THE PALLIAL ORGANS IN THE ASPIDOBRANCH GASTROPODA AND THEIR EVOLUTION THROUGHOUT THE MOLLUSCA

By C. M. YONGE, *University of Glasgow*

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[Plate 18]

CONTENTS

The pallial organs and the currents within the mantle cavity have been studied in many genera of aspidobranch Gastropoda including members of the Zeugobranchia, Fissurellidae, Patellacea (Docoglossa), Trochacea, Neritacea and Valvatacea. Relevant data on allied genera, not available alive, have been considered.

The aspidobranch condition has been retained in a diverse variety of Prosobranchia; its possession does not indicate close relationship.

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The mantle cavity of the Mollusca is a respiratory chamber unique in its primitively posterior position and the opening into it of the alimentary, renal and reproductive systems. The respiratory current is created by lateral cilia on filaments alternately arranged on either side of the axes of the paired ctenidia. The current passes between the filaments invariably from the efferent to the afferent surface, i.e. in the opposite direction to the flow of blood.

To withstand the water pressure the filaments are strengthened by skeletal rods under the zone of lateral cilia near the efferent surface. Frontal, abfrontal and terminal cilia (the last probably not primitive) are concerned with cleansing. Sediment is consolidated in mucus from hypobranchial glands situated on the roof of the mantle cavity where this is carried by the current. The osphradia always lie where the water current first impinges on the surface of the cavity; they are regarded as tactile organs for the estimation of sediment. Ctenidia, hypobranchial glands and osphradia form a functional unit. The anus and other openings discharge into the exhalant chamber dorsal to the ctenidia. There are correlated mechanisms in the gut for the consolidation of faeces.

The primitive Mollusca probably crawled on a hard substratum as do the modern Loricata and all aspidobranch Gastropoda, except the Valvatacea where the pallial organs have migrated forward in the mantle cavity. The more highly specialized pectinibranchs, together with the Scaphopoda and Lamellibranchia, invaded soft substrata. Other pectinibranchs, like many modern Cephalopoda, took to pelagic life.

In the evolution of the Gastropoda exogastric coiling of the shell probably preceded torsion.

Of the theories concerning the origin of torsion, that of Garstang, which postulates larval mutation, is the most probable. The process still occurs in the development of modern Prosobranchia. The immediate advantage to the larva explains the selection of the original mutation and the absence of intermediate forms. So far from being of immediate advantage to the adult, the occurrence of torsion presented a series of problems only successfully solved by the pectinibranchs and the equally specialized Patellacea.

The immediate problem, of 'sanitation', raised by the discharge of faeces and excrement into the anterior mantle cavity, was met by the appearance of a marginal slit (or aperture), with consequent withdrawal of the anus, which enabled the exhalant current carrying faeces and excretia to pass out clear of the head. The slit disappeared with the loss of the right ctenidium, when a left-right respiratory current was established and the rectum again extended to the margin of the cavity, and is now confined to the few surviving zygobranchiate genera.

The asymmetry of the pallial organs was caused by the asymmetrical coiling of the shell which probably followed torsion. The organs of the right side were reduced or lost except where, as in the Fissurellidae, secondary shell symmetry was attained before the complete disappearance of these organs.

The reproductive and renal organs are asymmetrical. There is no left gonoduct and possibly no left gonad (this loss may have preceded torsion); the right gonoduct opens into the reno-pericardial canal. In all Zeugobranchia (including Fissurellidae), Trochacea and Patellacea, the right kidney is retained and the left reduced; in the Neritacea, Valvatacea, Cocculinacea and all pectinibranchs, the right kidney disappears. Its loss is associated with the assumption of the monotocardiate condition and may be due to loss of the right ctenidium and so of the auricle. The retention of the right kidney in the other aspidobranchs cannot be correlated with changes in the pallial complex.

Aspidobranchs with the right kidney have been faced with fundamental reproductive limitations; the impossibility of internal fertilization has prevented them from invading fresh waters or the land (unlike Neritacea, Valvatacea and pectinibranchs) or the abyssal seas (unlike Cocculinacea).

In aspidobranchs four conditions have resulted from the initial asymmetrical coiling of the shell: (i) Asymmetrical shell with two asymmetrical ctenidia (Zeugobranchia); (ii) Secondarily symmetrical shell with two symmetrical ctenidia (Fissurellidae); (iii) Asymmetrical shell with loss of one ctenidium (Neritacea, Valvatacea, Trochacea); (iv) Secondarily symmetrical shell with loss of one or both ctenidia (Patellacea, Cocculinacea, some Neritacea, e.g. *Septaria*). The secondarily symmetrical limpet form has been acquired independently four times by these aspidobranchs as well as several times by other Gastropoda.

In the Patellacea a functional series, *Patelloida-Lottia-Patina-Patella*, indicates the manner in which the monobranchs may have evolved into types with a ring of pallial gills and no ctenidium.

With the loss of the left row of filaments in the remaining (left) ctenidium, the pectinibranch condition was assumed and the ideal solution found to the problem of respiratory circulation originally raised by torsion. Success is indicated by the wide range of adaptive radiation exhibited by the pectinibranchs.

The primitive molluscan ctenidium was probably essentially similar to that of a modern asymmetrical Zeugobranch, e.g. *Haliotis*. The ctenidium in the aspidobranchs has been variously specialized; in the zygobranchiate Fissurellidae in association with the retention of the marginal slit, with increased afferent attachment in the monobranchiate Trochacea, and with greater freedom in the monobranchiate Patellacea, Valvatacea and Neritacea where skeletal rods are also absent. In the pectinibranchs, apart from specialization for food collection, the ctenidium varies little.

In the Loricata, apart from multiplication and loss of skeletal rods, the ctenidia remain fundamentally unchanged. In the Scaphopoda they are lost.

In the Lamellibranchia attachment is exclusively afferent. The evolution of the complex food-collecting ctenidia, representing a change in the function of the frontal cilia, is traced by way of those of the Nuculidae. The elongated filaments of the Filibranchia and Eulamellibranchia probably evolved not by downward growth of the tip of the filaments and later reflexion, but by ventral extension of the *middle* of the originally horizontal filament. Only then could the food groove function during development (and evolution). Pumping ctenidia have been independently evolved by the Nuculanidae and the Septibranchia.

In the Cephalopoda respiratory currents are produced by contractions of the muscles of the funnel (*Nautilus*) and mantle (Dibranchia). The initial flow of water through the ctenidia is probably reversed, the exhalant chamber with anus and other openings being on the efferent side while skeletal rods appear in membranes on the afferent side of the filaments; but there may be some back-flow of water in the efferent-afferent direction. The evolution of this type of respiratory current made possible the swimming movements of the Cephalopoda.

The tetrabranchiate condition found in *Nautilus* is *not* regarded as primitive. There is no reason for assuming that primitive nautiloids were necessarily tetrabranchiate. The increased respiratory needs of the evolving Cephalopoda may have been met (i) by maintenance of the primitive circulatory system but duplication of the ctenidia, the current being produced by pulsations of the funnel only (e.g. *Nautilus*), or (ii) by retention of one pair of ctenidia, but increased efficiency by the acquisition of capillary circulation with branchial hearts and a more powerful respiratory current produced by the mantle musculature following the reduction and overgrowth of the shell (modern Dibranchia).

The relation between respiratory surface and body weight in Gastropoda, Loricata and *Nautilus* is approximately similar. With the elongation of the filaments in ciliary-feeding Lamellibranchia and Gastropoda the current is increased beyond the respiratory needs of the animal.

Hypobranchial glands occur in association with the ctenidia in all aquatic Gastropoda where sediment needs to be consolidated (i.e. *not* in Patellacea or Valvatacea); they disappear with the ctenidia, e.g. in *Caecum* and all terrestrial Gastropoda except the Neritacea. Similar glands occur in the Nuculidae and Solenomyidae (Protobranchia) and in *Monia* (Filibranchia); glands with similar functions occur in the pallial grooves of *Patina* and its allies (Patellacea) and in the Loricata.

Osphradia are associated with ctenidia in all aquatic Gastropoda, persisting after the loss of these in the Patellacea and in *Caecum*, and reappearing in aquatic Pulmonata. Their presence is nowhere correlated with existence in water of variable character or with the type of food. There is some correlation between their size and the degree of sediment normally encountered. In certain Patellacea and in the Loricata subpallial sensory streaks in the pallial grooves may have the same function. Similar organs, of dubious function, occur in the exhalant cavity in the Lamellibranchia, but in the Cephalopoda osphradia are confined to *Nautilus* where alone sediment will accumulate in the mantle cavity. In all but the Lamellibranchia sediment carried in by the respiratory current is carried over the osphradial surface.

Study of the bipectinate osphradium of *Neptunea* indicates that it is admirably adapted for the estimation of large quantities of sediment which passes slowly over its extensive sensory surface and is then rapidly removed by cilia and consolidated in mucus.

I. Introduction

The mantle cavity is one of the most characteristic features in the Mollusca. Primarily a respiratory chamber housing the ctenidia with associated organs, the alimentary, renal and reproductive systems all open into it. It is capable of remarkable modifications in form and function; it serves as a 'lung' in terrestrial Gastropoda and, while always retaining its respiratory function, as a feeding chamber in the Lamellibranchia and a few Gastropoda and as an organ of locomotion in the Cephalopoda and some Lamellibranchia.

The elucidation of the functional interrelationships between the pallial organs is essential to a full understanding of the Mollusca. Paradoxically more is known of conditions in the Lamellibranchia, and to some extent in the Cephalopoda, than in the less modified classes. The most primitive conditions amongst existing Mollusca are present in those Gastropoda in which both or one of the original bipectinate ctenidia are retained and which have been variously designated the Aspidobranchia, Diotocardia or Archaeogastropoda. Although much work has been done on the morphology of these animals since the pioneer investigations of Spengel (1881), notably the extensive studies of Bernard (1890 *a*, *b*) on the pallial organs of the Prosobranchia, there are no data on conditions *in life*. This is essential, most obviously in the case of the ctenidia, the shape and ciliation of which cannot be determined from preserved material. Previous work on the mantle cavity of pectinibranch Gastropoda (Yonge 1932, 1937*a*, 1938, 1942; Yonge & Iles 1939) and on the protobranch Lamellibranchia (Yonge 1939*b*) revealed that only after a functional study of conditions in primitive Gastropoda would a general survey of the mantle cavity throughout the Mollusca be possible.

This paper aims, therefore, at the interpretation first of conditions in the aspidobranch Gastropoda and second of those throughout the Mollusca. The question of torsion in the Gastropoda is dealt with particularly in connexion with its functional effects. As many aspidobranchs as possible have been examined in life, but where living animals were unobtainable, notably in the case of *Pleurotomaria* and *Scissurella*, relevant morphological data have been quoted. The classification and nomenclature used by Thiele (1925) and Winckworth (1932) has been followed. The term aspidobranch has been used in its widest sense, i.e. to denote all prosobranch Gastropoda with bipectinate ctenidia. It therefore includes both the Neritacea which, as Bourne (1908, 1911) has shown, should probably be elevated into an order on the same standing as the remaining Archaeogastropoda, and also the Valvatacea amongst the Mesogastropoda. In all of these the ctenidia have remained in a relatively unspecialized condition, but this does not necessarily indicate close relationship. While there is no intention of dealing with questions of classification it should be noted that Pelseneer's order Aspidobranchia is, for this reason, unsound.

The only group of the Mollusca possessing ctenidia which are not considered in the general sections of the paper are the Tectibranchia. Conditions in the mantle cavity of these animals will, it is hoped, form the subject-matter of a separate publication. Observations already made on living Tectibranchia confirm the general conclusions here reached.

II. Orientation and nomenclature

Any general account of the Mollusca, such as that of Pelseneer (1906), has necessarily to be preceded by a description of the hypothetical primitive mollusc to which alone the existing divergent classes can be related, although the structure of this postulated organism can only be deduced from a consideration of that of the various classes considered subsequently. For the same reason it has been found necessary for the better understanding of the subject-matter of this paper to make a preliminary statement on the primitive orientation of the pallial organs in the Gastropoda, which involves the important matter of nomenclature, although much of the data on which this is based is contained in subsequent sections of this paper. This might not have been necessary had it been possible to examine *in life* the disposition and functioning of the pallial organs in *Pleurotomaria* where very primitive conditions undoubtedly exist. The zygobranchous genera which have been examined alive, namely, *Haliotis*, *Diodora*, *Emarginula* and *Puncturella*, are all specialized in one way or another, and the primitive condition has had to be largely deduced from examination of conditions prevailing in these animals.

As shown in figure 1, the mantle cavity is bounded ventrally by the convex dorsal surface of the body and dorsally by the concave inner surface of the mantle. When, following contraction of the shell muscles in living zygobranchs, the animal is withdrawn fully within the shell, these two surfaces are closely applied, but when the animal is fully extended the pallial organs can function freely within the capacious cavity in which they lie protected. These organs consist of ctenidia, osphradia and hypobranchial glands. They will be described as they exist *after* torsion, i.e. in primitive zygobranchous Gastropoda. Their probable disposition *before* torsion is shown in figure 1.

The ctenidia, primitively paired, are pallial outgrowths which extend forwards from the posterior end of the cavity. Each consists of a laterally compressed axis with triangular filaments arranged alternately on the two sides. At the point of origin the axis is attached by membranes to the mantle both 'ventrally' and 'dorsally'. The 'ventral' membrane (*em*) is fused for variable distances with the margin of the mantle, near to its junction with the body, the tip of the ctenidium being always free, while the 'dorsal' membrane (*am*), usually much shorter, is attached to the base of the rectum (*r*) above. Through the axis run muscles, nerves and afferent and efferent blood vessels (*av*, *ev*). In all zygobranchous species which have been examined in life (when alone the normal disposition of the ctenidia can be determined with certainty because they shrink and twist after fixation) and also in the very similar Trochacea where the right ctenidium is lost, the ctenidia lie obliquely, the laterally compressed axis being inclined inwards at an angle of about 45°, as originally stated by Spengel (1881). It is therefore misleading to speak of their dorsal and ventral surfaces.

The ctenidial filaments, although capable of great modification, have a fundamentally triangular shape, one of the two free margins being distinguished in all zygobranchous and most other genera by the presence of a supporting skeletal rod (*sr*) which lies just within that margin against which the respiratory current, drawn into the mantle cavity and between the filaments by the lateral cilia, impinges. This is the frontal surface of the filament, the other being the abfrontal. But in certain genera, e.g. *Patelloida*, *Theodoxus* and *Valvata*, the skeletal rods, for reasons which will be discussed later, are absent, so that where the direction of water flow is unknown it is impossible to say which surface is frontal and which is abfrontal. For this reason it is inadvisable to employ these terms generally.

There remains the disposition of the blood vessels. The afferent blood vessel runs along the abfrontal margin of the axis, the efferent vessel along the frontal margin. There is a functional reason for this, just as there is for the presence of the skeletal rods, because the blood thus flows through the filaments in the *opposite direction* to the flow of water outside with consequent increase in respiratory efficiency. The arrangement of these vessels has been found to be constant throughout the Mollusca, and they provide the criterion on which is based the account of the evolutionary history of the molluscan ctenidium given later in this paper. Since they can be distinguished equally well by dissection or sectioning in both fresh and preserved material, they are here used to distinguish between the free surfaces of both the filaments and the ctenidial axes. Afferent surface thus replaces abfrontal or 'dorsal' and efferent surface frontal or 'ventral'. The 'dorsal' and 'ventral' ctenidial membranes will also be termed afferent and efferent respectively.

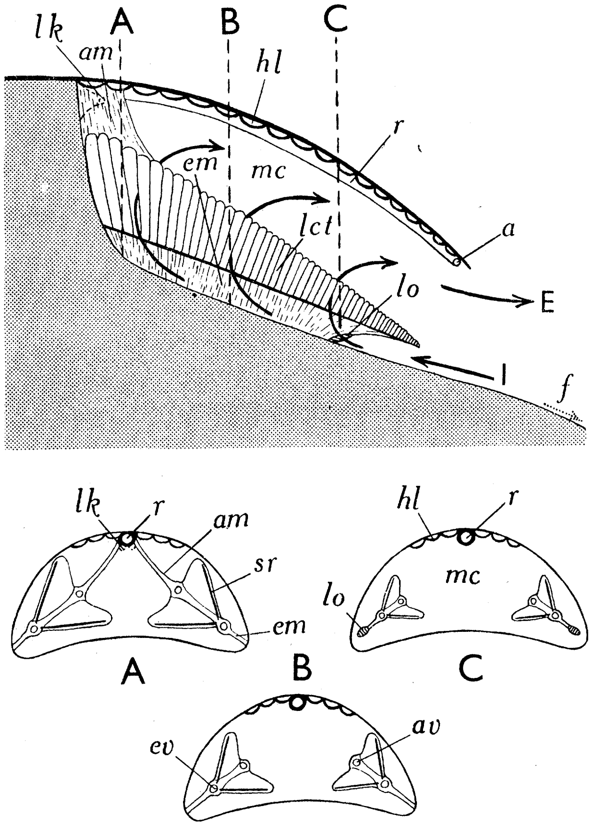

FIGURE 1. Diagrams showing probable arrangement of the pallial organs in the pre-torsional ancestors of the Gastropoda. Upper figure shows the mantle cavity viewed from the left side, the broken lines *A*, *B*, *C* indicating the position of the three similarly lettered sections each of which is drawn as viewed from the posterior. *a*, anus; *am*, afferent membrane; *av*, afferent blood vessel; *E*, exhalant current; *em*, efferent membrane; *ev*, efferent blood vessel; *f*, surface of foot with backward directed ciliary currents; *hl*, left hypobranchial gland; *I*, inhalant current; *lct*, left ctenidium; *lk*, left kidney aperture; *lo*, left osphradium; *mc*, mantle cavity; *r*, rectum; *sr*, skeletal rod in ctenidial filament.

The ctenidia divide the mantle cavity, functionally and in some specialized cases structurally, into inhalant or infrabranchial and exhalant or suprabranchial chambers. In the former lie the osphradia, against which the inhalant currents impinge. In the latter are the hypobranchial glands which, like the osphradia, are usually reduced when one ctenidium is lost but, unlike them, are sometimes absent. They are situated where the water current, after passing between the ctenidial filaments, strikes the roof of the cavity. The functional significance of the positions of these two sets of organs is discussed later. The renal and reproductive pores open into the exhalant chamber, excreta and sexual products being removed in the exhalant current. The rectum before torsion probably extended along the mid-line of the roof of the mantle cavity between the two hypobranchial glands, the anus opening, as indicated in figure 1, near the margin. The general disposition of all pallial organs is shown in lateral view and in sections in figure 1. The evidence furnished by existing Gastropoda on which the above account of primitive conditions is based will now be discussed.

III. The mantle cavity in the aspidobranch Gastropoda

For reasons which will become apparent later, the species here examined or discussed have been considered under six groups which, with two exceptions (B and F), agree with the classification into tribes of the Archaeogastropoda by Thiele (1925). These are: (A) Zeugobranchia *less* Fissurellidae, (B) Fissurellidae, (C) Patellacea (Docoglossa), (D) Trochacea, (E) Neritacea, (F) Valvatacea.

A. *Zeugobranchia* (*less Fissurellidae*)

(1) *Haliotidae*

Haliotis tuberculata was examined alive at Naples. Crofts (1929) has given the most recent and detailed account of the general anatomy and refers fully to previous literature, but the only accounts of ciliary currents in the mantle cavity are an incomplete statement by her and a brief note by Stephenson (1924). The position of the mantle cavity and the disposition of the contained organs are shown in figure 2. The disproportionate development of the right shell muscle (*rm*) displaces the mantle cavity (*mc*) to the left. The deep mantle cleft extends for the greater part of the roof of the cavity, the edges of the cleft (*me*) being closely applied in life. The position of the cleft, and so of the mantle cavity below, is indicated in the intact animal by the line of characteristic shell openings formed successively by it. The edges of the cleft bear three pallial tentacles, an anterior one (pt_1) on the left side, a second farther back on the right side (pt_2) and a third at the base of the cleft (pt_3). In life these project through certain of the shell openings. Thus in the specimen shown in figures 2 and 3, where there were five functional openings, a sixth being in process of formation anteriorly, the tentacles projected from the first, third and fifth holes counting from the anterior. But conditions vary and, according to Crofts (1929), the tentacles may not always project from the same openings in the same animal. In any case they must move forward during growth when new openings are formed anteriorly while old ones are closed posteriorly. When the shell muscles (*rm*, *lm*) are relaxed and the mantle cavity is functioning freely the mantle edges line the sides of the shell openings like fleshy lips, but when the muscles contract they are withdrawn.

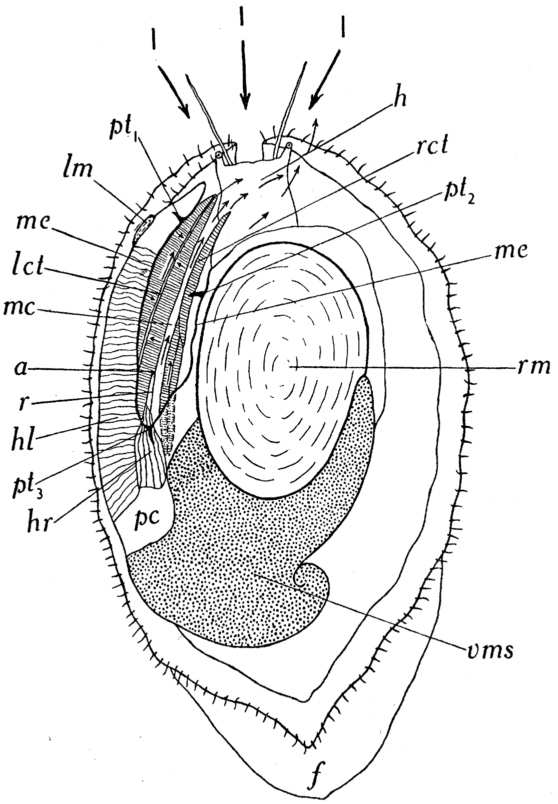

FIGURE 2. *Haliotis tuberculata*, dorsal view after removal of shell. × 1. *f*, foot; *h*, head; *hl*, *hr*, left and right hypobranchial glands; *lm*, left shell muscle; *me*, mantle edge; *pc*, pericardium; pt_1, pt_2, pt_3, pallial tentacles; *rct*, right ctenidium; *rm*, right shell muscle; *vms*, visceral mass. Other lettering as before. Arrows indicate direction of currents in mantle cavity.

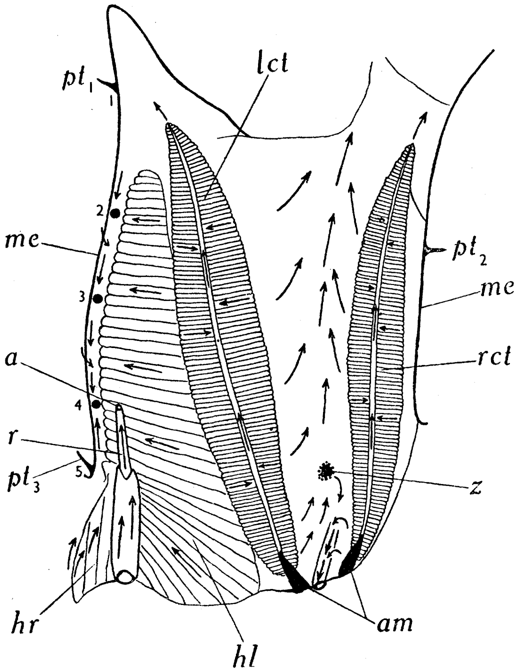

FIGURE 3. *Haliotis tuberculata*, mantle cavity exposed. × 5. *z*, region where material accumulates on floor of cavity; 1–5, positions of shell apertures. Black dots indicate regions where sediment accumulates on mantle edge. Other lettering as before.

The ctenidia (figures 2, 3, *rct*, *lct*) are of about equal length extending almost the complete length of the mantle cavity, but the right ctenidium is narrower. This asymmetry, as stated by Crofts (1929, 1937), is due to the hypertrophy of the right shell muscle and does not correspond to any evolutionary stage in the reduction and loss of the right ctenidium. The ctenidia taper at both ends and, except for a short distance anteriorly, each is attached by a long efferent membrane. The mantle curves under to such an extent on the left that the ctenidium on this side is almost upright and is attached by a very low membrane (figure 4, *em*), having thus little freedom. The efferent membrane of the right ctenidium is exceptionally deep, permitting the gill to bend over to an unusual angle to the left, as it does throughout its full length in life and not merely anteriorly as shown in figure 2. This is functionally advantageous owing to the reduction of the right side of the mantle cavity. Both ctenidia are attached to the roof of the mantle cavity posteriorly by a short afferent membrane (figure 3, *am*).

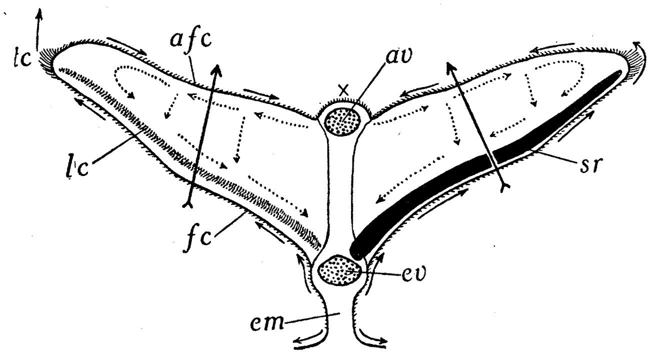

FIGURE 4. *Haliotis tuberculata*, lateral view of pair of filaments from left ctenidium, drawn from life (nerves and muscles in axis not visible). × 15. *afc*, abfrontal cilia; *fc*, frontal cilia; *lc*, lateral cilia (shown on left filament only; underlying skeletal rod on right filament); *tc*, terminal cilia. Other lettering as before. Feathered arrows indicate direction of respiratory current; unfeathered arrows direction of cleansing currents; dotted arrows course of blood.

The two hypobranchial glands lie in the roof of the mantle cavity (figures 2, 3, *hl*, *hr*). The left gland (*hl*) is much the larger, extending forward to between the first and second shell openings, while the right gland (*hr*) is confined to a small region at the posterior end and also covering the rectum (*r*) except for the region near the anus (*a*). The glandular region is everywhere deeply ridged, the intervening grooves being some 2 mm. deep. Crofts (1929) has described the histology of these glands which, when stimulated mechanically, secrete a copious transparent mucus. The epithelium is richly ciliated.

The osphradia (figure 5, *lo*) consist of yellowish coloured pleated grooves on the undersurface of the gill supports on either side of the entrance to the mantle cavity. Originally observed by Spengel (1881), the histology has been described by Bernard (1890*a*) and Crofts (1929). The rectum (figures 2, 3, 5, *r*) runs along the roof of the mantle cleft so that the anus (*a*) lies below the penultimate shell opening. The two renal openings, the right one being also the gonopore, are situated symmetrically on either side of the base of the rectum immediately above the line of the ctenidia (figure 5, *rk*).

Ctenidia. Each ctenidium is bipectinate, the laterally extended filaments of the two sides (figure 4) coming off the axis alternately. The mantle cavity is thus functionally divided into ventral inhalant and dorsal exhalant chambers (figure 5, *IC*, *EC*). In its essential features the structure of the ctenidium closely approaches that from which the condition in all Gastropoda, and indeed in the Mollusca generally, must have sprung. For this reason the ciliation of the filaments, never described except briefly in another connexion (Yonge 1939*a*), is especially important.

The respiratory current (figure 4, feathered arrows) is created by a zone of lateral cilia (*lc*) running parallel to the efferent surface. Underlying support provided by skeletal rods (*sr*), first described by Wegmann (1884), enables the filaments to resist the upward pressure of the current created by the lateral cilia. This explains their invariable presence on the efferent side. No other cilia occur on the lateral faces. Shorter frontal cilia (*fc*) on the efferent surface convey material to the tips of the filaments, weaker abfrontals (*afc*) on the afferent surface convey it to the axes. Both are concerned with their common function in primitive forms, the disposal of particles carried in with the respiratory current. Very long cilia (*tc*), up to 75μ in length, occur at the tips of the filaments. These assist in the transport of material round from the efferent to the afferent surface but also tend to throw light particles upwards to the roof of the mantle cavity, where they may become entangled in the mucus secreted by the hypobranchial glands. Along the dorsal surface of the axis material is carried anteriorly (figures 2, 3). There is a very weak ciliation on the efferent membrane (*em*) carrying material upwards into the region of the frontal cilia. On the floor of the mantle cavity material is carried away from the attachment of the ctenidia.

The circulation of blood within the filaments has been described by Crofts (1929) and previous authors. Blood passes laterally from the afferent vessel (figure 4, *av*) into the filaments and then down and inwards into the efferent vessel (*ev*), as shown by the dotted arrows in figure 4. The functional significance of this opposite flow of blood and respiratory current has not previously been noted. It has been shown by Hazelhoff (1938) that about 56 % of the oxygen is removed from the respiratory current as it flows through the mantle cavity of *Haliotis*. Thus the partial pressure of oxygen in the blood will be higher than that in the exhalant current, and this degree of efficiency would be impossible if the directions of flow of blood and of water were the same.

The gill filaments are very mobile, the presence of muscles attached to the skeletal bars enabling them to contract inward, thereby throwing the afferent surface into folds, the tips bending inward and upward. Longitudinal muscle in the gill axis enables the ctenidium to contract in length.

Currents in the mantle cavity. The action of the lateral cilia causes a powerful inhalant current (figure 2, *I*) to be drawn in above and on both sides of the head (not merely above and to the right as stated by Crofts (1929)). As in other zygobranchs, the exhalant current (*E*) passes out through the shell apertures, a fact noted by all who have observed these animals in life. The inhalant current, as indicated in figure 5, impinges on the osphradia when it enters the confines of the cavity. It has already been argued (Hulbert & Yonge 1937) that the osphradia are tactile organs concerned with the estimation of sediment brought in with the inhalant current. This matter will be reconsidered later. The heavier particles collect on the floor of the mantle cavity, those in the central and anterior regions being carried forward (figures 2, 3) and over the right side of the head to the exterior (figure 5, *R*), as observed by Stephenson (1924). Posteriorly, material from the left side collects in masses (figures 3, 5, *z*) beneath the penultimate shell opening through which it is ejected following contractions of the shell muscles. Posterior to this again there is a minor current carrying material on the right side back and then up the posterior surface of the mantle cavity, between the bases of the ctenidia, on to the upper surface of the rectum, whence it is carried to the region of the anus for ejection by the same opening.

The lightest material, carried upwards in the respiratory current, is removed in one of two ways (see arrows in figure 5). Particles conveyed from the frontal and abfrontal cilia on to the gill axis are carried anteriorly to join material on the floor of the mantle cavity (figures 2, 3, 5). The finest sediment which passes between the filaments, or is thrown upwards by the long terminal cilia on them (figure 4, *tc*), collects on the surface of the hypobranchial glands. Owing to the exceptional inward bending of the right ctenidium material from it will be largely carried on to the *left* gland. Here it is consolidated in the mucus its presence causes to be secreted. At the same time it is passed by cilia into the grooves and along these towards the left edge of the mantle cleft, i.e. inward on the left and forward on the right gland. There it accumulates in areas (marked with black circles in figure 3) beneath the second to the fourth shell openings, currents anterior to the fourth (penultimate) opening carrying material back and those posterior to it carrying it forward. On that portion of the right gland which covers the rectum, currents carry material to the anus, i.e. below the penultimate shell opening. Thus all material passed on to the surface of the glands is quickly accumulated around the openings through which the exhalant current passes (figure 5, *E*).

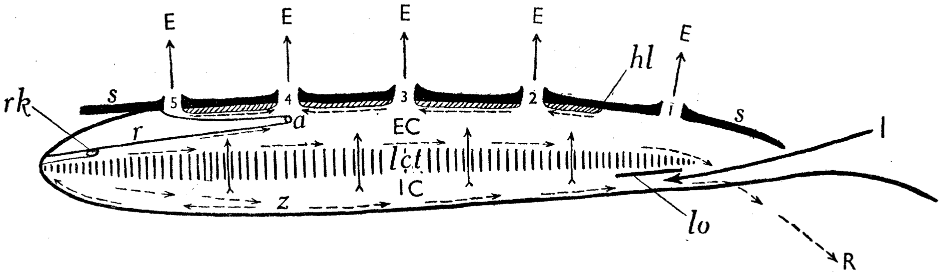

FIGURE 5. *Haliotis tuberculata*, diagrammatic lateral view of left half of mantle cavity to show course of currents. *EC*, *IC*, exhalant and inhalant chambers; *R*, rejection current on right of head; *rk*, right kidney aperture. Other lettering as before. Broken arrows indicate course of cleansing currents.

The exhalant current is apparently unable to remove all this material unaided. When large quantities of material, e.g. a heavy suspension of carmine, are introduced into the inhalant current, the animal reacts by the contraction of the shell muscles. This causes the shell to cant forward slightly so that fluid and suspended matter are expelled from the mantle cavity anteriorly as well as upward through the shell openings.

The faeces are expelled by way of the penultimate shell openings, defaecation being probably accompanied by some contraction of the shell muscles. The renal and genital openings (figure 5, *rk*) lie in the exhalant chamber, so that their products are also discharged through the shell openings.

(2) *Pleurotomariidae*

The pallial organs of Pleurotomaria have never been examined in life, the account here given being based on the morphological studies of Woodward (1901) and Bouvier & Fischer (1902) on *Pleurotomaria beyrichii* and confirmed by subsequent examination of a preserved specimen of the species.

This archaic genus, of which four species survive out of the several hundred known from the Silurian onward, is of especial interest. The broadly conical shell resembles that of the Trochacea, but with the characteristic slit in the outer lip. The left ctenidium is the larger, but neither extends to the posterior end of the mantle cavity; both are attached, except anteriorly, by an efferent membrane. Bouvier & Fischer also describe afferent membranes containing the afferent vessels (*av*), stretching from the posterior region of the ctenidium to the rectum and forming branchio-pallial partitions. The afferent and efferent blood vessels (*av*, *ev*) are in the same position as in *Haliotis*, Bouvier & Fischer showing that a vessel which runs within the mantle at the base of each efferent membrane, and described by Woodward as the efferent vessel, is really a collecting sinus (*cs*) into which this drains. Both accurately deduce the direction of the flow of blood through the filaments. Woodward's figures of sections through the filaments reveal the presence of frontal, abfrontal and lateral cilia (not so distinguished), the last being confined to the efferent region where skeletal bars are well developed. Thus the ctenidia resemble those of *Haliotis*. The osphradia occupy the same position, while hypobranchial glands (*hb*) cover the roof of the mantle cavity. Woodward describes larger anterior and smaller posterior areas, the latter behind the ctenidia, the anterior pair being separated only by a medium longitudinal furrow into which run grooves which traverse the surface of the glands as in *Haliotis*. Bouvier & Fischer demonstrated the great vascularity of this region and thought it of importance in

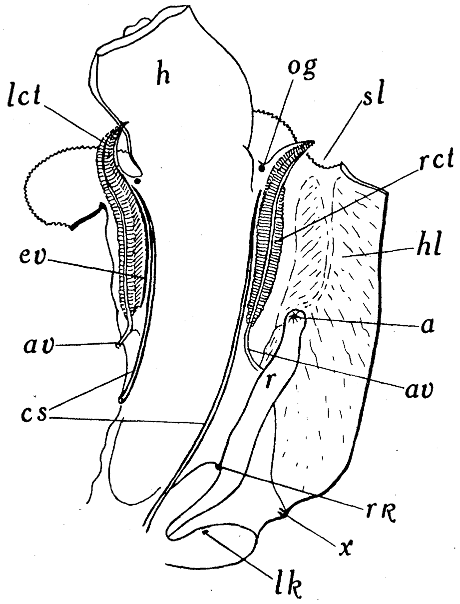

FIGURE 6. *Pleurotomaria beyrichii*, mantle cavity viewed from above. *cs*, collecting sinus; *og*, osphradial ganglion (right); *sl*, mantle slit; *x*, cut end of afferent vessel of left ctenidium. Other lettering as before. After Bouvier & Fischer (1902) with details of alimentary, nervous and circulatory systems omitted.

respiration: they considered the posterior regions as mainly concerned with secretion, but they do not figure these. The rectum (*r*) extends for some distance beneath the line of demarcation between the anterior glands, the anus (*a*) opening about half-way along this. The renal apertures (*lk*, *rk*), the right one being the gonopore, lie on either side of the base of the rectum.

Probable nature of currents in the mantle cavity. Before the author had the opportunity of examining a preserved specimen of *Pleurotomaria beyrichii* from the Hunterian Museum of Zoology, University of Glasgow, it was difficult to reconcile the statements of Woodward that the skeletal rods (and so lateral cilia) lie on the 'dorso-lateral' surface of the filaments, with those of Bouvier & Fischer that they occur on the 'outer' surface. The anatomical details supplied by both reveal that this is certainly the efferent surface. Personal examination has shown that the ctenidia have precisely the same mode of attachment and orientation as in *Haliotis* and other zygobranchous species. Woodward's statement is readily understood, especially in view of the lack of knowledge about the nature of the respiratory currents in the mantle cavity of the Gastropoda when he wrote. After fixation the free surface of the mantle surface collapses as a gently curved sheet over the body below, and when it is cut along its attachments to the body the ctenidia, no longer distended with blood and much contracted, hang down, the efferent surface being thus 'dorsal'.

It follows from the anatomical relations of the pallial organs in *Pleurotomaria* that, as in *Haliotis*, water will be drawn into the mantle cavity on either side of and above the head by the action of the lateral cilia. There it will first impinge on the osphradia and then be carried up between the ctenidial filaments and passed out as a single exhalant current by way of the base of the mantle cleft (*sl*) underlying the slit in the shell. The larger particles of sediment may be carried away from the floor of the mantle cavity by the agency of currents passing round the right of the head as in *Haliotis*, and into this may also pass material collected on the gill filaments and carried anteriorly along the upper border of the axis. Finer particles still may accumulate on the surface of the hypobranchial gland and be carried by currents in the grooves of these into the median longitudinal furrow. There they will probably pass forwards and so away, possibly assisted by contractions of the single shell muscle. Such contractions may also accompany defaecation.

As in *Haliotis*, the exhalant current, containing the finer sediment compacted in mucus, the faeces and the renal and reproductive products, would thus be discharged upwards some distance behind the head (as it is in the other zygobranchous genera). In this way the danger of discharging waste products immediately above the head is successfully countered.

(3) *Scissurellidae*

This family resembles the Haliotidae and the Pleurotomariidae in the spiral twisting of the shell in adult life. It is of especial interest because it indicates the lines along which the Fissurellidae possibly evolved. Observations on living species have been made only by Vayssière (1894) on *Scissurella costata* var. *laevigata*, but he did not examine the mantle cavity; Pelseneer (1899, 1903) described the chief morphological features of several species, but Bourne (1910), in his work on *Incisura* (*Scissurella*) *lytteltonensis*, has given the only detailed account of any species.

As shown in figures 7 and 8A, the shell is depressed with an enlarged terminal whorl in which the bulk of the animal is contained. But, unlike *Haliotis* and other 'limpets', the animal can be withdrawn into the shell, although, as in *Pleurotomaria*, the operculum is vestigial. The mantle slit (*sl*) is fringed with sensory processes and situated opposite the right tentacle. (This is not apparent in Vayssière's figures reproduced in figure 8A, which shows the head turned to the right.) As in *Haliotis* there are two shell muscles (*rm*, *lm*), but they are nearly the same size, the right one (*rm*) being slightly larger and extending farther back. The organs in the mantle cavity are displaced to the right in correlation with the site of the mantle slit. In life the anus (*a*) probably opens at the base of the slit. The right ctenidium (*rct*) is smaller than the left (*lct*) owing to restrictions of space. As shown by Bourne, both are bipectinate, not merely the left one as stated originally by Pelseneer (1899).

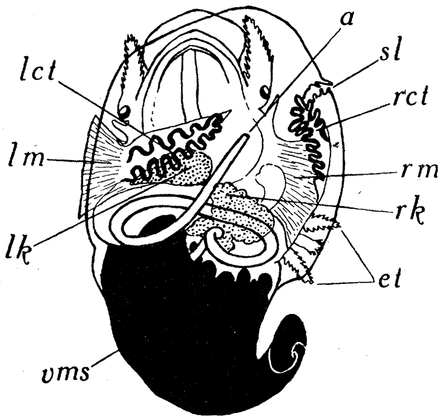

FIGURE 7. *Incisura lytteltonensis*, viewed from above after removal of shell and clearing of tissues. × 35. *et*, epipodial tentacles. Other lettering as before. After Bourne (1910).

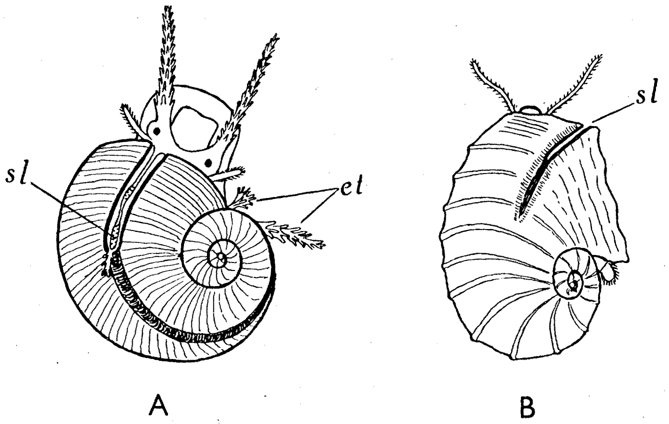

FIGURE 8. A, *Scissurella costata* var. *laevigata*, dorsal view of intact animal. × 22. B, *Fissurella* (*Diodora*) *reticulata*, developing animal in emarginuliform stage. Lettering as before. After Vayssière (1894) and Boutan (1885) respectively.

Bourne states that the left ctenidium 'lies almost transversely across the neck of the animal, its anterior extremity reaching nearly as far as the base of the right tentacle'. It is apparently largely free, although the posterior part of the axis is 'fused to the roof of the mantle cavity and extends back in the angle of that side of the mantle cavity'. His figure, reproduced in figure 7, would indicate that by the roof of the mantle cavity he means the margin of the mantle, i.e. in the typical position. The right ctenidium, for the greater part of its length, 'hangs vertically downwards in the space enclosed between the mantle and the outer edge of the foot'. It is attached to a greater extent, the fused portion of the axis 'extends far back in the extreme right-hand corner of the mantle cavity, lying close above the columellar muscle of that side'. The ctenidia are thus roughly symmetrically disposed on either side of the mantle slit (figure 7, *sl*) and also bend in towards this.

Bourne, in his account of the left ctenidium, speaks of the efferent branchial vessel as running 'along the dorsal, here the posterior margin, and the afferent vessel along the ventral, here the anterior margin of the axis'. These topographically anterior and posterior surfaces are shown in figure 7. But the same difficulty as before arises with regard to what is meant by dorsal and ventral. Reference to Bourne's figure of a section through two gill filaments from the right ctenidium (Bourne, plate 4, figure 18) reveals that the branch of the efferent vessel within the filaments is bounded by the skeletal rods, the epithelium above which carries long, clearly lateral, cilia. In other words Bourne's dorsal surface is the efferent surface and, as has been seen, the nature of the blood supply with the presence of skeletal rods and of lateral cilia combine to show that this is the surface against which the respiratory current first strikes the filaments. Bourne's description of the disposal of the left ctenidium would therefore imply that, *if this is the position in life*, the respiratory current will flow between the filaments anteriorly over the head carrying with it the faeces, etc. Since in all zygobranchous genera ever examined in life, *Haliotis*, *Diodora*, *Emarginula* and *Puncturella*, the marginal slit or shell aperture exists for the sole purpose of permitting the exhalant current, with contained waste products from anus and renal pores, to pass out clear of the head, the same must surely occur in this related genus. This would imply that the efferent surface is topographically anterior in life, the respiratory current being drawn in over the head and out by way of the marginal slit, the smaller right ctenidium providing a smaller complementary current of the same type on that side. The issue thus lies, as in *Pleurotomaria*, between a description based on examination of living species of four allied zygobranchous genera and many other aspidobranchs which reveals an unvarying course of the respiratory current with the functional needs which dictate this, and a description based on the examination of preserved material and especially of organs which are in life obliquely placed and are apt to suffer much distortion after fixation. Examination of a living specimen would settle the matter at once, but unfortunately the outbreak of war prevented a projected visit to Tromsö where *Scissurella* was known to be available.

The arrangement of cilia on the ctenidia Bourne's descriptions and figures show to be characteristic, the osphradia and hypobranchial glands lie in the same positions as in *Haliotis* and *Pleurotomaria*, the left gland being the smaller owing, in Bourne's opinion, to the relatively large size of the left kidney (*lk*). The renal openings, of which the right is also the gonopore, are in the usual positions, and the anus (*a*) opens a little distance behind the margin slit (*sl*).

The main differences from conditions in *Pleurotomaria* are thus the widening of the mantle cavity, the presence of two shell muscles, the greater freedom of the ctenidia, and the further reduction of the right ctenidium. The course of the respiratory current is probably essentially similar to that in *Haliotis*, fine sediment together with the faeces and the renal products passing out with it through the mantle slit, while heavier particles may be expelled on the right side of the head.

B. *Fissurellidae*

This family is here separated from the other Zeugobranchia because of the greater specialization of its constituent genera. The shell is secondarily symmetrical although spiral twisting is apparent during development (figure 8B). The animal is contained in what represents the enlarged, straightened, terminal whorl and, like all limpets, holds on to a hard substratum by the broad foot. This attachment enables the shell to be drawn firmly down by the contraction of the enlarged, horseshoe-shaped shell muscle which represents the backward extension and posterior union of the two shell muscles found in *Scissurella*. The capacious mantle cavity is symmetrical and has either a slit in the mid-line anteriorly or an aperture at the apex of the conical shell. The Fissurellidae are the only successful modern zygobranchiates. The family contains fifteen genera with many species compared with the five genera which make up the other three families (Thiele 1925). There is no account of the currents in the mantle cavity or of the appearance in life or mode of functioning of the ctenidia in any of the Fissurellidae.

(1) *Diodora* (*Fissurella*)

Three species were examined, *D. nubecula* and *D. mediterranea* at Naples and *D. apertura* at Plymouth. The structure and development of species of *Diodora* have been described by Boutan (1885) and the structure of others by Odhner (1932). The apex of the shell (figures 9, 10) lies somewhat anteriorly, the shell widening posteriorly. The elongated, anteriorly inclined aperture (figures 9, 10, *ap*) opens at the summit. According to Boutan (1885), this appears first in post-larval development as a marginal slit on the right side when the shell is still spirally twisted (figure 8B). With further shell growth it is cut off and, with the straightening of the shell, comes to lie in the mid-line. With the later enlargement of the aperture, due to resorption by the mantle, all trace of spiral twisting disappears and the aperture becomes apical.

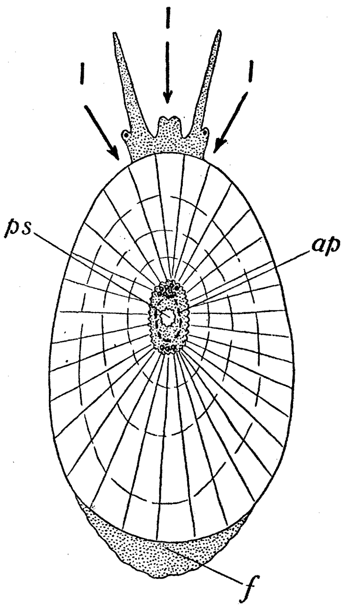

FIGURE 9. *Diodora nubecula*, dorsal view of intact animal. ×3. *ap*, shell aperture (extent indicated by broken line); *ps*, pallial siphon. Other lettering as before.

The most important difference between the three species is the extent to which the mantle extends upward around the shell margin. In *D. nubecula* (figure 9) it never extends beyond the shell; in *D. mediterranea*, a larger species, it extends upward for some 2 mm. and also outward for 3 or 4 mm.; in *D. apertura*, which is about the same size as *D. nubecula*, it extends relatively still farther (figure 10, *ma*). In an animal with a shell 11 mm. long, the mantle extended anteriorly for some 3 mm., obscuring the head, and laterally and posteriorly for 2 mm. It was reflected over the shell margin for 1 mm., terminating in a series of pinnate tentacles (figure 10, *pt*). This tendency for overgrowth by the mantle is taken further in the large

Pacific 'key-hole limpet', *Megathura crenatula*, where 'the black mantle of the living animal nearly covers the shell and the huge yellow foot is much larger than the shell' (Johnson & Snook 1927). In *Scutus* (*Parmophorus*) the shell is reduced, not extending over the mantle cavity, and is almost completely enclosed (Tobler 1902).

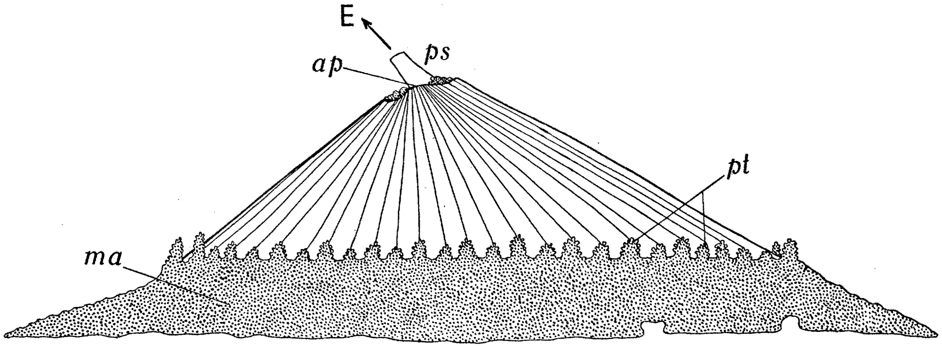

FIGURE 10. *Diodora apertura*, intact animal viewed from left side. × 7½. *ma*, mantle; *pt*, pallial tentacles. Other lettering as before.

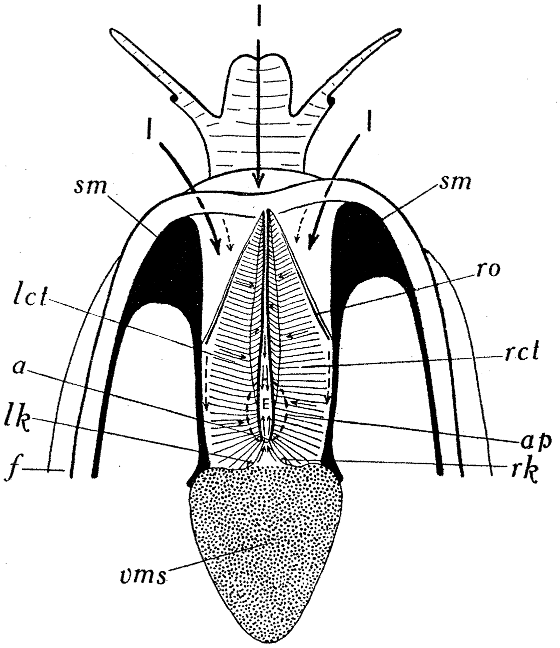

FIGURE 11. *Diodora nubecula*, mantle cavity from above. × 10. *sm*, shell muscle. Other lettering as before.

The mantle cavity, bounded laterally by the shell muscles (figure 11, *sm*), is occupied by the large, symmetrical ctenidia (*rct*, *lct*), the anterior halves being free. Each is inclined inward to such an extent that their afferent surfaces face one another and are closely apposed except for a slight posterior divergence (figure 11). The hypobranchial glands (figure 41, plate 18), the presence of which was denied by Bernard (1890*a*) and Boutan (1885) but demonstrated by Pelseneer (1899), extend for some distance posterior to the short afferent ctenidial membrane. They presumably discharge their secretion above the ctenidia, material being entangled in this after passing between or over the filaments. In section the cells are always empty (see figure 41, plate 18), which may explain the failure of Bernard and Boutan to identify the glands. The osphradia (*ro*) consist of sensory strips of epithelium along the free efferent surface of each ctenidial axis.

The anus (*a*) opens in the mid-line posteriorly, and slightly behind it are the renal openings (*rk*, *lk*), the right one being also the genital pore. The pallial siphon (figures 9, 10, *ps*) protrudes with an anterior inclination through the apical aperture and to a length of some 2 mm. in *D. nubecula* and *D. apertura.* The tissues around its base extend over the margin of the aperture and bear short tentacles, eight anterior and three posterior in *D. nubecula* (figure 9).

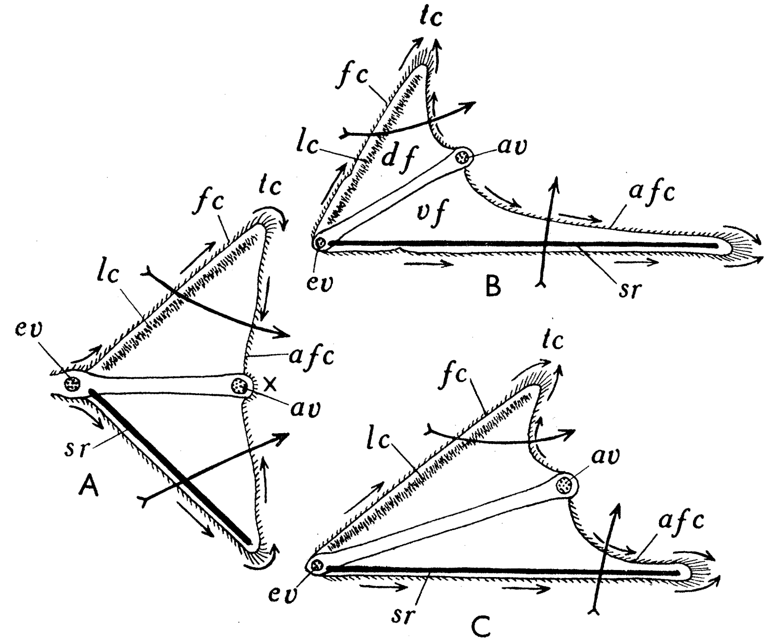

FIGURE 12. Lateral view of pair of ctenidial filaments, drawn from life, of: A, *Diodora nubecula*, × 20; B, *Emarginula reticulata*, × 68; C, *Puncturella noachina*, × 48. *df*, *vf*, dorsal and ventral filaments of B; *x*, current on free margin of axis. Other lettering as before.

Ctenidia. The filaments of the two sides (figure 12A) are symmetrical and essentially similar to those of *Haliotis* but shorter. There is the same system of lateral (*lc*), frontal (*fc*), abfrontal (*afc*) and terminal cilia (*tc*), the last reaching a length of 30μ. Skeletal rods (*sr*) are present along the efferent surface. The ciliary currents are similar to those of *Haliotis* (see arrows in figure 12A). The filaments are very mobile and can contract inwards until the efferent surfaces are almost parallel. This occurs on fixation, rendering any accurate picture of their condition in life impossible. The ctenidia can be shortened by contraction of longitudinal muscle in the axis. The direction of ciliary beat on the afferent axial surface varies. In *Diodora nubecula* (figure 11) cilia beat posteriorly over the anterior three-quarters of the axis, anteriorly behind that. Material thus accumulates immediately below the pallial siphon. In *D. mediterranea* and *D. apertura* cilia beat anteriorly along the entire axis. In all species the intact ctenidia exhibit continual movement, come together and separate, elongate and contract.

Currents in the mantle cavity. The inhalant current is very powerful owing to the extensive surface of lateral cilia on the enlarged ctenidia. Water passes between the filaments and then up in the mid-line to issue as one powerful exhalant current through the pallial siphon (figures 10, 11, *E*). In *D. nubecula* there are ingoing currents on the floor of the cavity on either side of the head and along the inner side of the base of the ctenidia (see broken arrows in figure 11). Material is carried in these to the base of the anal papilla and hence to its tip. There are no currents in the middle of the floor of the cavity or on the roof. Hence *all* rejection of sediment is by way of the pallial siphon, material collecting on the gill axis below this. The force of the current is sufficient to carry away unaided normal amounts of sediment, but larger accumulations are rejected following sudden contractions of the shell muscles. The mobile pallial siphon then lengthens and dilates. The faeces with renal and genital products pass out by the same opening. The force of the exhalant current is such that the secretion of the hypobranchial glands appears unnecessary, but it may aid in the consolidation of material which collects in posterior regions of the exhalant cavity.

In the other two species there *is* some rejection of sediment by way of the inhalant opening. Material is carried anteriorly along the gill axes, while there are no ingoing ciliary tracts on the sides of the head. This is probably correlated with the extension of the mantle round the margin of the shell (figure 10, *ma*). Whereas *D. nubecula* can draw the shell margins directly down upon the substratum, this takes longer when the mantle edge has first to be withdrawn. But minor sudden contractions, alone necessary for the expulsion of material *anteriorly*, will be possible in the other two species. The anterior extension of the mantle, the tissues of which are very sensitive to mechanical stimuli, may also aid by blocking the inhalant opening when much sediment is present. This may explain the association between increased size in *Diodora* and allied genera (e.g. *Megathura*), and greater extension of the mantle. Species may have been enabled to increase in size while countering the accompanying danger of the mantle cavity being blocked by the increased sediment drawn in by the enlarged ctenidia.

(2) *Emarginula reticulata*

This species was examined alive at Millport and Plymouth. The structure of species of *Emarginula* and of *Puncturella* (see later) has been described by Odhner (1932). Unexpected differences from *Diodora* and great specialization were revealed. The anterior marginal slit extends some one-third of the way up the conical shell. The appearance of the intact animal when expanded is shown in figure 13. The mantle does not extend beyond the shell. The mantle edges which bound the shell aperture are not fused, the pallial siphon (*ps*), which projects anteriorly, consisting of two applied surfaces. Dorsal to it are one pair, and ventral to it three pairs, of pallial tentacles (*pt*), one set on each margin of the mantle. These surfaces are not ciliated. When material is dropped on to the siphon this closes and the inhalant current (*I*) ceases until it reopens. When open, a powerful exhalant current (*E*) issues from it. From time to time the siphon extends and dilates, particles and faeces being extruded. But, unlike what occurs in *Diodora*, there is no accompanying contraction of the shell muscle. The siphon may remain distended for some time and, during the continued movement of the animal, material is shot out for considerable distances exclusively by ciliary action. Around the upper margins of the foot are eleven irregularly sized epipodial tentacles on each side. These are ciliated, material being carried to their tips. This is so in *Diodora*, but in *Emarginula* there are also currents on the sides of the foot and between this and the mantle, and these are directed into the mantle cavity (see arrows anterior to shell muscle in figure 14). There are no outgoing currents on the sides of the head, but there is a short process (figure 14, *q*), also present in *Puncturella* (figure 16), at the base of the right tentacle on which cilia beat to the tip. Dall (1889) has described a similar structure in the deep-sea genus, *Glyphis*, as a penis. But in *Emarginula* and *Puncturella* the spermatozoa would have to pass through the gill filaments, against the respiratory current, to reach it. In any case copulation is mechanically impossible in these genera. A similar structure was noted in the Trochidae by Randles (1904), who refused to regard it as a penis. Its function remains obscure.

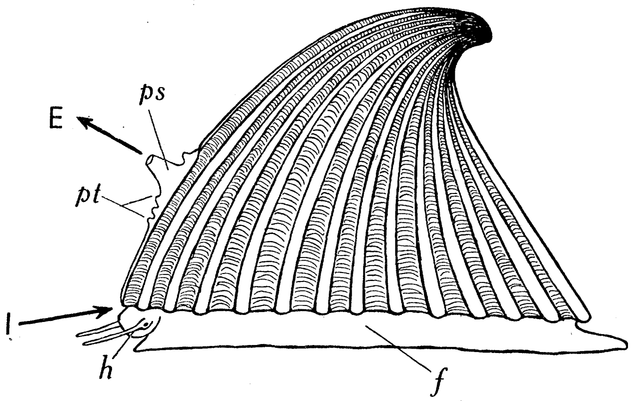

FIGURE 13. *Emarginula reticulata*, intact animal viewed from left side. × 12. Lettering as before.

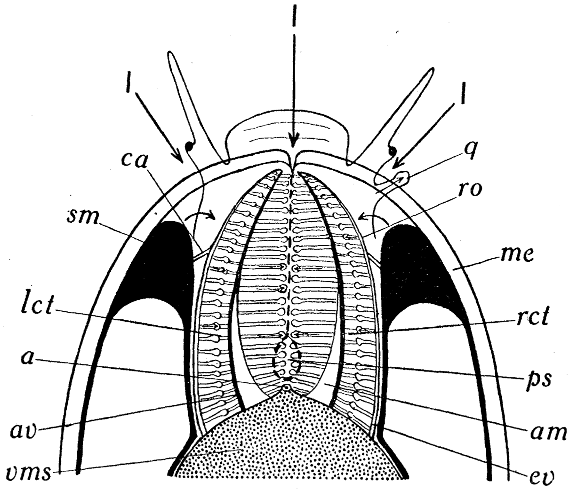

FIGURE 14. *Emarginula reticulata*, mantle cavity from above. × 20. *ca*, ctenidial attachment (efferent); *q*, appendage at base of right tentacle. Other lettering as before.

The mantle cavity (figure 14) although short is capacious and is completely occupied by the very large, symmetrical ctenidia (*rct*, *lct*). Apart from the size and form of these, the mantle cavity resembles that of *Diodora*, the osphradia (figure 42, plate 18), hypobranchial glands, anus (*a*) and renal and reproductive openings being all in the same positions. Only the anal papilla is ciliated.

Ctenidia. These are large and more specialized than in any other species examined. They are attached posteriorly, but are free laterally except for a band of tissue which stretches between the efferent axial margin and the mantle near the anterior end (figure 14, *ca*). But there is an extensive afferent membrane (*am*) which stretches forward from the region of the anus. The topographically ventral (morphologically inner) filament (figure 12B, *vf*) is twice as long as the dorsal filament (*df*). The tips of the ventral filaments are in close contact in life (see figure 15). The lateral cilia (*lc*) are unusually long, some 15μ, and very powerful. Skeletal rods (*sr*) occur as usual. The frontal cilia (*fc*) beat in the same direction as those of *Diodora*, but the abfrontals (*afc*) beat in the opposite direction, so that both sets of cilia carry material to the tips of the filaments. There the terminal cilia (*tc*) are conspicuous, attaining a length of over 30μ. There are no ciliary currents on the axis.

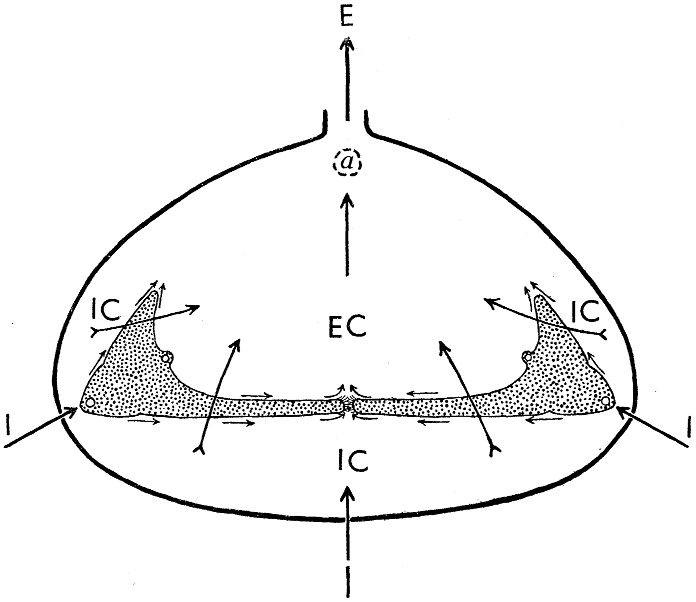

FIGURE 15. *Emarginula reticulata*, diagrammatic cross section through mantle cavity to show arrangement of ctenidia in life and course of currents. Lettering as before.

Currents in the mantle cavity. *Emarginula* (together with the allied genus, *Puncturella*) is unique in that *all* currents in the mantle cavity apart from those on the anal papilla are created by the cilia on the ctenidia. Currents on the head region are confined to those which bring material from the sides of the foot into the mantle cavity. Material is not carried along the ctenidial axis in either direction. The force of the respiratory current is such that *all* material, including the faeces, is expelled through the pallial siphon in suspension in the exhalant current (figure 15, *E*). No muscular contractions aid in this. The arrangement of the ctenidia in life is shown diagrammatically in figure 15. The terminal cilia of both sets of filaments interlock with those of the filaments on either side, while the cilia on the ventral filaments also interlock with the terminal cilia on the other ctenidium. Hence the mantle cavity is divided almost as effectively as in the Lamellibranchia into an inhalant chamber (lateral and ventral, figure 15, *IC*) and an exhalant chamber (median and dorsal, *EC*). But there are here no latero-frontal straining cilia to prevent particles from passing between the filaments. The bulk of suspended material passes between the filaments in the respiratory current; larger particles carried in the frontal or abfrontal currents are thrown upwards into the exhalant current by the action of the terminal cilia. The hypobranchial glands have presumably the same role as those in *Diodora*.

(3) *Puncturella noachina*

This species was examined alive at Millport. It resembles *Emarginula* closely, although the shell aperture is near the apex, as shown in figure 16, giving a superficial resemblance to *Diodora*. The aperture is short and linear and vaulted over internally by a forwardly projecting plate. As in *Emarginula* there is no outward extension of the mantle around the base of the shell, but there is the same series of epipodial tentacles (*et*). The pallial siphon (*ps*) is formed by applied surfaces, posterior to which is one pair, and anterior three pairs, of pallial tentacles (*pt*) which project with it through the shell aperture. The mantle slit extends anteriorly from the first of these pairs of tentacles to the thickened margin, where alone the two edges are fused. Conditions are thus very different from *Diodora*.

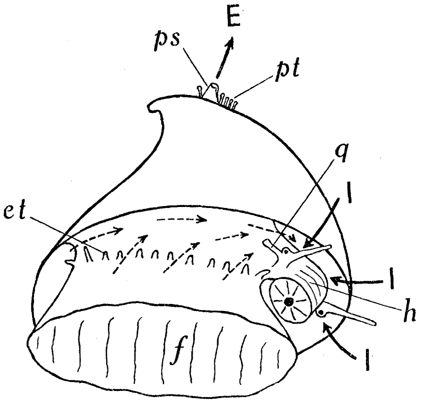

FIGURE 16. *Puncturella noachina*, ventro-lateral view of intact animal. × 5. Broken arrows indicate direction of currents on side of foot. Lettering as before.

The mantle cavity is long and narrow, and the ctenidia are attached by an efferent membrane for about half their length. They do not extend as far forward as in *Emarginula*, although much farther back. The filaments (figure 12C) have the same form but the dorsal filaments are relatively longer, some three-quarters the length of the ventral filaments, and the axis much deeper. The ciliation (figure 12C) is identical and the terminal cilia (*tc*) even longer, those of the ventral filaments being 45μ. These cilia also interlock and the arrangement of the ctenidia in the mantle cavity is the same. Material which collects around the foot passes into the mantle cavity around the sides of the head (see broken arrows in figure 16), otherwise cilia are confined to the ctenidia and anal papilla. The currents are as powerful as in *Emarginula*. It would appear from the above that *Puncturella*, in essentials, differs from *Emarginula* only in the conversion of the marginal slit into an aperture near the apex, and that this condition has been evolved independently of *Diodora*.

C. *Patellacea* (*Docoglossa*)

Although this group contains many genera, including those as ubiquitous as *Patelloida* (*Acmaea*) and *Patella*, and is one of the most successful in the Gastropoda, no account of the ciliation in the mantle cavity of any species has been found. All the Patellacea are limpets with a symmetrical conical shell and a horseshoe-shaped shell muscle, but without the shell slit or aperture of the Fissurellidae.

(1) *Lottiidae*

Patelloida tessulata (*Acmaea testudinalis*) and *Patelloida virginea* were examined alive at Millport and Plymouth. The habits and anatomy of these and allied species have been described by Willcox (1898, 1905, 1906) and Pelseneer (1899). To determine ciliary currents, animals were placed on glass slides and then inverted under water, and the mantle cavity studied in the intact animal from the ventral side. The nuchal cavity was also opened from above for examination of the osphradia and various apertures.

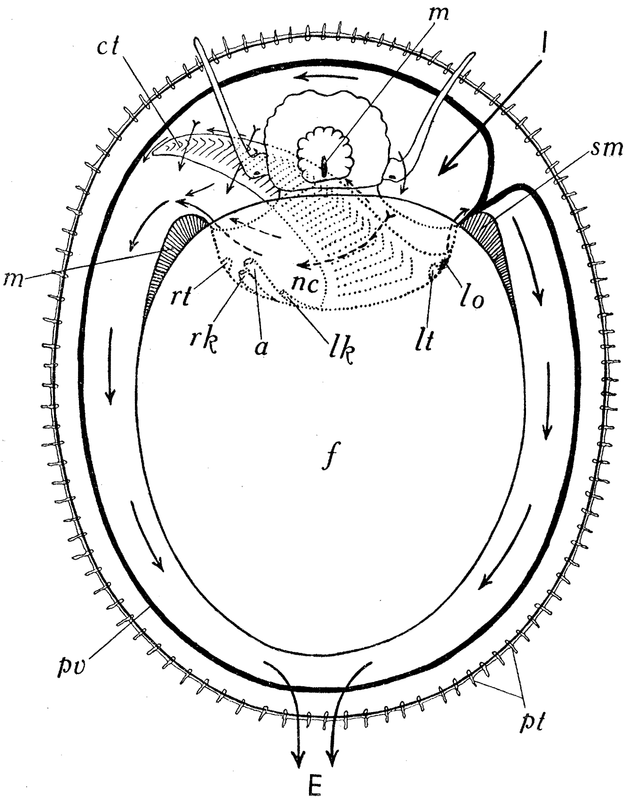

FIGURE 17. *Patelloida tessulata*, ventral view of intact animal. × 9. *ct*, ctenidium; *lt*, left tubercle; *m*, mouth; *nc*, nuchal cavity; *pv*, external pallial blood vessel; *rt*, right tubercle. Broken arrows indicate currents within nuchal cavity. Other lettering as before.

The ventral appearance of *P. tessulata* is shown in figure 17. As in all Patellacea, overgrowth by the mantle edges has increased the mantle cavity by formation of pallial grooves around the foot, the original, now nuchal, cavity being reduced. There is no epipodium, but the mantle margin bears tentacles (*pt*). The pallial groove is bounded externally by the conspicuous external pallial blood vessel (*pv*) which enters the heart on the left side anterior to the shell muscle (*sm*). The region outside the pallial vessel is glandular, especially in *P. virginea*. The nuchal cavity is bounded laterally by the anterior extensions of the shell muscle and largely occupied by the single, left ctenidium (*ct*). Thiele (1902, 1925) maintained that this is a secondary gill, but he has found no support, and Thiem (1917*b*) advanced conclusive arguments against this view. The ctenidium is an elongated triangle attached basally to the postero-lateral wall of the cavity. It stretches across the cavity and beyond it to the right (i.e. to the left in ventral aspect as in figure 17) often outside the shell. It is twisted to the right (when viewed from the dorsal aspect), so that the efferent surface faces to the left. Small tubercles (figure 17, *rt*, *lt*; figure 43, plate 18, *tu*), described by Bernard (1890*a*), Willcox (1898, 1905) and Pelseneer (1899) as osphradia, occur on each side of the neck at the base of the shell muscle, that on the left being the larger. Thiem (1917*b*), in his work on *Scurria*, regards them both as rudiments of the hinder region of the ctenidia, the anterior half of the left ctenidium only being retained. This is improbable; they arise on the neck, not on the pallial wall, and it is difficult to see how the posterior portion of the ctenidium could be lost and the anterior portion, retaining normal nervous and circulatory connexions, could persist. The tubercles, also present in *Patella*, contain blood spaces and have usually been regarded as lymphoid. Thiem maintains that in both *Scurria* and *Acmaea* (*Patelloida*) the osphradium consists of two streaks of sensory epithelium on each side of the frontal surface of the ctenidial axis. There is a thickening of the epithelium here in *Patelloida tessulata* but no indication of sense cells, and the epithelium is similarly thickened in all richly ciliated regions. Bernard (1890*a*) also failed to find sensory cells in this region. But anterior to the left tubercle there is a small but distinct sensory area situated on a small protruberance (figure 46, plate 18) overlying the osphradial ganglion (figure 46, plate 18, *og*), and this is here regarded as the left osphradium (figure 17, *lo*). No trace of a right osphradium has been found. There is *no* hypobranchial gland. The anal (*a*) and renal (*rk*, *lk*) openings are displaced to the right, lying on the summits of a small papillae. The right renal (and reproductive) opening is the larger.

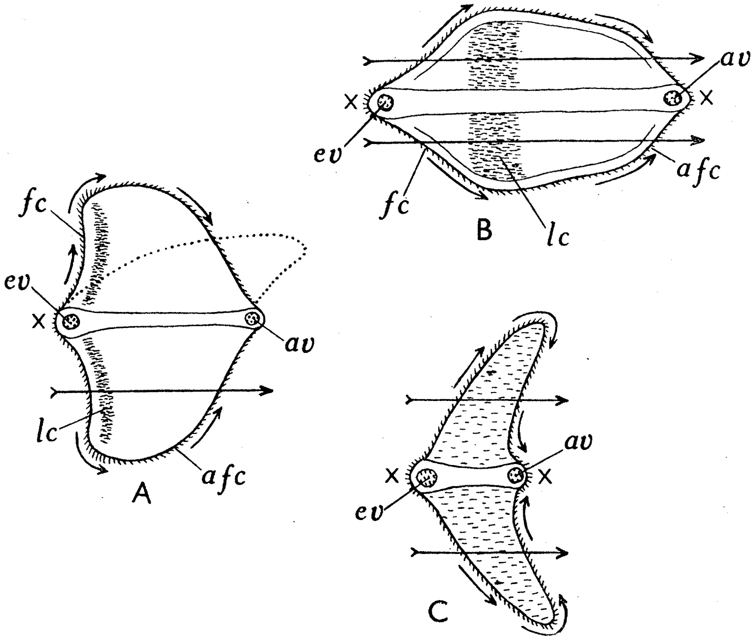

FIGURE 18. Lateral view of pair of ctenidial filaments, drawn from life of: A, *Patelloida tessulata*, × 22; B, *Theodoxus fluviatilis*, × 44; C, *Valvata piscinalis*, × 40. Lettering as before.

Ctenidium. As described by Thiem (1917*b*) for *Scurria*, this has the usual structure with alternating filaments identical on the two sides (figure 18A). Each filament possess bands of very active lateral cilia (*lc*); frontals and abfrontals (*fc*, *afc*) are large, but terminal cilia are poorly developed. Particles are carried directly round the filaments to the afferent surface. On the efferent surface of the axis particles are carried to the tip (figure 17), but there is no sign of currents along the afferent surface. The ctenidium is highly mobile with abundant muscle within both sides of the axis which enable it to bend freely and be contracted to one-third of its maximum expanded length, thereby withdrawing it completely within the nuchal cavity. Muscles within the filaments enable these to be drawn in towards the axis as indicated by the dotted outline in figure 18A. Skeletal rods are absent, thus permitting this great variation in shape.

Owing to the lateral disposition of the ctenidium, the respiratory current is drawn into the nuchal cavity on the left side (figure 17, *I*). But the oblique position of the ctenidium, increased by a certain backward curling towards the tip (see figure 17), directs the exhalant current posteriorly into the right pallial groove (i.e. left in ventral aspect) which it eventually leaves in the mid-line posteriorly (*E*).

Currents in the mantle cavity. Heavier particles carried in with the inhalant current will tend to impinge on the osphradium beneath the base of the ctenidium. Lighter particles will be carried between the widely spaced ctenidial filaments when the gill is fully expanded but will be conveyed over it by the action of the frontal and abfrontal cilia aided by the inward contraction of the filaments when the ctenidium is partly withdrawn. Some larger particles will be carried to the tip by the cilia on the efferent surface of the axis. The floor of the nuchal cavity is ciliated, material being carried to the right on the right of the osphradium and to the left of the other side of this (figure 17). The purely lateral passage of material through the cavity obviates the need for a hypobranchial gland. Material from the nuchal cavity passes into the pallial grooves in which powerful ciliary currents beat posteriorly. These unite in the mid-line posteriorly (figure 17, E), and there all sediment is rejected with the exhalant current. The characteristic faecal pellets described by Moore (1931) are consolidated in the intestine and rectum (see Graham (1932) for an account of this in *Patella*), and are expelled by the same route with the renal and reproductive products.

Allied to *Patelloida* is *Lottia* where, as shown in figure 23B, in addition to the ctenidium there is a ring of pallial gills within the line of the pallial vessel except anteriorly. Fisher (1904) has described the anatomy of *Lottia gigantea* and Thiem (1917*b*) that of a number of species of *Scurria* in which the pallial gills form a complete ring, but neither gives data on ciliary currents. The probable nature of these is discussed below.

(2) *Patellidae*

Patina (*Helcion*) *pellucida* and *Patella vulgata* were examined alive in the same manner as *Patelloida* at Millport and Plymouth. There is no ctenidium in these 'Cyclobranchs', instead secondary gills (figures 19 to 22, *g*) line the pallial groove as in *Lottia* and *Scurria* but in greater numbers. Each consists of a flap of tissue which hangs down from the roof of the groove (figure 22A). In *Patina* (figure 19) the ring is interrupted anteriorly, but in *Patella* it is complete. The nuchal cavity is further reduced, relatively more in *Patella*. As shown by Bernard (1890*a*) both possess small paired osphradia (figures 19, 21, *ro*, *lo*) on the neck. In each the sensory epithelium, which is well developed and lies over the nerve ganglion, is situated anterior to a patch of possibly lymphoid tissue as in *Patelloida* but which does not form a conspicuous projection (Pelseneer 1899; Davis & Fleure 1903). Thiem (1917*a*) maintains that the latter are rudimentary ctenidia but, for reasons given above, this appears improbable. As in *Patelloida*, there are no hypobranchial glands. The pallial vessels (*pv*) are relatively larger owing to their association with the organs of respiration, while pallial tentacles (*pt*) are more numerous and longer, especially in *Patella*.

In the Patellidae additional receptive surfaces in the form of subpallial sensory streaks are present in the mantle cavity. They were first described by Thiele in *Patinella* (1892), *Patina pellucida* and *Patella coerulea* (1893). Later (1902) he decided that they were not connected with the osphradia and were innervated from the mantle nerves. He ascribed considerable phylogenetic importance to them. Haller (1894) made similar observations on *Nacella vitrea*. Thiem (1917*a*) has reviewed the subject and described the streaks in *Helcioniscus ardosiaeus*, many species of *Patella* and *Nacella aenea*.

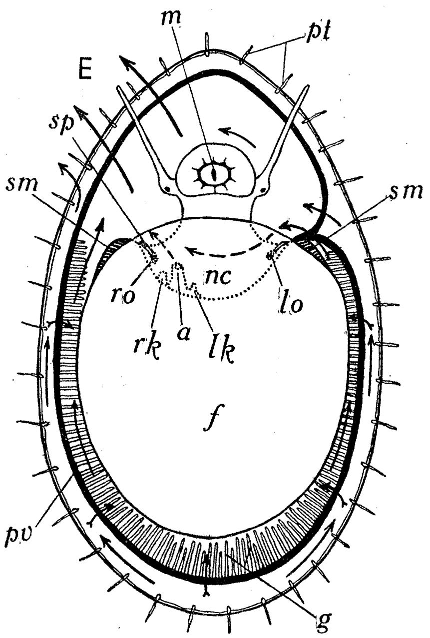

FIGURE 19. *Patina pellucida*, ventral view of intact animal. × 10. *g*, pallial gills; *sp*, subpallial sensory streak on right side. Other lettering as before.

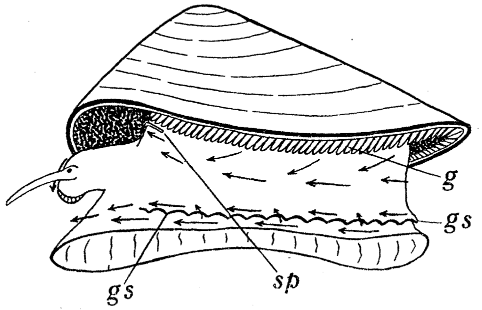

FIGURE 20. *Patina pellucida*, ventro-lateral view of intact animal. × 6. *gs*, glandular streak around foot; *sp*, subpallial sensory streak of left side. Other lettering as before.

In *Patina* they consist of thin ridges of sensory epithelium stretching from the osphradia round the anterior margins of the shell muscle (figures 19, 20, *sp*). In *Patella* (figures 21, 22) they extend along some one-third of the pallial grooves, being situated high up on the pedal side. In other species of *Patella* they extend for greater or less distances (Thiem 1917*a*). In *Nacella aenea* they are intermediate in length between those of *Patina* and *Patella vulgata*. In *Helcioniscus* there are a short anterior pair and a longer posterior pair, a condition which Thiem (1917*a*) states to be characteristic of this genus. He believes that all are innervated from the osphradial and pleural ganglia. Their presence in *Patina* and *Patella* has been confirmed macroscopically and in sections (figure 47, plate 18), the latter revealing a tenuous but distinct connexion with the osphradia. They are probably functionally equivalent to the latter, arising, as do the similar pallial streaks in the Loricata (Yonge 1939*a*), in correlation with the appearance of pallial grooves and the need for estimating the sediment which enters these. For this reason Thiele's views on their phylogenetical significance cannot be accepted.*

Ciliary currents. In *Patina* there is an exhalant current on the right of the head (figure 19 E), but water is drawn into the pallial grooves in all regions occupied by gills by the combined action of the cilia on these and in the pallial grooves, notably on the side of the foot. The respiratory current so created flows over and between the gills (see figure 22). Particles in suspension are carried anteriorly in both right and left grooves (figures 19, 20). Those in the left groove pass through the nuchal cavity where the currents beat, as in *Patelloida*, from left to right. Hence they pass over the sensory streaks and osphradia. This current, aided by others in the region above the head, is responsible for the exhalant current (E). The faeces and reproductive products are expelled in this. There are also anteriorly directed currents on the mantle margins outside the pallial vessels (figure 19).

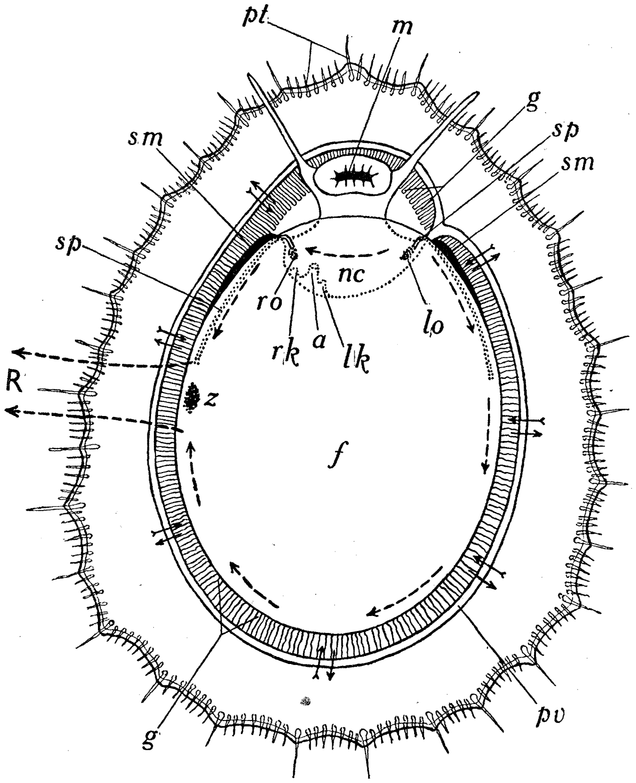

FIGURE 21. *Patella vulgata,* ventral view of intact animal. × 4. R, region where material accumulated at *z* is rejected by periodic contractions of shell muscle. Broken arrows indicate direction of currents in pallial grooves as well as nuchal cavity. Other lettering as before.

Boutan (1897) described the structure of a peripheral glandular streak around the foot in *Patina pellucida.* In life a ciliated furrow bordered dorsally by short tentacles (figure 20, *gs*) can be seen, while sections reveal that into the furrow (figure 45, plate 18, *cf*) open many relatively enormous mucous gland cells (figure 45, plate 18, *mg*) which penetrate

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* Thiele (quoted by Crofts 1929) identified similar sensory streaks around the anterior margins of the shell muscles in *Haliotis.* These were overlooked when *H. tuberculata* was examined alive, but, lying in the path of the inhalant streams, they could serve the same function as that suggested above for those of the Patellidae. But their presence in the Haliotidae and the Patellidae cannot be regarded as evidence of close relationship between these two groups.

deeply into the pedal musculature. The furrow is interrupted anteriorly. This structure was regarded by Pelseneer (1888 *b*, *c*, 1890, 1891 *a*) as homologous with the epipodium, but Haller (1894), Boutan (1897) and Thiele (1897) considered it to be of separate origin and homologous with similar structures in the allied genera, *Nacella*, *Patinastra* and *Patinella*. Boutan was uncertain as to its function but concluded that it was at once a receptor and an organ of defence, the extruded mucous being protective. The present investigation makes its presence easier of interpretation. As shown in figure 20, there are anteriorly directed currents on both sides of it, those on the dorsal side being the more powerful. Mucus is carried into the latter current by cilia on the sides of the groove and on the tentacles, and it is here that the bulk of the sediment is consolidated. *Patina*, unlike *Patelloida* or *Patella*, extrudes much mucus when handled and it comes from this source. Owing to the presence of gills posteriorly, sediment has to be carried forward and, if unconsolidated, might well foul the nuchal cavity and the region about the head. Actually when the animal is in motion much of this consolidated material is not extruded with the exhalant current but deposited in front of the foot which moves over it. The presence of this organ is thus associated with a definite need in *Patina* and its allies, and is analogous with the hypobranchial glands and even more with the pedal mucous tracts in the Loricata (Yonge 1939 *a*) which also arise in the elongated pallial grooves. The tentacles are sensory, Boutan having demonstrated the passage of nerves from them, and their stimulation by sediment probably causes secretion by the deep-seated mucous glands.

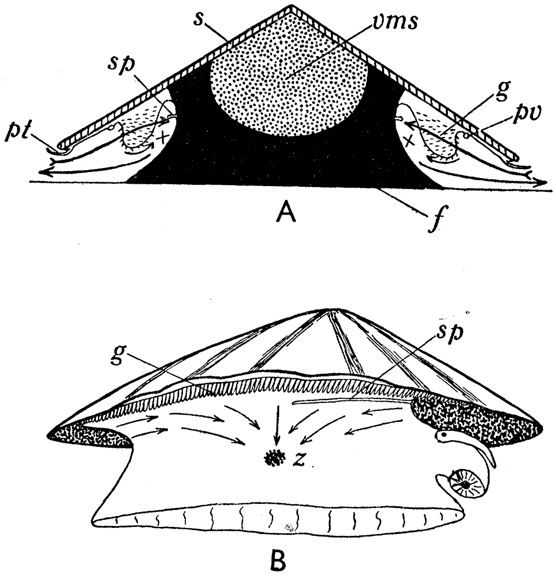

FIGURE 22. *Patella vulgata*. A, diagrammatic cross section through anterior half of animal in region of sensory streaks (*sp*). *x*, currents around side of foot. Other lettering as before. B, ventro-lateral view of intact animal showing accumulation of sediment (and faeces, etc.) at *z* on right side of foot. Lettering as before.

In *Patella*, where the pallial gills form a complete circle (figure 21, *g*), there is no restricted exhalant region. Owing to their larger size it was possible to examine excised gills which are irregularly ciliated on the outer, ventral and lateral faces, all cilia beating inwards (figure 22A). A gentle inhalant respiratory current is thus drawn in all around the margin of the mantle. As shown by Davis & Fleure (1903), the flow of blood through the gills is in the opposite direction so that, as in the ctenidia, most adequate oxygenation is ensured. An equally gentle and diffuse exhalant current passes out ventrally between the inhalant current and the substratum, as indicated in figure 22A. Material is conveyed round the sides of the foot in ciliary currents (figure 22A, B), which are more powerful in young than old animals. This material passes ventrally to the line of the subpallial sensory streaks (figure 22A, B, *sp*). Normally little sediment will be carried in with the gentle inhalant streams, although when the animal moves over muddy rocks considerable amounts may enter. There is no peripheral glandular region in adults, but traces are present in young animals as stated by Davis & Fleure (1903) and confirmed by section of animals 2–3 mm. long (figure 44, plate 18). Sediment will be thrown by the inhalant currents against the line of the subpallial streak, but the region of ciliary currents extends between this and a line some distance from the margin of the foot and which probably represents the original line of the glandular area. Ventrally to this the epithelium is flattened. Material is carried around the foot in these currents as indicated in figures 21 and 22B to a position midway along the right groove, where it accumulates in masses (*z*) at the ventral side of the ciliated region and immediately posterior to the end of the sensory streak. Faecal pellets (Moore 1931; Graham 1932) and other material from the nuchal cavity also pass direct to this region. The accumulations so formed are not removed by cilia—the absence of which along the ventro-lateral margins of the foot being possibly correlated with the presence of overhanging pallial gills—but from time to time sharp contractions of the shell muscle expel them in the region delimited by the broken arrows in figure 21, R. The process is somewhat similar to the rejection of material from the *inhalant* chamber in Lamellibranchs.

(3) *Modification within the Patellacea*

In the organization of the mantle cavity and in the means of respiration and of disposal of sediment, the Patellacea comprise an unusually complete evolutionary series. This can be most suitably discussed here, leaving the question of the origin of the group until later. The four significant stages in this series are represented by *Patelloida*, *Lottia*, *Patina* and *Patella*, as shown diagrammatically in figure 23 A to D.

In *Patelloida* (A) the loss of the right ctenidium with the elongation and horizontal disposition of that on the left have obviated the need for a marginal slit or aperture in the shell. The direction of the respiratory current in the nuchal cavity becomes lateral instead of vertical, while in the enlarged pallial grooves the currents are more powerful and beat posteriorly instead of anteriorly as in *Emarginula*. Correlated with the greater marginal extension of the mantle are the loss of the sensory epipodium, its function being taken over by the pallial tentacles, and the degeneration of the eyes. The inhalant current thus enters on the left and the exhalant current passes back along the right pallial groove. Sediment (see broken arrows in figure 23) is carried back on both sides, passing out with the exhalant current in the mid-line posteriorly. The speed of these currents and the open nature of the grooves obviate danger from accumulation of sediment, and the receptive surface is confined to the left osphradium on to which any abnormal concentration of sediment brought in with the inhalant current will impinge. The steady flow of water in the pallial grooves moves in the opposite direction to the blood in the pallial vein which probably plays some part in respiration.

In *Lottia* (B) pallial gills occur in addition to the ctenidium, but they appear late in development, and Fisher (1904) comments that when under 20 mm. long *L. gigantea* does not possess its generic character. Their presence will block the posterior passage of a sediment-laden exhalant current. There are no data on ciliary currents, but the presence of the ctenidium indicates that of an inhalant current on the left of the head. The pallial gills presumably produce diffuse inhalant streams into the pallial grooves, while conditions in *Patina* indicate the probability of a sediment-laden exhalant current on the right of the head. These currents are tentatively shown in figure 23B. Fisher mentions osphradia but not sensory streaks in *Lottia*, while, judging from the account by Thiem (1917*b*), receptive surfaces in *Scurria* are similar to those in *Patelloida* except in *Scurria viridula*, where there is a short, right, subpallial sensory streak. The presence of anterior pallial gills in *Scurria* probably does not affect the position of the exhalant current, because in *Patina* the gills in some cases extend far forward.

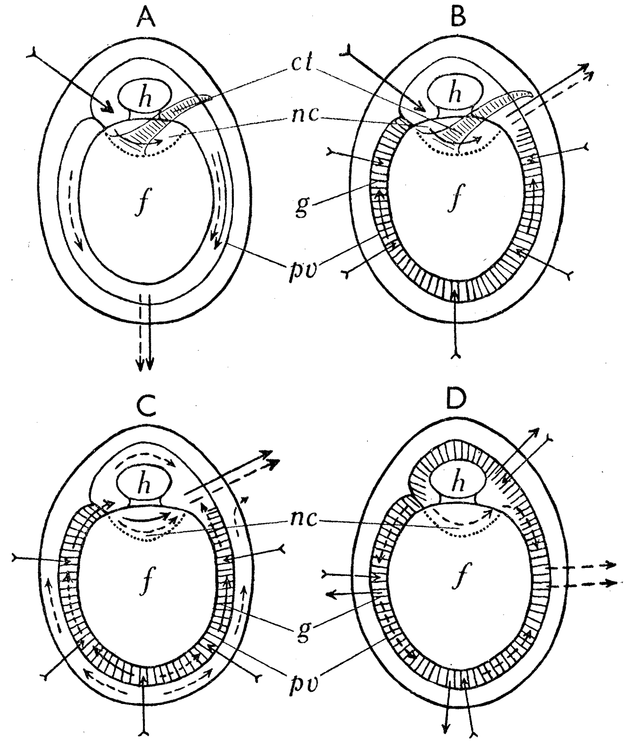

Figure 23. Diagrammatic comparison, from dorsal aspect, of the mantle cavity (nuchal cavity and pallial grooves) with contained organs and currents in: A, *Patelloida*; B, *Lottia* (currents deduced); C, *Patina*; D, *Patella*. Broken arrows indicate course of currents carrying sediment, etc., unbroken arrows course of respiratory current. Lettering as before.

Patina (C) resembles *Lottia* except for the loss of the ctenidium. Water enters exclusively between the pallial gills and is expelled, with some sediment, on the right of the head. But the bulk of the sediment is consolidated in the mucus from the glandular region round the foot. Currents in the nuchal cavity are unaltered, the receptive areas, i.e. two osphradia and two short sensory streaks, being confined to this region.

In *Patella* (D) the circle of gills is complete and there is no area where a single sediment- (and faecal-) laden exhalant current can pass out. The diffuse exhalant streams are too weak to remove sediment from the pallial grooves. Hence this collects in the middle of the right pallial groove and is expelled periodically by muscular action. The force of this renders a peripheral glandular region unnecessary, although its transitory presence in young animals indicates that *Patella* has passed through the stage now represented in *Patina*. The receptive surfaces resemble those of *Patina*, but the sensory streaks extend along the pallial grooves. In all the Patellacea the lateral course of the current through the nuchal cavity renders hypobranchial glands unnecessary.

D. Trochacea

This large group includes numerous temperate representatives, especially in the genera *Calliostoma* and *Gibbula*, and also large tropical species such as *Trochus niloticus* and *Turbo marmoratus*. The Trochacea are everywhere characteristic members of the intertidal fauna of rocky shores and find an ideal environment on the hard surfaces of coral reefs. The retention of the aspidobranch ctenidium probably debars them from life on a soft substratum with much suspended sediment in the water.

(1) *Trochidae*

Various species were examined, *Calliostoma zizyphinum* at Naples and Plymouth, *Gibbula magus*, *G. cineraria* and *G. umbilicalis* at Plymouth, and *G.* (*Monodonta*) *lineata* at Naples and Plymouth. The anatomy of the pallial organs has been described by Pelseneer (1899), Randles (1904), Fleure & Gettings (1907) and Frank (1914), but ciliary currents are not mentioned. The solitary elongated left ctenidium (figure 24, *ct*) is attached to the roof of the mantle cavity for some two-thirds of its length by a deep afferent membrane (figures 24, 25, *am*). This represents the forward extension of the short membrane in the Zeugobranchia. The filaments of the left (outer) side (figure 25, *lf*) are thus confined for this distance within a chamber enclosed on the inside by the afferent and efferent membranes and on the outside by the mantle. The efferent membrane extends farther forward, the unattached anterior end of the ctenidium being supported by a stout rod (figure 24, *sk*). At the base of this lies the rounded osphradium (*o*). The left hypobranchial gland (*hl*) varies in size in different species (see Randles) but is always large and folded; it covers the posterior half of the pallial roof between the ctenidium and the rectum. A vestige of the right gland (*hr*) lies on the right of the rectum adjoining the right renal aperture, but the right ctenidium and osphradium have gone. The epipodium is large with left and right cervical lobes which direct water into and out of the mantle cavity (Randles 1904), but only the tentacles are ciliated.

Ctenidia. Frank (1914) has described these; the structure is typical, but the filaments are asymmetrical in the region of the afferent membrane owing to the restricted function of those on the left (figure 25). This asymmetry is least in *Calliostoma zizyphinum* (figure 25A), increasing in the series *Gibbula cineraria*—*G. umbilicalis*—*G. lineata* (figure 25B). The cilia are powerful with well-developed terminals (*tc*). On the right filaments material is carried to the tip by both frontals and abfrontals and then passed on to the floor of the cavity or, by the action of the terminals, thrown up on to the left hypobranchial gland. On the left filaments material is carried round by the combined action of the frontals, terminals and abfrontals to the base of the afferent membrane (figure 25, *x*), where it is conveyed forward. This current ceases with the membrane; anterior to this material is carried across the afferent surface from left to right (figure 24). There is no current along the axis. The filaments frequently bend inwards, thereby throwing material clear. The free extremity of the ctenidium is very mobile.

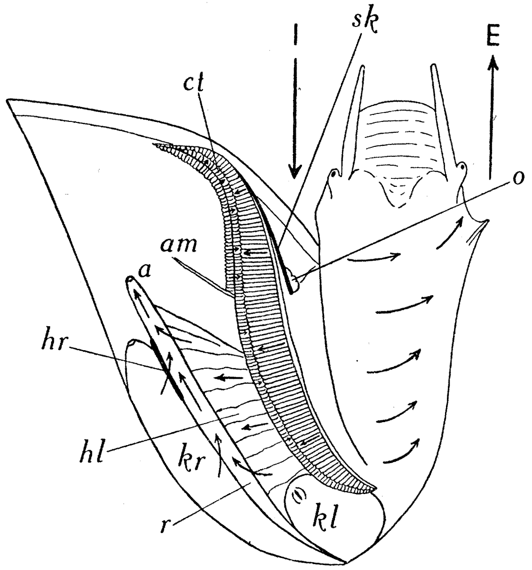

FIGURE 24. *Calliostoma zizyphinum*, mantle cavity cut open along right margin. × 4. *kl*, *kr*, left and right kidneys; *sk*, rod supporting free anterior portion of ctenidium. Other lettering as before.

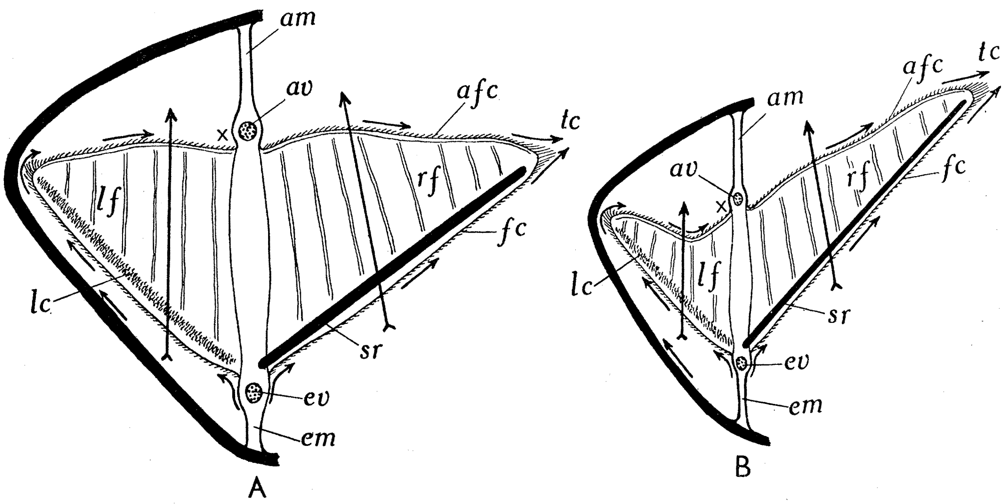

FIGURE 25. Lateral view of pair of filaments from posterior half of ctenidium viewed from posterior and drawn from life of: A, *Calliostoma zizyphinum*; B, *Gibbula lineata*. × 25. *lf*, *rf*, left (outer) and right (inner) filaments. Mantle shown solid black. Other lettering as before.

Currents in the mantle cavity. Water, guided in by the left cervical lobe, is drawn in left of the head (figure 24, I), passes between the ctenidial filaments and out on the right (E). Suspended material impinges first on the osphradium (*o*) and then, if relatively heavy, passes either directly or via the right margin of the filaments, on to the floor of the cavity and thence across this to the exhalant opening (figure 24). Fine particles pass between the filaments or are thrown up by the terminal cilia to be entangled in the copious secretion of the hypobranchial glands. They are then carried to the exhalant opening along the surface of the rectum. These two currents correspond to similar ones in pectinibranch gastropods (e.g. *Buccinum*, *Oxygyrus*; Yonge 1938, 1942), but there is no current carrying heavy material out by way of the *inhalant* opening as there is in these.

(2) *Turbinidae*

A single specimen of *Turbo rugosus* was examined at Naples. The pallial organs are similar to those in the Trochidae, but the left hypobranchial gland and the rectum extend farther forward. There is no supporting rod in the free extremity of the ctenidium although this is thickened. Anterior to the afferent membrane there is a forwardly directed ciliary current along the afferent surface of the axis (figure 34B), material from the abfrontal cilia on the left filaments being carried to the tip of the ctenidium and not to the right side. The evolutionary significance of this is discussed later.

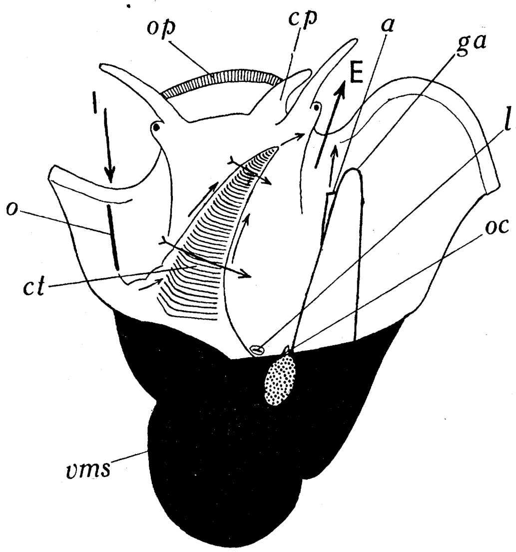

FIGURE 26. *Theodoxus fluviatilis*, mantle cavity exposed. × 9. *cp*, cephalic penis; *ga*, genital aperture; *oc*, 'organe creux' of Lenssen, possibly vestige of right ctenidium; *op*, operculum. Hypobranchial gland stippled. Other lettering as before.

E. *Neritacea*

Observations on this interesting group were confined to the sole British representative, the fresh-water *Theodoxus* (*Neritina*) *fluvatilis*. Thiele (1902) and Lenssen (1902) have described the pallial organs, but the exhaustive papers of Bourne (1908, 1911) are the main source of knowledge. No previous observations have been made on these structures in life.

The mantle cavity is relatively large and extends far back (figure 26). It is largely occupied by the single, left ctenidium (*ct*), which, like that of *Patelloida*, is attached by the base only and twisted laterally with the efferent surface to the left. It is very mobile. Between the efferent attachment and the inhalant opening extends the elongated osphradium (*o*) which is rounded in cross-section (figure 48, plate 18). Near the afferent attachment lies the opening of the solitary (left) kidney (*lk*). The anus (*a*) and complex genital ducts (*ga*) open on the right near the exhalant aperture. There is no left hypobranchial gland, but on the right of the rectum an extensive mucous gland (shown stippled in figure 26) opens by a small aperture. Both Thiele and Bourne regard this as homologous with the right hypobranchial gland. Histologically it certainly resembles such a gland. It opens at the base of a small projection named the 'organe creux' (*oc*) by Lenssen, who regarded it as the vestige of the right ctenidium, a view accepted by Bourne.

Although in other aspidobranchs reduction of the hypobranchial glands accompanies that of the corresponding ctenidia (except in the Patellacea where both glands disappear), it is possible that this view is correct. As Bourne has shown, the Neritacea have many unique features, resembling the other aspidobranchs in ctenidial structure but the pectinibranchs in the retention of the left, and loss of the right, kidney (see figure 30I), while their genital ducts are the most complex in the Prosobranchia. They may also, for reasons discussed below, be unique in retaining the *right* hypobranchial gland in association with the *left* ctenidium. If this is so then they are the only Gastropoda to retain the gland in terrestrial life, the Helicinidae possessing an enlarged mucous gland (Bourne 1911).

Ctenidium. Although superficially resembling that of *Patelloida*, important differences exist (figure 18B). The axis is unusually deep and the filaments short and capable of little change in shape. Restriction in length of the zone of lateral cilia (*lc*) is made good by increase in depth. Owing to the length of the cilia this zone appears as a broad band in the intact ctenidium. The shape of the filaments obviates the danger of buckling under the pressure of the respiratory current and, as noted by Bourne (1908), skeletal rods are absent. In this respect, in shape and in disposition of lateral cilia, these filaments resemble those of the Loricata (figure 32J). Frontal and abfrontal cilia (*fc*, *afc*) merge without the interposition of terminals at the gentle curve which represents the apex of the filaments (figure 18B), all material being carried to the afferent surface of the axis. On both this and the efferent surface material is carried to the tip of the ctenidium (figure 26). There are the usual blood vessels (figure 18B, *av*, *ev*), branchial nerves and muscles within the axis.

Currents in the mantle cavity. The powerful respiratory current enters on the left of the head (figure 26, I), passes between the filaments and out on the right (*E*). Suspended material will impinge on the surface of the osphradium (*o*). Fine particles are carried between the filaments, but larger ones caught on their surfaces are conveyed to the tip. No material is ejected through the inhalant opening. Apart from inward-beating cilia near the osphradium and outward-beating cilia anterior to the anus in the region of the exhalant opening, no ciliary currents were observed on either the floor or the roof of the mantle cavity. The current created by the lateral cilia is powerful enough to sweep material through the mantle cavity without such assistance. But, owing to the depth of the mantle cavity, it is possible that sediment may tend to accumulate posteriorly on the right side, where the secretion of the mucous gland would be available for its accumulation into masses which would later come under the influence of the outgoing current. This process was not observed, but in this case the opening of the mantle cavity for examination would certainly upset the system. The great depth of the mantle cavity certainly does introduce a need which is absent in the shallow nuchal cavity of *Patelloida*, and there is a functional justification for the views of Thiele and Bourne that the right, although not the left, hypobranchial gland has been retained.

After removal from the mantle cavity, sediment, together with the faeces, is carried back behind the exhalant opening by ciliary currents on the side of the foot. Here a ciliary vortex is formed which twists all this material into a mucus-laden mass. The whole mass rises above the surface and is finally carried away diagonally backwards over the side of the foot.

F. Valvatacea

This interesting group of fresh-water prosobranchs consists of a single family with one genus, *Valvata*. This is the only representative of the Monotocardia to possess an aspidobranch ctenidium; it is also hermaphrodite. Detailed examination was made of *V. piscinalis*, the structure of which has been described by Bernard (1890*b*) but without reference to ciliary currents.

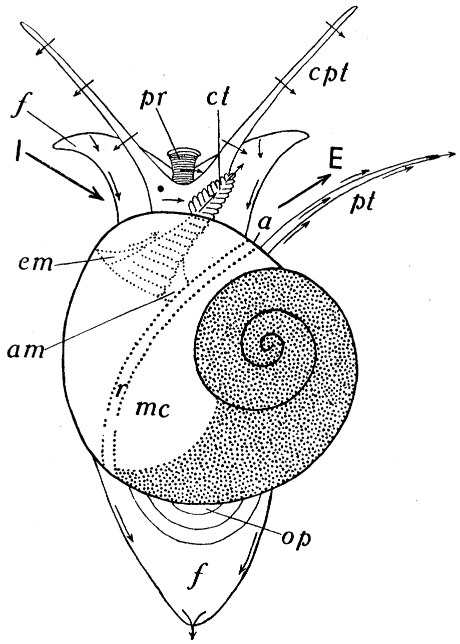

FIGURE 27. *Valvata piscinalis*, intact animal viewed from above, organs within mantle cavity shown by dotted lines. × 10. *cpt*, cephalic tentacle; *pr*, proboscis; *pt*, pallial tentacle. Other lettering as before.

The mantle cavity (figures 27, 28, *mc*) is capacious, but the ctenidium (*ct*) is attached so far forward that only the anterior third of the cavity is concerned with respiration, the remainder serving only to facilitate the withdrawal of the head and foot. Correlated with the forward migration of the ctenidium, the rectum (*r*) extends to the mantle edge, the anal region being free. To the right of this and only just within the mantle edge is the oviducal opening (figure 28, *ov*). The solitary left kidney possesses a ureter (unique in this respect amongst Prosobranchia with the exception of the *Paludina*, according to Bernard), so that the renal aperture opens far forward above the ctenidium in the pocket formed by its attaching membranes and the pallial roof. It is therefore obscured by the ctenidium in figure 28 but shown in section in figure 49, plate 18 (*ur*). At the base of the right tentacle is the long penis (figure 28, *cp*), which in life is normally folded back along the floor of the cavity, and so barely visible in the intact animal. The vas deferens opens at its tip.

When fully expanded *Valvata piscinalis*, like all species of the genus, is conspicuous for the amount of exposed tissue. The foot (figure 27, *f*) is broad and extended into two antero-lateral lobes, in the depression between which lies the downward-projecting proboscis (*pr*) which searches the substratum, continually taking in organic detritus. The two cephalic tentacles (*cpt*) are long and tapering, sweeping the substratum in advance of the animal. There is a long pallial tentacle (*pt*) attached to the base of the mantle edge on the right side which projects upward and outward, curling back somewhat at the tip. The ctenidium also projects beyond the mantle cavity. Bernard figures it as extended for almost half its length from the *left* side of the cavity; this was never observed in any of the specimens personally examined where, as shown in figure 27, it always projects for some half its length immediately to the *right* of the middle line.

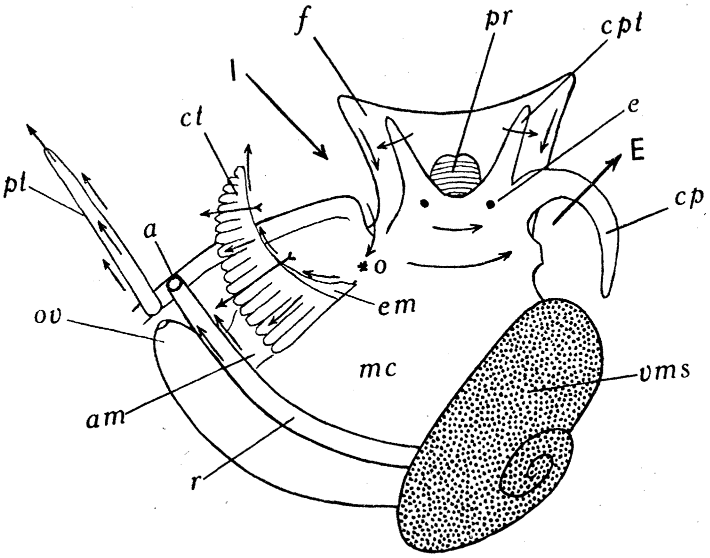

FIGURE 28. *Valvata piscinalis*, mantle cavity opened along right side. × 14. *e*, eye; *ov*, oviduct. Other lettering as before.

Ctenidium. The form and internal structure have been described by Bernard. There are some eighteen pairs of filaments each laterally elongated (figure 18C), but variable in shape owing, in part, to the absence of skeletal rods. The axis is attached for some quarter of its length by afferent and efferent membranes (figures 27, 28, *am*, *em*). The former remains attached to the side of the rectum and hence, owing to the forward migration of the ctenidium, this membrane has been carried to the right so that the axis now lies in the horizontal plane stretching from side to side across the mantle cavity. This it divides horizontally into two chambers (*not* inhalant and exhalant), the upper one, into which the ureter opens, being not more than one-quarter the size of the lower, as shown in figure 49, plate 18, and, diagrammatically, in figure 39E. The filaments extend vertically, but where the ctenidium extends outside the cavity it is always twisted with the afferent surface uppermost as shown in figure 27. When expanded, the ctenidium continually pulsates with the beating of the heart, while both the axis and the filaments are highly mobile owing to the abundant internal musculature. The entire ctenidial surface is ciliated and the resultant currents powerful. Cilia (figure 18C) cover the *entire* lateral surfaces of the filaments, frontal cilia beat to the tips of the filaments and abfrontals to the axis; there are no terminal cilia. Currents on both free surfaces of the axis (*x*) carry particles to the tip. The respiratory current thus flows from left to right within the mantle cavity and upwards outside this, all particles dropping on to the top of the head. One animal was found with a double ctenidium, i.e. with a second set of filaments on the afferent side of the axis; respiratory currents were therefore drawn in on either side of the gill, while the outgoing current streamed away in the line of the axis. Owing to the forward extension of the ctenidium this abnormality did not affect respiratory efficiency.

Ciliary currents. Owing to the outward extension of the ctenidium, only a portion of the respiratory current enters the mantle cavity. There is an inhalant current (*I*) on the left of the head, but no outgoing current on the floor of the mantle cavity here, as in all pectinibranch Monotocardia. To the left of the efferent attachment of the ctenidium is a small osphradium (figure 28, *o*) only revealed by sections and originally described by Bernard (1890*a*, *b*). Although a short distance from the base of the ctenidium, it lies in the same line as the axis, i.e. like *Theodoxus* and unlike *Patelloida.* According to Bernard the osphradium also extends along the frontal axis of the ctenidium. A branch of the ctenidial nerve, given off immediately before the osphradial ganglion, certainly passes into the axis, but no certain indication of sensory cells has been found in the epithelium of the axis. But this region may have some receptive capacity.

Particles collected on the ctenidium drop on to the top of the head where, as on the floor of the anterior region of the mantle cavity, currents beat to the exhalant region on the right. There are no cilia on the floor of the posterior regions of the cavity or on the mantle above the ctenidium. The ctenidial currents effectively clear the small region where particles might enter, and for the same reason there is *no* hypobranchial gland. Outgoing ciliary tracts are present on the terminal free region of the rectum, but there are none on the oviduct. The function of the pallial tentacle, hitherto obscure, is revealed by the dense covering of long cilia which beat to its tip, thereby assisting in the removal of faecal and genital products as well as of any sediment not removed in the exhalant current. It is noteworthy that the faecal pellets which are constantly being voided in the form of long rods are less firmly compacted than in the great majority of Prosobranchia where the anus opens in the mantle cavity. Correlated with this is the shortness of the gut after it leaves the stomach (see Bernard (1890*b*) for details). The pallial tentacle is an essential part of the pallial mechanism in this genus where so limited an area of the mantle cavity is swept by ciliary currents, and its presence is correlated with the forward extension of the rectum and oviduct. The powerful current it creates might affect the passage of spermatozoa along an open groove, and the opening of the vas deferens at the tip of the penis may therefore be correlated with the presence of the tentacle. The renal products will be carried out in the currents produced by the ctenidium.

All exposed surfaces are richly ciliated (figure 27); particles are carried posteriorly on both dorsal and ventral surfaces of the foot; cilia on the cephalic tentacles beat to the left on the left tentacle and to the right on the right one; on the upper surface of the proboscis they beat to the right.

Valvata cristata was subsequently examined. Although the shell is coiled in a flat spiral, the animal is very similar to *V. piscinalis*, and it behaves and feeds in essentially the same way. The ctenidium is even more exposed, some thirteen pairs of filaments protruding from the mantle cavity, again to the right of the middle line. The pallial tentacle is equally large and serves the same functions.

IV. Evolution of the mantle cavity in the Gastropoda

A. *Mantle cavity before torsion*

The posterior mantle cavity of the primitive Mollusca (figure 1) was probably a shallow chamber in which the ctenidia lay protected and was unique owing to its position in the mid-line where the gut and the urino-genital systems opened. An inhalant current would be drawn in on either side ventrally, and an exhalant current, carrying with it the renal and reproductive products, pass out in the mid-line dorsally where the anus opened near the margin (figure 1, *a*) as it does in modern pectinibranchs. Ciliary currents on the dorsal surface of the foot, indicated by the dotted arrow in figure 1, would remove the faecal pellets after extrusion. The great danger to which a respiratory chamber of this type would be exposed, especially when, with increasing size of the ctenidia, it became deeper, must have been sediment, the relatively weak current created by the cilia being insufficient, unaided, to remove heavy concentrations of this.

In association, therefore, with each ctenidium arose two organs. At the position where the water current, with its contained sediment, drawn in by each ctenidium impinged on the surface within the mantle cavity (actually at the anterior end of the efferent membrane) there appeared an osphradium. This, it is here maintained, is a tactile organ concerned with estimating the amount of sediment which enters the cavity, excessive stimulation causing closure of the cavity. On the pallial roof, above each ctenidium and on each side of the rectum, appeared a hypobranchial gland, the secretion of which consolidated the sediment carried upward in the respiratory current. All cilia on the ctenidia, other than the current-creating lateral cilia, were concerned with removing sediment.

In correlation with the opening of the anus into the respiratory chamber arose elaborate intestinal mechanisms for the consolidation of the faeces into compact pellets too heavy to be drawn in by the inhalant current. Such mechanisms have been described in the Prosobranchia (Graham 1932; Yonge 1935, 1937*a*), in the Loricata (Fretter 1937) and in the protobranchiate Lamellibranchia, where the mucus secreted for this purpose is probably the precursor of the crystalline style (Yonge 1939*b*). Moore (1931, 1932) has demonstrated the firm nature of the pellets. Where the danger of fouling the ciliated organs in the mantle cavity disappears so do these mechanisms, e.g. in the Nudibranchia (Graham 1938*b*), Septibranchia (Yonge 1928) and Cephalopoda.

Naef (1913, 1926) postulated the presence, primitively, of *two* pairs of ctenidia. He was certainly influenced by his preoccupation with the Cephalopoda. He considered that *Nautilus* retained the primitive condition, the Loricata had added further, secondary, gills on each side, while the remaining Mollusca had all lost at least one of the original pair. This view cannot be accepted. It is difficult to see how two pairs of ciliated ctenidia could have functioned in a restricted *posterior* mantle cavity—any more than they could in the anterior mantle cavity of a modern gastropod. Space would prevent their being arranged laterally, while if placed one above the other, the upper would have little functional value.* In the Loricata, on the other hand, where all the gills are structurally and func-

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* Dr C. F. A. Pantin, after reading this MS., inquires why it is necessary to postulate the possession of any definite number of pairs of ctenidia in the primitive mollusc. Might they not, he suggests, have had 'a variable number of simple respiratory excrescences which were specialized into ctenidia before the number

tionally identical (Yonge 1939*a*), ctenidial multiplication is correlated with the extension of the mantle cavity into narrow pallial grooves. The ctenidia are associated laterally and function as a unit (Yonge 1939*a*). The duplication which has occurred in the tetrabranchiate Cephalopoda may be ascribed to the increased respiratory needs of these animals. This matter will be discussed later. Here the pairs of ctenidia are arranged one above the other, but the respiratory current is greater and is created by pulsations of the funnel and *not* by cilia (Willey 1902).

In view of the symmetry of the renal and reproductive organs in the Lamellibranchia and the Loricata, there appears no reason for assuming an asymmetrical condition in the stock from which the Gastropoda evolved.

The form of the shell must remain a matter of conjecture, but probably, as suggested by Naef (1913, 1926) and Graham Kerr (1931), coiling preceded torsion. It would follow as a natural result of the consolidation and upward extension of the visceral mass represented in development by the ano-pedal flexure (Boutan 1899). Palaeontological evidence reveals that the early gastropod shell was coiled in a plano-spiral. If this coiling preceded torsion then the apex must have pointed forward, i.e. be exogastric as in *Nautilus*. The original plano-spiral shell is well displayed in the Bellerophontacea (Wenz 1938). Boutan (1899) contended that torsion and the coiling of the shell are independent processes, a view supported by later authors including Naef (1913, 1926). But the two processes continue to be confused.

Naef (1913, 1926) further contends that the marginal slit was present in the shell before torsion. But, as the foregoing descriptions of conditions in the modern Zeugobranchia reveal, the slit (or aperture) is intimately concerned with the physiology of an *anterior* mantle cavity in which two ctenidia are retained and disappears when one of these is lost. It is probably, as stated by Garstang (1928), a matter of 'sanitation'. Without this opening the faeces and renal products would be voided over the head of the animal. The appearance of the slit with consequent shortening of the rectum thus represent necessities imposed by torsion so long as two ctenidia are retained. There was no functional need of this nature for the slit when the mantle cavity was posterior and the faeces and renal products could be passed without harm over the dorsal surface of the foot. Boutan (1885) showed that in *Fissurella* the post-larval shell grows for some time *before* the slit appears, indicating, as Garstang (1928) has emphasized, that this may have been acquired late in evolution, i.e. after torsion. In *Haliotis* the slit does not appear until the 44th day (Crofts 1937). On the other hand, there is the possibility that the slit was initially concerned with the separation of the inhalant from the exhalant current. But although it is essential that the respiratory stream should not be contaminated by outgoing, deoxygenated water, the modern Brachiopoda, e.g. *Crania* and *Lingula*, which have a very similar arrangement of two ventral inhalant and one dorsal exhalant currents (Orton 1914), have no such slit. Both possess

was definitely fixed at one pair'? This raises the question, what is the criterion of a primitive mollusc? This has been taken to be the possession (amongst other things) of a posterior mantle cavity in which the ctenidia were enclosed and through which a respiratory current was created by the action of the lateral cilia on the filaments. And it is difficult, for the reasons given above, to see how more than one pair of ciliated ctenidia could have functioned in such a cavity. There may well have been numerous pairs of respiratory excrescences before the mantle cavity appeared, i.e. before the Mollusca evolved. I am grateful to Dr Pantin for raising this question.

an anus, but there is no head so that the need for a slit does not arise on that account. In *Lingula* there is a functional subdivision of the opening into the pallial cavity by apposition of the spinous pallial margins (Morse 1878), and some similar arrangement may have existed in primitive molluscs. Embayment of the shell margin in certain extinct Brachiopoda (see Orton 1914) may have arisen in connexion with separation of the currents, and it is similarly possible that the shallow sinus in such extinct Gastropoda as the Sinuitidae (Wenz 1938) may have had a similar functional origin. But the balance of evidence appears to the writer to be against the view that the sharply defined slit—so clearly correlated with the *withdrawal of the anus*—arose in connexion with the separation of the inhalant and exhalant currents. Naef regards the slit in the shell of primitive Mollusca as a factor in the later formation of the bivalve shell in the Lamellibranchia. But he fails to realize the functional significance of the slit, while the work of Jackson (1890) on the prodissoconch of the Lamellibranchia gives no support to this purely morphological contention. There is thus justification, on functional grounds, for refuting Naef's contention, based on the necessarily incomplete evidence of 'pure' morphology, and for regarding the slit as post-torsional.

The balance of evidence supports the view given here, that the primitive molluscs crawled on a hard substratum by means of a flat foot. In such an environment the tactile and possibly chemo-receptive powers of the sensory outgrowths from the epipodial ridge, which even Naef admits are probably primitive, would be of great importance as they still are in the modern Zeugobranchia and Trochacea. The Loricata, which must have diverged from the common stock before the Gastropoda, have never lost this dependence on life on a hard substratum, and have, indeed, become more highly specialized for it (Yonge 1939*a*). The early Gastropoda retained it, and their descendants still do so with the Patellacea as highly specialized in this respect as the Loricata. The more highly specialized Gastropoda successfully invaded soft substrata, the Lamellibranchia did so by way of forms not unlike the modern Protobranchia (Yonge 1939*b*), and so also did the Scaphopoda. The Cephalopoda, and a variety of different Gastropoda such as the Pteropoda and Heteropoda, took to pelagic life as a result of still greater specialization. It has been found impossible to accept Naef's view that the Mollusca were primitively free-swimming in habit.

B. *Torsion*

Since Spengel (1881), with characteristic perspicacity, first demonstrated that only torsion could explain the complex morphology of the Gastropoda, many theories have been advanced as to the nature and stimulating causes of this. The subject has been frequently reviewed, most recently by Naef (1913) and Crofts (1937), and only general conclusions need be considered. Broadly speaking the theories may be divided into the following five groups:

(i) Torsion occurred originally by stages in the adult.

(ii) Torsion occurred in the embryo due to antagonism between the growth of the foot and that of the shell.

(iii) Torsion occurred in the embryo but essentially to meet the needs of the adult.

(iv) Torsion occurred rapidly in post-larval life to meet the needs of adult life.

(v) Torsion occurred rapidly in embryonic life to meet purely embryonic needs.

A number of workers have given valuable accounts of the process of torsion in the larva without expressing personal views about its origin and possible value; they include Drummond (1902), Robert (1902), Smith (1935) and Crofts (1937).

(i) Lang (1891) and Plate (1895) produced the most important theories under this head. Lang postulated a top-heavy conical shell as the stimulating cause, Plate an asymmetry of the lobes of the 'liver' by which he attempted to explain both torsion and the asymmetrical coiling of the shell. Modern workers, notably Pelseneer (1911), Naef (1913, 1926), Garstang (1928) and Graham Kerr (1931), unite in dismissing these and similar theories on the sufficient ground of the anatomical difficulties they raise and the absence of any trace, in fossil forms, of intermediate stages or of any modern descendants of such forms, although in the existing Opisthobranchia are included genera showing many stages in the reverse process of detorsion. Andersen (1925), on the basis of work on the development of *Paludina*, has more recently suggested that the twisting of the visceral loop and the anterior movement of the mantle cavity are due to the spiral twisting of the visceral hump and shell in the late larva. His findings are in conflict with those of Drummond (1902), an earlier worker on the embryology of *Paludina*, while Crofts (1937) is unable to accept them in the light of her own very detailed study of the development of *Haliotis*. Andersen is the only recent worker to associate torsion and the asymmetrical coiling of the shell.

(ii) Boutan (1919 and earlier papers) is the protagonist of this view. It is difficult to summarize his unique views of torsion; he denies the occurrence of detorsion, and regards the nudibranchs as more primitive than the other Opisthobranchia. He appears to postulate no beneficial result of torsion either to the larva or the adult; torsion is merely a result of the antagonism of growth of the foot and of the shell during development.

(iii) Pelseneer (1911 and earlier papers) states his case briefly as follows: In the Mollusca, with the exception of the Cephalopoda, the foot extended for some distance posteriorly. This affected the development of the ctenidia in their original posterior position. This difficulty was met in the Lamellibranchia by their forward extension, in the Polyplacophora (Loricata) by their multiplication, and in the Gastropoda by torsion. This last change occurred in the embryo by a ventral flexion followed by a twisting round of the visceral mass in relation to the head and foot, i.e. lateral torsion. Pelseneer does not state that any advantage accrued to the embryo as a result of torsion, which he appears to regard purely as an adaptation for the future adult. But it is important to note that the backward extension of the foot which is so conspicuous a feature in the Gastropoda is more likely to be a *consequence* than a cause of torsion. This appears to have been overlooked.

(iv) Naef (1913), again preoccupied with the Cephalopoda, considered that the ancestral gastropod was free-swimming and nautiloid in form with the two major parts of the body, the head and foot (Kopfuss) and the visceral mass with mantle and shell (Eingeweidesack), connected by a narrow, very flexible 'waist'. The evolution of a crawling gastropod from this hypothetical ancestor demanded the reversal of the shell, the forwardly directed coil of which, Naef thought, would have pressed on the head and neck when the animal began to crawl. He assumed that flexibility of the 'waist' permitted an easy twisting round of the visceral mass and shell. When the animals settled permanently on the bottom this twist became permanent, the resting position of the shell being reversed. Naef suggested that in certain Cambrian Gastropoda, e.g. *Bellerophon*, the shell may have rested laterally with the mantle cavity pointed to the right so that it could easily be pulled either forward or backward.

This theory disregards the much greater structural affinities between Gastropoda and the Loricata on the one hand and the Lamellibranchia and Scaphopoda on the other. Garstang (1928), who has subjected Naef's views to a sound objective criticism, has rightly stressed these, and the majority of malacologists unite in regarding the primitive mollusc as a creeping animal with a flattened or dome-like shell and certainly with nothing in the nature of a flexible 'waist'! Pelseneer (1911) has emphasized the secondary nature of all pelagic Gastropoda; but Naef regards the veliger larva as a 'phylogenetic reminiscence' of his free-swimming primitive mollusc. Garstang is on much safer ground when he states that the velum is a special development of the prototroch of the trochosphere concerned only with the locomotion of the larva and having no phylogenetic significance.

(v) Garstang (1928) believes that torsion arose as a larval mutation, the process being essentially similar to that which still occurs in the development of modern forms. He shows that such a mutation would be of immediate advantage to the larvae. Before larval torsion the foot is adjacent to the mantle cavity so that the velum cannot be withdrawn into this. After torsion the head and velum can be withdrawn into the anterior mantle cavity followed by the foot. With the appearance of an operculum on this the opening could be closed. As Garstang points out, such a rapid change is more in accordance with modern views on the nature of evolutionary change than any fixation of characters acquired in adult or post-larval life. Moreover, this theory, unlike the teleological views considered under the previous section, does postulate an immediate advantage to the larva. The mutation would appear to have survival value. Apart, as already stated, from the posterior extension of the foot, the initial advantage to the adult of torsion is actually none too clear; indeed, it presents a series of problems the nature of which are discussed in the next section. It has been too readily assumed that because torsion has occurred it must have been of advantage to the adult. But the Cephalopoda, with similar ventral flexure and dorsal elongation of the visceral hump as the Gastropoda, have not undergone torsion, while the occurrence in the Opisthobranchia of detorsion, following the removal of the constraining influence of the shell and shell musculature, would indicate that torsion was imposed upon, rather than acquired by, the original adult Gastropoda.

With regard to the mechanics of larval torsion, Garstang states that the only mutation needed to start it would be an asymmetry in the development of the retractor muscles, 'thus bending the head and foot round during contraction'. In this connexion Smith (1935) states that in *Patella vulgata* only a dorsal retractor is present before torsion, which is brought about by the asymmetrical arrangement of this retractor together with the mutually antagonistic growth of the foot and shell. In *Haliotis*, Crofts (1937) found a single velar retractor muscle asymmetrically placed on the right side, torsion beginning as soon as the larval shell muscles are able to contract. There is thus pre-torsional asymmetry of the retractors, and although not of the type postulated by Garstang this is not surprising in view of the relatively specialized nature of both animals. There is also pre-torsional asymmetry of the gut and other organs, but this probably represents a pushing back into early developmental life of conditions acquired relatively late in evolution. Asymmetry actually first appears in the cleavage of the zygote, the cleavage planes of sinistral forms being the reverse of those of dextral forms, but it will not for that reason be contended that the ancestors of the Gastropoda were asymmetrical.

Garstang's theory also postulates the rapid completion of the torsional movement. Boutan (1899) claimed that 180° torsion occurs in a few minutes in both *Haliotis* and *Acmaea*, and Robert (1902) that it takes 6 to 8 hr. in *Trochus*. But Drummond (1902) states that torsion occurs gradually in *Paludina*, Smith found that in *Patella* the first half of torsion takes about 40 hr., the second stage being completed in a few hours, while in *Haliotis* Crofts (1937) found that a 90° torsion occurs in from 3 to 6 hr. in the pelagic larva some 29 to 35 hr. old. It then remains in this condition for several days, torsion not being completed until the sixth day when the animal is benthic. But *Haliotis*, owing to the hypertrophy of the right shell muscle, is possibly a special case. It would be helpful if the findings of Boutan and Robert on *Acmaea* and *Trochus* could be confirmed, these genera being less specialized than *Patella* or *Haliotis*.

Of the theories so far advanced in explanation of the origin of torsion that of Garstang appears inherently the most probable. It involves neither teleological assumptions nor the inheritance of acquired characters. The mechanism postulated, namely, larval torsion, is still exhibited during the development of all Gastropoda with pelagic larvae. The immediate advantage so acquired by the larvae appears a sufficient explanation for the selection of the original larval mutation and so for the absence of intermediate forms. Evidence advanced in this paper indicates that the immediate effects of torsion were by no means so advantageous to the adult as has previously been assumed.

C. *Mantle cavity after torsion*

As already stated the first problem presented to the Gastropoda with the mantle cavity opening immediately behind the head must, owing to the discharge into it of faeces and excrement, have been that of sanitation. This was met by the appearance of the slit in the mantle and shell and the withdrawal of the anus. Plate (1895), who regarded the slit as pre-torsional, first suggested that it was produced by the exhalant current, low in oxygen and laden with excreta, inhibiting the growth of the mantle edge. Garstang (1928) accepts this explanation but does not realize that such a cause would operate before, as well as after, torsion; and he insists that the slit is post-torsional. The exhalant current is low in oxygen, Hazelhoff (1938) showing that in *Haliotis tuberculata* some 56 % of the oxygen in the respiratory current is utilized. Bouvier & Fischer (1902), criticizing Plate's explanation, point out that if true there should be a slit along the right side of the shell opening in *all* monobranchiate Prosobranchia. This argument appears conclusive. The slit more probably arose by a series of changes in the gene complex, advantageous consequences ensuring its retention. With the loss of the right ctenidium the slit (or apertures) disappears and the rectum extends towards the margin of the mantle cavity. If the post-torsional origin of the slit be accepted, it follows that all fossil univalves possessing a slit, or its possible precursor a shallow sinus, which may, however, have been concerned with separation of inhalant and exhalant currents, as in the Sinuitidae (Wenz 1938), were Gastropoda. But earlier genera with no sinus, i.e. members of the Tryblidiacea, *may* have been pre-torsional.

So long as the bilaterally symmetrical plano-spiral shell was retained there appears no reason for assuming asymmetry in the mantle cavity. In fossil shells of this type the slit is always in the centre of the outer lip. The only changes would be deepening of the slit accompanying that of the mantle cavity. In habits the animals probably resembled their pre-torsional ancestors, being confined to a hard bottom with epipodial sense organs well developed.

D. *Effect of asymmetrical coiling of the shell*

When the innermost coils of the symmetrically twisted visceral mass began to be pushed out laterally leaving the longitudinal vertical axis, an asymmetrical condition was established from which evolved the characteristic form of the modern Gastropoda. This change, which disposed of the viscera more compactly, involved a rearrangement of these and also of the shell in relation to the foot on which it came to rest obliquely. Naef (1913) has described this process, his figures being reproduced in figure 29. The original transverse axis of the coiling (A) became directed posteriorly (B), while the apex was turned upward (C). Naef speaks of the first movement as 'regulatory detorsion', the second as 'inclination'. The further twisting of the visceral mass in relation to head and foot here involved had profound effects on the pallial complex, with secondary effects on the heart and on the renal and reproductive systems.

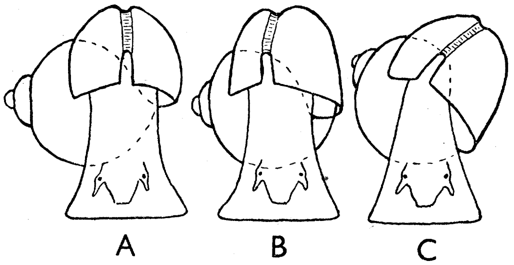

FIGURE 29. Diagrams illustrating regulation of the position of the gastropod shell following asymmetrical coiling. A, position of shell before regulation; B, original transverse axis of coiling directed posteriorly—the 'regulatory detorsion'; C, the spire of the shell is directed upwards so that balance is restored, the first whorl resting on the operculum—this is the 'inclination'. After Naef (1913).

Where coiling was dextral (sinistral coiling would produce opposite effects) compression of the right side of the mantle cavity would bring about reduction of the pallial organs on that side as stated by Naef (1913) and earlier workers. The organs on the left were correspondingly enlarged and the anus displaced towards the right. The new functional midpoint of the cavity was indicated by the position of the slit, also displaced to the right, as it is in the modern Zeugobranchia.

Although the right pallial organs are always reduced, the right kidney is enlarged and the left reduced in all aspidobranchs except the Neritacea and the Valvatacea (see figure 30), while in these and all other Gastropoda the left kidney is enlarged and the right one disappears, the duct becoming the gonoduct (although terminally this is ectodermal according to Krull (1935)). The right auricle is only retained when the right kidney persists. It is difficult to unravel cause and effect. Reduction of the right auricle will follow on that of the right ctenidium and efferent vessel, and this asymmetry in the heart might account for loss of the right kidney did not this persist in the monobranchiate Trochacea. But the retention of this kidney may be the reason why the right auricle persists after the loss of the ctenidium. In all other Mollusca the kidneys are symmetrical, which suggests that their asymmetry in the Gastropoda is connected with that of the pallial complex. But the reason why the right kidney is retained and the left reduced in most aspidobranchs remains obscure.

It is always the *left* (post-torsional) gonad which disappears—or at any rate gonoduct, because the gonad may represent the fusion of the original two indicated in figure 30A. This loss, or fusion, may have occurred before torsion (not so indicated in figure 30B). This is suggested by the single gonad in Loricata, Scaphopoda and Cephalopoda, with usually a single gonoduct except in the first. The transition from primitive to secondary condition is shown in figure 30A, B. Whatever its origin, the opening of the gonad on the right has had important results. In all aspidobranchs, except the Neritacea and Valvatacea, egg and sperm are discharged freely into the sea, which could be effected equally well from either side. But in the Neritacea, Valvatacea and pectinibranchs, which have yolky eggs with protective capsules demanding internal fertilization, the ducts *must* be on the right. Only here could a penis and an oviduct with accessory glands develop without impeding respiration. The elaboration of complex genital ducts could only follow suppression of the right kidney. It is noteworthy that the retention of the right kidney in the Zeugobranchia, Patellacea and Trochacea is associated with their restriction to a marine habitat. Free discharge of egg and sperm has made it impossible for them to penetrate fresh water.

In the Neritacea, Valvatacea and pectinibranchs, freeing of the oviduct from the renal duct permitted elaboration of accessory glands (present to a minor extent in some Trochacea, notably *Calliostoma zizyphinum*) and, with the appearance of a penis in the male, internal fertilization and direct development became possible. This permitted invasion of fresh water by members of all three groups; and, after suitable respiratory adjustments, of the land by certain Neritacea and pectinibranchs. Such is the somewhat surprising secondary result of renal adjustments associated with the asymmetrical coiling of the shell.

Mention should be made of the Cocculinacea included by Pelseneer (1906) in the Docoglossa (family Bathysciadidae), but more suitably separated by Thiele (1925) as a separate tribe. They include a number of somewhat obscure genera from deep water best described by Dall (1889) and Thiele (1908). All are limpets and more or less symmetrical. In most there is a single aspidobranch ctenidium, in some (e.g. *Addisonia*) large and curled back into the right pallial groove. They have lost the right kidney like the Neritacea and Valvatacea, and also resemble the latter in being hermaphrodite. In this case these changes have permitted descent into deep water where direct development is essential, internal fertilization being made possible by means of a penis developed at the base of the right tentacle. Unfortunately, no observations have been made on living representatives of this very interesting group.

The evolution of the reno-genital system in the Prosobranchia has been well summarized by Meyer (1913), and her diagrams, modified in various respects and extended to cover the Neritacea and with the relative positions of the Cocculinacea and Valvatacea indicated, are reproduced in figure 30 (references to literature being given in the legend). They illustrate the various points raised above and also the variety of conditions found in the Zeugobranchia, Patellacea and Trochacea (E, F, G, H). Here both the kidneys may open into the pericardium (G, H), or either the left (E) or right (F) exclusively. In the Patellacea (H) the gonad opens by rupture directly into the right kidney and not into the

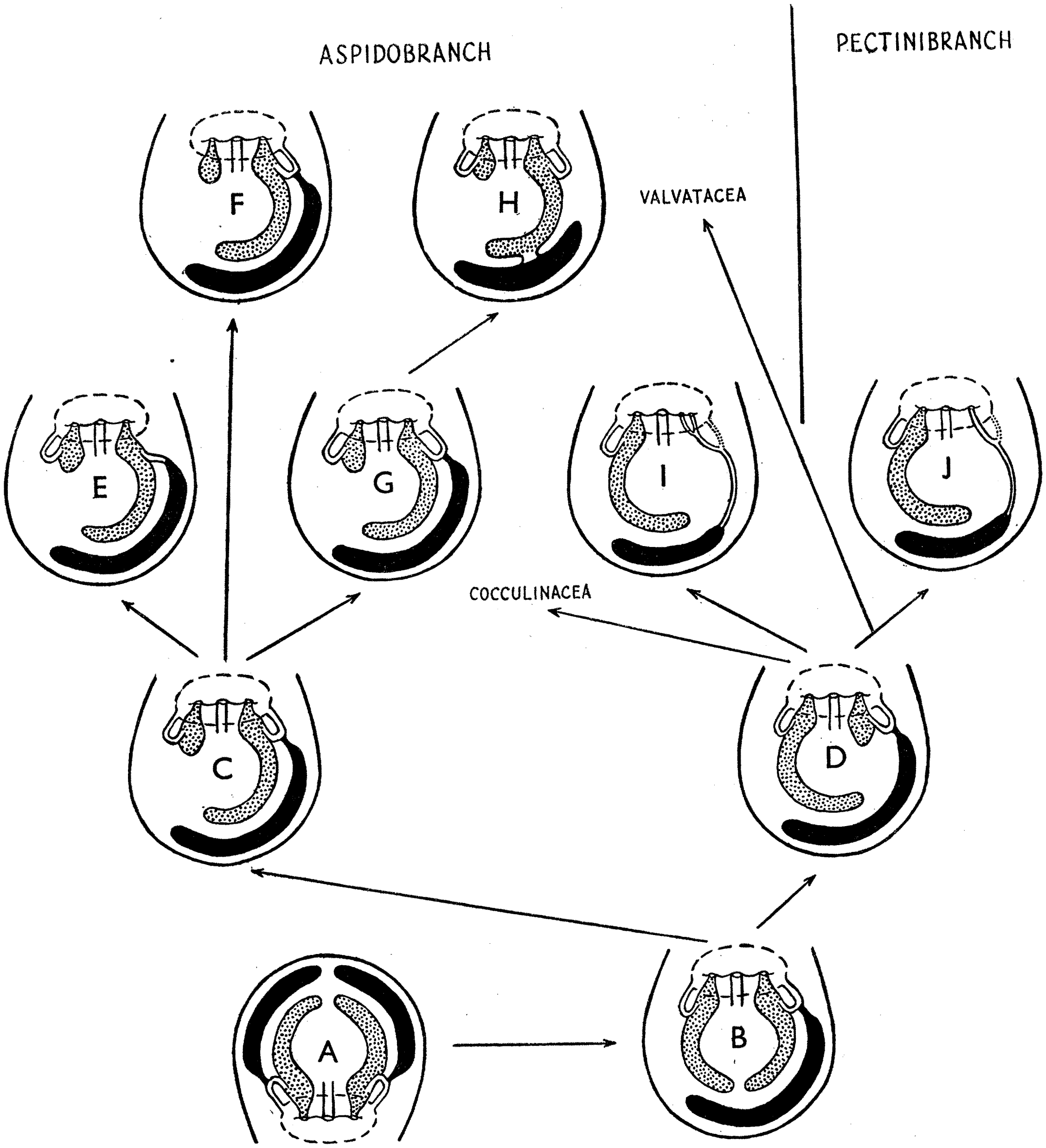

FIGURE 30. Diagrams illustrating arrangement of kidney and gonads throughout the Prosobranchia. Kidneys stippled, gonads black, pericardium indicated by broken line, anus shown between urinogenital openings into mantle cavity. A, hypothetical primitive condition (pro-gastropod), kidneys and gonads bilaterally symmetrical, gonads opening into reno-pericardial canals: B, loss of left, with increase of right (post-torsional) gonad; torsion may have occurred after this change: C, reduction of left, with retention of right, kidney; ancestral to conditions in Zeugobranchia (including Fissurellidae), Patellacea and Trochacea: D, reduction of right, with retention of left, kidney; ancestral to conditions in Neritacea, Cocculinacea, Valvatacea and all pectinibranchs: E, derived from C with loss of right reno-pericardial opening; found in *Pleurotomaria* (Woodward, 1901) and *Haliotis* (Crofts 1929): F, derived from C by loss of left reno-pericardial canal; found in *Diodora* (Pelseneer 1899): G, identical with C; found in *Puncturella* (Meyer 1913) and Trochidae (Randles 1904; Fleure & Gettings 1907; Frank 1914): H, derived from G by loss of connexion between gonad and reno-pericardial canal and discharge of former direct into lumen of kidney; found throughout the Patellacea: I, derived from D by complete loss of right kidney and development of long gonoduct, terminal portion of which represents remains of renal duct; found in the Neritacea where an ovo-pericardial canal (shown dotted) may be retained (*Septaria*) and the female ducts may be diaulic (as shown) or triaulic, the male being monaulic (Bourne 1908, 1911): J, derived from D in the same manner as I but, except for hermaphrodites, ducts always monaulic, an ovo-pericardial canal being retained (as indicated) in female (Krull 1935; Fretter 1941); found in all pectinibranchs. Conditions in the Valvatacea and Cocculinacea essentially similar to I and J respectively but both hermaphrodite.

reno-pericardial duct. In the variety of existing conditions, compared with the fundamental unity exhibited by the Neritacea (I), the pectinibranchs (including the Valvatacea) (J) and the Cocculinacea, is reflected the underlying difficulties presented by the retention of the right kidney.

In the aspidobranchs the following conditions have resulted from the initial coiling of the shell: (1) asymmetrical shell with two ctenidia; (2) secondarily symmetrical shell with two ctenidia; (3) asymmetrical shell with loss of one ctenidium; (4) secondarily symmetrical shell with loss of one or both ctenidia. These conditions, together with those in the pectinibranchs, are illustrated in figure 31, which indicates the separate origin of the Neritacea, and stresses the repeated independent assumption of the symmetrical limpet form by the Zeugobranchia (E), Patellacea (I, J), Neritacea (H) and pectinibranchs (M). In the remaining Gastropoda the same condition is attained in the deep-sea Cocculinacea (as indicated in figure 31) and also in the Umbrellidae among the Opisthobranchia and in the Siphonariidae and Ancylidae among the Pulmonata.

(1) *Asymmetrical shell with two ctenidia*

This condition is found in *Pleurotomaria*, the Scissurellidae and *Haliotis*, and only the first (figure 31B) has retained the primitive condition with the tightly wound spiral shell and single columellar muscle. In the Scissurellidae (C) the spire is reduced and the terminal whorl enlarged, with which is associated the appearance of a second, left shell muscle. In *Haliotis* (D) the limpet character has been attained but without complete loss of asymmetrical coiling of the shell. The terminal whorl is further enlarged, the shell much flattened and the right (original) shell muscle hypertrophied and centrally placed, the left shell muscle having been developed and then possibly reduced. In all other cases the left shell muscle tends to increase in size when once developed. The enlargement of the right shell muscle in *Haliotis* has had secondary effects on the mantle cavity which has been forced over to the left and, to compensate for this, elongated posteriorly. To overcome the difficulties presented by the consequent elongation of the marginal slit, this now takes the form of a series of apertures. The specialized nature of the Scissurellidae and Haliotidae is borne out by palaeontological evidence. According to Wenz (1938) both appear at the end of the Mesozoic, whereas the Pleurotomariidae are Ordovician or possibly Cambrian. *Haliotis*, with its numerous species and wide distribution, is a successful genus highly adapted for life in shallow water on a hard substratum, both in shell form and capacity for adhering tightly by means of the immense foot acting in co-operation with the large centrally placed shell muscle. In all three families intimate sensory contact is maintained with the environment by the agency of the highly developed epipodium.

(2) *Secondarily symmetrical shell with two ctenidia*

This condition is exhibited in the Fissurellidae (figure 31E) which form the majority of modern Zeugobranchia. The terminal whorl of the shell is further enlarged, the post-larval coils are lost and the mantle cavity becomes symmetrical. The secondary nature of this condition is revealed in development and by the continued asymmetry of renal and reproductive organs. At the same time the direct effect of the asymmetry of the shell on the pallial organs is revealed by the regained symmetry of these when this constraining factor is removed. Conditions in the Scissurellidae indicate the probable line of evolution

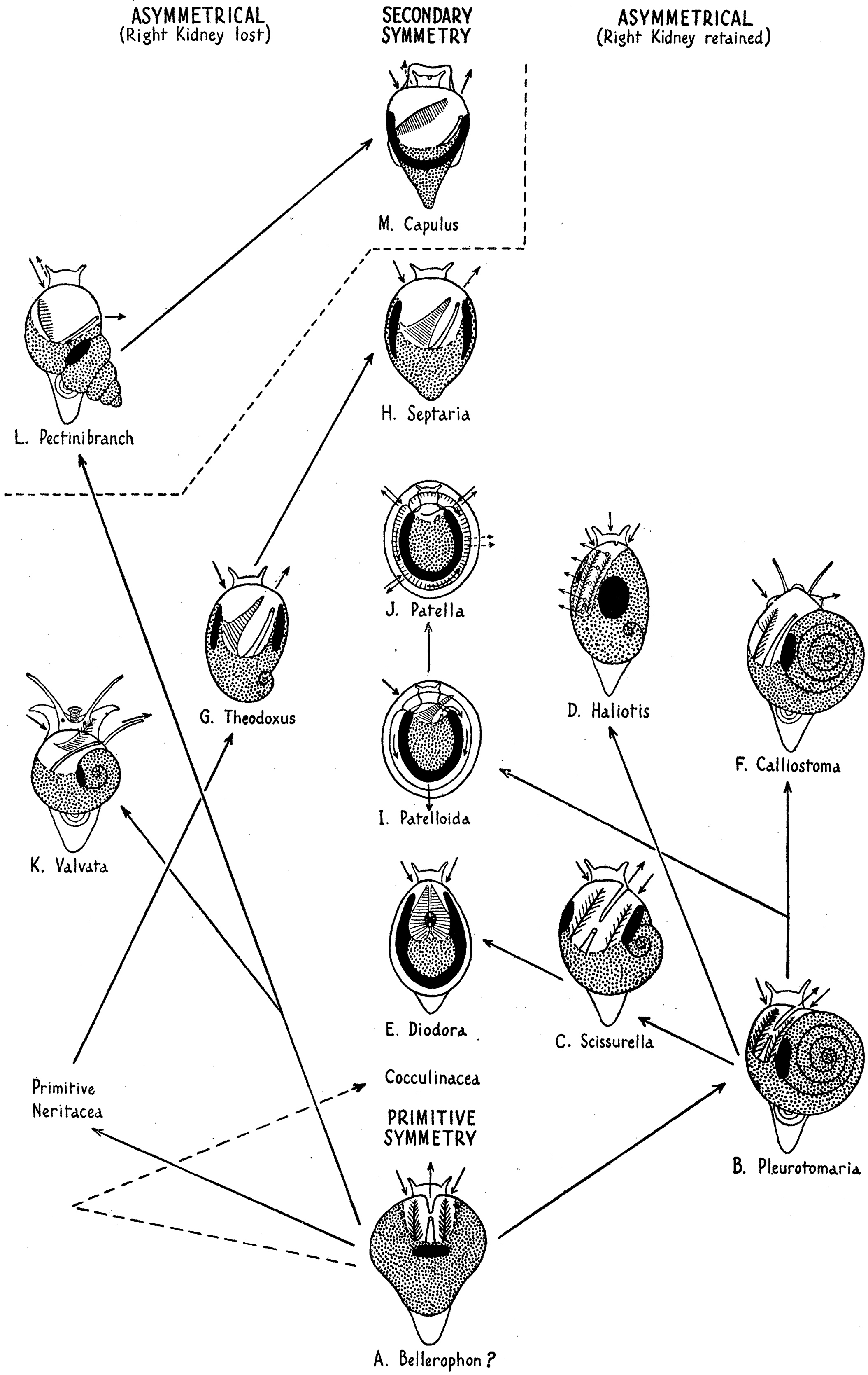
ASYMMETRICAL
(Right Kidney lost)
SECONDARY SYMMETRY
ASYMMETRICAL
(Right Kidney retained)
M. Capulus
L. Pectinibranch
H. Septaria
J. Patella
D. Haliotis
G. Theodoxus
F. Calliostoma
K. Valvata
I. Patelloida
E. Diodora
C. Scissurella
Cocculinacea
Primitive Neritacea
PRIMITIVE SYMMETRY
B. Pleurotomaria
A. Bellerophon ?

Figure 31

which led to this re-establishment of symmetry, and this is indicated in figure 31, but it is *not* suggested that the Scissurellidae are themselves ancestral to the Fissurellidae which actually appear earlier in evolution, in the middle of the Triassic (Wenz 1938).

The left shell muscle, after attaining the size of the right one, grew back with this to form a single horseshoe-shaped muscle in the same manner as in the Patellacea (Fleure 1904). The laterally constraining action of this caused a narrowing of the mantle cavity accompanied by a backward prolongation in the mid-line, and the consequent formation in many genera of an apical shell aperture, e.g. in *Diodora* and *Puncturella* where it has been evolved independently. The symmetrical ctenidia are highly specialized and represent the highest point reached in the evolution of these organs throughout the Gastropoda. In all the epipodium is retained, the enlarged foot, which has, like *Haliotis*, lost the operculum with the acquisition of the limpet form, extending beyond the shell when the animal moves, while there is a tendency for the overgrowth by the mantle of the shell which may then be reduced as in *Scutum*.

(3) *Asymmetrical shell with loss of one ctenidium*

This condition, with the accompanying loss of the shell aperture, has been acquired independently by the Trochacea (figure 31 F), Neritacea (G, H) and Valvatacea (K). The first may be derived directly from the Pleurotomariidae as shown in figure 31. Apart from the loss of the slit the shell is essentially similar, as are the reno-genital system and the foot and epipodium. With the loss of the right ctenidium a left-right respiratory circulation through the mantle cavity becomes possible for the first time, and the rectum now approaches the edge of the cavity on the right side. The loss of the right ctenidium is accompanied by that of the osphradium, but a trace of the right hypobranchial gland remains. The left ctenidium retains its primitive position and structure but has lengthened to compensate for the loss of the current originally produced by the right ctenidium. Problems of support raised by its increased length have been met by the extension anteriorly of the originally short afferent membrane. This involved loss of efficiency and so reduction in size of the filaments on the outer side of this. Within the limits imposed by the nature of this

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FIGURE 31. Diagrams illustrating the possible course of evolution within the Prosobranchia. Shell muscles shown black, visceral mass stippled, mantle cavity left clear with ctenidia and rectum shown, arrows indicating exhalant and inhalant currents. Primitive symmetry after torsion shown in A (*Bellerophon*). Evolution of asymmetry with retention of right kidney in Zeugobranchia (B) and Trochacea (F) shown on right; with loss of right kidney in Neritacea, Cocculinacea, Valvatacea (K) and pectinibranchs (L) on left. Partial return to secondary symmetry with duplication of the shell muscles is shown in the Zeugobranchia (C, D) on right and in the Neritacea (G) on left. Complete assumption of secondary symmetry is exhibited independently by the Fissurellidae (E) where the two shell muscles unite posteriorly and the ctenidia retain bilateral symmetry; in the Patellacea where the left ctenidium is retained (I) or pallial gills acquired (J); in the Cocculinacea (not figured); in the Neritacea (H) where the two shell muscles do not unite; in many pectinibranchs, e.g. *Capulus* (M) where there is a single shell muscle. The probable main lines of evolution are indicated by the large arrows, a broken line separating aspidobranchs from pectinibranchs. All figures based on original investigation except A (postulated), B (based on Woodward 1901), C (based on Vayssière 1894) and H (based on Bourne 1908).

respiratory apparatus, which would be readily blocked by sediment entering the chamber enclosed by the ctenidial membranes, this group has been successful and is widely distributed between tide marks and in shallow water on hard substrata. The Trochacea appear about the middle of the Triassic.

As discussed in detail by Bourne (1908, 1911), the Neritacea have evolved independently from the other Zeugobranchia and the Patellacea, and this is indicated in figure 31. The differences in the renal and genital systems have already been discussed. No modern representatives have two ctenidia or a shell aperture, and in all the coiling of the shell has undergone reduction, as in *Theodoxus* (figure 31 G), where conditions approximate to those in the Scissurellidae, with acquisition of a left shell muscle. In others practically all trace of asymmetry is lost, and a limpet form acquired with functional loss of the operculum and symmetrical development of the two shell muscles which do not, however, unite posteriorly. This is exhibited in *Septaria* (H) (Bourne 1908).

Any superficial resemblance between the Neritacea and the Trochacea is due to convergence; the two groups have little in common beyond the single aspidobranch ctenidium and the rhipidoglossan radula. The latter may also be due to convergence, the animals living on similar substrata and both feeding on encrusting vegetation. The Neritacea have the same environmental limitations in the sea, being confined to a hard substratum in shallow water in the tropics and subtropics (e.g. *Nerita*). But, although of separate sexes, their genital system is more complex than that of the higher Prosobranchia with the exception of the Valvatacea. With the evolution of a diaulic, in *Septaria* a triaulic, condition in the female they approximate to the Opisthobranchia and Pulmonata. On the other hand, the retention of a gono-pericardial canal in *Septaria* is a primitive feature found in only a few pectinibranchs (Krull 1935). The possession of large yolky eggs, internally fertilized and protected by complex capsules (Andrews 1935) has enabled them to penetrate into fresh waters where the bottom is hard (e.g. *Theodoxus* and *Septaria*), and also on to land where the pulmonate Helicinidae, Proserpinidae and Hydrocenidae are characteristic members of tropical faunas.

The Valvatacea (figure 30 K) resemble the pectinibranchs in all but the acquisition of hermaphroditism and the retention of the aspidobranch ctenidium. They are represented in figure 31 as an early offshoot from the pectinibranch stock. The inherent difficulties presented by the possession of an aspidobranch ctenidium have been met by its horizontal disposition but above all by its anterior migration, which has been accompanied by that of the openings of the alimentary, renal and reproductive systems. Respiration is largely carried on *outside* the mantle cavity. The reduction of currents within the cavity has led to the loss of the hypobranchial gland and a reduction in the size of the osphradium (even assuming it extends on to the gill axis), while the function of the exhalant current in the removal of faeces and genital products has been largely taken over by the pallial tentacle. *Valvata*, alone amongst aspidobranchs, is thus able to live on a soft substratum, there being little danger of much sediment entering the mantle cavity. The retention of the aspidobranch condition actually accompanies a high degree of specialization also revealed in the elaboration of a reproductive system as complex as that of the Pulmonata (Garnault 1890; Bernard 1890*b*; Furrow 1935). The Valvatacea are an old group dating from the beginning of the Jurassic and possibly earlier (Wenz).

(4) *Secondarily symmetrical shell with the loss of one or both ctenidia*

This condition occurs in the Patellacea, the Cocculinacea and in *Septaria* amongst the Neritacea. The Patellacea are the most successful of the aspidobranchs (in the Patellidae in part because they are no longer aspidobranchs!). The most reasonable explanation of their derivation is that they sprang from ancestors which had already lost the right ctenidium. Hence when secondary symmetry was attained (see figure 31I), in essentially the same manner as in the Fissurellidae, there was only one ctenidium, later lost in the Patellidae (figure 31J), and no shell aperture. This view opposes that of Fleure (1904), with which Naef (1913) is in essential agreement. He assumed that a shell slit was originally present but that this weakened the force of pedal attachment and was eliminated by natural selection. He thought that the forward displacement of the viscera, caused by the loss of all but the terminal whorl of the shell, pressed on the mantle cavity, especially on the right side, causing loss of the right ctenidium. But conditions in the Fissurellidae, and also in the Neritacea, indicate that reduction in the mantle cavity is *not* a necessary result of the assumption of a symmetrical limpet form. Fleure attributes the oblique arrangement of the left ctenidium to the reduction of the nuchal cavity, but it is oblique in the Neritacea and horizontal in the Valvatacea, in both of which the cavity is large. The arrangement represents one of the two ways in which a single aspidobranch gill can be disposed so as to create a left-right respiratory current, and the reduction of the nuchal cavity in the Patellacea is functionally correlated with the development of pallial grooves, as is the form and disposition of the ctenidium. In *Addisonia* amongst the Cocculinacea the ctenidium actually extends far along the right pallial groove (Dall 1889).

Fleure explains the loss of the hypobranchial glands by considerations of space, whereas they are functionally unnecessary because, as in the Valvatacea, sediment is not thrown against the roof of the cavity. Finally, he accounts for the loss of the ctenidium in *Patella* by increased risk of damage from 'excrement' owing to its position, by the loss of hypobranchial glands, by reduction in the size of the cavity and its 'imperfect currents', together with increased exposure to the air. Such statements reveal the inadequacy of exclusively morphological data and arguments.

The functional series exhibited within the Patellacea has already been discussed. The single ctenidium of *Patelloida* functions very efficiently, and its loss in the Patellidae may be attributed solely to the greater respiratory efficiency under shore conditions of the pallial gills acquired at the evolutionary stage represented by *Lottia* and *Scurria.* With their aid respiration is possible when little water is present; even if a thin layer of water covers the rock surface a respiratory current may be set up all around the animal, the water passed out being quickly reoxygenated. This transference of respiration from the nuchal cavity to the pallial grooves has raised difficulties about the disposal of sediment. These are met by the acquisition of peripheral glandular areas in *Patina* and its allies and, more successfully, by muscular extrusion in *Patella.* The abundance and size of species of *Patelloida* (*Acmaea*) in the Pacific would entitle this genus to be considered the most successful of all shore-living limpets were it not that on the eastern shores of the Atlantic its few and small species are clearly less efficient than those of *Patella.*

Fleure's other contentions can be largely accepted. He stresses the specialization of the method of adhesion, as opposed to retraction within the shell. This involved, as in the other limpets shown in the central column of figure 31, the formation of a broad adhesive surface and of a flattened shell capable of being held down symmetrically and providing the minimum of resistance to the waves. Hence the reduction of the tail process of the foot (still retained in some measure in the less specialized Fissurellidae) associated with creeping, and the formation of the horseshoe-shaped shell muscle. The downward and outward growth of the mantle enlarged the rim of the shell so as to form a cap over the animal which could be pulled evenly down on a hard substratum by the peripherally disposed muscle. In this way the pallial grooves were formed and the nuchal cavity in consequence reduced, i.e. not owing to pressure from the visceral mass. A second consequence was the restriction of contact between the foot and the environment—still intimate in the Fissurellidae—and hence the loss of the epipodium, the place of which was taken functionally by the marginal pallial tentacles. Fleure emphasizes the importance of the evolution of the 'homing instinct' in these shore-dwelling species. Without it the animals would have difficulty in finding and maintaining a clear area for attachment amongst the barnacle-encrusted rocks on which they live. Firm attachment is essential both when the surf breaks over them and when the rocks are left dry. The receptors concerned with homing are possibly resident in the pallial tentacles. The Patellacea are as highly specialized for life on a hard substratum as are the Loricata, and there is an interesting parallel in the evolution in both of a broad attaching sole and of pallial grooves with subpallial sensory streaks and glandular areas (Yonge 1939*a*).

Reference must be made to the Lepetidae, a small family of the Patellacea which live in relatively deep water and possess neither ctenidia nor pallial gills (Dall 1889; Pelseneer 1899, 1903). Attempts to dredge living specimens at Millport were unfortunately unsuccessful, and there are no data on conditions in life. Thiem (1917*b*) states that the reduced nuchal cavity contains neither osphradia nor sensory streaks, and possibly these animals have no currents in this cavity. On the basis primarily of the number of bundles into which the shell muscle is divided, Thiem (1917*b*) derives the Lepetidae from the Acmaeidae (by loss of the ctenidium), while he regards the Patellidae as being more closely associated with the Scurriidae. This view is not unreasonable; all that has been contended above is that, as indicated in figure 31 I, J, during the evolution of the Patellidae the animals must have passed through a stage corresponding to that of the modern *Patelloida* before proceeding to the stages represented by *Lottia-Patina-Patella*. This general sequence is supported by modern palaeontological opinion, Wenz (1938) putting the origin of the Acmaeidae in the middle of the Triassic, that of the Patellidae towards the end of the Jurassic, and of the Lepetidae at the beginning of the Miocene.

The Cocculinacea have acquired secondary symmetry with the limpet form and a very similar type of mantle cavity; but, as indicated in figure 31, from totally different origins. Moreover, as previously noted, they are adapted for deep-sea conditions and not for shore life. In the absence of data on the living animal no further comment is possible. Like the Lepetidae they are of relatively recent origin, appearing first at the beginning of the Miocene (Wenz).

E. *Mantle cavity in the pectinibranch Prosobranchia*

With the loss of the left row of filaments in the solitary ctenidium, the Gastropoda found the ideal solution for the problem of respiratory circulation presented after torsion.

Although a left-right circulation had been acquired by all aspidobranchs which had lost the right ctenidium, the complex gill was easily fouled by sediment, and the animals were thus unable to leave the clear water over a hard substratum. Only in the Valvatacea, where only a small area of the mantle cavity is concerned with respiration and in *Patella* where the ctenidium is lost, are the animals able to live in muddy areas, although the latter seldom do so. In the still waters of great depths the Lepetidae and the Cocculinacea must live on stones embedded in mud, but there will be little sediment in suspension, while it is questionable whether ciliary currents exist in the mantle cavity of the former.

But in the pectinibranchs (figure 31 L) the ctenidial axis becomes fused with the mantle wall from which the single row of filaments extend. In functional correlation with this the osphradium comes to lie parallel to the ctenidium ventrally. For the more efficient removal of sediment an additional ciliary current appears on the floor of the inhalant region, and in this the heaviest particles are immediately rejected (see broken arrows, figure 31 L, M). This current has been described in *Aporrhais*, *Buccinum*, *Oxygyrus* and other genera (Yonge 1937*a*, 1938, 1942). With the further evolution of an extensible inhalant siphon and suitable modification of the foot, the pectinibranchs became able to move through a soft substratum despite the amount of sediment suspended in the water. In the extreme case represented by *Aporrhais* they took to a largely quiescent life *under* mud, constructing inhalant and exhalant passages through this by means of the proboscis (Yonge 1937*a*). In certain cases secondary symmetry was attained with the limpet form, notably in the Capulidae (figure 31 M) and Calyptraeidae, a mode of life associated with ciliary feeding (Orton 1912; Yonge 1938). There is no need to dwell further on the remarkable display of adaptive radiation exhibited by the pectinibranchs which has enabled them to exploit all marine habitats, to become parasites, and also to pass into fresh water and on to land, although here, as in the Neritacea, the capacity for internal fertilization due to the loss of the right kidney is the supreme factor. But it should be emphasized that emancipation from dependence on a hard substratum was due to the greater efficiency of the mantle cavity attained with the assumption of the pectinibranch condition.

V. Evolution of the ctenidia throughout the Mollusca

The primitive character of the paired ctenidia of the unspecialized Zeugobranchia, postulated by previous workers on morphological grounds, has been confirmed by structural and functional analysis. It is possible, as displayed diagrammatically in figure 32, to derive, from the primitive condition they retain, the diverse and often highly complex ctenidia of all the Mollusca. The constant feature is the relation between the afferent and efferent blood vessels (the former being shown black). Failure to distinguish in all cases between these led to inaccuracy in the discussion of the molluscan ctenidia by Pelseneer (1906, pp. 10–12, figure 5).

A. *Primitive condition*

The ctenidia of the primitive Mollusca possessed, it is contended, the following characteristics:

(*a*) They consisted of a pair of outgrowths from the anterior end of the mantle cavity arising on either side of, and ventral to, the anus (figure 32A).

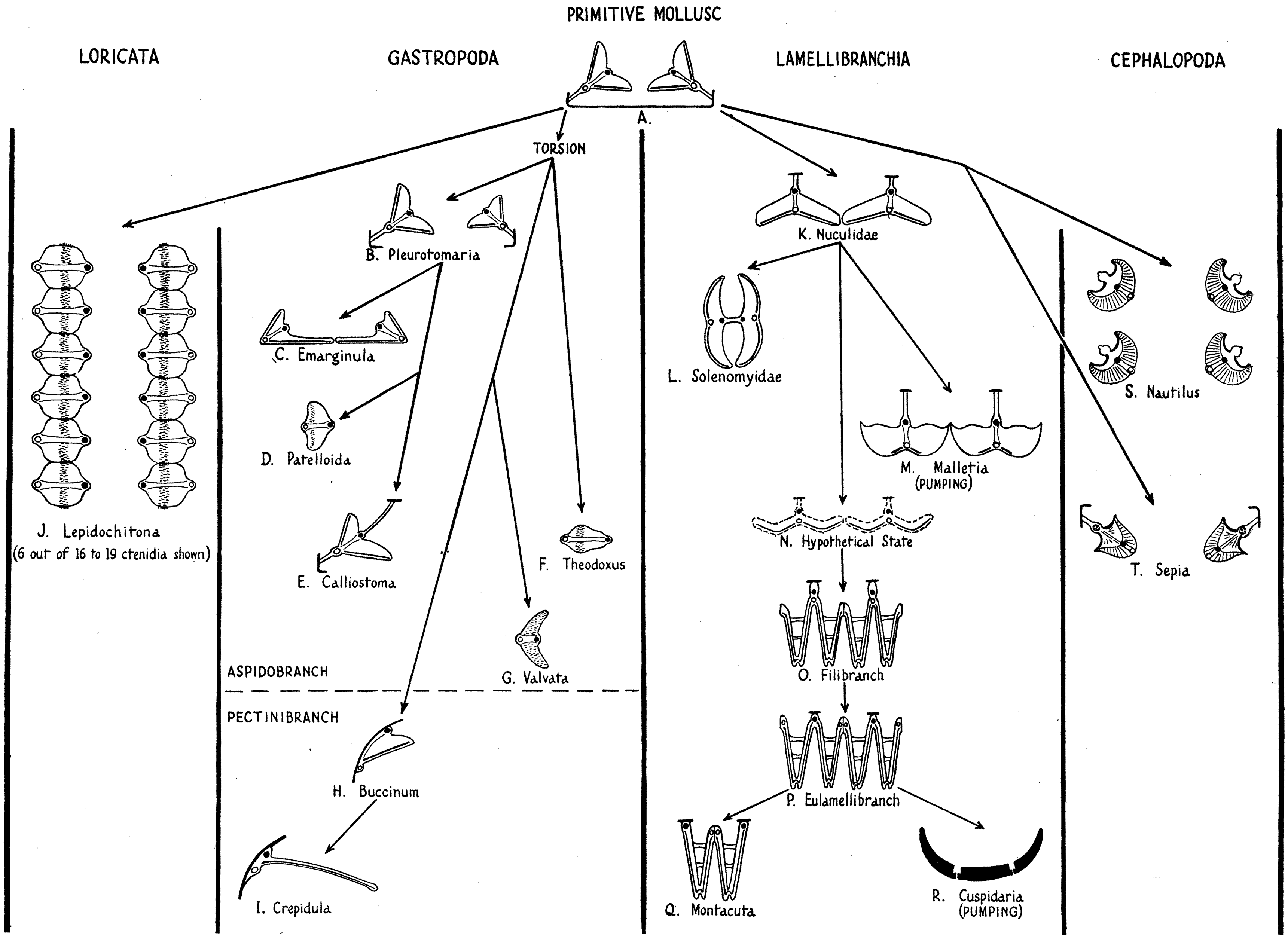

FIGURE 32. Diagrams illustrating the probable mode of evolution of the ctenidia throughout the Mollusca. Afferent blood vessel shown black throughout, efferent vessel as open circle, chitinous supporting rods indicated by thick black lines, where absent (D, F, G, J) the extent of the lateral cilia shown, supporting rods on afferent side of filaments in Cephalopoda (S, T) also shown. A, postulated; B, based on Woodward (1901); C–G, on present investigations; H, I, on Yonge (1938); J, on Yonge (1939*a*); K–M, on Yonge (1939*b*); N–P, original; Q, on Atkins (1937*b*); R, on Yonge (1928); S, on Joubin (1890); T, on Tompsett (1939). Other data in the text.

(*b*) Within a central axis ran afferent (dorsal) and efferent (ventral) blood vessels, the latter communicating directly with the single pair of auricles. Branchial muscles and nerves ran in close association with each blood vessel.

(*c*) Each ctenidium inclined inward (figure 1) and was attached by afferent and efferent membranes, the latter being the longer.

(*d*) Triangular filaments were given off alternately on the two sides of the axis; blood flowed into these from the afferent vessel and was re-collected in the efferent vessel.

(*e*) Lateral cilia on each face of the filaments near the efferent surface created an upwardly and inwardly directed respiratory current, i.e. in the opposite direction to the flow of blood.

(*f*) For support against this current skeletal rods appeared below the zones of lateral cilia. They were arranged in pairs, each like an elongated U, with the base embedded in connective tissue in the efferent region of the axis and the arms passing into adjacent filaments (figure 33).

(*g*) Sediment in the respiratory current was collected by frontal and abfrontal cilia along the efferent and afferent margins of the filaments respectively and carried away in currents on the afferent surface of the axis. (The presence primitively of enlarged terminal cilia is doubtful.)

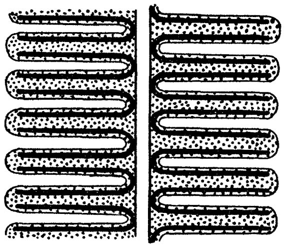

FIGURE 33. Diagram illustrating the arrangement of the chitinous supporting rods in the primitive ctenidium. Ctenidium viewed from frontal surface, rods shown as thick black lines.

B. *Gastropoda*

While probably unaffected by torsion, the ctenidia were, as stated above, profoundly influenced by the asymmetrical coiling of the visceral mass. Significant stages in the evolution and specialization of the gastropod ctenidia are shown in figure 32B–I. In unspecialized Zeugobranchia, e.g. *Pleurotomaria* (B), only the right ctenidium is reduced. In the Fissurellidae symmetry is regained with accompanying specialization, e.g. *Emarginula* (C). The right ctenidium is lost with extension in the left of the afferent attachment in the Trochacea, e.g. *Calliostoma* (E), but with freedom and specialization of the left ctenidium in the monobranchiate Patellacea, e.g. *Patelloida* (D), and in the Neritacea, e.g. *Theodoxus* (F). An early offshoot from the monotocardiate (pectinibranch) stock led to the appearance of the Valvatacea where the single left ctenidium (G) is specialized in structure and also position. The aspidobranch ctenidium has thus been diversely modified including: (*a*) shape of filaments, especially in C; (*b*) loss of skeletal rods in filaments of D, F, G; (*c*) loss of efferent attachment, partially in C, G, almost completely in D, F; (*d*) extension of the afferent attachment, slightly in G but notably in E, where alone the single ctenidium retains its primitive orientation. Apart from B and C, the respiratory current is left-right in direction.

Conditions in *Buccinum* (H) exemplify those in the pectinibranchs. Throughout the frontal cilia beat to the tip of filaments, but the abfrontals vary. A possible evolutionary sequence is indicated by comparison of conditions in *Haliotis*, *Turbo*, *Calliostoma* and *Buccinum* (figure 34). In *Haliotis* (A) the abfrontals beat towards the axis where cilia carry material anteriorly (probable primitive condition); in *Turbo* (B) (anterior to the afferent membrane) all abfrontals beat to the right, but a forwardly directed axial current carries material from the left filaments to the tip; in *Calliostoma* (C) axial currents are absent, all material being conveyed to the right; while in *Buccinum* (D) the abfrontals beat to the tips of the single, right row of filaments.

The uniformity of ctenidial structure in the pectinibranchs is in striking contrast to the variability in the less numerous aspidobranchs, and indicates the success of this final structural modification. The only major alterations are in connexion with ciliary feeding. The filaments are elongated, so providing additional surface for the frontal and abfrontal cilia which change in function from cleansing to food collection, material being conveyed to the mouth along the tips of the filaments. In the Lamellibranchia, where four greatly elongated filaments collect food compared with only one in these Gastropoda, frontal cilia only are concerned. In pectinibranchs ciliary feeding occurs in *Crepidula* (I) and its allies (Orton 1912), *Capulus* (Yonge 1938), certain species of *Vermetus* (Yonge 1932; Yonge & Iles 1939) and *Turritella* (Graham 1938*a*). The evolution of ciliary feeding in these Gastropoda has been discussed elsewhere (Yonge 1938). The only other major changes concern the loss of the ctenidium, e.g. in *Caecum* (Götze 1938), in *Firoloida*, the most specialized of the Heteropoda, and in parasites, e.g. many Eulimidae and all Entoconchidae (Pelseneer 1906).

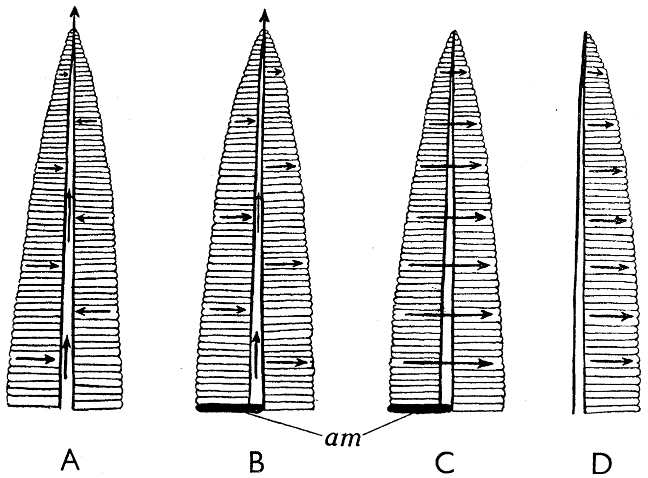

FIGURE 34. Evolution of the abfrontal ciliation in the Prosobranchs. A, *Haliotis*, B, *Turbo*, C, Trochidae, D, Pectinibranch. *am*, anterior end of afferent membrane in Trochacea.

In the Opisthobranchia the ctenidia are 'plicate' (Pelseneer 1906), with alternate furrows and ridges on the two sides of the axis, filaments being absent. They have certainly not been derived from the pectinibranch condition.

C. *Loricata*

Examination of the gills of *Lepidochitona cinereus* (figure 32J) (Yonge 1939*a*) has confirmed the original opinion of Spengel (1881) that these represent multiplied ctenidia and are not secondary. They divide the pallial grooves into inhalant and exhalant chambers, the alimentary, renal and reproductive systems opening into the latter. The axes contain the normal afferent and efferent vessels, nerves and muscles. The filaments are disposed alternately and are short, without skeletal rods but with broad zones of lateral cilia (figure 32J), which beat from the efferent to the afferent surface. At the margin of the areas occupied by these are long cilia whereby filaments of adjoining ctenidia are attached. Apart from possession of these cilia, the ctenidia are no further removed from the primitive condition than are those of *Patelloida*, *Theodoxus* or *Valvata*, where skeletal rods are also lacking. The multiplication of ctenidia is correlated with pedal elongation and consequent reduction of the posterior mantle cavity which is prolonged into narrow pallial grooves by the overgrowth laterally of the mantle, the inhalant current being drawn in anteriorly (Yonge 1939*a*).

D. *Scaphopoda*

Ctenidia are absent, but an inhalant current is produced in *Dentalium entalis* (Yonge 1937*b*) by the action of ciliated bands which extend across the ventral surface of the body anterior to the anus. These appear to have an exclusively current-producing function and are not gills. Periodic exhalant currents are produced by muscular contraction of the foot.

E. *Lamellibranchia*

Although the ctenidia in this class are the most complex in the Mollusca, they were the first to be described in detail, and an extraordinary volume of work has been done on them. A period of morphological study culminated in the exhaustive work of Ridewood (1903); functional study of ciliary currents was initiated by Wallengren (1905), continued by Orton (1912, 1913), Kellogg (1915), Yonge (1923, 1926, 1928) and others, and culminating in the detailed papers of Atkins (1936, 1937*a–c*, 1938*a–c*). Attention has been also directed, originally by Setna (1930) and more recently by Elsey (1935), Nelson (1938), Nelson & Allison (1940) and Atkins (1943), to the importance of muscular activity in these ctenidia. MacGinitie (1941) has stressed the significance of the mucous sheet secreted on the stimulation of food and other particles.

In the Lamellibranchia the mantle cavity extends anteriorly and ventrally owing to overgrowth of the body by the mantle lobes. This has involved forward migration of the ctenidia. The arrangement of the ctenidial blood vessels in the primitive Protobranchia is here a matter of great importance. Pelseneer (1891*b*) originally stated that the efferent vessel was ventral in *Nucula* and external (or pallial) in the vertically disposed ctenidia of *Solenomya* (see figure 32L); Stempell (1898, 1899) came to the same conclusion. But in his later account of the Mollusca (1906), Pelseneer figures the filaments of *Nucula* and *Solenomya* with the afferent vessel ventral, whether by error or deliberately is not clear. Mitsukuri (1881), Drew (1899, 1901) and Heath (1937) are all non-committal on this point, but previous work (Yonge 1939*b*) has confirmed Pelseneer's and Stempell's original statements, and re-examination of sections, especially of the relatively large *Malletia*, enables it to be stated that the efferent vessel does certainly run along the free, ventral surface of the axis, i.e. on the same side as the lateral cilia and skeletal rods exactly as in the Gastropoda. Conditions are similar in some Filibranchia (see below). The ctenidia of all Lamellibranchia are thus attached dorsally by an *afferent* membrane homologous with that of the aspidobranchs. Retention here of the efferent membrane would have carried the ctenidia ventrally to just within the margin of the mantle lobes with a corresponding reduction in the size of the inhalant chamber.

Their forward extension carried the ctenidia towards the mouth, a pair of labial palps on each side eventually bringing the two into functional association. Filaments increased in number while adjacent ones become attached, initially by ciliated junctions (cf. *Emarginula*). The mantle cavity was structurally as well as functionally divided into inhalant and exhalant chambers by the close application and final fusion of the outer filaments to the mantle and the inner ones to those of the other side or to the visceral mass. Increased danger of clogging with sediment the elaborate sieve-like tissue, owing to the greater respiratory and feeding current it created, was countered by the acquisition of additional latero-frontal cilia (for details of structure see Atkins 1938*c*). These prevent particles from passing between the filaments, and correlated with their appearance is the loss of abfrontals except in primitive genera such as *Nucula* (K). To resist the increased flow of water, the skeletal elements form tubes within the filaments (thickened below the zone of lateral cilia as indicated in figure 32 K to Q). These are connected with longitudinal elements in the efferent region of the axis (see description of the skeletal framework in *Nucula* by Mitsukuri (1881) and in Lamellibranchia generally by Ridewood (1903)). Food collection is always done by the frequently specialized frontal cilia which also exercise selective activity (see Atkins 1937*a*).

In the Protobranchia, the ctenidia of the Nuculidae (K) are relatively simple and easily derived from the primitive condition (A). They are primarily respiratory, although particles are passed forward in the middle line as shown by Orton (1912). But food is mainly collected by the palp proboscides, the presence of which is a necessary intermediate condition between loss of direct feeding by the mouth and acquisition of ciliary feeding by the modified ctenidia (Yonge 1939*b*). In *Solenomya* (L) the filaments are increased in area and number and, owing to the lateral compression of the body, they are vertical; the palps are reduced and feeding is the sole concern of the ctenidia (Yonge 1939*b*). This condition has been attained independently of that in the higher Lamellibranchia as indicated in figure 32. In both these families adjacent filaments are loosely united by ciliated disks; moreover, the inhalant current is *anterior*, probably a primitive characteristic of the Lamellibranchia (Yonge 1939*b*), its return posteriorly in the Nuculanidae and the higher Lamellibranchia being secondary.

In the Nuculanidae, e.g. *Malletia* (M), the palps are as complex as in the Nuculidae and the proboscides collect food. The ctenidia are very elaborate, forming delicate septal membranes perforated by four rows of small ciliated pores (two in each ctenidium). Adjacent filaments are united ventrally, except in the region of the pores, by highly efficient ciliary junctions which also connect the inner filaments of the two sides in some species (Yonge 1939*b*). Striated muscle in the afferent membrane, here very long, produces rhythmical upward movements best seen in *Yoldia* (Drew 1899) and *Malletia* (Yonge 1939*b*). The respiratory current is here produced almost exclusively by muscular action, the ctenidia forming pumping organs and attaining, in some respects, the most specialized condition found in the Mollusca.

In the more primitive Filibranchia (O), e.g. *Margaritifera* (Herdman 1904), *Placuna* (Hornell 1909) and *Pecten* (Dakin 1909), the efferent vessel runs immediately below the afferent, but in the others and in all eulamellibranchs the former has split, separate vessels running along the end of each filament (P, Q). In all the ctenidia are the sole organs of feeding, material being carried orally in special food grooves. The palps represent the lamellar region only of the more complex organs in the Protobranchia and retain their primitive function of selection (Yonge 1939*b*). These ctenidia may be derived from those of *Nucula* (K) by way of the hypothetical conditions represented in N. The classic view is that these elongate, reflected filaments evolved from the shorter ones by downgrowth of the tips of these which then bent back on themselves dorsally. The terms descending and ascending filaments, first used by Lacaze-Duthiers (1856) and later by Ridewood, assume this mode of origin. Embryological data (Rice 1908; Wasserloos 1911) is conflicting, but fundamentally this mode of origin is impossible. The filaments could not function until this process was completed. Only then could the region where reflexion occurs become modified to form the all-important food groove characteristic of these filaments. This difficulty is overcome if the filaments are regarded as arising from horizontal structures (as in *Nucula*) which, with *both* ends fixed, bent ventrally in the middle forming a downward-projecting V. In this case the area occupied by the food groove would remain as a fixed point throughout development and the filaments could function as soon as the requisite cilia appeared. This condition is illustrated in figure 32N.

The filibranch ctenidium (O) resembles that of *Nucula* in the presence of ciliary junctions only between adjacent filaments, but food grooves are present and the two arms of each reflected filament are united by interlamellar junctions. This is true of the eulamellibranch ctenidium (P), but here there are tissue and skeletal junctions between the filaments. The great variability in the route whereby food is passed to the mouth, by food grooves and axes, is described by Atkins (1937*b*). The ctenidia may also be modified by reduction or loss of one or both of the demibranchs. Atkins (1937*b*) has summarized existing knowledge; one such instance only is shown in figure 32, namely, that of *Montacuta* (Q) in which the outer filaments of each ctenidium are lost. The greatest reduction is in the specialized Teredinidae and Xylophaginidae where some only of the outer filaments are retained (Purchon 1939, 1941). The great elaboration of cilia, principal filaments, etc., in the ctenidia of the higher Lamellibranchia cannot here be discussed, but full details are contained in the papers quoted above, in particular those of Atkins and of Nelson.

Finally, in the Septibranchia the ctenidia have been practically replaced by a muscular septum, as in *Poromya* and *Cuspidaria* (R), which is perforated by a few pairs of ciliated pores (Pelseneer 1888*a*; Grobben 1892; Yonge 1928). In the absence of embryological data the exact mode of origin of the septum remains obscure, but there can be little doubt that it represents a modification and fusion of the ctenidia of the two sides. In *Poromya* the pores consist of two pairs of branchial sieves of obvious ctenidial origin and possessing lateral cilia (Yonge 1928); in *Cuspidaria*, where the septum is much thicker, the four or five pairs of pores are slit-like with dorsally directed valves edged with cilia in two regions and surrounded by a sphincter of plain muscle. Striated fibres compose the mass of the septal musculature in *Cuspidaria* but not in *Poromya*. A pumping organ has thus been evolved from the ctenidia for the second time in the Lamellibranchia, but in the Septibranchia the intake of water is powerful enough to draw into the mantle cavity small animals (probably dead or moribund) which are then pushed into the mouth by the reduced, muscular palps, the gut being appropriately modified (Yonge 1928). This remarkable culmination in the evolution of the lamellibranch ctenidium probably proceeded by way of the Anatinacea in which the ctenidia tend towards increasing muscularity.

F. *Cephalopoda*

In this class the mantle cavity is elongated dorso-ventrally and contains two pairs of ctenidia (Tetrabranchia, figure 32S) or one pair (Dibranchia, figure 32T). In *Nautilus* (Tetrabranchia) these are attached at the base only, but in the Dibranchia also along the afferent side of the axis (as in *Sepia*, figures 35, 36, *am*). A branchial gland (figures 36, 37, *bg*) extends along the afferent side of the axis in all Cephalopoda. The filaments are alternately arranged on either side of the axis and are unciliated (Joubin 1885), although Brooks (1880) found cilia on the gill primordia in *Loligo*. The respiratory surface of the filaments is greatly increased by lateral followed by secondary foldings, Joubin (1890) describing the following stages in complexity: (*a*) young *Sepia* with unfolded filaments; (*b*) older *Sepia* with primary lateral folds appearing; (*c*) *Nautilus* with secondary folds; (*d*) Decapoda with secondary folds further developed; (*e*) *Eledone* with secondary folding carried to the greatest complexity. With the exception of *Nautilus* (Willey 1902), blood flows through capillaries within the filaments, the branchial hearts found in all Dibranchia providing the necessary additional propulsion.

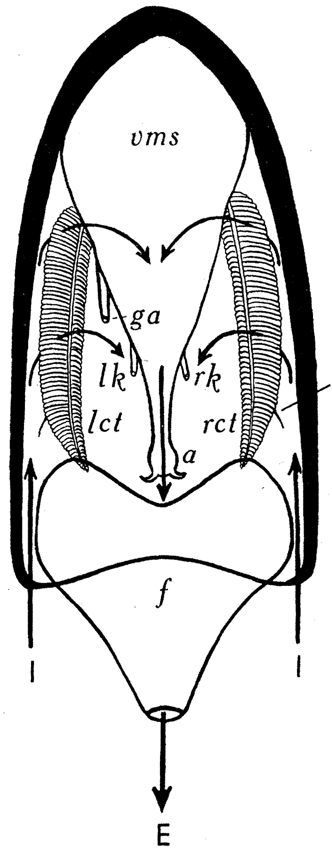

FIGURE 35. *Sepia officinalis*, mantle cavity, topographically under (morphologically posterior) surface, showing disposition of organs and course of respiratory currents. $\times \frac{1}{2}$. *ga*, genital aperture. Other lettering as before.

The respiratory current is created by muscular contraction; by pulsations of the funnel in *Nautilus* (Willey 1896, 1902), and by contractions of the circular muscles of the mantle and longitudinal muscles of the funnel and head in the Dibranchia. It is these movements, concerned primarily with respiration, that have made possible the characteristic swimming mechanism of these animals, water being expelled with great force through the funnel, the animal moving in the opposite direction to that in which this mobile organ is pointed. In *Loligo*, a typical squid in which these movements are best developed, the elaborate mechanism of nervous control has been beautifully demonstrated by Young (1936, 1938, 1939). Impulses are set up in either one of a structurally associated pair of giant nerve cells in the central nervous system, and from them conveyed to seven pairs of second-order giant neurons in the pallio-visceral ganglion. These control the muscles concerned with water movement, running direct to the retractor muscles of the funnel and head and, by way of the stellate ganglia, where they make synapse with third-order giant fibres, to the pallial muscles. An interesting parallel to this type of movement produced by extrusion of water from the mantle cavity occurs in certain lamellibranchs, e.g. *Pecten* and *Lima*, but here the adaptations for swimming are further developments of those originally acquired for the efficient cleansing of the mantle cavity (Yonge 1936).

In *Nautilus* water enters and leaves the mantle cavity by way of the funnel, and the exact course of the water currents within is not clear. In the Dibranchia it enters between the funnel and the mantle edge (figure 35, *I*) and leaves by the funnel (*E*). The direction of the currents within is difficult to determine because opening the cavity destroys the mechanism of current production. Supporting rods (figure 37, sr_2), originally described in *Sepia* by Burne (1899) and in *Nautilus* by Willey, occur but on the *afferent* side, where they arise within a membrane which extends from the afferent surface of the filaments to the afferent membrane (figures 36, 37, *at*). This important distinction between the gastropod and the cephalopod filament is shown diagrammatically in figure 37. Willey was mistaken when he homologized the rods in *Nautilus* with those in aspidobranchs such as *Haliotis*.

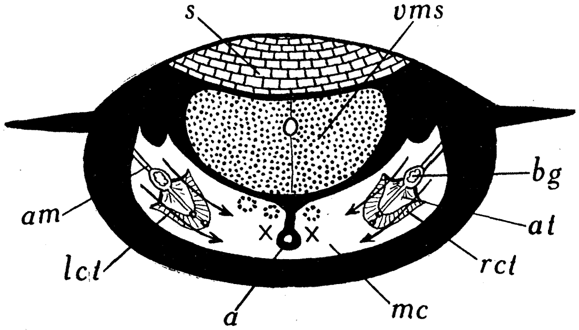

FIGURE 36. *Sepia officinalis*, diagrammatic cross section through mantle cavity. Genital and renal ducts dotted. *at*, membrane connecting afferent surface of filament with afferent membrane; *bg*, branchial gland. Other lettering as before. Modified after Tompsett (1939).

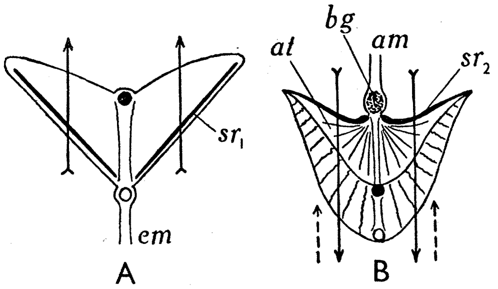

FIGURE 37. Comparison between A, unmodified aspidobranch ctenidial filaments of Gastropoda and B, ctenidial filaments of *Sepia*. sr_1, skeletal rod within efferent surface of gastropod filament; sr_2, skeletal rod along free border of supporting membrane on afferent side in cephalopod filament. Afferent blood vessels shown black, arrows indicate direction of respiratory current, broken arrows possible back-flow in *Sepia*. Other lettering as before.

At first sight it would appear that these filaments are fitted to withstand pressure of water from the afferent to the efferent side, and probably there is an initial flow of water between them in this direction as indicated by the arrows in figures 35–37. But it is by no means impossible that when the pallial muscles contract in the Dibranchia some water may not be forced through the ctenidia again in the reverse direction (i.e. in the same direction as in the Gastropoda) before being expelled through the funnel. The arrangement of the supporting rods, acting as ties between the margin of the filaments and the afferent membrane, may well enable the filaments to withstand pressure in this direction also. Such back-flow would presumably be only local, otherwise faeces and excrement, now passed into the mantle cavity on the *efferent* side of the ctenidia (cf. figure 38, A, C), would foul the filaments. The movements of water between the much-folded filaments are probably very complex.

The possible mode of evolution of the mantle cavity in the Cephalopoda, suggested by functional considerations, is indicated in figure 38A to C. The primitive condition, with the ctenidia attached by a long efferent membrane (A, *em*) and to a limited extent by an afferent membrane (*am*) and with the urinogenital openings and anus dorsal to them, is shown in A; the course of the respiratory current produced by lateral cilia being indicated by arrows. Hypobranchial glands (*hb*) and osphradia (*o*) probably occurred. In the hypothetical intermediate condition (B) the mantle cavity had elongated to some extent dorsally, the ctenidia at the same time migrating in that direction so that they came to lie on either side of the anus (as they do in *Nautilus*). The efferent attachment was reduced to the length of the afferent one so that the ctenidia (again as in *Nautilus*) were largely free. The foot (*f*) had formed the bilobed flap which presumably preceded the formation of an unfused funnel still retained in *Nautilus*. It is impossible to decide whether cilia were retained at this stage and the course of the respiratory current as in A, or whether the current was produced by muscular contraction and its initial course as in C. Hence the course of the respiratory currents is left undetermined in the diagram (see broken arrows). But at some such stage the change over must have occurred. Osphradia (*o*) were probably present but not hypobranchial glands. In the typical dibranchiate condition (C) the mantle cavity has become fully extended dorso-ventrally, the ctenidia have moved past the anus and other openings and become attached exclusively along the afferent side of the axis (C, *am*). With loss of the shell the mantle walls became muscular and the pedal flaps fused to form the funnel (*f*).* Owing to the reversal in direction of the respiratory

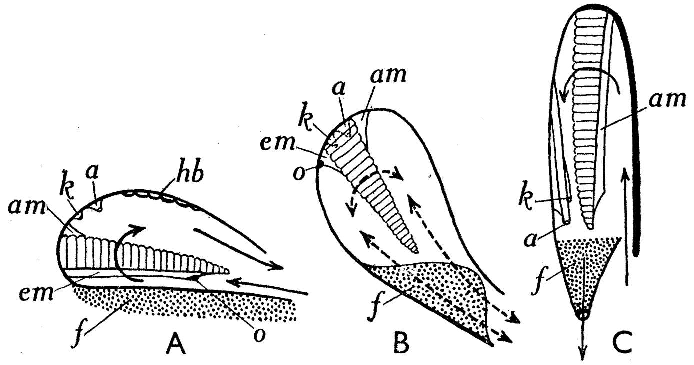

FIGURE 38. Diagrams illustrating postulated mode of evolution of cephalopod mantle cavity. A, primitive mollusc with posterior mantle cavity; B, postulated intermediate condition, broken arrows indicate alternative directions of respiratory current at this stage (i.e. as in A if produced by cilia; as in C if produced by muscular movements of pedal flaps); C, cephalopod mantle cavity. *hb*, hypobranchial gland. Other lettering as before.

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* The reduction of the opening into the mantle cavity in this way prevents the extrusion of a penis; hence the transference of sperm conveyance to the tentacles leading to the phenomenon of hectocotylization.

(now also locomotory) current following the substitution of muscular for ciliary mechanisms, the anus, renal and reproductive openings, although they now lie morphologically ventral to the ctenidia, are again in the *exhalant* chamber. By the acquisition of skeletal rods in the attaching membrane on the afferent side of the filaments these are able to withstand the powerful current which passes between them, possibly in both directions, when the mantle muscles relax and contract. With the assumption of a passive, benthic life by the Octopoda and the eventual change in some to swimming by means of the webbed arms, the opening into the mantle cavity is reduced and so are the ctenidia which become mere vestiges in the Vitreledonellidae where respiration must be carried on through the general surface of the body (Robson 1932).

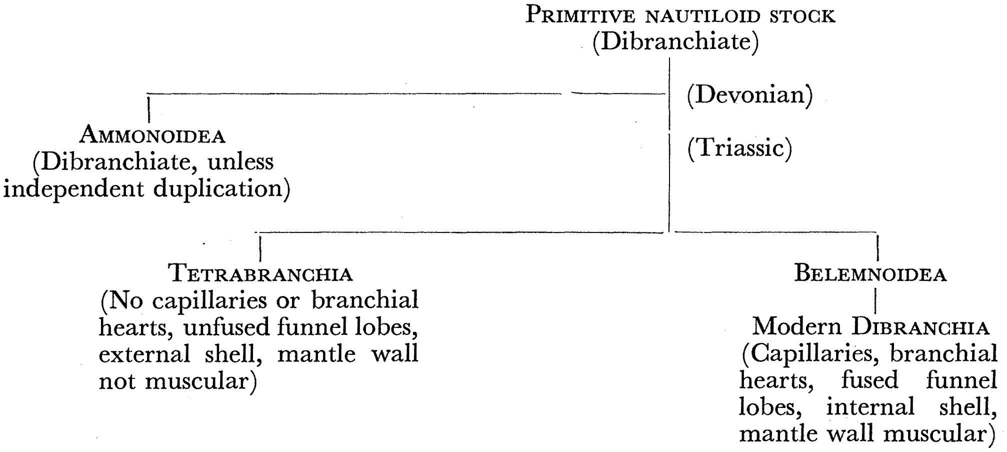
It is *not* suggested that the tetrabranchiate necessarily preceded the dibranchiate condition, i.e. that conditions in the mantle cavity of *Nautilus* approximate to those in the ancestors of the modern Dibranchia. The arguments against Naef's belief in a primitive tetrabranchiate condition in the Mollusca have already been stated (p. 480). It is here contended that the Mollusca were primitively dibranchiate, the tetrabranchiate condition, as indicated in figure 32, being secondary. Although the 'Tetrabranchia' are certainly the oldest of existing Cephalopoda, there is no evidence that their earlier representatives had two pairs of ctenidia; that has been assumed from conditions in the modern *Nautilus*. But there is no reason for supposing that primitively correlation existed between a nautiloid shell and two pairs of ctenidia. The early Cephalopoda were probably sluggish animals, and the duplication of the ctenidia in their capacious mantle cavity (i.e. unlike the multiplication of these organs in the restricted mantle cavity of the Loricata (Yonge 1939*a*)) cannot unreasonably be attributed to increased activity involving higher metabolism. While a subsequent reduction to the original single pair of ctenidia may have occurred in the Dibranchia it appears, for reasons given below, more probable that these animals evolved from primitive nautiloids in which the ctenidia were *never* duplicated.

Owing to the comparatively low oxygen-carrying powers of their haemocyanin and its slow rate of oxygenation (Redfield 1934), the increased respiratory needs of the evolving Cephalopoda could have been met by morphological changes which increased *either* the surface *or* the efficiency of the respiratory system, i.e. in the following ways:

(1) By the maintenance of the primitive circulatory system but increase of the respiratory surface by duplication of the unciliated ctenidia (figure 32S), an increased respiratory current being produced by the pulsations of the unfused funnel lobes, i.e. as in *Nautilus*.

(2) By the retention of the one pair of ctenidia (figure 32T) but increased efficiency of these by the acquisition of capillary circulation with accessory, branchial hearts, a more powerful respiratory current being produced by the mantle musculature which developed following the reduction and overgrowth of the shell, i.e. as in the Dibranchia.

The stage at which these two lines of cephalopod evolution could have diverged is about that represented by B in figure 38. This may possibly have been during the Triassic when the belemnites, from which the modern dibranchiate Cephalopoda probably evolved, first appear. If this be true it follows that the ammonites, which split off from the primitive nautiloid stock in the Devonian, need not have possessed two pairs of ctenidia—unless for the same metabolic need* these were duplicated independently. The postulated processes may be represented in the simplest form in the following evolutionary tree:



The second alternative, which permitted the evolution of rapid locomotion and, incidentally, the consequent assumption of pelagic life by the squids, proved the better; and the acquisition of a mantle cavity of this type probably represents a prime factor in the survival and continued success of the modern Dibranchia.

G. *Comparative respiratory surfaces*

Pelseneer (1935) made interesting comparisons between the respiratory surfaces presented by the lateral faces of the ctenidial filaments in a variety of Mollusca. His more important data are given in table 1.

TABLE 1

class	species	respiratory surface in sq.cm./g. body weight
LORICATA	*Chiton pellis serpentis*	8·66
GASTROPODA	*Trochus cinerarius*	8·64
	Patella vulgata (pallial gills)	9·36
	Buccinum undatum	7·936
	Purpura lapillus	7·1
CEPHALOPODA	*Nautilus macromphalus*	9·31

Thus, despite the multiplication of the ctenidia in the Loricata (in *Chiton pellis serpentis* there are fourty-four pairs), their duplication in *Nautilus* and their replacement by pallial gills in *Patella*, the respiratory surface remains approximately constant in relation to body weight. Pelseneer's figures for two lamellibranchs, *Mytilus edulis* and *Cardium echinatum*, are similar, about 8 sq.cm. in each, but here he estimated the superficial area of the ctenidia and not the lateral faces of the filaments. By estimating these in *Mytilus* a corrected figure of 13·50 has been obtained. This is to be expected in view of the great elongation of the filaments for feeding purposes in the Lamellibranchia.

In every instance where the ctenidia have been modified for food collection this involves an increase in the frontal surface, and the consequent elongation of the filaments reduces the lateral area in relation to the frontal length. This is revealed by the figures given in table 2, which has been prepared from data in the present and previous papers.

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* They probably resembled *Nautilus* in mode of life with some of them purely pelagic (see Trueman 1941).

Table 2

class	species	ratio lateral area to frontal length	function of ctenidia
Loricata (Yonge 1939*a*)	*Lepidochitona cinereus*	1:0·29	respiration only
Gastropoda			
Aspidobranchs (this paper)	*Haliotis tuberculata*	1:0·53	,, ,,
	Diodora nubecula	1:0·23	,, ,,
	Emarginula reticulata (both filaments)	1:0·51	,, ,,
	Patelloida tessulata	1:0·11	,, ,,
Pectinibranchs (Yonge 1938)	*Buccinum undatum*	1:0·21	,, ,,
	Capulus ungaricus	1:0·39	feeding and respiration
	Vermetus novae hollandiae	1:0·41	,, ,,
	Crepidula fornicata	1:1	ctenidium highly specialized for feeding
Lamellibranchia			
Protobranchia (Yonge 1939*b*)	*Malletia obtusata*	1:0·36	respiration only
	Nucula hanleyi	1:0·46	assist palps in feeding
	Solenomya togata	1:0·58	feeding and respiration
Filibranchia (this paper)	*Mytilus edulis*	1:35	,, ,,

In certain cases the form of the filament is affected by other factors; thus in *Haliotis* the filaments are elongated owing to the compression of the mantle cavity, while in *Emarginula* they are elongated to provide the additional lateral surface needed for the creation of a particularly powerful upward current. In *Patelloida*, on the other hand, the frontal surface is reduced owing to the elongation of the ctenidium and its oblique disposition in a reduced nuchal cavity. But where such factors do not operate, i.e. in *Lepidochitona*, *Diodora* and *Buccinum*, the ratio is very similar. In the ciliary feeding pectinibranchs the frontal length is increased, especially in the highly specialized *Crepidula*. It should be remembered that in these Gastropoda, unlike the Lamellibranchia, the abfrontal as well as the frontal surface is concerned with food collection. In *Nucula* there is an increase in the frontal surface relative to the lateral area with the taking over by the ctenidia of some responsibility for feeding from the palp proboscides. In *Solenomya* the number of filaments is also greatly increased. In the filibranchs, as exemplified by *Mytilus*, there is a vast increase in the frontal surface, and this is true also of the eulamellibranchs although, owing to the presence of complex interfilamentary junctions, any accurate estimate of the lateral areas on their filaments is impossible.

Valuable confirmatory data are provided by Hazelhoff (1938). He found that whereas in the three gastropods, *Haliotis tuberculata*, *Murex brancaris* and *Tritonium nodiferum*, the percentage of oxygen removed from the respiratory current was respectively 56, 38 and 79, and in *Octopus vulgaris* it was 63, in the three lamellibranchs, *Cardium edule*, *Solen siliqua* and *Pinna nobilis*, only between 5 and 9 % of the oxygen was utilized. Equally high figures were obtained for other non-particulate feeders, and similarly low ones for such fine particle feeders as sponges and ascidians. Hazelhoff considered that the greater metabolic needs of the former, which have to search for their food, was the sole cause of this difference; but, certainly in the case of the Mollusca, it is due primarily to the much greater water current produced by the lamellibranchs owing to the elongation of the ctenidial filaments for feeding purposes. Van Dam (1935, 1938) found very low oxygen utilization in both *Mya arenaria* and *Anodonta* (between 2 and 10%), and rightly attributes this to the increase in the water current for feeding.

VI. Hypobranchial glands

Bernard (1890*a*) described the anatomy and histology of these glands in many Prosobranchia, both aspidobranch and pectinibranch. His chief error was to deny their presence in the Fissurellidae and Neritacea. Later workers have described their histology in more detail, e.g. Bourne (1908, 1911) in the Neritacea, and Crofts (1929) in *Haliotis*. The mucus they secrete consolidates the fine sediment carried in with the respiratory current, and where such a function is unnecessary they are absent, e.g. in the Patellacea and Valvatacea. Graham (1938*a*) has suggested that in ciliary feeders, such as the Calyptraeidae and *Turritella*, their secretion may assist in the consolidation of the food particles. Owing to their intimate functional association with the ctenidia they vary in number with these, although a trace of the right gland persists in the Trochacea, while in the Neritacea the right gland appears to be associated with the left ctenidium. But possibly this is the left gland which, after being nipped off from the mantle cavity, has acquired a secondary opening for functional needs on the right side of the rectum. The gland varies greatly in size and complexity in the pectinibranchs according to the amount of sediment carried into the mantle cavity, being largest in mud or sand-dwellers, e.g. *Buccinum*, and smallest in sedentary forms living on a hard bottom in clear water, e.g. the Vermetidae, Calyptraeidae and in *Capulus** (Yonge 932, 1938; Yonge & Iles 1939). Amongst species of *Littorina* it is smallest in those which live highest on the shore (Pelseneer 1895). In *Caecum glabrum* the gland disappears with the ctenidium (Götze 1938). It is retained in association with the ctenidium in the Tectibranchia, but is absent in the Nudibranchia and Pulmonata where there are no ctenidia; on the other hand, it is retained in the Helicinidae and other terrestrial Neritacea (Bourne 1911).

Apart from the Gastropoda similar glands occur in certain Lamellibranchia. In the Protobranchia, complex hypobranchial glands are present in the Nuculidae and Solenomyidae in which sediment passes dorsally (in *Solenomya* inwards) between the indifferently attached ctenidial filaments (Yonge 1939*b*). They are absent in the Nuculanidae where particles are unable to pass through the fine pores in the septal membranes formed by the ctenidial filaments. In the remaining Lamellibranchia, where closely applied filaments prevent the passage of sediment between them, glands are absent with the exception of the filibranch *Monia* (Atkins 1936). In the Loricata there are neural, pedal, pallial and branchial tracts of mucous glands in the pallial grooves which are concerned with consolidation of sediment (Yonge 1939*a*). All are analogous with the hypobranchial glands, and the pallial tracts may be homologous. In the Scaphopoda, Distaso (1906) has described isolated glands which he believes are homologous with hypobranchial glands, although other authors believe they are absent; they will certainly have little function owing to the powerful exhalant current produced by pedal contractions. Their absence in the Cephalopoda can certainly be attributed to the powerful currents, although possibly the nidamental glands in the female may be homologous, as originally suggested by Haller (1894). In the protobranch, *Nucula delphinodonta*, the secretion from the hypobranchial glands has the secondary function of forming the broad-sac attached to the posterior end of the shell in the female (Drew 1901).

* The statement (Yonge 1938), based on morphological evidence, that hypobranchial glands are absent in *Crepidula* and *Capulus* is incorrect, Graham (1938*a*) has found evidence of them in sections.

VII. Osphradia

The osphradia have been regarded as chemoreceptors concerned with testing the water which enters the mantle cavity (Bernard 1890*a*), or, in carnivorous species, with the detection of food (Copeland 1918; Henschel 1932; Brock 1933). But there is no correlation between the presence, or size, of the osphradia and the need for 'water testing' (Hulbert & Yonge 1937). Osphradia are always present in aquatic Prosobranchia and Tectibranchia and are no larger in shore-living or estuarine species, where salinity varies or the water may be contaminated, than in the great majority of species which live invariably in pure sea water, on the bottom or pelagically. The second view as to its function fails to explain the presence of the osphradium in browsing herbivores, e.g. *Littorina* or *Pterocera* (Yonge 1932), in deposit feeders, e.g. *Aporrhais* (Yonge 1937*a*) and even less in sedentary plankton feeders, e.g. Calyptraeidae, Vermetidae or *Capulus* (Yonge 1938; Yonge & Iles 1939). Yet all have large osphradia. Moreover, there is nothing in the evidence produced by Copeland, Henschel or Brock inconsistent with the view that the chemoreceptive powers they found in *Allectrion*, *Busycon*, *Nassa* and *Buccinum* do not reside in the siphons. Similarly, the epipodial tentacles of the Zeugobranchia, Fissurellidae and Trochacea, the pallial tentacles of the Patellacea, and the cephalic tentacles of all Gastropoda, are probable sites of chemoreceptive powers.

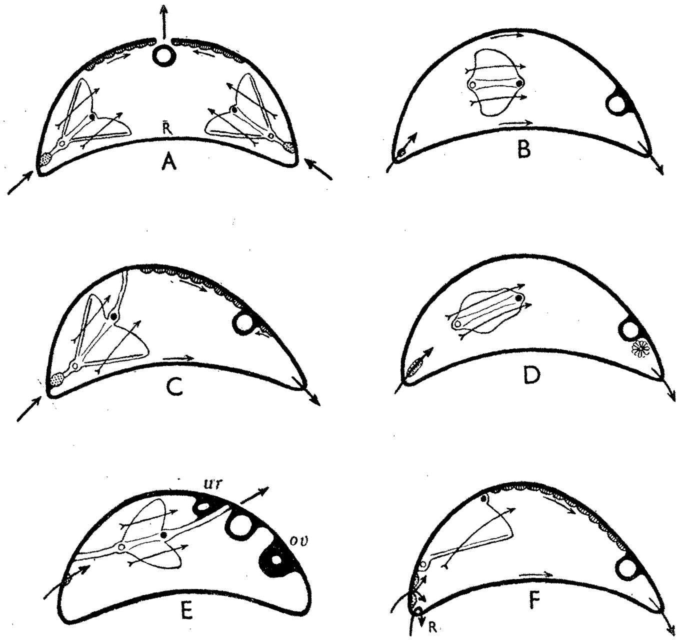

Figure 39. Diagrams illustrating relations between ctenidia, osphradia (stippled) and hypobranchial glands in A, zygobranchous aspidobranch; B, *Patelloida*; C, Trochacea; D, *Theodoxus* (hypobranchial gland opening at base of mantle cavity and to right of rectum); E, Valvatacea (showing anterior extension of *ov*, oviduct; *ur*, ureter); F, pectinibranch. Position of rectum indicated throughout. R, anteriorly directed rejection tracts carrying material out by way of inhalant opening in A and F.

It has been here shown that the osphradium always lies in the direct line of the current or, in zygobranchous species, the currents, produced by the ctenidia (see figure 39A to E). This is also true for pectinibranchs (figure 39F). Hence all suspended matter carried in with the respiratory current will impinge upon it, as seen in the intact animal in *Oxygyrus* (Yonge 1942). Additional evidence strengthened the previous view (Hulbert & Yonge 1937) that the osphradium is a tactile organ concerned with estimating the amount of sediment carried into the mantle cavity. There can be no doubt as to the importance of such a mechanism in animals which produce a respiratory current by ciliary means, while the universal presence of the osphradium, irrespective of habitat or food, in aquatic Gastropoda possessing a mantle cavity is thus explained by the equally universal danger from blocking or fouling of the mantle cavity with sediment.

Unlike the hypobranchial glands the osphradia may persist after the ctenidia have been lost. This is so in the Patellidae, although here they are reduced owing to the lessened importance of the nuchal cavity, but a similar function is probably served by the subpallial sensory streaks. The retention of the right osphradium in the Patellacea but not in the Neritacea or Valvatacea may well be due to the passage in the former of material over the floor of the nuchal cavity and thence posteriorly into the pallial groove on the right and not immediately to the exterior. In *Caecum*, where both ctenidium and hypobranchial gland are absent, but where a powerful respiratory current is created by the mantle ciliation, a large osphradium is present (Götze 1938).

There is some correlation between the size of the osphradium and the degree of sedimentation to which the animal is exposed. It is broad and bipectinate in siphonate Rachiglossa, e.g. *Buccinum*, *Fusus*, *Nassa* and *Murex*, which live on soft substrata and also in the Toxiglossa, e.g. *Conus*; it is linear in the non-siphonate Taenioglossa which are typically browsers, e.g. *Littorina*, and also in the pelagic Heteropoda. In the aspidobranchs which, except for *Valvata*, are confined to a hard bottom the osphradia are narrower than in the Taenioglossa, consisting of a single ridge, or papilla, instead of a multiple ridge. In *Valvata* the reduction in the respiratory function of the mantle cavity due to the forward displacement of the ctenidium is accompanied by a reduction in the osphradium. Among the Tectibranchia the osphradium is also reduced but probably in correlation with the reduction in size and exposure of the mantle cavity and with the rejection of sediment by cilia on the edge of grooves leading into the cavity. With the return to aquatic life in the Basommatophora (Pulmonata) the osphradium reappears (this does not involve the validity of Dollo's 'law' because even in terrestrial Pulmonata it is present during development).* It is, therefore, absent only in adult terrestrial Gastropoda and in the Nudibranchia.

In the Loricata there are sensory streaks in the pallial grooves which are analogous to those in the Patellidae, which these animals resemble so closely in habits, and possibly to the osphradia with which they may be homologous (Yonge 1939*a*). In the Cephalopoda osphradia are absent in the Dibranchia but present in *Nautilus* (Willey 1897, 1902). If they are tactile organs this is understandable because sediment is much more likely to accumulate in the mantle cavity of the bottom-living *Nautilus* with a relatively feeble respiratory current produced by the pulsations of the funnel than in the Dibranchia where water is violently expelled. In any case *Nautilus* has no more apparent need to 'test' the water than the Dibranchia and has other receptors more suited for detecting its food.

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* The ctenidia, on the other hand, having been lost by the terrestrial ancestors of the modern aquatic Basommatophora, were replaced by secondary gills (e.g. in *Siphonaria*) when these animals resumed aquatic respiration (Pelseneer 1895).

In the Scaphopoda, where water is also expelled violently (Yonge 1937*b*), Distaso (1906) alone states that osphradia occur. In the Lamellibranchia, where the ctenidia are free ventrally, small sensory patches histologically resembling osphradia normally occur on the under surface of the posterior adductor muscle, i.e. in the *exhalant* chamber. In *Pecten* and *Glycimeris* (Setna 1930) each extends as a ridge along the axis of the posterior extremities of the ctenidia. Their function is obscure. Dakin (1910) showed that it was not food detection, Monk (1928) rightly denies that it can be concerned with testing the respiratory current because water has to pass through the ctenidia before reaching these organs. The inhalant opening is fringed with sensory tentacles which could serve this function. For the same reason they could only estimate the small amount of material which passes between the filaments, although their greater extent in *Pecten* and *Glycimeris*, where more material will penetrate than through the closer knit eulamellibranch gill, suggests that such might be their function. The function of the somewhat similar and richly ciliated abdominal sense organs near the osphradia is also obscure. Elsey (1935), who found an organ of this type in the Ostreadae, suggests that it may be concerned with regulation of water flow brought about by the interaction of blood pressure, elastic skeletal bars and inter-filamentary muscles. This may be the explanation of the function of one or other of these sense organs.

Histologically the osphradia consist of raised patches of epithelium overlying the osphradial ganglion or nerve and containing sensory, mucous, and ciliated components. In Tectibranchia and Eulamellibranchia only sensory fibres from underlying ganglion cells penetrate the epithelium (Stork 1934). Dakin (1909, 1910) found similar conditions in *Pecten*, but Setna (1930) states that neuro-epithelial cells occur, as they certainly do in the Prosobranchia. These were first described by Bernard (1890*a*); Dakin (1912) denied their presence in *Buccinum*, but examinations of sections of the osphradium in this and the allied species *Neptunea antiqua* has confirmed Bernard's statements.

In all aspidobranchs the osphradium is not subdivided into specific areas and the epithelium contains mingled sensory, mucous and ciliated cells as in *Emarginula* (figure 42, plate 18) and *Theodoxus* (figure 48, plate 18). In the pectinibranchs it may be linear or bipectinate. In the former (e.g. *Littorina*) it is usually subdivided longitudinally into a major median ridge overlying the nerve with subsidiary minor ridges on each side. Cells of all three types occur, but mucous cells are sparse. Laterally the epithelium of the mantle cavity is thrown into ridges which contain numerous mucous cells. Material is carried by the cilia posteriorly along the main ridge and deflected to right and left by the action of the cilia on the subsidiary ridges. It is consolidated by mucus. Material which passes to the left is carried over the ctenidium; heavier particles pass to the right and are carried over the floor of the mantle cavity (figure 39F). In the species with bipectinate osphradia analysis of the structure of this in relation to the ciliary currents is instructive. *Neptunea antiqua*, the largest available species at Millport, was studied. In a specimen of shell length 12·5 cm., the osphradium when contracted was 1·7 cm. long and 0·4 cm. broad in the middle. There were some 130 filaments on the side nearest the ctenidium and some twenty less (owing to the curvature) on the other. The filaments on the former side were also appreciably longer (figure 40). As shown by Dakin (1912) for *Buccinum*, the epithelium of the filaments consist of three zones. The greater part of the lateral surface (*sz*) and also the exposed free edge is pigmented and contains sensory cells which are most numerous along the free edge. Branches of the osphradial nerve (*on*) extend between the epithelia of the two sides. The greater part of the epithelium consists of pigmented supporting cells; but, in addition to neuro-epithelial cells, there are scattered mucous and ciliated cells. Beneath and lateral to this zone is a narrow zone composed exclusively of ciliated cells (*cz*) and, beyond this again, a third zone of densely congregated mucous cells (*mz*). These are continued on the surface of the epithelium on either side.

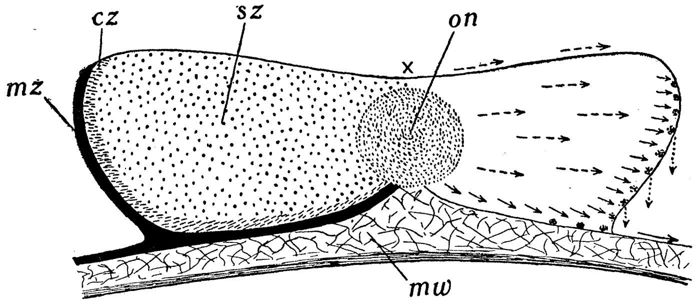

FIGURE 40. *Neptunea antiqua*, lateral view of pair of osphradial filaments with mantle and osphradial nerve. × 16. Left filament (ctenidial side) with epithelial zones shown semi-diagrammatically; right filament showing ciliary currents. *cz*, zone of ciliated cells; *mw*, mantle wall; *mz*, zone of mucous cells; *on*, osphradial nerve; *sz*, zone of pigmented cell containing neuro-epithelial cells. Broken arrows indicate slow currents, unbroken arrows rapid currents, dotted arrows sediment falling on to surface of mantle.

In life material is slowly passed laterally over the surface of the pigmented zone (see arrows in figure 40) owing to the sparse ciliation. But in the ciliated zone it moves rapidly on to the mucous zone where it is consolidated into masses which fall off on to the surface of the epithelium on either side. This slow passage of material over the sensory zone would permit the performance of its suggested tactile functions after which the sediment is quickly moved. The amount of surface provided by an osphradium of this type is very great. In the animal mentioned above the superficial area of the osphradium was 34 sq.mm., but the total area provided by this and the lateral faces of the 240 filaments amounted to about 514 sq.mm., i.e. some fifteen times greater. So extensive a surface is essential if the function of the osphradium is tactile but is much more difficult to explain if this organ is regarded as a chemoreceptor. Experimental work with modern technique on the osphradium is overdue, but, although planned, has been impossible under present conditions.

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Explanation of Plate 18

Key to lettering on Plate: *cf*, ciliated furrow; *ct*, ctenidium; *dm*, dorsal (i.e. afferent) ctenidial membrane; *hb*, hypobranchial gland; *mc*, mantle cavity; *mg*, mucous glands; *oe*, osphradial epithelium; *og*, osphradial ganglion; *on*, osphradial nerve; *ov*, oviduct; *pg*, pedal glands; *r*, rectum; *tu*, tubercle; *ur*, ureter; *vm*, ventral (i.e. efferent) ctenidial membrane.

Figure 41. *Diodora nubecula*, transverse section through mantle cavity showing opening of hypobranchial gland at base of ctenidium. × 110.

Figure 42. *Emarginula reticulata*, transverse section through ctenidium showing osphradium running along efferent margin of axis. × 215.

Figure 43. *Patelloida tessulata*, transverse section through posterior region of mantle cavity showing left tubercle. × 215.

Figure 44. *Patella vulgata*, transverse section through side of foot of animal about 2 mm. long showing restricted peripheral glandular region which disappears later. × 110.

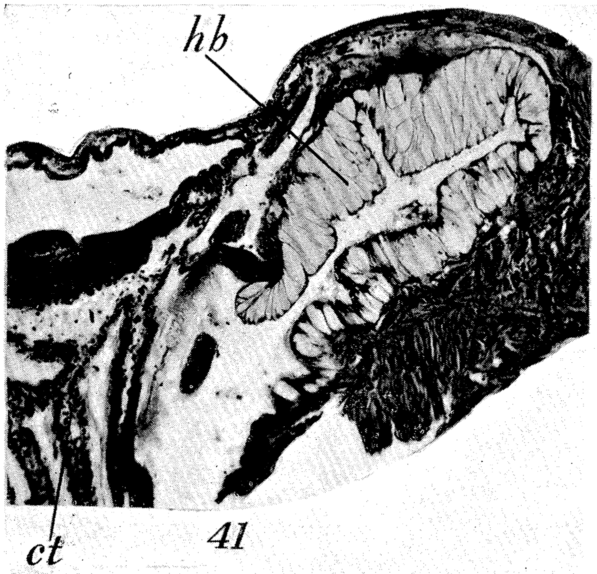
Figure 45. *Patina pellucida*, transverse section through middle of foot showing mucous cells of peripheral glandular region of the one side and also lateral opening of this (partly obscured by secreted mucus). × 110.

Figure 46. *Patelloida tessulata*, transverse section immediately anterior to figure 43 showing left osphradium. × 215.

Figure 47. *Patella vulgata*, transverse section through side of anterior half of foot showing the subpallial sensory streak. × 250.

Figure 48. *Theodoxus fluviatilis*, transverse section through elongated osphradium. × 215.

Figure 49. *Valvata piscinalis*, transverse section through anterior (respiratory) half of mantle cavity showing disposition of ctenidium and anterior prolongation of ureter and oviduct. × 60.



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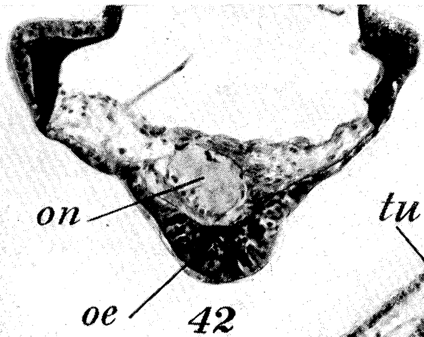

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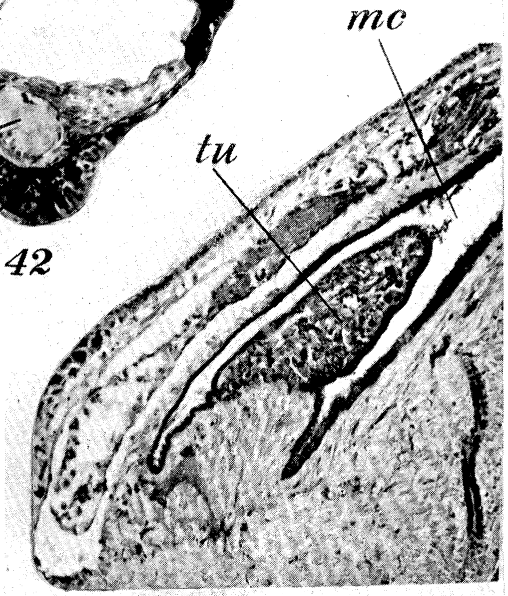

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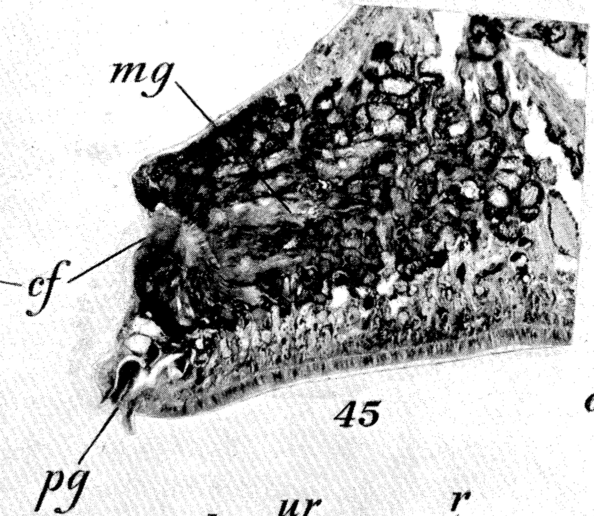

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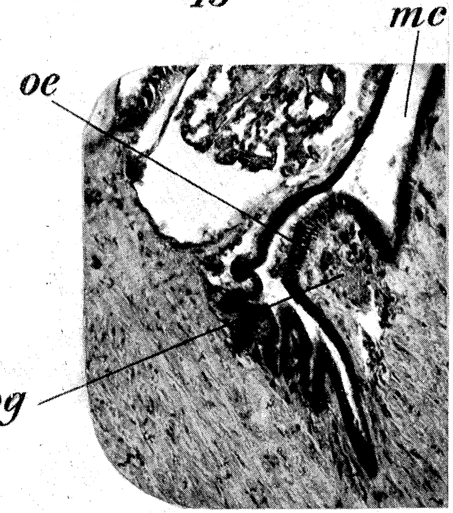

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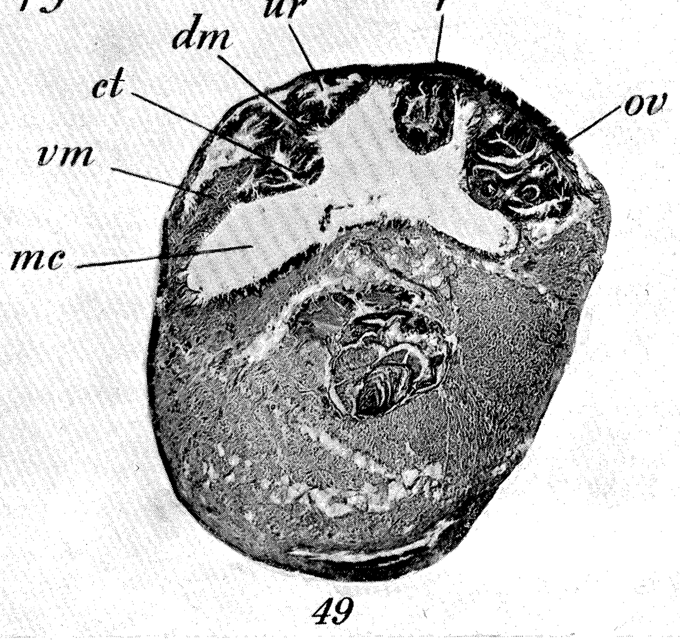

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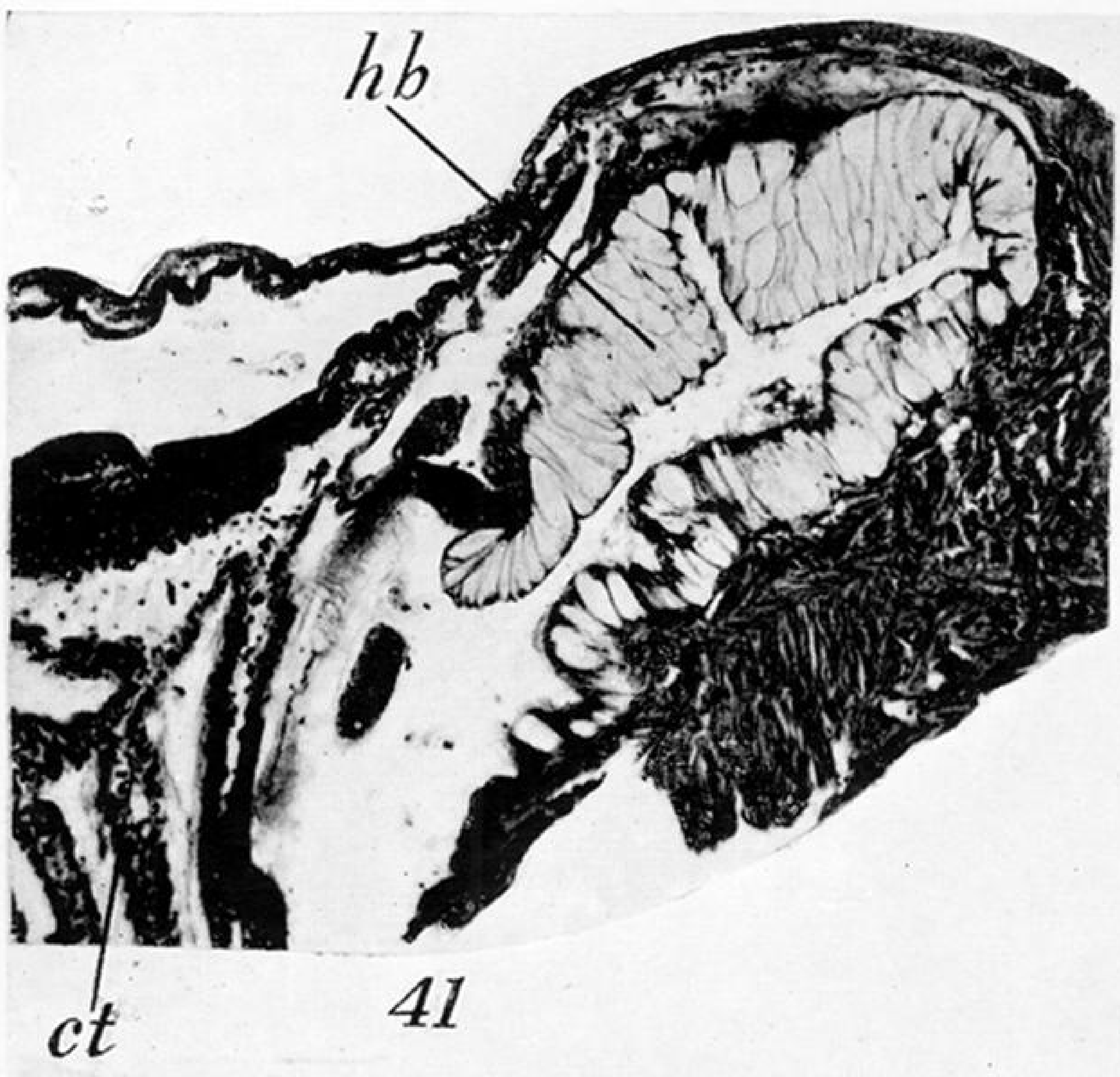

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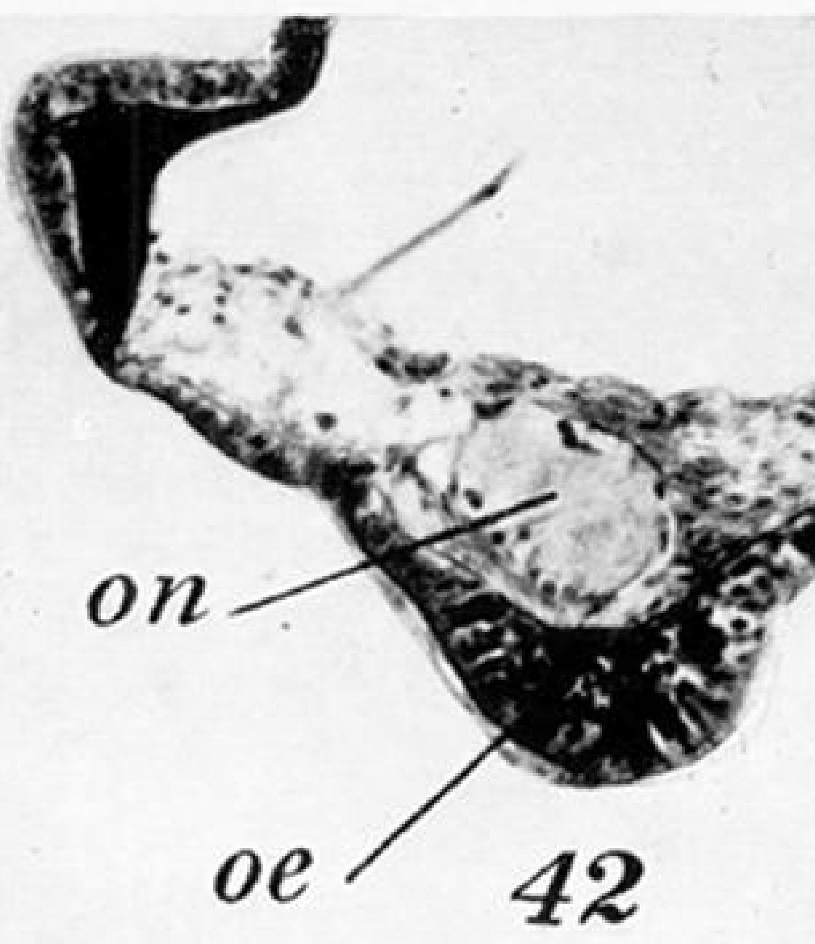

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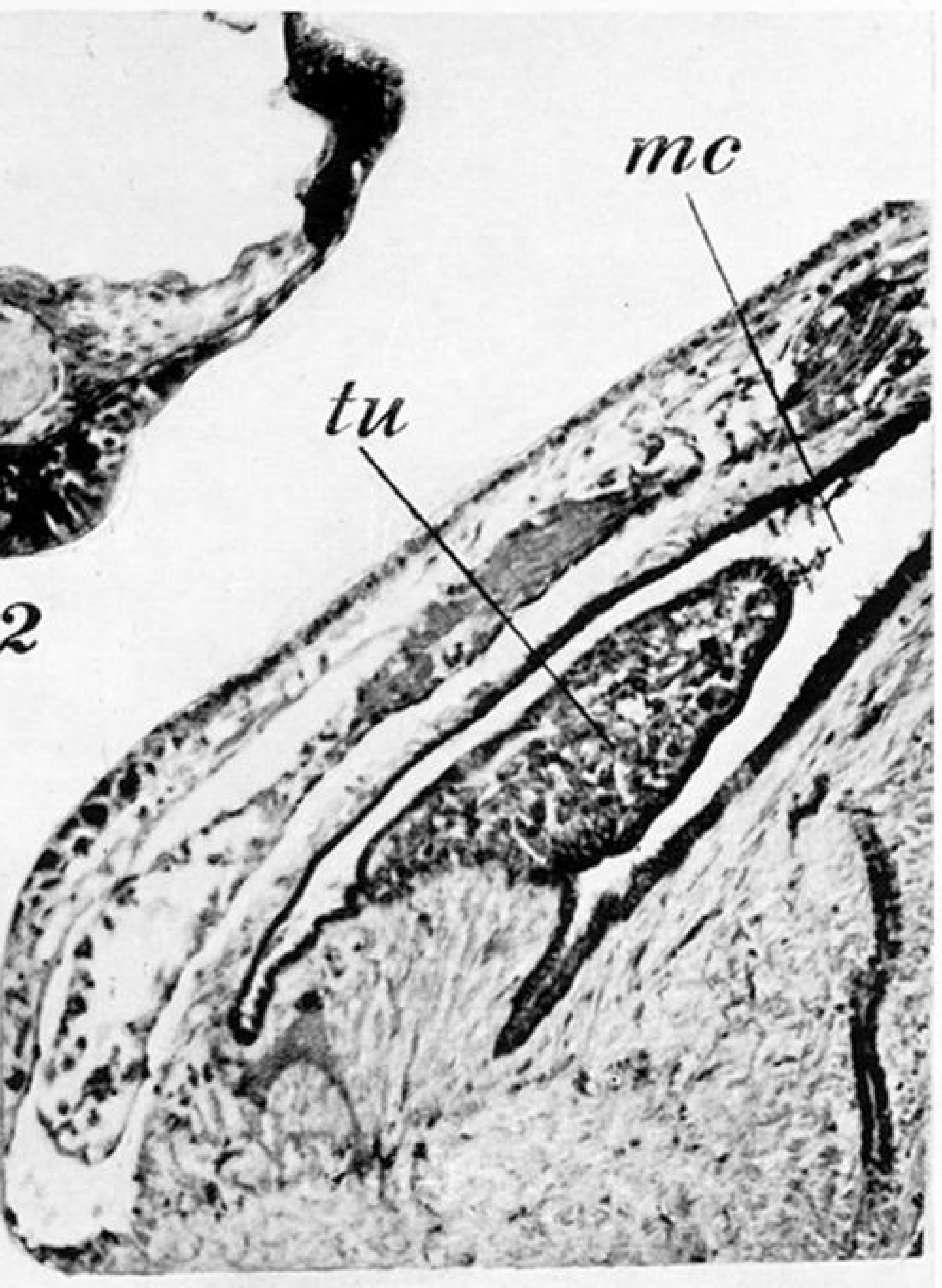

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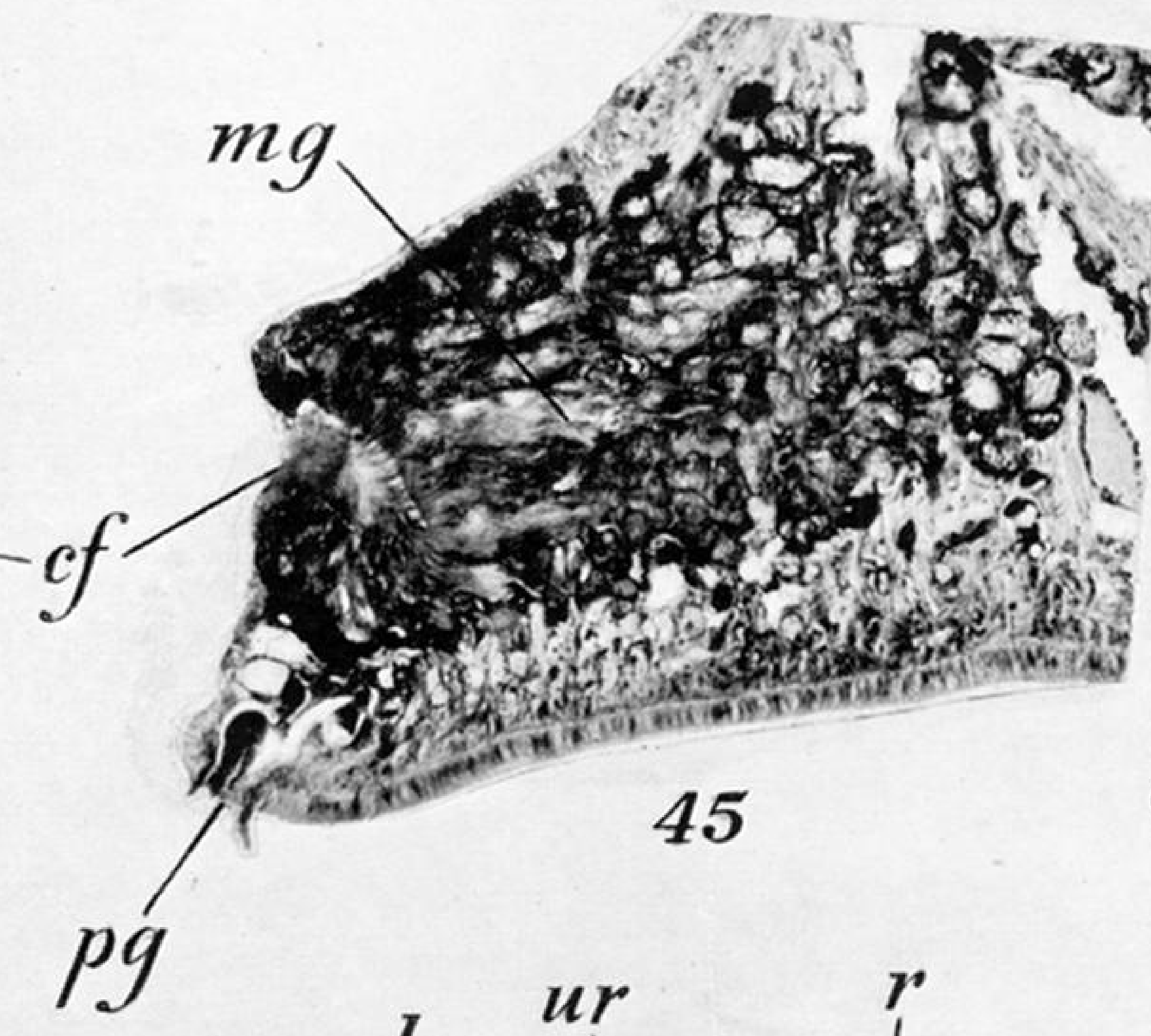

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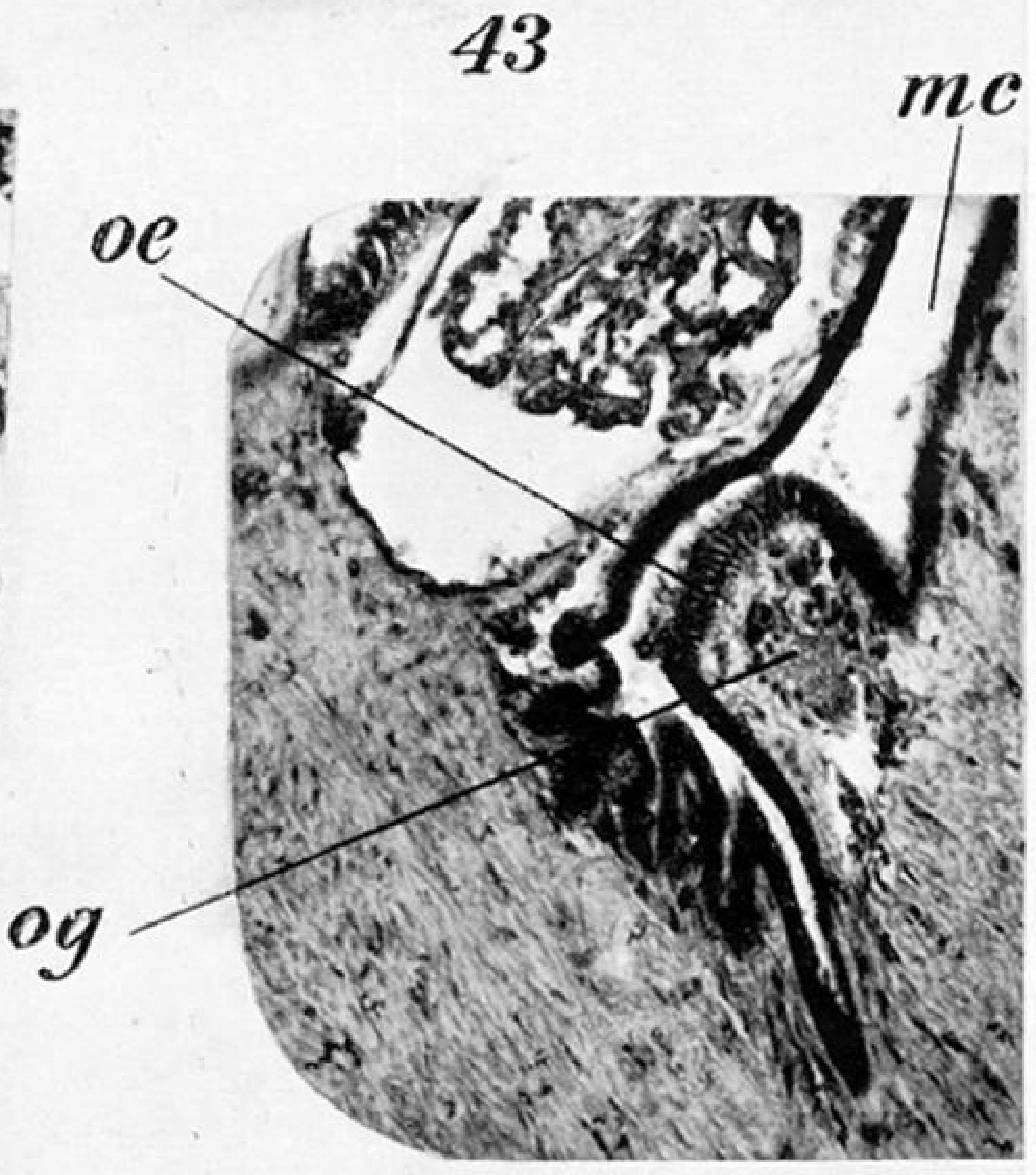

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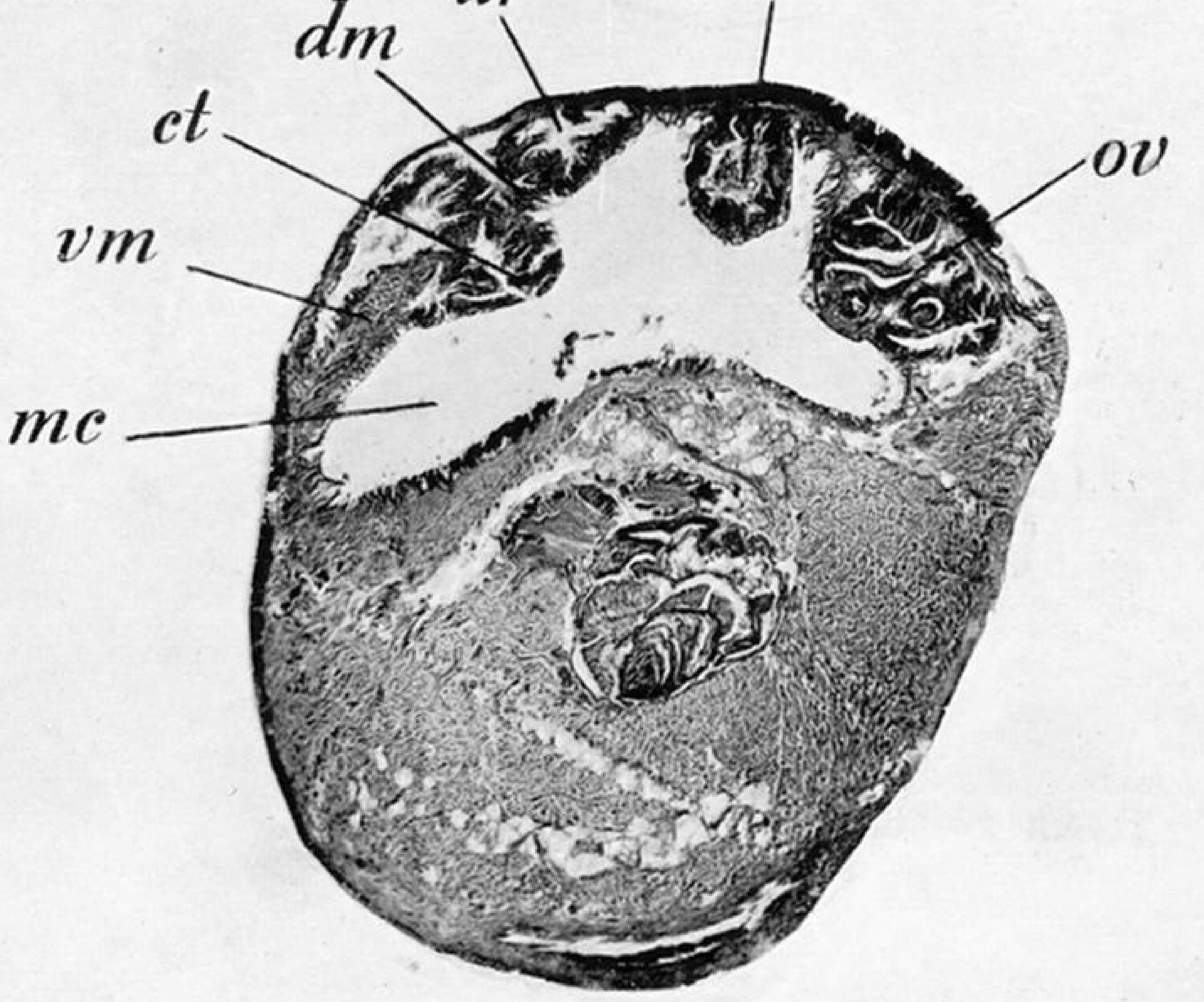

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Explanation of Plate 18

Key to lettering on Plate: *cf*, ciliated furrow; *ct*, ctenidium; *dm*, dorsal (i.e. afferent) ctenidial membrane; *hb*, hypobranchial gland; *mc*, mantle cavity; *mg*, mucous glands; *oe*, osphradial epithelium; *og*, osphradial ganglion; *on*, osphradial nerve; *ov*, oviduct; *pg*, pedal glands; *r*, rectum; *tu*, tubercle; *ur*, ureter; *vm*, ventral (i.e. efferent) ctenidial membrane.

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