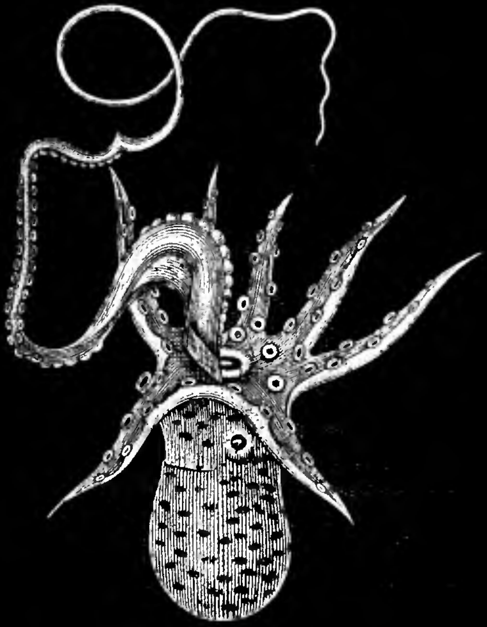
ZOOLOGICAL ARTICLES

LANKESTER ETC



ZOOLOGICAL ARTICLES

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CONTRIBUTED TO THE "ENCYCLOPÆDIA BRITANNICA"

BY

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PREFACE.

I HAVE been anxious to render the articles on various groups of Animals written by me for the *Encyclopædia Britannica* more readily accessible to the University student than they are when bound up in the large volumes of that great work. The Publishers have very kindly met my wishes in this respect by consenting to issue the present reprint. With my articles on Protozoa, Hydrozoa, Mollusca, Polyzoa, and Vertebrata, are here included, by the kind consent of the authors, the article on Sponges by Professor Sollas, that on Planarians by Professor von Graff, that on Nemertines by Professor Hubrecht, that on Rotifera by Professor Bourne, and that on Tunicata by Professor Herdman. The volume thus forms a treatise on a considerable section of the animal kingdom. Obviously it does not profess to be a complete handbook. Since the articles are reprinted from the original plates, and issued at a low price, it has not been possible to introduce any large additions into the text. Here and there an error, due to oversight, has been corrected, and one or two new figures have been added, rendering the work more complete. The chief additions are—the woodcut illustrating recent discoveries concerning the Dinoflagellata (p. 37); the note by Professor Sollas on the classification of Monaxonida (p. 39); the woodcut of Scyphomedusæ from the Deep-Sea (p. 57); the woodcut fig. 19 on p. 107, which replaces a similar but incorrect figure in the original article, and the woodcut, fig. 1A on p. 159, showing forms connecting the Eupolyzoa and other Gephyræa.

There are one or two matters, by way of addition to or correction of my own articles, which this preface gives me the opportunity of mentioning.

In regard to the Protozoa, the reader should note that Professor Bütschli's treatise in Bronn's *Thierreich* is now completed. He has rejected the classification of the Ciliata, which we owe to Stein, and adopts the following—Branch A. Gymnostoma (= Holotricha with chitinised pharynx, Prorodon, Trachelius, &c.); Branch B. Trichostoma (= the remaining Ciliata, all of which have the pharynx ciliated, if present). The Trichostoma are divided into two classes—the Aspirotricha, and the Spirotricha. The Aspirotricha are the rest of the Holotricha of Stein, not comprised in the Gymnostoma of this classification. The Spirotricha are characterised by all possessing the adoral "heterotrichal" band of large cilia; they are divided into the sub-classes Heterotricha, Hypotricha, Peritricha, and Oligotricha. The two first of these groups correspond with Stein's groups of the same names, whilst the Peritricha of Stein are now divided into Peritricha and Oligotricha, the latter sub-class being formed for such genera as Halteria, Strombidium, and Tintinnus. I consider Bütschli's classification an improvement upon Stein's, with the doubtful exception of the distinct position assigned to the Oligotricha.

In regard to the Hydrozoa, the most important additions to knowledge since the date of the article are to be found in the large and richly-illustrated monographs by Haeckel (*System der Medusen*, Jena, 1879–1880; "Report on the Deep-Sea Medusæ," *Challenger Reports*, vol. iv., 1882; "Reports on the Deep-Sea Siphonophora," *Challenger Reports*, vol. xxviii., 1888), and in the remarkable researches of Weissman on the origin of the sexual products (*Enstehung der Sexualzellen bei der Hydromedusen*, Jena, 1883). The student who takes in hand the actual examination of a specimen of *Aurelia aurita* by aid of the description given of it in the article Hydrozoa, should also refer to the plates of Ehrenberg's account of this animal (*Physikalische Abhandlungen der Konigl. Akad. d. Wissensch.*, Berlin, 1835), and Mr Minchin's brief but valuable paper on the enclosure of the embryos in minute brood pouches formed by sacculation of the grooves of the oral lobes (*Proc. Zool. Soc.*, 1889, No. xxxix.).

If I were rewriting the article Mollusca, I should adopt the conclusion of my friend and former pupil, Dr Paul Pelseneer, of Ghent, and remove the Pteropoda from association with the Cephalopoda, not to maintain them as a distinct class, but to place them, as he has done, among the Palliate or Tectibranchiate Opisthobranchiate Gastropoda, to which, it seems, they bear the same relation as do the Natantia to the Azygobranchiate Streptoneura. It appears that the Thecosomate Pteropods are nearly related to the Bullidæ and Tornatellidæ, whilst the Gymnosomate forms are derivable from the Aplysiidæ. A careful study of the nervous system convinced Dr Pelseneer that the sucker-bearing lobes of such Gymnosomate Pteropods as Pneumodermon are really cephalic in nature, and innervated from the cerebral ganglion, whilst the sucker-bearing lobes of the Cephalopoda are productions of the foot, and are convincingly demonstrated by Pelseneer (as maintained by me in the article "Mollusca") to be innervated by the pedal ganglia. The remarkable coincidence in the Pteropoda and Cephalopoda of adoral appendages provided with suckers which had been, to my mind, the chief ground for supposing a genetic relationship between these two sets of forms, proves to be a case of homoplasy.[1] It is, indeed, a very striking case of the parallelism of genetically distinct organs. The whole of this question is ably treated by Pelseneer in Part III. of his "Report on the Pteropoda," published in vol. xxiii. of the *Challenger Reports*, 1888. The student of molluscan anatomy should not fail to read this

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[1] The reader is referred for an explanation of this term, and a discussion of the phenomena concerned, to my article "On the use of the term Homology in Modern Zoology, and the distinction between Homogenetic and Homoplastic Agreements," *Ann. and Mag. Nat. Hist.*, 1870.

clear and well-illustrated discussion of the structure of the Pteropoda, and of the inferences which may be drawn therefrom as to their affinities.

In regard to the article Polyzoa, I may mention that I think it preferable to make use of the established term "Gephyræa" in place of that introduced in this article, viz., "Podaxonia." The Gephyræa, then, include the Sternaspidomorpha, Echiuromorpha, Sipunculomorpha, Phoronidomorpha, Polyzoa (Eupolyzoa of the article), Brachiopoda, and Pterobranchia. Concerning the affinities of the first four of these classes with one another, there is little doubt: as to the affinities of the last three with one another, and with the first four we are still in a very uncertain state, and are likely to remain so for some time, owing to the absence of satisfactory embryological data and the difficulty of obtaining such.

The subject matter of the article Vertebrata is much more extensive than that of the other chapters, and, owing to limited space, is treated in a much more general way than is the case with the latter. In regard to the Craniata, the intention was to give only a sketch of leading features which should be supplemented by the study of such works as Gegenbaur's *Comparative Anatomy*, Wiedersheim's *Anatomy of Vertebrates*, and the special articles on Fishes, Reptiles, Birds, and Mammals, written for the *Encyclopædia* by eminent authorities on those groups. The treatment of the Cephalochorda (Amphioxus) and its relations to the Urochorda is a little more complete, and I therefore take occasion to refer the reader to recent publications, in which our knowledge of this most interesting member of the Vertebrate group has been largely extended. They are—*Contributions to the Knowledge of Rhabdopleura and Amphioxus* (ubique citata), by E. Ray Lankester (London: J. & A. Churchill, 1889); "The Development of the Atrial Chamber of Amphioxus," by E. Ray Lankester and Arthur Willey, in the *Quart. Jour. of Mic. Sci.*, vol. xxxi., 1890; "The Later Larval Development of Amphioxus," by Arthur Willey, B.Sc., in the same Journal, vol. xxxii.; and "The Excretory Organs of Amphioxus," by F. E. Weiss, B.Sc., also in the *Quart. Jour. of Mic. Sci.*, vol. xxxi.

The article "Sponges," by Professor Sollas, contains the only summary account of the Porifera written since the recent extraordinary advances in our knowledge of this group. Its incorporation in the present volume cannot fail to be welcome to students. In Professor Bourne's article on Rotifera are given the only extant woodcuts of the important genus Pedalion. This most important form is not figured or discussed in any other general treatise accessible to students. The articles on Planarians and Nemertines, by Professor von Graff and Professor Hubrecht respectively, are brief summaries of what is known, written by the chief living authority on each group.

E. RAY LANKESTER.

OXFORD, *December* 1890.

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PROTOZOA

PROTOZOA is the name applied to the lowest grade of the animal kingdom, and originated as a translation of the German term "Urthiere." Whilst at first used some forty years ago in a vague sense, without any strict definition, so as to include on the one hand some simple organisms which are now regarded as plants and on the other some animals which are now assigned a higher place in the animal series, the term has within the last twenty years acquired a very clear signification.

The Protozoa are sharply and definitely distinguished from all the rest of the animal kingdom, which are known by the names "Metazoa" or "Enterozoa." They are those animals which are structurally single "cells" or single corpuscles of protoplasm, whereas the Enterozoa consist of many such units arranged definitely (in the first instance) in two layers—an endoderm or enteric cell-layer and an ectoderm or deric cell-layer—around a central cavity, the enteron or common digestive cavity, which is in open communication with the exterior by a mouth.

The Protozoa are then essentially unicellular animals. The individual or person in this grade of the animal kingdom is a single cell; and, although we find Protozoa which consist of aggregates of such cells, and are entitled to be called "multicellular," yet an examination of the details of structure of these cell-aggregates and of their life-history establishes the fact that the cohesion of the cells in these instances is not an essential feature of the life of such multicellular Protozoa but a secondary and non-essential arrangement. Like the budded "persons" forming, when coherent to one another, undifferentiated "colonies" among the Polyps and Corals, the coherent cells of a compound Protozoon can be separated from one another and live independently; their cohesion has no economic significance. Each cell is precisely the counterpart of its neighbour; there is no common life, no distribution of function among special groups of the associated cells, and no corresponding differentiation of structure. As a contrast to this we find even in the simplest Enterozoa that the cells are functionally and structurally distinguishable into two groups—those which line the enteron or digestive cavity and those which form the outer body wall. The cells of these two layers are not interchangeable; they are fundamentally different in properties and structure from one another. The individual Enterozoon is not a single cell; it is an aggregate of a higher order consisting essentially of a digestive cavity around which two layers of cells are disposed. The individual Protozoon is a single cell; a number of these individuals may, as the result of the process of fission (cell-division), remain in contact with one another, but the compound individual which they thus originate has not a strong character. The constituent cells are still the more important individualities; they never become differentiated and grouped in distinct layers differing from one another in properties and structure; they never become subordinated to the individuality of the aggregate produced by their cohesion; hence we are justified in calling even these exceptional aggregated Protozoa unicellular.

By far the larger number of Protozoa are absolutely single isolated cells, which, whenever they duplicate themselves by that process of division common to these units of structure (whether existing as isolated organisms or as constituents of the tissues of plants or of animals), separate at once into two distinct individuals which move away from one another and are thenceforward strangers.

Whilst it is easy to draw the line between the Protozoa and the Enterozoa or Metazoa which lie above them, on account of the perfectly definite differentiation of the cells of the latter into two primary tissues, it is more difficult to separate the Protozoa from the parallel group of unicellular plants.

Theoretically there is no difficulty about this distinction. There is no doubt that organisms present themselves to us in two great series starting in both cases from simple unicellular forms. The one series, the plants, can take up the carbon, hydrogen, oxygen, and nitrogen necessary to build up their growing protoplasm from mineral compounds soluble in water, compounds which constitute the resting stage of those elements in the present physical conditions of our planet. Plants can take their nitrogen in the form of ammonia or in the form of nitrates and their carbon in the form of carbonic acid. Accordingly they require no mouths, no digestive apparatus; their food being soluble in water and diffusible, they absorb at all or many points of their surface. The spreading diffuse form of plants is definitely related to this fact. On the other hand the series of organisms which we distinguish as animals cannot take the nitrogen, necessary to build up their protoplasm, in a lower state of combination than it presents in the class of compounds known as albumens; nor can they take carbon in a lower state of combination than it presents when united with hydrogen or with hydrogen and oxygen to form fat, sugar, and starch. Albumens and fats are not soluble in water and diffusible; they have to be seized by the animal in the condition of more or less solid particles, and by chemical processes superinduced in the living protoplasm of the animal by the contact of these particles they are acted upon, chemically modified, and rendered diffusible. Hence the animal is provided with a mouth and a digestive cavity, and with organs of locomotion and prehension by which it may search out and appropriate its scattered nutriment. Further the albumens, fats, sugars, and starch which are the necessary food of an animal are not found in nature excepting as the products of the life of plants or of animals; accordingly all animals are in a certain sense parasitic upon either plants or other animals. It would therefore seem to be easy to draw the line between even the most minute unicellular plants and the similarly minute unicellular animals—assigning those which feed on the albumens, &c., of other organisms by means of a mouth and digestive apparatus to the animal series, and those which can appropriate the elements of ammonia, nitrates, and carbonates to the plants.

Such absolute distinctions lending themselves to sharp definitions have, however, no place in the organic world; and this is found to be equally true whether we attempt to categorically define smaller groups in the classification of plants and animals or to indicate the boundaries of the great primary division which those familiar names imply. Closely allied to plants which are highly and specially developed as plants, and feed exclusively upon ammonia, nitrates, and carbonates, we find exceptionally modified kinds which are known as "insectivorous plants" and are provided with digestive cavities (the pitchers of pitcher-plants, &c.), and actually feed by acting chemically upon the albumens of insects which they catch in these digestive receptacles. No one would entertain for a moment the notion that these insectivorous plants should be considered as animals. The physiological definition separating plant from animal breaks down in their case; but the consideration of the probable history of their evolution as indicated by their various details of structure suffices at once to convince the most sceptical observer that they actually belong to the vegetable line of descent or family tree, though they have lost the leading physiological characteristic which has dominated the structure of other plants. In this extreme case it is made very obvious that in grouping organisms as plants or as animals we are not called upon to apply a definition but to consider the multifarious evidences of historical evolution. And we find in the case of the Protozoa and the Protophyta that the same principle holds good, although, when dealing with extremely simple forms, it becomes much more difficult to judge of the genetic relationship of an organism in proportion as the number of detailed points of possible agreement with and divergence from other forms to which it may be supposed to be related are few.

The feeding of plants upon carbonic acid is invariably accompanied by the presence of a peculiar green-colouring matter—chlorophyll. In virtue of some direct or indirect action of this chlorophyll the protoplasm of the plant is enabled to seize the carbon of the mineral world—the carbon which has sunk to the lowest resting stage of combination—and to raise it into combination with hydrogen and oxygen and ultimately with nitrogen. There are plants which have no chlorophyll and are thus unable to feed upon carbonic acid. They are none the less plants since they agree closely with particular chlorophyll-bearing plants in details of form and structure, mode of growth and reproduction. A large series of these are termed Fungi. Though unable to feed on carbonic acid, they do not feed as do animals. They can take their carbon from acetates and tartrates, which animals cannot do, and their nitrogen from ammonia. Even when it is admitted that some of these colourless plants, such as the Bacteria (Schizomycetes), can act upon albumens so as to digest them and thus nourish themselves, it is not reasonable to place the Bacteria among animals, any more than it would be reasonable so to place Nepenthes, Sarracenia, and Drosera (insectivorous Phanerogams). For the structure and mode of growth of the Bacteria is like that of well-known chlorophylligerous minute Algæ from which they undoubtedly differ only in having secondarily acquired this peculiar mode of nutrition, distinct from that which has dominated and determined the typical structure of plants.

So we find in a less striking series of instances amongst animals that here and there the nutritional arrangements which we have no hesitation in affirming to be the leading characteristic of animals, and to have directly and perhaps solely determined the great structural features of the animal line of descent, are largely modified or even altogether revolutionized. The green Hydra, the freshwater Sponge, and some Planarian worms produce chlorophyll corpuscles in the protoplasm of their tissues just as green plants do, and are able in consequence to do what animals usually cannot do—namely, feed upon carbonic acid. The possibilities of the protoplasm of the plant and of the animal are, we are thus reminded, the same. The fact that characteristically and typically plant protoplasm exhibits one mode of activity and animal protoplasm another does not prevent the protoplasm of even a highly developed plant from asserting itself in the animal direction, or of a thoroughly characterized animal, such as the green Hydra, from putting forth its chlorophylligenous powers as though it belonged to a plant.

Hence it is not surprising that we find among the Protozoa, notwithstanding that they are characterized by the animal method of nutrition and their forms determined by the exigencies of that method, occasional instances of partial vegetable nutrition such as is implied by the development of chlorophyll in the protoplasm of a few members of the group. It would not be inconsistent with what is observed in other groups should we find that there are some unicellular organisms which must, on account of their structural resemblances to other organisms, be considered as Protozoa and yet have absolutely given up altogether the animal mode of nutrition (by the ingestion of solid albumens) and have acquired the vegetable mode of absorbing ammonia, nitrates, and carbonic acid. Experiment in this matter is extremely difficult, but such "vegetable" or "holophytic nutrition" appears to obtain in the case of many of the green Flagellata, of the Dinoflagellata, and possibly of other Protozoa.

On the other hand there is no doubt that we may fall into an error in including in the animal line of descent all unicellular organisms which nourish themselves by the inception of solid nutriment. It is conceivable that some of these are exceptional creophagous Protophytes parallel at a lower level of structure to the insectivorous Phanerogams. In all cases we have to balance the whole of the evidence and to consider probabilities as indicated by a widely-reaching consideration of numerous facts.

The mere automatic motility of unicellular organisms was at one time considered sufficient indication that such organisms were animals rather than plants. We now know that not only are the male reproductive cells of ferns and similar plants propelled by vibratile protoplasm, but such locomotive particles are recognized as common products ("swarm-spores" and "zoospores") of the lowest plants.

The danger of dogmatizing erroneously in distinguishing Protozoa from Protophyta, and the insuperable difficulty in really accomplishing the feat satisfactorily, has led at various times to the suggestion that the effort should be abandoned and a group constituted confessedly containing both unicellular plants and unicellular animals and those organisms which may be one or the other. Haeckel has proposed to call this group the Protista (1).[1] On the whole, it is more satisfactory to make the attempt to discriminate those unicellular forms which belong to the animal line of descent from those belonging to the vegetable line. It is, after all, not a matter of much consequence if the botanist should mistakenly claim a few Protozoa as plants and the zoologist a few Protophyta as animals. The evil which we have to avoid is that some small group of unattractive character should be rejected both by botanist and zoologist and thus our knowledge of it should unduly lag. Bearing this in mind the zoologist should accord recognition as Protozoa to as wide a range of unicellular organisms as he can without doing violence to his conceptions of probability.

A very interesting and very difficult subject of speculation forces itself on our attention when we attempt to draw the line between the lowest plants and the lowest animals, and even comes again before us when we pass in review the different forms of Protozoa.

That subject is the nature of the first protoplasm which was evolved from not-living matter on the earth's surface. Was that first protoplasm more like animal or more like vegetable protoplasm as we know it to-day? By what steps was it brought into existence?

Briefly stated the present writer's view is that the earliest protoplasm did not possess chlorophyll and therefore did *not* possess the power of feeding on carbonic acid. A conceivable state of things is that a vast amount of albuminoids and other such compounds had been brought into existence by those processes which culminated in the development of the first protoplasm, and it seems therefore likely enough that the first protoplasm fed upon these antecedent steps in its own evolution just as animals feed on organic compounds at the present day, more especially as the large creeping plasmodia of some Mycetozoa feed on vegetable refuse. It indeed seems not at all improbable that, apart from their elaborate fructification, the Mycetozoa represent more closely than any other living forms the original ancestors of the whole organic world. At subsequent stages in the history of this archaic living matter chlorophyll was evolved and the power of taking carbon from carbonic acid. The "green" plants were rendered possible by the evolution of chlorophyll, but through what ancestral forms they took origin or whether more than once, *i.e.*, by more than one branch, it is difficult even to guess. The green Flagellate Protozoa (Volvocineæ) certainly furnish a connecting point by which it is possible to link on the pedigree of green plants to the primitive protoplasm; it is noteworthy that they cannot be considered as very primitive and are indeed highly specialized forms as compared with the naked protoplasm of the Mycetozoon's plasmodium.

Thus then we are led to entertain the paradox that though the animal is dependent on the plant for its food yet the animal preceded the plant in evolution, and we look among the lower Protozoa and not among the lower Protophyta for the nearest representatives of that first protoplasm which was the result of a long and gradual evolution of chemical structure and the starting point of the development of organic form.

The Protozoon Cell-Individual compared with the Typical Cell of Animal and Vegetable Tissues.

MORPHOLOGY.

The Protozoon individual is a single corpuscle of protoplasm, varying in size when adult from less than the $\frac{1}{1000}$th of an inch in diameter (some Sporozoa and Flagellata) up to a diameter of an inch (Nummulites), and even much larger size in the plasmodia of Mycetozoa. The substance of the Protozoa exhibits the same general properties—irritability, movement, assimilation, growth, and division—and the same irremediable chemical alteration as the result of exposure to a moderate heat, which are observed in the protoplasm constituting the corpuscles known as cells which build up the tissues of the larger animals and plants. There is therefore no longer any occasion to make use of the word "sarcode" which before this identity was established was very usefully applied by Dujardin (2) to the substance which mainly forms the bodies of the Protozoa. Like the protoplasm which constitutes the "cells" of the Enterozoa and of the higher plants, that of the Protozoon body is capable of producing, by chemical processes which take place in its substance (over and above those related merely to its nutrition), a variety of distinct chemical compounds, which may form a deposit in or beyond the superficial protoplasm of the corpuscle or may accumulate centrally. These products are therefore either ectoplastic or entoplastic. The chemical capacities of protoplasm thus exhibited are very diverse, ranging from the production of a denser variety of protoplasm, probably as the result of dehydration, such as we see in the nucleus and in the cortical substance of many cells, to the chemical separation and deposition of membranes of pure chitin or of cellulose or of shells of pure calcium carbonate or quasi-crystalline needles of silica.

NUCLEUS.—The nucleus is probably universally present in the Protozoon cell, although it may have a very simple structure and be of very small size in some cases. The presence of a nucleus has recently been demonstrated by means of appropriate staining reagents in some Protozoa (shell-bearing Reticularia or Foraminifera and many Mycetozoa) where it had been supposed to be wanting, but we are not yet justified in concluding absolutely that there are not some few Protozoa in which this central differentiation of the protoplasm does not exist; it is also a fact that in the young forms of some Protozoa which result from the breaking up of the body of the parent into many small "spores" there is often no nucleus present.

In contrast to this it is the fact that the cells which build up the tissues of the Enterozoa are all derived from the division of a nucleated egg-cell and the repeated division of its *nucleated* products, and are invariably nucleated. The same is true of tissue-forming plants.—though there are a few of the lowest plants, such as the Bacteria, the protoplasm of which presents no nucleus. In spite of recent statements (3) it cannot be asserted that the cells or protoplasmic corpuscles of the yeast-plant (Saccharomyces) and of the hyphæ of many simple moulds contain a true nucleus. We are here brought to the question "What is a true nucleus?" The nucleus which is handed on from the egg-cell of higher plants and Enterozoa to the cells derived from it by fission has lately been shown to possess in a wide variety of instances such very striking characteristics that we may well question whether every more or less distinctly outlined mass or spherule of protoplasm which can be brought into view by colouring or other reagents, within the protoplasmic body of a Protozoon or a Protophyte, is necessarily to be considered as quite the same thing as the nucleus of tissue-forming egg-cell-derived cells.

Researches, chiefly due to Flemming (4), have shown that the nucleus in very many tissues of higher plants and animals consists of a capsule containing a plasma of "achromatin" not deeply stained by reagents, ramifying in which is a reticulum of "chromatin" consisting of fibres which readily take a deep stain (Fig. I., A). Further it is demonstrated that, when the cell is about to divide into two, definite and very remarkable movements take place in the nucleus, resulting in the disappearance of the capsule and in an arrangement of its fibres first in the form of a wreath (Fig. I., D) and subsequently (by the breaking of the loops formed by the fibres) in the form of a star (E). A further movement within the nucleus leads to an arrangement of the broken loops in two groups (F), the position of the open ends of the broken loops being reversed

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[1] These numbers refer to the bibliography at p. 866.

as compared with what previously obtained. Now the two groups diverge, and in many cases a striated appearance of the achromatin substance between the two groups of loops of chromatin is observable (H). In some cases (especially egg-cells) this striated arrangement of the achromatin substance precedes the separation of the loops (G). The striated achromatin is then termed a "nucleus-spindle," and the group of chromatin loops (Fig. I., G, *a*) is known as "the equatorial plate." At each end of the nucleus-spindle in these cases there is often seen a star consisting of granules belonging to the general protoplasm of the cell (G, *c*). These are known as "polar stars." After the separation of the two sets of loops (H) the protoplasm of the general substance of the cell becomes constricted, and division occurs, so as to include a group of chromatin loops in each of the two fission products. Each of these then rearranges itself together with the associated achromatin into a nucleus such as was present in the mother-cell to commence with. This phenomenon is termed "karyokinesis," and has been observed, as stated above, in a large variety of cells constituting tissues in the higher animals and plants.

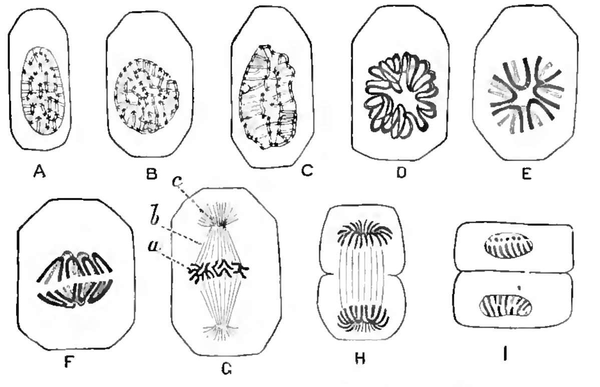

Fig. I.—Karyokinesis of a typical tissue-cell (epithelium of Salamander) after Flemming and Klein. The series from A to I represent the successive stages in the movement of the chromatin fibres during division, excepting G, which represents the "nucleus-spindle" of an egg-cell. A, resting nucleus; D, wreath-form; E, single star, the loops of the wreath being broken; F, separation of the star into two groups of U-shaped fibres; H, diaster or double star; I, completion of the cell-division and formation of two resting nuclei. In G the chromatin fibres are marked *a*, and correspond to the phase shown in F; they are in this case called the "equatorial plate"; *b*, achromatin fibres forming the nucleus-spindle; *c*, granules of the cell-protoplasm forming a "polar star." Such a polar star is seen at each end of the nucleus-spindle, and is not to be confused with the diaster H.

There is a tendency among histologists to assume that this process is carried out in all its details in the division of all cells in the higher plants and animals, and accordingly to assume that the structural differentiation of achromatin plasma and chromatin nucleus-fibres exists in the normal nucleus of every such cell. If this be true, it is necessary to note very distinctly that the nucleus of the Protozoon cell-individual by no means conforms universally to this model. As will be seen in the sequel, we find cases in which a close approach is made by the nucleus of Protozoa to this structure and to this definite series of movements during division (Fig. VIII. 3 to 12, and Fig. XXV.); and a knowledge of these phenomena has thrown light upon some appearances (conjugation of the Ciliata) which were previously misinterpreted. But there are Protozoa with a deeply-placed nucleus-like structure which does not present the typical structure above described nor the typical changes during division, but in which on the contrary the nucleus is a very simple homogeneous corpuscle or vesicle of more readily stainable protoplasm.

The difficulties of observation in this matter are great, and it is proportionately rash to generalize; but it appears that we are justified at the present moment in asserting that not all the cells even of higher plants and animals exhibit in full detail the structure and movement of the typical cell-nucleus above figured and described; and accordingly the fact that such structure and movement cannot always be detected in the Protozoon cell-nucleus must not be regarded as either an isolated phenomenon peculiar to such Protozoon cells, nor must it be concluded that we have only to improve our means of analysis and observation in order to detect this particular structure in all nuclei. It seems quite possible and even probable that nuclei may vary in these details and yet be true nuclei. Some nuclei which are observed in Protozoon cell-bodies may be regarded as being at a lower stage of differentiation and specialization than are those of the epithelial and embryonic cells of higher animals which exhibit typical karyokinesis. Others on the contrary, such as the nuclei of some Radiolaria (*vide infra*), are probably to be regarded as more highly developed than any tissue cell-nuclei, and will be found by further study to present special phenomena peculiar to themselves. In some of the highest Protozoa (the Ciliata) it has lately been shown that the nucleus may have no existence as such, but is actually dispersed throughout the protoplasm in the form of fine particles of chromatin-substance which stain on treatment with carmine but are in life invisible (**84**). This diffuse condition of the nuclear matter has no parallel, at present known, in tissue-cells, and curiously enough occurs in certain genera of Ciliata whilst in others closely allied to them a solid single nucleus is found. The new results of histological research have necessitated a careful study of the nucleus in its various stages of growth and division in the cell-bodies of Protozoa and a comparison of the features there observed with those established as "typical" in tissue-cells. Accordingly we have placed the figure and explanation of the typical cell-nucleus in the first place in this article for subsequent reference and comparison.

CORTICAL SUBSTANCE.—The superficial protoplasm of an embryonic cell of an Enterozoon in the course of its development into a muscular cell undergoes a change which is paralleled in many Protozoa. The cortical layer becomes dense and highly refringent as compared with the more liquid and granular medullary substance. Probably this is essentially a change in the degree of hydration of the protoplasm itself, although it may be accompanied by the deposition of metamorphic products of the protoplasm which are not chemically to be regarded as protoplasm. The differentiation of this cortical substance (which is not a frequent or striking phenomenon in tissue-cells) may be regarded as an ectoplastic (*i.e.*, peripheral) modification of the protoplasm, comparable to the entoplastic (central) modification which produces a nucleus.

The formation of "cortical substance" in the Protozoa furnishes the basis for the most important division into lower and higher forms, in this assemblage of simplest animals. A large number (the Gymnomyxa) form no cortical substance; their protoplasm is practically (excepting the nucleus) of the same character throughout. A nearly equally large number (the Corticata) develop a complete cortical layer of denser protoplasm, which is distinct from the deeper medullary protoplasm. This layer is permanent, and gives to the body a definite shape and entails physiological consequences of great moment. The cortical protoplasm may exhibit further specialization of structure in connexion with contractile functions (muscular).

ECTOPLASTIC PRODUCTS CHEMICALLY DISTINCT FROM PROTOPLASM.—The protoplasm of all cells may throw down as a molecular precipitate distinct from itself chemical compounds, such as chitin and horny matter and other nitrogenized bodies, or again non-nitrogenous compounds, such as cellulose. Very usually these substances are deposited not external to but *in* the superficial protoplasm. They are then spoken of as cell-cuticle if the cell bounds the free surface of a tissue, or as matrix or cell-wall in other cases. The Protozoon cell-body frequently forms such "cuticles," sometimes of the most delicate and evanescent character (as in some Amœbæ), at other times thicker and more permanent. They may give indications (though proper chemical examination is difficult) of being allied in composition to chitin or gelatin, in other instances to cellulose, which is rare in animals and usual in plants. These cuticular deposits may be absent, or may form thin envelopes or in other cases jelly-like substance intimately mixed with the protoplasm (Radiolaria). They may take the form of hooks, tubercles, or long spines, in their older and more peripheral parts free from permeation by protoplasm, though deeply formed in and interpenetrated by it. Such pellicles and cuticles, the deeper layers (if not the whole) of which are permeated by protoplasm, lead insensibly to another category of ectoplastic products in which the material produced by the protoplasm is separated from it and can be detached from or deserted by the protoplasm without any rupture of the latter. These are—

Shells and Cysts. — Such separable investments are formed by the cell-bodies of many Protozoa, a phenomenon not exhibited by tissue-cells. Even the cell-walls of the protoplasmic corpuscles of plant tissues are permeated by that protoplasm, and could not be stripped off without rupture of the protoplasm. The shell and the cyst of the Protozoon are, on the contrary, quite free from the cell-protoplasm. The shell may be of soft chitin-like substance (Gromia, &c.), of cellulose (Labyrinthula, Dinoflagellata), of calcium carbonate (Globigerina, &c.), or of silica (Clathrulina, Codonella). The term "cyst" is applied to completely closed investments ("shells" having one or more apertures), which are temporarily produced either as a protection against adverse external conditions or during the breaking up of the parent-cell into spores. Such cysts are usually horny.

Stalks.—By a localization of the products of ectoplastic activity the Protozoon cell can produce a fibre or stalk of ever-increasing length, comparable to the seta of a Chætopod worm produced on the surface of a single cell.

ENTOPLASTIC PRODUCTS DISTINCT FROM PROTOPLASM.—Without pausing here to discuss the nature of the finest granules which are embedded as a dust-cloud in the hyaline matrix of the purest protoplasm alike of Protozoa and of the cells of higher animals and plants, and leaving aside the discussion of the generalization that all protoplasm presents a reticular structure, denser trabeculæ of extreme minuteness traversing more liquid material, it is intended here merely to point to some of the coarser features of structure and chemical differentiation, characteristic of the cell-body of Protozoa.

With regard to the ultimate reticular structure of protoplasm it will suffice to state that such structure has been shown to obtain in not a few instances (*e.g.*, Lithamœba, Fig. V.), whilst in most Protozoa the methods of microscopy at present applied have not yielded evidence of it, although it is not improbable that a recticular differentiation of the general protoplasm similar to that of the nucleus may be found to exist in all cells.

Most vegetable cells and many cells of animal tissues exhibit vacuolation of the protoplasm; *i.e.*, large spaces are present in the protoplasm occupied by a liquid which is not protoplasm and is little more than water with diffusible salts in solution. Such vacuoles are common in Protozoa. They are either permanent, gastric, or contractile.

Permanent vacuoles containing a watery fluid are sometimes so abundant as to give the protoplasm a "bubbly" structure (Thalamophora, Radiolaria, &c.), or may merely give to it a trabecular character (Trachelius, Fig. XXIV. 14, and Noctiluca, Fig. XXVI. 18). Such vacuoles may contain other matters than water, namely, special chemical secretions of the protoplasm. Of this nature are oil-drops, and from these we are led to those deposits within the cell-protoplasm which are of solid consistence (see below).

Gastric vacuoles occur in the protoplasm of most Protozoa in consequence of the taking in of a certain quantity of water with each solid particle of food, such ingestion of solid food-particles being a characteristic process bound up with their animal nature.

Contractile vacuoles are frequently but not universally observed in the protoplasm of Protozoa. They are not observed in the protoplasm of tissue-cells. The contractile vacuole whilst under observation may be seen to burst, breaking the surface of the Protozoon and discharging its liquid contents to the exterior; its walls, formed of undifferentiated protoplasm, then collapse and fuse. After a short interval it re-forms by slow accumulation of liquid at the same or a neighbouring spot in the protoplasm. The liquid is separated at this point by an active process taking place in the protoplasm which probably is of an excretory nature, the separated water carrying with it nitrogenous waste-products. A similar active formation of vacuoles containing fluid is observed in a few instances (Arcella, some Amœbæ) where the protoplasm separates a gas instead of liquid, and the gas vacuole so produced appears to serve a hydrostatic function.

Corpuscular and Amorphous Entoplastic Solids.—Concretions of undetermined nature are occasionally formed within the protoplasm of Protozoon cells, as are starch and nitrogenized concretions in tissue-cells (Lithamœba, Fig. V. *conc.*). But the most important corpuscular products after the nucleus, which we have already discussed, are chlorophyll corpuscles. These are (as in plants) concavo-convex or spherical corpuscles of dense protoplasm resembling that of the nucleus, which are impregnated superficially with the green-coloured substance known as chlorophyll. They multiply by fission, usually tetraschistic, independently of the general protoplasm. They occur in representatives of many different groups of Protozoa (Proteomyxa, Heliozoa, Labyrinthulidea, Flagellata, Ciliata), but are confined to a few species. Similar corpuscles or band-like structures coloured by other pigments are occasionally met with (Dinoflagellata).

Recently it has been maintained (Brandt, 5) that the chlorophyll corpuscles of Protozoa and other animals are parasitic Algæ. But, though it is true that parasitic Algæ occur in animal tissues, and that probably this is the nature of the yellow cells of Radiolaria, yet there seems to be no more justification for regarding the chlorophyll corpuscles of animal tissue-cells and of Protozoa as parasites than there is for so regarding the chlorophyll corpuscles of the leaves of an ordinary green plant.

Corpuscles of starch, paramylum, and other amyloid substances are commonly formed in the Flagellata, whose nutrition is to a large extent plant-like.

Entoplastic Fibres.—A fibrillation of the protoplasm of the Protozoon cell-body may be produced by differentiation of less and more dense tracts of the protoplasm itself. But as distinct from this we find horny fibres occasionally produced within the protoplasm (Heliozoa) having definite skeletal functions. The threads produced in little cavities in the superficial protoplasm of many Ciliate Protozoa, known as trichocysts, may be mentioned here.

Entoplastic Spicules. — Needle-like bodies consisting either of silica or of a horny substance (acanthin) are produced in the protoplasm of many Protozoa (Heliozoa, Radiolaria). These are known as spicules; they may be free or held together in groups and arranged either radially or tangentially in reference to the more or less spherical body of the Protozoon. A similar production of siliceous spicules is observed in the tissue-cells of Sponges. Crystals of various chemical nature (silica, calcium carbonate, oxalate, &c.) are also frequently deposited in the protoplasm of the Protozoa, differing essentially from spicules in that their shape is due purely to crystallization.

General Form of the Protozoon Cell.—Those Protozoa which have not a differentiated cortical substance, and are known as Gymnomyxa, present very generally an extreme irregularity of contour. Their protoplasm, being liquid rather than viscous, flows into the most irregular shapes. Their fundamental form when at rest is in many cases that of the sphere; others are discoidal or may be monaxial, that is to say, show a differentiation of one region or "end" of the body from the other. Frequently the protoplasm is drawn out into long threads or filaments which radiate uniformly from all parts of the spherical or discoidal cell-body or originate from one region to the exclusion of other parts of the surface.

These non-corticate Protozoa can take solid particles of food into their protoplasm, there to be digested in an extemporized "gastric vacuole," at any part or most parts of their superficies. They have no permanent cell-mouth leading into the soft protoplasm since that soft protoplasm is everywhere freely exposed.

The corticate Protozoa have (with the exception of some parasites) one, and in the Acinetaria more than one, definite aperture in the cortical substance leading into the softer medullary protoplasm. This is the cell-mouth,—morphologically as distinct from the mouth of an Enterozoon as is the hole in a drain pipe from the front door of a house, but physiologically subserving the same distinctively animal function as does the mouth of multicellular animals. The general form of the body is in these Protozoa oblong, with either monaxial symmetry, when the mouth is terminal, or bilateral symmetry, when the body is oblong and flattened and the mouth is towards one end of what becomes by its presence the "ventral" surface. Though the protoplasm is not nakedly exposed in irregular lobes and long filaments in these corticate Protozoa so as to pick up at all points such food-particles as may fall in its way, yet the protoplasm does in most Corticata project in one or more peculiarly modified fine hair-like processes from the otherwise smooth surface of the cell-body. These processes are *vibratile cilia*, identical in character with the vibratile cilia of epithelial tissue-cells of Enterozoa. They are essentially locomotor and current-producing (therefore prehensile) organs, and, whilst unable to ingest solid food-particles themselves, serve to propel the organism in search of food and to bring food into the cell-mouth by the currents which they excite. Either a single vibratile filament is present, when it is called a flagellum, or a row or many rows of cilia are developed.

Constituent cells of the Enterozoa are well known which closely resemble some of the Gymnomyxa or non-corticate Protozoa in their general form. These are the colourless blood corpuscles or lymph corpuscles or phagocytes (Mecznikow, **6**) which float freely in the blood and ingest solid particles at any part of their surface as do non-corticated Protozoa; they exhibit a similar irregularity and mutability of outline, and actually digest the particles which they take in. The endodermal digestive cells of some Enterozoa (Cœlentera and Planarians) are also naked protoplasmic corpuscles and can take in solid food-particles.

No tissue-cells are known which present any close parallel to the mouth-bearing corticate Protozoa. The differentiation of the structure of a single cell has in these forms reached a very high degree, which it is not surprising to find without parallel among the units which build up the individual of a higher order known as an Enterozoon. Cilia are developed on such cell-units (ciliated epithelium), but not used for the introduction of food-particles into the cell. In rare cases (the ciliated "pots" of the vascular fluid of Sipunculus) they act so as to freely propel the ciliated cell through the liquid "blood" of the Enterozoon, as the cilia of a Protozoon propel it through water. An aperture in the cortical substance (or in the cuticular product) of a tissue-cell is sometimes to be observed, but is never (?) used for the ingestion of food-particles. Such an aperture occurs in unicellular glands, where it serves as the outlet of the secretion.

Physiology.

Motion.—As has just been hinted, the movement of protoplasm, which in the tissue-cells of Enterozoa and higher plants is combined and directed so as to produce effects in relation to the whole organism built up of countless cells, is seen in the Protozoa in a different relation, namely, as subserving the needs of the individual cell of which the moving protoplasm is the main substance. The phenomena known in tissue-cells as "streaming" (*e.g.*, in the cells of the hairs of Tradescantia), as local contraction and change of form (*e.g.*, in the corpuscles of the cornea), as muscular contraction, and as ciliary movement are all exhibited by the protoplasm of the cell-body of Protozoa, with more or less constancy, and are intimately related to the processes of hunting, seizing, and ingesting food, and of the intercourse of the individuals of a species with one another and their evasion of hostile agencies. Granule streaming and the implied movement of currents in the protoplasm are seen in the filamentous protoplasm of the Heliozoa, Radiolaria, Reticularia, and Noctiluca, and in the cyclosis of the gastric vacuoles of Ciliata. Local contraction and change of form is seen best in the Amœbæ and some Flagellata, where it results in locomotion. Definite muscular contraction is exhibited by the protoplasmic band in the stalk of Vorticella, by the leg-like processes of the Hypotrichous Ciliata, and by the cortical substance of some large Ciliata. Ciliary movement ranging from the vibration of filaments of protoplasm temporarily evolved, up to the rhythmic beat of groups of specialized cilia, is observed in all groups of Protozoa in the young condition if not in the adult, and special varieties of ciliary movement and of cilia-like organs will be noted below. For an account of the conditions and character of protoplasmic movement generally which cannot be discussed in the present article the reader is referred to Engelmann (7).

The protoplasm of the cell-body of the Protozoa is drawn out into lobes and threads which are motile and are used as locomotive and prehensile organs. These processes are of two kinds, which are not present on the same cell and are not capable of transmutation, though there are exceptions to both of these statements. The one kind are termed "pseudopodia," and are either lobose or filamentous or branched and even reticular (Figs. IV. and IX.). The Protozoa which exhibit them are sometimes termed Myxopods. The other kind are cilia and flagella, and are simple threads which are alternately bent and straightened almost incessantly during the life of the organism. These Protozoa are termed Mastigopods. Whilst the cilia and flagella are permanent organs, the pseudopodia vary greatly in character; they are in some cases rapidly expanded and withdrawn in irregular form, and can hardly be said to be more than lobose protuberances of the flowing moving mass of protoplasm. In other cases they are comparatively permanent stiff threads of protoplasm which can be contracted and can fuse with one another but rarely do so (Heliozoa, Radiolaria). Between these extreme forms of "pseudopodia" there are numerous intermediate varieties, and the whole protoplasmic body of the Protozoon may even assume the form of a slowly changing network of threads of greater or less tenuity (Chlamydomyxa, Fig. VI.).

Nutrition.—Typically—that is to say, by determinate hereditary tendency—the Protozoa take solid food-particles into their protoplasm which form and occupy with the water surrounding them "gastric vacuoles" in the protoplasm. The food-particle is digested in this vacuole, by what chemical processes is not ascertained. It has been shown that the contents of the gastric vacuole give in some cases an acid reaction, and it is not improbable that free acid is secreted by the surrounding protoplasm. It is not known whether any ferment[1] is separated by the protoplasm, but it is probable from observations made on the digestive process of Cœlentera (Actiniæ) that the ferment is not separated, but that actual contact of the food-particle with the protoplasm is necessary for a "ferment influence" to be exerted. The digestion of a food-particle by a Protozoon is intra-cellular, and has been contrasted with the cavitary digestion of higher animals. In the latter, ferments and acids are poured out by the cells bounding the enteric cavity into that space, and digestion is extra-cellular. In the lowest Enterozoa (many Cœlentera and some Planarian worms) it has been shown that food-particles are actually taken up in a solid state by the soft protoplasm of the enteric cells and thus subjected to intra-cellular digestion. There appears to be a gradual transition from this process, in which close contact with living protoplasm is necessary that the solution of an albuminous food-particle may be effected, onwards to the perfectly free cavitary digestion by means of secretions accumulated in the enteron.

We have not yet any satisfactory observations on the chemistry of intra-cellular digestion either of Protozoa or of Cœlentera.

Certain Protozoa which are parasitic do not take solid food particles; they (like higher parasites, such as the Tapeworms) live in the nutritious juices of other animals and absorb these by their general surface in a liquid state. The Gregarinæ (Sporozoa), many Ciliata, &c., are in this case. Other Protozoa are known which are provided with chlorophyll corpuscles and do not take in solid food, but, apparently as a result of exceptional adaptation in which they differ from closely-allied forms, nourish themselves as do green plants. Such are the Volvocinean Flagellata and some of the Dinoflagellata. It has also been asserted that other Protozoa (viz., some Ciliata)—even some which possess a well-developed mouth—can (and experimentally have been made to) nourish themselves on nitrogenous compounds of a lower grade than albumens—such, for instance, as ammonium tartrate. Any such assertions must be viewed with the keenest scepticism, since experimental demonstration of the absence of minute albuminous particles (*e.g.*, Bacteria) from a solution of ammonium tartrate in which Ciliate Protozoa are flourishing is a matter of extreme difficulty and has not yet been effected.

Undigested food-remnants are expelled by the protoplasm of the Protozoon cell either at any point of the surface or by the cell-mouth or by a special cell-anus (some Ciliata, see Fig. XXIV. 22).

Respiration and Excretion.—The protoplasm of the Protozoa respires, that is, takes up oxygen and liberates carbonic acid, and can readily be shown experimentally to require a supply of oxygen for the manifestation of its activity. No special respiratory structures are developed in any Protozoa, and as a rule also the products of oxidation appear to be washed out and removed from the protoplasm without the existence of any special apparatus. The contractile vacuole which exists in so many Protozoa appears, however, to be an excretory organ. It has been shown to rapidly excrete in a state of solution colouring matters (anilin blue) which have been administered with food particles (**8**). No evidence has been adduced to show whether traces of nitrogenous waste-products are present in the water expelled by the contractile vacuole.

Chemical Metamorphosis.—The form which the various products of the activity of the Protozoon's protoplasm may assume has been noted above. It will be sufficient here to point out that the range of chemical capacities is quite as great as in the cells of the higher Enterozoa. Chitin, cellulose, silicon, calcium carbonate, fats, pigments, and gases can be both deposited and absorbed by it. Owing to the minuteness of the Protozoa, we are at present unable to recognize and do justice to the variety of chemical bodies which undoubtedly must play a part in their economy as the result of the manufacturing activity of their protoplasm. See, however, Zopf (**13**), p. 71.

Growth and Reproduction.—The Protozoon cell follows the same course as tissue-cells, in that by assimilation of nutriment its protoplasm increases in volume and reaches a certain bulk, when its cohesion fails and the viscid droplet divides into two. The coefficient of cohesion varies in different genera and species, but sooner or later the disrupting forces lead to division, and thus to multiplication of individuals or reproduction. The phenomena connected with the division of the nucleus (already alluded to) will be noticed in particular cases below.

Whilst simple binary division is almost without exception a chief method of reproduction among the Protozoa, it is also very usual, and probably this would be found if our knowledge were complete to have few exceptions, that under given conditions the Protozoon breaks up rapidly into many (from ten to a hundred or more) little pieces, each of which leads an independent life and grows to the form and size of its parent. It will then multiply by binary division, some of the products of which division will in their turn divide into small fragments. The small fragments are called "spores." Usually the Protozoon before breaking up into spores forms a "cyst" (see above) around itself. Frequently, but not as a necessary rule, two (rarely three or more) Protozoon cell-individuals come together and fuse into one mass before breaking up into spores. This process is known as "conjugation;" and there can be no doubt that the physiological significance of the process is similar to that of sexual fertilization, namely, that the new spores are not merely fragments of an old individual but are something totally new inasmuch as they consist of a combination of the substance of individuals who have had different life experiences.

Whilst spore-formation is not necessarily preceded by conjugation, conjugation is not necessarily followed by spore-formation. Among the Mycetozoa the young individuals produced from spores conjugate at a very early period of growth in numbers and form "plasmodia," and after a considerable interval of feeding and growth the formation of spores takes place. Still more remarkable is the fact observed among the Ciliata where two individuals conjugate and after a brief fusion and mixture of their respective protoplasm separate, neither individual (as far as certain genera at least are concerned) breaking up into spores, but simply resuming the process of growth and recurrent binary division with increased vigour.

There is certainly no marked line to be drawn between reproduction by simple fission and reproduction by spore-formation; both are a more or less complete dividing of the parent protoplasm into separate masses; whether the products of the first fission are allowed to nourish themselves and grow before further fission is carried out or not

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[1] The digestive ferment pepsin has been detected by Krukenberg in the plasmodium of the Mycetozoon Fuligo (flowers of tan). See on this subject Zopf (**13**), p. 88.

does not constitute an essential difference. The fission of the Ciliate Protozoon, Opalina (see below Fig. XXIV. 4–8), is a step from the ordinary process of delayed binary division towards spore-formation. In some Protozoa spores are produced after encystation by a perfectly regular process of cleavage (comparable to the cleavage of the egg-cell of Enterozoa)—first two, then four, then eight, sixteen, and thirty-two fission products being the result (see Fig. XX. 24, 25, &c.).

But more usually there is a hastening of the process, and in these cases it is by no means clear what part the parent cell-nucleus takes. An encysted Gregarina (or two conjugated Gregarinæ) suddenly breaks up into a number of equal-sized spores, which do not increase in number by binary division and have not been formed by any such process. This multicentral segregation of the parent protoplasm is a marked development of the phenomenon of sporulation and remote from ordinary cell-division. How it is related to ordinary cell-division is not known, inasmuch as the changes undergone by the nucleus in this rapid multicentral segregation of the parent protoplasm have not been determined. The spores of Protozoa may be naked or encased singly or in groups in little envelopes, usually of a firm horny substance (see Fig. XX. 23 to 26, and Fig. XXIV. 15 to 18). Whenever the whole or a part of a Protozoon cell divides rapidly into a number of equal-sized pieces which are simultaneously set free and are destined to reproduce the adult form, the term spore is applied to such pieces, but the details of their formation may vary and also those of their subsequent history. In typical cases each spore produced as the result of the fission of an encysted Protozoon (conjugated or single) has its own protective envelope, as in the Mycetozoa (Fig. III.) and the Sporozoa (Fig. XVIII.), from which the contained protoplasm escapes by "germination" as a naked corpuscle either flagellate or amœbiform. In some terminologies the word "spore" is limited to such a "coated" spore, but usually the naked protoplasmic particles which issue from such "coated" spores, or are formed directly by the rapid fission of the parent Protozoon, are also called "spores." The former condition is distinguished as a "chlamydospore," whilst the latter are termed "gymnospores." Many Protozoa produce gymnospores directly by the breaking up of their protoplasm, and these are either "flagellulæ" (swarm-spores) or "amœbulæ" (creeping spores). The production of coated spores is more usual among the lower plants than it is among Protozoa, but is nevertheless a characteristic feature of the Gregarinæ (Sporozoa) and of the Mycetozoa. The term "gemma" or "bud-spore" is applied to cases, few in number, where (as in Acinetaria, Fig. XXVI., Spirochona, Fig. XXIII. 10, and Reticularia, Fig. X. 8) the spores are gradually nipped off from the parent-cell one or more at a time. This process differs from ordinary cell-division only in the facts (1) that the products of division are of unequal size—the parent-cell being distinguishable as the larger and more complete in structure, and (2) that usually the division is not binary, but more than one bud-spore is produced at a time.

Whilst in the binary cell-division of the Protozoa the two products are usually complete in structure at the period of separation, spores and spore-buds are not only of small size and therefore subject to growth before attaining the likeness of the parent, but they are also very often of simple and incomplete structure. The gap in this respect between the young spore and its parent necessarily varies according to the complexity of the parental form.

In the case of the Radiolaria, of the Gregarinæ, of Noctiluca, and of the Acinetaria, for instance, the spore has before it a considerable process of development in structure and not merely of growth, before attaining the adult characters. Hence there is a possible embryology of the Protozoa, to the study of which the same principles are applicable as are recognized in the study of the embryology of Enterozoa. Embryonic forms of great simplicity of structure, often devoid of nucleus, and consisting of simple elongate particles of protoplasm, are hatched from the spore-cases of the Gregarinæ (Fig. XVII. 13, 14) These gradually acquire a differentiated cortical protoplasm and a nucleus. A very large number of Gymnomyxa produce spores which are termed "monadiform," that is, have a single or sometimes two filaments of vibratile protoplasm extended from their otherwise structureless bodies. By the lashing of these flagella the spores (swarm-spores or zoospores) are propelled through the water. The resemblance of these monadiform young (best called "flagellulæ") to the adult forms known as Flagellata has led to the suggestion that we have in them a case of recapitulative development, and that the ancestors of the Gymnomyxa were Protozoa similar to the Flagellata. Again the Acinetaria produce spores which are uniformly clothed with numerous vibratile cilia (Fig. XXVI.), although the adults are entirely devoid of such structures; this is accounted for by the supposition that the Acinetaria have been developed from ancestors like the Ciliata, whose characters are thus perpetuated in their embryonic stages. There can be little doubt that these embryological suggestions are on the whole justified, and that the nucleated Protozoa are the descendants of non-nucleated forms similar to the spores of Gymnomyxa and Sporozoa, whilst it seems also extremely probable that the ancestral Protozoa were neither exclusively amœboid in the movement of their protoplasm nor provided with permanent vibratile filaments (flagella and cilia); they were neither Myxopods nor Mastigopods (to use the terms which have been introduced to express this difference in the character of the locomotor processes), but the same individuals were capable of throwing out their protoplasm sometimes in the form of flowing lobes and networks, sometimes in the form of vibratile flagella. A few such undifferentiated forms exist at the present day among the Proteomyxa and in a little more advanced condition among the lowest Flagellata, *e.g.*, Ciliophrys.

Death.—It results from the constitution of the Protozoon body as a single cell and its method of multiplication by fission that death has no place as a natural recurrent phenomenon among these organisms. Among the Enterozoa certain cells are separated from the rest of the constituent units of the body as egg-cells and sperm-cells; these conjugate and continue to live, whilst the remaining cells, the mere carriers as it were of the immortal reproductive cells, die and disintegrate. There being no carrying cells which surround, feed, and nurse the reproductive cells of Protozoa, but the reproductive cell being itself and alone the individual Protozoon, there is nothing to die, nothing to be cast off by the reproductive cell when entering on a new career of fission. The bodies of the higher animals which die may from this point of view be regarded as something temporary and non-essential, destined merely to carry for a time, to nurse, and to nourish the more important and deathless fission-products of the unicellular egg. Some of these fission-products of the new individual developed from an egg-cell—namely, the egg-cells and sperm-cells—are as immortal as the unicellular Protozoon. This method of comparing the unicellular and the multicellular organism is exceedingly suggestive, and the conception we thus gain of the individuality of the Enterozoon throws light upon the phenomena of reproduction and heredity in those higher organisms.

Experiment and observation in this matter are extremely difficult; but we have no reason to suppose that there is any inherent limit to the process of nutrition, growth, and fission, by which continuously the Protozoa are propagated. The act of conjugation from time to time confers upon the protoplasm of a given line of descent new properties, and apparently new vigour. Where it is not followed by a breaking up of the conjugated cells into spores, but by separation and renewed binary fission (Ciliata), the result is described simply as "rejuvenescence." The protoplasm originated by the successive division of substance traceable to one parent cell has become specialized, and in fact too closely adapted to one series of life-conditions; a fusion of substance with another mass of protoplasm equally specialized, but by experience of a somewhat differing character, imparts to the resulting mixture a new combination of properties, and the conjugated individuals on separation start once more on their deathless career with renewed youth.

CLASSIFICATION OF THE PROTOZOA.

In attempting a scheme of classification it would be most in accordance with the accepted probabilities of the ancestral history of the Protozoa to separate altogether those forms devoid of a nucleus from those which possess one, and to regard them as a lower "grade" of evolution or differentiation of structure.

By some systematists, notably Bütschli **(9)**, the presence or absence of a nucleus has not been admitted as a basis of classificatory distinction, whilst on the other hand both Haeckel **(1)** and Huxley **(10)** have insisted on its importance.

The fact is that during recent years many of those Protozoa which were at one time supposed to be devoid of nucleus even in a rudimentary form, and furnished therefore the tangible basis for a lowest group of "Protozoa Homogenea" or "Monera," have been shown by the application of improved methods of microscopic investigation to possess a nucleus, that is to say, a differentiated corpuscle of denser protoplasm lying within the general protoplasm, and capable when the organism is killed by alcohol or weak acids of taking up the colour of various dyes (such as carmine and hæmatoxylin) more readily and permanently than is the general protoplasm. In such cases the nucleus may be very small and exhibit none of the typical structure of larger nuclei. It is usually surrounded by a clear (*i.e.*, non-granular) halo of the general protoplasm which assists the observer in its detection. Nuclei have been discovered in many Reticularia (Foraminifera), a group in which they were supposed to be wanting, by Schultze **(11)** and the Hertwigs **(12)** and more recently in the Mycetozoa and in Vampyrella and Protomonas (Zopf, **13**), where so excellent an observer as Cienkowski had missed them.

It seems therefore not improbable that a nucleus is present though not observed in Protomyxa, Myxastrum, and other similar forms which have been by Haeckel and others classed as "Monera" or "Homogenea." The recently described **(14)** Archerina (Fig. II. **8, 11**) certainly possesses no nucleus in the usual sense of that term, but it is possible that the chlorophyll-coloured corpuscles of that organism should be considered as actually representing the nucleus. Whilst then refraining from asserting that there are no existing Protozoa devoid of nucleus corresponding in this character with non-nucleate Protophyta, such as the Bacteria, we shall not in our scheme of classification institute a group of Homogenea, but shall leave the taking of that step until it has been shown after critical examination that those forms now regarded by some observers as Homogenea are really so. In the meantime these forms will find their places alongside of the Nucleata most nearly allied to them in other characters.

The Protozoa with a definite permanent cortical substance of differentiated protoplasm are undoubtedly to be regarded as evolved from forms devoid of such differentiation of their substance, and we accordingly take this feature as the indication of a primary division of the Protozoa.[1] The lower grade, the Gymnomyxa, afford in other respects evidence of their being nearly related to the ancestral forms from which the Corticata (the higher grade) have developed. The Gymnomyxa all or nearly all, whilst exhibiting amœboid movement and the flowing of their protoplasm into "pseudopodia" of very varied shapes, produce spores which swim by means of one or two flagella of vibratile protoplasm (monadiform young or flagellulæ). These flagellate young forms are closely related to the Flagellata, a group of the Corticata from which it seems probable that the Dinoflagellata, the Ciliata, and the Acinetaria have been derived. The Gymnomyxa themselves cannot, on account of the small number of structural features which they offer as indications of affinity and divergence in genetic relationships *inter se*, be classified with anything like confidence in a genealogical system. We are obliged frankly to abandon the attempt to associate some of the simpler forms with their nearest genetic allies and to content ourselves with a more or less artificial system, which is not, however, artificial in so far as its main groups are concerned. Thus the genetic solidarity of each of the large classes Heliozoa, Reticularia, Mycetozoa, and Radiolaria is not open to question. The Lobosa on the other hand appear to be a more artificial assemblage, and it is difficult to say that genetically there is any wide separation between them and the Mycetozoa or between the Mycetozoa and some of the simpler forms which we bring together under the class Proteomyxa.

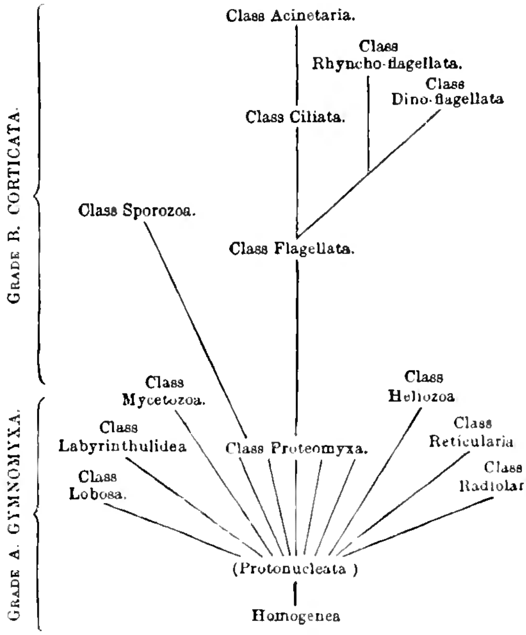
The scheme of classification which we adopt is the following:—

PROTOZOA.

Sections.	Grade A. *GYMNOMYXA.*
Proteana.	Class I. Proteomyxa. Ex. *Vampyrella*, *Protomyxa*, *Archerina*.
Plasmodiata.	Class II. Mycetozoa. Ex. The *Eu-mycetozoa* of Zopf.
Lobosa.	Class III. Lobosa. Ex. *Amœba*, *Arcella*, *Pelomyxa*.
Filosa.	Class IV. Labyrinthulidea. Ex. *Labyrinthula*, *Chlamydomyxa*.
	Class V. Heliozoa. Ex. *Actinophrys*, *Raphidiophrys*, *Clathrulina*.
	Class VI. Reticularia. Ex. *Gromia*, *Lituola*, *Astrorhiza*, *Globigerina*.
	Class VII. Radiolaria. Ex. *Thalassicolla*, *Eucyrtidium*, *Acanthometra*.

	Grade B. *CORTICATA.*
Lipostoma.	Class I. Sporozoa. Ex. *Gregarina*, *Coccidium*.
Stomatophora.	Class II. Flagellata. Ex. *Monas*, *Salpingœca*, *Euglena*, *Volvox*.
	Class III. Dinoflagellata. Ex. *Prorocentrum*, *Ceratium*.
	Class IV. Rhynchoflagellata. Ex. *Noctiluca*.
	Class V. Ciliata. Ex. *Vorticella*, *Paramœcium*, *Stentor*.
	Class VI. Acinetaria. Ex. *Acineta*, *Dendrosoma*.

The genetic relationships which probably obtain among these groups may be indicated by the following diagram:—



Literature.—Certain works of an older date dealing with microscopic organisms, and therefore including many Protozoa, have historical interest. Among these we may cite O. F. Müller, *Animalcula Infusoria*, 1786; Ehrenberg, *Infusionsthierchen*, 1838;

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[1] The "exoplasm" and "endoplasm" described in Amœbæ, &c., by some authors are not distinct layers but one and the same continuous substance—what was internal at one moment becoming external at another, no really structural difference existing between them.

Dujardin, *Histoire naturelle des Infusoires,* 1841; Pritchard, *Infusoria,* 1857.

The general questions relating to protoplasm and to the constitution of the Protozoon body as a single cell are dealt with in the following more recent treatises:—Max Schultze, *Ueber den Organismus der Polythalamien,* 1854, and *Ueber das Protoplasma der Rhizopoden und Pflanzenzellen,* 1863; and Engelmann, article "Protoplasma" in Hermann's *Handwörterbuch der Physiologie,* 1880.

Special works of recent date in which the whole or large groups of Protozoa are dealt with in a systematic manner with illustrations of the chief known forms are the following:—Bütschli, "Protozoa," in Bronn's *Classen und Ordnungen des Thierreichs,* a comprehensive and richly illustrated treatise now in course of publication, forming the most exhaustive account of the subject matter of the present article which has been attempted (the writer desires to express his obligation to this work, from the plates of which a large proportion of the woodcut figures here introduced have been selected); W. S. Kent, *Manual of the Infusoria,* 1882—an exhaustive treatise including figures and descriptions of all species of Flagellata, Dinoflagellata, Ciliata, and Acinetaria; Stein, *Der Organismus der Infusionsthiere,* 1867–1882; Haeckel, *Die Radiolarien,* 1862; Archer, "Résumé of recent contributions to our knowledge of freshwater Rhizopoda," *Quart. Jour. of Microscopical Science,* 1876–77; Zopf, "Pilzthiere" (Mycetozoa), in *Encyklopädie der Naturwissenschaften,* Breslau, 1884.

We shall now proceed to consider the classes and orders of Protozoa in detail.

PROTOZOA.

Characters.—Organisms consisting of a single cell or of a group of cells not differentiated into two or more tissues; incapable of assimilating nitrogen in its diffusible compounds (ammonia or nitrates) or carbon in the form of carbonates, except in special instances which there is reason to regard as directly derived from allied forms not possessing this capacity. The food of the Protozoa is in consequence as a rule taken in the form of particles into the protoplasm either by a specialized mouth or by any part of the naked cell-substance, there to be digested and rendered diffusible.

Grade A. *GYMNOMYXA,* Lankester, 1878 (**64**).

Characters.—Protozoa in which the cell-protoplasm is entirely or partially exposed to the surrounding medium, during the active vegetative phase of the life-history, as a naked undifferentiated slime or viscous fluid, which throws itself into processes or "pseudopodia" of various form either rapidly changing or relatively constant. Food can be taken into the protoplasm in the form of solid particles at any point of its surface or at any point of a large exposed area. The distinction into so-called "exoplasm" and "endoplasm" recognized by some authors, is *not* founded on a permanent differentiation of substance corresponding to the cortical and medullary substance of Corticata, but is merely due to the centripetal aggregation of granules lying in a uniform undifferentiated protoplasm. The cell-individual exhibits itself under four phases of growth and development—(1) as a swarm-spore (monadiform young or flagellula); (2) as an amœba form; (3) as constituent of a plasmodium or cell-fusion or conjugation; (4) as a cyst, which may be a flagellula(Schwärme)-producing cyst, an amœbula-producing cyst, a covered-spore(chlamydospore)-producing cyst (sporocyst *sens. stric.,* Zopf), or a simple resting cyst which does not exhibit any fission of its contents (hypnocyst). Any one of these phases may be greatly predominant and specialized whilst the others are relatively unimportant and rapidly passed through.

Class I. **PROTEOMYXA**, Lankester.

Characters.—Gymnomyxa which exhibit in the amœba phase various forms of pseudopodia often changing in the same individual, and do not produce elaborate spore cysts; hence they are not referable to any one of the subsequent six classes. Mostly minute forms, with small inconspicuous nucleus (absent in some ?).

A division into orders and families is not desirable, the group being confessedly an assemblage of negatively characterized or insufficiently known forms.

Genera.—*Vampyrella,* Cienkowski (**15**); *Vampyrellidium,* Zopf (**13**); *Spirophora,* Zopf (=*Amœba radiosa,* Perty); *Haplococcus,* Zopf; *Leptophrys,* Hertwig and Lesser (**16**); *Endyomena,* Zopf; *Bursulla,* Sorokin (**17**); *Myxastrum,* Haeckel (**1**); *Enteromyxa,* Cienkowski (**18**); *Colpodella,* Cienkowski (**19**); *Pseudospora,* Cienkowski (**20**); *Protomonas,* Cienkowski (**15**); *Diplophysalis,* Zopf (**13**); *Gymnococcus,* Zopf; *Aphelidium,* Zopf; *Pseudosporidium,* Zopf; *Protomyxa,* Haeckel (**1**); *Plasmodiophora,* Woronin (**21**); *Tetramyxa,* Göbel (**22**); *Gloidium,* Sorokin (**23**); *Gymnophrys,* Cienkowski (**24**); *Myxodictyum,* Haeckel (**1**); *Boderia,* Wright (**25**); *Biomyxa,* Leidy (**92**); *Protogenes,* Haeckel (**1**); *Protamœba,* Haeckel (**1**); *Nuclearia,* Cienkowski (**26**); *Monobia,* Aim. Schneider (**27**); *Archerina,* Lankester (**14**).

The forms here brought together include several genera (the first nineteen) referred by Zopf to the Mycetozoa, some again (Vampyrella, Myxastrum, Nuclearia, Monobia) which are by Bütschli associated with the Heliozoa, others (Protamœba, Gloidium) referred by the same authority to the Lobosa (Amœbæa) and others (Colpodella, Protomonas) which might be grouped with the lower Flagellata. By grouping them in the manner here adopted we are enabled to characterize those higher groups more satisfactorily and to give a just expression to our present want of that knowledge of the life-history both of these forms and of the higher Gymnomyxa which when it is obtained may enable us to disperse this heterogeneous class of Proteomyxa. The group has the same function in relation to the other classes of Gymnomyxa which the group Vermes has been made to discharge in relation to the better defined phyla of the Metazoa; it is a lumber-room in which obscure, lowly-developed, and insufficiently known forms may be kept until they can be otherwise dealt with.

It is true that, thanks to the researches of Continental botanists (especially Cienkowski and Zopf), we know the life-history of several of these organisms; but we are none the less unable to connect them by tangible characteristics with other Gymnomyxa.

Nearly all of the above-named genera are parasitic rather than "voracious," that is to say, they feed on the organized products of larger organisms both plants and animals (Haplococcus is parasitic in the muscles of the pig), into whose tissues they penetrate, and do not, except in a few cases (Protomyxa, Vampyrella), engulph whole organisms, such as Diatoms, &c., in their protoplasm. Many live upon and among the putrefying debris of other organisms (*e.g.*, rotting vegetable stems and leaves, excrements of animals), and like the Mycetozoa exert a digestive action upon the substances with which they come in contact comparable to the putrefying and fermentative activity of the Schizomycetes (Bacteria).

Fig. II. illustrates four chief genera of Proteomyxa.

Protomyxa aurantiaca was described by Haeckel (**1**), who found it on shells of Spirula on the coast of the Canary Islands, in the form of orange yellow flakes consisting of branching and reticular protoplasm nourishing itself by the ingestion of Diatoms and Peridinia. This condition is not a simple amœba phase but a "plasmodium" formed by the union of several young amœbæ. The plasmodium under certain conditions draws itself together into a spherical form and secretes a clear membranous cyst around itself, and then breaks up into some hundreds of flagellulæ or swarm-spores (Fig. II. 2). The diameter of the cyst is ·12 to ·2 millimetre. The flagellulæ subsequently escape (Fig. II. 3) and swim by the vibratile movement of one end which is drawn out in the form of a coarse flagellum. The swarm-spore now passes into the amœba phase (Fig. II. 4). Several of the small amœbæ creeping on the surface of the spirula-shell then unite with one another and form a plasmodium which continues to nourish itself by "voracious" inception of Diatoms and other small organisms. The plasmodia may attain a diameter of one millimetre and be visible by the naked eye.

A nucleus was not observed by Haeckel in the spores nor in the amœba phase, nor scattered nuclei in the plasmodium, but it is not improbable that they exist and escaped detection in the living condition, in consequence of their not being searched for by methods of staining, &c., which have since come into use. A contractile vacuole does not exist.

Vampyrella spirogyræ, Cienkowski (Fig. II. 5, 6, 7), is one of several species assigned to the genus Vampyrella, all of which feed upon the living cells of plants. The nucleus previously stated to be absent has been detected by Zopf (**13**). There is no contractile vacuole. The amœba phase has an actinophryd character (*i.e.*, exhibits fine radiating pseudopodia resembling those of the sun-animalcule, Actinophrys, one of the Heliozoa). This species feeds exclusively upon the contents of the cells of Spirogyra, effecting an entrance through the cell-wall (Fig. II. 5), sucking out the contents, and then creeping on to the next cell. In some species of Vampyrella as many as four amœba-individuals have been observed to fuse to form a small plasmodium. Cysts are formed which enclose in this species a single amœba-individual. The cyst often acquires a second or third inner cyst membrane by the shrinking of the protoplasmic body after the first encystment and the subsequent formation of a new membrane. The encysted protoplasm sometimes merely divides into four parts each of which creeps out of the cyst as an Actinophrys-like amœba (Fig. II. 7); in other instances it forms a dense spore, the product of which is not known.

Protogenes primordialis is the name given by Haeckel to a very simple form with radiating filamentous pseudopodia which he observed in sea-water. It appears to be the same organism as that described and figured by Max Schultze as *Amœba porrecta.* Schultze's figure is copied in Fig. II. 12. No nucleus and no contractile vacuole is observed in this form. It feeds voraciously on smaller organisms. Its life-history has not been followed over even a few steps. Hence we must for the present doubt altogether as to its true affinities. Possibly it is only a detached portion of the protoplasm of a larger nucleate Gymnomyxon. The same kind of doubt is justified in regard to Haeckel's *Protamœba primitiva*, which was observed by him in pond water and differs from Protogenes in having lobose pseudopodia, whilst agreeing with it in absence of nuclei, contractile vacuoles, and other differentiation of structure.

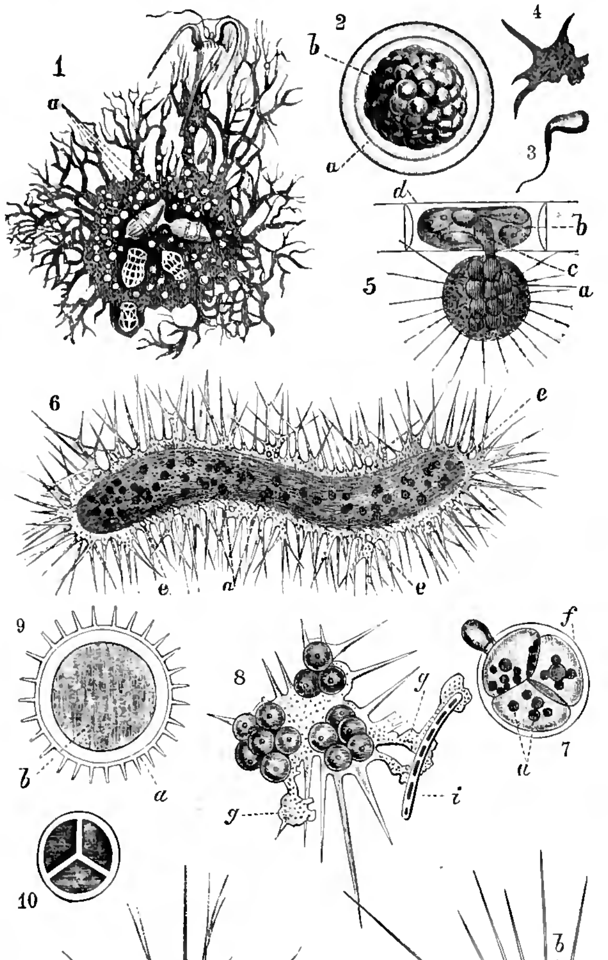


Fig. II.—Various **Proteomyxa.** 1. *Protomyxa aurantiaca*, Haeckel, plasmodium phase. The naked protoplasm shows branched, reticulate processes (pseudopodia), and numerous non-contractile vacuoles. It is in the act of engulphing a Ceratium. Shells of engulphed Ciliata (Tintinnabula) are embedded deeply in the protoplasm *a*. 2. Cyst phase of Protomyxa. *a*, transparent cyst-wall; *b*, protoplasm broken up into spores. 3. Flagellula phase of Protomyxa, the form assumed by the spores on their escape from the cyst. 4. Amœbula phase of the same, the form assumed after a short period by the flagellulæ. 5. *Vampyrella spirogyræ*, Cienk., amœba phase penetrating a cell of Spirogyra *b*, by a process of its protoplasm *c*, and taking up the substance of the Spirogyra cell, some of which is seen within the Vampyrella *a*. 6. Large individual of Vampyrella, showing pseudopodia *e*, and food particles *a*. The nucleus (though present) is not shown in this drawing. 7. Cyst phase of Vampyrella. The contents of the cyst have divided into four equal parts, of which three are visible. One is commencing to break its way through the cyst-wall *f*; *a*, food particles. 8. *Archerina Boltoni*, Lankester, showing lobose and filamentous protoplasm, and three groups of chlorophyll corpuscles. The protoplasm *g* is engulphing a Bacterium *i*. 9. Cyst phase of Archerina. *a*, spinous cyst-wall; *b*, green-coloured contents. 10. Chlorophyll corpuscle of Archerina showing tetraschistic division. 11. Actinophryd form of Archerina. *b*, chlorophyll corpuscles. 12. *Protogenes primordialis*, Haeckel (*Amœba porrecta*, M. Schultze), from Schultze's figure.

The structureless protoplasmic network described by Haeckel from spirit-preserved specimens of Atlantic ooze and identified by him with Huxley's (**28**) Bathybius, as also the similar network described by Bessels (**29**) as Protobathybius, must be regarded for the present as insufficiently known.

It is possible that these appearances observed in the ooze dredged from great depths in the Atlantic are really due to simple Protozoa. On the other hand it has been asserted by Sir Wyville Thomson, who at one time believed in the independent organic nature of Bathybius, that the substance taken for protoplasm by both Huxley and Haeckel is in reality a gelatinous precipitate of calcium sulphate thrown down by the action of alcohol upon sea-water. Other naturalists have pointed to the possibility of the protoplasmic network which Bessels studied in the living condition on board ship being detached portions of the protoplasm of Reticularia and Radiolaria. The matter is one which requires further investigation.

Archerina Boltoni is the name given by Lankester (**14**) to a very simple Gymnomyxon inhabiting freshwater ponds in company with Desmids and other simple green Algæ (Fig. II. 8 to 11). Archerina exhibits an amœba phase in which the protoplasm is thrown into long stiff filaments (Fig. II. 11), surrounding a spherical central mass about $\frac{1}{2000}$th inch in diameter (actinophryd form). A large vacuole (non-contractile) is present, or two or three small ones. No nucleus can be detected by careful use of reagents in this or other phases. The protoplasm has been seen to ingest solid food particles (Bacteria) and to assume a lobose form. The most striking characteristic of Archerina is the possession of chlorophyll corpuscles. In the actinophryd form two oval green-coloured bodies (*b*, *b*) are seen. As the protoplasm increases by nutrition the chlorophyll corpuscles multiply by quaternary division (Fig. II. 10) and form groups of four or of four sets of four symmetrically arranged. The division of the chlorophyll corpuscles is not necessarily followed by that of the protoplasm, and accordingly specimens are found with many chlorophyll corpuscles embedded in a large growth of protoplasm (Fig. II. 8); the growth may increase to a considerable size, numbering some hundreds of chlorophyll corpuscles, and a proportionate development of protoplasm. Such a growth is not a plasmodium, that is to say, is not formed by fusion of independent amœba forms, but is due to continuous growth. When nutrition fails the individual chlorophyll corpuscles separate, each carrying with it an investment of protoplasm, and then each such amœba form forms a cyst around itself which is covered with short spines (Fig. II. 9). The cysts are not known to give rise to spores, but appear to be merely hypnocysts.

The domination of the protoplasm by the chlorophyll corpuscles is very remarkable and unlike anything known in any other organism. Possibly the chlorophyll corpuscles are to be regarded as nuclei, since it is known that there are distinct points of affinity between the dense protoplasm of ordinary nuclei and the similarly dense protoplasm of normal chlorophyll corpuscles.

Class II. **MYCETOZOA**, De Bary.

Characters.—Gymnomyxa which, as an exception to all other Protozoa, are not inhabitants of water but occur on damp surfaces exposed to the air. They are never parasitic, as are some of the Proteomyxa most nearly allied to them (Plasmodiophora, &c.), but feed on organic debris. They are structurally characterized by the fact that the amœba forms, which develop either directly or through flagellulæ from their spores, always form large, sometimes very large, *i.e.*, of several square inches area, fusion plasmodia (or rarely aggregation plasmodia), and that the spores are always chlamydospores (*i.e.*, provided with a coat) and are formed either in naked groups of definite shape (sori) or on the surface of peculiar columns (conidiophors) or in large fruit-like cysts which enclose the whole or a part of the plasmodium and develop besides the spores definite sustentacular structures (capillitium) holding the spores in a mesh-work.

Three orders of Mycetozoa are distinguishable according to the arrangement of the spores in more or less complex spore-fruits.

Order 1. SOROPHORA, Zopf.

Characters.—Mycetozoa which never exhibit a vibratile (monadiform) swarmspore or flagellula phase, but hatch from the spore as amœbæ. A true fusion plasmodium is not formed, but an aggregation plasmodium by the contact without fusion of numerous amœba forms. The spore fruit is a naked aggregation of definitely arranged encysted amœbæ called a sorus, not enclosed in a common capsule; each encysted amœba has the value of a single spore and sets free on germination a single amœbula. They inhabit the dung of various animals.

Genera.—*Copromyxa*, Zopf; *Cynthulina*, Cienk.; *Dictyostelium*, Brefeld; *Acrasis*, Van Tieghem; *Polyspondylium*, Brefeld.

Order 2. ENDOSPOREA, Zopf.

Characters.—Mycetozoa always passing through the flagellula phase and always forming true plasmodia by fusion of amœba forms. The spore-fruit is in the form of a large cyst which encloses a quantity of the plasmodium; the latter then breaks up into (*a*) spores (one corresponding to each nucleus of the enclosed plasmodium) each of which has a cellulose coat, and (*b*) a capillitium of threads which hold the spores together. Each spore (chlamydospore) liberates on germination a single nucleated flagellula, which develops into an amœbula, which in turn fuses with other amœbulæ to form the plasmodium. The Endosporea are essentially dwellers on rotten wood and such vegetable refuse.

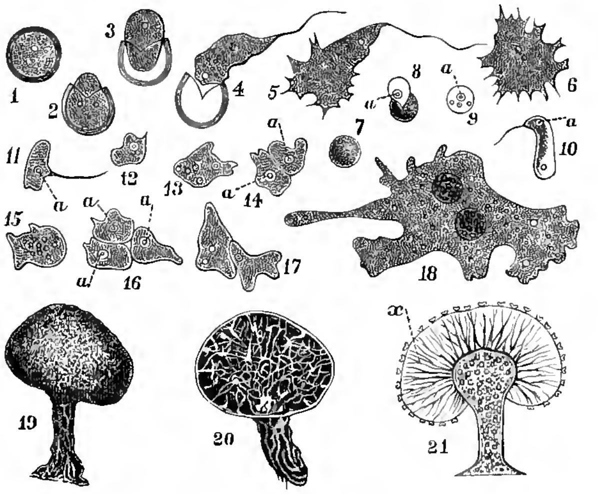


Fig. III.—**Mycetozoa** (after De Bary). 1–6. Germination of spore (1) of *Trichea varia*, showing the emerging "flagellula" (4, 5), and its conversion into an "amœbula" (6). 7–18. Series leading from spore to plasmodium phase of *Chondrioderma difforme*:—7, spore; 10, flagellula; 12, amœbula; 14, apposition of two amœbulæ; 15–17, fusions; 18, plasmodium. 19, 20, Spore-fruit (cyst) of *Physarum leucophæum*, Fr. (× 25), the former from the surface, the latter in section with the spores removed to show the sustentacular network or capillitium. 21. Section of the spore-cyst of *Didymium squamulosum*, with the spores removed to show the radiating capillitium *x* and the stalk.

Sub-order 1. PERITRICHEA, Zopf.

Fam. 1. CLATHROPTYCHIACEÆ, Rostafinski.
Genera.—*Clathroptychium*, Rost.; *Enteridium*, Ehr.
Fam. 2. CRIBRARIACEÆ.
Genera.—*Dictydium*, Pers.; *Cribraria*, Pers.

Sub-order 2. ENDOTRICHEA, Zopf.

Fam. 1. PHYSAREA.
Genera.—*Physarum*, Pers.; *Craterium*, Trentepol; *Badhamia*, Berkeley; *Leocarpus*, Link.; *Tilmadoche*, Fr.; *Fuligo* (*Æthalium*), Hall; *Æthaliopsis*, Z.
Fam. 2. DIDYMIACEÆ.
Genera.—*Didymium*; *Lepidoderma*, De Bary.
Fam. 3. SPUMARIACEÆ.
Genera.—*Spumaria*, Pers.; *Diachea*, Fries.
Fam. 4. STEMONITEA.
Genera.—*Stemonitis*, Gleditsch; *Comatricha*, Preuss; *Lamproderma*, Rost.
Fam. 5. ENERTHENEMEA.
Genera.—*Enerthema*, Bowman.
Fam. 6. RETICULARIACEÆ, Zopf.
Genera.—*Amaurochæte*, Rost.; *Reticularia*, Bull.
Fam. 7. TRICHINACEÆ.
Genera.—*Hemiarcyria*, Rost.; *Trichia*, Hall.
Fam. 8. ARCYRIACEÆ.
Genera.—*Arcyria*, Hall; *Cornuvia*, Rost.; *Lycogala*, Ehr.
Fam. 9. PERICHÆNACEÆ.
Genera.—*Perichæna*, Fries.; *Lachnobolus*, Fries.
Fam. 10. LICEACEÆ.
Genera.—*Licea*, Schrader; *Tubulina*, Pers.: *Lindbladia*, Fries.; *Tubulifera*, Zopf.

ORDER 3. EXOSPOREA, Zopf.

Characters.—The chlamydospore liberates an amœbula in the first instance, which develops into a flagellula. This subsequently returns to the amœba form, and by fusion with other amœbulæ it forms a true fusion plasmodium. The spores are not produced within a cyst but upon the surface of column-like up-growths of the plasmodium, each spore (conidum) forming as a little spherical outgrowth attached to the column (conidiophor) by a distinct pedicle.

Sole Genus.—*Ceratium*. [This name must be changed, since it was already applied to a genus of Dinoflagellata, when Famintzin and Woronin gave it to this Mycetozoon.]

Further Remarks on Mycetozoa.—About two hundred species of Mycetozoa have been described. Botanists, and especially those who occupy themselves with Fungi, have accumulated the very large mass of facts now known in reference to these organisms; nevertheless the most eminent botanist who has done more than any other to advance our knowledge of Mycetozoa, namely, De Bary, has expressed the view that they are to be regarded rather as animals than as plants. The fact is that, once the question is raised, it becomes as reasonable to relegate all the Gymnomyxa without exception to the vegetable kingdom as to do so with the Mycetozoa. Whatever course we take with the latter, we must take also with the Heliozoa, the Radiolaria, and the Reticularia.

The formation of plasmodia, for which the Mycetozoa are conspicuous, appears to be a particular instance of the general phenomenon of cell-conjugation. Small plasmodia are formed by some of the Proteomyxa; but among the other Gymnomyxa, excepting Mycetozoa, and among Corticate Protozoa, the fusion of two individuals (conjugation *sensu stricto*) is more usual than the fusion of several. Zopf (13) has attempted to distinguish arbitrarily between conjugation and plasmodium formation by asserting that in the former the nuclei of the cells which fuse are also fused, whereas in the latter process the nuclei retain their independence. Both statements are questionable. What happens to the nucleus in such conjugations as those of the Gregarinæ has not yet been made out, whilst it is only quite recently that Strasburger (30) has shown that the plasmodia of Mycetozoa contain numerous scattered nuclei, and it is not known that fusion does not occur between some of these. There is no doubt that the nuclei of plasmodia multiply by fission, though we have no detailed account of the process.

The Sorophora are exceptional in that the amœbæ which unite to form a cell-colony in their case do not actually fuse but only remain in close contact; with this goes the fact that there are no large spore-cysts, but an identification of spore and spore-cyst. The amœbæ arrange themselves in stalked clusters (sori), and each becomes encysted: one may, in this case, consider the cyst equally as a spore or as a spore-cyst which produces but a single spore. The amœbæ described by various writers as inhabiting the alimentary canal and the dung of higher animals (including man) belong to this group. The form described by Cunningham in the *Quart. Jour. Micr. Sci.*, 1881, as *Protomyxomyces coprinarius* is apparently related to the *Copromyxa* (*Guttulina*) *protea* of Fayod (31).

The spore-fruits of the Endosporeæ occur in various degrees of elaboration. Usually they are (1) spherical or pear-shaped cysts with or without an obvious stalk (Fig. III. 19, 20, 21), and often have a brilliant colour, and are of a size readily observed by the naked eye, the plasmodia which give rise to them being by no means microscopic. But they may present themselves (2) as irregular ridges growing up from the plasmodium, when they are termed serpula forms. Lastly, the cysts may be united side by side in larger or smaller groups instead of forming at various separate points of the plasmodium. These composite bodies are termed "fruit-cakes" or "æthalia," in view of the fact that the spore-cysts of Fuligo, also called Æthalium—the well-known "flowers of tan"—form a cake of this description.

The capillitium or network of threads which lies between the spores in the spore-cysts of Endosporeæ is a remarkable structure which exhibits special elaborations in detail in different genera, here not to be noticed for want of space. Although definite in form and structure, these threads are not built up by cells but are formed by a residual protoplasm (*cf.* Sporozoa) which is left in the cyst after the spores have been segregated and enclosed each in its special coat. They are often impregnated by calcium carbonate, and exhibit crystalline masses of it, as does also the cyst-wall.

The spores of the Mycetozoa are as a rule about the $\frac{1}{1500}$th inch in diameter. They are produced by millions in the large fruit-cakes of such forms as Fuligo. Often the spore-coat is coloured; it always consists of a substance which gives the cellulose reaction with iodine and sulphuric acid. This has been sometimes considered an indication of the vegetable nature of the Mycetozoa, but cannot be so regarded since many animals (especially the Tunicata and various Protozoa) produce substances giving this same reaction.

Dryness, low temperature, and want of nutriment lead to a dormant condition of the protoplasm of the plasmodium of many Mycetozoa and to its enclosure in cyst-like growths known as "sclerotia," which do not give rise to spores, but from which the protoplasm creeps forth unaltered when temperature, nutrition, and moisture are again favourable. The sclerotia are similar in nature to the hypnocysts of other Protozoa.

The physiological properties—chemical composition, digestive action, reaction to moisture, heat, light, and other physical influences—of the plasmodia of Mycetozoa have been made the subject of important investigations; they furnish the largest masses of undifferentiated protoplasm available for such study. The reader is referred to Zopf's admirable treatise (13) as to these matters, and also for a detailed account of the genera and species.

CLASS III. LOBOSA, Carpenter.

Characters.—Gymnomyxa in which (as in the succeeding four classes) the amœba-phase predominates over the others in permanence, size attained, and physiological importance. The pseudopodia are lobose, ranging in form from mere wave-like bulgings of the surface to blunt finger-like processes, but never having the character of filaments either simple, arborescent, or reticulate. Fusions of two individuals (conjugation) have been observed in a few cases, but not fusions of many individuals so as to form plasmodia; nevertheless the size attained by the naked protoplasm by pure growth is in some cases considerable, forming masses readily visible by the naked eye (Pelomyxa). The presence of more than one nucleus is a frequent character. A contractile vacuole may or may not be present. The formation of sporocysts and of chlamydospores (coated spores) has not been observed in any species, but naked spores (flagellulæ or amœbulæ) have been with more or less certainty observed as the product of the breaking up of some species (Amœba? Pelomyxa). The cyst phase is not unusual, but the cyst appears usually to be a hypnocyst and not a sporocyst. In the best observed case of spore-production (Pelomyxa) the spores were apparently produced without the formation of a cyst. Reproduction is undoubtedly most freely effected by simple fission (Amœba) and by a modified kind of bud-fission (Arcella). Fresh-water and marine. Two orders of the Lobosa are distinguished in accordance with the presence or absence of a shell.

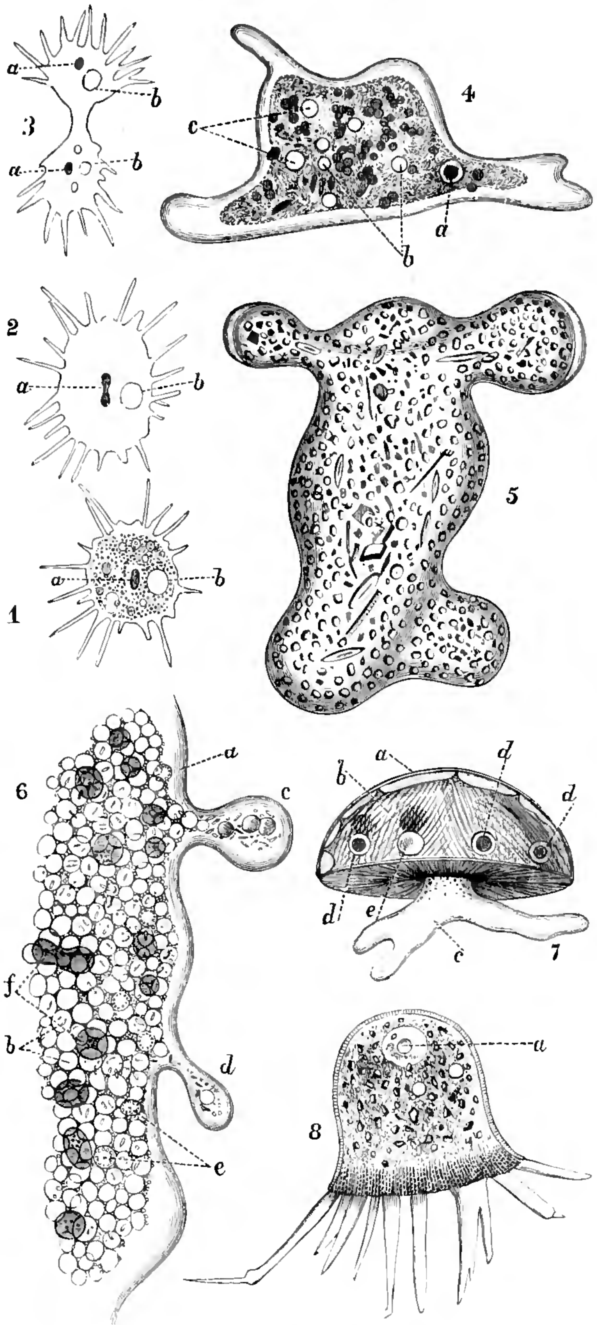


FIG. IV.—Various **Lobosa**. 1, 2, 3. *Dactylosphæra* (*Amœba*) *polypodia*, M. Schultze, in three successive stages of division; the changes indicated occupied fifteen minutes. *a*, nucleus; *b*, contractile vacuole (copied from F. E. Schultze, in *Archiv f. Mikrosk. Anat.*). 4. *Amœba princeps*, Ehr. (after Auerbach). *a*, nucleus; *b*, *c*, vacuoles (one or more contractile; the shaded granules are food-particles). 5. *Pelomyxa palustris*, Greeff (after Greeff), an example with comparatively few food-particles (natural size $\frac{1}{30}$th inch in length). 6. Portion of a Pelomyxa more highly magnified. *a*, clear superficial zone of protoplasm (so-called "exoplasm"); *b*, vacuoles, extremely numerous; *c*, lobose pseudopodium; *d*, a similar pseudopodium; *e*, nuclei; *f*, "refractive bodies" (reproductive?); scattered about in the protoplasm are seen numerous cylindrical crystals. 7. *Arcella vulgaris*, Ehr. *a*, shell; *b*, protoplasm within the shell; *c*, extended protoplasm in the form of lobose pseudopodia; *d*, nuclei; *e*, contractile vacuole; the dark bodies unlettered are gas vacuoles. 8. *Cochliopodium pellucidum*, Hert. and Less. *a*, nucleus surrounded by a hyaline halo sometimes mistaken for the nucleus, whilst the latter is termed nucleolus.

ORDER 1. NUDA.

Characters.—Lobosa devoid of a shell.

Genera.—*Amœba*, Auct. (Fig. IV. 4); *Ouramœba*, Leidy (with a villous tuft at one end, Wallich's *A. villosa*); *Corycia*, Duj. (low, ridge-like pseudopodia); *Lithamœba*, Lankester (Fig. V.); *Dinamœba*, Leidy (**92**) (covered with short stiff processes); *Hyalodiscus*, H. and L.; *Plakopus*, F. E. Schultze; *Dactylosphæra*, H. and L. (Fig. IV. 1, 2, 3); *Pelomyxa*, Greeff (Fig. IV. 5, 6); *Amphizonella*, Greeff (forms a gelatinous case which is broken through by the pseudopodia).

ORDER 2. TESTACEA.

Characters.—Lobosa which secrete a shell provided with an aperture from which the naked protoplasm can be protruded. The shell is either soft and membranous, or strengthened by the inclusion of sand-particles, or is hard and firm.

Genera.—*Cochliopodium* (Fig. IV. 8), H. and L.; *Pyxidicula*, Ehr.; *Arcella*, Ehr. (Fig. IV. 7); *Hyalosphenia*, Stein; *Quadrula*, F. E. Schultze (shell membraneous, areolated); *Difflugia*, Leclerc (shell with adventitious particles).

Further remarks on the Lobosa.—The Lobosa do not form a very numerous nor a very natural assemblage. Undoubtedly some of the forms which have been described as species of Amœba are amœba forms of Mycetozoa; this appears to be most probably the case in parasitic and stercoricolous forms. But when these are removed, as also those Proteomyxa which have pseudopodia of varying character, at one time lobose and at another filamentous, we have left a certain small number of independent lobose Gymnomyxa which it is most convenient to associate in a separate group. We know very little of the production of spores (whether it actually obtains or not) or of developmental phases among these Lobosa. The common Amœbæ are referable to the species *A. princeps*, *A. lobosa*, *Dactylosphæra polypodia*, *Ouramœba villosa*. Of none of these do we know certainly any reproductive phenomena excepting that of fission (see Fig. IV. 1, 2, 3). Various statements have been made pointing to a peculiar change in the nucleus and a production of spores having the form of minute Amœbæ, arising from that body; but they cannot be considered as established. Whilst the observed cases of supposed reproductive phenomena are very few, it must be remembered that we have always to guard (as the history of the Ciliata has shown, see below) against the liability to mistake parasitic amœbulæ and flagellulæ for the young forms of organisms in which they are merely parasitic. The remarkable *Pelomyxa palustris* of Greeff (**32**) was seen by him to set free (without forming a cyst) a number of amœbulæ which he considers as probably its young. Mr Weldon of St John's College, Cambridge, has observed the same phenomenon in specimens of Pelomyxa which made their appearance in abundance in an aquarium in the Morphological Laboratory, Cambridge. It seems probable that the amœbulæ in this case are not parasites but spore-like young, and this is the best observed case of such reproduction as yet recorded in the group.

Arcella is remarkable for the production of bud-spores, which may be considered as a process intermediate between simple fission and the complete breaking up of the parent body into spores. As many as nine globular processes are simultaneously pinched off from the protoplasm extruded from the shell of the Arcella; the nuclei (present in the parent Arcella to the number of two or three) have not been traced in connexion with this process. The buds then become nipped off, and acquire a shell and a contractile vacuole (**33**).

The presence of more than one nucleus is not unusual in Lobosa, and is not due to a fusion of two or more uninuclear individuals, but to a multiplication of the original nucleus. This has been observed in some Amœbæ (*A. princeps?*) as well as Arcella. Pelomyxa (Fig. IV. 6) has a great number of nuclei like the Heliozoon, Actinosphærium (Fig. VIII.).

Pelomyxa is the most highly differentiated of the Lobosa. The highly vacuolated character of its protoplasm is exhibited in a less degree by Lithamœba and resembles that of Heliozoa and Radiolaria. Besides the numerous nuclei there are scattered in the protoplasm strongly refringent bodies (Fig. IV. 6, *f*), the significance of which has not been ascertained. The superficial protoplasm is free from vacuoles, hyaline, and extremely mobile. Occasionally it is drawn out into very short fine filaments. Scattered in the protoplasm are a number of minute cylindrical crystals, of unascertained composition. Pelomyxa is of very large size for a Protozoon, attaining a diameter of $\frac{1}{16}$th of an inch. It takes into its substance a quantity of foreign particles, both nutrient organic matter such as Rotifera and Diatoms and sand particles. It occurs not uncommonly in old muddy ponds (such as duck-ponds), creeping upon the bottom, and has a white appearance to the naked eye. Lithamœba (Fig. V.) is distinguished by its large size, disk-like form, the disk-like shape of its pseudopodia, the presence of specific concretions, the vacuolation of its protoplasm, and the block-like form and peculiar tessellated appearance of its large nucleus, which has a very definite capsule. In Lithamœba it is easy to recognize a distinct pellicle or temporary cuticle which is formed upon the surface of the protoplasm, and bursts when a pseudopodium is formed. In fact it is the rupture of this pellicle which appears to be the proximate cause of the outflow of protoplasm as a pseudopodium. Probably a still more delicate pellicle always forms on the surface of naked protoplasm, and in the way just indicated determines by its rupture the form and the direction of the "flow" of protoplasm which is described as the "protrusion" of a pseudopodium.

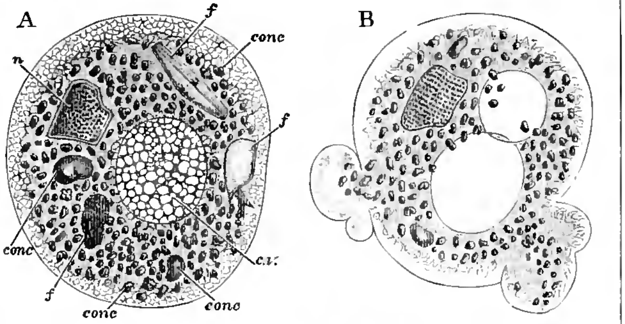


FIG. V.—*Lithamœba discus*, Lank. (after Lankester, 34). A, quiescent; B, throwing out pseudopodia. *c.v.*, contractile vacuole, overlying which the vacuolated protoplasm is seen; *conc*, concretions insoluble in dilute HCl and dilute KHO, but soluble in strong HCl; *n*, nucleus.

The shells of Lobosa Testacea are not very complex. That of Arcella is remarkable for its hexagonal areolation, dark colour, and firm consistence; it consists of a substance resembling chitin. That of Difflugia has a delicate membranous basis, but includes foreign particles, so as to resemble the built-up case of a Caddis worm.

Arcella is remarkable among all Protozoa for its power of secreting gas-vacuoles (observed also in an Amœba by Bütschli), which serve a hydrostatic function, causing the Arcella to float. The gas can be rapidly absorbed by the protoplasm, when the vacuole necessarily disappears and the Arcella sinks.

CLASS IV. LABYRINTHULIDEA.

Characters.—Gymnomyxa forming irregular heaps of ovoid nucleated cells, the protoplasm of which extends itself as a branching network or labyrinth of fine threads. The oval (spindle-shaped) corpuscles, consisting of dense protoplasm, and possessing each a well-marked nucleus (not observed in Chlamydomyxa), travel regularly and continuously along the network of filaments. The oval corpuscles multiply by fission; they also occasionally become encysted and divide into four spherical spores. The young forms developed from these spores presumably develop into colonies, but have not been observed.

Genera.—Two genera only of Labyrinthulidea are known:—*Labyrinthula*, Cienkowski; *Chlamydomyxa*, Archer.

Cienkowski (35) discovered Labyrinthula on green Algæ growing on wooden piles in the harbour of Odessa (marine). It has an orange colour and forms patches visible to the naked eye. Chlamydomyxa was discovered by Archer of Dublin (36) in the cells of Sphagnum and crawling on its surface; hence it is a freshwater form. Unlike Labyrinthula, the latter forms a laminated shell of cellulose (Fig. VI. 2, *c*), in which it is frequently completely enclosed, and indeed has rarely been seen in the expanded labyrinthine condition. The laminated cellulose shells are very freely secreted, the organism frequently deserting one and forming another within or adherent to that previously occupied. The network of Chlamydomyxa appears to consist of hyaline threads of streaming protoplasm, whilst that of Labyrinthula has a more horny consistence, and is not regarded by Cienkowski as protoplasm.

The spindle-shaped cells are much alike in form and size in the two genera; but no nucleus was detected by Archer in those of Chlamydomyxa. The encysting of the spindle-cells and their fission into spores has been seen only in Labyrinthula. Chlamydomyxa is often of a brilliant green colour owing to the presence of chlorophyll corpuscles, and may exhibit a red or mottled red and green appearance owing to the chemical change of the chlorophyll. It has been observed to take in solid nourishment, though Labyrinthula has not.

The Labyrinthulidea present strong resemblances to the Mycetozoa. The genus Dactylostelium (Sorophora) would come very close to Labyrinthula were the amœbæ of its aggregation plasmodium set upon a network of threads. Such a network, whether in the condition of soft protoplasm or hardened and horny, is represented in the higher Mycetozoa by the capillitium of the sporocysts.

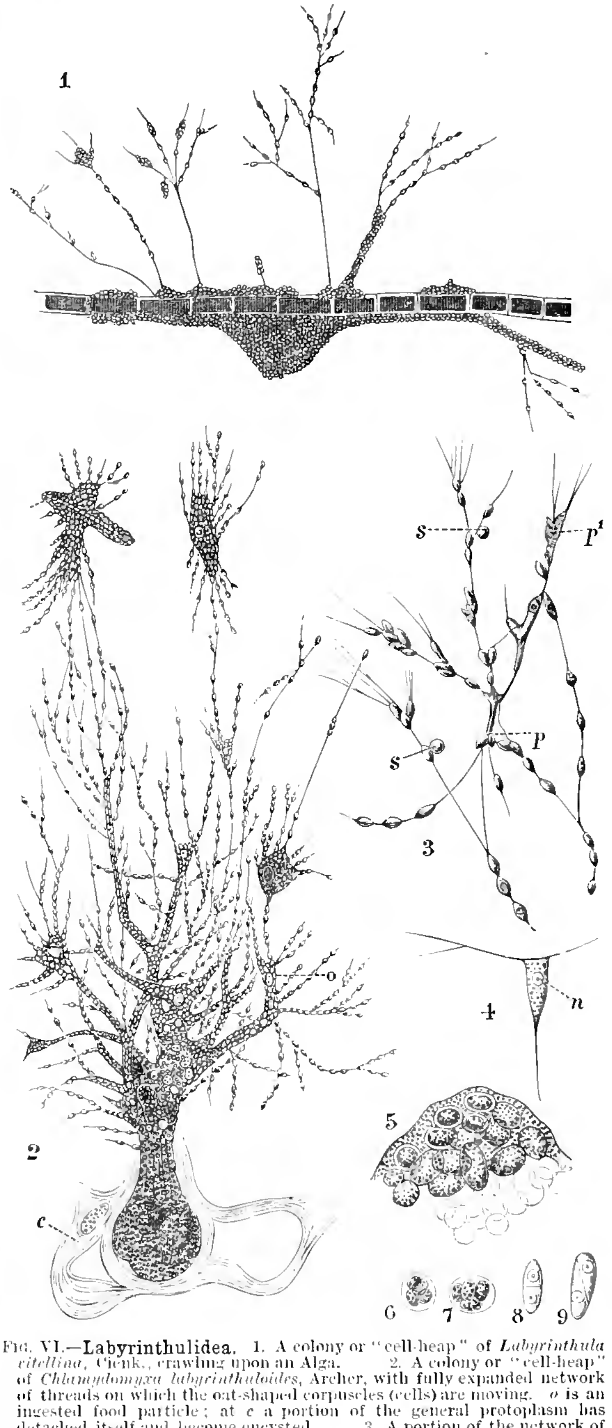


FIG. VI.—**Labyrinthulidea.** 1. A colony or "cell-heap" of *Labyrinthula vitellina*, Cienk., crawling upon an Alga. 2. A colony or "cell-heap" of *Chlamydomyxa labyrinthuloides*, Archer, with fully expanded network of threads on which the oat-shaped corpuscles (cells) are moving. *o* is an ingested food particle; at *c* a portion of the general protoplasm has detached itself and become encysted. 3. A portion of the network of *Labyrinthula vitellina*, Cienk., more highly magnified. *p*, protoplasmic mass apparently produced by fusion of several filaments; *p'*, fusion of several cells which have lost their definite spindle-shaped contour; *s*, corpuscles which have become spherical and are no longer moving (perhaps about to be encysted). 4. A single spindle cell and threads of *Labyrinthula macrocystis*, Cienk. *n*, nucleus. 5. A group of encysted cells of *L. macrocystis*, embedded in a tough secretion. 6, 7. Encysted cells of *L. macrocystis*, with enclosed protoplasm divided into four spores. 8, 9. Transverse division of a non-encysted spindle-cell of *L. macrocystis*.

The most important difference between Archer's Chlamydomyxa and Cienkowski's Labyrinthula is that in the former the threads of the network appear to consist of contractile protoplasm, whilst in the latter they are described as firm horny threads exuded by the spindle-cells. Neither form has been re-examined since its discovery; and it is possible that this apparent difference will be removed by further study.

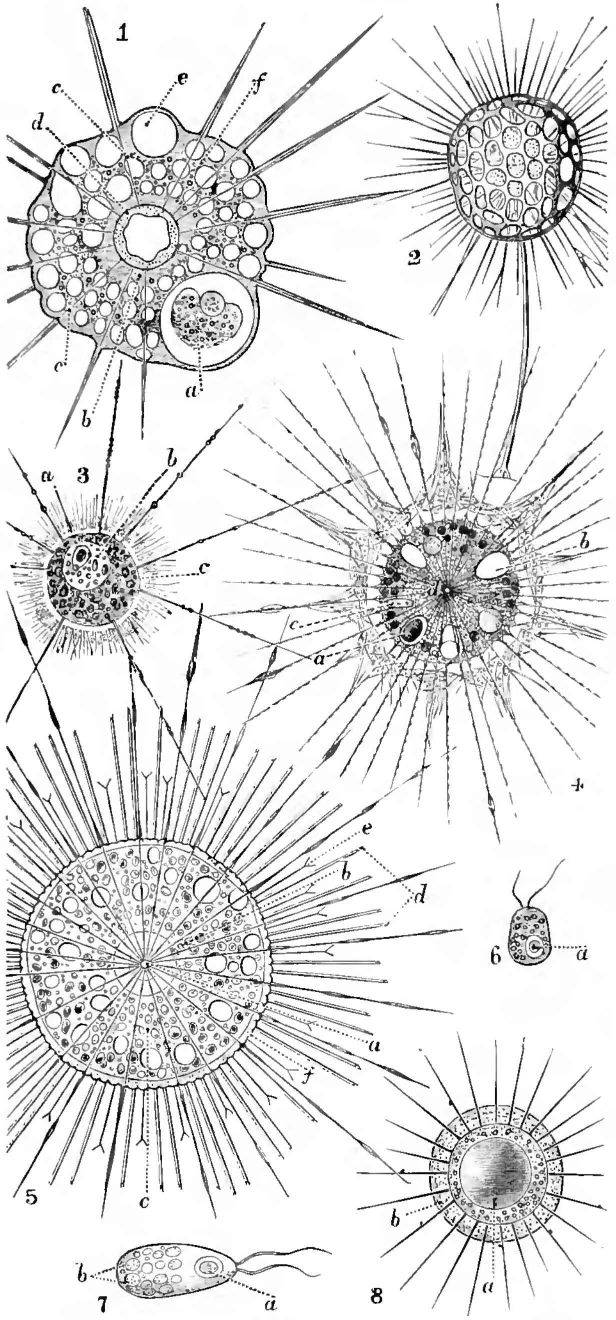


FIG. VII.—**Heliozoa.** 1. *Actinophrys sol*, Ehrb.; × 800. *a*. food-particle lying in a large food-vacuole; *b*, deep-lying finely granular protoplasm; *c*, axial filament of a pseudopodium extended inwards to the nucleus; *d*, the central nucleus; *e*, contractile vacuole; *f*, superficial much-vacuolated protoplasm. 2. *Clathrulina elegans*, Cienk.; × 200. 3. *Heterophrys marina*, H. and L. × 660. *a*, nucleus; *b*, clearer protoplasm surrounding the nucleus, *c*, the peculiar felted envelope. 4. *Raphidiophrys pallida*, F. E. Schultze; × 430. *a*, food-particle; *b*, the nucleus; *c*, contractile vacuole; *d*, central granule in which all the axis-filaments of the pseudopodia meet. The tangentially disposed spicules are seen arranged in masses on the surface. 5. *Acanthocystis turfacea*, Carter; × 240. *a*, probably the central nucleus; *b*, clear protoplasm around the nucleus; *c*, more superficial protoplasm with vacuoles and chlorophyll corpuscles; *d*, coarser siliceous spicules; *e*, finer forked siliceous spicules; *f*, finely granular layer of protoplasm. The long pseudopodia reaching beyond the spicules are not lettered. 6. Bi-flagellate "flagellula" of *Acanthocystis aculeata*. *a*, nucleus. 7. Ditto of *Clathrulina elegans*. *a*, nucleus. 8. *Astrodisculus ruber*, Greeff; × 320. *a*, red-coloured central sphere (? nucleus); *b*, peripheral homogeneous envelope.

Class V. **HELIOZOA**, Haeckel, 1866.

Characters.—Gymnomyxa in which the dominating amœba phase has the form of a spherical body from the surface of which radiate numerous isolated filamentous pseudopodia which exhibit very little movement or change of form, except when engaged in the inception of food-particles. The protoplasm of the spherical body is richly vacuolated; it may exhibit one or more contractile vacuoles and either a single central nucleus or many nuclei (Nuclearia, Actinosphærium). Skeletal products may or may not be present. Flagellulæ have been observed as the young forms of some species (Acanthocystis, Clathrulina), but very little has been as yet ascertained as to spore-formation or conjugation in this group, though isolated facts of importance have been observed. Mostly freshwater forms.

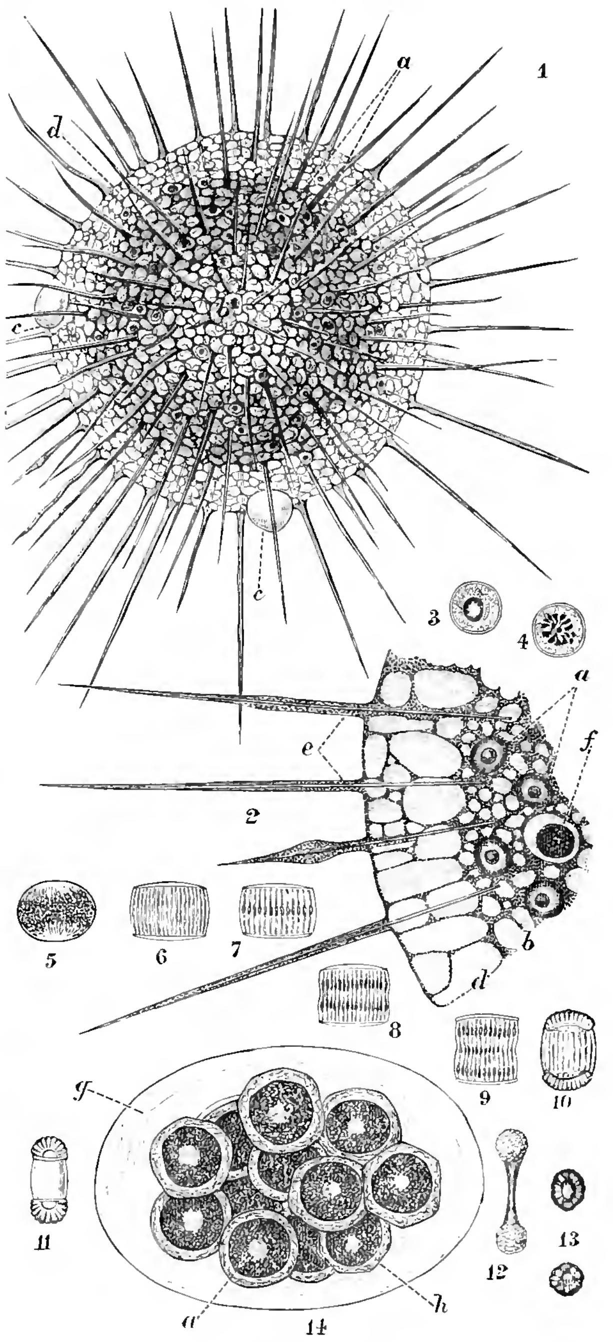


FIG. VIII.—**Heliozoa.** 1. *Actinosphærium Eichhornii*, Ehr.; × 200. *a*, nuclei; *b*, deeper protoplasm with smaller vacuoles and numerous nuclei; *c*, contractile vacuoles; *d*, peripheral protoplasm with larger vacuoles. 2. A portion of the same specimen more highly magnified and seen in optical section. *a*, nuclei; *b*, deeper protoplasm (so-called endosarc); *d*, peripheral protoplasm (so-called ectosarc); *e*, pseudopodia showing the granular protoplasm streaming over the stiff axial filament; *f*, food-particle in a food-vacuole. 3, 4. Nuclei of Actinosphærium in the resting condition. 5–13. Successive stages in the division of a nucleus of Actinosphærium, showing fibrillation, and in 7 and 8 formation of an equatorial plate of chromatin substance (after Hertwig). 14. Cyst-phase of *Actinosphærium Eichhornii*, showing the protoplasm divided into twelve chlamydospores, each of which has a siliceous coat; *a*, nucleus of the spore; *g*, gelatinous wall of the cyst; *h*, siliceous coat of the spore.

Order 1. APHROTHORACA, Hertwig (56).

Characters.—Heliozoa devoid of a spicular or gelatinous envelope, excepting in some a temporary membranous cyst.

Genera.—*Nuclearia*, Cienk. (37) (many nuclei; many contractile vacuoles; body not permanently spherical, but amœboid); *Actinophrys*, Ehr. (Fig. VII. 1; body spherical; pseudopodia with an axial skeletal filament; central nucleus; one large contractile vacuole; often forming colonies; *A. sol*, the Sun-animalcule); *Actinosphærium*, Stein (Fig. VIII.; spherical body; pseudopodia with axial filament; nuclei very numerous; contractile vacuoles 2 to 14); *Actinolophus*, F. E. Schulze (stalked).

Order 2. CHLAMYDOPHORA, Archer (57).

Characters.—Heliozoa with a soft jelly-like or felted fibrous envelope.

Genera.—*Heterophrys*, Archer (Fig. VII. 3); *Sphærastrum*, Greeff; *Astrodisculus*, Greeff (Fig. VII. 8).

Order 3. CHALAROTHORACA, Hertw. and Lesser (58).

Characters.—Heliozoa with a loose envelope consisting of isolated siliceous spicules.

Genera.—*Raphidiophrys*, Archer (Fig. VII. 4; skeleton in the form of numerous slightly curved spicules placed tangentially in the superficial protoplasm); *Pompholyxophrys*, Archer; *Pinacocystis* H. and L.; *Pinaciophora*, Greeff; *Acanthocystis*, Carter (skeleton in the form of radially disposed siliceous needles; encysted condition observed, and flagellula young, Fig. VII. 6); *Wagnerella*, Meresch.

Order 4. DESMOTHORACA, Hertw. and Less.

Characters.—Heliozoa with a skeletal envelope in the form of a spherical or nearly spherical shell of silica preforated by numerous large holes.

Genera.—*Orbulinella*, Entz (without a stalk); *Clathrulina*, Cienk. (with a stalk, Fig. VII. 2).

Further remarks on the Heliozoa.—The Sun-animalcules, Actinophrys and Actinosphærium, were the only known members of this group when Carter discovered in 1863 Acanthocystis. Our further knowledge of them is chiefly due to Archer of Dublin, who discovered the most important forms, and figured them in the *Quart. Jour. Micr. Sci.* in 1867.

Some of the Proteomyxa (*e.g.*, Vampyrella) exhibit "heliozoonlike" or "actinophryd" forms, but are separated from the true Heliozoa by the fact that their radiant pseudopodia are not maintained for long in the stiff isolated condition characteristic of this group. It is questionable whether Nuclearia should not be relegated to the Proteomyxa on account of the mobility of its body, which in all other Heliozoa has a constant spherical form.

Actinophrys sol is often seen to form groups or colonies (by fission), and so also is Raphidiophrys. It is probable from the little that is known that reproduction takes place not only by simple fission but by multiple fission, producing flagellate spores which may or may not be preceded by encystment. Only Clathrulina, Acanthocystis, Actinosphærium, and Actinophrys have been observed in the encysted state, and only the first two have been credited with the production of flagellated young. The two latter genera form covered spores within their cysts, those of Actinosphærium being remarkable for their siliceous coats (Fig. VIII. 14), but their further development has not been seen.

Class VI. RETICULARIA, Carpenter, 1862.

(*Foraminifera*, Auct., *Thalamophora*, Hertwig).

Characters.—Gymnomyxa in which the dominating amœba-phase, often of great size (an inch in diameter), has an irregular form, and a tendency to throw out great trunks of branching and often anastomosing filamentous pseudopodia, and an equally strong tendency to form a shell of secreted membrane or secreted lime or of agglutinated sand particles (only in one genus of secreted silex) into which the protoplasm (not in all ?) can be drawn and out of and over which it usually streams in widely spreading lobes and branches. One nucleus is present, or there are many. A contractile vacuole is sometimes, but not as a rule, present (or at any rate not described). Reproduction is by fission and (as in some other Protozoa) by the formation of peculiar bud-spores which remain for a time after their formation embedded in the parental protoplasm. No multiple breaking up into spores after or independent of the formation of a cyst is known. Marine and freshwater.

The Reticularia are divisible into several orders. The marked peculiarity of the shell structure in certain of these orders is only fitly emphasized by grouping them together as a sub-class Perforata, in contrast to which the remaining orders stand as a sub-class Imperforata. The distinction, however, is not an absolute one, for a few of the Lituolidea are perforate, that is, are sandy isomorphs of perforate genera such as Globigerina and Rotalia.

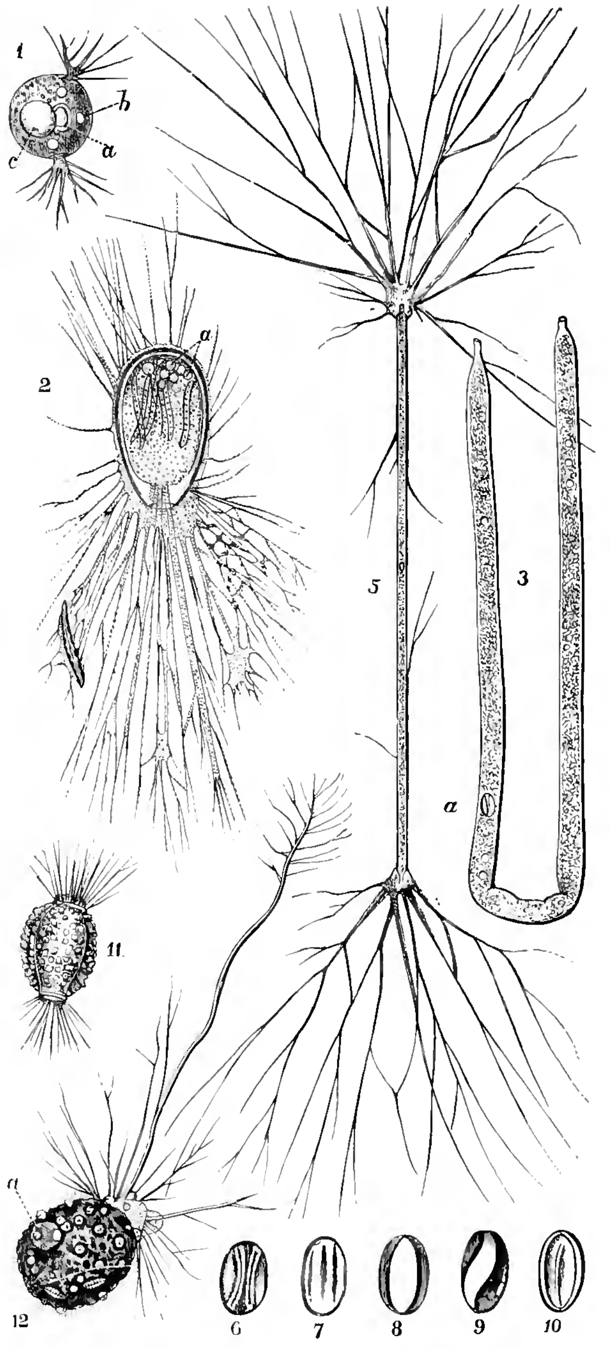


Fig. IX.—**Gromiidea (Reticularia membranosa).** 1. *Diplophrys Archeri*, Barker. *a*, nucleus; *b*, contractile vacuoles; *c*, the yellow oil-like body. Moor pools, Ireland. 2. *Gromia oviformis*, Duj. *a*, the numerous nuclei; near these the elongated bodies represent ingested Diatoms. Freshwater. 3. *Shepheardella tæniformis*, Siddall (*Quart. Jour. Micr. Sci.*, 1880); × 30 diameters. Marine. The protoplasm is retracted at both ends into the tubular case. *a*, nucleus. 5. *Shepheardella tæniiformis*; × 15; with pseudopodia fully expanded. 6–10. Varying appearance of the nucleus as it is carried along in the streaming protoplasm within the tube. 11. *Amphitrema Wrightianum*, Archer, showing membranous shell encrusted with foreign particles. Moor pools, Ireland. 12. *Diaphorophodon mobile*, Archer. *a*, nucleus. Moor pools, Ireland.

Sub-class A. Imperforata.

Characters.—Shell-substance not perforated by numerous apertures through which the protoplasm can issue, but provided with only one or two large apertures, or in branched forms with a few such apertures.

Order 1. GROMIIDEA, Brady.

Characters.—Shell or test membranous, in the form of a simple sac with a pseudopodial aperture either at one extremity or at both. Pseudopodia thread-like, long, branching, reticulated. Marine and freshwater.

Fam. 1. Monostomina, with a single aperture to the shell.

Genera.—*Lieberkuhnia*, Clap. and Lach.; *Gromia*, Duj. (Fig. IX. 2); *Mikrogromia*, Hertw.; *Euglypha*, Duj. (shell built up of hexagonal siliceous plates); *Diaphorophodon*, Archer (38) (many foreign particles cemented to form shell; small pseudopodia issue between these, hence resembling Perforata, and large long ones from the proper mouth of the shell, Fig. IX. 12).

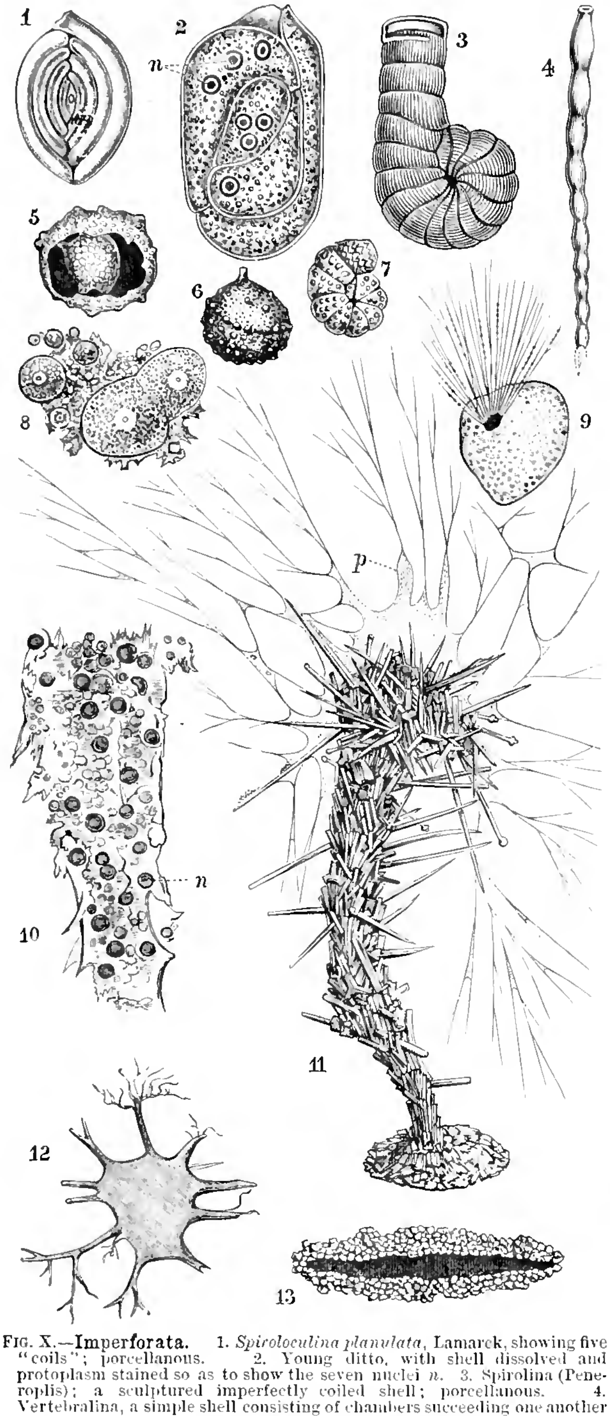


Fig. X.—**Imperforata.** 1. *Spiroloculina planulata*, Lamarck, showing five "coils"; porcellanous. 2. Young ditto, with shell dissolved and protoplasm stained so as to show the seven nuclei *n*. 3. Spirolina (Peneroplis); a sculptured imperfectly coiled shell; porcellanous. 4. Vertebralina, a simple shell consisting of chambers succeeding one another in a straight line; porcellanous. 5, 6. *Thurammina papillata*, Brady, a sandy form. 5 is broken open so as to show an inner chamber; recent. × 25. 7. *Lituola* (*Haplophragmium*) *canariensis*, a sandy form; recent. 8. Nucleated reproductive bodies (bud-spores) of Haliphysema. 9. *Squammulina lævis*, M. Schultze; × 40; a simple porcellanous Miliolide. 10. Protoplasmic core removed after treatment with weak chromic acid from the shell of *Haliphysema Tumanovitzii*, Bow. *n*, vesicular nuclei, stained with hæmatoxylin (after Lankester). 11. *Haliphysema Tumanovitzii*; × 25 diam.; living specimen, showing the wine-glass-shaped shell built up of sand-grains and sponge-spicules, and the abundant protoplasm *p*, issuing from the mouth of the shell and spreading partly over its projecting constituents. 12. Shell of *Astrorhiza limicola*, Sand.; $\times \frac{3}{4}$; showing the branching of the test on some of the rays usually broken away in preserved specimens (original). 13. Section of the shell of Marsipella, showing thick walls built of sand-grains.

Fam. 2. Amphistomina, with an aperture at each end of the shell.

Genera.—*Diplophrys*, Barker (Fig. IX. 1); *Ditrema*, Archer; *Amphitrema*, Archer (Fig. IX. 11); *Shepheardella*, Siddall (39) (membranous shell very long and cylindrical so as to be actually tubular, narrowed to a spout at each end, Fig. IX. 3; protoplasm extended from either aperture, Fig. IX. 5, and rapidly circulating within the tubular test during life, carrying with it the nucleus which itself exhibits peculiar movements of rotation, Fig. IX. 6, 7, 8, 9, 10).

Order 2. ASTRORHIZIDEA, Brady.

Characters.—Test invariably consisting of foreign particles; it is usually of large size and single-chambered, often branched or radiate with a pseudopodial aperture to each branch, the test often continued on to the finer branches of the pseudopodia (Fig. X. 12); never symmetrical. All marine.

Fam. 1. Astrorhizina, Brady. Walls thick, composed of loose sand or mud very slightly cemented.

Genera.—*Astrorhiza*, Sandahl (Fig. X. 12, very little enlarged); *Pelosina*, Brady; *Storthosphæra*, Brady; *Dendrophrya*, St. Wright; *Syringammina*, Brady.

Fam. 2. Pilulinina. Test single-chambered; walls thick, composed chiefly of felted sponge-spicules and fine sand, without calcareous or other cement.

Genera.—*Pilulina*, Carpenter; *Technitella*, Norman; *Bathysiphon*, Sars.

Fam. 3. Saccamminina. Chambers nearly spherical; walls thin, composed of firmly cemented sand grains.

Genera.—*Psammosphæra*, Schultze; *Sorosphæra*, Brady; *Saccammina*, M. Sars.

Fam. 4. Rhabdamminina. Test composed of firmly cemented sand-grains, often with sponge-spicules intermixed; tubular; straight, radiate, branched or irregular; free or adherent; with one, two, or more apertures; rarely segmented.

Genera.—*Jaculella*, Brady; *Marsipella*, Norman (Fig. X. 13); *Rhabdammina*, M. Sars; *Aschemonella*, Brady; *Rhizammina*, Brady; *Sagenella*, Brady; *Botellina*, Carp.; *Haliphysema*, Bowerbank (test wine-glass-shaped, rarely branched, attached by a disk-like base; generally beset with sponge-spicules, Fig. X. 11; pseudopodial aperture at the free extremity). This and Astrorhiza are the only members of this order in which the living protoplasm has been observed; in the latter it has the appearance of a yellowish cream, and its microscopic structure is imperfectly unknown (61). In Haliphysema the network of expanded pseudopodia has been observed by Saville Kent as drawn in Fig. X. 11. Lankester (59) discovered numerous vesicular nuclei scattered in the protoplasm (Fig. X. 10, *n*), and also near the mouth of the shell reproductive bodies (probably bud-spores) embedded in the protoplasm (Fig. X. 8). Haliphysema was described by Bowerbank as a Sponge, and mistaken by Haeckel (60) for a very simple two-cell-layered animal (Enterozoon), to which he assigned the class name of Physemaria.

Order 3. MILIOLIDEA, Brady.

Characters.—Test imperforate; normally calcareous and porcellanous, sometimes encrusted with sand; under starved conditions (*e.g.*, in brackish water) becoming chitinous or chitino-arenaceous; at abyssal depths occasionally consisting of a thin homogeneous, imperforate, siliceous film. The test has usually a chambered structure, being divided by septa (each with a hole in it) into a series of loculi which may follow one another in a straight line (Fig. X. 4) or the series may be variously coiled (Fig. X. 1 and 3). The chambering of the test does not express a corresponding cell-segmentation of the protoplasm; the latter, although growing in volume as the new shell-chambers are formed, remains one continuous cell-unit with many irregularly scattered nuclei (Fig. X. 2). The chambered and septate structure results in this group and in the other orders from the fact that the protoplasm, expanded beyond the last-formed chamber, forms a new test upon itself whilst it lies and rests upon the surface of the old test. The variations in such a formation are shown in Fig. XII. 1, 2, 3, 4.

Fam. 1. Nubecularina. Test free or adherent, taking various irregular asymmetrical forms, with variable aperture or apertures.

Genera.—*Squammulina*, Schultze (Fig. X. 9, showing the expanded pseudopodia); *Nubecularia*, Defrance.

Fam. 2. Miliolina. Shell coiled on an elongated axis, either symmetrically or in a single plane or inequilaterally; two chambers in each convolution. Shell aperture alternately during growth (addition of new chambers) at either end of the shell.

Genera.—*Biloculina*, D'Orb.; *Fabularia*, Defrance; *Spiroloculina*, D'Orb. (Fig. X. 1, 2); *Miliolina*, Williamson (Fig. XI.).

Fam. 3. Hauerinina. Shell dimorphous; chambers partly milioline, partly spiral or rectilinear.

Genera.—*Articulina*, D'Orb.; *Vertebralina*, D'Orb. (Fig X. 4); *Ophthalmidium*, Kubler; *Hauerina*, D'Orb.; *Planispirina*, Seguenza.

Fam. 4. Peneroplidina. Shell planospiral or cyclical, sometimes crosier-shaped, bilaterally symmetrical.

Genera.—*Cornuspira*, Schultze; *Peneroplis*, Montfort (Fig. X. 3);

Orbiculina, Lamarck; *Orbitolites*, Lamarck (by a division of the chambers regularly into chamberlets, and a cyclical mode of growth which results in shells of the size of a shilling, a very elaborate-looking structure is produced which has been admirably analysed by Carpenter (40), to whose memoir the reader is specially referred).

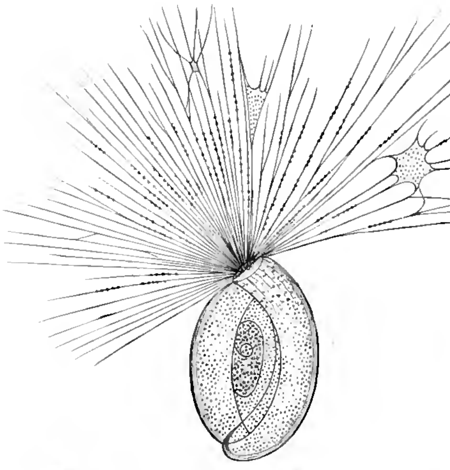


FIG. XI.—*Miliolina* (*Triloculina*) *tenera*. Young living animal with expanded pseudopodia (after Max Schultze). A single nucleus is seen in the innermost chamber.

Fam. 5. ALVEOLININA. Shell spiral, elongated in the line of the axis of the convolution; chambers divided into chamberlets.

Genus.—*Alveolina*, D'Orb.

Fam. 6. KERAMOSPHÆRINA. Shell spherical; chambers in concentric layers.

Genus.—*Keramosphæra*, Brady.

ORDER 4. LITUOLIDEA, Brady.

Characters.—Test arenaceous, usually regular in contour; septation of the many-chambered forms often imperfect, the cavity being labyrinthic. This order consists of sandy isomorphs of the simpler Miliolidea, and also of the simpler Perforata (Lagena, Nodosaria, Cristellaria, Globigerina, Rotalia, Nonionina, &c.); it also contains some peculiar adherent species.

Fam. 1. LITUOLINA. Test composed of coarse sand-grains, rough externally; often labyrinthic.

Genera.—*Reophax*, Montfort; *Haplophragmium*, Reuss (Fig. X. 7); *Coskinolina*, Stache; *Placopsilina*, D'Orb.; *Haplostiche*, Reuss; *Lituola*, Lamarck; *Bdelloidina*, Carter.

Fam. 2. TROCHAMMININA. Test thin, composed of minute sand-grains incorporated with calcareous and other organic cement, or embedded in a chitinous membrane; exterior smooth, often polished; interior smooth or rarely reticulated; never labyrinthic.

Genera.—*Thurammina*, Brady (test consisting typically of a single spherical chamber with several mammillate apertures, Fig. X. 5, 6); *Hippocrepina*, Parker; *Hormosina*, Brady; *Ammodiscus*, Reuss; *Trochammina*, Parker and Jones; *Carterina*, Brady; *Webbina*, D'Orb.

Fam. 3. ENDOTHYRINA. Test more calcareous and less sandy than in the other groups of Lituolidea; sometimes perforate; septation distinct.

Genera.—*Nodosinella*, Brady; *Polyphragma*, Reuss; *Involutina*, Terq.; *Endothyra*, Phillips; *Bradyina*, Moll.; *Stacheia*, Brady.

Fam. 4. LOFTUSINA. Test of relatively large size; lenticular, spherical, or fusiform; constructed either on a spiral plan or in concentric layers, the chamber cavities occupied to a large extent by the excessive development of the finely arenaceous cancellated walls.

Genera.—*Cyclammina*, Brady; *Loftusia*, Brady; *Parkeria*, Carpenter.

SUB-CLASS B. Perforata.

Characters.—Shell substance perforated by numerous minute apertures, through which as well as from the main aperture the protoplasm can issue.

ORDER 5. TEXTULARIDEA, Brady.

Characters.—Tests of the larger species arenaceous, either with or without a perforate calcareous basis; smaller forms hyaline and conspicuously perforated. Chambers arranged in two or more alternating series, or spiral or confused; often dimorphous.

Fam. 1. TEXTULARINA. Typically bi- or tri-serial; often bi-rarely tri-morphous.

Genera.—*Textularia* Defrance; *Cuneolina*, D'Orb.; *Verneuilina*, D'Orb.; *Tritaxia*, Reuss; *Chrysalidina*, D'Orb.; *Bigenerina*, D'Orb.; *Pavonina*, D'Orb.; *Spiroplecta*, Ehr.; *Gaudryina*, D'Orb.; *Valvulina*, D'Orb.; *Clavulina*, D'Orb.

Fam. 2. BULIMININA. Typically spiral; weaker forms more or less regularly biserial; aperture oblique, comma-shaped or some modification of that form.

Genera.—*Bulimina*, D'Orb.; *Virgulina*, D'Orb.; *Bifarina*, Parker and Jones; *Bolivina*, D'Orb.; *Pleurostomella*, Reuss.

Fam. 3. CASSIDULINA. Test consisting of a Textularia-like series of alternating segments more or less coiled upon itself.

Genera.—*Cassidulina*, D'Orb.; *Ehrenbergina*, Reuss.

ORDER 6. CHILOSTOMELLIDEA, Brady.

Characters.—Test calcareous, finely perforate, many-chambered. Segments following each other from the same end of the long axis, or alternately at the two ends, or in cycles of three, more or less embracing. Aperture a curved slit at the end or margin of the final segment.

Genera.—*Ellipsoidina*, Seguenza; *Chilostomella*, Reuss; *Allomorphina*, Reuss.

ORDER 7. LAGENIDEA, Brady.

Characters.—Test calcareous, very finely perforated; either single-chambered, or consisting of a number of chambers joined in a straight, curved, spiral, alternating, or (rarely) branching series. Aperture simple or radiate, terminal. No interseptal skeleton nor canal system.

Fam. 1. LAGENINA. Shell single-chambered.

Genera.—*Lagena*, Walker and Boys; *Nodosaria*, Lamk.; *Lingulina*, D'Orb.; *Frondicularia*, Defrance; *Rhabdogonium*, Reuss; *Marginulina*, D'Orb.; *Vaginulina*, D'Orb.; *Rimulina*, D'Orb.; *Cristellaria*, Lamk.; *Amphicoryne*, Schlumb.; *Lingulinopsis*, Reuss; *Flabellina*, D'Orb.; *Amphimorphina*, Neugeb.; *Dentalinopsis*, Reuss.

Fam. 2. POLYMORPHININA. Segments arranged spirally or irregularly around the long axis; rarely biserial and alternate.

Genera.—*Polymorphina*, D'Orb.; *Dimorphina*, D'Orb.; *Uvigerina*, D'Orb.; *Sagrina*, P. and J.

Fam. 3. RAMULININA. Shell branching, composed of spherical or pyriform chambers connected by long stoloniferous tubes.

Genus.—*Ramulina*, Rupert Jones.

ORDER 8. GLOBIGERINIDEA, Brady.

Characters.—Test free, calcareous, perforate; chambers few, inflated, arranged spirally; aperture single or multiple, conspicuous. No supplementary skeleton nor canal system. All the larger species pelagic in habit.

Genera.—*Globigerina*, D'Orb. (Fig. XII. 6): *Orbulina*, D'Orb (Fig. XII. 8); *Hastigerina*, Wy. Thomson (Fig. XII. 5); *Pullenia*, P. and J.; *Sphæroidina*, D'Orb.; *Candeina*, D'Orb.

ORDER 9. ROTALIDEA, Brady.

Characters.—Test calcareous, perforate; free or adherent. Typically spiral and "rotaliform" (Fig. XII. 2), that is to say, coiled in such a manner that the whole of the segments are visible on the superior surface, those of the last convolution only on the inferior or apertural side, sometimes one face being more convex sometimes the other. Aberrant forms evolute, outspread, acervuline, or irregular. Some of the higher modifications with double chamber-walls, supplemental skeleton, and a system of canals. The nature of this supplemental skeleton is shown in Fig. XII. 2 and 10.

Fam. 1. SPIRILLININA. Test a complanate, planospiral, non-septate tube; free or attached.

Genus.—*Spirillina*, Ehr.

Fam. 2. ROTALINA. Test spiral, rotaliform, rarely evolute, very rarely irregular or acervuline.

Genera.—*Patellina*, Williamson; *Cymbalopora*, Hay; *Discorbina*, P. and J.; *Planorbulina*, D'Orb.; *Truncatulina*, D'Orb.; *Anomalina*, P. and J.; *Carpenteria*, Gray (adherent); *Rupertia*, Wallick; *Pulvinulina*, P. and J.; *Rotalia*, Lamk.; *Calcarina*, D'Orb. [Shell rotaliform; periphery furnished with radiating spines; supplemental skeleton and canal system largely developed. This form is shown in a dissected condition in Fig. XII. 10. Outside and between the successive chambers with finely perforated walls a^2, a^3, a^4 a secondary shell-substance is deposited by the protoplasm which has a different structure. Whilst the successive chambers with their finely perforate walls (resembling dentine in structure) are formed by the mass of protoplasm issuing from the mouth of the last-formed chamber, the secondary or supplemental-shell substance is formed by the protoplasm which issues through the fine perforations of the primary shell substance; it is not finely canaliculated, but is of denser substance than the primary shell and traversed by coarse canals (occupied by the protoplasm) which make their way to the surface of the test (c', c'). In Calcarina a large bulk of this secondary shell-substance is deposited around each chamber and also forms the heavy club-like spines.]

Fam. 3. TINOPORINA. Test consisting of irregularly heaped chambers with (or sometimes without) a more or less distinctly spiral primordial portion; for the most part without any general pseudopodial aperture.

Genera.—*Tinoporus*, Carpenter; *Gypsina*, Carter; *Aphrosina*, Carter; *Thalamopora*, Roemer; *Polytrema*, Risso. [Shell parasitic, encrusting, or arborescent; surface areolated, coloured pink or white, Fig. XII. 9. Interior partly occupied by small chambers, arranged in more or less regular layers, and partly by non-segmented canal-like spaces, often crowded with sponge-spicules No true canal system. This is one of the most important types as exhibiting the arborescent and encrusting form of growth. It is fairly abundant.]

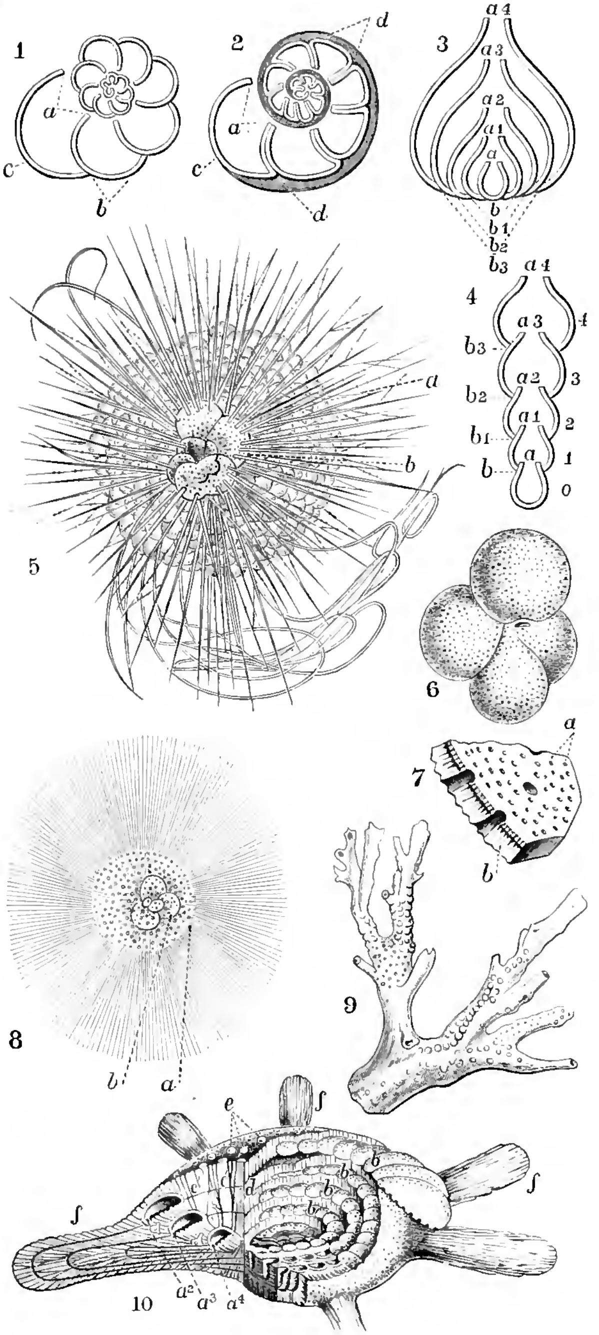


FIG. XII.—**Perforata.** 1. Spiral arrangement of simple chambers of a Reticularian shell. 2. Ditto, with double septal walls, and supplemental shell-substance (shaded). 3. Diagram to show the mode in which successively-formed chambers may completely embrace their predecessors. 4. Diagram of a simple straight series of non-embracing chambers. 5. *Hastigerina (Globigerina) Murrayi*, Wyv. Thomson. *a*, bubbly (vacuolated) protoplasm, enclosing *b*, the perforated Globigerina-like shell (conf. central capsule of Radiolaria). From the peripheral protoplasm project, not only fine pseudopodia, but hollow spines of calcareous matter, which are set on the shell, and have an axis of active protoplasm. Pelagic; drawn in the living state. 6. *Globigerina bulloides*, D'Orb., showing the punctiform perforations of the shell and the main aperture. 7. Fragment of the shell of Globigerina, seen from within, and highly magnified. *a*, fine perforations in the inner shell substances; *b*, outer (secondary) shell substance. Two coarser perforations are seen in section, and one lying among the smaller. 8. *Orbulina universa*, D'Orb. Pelagic example, with adherent radiating calcareous spines (hollow), and internally a small Globigerina shell. It is uncertain whether Orbulina is merely a developmental phase of Globigerina. *a*, Orbulina shell; *b*, Globigerina shell. 9. *Polytrema miniaceum*, Lin.; × 12. Mediterranean. Example of a branched adherent calcareous perforate Reticularian. 10. *Calcarina Spengleri*, Gmel.; × 10. Tertiary, Sicily. Shell dissected so as to show the spiral arrangement of the chambers, and the copious secondary shell substance. a^2, a^3, a^4, chambers of three successive coils in section, showing the thin primary wall (finely tubulate) of each; *b*, *b*, *b*, *b*, perforate surfaces of the primary wall of four tiers of chambers, from which the secondary shell substance has been cleared away; *c'*, *c'*, secondary or intermediate shell substance in section, showing coarse canals; *d*, section of secondary shell substance at right angles to *c'*; *e*, tubercles of secondary shell substance on the surface; *f*, *f*, club-like processes of secondary shell substance.

ORDER 10. NUMMULINIDEA, Brady.

Characters.—Test calcareous and finely tubulated; typically free, many-chambered, and symmetrically spiral. The higher modifications all possess a supplemental skeleton, and canal system of greater or less complexity.

Fam. 1. FUSULININA. Shell bilaterally symmetrical; chambers extending from pole to pole; each convolution completely enclosing the previous whorls. Shell-wall finely tubulated. Septa single or rarely double; no true interseptal canals. Aperture a single elongated slit, or a row of small rounded pores, at the inner edge of the final segment.

Genera.—*Fusulina*, Fischer; *Schwagerina*, Möller.

Fam. 2. POLYSTOMELLINA. Shell bilaterally symmetrical, nautiloid. Lower forms without supplemental skeleton or interseptal canals; higher types with canals opening at regular intervals along the external septal depressions.

Genera.—*Nonionina*, D'Orb.; *Polystomella*, Lamarck.

Fam. 3. NUMMULITINA. Shell lenticular or complanate; lower forms with thickened and finely tubulated shell-wall, but no intermediate skeleton; higher forms with interseptal skeleton and complex canal system.

Genera.—*Archæodiscus*, Brady; *Amphistegina*, D'Orb.; *Operculina*, D'Orb.; *Heterostegina*, D'Orb.; *Nummulites*, Lamarck; *Assilina*, D'Orb.

Fam. 4. CYCLOCLYPEINA. Shell complanate, with thickened centre, or lenticular; consisting of a disk of chambers arranged in concentric annuli, with more or less lateral thickening of laminated shell substance, or acervuline layers of chamberlets. Septa double and furnished with a system of interseptal canals.

Genera.—*Cycloclypeus*, Carpenter; *Orbitoides*, D'Orb.

Fam. 5. EOZOONINA. Test forming irregular, adherent, acervuline masses.

Genus.—*Eozoon* Dawson.

Further remarks on the Reticularia.—The name Thalamophora, pointing to the peculiar tendency which the larger members of the group have to form chamber after chamber and so to build up a complex shell, has been proposed by Hertwig (56) and adopted by many writers. The old name Foraminifera (which did not refer to the fine perforations of the Perforata but to the large pseudopodial aperture leading from chamber to chamber) has also been extended by some so as to include the simpler Gromia-like forms. On the whole Carpenter's term Reticularia (62) seems most suitable for the group, since they all present the character indicated. It has been objected that the Radiolaria are also reticular in their pseudopodia, but if we except the pelagic forms of Reticularia (Globigerina, Orbulina, &c.), we find that the Radiolaria are really distinguishable by their stiffer, straighter, radiating pseudopodia. No doubt the Labyrinthulid Chlamydomyxa and the plasmodia of some Mycetozoa are as reticular in their pseudopodia as the Reticularia, but they possess other distinctive features which serve, at any rate in an artificial system, to separate them.

The protoplasm of the majority of the Reticularia is unknown, or only very superficially observed; hence we have made a point of introducing among our figures as many as possible which show this essential part of the organism. It is only recently (1876) that nuclei have been detected in the calcareous-shelled members of the group, and they have only been seen in a few cases.

The protoplasm of the larger shell-making forms is known to be often strongly coloured, opaque, and creamy, but its minute structure remains for future investigation. Referring the reader to the figures and their explanation, we would draw especial attention to the structure of the protoplasmic body of Hastigerina (one of the Globigerinidea) as detected by the "Challenger" naturalists. It will be seen from Fig. XII. 5 that the protoplasm extends as a relatively enormous "bubbly" mass around the shell which is sunk within it; from the surface of this "bubbly" (vacuolated or alveolated) mass the pseudopodia radiate.

The reader is requested to compare this with Fig. XIII., representing the "bubbly" protoplasmic body of Thalassicolla. It then becomes obvious that the perforated central capsule CK of the latter holds the same relation to the mass of the protoplasm as does the central perforated shell of Globigerina (Hastigerina). The extreme vacuolation of the protoplasm in both cases (the vacuoles being filled with sea-water accumulated by endosmosis) and the stiff radiating pseudopodia are directly correlated with the floating pelagic life of the two organisms. All the Radiolaria are pelagic, and many exhibit this vacuolation; only a few of the Reticularia are so, and their structural correlation to that habit has only lately been ascertained.

The Reticularia are almost exclusively known by their shells, which offer a most interesting field for study on account of the very great complexity of form attained by some of them, notwithstanding the fact that the animal which produces them is a simple unicellular Protozoon. Space does not permit the exposition here of the results obtained by Carpenter in the study of the complex shells of Orbitolites, Operculina, Nummulites, &c.; it is essential that his work *Introduction to the Study of the Foraminifera* (Ray Society, 1862) should be consulted, and in reference to the sandy-shelled forms the monograph by Brady, in the *Challenger Reports*, vol. ix., 1883; and it must be sufficient here to point out the general principles of the shell-architecture of the Reticularia. Let us suppose that we have an ever-growing protoplasmic body which tends to produce a calcareous shell on its surface, leaving an aperture for the exit of its pseudopodia. It will grow too large for its shell and accumulate outside the shell. The accumulated external mass may then secrete a second chamber, resting on the first as chamber 1 rests on chamber 0 in Fig. XII. 4. By further growth a new chamber is necessitated, and so is produced a series following one another in a straight line, each chamber communicating with the newer one in front of it by the narrow pseudopodial aperture (a, a^1, a^2, a^3). Now it is possible for these chambers to be very variously arranged instead of simply as in Fig. XII. 4. For instance, each new chamber may completely enclose the last, as in Fig. XII. 3, supposing the protoplasm to spread all over the outside of the old chamber before making a new deposit. Again the chambers need not succeed one another in a straight line, but may be disposed in a spiral (Fig. XII. 1). And this spiral may be a flat coil, or it may be a helicine spiral with a rising axis; further it may be close or open. All these forms in various degrees of elaboration are exhibited by Miliolidea and various Perforata.

But the Perforata in virtue of their perforate shell-walls introduce a new complication. The protoplasm issues not only from the mouth of the last-formed chamber, but from the numerous pores in the wall itself. This latter protoplasm exerts its lime-secreting functions; it gathers itself into coarse branching threads which remain uncalcified, whilst all around a dense deposit of secondary or supplemental shell-substance is thrown down, thus producing a coarsely canalicular structure. The thickness and amount of this secondary shell and the position it may occupy between and around the chambers of primitive shell-substance vary necessarily in different genera according to the mode in which the primitive chambers are arranged and connected with one another. Calcarina is a fairly typical instance of an abundant secondary shell-deposit (Fig. XII. 10), and it is the existence of structure resembling the chambers of Calcarina with their surrounding primary and secondary shell-substances which has rendered it necessary to regard Eozoon (41) as the metamorphosed encrusting shell of a pre-Cambrian Reticularian.

The division of the Reticularia into Imperforata and Perforata which is here maintained has no longer the significance which was once attributed to it. It appears, according to the researches of Brady, that it is not possible to draw a sharp line between these sub-classes, since there are sandy forms which it is difficult to separate from imperforate Lituolidea and are nevertheless perforate, in fact are "sandy isomorphs of Lagena, Nodosaria, Globigerina, and Rotalia." It does not appear to the present writer that there can be any insurmountable difficulty in separating the Lituolidea into two groups—those which are sandy isomorphs of the porcellanous Miliolidea, and those which are sandy isomorphs of the hyaline Perforata. The two groups of Lituolidea thus formed might be placed in their natural association respectively with the Imperforata and the Perforata.

The attempt to do this has not been made here, but the classification of Brady has been adopted. In Butschli's large work on the Protozoa (9) the breaking up of the Lituolidea is carried out to a logical conclusion, and its members dispersed among the Miliolidea on the one hand and the various orders of Perforata on the other hand.

The calcareous shell-substance of the Miliolidea being opaque and white has led to their being called "Porcellana," whilst the transparent calcareous shells of the smaller Perforata has gained for that group the synonym of "Hyalina."

The shells of the calcareous Reticularia and of some of the larger arenaceous forms are found in stratified rocks, from the Palæozoic strata onwards. The Chalk is in places largely composed of their shells, and the Eocene Nummulitic limestone is mainly a cemented mass of the shells of Nummulites often as large each as a shilling. The Atlantic ooze is a chalky deposit consisting largely of the shells of Globigerina, &c.

Class VII. **RADIOLARIA**, Haeckel, 1862 (63) (*Polycystina*, Ehr.).

Characters.—Gymnomyxa in which the protoplasmic body of the dominant amœba phase has the form of a sphere or cone from the surface of which radiate filamentous pseudopodia, occasionally anastomosing, and encloses a spherical (homaxonic) or cone-shaped (monaxonic) perforated shell of membranous consistence known as the central capsule, and probably homologous with the perforated shell of a Globigerina. The protoplasm within the capsule (intracapsular protoplasm) is continuous through the pores or apertures of the capsule with the outer protoplasm. Embedded in the former lies the large and specialized nucleus (one or more). Gelatinous substance is frequently formed peripherally by the extracapsular protoplasm, constituting a kind of soft mantle which is penetrated by the pseudopodia. A contractile vacuole is never present.

Usually an abundant skeleton, consisting of spicules of silica or of a peculiar substance called acanthin arranged radially or tangentially, loose or united into a basket-work, is present. Oil globules, pigment, and crystals are found in greater or less abundance in the protoplasm.

In most but not all Radiolaria peculiar nucleated yellow corpuscles are abundantly present, usually regarded as parasitic Algæ. Reproduction by fission has been observed, and also in some few species a peculiar formation of swarm-spores (flagellulæ) within the central capsule, in which the nucleus takes an important part. All the Radiolaria are marine. The Radiolaria are divided into two sub-classes according to the chemical nature of their spicular skeleton, and into orders according to the nature and the disposition of the apertures in the wall of the central capsule.

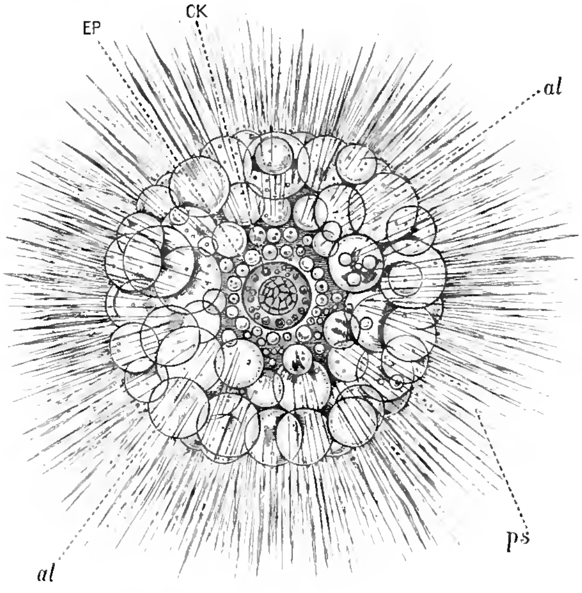


Fig. XIII.—*Thalassicolla pelagica*, Haeckel; × 25. CK, central capsule; EP, extracapsular protoplasm; *al*, alveoli, liquid-holding vacuoles in the protoplasm similar to those of Heliozoa, Pelomyxa, Hastigerina, &c.; *ps*, pseudopodia. The minute unlettered dots are the "yellow cells."

Sub-class I. **Silico-Skeleta**, Lankester.

Characters.—A more or less elaborate basket-work of tangential and radial elements consisting of secreted silica is present; in rare exceptions no skeleton is developed.

Order 1. PERIPYLÆA, Hertwig.

Characters.—Silico-skeletal Radiolaria in which the central capsule is uniformly perforated all over by fine pore-canals; its form is that of a sphere (homaxonic), and to this form the siliceous skeleton primarily conforms, though it may become discoid, rhabdoid, or irregular. The nucleus is usually single, but numerous nuclei are present in each central capsule of the Polycyttaria.

Fam. 1. Sphærida, Haeck. Spherical Peripylæa with a spherical basket-work skeleton, sometimes surrounded by a spongy outer skeleton, sometimes simple, sometimes composed of many concentric spheres (never discoid, flattened, or irregular). The central capsule sometimes encloses a part of the spherical skeleton, and often is penetrated by radiating elements.

Genera (selected).—*Ethmosphæra*, Haeck.; *Xiphosphæra*, Haeck.; *Staurosphæra*, Haeck.; *Heliosphæra*, Haeck. (Fig. XIV. 14); *Astromma*, Haeck.; *Haliomma*, Haeck.; *Actinomma*, Haeck. (Fig. XIV. 17; note the sphere within sphere, the smallest lying in the nucleus, and the whole series of spherical shells connected by radial spines); *Arachnosphæra*, Haeck.; *Plegmosphæra*, Haeck.; *Spongosphæra*, Haeck. (Fig. XVI. 8).

Fam. 2. Discida, Haeck. Discoid Peripylæa; both skeleton and central capsule flattened.

Genera (selected).—*Phacodiscus*, Haeck.; *Heliodiscus*, Haeck.; *Spongodiscus*, Haeck.; *Spongurus*, Haeck.

Fam. 3. THALASSICOLLIDA. Peripylæa devoid of a skeleton, or with a skeleton composed of loose siliceous spicules only. Nucleus single; central capsule and general protoplasm spherical.

Genera (selected).—*Thalassicolla*, Huxley (Fig. XIII., Fig. XIV. 1); *Thalassosphæra*, Haeck.; *Physematium*, Haeck.

Fam. 4. POLYCYTTARIA. Peripylæa consisting of colonies of many central capsules united by their extracapsular protoplasm. Central capsules multiplying by fission. Nuclei in each central capsule numerous. Siliceous skeleton either absent, or of loose spicules, or having the form of a spherical fenestrated shell surrounding each central capsule.

Genera (selected).—*Collosphæra*, Müller (with fenestrated globular skeleton); *Sphærozoum*, Haeck. (skeleton of numerous loose spicules which are branched); *Raphidozoum*, Haeck. (spicules simple); *Collozoum*, Müller (devoid of skeleton, Fig. XIV. 2, 3, 4, 5).

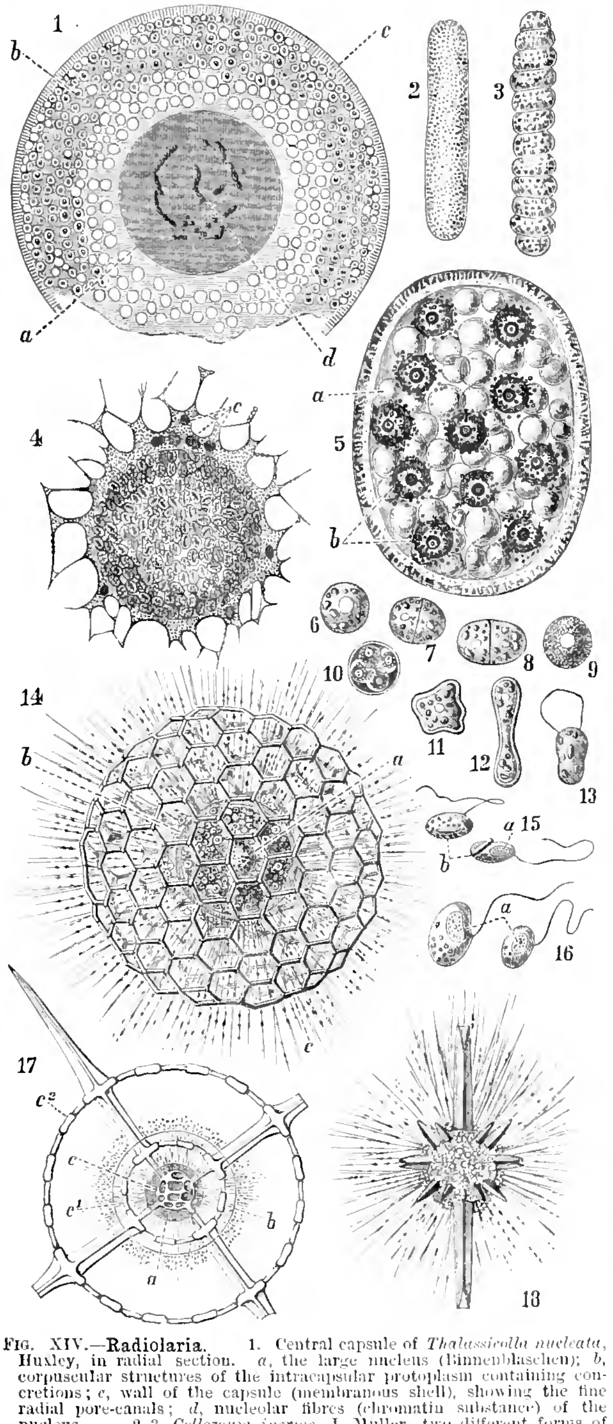


FIG. XIV.—**Radiolaria.** 1. Central capsule of *Thalassicolla nucleata*, Huxley, in radial section. *a*, the large nucleus (Binnenblaschen); *b*, corpuscular structures of the intracapsular protoplasm containing concretions; *c*, wall of the capsule (membranous shell), showing the fine radial pore-canals; *d*, nucleolar fibres (chromatin substance) of the nucleus. 2, 3. *Collozoum inerme*, J. Muller, two different forms of colonies, of the natural size. 4. Central capsule from a colony of *Collozoum inerme*, showing the intracapsular protoplasm and nucleus, broken up into a number of spores, the germs of swarm-spores or flagellulæ; each encloses a crystalline rod. *c*, yellow cells lying in the extracapsular protoplasm. 5. A small colony of *Collozoum inerme*, magnified 25 diameters. *a*, alveoli (vacuoles) of the extracapsular protoplasm; *b*, central capsules, each containing besides protoplasm a large oil-globule. 6-13. Yellow cells of various Radiolaria:—6, normal yellow cell; 7, 8. division with formation of transverse septum; 9, a modified condition according to Brandt; 10, division of a yellow cell into four; 11, amœboid condition of a yellow cell from the body of a dead Sphærozoon; 12, a similar cell in process of division; 13, a yellow cell the protoplasm of which is creeping out of its cellulose envelope. 14. *Heliosphæra inermis*, Haeck., living example; × 400. *a*, nucleus; *b*, central capsule; *c*, siliceous basket-work skeleton. 15. Two swarm-spores (flagellulæ) of *Collozoum inerme*, set free from such a central capsule as that drawn in 4; each contains a crystal *b* and a nucleus *a*. 16. Two swarm-spores of *Collozoum inerme*, of the second kind, viz., devoid of crystals, and of two sizes, a macrospore and a microspore. They have been set free from central capsules with contents of a different appearance from that drawn in 4. *a*, nucleus. 17. *Actinomma asteracanthion*, Haeck; × 260; one of the Peripylæa. Entire animal in optical section. *a*, nucleus; *b*, wall of the central capsule; *c*, innermost siliceous shell enclosed in the nucleus; c^1, middle shell lying within the central capsule; c^2, outer shell lying in the extracapsular protoplasm. Four radial siliceous spines, holding the three spherical shells together are seen. The radial fibrillation of the protoplasm and the fine extracapsular pseudopodia are to be noted 18. *Amphilonche messanensis*, Haeck; × 200; one of the Acanthometridea. Entire animal as seen living.

ORDER 2. MONOPYLÆA, Hertwig.

Characters.—Silico-skeletal Radiolaria in which the central capsule is not spherical but monaxonic (cone-shaped), with a single perforate area (pore-plate) placed on the basal face of the cone; the membrane of the capsule is simple, the nucleus single; the skeleton is extracapsular, and forms a scaffold-like or bee-hive-like structure of monaxonic form.

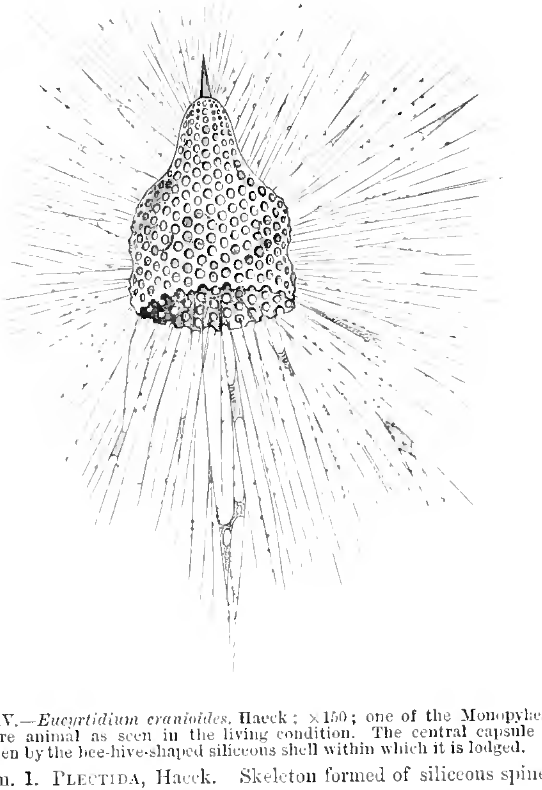


FIG. XV.—*Eucyrtidium cranioides*, Haeck; ×150; one of the Monopylæa. Entire animal as seen in the living condition. The central capsule is hidden by the bee-hive-shaped siliceous shell within which it is lodged.

Fam. 1. PLECTIDA, Haeck. Skeleton formed of siliceous spines loosely conjoined.

Genera (selected).—*Plagiacantha*, Haeck.; *Plegmatium*, Haeck.

Fam. 2. CYRTIDA, Haeck. Skeleton a monaxonic or triradiate shell, or continuous piece (bee-hive-shaped).

Genera (selected).—*Halicalyptra*, Haeck.; *Eucyrtidium*, Haeck. (Fig. XV.); *Carpocanium*, Haeck. (Fig. XVI. 3).

Fam. 3. BOTRIDA, Haeck. Irregular forms; the shell composed of several chambers agglomerated without definite order; a single central capsule.

Genera.—*Botryocyrtis*, Haeck.; *Lithobotrys*, Haeck.

Fam. 4. SPYRIDA, Haeck. Gemminate forms, with shell consisting of two conjoined chambers; a single central capsule.

Fam. 5. STEPHIDA, Haeck. Skeleton cricoid, forming a single siliceous ring or several conjoined rings.

Genera (selected).—*Acanthodesmia*, Haeck.; *Zygostephanus*, Haeck.; *Lithocircus*, Haeck. (Fig. XVI. 1).

ORDER 3. PHÆODARIA, Haeck. (*Tripylæa*, Hertwig).

Characters.—Silico-skeletal Radiolaria in which the central

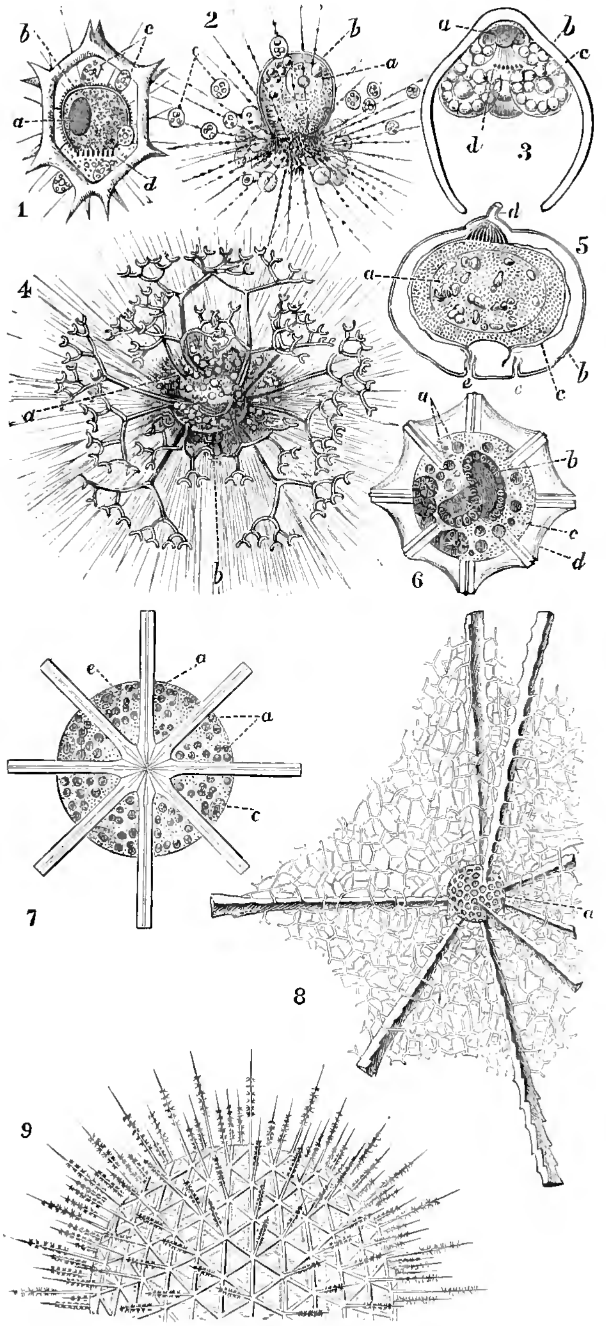


Fig. XVI.—**Radiolaria.** 1. *Lithocircus annularis*, Hertwig; one of the Monopylæa. Whole animal in the living state (optical section). *a*, nucleus; *b*, wall of the central capsule; *c*, yellow cells; *d*, perforated area of the central capsule (Monopylæa). 2. *Cystidium inerme*, Hertwig; one of the Monopylæa. Living animal. An example of a Monopylæon destitute of skeleton. *a*, nucleus; *b*, capsule-wall; *c*, yellow cells in the extracapsular protoplasm. 3. *Carpocanium diadema*, Haeck.; optical section of the bee-hive-shaped shell to show the form and position of the protoplasmic body. *a*, the tri-lobed nucleus; *b*, the siliceous shell; *c*, oil-globules; *d*, the perforate area (pore-plate) of the central capsule. 4. *Cœlodendrum gracillimum*, Haeck.; living animal, complete; one of the Tripylæa. *a*, the characteristic dark pigment (phæodium) surrounding the central capsule *b*. The peculiar branched siliceous skeleton, consisting of hollow fibres, and the expanded pseudopodia are seen. 5. Central capsule of one of the Tripylæa, isolated, showing *a*, the nucleus; *b*,*c*, the inner and the outer laminæ of the capsule-wall; *d*, the chief or polar aperture; *e*,*e*, the two secondary apertures. 6, 7. *Acanthometra Claparedei*, Haeck. 7 shows the animal in optical section, so as to exhibit the characteristic meeting of the spines at the central point as in all Acanthometridea; 6 shows the transition from the uninuclear to the multinuclear condition by the breaking up of the large nucleus. *a*, small nuclei; *b*, large fragments of the single nucleus; *c*, wall of the central capsule; *d*, extracapsular jelly (not protoplasm); *e*, peculiar intracapsular yellow cells. 8. *Spongosphæra streptacantha*, Haeck.; one of the Peripylæa. Siliceous skeleton not quite completely drawn on the right side. *a*, the spherical extracapsular shell (compare Fig. XIV. 17), supporting very large radial spines which are connected by a spongy network of siliceous fibres. 9. *Aulosphæra elegantissima*, Haeck.; one of the Phæodaria. Half of the spherical siliceous skeleton.

capsule has a double membrane and more than one perforate area, viz., one chief "polar aperture," and one, two, or more accessory apertures (Fig. XVI. 5). The nucleus is single. Around the central capsule is an abundant dark brown pigment (phæodium of Haeckel). The siliceous skeleton exhibits various shapes regular and irregular, but is often remarkable for the fact that it is built up of hollow tubes.

Fam. 1. Phæocystida, Haeck. The siliceous skeleton is either entirely absent or consists of hollow needles which are disposed outside the central capsule, regularly or irregularly.

Genera (selected).—*Aulacantha*, Haeck.; *Thalassoplancta*, Haeck.

Fam. 2. Phæogromida, Haeck. The siliceous skeleton consists of a single fenestrated shell, which may be spherical, ovoid, or often dipleuric, but always has one or more large openings.

Genera (selected).—*Challengeria*, Wy. Thomson; *Lithogromia*, Haeck.

Fam. 3. Phæosphærida. The siliceous skeleton consists of numerous hollow tubes which are united in a peculiar way to form a large spherical or polyhedral basket-work.

Genera (selected).—*Aulosphæra*, Haeck. (Fig. XVI. 9); *Auloplegma*, Haeck.; *Cannacantha*, Haeck.

Fam. 4. Phæoconchida. The siliceous skeleton consists of two separate fenestrated valves, similar to a mussel's shells; often there are attached to the valves simple or branched hollow tubes of silex.

Genera (selected).—*Conchidium*, Haeck.; *Cœlodendrum*, Haeck. (Fig. XVI. 4).

Sub-class II. **Acanthometridea**, Lankester (= *Acanthino-skeleta*).

Characters.—Radiolaria in which the skeleton is composed of a peculiar horny substance known as acanthin (rarely of silica). The central capsule is uniformly perforate (Peripylæa type). A divided or multiple nucleus is present in the capsule; the capsule-wall is single. The skeleton always has the form of spines which radiate from a central point within the capsule where they are all fitted to one another. Rarely a fenestrated tangential skeleton is also formed.

Fam. 1. Acanthonida, Haeck. Skeleton consisting of twenty spines of acanthin disposed in five parallel zones of four spines each, meeting one another at the central point of the organism; never forming a fenestrated shell.

Genera (selected).—*Acanthometra*, J. Müller (Fig. XVI. 6, 7); *Astrolonche*, Haeck.; *Amphilonche*, Haeck. (Fig. XIV. 18).

Fam. 2. Diploconida, Haeck. Skeleton a double cone.

Genus unicum.—*Diploconus*, Haeck.

Fam. 3. Dorataspida, Haeck. The twenty acanthin spines of the skeleton form by transverse outgrowths a spherical fenestrated shell.

Genera (selected).—*Stauraspis*, Haeck.; *Dorataspis*, Haeck.

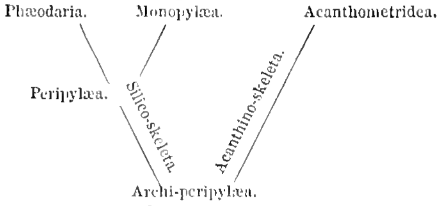
Fam. 4. Sphærocapsida, Haeck. The twenty acanthin spines are joined together at their free apices by a simple perforate shell of acanthin.

Genus unicum.—*Sphærocapsa.*

Fam. 5. Litholophida. Skeleton of many needles of acanthin radiating from a single point without definite number or order.

Genera.—*Litholophus*, Haeck.; *Astrolophus*, Haeck.

Further remarks on the Radiolaria.—It has not been possible in the systematic summary above given to enumerate the immense number of genera which have been distinguished by Haeckel (**42**) as the result of the study of the skeletons of this group. The important differences in the structure of the central capsule of different Radiolaria were first shown by Hertwig, who also discovered that the spines of the Acanthometridea consist not of silica but of an organic compound. In view of this latter fact and of the peculiar numerical and architectural features of the Acanthometrid skeleton, it seems proper to separate them altogether from the other Radiolaria. The Peripylæa may be regarded as the starting point of the Radiolarian pedigree, and have given rise on the one hand to the Acanthometridea, which retain the archaic structure of the central capsule whilst developing a peculiar skeleton, and on the other hand to the Monopylæa and Phæodaria which have modified the capsule but retained the siliceous skeleton.



Radiolaria.

The occasional total absence of any siliceous or acanthinous skeleton does not appear to be a matter of classificatory importance, since skeletal elements occur in close allies of those very few forms which are totally devoid of skeleton. Similarly it does not appear to be a matter of great significance that some forms (Polycyttaria) form colonies, instead of the central capsules separating from one another after fission has occurred.

It is important to note that the skeleton of silex or acanthin does not correspond to the shell of other Gymnomyxa, which appears rather to be represented by the membranous central capsule. The skeleton does, however, appear to correspond to the spicules of Heliozoa, and there is an undeniable affinity between such a form as Clathrulina (Fig. VII. 2) and the Sphærid Peripylæa (such as Heliosphæra, Fig. XIV. 14). The Radiolaria are, however, a very strongly marked group, definitely separated from all other Gymnomyxa by the membranous central capsule sunk in their protoplasm. Their differences *inter se* do not affect their essential structure. The variations in the chemical composition of the skeleton and in the perforation of the capsule do not appear superficially. The most obvious features in which they differ from one another relate to the form and complexity of the skeleton, a part of the organism so little characteristic of the group that it may be wanting altogether. It is not known how far the form-species and form-genera which have been distinguished in such profusion by Haeckel as the result of a study of the skeletons are permanent (*i.e.*, relatively permanent) physiological species. There is no doubt that very many are local and conditional varieties of a single Protean species. The same remark applies to the species discriminated among the shell-bearing Reticularia. It must not be supposed, however, that less importance is to be attached to the distinguishing and recording of such forms because we are not able to assert that they are permanent species.

The *yellow cells* (of spherical form, ·005 to 0·15 of a millimetre in diameter) which occur very generally scattered in the extra-capsular protoplasm of Radiolaria were at one time regarded as essential components of the Radiolarian body. Their parasitic nature is now rendered probable by the observations of Cienkowski (**43**), Brandt (**44**), and Geddes (**45**), who have established that each cell has a cellulose wall and a nucleus (Fig. XIV. 6 to 13), that the protoplasm is impregnated by chlorophyll which, as in Diatoms, is obscured by the yellow pigment, and that a starch-like substance is present (giving the violet reaction with iodine). Further, Cienkowski showed, not only that the yellow cells multiply by fission during the life of the Radiolarian, but that when isolated they continue to live; the cellulose envelope becomes softened; the protoplasm exhibits amœboid movements and escapes from the envelope altogether (Fig. XIV. 13) and multiplies by fission. Brandt has given the name *Zooxanthella nutricola* to the parasitic unicellular Alga thus indicated. He and Geddes have shown that a similar organism infests the endoderm cells of Anthozoa and of some Siphonophora in enormous quantities, and the former has been led, it seems erroneously, to regard the chlorophyll corpuscles of *Hydra viridis*, Spongilla, and Ciliata as also parasitic Algæ, for which he has coined the name Zoochlorella. The same arguments which Brandt has used to justify this view as to animal chlorophyll would warrant the creation of a genus "Phytochlorella" for the hypothetical Alga which has hitherto been described as the "chlorophyll corpuscles" of the cells of ordinary green plants.

Zooxanthella nutricola does not, for some unknown reason, infest the Acanthometridea, and it is by no means so universally present in the bodies of the Silico-skeleta as was supposed before its parasitic nature was recognized.

The *streaming of the granules of the protoplasm* has been observed in the pseudopodia of Radiolaria as in those of Heliozoa and Reticularia; it has also been seen in the deeper protoplasm; and granules have been definitely seen to pass through the pores of the central capsule from the intracapsular to the extracapsular protoplasm. A feeble vibrating movement of the pseudopodia has been occasionally noticed.

The *production of swarm-spores* has been observed only in Acanthometra and in the Polycyttaria and Thalassicollidæ, and only in the two latter groups have any detailed observations been made. Two distinct processes of swarm-spore production have been observed by Cienkowski (**43**), confirmed by Hertwig (**46**)—distinguished by the character of the resulting spores which are called "crystalligerous" (Fig. XIV. 15) in the one case, and "dimorphous" in the other (Fig. XIV. 16). In both processes the nucleated protoplasm within the central capsule breaks up by a more or less regular cell-division into small pieces, the details of the process differing a little in the two cases. In those individuals which produce crystalligerous swarm-spores, each spore encloses a small crystal (Fig. XIV. 15). On the other hand, in those individuals which produce dimorphous swarm-spores, the contents of the capsule (which in both instances are set free by its natural rupture) are seen to consist of individuals of two sizes "macrospores" and "microspores," neither of which contain crystals (Fig. XIV. 16). The further development of the spores has not been observed in either case. Both processes have been observed in the same species, and it is suggested that there is an alternation of sexual and asexual generations, the crystalligerous spores developing directly into adults, which in their turn produce in their central capsules dimorphous swarm-spores (macrospores and microspores), which in a manner analagous to that observed in the Volvocinean Flagellata copulate (permanently fuse) with one another (the larger with the smaller) before proceeding to develop. The adults resulting from this process would, it is suggested, produce in their turn crystalligerous swarm-spores. Unfortunately we have no observations to support this hypothetical scheme of a life-history.

Fusion or *conjugation* of adult Radiolaria, whether preliminary to swarm-spore-production or independently of it, has not been observed—this affording a distinction between them and Heliozoa, and an agreement, though of a negative character, with the Reticularia.

Simple fission of the central capsule of adult individuals and subsequently of the whole protoplasmic mass has been observed in several instances, and is probably a general method of reproduction in the group.

The siliceous shells of the Radiolaria are found abundantly in certain rocks. They furnish, together with Diatoms and Sponge-spicules, the silica which has been segregated as flint in the Chalk formation. They are present in quantity (as much as 10 per cent.) in the Atlantic ooze, and in the celebrated "Barbados earth" (a Tertiary deposit) are the chief components.

GRADE B. *CORTICATA*, Lankester, 1878 (**64**).

Characters.—Protozoa in which the protoplasm of the cell-body, in its adult condition, is permanently differentiated into two layers, an outer denser cortical substance and an inner more fluid medullary substance (not to be confused with the merely temporary distinction of exoplasm and endoplasm sometimes noted in Gymnomyxa, which is not structural but due to the gravitation and self-attraction of the coarser granules often embedded in the uniformly fluid protoplasm).

Since the Corticata have developed from simple Gymnomyxa exhibiting both amœboid and flagellate phases of form and activity, it results (1) that the forms of the body of many Corticata are traceable to modifications of these primitive forms; (2) that the young stages of the Corticata are in the lower classes of that group typical flagellulæ or amœbulæ; and (3) that there are certain archaic forms included in those lower classes whose position there is doubtful, and which might be with almost equal propriety assigned to the Gymnomyxa, since they are transitional from that lower grade to the higher grade of Corticata.

CLASS I. **SPOROZOA**, Leuckart (**47**); Syn. *Gregarinida*, Auct.

Characters.—Corticata parasitic in almost all classes and orders of animals, imbibing nutriment from the diffusible albuminoids of their hosts and therefore mouthless. In typical cases there is hatched from a chlamydospore one or more modified nucleate or non-nucleate flagellulæ (falciform young, drepanidium phase). The flagellula increases in size and differentiates cortical and medullary substance. Fission is common in the younger stages of growth. The movements now become neither vibratile nor amœboid but definitely restrained, and are best described as "euglenoid" (*cf.* Flagellata, Fig. XX. 27, 28). The nucleus is single, large, and spherical. No contractile vacuole and rarely any vacuole is present. A size of $\frac{1}{10}$th inch may be attained in this phase, which may be definitely spoken of as the euglena phase corresponding to the amœba phase of Gymnomyxa. It is usually of oblong form, with sac-like contractile wall of cortical substance, but may be spherical (Coccidiidea) or even amœboid (Myxosporidia).

Conjugation, followed directly or after an interval by sporulation, may now ensue. The conjugated individuals (two), or sometimes a single individual, become encysted. The contents of the cysts now rapidly divide (by a process the details of which are unknown) into minute ovoid nucleated (?) bodies; sometimes a portion of the protoplasm is not converted into spores but may form sporoducts (*cf.* capillitium of Mycetozoa). Each piece acquires a special chitin-like colourless coat, and is then a chlamydospore. Rarely one spore only is formed from the whole contents of a cyst. The spore-coat is usually thick, and remarkable for processes and other accessory developments. The included protoplasm of the chlamydospore frequently divides into several pieces before hatching. These usually, when set free from the spore-coat, have the form of modified nucleated flagellulæ, *i.e.*, flagellulæ in which the protoplasm is not drawn out into a thread-like flagellum but exhibits an elongate form, uniformly endowed with vibratile activity. With few (if any) exceptions, the falciform young thus characterized penetrates a cell of some tissue of its host and there undergoes the first stages of its growth (hence called Cytozoa). In some forms the pre-cystic phase never escapes from its cell host. In other cases it remains connected with the hospitable cell long after it has by growth exceeded by many hundred times the bulk of its quondam entertainer; often it loses all connexion with its cell host and is carried away to some other part of the infested animal before completing its growth and encysting.

The Sporozoa are divided into four sub-classes, differing from one another according to the form and development attained by the euglena phase. We shall place the most highly developed first, not only because our knowledge about it is most complete, but because it is possible that one at least of the other sub-classes is derived by degeneration from it.

SUB-CLASS I. **Gregarinidea**, Bütschli (9).

Characters.—Sporozoa in which the euglena phase is dominant, being relatively of large size, elongate in form, definitely shaped, having contractile but not viscid cortex, and exhibiting often active nutritional and locomotor phenomena. Though usually if not invariably cell-parasites in early youth, they become free before attaining adult growth, and inhabit either the body-cavity or the intestine of their hosts. Many spores are produced in the encysted phase. The spores have an oblong, sometimes caudate coat, and produce each one or several falciform young. At present only known as parasites of Invertebrata.

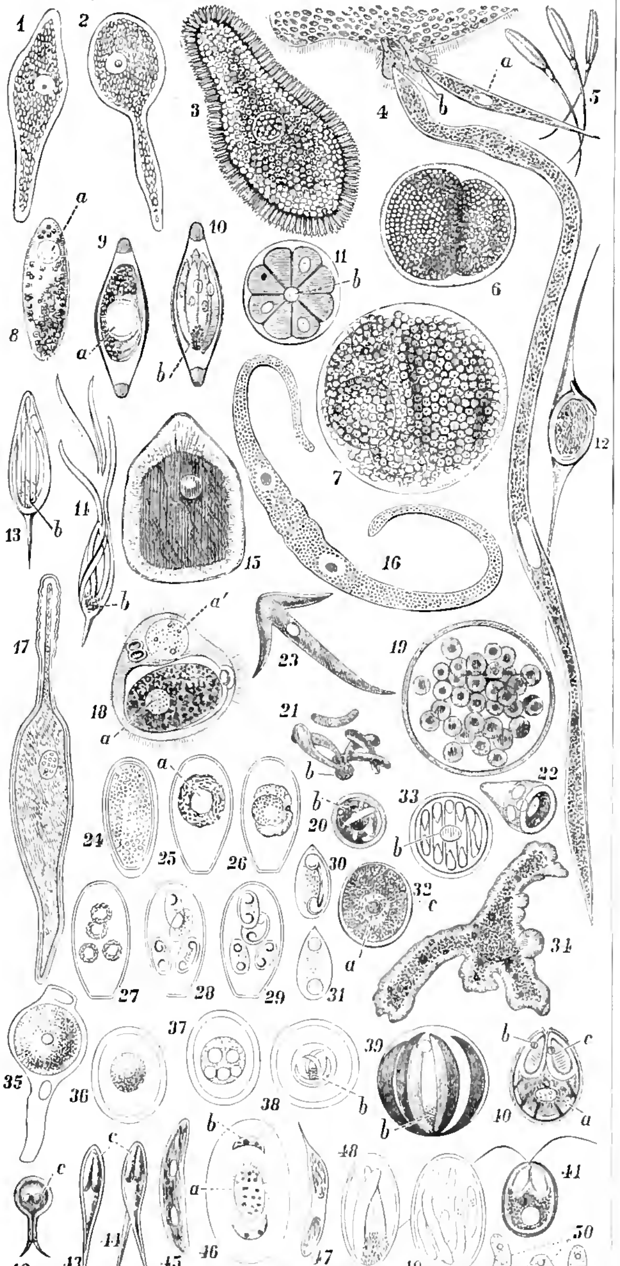


FIG. XVII.—**Sporozoa.** 1, 2. *Monocystis agilis*, Stein; × 250; from the testis of the Earthworm. Two phases of movement—a ring-like contraction passing along the body from one end to the other. 3. Individual of the same species which has penetrated in the young stage a sperm-cell of the Earthworm, and is now clothed as it were with spermatoblasts. 4. *Monocystis magna*, A. Schmidt, from the testis of the Earthworm (*L. terrestris*, L.). Two individuals, which are implanted by one extremity at *b* in two epithelial cells of the rosette of the spermatic duct. *a*, nucleus of the Monocystis. 5. Tailed chlamydospores of *Monocystis sænuridis*, Köll. 6. Two *M. agilis* encysted, spores forming on the surface of the protoplasm. 7. A similar cyst further advanced in spore-formation (see Fig. XVIII.). 8. Spore of *M. agilis*, now elongated but still naked. *a*, nucleus. × 1400. 9. The spore has now encased itself in a navicula-shaped coat. *a*, nucleus. 10. The spore protoplasm has now divided into several falciform swarm-spores, leaving a portion of the protoplasm unused. *b*, Schneider's residual core. 11. Optical transverse section of a completed spore. *b*, Schneider's residual core. 12. Chlamydospore of *Klossia chitonis*, nov. sp., from the liver of Chiton (original.) 13, 14. Chlamydospore of *Monocystis nemertis*, Köll., liberating falciform young. *b*, Schneider's residue. 15. *Monocystis pellucida*, Köll. (from Nereis); × 150; to show the very thick cortical substance and its fibrillation (after Lankester, **54**). 16. *Monocystis sænuridis*, Köll., two individuals adhering to one another (a syzygium). For spores see 5. 17. *Monocystis aphroditæ*, Lankester (**55**); × 60; remarkable among Monocystids for its long proboscis resembling the epimerite of some Septata. 18. *Klossia helicina*, Aim. Schn., from the kidney of *Helix hortensis*. A single cell of the renal epithelium in which a full-grown Klossia is embedded. *a*, nucleus of the Klossia; *a′*, nucleus of the renal cell. 19. Cyst of *Klossia helicina*, the contents broken up into spherical chlamydospores. 20. Single spore from the last, showing falciform young and a Schneider's residue *b*. 21. The contents of the same spore. 22. A small renal cell of Helix containing two of the youngest stage of Klossia. 23. *Monocystis sagittata*, Leuck., from the intestine of *Capitella capitata*; × 100. 24 to 31. *Coccidium oviforme*, Leuck., from the liver of the Rabbit:—24, adult individual encysted; 25, the protoplasm contracted—*a*, nucleus; 26, 27, division into four spores, as yet naked; 28, 29, the spores have acquired a covering, *i.e.*, are chlamydospores, and each contains a single falciform young; 30, 31, two views of a chlamydospore more highly magnified so as to show the single falciform young (from Leuckart). 32. *Klossia octopiana*, Aim. Schn., from Cephalopoda. *a*, nucleus; *b*, cyst-membrane. × 200 diam. 33. Single spherical spore of the same; × 1400 diam; showing numerous falciform young, and *b*, Schneider's residue. 34. *Myxidium Lieberkuhnii*, Butschli, one of the Myxosporidia, from the bladder of the Pike (Esox); creeping euglena phase, showing strongly lobed amœboid character (pseudopodia and undifferentiated (?) cortex); × 60 diam. 35-39. *Eimeria falciformis*, Eimer sp., from the Mouse:—35, an adult non-encysted individual inhabiting an epithelial cell of the intestine of the mouse; 36, encysted phase; 37, clear corpuscles appear in the encysted protoplasm; 38, the protoplasm now forms a single spore containing several falciform young; *b*, Schneider's residue; 39, isolated spore showing falciform young, and *b*, Schneider's residue. 40. Chlamydospore of *Myxobolus Mulleri*, Butschli, one of the Myxosporidia from the gills of Cyprinoid Fishes. *a*, nucleus; *b*, refringent corpuscle; *c*, polar body or thread-capsule. 41. A similar chlamydospore which has ejected the filaments from its thread capsules. 42. Chlamydospore of a Myxosporidium infesting the kidney of *Lota vulgaris*. *c*, polar body (psorosperm of authors). 43, 44. Chlamydospores of a Myxosporidium from the gills of Perca (psorosperm of authors). Compare with the tailed chlamydospore of *Monocystis sænuridis*, 5. 45-47. *Drepanidium ranarum*, Lankester, the falciform young of an unascertained Coccidiide infesting the Frog (supposed by Gaule to be produced by the blood corpuscles):—45, specimen stained by iodine; 46, red-blood corpuscle of Frog, showing *b*, two contained Drepanidia, and *a*, the nucleus of the blood corpuscle; 47, living Drepanidium. 48. Chlamydospore of Lieberkuhn's Coccidium of the Frog's kidney, perhaps belonging to the life-cycle of *Drepanidium ranarum*. The spore contains two falciform young (Drepanidia?) and a Schneider's residue. 49. Chlamydospore of *Monocystis thalassemæ*, Lankester, containing numerous falciform young. 50, 51. *Sarcocystis Miescheri*, Lankester:—50, falciform young escaped from chlamydospores; 51, adult euglena phase inhabiting a striated muscle fibre of the Pig.

ORDER 1. HAPLOCYTA, Lankester.

Characters.—Gregarinidea in which there is never at any time a partition of the medullary substance into two or more chambers. The euglenoid is always a single contractile sac with one mass of medullary substance in which floats the large vesicular transparent nucleus. Spores larger than in the next group, each producing several falciform young.

Genus unicum.—*Monocystis*, Stein, 1848. The various generic subdivisions proposed by Aim. Schneider (**48**), and accepted by Bütschli, appear to the present writer to have insufficient characters, and serve to complicate rather than to organize our knowledge of the subject. We do not yet know enough of the sporulation and subsequent development of the various monocystic Gregarinides to justify the erection of distinct genera.

Monocystis agilis, Stein, Fig. XVII. 1, 2, 3, 6, 7, 8, 9, 10, 11, and Fig. XVIII. is the type. The other species of Monocystis occur chiefly (and very commonly) in marine Annelids, Platyhelminthes, Gephyrea, and Tunicata; not in Arthropoda, Mollusca, nor Vertebrata. The only definite differences which they present of possibly more than specific worth, as compared with *M. agilis*, are in the form of the chlamydospores, which are sometimes tailed, as in *M. sænuridis* (Fig. XVII. 5), and in *M. nemertis* (Fig. XVII. 13) and *M. sipunculi*, and further also certain differences in the general form, as for instance the anchor-like *M. sagittata* (Fig. XVII. 23), and the proboscidiferous *M. aphroditæ* (Fig. XVII. 17). The fine parallel striation of the cuticule in some species (*M. serpulæ*, &c.) might also be made the basis of a generic or subgeneric group.

On the whole it seems best to leave all the species for the present in the one genus Monocystis, pending further knowledge. It seems probable that more than one species (at least two, *M. agilis* and *M. magna*) infest the common Earthworm.

ORDER 2. SEPTATA, Lankester.

Characters.—Gregarinidea in which in the adult the medullary substance is separated into two chambers—a smaller anterior (the protomerite) and a larger posterior (the deutomerite), in which lies the nucleus. There is frequently if not always present, either in early growth or more persistently, an anterior proboscis-like appendage (the epimerite) growing from the protomerite. The epimerite serves to attach the parasite to its host, and may for that purpose carry hooklets. It is always shed sooner or later. The phase in which it is present is called a "cephalont," the phase after it has broken off a "sporont" (see Fig. XIX. 22, 23). The spores are smaller than in the preceding group, often very minute, and sometimes the cyst is complicated by the formation of sporoducts, and by a kind of "capillitium" of residual protoplasm (Fig. XIX. 2). Spores producing each only a single (?) falciform young.

Genera.—*Gregarina*, Dufour; *Hoplorhynchus*, Von Carus.

[The numerous genera which have been proposed at different times by Hammerschmidt and others, and more recently by Aimé Schneider, appear to the present writer to be unserviceable, owing to the fact that our knowledge is as yet very incomplete. A good basis for generic or family distinctions might probably be found in the greater or less elaboration of the cyst and the formation or not of sporoducts. But of the majority of Septata we do not know the cysts or the history of sporulation; we merely know that some have simple cysts with complete sporulation leaving no residue of protoplasm, and that others form cysts with double walls and elaborate tubular ducts, whilst a part of the protoplasm is not sporulated but forms a capillitium (Fig. XIX. 2).

Another possible basis for generic division of the Septata may be found in the characters of the epimerite. This may be present or absent altogether. It may exist only in the young condition or persist until growth is completed. It may be simple, short, elongate, or provided with hooklets. The presence of hooklets on the epimerite is the only character which at present seems to serve conveniently for generic distinction. With regard to the other points mentioned we are not sufficiently informed, since we know the complete history of development from the young form set free from the spore in only one or two cases.]

The Septata are found exclusively in the alimentary canals of Arthropoda (Insects, Myriapods, Crustacea, not Arachnida). See Fig. XIX. for various examples of the group.

FIG. XVIII.—Cyst of *Monocystis agilis*, the common Gregarinide of the Earthworm; × 750 diam.; showing ripe chlamydospores and complete absence of any residual protoplasm or other material in the cyst (original).

SUB-CLASS II. Coccidiidea, Bütschli (9).

Sporozoa in which the euglena phase remains of relatively minute size, of spherical shape and simple egg-cell-like structure. It is not locomotive, but continues, until the cyst is formed, to inhabit a single cell of the host. Many, few, or one single chlamydospore are formed in the cyst. One or more falciform young escape from each spore, and exhibit active movements (flagellula-like) leading to a penetration of a tissue-cell by the young form as in Gregarinidea. Many are parasites of Vertebrata.

ORDER 1. MONOSPOREA, Aim. Schn.

Characters.—The whole content of the cyst forms but a single spore.

Genus unicum.—*Eimeria* (in the intestinal epithelium of Triton, Frog, Sparrow, Mouse, and the Myriapods Lithobius and Glomeris, Fig. XVII. 35 to 39).

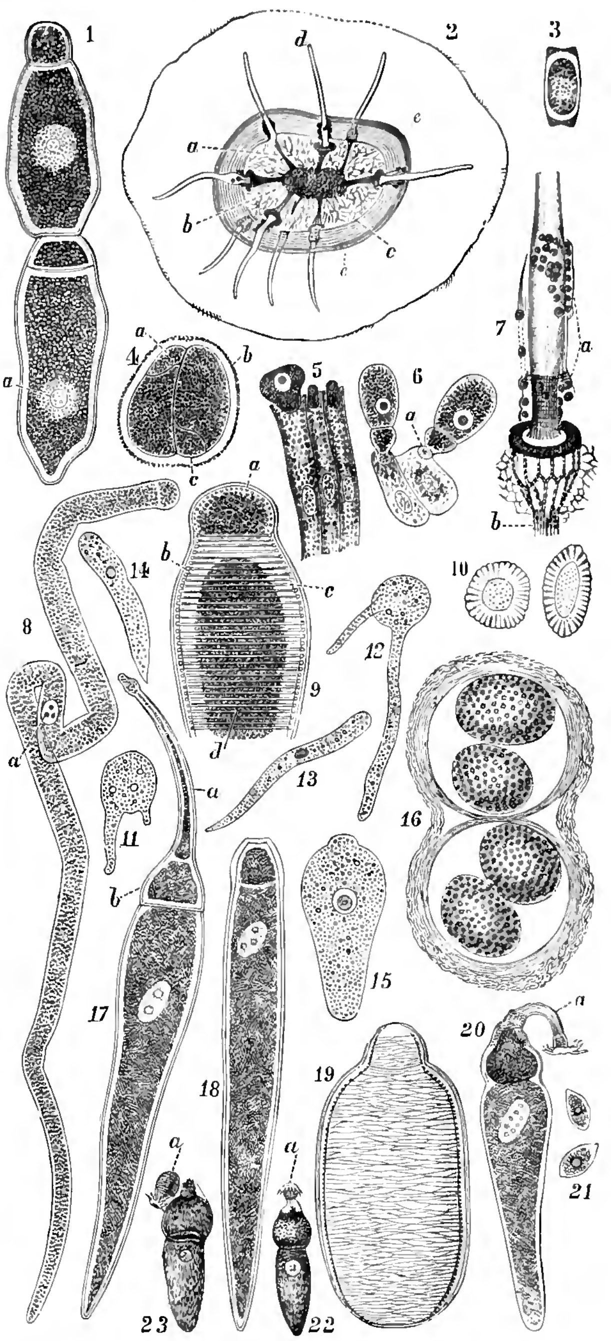


FIG. XIX.—**Sporozoa** (Septata). 1. *Gregarina blattarum*, Siebold, from the intestine of *Blatta orientalis*; × 80. A syzygium of two individuals. Each animal consists of a small anterior chamber, the protomerite, and a large posterior chamber, the deutomerite, in which is the nucleus *a*. 2. Over-ripe cyst of *Gregarina blattarum*, with thick gelatinous envelope *e*, and projecting sporoducts *d*. The spores have been nearly all discharged, but a mass of them still lies in the centre of the cyst *b*. The specimen has been treated with dilute KHO, and the granular contents of the cyst dissolved. Around the central mass of spores is rendered visible the network of protoplasmic origin in which the ejected spores were embedded. This distinctly resembles in origin and function the capillitium of Mycetozoa (Fig. III.). *a*, the plasmatic channels leading to the everted sporoducts; *b*, the still remaining spores; *c*, the proper cyst-wall; *d*, the everted sporoducts; *e*, the gelatinous envelope. 3. A ripe spore (chlamydo spore) of *Gregarina blattarum*, a long time after its escape from the cyst; × 1600 diam. 4. Commencing encystment of a syzygium of *G. blattarum*. *a*, protomerite of one individual; *b*, gelatinous envelope; *c*, protomerite of the second individual. 5. Three epithelial cells of the mid-gut of *Blatta orientalis*, into the end of each of which an extremely young *Gregarina blattarum* has made its way. 6. Further development of the young Gregarina; only the epimerite *a* is now buried in the substance of the epithelial cell, and this will soon break off and set the Gregarina free. It is now a "cephalont"; it will then become a "sporont." 7. Basal part of an everted sporoduct of *Gregarina blattarum*. *a*, granular-fibrous mass investing the base of the duct; *b*, commencement of the plasmatic channel in the interior of which the sporoduct was produced as an invaginated cuticular formation before its eversion. 8. *Gregarina gigantea*, E. Van Ben., from the intestine of the Lobster; × 150. *a*, nucleus.

9. Anterior end of the same more highly magnified. *a*, protomerite; *b*, layer of circular fibrillæ lying below the cuticle; *c*, cortical substance of the deutomerite; *d*, medullary substance of the deutomerite. 10. Two spores of *Gregarina gigantea* (after Butschli), showing the very thick coat of the spore. 11-15. Stages in the development of *Gregarina gigantea*:—11, recently escaped from the spore-coat, no nucleus; 12, still no nucleus, one vibratile and one motionless process; 13, the two processes have divided; one here drawn has developed a nucleus; 14, further growth; 15, the deutomerite commences to develop. 16. Cysts of *Gregarina gigantea*, from the rectum of the Lobster. The double contents are believed by Ed. Van Beneden to be due not to conjugation previous to encystment but to subsequent fission. 17, 18. *Gregarina longicollis*, Stein, from the intestine of *Blaps mortisaga*:—17, cephalont phase, with a long proboscis-like epimerite *a*, attached to the protomerite *b*; 18, sporont phase, the epimerite having been cast preliminarily to syzygy and encystment. 19. *Gregarina Manieri*, Aim. Schneider, from the intestine of *Timarcha tenebricosa*, to show the network of anastomosing fibres beneath the cuticle, similar to the annular fibrillæ of *G. gigantea* shown in 9. 20. *Gregarina* (*Hoplorhynchus*) *obligacanthus*, Stein, from the intestine of the larva of Agrion. Cephalont with spine-crowned epimerite *a*. 21. Spores of *Gregarina oligacanthus*. 22, 23. *Gregarina* (*Hoplorhynchus*) *Dujardini*, Aim. Schneider, from the intestine of *Lithobius forficatus*:—22, specimen with epimerite *a*, therefore a "cephalont"; 23, specimen losing its epimerite by rupture and becoming a "sporont."

ORDER 2. OLIGOSPOREA, Aim. Schn.

Characters.—The cyst-content develops itself into a definite and constant but small number of spores.

Genus unicum.—*Coccidium*, Leuck. (in intestinal epithelium and liver of Mammals, and some Invertebrates, Figs. XVII. 24 to 31).

ORDER 3. POLYSPOREA.

Characters.—The cyst-content develops itself into a great number of spores (sixty or more).

Genus unicum.—*Klossia*, Aim. Schn. Three species of Klossia are found in Mollusca—viz., in Helix, in Cephalopods, and in Chiton. Schneider's genus, Adelea, from Lithobius, appears to belong here. Kloss (**49**) discovered the parasite of the renal cells of *Helix hortensis* represented in Fig. XVII. 18, 19, 20, 21, and 22; Schneider that of Cephalopods, Fig. XVII. 32, 33. In Chiton Dr Tovey has discovered a third species with very remarkable spores, which are here figured for the first time (Fig. XVII. 12).

The *Drepanidium Ranarum* (Fig. XVII. 45, 46, 47), discovered by Lankester (**50**) in the Frog's blood, is probably the falciform young of a Coccidium parasitic in the Frog's kidney, and discovered there by Lieberkühn (**51**). A spore of this Coccidium is shown in Fig. XVII. 48; whilst in 46 two Drepanidia which have penetrated a red-blood corpuscle of the Frog are represented.

The Polysporous Coccidiidea come very close to the Gregarinide genus Monocystis, from which they may be considered as being derived by an arrest of development. The spores and falciform young of the Coccidiidea are closely similar to those of Monocystis, and the young in both cases penetrate the tissue-cells of their host; but in Monocystis this is only a temporary condition, and growth leads to the cessation of such "cell-parasitism." On the other hand, growth is arrested in the Coccidiidea, and the organism is permanently a cell-parasite.

Since the parasitism is more developed in the case of a cell-parasite than in the case of a parasite which wanders in the body cavity, it seems probable that the Coccidiidea have been derived from the Gregarinidea rather than that the reverse process has taken place.

SUB-CLASS III. **Myxosporidia**, Bütschli.

Characters.—Sporozoa in which the euglena-phase is a large multinucleate amœba-like organism (Fig. XVII. 34). The cysts are imperfectly known, but appear to be simple; some attain a diameter of two lines. The spores are highly characteristic, having each a thick coat which is usually provided with a bifurcate process or may have thread capsules (like nematocysts) in its substance (Fig. XVII. 40, 41, 42, 43, 44).

The spores contain a single nucleus, and are not known to produce falciform young, but in one case have been seen to liberate an amœbula. The further development is unknown. The Myxosporidia are parasitic beneath the epidermis of the gills and fins, and in the gall-bladder and urinary bladder of Fishes, both freshwater and marine.

Genera.—*Myxidium*, Bütschli (Pike, Fig. XVII. 34); *Myxobolus*, Bütschli (Cyprinoids); *Lithocystis*, Giard (the Lamellibranch Echinocardium).

The Myxosporidia are very imperfectly known. They present very close affinities to the Mycetozoa, and are to be regarded as a connecting link between the lower Gymnomyxa and the typical Sporozoa. Possibly their large multinucleate amœba phase is a plasmodium formed by fusion of amœbulæ set free from spores, though it is possible that the many nuclei are the result of a division of an original single nucleus, preparatory to sporulation.

Their spores are more elaborate in structure than those of any other Protozoa, and are more nearly paralleled by those of some species of Monocystis than by those of Mycetozoa. The thread-capsules of the spores are identical in structure with those of Hydrozoa, and probably serve as organs of attachment, as do the furcate processes of the spore-case. It is not certain that a definite cyst is always or ever formed, but as occurs rarely in some Gregarinidea, the spores may be formed in a non encysted amœba form.

Although pseudopodia, sometimes short and thread-like, have been observed in the amœba phase, yet it is also stated that a distinction of cortical and medullary substance obtains.

The "psorosperms" of J. Müller are the spores of Myxosporidia.

SUB-CLASS IV. **Sarcocystidia**, Bütschli.

(This division is formed by Bütschli for the reception of Sarcocystis, parasitic in the muscular fibres of Mammals, and of Amœbidium, parasitic in Crustacea. Both are very insufficiently known, but have the form of tubular protoplasmic bodies in which numerous ovoid spores are formed from which falciform young escape.)

Genera.—*Sarcocystis*, Lankester; *Amœbidium*, Cienkowski (**52**). Sarcocystis (Fig. XVII. 50, 51, *S. Miescheri*, Lank.), was first observed by Miescher in the striated muscle-fibres of the Mouse; then by Rainey in a similar position in the Pig, and taken by him for the youngest stage in the development of the cysts of *Tænia solium*; subsequently studied by Beale and others in connexion with the cattle-plague epidemic, and erroneously supposed to have a causal connexion with that disease. It is common in healthy butcher's meat. See Leuckart (**47**).

Further remarks on the Sporozoa.—The Sporozoa contrast strongly with the large classes of Gymnomyxa, the Heliozoa, Reticularia, and Radiolaria, as also with the Ciliate and Tentaculiferous Corticata, by their abundant and rapidly recurrent formation of spores, and agree in this respect with some Proteomyxa, with Mycetozoa, and some Flagellata. Their spores are remarkable for the firm, chitin-like spore-coat and its varied shapes, contrasting with the cellulose spherical spore-coat of Mycetozoa and with the naked spores of Radiolaria and Flagellata.

The protoplasm of the more highly developed forms (Gregarinidea) in the euglenoid phase exhibits considerable differentiation. Externally a distinct cuticle may be present, marked by parallel rugæ (*Monocystis serpulæ*) or by fine tubercles (*Monocystis sipunculi*). A circlet of hooks may be formed by the cuticle at one end of the body. Below the cuticle is sometimes developed a layer of fibrils running transversely to the long axis of the body (Fig. XIX. 9 and 19), which have been regarded as contractile, but are probably cuticular. The cortical layer of protoplasm below these cuticular structures is dense and refringent and sometimes fibrillated (*Monocystis pellucida*, Fig. XVII. 15). It is the contractile substance of the organism, and encloses the finely granular more liquid medullary substance. The granules of the latter have been shown by Bütschli (**9**) to give a starch-like reaction with iodine, &c. Probably the protoplasm in which they lie is finely reticulate or vacuolar, and when the granules are few it is actually seen to be so. No contractile vacuole is ever present. In Myxosporidia the medullary protoplasm is coloured yellow by hæmatoidin derived from the blood of its host or by absorbed bile-pigment, and also contains small crystals.

The nucleus of the Gregarinidea is a large clear capsule, with a few or no nucleolar granules. It has never been seen in a state of division, and it is not known what becomes of it during sporulation, though sporulating Gregarinidea have been observed with many minute nuclei scattered in their protoplasm, presumably formed by a breaking up of the single nucleus.

The habit of attaching themselves in pairs which is common in Gregarinidea is perhaps a reminiscence of a more extensive formation of aggregation plasmodia (compare Mycetozoa). The term "syzygium" is applied to such a conjunction of two Gregarinidea; it is not accompanied by fusion of substance. The formation of cysts is not connected with this pairing, since the latter occurs in young individuals long before encystment. Also cysts are formed by single Gregarinidea, as is always the case in the non-motile Coccidiidea.

The encystment always leads to the formation of spores, but in rare cases sporulation has been observed in unencysted Gregarinidea, and it occurs perhaps normally without true cyst-formation in the Myxosporidia.

The cell-parasitism of the young Sporozoa, and their flagellula-like (falciform) young and active vibratile movement, are points indicating affinity with the lower Gymnomyxa, and especially with those Proteomyxa, such as Vampyrella and Plasmodiophora, which are cell-parasites. Indeed it is probable that we have in this fact of cell-parasitism, and especially of parasitism in animal cells, a basis for the theoretical association of several unicellular organisms. The Haplococcus of Zopf (regarded by him as a Mycetozoon) is parasitic in the muscular cells of the Pig, and is probably related to Sarcocystis. Recently Von Lendenfeld (**53**) has described in Australia an amœba-like organism as parasitic in the skin of Sheep, which will probably be found to be either a Sporozoon or referable to those parasitic spore-producing Proteomyxa which are separated from Sporozoa only by their negative characters (see previous remarks on the negative characters of Proteomyxa).

The application of the name "Gregarines" has sometimes been made erroneously to external parasitic organisms, which have nothing in common with the Sporozoa. This was the case in regard to a fungoid growth in human hair—the so-called "chignon Gregarine." The Silk-worm disease known as "pebrine" has also been attributed to a Gregarine. It seems probable that the parasitic organism which causes that disease is (as is also the distinct parasite causing the disease known as "flaccidezza" in the same animals) one of the Schizomycetes (Bacteria). No disease is known at present as due to Sporozoa, although (*e.g.*, the *Klossia chitonis*) they may lead to atrophy of the organs of the animals which they infest, in consequence of their enormous numbers. Coccidia and Sarcocystis are stated to occur in Man.

CLASS II. FLAGELLATA,[1] Ehrenberg.

Characters.—Corticata in which the dominant phase in the life-history is a corticate flagellula, that is, a nucleated cell-body provided with one or a few large processes of vibratile protoplasm. Very commonly solid food particles are ingested through a distinct cell-mouth or aperture in the cortical protoplasm, though in some an imbibition of nutritive matter by the whole surface and a nutritional process chemically resembling that of plants (holophytic), chlorophyll being present, seems to occur.

Conjugation followed by a breaking up into very numerous minute naked spores is frequent in some; as also a division into small individuals (microgonidia), which is followed by their conjugation with one another or with big individuals (macrogonidia) and subsequent normal growth and binary fission.

Many have a well-developed cuticle, which may form collar-like outgrowths or stalk-like processes. Many produce either gelatinous or chitin-like shells (cups or cœnœcia), which are connected so as to form spherical or arborescent colonies; in these colonies the protoplasmic organisms themselves produce new individuals by fission, which separate entirely from one another but are held together by the continuity, with those already existing, of the new shells or jelly-houses or stalk-like supports produced by the new individuals. A single well-marked spherical nucleus, and one or more contractile vacuoles, are always present in the full-grown form.

Often, besides ingested food-particles, the protoplasm contains starch granules (amylon nucleus), paramylum corpuscles, chromatophors and chlorophyll corpuscles, some of which may be so abundant as to obscure the nucleus. One or two pigment spots (stigmata or so-called eye-spots) are often present at the anterior end of the body.

SUB-CLASS I. Lissoflagellata, Lankester.

Never provided with a collar-like outgrowth around the oral pole.

ORDER 1. MONADIDEA, Bütschli.

Characters.—Lissoflagellata of small or very small size and simple structure; often naked and more or less amœboid, sometimes forming tests. Usually colourless, seldom with chromatophors. With a single anterior large flagellum or sometimes with two additional paraflagella. A special mouth-area is often wanting, sometimes is present, but is never produced into a well-developed pharynx.

Fam. 1. RHIZOMASTIGINA, Bütschli. Simple mouthless forms with 1 to 2 flagella; either permanently exhibiting a Gymnomyxa-like development of pseudopodia or capable of passing suddenly from a firm-walled into a Gymnomyxa-like condition, when the flagella may remain or be drawn in. Ingestion of food by aid of the pseudopodia.

Genera.—*Mastigamœba*, F. E. Schultze; *Ciliophrys*, Cienkowski (**65**); *Dimorpha*, Gruber; *Actinomonas*, Kent; *Trypanosoma*, Gruby (parasitic in the blood of Frogs and other Amphibia and Reptiles, Fig. XX. 21, 22). The Rhizomastigina might all be assigned to the Proteomyxa, with which they closely connect the group of Flagellata. The choice of the position to be assigned to such a form as Ciliophrys must be arbitrary.

Fam. 2. CERCOMONADINA, Kent. Minute oblong cell-body which posteriorly may exhibit amœboid changes. One large anterior flagellum. Mouth at the base of this organ. Reproduction by longitudinal fission and by multiple fission producing spores in the encysted resting state.

Genera.—*Cercomonas*, Duj. (Fig. XX. 32, 33); *Herpetomonas*, S. Kent; *Oikomonas*, Kent (=*Monas*, James Clark; *Pseudospora*, Cienkowski, Fig. XX. 29, 30, 31); *Ancyromonas*, S. K.

Fam. 3. CODONŒCINA, Kent. Small colourless monads similar to Oikomonas in structure, which secrete a fixed gelatinous or membranous envelope or cup.

Genera.—*Codonœca*, James Clark; *Platytheca*, Stein.

Fam. 4. BIKŒCINA, Stein. Distinguished from the last family by the fact that the monad is fixed in its cup by a contractile thread-like stalk; cup usually raised on a delicate stalk.

Genera.—*Bicosœca*, J. Cl.; *Poteriodendron*, Stein.

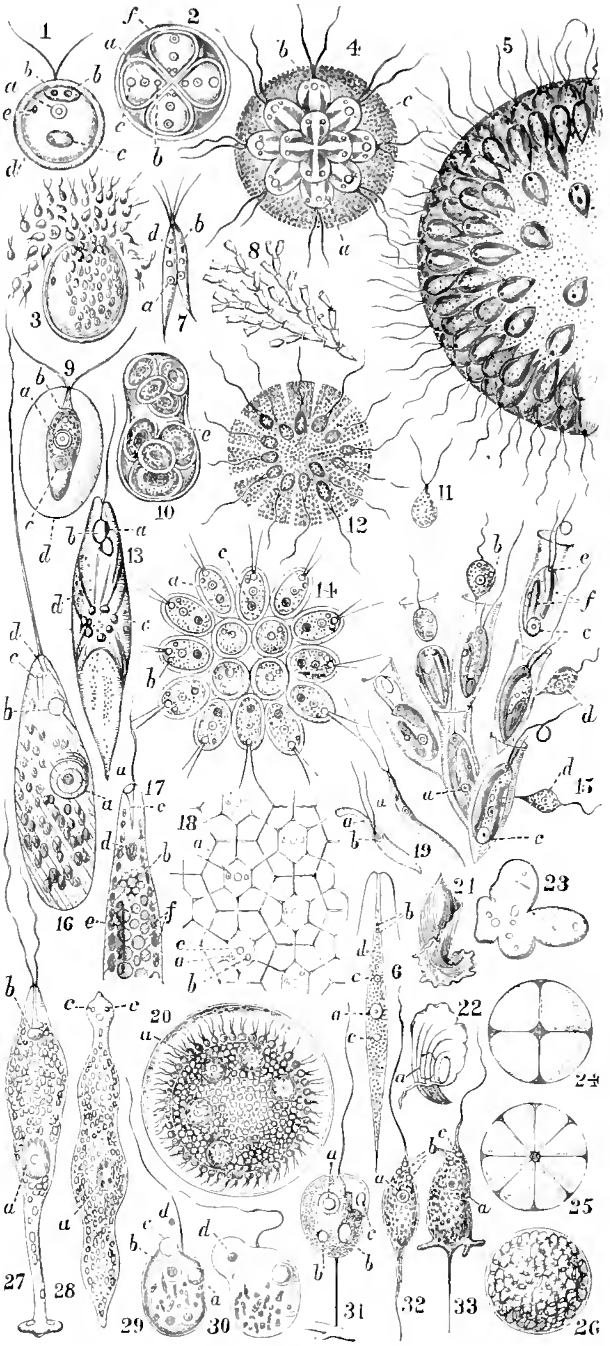


FIG. XX.—**Flagellata.** 1. *Chlamydomonas pulvisculus*, Ehr. (=*Zygoselmis*, From.); one of the Phytomastigoda; free-swimming individual. *a*, nucleus; *b*, contractile vacuole; *c*, starch corpuscle; *d*, cellulose investment; *e*, stigma (eye-spot). 2. Resting stage of the same, with fourfold division of the cell-contents. Letters as before. 3. Breaking up of the cell-contents into minute biflagellate swarm-spores, which escape, and whose history is not further known. 4. *Syncrypta volvox*, Ehr.; one of the Phytomastigoda. A colony enclosed by a common gelatinous test *c*. *a*, stigma; *b*, vacuole (non-contractile). 5. *Uroglena volvox*, Ehr.; one of the Monadidea. Half of a large colony, the flagellates embedded in a common jelly. 6. *Chlorogonium euchlorum*, Ehr.; one of the Phytomastigoda. *a*, nucleus; *b*, contractile vacuole; *c*, starch grain; *d*, eye-spot. 7. *Chlorogonium euchlorum*, Ehr., one of the Phytomastigoda. Copulation of two liberated microgonidia. *a*, nucleus; *b*, contractile vacuole; *d*, eye-spot (so-called). 8. Colony of *Dinobryon sertularia*, Ehr.; × 200; one of the Monadidea. 9. *Hæmatococcus palustris*, Girod (= *Chlamydococcus*, Braun, *Protococcus* Cohn), one of the Phytomastigoda; ordinary individual with widely separated test. *a*, nucleus; *b*, contractile vacuole; *c*, amylon nucleus (pyrenoid). 10. Dividing resting stage of the same, with eight fission products in the common test *c*. 11. A microgonidium of the same. 12. *Phalansterium consociatum*, Cienk., one of the Choanoflagellata; × 325. Disk-like colony. 13. *Euglena viridis*, Ehr.; × 300; one of the Englenoidea. *a*, pigment spot (stigma); *b*, clear space; *c*, paramylum granules; *d*, chromatophor (endochrome plate). 14. *Gonium pectorale*, O. F. Muller; one of the Phytomastigoda. Colony seen from the flat side. × 300. *a*, nucleus; *b*, contractile vacuole; *c*, amylon nucleus. 15. *Dinobryon sertularia*, Ehr.; one of the Monadidea. *a*, nucleus; *b*, con-

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[1] Butschli's work (**9**) has been pretty closely followed in the diagnosis of the groups of Flagellata and the enumeration of genera here given.

tractile vacuole ; *c*, amylon-nucleus ; *d*, free colourless flagellates, probably not belonging to Dinobryon ; *e*, stigma (eye-spot); *f*, chromatophors. 16. *Peranema trichophorum*, Ehr., (one of the Euglenoidea), creeping individual seen from the back ; × 140. *a*, nucleus ; *b*, contractile vacuoles ; *c*, pharynx ; *d*, mouth. 17. Anterior end of *Euglena acus*, Ehr., in profile. *a*, mouth ; *b*, contractile vacuoles ; *c*, pharynx ; *d*, stigma (eye-spot); *e*, paramylum-body ; *f*, chlorophyll corpuscles. 18. Part of the surface of a colony of *Volvox globator*, L. (Phytomastigoda), showing the intercellular connective fibrils. *a*, nucleus ; *b*, contractile vacuole ; *c*, amylum granule. 19. Two microgonidia of *Volvox globator*, L. *a*, nucleus ; *b*, contractile vacuole. 20. Ripe asexually produced daughter-individual of *Volvox minor*, Stein, still enclosed in the cyst of the partheno-gonidium. *a*, young partheno-gonidia. 21, 22. *Trypanosoma sanguinis*, Gruby ; one of the Rhizomastigina, from the blood of *Rana esculenta*. *a*, nucleus. × 500. 23–26. Reproduction of *Bodo caudatus*, Duj. (one of the Heteromastigoda), after Dallinger and Drysdale :—23, fusion of several individuals (plasmodium); 24, encysted fusion-product dividing into four ; 25, later into eight ; 26, cyst filled with swarm-spores. 27. *Astasia tenax*, O. F. Müll. (Proteus) ; one of the Euglenoidea ; × 440. Individual with the two flagella, and strongly contracting hinder region of the body. *a*, nucleus ; *b*, contractile vacuole, close to the pharynx. 28. The same devoid of flagella. *a*, nucleus ; *c*, *c*, the two dark pigment spots (so-called eyes) near the mouth. 29. *Oikomonas termo* (*Monas termo*) Ehr. ; one of the Monadidea. *a*, nucleus ; *b*, contractile vacuole ; *c*, food-ingesting vacuole ; *d*, food-particle. × 440. 30. The food-particle *d* has now been ingested by the vacuole. 31. *Oikomonas mutabilis*, Kent (Monadidea), with adherent stalk. *a*, nucleus ; *b*, contractile vacuole ; *c*, food-particle in food vacuole. 32, 33. *Cercomonas crassicauda*, Duj. (Monadidea), showing two conditions of the pseudopodium-protruding tail. *a*, nucleus ; *b*, contractile vacuoles ; *c*, mouth.

Fam. 5. Heteromonadina, Bütschli. Small colourless or green monads which possess, besides one chief flagellum, one or two smaller paraflagella attached near it, often forming colonies secreting a common stalk.

Genera.—*Monas* (Ehr.), Stein ; *Dendromonas*, Stein ; *Cephalothamnium*, Stein ; *Anthophysa*, Bory d. Vinc. (Fig. XXI. 12, 13); *Dinobryon*, Ehr. (Fig. XX. 8 and 15) ; *Epipyxis*, Ehr. ; *Uroglena*, Ehr. (Fig. XX. 5).

Order 2. EUGLENOIDEA, Bütschli.

Characters.—Generally somewhat large and highly developed monoflagellate forms, of monaxonic or slightly asymmetrical build. Cuticle present ; cortical substance firm, contractile, and elastic ; some forms quite stiff, others capable of definite annular contraction and worm-like elongation. At the base of the flagellum a small or large mouth leading into a more or less distinct pharyngeal tube. Near this is always the contractile vacuole. Rarely a pair of flagella instead of one.

Fam. 1. Cœlomonadina Coloured Euglenoidea, with numerous small chlorophyll corpuscles or 1 to 2 large plate-like green or brown chromatophors. Mouth and pharynx inconspicuous ; nutrition probably largely vegetal (holophytic).

Genera.—*Cœlomonas*, Stein ; *Gonyostomum*, Dies. ; *Vacuolaria*, Cienk. ; *Microglena*, Ehr. ; *Chromulina*, Cienk. ; *Cryptoglena*, Ehr.

Fam. 2. Euglenina, Stein. Body monaxonic, elongated, hinder end pointed. Spirally striated cuticle. A fine mouth-aperture leads into the well-developed tubular pharynx. Flagellum usually single, sometimes paired, often cast off. Near the pharynx is the "reservoir" of the contractile vacuoles and several of the latter. A single (sometimes two) stigma or colour-speck near the same spot. Chromatophors nearly always present, generally bright green. A large nucleus in the middle of the body. Multiplication by longitudinal fission. Encysted condition and attendant fission imperfectly studied. Copulation doubtful.

Genera.—(*a*) With flexible cuticle :—*Euglena*, Ehr. (Fig. XX. 13, 17 ; this is probably Priestley's "green matter," from which he obtained oxygen gas ; though one of the very commonest of all Protozoa, its life-history has yet to be worked out) ; *Colacium*, Ehr. ; *Eutreptia*, Perty.

(*b*) With stiff, shell-like cuticle :—*Ascoglena*, Stein ; *Trachelomonas*, Ehr. ; *Lepocinclis*, Perty ; *Phacus*, Nitzsch.

Fam. 3. Menoidina, Bütschli. Similar to the Euglenina, but devoid of chlorophyll, a deficiency connected with the saprophytic mode of life. Stigma always absent.

Genera.—(*a*) With flexible cuticle :—*Astasiopsis*, Butschli ; *Astasiodes*, Bütschli.

(*b*) With stiff cuticle and non-contractile body :—*Monoidium*, Perty ; *Atractonema*, Stein ; *Rhabdomonas*, Fresenius.

Fam. 4. Peranemina. Very contractile (metabolic) colourless Euglenoids. Mouth and pharynx large ; inception of solid nutriment certainly observed.

Genera.—*Peranema*, Duj. (Fig. XX. 16) ; *Urceolus*, Meresch.

Fam. 5. Petalomonadina. Colourless, non-metabolic forms. Mouth opening at the base of the single large flagellum.

Genera.—*Petalomonas*, Stein.

Fam. 6. Astasina. Colourless, metabolic, or stiff Euglenoids, differing from the rest in having a small or large paraflagellum in addition to the chief one. Nutrition partly saprophytic partly animal.

Genera.—*Astasia*, Ehr. emend. Stein (Fig. XX. 27, 28) ; *Heteronema*, Duj. ; *Zygoselmis*, Duj. ; *Sphenomonas*, Stein ; *Tropidoscyphus*, Stein.

Order 3. HETEROMASTIGODA, Bütschli.

Characters.—Small and large monads. Naked and even amœboid or with stiff cuticle. Two flagella at the anterior end differing in size : the smaller directed forwards subserves the usual locomotor function ; the larger is directed backwards and trailed, without movement. Sometimes two backwardly directed flagella are present. Always a mouth and animal nutrition. Always colourless.

Fam. 1. Bodonina, Bütschli. Size of the two flagella not very different.

Genera.—*Bodo*, Ehb. emend. Stein (Fig. XX. 23 to 26, and Fig. XXI. 10 ; the hooked monad and the springing monad of Dallinger and Drysdale (66) ; *Heteromita* of Dujardin and Kent); *Phyllomitus*, Stein ; *Colponema*, Stein ; *Dallingeria*, Kent ; *Trimastix*, Kent.

Fam. 2. Anisonemina, Kent. Large forms with cuticle ; difference of the two flagella considerable. Mouth, pharynx, and animal nutrition.

Genera.—*Anisonema*, Duj. ; *Entosiphon*, Stein.

Order 4. ISOMASTIGODA, Bütschli.

Characters.—Small and middle-sized forms of monaxonic rarely bilateral shape. Fore-end with 2, 4, or seldom 5 equal-sized and similar flagella. Some are coloured, some colourless ; naked or with strong cuticle or secreting an envelope. Mouth and pharynx seldom observed ; nutrition generally holophytic (*i.e.*, like a green plant), but in some cases, nevertheless, holozoic (*i.e.*, like a typical animal).

Fam. 1. Amphimonadina. Small, colourless, biflagellate Isomastigoda.

Genera.—*Amphimonas*, Duj. (? *Pseudospora*, Cienk.).

Fam. 2. Spongomonadina, Stein. Small colourless oval forms with two closely contiguous flagella. Chief character in the union of numerous individuals in a common jelly or in branched gelatinous tubes, the end of each of which is inhabited by a single and distinct individual.

Genera.—*Spongomonas*, Stein ; *Cladomonas*, Stein ; *Rhipidomonas*, Stein.

[Group **Phytomastigoda**, Bütschli. The following three families, viz., Chrysomonadina, Chlamydomonadina, and Volvocina, are so closely related to one another as to warrant their union as a sub-order. They are typical Isomastigoda, but have chlorophyll corpuscles and holophytic nutrition with correlated deficient mouth and pharynx. They are usually regarded by botanists as belonging to the unicellular Algæ.]

Fam. 3. Chrysomonadina, Bütschli. Single or colony-forming ; seldom an envelope. Spherical free-swimming colonies may be formed by grouping of numerous individuals around a centre. With two or rarely one brown or greenish brown chromatophor; a stigma (eye-speck) at the base of the flagella.

Genera.—*Stylochrysalis*, Stein; *Chrysopyxis*, Stein ; *Nephroselmis*, Stein ; *Synura*, Ehr. ; *Syncrypta*, Ehr. (Fig. XX. 4).

Fam. 4. Chlamydomonadina. Fore-end of the body with two or four (seldom five) flagella. Almost always green in consequence of the presence of a very large single chromatophor. Generally a delicate shell-like envelope of membranous consistence. 1 to 2 contractile vacuoles at the base of the flagella. Usually one eye-speck. Division of the protoplasm within the envelope may produce four, eight, or more new individuals. This may occur in the swimming or in a resting stage. Also by more continuous fission microgonidia of various sizes are formed. Copulation is frequent.

Genera.—*Hymenomonas*, Stein ; *Chlorangium*, Stein ; *Chlorogonium*, Ehr. (Fig. XX. 6, 7) ; *Polytoma*, Ehr. ; *Chlamydomonas*, Ehr. (Fig. XX. 1, 2, 3) ; *Hæmatococcus*, Agardh (= *Chlamydococcus*, A. Braun, Stein ; *Protococcus*, Cohn, Huxley and Martin ; *Chlamydomonas*, Cienkowski) ; *Carteria*, Diesing ; *Spondylomorum*, Ehr. ; *Coccomonas*, Stein ; *Phacotus*, Perty.

Fam. 5. Volvocina. Colony-building Phytomastigoda, the cell-individuals standing in structure between Chlamydomonas and Hæmatococcus, and always biflagellate. The number of individuals united to form a colony varies very much, as does the shape of the colony. Reproduction by the continuous division of all or of only certain individuals of the colony, resulting in the production of a daughter colony (from each such individual). In some, probably in all, at certain times copulation of the individuals of distinct sexual colonies takes place, without or with a differentiation of the colonies and of the copulating cells as male and female. The result of the copulation is a resting zygospore (also called zygote or oo-spermospore or fertilized egg-cell), which after a time develops itself into one or more new colonies.

Genera.—*Gonium*, O. F. Muller (Fig. XX. 14) ; *Stephanosphæra*, Cohn ; *Pandorina*, Bory de Vinc. ; *Eudorina*, Ehr. ; *Volvox*, Ehr. (Fig. XX. 18, 20).

[The sexual reproduction of the colonies of the Volvocina is one of the most important phenomena presented by the Protozoa. In some families of Flagellata full-grown individuals become amœboid, fuse, encyst, and then break up into flagellate spores which develop simply to the parental form (Fig. XX. 23 to 26). In the Chlamydomonadina a single adult individual by division produces small individuals, so-called "microgonidia." These copulate with one another or with similar microgonidia formed by other adults (as in Chlorogonium, Fig. XX. 7); or more rarely in certain genera a microgonidium copulates with an ordinary individual (macrogonidium). The result in either case is a "zygote," a cell formed by fusion of two which divides in the usual way to produce new individuals. The microgonidium in this case is the male element and equivalent to a spermatozoon; the macrogonidium is the female and equivalent to an egg-cell. The zygote is a fertilized egg-cell, or oo-spermospore. In the colony-building forms we find that only certain cells produce by division microgonidia; and, regarding the colony as a multicellular individual, we may consider these cells as testis-cells and their microgonidia as spermatozoa. In some colony-building forms the microgonidia copulate with ordinary cells of the colony which, when thus fertilized, become encysted as zygotes, and subsequently separate and develop by division into new colonies. In Volvox the macrogonidia are also specially-formed cells (not merely any of the ordinary vegetative cells), so that in a sexually ripe colony we can distinguish egg-cells as well as sperm mother-cells. Not only so, but in some instances (Eudorina and some species of Volvox) the colonies which produce sexual cells can not merely be distinguished from the asexual colonies (which reproduce parthenogenetically), but can be distinguished also *inter se* into male colonies, which produce from certain of their constituent cell-units spermatozoa or microgonidia only, and female colonies which produce no male cells, but only macrogonidia or egg-cells which are destined to be fertilized by the microgonidia or spermatozoa of the male colonies.

The differentiation of the cell-units of the colony into neutral or merely carrying cells of the general body on the one hand and special sexual cells on the other is extremely important. It places these cell-colonies on a level with the Enterozoa (Metazoa) in regard to reproduction, and it cannot be doubted that the same process of specialization of the reproductive function, at first common to all the cells of the cell-complex, has gone on in both cases. The perishable body which carries the reproductive cells is nevertheless essentially different in the two cases, in the Volvocina being composed of equipollent units, in the Enterozoa being composed of units distributed in two physiologically and morphologically distinct layers or tissues, the ectoderm and the endoderm.

The sexual reproduction of the Vorticellidæ may be instructively compared with that of the Phytomastigoda; see below.]

Fam. 6. TETRAMITINA. Symmetrical, naked, colourless, somewhat amœboid forms, with four flagella or three and an undulating membrane. Nutrition animal, but mouth rarely seen.

Genera.—*Collodictyon*, Carter; *Tetramitus*, Perty (Fig. XXI. 11, 14; calycine monad of Dallinger and Drysdale (66)); *Monocercomonas*, Grassi; *Trichomonas*, Donné; *Trichomastix*, Blochmann.

Fam. 7. POLYMASTIGINA. Small, colourless, symmetrical forms. Two flagella at the hinder end of the body and two or three on each side in front. Nutrition animal or saprophytic.

Genera.—*Hexamitus*, Duj. (Fig. XXI. 5); *Megastoma*, Grassi; *Polymastix*, Bütschli.

Fam. 8. TREPOMONADINA, Kent. As Polymastigina, but the lateral anterior flagella are placed far back on the sides.

Genera.—*Trepomonas*, Duj., described recently without name by Dallinger (67).

Fam. 9. CRYPTOMONADINA. Coloured or colourless, laterally compressed, asymmetrical forms; with two very long anterior flagella, placed a little on one side springing from a deep atrium-like groove or furrow (*cf.* Dinoflagellata and Noctiluca, to which these forms lead).

Genera.—*Cyathomonas*, From.; *Chilomonas*, Ehr.; *Cryptomonas*, Ehr.; *Oxyrrhis*, Duj.

Fam. 10. LOPHOMONADINA. A tuft of numerous flagella anteriorly.

Genus.—*Lophomonas*, Stein (Fig. XXI. 9, connects the Flagellata with the Peritrichous Ciliata).

Sub-class II. **Choanoflagellata**, Saville Kent.

Flagellata provided with an upstanding collar surrounding the anterior pole of the cell from which the single flagellum springs, identical in essential structure with the "collared cells" of Sponges. Single or colony-building. Individuals naked (*Codosiga*), or inhabiting each a cup (*Salpingœca*), or embedded in a gelatinous common investment (*Proterospongia*).

ORDER 1. NUDA, Lankester.

Characters.—Individuals naked, secreting neither a lorica (cup) nor a gelatinous envelope.

Genera.—*Monosiga*, S. Kent (solitary stalked or sessile); *Codosiga*, James Clark (united socially on a common stalk or pedicle, Fig. XXI. 3, 4); *Astrosiga*, S. Kent; *Desmarella*, S. Kent.

ORDER 2. LORICATA, Lankester.

Characters.—Each individual collared-cell unit secretes a horny cup or shell.

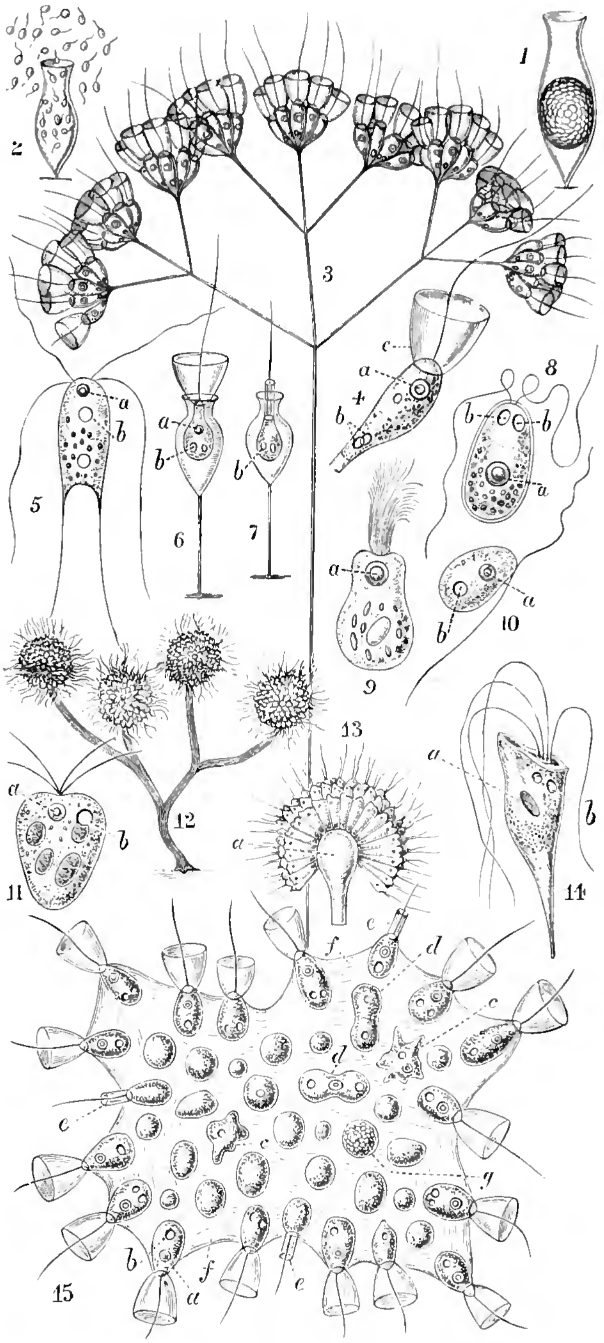

FIG. XXI.—**Flagellata.** 1. *Salpingœca fusiformis*, S. Kent; one of the Choanoflagellata. The protoplasmic body is drawn together within the goblet-shaped shell, and divided into numerous spores. × 1500. 2. Escape of the spores of the same as monoflagellate and swarm-spores. 3. *Codosiga umbellata*, Tatem; one of the Choanoflagellata; adult colony formed by dichotomous growth; × 625. 4. A single zooid of the same; × 1250. *a*, nucleus; *b*, contractile vacuole; *c*, the characteristic "collar" formed by cuticle on the inner face of which is a most delicate network of naked streaming protoplasm. 5. *Hexamita inflata*, Duj.; one of the Isomastigoda; × 650; normal adult; showing *a*, nucleus, and *b*, contractile vacuole. 6, 7. *Salpingœca urceolata*, S. Kent; one of the Choanoflagellata;—6, with collar extended; 7, with collar retracted within the stalked cup. *a*, nucleus; *b*, contractile vacuole. 8. *Polytoma uvella*, Mull. sp.; one of the Phytomastigoda. *a*, nucleus; *b*, contractile vacuole. × 800. 9. *Lophomonas blattarum*, Stein; one of the Isomastigoda, from the intestine of *Blatta orientalis*. *a*, nucleus. 10. *Bodo lens*, Mull.; one of the Heteromastigoda; × 800. *a*, nucleus; *b*, contractile vacuole; the wavy filament is a flagellum, the straight one is an immobile trailing thread. 11. *Tetramitus sulcatus*, Stein; one of the Isomastigoda; × 430. *a*, nucleus; *b*, contractile vacuole. 12. *Anthophysa vegetans*, O. F. Muller; one of the Monadidea; × 300. A typical, erect, shortly-branching colony stock with four terminal monad-clusters. 13. Monad cluster of the same in optical section (× 800), showing the relation of the individual monads or flagellate zooids to the stem *a*. 14. *Tetramitus rostratus*, Perty; one of the Isomastigoda; × 1000. *a*, nucleus; *b*, contractile vacuole. 15. *Proterospongia Haeckeli*, Saville Kent; one of the Choanoflagellata; × 800. A social colony of about forty flagellate zooids. *a*, nucleus; *b*, contractile vacuole; *c*, amœiform zooid sunk within the common jelly or test (compared by S. Kent to the mesoderm-cells of a sponge-colony); *d*, similar zooid multiplying by transverse fission; *e*, normal zooids with their collars contracted; *f*, hyaline mucilaginous common test or zoothecium; *g*, individual contracted and dividing into minute flagellate spores (microgonidia) comparable to the spermatozoa of a Sponge.

Genera.—*Salpingœca*, James Clark (sedentary, Fig. XXI. 6, 7); *Lagenœca*, S. Kent (free swimming); *Polyœca*, S. Kent (cups united socially to form a branching zoœcium as in Dinobryon).

ORDER 3. GELATINIGERA, Lankester.

The cell-units secrete a copious gelatinous investment and form large colonies.

Genera.—*Phalansterium*, Cienk. (Fig. XX. 12); *Proterospongia*, Saville Kent (Fig. XXI. 15).

[The Choanoflagellata were practically discovered by the American naturalist James Clark (68), who also discovered that the ciliated chambers of Sponges are lined by collared cells of the same peculiar structure as the individual Choanoflagellata, and hence was led to regard the Sponges as colonies of Choanoflagellata. Saville Kent (69) has added much to our knowledge of the group, and by his discovery of Proterospongia (see Fig. XXI. 15, and description) has rendered the derivation of the Sponges from the Flagellata a tenable hypothesis.]

Further remarks on the Flagellata.—Increased attention has been directed of late years to the Flagellata in consequence of the researches of Cienkowski, Bütschli, James Clark, Saville Kent, and Stein. They present a very wide range of structure, from the simple amœboid forms to the elaborate colonies of Volvox and Proterospongia. By some they are regarded as the parent-group of the whole of the Protozoa; but, whilst not conceding to them this position, but removing to the Proteomyxa those Flagellata which would justify such a view, we hold it probable that they are the ancestral group of the mouth-bearing Corticata, and that the Ciliata and Dinoflagellata have been derived from them. One general topic of importance in relation to them may be touched on here, and that is the nature of the flagellum and its movements. Speaking roughly, a flagellum may be said to be an isolated filament of vibratile protoplasm, whilst a cilium is one of many associated filaments of the kind. The movement, however, of a flagellum is not the same as that of any cilium; and the movement of all flagella is not identical. A cilium is simply bent and straightened alternately, its substance probably containing, side by side, a contractile and an elastic fibril. A flagellum exhibits lashing movements to and fro, and is thrown into serpentine waves during these movements. But two totally distinct kinds of flagella are to be distinguished, viz., (*a*) the pulsellum, and (*b*) the tractellum. An example of the pulsellum is seen in the tail of a spermatozoon which drives the body in front of it, as does the tadpole's tail. Such a "pulsellum" is the cause of the movement of the Bacteria. It is never found in the Flagellata. So little attention has been paid to this fact that affinities are declared by recent writers to exist between Bacteria and Flagellata. The flagellum of the Flagellata is totally distinct from the pulsellum of the Bacteria. It is carried in front of the body and draws the body after it, being used as a man uses his arm and hand when swimming on his side. Hence it may be distinguished as a "tractellum." Its action may be best studied in some of the large Euglenoidea, such as Astasia. Here it is stiff at the base and is carried rigidly in front of the animal, but its terminal third is reflected and exhibits in this reflected condition swinging and undulatory movements tending to propel the reflected part of the flagellum forward, and so exerting a traction in that direction upon the whole animal. It is in this way (by reflexion of its extremity) that the flagellum or tractellum of the Flagellata also acts so as to impel food-particles against the base of the flagellum where the oral aperture is situated.

Many of the Flagellata are parasitic (some hæmatozoic, see Lewis, 70); the majority live in the midst of putrefying organic matter in sea and fresh waters, but are not known to be active as agents of putrefaction. Dallinger and Drysdale have shown that the spores of Bodo and others will survive an exposure to a higher temperature than do any known Schizomycetes (Bacteria), viz., 250° to 300° Fahr., for ten minutes, although the adults are killed at 180°.

CLASS III. DINOFLAGELLATA, Bütschli.

Characters.—Corticate Protozoa of a bilaterally asymmetrical form, sometimes flattened from back to ventral surface (Diplopsalis, Glenodinium), sometimes from the front to the hinder region (Ceratium, Peridinium), sometimes from right to left (Dinophysis, Amphidinium, Prorocentrum)—the anterior region and ventral surface being determined by the presence of a longitudinal groove and a large flagellum projecting from it. In all except the genus Prorocentrum (Fig. XXII. 6) there is as well as a longitudinal groove a transverse groove (hence Dinifera) in which lies horizontally a second flagellum (Klebs and Bütschli), hitherto mistaken for a girdle of cilia. The transverse groove lies either at the anterior end of the body (Dinophysis, Fig. XXII. 3, 4; Amphidinium) or at the middle. In Gymnodinium it takes a spiral course. In Polykrikos (a compound metameric form) there are eight independent transverse grooves.

The Dinoflagellata are either enclosed in a cuticular shell (Ceratium, Peridinium, Dinophysis, Diplopsalis, Glenodinium, Prorocentrum, &c.) or are naked (Gymnodinium and Polykrikos). The cuticular membrane (or shell) consists of cellulose or of a similar substance (*cf.* Labyrinthulidea) and not, as has been supposed, of silica, nor of chitin-like substance; it is either a simple cyst or perforated by pores, and may be built up of separate plates (Fig. XXII. 10).

The cortical protoplasm contains trichocysts in Polykrikos.

The medullary protoplasm contains often chlorophyll and also diatomin and starch or other amyloid substance. In these cases (Ceratium, some species of Peridinium, Glenodinium, Prorocentrum, *Dinophysis acuta*) nutrition appears to be holophytic. But in others (Gymnodinium and Polykrikos) these substances are absent and food-particles are found in the medullary protoplasm which have been taken in from the exterior through a mouth; in these nutrition is holozoic. In others which are devoid of chlorophyll and diatomin, &c., there is found a vesicle and an orifice connected with the exterior near the base of the flagellum (*cf.* Flagellata) by which water and dissolved or minutely granular food-matter is introduced into the medullary protoplasm (*Protoperidinium pellucidum, Peridinium divergens, Diplopsalis lenticula, Dinophysis lævis*). It is important to note that these divergent methods of nutrition are exhibited by different species of one and the same genus, and possibly by individuals of one species in successive phases of growth (?).

No contractile vacuole has been observed in Dinoflagellata.

The nucleus is usually single and very large, and has a peculiar labyrinthine arrangement of chromatin substance.

Transverse binary fission is the only reproductive process as yet ascertained. It occurs either in the free condition (Fig. XXII. 2) or in peculiar horned cysts (Fig. XXII. 8). Conjugation has been observed in some cases (by Stein in Gymnodinium).

Mostly marine, some freshwater. Many are phosphorescent.

The Dinoflagellata are divisible into two orders, according to the presence or absence of the transverse groove.

ORDER 1. ADINIDA, Bergh.

Characters.—Body compressed laterally; both longitudinal and transverse flagellum placed at the anterior pole; a transverse groove is wanting; a cuticular shell is present.

Genera.—*Prorocentrum*, Ehr. (Fig. XXII. 6, 7); *Exuviella*, Cienk. (=*Dinopyxis*, Stein; *Cryptomonas*, Ehr.).

ORDER 2. DINIFERA, Bergh.

Characters.—A transverse groove is present and usually a longitudinal groove. The animals are either naked or loricate.

Fam. 1. DINOPHYIDA, Bergh. Body compressed; the transverse groove at the anterior pole; the longitudinal groove present; longitudinal flagellum directed backwards; loricate.

Genera.—*Dinophysis*, Ehr. (Fig. XXII. 3, 4); *Amphidinium*, Cl. & L.; *Amphisolenia*, Stein; *Histioneis*, Stein; *Citharistes*, Stein; *Ornithocercus*, Stein.

Fam. 2. PERIDINIDA, Bergh. Body either globular or flattened; transverse groove nearly equatorial; longitudinal groove narrow or broad; loricate.

Genera.—*Protoperidinium*, Bergh; *Peridinium* (Ehr.), Stein (Fig. XXII. 1, 2); *Protoceratium*, Bergh; *Ceratium*, Schrank (Fig. XXII. 15); *Diplopsalis*, Bergh; *Glenodinium*, Ehr.; *Heterocapsa*, Stein; *Gonyaulax*, Diesing; *Goniodoma*, Stein; *Blepharocysta*, Ehr.; *Podolampas*, Stein; *Amphidoma*, Stein; *Oxytoxum*, Stein; *Ptychodiscus*, Stein; *Pyrophacus*, Stein; *Ceratocorys*, Stein.

Fam. 3. GYMNODINIDA, Bergh. As Peridinida but no lorica (cuticular shell).

Genera.—*Gymnodinium* (Fig. XXII. 5), Stein; *Hemidinium*, Bergh.

Fam. 4. POLYDINIDA, Bütschli. As Gymnodinida, but with several independent transverse grooves.

Genus.—*Polykrikos*, Bütschli.

Further Remarks on the Dinoflagellata.—This small group is at the moment of the printing of the present article receiving a large amount of attention from Bergh (81), Klebs (83), and Bütschli (82), and has recently been greatly extended by the discoveries of Stein (80),—the last work of the great illustrator of the Ciliate Protozoa before his death. The constitution of the cell-wall or cuticle from cellulose, as well as the presence of chlorophyll and diatomin, and the holophytic nutrition of many forms recently demonstrated by Bergh, has led to the suggestion that the Dinoflagellata are to be regarded as plants, and allied to the Diatomaceæ and Desmidiaceæ. Physiological grounds of this kind have, however, as has been pointed out above, little importance in determining the affinities of Protozoa. Bütschli (82) in a recent very important article has shown in confirmation of Klebs that the Dinoflagellata do not possess a girdle of cilia as previously supposed, but that the structure mistaken for cilia is a second flagellum which lies horizontally in the transverse groove. Hence the name Cilioflagellata is superseded by Dinoflagellata (Gr. dinos, the round area where oxen tread out on a threshing floor).

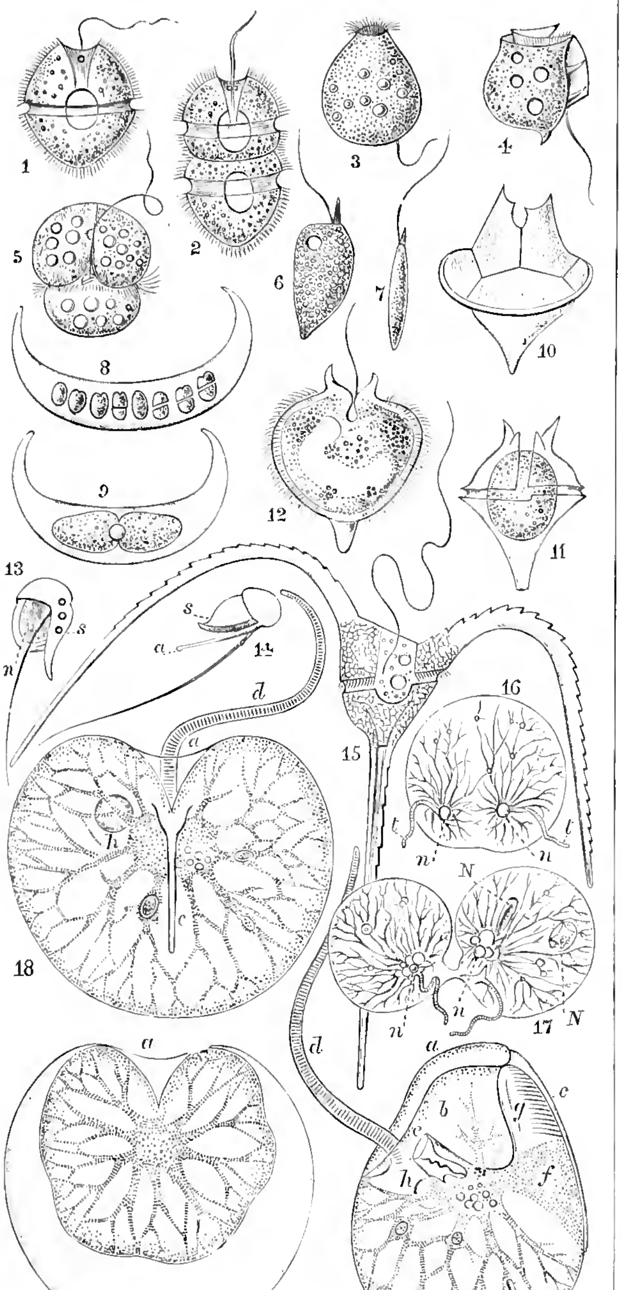

FIG. XXII.—**Dinoflagellata and Rhynchoflagellata.** *N.B.* In all these figures the apparent girdle of cilia is, accodring to Klebs and Bütschli's recent discovery, to be interpreted as an encircling flagellum lying in the transverse groove. 1. *Peridinium uberrimum*, Allman; × 300 (fresh-water ponds, Dublin). Probably (according to Butschli) the processes on the surface are not cilia nor flagellum. Both the longitudinal and the transverse groove are well seen. 2. The same species in transverse fission. 3. *Dinophysis ovata*, Cl. and L; × 350 (salt water, Norwegian coast). 4. *Dinophysis acuminata*, Cl. and L.; ×350 (salt water, Norwegian coast). 5. *Gymnodinium*, sp.; ×600. 6. *Prorocentrum micans*, Ehr.; ×300 (salt water). 7. Dorsal aspect of the same species. 8, 9. Cysts of Peridinia; the contents of 8 divided into eight minute naked Peridinia; ×300. 10. Empty cuirass of *Ceratium divergens.* Cl. and L.; ×500; showing the form and disposition of its component plates. 11. The same species with the animal contracted into a spherical form. The transverse groove well seen. 12. The same species in the normal state. The apparent girdle of cilia is really an undulating flagellum lying in the transverse groove. 13, 14. Young stages of *Noctiluca miliaris.* *n*, nucleus; *s*, the so-called spine (superficial ridge of the adult); *a*, the big flagellum; the unlettered filament is a flagellum which becomes the oral flagellum of the adult. 15. *Ceratium tripos*, Müll. The transverse groove well seen. The cilia really are a single horizontal flagellum. 16, 17. Two stages in the transverse fission of *Noctiluca miliaris*, Suriray. *n*, nucleus; N, food-particles; *t*, the muscular flagellum. 18. *Noctiluca miliaris*, viewed from the aboral side (after Allman, *Quart. Jour. Mic. Sci.*, 1872). *a*, the entrance to the atrium or flagellar fossa (=longitudinal groove of Dinoflagellata); *c*, the superficial ridge; *d*, the big flagellum (=the flagellum of the transverse groove of Dinoflagellata); *h*, the nucleus. 19. The animal acted upon by iodine solution, showing the protoplasm like the "primordial utricle" of a vegetable cell shrunk away from the structureless firm shell or cuirass. 20. Lateral view of Noctiluca, showing *a*, the entrance to the groove-like atrium or flagellar fossa in which *b* is placed; *c*, the superficial ridge; *d*, the big flagellum; *e*, the mouth and gullet, in which is seen Krohn's oral flagellum (=the chief flagellum or flagellum of the longitudinal groove of Dino-flagellata); *f*, broad process of protoplasm extending from the superficial ridge *c* to the central protoplasm; *g*, duplicature of the shell in connexion with the superficial ridge; *h*, nucleus.

Bütschli further suggests that the Dinoflagellata with their two flagella and their ⊥-shaped combination of longitudinal and transverse grooves may be derived from the Cryptomonadina (see p. 858). In the latter a groove-like recess is present in connexion with the origin of the two flagella. Bütschli thinks the large proboscis-like flagellum of Noctiluca (Rhynchoflagellata) represents the horizontal flagellum of the Dinoflagellata, whilst the prominent longitudinal flagellum of the Dinoflagellata is represented in that animal by the small flagellum discovered by Krohn within the gullet (see Fig. XXII. 20, *c*). The young form of Noctiluca (Fig. XXII. 14) has the longitudinal flagellum still of large size.

The phosphorescence of many Dinoflagellata is a further point of resemblance between them and Noctiluca.

Bergh has shown that there is a considerable range of form in various species of Dinoflagellata (Ceratium, &c.), and has also drawn attention to the curious fact that the mode of nutrition (whether holophytic or holozoic) differs in allied species. Possibly it may be found to differ according to the conditions of life in individuals of one and the same species.

The drawings in Fig. XXII. were engraved before the publication of Bütschli's confirmation of Klebs's discovery as to the non-existence of cilia in the transverse groove. The hair-like processes figured by Allman (91) external to the transverse groove in his *Peridinium uberrimum* (Fig. XXII. 1, 2) cannot, however, be explained as a flagellum. Bütschli inclines to the opinion that their nature was misinterpreted by Allman, although the latter especially calls attention to them as cilia, and as rendering his *P. uberrimum* unlike the Peridinium of Ehrenberg, in which the cilia (horizontal flagellum) are confined to the transverse groove.

N.B.—See Fig. XXVII., and explanation, p. 37.

CLASS IV. RHYNCHOFLAGELLATA, Lankester.

Characters.—Corticate Protozoa of large size ($\frac{1}{50}$th inch) and globular or lenticular form, with a firm cuticular membrane and highly vacuolated (reticular) protoplasm. In Noctiluca a deep groove is formed on one side of the spherical body, from the bottom of which springs the thick transversely striated proboscis or "big flagellum." Near this is the oral aperture and a cylindrical pharynx in which is placed the second or smaller flagellum (corresponding to the longitudinal flagellum of Dinoflagellata).

Nutrition is holozoic. No contractile vacuole is present; granule-streaming is observed in the protoplasm. An alimentary tract and anus have been erroneously described. The nucleus is spherical and not proportionately large (see for details Fig. XXII. 18 to 20).

Reproduction by transverse fission occurs, also conjugation and, either subsequently to that process or independently of it, a formation of spores (Cienkowski, 87), the protoplasm gathering itself, within the shell-like cuticular membrane, into a cake which divides rapidly into numerous flagellated spores (flagellulæ). These escape and gradually develop into the adult form (Fig. XXII. 13, 14).

The proboscis-like large flagellum is transversely striated, and exhibits energetic but not very rapid lashing movements.

Noctiluca is phosphorescent, the seat of phosphorescence being, as determined by Allman (86), the cortical layer of protoplasm underlying the cuticular shell or cell-wall as the primordial cuticle of a vacuolated vegetable cell underlies the vegetable cell-wall.

Genera.—Only two genera (both marine) are known:—*Noctiluca*, Suriray (90) (Fig. XXII. 17-20); *Leptodiscus*, Hertwig (88).

Further Remarks on the Rhynchoflagellata.—The peculiar and characteristic feature of Noctiluca appears to be found in its large transversely-striated flagellum, which, according to Butschli, is not the same as the longitudinal flagellum of the Dinoflagellata, but probably represents the horizontal flagellum of those organisms in a modified condition; hence the name here proposed—Rhynchoflagellata.

Noctiluca is further remarkable for its large size and cyst-like form, and the reticular arrangement of its protoplasm, like that of a vegetable cell. This is paralleled in *Trachelius ovum* among the Ciliata (Fig. XXIV. 14), where the same stiffening of the cuticle allows the vacuolation of the subjacent protoplasm to take place. The remarkable *Leptodiscus medusoides* of R. Hertwig (88) appears to be closely related to Noctiluca.

It would no doubt be not unreasonable to associate the Dinoflagellata and the Rhynchoflagellata with the true Flagellata in one class. But the peculiarities of the organization of the two former groups is best emphasized by treating them as separate classes derived from the Flagellata. Neither group leads on to the Ciliata or to any other group, but they must be regarded as forming a lateral branch of the family tree of Corticata. The relationship of Noctiluca to Peridinium was first insisted upon by Allman, but has quite recently been put in a new light by Bütschli, who identifies the atrial recess of Noctiluca (Fig. XXII. 20, *b*) with the longitudinal furrow or groove of the Dinoflagellata, and the large and minute flagella of the former with the transverse and longitudinal flagella respectively of the latter. The superficial ridge *c* of Noctiluca appears to represent the continuation of the longitudinal groove.

The phosphorescence of the sea, especially on northern coasts, is largely caused by Noctiluca, but by no means exclusively, since Medusæ, Crustaceans, Annelids, and various Protozoa often take part in the phenomenon. Not unfrequently, however, the phosphorescence on the British coasts seems to be solely due to Noctiluca, which then occurs in millions in the littoral waters.

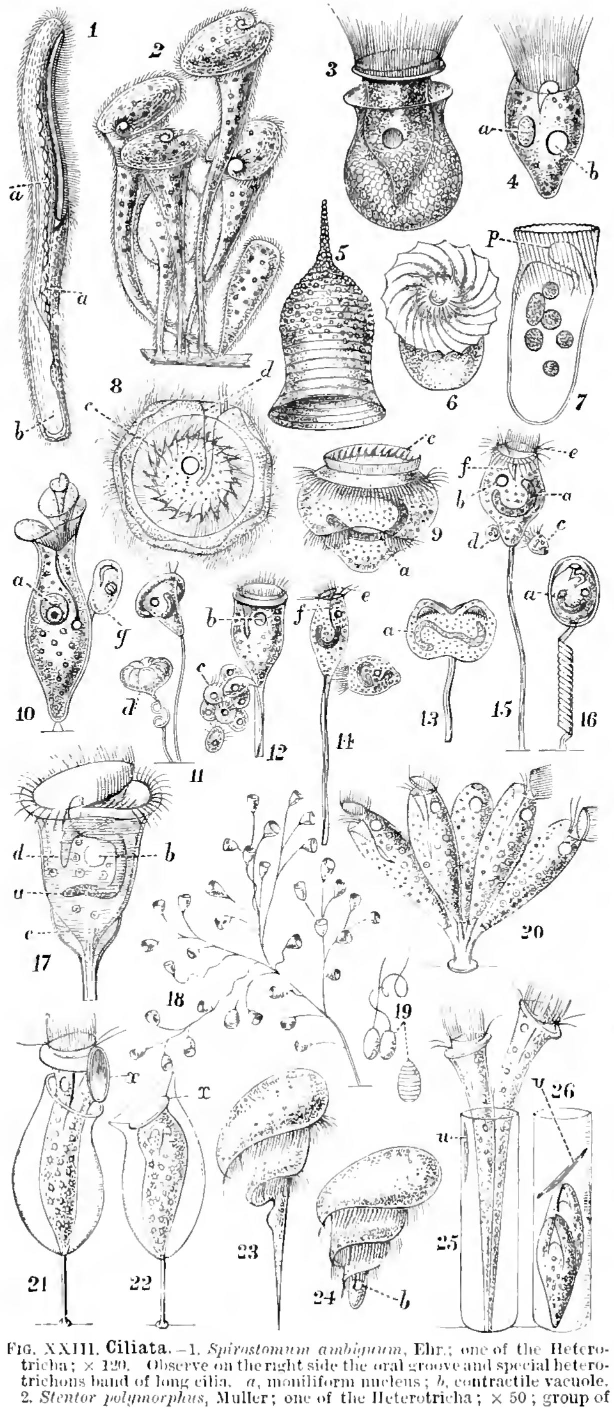

FIG. XXIII. **Ciliata.**—1. *Spirostomum ambiguum*, Ehr.; one of the Heterotricha; × 120. Observe on the right side the oral groove and special heterotrichous band of long cilia. *a*, moniliform nucleus; *b*, contractile vacuole. 2. *Stentor polymorphus*, Muller; one of the Heterotricha; × 50; group of individuals with the area fringed by the heterotrichous cilia expanded trumpet-wise. 3. *Tintinnus lagenula*, C. and L.; one of the Heterotricha; × 300. 4. *Strombidium Claparedii*, S. K.; one of the Peritricha; × 200. 5. Empty shell of *Codonella campanella*, Haeck.; one of the Heterotricha; × 180. 6, 7. *Torquatella typica*, Lankester. *p*, the supra-oral lobe seen through the membranous collar. 8, 9. View of the base and of the side of *Trichodina pediculus*, Ehr.; one of the Peritricha; × 300. *a*, nucleus; *c*, corneous collar; *d*, mouth. 10. *Spirochona gemmipara*, Stein; one of the Peritricha; × 350. *a*, nucleus; *g*, bud. 11. *Vorticella citrina*, Ehr.; × 150 (Peritricha). At *d* multiple fission of an individual cell to form "microgonidia." 12. *Vorticella microstoma*, Ehr. (Peritricha); × 300. At *e* eight "microgonidia" formed by fission of a single normal individual. 13. Same species, binary fission. *a*, elongated nucleus. 14. *Vorticella nebulifera*, Ehr.; free-swimming zooid resulting from fission in the act of detaching itself and swimming away, possessing a posterior circlet of cilia. *e*, ciliated disk; *f*, pharynx. 15. *Vorticella microstoma*, Ehr.; normal zooid with two microgonidia (or microzooids) *c*,*d*, in the act of conjugation. *a*, nucleus; *b*, contractile vacuole; *e*, ciliated disk; *f*, pharynx. 16. *Vorticella microstoma*, Ehr., with stalk contracted and body enclosed in a cyst. *a*, nucleus. 17. *Vorticella nebulifera*, Ehr. *a*, nucleus; *b*, contractile vacuole; *c*, muscular region of the body continuous with the muscle of the stalk; *d*, pharynx (the basal continuation of the oral vestibule which receives at a higher point the fœcal excreta and the ejected liquid from the contractile vacuole). 18. *Carchesium spectabile*, Ehr.; retractile colony; × 50. 19 Trichocysts of *Epistylis flavicans*, Ehr., as figured by Greeff. 20. *Opercularia stenostoma*, Stein; × 200; a small colony. Observe the ciliation of the oral vestibule and the upstanding ciliate disk (opercular-like). 21, 22. *Pyxicola affinis*, S. K.; one of the stalked loricate Peritricha, in expanded and retracted states. *x*, the true operculum. 23, 24. *Gyrocoris oxyura*, Stein; one of the free-swimming Peritricha, with spiral equatorial cilia-band; × 250. *b*, contractile vacuole. 25, 26. *Thuricola valvata*, Str. Wright; one of the sessile tubicolous Peritricha. Two individuals are as a result of fission temporarily occupying one tube; *u*, the valve attached to the tube, like the door of the trap-door spider's nest and the valve of the Gasteropod Clausilium.

CLASS V. **CILIATA**, Ehrenberg (*Infusoria* sensu stricto).

Characters.—Corticata of relatively large size, provided with either a single band of cilia surrounding the anteriorly placed oral aperture or with cilia disposed more numerously over the whole surface of the body. The cilia are distinguished from the flagella of Flagellata by their smaller size and simple movements of alternate flexion and erection; they serve always at some period of growth as locomotor organs, and also very usually as organs for the introduction of food particles into the mouth. Besides one larger oblong nucleus a second (the paranucleus) is invariably (?) present (Fig. XXV. 2), or the nucleus may be dispersed in small fragments. Conjugation of equal-sized individuals, not resulting in permanent fusion, is frequent. The conjugated animals separate and their nuclei and paranuclei undergo peculiar changes; but no formation of spores, either at this or other periods, has been decisively observed (Fig. XXV. 8 to 15). Multiplication by transverse fission is invariably observed in full-grown individuals (Fig. XXV. 16), and conjugation appears to take place merely as an interlude in the fissiparous process; consequently young or small Ciliata are (with few exceptions) unknown. Possibly spore-formation may hereafter be found to occur at rare intervals more generally than is at present supposed (Fig. XXIV. 15, 18). A production of microgonidia by rapid fission occurs in some Peritricha (Fig. XXIII. 11, 12, 14, 15), the liberated microgonidia conjugating with the normal individuals, which also can conjugate with one another.

The Ciliata, with rare exceptions (parasites), possess one or more contractile vacuoles (Fig. XXV. 3). They always possess a delicate cuticle and a body-wall which, although constant, in form is elastic. They may be naked and free-swimming, or they may form horny (Fig. XXIII. 21, 25) or siliceous cup-like shells or gelatinous envelopes, and may be stalked and form colonies like those of Choanoflagellata, sometimes with organic connexion of the constituent units of the colony by a branching muscular cord (Vorticellidæ). Many are parasitic in higher animals, and of these some are mouthless. All are holozoic in their nutrition, though some are said to combine with this saprophytic and holophytic nutrition.

The Ciliata are divisible into four orders according to the distribution and character of their cilia. The lowest group (the Peritricha) may possibly be connected through some of its members, such as Strombidium (Fig. XXIII. 4), with the Flagellata through such a form as Lophomonas (Fig. XXI. 9).

In the following synopsis, chiefly derived from Saville Kent's valuable treatise (**71**), the characters of the families and the names of genera are not given at length owing to the limitation of our space.

ORDER 1. PERITRICHA, Stein (**79**).

Characters.—Ciliata with the cilia arranged in one anterior circlet or in two, an anterior and a posterior; the general surface of the body is destitute of cilia.

Sub-order 1. NATANTIA (animals never attached).

Fam. 1. TORQUATELLIDÆ.

Genus.—*Torquatella*, Lankester, like *Strombidium*, but the cilia adherent so as to form a vibratile membranous collar (Fig. XXIII. 6, 7).

Fam. 2. DICTYOCYSTIDÆ. Animals loricate.

Fam. 3. ACTINOBOLIDÆ. Illoricate, with retractile tentacula.

Fam. 4. Halteriidæ.

Genera.—*Strombidium*, Cl. & L. (Fig. XXIII. 4); *Halteria*, Dujard., with a supplementary girdle of springing hairs; *Didinium*, Stein, (Fig. XXIV. 19).

Fam. 5. Gyrocoridæ.

Genera.—*Gyrocoris*, Stein, with an equatorial ciliary girdle spirally disposed (Fig. XXIII. 23, 24); *Urocentrum*, Nitzsch, girdle annular.

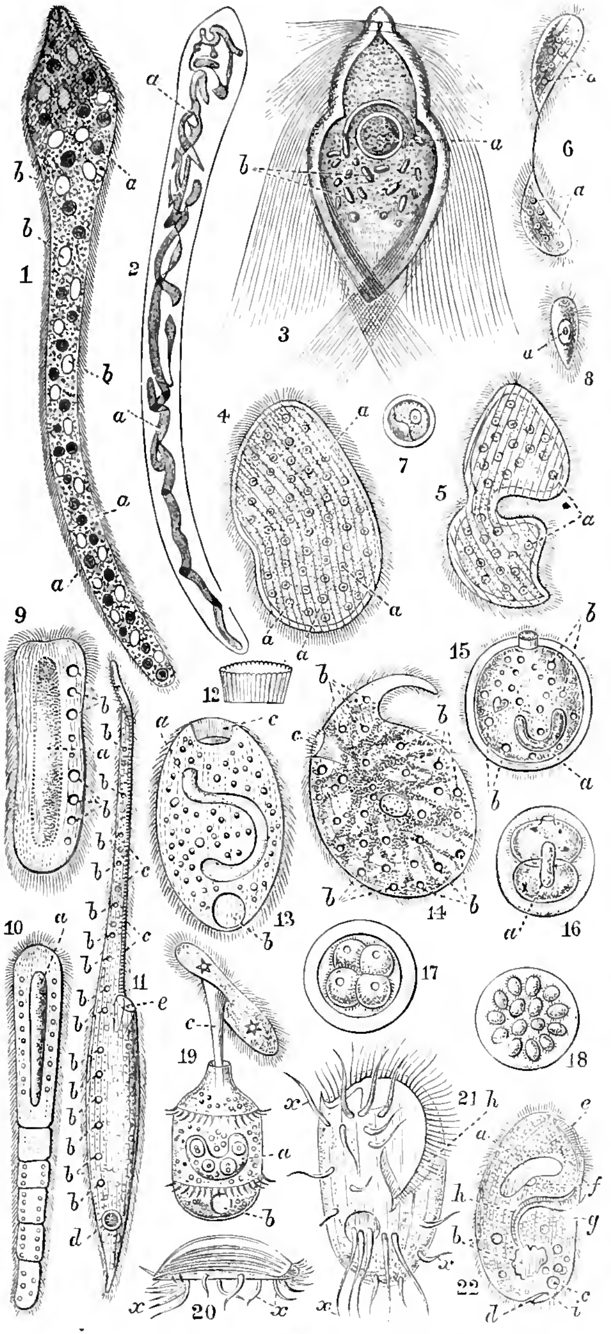

Fig. XXIV. **Ciliata**.—1. *Ophalinopsis sepiolæ*, Foett.; a parasitic Holotrichous mouthless Ciliate from the liver of the Squid. *a*, nuclei; *b*, vacuoles (non-contractile). 2. A similar specimen treated with picrocarmine, showing a remarkably branched and twisted nucleus; *a*, in place of several nuclei. 3. *Trichonympha agilis*, Leidy; parasitic in the intestine of the Termites (White Ants); × 600. *a*, nucleus; *b*, granules (food?). 4. *Opalina ranarum*, Purkinje; a Holotrichous mouthless Ciliate parasitic in the Frog's rectum; adult; × 100. *a*, *a*, the numerous regularly dispersed nuclei. 5. The same; an individual in process of binary fission. *a*, nuclei. 6. The same; the process of fission has now reduced the individuals to a relatively small size. 7. Smallest fission-produced fragment encysted, expelled from the Frog in this state and swallowed by Tadpoles. 8. Young uninucleate individual which has emerged from the cyst within the Tadpole, and will now multiply its nuclei and grow to full size before in turn undergoing retrogressive fission. 9. *Anoplophrya naidos*, Duj.; a mouthless Holotrichous Ciliate parasitic in the worm Nais; × 200. *a*, the large axial nucleus; *b*, contractile vacuoles. 10. *Anoplophrya prolifera*, C. and L.; from the intestine of Clitellio. Remarkable for the adhesion in a metameric series of incomplete fission-products. *a*, nucleus. 11. *Amphileptus gigas*, C. and L.; one of the Holotricha; × 100. *b*, contractile vacuoles; *c*, trichocysts (see Fig XXIII. 19); *d*, nucleus; *e*, pharynx. 12, 13. *Prorodon niveus*, Ehr.; one of the Holotricha; × 75. *a*, nucleus; *b*, contractile vacuole; *c*, pharynx with horny fascicular lining. 12. The fasciculate cuticle of the pharynx isolated. 14. *Trachelius ovum*, Ehr. (Holotricha); × 80; showing the reticulate arrangement of the medullary protoplasm. *b*, contractile vacuoles; *c*, the cuticle-lined pharynx. 15, 16, 17, 18. *Ichthyophthirius multifiliis*, Fouquet; one of the Holotricha; × 120. Free individual and successive stages of division to form spores. *a*, nucleus; *b*, contractile vacuoles. 19. *Didinium nasutum*, Müll.; one of the Peritricha; × 200. The pharynx is everted and has seized a Paramecium as food. *a*, nucleus; *b*, contractile vacuole; *c*, everted pharynx. 20. *Euplotes charon*, Müll.; one of the Hypotricha; lateral view of the animal when using its great hypotrichous processes, *x*, as ambulatory organs. 21. *Euplotes harpa*, Stein (Hypotricha); × 150. *h*, mouth; *x*, hypotrichous processes (limbs). 22. *Nyctotherus cordiformis*, Stein; a Heterotrichous Ciliate parasitic in the intestine of the Frog. *a*, nucleus; *b*, contractile vacuole; *c*, food particle; *d*, anus; *e*, heterotrichous band of large cilia; *f*, *g*, mouth; *h*, pharnyx; *i*, small cilia.

Fam. 6. Urceolariidæ.

Genera.—*Trichodina*, Ehr.; two ciliate girdles; body shaped as a pyramid with circular sucker-like base, on which is a toothed corneous ring (Fig. XXIII. 8, 9); *Licnophora*, Clap.; *Cyclochæta*, Hat. Jacks.

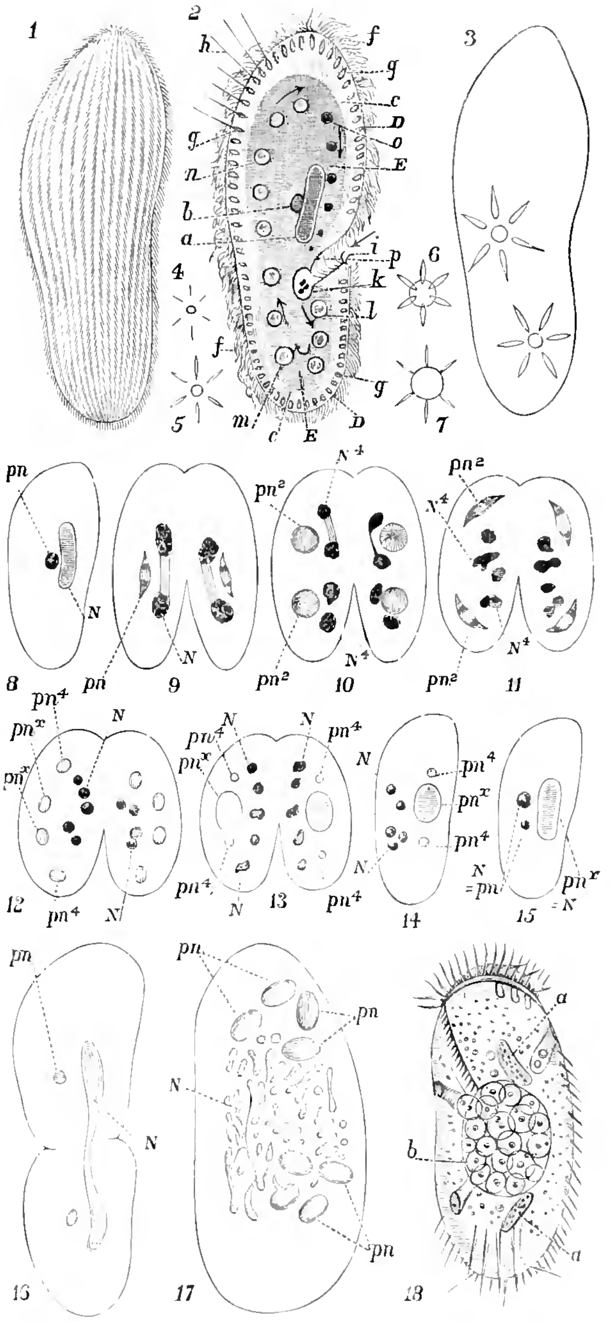

Fig. XXV. **Ciliata** (conjugation, &c.). 1. Surface view of Holotrichous Ciliate, showing the disposition of the cilia in longitudinal rows. 2.

Diagrammatic optical section of a Ciliate Protozoon, showing all structures except the contractile vacuoles. *a*, nucleus; *b*, paranucleus (so-called nucleolus); *c*, cortical substance; D, extremely delicate cuticle; E, medullary (more fluid) protoplasm; *f*, cilia; *g*, trichocysts; *h*, filaments ejected from the trichocysts; *i*, oral aperture; *k*, drop of water containing food-particles, about to sink into the medullary substance and form a food-vacuole; *l*, *m*, *n*, *o*, food-vacuoles, the successive order of their formation corresponding to the alphabetical sequence of the letters; the arrows indicate the direction of the movement of rotation of the medullary protoplasm; *p*, pharynx. 3. Outline of a Ciliate (Paramœcium), to show the form and position of the contractile vacuoles. 4-7. Successive stages in the periodic formation of the contractile vacuoles. The ray-like vacuoles discharge their contents into the central vacuole, which then itself bursts to the exterior. 8-15. Diagrams of the changes undergone by the nucleus and paranucleus of a typical Ciliate during and immediately after conjugation:—N, nucleus; *pn*, paranucleus; 8, condition before conjugation; 9, conjugation effected; both nucleus and paranucleus in each animal elongate and become fibrillated; 10, two spherical paranuclei pn^2 in each, two dividing or divided nuclei N^4; 11, the spherical paranuclei have become fusiform; 12, there are now four paranuclei in each (pn^4 and pn^x), and a nucleus broken into four or even more fragments; 13, the two paranuclei marked pn^x in 12 have united in each animal to form the new nucleus pn^x; the nuclear fragments are still numerous; 14, after cessation of conjugation the nuclear fragments N and the two unfused paranuclear pieces pm^4 are still present; 15, from a part or all of the fragments the new paranucleus is in process of formation, the new nucleus ($pn^x = N$) is large and elongated. 16. Diagram of a Ciliate in process of transverse fission. 17. Condition of the nucleus N, and of the paranucleus *pm* in *Paramœcium aurelia* after cessation of conjugation as observed by Bütschli. 18. *Stylonichia mytilus* (one of the Hypotricha), showing endoparasitic unicellular organisms *b*, formerly mistaken for spores; *a*, nuclei (after conjugation and breaking up).

Fam. 7. Ophryoscolecidæ.

Genera.—*Astylozoon*, Engelm.; *Ophryoscolex*, Stein.

Sub-order 2. Sedentaria, animals always attached or sedentary during the chief part of the life-history.

Fam. 1. Vorticellidæ. Animals ovate, campanulate, or subcylindrical; oral aperture terminal, eccentric, associated with a spiral fringe of adoral cilia, the right limb of which descends into the oral aperture, the left limb encircling a more or less elevated protrusible and retractile ciliary disk.

Sub-family 1. Vorticellinæ: animalcules naked.

α.—Solitary forms.

Genera.—*Gerda*, Cl. and L.; *Scyphidia*, Dujard.; *Spirochona*, Stein (sessile with peristome in the form of a spirally convolute membranous expansion, Fig. XXIII. 10); *Pyxidium*, Kent (with a non-retractile stalk); *Vorticella*, Linn. (with a hollow stalk in which is a contractile muscular filament).

β.—Forming dendriform colonies.

Genera.—*Carchesium*, Ehr. (Fig. XXIII. 18, with contractile stalks); *Zoothamnium*, Ehr. (contractile stalks); *Epistylis*, Ehr. (stalk rigid); *Opercularia*, Stein (stalk rigid, ciliated disk oblique; an elongated peristomial collar, Fig. XXIII. 20).

Sub-family 2. Vaginicolinæ: animalcules secreting firm cup-like or tube-like membranous shells.

Genera.—*Vaginicola*, Lamarck (no internal valve); *Thuricola*, Kent (with a door-like valve to the tube, Fig. XXIII. 25, 26); *Cothurina*, Ehr. (lorica or shell pediculate; no operculum); *Pyxicola*, Kent (lorica pedunculate, animal carrying dorsally a horny operculum, Fig. XXIII. 21, 22).

Sub-family 3. Ophrydina: animalcules secreting a soft gelatinous envelope.

Genera.—*Ophionella*, Kent; *Ophrydium*, Ehr.

Order 2. HETEROTRICHA, Stein.

Characters.—A band or spiral or circlet of long cilia is developed in relation to the mouth (the heterotrichous band) corresponding to the adoral circlet of Peritricha; the rest of the body is uniformly beset with short cilia.

α.—Heterotrichal band circular.

Genera (selected).—*Tintinnus*, Schranck (Fig. XXIII. 3); *Trichodinopsis*, Cl. and L.; *Codonella*, Haeck. (with a peri-oral fringe of lappet-like processes); *Calceolus*, Diesing.

β.—Heterotrichal band spiral.

Genera (selected).—*Stentor*, Oken (Fig. XXIII. 2); *Blepharisma*, Perty (with an undulating membrane along the oral groove); *Spirostomum*, Ehr. (oral groove linear and elongate, Fig. XXIII. 1); *Leucophrys*, Ehr. (oral groove very short).

γ.—Heterotrichal band in the form of a simple straight or oblique adoral fringe of long cilia.

Genera (selected).—*Bursaria*, Müller; *Nyctotherus*, Leidy (with well-developed alimentary tract and anus, Fig. XXIV. 22); *Balantidium*, Cl. and L. (*B. coli* parasitic in the human intestine).

Order 3. HOLOTRICHA, Stein.

Characters.—There is no special adoral fringe of larger cilia, nor a band-like arrangement of cilia upon any part of the body; short cilia of nearly equal size are uniformly disposed all over the surface. The adoral cilia sometimes a little longer than the rest.

α.—With no membraniform expansion of the body wall.

Genera.—*Paramœcium*, Ehr. (Fig. XXV. 1, 2); *Prorodon*, Ehr. (Fig. XXIV. 13); *Coleps*, Ehr.; *Enchelys*, Ehr.; *Trachelocerca*, Ehr.; *Trachelius*, Ehr.; *Amphileptus*, Ehr.; *Icthyophthirius*, Fouquet (Fig. XXIV. 15).

β.—Body with a projecting membrane, often vibratile.

Genera.—*Ophryoglena*, Ehr.; *Colpidium*, Stein; *Lembus*, Cohn; *Trichonympha*, Leidy (an exceptionally modified form, parasitic, Fig. XXIV. 3).

γ.—Isolated parasitic forms, devoid of a mouth.

Genera.—*Opalina*, Purkinje (nuclei numerous, no contractile vacuole, Fig. XXIV. 4 to 8); *Benedenia*, Foett.; *Opalinopsis*, Foett. (Fig. XXIV. 1, 2); *Anoplophrya*, Stein (large axial nucleus, numerous contractile vacuoles in two linear series, Fig. XXIV. 9 10); *Haptophrya*, Stein; *Hoplitophrya*, Stein.

Order 4. HYPOTRICHA, Stein.

Characters.—Ciliata in which the body is flattened and the locomotive cilia are confined to the ventral surface, and are often modified and enlarged to the condition of muscular appendages (setæ so-called). Usually an adoral band of cilia, like that of Heterotricha. Dorsal surface smooth or provided with tactile hairs only. Mouth and anus conspicuously developed.

α.—Cilia of the ventral surface uniform, fine, and vibratile.

Genera.—*Chilodon*, Ehr.; *Loxodes*, Ehr.; *Dysteria*, Huxl.; *Huxleya*, Cl. and L.

β.—Cilia of the ventral surface variously modified as setæ (muscular appendages), styles, or uncini.

Genera.—*Stylonichia*, Ehr. (Fig. XXV. 18); *Oxytricha*, Ehr.; *Euplotes*, Ehr. (Fig. XXIV. 20, 21).

Further remarks on the Ciliata.—The Ciliata have recently formed the subject of an exhaustive treatise by Mr Saville Kent (**71**) which is accessible to English readers. On the other hand Prof. Bütschli has not yet dealt with them in his admirable critical treatise on the Protozoa. Hence a large space has not been devoted in this article to the systematic classification and enumeration of their genera. See (**79**) and (**93**).

One of the most interesting features presented by the group is the presence in many of a cell anus as well as a cell mouth (Fig. XXIV. 22, *d*). In those devoid of an anus the undigested remnants of food are expelled either by a temporary aperture on the body-surface or by one opening into the base of the pharynx. In many parasitic Ciliata, as in higher animal parasites, such as the Cestoid worms, a mouth is dispensed with, nutriment being taken by general imbibition and not in the solid form. Many Ciliata develop chlorophyll corpuscles of definite biconcave shape, and presumably have so far a capacity for vegetal nutrition. In *Vorticella viridis* the chlorophyll is uniformly diffused in the protoplasm and is not in the form of corpuscles (**72**).

The formation of tubes or shells and in connexion therewith of colonies is common among the Peritricha and Heterotricha. The cuticle may give rise to structures of some solidity in the form of hooks or tooth-like processes, or as a lining to the pharynx (Fig. XXIV. 12).

The phenomena connected with conjugation and reproduction are very remarkable, and have given rise to numerous misconceptions. They are not yet sufficiently understood. It cannot be surely asserted that any Ciliate is at the present time known to break up, after encystment or otherwise, into a number of spores, although this was at one time supposed to be the rule. Icthyophthirius (Fig. XXIV. 15 to 18) and some Vorticellæ (**76**) have been stated, even recently, to present this phenomenon; but it is not impossible that the observations are defective. The only approach to a rapid breaking up into spores is the multiple formation (eight) of microgonidia or microzooids in Vorticellidæ (Fig. XXIII. 11, 12); otherwise the result of the most recent observations appears to be that the Ciliata multiply only by binary fission, which is very frequent among them (longitudinal in the Peritricha, transverse to the long axis in the others).

Several cases of supposed formation of spores within an adult Ciliate and of the production endogenously of numerous "acinetiform young" have been shown to be cases of parasitism, minute unicellular parasites, *e.g.*, parasitic Acinetæ (such as Sphaerophrya described and figured in Fig. XXVI.) being mistaken for the young.

The phenomenon of conjugation is frequent in the Ciliata, and is either temporary, followed by a separation of the fused individuals, as in most cases, or permanent, as in the case of the fertilization of normal individuals by the microgonidia of Vorticellidæ.

Since the process of conjugation or copulation is not followed by a formation of spores, it is supposed to have merely a fertilizing effect on the temporarily conjoined individuals, which nourish themselves and multiply by binary fission more actively after the process than before (hence termed "rejuvenescence)."

Remarkable changes have been from time to time observed in the nuclei of Ciliata during or subsequently to conjugation, and these were erroneously interpreted by Balbiani (**73**) as indicating the formation of spermatozoa and ova. The nuclei exhibit at one period great elongation and a distinct fibrillation, as in the dividing nuclei of tissue cells (compare Fig. I. and Fig. XXV. 9, 11, 17). The fibrillæ were supposed to be spermatozoids, and this erroneous view was confirmed by the observation of rod-like Bacteria (Schizomycetes) which in some instances infest the deeper protoplasm of large Ciliata.

The true history of the changes which occur in the nuclei of conjugating Ciliata has been determined by Bütschli (**74**) in some typical instances, but the matter is by no means completely understood. The phenomena present very great obstacles to satisfactory examination on account of their not recurring very frequently and passing very rapidly from one phase to another. They have not been closely observed in a sufficiently varied number of genera to warrant a secure generalization. The following scheme of the changes passed through by the nuclei must be regarded as necessarily referring to only a few of the larger Heterotricha, Holotricha, and Hypotricha, and is only probably true in so far as details are concerned, even for them. It is at the same time certain that some such series of changes occurs in all Ciliata as the sequence of conjugation.

In most of the Ciliata by the side of the large oblong nucleus is a second smaller body (or even two such bodies) which has been very objectionably termed the nucleolus (Fig. XXV. 8), but is better called the "paranucleus" since it has nothing to do with the nucleolus of a typical tissue-cell. When conjugation occurs and a "syzygium" is formed, both nucleus and paranucleus in each conjugated animal elongate and show fibrillar structure (Fig. XXV. 10). Each nucleus and paranucleus now divides into two, so that we get two nuclei and two paranuclei in each animal. Elongation and fibrillation are then exhibited by each of these new elements and subsequently fission, so that we get four nuclei and four paranuclei in each animal (11, 12). The fragments of the original nucleus (marked N in the figures) now become more dispersed and broken into further irregular fragments. Possibly some of them are ejected (so-called "cell excrement"); possibly some pass over from one animal to the other. Two of the pieces of the four-times-divided paranucleus now reunite (Fig. XXV. 13), and form a largish body which is the new nucleus. The remaining fragments of paranucleus and the broken down nucleus now gradually disappear, and probably as a remnant of them we get finally a few corpuscles which unite to form the new paranucleus (14, 15). The conjugated animals which have separated from one another before the later stages of this process are thus reconstituted as normal Ciliata, each with its nucleus and paranucleus. They take food and divide by binary fission until a new period of conjugation arrives, when the same history is supposed to recur.

The significance of the phenomena is entirely obscure. It is not known why there should be a paranucleus or what it may correspond to in other cells—whether it is to be regarded simply as a second nucleus or as a structurally and locally differentiated part of an ordinary cell-nucleus, the nucleus and the paranucleus together being the complete equivalent of such an ordinary nucleus. An attempt has been made to draw a parallel between this process and the essential features of the process of fertilization (fusion of the spermatic and ovicell nuclei) in higher animals; but it is the fact that concerning neither of the phenomena compared have we as yet sufficiently detailed knowledge to enable us to judge conclusively as to how far any comparison is possible. Whilst there is no doubt as to the temporary fusion and admixture of the protoplasm of the conjugating Ciliata, it does not appear to be established that there is any transference of nuclear or paranuclear matter from one individual to the other in the form of solid formed particles.

Conjugation resulting merely in rejuvenescence and ordinary fissive activity is observed in many Flagellata as well as in the Ciliata.

A noteworthy variation of the process of binary fission occurring in the parasite Opalina deserves distinct notice here, since it is intermediate in character between ordinary binary fission and that multiple fission which so commonly in Protozoa is known as spore-formation. In Opalina (Fig. XXIV. 4) the nucleus divides as the animal grows; and we find a great number of regularly disposed separate nuclei in its protoplasm. (The nuclei of many other Ciliata have recently been shown to exhibit extraordinary branched and even "fragmented" forms; compare Fig. XXIV. 2.) At a certain stage of growth binary fission of the whole animal sets in, and growth ceases. Consequently the products of fission become smaller and smaller (Fig. XXIV. 6). At last the fragments contain each but two, three, or four nuclei. Each fragment now becomes encased in a spherical cyst (Fig. XXIV. 7). If this process had occurred rapidly, we should have had a uninucleate Opalina breaking up at once into fragments (as a Gregarina does), each fragment being a spore and enclosing itself in a spore-case. The *Opalina ranarum* lives in the rectum of the Frog, and the encysted spores are formed in the early part of the year. They pass out into the water and undergo no change unless swallowed by a Tadpole, in the intestine of which they forthwith develop. From each spore-case escapes a uninucleate embryo (Fig. XXIV. 8), which absorbs nourishment and grows. As it grows its nucleus divides, and so the large multinucleate form from which we started is reattained.

This history has important bearings, not only on the nature of sporulation, but also on the question of the significance of the multinucleate condition of cells. Here it would seem that the formation of many nuclei is merely an anticipation of the retarded fissive process.

It is questionable how far we are justified in closely associating Opalina, in view of its peculiar nuclei, with the other Ciliata. It seems certain that the worm-parasites sometimes called Opalinæ, but more correctly Anaplophrya, &c., have no special affinity with the true Opalina. They not only differ from it in having one large nucleus, but in having numerous very active contractile vacuoles (**75**).

Recently it has been shown, more especially by Gruber (**84**), that many Ciliata are multinucleate, and do not possess merely a single nucleus and a paranucleus. In Oxytricha the nuclei are large and numerous (about forty), scattered through the protoplasm, whilst in other cases the nucleus is so finely divided as to appear like a powder or dust diffused uniformly through the medullary protoplasm (Trachelocerca, Choenia). Carmine staining, after treatment with absolute alcohol, has led to this remarkable discovery. The condition described by Foettinger (**85**) in his Opalinopsis (Fig. XXIV. 1, 2) is an example of this pulverization of the nucleus. The condition of pulverization had led in some cases to a total failure to detect any nucleus in the living animal, and it was only by the use of reagents that the actual state of the case was revealed. Curiously enough, the pulverized nucleus appears periodically to form itself by a union of the scattered particles into one solid nucleus just before binary fission of the animal takes place; and on the completion of fission the nuclei in the two new individuals break up into little fragments as before. The significance of this observation in relation to the explanation of the proceedings of the nuclei during conjugation cannot be overlooked. It also leads to the suggestion that the animal cell may at one time in the history of evolution have possessed not a single solid nucleus but a finely molecular powder of chromatin-substance scattered uniformly through its protoplasm, as we find actually in the living Trachelocerca.

Some of the Ciliata (notably the common Vorticellæ) have been observed to enclose themselves in cysts; but it does not appear that these are anything more than "hypnocysts" from which the animal emerges unchanged after a period of drought or deficiency of food. At the same time there are observations which seem to indicate that in some instances a process of spore-formation may occur within such cysts (76).

The differentiation of the protoplasm into cortical and medullary substance is very strongly marked in the larger Ciliata. The food-particle is carried down the gullet by ciliary currents and is forced together with an adherent drop of water into the medullary protoplasm. Here a slow rotation of the successively formed food-vacuoles is observed (Fig. XXV. 2, *l*, *m*, *n*, *o*), the water being gradually removed as the vacuole advances in position. It was the presence of numerous successively formed vacuoles which led Ehrenberg to apply to the Ciliata the not altogether inappropriate name "Polygastrica." The chemistry of the digestive process has not been successfully studied, but A. G. Bourne (**8**) has shown that, when particles stained with water-soluble anilin blue are introduced as food into a Vorticella, the colouring matter is rapidly excreted by the contractile vacuole in a somewhat concentrated condition.

The differentiation of the protoplasm of Ciliata in some special cases as "muscular" fibre cannot be denied. The contractile filament in the stalk of Vorticella is a muscular fibre and not simple undifferentiated contractile protoplasm; that is to say, its change of dimensions is definite and recurrent, and is not rhythmic, as is the flexion of a cilium. (Perhaps in ultimate analysis it is impossible to draw a sharp line between the contraction of one side of a cilium which causes its flexion and the rhythmical contraction of some muscular fibres.) The movements of the so-called "setæ" of the Hypotricha are also entitled to be called "muscular," as are also the general contractile movements of the cortical substance of large Ciliata. Haeckel (**77**) has endeavoured to distinguish various layers in the cortical substance; but, whilst admitting that, as in the Gregarinæ, there is sometimes a distinct fibrillation of parts of this layer, we cannot assent to the general distinction of a "myophane" layer as a component of the cortical substance.

Beneath the very delicate cuticle which, as a mere superficial pellicle of extreme tenuity, appears to exist in all Ciliata we frequently find a layer of minute oval sacs which contain a spiral thread; the threads are everted from the sacs when irritant reagents are applied to the animal (Fig. XXV. 2, *g*, *h*). These were discovered by Allman (**78**), and by him were termed "trichocysts." They appear to be identical in structure and mode of formation with the nematocysts of the Cœlentera and Platyhelmia. Similar trichocysts (two only in number) are found in the spores of the Myxosporidia (see *ante*, page 855).

The comparative forms of the nucleus and of the contractile vacuoles, as well as of the general body-form, &c., of Ciliata may be learnt from an examination of Figs. XXIII., XXIV., XXV., and the explanations appended to them.

CLASS VI. ACINETARIA, Lankester (*Tentaculifera*, Huxley).

Characters.—Highly specialized Corticate Protozoa, probably derived from Ciliata, since their young forms are provided with a more or less complete investment of cilia. They are distinguished by having no vibratile processes on the surface of the body in the adult condition, whilst they have few or many delicate but firm tentacle-like processes, which are either simply adhesive or tubular and suctorial. In the latter case they are provided at their extremity with a sucker-disk and have contractile walls, whereas in the former case they have more or less pointed extremities. The Acinetaria are sedentary in habit, even if not, as is usual, permanently fixed by a stalk. The nucleus is frequently arboriform. Reproduction is effected by simple binary fission, and by a modified fission (bud-fission) by which (as in Reticularia and Arcella) a number of small bud-like warts containing a portion of the branched parental nucleus are nipped off from the parent, often simultaneously (Fig. XXVI. 8). These do not become altogether distinct, but are for a time enclosed by the parental cell each in a sort of vacuole or brood-chamber, where the young Acinetarian develops a coat or band of cilia and then escapes from the body of its parent (Fig. XXVI. 10, 17). After a brief locomotive existence, it becomes sedentary, develops its tentacles, and loses its cilia.

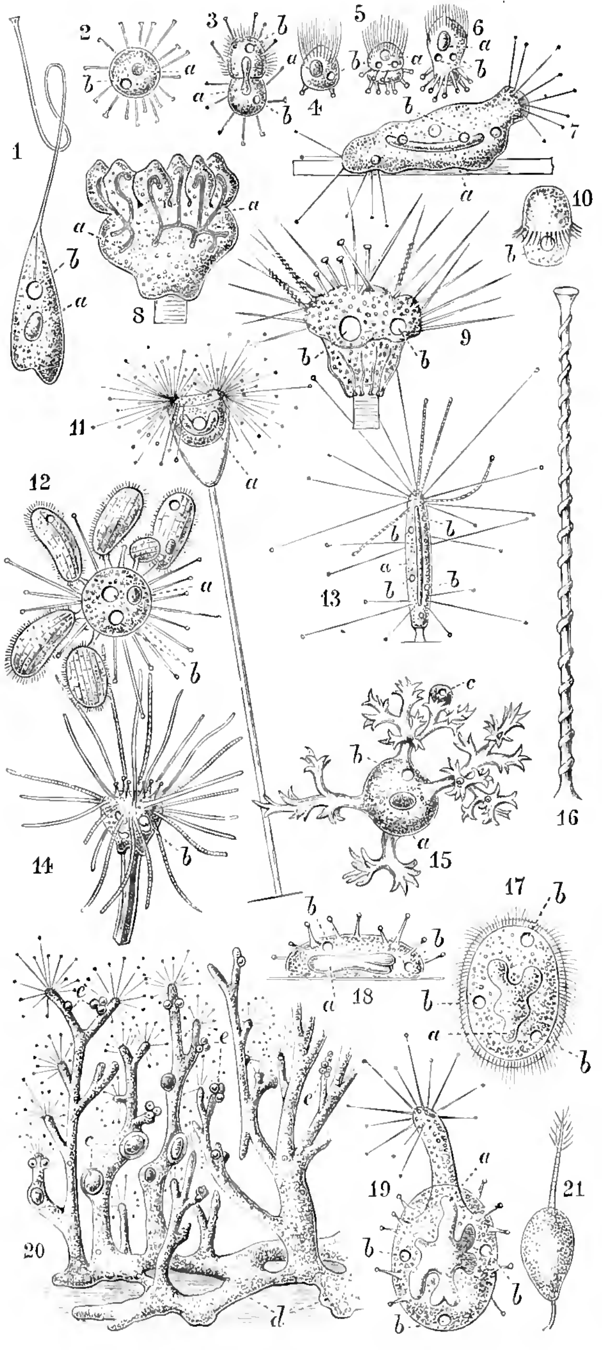

FIG. XXVI.—**Acinetaria.** 1. *Rhyncheta cyclopum*, Zenker. *a*, nucleus; *b*, contractile vacuole; only a single tentacle, and that suctorial; × 150. Parasitic on Cyclops. 2. *Sphærophrya urostylæ*, Maupas; normal adult; × 200. *a*, nucleus; *b*, contractile vacuole. Parasitic in Urostyla. 3. The same dividing by transverse fission, the anterior moiety with temporarily developed cilia. *a*, nucleus; *b*, contractile vacuole. 4, 5, 6. *Sphærophrya stentorea*, Maupas; × 200. Parasitic in Stentor, and at one time mistaken for its young. 7. *Trichophrya epistylidis*, Cl. and L.; × 150. *a*, nucleus; *b*, contractile vacuole. 8. *Hemiophrya gemmipara*, Hertwig; × 400. Example with six buds, into each of which a branch of the nucleus *a* is extended. 9. The same species, showing the two kinds of tentacles (the suctorial and the pointed), and the contractile vacuoles *b*. 10. Ciliated embryo of *Podophrya Steinii*, Cl. and L.; × 300. 11. *Acineta grandis*, Saville Kent; × 100; showing pedunculated lorica, and animal with two bunches of entirely suctorial tentacles. *a*, nucleus. 12. *Sphærophrya magna*, Maupas; × 300. It has seized with its tentacles, and is in the act of sucking out the juices of six examples of the ciliate *Colpoda parvifrons*. 13. *Podophrya elongata*, Cl. and L.; × 150. *a*, nucleus; *b*, contractile vacuole. 14. *Hemiophrya Benedenii*, Fraip.; × 200; the suctorial tentacles retracted. 15. *Dendrocometes paradoxus*, Stein; × 350. Parasitic on *Gammarus pulex*. *a*, nucleus; *b*, contractile vacuole; *c*, captured prey. 16. A single tentacle of Podophrya; × 800. (Saville Kent.) 17–20. *Dendrosoma radians*, Ehr.:—17, free-swimming ciliated embryo, × 600; 18, earliest fixed condition of the embryo, × 600; 19, later stage, a single tentaculiferous process now developed, × 600; 20, adult colony; *c*, enclosed ciliated embryos; *d*, branching stolon; *e*, more minute reproductive (?) bodies. 21. *Ophryodendron pedicellatum*, Hincks; × 300.

The Acinetaria have one or more contractile vacuoles. Their nutrition is holozoic.

The surface of the body in some cases is covered only by a delicate cuticle, but in other cases a definite membranous shell or cup (often stalked) is produced. Freshwater and marine. See Fraipont (89).

ORDER 1. SUCTORIA, Kent.

A greater or less proportion or often all of the tentacles are suctorial and terminated with sucker-like expansions.

Genera.—*Rhyncheta*, Zenker (stalkless, naked, with only one tentacle; epizoic on Cyclops; Fig. XXVI. 1); *Urnula*, C. and L.; *Sphærophrya*, C. and L. (naked, spherical, with distinctly capitate tentacles only; never with a pedicle; parasitic within Ciliata, supposed young; Fig. XXVI. 2–6, 12); *Trichophrya*, C. and L. (as *Sphærophrya*, but oblong and temporarily fixed without a pedicle); *Podophrya*, Ehr. (naked, solitary, globose, ovate or elongate, fixed by a pedicle; tentacles all suctorial, united in fascicles or distributed irregularly; Fig. XXVI. 10, 13, 16); *Hemiophrya*, S. Kent (as *Podophrya*, but the tentacles are of the two kinds indicated in the definition of the group; Fig. XXVI. 8, 9, 14); *Podocyathus*, S. Kent (secreting and inhabiting stalked membranous cups or loricæ; tentacles of the two kinds); *Solenophrya*, C. and L. (with a sessile lorica; tentacles only suctorial); *Acineta*, Ehr. (as *Solenophrya*, but the lorica is supported on a pedicle; Fig. XXVI. 11); *Dendrocometes*, Stein (cuticle indurated; solitary, sessile, discoid; tentacles peculiar, viz., not contractile, more or less branched, root-like, and perforated at the extremities and suctorial in function; Fig. XXVI. 15). *Dendrosoma*, Ehr. (forming colonies of intimately fused individuals, with a basal adherent protoplasmic stolon and upstanding branches the termination of which bear numerous capitate suctorial tentacles only; Fig. XXVI. 17–20).

ORDER 2. NON-SUCTORIA, Lankester (=*Actinaria*, Kent).

Characters.—Tentacles filiform, prehensile, not provided with a sucker.

Genera.—*Ephelota*, Str. Wright (solitary, naked, pedunculate, with many flexible inversible tentacles); *Actinocyathus*, S. Kent; *Ophryodendron*, C. and L. (sessile, with a long, extensile, anterior proboscis bearing numerous flexible tentacles at its distal extremity; Fig. XXVI. 21); *Acinetopsis*, Robin (ovate, solitary, secreting a stalked lorica; from the anterior extremity of the animal is developed a proboscis-like organ which does not bear tentacles).

Further remarks on the Acinetaria.—The independence of the Acinetaria was threatened some years ago by the erroneous view of Stein (79) that they were phases in the life-history of Vorticellidæ. Small parasitic forms (Sphaerophrya) were also until recently regarded erroneously as the "acinetiform young" of Ciliata.

They now must be regarded as an extreme modification of the Protozoon series, in which the differentiation of organs in a unicellular animal reaches its highest point. The sucker-tentacles of the Suctoria are very elaborately constructed organs (see Fig. XXVI. 16). They are efficient means of seizing and extracting the juices of another Protozoon which serves as food to the Acinetarian. The structure of Dendrosoma is remarkable on account of its multicellular character and the elaborate differentiation of the reproductive bodies.

The ciliation of the embryos or young forms developed from the buds of Acinetaria is an indication of their ancestral connexion with the Ciliata. The cilia are differently disposed on the young of the various genera (see Fig. XXVI. 10, 17).

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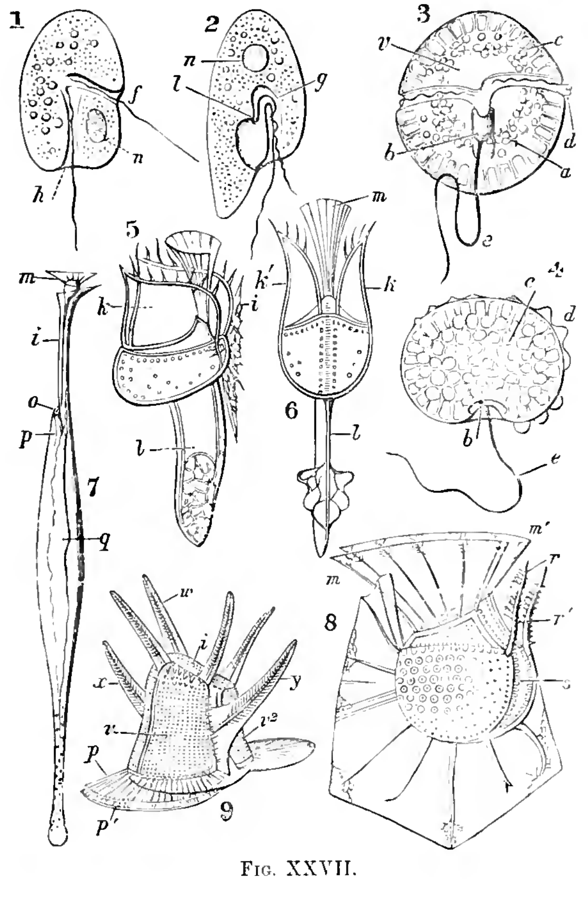

Fig. XXVII.

Fig. XXVII.—**Dinoflagellata.** This figure is not contained in the article as published in the *Encyclopædia Britannica.* It presents the recent discoveries of Klebs, Bütschli, and Stein.

1. Diagram of the Dinoflagellate *Hemidinium.* *n*, nucleus; *f*, flagellum of the transverse groove; *h*, flagellum of the vertical groove.
2. Diagram of the Cryptomonadine *Oxyrrhis* (to compare with the preceding). *n*, nucleus; *g*, the deep fossa or pit in which the two flagella are affixed; *l*, the origin of the flagellum which corresponds with that of the transverse groove of Dinoflagellata. The second flagellum is seen to be attached near the mouth of the fossa.
3. *Glenodinium cinctum*, Ehr., seen from the ventral surface. *a*, amyloid granules; *b*, eye-spot; *c*, chromatophores; *d*, flagellum of the transverse groove; *e*, flagellum of the vertical groove; *v*, vacuole.
4. The same, seen from the hinder pole (letters as in 3).
5. Cuticle of *Histioneis cymbalaria*, Stein, from the Atlantic. *i*, ventral process; *k*, cuticular collar; *l*, posterior process.
6. The same, seen from the dorsal surface. *m*, cephalic funnel (*k* and *l* as in 5).
7. Cuticle of *Amphisolenia globifera*, Stein, from the Atlantic, seen from the left side. *i*, narrow ventral processes; *m*, cephalic funnel; *o*, the mouth; *p*, pharynx; *q*, the shrunken protoplasm.
8. Cuticle of *Ornithocercus magnificus*, Stein, from the Atlantic. *mm'*, the cephalic funnel; *rr'*, the two large ribs of the cuticular collar (the collar itself similar to *k* in No. 5 is not drawn); *s*, the two rows of dorsal cuticular teeth.
9. Cuticle of *Ceratocorys horrida*, Stein, from the Southern Ocean. *i*, the large frontal plate; *pp'* the outgrown margins of the transverse groove; *v*, *v*², basal plates; *w*, one of the four frontal horns; *x*, the dorsal horn; *y*, the ventral horn.

SPONGES

(*By W. Johnson Sollas, LL.D., F.R.S., Professor of Geology, Trinity College, Dublin.*)

THE great advance which has been made during the past fifteen years in our knowledge of the sponges is due partly to the vivifying influence of the evolutional hypothesis, but still more to the opportunities afforded by novel methods of technique. To the strength and weakness of the deductive method Haeckel's work on the *Kalkschwämme* (*6*)[1] is a standing testimony, while the slow but sure progress which accompanies the scientific method is equally illustrated by the works of Schulze (*20*), who by a masterly application of the new processes has more than any one else reconstructed on a sure basis the general morphology of the sponges. In the general progress the fossil sponges have been involved, and the application of Nicol's method of studying fossil organisms in thin slices has led, in the hands of Zittel and others (*24, 35*), to a complete overthrow of those older classifications which relegated every obscure petrifaction to the fossil sponges, and consigned them all to orders no longer existing. But, whilst many problems have been solved, still more have been suggested. An almost endless diversity in details differentiates the sponges into a vast number of specific forms; the exclusive possession in common of a few simple characters closely unites them into a compact group, sharply marked off from the rest of the animal kingdom.[2]

Structure and Form.

Simple sponge.

Description of a Simple Sponge.—As an example of one of the simplest known sponges we select *Ascetta primordialis* (fig. 1), Haeckel. This is a hollow vase-like sac closed at the lower end, by which it is attached, opening above by a comparatively large aperture, the *osculum* or vent, and at the sides by numerous smaller apertures or *pores*, which perforate the walls. Except for the absence of tentacles and the presence of pores it offers a general resemblance to some simple form of *Hydrozoon.* Histologically, however, it presents considerable differences, since, in addition to an endoderm and an ectoderm, a third or mesodermic layer contributes to the structure of the walls; and the endoderm consists of cells (see fig. 21, *g*) each of which resembles in all essential features those complicated unicellular organisms known as choanoflagellate *Infusoria* (see PROTOZOA, vol. xix. p. 858). With this positive character is associated a negative one: nematocysts are entirely absent. The activity

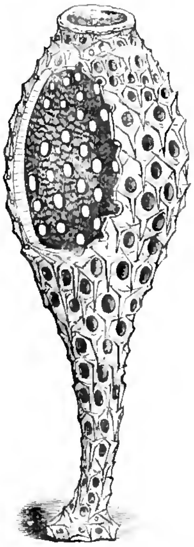

FIG. 1.—*Ascetta primordialis*, Haeckel. After Haeckel.

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[1] These italic numbers refer to the bibliography which will be found at page 54.

[2] Since this was written, in 1887, four large monographs, including considerably over 2000 pages of letterpress, have been published on the Sponges. Three of these, viz.:—Schulze on the *Hexactinellida*, Ridley and Dendy on the *Monaxonida*, and Sollas on the *Tetractinellida* appear as Reports of the "Challenger" Expedition, the fourth by Von Lendenfeld on the "Horny Sponges" as a special volume issued by the Royal Society. With this addition to our knowledge a longer preface than this would be possible, but for the general student the following amended classification of the *Monaxonida* will probably be found sufficient.

Order.—**Monaxonida.**

Sub-order 1. *ASEMOPHORA*, Sollas.

Family 1. HOMORAPHIDÆ, Ridley and Dendy.—Megascleres either oxeas or strongyles. No microscleres. Ex.: *Halichondria.*

Sub-order 2. *MENISCOPHORA*, Sollas.

The microscleres when present are sigmaspires, sigmas, or cymbas.

Family 1. HETERORAPHIDÆ, Ridley and Dendy.—Megascleres of various forms, microscleres never cymbas. Ex.: *Rhizochalina*, O.S.

Family 2. DESMACIDONIDÆ, O.S.—Megascleres usually monactinal, microscleres cymbas. Ex.: *Desmacidon*, O.S.

Sub-order 3. *SPINTHAROPHORA*, Sollas.

The microsclere when present is some form of aster.

Group 1. HOMOSCLERA.—The spicules are all microscleres.

Family 1. ASTROPEPLIDÆ.—The microscleres are microxeas and asters. Ex.: *Astropeplus*, Soll.

Group 2. HETEROSCLERA, Soll.—Megascleres are always present, and sometimes microscleres.

DEMUS 1. CENTROSPINTHARA, Soll.—The microsclere when present is a euaster.

Family 1. AXINELLIDÆ, O.S.—Non-corticate, mesoderm collenchymatous, chamber system eurypylous. The skeleton consists of axial and radial spicular fibres. Ex.: *Axinella*, O.S.

Family 2. DORYPLERIDÆ, Soll.—Non-corticate, mesoderm collenchymatous. Skeleton consisting of oxeas arranged without order. Ex.: *Dorypleres*, Soll.

Family 3. TETHYIDÆ, Vosm.—Corticate. Skeleton consisting of radially arranged oxeas. The microsclere is a spheraster. Ex.: *Tethya*, Lam.

DEMUS 2. SPIRASPINTHARA, Soll.—The microsclere is a spiraster.

Family 1. SCOLOPIDÆ, Soll.—The cortex is thin and fibrous, with radially arranged closely-packed microxeas and oxeas. The skeleton consists of oxeas collected into radially disposed fibres. The microsclere when present is an amphiaster. Ex.: *Scolopus*, Soll.

Family 2. SUBERITIDÆ, O.S.—Cortex with a skeleton of radially arranged styles. Microscleres usually absent. The megascleres are tylostyles. Ex.: *Suberites*, Nardo.

Family 3. SPIRASTRELLIDÆ, Ridley and Dendy.—The megascleres are rhabdi or styles. The microscleres are spirasters or discasters. Ex.: *Spirastrella*, O.S.

of the *Ascetta*, as of all sponges, is most obviously manifested, as Grant (*5*) first observed, by a rapid outflow of water from the oscule and a gentle instreaming through the pores,—a movement brought about by the energetic action of the flagella of the endodermic cells. The instreaming currents bear with them into the cavity of the sac (paragastric cavity) both protoplasmic particles (such as *Infusoria*, diatoms, and other small organisms) and dissolved oxygen, which are ingested by the flagellated cells of the endoderm. The presence of one or more contractile vacuoles in these cells suggests that they extricate water, urea, and carbonic acid. The insoluble residue of the introduced food, together with the fluid excreta, is carried out through the oscule by the excurrent water. New individuals are produced from the union of ova and spermatozoa, which develop from wandering amœboid cells in the mesoderm. The walls of *Ascetta* are strengthened by calcareous scleres, more especially designated as spicules, which have the form of triradiate needles. If we make abstraction of these we obtain an ideal sponge, which Haeckel has called *Olynthus* (*6*), and which may be regarded as the ancestral form from which all other sponges have been derived. To give greater exactness to our abstraction we should perhaps stipulate for the *Olynthus* a somewhat thicker mesoderm and more spherical form than a decalcified Ascon presents.

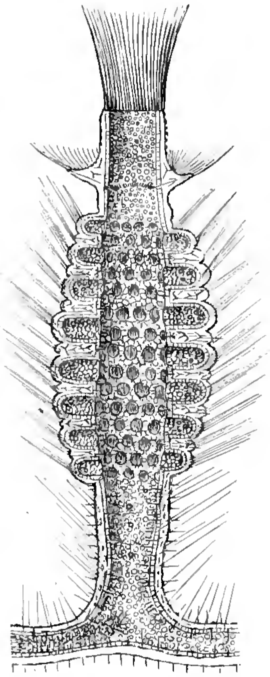
FIG. 2.—*Homoderma sycandra*, Lfd. One half cut away by a vertical median section. After V. Lendenfeld (×about 6).

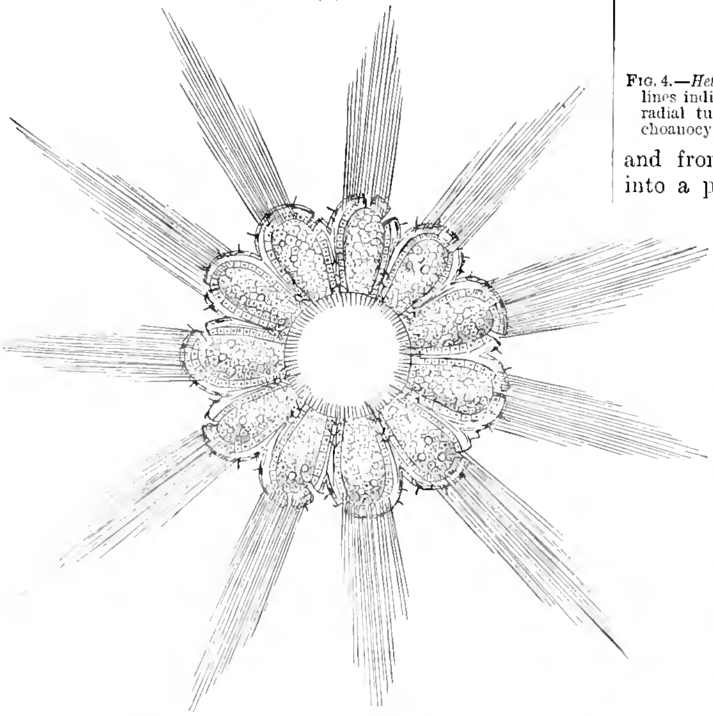
FIG. 3.—*Homoderma sycandra*, Lfd. Transverse section, showing radial tubes opening into central paragastric cavity. After V. Lendenfeld (×about 12).

Canal System.—We shall now trace the several modifications which the *Olynthus* has undergone as expressed in the different types of canal system.

Ascon type.

The simple paragaster of *Ascetta* may become complicated in a variety of ways, such as by the budding off from a parent form of stolon-like extensions, which then give rise to fresh individuals, or by the branching of the Ascon sac and the subsequent anastomosis of the branches; but in no case, so long as the sponge remains within the Ascon type, does the endoderm become differentiated into different histological elements. The most interesting modification of the Ascon form occurs in *Homoderma sycandra* (*12*), in which from the walls of a simple Ascon cæcal processes grow out radiately in close regular whorls, each process reproducing the structure of the parent sponge (figs. 2, 3). From this it is but a short step to the important departure which gives rise to the Sycons.

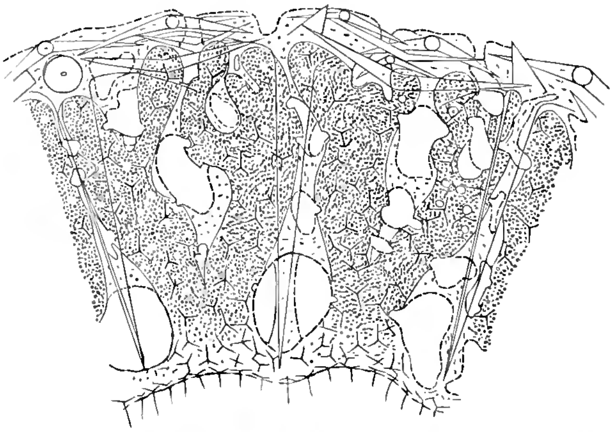
FIG. 4.—*Heteropegma nodus-gordii*, Pol. Part of a transverse section. The straight lines indicate spicules; the poriferous surface is uppermost; the branching radial tubes are rendered dark by numerous small circles representing choanocytes. After Polejaeff, "*Challenger*" *Report* (×50).

Sycon type.

In the simplest examples of this type the characters of *Homoderma sycandra* are reproduced, with the important exception that the endoderm lining the paragastric cavity of the original Ascon form loses its primitive character, and from a layer of flagellated cells becomes converted into a pavement epithelium, not in any distinguishable feature different from that of the ectoderm. The flagellated cells are thus restricted to the cæcal outgrowths or radial tubes. Concurrently with this differentiation of the endoderm a more abundant development of mesoderm occurs. In some Sycons (*Sycaltis*, Hk.) the radial tubes remain separate and free; in others they lie close together and are united by trabeculæ, or by a trabecular network, consisting of mesodermic strands surrounded by ectoderm (fig. 4). The spaces between the contiguous radial tubes thus become converted into narrow canals, through which water passes from the exterior to enter the pores in the walls of the radial tubes. These canals are the "intercanals" of Haeckel, now generally known by their older name of *incurrent* canals. The openings of the incurrent canals to the exterior are called pores, a term which we have also applied to the openings which lead directly into the radial tubes or paragastric cavity; to avoid ambiguity we shall for the future distinguish the latter kind of opening as a *prosopyle*. The term "pore" will then be restricted to the sense in which it was originally used by Grant. The mouth by which a radial tube opens into the paragaster is known as a *gastric ostium*. In the higher forms of Sycons the radial tubes no longer arise as simple outgrowths of the whole sponge-wall, but rather as outgrowths of the endoderm into the mesoderm, which, together with the ectoderm, exhibits an independent growth of its own; and this results in the formation of a thick investment, known as the *cortex* (fig. 5), to the whole exterior of the sponge. The radial tubes may branch, *Heteropegma* (fig. 4). If the branches are given off regularly, as the radial tubes were in the first plan, and if at the same time the original radial tube exchanges its flagellated for a pavement epithelium, a structure as shown in fig. 6 (*Polejna connexiva*, Pol.) will result. This form might also be brought about by unequal growth of the gastral endoderm leading to a folding of the inner part of the sponge-wall. Very little direct evidence exists as to which of these two plans has actually been followed. Phylogenetically the transition from a simple Ascon to the most complicated Sycon can be traced step by step; and ontogeny shows that such a Sycon form as *Grantia raphanus* passes through an Ascon phase in the course of its larval development.

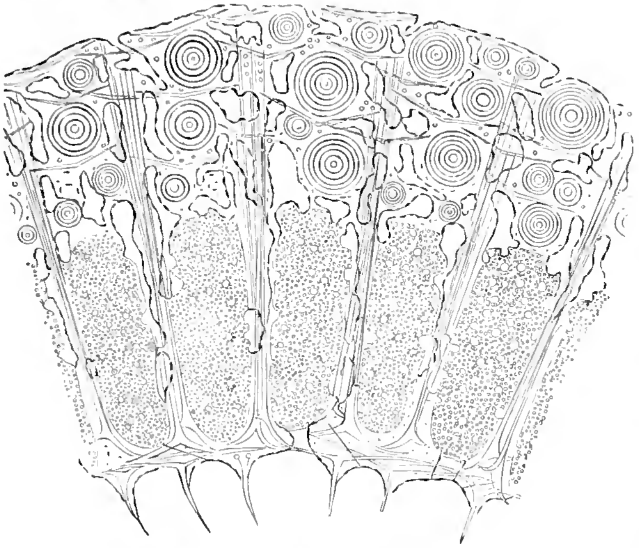
Fig. 5.—*Ute Argentea*, Pol. Part of a transverse section. The concentric circles, indicating transverse sections of spicules, lie within the cortex. After Polejaeff, "*Challenger*" *Report* (×100).

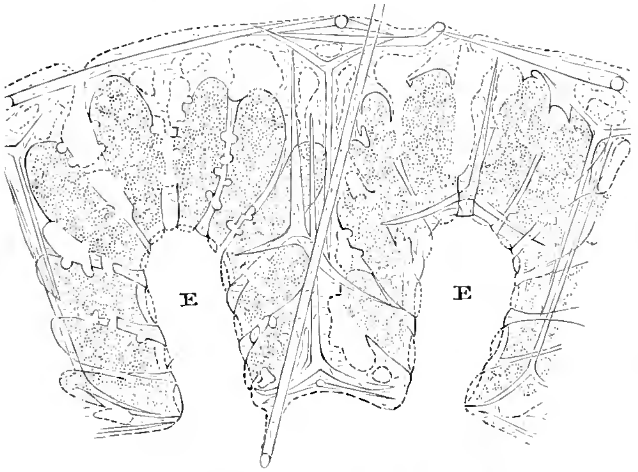

Fig. 6.—*Polejna connexiva*, Pol. Part of a transverse section. *E*, excurrent canals, into which the flagellated chambers open. After Polejaeff, "*Challenger*" *Report* (× 50).

Rhagon type.

Returning to the ancestral form of sponge, *Olynthus*, let us conceive the endoderm growing out into a number of approximately spherical chambers, each of which communicates with the exterior by a prosopyle and with the paragastric cavity by a comparatively large aperture, which we may term for distinction an *apopyle*; at the same time let the endoderm lose its flagellated character and become converted into a pavement epithelium, except in the spherical chambers. Such a form, called by Haeckel "dyssycus," may be more briefly named a *Rhagon* from the grape-like form of its flagellated chambers, which differ from those of a Sycon both by their form and their smaller dimensions. The Rhagon occurs as a stage in the early development of *Plakina monolopha* (Schulze) and *Reniera fertilis* (*9*) (fig. 7); a calcareous sponge which appears to approach it somewhat is *Leucopsis pedunculata*, Lfd. By the folding of the wall of a Rhagon, or by its outgrowth into lobes, a complicated structure such as that of *Plakina monolopha* (*20*) (see fig. 26 *f*) results. This is characterized by the chambers retaining their immediate communication with the incurrent and excurrent canals, opening into the latter by the widely open apopyle and receiving the former by one or several prosopyles. This may be termed the *eurypylous* type of Rhagon canal system. The folding of the sponge-wall may be simple, as in the example given, or too complex to unravel. In higher forms of sponges (*Geodinidæ*, *Stellettidæ*) the chambers cease to open abruptly into the excurrent canals: each is prolonged into a narrow canal, *aphodus*, or *abitus*, which usually directly, sometimes after uniting with one or more of its fellows, opens into an excurrent canal. The prosopyles, now restricted to one for each chamber, may remain unchanged in character, or at the most be prolonged into very short

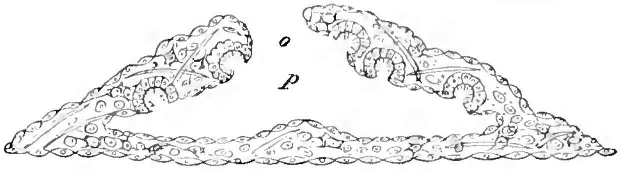

Fig. 7.—Vertical section of a Rhagon, partly diagrammatic. *o*, oscule; *p*, paragaster. After Keller (× about 100).

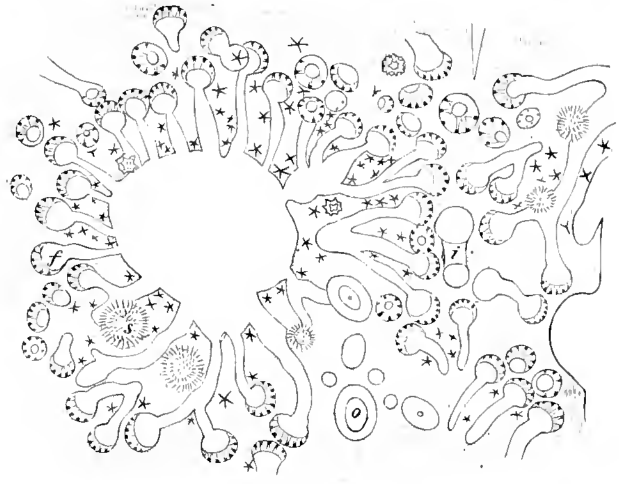

Fig. 8.—Transverse section across an excurrent canal and surrounding choanosome of *Cydonium eosaster*, Soll. *e*, excurrent canal; *f*, flagellated chambers communicating with it by aphodal canals; *i*, an incurrent canal cut across; *s*, a sterraster; *o*, an oxea cut across. After Sollas, "*Challenger*" *Report* (×125).

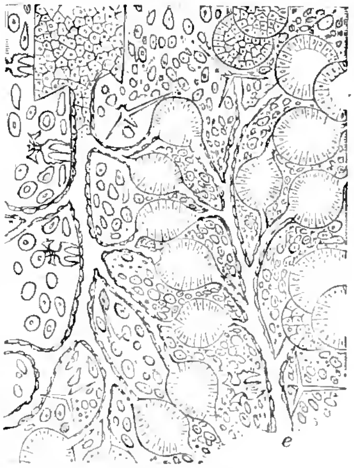

Fig. 9.—Diplodal canal system in *Corticium candelabrum*, O.S. *e*, excurrent canal; the incurrent canal is shown on the left-hand side, near its commencement in the cortex. After F. E. Schulze (× 200).

tubes, each a *prosodus* or *aditus* (fig. 8). This may be termed the *aphodal* or *racemose* type of Rhagon system, since the chambers at the ends of the aphodi radiating from the excurrent canal look like grapes on a bunch. As Haeckel, however, has used "racemose" in a different sense, we shall adopt here the alternative term. By the extension of the prosodal or adital canals into long tubes a still higher differentiation is reached (fig. 9). This, which from the marked presence of both prosodal and aphodal canals may be termed the *diplodal* type of the Rhagon canal system, occurs but rarely. *Chondrosia* is an example.

The following scheme will render clear the foregoing distinctions :—

1. Ascon type : simple, ex. *Ascetta*, Hk. ; strobiloid, ex. *Homoderma*, Lfd.
2. Sycon type : simple radial tubes, ex. *Sycetta*, Hk. ; branched radial tubes (cylindrical chambers), ex. *Heteropegma*, Fl. ; chamber-layer folded, ex. *Polejna*, Pol.
3. Rhagon type : eurypylous, with several prosopyles to each chamber, ex. *Spongelia* ; with a single prosopyle to each chamber, ex. *Oscarella*, *Thenea* ; aphodal, aphodal canals well developed, ex. *Geodia*, Lmk. ; diplodal, with both aphodal and prosodal canals well developed, ex. *Chondrosia*, O.S.

In the case of the calcareous sponges Polejaeff has argued forcibly that the eurypylous type arises directly from the Sycon and not from the Rhagon. It is therefore doubtful how far the Rhagon in other sponges is a primitive form derived directly from an *Olynthus*, or whether it may not be a secondary larval state resulting from the abbreviated development of a former Sycon predecessor. Whatever may have been its past history, the Rhagon serves now at all events as a starting-point for the development of the higher forms of canal system.

Subdermal cavities.

In the higher Rhagons, as in the Sycons, further complications ensue, owing to an independent growth of the external ectoderm and the adjacent mesoderm. While the endoderm, with its associated mesoderm, is growing out or folding to form the excurrent canal system, the superficial mesoderm increases in thickness, and the ectoderm, extending laterally from the sides of the incurrent sinuses, burrows into it, parallel to the surface of the sponge. Thus it forms beneath the skin (*i.e.*, the layer of superficial mesoderm and investing ectoderm) cavities which may be either simple and spacious or be broken up into a number of labyrinthine passages by a network of mesoblastic strands (invested with ectoderm) which extend irregularly from roof to floor of the chamber. These cavities are known as *subdermal chambers*.

Ectosome, choanosome.

With the appearance of subdermal chambers the sponge becomes differentiated into two almost independent regions, an outer or *ectosome* and an inner or *choanosome*, which is characterized by the presence of flagellated chambers. The ectosome forms the roof and walls of the subdermal chambers, and is in its simplest form merely an investing skin ; but in a large number of sponges it acquires considerable thickness and a very complicated histological structure. It is then known as a *cortex*. The thickening which gives rise to a cortex takes place chiefly beneath those parts of the skin which are not furnished with pores. Beneath the pores—in this case collected into sieve-like areas—dome-like cavities are left in the cortex ; they open freely into the subdermal cavities below and their roof is formed by the cribriform pore membrane above. In many sponges (*Geodia*, *Stelletta*) the cortical domes are constricted near their communication with the subdermal cavity (subcortical crypt) by a transverse muscular sphincter, which defines an outer division or *ectochone* from an inner or *endochone* (fig. 10), the whole structure being a *chone*. The endochone is frequently absent (fig. 10). The early development of the cortex has scarcely yet been studied. In *Stelletta phrissens* (Soll.), one of the "Challenger" *Stellettidæ*, an early form of the sponge (fig. 11), shows the choanosome already characteristically folded within the cortex, which forms a complete not-folded envelope around it. The roots of the incurrent sinuses form widely open spaces immediately beneath the cortex and are the rudiments of subcortical crypts. Again, in some sponges a part of the endoderm and associated mesoderm may likewise develop independently of the rest of the sponge, as in the *Hexactinellida*, where the choanosome forms a middle layer between a reticulation of ectosome on the one side and of endoderm and mesoderm, *i.e.*, *endosome*, on the other. Finally, the attached or lower half of a Rhagon may develop in an altogether different manner from the other or upper half, the endoderm not producing any flagellated chambers. In this case the upper portion alone is characterized by the flagellated chambers, which are the distinctive mark of a sponge, and hence may be called the *spongomere* ; the lower half, which consists of all three fundamental layers, may be called the *hypomere*.

Chone.

Endosome

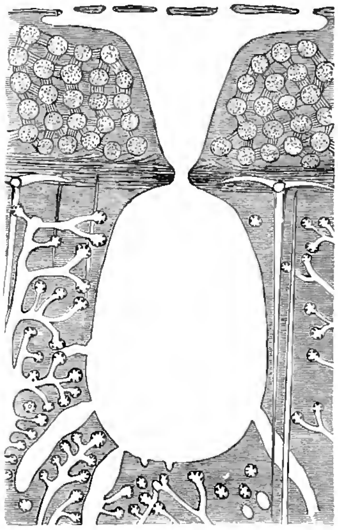

FIG. 10.—Section through the cortex of *Cydonium eosaster*, Soll., showing the pore-sieve overlying the chone, which communicates through a sphinctrate aperture with the subcortical crypt, lying in the choanosome with its flagellated chambers. The dotted circles in the cortex are sterrasters connected by fibrous strands. After Sollas, "*Challenger*" *Report* (×73).

FIG. 11.—Young sponge of *Stelletta phrissens*, Soll. Longitudinal median section, showing the choanosome folded within the cortex. *o*, oscule. After Sollas, "*Challenger*" *Report* (×50).

Oscule.

The form and general composition of sponges are exceedingly various and often difficult to analyse, presenting, along with some important differences, a remarkable general resemblance to the *Cœlentera* in these respects. Like them, some sponges are simple, and others, through asexual multiplication, compound. The only criterion by which the individual sponge can be recognized is the osculum ; and, as it is frequently difficult, and in many cases impossible, to distinguish this from the gastric opening of a large excurrent canal, there are many cases in which the simple or compound nature of the sponge must remain open to doubt. The oscule may also fail (*lipostomosis*), and so may the paragastric cavity (*lipogastrosis*) ; the problem then becomes insoluble. The loss of the oscule may in some cases be due to the continued growth of several endodermal folds towards the exterior, with a corresponding absorption of the mesoderm and ectoderm which lie in the way, till the folds penetrate to the ectoderm and open at the exterior, thus giving rise to excurrent openings, which are not readily distinguishable from pores. At the same time the original osculum closes up and entirely disappears. Lipogastrosis, on the other hand, may be produced by the growing together of the roots of the choanosomal folds, thus reducing the paragastric cavity to a labyrinth of canals, which may easily be confounded with the usual form of excurrent canals. While in some sponges the original oscule is lost, in others secondary independent openings, deceptively like oscules, are added. This pseudostomosis is due to a folding of the entire sponge, so as to produce secondary canals or cavities, which may be incurrent (*vestibular*) or excurrent (*cloacal*), the opening of the latter to the exterior being termed a *false oscule* or *pseudostome*. The faulty use of the term oscule for what is neither functionally nor morphologically a mouth is here obvious, for in one sense the oscule is always a pseudostome; it would be better if the term *pseudoproct* could be substituted.

Skeleton. *Skeleton.*—All sponges, except three or four genera belonging to the *Myxospongiæ*, possess some kind of skeletal structures. They may be either calcareous or silicious or horny scleres, the latter usually having the form of fibres, which sometimes enclose silicious needles (spicules) or foreign bodies introduced from without. Foreign bodies also contribute to the formation of the skeleton of some silicious sponges, and occasionally form the entire skeleton, no other hard parts being present.

Mineral spicules. Mineral scleres usually occur in the form of spicules. The spicules of calcareous sponges consist of carbonate of lime, having the crystalline structure and other properties of calcite (*29*). Each spicule, so far as its mineral component is concerned, is a single crystal, all the molecules of calcite of which it is built up being similarly oriented. On the other hand, its form and general structure are purely organic. Its surfaces are always curved, and usually it has the form of a cone or combination of cones, each of which consists of concentric layers of calcite surrounding an axial fibre of organic matter,—probably of the same nature as spongiolin or spongin, the chief constituent of the fibres of horny sponges. A thin layer of organic matter, known as the *spicule sheath*, forms an outer investment to the spicule and is best rendered visible as a residue by removing the calcite with weak acid. Silicious spicules consist of colloid silica or opal, and hence can be distinguished from calcareous by having no influence upon polarized light. Structurally the two kinds of spicules present no important difference. The spicules of different sponges differ greatly both in form and in size. They may be conveniently divided into two groups,—minute or flesh spicules, which usually serve as the support of a single cell only (*microscleres*), and larger or skeletal spicules, which usually contribute to the formation of a more or less consistent skeleton (*megascleres*). The distinction is not one that can be exactly defined, and must so far be regarded as of a provisional nature. There is usually but little difficulty in applying it in practice, except in some doubtful cases where large spicules do not form a continuous skeleton, or in others where flesh spicules appear to be passing into those of larger size. It is indeed highly probable that all large spicules have originated from flesh spicules (*12*).

Megascleres. (1) *Monaxon Biradiate Type* (*rhabdus*).—By far the commonest form is the oxea, a needle-shaped form pointed at both ends and produced by growth from a centre at the same rate in opposite directions along the same axis. It is therefore uniaxial and equibiradiate (fig. 12 *a*). (2) *Monaxon Uniradiate Type* (*stylus*).—By the suppression of one of the rays of an oxea, an acuate spicule or stylus results (fig. 12 *b*). (3) *Triaxon Triradiate Type*.—Linear growth from a centre in three directions inclined at an angle of 120° to each other gives rise to the primitive form of triradiate spicule so eminently characteristic of the calcareous sponges, but by no means confined to them (fig. 12 *c*). (4) *Tetraxon Quadriradiate Type* (*Calthrops*).—Growth from a centre in four directions inclined at about 110° to each other produces the primitive quadriradiate form of the *Tetractinellida* and of some calcareous sponges (fig. 12 *d*). (5) *Sexradiate Type*.—Growth in six directions along three rectangular axes produces the primitive sexradiate spicule of the *Hexactinellida* sponges (fig. 12 *e*). (6) *Multiradiate Type*.—Extensions radiating in many directions from a centre produce a stellate form (fig. 12 *f*). (7) *Spherical Scleres*.—Concentric growth of silica about an organic particle produces the sphere, which occurs as a reduction of the rhabdus in some species of *Pœcillastra*, or as an overgrown globule (flesh spicule) in *Caminus*.

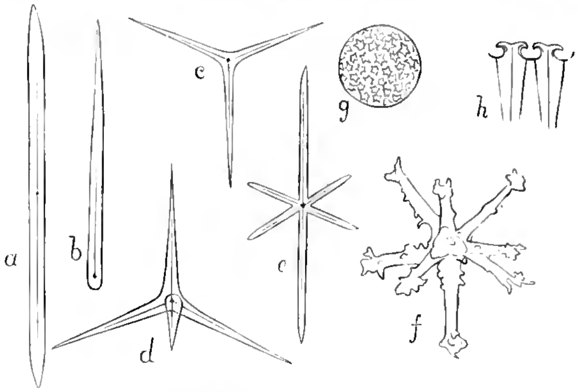

FIG. 12.—Typical megascleres. *a*, rhabdus (monaxon diactine); *b*, stylus (monaxon monactine); *c*, triod (triaxon triactine); *d*, calthrops (tetraxon tetractine); *e*, triaxon hexactine; *f*, desma of an anomocladine Lithistid (polyaxon); *g*, sterraster (polyaxon); *h*, radial section through the outer part of *g*, showing two actines soldered together by intervening silica, the free ends terminating in recurved spines and the axis traversed by a central fibre.

Uniaxial type. Usually conical, the spicular rays often become cylindrical; usually pointed (*oxeate*) at the ends, they are also frequently rounded off (*strongylate*), or thickened into knobs (*tylotate*), or branched (*cladose*). Their growth is not always rigorously confined to a straight line: frequently they are curved or even undulating. They are also liable to become spined, either by mere superficial thickening or by a definite outgrowth involving the axial fibre (fig. 13 *g*, *h*).

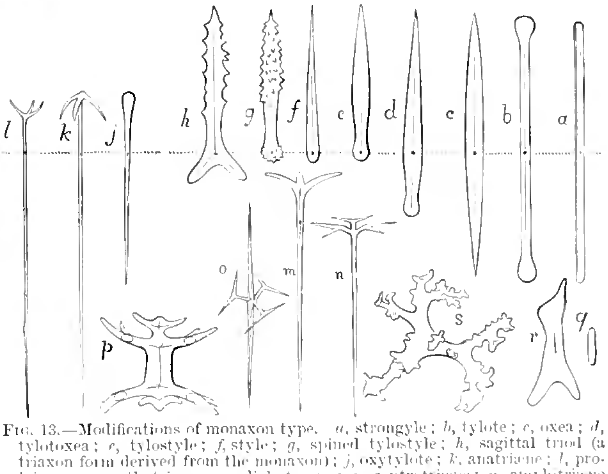

FIG. 13.—Modifications of monaxon type. *a*, strongyle; *b*, tylote; *c*, oxea; *d*, tylotoxea; *e*, tylostyle; *f*, style; *g*, spined tylostyle; *h*, sagittal triod (a triaxon form derived from the monaxon); *j*, oxytylote; *k*, anatriaene; *l*, protriaene; *m*, orthotriaene; *n*, dichotriaene; *o*, centrotriaene; *p*, amphitriaene (this is trichocladose); *q*, crepidial strongyle (basis of Rhabdocrepid Lithistid desma); *r*, young form of Rhabdocrepid desma, showing crepidial strongyle coated with successive layers of silica; *s*, Rhabdocrepid desma fully grown. The dotted line through the upper figures marks the origin of the actines.

The rhabdus if pointed at both ends is known as an *oxea* (fig. 13 *c*); if rounded at both ends as a *strongyle* (fig. 13 *a*); if knobbed at both ends as a *tylote* (fig. 13 *b*); the tylote if pointed at one end is a *tylotoxea* (fig. 13 *d*); the strongyle similarly becomes a *strongyloxea*. These last two forms are with difficulty distinguished from the stylus, which is usually pointed at the end, and strongylate (fig. 13 *f*) or tylotate (fig. 13 *e*) about the origin. A particular case of the cladose rhabdus, but one of the most frequent occurrence, is the *triæne*; in this form one ray of a rhabdus ends in three branches, which diverge at equal angles from each other. The rhabdus then becomes known as the shaft or *rhabdome*, and the secondary rays are the arms or *cladi*, collectively the head or *cladome* of the spicule. The arms make different angles with the shaft: when recurved a grapnel or *anatriæne* is produced (fig. 13 *k*), when projecting forwards a *protriæne* (fig. 13 *l*), and when extended at right angles an *orthotriæne* (fig. 13 *m*). The arms of a triæne may bifurcate (*dichotriæne*) once (fig. 13 *n*), twice, or oftener, or they may trifurcate. Again, they may extend laterally into undulating lamellæ, or unite to form a disk, the triæne character of which is indicated by the included axial fibre. The shaft may also become trifid at both ends, *amphitriæne* (fig. 13 *p*), and the resulting rays all bifurcate, or the cladome may arise from the centre of the rhabdome, *centrotriæne* (fig. 13 *o*). Amongst one group of Lithistid sponges (*Rhabdocrepida*) the normal growth of a strongyle is arrested at an early stage; it then serves as a nucleus upon which further silica is deposited, and in such a manner as to produce a very irregularly branching sclere or desma (fig. 13 *s*), within which the fundamental strongyle can be seen enclosed. In such a desma no axial fibre besides that of the enclosed strongyle is formed.

Triradiate type.

The chief modification of the triradiate spicule is due to an elongation of one ray, distinguished as *apical*, the shorter paired rays being termed *basal*, and the whole spicule a sagittal triradiate. The angle included by the basal rays is usually over 120° (fig. 14 *a*).

Quadriradiate type.

Some or all of the rays of the primitive calthrops (fig. 14 *b*) may subdivide into a number of terminal spines *candelabra* (fig. 14 *c*); or some or all of them may bifurcate once or twice and finally terminate by subdividing into numerous variously shaped processes; such a *tetracladine* desma (fig. 14 *e*) characterizes one division of the Lithistid sponges.

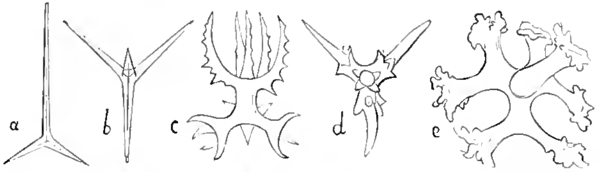

FIG. 14.—Modifications of the triaxon and tetraxon types. *a*, sagittal triradiate or triod; *b*, calthrops; *c*, candelabra (a polycladose microcalthrops); *d*, a spined microcalthrops; *e*, Tetracladine Lithistid desma.

Sexradiate type.

By the excess or defect of one or more rays a series of forms such as are represented in fig. 15 arise. In the oxea, which results from the suppression of all rays but two, the sexradiate character is sometimes preserved by the axial fibre, which gives off two or four processes in the middle of the spicule where the defective arms would arise. Let fig. 12 *e* represent a regular sexradiate spicule with its four horizontal arms extended beneath the dermis of its sponge; the over-development of the proximal ray and a reduction of the distal ray produce a form known as the *dagger* (fig. 15 *a*); the suppression of the proximal ray and the development of spines projecting forwards on the distal ray produce the *pinnulus* (fig. 15 *b*, *c*); the suppression of both proximal and distal rays gives the *staurus* (fig. 15 *f*), and the suppression of two of the remaining horizontal rays a dermal rhabdus (fig. 15 *g*). The suppression of a distal ray, excessive development of a proximal ray, and recurved growth of the remaining rays produce an *anchor*. In *Hyalonema* (glass rope sponge) anchors over a foot long occur, but their arms or teeth are not restricted to four, and the axial fibre gives off its processes before reaching the head of the spicule. Such a grapnel helps to support the sponge in the ooze of the sea-bed. Other characteristic spicules belonging to sponges distinguished by sexradiate spicules are the following:—the *uncinaria* (fig. 16 *a*), a spinose oxea with the spines all pointing one way; the *clavula*, a tylotate form with a toothed margin to the head (fig. 16 *b*); the *scopularia* (fig. 16 *c*), a besom-shaped spicule with tylotate rays, which vary in number from two to eight; the *amphidisk* (fig. 15 *d*), a shaft terminating at each end in a number of recurved rays. When the sexradiate spicules of the *Hexactinellida* unite together in a manner to be described later, the rays may be bent in a variety of ways out of the triaxial type, so that the sexradiate character alone remains.

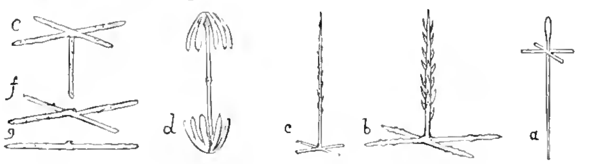

FIG. 15.—Modifications of the triaxon hexactine type. *a*, dagger; *b*, *c*, two varieties of pinnulus; *d*, amphidisk; *e*, pentactine; *f*, staurus; *g*, dermal rhabdus. After Schulze.

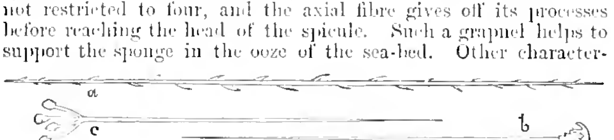

FIG. 16.—*a*, uncinaria; *b*, clavula; *c*, scopularia. After Schulze.

Multiradiate type.

Multiradiate Type.—The rays of an aster as of other spicules may be spined or tylotate. In one remarkable form known as a *sterraster* (fig. 12 *g*, *h*), and characteristic of the family *Geodinidæ*, the rays are almost infinite in number, and coalesced for the greater part of their length; the distal ends, however, remain separate, and, becoming slightly tylotate, are produced into four or five recurved spines, which give attachment to connective tissue fibres by which adjacent sterrasters are united together.

In one aberrant group of Lithistid sponges (*Anomocladina*) the skeleton is formed of desmas, which are multiradiate, each presenting a massive centrum (with an included cavity) produced into a variable number (4 to 8) of rays, which rays terminate in expanded ends (fig. 12 *f*).

Microscleres

It is doubtful whether a distinction between megascleres and microscleres can be maintained in the calcareous sponges, unless the minute oxeas which occur in *Eilhardia schulzei*, Pol. (*16*), are to be referred to this group. They are widely distributed throughout the silicious sponges, and by their different forms afford characters of the highest importance in classification.

One of the simplest forms is the *sigmaspire* (fig. 17 *a*, *b*); it looks like the letter C or S, according to the direction in which it is viewed, its actual form being that of a single turn of a cylindrical spiral. A turn and a part of a turn of a spiral of somewhat higher pitch than that of a sigmaspire gives the *toxaspire* (fig. 17 *c*); a continued spiral growth through several revolutions gives the *polyspire*. The sigmaspire becoming spined produces the *spiraster* or *spinispirula* (fig. 17 *d*); this, by losing its curvature, becomes the *sanidaster* (fig. 17 *e*), and by simultaneous concentration of its spines into a whorl at each end, the *amphiaster* (fig. 17 *f*). By reduction of the spire the spiraster passes into the *stellate* or *aster* (fig. 17 *n*). A thickening about the centre of the aster produces the *spheraster* (fig. 17 *m*), allied to which is the sterraster. By a reduction in the number of its rays the aster becomes a minute calthrops, from which, by increased growth, the skeletal calthrops may very well be derived; by further reduction to two rays a little rhabdus or microrabd results, and of this numerous varieties exist, of which the oxeate microrabd is the most interesting, since it only differs in size from the commonest of all skeletal spicules, the oxeate or acerate rhabdus. The sigmaspire is formed as a superficial spiral thickening in the wall of a spicule cell or scleroblast; as superficial deposits also the next group of spicules, the so-called *anchorates*, arise. Take a hen's egg as the model of a scleroblast, draw round it a broad meridional band, interrupted only on one side, for 30° above and below the equator; this will represent a truly C-shaped spicule, which differs from a sigmaspire by the absence of spiral twist. It may be termed a *cymba* (fig. 17 *g*). The back of the "C" is the *keel* or *tropis*; the points are the *prows* or *proræ*. Now broaden out the prora on the eggshell into oval lobes (*proral pteres*); and from each pole draw a lobe midway between the prora and the tropis (*pleural pteres*), and a common form of anchorate, the *pterocymba*

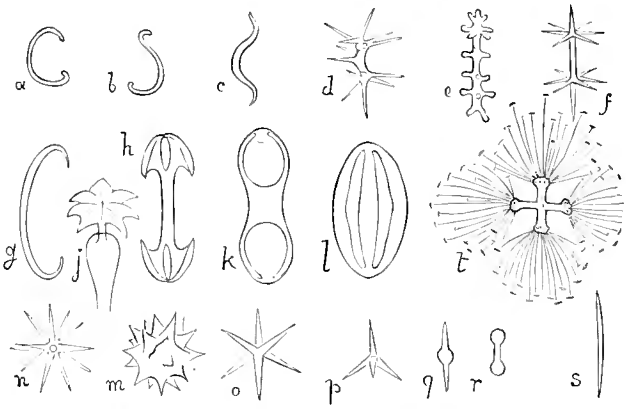

FIG. 17—Microscleres. *a*, *b*, sigmaspire viewed in different directions,—*a*, along axis, and *b*, obliquely; *c*, toxaspire; *d*, spiraster; *e*, sanidaster; *f*, amphiaster; *g*, sigma or cymba; *h*, cymba, with three ptera at each end,—the central one a proral pteron and the lateral, pleural ptera; *j*, one end of another form of cymba, showing seven ptera; *k*, monopteral cymba,—proral ptera only, developed at ends, tropidial ptera much enlarged; *l*, oocymba, in which proral and pleural ptera have grown towards each other and coalesced; *m*, spheraster; *n*, oxyaster; *o*, the same, with six actines; *p*, the same, with four actines; *q*, the same, with two actines (a centrotylote microxea); *r*, microtylote; *s*, microxea (*q*, *r*, and *s* are reduced asters); *t*, rosette.

results (fig. 17 *h*). The pterocymba is subject to considerable modifications: the prows may be similar (*homoproral*) or dissimilar (*heteroproral*); the pteres may be lamellar or ungual; additional lamellæ (*tropidial pteres*) may be produced by a lateral outgrowth of the keel (fig. 17 *k*); and by growing towards the equator the opposed proral and pleural pteres may conjoin, producing a spicule of two meridional bands (*oocymba*; fig. 17 *l*). A curious group of flesh spicules are the *trichites*. In this group silica, instead of being deposited in concentric coatings around an axial fibre, forms within the scleroblast a sheaf of immeasurably fine fibrillæ or trichites, which may be straight (fig. 17 *m*) or twisted. The trichite sheaf may be regarded as a fibrillated spicule. Trichite sheaves form in some sponges, as *Dragmastra* (*25*), a dense accumulation within the cortex. In Hexactinellid sponges the rays of the aster are limited to six, arranged as in a primitive sexradiate spicule, but divided at the ends into an indefinite number of slender filaments, which may or may not be tylotate, *rosettes* (fig. 17 *t*).

Spongin scleres. Spongin is a horny substance, most similar to silk in chemical composition, from which it differs in being insoluble in an ammoniacal solution of copper sulphate (cuproso-ammonium sulphate). In *Darwinella aurea*, F. Müller, it occurs in forms somewhat resembling tri-, quadri-, and sex-radiate spicules. But usually the spongin skeleton takes the form of fibres, consisting of a central core of soft granular substance around which the spongin is disposed in concentric layers, forming a hollow cylinder (fig. 23 *b*). The relative diameters of the soft core and of the spongin cylinder differ greatly in different sponges. The fibres branch so as to form antler-like twigs or bushy tree-like growths, or anastomose to form a continuous network, as in the bath sponge (*Euspongia officinalis*). The detailed characters of the network differ with the species, and are useful in classification. In *Ianthella* certain cells (sponginblasts) become included between the successive layers of the spongin cylinder, and their deep violet colour, contrasting with the amber tint of the spongin, renders them very conspicuous.

Union of scleres into a skeleton. In some sponges the scleres are simply scattered through the mesoderm and do not give rise to a continuous skeleton,—*Corticium*, *Chondrilla*, *Thrombus*. In the *Calcarea* and many silicious sponges they are dispersed through the mesoderm, but so numerously that by the overlapping of their rays a loosely felted skeleton is produced. In the calcareous sponges the spicules are frequently regularly disposed; and in the Sycons in particular a definite arrangement, on two plans, the *articulate* and *inarticulate*, can be traced in the skeleton of the radial tubes. On the latter plan the triradiate or quadriradiate spicules, the apical rays of which are of considerable length, are arranged in two sets, one having the basal rays lying in the mesoderm of the paragastral wall and the other with the corresponding rays in the dermal mesoderm. The apical rays of each set lie in the mesoderm of the radial tubes parallel to their length, but pointing in opposite directions (fig. 18 *b*). In the articulate division numerous spicules, small in comparison with the size of the radial tubes, form a series of rows round the tubes, their basal rays lying parallel to the paragastric surface and the apical pointing towards the ends of the radial tubes (fig. 18 *a*).

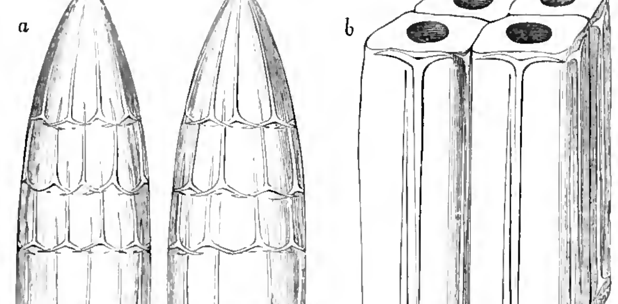

FIG. 18.—Articulate and inarticulate tubar skeletons of calcisponges. *a*, articulate; *b*, inarticulate skeleton. After Haeckel.

In the *Silicispongia* sheaves of long oxeate spicules radiate from the base of the sponge if of a plate-like form, or from the centre if globular, and extend to the surface. If triænes are present their arms usually extend within the mesoderm immediately below the dermal surface (fig. 19). Single spicules reach from centre to surface only in small sponges. As the sponge increases in size the spicules must either correspondingly lengthen, or fresh spicules must be added, if a continuous skeleton is to be formed. The latter is the plan followed in fact: the additional spicules overlap the ends of those first formed like the fusiform cells in a woody fibre. With the formation of a fibre, often strengthened by spongin or bound together with connective tissue, there appears to be a tendency for the constituent spicules to diminish in size, and the length of each in the most markedly fibrous sponges is insignificant when compared with the length of the fibre. The spicular fibre thus formed may be simple or echinated by spicules either similar to those which form its mass or different. More usually they are different, and generally styles, often spinose about their origin. The spongin which sometimes cements together the spicules of a fibre may progressively increase in quantity and the spicules diminish in number, till a horny fibre containing one or more rows of small oxeas results. In an echinated fibre the axial spicules may disappear and the echinating spicules persist. Finally all spicules may be suppressed and the horny fibre of the Ceratose sponges results. The horny fibres may next acquire the habit of embedding foreign bodies in their substance, though foreign enclosures are not confined to the *Ceratosa* but occur in some *Silicispongiæ* as well. The included foreign bodies may increase in quantity out of all proportion to the horny fibres; and finally the skeleton may consist of them alone, all spongin matter having disappeared.

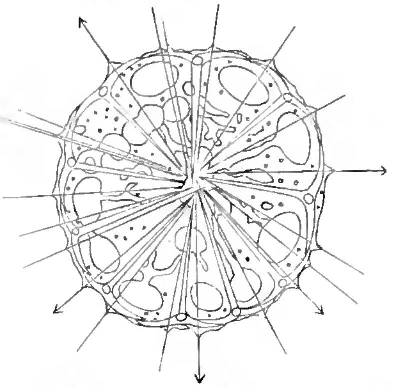

FIG. 19.—Mode of arrangement of spicules in a young Stellettid sponge, *Dragmastra normani*, Soll. After Sollas.

In the Lithistid sponges a skeleton is produced by the articulation of desmas into a network. The rays of the desmas (figs. 12 *f*, 13 *s*, 14 *c*) terminate in apophyses, which apply themselves to some part of adjacent desmas, either to the centrum, shaft, arms, or similar apophyses, and then, growing round them like a saddle on a horse's back, clasp them firmly without anchylosis. Thus they give rise to a rigid network, in conjunction with which fibres composed of rhabdus spicules may exist. In the *Hexactinellida* both spicular felts and fibres occur, and in one division (*Dictyonina*) a rigid network is produced, not, however, by a mere clasping of apophyses, but by a true fusion. The rays of adjacent spicules overlap and a common investment of silica grows over them.

Histology.

Ectoderm. The ectoderm usually consists of simple pavement epithelial cells (*pinnacocytes*), the margins of which can be readily rendered visible by treatment with silver nitrate, best by Harmer's method.[1] The nucleus and nucleolus are usually visible in preparations made from spirit specimens, the nucleus being often readily recognizable by its characteristic bulging beyond the general surface. In some sponges (*Theraphora*) the epithelium may be replaced locally by columnar epithelium, and the cells of both pavement and columnar epithelium may bear flagella (*Aplysilla violacea*, *Oscarella lobularis*). **Endoderm.** The endoderm presents the same characters as the ectoderm, except in the Ascons and the flagellated chambers of all other sponges, where it is formed of collared flagellated cells or *choanocytes*,—cells with a nearly spherical body in which a nucleus and nucleolus can be distinguished and one or more contractile vacuoles. The endoderm extends distally in a cylindrical neck or *collum*, which terminates in a long flagellum surrounded by a delicate protoplasmic frill or collar (fig. 21 *g*). In *Tetractinellida*, and probably in many other sponges—certainly in some—the collars of contiguous choanocytes coalesce at their margins so as to produce a fenestrated membrane, which forms a second inner lining to the flagel-

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[1] S. F. Harmer, "On a Method for the Silver Staining of Marine Objects," *Mitth. Zoolog. Station zu Neapel*, 1884, p. 445.

lated chamber (fig. 20, ii.). The presence of this membrane enables us readily to distinguish the excurrent from the incurrent face of the chamber, since its convex surface is always turned towards the prosopyle. In sponges with an aphodal canal system the flagellated chambers usually pass gradually into the aphodal canal, but the incurrent canal enters abruptly. This abrupt termination of the incurrent canal appears to mark the termination of the ectoderm and the commencement of the endoderm. The flagellated chambers differ greatly in size in different sponges, and evidently manifest a tendency to become smaller as the canal system increases in complexity; thus Sycon are always larger than Rhagon chambers, and eurypylous than aphodal Rhagon chambers. In most sponges except the Ascons the mesoderm is largely developed, and in many it undergoes a highly complex histological differentiation. In its commonest and simplest form it consists of a clear, colourless, gelatinous matrix in which irregularly branching stellate cells or connective tissue corpuscles are embedded; these may be termed *collencytes* (fig. 21 *a*) and the tissue *collenchyme*. In the higher sponges (*Geodia*, *Stelletta*) it consists of small polygonal granular cells either closely contiguous or separated by a very small quantity of structureless jelly, and in this form may be termed *sarcenchyme* (fig. 20). Collenchyme does not originate through the transformation of sarcenchyme, as one might expect, for it precedes the latter in development. Schulze (*20*), who has compared collenchyme to the gelatinous tissue which forms the chief part of the umbrella of "jelly-fish," describes it as becoming granular immediately in the neighbourhood of the flagellated chambers in the bath sponge, the granules becoming more numerous in sponges in which the canal system acquires a higher differentiation, till at length the collencytes are concealed by them. According to this view, sarcenchyme would appear to originate from a densely granular collenchyme. Amœboid wandering cells or *archæocytes* (fig. 22) are scattered through the matrix of the collenchyme. They evidently serve very different purposes: some appear to act as carriers of nourishment or as scavengers of useless or irritant foreign matter; others may possibly contribute to the formation of higher tissues, some certainly becoming converted into sexual products. Their parentage and early history are unknown.

Mesoderm.

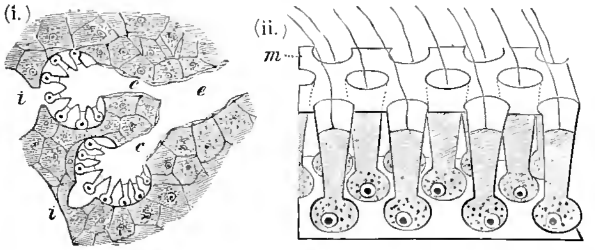

Fig. 20.—Choanocytes with coalesced collars. (i.) Longitudinal section through two flagellated chambers of *Anthastra communis*, Soll.; *i*, prosopyles; *c*, aphodal canals leading from the flagellated chambers; *e*, excurrent canal; the tissue surrounding the chambers is sarcenchyme (×360). (ii.) Diagram showing the fenestrated membrane (*m*) produced by coalesced collars of choanocytes. After Sollas, "*Challenger*" *Report*.

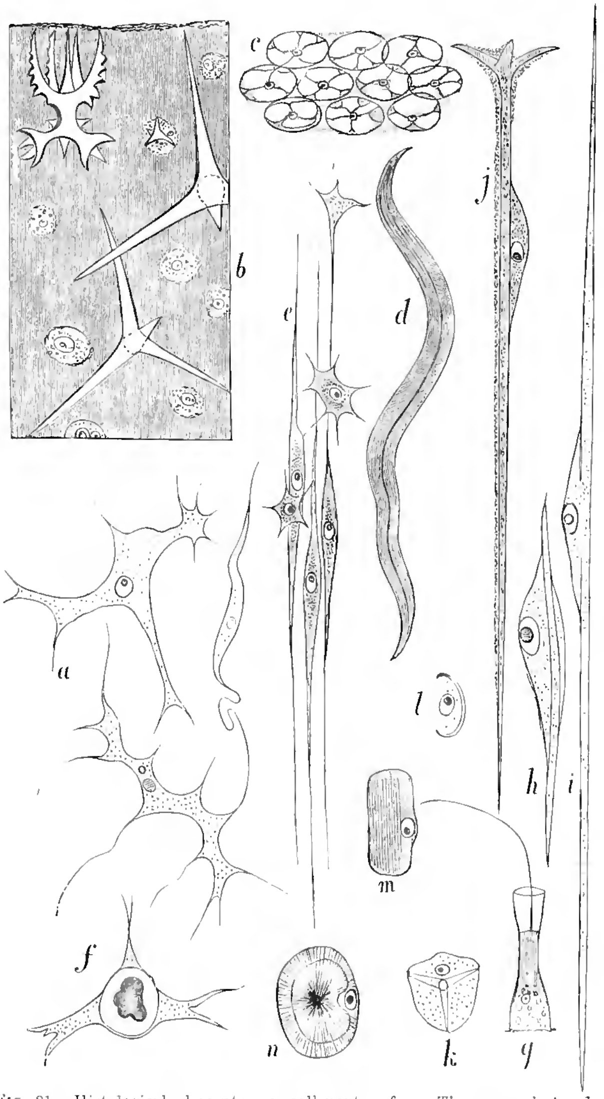

Fig. 21.—Histological elements. *a*, collencytes, from *Thenea muricata*; *b*, chondrenchyme, from cortex of *Corticium candelabrum* (the unshaded bodies are microscleres); *c*, cystenchyme, from *Pachymatisma johnstoni* (partly diagrammatic); *d*, desmacyte, from *Dragmastra normani*; *e*, myocytes in connexion with collencytes, from *Cinachyra barbata*; *f*, thesocyte, from *Thenea muricata*; *g*, choanocyte, from *Sycandra raphanus*; *h*–*n*, scleroblasts—*h*, of a young oxea, from an embryo of *Craniella cranium*; *i*, of a fully grown oxea, from an adult *C. cranium*; *j*, orthotriaene, with associated scleroblast from *Stelletta*; *k*, of a tetracladine desma, from *Theonella swinhoei*; *l*, of a sigmaspire, from *Craniella cranium*; *m*, of an orthodragma, from *Disyringa dissimilis*; *n*, of a sterraster, from *Geodia barretti*. Figs. *b* and *g* after Schulze, the others after Sollas.

A tissue (*cystenchyme*) which in some respects resembles certain forms of vegetable parenchyme occurs in some sponges, particularly *Geodinidæ* and other *Tetractinellida*. It consists of closely adjacent large oval cells, with thin well-defined walls and fluid contents. Somewhere about the middle of the cell is the nucleus with its nucleolus, supported by protoplasm, which extends from it in fine threads to the inner side of the wall, where it spreads out in a thin investing film (fig. 21 *c*). Cystenchyme very commonly forms a layer just below the skin of some *Geodinidæ*, particularly of *Pachymatisma*, and, as on teasing the cortex of this sponge a large number of refringent fluid globules immiscible with water are set free, it is just possible that it is sometimes a fatty tissue, and if so the contained oil must be soluble in alcohol, for alcoholic preparations show no trace of it. A tissue resembling cartilage, *chondrenchyme*, occurs in *Corticidæ* (fig. 21 *b*).

Desmacytes.

Connective-tissue cells or *desmacytes* are present in most sponges; they are usually long fusiform bodies, consisting of a clear, colourless, often minutely fibrillated sheath, surrounding a highly refringent axial fibre, which stains deeply with reagents (fig. 21 *d*). In other cases the desmacyte is simply a fusiform granular cell, with a nucleus in the interior and a fibrillated appearance towards the ends. The desmacytes are gathered together, their ends overlapping, into fibrous strands or felted sheets, which in the ectosome of some sponges may acquire a considerable thickness, often constituting the greater part of the cortex. The spicules of the sponge often furnish them with a surface of attachment, especially in the *Geodinidæ*, where each sterraster of the cortex is united to its neighbours by desmacytes, in the manner shown in fig. 10.

Myocytes.

Contractile fibre cells or *myocytes* occur in all the higher sponges. They appear to be of more than one kind. Most usually they are fine granular fusiform cells with long filiform terminations, and with an enclosed nucleus and nucleolus (fig. 21 *e*). In the majority of sponges both excurrent and incurrent canals are constricted at intervals by transverse diaphragms or *vela*, which contain myocytes concentrically and sometimes radiately arranged. The excessive development of myocytes in such a velum gives rise to muscular sphincters such as those which close the chones of many corticate sponges, such as *Pachymatisma*. In this sponge, which occurs on the British shores, the function of the oscular sphincters can be readily demonstrated, since irritation of the margin of the oscule is invariably followed after a short interval by a slow closure of the sphincter.

Æsthacytes. Supposed sense-cells or *æsthacytes* (fig. 22) were first observed by Stewart and have since been described by Von Lendenfeld (*12*). According to the latter, they are spindle-shaped cells, 0·01 mm. long by 0·002 thick; the distal end projects beyond the ectodermal epithelium in a fine hair or palpocil; the body is granular and contains a large oval nucleus; and the inner end is produced into fine threads, which extend into the collenchyme and are supposed—though this is not proved—to become continuous with large multiradiate collencytes, which Von Lendenfeld regards as multipolar ganglion cells (fig. 22).

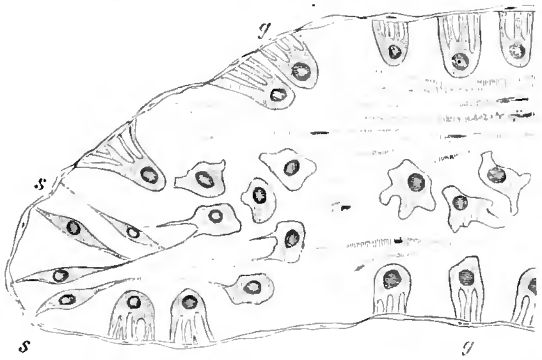

FIG. 22.—Transverse section through the edge of a pore in *Dendrilla cavernosa*, Lfd.; cells in the middle to the right, archæocytes; fusiform cells on each side of them, myocytes; *g*, above and below these, with processes terminating against the epithelium, gland cells; fusiform cells terminating against the epithelium at *s*, æsthacytes; at their inner ends these are continuous with ganglion cells. After Von Lendenfeld (× 800).

More recently he has described an arrangement of these cells curiously suggestive of a sense-organ. Numerous æsthacytes are collected over a small area, and at their inner ends pass into a granular mass of cells with well-marked nuclei, but with boundaries not so evident; these he regards as ganglion cells. From the sides of the ganglion other slender fusiform cells, which Von Lendenfeld regards as nerves, pass into the mesoderm, running tangentially beneath the skin. The inner end of the ganglion is in communication with a membrane formed of fusiform cells which Von Lendenfeld regards as muscular. If his observations and inferences are confirmed, it is obvious that we have here a complete apparatus for the conversion of external impressions into muscular movements.

Protoplasmic continuity. In most sponges a direct connexion can be traced by means of their branching processes between the collencytes of the mesoderm and the cells of the ectodermal and endodermal epithelium and the choanocytes of the flagellated chambers. As the collencytes are also united amongst themselves, they place the various histological constituents of the sponge in true protoplasmic continuity. Hence we may with considerable probability regard the collencytes as furnishing a means for the transmission of impulses: in other words, we may attribute to them a rudimentary nervous function. In this case the modification of some of the collencytes in communication with the ectoderm might readily follow and special æsthacytes arise. Fusiform collencytes perpendicular to the ectoderm, and with one end touching it, are common in a variety of sponges; but it is difficult to trace the inner end into connexion with the stellate collencytes, so that precisely in those cases in which it would be most interesting to find such a connexion absolute proof of it is wanting.

Pigment cells. The colour of sponges usually depends on the presence of cells containing granules of pigment; though dispersed generally through the mesoderm, these cells are most richly developed in the ectosome. Pigment granules also occur in the choanocytes of some sponges,—*Oscarella lobularis* and *Aplysina aerophoba*, for instance. In the latter the pigment undergoes a remarkable change of colour when the sponge is exposed to the air, and finally fades away. In many cases sponges borrow their colours from parasitic algæ (*Oscillatoria* and *Nostoc*) with which they are infested. The colours of sponge-pigments are very various. They have been examined by Krukenberg and Merejknovsky. Zoonerythin, a red pigment of the lipochrome series, is one of the most widely diffused; it is regarded as having a respiratory function. Reserve cells or *thesocytes* (fig. 21 *f*) have been described in several sponges as well as amylin and oil-bearing cells.

Scleroblasts. Each spicule of a sponge originates in a single cell (fig. 21 *h-n*), within which it probably remains enclosed until it has completed its full growth; the cell then probably atrophies. During its growth the spicule slowly passes from the interior to the exterior of the sponge, and is finally (in at least some sponges, *Geodia*, *Stelletta*) cast out as an effete product. The sponge is thus constantly producing and disengaging spicules; and in this way we may account for the extraordinary profusion of these structures in some modern marine deposits and in the ancient stratified rocks. Within the latter these deciduous spicules have furnished silica for the formation of flints, which have been produced by a silicious replacement of carbonate of lime (*26*).

The horny fibres of the *Ceratosa* are produced as a secretion of cells known as *sponginblasts*, which surround as a continuous mantle the sides of each growing fibre, and cover in a thick cap each growing point (fig. 23). The lateral sponginblasts are elongated radially to the fibre; the terminal cells are polygonal and depressed. The latter give rise to the soft granular core and the former to the spongin-walls of the fibre. Cells similar to the lateral sponginblasts, and regarded as homologous with them, occur in a single layer just below the outer epithelium of some horny sponges (*Aplysilla* and *Dendrilla*), and under certain circumstances secrete a large quantity of slimy mucus (*11*).

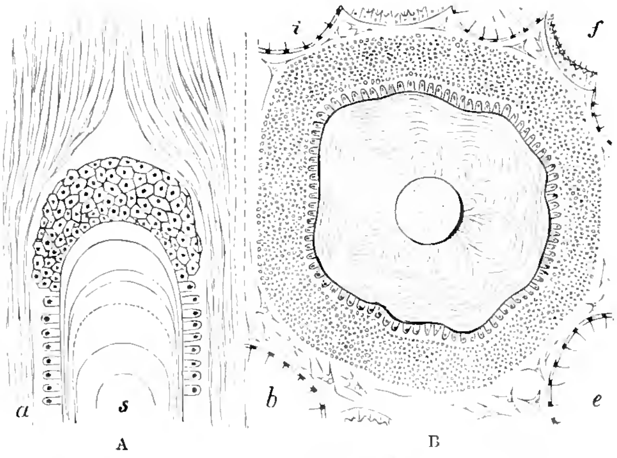

FIG. 23.—Section through the horny fibre and associated tissues of a horny sponge (*Dendrilla*). A, longitudinal section; *s*, layers of spongin, surrounded at the sides by the lateral mantle of sponginblasts, and at the ends by the terminal cap. A desmachymatous sheath, *a*, surrounds the whole (× 150). B, transverse section; in the centre is the soft core, surrounded by wavy spongin layers, the outermost being surrounded by sponginblasts, and these by a fibrous sheath; *i*, part of an incurrent canal lined by flagellated epithelium; *e*, part of an excurrent canal; *f*, part of a flagellated chamber (× 150). After Von Lendenfeld.

Classification.

Classification. The phylum *Parazoa* or *Spongiæ* consists of two main branches, as follows:—

Branch A.—*MEGAMASTICTORA.*
- Class CALCAREA, Grant.
  - Order 1.—*Homocœla*, Pol.
  - Order 2.—*Heterocœla*, Pol.

Branch B.—*MICROMASTICTORA.*
- Class I.—MYXOSPONGIÆ, Haeckel.
  - Order 1.—*Halisarcina.*
  - Order 2.—*Chondrosina.*
- Class II.—SILICISPONGIÆ.
  - Sub-class i.—HEXACTINELLIDA, O. Schmidt.
    - Order 1.—*Lyssacina*, Zittel.
    - Order 2.—*Dictyonina*, Zittel.
  - Sub-class ii.—DEMOSPONGIÆ, Sollas.
    - Tribe *a*.—**Monaxonida.**
      - Order 1.—*Monaxona.*
      - Order 2.—*Ceratosa*, Grant.
    - Tribe *b*.—**Tetractinellida**, Marshall.
      - Order 1.—*Choristida*, Sollas.
      - Order 2.—*Lithistida*, O.S.

Position in animal kingdom. By the possession of both sexual elements and a complex histological structure, and in the character of their embryological development, the sponges are clearly separated from the *Protozoa*; on the other hand, the choanoflagellate character of the endoderm, which it retains in the flagellated chambers throughout the group without a single exception, as clearly marks them off from the *Metazoa*. They may therefore be regarded as a separate phylum derived from the choanoflagellate *Infusoria*, but pursuing for a certain distance a course of development parallel with that of the *Metazoa*.

Different views have been propounded by other authors. Savile Kent regards the sponges as *Protozoa* (*10*); Balfour suggested that they branched off from the Metazoan phylum at a point below the *Cœlentera*, and considered them as intermediate between *Protozoa* and *Metazoa*; Schulze regards them as derived from a simple ancestral form of *Cœlentera* (*23*); Marshall advocates the view that they are degraded forms derived from Cœlenterates which were already in possession of tentacles and mesenteric pouches (*14*).

Subdivision in groups. As a phylum the *Spongiæ* are certainly divisible into two branches, one including the *Calcarea* and the other the remaining sponges, which Vosmaer has termed *Non-Calcarea*, and others *Plethospongiæ*. Since, however, the choanocytes of the *Calcarea* are usually, if not universally, larger than those of other sponges, we may make use of this difference in our nomenclature, and distinguish one branch as the *Megamastictora* (μαστίκτωρ, "scourger") and the other as the *Micromastictora*.

Branch A.—*MEGAMASTICTORA.*

Sponges in which the choanocytes are of comparatively large size, 0·005 to 0·009 mm. in diameter (Haeckel, *6*).

Class **CALCAREA.**

Calcarea. *Megamastictora* in which the skeleton is composed of calcareous spicules.

Order 1. HOMOCŒLA.—*Calcarea* in which the endoderm consists wholly of choanocytes. Examples: *Leucosolenia*, Bwk.; *Homoderma*, Lfd.

Order 2. HETEROCŒLA.—*Calcarea* in which the endoderm is differentiated into pinnacocytes, which line the paragastric cavity and excurrent canals, and choanocytes, which are restricted to special recesses (radial tubes or flagellated chambers). Examples: *Sycon*, O.S.; *Grantia*, Fl.; *Leuconia*, Bwk.

Branch B.—*MICROMASTICTORA.*

(*Non-Calcarea*, Vosmaer; *Plethospongiæ*, Sollas.) Sponges in which the choanocytes are comparatively small, 0·003 mm. in diameter.

Class I. **MYXOSPONGIÆ.**

Myxospongiæ. *Micromastictora* in which a skeleton or scleres are absent.

Order 1. HALISARCINA.—*Myxospongiæ* in which the canal system is simple, with simple or branched Sycon or eurypylous Rhagon chambers. An ectosome sometimes and a cortex always absent. Examples: *Halisarca*, Duj.; *Oscarella*, Vosm.; *Bajulus*, Lfd.

Order 2. CHONDROSINA.—*Myxospongiæ* in which the canal system is complicated, with diplodal Rhagon chambers and a well-developed cortex. Example: *Chondrosia*, O.S.

The *Halisarcina* are evidently survivals from an ancient and primitive type. The simplicity of the canal system is opposed to the view that they are degraded forms; we may therefore regard the absence of scleres as a persistent primary and not a secondary acquired character. They are as interesting, therefore, from one point of view (absence of scleres) as the Ascons are from another (undifferentiated endoderm). With the *Chondrosina* the case is different; they differ only from *Chondrilla* and its allies by the absence of asters; these differ only from the *Tethyidæ* by the absence of strongyloxeas; and we may very reasonably assume that in these three groups we have a series due to loss of characters, the *Chondrillæ* being reduced *Tethyidæ* and the *Chondrosina* reduced *Chondrillæ*. Still, as Huxley has well remarked, "classification should express not assumptions but facts"; and therefore till we are in possession of more direct evidence it will be well to exclude the *Chondrosina* from the *Silicispongiæ*.

Class II. **SILICISPONGIÆ.**

Micromastictora possessing a skeleton or scleres which are not calcareous.

Sub-class i. **HEXACTINELLIDA.**

Hexactinellida. *Silicispongiæ* characterized by sexradiate silicious spicules. Canal system usually simple, with Sycon chambers. Sponge differentiated into ecto-, choano-, and endo-some.

Order 1. LYSSACINA.—*Hexactinellida* in which the skeleton is formed of separate spicules, or, if united, then by a subsequent not a contemporaneous deposit of silica. Examples: *Euplectella*, Owen; *Asconema*, S. Kent; *Hyalonema*, Gray; *Rossella*, Crtr.

Order 2. DICTYONINA.—*Hexactinellida* in which sexradiate spicules are cemented together by a silicious deposit into a continuous network *pari passu* with their formation. Examples: *Farrea*, Bwk.; *Eurete*, Marshall; *Aphrocallistes*, Gray; *Myliusia*, Gray; *Dactylocalyx*, Stutchbury.

The *Hexactinellida* are a very sharply defined group, impressed with marked archaic features. No other *Silicispongiæ* possess, so far as is known, so simple a syconate canal system. The oldest known fossil sponge is a member of the *Lyssacina* (*7* and *24*), viz., *Protospongia*, Salter, from the Menevian beds, Lower Cambrian, St David's Head, Wales. The group is almost world-wide in distribution, chiefly affecting deep water, from 100 to 300 fathoms, but often extending into abyssal depths; occasionally, however, though rarely, it frequents shallow water (*Cystispongia superstes* dredged off Yucatan in 18 fathoms).

Sub-class ii. **DEMOSPONGIÆ.**

Demospongiæ *Silicispongiæ* in which sexradiate spicules are absent.

Tribe *a*. *MONAXONIDA.*

Demospongiæ in which the skeleton consists either of silicious spicules which are not quadriradiate, or of horny scleres or included foreign bodies, or of one or more of these constituents in conjunction.

Order 1. MONAXONA.—The skeleton is characterized by either uniaxial or polyaxial spicules. Examples: *Amorphina*, O.S. ("crumb of bread" sponge); *Spongilla*, Lmk. ("freshwater" sponge); *Chalina*, Bwk.; *Tethya*, Lmk.

Order 2. CERATOSA.—The skeleton consists of horny scleres which never include "proper" spicules, or of introduced foreign bodies, or of both these in conjunction. Examples: *Darwinella*, F. Müller; *Euspongia*, Bronn (the "bath" sponge).

Tribe *b*. *TETRACTINELLIDA.*

Demospongiæ possessing quadriradiate or triæne spicules or Lithistid scleres (desmas).

Order 1. CHORISTIDA.—*Tetractinellida* with quadriradiate or triæne spicules, which are never articulated together into a rigid network. Examples: *Tetilla*, O.S.; *Thenea*, Gray; *Geodia*, Lmk.; *Dercitus*, Gray.

Order 2. LITHISTIDA.—*Tetractinellida* with branching scleres (desmas), which may or may not be modified tetrad spicules, articulated together to form a rigid skeleton. Triæne spicules may or may not be present in addition. Examples: *Theonella*, Gray; *Corallistes*, O.S.; *Azorica*, Crtr.; *Vetulina*, O.S.

This large sub-class embraces the great majority of existing sponges. Its external boundaries are fairly well defined, its internal divisions much less so, as its various orders and families pass into each other at many points of contact. Although there does not appear to be much resemblance between a Lithistid sponge, such as *Theonella*, a Monaxonid such as *Amorphina*, and an ordinary "bath" sponge (*Euspongia*), yet between these extremes a long series of intermediate forms exists, so nicely graduated as to render their disruption into groups by no means an easy task. If the delimitation of orders is difficult, that of genera is often impossible, so that they are reduced to assemblages depending on the tact or taste of the author. Thus Polejaeff states that with a single exception "none of the genera of *Ceratosa* are separable by absolute characters." The chief spicules of *Monaxona* are uniaxial, often accompanied by characteristic microscleres. Although distinguished as a group by the absence of quadriradiate or triæne spicules, two exceptions are known in which these occur (*Tricentrion*, Ehlers, and *Acarnus*, Gray); these, however, present unusual characters which suggest an independent origin. The canal system of *Monaxona* has not yet been fully investigated; it appears usually to follow the eurypylous Rhagon type, but the aphodal is not unknown. The *Ceratosa* contain all sponges with a horny skeleton, except those in which the horny fibres are cored or spined with silicious spicules secreted by the sponge ("proper" spicules); these are arbitrarily assigned to the *Monaxona*. There is convenience in this proceeding, for horny matter is widely disseminated throughout the *Demospongiæ*, occurring even in the *Lithistida*, and it frequently serves to cement the oxeate spicules of the *Monaxona* into a fibre, without at the same time forming a preponderant part of the skeleton. It would be wellnigh impossible to say where the line should be drawn between a fibre composed of spicules cemented by spongin and one consisting of spongin with embedded spicules, while there is comparatively no difficulty in distinguishing between fibres containing spicules and fibres devoid of them. That the distinction, however, is entirely artificial is shown by the fact that, after spicules have disappeared from the horny fibre, they may still persist in the mesoderm; thus Von Lendenfeld announces the discovery of microscleres (cymba) in an Aplysillid sponge and of strongyles in a *Cacospongia*, both horny sponges. (A form intermediate between this Aplysillid and the *Desmacidonidæ* would appear to be *Toxochalina*, Ridley.) The *Ceratosa* frequently enclose sand, *Foraminifera*, deciduous spicules of other sponges and of compound Ascidians, and other foreign bodies within the horny fibres of their skeleton; they also sometimes attach this material, probably by a secretion of spongin, to their outer surface, and thus invest themselves in a thick protective crust. In some *Ceratosa* no other skeleton than that provided by foreign enclosures is present. The canal system is syconate or eurypylous in the simpler forms and diplodal in the higher. The *Monaxonida* make their earliest appearance in the Silurian rocks (*Climacospongia*, Hinde), and are now found in all seas at all depths. The only sponges inhabiting fresh water belong to this group. The *Tetractinellida* adhere to the *Monaxonida* at more than one point, and one of these groups has probably been a fruitful parent to the other, but which is offspring and which parent is still a subject for discussion. The *Choristida* in its simplest forms presents a eurypylous Rhagon system, in the higher an aphodal system. It is in this group that the most highly complex cortex is met with; in the *Geodinidæ*, for instance, it consists usually of at least five distinct layers. Thus, proceeding outwards, next to the choanosome is a layer of thickly felted desmachyme, passing into collenchyme on its inner face; then follows a thick stratum of sterrasters united together by desmacytes; this is succeeded by a layer of cystenchyme or other tissue of variable thickness; external to this is a single layer of small granular cells and associated dermal asters; and finally, the surface is invested by a layer of pavement epithelium. The *Lithistida*, like the *Ceratosa*, are possibly of polyphylitic origin; in one group (*Tetracladina*) the articulated scleres are evidently modified calthrops spicules (see fig. 14 *c*), and associated with them are free triænes, which support the dermis and resemble precisely the triænes of the *Choristida*. In another group (*Rhabdocrepida*) the scleres are moulded on a Monaxonid base (see fig. 13 *q-s*); but, associated with them, triænes sometimes occur similar to those of the *Tetracladina*. Both these groups are in all probability derived from the *Choristida*, and a distinct passage can be traced from the Tetracladose to the Rhabdocrepid group. In the *Rhabdocrepida* we find forms without triænes; these may possibly be degenerate forms. The third group of Lithistids is derived from the *Rhabdocrepida*, the Anomocladine desma being derivable from the Rhabdocrepid by a shortening of the main axis into a centrum. The thick centrum, from which the arms, variable in number, originate, is hollowed out by a cavity, which appears during life to have been occupied by a large nucleus, like that of a scleroblast, and it is quite conceivable that the scleroblast, which in the Tetracladine Lithistids lies in an angle between the arms, may have become enclosed in an overgrowth of silica, from which additional arms were produced. The constancy with which spicules in other sponges maintain their independence is very striking. When once a persistent character like this is disturbed, excessive variability may be predicted, as in the Anomocladine scleres.

Classification in families.

The classification of the sponges into families is shown in the following scheme.

Class *CALCAREA*.

Order 1. **HOMOCŒLA**, Pol.

Family 1. Asconidæ, Hk.—*Homocœla* which are simple or composite, but never develop radial tubes. Examples: *Ascetta*, Hk. (fig. 1); *Leucosolenia*, Bwk.

Family 2. Homodermidæ, Lfd.—*Homocœla* with radial tubes. Example: *Homoderma*, Lfd. (figs. 3, 4).

Order 2. **HETEROCŒLA**, Pol.

Tribe *a*. †Syconaria.[1]

The flagellated chambers are either radial tubes or cylindrical sacs.

Family 1. Syconidæ.—The radial tubes open directly into the paragastric cavity.

Sub-family *a*. **Syconina.**—The radial tubes are free for their whole length, or at least distally. Examples: *Sycetta*, Hk.; *Sycon*, O.S.

Sub-family *b*. **Uteina**, Lfd.—The radial tubes are simple and entirely united. The ectosome is differentiated from the choanosome and sometimes develops into a cortex. Examples: *Grantissa*, Lfd.; *Ute*, O.S. (fig. 5); *Sycortusa*, Hk.; *Amphoriscus*, Pol.

Sub-family *c*. **Grantina**, Lfd.—The radial tubes are branched. The incurrent canal system is consequently complicated. An ectosome is present. Examples: *Grantia*, Fl.; *Heteropegma*, Pol. (fig. 4); *Anamaxilla*, Pol.

Family 2. Sylleibidæ, Lfd.—The choanosome is folded. The flagellated chambers (which are partly rhagose in *Vosmaeria*) communicate with the paragastric cavity by excurrent canals. Examples: *Polejna*, Lfd. (fig. 6); *Vosmaeria*, Lfd.

Family 3. Teichonellidæ, Carter.—Composite *Sylleibidæ* with the oscules and pores occurring on different parts of the surface. Example: *Teichonella*, Crtr.

Tribe *b*. †Leuconaria.

The canal system belongs to the eurypylous Rhagon type.

Family 1. Leuconidæ, Hk.—The outer surface is not differentiated into osculiferous and poriferous areas. Examples: *Leucetta*, Hk.; *Leucaltis*, Hk.; *Leucortis*, Hk.

Family 2. Eilhardidæ, Pol.—Composite *Leuconaria*, with the outer surface differentiated into special osculiferous and poriferous areas. Example: *Eilhardia*, Pol.

The arrangement adopted above is founded on Von Lendenfeld's revision (*11*) of the classification propounded by Polejaeff (*16*), who in a masterly survey has thrown an unexpected light on the structure and inter-relationships of a group which Haeckel has rendered famous. It should not be overlooked that Vosmaer (*31*) had previously explained the structure of the Leucones. However erroneous in detail, Haeckel's views are confirmed in their broad outlines, and it was with true insight that he pronounced the *Calcarea* to offer one of the most luminous expositions of the evolutional theory. In this single group the development in general of the canal system of the sponges is revealed from its starting-point in the simple Ascon to its almost completed stage in the Leucon, with a completeness that leaves little further to be hoped for, unless it be the requisite physiological explanation.

Class *MYXOSPONGIÆ*.

Order 1. **HALISARCINA.**

Family 1. Halisarcidæ, Lfd.—The flagellated chambers are syconate. Examples: *Halisarca*, Duj. (with branched chambers); *Bajalus*, Lfd. (with simple chambers).

Family 2. Oscarellidæ, Lfd.—The flagellated chambers are eurypylous and rhagose. Example: *Oscarella*, Vosm.

Order 2. **CHONDROSINA.**

Family 1. Chondrosidæ.—With the characters of the order. Example: *Chondrosia*, O.S.

Class *SILICISPONGIÆ*.

Sub-class I. HEXACTINELLIDA.

Order 1. †**LYSSACINA.**

Family 1. Euplectellidæ.—The spicules of the dermal membrane are "daggers" (fig. 15 *a*). Examples: *Euplectella*, Owen; *Holascus*, E. Sch.; *Habrodictyum*, W.T.

Family 2. Asconematidæ.—The dermal spicules are "pinnuli" (fig. 15 *b*, *c*). Examples: *Asconema*, S. Kent; *Sympagella*, O.S.; *Caulophæus*, Schulze.

Family 3. Hyalonematidæ.—The dermal spicules are pinnuli and amphidisks (fig. 15 *d*). Example: *Hyalonema*, Gray.

Family 4. †Rosselidæ.—The dermal spicules are gomphi, stauri (fig. 15 *f*), and oxeas. Examples: *Rossella*, Crtr.; *Crateromorpha*, Gray; *Aulochona*, E. Sch.

Family 5. *Receptaculidæ, Hinde.—The distal ray of the dermal spicules is expanded horizontally into a polygonal plate. Example: **Receptaculites*, Defr.

Order 2. †**DICTYONINA.**

Sub-order 1. *UNCINITARIA*.

Uncinate spicules are present.

Tribe *a*. Clavularia.

Clavulæ (fig. 16 *c*) are present.

Family 1. Farreidæ.—Characters those of the tribe. Example: *Farrea*, Bwk.

Tribe *b*. Scopularia.

The dermal spicules are scopulariæ (fig. 16 *b*).

Family 1. †Euretidæ.—Branched anastomosing tubes, or goblet-shaped, with lateral outlets. Examples: *Eurete*, Marshall; *Periphragella*, Marshall; *Lefroyella*, Schulze.

Family 2. †Mellittonidæ.—Tubular or goblet-shaped, with honeycomb-like walls. Example: *Aphrocallistes*, Gray.

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[1] An * indicates that the group is only known in the fossil state, a † that it is both recent and fossil.

Family 3. †Chonelasmatidæ.—Flat or beaker-shaped; straight funnel-shaped canals perforating the wall perpendicularly and opening laterally on each side. Example: *Chonelasma*, Schulze.

Family 4. †Volvulinidæ.—Tubular, goblet-shaped, or massive; crooked canals more or less irregular in their course. Examples: *Volvulina*, Schulze; *Fieldingia*, S. Kent.

Family 5. Sclerothamnidæ.—Arborescent body; perforated at the ends and sides by round narrow radiating canals. Example: *Sclerothamnus*, Marshall.

Sub-order 2. *INERMIA.*

Dictyonina without uncinati, clavulæ, or scopulariæ.

Family 1. †Myliusidæ.—Depressed cup-shaped; a complex folding of the wall produces lateral excurrent tubes. Example: *Myliusia*, Gray.

Family 2. †Dactylocalycidæ.—Goblet-shaped or pateriform, with a thick wall consisting of numerous parallel anastomosing tubes, of uniform breadth, which terminate at the same level within and without. Examples: *Dactylocalyx*, Gray; *Scleroplegma*, O.S.; *Margaritella*, O.S.

Family 3. †Euryplegmatidæ.—Goblet-shaped or resembling ear-shaped saucers; the wall deeply folded longitudinally so as to produce a number of dichotomously branched canals or covered-in grooves. Example: *Euryplegma*, Schulze.

Family 4. †Aulocystidæ.—Of massive rounded form, with an axial cavity; wall consisting of a system of obscurely radiating anastomosing tubes and intervening inter-canals; both inter-canals and the external terminations of the tubes are covered by a thin membrane, which is perforated by slit-like openings over the lumina of the tubes, and thus assumes a sieve-like character. Examples: *Aulocystis*, Schulze; *Cystispongia*, Roemer.

This arrangement of the *Hexactinellida* is taken from the latest work on the subject, Schulze's *Preliminary Report on the "Challenger" Hexactinellida.* The reference of fossil forms to the families here instituted is rendered difficult by the disappearance of the requisite "guiding" spicules in the process of mineralization. A revision of the fossil families to bring them into harmony with the recent has certainly been rendered necessary, but this is too large a task to undertake in this place.

Sub-class II. DEMOSPONGIÆ.

Tribe *a.* Monaxonida.

Order 1. **MONAXONA.**

Family 1. Tethyidæ.—Skeleton consisting of radiately arranged strongyloxeas (except in the genus *Chondrilla*, which is without megascleres) and large spherasters. The ectosome is a thick fibrous cortex. Example: *Tethya*, Lmk.; *Chondrilla*, O.S.

Family 2. Polymastidæ.—Skeleton consisting of styles radiately arranged and cortical tylostyles. The oscules in many cases open at the ends of long papillæ. Examples: *Polymastia*, Bwk.; *Thecaphora*, O.S.; *Trichostemma*, Sars.

Family 3. Suberitidæ.—Skeleton consisting of strongylate or tylotate styles, arranged to form a felt. The flesh spicules when present are usually microrabds or spirasters. Examples: *Suberites*, Nardo; *Cliona*, Grant; *Poterion*, Schlegel.

Family 4. Desmacidonidæ.—The flesh spicules are cymbas. Examples: *Esperella*, Vosm.; *Desmacidon*, Bwk.; *Cladorhiza*, Sars.

Family 5. †Halichondridæ.—The flesh spicules when present are never cymbas. Examples: *Halichondria*, Fl.; *Reniera*, O.S.; *Chalina*, Bwk.; **Pharetrospongia*, Soll.

Family 6. Ectyonidæ.—The skeleton consists of fibres echinated by projecting spicules. Examples: *Plocamia*, O.S.; *Ectyon*, Gray; *Clathria*, O.S.

Family 7. †Spongillidæ.—*Halichondridæ* which are reproduced both sexually and by statoblasts. Habitat freshwater. Examples: *Spongilla*, Lmk.; *Ephydatia*, Lmk.; *Parmula*, Crtr.; *Potamolepis*, Marshall.[1]

The foregoing classification is purely provisional; the group requires a complete revision.

Order 2. **CERATOSA.**

Family 1. Darwinellidæ.—Canal system of the eurypylous Rhagon type. Flagellated chambers, pouch-shaped, large; the surrounding collenchyme not granular. Horny fibres with a thick core. Examples: *Darwinella*, Fritz Müller; *Aplysilla*, F.E.S.; *Ianthella*, Gray.

Family 2. Spongelidæ.—Canal system as in the *Darwinellidæ*, but the flagellated chambers more or less spherical. Horny fibres with a thin core, and usually containing foreign enclosures. Examples: *Velinea*, Vosm.; *Spongelia*, Nardo; *Psammoclema*, Marshall; *Psammopemma*, Marshall.

Family 3. Spongidæ.—Canal system aphodal. Chambers small and spherical; surrounding collenchyme granular. Fibres with a thin core. Examples: *Euspongia*, Bronn; *Coscinoderma*, Crtr.; *Phyllospongia*, Ehlers.

Family 4. Aplysinidæ.—Canal system diplodal; collenchyme surrounding the flagellated chambers densely granular. Fibres with a thick core. Examples: *Luffaria*, Duch. and Mich.; *Verongia*, Bwk.; *Aplysina*, Nardo.

The species of sponge in common use are three,—*Euspongia officinalis* (Linn.), the fine Turkey or Levant sponge; *E. zimocca* (O.S.), the hard Zimocca sponge; and *Hippospongia equina* (O.S.), the horse sponge or common bath sponge. The genus *Euspongia* is distinguished by the regular development of the skeletal network throughout the body, its narrow meshes, scarcely or not at all visible to the naked eye, and the regular radiate arrangement of its chief fibres. *Hippospongia* is distinguished by the thinness of its fibres and the labyrinthic character of the choanosome beneath the skin. As a consequence its chief fibres have no regular radiate arrangement. The species of *Euspongia* are distinguished as follows. In *E. officinalis* the chief fibres are of different thicknesses, irregularly swollen at intervals, without exception cored by sand grains; in *E. zimocca* they are thinner, more regular, and almost free from sand. In *E. officinalis*, again, the uniting fibres are soft, thin, and elastic; whilst in *E. zimocca* they are denser and thicker, to which difference the latter sponge owes its characteristic hardness. Finally, the skeleton of *E. officinalis* is of a lighter colour than that of *E. zimocca.* The common bath sponge (*Hippospongia equina*) has almost always a thick cake-like form; but its specific characters are not yet further defined.

Tribe *b.* Tetractinellida.

Order 1. **CHORISTIDA.**

Sub-order 1. *SIGMATOPHORA.*

The microsclere is a sigmaspire.

Family 1. Tetillidæ.—The characteristic megasclere is a protriæne. Canal system in the lower forms eurypylous, in the higher aphodal. The ectosome in the simpler forms is a dermal membrane, in the higher a highly differentiated cortex. Examples: *Tetilla*, O.S.; *Craniella*, O.S. (fig. 21 *h*, *l*).

Family 2. Samidæ.—The characteristic megasclere is an amphitriæne. Example: *Samus*, Gray.

Sub-order 2. *ASTEROPHORA.*

The microsclere is an aster.

Group 1. Spirastrosa.—A spiraster is usually present.

Family 1. Theneidæ, Carter.—The flesh spicule is a spiraster. Canal system eurypylous. Ectosome not differentiated to form a cortex. Examples: *Thenea*, Gray (fig. 21 *a*, *f*); *Pœcillastra* (*Normania*), Bwk.

Family 2. †Pachastrellidæ.—Canal system eurypylous in the lower, aphodal in the higher forms. Examples: *Plakortis*, F.E.S.; *Dercitus*, Gray.

Group 2. Euastrosa.—Spirasters are absent.

Family 1. †Stellettidæ.—Canal system aphodal, but approaching the eurypylous in the lower forms. The cortex chiefly consists of collenchyme in the lower forms; in the higher it is highly differentiated. Example: *Stelletta*, O.S. (fig. 11); *Ancorina*, O.S.; *Myriastra*, Soll.

Family 2. Tethyidæ.—Although this family has been placed in the *Monaxonida*, this seems to be its more natural position.

Group 3. Sterrastrosa.—A sterraster is present, usually in addition to a simple aster.

Family 1. †Geodinidæ.—The megascleres are partly triænes. Canal system always aphodal. Cortex highly differentiated. Examples: *Geodia*, Lmk. (fig. 21 *n*); *Pachymatisma*, Bwk. (fig. 21 *c*); *Cydonium*, Müller (fig. 10); *Erylus*, Gray.

Family 2. Placospongidæ.—The megasclere is a tylostyle. Triænes are absent. Example: *Placospongia*, Gray.

Sub-order 3. *MICROSCLEROPHORA.*

Microscleres only are present.

Family 1. Plakinidæ, Schulze.—Canal system very simple, belonging to eurypylons Rhagon type. Characteristic spicules candelabra. Examples: *Plakina*, F.E.S. (fig. 26).

Family 2. Corticidæ.—Canal system aphodal or diplodal. Mesoderm a collenchyme crowded with oval granular cells; the spicules either candelabra, amphitriænes, or triænes irregularly dispersed in it. Example: *Corticium*, O.S. (figs. 9, 21 *b*).

Family 3. Thrombidæ.—Canal system diplodal. Spicules trichotriænes. Example: *Thrombus*, Soll.

The *Pachastrellidæ* or the *Corticidæ* are probably the families from which the Tetracladine Lithistids have been derived. In the *Tetillidæ* the characteristic microsclere may occasionally fail, but there is never any difficulty in identifying the sponge in this case, as the triænes are of a very characteristic form: the arms of the protriænes are slender, simple, and directed very much forwards, making a very large angle with the shaft. Microscleres, having the form of little globules, are sometimes present with the sigmaspires.

Order 2. **LITHISTIDA**, O.S.

Sub-order 1. *TETRACLADINA*, Zittel.

The desmas are modified calthrops spicules.

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[1] Freshwater sponges without statoblasts are excluded from this family, and left for distribution amongst allied marine genera.

Family 1. Tetracladidæ.—With the characters of the sub-order. Examples: *Theonella*, Gray (fig. 21 *k*); *Discodermia*, Bocage; **Siphonia*, Parkinson.

Sub-order 2. *RHABDOCREPIDA.*

The desmas are of various forms, produced by the growth of silica over a uniaxial spicule.

Family 1. Megamorinidæ.—The desmas are comparatively large. Triænes, usually dichotriænes, help to support the ectosome. Microscleres usually spirasters. Examples: *Corallistes*, O.S.; **Hyalotragos*, Zittel; *Lyidium*, O.S.; **Dorydermia*, Zittel.

Family 2. Micromorinidæ.—The desmas are comparatively small. Triænes and microscleres are both absent. Examples: *Azorica*, Crtr.; **Verruclina*, Zittel.

Sub-order 3. *ANOMOCLADINA.*

Desmas with a massive nucleated centrum, from which a variable number of arms (*28*) extend radiately (see fig. 12 *f*). Examples: *Vetulina*, O.S.; **Astylospongia*, Roemer.

Reproduction and Embryology.

Fresh individuals arise by asexual gemmation, both external and internal, by fission, and by true sexual reproduction.

Asexual multiplication. Fission is probably one of the processes by which compound sponges are produced from simple individuals. Artificial fission has been practised with success in the cultivation of commercial sponges for the market. External gemmation has been observed in *Thenea*, *Tethya*, *Polymastia*, and *Oscarella*. A mass of indifferent sponge-cells accumulates at some point beneath the skin, bulges out, drops off, and gives rise to a new individual. Internal gemmation, which results in the formation of a statoblast, is only known to occur in the freshwater *Spongillidæ*. The statoblasts consist of a mass of yolk-bearing mesoderm cells, invested by a capsule, which in *Ephydatia fluviatilis* is composed of an inner cuticle of spongin separated from a similar outer layer by an intermediate zone of amphidisks and interspersed protoplasmic cells. On one side of the capsule is a hilum which leads into the interior.

Their development has recently been studied by Götte, with results that confirm the conclusions of Carter (*3*) and Lieberkühn (*13*). The process commences with an accumulation of amœboid cells within the mesoderm to form a globular cluster; yolk granules develop within them, especially in those that lie nearer the centre. The external cells give rise to the investing capsule; some resemble sponginblasts and secrete the inner and outer horny cuticle; others give rise to the amphidisks and interspersed cells of the middle layer. Under favourable conditions the interior cells creep out through the pore of the capsule, and form a spreading heap, which by subsequent differentiation gives rise to a young *Spongilla*. Since the freshwater sponges can only be regarded as modified descendants of ancient marine species (probably of the family *Halichondridæ*), we may consider the internal gemmules, like the similar statoblasts of the freshwater *Polyzoa*, as special adaptations to a changed mode of life. They appear primarily to serve a protective purpose, ensuring the persistence of the race, since they only appear in extreme climates on the approach of drought, and in cold ones on the approach of winter. As a secondary function they serve for the dispersal of the species; some are light enough to float down a stream, but not too far, so that there is no danger of their being carried to sea; others, which are characterized by large air-chambers, are possibly distributed by the wind.

Sexual reproduction. Both sexual elements may be formed in the same individual, *e.g.*, *Oscarella lobularis*, *Grantia raphanus*, and many others; but even in hermaphrodites one or other element usually occurs to excess in different individuals, so that some are predominantly male and others predominantly female. Polejaeff found only one such male form to 100 female forms in *Grantia raphanus*. In other sponges—*Reniera fertilis*, *Euspongia officinalis*—the sexes are distinct. The ova develop from archæocytes or wandering amœboid cells, which increase in size and acquire a store of reserve nourishment in the form of yolk granules; at first they exhibit lively amœboid movements, but later pass into a resting stage. The cavity of the mesoderm within which they are situated becomes lined by a layer of epithelium, which may not appear, however, till a late stage of segmentation. In *Euspongia officinalis* the ova occur congregated in groups within the mesoderm, thus presenting an early form of ovary. The spermatozoa, which also develop from wandering amœboid cells, are minute bodies with an oval or pear-shaped head and a long vibratile tail (fig. 24 *k*). Each amœboid cell produces a large number of spermatozoa, which occur in spherical clusters or sperm-balls. The heads of the spermatozoa, as in the *Metazoa*, are produced from the nucleus of the mother-cell, the tails from the surrounding protoplasm.

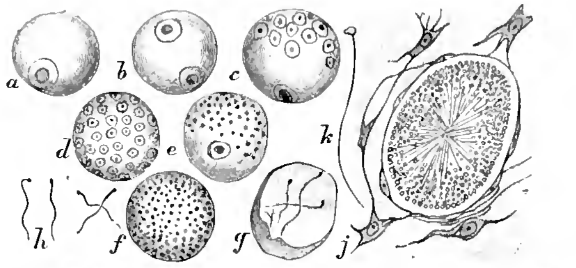

Fig. 24.—Spermatozoa. *a-h*, Development of spermatozoa in *Sycandra raphanus*, highly magnified; *h*, mature spermatozoa. After Polejaeff (×792). *j*, A sperm ball in *Oscarella lobularis* (×500); *k*, an isolated mature spermatozoon. After Schulze (×800).

The development in detail is upon two plans. In *Grantia raphanus* (*15*) the nucleus of the mother-cell divides into two (fig. 24 *b*); one of the resulting daughter nuclei undergoes no further change, but with a small quantity of peripheral protoplasm forms a "cover-cell" to the other or primitive sperm nucleus and its associated protoplasm. The sperm nucleus repeatedly divides, with-

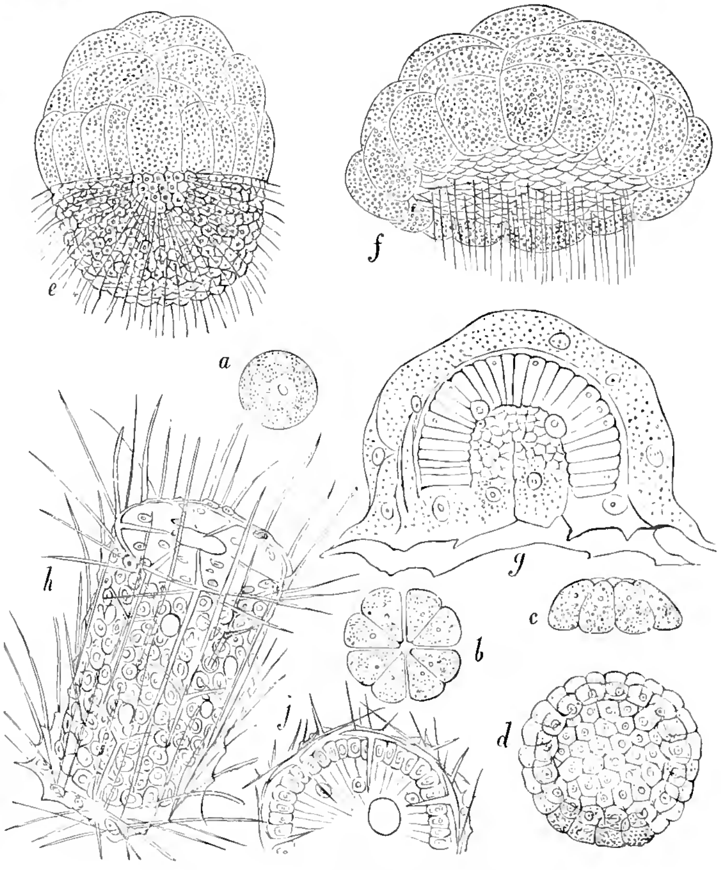

Fig. 25.—Development of a calcareous sponge (*Sycandra raphanus*). *a*, ovum; *b*, *c*, ovum segmented,—*b*, as seen from above, *c*, lateral view; *d*, blastosphere; *e*, amphiblastula; *f*, commencement of the invagination of the flagellated cells of the amphiblastula; *g*, gastrula attached by its oval face; *h*, *j*, young sponge (Ascon stage),—*h*, lateral view, *j*, as seen from above. After Schulze.

out involving the surrounding protoplasm (fig. 24 *c-f*). The resulting nuclei at length cease to exhibit a nucleolus, and become directly transformed into the heads of spermatozoa; the tails are appropriated by each head from the common protoplasmic residue. The mother-cell in this case undergoes no increase in volume as development proceeds, and it is not enclosed within an "endothelial" layer. In the second and apparently more usual case (*20*) no "cover-cell" is formed, but the mother-cell divides and subdivides, protoplasm as well as nuclei, till a vast number of minute cells results; the nucleus of each becomes the head of a spermatozoon and the protoplasm its tail. In this case the sperm-ball does increase in bulk: it grows as it develops, and the cavity containing it becomes lined by epithelium, or so-called "endothelium" (fig. 24 *j*). No doubt (*15*) the development of the epithelium stands in direct physiological connexion with the growth of the sperm-ball.

Embryology. Obscure as are the details of this subject, sufficient is known to enable us to make out two chief types of development. One, common amongst the calcareous sponges, and possibly occurring in a single genus (*Gummina*) of the *Micromastictora*, is characterized by what is known as the "amphiblastula" stage; the other, widely spread amongst the *Micromastictora* (*Reniera*, *Desmacidon*, *Euspongia*, *Spongelia*, *Aplysilla*, *Oscarella*), is characterized by a "planula" stage.

The first has been most thoroughly investigated in *Grantia raphanus* by Schulze (*20*). The ovum by repeated segmentation gives rise to a hollow vesicle, the wall of which is formed by a single layer of cells—*blastosphere* (fig. 25 *d*). Eight cells at one pole of the blastosphere now become differentiated from the rest; they remain rounded in form, comparatively large, and become filled with granules (stored nutriment), while the others, rapidly multiplying by division, become small, clear, columnar, and flagellated. By further change the embryo becomes egg-shaped; the granular cells, now increased in number to thirty-two, form the broader end, and the numerous small flagellated cells the smaller end. Of the granular cells sixteen are arranged in an equatorial girdle adjoining the flagellate cells. A blastosphere thus differentiated into two halves composed of different cells is known as an *amphiblastula*. The amphiblastula (fig. 25 *c*) now perforates the maternal tissue, and is borne along an excurrent canal to the oscule, where it is discharged to the exterior and swims about in a whirling lively dance. It then assumes a more spherical form, a change premonitory of the next most remarkable phase of its career. In this the flagellated layer becomes flattened, depressed, and finally invaginated within the hemisphere of granular cells, to the inner face of which it applies itself, thus entirely obliterating the cleavage cavity, but by the same process originating another (the invagination cavity) at its expense (fig. 25 *f*). The two-layered sac thus produced is a *paragastrula*; its outer layer, known as the *epiblast*, gives rise to the ectoderm, the inner layer or hypoblast to the endoderm. The paragastrula next becomes somewhat beehive-shaped, and the mouth of the paragastric cavity is diminished in size by an ingrowth of the granular cells around its margin. The larva now settles mouth downwards on some fixed object, and exchanges a free for a fixed and stationary existence (fig. 25 *g*). The granular cells completely obliterate the original mouth, and grow along their outer edge over the surface of attachment in irregular pseudopodial processes, which secure the young sponge firmly to its seat (fig. 25 *h*). The granular cells now become almost transparent, owing to the exhaustion of the yolk granules, and allow the hypoblast within to be readily seen; a layer of jelly-like material, the rudimentary mesoderm, is also to be discerned between the two layers. The spicules then become visible; slender oxeas appear first, and afterwards tri- and quadri-radiate spicules. The larva now elongates into a somewhat cylindrical form; the distal end flattens; and an oscule opens in its midst. Pores open in the walls; the endodermal cells, which had temporarily lost their flagella, reacquire them, at the same time extending the characteristic collar. In this stage (fig. 25 *h, j*) the young sponge corresponds to a true Ascon, no trace of radial tubes being visible; but as they characterize the parent sponge they must arise later, and thus we have clear evidence through ontogeny of the development of a Sycon sponge from an Ascon.

The three most striking features in the history of this larva are, first, the amphiblastula stage; next the invagination of the flagellate cells within the granular, instead of invagination in the reverse order; and third the attachment of the larva by the oral instead of the aboral surface. Should Schulze be correct in deriving the sponges from the *Cœlentera*, it is probable that the reversal of the Cœlenterate history as exemplified in the last two events will furnish an explanation of the remarkable divergencies which distinguish the two phyla. The history of the second or planula type has been thoroughly worked out by Schulze (*20*) in a little incrusting Tetraetinellid sponge (*Plakina monolopha*, Schulze). The ovum by regular segmentation produces a blastosphere, the blastomeres of which increase in number by further subdivision till they become converted into hyaline cylindrical flagellated cells (fig. 26 *f*). Thus a blastosphere is produced consisting wholly of similar flagellated cells. It becomes egg-shaped, and, hitherto colourless, assumes a rose-red tint, which is deepest over the smaller end. The larva (now a planula, fig. 26 *a*, by the filling in of the central cavity) escapes from the parent and swims about broad end foremost. In this stage thin sections show that the cleavage cavity is obliterated, its place being occupied by a mass of granular gelatinous material containing nuclei (fig. 26 *b*). In from one to three days after hatching the larva becomes attached. It then spreads out into a convex mass, and a cavity is produced within it by the splitting of the central jelly (fig. 26 *c, d*; compare *Eucope* and others amongst the Cœlenterates). This cavity becomes lined by short cylindrical cells (endoderm), while the flagellated cells of the exterior lose their flagella and become converted into pinnacocytes (ectoderm). The gelatinous material left between the two layers now formed acquires the characters of true collenchyme and thus becomes the mesoderm. The endoderm then sends off into the mesoderm, as buds, rounded chambers, which communicate with the paragastric cavity by a wide mouth and with the exterior by small pores (fig. 26 *c*). An oscule is formed later, and the sponge enters upon the Rhagon phase. Subsequent foldings of the sponge-wall give rise to a very simple canal system (fig. 26 *f*). In addition to these two well-ascertained modes of development others have been described which at present appear aberrant. In *Oscarella lobularis*, O.S. (*27*), a curious series of early developmental changes results in the formation of an irregular paragastrula, the walls of which become folded (while still within the parent sponge) in a complex fashion, so as to produce a form in which the incurrent and excurrent canals appear to be already sketched out before the flagellated chambers are differentiated off. In *Spongilla* Götte describes the ectoderm as becoming entirely lost on the attachment of the larva, so that the future sponge proceeds from the endoderm alone. As *Spongilla*, however,

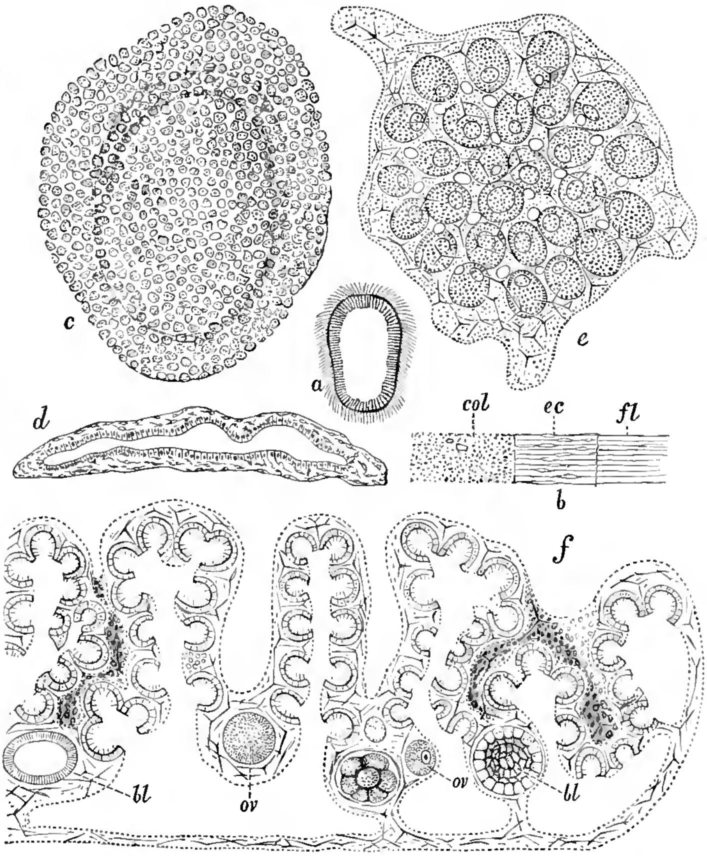

Fig. 26.—Development of a *Demospongia* (*Plakina monolopha*). *a*, planula (the central part should be shaded). *b*, Section through side of planula; *ec*, flagellated cells; *fl*, their flagella; *col*, cœnoblast. *c*, Attached gastrula (the paragaster is formed by fission). *d*, Section across the foregoing. *e*, Young sponge (Rhagon). *f*, Part of a section through fully grown sponge; the attached basal layer is the hypomere; the spongomere is folded so as to produce incurrent and excurrent canals; the canal system is eurypylous; *ov*, ova (a segmented ovum lies between two of them); *bl*, blastospheres. After Schulze.

is a freshwater form, anomalies in its development (which remind us of those in the development of the freshwater *Hydra*) might almost be expected.

Homoplasy. Probably in no other single group is the doctrine of homoplasy enunciated by Lankester more tellingly illustrated than in the sponges. The independent development of similar types of canal system in different groups, sometimes within the limits of a single family, is a remarkable fact. In the following table the sign × shows independent evolution of similar types of canal system in different groups:—

	Ascon.	Sycon.	Rhagon.		
			Eurypylous.	Aphodal.	Diplodal
Class *Calcarea*	×	×	×	...	...
Order *Halisarcina*......	...	×	×	...	...
Order *Monaxona*	...	...	×	×	...
Order *Ceratosa*	...	×	×	×	×
Sub-order *Microsclerophora*	...	...	×	×	×
Order *Choristida*	...	...	×	×	...
Family *Tetillidæ*	...	...	×	×	...

In the gross anatomy of the canal system similar homoplasy obtains; thus, to cite one case amongst many, a peculiar type of canal system characteristic of *Siphonia* (Lithistid) occurs also in *Emploca* (Hexactinellid), *Schmidtia* (Monaxonid), and other apparently unrelated genera. The development of a cortex has likewise taken place independently, but on parallel lines, in the *Syconidæ*, *Leuconidæ*, *Monaxona*, *Tetillidæ*, and *Stellettidæ*. Calcareous and silicious spicules have evidently an independent history, and yet all the chief forms of the former are repeated in the latter. Quite as remarkable is the similarity of the independently evolved horny spicules of *Darwinella aurea* to the quadri- and sex-radiate silicious spicules. We have now sufficient knowledge of the morphology and evolution of the sponge to furnish the physicist with data for an explanation of the skeleton, at least in its main outlines. The obvious conclusion from this is that variation does not depend upon accident, but on the operation of physical laws as mechanical in their action here as in the mineral world. Another important consequence follows: if homoplasy—*i.e.*, the independent evolution of similar structures —is of such certain and quite common occurrence in the case of the sponges, it is also to be looked for in other groups, and polyphylitic origin, so far from being improbable, is as likely an occurrence as monophylitic origin.

Physiology and Ætiology.

Physiology. Under the head of "physiology" we have almost a blank. At present we do not even know what cells of the sponge are primarily concerned in the ingestion of food. If a living sponge, such as *Spongilla*, be fed with carmine for a few minutes, then immersed in dilute osmic acid, and examined in thin sections, its flagellated chambers are found to be all marked out as red circular patches, and a closer investigation shows that the choanocytes, and they alone, have ingested the carmine. In this way we confirm the earlier observations of Carter made by teasing carmine-fed sponges. This might be thought to decide the question; but, though it effectually disposes of Polejaeff's argument that the choanocytes do not ingest nutriment because mechanical disadvantages (conceived *a priori*) make it impossible, it has not proved a final solution. Von Lendenfeld, by feeding sponges such as *Aplysilla* with carmine for a longer interval—a quarter of an hour—finds that amœboid cells crowd about the sides and particularly the floor of the subdermal cavities, and are soon loaded with carmine granules; after a time they wander away to the flagellated chambers and there cast out into the excurrent canals the carmine they have absorbed, apparently in an altered state. On the other hand, the choanocytes, though they at first absorb the carmine, soon thrust it out, apparently in an unaltered state. Hence Von Lendenfeld concludes that it is the epithelium of the subdermal cavities which is charged with the function of ingestion, and that the amœboid cells subsequently digest and distribute it, and finally cast out the worthless residues. There may be much truth in this view, but it requires to be supported by further evidence. (1) Sufficient proof is not adduced to show that the carmine granules expelled from the amœboid cells are really more decomposed than those rejected by the choanocytes. (2) There is at present no proof that carmine is a food, or that if it is sponges will readily feed upon it. In either case one would expect the amœboid cells to play the part which they perform in other organisms and to remove as soon as possible useless or irritant matter from the surface which it encumbers; at the same time the choanocytes, not having found the food to their liking, would naturally eject it. (3) If the choanocytes do not ingest food, how does the Ascon feed, since in this sponge all the pinnacocytes are external? It is, however, a very noticeable fact that, as the organization of a sponge increases in complexity, the choanocytal layers become reduced in volume relative to the whole bulk of the individual; and it is quite possible that as histological differentiation proceeds it may be accompanied by physiological differentiation which relieves the choanocytes to some extent of the ingestive part of their labours.

Ætiology. The origin of the sponges is to be sought for among the choanoflagellate *Infusoria*; and Savile Kent has described a colonial form of this group which is suggestively similar to a sponge. Its differences, however, are as marked as its resemblances, and have been sufficiently pointed out by Schulze (*23*). Kent has called this form *Protospongia*, a name already made use of, and fortunately, as the organism is not in any sense a true sponge; the present writer proposes, therefore, to call it *Savillia*, in honour of its discoverer. It consists of choanoflagellate *Infusoria* (see PROTOZOA, vol. xix. p. 858, fig. XXI., 15), half projecting from and half embedded in a structureless jelly or blastema, within which other cells of an amœboid character and reproductive function are immersed. Professor Haddon arrives at the generalization that conjugation amongst the *Protozoa* always takes place between individuals of the same order: flagellate cells conjugate with flagellate, amœboid with amœboid, but never with flagellate; while in true sexual reproduction the conjugation occurs between two individual cells in different stages of their life cycle: a flagellate cell conjugates with a resting amœboid cell. Now *Savillia* would appear to be extremely near such a true sexual process, since the simultaneous coexistence of cells in two different stages of life and within easy reach of each other—a necessary preliminary, one would think, to the union—has already been brought about. That coalescence between two different histological elements should result in products similarly histologically differentiated (compare amphiblastula stage of *Calcarea*) has in it a certain fitness, which, however, has still to be explained. The mode by which an organism like *Savillia* might become transformed into an Ascon cannot be suggestively outlined with any satisfactory results till our knowledge of the embryology of sponges is more advanced. The minute characters of the flagellate cells of the amphiblastula and other sponge larvæ are still a subject for research. They often possess a neck or collum; but the existence of a frill or collar is disputed. Kent asserts that it is present in several embryos which he figures; and Barrois makes the same assertion in respect to the larva of *Oscarella*, and illustrates his description with a figure. On the other hand, Schulze and Marshall both deny its existence, and the former attributes Kent's observations to error. One constant character they do possess: they are provided with flagella at some stage of their existence, but never with cilia. Ciliated cells, indeed, are unknown amongst the sponges, and, when pinnacocytes exceptionally acquire vibratile filaments, as in *Oscarella* and other sponges, these are invariably flagella, never cilia. An Ascon stage having been reached at some point in the history of the sponges, the Sycon tubes and Rhagon chambers would arise from it by the active proliferation of choanocytes about regularly distributed centres, possibly as a result of generous feeding. Vosmaer recognized as the physiological cause of Sycon an extension of the choanocytal layer. Polejaeff, relying on Von Lendenfeld's experiments, which seem to prove that it is the pinnacocytes and not the choanocytes which are concerned in the ingestion of nutriment, argues that, as in Sycon the pinnacocytal layer is increased relatively to the choanocytal, we have in this a true explanation of the transition. The existence of *Homoderma*, Lfd., however, shows that in the first stage there was not a replacement of choanocytes by pinnacocytes, but that this was a secondary change, following the development of radial tubes, and therefore cannot be relied upon to explain them. The radial tubes having been formed by a proliferation of choanocytal cells, the reduction of those lining the paragastric cavity to pinnacocytes would follow in consequence of the poisonous character of the water delivered from the radial tubes to the central cavity, since this water not only parts with its dissolved oxygen to the choanocytes it first encounters, but receives from them in exchange urea, carbonic acid, and fæcal residues. The development of subdermal cavities is explicable on Von Lendenfeld's hypothesis.

Distribution.

Distribution in space; Our knowledge of this subject is at present but fragmentary; we await fuller information in the remaining reports on the sponges obtained by the "Challenger." The sponges are widely distributed through existing seas, and freshwater forms are found in the rivers and lakes of all continents except Australia, and in numerous islands, including New Zealand. Many genera and several species are cosmopolitan, and so are most orders.

As instances of the same species occurring in widely remote localities we take the following from Polejaeff:—*Sycon arcticum* is found at the Bermudas and in the Philippine Islands, as also are *Leuconia multiformis* and *Leucilla uter*; *Sycon raphanus* occurs at Tristan da Cunha and the Philippines; *Heteropegma nodus-gordii* and *Leuconia dura* at the Bermudas and Torres Straits. We do not know, however, whether these species are isolated in their distribution or connected by intermediate localities. Of the *Calcarea* about eighty-one species have been obtained from the Atlantic, twenty-two from the Pacific, and twenty-two from the Indian Ocean; but these numbers no doubt depend largely on the extent to which the several oceans have been investigated, for the largest number of species has been found in the ocean nearest home. Schulze states that the *Hexactinellida* brought home by the "Challenger" were obtained at seventeen Atlantic stations, twenty-seven Pacific, and nineteen in the South Seas. In the last the number of species was greatest, in the Atlantic least. They flourish best on a bottom of diatomaceous mud. The *Calcarea* and *Ceratosa* are most abundant in shallow water and down to 40 fathoms, but they descend to from 400 to 450 fathoms. The *Hexactinellida* are most numerous over continental depths, *i.e.*, 100 to 200 fathoms; but they extend downwards to over 2500 fathoms and upwards into shallow water (10 to 20 fathoms). The *Lithistida* are not such deep-water forms as the *Hexactinellida*, being most numerous from 10 to 150 fathoms. Only one or two species have been dredged from depths greater than 400 fathoms, and none from 1000 fathoms. The *Choristida* range from shallow water to abyssal depths. A characteristic deep-sea Choristid genus is *Thenea*, Gray (= *Wyville Thompsonia*, Wright; *Dorvillia*, Kent). This is most frequently dredged from depths of from 1000 to 2000 fathoms; but it extends to 2700 fathoms on the one hand and to 100 on the other.

in time. Until about 1876 one of the chief obstacles to the interpretation of fossil sponges arose from a singular mineral replacement which most of them have undergone, leading to the substitution of calcite for the silica of which their skeletons were originally composed. This change was demonstrated by Zittel (*35*) and Sollas (*24*), and, though it was at first pronounced impossible, owing to objections founded on the chemical nature of silica, it has since become generally recognized. These observers also showed that the fossil sponges do not belong to extinct types, but are assignable to existing orders. Zittel in addition subjected large collections to a careful analysis and marshalled them into order with remarkable success. Since then several palæontologists have worked at the subject,—Počta, Dunikowski, and Hinde (*7*), who has published a *Catalogue*—which is much more than a catalogue—of the sponges preserved in the British Museum. The result of their labours is in general terms as follows. Fossil sponges are chiefly such as from the coarseness or consistency of their skeletons would be capable of preservation in a mineralized state. Thus the majority are *Hexactinellida*, chiefly *Dictyonina*; *Tetractinellida*, chiefly *Lithistida*; and *Calcarea*, chiefly *Leuconaria*. Monaxonid sponges rarely occur; the most ancient is *Climacospongia*, Hinde, found in Silurian rocks. A very common Halichondroid sponge of this group (*Pharetrospongia strahani*, Soll.) occurs in the Cambridge greensand; it owes its preservation to the collection of its small oxeate spicules into dense fibres. The *Choristida*, though not so common as the Lithistids, are commoner than the Monaxonids, particularly in Mesozoic strata.

The distribution of fossil sponges in the stratified systems may be summarized as follows. CALCAREA.—*Homocœla*, none. *Heterocœla*, a Syconid, in the Jurassic system. Numerous *Leuconaria* from the Devonian upwards. MYXOSPONGIÆ.—None; not fitted for preservation. HEXACTINELLIDA.—*Lyssacina*, from the Lower Cambrian upwards. *Dictyonina*, commencing in the Silurian; most numerous in the Mesozoic group; still existing. MONAXONIDA.—*Monaxona*, from the Silurian upwards. *Ceratosa*, none; few are fitted for preservation. TETRACTINELLIDA.—*Choristida*, from the Carboniferous upwards; most numerous in the Cretaceous system. *Lithistida*, from the Silurian upwards; most numerous in the Mesozoic group. In ancient times the Hexactinellids and Lithistids seem not to have been so comparatively uncommon in shallow water as they are at the present day. Thus, in the Lower Jurassic strata of the south-west of England we find Dictyonine Hexactinellids, Lithistids, and Leuconarian *Calcarea* associated together in a shelly breccia and in company with littoral shells, such as *Patella* and *Trochus*. Several Palæozoic Hexactinellids actually occur in a fine-grained sandstone. Of the Chalk, which is the great mine of fossil sponges, we must speak with caution, owing to the insufficient evidence as to the depth at which it was deposited.

As shown by *Protospongia*, the phylum of the sponges was in existence in very early Cambrian times, and probably much earlier. Before the end of the Silurian period its main branches had spread themselves out, and, developing fresh shoots since then, they have extended to the present day. Of the offshoots none of higher value than families are known to have become extinct, and of these decayed branches there are very few. The existence in modern seas of the *Asconidæ*, which must surely have branched off very near the base of the stem, is another curious instance of the persistence of simple types, which would thus appear not to be so vastly worse off in the struggle for existence than their more highly organized descendants.

Bibliography.—A fairly complete list of works on sponges published before 1882 will be found in Vosmaer's article "Porifera," in Bronn's *Klassen und Ordnungen*, vol. ii. D'Arcy Thompson's *Catalogue of Papers on Protozoa and Cœlenterata*, a still more complete list, extends to 1884.

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Commerce.

When the living matter is removed from a Ceratose sponge a network of elastic horny fibres, the skeleton of the animal, remains behind. This is the sponge of commerce. Of such sponges the softest, finest in texture, and most valued is the Turkey or Levant sponge, *Euspongia officinalis*, Lin. The other two varieties are the *Hippospongia equina*, O. Schmidt, and the Zimocca sponge, *Euspongia zimocca*, O.S., which is not so soft as the others (see p. 423 above). **Distribution.** All three species are found at from 2 to 100 fathoms along the whole Mediterranean coast, including its bays, gulfs, and islands, except the western half of its northern shores as far as Venice and the Balearic Isles, Corsica, Sardinia, and Sicily. Bath sponges occur around the shores of the Bahamas, and less abundantly on the north coast of Cuba. They are of several kinds, one not distinguishable from the fine Levant sponge; others, the "yellow" and "hardhead" varieties, resemble the Zimocca sponge; and of horse sponges there appear to be several varieties, such as the "lamb's-wool" and the "velvet" sponge (*Hippospongia gossypina* and *H. meandriformis*). The fine bath sponge occurs on the shores of Australia (Torres Straits, the west coast, and Port Phillip on the south coast). A sponge eminently adapted for bathing purposes (*Coscinoderma lanuginosum*, Crtr.; *Euspongia mathewsii*, Lfd.), but not yet brought into the market, occurs about the South Caroline Islands, where it is actually in use, and at Port Phillip in Australia. The fine bath sponge occurs in the North Pacific, South Atlantic, and Indian Oceans, so that its distribution is world-wide.

Fishing. The methods employed to get sponges from the bottom of the sea, where they grow attached to rocks, stones, and other objects, depend on the depths from which they are to be brought. In comparatively shallow water they may be loosened and hooked up by a harpoon; at greater depths, down to 30 or 40 fathoms, they are dived for; and at depths of from 50 to 100 fathoms they are dredged with a net. The method of harpooning was the earliest practised, and is still carried on in probably its most primitive form by the Dalmatian fishermen. Small boats are used, manned by a single harpooner with a boy to steer; when, however, the expedition is to extend over night the crew is doubled. The harpoon is a five-pronged fork with a long wooden handle, and if this is not long enough another harpoon is lashed on to it. The Greek fishers use a large boat furnished with two or three smaller ones, from which the actual harpooning is carried on; the crew numbers seven or eight. One of the chief difficulties is to see the bottom distinctly through a troubled surface. The Dalmatian fishers throw a smooth stone dipped in oil a yard or so in front of the boat; the stone scatters drops of oil as it flies and so makes a smooth track for the "lookout." The Greeks use a zinc-plate cylinder about 1½ feet long and 1 foot wide, closed at the lower end by a plate of glass, which is immersed below the surface of the sea; on looking through this the bottom may be clearly seen even in 30 fathoms. This plan is also adopted in the Bahamas, where harpooning carried on after the Greek system gives employment to over 5000 men and boys.

The primitive method of diving with no other apparatus than a slab of stone to serve as a sinker and a cord to communicate with the surface is still practised in the Mediterranean. The diver carries a net round his neck to hold the sponges. On reaching the bottom he hastily snatches up whatever sponge he sees. After staying down as long as he is able—an interval which varies from two to at the most three minutes—he tugs violently at the cord and is rapidly drawn up. On entering the boat from depths of 25 fathoms he quickly recovers from the effects of his plunge after a few powerful respirations; but after working at depths of 30 to 40 fathoms or more he reaches the surface in a swooning state. At the beginning of the season blood usually flows from the mouth and nose after a descent; this is regarded as a symptom of good condition; should it be wanting the diver will scarcely venture a second plunge for the rest of the season. The work is severe, and frequently the diver returns empty-handed to the boat. Diving is usually carried on in the summer months; in winter it is too cold, at all events without a diving-dress. The ordinary diver's dress with pumping apparatus is largely used by the Greeks. The diving is carried on from a ship manned by eight or nine men, including one, or rarely two, divers. At a depth of from 10 to 15 fathoms the diver can remain under for an hour, at greater depths up to 20 fathoms only a few minutes; the consequences of a longer stay are palsy of the lower extremities, stricture, and other complaints. Dredging is chiefly carried on along the west coast of Asia Minor, principally in winter after the autumn storms have torn up the seaweeds covering the bottom. The mouth of the dredge is 6 yards wide and 1 yard high; the net is made of camel-hair cords of the thickness of a finger, with meshes 4 inches square. It is drawn along the bottom by a tow-line attached to the bowsprit of a sailing vessel or hauled in from the shore.

Cultivation. Prompted by a suggestion made by Oscar Schmidt, that sponges might be artificially propagated from cuttings, the Italian Government supplied funds for experiments to determine the feasibility of cultivating sponges as an industrial pursuit. A station was established on the island of Lesina, off the Dalmatian coast, and experiments were carried on there for six years (1867-72) under the superintendence of Von Buccich. The results were on the whole successful, but all expectations of creating a new source of income for the sponge-fishers of Dalmatia were defeated by the hostility of the fishers themselves.

The details of the method of sponge-farming as practised by Von Buccich are briefly as follows. The selected specimens, which should be obtained in as uninjured a state as possible, are placed on a board moistened with sea water and cut with a knife or fine saw into pieces about 1 inch square, care being taken to preserve the outer skin as intact as possible. The operation is best performed in winter, as exposure to the air is then far less fatal than in summer. The sponge cuttings are then trepanned and skewered on bamboo rods; the rods, each bearing three cuttings, are secured in an upright position between two parallel boards, which are then sunk to the bottom of the sea and weighted with stones. In choosing a spot for the sponge-farm the mouths of rivers and proximity to submarine springs must be avoided; mud in this case, as in that of reef-building corals, is fatal. A favourable situation is a sheltered bay with a rocky bottom overgrown with green seaweed and freshened by gentle waves and currents. So favoured, the cuttings grow to a sponge two or three times their original size in one year, and at the end of five to seven years are large enough for the market. Similar experiments with similar results have more recently been carried on in Florida. The chief drawback to successful sponge-farming would appear to be the long interval which the cultivator has to wait for his first crop.

Preparation for market.

After the sponge has been taken from the sea, it is exposed to the air till signs of decomposition set in, and then without delay either beaten with a thick stick or trodden by the feet in a stream of flowing water till the skin and other soft tissues are completely removed. If this process is postponed for only a few hours after the sponge has been exposed a whole day to the air it is almost impossible to completely purify it. After cleaning it is hung up in the air to dry, and then with others finally pressed into bales. If not completely dried before packing the sponges "heat," orange yellow spots appearing on the parts attacked. The only remedy for this is to unpack the bale and remove the affected sponges. The orange-coloured spots produced by this "pest," or "cholera" as the Levant fishermen term it, must not be confounded with the brownish red colour which many sponges naturally possess, especially near their base. The sponges on reaching the wholesale houses are cut to a symmetrical shape and further cleaned. The light-coloured sponges often seen in chemists' shops have been bleached by chemical means which impair their durability. Sponges are sold by weight; sand is used as an "adulteration."

It is difficult to obtain recent statistics as to the extent of the sponge trade; the following tables gives a summary of the sponges sold in Trieste, the great European sponge market, in the year 1871:—

TABLE I.

Description of Sponge.	For Export.	
	Value in £.	Mean price per pound.
Horse sponge	£60,000	6s.
Zimocca sponge	20,000	6s.
Fine Levant sponge	20,000	14s.
Fine Dalmatian sponge	2,000	8s.

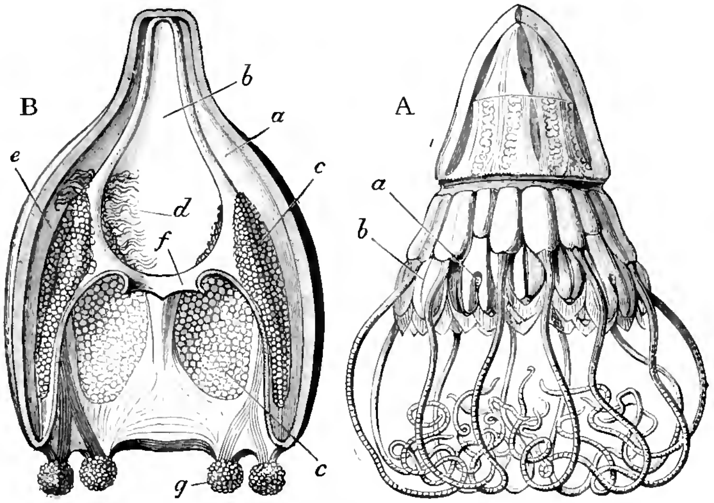
TABLE II.

Description of Sponge.	For Home Consumption.	
	Value in £.	Mean price per pound.
Horse sponge	£4400	6s.
Zimocca sponge	550	6s.
Fine Levant sponge	950	14s.
Fine Dalmatian sponge	...	...

(W. J. S.)

HYDROZOA

THE HYDROZOA form one of the three classes into which the *Cœlentera nematophora* (distinguished from the *Cœlentera porifera*, or Sponges) have been divided. It results from observations made by Ernst Haeckel that the *Ctenophora* should not be regarded as a class equivalent to the *Hydrozoa* and *Actinozoa*, nor as a subdivision of the latter class, but that they must be considered as a peculiar modification of the medusiform *Hydrozoa* (see final paragraph). If this conclusion be accepted, it will be necessary to divide the *Hydrozoa* into two primary groups or grades, for which the names *Polypomorpha* and *Ctenophora* are proposed.



Scyphomedusæ from the Deep Sea. (After Haeckel, *Challenger Reports*, vol. iv. 1882).

A. ***Periphylla mirabilis***, Haeck., one of the Peromedusæ, one-third the natural size. *a*, one of the four interradial tentaculocysts (sensory organs) sunk between its lappets; *b*, one of the sixteen subradial coronal lobes. The twelve tentacles (four perradial, eight adradial) are seen.

B. Perradial section through *Lucernaria bathyphila*, Haeck., nat. size. *a*, perradial gastral pouch; *b*, gastral axial cavity; *c*, ovary (four); *d*, gastral filaments; *e*, perradial gastral pouch; *f*, manubrium and mouth; *g*, the bunches of tentacles (eight, adradial).

The eight principal tentacles (four perradial and four interradial) are not in this species converted into adhesive anchors as in *L. auricula*, but are altogether suppressed.

The *Hydrozoa* correspond to the Linnæan genera *Hydra*, *Tubularia*, *Sertularia*, and *Medusa*. The name was applied by Huxley in 1856 to a group corresponding to that termed *Hydromedusæ* by Vogt (1851) and *Medusæ* by Leuckart (1853), and embracing the forms placed by Gegenbaur in his *Elements of Comparative Anatomy* (1878) in four classes, viz., *Hydromedusæ*, *Calycozoa*, *Thecomedusæ*, and *Medusæ*. Our knowledge of the structure and life-history of the *Hydrozoa*, many of which, on account of their delicacy and oceanic habits, are excessively difficult to obtain in a state fit for investigation, has greatly extended within the last five years. Whilst in the two decades preceding this period the admirable researches of Huxley, Gegenbaur, Agassiz, and Allman had brought to light and systematized a vast mass of information with regard to these organisms, the later observations of Claus, the Hertwigs, Haeckel, and Metschnikoff, have corrected, extended, and added to their history, especially in respect of embryological and histological detail. An epitome of the present condition of our knowledge of the group is afforded by the subjoined tabular classification of its families, orders, and sub-classes.

The definition and synonymy of the divisions recognized will be entered into, after a sketch has been given of the common structural features of typical *Hydrozoa*.

CLASS HYDROZOA.

	Examples.
Sub-Class I. **Scyphomedusæ** (syn. Ephyromedusæ).	
Order 1. LUCERNARIÆ.	
Fam. 1. Eleutherocarpidæ	Lucernaria (fig. 19). Halielystus.
,, 2. Cleistocarpidæ	Craterolophus. Manania.
Order 2. DISCOMEDUSÆ (Haeckel).	
Sub-Order 1. Cubostomæ.	
Fam. 1. Protephyridæ.	
,, 2. Nausithoidæ	Nausithoe.
,, 3. Ephyrellidæ.	
,, 4. Atollidæ.	
,, 5. Cyclorchidæ.	
Sub-Order 2. Semostomæ.	
Fam. 1. Pelagidæ	Chrysaora (fig. 24, *b*). Pelagia.
,, 2. Cyanæidæ	Cyanæa.
,, 3. Sthenonidæ	Sthenonia.
,, 4. Aurelidæ	Aurelia (figs. 26–31).
Sub-Order 3. Rhizostomæ.	
Fam. 1. Tetragameliæ	Cephea. Cassiopeia.
,, 2. Monogameliæ	Rhizostoma (fig. 24, *a*). Crambessa.
Order 3. CONOMEDUSÆ (Haeckel).	
Fam. 1. Charybdeidæ	Charybdæa (figs. 20–23).
,, 2. Bursaridæ.	
,, 3. Chiropsalmidæ.	
Order 4. PEROMEDUSÆ (Haeckel).	
Fam. 1. Periphyllidæ.	
,, 2. Pericryptidæ.	

Sub-Class II. **Hydromedusæ.**	
Order 1. GYMNOBLASTEA-ANTHOMEDUSÆ.	
Fam. 1. Tubularidæ	Tubularia (fig. 35). Hybocodon. Corymorpha (fig. 34).
„ 2. Pennaridæ	Pennaria. Vorticlava.
„ 3. Eudendridæ	Bougainvillia (figs. 36, 37). Perigonium. Lizzia (fig. 44).
„ 4. Cladonemidæ	Cladonema. Clavatella.
„ 5. Bimeridæ	Garveia. Stylactis.
„ 6. Dicorynidæ	Dicoryne (fig. 40).
„ 7. Corynidæ	Sarsiadæ (fig. 45). Coryne. Syncoryne (figs. 41, 46).
„ 8. Hydractinidæ	Hydractinia (fig. 39). Podocoryne.
„ 9. Clavidæ	Clava-Turris (fig. 38) Cordylophora.
„ 10. Hydridæ	Hydra (fig. 42). Protohydra(?).
Order 2. CALYPTOBLASTEA-LEPTOMEDUSÆ.	
Fam. 1. Plumularidæ	Plumularia. Antennularia.
„ 2. Sertularidæ	Sertularia. Halecium.
„ 3. Campanularidæ	Eucopidæ. Campanularia (fig. 43). Laomedea. Obelia.
„ 4. Thaumantiadæ	Thaumantias. Lafoea. Melicertum. Tima.
„ 5. Æquoridæ	Æquorea. Zygodactyla. Rhegmatodes.
Order 3. TRACHOMEDUSÆ (Haeckel).	
Fam. 1. Petasidæ	Petasus.
„ 2. Trachynemidæ	Rhopalonema.
„ 3. Aglauridæ	Aglaura.
„ 4. Geryonidæ	Liriope. Carmarina (figs. 48, 49).
Order 4. NARCOMEDUSÆ (Haeckel).	
Fam. 1. Cunanthidæ	Cunina (figs 50, 51).
„ 2. Peganthidæ	Polyxenia.
„ 3. Æginidæ	Ægina. Æginopsis
„ 4. Solmaridæ	Solmissus Solmaris.
Order 5. HYDROCORALLINÆ (Moseley).	
Fam. 1. Milleporidæ	Millepora (figs. 52, 53).
„ 2. Stylasteridæ	Sporadopora. Distichopora. Astylus (fig. 54).
Order 6. SIPHONOPHORA.	
Sub-Order 1. Physophoridæ.	
Fam. 1. Athorybiadæ	Athorybia.
„ 2. Physophoridæ	Physophora (fig. 57, C)
„ 3. Agalmidæ	Forskallia. Halistemma. Agalma (fig 57. E)
„ 4. Apolemiadæ	Apolemia.
„ 5. Rhizophysidæ	Rhizophysa.
Sub-Order 2. Physalidæ.	
Fam 1. Physalidæ	Physalia.
Sub-Order 3. Calycophoridæ	
Fam. 1. Hippopodiidæ	Gleba.
„ 2. Diphyidæ	Praya. Diphyes (fig. 57. A). Abyla.
„ 3. Monophyidæ	Sphæronectes.
Sub-Order 4. Discoideæ.	
Fam. 1. Velellidæ	Velella. Porpita.

The *Hydrozoa* present a greater simplicity of ultimate structure than do any animal organisms possessed of as great a complexity of external form. As in all *Metazoa* or *Enterozoa*, the life cycle of a hydrozoon starts with an egg which is at first a single cell or unit of protoplasm, but proceeds after fertilization to multiply by transverse fission in such a way that the resulting cells or units are arranged in two layers, each one cell deep, disposed around a central cavity—the enteron or archenteron. The sac thus formed is known as a diblastula (figs. 1, 2, and 25). By the formation[1] of a mouth to the sac, the enteron acquires the functions of a digestive retort in which food matters taken in at the mouth are brought into a chemical condition suitable for the nutrition of the surrounding cells. The two layers of cells (of which the outer only acquires additional layers[2] by the division of the primary cells, and that by no means in all cases) received from Allman (*Phil. Trans.*, 1855) the names respectively of the ectoderm and the endoderm, having previously been shown by Huxley (1849) to be the fundamental membranous constituents of which the most varied parts of the more complex *Hydrozoa*—such as tentacles, swimming bells, and air-bladders—are built up in the adult condition. Huxley also pointed out the identity of these membranes with the two primary layers of the vertebrate embryo. The endoderm and the ectoderm, which present themselves, as is now known, in the diblastula (or gastrula) phase of all *Enterozoa*, remain in *Hydrozoa* (and also in the allied groups of *Cœlentera*) as permanently distinguishable elements of structure. This important disposition is associated with and dependent on the simple character which the archenteron or primitive digestive space retains. Into whatever lobes or processes the sac-like body may be, so to speak, moulded, whether tentacles[3] or broader expansions, into these the cavity of the archenteron is extended in the first instance; and where the actual cavity is obliterated the endodermic cell-layer remains to represent it (Gefässplatte or endoderm-lamella, see figs. 7 and 16).

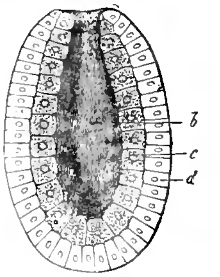


FIG. 1.—Diagram of a Diblastula. *a*, orifice of invagination (blastopore); *b*, archenteric cavity; *c*, endoderm: *d*, ectoderm. (From Gegenbaur's *Elements of Comparative Anatomy*)

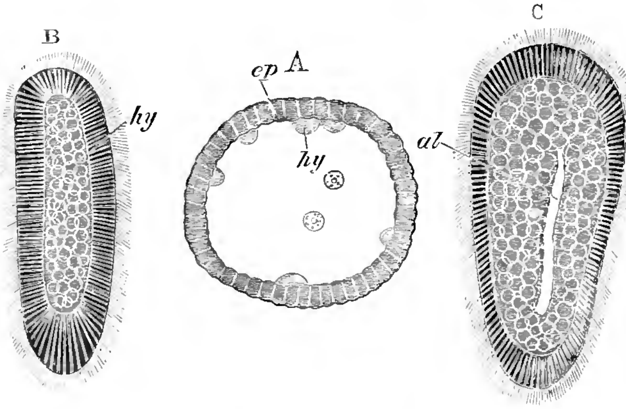


FIG. 2.—Formation of the Diblastula of *Eucope* (one of the Calyptoblastic *Hydromedusæ*) by delamination. (From Balfour, after Kowalewsky) A, B, C, three successive stages. *ep*, ectoderm; *hy*, endoderm; *al*, enteric cavity.

Conversely, whatever canals or spaces are discovered in the substance of a hydrozoon (excepting only the cavity of ectodermal otocysts) are simple and direct continuations of the one original enteric cavity of the diblastula, and all such spaces are permanently in free communication with one another.[4]

The whole of the *Hydrozoa* seem to present a lower grade of structure than the *Actinozoa*, in so far as the latter, whilst retaining permanently free communication between all parts of the archenteric space, yet exhibit a differentiation of this space into an axial and a periaxial portion—a digestive tube and a body cavity. The differentiation has only to proceed a step further, namely, to the closure or shutting off of the axial from the periaxial portion of the archenteric space, and we obtain the condition which characterizes the adult forms of the *Cœlomata*, or animals

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[1] In *Hydromedusæ* the inner layer of cells forms by delamination, in *Scyphomedusæ* by invagination. In the latter case the sac closes up, and the mouth is formed by a new opening.

[2] It is probable that the numerous rows of cells described in the endoderm of *Tubularia* and *Corymorpha* by Allman, in his great monograph of the *Tubularian Hydroids*, are due to a plication of the original endodermal cell-layer. The two kinds of cells in two layers figured by the same authority in the endoderm of *Gemmellaria implexa*, pl. vii. fig. 5, cannot, however, be thus explained.

[3] Some solid tentacles, with a single axial row of endodermal cells, form an exception to this statement.

[4] The observations of Eilhard Schulze cited in the article CŒLENTERA do not form any real exception to this statement.

with blood-lymph space distinct from digestive canal.[1] With the attainment of the cœlomate condition, the two fundamental cell-layers, ectoderm and endoderm, which still appear in the embryo, become so far interwoven, and their products so highly differentiated, that it is no longer possible to recognize them as anatomical structures in the adult.

The only deep-seated distinction between *Hydrozoa* and *Anthozoa* (the *Actinozoa* being thus termed when the *Ctenophora* are detached from them) appears to be the particular differentiation of the archenteric space in *Anthozoa* which has just been noted. It is no longer possible to separate the two groups from one another as *Exoarii* and *Endoarii*, as was proposed by Rapp (*Ueber die Polypen im Allgemeinen und die Actinien insbesondere*, Weimar, 1829)—the first term indicating the *Hydrozoa* as possessed of external generative organs, whilst by the latter term the *Anthozoa* are pointed to as having internal generative organs.[2] This distinction breaks down completely in the case of *Lucernaria*, and even in that of the so-called phanerocarpous and some other medusæ which discharge their genital products by the mouth, and quite rarely by rupture of the outer body-wall. The tendency to form calcareous deposits in the deep layers of the ectoderm, or mesoderm, as it has been termed, exhibited almost universally by the *Anthozoa* (whence the name *Coralligena* applied to them), is distinctive of them, though it has been shown first by Louis Agassiz, and more fully and recently by Moseley, to be paralleled among *Hydrozoa*, by the *external* calcareous deposits of the abundant and widely distributed Millepores and Stylasterids. A minute distinction between *Hydrozoa* and *Anthozoa*, which does not, however, hold good universally, is found in the form of the barbed threads ejected by the nematocysts. Instead of the complicated forms present in the latter group, the *Hydrozoa* are usually provided with either an unbarbed thread or one in which the barbs are confined to three at the base and a few minute barblets (fig. 5).

Fundamental Forms of the Hydrozoa.—The diblastula derived from the egg of a hydrozoon, when provided with a mouth, may be spoken of (as are the equivalent forms in other animals groups) as a person. Either this person elongates and develops tentacles in a circlet around or near the mouth, and usually becomes fixed by the aboral pole of the sac-like body, or the sac gradually assumes the form of a clapper-bell or of an umbrella with greatly thickened handle, the mouth being placed at the free end of the handle or of the clapper, and the animal freely swimming by the contractions and expansions of the dome of the bell (disc of the umbrella). The two forms of persons are known,—the former as the "hydriform" (2, 3 in fig. 16), the latter as the "medusiform" (4, 5, 6 in fig. 16).

The HYDRIFORM PERSONS usually occur as fixed branching colonies or trees (figs. 36 and 37) produced by lateral budding from an original hydra-form developed from a diblastula.

The hydriform person in its most fully developed state is seen in the colonies of *Tubularia*. In such a colony a number of hydriform persons are united like the flowers of a plant on its branches (whence Allman's terms hydranth, hydrophyton). Each hydriform person (fig. 35) has an elongated *body* with oral and aboral pole. The mouth is placed centrally at the oral pole, which is somewhat enlarged and conical. At the apex of the cone, immediately around the mouth, is a circlet of *small tentacles*; at the base of the cone is a second circlet of *larger tentacles*; the surface of the oral cone is termed the *hypostome*. In other genera (*e.g.*, *Hydra*, fig. 42) the smaller circle of tentacles is wanting; in others, again, the tentacles are irregularly placed and not concentrated into one circlet (fig. 38). We regard the former as the typical condition. In the hydriform persons of the *Scyphomedusæ* (figs. 26 and 27) the vertical axis is much shortened, the hypostome is flat, and the whole body cup-like or hemispherical.

The tentacles of the hydriform person are sometimes hollow (*Hydra*, *Garveia nutans*, *Hydrocorallinæ*), being mere prolongations of the sac-like body; but usually, though the endodermal cell-layer is continued into them, they are solid (2 in fig. 16). Very generally the tentacles of the hydra-form are indefinite in number, but in those belonging to the group of *Scyphomedusæ* a primary series indicating four radii (perradial) can be distinguished, to which are added four intermediate to these, marking four secondary radii (interradial), whilst eight more placed between the eight of the perradial and interradial series are known as adradial tentacles. The surface of the hydra-form may be entirely naked, or encased in a horny tube (perisarc) formed by the ectoderm: this may be confined to the aboral portion of the hydranth and to the common stem which unites the persons of a colony, or it may rise up and form a cup (or hydrotheca) around the oral region of the hydranth (figs. 32 and 33).

The bodies of all hydriform persons, as well as the tentacles, are excessively contractile, and when hydrothecæ are present can be withdrawn into them.

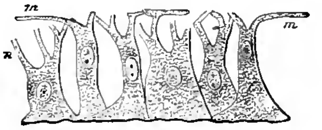

FIG. 3.—Epidermo-muscular cells of *Hydra*. *m*, muscular-fibre processes. (After Kleinenberg, from Gegenbaur.)

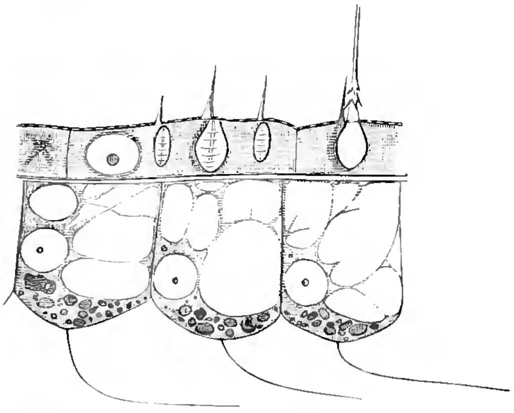

FIG. 4.—Portion of the body-wall of *Hydra*, showing ectoderm cells above, separated by "structureless lamella" from three flagellate endoderm cells below. The latter are vacuolated, and contain each a nucleus and several dark granules. In the middle ectoderm cell are seen a nucleus and three nematocysts, with trigger hairs projecting beyond the cuticle. A large nematocyst, with everted thread, is seen in the right-hand ectodermal cell. (After F. E. Schulze.)

The ectoderm or outer cell-layer furnishes the protective and contractile tissues of the hydra-form. Very usually it is not more than one or two cells deep, and is separated from the endoderm by a structureless lamella of firm consistence. In *Hydra* large cells of the ectoderm (neuro-muscular cells of Kleinenberg) bound the external surface (fig. 3) and give off horizontal muscular processes which lie side by side on the structureless lamella—forming thus a deep muscular coat, the fibrous elements of which are not independent cells. In larger species some of the fibres may become separated from the tegumentary or superficial cells, and acquire the character of independent nucleated corpuscles (*Hydractinia*, Van Beneden). No nervous elements nor sense-organs occur in any hydra-form (except perhaps the *Lucernariæ*). In *Antennularia* some ectoderm cells are amœbiform, and project processes which change shape (nematophors). Tactile hairs (palpocils),

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[1] The *Enterozoa* or *Metazoa* admit of division into two grades—(1) the *Cœlentera*, including sponges, polyps, jelly-fish, and corals, and (2) the *Cœlomata*, including all remaining forms.

[2] See, however, note to the paragraph headed *Definition of the Hydrozoa*, p. 555.

however, occur on the ectodermal cells, and the solid tentacles are essentially tactile organs. Placed in and between the large cells of the ectoderm (*Hydra*, *Cordylophora*, Allman, Kleinenberg, F. E. Schulze) are small nucleated cells which become converted into vesicles containing a three-barbed (figs. 4 and 5) or simple filament (nematocysts). These are frequently grouped on the surface in wart-like processes or "batteries." Nematocysts also are found in the endoderm; but it is probable that their presence there is due to their having been swallowed.

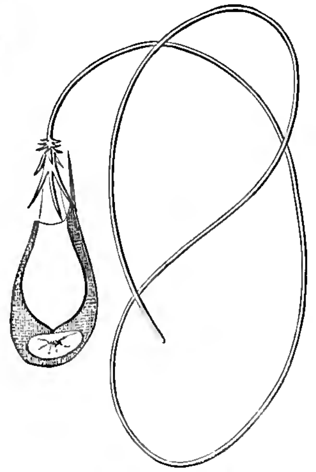

FIG. 5.—Nematocyst of *Hydra*, showing cell-substance and nucleus, cyst, trigger hair, and everted thread. (After F. E. Schulze.)

The endoderm is usually but one cell deep, and lines the entire cavity of the body starting from the margin of the mouth. In the region of the body proper, and in hollow tentacles, the cells are ciliated (fig. 4). In this region they are concerned in the secretion of digestive fluids and in absorption, and sometimes contain coloured granules (hepatic?). Allman found in *Myriothela* (*Phil. Trans.*, 1875) that the endoderm cells project processes like the pseudopodia of *Protozoa*, and suggests that solid food particles are incepted by them. T. J. Parker has published similar observation on *Hydra* (1880). In the solid tentacles the endodermal cells are greatly modified, forming a kind of skeletal tissue, each cell recalling by its vacuolation and firm cell-wall the characters of vegetable parenchyma (fig. 6). In the stems of *Siphonophora* endoderm cells give origin to muscular processes like those of the ectoderm (Claus). This latter fact has a morphological significance which cannot be too gravely estimated.

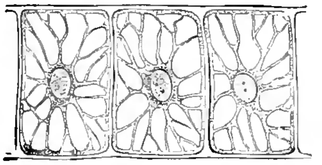

FIG. 6.—Vacuolated endoderm cells of cartilaginous consistence from the axis of the tentacle of a Medusa (*Cunina*). (From Gegenbaur's *Elements of Comparative Anatomy*.)

Generative products are not developed by any hydriform persons (excepting the *Lucernariæ*), the sexual process being carried on by a distinct set of buds developed on the sides of hydriform persons. These buds either become medusiform persons, or are degenerated representatives of such persons (sporosacs) (figs. 17 and 18). Even the fresh-water *Hydra* (fig. 42) does not appear to be an exception to this generalization. The single egg-cell of *Hydra* projects at the breeding season in an ectodermal covering, as a wart, from the lower part of the body. A conical eminence or two nearer the mouth contains the spermatozoa. Each ovarium and each spermarium represents an aborted generative person. According to Kleinenberg the egg-cell and the sperm-cells are both derived from the ectoderm. The *Lucernariæ* develop internal generative organs (fig. 19) which correspond closely with those of the medusiform persons of the group *Scyphomedusæ* (see below), with which they are classified. Both ova and testis are endodermal in origin in *Lucernaria* and in the medusiform persons of the *Scyphomedusæ*, whilst they appear to be ectodermal in origin in the complete medusiform persons of *Hydromedusæ*, though in the degenerate medusiform persons known as sporosacs they may either or both have an endodermal origin.

MEDUSIFORM PERSONS usually present themselves as isolated free-swimming individuals, but like hydriform persons they have the power of producing new persons by budding (figs. 44, 45, and 46), which may become detached or may remain connected with the primary person (fig. 57) to form a freely swimming colony (*Siphonophora*) comparable to the fixed colonies of hydriform persons. Medusiform persons are often produced as the immediate result of the development of the diblastula without any intermediate hydriform phase (*Pelagia* among *Scyphomedusæ*, *Trachomedusæ*, *Narcomedusæ*, and probably some *Anthomedusæ* and *Leptomedusæ*), but quite as frequently originate as lateral *buds* upon the body-walls of hydriform persons (figs. 34, 37, and 43), or of other medusiform persons (see below), or as metameric fission-products of hydra-forms. The typical medusa-form is a hemispherical cup (the *nectocalyx*, or *umbrella*, or *disc*), from the centre of which rises up a cylindrical or conical process (the *manubrium*, erroneously *polypite*) at the summit of which is the mouth (4, 5 in fig. 16). Four perradial (see above for use of this term) tentacle-like lobes very commonly surround the mouth, or numerous small tentacles (fig. 58), whilst the margin of the disc is beset with tentacles four in number, or a multiple of four (sometimes six, or one only, or indefinite). The aboral pole is dome-like, and is never attached except in those forms which take their origin as buds on a hydriform colony when the connexion exists at this point. The tentacles are, as in the hydriform persons, some solid, some hollow: both occur in the same individual.

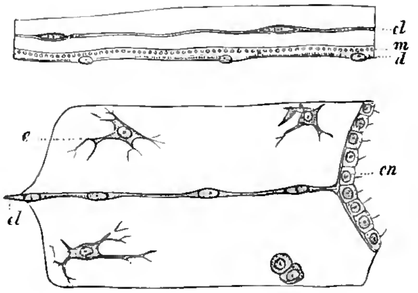

FIG. 7.—Portions of sections through the disc of medusæ,—the upper one of *Lizzia*, the lower of *Aurelia*. *el*, endoderm lamella, or vascular lamella; *m*, muscular processes of the ectoderm cells in cross section; *d*, ectoderm; *en*, endoderm lining the enteric cavity; *e*, wandering endoderm cells of the gelatinous substance. (After Hertwig.)

The body is not so completely hollowed out as in the hydriform persons. The mouth leads into a straight tube (the stomach) which occupies the axis of the manubrium, and expands at its insertion into the disc. The disc, even when thick and fleshy, is not fully excavated by the enteric cavity. In young forms the cavity does occupy it right up to the margin, but gradually the lumen disappears (fig. 29), leaving a series of canals and a continuous plate of endoderm (fig. 7) formed by the coalesced walls of the space (the endoderm-lamella of the Hertwigs, see *Organismus der Medusen*, 1878; the vascular-lamella of Claus, "Polypen und Quallen der Adria," *Wiener Denksch.*, 1878). The peripheral portion of the lumen of the original enteric cavity forms the ring-canal, which runs all round the margin of the disc, and is continued into the hollow tentacles. The lumen is further retained at intervals in the form of radiating canals connecting the axial enteric cavity with the ring-canal. These may be perradial, interradial, and adradial (see above as to tentacles of hydra-form), and may branch dichotomously in the disc or form networks.

The medusæ are thicker and more fleshy to the touch than are the hydra-forms, and are at the same time transparent. This is entirely due to the enormous development of a structureless substance between ectoderm and endoderm, corresponding to the "Stutz-lamella" or structureless lamella of the hydra-forms. (See figs. 49 and 51, representing sections of *Carmarina* and of *Cunina*.)

The remarkable development of this substance in a hyaline condition has led to the description of canals and spaces where none exist—the supposed spaces being really occupied by this hyaline substance. F. E. Schulze's statements as to extra-enteric spaces in *Sarsia* are thus explained—and more decidedly the supposed circular and longitudinal canals attributed by some authors to the scyphistoma phase of *Discomedusæ*. In the same manner (according to Claus) Allman's observations on *Stephanoscyphus* are reconciled with those of F. E. Schulze on *Spongicola*—clearly the same form. *Stephanoscyphus* is devoid of either circular or longitudinal canals, and though it has four remarkable ridges on the enteric wall like those of the scyphistoma of *Scyphomedusæ* (see fig. 26) stands in all probability very close indeed to the Tubularian genus, *Perigonimus*.

In a large number of medusa-forms the hyaline gelatinous substance is structureless, but in many of the larger *Scyphomedusæ* it is occupied by in-wandering amœboid cells derived from the endoderm and by fibrous trabeculæ (fig. 8).

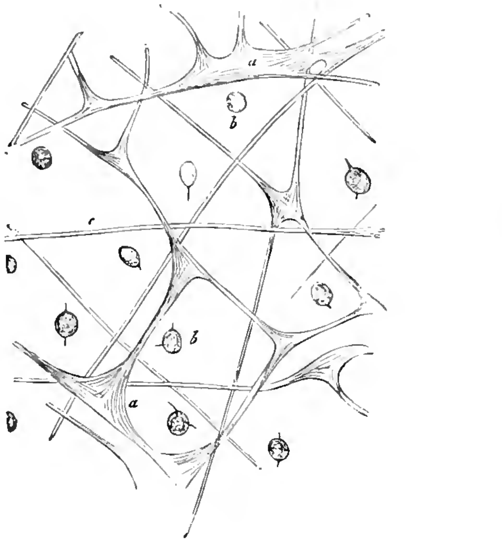

FIG. 8.—Gelatinous substance of the disc of *Aurelia*, showing—*a*, fibrous trabeculæ, and *b*, wandering endoderm cells, with amœboid movements. (From Gegenbaur.)

The wandering endodermal cells are nutrient in function, and represent so far isolated elements of the enteric canal system.

The medusiform person is fundamentally adapted to swimming movements. The muscular fibres are mostly transversely striated, and are as a rule outgrowths of superficial ectoderm cells as in *Hydra* (fig. 9), (though in some cases distinct cells); they are confined to a sheet spread on the oral face only of the disc or swimming-bell (sometimes called sub-umbrella), to the extensile manubrium and tentacles, and to an inwardly directed flap of the margin of the disc known as the *velum* (*Ve* in 4 of fig. 16), which is present in those medusæ that are not flattened but conical (bell-like). The muscular fibres on the oral face of the disc and on the velum have a circular direction, interrupted in some cases by radial tracts. The direction of the swimming movements is obvious from this arrangement.

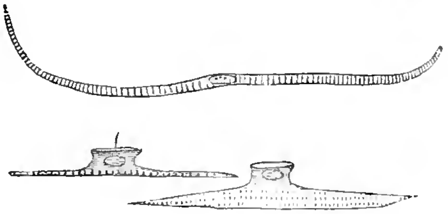

FIG. 9.—Muscular cells of medusæ (*Lizzia*). The uppermost is a purely muscular cell from the sub-umbrella; the two lower are epidermo-muscular cells from the base of a tentacle; the upstanding nucleated portion forms part of the epidermal mosaic on the free surface of the body. (After Hertwig.)

The velum is not a constant element in the medusa's disc; it serves to contract the space by which water is expelled from beneath the bell in the act of swimming. All fully-developed *Hydromedusæ* possess the velum, but only a few of the *Scyphomedusæ* (*Charybdæa*). In the former the endoderm plate (vascular lamella) is not continued into it; in the latter vessels of the enteric system are present in it (fig. 21), and, being probably morphologically distinct, it has been here termed the "pseudo-velum."

Unlike the hydra-forms, the medusa-forms of *Hydrozoa* possess in addition to the tentacles highly-developed sense-organs and ganglionic nerve-centres and nerves. The sense-organs appear to be either eye-spots, or else otocysts, or to combine the functions of both. In addition to these are olfactory tracts or pits connected with the preceding. The sense-organs are placed along the margin of the disc (hence called marginal bodies), and are of three kinds:—(1) ocelli—rounded pigment spots, rarely provided with a lens (*Lizzia*) (fig. 10), always placed at the base of a tentacle or in the radius of one on the oral surface (*Lizzia*), entirely ectodermal in origin; (2) vesiculi or otocysts—formed (as discovered by the Hertwigs, 1878) by an invagination of the ectoderm (fig. 11) containing concretions and hair cells; either open or entirely closed, generally numerous, and placed *between* tentacles, sometimes at the bases of tentacles (*Obelia*); (3) tentaculocysts—which are reduced and modified tentacles; into them alone of the three kinds of marginal bodies do the endoderm and, in the more complex, the enteric canal system enter (figs. 12, 13, and 30). The endodermal sac forms the axis of the tentaculocyst, its cells secrete crystalline concretions, and it functions as an otocyst; pigment spots, which may have cornea, lens, and retina well developed, are formed sometimes to the number of six (*Charybdæa*) on the ectoderm of the tentaculocyst (fig. 13). The olfactory sense-epithelium (fig. 14) is either distributed in a continuous band on the margin of the disc (*Hydromedusæ*, discovered here by the Hertwigs), or it is

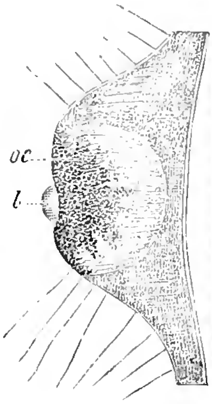

Fig. 10.

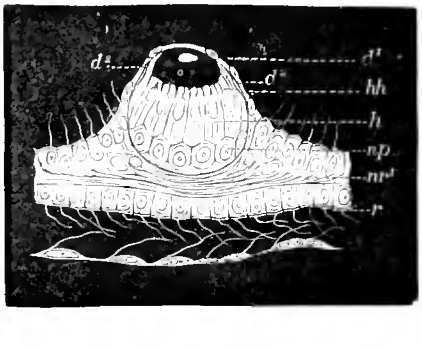

Fig. 11.

FIG. 10.—Ocellus of a medusa (*Lizzia Koellikeri*). *oc*, pigmented ectodermal cells; *l*, lens. (After Hertwig.)

FIG. 11.—Otocyst (formed entirely by ectoderm) of *Phialidium*, one of the vesiculate medusæ. *d*¹, superficial layer of ectoderm; *d*², deep layer of ectoderm; *h*, auditory cells of ectoderm; *hh*, auditory hairs; *np*, nerve body; *nr*¹, upper nerve-ring; *r*, endoderm cells of the circular canal. The otolith cavity is seen above *h*.

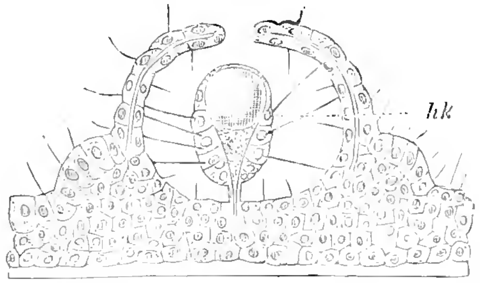

FIG. 12.—Simple tentaculocyst of one of the *Trachomedusæ* (*Rhopalonema velatum*). The process carrying the otolith or concretion *hk*, formed by endoderm cells, is enclosed by an upgrowth forming the "vesicle," which is not yet quite closed in at the top. (After Hertwig.)

confined to deep pits (foveæ nervosæ) from each of which a tentaculocyst arises (discovered in the *Scyphomedusæ* independently by Schäfer and Claus). With some exceptions, medusæ provided with ocelli are destitute of vesiculi, which alone occur in the vesiculate *Leptomedusæ*. Tentaculocysts characterize to the exclusion of the ocelli and vesiculi the *Trachomedusæ* and *Narcomedusæ* among *Hydromedusæ* and all the *Scyphomedusæ*, except *Lucernaria*, where they are replaced by "colleto-cystophors."

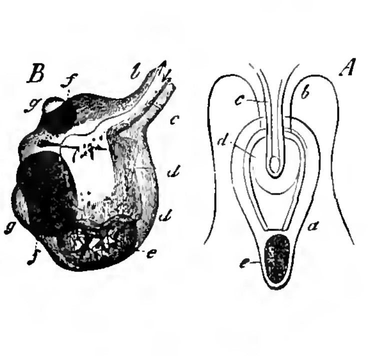

Fig. 13.

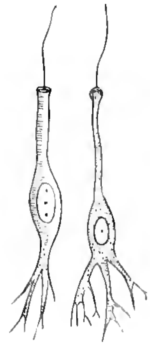

Fig. 14.

Fig. 13.—Tentaculocysts of medusæ (*A*, of *Pelagia*; *B*, of *Charybdæa*). *a*, the free tentacle hanging in the notch of the disc; *b*, stalk; *c*, enteric canal continued into it; *d*, enlarged portion of the canal; *e*, concretions on endodermal cells; *f*, pigmented ectoderm; *g*, lens. (From Gegenbaur.)

Fig 14.—Cells from the olfactory pits (foveæ nervosæ) of *Aurelia*. (After Schäfer.)

The nervous system has only recently been correctly recognized in medusæ, though seen by Agassiz as long ago as 1849, and described both by Fritz Müller and Haeckel in certain forms (*Geryonidæ*) more recently (1860). It differs remarkably in the two great groups into which the *Hydrozoa* are divisible. In the *Scyphomedusæ* there is no continuous nerve-centre, but around and about each tentaculocyst nerve-fibres and cells are grouped in such a way as to divide the disc into zones of nerve supply corresponding to the number of tentaculocysts (usually eight).

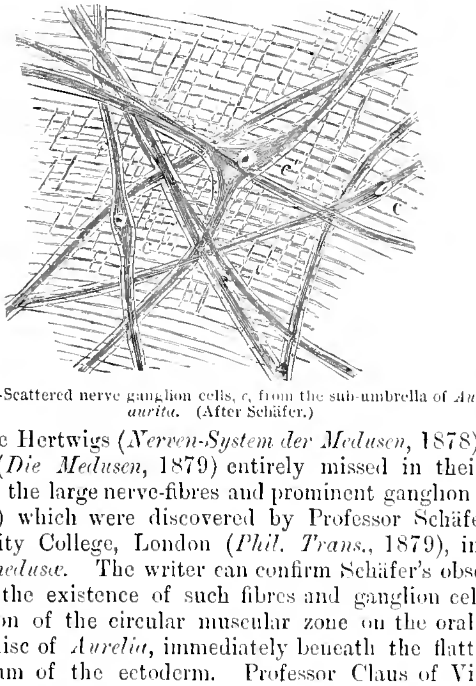

Fig. 15.—Scattered nerve ganglion cells, *c*, from the sub-umbrella of *Aurelia aurita*. (After Schäfer.)

Both the Hertwigs (*Nerven-System der Medusen*, 1878) and Eimer (*Die Medusen*, 1879) entirely missed in their researches the large nerve-fibres and prominent ganglion cells (fig. 15) which were discovered by Professor Schäfer of University College, London (*Phil. Trans.*, 1879), in the *Scyphomedusæ*. The writer can confirm Schäfer's observation of the existence of such fibres and ganglion cells in the region of the circular muscular zone on the oral face of the disc of *Aurelia*, immediately beneath the flattened epithelium of the ectoderm. Professor Claus of Vienna has independently described ("Polypen und Quallen der Adria," 1878) similar nerve-cells and fibres in *Chrysaora* and *Charybdæa*. Professor Schäfer failed to ascertain satisfactorily the origin and termination of the fibres, which appear, however, to originate in superficial ectodermal cells ("sense-epithelium") in the neighbourhood of the tentaculocysts and in the cells of those organs, and to terminate without any plexiform connexion with one another in the muscular fibres. Eimer has described very abundant and excessively fine fibres, often moniliform, which extend from epithelial cells in the neighbourhood of tentaculocysts and form a network traversing the gelatinous substance of the disc in every direction. This observation, though supported by the fact that such fibres are indicated by the extended experimental investigation of Eimer and of Romanes (Eimer, *Die Medusen*; Romanes, *Phil. Trans.*, 1876, *et seq.*), is not confirmed by other observers, and the fibres described are regarded as skeletal tissue. If Eimer's fibres do not exist, the muscular tissue of the medusæ must be regarded as acting to a large extent independently of nerve-control; and this is borne out by Claus's observation of the absence of sense-organs and nerve-fibres from the swimming-bells of the *Siphonophora* (compound medusæ). In the *Hydromedusæ* the nerve ganglion cells are grouped in a continuous ring around the margin of the disc, separated horizontally into an inferior and superior portion by the insertion of the velum. The difference in the form of the nervous system has led Eimer to propose the names *Cycloneura* for the *Hydromedusæ* and *Toponeura* for the *Scyphomedusæ*. Amongst the latter, however, *Charybdæa*, having a continuous velum like *Hydromedusæ*, has also a continuous nerve-ring.

Comparison and Relations of Hydriform and Medusiform Persons.—A simple shortening of the vertical axis, and a widening of the hypostome, with obliteration of the lumen (but not of the cells) of the endoderm over a considerable region of the disc thus produced, suffice to convert the hydraform into the medusa-form.[1] This change of proportion made (fig. 16), the sense-organs of the medusiform person have to be added, and the change is complete. Thus it becomes clear that we have to deal with one fundamental form, appearing in a lower, fixed, nutritive phase and a higher, locomotor, generative phase in the two cases respectively.

The phylogeny of the *Hydrozoa* and the historical relationship of the two phases (hydriform and medusiform) appears to be as follows.

A two-cell-layered sac-like form, with mouth and with or without tentacles, was the common ancestor of *Hydrozoa*, *Anthozoa*, and Sponges. The particular form which the proximate ancestor of the *Hydrozoa* took (1 in fig. 16) is most nearly exhibited at the present day in *Lucernaria* and in the scyphistoma larva (hydra-tuba) of *Discomedusæ*. It was a hemispherical cup-like polyp with tentacles in multiples of four, with four lobes to the wide enteric chamber. This polyp, after passing a portion of its life fixed by the aboral pole, loosened itself and swam freely by the contractions of the circular muscular fibres of its hypostome (sub-umbrella), and developed its ovaria and spermaria on the inner walls of the enteric chamber. This ancestor possessed, like its descendants, a very marked power of multiplication, either by buds or by detached fragments of its body. Accordingly it acquired definitely the character of multiplying by bud-formation during the earlier period of its life; each of the buds so formed completed in the course of time its growth into a free swimming person. We must suppose that the peculiarities of the two phases of development became more and more distinctly developed, the earlier budding phase exhibiting a more elongated form and simple enteric cavity (hydra-form), which subsequently

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[1] This relationship, demonstrated by the Hertwigs' discovery of the endoderm layer of the medusa's disc, differs from that supposed to obtain by Professor Allman. He supposed the medusa's disc to represent the coalesced tentacles of a hydra-form, and cited the webbed tentacles of *Laomedea flexuosa* in support of the identification, which had at the time very much to commend it.

became changed in the course of the ontogeny (development of the individual) into the umbrella or disc-like form, with coalesced enteric walls and radial and circular surviving spaces (medusa-form). And now the ancestry took two distinct lines, which have given rise respectively to the two great groups into which the *Hydrozoa* are divisible—the *Scyphomedusæ* and the *Hydromedusæ*. In the one set the hydriform persons of a colony, instead of each becoming metamorphosed into a medusiform person, proceeded each to break up into a series of transverse divisions; each division became a medusiform person, and was liberated in its turn as a free swimming organism (figs. 26 and 27). We must suppose that this process began historically by the outgrowth of new tentacles around the point where the disc of a person fully transformed from the hydriform to the medusiform phase was loosened in its attachment and about to separate from the colony. The "hastening of events," a well-known feature of organic growth-sequences, would complete the development of the newly sprouting person before the loosened medusa had got well away, and so on with a third, fourth, and even with twenty such successive buds. The separation of the adult form from its fixed larva by fission has been justly compared by Louis Agassiz to the separation of the *Comatula* from its pentacrinoid larval stalk. If the stalk could only produce new *Comatulæ*, the analogy would be complete. *Lucernaria* is in the same way comparable with the stalked crinoids, being an adult form which retains the characters exhibited by the immature phases of its congeners.

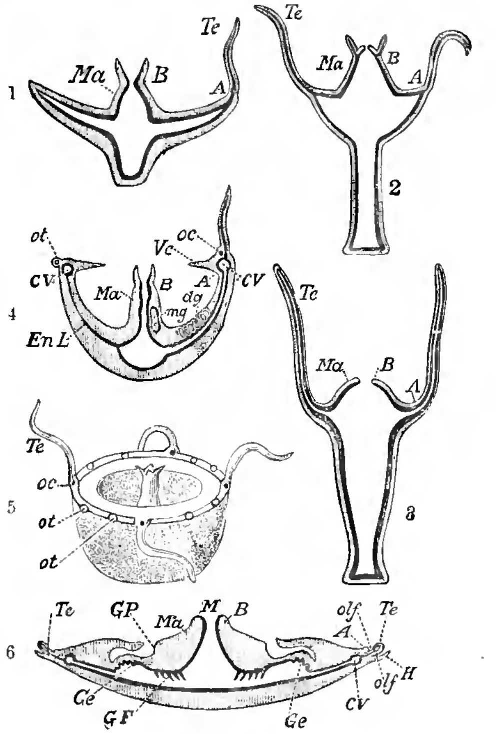

FIG. 16.—Diagrams to exhibit the plan of structure of hydriform and medusiform persons (all except 5 are vertical sections). *A*, base of tentacles, margin of the disc; *B*, oral margin; *Ma*, manubrium; *Te*, tentacle; *CV*, circular vessel; *EnL*, endoderm lamella; *ot*, otocyst; *oc*, ocellus *olf*, olfactory pit; *H*, hood of tentaculocyst; *mg*, genitalia developing in manubrium; *dg*, genitalia developing in the disc (wall of a radiating canal); *GP*, sub-genital pits of the sub-umbrella; *GF*, gastral filaments; *Ve*, velum. 1, Form intermediate between medusa-form and hydra-form. 2, Hydra-form with wide disc, manubrium, and solid tentacles (*Tubularian*). 3, Hydra-form with narrower disc, and hollow tentacles (*Hydra*). 4, Medusa-form with endoderm lamella on the left, the section passing through a radiating canal on the right; a velum, two possible positions of the genitalia, and two kinds of sense-organs are shown (*Hydromedusæ*). 5, A similar medusa-form seen from the surface. 6, Section of *Aurelia aurita*, to show especially the nature of the sub-genital pits, *GP*, outside the genital frills, and the position of the gastral filaments *GF*, as well as the flattened form of the disc.

The *Scyphomedusæ* do not, however, all exhibit a hydriform phase, and a production of medusæ by the "strobilation" or "metamerizing" of a scyphistoma. Some of them (*Pelagia*) "hasten events" so far that the diblastula never fixes itself, but becomes at once a single medusa, the hydriform phase of the ontogeny being altogether omitted. Certain peculiarities of the medusa's structure, above all the possession of gastral filaments (solid filaments like tentacles projecting in four interradial groups near the genitalia into the enteric cavity), serve to unite *Pelagia*, which has no larval stage, and *Lucernaria* (which is always of intermediate character between hydra-form and medusa-form) with the numerous species which develop by the strobilation of hydriform larvæ.

The second line of descent which has given rise to those *Hydrozoa* known as *Hydromedusæ* not only acquired at the start a different mode of producing medusiform persons, but the medusiform persons acquired characters differing from those of the *Scyphomedusæ* in important (but not fundamental) features. The larval stage in this series developed the property of budding to a very great degree, so as often to form fixed tree-like colonies of considerable size. Then the transformation of the identical colony-forming persons into free-swimming persons was finally and definitively abandoned, and only a late-appearing set of buds proceeded to complete the typical changes and to become medusæ. The earlier-produced buds were thus arrested in development, and became specially modified for the purposes of a fixed life as members of a colony. Thus they acquired the elongate form and the sporadic position of the tentacles which we see in some hydriform persons of the *Hydromedusæ* group (figs. 38 and 40), and were adapted to nutrition solely (hence the term trophosome applied by Allman to such colonies). The characters of the mature generative person, with its power of detachment and free locomotion, being confined to the later buds borne on the sides of the hydriform persons or on special portions of the colony, we find that the former became more and more specialized as *sexual* medusiform persons in proportion as the latter became specialized as *asexual* hydriform persons, and thus it is that we have the remarkable phenomenon of hydriform colonies, developed from the eggs of medusæ, producing as it were crops of medusæ (figs. 34 and 37) which detach themselves and swim away to deposit their eggs (alternation of generations). The *Hydromedusæ* never produce medusæ by strobilation or transverse division of a hydriform person, although in rare cases the cicatrix left by a detached medusa-bud has been observed to sprout and produce a hydriform person. Neither medusiform nor hydriform persons of the *Hydromedusæ* series ever have gastral filaments (unless they are represented by the "villi" of the *Siphonophora* described by Huxley, *Oceanic Hydrozoa*), whilst the medusa-forms always possess a velum and a comparatively simple set (four, six, or eight) of radiating canals in the disc, the remains of the enteric lumen.

The complete differentiation of hydriform and medusiform persons existing on one and the same colony having been attained in the *Hydromedusæ*, further changes of a most remarkable character were brought about in some of the descendants of these forms. The condition which we have so far noted is perpetuated at the present day in *Bougainvillia* (*Eudendrium*), *Campanularia*, and a vast number of the so-called hydroid polyps; others have undergone further adaptational changes. We have to notice at least four important additional modifications independent of one another.

(1.) The hydriform stage was suppressed altogether, and, as in some *Scyphomedusæ*, so here too the diblastula developed directly into a medusa (*Trachomedusæ*, *Narcomedusæ*, and probably some *Leptomedusæ* like *Thaumantias* and *Æquorea*, and some *Anthomedusæ* like *Oceania* and *Turritopsis*).

(2.) The medusiform persons being early produced did not separate themselves from the colony, but the whole colony became free (if it ever were fixed), the medusiform persons carrying the hydriform persons away with them. Thus the highly differentiated swimming and floating colonies of the *Siphonophora* originated.

(3.) The medusiform persons ceased to detach themselves from the fixed hydriform persons or colonies, and developed the ova and sperm within themselves, whilst still small in size and attached to the hydriform stock. Having once abandoned the detached, free-swimming life, the medusæ underwent in different genera a varying amount of degeneration and atrophy, of which we have in existence all possible degrees, leading from the fixed "phanerocodonic gonophors" (Allman, bell-like genital buds) of many *Siphonophora* through the "adelocodonic gonophors" (genital buds with the bell no longer open but closed by the union of the margins of the disc) of *Cordylophora* to the sporosacs of *Hydractinia*, and even to the simple genital warts of the little degenerate *Hydra viridis* of fresh waters (see fig. 17, and explanation). By this process a large number of *Hydromedusæ* (figs. 35, 38, 39, 40, and 42) have lost all evidence of the real characters of their medusa-forms, just as others have suppressed the evidence of their hydra-forms by direct development from the egg; and inasmuch as both these processes take place in genera having the closest affinity with genera in which both hydra-form and medusa-form are fully preserved, it is not possible to erect groups similar to the *Haplomorpha* of Carus or the *Monopsea* of Allman for their reception. The difficulty of classification is, however, rendered very great, for a double system becomes necessary, which shall deal with the characters of hydriform and medusiform persons in parallel equivalent series. The difficulty is considerably enhanced when we find that identical medusa-forms may spring from unlike hydra-forms, and, conversely, that closely allied hydra-forms may give rise to very different medusa-forms. The character first noticed by Rapp as distinguishing the hydroid polyps from the coral-polyps, namely, that of developing their genitalia as external bodies (*Exoarii*) instead of internally (*Endoarii*), is seen by the considerations just adduced to be fallacious. The *Hydromedusæ*, it is true, often (not always) develop their generative products from the ectoderm, and the genitalia frequently project as ridges and discharge themselves directly to the exterior in this division. The *Hydromedusæ* contrast in this respect with the *Scyphomedusæ* and *Anthozoa*, which develop their genitalia from the endoderm, and are (to use Rapp's terms) *Endoarii* whilst the former are *Exoarii*. But the bodies mistaken for external generative organs by Rapp and other early observers in many hydroids, and in *Hydra* itself, are aborted degenerate medusæ.

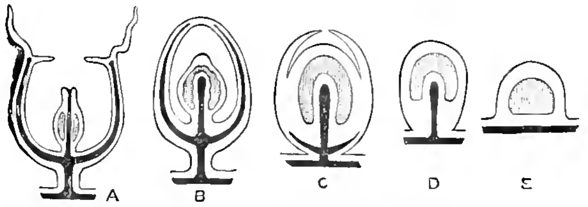

FIG. 17.—Diagrams illustrating the gradual degeneration of the medusa bud into the form of a sporosac. The black represents the enteric cavity and its continuations; the lighter shading represents the genital products (ova or sperm). A, medusiform person still attached by a stalk at the aboral pole to a colony (phanerocodonic gonophor of Allman); B, modified medusiform person, with margin of the disc (umbrella) united above and imperforate (mouthless) manubrium (adelocodonic gonophor of Allman); C, sporosac, with incomplete extension of the enteric cavity into the umbrella,—rudimentary invagination above to form the sub-umbrella cavity; D, sporosac with manubrial portion only of the enteric cavity; E, sporosac without any trace of manubrium.

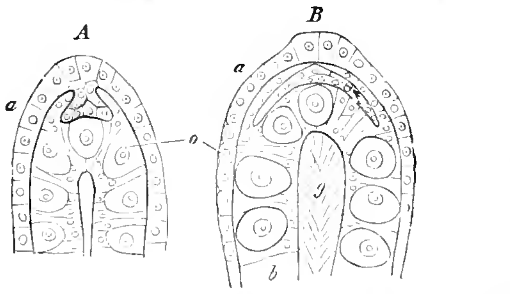

FIG. 18.—Two female sporosacs (degenerate medusæ) of *Hydractinia echinata*. (From Gegenbaur, after Van Beneden.) *a*, ectoderm; *b*, endoderm; *o*, egg-cells; *g*, enteric cavity. In A an invagination of the ectoderm, which is more complete in B, represents the rudiment of the sub-umbrella space.

(4.) A further set of changes, which have affected the original hydriform colonies and their medusa-buds so as to produce new complications of structure among the *Hydromedusæ*, are summed up under the head of "polymorphism." The differentiation of hydriform and medusiform persons is a case of dimorphism; a further distribution of functions, with corresponding modification of form, gives us "polymorphism." Polymorphism is unknown in the *Scyphomedusæ*, and it is chiefly confined to two groups of *Hydromedusæ* (the *Hydrocorallinæ* and the *Siphonophora*). In the hydriform colonies of *Hydractinia* (one of the *Gymnoblastea-Anthomedusæ*) the outer hydriform persons of the colony (fig. 39) differ in form from the rest, and have wart-like tentacles. In the same genus, and also in many *Calyptoblastea*, the hydriform persons which are destined especially to give origin to medusa-buds are devoid of tentacles and mouth, and are known as blastostyles (Allman), (fig. 43). In *Hydrocorallinæ* (fig. 53) elongated hydriform persons (dactylozooids) with no mouth and sporadic tentacles are set in series around a central short mouth-bearing person (gastrozooids) forming the "cyclo-systems" of Mr Moseley (figs. 52 and 55). In the *Siphonophora*, in addition to nutritive (hydriform) persons and generative (medusiform) persons, there may be rows of swimming-bells (medusæ devoid of mouth and of genitalia), covering-pieces (flattened medusæ), and tentacle-bearers (hydriform persons with one long highly-developed tentacle), (see figs. 56 and 57).

Hypothesis of the Individuation of Organs.—The building up of complex individualities, such as a hydrozoon colony, a flowering plant, or a segmented worm or arthropod—in any one of which a number of common units are repeated, but with varied form and function in each part of the compound body—is generally admitted to be explicable in two ways, and which of the two explanations may be adopted in any one case must depend on the ultimate inference from a wide series of observations. The first hypothesis, which undoubtedly applies to the ordinary hydriform colonies of *Hydrozoa*, to the segments of *Tænia*, and to plants formed by the repetition of phyllomes, is that an original unit like those which constitute the composite organism has freely budded, and repeated its own structure in the well-marked units which remain conjoined to form an aborescent or linear aggregate. This is "eumerogenesis," and such aggregates may be termed eumeristic. By a division of labour and consequent modification of form among the units of a eumeristic aggregate, such an aggregate may (in the course of phylogeny) acquire varied shape and definite grouping of its constituent units, and a high specialization as an individual. The high degree of individuation which may be thus attained is due to the more or less complete synthesis of a eumeristic colony. The more highly individuated Chætopods and Arthropods are synthesized linear colonies. The cyclo-systems of the *Hydrocorallinæ* are undoubted examples of synthesized colonies. The second hypothesis is one which is applicable to cases which, in the absence of special evidence to the contrary, might be regarded as highly synthesized colonies. According to this second hypothesis, such highly individuated composite organisms have not (in their phylogeny) passed through a eumeristic phase in which the units were well developed and alike, but the tendency to bud-formation (whether lateral, linear, or radial) has all along acted concurrently with a powerful synthetic tendency, so that new units have from the first made but a gradual and disguised appearance. This is "dysmerogenesis," and such aggregates as exhibit it may be called dysmeristic. In dysmeristic forms the individuality of the primary unit dominates from the first, and the merogenesis (segmentation or bud-formation) can only show itself by partially here and more completely there compelling (as it were) the organs or regions of the body of the primary unit to assume the form of new units. The arms of star-fishes are, when we consider them as derived from the antimera of a Holothurian, explained as examples of dysmerogenesis. So, too, the series of segments constituting a leech, and probably also the segments of a vertebrate. Eumerogenesis and dysmerogenesis are only variations of one process, merogenesis, and no sharp line can be drawn between them. Individuation may appear at *any* period in the phylogeny of a eumeristic aggregate and synthesize its units. On the other hand, individuation is more or less completely dominant *throughout* the history of a dysmeristic aggregate, and is gradually broken down as a more and more complete analysis of the primary unit into new units is effected. It will be observed, however, that in dysmerogenesis, the *form* which individuation tends to preserve is that of the primary unit (notably the case in leeches as compared with the ameristic flukes), whereas when we have eumerogenesis followed by synthesis the resulting form-individuality is something absolutely new. Thus, using the terms eumeromorph and dysmeromorph, we have—(1) synthesized eumeromorph simulates normal dysmeromorph; (2) analysized dysmeromorph simulates normal eumeromorph.

Whether the fixed hydriform colonies of the *Hydrozoa*, with their more or less complete medusiform buds, and further, the floating colonies of *Siphonophora*, with their polymorphous units, are to be regarded as synthesized eumeromorphs or as dysmeromorphs, more or less analysed, is perhaps still open to discussion. The former view (that adopted here) is that held by Allman (*Monograph of the Tubularian Hydroids*, 1874), by Leuckart (1851), by Gegenbaur (*Grundriss*, 1874), by Claus (*Grundzüge der Zoologie*, 1876), and by the Hertwigs (*Organismus der Medusen*, 1878). On the other hand, Huxley (*Oceanic Hydrozoa*, 1856), formerly Gegenbaur (*Zur Lehre der Generations-Wechsel*, 1854), and, more recently, Ed. Van Beneden ("De la distinction originelle du testicule et de l'ovaire," *Bull. Acad. Roy. Belg.*, 1874) have held that the medusiform person is a generative wart which has gradually assumed the characters of a bud, and that the various phases presented by it in different genera are so many more or less successful strivings after complete assumption of the hydra-form (from which the medusa-form is thus secondarily derived). Similarly the variously modified units of the siphonophorous colony have been regarded as the organs of a parent unit which have each more or less completely acquired the form of that parent unit, or, in other words, the colonies in question have been held to be dysmeromorphs. Recently ascertained facts as to the polymorphism of *Hydrocoralline*, but more especially the demonstration of the identity of structure of the medusæ of the Scyphomedusan and Hydromedusan groups, and, further, the mode of development of the *Scyphomedusæ* from the scyphistoma and the relations of the generative products to the enteric cavity, combine to render the view that the polymorphous and dimorphous colonies of *Hydrozoa* are synthesized eumeromorphs more probable, in the judgment of the present writer, than that which would explain them as dysmeromorphs.

The term "merogenesis," and its subordinate terms, "eumerogenesis, dysmerogenesis," &c., are applicable to units of the first order, namely, cells, as well as to the "persons" which are built up by them. Ordinary cell-division is an example of eumerogenesis; free-formation of nuclei, as in the fertilized ovum of Arthropods, is dysmerogenesis. A syncytium is usually a synthesized eumeromorph, but may be a dysmeromorph.

Definition of the Hydrozoa.—The *Hydrozoa* are *Cœlentera nematophora*, distinguished from the fellow-group *Anthozoa* (the name applied to *Actinozoa* when the *Ctenophora* are removed from them) by not possessing the latter's constant and sharp differentiation of the arch-enteric cavity into axial digestive and periaxial septate portions, usually by a simpler form of nematocyst, and generally by lower histological differentiation.[1]

The following is a brief summary of the chief characters of the larger divisions of the *Hydrozoa*:—

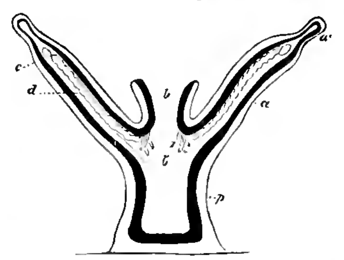

Fig. 19.—Diagrammatic vertical section of a *Lucernaria* in the plane of an interradius. *a*, one of the interradial angles of the disc, giving rise at *a'* to two groups of tentacles adradial in position; *b*, axial enteric cavity; *c*, endoderm; *d*, band-like genital gland (ovary or testis), adradial in position, and attached to the interradial septum which runs along the angular process of the disc, to which the letters *c*, *d* point; *p*, aboral region or "foot"; *z*, the interradial gastral filaments or phacellæ. (After Allman.)

Sub-class I. Scyphomedusæ.—These are *Hydrozoa* which in the adult condition always have four or eight interradial groups of gastral filaments ("phacellæ" of Haeckel) (figs. 16 (6), 23, and 26). The genitalia (ovaria and spermaria) are developed from endoderm, and are always interradial (in the four radii formed after the first four). The hydra-form is not a "hydroid," but a short polyp with broad hypostome—the "scyphistoma," which gives rise to medusa-forms by transverse fission (strobilation), or itself develops genitalia (*Lucernariæ*). Combined visual and auditory organs in the form of modified tentacles (tentaculocysts) to the number of four, eight, or more occur on the edge of the disc (except in *Lucernariæ*, where they are represented by the "colleto-cystophors"). The medusa-form in some cases develops from the egg without the intermediate scyphistoma-stage (*Pelagia*, *Charybdæa*?). The edge of its disc is provided with lappets, which cover the sensorial tentaculocysts (hence *Steganophthalmia* of Forbes), and is not provided with a velum (hence "*Acraspeda*" of Gegenbaur), excepting the rudimentary velum of *Aurelia* (fig. 31) and the well-developed vascular velum (pseudo-velum) of *Charybdæa* (fig. 21). There is no continuous marginal nerve-ring (except in *Charybdæa*), but several separate marginal nerve centres (hence *Toponeura* of Eimer). The

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[1] Quite recently the Hertwigs (*Jenaische Zeitschr.*, bd. vi., new series, 1879) have insisted that in the *Hydromedusæ* the genitalia (both ova and testes) are developed from the ectoderm, whilst in the *Scyphomedusæ* and in the *Anthozoa* they develop from the endoderm. On this account they propose to abandon the grouping into *Hydrozoa* and *Anthozoa* of *Cœlentera nematophora*, and suggest two groups, the *Ectocarpeæ* and the *Endocarpeæ*—the former equivalent to *Hydromedusæ*, the latter embracing *Scyphomedusæ* and *Anthozoa*. The *Anthozoa* exhibit a further predominance of the endoderm in its extensive origination in them of muscular fibre, which but rarely and in small quantity develops from endoderm in the *Hydromedusæ* or in the *Scyphomedusæ*. The Hertwigs base their generalization on their own studies of medusæ, but they have ignored the observations of Van Beneden on *Hydractinia* and of Ciamician on various Tubularians, in which the origin of either sperm or ova from endoderm is established. Recently Fraipont has repeated an observation of Van Beneden's on *Campanularia*, and shown conclusively that the ova in that form arise from endoderm. Weismann (*Zoologischer Anzeiger*, May 1880) shows the same for *Plumularidæ* and *Sertularidæ*; the reader is referred to his paper.

diblastula in all cases, as yet observed, is formed by invagination, the blastopore closing up (Balfour).

Fig. 20.

Fig 21.

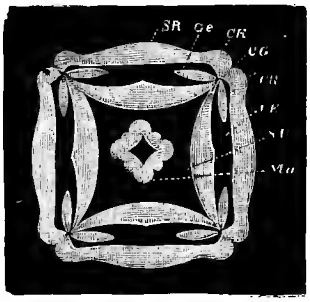

Fig. 22.

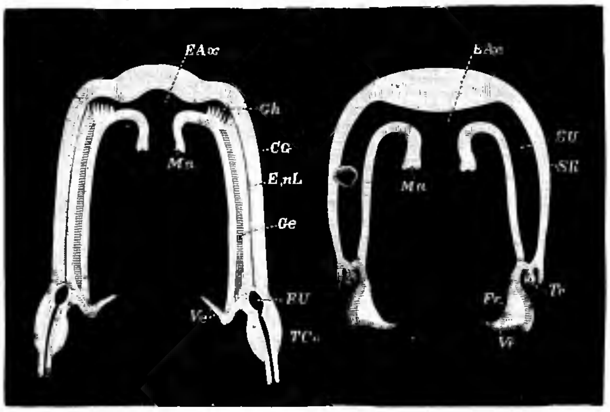

Fig. 23.

Fig. 20.—*Charybdæa marsupialis* (natural size, after Claus). The four annulated tentacles are seen depending from the four lappets placed at the four corners of the quadrangular umbrella. These are interradial. Two of the four perradial enteric pouches of the umbrella, representing radiating canals, are seen of a pale tint. *Fg*, gastral filaments (interradial); *R*, the modified perradial tentacles forming tentaculocysts; *G*, corner ridge facing the observer and dividing adjacent pouches of the umbrella; *GF*, position of one of the genital bands.

Fig. 21.—View of the margin of the umbrella of *Charybdæa marsupialis* (natural size, after Claus). At the four corners are seen the lappets which support the long tentacles, and in the middle of each of the four sides is seen a tentaculocyst. *Vel*, the vascular velum or pseudo-velum, with its branched vessels.

Fig. 22.—Horizontal section through the umbrella and manubrium of *Charybdæa marsupialis* (modified from Claus). *Ma*, manubrium; *SR*, side ridge (perradial); *CR*, corner ridges, separated by *CG*, the interradial corner groove; *Ge*, the genital lamellæ in section, projecting from the interradial angles on each side into *UE*, the enteric pouches of the umbrella; *SU*, the sub-umbrella space.

Fig. 23.—Vertical sections of *Charybdæa marsupialis*, to the left in the plane of an interradius, to the right in the plane of a perradius. *Ma*, manubrium; *EAx*, axial enteron; *Gh*, gastral filaments (*phacellæ*); *CG*, corner groove; *SR*, side ridge; *EnL*, endoderm lamella (line of concrescence of the walls of the enteric cavity of the umbrella, whereby its single chamber is broken up into four pouches); *Ge*, line of attachment of a genital band; *EU*, enteric pouch of the umbrella, in the left-hand figure, points to the cavity uniting neighbouring pouches near the margin of the umbrella and giving origin to *TCa*, the tentacular canal; *Ve*, velum; *Fr*, frenum of the velum; *Te*, tentaculocyst.

The binary division of the *Hydrozoa* was established by Eschscholtz (*System der Acalephen*, 1829) whose *Discophoræ phanerocarpæ* correspond to the *Scyphomedusæ*, whilst his *Discophoræ cryptocarpæ* represent the *Hydromedusæ*. The terms point to distinctions which are not valid. In 1853 Kolliker used the term *Discophora* for the *Scyphomedusæ* alone, an illegitimate limitation of the term which was followed by Louis Agassiz in 1860. Nicholson has used the term in the reverse sense for a heterogeneous assemblage of those medusæ not classified by Huxley as *Lucernaridæ*, nor as yet recognized as derived from hydroid trophosomes. This use of the term adds to the existing confusion, and renders its abandonment necessary. The term *Discomedusæ* was used for the *Scyphomedusæ* by Haeckel in his *Generelle Morphologie* (excluding *Charybdæa*)—whilst Carus (*Handbuch*, 1867) confines the term "*Medusæ*" to them alone, which is objectionable, since it belongs as justly to the *Hydromedusæ*. Forbes's term for them, *Steganophthalmia*, indicates a true characteristic, failing only in the *Lucernariæ*, but its complementary term *Gymnophthalmia* is inaccurate. Similarly the terms *Acraspeda* and its complement *Craspedota* are inacceptable. Eimer has proposed to use the terms *Toponeura* and *Cycloneura* for the two divisions—but *Charybdæa* appears to break down this division as so many others. The old term *Acalephæ*, which is retained by Gegenbaur in its proper sense for all the *Cœlentera nematophora*, is used as the designation of the *Scyphomedusæ* alone by Claus (*Grundzüge der Zool.*, 1878), which cannot fail to produce confusion. The term *Lucernaridæ*, proposed so long ago as 1856 by Huxley (*Med. Times and Gazette*), most truly indicates the relationships of these organisms which he was the first to recognize, but it seems desirable to restrict this term to the limited order in which *Lucernaria* is placed, and to employ for the larger group—*Scyphomedusæ*—a term which is the true complement of the convenient name assigned to the other division of *Hydrozoa*, viz., *Hydromedusæ*.[1]

Order 1. *Lucernariæ*,—*Scyphomedusæ* devoid of tentaculocysts, with the aboral pole of the body produced into an adhesive disc by which the organism (which possesses the power of swimming by contraction of the circular muscular zone of the hypostome) usually affixes itself. The enteric cavity is divided into four perradial chambers by four delicate interradial[2] septa. The genitalia are developed as four-paired ridges at the sides of the interradial septa on the oral wall of the chambers (fig. 19). No reproduction by fission nor "alternation of generations" is known in the group. At the edges of the disc capitate tentacles are developed in eight adradial[2] groups; between these are modified tentacles in some genera,—the marginal anchors or colleto-cystophors. The canal system which has sometimes been described in them is a product of erroneous observation. A very few genera and species of this order are known. They may be justly called the cœnotype of the medusæ (James Clark), and their relationship to the free swimming forms may be compared, as was done by L. Agassiz, to the relationship of the stalked Crinoids to such forms as *Comatula*. Three species are not uncommon on the British coasts.

By Milne Edwards the animals forming this group were termed *Podactinaria* and associated with the *Anthozoa*. By Leuckart they were termed *Calycozoa*; it is only of late that the closeness of their relationship to the *Scyphomedusæ* has been fully recognized, though long since insisted on by Huxley and by James Clark. Haeckel in his new system of the medusæ (*Sitzungsber. der Jenaische Gesellschaft für Medicin und Naturwiss.*, July 26, 1878) adopts for them the term *Scyphomedusæ* in allusion to their permanently maintaining the distinctive features of the scyphistoma larval form of the *Acraspedæ*, the term which he adopts from Gegenbaur for our *Scyphomedusæ*.

Order 2. *Discomedusæ*.—These are *Scyphomedusæ* developing as sexual medusiform persons by transverse fission from a scyphistoma, or else directly from the egg. They have eight tentaculocysts, four perradial, four interradial, and sometimes accessory ones (adradial). Four or eight genital lobes (ovaria or spermaria or hermaphrodite) are developed from the endoderm forming the oral floor of the central region of the enteric cavity, which is produced into a corresponding number of pouches. The mouth is either a simple opening at the termination of a rudimentary manubrium (sub-order *Cubostomæ*), or it is provided with four or eight arm-like processes (sub-orders *Semostomæ* and *Rhizostomæ*). In the sub-order *Rhizostomæ* (fig. 24, *a*), the

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[1] *Scyphomedusæ* (σκύφος, a cup) are medusæ which are related by strobilation to *Scyphistoma*,—a wide-mouthed polyp with four gastral ridges. *Hydromedusæ* are medusæ related to a *Hydra*,—a narrower polyp, devoid of gastral ridges,—by lateral gemmation.

[2] For use of these terms see paragraphs on *Aurelia* below.

edges of the oral opening fuse together at an early age and leave several sucker-like secondary mouths, which were formerly mistaken for independent persons. The central enteric chamber is continued through the disc by a complicated often reticulate system of radiating canals, which excavate the endoderm lamella.

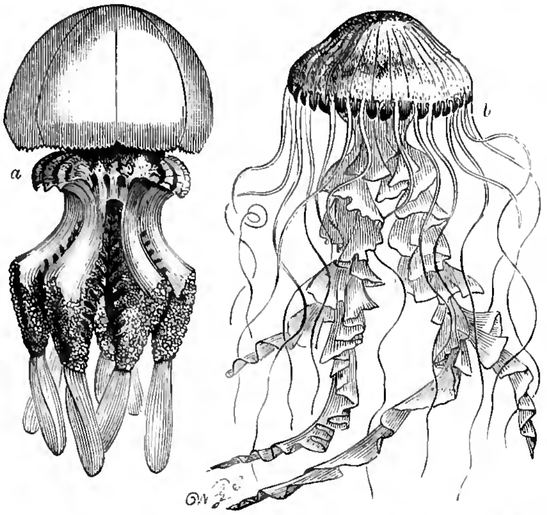

FIG. 24.—*Scyphomedusæ*. *a*, *Rhizostoma pulmo*; *b*, *Chrysaora hyosceua*.

In the *Semostomæ* and *Rhizostomæ* (not in the *Cubostomæ*) four remarkable (respiratory) sub-genital pits (fig. 28) are hollowed out in the gelatinous substance of the sub-umbrella (oral face of the umbrella). These do not communicate, as has been erroneously supposed, with the genital organs, the products of which normally are evacuated by the mouth. In the Tetragamelian *Rhizostomæ* these pits remain distinct from one another as in *Semostomæ*, but in the Monogamelian *Rhizostomæ* they unite to form one continuous sub-genital cavity placed between the wall of the enteric cavity and the polystomous oral disc. The common English forms, *Aurelia*, *Chrysaora*, and *Cyanæa*, are types of the *Semostomæ*, the somewhat less common *Rhizostoma* of the Monogamelian *Rhizostomæ*, whilst *Nausithoe* and *Discomedusa* represent the simple *Cubostomæ*.

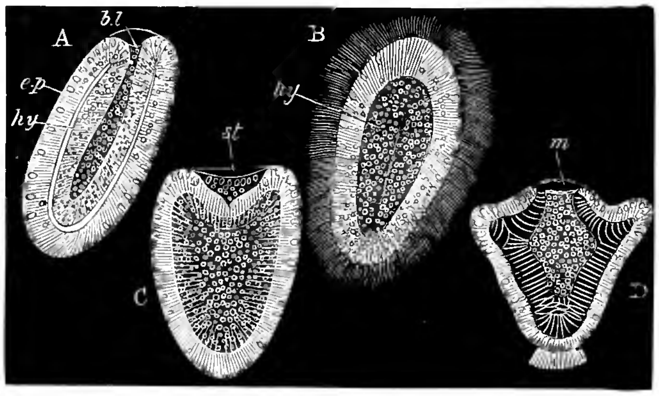

FIG. 25.—Four stages in the development of *Chrysaora*. A, Diblastula stage; B, stage after closure of blastopore; C, fixed larva with commencing stomodæum or oral ingrowth; D, fixed larva with mouth, short tentacles, &c.; *ep*, ectoderm; *hy*, endoderm; *st*, stomodæum; *m*, mouth; *bl*, blastopore. (From Balfour, after Claus.)

The writer has adopted the term used by Haeckel for this order, and is indebted to his preliminary notices of a large work on the *Medusæ*, now in the press, for outlines of the classification and definitions which have been introduced with modifications in relation to these and the other *Medusæ*. The term *Discophora* is used by Claus (*Grundzüge*) for the *Discomedusæ*. It is quite clear from the varied and inconsistent use by different authors of that term, and also of the terms *Acalephæ* and *Medusæ*, that they must be ejected altogether from use in systematic treatises.

The structure of the common *Aurelia aurita* and its development have recently formed the subject of investigation by Claus, Eimer, and others. As the current accounts in text-books are very inadequate, a short sketch of the morphology of that form is appended here.

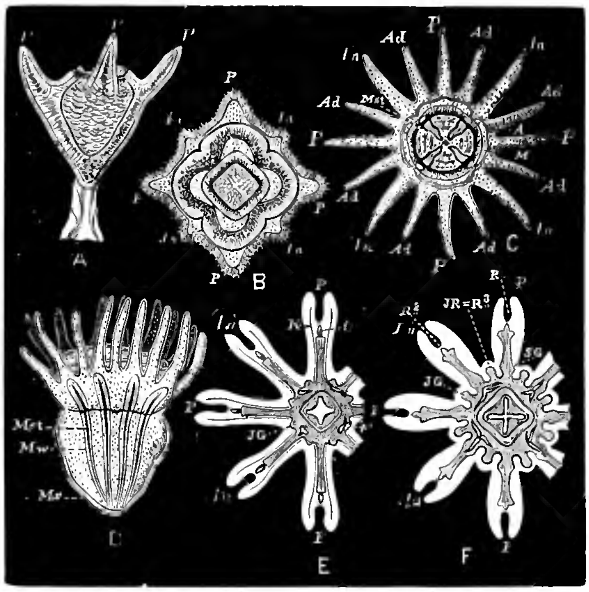

FIG. 26.—Later development of *Chrysaora* and *Aurelia* (after Claus). A, Scyphistoma of *Chrysaora*, with four perradial tentacles and horny basal perisarc. B, Oral surface of later stage of scyphistoma of *Aurelia*, with commencement of four interradial tentacles. The quadrangular mouth is seen in the centre; the outline of the stomach wall, seen by transparency around it, is nipped in four places interradially to form the four gastric ridges. C, Oral surface of a sixteen-tentacled scyphistoma of *Aurelia*. The four gastric interradial ridges are seen through the mouth. D, First constriction of the *Aurelia* scyphistoma to form the pile of ephyræ or young medusæ (see fig 27). The single ephyra carries the sixteen scyphistoma tentacles, which will atrophy and disappear The four longitudinal gastric ridges are seen by transparency. E, Young ephyra just liberated, showing the eight bifurcate arms of the disc and the interradial single gastral filaments. F, Ephyra developing into a medusa by the growth of the adradial regions. The gastral filaments have increased to three in each of the four sets. *A*, margin of the mouth; *Ad*, adradial radius; *F*, gastral filament; *In*, interradial radius; *JG*, adradial gastral canal; *JR*=*R*³, adradial lobe of the disc; *K*, lappet of a perradial arm; *M*, stomach wall; *Mst*, muscle of the gastral ridge; *Mw*, gastral ridge; *Ms*, mesoderm; *O*, tentaculocyst; *P*, perradial radius; *R*², interradial radius; *R*³, adradial radius; *SG*, commencement of lateral vessel.

From the egg, according to the researches of Claus (whose figures, here reproduced, refer more especially to the closely allied genus *Chrysaora*, up to the completion of the scyphistoma), a single-cell-layered blastula develops which forms a diblastula by invagination (fig. 25, A, B, C). The orifice of invagination closes up, and the ciliated "planula" (as this stage used to be termed in all *Cœlentera*), after swimming around for a time, fixes itself, probably by the blastoporal pole. The true mouth then forms by inruption at the opposite pole. Two tentacles now grow out near the mouth opposite to one another (fig. 25, D), and are followed by two more (fig. 26), these indicating the four primary radii of the body which pass through the angles of the four-sided mouth, and are termed *perradial*. Meanwhile the aboral pole narrows and forms a distinct stalk, which in *Chrysaora* secretes a horny perisarc (fig. 25,

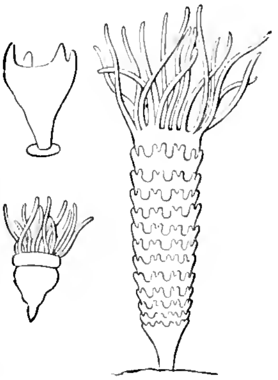

FIG. 27.—Development of *Aurelia*. Above to left, young scyphistoma with four perradial tentacles. Below to left, scyphistoma with sixteen tentacles and first constriction. To the right, strobila condition of the scyphistoma, consisting of thirteen metameric segments; the uppermost still possesses the sixteen tentacles of the scyphistoma; the remainder have no tentacles, but are ephyræ, each with eight bifid arms (processes of the disc). Each segment when detached becomes an ephyra, such as that drawn in fig. 26, E, F. (From Gegenbaur)

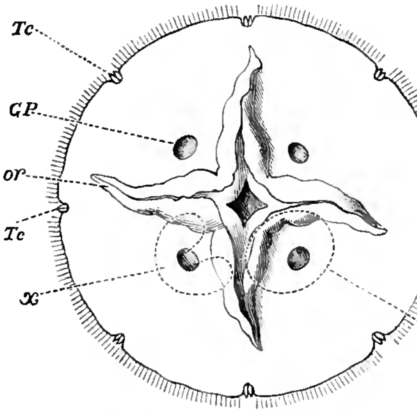

Fig. 28.—Surface view of the sub-umbrella or oral aspect of *Aurelia aurita*, to show the position of the openings of the sub-genital pits, *GP*. In the centre is the mouth, with four perradial arms corresponding to its angles (compare fig. 26). The four sub-genital pits are seen to be interradial. *x* indicates the outline of the roof (aboral limit) of a sub-genital pit; *y*, the outline of its floor or oral limit, in which is the opening (compare 6 of fig. 16).

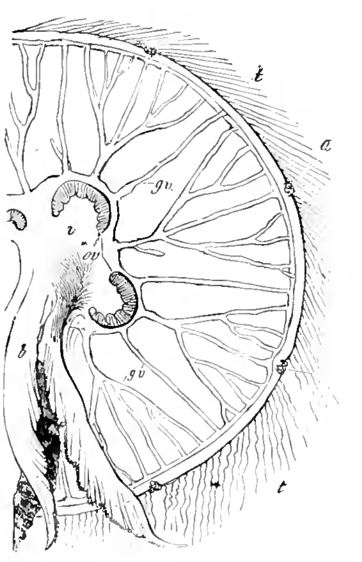

Fig. 29.—Half of the lower surface of *Aurelia aurita*. The transparent tissues allow the enteric cavities and canals to be seen through them. *a*, marginal lappets hiding tentaculocysts; *b*, oral arms; *v*, axial or gastric portion of the enteric cavity; *gv*, radiating and anastomosing canals of the enteric system; *ov*, ovaries. The gastral filaments near to these are not drawn. (From Gegenbaur.)

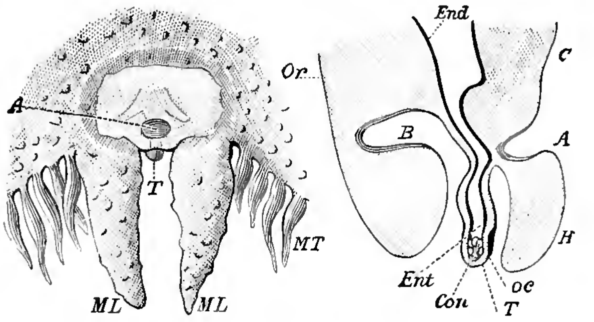

Fig. 30.—Tentaculocyst and marginal lappets of *Aurelia aurita*. In the left-hand figure—*ML*, marginal lappets; *T*, tentaculocyst; *A*, superior or aboral olfactory pit; *MT*, marginal tentacles of the disc. The view is from the aboral surface, magnified about 50 diameters. In the right-hand figure—*A*, superior or aboral olfactory pit; *B*, inferior or adoral olfactory pit; *H*, bridge between the two marginal lappets forming the hood; *T*, tentaculocyst; *End*, endoderm; *Ent*, canal of the enteric system continued into the tentaculocyst; *Con*, endodermal concretion (auditory); *oc*, ectodermal pigment (ocellus). The drawing represents a section, taken in a radial vertical plane so as to pass through the long axis of the tentaculocyst. (After Eimer.)

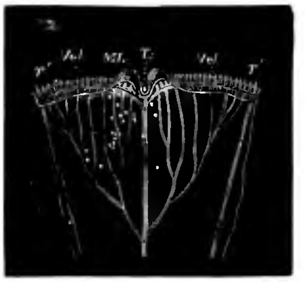

Fig. 31.—Part of the margin of the disc of a young *Aurelia*, to show the rudimentary velum, *Vel*, extending from the marginal lappets, *ML*, on either side; *T'*, the small tentacles fringing the disc.

D). Four new tentacles, those of the intermediate or secondary radii, now appear between the first four, and are termed *interradial*. At the same time four longitudinal ridges grow forward on the wall of the enteric cavity (fig. 26). These interradial ridges have sometimes been erroneously described as containing each a longitudinal canal connected with a circular canal at the base of the tentacles. They are in reality solid, as is the margin of the hypostome from which the tentacles spring. It is in connexion with these four ridges that the gastral filaments will subsequently appear, as also the genital organs either along their middle line or adradially to them. The ridges correspond to the mesenteries of the *Anthozoa*. Eight additional tentacles placed one on each side of the perradial tentacles (or of the interradial, according as we may choose to regard the matter) next appear, and are distinguished as *adradial*. All the tentacles reaching an equal size, we obtain the appearance seen in fig. 26, when the young scyphistoma is looked at from above. Looked at from the side, with its wide hypostome and short vertical axis, the scyphistoma differs widely from an ordinary hydra-form, and approaches the medusa-form, to which its four longitudinal gastral ridges further assimilate it. The little creature is now about an eighth of an inch in height; in other genera, but not in *Chrysaora*, it may now multiply by the production of a few buds from its fixed basal disc. After nourishing itself for a period, and increasing to four or five times the size just noted, the vertical axis elongates and a series of transverse constrictions appear on the surface, marking off the body of the scyphistoma into a series of discs (figs. 26 and 27), each of which by the development of tentacles and completion of the constriction will become a separate medusa (in its young state called "ephyra"). The tentacles of the *Aurelia* and the structure of the margin of its hypostome are very different from those of the scyphistoma. They are exhibited in their earliest condition (when the *Aurelia*-medusa is first liberated from its attachment and is an ephyra) in fig. 26, E, F. The margin of the hypostome is drawn out into eight arms (which are not to be confused with tentacles); the end of each arm is bifid, carrying a pair of lappets—the marginal lappets which persist in the adult (see figs. 30 and 31). Between the lappets is placed a short and peculiar tentacle, the tentaculocyst or sense-organ. The eight arms of the disc and their tentaculocysts are perradial and interradial. As the organism grows, a set of eight adradial tentacles appear in the notches between the eight arms, but never attain any relatively large size in *Aurelia*. The asteroid arm-bearing character of the margin of the disc is soon obliterated by the relative growth of the intermediate adradial areas, which become quite filled up, so that in the adult the tentaculocyst is carried in a notch instead of on a prominence, and is concealed by the two lappets (figs. 28 and 30). The margin of the disc between adjacent pairs of lappets gives rise to a fold which grows inwards (toward the mouth) during an early stage (fig. 31), and numerous small tentacles (the fringe) appear along the margin of the disc, which soon equal in size the first adradial tentacle. The ingrowing fold is the velum or "pseudo-velum," and never increases in size, so that in the adult it is not observable. The tentacles also remain very small and fine in *Aurelia*, forming a continuous fringe along the edge of the disc, interrupted only by the eight notches for the tentaculocysts (fig. 29).

The sixteen tentacles of the scyphistoma are necessarily attached to the most anterior of the pile of medusæ; they atrophy, but to what extent they may be metamorphosed to form the parts of the ephyra or young medusa has not been determined. The scyphistoma, having given rise to its pile of ephyræ, may (in some genera, *Aurelia?*) redevelop its own kind of tentacles below the constriction marking off the last ephyra. Hence scyphistoma tentacles appear sometimes at the top and sometimes at the bottom of the pile, which has led to diverse accounts of the mode of development of the ephyræ.

Whilst changes are going on in the configuration of the margin of the disc of an ephyra on its way to the perfect form of the adult *Aurelia*, the enteric cavity has also undergone most important changes. Foremost in importance is the development of a single gastral filament on each of the four gastral ridges which necessarily are present in the transverse slice (so to call it) of a scyphistoma, which becomes an ephyra (fig. 26). These rapidly increase in number as the ephyra grows. Further, the enteric cavity at first follows the outline of the ephyra, sending a process into each arm, but then by adhesion of its walls is converted into a four-lobed central chamber, a marginal canal, and an endoderm lamella. A system of canals, the arrangement of which is seen in figs. 29 and 31, subsequently opens out again certain lines and tracts of the conjoined endoderm walls.

In the adult *Aurelia* we find the mouth surrounded by four large arm-like perradial processes (figs. 25 and 29) (not tentacles), and leading through a short manubrium into a flattened four-lobed chamber, the lobes being interradial, and having on their oral floor numerous gastral filaments (rich in thread cells) (6 in fig. 16). Each pouch or lobe gives off a canal, which runs towards the circular canal at the margin of the disc, but breaks up into three or four secondary canals on its way. Between the pouches come off eight other "radiating" canals (adradial), which do not branch, but go straight to the circular canal.

The oral floor of the concavity of each lobe of the enteric cavity is occupied by a horse-shoe-shaped frill (fig. 29, *ov*), either testis or ovary (the sexes being in separate individuals). The open arms of the horse-shoe are turned towards the centre of the disc, and the folds of the genital frill are so deep as to show themselves on the outer ectodermal wall of the disc. Here, however, there is a very remarkable arrangement, which has rarely, if ever, been correctly described and figured in our common *Aurelia*. The gelatinous substance of the disc is hollowed out on that part of the oral face corresponding to the position of the genital frills, so as to form four separate extensive pits or chambers. Each of these sub-genital pits has in *Aurelia* a small round opening on the oral face of the disc (fig. 28, GP), but is otherwise entirely closed, having no communication with the genital tissues, from which it is separated by a delicate layer of ectoderm (6 in fig. 16). The pits probably serve to admit water for respiratory purposes into close proximity with the genital tissues.

The whole enteric surface, including canals, is ciliated, whilst the ectoderm is not ciliated, but provided with groups of nematocysts.

The tentaculocyst in the adult *Aurelia* is relatively an extremely minute body, completely hidden by the two large marginal lappets (fig. 30, T). Above it (that is, on the aboral surface, as the *Aurelia* swims) is a deep pit (A), Schäfer's fovea nervosa superior, sunk in a sort of bridge which connects the two lappets and overhangs the tentaculocyst. A similar pit (the fovea inferior) exists on the oral surface. These have been recognized by Claus, Eimer, and the Hertwigs as olfactory organs. The tentaculocyst is seen in section in fig. 30 (right-hand figure), which exhibits its central cavity continuous with the enteric cavity, its ectodermal pigment spot (eye), and its endodermal mass of concretions (auditory organ).

The chief muscular mass of *Aurelia*, except that of the oral arms, is a circular zone on the oral face of the disc. The muscular fibres are not distinct cells, but transversely-striated processes of the epidermic cells (epidermo-muscular cells) (fig. 9). In the "arms" of other medusæ, and presumably of *Aurelia*, the muscular fibre is formed by independent nucleated cells (fig. 9).

The nerve-epithelium from the olfactory pits of *Aurelia* is drawn in fig. 14. Starting from this and from the cells of the tentaculocysts are nerve-fibres, which spread themselves on the surface of the circular muscular zone in the neighbourhood of the tentaculocysts, and these are connected each and separately with large isolated nerve-ganglion cells (fig. 15). The nerve-fibre is continued beyond the cell, and in some instances has been traced into a broadened expansion lying on a muscular fibre (Schäfer). The nerve-ganglion cells lie very superficially immediately below the flat epithelium of the body surface and between it and its muscular processes.

The ova and spermatozoa of *Aurelia* develop in the genital frills from endoderm cells in separate individuals. They pass to the exterior through the mouth.

Order 3. *Conomedusæ*,—*Scyphomedusæ* with only four tentaculocysts, and these perradial. A broad velum (so-called pseudo-velum) of complete circular form is present, differing from that of the *Hydromedusæ* in the fact that it is penetrated by canals of the enteric system (*Charybdæa*). The whole umbrella is bell-shaped. The genital organs are four pairs of lamelliform ridges (fig. 22) which are attached to the four narrow interradial septa that divide the large enteric cavity of the umbrella into four perradial gastro-canal pouches. The lamelliform genital glands hang freely in these pouches. At the edge of the umbrella are four interradial lappet-like prolongations of the gelatinous substance of the disc, which support each a long tentacle (fig. 20). The nerve-ring is complete, like that of the *Hydromedusæ*.

There is now no doubt that *Charybdæa*, which has been placed in each of the two large divisions of the *Hydrozoa*, must be classed with the *Scyphomedusæ*. The recent investigations of Claus (*Arbeiten aus dem Zool. Institut zu Wien*, Bd. i. Hft. ii., 1878), as well as those of Haeckel and Fritz Müller, lead to this conclusion. The term *Conomedusæ* is adopted from Haeckel, who places here, besides *Charybdæa* and *Tamoya*, other forms, a fuller description of which may be expected in his forthcoming *System der Medusen*. In many respects—its quadrangular form, its marginal lappets, its broad enteric pouches in place of fine canals, its vascular velum, and its highly complicated tentaculocysts (fig. 13, B)—*Charybdæa* is peculiar. The simplicity of the enteric system and the arrangement of the genital glands bring it near to *Lucernaria*. The existence of four interradial groups of gastral filaments, and the disposition of the paired genital glands at the sides of the interradial septa, determine its position to be among the *Scyphomedusæ*. Its development is not known. Figs. 20 to 23 illustrate the structure of *Charybdæa*.

Order 4. *Peromedusæ*,—*Scyphomedusæ* with four interradial tentaculocysts. The enteric system consists of three divisions,—an aboral main stomach with four interradial gastral ridges and filament groups; a mid-stomach, which communicates by means of four perradial slits with a very large ring-sinus (occupying two-thirds of the umbrella); and thirdly, an oral portion or pharynx, with four wide perradial pouches. The genital organs are four pairs of sausage-shaped interradial ridges lying on the oral floor of the ring-sinus.

This is a new group founded by Haeckel, of which we have at present no further details.

Sub-class II. HYDROMEDUSÆ.—These are *Hydrozoa* devoid of gastral filaments; the sexual persons are always medusiform, the genital glands are developed sometimes from ectodermal cells, sometimes from endoderm, and are always perradial (in the radii of the first order). The medusiform persons always possess a muscular non-vascular velum (hence *Craspedota*) and a complete nerve-ring (hence *Cycloneura* of Eimer). The marginal sense-organs are either ocelli or otocysts or tentaculocysts. The diblastula, in all cases as yet observed, is formed by delamination (Balfour). The sexual medusiform persons may develop directly from the egg, but more usually the egg gives rise to a hydriform person—the hydroid—which differs from a scyphistoma in its elongate vertical axis, the indefinite number (often also position) of its tentacles, and its frequent formation of a colony of large size by lateral budding. By lateral budding (not by metameric fission) medusiform persons which alone develop sexual glands are produced on the hydriform colonies; these may separate from the colony, or may be retained in a more or less degenerate form adherent to it, as generative buds or warts.

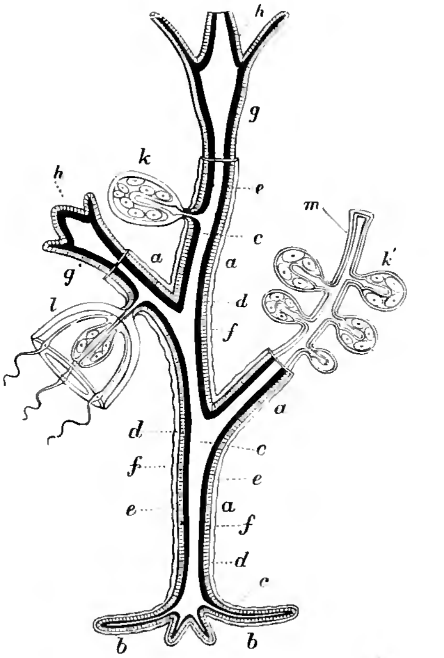

FIG. 32.—Diagram showing possible modifications of persons of a gymnoblastic *Hydromedusa*. *a*, hydrocaulus (stem); *b*, hydrorhiza (root); *c*, enteric cavity; *d*, endoderm; *e*, ectoderm; *f*, perisarc (horny case); *g*, hydranth (hydriform person) expanded; *g'*, hydranth (hydriform person) contracted; *h*, hypostome, bearing mouth at its extremity; *k*, sacciform gonophor (sporosac) springing from the hydrocaulus; *k'*, sporosac springing from *m*, a modified hydriform person (blastostyle): the genitalia are seen surrounding the spadix or manubrium; *l*, medusiform person or medusa; *m*, blastostyle. (After Allman.)

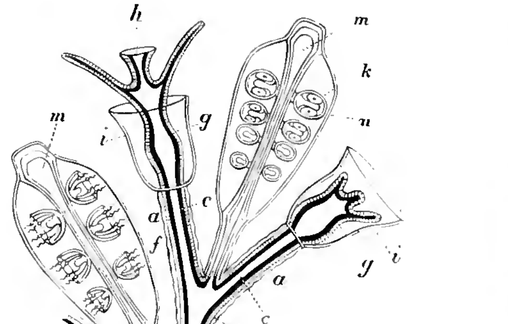

FIG. 33—Diagram showing possible modifications of the persons of a Calyptoblastic *Hydromedusa*. Letters *a* to *h* same as in fig. 32. *i*, the horny cup or hydrotheca of the hydriform persons; *l*, medusiform person springing from *m*, a modified hydriform person (blastostyle); *n*, the horny case or gonangium enclosing the blastostyle and its buds. This and the hydrotheca *i* give origin to the name *Calyptoblastea*. (After Allman.)

The medusiform persons of this group are the *Discophoræ cryptocarpæ* of Eschscholtz, the *Craspedota* of Gegenbaur (1854), and the *Hydromedusida* of Kölliker (1853)—the last two authors at that time separating the hydriform persons as *Hydroidea*. Louis Agassiz (1860) includes both sets of persons under the term *Hydroida* (together with *Lucernaria*), which also is the term adopted by Allman in his beautiful monograph (1871–74). J. V. Carus, amending the limitations given by Carl Vogt, was the first to use the term *Hydromedusæ* in the sense here adopted (*Handbuch der Zoologie*, 1863), and it is now employed in the same sense by Gegenbaur (*Elements of Comparative Anatomy*, London, 1878), namely, to embrace both the cryptocarpous medusæ of Eschscholtz and the hydroids related to them. The term *Hydromedusæ* is used unwisely by Claus (*Grundzüge d. Z.*) for the whole group of *Hydrozoa*. It has been the practice of some authors to give a double classification of the group—one based on the characters of the medusiform persons, the other on that of the hydriform persons. In the present article a double name will in some cases be assigned to a group—but the attempt is made to bring both sets of persons under one system.

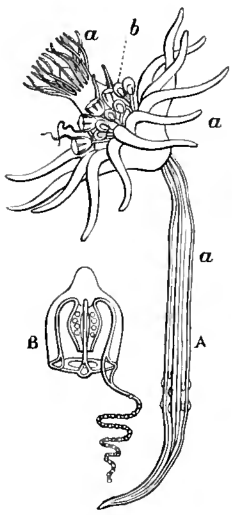

Fig. 34.

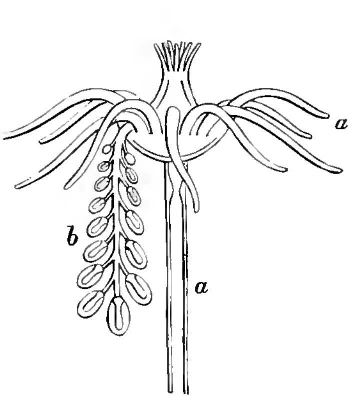

Fig. 35.

FIG. 34.—Diagram of *Corymorpha*. A, a hydriform person giving rise to medusiform persons by budding from the margin of the disc; B, free swimming medusa (*Steenstrupia* of Forbes) detached from the same, with manubrial genitalia (*Anthomedusæ*) and only one tentacle. (After Allman.)

FIG. 35.—Diagram of *Tubularia indivisa*. A single hydriform person *a* bearing a stalk carrying numerous degenerate medusiform persons or sporosacs *b*. (After Allman.)

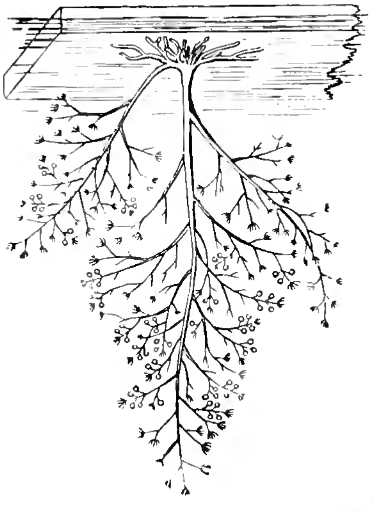

FIG. 36.—Colony of *Bougainvillea fruticosa*, natural size, attached to the underside of a piece of floating timber. (After Allman.)

Order 1. *Gymnoblastea-Anthomedusæ.*—These are *Hydromedusæ* which all, as far as is known, pass through a hydriform phase, but in which the medusiform persons may either reach full development or exhibit the extremest degeneration (*Hydra*). The ectoderm of the hydriform persons may secrete a horny tubular protective case (perisarc), but this does not form cups for the reception of the tentacular crown nor cases enclosing groups of medusiform buds (gonangia). The fully-developed medusiform persons never possess otocysts nor tentaculocysts, but always ocelli at the base of the tentacles. The latter are usually four or six, corresponding to the same number of simple radial enteric canals, but may be more numerous or reduced to one or to two; rarely they are branched (*Cladonema*). The sexual glands are placed in the wall of the manubrium, either equally distributed all round it or in four separate perradial groups, which are often divided into eight adradial groups by the perradial longitudinal muscles.

Fig. 37.—Portion of colony of *Bougainvillea* (*Endendrium*) *fruticosa* (*Anthomedusæ-calyptoblastea*) more magnified. (From Lubbock, after Allman.)

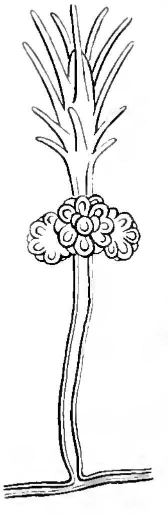

Fig. 38.

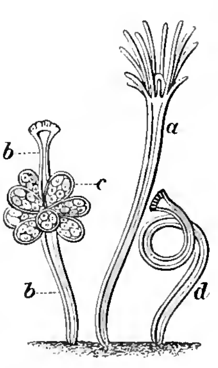

Fig. 39.

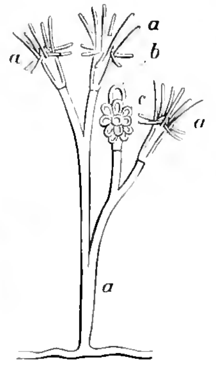

Fig. 40.

Fig. 38.—Diagram of *Clava*, showing a hydriform person surrounded by a verticil of degenerate medusiform persons (sporosacs) (After Allman.)

Fig. 39.—Diagram of a colony of *Hydractinia*, showing four forms of persons. *a*, hydriform person; *b*, modified hydriform person, or blastostyle, bearing *c*, degenerate medusiform persons or sporosacs; *d*, modified hydriform person situated at the margin of the colony (dactylozooid). (After Allman.)

Fig. 40.—Diagram of a colony of *Dicoryne*, showing three forms of persons *a*, normal hydriform person; *b*, modified bud-bearing hydriform person (blastostyle); *c*, degenerate medusiform persons (sporosacs). (After Allman.)

This is a very well defined group, since the *Gymnoblastea* of Allman, based on the characters of the hydriform persons—also known as *Tubulariæ* and *Gymnotoka*—correspond exactly with the *Anthomedusæ* of Haeckel's new system. *Hydra* is included here, though placed in a separate order by Allman. Some of the leading forms of hydriform and medusiform persons are given in the cuts (figs. 34 to 42). The greatest range in the amount of degeneration of the medusiform persons is seen even in genera of the same family—*e.g.*, *Turris* and *Clava*—the former producing free medusæ, the latter sessile sporosacs. The *Oceanidæ* of Gegenbaur (excluding the *Williadæ*, which Haeckel assigns to the next group) correspond on the whole to the medusa-forms of this order.

Fig. 41.

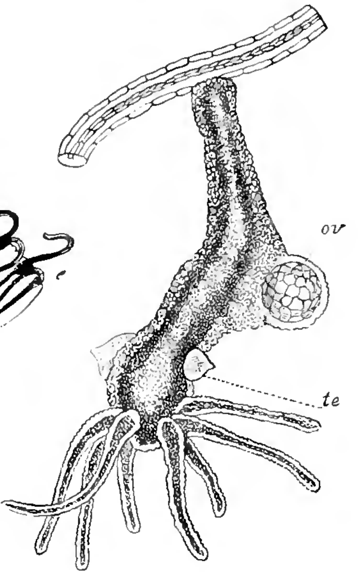

Fig. 42.

Fig. 41.—Hydriform person of *Syncoryne*, with medusiform persons budding from it, and shown in various stages of development, *a*, *b*, *c*, *d*, *e*. (From Gegenbaur, after Desor.)

Fig. 42.—*Hydra viridis*. *ov*, ovary; *te*, testis.

Order 2. *Calyptoblastea-Leptomedusæ*.—These are *Hydromedusæ* of which the hydriform phase is known in a large number of cases, whilst of others only the medusa-forms are known; none are *known* to develop directly from the egg to the medusa-form. As in the preceding group, the medusiform persons may reach full development or exhibit themselves as degenerate sexual sacs on the hydriform colonies. The ectoderm of the hydra-forms always secretes a perisarc which forms a cup-like protection (hydrotheca) to the tentacle-crown, and which also encloses the group of medusa-buds in peculiar horny cases (gonangia). The fully-developed medusiform persons (fig. 47) either

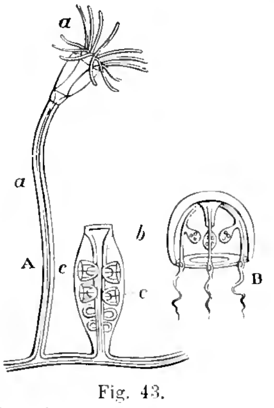

Fig. 43.

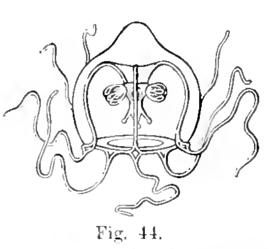

Fig. 44.

Fig. 43.—Diagram of a colony of *Campanularia*, showing four forms of persons A, portion of a fixed colony; *a*, hydriform person; *b*, bud-bearing hydriform person (blastostyle); B, free-swimming colony, being a sexless medusiform person (blastocheme of Allman), with modified medusiform persons budding from its radiating canals, as sporosacs. (After Allman.)

Fig. 44.—Medusiform person (*Lizzia*), one of the *Anthomedusæ*, detached from a hydroid colony of the family *Eudendridæ*. Ocelli are seen at the base of the tentacles, and two medusiform buds on the sides of the manubrium. (After Allman.)

have no otocysts, but only ocelli (*Ocellatæ*), or they have otocysts (fig. 11) (ectodermal sacs), four, eight, or over a hundred, not homologous with tentacles, and sometimes in addition ocelli (*Vesiculatæ*). The radial enteric canals are usually four or eight in number, but may be more numerous, whilst the marginal tentacles of the disc are either few or very numerous. The genital glands always are placed in the course of the radial canals of the disc (not in the manubrium), and stand out as groups of wart-like processes on the sub-umbrellar surface (fig. 43). Their mode of discharge is uncertain.

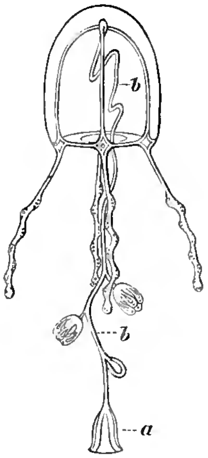

Fig. 45.

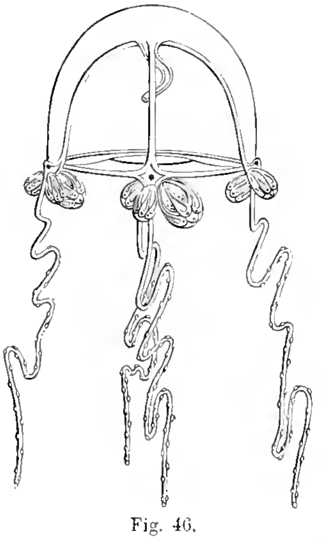

Fig. 46.

FIG. 45.—Medusiform person (*Sarsia*), one of the *Anthomedusæ*, detached from a hydroid colony of the family *Corynidæ*. *b*, the long manubrium, bearing (as an exception) medusiform buds; *a*, mouth.

FIG. 46.—Medusiform person, one of the *Anthomedusæ*, detached from a hydro- colony of *Syncoryne*. Ocelli are seen at the base of the tentacles, and also (as an exception) groups of medusiform buds.

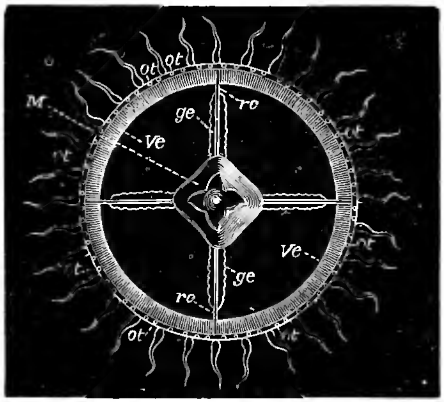

FIG. 47.—View of the oral surface of one of the *Leptomedusæ* (*Irene pellucida*, Haeckel), to show the numerous tentacles and the otocysts. *ge*, genital glands; *M*, manubrium; *ot*, otocysts; *rc*, the four radiating canals; *Ve*, the velum.

The *Calyptoblastea* of Allman, *Skenotoka* of Carus, and *Campanulariæ* of authors form a well-marked group of hydroids which, when they give rise to free medusæ, give rise to those termed *Leptomedusæ* by Haeckel, corresponding to the *Thaumantiadæ* and *Eucopidæ* of Gegenbaur's system. The calyptoblastic hydroid *Leptoscyphus*, which, according to Allman, gives rise to a *Lizzia*-like medusa (*Anthomedusæ*), is the only recorded exception to this correspondence. The *Æquoridæ* and other medusæ of similar structure have not been traced into connexion with any hydriform trophosome, but we are not justified therefore in concluding that they develop directly from the egg without hydriform phase. The chief point distinguishing the *Leptomedusæ* as a lot from the *Anthomedusæ* is the development of the generative bodies in the radial canals. This position is similar to that occupied by the same organs in *Trachomedusæ* and *Scyphomedusæ*. Allman, however, considers the genital glands of the *Leptomedusæ*, not as mere glands like those of *Aurelia* or *Charybdæa*, but as a series of buds—a generation of aborted medusæ or sporosacs. In consequence he terms the medusa of the *Leptomedusæ* a blastocheme (or bud-producer), as distinguished from a gonocheme (or genital-producer). In support of this view, Allman (*Monograph*, 1874) adduces the various remarkable cases of production of buds by medusæ which have been recorded (fig. 44, 45, 46), and, further, the very striking similarity between the structure of a lobe of the genital gland of *Obelia* and a sporosac such as we find in *Hydractinia*. It seems necessary to accept Allman's view on this matter, unless we are prepared to abandon the homology of sporosacs with medusæ in the case of hydriform persons.

The colonies of hydriform persons of the present group differ *inter se* according to the arrangement of the cups or hydrothecæ. In *Plumularidæ* they are sessile, and all on one side of a branch; in *Sertularidæ* they are sessile, and alternately placed on either side; in *Campanularidæ* each cup is raised on a pedicel or stalk. The medusiform persons sometimes remain abortive and sessile in their gonangia.

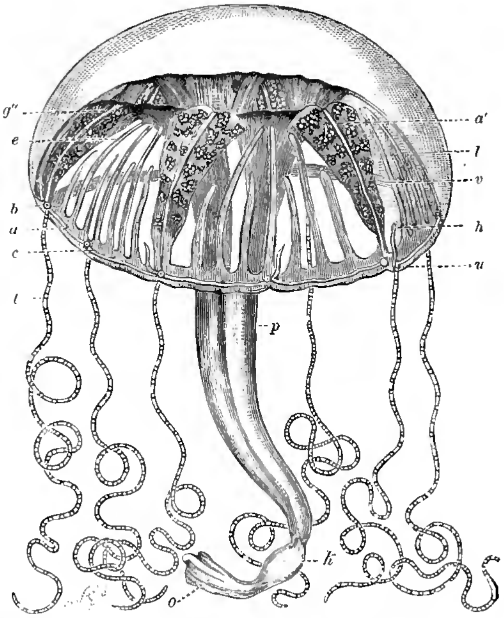

FIG. 48.—*Carmarina* (*Geryonia*) *hastata*, one of the *Trachomedusæ*. (After Haeckel.) *a*, nerve-ring; *a'*, radial nerve; *b*, tentaculocyst; *c*, circular canal; *e*, radiating canal; *g''*, ovary; *h*, peronia or cartilaginous process ascending from the cartilaginous margin of the disc centripetally in the outer surface of the jelly-like disc; six of these are perradial, six interradial, corresponding to the twelve solid larval tentacles, resembling those of *Cunina*; *k*, dilatation (stomach) of the manubrium; *l*, jelly of the disc; *p*, manubrium; *t*, tentacle (hollow and tertiary, *i.e.*, preceded by six perradial and six interradial solid larval tentacles); *u*, cartilaginous margin of the disc covered by thread-cells; *v*, velum.

Order 3. *Trachomedusæ*,—*Hydromedusæ* which have as sense-organs tentaculocysts. The otoliths (fig. 12) are formed by endodermic cells as in *Scyphomedusæ*, and ocelli may or may not be present on the tentaculocyst.

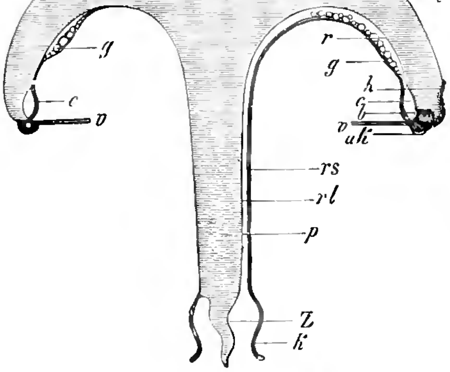

FIG. 49.—Diagram of a vertical section of *Carmarina hastata*, passing on the right through the whole length of a radiating canal, and on the left through the outspread lobe of an ovary. *l*, gelatinous substance of the disc and gastric stalk (manubrium); *r*, radiating canal; *rs*, its outer, *rl*, its inner wall; *g*, ovaries; *k*, stomach (dilatation of the manubrium); Z, tongue-like process of the gelatinous substance; *h*, cartilaginous process ascending from the marginal ring at the site of a tentaculocyst; *c*, circular canal; *b*, tentaculocyst; *v*, velum; *uk*, cartilaginous marginal ring. (From Gegenbaur.)

The genital glands have the form of wide outgrowths or lamelliform enlargements in the course of the radial canals (figs. 48, 49). No hydriform phase is known in any member of this group, and one at least (*Geryonia*) has been observed to develop from the egg directly into the medusa-form.

Order 4. *Narcomedusæ.*—These have the same characters as the *Trachomedusæ*, excepting that the genital glands are in the wall of the manubrium or in pocket-like radial outgrowths thereof (figs. 50 and 51). Further, the marginal tentacles of the disc possess peculiar "roots," which can be traced upwards into the gelatinous substance of the body. No hydriform phase has been observed in this group, whilst *Ægina* and *Æginopsis* have been shown to develop directly from the egg to the medusa-form.

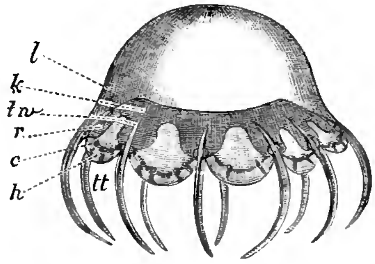

Fig. 50.—*Cunina rhododactyla*, one of the *Narcomedusæ*. *c*, circular canal; *h*, "otoporpæ" (ear-rivets) or centripetal process of the marginal cartilaginous ring connected with tentaculocyst; *k*, stomach; *l*, jelly of the disc; *r*, radiating canal (pouch of stomach); *tt*, tentacles; *tw*, tentacle root. (After Haeckel.) The lappets of the margin of the disc, separated by deep notches, above which (nearer the aboral pole) the tentacles project from the disc (not marginal therefore), are characteristic of many *Narcomedusæ* and *Trachomedusæ*. Cartilaginous strands (the mantle rivets or peroniæ) connect the tentacle root with the solid marginal ring.

The two orders *Trachomedusæ* and *Narcomedusæ* are established by Haeckel in his new "system" for the peculiar forms classed by Carus as *Haplomorpha*, and by Allman as *Monopsea*. These latter names have reference to the fact that no hydriform phase is *known* to occur in the life-history of these organisms, a fact which is not peculiar to them, and, if it should prove to be not universal amongst them, would by no means invalidate their claim to a distinct position on the grounds afforded by the characters above given. They are remarkable for a certain hardness and stiffness of the gelatinous substance of the disc, or at any rate of the cellular axis of the tentacles, on accout of which the orders are contrasted by Haeckel as *Trachylinæ* with *Anthomedusæ* and *Leptomedusæ*, which are termed *Leptolinæ*; a curious parallelism as to the position of the genitalia exists between *Anthomedusæ* and *Narcomedusæ* on the one hand and *Leptomedusæ* and *Trachomedusæ*, on the other. The orders present a very high degree of development, both in coarser and histological differentiation. At one time it was supposed, in accordance with Haeckel's observations, that *Geryonia* (*Carmarina*, fig. 48), one of the *Trachomedusæ*, gave rise by buds from its enteric walls to young *Cuninæ* (*Narcomedusæ*, fig. 50), but this has been explained by the observations of Franz Schulze and of Uljanin as due to parasitism, young *Cuninæ* in the condition of ciliated *Planulæ* entering the mouth and enteric chamber of the *Carmarina*. The same explanation probably applies (Claus) to the supposed internal buds of *Cunina* observed by Gegenbaur, Fritz Müller, and Metschnikow. The process is sufficiently remarkable according to the last observer, for the first generation of buds produce a second generation by external gemmation, before attaining the characters of the parent *Cunina*. The anatomy of these forms is fully given in Haeckel's memoirs in the *Jenaische Zeitschrift*, vols. i. and ii., 1864–66; also further details as to *Carmarina* are given in Eimer's *Medusen*, 1878.

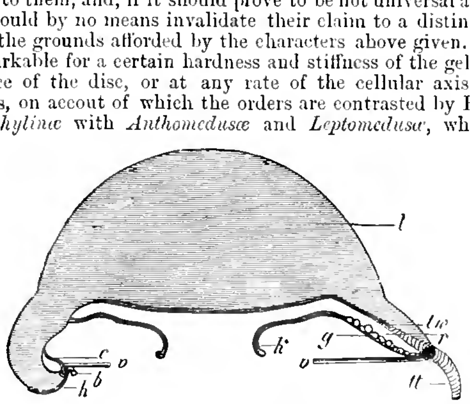

Fig. 51.—Diagram of a vertical section through a young *Cunina rhododactyla*, passing on the right side through a radiating pouch. *b*, tentaculocyst; *c*, circular canal; *g*, ovary; *h*, marginal cartilage and connecting process springing from a tentaculocyst (otoporpa); *k*, stomach; *l*, jelly of the disc; *r*, radiating canal or pouch; *tt*, tentacle (solid, cartilaginous); *tw*, tentacle root; *v*, velum. (From Gegenbaur.)

Order 5. *Hydrocorallinæ.*—These are *Hydromedusæ* in which the hydriform phase forms large colonies, presenting a copious calcareous deposit in the ectodermal tissue (cœnosteum of Moseley), leaving only the hydranths or tentacular region free from such hardening. The medusiform persons are, at present, only known in the degenerate form of sporosacs, which occupy cavities (ampullæ of Moseley) in the hardened base of the colony (*Stylasteridæ*). No such cavities have been detected in others (*Milleporidæ*), which may, therefore, give rise to complete medusiform persons. In all a marked polymorphism has been observed (fig. 53), consisting in the differentiation of longer tentacle-like persons (dactylozooids) and shorter mouth-bearing persons (gastrozooids). The persons of both kinds are either scattered irregularly or the dactylozooids are arranged around the gastrozooids in cyclosystems of greater or less definiteness, or in distinct rows (fig. 55). The position of these two kinds of hydriform persons is marked by definite groups of pits (cyclosystems) in the dried calcareous skeleton of the colonies, which simulate the calycles of the stony corals (*Anthozoa*).

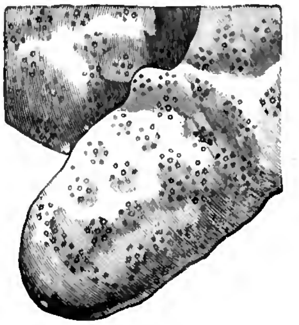

Fig. 52.—Portion of the calcareous corallum of *Millepora nodosa*, showing the cyclical arrangement of the pores occupied by the "persons" or hydranths. Twice the natural size. (From Moseley.)

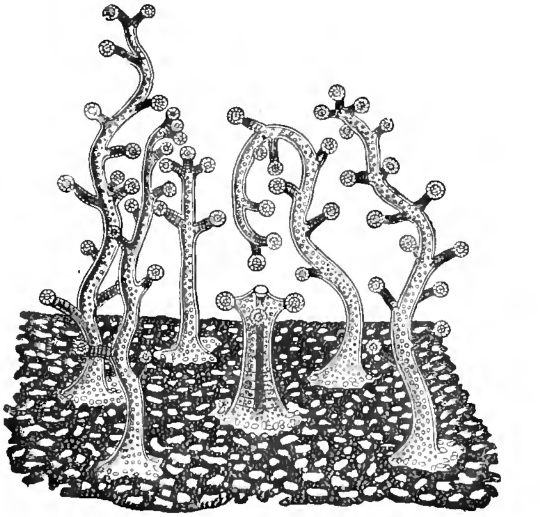

Fig. 53.—Enlarged view of the surface of a living *Millepora*, showing five dactylozooids surrounding a central gastrozooid. (From Moseley.)

Louis Agassiz was the first to recognize the true nature of the *Milleporidæ*, and his imperfect observations have been fully confirmed and greatly extended by Mr Moseley (*Phil. Trans.*, 1878) who added the *Stylasteridæ* previously regarded as *Anthozoa* to the category of calcigenous hydroids, and founded the order of *Hydrocorallinæ*. The *Stylasteridæ* differ from the *Milleporidæ* in possessing a calcified axial style at the base of the dilated portion of each gastrozooid, and further in the ascertained development of sporosacs, and in the greater complication of their cyclosystems. These forms are abundant in tropical seas, and contribute with the *Anthozoa* and Corallines to the formation of coral reefs. *Allopora* and *Stylaster* occur off the Norwegian coast. The woodcuts illustrating the structure of this group are borrowed from Mr Moseley's *Notes of a Naturalist on the "Challenger."*

The nearest allies of the *Hydrocorallinæ* are such polymorphic *Gymnoblastea* as *Hydractinia* (fig. 39); the definite division of labour and the polymorphism in the former, together with their calcigenous peculiarity, entitle them to rank as a distinct order.

Order 6. *Siphonophora.*—These are *Hydromedusæ* in which hydriform persons alone (*Velella*) or hydriform persons and sterile medusiform persons are united, under many special modifications of form, to constitute floating colonies of very definite shape and constitution. In addition to these are developed medusiform sexual persons which usually are sporosacs and only exceptionally attain full development so as to be liberated from the colony as free-swimming medusæ (*Velella*, as *Chrysomitra*; *Physalia*, only liberating female medusæ). The medusiform persons, where sufficiently developed, exhibit the velum characteristic of *Hydromedusæ*; the larger mouth-bearing hydriform persons, which are sometimes the only representatives of their kind, are remarkable for differentiation into four regions,—a proboscis, a stomach, a basal ring, and a short stalk on which the *single* tentacle of great length is situated (fig. 56, *f*). In the sub-order *Physophoridæ* (fig. 57, C) the persons are united by a short or long and spiral stem, terminated at one end by a flask-like air-sac (pneumatocyst); below the air-sac a biserial or multiserial range of swimming-bells (nectocalyces = medusæ with suppression of manubrium, tentacles, and sense-organs) are placed. Covering pieces (hydrophyllia, reduced medusæ) and dactylozooids are affixed to the succeeding region of the stem, and alternate in definite order with the mouth-bearing hydriform persons (polyps or nutritive persons) and generative medusiform persons. In the sub-order *Physalidæ* the stem is converted into an air-sac, enormously enlarged, and the nectocalyces and hydrophyllia are absent. In the sub-order *Calycophoridæ* the air-sac is not developed, the nectocalyces are in a biserial group, or reduced to two or to one. Dactylozooids are wanting. The modified persons (appendages, Huxley) arise from the stem in groups, and can be withdrawn into the cavity of a swimming-bell (fig. 57, B). Each group consists of a nutritive person, with long tentacle, of generative medusoids, and usually also an umbrella-shaped or funnel-like covering piece. The latter separate in some *Diphyidæ*, and lead an independent life as *Eudoxiæ*.

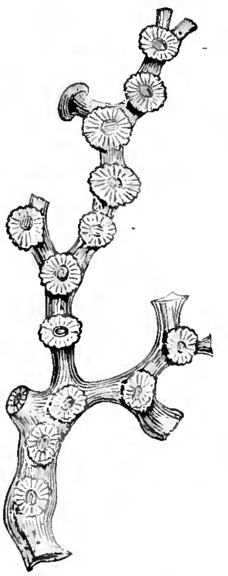

FIG. 54.—Portion of the corallum of *Astylus subviridis* (one of the *Stylasteridæ*), showing cyclosystems placed at intervals on the branches, each with a central gastropore and zone of slit-like dactylopores. (After Moseley.)

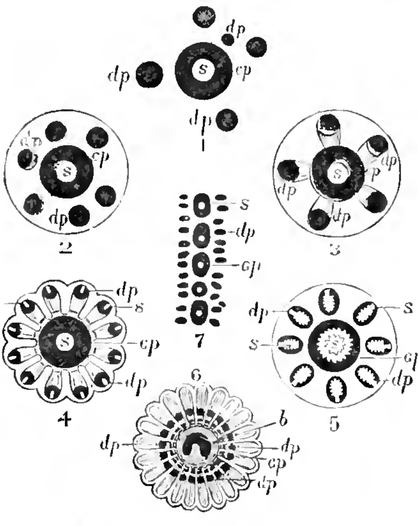

FIG. 55.—Diagrams illustrating the successive stages in the development of the cyclosystems of the *Stylasteridæ*. 1, *Sporadopora dichotoma*. 2, 3, *Allopora nobilis*. 4, *Allopora profunda*. 5, *Allopora miniacea*. 6, *Astylus subviridis*. 7, *Distichopora coccinea*. *s*, style; *dp*, dactylopore; *gp*, gastropore; *b*, in fig. 6, inner horseshoe-shaped mouth of gastropore. (After Moseley.)

In the suborder *Discoidæ* the stem is converted into a flattened disc with a system of canalicular cavities. Above this lies the air sac, a flattened reservoir of cartilaginous consistence. The hydriform persons depend from the disc, centrally a large nutritive person surrounded by smaller similar persons carrying at their bases the generative medusoids; near the edge of the disc are dactylozooids. The medusoids develop into complete medusiform persons, and develop the genital products after liberation from the colony, when they are known as *Chrysomitra*.

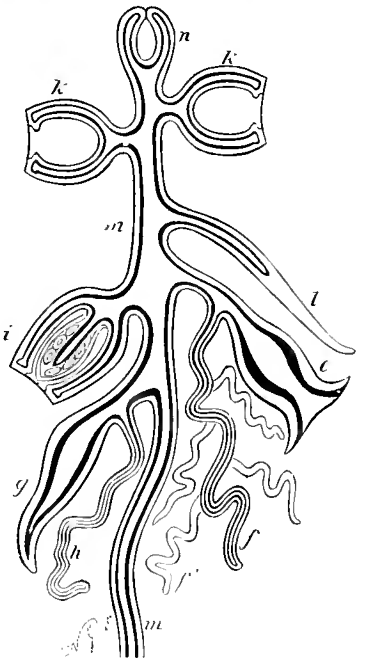

FIG. 56.—Diagram showing possible modifications of medusiform and hydriform persons of a colony of *Siphonophora*. *n*, pneumatocyst; *k*, nectocalyces (swimming bells); *l*, hydrophyllium (covering-piece); *i*, generative medusiform person; *g*, dactylozooid with attached tentacle, *h*; *c*, nutritive hydriform person, with branched grappling tentacle, *f*; *m*, stem. The thick black line represents endoderm, the thinner line ectoderm. (After Allman.)

The *Siphonophora* alone, amongst the colonies formed by *Hydrozoa*, exhibit a high degree of division of labour and consequent individuation. The mode of origin of such colonies has been discussed above. The locomotive habit, as contrasted with the sessile habit of other colonies, is no doubt correlated with the sharply defined individuality which they attain (compare *Cristatella* among *Polyzoa*). *Velella* and *Physalia* are occasionally seen on the southern and western shores of England, but as a rule the *Siphonophora* are met with only in the open ocean and in the Mediterranean. By some authorities the *Siphonophora* are assigned a distinct position among the *Hydrozoa*, side by side with the *Hydromedusæ* and *Scyphomedusæ*; their interpretation as floating colonies of *Hydromedusæ*, an interpretation necessitated by the structure of their medusiform persons, forbids their separation from that group.

FOSSIL HYDROZOA.—The researches of Moseley have necessitated a redistribution of the group of *Anthozoa* known as the *Tabulata*. Among these appear to be a few *Hydrocorallinæ*, which occur in the fossil state. The Palæozoic forms known as graptolites are by some authors assigned to the *Hydrozoa*, but the grounds for placing them in this position are very slight, owing to the imperfect nature of the remains. A discussion of the small amount of structure which they present would be out of place here.

Remarkable *Scyphomedusæ* have been obtained from the Solenhofen slates (Jurassic); excepting these, no noteworthy extinct *Hydrozoa* are known (see Haeckel in *Zeitsch. wiss.*

Zool., vols. xv., xix., and *Jenaische Zeitsch.*, vol. viii., 1874).

Relationship of the Ctenophora to the Hydrozoa.—The remarkable medusa-form recently described by Haeckel (*Sitzungsber. Jenaische Gesellsch.*, 1878) as *Ctenaria ctenophora*, and classed by him amongst the *Anthomedusæ*, seems to furnish a very direct transition from the structure of a medusa to that of such a ctenophor as *Cydippe* (*Pleurobrachia*). The woodcut and appended explanation (fig. 58) copied from Haeckel's memoir will render the relations of the two forms clear. *Ctenaria* has the margin of its disc narrowed so as to give the organism a spherical form. The approximated margins bound an orifice leading to the sub-umbrella space. This orifice corresponds to the so-called mouth of a *Cydippe*. Further, *Ctenaria* has two, and only two, long-fringed tentacles, like those of *Cydippe*, and each springing from a pocket as in that genus, and on the surface of its spheroidal umbrella eight rows of differentiated ectodermal cells, which though not ciliated correspond closely in position with the eight ctenophoral ambulacra of *Cydippe*. The disposition of the enteric canal-system of *Ctenaria* is, as shown in the cut, also transitional in the direction of *Cydippe*. Apart from the existence of *Ctenaria*, the homologies suggested by Haeckel between *Hydromedusæ* and *Ctenophora* are such as to commend themselves very strongly to acceptance (E. R. L.)

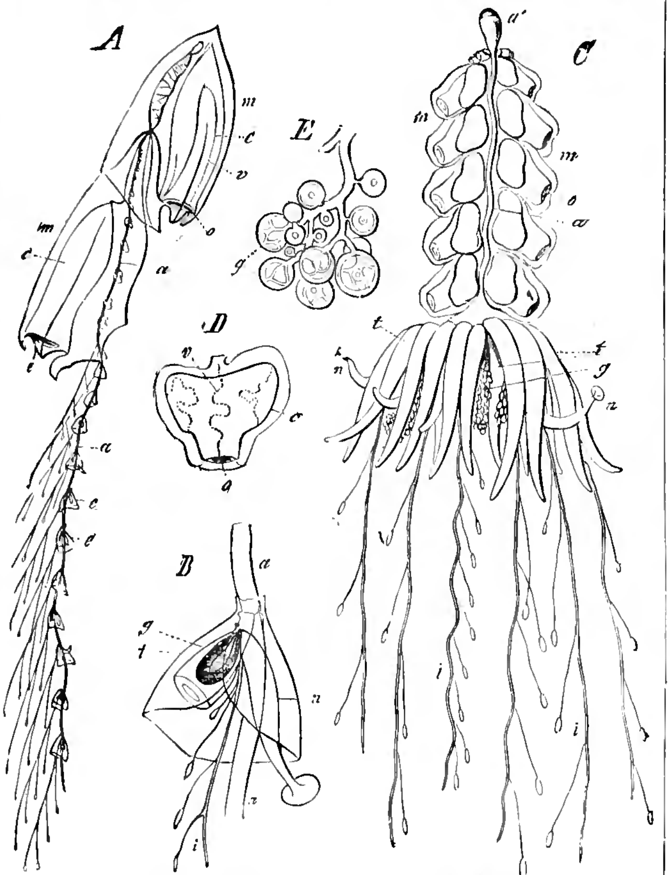

FIG 57.—Floating colonies of *Siphonophora*. *A*, *Diphyes campanulata* *B*, A group of appendages from the stem of the same *Diphyes*. *C*, *Physophora hydrostatica*. *D*, Separate nectocalyx of the same. *E*, Cluster of female sporosacs (aborted medusæ) of *Agalma sarsii*. *a*, stem or axis of the colony; *a'*, pneumatocyst (air-bladder); *m*, nectocalyx; *c*, sub-umbrellar cavity of nectocalyx; *v*, radiating canals of the umbrella of the nectocalyx; *o*, orifice formed by the margin of the umbrella; *t*, hydrophyllia in *B*, dactylozooids in *C*; *n*, stomach; *i*, tentacles; *g*, sporosacs. (From Gegenbaur.)

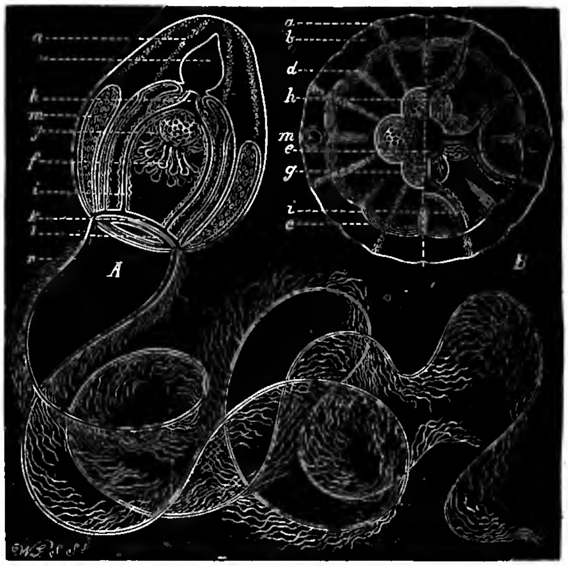

FIG. 58.—*Ctenaria Ctenophora* (Haeckel), one of the *Anthomedusæ*, connecting that group with the *Ctenophora*. *A*, lateral view of the entire medusa; *B*, two horizontal views, that to the left representing the surface of the aboral hemisphere, that to the right a section passing nearly equatorially. *a*, the eight (ciliated?) rows of thread-cells, adradial in position, and corresponding to the eight ctenophoral zones of *Pleurobrachia*; *b*, jelly of the umbrella; *c*, circular muscle of the sub-umbrella; *d*, longitudinal muscles of tho sub-umbrella; *e*, stomachal dilatation of the enteric cavity; *f*, the sixteen oral tentacles; *g*, the four perradial generative glands in the stomach wall (manubrium); *h*, the four perradial primary radiating canals; *i*, the eight adradial bifurcations of the preceding; *k*, ring canal in the margin of the umbrella; *l*, velum; *m*, the two lateral tentacle pouches; *n*, the two lateral unilaterally fringed tentacles; *o*, the apical cavity (infundibulum) above the stomach. The canal system, with its four primary and eight secondary rami agrees in *Ctenaria* and *Pleurobrachia*. The mouth of the latter is homologous with the margin of the umbrella of the former. The mouth of *Ctenaria* is homologous with the junction of the so-called funnel of *Pleurobrachia* with its so-called digestive cavity. This last is the homologue of the sub-umbrellar cavity of *Ctenaria*. The apical opening or openings of the funnel of *Ctenophora* is paralleled by the stalk canal of medusæ, whilst the agreement between the tentacles and their pouches in *Ctenaria* and *Pleurobrachia* is complete.

PLANARIANS

(*By Prof. Ludwig von Graff, University of Graz, Austria.*)

THE name *Planaria* was first applied by O. F. Müller in his *Prodromus Zoologiæ Danicæ* (1776) to a group of worms, inhabitants of fresh and salt water, characterized, so far as was then known, by a flattened leaf-like form. Ehrenberg in 1831 changed this name to *Turbellaria* on account of the cilia with which the body is furnished, by means of which the worms create a whirlpool in the surrounding water. The extent of this group was subsequently more restricted, and at present the name *Turbellaria* is applied to all those (mainly free-swimming) Platyhelminths whose body is clothed externally with a ciliated epidermis (fig. 9), and which possess a mouth and (with the exception of one division) an alimentary canal, but are without an anus. The Turbellarians, excluding the NEMERTINES (*q.v.*), which until recently were classed with them, form an order of the class *Platyhelminthes*, and the old name *Planaria* is now confined to a group of the freshwater representatives of this order.

Size and External Characters.—Many forms of the Turbellarians are so minute as to be hardly visible with the naked eye, while others attain to a length of several inches, and a land Planarian of no less than 9 inches in length has been described by Moseley. The freshwater forms are generally small, the largest representatives of the order being marine or terrestrial. The smaller species are mostly cylindrical, or convex dorsally and flat ventrally; the anterior extremity is commonly truncated and the posterior extremity pointed (fig. 1, *a*, *b*). The larger aquatic forms are thinner in proportion to the increasing surface of the body, so that they come to resemble thin leaf-like lamellæ (*d*), while the large land Planarians instead of increasing in superficies grow in length (*e* and *f*), so that they may be best compared to leeches. The larger aquatic forms are frequently provided with tentacles in the shape of paired finger-like processes or ear-like folds of the anterior part of the body (*d* and *g*); sometimes the tentacles are papillary outgrowths of the dorsal surface; the land Planarians are often to be distinguished by a crescent-shaped area at the fore end of the body, which is separated off from the rest (*f*). In many cases the whole dorsal surface is beset with papillæ (*d*). The aperture of the mouth varies greatly in its position; sometimes it is situated at the anterior extremity, sometimes in the middle of the ventral surface of the body, occasionally quite close to the posterior extremity; the single common or distinct male and female generative apertures are also situated upon the ventral surface of the body, and the former in rare cases open in common with the mouth; the genital apertures always lie behind the mouth. Many Turbellarians have a sucker which serves to attach the animal to surrounding objects, or to another individual during copulation.

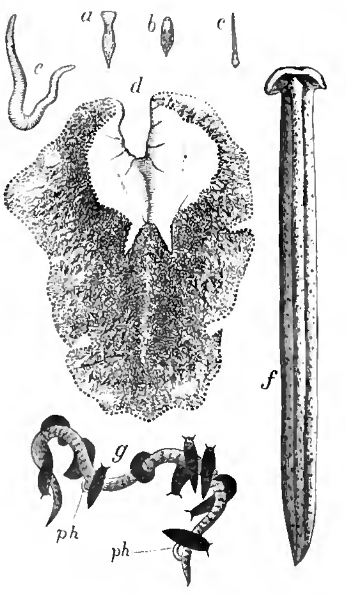

FIG. 1.—*a*, *Convoluta paradoxa*, Oe.; *b*, *Vortex viridis*, M. Sch.; *c*, *Monotus fuscus*, Gff.; *d*, *Thysanozoon brochii*, Gr., with elevated anterior extremity (after Joh. Schmidt); *e*, *Rhynchodemus terrestris*, O. F. Müller (after Kennel); *f*, *Bipalium ceres*, Mos. (after Moseley); *g*, *Polycelis cornuta*, O. Sch., attached by the pharynx (*ph*) to a dead worm (after Johnson). All the figures of natural size, and viewed from the dorsal surface.

Integument.—The integument is composed of a single layer of ciliated epithelium; between the cilia there are often long flagella and stiff tactile hairs and even (in a single instance) chitinous spines; these latter must be regarded as local thickenings of the firm cuticle which covers the epidermic cells. The epidermic cells are flat or columnar, and are united to each other by smooth opposed margins or by denticulate processes which fit into similar processes in the adjacent cells (fig. 2). Sometimes the epidermic cells are separated by an interstitial nucleated tissue. The structure and functions of the cells of the epidermis differ, and four varieties are to be found:—(*a*) indifferent ciliated cells; (*b*) cells containing certain definite structures (rhabdites, nematocysts); (*c*) gland cells; and (*d*) glutinous cells (Klebzellen). The rhabdites are refracting homogeneous rod-like bodies, of a firm consistency, which are met with in most Turbellaria, and often fill all the cells of the epidermis; they are not always found entirely within the cells, but the extremity often projects freely on to the exterior of the body. They are readily extruded from the cells by pressure, and are often found in great abundance in the mucus secreted by the glandular cells (many Turbellarians, like snails, deposit threads of mucus along their track); in this case the epidermic cells become perforated like a sieve. In many Turbellarians the rhabdites are chiefly massed in the anterior part of the body; frequently there are several varieties of rhabdites in one and the same species,—some being pointed at both ends, others cylindrical with truncated extremities. These structures are either formed directly in the ordinary epidermis cells as a kind of secreted product of the cell, or in special formative cells which lie beneath the integument and are connected with the epidermis cells by protoplasmic filaments, by means of which the rhabdites reach the surface of the body. These cells must be regarded as epidermic cells which have become disconnected with the epidermis itself, and wandered into the subjacent parenchyma. The function of the rhabdites seems to be to support the tactile sense. In rare instances nematocysts are present which in structure and development entirely resemble those of the *Cœlentera* (see vol. xii. p. 550). Very commonly structures known as pseudo-rhabdites are present; these have a rod-like form, but instead of being homogeneous are finely granular; they are an intermediate step between the rhabdites proper and a granulated secretion occasionally thrown off by the gland cells. The unicellular glands are either situated among the epidermic cells or in the parenchyma, in which case they are connected with the exterior only by the excretory duct. A peculiar modification of the epidermic cells are the so-called "glutinous cells," which occur on the ventral surface or at the hinder end of the body of many Turbellarians, and compensate for the suckers; the surface of these cells is furnished with numerous minute processes by means of which and a sticky secretion the animals can attach themselves to surrounding objects. Sometimes the epidermic cells contain calcareous concretions, and very commonly pigment is found either in the cells themselves or within the interstitial tissue. The colours of Turbellarians are, however, not always due to the pigment of the epidermis but to pigment contained in the parenchyma. Beneath the epidermis is a basement membrane (fig. 2, *bm*) which is in some cases very delicate and structureless, and in other cases much thicker and enclosing branched cells; this membrane is attached more firmly to the subjacent tissue than to the epidermis. Since this tissue is the strongest in the body, and serves as a surface of attachment for the muscles, it has been termed by Lang a skeletal membrane.

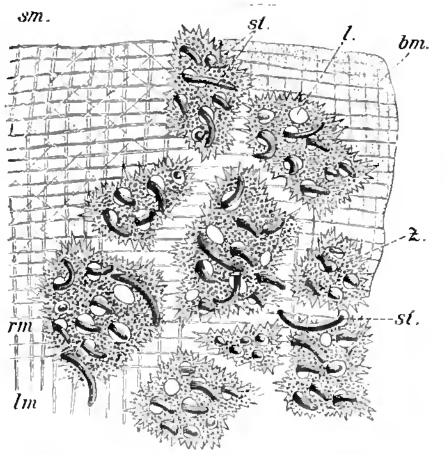

Fig. 2.—Integument of *Mesostoma lingua*, O. Sch. On the right hand is the epidermis (*z*) with perforations (*l*) through which the rhabdites (*st*) project. Beneath this the basement membrane (*bm*), and beneath this again the muscular layers consisting of circular (*rm*), diagonal (*sm*), and longitudinal (*lm*) fibres.

The third section of the integument is formed by the muscular layers. These form a continuous covering to the rest of the body, but their arrangement and thickness are very different in different forms. In the smaller species (*Rhabdocœlida*) there are two layers, an outer circular and an inner longitudinal, only in a few cases the circular layer is external to the longitudinal; sometimes there are three distinct layers, as in fig 2, where a diagonal layer is interposed. The larger forms (*Dendrocœlida*) have a much more complicated muscular system: in the most differentiated forms there are six separate layers (two circular, two diagonal, and two longitudinal), which are, however, always less developed upon the dorsal than upon the ventral surface in that the thickest layer of the ventral surface (the innermost longitudinal) is absent or very feebly developed upon the dorsal side. Besides the integumentary muscular system, there are also found dorso-ventral muscular bands which traverse the whole body from the dorsal to the ventral basement membrane, being branched at both extremities, and the special muscles of the pharynx, genital organs, and suckers.

The perivisceral cavity, bounded by the integument and traversed by the dorso-ventral muscles, contains the organs of the body—alimentary canal, excretory system, nervous system, and genital glands. The space left between these organs is filled with parenchyma; the latter varies much in appearance and is very difficult to study. Generally it consists of a network of fibres and trabeculæ, which contain nuclei, and between which is a system of cavities filled during life with the perivisceral fluid. These cavities are generally but few in number and vary with the stronger or feebler development of the reticulum; they occasionally contain free cells.

Alimentary Canal.—All Turbellarians are furnished with a mouth, which, as there is no anus, serves both to take in nutriment and expel the undigested remains of food. The alimentary canal consists of a muscular pharynx and an intestine. The pharynx (figs 3, 5 to 8, *ph*) is cylindrical in form, rather complicated in structure, and surrounded by a muscular sheath, which opens on to the exterior by the mouth (*m*). Often the pharynx consists merely of a circular fold lying within the pharyngeal pouch (fig. 8); it can be protruded through the mouth and acts like a sucker, so that the animal can fasten itself upon its prey and draw it into the intestine by suction. At the junction of the pharynx with the intestine open the salivary glands, which are frequently large and well-developed (fig. 5, *s*). The intestine (*i*) has a very characteristic form in the different sections, and has long served to divide the *Turbellaria* into two groups:—(1) *Rhabdocœlida*, with a straight unbranched intestine (figs. 5, 6), and (2) *Dendrocœlida*, with a branched intestine (figs. 7, 8). In the latter group Lang has recently called attention to further differences that exist in the form of the intestine: in the *Tricladida* (fig. 7) there is no central "stomach," but three equally-sized intestinal branches (which have secondary ramifications) unite together to open into the pharynx; in the second group, the *Polycladida* (fig. 8), there is a median stomach (*st*), from which numerous intestinal branches arise; this stomach communicates directly with the pharynx; the branches of the intestine are much ramified and often form an anastomosing network. The epithelium of the intestine is a single layer of cells generally not ciliated, capable of protruding amœboid processes by which the food is absorbed; the digestion of these animals is intracellular. Sometimes a muscular coat surrounds the intestine, the lumen of which is thus capable of being totally or partially contracted. To the above-mentioned divisions of the group, distinguished from each other by the varying form of the alimentary tract, another has been added, viz., the *Acœla* (Ulianin), which are characterized by the entire absence of any intestine. In these forms (fig. 4) the mouth leads directly into the parenchyma of the body by a short tube which is merely an invagination of the integument; the parenchyma is a syncytium, consisting of a soft protoplasmic mass with scattered nuclei, which represents the elements of the intestine and the body parenchyma (ento- and mesoderm) completely fused and without any traces of differentiation. This fact, as well as the disappearance of a nervous and excretory system, reduces the *Acœla* to the lowest position not only among the *Turbellaria*, but among the whole group of the *Vermes*.

Excretory System.—The excretory system of the Turbellarians is quite similar to that of the Trematodes and Cestoids; it consists of (1) the main trunks with their external aperture, (2) the secondary branches of these, and (3) the excretory cells with the fine tubules leading from them. Rarely is there but a single main excretory trunk present opening at the hinder end of the body (*Stenostoma*); generally there are a pair of such trunks which open in common at the hinder end of the body, or separately (most *Rhabdocœla*), or by the mouth (fig. 3). In the *Tricladida* there are two or four lateral trunks present which open by a number of pores arranged in pairs upon the dorsal surface of the body; the same appears to be the case in the *Polycladida*. The main trunks of the excretory system are generally much twisted in their course, and anastomose with each other; they receive the fine tubules either directly or, as in the *Rhabdocœla*, there is a network of secondary tubules interposed. The excretory cells are pear-shaped; they are branched and furnished with a nucleus and a large vacuole which is directly continuous with the lumen of the tubule; from the boundary wall of the vacuole springs a single flagellum, which depends into the lumen of the tubule and is capable of active movement. Lang discovered in a marine form of the *Tricladida* (*Gunda*) similar vacuolated cells with a single flagellum among the epithelial cells of the intestine, and came to the conclusion that the excretory cells were on that account derived from the epithelium of the intestine. The movements of the excretory fluid towards the external pore are directed by this flagellum as well as by cilia developed upon the walls of the fine tubules; the motion of all these cilia is such as to drive the contents of the tubules towards the excretory pore. The main trunks of the excretory system are either sparsely (*Tricladida* according to Jijima) or completely (*Polycladida* according to Lang) lined with cilia.

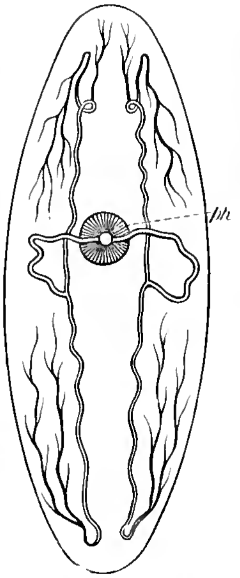

Fig. 3.—Main trunks of the excretory system of *Mesostoma ehrenbergii*, O. Sch. Open on to the exterior through the mouth. *ph*, pharynx.

Nervous System.—The central organ of the nervous system, the brain (*cn*), is a double ganglion at the anterior end of the body, and has been noticed in all the known forms with the exception of the *Acœla*. It is situated in front of or above the pharynx; in those species in which a process of the intestine extends beyond the region of the brain (*cf.* figs. 7 and 8 viewed from the ventral surface) it is placed below this. In such cases there is sometimes a commissure encircling the prolongations of the intestine. Each of the two ganglia gives off a strong longitudinal nerve cord (figs. 5–8, *ln*) from which arise branches going to the various organs of the body. The structure of the nervous system is somewhat different in the *Rhabdocœla*, *Tricladida*, and *Polycladida*. In the first group (figs. 5, 6) the two longitudinal cords and their branches are the most feebly developed, and there is but rarely (*Mesostoma*, *Monotus*) a transverse commissure uniting the longitudinal cords. These cords are very large in the *Tricladida*, where the brain is to be regarded as a simple thickening of them; in this group there are numerous transverse commissures between the longitudinal nerve cords (fig. 7), and the nerves arising from them and passing to the periphery form a subcutaneous nerve plexus within the muscular coat. Lang has observed a similar nerve plexus in the *Polycladida*, the central nervous system of which differs from that of the *Tricladida* in that a number of stout nerve cords radiate outwards from the brain as well as the two longitudinal cords; they are all united together by numerous commissures, and a network is thus formed which extends throughout the body.

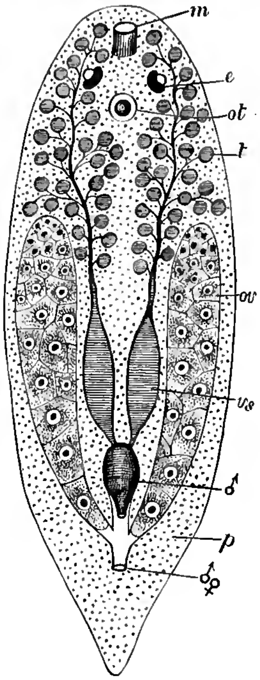

Fig. 4.

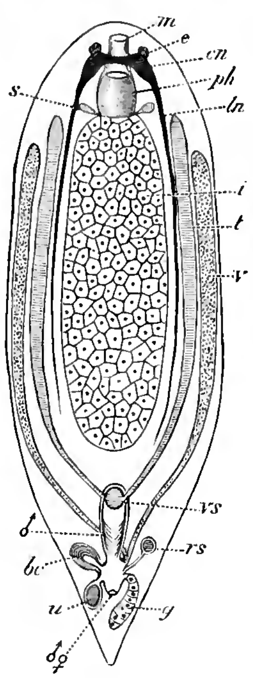

Fig. 5.

Fig. 4.—Plan of an Acœlous Turbellarian. *e*, eye; *m*, mouth; *ot*, otolith; *ov*, ovary; *p*, digesting parenchyma; *t*, testicular follicles; *vs*, vesicula seminalis ♂, male organ of copulation; ♂ ♀, common sexual aperture.

Fig. 5.—Plan of a Rhabdocœlous Turbellarian. *bc*, bursa copulatrix; *cn*, brain; *e*, eye; *g*, germarium; *i*, intestine; *ln*, longitudinal nerve trunk; *m*, mouth; *ph*, pharynx; *rs*, receptaculum seminis; *s*, salivary gland; *t*, testis; *u*, uterus (containing an egg); *v*, yelk gland; *vs*, vesicula seminalis; ♂, chitinous copulatory organ; ♂ ♀, common sexual aperture; *bc*, bursa copulatrix.

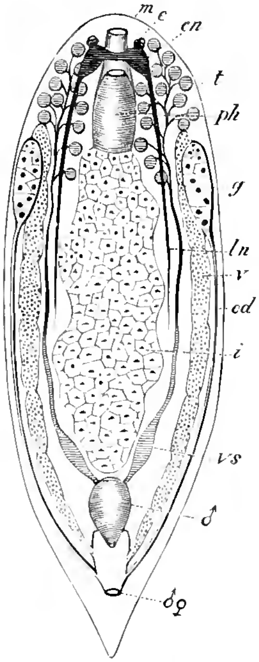

Fig. 6.

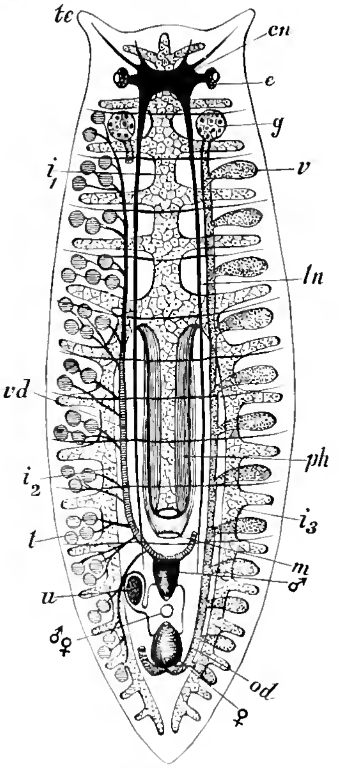

Fig. 7.

Fig. 6.—Plan of an Alloiocœlous Turbellarian. Lettering as in fig. 5.

Fig. 7.—Plan of a Tricladid. i_1, anterior, and i_2, i_3, paired posterior branches of intestine; *od*, oviduct; *tc*, tentacle; *vd*, vas deferens; ♂, male, and ♀, female copulatory organ. Other letters as in fig. 5.

Sense Organs.—These are represented by tactile organs, auditory organs (otoliths), and eyes. The whole surface of the body is very sensitive and (*e.g.*, in the *Polycladida*) contains cells which end in tufts of fine hairs, so that certain regions thus become specially sensitive and serve as tactile organs. The anterior pointed extremity of the body in the *Rhabdocœla* is characterized by an abundant development of rhabdites and tactile hairs, and thus becomes a special tactile organ; in other cases this region of the body is transformed into a conical tactile proboscis which can be retracted into a sheath (*Proboscida*). In the freshwater *Tricladida* the anterior margin of the head is richly innervated, and is beset with a special row of tactile cells which contain no rhabdites; in the terrestrial forms of the same family (*Bipalium*) Moseley has described a row of papillæ along the crescent-shaped anterior extremity which can be extended and form tactile organs; between the papillæ are peculiar ciliated grooves connected with nerves. In the *Polycladida* there are tactile cells with stiff hair-like processes on the summit of the dorsal papillæ and the various tentacular structures; the tentacles in this family also serve to support the eyes.

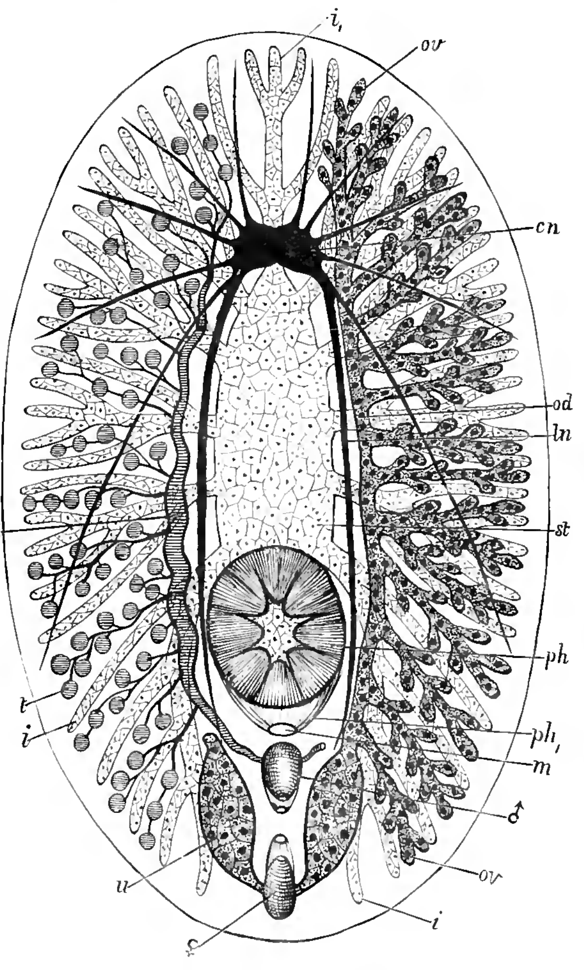

Fig. 8.—Plan of a Polycladid. *cn*, brain; *i*, intestinal branches; i_1, anterior unpaired intestinal branch; *ln*, longitudinal nerve cord; *m*, mouth; *od*, oviduct; *ov*, ovarian follicle; *ph*, pharynx; ph_1, pharyngeal pouch; *st*, stomach; *t*, testicular follicle; *u*, uterus; *vd*, vas deferens; ♂, male copulatory organ, with the male aperture behind; ♀, female copulatory organ, with the female aperture before it. The eyes are omitted.

The majority of the Turbellarians possess eyes; the *Rhabdocœlida* commonly have two or four, as also have the *Tricladida*; the latter, however, are in some instances furnished with a greater number arranged in a continuous row round the anterior end of the body; in the *Polycladida* there are from fourteen to several hundred eyes arranged in two symmetrical groups round the brain or scattered over the whole of the anterior margin of the body and upon the tentacles. The eyes are always situated beneath the integument within the parenchyma, sometimes directly upon the brain or connected with it by special optic nerves. In its simplest form the eye is a pigmented spot with or without a refractory lens-like body; the more complicated eyes consist of a pigmented sheath containing a number of refracting rods which are connected at their outer extremity with a series of retinal cells, one to each rod; the retinal cells are prolonged into a nerve thread running to the brain; the arrangement of the visual elements is therefore precisely the same as in the vertebrate eye. Of great interest is the fact that in the *Polycladida* the number of eyes increases with the growth of the animal, and Lang has shown that the eyes increase in number by actual division. On the other hand Carrière has discovered by experimenting with certain freshwater *Tricladida* that the compound eyes (those containing a number of rods) are formed by the coalescence of several simple eyes. Only a single eye is found in the *Monotida*, which has the form of a simple pigment spot in front of the otolith.

Auditory organs are found in the shape of vesicles filled with fluid and containing circular lenticular or spindle-shaped otoliths formed of carbonate of lime. Otolithic vesicles of this kind are found in many *Rhabdocœlida* (*Acœla*, *Monotida*, fig. 4, *ot*) embedded in a depression on the anterior surface of the brain. In the *Dendrocœlida* these organs are but rarely present.

As a sensory organ of unknown function must be mentioned the paired lateral ciliated grooves which are met with on either side of the brain in many *Rhabdocœla* (fig. 9, *c*); they are also found commonly in Nemertines (*q. v.*), but are here more complicated in structure.

Reproductive Organs.—With a few exceptions all the Turbellarians are hermaphrodite, and reproduce themselves sexually. Only among the *Microstomida* is there an asexual as well as a sexual reproduction. The male and female organs open to the exterior, either through a common cloaca (*atrium genitale*) on the ventral surface (most *Rhabdocœlida* and all *Tricladida*, figs. 4–7), or there are separate male and female apertures. In this case the male aperture is generally placed in front of the female aperture (some *Rhabdocœlida* and all *Polycladida*, fig. 8), but occasionally the positions are reversed (certain *Rhabdocœlida*). The genital glands display a primitive condition in being paired, though frequently the germarium (fig. 5, *g*) of the *Rhabdocœla*, and occasionally also the testis, is developed only upon one side of the body.

The structure of the female organs varies. In some cases there are simple ovaries (*ov* in figs. 4, 8) in which the ova originate and become fully mature without being furnished with the secretion of a second gland; in other cases there is a division into germarium (fig. 5–7, *g*) and yelk gland (*v*); the primordial ova or germs originate in the former, and absorb the products of the yelk gland in the atrium, where they become ready for fertilization. An intermediate condition is seen in those forms where there is but a simple gland present which produces germs in its upper portion and yelk in the lower portion. The ovaries are generally compact round or tubular glands (fig. 4); sometimes they are formed of a number of pear-shaped follicles (fig. 8); there is usually a simple or paired uterus (*u*) which retains the ova for some time before they are deposited; sometimes, however, the ova undergo their development within the uterus and are completely developed before expulsion; in some cases the egg-shell is detached within the uterus so that the young are produced alive.

In Turbellarians without a yelk gland the uterus is a simple widening of the oviduct (fig. 8); in those forms which possess additional yolk glands the uterus is a simple or paired diverticulum of the atrium genitale (figs. 5, 7). The ova are either surrounded by a more or less hard chitinous shell, or one shell contains a number of ova ("cocoon" of *Tricladida* and many *Polycladida*). The *Polycladida* deposit an egg-string which like that of the *Gastropoda* consists of a number of eggs bound together by a transparent albumen-like mass. Many Rhabdocœl Turbellarians (*e.g.*, *Mesostoma ehrenbergii*) produce two sorts of ova, thin-shelled summer ova and thick-shelled winter ova; the latter are capable of withstanding a considerable amount of dessication, and are deposited in the autumn. The accessory female organs of reproduction are represented by bursæ seminales, which receive the semen during copulation and retain it until fertilization is accomplished. A further division of labour is brought about by the presence of two diverticula of the atrium genitale, one of which serves as a bursa copulatrix (fig. 5, *bc*) and the other as a receptaculum seminis (*rs*) in the same sense as the equivalent organs of insects. In the place of a special receptaculum seminis the efferent duct of the ovary is often (*Mesostomida*) metamorphosed into a chamber to contain the semen. In the *Tricladida* and *Polycladida* the female efferent duct is often differentiated into a muscular vagina which closely resembles the penis (figs. 7, 8, ♀).

Finally, the female generative apparatus is furnished with a number of glands which have been termed cement glands, albuminiparous glands, and shell glands.

The male sexual glands (figs. 4–8, *t*) resemble the ovaries in being either compact tubular (fig. 5) or follicular (figs. 4, 6, 7, 8) structures. The vasa deferentia (*vd*) are often widened out into vesiculæ seminales (figs. 4, 6, *vs*); or there are special vesiculæ seminales present, formed by a portion of the penis (fig. 5, *vs*). In the male organ of copulation there is frequently found in addition to the spermatozoa an accessory granulated secretion produced by special glands, but of unknown function.

The muscular penis, especially in the *Rhabdocœla*, has a number of chitinous spines and hooks which serve to assist the animal in maintaining a firm hold during copulation, but also in capturing and retaining its prey. In *Macrorhynchus helgolandicus*, Gff., there is a peculiar poison dart connected with the male copulatory organ which only serves the latter purpose. Very remarkable is the opening of the penis into the mouth cavity in *Stylostomum* (*Polycladida*) and *Prorhynchus* (*Rhabdocœla*), and also the existence of several (2–15) pairs of male copulatory organs and genital apertures in certain *Polycladida*.

The spermatozoa vary much in form, especially in the *Rhabdocœlida*, where frequently the species of one and the same genus are distinguished by the different form of the spermatozoa. Copulation in the Turbellarians is generally reciprocal; only in those cases where both summer and winter ova (see above) are formed do the former arise from self-fertilization; the latter are the result of the copulation of two individuals. The fertilization of the ova always takes place in the atrium genitale. Many Turbellarians, especially the *Acœla*, display the phenomenon known as "successive hermaphroditism," the male organs of an individual attain to maturity first, and the female organs become ripe subsequently. During copulation, therefore, one individual is physiologically a male and the other a female.

Asexual generation is met with only in the *Microstomida*; it takes the form of transverse division accompanied by budding. The posterior third of the body becomes separated off by a septum running from the gut to the integument and an external furrow corresponding to this; this part of the body grows in length until it equals the anterior portion. By further repetition of this double procedure of separation and equalization there, chains of 4, then 8, 16, and 32 buds are formed, which remain attached (fig. 9), and, although fresh mouth apertures (m', m'', m''') have been formed, are still in communication by the intestinal lumen; this becomes closed before or after the several buds break off from their connexion with each other. Throughout the whole summer chains of zooids are met with; in autumn this asexual division probably ceases to occur; the several individuals become sexually mature, separate from each other, and lay eggs which remain quiescent during the winter and in the spring develop into fresh individuals reproducing asexually.

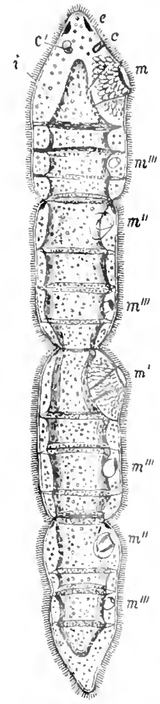

Fig. 9.

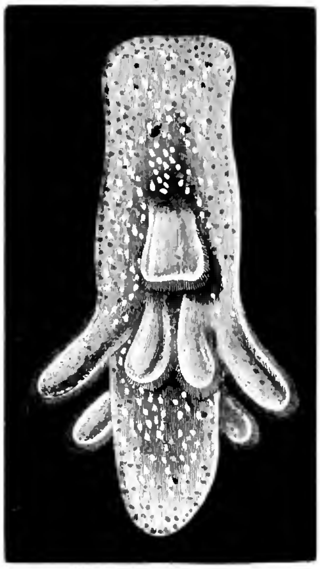

Fig. 10.

Fig. 9.—*Microstoma lineare*, Oe., undergoing division. There are 16 individuals, 8 with mouth apertures, showing the buds of the first (m), second (m'), third (m''), and fourth (m''') generation. The fifth generation has not yet acquired a mouth aperture. *c*, ciliated grooves; *e*, eye spots; *i*, intestine.

Fig. 10.—Larva of *Yungia aurantica*, L. (*Polycladida*), with provisional cillated processes (after A. Lang).

Development.—The study of the development of the Turbellarians is unfortunately not very far advanced, particularly among the small *Rhabdocœlida*, which are extremely difficult to investigate, and about which hardly any developmental facts are known. The larger fresh-water *Tricladida* and the *Polycladida* on the contrary have been recently very fully investigated. The *Rhabdocœla* and the *Tricladida* appear to develop directly without any metamorphosis, while a great part of the *Polycladida* undergo a metamorphosis and pass through a larval condition, during which they are furnished with provisional ciliated processes (fig. 10); the *Acœla* have also a free larval form; pelagic larvæ with a coat of long cilia apparently belonging to this group have been observed by Ulianin. The segmentation of the ovum is total, but unequal; an epibolic gastrula is formed and the aperture of invagination becomes the permanent mouth of the adult.

Systematic Arrangement and Mode of Life.—Order *Turbellaria*.—Platyhelminths with a ciliated integument, a mouth and pharynx, but no anus; with paired cerebral ganglia and two lateral nerve cords; sexual organs hermaphrodite; chiefly free-swimming.

Sub-order A. *Rhabdocœlida.*—Of small size; body cylindrical or depressed; without an intestine, or with a simple unbranched intestine; the female genital glands always compact, not follicular; genital apertures single or distinct.

Tribe I. *Acœla* (fig. 1, *a*).—With a digestive parenchyma not differentiated into intestine and parenchyma proper; with no nervous system or excretory organs; sexual organs hermaphrodite, with follicular testes and paired ovaries; generally without a pharynx, but having otoliths; all the forms marine. Many quite flat, with the lateral margins bent down towards the ventral surface (*Convoluta*), frequently with brown or green parasitic algæ in the parenchyma.

Tribe II. *Rhabdocœla* (fig. 1, *b*).—Intestinal tract and parenchyma separate; nervous system and excretory organs present; with compact testes and female generative glands (ovaries or separated germarium and yelk glands); with a complicated pharynx, but generally without otoliths. Numerous forms, freshwater and marine; the genus *Prorhynchus* (two species) also in damp earth. The *Microstomida* (fig. 9) propagate asexually. Freshwater forms mostly belong to the families *Mesostomida* and *Vorticida*, some of which contain green parasitic algæ. Marine forms include representatives of these two families and of the *Proboscida* (with a tactile proboscis). Of the family *Vorticida*, the genera *Graffilla* and *Anoplodium* are parasitic, the former in Gastropods the latter in Echinoderms (Holothurians).

Tribe III. *Alloiocœla* (fig. 1, *c*).—Intestinal tract and parenchyma separate; nervous system and excretory organs present; with follicular testes and compact female glands (as in the *Rhabdocœla*); pharynx similarly developed as a shorter or longer sac. One family (*Monotida*), with otoliths. All the species marine, with one exception, *Plagiostoma lemani*, which lives in the deep water of the Alpine lakes.

Sub-order B. *Dendrocœlida.*—Large forms, with a flattened body, branched intestine, follicular testes and follicular yelk glands or ovaries; without otoliths.

Tribe I. *Tricladida.*—Body elongate; intestine with three main branches uniting to open into a cylindrical retractile pharynx; with follicular testes, two round germariums, and numerous yelk follicles, with a single sexual aperture. *Planaria*, *Dendrocœlum*, *Polycelis* (fig. 1, *g*) are inhabitants of fresh water (with great power of reproduction). Terrestrial forms (fig. 1, *e*, *f*) of leech-like shape, especially met with in the tropics (only two European species *Rhynchodemus terrestris* and *Geodesmus bilineatus*); marine forms *Gunda* (characterized by a metameric structure), *Bdelloura* (external parasite of *Limulus*).

Tribe II. *Polycladida* (fig. 1, *d*).—Body leaf-like, thin, and broad, with numerous branched or retiform intestinal cœca which unite to form a central tube (stomach); with follicular testes and follicular ovaries, with two separated genital apertures, the male in front of the female; without (*Acotylea*) or with (*Cotylea*) a sucker situated behind the female generative opening. All marine.

Literature.—The most recent works, which also contain a full account of what has gone before, are the following:—*Rhabdocœla.*—L. v. Graff, *Monographie der Turbellarien*: 1. *Rhabdocœlida*, Leipsic, 1882, with 20 plates. *Marine and Freshwater Tricladida.*—A. Lang, "Der Bau von *Gunda segmentata* und die Verwandtschaft der Platyhelminthen mit Cœlenteraten und Hirudineen," in *Mitth. Zool. Stat. Neapel*, vol. iii., 1881; El. Metschnikoff, "Die Embryologie von *Planaria polychroa*," in *Zeitschr. f. wiss. Zool.*, vol. xxxviii., 1883; Isao Jijima, "Untersuchungen über den Bau und die Entwickelungsgeschichte der Süsswasser-Dendrocoelen," in *Zeitschr. f. wiss. Zool.*, vol. xl., 1884. *Land Planarians.*—H. N. Moseley, "On the Anatomy and Histology of the Land Planarians of Ceylon, with some Account of their Habits, and with a Description of Two New Species, and with Notes on the Anatomy of some European Aquatic Species," in *Phil. Trans.* (London, 1874), and "Notes on the Structure of several Forms of Land Planarians, with a Description of Two New Genera and Several New Species, and a List of all Species at present known," in *Quart. Jour. Micr. Sci.*, vol. xlvii., 1877; J. v. Kennel, "Die in Deutschland gefundenen Landplanarien *Rhynchodemus terrestris* und *Geodesmus bilineatus*," in *Arbeit. Zool.-Zootom. Instit. Würzburg*, v., 1879. *Polycladida.*—A. Lang, "Die Polycladen," in *Fauna und Flora des Golfes von Neapel*, No. 11, 39 plates, Leipsic, 1884-85.

(L. v. G.)

NEMERTINES

(*By A. A. W. Hubrecht, Ph.D., LL.D., Professor of Zoology, University of Utrecht.*)

NEMERTINES, or NEMERTEANS (*Nemertea*), is the name of a subdivision of worms,[1] characterized by the ciliation of the skin, by the presence of a retractile proboscis, by the simple arrangement of the generative apparatus, and in certain cases by a peculiar pelagic larval stage to which the name "pilidium" has been given. Many of them are long thread-shaped or ribbon-shaped animals, more or less cylindrical in transverse section. Even the comparatively shortest species and genera can always be termed elongate, the broadest and shortest of all being the parasitic *Malacobdella* and the pelagic *Pelagonemertes.* There are no exterior appendages of any kind. The colours are often very bright and varied. They live in the sea, some being common amongst the corals and algæ, others hiding in the muddy or sandy bottom, and secreting gelatinous tubes which ensheath the body along its whole length. Formerly, they were generally arranged amongst the Platyelminthes as a suborder in the order of the Turbellarians, to which the name of *Rhynchocœla* was applied, the other suborders being the *Dendrocœla* and the *Rhabdocœla.* With the advance of our knowledge of these lower worms it has been found desirable to separate them from the Turbellarians and to look upon the *Nemertea* as a seperate phylum of Platyelminthes. Lately the interest in their morphology has increased since it has been advanced (**6, 8**)[2] that certain points in their organization appear to indicate a remote degree of relationship to the ancestral forms which must have preceded the *Chordata* (to which the vertebrate animals also belong), and that this relationship is closer than that which exists between those *Protochordata* and any other group of invertebrate animals.

Classification.

CLASSIFICATION.—The Nemertines are subdivided into three suborders:—*Hoplonemertea, Schizonemertea,* and *Palæonemertea* (**5**). The (I) *Hoplonemertea* embrace all the species with a stylet in the proboscis, and also *Malacobdella,* which has an unarmed proboscis, but which, by the details of its organization and its development, must certainly be placed here (parasitism may be the cause of its incipient degeneration). The special characters of this suborder may be gathered from the anatomical descriptions hereafter to be given. In those species of which the embryology has been investigated the development was direct. The more common or more important genera are *Amphiporus* (*A. pulcher,* British coasts, Mediterranean; *A. splendidus,* Atlantic), which is comparatively short, *Nemertes* (*N. gracilis,* Atlantic and Mediterranean; *N. antonina,* Mediterranean; *N. echinoderma,* Mediterranean), which is long and thread-like, *Tetrastemma, Drepanophorus* (with more complicate armature in the proboscis), *Akrostomum, Malacobdella.* (2) In the *Schizonmertea* all those genera and species are united which have deep, longitudinal, lateral cephalic fissures. The development of some (*Lineus*) is characterized by the so-called larva of Desor, of others (*Cerebratulus*) by the curious and characteristic pilidium-larva. The principal genera are *Lineus* (*L. longissimus,* Atlantic; *L. obscurus*), *Cerebratulus* (*C. marginatus, C. bilineatus,* both Atlantic and Mediterranean; *C. urticans,* Mediterranean; *C. fasciolatus* and *aurantiacus, C. hepaticus* and *dohrnii,* Mediterranean; *C. macintoshii,* Madeira), *Langia* (*L. formosa*), *Borlasia* (*B. elizabethæ*). (3) Of the *Palæonemertea* the most typical and most characteristic genera are *Carinella* and *Cephalothrix.* They differ considerably both from Hoplo- and from Schizonemertines, and evidently belong to a lower stage of differentiation. The genera *Polia* (*P. delineata* and P. *curta,* Mediterranean) and *Valencinia* are provisionally arranged in this order because, though less primitive, they are not typical representatives of the other two suborders. The development of these species is not at all, or only very superficially, known. For the further characters of the last two suborders see the anatomical description below.

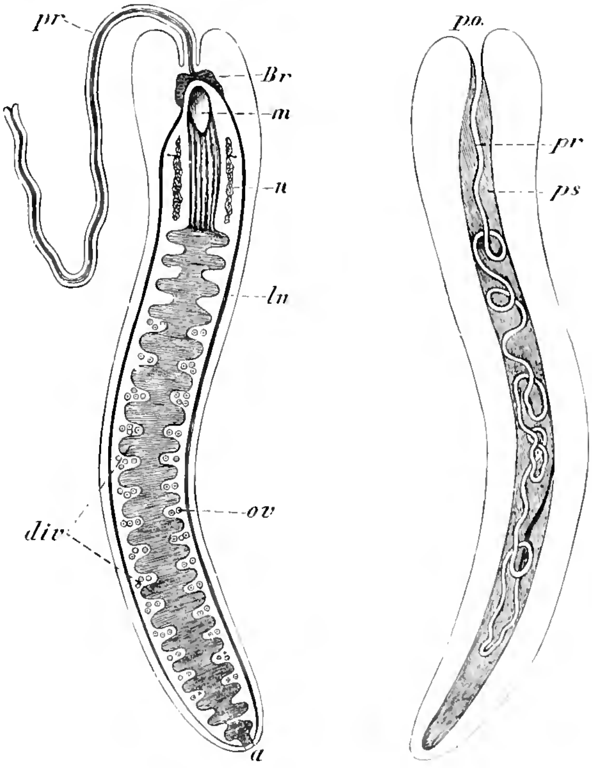

Fig. 1.   Fig. 2

FIGS. 1, 2.—Diagrams of the organs of a Nemertine, fig. 1 from below, fig. 2 from above. *m*, mouth; *div*, intestinal diverticula; *a*, anus; *ov*, ovaries; *n*, nephridia; *Br*, brain-lobes; *ln*, longitudinal nerve stems; *pr*, proboscis; *ps*, proboscidian sheath; *p.o.*, opening for proboscis.

Another subdivision generally current is that into the *Enopla* and the *Anopla* (**14**). This does not, however, take into sufficient account the primitive and diverging

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[1] Nemertes was a sea nymph, daughter of Nereus and Doris. One of the genera was named *Nemertes* by Cuvier.

[2] These figures refer to the bibliography at page 88.

characters disclosed by the very important less highly organized genera.

Anatomy

Anatomy.—(*a*) *Proboscis and Proboscidian Sheath.*—The organ most characteristic of a Nemertine is without doubt the proboscis. With very few exceptions (*Malacobdella*, *Akrostomum*, where it has fused with the mouth to a single exterior opening), there is a terminal opening (subterminal in *Valencinia*) at the foremost tip of the body, out of which the proboscis is seen shooting backwards and forwards, sometimes with so much force that both its interior attachments are severed and it is entirely expelled from the body. It then often retains its vitality for a long time, apparently crawling about as if it were itself a worm, a phenomenon which is at least partially explained by the extraordinary development of nervous tissue, equally distributed all through the walls of the proboscis, and either united (**10**) into numerous longitudinal nerve-stems (*Drepanophorus*, *Amphiporus*) or spread out into a uniform and comparatively thick layer (*Cerebratulus*, sp.). This very effective and elaborate innervation, which has been directly traced (**6**) to the brain, whence strong nerves (generally two) enter the proboscis, renders it exceedingly probable that the most important functions of the proboscis are of a sensiferous, tactile nature, a supposition which is again strengthened by the fact that amongst the Rhabdocœl Turbellarians an organ which may be called the forerunner of the Nemertean proboscis has been proved (**3**) to be the morphological equivalent of the foremost tip of the body, which, as an organ of delicate touch, has acquired the property of folding inwards. In Nemertines the everted proboscis is retracted in the same way as the tip of a glove finger would be if it were pulled backwards by a thread situated in the axis and attached to the tip. The comparison may be carried still further. The central thread just alluded to is represented in the Nemertean proboscis by that portion which is never everted, and the tip of the glove by the boundary between the evertible and non-evertible portion of the proboscis—a boundary which in the *Hoplonemertini* is marked by the presence of a pointed or serrated stylet. This stylet is thus situated terminally when the proboscis has reached its maximum eversion. It adds a decisively aggressive character to an organ the original significance of which, as we have seen, was tactile. This aggressive character has a different aspect in several genera which are destitute of a central stylet, but in which the surface that is turned outwards upon eversion of the proboscis is largely provided with nematocysts, sending the urticating rods of different sizes in all directions. In others this surface is beset with thick, glandular, adhesive papillæ.

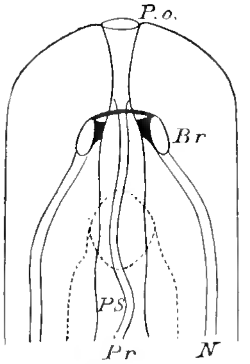

Fig. 3.—Anterior portion of the body of a Nemertine. *Br*, brain-lobes; *N*, lateral nerves; *PS*, proboscidian sheath; *Pr*, proboscis; *P.o.*, exterior opening through which the proboscis is everted. Œsophagus and mouth shown by dotted lines.

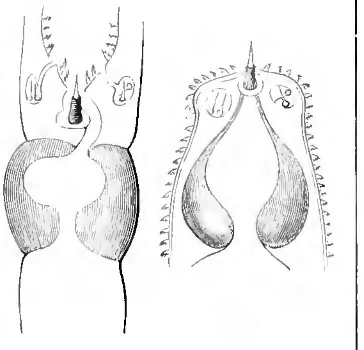

Fig. 4. Fig. 5.

Figs. 4, 5.—Proboscis with stylet, "reserve" sacs, and muscular bulb of a Hoplonemertine. Fig. 4 retracted; fig. 5 everted.

The comparison with the glove-finger is in so far insufficient as the greater portion of the non-evertible half of the proboscis is also hollow and clothed by glandular walls. Only at the very hindermost end does it pass into the so-called retractor-muscle (fig. 2), which is attached to the wall of the space (proboscidian sheath) in which the proboscis moves about. This retractor-muscle, indeed, serves to pull back with great rapidity the extruded proboscis, and is aided in its action by the musculature of the head. The extrusion itself depends entirely upon contraction of the muscular walls of the space just mentioned (proboscidian sheath). As it is (1) closed on all sides, and (2) filled with a corpuscular fluid, the contractions alluded to send this fluid to impinge against the anterior portion, where the proboscis, floating in its sheath, is attached with it to the muscular tissue of the head (fig. 3). Partial extrusion lessening the resistance in this region inevitably follows, and when further contractions of the walls of the sheath ensue total extrusion is the consequence. It is worthy of notice that in those Nemertines which make a very free use of their proboscis, and in which it is seen to be continually protruded and retracted, the walls of the proboscidian sheath are enormously muscular. On the other hand, they are much less considerably or even insignificantly so in the genera that are known to make a rather sparing use of their proboscis.

The proboscis, which is thus an eminently muscular organ, is composed of two or three, sometimes powerful, layers of muscles—one of longitudinal and one or two of circular fibres. In the posterior retractor the longitudinal fibres become united into one bundle, which, as noticed above, is inserted in the wall of the sheath. At the circular insertion of the proboscis in front of the brain the muscular fibres belonging to the anterior extremity of the body and those connected with the proboscis are very intimately interwoven, forming a strong attachment.

The proboscis broken off and expelled is generally reproduced, the posterior ribbon-like end of this reproduced portion again fusing with the walls of the sheath (**11**). There is reason to suppose that, when a wound is inflicted by the central stylet, it is envenomed by the fluid secreted in the posterior proboscidian region being at the same time expelled. A reservoir, a duct, and a muscular bulb in the region (fig. 4) where the stylet is attached serve for this purpose. The significance of two or more (in *Drepanophorus* very numerous) small sacs containing so-called "reserve" stylets resembling in shape that of the central dart is insufficiently known.

Fig. 6.—The armature from the proboscis of *Drepanophorus.*

The proboscidian sheath, which by its transverse contractions serves to bring about eversion of the proboscis in the way above traced, and the muscular walls of which were similarly noticed, is attached to the musculature of the head just in front of the ganglionic commissures (fig. 3). In nearly all Nemertines it extends backwards as far as the posterior extremity, just above the anus; in *Carinella* it is limited to the anterior body-region. The corpuscles floating in the fluid it contains are of definite shape, and in *Cerebratulus urticans* they are deep red from the presence of hæmoglobin. Internally the muscular layers are lined by an epithelium. In the posterior portion this epithelium in certain *Schizonemertea* has a more glandular appearance, and sometimes the interior cavity is obliterated by cell-proliferation in this region. Superiorly the sheath either closely adheres to the muscular body-wall, with which it may even be partly interwoven, or it hangs freely in the connective tissue which fills the space between the intestine and the muscular body-wall.

(*b*) *Cutaneous System.*—Externally in all species a layer of ciliated cells forms the outer investment. In it are, moreover, enclosed unicellular glands pouring their highly refracting contents, of a more or less rod-like shape, directly to the exterior. They appear to be the principal source of the mucus these animals secrete. In Schizonemertines these elements are separated by a thin homogeneous basement membrane (fig. 8) from the following,—that is, from a layer in which longitudinal muscular fibres are largely intermixed with tortuous glands, which by reason of their deeper situation communicate with the exterior by a much longer and generally very narrow duct. The pigment is also principally localized in this layer, although sometimes it is present even deeper down within the musculature. The passage from this tegumentary layer to the subjacent longitudinal muscular one is gradual, no membrane separating them. In *Carinella*, *Cephalothrix*, *Polia*, and the Hoplonemertines the two tegumentary layers with their different glandular elements are fused into one; a thick layer of connective tissue is situated beneath them (instead of between them) and keeps the entire cutaneous system more definitely separate from the muscular (figs. 7, 8).

(*c*) *Musculature and Connective Tissue.*—The muscular layers by which the body-wall is constituted have been very differently and to some extent confusingly described by the successive authors on Nemertean anatomy. There is sufficient reason for this confusion. The fact is that not only have the larger subdivisions a different arrangement and even number of the muscular layers, but even within the same genus, nay, in the same species, well-marked differences occur. Increase in size appears sometimes to be accompanied by the development of a new layer of fibres, whereas a difference in the method of preparation may give to a layer which appeared homogeneous in one specimen a decidedly fibrous aspect in another. Nevertheless there are three principal types under which the different modifications can be arranged. One of them is found in the two most primitively organized genera, *Carinella* and *Cephalothrix*, *i.e.*, an outer circular, a longitudinal, and an inner circular layer of muscular fibres (fig. 7). The second is common to all the Schizonemertines as well as to *Polia* and *Valencinia*, and also comprehends three layers, of which, however, two are longitudinal, viz., the external and the internal one, there being a strong circular layer between them (fig. 9). To the third type all the *Hoplonemertea* correspond; their muscular layers are only two, an external circular and an internal longitudinal one (fig. 8).

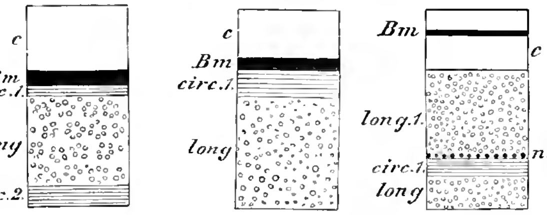

Fig. 7. Fig. 8. Fig. 9.

FIGS. 7-9.—The layers of the body-wall in *Carinella* (fig. 7), the *Hoplonemertea* (fig. 8), and the *Schizonemertea* (fig. 9). *c*, cellular tissue of the integument; *Bm*, basement membrane; *circ.* 1, outer circular, and *long*, longitudinal layer of muscular tissue; *circ.* 2, *long.* 1, additional circular and longitudinal layers of the same; *nl*, nervous layer.

The *Schizonemertea* thus appear to have developed an extra layer of longitudinal fibres internally to those which they inherited from more primitive ancestors, whereas the *Hoplonemertea* are no longer in possession of the internal circular layer, but have on the contrary largely developed the external circular one, which has dwindled away in the *Schizonemertea*. In only one instance has the present writer met with a thin exterior circular layer in a very large specimen of *Cerebratulus*; younger specimens of the same species did not show it. It is noticeable that Kefferstein (**9**) also observed four layers similarly arranged in one of the specimens of *Cerebratulus* which he investigated. The situation of the lateral nerve-stems in the different genera with respect to the muscular layers lends definite support to the interpretation of their homologies here given.

In *Carinella*, *Cephalothrix*, and *Polia*, as well as in all Hoplonemertines, the basement membrane of the skin already above alluded to is particularly strong and immediately applied upon the muscular layers. In the Schizonemertines there is a layer in which the cutaneous elements are largely represented below the thin basement membrane (fig. 8), between it and the bulk of the outer longitudinal muscles. The difference in the appearance of the basement membrane—sometimes wholly homogeneous, sometimes eminently fibrillar—can more especially be observed in differently preserved specimens of the genus *Polia*.

The connective tissue of the integument and basement membrane imperceptibly merges into that which surrounds the muscular bundles as they are united into denser and definite layers, and this is especially marked in those forms (*Akrostomum*) where the density of the muscular body-wall has considerably diminished, and the connective tissue has thus become much more prominent. It can then at the same time be observed, too, that the compact mass of connective tissue ("reticulum," Barrois) which lies between the muscular body-wall and the intestine (**1**) is directly continuous with that in which the muscular layers are imbedded. Nuclei are everywhere present. The omnipresence of this connective tissue excludes the idea of any true body cavity in Nemertines.

In *Polia* the connective tissue enclosed in the external muscular layer is eminently vacuolar,—all the intermediate stages between such cells in which the vacuole predominates and the nucleus is peripheral and those in which the granular protoplasm still entirely fills them being moreover present.

In addition to the musculature of the proboscis and proboscidian sheath, longitudinal muscular fibres are found in the walls of the œsophagus, whilst transverse ones are numerous and united into vertical dissepiments between the successive intestinal cæca, thus bringing about a very regular internal metamerization (**4**). The genital products develop in intermediate spaces similarly limited by these dissepiments and alternating with the digestive cæca.

(*d*) *Nervous System and Sense Organs.*—The nervous system of Nemertines presents several interesting peculiarities. As central organs we have to note the brain-lobes and the longitudinal lateral cords which form one continuous unsegmented mass of fibrous and cellular nerve-tissue. The fibrous nerve-tissue is more dense in the higher differentiated, more loose and spongy in the lower organized forms; the cellular nerve-tissue is similarly less compact in the forms that are at the base of the scale. No ganglionic swellings whatever occur in the course of the longitudinal cords. The brain must be looked upon as the anterior thickening of these cords, and at the same time as the spot where the two halves of the central nerve system intercommunicate. This is brought about by a double commissure, of which the ventral portion is considerably thicker than the dorsal, and which, together with the brain-lobes, constitutes a ring through which both proboscis and proboscidian sheath pass. The brain-lobes are generally four in number, a ventral and a dorsal pair, respectively united together by the above-mentioned commissures, and moreover anteriorly interfusing with each other, right and left. In *Carinella* this separation into lobes of the anterior thickenings of the cords has not yet commenced, the ventral commissure at the same time being extremely bulky. There is great probability that the central stems, together with the brain,

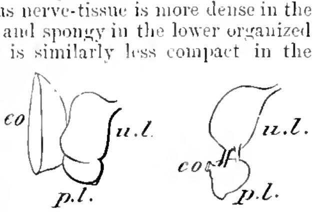

Fig. 10. Fig. 11.

FIGS. 10, 11.—Brain and lateral organ of a Schizonemertine (fig. 10) and a Hoplonemertine (fig. 11). *co*, exterior opening; *u.l.*, superior brain-lobe; *p.l.*, posterior brain-lobe.

must be looked upon as local longitudinal accumulations of nervous tissue in what was in more primitive ancestors a less highly differentiated nervous plexus, situated in the body-wall in a similar way to that which still is found in the less highly organized Cœlenterates. Such a nervous plexus indeed occurs in the body-wall of all Schizonemertines (**7**), sometimes even as a comparatively thick layer, situated, as are the nerve stems, between the external longitudinal and the circular muscles (fig. 9). In *Carinella*, where the longitudinal nerve-stems are situated exteriorly to the muscular layers, this plexus, although present, is much less dense, and can more fitly be compared to a network with wide meshes. In both cases it can be shown to be in immediate continuity with the coating of nerve-cells forming part of the longitudinal cords. It stretches forward as far as the brain, and in *Carinella* is again continued in front of it, whereas in the Schizonemertines the innervation of the anterior extremity of the head, in front of the brain, takes the form of more definite and less numerous branching stems. The presence of this plexus in connexion with the central stems, sending out nervous filaments amongst the muscles, explains the absence, both in Palæo- and Schizonemertines, of separate and distinct peripheral nerve stems springing from the central stems innervating the different organs and body-regions, the only exceptions being the nerves for the proboscis, those for the sense organs in the head, and the strong nerve pair (*n. vagus*) for the œsophagus. At the same time it renders more intelligible the extreme sensitiveness of the body-wall of the Nemertines, a local and instantaneous irritation often resulting in spasmodic rupture of the animal at the point touched.

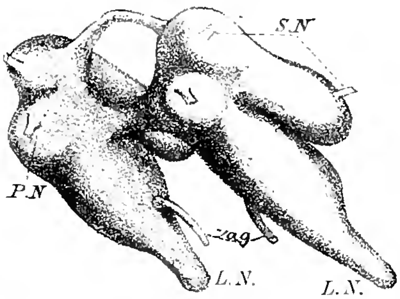

Fig. 12.—The brain of a Nemertine, with its lobes and commissures. *S.N.*, nerves to sensory apparatus; *P.N.*, nerves for proboscis; *vag.* nerves for œsophagus; *L.N.*, lateral nerve stems.

In the *Hoplonemertea*, where the longitudinal stems lie inside the muscular body-wall, definite and metamerically placed nerve branches spring from them and divide dichotomously in the different tissues they innervate. A definite plexus can here no longer be traced. In certain Hoplonemertines the lateral stems have been noticed to unite posteriorly by a terminal commissure, situated above the anus, the whole of the central nervous system being in this way virtually situated above the intestine. In others there is an approximation of the lateral stems towards the median ventral line (*Drepanophorus*); in a genus of Schizonemertines (*Langia*), on the other hand, an arrangement occurs by which the longitudinal stems are no longer lateral, but have more or less approached each other dorsally (**6**).

In addition to the nerves starting from the brain-lobes just now especially mentioned, there is a double apparatus which can hardly be treated of in conjunction with the sense organs, because its sensory functions have not been sufficiently made out, and which will therefore rather be considered along with the brain and central nervous system. This apparatus is usually known under the name of the lateral organs. To it belong (*a*) superficial grooves or deeper slits situated on the integument near the tip of the head, (*b*) nerve lobes in immediate connexion with the nervous tissue of the brain, and (*c*) ciliated ducts penetrating into the latter and communicating with the former. Embryology shows that originally these different parts are separately started, and only ultimately become united into one. Two lateral outgrowths of the foremost portion of the œsophagus, afterwards becoming constricted off, as well as two ingrowths from the epiblast, contribute towards its formation, at least as far as both Hoplo- and Schizonemertines are concerned. As to the *Palæonemertea*, their embryology has not yet been studied, and in the most primitive genus, *Carinella*, we do not find any lateral organs answering to the description above given. What we do find is a slight transverse furrow on each side of the head, close to the tip, but the most careful examination of sections made through the tissues of the head and brain shows the absence of any further apparatus comparable to that described above. Only in one species, *Carinella inexpectata*, a step in advance has been made, in so far as in connexion with the furrow just mentioned, which is here also somewhat more complicated in its arrangement, a ciliated tube leads into the brain, there to end blindly amidst the nerve-cells. No other intermediate stages have as yet been noticed between this arrangement and that of the *Schizonemertea*, in which a separate posterior brain-lobe receives a similar ciliated canal, and in which the œsophageal outgrowths have made their appearance and are coalesced with the nerve-tissue in the organ of the adult animal. The histological elements of this portion remain distinct both by transmitted light and in actual sections.

These posterior brain-lobes, which in all Schizonemertines are in direct continuity of tissue with the upper pair of principal lobes, cease to have this intimate connexion in the *Hoplonemertea*; and, although still constituted of (1) a ciliated duct, opening out externally, (2) nervous tissue surrounding it, and (3) histological elements distinctly different from the nervous, and most probably directly derived from the œsophageal outgrowths, they are nevertheless here no longer constantly situated behind the upper brain lobes and directly connected with them, but are found sometimes behind, sometimes beside, and sometimes before the brain-lobes. Furthermore, they are here severed from the principal lobes and connected with them by one or more rather thick strings of nerve-fibres. In some cases, especially when the lobes lie before the brain, their distance from it, as well as the length of these nervous connexions, has considerably increased.

With the significance of these parts we are still insufficiently acquainted. There appear to be analogous organs amongst Platyelminthes, but a careful comparative study is wanted. A partial comparison has been hazarded (**8**) with the anterior œsophageal outgrowths in *Balanoglossus* and *Amphioxus*, and for the Schizonemertines arguments have been adduced (**6**) to prove that here they have the physiological significance of a special respiratory apparatus for the central nervous tissue, which in all these forms is strongly charged with hæmoglobin. The hæmoglobin would, by its pre-eminent properties of fixing oxygen, serve to furnish the nerve system, which more than any other requires a constant supply, with the necessary oxygen. Such could hardly be obtained in any other way by those worms that have no special respiratory apparatus or delicately ramifying blood-vessels, and that live in mud and under stones, where the natural supply of freshly oxygenated sea-water is practically limited. Whether in the Hoplonemertines, where the blood fluid is often provided with hæmoglobiniferous disks, the chief functions of the side organs may not rather be a sensory one must be further investigated.

The exterior opening of the duct has been several times alluded to. In the Hoplonemertines it is generally situated towards the middle of a lateral transverse groove on either side of the head, as was noticed for *Carinella*, and as is also present in *Polia*. Generally a row of shorter grooves perpendicular to the first, and similarly provided with strong cilia, enlarges the surface of these furrows (fig. 14). In *Valencinia* there is nothing but a circular opening without furrow. In all Schizonemertines there is on each side of the head a longitudinal slit of varying length but generally considerable depth, in the bottom of which the dark red brain is very plainly visible by transparency. These slits are continued into the ciliated duct, being at the same time themselves very strongly ciliated. In life they are commonly rhythmically opened and shut by a wavy movement. They are the head slits (cephalic fissures, "Kopfspalten") so characteristic of this subdivision (figs. 10 and 13).

Fig. 13. Fig. 14.

Figs. 13, 14.—Lateral views of head of a Schizonemertine (fig. 13) with longitudinal slit, and of a Hoplonemertine (fig. 14) with transverse groove and furrows.

With respect to the sense organs of the Nemertines, we find that eyes are of rather constant occurrence, although many Schizonemertines living in the mud appear to be blind. The more highly organized species have often very numerous eyes (*Amphiporus*, *Drepanophorus*), which are provided with a spherical refracting anterior portion, with a cellular "vitreous body," with a layer of delicate radially arranged rods, with an outer sheath of dark pigment, and with a separate nerve-twig each, springing from a common or double pair of branches which leave the brain as *n. optici.* for the innervation of the eyes. Besides these more highly differentiated organs of vision, more primitive eyes are present in others down to simple stellate pigment specks without any refracting apparatus.

Organs of hearing in the form of capsules containing otoliths have only been very rarely observed, apparently only in *Hoplonemertea*.

As to the organ of touch, the great sensitiveness of the body has already been noticed, as well as the probable primary significance of the proboscis. Small tufts of tactile hairs or papillæ are sometimes observed in small number at the tip of the head (**11**); sometimes longer hairs, apparently rather stiff, are seen on the surface, very sparingly distributed between the cilia, and hitherto only in a very limited number of small specimens. They may perhaps be considered as sensory.

(*c*) *Digestive System.*—The anterior opening, the mouth, is situated ventrally, close to the tip of the head and in front of the brain in the *Hoplonemertea*, somewhat more backward and behind the brain in the other Nemertines. In most Schizonemertines it is found to be an elongated slit with corrugated borders; in the

Hoplonemertines it is smaller and rounded; in *Malacobdella* and *Akrostomum* it, moreover, serves for the extrusion of the proboscis, which emerges by a separate dorsal opening just inside the mouth. The œsophagus is the anterior portion of the digestive canal; its walls are folded longitudinally, comparatively thick, and provided with longitudinal muscular fibres. Two layers are specially obvious in its walls,—the inner layer bordering the lumen being composed of smaller ciliated cells, the outer thicker one containing numerous granular cells and having a more glandular character. Outside the wall of the œsophagus a vascular space has been detected (**11**) which is in direct continuity with the longitudinal blood-vessels. In certain cases, however, the walls of the œsophagus appear to be very closely applied to the muscular body-wall, and this vascular space thereby considerably reduced.

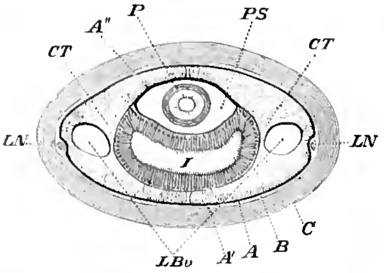

Fig. 15.

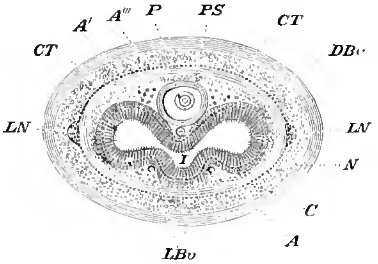

Fig. 16.

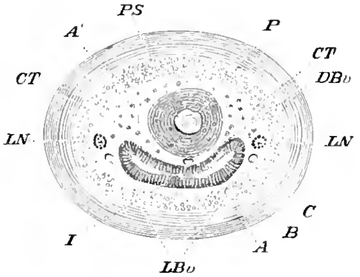

Fig. 17.

FIGS. 15-17.—Diagrammatic sections to show disposition of internal organs in *Carinella* (*Palæonemertea*), fig. 15, *Schizonemertea*, fig. 16, and *Hoplonemertea*, fig. 17. *C*, cellular portion of integument; *B*, basement membrane; *A*, circular muscular layer; *A'*, longitudinal do.; *A''*, second circular (in *Carinella*); *A'''*, second longitudinal (in *Schizonemertea*); *N*, nervous layer; *LN*, lateral nerves; *PS*, cavity of proboscidian sheath (the sheath itself of varying thickness); *P*, proboscis; *I*, intestine; *LBv*, lateral blood-vessel; *DBv*, dorsal do.; *CT*, connective tissue.

The posterior portion of the intestine is specially characterized by the appearance of the intestinal diverticula horizontally and symmetrically placed right and left and opposite to each other. Sometimes this region, into which the œsophagus leads, stretches forwards under the œsophagus (Hoplonemertines) for a certain distance, anteriorly terminating by a cul-de-sac. Cases of asymmetry or irregularity in the arrangement of the cæca, though sometimes occurring, are not normal. At the tip of the tail, where the growth of the animal takes place, the cæca are always eminently regular. So they are throughout the whole body in most of the Hoplonemertines. In *Carinella* they are generally deficient and the intestine straight; in young specimens of this species, however, they occur, though less regular and more in the form of incipient foldings by which the digestive surface is increased. The inner surface of the intestinal cæca is ciliated, the cæca themselves are sometimes—especially in the hindermost portion of the body—of a considerably smaller lumen than the intermediate genital spaces; sometimes, however, the reverse is the case, and in both cases it is the smaller lumen that appears enclosed between and suspended by the transverse fibres constituting the muscular dissepiments above mentioned.

The anus is situated terminally, the muscular body-wall through which the intestine must find its way outwards probably acting in this region the part of a sphincter. The lateral nerve stems mostly terminate on both sides in closest proximity to the anus; in certain species, however, they interfuse by a transverse connexion *above* the anus. The longitudinal blood-vessels do the same. The question has been raised whether the regular intestinal cæca of Nemertines might not be compared with those intestinal diverticula of the embryo *Amphioxus* which ultimately become the mesoblastic somites of the adult (**8**). This view would be a further extension of the views concerning the cœlom first propounded by Huxley.

(*f*) *Circulatory Apparatus.*—This consists of three longitudinal trunks, a median and two lateral ones. They are in direct connexion with each other both at the posterior and at the anterior end of the body. At the posterior end they communicate together by a T-shaped connexion in a simple and uniform way. Anteriorly there is a certain amount of difference in the arrangement. Whereas in the Hoplonemertines an arrangement prevails as represented in fig. 18, the lateral stems in the Schizonemertines, while entirely uniform all through the posterior portion of the body, no longer individually exist in the œsophageal region, but here dissolve themselves into a network of vascular spaces surrounding this portion of the digestive tract (**11**). The median dorsal vessel, however, remains distinct, but instead of continuing its course beneath the proboscidian sheath it is first enclosed by the ventral musculature of this organ, and still farther forwards it even bulges out longitudinally into the cavity of the sheath. Anteriorly it finally communicates with the lacunæ just mentioned, which surround the œsophagus, bathe the posterior lobes of the brain, pass through the nerve ring together with the proboscidian sheath, and are generally continued in front of the brain as a lacunar space in the muscular tissue, one on each side.

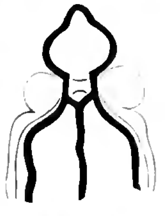

FIG. 18.—Diagram of the circulatory apparatus in the anterior body-region of a Hoplonemertine.

Special mention must be made of the delicate transverse vessels regularly connecting the longitudinal and the lateral ones. They are metamerically placed, and belong to the same metamer as the digestive cæca, thus alternating with the generative sacs. The blood fluid does not flow in any definite direction; its movements are largely influenced by those of the muscular body-wall. It is colourless, and contains definite corpuscles, which are round or elliptical, and in many Hoplonemertines are coloured red by hæmoglobin, being colourless in other species. The circulatory system of *Carinella* is considerably different, being more lacunar and less restricted to definite vascular channels. Two lateral longitudinal lacunæ form, so to say, the forerunners of the lateral vessels. A median longitudinal vessel and transverse connecting trunks have not as yet been detected. There are large lacunæ in the head in front of the ganglia.

(*g*) *Nephridia.*—Although these organs were already very well known to Max Schultze (**14**), their presence in Nemertines was repeatedly and seriously disputed until Von Kennel (**10**) definitely proved their existence and gave details concerning their histology. With the exception of a few genera where they have not as yet been discovered (*Carinella*), one pair of nephridia appears to be very generally present. They essentially consist of a complex coiled tube, one on each side of the œsophagus (fig. 1), communicating with the exterior by a duct piercing the body-wall. The two openings of the nephridia are situated sometimes more towards the ventral, at other times more towards the dorsal side. Even in the larger Schizonemertines these pores are only a few millimetres behind the mouth region. Internal funnel-shaped openings, although sought for, have as yet not been detected. The coiled tubes extend both forwards and backwards of the external opening, by far the greater portion being situated backwards. The anterior coils reach forwards till in the immediate vicinity of the posterior brain-lobes. The coils are tubiform, with an internal lumen, only one layer of rather large cells constituting the walls. These cells are ciliated; in some transparent species the internal ciliary movement can be observed during life. In transverse sections the nephridia can be shown to be generally situated in the region limited by (1) the proboscidian sheath, (2) the upper wall of the intestine, (3) the muscular body-wall. No trace of nephridia is found posterior to the œsophagus.

(*h*) *Generative System.*—In the Nemertines the sexes are separate, with only very few exceptions (**12**) (*Tetrastemma hermaphroditica*, Marion). The generative products are contained in separate pouches placed metamerically in the way noticed above in treating of the digestive system. They are conveyed outwards along narrow canals, one pair for each metamer piercing the muscular body-wall, and visible on the outside in mature individuals as minute light-coloured specks. The ova and spermatozoa, when mature, present no peculiarities. As the ova are in many species deposited in a gelatinous tube secreted by the body-walls, in which they are arranged (three or more together) in flask-shaped cavities, impregnation must probably take place either before or at the very moment of their being deposited. The exact mode has not yet been noticed. Another point not yet sufficiently settled is the oogenesis in Nemertines. In several cases the ova appear to originate directly as the lining of the generative pouches, but the exact part which the mesoblastic connective tissue plays, both with regard to these pouches and to the generative products themselves, remains yet to be settled.

Prosorhochmus claparedii is a viviparous form.

Development.

DEVELOPMENT.—The embryology of the Nemertines offers some very remarkable peculiarities. Our knowledge of the development of the most primitive forms is very scanty. Of that of *Carinella* absolutely nothing is known. On *Cephalothrix* we have observations, in certain respects contradictory. Both *Schizo-* and *Hoplonemertea* have been more exhaustively studied, the first, as was noticed above, being characterized by peculiar larval forms, the second developing without metamorphosis.

The larva of *Cerebratulus* is called the pilidium. In exterior shape it resembles a helmet with spike and ear-lobes, the spike being a strong and long flagellum or a tuft of long cilia, the ear-lobes lateral ciliated appendages (fig. 19). It encloses the primitive alimentary tract. Two pairs of invaginations of the skin, which originally are called the prostomial and metastomial disks, grow round the intestine, finally fuse together, and form the skin and muscular body-wall of the future Nemertine, which afterwards becomes ciliated, frees itself from the pilidium investment, and developes into the adult worm without further metamorphosis (**2, 13**).

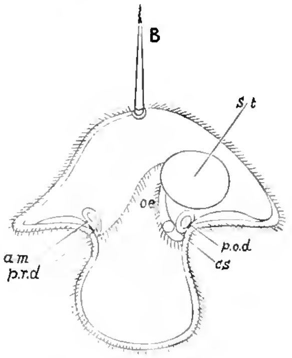

FIG. 19.—Pilidium larva. *B*, bunch of cilia or flagellum; *œ*, œsophagus; *st*, stomach; *cs*, œsophageal outgrowth for lateral organ; *am*, amnion; *pr.d.*, prostomial disk; *po.d.*, metastomial disk.

The eggs of these species are not enveloped by such massive gelatinous strings as are those of the genus *Lineus*. In the latter we find the young Nemertines crawling about after a period of from six to eight weeks, and probably feeding upon a portion of this gelatinous substance, which is found to diminish in bulk. In accordance with these more sedentary habits during the first phases of life, the characteristic pilidium larva, which is so eminently adapted for a pelagic existence, appears to have been reduced to a close-fitting exterior layer of cells, which is striped off after the definite body-wall of the Nemertine has similarly originated out of four ingrowths from the primary epiblast. To this reduced and sedentary pilidium the name of "larva of Desor" has been given (**1**).

In the *Hoplonemertea*, as far as they have been investigated, a direct development without metamorphosis has been observed. It appears probable that this is only a further simplification of the more complicated metamorphosis described above.

As to the development of the different organs, there is still much that remains doubtful. The hypoblast in some forms originates by invagination, in others by delamination. The proboscis is an invagination from the epiblast; the proboscidian sheath appears in the mesoblast, but is perhaps originally derived from the hypoblast. The origin of the lateral organs has already been noticed; that of the nerve system is essentially epiblastic.

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(**11**) W. C. MacIntosh, *A Monograph of British Annellida: I. Nemerteans*, Ray Society, 1873–74.

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(**13**) E. Metschnikoff, "Studien über die Entwickelung der Echinodermen und Nemertinen," *Mém. de l'Acad. Imp. de St. Petersb.*, xiv., 1869.

(**14**) Max Schultze, *Beiträge zur Naturgeschichte der Turbellarien*, Greifswald, 1851, and *Zeitschr. für wissensch. Zool.*, iv., 1852.

(A. A. W. H.)

ROTIFERA

(By Prof. A. G. Bourne, Presidency College, Madras.)

THE *Rotifera* or *Rotatoria* form a small, in many respects well-defined, but somewhat isolated class of the animal kingdom. They are here treated of separately, partly on account of the difficulty of placing them in one of the large phyla, partly on account of their special interest to microscopists.

Now familiarly known as "wheel animalcules" from the wheel-like motion produced by the rings of cilia which generally occur in the head region, the so-called rotatory organs, they were first discovered by Leeuwenhoek (**1**),[1] to whom we also owe the discovery of *Bacteria* and ciliate *Infusoria*. Leeuwenhoek described the *Rotifer vulgaris* in 1702, and he subsequently described *Melicerta ringens* and other species. A great variety of forms were described by other observers, but they were not separated as a class from the unicellular organisms (*Protozoa*) with which they usually occur until the appearance of Ehrenberg's great monograph (**2**), which contained a mass of detail regarding their structure. The classification there put forward by Ehrenberg is still widely adopted, but numerous observers have since added to our knowledge of the anatomy of the group (**3**). At the present day few groups of the animal kingdom are so well known to the microscopist, few groups present more interesting affinities to the morphologist, and few multicellular animals such a low physiological condition.

General Anatomy.—The *Rotifera* are multicellular animals of microscopic size which present a cœlom. They are bilaterally symmetrical and present no true metameric segmentation. A head region is generally well marked, and most forms present a definite tail region. This tail region has been termed the "pseudopodium." It varies very much in the extent to which it is developed. It attains its highest development in forms like *Philodina*, which affect a leech-like method of progression and use it as a means of attachment. We may pass from this through a series of forms where it becomes less and less highly developed. In such forms as *Brachionus* it serves as a directive organ in swimming, while in a large number of other forms it is only represented by a pair of terminal styles or flaps. In the sessile forms it becomes a contractile pedicle with a suctorial extremity. A pseudopodium is entirely absent in *Asplanchna*, *Triarthra*, *Polyarthra*, and a few other genera. The pseudopodium, when well developed, is a very muscular organ, and it may contain a pair of glands (fig. 2, A, *gl*) which secrete an adhesive material.

The surface of the body is covered by a firm homogeneous structureless cuticle. This cuticle may become hardened by a further development of chitin, but no calcareous deposits ever take place in it. The cuticle remains softest in those forms which live in tubes. Among the free-living forms the degree of hardening varies considerably. In some cases contraction of the body merely throws the cuticle into wrinkles (*Notommata*, *Asplanchna*); in others definite ring-like joints are produced which telescope into one another during contraction; while in others again it becomes quite firm and rigid and resembles the carapace of one of the *Entomostraca*; it is then termed a "lorica." The lorica may be prolonged at various points into spines, which may attain a considerable length. The surface may be variously modified, being in some cases smooth, in others marked, dotted, ridged, or sculptured in various ways (fig. 1, K). The curved spines of *Philodina aculeata* (fig. 1, G) and the long rigid spines of *Triarthra* are further developments in this direction. The so-called setæ of *Polyarthra* on the other hand are more complex in nature, and are moved by muscles, and thus approach the "limbs" of *Pedalion*.

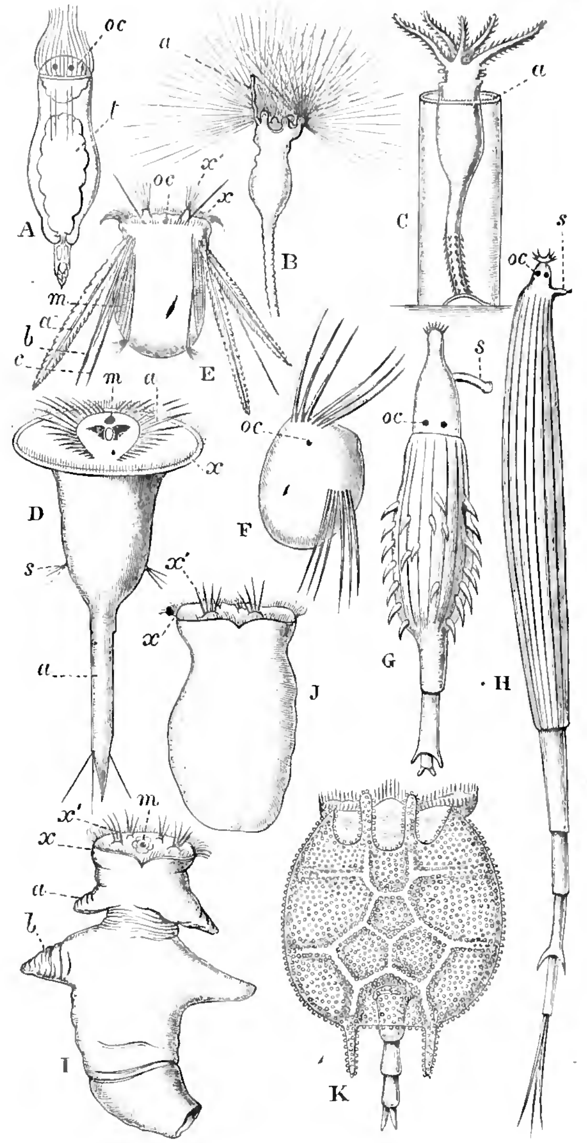

FIG. 1.—A, *Floscularia campanulata*, an adult male, drawn from a dead specimen (after Hudson): *t*, testis; *oc*, eye-spots. B, *Floscularia appendiculata*, an adult female (after Gegenbaur): *a*, the ciliated flexible proboscis. C, *Stephanoceros eichhornii*: *a*, the urceolus. D, *Microcodon clavus*, ventral view (after Grenacher): *m*, mouth; *a*, bristles; *x*, architroch; *s*, lateral sense-organs. E, *Polyarthra platyptera*: *oc*, eye-spot; *x'*, isolated tufts representing a cephalotroch; *x*, branchiotroch; *a*, *b*, and *c*, three pairs of appendages which are moved by the muscles *m*. F, another figure of *Polyarthra*, to show the position which the appendages may take up. G, *Philodina aculeata*: *oc*, eye-spots; *s*, calcar. H, *Actinurus neptunius*: *oc*, eye-spots; *s*, calcar. I, *Asplanchna sieboldii*, male, viewed from the abdominal surface: *a*, anterior short arms; *b*, posterior longer arms; *m*, mouth; *x'*, cephalotrochic tufts; *x*, branchiotroch. J, *Asplanchna sieboldii*, female; letters as before. K, *Noteus quadricornis*, to show the extent to which the lorica may become sculptured. (All, except where otherwise stated, from Pritchard.)

Several genera present an external casing or sheath or tube which is termed an "urceolus." In *Floscularia* and *Stephanoceros* the urceolus is gelatinous and perfectly hyaline; in *Conochilus* numerous individuals live in such a hyaline urceolus arranged in a radiating manner. The urceolus, which is secreted by the animal itself, may become covered with foreign particles, and in one species, the well-known *Melicerta ringens*, the animal builds up its urceolus with pellets which it manufactures from foreign

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[1] These numbers refer to the bibliography at p. 93.

particles, and deposits in a regular oblique or spiral series, and which are cemented together by a special secretion. The urceolus serves as a defence, as the animal can by contracting its stalk withdraw itself entirely within the tube.

Locomotor Organs.—While, as mentioned above, several genera or individual species present long spines, these become movable, and may be spoken of as appendages, in two genera only. In *Polyarthra* (fig. 1, E, F) there are four groups of processes or plumes placed at the sides of the body, each of which groups can be separately moved up and down by means of muscular fibres attached to their bases, which project into the body. The processes themselves are unjointed and rigid. In *Pedalion* (fig. 3), a remarkable form discovered by Dr C. J. Hudson in 1871 (**12**, **13**, **14**, and **15**), and found in numbers several times since, these appendages have acquired a new and quite special development. They are six in number. The largest is placed ventrally at some distance below the mouth. Its free extremity is a plumose fan-like expansion (fig. 3, A, *a*, and H). It is (in common with the others) a hollow process into which run two pairs of broad, coarsely transversely striated muscles. Each pair has a single insertion on the inner wall—the one pair near the free extremity of the limb, the other near its attachment; the bands run up, one of each pair on each side and run right round the body forming an incomplete muscular girdle, the ends approximating in the median dorsal line. Below this point springs the large median dorsal limb, which terminates in groups of long setæ. It presents a single pair of muscles attached along its inner wall which run up and form a muscular girdle round the body in its posterior third. On each side is attached a superior dorso-lateral and an inferior ventro-lateral appendage, each with a fan-like plumose termination consisting of compound hairs, found elsewhere only among the *Crustacea*; each of these is moved by muscles running upwards towards the neck and arising immediately under the trochal disk, the inferior ventro-lateral pair also presenting muscles which form a girdle in the hind region of the body. Various other muscles are present: there are two complete girdles in the neck region immediately behind the mouth; there are also muscles which move the hinder region of the body. In addition to these the body presents various processes which are perhaps some of them unrepresented in other Rotifers. In the median dorsal line immediately below the trochal disk there is a short conical process presenting a pair of muscles which render it capable of slight movement. From a recess at the extremity of this process spring a group of long setose hairs the bases of which are connected with a filament probably nervous in nature. This doubtless represents a structure found in many Rotifers, and variously known as the "calcar," "siphon," "tentaculum," or "antenna." This calcar is double in *Tubicolaria* and *Melicerta*. It is very well developed in the genera *Rotifer*, *Philodina*, and others, and is, when so developed, slightly retractile. It appears to be represented in many forms by a pit or depression set with hairs. The calcar has been considered both as an intromittent organ and a respiratory tube for the admission of water. It is now, however, universally considered to be sensory in nature. Various forms present processes in other parts of the body which have doubtless a similar function, *e.g.*, *Microcodon* (fig. 1, D, *s*) with its pair of lateral organs. *Pedalion* presents a pair of ciliated processes in the posterior region of the body (fig. 3, B, C, and D, *e*), which it can apparently use as a means of attachment; Dr Hudson states that he has seen it anchored by these and swimming round and round in a circle. They possibly re-

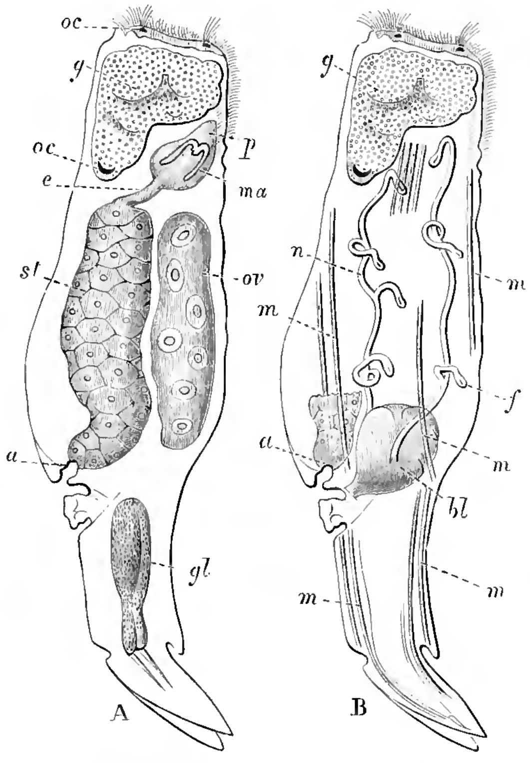

FIG. 2.—*Floscularia appendiculata.* A and B represent the same animal, some of the organs being shown in one figure and some in the other. *oc*, eye-spots; *g*, nerve ganglion; *p*, pharynx (the mouth should be shown opening opposite the letter); *ma*, the mastax; *e*, œsophagus; *st*, stomach; *a*, anus, opening the cloaca; *gl*, mucous glands in the pseudopodium; *n*, nephridia; *f*, flame-cells; *bl*, contractile vesicle; *m*, *m*, muscles.

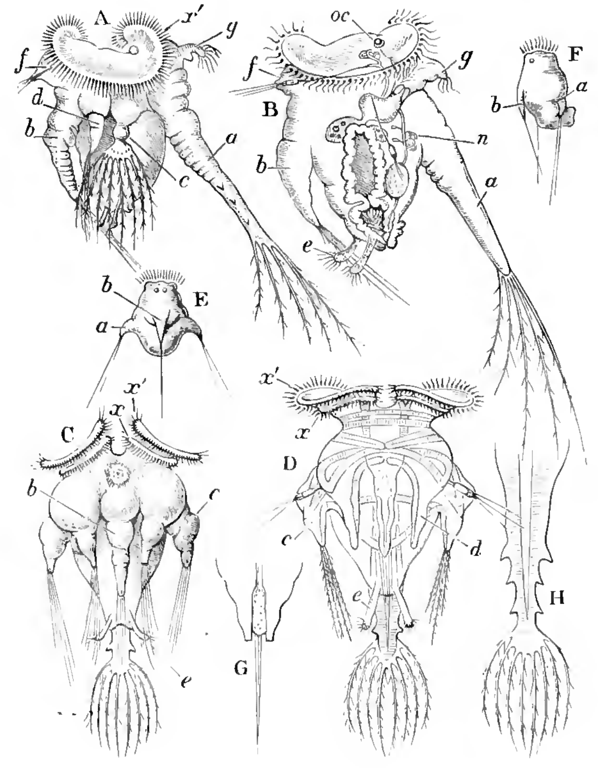

FIG. 3.—*Pedalion mira.* A, Lateral surface view of an adult female: *a*, median ventral appendage; *b*, median dorsal appendage; *c*, inferior ventro-lateral appendage; *d*, superior dorso-lateral appendage; *f*, dorsal sense-organ (calcar); *g*, "chin;" *x*, cephalotroch. B, lateral view, showing the viscera: *oc*, eye-spots; *n*, nephridia; *e*, ciliated processes, probably serving for attachment; other letters as above. C, ventral view: *x'*, cephalotroch; *x*, branchiotroch; other letters as above. D, ventral view, showing the musculature (*cf.* text). E, dorsal view of a male: *a*, lateral appendages; *b*, dorsal appendage. F, lateral view of a male. G, enlarged view of the sense-organ marked *f*. H, enlarged view of the median ventral appendage. (All after Hudson.)

present the flaps found on the tail of other forms. *Pedalion* also has a small ciliated muscular process (fig. 3, A, *g*) placed immediately below the mouth, and termed a "chin," which appears to be merely a greater development of a sort of lower lip which occurs in many Rotifers.

Muscular System.—All the *Rotifera* present a muscular system which is generally very well developed. Transverse striation occurs among the fibres to a varying extent, being well marked in cases where the muscle is much used. The muscles which move the body as a whole are arranged as circular and longitudinal series, but they are arranged in special groups and do not form a complete layer of the body-wall as in the various worms. Some of the longitudinal muscles are specially developed in connexion with the tail or pedicle. Other muscles are developed in connexion with special systems of organs,—the trochal disks, the jaw apparatus, and the reproductive system. The muscles in connexion with the trochal disk serve to protrude or withdraw it, and to move it about, when extruded, in various directions. The protrusion is probably, however, generally effected by the elasticity of the integument coming into play during the relaxation of the retractor muscles, and by a general contraction of the body wall. The tentaculiferous apparatus of *Polyzoa* and *Gephyrea* is protruded in the same manner.

Trochal Disk.—This structure is the peculiar characteristic of the class. It is homologous with the ciliated bands of the larvæ of Echinoderms, Chætopods, Molluscs, &c., and with the tentaculiferous apparatus of *Polyzoa* and *Gephyrea*, and has been termed in common with these a "velum." This velum presents itself in various stages of complexity. It is found as a single circum-oral ring (*pilidium*), as a single præ-oral ring (Chætopod larvæ), or as a single præ-oral ring coexisting with one or more post-oral rings (Chætopod larvæ, Holothurian larvæ). We may here assume that the ancestral condition was a single circum-oral ring associated with a terminal mouth and the absence of an anus, and that the existence of other rings posterior to this is an expression of metameric segmentation, *i.e.*, a repetition of similar parts. With the development of a prostomiate condition a certain change necessarily takes place in the position of this band: a portion of it comes to lie longitudinally; but it may still remain a single band, as in the larva of many Echinoderms. How have the other above-mentioned conditions of the velum come about? How has the præ-oral band been developed? Two views have been held with regard to this question. According to the one view, the fact whether the single band is a præ-oral or a post-oral one depends upon the position in which the anus is about to develop. If the anus develops in such a position that mouth and anus lie on one and the same side of the band, the latter becomes præ-oral; if, however, the anus develops so that the mouth and anus lie upon opposite sides of the band, the band becomes post-oral. If we hold this view we must consider any second band, whether præ- or post-oral, to arise as a new development. The other view premises that the anus always forms so as to leave the primitive ring or "architroch" post-oral, *i.e.*, between mouth and anus. Concurrently with the development of a prostomium this architroch somewhat changes its position and the two lateral portions come to lie longitudinally; these may be supposed to have met in the median dorsal line and to have coalesced so as to leave two rings—the one præ-oral (a "cephalotroch"), the other post-oral (a "branchiotroch"); this latter may atrophy, leaving the single præ-oral ring, or it may become further developed and thrown into more or less elaborate folds. The existing condition of the trochal disk or velum in the *Rotifera* seems to the writer of this article to bear out the latter view as to the way in which modifications of the velum may have come about.

In its simplest condition it forms a single circum-oral ring, as in *Microcodon* (fig. 1, D). The structures at the sides of the mouth in this form are stated to be bristles, and have therefore nothing to do with the velum (fig. 4, A, *p*). This simple ring may become thrown into folds, so forming a series of processes standing up around the mouth; this is the condition in *Stephanoceros* (fig. 4, B, *p*). There are, however, but few forms presenting this simple condition; and it must be remembered that the evidence for the assumption here made, that this is a persistent architroch and not a branchiotroch persisting where a cephalotroch has vanished, is not at present conclusive. This band, may, while remaining single and perfectly continuous, become prolonged around a lobe overhanging the mouth—a prostomium. This condition occurs in *Philodina* (fig. 4, E, F, *p*); the two sides of the post-oral ring do not meet dorsally, but are carried up and are continuous with the row of cilia lining the "wheels." There is thus one continuous ciliated band, a portion of which runs up in front of the mouth. This condition corresponds to that of the Auricularian larva. The folding of the band has become already somewhat complicated; a hypothetical intermediate condition is shown in fig. 4, C, D. The next stage in the advancing complexity is that the prostomial portion of the band (fig. 4, G, H, *p'*) becomes separated as a distinct ring, a cephalotroch; we find such a stage in *Lacinularia* (fig. 4, G, H), where both cephalotroch and branchiotroch remain fairly simple in shape. In *Melicerta* (fig. 4, I, J) both cephalotroch and branchiotroch are thrown into folds. Lastly, we find that in such forms as *Brachionus* the cephalotroch becomes first convoluted and then discontinuous (fig. 4, K, L, *c*), and further it may become so reduced as to be represented only by a few isolated tufts, as in *Asplanchna* (fig. 1, I, *x* and *x'*); in such a form as *Lindia* (fig. 6, C) the branchiotroch has vanished and the cephalotroch has become reduced to the two small patches at the sides of the head.

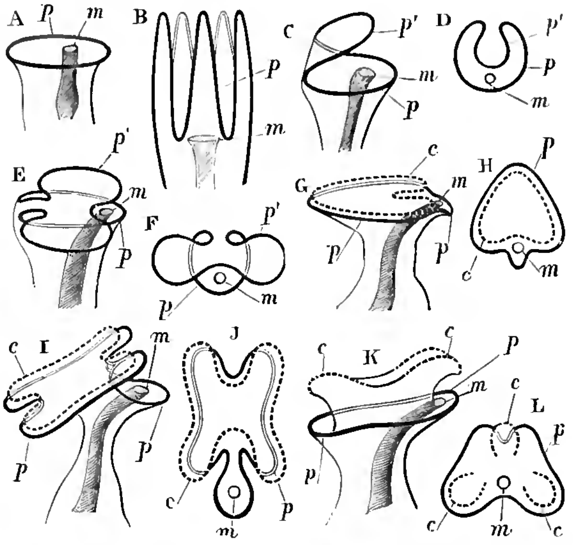

Fig. 4.—Diagrams of the Trochal Disk. A, *Microcodon*. B, *Stephanoceros*; the mouth lies in the centre of a group of tentacles. C, hypothetical intermediate form between *Microcodon* and *Philodina*, showing the development of a prostomial portion of the velum. D, dorsal view of the same. E, *Philodina*. F, dorsal view of the same. G, *Lacinularia*; the dotted line represents the portion of the velum which has become separated as a special ring—a cephalotroch. H, dorsal view of the same. I, *Melicerta*; the dotted line represents the cephalotroch; both this and the branchiotroch have become thrown into folds. J, dorsal view of the same. K, *Brachionus*; there is a large præ-oral lobe with three ciliated regions, shown by the dotted lines *c*, *c*, a discontinuous cephalotroch. L, dorsal view of the same.

m, mouth; *p*, *p'*, velum; *p*, architroch; *p'*, portion of the architroch which becomes carried forward to line the prostomial region, but does not become separated; *c*, cephalotroch. (Original.)

The trochal apparatus serves the *Rotifera* as a locomotive organ and to bring the food particles to the mouth; the cilia work so as to produce currents towards the mouth.

Digestive System.—This consists of the following regions:—(1) the oral cavity; (2) the pharynx; (3) the œsophagus; (4) the stomach; (5) the intestine, which terminates in an anus. The anus is absent in one group.

The pharynx contains the *mastax* with its teeth; these are calcareous structures, and are known as the *trophi*. In a typical mastax (8, 9) (*Brachionus*, fig. 5, A) there are a median anvil or *incus* and two hammer-like portions, *mallei*. The incus consists of two *rami* (*e*) resting upon a central *fulcrum* (*f*); each malleus consists of a handle or *manubrium* (*c*) and a head or *uncus* (*d*), which often presents a comb-like structure. Fig. 5 shows some of the most important modifications which the apparatus may exhibit. The parts may become very slender, as in *Diglena forcipata* (fig. 5, B); the mallei may be absent, as in *Asplanchna* (fig. 5, C), the rami being highly developed into curved forceps and movable one on the other; or, the manubria being absent and the fulcrum rudimentary, the rami may become massive and subquadratic, as in *Philodina* (fig. 5, D). All the true Rotifers possess a mastax. Ehrenberg's group of the *Agomphia* consisted of a heterogeneous collection of forms,—*Ichthydium* and *Chætonotus* being *Gastrotricha*, and *Cyphonautes*

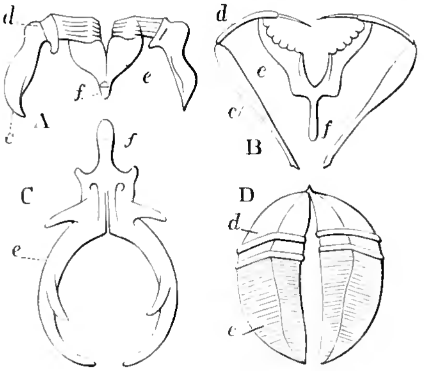

Fig. 5.—Trophi of various forms: A, *Brachionus*; B, *Diglena forcipata*; C, *Asplanchna*; D, *Philodina*. *f*, fulcrum, and *e*, *e*, rami, forming the incus; *c*, manubrium, and *d*, uncus, forming the malleus. (After Hudson.)

a Polyzoan larva, while *Enteroplea* is probably a male Rotifer, and, like the other males, in a reduced condition. There is no reason for considering this mastax as the homologue of either the gastric mill of Crustaceans on the one hand or the teeth in the Chætopods' pharynx on the other; it is merely homoplastic with these structures, but has attained a specialized degree of development. Both the pharynx and the œsophagus which follows it are lined with chitin. The œsophagus varies in length and in some genera is absent (*Philodinadæ*), the stomach following immediately upon the pharynx. The stomach is generally large; its wall consists of a layer of very large ciliated cells, which often contain fat globules and yellowish-green or brown particles, and outside these a connective tissue membrane; muscular fibrillæ have also been described. Very constantly a pair of glands open into the stomach, and probably represent the hepato-pancreatic glands of other Invertebrates.

Following upon the stomach there is a longer or shorter intestine, which ends in the cloaca. The intestine is lined by ciliated cells. In forms living in an urceolus the intestine turns round and runs forward, the cloaca being placed so as to debouch over the margin of the urceolus. The cloaca is often very large; the nephridia and oviducts may open into it, and the eggs lodge there on their way outwards; they are thrown out, as are the fæcal masses, by an eversion of the cloaca. *Asplanchna*, *Notommata sieboldii*, and certain species of *Ascomorpha* are said to be devoid of intestine or anus, excrementitious matters being ejected through the mouth (**11**).

Nephridia.—The cœlom contains a fluid in which very minute corpuscles have been detected. There is no trace of a true vascular system. The nephridia (fig. 2, B, *n*) present a very interesting stage of development. They consist of a pair of tubules with an intracellular lumen running up the sides of the body, at times merely sinuous, at others considerably convoluted. From these are given off at irregular intervals short lateral branches, each of which terminates in a flame-cell precisely similar in structure to the flame-cells found in Planarians, Trematodes, and Cestodes; here as there the question whether they are open to the cœlom or not must remain at present undecided. At the base these tubes open either into a permanent bladder which communicates with the cloaca or into a structure presenting apparently no advance in its development upon the contractile vacuole of a ciliate Infusorian.

Nervous System and Sense-Organs.—Various structures have been spoken of as nervous which are now acknowledged to have been erroneously so described (**18**). There is a supra-œsophageal ganglion which often attains considerable dimensions, and presents a lobed appearance (fig. 2, A and B, *g*). Connected with this are the eye-spots, which are seldom absent. Where these are most highly developed a lens-like structure is present, produced by a thickening of the cuticle. In the genus *Rotifer* and other forms these are placed upon the protrusible portion of the head, and so appear to have different positions at different moments. The number of eye-spots varies from one to twelve or more. They are usually red, reddish-brown, violet, or black in colour. Other structures are found which doubtless act as sense-organs. The calcar above-mentioned generally bears at its extremity stiff hairs which have been demonstrated to be in connexion with a nerve fibril. On the ventral surface of the body just below the mouth a somewhat similar structure is often developed—the chin. There are besides at times special organs, like the two lateral organs in *Microcodon* (fig. 1, D, *s*), which no doubt in common with the calcar and chin have a tactile function.

Reproductive Organs and Development.—The *Rotifera* were formerly considered to be hermaphrodite, but, while the ovary was always clear and distinct, there was always some difficulty about the testis, and various structures were put forward as representing that organ. One by one, however, small organisms have been discovered and described as the males of certain species of Rotifers, until at the present time degenerated males are known to occur in all the families except that of the *Philodinadæ*. The male Rotifers are provided with a single circlet of cilia (a peritroch), a nerve ganglion, eye-spots, muscles, and nephridial tubules all in a somewhat reduced condition, but there is usually no trace of mouth or stomach, the main portion of the body being occupied by the testicular sac. There is an aperture corresponding with the cloaca of the female, where the testis opens into the base of an eversible penis. The males of *Floscularia* are shown in fig. 1. The male of *Pedalion mira* possesses rudimentary appendages. The ovary is usually a large gland lying beside the stomach connected with a short oviduct which opens into the cloaca. The ova often present a reddish hue (*Philodina roseola*, *Brachionus rubens*), due doubtless, like the red colour of many Crustacean ova, to the presence of tetronerythrin.

Up to the present our embryological knowledge of the group is very incomplete. Many Rotifers are known to lay winter and summer eggs of different character. The winter eggs are provided with a thick shell and probably require fertilization. Two or three of them are often carried about attached to the parent (*Brachionus*, *Notommata*), but they are usually laid and fall into the mud, there to remain till the following spring. The summer eggs are of two kinds, the so-called male and female ova, both of which are stated to develop parthenogenetically. They may be carried about in large numbers in the cloaca or oviduct or attached to the body of the parent. The female ova give rise to female and the male ova to male individuals. Male individuals are only formed in the autumn in time to fertilize the winter ova.

Habitat and Mode of Life.—The *Rotifera* are distributed all over the earth's surface, inhabiting both fresh and salt water. The greater number of species inhabit fresh water, occurring in pools, ditches, and streams. A few species will appear in countless numbers in infusions of leaves, &c., but their appearance is generally delayed until the putrefaction is nearly over. Species of *Rotifer* and *Philodina* appear in this way. A few marine forms only have been described—*Brachionus mülleri*, *B. heptatonus*, *Synchæta baltica*, and others.

A few forms are parasitic. *Albertia* lives in the intestine of the earthworm; a form has been described as occurring in the body-cavity of *Synapta*; a small form was also observed to constantly occur in the velar and radial canals of the freshwater jelly-fish, *Limnocodium*. *Notommata parasitica* leads a parasitic existence within the hollow spheres of *Volvox globator*, sufficient oxygen being given off by the *Volvox* for its respiration.

Many Rotifers exhibit an extraordinary power of resisting drought. Various observers have dried certain species upon the slide, kept them dry for a certain length of time, and then watched them come to life very shortly after the addition of a drop of water. The animal draws itself together, so that the cuticle completely protects all the softer parts and prevents the animal itself from being thoroughly dried. This process is not without parallel in higher groups; *e.g.*, many land snails will draw themselves far into the shell, and secrete a complete operculum, and can remain in this condition for an almost indefinite amount of time. The eggs are also able to withstand drying, and are probably blown about from place to place. The *Rotifera* can bear great variations of temperature without injury.

Since their removal from among the *Protozoa* various attempts have been made to associate the *Rotifera* with one or other large phylum of the animal kingdom. Huxley, insisting upon the importance of the trochal disk, put forward the view that they were "permanent Echinoderm larvæ," and formed the connecting link between the *Nemertidæ* and the Nematoid worms. Ray Lankester proposed to associate them with the *Chætopoda* and *Arthropoda* in a group *Appendiculata*, the peculiarities in the structure of *Pedalion* forming the chief reason for such a classification. There is, however, no proof that we thus express any genetic relationship. The well-developed cœlom, absence of metameric segmentation, persistence of the trochal disk in varying stages of development, and the structure of the nephridia are all characters which point to the *Rotifera* as very near representatives of the common ancestors of at any rate the *Mollusca*, *Arthropoda*, and *Chætopoda*. But the high development of the mastax, the specialized character of the lorica in many forms, the movable spines of *Polyarthra*, the limbs of *Pedalion*, and the lateral appendages of *Asplanchna*, the existence of a diminutive male, the formation of two varieties of ova, all point to a specialization in the direction of one or other of the above mentioned groups. Such specialization is at most a slight one, and does not justify the definite association of the *Rotifera* in a single phylum with any of them.

Classification.—The following classification has been recently put forward by Dr C. T. Hudson (**19**).

CLASS ROTIFERA.

Order 1.—**Rhizota.**

Fixed forms; foot attached, transversely wrinkled, non-retractile truncate.

Fam. 1. FLOSCULARIADÆ. *Floscularia*, *Stephanoceros*.
Fam. 2. MELICERTADÆ. *Melicerta*, *Cephalosiphon*, *Megalotrocha*, *Limnias*, *Æcistes*, *Lacinularia*, *Conochilus*.

Order II.—Bdelloida.

Forms which swim and creep like a leech; foot retractile jointed, telescopic, termination furcate.

Fam. 3. PHILODINADÆ. *Philodina, Rotifer, Callidina.*

Order III.—Ploïma.

Forms which swim only.

Grade A. ILLORICATA.

Fam. 4. HYDATINADÆ. *Hydatina, Rhinops.*
Fam. 5. SYNCHÆTADÆ. *Synchæta, Polyarthra.*
Fam. 6. NOTOMMATADÆ. *Notommata, Diglena, Furcularia, Scaridium, Pleurotrocha, Distemma.*
Fam. 7. TRIARTHRADÆ. *Triarthra.*
Fam. 8. ASPLANCHNADÆ. *Asplanchn*

Grade B. LORIÇATA.

Fam. 9. BRACHIONIDÆ. *Brachionus, Noteus, Anuræa, Sacculus.*
Fam. 10. PTERODINADÆ. *Pterodina, Pompholyx.*
Fam. 11. EUCHLANIDÆ. *Euchlanis, Salpina, Diplax, Monostyla, Colurus, Monura, Metopodia, Stephanops, Monocerca, Mastigocerca, Dinocharis.*

Order IV.—Scirtopoda.

Forms which swim with their ciliary wreath, and skip by means of hollow limbs with internal locomotor muscles.

Fam. 12. PEDALIONIDÆ. *Pedalion.*

The above list includes only the principal genera. There are, however, a number of forms which could not be placed in any of the above families.

ABERRANT FORMS.

Trochosphæra æquatorialis (fig. 6, G), found by Semper in the Philippine Islands, closely resembles a monotrochal polychætous larva while possessing undoubtedly Rotiferal characters. Mecznikow has described a remarkable form, *Apsilus lentiformis* (fig. 6, D, E, and F), the adult female of which is entirely devoid of cilia but possesses a sort of retractile hood; the young female and the males are not thus modified. Claparède discovered fixed to the bodies of small Oligochætes a curious non-ciliated form, *Balatro calvus* (fig. 6, A), which has a worm-like very contractile body and a well-developed mastax. As mentioned above, the ciliation is reduced to a minimum in the curious worm-like form *Lindia* (fig. 6, C). *Seison nebaliæ* (fig. 6, B), living on the surface of *Nebaliæ*, which was described originally by Grube, is the same form as the *Saccobdella nebaliæ*, which was supposed by Van Beneden and Hesse to be a leech. It has been shown by Claus to be merely an aberrant Rotifer.

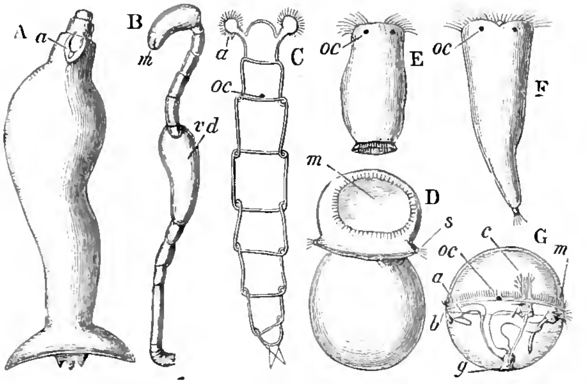

FIG. 6.—Various aberrant forms. A, *Balatro calvus* (after Claparède): *a*, mastax. B, *Seison nebaliæ* (after Claus): *m*, mouth; *vd*, position of the aperture of the vas deferens. C, *Lindia torulosa*: *a*, ciliated processes at the sides of the head representing cephalotroch; *oc*, eye-spots. D, E, and F, *Apsilus lentiformis* (after Mecznikow). D, adult female with expanded proboscis: *m*, position of the mouth; *s*, lateral sense-organs. E, young free-swimming female. F, adult male. G, *Trochosphæra æquatorialis* (after Semper): *m*, mouth; *g*, ganglion; *a*, anus; *b*, velum; *oc*, eye-spot; *c*, muscles.

Of the curious aquatic forms *Icthydium, Chætonotus, Turbanella, Dasyditis, Cephalidium, Chætura*, and *Hemidasys*, which Mecznikow and Claparède included under the name *Gastrotricha*, no further account can be given here. They are possibly allied to the *Rotifera*, but are devoid of mastax and trochal disk.

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(A. G. B.)

MOLLUSCA

The Mollusca form one of the great "phyla," or sub-kingdoms of the Animal Pedigree or Kingdom.

Literary History of the Group.—The shell-bearing forms belonging to this group which were known to Linnæus were placed by him (in 1748) in the third order of his class Vermes under the name "Testacea," whilst the Echinoderms, Hydroids, and Annelids, with the naked Molluscs, formed his second order, termed "Zoophyta." Ten years later he replaced the name "Zoophyta" by "Mollusca," which was thus in the first instance applied, not to the Mollusca at present so termed, but to a group consisting chiefly of other organisms. Gradually, however, the term Mollusca became used to include those Mollusca formerly placed among the "Testacea," as well as the naked Mollusca.

It is important to observe that the term μαλάκια, of which Mollusca is merely a Latinized form, was used by Aristotle to indicate a group consisting of the Cuttle-fishes only.

The definite erection of the Mollusca into the position of one of the great primary groups of the animal kingdom is due to George Cuvier (1788-1800), who largely occupied himself with the dissection of representatives of this type (**1**).[1] An independent anatomical investigation of the Mollusca had been carried on by the remarkable Neapolitan naturalist Poli (1791), whose researches (**2**) were not published until after his death (1817), and were followed by the beautiful works of another Neapolitan zoologist, the illustrious Delle Chiaje (**3**).

The "embranchement" or sub-kingdom Mollusca, as defined by Cuvier, included the following classes of shell-fish:—1, the cuttles or poulps, under the name Cephalopoda; 2, the snails, whelks, and slugs, both terrestrial and marine, under the name Gastropoda; 3, the sea-butterflies or winged-snails, under the name Pteropoda; 4, the clams, mussels, and oysters, under the name Acephala; 5, the lamp-shells, under the name Brachiopoda; 6, the sea-squirts or ascidians, under the name Nuda; and 7, the barnacles and sea-acorns, under the name Cirrhopoda.

The main limitations of the sub-kingdom or phylum Mollusca, as laid down by Cuvier, and the chief divisions thus recognized within its limits by him, held good to the present day. At the same time, three of the classes considered by him as Mollusca have been one by one removed from that association in consequence of improved knowledge, and one additional class, incorporated since his day with the Mollusca with general approval, has, after more than forty years, been again detached and assigned an independent position owing to newly-acquired knowledge.

The first of Cuvier's classes to be removed from the Mollusca was that of the Cirrhopoda. Their affinities with the lower Crustacea were recognized by Cuvier and his contemporaries, but it was one of the brilliant discoveries of that remarkable and too-little-honoured naturalist, J. Vaughan Thompson of Cork, which decided their position as Crustacea. The metamorphoses of the Cirrhopoda were described and figured by him in 1830 in a very complete manner, and the legitimate conclusion as to their affinities was formulated by him (**4**). Thus it is to Thompson (1830), and not to Burmeister (1834), as erroneously stated by Keferstein, that the merit of this discovery belongs. The next class to be removed from Cuvier's Mollusca was that of the Nuda, better known as Tunicata. In 1866 the Russian embryologist Kowalewsky startled the zoological world with a minute account of the developmental changes of Ascidia, one of the Tunicata (**5**), and it became evident that the affinities of that class were with the Vertebrata, whilst their structural agreements with Mollusca were only superficial. The last class which has been removed from the Cuvierian Mollusca is that of the Lamp-shells or Brachiopoda. The history of its dissociation is connected with that of the class, viz., the Polyzoa or Bryozoa, which has been both added to and again removed from the Mollusca between Cuvier's date and the present day. The name of J. Vaughan Thompson is again that which is primarily connected with the history of a Molluscan class. In 1830 he pointed out that among the numerous kinds of "polyps" at that time associated by naturalists with the Hydroids, there were many which had a peculiar and more elaborate type of organization, and for these he proposed the name Polyzoa (**6**). Subsequently (**7**) they were termed Bryozoa by Ehrenberg (1831).

Henri Milne-Edwards in 1844 demonstrated (**8**) the affinities of the Polyzoa with the Molluscan class Brachiopoda, and proposed to associate the three classes Brachiopoda, Polyzoa, and Tunicata in a large group "Molluscoidea," coordinate with the remaining classes of Cuvier's Mollusca, which formed a group retaining the name Mollusca. By subsequent writers the Polyzoa have in some cases been kept apart from the Mollusca and classed with the "Vermes;" whilst by others (including the present writer) they have, together with the Brachiopoda, been regarded as true Mollusca. The recent investigation by Mr. Caldwell (1882) of the developmental history of Phoronis (**9**), together with other increase of knowledge, has now, however, established the conclusion that the agreement of structure supposed to obtain between Polyzoa and true Mollusca is delusive; and accordingly they, together with the Brachiopoda, have to be removed from the Molluscan phylum. Further details in regard to this, the last revolution in Molluscan classification, will be found in the article Polyzoa.

As thus finally purified by successive advances of embryological research, the Mollusca are reduced to the Cuvierian classes of Cephalopoda, Pteropoda, Gastropoda, and Acephala. Certain modifications in the disposition of these classes are naturally enough rendered necessary by the vast accumulation of knowledge as to the anatomy and embryology of the forms comprised in them during fifty years. Foremost amongst those who have within that period laboured in this group are the French zoologists Henri Milne-Edwards (**20**) and Lacaze Duthiers (**21**), to the latter of whom we owe the most accurate dissections and beautiful illustrations of a number of different types. To Kölliker (**22**), Gegenbaur (**23**), and more recently Spengel (**24**), amongst German anatomists, we are indebted for epoch-making researches of the same kind. In England, Owen's anatomy of the Pearly Nautilus (**10**), Huxley's discussion of the general morphology of the Mollusca (**11**), and Lankester's embryological investigations (**12**), have aided in advancing our knowledge of the group. Two remarkable works of a systematic character dealing with the Mollusca deserve mention here—the *Manual of the Mollusca* by the late Dr. S. P. Woodward, a model of clear systematic exposition, and the exhaustive treatise on the Malacozoa or Weichthiere by the late Professor Keferstein of Göttingen, published as part of Bronn's *Classen und Ordnungen des Thier-Reichs*. The latter work is the most completely illustrated and most exhaustive survey of existing knowledge of a large division of the animal kingdom which has ever been produced, and, whilst forming a monument to its lamented author, places the student of Molluscan morphology in a peculiarly favourable position.

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[1] These figures refer to the bibliography at the end of the article, p. 695.

Classes of the Mollusca.—The classes of the Mollusca which we recognize are as follows:—

Phylum MOLLUSCA.

BRANCH A.—**Glossophora.**

Class 1.—GASTROPODA.
  Br. a.—Isopleura.
    Examples — Chiton, Neomenia.
  Br. b.—Anisopleura.
    Examples—Limpet, Whelk, Snail, Slug.
Class 2.—SCAPHOPODA.
  Example—Tooth-shell.
Class 3.—CEPHALOPODA.
  Br. a.—Pteropoda.
    Examples—Hyalæa, Pneumodermon.
  Br. b.—Siphonopoda.
    Examples — Nautilus, Cuttles, Poulp.

BRANCH B.—**Lipocephala**
(=Acephala, *Cuvier*).

Class 1.—LAMELLIBRANCHIA
  (Syn. Conchifera).
  Examples—Oyster, Mussel, Clam, Cockle.

General Characters of the Mollusca.—The forms comprised in the above groups, whilst exhibiting an extreme range of variety in shape, as may be seen on comparing an Oyster, a Cuttle-fish, and a Sea-slug such as Doris; whilst adapted, some to life on dry land, others to the depths of the sea, others to rushing streams; whilst capable, some of swimming, others of burrowing, crawling, or jumping, some, on the other hand, fixed and immobile; some amongst the most formidable of carnivores, others feeding on vegetable mud, or on the minutest of microscopic organisms—yet all agree in possessing in common a very considerable number of structural details which are not possessed in common by any other animals.

The structural features which the Mollusca do possess in common with other animals belonging to other great phyla of the animal kingdom are those characteristic of the Cœlomata, one of the two great grades (the other and lower being that of the Cœlentera) into which the higher animals, or Enterozoa as distinguished from the Protozoa, are divided (**13**). The Enterozoa all commence their individual existence as a single cell or plastid, which multiplies itself by transverse division. Unlike the cells of the Protozoa, these embryonic cells of the Enterozoa do not remain each like its neighbour and capable of independent life, but proceed to arrange themselves in two layers, taking the form of a sac. The cavity of the two-cell-layered sac or Diblastula thus formed is the primitive gut or ARCH-ENTERON. In the Cœlentera, whatever subsequent changes of shape the little sac may undergo as it grows up to be Polyp or Jelly-fish, the original arch-enteron remains as the one cavity pervading all regions of the body. In the Cœlomata the arch-enteron becomes in the course of development divided into two totally distinct cavities shut off from one another—an axial cavity, the MET-ENTERON, which retains the function of a digestive gut; and a peri-axial cavity, the CŒLOM or body-cavity, which is essentially the blood-space, and receives the nutritive products of digestion and the waste products of tissue-change by osmosis. The Mollusca agree in being Cœlomate with the phyla Vertebrata, Platyhelmia (Flat-worms), Echinoderma, Appendiculata (Insects, Ringed-worms, &c.), and others,—in fact, with all the Enterozoa except the Sponges, Corals, Polyps, and Medusæ.

In common with all other Cœlomata, the Mollusca are at one period of life possessed of a PROSTOMIUM or region in front of the mouth, which is the essential portion of the "head," and is connected with the property of forward locomotion in a definite direction and the steady carriage of the body (as opposed to rotation of the body on its long axis). As a result, the Cœlomata, and with them the Mollusca, present (in the first instance) the general condition of body known as BILATERAL SYMMETRY; the dorsal is differentiated from the ventral surface, whilst a right and a left side similar to, or rather the complements of, one another are permanently established. In common with all other Cœlomata, the Mollusca have the mouth and first part of the alimentary canal which leads into the met-enteron formed by a special invagination of the outer layer of the primitive body-wall, not to be confounded with that which often, but not always, accompanies the antecedent formation of the arch-enteron; this invagination is termed the STOMODÆUM. Similarly, an anal aperture is formed in connexion with a special invagination which meets the hinder part of the met-enteron, and is termed the PROCTODÆUM.

In common with many (if not all) Cœlomata, the Mollusca are provided with at least one pair of tube-like organs, which open each by one end into the cœlom or body cavity, and by the other end to the exterior, usually in the neighbourhood of the anus. These are the NEPHRIDIA.

Like all other Cœlomata, the Mollusca are also provided with special groups of cells forming usually paired or median growths upon the walls of the cœlomic cavity, the cells being specially possessed of reproductive power, and differentiated as egg-cells and sperm-cells. These are the GONADS. As in other Cœlomata, the cells of the gonads may escape to the exterior in one of two ways—either through the nephridia, or, on the other hand, by special apertures.

As in all other Cœlomata, the cells, which build up respectively the primary outer layer of the body, the lining layer of the met-enteron, and the lining layer of the cœlom, are multiplied and differentiated in a variety of ways in the course of growth from the early embryonic condition. TISSUES are formed by the adhesion of a number of similarly modified cells in definite tracts. As in all Cœlomata, there is a considerable variety of tissues characterized by, and differentiated in relation to, particular physiological activities of the organism. Not only the Cœlomata but also many Cœlentera show, in addition to the EPITHELIA (the name given to tissue which bounds a free surface, whether it be that of the outer body-wall, of the gut, or of a blood-space), also deeper lying tissues, of which the first to appear is MUSCULAR tissue, and the second NERVOUS tissue.

The epithelia are active in throwing off their constituent cells (blood-corpuscles from the wall of the cœlom), or in producing secretions (glands of body-wall and of gut), or in forming horny or calcareous plates, spines, and processes, known as CUTICULAR PRODUCTS (shells and bristles of the body-wall, teeth of the tongue, gizzard, &c.).

In the Mollusca, as in all other Cœlomata, in correspondence with the primary bilateral symmetry and in relation to the special mechanical conditions of the prostomium, the nervous tissue which is in Cœlentera, and even in Flatworms, diffused over the whole body in networks, tends to concentrate in paired lateral tracts, having a special enlargement in the prostomium. The earlier plexiform arrangement is retained in the nervous tissue of the walls of the alimentary canal of many Cœlomata, whilst a concentration to form large nerve-masses (GANGLIA), to which numerous afferent and efferent fibres are attached, affects the nervous tissue of the body-wall.

In all Cœlomata, including Mollusca, muscular tissue is developed in two chief layers, one subjacent to the deric or outer epithelium (SOMATIC MUSCULATURE), and a second surrounding the alimentary canal (SPLANCHNIC MUSCULATURE). Thus, primarily, in Cœlomata the body has the character of two muscular sacs or tubes, placed one within the other and separated from one another by the cœlomic space. The somatic musculature is the more copious and develops very generally an outer circular layer (*i.e.*, a layer in which the muscular fibres run in a direction transverse to the long axis of the body) and a deeper longitudinal layer; to these oblique and radiating fibres may be added. The splanchnic musculature, though more delicate, exhibits a circular layer nearer the enteric epithelium, and a longitudinal layer nearer the cœlomic surface.

In Cœlomata and in many Cœlentera there are found distributed between the tracts of muscular tissue, bounding them and giving strength and consistency also to the walls of the body, of the alimentary canal, of the cœlom, and of the various organs and tissue-masses (such as nerve-centres, gonads, &c.) connected with these, tracts of tissue the function of which is skeletal. The SKELETAL TISSUE of Mollusca, in common with that of other Cœlomata, exhibits a wide range of minute structure, and is of differing density in various parts; it may be fibrous, membranous, or cartilaginous. The Mollusca, in common with the other Cœlomata, exhibit a remarkable kind of association between the various forms of skeletal tissue and the epithelium which lines the cœlomic cavity. The cœlomic cavity contains a liquid which is albuminous in chemical composition (BLOOD-LYMPH OR HÆMOLYMPH), and into this liquid cells are shed from the cœlomic epithelium. They float therein and are known as BLOOD CORPUSCLES or LYMPH CORPUSCLES. The cœlomic space with its contained hæmolymph is not usually in Cœlomata, and is not in Mollusca, a simple even-walled cavity, but is broken up into numerous passages and recesses by the outgrowths, both of the alimentary canal and of its own walls. By the adhesion of its opposite walls, and by an irregularity in the process of increase of its area during growth, the cœlom becomes to a very large extent a spongy system of intercommunicating LACUNÆ or irregular spaces, filled with the cœlomic fluid. At the same time, the cœlomic space has a tendency to push its way in the form of narrow canals and sinuses between the layers of skeletal tissue, and thus to permeate together with the skeletal tissue in the form of a spongy, or it may be a tubular, network all the apparently solid portions of the animal body. This association of the nutritive and skeletal functions is accompanied by a complete identity of the tissues concerned in these functions. Not only is there complete gradation from one variety of skeletal tissue to another (*e.g.*, from membranous to fibrous, and from fibrous to cartilaginous) even in respect of the form of the cells and their intercellular substance, but the cœlomic epithelium, and consequently the hæmolymph with its floating corpuscles derived from that epithelium, is brought into the same continuity. The skeletal and blood-containing and -producing tissues in fact form one widely-varying but continuous whole, which may be called the SKELETO-TROPHIC SYSTEM OF TISSUES.

In many Cœlomata not only do the skeletal tissues allow the cœlomic space with its fluid and corpuscles to penetrate between their layers, but a special mode of extension of that space is found, which consists in the hollowing out of the solid substance of elongated cells having the form of fibres, which thus become tubular, and, admitting the nutritive fluid, serve as channels for its distribution. These are "capillary vessels," and it has yet to be shown that such are formed in the Mollusca. Larger vessels, however, concerned in guiding the movement of the cœlomic fluid in special directions are very usually developed in the Mollusca, as in other Cœlomata, by the growth of skeletal tissue around what are at first ill-defined extensions of the cœlomic space. In this way a portion of the cœlomic space becomes converted into vessels, whilst a large part remains with irregular walls extending in every direction between the skeletal tissues and freely communicating with the system of vessels. As in many other Cœlomata, muscular tissue grows around the largest vessel formed from the primitive cœlom, which thus becomes a contractile organ for propelling the blood-lymph fluid. This "HEART" has in Mollusca, as in most other Cœlomata in which it is developed, a dorsal position. A communication of the blood-lymph space with the exterior by means of a pore situated in the foot or elsewhere has been very generally asserted to be characteristic of Mollusca. It has been maintained that water is introduced by such a pore into the blood, or admitted into a special series of water-vessels. It has also been asserted that the blood-fluid is expelled by the Mollusca from these same pores. Recent investigation (**14**) has, however, made it probable that the pores are the pores of secreting glands, and do not lead into the vascular system. There is, it therefore appears, no admission or expulsion of water through such pores in connexion with the blood, although in some other Cœlomata it is established that water is taken into the cœlomic space through a pore (Echinoderms), whilst in some others there is no doubt that the cœlomic hæmolymph is occasionally discharged in quantity through pores of definite size and character (Earthworm, &c.).

We have thus seen that the Mollusca possess, in common with the other Cœlomata—1, a body composed of a vast *number of cells* or plastids, arranged so as to form a sac-like *body-wall*, and within that a second sac, the *met-enteron*, the wall of which is separated from the first by a *cœlom* or blood-lymph space; 2, a *stomodæum* and a *proctodæum*; 3, a *prostomium*, together with a differentiated *dorsal* and *ventral* surface, and consequently *right* and *left sides*, *i.e.*, bilateral symmetry; 4, a pair of *nephridia*; 5, *gonads* developed on the wall of the cœlom; 6, *deric* epithelium (producing horny and calcareous deposits on its surface), *enteric* epithelium, and *cœlomic* epithelium; 7, laterally paired masses of *nerve-tissue*, especially large in the prostomial region (nerve-centres or *ganglia*); 8, *muscular tissue*, forming a *somatic* tunic and a *splanchnic* tunic; 9, *skeleto-trophic tissues*, consisting of membranous, fibrous, and cartilaginous *supporting tissues*, and of *blood-vessels* and the walls of *blood-spaces*, the *cœlomic epithelium*, and the liquid tissue known as *hæmolymph* (commonly blood).

Schematic Mollusc.—Starting from this basis of structural features common to them and the rest of the Cœlomata, we may now point out what are the peculiar developments of structure which characterize the Mollusca and lead to the inference that they are members of one peculiar branch or phylum of the animal pedigree. In attempting thus to set forth the dominating structural attributes of a great group of organisms it is not possible to make use of arbitrary definitions. Of Mollusca, as of other great phyla, it is not possible categorically to enunciate a series of structural peculiarities which will be found to be true in reference to every member of the group. We have to remember that the process of adaptation in the course of long ages of development has removed in some cases one, in other cases another, of the original features characteristic of the ancestors from which the whole group may be supposed to have taken origin, and that it is possible (and actually is realized in fact) that some organisms may have lost all the *primary* characteristics of Molluscan organization, and yet be beyond all doubt definitely stamped as Mollusca by the retention of some *secondary* characteristic which is so peculiar as to prove their relationship with other Mollusca. An example in point is found in the curious fish-like form Phyllirhoë (fig. 58), which has none of the primary characteristics of a Mollusc, and yet is indisputably proved to belong to the Molluscan phylum by possessing the peculiar and elaborate lingual apparatus present in one branch of the phylum, the Glossophora.

In order to exhibit concisely the peculiarities of organization which characterize the Mollusca, we find it most convenient to construct a schematic Mollusc, which shall possess in an unexaggerated form the various structural arrangements which are more or less specialized, exaggerated, or even suppressed in particular members of the group. Such a schematic Mollusc is not to be regarded as an archetype, in the sense which has been attributed to that word, nor as the embodiment of an idea present to a creating mind, nor even as an epitome of developmental laws. Were knowledge sufficient, we should wish to make this schematic Mollusc the representation of the actual Molluscan ancestor from which the various living forms have sprung. To definitely claim for our schematic form any such significance in the present state of knowledge would be premature, but it may be taken as more or less coinciding with what we are justified, under present conditions, in picturing to ourselves as the original Mollusc or archi-Mollusc (more correctly Archimalakion). After describing this schematic form, we shall proceed to show how far it is realized or justified in each class and order of Mollusca successively.

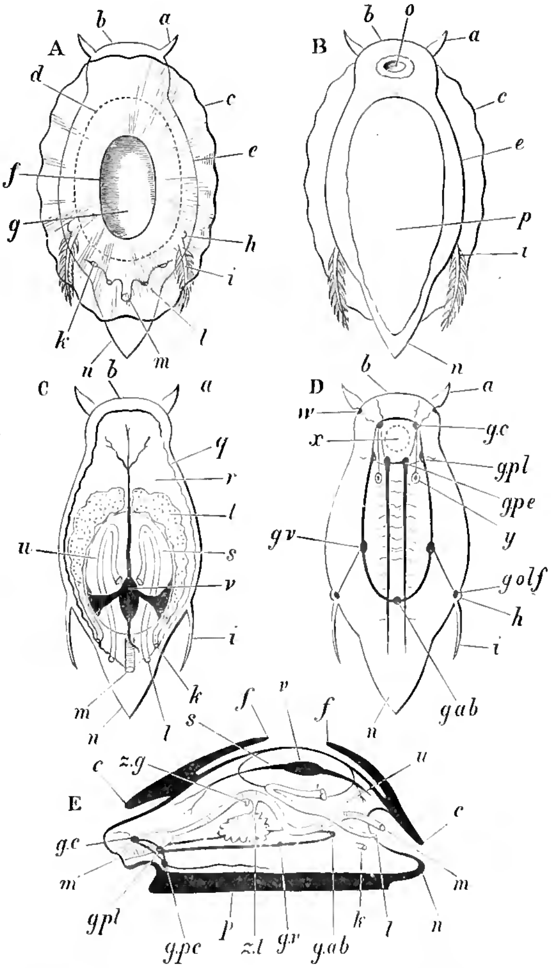

FIG. 1.—Schematic Mollusc. A. Dorsal aspect. B. Ventral aspect. C. The heart, pericardium, gonads, and nephridia shown in position. D. The nervous system; the reader is requested to note that the cord passing backwards from *g.pe* lies beneath, and does not in any way unite with the cord which passes from *g.ab* to *g.pl*. E. Diagram in which the body-wall is represented as cut in the median antero-posterior plane, so as to show organs in position,—the shell-sac is seen in section, but the shell is omitted.

Letters in all the figures as follows:—*a*, cephalic tentacle; *b*, head; *c*, edge of the mantle-skirt or limbus pallialis; *d*, dotted line indicating the line of origin of the free mantle-skirt from the sides of the visceral hump; *e*, outline of the foot seen through the mantle-skirt in A, which is supposed to be transparent, allowing the position of this and of the various parts *h*, *i*, *k*, *l*, *m*, to be seen through its substance; *f*, edge of the shell-follicle; *g*, the shell; *h*, the osphradium, paired (Spengel's olfactory organ); *i*, the ctenidium, paired (gill-plume); *k*, aperture of the gonad, paired; *l*, aperture of one of the two nephridia; *m*, anus; *n*, posterior region of the foot reaching farther back than the mass of viscera (dorsal hump) which it carries; *o*, mouth; *p*, plantar surface of the foot; *q*, cut edge of the body-wall of the dorsal region; *r*, cœlomic space (blood-lymph space or body-cavity), mostly occupied by liver, but to some extent retained as blood-channels and lacunæ; *s*, pericardial cavity; *t*, gonad (ovary or spermary), paired; *u*, nephridium, paired; *v*, ventricle of the heart receiving the right and the left auricles at its sides, and sending off anteriorly a large vessel, posteriorly a small one; *w*, the cephalic eye, paired; *x*, dotted ring to show the position occupied by the œsophagus in relation to the nerve ganglia and cords; *y*, the otocyst, paired; *z.l*, the digestive gland (so-called "liver") of the left side; *z.g*, duct of the digestive gland of the right side; *g.c*, cerebral ganglion united by the cerebral commissure to its fellow; *g.pl*, pleural ganglion united by the cerebro-pleural connective to the cerebral ganglion, and by the pleuro-pedal connective to the pedal ganglion; *g.pe*, the pedal ganglion united to its fellow by the pedal commissure—the two sending off posteriorly the long ladder-like pair of pedal nerves; *g.v*, the visceral ganglion (of the left side) united by the visceral loop or commissure to the similar ganglion on the right side, and by the viscero-pleural connective to the pleural ganglion; *g.ab*, abdominal ganglion developed on the course of the visceral loop; *g.olf*, olfactory ganglion placed near the osphradium on a nerve taking its origin from the visceral ganglion.

The schematic Mollusc (fig. 1, A to E) is oblong in shape, bilaterally symmetrical, with strongly differentiated dorsal and ventral surface, and has a well-marked **HEAD**, consisting of the prostomium (*b*) and the region immediately behind the mouth. Upon the head we place a pair of short **CEPHALIC TENTACLES** (*a*). The *mouth* is placed in the median line anteriorly, and is overhung by the prostomium (B, *o*); the *anus* is placed in the median line posteriorly, well raised on the dorsal surface (A, *m*). The apertures of a pair of **NEPHRIDIA** are seen in the neighbourhood of the anus right and left (A, *l*). Near the nephridial apertures, and in front of them, right and left, are the pair of apertures (*k*) appropriate to the ducts of the **GONADS** (generative pores).

The most permanent and distinctive Molluscan organ is the **FOOT** (Podium). This is formed by an excessive development of the somatic musculature along the ventral surface, distinctly ceasing at the region of the head, below which it suddenly projects as a powerful muscular mass (B, *p*; E, *p*). It may be compared, and is probably genetically identical, with the muscular ventral surface of the Planarians and with the suckers of Trematoda, but is more extensively developed than are those corresponding structures. The muscular tissue of the foot, and of all other parts of the body of all Mollusca, is cellular and unstriated, as distinguished from the composite muscular fibre (consisting of cell-fusions instead of separable cells) which occurs in Arthropoda and in Vertebrata, and which has the further distinction of being composed of alternating bands of substance of differing refractive power (hence "striated"). The appearance of cross striation seen in the muscular cells of some Molluscs (odontophore of Haliotis, Patella, &c.) requires further investigation. It is by no means altogether the same thing as the marking characteristic of striated muscular fibre.

Contrasting with the ventral foot is the thin-walled dorsal region of the body, which may be termed the antipodial region. This thin-walled region is formed by soft viscera covered in by the comparatively delicate and non-muscular body-wall (fig. 1, E). As the ventral foot is clearly separate from the projecting head, so is this dorsal region, and it is conveniently spoken of as the **VISCERAL HUMP** or "dome" (cupola). Protecting the visceral dome is a **SHELL** (conchylium) consisting of a horny basis impregnated with carbonate of lime,[1] and secreted by the deric epithelium of this region of the body (*g*). The shell in our schematic Mollusc is single, cap-shaped, and symmetrical. It does not lie entirely naked upon the surface of the visceral dome, but is embedded all round its margin, to a large extent in the body-wall. In fact, the integument of the visceral dome forms an open flattened sac in which the shell lies. This is the **PRIMARY SHELL-SAC**, or **FOLLICLE** (A and E, *f*). The wall of the body projects all round the visceral dome in the form of a flap or skirt, so as to overhang and conceal to some extent the head and the sides of the foot. This skirt, really an out-

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[1] As to the minute structure of the shell in various classes, see Carpenter's article "Shell" in the *Cyclop. of Anat. and Physiol.* The limits of our space do not permit us to deal with this or other histological topics.

growth of the dorsal body-wall, is called the MANTLE-FLAP (limbus pallialis), or more shortly the MANTLE or PALLIUM (*c*). The space between the overhanging mantle-flap and the sides and neck of the animal which it overhangs is called the SUB-PALLIAL SPACE or CHAMBER. Posteriorly in this space are placed the anus and the pair of nephridial apertures (see fig. 1, E).

The development of the mantle-skirt and its sub-pallial space appears to have a causal relation, in the way of protection, to a pair of processes of the body-wall which spring, one on the right and one on the left, from the sides of the body, nearer the anus than the mouth, and are concealed by the mantle-flap to some extent (A, B, *i*). These processes have an axis in which are two blood-vessels, and are beset with two rows of flattened filaments, like the teeth of a comb in double series. These are the CTENIDIA or gill-combs. Usually, as will be seen in the sequel, they play the part of gills, but since in many Molluscs (Lamellibranchs) their function is not mainly respiratory, and since also other completely-formed gills are developed as special organs in some Molluscs to the exclusion of these processes, it is well not to speak of them simply as "gills" or "branchiæ," but to give them a non-physiological name such as that here proposed. Near the base of the stem of each ctenidium is a patch of the epithelium of the body-wall, peculiarly modified and supplied with a special nerve and ganglion. This is Spengel's olfactory organ, which tests the respiratory fluid, and is persistent in its position and nerve-supply throughout the group Mollusca. We propose to call it the OSPHRADIUM.

Passing now to the internal organs, our schematic Mollusc is found to possess an ALIMENTARY CANAL, which passes from mouth to anus in the middle line, leaving between it and the muscular body-wall a more or less spongy, in parts a spacious, CŒLOM. The *stomodæum* is large and muscular, the *proctodæum* short; the bulk of the alimentary canal is therefore developed from the metenteron or remnant of the arch-enteron after the cœlom has been pinched off from it. A paired outgrowth of the met-enteron forms the glandular diverticulum known as the digestive gland or (commonly) liver (E, *zg*, *zl*).

Dorsally to the alimentary tract the cœlom is spacious. The space (C, E, *s*) is termed the PERICARDIUM, since it is traversed by a vessel running fore and aft in the median line, which has contractile muscular walls and serves as a heart to propel the cœlomic blood-fluid. This pericardial space, although apparently derived from the original cœlom, is not in communication with the other spaces and blood-vessels derived from the cœlom; it never (or perhaps in a very few instances) contains in the adult the Molluscan blood or hæmolymph, and is always in free communication with the exterior through the tubes called *nephridia* (renal organs). The HEART receives symmetrically on each side, right and left, a dilated vessel bringing aerated blood from the ctenidia. These dilated vessels are termed the *auricles of the heart*, whilst the median portion itself, at the point where these vessels join it, is termed the *ventricle of the heart* (C, *v*). The vessel passing fore and aft from the ventricle gives off a few trunks which open into spaces of the cœlom, the so-called lacunæ; these are excavated in every direction between the viscera and the various bundles of fibrous and muscular tissue, and may assume more or less the character of tube-like vessels with definite walls. Right and left opening into the pericardial cœlom is a coiled tube, the farther extremity of which opens to the exterior by the side of the anus. These two tubes (C, *u*) are the symmetrically disposed NEPHRIDIA (renal organs).

The GONADS (ovaries or spermaries) are placed in the mid-dorsal region of the cœlom (C, *t*), and have their own apertures in the immediate neighbourhood of those of the nephridia. The apertures are paired right and left, and so are the ducts into which they lead; but at present we have no ground for determining whether the gonad itself was primarily in Molluscs a paired organ or a median organ, nor have we any well-founded conception as to the nature of the ducts when present, and their original relationship to the gonads. The genital ducts of some organisms are modified nephridia, but the nature of those of Mollusca, of Arthropoda, of Echinoderma, of Nematoidea, and of some Vertebrata has yet to be elucidated.

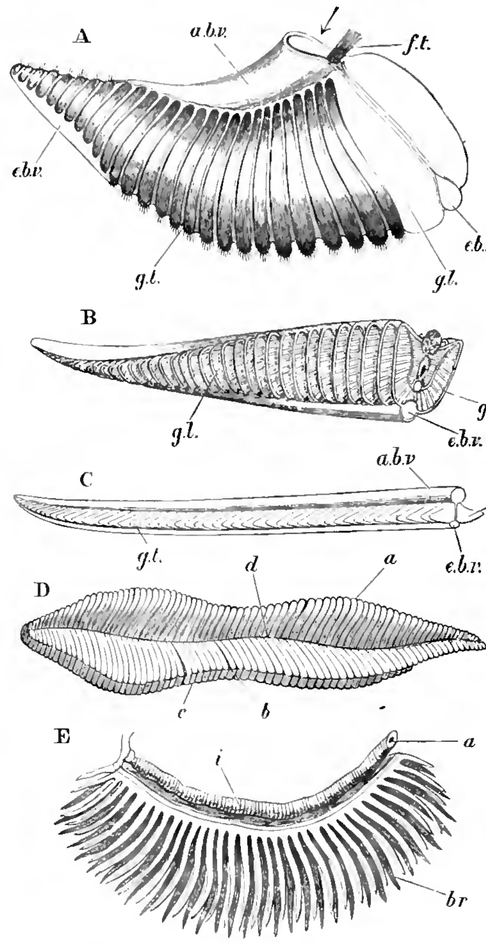


FIG. 2.—Ctenidia of various Mollusca (original). A. Of Chiton; *f.t.*, fibrous tissue; *a.b.v.*, afferent blood-vessel; *e.b.v.*, efferent blood-vessel; *g.l.*, laterally paired lamellæ. B. Of Sepia; letters as in A. C. Of Fissurella; letters as in A. D. Of Nucula; *d*, position of axis with blood-vessels; *a*, inner; *b* and *c*, outer row of lamellæ. E. Of Paludina; *i*, intestine running parallel with the axis of the ctenidium and ending in the anus *a*; *br*, rows of elongate processes corresponding to the two series of lamellæ of the upper figures.

The disposition of the nerve-centres is highly characteristic. There are four long cords composed of both nerve-fibres and nerve-cells which are disposed in pairs, two right and left of the pedal area or foot, two more dorsally and tending to a deeper position than that occupied by the pedal cords, so as to lie freely within the cœlomic space unattached to the body-wall. These are respectively the PEDAL NERVE-CORDS and the VISCERAL NERVE-CORDS. The latter meet and join one another posteriorly. A right and left (D, *g.v*), and a median abdominal (*g.ab*) ganglion are placed on these cords, and from them are given off the osphradial nerves which have special ganglia (*g.olf*). In the region of the prostomium the pedal nerve-cords are enlarged behind the mouth, forming the *pedal ganglia* (*g.pe*), and are united by nerve-fibres to one another. From this spot they are continued forward into the prostomium, where they enlarge to form the right and left *cerebral ganglia* (*g.c*), which are united to one another by nerve-fibres in front of the mouth, just as the pedal ganglia are behind it. The right and left pedal ganglia are joined by transverse cords to the right and left visceral cords respectively, the point of union being marked on either side by a swelling (*g.pl*) known as the pleural ganglion. The visceral nerve-cord can also be traced up on each side beyond the pleural ganglion to the cerebral ganglion. Thus we have a nearly complete double nerve-ring formed around the œsophagus by the two pairs of nerve-cords which are in this region drawn, as it were, towards each other and away from their lateral position both behind and before the stomodæal invagination. Whilst the swollen parts of the nerve-tracts are termed *ganglia*, the connecting cords are conveniently distinguished either as *connectives* or as *commissures*. Commissures connect two ganglia of the same pair We have a cerebral commissure, a pedal commissure and a visceral commissure. Connectives connect ganglia of dissimilar pairs, and we speak accordingly of the cerebro-pedal connective, the cerebro-pleural connective, the pleuro-pedal connective, and the viscero-pleural connective.

An ENTERIC NERVOUS SYSTEM forming a plexus on the walls of the alimentary canal exists, but does not exhibit cords and ganglia visible to the naked eye except in the large Dibranchiate Cephalopods.

Our schematic Mollusc is provided with certain ORGANS OF SPECIAL SENSE. Tactile organs occur on the head in the form of short CEPHALIC TENTACLES (*a*). Deeply placed are a pair of closed vesicles containing each a calcareous concretion and acting as auditory organs; these are known as OTOCYSTS (D, *y*). They are situated behind the mouth in the foremost portion of the foot. At the base of each cephalic tentacle is a pigmented eye-spot—the CEPHALIC EYE (D, *w*). The OSPHRADIUM (*h*), or peculiar patch of olfactory epithelium at the base of the ctenidium, has already been mentioned.

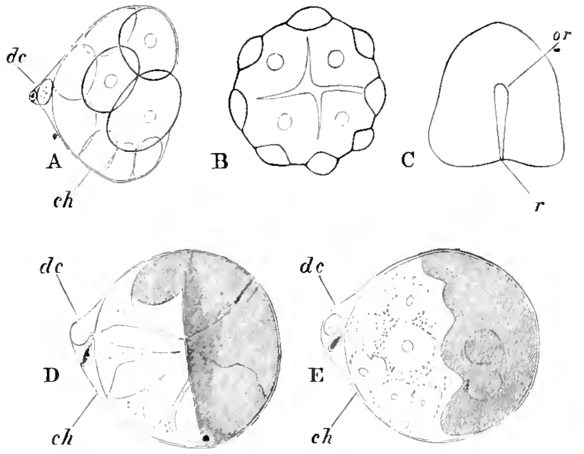


FIG. 3.—Development of the Pond-Snail, *Limnæus stagnalis* (after Lankester, 15). *dc*, directive corpuscles (præseminal outcast cells); *ch*, egg-envelope or chorion; *or*, oral end of the blastopore; *r*, anal end of the blastopore. A. Formation of the Diblastula by the invagination of larger cells into the area of smaller cells (optical section). B. View of the same specimen from the surface of invagination; the smaller cells are seen at the periphery; by division they will multiply and extend themselves over the four larger cells. C. Fully-formed Diblastula, surface view to show the elongated form of the orifice of invagination or blastopore; its middle portion closes up and coincides with the region of the foot; the extremity, *or*, coincides with the mouth and stomodæum, the opposite extremity, *r*, with the anus. D. Optical section of an embryo a little older than A. E. Surface view of the same embryo.

To the scheme thus exhibited of the possible organization of the ancestral Mollusc we shall now add a sketch of the mode in which this form of body and series of internal organs are developed from the egg.

The egg-cell of Mollusca is either free from food material a simple protoplasmic corpuscle—or charged with food material to a greater or less extent. Those cases which appear to be most typical—that is to say, which adhere to a procedure which was probably common at one time to all then existing Mollusca, and which has been departed from only in later and special lines of descent—show approxi-

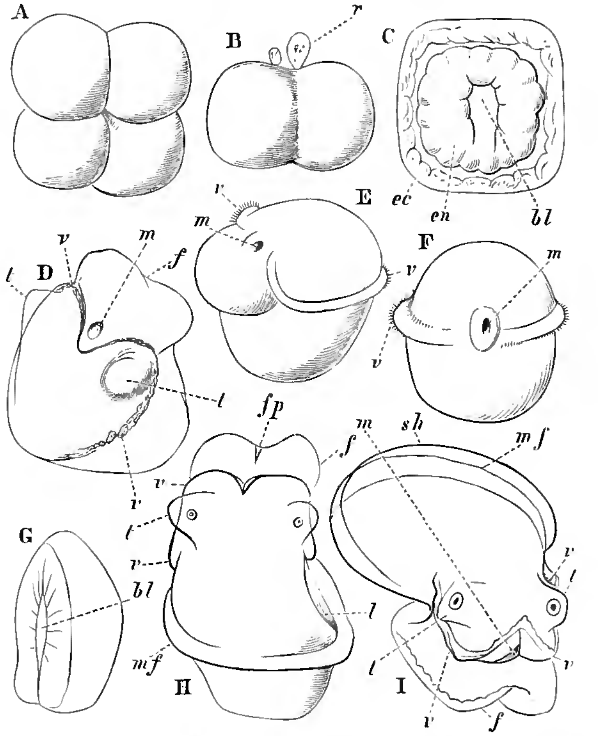


FIG. 4.—Development of the Pond-Snail, *Limnæus stagnalis* (after Lankester, 15). *r*, directive corpuscle; *bl*, blastopore; *en*, endoderm or enteric cell layer; *ec*, ectoderm or deric cell-layer; *v*, velum; *m*, mouth; *f*, foot; *t*, tentacles; *fp*, pore in the foot (belonging to the pedal gland?); *mf*, the mantle-flap or limbus pallialis; *sh*, the shell; *l*, the sub-pallial space, here destined to become the lung. A. First four cells resulting from the cleavage of the original egg-cell. B. Side view of the same. C. Diblastula stage (see fig. 3), showing the two cell-layers and the blastopore. D, E, F. Trochosphere stage, D older than E or F. G. Three-quarter view of a Diblastula, to show the orifice of invagination of the endoderm or blastopore, *bl*. H, I. Veliger stage later than D. (Compare fig. 70 and fig. 72***).

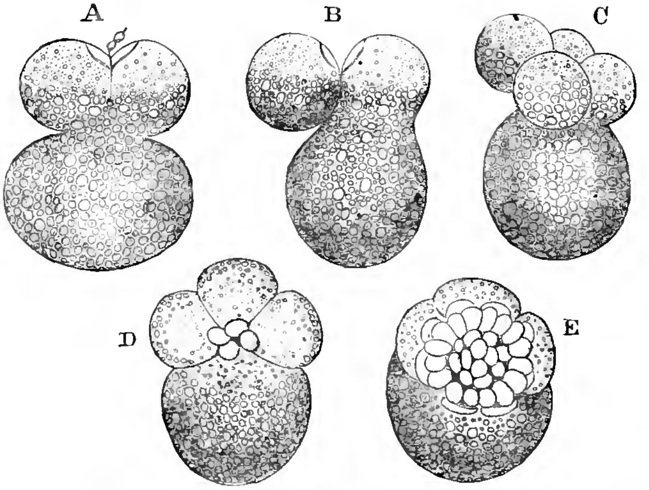


FIG. 5.—Early stages of division of the fertilized egg-cell in *Nassa mutabilis* (from Balfour, after Bobretzky). A. The egg-cell has divided into two spheres, of which the lower contains more food-material, whilst the upper is again incompletely divided into two smaller spheres. Resting on the dividing upper sphere are the eight-shaped "directive corpuscles," better called "præseminal outcast cells or apoblasts," since they are the result of a cell-division which affects the egg-cell before it is impregnated, and are mere refuse, destined to disappear. B. One of the two smaller spheres is reunited to the larger sphere. C. The single small sphere has divided into two, and the reunited mass has divided into two, of which one is oblong and practically double, as in B. D. Each of the four segment-cells gives rise by division to a small pellucid cell. E. The cap of small cells has increased in number by repeated formation of pellucid cells in the same way, and by division of those first formed. The cap will spread over and enclose the four segment-cells, as in fig. 3, A, B.

mately the following history. By division of the egg-cell (fig. 3, A, B; fig. 4, A, B; and fig. 5) a mulberry-mass of embryonic-cells is formed (Morula), which dilates, forming a one-cell-layered sac (Blastula). By invagination one portion of this sphere becomes tucked into the other—as in the preparation of a woven night-cap for the head (fig. 6, B; fig. 7, A). The orifice of invagination (blastopore) narrows, and we now have a two-cell-layered sac,—the Diblastula. The invaginated layer is the enteric cell-layer or endoderm; the outer cell-layer is the deric cell-layer or ectoderm. The cavity communicating with the blastopore and lined by the endoderm is the arch-enteron. The blastopore, together with the whole embryo, now elongates. The blastopore then closes along the middle portion of its extent, which corresponds with the later developed foot. At the same time the stomodæum or oral invagination forms around the anterior remnant of the blastopore, and the proctodæum or anal invagination forms around the posterior remnant of the blastopore. There are, however, variations in regard to the relation of the blastopore to the mouth and to the anus which are probably modifications of the original process described above. An examination of figs. 3, 4, 5, 6, 7, and of others illustrative of the embryology of particular forms which occur later in this article, is now recommended to the reader. The explanation of the figures has been made very full so as to avoid the necessity of special descriptions in the text. Internally, by the nipping off of a pair of lateral outgrowths (forming part of the indefinable "mesoblast") from the enteric cell-layer the foundations of the cœlomic cavity are laid. In some Cœlomata these outgrowths are hollow and of large size. In Mollusca they are not hollow and large, which is probably the archaic condition, but they consist at first of a few cells only, adherent to one another; these cells then diverge, applying themselves to the body-wall and to the gut-wall so as to form the lining layer of the cœlomic cavity. Muscular tissue develops from deep-lying cells, and the rudiments of the paired nerve-tracts from thickenings of the deric-cell layer or ectoderm.

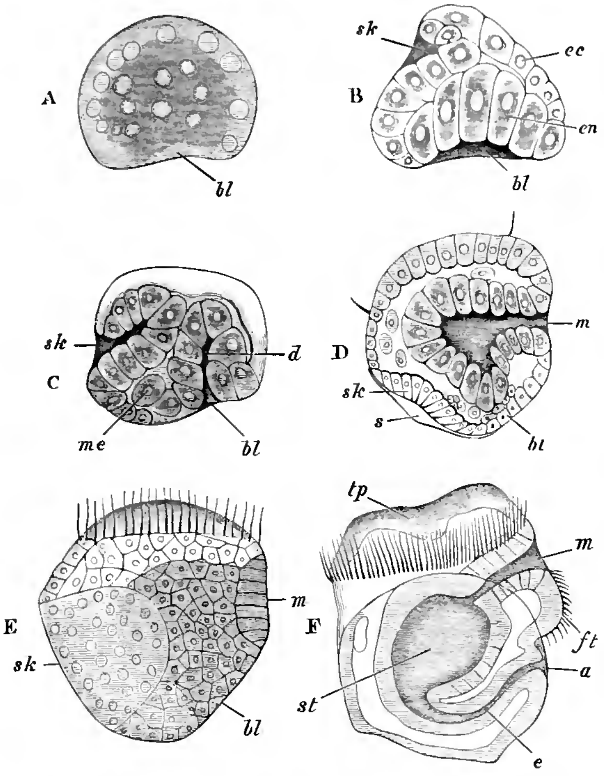


Fig. 6.—Development of the Oyster, *Ostrea edulis* (modified from Horst, 16). A. Blastula stage (one-cell-layered sac), with commencing invagination of the wall of the sac at *bl*, the blastopore. B. Optical section of a somewhat later stage, in which a second invagination has commenced—namely, that of the shell-gland *sk*; *bl*, blastopore; *en*, invaginated endoderm (wall of the future arch-enteron); *ec*, ectoderm. C. Similar optical section at a little later stage. The invagination connected with the blastopore is now more contracted, *d*; and cells, *me*, forming the mesoblast from which the cœlom and muscular and skeleto-trophic tissues develop, are separated. D. Similar section of a later stage. The blastopore, *bl*, has closed; the anus will subsequently perforate the corresponding area. A new aperture, *m*, the mouth, has eaten its way into the invaginated endodermal sac, and the cells pushed in with it constitute the stomodæum. The shell-gland, *sk*, is flattened out, and a delicate shell, *s*, appears on its surface. The ciliated velar ring is cut in the section, as shown by the two projecting cilia on the upper part of the figure. The embryo is now a Trochosphere. E. Surface view of an embryo at a period almost identical with that of D. F. Later embryo seen as a transparent object. *m*, mouth; *ft*, foot; *a*, anus; *e*, intestine; *st*, stomach; *tp*, velar area of the prostomium. The extent of the shell and commencing upgrowth of the mantle-skirt is indicated by a line forming a curve from *a* to F.

N.B.—In this development, as in that of Pisidium (figs. 150, 151), no part of the blastopore persists either as mouth or as anus, but the aperture closes,—the pedicle of invagination, or narrow neck of the invaginated arch-enteron, becoming the intestine. The mouth and the anus are formed as independent in-pushings, the mouth with stomodæum first, and the short anal proctodæum much later. This interpretation of the appearances is contrary to that of Horst (**16**), from whom our drawings of the oyster's development are taken. The account given by the American naturalist Brooks (**19**) differs greatly as to matter of fact from that of Horst, and appears to be erroneous in some respects.

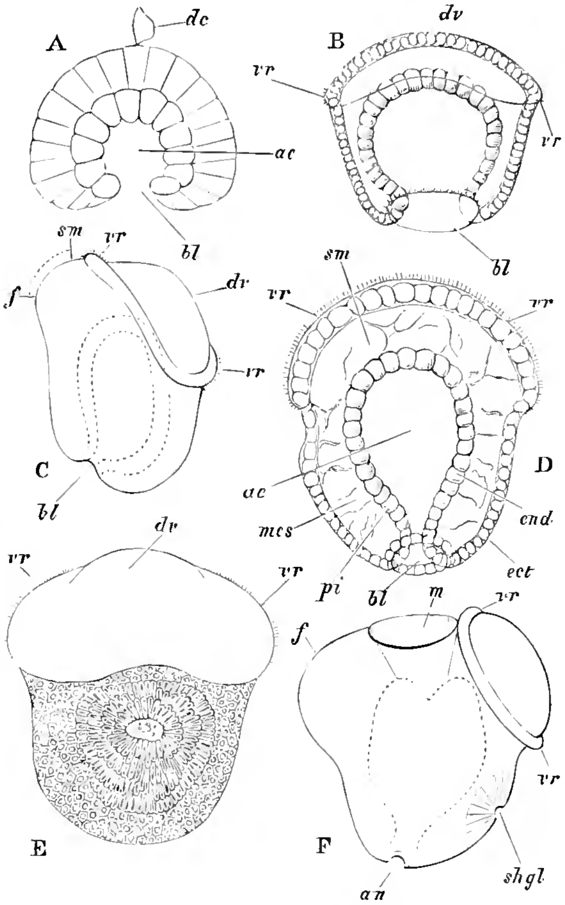


Fig. 7.—Development of the River-Snail, *Paludina vivipara* (after Lankester, **17**). *dc*, directive corpuscle (outcast cell); *ac*, arch-enteron or cavity lined by the enteric cell-layer or endoderm; *bl*, blastopore; *vr*, velum or circlet of ciliated cells; *dv*, velar area or cephalic dome; *sm*, site of the as yet unformed mouth; *f*, foot; *mes*, rudiments of the skeleto-trophic tissues; *pi*, the pedicle of invagination, the future rectum; *shgl*, the primitive shell-sac or shell-gland; *m*, mouth; *an*, anus. A. Diblastula phase (optical section). B. The Diblastula has become a Trochosphere by the development of the ciliated ring *vr* (optical section). C. Side view of the Trochosphere with commencing formation of the foot. D. Further advanced Trochosphere (optical section). E. The Trochosphere passing to the Veliger stage, dorsal view showing the formation of the primitive shell-sac. F. Side view of the same, showing foot, shell-sac (*shgl*), velum (*vr*), mouth, and anus.

N.B.—In this development the blastopore is not elongated; it persists as the anus. The mouth and stomodæum form independently of the blastopore.

The external form meanwhile passes through highly characteristic changes, which are on the whole fairly constant throughout the Mollusca. A circlet of cilia forms when the embryo is still nearly spherical (fig. 4, F; fig. 6, E; fig. 7, B), in an equatorial position. As growth proceeds, one hemisphere remains relatively small, the other elongates and enlarges. Both mouth and anus are placed in the larger area; the smaller area is the prostomium simply; the ciliated band is therefore in front of the mouth. The larval form thus produced is known as the Trochosphere. It exactly agrees with the larval form of many Chætopod worms and other Cœlomata. Most remarkable is its agreement with the adult form of the Wheel animalcules or Rotifera, which retain the præ-oral ciliated band as their chief organ of locomotion and prehension throughout life. So far the young Mollusc has not reached a definitely Molluscan stage of development, being only in a condition common to it and other Cœlomata. It now passes to the veliger phase, a definitely Molluscan form, in which the disproportion between the area in front of the ciliated circlet and that behind it is very greatly increased, so that the former is now simply an emarginated region of the head fringed with cilia (fig. 8; fig. 6, F; fig. 7, F; and fig. 60, A). It is termed the "velum," and is frequently drawn out into lobes and processes. As in the Rotifera, it serves the veliger larva as an organ of locomotion. In a very few Molluscs, but notably in the Common Pond-Snail, the emarginated bilobed velum is retained in full proportions in adult life (fig. 70), having lost its marginal fringe of specially long cilia and its locomotor function. The body of the Veliger is characterized by the development of the visceral hump on one surface, and by that of the foot on the other. Growth is greater in the vertical dorso-ventral axis than in the longitudinal oro-anal axis; consequently the foot is relatively small and projects as a blunt process between mouth and anus, which are not widely distant from one another, whilst the antipedal area projects in the form of a great hump or dome. In the centre of this antipedal area there has appeared (often at a very early period) a gland-like depression or follicle of the integument (fig. 6, C, *sk*; fig. 7, E, F, *shgl*; fig. 60, B; fig. 68, *shs*; fig. 72^{***}, *ss*). This is the primitive shell-sac discovered by Lankester (**18**) in 1871, and shown by him to precede the development of the permanent shell in a variety of Molluscan types. The cavity of this small sac becomes filled by a horny substance, and then it very usually disappears, whilst a delicate shell, commencing from this spot as a centre, forms and spreads upon the surface of the visceral dome.

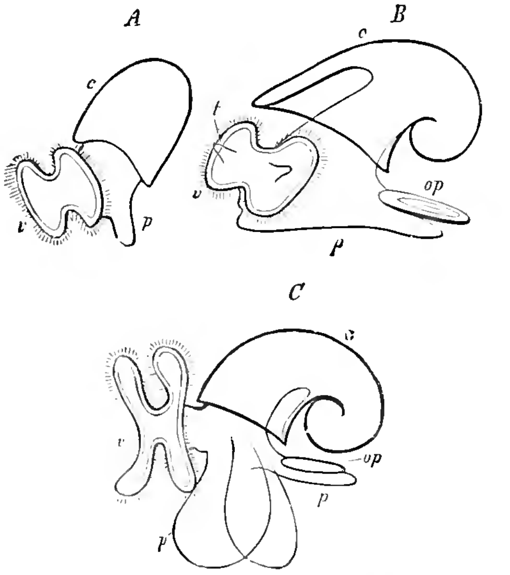


Fig. 8.—"Veliger" embryonic form of Mollusca (from Gegenbaur). *v*, velum; *c*, visceral dome with dependent mantle-skirt; *p*, foot; *t*, cephalic tentacles; *op*, operculum. A. Earlier, and B, later, Veliger of a Gastropod. C. Veliger of a Pteropod showing lobe-like processes of the velum and the great paired outgrowths of the foot.

The embryonic shell-sac or shell-gland represents in a transient form, in the individual development of most Mollusca, that condition of the shell-forming area which we have sketched above in the schematic Mollusc. In very few instances (in Chiton, and probably in Limax), as we shall see below, the *primitive shell-sac* is retained and enlarged as the permanent shell-forming area. It is supplanted in other Molluscs by a *secondary shell-forming area*, namely, that afforded by the free surface of the visceral hump, the shell-forming activity of which extends even to the surface of the depending mantle-skirt. Accordingly, in most Mollusca the *primitive shell* is represented only by the horny plug of the primitive shell-sac. The permanent shell is a new formation on a new area, and should be distinguished as a *secondary shell.*

The ctenidia, it will be observed, have not yet been mentioned, and they are indeed the last of the characteristic Molluscan organs to make their appearance. Their possible relation to the præ-oral and post-oral ciliated bands of embryos similar to the Trochosphere are discussed by the writer in the *Quart. Jour. Micr. Sci.*, vol. xvii. p. 423. The Veliger, as soon as its shell begins to assume definite shape, is no longer of a form common to various classes of Mollusca, but acquires characters peculiar to its class. At this point, therefore, we shall for the present leave it.

Systematic Review of the Classes and Orders of Mollusca.

We are now in a position to pass systematically in review the various groups of Mollusca, showing in what way they conform to the organization of our schematic Mollusc, and in what special ways they have modified or even suppressed parts present in it, or phases in the representative embryonic history which has just been sketched. It will be found that the foot, the shell, the mantle-skirt, and the ctenidia, undergo the most remarkable changes of form and proportionate development in the various classes—changes which are correlated with extreme changes and elaboration in the respective functions of those parts.

Division of the Phylum into two Branches.—The Mollusca are sharply divided into two great lines of descent or branches, according as the prostomial region is atrophied on the one hand, or largely developed on the other.

The probabilities are in favour of any ancestral form—the hypothetical archi-Mollusc which connected the Mollusca with their non-Molluscan forefathers—having possessed, as do all the more primitive forms of Cœlomata, a well-marked prostomium, and consequently a head. The one series of Mollusca descended from the primitive head-bearing Molluscs have acquired an organization in which the Molluscan characteristics have become modified in definite relation to a sessile inactive life. As the most prominent result of the adaptation to such sessile life they exhibit an atrophy of the cephalic region. They form the branch LIPOCEPHALA—the mussels, oysters, cockles, and clams. The other series have retained an active, in many cases a highly aggressive, mode of life; they have, correspondingly, not only retained a well-developed head, but have developed a special aggressive organ in connexion with the mouth, which, on account of its remarkable nature and the peculiarities of the details of its mechanism, serves to indicate a very close genetic connexion between all such animals as possess it. This remarkable organ is the odontophore, consisting of a lingual ribbon, rasp, or radula, with its cushion and muscles. On account of the possession of this organ this great branch of the Molluscan phylum may be best designated GLOSSOPHORA. Any term which merely points to the possession of a head is objectionable, since this is common to them and the hypothetical archi-Mollusca from which they descend. The term Odontophora, which has been applied to them, is also unsuitable, since the organ which characterizes them is not a tooth, but a tongue.

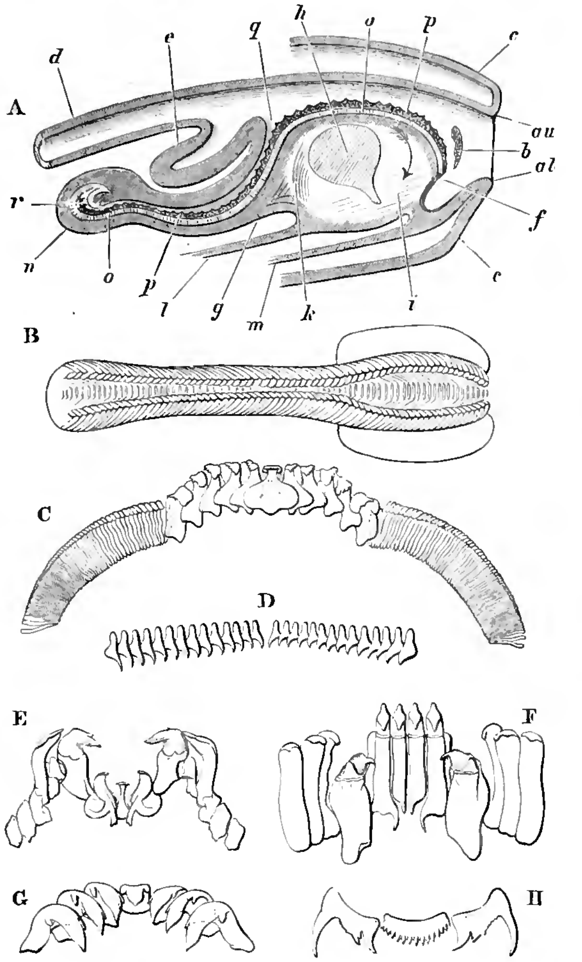


Fig. 9.—Odontophore of Glossophorous Mollusca.

A. Diagram showing mouth, œsophagus, and lingual apparatus of a Gastropod in section. *au*, upper lip; *al*, lower lip; *b*, calcareo-corneous jaw of left side; *c*, outer surface of the snout; *d*, œsophagus; *e*, fold in the wall of the œsophagus behind the radular sac (*n*); *f*, anterior termination of the radula and its bed, the point at which it wears away; *g*, base of the radular sac or recess of the pharynx; *h*, cartilaginous piece developed in the floor of the pharynx beneath the radula, and serving for the attachment of numerous muscles, and for the support of the radula; *i*, anterior muscles; *k*, posterior muscles attached to the cartilage; *l*, muscle acting as a retractor of the buccal mass; *m*, muscle attached to the lower lip; *n*, posterior extremity of the radular sac; *o*, the bed of the radula or layer of cells by which its lower surface is formed; *p*, the horny radula or lingual ribbon; *q*, opening of the radular sac into the pharynx or buccal cavity; *r*, cells at the extreme end of the inner surface of the radular sac which produce as a "cuticular secretion" the rows of teeth of the upper surface of the radula.

B. Radula or lingual ribbon of *Paludina vivipara*, stripped from its bed,—a horny, cuticular product.

C. A single row of teeth from the radula of *Trochus cinerarius*. Rhipidoglossate; formula, x.5.1.5.x.

D. A single row of teeth from the radula of *Faultima fragilis*. Ptenoglossate; formula, x.0.x.

E. A single row of teeth from the radula of *Chiton cinereus*. Too elaborate for formulation.

F. A single row of teeth from the radula of *Patella vulgata*. Formula, 3.1.4.1.3.

G. A single row of teeth from the radula of *Cypræa helvola*. Tænioglossate; formula, 3.1.3.

H. A single row of teeth from the radula of *Nassa annulata*. Rachiglossate; formula, 1.1.1. The Common Whelk is similar to this.

The general structure of the odontophore (= tooth-bearer, in allusion to the rasp-like ribbon) of the glossophorous Mollusca may be conveniently described at once. Essentially it is a tube-like outgrowth—the *radular sac* (fig. 9, A, *g*, *n*)—in the median line of the ventral floor of the stomodæum, upon the inner surface of which is formed a chitinous band (the radula) beset with minute teeth like a rasp (*p*). Anteriorly the ventral wall of the diverticulum is converted into cartilage (*h*), to which protractor and retractor muscles are attached (*k*, *i*), so that by the action of the former the cartilage, with the anterior end of the ribbon resting firmly upon it, may be brought forward into the space between the lips of the oral aperture (*au*, *al*), and made to exert there a backward and forward rasping action by the alternate contraction of retractor and protractor muscles attached to the cartilage. But in many Glossophora (*e.g.*, the Whelk) the apparatus is complicated by the fact that the diverticulum itself, with its contained radula, rests but loosely on the cartilage, and has special muscles attached to each end of it, arising from the body wall; these muscles pull the whole diverticulum or radular sac alternately backwards and forwards over the surface of the cartilage. This action, which is quite distinct from the movement of the cartilage itself, may be witnessed in a Whelk if the pharynx be opened whilst it is alive. It has also been seen in living transparent Gastropods. The chitinous ribbon is continuously growing forward from the tube-like diverticulum as a finger-nail does on its bed, and thus the wearing away of the part which rests on the cartilage and is brought into active use, is made up for by the advance of the ribbon in the same way as the wearing down of the finger-nail is counterbalanced by its own forward growth. And, just as the new substance of the finger-nail is formed in the concealed part, sunk posteriorly below a fold of skin, and yet is continually carried forward with the forward movement of the bed on which it rests, and which forms its undermost layers, so is the new substance of the radula formed in the compressed extremity of the radular sac (*n*), and carried forward by the forward movement of the bed (*o*) on which it rests, and by which is formed its undermost layer. This forward-moving bed is not merely the ventral wall of the radular diverticulum, but includes also that portion of the floor of the oral cavity to which the radula adheres (as far forward as the point *f* in fig. 9, A). At the spot where the radula ceases, the forward growth-movement of the floor also ceases, just as in the case of the finger-nail the similar growth-movement ceases at the line where the nail becomes free.

The radula or cuticular product of the slowly-moving bed can be stripped off, and is then found to consist of a ribbon-like area, upon which are set numerous tooth-like processes of various form in transverse rows, which follow one another closely, and exactly resemble one another in the form of their teeth (fig. 9, B). The tooth-like processes in a single transverse row are of very different shape and number in different members of the Glossophora, and it is possible to use a formula for their description. Thus, when in each row there is a single median tooth with three teeth on each side of it more or less closely resembling one another, as in fig. 9, G, we write the formula 3.1.3. When there are additional lateral pieces of a different shape to those immediately adjoining the central tooth, we indicate them by the figure 0, repeated to represent their number, thus 0000.1.1.1.0000 is the formula for the lingual teeth of *Chiton Stelleri*. A single median tooth, an admedian series, and a lateral series may be thus distinguished. In some Glossophora only median teeth are present, or large median teeth with a single small admedian tooth on each side of it (fig. 9, H); these are termed Rachiglossa (formula, —.1.— or 1.1.1). In a large number of Glossophora we have three admedian on each side and one median, no lateral pieces (fig. 9, G); these are termed Tænioglossa (formula, 3.1.3). Those with numerous lateral pieces, four to six or more admedian pieces, and a median piece or tooth (fig. 9, C) are termed Rhipidoglossa (formula, x.6.1.6.x, where x stands for an indefinite number of lateral pieces). The Toxoglossa have

1.0.1, the central tooth being absent and the lateral teeth peculiarly long and connected with muscles. The term Ptenoglossa (fig. 9, D) is applied to those Glossophora in which the radula presents no median tooth, but an indefinite and large number of admedian teeth, giving the formula x.0.x. When the admedian teeth are indefinite (forty to fifty), and a median tooth is present, the term Myriaglossa is applied (formula, x.1.x). It must be understood that the pieces or teeth thus formulated may themselves vary much in form, being either flat plates, or denticulated, hooked, or spine-like bodies. We shall revert to the terms thus explained in the systematic descriptions of the groups of Glossophora.

The muscular development in connexion with the whole buccal mass, and with each part of the radular apparatus, is exceedingly complicated,—as many as twenty distinct muscles having been enumerated in connexion with this organ. In addition to the radula, and correlated with its development, we find almost universally present in the Glossophora a pair of horny jaws (usually calcified) developed as cuticular productions upon the epidermis of the lips (fig. 9, A, *b*). The radula and the shelly jaws of the Glossophora enable their possessors not only to voraciously attack vegetable food, but the radula is used in some instances for boring the shells of other Mollusca, and the jaws for crushing the shells of Crustacea, and for wounding even Vertebrata.

Phylum MOLLUSCA.

Branch A.—*GLOSSOPHORA.*

Characters.—Mollusca with head-region more or less prominently developed; always provided with a peculiar rasping-tongue—the odontophore—rising from the floor of the buccal cavity.

The Glossophora comprise three classes, chiefly distinguished from one another by the modifications of the foot.

Class I.—**GASTROPODA.**

Characters.—Glossophora in which (with special exception of swimming forms) the FOOT is simple, median in position, and flattened so as to form a broad sole-like surface, by the contractions of which the animal crawls, often divided into three successive regions—the pro-, meso-, and meta-podium—by lateral constrictions.

The Gastropoda exhibit two divergent lines of descent indicated by the term sub-class (see p. 649).

Sub-class 1.—GASTROPODA ISOPLEURA.

Characters.—Gastropoda in which not only the head and foot but also the visceral dome with its contents and the mantle retain the primitive BILATERAL SYMMETRY of the archi-Mollusc. The anus retains its position in the median line at the posterior end of the body. The whole visceral mass together with the foot is elongated, so that the axis joining mouth and anus is relatively long, whilst the dorso-pedal axis at right angles to it is short. The CTENIDIA, the NEPHRIDIA, GENITAL DUCTS, and CIRCULATORY ORGANS are paired and bilaterally symmetrical. The pedal and visceral NERVE-CORDS are straight, parallel with one another, and all extend the whole length of the body; the ganglionic enlargements are feebly or not at all developed. The Isopleura comprise three orders.

Order 1.—**Polyplacophora** (the Chitons).

Characters.—Gastropoda Isopleura with a metameric repetition of the shell to the number of eight. The shells of the primitive type are partially or wholly concealed in shell-sacs comparable to the single embryonic shell-sac of other Mollusca. On the surface of the mantle-flap numerous calcified spines and knobs are frequently developed. The ctenidia are of the typical form, small in size and metamerically repeated along the sides of the body to the number of sixteen or more; an osphradium or area of "olfactory epithelium" (Spengel) is found at the base of each ctenidium. The other organs are not subject to metameric repetition. The odontophore is highly developed; the teeth of the lingual ribbon are varied in form,—several in each transverse row (fig. 9, E). Paired genital ducts distinct from the paired nephridia are present.

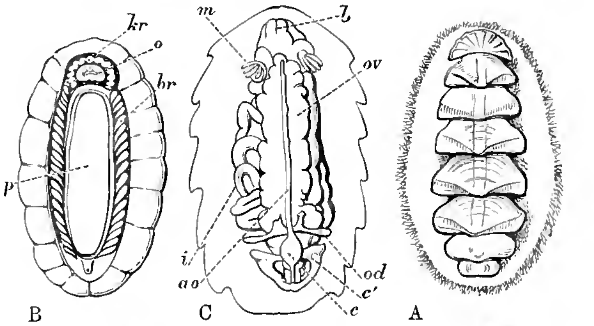


FIG. 10.—Three views of Chiton. A. Dorsal view of *Chiton Wosnessenksii*, Midd., showing the eight shells. (After Middendorf.) B. View from the pedal surface of a species of Chiton from the Indian Ocean. *p*, foot; *o*, mouth (at the other end of the foot is seen the anus raised on a papilla); *kr*, oral fringe; *br*, the numerous ctenidia (branchial plumes); spreading beyond these, and all round the animal, is the mantle-skirt. (After Cuvier.) C. The same species of Chiton, with the shells removed and the dorsal integument reflected. *b*, buccal mass; *m*, retractor muscles of the buccal mass; *ov*, ovary; *od*, oviduct; *i*, coils of intestines; *ao*, aorta; *c′*, left auricle; *c*, ventricle.

The order Polyplacophora contains but one family, the *Chitonidæ*, with the genera: *Chiton*, Lin. (figs. 10, 15, &c.); *Cryptochiton*, Midd., 1847; and *Cryptoplax* (= *Chitonellus*), Blainv., 1818.

Order 2.—**Neomeniæ.**

Characters.—Gastropoda Isopleura devoid of a shell, which is replaced by innumerable microscopic calcified plates or spicules set in the dorsal epidermis; mantle-flap not lateral, but reduced to a small collar surrounding the anus; ctenidia represented by a symmetrical group of branchial filaments on either side of the anus; foot very narrow, sunk in a groove; odontophore feebly developed, but the radula many-toothed; gonads placed in the pericardium discharging by the nephridia; no special generative ducts.

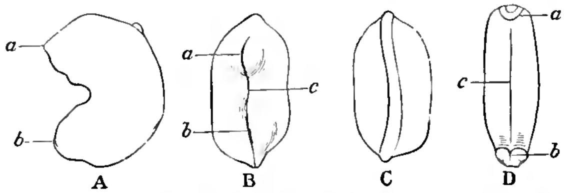


FIG. 11.—*Neomenia carinata*, Tullberg (after Tullberg). A. Lateral view. B. Ventral view. C. Dorsal view. D. Ventral view of a more extended specimen. *a*, anterior; *b*, posterior extremity; *c*, furrow, in which the narrow foot is concealed.

The order Neomeniæ contains the two genera *Neomenia*, Tullberg (*Solenopus*, *Sars*) (fig. 11); and *Proneomenia*, Hubrecht.

Order 3.—**Chætoderma.**

Characters.—Gastropoda Isopleura devoid of a shell, which is replaced by numerous minute calcareous spines standing up like hairs on the surface of the body; body

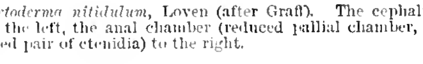


FIG. 12.—*Chætoderma nitidulum*, Loven (after Graff). The cephalic enlargement is to the left, the anal chamber (reduced pallial chamber, containing the concealed pair of ctenidia) to the right.

much elongated so as to be vermiform; mantle-flap as in Neomeniæ; ctenidia in the form of a pair of branchial plumes, one on each side of the anus; foot aborted, its position being indicated by a longitudinal furrow; odontophore greatly reduced, the radula only represented by a single tooth; gonads and nephridia as in Neomenia.

The order Chætoderma contains the single genus *Chætoderma* (fig. 12).

Further remarks on the Isopleurous Gastropods.—The union of the Chitons with the remarkable worm-like forms Neomenia and Chætoderma was rendered necessary by Hubrecht's discovery (**25**) in 1881 of a definitely constituted radula and odontophore in his new genus Proneomenia, founded on two specimens brought from the arctic regions by the Barents Dutch expedition.

By some writers—*e.g.*, Keferstein—the Chitons have been too intimately associated with the other Gastropoda, whilst, on the other hand, Gegenbaur seems to have gone a great deal too far in separating them altogether from the other Mollusca as a primary subdivision of that phylum, inasmuch as they are intimately bound to the other Glossophora by the possession of a thoroughly typical and well-developed odontophore. They undoubtedly stand nearer to the archi-Mollusca than any other Glossophora in having retained a complete bilateral symmetry and the primitive shell-sac, though the metameric repetition of this organ and of the ctenidia is a complication of, and departure from, the primitive character. It is not improbable that in the calcareous spines and plates of the dorsal integument of Neomenia and Chætoderma, which occur also on the part of the dorsum uncovered by shell in Chiton, we have the retention of a condition preceding the development of the solid Molluscan shell, or a reversion to it. The minute calcareous bodies may have the same relation to a compact shell which the shagreen denticles of the sharks have to a continuous dermal bone.

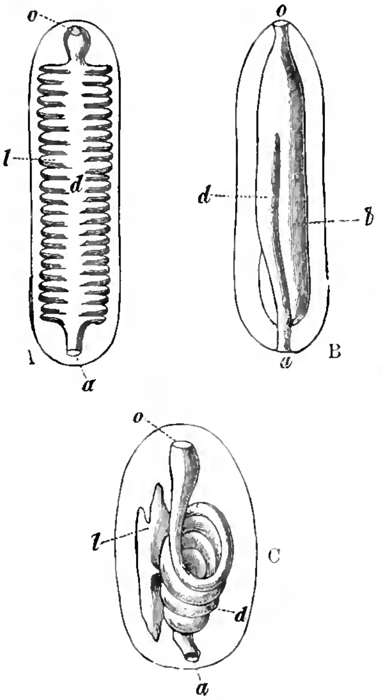


Fig. 13.—Diagrams of the alimentary canal of Isopleura (from Hubrecht). *o*, mouth; *a*, anus; *d*, alimentary canal; *l*, liver (digestive gland). A. Neomenia and Proneomenia. B. Chætoderma. C. Chiton.

The anatomy of the Gastropoda Isopleura has been largely elucidated within the past year by the researches of Hubrecht and of Sedgwick, who have been the first to apply the method of sections to the study of this group.

The leading points in the modifications of mantle-flap, foot, and ctenidia are set forth in the preceding summaries, and in the accompanying references to the figures. With regard to other organs, we have to note the form of the alimentary canal (fig. 13), which is simplest in Chætoderma, symmetrically sacculated in Neomenia, and wound upon itself, forming a few coils, in Chiton. The latter has a compact liver with arborescent duct, which is represented by the sacculi in Neomenia and by a single cæcum in Chætoderma. Salivary glands are present in Chiton and in Proneomenia. The radula is highly developed in Chiton, and, though present in Proneomenia, has not been described in Neomenia. A single tooth in Chætoderma appears to represent the radula in a reduced state. The circulatory organs of Chiton alone are known with any degree of detail (fig. 10, C). There is a median dorsal blood-vessel—the aorta—which is enlarged to form a ventricle in the posterior region of the body. On either side the ventricle is connected to a well-developed auricle, which pours into it the aerated blood from the gills (ctenidia). The extent to which vascular trunks are developed has not been determined, but vessels to and from the ctenidia, and in the mid-line of the foot, are known. As in other Mollusca, the vessels do not extend far, but lead into lacunæ between the organs and tissues. Dorsal and ventral vessels have been detected in Neomenia and Chætoderma, but no specialized heart.

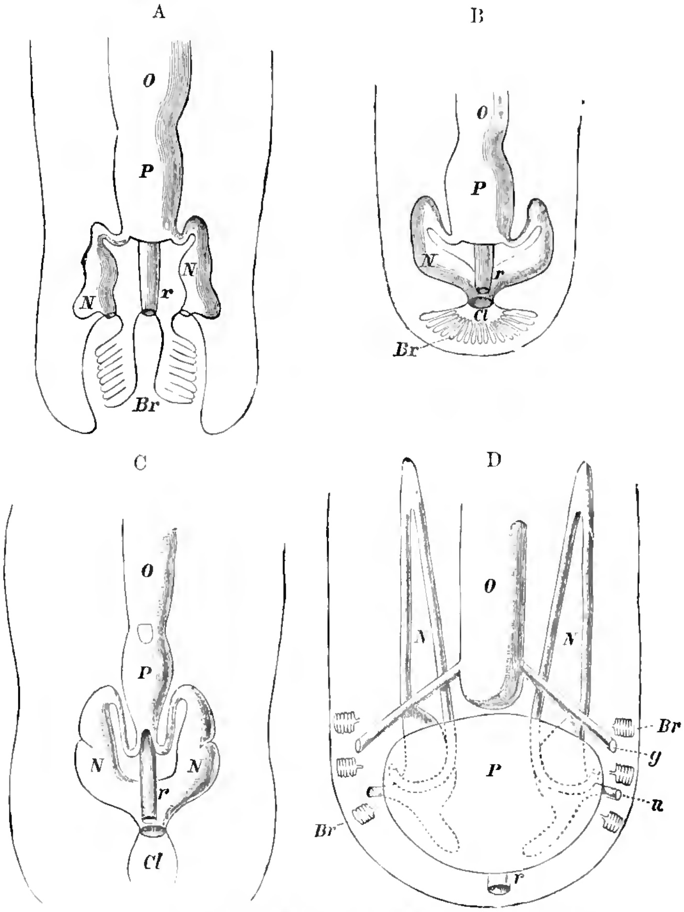


Fig. 14.—Diagrams of the excretory and reproductive organs of Isopleura (after Hubrecht). *O*, ovary; *P*, pericardium; *N*, nephridium; *n*, external aperture of nephridium; *g*, external aperture of the genital duct of Chiton; *r*, rectum; *Cl*, cloacal or pallial chamber of Neomeniæ and Chætoderma; *Br*, ctenidia (branchial plumes). A. Chætoderma. B. Neomenia. C. Proneomenia. D. Chiton.

The heart of Chiton lies in a space which is to be regarded as a specialized part of the cœlom, and, as in other Molluscs, is termed the pericardium. In front of this space in Chiton lies the ovary (fig. 14, D). In the other Isopleura the genital bodies (gonads) lie in the pericardium, which has a longer form and extends dorsally above the intestine. Opening into the pericardium equally in all the Isopleura (fig. 14) is a pair of bent tubes which lead to the exterior. These are the nephridia, which in Chiton are essentially renal in function. Their disposition has been determined by Sedgwick (**26**), who has shown that each nephridium is much bent on itself, so that, as in the nephridia of Conchifera (organ of Bojanus), the internal aperture lies near the external. From the folded stem of the nephridium very numerous secreting cæca are given off,—omitted in the diagram (fig. 14, D), but accurately drawn in fig. 15. The sexes in Chiton are distinct, and the ovary or testis, as the case may be, though lying in and filling a chamber of the original cœlom, does not discharge into the pericardium, but has its own ducts, which pass to the exterior just in front of those of the nephridia (fig. 14, D, *g*, and fig. 16). In this respect Chiton is less primitive than the other Isopleura, and even than some other Gastropods (the Zygobranchia), and some Conchifera (Spondylus, &c.), which have no special genital apertures, but make use of the nephridia for this purpose. In *Chiton discrepans*, in which there are sixteen pairs of ctenidia, the orifices of the nephridia are coincident with the sixteenth pair of ctenidia, those of the genital ducts with a point between the thirteenth and fourteenth ctenidia.

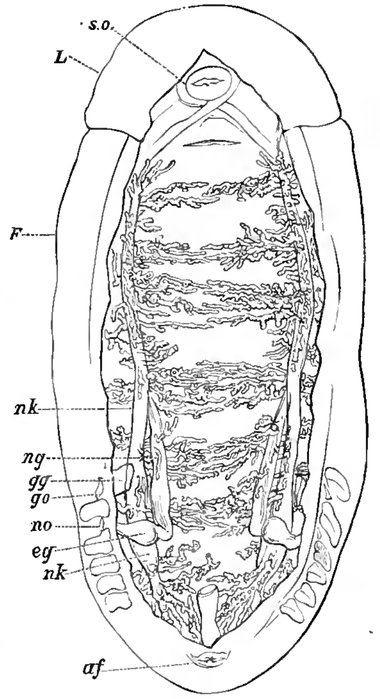


Fig. 15.—Dissection of the renal organs (nephridia) of *Chiton siculus*, after Haller (*Arbeiten, Zool. Instit.*, Vienna, 1882). *F*, foot; *L*, edge of the mantle not removed in the front part of the specimen; *s.o.*, œsophagus; *af*, anus; *gg*, genital duct; *go*, external opening of the same; *eg*, stem of the nephridium leading to *no*, its external aperture; *nk*, reflected portion of the nephridial stem; *ng*, fine cæca of the nephridium, which are seen ramifying transversely over the whole inner surface of the pedal muscular mass.

In the Neomeniæ and Chætoderma the nephridia are short and wide (*N* in fig. 14, A, B, C), and function as excretory ducts for the genital products, the gonads being lodged in the long pericardium. Their separate or united apertures open near the anus into the small chamber formed by the restriction of the mantle-skirt to the immediate neighbourhood of the anus.

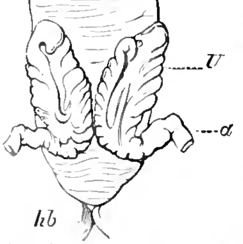


Fig. 16.—Ovary and oviducts of *Chiton siculus* (after Haller, *loc. cit.*). *vb*, *hb*, anterior and posterior suspensor of the ovary; *U*, uterus (enlarged part of oviduct); *o*, oviduct.

The nervous system of the Gastropoda Isopleura is represented in the diagram fig. 17. In all it is important to observe that nerve-ganglion cells are by no means limited to special swellings—the ganglia—but are abundant along the whole course of the four great longitudinal trunks. This is a primitive character comparable to that presented by the nerve-cords of Nemertine worms, and of the Arthropod Peripatus. Higher differentiation in other Mollusca leads to predominance if not an exclusive presence of nerve-*fibres* in the cords, and of nerve-*ganglion cells* in the specialized ganglia. The numerous transverse connexions of the pedal nerve-cords in Chiton and Neomenia (seen also in Fissurella (fig. 36) and some other Gastropods) are comparable to the transverse connexions of the ventral nerve-cords of Chætopod worms and Arthropods. In the abundance of the nervous network connected with its longitudinal nerve-tracts, Chiton appears to retain something of the early condition of the Cœlomate nervous system when it had the form of a sub-epidermic network or nerve-tunic (seen more clearly in Planarians and some Nemertines), and when the concentration into definitely compacted cords had not set in.

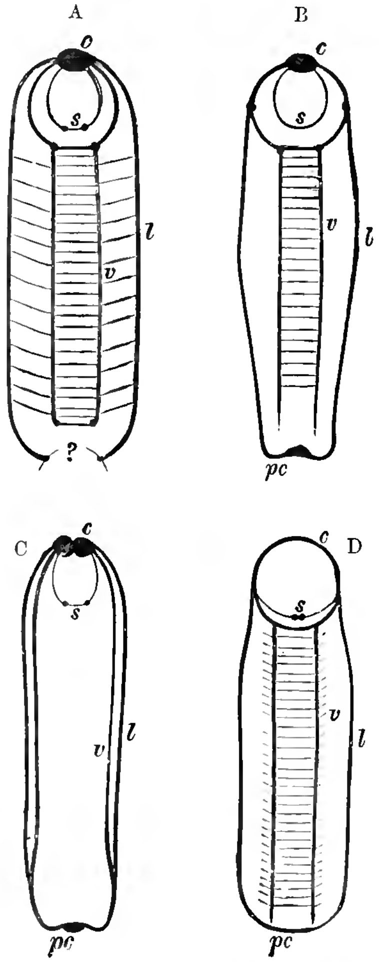


Fig. 17.—Diagrams of the nervous system of Isopleura (after Hubrecht, *loc. cit.*). *c*, cerebral ganglia; *s*, sublingual ganglia; *v*, pedal (ventral) nerve-cord; *l*, visceral (lateral) nerve-cord; *pc*, post-anal junction of the visceral nerve-cords. A. Proneomenia. B. Neomenia. C. Chætoderma. D. Chiton.

Ganglia are, however, distinguishable upon the nervous cords of Chiton (fig. 18). The cerebral ganglia are not distinguishable as such, but a pair of buccal ganglia (B in fig. 18) are developed on two connectives which pass forward from the cerebral region to the great muscular mass of the mouth. These buccal ganglia are special developments connected with the special muscularity of the lips and odontophore, and are found in all Glossophora, but not in the Lipocephala. Such special ganglia related to special organs (and not introduced in our schematic Mollusc, fig. 1) we find in connexion with the siphons of the Lipocephala, and in various positions upon the visceral nerve-cords of other Mollusca, both Glossophora and Lipocephala. A pair of pedal ganglia but little developed (*p* in fig. 18), and a special group of sublingual ganglia are present in Chiton. On the whole, the nervous system of the Isopleura is exceedingly simple and archaic, whilst it does not well serve as a type with which to compare that of other Mollusca on account of the small amount of concentration of its nerve-ganglion cells into ganglia, such as we find well developed in other forms.

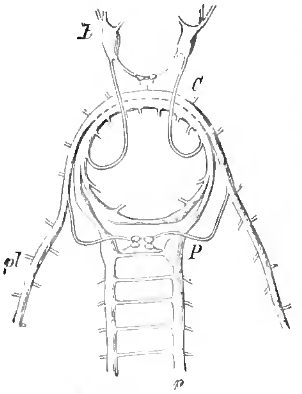


Fig. 18.—Anterior part of the nervous system of *Chiton cinereus*, in more detail (from Gegenbaur, *Elements of Comp. Anatomy*). *B*, buccal ganglia (concerned with the odontophore); *C*, cerebral nerve-mass; *P*, pedal ganglion and commencement of pedal nerve-cord; *pl*, visceral nerve-cord. The sublingual ganglia are not lettered.

The development of Neomenia and Chætoderma from the egg is entirely unknown, that of Chiton only partially. Impregnation is effected when the eggs have been discharged and are lying beneath the mantle-skirt. A trochosphere larva is developed from the Diblastula of Chiton (Loven).

The Chitons are found in the littoral zone in all parts of the world, and are exclusively marine. Neomenia, Proneomenia, and Chætoderma have hitherto been dredged from considerable depths (100 fathoms and upwards) in the North Sea, Proneomenia also in the Mediterranean (Marion).

Sub-class 2.—GASTROPODA ANISOPLEURA.

Characters.—Gastropoda in which, whilst the head and foot retain the bilateral symmetry of the archi-Mollusca, the visceral dome, including the mantle-flap dependent from it, and the region on which are placed the ctenidia, anus, generative and nephridial apertures, have been subjected to a ROTATION tending to bring the anus from its posterior median position, by a movement along the right side, forwards to a position above the right side of the animal's neck, or even to the middle line above the neck. This torsion is connected mechanically with the excessive vertical growth of the visceral hump and the development upon its surface of a heavy shell. The SHELL is not a plate enclosed in a shell-sac, but the primitive shell-sac appears and disappears in the course of embryonic development, and a relatively large nautiloid shell (with rare exceptions) develops over the whole surface of the visceral hump and mantle-skirt. Whilst such a shell might retain its median position in a swimming animal, it and the visceral hump necessarily fall to one side in a creeping animal which carries them uppermost.

The shell and visceral hump in the Anisopleura incline normally to the right side of the animal. As mechanical results, there arise a one-sided pressure and a one-sided strain, together with a one-sided development of the muscular masses which are related to the shell and foot. Both the TORSION THROUGH A SEMICIRCLE of the base of the visceral dome and the continued leiotropic spiral growth of the visceral dome itself, which is very usual in the Anisopleura, appear to be traceable to these mechanical conditions. ATROPHY of the representatives on one side of the body of paired organs is very usual. Those placed primitively on the left side of the rectum, which in virtue of the torsion becomes the right side, are the set which suffer (see fig. 19). Some Anisopleura, after having thus acquired a strongly-marked inequilateral character in regard to such organs as the ctenidia, nephridia, genital ducts, heart, and rectum, appear by further change of conditions of growth to have acquired a superficial bilateral symmetry, the secondary nature of which is revealed by anatomical examination (Opisthobranchia, Natantia).

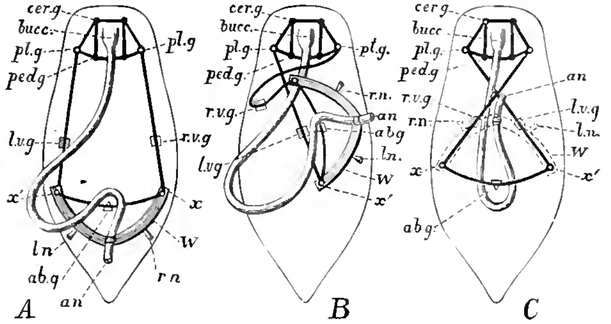


FIG. 19.—Sketch of a model designed so as to show the effect of torsion or rotation of the visceral hump in Streptoneurous Gastropoda; *A*, unrotated ancestral condition, *B*, quarter-rotation; *C*, complete semi-rotation (the limit); *an*, anus; *ln*, *rn*, primarily left nephridium and primarily right nephridium; *lvg*, primarily left (subsequently the sub-intestinal) visceral ganglion; *rvg*, primarily right (subsequently the sub-intestinal) visceral ganglion; *cerg*, cerebral ganglion; *plg*, pleural ganglion; *pedg*, pedal ganglion; *abg*, abdominal ganglion; *bucc*, buccal mass; *W*, wooden arc representing the base-line of the wall of the visceral hump; *x*, *x'*, pins fastening the elastic cord (representing the visceral nerve loop) to *W*.

In all groups of Anisopleura examples are numerous in which the shell is greatly developed, forming a "house" into which the whole animal can be withdrawn, the entrance being often closed by a second shelly piece carried upon the foot (the operculum). The power of rapidly extending and of again contracting large regions of the body to an enormous degree is usual, as in the Lipocephalous Mollusca. In spite of the theories which have been held on this matter, it appears highly probable that no fluid from without is introduced into the blood, nor is any expelled during these changes of form. A large mucous gland with a median pore is usually developed on the ventral surface of the foot, comparable to the similar gland and pore in Lipocephala, and in some cases (*e.g.*, Pyrula, fig. 37, B) this has been mistaken for a water-pore.

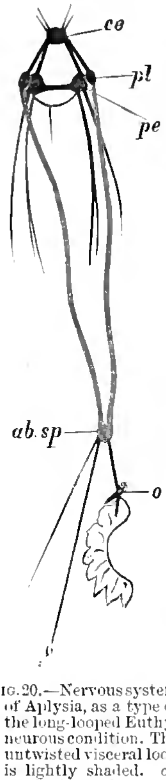


FIG. 20.—Nervous system of Aplysia, as a type of the long-looped Euthyneurous condition. The untwisted visceral loop is lightly shaded. *ce*, cerebral ganglion; *pl*, pleural ganglion; *pe*, pedal ganglion; *ab. sp*, abdominal ganglion, which represents also the supra-intestinal ganglion of Streptoneura and gives off the nerve to the osphradium (olfactory organ) *o*, and another to an unlettered so-called "genital" ganglion. The buccal nerves and ganglia are omitted. (After Spengel.)

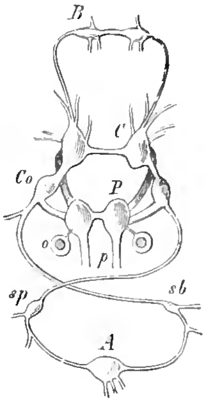


FIG. 21.—Nervous system of Paludina as a type of the Streptoneurous condition. *B*, buccal (sub-œsophageal) ganglion; *C*, cerebral ganglion; *Co*, pleural ganglion; *P*, pedal ganglion with otocyst attached; *p*, pedal nerve; *A*, abdominal ganglion at the extremity of the twisted visceral "loop"; *sp*, supra-intestinal visceral ganglion on the course of the right visceral cord; *sb*, sub-intestinal ganglion on the course of the left visceral cord. (From Gegenbaur, after Jhering.)

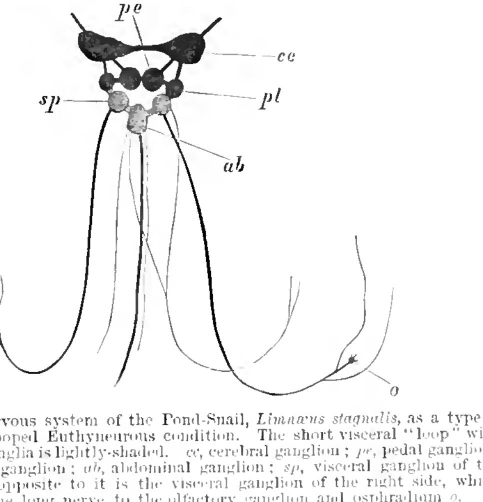


FIG. 22.—Nervous system of the Pond-Snail, *Limnæus stagnalis*, as a type of the short-looped Euthyneurous condition. The short visceral "loop" with its three ganglia is lightly-shaded. *ce*, cerebral ganglion; *pe*, pedal ganglion; *pl*, pleural ganglion; *ab*, abdominal ganglion; *sp*, visceral ganglion of the left side; opposite to it is the visceral ganglion of the right side, which gives off the long nerve to the olfactory ganglion and osphradium *o*. In Planorbis and in Auricula (Pulmonata, allied to Limnæus) the olfactory organ is on the *left* side and receives its nerve from the *left* visceral ganglion. (After Spengel.)

The leiotropic torsion of the visceral dome has had less deep-seated effect in one series of Anisopleura than in another. Accordingly, as the loop formed by the two VISCERAL NERVES (fig. 19) is or is not caught, as it were, in the twist, we are able to distinguish one branch or line of descent with straight visceral nerves—the EUTHYNEURA (fig. 20)—from a second branch with the visceral nerves twisted into a figure-of-eight—the STREPTONEURA (fig. 21). Probably the Euthyneura and the Streptoneura have developed independently from the ancestral bilaterally symmetrical Gastropods. The escape of the visceral nerve-loop from the torsion depends on its having acquired a somewhat deeper position and shorter extent, previously to the commencement of the phenomenon of torsion, in the ancestors of the Euthyneura than in those of the Streptoneura. In the ancestral Streptoneura the visceral loop was lateral and superficial as in the living Isopleura.

Branch *a.*—*STREPTONEURA* (Spengel, 1881).

Characters.—Gastropoda Anisopleura in which the visceral "loop" (the conterminous visceral nerves) was adherent to the body-wall and so shared in the torsion of the visceral hump, the right cord crossing above the left so as to form a figure-of-eight (see fig. 19).

The Streptoneura comprise two orders—the Zygobranchia and the Azygobranchia.

Order 1.—**Zygobranchia.**

Characters.—Streptoneura in which, whilst the visceral torsion is very complete so as to bring the anus into the middle line anteriorly or nearly so, the atrophy of the primitively left-side organs is not carried out. The right and left ctenidia, which have now become left and right respectively, are of equal size, and are placed symmetrically on either side of the neck in the pallial space. Related to them is a simple pair of osphradial patches. Both right and left nephridia are present, the actual right one being much larger than the left. Two auricles may be present right and left of a median ventricle (Haliotis), or only one (Patella). The Zygobranchia are further very definitely characterized by the archaic character of absence of special genital ducts. The generative products escape by the larger nephridium. The sexes are distinct, and there is no copulatory or other accessory generative apparatus. The teeth of the lingual ribbon are highly differentiated (Rhipidoglossate). The visceral dome lies close upon the oval sucker-like foot, and is coextensive with its prolongation in the aboral direction.

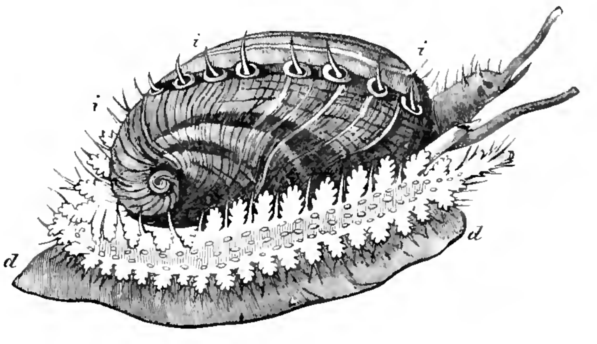


FIG. 23.—*Haliotis tuberculata.* *d*, foot; *i*, tentacular processes of the mantle. (From Owen, after Cuvier.)

The Zygobranchia comprise three families, arranged in two sub-orders.

Sub-order 1. *Ctenidiobranchia.*

Character.—Large paired ctenidia acting as gills.

Family 1.—*Haliotidæ.*

Genera: *Haliotis* (Ear-Shell, Ormer in Guernsey); mostly tropical; *Teinotis.*

Family 2.—*Fissurellidæ.*

Genera: *Fissurella* (Key-hole Limpet) (figs. 24, 36), *Emarginula, Parmophorus* (fig. 25); mostly tropical.

Sub-order 2. *Phyllidiobranchia.*

Characters.—Ctenidia reduced to wart-like papillæ; special sub-pallial lamellæ, similar to those of the Opisthobranch Pleurophyllidia, perform the function of gills.

Family 3.—*Patellidæ.*

Genera: *Patella* (Limpet, figs. 26, &c.), *Nacella* (Bonnet-Limpet), *Lottia.*

Further Remarks on Zygobranchia.—The Common Limpet is a specially interesting and abundant example of the remarkable order Zygobranchia. A complete and accurate account of its anatomy has yet to be written. Here we have only space for a brief outline. The foot of the Limpet is a nearly circular disc of muscular tissue; in front, projecting from and raised above it, are the head and neck (figs. 26, 30). The visceral hump forms a low conical dome above the subcircular foot, and standing out all round the base of this dome so as to completely overlap the head and foot, is the circular mantle-skirt. The depth of free mantle-skirt is greatest in front, where the head and neck are covered in by it. Upon the surface of the visceral dome, and extending to the edge of the free mantle-skirt, is the conical shell. When the shell is taken away (best effected by immersion in hot water) the surface of the visceral dome is found to be covered by a black-coloured epithelium, which may be removed, enabling the observer to note the position of some organs lying below the transparent integument (fig. 27). The muscular columns (*c*) attaching the foot to the shell form a ring incomplete in front, external to which is the free mantle-skirt. The limits of the large area formed by the flap over the head and neck (*ecr*) can be traced, and we note the anal papilla showing through and opening on the right shoulder, so to speak, of the animal into the large anterior region of the sub-pallial space. Close to this the small renal organ (*i*, mediad) and the larger renal organ (*k*, to the right and posteriorly) are seen, also the pericardium (*l*) and a coil of the intestine (*int*) embedded in the compact liver.

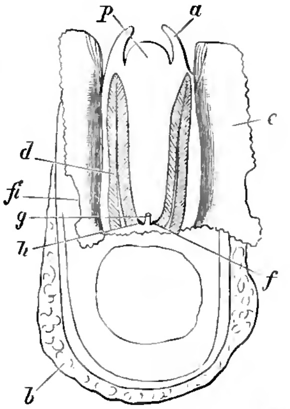


FIG. 24.—Dorsal aspect of a specimen of Fissurella from which the shell has been removed, whilst the anterior area of the mantle-skirt has been longitudinally slit and its sides reflected. *a*, cephalic tentacle; *b*, foot; *d*, left (archaic right) gill-plume; *e*, reflected mantle-flap; *fi*, the fissure or hole in the mantle-flap traversed by the longitudinal incision; *f*, right (archaic left) nephridium's aperture; *g*, anus; *h*, left (archaic right) aperture of nephridium; *p*, snout. (Original.)

On cutting away the anterior part of the mantle-skirt so as to expose the sub-pallial chamber in the region of the neck, we find the right and left renal papillæ (discovered by Lankester (**27**) in 1867) on either side the anal papilla (fig. 28), but no gills. If a similar examination be made of the allied genus Fissurella (fig. 24, *d*), we find right and left of the two renal apertures a right and left gill-plume or ctenidium, which by their presence here and in Haliotis furnish the distinctive character to which the name Zygobranchia refers. In Patella no such plumes exist, but right and left of the neck are seen a pair of minute oblong yellow bodies (fig. 28, *d*), which were originally described by Lankester as orifices possibly connected with the evacuation of the generative

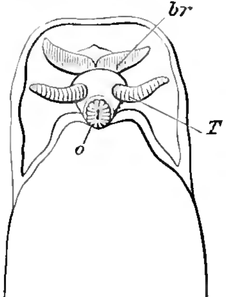


FIG. 25.—Parmophorus, seen from the pedal surface. *o*, mouth; *T*, cephalic tentacle; *br*, one of the two symmetrical gills placed on the neck. (Original.)

products. On account of their position they were termed by him the "capito-pedal orifices," being placed near the junction of head and foot. Spengel (**24**) has, however, in a most ingenious way shown that these bodies are the representatives of the typical pair of ctenidia, here reduced to a mere rudiment. Near to each rudimentary ctenidium Spengel has discovered an olfactory patch or osphradium (consisting of modified epithelium) and an olfactory nerve-ganglion (fig. 32). It will be remembered that, according to Spengel, the osphradium of Mollusca is definitely and intimately related to the gill-plume or ctenidium, being always placed near the base of that organ; further, Spengel has shown that the nerve-supply of this olfactory organ is always derived from the visceral loop. Accordingly, the nerve-supply affords a means of testing the conclusion that we have in Lankester's capito-pedal bodies the rudimentary ctenidia. The accompanying diagrams (figs. 34, 35) of the nervous systems of Patella and of Haliotis, as determined by Spengel, show the identity in the origin of the nerves passing from the visceral loop to Spengel's olfactory ganglion of the Limpet, and that of the nerves which pass from the visceral loop of Haliotis to the olfactory patch or osphradium, which lies in immediate relation on the right and on the left side to the right and the left gill-plumes (ctenidia) respectively. The same diagrams serve to demonstrate the Streptoneurous condition of the visceral loop in Zygobranchia.

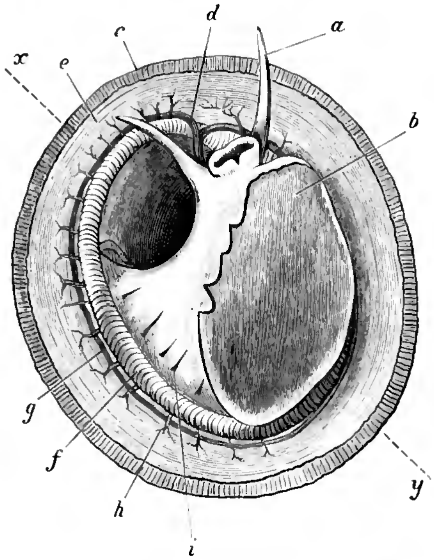


FIG. 26.—The Common Limpet (*Patella vulgata*) in its shell, seen from the pedal surface. *x*, *y*, the median antero-posterior axis; *a*, cephalic tentacle; *b*, plantar surface of the foot; *c*, free edge of the shell; *d*, the branchial efferent vessel carrying aerated blood to the auricle, and here interrupting the circlet of gill lamellæ; *e*, margin of the mantle-skirt; *f*, gill lamellæ (*not* ctenidia, but special pallial growths, comparable to those of Pleurophyllidia); *g*, the branchial efferent vessel; *h*, factor of the branchial advehent vessel; *i*, interspaces between the muscular bundles of the root of the foot, causing the separate areæ seen in fig. 27, *c*. (Original.)

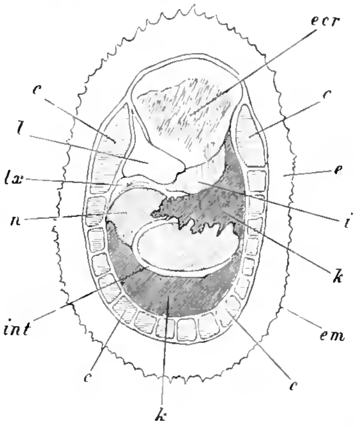


FIG. 27.—Dorsal surface of the Limpet removed from its shell and deprived of its black pigmented epithelium; the internal organs are seen through the transparent body-wall. *c*, muscular bundles forming the root of the foot, and adherent to the shell; *e*, free mantle-skirt; *em*, tentaculiferous margin of the same; *i*, smaller (left) nephridium; *k*, larger (right) nephridium; *l*, pericardium; *lx*, fibrous septum, behind the pericardium; *n*, liver; *int*, intestine; *ecr*, anterior area of the mantle-skirt overhanging the head (cephalic hood). (Original.)

Thus, then, we find that the Limpet possesses a symmetrically-disposed pair of ctenidia in a rudimentary condition, and justifies its position among Zygobranchia. At the same time it possesses a totally distinct series of *functional* gills, which are not derived from the modification of the typical Molluscan ctenidium. These gills are in the form of delicate lamellæ (fig. 26, *f*), which form a series extending completely round the inner face of the depending mantle-skirt. This circlet of gill-lamellæ led Cuvier to class the Limpets as Cyclobranchiata, and, by erroneous identification of them with the series of metamerically repeated ctenidia of Chiton, to associate the latter Mollusc with the former. The gill-lamellæ of Patella are processes of the mantle comparable to the plait-like folds often observed on the roof of the branchial chamber in other Gastropoda (*e.g.*, Buccinum and Haliotis). They are termed pallial gills. The only other Molluscs in which they are exactly represented are the curious Opisthobranchs Phyllidia and Pleurophyllidia (fig. 57). In these, as in Patella, the typical ctenidia are aborted, and the branchial function is assumed by close-set lamelliform processes arranged in a series beneath the mantle-skirt on either side of the foot. In fig. 26, *d* the large branchial vein of Patella bringing blood from the gill-series to the heart is seen; where it crosses the series of lamellæ there is a short interval devoid of lamellæ.

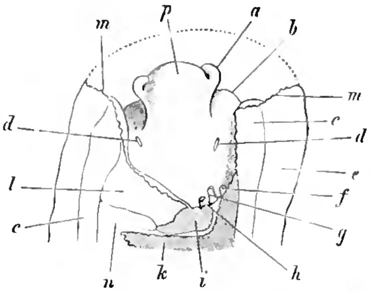


FIG. 28.—Anterior portion of the same Limpet, with the overhanging cephalic hood removed. *a*, cephalic tentacle; *b*, foot; *c*, muscular substance forming the root of the foot; *d*, the capito-pedal organs of Lankester (=rudimentary ctenidia); *e*, mantle-skirt; *f*, papilla of the larger nephridium; *g*, anus; *h*, papilla of the smaller nephridium; *i*, smaller nephridium; *k*, larger nephridium; *l*, pericardium; *m*, cut edge of the mantle-skirt; *n*, liver; *p*, snout. (Original.)

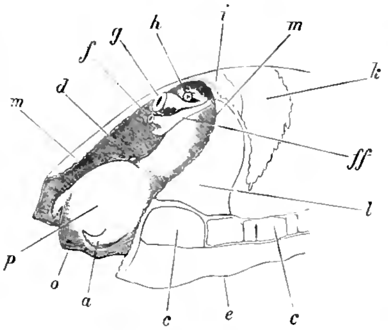


FIG. 29.—The same specimen viewed from the left front, so as to show the sub-anal tract (*ff*) of the larger nephridium, by which it communicates with the pericardium. *o*, mouth; other letters as in fig. 28.

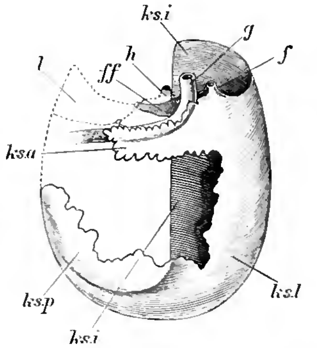


FIG. 30.—Diagram of the two renal organs (nephridia), to show their relation to the rectum and to the pericardium. *f*, papilla of the larger nephridium; *g*, anal papilla with rectum leading from it; *h*, papilla of the smaller nephridium, which is only represented by dotted outlines; *l*, pericardium indicated by a dotted outline,—at its right side are seen the two reno-pericardial pores; *ff*, the sub-anal tract of the large nephridium given off near its papilla and seen through the unshaded smaller nephridium; *ks.a*, anterior superior lobe of the large nephridium; *ks.l*, left lobe of same; *ks.p*, posterior lobe of same; *ks.i*, inferior sub-visceral lobe of same. (Original.)

The heart in Patella consists of a single auricle (not two as in Haliotis and Fissurella) and a ventricle; the former receives the blood from the branchial vein, the latter distributes it through a large aorta which soon leads into irregular blood-lacunæ.

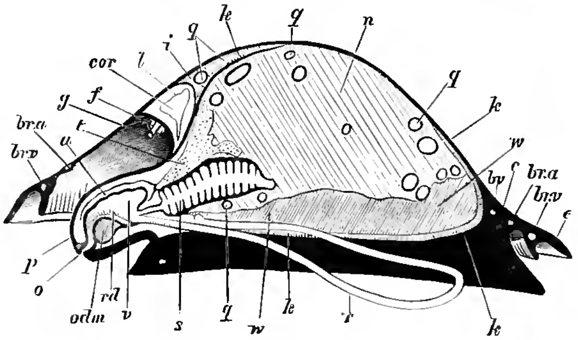


FIG. 31.—Diagram of a vertical antero-postero median section of a Limpet. Letters as in figs. 28, 29, with following additions: *q*, intestine in transverse section; *r*, lingual sac (radular sac); *rd*, radula; *s*, lamellated stomach; *t*, salivary gland; *u*, duct of same; *v*, buccal cavity; *w*, gonad; *br.a*, branchial advehent vessel (artery); *br.v*, branchial efferent vessel (vein); *bv*, blood-vessel; *odm*, muscles and cartilage of the odontophore; *cor*, heart within the pericardium. (Original.)

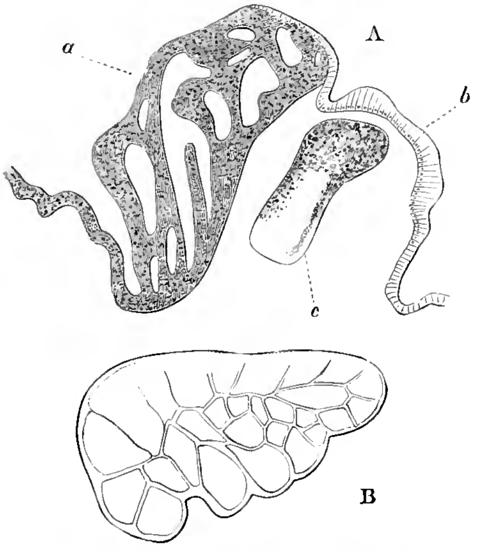


FIG. 32.—A. Section in a plane vertical to the surface of the neck of Patella through *a*, the rudimentary ctenidium (Lankester's organ), and *b*, the olfactory epithelium (osphradium); *c*, the olfactory (osphradial) ganglion. (After Spengel.) B. Surface view of a rudimentary ctenidium of Patella, excised and viewed as a transparent object. (Original.)

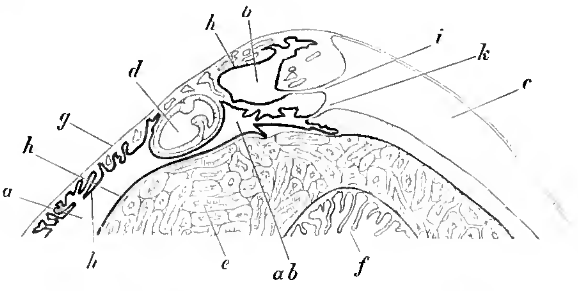


FIG. 33.—Vertical section in a plane running right and left through the anterior part of the visceral hump of Patella, to show the two renal organs and their openings into the pericardium. *a*, large or external or right renal organ; *ab*, narrow process of the same running *below* the intestine and leading by *k* into the pericardium; *b*, small or median renal organ; *c*, pericardium; *d*, rectum; *e*, liver; *f*, manyplies; *g*, epithelium of the dorsal surface; *h*, renal epithelium lining the renal sacs; *i*, aperture connecting the small sac with the pericardium; *k*, aperture connecting the large sac with the pericardium. (From an original drawing by Mr J. T. Cunningham, Fellow of University College, Oxford.)

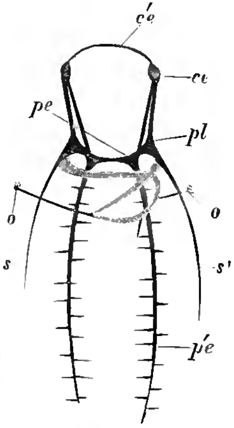


FIG. 34.—Nervous system of Patella; the visceral loop is lightly shaded; the buccal ganglia are omitted. *ce*, cerebral ganglia; *c'e*, cerebral commissure; *pl*, pleural ganglion; *pe*, pedal ganglion; *p'e*, pedal nerve; *s*, *s'*, nerves (right and left) to the mantle; *o*, olfactory ganglion, connected by nerve to the Streptoneurous visceral loop. (After Spengel.)

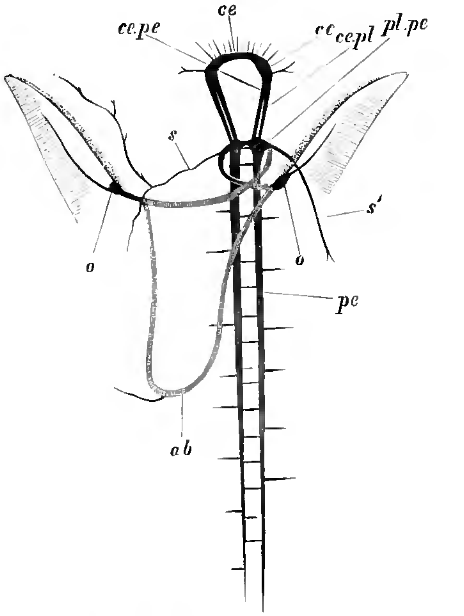


FIG. 35.—Nervous system of Haliotis; the visceral loop is lightly shaded; the buccal ganglia are omitted. *ce*, cerebral ganglion; *pl.pe*, the fused pleural and pedal ganglia; *pe*, the right pedal nerve; *ce.pl*, the cerebro-pleural connective; *ce.pe*, the cerebro-pedal connective; *s*, *s'*, right and left mantle nerves; *ab*, abdominal ganglion or site of same; *o*, *o*, right and left olfactory ganglia and osphradia receiving nerve from visceral loop. (After Spengel.)

The existence of two renal organs in Patella, and their relation to the pericardium (a portion of the cœlom), is important. Each renal organ is a sac lined with glandular epithelium (ciliated cells with concretions) communicating with the exterior by its papilla, and by a narrow passage with the pericardium. The connexion with the pericardium of the smaller of the two renal organs was demonstrated by Lankester in 1867, at a time when the fact that the renal organ of the Mollusca, as a rule, opens into the pericardium, and is therefore a typical nephridium, was not known. Subsequent investigations (**27**) carried on under the direction of the same naturalist have shown that the larger as well as the smaller renal sac is in communication with the pericardium. The walls of the renal sacs are deeply plaited and thrown into ridges. Below the surface these walls are excavated with blood-vessels, so that the sac is practically a series of blood-vessels covered with renal epithelium, and forming a mesh-work within a space communicating with the exterior. The larger renal sac (remarkably enough, that which is aborted in other Anisopleura) extends between the liver and the integument of the visceral dome very widely. It also bends round the liver as shown in fig. 30, and forms a large sac on half of the upper surface of the muscular mass of the foot. Here it lies close upon the genital body (ovary or testis), and in such intimate relationship with it that, when ripe, the gonad bursts into the renal sac, and its products are carried to the exterior by the papilla on the right side of the anus (Robin, Dall). This fact led Cuvier erroneously to the belief that a duct existed leading from the gonad to this papilla. The position of the gonad, best seen in the diagrammatic section (fig. 31), is, as in other Zygobranchia, devoid of a special duct communicating with the exterior. This condition, probably an archaic one, distinguishes the Zygobranchia among all Glossophorous Mollusca.

The digestive tract of Patella offers some interesting features. The odontophore is powerfully developed; the radular sac is extraordinarily long, lying coiled in a space between the mass of the liver and the muscular foot. The radula has 160 rows of teeth with twelve teeth in each row. Two pairs of salivary ducts, each leading from a salivary gland, open into the buccal chamber. The œsophagus leads into a remarkable stomach, plaited like the manyplies of a sheep, and after this the intestine takes a very large number of turns embedded in the yellow liver, until at last it passes between the two renal sacs to the anal papilla. A curious ridge (spiral? valve) which secretes a slimy cord is found upon the inner wall of the intestine. The general structure of the Molluscan intestine has not been sufficiently investigated to render any comparison of this structure of Patella with that of other Mollusca possible. The eyes of the Limpet (**28**) deserve mention as examples of the most primitive kind of eye in the Molluscan series. They are found one on each cephalic tentacle, and are simply minute open pits or depressions of the epidermis, the epidermic cells lining them being pigmented and connected with nerves (compare fig. 118).

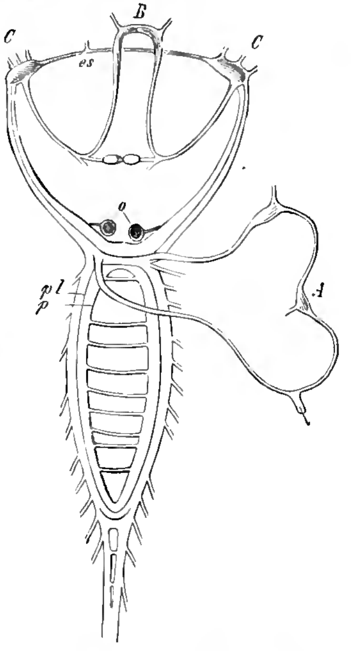


Fig. 36.—Nervous system of Fissurella. *pl*, pallial nerve; *p*, pedal nerve; *A*, abdominal ganglia in the Streptoneurous visceral commissure, with supra- and sub-intestine ganglion on each side; *B*, buccal ganglia; *C*, *C*, cerebral ganglia; *es*, cerebral commissure; *o*, otocysts attached to the cerebro-pedal connectives. (From Gegenbaur, after Jhering.)

The Limpet breeds upon the southern English coast in the early part of April, but its development has not been followed. It has simply been traced as far as the formation of a Diblastula which acquires a ciliated band, and becomes a nearly spherical Trochosphere. It is probable that the Limpet takes several years to attain full growth, and during that period it frequents the same spot, which becomes gradually sunk below the surrounding surface, especially if the rock be carbonate of lime. At low tide the Limpet (being a strictly inter-tidal organism) is exposed to the air, and is to be found upon its spot of fixation; but when the water again covers it, it (according to trustworthy observers) quits its attachment and walks away in search of food (minute encrusting algæ), and then once more as the tide falls returns to the identical spot, not an inch in diameter, which belongs, as it were, to it. Several million Limpets —twelve millicn in Berwickshire alone—are annually used on the east coast of Britain as bait.

Order 2.—**Azygobranchia.**

Characters.—Streptoneura which, as a sequel to the torsion of the visceral hump, have lost by atrophy the originally left ctenidium and the originally left nephridium, retaining the right ctenidium as a comb-like gill-plume to the actual left of the rectum, and the right nephridium (that which is the smaller in the Zygobranchia) also to the actual left of the rectum, between it and the gill-plume. The right olfactory organ only is retained, and may assume the form of a comb-like ridge to the actual left of the ctenidium or branchial plume. It has been erroneously described as the second gill, and is known as the parabranchia. The rectum itself lies on the animal's right shoulder. The presence of glandular plication of the surface of the mantle-flap (fig. 46, *x*) and an adrectal gland (purple-gland, fig. 47, *gp*) are frequently observed. The sexes are always distinct; a special genital duct (oviduct or sperm duct) unpaired is present, opening either by the side of the anus or, in the males, on the right side of the neck in connexion with a large penis. The shell is usually large and spiral; often an operculum is developed on the upper surface of the hinder part of the foot. The dentition of the lingual ribbon is very varied. In most cases the visceral hump and the foot increase along axes at right angles to one another, so that the foot is extended far behind the visceral hump in the ab-oral direction, whilst the visceral hump is lofty and spirally twisted.

This is a very large group, and is conveniently divided into two sections, the Reptantia and the Natantia. The former, containing the immense majority of the group, breaks up into three sub-orders, the Holochlamyda, Pneumonochlamyda, and Siphonochlamyda, characterized by the presence or absence of a trough-like prolongation of the margin of the mantle-flap, which conducts water to the respiratory chamber (sub-pallial space where the gill, anus, &c., are placed), and notches the mouth of the shell by its presence, or again by adaptation to aerial respiration. The sub-orders are divided into groups according to the characters of the lingual dentition. In some Azygobranchia the mouth is placed at the end of a more or less elongated snout or rostrum which is not capable of introversion (Rostrifera); in the others (Proboscidifera) the rostrum is partly invaginated and is often of great length. It is only everted when the animal is feeding, and is withdrawn (introverted) by the action of special muscles; the over-worked term "proboscis" is applied to the retractile form of snout. The term "introversible snout," or simply "introvert," would be preferable. The presence or absence of this arrangement does not seem to furnish so natural a division of the Reptant Azygobranchia as that afforded by the characters of the mantle-skirt.

Section α.—*REPTANTIA.*

Characters.—Azygobranchia adapted to a creeping life; foot either wholly or only the mesopodium in the form of a creeping disc.

Sub-order 1.—*Holochlamyda.*

Characters.—Reptant Azygobranchia with a simple margin to the mantle-skirt, and, accordingly, the lip of the shell unnotched; mostly Rostrifera (*i.e.*, with a non-introversible snout), and vegetarian; marine, brackish, fresh-water, terrestrial.

α. *Rhipidoglossa* (x.4 to 7.1.4 to 7.x).

Family 1.—*Trochidæ.*
Genera: *Turbo*, Lin.; *Phasianella*, Lam.; *Imperator*, Montf.; *Trochus*, Lin.; *Rotella*, Lam.; *Euomphalus*, Low.
Family 2.—*Neritidæ.*
Genera: *Nerita*, L.; *Neritina*, Lam.; *Pileolus*, Low; *Navicella*, Lam.
Family 3.—*Pleurotomaridæ.*
Genera: *Pleurotomaria*, Defr.; *Anatomus*, Montf.; *Stomatia*, Helbing.

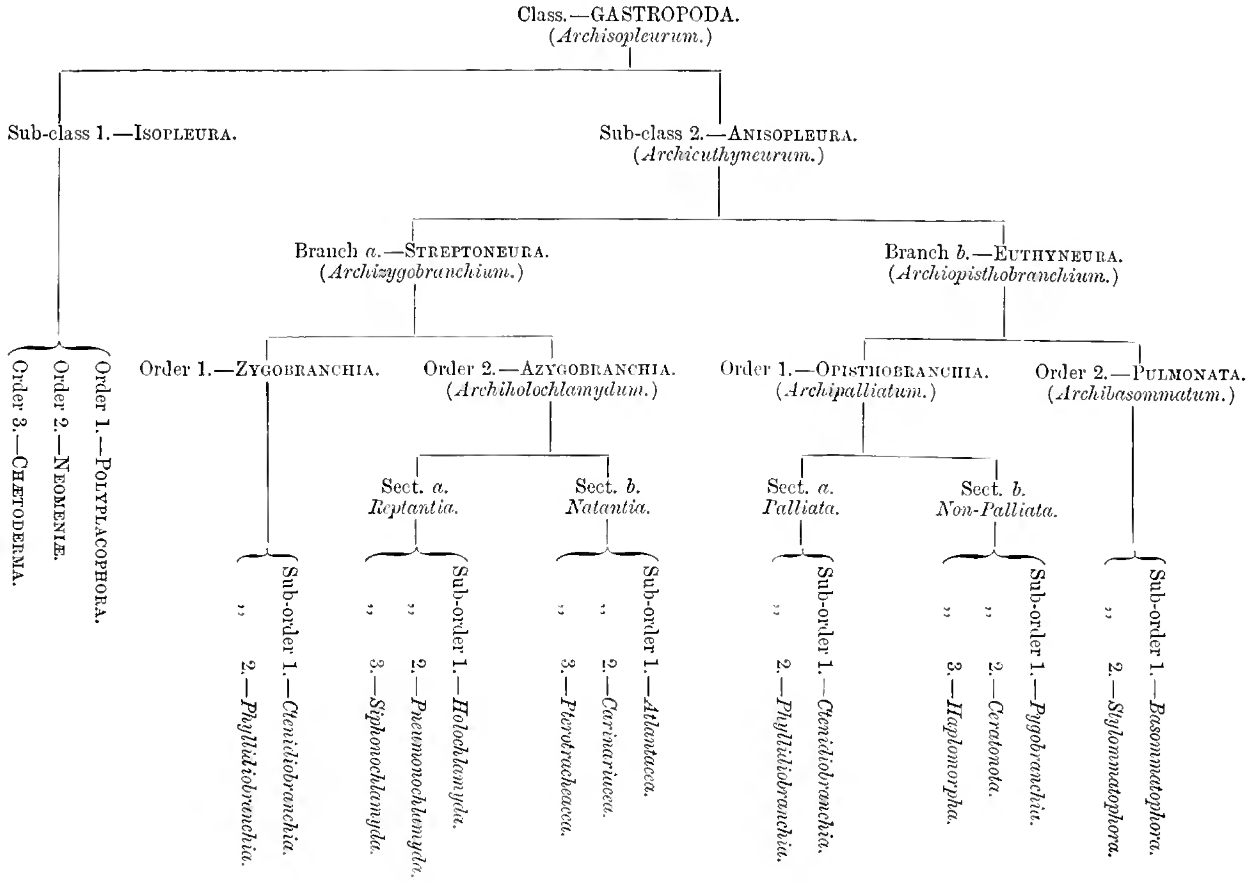
β. *Ptenoglossa* (x.0.x).

Family 4.—*Scalaridæ.*
Genus: *Scalaria*, Lam.
Family 5.—*Janthinidæ.*
Genera: *Janthina*, Lam. (fig. 44); *Recluzia*, Petit.

γ. *Tænioglossa* (3.1.3).

Family 6.—*Cerithidæ.*
Genera: *Cerithium*, Brug.; *Potamides*, Brong.; *Nerinæa*, Defr.
Family 7.—*Melanidæ.*
Genera: *Melania*, Lam.; *Melanopsis*, Fér.; *Ancylotus*, Lay.
Family 8.—*Pyramidellidæ.*
Genera: *Pyramidella*, Lam.; *Stylina*, Flem.; *Aclis*, Loven.
Family 9.—*Turritellidæ.*
Genera: *Turritella*, Lam.; *Cæcum*, Flem.; *Vermetus*, Adans.; *Siliquaria*, Brug.
Family 10.—*Xenophoridæ.*
Genus: *Phorus*, Montf. (fig. 39).

TABULAR VIEW OF THE SUBDIVISIONS OF THE CLASS GASTROPODA, ARRANGED SO AS TO SHOW THEIR SUPPOSED GENETIC RELATIONSHIPS.



Family 11.—*Naticidæ.*
Genera: *Natica,* Lam.; *Sigarctus,* Lam.; *Neritopsis,* Gratel.
Family 12.—*Entoconchidæ.*
The single genus and species *Entoconcha mirabilis,* discovered by Joh. Müller in 1851, parasitic in *Synapta digitata.* The adult form is not known.
Family 13.—*Marsenidæ.*
Genera: *Marsenia,* Leach; *Onchidiopsis,* Beck.
Family 14.—*Acmæidæ.*
Genera: *Acmæa,* Eschsch.; *Lottia,* Gr.; (probably these will be found to belong to the Zygobranchia).
Family 15.—*Capulidæ.*
Genera: *Capulus,* Montf.; *Calyptræa,* Lam. (fig. 40); *Trochita,* Schum.
Family 16.—*Littorinidæ.*
Genera: *Littorina* (the Periwinkles, fig. 46); *Modulus,* Gray; *Lacuna,* Turt.; *Rissoa,* Frem.; *Hydrobia,* Hartm.; *Assiminia,* Leach.
Family 17.—*Paludinidæ.*
Genera: *Paludina* (River-Snail) (figs. 7, 21); *Bithynia,* Gray; *Tanalia,* Gray.
Family 18.—*Valvatidæ.*
Genus: *Valvata* (fig. 45), fresh-water.
Family 19.—*Ampullaridæ.*
Genus: *Ampullaria* (can breathe air by means of the walls of the pallial chamber as well as water by the gill; fresh-waters of tropical America, Africa, and East Indies).

Sub-order 2.—*Pneumonochlamyda.*

Characters.—Pallial chamber a lung-sac; no gill; mouth on a rostrum, not a retractile proboscis; terrestrial habit.

Family 20.—*Cyclostomidæ.*
Genera: *Cyclostoma,* Lam.; *Cyclophorus,* Montf.; *Ferussina,* Gratel.; *Pupina,* Vignard.
Family 21.—*Helicinidæ* (radula rhipidoglossate rather than tænioglossate).
Genera: *Stoastoma,* Adams; *Trochatella,* Swains.; *Helicina,* Lam.; *Proserpina,* Guild.
Family 22.—*Aciculidæ.*
Genera: *Acicula,* Hartm.; *Geomelania,* Pfr.

Sub-order 3.—*Siphonochlamyda.*

Characters.—Reptant Azygobranchia with the margin of the mantle drawn out to form a trough-like siphon which notches the lip of the shell; shell always spiral; usually an operculum, horny or lamelliform; either a rostrum or a retractile proboscis; exclusively marine; mostly carnivorous.

**Tænioglossa* (3.1.3).

Family 1.—*Strombidæ.*
Genera: *Strombus,* L.; *Pterocerus,* Lam.; *Rostellaria,* Lam. (fig. 43).
Family 2.—*Aporrhaidæ.*
Genus: *Aporrhais,* Da Costa.
Family 3.—*Pedicularidæ.*
Genus: *Pedicularia,* Swains.
Family 4.—*Doliidæ.*
Genera: *Cassis,* Lam.; *Cassidaria,* Lam.; *Dolium,* Lam.; *Ficula,* Swains.
Family 5.—*Tritonidæ.*
Genera: *Tritonium,* Cuv. (fig. 42); *Ranella,* Lam.
Family 6.—*Cypræidæ* (the Cowries).
Genera: *Cypræa,* L.; *Ovulum,* Brug. (fig. 41); *Erato,* Risso.

**Toxiglossa* (1.0.1).

Family 7.—*Conidæ.*
Genus: *Conus,* L.
Family 8.—*Terebridæ.*
Genus: *Terebra,* Adans.
Family 9.—*Pleurotomidæ.*
Genus: *Pleurotoma,* Lam.
Family 10.—*Cancellaridæ.*
Genus: *Cancellaria,* Lam.

**Rachiglossa* (1.1.1 or .1.).

Family 11.—*Muricidæ.*
Genera: *Murex,* L.; *Trophon,* Montf.; *Fusus,* Brug.; *Pyrula,* Lam. (fig. 38); *Turbinella,* Lam.
Family 12.—*Buccinidæ.*
Genera: *Buccinum,* L.; *Nassa,* Lam. (fig. 5); *Purpura,* Brug. (fig. 47): *Concholepas,* Lam.; *Magilus,* Montf.
Family 13.—*Mitridæ.*
Genus: *Mitra,* Lam.

Family 14.—*Olividæ*.
Genera: *Oliva*, Brug.; *Ancilla*, Lam.; *Harpa*, Lam.
Family 15.—*Volutidæ*.
Genera: *Voluta*, L.; *Cymbium*, Montf.; *Marginella*, Lam.; *Volvaria* Lam.

Further Remarks on the Reptant Azygobranchia.—The very large assemblage of forms coming under this order comprise the most highly developed predaceous sea-snails, numerous vegetarian species, a considerable number of fresh-water, and some terrestrial forms. The partial dissection of a male specimen of the Common Periwinkle, *Littorina littoralis*, drawn in fig. 46, will serve to exhibit the disposition of viscera which prevails in the group.

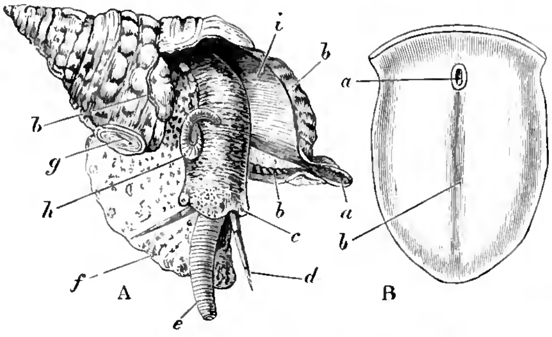


Fig. 37.—A. *Triton variegatum*, to show the proboscis or buccal introvert (*e*) in a state of eversion. *a*, siphonal notch of the shell occupied by the siphonal fold of the mantle-skirt (Siphonochlamyda); *b*, edge of the mantle-skirt resting on the shell; *c*, cephalic eye; *d*, cephalic tentacle; *e*, everted buccal introvert (proboscis); *f*, foot; *g*, operculum; *h*, penis; *i*, under surface of the mantle-skirt forming the roof of the sub-pallial chamber. B. Sole of the foot of *Pyrula tuba*, to show *a*, the pore usually said to be "aquiferous" but probably the orifice of a gland; *b*, median line of foot.

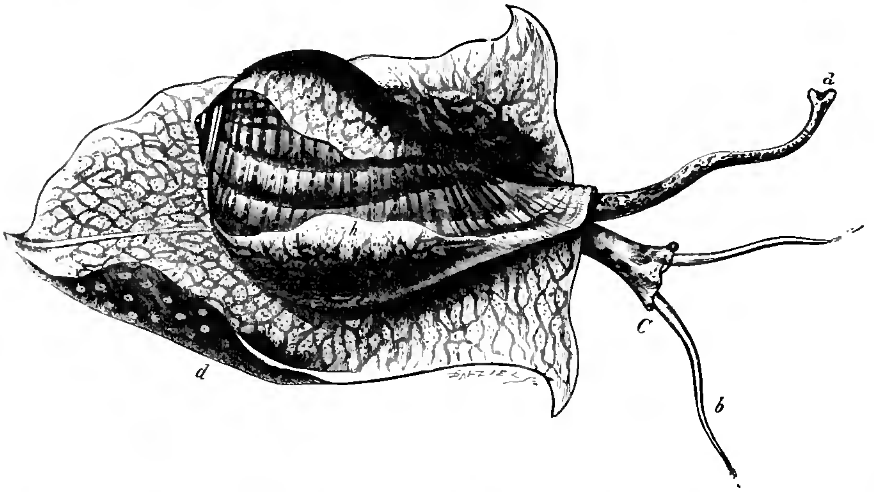


Fig. 38.—Animal and shell of *Pyrula lævigata*. *a*, siphon; *b*, head-tentacles; *C*, head, the letter placed near the right eye; *d*, the foot, expanded as in crawling; *h*, the mantle-skirt reflected over the sides of the shell. (From Owen.

The branchial chamber formed by the mantle-skirt overhanging the head has been exposed by cutting along a line extending backward from the letters *vd* to the base of the columella muscle *mc*, and the whole roof of the chamber thus detached from the right side of the animal's neck has been thrown over to the left, showing the organs which lie upon the roof. No opening into the body-cavity has been made; the organs which lie in the coiled visceral hump show through its transparent walls. The head is seen in front resting on the foot and carrying a median non-retractile snout or rostrum, and a pair of cephalic tentacles at the base of each of which is an eye. In many Gastropoda the eyes are not thus sessile but raised upon special eye-tentacles (figs. 43, 69). To the right of the head is seen the muscular penis *p* close to the termination of the vas deferens (spermatic duct) *vd*. The testis *t* occupies a median position in the coiled visceral mass. Behind the penis on the same side is the hooklike columella muscle, a development of the retractor muscle of the foot, which clings to the spiral column or columella of the shell (see fig. 42). This columella muscle is the same thing as the muscular surface marked *c* in the figures of Patella, marked *k* in fig. 91 of Nautilus, and the posterior adductor of Lamellibranchs (fig. 131).

The surface of the neck is covered by integument forming the floor of the branchial cavity. It has not been cut into.

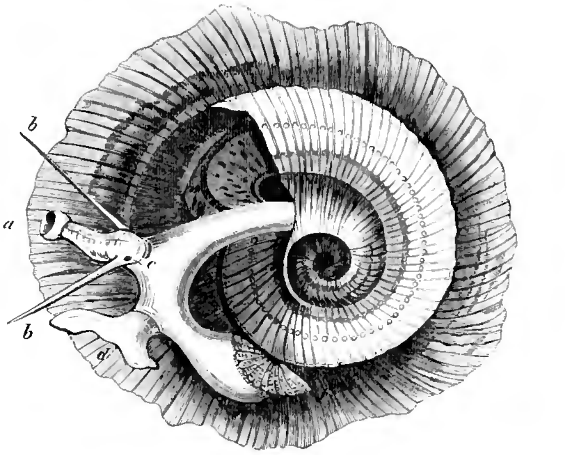


Fig. 39.—Animal and shell of *Phorus exutus*. *a*, snout (not introversible); *b*, cephalic tentacles; *c*, right eye; *d*, pro- and meso-podium,—to the right of this is seen the metapodium bearing the sculptured operculum.

Of the organs lying on the reflected mantle-skirt, that which in the natural state lay nearest to the vas deferens on the right side of the median line of the roof of the branchial chamber is the rectum *i'*, ending in the anus *a*. It can be traced back to the intestine *i* near the surface of the visceral hump, and it is found that the apex of the coil formed by the hump is occupied by the liver *h* and the stomach *v*. Pharynx and œsophagus are concealed in the head. The enlarged glandular structure of the walls of the rectum is frequent in the Azygobranchia, as is also though not universally the gland marked *y*, next to the rectum. It is the adrectal gland, and in the genera Murex and Purpura secretes a colourless liquid which turns purple upon exposure to the atmosphere, and was used by the ancients as a dye. Near this, and less advanced into the branchial chamber, is the single renal organ or nephridium *r* with its opening to the exterior *r'*. Internally this glandular sac presents a second slit or aperture which leads into the pericardium (as is now found to be the case in all Mollusca). The heart *c* lying in the pericardium is seen in close proximity to

Fig. 40.—Shell of Calyptræa, seen from below so as to show the inner whorl *b*, concealed by the cap-like outer whorl *a*.

the renal organ, and consists of a single auricle receiving blood from the gill, and of a single ventricle which pumps it through the body by an anterior and posterior aorta (see fig. 105). The surface *x* of the mantle between the rectum and the gill-plume is thrown into folds which in many sea-snails (Whelks, &c.) are very strongly developed. The whole of this surface appears to be active in the secretion of a mucous-like substance. The single gill-plume *br* lies to the left of the median line in natural position. It corresponds to the right of the two primitive ctenidia in the untwisted archaic condition of the Molluscan body, and does not project freely into the branchial cavity, but its axis is attached (by concrescence) to the mantle-skirt (roof of the branchial chamber). It is rare for the gill-plume of an Anisopleurous Gastropod to stand out freely as a plume, but occasionally this more archaic condition is exhibited, as in Valvata (fig. 45). Next beyond (to the left of) the gill-plume we find the so-called parabranchia, which is here simple, but sometimes lamellated as in Purpura (fig. 47). This organ has, without reason, been supposed to represent the second ctenidium of the typical Mollusc, which it cannot do on account of its position. It should be to the right of the anus were this the case. Recently Spengel has shown that the parabranchia of Gastropods is the typical olfactory organ or osphradium in a highly-developed condition The minute structure of the epithelium which clothes it, as well as the origin of the nerve which is distributed to the parabranchia, proves it to be the same organ which is found universally in Molluscs at the base of each gill-plume, and tests the indrawn current of water by the sense of smell. The nerve to this organ is given off from the superior (original right, see fig. 19) visceral ganglion.

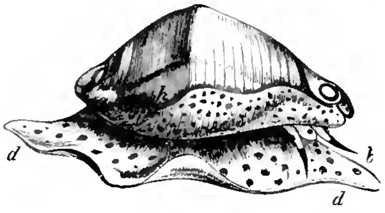


FIG. 41.—Animal and shell of Ovulum. *h*, cephalic tentacles; *d*, foot; *h*, mantle-skirt, which is naturally carried in a reflected condition so as to cover in the sides of the shell.

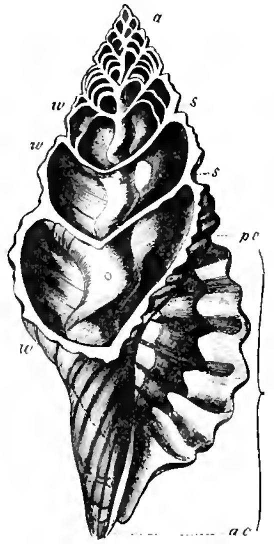


FIG. 42.—Section of the shell of Tritonium, Cuv. *a*, apex; *ac*, siphonal notch of the mouth of the shell; *ac* to *pe*, mouth of the shell; *w*, *w*, whorls of the shell; *s*, *s*, sutures. Occupying the axis, and exposed by the section, is seen the "columella" or spiral pillar. The upper whorls of the shell are seen to be divided into separate chambers by the formation of successively formed "septa." (From Owen.)

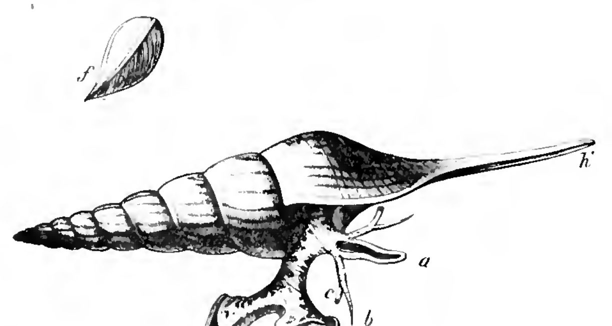


FIG. 43.—Animal and shell of *Rostellaria rectirostris*. *a*, snout or rostrum; *b*, cephalic tentacle; *c*, eye; *d*, propodium and mesopodium; *e*, metapodium; *f*, operculum; *h'*, prolonged siphonal notch of the shell occupied by the siphon, or trough-like process of the mantle-skirt. (From Owen.)

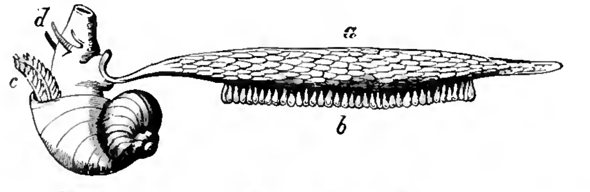


FIG. 44.—Female Janthina, with egg-float (*a*) attached to the foot; *b*, egg-capsules; *c*, ctenidium (gill-plume); *d*, cephalic tentacles.

The figures which are here given of various Azygobranchia are in most cases sufficiently explained by the references attached to them. As an excellent general type of the nervous system, attention may be directed to that of Paludina drawn in fig. 21. On the whole, the ganglia are strongly individualized in the Azygobranchia, nerve-cell tissue being concentrated in the ganglia and absent from the cords (contrast with Zygobranchia and Isopleura). At the same time, the junction of the visceral loop above the intestine prevents in all Streptoneura the shortening of the visceral loop, and it is rare to find a fusion of the visceral ganglia with either pleural, pedal, or cerebral—a fusion which can and does take place where the visceral loop is not above but below the intestine, *e.g.*, in the Euthyneura (fig. 67), Cephalopoda (fig. 112), and Lamellibranchia (fig. 144). As contrasted with the Zygobranchia and the Isopleura, we find that in the Azygobranchia the pedal nerves are distinctly nerves given off from the pedal ganglia, rather than cord-like nerve-tracts containing both nerve-cells or ganglionic elements and nerve-fibres. Yet in some Azygobranchia (Paludina) a ladder-like arrangement of the two pedal nerves and their lateral branches has been detected (**30**). The histology of the nervous system of Mollusca has yet to be seriously inquired into.

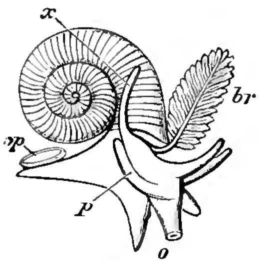


FIG. 45.—*Valvata cristata*, Müll. *o*, mouth; *op*, operculum; *br*, ctenidium (branchial plume); *x*, filiform appendage (? rudimentary ctenidium). The freely projecting ctenidium of typical form not having its axis fused to the roof of the branchial chamber is the notable character of this genus.

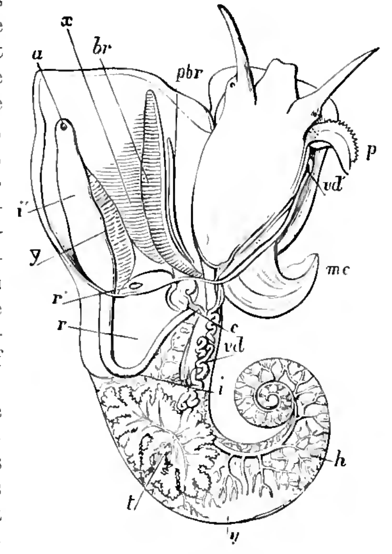


FIG. 46.—Male of *Littorina littoralis*, Lin., removed from its shell; the mantle-skirt cut along its right line of attachment and thrown over to the left side of the animal so as to expose the organs on its inner face. *a*, anus; *i*, intestine; *r*, nephridium (kidney); *r'*, aperture of the nephridium; *c*, heart; *br*, ctenidium (gill-plume); *pbr*, parabranchia (=the osphradium or olfactory patch); *x*, glandular lamellæ of the inner face of the mantle-skirt; *y*, adrectal (purpuriparous) gland; *t*, testis; *vd*, vas deferens; *p*, penis; *mc*, columella muscle (muscular process grasping the shell); *v*, stomach; *h*, liver. *N.B.* Note the simple snout or rostrum not introverted as a "proboscis."

The alimentary canal of the Azygobranchia presents little diversity of character, except in so far as the buccal region is concerned. Salivary glands are present, and in some carnivorous forms (Dolium) these secrete free sulphuric acid (as much as two per cent is present in the secretion), which assists the animal in boring holes by means of its rasping tongue through the shells of other Molluscs upon which it preys. A crop-like dilatation of the gut and a recurved intestine, embedded in the compact yellowish-brown liver, the ducts of which open into it, form the rest of the digestive tract and occupy a large bulk of the visceral hump. The buccal region presents a pair of shelly jaws placed laterally upon the lips, and a wide range of variation in the form of the denticles of the lingual ribbon or radula, the nature of which will be understood by a reference to fig. 9, whilst the systematic list of families given above shows the particular form of dentition characteristic of each division of the order.

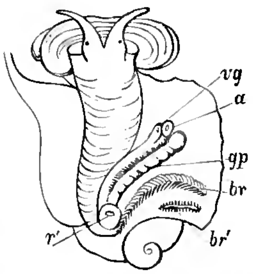


Fig. 47.—Female of *Purpura lapillus* removed from its shell; the mantle-skirt cut along its left line of attachment and thrown over to the right side of the animal so as to expose the organs on its inner face. *a*, anus; *vg*, vagina; *gp*, adrectal purpuriparous gland; *r′*, aperture of the nephridium (kidney); *br*, ctenidium (branchial plume); *br′*, parabranchia (= the comb-like osphradium or olfactory organ).

The modification in the form of the snout upon which the mouth is placed, leading to the distinction of "proboscidiferous" and "rostriferous" Gastropods, requires further notice. The condition usually spoken of as a "proboscis" appears to be derived from the condition of a simple rostrum (having the mouth at its extremity) by the process of *incomplete introversion* of that simple rostrum. There is no reason in the actual significance of the word why the term "proboscis" should be applied to an alternately introversible and eversible tube connected with an animal's body, and yet such is a very customary use of the term. The introversible tube may be completely closed, as in the "proboscis" of Nemertean worms, or it may have a passage in it leading into a non-eversible œsophagus, as in the present case, and in the case of the eversible pharynx of the predatory Chætopod worms. The diagrams here introduced (fig. 48) are intended to show certain important distinctions which obtain amongst the various "introverts," or intro- and e-versible tubes so frequently met with in animal bodies. Supposing the tube to be completely introverted and to commence its eversion, we then find that eversion may take place, either by a forward movement of the side of the tube near its attached base, as in the proboscis of the Nemertine worms, the pharynx of Chætopods, and the eye-tentacle of Gastropods, or, by a forward movement of the inverted apex of the tube, as in the proboscis of the Rhabdocœl Planarians, and in that of Gastropods here under consideration. The former case we call "pleurecbolic" (fig. 48, A, B, C, H, I, K), the latter "acrecbolic" tubes or introverts (fig. 48, D, E, F, G). It is clear that, if we start from the condition of full eversion of the tube and watch the process of introversion, we shall find that the pleurecbolic variety is introverted by the apex of the tube sinking inwards; it may be called acrembolic, whilst conversely the acrecbolic tubes are pleurembolic. Further, it is obvious enough that the process either of introversion or of eversion of the tube may be arrested at any point, by the development of fibres connecting the wall of the introverted tube with the wall of the body, or with an axial structure such as the œsophagus; on the other hand, the range of movement of the tubular introvert may be unlimited or complete. The acrembolic proboscis or frontal introvert of the Nemertine worms has a complete range. So has the acrembolic pharynx of Chætopods, if we consider the organ as terminating at that point where the jaws are placed and the œsophagus commences. So too the acrembolic eye-tentacle of the snail has a complete range of movement, and also the pleurembolic proboscis of the Rhabdocœl prostoma. The introverted rostrum of the Azygobranch Gastropods presents in contrast to these a limited range of movement. The "introvert" in these Gastropods is not the pharynx as in the Chætopod worms, but a præ-oral structure, its apical limit being formed by the true lips and jaws, whilst the apical limit of the Chætopod's introvert is formed by the jaws placed at the junction of pharynx and œsophagus, so that the Chætopod's introvert is part of the stomodæum or fore-gut, whilst that of the Gastropod is external to the alimentary canal altogether, being in front of the mouth, not behind it, as is the Chætopod's. Further, the Gastropod's introvert is pleurembolic (and therefore acrecbolic), and is limited both in eversion and in introversion; it cannot be completely everted owing to the muscular bands (fig. 48, G), nor can it be fully introverted owing to the bands (fig. 48, F) which tie the axial pharynx to the adjacent wall of the apical part of the introvert. As in all such intro- and e-versible organs, eversion of the Gastropod proboscis is effected by pressure communicated by the muscular body-wall to the liquid contents (blood) of the body-space, accompanied by the relaxation of the muscles which directly pull upon either the sides or the apex of the tubular organ. The inversion of the proboscis is effected directly by the contraction of these muscles. In various members of the Azygobranchia the mouth-bearing cylinder is introversible (*i.e.*, is a *proboscis*)—with rare exceptions these forms have a siphonate mantle-skirt. On the other hand, many which have a siphonate mantle-skirt are not provided with an introversible mouth-bearing cylinder, but have a simple non-introversible rostrum, as it has been

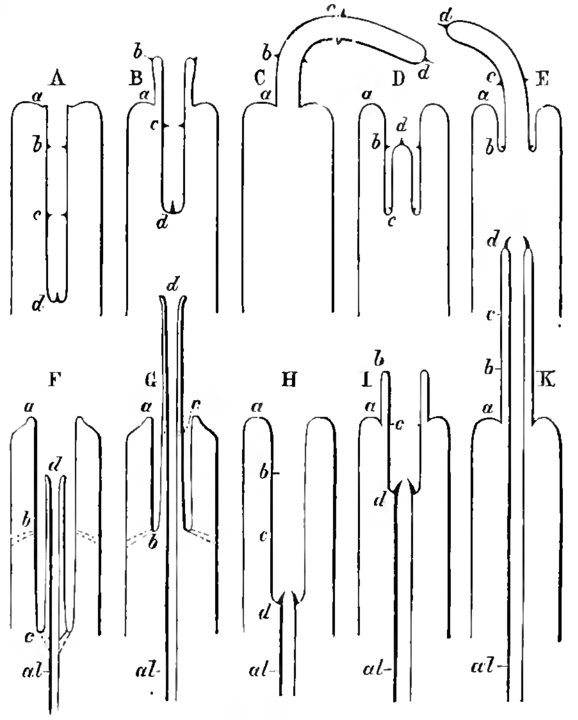


Fig. 48.—Diagrams explanatory of the nature of so-called proboscides or "introverts." A. Simple introvert completely introverted. B. The same, partially everted by eversion of the sides, as in the Nemertine proboscis and Gastropod eye-tentacle = pleurecbolic. C. The same, fully everted. D, E. A similar simple introvert in course of eversion by the forward movement, not of its sides, but of its apex, as in the proboscidean Rhabdocœls = acrecbolic. F. Acrecbolic (= pleurembolic) introvert, formed by the snout of the proboscidiferous Gastropod. *al*, alimentary canal; *d*, the true mouth. The introvert is not a simple one with complete range both in eversion and introversion, but is arrested in introversion by the fibrous bands at *c*, and similarly in eversion by the fibrous bands at *b*. G. The acrecbolic snout of a proboscidiferous Gastropod, arrested short of complete eversion by the fibrous band *b*. H. The acrembolic (= pleurecbolic) pharynx of a Chætopod fully introverted. *al*, alimentary canal; at *d*, the jaws; at *a*, the mouth; therefore *a* to *d* is stomodæum, whereas in the Gastropod (F) *a* to *d* is inverted body-surface. I. Partial eversion of H. K. Complete eversion of H. (Original.)

termed, which is also the condition presented by the mouth-bearing region in nearly all other Gastropoda. One of the best examples of the introversible mouth-cylinder or proboscis which can be found is that of the Common Whelk and its immediate allies. In fig. 37 the proboscis is seen in an everted state; it is only so carried when feeding, being withdrawn when the animal is at rest. Probably its use is to enable the animal to introduce its rasping and licking apparatus into very narrow apertures for the purpose of feeding, *e.g.*, into a small hole bored in the shell of another Mollusc.

The foot of the Azygobranchia, unlike the simple muscular disc of the Isopleura and Zygobranchia, is very often divided into lobes, a fore, middle, and hind lobe (pro-, meso-, and meta-podium, see figs. 39 and 43). Very usually, but not universally, the meta-podium carries an operculum. The division of the foot into lobes is a simple case of that much greater elaboration or breaking up into processes and regions which it undergoes in the class Cephalopoda. Even among some Gastropoda (viz., the Opisthobranchia), we find the lobation of the foot still further carried out by the development of lateral lobes, the epipodia, whilst there are many Azygobranchia, on the other hand, in which the foot has a simple oblong form without any trace of lobes.

The development of the Azygobranchia from the egg has been followed in several examples, *e.g.*, Paludina, Purpura, Nassa, Vermetus, Neritina. As in other Molluscan groups, we find a wide variation in the early process of the formation of the first embryonic cells, and their arrangement as a Diblastula dependent on the greater or less amount of food-yelk which is present in the egg-cell when it commences its embryonic changes. In fig. 7, the early stages of *Paludina vivipara* are represented. There is but very little food-material in the egg of this Azygobranch, and consequently the Diblastula forms by invagination; the blastopore or orifice of invagination coincides with the anus, and never closes entirely. A well-marked Trochosphere is formed by the development of an equatorial ciliated band; and subsequently, by the disproportionate growth of the lower hemisphere, the Trochosphere becomes a Veliger. The primitive shell-sac or shell-gland is well marked at this stage, and the pharynx is seen as a new ingrowth (the stomodæum), about to fuse with and open into the primitively invaginated arch-enteron (fig. 7, F).

In other Azygobranchs (and such variations are representative for all Mollusca, and not characteristic only of Azygobranchia), we find that there is a very unequal division of the egg-cell at the commencement of embryonic development, as in Nassa (fig. 5). Consequently there is strictly speaking no invagination (emboly), but an overgrowth (epiboly) of the smaller cells to enclose the larger. The general features of this process and of the relation of the blastopore to mouth and anus have been explained above in treating of the development of Mollusca generally. In such cases the blastopore may entirely close, and both mouth and anus develop as new ingrowths (stomodæum and proctodæum), whilst, according to the observations of Bobretzky, the closed blastopore may coincide in position with the mouth in some instances (Nassa, &c.), instead of with the anus. But in these epibolic forms, just as in the embolic Paludina, the embryo proceeds to develop its ciliated band and shell-gland, passing through the earlier condition of a Trochosphere to that of the Veliger. In the veliger stage many Azygobranchia (Purpura, Nassa, &c.) exhibit, in the dorsal region behind the head, a contractile area of the body-wall. This acts as a larval heart, but ceases to pulsate after a time. Similar rhythmically contractile areas are found on the foot of the embryo Pulmonate Limax and on the yelk-sac (distended foot-surface) of the Cephalopod Loligo (see fig. 72**).

The history of the shell in the development of Azygobranchia (and other Gastropods) is important. Just as the primitive shell-sac aborts and gives place to a cap-like or boat-like shell, so in some cases (Marsenia, Krohn) has this first shell been observed to be shed, and a second shell of different shape is formed beneath it.

A detailed treatment of what is known of the histogenesis in relation to the cell-layers in these Mollusca would take us far beyond the limits of this article, which aims at exposing only the well-ascertained characteristic features of the Mollusca and the various subordinate groups. There is still a great deficiency in our knowledge of the development of the Gastropoda, as indeed of all classes of animals. The development of the gill (ctenidium) as well as of the renal organ, and details as to the process of torsion of the visceral hump, are still quite insufficiently known.

One further feature of the development of the Azygobranchia deserves special mention. Many Gastropoda deposit their eggs, after fertilization, enclosed in capsules; others, as Paludina, are viviparous; others, again, as the Zygobranchia, agree with the Lamellibranch Conchifera (the Bivalves) in having simple exits for the ova without glandular walls, and therefore discharge their eggs unenclosed in capsules freely into the sea-water; such unencapsuled eggs are merely enclosed each in its own delicate chorion. When egg-capsules are formed they are often of large size, have tough walls, and in each capsule are several eggs floating in a viscid fluid. In some cases all the eggs in a capsule develop; in other cases one egg only in a capsule (Neritina), or a small proportion (Purpura, Buccinum), advance in development; the rest are arrested either after the first process of cell-division (cleavage) or before that process. The arrested embryos or eggs are then swallowed and digested by those in the same capsule which have advanced in development. The details of this history require renewed study, our present knowledge of it being derived from the works of Koren and Danielssen, Carpenter and Claparède. In any case it is clearly the same process in essence as that of the formation of a vitellogenous gland from part of the primitive ovary, or of the feeding of an ovarian egg by the absorption of neighbouring potential eggs; but here the period at which the sacrifice of one egg to another takes place is somewhat late. What it is that determines the arrest of some eggs and the progressive development of others in the same capsule is at present unknown.

Section *b* (of the Azygobranchia).—*NATANTIA.*

Characters.—Azygobranchiate Streptoneura which have the form and texture of the body adapted to a free-swimming pelagic habit. They appear to be derived from holochlamydic forms of Reptant Azygobranchia. The foot takes the form of a swimming organ. The nervous system and sense-organs (eyes, otocysts, and osphradium) are highly developed. The odontophore also is remarkably developed, its admedian teeth being mobile, and it serves as an efficient organ for attacking other pelagic forms upon which the Natantia prey. The sexes are distinct as in all Streptoneura; and genital ducts and accessory glands and pouches are present as in all Azygobranchia. The Natantia exhibit a series of modifications of the form and proportions of the visceral mass and foot, leading from a condition readily comparable with that of a typical Azygobranch such as Rostellaria, with the three regions of the foot (pro-, meso-, and meta-podium) strongly marked, and a coiled visceral hump of the usual proportions, up to a condition in which the whole body is of a tapering cylindrical shape, the foot a plate-like vertical fin, and the visceral hump almost completely atrophied. Three steps of this modification may be distinguished as three sub-orders, the *Atlantacea*, the *Carinariacea*, and the *Pterotracheacea*.

Sub-order 1.—*Atlantacea.*

Characters.—Natantia with a large spirally-wound visceral hump, covered by a hyaline spiral shell; mantle-skirt large, overhanging a well-developed sub pallial branchial chamber as in Azygobranchia, to the wall of which is attached the branchial ctenidium; foot well developed, divisible into a mobile propodium, a mesopodium on which is formed a sucker, and a metapodium which, when the animal is expanded, extends backwards beyond the shell and visceral hump; upon the upper surface of the metapodium is developed an operculum.

Genera: *Atlanta, Oxygurus.* Probably here belong the Palæozoic fossils *Bellerophon.*

Sub-order 2.—*Carinariacea.*

Characters.—Visceral hump greatly reduced in relative size; shell small, cap-like, hyaline; ctenidium (branchial plume) projecting from the small sub-pallial chamber; body cylindrical; of the foot-lobes only the mesopodium is prominent, provided with a sucker, and compressed laterally so as to form a vertical plate-like fin projecting from the ventral surface; the propodium forms simply the ventral surface of the anterior region of the cylindrical body whilst the metapodium forms its posterior region.

Genera: *Carinaria, Cardiopoda.*

Sub-order 3.—*Pterotracheacea.*

Characters.—Visceral hump still further reduced, forming a mere oval sac embedded in the posterior dorsal region of the cylindrical body; no shell; foot as in Carinariacea, except that the sucker is absent from the mesopodium in the females.

Genera: *Pterotrachea, Firuloides.*

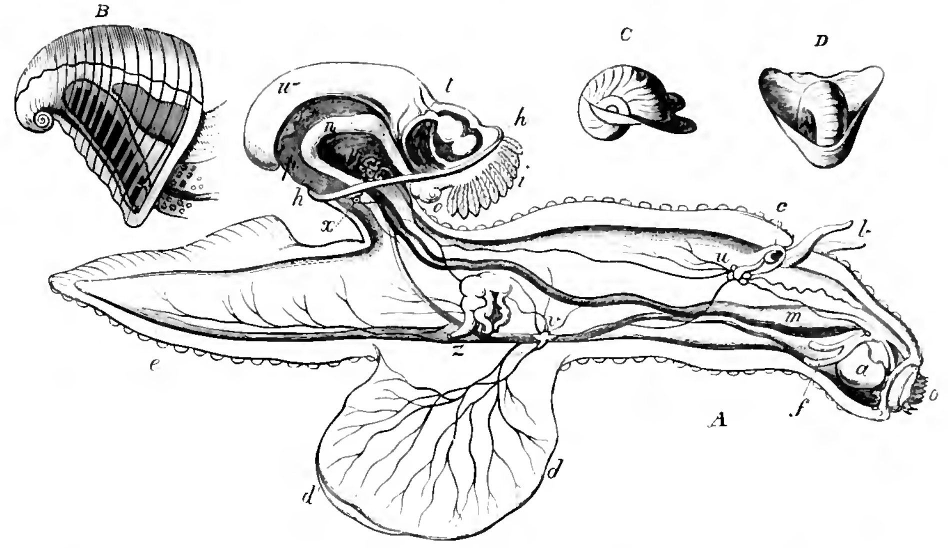


Fig. 50.—*Carinaria mediterranea.* A. The animal. B. The shell removed. C, D. Two views of the shell of Cardiopoda. *a*, mouth and odontophore; *b*, cephalic tentacles; *c*, eye; *d*, the fin-like mesopodium; *d'*, its sucker; *e*, metapodium; *f*, salivary glands; *h*, border of the mantle-flap; *i*, ctenidium (gill-plume); *m*, stomach; *n*, intestine; *o*, anus; *p*, liver; *t*, aorta, springing from the ventricle; *u*, cerebral ganglion; *v*, pleural and pedal ganglion; *w*, testis; *x*, visceral ganglion; *y*, vesicula seminalis; *z*, penis. (From Owen.)

Further Remarks on the Natantia Azygobranchia.—Logically the Natantia should stand as we have placed them, viz., as a special branch or section of the Azygobranchia, related to them somewhat as are the Birds to the Reptiles. They are true Azygobranchia which have taken to a pelagic life, and the peculiarities of structure which they exhibit are strictly adaptations of the structure common to them and the Azygobranchia consequent upon their changed mode of life. Such adaptations are the transparency and colourlessness of the tissues, and the modifications of the foot, which still shows in Atlanta the form common in Azygobranchia (compare fig. 49 and fig. 39).

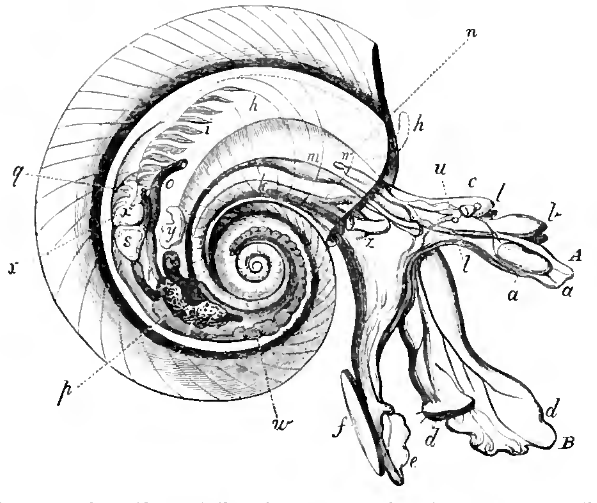


Fig. 49.—*Atlanta* (*Oxygura*) *Keraudrenii* (magnified 20 diameters). *a*, mouth and odontophore; *b*, cephalic tentacles; *c*, eye; *d*, propodium (*B*) and mesopodium; *e*, metapodium; *f*, operculum; *h*, mantle-chamber; *i*, ctenidium (gill-plume); *k*, retractor muscle of foot; *l*, optic tentacle; *m*, stomach; *n*, dorsal surface overhung by the mantle-skirt, the letter is close to the salivary gland; *o*, rectum and anus; *p*, liver; *q*, renal organ (nephridium); *s*, ventricle; *u*, the otocyst attached to the cerebral ganglion; *w*, testis; *x*, auricle of the heart; *y*, vesicle on genital duct; *z*, penis. (From Owen.)

The cylindrical body of Pterotracheacea is paralleled by the slug-like forms of Euthyneura. Spengel has shown that the visceral loop of the Natantia is Streptoneurous. Special to the Natantia is the high elaboration of the lingual ribbon, and, as an agreement with some of the Opisthobranchiate Euthyneura but as a difference from the Azygobranchia, we find the otocysts closely attached to the cerebral ganglia. This is, however, less of a difference than it was at one time supposed to be, for it has been shown by Lacaze Duthiers, and also by Leydig, that the otocysts of Azygobranchia even when lying close upon the pedal ganglion (as in fig. 21) yet receive their special nerve (which can sometimes be readily isolated) from the cerebral ganglion (see fig. 36). Accordingly the difference is one of position of the otocyst and not of its nerve-supply. The Natantia are further remarkable for the high development of their cephalic eyes, and for the typical character of their osphradium (Spengel's olfactory organ). This is a groove, the edges of which are raised and ciliated, lying near the branchial plume in the genera which possess that organ, whilst in Firuloides, which has no branchial plume, the osphradium occupies a corresponding position. Beneath the ciliated groove is placed an elongated ganglion (olfactory ganglion) connected by a nerve to the supra-intestinal (therefore the primitively dextral) ganglion of the long visceral nerve-loop, the strands of which cross one another,—this being characteristic of Streptoneura (Spengel).

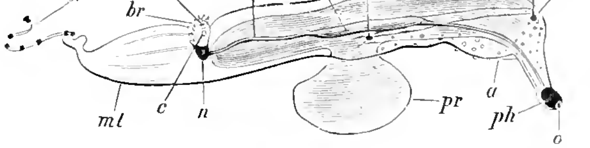


Fig. 51.—*Pterotrachea mutica* seen from the right side. *a*, pouch for reception of the snout when retracted; *c*, pericardium; *ph*, pharynx; *oc*, cephalic eye; *g*, cerebral ganglion; *g'*, pleuro-pedal ganglion; *pr*, foot (mesopodium); *v*, stomach; *i*, intestine; *n*, so-called nucleus; *br*, branchial plume (ctenidium); *w*, osphradium; *mt*, foot (metapodium); *z*, caudal appendage. (After Keferstein.)

The Natantia belong to the "pelagic fauna" occurring near the surface in the Mediterranean and great oceans in company with the Pteropoda, the Siphonophorous Hydrozoa, Salpæ, Leptocephali, and other specially-modified transparent swimming representatives of various groups of the animal kingdom. In development they pass through the typical trochosphere and veliger stages provided with boat-like shell.

Branch *b*.—*EUTHYNEURA* (Spengel, 1881).

Characters. — Gastropoda Anisopleura in which the visceral loop (the conterminous visceral nerves) does not share in the torsion of the visceral hump, but, being sunk entirely below the body-wall, remains straight and untwisted. Although the anus is not brought so far forward by the visceral torsion as in the Streptoneura, and may even by *secondary* growth assume a posterior median position, yet, as fully developed, an asymmetry has resulted as in the Azygobranchia, only the original right renal organ, right ctenidium (if any), right osphradium, right side of the heart, and right genital ducts being retained. All the Euthyneura are hermaphrodite. The lingual ribbon has very usually numerous fine denticles undifferentiated into series in each row. The shell is light and little calcified; often it is not developed in the adult, though present in the embryo. An operculum, often found in the embryo, is never present in the adult (except in Tornatella, fig. 53). Many Euthyneura show a tendency to, or a complete accomplishment of, the suppression of the mantle-skirt as well as of the shell, also of the ctenidium, and acquire at the same time a more or less cylindrical (slug-like) form of body.

Fig. 52.—*Bulla vexillum* (Chemnitz), as seen crawling. *a*, oral hood (compare with Tethys, fig. 62, B), possibly a continuation of the epipodia; *b*, *b′*, cephalic tentacles. (From Owen.)

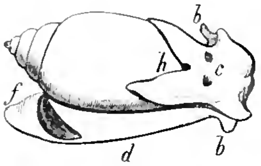


Fig. 53.—Tornatella. *h*, shell; *b*, oral hood; *d*, foot; *f*, operculum.

The Euthyneura comprise two orders, the Opisthobranchia and the Pulmonata.

Order 1.—**Opisthobranchia**.

Marine Euthyneura the more archaic forms of which have a relatively large foot and a small visceral hump, from the base of which projects on the right side a short mantle-skirt. The anus is placed in such forms far back beyond the mantle-skirt. In front of the anus, and only partially covered by the mantle-skirt, is the ctenidium with its free end turned backwards. The heart lies in front of, instead of to the side of, the attachment of the ctenidium,—hence Opisthobranchia as opposed to "Prosobranchia," which correspond to the Streptoneura. A shell is possessed in the adult state by but few Opisthobranchia, but all pass through a veliger larval stage with a nautiloid shell (fig. 60).

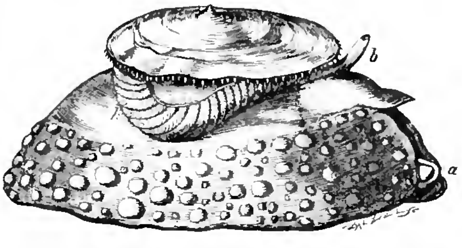


Fig. 54.—*Umbrella mediterranea*. *a*, mouth; *b*, cephalic tentacle; *h*, gill (ctenidium). The free edge of the mantle is seen just below the margin of the shell (compare with Aplysia, fig. 63). (From Owen.)

Many Opisthobranchia have by a process of atrophy lost the typical ctenidium and the mantle-skirt, and have developed other organs in their place. As in some Azygobranchia, the free margin of the mantle-skirt is frequently reflected over the shell when a shell exists; and, as in some Azygobranchia, broad lateral outgrowths of the foot (epipodia) are often developed, which, as does *not* occur in Azygobranchia, may be thrown over the shell or naked dorsal surface of the body.

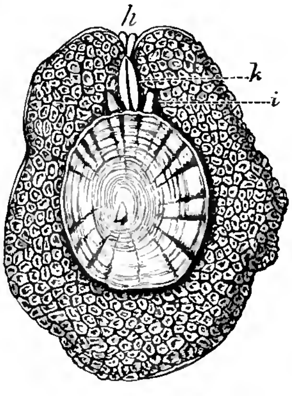


Fig. 55.—*Umbrella mediterranea*, seen from above. *h*, mouth; *i*, cephalic tentacles; *k*, penis-sheath. (After Keferstein.)

The variety of special developments of structure accompanying the atrophy of typical organs in the Opisthobranchia and general degeneration of organization is very great, and renders their classification difficult. Two sections of the order may be distinguished, according as the typical Molluscan mantle-skirt (limbus pallialis) is or is not atrophied, and within each section certain sub-orders.

Section *a*.—*PALLIATA* (= *Tectibranchiata*, Woodward)—the typical Molluscan mantle-skirt or pallium retained.

Sub-order 1.—*Ctenidiobranchia*.

Characters.—Palliata in which the ctenidium is retained as the branchial organ; with rare exceptions a delicate shell, which may be very small or completely enclosed by the reflected margin of the mantle; epipodia (lateral outgrowths of the foot) frequently present.

Family 1.—*Tornatellidæ*.
  Genera: *Tornatella*, Lam. (fig. 53); *Cinulia*, Gray, &c.
Family 2.—*Bullidæ*.
  Genera: *Bulla*, Lam. (fig. 52); *Acera*, Müller; *Scaphander*, Montf.; *Bullæa*, Lam.; *Doridium*, Meckel; *Gastropteron*, Meckel, &c.
Family 3.—*Aplysiidæ*.
  Genera: *Aplysia*, Gmelin (the Sea-Hare) (figs. 20, 56, &c.); *Dolobella*, Lam.; *Lobiger*, Krohn, &c.
Family 4.—*Pleurobranchidæ*.
  Genera: *Pleurobranchus*, Cuvier; *Umbrella*, Chemnitz (figs. 54, 55); *Runcina*, Forbes, &c.

Sub-order 2.—*Phyllidiobranchia*.

Characters.—Palliata in which the ctenidia have atrophied; much as in Patellidæ among the Zygobranchiate Streptoneura their place is taken by laterally-placed lamellæ, developed from the inner surfaco of the bilaterally-disposed mantle-skirt in two lateral rows.

Family 5.—*Phyllidiidæ*.
  Genera: *Phyllidia*, Cuiver; *Pleurophyllidia*, Meck. (fig. 57).

Section *b*.—*NON-PALLIATA*.

Characters.—The typical Molluscan mantle-skirt is atrophied in the adult. No shell is present in the adult, though the dorsal integument may be strengthened by calcareous spicules (Doris). The otocysts are not sessile on the pedal ganglia as in other Gastropods, but, as in the Natantia Azygobranchia, lie close to the cerebral ganglia. In one sub-order (Pygobranchia) the typical ctenidium appears to be retained in a modified form; in the others special developments of the body-wall take its place, or no special respiratory processes exist at all. The general form of the body is slug-like, the foot and visceral hump being coextensive, and a secondary bilateral symmetry is asserted by the usually median (sometimes right-sided) dorsal position of the anus on the hinder part of the body.

Sub-order 1.—*Pygobranchia*.

Characters.—The ctenidium assumes the form of a circlet of pinnate processes surrounding the median dorsal anus; a strongly-marked epipodial fold may occur all round the foot and simulate a mantle-skirt (see fig. 62, C, Doris); papillæ or "cerata" of the dorsal integument may occur as well as the true ctenidium (fig. 61).

Family 6.—*Dorididæ*.
  Genera: *Doris*, L.; *Goniodoris*, Forbes; *Triopa*, Johnst.; *Ægirus*, Loven; *Thecacera*, Fleming; *Polycera*, Cuvier; *Idalia*, Leuckart; *Ancula*, Loven; *Ceratosoma*, Adams; *Onchidoris*, Blainv.

Sub-order 2.—*Ceratonota.*

Characters.—The typical Molluscan ctenidium is not developed; upon the dorsal area is developed a more or less numerous series of cylindrical or branched processes (the cerata) into each of which the intestine usually sends a process; anus dorsal, median, or right-sided.

Family 7.—*Tritoniadæ.*
Genera: *Tritonia*, Cuvier; *Scyllæa*, L.; *Tethys*, L. (fig. 62, B); *Dendronotus*, A. and H.; *Doto*, Oken.

Family 8.—*Eolidæ.*
Genera: *Eolis*, Cuvier (fig. 62, A); *Glaucus*, Forster; *Fiona*, A. and H. (fig. 67); *Embletonia*, A. and H.; *Proctonotus*, A. and H.; *Antiopa*, A. and H.; *Hermæa*, Loven; *Alderia*, Allman.

Sub-order 3.—*Haplomorpha.*

Characters.—No ctenidia, cerata, mantle-skirt, or other processes of the body-wall; degenerate forms of small size.

Family 9.—*Phyllirhoidæ.*
Genera: *Phyllirhoë*, Peron and Lesueur (fig. 58); *Acura*, Adams.

Family 10.—*Elysiadæ.*
Genera: *Elysia*, Risso (fig. 62, D, E); *Acteonia*, Quatref.; *Cenia*, A. and H.; *Limapontia*, Johnston; *Rhodope*, Köll.

Further Remarks on the Opisthobranchia.—The Opisthobranchia present the same wide range of superficial appearance as do the Azygobranchiate Streptoneura, forms carrying well-developed spiral shells and large mantle-skirts being included in the group, together with flattened or cylindrical slug-like forms. But in respect of the substitution of other parts for the mantle-skirt and for the gill which the more degenerate Opisthobranchia exhibit, this Order stands alone. Some Opisthobranchia are striking examples of degeneration (some Haplomorpha), having none of those regions or processes of the body developed which distinguish the archaic Mollusca from such flat-worms as the Dendrocœl Planarians. Indeed, were it not for their retention of the characteristic odontophore we should have little or no indication that such forms as Phyllirhoë and Limapontia really belong to the Mollusca at all. The interesting little *Rhodope Veranyii*, which has no odontophore, has been associated by systematists both with these simplified Opisthobranchs and with Rhabdocœl Planarians (**29**).

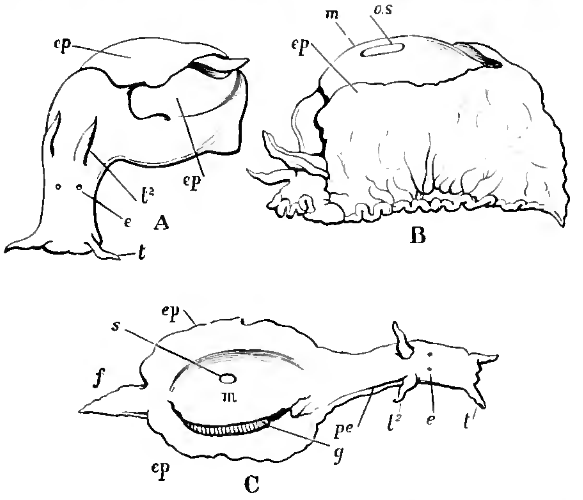


FIG. 56.—Three views of Aplysia sp., in various conditions of expansion and retraction. *t*, anterior cephalic tentacles; t^2, posterior cephalic tentacles; *e*, eyes; *f*, metapodium; *ep*, epipodium; *g*, gill-plume (ctenidium); *m*, mantle-flap reflected over the thin oval shell; *os*, *s*, orifice formed by the unclosed border of the reflected mantle-skirt, allowing the shell to show; *pe*, the spermatic groove. (After Cuvier.)

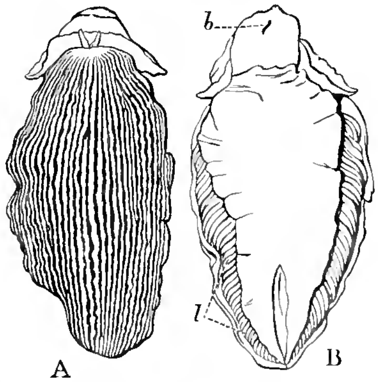


FIG. 57.—Dorsal and ventral view of *Pleurophyllidia lineata* (Otto), one of the Phyllidiobranchiate Palliate Opisthobranchs. *b*, the mouth; *l*, the lamelliform sub-pallial gills, which (as in Patella) replace the typical Molluscan ctenidium. (After Keferstein.)

In many respects the Sea-Hare (Aplysia) of which several species are known (some occurring on the English coast), serves as a convenient example of the fullest development of the organization characteristic of Opisthobranchia. The woodcut (fig. 56) gives a faithful representation of the great mobility of the various parts of the body. The head is well marked and joined to the body by a somewhat constricted neck. It carries two pairs of cephalic tentacles and a pair of sessile eyes. The visceral hump is low and not drawn out into a spire. The foot is long, carrying the oblong visceral mass upon it, and projecting (as metapodium) a little beyond it (*f*). Laterally the foot gives rise to a pair of mobile fleshy lobes, the epipodia (*ep*), which can be thrown up so as to cover in the dorsal surface of the animal. Such epipodia are common, though by no means universal, among Opisthobranchia. The torsion of the visceral hump is not carried out very fully, the consequence being that the anus has a posterior position a little to the right of the median line above the metapodium, whilst the branchial chamber formed by the overhanging mantle-skirt faces the right side of the body instead of lying well to the front as in Streptoneura and as in Pulmonate Euthyneura. The gill-plume which in Aplysia is the typical Molluscan ctenidium is seen in fig.

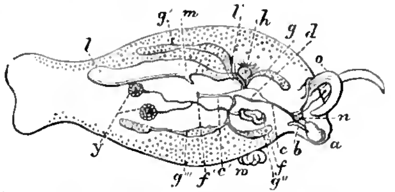


FIG. 58.—*Phyllirhoë bucephala*, twice the natural size, a transparent pisciform pelagic Opisthobranch. The internal organs are shown as seen by transmitted light. *a*, mouth; *b*, radular sac; *c*, œsophagus; *d*, stomach; *c'*, intestine; *f'*, anus; *g*, *g'*, *g''*, *g'''*, the four lobes of the liver; *h*, the heart (auricle and ventricle); *l*, the renal sac (nephridium); *l'*, the ciliated communication of the renal sac with the pericardium; *m*, the external opening of the renal sac; *n*, the cerebral ganglion; *o*, the cephalic tentacles; *f*, the genital pore; *y*, the ovo-testes; *w*, the parasitic hydromedusa *Mnestra*, usually found attached in this position by the aboral pole of its umbrella. (After Keferstein.)

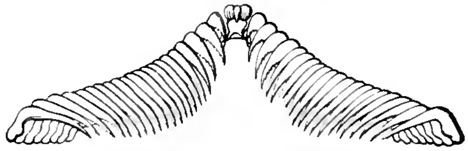


FIG. 59.—*Acera bullata.* A single row of teeth of the radula. (Formula, x.1.x.)

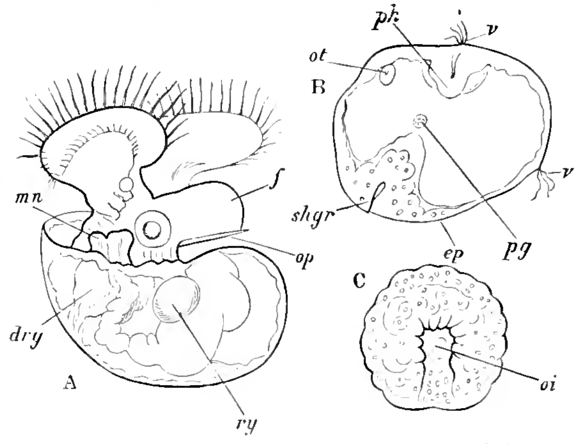


FIG. 60.—A. Veliger-larva of an Opisthobranch (Polycera). *f*, foot; *op*, operculum; *mn*, anal papilla; *ry*, *dry*, two portions of unabsorbed nutritive yelk on either side the intestine. The right otocyst is seen at the root of the foot. B. Trochosphere of an Opisthobranch (Pleurobranchidium) showing: *shgr*, the shell-gland or primitive shell-sac; *v*, the cilia of the velum; *ph*, the commencing stomodæum or oral invagination; *ot*, the left otocyst; *pg*, red-coloured pigment spot. C. Diblastula of an Opisthobranch (Polycera) with elongated blastopore *oi*. (All from Lankester.)

63 projecting from the branchial sub-pallial space. The relation of the delicate shell to the mantle is peculiar, since it occupies an oval area upon the visceral hump, the extent of which is indicated in fig. 56, C, but may be better understood by a glance at the figures of the allied genus Umbrella (figs. 54, 55), in which the margin of the mantle-skirt coincides, just as it does in the Limpet, with the margin of the shell. But in Aplysia the mantle is reflected over the edge of the shell, and grows over its upper surface so as to completely enclose it, excepting at the small central area *s* where the naked shell is exposed. This enclosure of the shell is a permanent development of the arrangement seen in many Streptoneura (*e.g.*, Pyrula, Ovulum, see figs. 38 and 41), where the border of the mantle can be, and usually is, drawn over the shell, though it is withdrawn (as it cannot be in Aplysia) when they are irritated. From the fact that Aplysia commences its life as a free-swimming Veliger with a nautiloid shell not enclosed in any way by the border of the mantle, it is clear that the enclosure of the shell in the adult is a secondary process. Accordingly, the shell of Aplysia must not be confounded with a primitive shell in its shell-sac, such as we find realized in the shells of Chiton and in the plugs which form in the remarkable transitory "shell-sac" or "shell-gland" of Molluscan embryos (see figs. 7, 68, and 72***). Aplysia, like other Mollusca, develops a primitive shell-sac in its trochosphere stage of development (fig. 68), which disappears and is succeeded by a nautiloid shell (fig. 60). This forms the nucleus of the adult shell, and, as the animal grows, becomes enclosed by a reflexion of the mantle-skirt. In reference to the possible comparison of the enclosed shell of Aplysia and its allies with those of some Slugs and of Cuttle-fishes, the reader is referred to the paragraphs dealing especially with those Molluscs. When the shell of an Aplysia enclosed in its mantle is pushed well to the left, the sub-pallial space is fully exposed as in fig. 63, and the various apertures of the body are seen. Posteriorly we have the anus, in front of this the lobate gill-plume, between the two (hence corresponding in position to that of the Azygobranchia) we have the aperture of the renal organ. In front, near the anterior attachment of the gill-plume, is the osphradium (olfactory organ) discovered by Spengel, yellowish in colour, in the typical position, and overlying an olfactory ganglion with typical nerve-connexion (see fig. 20). To the right of Spengel's osphradium is the opening of a peculiar gland which has, when dissected out, the form of a bunch of grapes; its secretion is said to be poisonous. On the under side of the free edge of the mantle are situated the numerous small cutaneous glands which, in the large *Aplysia camelus* (not in other species), form the purple secretion which was known to the ancients. In front of the osphradium is the single genital pore, the aperture of the common or hermaphrodite duct. From this point there stretches forward to the right side of the head a groove—the spermatic groove—down which the spermatic fluid passes. In other Euthyneura this groove may close up and form a canal. At its termination by the side of the head is the muscular introverted penis. In the hinder part of the foot (not shown in any of the diagrams) is the opening of a large mucous-forming gland very often found in the Molluscan foot.

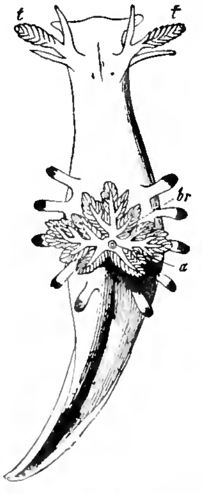


Fig. 61.—*Polycera cristata*, one of the Pygobranchiate Opisthobranchs (dorsal view). *a*, anus; *br*, the ctenidium peculiarly modified so as to encircle the anus; *t*, cephalic tentacles. External to the branchial ctenidium are seen ten club-like processes of the dorsal wall, these are the "cerata" which are characteristically developed in another sub-order of Opisthobranchs, the Ceratonota (see fig. 62, A). (From Gegenbaur, after Alder and Hancock.)

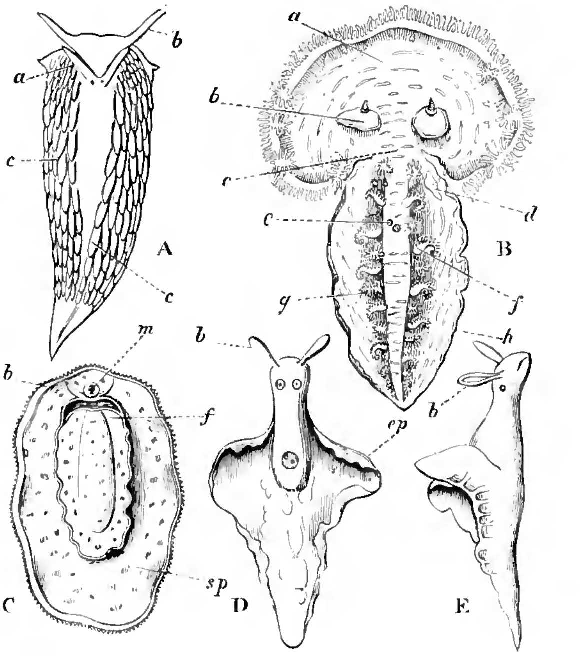


Fig. 62.

A. *Eolis papillosa* (Lin.), dorsal view. *a*, *b*, posterior and anterior cephalic tentacles; *c*, the dorsal "cerata" (hence Ceratobranchia).

B. *Tethys leporina*, dorsal view. *a*, the cephalic hood; *b*, cephalic tentacles; *c*, neck; *d*, genital pore; *e*, anus; *f*, large cerata; *g*, smaller cerata; *h*, margin of the foot.

C. *Doris* (*Actinocyclus*) *tuberculatus* (Cuv.), seen from the pedal surface. *m*, mouth; *b*, margin of the head; *f*, sole of the foot; *sp*, the mantle-like epipodium.

D, E. Dorsal and lateral view of *Elysia* (*Actaeon*) *viridis*. *ep*, epipodial outgrowths. (After Keferstein.)

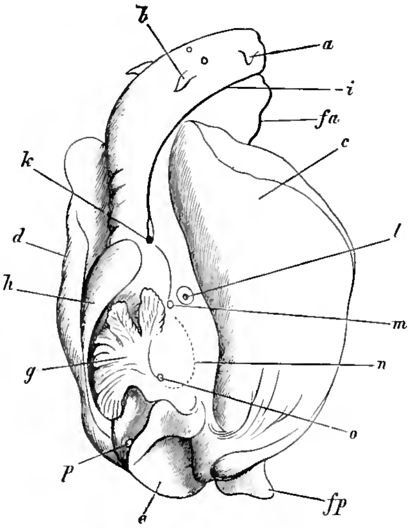


Fig. 63.—*Aplysia leporina* (*camelus*, Cuv.), with epipodia and mantle reflected away from the mid-line. *a*, anterior cephalic tentacle; *b*, posterior do.; between *a* and *b*, the eyes; *c*, right epipodium; *d*, left epipodium; *e*, hinder part of visceral hump; *fp*, posterior extremity of the foot; *fa*, anterior part of the foot underlying the head; *g*, the ctenidium (branchial plume); *h*, the mantle-skirt tightly spread over the horny shell and pushed with it towards the left side; *i*, the spermatic groove; *k*, the common genital pore (male and female); *l*, orifice of the grape-shaped (supposed poisonous) gland; *m*, the osphradium (olfactory organ of Spengel); *n*, outline of part of the renal sac (nephridium) below the surface; *o*, external aperture of the nephridium; *p*, anus. (Original.)

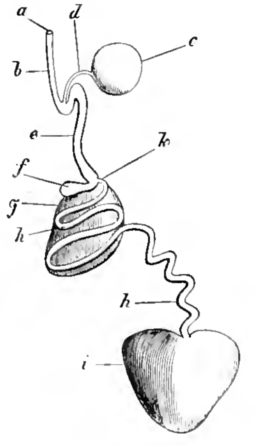


Fig. 64.—Gonad, and accessory glands and ducts of Aplysia. *i*, ovo-testis; *h*, hermaphrodite duct; *g*, albuminiparous gland; *f*, vesicula seminalis; *k*, opening of the albuminiparous gland into the hermaphrodite duct; *e*, hermaphrodite duct (uterine portion); *b*, vaginal portion of the uterine duct; *c*, spermatheca; *d*, its duct; *a*, genital pore. (Original.)

With regard to internal organization we may commence with the disposition of the renal organ (nephridium), the external opening of which has already been noted. The position of this opening and other features of the renal organ have been determined recently by Mr. J. T. Cunningham, Fellow of University College, Oxford, who writes as follows from Naples, February 1883:—

"There is considerable uncertainty with respect to the names of the species of Aplysia. There are two forms which are very common in the Gulf of Naples, and which I have used in studying the anatomy of the renal organ in the genus. One is quite black in colour, and measures when outstretched eight or nine inches in length. The other is light brown and somewhat smaller, its length usually not exceeding seven inches. The first is flaccid and sluggish in its movements, and has not much power of contraction; its epipodial lobes are enormously developed and extend far forward along the body; it gives out when handled an abundance of purple liquid, which is derived from cutaneous glands situated on the under side of the free edge of the mantle. In the Zoological Station this form is known as *Ap. leporina*; but according to Blochmann it is identical with *A. Camelus* of Cuvier. The other species is *A. depilans*; it is firm to the touch, and contracts forcibly when irritated; the secretion of the mantle-glands is not abundant, and is milky white in appearance. The kidney has similar relations in both genera, and is identical with the organ spoken of by many authors as the triangular gland. Its superficial extent is seen when the folds covering the shell are cut away and the shell removed; the external surface forms a triangle with its base bordering the pericardium and its apex directed posteriorly and reaching to the left-hand posterior corner of the shell-chamber. The dorsal surface of the kidney extends to the left beyond the shell-chamber beneath the skin in the space between the shell-chamber and the left epipodium.

"When the animal is turned on its left-hand side and the mantle-chamber widely opened, the gill being turned over to the left, a part of the kidney is seen beneath the skin between the attachment of the gill and the right epipodium (fig. 63). On examination this is found to be the under surface of the posterior limb of the gland, the upper surface of which has just been described as lying beneath the shell. In the posterior third of this portion, close to that edge which is adjacent to the base of the gill, is the external opening (fig. 63, *o*).

"When the pericardium is cut open from above in an animal otherwise entire, the anterior face of the kidney is seen forming the posterior wall of the pericardial chamber; on the deep edge of this face, a little to the left of the attachment of the auricle to the floor of the pericardium, is seen a depression; this depression contains the opening from the pericardium into the kidney.

"To complete the account of the relations of the organ: the right anterior corner can be seen superficially in the wall of the mantle-chamber above the gill. Thus the base of the gill passes in a slanting direction across the right-hand side of the kidney, the posterior end being dorsal to the apex of the gland, and the anterior end ventral to the right-hand corner.

"As so great a part of the whole surface of the kidney lies adjacent to external surfaces of the body, the remaining part which faces the internal organs is small; it consists of the left part of the under surface; it is level with the floor of the pericardium, and lies over the globular mass formed by the liver and convoluted intestine.

"Mere dissection does not give sufficient evidence concerning such communications as these of the kidney in Aplysia. I studied the external opening by taking a series of sections through the surrounding region of the gland; to demonstrate the internal aperture injected a solution of Berlin blue into the pericardium; it did not fill the whole kidney easily, but ran down into the part adjacent to the base of the gill."

Thus the renal organ of Aplysia is shown to conform to the Molluscan type. The heart lying within the adjacent pericardium has the usual form, a single auricle and ventricle. The vascular system is not extensive, the arteries soon ending in the well-marked spongy tissue which builds up the muscular foot, epipodia, and dorsal body-wall.

The alimentary canal commences with the usual buccal mass; the lips are cartilaginous, but not armed with horny jaws, though these are common in other Opisthobranchs; the lingual ribbon is multidenticulate, and a pair of salivary glands pour in their secretion. The œsophagus expands into a curious gizzard, which is armed internally with large horny processes, some broad and thick, others spinous, fitted to act as crushing instruments. From this we pass to a stomach and a coil of intestine embedded in the lobes of a voluminous liver; a cæcum of large size is given off near the commencement of the intestine. The liver opens by two ducts into the digestive tract.

The generative organs lie close to the coil of intestine and liver, a little to the left side. When dissected out they appear as represented in fig. 64. The essential reproductive organ or gonad consists of both ovarian and testicular cells (see fig. 65). It is an ovo-testis. From it passes a common or hermaphrodite duct, which very soon becomes entwined in the spire of a gland—the albuminiparous gland. The latter opens into the common duct at the point *x*, and here also is a small diverticulum of the duct *y*. Passing on, we find not far from the genital pore a glandular spherical body (the spermatheca *a*) opening by means of a longish duct into the common duct, and then we reach the pore (fig. 63, *k*). Here the female apparatus terminates. But when the male secretion of the ovo-testis is active, the seminal fluid passes from the genital pore along the spermatic groove (fig. 63,) to the penis, and is by the aid of that eversible muscular organ introduced into the genital pore of a second Aplysia, whence it passes into the spermatheca, there to await the activity of the female element of the ovo-testis of this second Aplysia. After an interval of some days—possibly weeks—the ova of the second Aplysia commence to descend the hermaphrodite duct; they become enclosed in a viscid secretion at the point where the albuminiparous gland opens into the duct intertwined with it; and on reaching the point where the spermathecal duct debouches they are impregnated by the spermatozoa which escape now from the spermatheca and meet the ova.

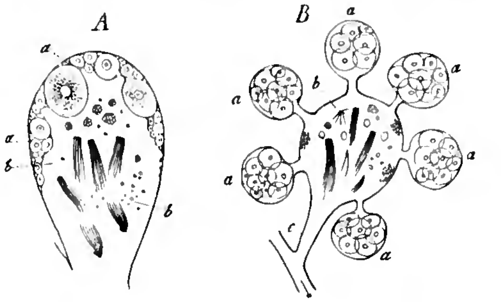


Fig. 65.—Follicles of the hermaphrodite gonads of Euthyneurous Anisopleura. —*A*, of Helix; *B*, of Eolidia. *a*, ova; *b*, developing spermatozoids; *c*, common efferent duct.

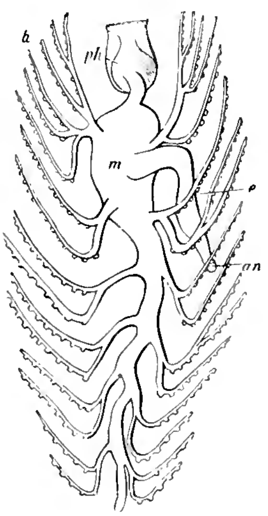


Fig. 66. Enteric canal of *Æolidia papillosa*. *ph*, pharynx; *m*, mid-gut, with its hepatic appendages *h*, all of which are not figured; *e*, hind gut; *an*, anus. (From Gegenbaur, after Alder and Hancock.)

The development of Aplysia from the egg presents many points of interest from the point of view of comparative embryology, but in relation to the morphology of the Opisthobranchia it is sufficient to point to the occurrence of a trochosphere and a veliger stage (fig. 60), and of a shell-gland or primitive shell-sac (fig. 68, *shs*), which is succeeded by a nautiloid shell.

The nervous system of Aplysia will be found on comparison of fig. 20, which represents it, with our schematic Mollusc (fig. 1, D) to present but little modification. It is in fact a nervous system in which the great ganglion-pairs are well developed and distinct. The Euthyneurous visceral loop is long, and presents only one ganglion (in *Aplysia camelus*, but two distinct ganglia joined to one another in

Aplysia hybrida of the English coast), placed at its extreme limit, representing both the right and left visceral ganglia and the third or abdominal ganglion, which are so often separately present. The diagram (fig. 20) shows the nerve connecting this abdomino-visceral ganglion with the olfactory ganglion of Spengel. It is also seen to be connected with a more remote ganglion—the genital. Such special irregularities in the development of ganglia upon the visceral loop, and on one or more of the main nerves connected with it, are, as the figures of Molluscan nervous systems given in this article show, very frequent. Our figure of the nervous system of Aplysia does not give the small pair of buccal ganglia which are, as in all Glossophorous Molluscs, present upon the nerves passing from the cerebral region to the odontophore.

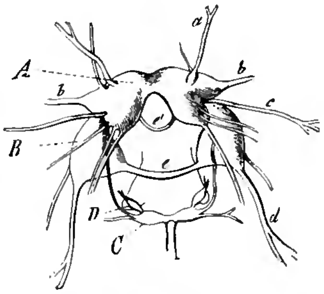


Fig. 67.—Central nervous system of Fiona (one of the Ceratonotous Opisthobranchs), showing a tendency to fusion of the great ganglia. *A*, cerebral, pleural, and visceral ganglia united; *B*, pedal ganglion; *C*, buccal ganglion; *D*, œsophageal ganglion connected with the buccal; *a*, nerve to superior cephalic tentacle; *b*, nerves to inferior cephalic tentacles; *c*, nerve to generative organs; *d*, pedal nerve; *e*, pedal commissure; *e′*, visceral loop or commissure (?). (From Gegenbaur, after Bergh.)

For a comparison of various Opisthobranchs, Aplysia will be found to present a convenient starting-point. It is one of the more typical Opisthobranchs, that is to say, it belongs to the section Palliata, but other members of the Palliata, namely, Bulla and Tornatella (figs. 52 and 53), are less abnormal than Aplysia in regard to their shells and the form of the visceral hump. They have naked spirally-twisted shells which may be concealed from view in the living animal by the expansion and reflexion of the epipodia, but are not enclosed by the mantle, whilst Tornatella is remarkable amongst all Euthyneura for possessing an operculum like that of so many Streptoneura.

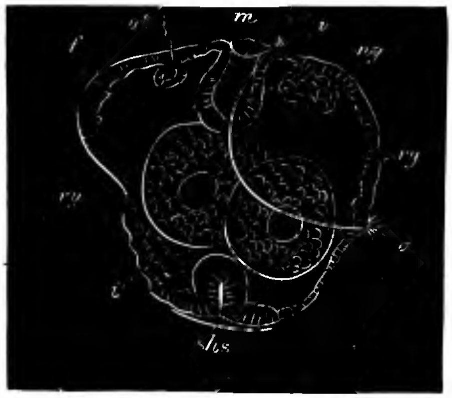


Fig. 68.—Young veliger larva of an Opisthobranch (Pleuro-branchidium). *m*, mouth; *v*, ciliated band marking off the velum; *ng*, cerebral ganglion developing from epiblast, within the velar area; *ot*, otocyst also developing from epiblast; *f*, foot; *i*, intestine; *ry*, residual nutritive yelk; *shs*, primitive shell sac or shell-gland. (From Lankester.)

The great development of the epipodia seen in Aplysia is usual in Palliate Opisthobranchs; it occurs also in Elysia (fig. 62, D) among Non-Palliata; in Doris it seems probable that the mantle-like fold overhanging the foot is to be interpreted as epipodium, the mantle-skirt being altogether absent, as shown by the naked position of the gills and anus on the dorsal surface (figs. 61 and 62, C). The whole surface of the body becomes greatly modified in those Non-Palliate forms which have lost, not only the mantle-skirt and the shell, but also the ctenidium. Many of these (Ceratonota) have peculiar processes developed on the dorsal surface (fig. 62, A, B), or retain purely negative characters (fig. 62, D). The chief modification of internal organization presented by these forms, as compared with Aplysia, is found in the condition of the alimentary canal. The liver is no longer a compact organ opening by a pair of ducts into the median digestive tract, but we find very numerous hepatic diverticula on a shortened axial tract (fig. 66). These diverticula extend usually one into each of the dorsal papillæ or "cerata" when these are present. They are not merely digestive glands, but are sufficiently wide to act as receptacles of food, and in them the digestion of food proceeds just as in the axial portion of the canal. A precisely similar modification of the liver or great digestive gland is found in the Scorpions, where the axial portion of the digestive canal is short and straight, and the lateral ducts sufficiently wide to admit food into the ramifications of the gland there to be digested; whilst in the Spiders the gland is reduced to a series of simple cæca.

The typical character is retained by the heart, pericardium, and the communicating nephridium or renal organ in all Opisthobranchs. An interesting example of this is furnished by the fish-like transparent Phyllirhoë (fig. 58), in which it is possible most satisfactorily to study in the living animal, by means of the microscope, the course of the blood-stream, and also the reno-pericardial communication. With reference to the existence of pores placing the vascular system in open communication with the surrounding water, see the paragraph as to Mollusca generally. In a form closely allied to Aplysia (Pleurobranchus) such a pore leading outwards from the branchial vein has been precisely described by Lacaze Duthiers. No such pore has been detected in Aplysia. In many of the Non-Palliate Opisthobranchs the nervous system presents a concentration of the ganglia (fig. 67), contrasting greatly with what we have seen in Aplysia. Not only are the pleural ganglia fused to the cerebral, but also the visceral to these (see in further illustration the condition attained by the Pulmonate Limnæus, fig. 22), and the visceral loop is astonishingly short and insignificant (fig. 67, *e′*). That the parts are rightly thus identified is probable from Spengel's observation of the osphradium and its nerve-supply in these forms; the nerve to that organ, which is placed somewhat anteriorly—on the dorsal surface—being given off from the hinder part (visceral) of the right compound ganglion—the fellow to that marked A in fig. 67. The Ceratonotous Opisthobranchs, amongst other specialities of structure, are stated to possess (in some cases at any rate) apertures at the apices of the "cerata" or dorsal papillæ, which lead from the exterior into the hepatic cæca. This requires confirmation. Some amongst them (Tergipes, Eolis) are also remarkable for possessing peculiarly modified epidermic cells placed in sacs at the apices of these same papillæ, which resemble the "thread-cells" of the Planarian Flatworms and of the Cœlentera. The existence of these thread-cells is sufficiently remarkable, seeing that the Non-Palliate Opisthobranchs resemble in general form and habit the Planarian worms, many of which also possess thread-cells. But it is not conceivable that their presence is an indication of genetic affinity between the two groups, rather they are instances of homoplasy. The development of many Opisthobranchia has been examined—*e.g.*, Aplysia, Pleurobranchidium, Elysia, Polycera, Doris, Tergipes. All pass through trochosphere and veliger stages, and in all a nautiloid or boat-like shell is developed, preceded by a well-marked "shell-gland" (see figs. 60 and 68). The transition from the free-swimming veliger larva with its nautiloid shell (fig. 60) to the adult form has not been properly observed, and many interesting points as to the true nature of folds (whether epipodia or mantle or velum) have yet to be cleared up by a knowledge of such development in forms like Tethys, Doris, Phyllidia, &c.

As in other Molluscan groups, we find even in closely-allied genera (for instance, in Aplysia and Pleurobranchidium, and other genera observed by Lankester) the greatest differences as to the *amount* of food-material by which the egg-shell is encumbered. Some form their Diblastula by emboly (fig. 7), others by epiboly (fig. 5); and in the later history of the further development of the enclosed cells (arch-enteron) very marked variations occur in closely-allied forms, due to the influence of a greater or less abundance of food-material mixed with the protoplasm of the egg.

Order 2 (of the Euthyneura).—**Pulmonata.**

Characters.—Euthyneurous Anisopleurous Gastropoda, probably derived from ancestral forms similar to the Palliate Opisthobranchia by adaptation to a terrestrial life. The ctenidium is atrophied, and the edge of the mantle-skirt is fused to the dorsal integument by concrescence, except at one point which forms the aperture of the mantle-chamber, thus converted into a nearly closed sac. Air is admitted to this sac for respiratory and hydrostatic purposes, and it thus becomes a lung. An operculum is never present; a contrast being thus afforded with the operculate Pulmonate Streptoneura (Cyclostoma, &c.), which differ in other essential features of structure from the Pulmonata. The Pulmonata are, like the other Euthyneura, hermaphrodite, with elaborately-developed copulatory organs and accessory glands. Like other Euthyneura, they have very numerous small denticles on the lingual ribbon. The ancestral Pulmonata appear to have retained both the right and the left osphradia (Spengel's olfactory organs), since in some (Planorbis, Auricularia) we find the single osphradium to be that of the original left side, whilst in others (Limnæus) it is that of the original right side.

In some Pulmonata (Snails) the foot is extended at right angles to the visceral hump, which rises from it in the form of a coil as in Streptoneura; in others the visceral hump is not elevated, but is extended with the foot, and the shell is small or absent (Slugs).

The Pulmonata are divided into two sub-orders according to the position of the cephalic eyes.

Sub-order 1.—*Basommatophora.*

Characters.—Eyes placed mediad of the cephalic tentacles at their base; the embryonic velar area retained in adult life as a pair of cephalic lobes (fig. 70, *v*); male and female generative apertures separate, placed (as is typical in Anisopleura) on the right side of the neck; visceral hump well developed, with a well-developed shell; aquatic in habit.

Family 1.—*Limnæidæ.*

Genera: *Limnæus*, Lam. (figs. 3, 4, &c.); *Chilinia*, Gray; *Physa*, Draparn.; *Ancylus*, Geoff.; *Planorbis*, Mull., &c.

Family 2.—*Auriculidæ.*

Genera: *Auricula*, Lam.; *Conovulus*, Lam.; *Pitharella*, Wood. &c.

Sub-order 2.—*Stylommatophora.*

Characters.—Eyes placed on the summit of two hollow tentacles; visceral hump well or not at all developed; shell large and coiled, or minute or absent; almost exclusively terrestrial.

Family 1.—*Helicidæ.*

Genera: *Helix*, L. (figs. 69, A; 72*); *Vitrina*, Draparn.; *Succinea*, Draparn.; *Bulimus*, Scopoli; *Achatina*, Lam.; *Pupa*, Lam.; *Clausilia*, Draparn., &c.

Family 2.—*Limacidæ* (Slugs).

Genera: *Limax*, L.; *Incilaria*, Benson; *Arion*, Ferussac (fig. 69, D); *Parmacella*, Cuvier; *Testacella*, Cuvier (fig. 69, C), &c.

Family 3.—*Oncidiadæ.*

Genera: *Oncidium*, Buchanan; *Peronia*, Blainv. (fig. 72); *Vaginulus*, Ferussac, &c.

Further Remarks on Pulmonata.—The land-snails and slugs forming the group Pulmonata are widely distinguished from a small set of terrestrial Azygobranchia, the Pneumonochlamyda (see above), at one time associated with them on account of their mantle-chamber being converted, as in Pulmonata, into a lung, and the ctenidium or branchial plume aborted. The Pneumonochlamyda (represented in England by the common genus Cyclostoma) have a twisted visceral nerve-loop, an operculum on the foot, a complex rhipidoglossate or tænioglossate radula, and are of distinct sexes; they are, in fact, Azygobranchiate Streptoneura. The Pulmonata have a straight visceral nerve-loop, never an operculum (even in the embryo), and a multidenticulate radula, the teeth being equi-formal; and they are hermaphrodite. Some Pulmonata (Limnæus, &c.) live in fresh-waters although breathing air. The remarkable discovery has been made that in deep lakes such Limnæi do not breathe air, but admit water to the lung-sac and live at the bottom. The lung-sac serves undoubtedly as a hydrostatic apparatus in the aquatic Pulmonata, as well as assisting respiration. It is not improbable that here, and in other air-breathing animals, the hydrostatic function was the primary one, and the respiratory a later development.

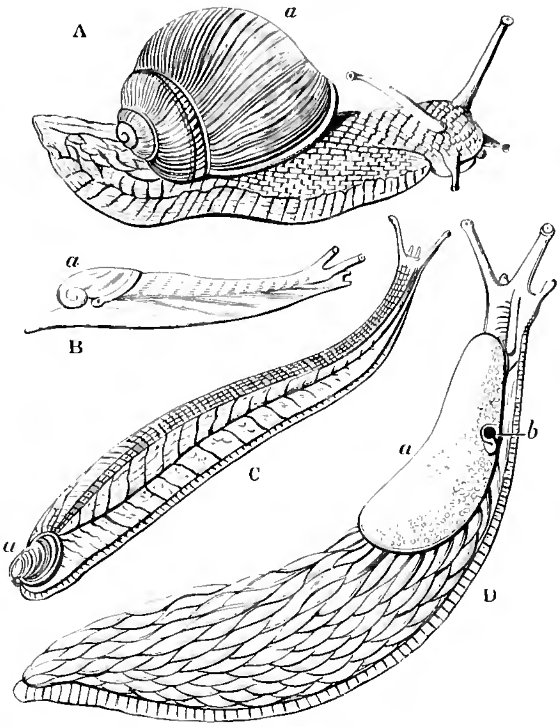


Fig. 69.—A series of Stylommatophorous Pulmonata, showing transitional forms between snail and slug.
A. *Helix pomatia* (from Keferstein).
B. *Helicophanta brevipes* (from Keferstein, after Pfeiffer).
C. *Testacella haliotidea* (from Keferstein).
D. *Arion ater*, the great Black Slug (from Keferstein).
a, Shell in A, B, C, shell-sac (closed) in D; *b*, orifice leading into the subpallial chamber (lung).

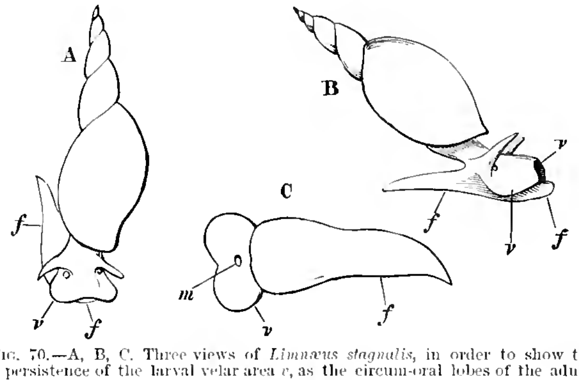


Fig. 70.—A, B, C. Three views of *Limnæus stagnalis*, in order to show the persistence of the larval velar area *v*, as the circum-oral lobes of the adult. *m*, mouth; *f*, foot; *v*, velar area, the margin *v* corresponding with the ciliated band which demarcates the velar area or velum of the embryo Gastropod (see fig. 4, D, E, F, H, I, *v*). (Original.)

The same general range of body-form is shown in Pulmonata as in the Natant Azygobranchia and in the Opisthobranchia; at one extreme we have Snails with coiled visceral hump, at the other cylindrical or flattened Slugs (see fig. 69). Limpet-like forms are also found (fig. 71, Ancylus). The foot is always simple, with its flat crawling surface extending from end to end, but in the embryo Limnæus (fig. 4, H) it shows a bilobed character, which leads on to the condition characteristic of Pteropoda.

Fig. 71.—*Ancylus fluviatilis*, a patelliform aquatic Pulmonate.

The adaptation of the Pulmonata to terrestrial life has entailed little modification of the internal organization. The vascular system appears to be more complete in them than in other Gastropoda, fine vessels and even capillaries being present in place of lacunæ, in which arteries and veins find their meeting-point. The subject has not, however, been investigated by the proper methods of recent histology, and our knowledge of it, as of the vascular system of Molluscs generally, is most unsatisfactory. In one genus (Planorbis) the plasma of the blood is coloured red by hæmoglobin, this being the only instance of the presence of this body in the blood of Glossophorous Mollusca, though it occurs in corpuscles in the blood of the bivalves Arca and Solen (Lankester, **31**).

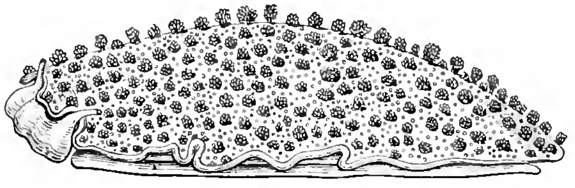


Fig. 72.—*Peronia Tongæ*, a littoral Pulmonate, found on the shores of the Indian and Pacific Oceans (Mauritius, Japan).

The generative apparatus of the Snail (Helix) may serve as an example of the hermaphrodite apparatus common to the Pulmonata and Opisthobranchia (fig. 72*). From the ovo-testis, which lies near the apex of the visceral coil, a common hermaphrodite duct *v.e* proceeds, which receives the duct of the compact white albuminiparous gland *E.d.*, and then becomes much enlarged, the additional width being due to the development of glandular folds, which are regarded as forming a uterus *u*. Where these folds cease the common duct splits into two portions, a male and a female. The male duct *v.d* becomes fleshy and muscular near its termination at the genital pore, forming the penis *p*. Attached to it is a diverticulum *fl.*, in which the spermatozoa which have descended from the ovo-testis are stored and modelled into sperm ropes or spermatophores. The female portion of the duct is more complex. Soon after quitting the uterus it is joined by a long duct leading from a glandular sac, the spermatheca (*R.f*). In this duct and sac the spermatophores received in copulation from another snail are lodged. In *Helix hortensis* the spermatheca is simple. In other species of Helix a second duct (as large in *Helix aspersa* as the chief one) is given off from the spermatheeal duct, and in the natural state is closely adherent to the wall of the uterus. This second duct has normally no spermatheeal gland at its termination, which is simple and blunt. But in rare cases in *Helix aspersa* a second spermatheca is found at the end of this second duct. Tracing the widening female duct onwards we now come to the openings of the digitate accessory glands *d*, *d*, which probably assist in the formation of the egg-capsule. Close to them is the remarkable dart-sac *ps*, a thick-walled sac, in the lumen of which a crystalline four-fluted rod or dart consisting of carbonate of lime is found. It is supposed to act in some way as a stimulant in copulation, but possibly has to do with the calcareous covering of the egg-capsule. Other Pulmonata exhibit variations of secondary importance in the details of this hermaphrodite apparatus.

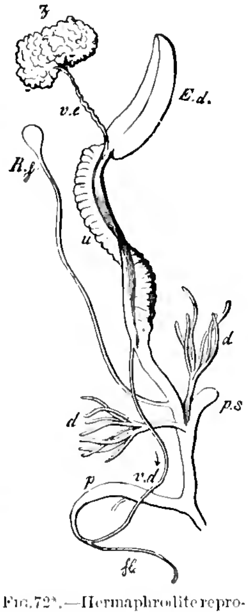


Fig. 72*.—Hermaphrodite reproductive apparatus of the Garden Snail (*Helix hortensis*). *z*, ovo-testis; *v.e*, hermaphrodite duct; *E.d.*, albuminiparous gland; *u*, uterine dilatation of the hermaphrodite duct; *d*, digitate accessory glands on the female duct; *p.s*, calciferous gland or dart-sac on the female duct; *R.f*, spermatheca or receptacle of the sperm in copulation, opening into the female duct; *v.d*, male duct (vas deferens); *p*, penis; *fl.*, flagellum.

The nervous system of Helix is not favourable as an example on account of the fusion of the ganglia to form an almost uniform ring of nervous matter around the œsophagus. The Pond-Snail (Limnæus) furnishes, on the other hand, a very beautiful case of distinct ganglia and connecting cords (fig. 22). The demonstration which it affords of the extreme shortening of the Euthyneurous visceral nerve-loop is most instructive and valuable for comparison with and explanation of the condition of the nervous centres in Cephalopoda, as also of some Opisthobranchia. The figure (fig. 22) is sufficiently described in the letterpress attached to it; the pair of buccal ganglia joined by the connectives to the cerebrals are, as in most of our figures, omitted. Here we need only further draw attention to the osphradium, discovered by Lacaze Duthiers (**32**), and shown by Spengel to agree in its innervation with that organ in all other Gastropoda. On account of the shortness of the visceral loop and the proximity of the right visceral ganglion to the œsophageal nerve-ring, the nerve to the osphradium and olfactory ganglion is very long. The position of the osphradium corresponds more or less closely with that of the vanished right ctenidium, with which it is normally associated. In Helix and Limax the osphradium has not been described, and possibly its discovery might clear up the doubts which have been raised as to the nature of the mantle-chamber of those genera. In Planorbis, which is dexiotropic (as are a few other genera or exceptional varieties of various Anisopleurous Gastropods) instead of being leiotropic, the osphradium is on the left side, and receives its nerve from the left visceral ganglion, the whole series of unilateral organs being reversed. This is, as might be expected, what is found to be the case in all "reversed" Gastropods. It is also the case in the Pulmonate Auricula, which is leiotropic.

The shell of the Pulmonata, though always light and delicate, is in many cases a well-developed spiral "house," into which the creature can withdraw itself; and, although the foot possesses no operculum, yet in Helix the aperture of the shell is closed in the winter by a complete lid, the "hybernaculum," more or less calcareous in nature, which is secreted by the foot. In Clausilia a peculiar modification of this lid exists permanently in the adult, attached by an elastic stalk to the mouth of the shell, and known as the "clausilium." In Limnæus the permanent shell is preceded in the embryo by a well-marked shell-gland or primitive shell-sac (fig. 72***), at one time supposed to be the developing anus, but shown by Lankester to be identical with the "shell-gland" discovered by him in other Mollusca (Pisidium, Pleurobranchidium, Neritina, &c.). As in other Gastropoda Anisopleura, this shell-sac may abnormally develop a plug of chitonous matter, but normally it flattens out and disappears, whilst the cap-like rudiment of the permanent shell is shed out from the dome-like surface of the visceral hump, in the centre of which the shell-sac existed for a brief period.

In Clausilia, according to the observations of Gegenbaur, the primitive shell-sac does not flatten out and disappear, but takes the form of a flattened closed sac. Within this closed sac a plate of calcareous matter is developed, and after a time the upper wall of the sac disappears, and the calcareous plate continues to grow as the nucleus of the permanent shell. In the slug Testacella (fig. 69, C) the shell-plate never attains a large size, though naked. In other slugs, namely, Limax and Arion, the shell-sac remains permanently closed over the shell-plate, which in the latter genus consists of a granular mass of carbonate of lime. The permanence of the primitive shell-sac in these slugs is a point of considerable interest. It is clear enough that the sac is of a different origin from that of Aplysia (described in the section treating of Opisthobranchia), being primitive instead of secondary. It seems probable that it is identical with one of the open sacs in which each shell-plate of a Chiton is formed, and the series of plate-like imbrications which are placed behind the single shell-sac on the dorsum of the curious slug, Plectrophorus, suggest the possibility of the formation of a series of shell-sacs on the back of that animal similar to those which we find in Chiton. Whether the closed primitive shell-sac of the slugs (and with it the transient embryonic shell-gland of all other Mollusca) is precisely the same thing as the closed sac in which the calcareous pen or shell of the Cephalopod Sepia and its allies is formed, is a further question, which we shall consider when dealing with the Cephalopoda. It is important here to note that Clausilia furnishes us with an exceptional instance of the *continuity* of the shell or secreted product of the primitive shell-sac with the adult shell. In most other Mollusca (Anisopleurous Gastropods, Pteropods, and Conchifera) there is a want of such continuity; the primitive shell-sac contributes no factor to the permanent shell, or only a very minute knob-like particle (Neritina and Paludina). It flattens out and disappears before the work of forming the permanent shell commences. And just as there is a break at this stage, so (as observed by Krohn in Marsenia = Echinospira) there *may* be a break at a later stage, the nautiloid shell formed on the larva being cast, and a new shell of a different form being formed afresh on the surface of the visceral hump. It is, then, in this sense that we may speak of primary, secondary, and tertiary shells in Mollusca, recognizing the fact that they *may* be merely phases fused by continuity of growth so as to form but one shell, or that in other cases they *may* be presented to us as separate individual things, in virtue of the non-development of the later phases, or in virtue of sudden changes in the activity of the mantle-surface causing the shedding or disappearance of one phase of shell-formation before a later one is entered upon.

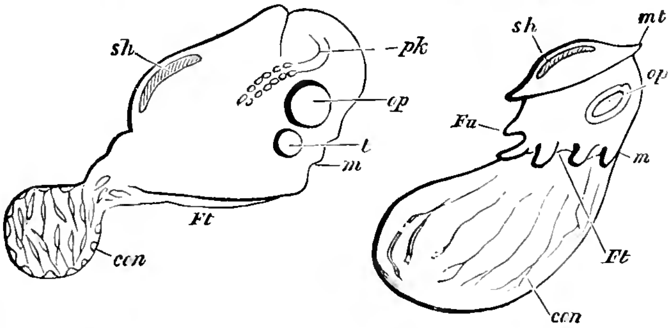


FIG. 72**.—Comparative diagrams of an embryo Slug, Limax (left), and an embryo Cuttle-fish, Loligo (right). *sh*, internal shell; *pk*, embryonic renal organ (Stiebel's canal) in Limax; *mt*, edge of the mantle-flap in Loligo; *op*, cephalic eye; *t*, cephalic tentacle; *m*, position of the mouth; *Ft*, the foot; *Fu*, the hinder part of the foot drawn out to form the funnel of Loligo; *con*, the contractile yelk-sac or hernia-like protrusion of the mid-region of the foot, corresponding to the line of closure of the blastopore in Limnæus. *N.B.*—The blastopore in the embryo of Loligo, which, like that of a bird, is much distorted by excess of food-yelk, *does* close at the extremity of the yelk-sac *con*. (Original.)

The development of the aquatic Pulmonata from the egg offers considerable facilities for study, and that of Limnæus has been elucidated by Lankester, whilst Rabl has with remarkable skill applied the method of sections to the study of the minute embryos of Planorbis. The chief features in the development of Limnæus are exhibited in the woodcuts (figs. 3, 4, and 72***). There is not a very large amount of food-material present in the egg of this snail, and accordingly the cells resulting from division are not so unequal as in many other cases. The four cells first formed are of equal size, and then four smaller cells are formed by division of these four so as to lie at one end of the first four (the pole corresponding to that at which the "directive corpuscles" *dc* are extruded and remain). The smaller cells now divide and spread over the four larger cells (fig. 3); at the same time a space—the cleavage cavity or blastocœl—forms in the centre of the mulberry-like mass. Then the large cells recommence the process of division and sink into the hollow of the sphere, leaving an elongated groove, the blastopore, on the surface (fig. 3, C, and fig. 4, G). The invaginated cells (derived from the division of the four big cells) form the endoderm or arch-enteron; the outer cells are the ectoderm. The blastopore now closes along the middle part of its course, which coincides in position with the future "foot." One end of the blastopore becomes nearly closed, and an ingrowth of ectoderm takes place around it to form the stomodæum or fore-gut and mouth. The other extreme end closes, but the invaginated endoderm cells remain in continuity with this extremity of the blastopore, and form the "rectal peduncle" or "pedicle of invagination" of Lankester (see also the account and figures (fig. 151, A) of the development of the bivalve Pisidium), although the endoderm cells retain no contact with the middle region of the now closed-up blastopore. The anal opening forms at a late period by a very short ingrowth or proctodæum coinciding with the blind termination of the rectal peduncle (fig. 72***, *pi*).

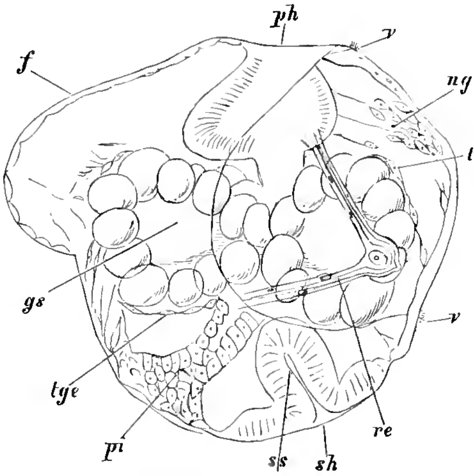


FIG. 72***.—Embryo of *Limnæus stagnalis*, at a stage when the Trochosphere is developing foot and shell-gland and becoming a Veliger, seen as a transparent object under slight pressure. *ph*, pharynx (stomodæal invagination); *v*, *v*, the ciliated band marking out the velum; *ng*, cerebral nerve-ganglion; *re*, Stiebel's canal (left side), probably an evanescent embryonic nephridium; *sh*, the primitive shell-sac or shell-gland; *pi*, the rectal peduncle or pedicle of invagination, its attachment to the ectoderm is coincident with the hindmost extremity of the elongated blastopore of fig. 3, C; *tge*, mesoblastic (skeletotrophic and muscular) cells investing *gs*, the bilobed arch-enteron or lateral vesicles of invaginated endoderm, which will develop into liver; *f*, the foot. (Original.)

The body-cavity and the muscular, fibrous, and vascular tissues are traced partly to two symmetrically-disposed "mesoblasts," which bud off from the invaginated arch-enteron, partly to cells derived from the ectoderm, which at a very early stage is connected by long processes with the invaginated endoderm, as shown in fig. 3, D. The external form of the embryo goes through the same changes as in other Gastropods, and is not, as was held previously to Lankester's observations, exceptional. When the middle and hinder regions of the blastopore are closing in, an equatorial ridge of ciliated cells is formed, converting the embryo into a typical "Trochosphere" (fig. 4, E, F).

The foot now protrudes below the mouth (fig. 4), and the post-oral hemisphere of the Trochosphere grows more rapidly than the anterior or velar area. The young foot shows a bilobed form (fig. 4, D, *f*). Within the velar area the eyes and the cephalic tentacles commence to rise up (fig. 4, D, *t*), and on the surface of the post-oral region is formed a cap-like shell and an encircling ridge, which gradually increases in prominence and becomes the freely depending mantle-skirt. The outline of the velar area becomes strongly emarginated and can be traced through the more mature embryos to the cephalic lobes or labial processes of the adult Limnæus (fig. 70).

This permanence of the distinction of the part known as the velar area through embryonic life to the adult state is exceptional among Mollusca, and is therefore a point of especial interest in Limnæus. None of the figures of adult Limnæus in recent works on Zoology show properly the form of the head and these velar lobes, and accordingly the figures here given have been specially sketched for the present article. The increase of the visceral dome, its spiral twisting, and the gradual closure of the space overhung by the mantle-skirt so as to convert it into a lung-sac with a small contractile aperture, belong to stages in the development later than any represented in our figures.

We may now revert briefly to the internal organization at a period when the Trochosphere is beginning to show a prominent foot growing out from the area where the mid-region of the elongated blastopore was situated, and having therefore at one end of it the mouth and at the other the anus. Fig. 72*** represents such an embryo under slight compression as seen by transmitted light. The ciliated band of the left side of the velar area is indicated by a line extending from *v* to *v*; the foot *f* is seen between the pharynx *ph* and the pedicle of invagination *pi*. The mass of the arch-enteron or invaginated endodermal sac has taken on a bilobed form (compare Pisidium, fig. 151), and its cells are swollen (*ys* and *tye*). This bilobed sac becomes *entirely* the liver in the adult; the intestine and stomach are formed from the pedicle of invagination, whilst the pharynx, œsophagus, and crop form from the stomodæal invagination *ph*. To the right (in the figure) of the rectal peduncle is seen the deeply invaginated shell-gland *ss*, with a secretion *sh* protruding from it. The shell-gland is destined in Limnæus to become very rapidly stretched out, and to disappear. Farther up, within the velar area, the rudiments of the cerebral nerve-ganglion *ng* are seen separating from the ectoderm. A remarkable cord of cells having a position just below the integument occurs on each side of the head. In the figure the cord of the left side is seen, marked *re*. This paired organ consists of a string of cells which are perforated by a duct. The opening of the duct at either end is not known. Such cannulated cells are characteristic of the nephridia of many worms, and it is held that the organs thus formed in the embryo Limnæus are embryonic nephridia. The most important fact about them is that they disappear, and are in no way connected with the typical nephridium of the adult. In reference to their first observer they are conveniently called "Stiebel's canals." Other Pulmonata possess, when embryos, Stiebel's canals in a more fully-developed state, for instance, the common slug Limax (fig. 72**, *pk*). Here too they disappear during embryonic life. Further knowledge concerning them is greatly needed. It is not clear whether there is anything equivalent to them in the embryos of marine Gastropoda or other Mollusca, the ectodermal cells called "embryonic renal organs" in some Gastropod embryos having only a remote resemblance to them. The three pairs of transient embryonic nephridia of the medicinal leech, the ciliated cephalic pits of Nemertines, and the anterior nephridia of Gephyræans, all suggest themselves for comparison with these enigmatical canals.

Marine Pulmonata.—Whilst the Pulmonata are essentially a terrestrial and fresh-water group, there is one genus of slug-like Pulmonates which frequent the sea-coast (Peronia, fig. 72), whilst their immediate congeners (Onchidium) are found in marshes of brackish water. Semper (**33**) has shown that these slugs have, in addition to the usual pair of cephalic eyes, a number of eyes developed upon the dorsal integument. These dorsal eyes are very perfect in elaboration, possessing lens, retinal nerve-end cells, retinal pigment, and optic nerve. Curiously enough, however, they differ from the cephalic Molluscan eye (for an account of which see fig. 118) in the fact that, as in the vertebrate eye, the filaments of the optic nerve penetrate the retina, and are connected with the surfaces of the nerve-end cells nearer the lens instead of with the opposite end. The significance of this arrangement is not known, but it is important to note, as shown by Hensen, Hickson, and others, that in the bivalves Pecten and Spondylus, which also have eyes upon the mantle quite distinct from typical cephalic eyes, there is the same relationship as in Onchidiadæ of the optic nerve to the retinal cells (fig. 145). In both Onchidiadæ and Pecten the pallial eyes have probably been developed by the modification of tentacles, such as coexist in an unmodified form with the eyes. The Onchidiadæ are, according to Semper, pursued as food by the leaping fish Periophthalmus, and the dorsal eyes are of especial value to them in aiding them to escape from this enemy.

Class II.—**SCAPHOPODA.**

Characters.—Mollusca Glossophora with the FOOT adapted to a BURROWING life in sand (figs. 73, 74, *f*). The body, and to a much greater extent the mantle-skirt and the foot, are elongated along the primitive antero-posterior (oro-anal)

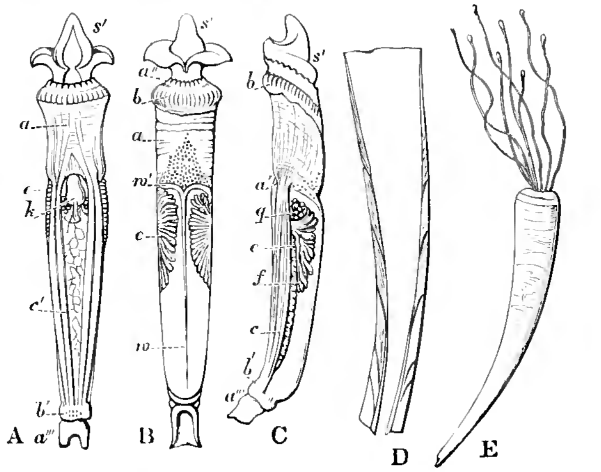


FIG. 73.—*Dentalium vulgare*, Da C. (after Lacaze Duthiers). A. Ventral view of the animal removed from its shell. B. Dorsal view of the same. C. Lateral view of the same. D. The shell in section. E. Surface view of the shell with gill-tentacles exserted as in life. *a*, mantle; *a'*, longitudinal muscle; *a''*, fringe surrounding the anterior opening of the mantle-chamber; *a'''*, the posterior appendix of the mantle; *b*, anterior circular muscle of the mantle; *b'*, posterior do.; *c*, *c'*, longitudinal muscle of mantle; *e*, liver; *f*, gonad; *k*, buccal mass (showing through the mantle); *q*, left nephridium; *s'*, club-shaped extremity of the foot; *w*, *w'*, longitudinal blood-sinus of the mantle.

axis, and retain, both externally and in the disposition of internal organs, the archi-Molluscan BILATERAL SYMMETRY. The margins of the mantle-skirt of opposite sides (right and left) meet below the foot and fuse by concrescence; only a small extent in front and a small extent behind of the mantle-margin is left unfused. Thus a CYLINDRICAL FORM is attained by the mantle, and on its surface a TUBULAR shell (incomplete along the ventral line in the youngest stages) is secreted (fig. 73, D). The FOOT is greatly elongated, and can be protruded from the anterior mantle-aperture. It has a characteristic clavate form (fig. 74, *f*).

The pair of typical CTENIDIA are symmetrically developed in the form of numerous gill-filaments (fig. 74, A, *g*) placed at the base of the cylindrical cephalic prominence or snout (fig. 74, *e*). A pair of NEPHRIDIA (fig. 74, *l*) are present, opening near the anus (fig. 74, *k*). The right serves as a genital duct, the left is apparently renal in function. The LIVER (*p*) is large and bilobed, the lobes divided into parallel lobules. The NERVE-GANGLIA are present (fig. 74, C) as well-marked cerebral, pleural, pedal, and visceral pairs, the typical pleural pair being closely joined to the cerebral. The visceral loop or commissure is untwisted, that is to say, the Scaphopoda are EUTHYNEUROUS. HEART and distinct VESSELS are not developed; a colourless blood is contained in the sinuses and networks formed by the body-cavity. The GONADS are either male or female, the sexes being distinct.

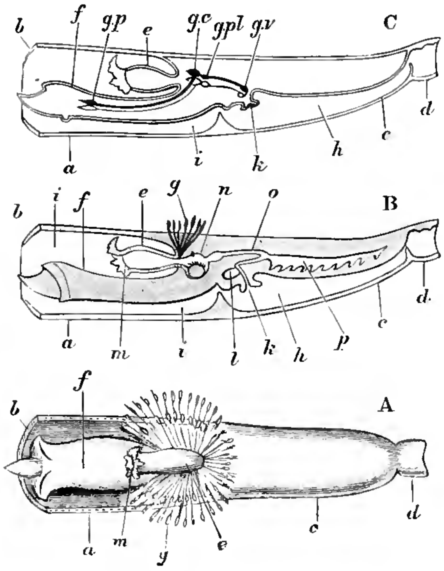


Fig. 74.—Diagrams of the anatomy of Dentalium. A. The anterior portion of the tubular mantle is slit open along the median dorsal line, and its cut margins (*a*) reflected so as to expose the foot, snout, and gills. B. Lateral view with organs showing as though by transparency. C. Similar lateral view to show the number and position of the nerve-ganglia and cords. *a*, the mantle-skirt; *b*, anterior free margin of the same; *c*, hinder extension of the mantle-skirt; *d*, the appendix of the mantle-skirt separated by a valve from the peri-anal portion of the sub-pallial chamber, *h*; *e*, the snout or oral process; *f*, the foot; *g*, the ctenidial filaments; *h*, the peri-anal part of the sub-pallial chamber; *i*, the peri-oral part of the same chamber; *k*, the anus; *l*, the left nephridium; *m*, the mouth surrounded by pinnate tentacles; *n*, the buccal mass and odontophore; *o*, œsophagus; *p*, the left lobe of the liver; *g.p*, pedal ganglion-pair; *g.c*, cerebral ganglion-pair; *g.pl*, pleural ganglion-pair; *g.v*, visceral ganglion-pair. Possibly further research will show that *g.pl* is the typical visceral ganglion-pair, and that *g.v* is a pair of olfactory ganglia placed on the visceral loop as in the Lipocephala according to Spengel.

The embyro is remarkable for developing five ciliated rings posterior to the ciliated ring and tuft characteristic of the trochosphere larval condition of Molluscs generally. These rings are comparable to those of the larva of Pneumodermon (fig. 84), and like them disappear.

The class Scaphopoda is not divisible into orders or families. It contains only three genera: *Dentalium*, L. (figs. 73, 74); *Siphonodentalium*, Sars.; and *Entalium*, Dfr. They inhabit exclusively the sand on the sea-coast in depths of from 10 to 100 fathoms.

It is worthy of remark that the Scaphopoda constitute among the Glossophora a parallel to the sand-boring forms so common among the Lipocephala (such as Solen and Mya). This parallelism is seen in the special mode of elongation of the body, in the form of the foot, and in the tubular form of the mantle brought about by the concrescence of its ventral margins, as in the Lipocephala mentioned. The cylindrical shell of Dentalium is also comparable to the two semi-cylindrical valves of the shell of Solen; or, better, to the tubular shell of Aspergillum and Teredo. Nevertheless, it is necessary to consider the Scaphopoda as standing far apart from the Lipocephala, and as having no special genetic but only a homoplastic relationship to them, in consequence of their possessing a well-developed odontophore, the characteristic organ of the Glossophora never possessed by any Lipocephala.

Class III.—**CEPHALOPODA**.

Characters.—Mollusca Glossophora with the FOOT primarily adapted to a FREE-SWIMMING mode of life. The archi-Molluscan BILATERAL SYMMETRY predominates both in the external and internal organs generally, though in many cases (especially the smaller forms) a one-sided displacement of primitively median organs and a suppression of one of the primitively paired organs is to be noted.

An ANTERIOR, MEDIAN, and POSTERIOR region of the FOOT can be distinguished (fig. 75, (4), (5), (6)), corresponding to but probably not derived from the pro-, meso-, and meta-podium of Gastropoda. The fore-foot invariably has the HEAD MERGED into it, and grows up on each side (right and left) of that part so as to surround the mouth, the two upgrowths of the fore-foot meeting on the dorsal aspect of the snout,—whence the name Cephalopoda. In the more typical forms of both branches of the class, the peri-oral portion of the foot is drawn out into paired arm-

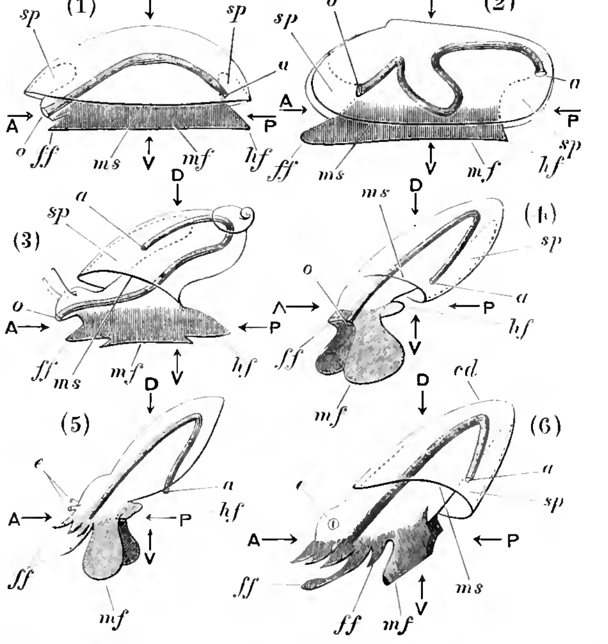


Fig. 75.—Diagrams of a series of Molluscs to show the form of the foot and its regions, and the relation of the visceral hump to the antero-posterior and dorso-ventral axes. (1) A Chiton. (2) A Lamellibranch. (3) An Anisopleurous Gastropod. (4) A Thecosomatous Pteropod. (5) A Gymnosomatous Pteropod. (6) A Siphonopod (Cuttle) A, P, antero-posterior horizontal axis; D, V, dorso-ventral vertical axis at right angles to A, P; *o*, mouth; *a*, anus; *ms*, edge of the mantle-skirt or flap; *sp*, sub-pallial chamber or space; *ff*, fore-foot; *mf*, mid-foot; *hf*, hind-foot; *e*, cephalic eyes; *cd*, centro-dorsal point (in 6 only).

like processes, either very short and conical (Clio, Eurybia), or lengthy (Pneumodermon, Octopus); these may be beset with suckers or hooks, or both. The mid-foot (fig. 75, *mf*) is expanded into a pair of muscular lobes right and left, which either are used for striking the water like the wings of a butterfly (Pteropoda), or are bent round towards one another so that their free margins meet and constitute a short tube,—the siphon or funnel (Siphonopoda). The hind foot is either very small or absent.

A distinctive feature of the Cephalopoda is the ABSENCE of anything like the TORSION of the visceral mass seen in the Anisopleurous Gastropoda, although as an exception this torsion occurs in one family (the Limacinidæ).

The ANUS, although it may be a little displaced from the median line, is (except in Limacinidæ) approximately median and posterior. The MANTLE-SKIRT may be aborted (Gymnosomatous Pteropoda); when present it is deeply produced posteriorly, forming a large sub-pallial chamber around the anus. As in our schematic Mollusc, by the side of the anus are placed the single or paired apertures of the NEPHRIDIA, the GENITAL APERTURES (paired only in Nautilus, in female Octopoda, female Ommastrephes, and male Eledone), and the paired CTENIDIA (absent in all Pteropoda). The VISCERAL HUMP or dome is elevated, and may be very much elongated (see fig. 75, (4), (5), (6)) in a direction almost at right angles to the primary horizontal axis (**A**, **P** in fig. 75) of the foot.

A SHELL is frequently, but not invariably, secreted on the visceral hump and mantle-skirt of Cephalopoda; but there are both Pteropoda and Siphonopoda devoid of any shell. The shell is usually light in substance or lightened by air-chambers in correlation with the free-swimming habits of the Cephalopoda. It may be external, when it is box-like or boat-like, or internal, when it is plate-like. Very numerous minute pigmented sacs capable of expansion and contraction, and known as CHROMATOPHORES, are usually present in the integument in both branches of the class. The GONADS of both sexes are developed in one individual in some Cephalopoda (Pteropoda), in others the sexes are separate.

SENSE-ORGANS, especially the cephalic eyes and the otocysts, are very highly developed in the higher Cephalopoda. The osphradia have the typical form and position in the lower forms, but appear to be more or less completely replaced by other olfactory organs in the higher. The normal NERVE-GANGLIA are present, but the connectives are shortened, and the ganglia concentrated and fused in the cephalic region. Large special ganglia (optic, stellate, and supra-buccal) are developed in the higher forms (Siphonopoda).

The Cephalopoda exhibit a greater range from low to high organization than any other Molluscan class, and hence they are difficult to characterize in regard to several groups of organs; but they are definitely held together by the existence in all of the encroachment of the fore-foot so as to surround the head, and by the functionally important BILOBATION OF THE MID-FOOT.

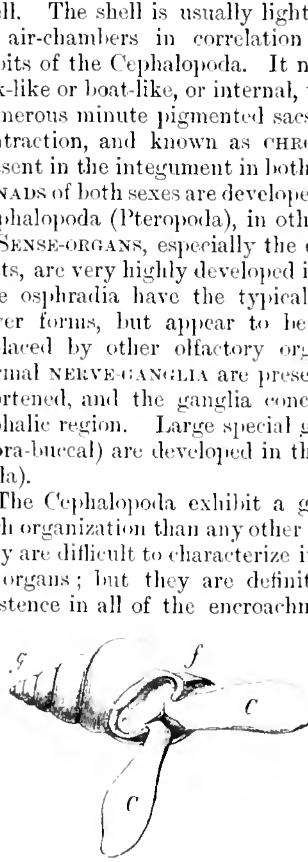


Fig. 76.

Fig. 77.

FIG. 76.—*Spirialis bulimoides*, Soul., one of the Limacinidæ enlarged (from Owen). *C C*, pteropodial lobes of the mid-foot; *f*, operculum carried on the hind-foot; *q*, spiral shell.
FIG. 77.—Operculum of Spirialis enlarged.

Two very distinct branches of the Cephalopoda are to be recognized: the one, the Pteropoda, more archaic in the condition of its bilobed mid-foot, including a number of minute, and in all probability degenerate, oceanic forms of simplified and obscure organization; the other, the Siphonopoda, containing the Pearly Nautilus and the Cuttles, which have for ages (as their fossil remains show) dominated among the inhabitants of the sea, being more highly gifted in special sense, more varied in movement, more powerful in proportion to size, and more heavily equipped with destructive weapons of offence than any other marine organisms.

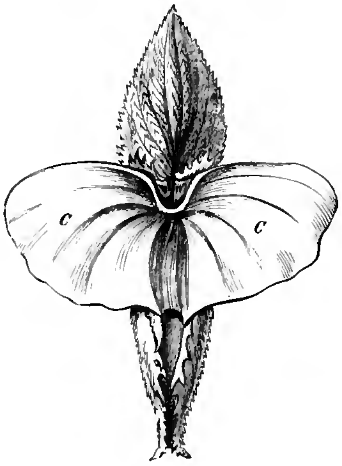


FIG. 77*a*.—*Cymbulia Peronii*, Cuvier (from Owen). *C*, *C*, the expanded pteropodial lobes or wing-like fins of the mid-foot.

Branch *a*.—*PTEROPODA.*

Characters.—Cephalopoda in which the mid-region of the foot is (as compared with the Siphonopoda) in its more primitive condition, being relatively largely developed and drawn out into a pair of wing-like muscular lobes (identical with the two halves of the siphon of the Siphonopoda) which are used as paddles (see figs. 76-86). The hind-region of the foot is often aborted, but may carry an operculum (figs. 76, 77). The fore-region of the foot (that embracing the head) is also often rudimentary, but may be drawn out into one or more pairs of tentacles, simulating cephalic tentacles, and provided with suckers (figs. 84, 85).

Though the visceral hump is not twisted except in the Limacinidæ (fig. 76), there is a very general tendency to one-sided development of the viscera, and of their external apertures (as contrasted with Siphonopoda). The ctenidia are aborted, with the possible exception of the processes (fig. 85, *c*) at the end of the body of Pneumodermon. The vascular system resembles that of the Gastropoda. The nephridium is a single tubular body corresponding to the right nephridium of the typical pair of the archi-Mollusc. The anal aperture is usually placed a little to the left of the median line, more rarely to the right. In the Limacinidæ it has an exceptional position, owing to the torsion of the visceral mass, as in Anisopleurous Gastropoda.

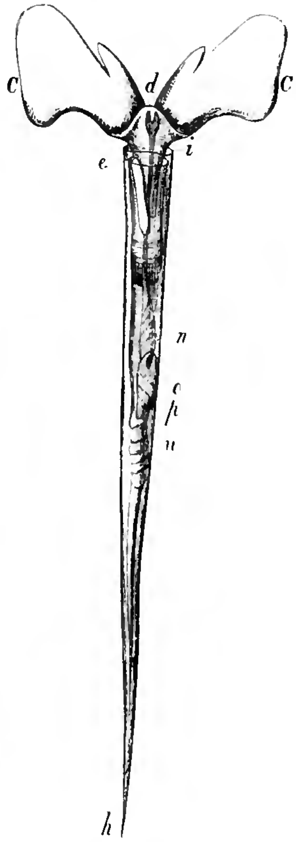


FIG. 78.—*Styliola acicula*, Rang. sp. enlarged (from Owen). *C*, *C*, the wing-like lobes of the mid-foot; *d*, median fold of same; *e*, copulatory organ; *h*, pointed extremity of the shell; *i*, anterior margin of the shell; *n*, stomach; *o*, liver; *u*, hermaphrodite gonad.

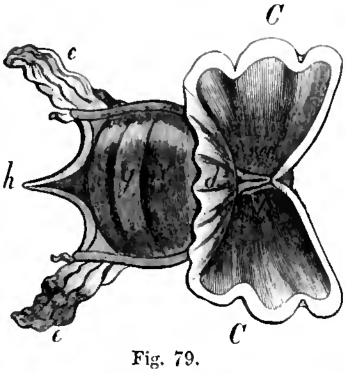


Fig. 79.

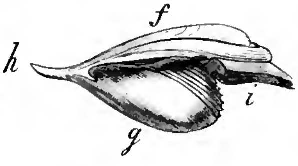


Fig. 80.

Fig. 79.—*Cavolinia tridentata*, Forsk. from the Mediterranean, magnified two diameters (from Owen). *a*, mouth; *b*, pair of cephalic tentacles; *C*, *C*, pteropodial lobes of the mid-foot; *d*, median web connecting these; *e*, *e*, processes of the mantle-skirt reflected over the surface of the shell; *g*, the shell enclosing the visceral hump; *h*, the median spine of the shell.

Fig. 80.—Shell of *Cavolinia tridentata*, seen from the side. *f*, postero-dorsal surface; *g*, antero-ventral surface; *h*, median dorsal spine; *i*, mouth of the shell.

Jaws and a lingual ribbon are present as in typical Glossophora, the dentition of the ribbon and the number of jaw-pieces presenting a certain range of variation. Sense-organs are present in the form of cephalic eyes in very few forms (Cavolinia, Clione, and in an undescribed form discovered by Suhm during the "Challenger" Expedition); otocysts are universally present. The osphradia are present in typical form, although the ctenidia are aborted; only one osphradium (the right of the typical pair) is present (fig. 87). The gonads are both male and female in the same individual. The genital aperture is single. Copulatory organs, often of considerable size, are present (fig. 86, *z*).

The mantle-skirt is present in one division of the Pteropoda (Thecosomata), and in these an extensive sub-pallial chamber is developed, the walls of which in the absence of ctenidia have a branchial function. In a second division (Gymnosomata), which comprises forms highly developed in regard to the processes of the fore-foot, the mantle-skirt is aborted. A shell is developed on the surface of the visceral hump and mantle-skirt of the Thecosomata, whilst in the Gymnosomata, which have no mantle-skirt, there is in the adult animal no shell. The embryo passes through a trochosphere and a veliger stage (fig. 81), provided with boat-like shell, except in some Gymnosomata in which the Trochosphere with its single velar ciliated band becomes metamorphosed into a larva which has three additional ciliated bands but no velum (resembling the larva of the Scaphopod Dentalium); this banded larva does *not* form a larval shell (fig. 84).

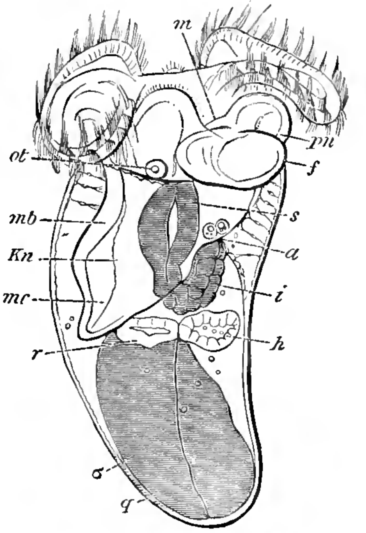


Fig. 81.—Embryo of *Cavolinia tridentata* (from Balfour, after Fol.). *a*, anus; *f*, median portion of the foot; *pn*, pteropodial lobe of the foot; *h*, heart; *i*, intestine; *ot*, otocyst; *q*, shell; *r*, nephridium; *s*, œsophagus; σ, sac containing nutritive yelk; *mb*, mantle-skirt; *mc*, sub-pallial chamber; *Kn*, contractile sinus.

The Pteropoda are divided into two orders.

Order 1.—**Thecosomata.**

Characters.—Pteropoda provided with a mantle-skirt, and with a delicate hyaline shell developed on the surface of the visceral hump and mantle-skirt; visceral hump, and consequently the shell, spirally twisted in one family, the Limacinidæ; shell often with contracted mouth and dilated body, its walls sometimes drawn out into spine-like processes, which are covered by reflexions of the free margin of the mantle (Cavolinia, figs. 79, 80).

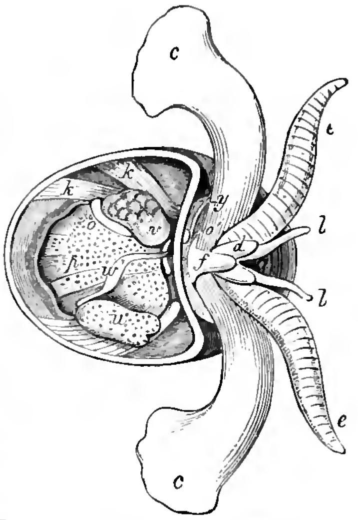


Fig. 82.—*Theceurybia Gaudichaudii*, Soul., (from Owen). Much enlarged; the body-wall removed. *a*, the mouth; *c*, the pteropodial lobes of the foot; *f*, the centrally-placed hind-foot; *d*, *l*, *e*, three pairs of tentacle-like processes placed at the sides of the mouth, and developed (in all probability) from the fore-foot; *o'*, anus; *y*, genital pore; *k*, retractor muscles; *o* and *p*, the liver; *u*, *v*, *w*, genitalia.

Family 1.—*Cymbuliidæ.*
  Genera: *Tiedemannia*, Chj.; *Halopsyche*, *Theceurybia* (figs. 82, 83), *Cymbulia*, P. and L. (fig. 77*a*).
Family 2.—*Conulariidæ* (fossil).
  Genus: *Conularia*, Mill.
Family 3.—*Tentaculitidæ* (fossil).
  Genera: *Tentaculites*, Schlth.; *Cornulites*, Schlth.; *Colcoprion*, Sandb.
Family 4.—*Hyaleidæ.*
  Genera: *Triptera*, Q. and G.; *Styliola*, Les. (fig. 78); *Balantium*, Lch.; *Vaginella*, Dand.; *Cleodora*, P. and L.; *Diacria*, Gr.; *Pleuropus*, Esch.; *Cavolinia*, Gioni. (figs. 79, 80, 81).
Family 5.—*Thecidæ.*
  Genera: *Theca*, Low; *Pterotheca*, Salt.
Family 6.—*Limacinidæ.*
  Genera: *Eccyliomphalus*, Porti.; *Heterofusus*, Flg.; *Spirialis*, E. S. (fig. 76); *Limacina*, Cuv.

Order 2.—**Gymnosomata.**

Characters.—Pteropoda devoid of mantle-skirt and shell; tentacular processes of the fore-foot well developed and provided with suckers.

Family 1.—*Pterocymodoceidæ.*
  Genus: *Pterocymodoce*, Kef.
Family 2.—*Clionidæ.*
  Genera: *Cliodita*, Q. and G.; *Clionopsis*, Trosch.; *Clione*, Pall. (fig. 86).
Family 3.—*Pneumodermidæ.*
  Genera: *Trichocyclus*, Esch.; *Spongobranchia*, d'Orb.; *Pneumodermopsis*, Kef.; *Pneumodermon*, Cuv. (fig. 85).

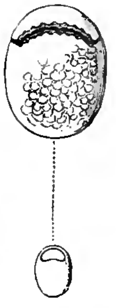


Fig. 83.—Shell of *Theceurybia norfolkensis*; the lower figure shows the natural size.

Branch *b*.—*SIPHONOPODA.*

Cephalopoda in which the two primarily divergent right and left lobes of the mid-region of the foot have their free borders recurved towards the middle line, where they are either held in apposition (Tetrabranchiata), or fused with one another to form a complete cylinder open at each end (Dibranchiata). This fissured or completely closed tube is the siphon (fig. 75, (6), *mf*) characteristic of the Siphonopoda, and is used to guide the stream of water expelled by the contractions of the walls of the branchial chamber. The pallial skirt is accordingly well developed and muscular, subserving by its contractions not only respiration but locomotion. The visceral hump is never twisted, and accordingly the main development of the pallial skirt and chamber is posterior, the excretory apertures, anus, and gills having a posterior position, as in the archi-Mollusc. At the same time the visceral hump is usually much elongated in a direction corresponding to an oblique line between the vertical dorso-ventral and the horizontal antero-posterior axes (see fig. 75, (6)).

The fore-part of the foot which surrounds the mouth, as in all Cephalopoda, is drawn out into four or five pairs of lobes, sometimes short, but usually elongated and even filiform. These lobes either carry peculiar sheathed tentacles (Nautilus), or, on the other hand, acetabuliform suckers, which may be associated with claw-like hooks (Dibranchiata). The hind-foot is probably represented by the valve which depends from the inner wall of the siphon in many cases.

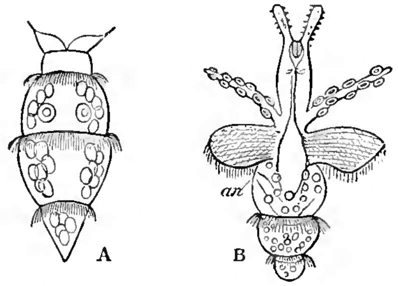


Fig. 84.

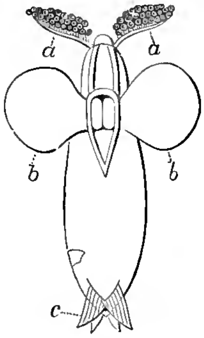


Fig. 85.

FIG. 84.—Larvæ of Pneumodermon (from Balfour, after Gegenbaur). The præ-oral ciliated band of the trochosphere stage (velum) has atrophied. In A three post-oral circlets of cilia are present. The otocysts are seen, and the rudiments of a pair of processes growing from the head. In B the foremost ciliated ring has disappeared; the cephalic region is greatly developed, and, as compared with the adult (fig. 85), is large and free; the pair of hook-bearing processes on each side of the mouth are retractile, probably part of the fore-foot. At the base of the cephalic snout are seen the pair of arm-like processes (fore-foot) provided with suckers, and behind these the broad pteropodial lobes or wing-like fins of the mid-foot.

FIG. 85.—*Pneumodermon violaceum*, d'Orb.; magnified five diameters. *a*, the sucker-bearing arms; *b*, the fins of the mid-foot (in the middle line, between these, is seen the sucker-like median portion of the foot, by means of which the animal can crawl as a Gastropod); *c*, the four branchial processes. (After Keferstein.)

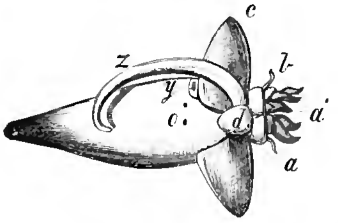


FIG. 86.—*Clione borealis*, L.; magnified two diameters,—postero-ventral aspect. *a*, the cephalic region carrying *a'*—three pairs of cephalic cones provided each with very numerous minute sucker-like processes, and surrounded by a hood-like upgrowth,—and *b*, the more elongated tentacles (the retractile eye-tentacles are not seen, being placed dorsally); *c*, the pteropodial fins; *d*, the median portion of the foot; *o*, the anus; *y*, the vagina; *z*, the penis. (From Owen, after Eschricht.)

A shell (figs. 89, 100) is very generally present, affording protection to the visceral mass and attachment for muscles. It may be external or enclosed in dorsal upgrowing folds of the mantle, which (except in Spirula) close up at an early period of development, so as to form a shut sac in which the shell is secreted. The ctenidia are well developed as paired gill-plumes, serving as the efficient branchial organs (figs. 101, 103, and fig. 2, B).

The vascular system is very highly developed; the heart consists of a pair of auricles and a ventricle (figs. 104, 105). Branchial hearts are formed on the advehent vessels of the branchiæ. It is not known to what extent the minute subdivision of the arteries extends, or whether there is a true capillary system.

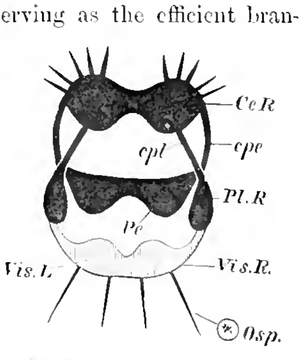


FIG. 87.—Enlarged diagram of the nerve-centres of Pneumodermon (from Spengel, after Souleyet). *CeR*, right cerebral ganglion; *Pl.R*, right pleural ganglion; *Pe*, right pedal ganglion; *Vis.R.*, right visceral ganglion; *Vis.L.*, left visceral ganglion; *cpe*, right cerebro-pedal connective; *cpl*, right cerebro-pleural connective; *Osp.*, osphradium connected by a nerve with the right visceral ganglion.

The pericardium is extended so as to form a very large sac passing among the viscera dorsalwards and sometimes containing the ovary or testis—the viscero-pericardial sac—which opens to the exterior either directly or through the nephridia. It has no connexion with the vascular system. The nephridia are always paired sacs, the walls of which invest the branchial advehent vessels (figs. 104, 108). They open each by a pore into the viscero-pericardial sac except in Nautilus. The anal aperture is median and raised on a papilla. Jaws (fig. 88, *e*) and a lingual ribbon (fig. 107) are well developed. The jaws have the form of a pair of powerful beaks, either horny or calcified (Nautilus), and are capable of inflicting severe wounds.

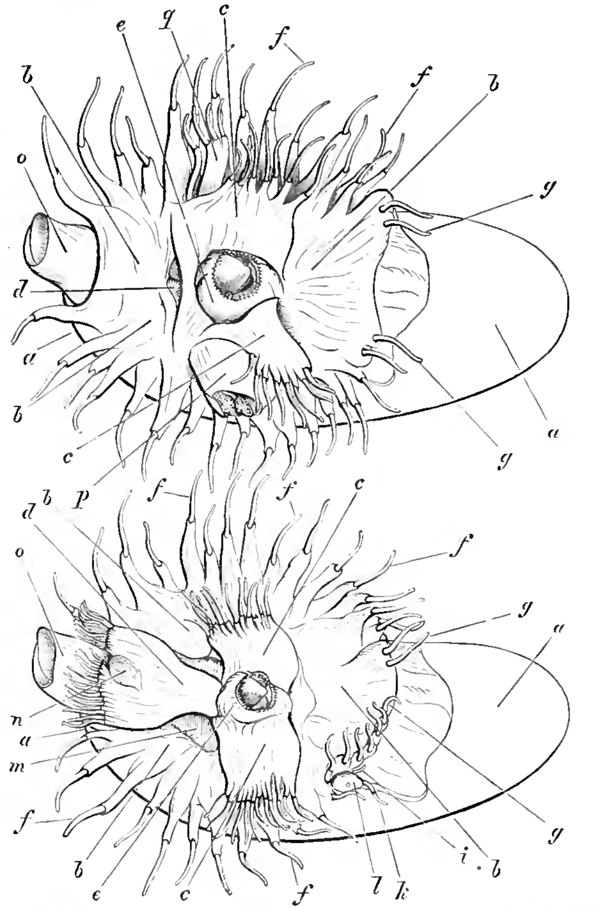


FIG. 88.—Male (upper) and female (lower) specimens of *Nautilus pompilius* as seen in the expanded condition, the observer looking down on to the buccal cone *e*; one-third the natural size linear. The drawings have been made from actual specimens by A. G. Bourne, B.Sc., and serve to show the natural disposition of the tentaculiferous lobes and tentacles of the circum-oral portion of the foot in the living state, as well as the great differences between the two sexes. *a*, the shell; *b*, the *outer* ring-like expansion (annular lobe) of the circum-oral muscular mass of the fore-foot, carrying nineteen tentacles on each side—posteriorly this is enlarged to form the "hood" (marked *v* in fig. 89 and *m*, in figs. 90 and 91), giving off the pair of tentacles marked *g* in the present figure; *c*, the right and left inner lobes of the fore-foot, each carrying twelve tentacles in the female, in the male subdivided into *p*, the "spadix" or hectocotylus on the left side, and *q*, the "anti-spadix," a group of four tentacles on the right side,—it is thus seen that the subdivided right and left inner lobes of the male correspond to the undivided right and left inner lobes of the female; *d*, the inner inferior lobe of the fore-foot, a bilateral structure in the female carrying two groups, each of fourteen tentacles, separated from one another by a lamellated organ *n*, supposed to be olfactory in function—in the male the inner inferior lobe of the fore-foot is very much reduced, and has the form of a paired group of lamellæ (*d* in the upper figure); *e*, the buccal cone, rising from the centre of the three inner lobes, and fringing the protruded calcareous beaks or jaws with a series of minute papillæ; *f*, the tentacles of the outer circum-oral lobe or annular lobe of the fore-foot projecting from their sheaths; *g*, the two most posterior tentacles of this series belonging to that part of the annular lobe which forms the hood (*m*. in figs. 90 and 91); *i*, superior ophthalmic tentacle; *k*, inferior ophthalmic tentacle; *l*, eye; *m*, paired laminated organ on each side of the base of the inner inferior lobe (*d*) of the female, probably olfactory in function; *n*, olfactory lamellæ upon the inner inferior lobe (in the female); *o*, the siphon (mid-foot); *p*, the spadix (in the male), the hectocotylized portion of the left inner lobe of the fore-foot representing four modified tentacles, eight being left unmodified; *q*, the anti-spadix (in the male), being four of the twelve tentacles of the right inner lobe of the fore-foot isolated from the remaining eight, and representing on the right side the differentiated spadix of the left side. The four tentacles of the anti-spadix are set, three on one base and one on a separate base.

There are thus in the female, where they are most numerous, ninety-four tentacles, thirty-eight on the outer annular lobe, four ophthalmic (a pair to each eye), twelve on each of the right and left inner lobes, and twenty-eight on the inner inferior lobe.

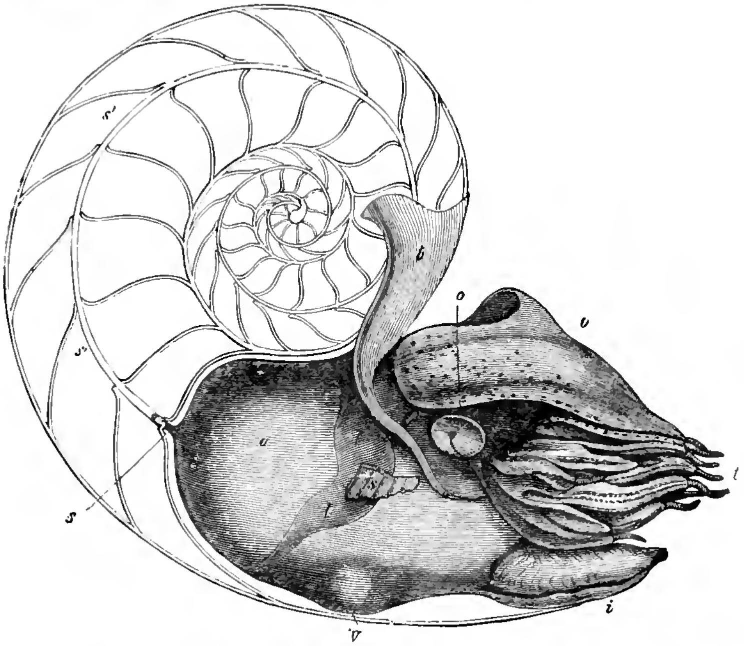


Fig. 89.—Lateral view of the female Pearly Nautilus, contracted by spirit and lying in its shell, the right half of which is cut away (from Gegenbaur, after Owen). *a*, visceral hump; *b*, portion of the free edge of the mantle-skirt reflected on to the shell,—the edge of the mantle-skirt can be traced downwards and forwards around the base of the mid-foot or siphon *i*; *l*, *l*, superficial origin of the retractor muscle of the mid-foot (siphon), more or less firmly attached to the shell, of which a small piece (*s*) is seen between the letters *l*, *l*; *s* (farther back) points to the siphuncular pedicle, which is broken off short and not continued, as in the perfect state, through the whole length of the siphuncle of the shell, also marked *s* and *s'*; *o* points to the right eye; *t* is placed near the extremities of the contracted tentacles of the outer or annular lobe of the fore-foot,—the jointed tentacles are seen protruding a little from their long cylindrical sheaths; *c*, the dorsal "hood" formed by an enlargement in this region of the annular lobe of the fore-foot (*m.* in figs. 90, 91); *V*, a swelling of the mantle-skirt, indicating the position on its inner face of the nidamental gland (see fig. 101, *g.n.*).

Sense-organs are highly developed; the eye exhibits a very special elaboration of structure in the Dibranchiata, and a remarkable archaic form in the Nautilus. Otocysts are present in all. The typical osphradium is not present, except in Nautilus, but other organs are present in the cephalic region, to which an olfactory function is ascribed both in Nautilus and in the other Siphonopoda.

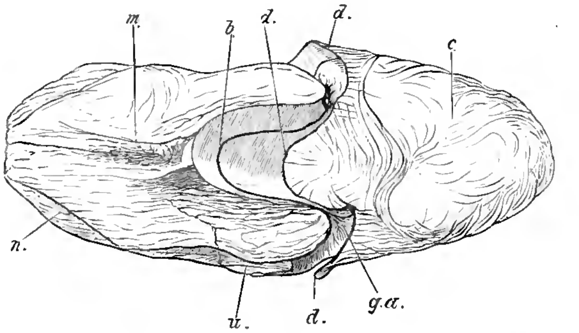


Fig. 90.—Spirit specimen of female Pearly Nautilus, removed from its shell, and seen from the antero-dorsal aspect (drawn from nature by A. G. Bourne). *m.*, the dorsal "hood" formed by the enlargement of the outer or annular lobe of the fore-foot, and corresponding to the sheaths of two tentacles (*g*, *g* in fig. 88); *n.*, tentacular sheaths of lateral portion of the annular lobe; *u.*, the left eye; *b.*, the nuchal plate, continuous at its right and left posterior angles with the root of the mid-foot, and corresponding to the nuchal cartilage of Sepia; *c.*, visceral hump; *d.*, the free margin of the mantle-skirt, the middle letter *d.* points to that portion of the mantle-skirt which is reflected over a part of the shell as seen in fig. 89, *b*; the cup-like fossa to which *b.* and *d.* point in the present figure is occupied by the coil of the shell; *g.a.* points to the lateral continuation of the nuchal plate *b.* to join the root of the mid-foot or siphon.

The gonads are always separated in male and female individuals. The genital aperture and duct is sometimes single, when it is the left; sometimes the typical pair is developed right and left of the anus. The males of nearly all Siphonopoda have been shown to be characterized by a peculiar modification of the arm-like processes or lobes of the fore-foot, connected with the copulative function. The term hectocotylization is applied to this modification (see figs. 88, 95, 96). Elaborate spermatophores or sperm-ropes are formed by all Siphonopoda, and very usually the female possesses special capsule-forming and nidamental glands for providing envelopes to the eggs (fig. 101, *g.n.*). The egg of all Siphonopoda is large, and the development is much modified by the presence of an excessive amount of food-material diffused in the protoplasm of the egg-cell. Trochosphere and veliger stages of development are consequently not recognizable.

The Siphonopoda are divisible into two orders, the names of which (due to Owen) describe the number of gill-plumes present; but in fact there are several characters of as great importance as those derived from the gills by which the members of these two orders are separated from one another.

Order 1.—**Tetrabranchiata** (= Schizosiphona, Tentaculifera).

Characters.—Siphonopodous Cephalopods in which the inrolled lateral margins of the mid-foot are not fused, but form a siphon by apposition (fig. 101). The circum-oral lobes of the fore-foot carry numerous sheathed tentacles (not suckers) (fig. 88). There are two pairs of ctenidial gills (hence Tetrabranchiata), and two pairs of nephridia, consequently four nephridial apertures (fig. 101). The viscero-pericardial chamber opens by two independent apertures to the exterior and not into the nephridial sacs. There are two oviducts (right and left) in the female and two sperm-ducts in the male, the left duct in both sexes being rudimentary.

A large external shell either coiled or straight is present, and is not enclosed by reflexions of the mantle-skirt, except such narrow-mouthed shells as that of Gomphoceras, which were probably enclosed by the mantle as in the Dibranch Spirula. The shell consists of a series of chambers, the last formed of which is occupied by the body of the animal, the hinder ones (successively deserted) containing gas (fig. 89).

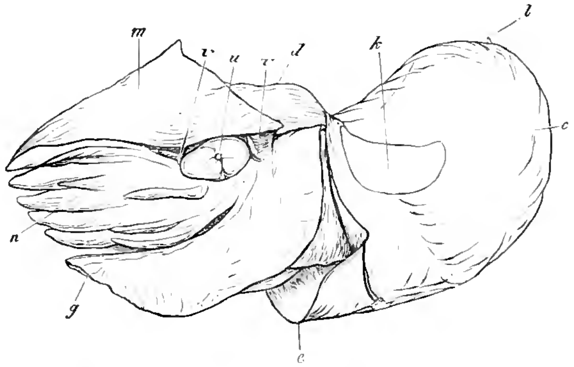


Fig. 91.—Lateral view of the same specimen as that drawn in fig. 90. Letters as in that figure with the following additions—*c* points to the concave margin of the mantle-skirt leading into the sub-pallial chamber; *g*, the mid-foot or siphon; *k*, the superficial origin of its retractor muscles closely applied to the shell and serving to hold the animal in its place; *l*, the siphuncular pedicle of the visceral hump broken off short; *v*, *v*, the superior and inferior ophthalmic tentacles.

The pair of cephalic eyes are hollow chambers (fig. 118, A) opening to the exterior by minute orifices (pinhole camera), and devoid of refractive structures. A pair of osphradia are present at the base of the gills (fig. 101, *olf*). Salivary glands are wanting. An ink-sac is *not* present. Branchial hearts are *not* developed on the branchial advehent vessels.

Family 1.—*Nautilidæ.*
  Genera: [*Orthoceras*], Breyn.; [*Cyrtoceras*], Goldfuss; [*Gomphoceras*], Münster; [*Phragmoceras*], Brod.; [*Gyroceras*], Meyer; [*Ascoceras*], Barrande; [*Oncoceras*], Hall; [*Lituites*], Breyn.; [*Trochoceras*], Barrande; *Nautilus*, L. (figs. 88, 89, 90, &c.); [*Clymenia*], Münst.; [*Nothoceras*], Barrande.
Family 2.—*Ammonitidæ.*
  Genera: [*Bactrites*], Sanderg.; [*Goniatites*], de Haan; [*Rhabdoceras*], Hauer; [*Clydonites*], Hauer; [*Cochloceras*], Hauer; [*Baculina*], d'Orb.; [*Ceratites*], de Haan; [*Baculites*], Lam.; [*Toxoceras*], d'Orb.; [*Crioceras*], Leveillé; [*Ptychoceras*], d'Orb.; [*Hamites*], Parkinson; [*Ancyloceras*], d'Orb.; [*Scaphites*], Parkinson; [*Ammonites*], Breyn.; [*Turrilites*], Lam.; [*Helioceras*], d'Orb.; [*Heteroceras*], d'Orb.
  N.B.—The names in brackets are those of extinct genera.

Order 2.—**Dibranchiata** (= Holosiphona, Acetabulifera).

Characters.—Siphonopodous Cephalopods in which the inflected lateral margins of the mid-foot are fused so as to form a complete tubular siphon (fig. 96, *i*). The circumoral lobes of the fore-foot carry suckers disposed upon them in rows (as in the Pteropod Pneumodermon), *not* tentacles (see figs. 92, 95, 96). There is a single pair of typical ctenidia (fig. 103) acting as gills (hence Dibranchiata), and a single pair of nephridia opening by apertures right and left of the median anus (fig. 103, *r*), and by similar internal pores into the pericardial chamber, which consequently does not open directly to the surface as in Nautilus. The oviducts are sometimes paired right and left (Octopoda), sometimes that of one side only is developed (Decapoda, except Ommastrephes). The sperm-duct is always single except, according to Keferstein, in *Eledone moschata*.

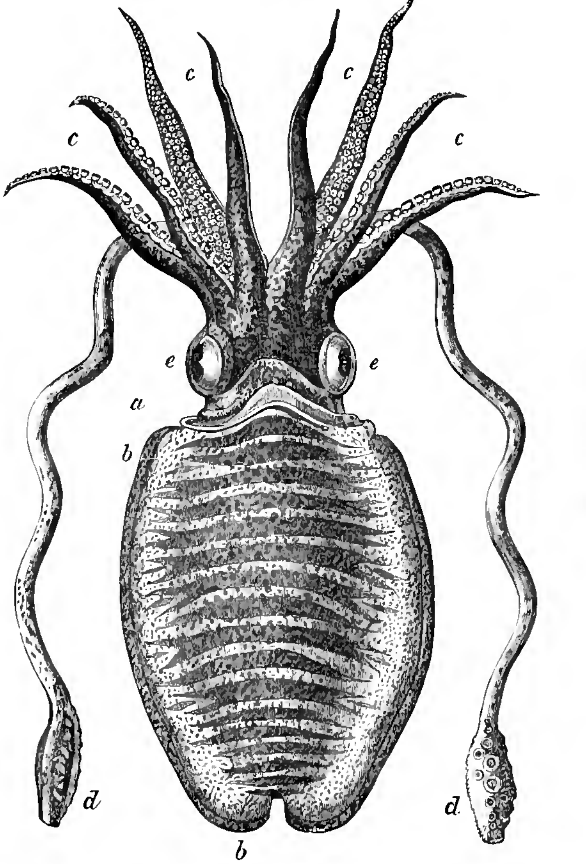


Fig. 92.—*Sepia officinalis*, L., half the natural size, as seen when dead, the long prehensile arms being withdrawn from the pouches at the side of the head, in which they are carried during life when not actually in use. *a*, neck; *b*, lateral fin of the mantle-sac; *c*, the eight shorter arms of the fore-foot; *d*, the two long prehensile arms; *e*, the eyes.

A plate-like shell is developed in a closed sac formed by the mantle (figs. 98, 99), except in the Octopoda, which have none, and in Spirula (fig. 100, D) and the extinct Belemnitidæ, which have a small chambered shell resembling that of Nautilus with or without the addition of plate-like and cylindrical accessory developments (fig. 100, C).

The pair of cephalic eyes are highly-developed vesicles with a refractive lens (fig. 120), cornea, and lid-folds,—the vesicle being in the embryo an open sac like that of Nautilus (fig. 119). Osphradia are not present, but cephalic olfactory organs are recognized. One or two pairs of large salivary glands with long ducts are present. An ink-sac formed as a diverticulum of the rectum and opening near the anus is present in all Dibranchiata (fig. 103, *t*), and has been detected even in the fossil Belemnitidæ. Branchial hearts are developed on the two branchial advehent blood-vessels (fig. 104, *vc'*, *vi*).

The Dibranchiata are divisible into two sub-orders, according to the number and character of the arm-like sucker-bearing processes of the fore-foot.

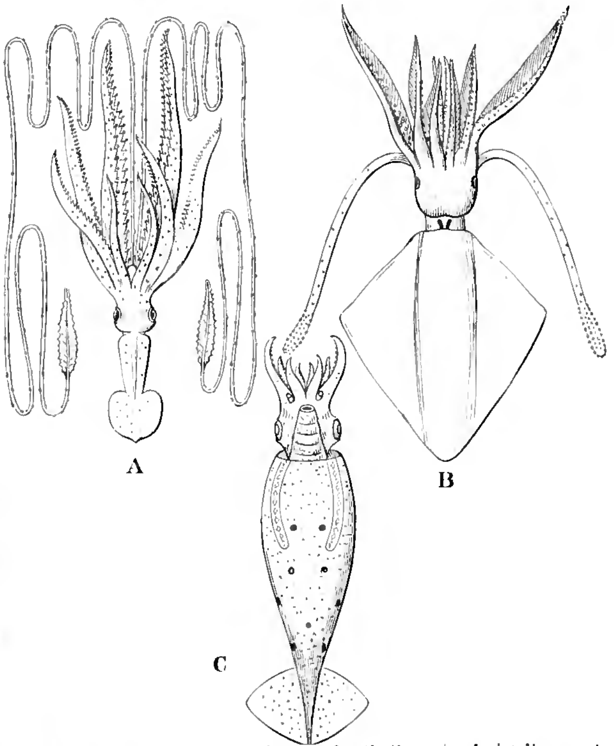


Fig. 93.—Decapodous Siphonopods; one-fourth the natural size linear. A. *Cheiroteuthis Verangi*, d'Orb. (from the Mediterranean) B. *Thysanoteuthis rhombus*, Troschel (from Messina). C. *Loligopsis cyclura*, Fer. and d'Orb. (from the Atlantic Ocean).

Sub-order 1.—*Decapoda.*

Characters.—Dibranchiata with the fore-foot drawn out into eight shorter and two longer arms (prehensile arms), the latter being placed right and left between the third and fourth shorter arms. The suckers are stalked and strengthened by a horny ring. The eyes are large and have a horizontal in place of a sphincter-like lid. The body is elongated and provided with lateral fins (lamelliform expansions of the mantle). The mouth has a buccal membrane. The mantle-margin is locked to the base of the siphon by a specially-developed cartilaginous apparatus. Numerous water-pores are present in the head and anterior region of the body, leading into recesses of the integument of unknown significance. The oviduct is single; large nidamental glands are present. The viscero-pericardial space is large, and lodges the ovary (Sepia). There is always a shell present which is enclosed by the upgrowth of the mantle, so as to become "internal."

Section *a.*—*Decapoda Calciphora.*

Character.—Internal shell calcareous.

Family 1.—*Spirulidæ.*
  Genus: *Spirula*, Lam. (fig. 100, D).
Family 2.—*Belemnitidæ.*
  Genera: [*Spirulirostra*], d'Orb. (fig. 100, C); [*Beloptera*], Desh.; [*Belemnosis*], Edw.; [*Conoteuthis*], d'Orb. (fig. 100, A); [*Acanthoteuthis*], R. Wag.; [*Belemnites*], Lister, 1678; [*Belemnitella*], d'Orb.; [*Xiphoteuthis*], Huxley.
Family 3.—*Sepiadæ.*
  Genera: *Sepia*, L. (figs. 92, 98, &c.); [*Belosepia*], Voltz; *Coccoteuthis*, Owen.

Section *b*.—*Decapoda Chondrophora*.

Character.—Internal shell horny.

Sub-section *α*.—*Myopsidæ* (d'Orb.).

Eye with closed cornea, so that the surrounding water does not touch the lens; mostly frequenters of the coast.

Family 1.—*Loligidæ*.
  Genera: *Loligo*, Schneid. (figs. 99, &c.); *Loliolus*, Steenstrup; *Sepioteuthis*, Blv.; [*Teuthopsis*], Desl.; [*Leptoteuthis*], Meyer; [*Belemnosepia*], Ag.; [*Beloteuthis*], Münst.
Family 2.—*Sepiolidæ*.
  Genera: *Sepiola*, Schneid.; *Rossia*, Owen.

Sub-section *β*.—*Oigopsidæ* (d'Orb.).

Eye with open cornea, so that the surrounding water bathes the anterior surface of the lens; mostly pelagic animals.

Family 3.—*Cranchiadæ*.
  Genus: *Cranchia*, Leach (fig. 94, C).
Family 4.—*Loligopsidæ*.
  Genus: *Loligopsis*, Lam. (fig. 93, C).
Family 5.—*Cheiroteuthidæ*.
  Genera: *Cheiroteuthis*, d'Orb. (fig. 93, A); *Histioteuthis*, d'Orb.
Family 6.—*Thysanoteuthidæ*.
  Genus: *Thysanoteuthis*, Troschel (fig. 93, B).
Family 7.—*Onychoteuthidæ*.
  Genera: *Gonatus*, Gray; *Onychoteuthis*, Lichtenst. (fig. 97); *Onychia*, Lesueur; *Enoploteuthis*, d'Orb., *Veranya*, Krohn; [*Plesioteuthis*], A. Wag.; [*Celæno*], Münst.; *Dosidicus*, Steenstrup; *Ommastrephes*, d'Orb.

Sub-order 2.—*Octopoda*.

Characters.—Dibranchiata with the fore-foot drawn out into eight arms only; suckers sessile, devoid of horny ring; eyes small, the outer skin can be closed over them by a sphincter-like movement. The body is short and rounded; the mantle has no cartilaginous locking apparatus, and is always fused to the head dorsally by a broad nuchal band. No buccal membrane surrounds the mouth. The siphon is devoid of valves. The oviducts are paired; there are no nidamental glands. The viscero-pericardial space is reduced to two narrow canals, passing from the nephridia to the capsule of the genital gland. There is no shell on or in the visceral hump.

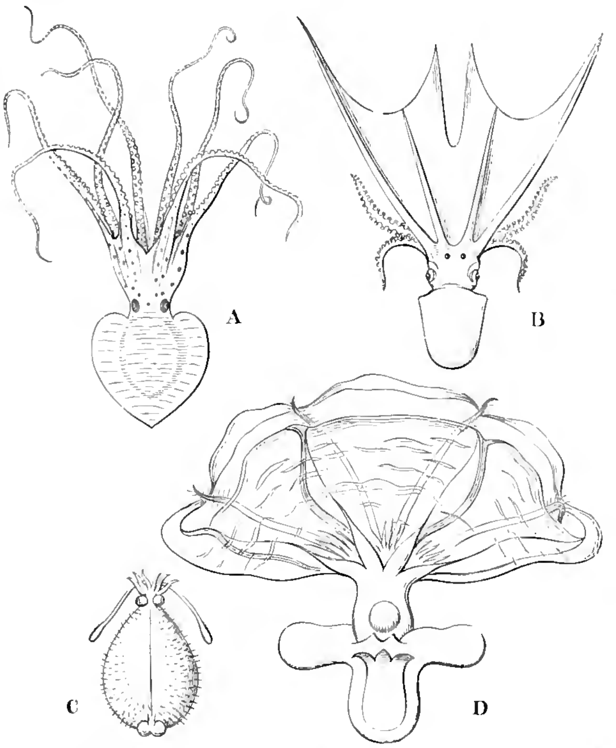


Fig. 94.—Octopodous Siphonopods; one-fourth the natural size linear. A. *Pinnoctopus cordiformis*, Quoy and Gain (from New Zealand). B. *Tremoctopus violaceus*, Ver. (from the Mediterranean). C, *Cranchia scabra*, Owen (from the Atlantic Ocean; one of the Decapoda). D. *Cirrhoteuthis Mulleri*, Esch. (from the Greenland coast).

Family 1.—*Cirrhoteuthidæ*.
  Genus: *Cirrhoteuthis*, Esch. (*Sciadephorus*, Reinh.) (fig. 94, D).
Family 2.—*Octopodidæ*.
  Genera: *Pinnoctopus*, d'Orb. (fig. 94, A); *Octopus*, Lam. (fig. 95); *Scæurgus*, Trosch.; *Eledone*, Leach; *Bolitæna*, Steenstrup.
Family 3.—*Philonexidæ*.
  Genera: *Tremoctopus*, Delle Chiaje (*Philonexis*, d'Orb.) (fig. 94, B); *Parasira*, Steenstrup (*Octopus catenulatus*, Fér., is the female, and *Octopus carena*, Ver., is the male of the one species of this genus according to Steenstrup (fig. 96)); *Argonauta*, L. (the shell of this genus is formed only in the female by the expanded ends of the two large "arms" of the fore-foot).

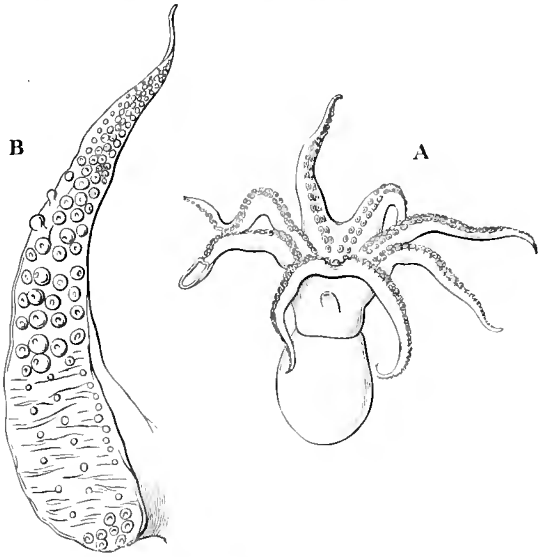


Fig. 95.—A. Male specimen of *Octopus grœnlandicus*, with the third arm of the right side hectocotylized. B. Enlarged view of the hectocotylized arm of Sepia.

Further Remarks on the Cephalopoda.—In order to give a more precise conception of the organization of the Cephalopoda in a concrete form we select the Pearly Nautilus for further description, and in passing its structure in review we shall take the opportunity of comparing here and there the peculiarities presented by that animal with those obtaining in allied forms. In the last edition of this work the Pearly Nautilus was made the subject of a detailed exposition by Professor Owen, and it has seemed accordingly appropriate that it should be somewhat fully treated on the present occasion also. The figures which illustrate the present description are (excepting fig. 89) original, and prepared from dissections (made under the direction of the writer) of a male and female *Nautilus pompilius*, lately purchased for the Museum of University College, London.

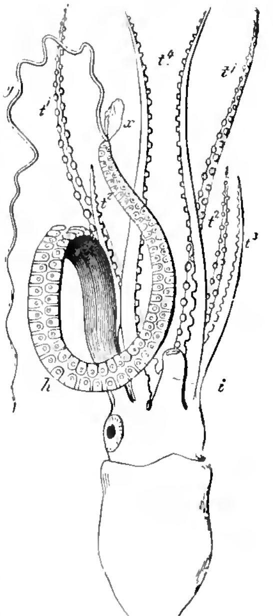


Fig. 96.—Male of *Parasira catenulata*, Steenstrup (*Octopus carena*, Ver.), showing the hectocotylized arm. *t*1, *t*2, *t*3, *t*4, the first, second, third, and fourth arms or processes of the fore-foot; *h*, the third arm of the right side hectocotylized; *x*, the apical sac of the hectocotylized arm; *y*, the filament which issues from the sac when development is complete; *i*, the siphon. (From Gegenbaur.)

Visceral Hump and Shell.—The visceral hump of Nautilus (if we exclude from consideration the fine siphuncular pedicle which it trails, as it were, behind it) is very little, if at all, affected by the coiled form of the shell which it carries, since the animal always slips forward in the shell as it grows, and inhabits a chamber which is practically cylindrical (fig. 89). Were the deserted chambers thrown off instead of being accumulated behind the inhabited chamber as a coiled series of air-chambers, we should have a more correct indication in the shell of the extent and form of the animal's body. Amongst Gastropods it is not very unusual to find the animal slipping forward in its shell as growth advances and leaving an unoccupied chamber in the apex of the shell. This may indeed become shut off from the occupied cavity by a transverse septum, and a series of such septa may be formed (fig. 42), but in no Gastropod are these apical chambers known to contain a gas during the life of the animal in whose shell they occur. A further peculiarity of the Nautilus shell and of that of the allied extinct Ammonites, Scaphites, Orthoceras, &c., and of the living Spirula, is that the series of deserted air-chambers are traversed by a cord-like pedicle extending from the centro-dorsal area of the visceral hump to the smallest and first-formed chamber of the series. No structure comparable to this siphuncular pedicle is known in any other Mollusca. Its closest representative is found in the so-called "contractile cord" of the remarkable form Rhabdopleura, referred according to present knowledge to the Polyzoa. There appears to be no doubt that the deserted chambers of the Nautilus shell contain in the healthy living animal a gas which serves to lessen the specific gravity of the whole organism. The gas is said to be of the same composition as the atmosphere, with a larger proportion of nitrogen. With regard to its origin we have only conjectures. Each septum shutting off an air-containing chamber is formed during a period of quiescence, probably after the reproductive act, when the visceral mass of the Nautilus may be slightly shrunk, and gas is secreted from the dorsal integument so as to fill up the space previously occupied by the animal. A certain stage is reached in the growth of the animal when no new chambers are formed. The whole process of the loosening of the animal in its chamber and of its slipping forward when a new septum is formed, as well as the mode in which the air-chambers may be used as a hydrostatic apparatus, and the relation to this use, if any, of the siphuncular pedicle, is involved in obscurity, and is the subject of much ingenious speculation. In connexion with the secretion of gas by the animal, besides the parallel cases ranging from the Protozoon Arcella to the Physoclistic Fishes, from the Hydroid Siphonophora to the insect-larva Corethra, we have the identical phenomenon observed in the closely-allied Sepia when recently hatched. Here, in the pores of the internal rudimentary shell, gas is observable, which has necessarily been liberated by the tissues which secrete the shell, and not derived from any external source (Huxley).

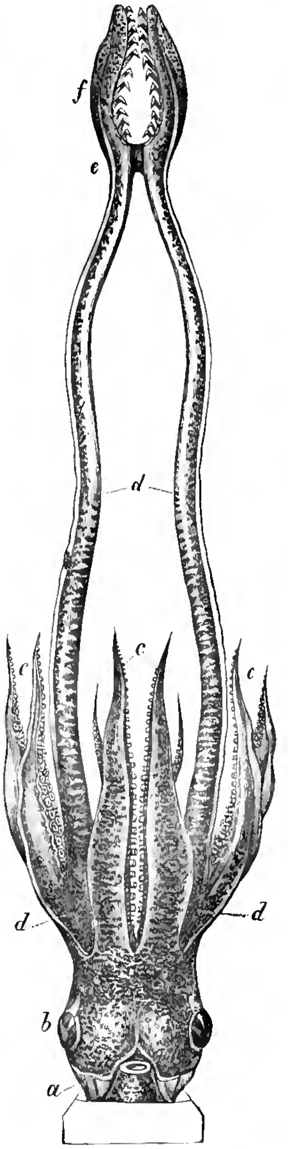


Fig. 97.—Head and circum-oral processes of the fore-foot of Onychoteuthis (from Owen). *a*, neck; *b*, eye; *c*, the eight short arms; *d*, long prehensile arms, the clavate extremities of which are provided with suckers at *e*, and with a double row of hooks beyond at *f*. The temporary conjunction of the arms by means of the suckers enables them to act in combination.

The coiled shell of Nautilus, and by analogy that of the Ammonites, is peculiar in its relation to the body of the animal, inasmuch as the curvature of the coil proceeding from the centro-dorsal area is towards the head or forward, instead of away from the head and backwards as in other discoid coiled shells such as Planorbis; the coil is in fact absolutely reversed in the two cases. Amongst the extinct allies of the Nautilus (Tetrabranchiata) we find shells of a variety of shapes, open coils such as Scaphites, leading on to perfectly cylindrical shells with chamber succeeding chamber in a straight line (Orthoceras), whence again we may pass to the cork-screw spires formed by the shell of Turrilites.

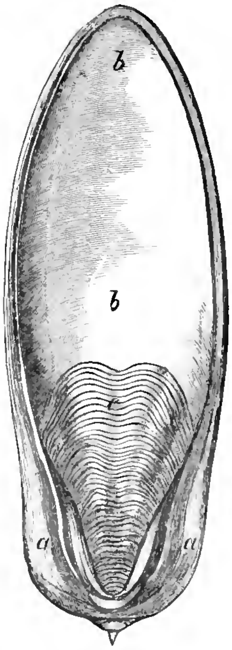


Fig. 98.

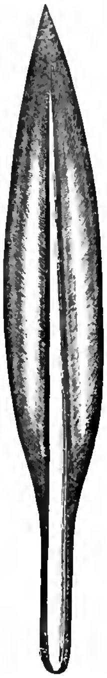


Fig. 99.

Fig. 98.—The calcareous internal shell of *Sepia officinalis*, the so-called cuttle-bone. *a*, lateral expansion; *b*, anterior cancellated region; *c*, laminated region, the laminæ enclosing air.

Fig. 99.—The horny internal shell or gladius or pen of Loligo.

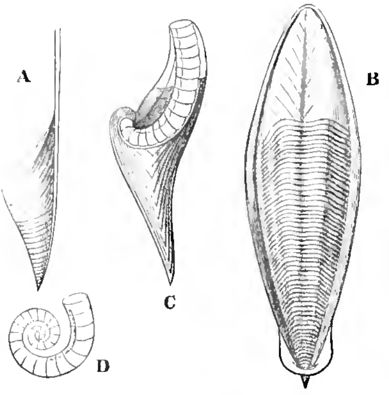


Fig. 100.—Internal shells of Cephalopoda Siphonopoda. A. Shell of *Conoteuthis dupiniana*, d'Orb. (from the Neocomian of France). B. Shell of *Sepia orbigniana*,' Fer. (Mediterranean). C. Shell of *Spirulirostra Bellardii*, d'Orb. (from the Miocene of Turin). The specimen is cut so as to show in section the chambered shell and the laminated "guard" deposited upon its surface. D. Shell of *Spirula lævis*, Gray (New Zealand).

Whilst the Tetrabranchiata, so far as we can recognize their remains, are characterized by these large chambered shells, which, as in Nautilus, were with the exception of some narrow-mouthed forms such as Gomphoceras but very partially covered by reflexions of the mantle-skirt (fig. 89, *b*), the Dibranchiata present an interesting series of gradations, in which we trace—(*a*) the diminution in relative size of the chambered shell; (*b*) its complete investiture by reflected folds of the mantle (Spirula, fig. 100, D); (*c*) the concrescence of the folds of the mantle to form a definitely-closed shell-sac; (*d*) the secretion by these mantle-folds or walls of the shell-sac of additional laminæ of calcareous shell-substance, which invest the original shell and completely alter its appearance (Spirulirostra, fig. 100, C; Belemnites); (*e*) the gradual dwindling and total disappearance of the original chambered shell, and survival alone of the calcareous laminæ deposited by the inner walls of the sac (Sepia, fig. 100, B); (*f*) the disappearance of all calcareous substance from the pen or plate which now represents the contents of the shell-sac, and its persistence as a horny body simply (Loligo, fig. 99); (*g*) the total disappearance of the shell-sac itself, and consequently of its pen or plate, nevertheless the rudiments of the shell-sac appearing in the embryo and then evanescing (Octopus). The early appearance of the sac of the mantle in which the shell is enclosed, in Dibranchiata, has led to an erroneous identification of this sac with the primitive shell-sac of the archi-Mollusc (fig. 1), of Chiton (fig. 10, A), of Arion (fig. 69, D, *a*), and of the normally-developing Molluscan embryo (figs. 68 and 72***, *sh*). The first appearance of the shell-sac of Dibranchiata is seen in figs. 121 and 122, its formation as an open upgrowth of the centro-dorsal area of the embryo having been demonstrated by Lankester (**34**) in 1873, who subsequently showed (**35**) that the same shell-sac appears and disappears without closing up in Argonauta and Octopus, and pointed out the distinctness of this sac and the primitive shell-gland. The shell of the female Argonauta is not formed by the visceral hump, but by the enlarged arms of the foot, which are in life always closely applied to it.

The shell of such Pteropoda as have shells (the Thecosomata) is excessively light, and fits close to the animal, no air-chambers being formed. It is important to note that in this division of the Cephalopoda there is the same tendency, which is carried so far in the Dibranchiate Siphonopods, for the mantle-skirt to be reflected over and closely applied to the shell (*e.g.*, Cavolinia, figs. 79 and 80). But in Pteropoda there is no complete formation of a closed sac by the reflected mantle, no thickening of the enclosed shell, no dwindling of the original shell and substitution for it of a laminated plate. The variety of form of the glass-like shells of Pteropoda is a peculiarity of that group.

Head, Foot, Mantle-skirt, and Sub-pallial Chamber.—In the Pearly Nautilus the ovoid visceral hump is completely encircled by the free flap of integument known as mantle-skirt (fig. 91, *d*, *e*). In the antero-dorsal region this flap is enlarged so as to be reflected a little over the coil of the shell which rests on it. In the postero-ventral region the flap is deepest, forming an extensive sub-pallial chamber, at the entrance of which *e* is placed in fig. 91. A view of the interior of the sub-pallial chamber, as seen when the mantle-skirt is retroverted and the observer faces in the direction indicated by the reference line passing from *e* in fig. 91, is given in fig. 101. With this should be compared the similar view of the sub-pallial chamber of the Dibranchiate Sepia (fig. 103). It should be noted as a difference between Nautilus and the Dibranchiates that in the former the nidamental gland (in the female) lies on that surface of the pallial chamber formed by the dependent mantle-flap (figs. 101, *g.n.*; 89, *V*), whilst in the latter it lies on the surface formed by the body-wall; in fact in the former the base of the fold forming the mantle-skirt comprises in its area a part of what is unreflected visceral hump in the latter.

The apertures of the two pairs of nephridia, of the viscero-pericardial sac, of the genital ducts, and of the anus are shown in position on the body-wall of the pallial chamber of Nautilus in figs. 101, 102. There are nine apertures in all, one median (the anus), and four paired. Besides these apertures we notice *two* pairs of gill-plumes which are undoubtedly typical ctenidia, and a short papilla (the osphradium) between each anterior and posterior gill-plume (see figs. 101, 102, and explanation). As compared with this in a Dibranchiate, we find (fig. 103) only four apertures, viz., the median anus with adjacent orifice of the ink-sac, the single pair of nephridial apertures, and one asymmetrical genital aperture (on the left side), except in female Octopoda and a few others where the genital ducts and their apertures are paired. No viscero-pericardial pores are present on the surface of the pallial chamber, since in the Dibranchiata the viscero-pericardial

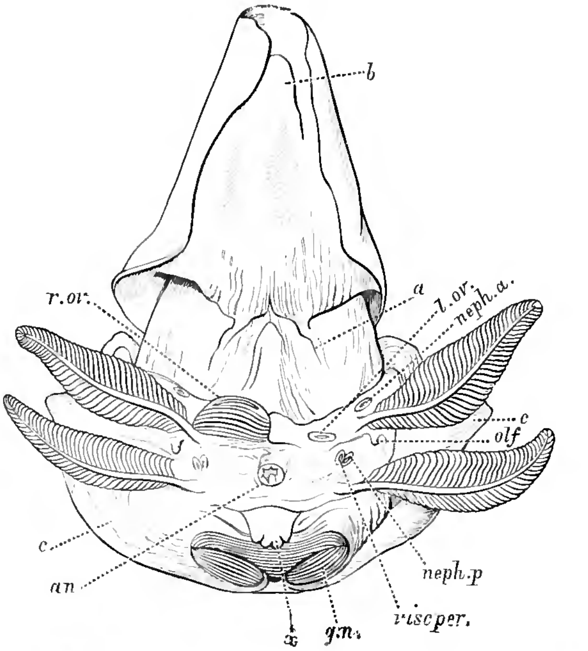


FIG. 101.—View of the postero-ventral surface of a female Pearly Nautilus, the mantle-skirt (*c*) being completely reflected so as to show the inner wall of the sub-pallial chamber (drawn from nature by A. G. Bourne). *a*, muscular band passing from the mid-foot to the integument; *b*, the valve on the surface of the funnel-like mid-foot, partially concealed by the inrolled lateral margin of the latter; *c*, the mantle-skirt retroverted; *an*, the median anus; *x*, post-anal papilla of unknown significance; *g.n.*, nidamental gland; *r.ov.*, aperture of the right oviduct; *l.ov.*, aperture of the rudimentary left oviduct (pyriform sac of Owen); *neph.a.*, aperture of the left anterior nephridium; *neph.p*, aperture of the left posterior nephridium; *visc.per.*, left aperture of the viscero-pericardial sac; *olf*, the left osphradium placed near the base of the anterior gill-plume. The four gill-plumes (ctenidia) are not lettered.

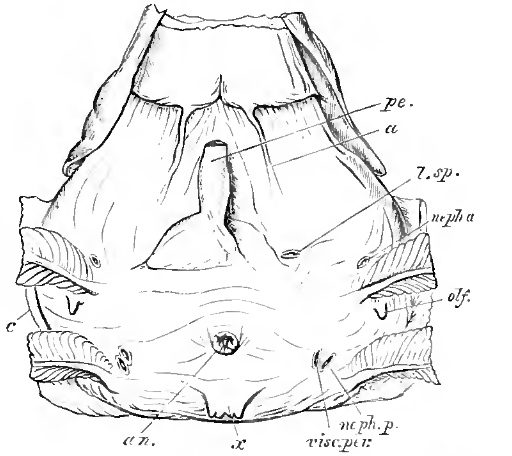


FIG. 102.—View of the postero-ventral surface of a male Pearly Nautilus, the mantle-skirt (*c*) being completely reflected so as to show the inner wall of the sub-pallial chamber, and the four ctenidia and the foot cut short (drawn from nature by A. G. Bourne). *pe.*, penis, being the enlarged termination of the right spermatic duct; *l.sp.*, aperture of the rudimentary left spermatic duct (pyriform sac of Owen). Other letters as in fig. 101.

sac opens by a pore into each nephridium instead of directly to the surface. A single pair of ctenidia (gill-plumes) is present instead of the two pairs in Nautilus. The existence of two pairs of ctenidia and of two pairs of nephridia in Nautilus, placed one behind the other, is highly remarkable. The interest of this arrangement is in relation to the general morphology of the Mollusca, for it is impossible to view this repetition of organs in a linear series as anything else than an instance of metameric segmentation, comparable to the segmentation of the ringed worms and Arthropods. The only other example which we have of this metamerism in the Mollusca is presented by the Chitons. There we find not two pairs of ctenidia merely, but sixteen pairs (in some species more) accompanied by a similar metamerism of the dorsal integument, which carries eight shells. In Chiton the nephridia are not affected by the metamerism as they are in Nautilus. It is impossible on the present occasion to discuss in the way which their importance demands the significance of these two instances among Mollusca of incomplete or partial metamerism; but it would be wrong to pass them by without insisting upon the great importance which the occurrence of these isolated instances of metameric segmentation in a group of otherwise unsegmented organisms possesses, and the light which they may be made to throw upon the nature of metameric segmentation in general.

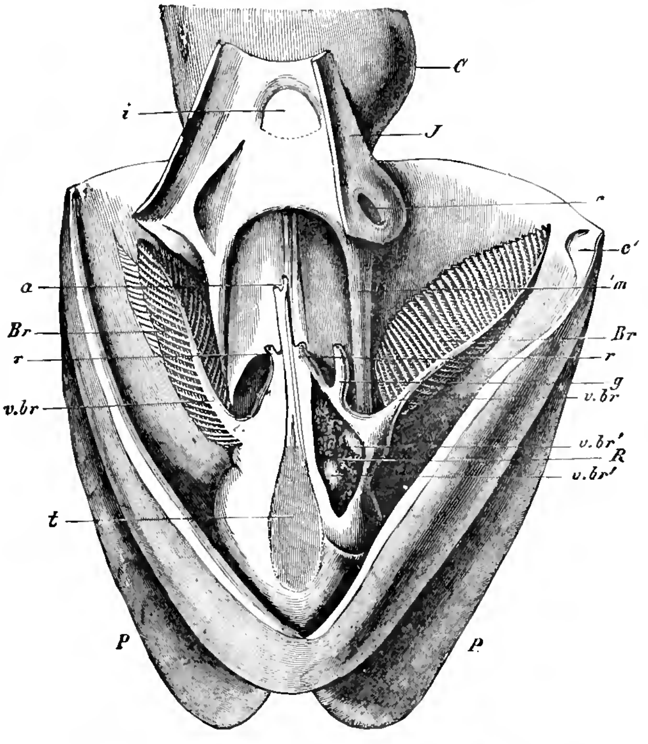


Fig. 103.—View of the postero-ventral surface of a male Sepia, obtained by cutting longitudinally the firm mantle-skirt and drawing the divided halves apart. This figure is strictly comparable with fig. 101. *C*, the head; *J*, the mid-foot or siphon, which has been cut open so as to display the valve *i*; *R*, the glandular tissue of the left nephridium or renal-sac, which has been cut open (see fig. 108); *P*, *P*, the lateral fins of the mantle-skirt; *Br*, the single pair of branchiæ (ctenidia); *a*, the anus,—immediately below it is the opening of the ink-bag; *c*, cartilaginous socket in the siphon to receive *c'*, the cartilaginous knob of the mantle-skirt,—the two constituting the "pallial hinge apparatus" characteristic of Decapoda, not found in Octopoda; *g*, the azygos genital papilla and aperture; *'i*, valve of the siphon (possibly the rudimentary hind-foot); *m*, muscular band connected with the fore-foot and mid-foot (siphon) and identical with the muscular mass *k* in fig. 91; *r*, renal papillæ, carrying the apertures of the nephridia; *v.br*, branchial efferent blood-vessel; *v.br'*, bulbous enlargements of the branchial blood vessels (see figs. 104, 108); *t*, ink-bag. (From Gegenbaur.)

The foot and head of Nautilus are in the adult inextricably grown together, the eye being the only part belonging primarily to the head which projects from the all-embracing foot. The fore-foot or front portion of the foot in Nautilus has the form of a number of lobes carrying tentacles and completely surrounding the mouth (figs. 88, 89, 91). The mid-foot is a broad median muscular process which exhibits in the most interesting manner a curling in of its margins so as to form an incomplete siphon (fig. 101), a condition which is completed and rendered permanent in the tubular funnel, which is the form presented by the corresponding part of Dibranchiata (fig. 96). The hind-foot possibly is represented by the valvular fold on the surface of the siphon-like mid-foot. In the Pteropoda the wing-like swimming lobes (epipodia or pteropodia) correspond to the two halves of the siphon, and are much the largest element of the foot. The fore-foot surrounding the head is often quite small, but in Clione and Pneumodermon carries lobes and suckers. A hind-foot is in Pteropoda often distinctly present; it is open to doubt as to whether the corresponding region of the foot in Siphonopoda is developed at all.

The lobes of the fore-foot of Nautilus and of the other Siphonopoda require further description. It has been doubted whether these lobes were rightly referred (by Huxley) to the fore-foot, and it has been maintained by some zoologists (Grenacher, Jhering) that they are truly processes of the head. It appears to the present writer to be impossible to doubt that the lobes in question are the fore-portion of the foot when their development is examined (see fig. 121, and especially fig. 72**), further, when the fact is considered that they are innervated by the pedal ganglion, and, lastly, when the comparison of such a Siphonopod as Sepia is made with such a Pteropod as Pneumodermon in its *larval* (fig. 84) as well as in its adult condition (fig. 85). The larval Pneumodermon shows clearly that the sucker-bearing processes of that Mollusc are originally far removed from the head and close in position to the pteropodial lobes of the foot. By differential growth they gradually embrace and obliterate the head, as do the similar sucker-bearing processes of Sepia. In both cases the sucker-bearing processes are "fore-foot." The fore-foot of Nautilus completely surrounds the buccal cone (fig. 88, *e*), so as to present an appearance with its expanded tentacles similar to that of the disc of a sea-anemone (Actinia). No figure has hitherto been published exhibiting this circum-oral disc with its tentacles in natural position as when the animal is alive and swimming, the small figure of Valenciennes being deficient in detail. All the published figures represent the actual appearance of the contracted spirit-specimens. Mr A. G.

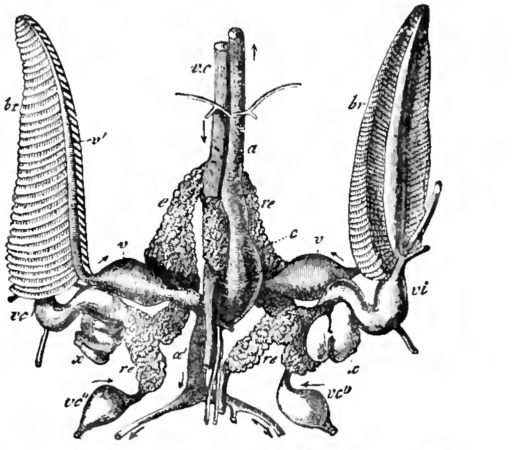


Fig. 104.—Circulatory and excretory organs of Sepia (from Gegenbaur, after John Hunter). *br*, branchiæ (ctenidia); *c*, ventricle of the heart; *a*, anterior artery (aorta); *a'*, posterior artery; *v*, the right and left auricles (enlargements of the efferent branchial veins); *v'*, efferent branchial vein on the free face of the gill-plume; *v.c*, vena cava; *vi*, *vc'*, advehent branchial vessels (branches of the vena cava, see fig. 108); *vc''*, abdominal veins; *x*, branchial hearts and appendages; *re*, *e*, glandular substance of the nephridia developed on the wall of the great veins on their way to the gills. The arrows indicate the direction of the blood-current.

Bourne, B.Sc., of University College, has prepared from actual specimens the drawings of this part in the male and female Nautilus reproduced in fig. 88, and has restored the parts to their natural form when expanded. The drawings show very strikingly the difference between male and female. In the female (lower figure), we observe in the centre of the disc the buccal cone *e* carrying the beak-like pair of jaws which project from the finely papillate buccal membrane. Three tentaculiferous lobes of the fore-foot are in immediate contact with this buccal cone; they are the right and left (*c*, *c*) inner lobes, as we propose to call them, and the inferior inner lobe (*d*),—called inferior because it really lies ventralwards of the mouth. This inner inferior lobe is clearly a double one, representing a right and left inner inferior lobe fused into one. A lamellated organ on its surface, probably olfactory in function (*n*), marks the separation of the constituent halves of this double lobe. Each half carries a group of fourteen tentacles. The right and the left inner lobes (*c*, *c*) each carry twelve tentacles. External to these three lobes the muscular substance of the mouth-embracing foot is raised into a wide ring, which becomes especially thick and large in the dorsal region where it is notably modified in form, offering a concavity into which the coil of the shell is received, and furnishing a protective roof to the retracted mass of tentacles. This part of the external annular lobe of the fore-foot is called the "hood" (figs. 90, 91, *m*.). The median antero-posterior line traversing this hood exactly corresponds to the line of concrescence of the two halves of the fore-foot, which primitively grew forward one on each side of the head, and finally fused together along this line in front of the mouth. The tentacles carried by the great annular lobe are nineteen on each side, thirty-eight in all. They are somewhat larger than the tentacles carried on the three inner lobes. The dorsalmost pair of tentacles (marked *g* in fig. 88) are the only ones which actually belong to that part of the disc which forms the great dorsal hood *m*. The hood is, in fact, to a large extent formed by the enlarged sheaths of these two tentacles. In the Ammonites (fossil Tetrabranchiata allied to Nautilus) the dorsal surface of the hood secreted a shelly plate in two pieces, known to palæontologists as Trigonellites and Aptychus. Possibly, however, this double plate was carried on the surface of the bilobed nidamental gland with the form and sculpturing of which, in Nautilus, it closely agrees. All the tentacles of the circum-oral disc are set in remarkable tubular sheaths, into which they can be drawn. The sheaths of some of those belonging to the external or annular lobe are seen in fig. 91, marked *n*. The sheaths are muscular as well as the tentacles, and are simply tubes from the base of which the solid tentacle grows. The functional significance of this sheathing arrangement is as obscure as its morphological origin. With reference to the latter, it appears highly probable that the tubular sheath represents the cup of a sucker such as is found on the fore-foot of the Dibranchiata. In any case, it seems to the writer impossible to doubt that each tentacle, and its sheath on a lobe of the circum-oral disc of Nautilus, corresponds to a sucker on such a lobe of a Dibranchiate. Keferstein follows Owen in strongly opposing this identification, and in regarding such tentacle as the equivalent of a whole lobe or arm of a Decapod or Octopod Dibranch. We find in the details of these structures, especially in the facts concerning the hectocotylus and spadix, the most conclusive reasons for dissenting from Owen's view. We have so far enumerated in the female Nautilus ninety tentacles. Four more remain which have a very peculiar position, and almost lead to the suggestion that the eye itself is a modified tentacle. These remaining tentacles are placed one above (before) and one below (behind) each eye, and bring up the total to ninety-four (fig. 91, *v*, *v*). They must be considered as also belonging to the fore-foot which thus surrounds the eye.

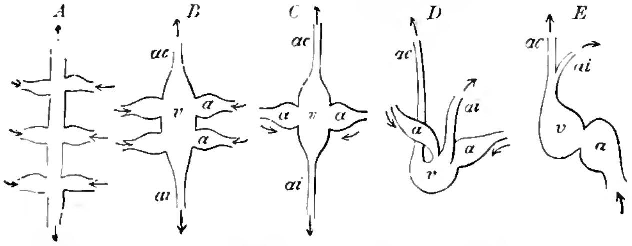


Fig. 105.—Diagram to show the relations of the heart in the Mollusca (from Gegenbaur). *A*. Part of the dorsal vascular trunk and transverse trunks of a worm. *B*. Ventricle and auricles of Nautilus. *C*. Of a Lamellibranch, of Chiton, or of Loligo. *D*. Of Octopus. *E*. Of a Gastropod. *a*, auricle; *v*, ventricle; *ac*, arteria cephalica (aorta); *ai*, arteria abdominalis. The arrows show the direction of the blood-current.

In the adult male Nautilus we find the following important differences in the tentaculiferous disc as compared with the female (see upper drawing in fig. 88). The inner inferior lobe is rudimentary, and carries no tentacles. It is represented by three groups of lamellæ (*d*), which are not fully exposed in the drawing. The right and left inner lobes are subdivided each into two portions. The right shows a larger portion carrying eight tentacles, and smaller detached groups (*q*) of four tentacles, of which three have their sheaths united whilst one stands alone. These four tentacles may be called the "anti-spadix." The left inner lobe shows a similar larger portion carrying eight tentacles, and a curious conical body in front of it corresponding to the anti-spadix. This is the "spadix" of Van der Hoeven (**36**). It carries no tentacles, but is terminated by imbricated lamellæ. These lamellæ appear to represent the four tentacles of the anti-spadix of the right internal lobe, and are generally regarded as corresponding to that modification of the sucker-bearing arms of male Dibranchiate Siphonopods to which the name "hectocotylus" is applied. The spadix is in fact the hectocotylized portion of the fore-foot of the male Nautilus. The hectocotylized arm or lobe of male Dibranchiata is connected with the process of copulation, and in the male Nautilus the spadix has probably a similar significance, though it is not possible to suggest how it acts in this relation. It is important to observe that the modification of the fore-foot in the male as compared with the female Nautilus is not confined to the existence of the spadix. The anti-spadix and the reduction of the inner inferior lobe are also male peculiarities. The external annular lobe in the male does not differ from that of the female; it carries nineteen tentacles on each side. The four ophthalmic tentacles are also present. Thus in the male Nautilus we find altogether sixty-two tentacles, the thirty-two additional tentacles of the female being represented by lamelliform structures.

If we now compare the fore-foot of the Dibranchiata with that of Nautilus, we find in the first place a more simple arrangement of its lobes, which are either four or five pairs of tapering processes (called "arms") arranged in a series around the buccal cone, and a substitution of suckers for tentacles on the surface of these lobes (figs. 92, 95, 96). The most dorsally-placed pair of arms, corresponding to the two sides of the hood of Nautilus, are in reality the most anterior (see fig. 75, (6)), and are termed the first pair. In the Octopoda there are four pairs of these arms (figs. 94, 95), in the Decapoda five pairs, of which the fourth is greatly elongated (figs. 92, 93). In Sepia and other Decapoda (not all) each of these long arms is withdrawn into a pouch beside the head, and is only ejected for the purpose of prehension. The figures referred to show some of the variations in form which these arms may assume. In the

Octopoda they are not unfrequently connected by a web, and form an efficient swimming-bell. The suckers are placed on the ad-oral surface of the arms, and may be in one, two, or four rows, and very numerous. In place of suckers in some genera we find on certain arms or parts of the arms horny hooks; in other cases a hook rises from the centre of each sucker. The hooks on the long arms of Onychoteuthis are drawn in fig. 97. The fore-foot, with its apparatus of suckers and hooks, is in the Dibranchiata essentially a prehensile apparatus, though the whole series of arms in the Octopoda serve as swimming organs, and in many (*e.g.*, the Common Octopus or Poulp) the sucker-bearing surface is used as a crawling organ.

In the males of the Dibranchiata one of the arms is more or less modified in connexion with the reproductive function, and is called the "hectocotylized arm." This name is derived from the condition assumed by the arm in those cases in which its modification is carried out to the greatest extent. These cases are those of the Octopods *Argonauta argo* and *Parasira catenulata* (fig. 96). In the males of these the third arm (on the left side in Argonauta, on the right side in Parasira) is found before the breeding season to be represented by a globular sac of integument. This sac bursts, and from it issues an arm larger than its neighbours, having a small sac at its extremity in Parasira (fig. 96, *x*), from which subsequently a long filament issues. Before copulation the male charges this arm with the spermatophores or packets of spermatozoa removed from its generative orifice beneath the mantle-skirt, and during coitus the arm becomes detached and is left adhering to the female by means of its suckers. A new arm is formed at the cicatrix before the next breeding season. The female, being much larger than the male, swims away with the detached arm lodged beneath her mantle-skirt. There, in a way which is not understood, the fertilization of the eggs is effected. Specimens of the female Parasira with the detached arm adherent were examined by Cuvier, who mistook the arm for a parasitic worm and gave to it the name Hectocotylus. Accordingly, the correspondingly modified arms of other Siphonopoda are said to be hectocotylized. Steenstrup has determined the hectocotylized condition of one or other of the arms in a number of male Dibranchs as follows:—in all, excepting Argonauta and Parasira, the modification of the arm is slight, consisting in a small enlargement of part or the whole of the arm, and the obliteration of some of its suckers, as shown in fig. 95, A, B; in Octopus and Eledone the third right arm is hectocotylized; in Rossia the first left arm is hectocotylized along its whole length, and the first right arm also in the middle only; in Sepiola only the first left arm along its whole length; in Sepia it is the fourth left arm which is modified, and at its base only; in Sepioteuthis, the same at its apex; in Loligo, the same also at its apex; in Loliolus, the same along its whole length; in Ommastrephes, Onychoteuthis, and Loligopsis no hectocotylized arm has hitherto been observed.

In the females of several Dibranchs (Sepia, &c.) the packets of spermatozoa or spermatophores received from the male have been observed adhering to the smaller arms. How they are passed in this case by the female to the ova in order to fertilize them is unknown.

Musculature, Fins, and Cartilaginous Skeleton.—Without entering into a detailed account of the musculature of Nautilus, we may point out that the great muscular masses of the fore-foot and of the mid-foot (siphon) are ultimately traceable to a large transverse mass of muscular tissue, the ends of which are visible through the integument on the right and left surfaces of the body dorsal of the free flap of the mantle-skirt (fig. 89, *l*, *l*, and fig. 91, *k*). These muscular areæ have a certain adhesion to the shell, and serve both to hold the animal in its shell and as the fixed supports for the various movements of the tentaculiferous lobes and the siphon. They are to be identified with the ring-like area of adhesion by which the foot-muscle of the Limpet is attached to the shell of that animal (see fig. 27). In the Dibranchs a similar origin of the muscular masses of the fore-foot and mid-foot from the sides of the shell—modified, as this is, in position and relations—can be traced.

In Nautilus there are no fin-like expansions of the integument, whereas such occur in the Decapod Dibranchs along the sides of the visceral hump (figs. 92, 93). As an exception among Octopoda lateral fins occur in Pinnoctopus (fig. 94, A), and in Cirrhoteuthis (fig. 94, D). In the Pteropodous division of the Cephalopoda such fin-like expansions of the dorsal integument do not occur, which is to be connected with the fact that another region, the mid-foot, which in Siphonopods is converted into a siphon, is in them expanded as a pair of fins.

In Nautilus there is a curious plate-like expansion of integument in the mid-dorsal region just behind the hood, lying between that structure and the portion of mantle-skirt which is reflected over the shell. This is shown in fig. 90, *b*. If we trace out the margin of this plate we find that it becomes continuous on each side with the sides of the siphon or mid-foot. In Sepia and other Decapods (not in Octopods) a closely similar plate exists in an exactly corresponding position (see *b* in figs. 110, 111). In Sepia a cartilaginous development occurs here immediately below the integument forming the so-called "nuchal plate," drawn in fig. 116, D. The morphological significance of this nuchal lamella, as seen both in Nautilus and in Sepia, is not obvious. Cartilage having the structure shown in fig. 117 occurs in various regions of the body of Siphonopoda. In all Glossophorous Mollusca the lingual apparatus is supported by internal skeletal pieces, having the character of cartilage; but in the Siphonopodous Cephalopoda such cartilage has a wider range.

In Nautilus a large H-shaped piece of cartilage is found forming the axis of the mid-foot or siphon (fig. 116, A, B). Its hinder part extends up into the head and supports the peri-œsophageal nerve-mass (*a*), whilst its two anterior rami extend into the tongue-like siphon. In Sepia, and Dibranchs generally, the cartilage takes a different form, as shown in fig. 116, C. The processes of this cartilage cannot be identified in any way with those of the capito-pedal cartilage of Nautilus. The lower larger portion of this cartilage in Sepia is called the cephalic cartilage, and forms a complete ring round the œsophagus; it completely invests also the ganglionic nerve-collar, so that all the nerves from the latter have to pass through foramina in the cartilage. The outer angles of this cartilage spread out on each side so as to form a cup-like receptacle for the eyes. The two processes springing right and left from this large cartilage in the median line (fig. 116, C) are the "præ-orbital cartilages;" in front of these, again, there is seen a piece like an inverted T, which forms a support to the base of the "arms" of the fore-foot, and is the "basi-brachial" cartilage. The Decapod Dibranchs have, further, the "nuchal cartilage" already mentioned, and in Sepia, a thin plate-like "sub-ostracal" or (so-called) dorsal cartilage, the anterior end of which rests on and fits into the concave nuchal cartilage. In Octopoda there is no nuchal cartilage, but two band-like "dorsal cartilages." In Decapods there are also two cartilaginous sockets on the sides of the funnel —"siphon-hinge cartilages"—into which fleshy knobs of the mantle-skirt are loosely fitted. In Sepia, along the whole base-line of each lateral fin of the mantle (fig. 92), is a "basi-pterygial cartilage." It is worthy of remark that we have, thus developed, in Dibranch Siphonopods a more complete internal cartilaginous skeleton than is to be found in some of the lower Vertebrates. There are other instances of cartilaginous endo-skeleton in groups other than the Vertebrata. Thus in some capito-branchiate Chætopods cartilage forms a skeletal support for the gill-plumes, whilst in the Arachnids (Mygale, Scorpio) and in Limulus a large internal cartilaginous plate—the ento-sternite—is developed as a support for a large series of muscles.

Alimentary Tract.—The buccal cone of Nautilus is terminated by a villous margin (buccal membrane) surrounding the pair of beak-like jaws. These are very strong and dense in Nautilus, being calcified. Fossilized beaks of Tetrabranchiata are known under the name of Rhyncholites. In Dibranchs the beaks are horny, but similar in shape to those of Nautilus. They resemble in general those of a parrot, the lower beak being the larger, and overlapping the upper or dorsal beak. The lingual ribbon and odontophoral apparatus has the structure which is typical for Glossophorous Mollusca. In fig. 107, A is represented a single row of teeth from the lingual ribbon of Nautilus, and in fig. 107, B, C, of other Siphonopoda.

Fig. 106.—Alimentary canal of *Loligo sagittata* (from Gegenbaur). The buccal mass is omitted. *oe*, œsophagus; *v*, the stomach opened longitudinally; *x*, probe passed through the pylorus; *c*, commencement of the cæcum; *e*, its spiral portion; *i*, intestine; *a*, ink-bag; *b*, its opening into the rectum.

In Nautilus a long and wide crop or dilated œsophagus (*cr*, fig. 110) passes from the muscular buccal mass, and at the apex of the visceral hump passes into a highly muscular stomach, resembling the gizzard of a bird (*gizz*, fig. 110). A nearly straight intestine passes from the muscular stomach to the anus, near which it develops a small cæcum. In other Siphonopods the œsophagus is usually narrower (fig. 106, *oe*), and the muscular stomach more capacious (fig. 106, *v*), whilst a very important feature in the alimentary tract is formed by the cæcum. In all but Nautilus the cæcum lies near the stomach, and may be very capacious—much larger than the stomach in *Loligo vulgaris*—or elongated into a spiral coil, as in fig. 106, *e*. The simple U-shaped flexure of the alimentary tract as seen in fig. 106, and in fig. 110, is the only important one which it exhibits in the Cephalopoda,—the Pteropoda (except the Limacinida) agreeing with the Siphonopoda in this simplicity in consequence of their visceral hump being untwisted. The acini of the large liver of Nautilus are compacted into a solid reddish-brown mass by a firm membrane, as also is the case in the Dibranchiata. The liver has four paired lobes in Nautilus, which open by two bile-ducts into the alimentary canal at the commencement of the intestine. The bile-ducts unite before entering the intestine. In Dibranchiata the two large lobes of the liver are placed antero-dorsally (beneath the shell in Decapoda), and the bile-ducts open into the cæcum. Upon the bile-ducts in Dibranchiata are developed yellowish glandular diverticula, which are known as "pancreas," though neither physiologically nor morphologically is there any ground for considering either the so-called liver or the so-called pancreas as strictly equivalent to the glands so denominated in the Vertebrata. In Nautilus the equivalents of the pancreatic diverticula of the Dibranchs can be traced upon the relatively shorter bile-ducts.

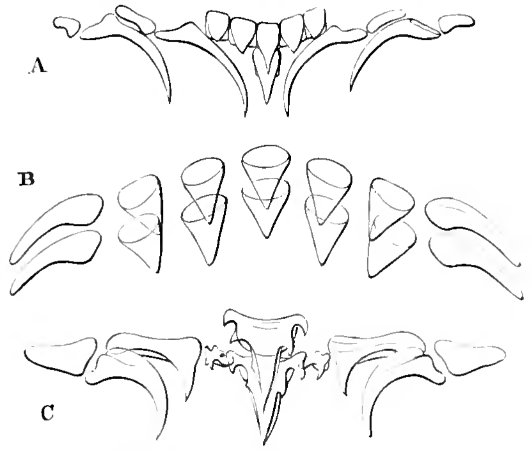


Fig. 107.—Lingual dentition of Siphonopoda. A. A single row of lingual teeth of *Nautilus pompilius* (after Keferstein). B. Two rows of lingual teeth of *Sepia officinalis* (after Troschel). C. Lingual teeth of *Eledone cirrhosa* (after Loven).

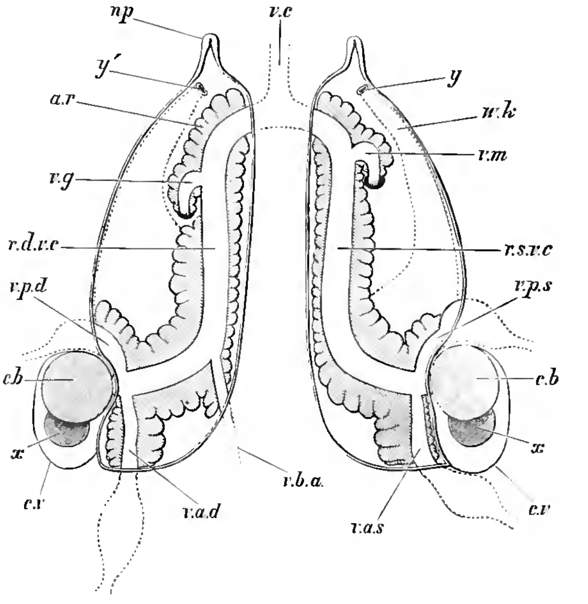


Fig. 108.—Diagram of the nephridial sacs, and the veins which run through them, in *Sepia officinalis* (after Vigelius). The nephridial sacs are supposed to have their upper walls removed. *v.c*, vena cava; *r.d.v.c*, right descending branch of the same; *r.s.v.c*, left descending branch of the same; *v.b.a.*, vein from the ink-bag; *v.m*, mesenteric vein; *v.g*, genital vein; *v.a.d*, right abdominal vein; *v.a.s*, left abdominal vein; *v.p.d*, right pallial vein; *v.p.s*, left pallial vein; *c.b*, branchial heart; *x*, appendage of the same; *c.v*, capsule of the branchial heart; *np*, external aperture of the right nephridial sac; *y*, reno-pericardial orifice placing the left renal sac or nephridium in communication with the viscero-pericardial sac, the course of which below the nephridial sac is indicated by dotted lines; *y'*, the similar orifice of the right side; *a.r*, glandular renal outgrowths; *w.k*, viscero-pericardial sac (dotted outline).

Salivary Glands are not developed in Nautilus unless a pair of glandular masses lying on the buccal cavity are to be considered as such. In the Dibranchs, on the contrary, one (Sepia, Loligo) or two pairs of large salivary glands are present, an anterior and a posterior (Octopus, Eledone, Onychoteuthis). Each pair of salivary glands has its paired ducts united to form a single duct, which runs forward from the glands and opens into the buccal cavity near the radula. The anterior pair of glands when present lie in the head near the buccal mass, the posterior pair lie much farther back beneath the liver, at the sides of the œsophagus. It is the posterior pair which alone are present in Sepia and Loligo. The ink-bag is to be considered as an appendage of the rectum. It is not developed in Nautilus, nor in the Pteropoda; in all Dibranchiata (even in the fossil Belemnites) it is present (fig. 106, *a*; fig. 103, *t*), and has been observed to develop as a diverticulum of the rectum, with spirally plaited walls which very early secrete a black pigment. The spiral plaitings of the walls diminish in relative size as the volume of the sac increases. Its outer surface acquires a metallic iridescence similar to that of the integuments of many fishes. The opening of the ink-sac is in the adult sometimes distinct from but near to the anus (Sepia); in other cases it opens into the rectum near the anus. The ink-bag of Dibranch Siphonopoda is possibly to be identified with the adrectal (purpuriparous) gland of some Gastropoda.

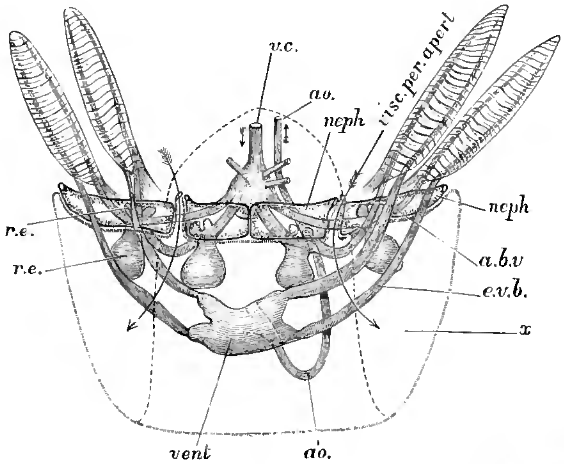


Fig. 109.—Diagram to show the relations of the four nephridial sacs, the viscero-pericardial sac, and the heart and large vessels in Nautilus (drawn by A. G. Bourne). *neph*, *neph*, on the right side point to the two nephridia of that side (the two of the opposite side are not lettered),—each is seen to have an independent aperture; *x* is the viscero-pericardial sac, the dotted line indicating its backward extension; *visc.per.apert* marks an arrow introduced into the right aperture of the viscero-pericardial sac; *r.e.*, *r.e.*, point to the glandular enlarged walls of the advehent branchial vessels,—two small glandular bodies of the kind are seen to project into each nephridial sac, whilst a larger body of the same kind depends from each of the four branchial advehent vessels into the viscero-pericardial sac; *v.c.*, vena cava; *vent*, ventricle of the heart; *ao.*, cephalic aorta (the small abdominal aorta not drawn); *a.b.v*, advehent branchial vessel; *e.v.b.*, efferent branchial vessel.

Cœlom, Blood-vascular System, and Excretory Organs.—Nautilus and the other Siphonopoda conform to the general Molluscan characters in regard to these organs. Whilst the general body-cavity or cœlom forms a lacunar blood-system or series of narrow spaces, connected with the trunks of a well-developed vascular system, that part of the original cœlom surrounding the heart and known as the Molluscan pericardium becomes shut off from this general blood-lymph system, and communicates, directly in Nautilus, in the rest through the nephridia, with the exterior. In the Siphonopoda this specialized pericardial cavity is particularly large, and has been recognized as distinct from the blood-carrying spaces, even by anatomists who have not considered the pericardial space of other Mollusca to be thus isolated. The enlarged pericardium, which may even take the form of a pair of sacs, has been variously named, but is best known as the viscero-pericardial sac or chamber. In Nautilus this sac occupies the whole of the postero-dorsal surface and a part of the antero-dorsal (see fig. 110, *x*), investing the genital and other viscera which lie below it, and having the ventricle of the heart suspended in it. Certain membranes forming incomplete septa, and a curious muscular band—the pallio-cardiac band—traverse the sac. The four branchial advehent veins, which in traversing the walls of the four nephridial sacs give off, as it were, glandular diverticula into those sacs, also give off at the same points four much larger glandular masses, which hang freely into the viscero-pericardial chamber (fig. 109, *r.e*). In Nautilus the viscero-pericardial sac opens to the exterior directly by a pair of apertures, one placed close to the right and one close to the left posterior nephridial aperture (fig. 101, *visc.per.*). This direct opening of the pericardial sac to the exterior is an exception to what occurs in all other Mollusca. In all other Molluscs the pericardial sac opens into the nephridia, and through them or the one nephridium to the exterior. In Nautilus there is no opening from the viscero-pericardial sac into the nephridia. Therefore the external pore of the viscero-pericardial sac may possibly be regarded as a shifting of the reno-pericardial orifice from the actual wall of the nephridial sac to a position alongside of its orifice. Parallel cases of such shifting are seen in the varying position of the orifice of the ink-bag in Dibranchiata, and in the orifice of the genital ducts of Mollusca, which in some few cases (*e.g.*, Spondylus) open into the nephridia, whilst in other cases they open close by the side of the nephridia on the surface of the body. The viscero-pericardial sac of the

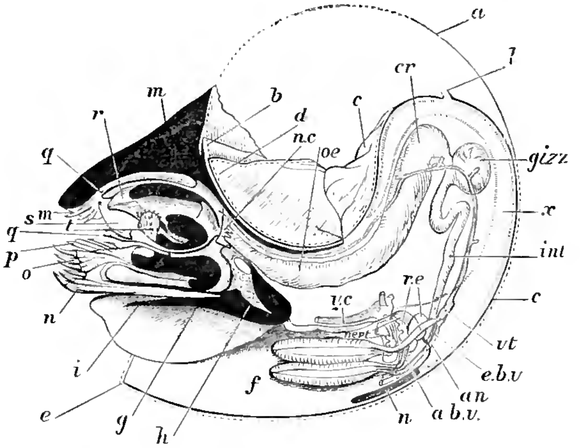


Fig. 110.—Diagram representing a vertical approximately median antero posterior section of *Nautilus pompilius* (from a drawing by A. G. Bourne). The parts which are quite black are the cut muscular surfaces of the foot and buccal mass. *a*, the shell; *b*, the nuchal plate identical with the nuchal cartilage of Sepia (see fig. 90, *b*); *c*, the integument covering the visceral hump; *d*, the mantle flap or skirt in the dorsal region where it rests against the coil of the shell; *e*, the inferior margin of the mantle-skirt resting on the lip of the shell represented by the dotted line; *f*, the pallial chamber with two of the four gills; *g*, the vertically cut median portion of the mid-foot (siphon); *h*, the capito-pedal cartilage (see fig. 116); *i*, the valve of the siphon; *l*, the siphuncular pedicle (cut short); *m*, the hood or dorsal enlargement of the annular lobe of the fore-foot; *n*, tentacles of the annular lobe; *p*, tentacles of the inner inferior lobe; *q*, buccal membrane; *r*, upper jaw or beak; *s*, lower jaw or beak; *t*, lingual ribbon; *x*, the viscero-pericardial sac; *n.c*, nerve-collar; *oe*, œsophagus; *cr*, crop; *gizz*, gizzard; *int*, intestine; *an*, anus; *ni*, nidamental gland; *nept*, aperture of a nephridial sac; *r.e*, renal glandular masses on the walls of the afferent branchial veins (see fig. 109); *a.b.v.*, afferent branchial vessel; *e.b.v*, efferent branchial vessel; *vt*, ventricle of the heart.

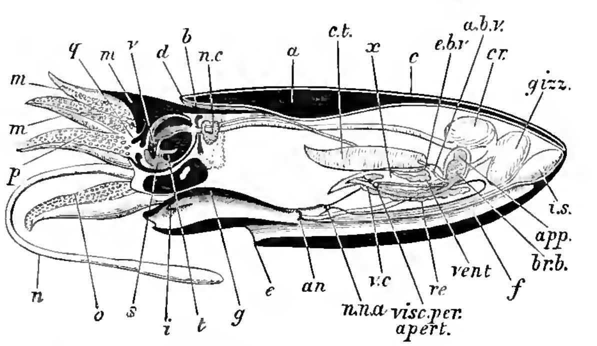


Fig. 111.—Diagram representing a vertical approximately median antero-posterior section of *Sepia officinalis* (from a drawing by A. G. Bourne). The lettering corresponds with that of fig, 110, with which this drawing is intended to be compared. *a*, shell (here enclosed by a growth of the mantle); *b*, the nuchal plate (here a cartilage); *c* (the reference line should be continued through the black area representing the shell to the outline below it), the integument covering the visceral hump; *d*, the reflected portion of the mantle-skirt forming the sac which encloses the shell; *e*, the inferior margin of the mantle-skirt (mouth of the pallial chamber); *f*, the pallial chamber; *g*, the vertically cut median portion of the mid-foot (siphon); *i*, the valve of the siphon; *m*, the two upper lobes of the fore-foot; *n*, the long prehensile arms of the same; *o*, the fifth or lowermost lobe of the fore-foot; *p*, the third lobe of the fore-foot; *q*, the buccal membrane; *v*, the upper beak or jaw; *s*, the lower beak or jaw; *t*, the lingual ribbon; *x*, the viscero-pericardial sac; *n.c*, the nerve-collar; *cr.*, the crop; *gizz.*, the gizzard; *an*, the anus; *c.t.*, the left ctenidium or gill-plume; *vent*, ventricle of the heart; *a.b.v.*, afferent branchial vessel; *e.b.v*, efferent branchial vessel; *re*, renal glandular mass; *n.n.a*, left nephridial aperture; *visc.per.apert.*, viscero-pericardial aperture (see fig. 108); *br.b.*, branchial heart; *app.*, appendage of the same; *i.s.*, ink-bag.

Dibranchs is very large also, and extends into the dorsal region. It varies in shape—that is to say, in the extensions of its area right and left between the various viscera—in different genera, but in the Decapods is largest. In an extension of this chamber is placed the ovary of Sepia, whilst the ventricle of the heart and the branchial hearts and their appendages also lie in it. It is probable that water is drawn into this chamber through the nephridia, since sand and other foreign matters are found in it. In all it opens into the pair of nephridial sacs by an orifice on the wall of each, not far from the external orifice (fig. 108, *y*, *y'*). There does not seem any room for doubting that each orifice corresponds to the reno-pericardial orifice which we have seen in the Gastropoda, and shall find again in the Lamellibranchia. The single tube-like nephridium and the pericardium of the Pteropoda also communicate by an aperture.

The circulatory organs, blood-vessels, and blood of Nautilus do not differ greatly from those of Gastropoda. The ventricle of the heart is a four-cornered body, receiving a dilated branchial efferent vessel (auricle) at each corner (fig. 109). It gives off a cephalic aorta anteriorly, and a smaller abdominal aorta posteriorly. The diagram, fig. 105, serves to show how this simple form of heart is related to the dorsal vessel of a worm or of an Arthropod, and how by a simple flexure of the ventricle (D) and a subsequent suppression of one auricle, following on the suppression of one branchia, one may obtain the form of heart characteristic of the Anisopleurous Gastropoda (excepting the Zygobranchia). The flexed condition of the heart is seen in Octopus, and is to some extent approached by Nautilus, the median vessels not presenting that perfect parallelism which is shown in the figure (B). The most remarkable feature presented by the heart of Nautilus is the possession of four instead of two auricles, a feature which is simply related to the metamerism of the branchiæ. By the left side of the heart of Nautilus, attached to it by a membrane, and hanging loosely in the viscero-pericardial chamber, is the pyriform sac of Owen. This has recently been shown to be the rudimentary left oviduct or sperm-duct, as the case may be (Lankester and Bourne, **37**), the functional right ovi-sac and its duct being attached by a membrane to the opposite side of the heart.

The cephalic and abdominal aortæ of Nautilus appear, after running to the anterior and posterior extremes of the animal respectively, to open into sinus-like spaces surrounding the viscera, muscular masses, &c. These spaces are not large, but confined and shallow. Capillaries are stated to occur in the integument. In the Dibranchs the arterial system is very much more complete; it appears in some cases to end in irregular lacunæ or sinuses, in other cases in true capillaries which lead on into veins. An investigation of these capillaries in the light of modern histological knowledge is much needed. From the sinuses and capillaries the veins take origin, collecting into a large median trunk (the vena cava), which in the Dibranchs as well as in Nautilus has a ventral (postero-ventral) position, and runs parallel to the long axis of the animal. In Nautilus this vena cava gives off at the level of the gills four branchial advehent veins (fig. 109, *v.c.*), which pass into the four gills without dilating. In the Dibranchs at a similar position the vena cava gives off a right and a left branchial advehent vein (fig. 108, *r.s.v.c*, *r.d.v.c*), each of which, traversing the wall of the corresponding nephridial sac and receiving additional factors (fig. 108, *v.g*, *v.p.d*, *v.a.d*, *v.b.a*), dilates at the base of the corresponding branchial plume, forming there a pulsating sac—the branchial heart (fig. 104, *x*; and fig 108, *c.b*). Attached to each branchial heart is a curious glandular body, which may possibly be related to the larger masses (*r.e* in fig. 109) which depend into the viscero-pericardial cavity from the branchial advehent veins of Nautilus. From the dilated branchial heart the branchial advehent vessel proceeds, running up the ad-pallial face of the gill-plume (*vi*, *vc'*, fig. 104). From each gill-plume the blood passes by the branchial efferent vessels (*v'*, fig. 104) to the heart, the two auricles being formed by the dilatation of these vessels (*v*, *v* in fig. 104).

The blood of Siphonopoda contains the usual amœboid corpuscles, and a diffused colouring matter—the hæmocyanin of Fredericque—which has been found also in the blood of Helix, and in that of the Arthropods Homarus and Limulus. It is colourless in the oxidized, blue in the deoxidized state, and contains copper as a chemical constituent.

The nephridial sacs and renal glandular tissue are closely connected with the branchial advehent vessels in Nautilus and in the other Siphonopoda. The arrangement is such as to render the typical relations and form of a nephridium difficult to trace. In accordance with the metamerism of Nautilus already noticed, there are two pairs of nephridia. Each nephridium assumes the form of a sac opening by a pore to the exterior. As is usual in nephridia, a glandular and a non-glandular portion are distinguished in each sac; these portions, however, are not successive parts of a tube, as happens in other cases, but they are localized areæ of the wall of the sac. The glandular renal tissue is, in fact, confined to a tract extending along that part of the sac's wall which immediately invests the great branchial advehent vein. The vein in this region gives off directly from its wall a complete herbage of little venules, which branch and anastomose with one another, and are clothed by the glandular epithelium of the nephridial sac. The secretion is accumulated in the sac and passed by its aperture to the exterior. Probably the nitrogenous excretory product is very rapidly discharged; in Nautilus a pink-coloured powder is found accumulated in the nephridial sacs, consisting of calcium phosphate. The presence of this phosphatic calculus by no means proves that such was the sole excretion of the renal glandular tissue. In Nautilus a glandular growth like that rising from the wall of the branchial vessel into its corresponding nephridial sac, but larger in size, depends from each branchial advehent vessel into the viscero-pericardial sac,—probably identical with the "appendage" of the branchial hearts of Dibranchs.

The chief difference, other than that of number between the nephridia of the Dibranchs and those of Nautilus, is the absence of the accessory growths depending into the viscero-pericardial space just mentioned, and, of more importance, the presence in the former of a pore leading from the nephridial sac into the viscero-pericardial sac (*y*, *y'* in fig. 108). The external orifices of the nephridia are also more prominent in Dibranchs than in Nautilus, being raised on papillæ (*np* in fig. 108; *r* in fig. 103). In Sepia, according to Vigelius (**38**), the two nephridia give off each a diverticulum dorsalwards, which unites with its fellows and forms a great median renal chamber, lying between the ventral portions of the nephridia and the viscero-pericardial chamber. In Loligo the fusion

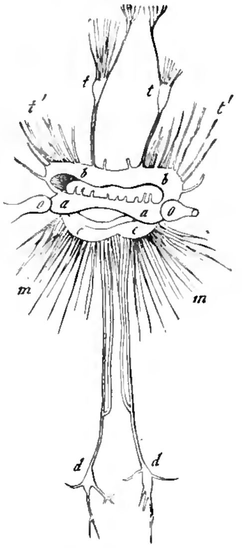


Fig. 112.—Nervous system of *Nautilus pompilius* (from Gegenbaur, after Owen). *t*, *t*, ganglion-like enlargements on nerves passing from the pedal ganglion to the inner series of tentacles; *t'*, nerves to the tentacles of the outer or annular lobe; *b*, pedal ganglion-pair; *a*, cerebral ganglion-pair); *c*, pleuro-visceral ganglionic band (fused pleural and visceral ganglion-pairs); *d*, genital ganglion placed on the course of the large visceral nerve, just before it gives off its branchial and its osphradial branches; *m*, nerves from the pleural ganglion to the mantle-skirt.

of the two nephridia to form one sac is still more obvious, since the ventral portions are united. In Octopus the nephridia are quite separate.

Tegumental pores have not been described in Nautilus, but exist in Dibranchiata, and have been (probably erroneously, but further investigation is needed) supposed to introduce water into the vascular system. A pair of such pores leading into sub-tegumental spaces of considerable area, the nature of which is imperfectly known, exist on the back of the head in Philonexis, Tremoctopus, and Argonauta. At the base of the arms and mouth four such pores are found in Histioteuthis and Ommastrephes, six in Sepia, Loligo, Onychoteuthis. Lastly, a pair of such pores are found in the Decapoda at the base of the long arms, leading into an extensive sub-tegumental pouch on each side of the head into which the long arms can be, and usually are, withdrawn. In Sepia, Sepiola, and Rossia the whole arm is coiled up in these sacs; in Loligo only a part of it is so; in Histioteuthis, Ommastrephes, and Onychoteuthis, the sacs are quite small and do not admit the arms.

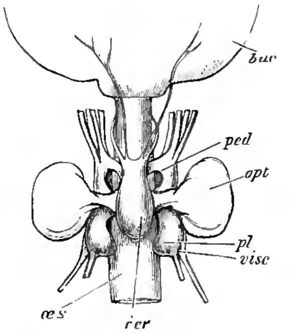


Fig. 113.

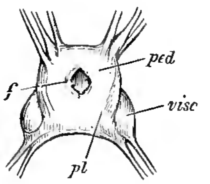


Fig. 114.

Figs. 113, 114.—Nerve-centres of Octopus. Figure 113 gives a view from the dorsal aspect, figure 114 one from the ventral aspect. *buc*, the buccal mass; *ped*, pedal ganglion; *opt*, optic ganglion; *cer*, cerebral ganglion; *pl*, pleural ganglion; *visc*, visceral ganglion; *œs*, œsophagus; *f*, foramen in the nerve-mass formed by pedal, pleural, and visceral ganglion-pairs, traversed by a blood-vessel.

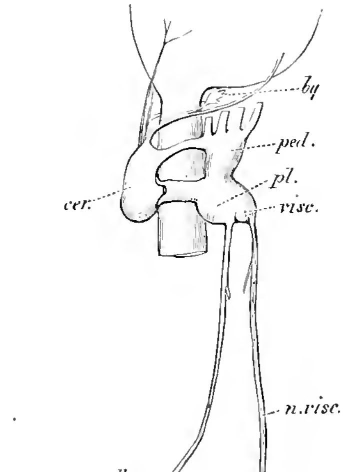


Fig. 115.—Lateral view of the nervous centres and nerves of the right side of *Octopus vulgaris* (from a drawing by A. G. Bourne). *bg*, buccal ganglion; *cer.*, cerebral ganglion; *ped.*, pedal ganglion; *pl.*, pleural, and *visc.*, visceral region of the pleuro-visceral ganglion; *gang. stell.*, the right stellate ganglion of the mantle connected by a nerve to the pleural portion; *n.visc.*, the right visceral nerve; *n.olf.*, its (probably) olfactory branches; *n.br.*, its branchial branches.

Nervous System.—Nautilus, like the other Cephalopoda (*e.g.*, Pneumodermon, fig. 87; Octopus, fig. 113), exhibits a great concentration of the typical Molluscan ganglia, as shown in fig. 112. The ganglia take on a band-like form, and are but little differentiated from their commissures and connectives,—an archaic condition reminding us of Chiton. The special optic outgrowth of the cerebral ganglion, the optic ganglion (fig. 112, *o*), is characteristic of the big-eyed Siphonopoda. The cerebral ganglion-pair (*a*) lying above the œsophagus is connected with two sub-œsophageal ganglion-pairs of band-like form. The anterior of these is the pedal *b*, *b*, and supplies the fore-foot with nerves *t'*, *t*, as also the mid-foot (siphon). The hinder band is the visceral and pleural pair fused (compare fig. 112 with fig. 87, and especially with the typical Euthyneurous nervous system of Limnæus, fig. 22); from its pleural portion nerves pass to the mantle, from its visceral portion nerves to the branchiæ and genital ganglion (*d* in fig. 112), and in immediate connexion with the latter is a nerve to the osphradium or olfactory papilla. No buccal ganglia have been observed in Nautilus, nor has an enteric nervous system been described in this animal, though both attain a special development in the Dibranchiata. The figures (114 and 115) representing the nerve-centres of Octopus serve to exhibit the disposition of these parts in the Dibranchiata. The ganglia are more distinctly swollen than in Nautilus. In Octopus an infra-buccal ganglion-pair are present corresponding to the buccal ganglion-pair of Gastropoda. In Decapoda a supra-buccal ganglion-pair connected with these are also developed. Instead of the numerous radiating pallial nerves of Nautilus, we have in the Dibranchiata on each side (right and left) a large pleural nerve passing from the pleural portion of the pleuro-visceral ganglion to the mantle, where it enlarges to form the stellate ganglion. From each stellate ganglion nerves radiate to supply the powerful muscles of the mantle-skirt. The nerves from the visceral portion of the pleuro-visceral ganglion have the same course as in Nautilus, but no osphradial papilla is present. An enteric nervous system is richly developed in the Dibranchiata, connected with the somatic nervous centres through the buccal ganglia, as in the Arthropoda through the stomato-gastric ganglia, and anastomosing with deep branches of the visceral nerves of the viscero-pleural ganglion-pair. It has been especially described by Hancock (**39**) in Ommastrephes. Upon the stomach it forms a single large and readily-detected gastric ganglion. It is questionable as to how far this and the "caval ganglion" formed in some Decapoda by branches of the visceral nerves which accompany the vena cava are to be considered as the equivalents of the "abdominal ganglion," which in a typical Gastropod nervous system lies in the middle of the visceral nerve-loop or commissure, having the right and left visceral ganglia on either side of it, separated by a greater or less length of visceral nerve-cord (see figs. 20, 21, 22). There can be little doubt that the enteric nervous system is much more developed in the Dibranchiata than in other Mollusca, and that it effects a fusion with the typical "visceral" cords more extensive than obtains even in Gastropoda, where such a fusion no doubt must also be admitted.

Special Sense-Organs.—Nautilus possesses a pair of osphradial papillæ (fig. 101, *olf*) corresponding in position and innervation to Spengel's organ placed at the base of the ctenidia (branchiæ) in all classes of Mollusca. This organ has not been detected in other Siphonopoda. In Pteropoda it is well developed as a single ciliated pit, although the ctenidia are in that group aborted (fig. 87, *Osp.*). Nautilus possesses other olfactory organs in the region of the head. Just below the eye is a small triangular process (not seen in our figures), having the structure of a shortened and highly-modified tentacle and sheath. By Valenciennes, who is followed by Keferstein, this is regarded as an olfactory organ. The large nerve which runs to this organ originates from the point of juncture of the pedal with the optic ganglion. The lamelliform organ upon the inner inferior tentacular lobe of Nautilus is possibly also olfactory in function. In Dibranchs behind the eye is a pit or open canal supplied by a nerve corresponding in origin to the olfactory nerve of Nautilus above mentioned.

Possibly the sense of taste resides in certain processes within the mouth of Nautilus and other Siphonopoda.

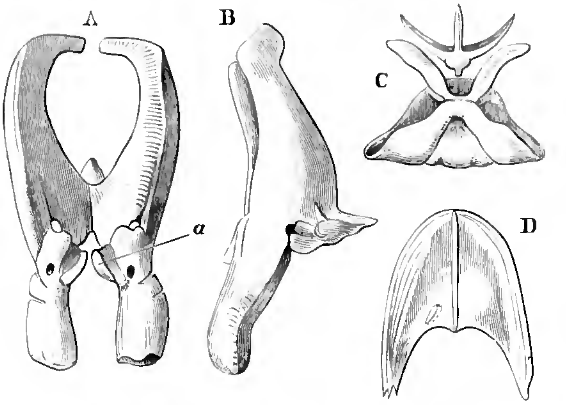


FIG. 116.—Cartilaginous skeleton of Siphonopoda (after Keferstein). A. Capito-pedal cartilage of *Nautilus pompilius*; *a* points to the ridge which supports the pedal portion of the nerve-centre. B. Lateral view of the same,—the large anterior processes are sunk in the muscular substance of the siphon. C. Cephalic cartilages of *Sepia officinalis*. D. Nuchal cartilage of *Sepia officinalis*.

The otocysts of Nautilus were discovered by Macdonald (**40**). Each lies at the side of the head, ventral of the eye, resting on the capito-pedal cartilage, and supported by the large auditory nerve which arises from the pedal ganglion. It has the form of a small sac, 1 to 2 mm. in diameter, and contains whetstone-shaped crystals, such as are known to form the otoliths of other Mollusca. The otocysts of Dibranchiata are larger and deeply sunk in the cephalic cartilage. It has been shown by Lankester that they develop as open pits (fig. 121, (5), (6), *o*), which gradually close up, the communication with the exterior becoming narrowed into a fine canal, which is reflected over one end of the sac, and finally has its external opening obliterated. A single otolith only is found in all Dibranchiata.

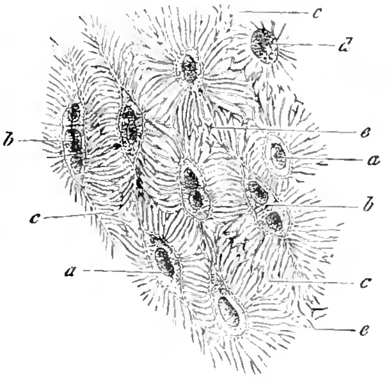


FIG. 117.—Minute structure of the cartilage of Loligo (from Gegenbaur, after Furbringer). *a*, simple, *b*, dividing, cells; *c*, canaliculi; *d*, an empty cartilage capsule with its pores; *e*, canaliculi in section.

The eye of Nautilus is among the most interesting structures of that remarkable animal. No other animal which has the same bulk and general elaboration of organization has so simple an eye as that of Nautilus. When looked at from the surface no metallic lustre, no transparent coverings, are presented by it. It is simply a slightly projecting hemispherical box like a kettle-drum, half an inch in diameter, its surface looking like that of the surrounding integument, whilst in the middle of the drum-membrane is a minute hole (fig. 91, *u*). Owen very naturally thought that some membrane had covered this hole in life, and had been ruptured in the specimen studied by him. It, however, appears from the researches of Hensen (**41**) that the hole is a normal aperture leading into the globe of the eye, which is accordingly filled by sea-water during life. There is no dioptric apparatus in Nautilus, and in place of refracting lens and cornea we have actually here an arrangement for forming an image on the principle of "the pin-hole camera." There is no other eye known in the whole animal kingdom which is so constructed. The wall of the eye-globe is tough, and the cavity is lined solely by the naked retina, which is bathed by sea-water on one surface and receives the fibres of the optic nerve on the other (see fig. 118, A). As in other Siphonopods (*e.g.*, fig. 120, *Ri*, *Re*, *p*), the retina consists of two layers of cells separated by a layer of dark pigment. The most interesting consideration connected with this eye of Nautilus is found when the further facts are noted—(1) that the elaborate lens-bearing eyes of Dibranchiata pass through a stage of development in which they have the same structure as the eye of Nautilus—namely, are open sacs (fig. 119); and (2), that amongst other Mollusca examples of cephalic eyes can be found which in the adult condition are, like the eye of Nautilus and the developing eye of Dibranchs, simple pits of the integument, the cells of which are surrounded by pigment and connected with the filaments of an optic nerve. Such is the structure of the eye of the Limpet (Patella); and in such a simple eye we obtain the clearest demonstration of the fact that the retina of the Molluscan cephalic eye, like that of the Arthropod cephalic eye and unlike that of the Vertebrate myelonic eye, is essentially a modified area of the general epiderm, and that the sensitiveness of its cells to the action of light and their relation to nerve-filaments is only a specialization and intensifying of a property common to the whole epiderm of the surface of the body. What, however, strikes us as especially remarkable is that the simple form of a pit, which in Patella serves to accumulate a secretion which acts as a refractive body, should in Nautilus be glorified and raised to the dignity of an efficient optical apparatus. Natural selection has had an altogether exceptional opportunity in the ancestors of Nautilus. In all other Mollusca, starting as we may suppose from the follicular or pit-like condition, the eye has proceeded to acquire the form of a *closed* sac, the cavity of the closed vesicle being then filled partially or completely by a refractive body (lens) secreted by its walls (fig. 118, B). This is the condition attained in most Gastropoda. It presents a striking contrast to the simple Arthropod eye, where, in consequence of the existence of a dense exterior cuticle, the eye does not form a vesicle, and the lens is always part of that cuticle.

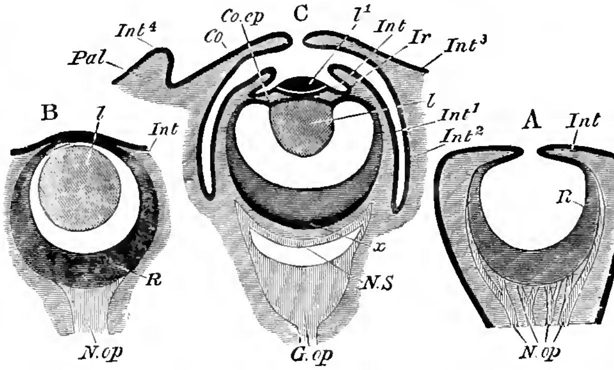


FIG. 118.—Diagrams of sections of the eyes of Mollusca. A. Nautilus (and Patella). B. Gastropod (Limax or Helix). C. Dibranchiate Siphonopod (Oigopsid). *Pal*, eyelid (outermost fold); *Co*, cornea (second fold); *Ir*, iris (third fold); *Int*$^{1, 2, 3, 4}$, different parts of the integument; *l*, deep portion of the lens; l^1, outer portion of the lens; *Co.ep*, ciliary body; *R*, retina; *N.op*, optic nerve; *G.op*, optic ganglion; *x*, inner layer of the retina; *N.S*, nervous stratum of the retina. (From Balfour, after Grenacher.)

In the Dibranchiate division of the Siphonopoda the greatest elaboration of the dioptric apparatus of the eye is attained, so that we have in one sub-class the extremes of the two lines of development of the Molluscan eye, those two lines being the punctigerous and the lentigerous. The structure of the Dibranchiate's eye is shown in section in fig. 118, C, and in fig. 120, and its development in fig. 119 and fig. 123. The open sac which forms the retina of the young Dibranchiate closes up, and constitutes the posterior chamber of the eye, or primitive optic vesicle (fig. 123, A, *poc*). The lens forms as a structureless growth, projecting inwards from the front wall of this vesicle (fig. 123, B, *l*). The integument around the primitive optic vesicle which has sunk below the surface now rises up and forms firstly nearest the axis of the eye the iridian folds (*if* in B, fig. 123 ; *ik* in fig. 120 ; *Ir* in fig. 118), and then secondly an outer circular fold grows up like a wall and completely closes over the iridian folds and the axis of the primitive vesicle (fig. 120, C). This covering is transparent, and is the cornea. In the oceanic Decapoda the cornea does not completely close, but leaves a central aperture traversed by the optic axis. These forms are termed Oigopsidæ by d'Orbigny (**42**), whilst the Decapoda with closed cornea are termed Myopsidæ. In the Octopoda the cornea is closed, and there is yet another fold thrown over the eye. The skin surrounding the cornea presents a free circular margin, and can be drawn over the surface of the cornea by a sphincter muscle. It thus acts as an adjustable diaphragm, exactly similar in movement to the iris of Vertebrates. Sepia and allied Decapods have a horizontal lower eyelid, that is to say, only one-half of the sphincter-like fold of integument is movable. The exact history of the later growth of the lens in the Dibranchs' eye is not clear. As seen in fig. 120, it appears, after attaining a certain size, to push through the front wall of the primitive optic vesicle at the point corresponding to its centre of closure, and to project a little into the anterior chamber formed by the cornea. The wall of the primitive optic vesicle adjacent to the embedded lens (L) now becomes modified, forming a so-called "ciliary body," in which muscular tissue is present, serving to regulate the focus of the lens (*ci* in fig. 120). Bobretzky (**43**) differs from Lankester, whose view is above given, in assigning a distinct origin to the protruding anterior segment of the lens (l^1 in fig. 118). The optic ganglion, as well as the other large ganglia of the Dibranchiata, originate in the mesoblast of the embryo. The connexion between the cells of the retina and the nerve-fibres proceeding from the optic ganglion must therefore be a secondary one.

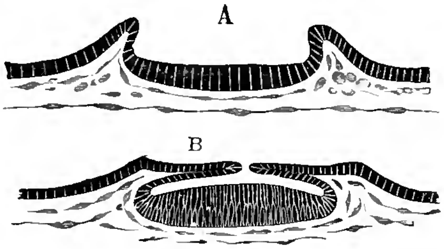


Fig. 119.—Diagrams of sections showing the early stage of development of the eye of Loligo when it is, like the permanent eye of Nautilus and of Patella, an open sac. A. First appearance of the eye as a ring-like upgrowth. B. Ingrowth of the ring-like wall so as to form a sac, the primitive optic vesicle of Loligo. (From Lankester.)

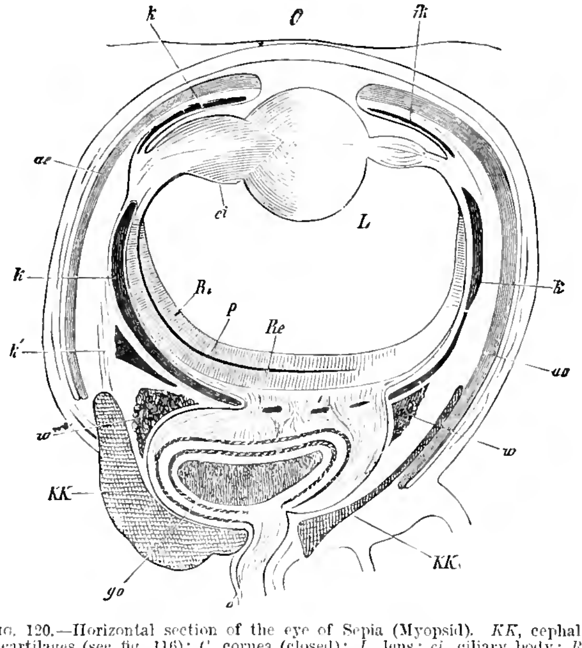


Fig. 120.—Horizontal section of the eye of Sepia (Myopsid). *KK*, cephalic cartilages (see fig. 116); *C*, cornea (closed); *L*, lens; *ci*, ciliary body; *Ri*, internal layer of the retina; *Re*, external layer of the retina; *p*, pigment between these; *o*, optic nerve; *go*, optic ganglion; *k* and *k'*, capsular cartilage; *ik*, cartilage of the iris; *w*, white body; *ae*, argentine integument. (From Gegenbaur, after Hensen.)

Chromatophores.—In Nautilus these remarkable structures, which we mention here as being intimately associated with the nervous system, appear to be absent. In Dibranchiata they play an important part in the economy, enabling their possessor, in conjunction with the discharge of the contents of the ink-bag, to elude the observation of either prey or foe. They consist of large vesicular cells (true nucleated cells converted into vesicles), arranged in a layer immediately below the epidermis. Each chromatophore-cell has from six to ten muscular bands attached to its walls, radiating from it star-wise. The contraction of these fibres causes the chromatophore-cell to widen out; it returns to its spherical resting state by its own elasticity. In the spherical resting state such a cell may measure ·01 mm., whilst when fully stretched by its radiating muscles it covers an area of ·5 mm. The substance of the chromatophore-cells is intensely coloured with one of the following colours—scarlet, yellow, blue, brown—which are usually of the greatest purity and brilliance. The action of the chromatophores may be watched most readily in young Loligo, either under the microscope or with the naked eye. The chromatophores are suddenly expanded, and more slowly retracted with rapidly-recurring alternation. All the blue, or all the red, or all the yellow may be expanded and the other colours left quiescent. Thus the animal can assume any particular hue, and change its appearance in a dazzling way with extraordinary rapidity. There is a definite adaptation of the colour assumed in the case of Sepia and others to the colour of the surrounding rock and bottom.

Gonads and Genital Ducts.—In Nautilus it has recently been shown by Lankester and Bourne (**37**) that the genital ducts of both sexes are paired right and left, the left duct being rudimentary and forming the "pyriform appendage," described by Owen as adhering by membranous attachment to the ventricle of the heart, and shown by Keferstein to communicate by a pore with the exterior. Thus the Cephalopoda agree with our archi-Mollusc in having bilaterally symmetrical genital ducts in the case of the most archaic member of the class. The ovary (female gonad) or the testis (male gonad) lies in Nautilus as in the Dibranchs in a distinct cavity walled off from the other viscera, near the centro-dorsal region. This chamber is formed by the cœlomic or peritoneal wall; the space enclosed is originally part of the cœlom, and in Sepia and Loligo is, in the adult, part of the viscero-pericardial chamber. In Octopus it is this genital chamber which communicates by a right and a left canal with the nephridium, and is the only representative of pericardium. The ovary or testis is itself a growth from the inner wall of this chamber, which it only partly fills. In Nautilus the right genital duct, which is functional, is a simple continuation to the pore on the postero-dorsal surface of the membranous walls of the capsule in which lies the ovary or the testis, as the case may be. The gonad itself appears to represent a single median or bilateral organ.

The true morphological nature of the genital ducts of the Cephalopoda and of other Mollusca is a subject which invites speculation and inquiry. In all the cases in which such ducts continuous with the tunic of the gonad itself occur—viz., in Nematoid worms, in Arthropoda, and in Teleostean fishes, besides Mollusca—there is an absence of definite knowledge as to the mode of development of the duct. It seems, however, from such facts as have been ascertained that the gonad lies at first freely in the cœlom, and that the duct develops in connexion with the genital pore, and attaches itself to the embryonic gonad, or to the capsule which grows around it. The question then arises as to the nature of the pore. In other groups of animals we find that the pore, and funnel or tube connected with it by which the genital products are conveyed to the exterior, is a modified nephridium (usually a pair, one right and one left). Is it possible that this is also the case where the duct very early becomes united to the gonad, and even gives rise to the appearance of a tubular ovary or testis? Probably this is the case in Teleostean fishes (see Huxley's observations on the oviducts of the smelt, **44**); but it seems to be a tenable position that in other cases, including the Mollusca, the genital pore is a simple opening in the body-wall leading into the body-cavity or cœlom, such as we find on the dorsal surface of the earth-worm, which has become specialized for the extrusion of the genital products. Possibly, as in Nemertine and Chætopod worms, the condition preceding the development of these definite genital pores was one in which a temporary rupture of the body-wall occurred at the breeding season, and this temporary aperture has gradually become permanent. The absence of genital pores in Patella, and some Lamellibranchs which make use of the nephridia for the extrusion of their genital products, suggests that the very earliest Mollusca or their forefathers were devoid of genital ducts and pores. In no Mollusca, however, is the nephridium used in the same way as a genital duct as it is in the Chætopoda, the Gephyræa, and the Vertebrata; for the open mouth of the nephridium in Mollusca leads into the pericardial space, and it is not through this space and this mouth that the genital products of any Mollusca enter the nephridium (except perhaps in Neomenia), although it is by this mouth that the genital products enter the nephridium in the former classes above named. Hence the arrangement in Patella, &c., is to be looked upon as a special development from the simpler condition when the Mollusca brought forth by rupture (= schizodinic, from ὠδίς, travail), and not as derived from the common arrangement of adaptation of a nephridium to the genital efferent function (= nephrodinic).[1]

The functional oviduct of Nautilus forms an albuminiparous gland as a diverticulum, which appears to correspond to a dilatation in the male duct, which succeeds the testis itself, and is called the "accessory gland." The male duct has a second dilatation (Needham's sac), and then is produced in the form of a large papilla. In Dibranchs the genital ducts are but little more elaborated. They are ciliated internally. In female Octopoda, in Ommastrephes, and in one male Octopod (*Eledone moschata*) the genital ducts are paired, opening right and left of the anus. But in all other Dibranchs a single genital duct only is developed, viz., that of the left side, and leads from the genital capsule or chamber of the gonad to an asymmetrically-placed pore. In the male Dibranchs the genital duct is coiled and provided with a series of glandular dilatations and receptacles. These are connected with the formation of the spermatophores. In the Siphonopoda the spermatic fluid does not flow as a liquid from the genital pore, but the spermatozoa are made up into little packets before extrusion. In other Mollusca (Pulmonata) and in other animals (Chætopoda) this formation of "sperm-ropes" is known, but in the Siphonopoda it attains its highest development. Exceedingly complicated structures of a cylindrical form (sometimes an inch in length) are formed in the male genital duct by a secretion which embeds and cements together the spermatozoa. They are formed in Nautilus as well as in Dibranchs, the actual manner in which their complicated structure is produced being not easily conjectured. Accessory glands not forming part of the oviduct, but furnishing the material for enclosing the eggs in an elastic envelope, are found as paired structures, opening some way behind the anus in Nautilus (101, *g.n.*) and in the Dibranchs. They are known as the nidamental glands. In the female Sepia they are particularly large and prominent, and are accompanied by a second smaller pair.

Reproduction and Development.—The details of sexual congress and of the actual fertilization of the egg are quite unknown in Nautilus, and imperfectly in the Dibranchs and the Pteropoda. Allusion has already been made to the subject in connexion with the hectocotylized arm. The mature eggs of Nautilus are unknown, as well as the appearance which they present when deposited. In the Dibranchs the eggs are always very large; in some cases the amount of food-yelk infused into the original egg-cell is so great as to give it the size of a large pea. This results in that mode of development which is only known outside this class among the Vertebrata; it is discoblastic. The protoplasm of the fertilized egg-cell segregates to one pole of the egg, and there undergoes cell-division, resulting in the formation of a disc of cleavage cells (fig. 121, (1)) resembling the cicatricula of the hen's egg, which subsequently spreads over and invests the whole egg (fig. 121, (2)). For details of this process we must refer the reader to other works (**45, 46**); but it may here be noted that in addition to the layer of cleavage cells, which consists of more than one stratum of cells in the future embryonic area as opposed to the yelk-sac area, additional cells are formed in the mass of residual yelk apparently by an independent process of segregation, each cell having a separate origin, whence they are termed "autoplasts." The autoplasts eventually form a layer of fusiform cells (fig. 121, (7), *h*; fig. 122, *m*, and fig. 123, *ps*),—the "yelk-membrane" which everywhere rests upon and encloses the residual yelk. The cleavage cells form a single layer on the yelk-sac area and two layers on the embryonic area, an outer layer one cell deep (fig. 122, *ep*), and an inner—the middle layer of the three—which is often thick and many cells deep (fig. 122, *m*). There is great difficulty here in identifying the layers with the three typical layers of other animal embryos, except in regard to the outermost, which corresponds with the epiblast of Vertebrates in many respects. The middle layer, however, gives rise to the nerve-ganglia as well as to the muscles, cœlom, and skeleto-trophic tissues, and to the mid-portion of the alimentary canal with its hepatic diverticula, the liver (see fig. 121, (7) and explanation, where the origin of the mid-gut as a vesicle *r* is seen). It is clearly, therefore, something more than the mesoblast of the Vertebrate, giving rise, as it does, to important organs formed both by epiblast and hypoblast in other animals. Lastly, the yelk-membrane, though corresponding to the Vertebrate hypoblast in position and structure, furnishes no part of the alimentary tract, but disappears when the yelk is completely absorbed. In fact, the developmental phenomena in Sepia, Loligo, and Octopus are profoundly perturbed by the excessive proportion of food-yelk. Balfour has shown

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[1] Cœlomate animals are, according to this nomenclature, either Schizodinic or Porodinic. The Porodinic group is divisible into Nephrodinic and Idiodinic, in the former the nephridium serving as a pore, in the latter a special (ἴδιος) pore being developed. In each of these latter groups the pore may be—(1) devoid of a duct, (2) provided with a duct which is unattached to the gonad and opens into the body-cavity, (3) provided with a duct which fuses with the gonad. The genital ducts of Idiodinic forms may be called Idiogonaducts, as distinguished from the Nephrogonaducts of nephrodinic forms.

that in the chick the orifice of closure of the overspreading blastoderm does not represent the whole of the blastopore, but that this is in part to be sought in the widely-separated primitive streak. The present writer has little doubt that a structure corresponding to the primitive streak of the chick, and lying near the klastic pole, will be found in Sepia and Loligo, and the strange vesicular origin of the mid-gut will be traced to and explained by it.

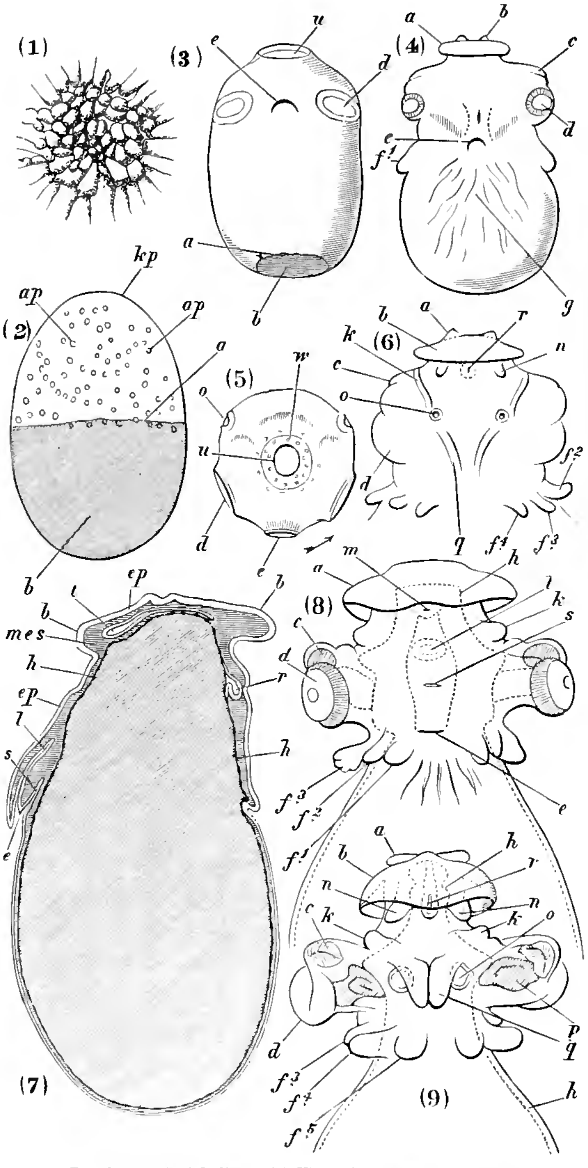

FIG. 121.—Development of Loligo. (1) View of the cleavage of the egg during the first formation of embryonic cells. (2) Lateral view of the egg at a little later stage. *a*, limit to which the layer of cleavage-cells has spread over the egg; *b*, portion of the egg (shaded) as yet uncovered by cleavage-cells; *ap*, the autoplasts; *kp*, cleavage-pole where first cells were formed. (3) Later stage, the limit *a* now extended so as to leave but little of the egg-surface (*b*) unenclosed. The eyes (*d*), mouth (*e*), and mantle-sac (*u*) have appeared. (4) Later stage, anterior surface, the embryo is becoming nipped off from the yelk sac (*g*). (5) View of an embryo similar to (3) from the cleavage-pole or centro-dorsal area. (6) Later stage, posterior surface. (7) Section in a median dorso-ventral and antero-posterior plane of an embryo of the same age as (4). (8) View of the anterior face of an older embryo. (9) View of the posterior face of an embryo of the same age as (8). Letters in (3) to (9):—*a*, lateral fins of the mantle; *b*, mantle-skirt; *c*, supra-ocular invagination to form the "white body"; *d*, the eye; *e*, the mouth; f^1, ^{2}, ^{3}, ^{4}, ^{5}, the five paired processes of the fore-foot; *g*, rhythmically contractile area of the yelk-sac, which is itself a hernia-like protrusion of the median portion of the fore foot (see fig. 72**); *h*, dotted line showing internal area occupied by yelk (food-material of the egg); *k*, first rudiment of the mid-foot (paired ridges which unite to form the siphon or funnel); *l*, sac of the radula or lingual ribbon; *m*, stomach; *n*, rudiments of the gills (paired ctenidia); *o*, the otocysts,—a pair of invaginations of the surface of the mid-foot; *p*, the optic ganglion; *q*, the distal portion of the ridges which form the siphon or mid-foot, *k* being the basal portion of the same structure; *r*, the vesicle-like rudiment of the intestine formed independently of the parts connected with the mouth, *s*, *k*, *m*, and without invagination; *s*, rudiment of the salivary glands; *t* in (7), the shell-sac at an earlier stage open (see fig. 122), now closed up; *u*, the open shell-sac formed by an uprising ring-like growth of the centro-dorsal area; *w* in (5), the mantle-skirt commencing to be raised up around the area of the shell-sac. In (7) *mes* points to the middle cell-layer of the embryo, *ep* to the outer layer, and *h* to the deep layer of fusiform cells which separates everywhere the embryo from the yelk or food-material lying within it. (Original.)

Leaving this difficult question of the cell-layers of the embryo, we would draw the reader's attention to the series of sketches representing the semi-transparent embryo of Loligo, drawn in fig. 121. When the cleavage cells have nearly enclosed the yelk, the upper or embryonic area shows the rudiments of the centro-dorsal mantle-sac or pen-sac, the mouth, the paired optic pits, and the paired otic pits (fig. 121, (3), (5)). The eye-pits close up (fig. 119), the orifice of the mantle-sac narrows, and its margin becomes raised and freely produced as mantle-skirt; at the same time an hour-glass-like pinching in of the whole embryo commences, separating the embryo proper from the so-called yelk-sac (fig. 121, (4)). Around the "waist" of constriction, pair by pair, ten lobes arise (fig. 121, (8)),—the arms of the fore-foot. It now becomes obvious that the yelk-sac is but the median surface of the fore-foot bulged out inordinately by food-yelk, just as the hind region of the foot is in the embryo slug (see fig. 72**, and explanation). Just as in the slug, this dilated yelk-holding foot is rhythmically contractile, and pulsates steadily over the area *g* in fig. 121, (4). At this stage, and long subsequently, the mouth of the young Cephalopod is in no way surrounded by the fore-foot, but lies well above its nascent lobes (*e* in fig. 121). Subsequently it sinks, as it were, between the right and left most anterior pair of the series, which grow towards one another and fuse above it, and leave no trace of their original position and relations. Fig. 121, (6) gives a view of the postero-dorsal surface of an embryo, in which the important fact is seen of the formation of the funnel or siphon by the union of two pieces (*q*), which grow up each independently, one right and one left, like the sides of the siphon of Nautilus or the swimming lobes of a Pteropod, and subsequently come together, as shown in (9), where the same letter *q* indicates the same part. The explanations of figs. 121 and 123 are given very full, and here, therefore, we shall only allude to two additional points. A curious mass of tissue of unknown significance occurs in the orbit of Dibranchs, known as the white body (*w* in fig. 120). A strongly-marked invagination just above the orbit is a very prominent feature in the embryo of Loligo, Sepia, and Octopus, and appears to give rise to this so-called white body. This invaginated portion of the outer cell-layer is seen in fig. 121, (8) and (9), lettered *c*; in fig. 123, A and B, it is lettered *wb*.

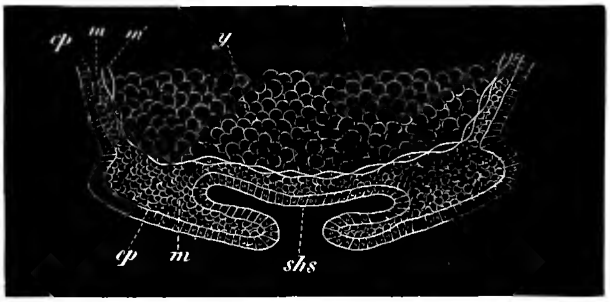

FIG. 122.—Section through the still open shell-sac occupying the centro-dorsal area of an embryo of Loligo; the position is inverted as compared with fig. 121 (3) and (7). *ep*, outer cell-layer; *m*, middle cell-layer; *m'*, deep cell-layer of fusiform cells; *y*, the granular yelk or food-material of the egg; *shs*, the still open shell-sac. (From Lankester.)

Lastly, in fig. 123, A, the origin of the optic nerve-ganglion *ng* from the cells of the middle layer should be especially noticed. In some other Molluscs the nerve-ganglia have been definitely traced to the outer cell-layer, whilst in some Gastropods, according to Bobretzky, they originate, as here shown, for Loligo.

The egg-coverings of the Dibranchiate are very complete. Argonauta and Octopus deposit each egg in a firm oval case, thin and transparent, which has a long stalk by which (in Octopus) the egg is fixed in company with two or three hundred others to some foreign object. Sepia encloses each egg in a thick envelope of many layers resembling india-rubber. Loligo encloses many rows of eggs in a copious tough jelly, and affixes a dozen or twenty such egg-strings to one spot. Sepia and Loligo desert their eggs when laid. The female Octopus most jealously guards them, building a nest of stones and incubating. Argonauta carries hers with her in a special brood-holding shell.

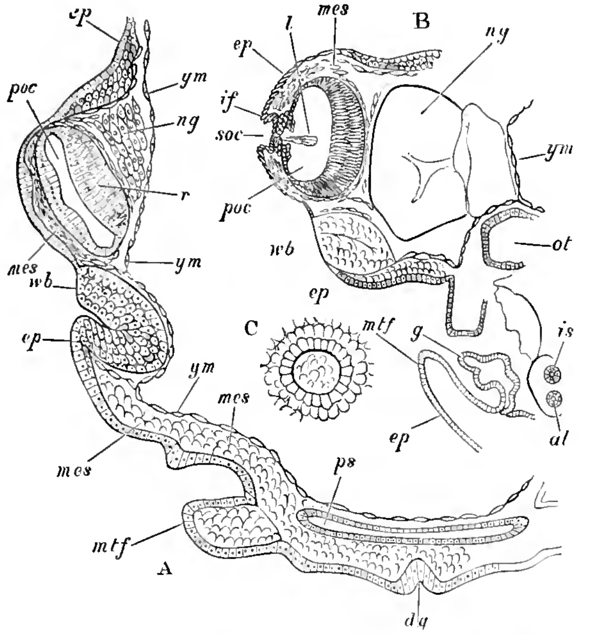

Fig. 123.—Right and left sections through embryos of Loligo. A. Same stage as fig. 121 (4). B. Same stage as fig. 121 (8); only the left side of the sections is drawn, and the food-material which occupies the space internal to the membrane *ym* is omitted. *al*, rectum; *is*, ink-sac; *ep*, outer cell-layer; *mes*, middle cell-layer; *ym*, deep cell-layer of fusiform cells (yelk-membrane); *ng*, optic nerve-ganglion; *ot*, otocyst; *wb*, the "white body" of the adult ocular capsule forming as an invagination of the outer cell-layer; *mtf*, mantle-skirt; *g*, gill; *ps*, pen-sac or shell-sac, now closed; *dg*, dorsal groove; *poc*, primitive optic vesicle, now closed (see fig. 119); *l*, lens; *r*, retina; *soc*, second or anterior optic chamber still open; *if*, iridean folds. C. The primitive invagination to form one of the otocysts, as seen in fig. 121 (5) and (6). (After Lankester.)

The development of the Pteropoda, so far as is known, presents no points of contact with that of the Siphonopoda rather than with that of the Gastropoda, owing to the fact that in them the egg has not an excess of food-yelk. Consequently, we find typical trochosphere and veliger larvæ among the Thecosomata (fig. 8, C, and fig. 81), whilst the isolated observation of Gegenbaur has made known very remarkable larvæ referable to the Gymnosomata, and with little doubt to Pneumodermon (fig. 84). The former set of larvæ are sufficient to demolish once for all the view which has been entertained by some zoologists, viz., that the velar disc of the veliger larva is the same thing as the pteropodial lobes of the mid-foot of Pteropoda. The latter larvæ are of importance in showing that, as in embryo Siphonopods so in embryo Pteropods, the sucker-bearing lobes of the fore-foot are truly podial structures, and only embrace the head and surround the mouth as the result of late embryonic growth.

Branch B.—*LIPOCEPHALA.*

Characters.—Mollusca with the head region undeveloped. No cephalic eyes are present; the buccal cavity is devoid of biting, rasping, or prehensile organs. The animal is sessile, or endowed with very feeble locomotive powers. The Lipocephala comprise but one class, the Lamellibranchia, also known as Elatobranchia and Conchifera.

Class **LAMELLIBRANCHIA**.

Characters.—Lipocephala in which the archaic BILATERAL SYMMETRY of the Mollusca is usually fully retained, and raised to a dominant feature of the organization by the lateral compression of the body and the development of the shell as two bilaterally symmetrical plates or valves covering each one side of the animal. The FOOT is commonly a simple cylindrical or ploughshare-shaped organ, used for boring in sand and mud, and more rarely presents a crawling disc similar to that of Gastropoda; in some forms it is aborted. The paired CTENIDIA are very greatly developed right and left of the elongated body, and form the most prominent organ of the group. Their function is chiefly not respiratory but nutritive, since it is by the currents produced by their ciliated surface that food-particles are brought to the feebly-developed mouth and buccal cavity.

The Lamellibranchia present as a whole a somewhat uniform structure, so that, although they are very numerous, it is not possible to divide them into well-marked sub-classes or sections, and orders. The chief points in which they vary are—(1) in the structure of the ctenidia or branchial plates; (2) in the presence of one or of two chief muscles, the fibres of which run across the animal's body from one valve of the shell to the other (adductors); (3) in the greater or less elaboration of the posterior portion of the mantle-skirt so as to form a pair of tubes, by one of which water is introduced into the sub-pallial chamber, whilst by the other it is expelled; (4) in the perfect or deficient symmetry of the two valves of the shell and the connected soft parts, as compared with one another; (5) in the development of the foot as a disc-like crawling organ (Arca, Nucula, Pectunculus, Trigonia, Lepton, Galeomma), as a simple plough-like or tongue-shaped organ (Unionacea, &c.), as a re-curved saltatory organ (Cardium, &c.), as a long burrowing cylinder (Solenacea, &c.), or its partial (Mytilacea) or even complete abortion (Ostracea).

The essential Molluscan organs are, with these exceptions, uniformly well developed. The MANTLE-SKIRT is always long, and hides the rest of the animal from view, its dependent margins meeting in the middle line below the ventral surface when the animal is retracted; it is, as it were, slit in the median line before and behind so as to form two flaps, a right and a left; on these the right and the left calcareous valves of the shell are borne respectively, connected by an uncalcified part of the shell called the ligament. In many embryo Lamellibranchs a centro-dorsal PRIMITIVE SHELL-GLAND or follicle has been detected (figs. 8 and 151). The MOUTH lies in the median line anteriorly, the ANUS in the median line posteriorly.

Both CTENIDIA right and left are invariably present, the axis of each taking origin from the side of the body as in the schematic archi-Mollusc (see fig. 1 and fig. 131). A pair of NEPHRIDIA opening right and left, rather far forward on the sides of the body, are always present. Each opens by its internal extremity into the pericardium. A pair of GENITAL APERTURES, connected by genital ducts with the paired gonads, are found right and left near the nephridial pores, except in a few cases where the genital duct joins that of the nephridium (Spondylus). The sexes are often, but not always, distinct. No accessory glands or copulatory organs are ever present in Lamellibranchs. The ctenidia often act as brood-pouches.

A dorsal contractile HEART, with symmetrical right and left auricles (fig. 143, A) receiving aerated blood from the ctenidia and mantle-skirt, is present, being unequally developed only in those few forms which are inequivalve. The typical PERICARDIUM is well developed. It appears, as in other Mollusca, not to be a blood-space although developed from the cœlom, and it communicates with the exterior by the pair of nephridia. As in Cephalopoda (and possibly other Mollusca) water can be introduced through the nephridia into this space. The ALIMENTARY CANAL keeps very nearly to the median vertical plane whilst exhibiting a number of flexures and loopings in this plane. A pair of large glandular outgrowths, the so-called "liver" or great digestive gland, exists as in other Molluscs. A pair of pedal OTOCYSTS, and a pair of OSPHRADIA at the base of the gills, appear to be always present. A typical NERVOUS SYSTEM is present (fig. 144), consisting of a cerebro-pleuro-visceral ganglion-pair, united by connectives to a pedal ganglion-pair and an osphradial ganglion-pair (parieto-splanchnic).

A special cæcum connected with the pharynx is sometimes found, containing a tough flexible cylinder of transparent cartilaginous appearance and unknown significance, called the "crystalline style" (Mactra), which possibly represents the radular sac of Glossophora. In many Lamellibranchs a gland is found on the hinder surface of the foot in the mid line, which secretes a substance which sets into the form of threads—the so-called "byssus"—by means of which the animal can fix itself. Sometimes this gland is found in the young and not in the adult (Anodon, Unio, Cyclas). In some Lamellibranchs (Pecten, Spondylus, Pholas, Mactra, Tellina, Pectunculus, Galeomma, &c.), although cephalic eyes are always absent, special eyes are developed on the free margin of the mantle-skirt, apparently by the modification of tentacles which are commonly found there (fig. 145). The existence of pores in the foot and elsewhere in Lamellibranchia by which liquid can pass into and out of the vascular system, although asserted as in the case of other Mollusca, appears to be improbable. It has yet to be shown by satisfactory microscopic sections that the supposed pores are anything but epidermal glands.

The Lamellibranchia live chiefly in the sea, some in fresh waters. A very few have the power of swimming by opening and shutting the valves of the shell (Pecten, Lima); most can slowly crawl or rapidly burrow; others are, when adult, permanently fixed to stones or rocks either by the shell or the byssus. In development some Lamellibranchia pass through a free-swimming trochosphere stage with præoral ciliated band; other fresh-water forms which carry the young in brood-pouches formed by the ctenidia have suppressed this larval phase.

The following classification and enumeration of genera are based primarily upon the characters of the adductor muscles. The Heteromya and Monomya must be conceived of as derived from forms resembling such Gastropodous Isomya as Nucula and Trigonia, which undoubtedly are the nearest living representatives of the ancestral Lipocephala, and bring us nearest to the other branch of the Mollusca, the Glossophora.

Order 1.—Isomya.

Character.—Anterior and posterior adductor muscles of approximately equal size.

Sub-order 1.—*Integripallia.*

Characters.—Marginal attachment of the mantle to the shell not inflected to form a sinus; siphons not developed in some, present in most.

Family 1.—*Arcacea.*
Genera: *Arca*, L. (fig. 132); *Cucullæa*, Lam.; *Pectunculus*, Lam.; *Limopsis*, Sassi; *Nucula*, Lam. (fig. 134); *Isoarca*, Munster; *Leda*, Schu.; *Yoldia*, Moll.; *Solenella*, Sowerby, &c.
Family 2.—*Trigoniacea.*
Genera: *Trigonia*, Brug.; *Axinus*, Sow.; *Lyrodesma*, Conrad.
Family 3.—*Unionacea.*
Genera: *Unio*, Retz.; *Castalia*, Lam.; *Anodon*, Cuv. (figs. 124, &c.); *Iridina*, Lam.; *Mycetopus*, d'Orb., &c.
Family 4.—*Lucinacea.*
Genera: *Lucina*, Brug.; *Corbis*, Cuv.; *Diplodonta*, Brown; *Kellia*, Turton; *Montacuta*, Turton; *Lepton*, Turton; *Galeomma*, Turton; *Astarte*, Sow.; *Crassatella*, Lam.; *Cardinia*, Ag.; *Cardita*, Brug., &c.
Family 5.—*Cyprinacea.*
Genera: *Tridacna*, Da C.; *Chama*, L.; *Dimya*, Ron.; *Diceras*, Lk.; *Isocardia*, Lam.; *Hippopodium*, Sow.; *Cardium*, L.; *Corbicula*, Meg.; *Cyrena*, Lk.; *Cyclas*, Brug. (fig. 146); *Pisidium*, Pfr. (figs. 148-153); *Cyprina*, Lam., &c.

Sub-order 2.—*Sinupallia.*

Characters.—Marginal attachment of the mantle to the shell inflected so as to form a sinus into which the pallial siphons can be withdrawn; siphons always present, and large.

Family 6.—*Veneracea.*
Genera: *Cypricardia*, Lam.; *Tapes*, Megl.; *Cyclina*, Desh.; *Cytherea*, Lam. (figs. 125, &c.); *Chione*, Megl.; *Venus*, L.; *Lucinopsis*, F. H.; *Sanguinolaria*, Lam.; *Psammobia*, Lam. (fig. 130); *Tellina*, L.; *Donax*, L.; *Scrobicularia*, Schu.; *Cumingia*, Sow.; *Rangia*, Dsml.; *Mactra*, L. (fig. 140); *Trigonella*, Da C.; *Vaganella*, Gr.; *Lutraria*, Lam.
Family 7.—*Myacea.*
Genera: *Myochama*, Stb.; *Chamostrea*, Rois; *Pandora*, Sol.; *Thracia*, Leach; *Thetis*, Sow.; *Pholadomya*, Sow.; *Corbula*, Brug.; *Mya*, Lam.; *Saxicava*, Fleur; *Panopæa*, Ad.; *Glycimeris*, Lam.; *Siliqua*, Mhlf., &c.; *Solen*, L.
Family 8.—*Pholadacea.*
Genera: *Clavagella*, Lam.; *Aspergillum*, Lam. (figs. 128, 129); *Humphreyia*, Gr.; *Pholas*, L.; *Pholadidea*, Turt.; *Teredo*, L.; *Teredina*, Lam.; *Furcella*, Oken, &c.

Order 2.—Heteromya.

Characters.—Anterior adductor (pallial adductor) much smaller than the posterior adductor (pedal adductor); siphons rarely present.

Family 1.—*Mytilacea.*
Genera: *Mytilus*, L. (fig. 133); *Modiola*, Lam.; *Crenella*, Brown; *Lithodomus*, Cuv.; *Dreissena*, Ben. (fig. 136); *Modiolarca*, Gr., &c.
Family 2.—*Mulleriacea.*
Genera: *Aetheria*, Lam.; *Mulleria*, Fér.

Order 3.—Monomya.

Characters.—Anterior adductor absent in the adult; siphons never developed.

Family 1.—*Aviculacea.*
Genera: *Cardiola*, Brdp.; *Avicula*, Kl.; *Malleus*, Lam.; *Inoceramus*, Sow.; *Crenatula*, Lam.; *Perna*, Brug., &c.
Family 2.—*Ostracea.*
Genera: *Ostrea*, L. (fig. 6); *Anomia*, L.; *Spondylus*, L.; *Plicatula*, Lam.; *Vulsella*, Lam.; *Lima*, Brug.; *Pecten*, L.; *Hinnites*, Dfr., &c.

Further Remarks on the Lamellibranchia.—The Lamellibranchia are the only members of the Lipocephalous branch of Mollusca existing at the present day; and we must suppose that, whilst on the one hand the earliest Glossophorous forms were developing from the archi-Mollusca by the elaboration of the buccal apparatus, the bivalved sessile Lamellibranchs were developing in another direction from univalve cephalophorous ancestors. The large bilobed mantle-flap with its pair of shells covering in the whole animal, the current-producing largely-expanded ctenidia, and the reduced cephalic region are characters which go hand in hand, and were simultaneously acquired, each being related to the development of the others. Unless the "crystalline style" of Lamellibranchs is to be considered as the rudiment of the "radular sac" of Glossophora, as suggested by Balfour, there is no indication whatever that the ancestors of the Lamellibranchia had acquired a representative of the buccal apparatus—so highly developed in Glossophora—before diverging from the archi-Mollusca; that is to say, the common ancestors of the two great branches of Mollusca presented the distinctive character of neither branch—they had not an aborted cephalic region, and they had not a lingual ribbon.

As an example of the organization of a Lamellibranch, we shall review the structure of the Common Pond-Mussel (*Anodonta cygnea*), comparing its structure with those of other Lamellibranchia. The Swan Mussel has superficially a perfectly-developed bilateral symmetry. The left side of the animal is seen as when removed from its shell in fig. 124 (1). The valves of the shell have been removed by severing their adhesions to the muscular areæ *h*, *i*, *k*, *l*, *m*, *u*.

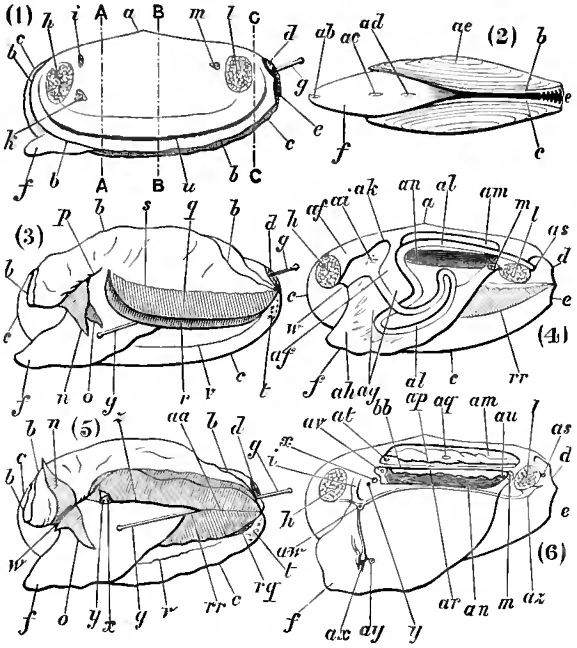

FIG. 124.—Diagrams of the external form and anatomy of *Anodonta cygnea*, the Pond-Mussel; in all the figures the animal is seen from the left side, the centro-dorsal region uppermost, as in the drawings of fig. 75, which compare. (1) Animal removed from its shell, a probe *g* passed into the sub-pallial chamber through the excurrent siphonal notch. (2) View from the ventral surface of an Anodon with its foot expanded and issuing from between the gaping shells. (3) The left mantle-flap reflected upwards so as to expose the sides of the body. (4) Diagrammatic section of Anodon to show the course of the alimentary canal. (5) The two gill-plates of the left side reflected upwards so as to expose the fissure between foot and gill where the probe *g* passes. (6) Diagram to show the positions of the nerve-ganglia, heart, and nephridia.

Letters in all the figures as follows:—*a*, centro-dorsal area; *b*, margin of the left mantle-flap; *c*, margin of the right mantle-flap; *d*, excurrent siphonal notch of the mantle margin; *e*, incurrent siphonal notch of the mantle margin; *f*, foot; *g*, probe passed into the superior division of the sub-pallial chamber through the excurrent siphonal notch, and issuing by the side of the foot into the inferior division of the sub-pallial chamber; *h*, anterior (pallial) adductor muscle of the shells; *i*, anterior retractor muscle of the foot; *k*, protractor muscle of the foot; *l*, posterior (pedal) adductor muscle of the shells; *m*, posterior retractor muscle of the foot; *n*, anterior labial tentacle; *o*, posterior labial tentacle; *p*, base-line of origin of the reflected mantle-flap from the side of the body; *q*, left external gill-plate; *r*, left internal gill-plate; *rr*, inner lamella of the right inner gill-plate; *rg*, right outer gill-plate; *s*, line of concrescence of the outer lamella of the left outer gill-plate with the left mantle-flap; *t*, pallial tentacles; *u*, the thickened muscular pallial margin which adheres to the shell and forms the pallial line of the left side; *v*, that of the right side; *w*, the mouth; *x*, aperture of the left organ of Bojanus (nephridium) exposed by cutting the attachment of the inner lamella of the inner gill-plate; *y*, aperture of the genital duct; *z*, fissure between the free edge of the inner lamella of the inner gill-plate and the side of the foot, through which the probe *g* passes into the upper division of the sub-pallial space; *aa*, line of concrescence of the inner lamella of the right inner gill-plate with the inner lamella of the left inner gill-plate; *ab*, *ac*, *ad*, three pit-like depressions in the median line of the foot supposed by some writers to be pores admitting water into the vascular system; *ae*, left shell valve; *af*, space occupied by liver; *ag*, space occupied by gonad; *ah*, muscular substance of the foot; *ai*, duct of the liver on the wall of the stomach; *ak*, stomach; *al*, rectum traversing the ventricle of the heart; *am*, pericardium; *an*, glandular portion of the left nephridium; *ap*, ventricle of the heart; *aq*, aperture by which the left auricle joined the ventricle; *ar*, non-glandular portion of the left nephridium; *as*, anus; *at*, pore leading from the pericardium into the glandular sac of the left nephridium; *au*, pore leading from the glandular into the non-glandular portion of the left nephridium; *av*, internal pore leading from the non-glandular portion of the left nephridium to the external pore *x*; *aw*, left cerebro-pleuro-visceral ganglion; *ax*, left pedal ganglion; *ay*, left otocyst; *az*, left olfactory ganglion (parieto-splanchnic); *bb*, floor of the pericardium separating that space from the non-glandular portion of the nephridia.

The free edge of the left half of the mantle-skirt *b* is represented as a little contracted in order to show the exactly similar free edge of the right half of the mantle-skirt *c*. These edges are not attached to, although they touch, one another; each flap (right or left) can be freely thrown back in the way which has been carried out in fig. 124, (3) for that of the left side. This is not always the case with Lamellibranchs; there is in the group a tendency for the corresponding edges of the mantle-skirt to fuse together by concrescence, and so to form a more or less completely closed bag, as in the Scaphopoda (Dentalium). In this way the notches *d*, *e* of the hinder part of the mantle-skirt of Anodon are in the Siphonate forms converted into two separate holes, the edges of the mantle being elsewhere fused together along this hinder margin. Further than this, the part of the mantle-skirt bounding the two holes is frequently drawn out so as to form a pair of tubes which project from the shell (figs. 130, 141). In such Lamellibranchs as the oysters, scallops, and many others which have the edges of the mantle-skirt quite free, there are numerous tentacles upon those edges. In Anodon these pallial tentacles are confined to a small area surrounding the inferior siphonal notch (fig. 124, (3), *t*).

The centro-dorsal point *a* of the animal of Anodonta (fig. 124, (1)) is called the umbonal area; the great anterior muscular surface *h* is that of the anterior adductor muscle, the posterior similar surface *i* is that of the posterior adductor muscle; the long line of attachment *u* is the simple "pallial muscle,"—a thickened ridge which is seen to run parallel to the margin of the mantle-skirt in this Lamellibranch. In some of the Siphonate Isomya, which are hence termed "Sinupallia," the pallial muscle is not simple but deeply incurved at the posterior region so as to allow of the large pallial siphons being retracted within the shell or expanded at will (fig. 127, and figs. 140, 141).

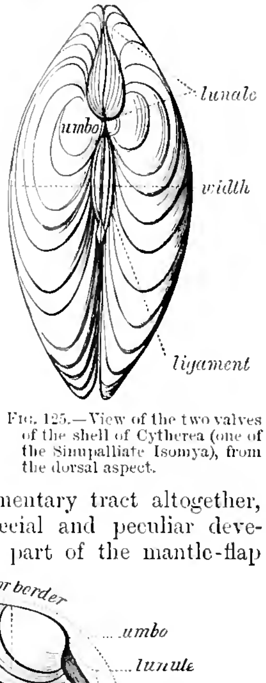

FIG. 125.—View of the two valves of the shell of Cytherea (one of the Sinupalliate Isomya), from the dorsal aspect.

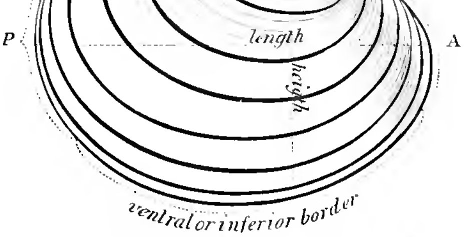

FIG. 126.—Right valve of the same shell from the outer face.

It is the approximate equality in the size of the anterior and posterior adductor muscles which has led to the name Isoyma for the group to which Anodon belongs. The hinder adductor muscle may be considered as representing morphologically the transverse fibres of the root of the foot of Nautilus by which it adheres to its shell (fig. 91, *k*), the annular muscular area of Patella (fig. 27, *c*), and the columella muscle of the Gastropods generally. It is always large in Lamellibranchs, but the anterior adductor may be very small (Heteromya), or absent altogether (Monomya). The anterior adductor muscle is in front of the mouth and alimentary tract altogether, and must be regarded as a special and peculiar development of the median anterior part of the mantle-flap in Heteromya and Isomya. Amongst those Lamellibranchs which have only a posterior adductor (Monomya), it is remarkable that the oyster has been found (by Huxley) to possess, when the young shells and muscles first develop, a well-marked anterior adductor as well as a posterior one. Accordingly there is ground for supposing that the Monomya have been developed from Isomya-like ancestors, and have lost by atrophy their anterior adductor. The single adductor muscle of the Monomya is separated by a difference of fibre into two portions, but neither of these can be regarded as possibly representing the anterior adductor of the other Lamellibranchs. One of these portions is more ligamentous, and serves to keep the two shells constantly attached to one another, whilst the more fleshy portion serves to close the shell rapidly when it has been gaping.

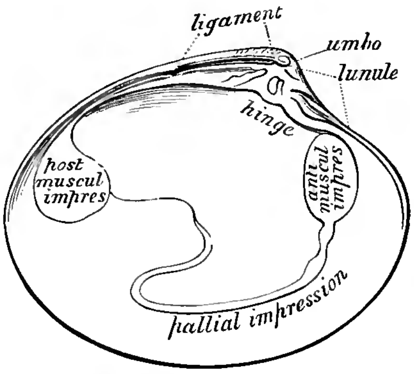

Fig. 127.—Left valve of the same shell from the inner face. (Figs. 125, 126, 127 from Owen.)

In removing the valves of the shell from an Anodon, it is necessary not only to cut through the muscular attachments of the body-wall to the shell but to sever also a strong elastic ligament, or spring resembling india-rubber, joining the two shells about the umbonal area. The shell of Anodon does not present these parts in the most strongly marked condition, and accordingly our figures (figs. 125, 126, 127) represent the valves of the Sinupalliate genus Cytherea. The corresponding parts are recognizable in Anodon. Referring to the figures (125, 126) for an explanation of terms applicable to the parts of the valve and the markings on its inner surface—corresponding to the muscular area which we have already noted on the surface of the animal's body—we must specially note here the position of that denticulated thickening of the dorsal margin of the valve which is called the hinge (fig. 127). By this hinge one valve is closely fitted to the other. Below this hinge each shell becomes concave, above it each shell rises a little to form the umbo, and it is into this ridge-like upgrowth of each valve that the elastic ligament or spring is fixed (fig. 127). As shown in the diagram (fig. 127*) representing a transverse section of the two valves of a Lamellibranch, the two shells form a double lever, of which the toothed-hinged is the fulcrum. The adductor muscles placed in the concavity of the shells act upon the long arms of the lever at a mechanical advantage; their contraction keeps the shells shut, and stretches the ligament or spring *h*. On the other hand, the ligament *h* acts upon the short arm formed by the umbonal ridge of the shells; whenever the adductors relax, the elastic substance of the ligament contracts, and the shells gape. It is on this account that the valves of a dead Lamellibranch always gape; the elastic ligament is no longer counteracted by the effort of the adductors. The state of closure of the valves of the shell is not, therefore, one of rest; when it is at rest—that is, when there is no muscular effort—the valves of a Lamellibranch are slightly gaping, and are closed by the action of the adductors when the animal is disturbed. The ligament is simple in Anodon; in many Lamellibranchs it is separated into two layers, an outer and an inner (thicker and denser). That the condition of gaping of the shell-valves is essential to the life of the Lamellibranch appears from the fact that food to nourish it, water to aerate its blood, and spermatozoa to fertilize its eggs, are all introduced into this gaping chamber by currents of water, which are set going by the highly-developed ctenidia. The current of water enters into the sub-pallial space at the spot marked *e* in fig. 124, (1), and, after passing as far forward as the mouth *w* in fig. 124, (5), takes an outward course and leaves the sub-pallial space by the upper notch *d*. These notches are known in Anodon as the afferent and efferent siphonal notches respectively, and correspond to the long tube-like afferent inferior and efferent superior "siphons" formed by the mantle in many other Lamellibranchs (fig. 130).

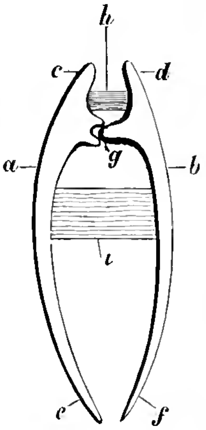

Fig. 127*.—Diagram of a section of a Lamellibranch's shells, ligament, and adductor muscle. *a*, *b*, right and left valves of the shell; *c*, *d*, the umbones or short arms of the lever; *e*, *f*, the long arms of the lever; *g*, the hinge; *h*, the ligament; *i*, the adductor muscle.

Whilst the valves of the shell are equal in Anodon we find in many Lamellibranchs (Ostræa, Chama, Corbula, &c.) one valve larger, and the other smaller and sometimes flat, whilst the larger shell may be fixed to rock or to stones (Ostræa, &c.). A further variation consists in the development of additional shelly plates upon the dorsal line between the two large valves (Pholadidæ). In *Pholas dactylus* we find a pair of umbonal plates, a dors-umbonal plate and a dorsal plate. It is to be remembered that the whole of the cuticular hard product produced on the dorsal surface and on the mantle-flaps is to be regarded as the "shell," of which a median band-like area, the ligament, usually remains uncalcified, so as to result in the production of two valves united by the elastic ligament. But the shelly substance does not always in boring forms adhere to this form after its first growth. In Aspergillum the whole of the tubular mantle area secretes a continuous shelly tube, although in the young condition two valves were present. These are seen (fig. 129) set in the firm substance of the adult tubular shell, which has even replaced the ligament, so that the tube is complete. In Teredo a similar tube is formed as the animal elongates (boring in wood), the original shell-valves not adhering to it but remaining movable and provided with a special muscular apparatus in place of a ligament.

Let us now examine the organs which lie beneath the mantle-skirt of Anodon, and are bathed by the current of water which circulates through it. This can be done by lifting up and throwing back the left half of the mantle-skirt as is represented in fig. 124, (3). We thus expose the plough-like foot (*f*), the two left labial tentacles, and the two left gill-plates or left ctenidium. In fig. 124, (5), one of the labial tentacles *n* is also thrown back so as to show

Fig. 128.

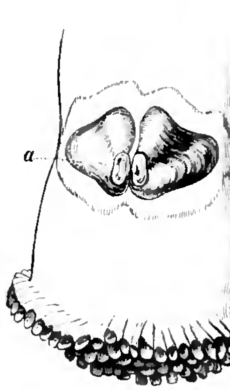

Fig. 129.

Fig. 128.—Shell of *Aspergillum vaginiferum* (from Owen).
Fig. 129.—Shell of *Aspergillum vaginiferum* to show the original valves *a*, now embedded in a continuous calcification of tubular form (from Owen).

the mouth *w*, and the two left gill-plates are reflected so as to show the gill-plates of the right side (*rr*, *rq*) projecting behind the foot, the inner or median plate of each side being united by concrescence to its fellow of the opposite side along a continuous line (*aa*). The left inner gill-plate is also snipped so as to show the subjacent orifices of the left nephridium *x*, and of the genital gland (testis or ovary) *y*. The foot thus exposed in Anodon is a simple muscular tongue-like organ. It can be protruded between the flaps of the mantle (fig. 124, (1), (2)) so as to issue from the shell, and by its action the Anodon can slowly crawl, or burrow in soft mud or sand. It has been supposed that water is taken into the blood-vessels of the Anodon through pores in the foot, and in spite of opposition this view is still maintained (Griesbach, **47**). In fig. 124, (2) the letters *ab*, *ac*, *ad*, point to three pit-like depressions, supposed by Griesbach to be pores leading into the blood-system. According to Carrière (**48**) these pits are nothing but irregularities of the surface; in some cases they are the entrances to ramified glands. Other Lamellibranchs may have a larger foot relatively than has Anodon. In Arca it has a sole-like surface. In Arca too and many others it carries a byssus-forming gland and a byssus-cementing gland. In the Cockles, in Cardium, and in Trigonia, it is capable of a sudden stroke, which causes the animal to jump when out of the water, in the latter genus to a height of four feet. In Mytilus the foot is reduced to little more than a tubercle carrying the apertures of these glands. In the Oyster it is absent altogether.

FIG 130.—*Psammobia florida*, right side, showing expanded foot *e*, and *g* incurrent and *g'* excurrent siphons (from Owen).

The labial tentacles of Anodon (*n*, *o* in fig. 124, (3), (5)) are highly vascular flat processes richly supplied with nerves. The left anterior tentacle (seen in the figure) is joined at its base in front of the mouth (*w*) to the right anterior tentacle, and similarly the left (*o*) and right posterior tentacles are joined behind the mouth. Those of Arca (*i*, *k* in fig. 132) show this relation to the mouth (*a*). These organs are characteristic of all Lamellibranchs; they do not vary except in size, being sometimes drawn out to streamer-like dimensions. Their appearance and position suggest that they are in some way related morphologically to the gill-plates, the anterior labial tentacle being a continuation of the outer gill-plate, and the posterior a continuation of the inner gill-plate. There is no embryological evidence to support this suggested connexion, and, as will appear immediately, the history of the gill-plates in various forms of Lamellibranchs does not directly favour it. Yet it is very probable that the labial tentacles and gill-plates are modifications of a double horseshoe-shaped area of ciliated filamentous processes which existed in ancestral Mollusca much as in Phoronis and the Polyzoa, and is to be compared with the continuous præ- and post-oral ciliated band of the Echinid larva Pluteus and of Tornaria (**49**).

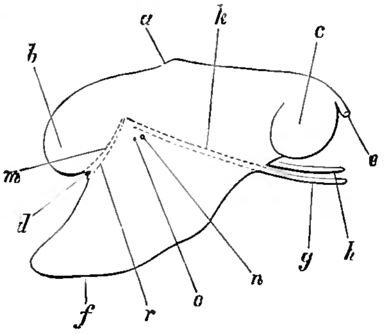

FIG. 131.—Diagram of a view from the left side of the animal of *Anodonta cygnæa*, from which the mantle-skirt, the labial tentacles, and the gill-filaments have been entirely removed so as to show the relations of the axis of the gill-plumes or ctenidia *g*, *h*. *a*, centro-dorsal area; *b*, anterior adductor muscle; *c*, posterior adductor muscle; *d*, mouth; *e*, anus; *f*, foot; *g*, free portion of the axis of left ctenidium; *h*, axis of right ctenidium; *k*, portion of the axis of the left ctenidium which is fused with the base of the foot, the two dotted lines indicating the origins of the two rows of gill-filaments; *m*, line of origin of the anterior labial tentacle; *n*, nephridial aperture; *o*, genital aperture; *r*, line of origin of the posterior labial tentacle. (Original.)

The gill-plates have a structure very different from that of the labial tentacles, and one which in Anodon is singularly complicated as compared with the condition presented by these organs in some other Lamellibranchs, and with what must have been their original condition in the ancestors of the whole series of living Lamellibranchia. The phenomenon of "concrescence" which we have already had to note as showing itself so importantly in regard to the free edges of the mantle-skirt and the formation of the siphons, is what, above all things, has complicated the structure of the Lamellibranch ctenidium. Our present knowledge of the interesting series of modifications through which the Lamellibranch gill-plates have developed to their most complicated form is due to R. Holman Peck (**50**) and to Mitsukuri (**51**). The Molluscan ctenidium is typically, as shown in fig. 2, a plume-like structure, consisting of a vascular axis, on each side of which is set a row of numerous lamelliform or filamentous processes. These processes are hollow, and receive the venous blood from, and return it again aerated into, the hollow axis, in which an afferent and an efferent blood-vessel may be differentiated. In the genus Nucula (fig. 134), one of the Arcaceæ, we have an example of a Lamellibranch retaining this plume-like form of gill. In other Arcaceæ (*e.g.*, Arca and Pectunculus) the lateral processes which are set on the axis of the ctenidium are not lamellæ, but are slightly-flattened, very long tubes or hollow filaments. These filaments are so fine and are set so closely together that they appear to form a continuous membrane until examined with a lens. The microscope shows that the neighbouring filaments are held together by patches of cilia, called "ciliated junctions," which interlock with one another just as two brushes may be made to do. In fig. 133, A a portion of four filaments of a ctenidium of the Sea-Mussel (Mytilus) is represented, having precisely the same structure as those of Arca. The filaments of the gill (ctenidium) of Mytilus and Arca thus form two closely set rows which depend from the axis of the gill like two parallel plates. Further, their structure is profoundly modified by the curious condition of the free ends of the depending filaments. These are actually reflected at a sharp angle—

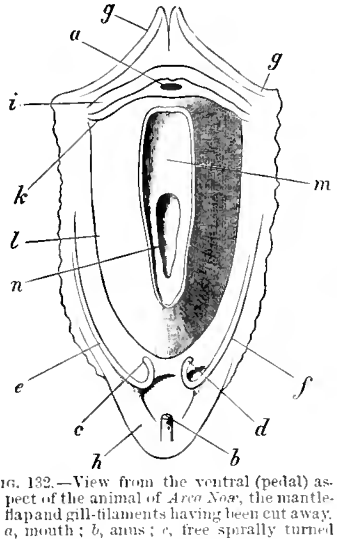

FIG. 132.—View from the ventral (pedal) aspect of the animal of *Arca Noæ*, the mantle-flap and gill-filaments having been cut away. *a*, mouth; *b*, anus; *c*, free spirally turned extremity of the gill-axis or ctenidial axis of the right side; *d*, do. of the left side; *e*, *f*, anterior portions of these axes fused by concrescence to the wall of the body; *g*, anterior adductor muscle; *h*, posterior adductor; *i*, anterior labial tentacle; *k*, posterior labial tentacle; *l*, base line of the foot; *m*, sole of the foot; *n*, callosity. (Original.)

doubled on themselves in fact—and thus form an additional row of filaments (see fig. 133, B). Consequently, each primitive filament has a descending and an ascending ramus, and instead of each row forming a simple plate, the plate is double, consisting of a descending and an ascending lamella. As the axis of the ctenidium lies by the side of the body, and is very frequently connate with the body, as so often happens in Gastropods also, we find it convenient to speak of the two plate-like structures formed on each ctenidial axis as the outer and the inner gill-plate; each of these is composed of two lamellæ, an outer (the reflected) and an adaxial in the case of the outer gill-plate, and an adaxial and an inner (the reflected) in the case of the inner gill-plate. This is the condition seen in Arca and Mytilus, the so-called plates dividing upon the slightest touch into their constituent filaments, which are but loosely conjoined by their "ciliated junctions." Complications follow upon this in other forms. Even in Mytilus and Arca a connexion is here and there formed between the ascending and descending rami of a filament by hollow extensible outgrowths called "interlamellar junctions" (*il.j* in B, fig. 133). Nevertheless the filament is a complete tube formed of chitonous substance and clothed externally by ciliated epithelium, internally by endothelium and lacunar tissue—a form of connective tissue—as shown in fig. 133, C. Now let us suppose, as happens in the genus Dreissena—a genus not far removed from Mytilus—that the ciliated inter-filamentar junctions (fig. 136) give place to solid permanent inter-filamentar junctions, so that the filaments are converted, as it were, into a trellis-work. Then let us suppose that the inter-lamellar junctions which we have already noted in Mytilus become very numerous, large, and irregular; by them the two trellis-works of filaments would be united so as to leave only a sponge-like set of spaces between them. Within the trabeculæ of the sponge-work blood circulates, and between the trabeculæ the water passes, having entered by the apertures left in the trellis-work formed by the united gill-filaments (fig. 138, A, B). The larger the intra-lamellar spongy growth becomes, the more do the original gill-filaments lose the character of blood-holding tubes and tend to become dense elastic rods for the simple purpose of supporting the spongy growth. This is seen both in the section of Dreissena gill (fig. 136) and in those of Anodon (fig. 137, A, B, C). In the drawing of Dreissena the individual filaments *f, f, f* are cut across in one lamella at the horizon of an inter-filamentar junction, in the other (lower in the figure) at a point where they are free. The chitonous substance *ch* is observed to be greatly thickened as compared with what it is in fig. 133, C, tending in fact to obliterate altogether the lumen of the filament. And in Anodon (fig. 137, C) this obliteration is effected. In Anodon, besides being thickened, the skeletal substance of the filament develops a specially dense rod-like body on each side of each filament. Although the structure of the ctenidium is thus highly complicated in Anodon, it is yet more so in some of the Siphonate genera of Lamellibranchs. The filaments take on a secondary grouping, the surface of the lamella being thrown into a series of half-cylindrical ridges, each consisting of ten or twenty filaments; a filament

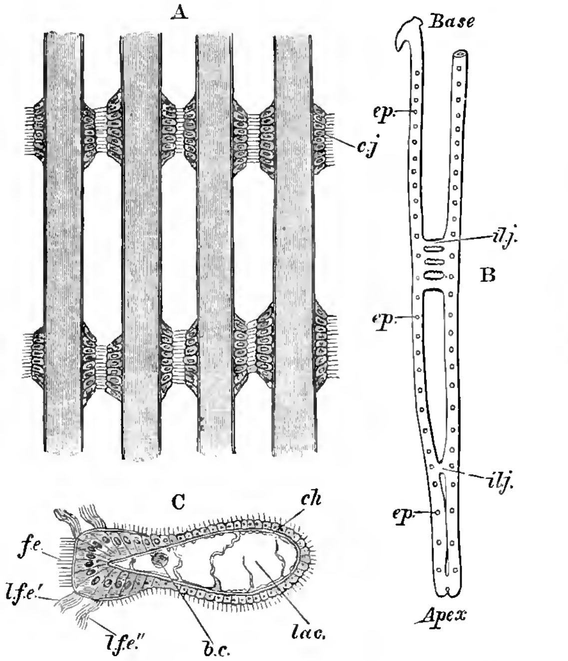

Fig. 133.—Filaments of the ctenidium of *Mytilus edulis* (after Holman Peck). A. Part of four filaments seen from the outer face in order to show the ciliated junctions *c.j.* B. Diagram of the posterior face of a single complete filament with descending ramus and ascending ramus ending in a hook-like process. *ep.*, *ep.*, the ciliated junctions; *il.j.*, inter-lamellar junction. C. Transverse section of a filament taken so as to cut neither a ciliated junction nor an inter-lamellar junction. *f.e.*, frontal epithelium; *l.f.e'.*, *l.f.e''.*, the two rows of latero-frontal epithelial cells with long cilia; *ch*, chitonous tubular lining of the filament; *lac.*, blood lacuna traversed by a few processes of connective tissue cells; *b.c.*, blood-corpuscle.

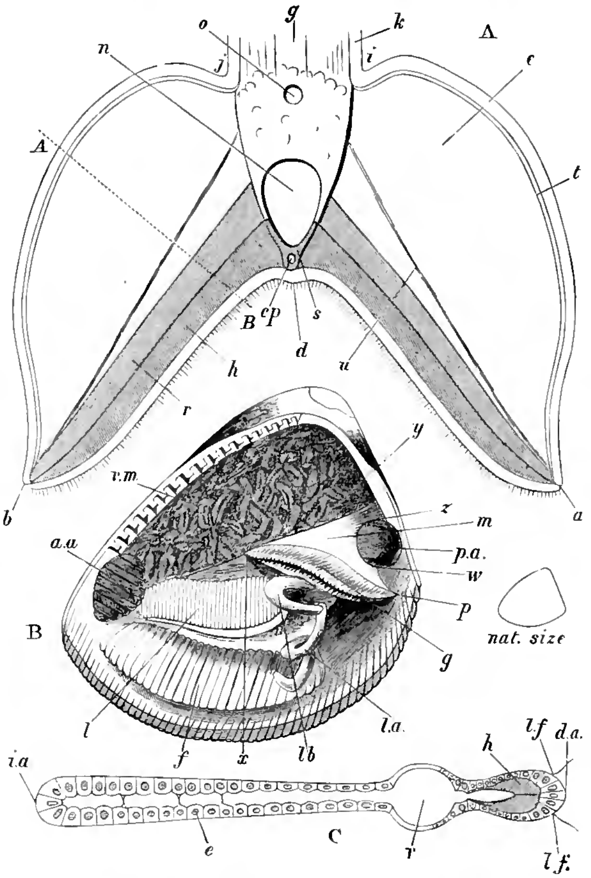

Fig. 134.—Structure of the ctenidia of Nucula (after Mitsukuri); see also fig. 2. A. Section across the axis of a ctenidium with a pair of plates—flattened and shortened filaments—attached. *i, j, k, g* are placed on or near the membrane which attaches the axis of the ctenidium to the side of the body; *a, b*, free extremities of the plates (filaments); *d*, mid-line of the inferior border; *e*, surface of the plate; *t*, its upper border; *h*, chitonous lining of the plate; *r*, dilated blood-space; *u*, fibrous tract; *o*, upper blood-vessel of the axis; *n*, lower blood-vessel of the axis; *s*, chitonous framework of the axis; *cp*, canal in the same; *A, B*, line along which the cross-section C of the plate is taken. B. Animal of a male *Nucula proxima*, Say, as seen when the left valve of the shell and the left half of the mantle-skirt are removed. *a.a.*, anterior adductor muscle; *p.a.*, posterior adductor muscle; *v.m*, visceral mass; *f*, foot; *g*, gill; *l*, labial tentacle; *l.a.*, filamentous appendage of the labial tentacle; *lb*, hood-like appendage of the labial tentacle; *m*, membrane suspending the gill and attached to the body along the line *x, y, z, w*; *p*, posterior end of the gill (ctenidium). C. Section across one of the gill-plates (*A, B*, in A) comparable with fig. 133, C. *i.a.*, outer border; *d.a.*, axial border; *l.f.*, latero-frontal epithelium; *e*, epithelium of general surface; *r*, dilated blood-space; *h*, chitonous lining (compare A).

of much greater strength and thickness than the others may be placed between each pair of groups. In Anodon, as in many other Lamellibranchs, the ova and hatched embryos are carried for a time in the ctenidia or gill apparatus, and in this particular case the space between the two lamellæ of the outer gill-plate is that which serves to receive the ova (fig. 137, A). The young are nourished by a substance formed by the cells which cover the spongy inter-lamellar outgrowths.

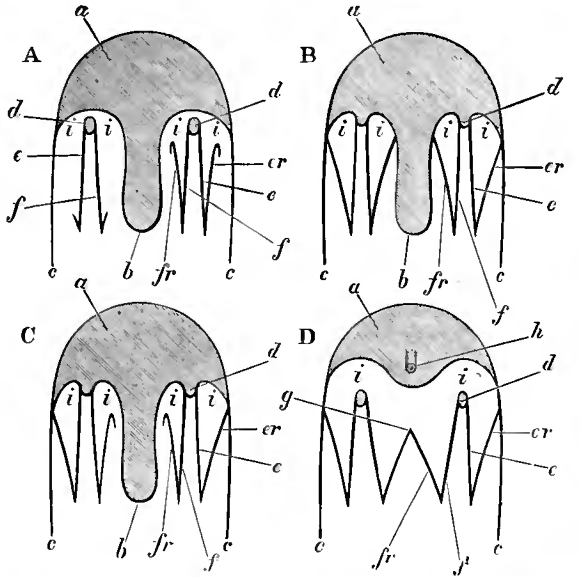

FIG. 135.—Diagrams of transverse sections of a Lamellibranch to show the adhesion, by concrescence, of the gill-lamellæ to the mantle-flaps, to the foot, and to one another. A shows two conditions with free gill-axis; B, condition at foremost region in Anodon; C, hind region of foot in Anodon; D, region altogether posterior to the foot in Anodon. *a*, visceral mass; *b*, foot; *c*, mantle flap; *d*, axis of gill or ctenidium; *e*, adaxial lamella of outer gill-plate; *er*, reflected lamella of outer gill-plate; *f*, adaxial lamella of inner gill-plate; *fr*, reflected lamella of inner gill-plate; *g*, line of concrescence of the reflected lamellæ of the two inner gill-plates; *h*, rectum; *i*, supra-branchial space of the sub-pallial chamber. (Original.)

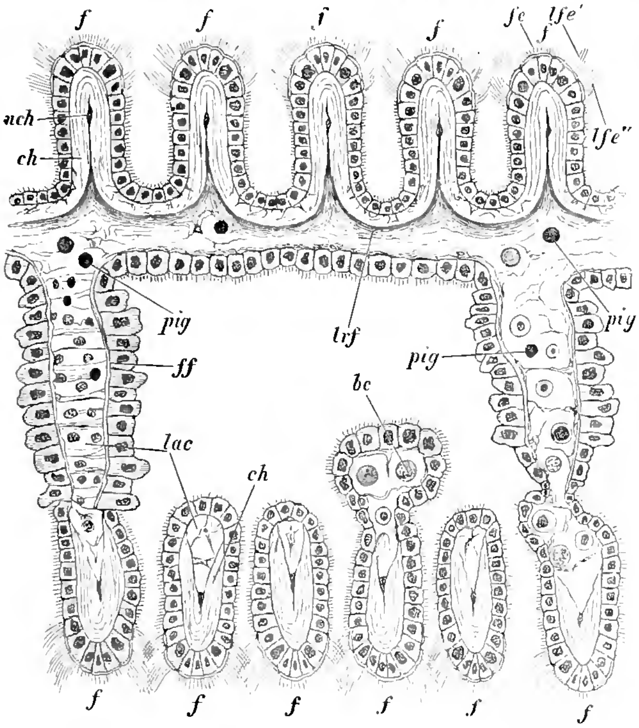

FIG. 136.—Transverse section of the outer gill-plate of *Dreissena polymorpha* (after Holman Peck). *f*, constituent gill-filaments; *ff*, fibrous sub-epidermic tissue; *ch*, chitonous substance of the filaments; *nch*, cells related to the chitonous substance; *lac*, lacunar tissue; *pig*, pigment-cells; *bc*, blood-corpuscles; *fe*, frontal epithelium; *lfe'*, *lfe''*, two rows of latero-frontal epithelial cells with long cilia; *lrf*, fibrous, possibly muscular, substance of the inter-filamenter junctions.

There are certain other points in the modification of the typical ctenidium which must be noted in order to understand the ctenidium of Anodon. The axis of each ctenidium, right and left, starts from a point well forward near the labial tentacles, but it is at first only a ridge, and does not project as a free cylindrical axis until the back part of the foot is reached. This is difficult to see at all in Anodon, but if the mantle-skirt be entirely cleared away, and if the dependent lamellæ which spring from the ctenidial axis be carefully cropped away so as to leave the axis itself intact, we obtain the form shown in fig. 131, where *g* and *h* are respectively the left and the right ctenidial axes projecting freely beyond the body. In Arca this can be seen with far less trouble, for the filaments are more easily removed than are the consolidated lamellæ formed by the filaments of Anodon, and in Arca the free axes of the ctenidia are large and firm in texture (fig. 132, *c*, *d*).

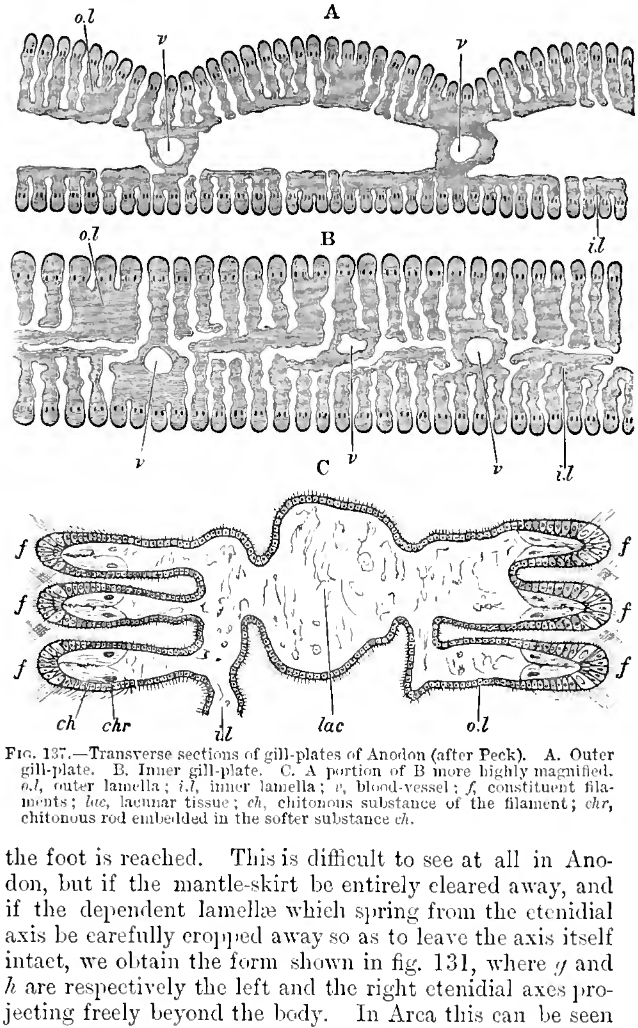

FIG. 137.—Transverse sections of gill-plates of Anodon (after Peck). A. Outer gill-plate. B. Inner gill-plate. C. A portion of B more highly magnified. *o.l*, outer lamella; *i.l*, inner lamella; *v*, blood-vessel; *f*, constituent filaments; *lac*, lacunar tissue; *ch*, chitonous substance of the filament; *chr*, chitonous rod embedded in the softer substance *ch*.

If we were to make a vertical section across the long axis of a Lamellibranch which had the axis of its ctenidium free from its origin onwards, we should find such relations as are shown in the diagram fig. 135, A. The gill axis *d* is seen lying in the sub-pallial chamber between the foot *b* and the mantle *c*. From it depend the gill-filaments or lamellæ—formed by united filaments—drawn as black lines *f*. On the left side these lamellæ are represented as having only a small reflected growth, on the right side the reflected ramus or lamella is complete (*fr* and *er*). The actual condition in Anodon at the region where the gills commence anteriorly is shown in fig. 135, B. The axis of the ctenidium is seen to be adherent to, or fused by concrescence with, the body-wall, and moreover on each side the outer lamella of the outer gill-plate is fused to the mantle, whilst the inner lamella of the inner gill-plate is fused to the foot. If we pass a little backwards and take another section nearer the hinder margin of the foot, we get the arrangement shown diagrammatically in fig. 135, C, and more correctly in fig. 142. In this region the inner lamellæ of the inner gill-plates are no longer affixed to the foot. Passing still further back behind the foot, we find in Anodon the condition shown in the section D, fig. 135. The axes *i* are now free; the outer lamellæ of the outer gill-plates (*er*) still adhere by concrescence to the mantle-skirt, whilst the inner lamellæ of the inner gill-plates meet one another and fuse by concrescence at *g*. In the lateral view of the animal with reflected mantle-skirt and gill-plates, the line of concrescence of the inner lamellæ of the inner gill-plates is readily seen; it is marked *aa* in fig. 124, (5). In the same figure the free part of the inner lamella of the inner gill-plate resting on the foot is marked *z*, whilst the attached part—the most anterior—has been snipped with scissors so as to show the genital and nephridial apertures *x* and *y*. The concrescence, then, of the free edge of the reflected lamellæ of the gill-plates of Anodon is very extensive. It is important, because such a concrescence is by no means universal, and does not occur, for example, in Mytilus or in Arca; further, because when its occurrence is once appreciated, the reduction of the gill-plates of Anodon to the plume-type of the simplest ctenidium presents no difficulty; and, lastly, it has importance in reference to its physiological significance. The mechanical result of the concrescence of the outer lamellæ to the mantle-flap, and of the inner lamellæ to one another as shown in section D, fig. 135, is that the sub-pallial space is divided into two spaces by a horizontal septum. The upper space (*i*) communicates with the outer world by the excurrent or superior siphonal notch of the mantle (fig. 124, *d*); the lower space communicates by the lower siphonal notch (*e* in fig. 124). The only communication between the two spaces, excepting through the trellis-work of the gill-plates, is by the slit (*z* in fig. 124, (5)) left by the non-concrescence of a part of the inner lamella of the inner gill-plate with the foot. A probe (*g*) is introduced through this slit-like passage, and it is seen to pass out by the excurrent siphonal notch. It is through this passage, or indirectly through the pores of the gill-plates, that the water introduced into the lower sub-pallial space must pass on its way to the excurrent siphonal notch. Such a subdivision of the pallial chamber, and direction of the currents set up within it do not exist in a number of Lamellibranchs which have the gill-lamellæ comparatively free (Mytilus, Arca, Trigonia, &c.), and it is in these forms that there is least modification by concrescence of the primary filamentous elements of the lamellæ. Probably the gill-structure of Lamellibranchs will ultimately furnish some classificatory characters of value when they have been thoroughly investigated throughout the class.

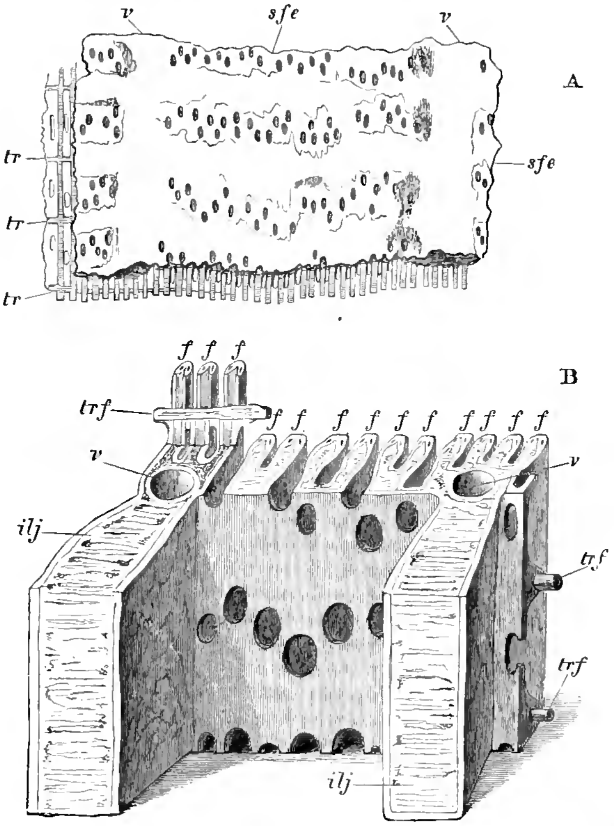

FIG. 138.—Gill-lamellæ of Anodon (after Peck). A. Fragment of the outer lamella of an inner gill-plate torn from the connected inner lamella, the sub-filamentar tissue also partly cut away round the edges so as to expose the filaments, their transverse junctions *tr*, and the "windows" left in the lattice-work; *sfe*, internal surface of the lamella; *v*, vessel. B. Diagram of a block cut from the outer lamella of the outer gill-plate and seen from the inter-lamellar surface (after Peck). *f*, constituent filaments; *trf*, fibrous tissue of the transverse inter-filamentar junctions; *v*, blood-vessel; *ilj*, inter-lamellar junction. The series of oval holes on the back of the lamella are the water-pores which open between the filaments in irregular rows separated horizontally by the transverse inter-filamentar junctions.

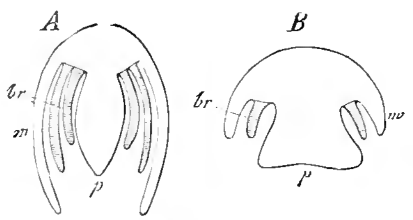

FIG. 139.—Transverse sections of *A*, a Lamellibranch, and *B*, an Isopleurous Gastropod (Chiton), to show the relations of *p*, the foot; *br*, the branchiæ; and *m*, the mantle. (From Gegenbaur.)

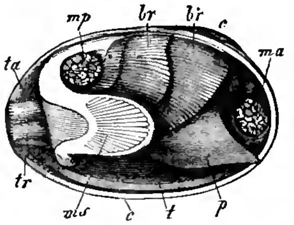

FIG. 140.—Lateral view of a Mactra, the right valve of the shell and right mantle-flap removed, and the siphons retracted. *br*, *br′*, outer and inner gill-plates; *t*, labial tentacle; *ta*, *tr*, upper and lower siphons; *ms*, siphonal muscle of the mantle-flap; *ma*, anterior adductor muscle; *mp*, posterior adductor muscle; *p*, foot; *c*, umbo. (From Gegenbaur.)

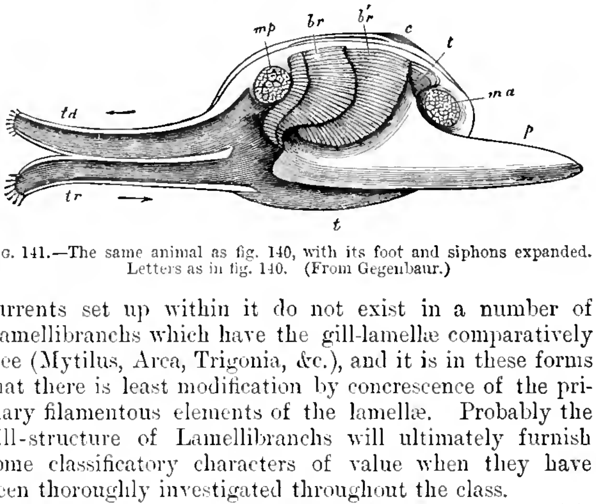

FIG. 141.—The same animal as fig. 140, with its foot and siphons expanded. Letters as in fig. 140. (From Gegenbaur.)

The alimentary canal of Anodon is shown in fig. 124, (4). The mouth is placed between the anterior adductor and the foot; the anus opens on a median papilla overlying the posterior adductor, and discharges into the superior pallial chamber along which the excurrent stream passes. The coil of the intestine in Anodon is similar to that of other Lamellibranchs, but the crystalline style and its diverticulum are not present here. The rectum traverses the pericardium, and has the ventricle of the heart wrapped, as it were, around it. This is not an unusual arrangement in Lamellibranchs, and a similar disposition occurs in some Gastropoda (Haliotis). A pair of ducts (*ai*) lead from the first enlargement of the alimentary tract called stomach into a pair of large digestive glands, the so-called liver, the branches of which are closely packed in this region (*af*). The food of the Anodon, as of other Lamellibranchs, consists of microscopic animal and vegetable organisms, which are brought to the mouth by the stream which sets into the sub-pallial chamber at the lower siphonal notch (*e* in fig. 124). Probably a straining of water from solid particles is effected by the lattice-work of the ctenidia or gill-plates.

The heart of Anodon consists of a median ventricle embracing the rectum (fig. 143, A), and giving off an anterior and a posterior artery, and of two auricles which open into the ventricle by orifices protected by valves.

The blood is colourless, and has colourless amœboid corpuscles floating in it. In two Lamellibranchs, *Solen* (*Ceratisolen*) *legumen* and *Arca Noæ*, the blood is crimson, owing to the presence of corpuscles impregnated with hæmoglobin (Lankester, **31**). In Anodon the blood is driven by the ventricle through the arteries into vessel-like spaces, which soon become irregular lacunæ surrounding the viscera, but in parts—*e.g.*, the labial tentacles and walls of the gut—very fine vessels with endothelial cell-lining are found. The blood makes its way by large veins to a venous sinus which lies in the middle line below the heart, having the paired renal organs (nephridia) placed between it and that organ. Hence it passes through the vessels of the glandular walls of the nephridia right and left into the gill-lamellæ, whence it returns through many openings into the widely-stretched auricles. A great deal more precision has been given to accounts of the structure of arteries, veins, and capillaries in Anodon than the facts warrant. The course of the blood-stream can only be somewhat vaguely inferred except in its largest outlines. Distinct arterial and venous channels cannot be distinguished in the gill-lamellæ, in spite of what Langer (**52**) has written on the subject, though it is highly probable that there is some kind of circulation in the gills. In the filaments of the gill of Mytilus the tubular cavity is divided by a more or less complete fibrous septum into two channels, presumably for an ascending and a descending blood-current. The ventricle and auricles of Anodon lie in a pericardium which is clothed with a pavement endothelium (*d*, fig. 143). Veins are said by Keber and others to open anteriorly into it, but this appears to be an error. It does not contain blood or communicate directly with the blood-system; this isolation of the pericardium we have noted already in Gastropods and Cephalopods. A good case for the examination of the question as to whether blood enters the pericardium of Lamellibranchs, or escapes from the foot, or by the renal organs when the animal suddenly contracts, is furnished by the *Solen legumen*, which has red blood-corpuscles. According to observations made by Penrose (**53**) on an uninjured *Solen legumen*, no red corpuscles are to be seen in the pericardial space, although the heart is filled with them, and no such corpuscles are ever discharged by the animal when it is irritated.

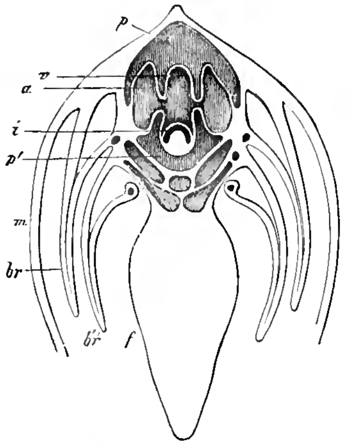

Fig. 142.—Vertical section through an Anodonta, about the mid-region of the foot. *m*, mantle-flap; *br*, outer, *b′r′*, inner gill-plate—each composed of two lamellæ; *f*, foot; *v*, ventricle of the heart; *a*, auricle; *p*, *p′*, pericardial cavity; *i*, intestine.

The pair of nephridia of Anodon, called in Lamellibranchs the organ of Bojanus, lie below the membranous floor of the pericardium, and open into it by two well-marked apertures (*e* and *f* in fig. 143). Each nephridium, after being bent upon itself as shown in fig. 143, C, D, opens to the exterior by a pore placed at the point marked *x* in fig. 124, (5), (6). It is no doubt possible, as in the Gastropoda and Cephalopoda, for water to enter from the exterior by the nephridia into the pericardium, but that it ever does so is as yet not proved. What is certain from the set of the ciliary currents is that liquid generally passes out of the pericardium by the nephridia. One half of each nephridium is of a dark-green colour and glandular (*h* in fig. 143). This opens into the reflected portion which overlies it as shown in the diagram fig. 143, D, *i*; the latter has non-glandular walls, and opens by the pore *k* to the exterior. The nephridia may be more ramified in other Lamellibranchs than they are in Anodon. In some they are difficult to discover. That of the common oyster has recently (1882) been detected by Hoek (**54**). Each nephridium in the oyster is a pyriform sac, which communicates by a narrow canal with the urino-genital groove placed to the front of the great adductor muscle; by a second narrow canal it communicates with the pericardium. From all parts of the pyriform sac narrow stalk-like tubes are given off, ending in abundant widely-spread branching glandular cæca, which form the essential renal secreting apparatus. The genital duct opens by a pore into the urino-genital groove of the oyster (the same arrangement being repeated on each side of the body) close to but distinct from the aperture of the nephridial canal. Hence, except for the formation of a urino-genital groove, the apertures are placed as they are in Anodon. Previously to Hoek's discovery a brown-coloured investment of the auricles of the heart of the oyster had been supposed to represent the nephridia in a rudimentary state. This investment, which occurs also in Mytilus but not in Anodon, may possibly consist of secreting cells, and may be comparable to the pericardial accessory glandular growths of Cephalopoda.

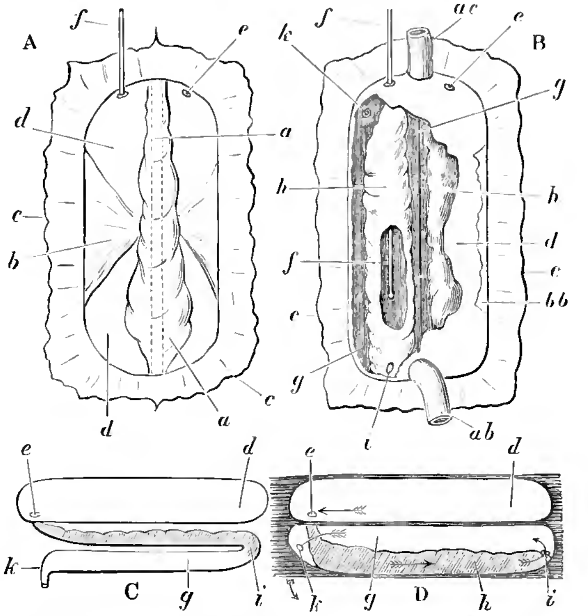

Fig. 143.—Diagrams showing the relations of pericardium and nephridia in a Lamellibranch such as Anodon. A. Pericardium opened dorsally so as to expose the heart and the floor of the pericardial chamber *d*. B. Heart removed and floor of the pericardium cut away on the left side so as to open the non-glandular sac of the nephridium, exposing the glandular sac *b*, which is also cut into so as to show the probe *f*. C. Ideal pericardium and nephridium viewed laterally. D. Lateral view showing the actual relation of the glandular and non-glandular sacs of the nephridium. The arrows indicate the course of fluid from the pericardium outwards. *a*, ventricle of the heart; *b*, auricle; *bb*, cut remnant of the auricle; *c*, dorsal wall of the pericardium cut and reflected; *e*, reno-pericardial orifice; *f*, probe introduced into the left reno-pericardial orifice; *g*, non-glandular sac of the left nephridium; *h*, glandular sac of the left nephridium; *i*, pore leading from the glandular into the non-glandular sac of the left nephridium; *k*, pore leading from the non-glandular sac to the exterior; *ac*, anterior, *ab*, posterior, cut remnants of the intestine and ventricle.

Nervous System and Sense-organs.—In Anodon there are three well-developed pairs of nerve-ganglia (fig. 144, B and fig. 124, (6)). An anterior pair, lying one on each side of the mouth (fig. 144, B, *a*) and connected in front of it by a commissure, are the representatives of the cerebral, pleural, and visceral ganglia of the typical Mollusc, which are not here differentiated as they are in Gastropods (compare, however, fig. 67). A pair placed close together in the foot (fig. 144, B, *b*, and fig. 124, (6), *ax*) are the typical pedal ganglia; they are joined to the cerebro-pleuro-visceral ganglia by connectives.

Posteriorly beneath the posterior adductors, and covered only by a thin layer of elongated epidermal cells, are the olfactory ganglia, their epidermal clothing constituting the pair of osphradia, which are thus seen in Lamellibranchs to occupy their typical position and to have the typical innervation,—the nerve to each osphradium being given off by the visceral ganglion—that is to say, by the undifferentiated cerebro-pleuro-visceral ganglion of its proper side. This identification of the posterior ganglion-pair of Lamellibranchs is due to Spengel (**11**). Other anatomists have considered this ganglion-pair as corresponding to either the pleural or the visceral of Gastropoda, or to both, and very usually it is termed "the parieto-splanchnic" (Huxley).

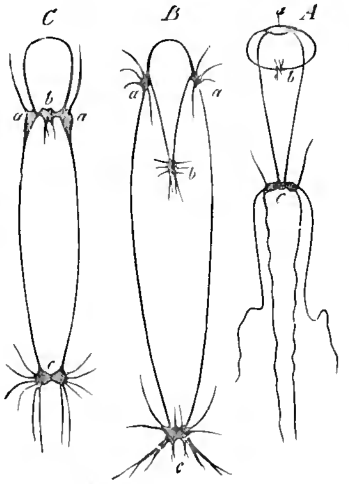

Fig. 144.—Nerve-ganglia and cords of three Lamellibranchs (from Gegenbaur): *A*, of Teredo; *B*, of Anodonta; *C*, of Pecten. *a*, cerebral ganglion-pair (=cerebro-pleuro-visceral); *b*, pedal ganglion-pair; *c*, olfactory (osphradial) ganglion-pair.

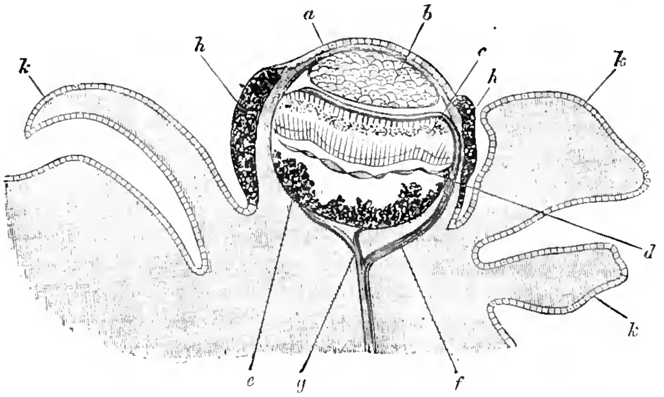

Fig. 145.—Pallial eye of Spondylus (from Hickson). *a*, præ-corneal epithelium; *b*, cellular lens; *c*, retinal body; *d*, tapetum; *e*, pigment; *f*, retinal nerve; *g*, complementary nerve; *h*, epithelial cells filled with pigment; *k*, tentacle

The sense-organs of Anodon other than the osphradia consist of a pair of otocysts attached to the pedal ganglia (fig. 124, (6), *ay*). The otocysts of Cyclas are peculiarly favourable for study on account of the transparency of the small foot in which they lie, and may be taken as typical of those of Lamellibranchs generally. The structure of one is exhibited in fig. 146. A single otolith is present as in the veliger embryos of Opisthobranchia. In adult Gastropoda there are frequently a large number of rod-like otoliths instead of one.

Anodon has no eyes of any sort, and the tentacles on the mantle edge are limited to its posterior border. This deficiency is very usual in the class; at the same time, many Lamellibranchs have tentacles on the edge of the mantle supplied by a pair of large well-developed nerves, which are given off from the cerebro-pleuro-visceral ganglion-pair, and very frequently some of these tentacles have undergone a special metamorphosis converting them into highly-organized eyes. Such eyes on the mantle-edge are found in Pecten, Spondylus, Lima, Ostrea (?), Pinna, Pectunculus, Modiola, Mytilus (?), Cardium, Tellina, Mactra, Venus, Solen, Pholas, and Galeomma. They are totally distinct from the cephalic eyes of typical Mollusca, and have a different structure and historical development. They have not originated as pits but as tentacles. They agree with the dorsal eyes of Onchidium (Pulmonata) in the curious fact that the optic nerve penetrates the capsule of the eye and passes in front of the retinal body (fig. 145), so that its fibres join the anterior faces of the nerve-end cells as in Vertebrates, instead of their posterior faces as in the cephalic eyes of Mollusca and Arthropoda; moreover, the lens is not a cuticular product but a cellular structure, which, again, is a feature of agreement with the Vertebrate eye. It must, however, be distinctly borne in mind that there is a fundamental difference between the eye of Vertebrates and of all other groups in the fact that in the Vertebrata the retinal body is itself a part of the central nervous system, and not a separate modification of the epidermis—myelonic as opposed to epidermic. The structure of the reputed eyes of several of the above-named genera has not been carefully examined. In Pecten and Spondylus, however, they have been fully studied (see fig. 145, and explanation).

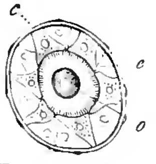

Fig. 146.—Otocyst of Cyclas (from Gegenbaur). *c*, capsule; *e*, ciliated cells lining the same; *o*, otolith.

The gonads of Anodon are placed in distinct male and female individuals. In some Lamellibranchs—for instance, the European Oyster and the *Pisidium pusillum*—the sexes are united in the same individual; but here, as in most hermaphrodite animals, the two sexual elements are not ripe in the same individual at the same moment. It has been conclusively shown that the *Ostrea edulis* does not fertilize itself. The American Oyster (*O. virginiana*) and the Portuguese Oyster (*O. angulata*) have the sexes separate, and fertilization is effected in the open water after the discharge of the ova and the spermatozoa from the females and males respectively. In the *Ostrea edulis* fertilization of the eggs is effected at the moment of their escape from the uro-genital groove, or even before, by means of spermatozoa drawn into the sub-pallial chamber by the incurrent ciliary stream, and the embryos pass through the early stages of development whilst entangled between the gill-lamellæ of the female parent (fig. 6). In Anodon the eggs pass into the space between the two lamellæ of the outer gill-plate, and are there fertilized, and advance whilst still in this position to the glochidium phase of development (fig. 147). They may be found here in thousands in the summer and autumn months. The gonads themselves are extremely simple arborescent glands which open to the exterior by two simple ducts, one right and one

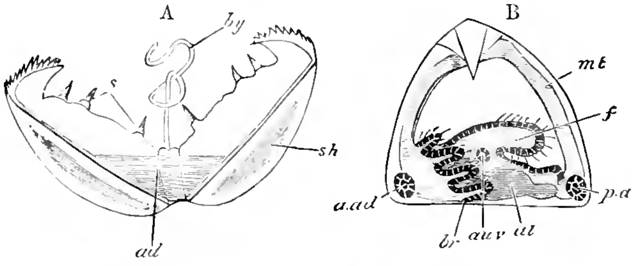

Fig. 147.—Two stages in the development of Anodonta (from Balfour). Both figures represent the glochidium stage. A, when free swimming, shows the two dentigerous valves widely open. B, a later stage, after fixture to the fin of a fish. *sh*, shell; *ad*, adductor muscle; *s*, teeth of the shell; *by*, byssus; *a.ad*, anterior adductor; *p.ad*, posterior adductor; *mt*, mantle-flap; *f*, foot; *br*, branchial filaments; *au.v*, otocyst; *al*, alimentary canal.

left, continuous with the wall of the tubular branches of the gland (fig. 124, (5), (6), *y*). In no Lamellibranch is there a divergence from this structure, excepting that in some (Ostrea) the contiguous nephridial and the genital aperture are sunk in a urino-genital groove, which in other cases (Spondylus?) may partially close up so as to constitute a single pore for the nephridial and genital ducts. No accessory genital glands are present.

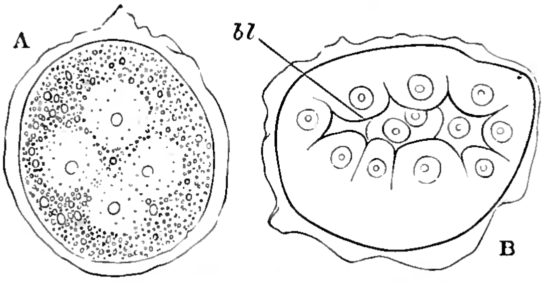

Fig. 148.—Embryos of *Pisidium pusillum* (after Lankester). A. Only four embryonic cells are present, still enclosed in the egg envelope. B. The cells have multiplied and commenced to invaginate, forming a blastopore or orifice of invagination, *bl*.

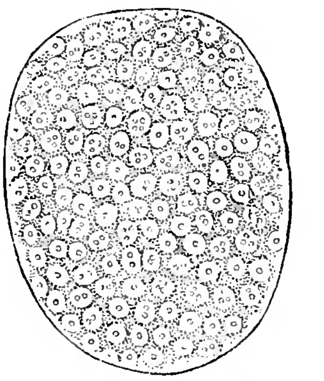

Fig. 149.

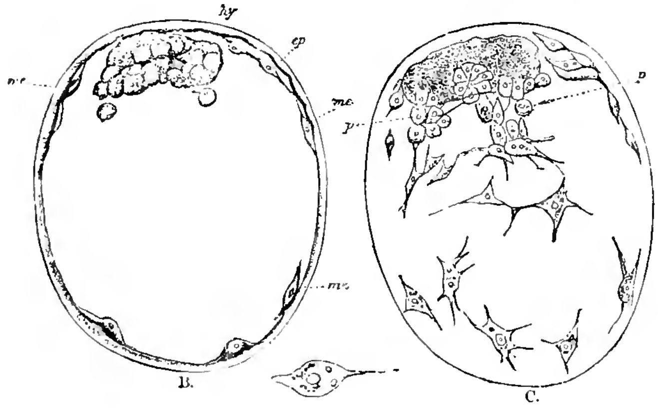

Fig. 150.

Fig. 149.—Embryo of *Pisidium pusillum* in the diblastula stage, surface view (after Lankester). The embryo has increased in size by accumulation of liquid between the outer and the invaginated cells. The blastopore has closed.

Fig. 150.—B. Same embryo as fig. 149, in optical median section, showing the invaginated cells *hy* which form the arch-enteron, and the mesoblastic cells *me* which are budded off from the surface of the mass *hy*, and apply themselves to the inner surface of the deric or epiblastic cell-layer *ep*. C. The same embryo focused so as to show the mesoblastic cells which immediately underlie the outer cell-layer.

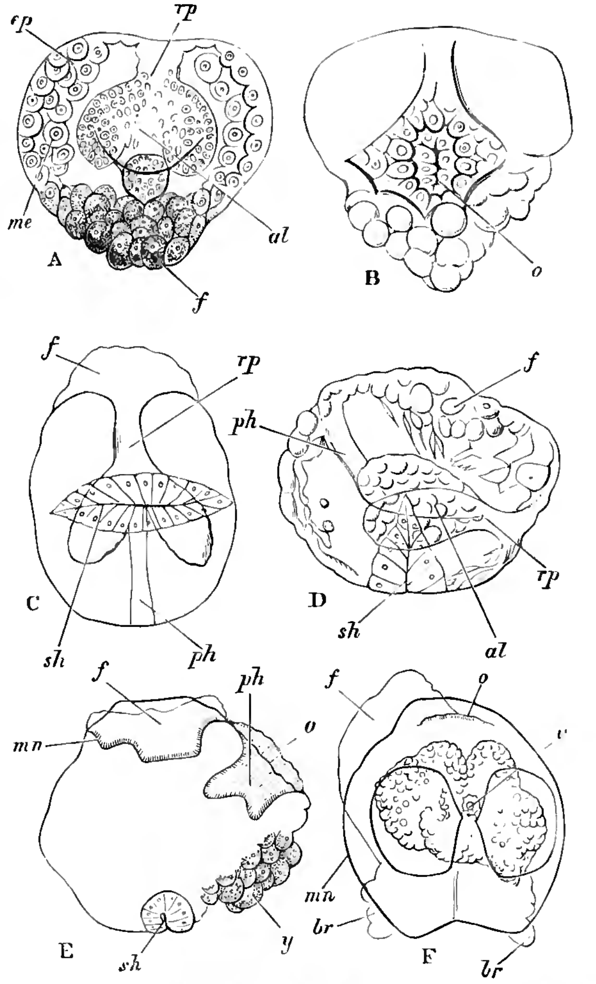

Fig. 151.—Further stages in the development of *Pisidium pusillum* (after Lankester). A. Optical section of an embryo in which the foot has begun to develop. B. The same embryo focused to its surface plane to show the mouth *o*. C. Later embryo, showing the shell-gland *sh*. D. Lateral view of the same embryo. E. Later stage, with rudiments of the mantle-flap, lateral view. F. Still later stage, with shell-valves and branchial filaments. *ep*, epiblast; *me*, mesoblast; *al*, met-enteron; *rp*, rectal peduncle or pedicle of invagination connecting the met-enteron with the cicatrix of the blastopore; *o*, mouth; *ph*, pharynx; *sh*, shell-gland; *mn*, mantle-flap; *br*, branchial filaments; *y*, granular cells of doubtful significance; *v*, vesicular structure of unknown significance.

The development of Anodon is remarkable for the curious larval form known as Glochidium (fig. 147). The Glochidium quits the gill-pouch of its parent and swims by alternate opening and shutting of the valves of its shell, as do adult Pecten and Lima, trailing at the same time a long byssus thread. By this it is brought into contact with the fin of a fish, such as Perch, Stickleback, or others, and effects a hold thereon by means of the toothed edge of its shells. Here it becomes encysted, and is nourished by the exudations of the fish. A distinct development of its internal organs has been traced by the late Professor Balfour, but no one has followed it to the moment at which it drops from the fish's fin and assumes the form of shell characteristic of the parent. Other Lamellibranchs exhibit either a trochosphere larva which becomes a Veliger, differing only from the Gastropod's and Pteropod's Veliger in having bilateral shell-calcifications instead of a single central one; or, like Anodon, they may develop within the gill-plates of the mother, though without presenting such a specialized larva as the Glochidium. An example of the former is seen in the development of the European Oyster, to the figure of which and its explanation the reader is specially referred (fig. 6). An example of the latter is seen in a common little fresh-water bivalve, the *Pisidium pusillum*, which has been studied by Lankester (12). The successive stages of the development of this Lamellibranch are illustrated in the woodcuts figs. 148 to 153 inclusive. These should be compared with the figures of Gastropod development (figs. 3, 4, 5, 7, and 72***). Fig. 148 shows the cleavage of the egg-cell into four (A), and at a later stage the tucking in of some of the cells to form an invaginated series (B).

The embryonic cells continue to divide, and form an oval vesicle containing liquid (fig. 149); within this, at one pole, is seen the mass of invaginated cells (fig. 150, *hy*). These invaginated cells are the arch-enteron; they proliferate and give off branching cells, which apply themselves (fig. 150, C) to the inner face of the vesicle, thus forming the mesoblast or cœlomic outgrowths. The outer single layer of cells which constitutes the surface of the vesicle (fig. 147) is the ectoderm or epiblast or deric cell-layer. The little mass of hypoblast or enteric cell-mass now enlarges, but remains connected with the cicatrix of the blastopore or orifice of invagination by a stalk, the rectal peduncle (fig. 151, A, *rp*). The enteron itself becomes bilobed and is joined by a new invagination, that of the mouth and stomodæum, *ph*. Fig. 151, B shows the origin of the mouth *o*, being a deeper view of the same specimen in the same position which is drawn in fig. 151, A. The mesoblast multiplies its cells, which become partly muscular and partly skeleto-trophic. Centro-dorsally now appears the embryonic shell-gland (fig. 151, C, *sh*). The pharynx or stomodæum is still small, the foot not yet prominent. A later stage is seen in fig. 152, where the pharynx is widely open and the foot prominent. No ciliated velum or præ-oral (cephalic) lobe ever develops. The shell-gland disappears, the mantle-skirt is raised as a ridge (fig. 151, E, *mn*), the paired shell-valves are secreted, the anus opens by a proctodæal ingrowth into the rectal peduncle, and the rudiments of the gills (*br*) and of the nephridia (B) appear (figs. 151, F, and 153, dorsal and lateral views of same stage), and thus the chief organs and general form of the adult are acquired. Later changes, not drawn here, consist in the growth of the shell-valves over the whole area of the mantle-flaps, and in the multiplication of the gill-filaments and their consolidation to form gill-plates. It is important to note that the gill-filaments are formed one by one *posteriorly*. The labial tentacles are formed late. In the allied genus Cyclas, a byssus gland is formed in the foot and subsequently disappears, but no such gland occurs in Pisidium. The nerve-ganglia and the otocysts probably form from thickenings of the epiblast, but detailed observation on this and other points of histogenesis in the Lamellibranchia is still wanting.

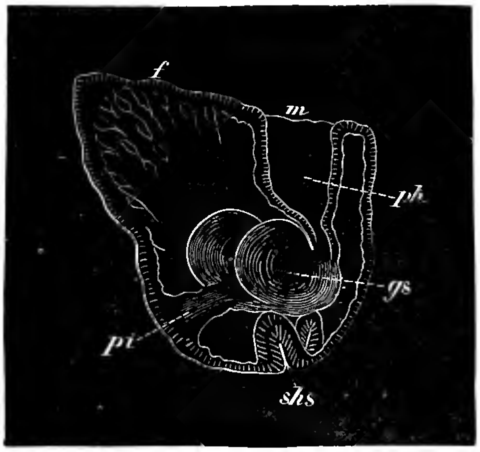

Fig. 152.—Diagram of embryo of Pisidium in the same stage as E in fig. 151. *m*, mouth; *f*, foot; *ph*, pharynx; *gs*, met-enteron; *pi*, rectal peduncle or pedicle of invagination; *shs*, shell-gland. (From Lankester.)

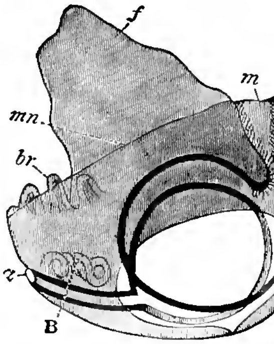

Fig. 153.—Diagram of embryo of Pisidium, in same stage as F in fig. 151 (after Lankester). *m*, mouth; *x*, anus; *f*, foot; *br*, branchial filaments; *mn*, margin of the mantle-skirt; *B*, organ of Bojanus (nephridium). The unshaded area gives the position of the shell-valve.

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(E. R. L.)

POLYZOA

POLYZOA is the name applied by J. Vaughan Thompson in 1730 (1)[1] to a group of minute polyp-like organisms which were subsequently (1834) termed "Bryozoa" by Ehrenberg (2). The forms included in this group were stated by Thompson to be "in a general way the whole of the Flustraceæ, in many of which I have clearly ascertained the animals to be Polyzoæ," they having been previously considered by zoologists to be allied to the Hydra-like polyps. These organisms had previously been known by the hard corneous "cells" or chambers which are formed by the animals on the surface of their bodies, and build up, in consequence of the formation of dense colonies by budding, complex aggregates known as "sea mats" and "sea mosses." Thompson expressly stated the opinion that the organization of the animals detected by him led to the conclusion that "they must be considered as a new type of the Mollusca Acephala."

Subsequently (1844) Henri Milne-Edwards (3) pointed out the relationship of Thompson's Polyzoa to the Brachiopoda, and, adopting the latter's view as to their Molluscan affinities, proposed to unite these two classes with the Tunicata in a group to be called "Molluscoidea." Recent researches have entirely separated the Tunicata from this association, and have demonstrated that they belong to the great phylum of Vertebrata. On the other hand, the association of the Polyzoa with the Brachiopoda appears at present to be confirmed, though the relationship of these two classes to the Mollusca has been shown to rest on mistaken identification of parts; see, however, Harmer (18).

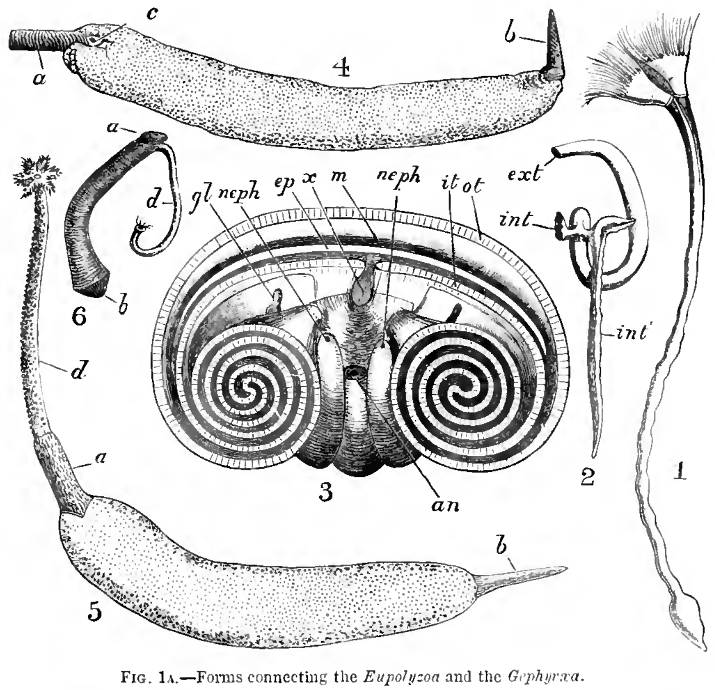

FIG. 1A.—Forms connecting the *Eupolyzoa* and the *Gephyræa*.

1. *Phoronis australis*, Haswell.
2. One of the two nephridia of the same; *ext*, external aperture; *int*, *int'*, the two internal funnel-like apertures.
3. View of the tentacular area of *Phoronis australis*—the tentacles cut to their bases. *ot*, outer line of tentacles; *it*, inner line of tentacles; *m*, mouth; *ep*, epistome; *x*, gap in the inner series of tentacles; *neph*, nephridio-pores; *an*, anus; *gl*, glandular pit. (After Benham, *Quart. Journ. Micr. Sci.*, vol. 30, 1889.)
4. *Golfingia M'Intoshii*, Lankester. Specimen in which the introvert is telescoped into the body. *a*, the sclerorhynchus, which with *b*, the scleropyge, represents the hard zoœcium of Eupolyzoa; *c*, anus.
5. View of the same in an expanded condition. *a*, sclerorhynchus; *b*, scleropyge; *d*, the soft introvert carrying mouth, surrounded by six pinnate tentacles. (After Lankester, *Trans. Linn. Soc.*, 2nd ser., "Zoology," vol. ii., 1885.)
6. *Aspidosiphon Steenstrupii*, Diesing. *a*, anterior corneous plate; *b*. terminal posterior plate; *d*, introvert. (After Selenka, *Die Sipunculiden*, 1883.)

The Polyzoa appear to be related to the Sipunculoid Gephyræan worms (Gephyræa inermia) more nearly than to any other class of the animal kingdom. The study and interpretation of the facts of their ontogeny (growth from the egg) presents such extreme difficulty that in the present state of our knowledge it is necessary to regard them

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[1] These numbers refer to the bibliography which will be found in page 171.

ad interim as forming with the Brachiopoda and Sipunculoids an isolated group, to which the name "Podaxonia" may be applied, pending the decision of their affinities by the increase of our knowledge of the embryology of important members of the group.[1]

The forms included at the present day in Thompson's class of "Polyzoa" may then be thus classified :—

PHYLUM PODAXONIA.

- CLASS I.—*SIPUNCULOIDEA.*
- CLASS II.—*BRACHIOPODA.*
- CLASS III.—*POLYZOA.*
  - Section 1.—VERMIFORMIA.
    - Sole genus: *Phoronis* (figs. 4 and 5).
  - Section 2.—PTEROBRANCHIA.
    - Genus 1: *Rhabdopleura* (fig. 7).
    - Genus 2: *Cephalodiscus* (figs. 8, 9, 10).
  - Section 3.—EUPOLYZOA.
    - Sub-class 1.—**Ectoprocta.**
      - Order 1.—PHYLACTOLÆMA.
        - Examples: *Lophopus*, *Plumatella* (fig. 2, B), *Cristatella* (fig. 3), *Fredericella.*
      - Order 2.—GYMNOLÆMA.
        - Sub-order 1.—Cyclostoma.
          - Examples: *Crisia* (fig. 13, A), *Hornera*, *Tubulipora*, *Discoporella.*
        - Sub-order 2.—Ctenostoma.
          - Examples: *Alcyonidium*, *Vesicularia*, *Serialaria*, *Bowerbankia* (fig. 1, A), *Paludicella* (fig. 1, E and fig. 2, A).
        - Sub-order 3.—Chilostoma.
          - Examples: *Cellularia*, *Scrupocellaria*, *Kinetoskias* (fig. 14), *Bugula*, *Bicellaria*, *Flustra* (fig. 1, G), *Mucronella* (fig. 1, C, D, F), *Membranipora*, *Lepralia*, *Eschara*, *Cellepora*, *Retepora.*
    - Sub-class 2.—**Entoprocta.**
      - Genera: *Pedicellina* (fig. 15), *Loxosoma* (fig. 16), *Urnatella*, *Ascopodaria.*

We shall most readily arrive at a conception of the essential structure of a Polyzoon, and of the variations to which that essential structure is subject within the class, by first examining one member of the group in detail and subsequently reviewing the characters presented by the divergent sub-classes, orders, &c., above indicated.

The most convenient form for our purpose is *Paludicella Ehrenbergii* (fig. 2, A), belonging to the typical section of the class (the Eupolyzoa) and to the order Gymnolæma. The organism occurs as minute tree-like growths (figs. 2, A and 1, E) attached to stones in freshwater streams and canals. The branches of the little tree are rarely more than an inch in length, and are regularly swollen and jointed at intervals. Each of the very numerous joints is about one-fifth of an inch long, and is in reality a tubular horny box attached above and below to the preceding and succeeding joints, and having on one side of it a spout-like aperture from which a crown of tentacles can be protruded. Each joint is thus inhabited by a distinct animal which is more or less completely shut off from the one in front of it and the one behind it, although it originated from the hinder and has given rise to the fore-lying individual by a process of budding, and retains a continuity of substance with both. A single cell or joint with its contained animal is represented in fig. 2, A.

Paludicella produces an arboriform colony, the main trunk or stolon being adherent to some stone or piece of wood. The substance of the wall of the cells is formed by a chemical body allied to chitin. Other Polyzoa may form mat-like expansions—the cells being placed in one plane, side by side (fig. 1, C, D, F, G), as well as in linear series; others again form solid masses, whilst many agree with Paludicella in the simple linear arrangement of their units. Phoronis and Loxosoma, on the other hand, do not form colonies at all—the former because it does not bud, the latter because the buds become detached from their parent as soon as formed, as do the buds of the Hydrozoon Hydra.

On the whole Paludicella presents us with a very simple form of Polyzoon-colony (technically termed a "zoarium"), in which the aggregate of budded persons, each of which is called a "polypide," does not exhibit any marked individuation, but is irregular and tree-like. But, just as in the Hydrozoa we find the Siphonophora presenting us with a very definite shape and individuality of the aggregate or colony, so in the Polyzoa we find instances of high indi-

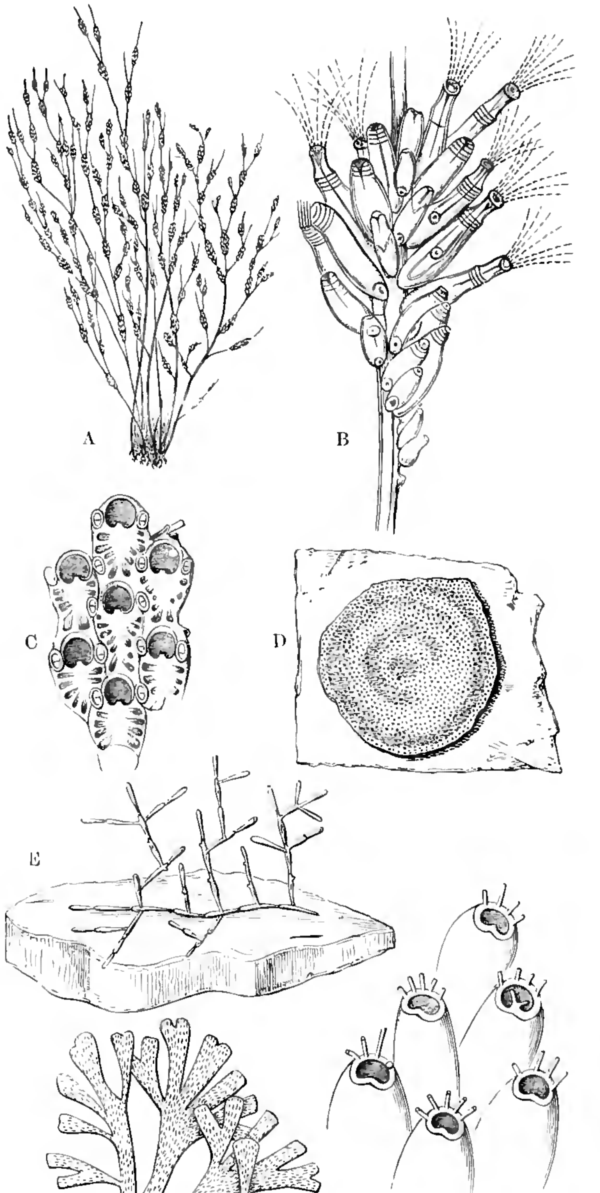

FIG. 1.—Various forms of zoaria of Eupolyzoa.
A. *Bowerbankia pustulosa*, one of the Ctenostoma; natural size.
B. A cluster of polypides of *Bowerbankia pustulosa*, some with expanded tentacles; more highly magnified.
C. Zoœcia of *Mucronella pavonella* (Chilostoma); highly magnified.
D. Zoarium of *Mucronella pavonella*, forming a disk-like encrustation on a piece of stone; natural size.
E. Zoarium of *Paludicella Ehrenbergii* (Ctenostoma), natural size.
F. Zoœcia of *Mucronella Peachii*; highly magnified. Compare with C in order to note specific characters.
G. Zoarium of *Flustra securifrons*; natural size.

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[1] The research of Harmer (18) on Loxosoma is published too late for due notice in this article. It tends to the conclusion that the Eupolyzoa are after all degraded Mollusca, and have no connexion with the Vermiformia, Pterobranchia, Brachiopoda, and Sipunculoidea. The reader is referred to Mr Harmer's memoir.

viduation of the zoarium of a similar kind. The most remarkable example is afforded by the locomotive zoarium or colony of Cristatella (fig. 3); and another very striking instance is that of the stalked zoaria of Kinetoskias (fig. 14) and Adeona.

The horny consistence of the cells which are produced by Paludicella is very usual in other Polyzoa; but we find frequently that the substance which forms the cells is gelatinous and soft instead of being horny, or again may be strongly calcareous. The term *cœnœcium* is applied to the mass of cells belonging to a colony or zoarium when considered apart from the living polypides which form it. Often such cœnœcia are found retaining form and structure when the soft living polypides have decomposed and disappeared. A single cell of the cœnœcium, corresponding to a single polypide, is called by the special students of the Polyzoa a *zoœcium*.

If we examine a single cell or zoœcium of Paludicella more carefully whilst its polypide is alive, we discover that the horny cell is nothing more than the cuticle of the polypide itself, to which it is absolutely adherent. At the so-called "mouth" or spout of the cell the cuticle suddenly changes its character and becomes a very delicate and soft pellicle instead of being thick and horny. There is no real discontinuity of the cuticle at this region, but merely a change in its qualities. This gives to that portion of the body of the polypide which lies beyond the spout a mobility and capacity for folding and pleating which is entirely denied to that part where the cuticle is more dense (fig. 2, A). Accordingly we find that the anterior portion of the body of the polypide can be pulled into the hinder part as the finger of a glove may be tucked into the hand. It is, in fact, an "introvert" (for the use of this term see MOLLUSCA, vol. xvi. p. 652). This arrangement is universal in the Ectoproctous Eupolyzoa, but does not obtain either in the Entoprocta, the Pterobranchia, or the Vermiformia. In Phoronis, Rhabdopleura, and Cephalodiscus the anterior part of the body can *not* be tucked or telescoped into the hinder part as it can in typical Eupolyzoa. On the other hand it is very important to note that the Sipunculoid Gephyræans are all pre-eminently characterized by possessing identically this arrangement. The introversion is effected in Paludicella (as in other Eupolyzoa) by a series of long detached retractor muscles of considerable power (fig. 2, A, *mr*, *r'*, *m*); the same is true of Sipunculus.

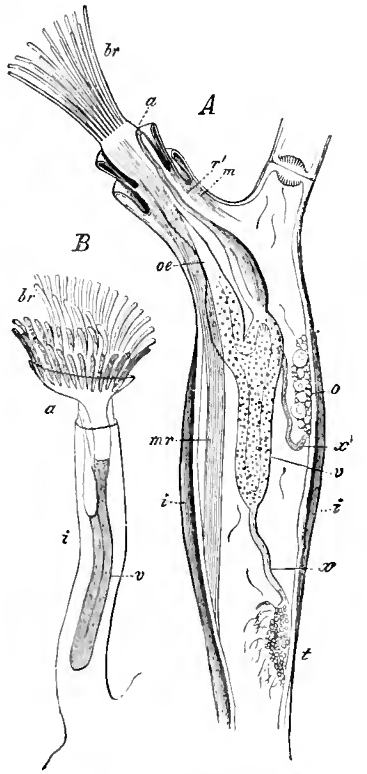

FIG. 2 —A. Polypide of *Paludicella Ehrenbergii*, seen as a transparent object in optical section and highly magnified (from Gegenbaur, after Allman). For natural size see fig. 1, E. *a*, anus; *br*, peristomial circlet of ciliated tentacles; *i*, thickened cuticle of the body-wall, forming the horny cell or zoœcium; *m*, median retractor muscle of the introversible part of the body; *r'*, anterior retractor of the same; *mr*, great retractor muscle of the same; *o*, ovary, passing from which to the stomach is the anterior mesentery or funiculus; *t*, testis; *œ*, œsophagus; *v*, stomach; *x*, posterior mesentery or funiculus; *x'*, anterior mesentery or funiculus. Observe at the right upper corner of the figure the base of a second polypide and the "rosette-plate" of separation.

B. Diagram of a polypide of Plumatella. Letters as above.

The view has been advanced by Allman (**4**) that the retractile part of the polypide is to be considered as a distinct individual budded from the basal portion, which is regarded as an equivalent individual. It does not appear to the present writer that such a theoretical conception tends to facilitate the understanding of the structure and relations of these animals.

An "ectocyst" and "endocyst" have also been distinguished in former treatises, and these terms form part of a special "polyzoarial" nomenclature, but do not appear to be any longer needful. Equally undesirable is the misapplied term "endosarc" lately introduced by Jolliet (**5**) to denote a certain portion of the Polyzoon structure which will not be referred to here by that name.

The retractile or introversible portion of the body of the polypide of Paludicella is terminated by a crown of sixteen stiff non-contractile tentacles (fig. 2, A, *br*) which form a circle around a central aperture—the animal's mouth. These tentacles are hollow and beset with vibratile cilia. The beating of the cilia causes a powerful current in the water by which food is brought to the animal's mouth. Each tentacle is also muscular, and can be bent and straightened at will. The tentacles not only serve to bring food into the mouth, but they are efficient as gill-filaments, being possibly homologous with (as well as functionally similar to) the gill-filaments of Lamellibranch Molluscs. They also serve as delicate tactile organs, and are the only sense organs possessed by the Eupolyzoa.

In Paludicella the platform around the mouth from which the tentacles arise, or *lophophore*, as it is termed, is circular. This is the case in all members of the large group of Gymnolæma and in the Entoprocta. But in the Phylactolæma the lophophore is drawn out on each side, right and left, so as to present a horse-shoe shape (fig. 2, B), and in some forms, notably Lophopus and Alcyonella, the two arms or diverging rami of the horse-shoe are very strongly developed.

In the Pterobranchia the tentacles are confined in one genus (Rhabdopleura) to the two arm-like outgrowths of the lophophore, and are not simply hollow but contain a well-developed cartilaginoid skeleton (fig. 7). In the allied genus Cephalodiscus there are not merely a single pair of such arm-like processes, each bearing two rows of tentacles, but the lophophore is developed into twelve arm-like processes (fig. 9), which form a dense tuft of filaments around the anterior extremity of the animal.

In the Vermiformia (Phoronis) we again meet with a very perfect horse-shoe-shaped lophophore (fig. 4). The tentacles upon the crescentic or otherwise lobed circumoral region of the Sipunculoids are the representatives of the tentacles of the Polyzoa; whilst the tentaculiferous "arms" of the Brachiopoda appear to be the equivalents of the Polyzoon's lophophore much drawn out and in most cases spirally rolled.

Just below the circular crown of tentacles in Paludicella we find an aperture which the study of internal anatomy proves to be the anus. In all Polyzoa the anus has this position near the mouth; and in this respect we again note an agreement with Sipunculus and the other so-called Gephyræa inermia. In one division of the Polyzoa alone is there any noteworthy variation in the position of the anus, namely, in the Entoprocta (sub-class of the section Eupolyzoa). In these forms the anus, instead of lying just below the lophophore or platform from which the tentacles spring, is included like the mouth within its area (fig. 15, C).

Passing now to the deeper structure of Paludicella, we find that it is a Cœlomate animal; that is to say, there exists between the body-wall and the wall of the alimentary tract a distinct space termed "perigastric space," "body-cavity," or "cœlom." This is true of all Polyzoa, though it has been erroneously stated by G. O. Sars that Rhabdopleura does not possess such a cœlom. In Eupolyzoa (excepting the Entoprocta) the cœlom is very capacious; it is occupied by a coagulable hæmolymph in which float cellular corpuscles, and also the generative products, detached, as is usual in Cœlomata, from definite "gonads" developed on its lining membrane (fig. 2, A, *o*, *t*). This lining membrane or "cœlomic epithelium" is ciliated in the Phylactolæma, but its characters appear not to have been definitely determined in other Eupolyzoa. The cœlomic space and the tissues bounding it are continuous throughout the colony or zoarium of a Polyzoon—either directly without any constriction marking off one polypide from another, or through perforate septum-like structures as in Paludicella (see right-hand upper process of fig. 2, A), which form incomplete barriers between juxtaposed zoœcia, and are termed "rosette-plates" or "communication-plates." The cœlomic cavity is continued in Paludicella and probably in all Polyzoa into the tentacles, so that these organs expose the hæmolymph fluid to a respiratory action, and hence may be called branchial.

The body-wall of Paludicella consists, alike in the anterior introversible region and in the posterior region, of an outer cuticle which has already been spoken of as thickened around the base of the polypide so as to become there the hard tube-like zoœcium. Beneath this is the delicate layer of living epidermic cells which are the mother-cells or matrix of that cuticle. Beneath this again are a few scattered annuli of muscular fibre-cells arranged ring-wise around the cylindrical body; more deeply placed than these are five large bundles of longitudinally placed muscular fibre-cells which are attached at three different levels to the soft introversible portion of the body, and by their retraction pull it in three folds or telescopic joints into the capacious hinder part of the body. In some Polyzoa the muscular fibre-cells present transverse striations. These folds are shown in fig. 2, A; but when the longitudinal muscles are completely contracted the tentacular crown would be pulled down far out of sight into the midst of the body by the great longitudinal muscle *mr*. Deeper than the longitudinal muscles, and clothing them and everything else which projects into the cœlom, is the cœlomic epithelium, not easily observed, and sufficiently known only in the Phylactolæma. Part of it gives rise to the generative products (fig. 2 A, *o*, *t*). Other Eupolyzoa have a similar but not identical arrangement of the longitudinal muscles—acting essentially as retractors of the "introvert" or soft anterior region of the body—and a similar structure of the body-wall which is in essential features identical with that of the Sipunculoid worms, the Chætopod worms, and other typical Cœlomate animals.

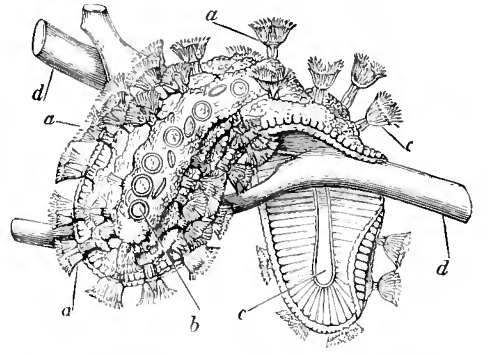

Fig. 3.—The locomotive zoarium of the freshwater Phylactolæmous Polyzoon *Cristatella mucedo*; magnified six times linear (after Allman). *a*, individual polypides with their horse-shoe-shaped crown of tentacles exserted; *b*, statoblasts seen through the transparent tissues; *c*, the muscular foot or base of the colony by means of which it crawls; *d*, portion of water-weed upon which the Cristatella is crawling.

The alimentary canal of Paludicella forms a closely compressed U-shaped loop depending from the closely approximated mouth and anus into the capacious cœlom. It is clothed on its cœlomic surface (in Phylactolæma at any rate) with cœlomic epithelium, and beneath this are extremely delicate muscular layers. Within it is lined, except in the immediate region of the mouth (which is lined by the in-pushed outer cell-layer), by the enteric cell-layer—the digestive cells derived from the archenteron of the embryo. We can distinguish in Paludicella a contractile pharyngo-œsophagus (fig. 2, A, *œ*), a digestive stomach *v* (the lining cells of which have a yellow colour), and an intestine which forms that arm of the loop connected with the anus. This simple form of alimentary canal is uniformly present in Polyzoa. In *Bowerbankia* and its allies a muscular gizzard with horny teeth is interposed between œsophagus and digestive stomach.

The alimentary canal of Paludicella does not hang quite freely in the cœlomic cavity, but, as is usually the case in other classes where the cœlom is large, *mesenteries* are present in the form of fibrous (muscular?) bands clothed with cœlomic epithelium and suspending the gut to the body-wall. In Paludicella there are two of these mesenteries, an anterior (*x'*) and a posterior (*x*). The presence of two mesenteric bands is exceptional. Usually in the Eupolyzoa we find one such mesentery only, corresponding to the hinder of the two in Paludicella. The special name *funiculus* (Huxley) is applied to this mesenteric band, and it is noteworthy that the cells of the cœlomic epithelium, either upon its surface or at its point of insertion into the body-wall, are modified as reproductive elements, forming either the testis or ovary; in the Phylactolæma they form here also special asexual reproductive bodies, the statoblasts. The nervous tissue and organs of Paludicella have not been specially investigated, but in many Eupolyzoa an oval mass of nerve-ganglion cells is found lying between the mouth and anus, and there is no doubt that it is present in this case. In Plumatella nerve-fibres have been traced from this ganglion to the tentacles and other parts around the mouth (fig. 11, *w*, *x*, *y*). A "colonial nervous system" was described some years ago by Fr. Müller in Serialaria; but modern histologists do not admit that the tissue so named by Müller is nerve-tissue. The ganglion above mentioned is the only nervous tissue at present known in Polyzoa (but see fig. 17, *x*).

No heart or blood-vessels of any kind exist in Paludicella nor in any of the Eupolyzoa or Pterobranchia. On the other hand the isolated vermiform genus Phoronis presents a closed contractile system of longitudinal vessels (dorsal and ventral) which contain nucleated corpuscles coloured red by hæmoglobin (figs. 4, 5).

No excretory organs (nephridia) or genital ducts have been observed in Paludicella, nor have such organs been detected in the majority of the Polyzoa which have been studied. In the Entoprocta, however, a pair of minute ciliated canals are found in the nearly obliterated body-cavity opening to the exterior near the tentacular crown in both Pedicellina and Loxosoma, which represent the cephalic nephridia of worms. A definite pair of nephridia occur in Phoronis. A similar significance is perhaps to be attributed to the "intertentacular organ" of Farre—a ciliated passage opening between two tentacles of the lophophore in Membranipora, Alcyonidium, and other forms—through which Hincks has observed the spermatozoa to escape in large numbers. This organ occurs equally in female specimens of Membranipora, and is not therefore simply a spermatic duct.

Paludicella, as we have seen, develops both ova and spermatozoa in one and the same polypide. The details of impregnation and development have not been followed in this instance, but in some of the marine Eupolyzoa (Gymnolæma) remarkable bud-like structures termed *oœcia* are developed for the special reception of the ova, and in these organs fertilization takes place. In the Entoprocta there is a peculiar brood-pouch. The spermatozoa of one polypide probably in all cases fertilize the ova of another, but we have not yet in many cases a knowledge of how the spermatozoa get to the eggs, or how the eggs escape from the body-cavity of the parent. In the hippocrepian freshwater Polyzoa (Phylactolæma) the ova appear to be fertilized and undergo the early stages of development within the body-cavity of the parent or in a hernia-like protrusion of it. Probably in such cases the embryos escape by the death of the parent and rupture of the parental tissues, as do also the peculiar asexual internal buds or statoblasts of these forms.

The embryo Polyzoon or "larva" swims freely in its early condition by means of cilia, and is in this condition a single polypide or "person." The forms assumed by these ciliated larvæ in different Polyzoa are very various and exceedingly difficult of interpretation. We shall have more to say with regard to them below (see figs. 19, 20, 21). The ciliated larva then fixes itself and commences to produce polypides by a process of budding, the buds remaining not merely in contact but in organic continuity, and increasing continually in number so as to form a large colony or zoarium. In Paludicella we have seen that this colony has a simple tree-like form. The new buds form as wart-like growths, usually one, sometimes two in number, at the free end of a cell or zoœcium near the spout-like process from which the tentacular crown is everted. In Paludicella all the polypides of a colony are alike; there is no differentiation of form or distribution of function amongst the members of the colony. In many Eupolyzoa this simplicity is by no means maintained, but a great variety of form and function is assumed by various members of the aggregate. The only approach to a differentiation of the polypides in Paludicella is in the arrest of growth of some of the buds of a colony in autumn, which, instead of advancing to maturity, become conical and invested with a dark-coloured cuticle. They are termed *hybernacula*. Should the rest of the polypides die down in winter, these arrested buds survive and go on to complete development on the return of spring.

In Paludicella we have thus seen a fairly simple and central example of Polyzoon structure and life-history. The variations upon this theme presented in different groups of Polyzoa have been to some small extent noted in the preceding account, but we shall now be able to indicate them more precisely by considering the various groups of Polyzoa in succession. The limit assigned to this article necessitates very large omissions. The reader who wishes to have the fullest information on the many difficult and uncertain matters connected with this subject is referred to Allman, *Freshwater Polyzoa* (Ray Society, 1856); Hincks, *British Marine Polyzoa* (Van Voorst, 1880); Haddon, "Budding in Polyzoa," *Quart. Journ. Micr. Sci.*, 1883; Balfour, *Embryology*, vol. i. p. 242; and the original memoirs cited by these writers.

THE VERMIFORMIA.

The first section of the Polyzoa comprises but a single genus, Phoronis. It differs from all other Polyzoa first in its greater size (species 2 inches long are known) and elaboration of organization, and correlatively with that in the fact that it does not produce buds. Further, it does not produce a closely adherent cuticular zoœcium as do Paludicella and the Eupolyzoa generally, but a leathery tube in which the animal freely moves, resembling that of some Chætopods (Sabella). Like some Sabellæ, Phoronis forms closely packed aggregates of individuals not brought together by any process of budding, but each separately developed from an egg. Phoronis has an elongate, worm-like, unsegmented body, with a conical posterior termination (like Sipunculus), and anteriorly provided with a horse-shoe-shaped crown of tentacles surrounding the mouth (figs. 4, 5). There is an intertentacular "web" between the bases of the tentacles as in the Phylactolæma. Caldwell (6) has recently shown that the tentacles are supported by a mesoblastic skeleton, as is also the case in Rhabdopleura, but apparently not the case in any other Polyzoa. Close to the mouth, as in all Polyzoa, is placed the anus, outside the horse-shoe-shaped lophophore or tentacular platform (fig. 11, *i*). The tentacular crown is not introversible; in this point Phoronis differs from Paludicella and the Ectoproctous Eupolyzoa, and agrees with the Entoprocta and the Pterobranchia. Overhanging the mouth is a small præ-oral lobe or "epistome" (figs. 4, 5, *c*). This organ is aborted in Paludicella, and indeed in all the Gymnolæma, but is present in the other Polyzoa, and is especially large and well developed in Rhabdopleura and Cephalodiscus. It has been compared to the Molluscan foot, but undoubtedly in Phoronis it is the persistent representative of the præ-oral

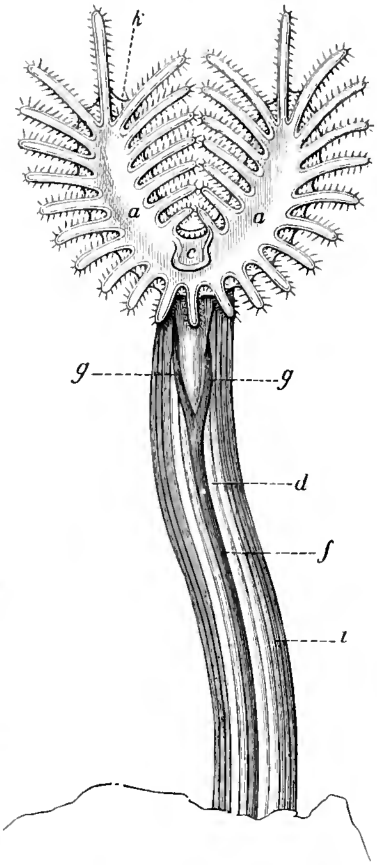

FIG. 4.—*Phoronis hippocrepia*, Wright; magnified six times linear (from Allman). *a*, horse-shoe-shaped lophophore with tentacles; *c*, epistome (præ-oral lobe or prostomium); *d*, œsophagus; *f*, ventral vessel; *g*, *g*, two anterior vessels which unite to form *f*; *i*, longitudinal muscular coat of the body-wall; *k*, intertentacular membrane.

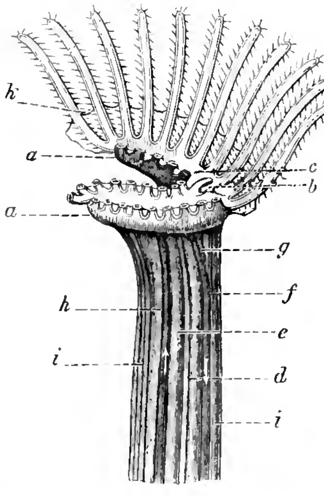

FIG. 5.—Lateral view of the anterior region of Phoronis. The tentacles of the right arm of the lophophore are cut short in order to expose clearly the mouth *b* and the overhanging "epistome" or præ-oral lobe *c*. *e*, intestine; *h*, dorsal vessel. Other letters as in fig. 4.

lobe of the larva (fig. 6), and therefore cannot be compared to the Molluscan foot. If we are right in associating Phoronis with the Polyzoa, this fact is sufficient to show that the epistome of the Phylactolæma (fig. 11, *e*) and the buccal shield of Rhabdopleura (fig. 7, *d*) and of Cephalodiscus (fig. 9, *b*) are also cephalic in nature, and cannot rightly be identified with the post-oral and ventral muscular lobe known as the foot in Mollusca. A circum-oral nerve ring occurs at the base of the tentacles and sends off a cord which runs along the left side of the body. The alimentary canal presents the same general form and regions as in Paludicella. It hangs in the body-cavity, to the walls of which it is suspended by definite mesenteries.

Phoronis presents a closed contractile vascular system containing red-coloured blood-corpuscles (figs. 4, 5, *f*, *g*, *h*). A pair of ciliated canals acting as genital pores is found near the anus; these have been shown by Caldwell to be typical nephridia.

The development of Phoronis is remarkable. The egg gives rise (after the usual phases of cleavage and gastrulation) to the larval form known as *Actinotrocha* (fig. 6). This larva possesses a hood-like region overhanging the mouth and a number of ciliated post-oral processes or tentacles. The anus is placed at the extremity of the elongate body opposite to that bearing the mouth and præ-oral hood. The præ-oral hood becomes the epistome, and the tentacles, by further development (new tentacles replacing the larval ones), become the horse-shoe-shaped group of tentacles of the adult. A very curious process of growth changes the long axis of the body and results in the anus assuming its permanent position near the mouth. An invagination appears on the ventral face of the larva between the anus and mouth, and attains considerable size. At a definite moment in the course of growth this invagination is suddenly everted, carrying with it in its cavity the intestine in the form of a loop. Thus a new long axis is suddenly established at right angles to the original oro-anal axis, and continues to develop as the main portion of the body. The short area extending from the præ-oral hood to the anus is thus the true *dorsal* surface of Phoronis, whilst the elongated body is an outgrowth of the ventral surface perpendicular to the primary oro-anal axis, as conversely in many Mollusca we find a short *ventral* area (the foot) between mouth and anus, and an outgrowth of the dorsal surface (the visceral hump) perpendicular to the primary oro-anal axis, forming the chief body of the animal. In these relations Phoronis (and with it the other Polyzoa) agrees with Sipunculus. On the other hand Echiurus, the Chætopods, Nemertine worms, and some other groups which start from a simple larval form not unlike that of Phoronis, present a continual elongation of the original oro-anal axis, and no transference of the long axis by the perpendicular or angular growth of either the ventral or the dorsal surface of the larva.

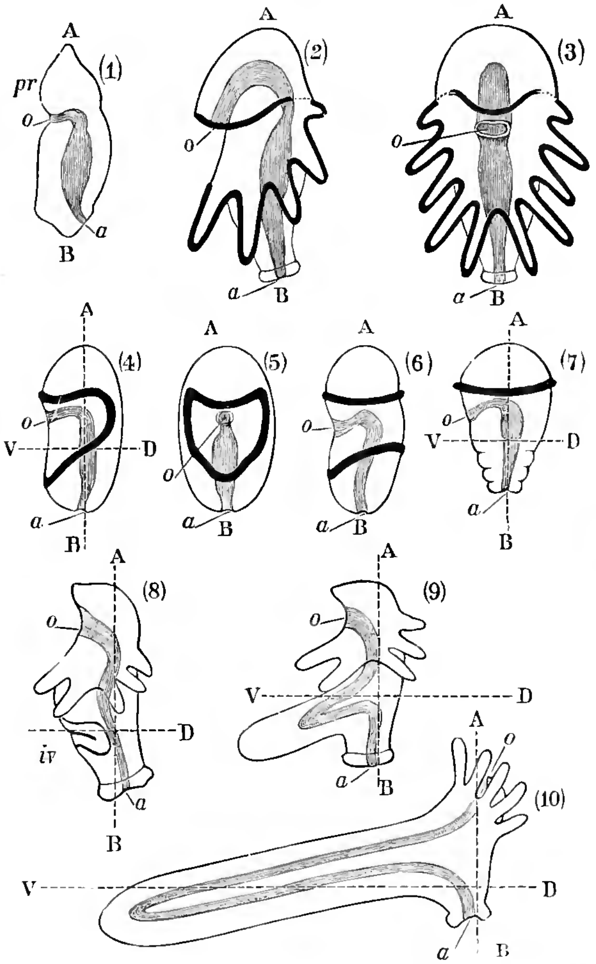

FIG. 6.—Development of Phoronis and typical ciliate larvæ. (1), (2), (3), (8), (9), (10), stages in the development of Phoronis—(1), earliest larva; (2), lateral view of the Actinotrocha; (3), ventral view of the same; (8), the ventral invagination *iv* is formed; (9), the ventral invagination is everted, carrying with it a loop of intestine; (10), the permanent relations of mouth, anus, and body (Podaxonia) are attained. (4), (5), Echinoderm larva with architroch, as in Actinotrocha, but band-like, not digitate. (6), Echinoderm larva, with the architroch divided into a præ-oral cephalotroch (Molluscan and Rotifer's velum), and a post-oral branchiotroch. (7), Chætopod trochosphere larva with cephalotroch only, and elongation and segmentation of the oro-anal axis. *a*, anus; *o*, mouth; *pr*, prostomium; *iv*, ventral invagination of Phoronis larva. A B, oro-anal axis; V D, dorso-ventral axis.

Phoronis was discovered originally in the Firth of Forth by Dr Strethill Wright. It occurs in the Mediterranean and in Australian seas (Port Jackson).

THE PTEROBRANCHIA.

This section of the Polyzoa also comprises forms which differ very widely from Paludicella. Inasmuch as their development from the egg is at present quite unknown, it may possibly prove that they have other affinities. Only two genera are known, Rhabdopleura (Allman) and Cephalodiscus (M'Intosh), the former dredged by Dr Norman in deep water off the Shetlands (and subsequently in Norway), the latter taken by the "Challenger" expedition in 250 fathoms off the coast of Patagonia.

The Pterobranchia have the mouth and anus closely approximated, and immediately below the mouth are given off a series of ciliated tentacles, but these do not form a complete circle as in Paludicella, nor is the lophophore (the platform of their origin) horse-shoe-shaped as in Phoronis. The lophophore is drawn out into a right and a left arm in Rhabdopleura (fig. 7), upon each of which are two rows of ciliated tentacles; no tentacles are developed centrally in the region between the two arms, so that the mouth is not completely surrounded by these processes. The horse-shoe-shaped lophophore of Phoronis could be modified so as to represent the tentaculiferous arms of Rhabdopleura by suppressing both rows of tentacles at the curve of the horse-shoe, and leaving only those which occur on the arms or rami of the horse shoe (see fig. 4). The lophophore of Cephalodiscus presents us with twelve processes, each carrying two rows of ciliated tentacles; in fact we have six pairs of tantaculiferous arms instead of a single pair, and each of these arms is precisely similar to one of the arms of Rhabdopleura (fig. 9), excepting that it terminates in a knob instead of tapering. There is no arrangement for introverting the anterior portion of the body into the hinder portion in the Pterobranchia.

The little epistome or præ-oral lobe of Phoronis is represented in the Pterobranchia by a large muscular shield or disk-like structure (fig. 7, *d* and fig. 9, *b*) which overhangs the mouth and has an actively secreting glandular surface by which the tube or case (tubarium) in which the polypide is enclosed is secreted.

Both Rhabdopleura and Cephalodiscus produce colonies by budding; but the colonies of the former are large, definite, and arborescent, whilst those of Cephalodiscus are remarkable for the fact that the buds do not remain long in organic continuity with their parent, but become detached and nevertheless continue to be enclosed by the same common envelope or secretion. The bud-formation of Rhabdopleura recalls that of Paludicella in the fact that it leads to the formation of continuous arboriform communities. That of Cephalodiscus resembles the budding of Loxosoma, since no two fully-formed individuals remain in organic continuity. Both Rhabdopleura and Cephalodiscus (like Phoronis) produce cases or investments in which they dwell. These are free secretions of the organism, and are not, like the cœnœcia of Eupolyzoa, cuticular structures adherent to and part of the polypide's integument. The dwelling of Rhabdopleura is a branched system of annulated tubes of a delicate membranous consistency, each tube corresponding to a single polypide, the rings of which it is built being successively produced at the termination of the tube by the secreting activity of the præ-oral disk (fig. 7, E). The polypides freely ascend and descend in these tubes owing to the contractility of their stalks. On the other hand the dwelling of Cephalodiscus is a gelatinous, irregularly branched, and fimbriated mass (fig. 8), excavated by numerous cavities which communicate with the exterior. In these cavities are found the numerous *detached* small colonies of Cephalodiscus (fig. 9), or we should rather say the isolated budding polypides. The remaining important feature in the organization of the Pterobranchia, namely, the parts connected with the formation of buds, are best understood by first examining Cephalodiscus. The body of Cephalodiscus is seen (fig. 9) to be an oval sac; in this is suspended the U-shaped alimentary canal, and from the walls of its cavity (cœlom) the ova and the spermatozoa are developed. Projecting from the ventral face of this oval sac is a muscular cylindrical stalk, into which the viscera do not pass, though the cœlom is continued into it (fig. 9, *c*). This stalk is merely the outdrawn termination of the body. It is about as long as the whole of the rest of the animal, and it is from its extremity that the buds are produced (fig. 9, *a*). Before the buds have attained half the size of their parent they become detached, but continue to occupy some portion of the common gelatinous dwelling.

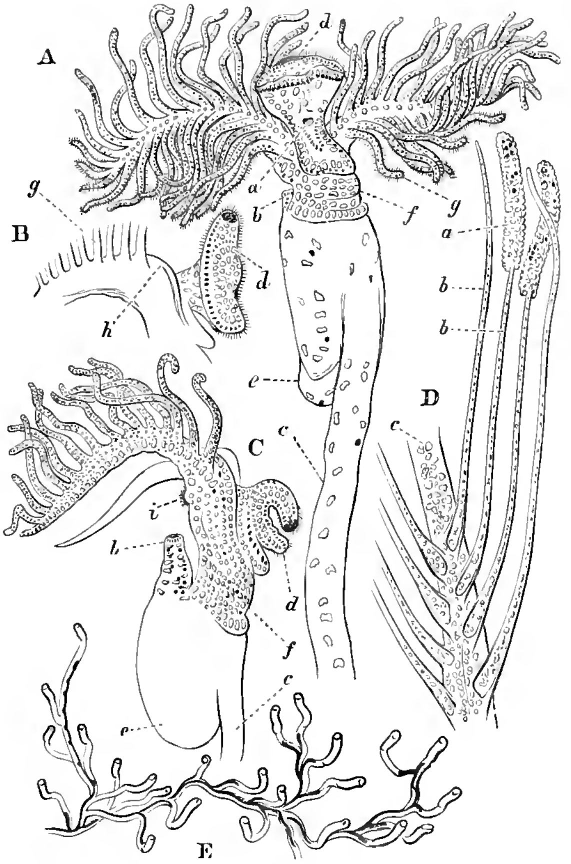

Fig. 7.—*Rhabdopleura Normani*, Allman (original drawings, Lankester). A. A single polypide removed from its tube and greatly magnified. *a*, mouth; *b*, anus; *c*, polypide-stalk or gymnocaulus, the "contractile cord" of Sars; *d*, the præ-oral lobe (buccal shield or disk of Allman); *e*, intestine; *f*, thoracic region of the polypide; *g*, one of the ciliated tentacles. B. Lateral view to show the form of the buccal shield and its pigment spot. *g*, ciliated tentacle (in outline); *h*, basal ridge of the right arm of the lophophore. C. Lateral view of a polypide. *i*, ciliated patch (Sars's organ) at the base of the lophophore-arm. Other letters as above. D. Part of a lophophore-arm, with soft tissues rubbed off to show the cartilaginoid skeleton. *a*, epithelium and soft tissues still adherent at the tip of a tentacle; *b*, skeleton of tentacle; *c*, skeleton of axis. E. Portion of a colony of *Rhabdopleura Normani*, showing the branched tube-like cases formed by the polypides. The black line within the tubes represents the retracted polypides connected together by their common stalk, the pectocaulus. Magnified to three times the size of nature.

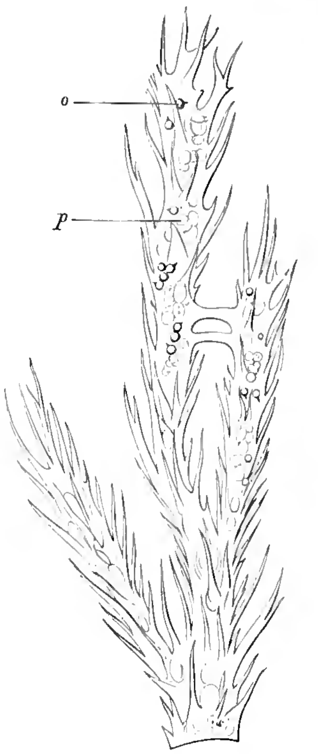

Fig. 8.—Dwelling of gelatinous consistence and brown colour formed by the polypides of *Cephalodiscus dodecalophus*, M'Intosh; natural size (from an original drawing kindly supplied by Prof. M'Intosh, F.R.S.). *o*, polypide within the jelly; *p*, cavity once occupied by polypides.

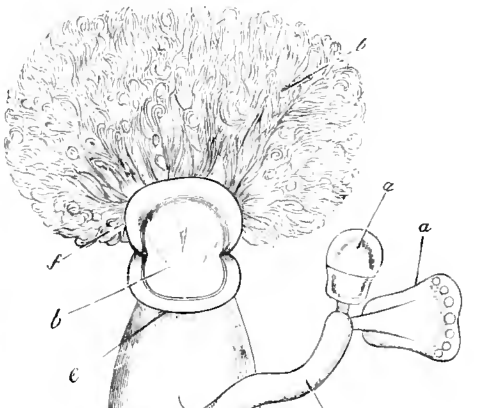

Fig. 9.—A polypide of *Cephalodiscus dodecalophus* removed from the gelatinous house (from an original drawing by Prof. M'Intosh). No organic connexion has been severed in thus isolating this polypide with its attached buds *a*, *a*. The figure represents the furthest point to which colony-formation attains in this form. *a*, buds growing from the base of the polypide-stalk; *b*, the præ-oral lobe (buccal shield or disk); *c*, the polypide-stalk; *d*, the ciliated tentacles of the twelve lophophore arms (six pairs, each like the single pair of Rhabdopleura) inextricably matted and confused; *e*, anterior margin of the præ-oral lobe; *f*, posterior margin of the same. Magnified about fifty times linear

Turning to Rhabdopleura, we find that each polypide has a body of similar shape and character to that described for Cephalodiscus, and a similar ventrally developed "stalk" (fig. 7, A, *c*). But, inasmuch as the buds developed on the stalk of a Rhabdopleura polypide do not detach themselves, we find that we can trace the stalk of each polypide of a colony into connexion with the stalk of the polypide from which it was originally budded, which may now be considered as a "branch" bearing many-stalked polypides upon its greatly extended length, and such a "branch-stalk" may be further traced to its junction with the "stem-stalk" of the whole colony. The stem-stalk was at one time the simple terminal stalk of a single polypide, but by lateral budding it gave rise to other polypides, and so became a gemmiferous "branch"; and further, when some of these in their turn budded and became branches, it became the main "stem" of a copious colony.

A serious error has been made in comparing the contractile stalk of the Pterobranchiate polypide to the "funiculus" or cord-like mesentery of Eupolyzoa. With this it has morphologically nothing in common, since it is not an internal organ, but simply the elongated termination or stalk of the body, comparable to the stalk of Pedicellina (fig. 15) and Loxosoma (fig. 16), or to the hydrocaulus of such a Hydrozoon colony as Cordylophora. The stalk where it bears only very young buds, or none at all, as is always its condition in Cephalodiscus and in many polypides of a Rhabdopleura colony, may be called a "gymnocaulus"; when once its buds have developed into full grown polypides, and it has elongated proportionally with their growth, it becomes a "pectocaulus"; that is to say, it is to that part of it which bears such polypides that this term may be conveniently applied. The pectocaulus of Rhabdopleura, both in the form of branch and stem, undergoes remarkable change of appearance as compared with the gymnocaulus. It loses its contractility, shrinks, and develops on its surface a hard, dark, horny cuticle (whence its name), comparable precisely in its nature to the hardened cuticle which forms the zoœcia of Eupolyzoa. It now has the appearance of a black cord or rod-like body lying within and adherent to the inner face of the much wider tubular stem, and branches formed by the gradual building up and arborescent extension of the annulated tubarium secreted by the individual polypides. It has been regarded both by Allman and by Sars as a special structure, and called by the former "the chitinous rod" or "blastophore," by the latter "the axial cord."

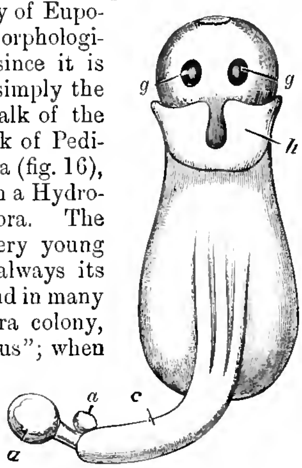

Fig. 10.—A polypide of *Cephalodiscus dodecalophus*, from which the lophophore-tentacles and buccal shield have been removed in order to show the remarkable eyes. *a*, buds; *c*, stalk; *g*, eyes; *h*, post-oral collar, hidden by the buccal shield in fig. 9. (Original drawing by Prof. M'Intosh F.R.S.)

In reality it is the black-coloured pectocaulus of Rhabdopleura which corresponds to the cœnœcium of an ordinary Polyzoon; whilst the term "cœnœcium" is totally inapplicable morphologically to the annulated branched tube in which the Rhabdopleura colony lives, this having absolutely no parallel in the Eupolyzoa.

A sac-like testis has been discovered in Rhabdopleura opening by the side of the anus (Lankester, 7); but the ova have not yet been seen, nor is anything known of its development. Similarly the eggs of Cephalodiscus are observed within the body of the parent in the "Challenger" specimens, but nothing further is known of its life-history.

A body-cavity is present (Lankester), though its existence has been denied by Sars and by M'Intosh. Nephridia and nerve ganglia are not described. Cephalodiscus has two remarkable eye spots dorsal to the cephalic disk (fig. 10, *g*).

THE EUPOLYZOA.

Whilst it is necessary to include in the group Polyzoa the forms we have already noticed as Vermiformia and Pterobranchia, there can be no doubt that those organisms to which we assign the name Eupolyzoa are primarily those upon which naturalists have framed their conception of the group, and that they constitute a very consistent assemblage, held together by well-defined characters, and yet presenting an immense number of varied forms showing a wide range of modifications.

All the Eupolyzoa have closely approximated mouth and anus, and, like Paludicella, a complete range of hollow ciliate tentacles, describing either a circle or a horse shoe, surrounding the mouth. The anus as well as the mouth is included in this area in a few exceptional forms (the Entoprocta); it lies near but outside the lophophore (as the area is termed) in the vast majority (the Ectoprocta). Except in the Entoprocta, where the movement is limited, the whole anterior portion of the body bearing the lophophore can be invaginated into the hinder part (as described above for the typical Eupolyzoon Paludicella). This character distinguishes the Eupolyzoa from both Vermiformia and Pterobranchia. The polypides of all the Eupolyzoa are minute, but all produce buds which remain in organic continuity with their parent (except in Loxosoma) and build up very considerable and sometimes massive colonies.

In all Eupolyzoa the cuticle of the hinder part of each polypide is thick and dense, thus forming a hard-walled sac, the zoœcium. This is peculiar to and universal in the Eupolyzoa (except Loxosoma), and is not to be confounded with the non-adherent tubes of Phoronis and Rhabdopleura or the jelly-house of Cephalodiscus. The connected zoœcia of a colony of Eupolyzoa constitute a cœnœcium. A simple nerve ganglion between mouth and anus, a large body-cavity (except in Entoprocta), simple gonads without accessory glands or ducts, usually testis and ovary in the same polypide, absence of a blood-vascular system, of any but the most rudimentary nephridia, and of eyes, otocysts, or other special sense-organs, are features characterizing all adult Eupolyzoa.

The section Eupolyzoa, with its vast number of species and genera, requires a somewhat elaborate classification. The forms in which the anus is enclosed within the tentacular circle are very few, and are peculiar in other respects. We follow Nitsche (8) in separating them as the sub-class Entoprocta from the majority of Eupolyzoa forming the sub-class Ectoprocta.

Sub-class 1. **Ectoprocta**, Nitsche.

Eupolyzoa with the anus not included within the area of the lophophore. Anterior portion of the body of the normal polypide introversible. Tentacles not individually capable of being coiled or flexed.

Order I. Phylactolæma, Allman.

Ectoproctous Eupolyzoa in which the polypide possesses a præ-oral lobe or epistome, similar to that of Phoronis, and comparable to the more highly developed buccal shield or disk of the Pterobranchia. Lophophore (except in Fredericella, where it is nearly circular) horse-shoe-shaped (hippocrepian). Polypides of a colony equi-formal, that is, not differentiated in structure and function. Neighbouring zoœcia are in free and open communication, the bud never becoming shut off by a perforated cuticular plate from its parent. Cuticle of the zoœcia either gelatinous or horny, forming massive or else arborescent cœnœcia, in one genus

(Cristatella) having the form of a plano-convex ellipse and locomotive (fig. 3). In addition to the multiplication of polypides in a colony by budding, and to the annual production of new individuals from fertilized eggs which initiate new colonies, a reproduction by internal buds called "statoblasts," comparable to the gemmæ of Spongilla, has been observed in all the genera (fig. 3, *b*). The statoblasts are developed from the funiculus (mesentery), and are enclosed in ornate lenticular capsules of chitinous substance, characteristic in form in each species.

The fertilized egg of the Phylactolæma does not give rise to a zonociliate larva, but to a uniformly ciliate cyst-like diblastula, which develops directly and produces polypides by budding. The Phylactolæma are all inhabitants of fresh water (lacustrine).

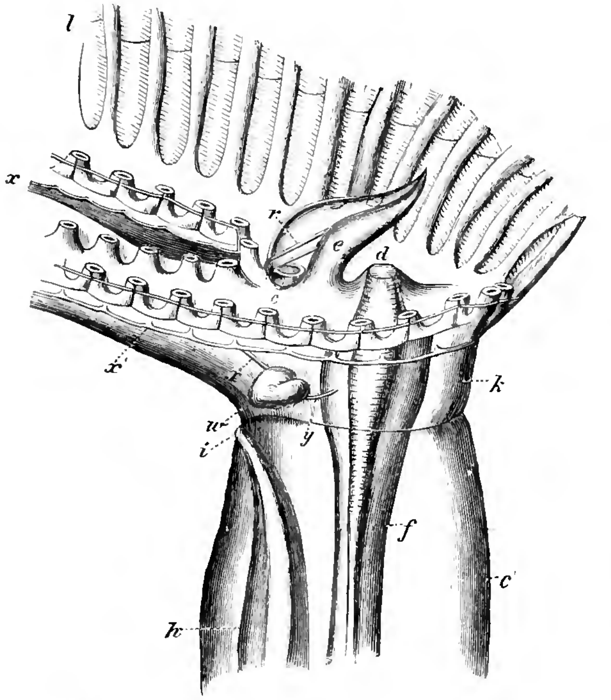

FIG. 11.—Semi-ideal view of part of the lophophore of *Lophopus* and its tentacles,—intended to show the nerve-ganglion, nerves, and parts around the mouth. The tentacles have been cut away all along the right arm of the lophophore and from the inner margin of the left arm. *c*, foramen placing the cavity of the epistome in communication with the body-cavity; *c'*, body-wall; *d*, mouth; *e*, the epistome or præ-oral lobe; *f*, wall of the pharynx; *h*, wall of the intestine; *i*, anus; *k*, lophophore; *l*, a ciliated tentacle; *r*, elevator muscle of the epistome; *w*, the nerve-ganglion; *x*, *x'*, nerves to lophophore and tentacles· *y*, nerve to pharynx.

The Phylactolæma include the genera Lophopus, Cristatella, Alcyonella, Plumatella, and Fredericella, which have been beautifully figured and described in Allman's classical *Freshwater Polyzoa*, Ray Society, 1856. The colonies of Lophopus are small, consisting of half a dozen polypides embedded in a massive glass-like cœnœcium. Cristatella (fig. 3) is remarkable amongst all Polyzoa for its locomotive zoarium. Alcyonella forms massive cœnœcia of many hundred polypides, as large as a man's fist. Plumatella and Fredericella are delicate arborescent forms commonly encrusting stones and the leaves of water-plants. All the genera known are British.

The Phylactolæma furnish a remarkable instance of a well-marked zoological group being confined to fresh water. Their reproduction by statoblasts (not known in the marine Polyzoa) appears to be related to the special conditions of lacustrine life, since it is also observed under the same exceptional conditions in the single freshwater genus of another great group of animals, viz., Spongilla. Also related to their non-marine conditions of life is the development of the fertilized egg, which, as in so many similar cases, does not produce the remarkable banded forms of locomotive larvæ which are characteristic of their marine congeners.

Order 2. GYMNOLÆMA, Allman.

Ectoproctous Eupolyzoa in which the polypide is devoid of any trace of the præ-oral lobe or epistome, whilst the lophophore is perfectly circular. The polypides of a colony are frequently highly differentiated as avicularia, vibracularia, oœcia (egg-receptacles), and even as root and stem segments. The neighbouring polypides of a colony communicate (?) with one another by "rosette-plates" or "communication-plates"—perforated areas in the walls of contiguous zoœcia. The greatest variety in the character of the cuticle forming the zoœcia (gelatinous, horny, calcareous) and in the grouping of the polypides, as well as in the shape of their zoœcia, is observed in different sub-orders and families. In addition to the ordinary sexual reproduction, there are various modifications of the process of budding, the full exposition of which would necessitate more space than is here allotted, and is not yet indeed within the possibilities of present knowledge. The fertilized egg of the Gymnolæma gives rise to remarkable ciliate larvæ of various forms (figs. 19, 20, 21), from which the first polypide of a colony is developed by an extraordinary and unexplained series of changes. The Gymnolæma are, with the single exception of the genus Paludicella, inhabitants of the sea.

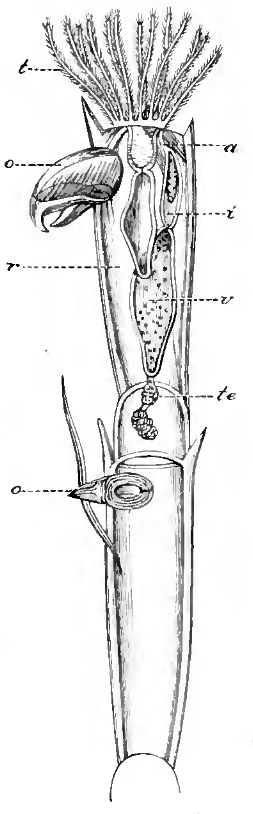

FIG. 12.—Two zoœcia of *Acamarchis (Bugula) avicularia*, Lmx. (Chilostoma), of which the anterior contains a living polypide, whilst the posterior is empty. To each is attached one of the characteristically modified polypides known as an "avicularium" *o*; the hinder of these has grasped and holds in its beak a small worm. *a*, anus; *i*, intestine; *v*, stomach; *r*, body-cavity (cœlom); *t*, tentacular crown surrounding the mouth; *te*, testis cells developed on the surface of the terminal mesentery or "funiculus"; *o*, *o*, avicularia.

The Gymnolæma are divided, according to the system of Busk, into three sub-orders characterized by the shape of their zoœcia, and the nature of the mouth-like margin which it presents when the exsertile portion of the polypide is withdrawn within it. The **Cyclostoma** have long tubular zoœcia, often of large size and often calcified, placed side by side in cylindrical bundles, or in other definite grouping; the mouth of the zoœcium is circular and devoid of processes. There is little or no differentiation of the polypides constituting a colony. Most of this group are fossil, and the living genera belong mostly to southern seas. The genera Crisia (fig. 13, A), Diastopora, Tubulipora, and Hornera are typical. The **Ctenostoma** have usually a soft zoœcium; its orifice is closed by the folds of the retracted polypide or by a circlet of bristles which surround it. *Alcyonidium gelatinosum* is the commonest representative of this group on the British coasts. Bowerbankia (fig. 1, A) and Paludicella (fig. 1, E) also belong here. The **Chilostoma** form the largest and most varied sub-order of Gymnolæma. The zoœcia are horny or calcified; their orifices can be closed by a projecting lip in the form of an operculum. The operculum is a separable plate developed on the cuticle of the retractile part of the polypide, and has muscles attached to it (fig. 13, B, C, D). The surface of the zoœcia is frequently sculptured, and its orifice provided with processes and spines (fig. 1, C, F). Very usually some of the polypides of a colony are modified as avicularia, vibracularia, radical fibres, and oœcia. The avicularium is a polypide reduced to a simple muscular apparatus working upon the modified operculum and zoœcium so as to cause these hard parts to act as a snapping apparatus comparable to a bird's head (fig. 12, *o*). They are frequently found regularly distributed among the normal cells of a colony, and probably have a cleansing function similar to that attributed to the Pedicellariæ of the Echinoderms. "Vibracularia" are even more simplified polypides, being little more than motile filaments, probably tactile in function. The opercula of zoœcia, oœcia, and avicularia have recently been used by Busk in characterizing genera and species, in a systematic way. Stem-building and root-forming polypides are frequently found, being closed polypides which subserve anchoring or supporting functions for the benefit of the whole colony. The stem of Kinetoskias (fig. 14) is produced in this way. The Chilostoma include a large series of genera arranged in the sections Cellularina, Flustrina, Escharina, and Celleporina. For the systematic description of the highly complex and very varied colonial skeletons or cœnœcia of the Gymnolæma, the reader is referred to the works of Busk (9), Hincks (10), Smitt (11), and Heller (12). See also Ehlers (13) on Hypophorella.

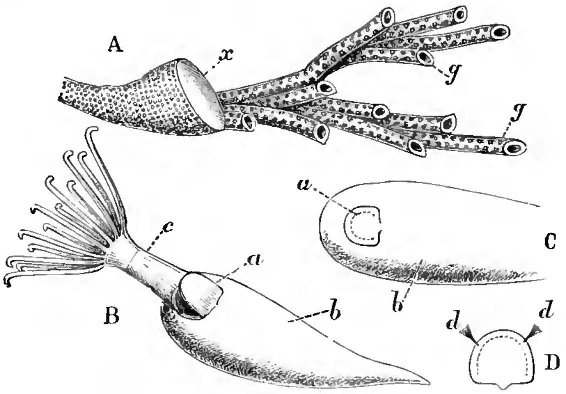

Fig. 13.—A. Cænœcium of *Crisia eburnea*, Lin., one of the Cyclostoma; *g*, *g*, tubular zoœcia with circular terminal mouths; *x*, oœcium, being a zoœcium modified to serve as a brood-chamber.
B. Diagram of a single polypide of one of the Chilostoma in a state of expansion, in order to show the position and action of the operculum. *a*, operculum, a plate of thickened cuticle hinged or jointed to *b*, the main area of dense cuticle of the antitentacular region known as the zoœcium; *c*, the soft-walled portion of the polypide in expansion.
C. The same zoœcium with the polypide invaginated (telescoped) and the operculum *a* shut down over the mouth of the zoœcium.
D. Operculum detached, and seen from its inner face, to show the occlusor muscles *d d*.

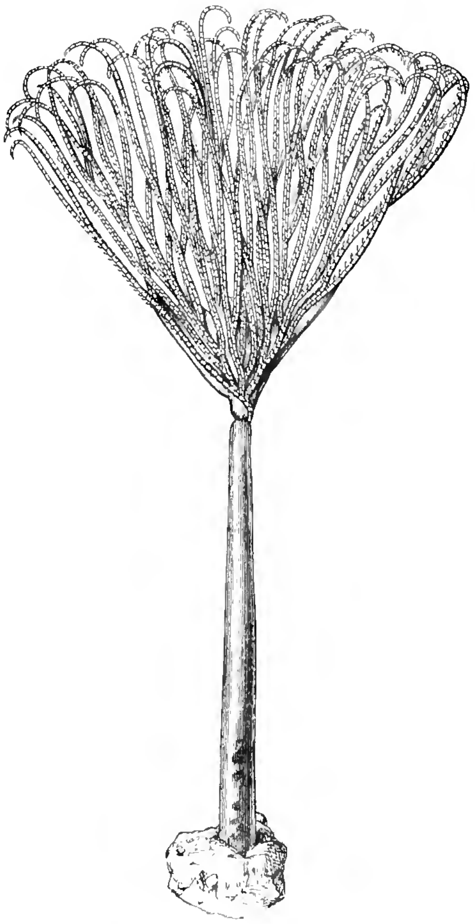

Fig. 14.—*Kinetoskias* (*Naresia*) *cyathus* (from Sir Wyville Thomson). The polypides and zoœcia are allied to *Bugula*, but the zoarium as a whole is remarkable for its definite shape, consisting of a number of slightly branched gracefully bending filaments supported like the leaves of a palm on a long transparent stalk. (See Busk, in *Quart. Journ. Micr. Sci.*, 1881, for further details.)

Sub-class 2. **Entoprocta**, Nitsche.

Eupolyzoa in which the anal aperture lies close to the mouth within the tentacular area or lophophore. Lophophore sunk within a shallow basin formed by the inversion of the broad truncated extremity of the cup-shaped body. Tentacular crown not further introversible, the individual tentacles (as in the Pterobranchia and unlike the Ectoprocta) capable of being flexed and partially rolled up so as to overhang the mouth (see fig. 15, B and C). Body-cavity (cœlom) almost completely obliterated. The antitentacular region of the polypide's body is drawn out to form a stalk similar to the gymnocaulus of the Pterobranchia. The extremity of this stalk is provided with a cement gland in the young condition which persists in the adult of some species (*Loxosoma neapolitanum*, fig. 16, *shs*). Cuticular investment (zoœcium) of the polypides feebly developed. A pair of small nephridia are present.

The Entoprocta consist of the marine genera Pedicellina (fig. 15), Loxosoma (fig. 16), and probably the insufficiently known freshwater American genus Urnatella of Leidy. To these must be added Busk's new genus Ascopodaria, as yet undescribed, based on a specimen dredged by the "Challenger," showing a number of Pedicellina-like polypides, carried as an umbel on a common stalk of very peculiar structure. Pedicellina is found attached to algæ, shells, zoophytes, &c., and to the integument of some Gephyræan worms (*Sipunculus punctatus*) and Annelids (Aphrodite); Loxosoma occurs on various worms, &c. Whilst the buds of Pedicellina remain connected so as to constitute a colony, those produced by Loxosoma are continually detached, so that the polypide is solitary. Further, the cup-like body of Pedicellina is deciduous, and frequently falls from the stalk and is replaced by new growth. There is less distinction between body and stalk in Loxosoma, and the former does not become detached. Apparently a very important feature in the structure of the Entoprocta is the absence of a body-cavity. This is, however, more apparent than real. The Entoprocta are true Cœlomata, but the cœlom is partially obliterated by the growth of mesoblastic tissue. The nephridia presumably lie in a space which, small as it is, represents the cœlom. See Harmer (18) for details.

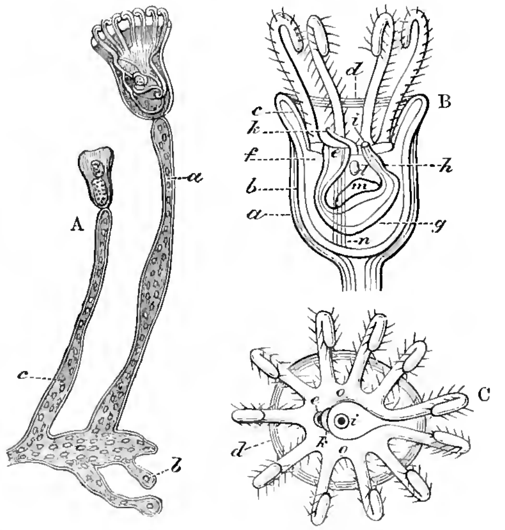

Fig. 15.—A. Two polypides and buds of *Pedicellina belgica*, Van B. (after Van Beneden); greatly magnified. *a*, the polypide-stalk of a fully developed polypide; *c*, that of a less mature individual; *b*, a bud. All are connected by a common stalk or stolon. B. and C. Two views of the body of the polypide of Pedicellina (after Allman). *a*, cuticle; *b*, body-wall; *c*, permanently introverted anterior region of the body; *d*, margin of the tentacular cup or calyx thus formed; *e*, mouth; *f*, pharynx; *g*, stomach; *h*, intestine; *i*, anus; *k*, epistome or præ-oral lobe; *l*, nerve-ganglion; *m*, gonad; *n*, retractor muscle of the lophophore; *o*, lophophore.

Genealogical Relationships of the Groups of Polyzoa.

It is necessary that we should try to form some opinion as to which of the various groups of Polyzoa are most like the ancestral form from which they have all sprung, and what are the probable lines of descent within the group. Any attempt of the kind is speculative, but it is absolutely needful since zoology has become a science—that is to say, an investigation of causes and not merely a record of unexplained observations—to enter upon such questions. Colonial organisms have necessarily descended from solitary ancestors, and it is probable that the ancestral form of Polyzoa was not only solitary, as are Phoronis and Loxosoma at the present day, but of relatively large size and more elaborately organized than the majority of living Polyzoa. Whilst the polypides have dwindled in size and lost some of their internal organs, the modern Polyzoa have developed *pari passu* with this degeneration an elaborate system of bud-production and colony-formation. The new individuality (the tertiary aggregate) attains a high degree of development (Cristatella, Kinetoskias) in proportion as the constituent units merged in this new individuality have suffered a degeneration. The præ-oral lobe (epistome, buccal disk) present in all Polyzoa except the most minute and most elaborately colonial forms—namely, the Gymnolæmia—is to be regarded as an ancestral structure which has been lost by the Gymnolæma. The horse-shoe-shaped lophophore, such as we see it in Phoronis and in Lophopus, is probably the ancestral form, and has given rise to the two other extreme forms of lophophore,—namely, the "pterobranchiate," associated with a great development of the epistome, and the "circular," associated with a complete suppression of the epistome. The entoproctous lophophore is a special modification of the horse-shoe-shaped, as shown in the diagram fig. 15, C. The formation of zoœcia, and so of an elaborate colonial skeleton, was not a primary feature of the Polyzoa. Even after budding and colony-formation had been established zoœcia were not at once produced, but possibly dwellings of another kind (Pterobranchia). We are thus led to look upon the Gymnolæma as the extreme modification of the Polyzoon type. Starting with an organism similar to Phoronis, we may suppose the following branchings in the pedigree to have occurred.

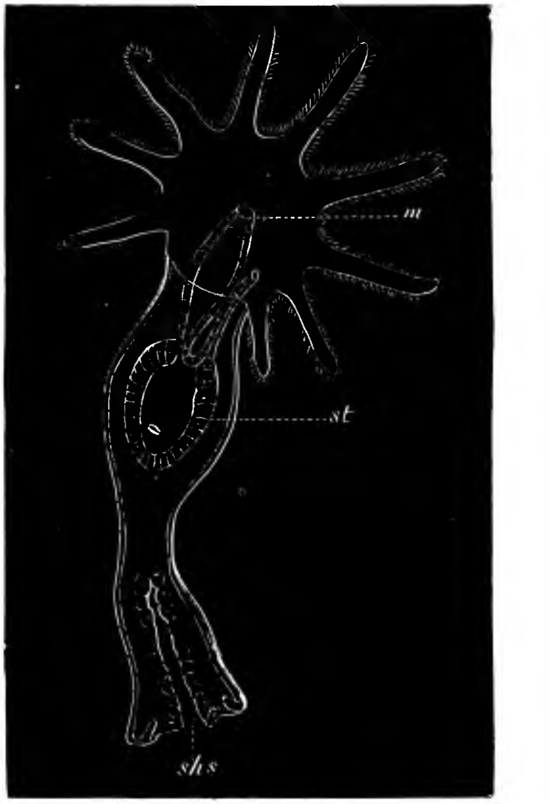

FIG. 16.—Diagram of *Loxosoma Neapolitanum* (after Kowalewsky). A single polypide devoid of buds. *m*, mouth; *st*, stomach; *shs*, basal gland of the polypide-stalk.

VERMIFORMIA

A. The complete hippocrepian lophophore becomes specialized in the form of ctenidia or gill-plumes; the epistome enlarged.
= PTEROBRANCHIA.

α. The anti-tentacular region of the body elongated as a stalk gives rise to one or two rapidly detached buds (Cephalodiscus).

β. The stalk gives rise to buds which do not detach themselves, but remain in continuity so as to form a colony of a hundred or more individuals (Rhabdopleura).

B. The complete hippocrepian lophophore retains its form, but acquires a gradually increasing power of being telescoped into the hinder part of the body.
= The Pro-Eupolyzoon.

A. The anti-tentacular region of the body becomes stalk-like, and develops buds which either detach themselves as they form (Loxosoma) or remain to form a small colony (Pedicellina). The telescopic introversibility of the lophophore does not advance beyond an initial stage. The arms of the lophophore grow round so as to embrace the anus.
= Sub-class 1 (of the Eupolyzoa) Entoprocta.

B. The complete hippocrepian lophophore remains in its original form, and also the præ-oral epistome, but the telescopic introversibility of the anterior region of the body is greatly developed at the same time that the cuticle of the hinder part of the body is increased in thickness and toughness. Bud production, not from a stalk-like pedicle, but from all parts of the body, now becomes characteristic, the buds, which were at first deciduous, now remaining in permanent continuity so as to form colonies.
= The Pro-Ectoprocton.

A. The polypides acquire the property of carrying their young so as to avoid the disastrous influences of fluviatile currents, and also the property of producing resistent statoblasts, and thus are enabled to become isolated and to persist in the peculiar conditions of fresh waters.
= The 1st order (of Ectoprocta) Phylactolæma.

B. The polypides forming relatively larger colonies, and themselves becoming relatively more minute, lose by atrophy the præ-oral epistome; and simultaneously the arms of the hippocrepian lophophore dwindle, and a simple circum-oral circlet of tentacles is the result. The cuticle of the hinder part of the polypide becomes more and more specialized as the cell or zoœcium, and in different polypides in various parts of the colony acquires special forms—as egg-cases, snappers (avicularia), tentacles, stalk and root segments.
= The 2d order (of Ectoprocta) Gymnolæma.

Distinctive Characters of the Polyzoa.

From all that has preceded it appears that the really distinctive characters common to all the Polyzoa may be summed up as follows:—

Cœlomata with closely approximated mouth and anus, the bulk of the body forming a more or less elongate growth at right angles to the original (ancestral) oro-anal axis, and starting from the original ventral (*i.e.*, oral) surface. A variously modified group of ciliated tentacles is disposed around the mouth, being essentially the development by digitiform upgrowth of a post-oral ciliated band.

As negative characters it is important to note the absence of all trace of metameric segmentation, of setæ, and of paired lateral (parapodia of Appendiculata) or median ventral (podium of Mollusca) outgrowths of the body-wall.

Larval Forms of Polyzoa.

In the consideration of the probable pedigree and affinities of the Polyzoa, we are not at present able to make use of the facts of development from the egg, on account of the extreme difficulty which the study of the young stages of these organisms presents. In the case of Phoronis we have the only readily intelligible history. The larva, to start with, is of that form known as an architroch (see Lankester, "Notes on Embryology and Classification," *Quart. Journ. Micr. Sci.*, 1876), having a præ-oral ciliated area (velum or cephalotroch) continuous with a post-oral ciliated band (the branchiotroch), which latter becomes developed into the tentacular crown of the adult.

The actinotrocha (Phoronis) larva is readily comparable with the trochosphere larvæ of Echinoderms, Chætopods, Gephyræans, and Molluscs. Its special character consists in the strong development of the post-oral ciliated band, whereas the præ-oral ciliated band is in most other classes (the Sipunculoids excepted) the predominant one. The Phoronis larva exhibits first of all an oro-anal long axis, and this is suddenly abandoned for a new long axis by the growth of the ventral surface of the larva at right angles to the primary axis (hence the term Podaxonia).

In the other Polyzoa we do not at present know of any larva which retains even in its earliest phases the original oro-anal long axis. They all appear to start at once with the peculiar and secondary long axis of the adult Phoronis, so that Balfour has diagrammatically represented the Polyzoon larva by the sketch given in fig. 19. This diagram applies, however, more especially to the Entoprocta, since the anus is represented as included in the area of the post-oral ciliated ring. The development of Pedicellina has been very carefully followed by Hatschek, and may be said to be the only instance among the Eupolyzoa in which the growth of the different organs and the consequent relation of the form of the larva to the form of the adult is understood (see figs. 17 and 18).

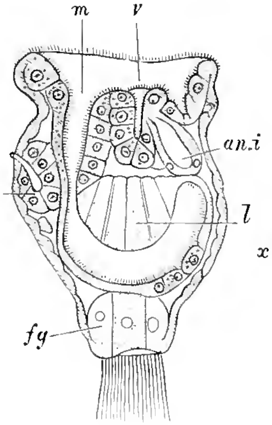

Fig. 17.

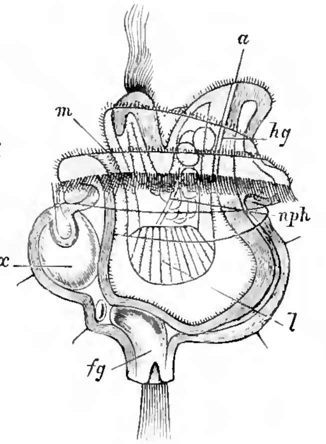

Fig. 18.

Fig. 17.—Larva of Pedicellina (from Balfour, after Hatschek). *v*, vestibule (the cup-like depression of the tentaculiferous end of the body); *m*, mouth; *l*, digestive gland; *an.i*, anal invagination; *fg*, the ciliated disk (corresponding to the cement gland of Loxosoma (fig. 16, *shs*); *x*, so-called "dorsal organ," supposed by Balfour to be a bud, by Harmer (**18**) regarded as the cephalic ganglion.

Fig. 18.—Later stage of the same larva as fig. 17. Letters as before, with the addition of *nph*, duct of the right nephridium; *a*, anus; *hg*, hind-gut.

In the other Polyzoa, in spite of the painstaking and minute studies of Barrois (**14**), the fact is that we do not know what face of the larva corresponds to the tentacular area, what to the stalk or anti-tentacular extremity, what to the anterior and what to the posterior surface. The conversion of the larva into the first polypide has not been observed in the case of these free-swimming forms, and it is even probable that no such conversion ever takes place, but that the first polypide forms as a bud upon the body-wall of the larva.

Two of the most remarkable forms of free-swimming larvæ of Gymnolæma are represented in figs. 20 and 21. In both, in addition to the chief post-oral ciliated band, a smaller ciliated ring is observed, which is identified by Balfour with that which is found at the anti-tentacular extremity (base of the stalk) in the Pedicellina larva.

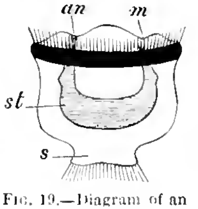

Fig. 19.—Diagram of an ideal Polyzoon larva (from Balfour). *an*, anus; *m*, mouth; *st*, stomach; *s*, ciliated disk (*fg* in figs. 17, 18, and 21).

It does not seem justifiable, in the face of the existing uncertainties as to identification of parts, and in view of the high probability that the Gymnolæma are extremely modified and degenerate forms (a consideration which applies in some respects even more strongly to the Entoprocta), to assume that the larval form schematized in fig. 19 represents an ancestral condition of the Polyzoa. Professor Balfour (**15**) was, however, led to entertain such a view; and, assuming that the chief ciliated band (drawn as a broad black line) corresponds to the single præ-oral ciliated band of the trochosphere larva of Echiurus, Polygordius, Chætopods, and Mollusca, he pointed out that in both cases the ciliated girdle divides the larva into a hemisphere in which mouth and anus lie and a hemisphere which is the complement of this; in most classes the first hemisphere elongates and forms the bulk of the body, whilst the second hemisphere forms the prostomium or præ-oral lobe. But, according to Balfour's theory, in Polyzoa it is the second hemisphere which enlarges and becomes the stalk-like body of the adult, whilst the first hemisphere remains small and insignificant. Thus the Polyzoa would fix themselves in later growth by what corresponds to the head or prostomium of other animals, as do the Barnacles and the Ascidians. Ingenious as this speculation is, we must remember that it takes no account of the facts known as to Phoronis, nor of the Pterobranchia, and that it is confessedly based upon the assumption that the larvæ of extremely degenerate and peculiar members of the group are not adaptive and modified, but retain primary and archaic characters. Further, it is to be distinctly borne in mind that the interpretation of parts upon which this speculation rests is, except in the case of Pedicellina, altogether hypothetical.

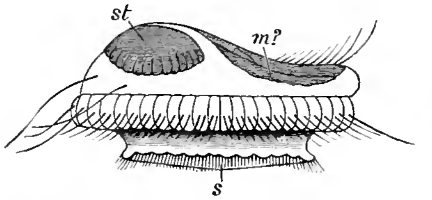

Fig. 20.—Larva of *Alcyonidium mytili* (from Balfour after Barrois). *m* ?, problematic structure; *st*, oral invagination (?) = Harmer's cephalic ganglion; *s*, ciliated disk (corresponding to *fg* in figs. 17, 18, and 21).

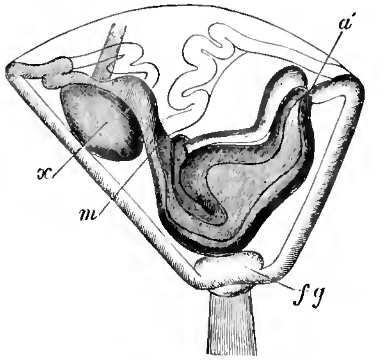

Fig. 21.—Larva of Membranipora (known as Cyphonautes). *m*, mouth; *a'*, anus; *fg*, ciliated body; *x*, problematical body, supposed by Balfour to be a bud, similar to the dorsal organ *x* in figs. 17, 18, and to either *st* or *m* in fig. 20.

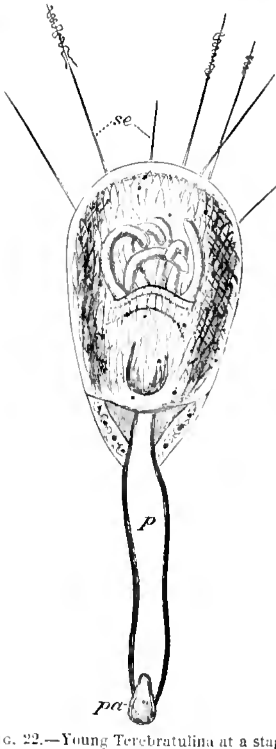

Fig. 22.—Young Terebratulina at a stage when only six tentacles are present. *se*, setæ at the margin of the calyx; *p*, stalk comparable to the stalk of Pedicellina, Loxosoma, Cephalodiscus, and Rhabdopleura; *pa*, cement gland at the apex of the stalk (after Morse).

Relations of the Polyzoa to the Brachiopoda.

The Polyzoa were first associated with the Brachiopoda by H. Milne-Edwards. The investigation of the development of Terebratulina by Morse (**16**) led to a further perception of the points of agreement in structure between these two groups. Lastly, Caldwell (**6**) has shown that the mesenteries of Phoronis have precisely similar relations to the lophophore, the nephridia, and the termination of the intestine as have the gastro-parietal and ilio-parietal bands or mesenteries of the Terebratulidæ. The young Terebratulina (fig. 22) may be readily compared with Loxosoma (fig. 16),—the peduncle with its cement glands in the former being identical with the stalk and basal gland of the latter. The form of the alimentary canal and the disposition of the tentacular arms (fig. 23) is the same in Brachiopoda and Polyzoa. The nephridia (oviducts) of Terebratula have a position and relations similar to those of the nephridia (genital ducts) of Phoronis. The chief difference between Polyzoa and Brachiopoda consists in the special development of the margin of the cupped end of the body, into which the lophophore is sunk, as in Pedicellina (see fig. 15, B, *c*). This up-standing margin is enormously increased in the Brachiopoda, so as to form a voluminous hood or collar, which surrounds the large tentacular arms, and forms a protective chamber for them. It is notched right and left so as to be divided into two lobes, and on its surface is developed a horny or a calcareous shell in two corresponding moieties. Until recently it was held (see Lankester, 17) that both Brachiopoda and Polyzoa were modifications of the Molluscan type, and the Brachiopods' collar was identified with the pallial fold of Mollusca. The resemblance of the two structures must now be considered as purely homoplastic, and not as having any real morphological (homogenetic) significance.

Fig. 23.

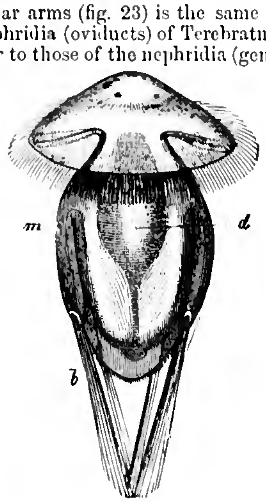

Fig. 24.

FIG. 23.—Lophophore and epistome of young Terebratulina, showing the horseshoe shape; the arms are turned in the direction the reverse of that taken by the lophophore-arms in Polyzoa (see fig. 4). In later growth they will become spirally coiled. (After Morse.)

FIG, 24.—Larva of the Brachiopod Argiope (from Gegenbaur, after Kowalewsky). *m*, setigerous lobe; *b*, setæ; *d*, enteron.

The larvæ of the Brachiopoda (figs. 24, 25) are as exceptional and difficult of interpretation as those of Polyzoa, but no attempt has been yet made to show that the one can be reduced to a common form with the other. The three segments presented by some Brachiopod larvæ (fig. 25) have been compared to the segments of Chætopod worms by some writers; and these, together with the presence of setæ, have been regarded as indicative of affinity between the Brachiopoda and Chætopoda (Morse). But it is sufficient, in order to dispose of this suggestion, to point out that the segments of the Chætopoda follow one another along the primary oro-anal axis, whilst those of Brachiopoda are developed along an axis at right angles to this (Caldwell).

The Brachiopoda must be classified together with the Polyzoa and Sipunculoidea in a phylum (Podaxonia) characterized by the development of this secondary axis.

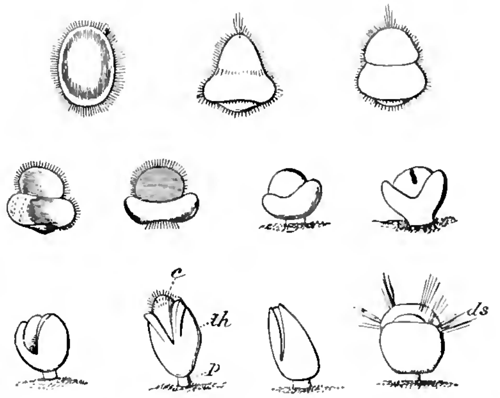

FIG. 25.—Surface views of ten stages in the development of Terebratulina, showing the free-swimming larva and its mode of fixation (after Morse). *c*, lophophoral segment; *th*, thoracic segment; *p*, peduncular segment; *ds*, deciduous setæ.

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VERTEBRATA

Lamarck's and Cuvier's classifications.

VERTEBRATA, the name of a great branch or phylum of the Animal Kingdom which comprises those animals having bony "vertebræ", or pieces of bone jointed so as to form a spinal column. The first recognition of the group is due to Lamarck (1797), who united the four highest classes of Linnæus's system as "animaux à vertèbres," whilst distinguishing the rest of the animal world as "animaux sans vertèbres." The same union of the four Linnæan classes had been previously made by Batsch in 1788, who, however, proposed for the great division thus constituted the name "Knochenthiere." The significance of Lamarck's classification was materially altered, and the foundation laid of our present attempts to represent by our classifications the pedigree of the animal kingdom, when Cuvier propounded his doctrine of "types," and recognized the *Vertebrata* as one of four great types or plans of structure to be distinguished in the animal world (*1*).[1]

Essential structures of Vertebrates.

The *Vertebrata* of Lamarck and Cuvier included beasts, birds, reptiles, and fishes, and until recently the group was considered as one of the most sharply limited in the animal kingdom. The progress of anatomical studies very soon rendered it clear that all *Vertebrata* did not possess bony vertebræ; for, besides the commoner sharks and skates, with their purely cartilaginous skeletons, naturalists became acquainted with the structure of fishes, such as the sturgeons and the lampreys, which possess no vertebræ at all, but merely a continuous elastic rod (the notochord) in the place of the jointed spinal column. The muscles and their skeletal septa were seen in these fishes to be arranged in a series of segments attached to the sides of this continuous rod; and hence the structural character of bony vertebræ, as distinguishing the *Vertebrata*, gave place to the character of segmental arrangement of the muscles of the body-wall, such muscles being supported by a skeletal axis which might be itself unsegmented (notochord), or replaced by segmental cartilaginous or bony vertebræ. The studies of embryologists furnished a sound foundation for this conception by demonstrating that in the embryos of *Vertebrata* with true vertebræ these structures are preceded by an unsegmented continuous notochord. The inquiry into the structural characteristics of *Vertebrata* led further to the recognition of several additional points of structure, the combination of which was present only in the group which had been recognized by Lamarck on superficial grounds. It was found that all *Vertebrata* possess laterally-placed passages leading from the pharynx to the exterior, serving in the aquatic forms as the exits for water taken in by the mouth, and provided with vascular branchial processes, whilst in the embryos of the higher air-breathing classes they appear only as temporary structures. It was further established that the great mass of nervous tissue lying dorsally above the spinal column, and known as the cerebro-spinal nerve-centre or brain and spinal cord, is in all cases a tube, and originates as part of the dorsal surface of the embryo, which becomes depressed in the form of a long groove and finally closed in by the adhesion of its opposite edges, thus forming a tube or canal. The three structures,—notochord, gill-slits, and tubular dorsal nerve-cord,—were more than twenty years ago recognized as characterizing, together with the metameric segmentation of the musculature of the body-wall, all *Vertebrata* at some one or other period of their existence.

Question of Vertebrate ancestry.

Kowalewsky's labours.

The establishment by Darwin of the doctrine of organic evolution in 1859 led naturalists consciously to make the attempt to determine the genetic affinities and the probable ancestry of the various groups of animals, and enabled them to recognize in the classifications by "type", and other such conceptions of earlier systematists, the unconscious striving after genealogical representation of the relationships of organic beings. The question naturally arose in regard to the *Vertebrata*, as in regard to other great divisions of the animal kingdom, What were the characters of the earliest forms, the ancestors of those now living? Then came the further questions as to whether any surviving *Vertebrata* closely resemble the ancestral form, and whether any animals are still in existence which retain the general characters of those primeval forms which were the common ancestors at once of Vertebrates and of other large and equally well-marked phyla or branches of the animal kingdom, such as the Molluscs, the Annulates, &c. This fascinating subject of inquiry received its most important impulse from the embryological investigations of the Russian naturalist Kowalewsky, and has been for nearly a quarter of a century the fertile source of speculation and its indispensable accompaniments, new observation and research. Kowalewsky published in 1866 an account of the embryology of the lowest and simplest of then recognized Vertebrates, the lancelet (*Amphioxus lanceolatus*), in which he attempted to trace, cell for cell from the fertilized egg-cell, the origin of the characteristic

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[1] These numerals refer to the bibliography at the end of the article.

Vertebrate organs of this animal (*2*). This work alone would not have acquired historic importance, although it is the starting-point of what may be called strict cellular embryology, as compared with the less severely histological works of previous students. But it was accompanied by an account (*3*) of the development of *Ascidia mamillata*, one of the so-called Tunicate Molluscs, in which it was demonstrated by Kowalewsky, not only that this supposed Mollusc possesses when first hatched from its egg-envelope a notochord, pharyngeal gill-slits, and a tubular dorsal nerve-cord and brain, but that these three characteristically Vertebrate features of organization originate from the same cell-layers of the embryo, and in essentially the same way as in *Amphioxus*, whilst the cell-layers themselves originate from the egg-cell in the two animals by precisely similar movements of cell division and invagination (see figs. 1 and 2). Kowalewsky's discoveries established once for all that the Ascidian tadpole is identical in three very special and distinct features of structure with the frog's tadpole. No classification which pretended to set forth the genetic affinities of animals could henceforth separate the Ascidian from the *Vertebrata*, and with it the Ascidian brought the whole series of *Tunicata*.

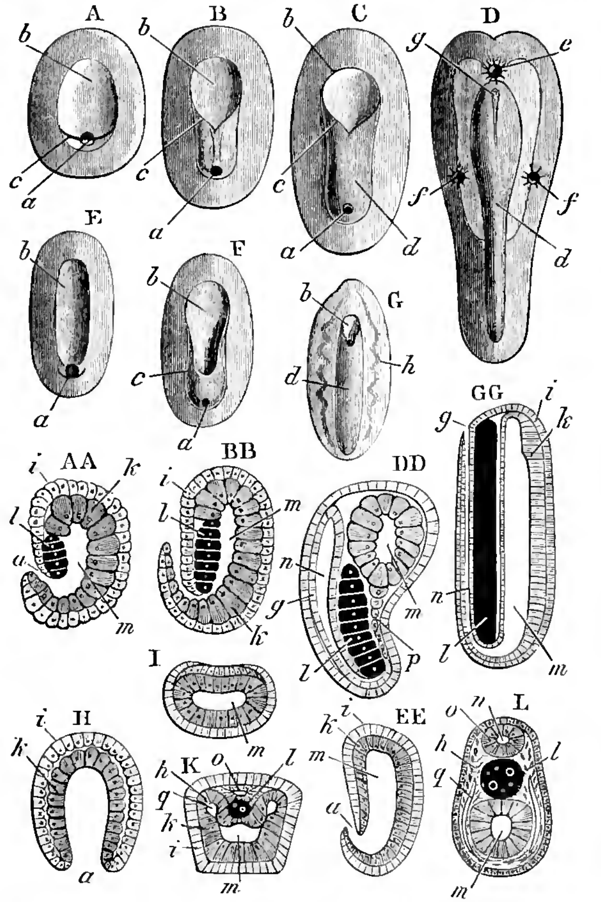

Fig. 1.—Early stages of *Ascidia* and *Amphioxus*. *a*, blastopore; *b*, neural groove; *c*, neural folds; *d*, closed portion of neural tube; *e*, commencing oral invagination (stomodæum) of Ascidian tadpole; *f*, right and left cloacal invaginations of Ascidian tadpole; *g*, anterior opening of neural tube of *Amphioxus*, coincident with the later developed olfactory pit; *h*, wall of one of the series of paired outgrowths of archenteron or cœlomic pouches of *Amphioxus*; *i*, ectoderm; *k*, endoderm (of diblastula phase); *l*, notochord, derived from endoderm; *m*, cavity of gut; *n*, cavity of nerve-tube; *o*, wall of nerve-tube, formed by upgrowth and union of neural folds; *p*, mesoblast of tail of Ascidian tadpole, derived from endoderm; *q*, lumen of cœlomic pouches of *Amphioxus*, once continuous with *m*, but nipped off in the course of development.

A, B, C, D. Four stages in development of *Ascidia*, surface views showing gradual enclosure of neural area. E, F, G. Three similar stages in development of *Amphioxus*. AA. Vertical antero-posterior median section of A. BB. Similar section of B. DD. Similar section of a stage a little earlier than D. EE. Similar section of E (*Amphioxus*). GG. Similar section of embryo represented in G. H. Transverse section of diblastula stage of *Amphioxus*, with widely open blastopore (earlier than A or E). I. Transverse (right and left) section about the middle of F, showing neural area. K. Transverse section about middle of G, showing nerve-tube, notochord, and cœlomic pouches or mesoblastic somites *q*. L. Transverse section of a much further advanced embryo of *Amphioxus*, showing nerve-tube, notochord, and gut; the walls of the cœlomic pouches are now converted into muscular tissue and the pouch cavity (*q*) compressed. (All the figures after Kowalewsky, *17*, *18*.)

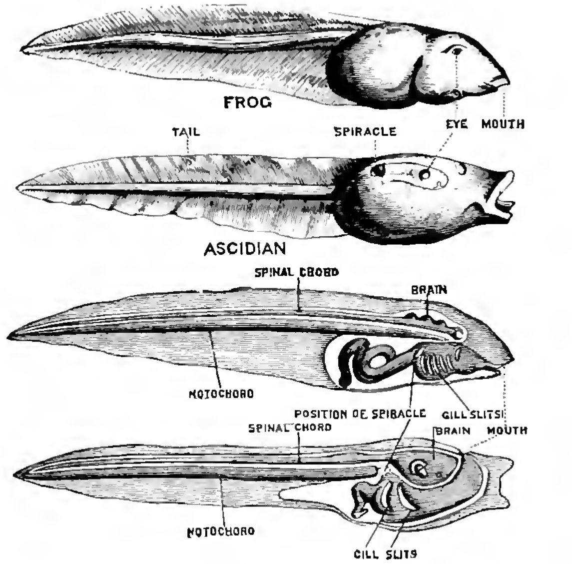

Fig. 2.—Diagram illustrating relationship of tadpoles of Frog and Ascidian. The two upper figures represent surface views of the tadpoles; the two lower ones show in place the chief Vertebrate organs, viz., notochord, gill-slits, nerve-tube, and myelonic eye. (From Lankester's *Degeneration*.)

Admission of *Tunicata* as Vertebrates.

The admission of *Tunicata* as a group of *Vertebrata* was proposed by the present writer as long ago as 1877 (*4*); but it required the intermediate proposition by Balfour of a group *Chordata*, to comprise the two divisions *Tunicata* and *Vertebrata*, in order to render the final admission of *Tunicata* to their proper association with the *Vertebrata* of Cuvier palatable to systematists. As an objection to the simple inclusion of *Tunicata* in the great phylum *Vertebrata* it has been urged that *Tunicata* do not possess vertebræ,—a proposition which is equally true of *Amphioxus* and of some Fishes. Shifting the objection, some writers have maintained that the vertebration of the *Vertebrata* may be understood as having reference to the segmentation of the muscles of the body-wall, which is exhibited by all Cuvier's *Vertebrata* without exception, inclusive of *Amphioxus*, though not by *Tunicata*. To this it may be replied that the Ascidian tadpole, and more clearly the free-swimming Tunicate *Appendicularia* (see fig. 9), do exhibit a segmentation of the muscles of the hinder part of the body-wall similar to and identical with that of *Amphioxus*, whilst no such strict application of a name in its original descriptive sense is desirable in systematic nomenclature. All *Gastropoda* (it has been pointed out) are not gastropodous; all *Arthropoda* are not arthropodous; and many *Echinoderma* are not echinodermous. It is, in the present writer's opinion, better to retain an historic and familiar name for the great branch of the animal pedigree to which it has become necessary to admit forms whose affinities therewith were at one time unsuspected rather than to sacrifice historical significance to a futile striving after etymological accuracy.

Inclusion of *Balanoglossus* in Vertebrate phylum.

The admission of *Tunicata* to association with Cuvier's *Vertebrata* has been followed by a further innovation. The remarkable marine worm *Balanoglossus*—originally described by Della Chiaje at the end of the 18th century—was shown in 1866 by Kowalewsky (*5*) to possess a series of pharyngeal gill-slits similar to those of *Tunicata* and *Amphioxus*. Later researches by Bateson (*6*) have demonstrated that *Balanoglossus* develops in embryonic life a short notochord, whilst its nerve-cord is, in part at least, tubular, and similar in position and relations to the median epidermal tract by the infolding of which the nerve-tube of *Tunicata* and the other *Vertebrata* is formed. Hence it seems impossible to exclude *Balanoglossus* from a place in the phylum *Vertebrata*. The possession of pharyngeal gill-slits alone might not justify the association; but, when this is combined with the presence of the notochord, though rudimentary and with a special condition and position of the main nerve-centre, it becomes impossible to ignore *Balanoglossus* in our conception of the Vertebrate phylum. The recent discoveries of Harmer (7) with regard to *Cephalodiscus* will hereafter render it necessary to associate that form, and in all probability *Rhabdopleura* also, with *Balanoglossus* in the Vertebrate phylum. The further consequences of such an association in regard especially to the affinities of *Polyzoa* and of *Gephyræa* open up a large field of speculation and of consequent embryological and anatomical research.

Ancestral form of Vertebrates.

The Cuvierian *Vertebrata*, *Amphioxus*, *Tunicata*, and *Balanoglossus* being thus indisputably connected by a remarkable combination of structural points, which admit of no explanation consistent with the principles of evolutional morphology except that of the genetic relationship of the forms thus enumerated, we are at once confronted by those questions as to the ancestral history of *Vertebrata* which have been already mentioned above as stimulated by Kowalewsky's discoveries. Undoubtedly *Amphioxus* is lower and simpler in structure than any Fish, *Tunicata* as low as or lower than *Amphioxus*, and *Balanoglossus*, in some respects, more archaic than either *Amphioxus* or the Ascidian tadpole. The first tendency arising from the discovery of the affinities of these simpler forms with the Cuvierian *Vertebrata* was to see in them the representatives of the ancestors of all *Vertebrata*. *Amphioxus* has been pointed to by authorities in morphology as the living presentation of our common Vertebrate ancestor; a similar position corresponding to an earlier stage of development has been admitted by no less an authority than Darwin for the Ascidian. It appears, nevertheless, that all such simple solutions of the problem of Vertebrate ancestry are without warrant. They arise from a very common tendency of the mind, against which the naturalist has to guard himself,—a tendency which finds expression in the very widespread notion that the existing anthropoid apes, and more especially the gorilla, must be looked upon as the ancestors of mankind, if once the doctrine of the descent of man from ape-like forefathers is admitted. A little reflexion suffices to show that any given living form, such as the gorilla, cannot possibly be the ancestral form from which man was derived, since *ex hypothesi* that ancestral form underwent modification and development, and in so doing ceased to exist. The same considerations apply to the question of the ancestry of *Vertebrata*. Probably no existing low form of Vertebrate *closely* represents the ancestral form by the modification of which higher forms have been developed. We have no justification for assuming that such low forms do more than present to us a collateral branch of the family, and that collateral branch must, in all probability, have experienced its own special series of modifications of structure. Not only this, but we have no sufficient ground for assuming that, even in respect of the simplicity of their structure, any given animal forms at present existing exhibit a mere survival of a corresponding degree of simplicity in their remote ancestors. Such an assumption was almost universally made, until a more correct view was pressed on the attention of naturalists by Dr Anton Dohrn, the founder of the zoological station of Naples (*8*). So far from its being the case that simplicity of organization necessarily implies the continuous hereditary transmission of a low stage of structural development from remote ancestors, there are numerous instances in which it is certain that the existing simplicity of structure is due to a process of degeneration, and that an existing form of simple structure is thus descended from ancestors of far higher complexity of organization than itself. Such are various parasitic worms and *Crustacea*. The evidence in favour of the occurrence of progressive simplification of structure or degeneration, in place of progressive elaboration, depends (1) upon the comparison of the adult structure of the degenerate organism with that of its nearest allies, by which it is often rendered clear that the *ensemble* of the organization of the simpler organism cannot be explained on the hypothesis that it represents an ancestral or archaic condition common to it and its more elaborate congeners, and (2) on the direct evidence of individual development or life-history. The latter evidence is conclusive, when we find, as in the case of Cirrhipede Crustaceans and of Ascidian Tunicates, that the embryo on its way to the adult condition passes through stages of development presenting a higher degree of organization than that ultimately reached, so that, as in the Cirrhipede larva and the Ascidian tadpole, the young form resembles allied organisms of a higher stage of development, and subsequently degenerates from the point of progressive elaboration to which it had attained, and becomes greatly simplified in the final stage of its growth. Conclusive as such evidence is, there is no law of development which necessitates its preservation. If it be an advantage to the organism, the full force of heredity has play, and what are called the "recapitulative phases" of ancestral development are passed through by the individual in the course of development from the egg. But with remorseless thoroughness all such hereditary tendencies may be removed when such removal is an advantage to the organism, and the development from the egg *may* proceed directly to the adult degenerate form. Such is the case with many *Tunicata*, the young of which never exhibit notochord and tadpole form; indeed, were it not for the preservation of a few exceptional cases, like that of the Ascidian section of the group, we should have no direct evidence of the degeneration of *Tunicata* from tadpole-like ancestry.

Arguments from simplicity of structure.

Hypothesis of degeneration.

The general result of the considerations which have been urged with regard to degeneration is this, that it is *primâ facie* as legitimate an hypothesis, that any existing animal has developed by progressive simplification from more elaborate ancestors, as it is that such an animal has developed by a continuous and unbroken progress in elaboration from simpler ancestors; and we are specially called upon to apply the hypothesis of degeneration where the animal under consideration is likely from its mode of life to have undergone that process. Such modes of life, tending to degeneration, are parasitism, sessile or adherent habit, burrowing in the sea-bottom, and diffuse feeding. The animal which pursues living prey, and contends with other organisms for the dominion of the regions of earth and water that are flooded with light and richly supplied with oxygen gas, is the animal which represents the outcome of a longer or shorter period of progressive elaboration. It is worth while noting in parenthesis that in all cases the "whirligig of time" has probably brought its revenges, and that the ancestry of a form evolved through a long period of progressive elaboration was at an antecedent period subject to simplification and degeneration, whilst in the past records of the present exemplars of the latter process there must certainly have been long stretches of continuous elaboration.

Genealogical tree.

Applying these considerations to the construction of the genealogical tree of *Vertebrata*, we find that the task is by no means simplified. We cannot with the earliest evolutionists adopt a scale or ladder-like series, placing the simplest form on the lowest step; nor can we be satisfied with a tree-like arrangement, in which the forms at the ends of the branches are always more elaborate than those nearer the trunk. Our genealogical tree will more strictly conform to that of a parvenu human family, if we take worldly prosperity in the latter case as corresponding to elaboration of structure in the former. The strict family genealogist will include in the successive ramifications of the tree the five sons of the founder of the family, one of whom remained an agricultural labourer, whilst two became brewers and two emigrated. The cousins in the next generation will be set forth in place, the sons of one brewer becoming paupers, whilst those of the other advance to the position of Government employés, and one to the peerage. Thus in successive branchings of the family history there may be alternate progress and degeneration. And so it must be in the genealogical trees constructed by the naturalist: the fact that a branch is later in origin will not imply that it is higher in elaboration than those below it, and accordingly we must not expect to draw our tree so as to be able to trace all simpler forms to lower off-sets of the tree.

Divisions of Vertebrate phylum. The structural features of those animals which must be admitted to the Vertebrate phylum in consequence of possessing notochord, pharyngeal gill-slits, and dorsal nerve-plate, tubular or unrolled, are such as enable us very readily to group them in four great divisions, which appear to be equally distinct from one another. As to what may be the genetic relations to one another of these four groups we will inquire subsequently; for the present we term these groups "branches." They are as follows:—

Phylum VERTEBRATA.
Branch *a*—*Craniata* (Cuvierian *Vertebrata*).
,, *b*—*Cephalochorda* (*Amphioxus*).
,, *c*—*Urochorda* (*Tunicata*).
,, *d*—*Hemichorda* (*Balanoglossus*).

The *Vertebrata* thus limited may be defined as Cœlomate *Enterozoa* (*Metazoa*) with well-developed cœlom. In all, with the exception of the more degenerate members of *Urochorda*, an elastic skeletal rod—the notochord—is developed dorsally by an outgrowth of cells forming the wall of the primitive archenteron; the notochord may or may not persist in adult life. Pharyngeal gill-slits, which may or may not persist in adult life, are developed in all Vertebrates. In all, except in certain *Urochorda*, the chief nerve-centre has the form of a dorsal, median, elongate tract, derived from the epiblast, which becomes sunk below the surface and invaginated so as to form a tube. In all there is a tendency to metameric repetition of parts, which may find its expression in a strongly-marked segmentation of the musculature of the body-wall and its skeleton, or may be recognizable only in a limited degree, as exhibited by the successive gill-slits or successive gonads.

We shall now examine the distinctive features of each of these large groups, and form an estimate of their relations to one another, and of their probable ancestry, this being the task to which we must limit ourselves in the brief space here afforded.

THE CRANIATA.

Characters of *Craniata*. The *Craniata* are *Vertebrata* in which the tubular cerebro-spinal nerve-mass is swollen anteriorly to form a brain, consisting primarily of three successive vesicles, in connexion with the anterior of which the special nerves of the olfactory organs and of the eyes originate. The notochord, whilst extending posteriorly to the extremity of the body, does not reach quite so far forward anteriorly as the termination of the nerve-tube. A cartilaginous cranium or brain-case develops round the anterior extremity of the nerve-cord, and rises up laterally so as to enclose and protect the brain (hence *Craniata*). Cartilage is developed in other parts of the body as a skeletal substance, though it may be subsequently replaced in the cranium, as elsewhere, by bone. The longitudinal muscles of the body-wall are divided by transverse fibrous septa into a series of segments, varying in the adult from ten to one hundred or more in number. Cartilaginous neural arches, corresponding in number and position to the fibrous septa, and resting on the notochord, are developed so as to protect the nerve-cord. Cartilaginous bars also pass outwards, with a direction at first horizontal and then ventral, from the sides of the notochord into the intermuscular fibrous septa. Very generally, but not always, a tubular cartilaginous sheath forms round the notochord; this sheath with rare exceptions becomes segmented to form a series of vertebral bodies, which lie in the planes of the fibrous intersegmental septa, and, increasing in thickness by encroaching upon the substance of the notochord, finally obliterate it almost entirely.

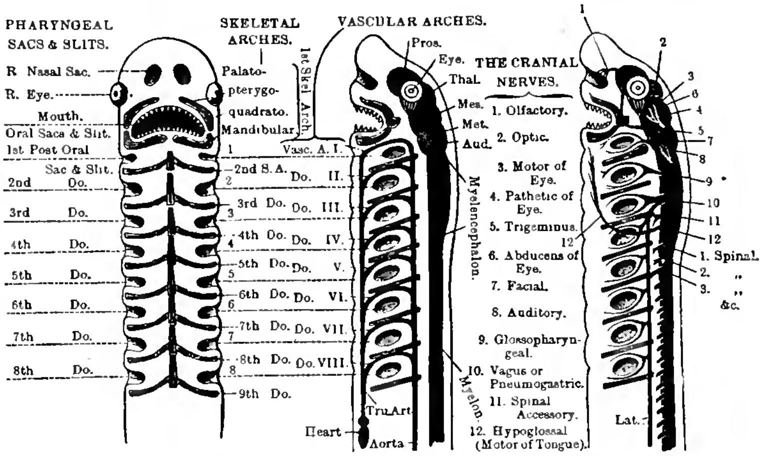

FIG. 3.—Three diagrams showing characteristic disposition of gill-slits, skeletal arches, vascular arches, and furcal nerves in a primitive ideal Craniate. The following abbreviations require explanation:—*pros.*, prosencephalon; *thal.*, thalamencephalon; *mes.*, mesencephalon; *met.*, metencephalon; *aud.*, otocyst or auditory sac; *tru. art.*, truncus arteriosus. (Original.)

The pharyngeal slits follow closely upon the mouth, and in existing *Craniata* never number more than eight pairs (see fig. 3). They are separated from one another and their apertures strengthened by a series of cartilaginous hoops, the first of which, that between the mouth and the first gill-slit, forms the primitive upper and lower jaw in all but the small and degenerate group *Cyclostoma*. The gill-slits when functional are generally protected by an opercular fold of the body-wall, which overhangs them and corresponds to the epipleural fold of *Amphioxus*, the collar of *Balanoglossus*, and doubtfully to the wall of the atrial chamber of *Urochorda*. The extension of this fold along the sides of the middle third of the body (between the pharyngeal region and the anus) acquired in ancestral *Craniata* the function of a continuous right and left lateral fin (see fig. 4). At the same time a continuous median fin, corresponding to the dorsal, caudal, and anal fins of existing Fishes, was developed. In both lateral and median fins a cartilaginous skeleton was developed, consisting of a basal longitudinal bar, supporting a number of rods like the teeth of a comb. The primitive form of fin skeleton is retained in the median fins of some sharks; the primitive lateral fin has in all cases either

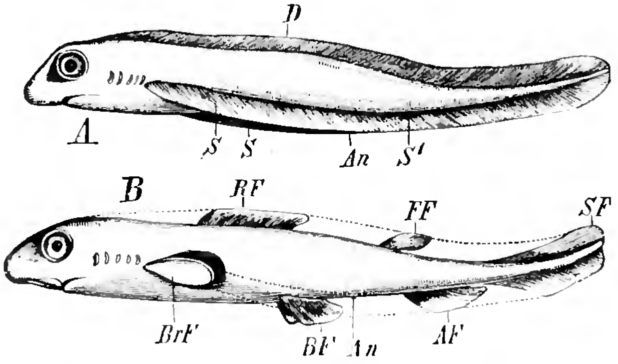

FIG. 4.—A. Hypothetical primitive Fish, with continuous lateral fins S, S (paired right and left), confluent with median azygos fin (*An*), the post-anal part of which is marked S', whilst its dorsal part is marked D. B. Actual Fish, showing relation of isolated lateral and median fins to original hypothetical fins of the upper figure. BrF, left pectoral fin (paired); BF, left pelvic fin (paired); AF, anal (post-anal) azygos fin; SF, caudal azygos fin; RF and FF, anterior and posterior azygos dorsal fins; An, anus. (From Wiedersheim.)

entirely disappeared (*Cyclostoma*) (as has their anterior extension, the operculum, in many cases) or it has become, together with its skeletal elements, concentrated in two regions—forming the pectoral and the pelvic paired appendages or limbs, with their respective girdles.

The cerebro-spinal nerve-centre and the disposition of the nerves issuing from it present a remarkable complexity, and at the same time uniformity, of structure in all *Craniata* (see fig. 5). The foremost of the three primary cerebral vesicles gives rise to paired anterior outgrowths, the prosencephala, to a median dorsal outgrowth, the stalk of the pineal eye (rudimentary in all existing *Craniata*), and to a median ventral outgrowth, which is met by an invagination of the epidermis of the oral cavity forming the pituitary body, further, to a pair of lateral outgrowths, which become the right and left optic nerves and retinæ respectively. The modifications of the hindmost of the three primary vesicles are also extremely definite and persistent throughout the group: its anterior dorsal surface enlarges and becomes the cerebellum (the metencephalon), whilst the cavity of its hinder part (the medulla oblongata or the epencephalon) becomes comparatively wide, and is covered dorsally by a thin membrane only, in which nervous tissue does not take a part. The intermediate primary cerebral vesicle (the mesencephalon) does not give rise to outgrowths.

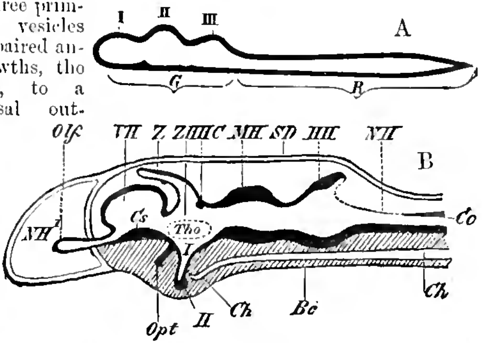

FIG. 5.—Diagrams of Craniate brain. A. Embryonic condition of neural tube. G, Cerebral portion; R, spinal cord; I, II, III, three primary cerebral vesicles. B. Longitudinal section of adult brain, applicable to any and every Craniate Vertebrate. *Bc*, Floor of skull; *Ch*, notochord; *SD*, roof of skull; NH¹, nasal cavity; VH, fore-brain, prosencephalon, or cerebrum; *Olf*, olfactory lobe; *Cs*, corpus striatum; ZH, thalamencephalon, corresponding to primary anterior vesicle, from which the prosencephalon has grown out as well as Z, the epiphysis or pineal body; I, infundibulum, with attached hypophysis or pituitary body H; *Opt*, optic nerve; *Tho*, thalamus opticus; HC, posterior commissure; MH, mesencephalon (*corpora quadrigemina* or optic lobes or mid-brain); HH, cerebellum or metencephalon; NH, medulla oblongata or epencephalon (the reference line touches the membranous roof of the so-called "fourth ventricle" of the brain); *Co*, canal of the spinal cord or myelon. (From Wiedersheim.)

In all *Craniata* nerves are given off from the cerebro-spinal cord or tube with great regularity, one right and left in each successive myomere or segment of the body-wall. Each nerve has two roots, a dorsal (sensory) and a ventral (motor). A commissure between each successive pair of deep or intestinal branches of the spinal nerves forms the so-called sympathetic nerve-cords, one on each side of the vertebral column. Nerves similar to the spinal nerves, but not identical with them, are given off from the brain, and perforate the cranial box right and left. In all *Craniata* there are ten pairs of nerves which originate thus, and in the higher forms two more pairs (elsewhere spinal) are included amongst those which thus perforate the cranium (spinal accessory and hypoglossal). The order and character of the cranial nerves are the same in all *Craniata*. The first (olfactory) and the second (optic) are unlike spinal nerves in both distribution and origin. As we pass backwards along the series, the cranial nerves are found to resemble more and more the ordinary spinal nerves. Hence it has been inferred that the cranial region consisted at one time of a number of distinct myomeres (as many as nine), which have become fused and modified to form the typical craniate "head." The oculo-motor or 3d nerve indicates the first of these segments, the trochlear or 4th nerve the second, the abducens or 6th the third, the facial and auditory (7th and 8th) the fourth, the glosso-pharyngeal or 9th the fifth, and the vagus or 10th, with certain of its branches supposed to have been originally distinct nerves, the sixth, seventh, eighth, and ninth. It is probable that in *Craniata* the metamerism of the gill-slits does not correspond to the metamerism of the body-wall. The mouth and each successive gill-slit are related to a bifurcate branch of a cranial nerve (furcal nerve) in lower *Craniata* (see fig. 3); these furcal nerves do not correspond, so far as we can at present judge, with cranial myomeres.

The lateral pair of eyes (as opposed to the rudimentary pineal or parietal eye) present a striking uniformity of origin and structure throughout *Craniata*. Not only are they uniformly developed from three elements, viz., the retinal cup which grows out from the anterior of the primary cerebral vesicles, the epidermal lens which grows inwards from the surface of the skin, and the connective tissue between these two, but we find that the muscles attached to the eyeball are identical throughout the series: that is, the superior, inferior, and internal rectus, and the inferior oblique muscles represent the first cranial myomere, the superior oblique represent the second, and the external rectus represent the third cranial myomere.

The olfactory sacs are paired in all except *Cyclostoma*, in which they are represented by a single sac which may or may not be archaic in its azygos character. The auditory sacs are paired organs which develop as invaginations from the surface,—the orifice of invagination closing up,—at the hinder part of the cranial region. They present a gradually increasing complexity of form as we pass from aquatic to terrestrial forms, but are identical in essential structure throughout.

All *Craniata*, except some Fishes, possess a muscular process on the floor of the oral cavity which may carry teeth, or act as a licking organ, or assist in suction. This is the tongue.

All *Craniata*, with degradational exceptions, possess an outgrowth, single or paired, of the post-pharyngeal region of the alimentary canal, which is filled with gas. In many Fishes this becomes shut off from the gut; in others it remains in communication with the gut by an open duct. In Fishes it functions as a hydrostatic apparatus. In terrestrial *Craniata* it is subservient to the gas-exchange of the blood and becomes the lungs.

All *Craniata* have a large and compact liver; and a pancreas is also uniformly present, except in *Cyclostoma*, some bony Fishes, and the lower *Amphibia*.

All *Craniata* have a thick-walled muscular heart, which appears first as an "atrium," receiving the great veins, attached to a "ventricle" by which the blood received from the atrium is propelled through a number of arteries, right and left, corresponding in number to the pharyngeal gill-slits between which they pass. A præatrial chamber (the sinus) and an extra-ventricular chamber (the conus) are added to the primitive chambers; but the most important modifications arise in consequence of the development of pulmonary respiration and the gradual separation of the cavities of the heart by median septa into a double series, a right and a left. The plan of the great arteries in all *Craniata* is in origin the same, and is determined by the primitive existence of a branchial circulation in the gill-slits, which is obliterated in higher forms. Similarly the plan of the great veins is identical, the primitive posterior vertebral veins of lower *Craniata*, though persistent in higher members of the group, having their function gradually usurped by the excessive development of the renal vein, and of renal-portal and ultimately of iliac veins.

All *Craniata* have a lymphatic system or series of channels by which the exudation from the capillary blood-vessels is returned to the vascular system. It includes in its space-system the cœlom and a variety of irregular and canalicular spaces in the connective tissues. Masses of spongy tissue (adenoid tissue, lymphatic glands) exist, through which the lymph filters, and there acquires corpuscular elements as well as chemical elaboration. At various points in various *Craniata* pulsating or simple communications are established between the lymphatic system and the veins. A special and characteristic communication is established in the spleen, an organ which is found in all *Craniata*, either as a single mass or as scattered masses of spongy tissue in which blood-vessels and lymphatics unite.

The renal organs of *Craniata* are primitively a series of nephridia corresponding in number to the myotomes of the mid-region of the body in which they exist. They are connected in the simplest *Craniata* by a right and a left archinephric duct, which appear to be in origin lateral grooves of the epidermal surface. This primitive renal system has been modified in some lower forms (*Cyclostoma* and Teleostean Fishes) by the atrophy of its anterior portion. But in all other *Craniata* it acquires relations to the gonads or ovary and testes, so that an anterior portion of the archinephros and a corresponding longitudinal tract of the duct become separated to serve as oviduct, a middle portion to serve as sperm-duct, while a posterior portion retains exclusively or shares with the middle portion the function of urinary excretion. The male and female gonads are, with the rarest exceptions, developed in distinct individuals, though the rudiments of the suppressed gonad may in some cases (*Amphibia*) be traceable in either sex.

Sub-divisions of *Craniata.*

The group of Craniate *Vertebrata* thus anatomically described, whilst retaining the essential unity indicated, presents an immense variety of modifications. The chief modifications are distinctly traceable to and accounted for by mechanical and physiological adaptation to a terrestrial and air-breathing life, as opposed to the earlier aquatic and branchial condition. The existing forms of *Craniata* have been arrested at several points, in the progress towards the most extreme adaptation to terrestrial conditions, which is presented by those forms that can not only breath air and live on dry ground but fly habitually in the air. The organs most obviously affected by this progressive adaptation are the skin, the skeleton, especially of the limbs, the pharyngeal gills, and the air-bladder. This fact will appear most clearly in the subjoined classification of *Craniata*; for space does not permit us to pursue further the history of these modifications.

Classification of CRANIATA.[1]

Grade A. CYCLOSTOMA.
Class I. *Myxinoidea.*
II. *Petromyzontia.*
Grade B. GNATHOSTOMA.
Grade a. **Branchiata heterodactyla.**
Class I. *Pisces.*
II. *Dipnoi.*
Grade b. **Branchiata pentadactyla.**
Class. *Amphibia.*
Grade c. **Pentadactyla lipobranchia.**
Branch a. Monocondyla. *Branch b. Amphicondyla.*
Class I. *Reptilia.* Class. *Mammalia.*
II. *Aves.*

Ancestral form of *Craniata.* If we now briefly consider what must have been the common ancestral form from which these *Craniata* have proceeded, making use of such internal evidence as their structure affords, we find that we get no further back than such an animal as would fit the description given above, with the exception that we should be warranted in substituting in the ancestor a pair of continuous lateral fins, with comb-like cartilaginous skeleton, in place of the two pairs of fins, or their total defect, seen in living *Craniata.* We get no clear suggestion from the study of *Craniata* themselves as to the meaning of the curious shape of the brain and its outgrowths (though the pineal outgrowth has recently been explained as an eye), nor as to the original genesis of the notochord. We should, however, be justified in representing that region which now corresponds to the hinder part of the skull and brain as more fully developed and segmented, so as to give a series of separate myotomes and perhaps separate nerves corresponding to the several furcal branches of the vagus; and we may very well suppose that the number of pharyngeal gill-slits was larger in the ancestral than in any living form, though it seems improbable that in any true Craniate did each gill-slit correspond to a distinct muscular segment.

An attempt to go further than this has been made by Dr Anton Dohrn by the method of hypothesis and subsequent corroborative inquiry into facts of minute structure and embryological history. Making use of the principle of degeneration, Dohrn started with the legitimate hypothesis that the branches of *Vertebrata* other than *Craniata*—viz., *Cephalochorda*, *Urochorda*, and (though at the time he commenced his work their structure was not fully understood) *Hemichorda*—were not to be regarded as permanent records of steps in the evolution of *Craniata*, but rather as greatly degenerate offshoots from the ancestors of that group, which could throw but little light on the character of their non-degenerate ancestors. A second fundamental assumption which led Dohrn to his position was that the segmentation of the Craniates' body-wall is a primitive and essential feature in their structure, and becomes more and more fully expressed instead of less developed the further we go back in their ancestry. Dohrn, in fact, assumes that what is called metameric segmentation is a phenomenon of structure which has occurred once only in the history of animal form, and that all segmented animals are genetically related and descended from a common segmented ancestor. Assuming this, he pointed to the existing Chætopod Worms as most nearly representing at the present day the common ancestor of segmented animals. They have, as he pointed out, a high organization, little inferior to that of the lowest *Craniata*; they possess a well-developed cœlom, blood-vessels with red blood, a segmental series of nephridia (modified in some as gonaducts), segmental branchiæ, and lateral locomotive organs; not a few develop cartilage as a skeletal support; and many show a concentration and fusion of segments to form a complex head, which resembles, so far, that of *Craniata.* The ventral in place of the dorsal position of the nerve-cord led Dohrn to accept De Blainville's conception that the dorsal and ventral surfaces are reversed in *Vertebrata*, as compared with Annelids, Crustaceans, and Insects, so that the Vertebrate is compared to an Insect walking with its ventral surface upward. This led further to the notion that the mouth of the Chætopod or Annelid, which penetrates the nerve-cord, or rather passes between its two divaricated lateral constituents in those animals, has in *Craniata* disappeared, its place being taken by a new mouth derived from the modification of a pair of gill-slits. The remnant of the old mouth, which should, if the comparison instituted holds good, lie in *Craniata* somewhere on the dorsal surface of the cranial region, was sought by Dohrn in some of the peculiar and hitherto unexplained median structures of the brain: at one time the fourth ventricle with its deficient roof was suggested as thus to be explained, whilst subsequently the curious median structures,—the pineal and pituitary bodies,—were called in as possibly thus significant.

Without pursuing further the elaboration of Dohrn's views, it must be at once noted that, whilst the legitimacy of the assumption of degeneration must be admitted, the second assumption, viz., that metameric segmentation is a character bringing all forms showing it into a special genetic continuity, cannot be accepted. The property of repeating units of structure, so as to build up a complex of many similar parts united to form one individual, is a very general one in organic forms, and is exhibited in various conditions by both animals and plants. Its simplest expression is found in cell-structure and the binary division of cells. It shows itself as affecting larger masses of structure in the arborescent colonies of *Cœlentera*, in the radial or antimeric composition of Echinoderms and of Compound Ascidians, and in the linear or metameric segmentation of Worms, Arthropods, and Vertebrates. There is abundant evidence that this property is a general one, which may assert itself at any period in the history of a group of animals, and does not imply special unity of origin in forms which exhibit it. As pointed out in the article HYDROZOA, merogenesis—the name applicable to this phenomenon generally—may take an extreme and complete character, leading to the separation and independence of the units of structure produced; in that case it may be termed eumerogenesis. Or the process may be very partial, occurring only during a period of embryonic growth, and subsequently ceasing, so that later growth obscures or obliterates it altogether (dysmerogenesis). There is no ground for assuming that either one of these extremes is fundamental or original. Any mechanical or nutritional condition may lead to merogenesis in an organism in which the tissues have a certain reproductive capacity, or have not acquired final differentiation; and it will depend upon the balance of advantage, determined by natural selection, whether the segmentation (supposing the merogenesis to take the linear form) results in the separation of segment-buds, or in the formation of an annulate body, or leaves traces of its occurrence only in certain tissues and organs. The Cestoid Worms present within the range of a single group almost every grade of eumerogenesis and dysmerogenesis (*Caryophyllæus*, *Ligula*, *Tænia*). In the otherwise amerogenetic *Mollusca*, Chiton and the pearly Nautilus show dysmerogenesis in certain organs, whilst the Planarian Worms frequently exhibit eumerogenesis in their bud-segmentation (to be compared with that of the Annelid *Ctenodrilus* described by Zeppelin, *9*) and the elongated Nemertines only slight traces of dysmerogenesis.

If we deny Dohrn's assumption with reference to segmentation, we are no longer led in the direction of the Annelids (Chætopods) in our search for the ancestry of the Craniate *Vertebrata.*

The fact that the notochord is the forerunner of the segmented vertebral column, and is itself never segmental, instead of being a difficulty, acquires directive significance. The fact that the nerve tube is dorsal, and not ventral, no longer requires the large assumption that animals have reversed their habitual carriage, but suggests that the Craniates' ancestor had a dorsal median nerve, which has increased in size and importance so as to become the nerve-tube of existing forms. The explanation of the curious structure of the brain will have to be found otherwise than in the assumption of a perforating pharynx,—an assumption which the recent discovery of the true nature of the pineal body has rendered untenable in the latest form advocated by its ingenious author, whose speculations, nevertheless, deserve the fullest recognition as having stimulated inquiry and guided observation.

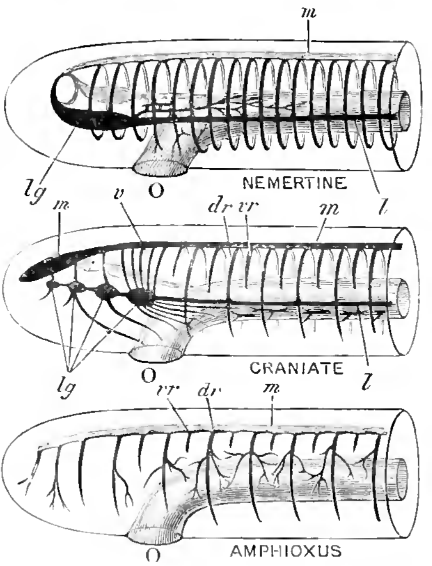

FIG. 6.—Comparison of nervous systems of a Nemertine, a primitive Craniate, and *Amphioxus.* *m*, Median dorsal nerve, which becomes the myelon in the Craniate and *Amphioxus*, acquiring an anterior enlargement in the former; *l*, lateral nerve (right and left), absent by degeneration in *Amphioxus*; *lg*, ganglia of lateral nerve, forming a single large lobe on each side in the Nemertine, and broken into a metameric series in the Craniate; *v*, roots of vagus nerve of the Craniate; *dr*, dorsal roots of nerves given off from myelon or median dorsal nerve; *vr*, ventral roots of these nerves, here represented as separate nerves; *O*, mouth. (After Hubrecht.)

Balfour (*10*) in 1878 refused to adopt Dohrn's views, and considered it probable that the dorsal position of the nerve-cord in *Vertebrata* could be accounted for, without any assumption of a substitution of a pair of gill-slits for the original mouth, by assuming that primitively the nerve-cord consisted of two lateral cords, as seen at the present time in the Nemertine Worms, and that these cords have coalesced *dorsally* in *Vertebrata*, just as it is clearly demon

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[1] The classes here enumerated are described in separate articles, whilst *Cyclostoma* and *Dipnoi* are included in the article ICHTHYOLOGY.

strable that two originally lateral cords have coalesced *ventrally* to form the Annelid's ventral nerve-chain.

The comparison of the Vertebrates' nervous system with that of the Nemertines had already been made by the present writer, as cited by Hubrecht (*11*) in connexion with the latter's discovery of a complete sub-epidermal nerve-tunic in those worms. Hubrecht has more recently on two occasions (*12* and *13*) developed an interesting and important comparison of Nemertine and Vertebrate structure. He has in the first place suggested that the notochord of *Vertebrata* is nothing more than a modified survival of the proboscidean sheath of the Nemertines, whilst the oral invagination of the epidermis, in connexion with the hypophysis cerebri of the Vertebrate, may be a last remnant of the proboscis itself. More conclusively he has drawn attention to the median dorsal nerve of Nemertines as corresponding to the Vertebrate cerebro-spinal nerve-cord, whilst the great lateral nerve-cords of Nemertines, and the lateral ganglia in which they expand anteriorly, are compared to the lateral ganglia of the cephalic region of Craniate *Vertebrata* and the nerve of the lateral line (see fig. 6). The comparison is strengthened by the existence of a metameric series of transverse nerves in the Nemertine, which correspond in respect of their metamerism and their connexion with a dorsal median trunk, with the spinal nerves of *Craniata*. Hubrecht is careful to insist that he does not regard the Nemertines as representing the direct ancestry of *Vertebrata*; but he points out that from the primitive condition of an elongate animal, with a plexiform nerve-tunic, it is readily conceivable that a form was developed in which the nervous tissue was concentrated in three cords,—a median dorsal and two lateral,—and from such a form we can derive the Craniates' condition by excessive development of the median tract and relatively small development of the lateral cords, whilst the Nemertines' condition would be attained by the converse process. The tubular condition of the cerebro-spinal nerve-cord of *Vertebrata*, it may here be remarked, is now very generally regarded as being in its origin a purely developmental feature. It was primitively separated from the epidermis by delamination and in-sinking, and the mode of formation by invagination of a canal has been substituted in accordance with a general embryological law of growth, which is that bulky structures originating beneath a surface from the cells forming that surface take up their position in embryonic growth by invagination of the parent surface. The tubular form, having thus started, seems to have been utilized during one phase of Vertebrate evolution for the respiration of the nervous tissue, by the introduction through an anterior unclosed pore of a current of water, which escaped by the neuranal canal (as in larval *Amphioxus*).

There is a wide gap between any form presenting an approach to a Nemertine Worm and the most simple Craniate Vertebrate which can be imagined still provided with the organization characteristic of all *Craniata*. To pass from such a Worm-like animal to a Craniate, we have to account for and introduce, amongst other new developments, (1) a greatly increased metamerism, showing itself in the segmentation of the muscles of the body-wall and in the repetition of the nephridia; (2) the characteristic sense organs; (3) the lateral and median longitudinal folds or continuous fins; (4) the cartilaginous rods and bars of the skeleton; (5) the gill-slits, even if we admit the notochord to be represented by the proboscidean sheath.

It remains to inquire whether the structure of the other *Vertebrata* throws light on this long hypothetical passage from the simple Worm phase to the elaborate Craniate, or suggests any other ancestry.

THE CEPHALOCHORDA.

Characters of *Cephalochorda.*

Cephalochorda are *Vertebrata* in which there is no anterior dilatation of the nerve-tube to form a brain (see fig. 6) and no specialized skeletal brain-case. The notochord extends from one extremity of the elongate body to the other as a tapering unconstricted rod, passing anteriorly some distance in front of the nerve-cord. The longitudinal muscles of the body-wall are divided by transverse fibrous septa into a series of segments (sixty-two in *Amphioxus lanceolatus*), the more anterior of which are in front of the mouth and not in any way fused to form a head or cranial structure. Dense connective tissue (differing but little from cartilage) forms an unsegmented sheath to the notochord and an unbroken neural canal above it, in which the nerve-cord lies. The same tissue forms a series of metamerically repeated fin rays, which support the base of a median fin extending along the entire dorsal surface. The fin is continued ventrally from the caudal extremity as far forward as the anus, but without fin rays. Two lateral up-growths of the body-wall (the epipleura) extend one on either side from the head as far back as the anus. Each of these is divided into three regions,—(1) an anterior, which forms the præoral hood; (2) a median, which forms the wall of the great branchial chamber, the two folds meeting one another and coalescing in the ventral mid-line, excepting where they leave a posterior median aperture, the atriopore; and (3) the post-atrioporal præanal ventral fin (extending between atriopore and anus), which is formed by the complete coalescence of the two folds behind the atriopore.

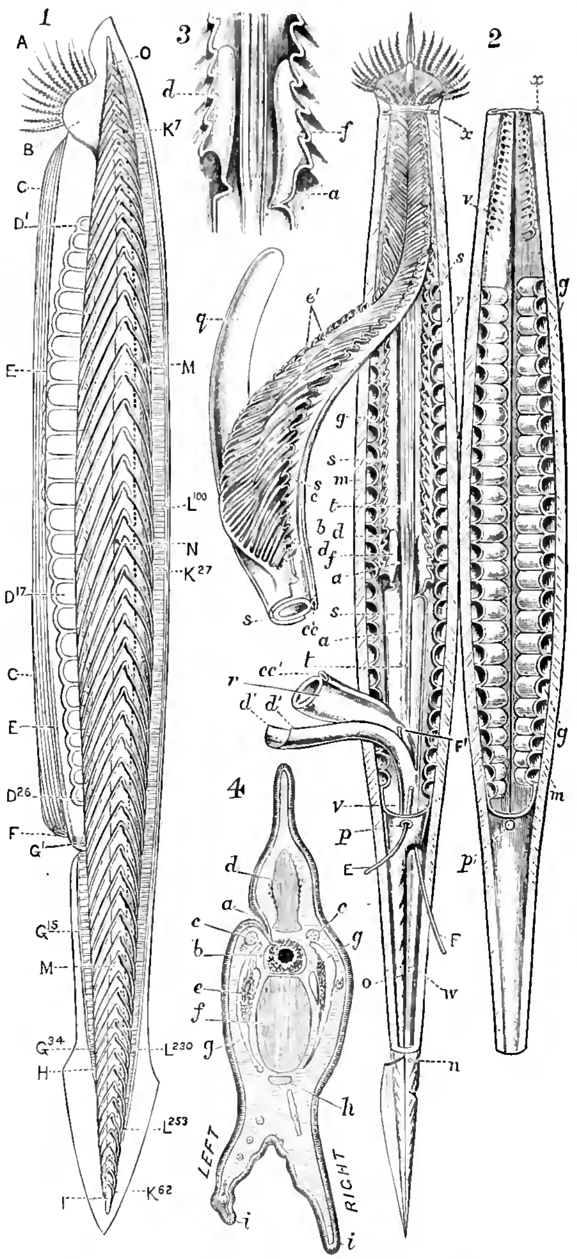


FIG. 7.—*Amphioxus lanceolatus*, Yarrell (*Branchiostoma lubricum*, Coste). (Original drawings.) (1) Lateral view of adult, to show general form, the myomeres, fin rays, and gonads. A, oral tentacles (28 to 32 in full-grown animals, 20 to 24 in half-grown specimens); B, præoral hood or præoral epipleur; C, plicated ventral surface of atrial chamber; D^1, D^{17}, D^{26}, gonads, twenty-six pairs, coincident with myotomes 10 to 36; E, metapleur or lateral ridge on atrial epipleur; F, atriopore, coincident with myotome 36; G^1, G^{15}, G^{34}, double ventral fin rays, extending from myotomes 37 to 52, but having no numerical relation to them; H, position of anus, between myotomes 51 and 52; I, notochord, projecting beyond myotomes; K^7, K^{27}, K^{62}, myotomes or muscular segments of body-wall, 62 in number; L^{100}, L^{230}, L^{253}, dorsal fin rays, about 250 in number, the hard substance of the ray being absent at the extreme ends of the body (these have no constant numerical relation to the myomeres); M, notochord as seen through the transparent myotomes, the thin double-lined spaces being the connective-tissue septa and the broader spaces the muscular tissue of the myotomes; N, position of brown funnel of left side (atrio-cœlomic canal); O, nerve-tube resting on notochord.

(2) Dissection of *Amphioxus*. By a horizontal incision on each side of the body a large ventral area has been separated and turned over, as it were on a hinge, to the animal's left side. The perforated pharyngeal region has then been detached from the adherent epipleura or opercular folds (wall of atrial or branchial chamber) by cutting the fluted pharyngo-pleural membrane *d*, and separated by a vertical cut from the intestinal region. *a*, Edge of groove formed by adhesion of median dorsal surface of alimentary canal to sheath of notochord; *b*, median dorsal surface of alimentary canal; *c*, left dorsal aorta; *cc*, single dorsal aorta, formed by union of the two anterior vessels; *cc'*, same vessel resting on intestine; *d*, cut edge of pharyngo-pleural folds of atrial tunic, really the original outer body-wall before the downgrowth of epipleura; *d'*, atrial tunic (original body-wall) at non-perforate region, cut and turned back so as to expose peri-enteric cœlom and intestine *r*; *e'*, upstanding folds of body-wall (pharyngo-pleural folds) on alternate bars of perforate region of body; *f*, atrio-cœlomic canals or brown funnels (collar-pores of *Balanoglossus*); *g*, cavity of a gonad-sac; *m*, cut musculature of body-wall; *n*, anus; *o*, post-atrioporal extension of atrial chamber in form of a

tubular cæcum; *p*, atriopore; *q*, hepatic cæcum; *r*, intestine; *s*, cœlom; *t*, area of adhesion between alimentary canal and sheath of notochord; *v*, atrial chamber or branchial cavity; *w*, post-atrioporal portion of intestine; *x*, canals of metapleura exposed by cutting; E, probe passing through atriopore into atrial or branchial chamber; FF′, probe passed from cœlom, where it expands behind the atriopore, into narrower pericenteric cœlom of præatrioporal region.

(3) Portion of (2) enlarged to show atrio-cœlomic canals ("brown funnels" of Lankester). Lettering as in (2).

(4) Section taken transversely through præoral region near termination of nerve-tube. *a*, Olfactory ciliated pit on animal's left side, its wall confluent with substance of nerve-tube; *b*, pigment spot (rudimentary eye) on anterior termination of nerve-tube; *c*, first pair of nerves in section; *d*, fin ray; *e*, myotome; *f*, notochord; *g*, space round myotome (? artifact or cœlom); *h*, subchordal canal (? blood-vessel); *i*, a symmetrical epipleura of præoral hood.

The originally double character of this part of the ventral fin is indicated by the double series of metameric fin rays which support it. It is probable that these "epipleural" folds of *Amphioxus* correspond to the opercular folds and lateral fins of *Craniata*. No cartilaginous fin rays are developed in the atrio-pleural (opercular) region of the epipleura; but a longitudinal unsegmented bar of cartilaginous consistency strengthens its side and bounds a lymph-holding canal (*x* in fig. 8).

The gill-slits in *Amphioxus* are very numerous (one hundred or more), and have no numerical relation to the metameres of the muscular body-wall, though the first few which appear in the embryo correspond at the time to successive myomeres,—a relation which they subsequently lose. The sides of the gill-slits are supported by chitinous (?) bars, and each slit is divided into two equal portions by a longitudinal tongue or bar, which grows out from the dorsal margin of the slit soon after its first formation. The number of gill-slits increases continually throughout the life of *Amphioxus* by the formation of new ones at the posterior border of the pharynx, whilst the myomeres do not increase in number after early embryonic life.

The nerves given off from the dorsal nerve-cord of *Amphioxus* are of two kinds,—dorsal and ventral. The dorsal nerves correspond in number and position to the myomeres, right and left, except in the most anterior region of the body, where two larger pairs of dorsal nerves are given off from near the extremity of the nerve-cord, and pass forward, supplying the region which lies in front of the termination of the musculature. The ventral nerves are minute, and are given off numerously, right and left, from the nerve-tube throughout its length. The dorsal and ventral nerves of a single myomere appear to correspond, respectively, to the dorsal and ventral roots of a spinal nerve of a Craniate.

There is a single olfactory pit in *Amphioxus*, which rests upon the left side of the anterior termination of the nerve-cord (see fig. 7, 4). Within the cavity of the nerve-cord at the same point a patch of brown pigment is present (eye-spot). There are no representatives of the lateral eyes of *Craniata* and no otocysts.

There is no representative of the Craniates' swim-bladder in *Amphioxus*. A single wide diverticulum of the alimentary canal represents the liver of *Craniata*; the pancreas is unrepresented.

The vascular system is singularly incomplete: large trunks exist, but few branches and no heart, whilst the blood itself is colourless, and communicates (as in *Craniata* by the lymphatic "hearts") with the cœlomic fluid at various points. A contractile ventral trunk runs along the lower face of the slit pharynx, and sends vessels right and left up the successive bars; these vessels unite above, as in *Craniata*, to form a double "dorsal aorta," which posteriorly becomes a single vessel. A portal system of veins can be traced in connexion with the hepatic cæcum.

No system of lymphatic vessels, nor lymphatic "glands," nor a spleen exist; but the cœlom, and certain other spaces in the connective tissue, contain coagulable lymph, and correspond to the lymph spaces of *Craniata*.

There is no series of nephridia, nor a renal organ formed by the coalescence of nephridia, nor are gonaducts present. The "brown funnels," a pair of funnel-shaped tubes discovered by Lankester (*14*), place the cœlomic space of the opercular (epipleural) downgrowths of the body-wall in communication with the space which these folds enclose. They appear to be identical with the "collar-pores" of *Balanoglossus*, and it is doubtful whether they represent nephridia.

In the larval *Amphioxus* there is developed from the left anterior cœlomic pouch a glandular tube and a sense-organ, which are represented in the adult by the structures marked *f* in fig. 8, B. This tube is probably the same thing as the subneural gland of Ascidians and as the proboscidean gland and pore of *Balanoglossus*. Quite distinct from the foregoing is a nephridial tube lying on the left side behind the mouth of the larval *Amphioxus*. All are probably of the nature of nephridia. In the adult *Amphioxus* the nephridial tube is in an atrophied condition, though large and active in a *late* larval stage, when the olfactory pit opens into the neural canal. Hatschek (*15*) describes this condition in "*ausgebildete*" but not in *adult* examples.

The gonads are distinct ovaries and testes; they are developed in distinct male and female individuals in corresponding positions, viz., in that part of the cœlom which is carried downwards in the descending right and left outgrowth (epipleura, opercula) of the body-wall, which encloses the atrial or branchial chamber. The gonads are twenty-six pairs in number, corresponding to the 10-36 myomeres. They are devoid of ducts, and discharge their products by dehiscence into the atrial chamber, whence they pass to the exterior, either by the atriopore or by entering the pharynx through its slits, when they are ejected by the mouth.

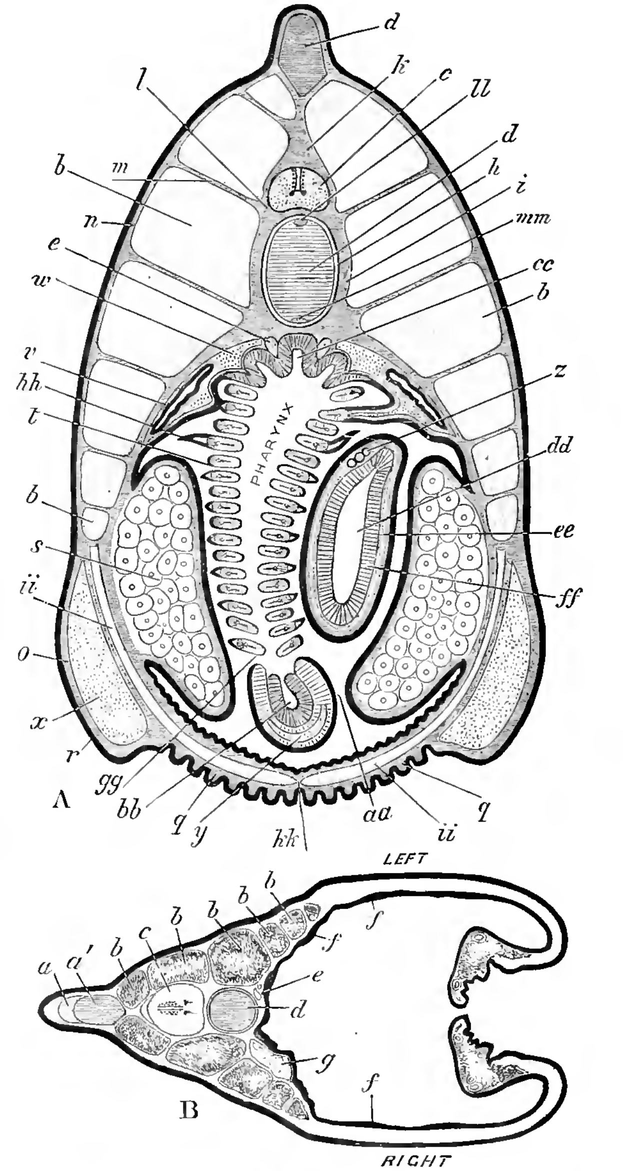


Fig. 8.—Transverse sections of *Amphioxus*. (Original.) A. Section through region of atrio-cœlomic canals, *v*. B. Section in front of mouth; the right and left sides are transposed. *a*, Cavity surrounding fin ray; *a′*, fin ray; *b*, muscular tissue of myotome; *c*, nerve-cord; *d*, notochord; *e*, left aorta; *f*, thickened ridges of epithelium of præoral chamber (Rader organ); *g*, coiled tube lying in a cœlomic space on *right* side of præoral hood, apparently an artery; *h*, cuticle of notochord; *i*, connective-tissue sheath of notochord; *k*, median ridge of skeletal canal of nerve-cord; *l*, skeletal canal protecting nerve-cord; *m*, inter-segmental skeletal septum of myotome; *n*, subcutaneous skeletal connective tissue; *o*, ditto of metapleur (this should be relatively thicker than it is); *q*, subcutaneous connective tissue of ventral surface of atrial wall (not a canal, as supposed by Stieda and others); *r*, epiblastic epithelium; *s*, gonad-sac containing ova; *t*, pharyngeal bar in section, one of the "tongue" bars alternating with the main bars and devoid of pharyngo-pleural fold and cœlom; *v*, atrio-cœlomic funnel; *w*, so-called "dorsal" cœlom; *x*, lymphatic space or canal of metapleur; *y*, sub-pharyngeal vascular trunk; *z*, blood-vessel (portal vein) on wall of hepatic cæcum; *aa*, space of atrial or branchial chamber; *bb*, ventral groove of pharynx (anteriorly this takes the form of a ridge); *cc*, hyperbranchial groove of pharynx; *dd*, lumen or space of hepatic cæcum; *ee*, narrow cœlomic space surrounding hepatic cæcum; *ff*, lining cell-layer of hepatic cæcum; *gg*, inner face of a pharyngeal bar clothed with hypoblast, the outer face covered with epiblast (represented black); *hh*, a main pharyngeal bar with projecting pharyngeal fold (on which the reference line rests) in section, showing cœlomic space beneath the black epiblast; *ii*, transverse ventral muscle of epipleura; *kk*, raphe or plane of fusion of two down-grown epipleura; *ll*, space and nucleated cells on dorsal face of notochord; *mm*, similar space and cells on its ventral face.

In many respects *Amphioxus*, the only representative of *Cephalochorda*, bears evidence of being derived from a more highly organized

Relationship of *Cephalochorda* to *Craniata* and the Vertebrate ancestry.

ancestry. Its mode of life (burrowing in the sand in shallow water, whilst its general build is that of a swimming animal) and the nature of its food (diatoms, &c., carried into the pharynx by ciliary currents) in themselves suggest such a history. The vascular system is elaborate in plan yet incomplete in detail, suggesting an atrophy of its finer branches, which is consistent with the small size of *Amphioxus* and the general principle that a complex vascular system can only be developed in an animal which has attained to a certain bulk. The absence of well-developed sense organs and of "cephalization" in an animal which has attained to such elaboration of structure as is shown by the pharynx and atrial chamber, and which has such well-developed muscles to the body-wall, is an inconsistency best explicable by degeneration ; so, too, the existence of the elaborate series of fin rays, which are out of proportion to the mechanical requirements of so small a form.

Degenerate though *Amphioxus* must be, the ancestor from which it started on its retrogressive course was probably a long way behind any living Craniate. There is no reason to suppose that this ancestor had a cranium, or that the muscular segments and segmental nerves in its cephalic region were fused and welded. *Amphioxus* has probably lost, as compared with that ancestor, lateral eyes and otocysts, nephridia, and, above all, size. The epipleural folds which now form oral hood, branchial opercula, and coalesced ventral fin were probably originally less developed lateral ridges, protecting the gill-slits anteriorly and posteriorly, serving by their undulations to assist in locomotion, whilst the median fin and its rays were large and functional.

One of the most curious features in the structure of *Amphioxus* is its asymmetry. The anus is on the animal's left side ; the nasal pit upon its left ; the myomeres on the two sides of the notochord do not coincide ; and the right and left dorsal spinal nerves do not arise *vis-à-vis* to one another. There is no conclusive reason for regarding this as an ancestral feature, although the early larval form is as curiously asymmetrical as the adult. *Amphioxus* habitually rests upon the sand, lying upon one side of the body, and it is possible that the distortion is related to this habit, as in the case of the Pleuronectid Fishes.

However we may estimate *Amphioxus*, we are not led by it, though its muscular metamerism is so well marked, a single step in the direction of the Annelids, neither are we led directly, it is true, in the direction of *Nemertina* in connexion with those points, as to relationship of notochord with proboscis sheath and nerve-cord with median dorsal nerve, insisted on by Hubrecht. But it will be seen below that, by the agreement of *Amphioxus* with *Balanoglossus* in the structure of the perforations of the pharynx, in the possession of collar pores, and in the præoral glandular body, we do arrive at an important connexion with Nemertine-like forms.

THE UROCHORDA.

Characters of *Urochorda.*

Urochorda are *Vertebrata* which, with the exception of the group *Larvalia* (*Appendicularia*, *Fritillaria*, *Oikopleura*), have receded very far indeed from the characteristic Vertebrate structure, showing neither notochord nor nerve-cord, and gill-slits only of the most highly modified and aberrant form ; some, however (certain Ascidians), pass through a larval condition in which these structures are present in the normal form. It is necessary for the purposes of the present article to confine our attention to *Larvalia* and to the larval forms which retain ancestral characters. (For a description of the whole group, see the article TUNICATA.) In *Urochorda* thus signalized the notochord never reaches forward into the anterior part of the body, but is confined to the tail (hence *Urochorda*). The longitudinal muscles of the region traversed by the notochord show traces of metameric segmentation, which are probably survivals of a more complete development of myomeres in ancestral forms (*16*). There is no trace in *Larvalia* of fin rays or other skeletal structure. Corresponding to the opercular folds and epipleura of *Craniata* and *Cephalochorda* are ridges of the body-wall, which protect the pharyngeal gill-slits, and may give rise, as in *Cephalochorda*, to an enclosed atrial chamber with atriopore. The gill-slits in these larval forms are few in number (one or two pairs), but in many of the aberrant *Urochorda* (by far the majority of the group) they become excessively numerous and complicated in structure, and are supported by a chitinous (?) framework, as in *Cephalochorda*. It has been suggested that the fenestrated structure of the pharyngeal wall in *Tunicata* does not represent a series of gill-slits, but a single pair of slits subdivided. This suggestion is worthy of further consideration.

The cerebro-spinal nerve-cord is tubular and presents itself as a dilated cerebral vesicle in front of the notochord, and as a narrower part running along the whole length of the notochord.

Sense organs are present—a single eye with pigment and lens, a single otocyst, and an olfactory pit (*Larvalia*). The mouth is dorsal in position in the Ascidian tadpole, but subterminal in *Larvalia*. The pharynx is wide, and is followed by a narrow œsophagus, stomach, and intestine, which does not open ventrally but turns upwards to the anus. The *Larvalia* have a rudimentary heart and no vascular system,—a fact connected with their diminutive size. For the same reason no vascular system develops in the Ascidian tadpole until it has ceased to be locomotive and has entered upon its later development ; but in the larger adult *Urochorda* a contractile heart and a well-developed vascular system are present.

No undeniable nephridia are present in *Larvalia* nor in the larval Ascidian, and no structure comparable to the collar pores of *Balanoglossus* or the atrio-cœlomic funnels of *Amphioxus* is known in them.

The subneural gland, however, a glandular tube opening anteriorly near the mouth of the pharynx, appears to be identical with the præoral larval gland of *Amphioxus* and the proboscis pore and gland of *Balanoglossus*. It is probably to be regarded as a nephridium, and has been compared by Julin and Van Beneden to the pituitary body of *Craniata*, with which it corresponds in position and development.

The gonads of *Larvalia* are developed in irregular masses on the walls of the cœlom, ovaries and testes in the same individual.

Classification of *Urochorda.*

As above indicated, there is a small section of *Urochorda* which retain in adult life the tadpole-like form and the essential Vertebrate organs which are exhibited by the larvæ only of other *Urochorda*, and by a few only of these. This necessitates a primary division of the branch into two grades.

Grade A.—LARVALIA (*Appendicularia, Fritillaria, Oikopleura*).
Grade B.—SACCATA.
Class I.—*Ascidiæ* (*Simplices, Sociales, Compositæ, Pyrosomiidea*).
Class II.—*Salpiformia* (*Salpiidea, Dolioliidea*).

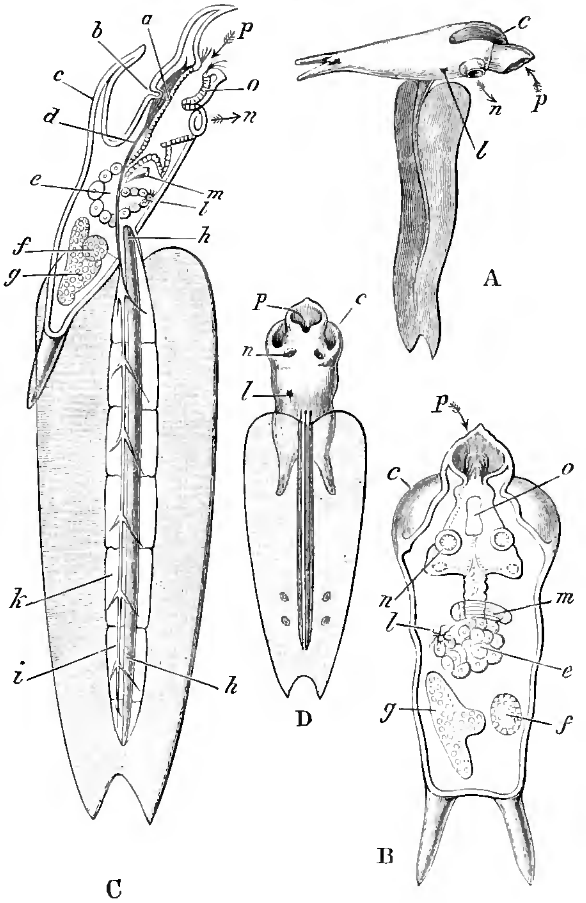


FIG. 9.—*Fritillaria* (*Appendicularia*) *furcata*, one of the *Urochorda*. (Original drawings.) A. Lateral surface view, showing habitual carriage of "body" at right angles to "tail." B. Organs of body as seen by transparency. C. Lateral view of body with tail in morphological position, showing organs by transparency. D. Surface view of animal from below to show apertures. *a*, Otocyst in connexion with brain ; *b*, olfactory pit ; *c*, dorsal hood ; *d*, nerve-tube passing from enlarged brain to caudal region, where it forms one true ganglion and a series of minor enlargements, corresponding to the rudimentary "myotomes" or "myomeres" of the tail ; *e*, stomach ; *f*, ovary ; *g*, testis ; *h*, notochord (urochord) ; *i*, nerve-tube or myelon in tail ; *k*, fifth myomere of tail ; *l*, anus ; *m*, heart ; *n*, gill-slit ; *o*, endostyle or hypobranchial groove ; *p*, mouth.

Relations of *Urochorda* to Vertebrate ancestry.

Urochorda are so extremely aberrant, and show so little more than a transient developmental indication of the essential Vertebrate organs, that we cannot hope to get much positive information from them on the subject of Vertebrate ancestry. Only the minute *Appendiculariæ* (*Larvalia*) retain the Vertebrate structure through life, and they are obviously, on account of their minute size, extremely degenerate. It is possible to make hypotheses as to the greater or less elaboration of the ancestors of *Urochorda*, and to maintain even that their ancestry had reached as high a condition as that shown by *Craniata*; on the other hand, it does not seem likely that their point of divergence from the main ancestral line leading to *Craniata* was lower than, or even so low as, that at which *Amphioxus* branched off. The differentiation of trunk and tail by the limitation of the notochord anteriorly is a nearer approach to Craniate structure than that shown by *Amphioxus*, whilst the definite development of a brain of considerable relative size places *Urochorda* nearer to the Craniates than is *Amphioxus*. The metameric myomeres so strongly developed in this last are not absent in *Urochorda*, as is often maintained, but exist in a rudimentary form, indicating that they had once a fuller development.

THE HEMICHORDA.

Characters of *Hemichorda*.

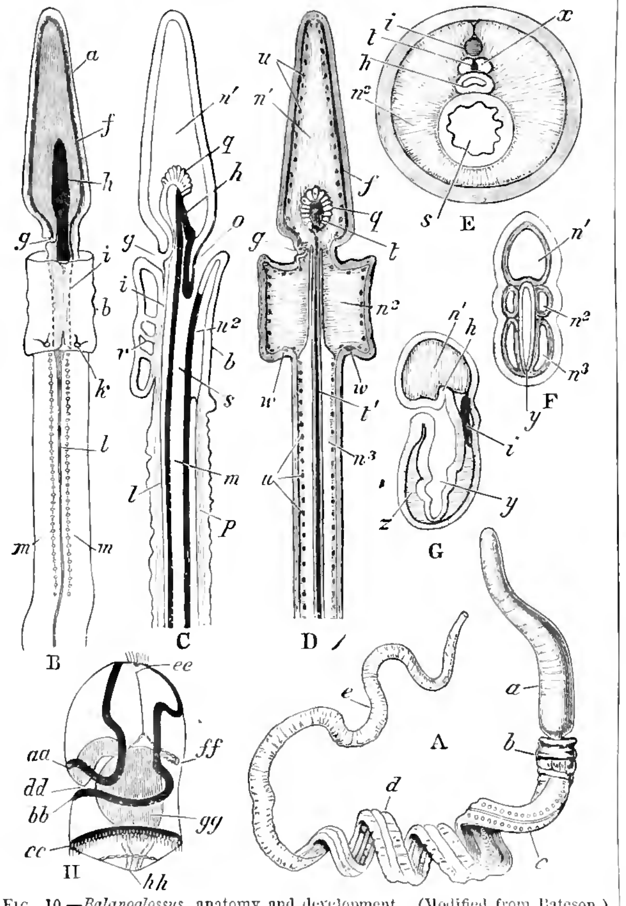


FIG. 10.—*Balanoglossus*, anatomy and development. (Modified from Bateson.) A. *Balanoglossus kowalewskii*, Bateson; from the coast of Virginia, U.S.; natural size; *a*, proboscis; *b*, collar; *c*, perforate region; *d*, flattened digestive region; *e*, cylindrical hind region. B. Diagram of dorsal view, showing certain organs as though the body-wall were transparent. C. Diagram of a vertical antero-posterior section. D. Diagram of a dorsal view to show vessels and nerves by transparency. E. Diagram of a transverse section through the collar. F. Larva of *B. kowalewskii*; diagram of horizontal section. G. Vertical longitudinal section of an older larva of the same. Lettering B-G:—*a*, proboscis; *b*, collar; *f*, nerve-tunic of proboscis; *g*, proboscis pore (ciliated orifice); *h*, notochord (limited to a small tract of modified tissue derived from præoral extension of alimentary canal); *i*, dorsal nerve-plate; *k*, collar-pore (right and left), opening to exterior from collar cœlom just beneath the collar; *l*, continuation of dorsal nerve-plate as a nerve-cord; *m*, pharyngeal perforations (gill-slits); *n'*, cœlom of proboscis (anterior azygos primitive cœlomic pouch); *n²*, collar cœlom (right and left middle cœlomic pouches of embryo); *n³*, body cœlom (right and left posterior cœlomic pouches of embryo); *o*, mouth; *p*, ventral nerve-tunic of body-wall; *x*, proboscis gland; *r*, strands connecting dorsal nerve-plate with outer wall of collar; *s*, cavity of pharynx in front of perforate region; *t*, dilated part (heart) of dorsal vessels within proboscis-gland; *t'*, dorsal vessel; *u*, blood-vessels of body-wall in section; *w*, paired nerves of collar region in transverse section; *x*, perihæmal cœlom, surrounding dorsal vessel in collar region; *y*, digestive region of gut (in embryo); *z*, mesoblast. H. Larva of another species of *Balanoglossus*, known as the *Tornaria* larva of Johann Muller, and resembling an Echinoderm larva. *aa*, præoral ciliated band of *Tornaria*; *bb*, post-oral ditto; *cc*, terminal ditto; *dd*, mouth; *ee*, apical plate and sense organ; *ff*, canal system and pore; *gg*, gut; *hh*, anus.

Hemichorda comprise the single genus *Balanoglossus*—formerly classified by Gegenbaur as *Enteropneusta*, an independent phylum of the animal kingdom. They are *Vertebrata* of worm-like form, elongate and somewhat flattened from above downwards. In front of the mouth is a long cylindrical proboscis, and behind it a collar, the free margin of which is turned backwards, and corresponds to the opercular epipleural folds of *Cephalochorda* and *Craniata*. This agreement is supported by the existence of a pair of collar pores opening into the cœlom of the collar, as the "brown funnels" of *Amphioxus* open into the epipleural cœlom of that animal. A proboscis pore, opening on the left side into the præoral cœlom of the proboscis (paired in *B. kupfferi*), is exactly representative of the similarly placed pore which in the young *Amphioxus* (according to Hatschek, *15*) leads into the tubular organ derived from the left cœlomic chamber of the præoral lobe of that animal. The whole surface of the body is ciliated, as in Nemertines and Echinoderms, and as in no other Vertebrates. Following the collar is a perforated region of the body,—gill-slits opening from the outer surface into the pharynx. In the young form there is for a time, as in *Appendiculariæ* and the Ascidian tadpole, only one pair of gill-slits, but they subsequently increase in number as the animal grows in length. They resemble in form and structure those of *Amphioxus*. The notochord (*h* in fig. 10) arises at the anterior end of the hypoblast in the young, and grows forward, forming a support for the base of the proboscis. It is limited to this very small region. The cerebro-spinal nerve-cord originates by a delamination of a solid cord of epiblast in the mid-dorsal line of the middle third of the body; then by invagination of its two ends it extends as a tube both anteriorly and posteriorly. A general network of nerve-fibres (and cells?) exists beneath the epidermis all over the body. The blood-system is peculiar, consisting of an anterior heart and a dorsal and ventral vessel; these are united by a plexus of subcutaneous vessels. The musculature of the body-wall is not broken into successive myomeres; but, on the other hand, the gonads (ovaries or testes) are sac-like, and, as in *Amphioxus*, are repeated in a series throughout a great length of the body. In the pharyngeal region the gonad sacs agree in number with the gill-slits. There are no nephridia (unless proboscis pore and collar pores are to be so regarded); but the connective-tissue cells of the body-cavity are active as excreting agents, as in Echinoderms and in *Urochorda*, and a large glandular organ in the proboscis attached to the end of the notochord appears to have to do with this function. Not the least remarkable fact about *Hemichorda* is the nature of their larvæ. No other *Vertebrata* present larval forms which indicate the nature of the early ancestral history in what we may call præ-chordal times; however interesting the Ascidian larva, or the young *Amphioxus*, and the embryo dog-fish, they do not take us out of the Vertebrate area. Some species of *Balanoglossus* (? *B. minutus*), however, pass through a banded ciliate larval condition, which was known as *Tornaria*, and was considered to be an Echinoderm larva allied to *Bipinnaria*, before its relation to *Balanoglossus* was discovered. It is not possible to view the *Tornaria* larva of *Balanoglossus* as otherwise than identical with Echinoderm larvæ, and it results that *Balanoglossus* and the Echinoderms have remote genetic affinities of a special kind.

Species of *Hemichorda*.

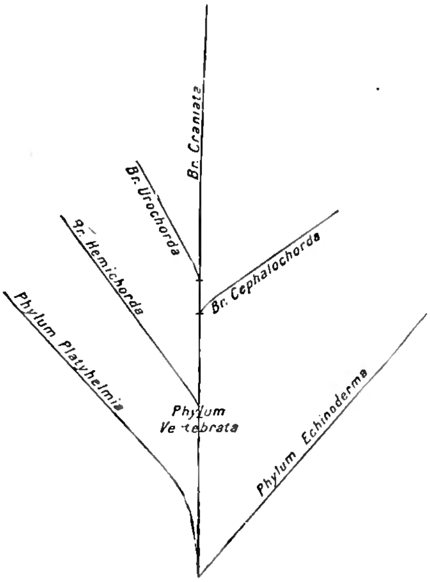
No classification of *Hemichorda* is possible beyond an enumeration of the species:—

1. *Balanoglossus clavigerus* (Della Chiaje), Naples.
2. *B. minutus* (Kowalewsky), ,,
3. *B. kowalewskii* (Al. Agassiz), east coast, United States.
4. *B. brooksii* (Bateson), ,, ,,
5. *B. salmoneus* (Giard), Brittany.
6. *P. robinii* (Giard), ,,

It seems that in *Balanoglossus* we at last find a form which, though no doubt specialized for its burrowing

Relations of *Hemichorda* to Vertebrate ancestry.

sand-life, and possibly to some extent degenerate, yet has not to any large extent fallen from an ancestral eminence. The ciliated epidermis, the long Worm-like form, and the complete absence of segmentation of the body-muscles lead us to forms like the Nemertines. The great proboscis of *Balanoglossus* may well be compared to the invaginable organ similarly placed in the Nemertines. The collar is the first commencement of a structure destined to assume great importance in *Cephalochorda* and *Craniata*, and perhaps protective of a single gill-slit in *Balanoglossus* before the number of those apertures had been extended. Borrowing, as we may, the nephridia from the Nemertines, and the lateral in addition to the dorsal nerve, we find that *Balanoglossus* gives the most hopeful hypothetical solution of the pedigree of Vertebrates. Space has not permitted us to go so fully into *pros* and *cons* as the speculative nature of the subject requires; but we give the final conclusion to which our consideration of the structure of the four great branches of the *Vertebrata* leads in the form of the accompanying genealogical tree.



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TUNICATA

(*By W. A. Herdman, D.Sc., Professor of Natural History, University College, Liverpool.*)

THIS group of animals was formerly regarded as constituting along with the *Polyzoa* and the *Brachiopoda* the invertebrate class *Molluscoidea*. It is now known to be a degenerate branch of the *Chordata*, and to be more nearly related to the *Vertebrata* than to any group of the *Invertebrata*.

HISTORY.[1]

Simple Ascidians. **Compound Ascidians.** **Cuvier and Savigny.** **Lamarck.**

More than two thousand years ago Aristotle gave a short account of a Simple Ascidian under the name of *Tethyum*. He described the appearance and some of the more important points in the anatomy of the animal. From that time onwards to little more than a century ago, although various forms of Ascidians had been briefly described by writers on marine zoology, comparatively little advance was made upon the knowledge of Aristotle. Schlosser and Ellis, in a paper containing a description of *Botryllus*, published in the *Philosophical Transactions* of the Royal Society for 1756, first brought the Compound Ascidians into notice; but it was not until the commencement of the 19th century, as a result of the careful anatomical investigations of Cuvier (*1*) upon the Simple Ascidians and of Savigny (*2*) upon the Compound, that the close relationship between these two groups of the *Tunicata* was conclusively demonstrated. Up to 1816, the date of publication of Savigny's great work (*2*), the few Compound Ascidians then known had been generally regarded as *Alcyonaria* or as Sponges; and, although many new Simple Ascidians had been described by O. F. Müller (*4*) and others, their internal structure had not been investigated. Lamarck (*3*) in 1816, chiefly as the result of the anatomical discoveries of Savigny and Cuvier, instituted the class *Tunicata*, which he placed between the *Radiata* and the *Vermes* in his system of classification. The *Tunicata* included at that time, besides the Simple and the Compound Ascidians, the pelagic forms *Pyrosoma*, which had been first made known by Péron in 1804, and *Salpa*, described by Forskål in 1775.

Chamisso and alternation of generations. **Circulation.** **Milne-Edwards.**

Chamisso in 1820 made the important discovery that *Salpa* in its life-history passes through the series of changes which were afterwards more fully described by Steenstrup in 1842 as "alternation of generations"; and a few years later Kuhl and Van Hasselt's investigations upon the same animal resulted in the discovery of the alternation in the directions in which the wave of contraction passes along the heart and in which the blood circulates through the body. It has since been found that this observation holds good for all groups of the *Tunicata*. In 1826 H. Milne-Edwards and Audouin made a series of observations on living Compound Ascidians, and amongst other discoveries they found the free-swimming tailed larva, and traced its development into the young Ascidian. Milne-Edwards (*5*) also founded the group of "Social" Ascidians, now known as the *Clavelinidæ*, and gave a classification of the Compound Ascidians which was universally accepted for many years. From the year 1826 onwards a number of new and remarkable forms were discovered, as, for instance, some of the *Boltenina* (Macleay), *Chelyosoma* (Broderip and Sowerby, and afterwards Eschricht), *Oikopleura* (Mertens), *Perophora* (Lister), *Pelonaia* (Forbes and Goodsir), *Chondrostachys* and *Diplosoma* (Denis Macdonald), *Diazona* (Forbes and Goodsir), and *Rhodosoma* (Ehrenberg, and afterwards Lacaze-Duthiers).

Carl Schmidt. **Huxley.** **Kowalevsky.** **Tailed larva.** **Relationship to Vertebrates.** **Kupffer, Giard, &c.** **Gemmation.**

In 1845 Carl Schmidt (*6*) first announced the presence in the test of some Ascidians of "tunicine," a substance very similar to cellulose, and in the following year Löwig and Kölliker (*7*) confirmed the discovery and made some additional observations upon this substance and upon the structure of the test in general. Huxley (*8*), in an important series of papers published in the *Transactions* of the Royal and Linnean Societies of London from 1851 onwards, discussed the structure, embryology, and affinities of the pelagic Tunicates *Pyrosoma*, *Salpa*, *Doliolum*, and *Appendicularia*. These important forms were also investigated about the same time by Gegenbaur, Vogt, H. Müller, Krohn, and Leuckart. The most important epoch in the history of the *Tunicata* is the date of the publication of Kowalevsky's celebrated memoir upon the development of a Simple Ascidian (*9*). The tailed larva had been previously discovered and investigated by several naturalists—notably H. Milne-Edwards (*5*), J. P. van Beneden (*10*), and Krohn (*11*); but its minute structure had not been sufficiently examined, and the meaning of what was known of it had not been understood. It was reserved for Kowalevsky in 1866 to demonstrate the striking similarity in structure and in development between the larval Ascidian and the vertebrate embryo. He showed that the relations between the nervous system, the notochord, and the alimentary canal are much the same in the two forms, and have been brought about by a very similar course of embryonic development. This discovery clearly indicated that the *Tunicata* are closely allied to *Amphioxus* and the *Vertebrata*, and that the tailed larva represents the primitive or ancestral form from which the adult Ascidian has been evolved by degeneration, and this led naturally to the view usually accepted at the present day, that the group is a degenerate side-branch from the lower end of the phylum *Chordata*, which includes the *Tunicata* (*Urochorda*), *Amphioxus* (*Cephalochorda*), and the *Vertebrata*. Kowalevsky's great discovery has since been confirmed and extended to all other groups of the *Tunicata* by Kupffer (*12*), Giard (*13* and *15*), and others. Important observations upon the process of gemmation and the formation of colonies in various forms of Compound Ascidians have been made by Krohn, Metschnikoff, Kowalevsky, Ganin, Giard, Della Valle, and others, and have gradually led to the establishment of the general principle, that all the more important layers of the bud are derived more or less directly from the corresponding regions in the body of the parent.

Fol, &c. **Sub-neural gland and dorsal tubercle.**

In 1872 Fol (*14*) added largely to the knowledge of the *Appendiculariidæ*, and Giard (*15*) to that of the Compound Ascidians. The latter author described a number of new forms and remodelled the classification of the group. The most important additions which have been made to the Compound Ascidians since Giard's work have been those described by Von Drasche (*16*) from the Adriatic and those discovered by the "Challenger" expedition (*17*). The structure and the systematic arrangement of the Simple Ascidians have been mainly discussed of recent years by Alder and Hancock (*18*), Heller (*19*), Lacaze-Duthiers (*20*), Traustedt (*21*), and Herdman (*17*, *22*). In 1874 Ussoff (*23*) investigated the minute structure of the nervous system and of the underlying gland, which was first discovered by Hancock, and showed that the gland has a duct which communicates with the front of the branchial sac or pharynx by an aperture in the dorsal (or "olfactory") tubercle. In an important paper published in 1880 Julin (*24*) drew attention to the similarity in structure and relations between this gland and the *hypophysis cerebri* of the vertebrate brain, and insisted upon their homology. He suggests that they perform a renal function. The *Thaliacea*

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[1] Only the more important works can be mentioned here. For a more detailed account of the history of the group and a full bibliography, see (*17*) in the list of works at the end of this article.

Thaliacea. have of late years been the subject of several very important memoirs. The researches of Todaro, Brooks (*25*), Salensky (*26*), and others have elucidated the embryology, the gemmation, and the life-history of the *Salpidæ*; and Grobben, Barrois (*27*), and more especially Uljanin (*28*) have elaborately worked out the structure and the details of the complicated life-history of the *Doliolidæ*. Finally, in an important work published in 1886 on the morphology of the *Tunicata*, E. van Beneden and Julin (*30*) have, mainly as the result of a close comparison of the embryology of Ascidians with that of *Amphioxus* and other *Chordata*, added considerably to our knowledge of the position and affinities of the *Tunicata*, and of the exact relations of their organs to the corresponding parts of the body in the *Vertebrata*.

Van Beneden and Julin.

ANATOMY.

Ascidia mentula. As a type of the *Tunicata*, *Ascidia mentula*, one of the larger species of the Simple Ascidians, may be taken. This species is found in most of the European seas, generally in shallow water on a muddy bottom.

External characters. It has an irregularly ovate form, and is of a dull grey colour. It is attached to some foreign object by one end (fig. 1). The opposite end of the body is usually narrow, and it has a terminal opening surrounded by eight rounded lobes. This is the mouth or branchial aperture, and it always indicates the anterior end [1] of the animal. About half-way back from the anterior end, and on a rounded projection, is the atrial or cloacal aperture—an opening surrounded by six lobes—which is always placed upon the dorsal region. When the Ascidian is living and undisturbed, water is being constantly drawn in through the branchial aperture and passed out through the atrial. If coloured particles be placed in the water near the apertures, they are seen to be sucked into the body through the branchial aperture, and after a short time some of them are ejected with considerable force through the atrial aperture. The current of water passing in is for respiratory purposes, and it also conveys food into the animal. The atrial current is mainly the water which has been used in respiration, but it also contains all excretions from the body, and at times the ova and spermatozoa or the embryos.

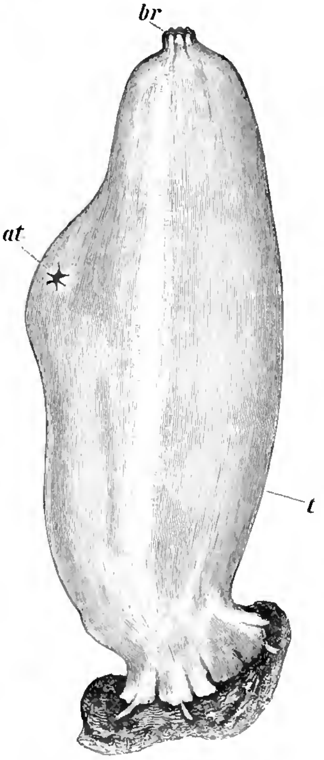

Fig. 1.—*Ascidia mentula* from the right side. *at*, atrial aperture; *br*, branchial aperture; *t*, test. (Original.)

The test. The outer grey part of the body, which is attached at or near its posterior end and penetrated by the two apertures, is the "test." This is a firm gelatinous cuticular secretion from the outer surface of the ectoderm, which is a layer of flat cells lining its inner surface. Although at first produced as a cuticle, the test soon becomes organized by the migration into it of cells derived from the ectoderm (see fig. 2). These test cells may remain as rounded or fusiform or stellate cells imbedded in the gelatinous matrix, to which they are constantly adding by secretions on their surfaces; or they may develop vacuoles in their protoplasm, which become larger and fuse to form a huge ovate clear cavity (a "bladder cell"), surrounded by a delicate film of protoplasm and having the nucleus still visible at one point; or they may form pigment granules in the protoplasm; or, lastly, they may deposit carbonate of lime, so that one or several of them together produce a calcareous spicule in the test. Only the unmodified test cells and the bladder cells are found in *Ascidia mentula*. Calcareous spicules are found chiefly in the *Didemnidæ*, amongst Compound Ascidians; but pigmented cells may occur in the test of almost all groups of *Tunicata*. The matrix in which these structures are imbedded is usually clear and apparently homogeneous; but in some cases it becomes finely fibrillated, especially in the family *Cynthiidæ*. It is this matrix which contains tunicine. At one point on the left side near the posterior end a tube enters the test, and then splits up into a number of branches, which extend in all directions and finally terminate in rounded enlargements or bulbs, situated chiefly in the outer layer of the test. These tubes are known as the "vessels" of the test, and they contain blood. Each vessel is bounded by a layer of ectoderm cells lined by connective tissue (fig. 3, *B*), and is divided into two tubes by a septum of connective tissue. The septum does not extend into the terminal bulb, and consequently the two tubes communicate at their ends (fig. 3, *A*). The vessels are formed by an outgrowth of a blood sinus (derived originally from the blastocœle of the embryo) from the body wall (mantle) into the test, the wall of the sinus being formed by connective tissue and pushing out a covering of ectoderm in front of it (fig. 2, *s'*). The test is turned inwards at the branchial and atrial apertures to line two funnel-like tubes,—the branchial siphon leading to the branchial sac and the atrial siphon leading to the atrial or peribranchial cavity.

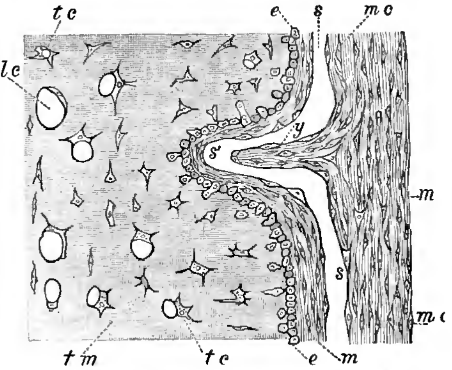

Fig. 2.—Diagrammatic section of part of mantle and test of an Ascidian, showing the formation of a vessel and the structure of the test. *m*, mantle; *e*, ectoderm; *tc*, test cell; *tm*, matrix; *ble*, bladder cell; *s*, *s'*, blood sinus in mantle being drawn out into test; *mc*, mantle cells; *y*, septum of vessel. (From Herdman, Challenger *Report*.

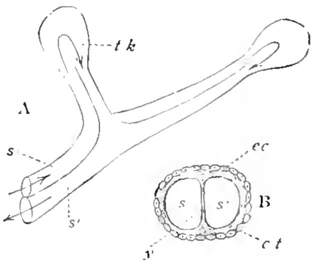

Fig. 3.—*A*, a vessel from the test. *B*, diagrammatic transverse section of a vessel. *ec*, ectoderm; *ct*, connective tissue; *s*, *s'*, the two tubes; *y*, septum; *tk*, terminal bulb. (Original.)

The body wall, inside the test and the ectoderm, is formed of a layer (the somatic layer of mesoderm) of connective tissue, inclosing muscle fibres, blood sinuses, and nerves. This layer (the mantle) has very much the shape of the test outside it, but at the two apertures it is drawn out to form the branchial and atrial siphons (fig. 4). In the walls of these siphons the muscle fibres form powerful circular bands, the sphincter muscles. Throughout the rest of the mantle the bands of muscle fibres form a rude irregular network. They are numerous on the right side of the body, and almost totally absent on the left. The muscles are all formed of very long fusiform non-striped fibres. The connective tissue of the mantle is chiefly a clear gelatinous Mantle.

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[1] Some writers use a different nomenclature of regions; see (*17*).

matrix, containing cells of various shapes; it is frequently pigmented and is penetrated by numerous lacunæ, in which the blood flows. Inside the mantle, in all parts of the body, except along the ventral edge, there is a cavity,—the atrial or peribranchial cavity,—which opens to the exterior by the atrial aperture. This cavity is lined by a layer of cells derived originally from the ectoderm[1] and directly continuous with that layer through the atrial aperture (fig. 5); consequently the mantle is covered both externally and internally by ectodermal cells.

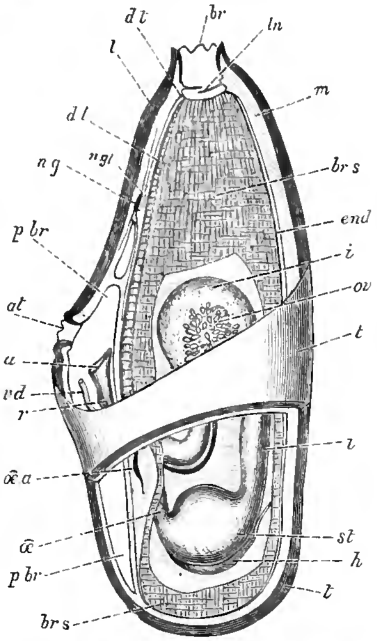

Fig. 4.—Diagrammatic dissection of *A. mentula* to show the anatomy. *at*, atrial aperture; *br*, branchial aperture; *a*, anus; *brs*, branchial sac; *dl*, dorsal lamina; *dt*, dorsal tubercle; *end*, endostyle; *h*, heart; *i*, intestine; *m*, mantle; *ng*, nerve ganglion; *œ*, œsophagus; *œa*, œsophageal aperture; *ov*, ovary; *pbr*, peribranchial cavity; *r*, rectum; *st*, stomach; *t*, test; *tn*, tentacles; *vd*, vas deferens; *ngl*, subneural gland. (Original.)

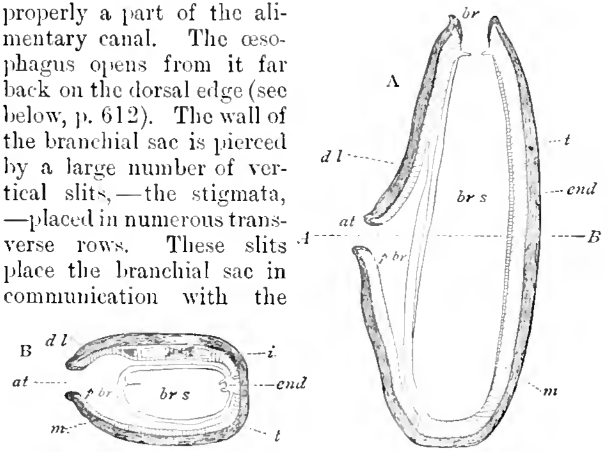

Fig. 5.—Diagrammatic longitudinal (A) and transverse (B) sections through *Ascidia* to show the position of the ectoderm and the relations of the branchial and peribranchial cavities. The lettering is the same as for fig. 4. B represents a section taken along the dotted line *A-B* in A. (Original.)

Branchial sac and neighbouring organs. The branchial aperture (mouth) leads into the branchial siphon (buccal cavity or stomodæum), and this opens into the anterior end of a very large cavity (the branchial sac) which extends nearly to the posterior end of the body (see figs. 4 and 5). This branchial sac is an enlarged and modified pharynx, and is therefore properly a part of the alimentary canal. The œsophagus opens from it far back on the dorsal edge (see below, p. 612). The wall of the branchial sac is pierced by a large number of vertical slits,—the stigmata,—placed in numerous transverse rows. These slits place the branchial sac in communication with the peribranchial or atrial cavity, which lies outside it (fig. 5, *B*). Between the stigmata the wall of the branchial sac is traversed by blood-vessels, which are arranged in three regular series (fig. 6),—(1) the transverse vessels, which run horizontally round the wall and open at their dorsal and ventral ends into large longitudinal vessels, the dorsal and ventral sinuses; (2) the fine longitudinal vessels, which run vertically between adjacent transverse vessels and open into them, and which bound the stigmata; and (3) the internal longitudinal bars, which run vertically in a plane internal to that of the transverse and fine longitudinal vessels. These bars communicate with the transverse vessels by short side branches where they cross, and at these points are prolonged into the lumen of the sac in the form of hollow papillæ. The edges of the stigmata are richly set with cilia, which drive the water from the branchial sac into the peribranchial cavity, and so cause the currents that flow in through the branchial aperture and out through the atrial.

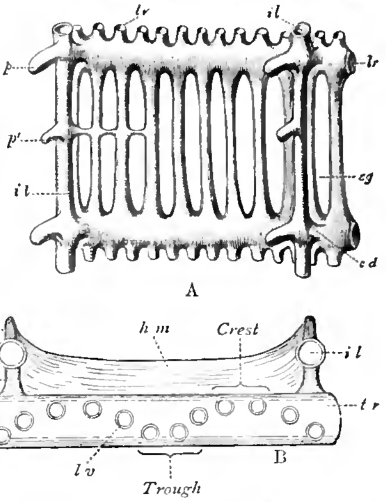

Fig. 6.—*A*. Part of branchial sac of *Ascidia* from inside. *B*. Transverse section of same. *tr*, transverse vessel; *cd*, connecting duct; *hm*, horizontal membrane; *il*, internal longitudinal bar; *lv*, fine longitudinal vessels; *p*, *p′*, papillæ; *sg*, stigmata. A and B are drawn to different scales. (From Herdman, Challenger *Report*.)

Endostyle. Along its ventral edge the wall of the branchial sac is continuous externally with the mantle (fig. 5, *B*), while internally it is thickened to form two parallel longitudinal folds bounding a groove, the "endostyle," hypobranchial groove, or ventral furrow (figs. 4, 5, *end*). The endoderm cells which line the endostyle are greatly enlarged at the bottom and on parts of the sides of the furrow so as to form projecting pads, which bear very long cilia. It is generally supposed that this organ is a gland for the production of the mucous secretion which is spread round the edges of the branchial sac and catches the food particles in the passing current of water; but it has recently been pointed out that there are comparatively few gland cells in the epithelium of the endostyle, and that it is more probable that this furrow is merely a ciliated path along which the mucous secretion (produced possibly by the subneural gland) is conveyed posteriorly along the ventral edge of the branchial sac. **Peripharyngeal bands.** At its anterior end the edges of the endostyle become continuous with the right and left halves of the posterior of two circular ciliated ridges,—the peripharyngeal bands,—which run parallel to one another round the front of the branchial sac. **Dorsal lamina.** The dorsal ends of the posterior peripharyngeal band bend posteriorly (enclosing the epibranchial groove), and then join to form the anterior end of a fold which runs along the dorsal edge of the branchial sac as far as the œsophageal aperture. This fold is the dorsal lamina (figs. 4, 5, *dl*). It probably serves to direct the stream of food particles entangled in a string of mucus from the anterior part of the dorsal lamina to the œsophagus. **Dorsal languets.** In many Ascidians this organ, instead of being a continuous membranous fold as in *A. mentula*, is represented by a series of elongated triangular processes—the dorsal languets,—one attached in the dorsal median line opposite to each transverse vessel of the branchial sac. The anterior peripharyngeal band is a complete circular ridge, having no connexion with either the endostyle or the dorsal lamina. In front of it lies the prebranchial zone, which separates the branchial sac behind from the branchial siphon in front. The prebranchial zone is bounded anteriorly by a muscular band—the posterior edge of the sphincter muscle,—which bears a circle of long delicate processes, the tentacles (figs. 4, 7, 8, *tn*). **Tentacles.** These project inwards at right angles so as to form a network across the entrance to the branchial sac. Each tentacle consists of connective tissue covered with epithe-

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[1] According to E. van Beneden and Julin's recent investigations (*30*) only the outer wall of the atrium is lined with epiblast, the inner wall being derived from the hypoblast of the primitive branchial sac.

lium (endoderm), and contains two or more cavities which are continuous with blood sinuses in the mantle. In the dorsal median line near the anterior end of the body, and imbedded in the mantle on the ventral surface of the nerve ganglion, there lies a small glandular mass—the subneural gland—which, as Julin has shown (*24*), there is reason to regard as the homologue of the *hypophysis cerebri* of the vertebrate brain. Julin and E. van Beneden have suggested that the function of this organ may possibly be renal.[1] The subneural gland, which was first noticed by Hancock, communicates anteriorly, as Ussoff (*23*) pointed out, by means of a narrow duct with the front of the branchial sac (pharynx). The opening of the duct is enlarged to form a funnel-shaped cavity, which may be folded upon itself, convoluted, or even broken up into a number of smaller openings, so as to form a complicated projection, called the dorsal tubercle, situated in the dorsal part of the prebranchial zone (fig. 7). The dorsal tubercle in *A. mentula* is somewhat horse-shoe-shaped (fig. 8); it varies in form in most Ascidians according to the genus and species, and in some cases in the individual also. Possibly, besides being the opening of the duct from the subneural gland, it may be a sense-organ for testing the quality of the water entering the branchial sac.

Subneural gland.

Dorsal tubercle.

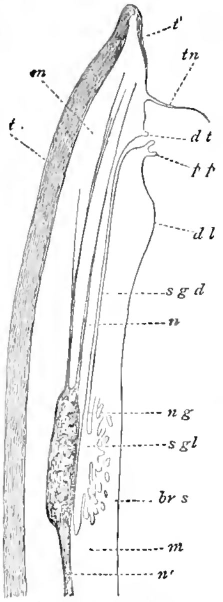

FIG. 7.—Diagrammatic section through anterior dorsal part of *A. mentula*, showing the relations of the nerve ganglion, subneural gland, &c. Lettering as for fig. 4; *n*, nerve; *n'*, myelon; *pp*, peripharyngeal band; *sgl*, subneural gland; *sgd*, its duct; *t'*, test lining branchial siphon. (Original.)

Nervous system.

The single elongated ganglion in the median dorsal line of the mantle between the branchial and atrial siphons is the only nerve-centre in *A. mentula* and most other *Tunicata*. It is the degenerate remains of the anterior part of the cerebro-spinal nervous system of the tailed larval Ascidian (see below, p. 614). The posterior or spinal part has entirely disappeared in most *Tunicata*. It persists, however, in the *Appendiculariidæ*, and traces of it are found in some Ascidians (*e.g.*, *Clavelina*; see Julin). The ganglion gives off distributory nerves at both ends, which run through the mantle to the neighbourhood of the apertures, where they divide and subdivide. The only sense-organs are the pigment spots between the branchial and atrial lobes, the tentacles at the base of the branchial siphon, and possibly the dorsal tubercle and the languets or dorsal lamina. These are all in a lowly developed condition. The larval Ascidians on the other hand have well-developed intra-cerebral optic and auditory sense-organs; and in some of the pelagic *Tunicata* otocysts and pigment spots are found in connexion with the ganglion.

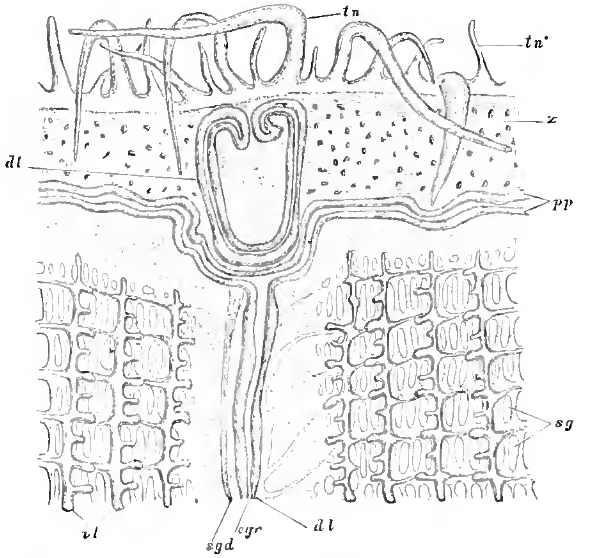

FIG. 8.—Dorsal tubercle and neighbouring organs of *A. mentula*. Lettering as before; *egr*, epibranchial groove; *z*, prebranchial zone. (Original.)

Sense organs.

Alimentary canal.

The mouth and the pharynx (branchial sac) have already been described. The remainder of the alimentary canal is a bent tube which in *A. mentula* and most other Ascidians lies imbedded in the mantle on the left side of the body, and projects into the peribranchial cavity. The œsophagus leaves the branchial sac in the dorsal middle line near the posterior end of the dorsal lamina (see fig. 4, *œa*). It is a short curved tube which leads ventrally to the large fusiform thick-walled stomach. The intestine emerges from the ventral end of the stomach, and soon turns anteriorly, then dorsally, and then posteriorly so as to form a curve—the intestinal loop—open posteriorly. The intestine now curves anteriorly again, and from this point runs nearly straight forward as the rectum, thus completing a second curve—the rectal loop—open anteriorly (see fig. 4). The wall of the intestine is thickened internally, to form the typhlosole, a pad which runs along its entire length. The anus opens into the dorsal part of the peribranchial cavity near to the atrial aperture. The walls of the stomach are glandular; and a system of delicate tubules with dilated ends, which ramifies over the outer wall of the intestine and communicates with the cavity of the stomach by means of a duct, is probably a digestive gland.

Excretory organs.

A mass of large clear vesicles which occupies the rectal loop, and may extend over the adjacent walls of the intestine, is a renal organ without a duct. Each vesicle is the modified remains of a part of the primitive cœlom or body-cavity, and is formed of cells which eliminate nitrogenous waste matters from the blood circulating in the neighbouring blood-lacunæ and deposit them in the cavity of the vesicle, where they form a concentrically laminated concretion of a yellowish or brown colour. These concretions contain uric acid, and in a large Ascidian are very numerous. The nitrogenous waste products are thus deposited and stored up in the renal vesicles in place of being excreted from the body. In other Ascidians the renal organ may differ from the above in its position and structure; but in no case has it an excretory duct, unless the subneural gland is to be regarded as a renal organ.

Blood-vascular system and cœlom.

The heart is an elongated fusiform tube placed on the ventral and posterior edge of the stomach, in a space (the pericardium) which is part of the original cœlom or body-cavity, the rest of which exists merely in the form of lacunæ and of the cavities of the reproductive organs and renal vesicles in the adult Ascidian. The wall of the heart is formed of a layer of epithelio-muscular cells, the inner ends of which are cross-striated; and waves of contraction pass along it from end to end, first for a certain number of beats in one direction and then in the other, so as to reverse the course of circulation periodically. At each end the heart is continued into a vessel (see fig. 9), a large sinus or lacuna lined with a delicate endothelial layer. The sinus leaving the ventral end of the heart is called the branchio-cardiac vessel,[2] and the heart itself is merely the differentiated posterior part of this sinus and is therefore a ventral vessel. The branchio-cardiac vessel, after giving off a branch which, along with a corresponding branch from the cardio-visceral vessel, goes to the test, runs along the

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[1] See also Herdman, *Nature*, vol. xxviii. p. 284.

[2] On account of the periodic reversal of the circulation none of the vessels can be called arteries or veins.

ventral edge of the branchial sac externally to the endostyle, and communicates laterally with the ventral ends of all the transverse vessels of the branchial sac. The sinus leaving the dorsal end of the heart is called the cardio-visceral vessel, and this, after giving off to the test the branch above mentioned, breaks up into a number of sinuses, which ramify over the alimentary canal and the other viscera. These visceral lacunæ finally communicate with a third great sinus, the viscero-branchial vessel, which runs forward along the dorsal edge of the branchial sac externally to the dorsal lamina and joins the dorsal ends of all the transverse vessels of the branchial sac. Besides these three chief systems there are numerous lacunæ in all parts of the body, by means of which anastomoses are established between the different currents of blood. All these blood spaces and lacunæ are to be regarded as derived from the blastocœle of the embryo, and not, as has been usually supposed, from the cœlom (*30*). Course of circulation. When the heart contracts ventro-dorsally, the course of the circulation is as follows: the blood which is flowing through the vessels of the branchial sac is collected in an oxygenated condition in the branchio-cardiac vessel, and, after receiving a stream of blood from the test, enters the heart. It is then propelled from the dorsal end of the heart into the cardio-visceral vessels, and so reaches the test and digestive and other organs; then, after circulating in the visceral lacunæ, it passes into the viscero-branchial vessel in an impure condition, and is distributed to the branchial vessels to be purified again. When the heart on the other hand contracts dorso-ventrally, this course of circulation is reversed. As the test receives a branch from each end of the heart, it follows that it has afferent and efferent vessels whichever way the blood is flowing. In some Ascidians the vessels in the test become very numerous and their end branches terminate in swollen bulbs close under the outer surface of the test. In this way an accessory respiratory organ[1] is probably formed in the superficial layer of the test. The blood corpuscles are chiefly colourless and amœboid; but in most if not all Ascidians there are also some pigmented corpuscles in the blood. These are generally of an orange or reddish brown tint, but may be opaque white, dark indigo-blue, or of intermediate colours. Precisely similarly pigmented cells are found throughout the connective tissue of the mantle and other parts of the body.

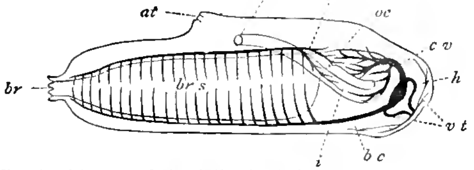

Fig. 9.—Diagram of circulation in *Ascidia*. Lettering as before; *bc*, branchio-cardiac or ventral vessel; *cv*, cardio-visceral vessels; *vb*, viscero-branchial or dorsal vessel; *vt*, vessels to test. (Original.)

Reproductive organs. *A. mentula* is hermaphrodite, and the reproductive organs lie, with the alimentary canal, on the left side of the body. The ovary is a ramified gland which occupies the greater part of the intestinal loop (see fig. 4). It contains a cavity which, along with the cavities of the testis, is derived from a part of the original cœlom, and the ova are formed from its walls and fall when mature into the cavity. The oviduct is continuous with the cavity of the ovary and leads forwards alongside the rectum, finally opening near the anus into the peribranchial cavity. The testis is composed of a great number of delicate branched tubules, which ramify over the ovary and the adjacent parts of the intestinal wall. Those tubules terminate in ovate swellings. Near the commencement of the rectum the larger tubules unite to form the vas deferens, a tube of considerable size, which runs forwards alongside the rectum, and, like the oviduct, terminates by opening into the peribranchial cavity close to the anus. The lumen of the tubules of the testis, like the cavity of the ovary, is a part of the original cœlom, and the spermatozoa are formed from the cells lining the wall. In some Ascidians reproductive organs are present on both sides of the body, and in others (*Polycarpa*) there are many complete sets of both male and female systems, attached to the inner surface of the mantle on both sides of the body and projecting into the peribranchial cavity.[2]

EMBRYOLOGY[3] AND LIFE HISTORY.

Embryology. In most Ascidians the eggs are fertilized in the peribranchial cavity, and undergo most of their development before leaving the parent; in some cases, however, the eggs are laid, and fertilization takes place in the surrounding water. The segmentation is complete and regular (fig. 10, A) and results in the formation of a spherical blastula, which then undergoes invagination (fig. 10, B). The embryo elongates, and the blastopore or invagination opening comes to be placed on the dorsal edge near the posterior end (fig. 10, C). The hypoblast cells lining the archenteron are columnar in form, while the epiblast cells are more cubical (fig. 10, B, C, D). The dorsal surface of the embryo now becomes flattened and then depressed to form a longitudinal groove, extending forwards from the blastopore to near the front of the body. This "medullary groove" now becomes converted into a closed canal by its side walls growing up, arching over, and coalescing in the median dorsal line (fig. 10, D). This union of the *laminæ dorsales* to form the neural canal commences at the posterior end behind the blastopore and gradually extends forwards. Consequently the blastopore comes to open into the posterior end of the neural canal (fig. 10, D), while the anterior end of that cavity remains open to the exterior. In this way the archenteron communicates indirectly with the exterior. The short canal leading from the neural canal to the archenteron is known as the neurenteric canal (fig. 10,

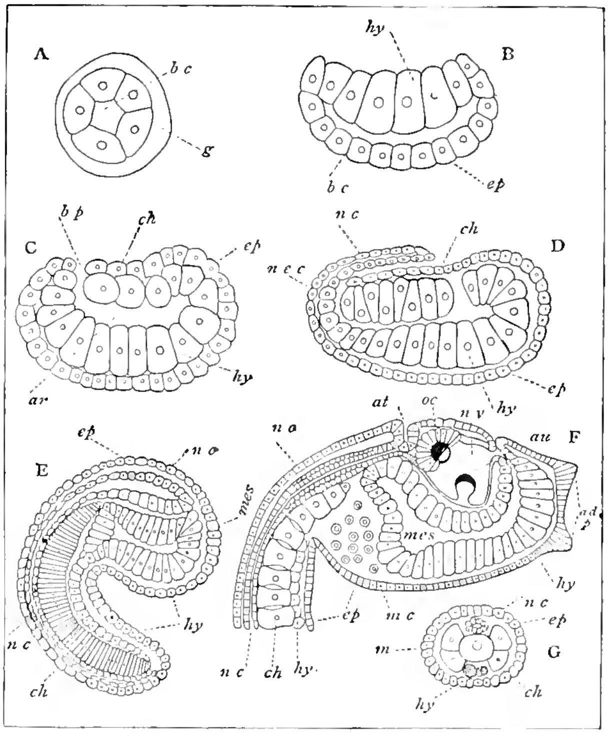

Fig. 10.—Stages in the embryology of a Simple Ascidian (after Kowalevsky). A to F. Longitudinal vertical sections of embryos, all placed with the dorsal surface uppermost and the anterior end at the right. A. Early blastula stage, during segmentation. B. Early gastrula stage. C. Stage after gastrula, showing commencement of notochord. D. Later stage, showing formation of notochord and of neural canal. E. Embryo showing body and tail and completely formed neural canal. F. Larva just hatched; end of tail cut off. G. Transverse section of tail of larva.
adp, adhering papillæ of larva; *at*, epiblastic (atrial) involution; *au*, auditory organ of larva; *ar*, archenteron; *bc*, blastocœle; *bp*, blastopore; *ch*, notochord; *ep*, epiblast; *hy*, hypoblast; *nc*, neural canal; *nec*, neurenteric canal; *oc*, ocular organ of larva; *g*, gelatinous investment of embryo; *m*, muscle cells of tail; *mes*, mesenteron; *mc*, mesoderm cells; *nv*, cerebral vesicle at anterior end of neural canal.

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[1] See Herdman, *Nature*, vol. xxxi. p. 247.

[2] For structure of other forms, see p. 614 *sq.* below.

[3] For reproduction by gemmation, see under "Classification," p. 614 *sq.* below.

D, *nec*). Previous to this stage some of the hypoblast cells at the front edge of the blastopore and forming part of the dorsal wall of the archenteron (fig. 10, C, *ch*) have become separated off, and then arranged to form an elongated band, two cells wide, underlying the posterior half of the neural canal (fig. 10, D, E, *ch.*). This is the origin of the notochord. Outgrowths from the sides of the archenteron give rise to laterally placed masses of cells, which are the origin of the mesoblast. These masses show no trace of metameric segmentation. The cavities (reproductive and renal vesicles) which are formed later in the mesoblast represent the cœlom. Consequently the body-cavity of the *Tunicata* is a modified form of enterocœle. The anterior part of the embryo, in front of the notochord, now becomes enlarged to form the trunk, while the posterior part elongates to form the tail (fig. 10, E). In the trunk the anterior part of the archenteron dilates to form the mesenteron, the greater part of which becomes the branchial sac; at the same time the anterior part of the neural canal enlarges to form the cerebral vesicle, and the opening to the exterior at the front end of the canal now closes. In the tail part of the embryo the neural canal remains as a narrow tube, while the remains of the wall of the archenteron—the dorsal part of which becomes the notochord—are converted into lateral muscle bands (fig. 10, G) and a ventral cord of cells, which eventually breaks up to form blood corpuscles. As the tail grows longer, it becomes bent round the trunk of the embryo inside the egg-membrane. About this period the epiblast cells begin to form the test as a cuticular deposit upon their outer surface. The test is at first devoid of cells and forms a delicate gelatinous investment, but it shortly afterwards becomes cellular by the migration into it of test cells formed by proliferation from the epiblast.[1]

Larval stage.

The embryo is hatched about two or three days after fertilization, in the form of a tadpole-like larva, which swims actively through the sea by vibrating its long tail. The anterior end of the body is provided with three adhering papillæ (fig. 10, F, *adp*) in the form of epiblastic thickenings. In the free-swimming tailed larva the nervous system, formed from the walls of the neural canal, becomes considerably differentiated. The anterior part of the cerebral vesicle remains thin-walled (fig. 10, F), and two unpaired sense organs develop from its wall and project into the cavity. These are a dorsally and posteriorly placed optic organ, provided with retina, pigment layer, lens, and cornea, and a ventrally placed auditory organ, consisting of a large spherical partially pigmented otolith, attached by delicate hair-like processes to the summit of a hollow *crista acustica* (fig. 10, F, *au*). The posterior part of the cerebral vesicle thickens to form a solid ganglionic mass traversed by a narrow central canal. The wall of the neural canal behind the cerebral vesicle becomes differentiated into an anterior thicker region, placed in the posterior part of the trunk and having a superficial layer of nerve fibres, and a posterior narrower part which traverses the tail, lying on the dorsal surface of the notochord, and gives off several pairs of nerves to the muscles of the tail. Just in front of the anterior end of the nervous system a dorsal involution of the epiblast breaks through into the upturned anterior end of the mesenteron and thus forms the mouth opening. Along the ventral edge of the mesenteron, which becomes the branchial sac, the endostyle is formed as a narrow groove with thickened side walls. It probably corresponds to the median portion of the thyroid body of *Vertebrata*. A curved outgrowth from the posterior end of the mesenteron forms the alimentary canal (œsophagus, stomach, and intestine), which at first ends blindly. An anus is formed later by the intestine opening into the left of two lateral epiblastic involutions (the atria), which rapidly become larger and fuse dorsally to form the peribranchial cavity. Outgrowths from the wall of the branchial sac meet these epiblastic involutions and fuse with them to give rise to the first formed pair of stigmata, which thus come to open into the peribranchial cavity; and these alone correspond to the gill clefts of *Amphioxus* and the *Vertebrata*.

Metamorphosis to adult form.

After a short free-swimming existence the fully developed tailed larva fixes itself by its anterior adhering papillæ to some foreign object, and then undergoes a remarkable series of retrogressive changes, which convert it into the adult Ascidian. The tail atrophies, until nothing is left but some fatty cells in the posterior part of the trunk. The adhering papillæ disappear and are replaced functionally by a growth of the test over neighbouring objects. The nervous system with its sense organs atrophies until it is reduced to the single small ganglion, placed on the dorsal edge of the pharynx, and a slight nerve cord running for some distance posteriorly (Van Beneden and Julin). Slight changes in the shape of the body and a further growth and differentiation of the branchial sac, peribranchial cavity, and other organs now produce gradually the structure found in the adult Ascidian.

The most important points in connexion with this process of development and metamorphosis are the following. (1) In the Ascidian embryo all the more important organs (*e.g.*, notochord, neural canal, archenteron) are formed in essentially the same manner as they are in *Amphioxus* and other *Chordata*. (2) The free-swimming tailed larva possesses the essential characters of the *Chordata*, inasmuch as it has a longitudinal skeletal axis (the notochord) separating a dorsally placed nervous system (the neural canal) from a ventral alimentary canal (the archenteron); and therefore during this period of its life-history the animal belongs to the *Chordata*. (3) The Chordate larva is more highly organized than the adult Ascidian, and therefore the changes by which the latter is produced from the former may be regarded as a process of degeneration (*31*). The important conclusion drawn from all this is that the *Tunicata* are the degenerate descendants of a group of the primitive *Chordata* (see below p. 618).

Classification and Characters of Groups.

Order I.—LARVACEA.

Characters of *Larvacea*.

Free-swimming pelagic forms provided with a large locomotory appendage (the tail), in which there is a skeletal axis (the urochord). A relatively large test (the "Haus") is formed with great rapidity as a secretion from the ectoderm; it is merely a temporary structure, which is cast off and replaced by another. The branchial sac is simply an enlarged pharnyx with two ventral ciliated openings (stigmata) leading to the exterior. There is no separate peribranchial cavity. The nervous system consists of a large dorsally placed ganglion and a long nerve cord, which stretches backwards over the alimentary canal to reach the tail, along which it runs on the left side of the urochord. The anus opens ventrally on the surface of the body in front of the stigmata. No reproduction by gemmation or metamorphosis is known in the life-history.

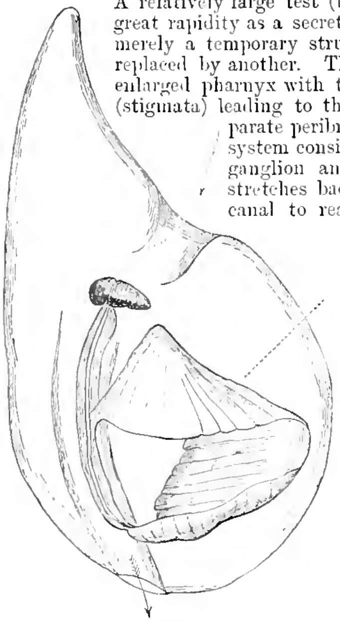

Fig. 11.—*Oikopleura cophocerca* in "Haus" (after Fol), seen from right side, magnified six times. The arrows indicate the course of the water; *x*, lateral reticulated parts of "Haus."

This is one of the most interesting groups of the *Tunicata*, as it shows more completely than any of the rest the characters of the original ancestral forms. It has undergone little or no degeneration, and consequently corresponds more nearly to the tailed-larval condition than to the adult forms of the other groups. The order includes a single family, the Appendiculariidæ, all the members of which are minute and free-swimming. They occur on the surface of the sea in most parts of the world. They possess the power to form with great rapidity an enormously large investing gelatinous layer (fig. 11), which corresponds to the test of other groups. This was first described by Von Mertens and by him named "Haus." It is only loosely attached to the body and is frequently thrown off soon after its formation. The tail in the *Appendiculariidæ* is attached to the ventral surface of the body (fig. 12), and usually

Structure of *Appendicularia*.

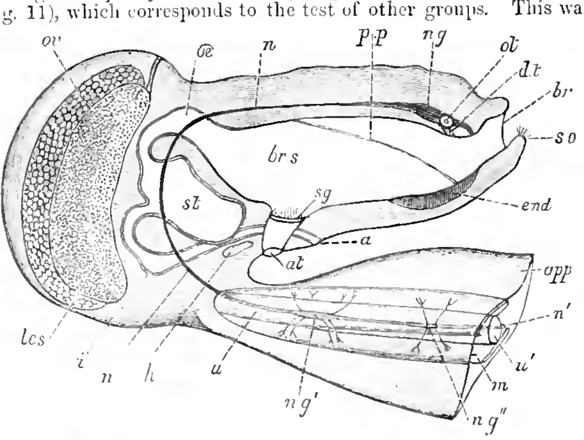

Fig. 12.—Semi-diagrammatic view of *Appendicularia* from the right. *a*, anus; *at*, one of the atrial apertures; *app*, tail; *br*, branchial aperture; *brs*, branchial sac; *dt*, dorsal tubercle; *end*, endostyle; *h*, heart; *i*, intestine; *m*, muscle band of tail; *n*, nerve cord in body; *n'*, nerve cord in the tail; *œ*, œsophagus; *ot*, otocyst; *ov*, ovary; *pp*, peripharyngeal band; *ng*, cerebral ganglion; *ng'*, caudal ganglion; *ng''*, enlargement of nerve cord in tail; *so*, sense organ (tactile) on lower lip; *sg*, ciliated aperture in pharynx; *st*, stomach; *tes*, testis; *u*, urochord; *u'*, its cut end. (Original.)

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[1] Some of the first test cells are also probably derived from the epithelium of the egg follicle.

points more or less anteriorly. It shows distinct traces of metameric segmentation, having its muscle bands broken up into myotomes, while the nerve cord presents a series of enlargements from which distributary nerves are given off (fig. 12, *ng''*). Near the base of the tail there is a distinct elongated ganglion (fig. 12, *ng'*). The anterior (cerebral) ganglion has connected with it an otocyst, a pigment spot, and a tubular process opening into the branchial sac and representing the dorsal tubercle and associated parts of an ordinary Ascidian. The branchial aperture or mouth leads into the branchial sac or pharynx. There are no tentacles. The endostyle is short. There is no dorsal lamina, and the peripharyngeal bands run dorsally and posteriorly. The wall of the branchial sac has only two ciliated apertures. They are homologous with the primary stigmata of the typical Ascidians and the gill clefts of Vertebrates. They are placed far back on the ventral surface, one on each side of the middle line, and lead into short funnel-shaped tubes which open on the surface of the body behind the anus (fig. 12, *at*). These tubes correspond to the right and left atrial involutions which, in an ordinary Ascidian, fuse to form the peribranchial cavity. The heart, according to Lankester, is formed of two cells, which are placed at the opposite ends and connected by delicate contractile protoplasmic fibrils. The large ovary and testis are placed at the posterior end of the body. The remainder of the structural details can be made out from fig. 12.

The family *Appendiculariidæ* comprises the genera,—*Oikopleura* (Mertens), and *Appendicularia* (Cham.), in both which the body is short and compact and the tail relatively long, while the endostyle is straight; *Fritillaria* (Q. and G.), in which the body is long and composed of anterior and posterior regions, the tail relatively short, the endostyle recurved, and an ectodermal hood is forming over the front of the body; and *Kowalevskia* (Fol), a remarkable form described by Fol (*14*), in which the heart, endostyle, and intestine are said to be absent, while the branchial sac is provided with four rows of ciliated tooth-like processes.

Order II.—THALIACEA.

Thaliacea.

Free-swimming pelagic forms which may be either simple or compound, and the adult of which is never provided with a tail or a notochord. The test is permanent and may be either well developed or very slight. The musculature of the mantle is in the form of more or less complete circular bands, by the contraction of which locomotion is effected. The branchial sac has either two large or many small apertures, leading to a single peribranchial cavity, into which the anus opens. Alternation of generations occurs in the life-history, and may be complicated by polymorphism. The *Thaliacea* comprises two groups, *Cyclomyaria* and *Hemimyaria*.

Sub-order 1.—**Cyclomyaria.**

Characters of *Cyclomyaria.*

Free-swimming pelagic forms which exhibit alternation of generations in their life-history but never form permanent colonies. The body is cask-shaped, with the branchial and atrial apertures at the opposite ends. The test is more or less well developed. The mantle has its musculature in the form of circular bands surrounding the body. The branchial sac is fairly large, occupying the anterior half or more of the body. Stigmata are usually present in its posterior part only. The peribranchial cavity is mainly posterior to the branchial sac. The alimentary canal is placed ventrally close to the posterior end of the branchial sac. Hermaphrodite reproductive organs are placed ventrally near the intestine.

This group forms one family, the Doliolidæ, including two genera, *Doliolum* (Quoy and Gaimard) and *Anchinia* (C. Vogt).

Structure of *Doliolum.*

Doliolum, of which several species are known from various seas, has a cask-shaped body, usually from 1 to 2 cm. in length. The terminal branchial and atrial apertures (fig. 13) are lobed, and the lobes are provided with sense organs. The test is very slightly developed and contains no cells. The mantle has eight or nine circular muscle bands surrounding the body. The most anterior and posterior of these form the branchial and atrial sphincters. The wide branchial and atrial apertures lead into large branchial and peribranchial cavities, separated by the posterior wall of the branchial sac, which is pierced by stigmata; consequently there is a free passage for the water through the body along its long axis, and the animal swims by contracting its ring-like muscle-bands, so as to force out the contained water posteriorly. Stigmata may also be found on the lateral walls of the branchial sac, and in that case there are corresponding anteriorly directed diverticula of the peribranchial cavity. There is a distinct endostyle on the ventral edge of the branchial sac and a peripharyngeal band surrounding its anterior end, but there is no representative of the dorsal lamina on its dorsal edge. The œsophagus commences rather on the ventral edge of the posterior end of the branchial sac, and runs backwards to open into the stomach, which is followed by a curved intestine opening into the peribranchial cavity. The alimentary canal as a whole is to the right of the middle line. The hermaphrodite reproductive organs are to the left of the middle line alongside the alimentary canal. They open into the peribranchial cavity. The ovary is nearly spherical, while the testis is elongated, and may be continued anteriorly for a long distance. The heart is placed in the middle line ventrally, between the posterior end of the endostyle and the œsophageal aperture. The nerve ganglion lies about the middle of the dorsal edge of the body, and gives off many nerves. Under it is placed the subneural gland, the duct of which runs forward and opens into the anterior end of the branchial sac by a simple aperture, surrounded by the spirally twisted dorsal end of the peripharyngeal band (fig. 13, *dt*).

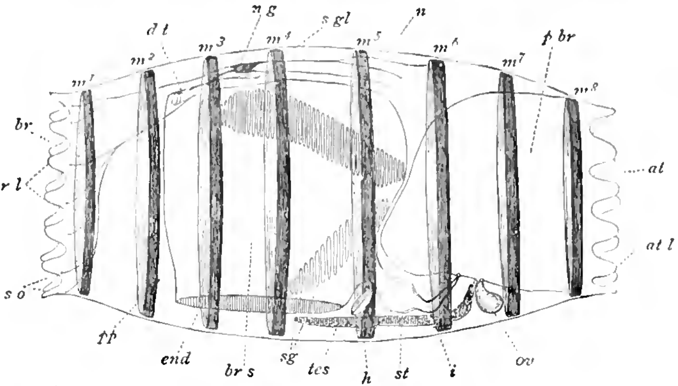

Fig. 13.—*Doliolum denticulatum*, sexual generation, from the left side. Lettering as for fig. 12; *m^1—m^8*, muscle bands; *ng*, nerve ganglion; *sg*, stigmata; *sgl*, subneural gland; *pbr*, peribranchial cavity; *atl*, atrial lobes; *so*, sense organs; *brl*, branchial lobes. (Original.)

Development of *Doliolum.*

The ova of the sexual generation produce tailed larvæ; these develop into forms known as "nurses" (blastozooids), which are asexual, and are characterized by the possession of nine muscle bands, an auditory sac on the left side of the body, a ventrally-placed stolon near the heart, upon which buds are produced, and a dorsal outgrowth near the posterior end of the body. The buds give rise eventually to the sexual generation, which is polymorphous, having three distinct forms, in two of which the reproductive organs remain undeveloped. The buds while still very young migrate from their place of origin on the stolon, divide by fission, and become attached to the dorsal outgrowth of the body of the nurse, where they develop. The three forms produced are as follows. (1) Nutritive forms (trophozooids), which remain permanently attached to the nurse and serve to provide it with food; they have the body elongated dorso-ventrally, and the musculature is very slightly developed. (2) Foster forms (phorozooids), which, like the preceding, do not become sexually mature, but, unlike them, are set free as cask-shaped bodies with eight muscle bands and a ventral outgrowth, which is formed of the stalk by which the body was formerly united to the nurse. On this outgrowth the (3) forms (gonozooids) which become sexually mature are attached while still young buds, and after the foster forms are set free these reproductive forms gradually attain their complete development, and are eventually set free and lose all trace of their connexion with the foster forms. They resemble the foster forms in having a cask-shaped body with eight muscle bands, but differ in having no outgrowth or process, and in having the reproductive organs fully developed.[1]

Anchinia.

Anchinia, of which only one species is known, *A. rubra*, from the Mediterranean, has the sexual forms permanently attached to portions of the dorsal outgrowth from the body of the unknown nurse. The body is elongated dorso-ventrally. The test is well developed and contains branched cells. The musculature is not so well developed as in *Doliolum*. There are two circular bands at the anterior end and two at the posterior, and two on the middle of the body. The stigmata are confined to the obliquely placed posterior end of the branchial sac. The alimentary canal forms a U-shaped curve. The reproductive organs are placed on the right side of the body. The life-history is still imperfectly known. As in the case of *Doliolum* the sexual generation is polymorphous, and has three forms, two of which remain in a rudimentary condition so far as the reproductive organs are concerned. In *Anchinia*, however, the three forms do not occur together on one stolon or outgrowth, but are produced successively, the reproductive forms of the sexual generation being independent of the "foster forms" (see Barrois, *27*).

Sub-order 2.—**Hemimyaria.**

Characters of *Hemimyaria.*

Free-swimming pelagic forms which exhibit alternation of generations in their life-history and in the sexual condition form colonies. The body is more or less fusiform, with the long axis antero-posterior, and the branchial and atrial apertures nearly terminal. The test is well developed. The musculature of the mantle is in the form of a series of transversely-running bands, which do not form complete independent rings as in the *Cyclomyaria*. The branchial and

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[1] For further details see Uljanin (*28*).

peribranchial cavities form a continuous space in the interior of the body, opening externally by the branchial and atrial apertures, and traversed obliquely from the dorsal and anterior end to the ventral and posterior by a long narrow vascular band, which represents the dorsal lamina, the dorsal blood-vessel, and the neighbouring part of the dorsal edge of the branchial sac of an ordinary Ascidian. The alimentary canal is placed ventrally. It may either be stretched out so as to extend for some distance anteriorly, or—as is more usual—be concentrated to form along with the reproductive organs a rounded opaque mass near the posterior end of the body, known as the visceral mass or "nucleus." The embryonic development is direct, no tailed larva being formed.

This sub-order contains two very distinct families, the SALPIDÆ, which are the typical members, and the OCTACNEMIDÆ, including a single very remarkable form (*Octacnemus bythius*), which in some respects does not conform with the characters given above.

Salpidæ.

The *Salpidæ* includes the single genus *Salpa* (Forskål), which, however, may be divided into two well-marked groups of species,—(1) those, such as *S. pinnata*, in which the alimentary canal is stretched out along the ventral surface of the body, and (2) those, such as *S. fusiformis* (fig. 14, A), in which the alimentary canal forms a compact globular mass, the "nucleus," near the posterior end of the body. About fifteen species altogether are known; they are all pelagic forms and are found in nearly all seas.

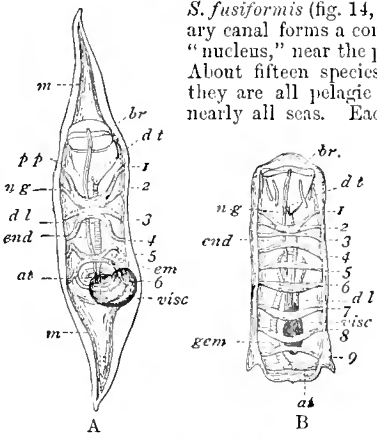


FIG. 14.—*Salpa runcinata-fusiformis.* A. Aggregated form. B. Solitary form. Lettering as before; 1-9, muscle bands; *em*, embryo; *gem*, gemmiparous stolon; *m*, mantle; *visc*, visceral mass (nucleus). (Original.)

Each species occurs in two forms—the solitary asexual (*proles solitaria*) and the aggregated sexual (*proles gregaria*)—which are usually quite unlike one another. The solitary form (fig. 14, B) gives rise by internal gemmation to a complex tubular stolon, which contains processes from all the more important organs of the parent body and which becomes segmented into a series of buds or embryos. As the stolon elongates, the embryos near the free end which have become advanced in their development are set free in groups, which remain attached together by processes of the test, each enclosing a diverticulum from the mantle so as to form "chains" (fig. 15). Each member of the chain is a *Salpa* of the sexual or aggregated form, and when mature may—either still attached to its neighbours or separated from them (fig. 14, A)—produce one or several embryos, which develop into the solitary *Salpa*. Thus the two forms alternate regularly.

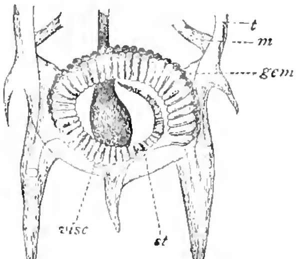


FIG. 15.—Posterior part of solitary form of *Salpa democratica-mucronata*, showing a chain of embryos nearly ready to be set free. *gem*, young aggregated *Salpæ* forming the chain; *st*, stolon; *m*, muscle band of the mantle. (Original.)

Structure of Salpa.

The more important points in the structure of a typical *Salpa* are shown in fig. 16. The branchial and atrial apertures are at opposite ends of the body, and each leads into a large cavity, the branchial and peribranchial sacs, which are in free communication at the sides of the obliquely-running dorsal lamina or "gill." The test is well developed and adheres closely to the surface of the mantle. The muscle bands of the mantle do not completely encircle the body. They are present dorsally and laterally, but the majority do not reach the ventral surface. In many cases neighbouring bands join in the median dorsal line, (fig. 14). The anterior end of the dorsal lamina is prolonged to form a prominent tentacular organ, the languet, projecting into the branchial sac.

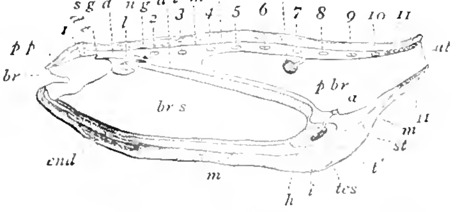


FIG. 16.—Semi-diagrammatic representation of *Salpa* from left side. Lettering as before; *emb*, embryo; *m*, mantle; *l*, languet; *sgd*, duct of subneural gland; 1-11, muscle bands of mantle; *t'*, thickening of test over nucleus; *dl*, gill or branchia. (Original.)

The nerve ganglion, subneural gland, dorsal lamina, peripharyngeal bands, and endostyle are placed in the usual positions. A pigment spot and an otocyst are found in connection with the ganglion. The large spaces at the sides of the dorsal lamina (often called the gill or branchia of *Salpa*), by means of which the cavity of the branchial sac is placed in free communication with the peribranchial cavity, are to be regarded as gigantic stigmata formed by the suppression of the lateral walls of the branchial sac. Fig. 16 represents an aggregated or sexual *Salpa* which was once a member of a chain, since it shows a testis and a developing embryo. The ova (always few in number, usually only one) appear at a very early period in the developing chain *Salpa*, while it is still a part of the gemmiparous stolon in the body of the solitary *Salpa*. This gave rise to the view put forward by Brooks (*25*), that the ovary really belongs to the solitary *Salpa*, which is therefore a female producing a series of males by asexual gemmation, and depositing in each of these an ovum, which will afterwards, when fertilized, develop in the body of the male into a solitary or female *Salpa*. This idea would of course entirely destroy the view that *Salpa* is an example of alternation of generations. The sexual or chain *Salpa*, although really hermaphrodite, is always protogynous: *i.e.*, the female elements or ova are produced at an earlier period than the male organ or testis. This prevents self-fertilization.

Development of Salpa.

The ovum is fertilized by the spermatozoa of an older *Salpa* belonging to another chain, and the embryo is far advanced in its development before the testis is formed. At an early period in its development a part of the embryo becomes separated off, along with a part of the wall of the cavity in which it lies, to form the "placenta," in which the embryonic and the maternal blood streams circulate in close proximity (or actually coalesce during one period) and so allow of the passage of nutriment to the developing embryo. At a somewhat later stage a number of cells placed at the posterior end of the body alongside the future nucleus become filled up with oil-globules to form a mass of nutrient material—the elæoblast—which is used up later on in the development. Many suggestions have been made as to the homology of the elæoblast. The most probable is that it is the disappearing rudiment of the tail found in the larval condition of most Ascidians.

Octacnemidæ.

The family *Octacnemidæ* includes the single remarkable form *Octacnemus bythius*, found during the "Challenger" expedition, and first described by Moseley (*29*). It is apparently a deep-sea representative of the pelagic *Salpidæ*, and may possibly be fixed. The body is somewhat discoid, with its margin prolonged to form eight tapering processes, on to which the muscle bands of the mantle are continued. The alimentary canal forms a compact nucleus (fig. 17); the endostyle is very short; and the dorsal lamina is apparently absent. The reproduction and life-history are entirely unknown.

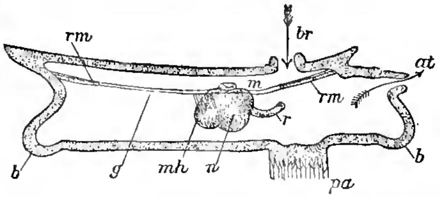


FIG. 17.—Diagrammatic vertical longitudinal section of *Octacnemus bythius* (after Moseley). *br*, branchial aperture; *m*, opening of œsophagus; *r*, rectum; *at*, atrial aperture; *rm*, *rm*, radiating muscles; *n*, nucleus; *mh*, muscles of nucleus; *g*, respiratory membrane; *b*, thickened margin of base of test; *pa*, pedicle of attachment.

Order III.—ASCIDIACEA.

Ascidiacea.

Fixed or free-swimming Simple or Compound Ascidians which in the adult are never provided with a tail and have no trace of a notochord. The free-swimming forms are colonies, the Simple Ascidians being always fixed. The test is permanent and well developed; as a rule it increases with the age of the individual. The branchial sac is large and well developed. Its walls are perforated by numerous slits (stigmata) opening into the peribranchial cavity, which communicates with the exterior by the atrial aperture. Many of the forms reproduce by gemmation, and in most of them the sexually-produced embryo develops into a tailed larva.

The *Ascidiacea* includes three groups,—the Simple Ascidians, the Compound Ascidians, and the free-swimming colonial *Pyrosoma*.

Sub-order I.—**Ascidiæ Simplices.**

Simple Ascidians.

Fixed Ascidians which are solitary and very rarely reproduce by gemmation; if colonies are formed, the members are not buried in a common investing mass, but each has a distinct test of its own. No strict line of demarcation can be drawn between the Simple and the Compound Ascidians, and one of the families of the former group, the *Clavelinidæ* (the Social Ascidians), forms a transition from the typical Simple forms, which never reproduce by gemmation, to the Compound forms, which always do (see p. 618 below). The *Ascidiæ Simplices* may be divided into the following families:—

Family I.—CLAVELINIDÆ. Simple Ascidians which reproduce by gemmation to form small colonies in which each ascidiozooid has a distinct test, but all are connected by a common blood-system.

Buds formed on stolons which are vascular outgrowths from the posterior end of the body, containing prolongations from the ectoderm, mesoderm, and endoderm of the ascidiozooid. Branchial sac not folded; internal longitudinal bars usually absent; stigmata straight; tentacles simple. This family contains three genera: *Ecteinascidia* (Herdman), with internal longitudinal bars in branchial sac; *Clavelina* (Savigny), with intestine extending behind branchial sac; and *Perophora* (Wiegmann), with intestine alongside branchial sac.

Family II.—Ascidiidæ. Solitary fixed Ascidians with gelatinous test; branchial aperture usually eight-lobed, atrial aperture usually six-lobed. Branchial sac not folded; internal longitudinal bars usually present; stigmata straight or curved; tentacles simple. This family is divided into three sections:—

Sub-family 1.—Hypobythinæ. Branchial sac with no internal longitudinal bars. One genus, *Hypobythius* (Moseley).

Sub-family 2.—Ascidinæ. Stigmata straight. Many genera, of which the following are the more important:—*Ciona* (Fleming), dorsal languets present; *Ascidia* (Linnæus, =*Phallusia*, Savigny), dorsal lamina present (see figs. 1 to 10); *Rhodosoma* (Ehrenberg), anterior part of test modified to form operculum; *Abyssascidia* (Herdman), intestine on right side of branchial sac.

Sub-family 3.—Corellinæ. Stigmata curved. Three genera:—*Corella* (Alder and Hancock), test gelatinous, body sessile; *Corynascidia* (Herdman), test gelatinous, body pedunculated; *Chelyosoma* (Brod. and Sow.), test modified into horny plates.

Family III.—Cynthiidæ. Solitary fixed Ascidians, usually with leathery test; branchial and atrial apertures usually both four-lobed. Branchial sac longitudinally folded; stigmata straight; tentacles simple or compound. This family is divided into three sections:—

Sub-family 1.—Stylinæ, not more than four folds on each side of branchial sac; tentacles simple. The more important genera are—*Styela* (Macleay), stigmata normal, and *Bathyoncus* (Herdman), stigmata absent or modified.

Sub-family 2.—Cynthinæ, more than eight folds in branchial sac; tentacles compound; body sessile. The chief genus is *Cynthia* (Savigny), with a large number of species.

Sub-family 3.—Boltenin.e, more than eight folds in branchial sac; tentacles compound; body pedunculated (fig. 18, A). The chief genera are—*Boltenia* (Savigny), branchial aperture four-lobed, stigmata normal; and *Culeolus* (Herdman), branchial aperture with less than four lobes, stigmata absent or modified (fig. 18, B). This last is a deep-sea genus discovered by the "Challenger" expedition (see *17*).

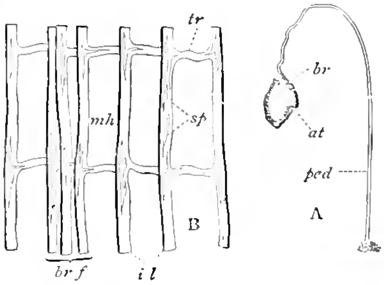


Fig. 18.—*Culeolus willemoesi*. A. Entire body, natural size. B. Part of branchial sac magnified. *at*, atrial aperture; *br*, branchial aperture; *ped*, peduncle; *br f*, slight fold of branchial sac; *i l*, internal longitudinal bar; *mh*, mesh; *sp*, calcareous spicules in vessels; *tr*, transverse vessels. (After Herdman, Challenger *Report*.)

Family IV.—Molgulidæ. Solitary Ascidians, sometimes not fixed; branchial aperture six-lobed, atrial four-lobed. Test usually incrusted with sand. Branchial sac longitudinally folded; stigmata more or less curved, usually arranged in spirals; tentacles compound. The chief genera are—*Molgula* (Forbes), with distinct folds in the branchial sac, and *Eugyra* (Ald. and Hanc.), with no distinct folds, but merely broad internal longitudinal bars in the branchial sac. In some of the *Molgulidæ* (genus *Anurella*, Lacaze-Duthiers, *20*) the embryo does not become converted into a tailed larva, the development being direct, without metamorphosis. The embryo when hatched assumes gradually the adult structure, and never shows the features characteristic of larval Ascidians, such as the urochord and the median sense-organs.

Sub-order 2.—**Ascidiæ Compositæ.**

Compound Ascidians.

Fixed Ascidians which reproduce by gemmation, so as to form colonies in which the ascidiozooids are buried in a common investing mass and have no separate tests. This is probably a somewhat artificial assemblage formed of two or three groups of Ascidians which produce colonies in which the ascidiozooids are so intimately united that they possess a common test or investing mass. This is the only character which distinguishes them from the *Clavelinidæ*, but the property of reproducing by gemmation separates them from the rest of the *Ascidiæ Simplices*. The *Ascidiæ Compositæ* may be divided into the following families:—

Family I.—Distomidæ. Ascidiozooids divided into two regions, thorax and abdomen; testes numerous; vas deferens not spirally coiled. The chief genera are—*Distoma* (Gaertner); *Distaplia* (Della Valle); *Colella* (Herdman), forming a pedunculated colony (see fig. 19, A) in which the ascidiozooids develop incubatory pouches, connected with the peribranchial cavity, in which the embryos undergo their development (*17*); and *Chondrostachys* (Macdonald).

Family II.—Cœlocormidæ. Colony not fixed, having a large axial cavity with a terminal aperture. Branchial apertures five-lobed. This includes one species, *Cœlocormus huxleyi* (Herdman), which is a transition form between the ordinary Compound Ascidians (*e.g.*, *Distomidæ*) and the *Ascidiæ Salpiformes* (*Pyrosoma*).

Family III.—Didemnidæ. Colony usually thin and incrusting. Test containing stellate calcareous spicules. Testis single, large; vas deferens spirally coiled. The chief genera are—*Didemnum* (Savigny), in which the colony is thick and fleshy and there are only three rows of stigmata on each side of the branchial sac; and *Leptoclinum* (Milne-Edwards), in which the colony is thin and incrusting (fig. 19, B) and there are four rows of stigmata on each side of the branchial sac.

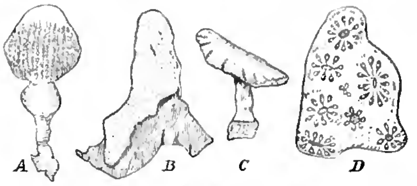


Fig. 19.—Colonies of *Ascidiæ Compositæ* (natural size). A. *Colella quoyi*. B. *Leptoclinum neglectum*. C. *Pharyngodictyon mirabile*. D. *Botryllus*, showing arrangement of ascidiozooids in circular systems each of which has a central common cloaca. (After Herdman, Challenger *Report*.)

Family IV.—Diplosomidæ. Test reduced in amount, rarely containing spicules. Vas deferens not spirally coiled. In *Diplosoma* (Macdonald), the most important genus, the larva is gemmiparous.

Family V.—Polyclinidæ. Ascidiozooids divided into three regions,—thorax, abdomen, and post-abdomen. Testes numerous; vas deferens not spirally coiled. The chief genera are—*Pharyngodictyon* (Herdman), with stigmata absent or modified, containing one species, *Ph. mirabile* (fig. 19, C), the only Compound Ascidian known from a depth of 1000 fathoms; *Polyclinum* (Savigny), with a smooth-walled stomach; *Aplidium* (Savigny), with the stomach wall longitudinally folded; and *Amaroucium* (Milne-Edwards), in which the ascidiozooid has a long post-abdomen and a large atrial languet.

Family VI.—Botryllidæ. Ascidiozooids having the intestine and reproductive organs alongside the branchial sac. Dorsal lamina present; internal longitudinal bars present in branchial sac. The chief genera are—*Botryllus* (Gaertn. and Pall.), with simple stellate systems (fig. 19, D), and *Botrylloides* (Milne-Edwards), with elongated or ramified systems.

Family VII.—Polystyelidæ. Ascidiozooids not grouped in systems. Branchial and atrial apertures four-lobed. Branchial sac may be folded; internal longitudinal bars present. The chief genera are—*Thylacium* (Carus), with ascidiozooids projecting above general surface of colony; *Goodsiria* (Cunningham), with ascidiozooids completely imbedded in investing mass; and *Chorizocormus* (Herdman), with ascidiozooids united in little groups which are connected by stolons. The last genus contains one species, *Ch. reticulatus*, a transition form between the other *Polystyelidæ* and the *Stylinæ* amongst Simple Ascidians.

Reproduction by gemmation

The methods of reproduction by gemmation differ in their details in the various groups of Compound Ascidians; but in all cases the process is essentially a giving off from the parent body of groups of cells representing the ectoderm, the mesoderm, and the endoderm, which develop into the corresponding layers of the bud. The first ascidiozooid of the colony produced by the tailed larva does not form sexual reproductive organs, but reproduces by gemmation so as to make a colony. Thus there is alternation of generations in the life-history. In the most completely formed colonies (*e.g.*, *Botryllus*) the ascidiozooids are arranged in groups (systems or cœnobii), and in each system are placed with their atrial apertures towards one another, and all communicating with a common cloacal cavity which opens to the exterior in the centre of the system (fig. 19 D).

Sub-order 3.—**Ascidiæ Salpiformes.**

Ascidiæ Salpiformes.

Free-swimming pelagic colonies having the form of a hollow cylinder closed at one end. The ascidiozooids forming the colony are imbedded in the common test in such a manner that the branchial apertures open on the outer surface and the atrial apertures on the inner surface next to the central cavity of the colony. The ascidiozooids are produced by gemmation from a rudimentary larva (the cyathozooid) developed sexually.

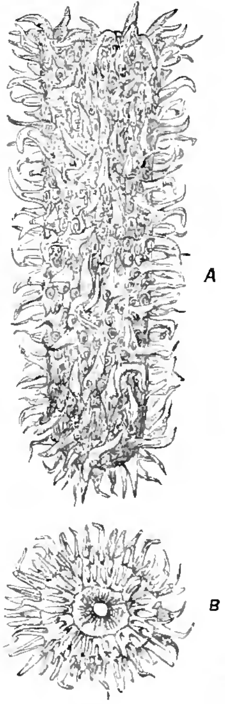


Fig. 20.—*Pyrosoma elegans*, natural size. A. Side view of entire colony. B. End view of open extremity. (Original.)

Structure of *Pyrosoma.*

This sub-order includes a single family, the Pyrosomidæ, containing one well-marked genus, *Pyrosoma* (Péron), with several species. They are found swimming near the surface of the sea, chiefly in tropical latitudes, and are brilliantly phosphorescent. A fully developed *Pyrosoma* colony may be from an inch or two to upwards of four feet in length. The shape of the colony is seen in fig. 20. It tapers slightly towards the closed end, which is rounded. The opening at the opposite end is reduced in size by the presence of a membranous prolongation of the common test (fig. 20, B). The branchial apertures of the ascidiozooids are placed upon short papillæ projecting from the general surface, and most of the ascidiozooids have long conical processes of the test projecting outwards beyond their branchial apertures (figs. 20, 21, and 22). There is only a single layer of ascidiozooids in the *Pyrosoma* colony, as all the fully developed ascidiozooids are placed with their antero-posterior axes at right angles to the surface and communicate by their atrial apertures with the central cavity of the colony (fig. 21).

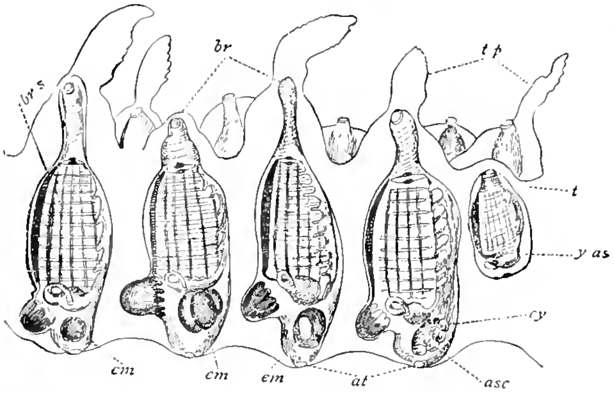


Fig. 21.—Part of a longitudinal section through wall of *Pyrosoma*, showing arrangement of ascidiozooids, magnified (partly after Savigny). *at*, atrial apertures; *br*, branchial apertures; *asc*, young ascidiozooid of a future colony produced by budding from *cy*, cyathozooid; *cm*, embryos in various stages; *t*, test; *tp*, processes of test; *brs*, branchial sac; *yas*, young ascidiozooid.

Their dorsal surfaces are turned towards the open end of the colony. The more important points in the structure of the ascidiozooid of *Pyrosoma* are shown in fig. 22. A circle of tentacles, of which one, placed ventrally (fig. 22, *tn*), is larger than the rest, is found just inside the branchial aperture. From this point a wide cavity, with a few circularly-placed muscle bands running round its walls, leads back to the large branchial sac, which occupies the greater part of the body. The stigmata are elongated transversely and crossed by internal longitudinal bars. The dorsal lamina is represented by a series of eight languets (*l*). The nerve ganglion (on which is placed a small pigmented sense organ), the subneural gland, the dorsal tubercle, the peripharyngeal bands, and the endostyle are placed in the usual positions. On each side of the anterior end of the branchial sac, close to the peripharyngeal bands, is a mass of rounded gland cells which are the source of the phosphorescence. The alimentary canal is placed posteriorly to the branchial sac, and the anus opens into a large peribranchial (or atrial) cavity, of which only the median posterior part is shown (*pbr*) in fig. 22. The reproductive organs are developed in a diverticulum of the peribranchial cavity, and consist of a lobed testis and a single ovum at a time. The development takes place in a part of the peribranchial cavity (fig. 21, *em*). The segmentation is meroblastic, and an elongated embryo is formed on the surface of a mass of yolk. The embryo, after the formation of an alimentary cavity, a tubular nervous system, and a pair of laterally placed atrial tubes, divides into an anterior and a posterior part. The anterior part then segments into four pieces, which afterwards develop into the first ascidiozooids of the colony, while the posterior part remains in a rudimentary condition, and was called by Huxley the "cyathozooid"; it eventually atrophies. As the four ascidiozooids increase in size, they grow round the cyathozooid and soon encircle it (fig. 21, *asc* and *cy*). The cyathozooid absorbs the nourishing yolk upon which it lies, and distributes it to the ascidiozooids by means of a heart and system of vessels which have been meanwhile formed. When the cyathozooid atrophies and is absorbed, its original atrial aperture remains and deepens to become the central cavity of the young colony, which now consists of four ascidiozooids placed in a ring, around where the cyathozooid was, and enveloped in a common test. The colony gradually increases by the formation of buds from these four original ascidiozooids.

Development of *Pyrosoma.*

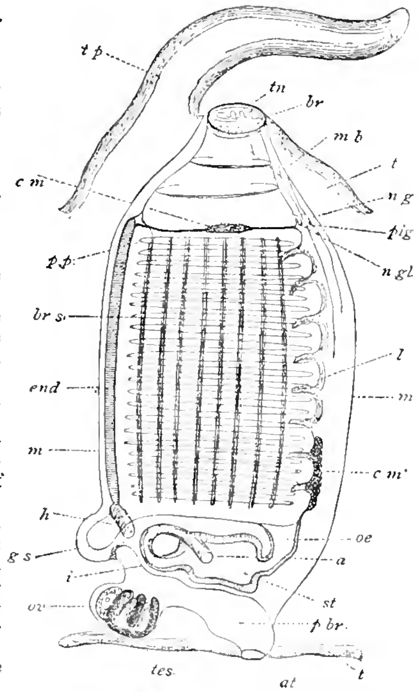
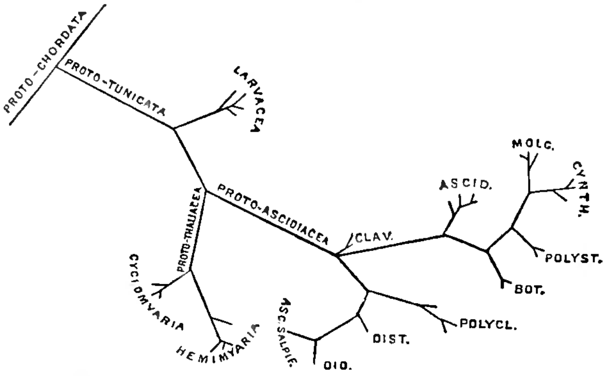


Fig. 22.—Mature ascidiozooid of *Pyrosoma*, from left side (partly after Keferstein). Lettering as before; *cm*, cellular mass, the seat of phosphorescence; *cm'*, posterior cellular mass; *gs*, gemmiparous stolon; *mb*, muscle band; *ngl*, subneural gland; *pig*, pigment spot on ganglion; *tp*, process of test.

Phylogeny.

Phylogeny.



The accompanying diagram shows graphically the probable origin and course of evolution of the various groups of *Tunicata*, and therefore exhibits their relations to one another much more correctly than any system of linear classification can do. The ancestral *Proto-Tunicata* are here regarded [1] as an offshoot from the *Proto-Chordata*—the common ancestors of the *Tunicata* (*Urochorda*), *Amphioxus* (*Cephalochorda*), and the *Vertebrata*. The ancestral *Tunicata* were probably free-swimming forms, not very unlike the existing *Appendiculariidæ*, and are represented in the life-history of nearly all sections of the *Tunicata* by the tailed larval stage. The *Larvacea* are the first offshoot from the ancestral forms which gave rise to the two lines of descendants, the *Proto-Thaliacea* and the *Proto-Ascidiacea*. The *Proto-Thaliacea* then split into the ancestors of the existing *Cyclomyaria* and *Hemimyaria*. The *Proto-Ascidiacea* gave up their pelagic mode of life and became fixed. This ancestral process is repeated at the present day when the free-swimming larva of the Simple and Compound Ascidians becomes attached. The *Proto-Ascidiacea*, after the change, are probably most nearly represented by the existing genus *Clavelina*. They have given rise directly or indirectly to the various groups of Simple and Compound Ascidians and the *Pyrosomidæ*. These groups form two lines, which appear to have diverged close to the position of the family *Clavelinidæ*. The one line leads to the more typical Compound Ascidians, and includes the *Polyclinidæ*, *Distomidæ*, *Didemnidæ*, *Diplosomidæ*, *Cœlocormidæ*, and finally the *Ascidiæ Salpiformes*. The second line gave rise to the Simple Ascidians, and to the *Botryllidæ* and *Polystyelidæ*, which

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[1] By Dohrn and others their point of origin is placed considerably further up on the stem of the *Chordata*, thus causing the *Tunicata* to be regarded as very degenerate *Vertebrata* (see 32).

are, therefore, not closely allied to the other Compound Ascidians. The later *Proto-Ascidiacea* were probably colonial forms, and gemmation was retained by the *Clavelinidæ* and by the typical Compound Ascidians (*Distomidæ*, &c.) derived from them. The power of forming colonies by budding was lost, however, by the primitive Simple Ascidians, and must, therefore, have been regained independently by the ancestral forms of the *Botryllidæ* and the *Polystyelidæ*. If this is a correct interpretation of the course of evolution of the *Tunicata*, we arrive at the following important conclusions. (1) The *Tunicata*, as a whole, form a degenerate branch of the *Proto-Chordata*; (2) the *Ascidiæ Salpiformes* (*Pyrosoma*) are much more closely related to the typical Compound Ascidians than to the other pelagic *Tunicata*, viz., the *Larvacea* and the *Thaliacea*; and (3) the *Ascidiæ Compositæ* form a polyphyletic group, the sections of which have arisen at several distinct points from the ancestral Simple Ascidians.

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