V. *On the Structure of the Gills of the Lamellibranchia.*

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INTRODUCTION.

THE comparative study of the gill structure of the Lamellibranchia may be said to date from 1875. WILLIAMS, it is true, had in 1854* published two papers on the subject, but owing to the fact that the morphological relations of the gill lamellæ to the gill axis and to other parts of the body were not then understood, and owing to the somewhat wild and fantastic mode of argument affected by this author, they cannot claim to be seriously regarded as the first important contribution to the literature of the subject. The few remarks on the different types of Lamellibranch gills made by LEUCKART in 1848* (p. 113), HANCOCK in 1853 (p. 290), and

* See alphabetical list of references, pp. 278–284.

DUVERNOY in 1854 (p. 37) are of interest only from an historical point of view, and do not come within the range of the modern treatment of the subject; and the excellent figures and remarks on gill structure made by DESHAYES in 1844–1848 cannot claim to be considered in the present connection, being purely descriptive and not comparative.

It was POSNER who first attempted a systematic investigation of the subject, and in his memoir of 1875 he discussed, not very astutely, the minute structure of the gills of *Anodonta* and eleven other genera of bivalve Mollusca. Some fifteen months later PECK, who in 1875, independently of POSNER's work, had commenced a similar investigation, published his important observations on the gills of *Arca*, *Mytilus*, *Dreissensia* and *Anodonta*. It was this paper which first placed the comparative study of the gills upon a sound basis. The investigation was conducted in the laboratory of Professor RAY LANKESTER and under his direction, and the working hypothesis around which the paper was written, and which has stood the test of time ever since, was, as the author explains, supplied by Professor LANKESTER. An adequate terminology was propounded for the grosser and finer parts of the gill, and this terminology remains in general use at the present day.

In the same year (1877) BONNET produced his dissertation on the gills of *Arca*, *Mytilus*, *Venus*, *Ostrea*, *Anodonta*, *Unio*, *Pinna* and *Pecten*, and in the following year there appeared an unsatisfactory paper by SLUITER, treating of the genera *Mytilus*, *Donax*, *Mactra*, *Mya*, *Venus*, *Ostrea*, *Solen* and *Anodonta*.

MITSUKURI, in 1881, sustained in some measure the interest in the subject by the publication of his excellent account of the structure of the gills of *Nucula* and *Yoldia*, together with some general observations on the evolution of gills in the Lamellibranchia from these primitive forms; and in the same year HAREN-NORMAN described and compared the gills of *Pecten*, *Lima*, *Arca*, *Modiolaria*, *Cardium* and *Astarte*. The study received a fresh impetus in 1888, and during the six years 1888 to 1893 many important contributions were made by PELSENEER, DALL, MÉNÉGAUX, KELLOGG and JANSSENS.* The first-named of these authors produced in 1892 that classification of the Lamellibranchia, based largely on their gill structure, which has remained more or less in favour ever since, although in several of its details it has ceased to command confidence.

In 1894 DALL (**14**, pp. 692–697) made the startling announcement that the gills of *Callocardia* (a genus of the Eulamellibranchiate family Cyprinidæ) and *Euciroa* (a genus of the Verticordiidæ) were of the Foliobranchiate type exemplified by *Nucula*, or at least were intermediate between this and the Eulamellibranchiate type. This fact, if true, threatened the very foundations of PELSENEER's scheme of classification, and pointed to the futility of any attempt to utilise the minute structure of the gill as a taxonomic character.

The interest in the subject being now more keen than ever, Professor LANKESTER

* See alphabetical list of references, pp. 278–284.

was moved to reopen the investigation which PECK had made in his laboratory, and with the aid of a grant from the Royal Society the present exhaustive inquiry was instituted.

Three species (*Ostrea edulis, Pecten opercularis* and *Avicula tarentina*) were fully investigated by Mr. J. W. JENKINSON, B.A., and nineteen more (*Cardita sulcata, Kellya suborbicularis, Tellina nitida, Mactra stultorum, Circe minima, Tapes pullastra, Petricola lithophaga, Cardium edule, Tridacna sp., Psammobia ferroensis, Corbula gibba, Ceratisolen legumen, Saxicava rugosa, Rocellaria dubia, Pholadidea papyracea, Teredo navalis, Pandora inæquivalvis, Lyonsia norvegica* and *Thracia papyracea*) were examined, rather less fully, by Mr. R. EVANS, M.A., B.Sc. The remarks on these species in the following pages are in large measure culled from their notes, which were handed over to me by Professor LANKESTER in the spring of 1900, when he confided to me the further prosecution of the research.

Since that time 193 species have been examined, making with the foregoing 22 a total of 215 species, belonging to 118 genera. Professor LANKESTER has throughout watched the progress of the research. It is due to his personal influence that much of the rarer material was obtained, and I have to thank him also for many fertile suggestions and much valuable advice.

Material.

The material has been furnished most liberally by zoologists in various parts of the world, and special acknowledgments are due, and on behalf of Professor LANKESTER and myself are hereby tendered, to Professor W. H. DALL, of the United States National Museum, for most of the Septibranchia examined, for specimens of *Dimya argentea, Vesicomya stearnsi, Periploma sp., Entodesma saxicola, Vanganella taylori, Rangia cyrenoides* and twenty-eight other species, and for the loan of slides of *Verticordia, Euciroa* and *Chlamydoconcha*; to Dr. A. ALCOCK, of the Indian Museum, Calcutta, for specimens of *Euciroa eburnea, Anatina flexuosa, Venus calophylla, Mactra violacea, Crassatella indica, Lucina bengalensis* and eleven others; and to Professor PERRIER, of the Muséum d'Histoire Naturelle, Paris, the late Mr. M. F. WOODWARD, of the Royal College of Science, London, Dr. A. WILLEY, and Mr. J. STANLEY GARDINER. Many specimens were utilised from the collection of Mollusca in spirit at the Natural History Museum, London, and much well-preserved material was obtained from the collections made during the "Skeat Expedition" in Siam, 1900, and by purchase from the Zoological Station of Naples, and the Marine Laboratory of Plymouth. The identification of the unnamed specimens and the checking of those already provided with labels was kindly undertaken by Mr. E. A. SMITH, of the Natural History Museum, London; and the opportunity may here be taken to express the debt of gratitude which morphologists owe to the systematists, since anatomical comparisons are valueless unless the species studied are correctly named.

Methods.

The methods of investigation naturally varied with the forms under examination. In the majority of cases the sections of the gill-lamellæ were cut parallel to the axis of the gill. The whole lamella was cut into sections, and five or six slides were prepared by mounting thirty or forty consecutive sections selected from five or six different parts of the continuous ribbon. Sections cut parallel to the filaments were found useful for deciding special points of structure, e.g., in *Mactra* and *Anodonta*. The mode of section employed in the case of the Protobranchia and Septibranchia, and such aberrant genera as *Euciroa* and *Vesicomya* will be found explained in the pages devoted to a description of these forms. It was early found to be important not to rely too exclusively upon serial sections, since much that might escape notice, or be liable to an erroneous interpretation, can frequently be made out in dissected preparations, stained, clarified with clove oil, and mounted in Canada balsam. This applies particularly to the leaflets of the Protobranchia, isolated filaments of the Filibranchia showing the arrangement of the ciliated discs and inter-lamellar junctions, isolated portions of the lamellæ of the Eulamellibranchia showing the form of the water-pores, and isolated gill-vestiges of the Septibranchia. The staining fluids were in almost all cases borax-carmine and picro-nigrosin. By employing these in succession the chitinous framework of the gill is left blue, the cytoplasm bluish-purple, and the nuclei red.

Terminology.

No radical change is here proposed with respect to the nomenclature of the parts of the Lamellibranch gill. PELSENEER has already clearly demonstrated in his numerous writings the morphological identity of the ctenidia of the Lamellibranchia with those of other Mollusca, and has shown the error of regarding the Lamellibranchia as possessed of *two* gills on each side of the body. And PECK, many years before this, introduced a rational terminology for the constituent parts which still remains in use; its main features are incorporated in the following paragraphs.

The commonest type of gill in the Lamellibranchia is that which in section presents the form of the letter W (fig. 1A). The outermost lines of the letter represent the *ascending filaments*,* the other two lines the *descending filaments*. The *axis* is situated along the top of the descending filaments at right angles to the plane of section. The descending filaments depend from the axis in two regular series, each known as a *descending lamella*; the ascending filaments in a similar manner are units of the *ascending lamellæ*. A descending lamella and its corresponding ascending lamella together constitute a *demibranch*. The demibranchs are

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* Since each complete filament consists of a descending and an ascending portion, it would be more correct to speak of these as the descending and ascending *portions* of the filaments; but the conventional and very convenient abbreviation is so well established that no misunderstanding is likely to arise.

inner and *outer*, lying towards the visceral mass and the mantle respectively. The space between the two lamellæ of each demibranch is spoken of as the *interlamellar cavity*, and those edges of the filaments which are directed towards this space are *interlamellar edges*, the opposite edges *incurrent* or *frontal* (*morphologically ventral*, PELSENEER, **71**, p. 185).

Although the words descending and ascending as applied to filaments and lamellæ
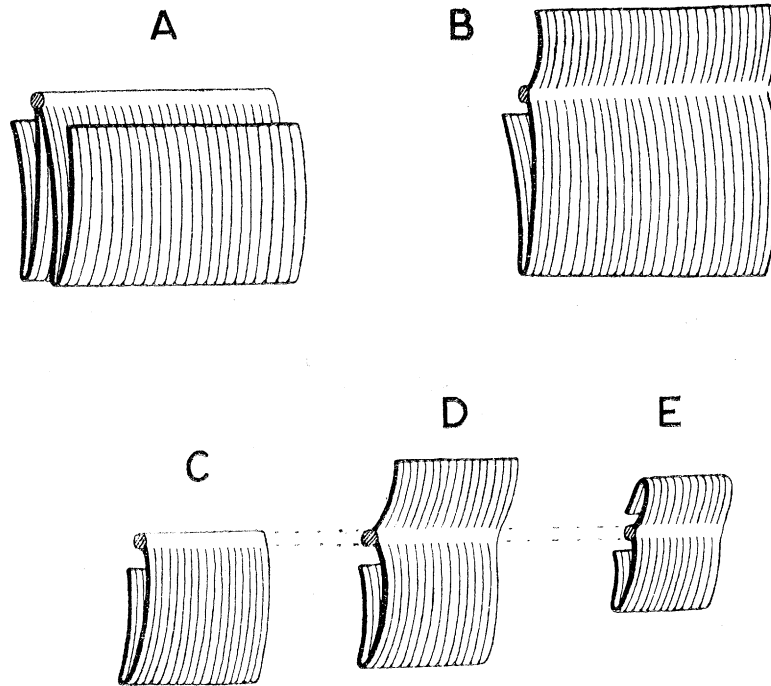
A B

C D E

FIG. 1.—A, portion of a typical Lamellibranch gill, showing the descending and ascending lamellæ of the inner and outer demibranchs. B, portion of the gill of *Lyonsia* or *Scrobicularia*, showing the outer demibranch upturned and consisting of a direct lamella only. C, D and E, middle portions of the anterior, middle and posterior thirds of the gill of *Tellina*. The outer demibranch is wanting in the first, it consists of an upturned direct lamella in the second, and of an upturned direct and a downwardly-directed reflected lamella in the third.

are so convenient and so familiar in writings on the subject, yet it will be necessary in certain cases (*e.g.*, *Lyonsia*, *Scrobicularia*) to substitute for them the words *direct* and *reflected*,* since in these cases the outer demibranch is upturned, so that the normally descending lamella is in reality ascending (see fig. 1B). In *Lyonsia* and *Scrobicularia* the reflected lamella of the outer demibranch is wanting, but in the hinder portion of the gill of *Tellina* it is present, and, owing to the upturning of the demibranch, is descending (fig. 1E). It is interesting to note that in its anterior third (fig. 1C) the gill of *Tellina* resembles that of *Lucina*, since the outer demibranch is wanting; in its middle third (fig. 1D) it is comparable with that of

* The terms *direct* and *réfléchi* were employed by LACAZE DUTHIERS as far back as 1856 (**47**, p. 12).

Lyonsia, while in its posterior third it is peculiar, no other form being known to possess an upturned outer demibranch with a reflected lamella.

The figures 2A to 2K, representing a further elaboration of the scheme of comparison instituted by PELSENEER (**68** and **69**), will serve to explain some of the more important forms assumed by the lamellæ of the gills. In the first two figures, representing *Nucula* and *Solenomya*, the term "lamella" can hardly be applied. The gill is made up of two demibranchs, each composed of a series, not of filaments, but of broad *leaflets*. In *Dimya agentea* and *Anomia aculeata* (fig. 2C) there are no ascending lamellæ. In *Donax faba* (fig. 2E) the descending lamella of the outer demibranch is exceptionally short. In *Donax variabilis* the relations are those shown in fig. 2F. There is a *supra-axial extension* of the ascending lamella of the
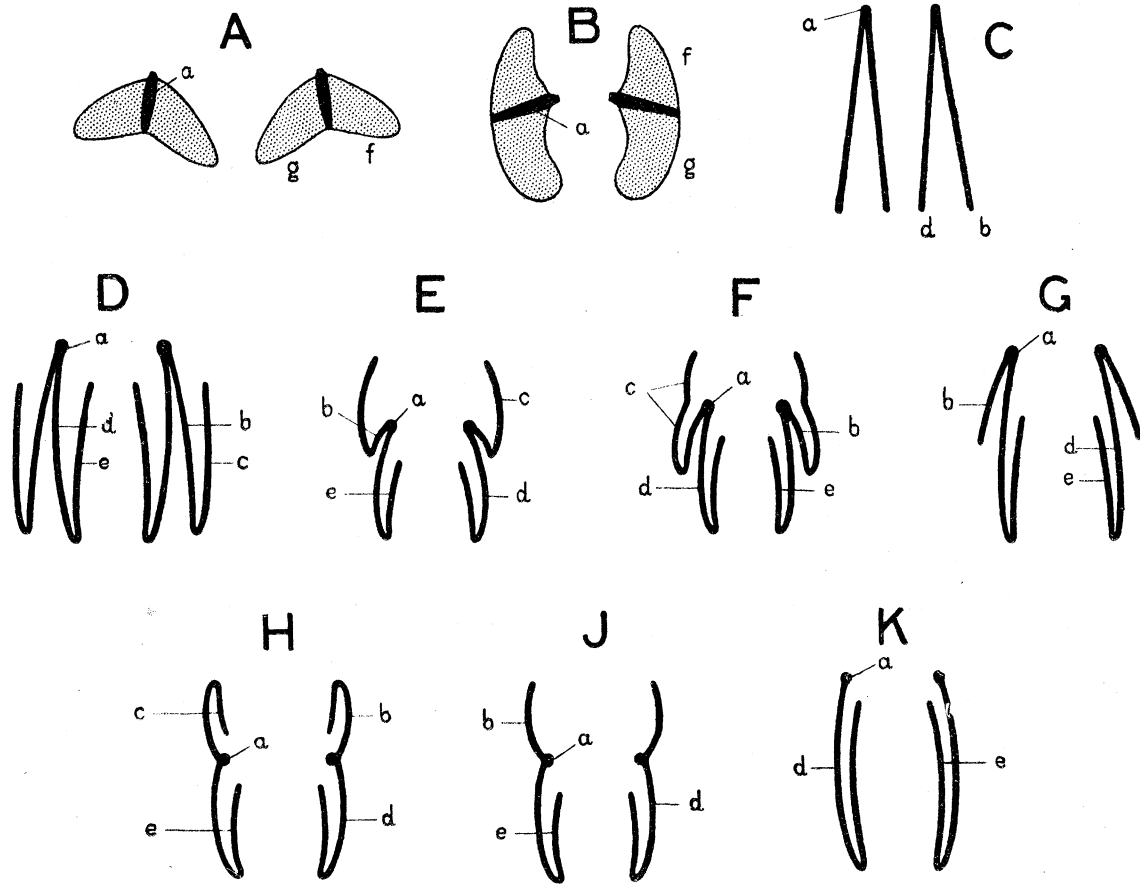

FIG. 2.—Diagrammatic sections taken transversely to the axes of the gills of A, *Nucula*; B, *Solenomya*; C, *Dimya* or *Anomia aculeata*; D, the majority of the Lamellibranchia; E, *Donax faba*; F, *Donax variabilis, Cyrena, Tapes, Venus* or *Isocardia*; G, *Lasaea*; H, *Tellina* (hinder portion of gill); J, *Lyonsia, Pandora* or *Scrobicularia*; K, *Lucina* or *Montacuta*.

  a, axis; *b*, direct (usually descending) lamella of the outer demibranch; *c*, reflected (usually ascending) lamella of the outer demibranch; *d*, direct or descending lamella of the inner demibranch; *e*, reflected or ascending lamella of the inner demibranch; *f*, leaflets of the outer demibranch; *g*, leaflets of the inner demibranch.

outer demibranch, so that the total height of this ascending lamella is considerably greater than that of the corresponding descending lamella.   This supra-axial extension is much better developed in *Psammobia, Asaphis* (fig. 39D, p. 250), *Tapes, Venus, Cyrena,* and *Isocardia* than in *Cardium,* which PELSENEER chose to represent this type of gill structure.   *Lasaea* (fig. 2G) possesses no ascending lamella to the outer demibranch ; and *Lucina* and *Montacuta* (fig. 2K) lack both lamellæ of the outer demibranch.   The Anatinacea are remarkable in having the outer demibranch upturned, and consisting of a direct lamella only (fig. 2J).   This character is shared by *Scrobicularia,* and, as has just been mentioned, is met with also in the middle portion of the gill of *Tellina.*

It might perhaps be here suggested that in the upturned lamella of the Anatinacea the whole of the normal outer demibranch is present, and that the position of the bend in the filaments has gradually approached the axis, or retreated from it, and finally disappeared.   The series of changes might be represented by the figures 2D, 2F, 2E, 2J, taken in this order.   There is an attractive plausibility in the hypothesis, but it is rather beyond the scope of the present work to investigate the matter to its final solution.   The condition found in *Tellina* does not help one much.   In passing from the middle to the hinder part of the gill one notices that the upper edge begins to turn over, but it does not follow that in the middle part the filaments are at all abbreviated.   It may be merely that they exhibit no bending.   In the case of three sticks of equal length, one bent into two equal parts, the second into two unequal parts, and the third not bent at all, it is hardly worth discussing the equivalence of the various parts ; and although embryological evidence goes to show that the reflected filaments are outgrowths, in a different direction, from the extremities of the direct filaments, yet it is not unreasonable to suppose that the change in the direction of growth may occur in some species earlier, in others later.   The position of the actual bend in the filaments is thus subject to as much variation as the bending of the sticks of wood.   One might, for instance, say that in the case of *Anomia aculeata* (fig. 2C) the upper half of the filament is direct, and the lower half is the reflected filament which has failed to alter its course during growth.

The filaments of the same gill-lamella may be arranged in a flat, uniform series, or the lamella may be thrown into vertical folds or *plicæ.*   The *apex* of the plica is that part farthest from the interlamellar cavity.   The filament that occupies the bottom of the depression between two successive plicæ of a plicate lamella is in most species of greater size than the others.   It will be spoken of as the *principal filament,* the others as *ordinary filaments.*   *Homorhabdic* gills* are those with all the filaments

* The terms homorhabdic and heterorhabdic we owe to Professor LANKESTER, who first made use of them in the course of lectures on the Mollusca which he delivered a few years back at the Royal Institution in his capacity of Fullerian Professor.   The terms were introduced on the assumption that the difference was an important one, and Professor LANKESTER was curious to learn how far the present investigation would bear out his contention.   As will be seen in the sequel, the results are largely

alike ; *heterorhabdic* gills are those which exhibit the above-mentioned differentiation into principal and ordinary filaments.

In those Lamellibranchia in which gill filaments are present (*i.e.*, all excepting the Protobranchia, and forms with obsolete gills, such as *Cuspidaria*) the filaments may be united with their neighbours in one of two ways. They may bear on their broader, mutually opposed surfaces uniformly disposed brushes of stiff cilia which interlock and serve to keep the filaments in position ; or there may be definite strands of cellular tissue extending horizontally at various levels, and connecting up the interlamellar edges of the filaments. The former are known as *ciliated inter-filamentar junctions*, or *junctions by ciliated discs*, the latter as *organic interfila-mentar junctions*. Although in teased preparations of the filaments ciliated discs may tear away from the filaments rather than unlock from the cilia of the opposed disc, yet it can be observed, by watching a living *Mytilus*, that if the filaments be separated by a needle, they soon recover themselves by a fresh interlocking of the cilia. There is no organic connection between the ciliated discs ; it is merely a mechanical interlocking such as occurs when two hair-brushes are pressed together.

By reason of the relative freedom from one another of the filaments provided with ciliated discs, the gills composed of such filaments may be conveniently referred to as *eleutherorhabdic* ; while gills with filaments united by organic interfilamentar junctions, with consequent division of the interfilamentar spaces into series of fenestræ, so that the lamellæ appear reticulate, may be termed *synaptorhabdic*. Synaptorhabdic gills have no ciliated discs ; but eleutherorhabdic gills are not neces-sarily devoid of all organic interfilamentar connection. The upper extremities of the ascending filaments of *Mytilus*, for instance, are in mutual organic connection, and in *Avicula* and *Meleagrina* the lower as well as the upper ends of the ascending filaments are organically united.

In the instances just cited the organic junction is established between the broad mutually opposed faces of the filaments, but in the synaptorhabdic type of gill the interfilamentar junctions arise from outgrowths, sometimes of considerable bulk, of rather loose cellular tissue, described by PECK as *subfilamentar tissue*, on the inter-lamellar edges of the filaments.

Evolution of the Synaptorhabdic Gill.

The theory of POSNER (**76**), that the eleutherorhabdic gill has been evolved by the splitting up of a reticulate gill such as that of *Anodonta*, was destined to be short-lived, for PECK, writing shortly afterwards, showed conclusively that the reverse was far more probably the case. At the present time POSNER's view can hardly claim any adherents at all ; and KORSCHELT and HEIDER (**44**, p. 966) stand alone in even

destructive of the hypothesis, since homorhabdic and heterorhabdic gills may occur within the limits of the same genus.

questioning the evolution of the synaptorhabdic from the eleutherorhabdic gill. It is barely conceivable that the ciliated junctions should be the relics of a broken down organic interfilamentar connection,* while on the other hand we have evidence from at least two sources in support of the view that the ciliated junctions are the predecessors of the organic junctions.

In *Avicula argentea* the interlamellar edges of the filaments, particularly in the region of the ciliated discs, have a tendency towards the proliferation of subfilamentar tissue, which, although not uncommon in the Synaptorhabda, is in the case of Eleutherorhabda only displayed in the formation of interlamellar junctions. These proliferations on the inner sides of the filaments are, owing largely to the plication of the lamellæ, brought into mutual contact, and a cellular fusion follows. A section, therefore, through such a part, if taken transversely to the filaments, shows both ciliary and organic interfilamentar junctions (see fig. 16, *org.*, p. 212). The other species of *Avicula* examined possess the ciliated junctions only, and throughout the whole investigation no other instance of the simultaneous presence of ciliated and organic interfilamentar junctions was met with.† The nearest approach to it was in *Lima inflata*, a synaptorhabdic form with just a suspicion of obsolete ciliated discs (see fig. 18*a*, p. 216).

The other argument lies in the substitution of a cellular connection between the upper extremities of the ascending filaments in certain eleutherorhabdic forms for the ciliated junctions which persist in such genera as *Pectunculus*, for JACKSON (**38**, p. 358) has noted that, although in the adults of *Anomia glabra* the ascending filaments are organically united at their tips, in very young stages the filaments are simple, not reflected, and free at their tips. This, to a certain extent, is also the case in *Mytilus*, for the descending filaments develop independently the one of the other. They unite at their tips, however, before becoming reflected, and the ascending lamella grows up as a continuous membrane, to be subsequently perforated and split, except at the uppermost edge, into the ascending filaments (LACAZE DUTHIERS, **47**).

It may be freely assumed that although ciliated discs as interfilamentar junctions are more ancestral than organic interfilamentar junctions, they themselves indicate a certain advance upon the absolute freedom of filaments. This is supported by embryological evidence, for JACKSON (**38**, p. 336) has described an early stage of *Pecten irradians* in which the filaments are ciliated, but " have not yet the ciliated interfilamental knobs or processes existing in the adult."

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* It is important to note, however, that according to the observations of LACAZE DUTHIERS (**47**) on the development of the gills of *Mytilus*, the freedom of the filaments along the ventral edge of the demibranch is secondary, and is due to the solution of an organic continuity which is not destroyed until after the ascending lamella has become fenestrated.

† Except, perhaps, in *Meleagrina vulgaris*, the specimen of which was not sufficiently well preserved to enable one to determine the point.

In spite of the evidence furnished by a study of the gill of *Avicula argentea,* it is not necessary to suppose that the organic interfilamentar junctions are invariably preceded by the ciliated junctions. It is quite possible that in the history of the Lamellibranchia the reticulate lamella may have been evolved directly from one consisting of plain uniformly ciliated filaments. In ontogeny this is certainly some-times the case. JACKSON has shown that in the young *Ostrea* the gills begin to develop as "two rows of filamentous appendages" (**38**, p. 303) or "tubular discon-nected bags" (p. 305), and that the interfilamentar connections are brought about by the concrescence of fleshy processes from the margins of adjoining filaments, the first formed junction being that connecting the not yet reflected tips of the filaments. In this he confirms the earlier researches of HORST on the same genus (**34**, fig. 19, and p. 303).

The fact that in ontogeny the reticulate or synaptorhabdic gill-lamella may arise by the perforation of a continuous membrane, and not by the actual concrescence of separate filaments by a new growth of subfilamentar tissue, does not in reality invalidate the argument that the filamentous condition is the more archaic, since the process may not unreasonably be regarded as an abbreviation of the normal mode such as is indicated by the comparative study of the gills of adult forms. No embryonic gills were examined in the present investigation, but it may be noted that the observation of STEPANOFF'S on the perforation of the gill-membrane of *Cyclas* (= *Sphærium*) (**98**, p. 27, and figs. 17, 19, 20), upon which POSNER'S line of argu-ment was largely based, was in complete accord with the earlier observations of LEYDIG (*Cyclas* (= *Sphærium*), **54**, figs. 17 and 18); and the mode of development has since been found to occur in *Teredo* (HATSCHEK, **32**, p. 22, and figs. 26–29, and SIGERFOOS, **93**), and in *Scioberetia* (BERNARD, **2**, pp. 376 and 382).

Although, therefore, subsequent discoveries have shown that POSNER (**76**, p. 554) was wrong in deriving the gill structure of *Pecten* from that of *Anodonta* by a solution of the organic continuity between the filaments, it would yet seem that PECK (**66**, p. 46) was a little severe on this author in respect of the implicit reliance which he placed upon STEPANOFF'S observation.

In this connection it should be noted that ZIEGLER'S observations on *Cyclas* (= *Sphærium*) (**110**, p. 560, and figs. 29*a* and 30) are not quite in accord with those of other authorities. He states that the outer and inner surfaces of the continuous gill-fold show groove-like depressions, disposed at right angles to the gill axis, and extending from the free margin of the fold to near the axis. These grooves deepen, and meeting the corresponding grooves of the opposite surface, become fissures or slits extending from the margin to the axis. Even this slitting of a continuous membrane into filaments is, however, not exactly the same thing as the downgrowth of primarily independent filaments. LANKESTER, referring to *Pisidium pusillum,* speaks of "buds, separate from the first," and "short, stump-like tentacles which elongate and become ciliated" (**50**, p. 10, and figs. 46 and 52). JACKSON also has

described a young *Sphærium securis* with filamentous gills (**38**, p. 369 and Plate 30, fig. 4), but he does not explain by what means they arrived at this condition.

F. SCHMIDT (**90**, p. 219, Plate 12, fig. 13) has figured and described the inner demibranch of *Anodonta* as arising by the outgrowth of a series of separate papillæ, and BALFOUR ('Treatise of Comp. Embryology,' I, London, 1880, p. 223) states that the gills of *Anodonta* "arise as solid and at first somewhat knobbed papillæ"; yet SCHIERHOLZ (**89**, p. 208) speaks of the inner demibranch of *Unio* as arising by the outgrowth of a process which divides into an anterior and a posterior part, each of which divides again, forming a series of gill papillæ.

In the presence of such conflicting descriptions in closely allied forms, one is led to conclude that the phenomena of gill ontogeny are extremely difficult to make out. The difficulty, indeed, is not denied; for KORSCHELT (**45**, p. 143) in his account of the development of *Dreissensia*, writes "Zwischen Mantelfalte und Fuss wurden die Kiemen angelegt. Sie erscheinen zu dieser Zeit als wenige ziemlich umfangreiche Papillen von seitlich plattgedrückter Form, deren gegen einander gerichtete Kanten mit starken Wimperhaaren besetzt sind, so dass man stark wimpernde Spalten vor sich zu haben glaubt. . . . . Ob sie in Form einer Falte angelegt werden, die sich schon sehr bald einkerbt und so jene vermeintlichen Papillen entstehen lässt, oder ob sie als wirklich Papillen hervorsprossen, ist schwer zu entscheiden." WELTNER (**104**, fig. 2, p. 450) shows, in a young *Dreissensia*, separate gill filaments at the back part of the gill, while the extremities of the anterior filaments are united in series. He does not say, however, how this condition is arrived at. MEISENHEIMER, quite recently (**56**, p. 58) also admits the difficulty in deciding the exact mode of the origin of the gills of *Dreissensia*; but he confesses that he did not specially investigate this point It is not possible to draw one's own conclusions from his figures (figs. 56–59).

In view, therefore, of the uncertainty that exists as to the exact details of the development of the gills of the commonest and most investigated species; and secondly, of the fact that DREW (**22**) has shown that the gill leaflets of *Nucula* develop as papillæ which later become flattened out; and thirdly, of the fact that the Protobranchia are almost universally admitted to be the most archaic representatives of the Lamellibranchiate Mollusca,* we may, pending further investigations specially directed to this object, conclude that the perforation or the slitting into filaments of a continuous gill-membrane is an infraction of the rule that ontogeny is a repetition of phylogeny.

Labial Palps.

It is of no little interest to observe that throughout the wide range of the Lamellibranchia the palps do not share in the remarkable diversity of structure which the ctenidia exhibit. A minute examination of the palps was not made in

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* DREW (**22**, p. 363) is a little loath to admit the primitive nature of the Protobranchiate gill.

every species under consideration, but in genera with gill-structure so diverse as *Nucula, Yoldia, Anomia, Mytilus, Lithodomus, Meleagrina, Ostrea, Astarte, Anodonta, Tellina, Mya,* and *Lyonsia* the palps have the same essential structure. They are imperforate flaps, generally of triangular shape, deeply corrugated on their mutually opposed surfaces, and smooth on the sides which face the mantle and visceral mass (see THIELE, J., " Die Mundlappen der Lamellibranchiaten," ' Zeitschr. f. wiss. Zool.,' xliv, 1886, Leipzig, pp. 239–272, with two plates).

That the palps are not dismembered portions of the ctenidium is indicated not only by the above fact that their structure remains invariable however much the gill may become modified, but also by the relative positions assumed in certain cases. In *Lyonsia* and *Nucula,* for instance, the attachment of the palps to the body is at a much lower level than the ctenidial axis, and in *Mytilus, Venus,* and *Psammobia,* the front part of the gill lies between the inner and outer palps. The palps are supplied with arterial blood by a branch of the anterior aorta; but even if, as has been suggested by MITSUKURI (**63**) and DREW (**22**), they have a respiratory function, it does not follow that they are on that account to be regarded as of ctenidial origin, since the same function is ascribed to the mantle. The palps, also, are innervated from the cerebral ganglion, whereas the gills are innervated from the visceral.

In the Nuculidæ the palps are exceptionally large, and are provided at their posterior ends with an elongated muscular appendage, with close transverse plications on its inner surface. In *Solenomya* the palps have disappeared entirely, and only this appendage remains.

Plication of the Lamellæ.

The plicate gills are so strikingly different in appearance from the non-plicate gills that one is not surprised to find that much importance has been attached to this feature in the past. The term *plica* was first employed in 1853 by HANCOCK, who made plication of the gill lamella a distinctive character of his third type of gill. He described his three types thus (**30**, p. 290):—" In the first the laminæ forming the gill-plate are composed of filaments, either free or only slightly united to each other at distant intervals, as in *Anomia* and *Mytilus*; in the second they are formed of a simple vascular network, as in *Mya,** *Pholas,* &c., and in the third the laminæ of the gill-plate are complicated by the addition of transverse plicæ composed of a minute reticulation of vessels, as in *Chamostrea, Myochama, Cochlodesma,* &c."

DUVERNOY, also, in 1854 attached considerable importance to the plication of the lamellæ. His three types of gills were (**23**, p. 37):—

(1.) Les branchies à surface unie des *Anodontes.*

(2.) Les branchies plissées en travers, dont les unes sont à larges plis uniformes (les *Tridacnes*), dont les autres sont réunis par paires, sont courts et forment de fortes cannelures (les *Vénus*).

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* One would conclude from this that he regarded the gill of *Mya* as non-plicate.

(3.) Enfin la troisième structure est celle des branchies filamenteuses, ou en franges, des *Peignes*, de la *Moule comestible*, &c.

In more recent years, in proportion as attention was paid to the minuter structure of the gills, the plication of the lamellæ came to be regarded as of less value than the differentiation of principal filaments.

Every gradation of plication is met with, from the barely perceptible undulation of the surface of the lamella in *Monocondylæa* (fig. 28, p. 232) and *Ensis siliqua* (fig. 47, p. 257), and the inner demibranch of *Anodonta*, to the great flattened folds of *Tridacna* (fig. 37, p. 246) and *Hippopus*, which project like the leaves of a book. The plication is usually less marked in the outer than in the inner demibranch (*e.g.*, *Venus*, *Tapes*) and the filaments in each plica fewer; but this is not always the case (*e.g.*, *Ostrea*, *Pinna*). The number of filaments composing a plica may vary from about 7 (*Pandora inæquivalva*) to 80 or 100 (*Tridacna* and *Hippopus*). The number is usually greater in the plicæ of the middle part of the lamella than in those of the front and hinder parts. The number is also greater in the adult than in the young (as I have ascertained to be the case in *Solen ensis*), and it is greater in the upper part of a plica than in the lower (RICE, **84**, *Cardium*, &c.). Oddly enough RICE regards this numerical discrepancy as due to filamentar fusion in the lower parts of the plica rather than to branching in the upper parts.

Principal Filaments.

Principal filaments (*Filaments principaux* of PELSENEER; *Segments primaires* of JANSSENS; *Canals principaux* of MÉNÉGAUX; *Grenzfilamente* of RICE; *Filaments of the re-entering angle* of KELLOGG) are confined to the Pseudolamellibranchia, and the Eulamellibranchia. They are not met with in all the Pseudolamellibranchia, as PELSENEER imagined, for the gills of such forms as *Malleus*, *Melina*, *Amussium* and *Plicatula* are homorhabdic. In the Eulamellibranchia they occur in a large proportion of forms, but in such a manner as to preclude the possibility of framing any generalisations with respect to the families, or even genera in which they are found. Instances will be cited later of cases in which two species of the same genus have homorhabdic and heterorhabdic gills respectively.

Principal filaments do not occur in non-plicate gills. There are well differentiated principal filaments in *Ensis siliqua* (fig. 47, p. 257) and *Monocondylæa* (fig. 28, p. 232), in which the plication is at a minimal degree of development; but none occur in lamellæ which are absolutely flat, unless one considers that those filaments which in the gills of *Lithodomus dactylus* and *Modiola barbata* are provided with interlamellar septa are principal filaments in their initial stage of differentiation. The condition in *Lithodomus* (p. 204) is a most interesting one, since the filaments in question are slightly larger and with wider cavity than the others. They occur at intervals of about eight filaments in the outer demibranch, and about eleven fila-

ments in the inner.   If, however, these are recognised as principal filaments, how is one to regard the gill of *Malleus* (fig. 14A, p. 207), in which every filament has a septum of some sort, high, low, or of intermediate extent ?   A gill cannot be composed of principal filaments alone.   Another matter for serious consideration is the impossibility of distinguishing these septum-bearing filaments of *Lithodomus* from the others in sections taken at a higher level than the upper edge of the septum.

Principal filaments are always developed in relation with interlamellar septa, so that the ascending and descending parts of the same principal filament are connected by a continuous sheet of membrane* which extends to varying heights in different species.   Interlamellar septa may, however, exist without special modification of the filaments which they connect (*e.g., Mactra stultorum, Saxicara rugosa, Mactrinula plicataria, Rocellaria dubia, Pholas crispata, Dreissensia polymorpha,* &c.) ; so that the converse deduction is not true ; and this still further weakens the case for *Lithodomus.*

In cases where the lamellæ are plicate there may be at the bottom of the groove between two plicæ, and connected with the interlamellar septum :—

(1.) One filament† not enlarged nor otherwise differentiated ; or very slightly enlarged, or with the chitin slightly thicker than usual.   (*e.g., Diplodonta oblonga,* fig. 24B, p. 227, *Petricola monstrosa,* fig. 35, p. 243.)

(2.) One filament, enlarged, but not differing greatly in shape from the ordinary filaments.   The frontal surface has the form of a fairly sharp ridge.   Occasionally there are two such filaments, or else the filaments adjacent to the principal filaments are slightly larger than usual.   (*e.g., Tapes aureus,* fig. 34, p. 242.)

(3.) One filament, considerably enlarged and with the frontal surface either flattened, or with a ridge, or grooved so as to appear U-shaped in section.   (*e.g., Ensis siliqua,* fig. 47, p. 257, *Pinna virgata,* fig. 17B, p. 214.)

(4.) Several filaments, not differentiated.   (*e.g., Venus callophylla,* fig. 33, p. 241, *Ensis macha,* fig. 48, p. 257.)

To draw any sharp line between the first and fourth groups is by no means easy, since, as in *Mesodesma donacia* and *Mesodesma novæ-zelandiæ,* it not infrequently happens that the interlamellar septum is connected with one filament on one side and with three or four on the other.   Neither is it possible to subdivide the third group, into which the bulk of the examples fall, for the character of the principal filament may vary at different levels.   One of the most striking instances of this is seen in *Lima.*   In sections of the gill of *Lima fragilis* taken high up the demibranch, the frontal surface of the principal filament has the shape of the letter U, whereas in sections taken low down, *i.e.,* near the free edge of the demibranch, it has more the form of a W.   There is a ridge which occupies the centre of the U, and which is more

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* In *Pinna* the septum is so far fenestrated as to be reduced to a few cross bars.

† If the section is taken through or near an interfilamentar junction, several filaments will be found united with the interlamellar septum.

strongly developed the nearer one approaches the ventral edge of the demibranch (*cf.* figs. 19A and B, p. 217). In sections of *Lima squamosa* taken high up the demibranch, the ridge is as well developed as in sections of *Lima fragilis* taken low; and this ridge also enlarges in the lower parts, so that in sections taken near the edge of the demibranch, it has obliterated the cavity of the U entirely (*cf.* figs. 19B and C, p. 217). A somewhat similar disappearance of the groove, but without any corresponding enlargement of the ridge, is observable in *Spondylus* (figs. 15A and B, p. 209).

A different state of things is found in *Psammobia ferroensis.* Here the principal filament shows throughout the greater part of its length a deep narrow groove (fig. 38, p. 249). Towards the free edge of the demibranch this becomes shallower, and ultimately disappears, causing the principal filament to resemble an ordinary filament. Since the groove does not necessarily die away at precisely the same level in the ascending and descending principal filaments, the appearance presented in fig. 39A, p. 250, is sometimes met with. This dying away of the frontal groove in sections taken near the extreme ventral edge of the demibranch is probably of very general occurrence; see *Solen ensis* (figs. 44 and 45, pp. 255 and 256), and *Pandora obtusa* (figs. 53B and C, p. 264).

Exactly the reverse occurs in *Asaphis deflorata.* The groove is wanting for the greater part of the length of the principal filament, and only appears in sections taken very low down. It is a shallow depression, but the appearance of the section is very striking, since the thickened chitin bands, which in the sections at most levels are in contact by those edges directed towards the interplical space, are here divaricated and more nearly parallel (see figs. 39F and G, p. 250).

In *Cardium edule* the different principal filaments vary in shape even at the same level. Some have a groove only, others a ridge only, others a ridge rising from the bottom of a groove, and others again have a perfectly flat frontal surface (fig. 36, p. 245).

The differences presented by *Solen* and its immediate allies show that the plication of the lamellæ and the differentiation of principal filaments are of not more than specific, or at most subgeneric, value. *Solen ensis* and *Solen fonesi* have strongly plicate lamellæ, and principal filaments with the frontal surface nearly flat, but with a shallow, narrow groove (fig. 44, p. 255). The gills of *Solen vagina* and *Solena rudis* are strongly plicate, and have principal filaments with a wide, shallow, U-shaped groove (fig. 43, p. 255). *Ceratisolen legumen* has flat lamellæ, with no principal filaments (fig. 46, p. 256). *Pharella orientalis* has moderately plicate lamellæ, and feebly differentiated principal filaments with a ridge-like frontal surface. *Ensis macha* has moderately plicate lamellæ, with several undifferentiated or barely differentiated filaments at the base of the interplical space (fig. 48, p. 257). *Ensis siliqua* has lamellæ nearly flat, but with large principal filaments, with sharp frontal edges (fig. 47, p. 257).

Similar incongruities have been pointed out by RICE in *Donax* (**83**). He has shown that the lamellæ of *Donax trunculus* are flat, those of *Donax politus* slightly plicate, and those of *Donax serra* strongly plicate.* Two species of Donax were examined in the course of the present investigation, *Donax variabilis* and *Donax faba*. The former has flat, homorhabdic lamellæ, the latter plicate, heterorhabdic lamellæ (figs. 31A and B, p. 236). Judging by the illustrations, the three species of *Donax* described by RICE are all homorhabdic.

Cyrena floridana, again, has flat, homorhabdic lamellæ, but *Cyrena sinuosa* plicate, heterorhabdic lamellæ. *Crassatella cumingi* and *Crastella indica* have simple homorhabdic, flat lamellæ, and interlamellar junctions of the form of isolated bars, whereas *Crassatella floridana* has plicate, heterorhabdic gills with interlamellar septa. *Rocellaria dubia* has flat lamellæ and interlamellar septa not regularly arranged, while *Rocellaria gigantea* has plicate lamellæ with interlamellar septa at regular intervals. Both are homorhabdic.

The differentiation of principal filaments may possibly be connected in some obscure way with the fact that these alone contain the afferent branchial blood channels, the arterialised blood finding its way back to the auricle from the ordinary filaments. This direction of the blood stream is a matter upon which BONNET,† SLUITER and HAREN-NORMAN are agreed; but I am not in a position to express an opinion upon it since, the whole of the material available being preserved in alcohol, I have not injected any specimens. MÉNÉGAUX, it should be noted, regards the blood as passing down one principal filament and back by the next, the principal filaments of each lamella being thus alternately afferent and efferent (**62**, p. 175. *Solen* and some other forms), and JOHNSTONE (**40**, fig. 26) in his investigations of *Cardium* has arrived at the same conclusion.

What it is important to note in this connection is the fact that principal filaments are ontogenetically a secondary differentiation. No genus could be better adapted for an investigation of this point than *Pecten*, since in this genus there is a remarkably strong contrast in size between the principal and ordinary filaments. In *Pecten irradians* JACKSON has described (**38**, p. 336) a stage in which the filaments are fully reflected, and yet the interlamellar septa which, he remarks, occur on every eleventh to fifteenth filament of the adult gill, are not developed; and (judging by his figure, Plate 28, fig. 1) the filaments are all alike in size and shape.

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* It is worthy of note that he regards the simplicity of the flat forms as secondary, and derived by retrogression from the plicate condition.

† In *Pecten jacobæus*, however, BONNET considers the principal filament to be carrying arterial blood. (See **5**, figs. 25 and 26). JANSSENS states that the channel on the frontal side of the septum of the principal filament of *Pecten* is efferent, and the deeper one afferent (**39**, fig. 91), and MÉNÉGAUX gives a similar relation (**62**. p. 99).

Apical Filaments.

In certain plicate gills the filaments at the apex ot the plica, *i.e.*, at the part of the fold most remote from the interlamellar space, are larger than the ordinary filaments. The differentiation may be confined to the single filament that occupies the very summit of the plica, or may be shared by two or three filaments. In the latter case the central filament of the three is larger than the lateral. This differentiation of apical filaments was first noticed by HANCOCK in *Chamostrea* (**29**, Plate 4, fig. 5), and has since been recorded by PELSENEER in *Lyonsia norvegica* (**71**, p. 212). The present investigation has revealed the presence of enlarged apical filaments in *Pinna nobilis*, *P. pectinata*, and *P. virgata* (fig. 17B, p. 214), and slightly enlarged filaments in *Pinna nigra*. They occur in *Lima fragilis*, *L. inflata* (fig. 18, p. 216), *L. squamosa* and *L. hians*, but not in *Lima californica*; in *Meleagrina margaritfera* but not in *Meleagrina anomioides*, or *M. vulgaris*; in *Solen fonesi*, *Pharella orientalis* and *Solenocurtus philippinarum* (fig. 42, p. 254), but not in the other examples of the Solenidæ examined; in *Anatina flexuosa*, but not in *Anatina truncata*. The meaning of these enlarged apical filaments is as inscrutable as that of the principal filaments, and no attempt at an explanation is here contemplated.

Cilia.

Those curious isolated patches ot stiff cilia constituting the "ciliated discs" have already been referred to (p. 154). As a general rule they project slightly from the anterior and posterior sides of the filament, owing to the fact that the columnar cells bearing them are taller than the ordinary epithelial cells, *e.g.*, *Lithodomus dactylus* (fig. 3A). In certain instances, however, they are set upon definite outgrowths or "spurs" of the filament, arising from the anterior and posterior sides, *e.g.*, *Modiola polita* (fig. 3B), or from the interlamellar edge, *e.g.*, *Spondylus nicobaricus* (fig. 3C).

The other cilia of the filaments are usually arranged in vertical strips or bands, one down the frontal surtace of the filament—the *frontal cilia*—and one on each of the sides of the filament—the *lateral cilia*—separated from the frontal cilia by a narrow space. The marginal cilia of the frontal band are usually, though not invariably, longer than the median ones, and these are known as the *latero-frontal cilia*. (These terms are not employed in exactly the same sense as by PECK, whose figures are mostly incorrect as regards arrangement of the cilia.) The disposition of the cilia in the great majority (nine-tenths or more) of the Lamellibranchia is that shown in fig. 3A. The transition from the frontal to the long latero-frontal cilia is usually gradual, as shown in this figure, but, owing to the curvature of the latero-frontal cilia, these frequently appear to be more sharply differentiated, as in fig. 3D. Since both arrangements are to be found in the same gill, the difference may evidently be disregarded.

Although PECK noticed the lateral cilia as distinct from the latero-frontal cilia in *Mytilus* (**66**, fig. 6) and *Dreissensia* (**66**, fig. 25), he failed to recognise them in *Anodonta* (**66**, figs. 12 and 13). Yet they are well developed in the Unionidæ, and have been figured by RABL in *Unio* (**81**), by POSNER (**77**, fig. 2) in *Anodonta*, and by JANSSENS (**39**) in both of these genera. Certain of the cells lining the inter-lamellar cavities also bear cilia. Such cilia are shown by POSNER and RABL in their figures above cited. PECK showed in his figures 12 and 13 a uniform clothing of
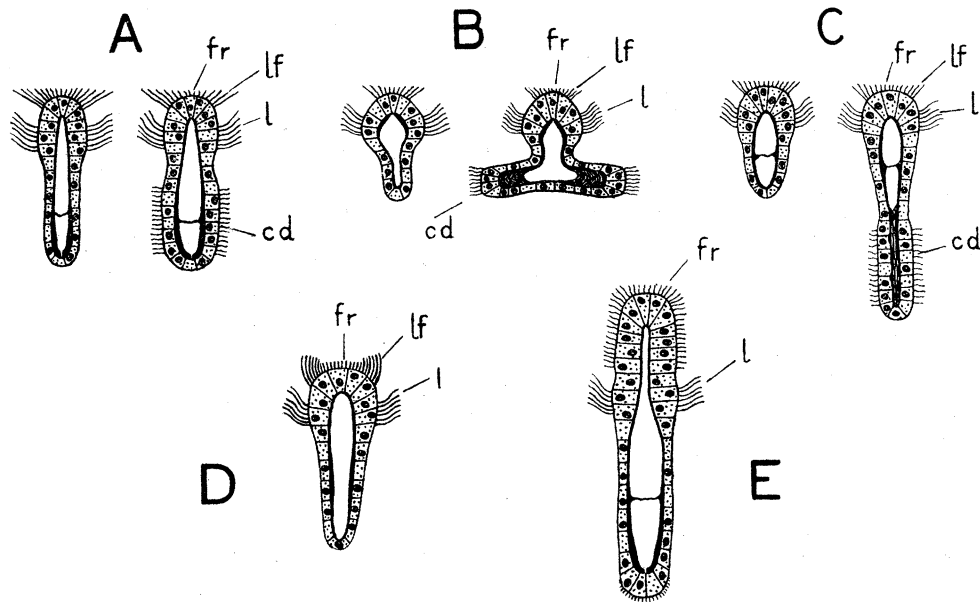
FIG. 3.—A, B and C, sections of the filaments of *Lithodomus dactylus*, *Modiola polita* and *Spondylus nicobaricus* respectively. The right-hand section of each pair is taken through a ciliated disc (*cd*), the left-hand one passes through the filament between one ciliated disc and the next above it ; *fr*, frontal cilia ; *lf*, latero-frontal cilia ; *l*, lateral cilia. D, section showing normally disposed cilia as they appear if the latero-frontal cilia are curved over the frontal cilia. E, section of a filament of *Arca granosa*.

short cilia over the whole of that part of the surface of the filament that was not covered by larger cilia, but this error was exposed by POSNER in his second paper (**77**, pp. 136–137). Short cilia occur also on the interlamellar edges of the filaments in the Oyster, where they were first noticed by LANKESTER (**52**). They are figured by JANSSENS in *Mytilus* (**39**, figs. 77 and 78), and I can attest their presence in *Arca granosa* (fig. 3E), *Monocondylæa* (fig. 28, p. 232), and *Teredo* (fig. 50, p. 260). It may be remarked that in many cases it is extremely difficult to distinguish cilia from coagulated mucus secreted by the abfrontal cells.

Where, as in *Arca granosa* (fig. 3E) and *Pectunculus glycimeris* (fig. 11A, p. 201), the filament is broad, the frontal cilia may extend round on to the sides of the filament beyond the region where the latero-frontal cilia are usually located. A similar disposition is figured by KELLOGG in *Arca pexata* (**42**, fig. 66) ; but in the

figures of *Arca barbata* and *Pectunculus glycimeris* by PELSENEER (**71**, figs. 36 and 34), the arrangement conforms with the normal plan.

The non-ciliated interval between the latero-frontal and the lateral cilia appears to be wanting in *Solenomya* (fig. 7 E, p. 192). The specimens examined in the course of this investigation were not sufficiently well preserved to enable one to deny its presence with any degree of confidence, although the cilia certainly seemed to be continuous; but it is a significant fact that in the figures given by PELSENEER (**71**, fig. 28), KELLOGG (**42**, fig. 77), and STEMPELL (**97**, fig. 20) it is not shown. If this be a correct conclusion, *Solenomya* stands alone as the sole example of a Lamellibranch with the frontal and lateral cilia continuous. HAREN-NORMAN, it is true, shows some small cilia occupying the interval between the lateral and the latero-frontal cilia in *Cardium ciliatum* and *Astarte sulcata* (**31**, figs. 44 and 48), but, although I have examined neither of these species, I have little hesitation in regarding this as an error of observation. He is probably also unfortunate in his representations of *Pecten groenlandicum* and *Modiolaria discors* (**31**, figs. 35 and 40), for he shows the sides of the filaments of the latter as possessing a uniform covering of short cilia, and the frontal surface of the former as devoid of cilia.

Chitin Skeleton.

The gill-filaments in all cases are strengthened by a skeletal substance to which the name *Chitin* has almost invariably been applied; and although there can be little doubt that this is the same substance which is found, in conjunction with salts of lime, in the valves of the shell and in pearls, and known under the name of *Conchyolin*, it will be well, in view of our present ignorance of the chemical and physical differences between Chitin and Conchyolin, to fall in with the general custom and adopt the term *Chitin*. It is elastic and resistant in character. It resists dilute acids and alkalies, and the skeleton of a gill may be prepared by prolonged maceration in warm dilute potassic hydrate. Preparations made in this way are best examined in weak glycerin.

In sections of the gill, cut by means of a microtome, the chitin framework can be made to stand out well by differential staining. It has a strong affinity for the aniline dyes, and as the result of extensive trials the blue known as " Bleu de Lyon " was found to give the best results. Unfortunately the colour is fugitive, and so the bulk of the sections prepared were double-stained with borax-carmine and picro-nigrosin. Under this treatment the chitin becomes a clear blue.

In simple filamentous gills the chitin takes the form of a complete tube, compressed in such a way that the broader surfaces are anterior and posterior, while the narrower surfaces are towards the pallial cavity and the interlamellar space respectively. The thickness of the chitin is probably in no case absolutely uniform, but the broader sides of the tube have each a thickened area. Concerning this,

PELSENEER has already stated (**72**, p. 177) that " cet épaississement est surtout développé vers le côté interne des feuillets chez les Anomiidæ, Arcidæ, et Trigoniidæ, et surtout vers le côté externe (donc ventral des filaments) dans les autres Lamellibranches ;" but although this statement is correct in the main, and may be allowed to pass as a text-book generalisation, it fails to take into account the fact that the position of the thickened band frequently varies at different levels. The general tendency is for the thickening to be nearer the interlamellar edge of the filament in sections taken towards the ventral edge of the demibranch than in those taken at higher levels. Occasionally there are two thickened bands on each broad face, one towards the incurrent and one towards the interlamellar side (figs. 11 A and C, and fig. 13 C *b*).

The cavity of the tube of chitin may be traversed by a continuous membrane of chitin (intrafilamentar septum), running lengthwise down the filament, and dividing the tube into two tubes, or there may occur isolated strands of chitin running from side to side. A careful examination of serial sections is necessary to distinguish these latter from the intrafilamentar septa. The presence of the septum must have a marked influence on the course of the blood stream, and a few paragraphs devoted to the discussion of this point will be found on p. 170. Speaking in a general way, the intrafilamentar septum is common among the Filibranchia, and occurs in two Pseudo-lamellibranch families—Spondylidæ and Pectinidæ. So far as present observations go, it is met with in none of the Eulamellibranchia except *Lyonsia nitida* and *Astarte borealis.*

In those cases where the filaments are in organic connection, either of an inter-lamellar or interfilamentar kind, the chitin also is continuous. These connections are mainly of loose lacunar tissue, covered by epithelium ; and extremely thin films of chitin cover the lacunar cells, and, in fact, form a sponge-work in which the cells are embedded. The continuity of this chitin with the thicker chitin of the filaments can be easily made out in well preserved and well stained material.

In those Lamellibranchia with organic interfilamentar junctions (*i.e.*, the Eulamellibranchia *plus* the Pinnidæ, Ostreidæ, and Limidæ—an assemblage which it is proposed to term the Synaptorhabda, see p. 186), the chitin in these junctions is remarkably thick and fibrous in character. It is continuous with the chitin of the filaments, which at the levels of the interfilamentar junctions is much thicker than usual, the thickening taking place at the expense of the filamentar cavity. In fact, in a great many of the forms the cavity of the filament, even in the regions between the interfilamentar junctions, can hardly be said to exist, an obliteration of the space being effected either by the excessive thickening of the chitin, or by an exceptional development of lacunar tissue which has intruded into the filamentar cavity (*e.g.*, *Anodonta, Lucina*, fig. 24A, p. 227).

A pale-staining chitin is sometimes met with in conjunction with the normal, deeply staining chitin. The two are found in close association, and the transition

may be gradual, but is more frequently abrupt. In the principal filaments of *Pecten opercularis, Spondylus ducalis,* and *Lima inflata* (see fig. 15, p. 209 and fig. 18, p. 216), the pale chitin lies towards the outer or epithelial side of the ordinary chitin, and a similar relation is found beneath the ciliated discs of *Trigonia* and *Malleus* (fig. 14B, p. 207) ; in these instances the pale chitin is perfectly homogeneous in character, or slightly fibrous, and would appear to be a softer, less concentrated variety of the normal chitin. Another kind of pale chitin, however, is sometimes met with, which exhibits a distinctly vesicular structure, the meshes of the sponge-work being occupied by rounded nucleated cells (*e.g., Lyonsiella papyracea,* fig, 54, p. 267, *Euciroa eburnea,* fig. 56, p. 270, and the principal filaments of *Tridacna elongata,* fig. 37, p. 246).

In effecting a comparison between the gills of Lamellibranchia and those of other Mollusca, one naturally selects such a form as *Nucula* for the purpose. In *Nucula* the columnar epithelium with differentiated cilia, and the thickened bands of chitin, lie towards the ventral edges of the leaflets, on the side of the axis nearest the efferent* vessel, and on the side farthest from the supporting membrane by means of which the gill axis is concrescent longitudinally with the side of the body.

Owing to the fact that in *Pleurotomaria* the supporting " rods " lie in the edges of the leaflets nearest the supporting membrane of the axis, WOODWARD† (p. 225) has seen a grave difficulty in the way of homologising the ctenidia of the Lamellibranchia with those of the Gastropoda. But the strengthened edges of the leaflets are still towards the efferent side of the axis, and all that is necessary for a rational explanation of the facts is to allow that the concrescence of the gill axis with the body is secondary, and that if the gill is backwardly directed, as in *Nucula,* that side of the axis which carries the afferent vessel may become concrescent with the side of the body, whereas if the gill is forwardly rotated over the back, and has a further translation from right side to left, and *vice versâ,* as in Streptoneurous Gastropods, the concrescence is effected between the body and that side of the gill axis carrying the efferent vessel. This admission as to the concrescence being secondary appears to be legitimate, in spite of the fact that DREW has shown that the gill leaflets of *Nucula* arise as papillæ from the sides of the body, and not from the sides of an axis which subsequently becomes concrescent with the body.

Endothelium.

A very keen controversy has long been rife concerning the cells which are found on the inner surface of the chitinous tube, and the warmth of the discussion appears to

* This is on the authority of PELSENEER (**71**, p. 164), and STEMPELL (**96**, pp. 395 and 396). MITSUKURI, KELLOGG and MÉNÉGAUX furnish no information. DREW, on the other hand, says that the vessel nearest the body communicates with the auricle (**22**, p. 360).

† WOODWARD, M. F., " The Anatomy of *Pleurotomaria beyrichii,*" 'Quart. Journ. Micro. Sci.,' 44, 1901, pp. 215-268, with four plates.

be quite disproportionate to the merits of the subject. The question is whether or no the chitin is lined by a definite and continuous layer of endothelial cells. The earlier observers BONNET (**5**) and SLUITER (**95**) described a definite endothelium in *Mytilus*, and KOLLMANN (**43**, p. 560) in *Mytilus, Pinna,* and *Anodonta*; and an endothelial lining has been recorded in *Modiolaria* and in the principal filaments of *Lima* by HAREN-NORMAN (**31**, pp. 35 and 32), in *Avicula* and *Pectunculus* by MÉNÉGAUX (**62**, pp. 41 and 88), and in *Yoldia, Solenomya, Pecten, Mytilus, Anodonta,* and *Venus* by KELLOGG (**42**, pp. 416–424). The last two authors are very positive as to its occurrence, KELLOGG declaring that there is no possibility of mistaking these cells for deposited blood corpuscles, and MÉNÉGAUX (**62**, p. 243) concludes a lengthy argument on the point with the words : " Il n'y a pas de lacunes dans les branchies des Pélécypodes marins, que le sang y circule toujours dans les vaisseaux à parois propres, tapissées par un endothélium formant une couche non interrompue." PELSENEER (**71**) and JANSSENS (**39**, pp. 16 and 72), on the other hand, are equally confident that a continuous endothelium does not exist.

It is, however, really immaterial whether there is an endothelium or not in the fully formed filament. The chitin must be secreted by the cells of the lacunar tissue and not by the superficial epithelium, since it is found in places far removed from the epithelial layer (*e.g.*, in the middle of a filament as an intrafilamentar septum,* in the middle of large thick interlamellar septa, and in the principal filaments of *Ostrea, Tridacna*, &c.), and on its first formation must be in relation with internal cells, probably disposed with their edges in contact to form an endothelium. In the filaments of the adult, however, the appearances presented are those of isolated cells or groups of cells flattened against the surface of the chitin. A special search was made for a continuous endothelium in all the sections in which the finer histological details were to be made out, but in no case were there evidences of more than two or three cells in continuity. The silver nitrate test, also, applied to longitudinal sections of *Mactra, Ostrea*, and *Mytilus*, failed to provide any unequivocal evidence.

Calcified Rods.

These are calcified structures peculiar to the filaments of the Unionidæ and *Mülleria*. Much confusion has arisen from the fact that some authors, such as LANGER (**49**, p. 44), POSNER (**76**), RABL (**81**, p. 352), and SIMPSON (**94**, p. 182) failed to discriminate between the thickened bands of chitin (Stäbchen) such as occur in the majority of Eulamellibranch gills and these calcareous rods embedded in the chitin, first noted by RENGARTEN in 1853 (**82**), and described by HESSLING in 1859 (**33**, p. 228) as " Kalkstäbchen." The Stäbchen of chitin are but local thickenings of what must be regarded as a general lining of the filamentar, and

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* KELLOGG, curiously enough, does not admit that the intrafilamentar septum is composed of chitin (**42**, p. 421, *Pecten irradians*). He regards it as cellular—endothelium, in fact.

frequently also the lacunar cavities, and it is only by disregarding the thinner parts of the chitin that these thickenings can be taken for rods at all. It is true that they bear a certain resemblance to rods in some cases, *e.g.*, *Panopea generosa* (fig. 49, p. 258) and *Pholas crispata*, but a few simple reactions, such as the employment of acids, alkalies, and differential stains, soon enable one to distinguish that these are not the calcified rods under discussion. BONNET did not fall into the common error, and it was he who first remarked that these structures are not met with outside the family Unionidæ (**5**, p. 322). KOLLMANN (**43**, p. 592) correctly regarded the calcified rods as local calcifications of the " Gallertgewebe," and PECK (**66**, p. 62) also discriminated between the calcified rods and the chitin thickenings, but since he failed to note POSNER's confusion, he alluded to the former as the " well-known Stäbchen of the German authors." The best account of them is that given by JANSSENS (**39**, p. 56), who called them " baguettes calcifiées," and showed that they are composed of calcium phosphate, with a little calcium carbonate, and a chitin or conchylin base which remains after the removal of the calcium salts by dilute acids.

They are not continuous rods of uniform width extending the full height of the demibranch, but consist of a succession of short rods which taper off to nothing in the middle of each interfilamentar junction. The length of each rod is thus slightly less than the mean distance between one interfilamentar junction and the next above it. This fact is easily demonstrated by soaking in 10 per cent. potassic hydrate for 24 hours a piece of the lamella of the *Anodonta* or *Unio* gill, and examining in glycerine under the low power of the microscope; but it is also apparent in a continuous series of sections taken transversely to the filaments. As an interfilamentar junction is approached the sections of the rods become smaller and smaller, and in the middle of the interfilamentar junction are wanting entirely. The rods are extremely brittle, and in sections taken as above the pieces are frequently seen dislocated and thrown on their sides, especially if the section is thicker than the width of the rod and if the razor employed was at all dull. According to SIMPSON (**94**, p. 182, and Plate 7, fig. 1), JANSSENS (**39**, p. 58, and figs. 44 and 55), and PECK (**66**, p. 62), the rods persist, in an attenuated form, through the interfilamentar junctions. This may possibly be true in old specimens, but it was not the case in the numerous examples examined for the purposes of this research. HESSLING, it may be noted, spoke of the rods (**33**, p. 228) as " vielfach gegliederte Kalkstäbchen," and LANGER (**49**, Plate 2, fig. 9) has figured them as completely separated structures.

Intrafilamentar Septa.

The filaments of *Arca* have intrafilamentar septa, whereas those of *Trigonia* have not. The upper extremities of the ascending filaments of *Arca* are in ciliary connection with one another, whereas those of *Trigonia* are in organic connection. In these

two facts, taken together, there lies a fascinating suggestion that when the ascending filaments are not in mutual organic connection the blood circulating in them must come back again to the gill-axis, and that the intrafilamentar septum serves to keep the two currents distinct ; whereas when the ascending filaments are united, the blood passes in one direction only along the filament, either down the descending filament and up the ascending filament and out into adjacent parts, or the reverse,* and an intrafilamentar septum is in such case no longer essential.   This tempting hypothesis has not escaped previous writers.   MÉNÉGAUX, for instance, states that the difference in the circulation in the gills of the Mytilidés and the Arcadés (**62**, pp. 226 and 227) is related to the absence or presence of the intrafilamentar septum, and PELSENEER (**71**, p. 245) states even more definitely that the difference " peut s'expliquer par le fait que le septum a dû disparaître aussitôt que la concrescence, par leur bord dorsal, des filaments réfléchis, a permis la communication entre les filaments successifs."   KELLOGG (**42**, p. 408), again, writes : " In forms with a descending and ascending portion in the filament, and where the latter is not in concrescence at its extremity with the mantle or neighbouring filaments, the blood must flow out to the extremity of a filament and then back again, perhaps, however, not taking exactly the same path.   It will be noticed that in gills of this kind the blood space of the filament is divided by a septum or is greatly flattened out, and shows in section a long, narrow blood channel."†

On putting the above hypothesis to the test, one finds that the evidence barely justifies the generalisation ; for although one may conclude that the intrafilamentar septum is present when the upper ends of the ascending filaments are in ciliary connection only, yet there are several instances of species having the ends of the filaments fused up, and yet retaining the septum.   In the list below, the term " present at intervals " means that when following a single filament through a long series of sections cut by means of a microtome, the septum is seen to be present in some three, four or more sections, is not apparent in several more sections, and then reappears in those that follow.   I take this to signify an incomplete septum.   The word

* That it is not easy to decide which is the course actually taken by the blood is evident from the discrepancies in the published accounts.   With regard to *Mytilus*, or its allies, BONNET (**5**), SABATIER (**86**), PECK (**66**, p. 49), SLUITER (**95**) and HAREN-NORMAN (**31**, p. 33) are of opinion that the blood passes from the axis down the descending filaments and up the ascending, whereas the reverse direction is given by MÉNÉGAUX (**62**, p. 226), PELSENEER (**72**, p. 177) and RICE (**83**, p. 43).

† His observations on the living *Arca* are, however, at variance with this deduction.   Concerning *Arca pexata*, he writes (**42**, p. 409) :—" Under the microscope the pale yellow corpuscles could be seen in motion in the blood stream.   In both outer and inner lamellæ the currents would keep up a constant flow for half-a minute, at times, though the rate of the current did not remain constant.   The streams would become slower, finally stop, and then a back-flow would set in.   After a short time these ceased, and the currents resumed their original course.   I did not confound two separate currents, but could see individual corpuscles being carried in one direction and then back in the other.   The currents in the different filaments were independent of one another, and there seemed to be a somewhat irregular channel for them."

"present" means that the septum is so commonly visible in the sections, that its occasional absence may be regarded as due to the rupture of the membrane in the act of cutting.

(1.) Upper ends of the ascending filaments in ciliary connection with one another :—

*Dimya argentea**	{ intrafilamentar septum present at rare intervals.
*Anomia aculeata**	present.
Anomia patelliformis . . .	present.
Anomia laqueata	present at rare intervals.
Arca granosa	present.
Pectunculus glycimeris . .	present.
Limopsis indica	present at intervals.
Pecten opercularis . . .	present.
Amussium dalli	present.
Spondylus calcifer . . .	present.
Spondylus nicobaricus . .	present.
Plicatula australis . . .	present.

(2.) Upper ends of the ascending filaments fused with one another :—

Anomia ephippium . . .	present.
Placuna placenta . . .	present.
Trigonia lamarcki . . .	absent.
Mytilus edulis	present at intervals.
Modiola polita	present at intervals.
Modiola evansi	absent.
Modiola barbata . . .	absent.
Modiolaria discors . . .	absent.
Lithodomus dactylus . .	present.
Lithodomus teres . . .	present.
Lithodomus malaccanus . .	present.
Botula cinnamonia . . .	present.
Septifer bilocularis . . .	present.
Avicula argentea . . .	absent.
Avicula radiata	absent.
Meleagrina margaritifera .	absent.
Malleus albus	absent.
Melina perna	absent.

* These have no ascending filaments, but since the extremities of the filaments are in ciliary connection, they may be located here.

Melina linguæformis . . . absent.

Melina serratula . . . . absent.

Pinna virgata . . . . . absent.

Pinna nobilis . . . . . absent.

*Ostrea edulis** . . . . . absent.

Lima inflata . . . . . absent.

Lima calfornica . . . . . absent.

Lima fragilis . . . . . absent.

Lima hians . . . . . . present.

Spondylus varians . . . . present.

Interlamellar Junctions.

The interlamellar junctions may have the form of horizontal bars extending from the descending to the ascending filaments, or of continuous septa. It is very doubtful whether any great significance need be attached to the difference. Judging from the embryological data available, they are in all cases of secondary origin, since the descending filaments are formed prior to the appearance of the ascending filaments. As will be seen by a reference to the chapter on the non-plicate Eleutherorhabda, pp. 193—208, there is a most inconsequent distribution of the varieties of interlamellar junctions in the species examined. There may be no interlamellar junctions at all (*Anomia*, *Pectunculus*); septa may occur in certain filaments at regular intervals (*Lithodomus*); septa of various heights in all filaments (*Malleus*); a single cross bar in all filaments (*Septifer*); a cross bar and a low septum (*Trigonia*); a cross bar situated high up and restricted to certain filaments at intervals (*Melina*); or three cross bars in all filaments (*Mytilus edulis*). In the case of *Melina* the bar is unusually thick, and is connected with the upper ends of several filaments at each of its extremities.

In the plicate Eleutherorhabda (*Spondylus, Pecten, Avicula, Meleagrina*), and in the plicate Synaptorhabda (except *Pinna*) the interlamellar junctions have the form of septa, and are confined to the principal filaments, if such are differentiated. It is a curious fact that in the great majority of these the septa are alternately high and low, the former extending the full height of the ascending lamella, the latter not rising more than one-half or three-quarters of the height. In a few cases (*e.g.*, *Psammobia ferroensis, Solen ensis, Solenocurtus rufus, Panopea generosa, Tapes pullastra, Diplodonta oblonga*) all the septa are high.

Septa are not uncommon in the non-plicate Synaptorhabda, and are frequently thick and related at their edges with three or four filaments, particularly at the levels of the interfilamentar junctions.

* KELLOGG (**42**, p. 423) says that in *Ostrea virginiana* "there is no constant septum," thereby, I take it, implying that it is present at intervals.

Within the group Synaptorhabda interlamellar bars appear to be confined to the non-plicate forms of Submytilacea. They occur in *Cardita, Astarte, Kellya, Lasæa, Galeomma, Crassatella cumingi* and *Crassatella indica*. (The gill of *Crassatella floridana* is plicate, and has septa.) *Dreissensia, Lucina,* and some other non-plicate Submytilacea have septa.

Pinna stands rather alone among the Synaptorhabda, since its principal filaments are provided with two or three horizontal bars.

The distinction that has been drawn by many authors between vascular and non-vascular interlamellar junctions is difficult of application, and probably of no great morphological value. If the animal be killed in such a way that the gills are gorged with blood, there are numerous large spaces in the subfilamentar tissue and interlamellar junctions, whereas if the killing reagent causes a contraction of the gill, the tissues appear more solid. An *Anodonta* which has died in an aquarium, or has been killed by very gradually warming up the water to 60° C., has its gills full of blood, but if the animal be dropped into alcohol, or is bled to death by incision into the auricles, the lacunar tissue shows few cavities. The differences presented by the lacunar tissue of different individuals of the same species may in many cases be attributed to such causes.

Interlamellar Extensions of the Filaments.

In many forms of Lamellibranchia the interlamellar edges of the filaments exhibit a marked tendency to secondary growth. Interlamellar junctions and organic inter-filamentar junctions owe their origin to this capacity for proliferation of subfila-mentar tissue. Taking a genus such as *Astarte* (fig. 22, p. 222) or *Kellya*, in which the tendency is slight, one notices, on comparing a section taken through an inter-filamentar junction with one taken through a free part of the filament, that the inter-filamentar junction lies internally to, *i.e.*, on the interlamellar side of, the filament proper. This gives one a means of distinguishing in more difficult cases between the filament proper and such secondary growths as may give an exaggerated appearance to the width of the filament—width here referring to the measurement from the interlamellar edge to the frontal surface. The increment may be spoken of as the *interlamellar extension* of the filament. A comparative glance at sections of *Astarte* and *Ephippodonta* (figs. 22 and 25) will render it clear that, in the latter, what might at first appear to be very broad laminate filaments united by interfilamentar junctions at a distance of one-third of their width from the frontal edges, are in reality composite structures, the outer third of which is constituted by the filament proper and the inner two-thirds by the interlamellar extension. A further means of dis tinguishing the filament proper in such cases as this is the fact that the chitinous lining is thickened in the filament proper but not in its interlamellar extension.

If the interlamellar extensions of a descending filament and its corresponding

ascending filament become united across the interlamellar space, an interlamellar septum is formed; and in the filaments of *Arca granosa* and *Arca americana* (fig. 10A, p. 199), and the principal filaments of *Pecten* and *Spondylus*, the appearances are decidedly suggestive of the fact that the great flap developed on the upper part of the descending filament has been unable to produce a high septum in consequence of the failure on the part of the ascending filament to respond to a sufficient degree in the same direction.

It is a significant fact that interlamellar junctions having the form of rods occur only in those genera with feeble development of subfilamentar tissue, viz., certain Filibranchia and Submytilacea. *Pinna*, it is true, is an exception, but there is reason for believing that the three interlamellar bars to each principal filament of this genus are the relics of a fenestrate septum (fig. 17A, p. 214).

Like so many features of gill structure this proneness of the filaments to extension in an interlamellar direction is of little, if any, systematic value. It is possibly related to the conditions under which the animal is living, and is the outcome of a permanently altered metabolism of the tissues of the gills. Perhaps it indicates abundant nutrition, or may be ascribable to increased temperature or diminished salinity of the water, or to the depth below the surface at which the animal lives. Since, however, there is abundant subfilamentar tissue in *Unio pictorum* and *Psammobia pallida*, but little in *Unio ambiguus* and *Psammobia ferroensis*, one hesitates to frame generalisations.

In their elementary state the interlamellar extensions of filaments have the form of free vertical plates directed into the interlamellar cavity (*e.g.*, *Ephippodonta*), but if they have attained any considerable size, they usually become connected the one with the other by lateral extensions of the subfilamentar tissue, forming what appear to be deeply situated interfilamentar junctions (*e.g.*, *Lucina bengalensis*, fig. 24A *a*, p. 227, *Donax variabilis*, fig. 31A, p. 236, *Tridacna elongata*, fig. 37 *b* and *c*, p. 246). These deep interfilamentar junctions differ from the more superficial true interfilamentar junctions in being less regular in their arrangement, and in not containing thick horizontal rods of chitin. Chitin is present, but, as in the interlamellar extensions themselves, it has a delicate vesicular structure.

In extreme cases, where the growth of subfilamentar tissue is excessive, the interlamellar extensions fuse up into bulky masses of lacunar tissue (*e.g.*, *Anodonta cygnea*, *Mactrinula plicataria*, *Psammobia pallida*, *Mya arenaria*). It would appear that this condition has been brought about by the addition of new struts between the interlamellar extensions rather than by the swelling of those already present. In many cases, however, the effect of deep interfilamentar junctions is due to the spreading of the inner part of the normal interfilamentar junctions in an upward and downward direction along the edges of the interlamellar extensions.

As might have been expected, this copious proliferation has the effect of reducing the size of the fenestrations, so that the lamella, instead of presenting the appearance

of a regular rectangular meshwork, shows a number of small water-pores, disposed usually in irregular sinuous horizontal lines (*e.g.*, *Anodonta*).   In extreme cases many of the water-pores are completely occluded (*e.g.*, *Lucina* and *Tellina*).

In *Dreissensia* the interlamellar extensions occur on alternate filaments only; and they swell out in such a way that there is but one vertical row of interlamellar openings corresponding to two rows of external or interfilamentar pores (fig. 29 *ile.*).

In certain plicate Eulamellibranchia, notably the Tellinacea, Veneracea and Myacea, there are vertically disposed blood tubes within the apex of the plica.   They are conspicuously developed in *Semele, Paphia, Donax faba* (fig. 31B, p. 236); *Venus* (fig. 33, p. 241); *Circe, Dosinia, Tapes* (fig. 34, p. 242); *Petricola* (fig. 35, p. 243); *Psammobia* (fig. 38, p. 249); *Asaphis, Tagalus.*   They do not occur in the Pseudolamellibranchia, and there may be some functional significance in the fact that they are not found in gills which have enlarged apical filaments.   What is probably more to the point is the fact that, in the forms mentioned above, the interlamellar septa are all high septa, not alternately high and low.   It is as though in such forms as *Cyrtodaria* or *Lutraria* (fig. 40, p. 251), the two blood tubes continued upward from the low or incomplete septa were so widely divaricated that each two adjacent plicæ of the same lamella were thrown into one large plica, with the vessel occupying its apex.   The interlamellar septa that remained would then all be high septa.

The failure to grasp the full significance of the interlamellar extensions of the filaments has resulted in many misconceptions in the past, and was one of the prime causes which contributed to the erroneous interpretation put by DALL upon the gill structure of *Vesicomya* and *Euciroa.*   Both of these genera have interlamellar extensions of plate-like form; and since, owing to the obliquity of his sections, this author failed to recognise the presence of regular organic interfilamentar junctions, it was but natural that he should take these extensions to be the central parts of such leaflets as occur in the Protobranchia.   In *Euciroa* there is no acute angle between the descending and ascending parts of each filament at the ventral edge of the demi-branch, but a uniform curve, which suggests at first glance a resemblance to the Protobranch gill.

According to DALL's view, the interlamellar septum in the gills of the majority of Lamellibranchia is the persistent central portion of the Protobranch leaflet, the filament proper being the equivalent of the swollen lower edge, which alone is provided with cilia and thickened chitin.   This hypothesis necessitates the admission that in the gradual increase of the vertical extent of the gill lamella the abaxial end of the thickened rim is as relatively fixed as the axial end, and that the extreme ventral point of the filament at the lower edge of the demibranch of the ordinary Lamellibranch gill represents a point halfway along the thickened rim of the leaflet, as shown in fig. 4 (p. 176).

That this is an untenable view is rendered more than probable by the fact that all

embryological evidence points to the formation of the descending filaments first, the ascending filaments afterwards, and the interlamellar junctions at a still later date. KELLOGG (**42**, p. 428) states at the conclusion of a discussion on the evolution of gill
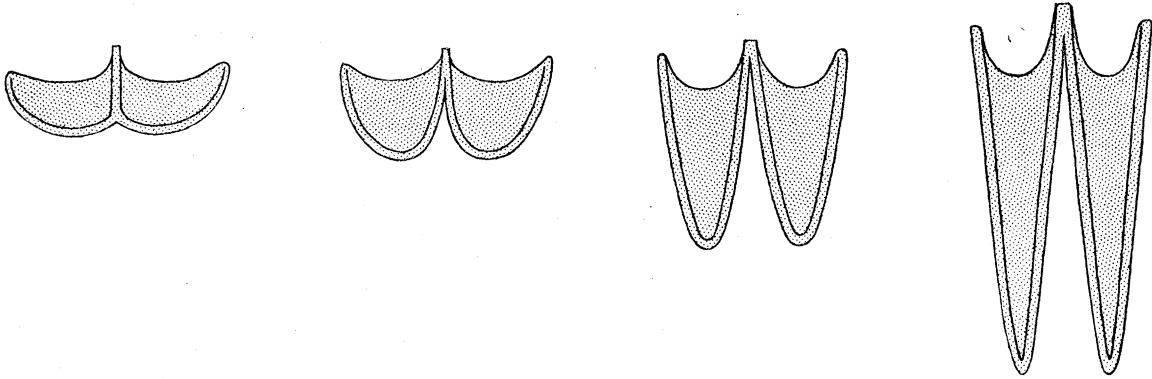

FIG. 4.—Erroneous mode of regarding the evolution of the Lamellibranch gill filament and its inter-lamellar septum from the Protobranch leaflet.

filaments that " it seems as if we ought to regard the gill plate of *Nucula* as being homologous, not alone to the descending limb of a filament, as MITSUKURI has done, but to both descending and ascending limbs." It is not clear, however, to what extent he is prepared to countenance the above hypothesis.

On the same page KELLOGG suggests, with apparent diffidence, that the Proto-branch leaflet has originated from the filamentous type by a process of shortening up, accompanied perhaps by a degeneration of the ascending limb. This, of course, is not altogether impossible, but seeing what a good case PELSENEER (**71**, pp. 246–250, and p. 274) has made out in favour of the antiquity of the Protobranchia and the primitive nature of their gills, it seems hardly worth while to discuss the matter further.

Euciroa and *Vesicomya*, even admitting that they have a mutually similar type of gill as DALL maintains, cannot by themselves bridge the great gap between *Nucula* and *Arca* as this malacologist suggests (**15**, p. 505). Owing to their possession of organic interfilamentar junctions, their relations with the Eulamellibranchia are such that, if it be satisfactorily demonstrated that the Protobranchia are degenerate Eulamellibranchia which have been further modified along the *Euciroa* line, then the whole of the Eulamellibranchia must come between the Filibranchia (which now must begin the series) and the Protobranchia (which now would stand at the end).

Classification.

One of the most important results of the present investigation is the confirmation of the accepted view that ctenidial filaments held together by ciliated discs are of essentially simpler structure than those connected by subfilamentar tissue ; and one

of the most obvious conclusions to be drawn from the results as a whole, and more particularly from the condition found to exist in *Lima inflata* and *Avicula argentea*, is that the ciliated disc is a more archaic mode of junction than the cellular junction. This deduction is supported by the absence of tissue junctions between the leaflets of the Protobranchia, the ctenidia of which may on other grounds be regarded as more primitive than those of other Lamellibranchia. In so far, then, as it is possible to distinguish in the Lamellibranchia three grades of gill complexity, characterised respectively by the freedom of leaflets, the union of filaments by ciliated discs, and the union of filaments by organic junctions, the results of the investigation realise the anticipations expressed by LANKESTER in 1883 (**51**, p. 691), that "probably the gill-structure of Lamellibranchs will ultimately furnish some classifactory characters of value when they have been thoroughly investigated throughout the class." To this extent, also, they confirm the conclusion of PELSENEER (**71**, p. 290):—" La complication de la branchie ·indique le degré de spécialisation des différents groupes de Lamellibranches." But, for the subdivision of these groups, the gill-structure is of little, if indeed of any, value for indicating genetic relationships.

The order Protobranchia, as at present constituted, was founded by PELSENEER in 1889 (**69**), but the primitive nature of the gills of the included genera had been noted long before this. LEUCKART, in 1848 (**53**, p. 133), stated that *Solenomya* has a primitive form of gill, from which, by the elongation of the leaflets (Blättchen), are derived two types of gill, the first with narrow and free filaments (example— *Pectunculus* and *Arca*), and the second with the filaments united so as to form a membrane or lamella. HUXLEY (' Anatomy of Invertebrated Animals,' 1877, p. 408) wrote that " in its simplest form the branchia of a Lamellibranch consists of a stem fringed by a double series of filaments (*e.g., Nucula*)," and that " the next degree of complication arises from these filaments becoming as it were doubled upon themselves," as in *Mytilus* and *Pecten*. VON IHERING, in the same year, remarked in a footnote to his paper on the Molluscan kidney (1877,* p. 610):—" Die Differenzen im Baue der Kiemen bestehen darin, dass entweder nur die primären Blätter existiren (*Nucula, Nuculana, Solemya*) oder . . . . Da wo nur die primären Blätter existiren, bestehen sie aus einzelnen Blättern, die nicht quer verbunden sind." And LANKESTER, in 1883, wrote (**51**, p. 688):—" The Molluscan ctenidium is typically . . . . a plume-like structure . . . . In the genus *Nucula* . . . . . we have an example of a Lamellibranch retaining this plume-like form of gill."

The first figure showing the form of the leaflets of the gill ot *Nucula* was published by DESHAYES in his memoir on the Mollusca of Algeria (**17**, Plate 117, fig. 7), a work which has been largely overlooked by investigators on the gill structure of Lamellibranchia. MITSUKURI was the first to apply modern methods of microscopical

* IHERING, H. VON :—" Zur Morphologie der Niere der sogennanten ' Mollusken.' " ' Zeitschr. f. wiss. Zool.,' 29. Leipzig, 1877, pp. 583–614.

research to this type of gill, and PELSENEER, in the works cited on p. 188, contributed further to our knowledge of the structure of the Protobranch gill, and discussed the derivation of other Lamellibranch gills from such a simple type.

The term Foliobranchia was suggested by MÉNÉGAUX in 1890 (**62**) as a substitute for Protobranchia, as referring to a structural peculiarity rather than to the relation which this form of gill may be deemed to bear to other types. He agreed, however, with earlier observers in regarding the type as archaic. The most recent contributions to the literature of the subject are those of KELLOGG (**42**), STEMPELL (**96** and **97**), and DREW (**22**), all of which, though valuable as additions to our knowledge of the more detailed structure of the leaflets, leave the subject as a whole much as it was.

The only writers who have at all contested the right of the Protobranch gill to rank as the ancestral type are KELLOGG and DREW, both of whom throw out suggestions, but do not definitely argue in favour of the derivation of the Protobranch from the Filibranch type. The former writes (**42**, p. 428):—" PELSENEER now regards *Nucula* as the most primitive form. He believes *Anomia* and also the Arcidæ to be directly descended from forms with plate gills. As I have said, these relations may be the true ones, and yet it seems difficult to explain the structure of the gills of the former in terms of those of the latter. One might much more easily suppose, *a priori*, that the latter had developed from the filamentous type, perhaps by the degeneration of the ascending portion of its filament." And DREW says (**22**, p. 363):—" There is much in the structure and embryology of *Nucula* that points to a generalised type, and in this much it seems natural to look at the gills as primitive; but the gills of *Yoldia*—its undoubted near relative—are so remarkably well adapted for the performance of a special function, that it hardly seems safe to regard them as slightly modified gills until there are more careful observations on the habits of other forms. I recognise fully the mass of evidence in favour of the primitive form of the plate-like gill. My only plea is for caution."

It is true that the gill with leaflets may have been evolved from a simple fili-branchiate gill without ciliated discs or interfilamentar fusions, on the assumption that each filament has an extensive interlamellar septum, and that the vertical extent of the demibranch has become reduced. But, after all, the Protobranch ctenidium conforms more nearly with that of the Gastropod and Cephalopod than does the Filibranch, and it is thus more reasonable to consider it as the more primitive form. The fact that the other anatomical features of these Protobranch Molluscs, as well as their antiquity in geological time, point to their primitive nature must be allowed to carry weight. The ablest arguments put forward in favour of the archaic character of the Protobranch gill are those published by PELSENEER in 1891 (**71**, pp. 246–250, and p. 274). He has shown (**71**, figs. 99, 100, and 103) how closely the gill-structure of the Protobranchia resembles that of *Fissurella*, *Chitonellus* (= *Cryptoplax*), and *Trochus*. It is, further, not a little remarkable how closely the figure of the section

of the gill of *Chiton* (*Enoplochiton niger*), given by PLATE,* resembles that of a *Yoldia*. And, allowing for the difference in the position of the supporting membrane of the axis (see p. 167), the structure of the gill of *Pleurotomaria*, as described by WOODWARD,† is very much like that of the gill of one of the Nuculidæ.

As regards the Pseudolamellibranchia, it becomes expedient, in the circumstances, to abolish this extremely unsatisfactory group.‡ This was done as far back as 1889 by MÉNÉGAUX (**61**), but the step did not appear to meet with general approval. In spite of the extreme probability, supported in no small degree by the mode of ontogeny of the adductor muscles, that the monomyarian condition has been evolved in several families quite independently, there is still a wide-spread mistrust of any scheme of classification which involves the dissociation of the monomyarian forms.§ The gill of *Ostrea* will, however, in its minuter structure bear a much closer comparison with that of *Lyonsia, Psammobia, Asaphis, Solen ensis, Tridacna*, or other plicate heterorhabdic Eulamellibranch than with that of *Avicula* or *Pecten*. It is, indeed, typically Eulamellibranchiate.

What is now proposed, therefore, is to remove *Pinna* from the family Aviculidæ to constitute a separate family, the Pinnidæ, and to include this, together with the Ostreidæ and Limidæ, in the Eulamellibranchia. The Aviculidæ that remain after removal of *Pinna* must then, with the Pectinidæ, Spondylidæ, and Dimyidæ, be joined to the Filibranchia to constitute the new group Eleutherorhabda,‖ characterised by

* PLATE, "Die Anatomie und Phylogenie der Chitonen," 'Zool. Jahrb.,' Suppl. Bd. iv, 1, Jena, 1898, pl. 9, fig. 89.

† WOODWARD, M. F.—"The Anatomy of *Pleurotomaria beyrichii*," 'Quart. Journ. Micro. Sci.,' vol. 44, 1901, pp. 215–268.

‡ The unsatisfactory nature of the group is evident from PELSENEER'S original diagnosis (**69**, p. 52) :—
"Un troisième (groupe), dans lequel on peut réunir les animaux à branchies filamenteuses, mais dont les filaments branchiaux n'ont plus la même liberté que dans le groupe précédent; les deux branches d'un même filament présentent des réunions transversales, en même temps que les filaments d'un même feuillet sont réunies par des brides longitudinales. Le nom *Pseudolamellibranchiés* conviendrait à ce groupe qui serait composé des Mytilacea, Pectinacea, Ostracea."

§ That no great value can be attached to the presence or the absence of the anterior adductor muscle is shown by the fact that this muscle is present in *Anodonta* and *Unio*, but is wanting in *Mülleria*; and yet these are universally admitted to be closely related genera. This has been pointed out by PELSENEER (**69**), and has more recently been alluded to by WOODWARD (**108**, pp. 87 and 89). PURDIE, again, has stated (**78**, p. 9) that the anterior adductor is wanting in *Mytilus latus*, although present in *Mytilus edulis* and *Mytilus magellanicus*.

‖ By the suppression of the Pseudolamellibranchia the resulting classification comes to resemble fairly closely that of MÉNÉGAUX (**62**, p. 270), who wrote :—" D'après la structure anatomique des branchies, on peut diviser les Lamellibranches en :—

    Foliobranches—Nuculidés, Solemya.
    Filibranches—Mytilidés, Trigoniidés, Aviculidés, Arcadés, Pectinidés, et à côté les Ostréidés.
    Eulamellibranches—Naiadés, tous les Siphonés.
    Septibranches—Poromyidés, Cuspidariidés."

the relative freedom of the gill filaments. Interfilamentar junctions by means of interlocking cilia are confined to this group. The upper extremities of the ascending filaments may be fused in longitudinal series (*e.g.*, *Trigonia*, *Mytilus*, *Avicula*), or (as in *Pecten*, *Spondylus*, *Arca*) remain in ciliary connection only—the latter condition being evidently the more primitive. And at the ventral edge of the demibranch, where the descending filaments turn and begin to ascend, an organic connection may become established from one filament to the next, as for instance in *Malleus*, *Meleagrina*, and *Avicula*. But the organic interfilamentar junctions occurring at more or less regular intervals up the lamellæ are characteristic of the Eulamellibranchia, and with one exception do not occur in the Eleutherorhabda. In *Avicula argentea*, as already mentioned, there is to be seen a most interesting combination of the ciliary junction with that of the cellular type (fig. 16, *org.* p. 212). Several other species of *Avicula* were examined, but in all of these the ciliated discs were of the normal type, and exhibited no tendency towards such proliferation of subfilamentar tissue as might put adjacent filaments into organic union. This condition, taken in conjunction with what is seen in *Lima inflata*, where there is a suggestion of obsolete ciliated discs, indicates with tolerable clearness how the former junctions have come to be replaced by the latter.

While in the Eulamellibranchia it is usual, though by no means universal, for the upper edge of the ascending lamella of the outer demibranch to be concrescent with the mantle, and that of the inner demibranch to be united with the side of the visceral mass for a certain distance, and behind the visceral mass to be united with the corresponding ascending lamella of the opposite side, such connections are exceptional in the Eleutherorhabda. As will be shown shortly, no great importance need be attached to this feature.

The Filibranchia as recognised by PELSENEER, include the Anomiidæ, Arcidæ, Trigoniidæ and Mytilidæ, all the genera of which have flat gill lamellæ. Although principal filaments are not differentiated, a very interesting condition is observable in *Lithodomus dactylus*, each tenth or twelfth filament in the inner demibranch, and each seventh or eighth filament in the outer, possessing an interlamellar septum, whereas the intervening filaments do not (figs. 12 and 13, p. 204). We have here what is presumably an early stage in the differentiation of principal filaments, although the filaments in question are barely, if at all, wider than the average. There is no indication of folding of the lamellæ, so that the evolution of plicæ would appear to be subsequent to that of the principal filaments. If, after the stablishment of such a condition as occurs in *Lithodomus*, there should arise a tendency for the gill axis to shorten, the bulging of the lamellæ between each two septum-provided filaments would be the natural consequence, and the gill lamella becomes plicate. A condition similar to that found in *Lithodomus dactylus* occurs in the other species of *Lithodomus* examined, and in *Botula cinnamonia* and *Modiola barbata*, the septum-bearing filaments in these species recurring more frequently, at

intervals of four filaments or so. The other Filibranchia have no interlamellar junctions at all (e.g., *Pectunculus glycimeris*), or have all the filaments provided with septa of varying height (e.g., *Arca americana*), or with one (e.g., *Trigonia lamarcki*) or more (e.g., *Mytilus edulis*) horizontal bars of tissue stretching between the ascending and descending filaments.

Of the genera of the Pseudolamellibranchia which it is now proposed to associate with the Filibranchia under the title Eleutherorhabda, some have well developed principal filaments and plicate lamellæ (e.g., *Avicula, Meleagrina, Pecten, Spondylus*), whereas others have flat lamallæ and filaments undifferentiated (e.g., *Plicatula, Malleus, Melina, Amussium* and *Dimya*). So sharply marked off are these first four genera from all the rest of the Eleutherorhabda by reason of their strongly differentiated principal filaments and their plicate lamellæ, that it is well to let them constitute a sub-order by themselves. *Dimya*, also, may with advantage be joined with *Anomia aculeata* in a special sub-order characterised by the absence of ascending lamellæ.

The amount of family disruption which this scheme involves will doubtless prove startling to the systematic malacologist, who has long been accustomed to the association of *Amussium* with *Pecten*, and *Plicatula* with *Spondylus*. It remains for an exhaustive study of the general anatomy of these forms to demonstrate whether the similarity in their more obvious features is a family trait or is a phenomenon of convergence. We have, curiously enough, in the Eleutherorhabda no intermediate gradations between the homorhabdic and heterorhabdic conditions such as are to be seen in the Synaptorhabda; for even in the case of *Lithodomus* and its allies, the approach to the heterorhabdic condition lies rather in the limitation of the interlamellar septa to certain filaments at intervals than in the enlargement and specialisation of the septum-bearing filaments themselves.

In reviewing the species included in the second and third divisions of the Eleutherorhabda, it becomes apparent that in those forms in which the upper extremities of the ascending filaments are in organic connection, no great importance can be attached to the fact that the upper edge of the ascending lamella remains free from adjacent parts in some, while it is concrescent with them in others. Thus, while in *Melina serratula* the upper edges of the ascending lamellæ show no concrescence with the mantle, visceral mass, nor with one another, in *Melina perna* the inner lamellæ fuse with one another behind the visceral mass, the outer lamellæ remaining free from the mantle. In *Melina linguæformis* the inner ascending lamellæ are fused with the visceral mass, and behind this with one another, while the outer ascending lamella is fused with the mantle for the full extent of its upper edge.

Concrescence of the inner ascending lamellæ behind the visceral mass occurs in *Anomia ephippium*, but not in *Anomia laqueata* nor *Anomia patelliformis*. In *Aulacomya ovalis* and in *Septifer bilocularis* the outer ascending lamellæ are fused with the mantle, and the inner lamellæ with the visceral mass, but not with one

another behind the visceral mass. The upper edges of the ascending lamellæ are fused with mantle, visceral mass and with one another in *Modiola evansi* and *Modiolaria marmorata*, although no fusions of these edges with adjacent parts is to be observed in *Modiola barbata*, *Modiola polita* and *Modiolaria discors*. PURDIE, also (**78**, p. 8), has remarked that the upper edges of the ascending lamellæ of *Mytilus latus* are fused with the visceral mass and mantle, instead of being free from these parts as in *Mytilus edulis* and *Mytilus magellanicus*.

In *Meleagrina anomioides* there is fusion between the hinder parts of the inner ascending lamellæ, and between the hinder part of the outer lamella and the mantle, but in the front part of the gill the edges are free. In *Meleagrina vulgaris* and *Meleagrina margaritifera* there is no fusion with adjacent parts. In *Avicula tarentina* the posterior part of the outer lamella is fused with the mantle, but this is not the case in the other species of *Avicula* examined. (PELSENEER's description " branchies soudées au manteau " as a character of the family Aviculidæ (**72**, p. 190) is, therefore, open to objection.)

One feels no more confidence in attaching any degree of importance to the character of the interlamellar junctions in the Eleutherorhabda. Indeed, when one discovers that *Modiola polita* has no interlamellar junctions at all, that *Modiola barbata* has septa on certain filaments at intervals, while *Modiola evansi* has, in all filaments, a cross strand and low septum, one may suspect either that the generic identity of these species will on further investigation prove to be based on insufficient grounds, or else that the interlamellar junctions afford no test of affinity.

The main types of interlamellar junctions occurring in the second group of the Eleutherorhabda will be comprehended by reference to the chapter devoted to the Mytilacea (p. 195).

In the third group (Pectinacea) interlamellar junctions are confined to the principal filaments, all of which have interlamellar septa of some sort.

In considering the subdivision of the Synaptorhabda (including all the Lamellibranchia except the Protobranchia and Eleutherorhabda) it is convenient, and perhaps natural, to keep the Ostreidæ, Limidæ, and Pinnidæ together, and to separate them from the rest as a new sub-order, the Ostreacea.

As regards the Septibranchia some rearrangement seems to be called for. The first intimation of the anomalous condition of the branchial organs in these forms was made by DALL in 1886 (**10**), in a letter to ' Nature,' in which he expressed his inability to discover the gills of *Neæra* (*Cuspidaria*). In the same year he described the breathing organs of *Cuspidaria*, *Cetoconcha*, *Verticordia*, and *Lyonsiella* (**9**, pp. 280–281), and considered them as representing the successive stages of development of a typical ctenidium.* PELSENEER, in 1888 (**67**), confirmed the absence of

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* He modified this view later (**13**, p. 437), and considered the gill of *Lyonsiella* as of the ordinary type, but the lamellæ of *Cetoconcha* and *Poromya* as new structures succeeding the total obliteration of the normal ctenidium.

free gills in *Cuspidaria, Silenia,* and *Poromya,* and established the Order Septi-branchia to include these genera. He classified them as follows :—

1. Cloison branchiale présentant des orifices réunis en groupes :—

  A. Deux groupes d'orifices de chaque côté—*Poromya.*
  B. Trois groupes d'orifices de chaque côté—*Silenia.*

2. Cloison branchiale présentant quatre paires d'orifices séparés—*Cuspidaria.*

DALL (**11** and **13**, p. 449) objected that PELSENEER's branchial septum was not branchial at all, but was pallial in origin, or was a forward growth of the siphonal septum. In reply to this, PELSENEER (**70**) stoutly contested the position he had taken up, and in 1891 (**71**, p. 219) explained that the septum must be branchial in origin, since its tissue is supplied by the branchial nerve arising from the antero-lateral angle of the visceral ganglion, and not by the siphonal or pallial nerve ; and, noting the fact that the nerve runs at the outer edge of the septum, near the mantle (**71**, p. 243), concluded that the septum represented the inner demibranch, the outer being entirely absent. GROBBEN's researches (**28**) have led him also to the conclusion that at least the front part of the septum is branchial.

But DALL, in 1894 (**14**, p. 697), and 1895 (**15**, p. 537), still maintained that the septum was an ingrowth from the mantle and siphon ; and in 1897 he received the support of PLATE (**75**), who, speaking of *Cuspidaria obesa,* regarded the septum as pallial, since he found it to be innervated, not by the branchial branch of the visceral nerve, but by a nerve arising, together with the visceral commissure, from the cerebral ganglion.

As the result of an examination of the branchial structures of *Poromya, Cetoconcha,* and *Cuspidaria,* I do not consider that there is sufficient evidence to warrant the removal of the Septibranchia from the Eulamellibranchia as a separate Order, and in adopting a course which shall obviate this it is not entirely new ground which is being broken, for GROBBEN, in 1892 (**28**, p. 41), expressed himself dissatisfied with PELSENEER's step. The reduction of the branchial organs is certainly very remark-able, but there are greater differences between the three genera included in the Septibranchia than between a form like *Poromya malespinæ,* on the one hand, and *Verticordia* on the other. The conditions found in *Poromya, Cetoconcha,* and *Cuspi-daria* may be considered to have been evolved independently, although following the same general trend. The relations between these three forms and the Verticordiidæ being obvious, it is proposed, in the absence of much accurate information as to general anatomy, to place the three families, Poromyidæ, Cetoconchidæ, and Cuspi-dariidæ after the Verticordiidæ in a terminal sub-order (Poromyacea) of the Synaptorhabda.

The sub-order Poromyacea as thus constituted is an apparently natural assemblage of forms with reduced ctenidial structures. The constitution of the sub-order differs

somewhat from that of the super-family Poromyacea founded by DALL (**15**, p. 534). The Cetoconchidæ are now separated from the Poromyidæ, although included in that family by DALL, and *Lyonsiella* and *Euciroa* are restored to the Verticordiidæ, whereas in DALL's system the Lyonsiellidæ were included in the Anatinacea, while the Euciroidæ and Verticordiidæ were treated as two distinct families of the Poromyacea. The latter reinstatements are based on the discovery that the distinction drawn by DALL between the gill structures of *Lyonsiella*, *Verticordia*, and *Euciroa* originated in a misinterpretation of the finer details of the gills in the latter two genera. There is really nothing in these genera to suggest affinity with the Protobranchia, while on the other hand their gill structure will bear a close comparison with that of *Lyonsiella*. In none of the Poromyacea as above constituted is there any trace of plication or lamellæ, or of differentiation of principal filaments; and thus a sharp line can be drawn between this sub-order and the Anatinacea, which latter appears to contain the nearest allies of *Lyonsiella*, the least aberrant genus of the sub-order Poromyacea.

As regards the sub-orders Submytilacea, Tellinacea, Veneracea, Cardiacea, Myacea, and Pholadacea, the modern classification—that of PELSENEER* (**72**)—to which we have now become so accustomed, is allowed to stand. The attempt to place the genera and families concerned in other positions in the scheme of taxonomy would have involved a study of the detailed anatomy of other organs of the body besides the gills, and would have opened up an investigation of such magnitude as would have necessitated an indefinite postponement of the publication of the results at present obtained. Having pointed out the incongruities of certain associations of forms, it may well be left for the malacologists of the future to rectify the anomalies.

It is not claimed that the scheme of classification set forth in the following pages represents the genetic affinities of the forms included; but while disinclined to inflict upon a long-suffering world of zoologists a new classification of the Lamellibranchia in which I myself have no great confidence, I have, for reasons similar to those stated in a previous paper ("On the Efferent Branchial Blood-vessels of Teleostean Fishes," 'Proc. Zool. Soc.,' 1899), arrived at the conclusion that, for purposes of ready reference, a key to the species examined based on the particular feature under consideration is not only justifiable, but even useful.

* It is somewhat curious that DALL's classification (**15**) is so little adopted in European works on Malacology. Since it is the outcome of a life-long study of Mollusca on the part of one who, by virtue of his official position has at his disposal a wealth of material greatly to be envied, it is not to be lightly passed over. It may, perhaps, be objected that he accords too much value to the degree of fusion of the mantle edges—an obviously adaptive feature—and, since he subordinates the minuter structure of the gills to the coarser, and practically disregards such features as ciliated discs, the classification is less adapted for the present purpose than that of PELSENEER's. That the grosser structure of the gill, on which PAUL FISCHER placed so much reliance (Manuel de Conch.) is no criterion of affinity has been ably exposed by PELSENEER (**68**, p. 37, and **69**, p. 38) in his discussion of the three Erycinid genera *Kellya*, *Lasæa*, and *Montacuta*, and by MÉNÉGAUX (**62**, pp. 237–238) in his comparison of *Lucina* and *Diplodonta*.

The Lamellibranchia have ever been a most troublesome group to classify—witness the inadequacy of such features as the shell, hinge-teeth, ligament, pallial sinus, fusion of mantle edges, siphons, adductor muscles, otoliths, and nerve ganglia to constitute a reliable basis of taxonomy,*—and an arrangement of genera and families founded on the features of a single organ must always be accepted with great reserve. What it is well to aim at, however, is the formation of classificatory tables, admittedly artificial and based each on a single character, so that the taxonomist of the future may, by a process of correlation of these tables and a careful weighing of the respective values of the facts therein laid before him in a compact and readily assimilable form, arrive at the truth concerning the phylogenetic history of the Lamellibranchia. In spite of the fact that DALL's mistrust of the classification of the Lamellibranchia by their gills was occasioned by an erroneous interpretation of certain forms (*Vesicomya* and *Euciroa*), I am nevertheless in complete accord with him in his conclusion "that systems based on a single character, whether gills, siphons, muscles or what not, are bound to prove unsatisfactory as our knowledge of intermediate types advances; and that almost any group may have among its members some which retain archaicisms longer than the rest. In such cases the persistency of these characteristics should not oblige us to ignore relationships indicated by other features of the animal. Any permanent classification must necessarily be ecletic, considering all characters and distinguishing sufficiently between genetic and adaptive features." (**15**, p. 505.)

SCHEME OF CLASSIFICATION OF THE LAMELLIBRANCHIA BASED LARGELY UPON THE CHARACTERS OF THE GILLS.

(1.) Order PROTOBRANCHIA.—Arranged on the two sides of the gill axis are closely-set leaflets or platelets. (This is PELSENEER's Order Protobranchia adopted without alteration.)

<div align="center">Nuculidæ.   Solenomyidæ.</div>

(2). Order ELEUTHERORHABDA.—Arranged in series on the two sides of the gill axis are elongated filaments. Adjacent filaments are held in position by stiff cilia disposed in isolated patches (ciliated discs).

Sub-order DIMYACEA. (Gill lamellæ flat and homorhabdic. No ascending filaments) . . . . } Dimyidæ.

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* This matter has been ably discussed by PELSENEER (**69**, pp. 27–52), and by RICE (**83**, pp. 30–36).

Sub-order MYTILACEA. (Gill lamellæ flat and homo-
rhabdic. With ascending filaments) . . . .
$\left\{\begin{array}{l}\text{Anomiidæ (exclud-} \\ \quad\text{ing } \textit{Anomia acu-} \\ \quad\textit{leata}) \\ \text{Arcidæ.} \\ \text{Trigoniidæ.} \\ \text{Mytilidæ.} \\ \text{Melinidæ.} \\ \text{Amussiidæ.}\end{array}\right.$

Sub-order PECTINACEA. (Gill lamellæ plicate and
heterorhabdic. With ascending filaments) . . . .
$\left\{\begin{array}{l}\text{Spondylidæ.} \\ \text{Pectinidæ.} \\ \text{Aviculidæ.}\end{array}\right.$

(3.) Order SYNAPTORHABDA.—There are no ciliated discs. The interlamellar edges of adjacent filaments are connected by cellular tissue. These organic interfilamentar junctions are situated at uniform intervals up the filaments, and convert the linear interfilamentar spaces into series of fenestræ. (This order includes the orders Eulamellibranchia and Septibranchia of PELSENEER, together with the genera *Pinna, Lima* and *Ostrea*. As regards the sub-orders Submytilacea, Tellinacea, Veneacea, Cardicea, Myacea and Pholadacea the subdivision into families is exactly the same as that proposed by PELSENEER). Brief diagnoses of the sub-orders are not possible.

Sub-order OSTREACEA . . . .
$\left\{\begin{array}{l}\text{Pinnidæ.} \\ \text{Limidæ.} \\ \text{Ostreidæ.}\end{array}\right.$

Sub order SUBMYTILACEA . . . .
$\left\{\begin{array}{l}\text{Carditidæ.} \\ \text{Astartidæ.} \\ \text{Crassatellidæ.} \\ \text{Cyprinidæ.} \\ \text{Lucinidæ.} \\ \text{Erycinidæ.} \\ \text{Galeommidæ.} \\ \text{Cyrenidæ.} \\ \text{Rangiidæ.} \\ \text{Ætheriidæ.} \\ \text{Unionidæ.} \\ \text{Dreissensiidæ.}\end{array}\right.$

Sub-order TELLINACEA . . . .
$\left\{\begin{array}{l}\text{Tellinidæ.} \\ \text{Scrobiculariidæ.} \\ \text{Donacidæ.} \\ \text{Mesodesmatidæ.} \\ \text{Mactridæ.}\end{array}\right.$

Sub-order VENERACEA . . . . $\left\{\begin{array}{l}\text{Veneridæ.}\\ \text{Petricolidæ.}\\ \text{Glaucomyidæ.}\end{array}\right.$

Sub-order CARDIACEA . . . . $\left\{\begin{array}{l}\text{Cardiidæ.}\\ \text{Tridacnidæ.}\\ \text{Chamidæ.}\end{array}\right.$

Sub-order MYACEA . . . . $\left\{\begin{array}{l}\text{Psammobiidæ.}\\ \text{Myidæ.}\\ \text{Solenidæ.}\\ \text{Saxicavidæ.}\\ \text{Rocellariidæ.}\end{array}\right.$

Sub-order PHOLADACEA . . . . $\left\{\begin{array}{l}\text{Pholadidæ.}\\ \text{Teredinidæ}\end{array}\right.$

Sub-order ANATINACEA . . . . $\left\{\begin{array}{l}\text{Clavagellidæ.}\\ \text{Anatinidæ.}\\ \text{Pandoridæ.}\\ \text{Lyonsiidæ.}\end{array}\right.$

Sub-order POROMYACEA . . . . $\left\{\begin{array}{l}\text{Verticordiidæ.}\\ \text{Poromyidæ.}\\ \text{Cetoconchidæ.}\\ \text{Cuspidariidæ.}\end{array}\right.$

Order PROTOBRANCHIA.

SPECIES EXAMINED :—

Nuculidæ .
{
Nucula nucleus.
Nucula (Acila) fultoni.
Nuculana pella.
Nuculana pernula.
Nuculana (Adrana) elongata.
Yoldia glacialis.
Yoldia amygdalea.
Yoldia subæquilateralis.
Yoldia isonota.
Neilo australis.
Malletia angulata.
Malletia magellanica.
}

Solenomyidæ .   *Solenomya togata.*

PREVIOUS ACCOUNTS :—

Nucula margaritacea, DESHAYES, **17**, 1844–1848, Plate 117, fig. 7.

Nucula proxima, MITSUKURI, **63**, 1881, and **64**, 1882.

Nucula nucleus, MÉNÉGAUX, **60**, 1889, and **62**, 1890, p. 70.

Nucula nucleus, PELSENEER, **71**, 1891, p. 162, and figs. 1, 2 and 5.

Nucula delphinodonta, DREW, **22**, 1901, Plate 24, fig. 53.

Nuculana pella (Leda pella). PELSENEER, **71**, 1891, p. 171.

Nuculana sulculata (Leda sulculata), STEMPELL, **96**, 1898, pp. 395–398, and fig. 33.

Yoldia limatula, MITSUKURI, **63**, 1881, and **64**, 1882.

Yoldia limatula, PELSENEER, **71**, 1891, p. 174.

Yoldia limatula, KELLOGG, **42**, 1892, p. 414, and figs. 48, 78–82, and 92.

Yoldia limatula, DREW, **19**, 1897 ; **21**, 1899, pp. 11–16, and figs. 19 and 20 ; **20**, 1899, and **22**, 1901, fig. U, p. 360.

Malletia pallida, PELSENEER, **68**, 1888, p. 11, and Plate 1, fig. 8.

Malletia chilensis, STEMPELL, **96**, 1898, p. 397.

Solenomya mediterranea, PHILIPPI, **74**, 1835.

Solenomya mediterranea, DESHAYES, **17**, 1844–1848, pp. 124–126, Plate 19, fig. 6 ; Plate 19A, fig. 3 ; Plate 19B, fig. 1.

Solenomya, LEUCKART, **53**, 1848.

Solenomya togata, PELSENEER, **71**, 1891, p. 180, and Plates 9, 10 and 11.

Solenomya velum, KELLOGG, **42**, 1892, p. 418, and figs. 77 and 91.

Solenomya togata, STEMPELL, **97**, 1900, pp. 136–141, and figs. 20, 21 and 28.

Nuculidæ.

The ctenidium is made up of two rows of gill-plates or gill-leaflets, attached to a ctenidial axis, which slopes downwards and backwards, and which is concrescent with the body by means of a suspensory membrane, except in its posterior sixth, where it projects freely beneath the posterior adductor muscle. The leaflets stand out laterally form the axis towards the visceral and pallial sides respectively. Considering how large are the gills in most Lamellibranchia relatively to the size of the body, those of the Nuculidæ are small, and their diminutive size is correlated with an enlargement of the labial palps, the outer of which is provided at its posterior edge with curious grooved appendages, a short upper and a remarkably long lower one.

In *Nucula* the leaflets vary in shape as well as in size at different positions along the axis, and in *Nucula nucleus* the leaflets of the middle part of the inner demibranch depend as much as is shown in fig. 5A. In the axis are two blood-vessels, the upper one in the anterior part of the gill being really in the suspensory membrane. The lower one is separated from the ventral edge of the gill by a complex chitin skeleton, the characters of which, in *Nucula proxima*, have been fully worked out by MITSUKURI (**63**, figs. 5 and 7).

Most of the epithelium is quite thin and destitute of cilia, as was shown by DREW (**22**, p. 361) to be the case in *Nucula delphinodonta*, and not uniformly ciliated as was assumed to be the case by MITSUKURI (**63**, p. 600) in *Nucula proxima*. The edges of the leaflets marked *cd*, *cc* in fig. 5A differ from those marked *ef*, *dg*, in having a more prismatic epithelium (fig. 5B) bearing cilia in three rows—one frontal, and one lateral on each side—and supported by a thickening of the layer of chitin which lines the whole of the lacunar tissue of the interior of the leaflet. In the terminology adopted for the filaments of the higher forms, this thickened edge would be the " filament proper," and the rest of the leaflet a " subfilamentar extension." The outer edges of the leaflets (*fe* and *gd* in fig. 5A) are also thickened, and the epithelial cells are slightly larger than those in the middle of the leaflet, and are provided with cilia. In certain of the leaflets this edge is very much distended, an irregularity which is probably due to unequal distribution of the blood in the different leaflets when the animal was thrown into the killing fluid.

Nucula (Acila) fultoni differs from the former species in that the leaflets stand out more nearly in the horizontal plane, and the suspensory membrane of the axis is thicker. The thickened chitin bands, also, are more remote from the edge of the leaflet (fig. 5C).

The specimens of *Nuculana* were too badly preserved to enable one to make out much of their finer structure, but the gills appeared to agree in most respects with those of *Nucula*. The leaflets, as has been pointed out by PELSENEER in *Nuculana pella* (**71**, p. 171), do not hang down. Two sections, through the middle of the length of the gill and at a distance of one-sixth of its length from the posterior end,
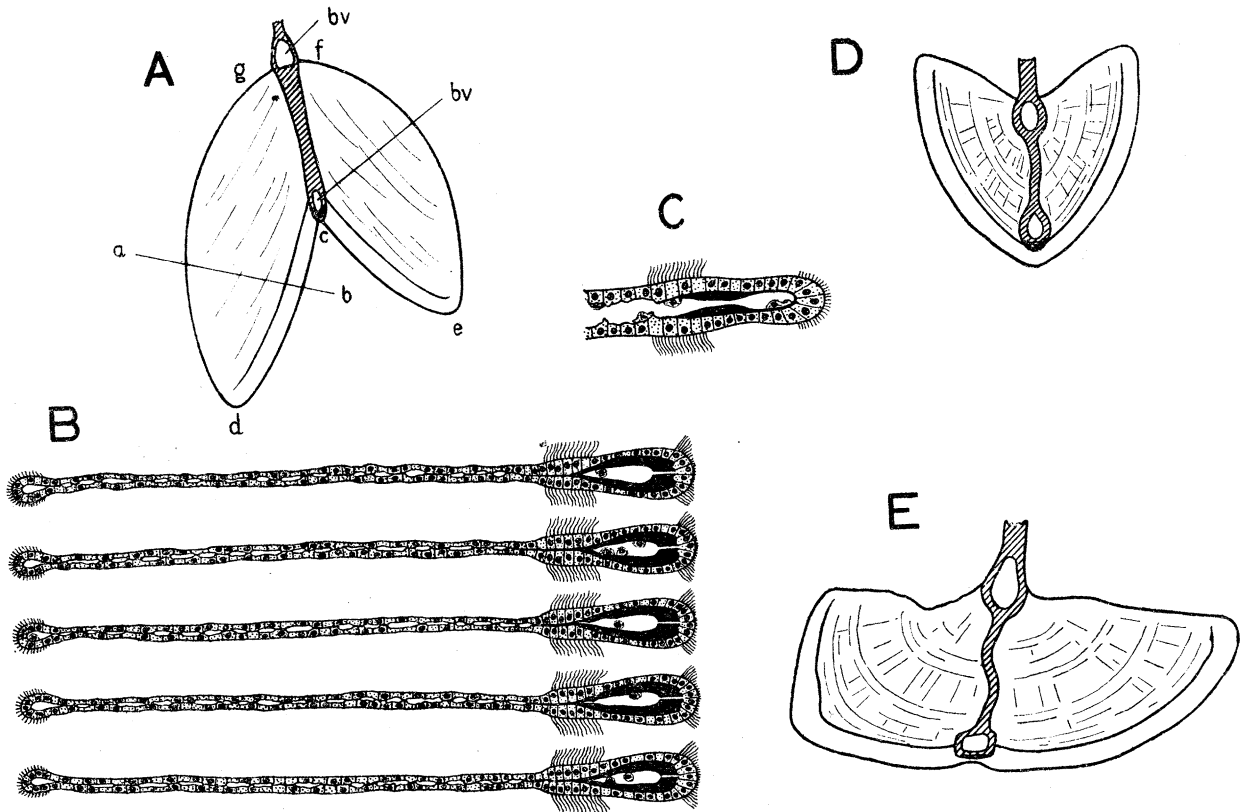
FIG. 5.—A, *Nucula nucleus*. Section of the gill taken through the middle of its length. *d*, extremity of inner leaflet; *e*, extremity of outer leaflet; *bv*, blood-vessels in the gill axis. B, section of five leaflets of the inner demibranch taken in the direction *ab* in fig. A. C, *Nucula (Acila) fultoni*. Portion of a section similar to the right-hand end of one of the leaflets of fig. B. D, *Nuculana pernula*. Section of the gill taken transversely to the axis at a distance of one-sixth of the length from the posterior end. E, similar section taken through the middle of the gill.

are shown in figs. 5E and 5D. In the long-bodied *Nuculana (Adrana) elongata* the gills are relatively smaller than in the other species. The leaflets are stunted, and the axis stout.

Concerning the genus *Yoldia* but little need be said, since the gills of the four species examined agree closely with those of *Yoldia limatula*, our knowledge of which, thanks to MITSUKURI, PELSENEER, KELLOGG, and DREW, is very complete. The part of the gill axis between the afferent and efferent blood vessels is in this species thin; and a horizontal section of the gill shows that the leaflets on the visceral and pallial

sides of it are disposed alternately. The muscle fibres which radiate in the leaflet from the region of the upper vessel are a prominent feature, and are evidently related to the extraordinary changes in superficial extent of which the leaflets are capable (KELLOGG and DREW). There are also longitudinal muscles in the axis, lying below the upper and lower blood-vessels respectively. The bands of thickened chitin in the leaflets do not extend more than half-way up the edges in *Yoldia limatula* and *Yoldia glacialis*. In *Yoldia subæquilateralis* they extend considerably less than half-way up,
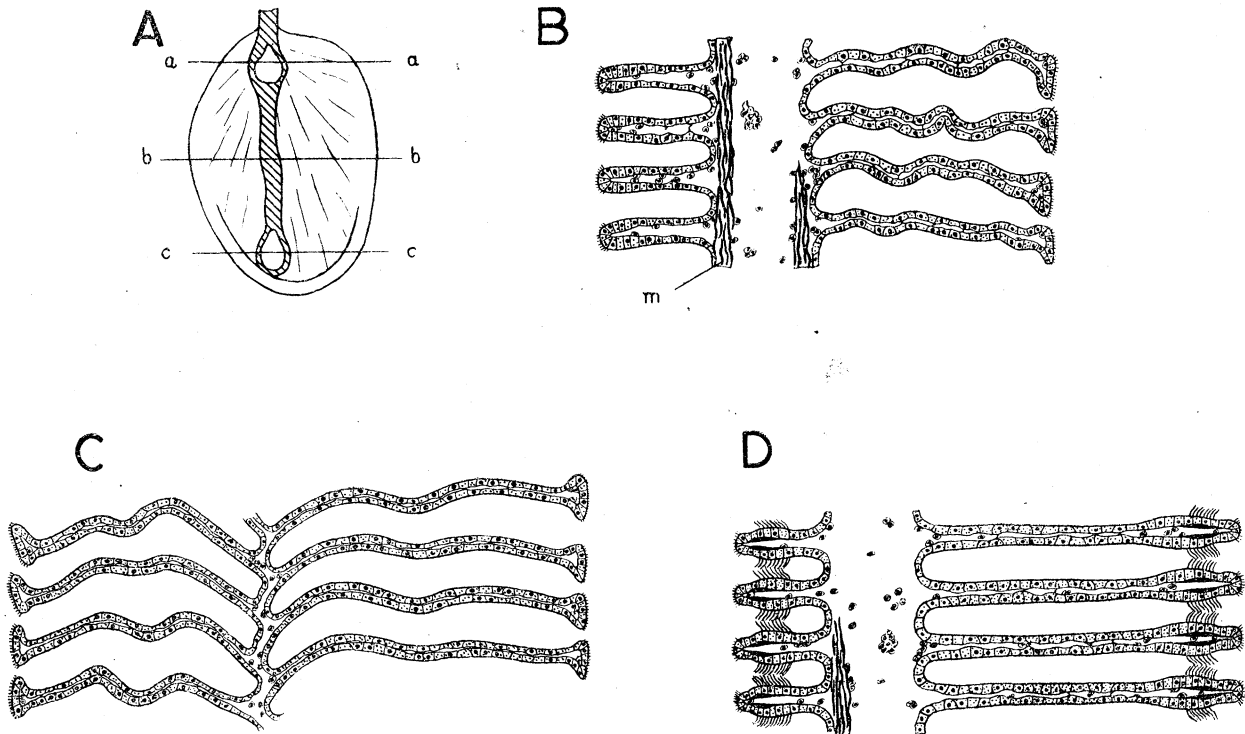
FIG. 6.—A, *Yoldia subæquilateralis*. Section through the middle of the gill. B, horizontal section through four pairs of leaflets, taken at the level *a* in fig. A ; *m*, muscle lying below and at the sides of the upper blood-vessel. C and D, similar sections taken at levels *b* and *c*.

whereas in the leaflets of *Yoldia isonota* and *Yoldia amygdaloides* they support about three-fourths of the edge.

MITSUKURI, KELLOGG, and DREW are agreed that the leaflets of *Yoldia limatula* have pointed upper extremities. In *Yoldia glacialis* and *Yoldia amygdaloides*, however, I find the upper edges to be evenly rounded, while in *Yoldia subæqui-lateralis* the section through the middle of the length of the gill is of elliptical contour (fig. 6A). Longitudinal muscle fibres are abundant around and below both upper and lower vessels. It will be noticed that in the axis the chitinous lining of each leaflet is continuous with that of the next leaflet of the same side, and that the thickened bands of chitin in the lower edges of the leaflet do not rise high enough to be included in section C, which is taken midway between B and D.

The cilia, as in *Nucula*, consist of a frontal series and a paired lateral series. KELLOGG is probably in error in representing two lateral series on each side of the thickened margin of the leaflet (**42**, fig. 79). These lateral cilia, also, judging from their relation to the thickened chitin bands, are the straining cilia of the higher Lamellibranchia, and not the interlocking cilia, as KELLOGG states (p. 415). The true interlocking cilia of Lamellibranchia always occur in patches—ciliated discs— and not in continuous series. The frontal cilia are continued along the edges of the leaflets in the higher levels, but the lateral cilia are conterminous with the thickened bands of chitin.

Of the gill of *Neilo australis* no sections were cut, since the tissues were in a poor state of preservation. So far as could be made out by examination with a dissecting lens, the gills are like those of the other Nuculidæ examined. The palps in this species are relatively small, but the appendage is disproportionately large.

The two species of *Malletia* examined (*Malletia angulata* and *Malletia magellanica*) agree tolerably closely with one another, and with *Yoldia*. The outline of a
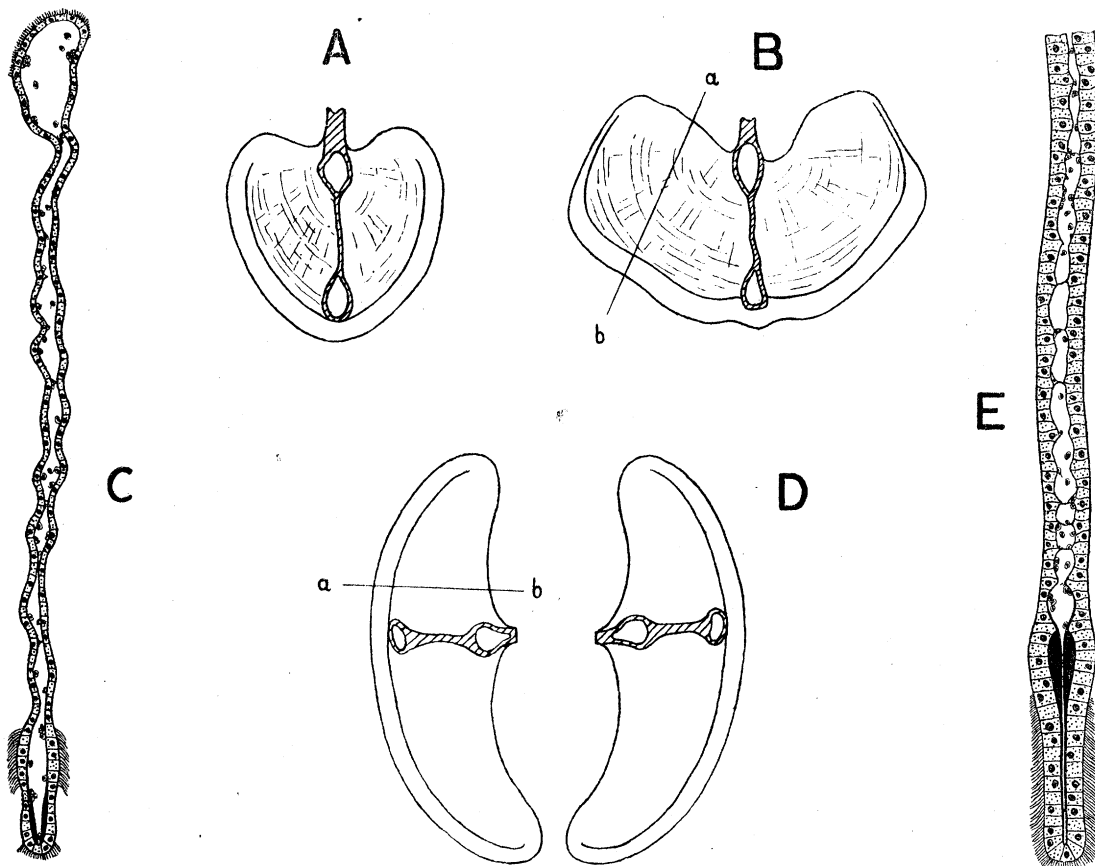
FIG. 7.—A, *Malletia magellanica*. Section of the gill taken near the posterior end. B, section taken through the middle of the gill. C, Single leaflet cut in the direction *ab* in fig. B. D, *Solenomya togata*. Section of both gills taken about the middle of their length. E, part of a section of one of the upper leaflets cut in the direction *ab* in fig. D.

section across the hinder part of the gill is nearly elliptical, with a truncated upper edge (fig. 7A), but in the anterior part the leaflets are relatively broader (fig. 7B). A section of a leaflet (fig. 7C) taken in the direction *ab* in fig. 7B shows no important departure from the structure already described in the case of *Yoldia*.

Solenomyidæ.

As is well known, the gill of *Solenomya* differs from that of the Nuculidæ in having the leaflets of the outer demibranch upturned (fig. 7D). It is larger in proportion to the size of the body, and is a conspicuous feature in a side dissection. The leaflets are very numerous and thickly set. The curvatures of the pallial surfaces of the upper and lower demibranchs are continuous, and the line of separation between them is not always easy to distinguish. In correlation, apparently, with the large size of the gill the labial palps are extremely reduced, the appendage normally projecting from the posterior edge of the outer palp alone being represented.

The thickened margin of the leaflets of *Solenomya* is extensive, and reaches as far as the extreme upper end of the leaflets of the upper demibranch, and as far as the ventro-internal portion of the edge of the lower leaflets. This margin is fairly wide, and the thickened bands of the chitinous lining (fig. 7E) are farther removed from the actual edge than is the case in the Nuculidæ.

The interior of the leaflet is lacunar; muscular tissue is scarce, and the epithelium, even in parts remote from the thickened edge, is of a columnar nature. Cilia are confined to the thickened edge, and appear to form a continuous investment of it, not differentiated into frontal and lateral tracts. The material available is not sufficiently well preserved to allow of a definite statement upon this point, but it is worthy of remark that no gap between the frontal and lateral cilia is shown in the figures given by PELSENEER (**71**, fig. 28), KELLOGG (**42**, fig. 77), and STEMPELL (**97**, fig. 20). The cilia extend as far as the level of the outer edge of the thickened chitin bands, and the shortest are those on the frontal surface. PELSENEER shows large latero-frontal cilia, but this is possibly an error.

Order ELEUTHERORHABDA.

Sub-order DIMYACEA.

SPECIES EXAMINED :—

> *Dimya argentea* and *Anomia aculeata.*

PREVIOUS ACCOUNTS :—

> *Dimya argentea,* DALL, **8**, 1883.
> *Dimya argentea,* DALL, **9**, 1886, p. 230.
> *Dimya argentea,* DALL, **13**, 1889, p. 434.
> *Dimya argentea,* DALL, **15**, 1895, pp. 504 and 526.

In *Dimya argentea*—a rare form, of which a specimen was kindly supplied by Professor DALL—each gill consists of two demibranchs, the filaments of which have no ascending portions. The lamellæ are flat and homorhabdic. Each filament has but two ciliated discs—one on the anterior and one on the posterior surface of its lower extremity. The transverse sections of the filaments show that the thickenings of the chitinous lining of the filament are situated rather nearer the frontal edge of the filament than the other. An intrafilamentar septum is visible but rarely. The epithelium on the frontal edge of the filament is seen to be more prismatic than that on the other (morphologically interlamellar) edge, but the material is not sufficiently well preserved to enable one to judge of the arrangement of the frontal and lateral cilia. I fail to recognise the " central more solid rod with a tube on each side of it," described by DALL (**9**, p. 230).

DALL appears to have overlooked the inner demibranch entirely, for he states (**13**, p. 434):—" In *Dimya* we have . . . . a stem with only a single series of filaments," and (**15**, p. 526) in *Dimya* the gills are " filibranchiate, the stem distally attached to the mantle; the inner direct filaments wanting, the outer filaments not reflected."

In *Anomia aculeata* the general disposition of the gill filaments is exactly the same as in *Dimya*, but since the material available was in a better state of preservation, and more abundant—fifteen specimens being obtained from Plymouth—the relation of the parts and their minute structure could be studied more accurately. The filaments are united in longitudinal series by ciliated discs situated at their
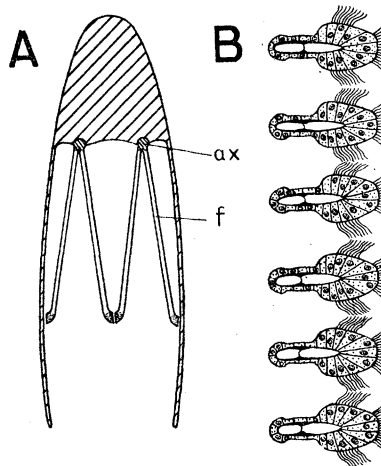
FIG. 8.—A, *Anomia aculeata*. Section of the body at right-angles to the gill axes. *ax*, gill axis; *f*, gil filament. B, series of six filaments in transverse section.

lower extremities. Besides this, however, there are patches of interlocking cilia on the ab-frontal margins of the lower extremities, by means of which the lower edges of the two inner demibranchs are held in juxtaposition, while the edges of the outer demibranchs are affixed to the mantle (fig. 8A). In the posterior third of the gill

the axis is free ; the filaments here are shorter, and have free, rounded ends, without ciliated discs.

The frontal and lateral cilia are disposed as in the great majority of Lamellibranchia (fig. 8B), and the marginal cilia of the frontal series are longer than the central ones. The epithelial cells that bear these cilia are very large. An intra-filamentar septum is present, and the chitinous lining of the filament is only slightly thickened at the sides.

Particular interest attaches to these two forms in that they are concrete examples of the hypothetical type of gill which PELSENEER conceived to be the annectant link between the Protobranchiate and the Filibranchiate types (**69**, p. 43, and p. 47, fig. 4c).

Sub-order MYTILACEA.

SPECIES EXAMINED :—

Anomiidæ . . { *Anomia ephippium.*
(excluding *Anomia patelliformis.*
Anomia *Anomia laqueata.*
aculeata). *Placuna placenta.*

Arcidæ . . . { *Arca americana.*
Arca (Andara) granosa.
Arca tetragona.
Arca zebra.
Arca (Scaphula) ? n.sp.
Pectunculus* glycimeris.
Limopsis indica.

Trigoniidæ . . *Trigonia lamarcki.*

Mytilidæ . . . { *Mytilus edulis.*
Mytilus (Aulacomya) ovalis.
Modiola† polita.
Modiola evansi.
Modiola barbata.
Modiolaria discors.
Modiolaria marmorata.
Lithodomus dactylus.
Lithodomus teres.
Lithodomus stramineus.
Lithodomus malaccanus.
Botula cinnamonia.
Septifer bilocularis.

* *Pectunculus* = *Glycimeris*, Da Costa *nec* Lamarck.
† *Modiola* = *Volsella*, Scopoli.

Melinidæ . . . $\left\{\begin{array}{l} \textit{Melina perna.} \\ \textit{Melina linguæformis.} \\ \textit{Melina serratula.} \\ \textit{Malleus albus.} \end{array}\right.$

Amussiidæ . . $\left\{\begin{array}{l} \textit{Amussium dalli.} \\ \textit{Amussium lucidum.} \\ \textit{Amussium meridionale.} \\ \textit{Plicatula australis.} \end{array}\right.$

PREVIOUS ACCOUNTS :—

Anomia ephippium, LACAZE DUTHIERS, **46**, 1854.

Anomia ephippium, WOODWARD, **109**, 1855.

Anomia glabra, JACKSON, **38**, 1890, p. 358.

Anomia ephippium, PELSENEER, **71**, 1891, pp. 184 and 242, and fig. 32 ; and **72**, 1892, p. 177, fig. 98.

Anomia ephippium, RICE, **83**, 1897.

Arca noae, DESHAYES, **17**, 1844–48, Plate 121.

Arca, PECK, **66**, 1877.

Arca noë, BONNET, **5**, 1877.

Arca glacialis, HAREN-NORMAN, **31**, 1881.

Arca ectocomata, DALL, **13**, 1889, p. 434.

Arca barbata, PELSENEER, **71**, 1891, p. 188 and fig. 36.

Arca (Argina) pexata, KELLOGG, **42**, 1892, p. 419 and figs. 50 and 66.

Arca transversa, RICE, **83**, 1897.

Pectunculus glycimeris, MÉNÉGAUX, **62**, 1890, p. 87.

Pectunculus glycimeris, PELSENEER, **71**, 1891, p. 189.

Limopsis pelagica, PELSENEER, **68**, 1888, p. 12 and Plate 2, figs. 1 and 2.

Trigonia, HUXLEY, **35**, 1849.

Trigonia margaritacea, SELENKA, **92**, 1868, p. 68.

Trigonia pectinata, MÉNÉGAUX, **62**, 1890, p. 66.

Trigonia pectinata, PELSENEER, **71**, 1891, p. 193, and figs. 43 and 44.

Mytilus edulis, LACAZE DUTHIERS, **47**, 1856.

Mytilus edulis, POSNER, **76**, 1875, Plate 32, figs. 22 and 27.

Mytilus, PECK, **66**, 1877.

Mytilus edulis, BONNET, **5**, 1877, Plate 15, fig. 14.

Mytilus edulis, SABATIER, **86**, 1877.

Mytilus edulis, SLUITER, **95**, 1878, Plate 7, fig. 1.

Mytilus edulis, *M. latus* and *M. magellanicus*, PURDIE, **78**, 1887.

Mytilus edulis, PELSENEER, **71**, 1891, p. 197.

Mytilus edulis, KELLOGG, **42**, 1892, p. 424 and fig. 49.

Mytilus edulis, JANSSENS, **39**, 1893, figs. 77–82.

Mytilus edulis, RICE, **83**, 1897, p. 48 and fig. 3.

Modiola plicatula, RICE, **83**, 1897, Plate 3, fig. 1.

Modiolaria discors, HAREN-NORMAN, **31**, 1881, fig. 40.

Modiolaria marmorata, PELSENEER, **71**, 1891, p. 196 and fig. 45.

Lithodomus (*Mytilus lithophagus*), DESHAYES, **17**, 1844–48, Plate 130, fig. 7.

Lithodomus dactylus, MÉNÉGAUX, **62**, 1890, p. 63.

Vulsella and *Crenatula*, VAILLANT, **100**, 1868, p. 293.

Vulsella lingulata, MÉNÉGAUX, **62**, 1890, p. 47.

Amussium dalli, DALL, **13**, 1889, p. 434.

Amussium lucidum and *A. meridionale*, PELSENEER, **68**, 1888, p. 13.

Anomiidæ (excluding *Anomia aculeata*).

In *Anomia ephippium* the upper ends of the ascending filaments are organically united in longitudinal series. The upper edge of the ascending lamella of the outer demibranch is traversed by a longitudinal blood-vessel; it is free from the mantle, and has a dependent membranous flap or velum, the depth of which is about one-fifth of the height of the lamella (fig. 9A). This membrane is evidently the " fifth lamella of the gill," mentioned by LACAZE DUTHIERS (**46**, p. 15). The upper edges of the ascending lamellæ of the inner demibranchs are united across the median plane of the body, and have a longitudinal vessel.

The ascending filaments are connected with the descending filaments only by a small septum which extends up about one-tenth of the height of the demibranch. One might thus almost say that there are no interlamellar junctions. A single row of ciliated discs occurs along the ventral edge of the demibranch, but nowhere else (fig. 9A). These ciliated discs were overlooked by PELSENEER (**71**, p. 184). The frontal and lateral cilia of the filaments are normal (fig. 9B), an intrafilamentar septum is present, and the thickenings of the chitinous lining of the filament are nearer the interlamellar than the frontal edge of the filaments.

Anomia patelliformis and *Anomia laqueata*, like *Anomia ephippium*, have a row of large ciliated discs along the ventral edge of the demibranch, but they differ from this species in having other ciliated discs distributed along the faces of the filaments (fig. 9C), and in having the upper ends of the ascending filaments held in juxtaposition by ciliated discs. The upper edges of the ascending lamellæ are free from adjacent parts. There is no velum to the outer lamella of the outer demibranch, but in *Anomia laqueata* there is a somewhat similar membrane depending from the axis between the two descending lamellæ. In *Anomia patelliformis* the smaller ciliated discs are situated at three or four levels in each lamella, in *Anomia laqueata* there are but two or three rows (fig. 9C). The transverse sections of the filaments resemble those of *Anomia ephippium*, unless, of course, the section passes through a ciliated

disc. The intrafilamentar septum, however, is seen but rarely in the sections of *Anomia laqueata.*

The fact that in the genus *Anomia* there are three distinct types of gill structure exemplified by *Anomia aculeata, A. laqueata* and *A. ephippium,* suggests that some division into sub-genera is demanded. It was foreign to the purpose of the present
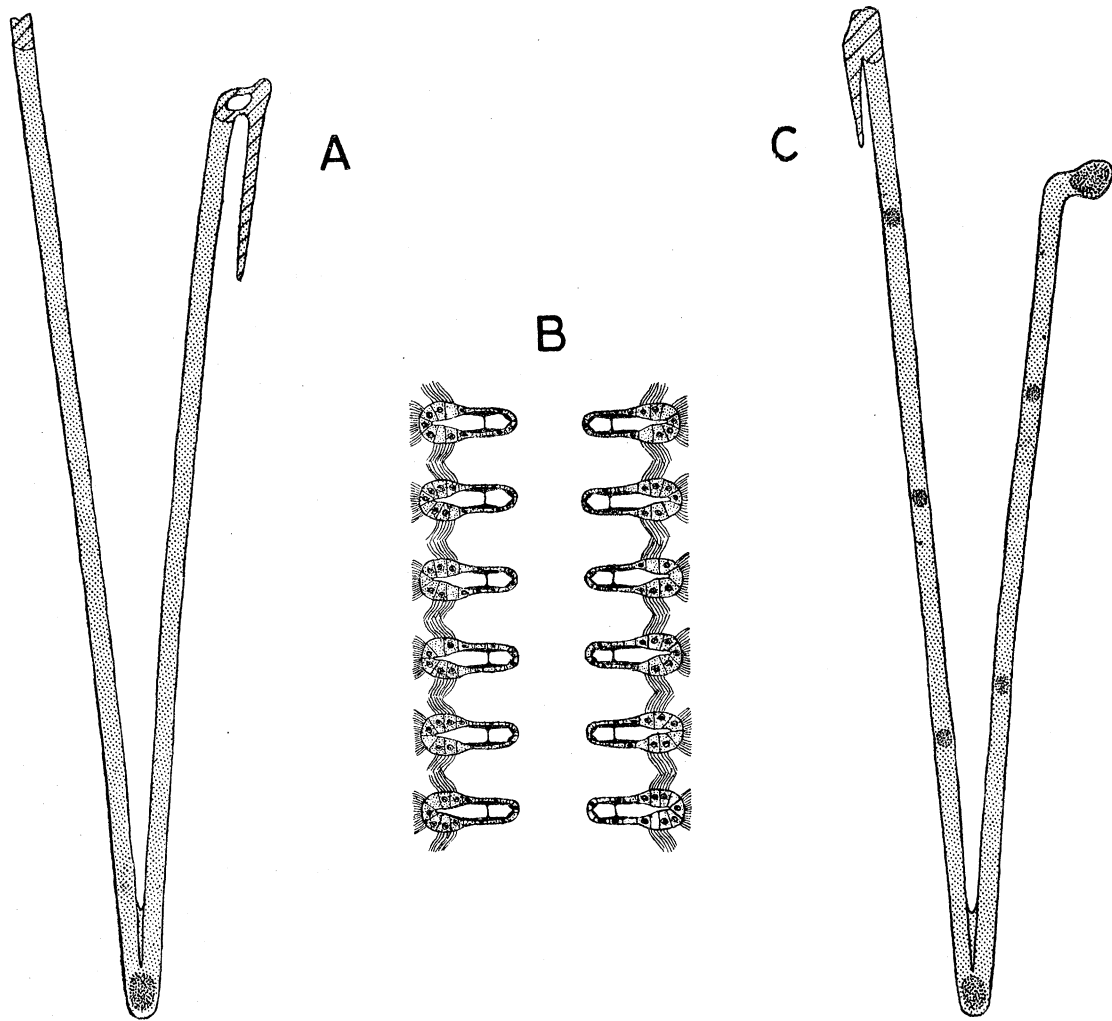
Fig. 9.—A, *Anomia ephippium.* Single filament of the outer demibranch. B, section of portion of the demibranch, about half-way up. C, *Anomia laqueata.* Single filament.

inquiry to make an exhaustive study of the general anatomy of the various species, and the material available was not adequate for the purpose ; but it may be pointed out that there are other features besides those of the gills, which suggest that a revision of the genus is desirable. The muscle impressions in the imperforate valve of the shell, for instance, are three in number in *Anomia ephippium,* whereas in *Anomia patelliformis* there is a single impression incompletely divided into two.

Except in the fact that the two inner lamellæ of the inner demibranchs are not united at their upper edges, the gills of *Placuna placenta* agree exactly, both in general and minute structure, with those of *Anomia ephippium*.

Arcidæ.

In all the species of Arcidæ examined, the upper ends of the ascending filaments are in ciliary connection, but it would appear that the upper ends are fused in longitudinal series in *Arca barbata* (PELSENEER, **71**, p. 188, footnote) and *Arca glacialis* (HAREN-NORMAN, **31**, Pl. 2, figs. 22 and 23). The upper edges of the ascending lamellæ are free from adjacent parts. Interlamellar extensions of the descending filaments are well developed in *Arca americana* (fig. 10A) and *Arca granosa*, similar to those described by KELLOGG for *Arca pexata* (**42**, p. 419 and fig. 50);
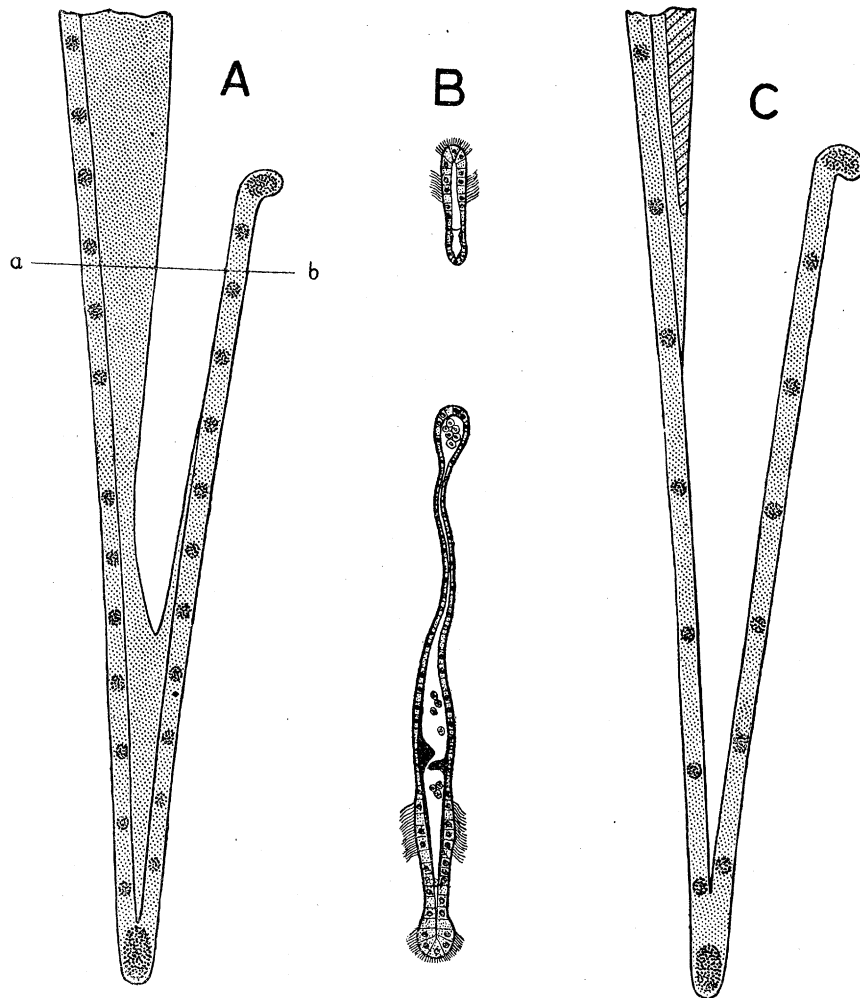
FIG. 10.—A, *Arca americana*. Single filament. B, section of same at level *ab*; the upper section is that of the ascending filament. C, *Arca tetragona*. Single filament.

and interlamellar septa extend to varying heights in the different filaments, the average height being one-third that of the demibranch. In *Arca tetragona* (fig. 10C) and *Arca zebra* there are narrow interlamellar extensions at the upper ends of the descending filaments only, and these are fused together and present a smooth surface to the interlamellar cavity. There are no interlamellar septa at all. In an apparently new species of *Arca (Scaphula)* obtained from Siam there are no interlamellar extensions, but interlamellar septa of fairly uniform height rise one-fourth or one-fifth of the way up the demibranch. There are about thirteen horizontal rows of ciliated discs in the lamellæ of *Arca americana* and *Arca granosa*, three to seven in *Arca tetragona*, and about twenty in *Arca zebra*. In *Arca (Scaphula) sp.* there is only one row to the descending lamella, about one-third of the way up, but the ascending lamella may have one, two or three rows.

The lateral cilia are situated at some distance from the frontal edge, and in *Arca granosa* the frontal cilia extend round so as to cover part of the anterior and posterior faces of the filaments (fig. 3E, p. 164). Some cilia occur on the interlamellar side of the filament. The thickest part of the chitin lies close to the interlamellar edge of the filament (fig. 3E); in *Arca americana* it is very pronounced, especially in the higher parts of the filaments (fig. 10B).

DALL (**13**, p. 435) speaks of *Arca ectocomata* as having gills with descending filaments only, and as differing in this respect from *Arca noæ*. This may be so, but it is just possible, judging by the fact that he speaks of the filaments as much " contorted in all directions, twisted and curled," that this is a species without interlamellar septa, like *Arca tetragona*, for instance, and that the ascending parts of the filaments have fallen down, as in badly preserved specimens of the latter species they are very liable to do.

The isolated filaments of *Pectunculus glycimeris* bear a close resemblance to those of *Arca tetragona* (fig. 10C), except that the large ciliated disc at the lower angle is wanting. There are fifteen or sixteen ciliated discs on each side of the ascending filament, and the same number on the descending. There are no interlamellar septa; the upper ends of the ascending filaments are in ciliary connection only, and the upper edges of the ascending lamellæ are not united with adjacent parts of the body. The filaments are broad and thin (fig. 11A); an intrafilamentar septum is present, and irregular strands of chitin may run across the filamentar cavity. There is a paired thickening of the chitin at the interlamellar edge of the filament, and another thickening in the vicinity of the intrafilamentar septum. The ciliated discs are equidistant from the frontal and interlamellar edges of the filament, and are not raised above the general surface of the side of the filament. The arrangement of the frontal and lateral cilia is shown in fig. 11A.

In *Limopsis indica* ciliated discs connect the filaments at the ventral edge of the demibranch, and another series holds the upper ends of the ascending filaments in juxtaposition. The only other ciliated discs are a single row occurring half way up

each of the lamellæ. There are no interlamellar junctions. The features of the chitin as seen in transverse sections are similar to those of *Pectunculus*.

Trigoniidæ.

The upper ends of the ascending filaments oɪ *Trigonia lamarcki* are fused in longitudinal series, but the upper edges of the ascending lamellæ are not united with adjacent parts. The interlamellar junctions are similar in all the filaments, and
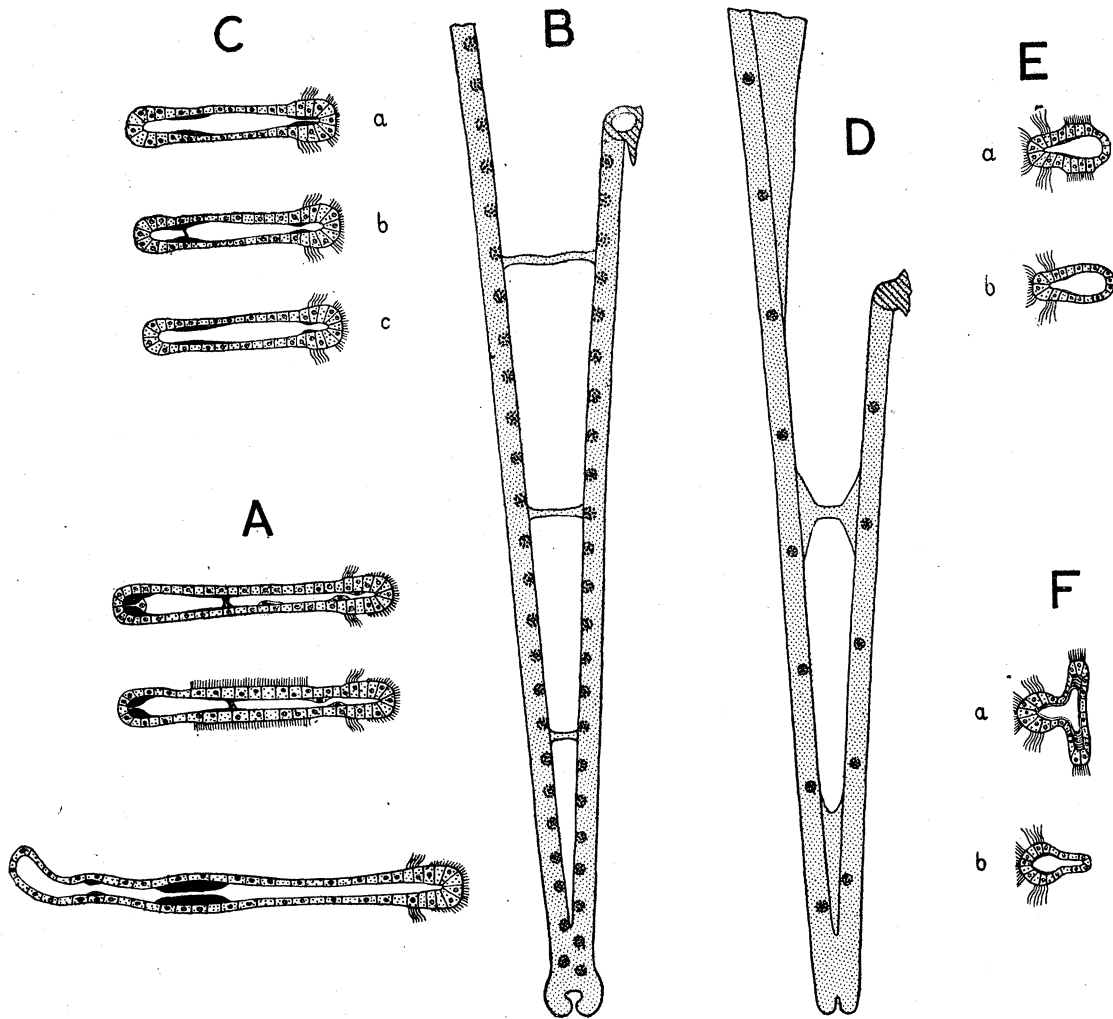
Fɪɢ. 11.—*Pectunculus glycimeris.* The upper section is taken about half-way up the filament; the second, taken at a similar level, passes through a ciliated disc; the third section is from the upper part of a descending filament. B, *Mytilus edulis.* Single filament. (The full complement of ciliated discs is not shown.) C, sections of a descending filament taken at high (*a*), middle (*b*), and low (*c*) levels. D, *Modiola evansi.* Single filament of the outer demibranch. E, sections taken about half-way up the filament; *a*, through a ciliated disc; *b*, not through a ciliated disc. F, similar sections, taken rather high up, of *Modiola polita.*

consist of a narrow septum extending up the lower fifth of the filaments, and just above this a short horizontal bar. The bar is narrow in the middle, but enlarged at its junction with the ascending and descending filaments. The interval between the bar and the septum is thus elliptical in shape. Except in the lower position of the bar, the features of the interlamellar junctions are similar to those of *Modiola evansi*, shown in fig. 11D. The ciliated discs project slightly from the faces of the filaments. There are about ten horizontal rows of them in each lamella of the inner demibranch, but in the outer demibranch, which is not so deep as the inner, there are only seven. The ciliated discs are quite close to the interlamellar edge of the filament, and not as shown in PELSENEER's figure (**71**, fig. 43) of *Trigonia pectinata*. The frontal and lateral cilia are normal. There is no intrafilamentar septum, and the thickest part of the chitin is near the interlamellar edge of the filament.

Mytilidæ.

The gill structure of *Mytilus edulis* has been so repeatedly and thoroughly described by previous writers that it may here be dealt with very briefly. The upper ends of the ascending filaments are in organic continuity, and are traversed by a longitudinal blood-vessel. The upper edges of the ascending lamellæ are free from adjacent parts. The ventral angle of each complete filament (*i.e.*, ascending and descending parts together) has a deep notch (fig. 11B), which is not present in any of the families of the Mytilacea just treated of. The interlamellar junctions have the form of bars, and are usually four in number for each filament, sometimes three. They are uniformly spaced (fig. 11B), as is shown in KELLOGG's figure (**42**, fig. 49), and not crowded in one place as figured by PECK (**66**, fig. 10). They occur at the same levels in adjacent filaments, or very nearly so; occasionally, however, the rows interlamellar junctions in the different filaments are not parallel with the ventral edge of the demibranch, but rather oblique.

The ciliated discs project slightly from the anterior and posterior faces of the filament, and are situated close to the interlamellar edge, not in the middle of the face as shown by PECK. There are about thirty on each face of the ascending filament, and slightly more on the descending filament. The frontal and lateral cilia are normal. The intrafilamentar septum appears not to be at all constant. When present, it is situated rather near the interlamellar edge of the filament (fig. 11C*b*). The chitin is thickened beneath the lateral cilia (less so in sections taken at low levels of the demibranch), and also at the interlamellar edge of the filament.

Mytilus (Aulacomya) ovalis resembles *Mytilus edulis*, except in the following respects :—The upper edge of the ascending lamella of the outer demibranch is fused with the mantle ; that of the inner demibranch is fused with the visceral mass in front, while the hinder part, behind the visceral mass, is free, and not fused with its fellow of the opposite side. A similar condition has been recorded by PURDIE (**78**, p. 8) in

the case of *Mytilus latus*. There are about fifteen horizontal rows of ciliated discs in each lamella. The interlamellar bars are wanting.

In the three species of *Modiola* examined the upper ends of the ascending filaments are in serial organic connection. The upper edges of the ascending lamellæ are free from adjacent parts in *Modiola polita* and *Modiola barbata*, but in a new species of *Modiola* collected by Mr. R. EVANS in South Siam, which Mr. E. A. SMITH proposes to describe under the name *Modiola evansi*, the upper edges of the ascending lamellæ of the outer demibranch are coherent with the mantle, and those of the inner with the visceral mass and with one another. Interlamellar junctions are wanting in *Modiola polita*. In *Modiola evansi* there is a low septum, extending not more than one-fourth of the height of the ascending filament, and a cross bar situated at about half or two-thirds of the height (fig. 11D). The upper part of the descending filament has an interlamellar extension. In *Modiola barbata* most of the filaments have no interlamellar junctions, but each fourth to eighth filament has an inter-lamellar septum, extending more than half way up the filament. A similar condition has been shown by RICE to occur in *Modiola plicatula* (**83**, Plate 3, fig. 1). It also occurs in *Lithodomus* (fig. 13).

The ciliated discs are tall, projecting considerably from the faces of the filament, in *Modiola polita* (fig. 11Fa). In the other two species they are lower, and the filaments are in consequence closer together. In *Modiola polita* the ciliated discs are arranged usually in 2, 3, or 4 horizontal rows in each lamella. In *Modiola evansi* there are 5–7 rows, and in *Modiola barbata* about 30 rows. An intrafilamentar septum is common in the lower parts of the filaments of *Modiola polita*, but not in the upper. It is wanting altogether in the other two species. In *Modiola polita* the chitin thickenings are towards the frontal surface in sections taken through the upper parts of the demibranch (fig. 11Fb), but in the lower parts they are towards the inter-lamellar edge. In the intermediate regions the chitinous lining is of uniform thickness. In *Modiola evansi* the thickenings are towards the frontal edge in upper parts, and in the middle of the faces of the filament in the lower parts. In *Modiola barbata* two paired thickenings are present in most sections, one pair near the frontal edge, and the other near the interlamellar edge.

In *Modiolaria discors* the upper ends of the ascending filaments are in organic continuity, and the upper edges of the ascending lamellæ are free from adjacent parts; but in *Modiolaria marmorata* the upper edges of the outer ascending lamellæ are fused with the mantle, and those of the inner are united with the visceral mass in front and with one another behind. In both species the interlamellar junctions are exactly as in *Mytilus edulis*—three or four cross bars at similar levels in adjacent filaments. There are about thirty horizontal rows of ciliated discs in each lamella in *Modiolaria discors* and ten in *Modiolaria marmorata*. The intrafilamentar septum is absent, and the chitinous lining is of uniform thickness.

In *Lithodomus dactylus* the upper ends of the ascending filaments are in serial

organic continuity. The upper edges of the ascending lamellæ are free from adjacent parts, and a longitudinal blood-vessel traverses each edge. The number of horizontal rows of ciliated discs in each lamella varies from ten to twenty-four. When the demibranch is laid flat on a slide and examined under the low power of the micro-
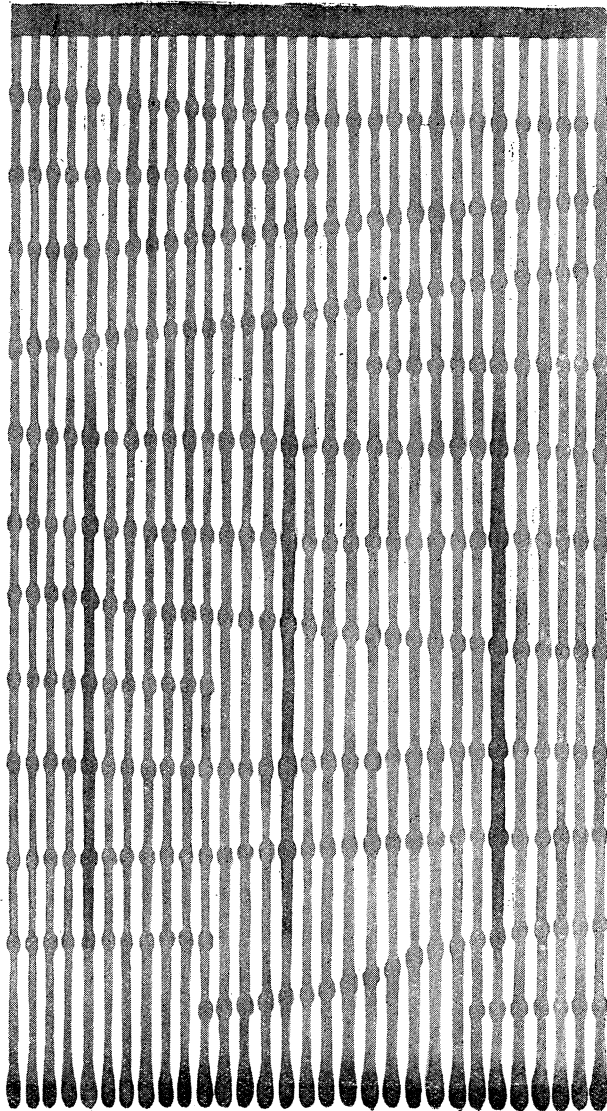
Fig. 12.—*Lithodomus dactylus.* Surface view of portion of inner demibranch showing three dark septum-bearing filaments.

scope, certain of the filaments appear darker and slightly thicker than the others. The distinction is not visible, however, in the upper third or the lower eighth of the demibranch (fig. 12). The differentiated filaments occur at intervals of 10 or 12 filaments in the inner demibranch, and 6 or 7 in the outer. On isolating the filaments it is seen that these differentiated filaments have an interlamellar septum

extending about half-way up, whereas the others have no interlamellar junctions at all (fig. 13A and B). This condition is of considerable interest as indicating what is presumably an early stage in the differentiation of principal filaments.
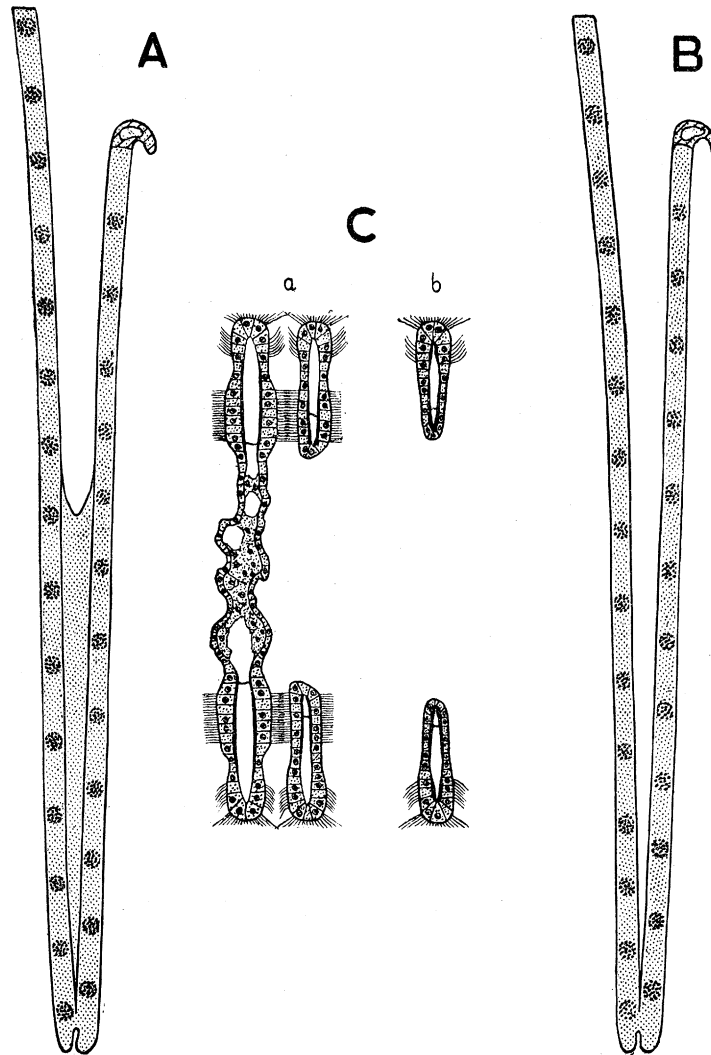
FIG. 13.—*Lithodomus dactylus.* A, septum-bearing filament. B, ordinary filament, without interlamellar septum. C, sections taken (*a*) half-way up the demibranch, and (*b*) high up. The left-hand filament of section *a* has an interlamellar septum, the right-hand one has not. This section is taken at the level of a row of ciliated discs. Section *b* is not taken through ciliated discs.

An intrafilamentar septum is present. The chitin is thickened towards the inter-lamellar edge (fig. 13C*a*), and in the upper parts of the filaments towards the frontal edge also (fig. 13C*b*). In the septum-bearing filaments the chitin is thickest in the middle of the face of the filament, but in the upper parts, above the septa, these filaments do not differ in size or in the position of the chitin thickenings from the other filaments. The latero-frontal cilia are long and fairly stiff, and those or

adjacent filaments frequently cross. In a surface view of one of the lamellæ the filaments appear to have a comb-like edge.

In *Lithodomus teres, Lithodomus stramineus, Lithodomus malaccanus* and *Botula cinnamonia* the features of gill structure are essentially the same as in *Lithodomus dactylus*, the differences being merely numerical, and affecting the intervals at which the septum-bearing filaments recur, the height of the septa, and the number of horizontal rows of ciliated discs. These species were, therefore, not examined in minute detail.

DESHAYES (**17**, Plate 130, fig. 7) shows the filaments of *Lithodomus lithophagus* (*Mytilus lithophagus*, LINNÉ) as having *organic* interfilamentar junctions. I have not examined this species, but in view of the uniformity of structure seen in the above five species, I should be very much surprised if this proves to be correct.

In *Septifer bilocularis* the upper edges of the ascending lamella of the outer demibranch is fused with the mantle, and that of the inner demibranch with the visceral mass, but behind the visceral mass the two ascending lamellæ of the inner demibranchs do not fuse. At about one-third of the height of the demibranch each filament has a bar-like interlamellar junction. The bars are not all strictly at the same level, but vary slightly in adjacent filaments. Here and there a filament has no interlamellar junction. The material was too badly preserved to enable one to udge of the number of ciliated discs.

Melinidæ.

In the three species of *Melina* examined the upper ends of the ascending filaments are fused in series. In *Melina perna* and *Melina serratula* the upper edges of the outer ascending lamellæ are free from the mantle, while in *Melina linguæformis* they are fused with it ; those of the inner demibranchs are united acoss the median plane of the body in *Melina perna* and *Melina linguæformis*, but not in *Melina serratula*. In *Melina perna* a continuous membrane or web runs along the upper fifths of the descending filaments, developed apparently by the fusion of their narrow interlamellar extensions, and in *Melina serratula* a similar web occurs in the upper part of the ascending lamellæ. At intervals of 8–12 filaments there is an interlamellar junction in the upper part of the demibranch (fig. 14D), involving 2, 3, or 4 filaments. There are no other interlamellar junctions, except in the case of *Melina serratula*, in which every filament has a low septum extending up the lower twelfth of the demibranch. In *Melina perna* there are three horizontal rows of ciliated discs (fig. 14C and D) ; there are about four in *Melina linguæformis*, and about fourteen in *Melina serratula*. The chitin is thickest towards the interlamellar edge of the filament, and there is no intrafilamentar septum.

In *Malleus albus* the upper ends of the ascending filaments are fused in series, and the upper edges of the ascending lamellæ are free from adjacent parts. The apex of the ctenidium is fused with the mantle edge. At the ventral edge of the demi-

branch the filaments are in organic continuity, a feature not met with in the other Mytilacea. There is a longitudinal muscle and a blood-vessel in this ventral edge. The ciliated discs are arranged in about six horizontal rows in each lamella. Every
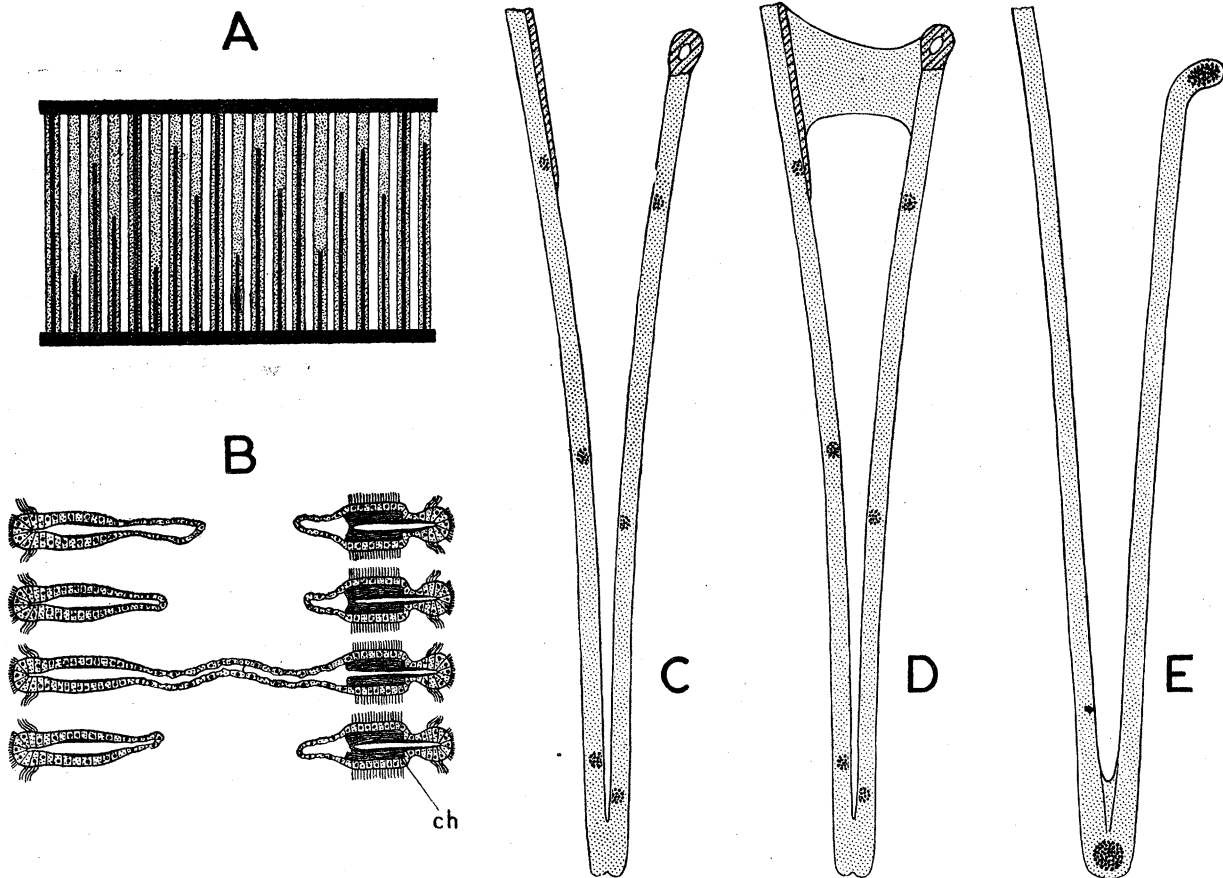
FIG. 14.—A, *Malleus albus*. Interlamellar aspect of a portion of the ascending lamella of the outer demibranch, as seen after stripping the two lamellæ apart. The dotted bands are the filaments; the black lines upon them are the torn edges of the interlamellar septa, which vary considerably in height. The upper and lower black lines represent the organic continuity between the filaments at the upper and lower edges of the lamella. B, section of a portion of the demibranch. Ciliated discs are shown in the right-hand side of the figure; *ch*, pale-staining chitin of the ciliated disc. C, *Melina perna*. Single filament. D, a filament with an interlamellar bar. E, *Amussium dalli*. Single filament.

filament has an interlamellar septum, the height ot which is very inconstant (fig. 14A). About each fourth septum extends the full height of the demibranch. Beneath the epithelium of the ciliated disc is a thick mass of pale-staining chitin (fig. 14B).

Amussiidæ.

In the three species ot *Amussium* examined the upper edges of the ascending lamellæ are free from adjacent parts. The upper ends of the ascending filaments are

united in series by ciliated discs, as also are the lower ends of the filaments along the ventral edge of the demibranch. ·There are no ciliated discs besides these two rows (fig. 14E).   There are no interlamellar junctions of any kind.   The ascending lamellæ of *Amussium dalli* reach nearly as high as the descending, but those of *Amussium lucidum* and *Amussium meridionale* only extend half-way up the descending lamellæ, or a little higher.   An intrafilamentar septum is present, and the chitinous lining is of fairly uniform thickness.   The specimen of *Amussium dalli* was kindly supplied by Professor DALL, and I have no hesitation in assuring him that the gills do not consist of direct filaments only as he has described (**13**, p. 434, and **15**, p. 525).

The gills of *Plicatula australis* agree exactly with those of *Amussium*, and demand no special notice.   The ascending lamellæ extend about half-way up the descending, as in *Amussium lucidum* and *Amussium meridionale*.

Sub-order PECTINACEA.

SPECIES EXAMINED :—

Spondylidæ . . { *Spondylus nicobaricus.*
Spondylus ducalis.
Spondylus ocellatus.
Spondylus calcifer.
Spondylus varians.

Pectinidæ. . . { *Pecten opercularis.*
Janira pyxidatus.
Pedum spondyloideum.

Aviculidæ . . { *Avicula* tarentina.*
Avicula argentea.
Avicula americana.
Avicula radiata.
Meleagrina† margaritifera.
Meleagrina vulgaris.
Meleagrina anomioides.

PREVIOUS ACCOUNTS :—

Pecten varius, POSNER, **76**, 1875, p. 554 and fig. 21.
Pecten jacobea, BONNET, **5**, 1877.
Pecten groenlandicus, HAREN-NORMAN, **31**, 1881, pp. 28-30, fig. 35.
Pecten jacobaeus and *Pecten maximus*, MÉNÉGAUX, **57**, 1889.
Pecten, MÉNÉGAUX, **62**, 1890, p. 98.

* *Avicula* = *Pteria*, SCOPOLI.
† *Meleagrina* = *Margaritifera*, BROWNE.

Pecten opercularis, PELSENEER, **71**, 1891, p. 200, and fig. 47.

Pecten irradians, KELLOGG, **42**, 1892, p. 420, and figs. 83, 84 and 86.

Pecten jacobaeus, *Pecten varius* and *Pecten maximus*, JANSSENS, **39**, 1893,
pp. 24–36, and figs. 83–103.

Pecten opercularis, RICE, **83**, 1897.

Avicula tarentina, DESHAYES, **17**, 1844–1848, Plate 139.

Avicula tarentina, MÉNÉGAUX, **62**, 1890, p. 41.

Avicula tarentina, PELSENEER, **71**, 1891, p. 198.

Meleagrina fucata, PELSENEER, **71**, 1891, p. 198.

Spondylidæ.

In *Spondylus* the two demibranchs are of nearly the same size, and the ascending lamella is of about two-thirds the height of the descending. The upper edges of the ascending lamellæ are free from adjacent parts of the body. In *Spondylus varians*
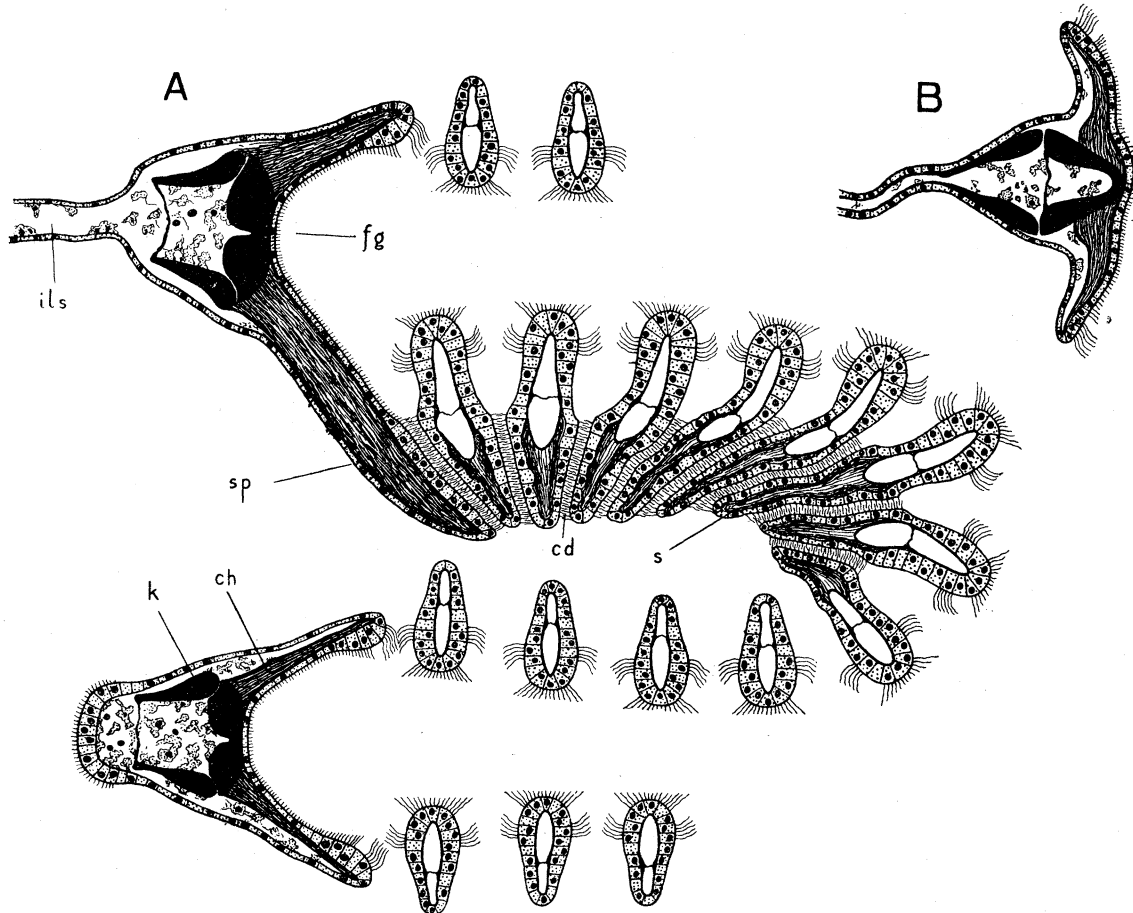
FIG. 15.—*Spondylus ducalis.* A, section taken about half-way up the lamella, including a complete plica and two principal filaments. *cd*, cilia of the ciliated disc; *ch*, pale-staining chitin, and *k*, darkly-staining chitin of the principal filament; *fg*, frontal groove; *ils*, interlamellar septum; *s*, spur of the ordinary filament; *sp*, spur of the principal filament. B, section of a principal filament taken near the lower edge of the demibranch.

the upper ends of the ascending filaments are fused in longitudinal series, but in the other species examined they are united by ciliated discs. At the lower edge of the demibranch the filaments are not in serial organic connection. The interlamellar junctions have the form of low septa extending one-eighth of the height of the ascending principal filaments in *Spondylus varians*, two-fifths in *Spondylus calcifer*, and one-fifth to one-fourth in the other species. A lamellate interlamellar extension occurs on the upper third of the descending principal filament. The edge of this contains a vertical blood vessel, and the cells of the extreme margin are ciliated.

There are on an average thirteen filaments to the plica. The plicæ are flatter in the lower parts of the demibranch than in the upper. Ciliated discs are situated on the sides of long spurs or ingrowths from the interlamellar (intraplical) edge of the filament (fig. 15A, *s*), filled with pale-staining chitin. The principal filaments are large, with frontal surface concave in the upper parts, and convex in the lower parts of the demibranch. The difference in the shape of the principal filaments is perhaps not altogether a natural one, but may be due to an accidental bending back of the lateral flaps. Towards the lower part of the demibranch a principal filament, such as that shown in fig. 15B, may have as its neighbour one with a frontal groove, less deep, however, than those shown in fig. 15A. Principal filaments have two vertical rows of spurs, bearing ciliated discs on one aspect only. In certain of the plicæ of *Spondylus ocellatus* the 2, 3 or 4 apical filaments are slightly larger than the ordinary filaments. An intrafilamentar septum is present.

Pectinidæ.

In *Pecten opercularis* the gills exactly resemble those of *Spondylus ducalis* except in the following respects. The ascending lamellæ extend two-thirds of the height of the descending lamellæ. The interlamellar septa of the principal filaments extend about half-way up the ascending lamellæ, and the interlamellar extensions of the descending principal filaments reach so low down as to be continuous with the septa. The spurs that bear the ciliated discs are short, although they are quite long in *Pecten irradians* (KELLOGG, **42**, fig. 84). There are about sixteen filaments to the plica.

Janira pyxidatus and *Pedum spondyloideum* differ from *Pecten opercularis* in no essential respects. The ciliated spurs of *Pedum* are quite as long as those of *Spondylus*.

The section of the gill of *Pecten* given by POSNER (**76**, fig. 21) shows a great amount of subfilamentar tissue. He admits (**76**, p. 554) that the section is not taken through the part of the gill where the filaments are free, but even admitting that it is taken through the " Kiemenbasis, wo bekanntlich die Fäden noch ver-bunden sind " the figure is impossible ; for it represents not two descending lamellæ, but an ascending and a descending lamella—and at no part of the ascending lamella

are the filaments in organic union. This figure, even if admitted to stand for *Lima*, as the sentence " *Lima* scheint, soweit ich sie untersucht habe, ein völlig identisches Verhalten zu bieten (vgl. fig. 21)" might imply, would still be incorrect, for at high levels, near the axis, the interlamellar junctions are wanting.

HAREN-NORMAN (**31**, pp. 28—30) states that in *Pecten groenlandicus* the interlamellar septa are completely wanting, and that only one row of ciliated discs is present, at the lower edge of the demibranch. The lamellæ, also, are homorhabdic, so that if the observations are correctly stated, this species would come nearer to *Amussium* than to *Pecten*.

Aviculidæ.

In *Avicula* (= *Pteria* of SCOPOLI) and *Meleagrina* (= *Margaritifera* of BROWNE) the upper ends of the ascending filaments are in serial organic continuity, and a longitudinal blood-vessel traverses the upper edge of the ascending lamella. The filaments are in serial organic continuity along the ventral edge of the demibranch, and a longitudinal blood-vessel occurs here also. The upper edges of the ascending lamellæ are free from adjacent parts in all the species examined except *Avicula tarentina* and *Meleagrina anomioides*. In the former the posterior part of the upper edge of the outer ascending lamella is fused with the mantle. There is, however, probably some variation in this respect, for PELSENEER (**71**, p. 198) states that the edge is " soudée au manteau sur toute sa longueur." In *Meleagrina anomioides* the anterior part of the outer ascending lamella is fused with the mantle; the upper edges of the inner lamellæ are fused with one another behind the visceral mass. Their anterior parts are not united with the visceral mass.

Every principal filament has an interlamellar septum. Most of these rise one-third or two-fifths of the height of the demibranch in *Avicula*, and one-fifth of the height in *Meleagrina*; but some extend the full height of the demibranch. High septa are scarce in the anterior part of the gill; they occur at intervals of three to five plicæ in the middle regions, while in the posterior part of the gill every principal filament or every alternate one has a high septum. In *Meleagrina margaritifera* many of the high septa in the middle of the length of the gill are incomplete in their middle, so that the thickened upper edge remains as a cross-bar stretching from the upper edge of the ascending lamella to the axis.

The principal filaments are large, and have a deeply grooved frontal surface in the upper and middle parts of the demibranch (fig. 16). The groove becomes shallow in the lower parts of the demibranch. There are about 12 or 13 filaments to the plica in *Avicula* and 10 or 11 in *Meleagrina*. The 2 or 3 apical filaments are smaller than the average in *Avicula tarentina* and *Avicula argentea*, while in *Meleagrina margaritifera* they are larger. In the other species they do not differ from the filaments at the sides of the plicæ. The ciliated discs are borne on spurs or processes of the inner edge of the filament. There are no intrafilamentar septa. The

chitin is of some thickness beneath the ciliated discs, and the intrafilamentar cavity is here largely obliterated.
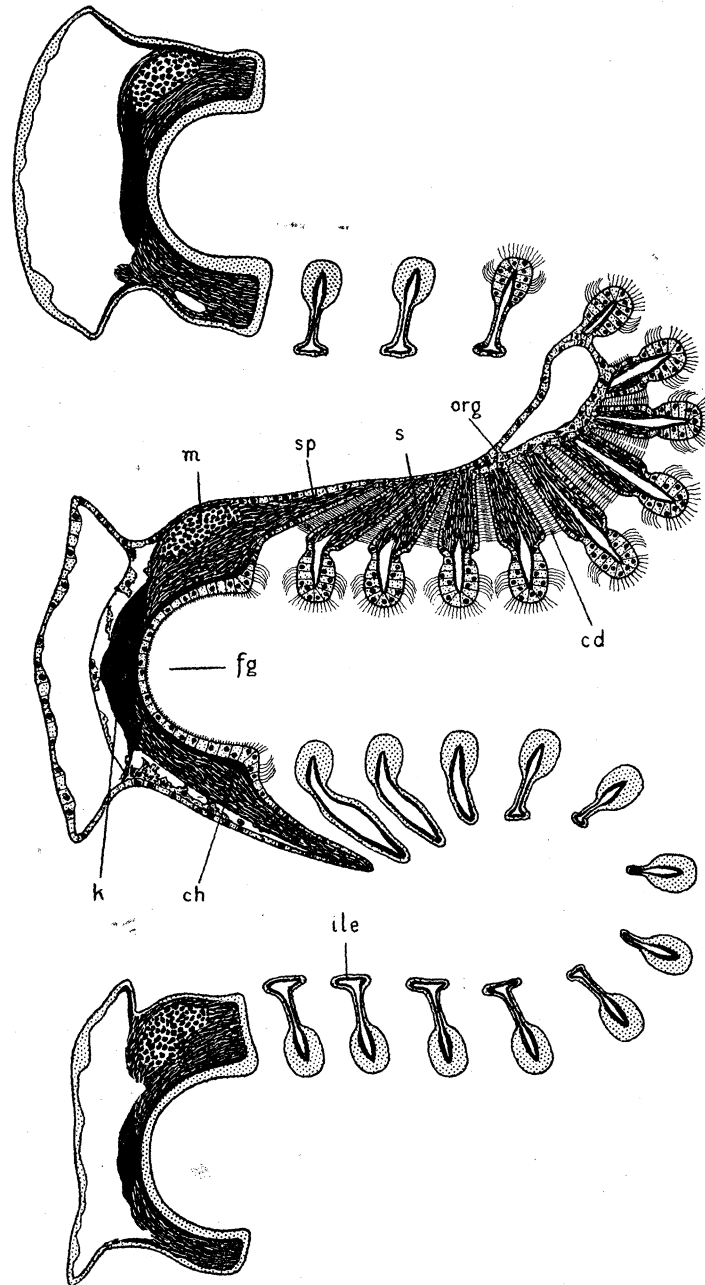
Fig. 16.—*Avicula argentea.* Section including two plicæ and three principal filaments. *ile*, interlamellar extension of one of the ordinary filaments; *org*, organic or cellular union between the interlamellar edges of the ciliated spurs; *m*, vertical muscles in the principal filaments. Other letters as in fig. 15.

Avicula argentea proves to be a form of intense interest, since the interfilamentar junctions are of a compound nature, an organic union having taken place between the

intraplical edges of the spurs that bear the ciliated discs (fig. 16, *org.*). The tendency to form subfilamentar tissue is not confined to the levels of the ciliated discs, but is exhibited all along the inner edge of the filaments (fig. 16, *ile.*). Possibly a similar cellular connection obtains in *Meleagrina vulgaris.* The chitin appears to be continuous from spur to spur, but the material was not sufficiently well preserved to show cellular continuity.

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Order SYNAPTORHABDA.

Sub-order OSTREACEA.

</div>

SPECIES EXAMINED :—

Pinnidæ . . .
- *Pinna pectinata.*
- *Pinna zealandica.*
- *Pinna nobilis.*
- *Pinna nigra.*
- *Pinna virgata.*

Limidæ . . .
- *Lima fragilis.*
- *Lima californica.*
- *Lima inflata.*
- *Lima squamosa.*
- *Lima hians.*
- *Lima excavata.*

Ostreidæ . . . *Ostrea edulis.*

PREVIOUS ACCOUNTS :—

Pinna nobilis, POSNER, **76**, 1875.

Pinna nobilis, BONNET, **5**, 1877.

Pinna pectinata, MÉNÉGAUX, **62**, 1890, p. 55, and fig. 15.

Pinna nobilis, PELSENEER, **71**, 1891, p. 199.

Lima elliptica, HAREN-NORMAN, **31**, 1881, fig. 36.

Lima hians, PELSENEER, **71**, 1891, p. 201, and fig. 49B.

Lima, KELLOGG, **42**, 1892, p. 420.

Ostrea edulis, POSNER, **76**, 1875.

Ostrea edulis and *Ostrea hippopus,* BONNET, **5**, 1877.

Ostrea edulis, SLUITER, **95**, 1878.

Ostrea edulis, LANKESTER, **52**, 1886.

Ostrea, MÉNÉGAUX, **58**, 1889, pp. 121–126.

Ostrea edulis, MÉNÉGAUX, **62**, 1890, p. 116.

Ostrea virginiana, KELLOGG, **42**, 1892, p. 422 and fig. 76.

Ostrea edulis, JANSSENS, **39**, 1893, fig. 62.

Ostrea virginiana, RICE, **83**, 1897.

Pinnidæ.

The upper ends of the ascending filaments are fused in series, and there is a longitudinal blood-vessel in this edge.   Except in *Pinna nobilis*, where the upper edge of the outer ascending lamella is fused with the mantle, the upper edges of the ascending lamellæ are free from adjacent parts.   Near the lower edge of the demibranch
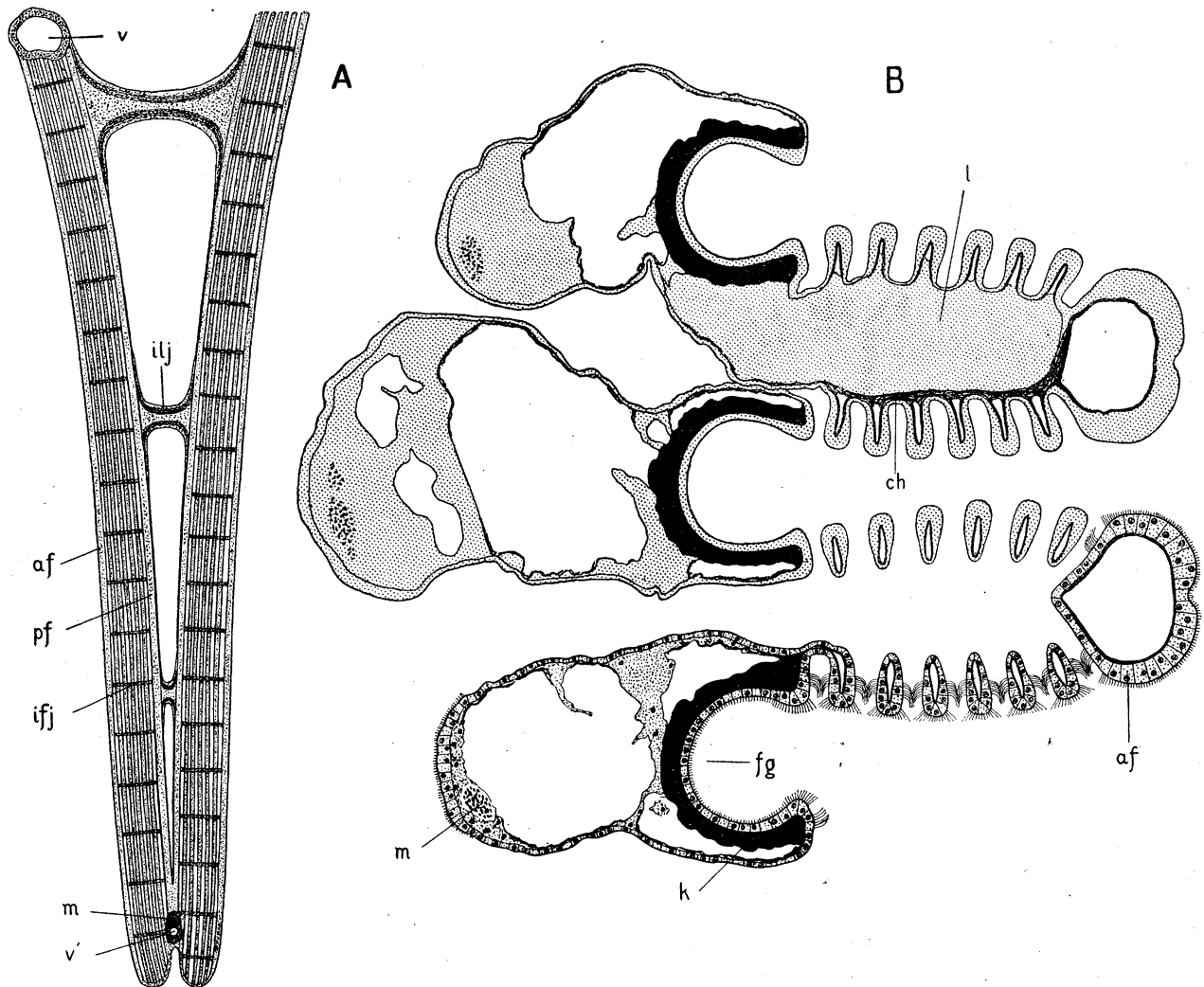
FIG. 17.—*Pinna virgata.*   A, vertical section of a demibranch, one-half of a plica in thickness, flattened out.   (Owing to the flattening-out, the true relations of the ascending and descending filaments at the lower edge of the demibranch cannot be shown.)   B, horizontal section of portion of a lamella, including two plicæ and three principal filaments.

af, apical filament: *ch*, chitin of the interfilamentar junction, fibrous in character, and continuous from filament to filament; *fg*, frontal groove of the principal filament; *ifj*, interfilamentar junction; *ilj*, interlamellar junction; *k*, darkly-staining chitin of the principal filament; *l*, lacunar tissue of the interfilamentar junction forming a horizontal septum across the plica; *m*, muscular tissue; *pf*, principal filament; *v*, blood-vessel in the edge of the ascending lamella; *v′*, blood-vessel at the lower edge of the demibranch.

the filaments are in serial continuity, and in this connective is a longitudinal blood-vessel, with a muscle above it (fig. 17A, v' and m). The actual lower edge of the demibranch has a longitudinal groove. The interlamellar junctions are two or three bands (fig. 17A, ilj). They are of varied heights in the different principal filaments, and do not occur in rows along the demibranch. They usually involve single principal filaments, but the uppermost ones are often broader, and extend across the plical opening so as to be in relation with two adjacent principal filaments. Muscle strands run in the upper and lower edges of the interlamellar bands, and are continued upward and downward along the interlamellar edges of the principal filaments for some distance.

There are 16 or 17 filaments to the plica in *Pinna pectinata*, 10 or 11 in *Pinna nobilis*, *Pinna nigra*, and *Pinna zealandica*, 12 or 13 in *Pinna virgata*. In all cases the frontal surface of the principal filament has the form of a semi-cylindrical groove (fig. 17B, *fg*). The interfilamentar junctions are horizontal septa, arranged in regular horizontal rows in the different plicæ. As has already been shown by MÉNÉGAUX (**62**, p. 55, fig. 15), the apical filament is larger than the ordinary filaments in *Pinna pectinata*. It is very large in *Pinna nobilis* and *Pinna virgata* (fig. 17B, *af*), but in *Pinna nigra* it is very slightly, if at all, larger than the ordinary filaments. There is no intrafilamentar septum.

Limidæ.

The upper ends of the ascending filaments are united organically in longitudinal series, and the upper edges of the ascending lamellæ are free from adjacent parts. The interlamellar junctions are septa. In *Lima fragilis* they extend only one-twelfth of the height of the demibranch ; in fact, as septa, they may be said to be absent, for the junction practically represents the bend of the filament. In the other species they extend up from one-fifth to one-third of the height of the demibranch. They are, of course, confined to the principal filaments. In *Lima californica* there is a longitudinal blood-vessel in the ventral edge of the demibranch, but this appears to be wanting in the other species. The interfilamentar junctions do not run across the plica as horizontal septa, and the plical cavity is, therefore, freely open in a vertical direction.

The apical filament is large in *Lima fragilis*, *Lima hians*, and *Lima squamosa*. It is very large in *Lima inflata*, but in *Lima fragilis* it is of about the same size as the other filaments. The average number of filaments in a plica is 11 in *Lima squamosa*, 12 in *Lima fragilis* and *Lima californica*, 15 in *Lima hians*, and 18 in *Lima inflata*.

The shape of the frontal surface of the principal filament is variable, not only in the different species, but also at different levels of the same filament. In the upper parts of the demibranch of *Lima inflata* and *Lima fragilis* the frontal surface of the

principal filament has the form of a deep groove (fig. 19A), the groove having a
flatter bottom in the descending than in the ascending filament.   On taking sections
at successively lower levels one notices the appearance of a ridge rising from the
bottom of the groove (fig. 18), small at first, but increasing in height so that in
sections taken near the lower edge of the demibranch its summit is level with the
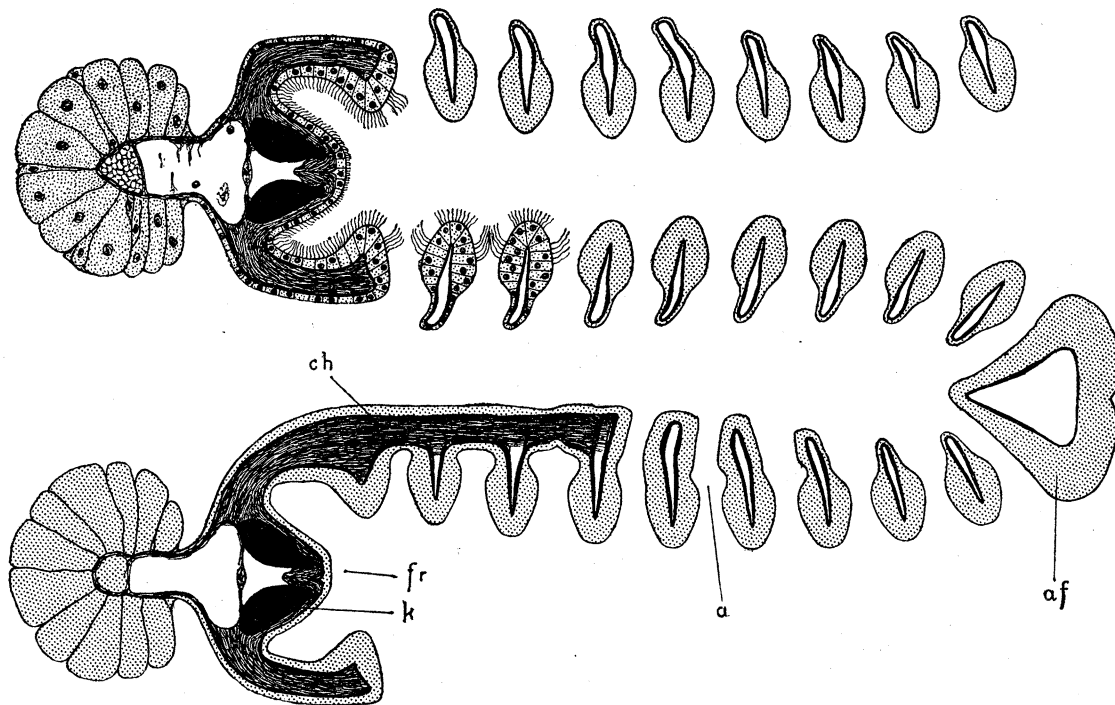
Fig. 18.—*Lima inflata.*   *a,* part of the section in which the epithelium is rather suggestive of obsolete
    ciliated discs; *af,* apical filament; *ch,* pale-staining chitin of the principal filament and interfilamentar
    junction; *fr,* frontal ridge of the principal filament; *k,* darkly-staining chitin.

sides of the groove (fig. 19B).   A further increase in the size of the ridge may be
seen by examining a series of sections of *Lima squamosa,* for here, in sections taken
high up, the principal filament has the shape shown in fig. 19B, whereas in the lower
parts of the demibranch the ridge is so large as to have obliterated the groove
entirely (fig. 19C).   In sections of *Lima hians,* and according to HAREN-NORMAN in
Lima elliptica also (**31**, fig. 36), the principal filaments appear as shown in fig. 19B.
For *Lima californica,* see fig. 19D.

The thickest part of the chitinous lining is situated nearer the interlamellar than
the frontal edge of the ordinary filament.   In *Lima hians* an intrafilamentar septum
is not uncommonly seen, but it is wanting in the other species.   *Lima inflata* is
interesting in that in certain parts of the sections the interfilamentar junctions
present the appearance shown in fig. 18 at *a.*   In view of the occurrence of both
organic interfilamentar connections and ciliated discs in *Avicula argentea* (p. 212),

where the former junctions appear to be superadded on the latter, one may regard this condition in *Lima inflata* as a further step in the same direction, the main junctions being here the organic, while the obsolete ciliated discs are merely suggested by the regularity of the prismatic epithelium.
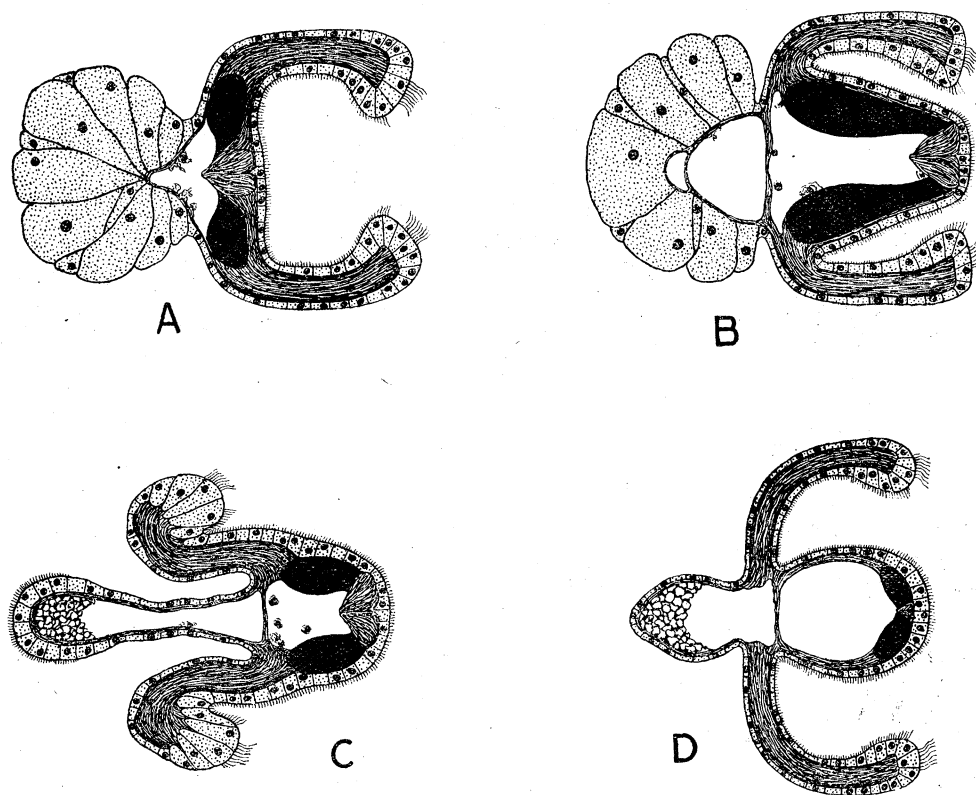
FIG. 19.—Transverse sections of principal filaments. A, *Lima fragilis*, section taken through the upper part of the filament. B, *Lima hians*, section taken half-way up; or *Lima fragilis*, section taken low down; or *Lima squamosa*, section taken high up. C, *Lima squamosa*, section taken low down. D, *Lima californica*, section taken half-way up.

Ostreidæ.

The upper edges of the ascending lamellæ of the inner demibranchs of *Ostrea edulis* are united in the middle line; those of the outer are fused with the mantle. There are 9–12 filaments to the plica. The front of the principal filament has the form of a broad ridge. The filaments adjacent to the principal filament are slightly larger than usual, and have been called *transitional filaments* by KELLOGG (**42**, p. 422). They were first noticed by LANKESTER in his memoir on "Green Oysters" (**52**). The interlamellar junctions have the form of septa. At low levels all the principal filaments have septa. At a short distance up, the interlamellar septa occur only in relation with alternate principal filaments, but the order is not absolutely regular. Higher up still each fourth septum only persists. The bars which run

across the floor of the suprabranchial cavity from descending to ascending lamella are the thickened upper edges of alternate high septa.   They recur at intervals of about eight plicæ.

Most of the interfilamentar junctions are bands of tissue running horizontally round the inner surface of the plica (fig. 20, *l'*), but each third or fourth in a vertical
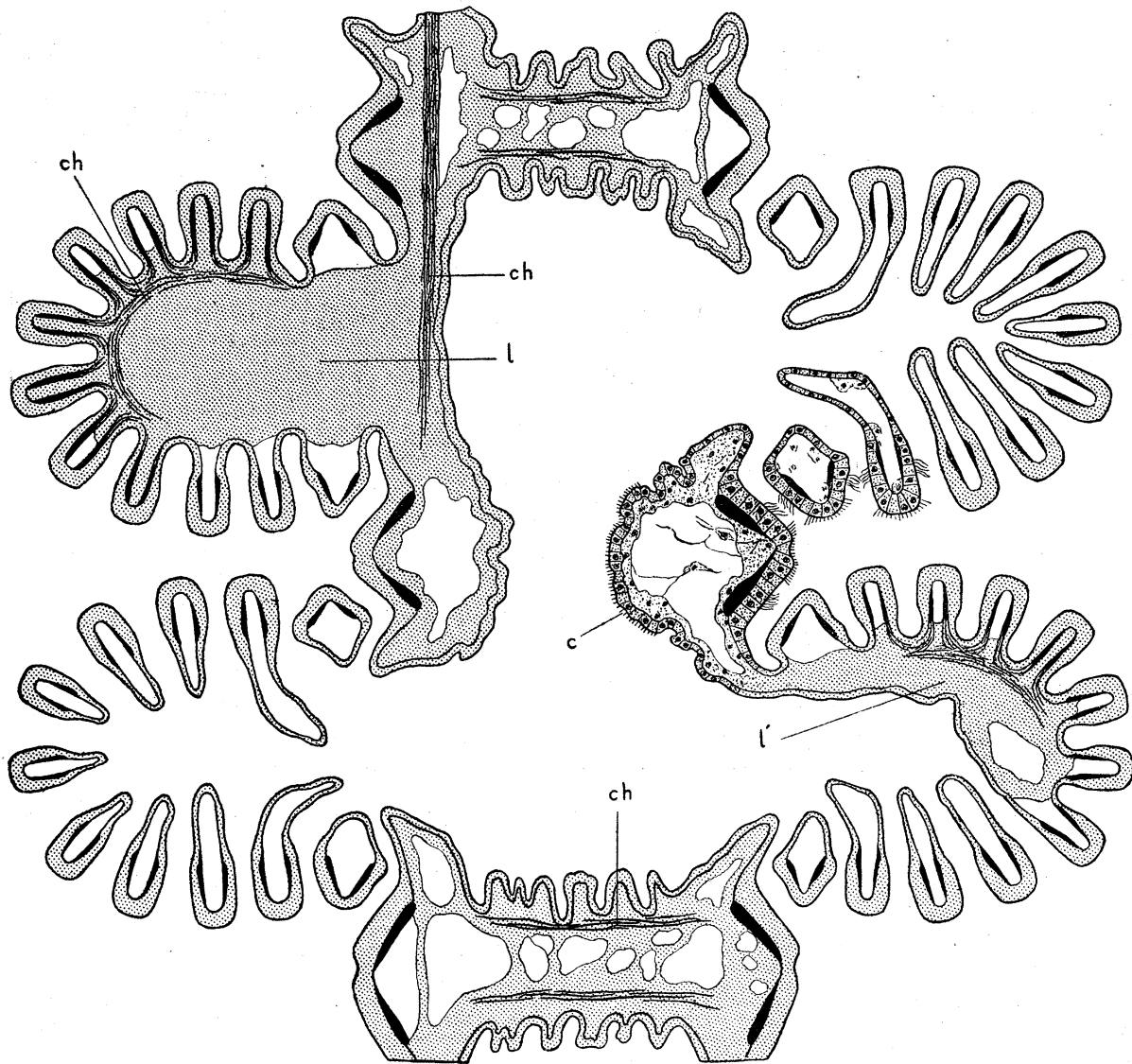
Fig. 20.—*Ostrea edulis.*   *c*, cilia on the interlamellar edge of the principal filament; *ch*, chitin of a fibrous nature; *l*. lacunar tissue of the interfilamentar junction, which in this instance has the form of a horizontal septum; *l'*, an interfilamentar junction of the form of an intra-plical band.   Owing to the slight obliquity of section the band does not extend all the way round the plica.

series extends across the plica as a horizontal septum (fig. 20, *l*).   Such plates of subfilamentar tissue are shown in fig. 62 of JANSSENS (**39**), but they are not as numerous as his figure would suggest.   The frontal and lateral cilia are normal.

There are short cilia on the interlamellar edges of the principal filaments (fig. 20c).
No intrafilamentar septum is present. There is a fair amount of muscle in the inter-
filamentar junctions and in the inner edge of the horizontal septa, but it becomes
very difficult in places to discriminate between muscle fibre and fibrous chitin.

Why KELLOGG (42) should regard the gill of *Ostrea* as "very degenerate" it is
difficult to conjecture. It belongs to a highly specialised, heterorhabdic and much
plicate type.

Sub-order SUBMYTILACEA.

SPECIES EXAMINED :—

Carditidæ

{ *Cardita (Venericardia) sulcata.*
Cardita (Venericardia) granulata.
Cardita (Mytilicardia) crassicostata.
Carditamera floridana. }

Astartidæ.

{ *Astarte borealis.*
Astarte crebicostata. }

Crassatellidæ

{ *Crassatella cumingi.*
Crassatella indica.
Crassatella floridana. }

Cyprinidæ

{ *Cyprina islandica.*
Trapezium vellicatum.
Isocardia cor (= humana).
Vesicomya (Callocardia) stearnsi. }

Lucinidæ

{ *Lucina borealis.*
Lucina bengalensis.
Lucina aequicostata.
Loripes leucoma.
Diplodonta oblonga.
Montacuta substriata. }

Erycinidæ

{ *Kellya cycladiformis.*
Kellya suborbicularis.
Lasaea rubra. }

Galeommidæ

{ *Scintilla ambigua.*
Scintilla philippinensis.
Galeomma turtoni.
Chlamydoconcha orcutti.
Ephippodonta lunata. }

Cyrenidæ. . . . {
  Cyrena (Egeta) floridana.
  Cyrena sinuosa.
  Corbicula lydigiana.
  Corbicula minor.
  Sphaerium pallidum

Rangiidæ. . . . { *Rangia cyrenoides.*

Ætheriidæ . . . {
  Ætheria plumbea
  Mülleria dalyi.

Unionidæ. . . . {
  Unio pictorum.
  Unio ambiguus.
  Anodonta cygnea.
  Monocondylaea sp.

Dreissensiidæ . { *Dreissensia polymorpha.*

PREVIOUS ACCOUNTS :—

Cardita calyculata, DESHAYES, **17**, 1844–1848, pl. 107, fig. 6.
Cardita sulcata, PELSENEER, **71**, 1891, p. 202, and figs. 50 and 51.
Cardita calyculata, RICE, **83**, 1897.
Cardita sulcata, RICE, **83**, 1897, figs. 9 and 10.
Astarte sulcata, HAREN-NORMAN, **31**, 1881, p. 39 and figs. 45 and 46.
Astarte fusca, RICE, **83**, 1897, fig. 8.
Cyprina islandica, RICE, **83**, 1897.
Callocardia stearnsii, DALL, **14**, 1894, pp. 692–697.
Lucina lactea, DESHAYES, **17**, 1844–1848, pl. 79, fig. 3.
Lucina, VALENCIENNES, **101**, 1845, p. 1688.
Lucina, DESHAYES, **18**, 1845, p. 1794.
Lucina jamaicensis and *Lucina interrupta*, MÉNÉGAUX, **59**, 1889, p. 130–132.
Lucina, MÉNÉGAUX, **62**, 1890, p. 148.
Lucina lactea, PELSENEER, **71**, 1891, p. 202.
Diplodonta, PELSENEER, **68**, 1888, p. 16.
Montacuta, LOVEN, **55**, 1849.
Montacuta ferruginosa, PELSENEER, **71**, 1891, p. 203.
Scioberetia australis, BERNARD, **2**, 1896.
Entovalva mirabilis, VOELTZKOW, **103**, 1891.
Chlamydoconcha orcutti, BERNARD, **3**, 1896.
Ephippodonta macdougalli, WOODWARD, **107**, 1893.
Cyclas cornea (= *Sphaerium corneum*), ZIEGLER, **110**, 1885, p. 561 and fig. 23.
Cyclas cornea (= *Sphaerium corneum*), JANSSENS, **39**, 1893.
Mülleria dalyi, WOODWARD, **108**, 1898.

Unio, HESSLING, **33**, 1859.

Unio pictorum, POSNER, **76**, 1875.

Unio margaritifera, BONNET, **5**, 1877.

Unio pictorum, RABL, **81**, 1877.

Unio margaritifer, JANSSENS, **39**, 1893.

Anodonta, RENGARTEN, **82**, 1853.

Anodonta, LANGER, **49**, 1856.

Anodonta, STEPANOFF, **98**, 1865, fig. 21.

Anodonta anatina, POSNER, **76**, 1875.

Anodonta, PECK, **66**, 1877.

Anodonta piscinalis, BONNET, **5**, 1877.

Anodonta, KOLLMANN, **43**, 1877.

Anodonta cygnea, SLUITER, **95**, 1878.

Anodonta fluviatilis, SIMPSON, **94**, 1884.

Anodonta anatina, JANSSENS, **39**, 1893.

Dreissensia polymorpha, PECK, **66**, 1877.

Dreissensia polymorpha, JANSSENS, **39**, 1893.

Dreissensia polymorpha, RICE, **83**, 1897.

Carditidæ.

The gills of the four species examined *Cardita* (*Venericardia*) *sulcata*, *Cardita* (*Venericardia*) *granulata*, *Cardita* (*Mytilicardia*) *crassicostata*, *Carditamera floridana*), agree in both general and minute structure with those of *Astarte*, described under the next family, except that their subfilamentar tissue exhibits a proneness to dilatation into large vertical blood tubes, running along the interlamellar side of certain of the filaments. It would appear from this that the circulation of the blood has been largely transferred from the filamentar cavities to the subfilamentar tissue; yet the filamentar cavities do not appear smaller than in *Astarte*.

Astartidæ.

The type of gill seen in *Astarte* is probably the simplest of the numerous Eulamellibranch varieties. It is homorhabdic and non-plicate, and the subfilamentar tissue is scanty. The interfilamentar junctions are very regular horizontal bars (fig. 21), and the fenestrations are regular and comparatively large. The interlamellar junctions have the form of rods or bars, few in number and irregularly disposed. They are apparently not vascular, since an examination of horizontal sections of the demibranch, and of the torn ends of the bars seen when one lamella is stripped away from the other of the same demibranch, fails to disclose any definite and continuous cavities in the interior. The usual form of horizontal section of the demibranch is that shown in fig. 22.

The interfilamentar junctions may be seen joining up two, three, or more filaments. It is only the slight sinuosity of the interfilamentar junction, and the almost inevitable obliquity of the plane of section, that prevents one getting an interfilamentar
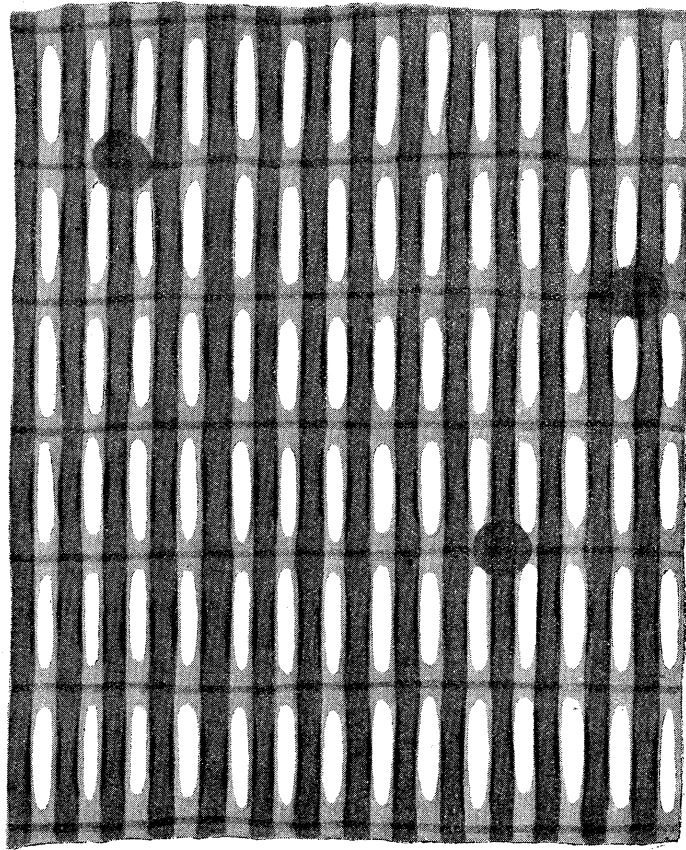
FIG. 21.—*Astarte borealis.* Interlamellar aspect of a portion of one lamella. The vertical bands are the filaments, the horizontal dark lines the chitin in the interfilamentar junctions, and the three dark patches are interlamellar bars.
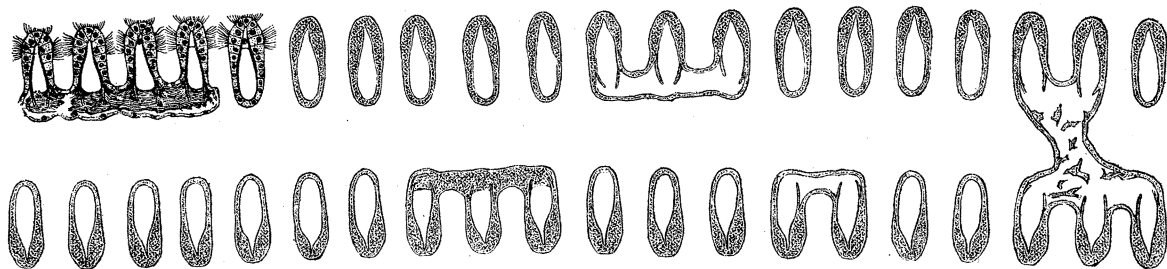
FIG. 22.—*Astarte borealis.* Horizontal section of a portion of one demibranch.

junction continuous from one end of the section to the other. The interfilamentar junctions are supported by a thick rod of rather fibrous chitin, which is continuous with the chitin that lines and supports the filaments they connect. The filaments

are quite simple in character, their cilia are normal, and their chitinous lining is only slightly thickened at the two sides of the filament. Intrafilamentar septa may occasionally be seen in the cavity, and also a few nucleated cells, especially towards the frontal side of the filament. That the gills are of a primitive nature is indicated not only by the simplicity of their finer structure, but also by the freedom of the posterior parts of the gill axis and the ascending lamellæ from adjacent organs.

Crassatellidæ.

The gills of *Crassatella cumingi* and *Crassatella indica* are almost identical in structure with those of *Astarte*. The lamellæ are flat and homorhabdic, the interfilamentar junctions regular, the development of subfilamentar tissue feeble, and the interlamellar bars scarce, even in sections taken close to the lower margin of the demibranch.

The gill lamellæ of *Crassatella floridana*, on the other hand, are strongly plicate, with about 26–28 filaments to the plica in both demibranchs, with well-differentiated principal filaments with broad, flat frontal surface and large blood cavity. The interlamellar junctions are septa, alternately high and low. Muscular tissue is fairly abundant, and most of the sections of the plicæ are seen to be partially choked up by subfilamentar tissue, which is thus not confined to the levels of the interfilamentar junctions. The apical filaments are slightly enlarged. The chitinous lining is but slightly thickened at the sides of the filaments, and exhibits a curious arborising, due apparently to vacuolation, in that part which lies beneath the frontal epithelium. The intrafilamentar cavity is almost obliterated by the close approximation of the two sides of the filament. The single specimen examined of this species was kindly furnished by Professor DALL, and the identification has been confirmed by Mr. E. A. SMITH, but it is highly probable that when the revision of the genus is undertaken, it may be necessary to separate this from forms like *Crassatella cumingi* and *Crassatella indica*, since it not only differs from them in its gill structure, but also in having a relatively huge saltatory foot, which they do not possess.

Cyprinidæ.

Cyprina islandica has homorhabdic, plicate gills, with about forty-five filaments to the plica. The specimen examined was in a bad state of preservation, and this may account for a certain irregularity in the folding of the lamellæ seen in the sections. The interlamellar junctions are septa, alternately high and low ; muscular tissue and subfilamentar tissue are fairly abundant. The chitin is but feebly thickened at the sides of the filaments.

The lamellæ of *Trapezium vellicatum* are strongly plicate, with 24–32 filaments to the plica, and heterorhabdic, the frontal surface of the principal filaments being flat, or very slightly grooved. The interlamellar junctions are septa, alternately high and

low.   The chitin of the two or three filaments adjacent to the principal filament is thicker than in the other filaments.

Isocardia cor (= *humana*) also has plicate gills, with about twenty filaments to the plica.   The principal filaments have a ridged frontal surface, and the ascending and descending parts of each are close together in consequence of the narrowness of the interlamellar septa.   In the specimen examined the plications of the same lamella were not uniformly spaced, but were arranged in pairs in such a way that one principal filament was in relation with two closely approximated plicæ, while the next was situated in a nearly flat portion of the lamella.   Whether this is natural or due to imperfect preservation is open to question.

Vesicomya stearnsi (*Callocardia stearnsi*) is a form to which considerable interest attaches, in consequence of Professor DALL having claimed for it affinity with the Protobranchia.   In 1894 (**14**, p. 696) he wrote :—" The single ctenidium in *Callocardia stearnsii*, DALL, is composed of the central stem and two sets of ribbon-like lamellæ, which spring from either side.   These lamellæ are thick and fleshy (relatively to their size), and are attached to each other at their proximal ends by the common adhesion of the stem, and at their distal ends by a narrow fibrous strip, which may possibly contain a vascular channel, but did not show any in the present condition of the specimens.   There are indications of a lateral band of cilia ; at all events, the edges of the lamellæ are distinctly marginate and yet not organically connected. .   .   .   . It can be positively stated, however, that there are neither fibrous nor vascular connectives between the lamellæ, except as above mentioned, and the chief difference between the ctenidium of *Callocardia* and that of *Solemya* is obviously that the lamellæ are united by a narrow band distally and reflected in the former, while they are comparatively free and not reflected in the latter.   It may be added that the entire ctenidium is solid and fleshy as in *Nucula*, and when lifted separates from the body in a single mass.   The two ctenidia are united to the siphonal septum behind the foot, but not to each other, so there is no complete anal chamber.   .   .   . The discovery of this type may be said to practically complete the series uniting the foliobranch with the reticulate gill and give the quietus to the classification based solely on the divergencies of the ctenidia."

Writing again in 1895, he said (**15**, p. 505) : " In *Callocardia* the greatly elongated and reflected ribbon-like plates on either side of the stem are fleshy and free, as in *Nucula*, without any trace of reticulation, but are united by a slender band of connective tissue at their tips.   If the strap-like plates of *Callocardia* were narrowed until they became rod-like, and the distal fibres omitted, there would be hardly anything except the chitinous skeleton of the filibranch to separate the two types of ctenidia."

I am sorry to have to traverse the main thesis of the above citations, but as the result of an examination of a specimen, kindly supplied by Professor DALL himself, I find the structure of the lamellæ to be that of a Eulamellibranch not more aberrant

than *Lucina*. The filaments are very closely packed, so that to the naked eye the striation of the lamella is barely apparent (fig. 23A). The outer demibranch is small as compared with the inner. Both inner and outer demibranchs have the usual descending and reflected lamellæ, and the filaments are broad (fig. 23B), *i.e.*, each has a wide interlamellar extension. The upper edge of the ascending lamella of the outer demibranch appears to be free from the mantle, and that of the inner demibranch from the visceral mass and from the fellow lamella of the opposite side, but the relations are not easy to determine, for the lamellæ are so rigid that they would come away readily from the adjacent parts even if organically united to them.
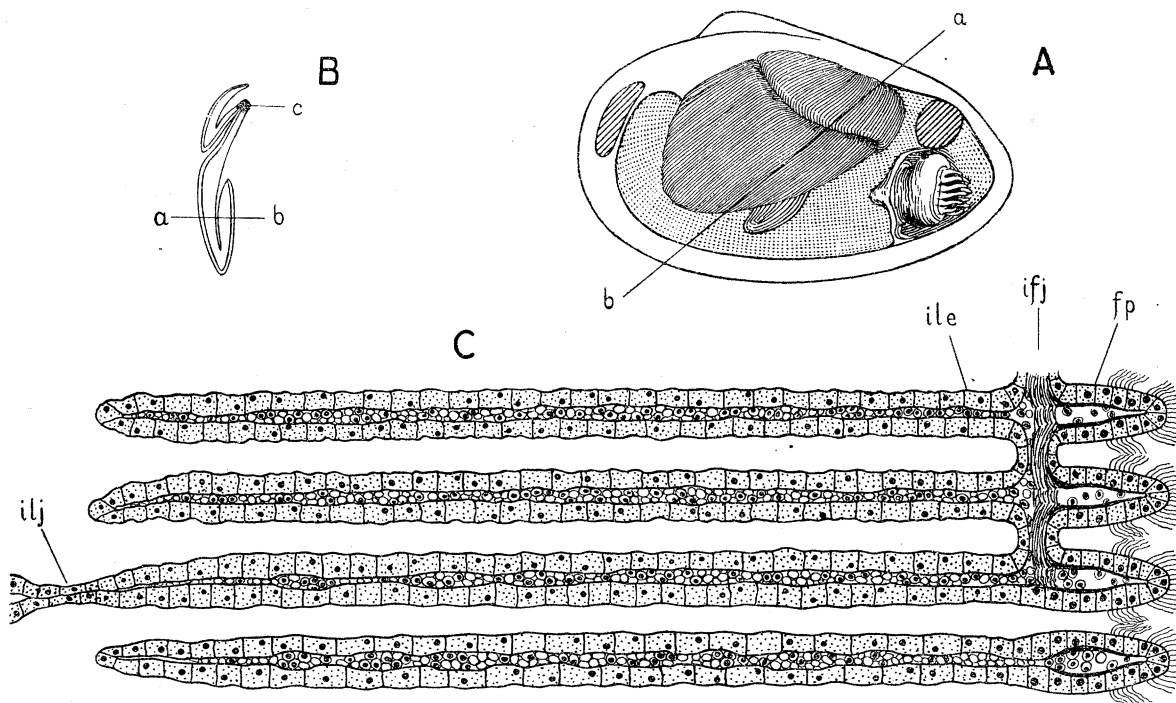
Fig. 23.—*Vesicomya stearnsi*. A, sketch of left side of body, showing the relative size of the gill. B, section of the gill in the direction *ab* in fig. A; *c*, gill axis. C, section of four filaments of the ascending lamella of the inner demibranch taken as *ab* in fig. B. *fp*, filament proper; *ifj*, interfilamentar junction; *ile*, interlamellar extension; *ilj*, interlamellar junction.

A horizontal section of four filaments of one lamella of the inner demibranch, taken in the direction *ab* in fig. 23B, is shown in fig. 23C. The "filaments proper" are quite normal, both as regards their epithelium, thickenings of the chitin, and arrangement of the cilia. The intrafilamentar cavity, as also that of the interlamellar extension, is filled with blood corpuscles. The interfilamentar junctions are normal, and are supported by chitin of a fibrous character. The epithelium of the interlamellar extensions consists of large cells with clearly marked outlines, as in *Lucina*, and with small nuclei. The interlamellar extensions of the filaments of the same lamella show very little disposition to fuse the one with the other

on the interlamellar side of the interfilamentar junctions, and it is this feature which causes a teased lamella to separate into plates; but this feature also may be noticed in some species of *Lucina* (*e.g.*, *Loripes leucoma*). Interlamellar septa of very narrow extent are found on every third or fourth filament in the inner demibranch.

The general conclusions, therefore, so far as the gill structure alone is concerned, point to resemblances between *Vesicomya* and *Lucina*, and not to any near affinity with the Protobranchia. The small size of the outer demibranch of *Vesicomya*, also, suggests a process of reduction which has reached a maximum in *Lucina*.

Lucinidæ.

The gills of *Lucina borealis*, *Lucina bengalensis*, and *Lucina* (*Loripes*) *leucoma* agree tolerably closely in their general structure. As is well known, the inner-demibranch alone is present. The surface is smooth, and the striations are faint, in consequence of the close packing of the filaments. The lamellæ are thick, owing to the great development of the interlamellar extensions of the filaments (fig. 24 A). The water-pores are greatly reduced in size; many, indeed, are completely occluded. In sections taken near the ventral edge of the demibranch the ascending and descending portions of each filament are seen to be connected by an interlamellar septum. In sections taken about half-way up, only each third, fourth, or fifth has a complete septum, and at higher levels each sixth or eighth.

The epithelium of the interlamellar extensions consists of large, well-defined cells; the cavity is almost obliterated, except in the innermost edges and in the inter-lamellar septa. The filamentar cavity is closed by a vesicular chitinous mass in *Lucina borealis*, *Lucina bengalensis*, and *Lucina æquicostata*, but in *Loripes leucoma* by the approximation of the greatly thickened chitin-bands that line the sides of the filaments. In *Lucina borealis*, *Lucina bengalensis*, and *Loripes leucoma* the inter-lamellar extensions of filaments of the same lamella very rarely fuse with one another at their internal (*i.e.*, interlamellar) edges (fig. 24 A, *a*), but such union is fairly common in *Lucina æquicostata*, so that here deep interfilamentar junctions are present as well as the true, chitin-supported interfilamentar junctions which lie just internal to the filaments proper. In this species the interlamellar septa are fewer, and the interfilamentar spaces wider than in the other three.

Diplodonta oblonga, although usually placed in the family Lucinidæ, has the outer demibranch present. The degree of importance to be attached to this fact has been discussed by PELSENEER (**68**, p. 16), by MÉNÉGAUX (**62**, p. 237), and by DALL (**15**, p. 545), the last recommending the separation of *Diplodonta* from the Lucinidæ to constitute a new family, the Diplodontidæ. The lamellæ are homorhabdic, and moderately plicate (fig. 24 B) with about fifteen filaments to the plica. The filaments have interlamellar extensions, rather less well-developed than in *Lucina*, which fuse

up in places to form bulky masses of subfilamentar tissue. The interlamellar junctions are septa, all of which rise high up the demibranch, and have large blood cavities.
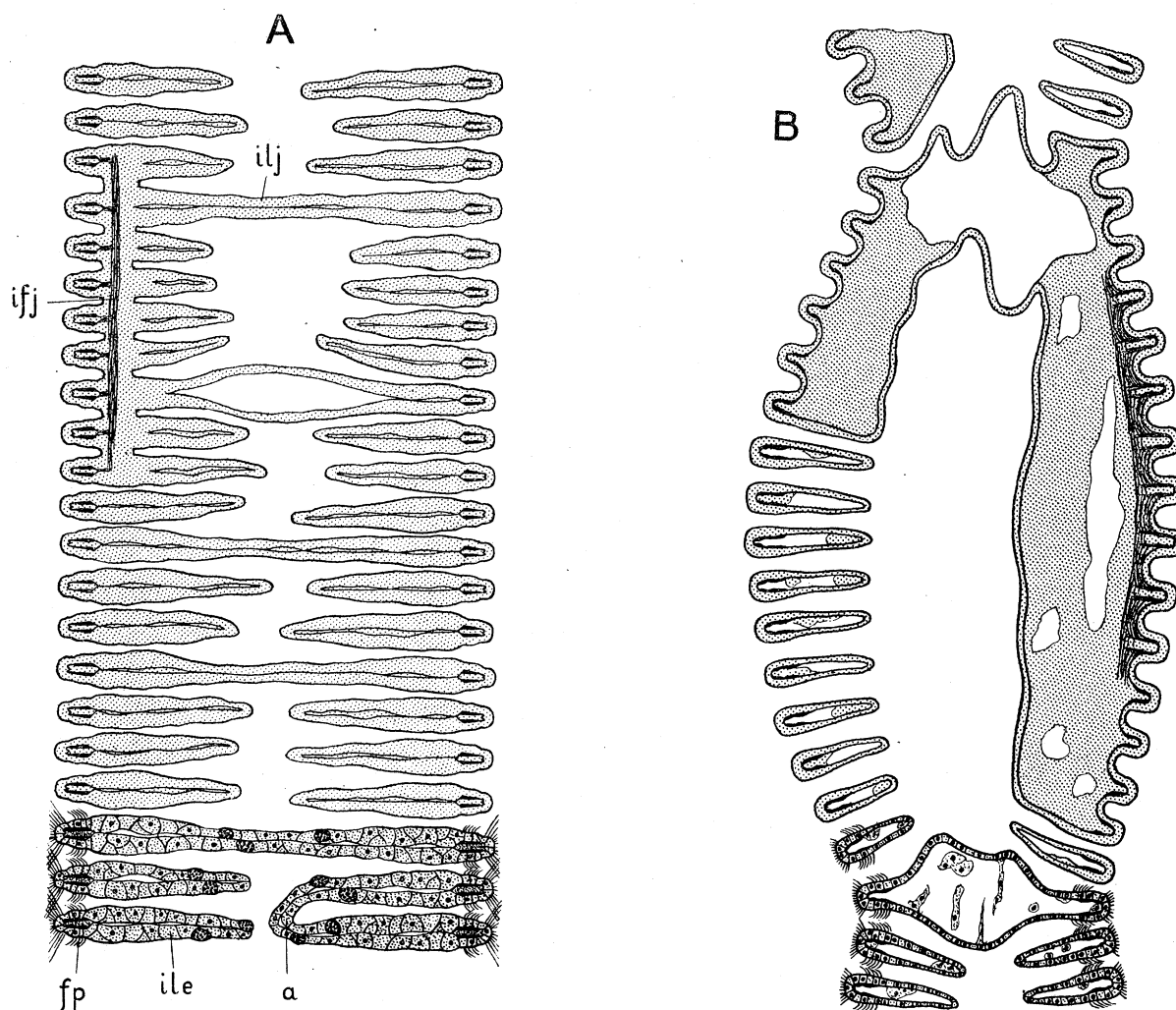
FIG. 24.—A, *Lucina bengalensis*. *a*, union of inner edges of adjacent interlamellar extensions. Other letters as in fig. 23. B, *Diplodonta oblonga*.

Montacuta substriata has no outer demibranch. The gill lamellæ are, like those of *Astarte*, very simple, flat, homorhabdic, with scanty development of subfilamentar tissue, without interlamellar extensions to the filaments, with interlamellar junctions in the form of bars, few in number and irregularly scattered.

Erycinidæ.

The disposition of the gill lamellæ of *Kellya cycladiformis* and *Kellya suborbicularis* is normal, but in *Lasæa*, as has already been made known by PELSENEER (**72**, fig. 96G) and DALL (**15**, p. 506), the reflected lamella of the outer demibranch is

wanting (fig. 2G, p. 152). The lower edge of the descending lamella of the outer demibranch of *Lasæa rubra* is confluent with the mantle, and the lamella is also held against the mantle by several short bars, which in a more normal demibranch would be the interlamellar junctions. The lamella has only three rows of interfilamentar junctions, and these are extremely delicate. The inner demibranch of *Lasæa* and both demibranchs of *Kellya* are exactly like those of *Astarte*, being homorhabdic, non-plicate, with very little subfilamentar tissue, and with interlamellar junctions in the form of scattered bars.

Galeommidæ.

The gill lamellæ of *Scintilla ambigua*, *Scintilla philippinensis*, *Galeomma turtoni* and *Chlamydoconcha orcutti* may be dismissed with the remark that they are simple and Astartiform. In *Galeomma* the outer demibranch hangs lower than the inner, but whether this is related to the gaping of the valves of the shell is doubtful, since in *Ephippodonta*, where the valves are so divaricated as to lie almost in one plane, the inner demibranch is far more extensive than the outer. The gills of *Ephippo-*
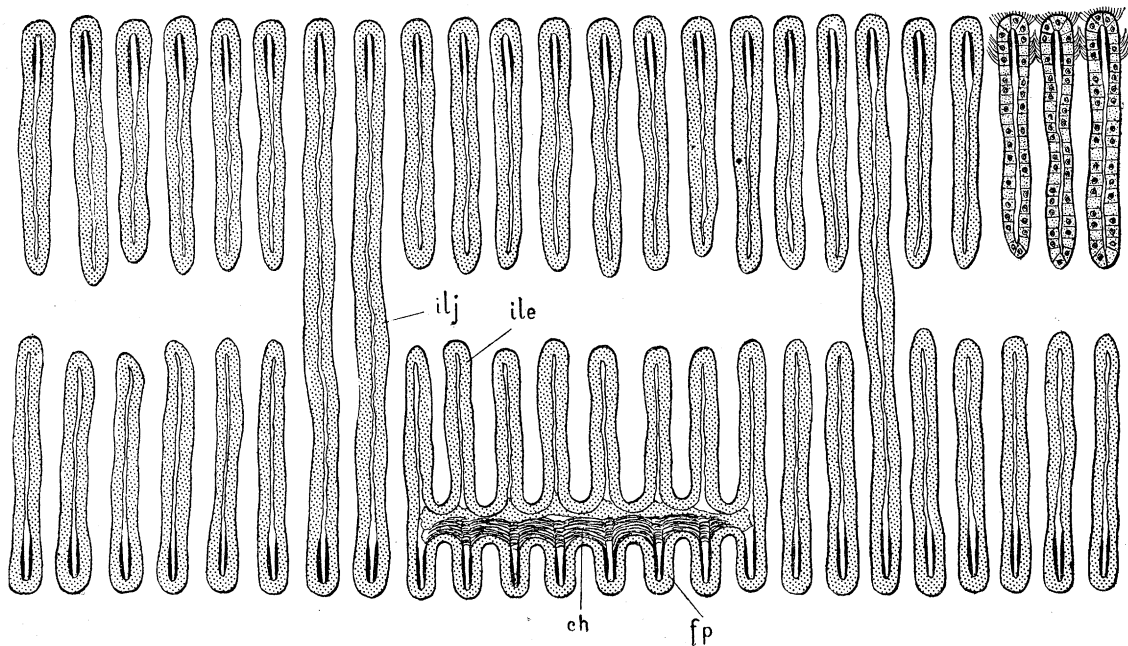
Fig. 25.—*Ephippodonta lunata.* *ch*, fibrous chitin in the interfilamentar junction; *fp*, filament proper; *ile*, interlamellar extension of the filament; *ilj*, interlamellar junction.

donta lunata differ from those of the other four species of Galeommidæ examined, in that all the filaments have interlamellar extensions. These exhibit no tendency to unite with their neighbours of the same lamella (fig. 25). The interlamellar junctions have the form of short bands, about six times as high as thick. Though doubtless related primarily to the interfilamentar junctions, they extend above and below the

levels of these junctions, so that, as shown in the figure, they may in some sections appear to be independent of them. Interlamellar junctions may occasionally be seen at the same level in adjacent filaments (fig. 25, *ilj*).

Cyrenidæ.

In the two species of *Cyrena* examined (*Cyrena sinuosa* and *Cyrena* (*Egeta*) *floridana*) the ascending lamella of the outer demibranch rises considerably above the level of the gill axis, forming a " supra-axial extension." In their structure the gill lamellæ of these two species differ remarkably, since those of *Cyrena floridana* are flat, homorhabdic, and with interlamellar septa of various heights, only each sixth or
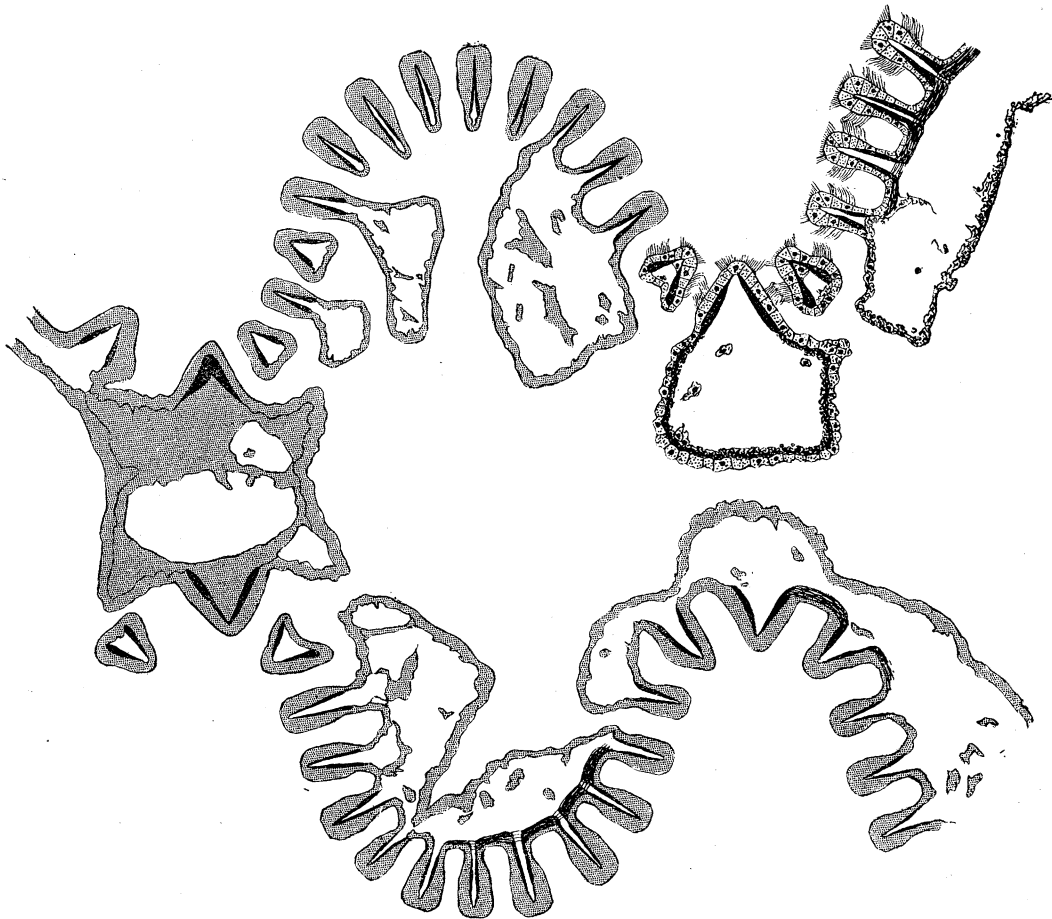
FIG. 26.—*Corbicula lydigiana.*

seventh rising more than half-way up the demibranch, whereas in *Cyrena sinuosa* the lamellæ are plicate and heterorhabdic. The principal filaments of *Cyrena sinuosa* have a frontal surface in the form of a shallow ridge, and the interlamellar septa are alternately high and low. Subfilamentar tissue is not very abundant, and the two or

three filaments adjacent to the principal filament are slightly larger than the average. There are about 20—25 filaments to the plica in both demibranchs.

The outer demibranch of *Corbicula lydigiana* has no supra-axial extension. The lamellæ are plicate, and the principal filaments, though slightly wider than the ordinary filaments, are not much larger (fig. 26). There are about 10—14 filaments to the plica. The subfilamentar tissue is highly lacunar in the specimen examined, and there are large blood-tubes, usually two in number, in the interlamellar septa. *Corbicula minor* agrees in the main with *Corbicula lydigiana*, but has about 12—15 filaments to the plica.

Sphærium pallidum has flat, homorhabdic gill lamellæ. In the lower part of the demibranch each of the filaments has its own interlamellar septum, but these septa all cease at about the same level, so that the upper parts of the two lamellæ of a demibranch dissected from the body tend to fall apart.

Rangiidæ.

The lamellæ of *Rangia cyrenoides* are homorhabdic and flat. The interlamellar junctions are septa, which in sections taken half-way up the demibranch are set at intervals of 10 or 12 filaments. There is a very considerable development of subfilamentar tissue, containing here and there large vertical and horizontal blood-tubes, and the water-pores are much reduced in size. The chitin lining the filaments is thin, with a tendency to sponginess on its inner surface; and the cavities are choked by cells, which appear not to be blood corpuscules.

Ætheriidæ.

The gills of *Ætheria plumbea* are plicate, with 15 to 20 filaments to the plica. They might almost be said to be homorhabdic, since although one or more filaments occupying a basal position between two plicæ may be rather broader than usual, with the chitin-bands set at a less acute angle, this is by no means invariably the case, and further, such filaments are occasionally to be found in groups of 2 or 3 on the sides of the plicæ. Subfilamentar tissue is fairly abundant, and tends to fill up the plical cavity. The interlamellar septa are alternately high and low.

Mülleria dalyi has flat, homorhabdic lamellæ, with such profuse development of subfilamentar tissue, extending across the interlamellar space, that it becomes difficult to distinguish any regularity in the arrangement of the interlamellar junctions (fig. 27). The general structure recalls that of *Anodonta* or *Unio*, and the resemblance is emphasised by the presence of brittle calcified rods (*cr*) in the thickened chitin-bands at the sides of the filaments, and of spherical concretions in the masses of subfilamentar tissue. As WOODWARD (**108**, p. 91) has

already suggested, this genus may ultimately find a resting place in the family Unionidæ.
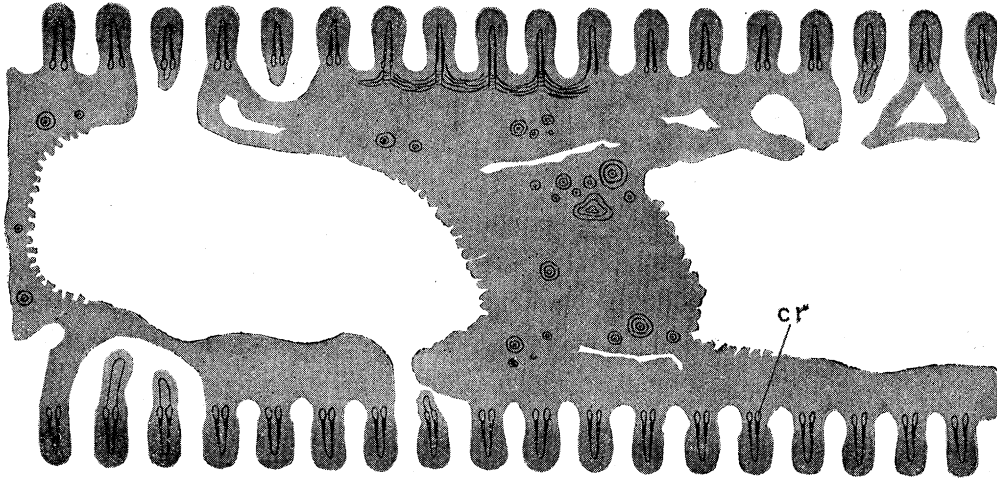
FIG. 27.—*Mülleria dalyi.* *cr*, calcified rod.

Unionidæ.

The gill-structure of *Anodonta* and *Unio* has been so repeatedly and thoroughly investigated that little need be said here. The outer demibranch of *Anodonta* has flat homorhabdic lamellæ, with numerous interlamellar septa, especially in sections taken towards the lower edge of the demibranch. The alternation of the high and low septa is by no means regular, and in many places there are two high to each low one. The high septa occur at intervals of 5 to 7 filaments.

The inner demibranch is usually described as moderately plicate, but in the living animal the lamellæ are flat. They become plicate, however, if some alcohol be dropped upon them, or if they are irritated with the point of a pin—probably by the contraction of the muscle tracts horizontally disposed in the subfilamentar tissue. On killing in spirit the plications become very marked. If, however, the whole gill be dissected out, and while still in water, clamped at its two ends to a piece of cork or wood, and then transferred bodily to absolute alcohol, the inner demibranch can be fixed in such a way as not to exhibit these foldings. The interlamellar septa are more regular than in the outer demibranch, and in sections taken about half-way up, the septa occur at intervals of about twenty filaments.

But little circulation can occur in the intrafilamentar cavities, since these are almost, if not quite, obliterated by the excessive thickening of the chitin which occurs at the level of each interfilamentar junction. Large blood-tubes, however, are seen at the sides of the interlamellar septa, one to each septum in the inner demibranch, and two in the outer, and these are connected up by smaller irregular channels running horizontally in the subfilamentar tissue of the interfilamentar

junctions. The interlamellar extensions of the filaments are very broad, and tend to fuse up into great masses of loose lacunar tissue, and the water-pores are reduced to small elliptical apertures, arranged in sinuous or irregular horizontal lines.

The calcified rods have already been treated of in the General Part of this paper (p. 168). They extend from one interfilamentar junction to the next, but are not continued through the interfilamentar junctions. JANSSENS (39) has shown that these rods are deposits of calcium phosphate, with a little calcium carbonate, in the chitin-bands that line the sides of the filaments. The spherical concentrically striated concretions, that in some specimens occur in such abundance in the loose subfilamentar tissue, he has shown (p. 61) to be of a similar nature—calcium salts and a chitin basis. These are not to be confounded with the yellow granules which PECK described (66, p. 69, *yg*) as food reserves for the nourishment of the Glochidia.

The cilia of the filament proper are normal, and are arranged in frontal and lateral tracts. The epithelium of the interlamellar extensions consists of low flattened cells, but those at the inner edges of the extensions, forming the lining of the inter-lamellar spaces, are larger and taller, and many of these are ciliated. There is not a uniform layer of ciliated epithelium here, but groups of three or four ciliated cells occur scattered among the mucus-secreting cells.

The gills of the *Unio pictorum* agree very closely with those of *Anodonta*, and have a vast amount of subfilamentar tissue, but those of *Unio ambiguus* have the subfila-mentar tissue more sparingly developed. The calcified rods are larger in proportion than in *Unio pictorum*.
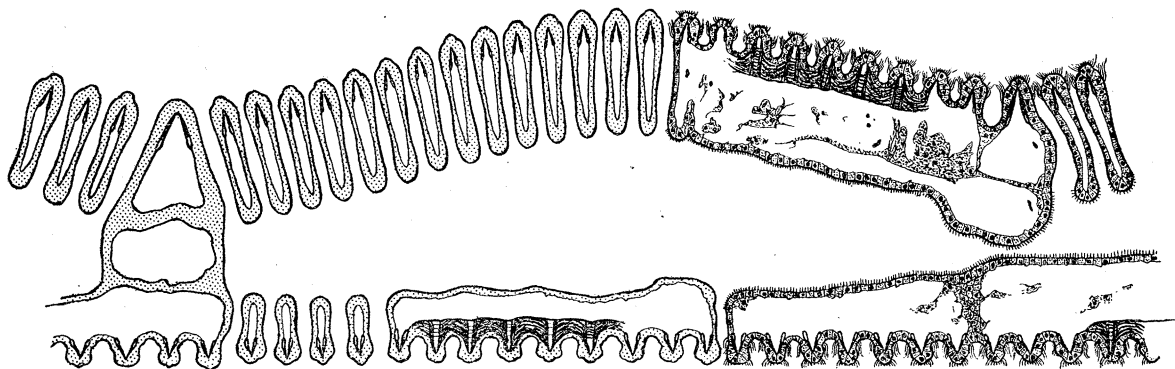
FIG. 28.—*Monocondylœa sp.* The upper part of the figure is the descending lamella, which is slightly plicate. Two principal filaments are shown.

The outer and inner demibranchs of *Monocondylœa sp.* are similar in structure, and in each there is a curious difference between the descending and ascending lamellæ. The descending lamella is slightly plicate and heterorhabdic (fig. 28). The principal filaments have a ridged front, and are situated at intervals of 15–25 fila-ments. Each is in relation with a narrow, thick interlamellar septum, containing a large central blood-tube. The ascending lamella, however, is flat, and the filaments

in connection with the interlamellar septa are not differentiated as principal filaments, or are but very slightly so.

The interlamellar extensions of the descending filaments are broader than those of the ascending filaments, and, since the water-pores are larger than in *Anodonta*, more disconnected filaments are seen in such sections as do not actually pass through an interfilamentar junction. The filamentar cavities are more patent, and the calcified rods more strap-shaped than in *Anodonta*. Muscle fibre is recognisable in the interfilamentar junctions. The interlamellar edges of the filaments are ciliated.

Dreissensiidæ.

The lamellæ of *Dreissensia polymorpha* are flat and homorhabdic. The interlamellar junctions are septa reaching to various heights. The highest of all are about ten filaments apart in both demibranchs. Subfilamentar tissue is less abundant than in *Anodonta*, but it is present in sufficient amount to reduce the fenestræ to elliptical water-pores. Except in the lowest parts of the lamellæ, the vertical rows of water-pores are only half as numerous as the filaments, a feature already
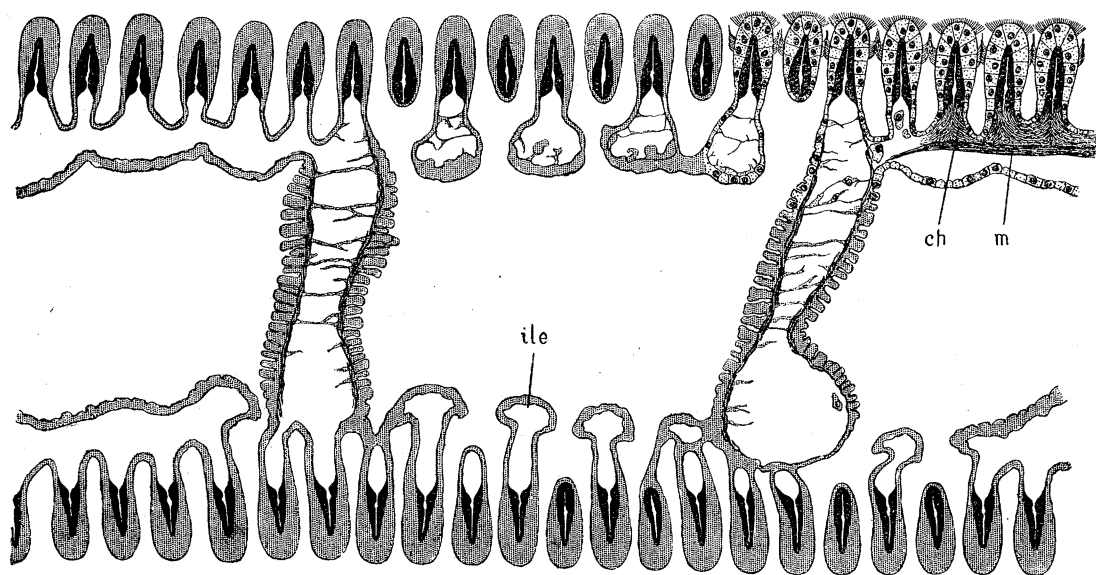
FIG. 29.—*Dreissensia polymorpha*. *ch*, fibrous chitin in the interfilamentar junction; *ile*, interlamellar extensions on alternate filaments; *m*, muscular tissue.

noted by JANSSENS (**39**, p. 22). This fact is due to each alternate filament having an interlamellar extension which spreads antero-posteriorly, and brings the internal or interlamellar opening of the water-passage opposite the internal edges of the intervening filaments (fig. 29, *ile*). It is worthy of remark that RICE (**83**, pp. 51–55), in spite of the enormous differences in the gill-structure of *Dreissensia* and *Mytilus*, objects to the dissociation of these genera.

Sub-order TELLINACEA.

Species Examined :—

Tellinidæ . . . { *Tellina nitida.*
                  Tellina (Arcopagia) capsoides,

Scrobiculariidæ . { *Scrobicularia piperata.*
                    Semele orbiculata.
                    Semele cordiformis.

Donacidæ . . { *Donax variabilis.*
               Donax faba.

Mesodesmatidæ . { *Donacilla cornea.*
                  Paphia glabrata.
                  Mesodesma (Ceronia) donacia.
                  Mesodesma novæ-zelandiæ.

Mactridæ . . { *Mactra stultorum.*
               Mactra violacea.
               Mactrinula plicataria.
               Mulinia sp.
               Vanganella taylori.

Previous Accounts :—

> *Tellina,* Valenciennes, **102**, 1845, p. 511.
> *Tellina,* Pelseneer, **68**, 1888, Plate 4, fig. 10.
> *Tellina planata,* Ménégaux, **61**, 1889, p. 142.
> *Tellina planata* and *Tellina nitida,* Rice, **83**, 1897.
> *Capsa fragilis,* Rice, **83**, 1897.
> *Scrobicularia sp.,* Posner, **76**, 1875.
> *Scrobicularia piperata,* Rice, **83**, 1897.
> *Donax trunculus,* Sluiter, **95**, 1878.
> *Donax serra, Donax politus,* and *Donax trunculus,* Rice, **83**, 1897.
> *Mactra stultorum,* Sluiter, **95**, 1878, fig. 9.

Tellinidæ.

The direct lamella of the outer demibranch of *Tellina nitida* and *Tellina (Arcopagia) capsoides* is upturned, and has a reflected lamella in its posterior portion only (see fig. 1, C, D, and E, p. 151). The anterior third of the gill has no outer demibranch. The lamellæ are flat and homorhabdic. All the filaments have interlamellar septa, which rise the full height of the inner demibranch in *Tellina capsoides,* but which in *Tellina nitida* are alternately high and low (fig. 30B). The low septa, however, of the latter species are continued as interlamellar extensions, or incomplete septa, up

the filaments to which they belong. The subfilamentar tissue of the interfilamentar junctions extends upward and downward to a very considerable distance, so as to obliterate most of the water-pores. To such an extent is this carried in *Tellina nitida* that a lamella mounted whole shows water-pores only at rare intervals. The structure of the lamellæ of *Tellina capsoides*, and, according to RICE (**83**, Plate 4), that of *Tellina planata*, is less abnormal. In the outer or upturned demibranch of
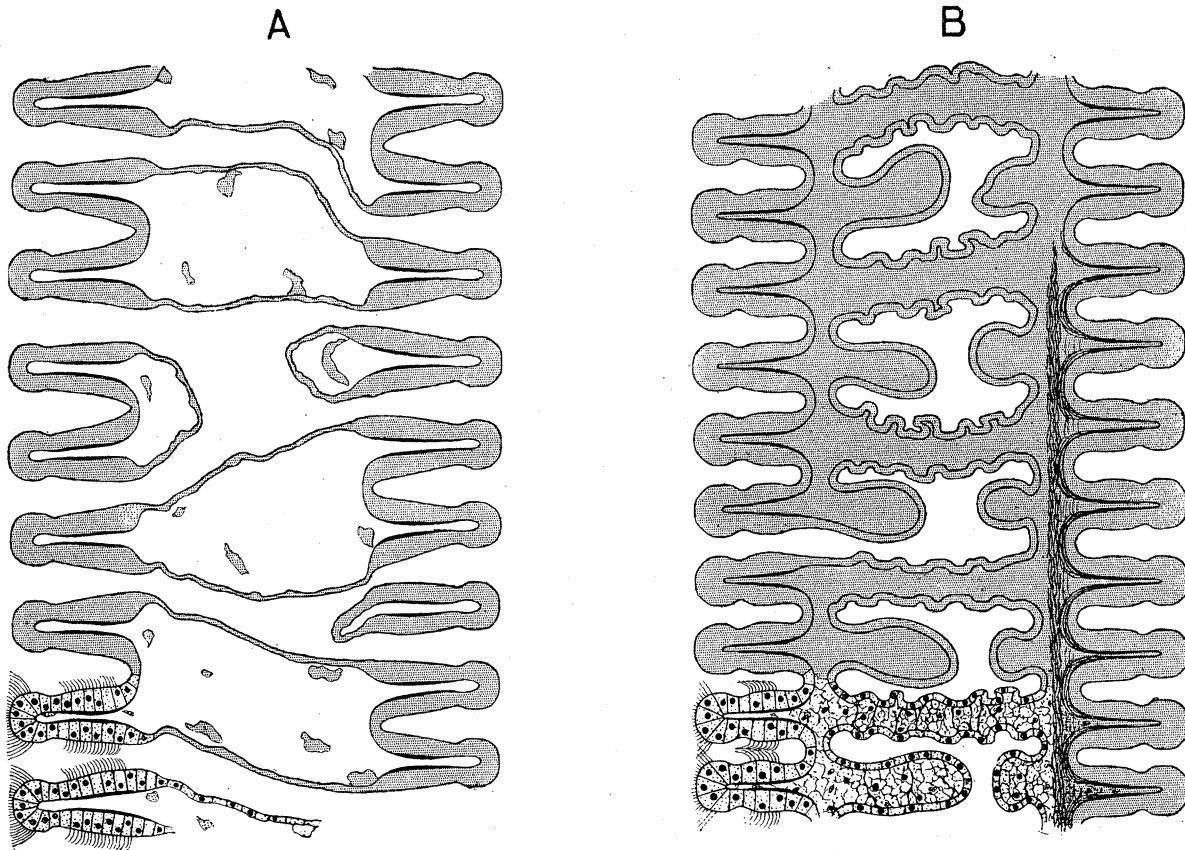
FIG. 30.—A, *Scrobicularia piperata.* B, *Tellina nitida.*

Tellina the structure is similar to that of the inner, and in the part which has no reflected lamella the interlamellar extensions are concrescent with the visceral mass.

Scrobiculariidæ.

The outer demibranch of *Scrobicularia piperata* is upturned, and consists of a direct lamella only. The lamellæ of both demibranchs are flat and homorhabdic. There is no regular succession of high and low septa in the inner demibranch, and the high septa are attached at their sides to 1, 2, or 3 filaments, and are swollen in the middle (fig. 30A) and highly lacunar. The interlamellar extensions of the upper demibranch are fused with the visceral mass. The tracts of lateral cilia on the filaments are rather wide.

In *Semele orbiculata* and *Semele cordiformis* the outer demibranch is upturned and has no reflected lamella. The lamellæ are strongly plicate, and have large intraplical blood-tubes. Between the interfilamentar junctions the tubes are free from the filaments. There are 32–35 filaments to the plica. Principal filaments are barely differentiated in the lower parts of the inner demibranch, but in the upper parts they may be distinguished by their chitin-bands being set at a wider angle than usual. Owing to the narrowness of the interlamellar septa, the ascending and descending parts of each principal filament are closely approximated. Subfilamentar tissue is moderately abundant, and at the levels of the interfilamentar junctions forms a horizontal septum across the plical cavity. Muscular tissue is recognisable in these septa and in the interlamellar septa.

Donacidæ.

The ascending lamella of the outer demibranch of *Donax variabilis* and *Donax faba* has a marked supra-axial extension, which, in the latter species, is not clearly marked off from the sub-axial part (fig. 2E, p. 152). The lamellæ of the different species of *Donax* have already been shown by RICE (**83**, pp. 70–71, and Plate 4) to exhibit great variety, *Donax trunculus* having flat lamellæ, *Donax politus*
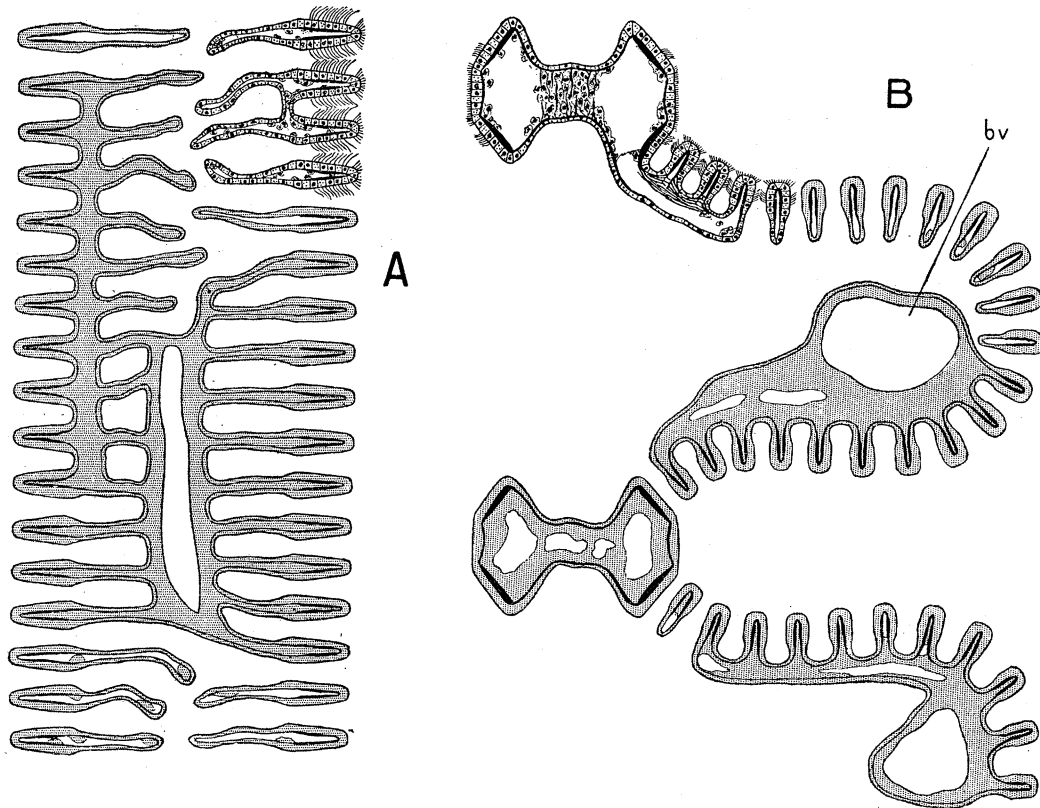
FIG. 31.—A, *Donax variabilis*. B, *Donax faba*. *bv*, blood-vessel running vertically within the apex of the plica.

slightly plicate, and *Donax serra* strongly plicate lamellæ. The figure of *Donax trunculus* given by SLUITER (**95**, fig. 7) shows the lamellæ slightly plicate, but since this author represents in his fig. 8 the interfilamentar junctions as effected by ciliated discs, it is evident that no great reliance can be placed on his illustrations. The species *Donax variabilis* and *Donax faba* bear out the observations of RICE as to the diversity of gill-structure in this genus, the former having flat homo-rhabdic lamellæ (fig. 31A), and the latter plicate heterorhabdic (fig. 31B).

In *Donax variabilis* each filament has an interlamellar extension about as wide as the filament itself, and, except in the lower parts of the demibranch, these do not unite across to form interlamellar septa, but unite in an irregular manner to enclose large blood-sinuses. The lateral tracts of cilia are unusually wide, and the cilia themselves are long. *Donax faba* has about twenty-two filaments to the plica (fig. 31B). Each plica has a vertical blood-tube (*bv*) in its interior. The principal filaments are well-differentiated, and have a frontal surface in the form of a shallow truncated ridge. The interlamellar septa are narrow.

Mesodesmatidæ.

Donacilla cornea has strongly-marked plicæ, antero-posteriorly compressed, and consisting of about twenty-five filaments each. The principal filaments are large, and have a broad shallow frontal groove. The interlamellar septa are alternately high and low. The ordinary filaments have no interlamellar extensions; subfila-mentar tissue is scanty, and, except in the regions of interfilamentar junctions, the filaments are free.

The lamellæ of both demibranchs of *Paphia glabrata* are plicate, each plica consisting of 20–26 filaments. The supra-axial extension, however, of the ascending lamella of the outer demibranch is barely plicate. Principal filaments are not differen-tiated, but the 2, 3, or 4 filaments occupying a basal position between the two plicæ may have thicker chitin-bands than usual. The filaments have no interlamellar extensions. A small vertical blood-tube occurs in the apex of each plica, and, except in the region of the interfilamentar junctions, this is connected with a single apical filament.

Mesodesma (Ceronia) donacia has moderately plicate lamellæ, with about twenty-five filaments to the plica. In *Mesodesma novæ-zelandiæ* the plications are less marked, and there are 14–20 filaments to the plica. No principal filaments are differentiated in either species. All the septa rise high, and each has a single vertical blood-tube, communicating with horizontal vessels in the interfilamentar junctions. The filaments have wide interlamellar extensions.

Mactridæ.

Both *Mactra stultorum* and *Mactra violacea* have flat homorhabdic lamellæ. In the latter species all the filaments have interlamellar extensions, about one and a half

times the width of the filament proper.   At the lowest levels of the demibranch
these extensions are continuous across the interlamellar space as septa.   There is no
alternation of low and high septa, but their heights are irregularly varied.   About
every fifth septum extends half-way up the demibranch ; none extend higher.

Muscle fibres are horizontally disposed in the interfilamentar junctions and inter-
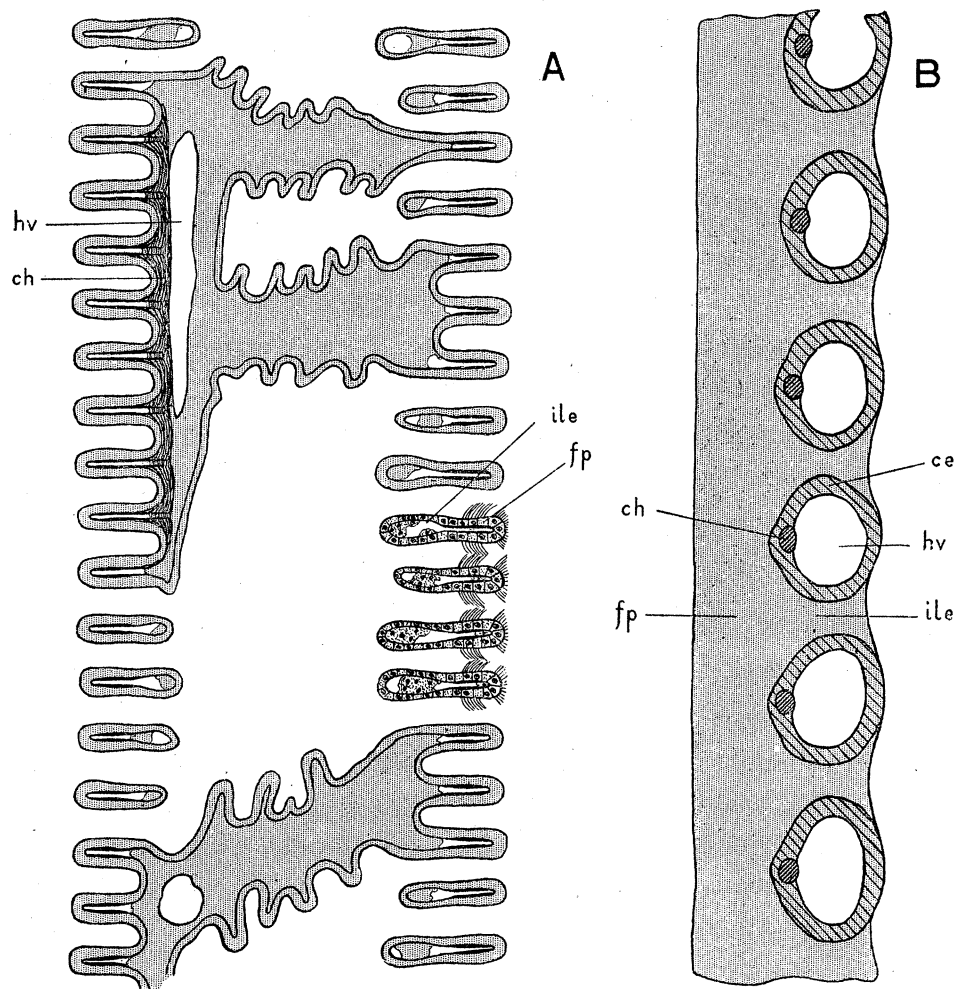lamellar septa.   The muscle strands of the upper edges of the interlamellar septa

Fig. 32.—*Mactra stultorum*.   A, horizontal section of a portion of one demibranch.   B, vertical section of
    one lamella showing the side view of a filament.   The section is taken in the direction of the line *hv*,
    fig. A.   *ce*, cellular tissue of the interfilamentar junction; *ch*, fibrous chitin of the interfilamentar
    junction; *fp*, filament proper; *hv*, horizontal blood-vessel in the interfilamentar junction; *ile*, inter-
    lamellar extension of the filament.

curve upward, and are continued for some distance along the inner border of the
filament.   The inner edges of the interlamellar extensions of the same lamella
frequently unite and form a common mass of subfilamentar tissue traversed by a
large vertical blood-sinus.   Sometimes a vertical blood-tube is in relation with a

single filament only.   Large blood-tubes running in the interfilamentar junctions are a conspicuous feature in *Mactra stultorum* (fig. 32A and B, *hv*), but they are barely recognisable in *Mactra violacea*.

In *Mactra stultorum* the high septa, some of which reach the full height of the demibranch, are disposed at very irregular intervals, varying from 3 to 10 filaments. They may have a unilateral vertical blood-tube, communicating with the large horizontal tubes of the interfilamentar junctions.   The figure of this species given by SLUITER (**95**, fig. 9) is incorrect, in that no interfilamentar junctions at all are represented.

Mactrinula plicataria has flat homorhabdic lamellæ, all the filaments of which have interlamellar extensions about one and a half times as wide as the filaments proper.   The interlamellar extensions of the filaments of the same lamella show a remarkable tendency to fuse up into relatively solid masses of subfilamentar tissue, not confined to the regions of the interfilamentar junctions.   The water-pores are thus greatly reduced in size.   High septa recur at intervals of 10 or 12 filaments, and have unilateral vertical blood-tubes situated alternately on the ascending and descending sides of the demibranch.

Mulinia has flat homorhabdic lamellæ, the filaments of which have interlamellar extensions about as wide as those of *Mactrinula*; but it is only the inner edges of these extensions which tend to unite with those of adjacent filaments.   The result is the formation of deep interfilamentar junctions, independent of the true or superficial interfilamentar junctions.   High interlamellar septa are disposed at intervals of 10 or 14 filaments.

The gills of *Vanganella taylori* (*Resania lanceolata*) are intermediate in character between those of *Mulinia* and *Mactrinula*, since adjacent interlamellar extensions of the filaments may unite at their inner edges only, or by projections from the middle of their faces, or by the whole of their faces, in the last instance giving rise to a comparatively solid mass of subfilamentar tissue.   The high septa are situated about twelve filaments apart, and are very narrow, so that the two lamellæ are brought close together.   Each septum has a single median vertical vessel.

Sub-order VENERACEA.

SPECIES EXAMINED :—

Veneridæ . . .
{
Venus striatula.
Venus fasciata.
Venus casina.
Venus (Anaitis) calophylla.
Meretrix petechialis.
Circe minima.
Circe pectinata.
Circe dispar.
Dosinia exoleta.
Tapes pullastra.
Tapes decussatus.
Tapes aureus.
Tapes virgineus.
Venerupis pulcherrima.
}

Petricolidæ . . {
Petricola lithophaga.
Petricola monstrosa.
}

Glaucomyidæ . { *Glaucomya chinensis.* }

PREVIOUS ACCOUNTS :—

Venus sp., POSNER, **76**, 1875, p. 552, and Plate 31, fig. 15.
Venus chione, BONNET, **5**, 1877.
Venus gallina, SLUITER, **95**, 1878, fig. 13.
Venus mercenaria, KELLOGG, **42**, 1892, p. 422 and fig. 70.
Venus verrucosa, RICE, **83**, 1897, Plate 4, fig. 11.
Cytherea chione, RICE, **83**, 1897.
Dosinia (Arthemis) lupinus, DESHAYES, **17**, 1844–48, Plate 94A, fig. 4.
Petricola pholadiformis, RICE, **83**, 1897.

The Veneracea may be dismissed somewhat curtly, since the gills of all the species examined (see list above) conform to the same general type. There is a supra-axial extension of the ascending lamella of the outer demibranch, which differs from the subaxial part in the obliquity of its filaments, and in being almost devoid of plication. The lamellæ of the inner demibranch are usually strongly plicate ; in *Venus striatula* and *Circe minima* they are only slightly so. The lamellæ of the outer demibranch have shallow plications as a rule ; in *Meretrix petechialis*, however, the plication is almost as strongly marked as in the inner demibranch, while in *Circe minima* the plication is practically absent.

The average number of filaments in a plica of the inner demibranch varies in the different forms. In *Venus striatula* it is 16, *Venus fasciata* 20, *Venus casina* 25, *Venus calophylla* 26 (fig. 33), *Meretrix petechialis* 42, *Circe minima* 13, *Circe*
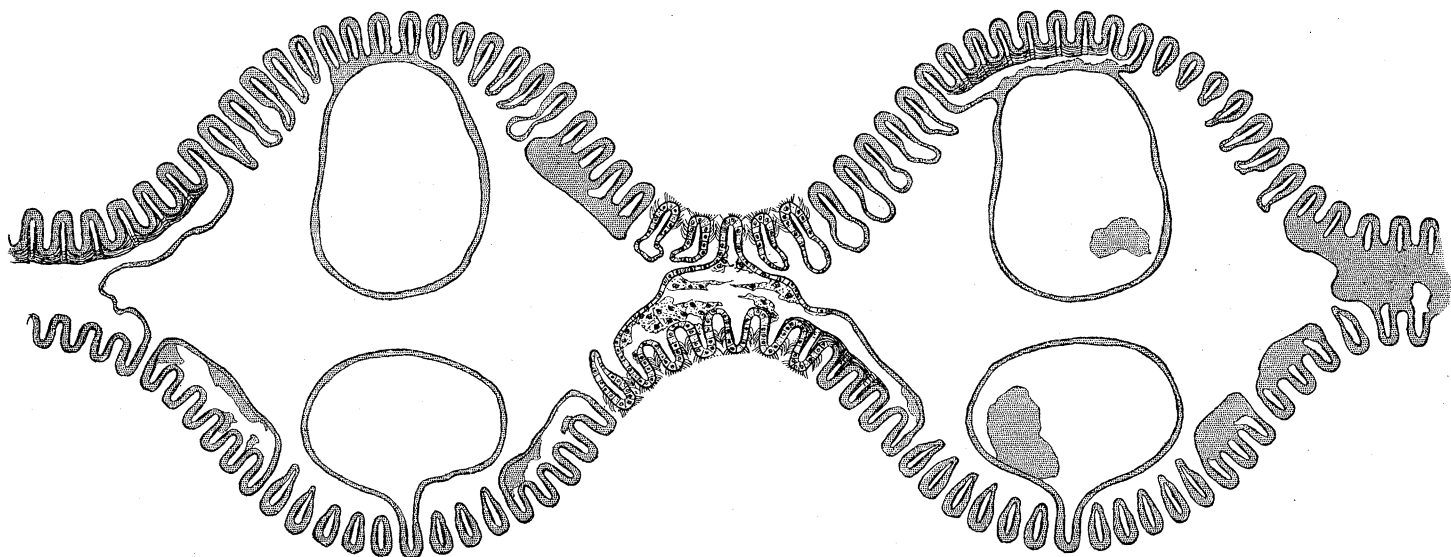
FIG. 33.—*Venus calophylla.*

pectinata, Circe dispar, Tapes pullastra, Tapes decussatus and *Tapes virgineus* 30, *Tapes aureus* 22 (fig. 34), *Venerupis pulcherrima* 13, *Petricola lithophaga* 18, *Petricola monstrosa* 24 (fig. 35), and *Glaucomya chinensis* 22. In the outer demibranch the plicæ are rather unequal in size, and considerable variation may be noticed in the number of filaments in the different plicæ of the same lamella. Roughly speaking, the number of filaments is about two-thirds of that found in the plicæ of the inner demibranch, but in *Glaucomya chinensis* the numbers are nearly equal in the two demibranchs.

At the anterior, posterior and ventral parts of the demibranchs the lamellæ may be said to be homorhabdic, but in the middle part of each lamella, where one naturally looks for characteristic features, the one, two, three or four filaments which occupy a basal position between two plicæ may be slightly wider than usual, and have the chitin-bands rather thicker, and set at a less acute angle than in the ordinary filaments of the plica. Where three filaments are so differentiated, the middle one is larger than its neighbours. In *Venus fasciata* the principal filaments are quite as much differentiated as those of Tapes aureus (fig. 34), but in *Venus calophylla* (fig. 33) the basal areas are wider, and the basal filaments do not differ from the ordinary filaments. In the inner demibranch of *Circe dispar* the middle one of the enlarged basal filaments may have its frontal ridge truncated or even slightly grooved, but this feature is not constant even in different parts of the same lamella.

The interlamellar septum which is in relation with these differentiated filaments invariably rises nearly to the upper edge of the demibranch.   If any vertical blood-tube is at all discernible, it is usually unilateral, but if the interlamellar septa are so narrow that the plical bases which they connect are closely approximated, the tube
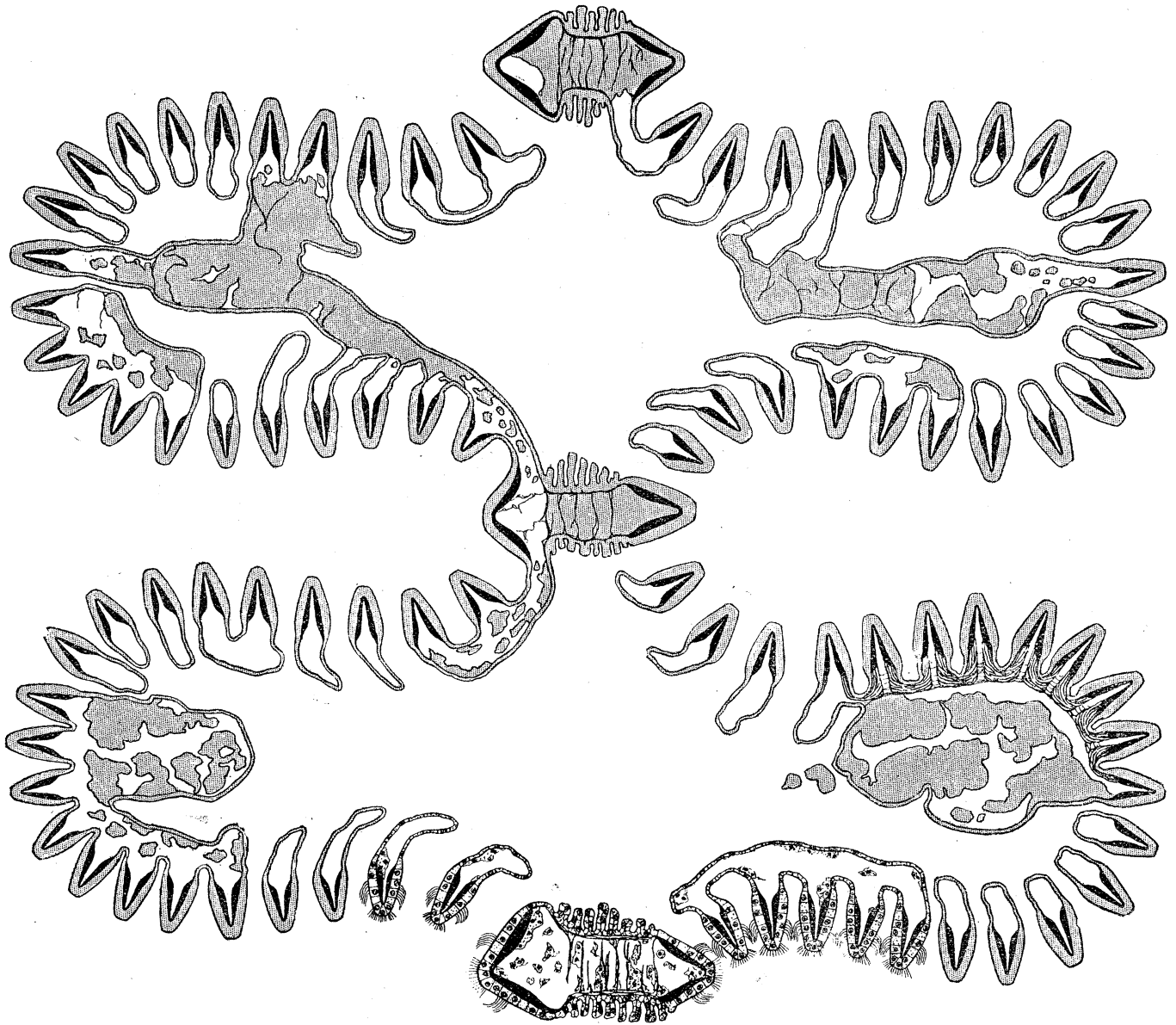
FIG. 34.—*Tapes aureus.*

is median (*e.g., Petricola lithophaga*).   The apical filaments of each plica are connected with a vertical intra-plical blood-tube, small in some species, large in others   The tubes in the descending lamella are larger than those in the ascending.   Where the plications are shallow, as in the lower parts of the outer demibranchs and the lowest

parts of the inner, the two tubes may be united across, forming an interlamellar septum ; and at still lower levels the two tubes become a single one.
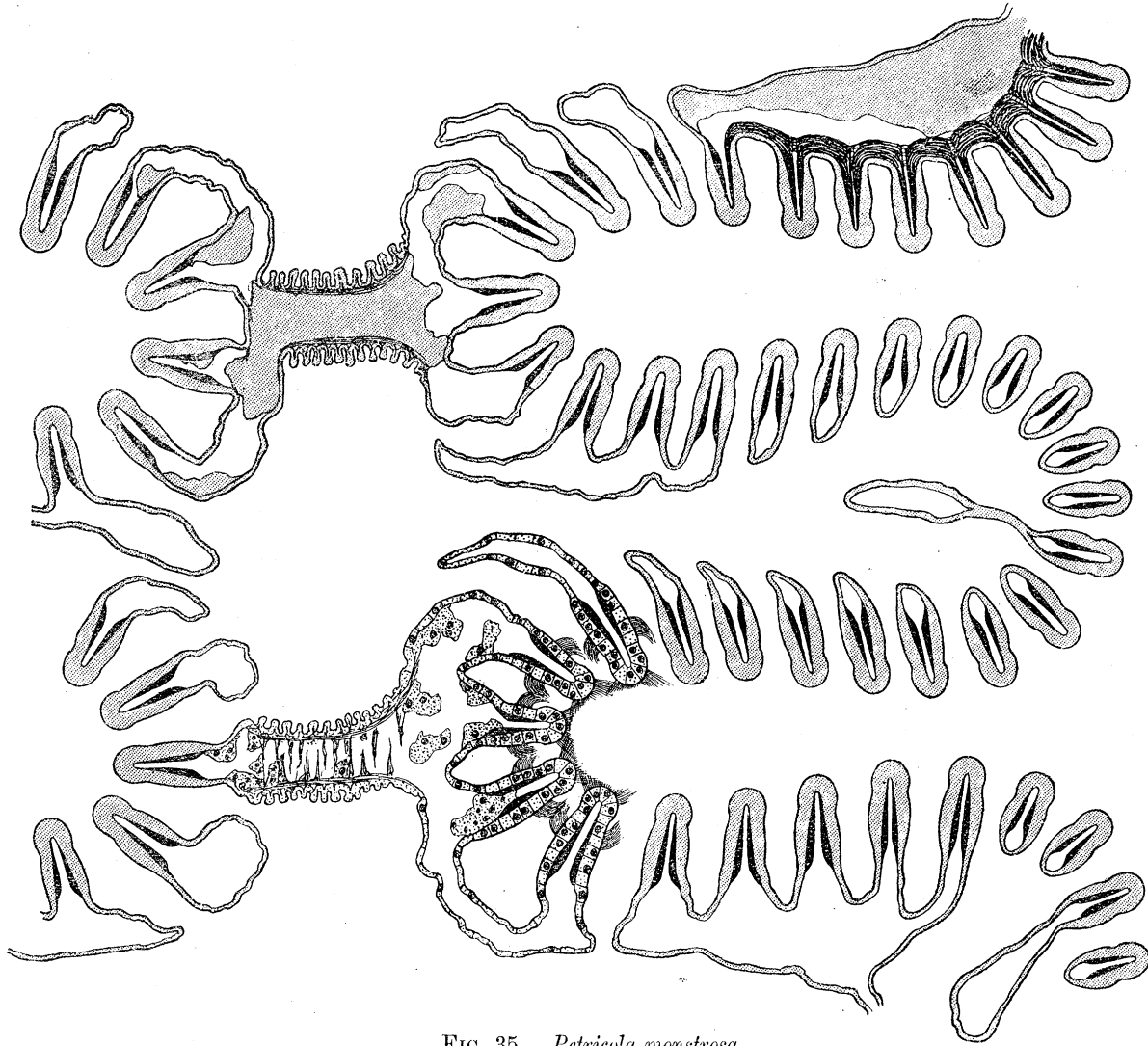
FIG. 35.—*Petricola monstrosa.*

This is very interesting when considered in relation with the figure of *Venus mercenaria* given by KELLOGG (**42**, fig. 70), in which the plicæ have inturned apices. There is a suggestion of a definite connection between the presence of these intra-plical tubes and the fact that all the interlamellar septa rise high. It is shown elsewhere that at least in some cases where the interlamellar septa are alternately high and low (*e.g., Lutraria*), the low septa have median vertical blood-tubes, which fork at the upper border of the septum, and one limb of the tube is continued up the ascending and one up the descending lamella (see remarks on intraplical blood-tubes on p. 175). One might, indeed, be tempted to propound the hypothesis that plication is the outcome of the failure of the incomplete or low septa

to hold the two lamellæ together, were it not for the disturbing fact that there are many plicate gills (*e.g.*, that of *Lutraria* just mentioned) which have the inter-lamellar septa of the *plical bases* alternately high and low; which have, in other words, their low septa related to plical bases and not to plical apices.

Sub-order CARDIACEA.

SPECIES EXAMINED :—

Cardiidæ . . . $\left\{\begin{array}{l}\text{\textit{Cardium edule.}} \\ \text{\textit{Cardium echinatum.}} \\ \text{\textit{Cardium (Fragum) unedo.}} \\ \text{\textit{Cardium (Fragum) hemicardium.}} \\ \text{\textit{Cardium (Laevicardium) norvegicum.}} \\ \text{\textit{Cardissa cardissa.}} \\ \text{\textit{Serripes groenlandicum.}}\end{array}\right.$

Tridacnidæ . . $\left\{\begin{array}{l}\text{\textit{Tridacna elongata.}} \\ \text{\textit{Tridacna crocea.}} \\ \text{\textit{Hippopus hippopus.}}\end{array}\right.$

Chamidæ . . $\left\{\begin{array}{l}\text{\textit{Chama gryphoides.}}\end{array}\right.$

PREVIOUS ACCOUNTS :—

Cardium edule, POSNER, **76**, 1875.

Cardium ciliatum, HAREN-NORMAN, **31**, 1881.

Cardium, DALL, **13**, 1889, p. 434, fig. G.

Cardium (five species), MÉNÉGAUX, **62**, 1890, p. 141.

Cardium edule, JOHNSTONE, **40**, 1899, pp. 43-48, and figs. 26-28.

Cardium edule, RICE, **84**, 1900.

Tridacna, VAILLANT, **99**, 1865, p. 156.

Hippopus maculatus (= *Hippopus hippopus*), PELSENEER, **71**, 1891, p. 205, and figs. 54 and 55.

Chama ruppelli, MÉNÉGAUX, **62**, 1890, p. 128.

Cardiidæ.

In *Cardium edule* the height of the outer demibranch is only one-fourth of that of the inner. Both demibranchs, however, are normal in their disposition, and DALL's diagram of the gill of *Cardium* (**13**, p. 434, fig. G) is quite incomprehensible to me. The lamellæ are strongly plicate, and each plica consists of 20 to 30 filaments. The principal filaments vary enormously in form, the frontal surface being flat (fig. 36, *a*), ridged (*b*), grooved (*c*), or with a ridge rising from the bottom of a

groove (*d*). Their chitin is thick, and inclined to vacuolation. Subfilamentar tissue is abundant, and at the levels of the interfilamentar junctions the plical cavities are frequently seen to be choked up by it. The interlamellar septa are alternately high and low, and the high septa do not rise the full height of the demibranch.
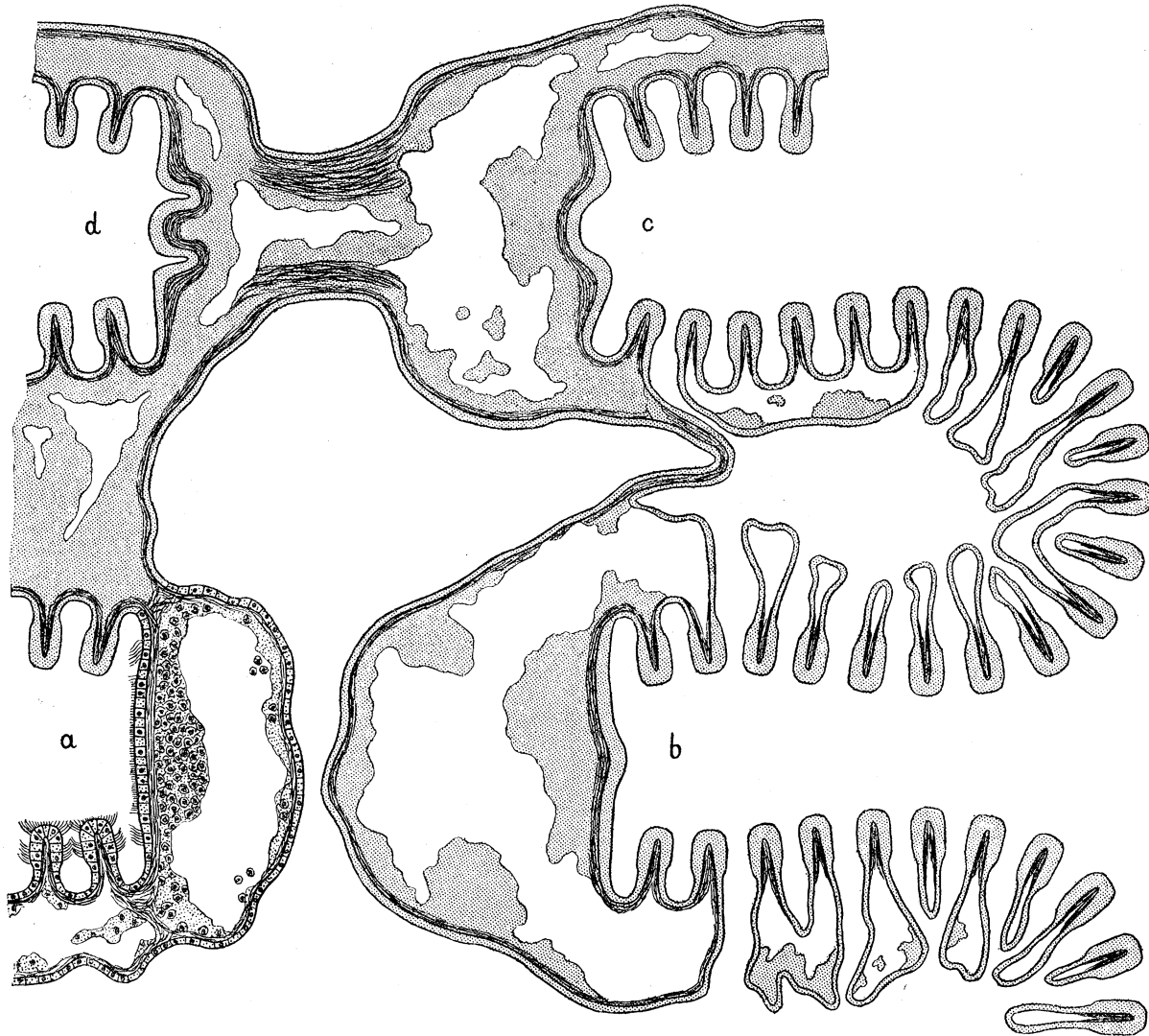
FIG. 36.—*Cardium edule.* *a, b, c* and *d*, various forms of principal filaments.

Four other species of *Cardium* were examined (*Cardium echinatum, Cardium (Fragum) unedo, Cardium (Fragum) hemicardium, Cardium (Lævicardium) norvegicum*). Their gills do not differ materially from those of *Cardium edule.* The principal filaments are less variable in shape, and the general form of their frontal surface is that of a broad shallow groove. In *Cardium norvegicum* the plicæ are antero-posteriorly compressed, and the subfilamentar tissue tends to form trabeculæ between the anterior and posterior sides of the plica. In *Cardium hemicardium* the

interlamellar extensions of the filaments were found to be greatly dilated, but this may possibly be due to the fact that the mode of killing caused the gills to become gorged with blood.

The gills of *Cardissa cardissa* (*Hemicardium cardissa*) have about twenty-four filaments to the plica. The principal filaments are not much larger than the ordinary filaments; their frontal surface has the form of a shallow ridge.

Serripes groenlandicum has 12–14 filaments to the plica in the outer demibranch, and 20–22 in the inner. The principal filaments have a deep frontal groove, which is broadest at its base. Near the lower border of the demibranch, however, the groove disappears, and the frontal surface has the form of a moderately sharp ridge.

Tridacnidæ.

Tridacna elongata has plicæ of considerable size (about eighty filaments), antero-posteriorly compressed so as to resemble the leaves of a book. All the interlamellar septa rise fairly high, but there is yet an alternation of high and moderately high
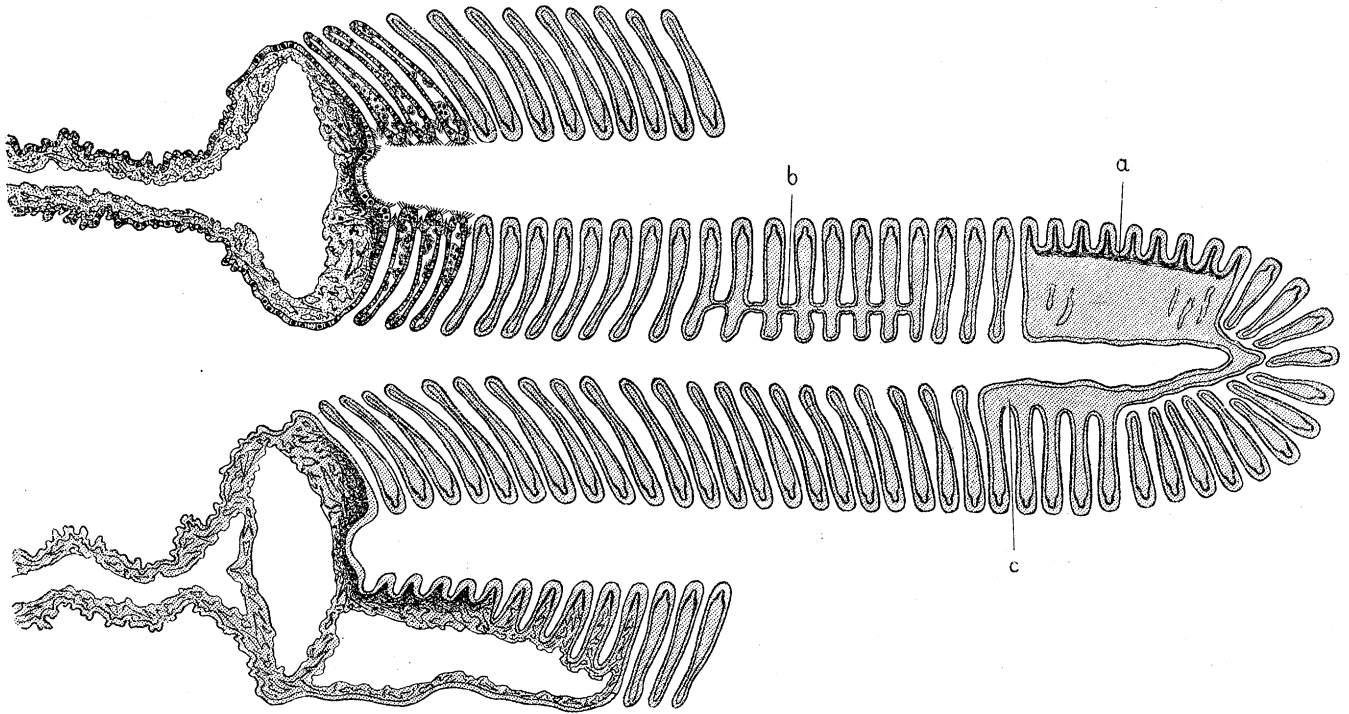
Fig. 37.—*Tridacna elongata*. At *a* the section passes through an interfilamentar junction, with chitin continuous from filament to filament, and with a large mass of subfilamentar tissue. At *b* and *c* the inner parts of the interlamellar extensions alone are connected up.

septa. The principal filaments are large, and with a semi-cylindrical groove on the frontal surface (fig. 37). The chitin next the epithelium is a thin, compact layer, and on the inner side of this is more chitin of a spongy nature. All the ordinary filaments have plate-like interlamellar extensions, which at the levels of the interfila-

mentar junctions fuse up by the whole of their faces (fig. 37, *a*), but at other levels may remain free, or fuse by their inner edges only (fig. 37, *b* and *c*); that is to say, the common mass of subfilamentar tissue at the interfilamentar junctions spreads upward and downward along the edges of the interlamellar extensions of the filaments.

Tridacna crocea is much the same as the above, but has 60–70 filaments to the plica, and has a shallower frontal groove to the principal filaments—in some of the sections the frontal surface is nearly flat.

Hippopus hippopus has gills like those of *Tridacna*. The principal filaments are like those of *Tridacna crocea*, with frontal surface nearly flat, and there are about ninety filaments to the plica. I have not seen the "plusieurs centaines" said to be present in this species by PELSENEER (**71**, p. 206).

Chamidæ.

In *Chama gryphoides* there are 14–26 filaments in a plica, and the principal filaments are flat-fronted or very slightly concave. The ordinary filaments have no interlamellar extensions, and the interlamellar septa are alternately high and low.

Sub-order MYACEA.

SPECIES EXAMINED :—

Psammobiidæ
- *Psammobia* ferroensis.*
- *Psammobia vespertina.*
- *Psammobia togata.*
- *Psammobia pallida.*
- *Asaphis deflorata.*

Myidæ
- *Mya arenaria.*
- *Corbula fasciata.*
- *Corbula gibba.*
- *Corbula laevis.*
- *Lutraria elliptica.*

Solenidæ
- *Solenocurtus strigillatus.*
- *Solenocurtus (Tagalus) rufus.*
- *Solenocurtus (Macha) philippinarum.*
- *Solen vagina.*
- *Solen ensis.*
- *Solen fonesi.*
- *Solen (Solena) rudis.*
- *Solen (Pharella) orientalis.*
- *Ceratisolen legumen.*
- *Ensis siliqua.*
- *Ensis macha.*

* *Psammobia* = *Gari* of SCHUMACHER.

Saxicavidæ . . $\left\{\begin{array}{l}\textit{Panopea generosa.}\\\textit{Saxicava rugosa.}\\\textit{Saxicava arctica.}\\\textit{Cyrtodaria siliqua.}\end{array}\right.$

Rocellariidæ . . $\left\{\begin{array}{l}\textit{Rocellaria dubia.}\\\textit{Rocellaria gigantea.}\end{array}\right.$

PREVIOUS ACCOUNTS :—

Psammobia vespertina, RICE, **83**, 1897, Plate 4, fig. 16.

Asaphis dichotoma, RICE, **83**, 1897.

Mya arenaria, POSNER, **76**, 1875.

Mya truncata, SLUITER, **95**, 1878.

Lutraria solenoides, DESHAYES, **17**, 1844–1848, Plate 32, fig. 2.

Lutraria elliptica and *Lutraria oblonga*, MÉNÉGAUX, **62**, 1890, p. 165.

Solenocurtus sp., POSNER, **76**, 1875.

Solen radiatus, VALENCIENNES, **102**, 1845, p. 513.

Solen vagina, POSNER, **76**, 1875.

Solen vagina, SLUITER, **95**, 1878.

Solen ensis and *Solen vagina*, MÉNÉGAUX, **62**, 1890, p. 175.

Macha candida, RICE, **83**, 1897.

Psammobiidæ.

In *Psammobia* and *Asaphis* the inner demibranch hangs much lower than the outer, and the ascending lamella of the latter rises considerably above the level of the gill-axis, forming a supra-axial extension (see figs. 39D and E). The gill lamellæ of the four species of *Psammobia* examined are plicate, and have enlarged principal filaments with a grooved frontal border. In *Psammobia ferroensis* the plicæ of the outer demibranch have about 14, those of the inner about 18 filaments (fig. 38). In *Psammobia vespertina*, *Psammobia togata*, and *Psammobia pallida* the numbers are the same in both demibranchs, and run 24–30, 35–40, and 18–20 respectively. In all four species there is a fairly large blood-tube in the subfilamentar tissue in the apex of the plica, and all the interlamellar septa, and not the alternate ones only, extend high up the demibranch. The ordinary filaments present no exceptional features. In *Psammobia pallida* there is a much more copious proliferation of sub-filamentar tissue, tending to choke up the interior of the plica, than in the other species. There is a fair amount of muscle fibre around the interlamellar spaces and in the interlamellar septa in *Psammobia vespertina*.

The principal filament of *Psammobia ferroensis* bears a false resemblance to a couple of ordinary filaments (see fig. 38), due to the sharply-cut sides of the frontal

groove, and to the fact that each of the halves is about the same size as an ordinary filament. The illusion is dispelled, however, on examining sections near the ventral
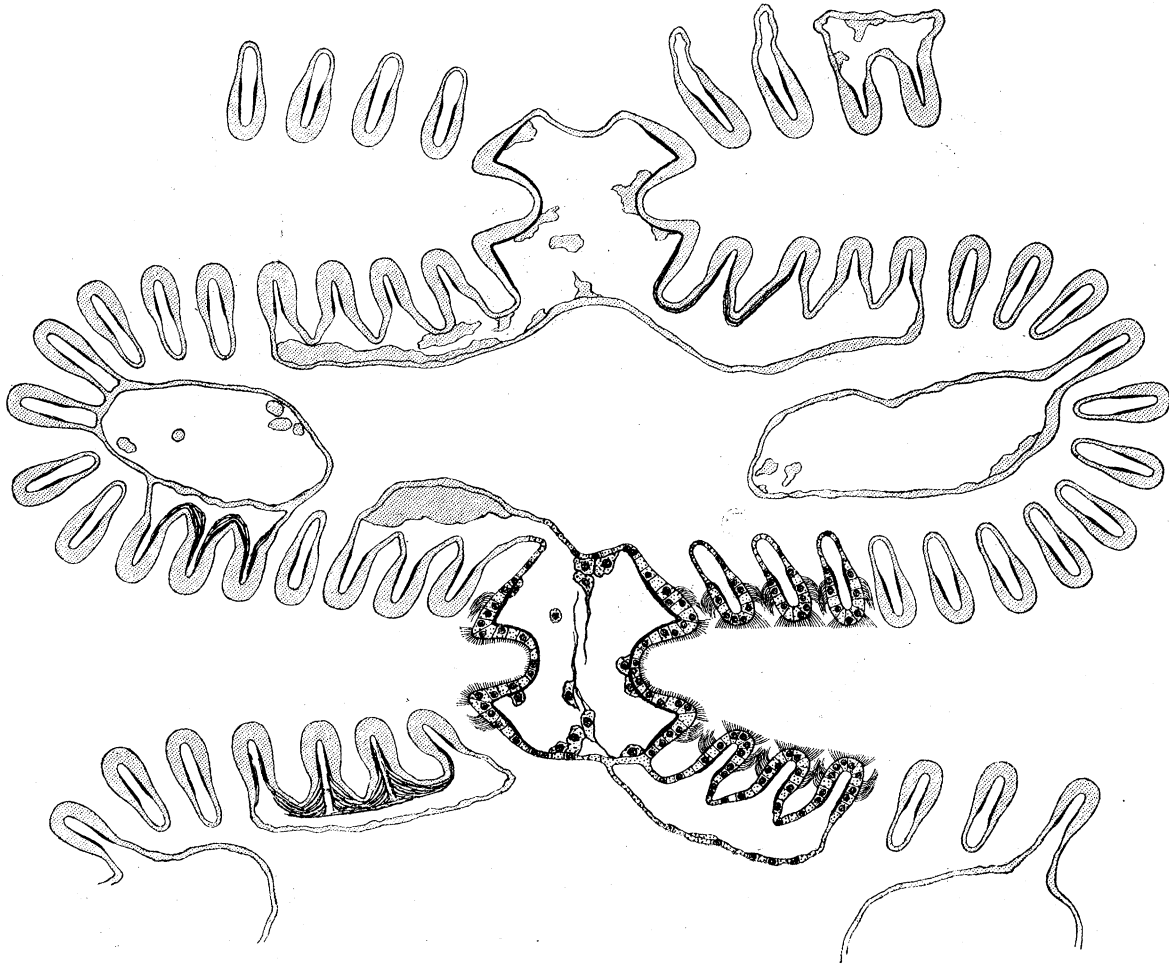

FIG. 38.—*Psammobia ferroensis*. Section of portion of the inner demibranch, taken about half-way up.

edge of the demibranch, since here the groove becomes less and less pronounced, and finally disappears. The appearance presented in fig. 39A may sometimes be seen, owing to the frontal groove disappearing on one side before the other. Apart from this, the fallacy may be exposed by a critical examination of the cilia of the principal filaments (fig. 38).

In *Psammobia ferroensis* the sides of the principal filament slope away abruptly from the edges of the groove, but in *Psammobia vespertina* (fig. 39B) and *Psammobia togata* they lie nearly in the same plane, or indeed rise slightly, giving to the frontal surface the appearance of a narrow, deep groove in the middle of a wider shallow groove. *Psammobia pallida* has a wide central groove, the epithelium of the bottom of which is thick and supported by extensions of the chitin-layer (fig. 39 C).

In *Asaphis deflorata* there are about 36–40 filaments in a plica, and the principal filament has a ridge-like frontal surface, without any central groove (fig. 39F). Towards the ventral edge of the demibranch, however, the apex of the frontal ridge
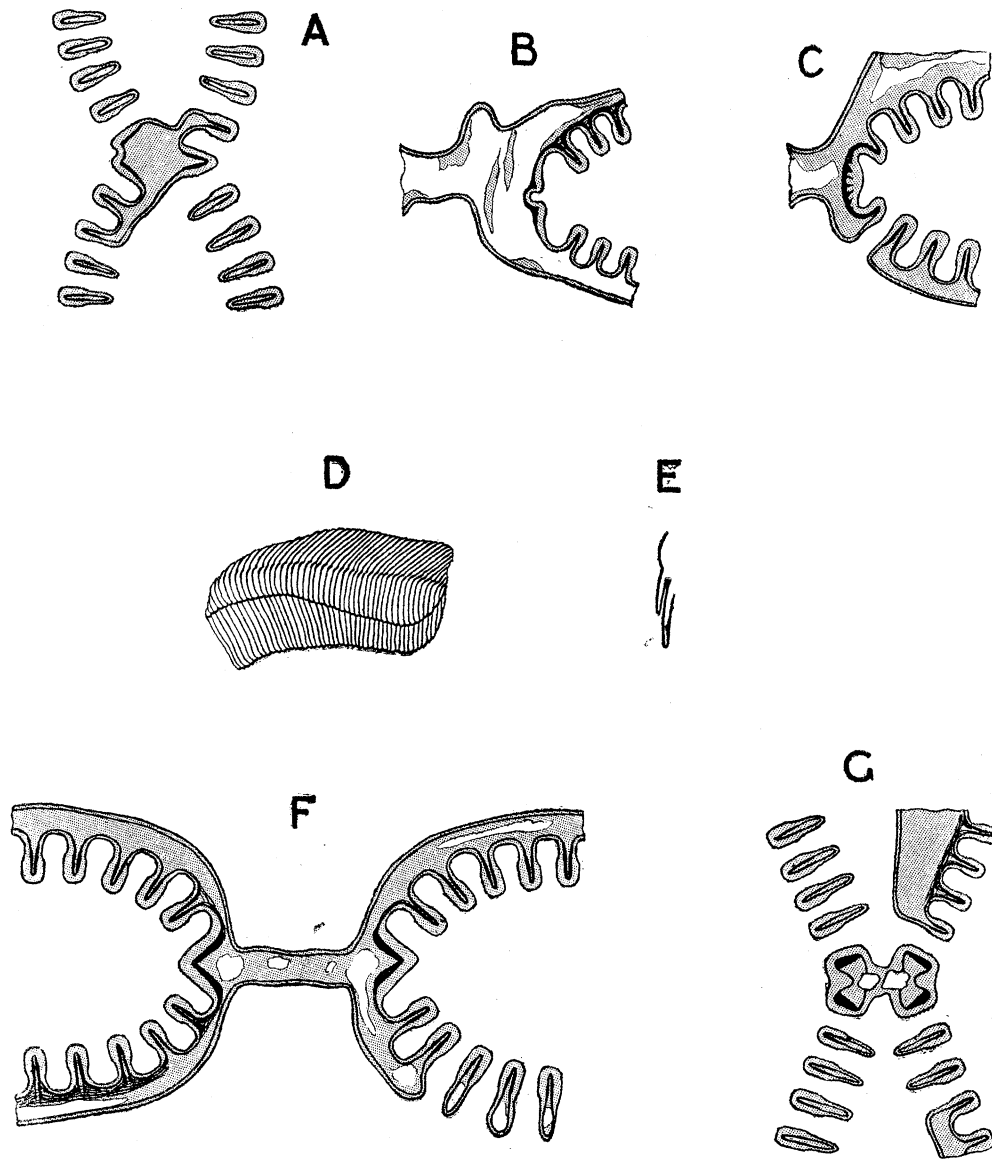
FIG. 39.—A, *Psammobia ferroensis.* Section from lowest part of inner demibranch. The plicæ are seen to be very shallow. The principal filament on the right side has a frontal ridge, that on the left a small groove (*cf.* fig. 38). B, *Psammobia vespertina.* Principal filament and a few adjoining ordinary filaments from section taken about half-way up the demibranch. C, similar section of *Psammobia pallida.* D *Asaphis deflorata.* Pallial aspect of left gill, showing the large supra-axial extension of the ascending lamella of the outer demibranch. E, vertical section of the gill. F, portion of horizontal section taken half-way up the inner demibranch. The ascending and descending parts of one principal filament are shown, together with a few adjacent ordinary filaments. G, similar section taken very close to the lower edge of the demibranch.

flattens (fig. 39G), and the outer edges of the thickened chitin-bands become divaricated. In the supra-axial extension of the outer lamella of the outer demibranch the structure is much the same as that of a single lamella of the demibranch below the level of the axis, but the interlamellar septa are wanting, and the principal filaments have their chitin-bands more obtusely set. There are about twenty-six filaments to the plica.

<center>*Myidæ.*</center>

In *Mya arenaria* and *Lutaria elliptica* the lamellæ are plicate, but there is no differentiation of principal filaments. In the latter form the interlamellar septa are alternately very high and very low, and each has a single blood channel running up the middle. At the upper edge of the low septa the blood-vessel forks, one part
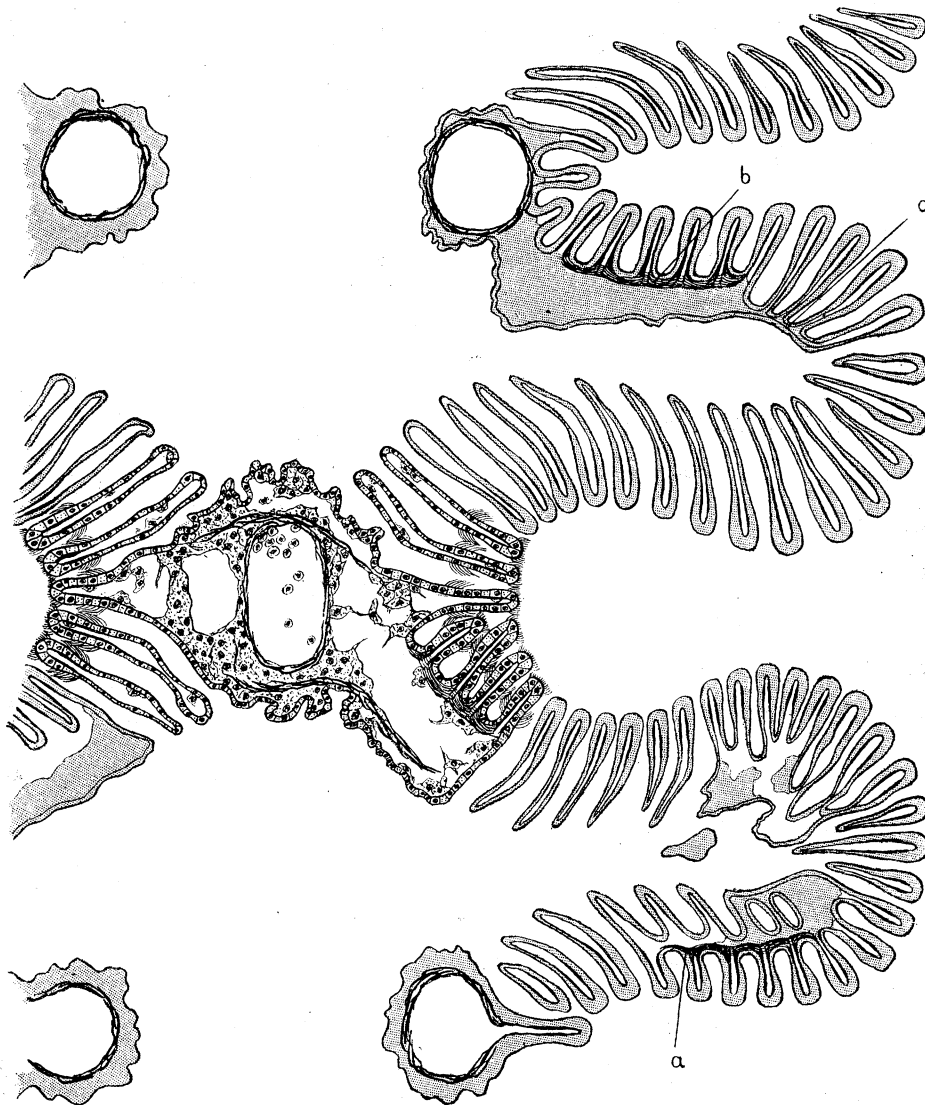
FIG. 40.—*Lutraria elliptica.* *a*, *b* and *c*, three aspects presented by interfilamentar junctions.

<center>2 K 2</center>

being continued up each of the plical bases in relation with it (fig. 40).   In the upper
parts of the demibranch, near the axis, the vessel in the descending lamella is larger
than in the ascending.   The median vessel, also, in each high septum becomes much
larger, and approaches the descending lamella.   In *Mya arenaria* all the septa rise
to the top of the demibranch.

Fig. 41.—A, *Corbula gibba*.   Interlamellar aspect of a portion of a single lamella stripped away from its
     fellow.   The dark patches are the interlamellar junctions; the fenestræ are bounded at the sides by
     the filaments, and above and below by the interfilamentar junctions.   The dark line in each
     interfilamentar junction is the chitin-strand.   B, similar preparation of *Corbula laevis*.   The subfila-
     mentar tissue is much more profuse, both as regards the interlamellar and interfilamentar junctions.
     C, section taken horizontally through a row of fenestræ, in the direction of the upper pen-line in
     fig. B.   D, similar section through interfilamentar junctions, in the direction of the lower line in
     fig. B.

In *Mya* and *Lutraria* there are about 25–38 filaments to the plica. In both there is a considerable development of subfilamentar tissue, so that at the levels of the interfilamentar junctions the interior of the plica may be completely choked up. In *Lutraria* it may be noticed that the interlamellar extension of the filament is about as wide as the filament proper, and that fusions may occur in three ways; by the normal interfilamentar junction only, leaving the interlamellar extensions free (fig. 40, *a*), by the normal interfilamentar junction combined with a complete fusion of the interlamellar extensions into a bulky mass (*b*), or by the inner (*i.e.*, intraplical) edges of the interlamellar extensions uniting (*c*). The latter appearance is due to the inner face of such a mass of subfilamentar tissue as is seen at *b*, extending higher or lower than the real interfilamentar junction. The normal interfilamentar junction is, of course, recognised by the thick chitin (*a* and *b*). The choking up of the plical cavity is due to the union of such masses as shown at *b*, from one side of the plica to the other.

In the three species of *Corbula* examined the lamellæ are simple, flat and homorhabdic. The main interest in connection with these forms centres around the interlamellar junctions, since the two lamellæ of the same demibranch are joined by septa, in relation with alternate filaments, in *Corbula lævis* (figs. 41B, C, and D), but by irregular bars in *Corbula gibba* (fig. 41A). The bars of *Corbula gibba* are not simple horizontal rods such as occur in *Astarte*, but have a tendency to spread down the filaments, and to run along the interfilamentar junctions. They thus form what are practically irregular and partial septa. Further than this, they do not always reach across, or only do so for a certain portion of their full extent. Whether any great importance need be attached to the difference in the form of the interlamellar junctions in these two species is doubtful. The difference is probably due to the fact that *Corbula lævis*, having a greater capacity for forming subfilamentar tissue than *Corbula gibba*, is enabled to develop complete septa, whereas the latter is not. The condition in *Corbula gibba* may, therefore, be the more primitive, or, on the other hand, it may indicate a defection from the septal condition.

Solenidæ.

The gills of the three species of *Solenocurtus* examined agree tolerably closely in their general structure. The lamellæ are highly plicate, the plicæ being flattened antero-posteriorly so as to resemble the leaves of a book. The numbers of filaments in a plica are about 30 in the outer, and 40 in the inner demibranch in *Solenocurtus strigillatus* and *Solenocurtus* (*Tagalus*) *rufus*, while in *Solenocurtus* (*Macha*) *philippinarum* the numbers are about 24 and 30. In *Solenocurtus rufus* all the interlamellar septa rise high up the demibranch, but in the other two species alternate septa are of small vertical extent. *Solenocurtus rufus* also has, in the apex of the plica, a blood-tube which is not noticeable in the

other two.   The apical filaments, one or two in number, of *Solenocurtus philip-pinarum* are slightly larger than the ordinary (fig. 42).   The intra-plical tissue has more or less the form of bands or trabeculæ, running from side to side of the plica.   The principal filaments in all three species are large, and have a broad,
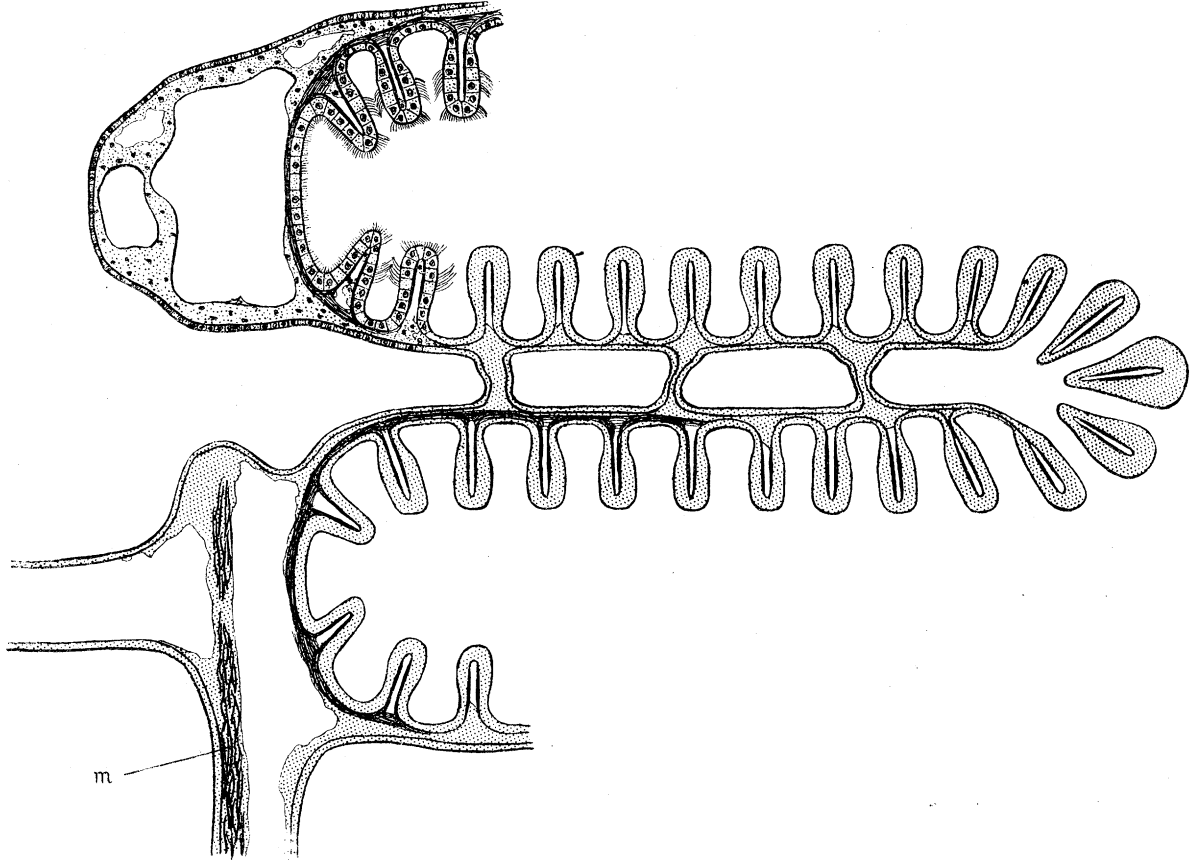

Fig. 42.—*Solenocurtus (Macha) philippinarum.*   *m,* muscle fibres.   The upper principal filament shows a broad groove, the lower a narrower groove.

shallow frontal groove, from the middle of which there sometimes rises, particularly in *Solenocurtus strigillatus,* a ridge of tall epithelial cells.   There is a fair amount of muscle fibre, running some vertically and some horizontally (*m*), in relation with the principal filaments.

In the five species of *Solen* examined the lamellæ are heterorhabdic and plicate, the plication being shallower in *Solen orientalis* than in the others.   The numbers of filaments in a plica are nearly the same in the two demibranchs, and run approximately 26 in *Solen vagina,* 17 in *Solen ensis,* 12 in *Solen fonesi,* 22 in *Solen (Solena) rudis,* and 16 in *Solen (Pharella) orientalis.*   In *Solen rudis* alternate interlamellar septa fail to reach more than half-way up the demibranch, but in the other four all septa rise high.   In *Solen vagina* (fig. 43) the interlamellar space is divided by the septa into a number of vertical cylindrical

tubes, the openings into which from the plical cavities are scarce. The epithelial lining of the interlamellar spaces is thrown into vertical folds, probably an unnatural
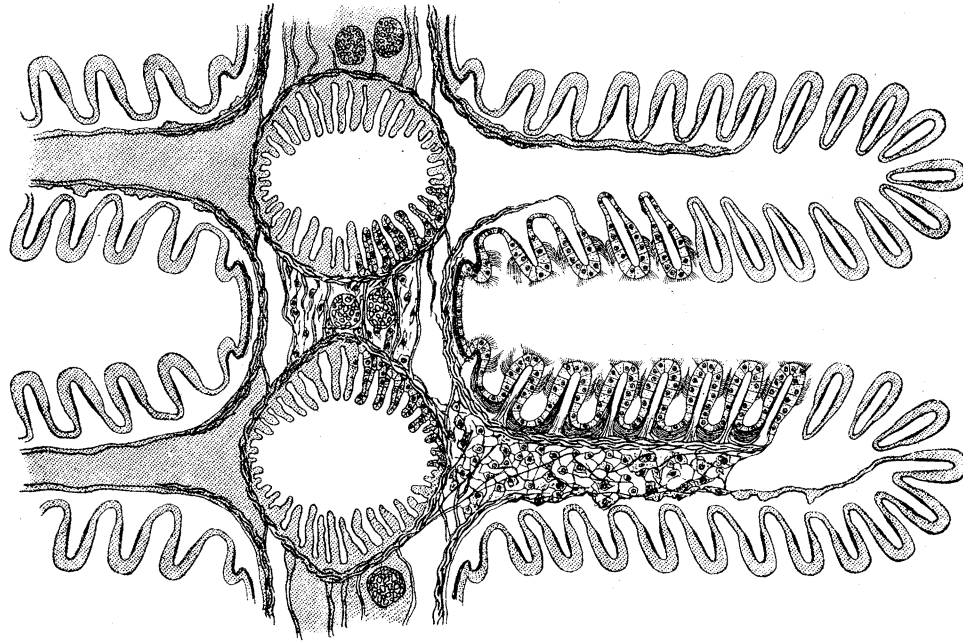
FIG. 43.—*Solen vagina.*
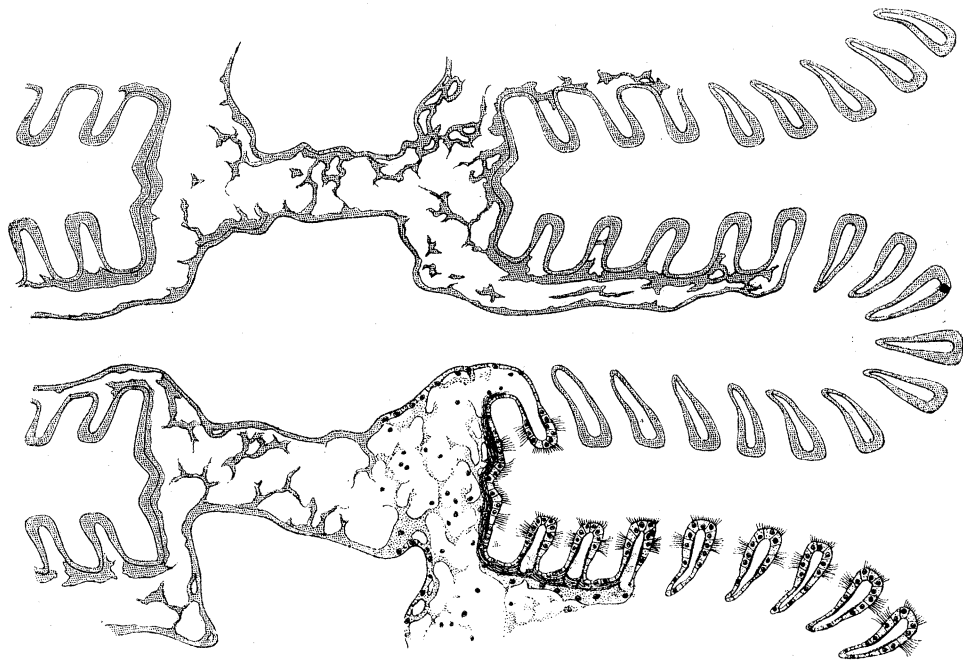
FIG. 44.—*Solen ensis.*

effect due to the contraction, at the time of death, of the muscular tissue, which is abundant around these tubes. One or two vertical muscles in the interlamellar septa are also a conspicuous feature.

The two or three filaments at the apex of the plica are enlarged in *Solen fonesi* and *Solen orientalis*. The principal filaments of *Solen vagina* (fig. 43) and *Solen rudis* have a broad, shallow frontal groove, but the groove is narrow in *Solen ensis* (fig. 44) and *Solen fonesi*. In *Solen orientalis* there is every gradation from a shallow frontal groove to a shallow frontal ridge, even in filaments cut at the same horizontal level. In all five cases the frontal groove disappears at the ventral edge of the demibranch, where the principal filament presents a distinct frontal ridge (fig. 45).
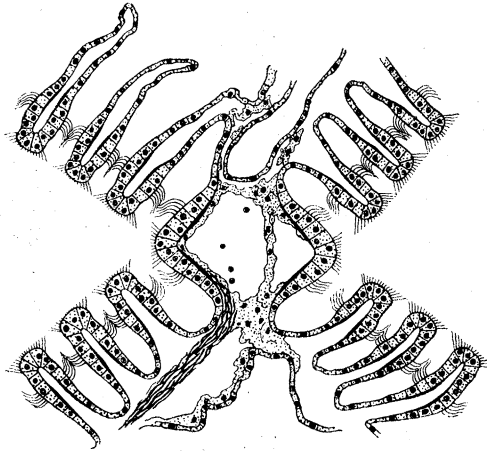
FIG. 45.—*Solen ensis.* Section taken quite near the lower edge of the demibranch. The principal filaments have a fairly sharp frontal ridge (*cf.* fig. 44).

Ceratisolen legumen has a non-plicate, homorhabdic gill, in striking contrast with those of the other genera of the Solenidæ. The interlamellar septa (fig. 46) are very
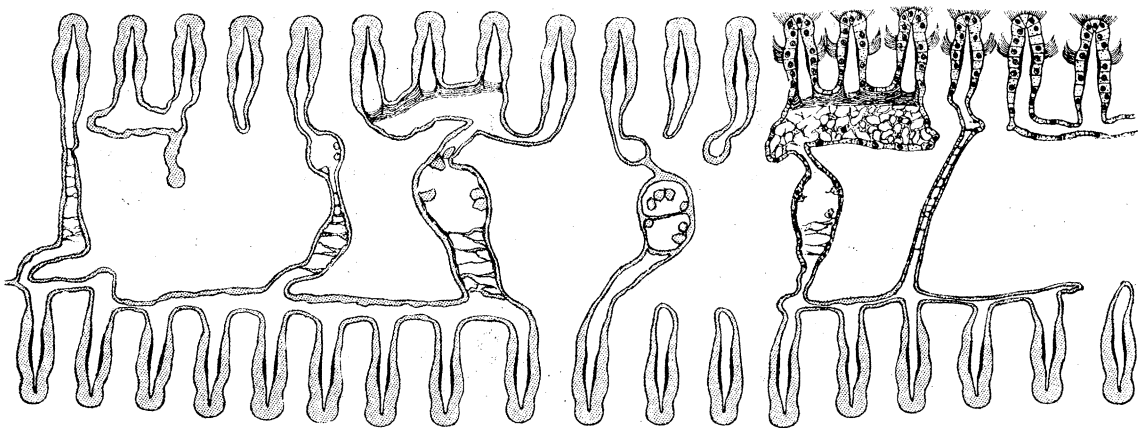
FIG. 46.—*Ceratisolen legumen.*

irregular in their disposition and in their vertical extent. They may contain two vertical tubes, or one, or none. The chitinous lining is rather feebly developed.

The lamellæ of *Ensis siliqua* are markedly heterorhabdic, and very feebly plicate

(fig. 47). The plicæ of both demibranchs contain about twenty-four filaments, and there is a very considerable development of muscular tissue in the interfilamentar junctions. Curious layers of subfilamentar tissue arch across what in a more strongly plicate lamella would be the intraplical cavity. They appear to have a
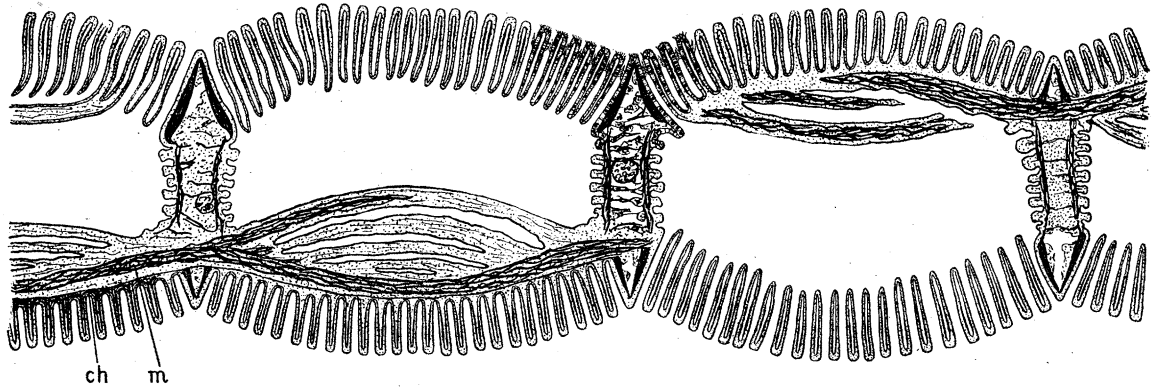

FIG. 47.—*Ensis siliqua.* *ch*, chitin in the interfilamentar junction ; *m*, muscle.

definite relation to the interfilamentar junctions, and are wanting at levels where the filaments are free from one another. The principal filament presents a sharp ridge, and has a much thickened chitin skeleton.
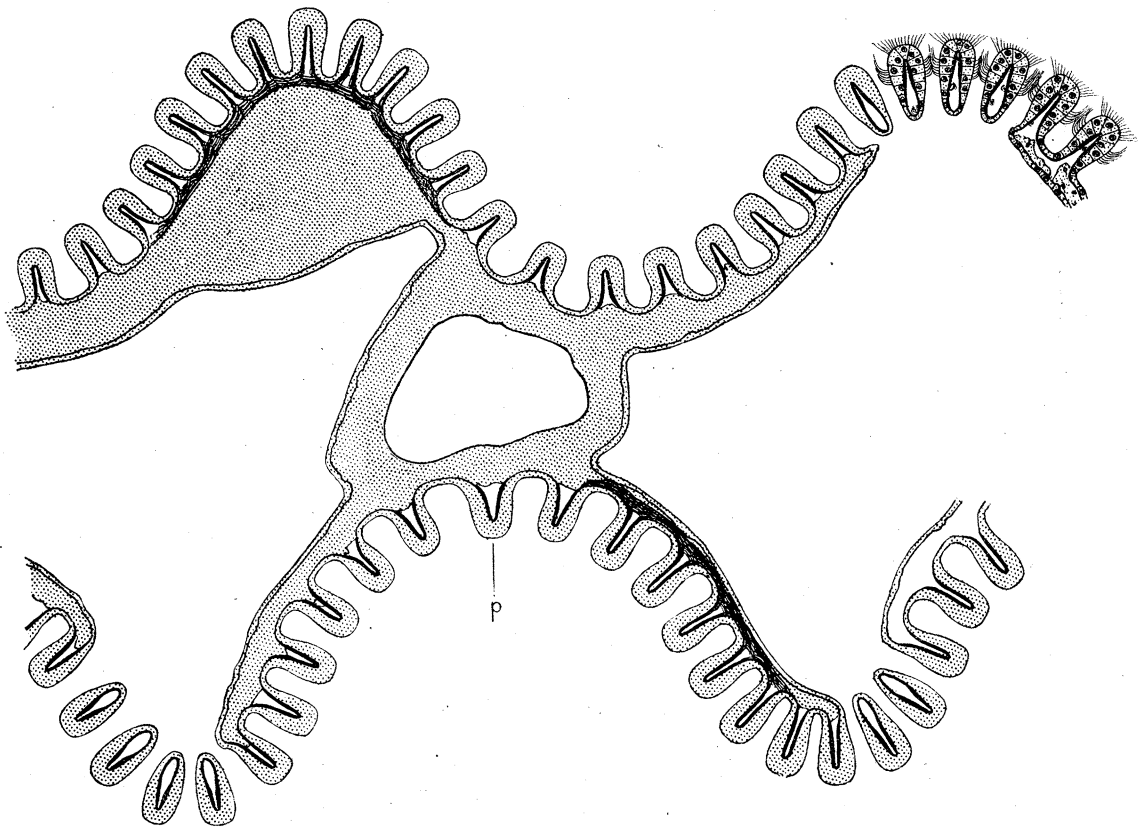
FIG. 48.—*Ensis macha.* *p*, barely differentiated principal filament.

In *Ensis macha*, on the other hand, the horizontal section of the lamella shows a sinuous curve, and at the bases of the plications there occur three or four filaments apparently differing in no respect from the ordinary filaments. A careful examination of a large series of sections, however, shows that in certain places the middle one of the group has its chitin-bands set at a slightly wider angle than usual (fig. 48, *p*), and that occasionally the interlamellar septum is related to a single filament, which may thus be taken to represent a principal filament. There is, at all events, but a minimal approach to the heterorhabdic condition in this species. The subfilamentar tissue spreads considerably upwards and downwards from the interfilamentar junctions, so that the water-pores are scarce. They are usually towards the apices of the plicæ.

Saxicavidæ.

The gills of *Saxicava rugosa* and *Saxicava arctica* are simple, non-plicate, and homorhabdic; with regularly-arranged interlamellar septa, related at their sides with one or more filaments according to the remoteness or proximity of the plane of section with respect to the interfilamentar junctions. The septa are disposed at intervals of 6–8 filaments in the former species, 10–14 filaments in the latter.

Panopea generosa has homorhabdic, strongly-plicate lamellæ, with about 50–55 filaments in a plica. All interlamellar septa rise high up the demibranch, and contain each two vertical blood-vessels. In both interlamellar and interfilamentar junctions there is a considerable quantity of muscle fibre. The middle filament of the group of four or five occupying the basal position between two plicæ may sometimes be very slightly broader than the others; and at certain levels of section the interlamellar septa may be seen to be connected with a single filament, but this is not common. The chitin is thickened in the filaments in a very abrupt manner (fig. 49), so that one might here be pardoned for speaking of " chitin-rods."

FIG. 49.—*Panopea generosa.* Transverse section of a single filament.

In *Cyrtodaria siliqua* the lamellæ are plicate, and homorhabdic, or with the barest possible differentiation of principal filaments, as in *Panopea*. There are about twenty filaments in a plica, and the interlamellar septa are alternately high and low. Where the plical bases of opposed lamellæ are connected by an interlamellar septum, there is a single vertical blood-tube in the middle of the septum, but at higher levels of section, above the upper edge of the low septa, each plical base has its own vessel.

Rocellariidæ.

The gills of *Rocellaria dubia* and *Rocellaria gigantea* are homorhabdic. The former are non-plicate, and with interlamellar septa irregularly disposed at intervals of 3–8 filaments. The lamellæ of the inner demibranch of *Rocellaria gigantea* are

moderately plicate, and with interlamellar septa, all rising high, at intervals of 24–30 filaments; those of the outer demibranch are very slightly plicate, with interlamellar septa at variable intervals of 6–25 filaments.

Sub-order PHOLADACEA.

SPECIES EXAMINED :—

Pholadidæ . .	Pholas dactylus.
	Pholas crispata.
	Pholas parva.
	Pholas candida,
	Pholadidea papyracea.
	Jouannetia cumingi.
Teredinidæ . .	Teredo navalis.

PREVIOUS ACCOUNTS :—

Pholas crispata, ALDER and HANCOCK, 1, 1851, Plate 15, figs. 2 and 3.
Pholas dactylus, POSNER, 76, 1875.
Jouannetia cumingi, EGGER, 24, 1887.
Teredo, DESHAYES, 17, 1844–48, Plate 6, fig. 5.
Teredo, QUATREFAGES, 79, 1849, p. 59.
Teredo, MÉNÉGAUX, 62, 1890, p. 197.

Pholadidæ.

The gills of the four species of Pholas examined are homorhabdic, and have interlamellar septa arranged in a very irregular succession, so that the plicæ (which are very feebly marked in Pholas crispata, Pholas parva, and Pholas candida) are unequal. In Pholas dactylus there may be secondary plicæ superposed on the larger primary plicæ. Subfilamentar tissue is rather scanty in Pholas crispata, but is fairly abundant in the other three species. Open passages between the filaments are consequently not often seen in the sections. The interlamellar septa are thick, and even midway between an interfilamentar junction and the next above they may be in relation with three, four or more filaments. The single vertical blood-tube found in each interlamellar septum forks at the upper edge of the septum, so that at levels above this a pair of tubes may be seen.

The lamellæ of the specimen of Pholadidea papyracea examined were crumpled, but essentially flat and non-plicate. No principal filaments are differentiated, and most of the filaments have small hollow interlamellar extensions, which give one the impression that the blood circulates in these extensions rather than in the filamentar cavities. In sections taken half-way up the demibranch the interlamellar septa occur at irregular intervals of about 5–18 filaments. The blood-tube in the interlamellar

septum forks, as in *Pholas*, and horizontal tubes occur in the subfilamentar tissue lying on the interlamellar side of the interfilamentar junctions.

Jouannetia cumingi has strongly plicate lamellæ, with about twenty-five filaments to the plica in both demibranchs. One, two or three filaments occupying a basal position between two plicæ may be slightly larger, and with thicker chitin-bands than usual, but the lamellæ are not markedly heterorhabdic. The lamellæ are thick, in consequence of the well-developed interlamellar extensions of the filaments.

Teredinidæ.

The gill of *Teredo navalis* is aberrant, having but a vestige of the external demibranch (MÉNÉGAUX, **62**, pp. 197–199; DALL, **15**, p. 559; SIGERFOOS, **93**). The
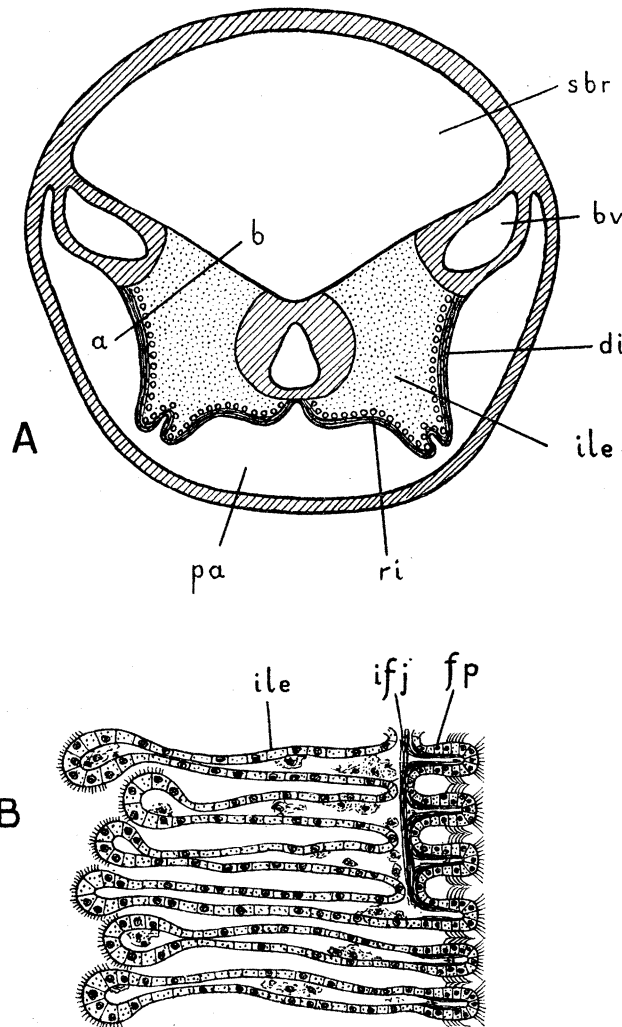
FIG. 50.—*Teredo navalis*. A, section across the body behind the visceral mass. *bv*, blood-vessel in the gill axis; *di*, descending filament of the inner demibranch; the small circles to the left of it are the transverse sections of the interfilamentar junctions; *ile*, interlamellar extension; *pa*, pallial cavity; *ri*, reflected filament of the inner demibranch; *sbr*, suprabranchial cavity. B, section of descending lamella taken in the direction *ab* in fig. A. *fp*, filament proper; *ifj*, interfilamentar junction.

direct lamellæ of the inner demibranchs descend, but the reflected lamellæ pass horizontally inward and unite with one another in the median line (fig. 50A). This junction consists of a large mass of rather firm tissue traversed by a longitudinal blood cavity. The filaments have plate-like interlamellar extensions of considerable size (fig. 50B), recalling those of *Lucina*. The inner edges of the extensions, which, in the absence of an interlamellar cavity, form the floor of the supra-branchial chamber, are swollen, and have large ciliated epithelial cells. The filaments proper are quite normal.

Sub-order ANATINACEA.

SPECIES EXAMINED :—

Clavagellidæ . . { *Clavagella melitensis.*
                    Brechites javanicus.

Anatinidæ . . { *Anatina truncata.*
                 Anatina flexuosa.
                 Periploma sp.
                 Thracia corbuloides.
                 Thracia papyracea.

Pandoridæ . . { *Pandora obtusa.*
                 Pandora inæquivalva.

Lyonsiidæ . . { *Lyonsia norvegica.*
                 Lyonsia nitida.
                 Entodesma saxicula.
                 Mytilimeria nuttalli.

PREVIOUS ACCOUNTS :—

Clavagella lata, OWEN, **65**, 1835.
Aspergillum dichotomum, LACAZE-DUTHIERS, **48**, 1883, pp. 713-716.
Pandora oblonga, DESHAYES, **17**, 1844-1848, Plate 25, fig. 3.
Myochama anomioides, HANCOCK, **30**, 1853.
Chamostrea albida, HANCOCK, **29**, 1853.
Lyonsia norvegica, PELSENEER, **71**, 1891, p. 212, and fig. 70.

There is a marked uniformity in the gross and minute structure of the gills in the investigated species of the families Clavagellidæ, Anatinidæ, Pandoridæ and Lyonsiidæ. *Chamostrea*, the sole genus of the family Chamostreidæ, was not examined, but, judging from HANCOCK's account (**29**) the structure of the gill is similar to that seen in the above four families. The inner demibranch in all the above is normal, while the outer is upturned, and consists of direct lamella only. These relations could not

be made out exactly in the single specimen of *Brechites* available, owing to the excessive crumpling of the gills, but LACAZE-DUTHIERS has stated (**48**, p. 715):— " Dans la branchie de l'Arrosoir on ne trouve que trois feuillets, deux directs et un réfléchi," and his figure 4, plate 27, shows that the disposition of the gill lamellæ is typically Anatinaceous.   Concerning *Clavagella*, OWEN's remark (**65**, p. 272), " The laminæ are arranged in three layers instead of two on either side the foot," is rather puzzling.   In *Clavagella melitensis* the lamellæ are arranged as in the other forms included in the above families.   The inner or descending demibranch of his specimen (*Clavagella lata*) appears from his figures to be wrinkled longitudinally in such a way as to appear double.

As regards the finer structure of the gill, it may be said at once that the lamellæ of the Clavagellidæ, Anatinidæ, Pandoridæ, Chamostreidæ, and Lyonsiidæ are plicate and heterorhabdic.   The interlamellar septa of the lower demibranch are alternately high and low, and, as a rule, the low septa extend but a very short distance up.   A fair amount of muscular tissue is present.   The average number of filaments in the
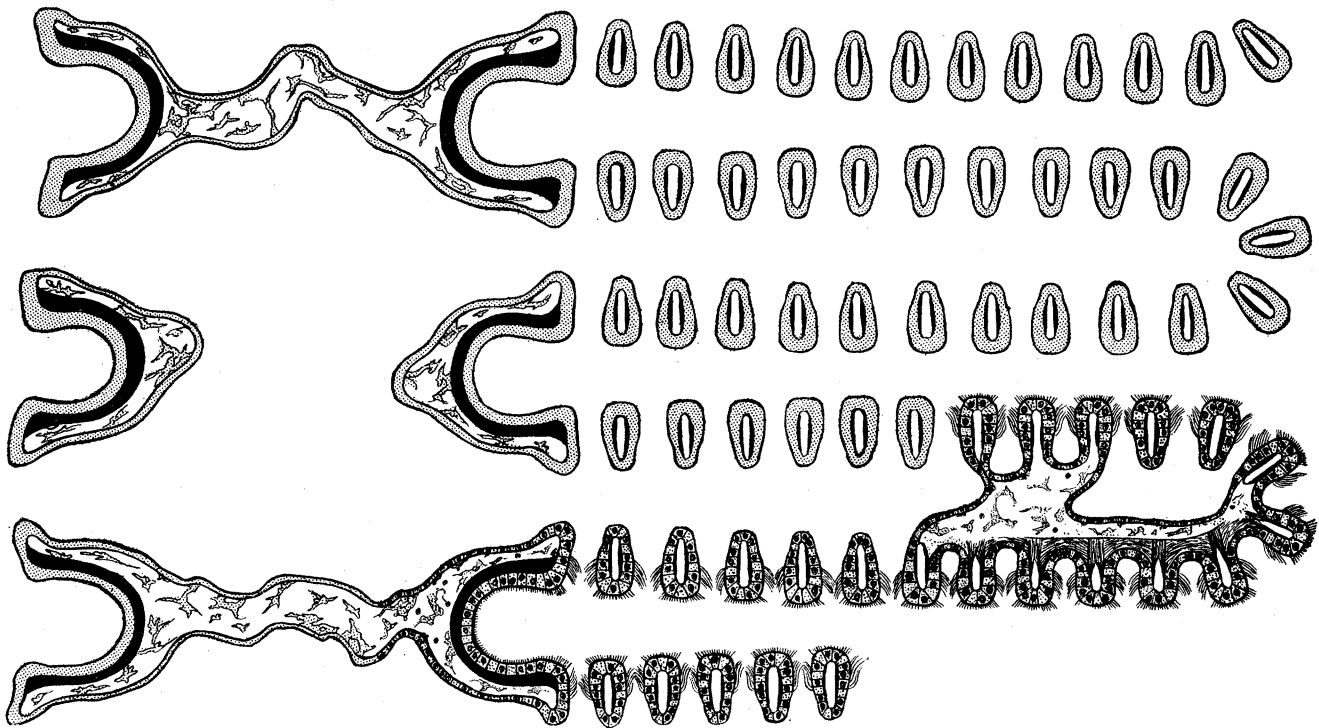

FIG. 51.—*Clavagella melitensis.* Inner demibranch.

plicæ of the lower demibranch is 20 in *Brechites javanicus*, 24 in *Clavagella melitensis*, 25 in *Anatina truncata*, 20 in *Anatina flexuosa*, 31 in *Periploma sp.*, 27 in *Thracia corbuloides*, 15 in *Thracia papyracea*, 9 in *Pandora obtusa*, 7 in *Pandora inæqui-valva*, 13 in *Lyonsia norvegica* and *Lyonsia nitida*, 20 in *Entodesma saxicola* and *Mytilimeria nuttalli*,

The frontal surface of the principal filament is flat, with a semi-cylindrical groove in the middle third of the total width, in *Brechites javanicus* and *Entodesma saxicola*. The groove is very large and deep in *Clavagella melitensis* (fig. 51), *Anatina truncata*, and *Lyonsia norvegica*.   It is broader and shallower in *Anatina flexuosa*, *Lyonsia nitida*, *Mytilimeria nuttalli*, *Thracia corbuloides*, and *Thracia papyracea* (fig. 52).   In *Pandora obtusa* some of the sections of the principal filaments show a
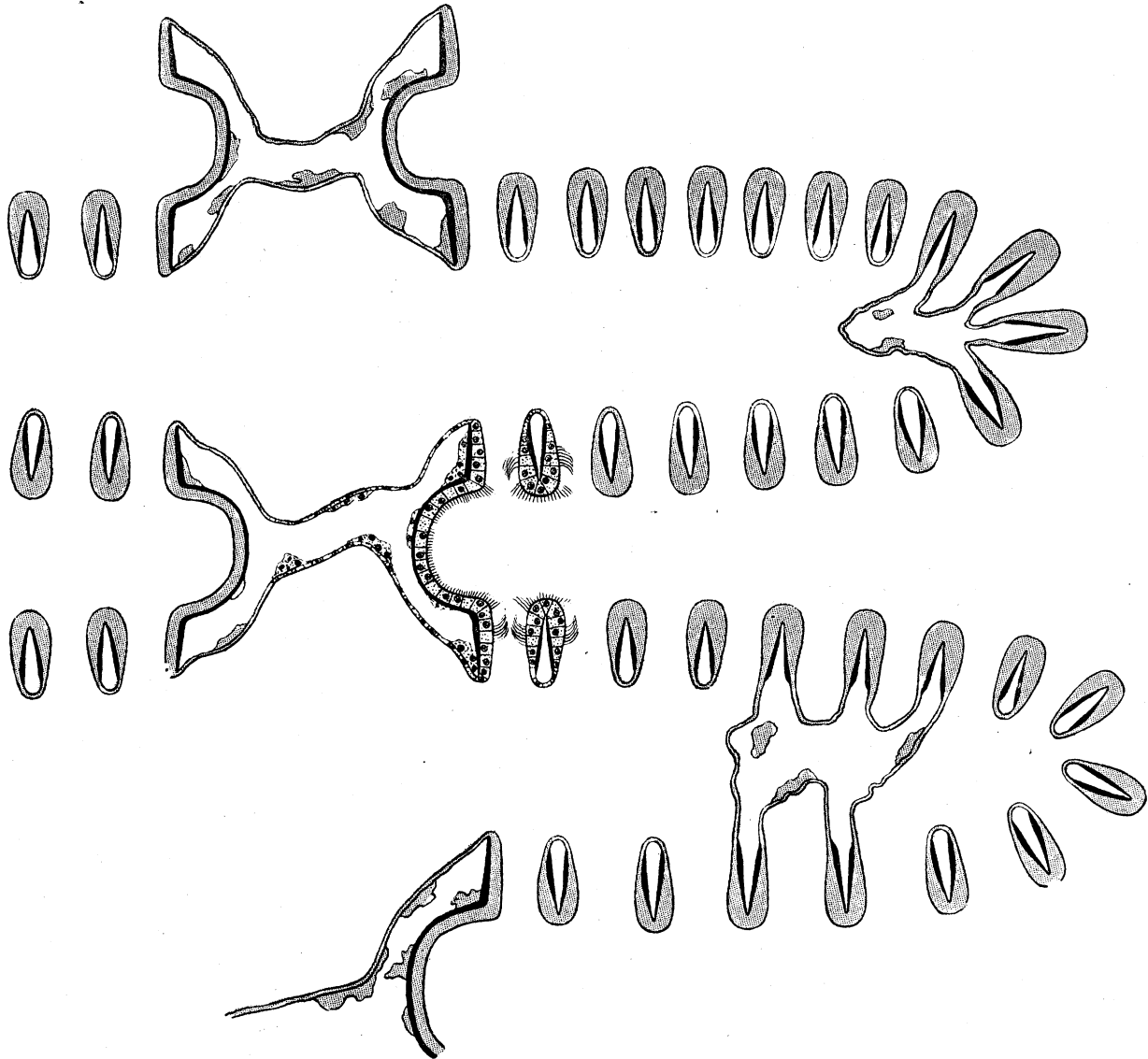
FIG. 52.—*Thracia papyracea.*   Inner demibranch.

large semi-circular space in the frontal surface (fig. 53B), but more usually, especially at the higher levels of the demibranch, the outline is cusp-like, owing to the presence of a sharp ridge at the bottom of the groove (fig. 53A).   As in other sub-orders, the characteristic features of the principal filaments disappear at the lowest parts of the
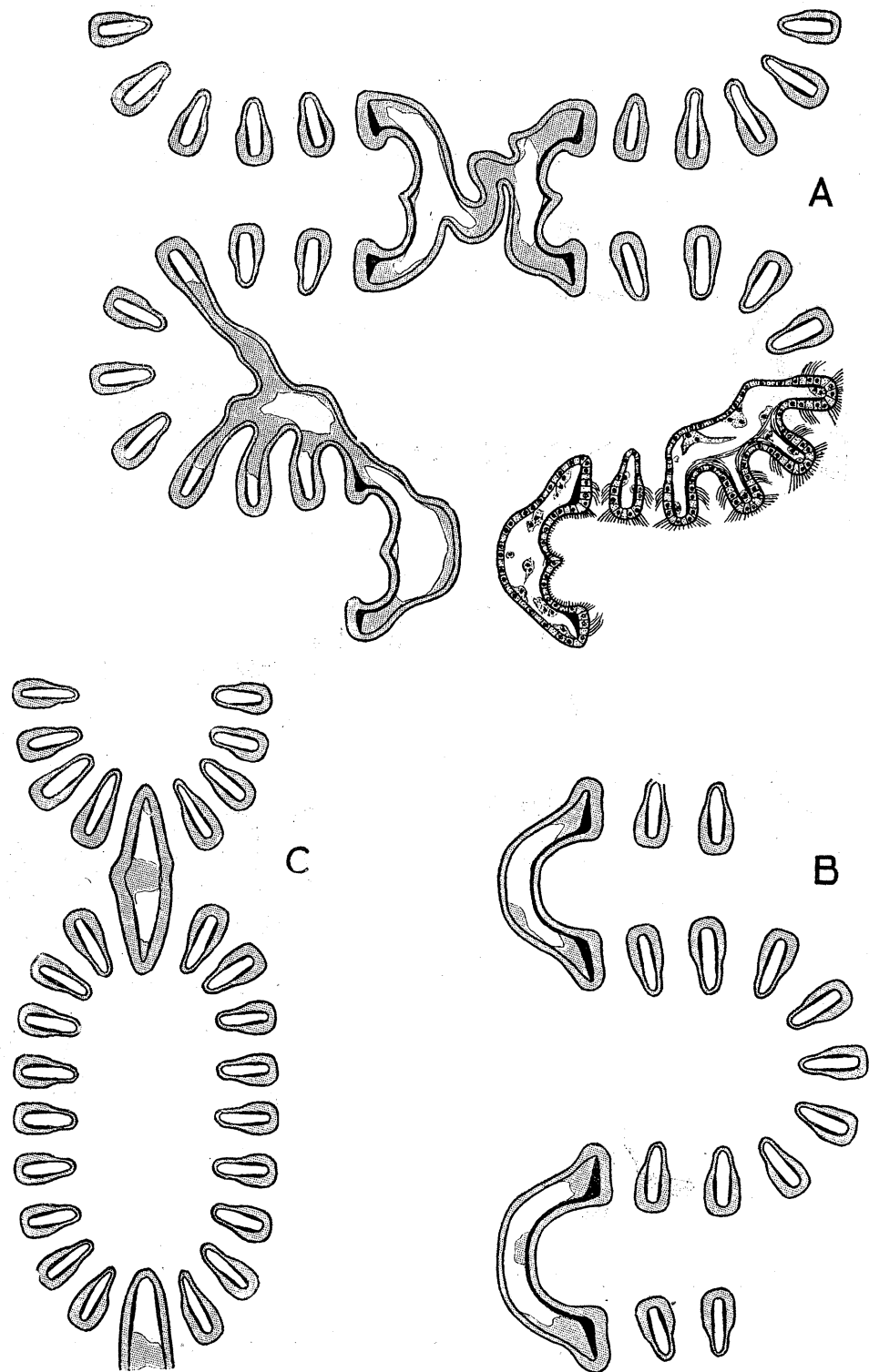
FIG. 53.—*Pandora obtusa.* A, B and C, sections of inner demibranch from high, middle and low levels respectively.

demibranch, and differences as striking as those seen in figs. 53B and C are sometimes met with.

At the levels of the interfilamentar junctions, and extending for a little distance above and below them, trabeculæ may stretch across from the anterior to the posterior side of the plica (*e.g.*, *Lyonsia norvegica*), or where subfilamentar tissue is more abundant, a complete horizontal septum may extend across the plical cavity (*e.g.*, *Anatina flexuosa*, *Thracia corbuloides*, and *Entodesma saxicola*).

The one or two filaments at the apex of the plica are larger than usual in *Chamostrea albida* (HANCOCK, **29**), *Pandora inæquivalva* and *Anatina flexuosa* (not in *Anatina truncata*). As already noted by PELSENEER (**71**, p. 212), the apical filaments of *Lyonsia norvegica* are slightly differentiated. The frontal surfaces of such enlarged filaments are more convex than usual, semi-cylindrical in fact. An intrafilamentar septum is not uncommonly seen in the ordinary filaments of *Lyonsia nitida*.

In the upper demibranch the plicæ are smaller, and contain some three-fourths of the number of filaments composing the plicæ of the lower demibranch. The frontal surface of the principal filament is usually quite flat. The plates of the upper demibranch which, in the presence of a reflected lamella, would be interlamellar septa, are usually present on alternate principal filaments only. Their mesial edges end freely, so that the upper demibranch is attached to the visceral mass by its edge only. In *Thracia corbuloides* the principal filaments have no septa, and are free from the visceral mass except at their upper ends. In *Periploma sp.* the interlamellar septa are all complete, and are united at their mesial edges to a fibrous membrane, which is free from the visceral mass. *Mytilimeria nuttalli* and *Entodesma saxicola* also have an upper demibranch which is free from the visceral mass, but the fibrous membrane is wanting.

Sub-order POROMYACEA.

SPECIES EXAMINED :—

Verticordiidæ .	*Lyonsiella papyracea.* *Verticordia acuticostata.* *Euciroa eburnea.* *Euciroa pacifica.*
Poromyidæ . .	*Poromya malespinæ.* *Poromya oregonensis.*
Cetoconchidæ .	*Cetoconcha sarsi.* *Cetoconcha smithi.*
Cuspidariidæ .	*Cuspidaria glacialis.*

PREVIOUS ACCOUNTS :—

> *Lyonsiella abyssicola*, SARS, **87**, 1872.
>
> *Lyonsiella* and *Verticordia*, DALL, **9**, 1886.
>
> *Lyonsiella jeffreysi*, PELSENEER, **68**, 1888.
>
> *Lyonsiella*, PELSENEER, **67**, 1888.
>
> *Lyonsiella* and *Verticordia*, DALL, **13**, 1889, p. 437.
>
> *Lyonsiella abyssicola*, PELSENEER, **71**, 1891, p. 215, and figs. 74–77.
>
> *Lyonsiella alaskana*, *Halicardia flexuosa*, and *Euciroa pacifica*, DALL, **14**, 1894, pp. 687–705, and Plate 23.
>
> *Poromya tornata* and *Poromya granulata*, PELSENEER, **68**, 1888.
>
> *Poromya granulata*, PELSENEER, **71**, 1891, p. 218, and fig. 84.
>
> *Silenia sarsii*, PELSENEER, **68**, 1888.
>
> *Cuspidaria fragilissima*, *Cuspidaria curta*, *Cuspidaria rostrata* and *Cuspidaria platensis*, PELSENEER, **68**, 1888.
>
> *Cuspidaria rostrata*, PELSENEER, **71**, 1891, p. 224, and figs. 92 and 96.
>
> *Cuspidaria cuspidata*, GROBBEN, **28**, 1892.
>
> *Cuspidaria obesa*, PLATE, **75**, 1897.

For observations on the Septibranchia generally, see :—DALL, **10**, 1886 ; DALL, **9**, 1886, pp. 280–310 ; PELSENEER, **67**, 1888 ; DALL, **11**, 1888 ; PELSENEER, **70**, 1889 ; DALL, **12**, 1889 ; DALL, **13**, 1889 ; PELSENEER, **69**, 1889 ; DALL, **14**, 1894 ; DALL, **15**, 1895.

Verticordiidæ.

What renders the gills of *Lyonsiella papyracea* remarkable at first glance is the small extent to which they descend into the pallial cavity. By the sides of the visceral mass the ascending and descending lamellæ of the inner demibranchs are recognisable as such, but the interlamellar cavity is wide, and the lower edge of the demibranch is very much rounded. Just behind the foot the lamellæ have a continuous curve (fig. 54A, *id*). There are no interlamellar junctions of any kind. The outer demibranch is narrow and upturned, and consists of direct lamella only. The ctenidial axis is concrescent with the body in its front portion, the union being effected through the intermediation of a kind of suspensory membrane. This membrane does not reach back as far as the hind edge of the foot, so that the axis is free for a considerable portion of its length.

The suprabranchial cavity is large, and into it there projects, from the mantle just above the outer demibranch, a curious flap with a free lower edge. The flap was very thick in the specimen of which a section is figured (fig. 54A, *f*), but in a second specimen of the same species, it was a comparatively thin membrane. This is evidently the equivalent of the " free lamina " figured by DALL (**14**, Plate 23,

fig. 3nn') in *Halicardia*, and referred to in his remarks on *Lyonsiella alaskana* (p. 704). He notes that PELSENEER did not mention it in his account of *Lyonsiella* in the " Challenger Report " (**68**).

The anterior parts of the upper edges of the ascending lamellæ of the inner demi-branchs are fused with the sides of the visceral mass. The edges are free from the
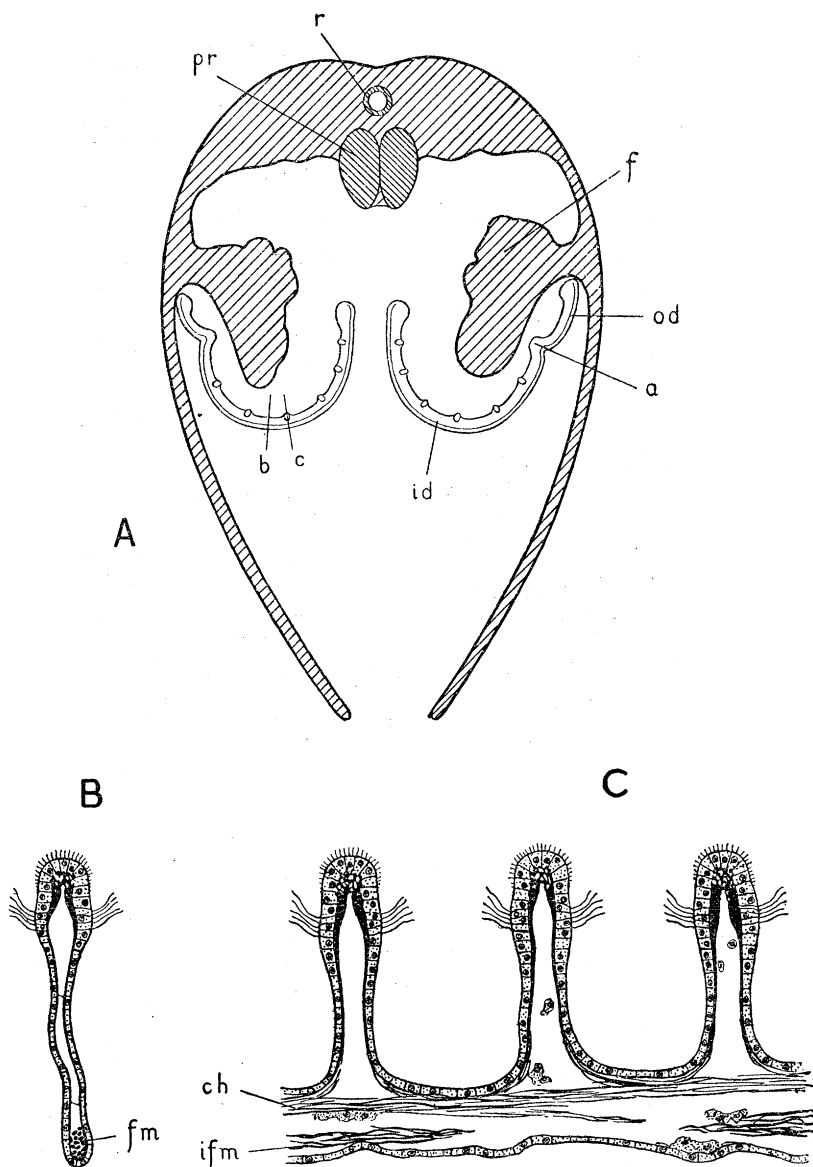

FIG. 54.—*Lyonsiella papyracea.*—A, transverse section of the body just behind the foot.   *a*, gill axis; *b* and *c*, directions of the sections B and C; *f*, curious fold which descends into the suprabranchial cavity; *id*, inner demibranch, with six interfilamentar junctions; *od*, outer demibranch, with no interfilamentar junctions; *pr*, pedal retractors; *r*, rectum.   B, section of a filament in the direction *b* in fig. A. *fm*, muscle running in the direction of the filament.   C, section of three filaments taken through an interfilamentar junction, in the direction *c* in fig. A.   *ch*, continuous chitin of the interfilamentar junction; *ifm*, muscle running in the interfilamentar junction.

hinder part of the visceral mass, and for a short distance behind it. They are fused with one another in the posterior fourth of their length. The apices of the ctenidia are united ; they touch the siphonal septum, but are not fused with it. The edge of the upper demibranch is in feeble organic connection with the mantle.

There are not more than 6 or 7 interfilamentar junctions in the inner demibranch (6 are shown in fig. 54A), and there are none at all in the outer. No trace of plication of the lamellæ can be detected, and the filaments are all of one kind.

The part of the filament lying towards the pallial cavity has large prismatic epithelial cells and a lining of thickened chitin (fig. 54B). Just below the frontal epithelium the chitin is not only thick, but highly vesicular, with nucleated cells in the meshes. The cilia at the edges of the frontal tracts are smaller than those in the middle ; the lateral cilia are normal and fairly long. The rest of the filament is thinner than the part just mentioned, and has flatter epithelial cells, a thin lining of chitin, and at its inner (interlamellar) edge has a well-defined strand of muscle running lengthwise along the filament. This latter part of the filament might at first be taken for an interlamellar extension of the former part, which appears to correspond with the filament proper of other forms ; but the whole must be regarded as filament proper, since the interfilamentar junctions are situated at the inner edges, and not where the former part passes into the latter (fig. 54C).

A specimen of *Euciroa eburnea* in excellent preservation was kindly supplied by Dr. ALCOCK, of the Indian Museum, Calcutta. The gills resemble those of *Lyonsiella papyracea*, in that the demibranchs do not project much into the pallial cavity. The outer demibranch cannot be said to be upturned in this case, since it is disposed almost horizontally (fig. 55A) ; and although the two equivalents of the descending and ascending lamellæ of the inner demibranch can be recognised, they also are disposed nearly horizontally. In the greater part of the length of the gill the morphological ventral edge of the inner demibranch has the form of a groove (fig. 55A, *f*), but the groove dies away at one-sixth of the length from the posterior end, and sections across the hinder parts show a uniform curve below.

The axis has two blood-vessels, the upper larger than the lower, and in its posterior fourth is not concrescent with the body, so that the inner and outer suprabranchial chambers are here continuous. The edge of the outer demibranch is united with the mantle for the whole of its length ; that of the inner is free from the visceral mass, but behind the visceral mass it fuses with the edge of the corresponding demibranch of the opposite side. The hinder extremities of the gills are not pointed, and are fused with the front edge of the siphonal septum. The relations of the parts are thus the same as those described by DALL for *Euciroa pacifica* (**14**, pp. 691 and 692). A blood-vessel runs longitudinally along the outer edge of the outer demibranch, another along the inner edge of the inner demibranch, and yet another just above the groove that represents the ventral edge of the inner demibranch.

The filaments are not disposed transversely to the axis, but rather obliquely, and

fig. 55A represents a dissection exposing the full length of one filament of each demibranch rather than an actual transection of the body. The filaments are close-set, so that the striation of the lower or incurrent surface of the gill is faint. All the filaments have interlamellar extensions of considerable width. Although not alternately high and low, these interlamellar extensions vary somewhat, each second, third, or fourth rising a little higher than the intermediate ones. When the gill is removed from the body, its upper surface shows the edges of these higher interlamellar extensions running outwards, a little obliquely, from each side of the axis to the
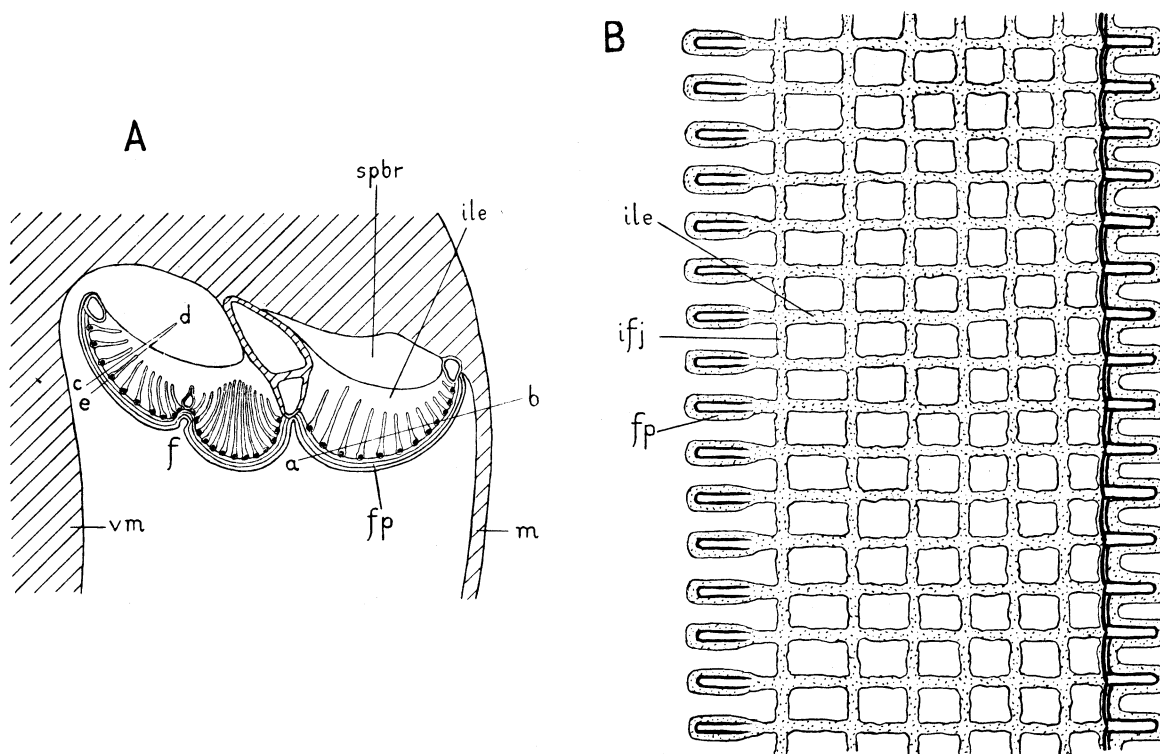
FIG. 55.—*Euciroa eburnea.* A, transverse section of gill and adjacent parts. *ab, cd* and *ed,* directions of sections 55B, 56A and 56B respectively; *f,* morphological ventral edge of inner demibranch; *fp,* filament proper; *ile,* interlamellar extension of filament; *m,* mantle; *spbr,* suprabranchial cavity of outer demibranch; *vm,* visceral mass. B, section taken in the direction *ab* in fig. A. *ifj,* one of the seven interfilamentar junctions that are included in this section; that on the extreme right shows the chitin-strand.

edges of the inner and outer demibranchs respectively. Since they are less numerous than the filaments themselves, they are more clearly distinguishable than are the latter when examined in a ventral view of the gill. It was evidently the plate-like aspect of these interlamellar extensions, as viewed from above, which led DALL to see in them the equivalents of the leaflets or platelets of the Protobranch ctenidium (**14**, p. 692, and **15**, p. 504). The species to which allusion is made in these references is *Euciroa pacifica* and not *Euciroa eburnea,* but Professor DALL was good

enough to lend the slide on which his remarks were based, and I have no hesitation in regarding the structural features as identical in the two species. The appearances presented by the sections are accurately represented in Professor DALL's figure (**14**, p. 693), but the plane of section is transverse to the ctenidial axis, and since the filaments are set obliquely on the axis the result is not a little confusing.

The number of interfilamentar junctions in the outer demibranch is twelve. Thirteen are present in the descending lamella, and ten in the ascending lamella ot the inner demibranch (fig. 55A). Each has a strand of rather fibrous chitin, and some muscle fibres, at its outer (*i.e.*, lower) edge, which is coincident with the inner (upper) edge of the filaments proper. The strands are shown in the figure as black dots. The interfilamentar junction is, however, prolonged considerably in an upward direction, so that it connects the interlamellar extensions for about two-thirds of their width (fig. 56B). The water-passages thus have the form of four-sided tubes, two of the sides being formed by the interlamellar extensions and two by the interfilamentar junctions (fig. 55B).

When the upper surface of the whole gill is examined, the upper edges of these interfilamentar junctions can be seen by slightly separating the edges of the higher of the interlamellar extensions. It is abundantly clear that these are the "fibers" alluded to by DALL in the following passages :—" The upper surface of the gill is furnished with numerous longitudinal fibers, at about equal distances apart, which firmly connect the upper edges of the lamellæ." " The close set oblique plates, or
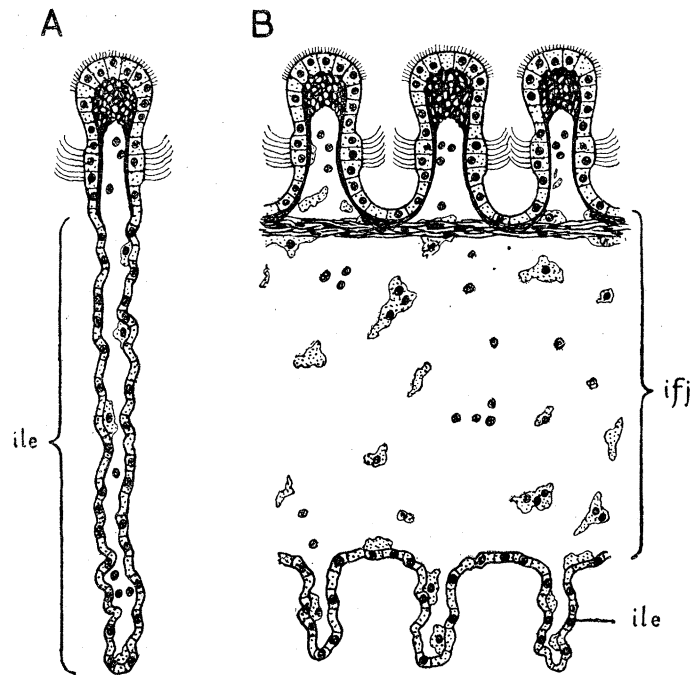

FIG. 56.—*Euciroa eburnea.* A, section of a filament taken in the direction *cd* in fig. 55A. B, similar section of three filaments taken through an interfilamentar junction, in the direction *ed* in fig. 55A. *ifj*, interfilamentar junction; *ile*, interlamellar extension.

lamellæ, are connected at their dorsal edges by a delicate series of connective fibers running in an antero-posterior direction." "Here and there a fibrous link united the faces of two plates near their dorsal margins" (**14**, pp. 693 and 695). The upper part of one such interfilamentar junction is shown cut obliquely at 7 and 8 in his fig. 2, p. 694.

There is nothing abnormal in the disposition of the cilia on the filaments (fig. 56). The frontal edge of the filament is convex, and is uniformly clothed with short cilia : the latero-frontal cilia are not longer than the median ones. The "interlocked giant cilia" upon which DALL laid so much stress (**14**, p. 694), are the normal lateral cilia. There is a profuse development of faintly staining vesicular chitin beneath the frontal epithelium. The inner demibranch has more muscular tissue than the outer demibranch, but on the whole there is less muscle present than in *Lyonsiella*.

No specimen of *Verticordia* was available, but Professor DALL was good enough to submit for inspection the slide of serial sections of the gill of *Verticordia acuticostata*, upon which he based his conclusion that the gill was *foliobranchiate* and *simple* (**15**, p. 535). I am satisfied from an examination of this slide that the gill of *Verticordia* differs · in no essential respects from those of *Lyonsiella* and *Euciroa*. Since, however, the matter cannot be dismissed by a mere expression of opinion, I take the liberty of figuring one of the most comprehensive sections on Professor DALL's slide (fig. 57), and of explaining my own interpretation of it. What makes the slide rather perplexing is that the sections are cut nearly parallel to the length of the gill, in a more or less horizontal direction as regards the body placed in the conventional position. They appear also to be taken parallel to the flattest part of the lamellæ, and in consequence the thickened, ciliated edges of the filaments are bound to be cut obliquely.

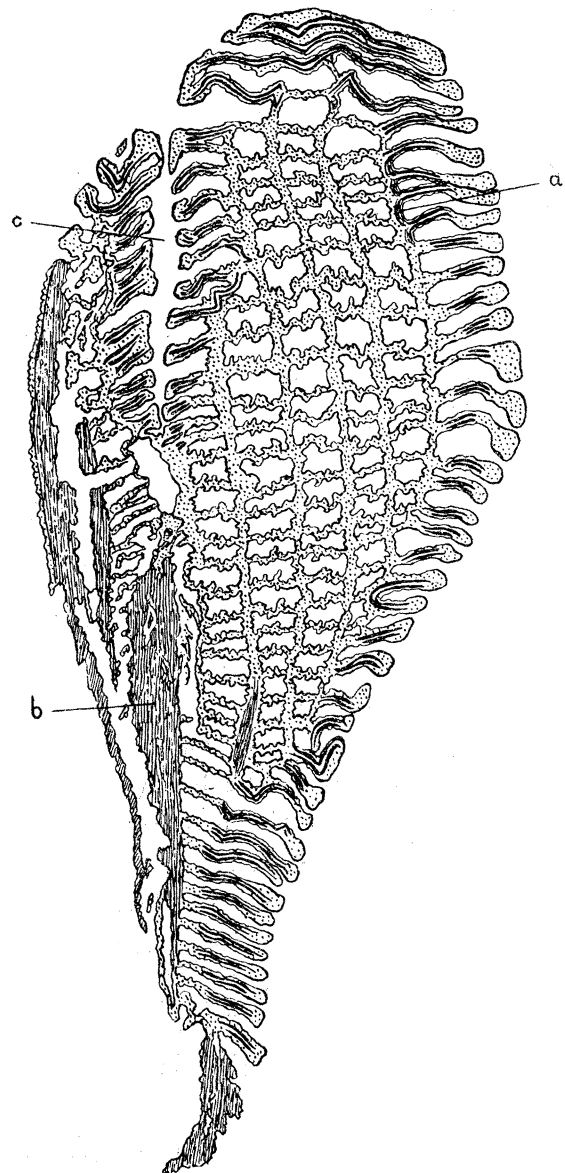A section of the gill of *Euciroa eburnea* taken in the direction *ab* in fig. 55A, is

FIG. 57.—*Verticordia acuticostata.* For explanation of *a, b* and *c* see text.

shown in fig. 55 B. It passes on the right-hand side through the continuous chitin-strand of an interfilamentar junction, and includes six other interfilamentar junctions cut at a higher level. The filaments proper are necessarily cut obliquely on both sides. This semi-diagrammatic section, although taken for convenience through the outer demibranch, supplies the key for the proper understanding of fig. 57. In the upper part of the latter figure the filaments proper alone are cut. They are the anterior filaments of the inner demibranch cut tangentially, and ventrally to the interfilamentar junctions. At a the section passes through the chitin-strand of an interfilamentar junction, and to the left of this are seen three other interfilamentar junctions cut at higher levels than those at which the chitin-strands occur. The plane of section is oblique to the ctenidial axis, including the latter behind (at b), but passing through the groove between the two demibranchs anteriorly (at c). The part to the left of the space c is the small outer demibranch.

As regards the extensiveness of the interfilamentar junctions in an upward (morphologically interlamellar) direction *Verticordia acuticostata* agrees with *Euciroa*, but in the absence of the groove that represents the morphological ventral edge of the inner demibranch, and in the smallness of the number of interfilamentar junctions, it corresponds more nearly with *Lyonsiella*. Examination of the complete series of sections of the gill of *Verticordia* shows that there are six interfilamentar junctions in the broadest part of the inner demibranch, and none in the outer, *i.e.*, exactly as in *Lyonsiella papyracea* (fig. 54 A).

Poromyidæ.

Professor DALL was good enough to send, among other material, a well-preserved specimen of *Poromya*, dredged from 1569 fathoms in the North Pacific, broad off the harbour of Sitka, Alaska. It is an undescribed species, but Professor DALL tells me he intends to describe it under the name *Poromya malespinæ*.

The gill filaments are disposed in two patches in the right half of the branchial septum, and two in the left (fig. 58 B, a and b). Each has the form of a shallow convex sieve, with the convexity directed downward and outward into the pallial cavity, and is attached all round its edge to the branchial septum by a thickened border. The anterior one is level with the front of the foot, and is continuous with the posterior palp; the posterior one is level with the hinder edge of the foot. They both lie a little obliquely. The branchial septum is rather thin and membranous for the greater part of its extent, but the posterior fourth is thicker and more muscular. The transition is abrupt, and occurs at a short distance behind the posterior branchial sieve.

The hinder sieve consists of ten free filaments crossed by four interfilamentar junctions (fig. 58 A), the anterior one of eight free filaments and four interfilamentar junctions. The filaments, as seen in a section through the middle part of the sieve,

prove to be of normal construction (fig. 58C). They have no interlamellar extensions; the cilia are disposed in one frontal and two lateral tracts, and the chitin is thickest beneath the cells that bear the lateral cilia. The upper (morphologically interlamellar) part of the filament is narrower than the ciliated part, and a sharply-defined strand of muscle lies in its edge. A section taken along one of the interfila-
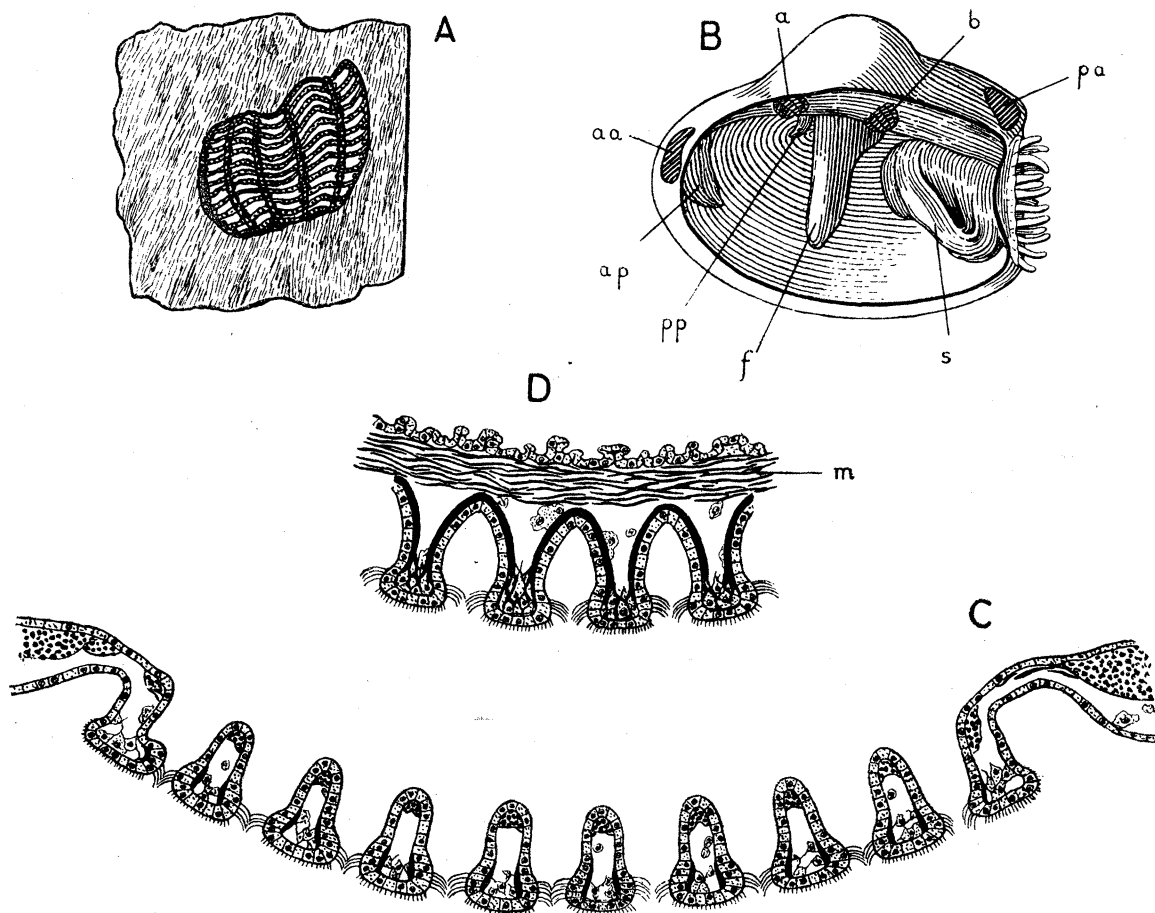

Fig. 58.—*Poromya malespinæ.* B, general dissection from the left side. *a* and *b*, anterior and posterior gill vestiges; *aa* and *pa*, anterior and posterior adductor muscles; *ap* and *pp*, anterior and posterior palps; *f*, foot; *s*, retracted siphon. A, pallial aspect of the right posterior gill vestige or sieve, with a portion of the branchial septum. The straight edge on the right-hand side is the mesial edge, applied to the side of the foot. C, section across the anterior gill vestige, taken transversely to the filaments. Eight filaments are free, and two more are confluent with the branchial septum. D, similar section of four filaments only, taken through an interfilamentar junction. *m*, muscle in the interfilamentar junction.

mentar junctions (fig. 58D) shows that the chitin is continuous from filament to filament, but that there is no continuous rod of chitin. A muscle tract in contact with the upper epithelium is a conspicuous feature.

It is doubtful whether in these two branchial sieves one can recognise the vestiges

of the inner and outer demibranchs respectively. No large blood-vessels such as might mark the position of the degenerate ctenidial axis can be recognised in the branchial septum.

In *Poromya oregonensis* (a well-preserved specimen of which was also supplied by Professor DALL) the gill vestiges occupy the same positions as in the former species. They are relatively larger in size, and are not set so obliquely. The vestiges have the form of convex grids rather than sieves, for there are no interfilamentar junctions. The filaments, of which there are seven in each of the vestiges (five free and two confluent by one edge with the branchial septum), are comparatively wide tubular structures. The six slits do not extend as close to the mesial as to the lateral edge of the convexity (fig. 59B), *i.e.*, they open downwards and outwards rather than strictly downwards.

A section taken lengthwise through the vestige (see fig. 59C) shows that the filaments have lateral tracts of cilia, borne on tall epithelial cells; but the cubical cells of the frontal surface seem to have no cilia, although small latero-frontal cilia,
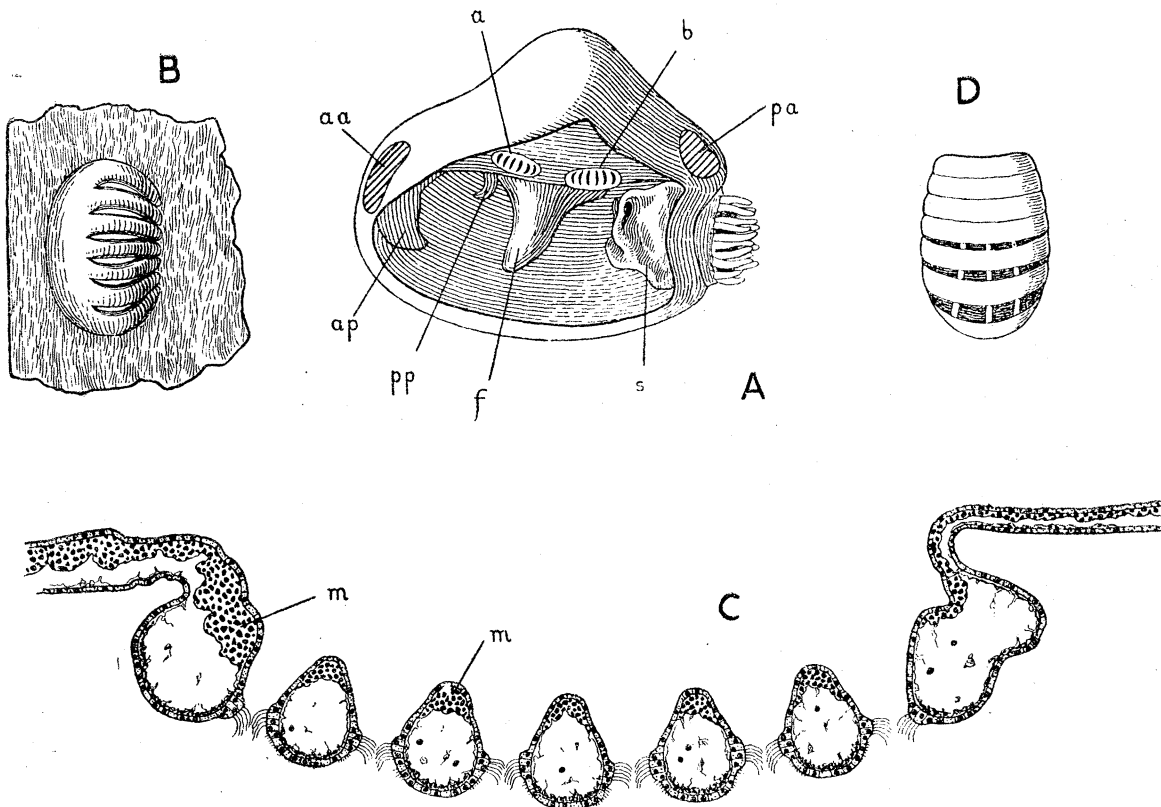

FIG. 59.—*Poromya oregonensis.* A, general dissection from the left side. Letters as in fig. 58B. B, pallial aspect of one of the posterior gill vestiges, with a portion of the branchial septum. The straight edge on the left-hand side is the mesial edge, applied to the side of the foot. C, section across the filaments, *i.e.*, in the direction of a vertical line drawn through fig. B. *m*, muscle. D, gill vestige of *Poromya tornata*, after PELSENEER.

separated by a small gap from the lateral cilia, can be distinguished. The chitin is thickest beneath the frontal epithelium; it stains rather faintly, and is vacuolated, with nucleated cells in the meshes. Straggling threads of the chitin project into the large filamentar cavity from all sides. Muscle fibres running lengthwise along the filaments occur in the upper edges of the filaments.

Poromya tornata I have not had an opportunity of examining, but, according to PELSENEER's account, and according to his figure of the anterior vestige (**68**, Plate 3, fig. 5), seven filaments are present, and three interfilamentar junctions (see fig. 59D), and the filaments are much thicker than the junctions. In this respect the species occupies an intermediate position between *Poromya oregonensis*, which has thick filaments and no interfilamentar junctions, and *Poromya malespinæ*, which has the interfilamentar junctions thicker than the filaments.

In *Poromya malespinæ* and *Poromya oregonensis*, and, according to PELSENEER (**68**, p. 20), in *Poromya tornata* and *Poromya granulata* also, there is no fusion between the inner edge of the branchial septum and the side of the foot.

It is worthy of mention here that DALL has observed that the pores of *Poromya* are closed in the young, and only open on the attainment of sexual maturity (**13**, p. 451).

Cetoconchidæ.

The general arrangement of the branchial pores of *Cetoconcha sarsi* (= *Silenia sarsi*) has already been clearly explained by PELSENEER (**68**), who states that they are arranged in 3 paired groups, the anterior group having 5 pores, the second 5 or 6, and the posterior 3. The disposition of the pores can be better comprehended by a glance at fig. 60A than by following a verbal description. This figure is substantially identical with the fig. 9, Plate 3, of PELSENEER, and its object in the present instance is to explain the direction in which the section shown in fig. 60B is taken.

The anterior palps are large, the posterior small. The branchial septum is only moderately thick. Its inner edge is fused with the sides of the foot, and in its hinder portion is continuous with the siphonal septum.

A section through the five anterior pores appears as shown in fig. 60B. The lower epithelium of the bars between the pores consist of sharply-outlined cubical cells, rather wrinkled in the actual sections, but represented in the figure in what may be assumed to be its normal condition—a uniformly-curved layer. I fail to distinguish any cilia. The upper epithelium is flatter, and is in contact with great tracts of muscle, seen cut traversely. The interior is partly occupied by loose cells; and thick vesicular chitin lines the cubical epithelium, while a thin layer of chitin may be recognised on the lower surface of the muscle. In a slide of transverse sections of the whole body of *Cetoconcha smithi*, lent by Professor DALL, there are evidences of cilia, but I am unable to distinguish the limits of the ciliated areas.

These appearances are so little different from those seen in the transverse sections of the gill filaments of *Poromya oregonensis*, that it is not unreasonable to suppose that the boundaries between each two pores of *Cetoconcha* are shortened gill
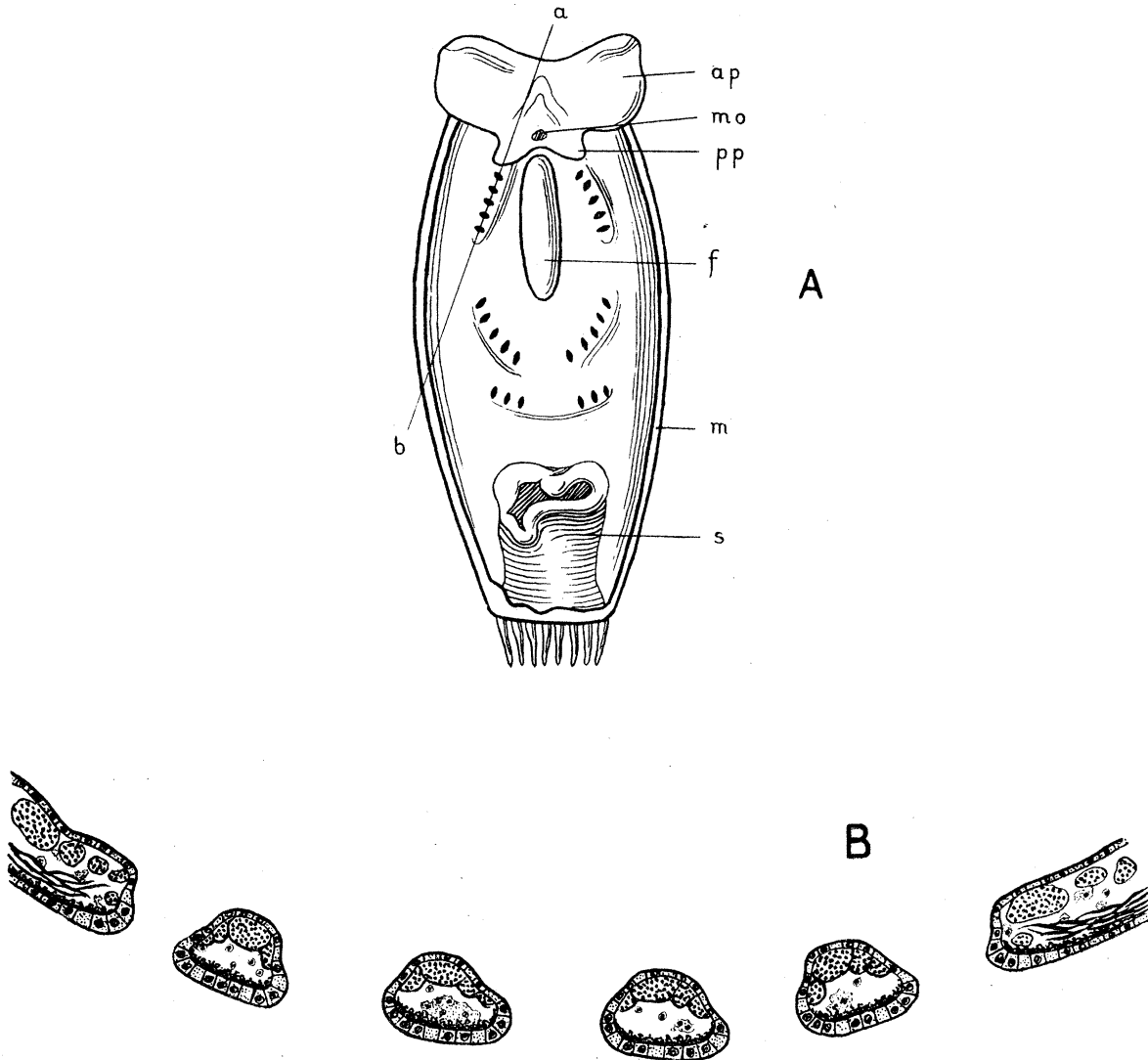

Fig. 60.—*Cetoconcha sarsi*. Ventral aspect of the branchial septum and associated parts. *ap* and *pp*, anterior and posterior palps; *f*, foot; *m*, mantle; *mo*, mouth; *s*, retracted siphon. B, section through one of the anterior groups of pores taken in the direction *ab* in fig. A.

filaments. If in *Poromya oregonensis* the branchial slits were shortened until circular in outline, there would result a series of six pores disposed in an antero-posterior direction. Without the series *Lyonsiella papyracea—Poromya malespinæ—Poromya tornata—Poromya oregonensis* one might hesitate to recognise the wide tubes of the latter species as modified gill filaments, but with the help of this series one is enabled to go even farther, and to comprehend the morphological nature of the tissue between each two consecutive pores of *Cetoconcha*. The anterior and middle

groups of pores of *Cetoconcha* may thus be compared with the two groups of branchial slits in *Poromya oregonensis*. Since, however, the posterior groups of pores of *Cetoconcha* have no equivalent in the known species of *Poromya*, it is well to place the two genera in separate families—Cetoconchidæ and Poromyidæ.

Cuspidariidæ.

The branchial pores of *Cuspidaria* have already been so fully treated of by previous authorities (see references on p. 266) that little remains to be added. The branchial septum in *Cuspidaria glacialis* is thick and muscular, and has five pores on each side of the body (fig. 61, *p*). The first pair are in front of the posterior palps (the anterior palps are wanting in this species), the second pair just behind these palps. The fourth pair are on a level with the hinder part of the foot. While some species of *Cuspidaria* have five pairs of pores, *e.g.*, *Cuspidaria glacialis*
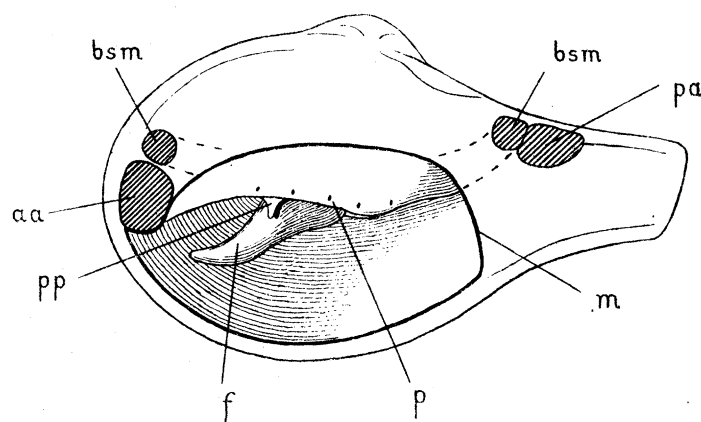

Fig. 61.—*Cuspidaria glacialis*. General dissection from the left side. *aa* and *pa*, anterior and posterior adductor muscles; *bsm*, muscles of the branchial septum, attached to the shell; *f*, foot; *m*, cut edge of mantle; *p*, the middle of the five pores; *pp*, posterior palp.

(DALL, **11**, p. 209), and *Cuspidaria cuspidata* (GROBBEN, **28**, p. 10), others have only four pairs, *e.g.*, *Cuspidaria patagonica* and *Myonera paucistriata* (DALL, **11**, p. 209), and *Cuspidaria curta*, *C. fragilissima*, *C. platensis*, and *C. rostrata* (PELSENEER, **68**, p. 24).

The sections of the branchial septum of the specimen examined fail to show any special features of the pores. The material is evidently in a poorer state of preservation than that studied by GROBBEN, who was able to distinguish a prismatic epithelium and two tracts of cilia (*Cuspidaria cuspidata*, **28**, Plate 4, fig. 25). The valves shown by PELSENEER (*Cuspidaria rostrata*, **71**, fig. 92) cannot be recognised in my sections : they are not shown in GROBBEN's figure.

After what has just been said concerning *Cetoconcha*, and the series of species showing gradual reduction of the interfilamentar slits, there is little difficulty in

recognising in the four or five pairs of branchial stigmata of *Cuspidaria* the reduced gill-slits such as occur in the middle group of pores of *Cetoconcha*. This is not intended to imply direct parentage on the part of the Cetoconchidæ, but that the appearances presented in the Poromyidæ and Cetoconchidæ supply the key to the proper understanding of the nature of the stigmata of *Cuspidaria*.

It must be noted that the pores are wider apart than in *Cetoconcha*, and the amount of muscular tissue in the intervening parts is relatively enormous. It becomes a pertinent question, therefore, whether the other parts of the branchial septum may not also be really branchial in origin. In the series *Pandora* (or any other typical form of Anatinacea), *Lyonsiella*, *Poromya*, *Cetoconcha* and *Cuspidaria*, there is a gradual increase in the amount of muscle fibre in the inner or interlamellar edge of the filaments or their reduced equivalents, so that DALL's objection to the branchial origin of the septum because of its muscularity (**15**, p. 537) cannot hold good. At the same time it is difficult to understand how a muscular structure of ctenidial origin could have extended forwards and backwards so as to gain such important attachments to the valves of the shell as is seen in Cuspidaria (fig. 61, *bsm*). A historical review of the discussion as to the branchial or pallial nature of the septum is given on page 183, and I prefer to leave the question entirely open.

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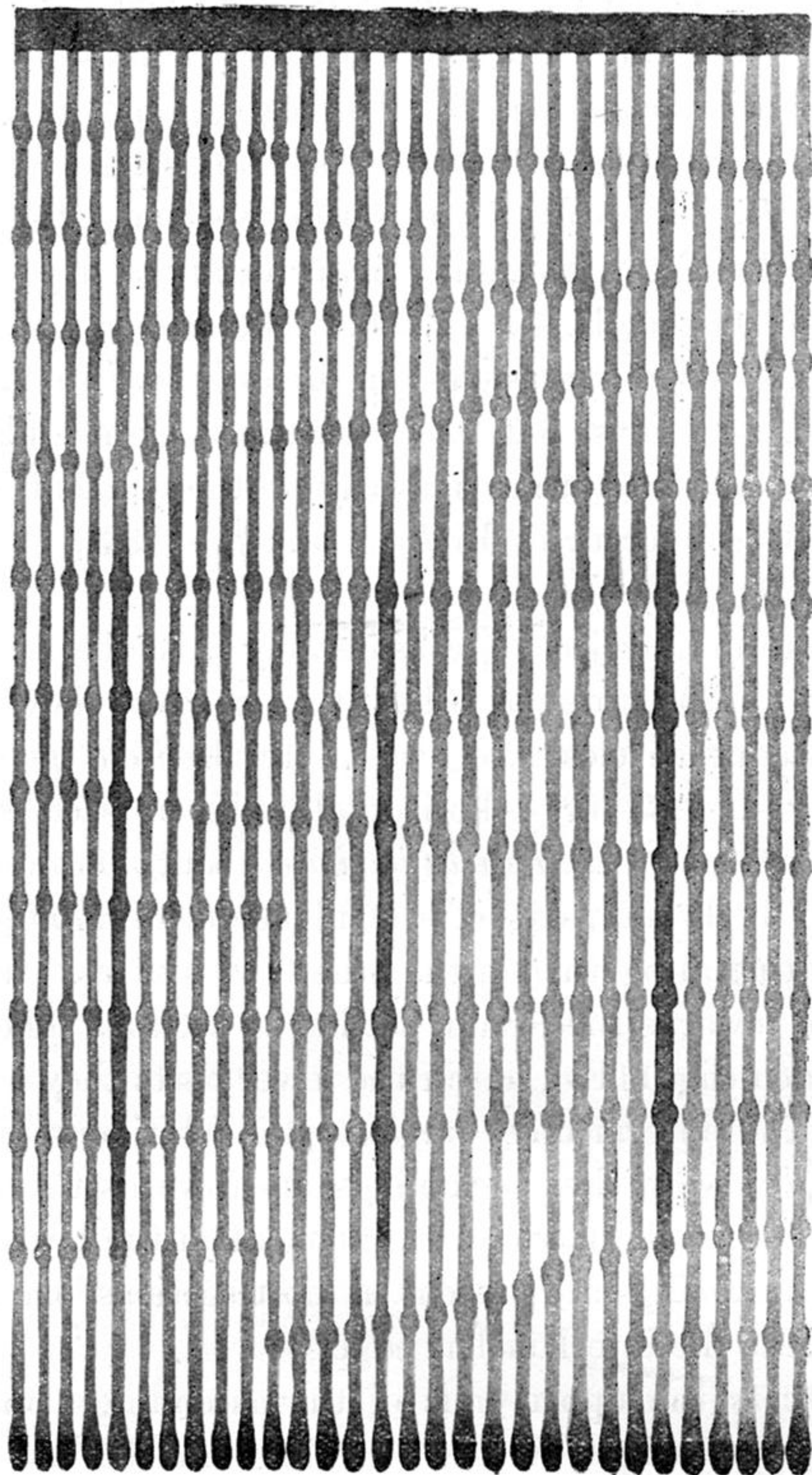
FIG. 12.—*Lithodomus dactylus*. Surface view of portion of inner demibranch showing three dark septum-bearing filaments.
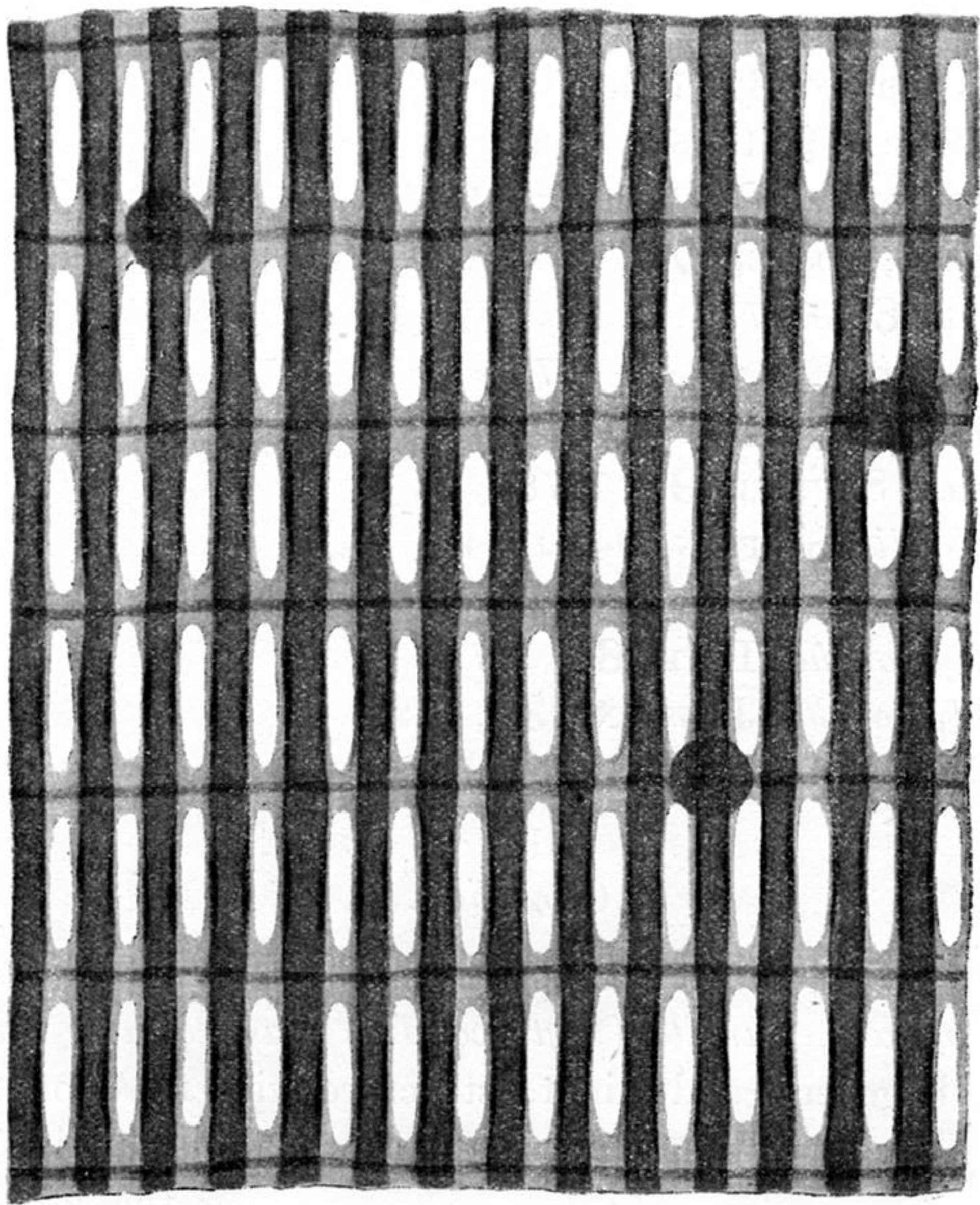
FIG. 21.—*Astarte borealis*. Interlamellar aspect of a portion of one lamella. The vertical bands are the filaments, the horizontal dark lines the chitin in the interfilamentar junctions, and the three dark patches are interlamellar bars.
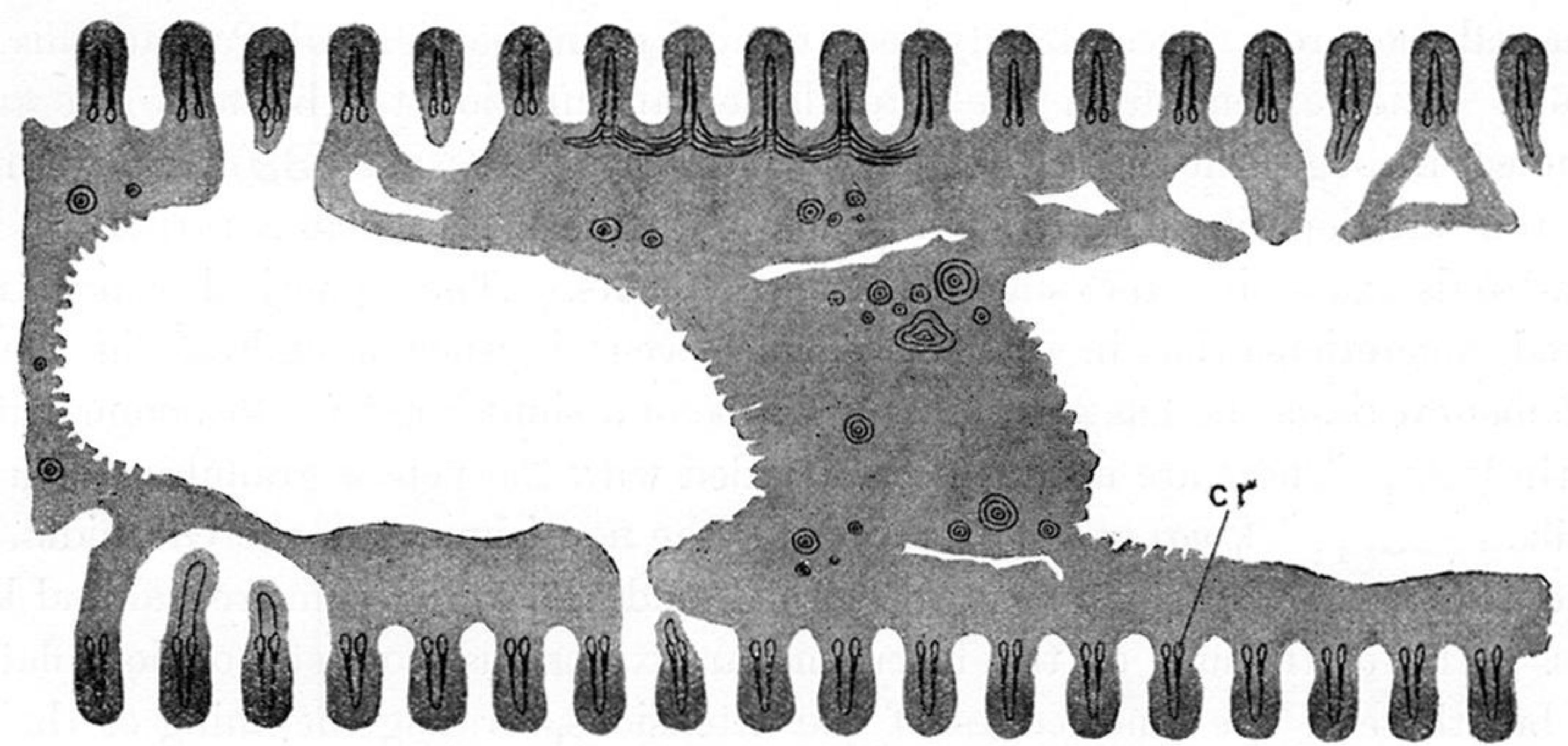
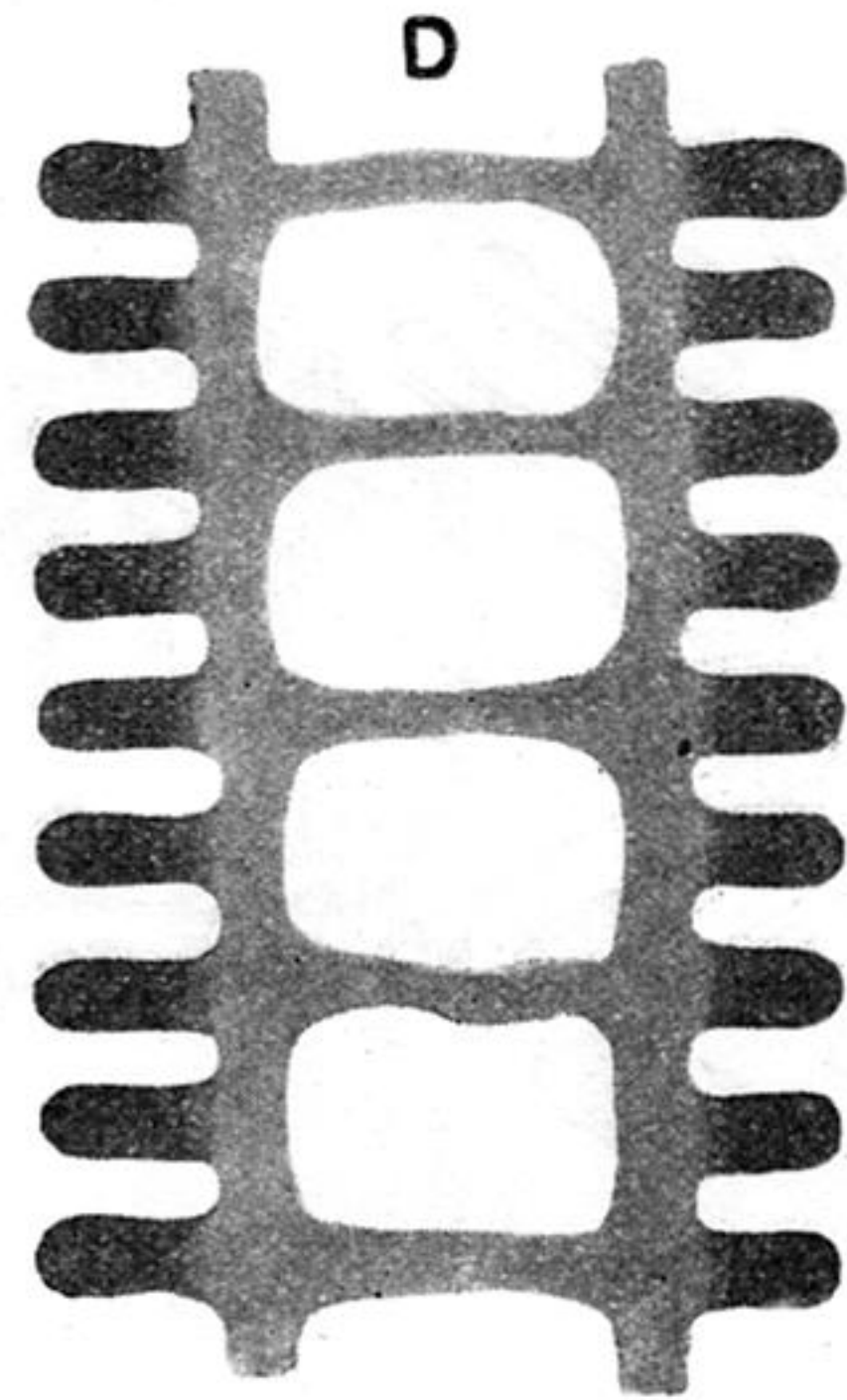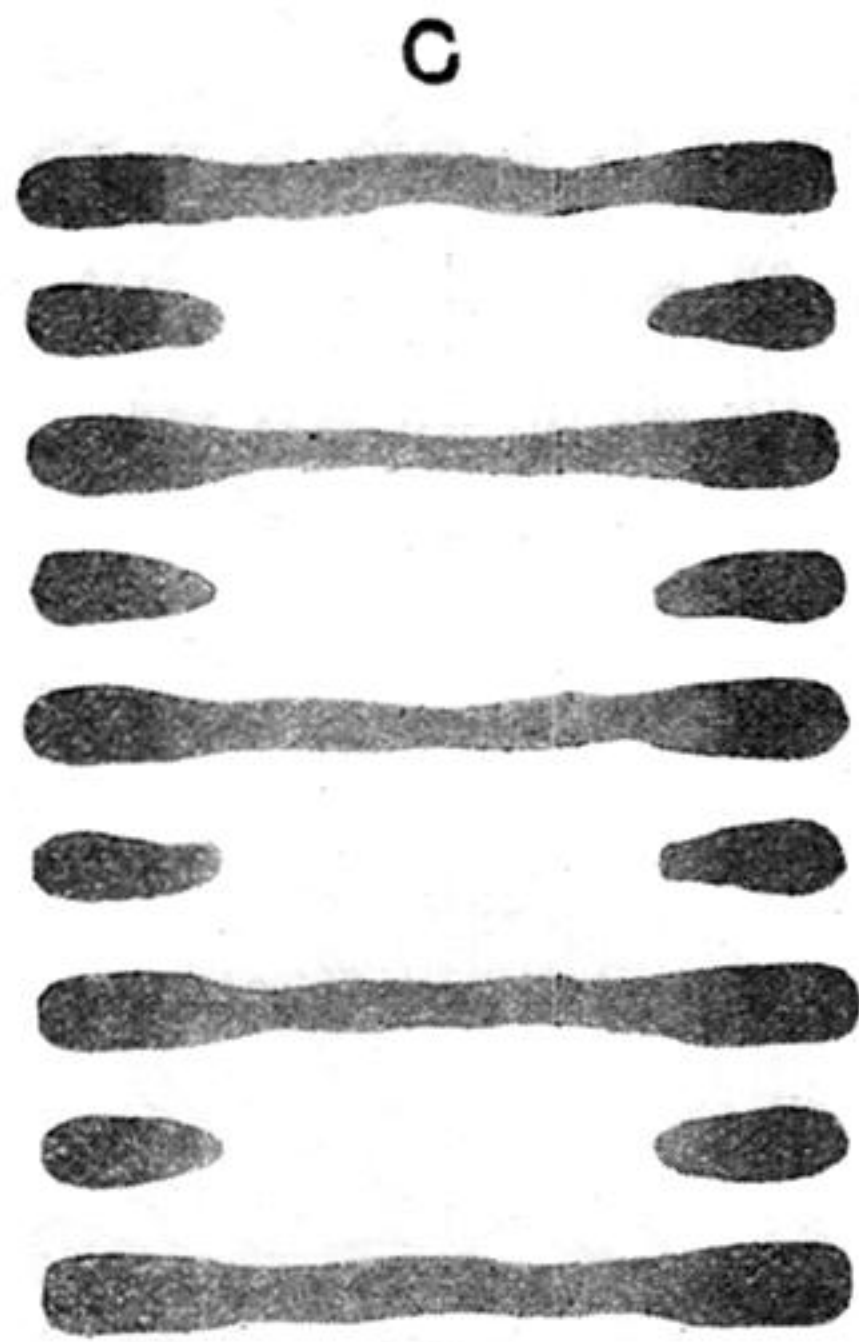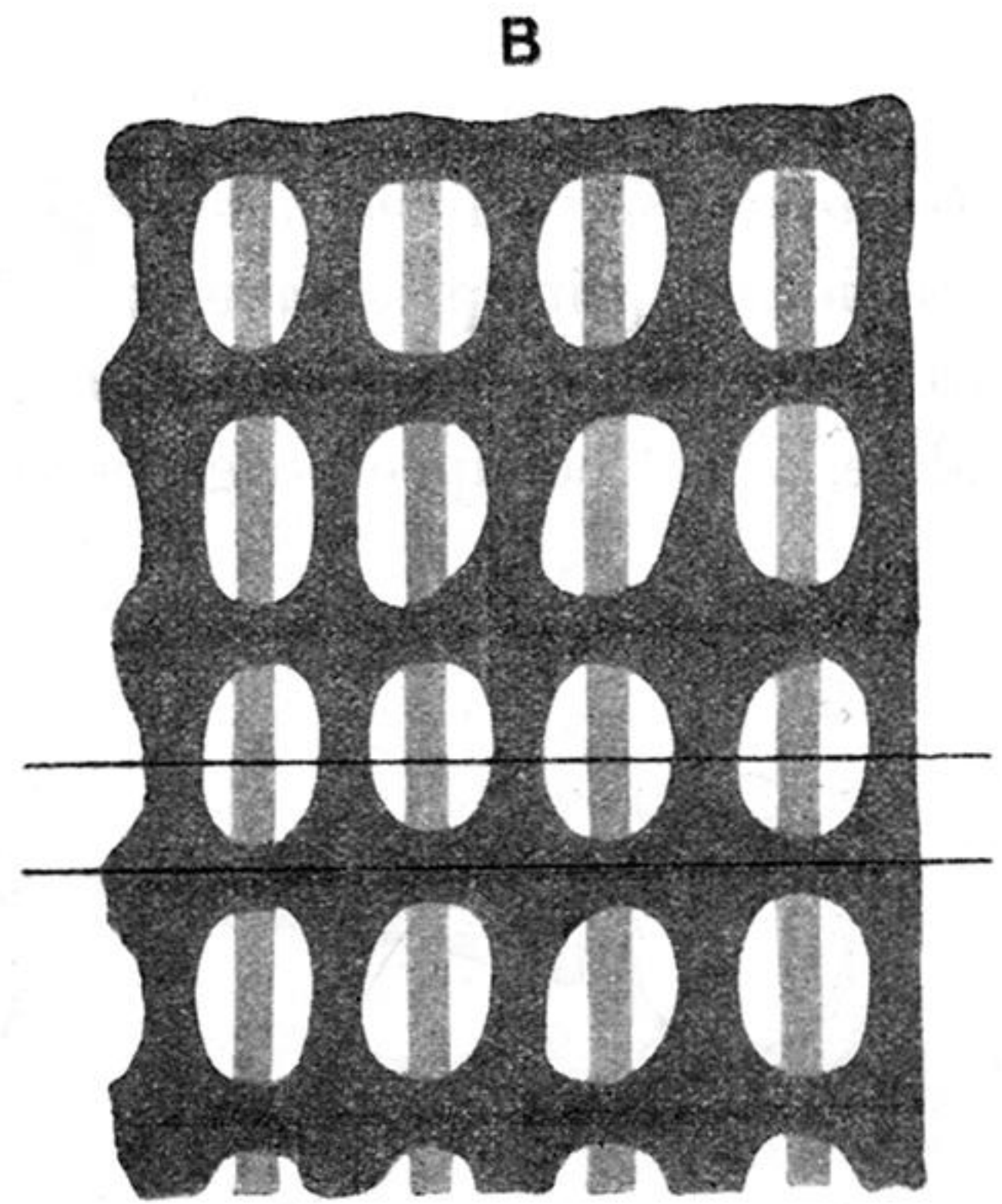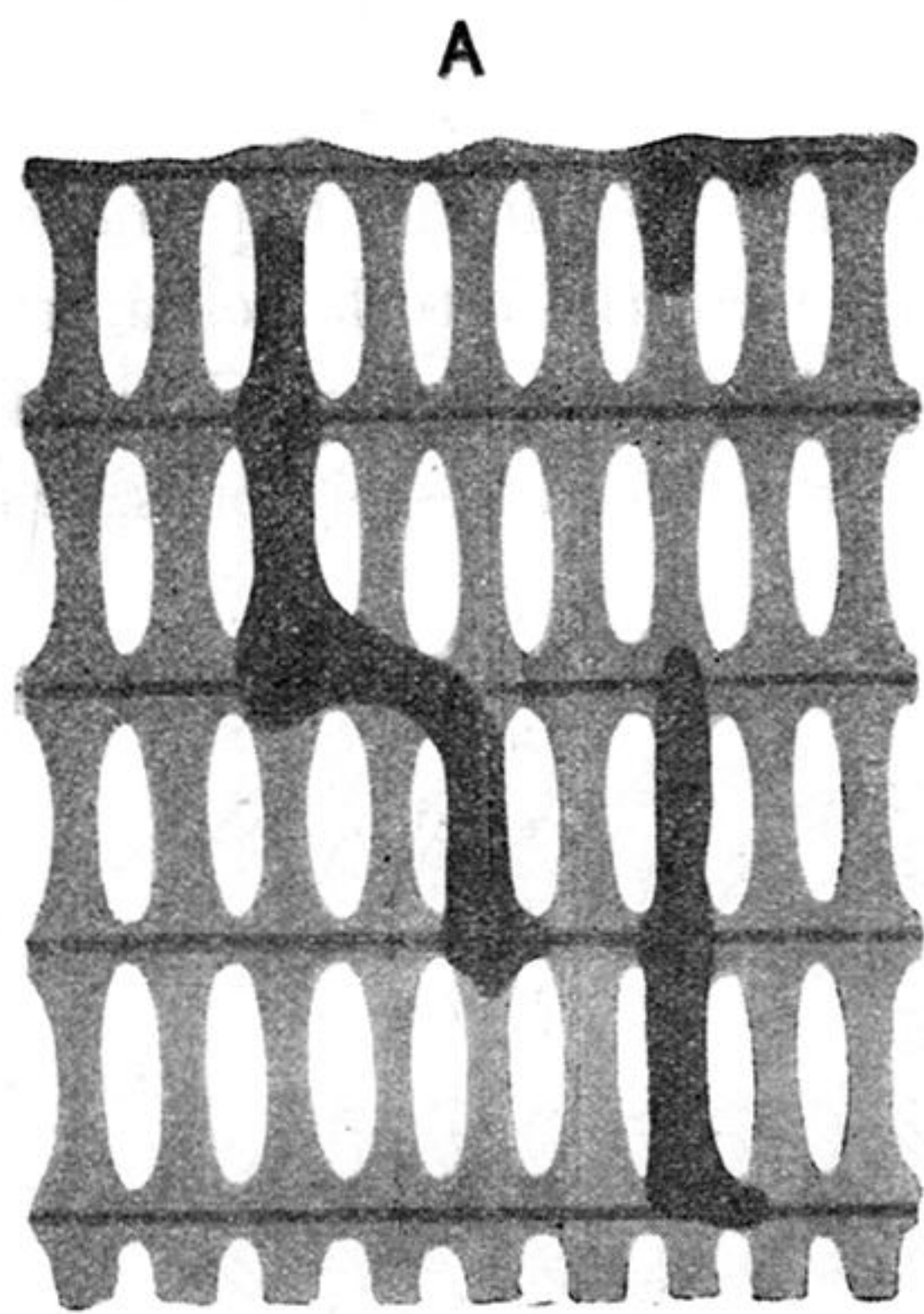FIG. 27.—*Mülleria dalyi.* *cr*, calcified rod.

FIG. 41.—A, *Corbula gibba*. Interlamellar aspect of a portion of a single lamella stripped away from its
fellow. The dark patches are the interlamellar junctions; the fenestræ are bounded at the sides by
the filaments, and above and below by the interfilamentar junctions. The dark line in each
interfilamentar junction is the chitin-strand. B, similar preparation of *Corbula laevis*. The subfila-
mentar tissue is much more profuse, both as regards the interlamellar and interfilamentar junctions.
C, section taken horizontally through a row of fenestræ, in the direction of the upper pen-line in
fig. B. D, similar section through interfilamentar junctions, in the direction of the lower line in
fig. B.