# THE PROTOBRANCHIATE MOLLUSCA; A FUNCTIONAL INTERPRETATION OF THEIR STRUCTURE AND EVOLUTION

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[Plate 15]

CONTENTS

## 1. Introduction

Examination of the structure of species of *Nucula*, *Leda*, *Yoldia* and *Solenomya* led Pelseneer (1891), in his classic work on the morphology of the Lamellibranchia, to establish for their inclusion the order Protobranchia. He regarded them as in almost all respects a primitive group, and Stempell (1898*a*, 1898*b*, 1899) came to very similar conclusions. Later (1898, 1911) Pelseneer extended his work on these animals, grouping all recent species in the three families Solenomyidae, Nuculidae and Ledidae (= Nuculanidae). On the other hand, Neumayr (1891), on the basis of the hinge characters, grouped all but the first of these families with the Arcidae, Glycymeridae and Limopsidae in the order Taxodonta. Thiele (1934) elaborated this classification, dividing the Taxodonta into two divisions, Nuculacea and Arcacea, and subdividing the former into the four families Nuculidae, Malletiidae, Ledidae (= Nuculanidae) and Solenomyidae. Finally, Douvillé (1912), in his illuminating sketch of a possible classification of the Lamellibranchia, regarded the Nuculidae and the Nuculanidae as affording some indication of the original characters of those Lamellibranchia which took to a more or less active life on the sea bottom, and the Solenomyidae as representing to some extent ancestral conditions to those which assumed life in burrows. Douvillé's views have been well summarized by Davies (1933, 1935).* Verrill and Bush (1897, 1898) have given the best account of the shell characters of the Protobranchia, while knowledge of many aspects of their morphology has recently been extended by Heath (1937).

Two questions of considerable importance remain to be decided. First, whether the Protobranchia, as defined by Pelseneer, are to be regarded, in view of their many unique morphological characters, as an order of the Lamellibranchia, or whether these differences are outweighed by the taxodont shell they possess in common with the Arcacea. Second, to what extent the Protobranchia are truly primitive and to what extent they have evolved along lines different from, though possibly to some degree parallel with, the other Lamellibranchia.

The answers to these questions can only be obtained as a result of a more detailed investigation than any hitherto attempted into the habits and mode of functioning of these animals. Only by the simultaneous study of form and function of species of all families of the Protobranchia can it be determined which structures are truly primitive and which modifications for a particular mode of life. The interrelationships between the different families, at present obscure, may also be elucidated. With the notable exception of *Yoldia limatula*, which has been studied in detail by Drew (1899, 1900) and Kellogg (1892, 1915), there exist only imperfect accounts of the habits and mode of life of the commoner species of *Nucula*, *Nuculana* and *Solenomya*. No species of *Malletia*, *Lembulus* or *Yoldiella* has ever been studied in life. Moreover, previous work has been limited in scope to some particular species and has not been concerned with the Protobranchia as a whole.

It was to remedy this omission that the present work was undertaken. *Malletia obtusata*, *Nuculana* [= *Leda*] *minuta* and *Yoldiella* (*Portlandia*) *lucida* were examined at the Bergens Museum Biologiska Stasjon, Herdla, during the summer of 1936, *Nucula hanleyi* (= *radiata*), *N. nucleus* and *N. turgida* at the Marine Biological Laboratory, Plymouth, during the summers of 1937 and 1938, and *Solenomya togata* with *Lembulus* [= *Leda*]† *pella* at the Stazione Zoologica, Naples, in April 1938. Particular attention was paid to the habits of the animals, the circulation of water through the mantle

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* Iredale (1939), in an important communication published since this paper went to the Press, has given a good résumé of the history of Lamellibranch classification.

† See footnote on p. 87.

cavity and the removal of sediment, the nature and physiology of the ctenidia and palps, i.e. the mechanisms of respiration and feeding, and finally the structure and physiology of the alimentary canal. Previous work on the Lamellibranchia (Yonge 1923, 1926*a*, 1926*b*, 1928, 1936*a*, 1936*b*) has convinced the author that it is an adequate knowledge of these aspects of their biology which provides the key to the interpretation of structure in members of this class. Other details of structure will be considered in the discussion at the end of this paper.

It is a pleasure to record thanks to Professor Dr A. Brinkmann, Professor Dr R. Dohrn and Dr S. Kemp, F.R.S., Directors of the Laboratories at Herdla, Naples and Plymouth respectively, for their kindness and help. Acknowledgements are also due to Amanuensis D. Rustad of the Bergens Museum Biologiska Stasjon, to Mr A. Graham, M.A., B.Sc., for information about then unpublished work on the Gastropoda, to Mr R. Winckworth, M.A., for assistance in matters of nomenclature, to Mr H. F. Steedman for taking microphotographs and for cutting sections, and finally to the Colston Research Society of the University of Bristol for financial assistance which made possible the visits to Bergen and to Naples.

## 2. Form and habits

For reasons which will become apparent in the course of this paper, the species examined will be regarded as belonging to the three families, Nuculidae, Solenomyidae and Nuculanidae (i.e. regarding *Malletia* as a genus of the Nuculanidae and disregarding Thiele's family Malletiidae), and they will in most cases be dealt with in this order.

### (*a*) *Nuculidae*

The anatomy of species of the genus *Nucula* is better known than that of any other genus of Protobranchia owing to the work of Pelseneer (1891, 1898, 1911), Stempell (1898*a*) and Heath (1937). Drew (1901) has described the embryology of *N. delphinodonta*, while Schenck (1934) has reviewed the classification of the Nuculidae and given detailed accounts of the shell characters. But there is no full account of the mode of life of any species of *Nucula*. Drew (1900, 1901) described the burrowing action of the foot, erroneously described by Forbes and Hanley (1853), Pelseneer (1891) and Verrill and Bush (1897, 1898) as a creeping organ, and states that *N. delphinodonta* moves about slowly under mud, never coming to the surface for any length of time. Hirasaka (1927), in his account of feeding in *N. nucleus*, also notes that the foot is a burrowing organ.

Three species of *Nucula* were examined at Plymouth, *N. hanleyi*, *N. nucleus* and *N. turgida* (the terminology is taken from Winckworth 1932). Of these the first and largest occurs on shell gravel, the second on a bottom of thick muddy sand mixed with gravel, and the last and smallest on fine muddy sand or silt. Owing to its large size *N. hanleyi* was examined in most detail for structure and currents in the mantle cavity—the three species not differing significantly in these respects. The habits of *N. nucleus* were studied, an adequate supply of bottom material being available. When placed on this the animal quickly extruded the foot which first appears ventrally, then extends outwards and forwards as shown in fig. 1. At the same time the two halves of the sole open out widely and are finally withdrawn between the anterior margins of the shell valves, when they come together again. Usually after a few ineffective attempts the foot succeeds in extending under the mud. This is gripped by the two halves of the sole when these open out and the animal is able to erect itself and is pulled down and forward. In some cases burrowing follows immediately, in others the animal moves about on the surface for some time, forming a groove in the mud. But burrowing always eventually occurs. The foot is repeatedly extended obliquely downwards and, with the co-operation of the pedal retractors, the animal is pulled under the mud. The hinder margin of the shell remains visible when the umbo is buried, but finally mud falls in and obliterates the pit behind the shell.

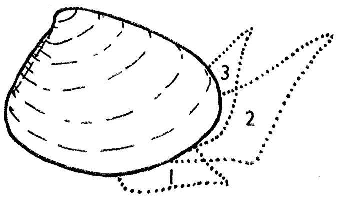

FIG. 1. *Nucula nucleus*, viewed from right side. × 3. 1, 2, 3, successive stages in movements of foot.

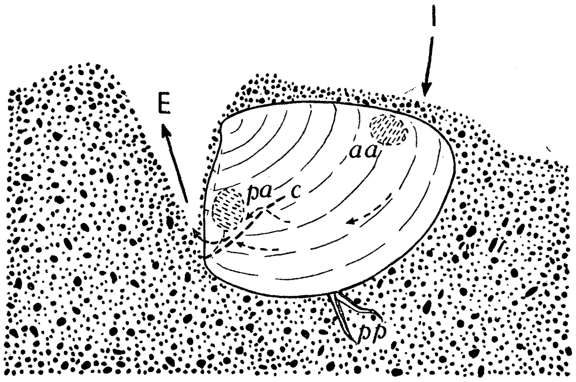

FIG. 2. *Nucula nucleus*, semi-diagrammatic representation of the animal *in situ* when feeding and respiring. × 4½. *aa*, anterior adductor; *c*, ctenidia (represented by broken line); *E*, exhalant current; *I*, inhalant current; *pa*, posterior adductor; *pp*, palp proboscides. Broken arrows indicate currents within mantle cavity.

When completely buried the animals cease moving. They then lie with the anterior margin of the shell parallel to the surface of the substratum and covered to a depth of about 1 mm. An opening to the exterior is then remade at the posterior end, in the first place by a sudden contraction of the adductors which forces water out through the posterior end of the mantle aperture. The opening so made is about 0·5 mm. in diameter, rounded if edged with mud, irregular if with gravel. A mound composed largely of faecal pellets is gradually built up around the margin. There are no siphons and no portion of the palps was ever observed. The statement of Drew (1901) that *Nucula* feeds below the surface was confirmed. There is a continuous but very slow extrusion of water by way of the pit posterior to the animal (see fig. 2), varied only by occasional sudden extrusions caused by contractions of the adductors usually stimulated by mud falling into the cavity. The faeces are also driven clear of the shell by this means. There is no evidence, when the animal is so buried, of any inhalant current; this is anterior and possibly to some extent ventral as shown in fig. 2. *N. nucleus* may remain buried in the same position for long periods, often several days.

No species of *Acila* has been available for examination but, judging from the figures and descriptions of Heath (1937) who deals with four species, this genus has essentially the same structure as *Nucula* and may therefore be assumed to have similar habits.

### (*b*) *Solenomyidae*

The morphology of *Solenomya togata* has been well described by Pelseneer (1891, 1899) and Stempell (1898*b*, 1899). Kellogg (1892) gave an account of some aspects of the morphology of *S. velum*, while Drew (1900) and Morse (1913) have both studied the habits of this American species. *S. togata* was examined alive at Naples, but the very small size of the specimens obtained, never more than 5 mm. long, rendered this difficult. Preserved specimens of the very much larger *S. velum* were purchased from Wood's Hole.

*S. togata* occurs in shallow water in a bottom of fine muddy sand containing much flocculent organic matter. *S. velum* is found in somewhat similar conditions (Morse 1913). The animals are elongated and almost cylindrical, resembling *Ensis* in this respect as well as in habits. The elongated foot (fig. 11, *f*) occupies when withdrawn the anterior half of the mantle cavity. When placed on the appropriate bottom material the foot is protruded anteriorly. It is pointed and the two halves of the sole are applied. Further expansion brings about a downward movement and the point of the foot passes into the mud where the two halves open out. The purchase so obtained enables the animal to erect itself. Preliminary movements bring about only the formation of a shallow pit in front of the animal, but later a firm grip is obtained and the animal is raised diagonally with the anterior end downwards (fig. 3). It then moves diagonally down with considerable speed. From the first entrance some eight to ten movements of the foot suffice for complete burial, only the posterior opening being visible. But the animal does not remain in contact with the surface. In every case where burrowing was followed this continued until the animal disappeared from view, slight movements of the sand revealing that burrowing was still progressing. On several occasions the animals were later seen through the bottom of the glass vessel under between 1 and 2 cm. of bottom material. One specimen about 4 mm. long burrowed in a dish containing a layer of mud 1·2 cm. deep. It remained so for 2 days while kept under gentle circulation. It was never observed to come to the surface, and in no case was there any indication of an opening to the surface for respiratory or feeding purposes.

According to Morse (1913) *S. velum* and *S. borealis* frequently burrow with the posterior end downwards. This was never observed for *S. togata* and is very difficult to understand. Morse states that *S. velum* on occasion "pushes itself backward by means of its foot which, assuming a pointed tongue-like shape, is thrust forward and downward lifting the anterior end and thus depressing the posterior end". He also found a specimen with sponge attached to the anterior end, indicating that this had been protruded, and for some considerable period, from beneath the mud. These statements will be discussed later.

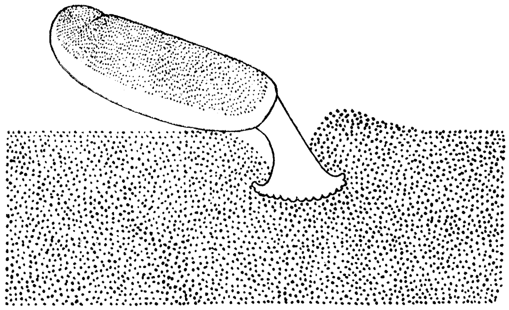

FIG. 3. *Solenomya togata*, animal viewed from right side when beginning to burrow. × 6. Unstippled, ventral region of shell indicates area not calcified.

The remarkable agility with which *Solenomya* burrows has made possible the swimming movements which may be executed when the animal is placed in a dish without mud. These movements have been well described by Drew (1900). By extensions followed by sudden withdrawals of the foot, water is expelled rapidly through the posterior opening and the animal moves forward in a series of short darts. As Drew pointed out, the ejection of water is further assisted by the intucking of the fused ventral margins of the shell. In all species of *Solenomya* the shell is composed largely of periostracum, which is notably water repellant, and the ventral quarter of the shell is entirely uncalcified (fig. 3). This region, as shown by Drew (1900), is infolded when the shell valves are drawn together. The periostracum is composed of alternate thick and thin portions radiating from the umbo to the free margins of the shell. The former provide elasticity, the latter permit plaiting when the shell is folded under. The intucking process is brought about by the action of muscles attached to this region of the shell (fig. 13, *mr*). The radial pallial muscles associated in genera such as *Pecten* or *Ostrea* (Yonge 1936*b*) with the withdrawal of the pallial curtain (velum) are well developed, extending in a series of bundles from the ventral extremity of the calcareous region of the shell to the free edge of the periostracum. Longitudinal muscle fibres (fig. 13, *lm*) extend along the line of union of the two mantle lobes, and after crossing over immediately behind the pedal opening, continue forward on either side of this. The action of these muscles, working in co-operation with the withdrawal of the foot, causes almost complete obliteration of the mantle cavity. The foot, and the intucking of the mantle and shell ventral to this which follows its withdrawal, prevents passage of water anteriorly so that all must be ejected posteriorly by way of the infrabranchial chamber and through the posterior aperture. This provides the mechanism for the powerful swimming movements and also explains the depth to which and the speed with which the animals burrow. Swimming, as will be indicated later, is probably merely the incidental consequence of mechanisms elaborated for burrowing and for the removal of sediment from the mantle cavity. Small specimens of *Ensis* or *Cultellus* have been observed to execute similar darting movements although they seldom actually swim.

*Solenomya* resembles *Nucula* in the absence of siphons but differs in that no portion of the palps is ever extruded beyond the margin of the shell.

### (*c*) *Nuculanidae*

Species of four genera of this family, *Nuculana*, *Yoldiella*, *Lembulus* and *Malletia*, were studied in life. Unfortunately, no species of *Yoldia* is available for examination in any European marine laboratory, although preserved material of *Y. limatula* was purchased from Wood's Hole. Happily no genus of Protobranchia has been studied in such detail in the living condition, notably by Drew (1899, 1900), Kellogg (1892, 1915) and Morse (1919). Statements as to the habits of this genus, essential for completeness, are taken from their work.

The structure of species of *Nuculana* (better known as *Leda*) has been described by Stempell (1898*a*), Pelseneer (1903, 1911) and Heath (1937). Pelseneer's earlier papers (1891, 1898) deal with *Leda pella* which, for reasons given later, appears more suitably assigned to the genus *Lembulus* than to *Nuculana*. Morse (1919) describes the appearance in life of *N. tenuisulcata* and Atkins (1936) gives a detailed account of the ciliary currents and of the ctenidia in *N. minuta*. But there is no account of the habits of any species of this genus.

*N. minuta* was obtained by means of an Agassiz trawl at Ypsøsund near Herdla at a depth of 60 m. in mud of medium consistency containing some fine gravel. When placed on this bottom material in the laboratory the animals soon extruded the large foot in much the same manner as in *Nucula*, erected themselves by the gripping action of the two sides of the sole and then moved along the surface, cutting grooves as deep as the height of the shell. Finally they burrowed under the surface, but in this case the presence of the animals was indicated by the presence of united siphons (see fig. 14) which extend, curling upwards, for 1·3 mm. in the case of an animal of shell length 1·1 cm. They project from the base of a small pit formed immediately behind the posterior margin of the shell. When observed under the binocular microscope, sudden ejections of water through the exhalant siphon accompanied by a closure of the inhalant opening were noted. These occurred on the average every $5\frac{1}{2}$ sec. Between these expulsions there was a very slow intake of water through the inhalant siphon, culminating in a sudden intake preceding the expulsion. The thread-like extremities of the palp proboscides (fig. 14, *pp*) extend to the posterior margins of the shell immediately ventral to the siphons. The palp proboscides collect food from the surface of the mud. Their extrusion has been noted by Atkins (1936) and also by Morse (1919) in *Nuculana tenuisulcata*, but he regarded them as probably "a double siphonal tentacle". Actually no such tentacle was found in this species, confirming the statement of Atkins (1936).

Specimens of *Yoldiella lucida* were abundant in the Bergen Fjord on the same bottom as *Nuculana minuta*. As shown in fig. 4, the shell is relatively shorter than that of *N. minuta*, the posterior rostrum being absent. It is also relatively wider. Although no specimen exceeded 6 mm. in length, extensive observations were made on this interesting species never previously examined in life, although Stempell (1898*a*) has described the anatomy of *Yoldiella* [= *Leda*] *sulculata* and *Y.* [= *L.*] *pygmaea* and Heath (1937) that of *Y. inflata* and *Y. iris*.

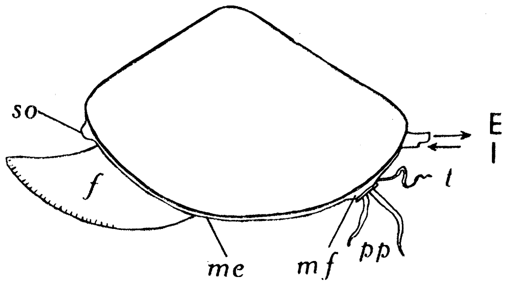

FIG. 4. *Yoldiella lucida*, animal viewed from left side with organs extruded. × 8. *f*, foot (partially extruded); *me*, mantle edge; *mf*, posterior mantle fold around region where palp proboscides extruded; *so*, marginal sense organ; *t*, posterior, unpaired tentacle. Other lettering as before.

In habits the animal resembles *Nuculana minuta*, burrowing in the same manner and projecting the relatively shorter siphons posteriorly (fig. 4). The foot (*f*) is relatively of enormous size when fully extended, being about equal in bulk to the rest of the body. When placed in a glass dish without mud the animals extended the foot repeatedly making futile attempts at burrowing. The same alternations between sudden expulsions of water through the exhalant siphon and periods of very slow intake through the inhalant siphon were noted. The former occurred on the average every 5 sec. The tips of the palp proboscides (*pp*) were extended beyond the shell valves with great readiness and were seen to grope about on the surface of the mud behind the burrowed animal. As shown in fig. 4, they appear in the same position as in *N. minuta*. The mantle edges in this region (*mf*) are extended somewhat and curled back over the shell. Immediately dorsal to the palp proboscides projects the long, unpaired posterior tentacle (*t*). The exact function of this organ, which appears in all further species of the Nuculanidae examined, is obscure although presumably receptive. It arises from a pit in the mantle edge usually on the right side of the body, although, as observed by Stempell (1898*a*) there is considerable variation in all species which possess it and it may appear on the left side.

*Lembulus pella** occurs in a substratum of fine silty mud in shallow water and is common in such localities at Naples. It is relatively large, individuals often exceeding 1 cm. in length and, like *Yoldiella lucida*, is considerably more rounded than *Nuculana minuta*, being about half as wide as it is long. The thick white shell is diagonally sculptured and possesses a short posterior rostrum bounded ventrally by a ledge (fig. 5). It expands readily when placed in a dish of sea water, unusually large areas of the mantle edges (*mf*) being protruded posteriorly. Between these are extruded the tips of the palp proboscides (*pp*), the delicate posterior tentacle (*t*) and, dorsal to these, the siphons. The inhalant siphon (*is*) is wider but slightly shorter than the exhalant siphon (*es*).

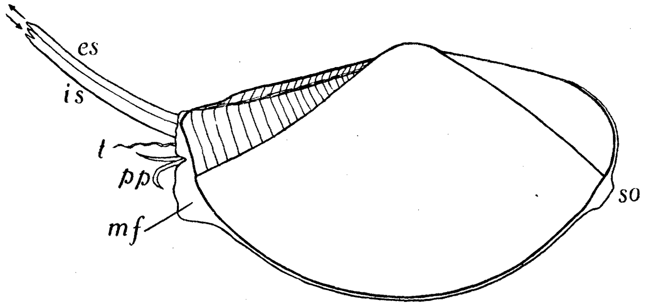

FIG. 5. *Lembulus pella*, animal viewed from right side with organs extruded. × 5. *es*, exhalant siphon; *is*, inhalant siphon. Other lettering as before.

The animal burrows diagonally downward, movement usually stopping with the hind end of the shell still exposed. The siphons are from time to time, every 16–18 sec. in the specimen observed, protruded very quickly to an extent of about 4 mm. in an animal 1·15 cm. long. They are thus relatively longer than those of *N. minuta* (cf. figs. 5, 14). When fully extended first the inhalant and then the exhalant siphon opens, a sudden intake of water through the former being succeeded by an equally powerful expulsion through the latter. Stimulation of the animal causes further burrowing by a series of sudden movements. Invariably contact is soon remade with the water above by the protrusion of the siphons from below the mud. Under these conditions they remain partially protruded but with the openings closed, only expanding fully and opening at the same regular intervals as before. In time, as a result of a series of violent expulsions of water due to contractions of the adductors, a permanent opening is made in the substratum and the siphons withdrawn except for the periodic extrusions. Occasionally, during movement under the sand, the anterior end is exposed.

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* In their descriptions of its morphology both Pelseneer (1891, 1899) and Stempell (1898*a*) refer to this species as *Leda pella*. Thiele (1934), on the basis of the shell characters, refers it to the subgenus *Lembulus* Risso, a section of the genus *Leda* [*Nuculana*]. It is certainly generically distinct from both *Nuculana* and *Yoldiella*. Apart from shell characters, it differs from *Nuculana minuta* in the presence of a posterior tentacle and from both this species and *Yoldiella lucida* in the complete fusion of the ventral surface of both siphons (see fig. 18) and also the lack of union between the inner filaments of the ctenidia of the two sides (cf. figs. 22–24).

An inward current can then be detected in this region. But the siphons are not in operation and particles drawn in with this current are expelled ventrally by sudden contractions of the adductors. The animals apparently feed under the surface.

Knowledge of the deep-water genus *Malletia* is based on the morphological studies of Sars (1872), Pelseneer (1888, 1911), Stempell (1898*a*) and Heath (1937). Sars's account of "*Yoldia obtusa*" is of great interest historically, being the first description of the structure of any species in this interesting genus. His figure is excellent, although he not unnaturally describes the palps as gills and the region where the palp proboscides are extruded as the branchial siphon. He is the only person to have given any account of a species of this genus in life. He notes that it is widely distributed in deep water, between 200 and 500 fm. off the coast of Norway. The other known species, such as *Malletia pallida* (Pelseneer 1888) from Station 137 of the *Challenger* between Tristan da Cunha and the Cape of Good Hope, *M. abyssorum* and *M. polita* (Verrill and Bush 1898) from off Chesapeake Bay, *M. chilensis* (Stempell 1898*a*; Heath 1937) from off the coast of Chili and *M. sibogae* (Pelseneer 1911) from the East Indies, are all from very deep water.

Numbers of *M. obtusata* (= *Yoldia obtusa* of Sars) were obtained by trawling at depths of about 350 m. in the Manger Fjord, in the classic collecting grounds of Michael Sars. The animals live on a bottom of extremely fine-grained, soft mud. They lived for several days in captivity, burrowing in mud collected from their normal habitat.

*M. obtusata* is flattened from side to side. The shell is thin and, being composed primarily of periostracum, so transparent that the tissues can be seen through it. This had the great advantage of permitting the movements of the ctenidia to be observed in the intact animal. The foot has the typical structure, but is thinner and more blade-like than in the other genera. The fused siphons are very characteristic. They are, as originally stated by Sars (1872) for the "anal" siphon, of great length, extending for as much as 2 cm. in the case of an animal 1·4 cm. long. But whereas Sars figures them as extended backward and curling down at the tip, normally they extend upwards and then arch forward parallel to the dorsal edge of the shell as shown in the upper drawing in fig. 6. Sars probably figured a moribund specimen.

When placed on mud the animals soon extruded the foot, erected themselves and began to move about, forming a deep groove in this soft substratum. The foot has remarkable powers of extension, and the two sides of the sole open out very widely the better to grip the soft mud. Movement is accompanied by a typical dipping action. The foot first pushes downward with the two halves of the sole applied and then moves upward and forward with the sole extended (fig. 6), finally being withdrawn within the anterior margins of the shell. Owing to the softness of the mud, this frequently falls in and may completely cover the animal, but the length and great mobility of the fused siphons enable communication to be maintained with the water above. The animals never burrow downwards but will burrow through any slight elevation in the mud. Typical conditions are shown in fig. 6. Unlike the other species examined, *M. obtusata* tends to keep moving about; this may well be correlated with the greater paucity of food at the great depths in which it lives.

Water is expelled violently from the exhalant siphon at fairly regular intervals, on the average every 28 sec. During the remaining time there is a very slow intake of water through the inhalant siphon. Below the siphon there extends the long, unpaired tentacle similar to that of *Yoldiella* and *Lembulus*. Below that again, as shown in fig. 16, the tips of the palp proboscides are occasionally protruded.

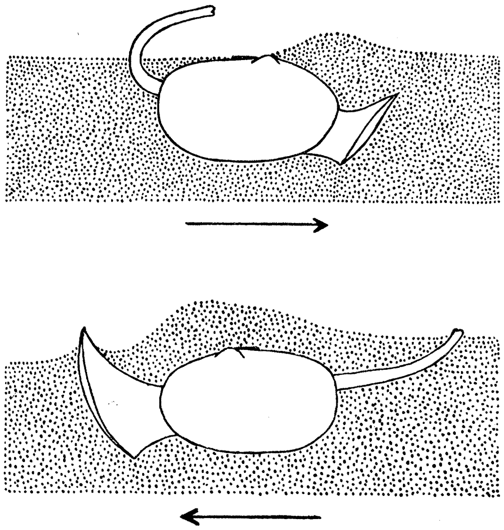

FIG. 6. *Malletia obtusata*, animal viewed from right side (above) and left side (below) showing manner of progression through mud and extrusion of siphons and foot. × 2.

*Yoldia limatula* is abundant on a soft mud bottom of high organic content in shallow coves and inlets along the coasts of Maine and adjacent regions (Drew 1899). The shell is smooth, laterally compressed and tapers somewhat posteriorly. It is fairly heavily calcified. In form and structure, therefore, it may be regarded as somewhat intermediate between the shell of *Nuculana minuta* which has a pronounced posterior rostrum and is heavily calcified and that of *Malletia obtusata* which is flatter, has no rostrum and is so very slightly calcified. But *Yoldia limatula* is larger with an average length of some 3·5 cm. The siphons (see fig. 8), which are fused like those of *Malletia*, are long, extending almost directly backwards for a length equal to about half that of the shell. Beneath lies an equally long unpaired tentacle (fig. 8, *t*). The foot is very large with the usual structure. By its aid the animal burrows vertically. In the words of Drew: "The movements of burrowing consist of thrusting the closed foot far out of the shell anteriorly (fig. 7 A), spreading the flaps, and with the flaps spread (fig. 7 B) withdrawing it (fig. 7 C). The spread flaps are closed together when they come to the margin of the shell, and the foot is ready for another thrust." Contraction of the retractor muscles of the foot when the animal is anchored by the extended flaps causes rapid burrowing in mud, "after the animal has righted itself, two thrusts and retractions generally suffice to carry it beneath the surface". The animals are normally preyed upon by cormorants and flounders, and this efficient mode of burrowing must be an effective method of escape. When feeding (fig. 8), the animal (Drew 1899) "is usually slightly tipped ventrally from the perpendicular, and frequently has about one-third of its posterior end above the mud. While in this position, the palp appendages are thrust out of the shell and one, at least, bends over and inserts its tip in the mud. The cilia lining its longitudinal groove immediately begin to elevate the mud, which is rich in living organisms. The stream of particles passing along the groove is large enough to be distinguished at a distance of some feet."

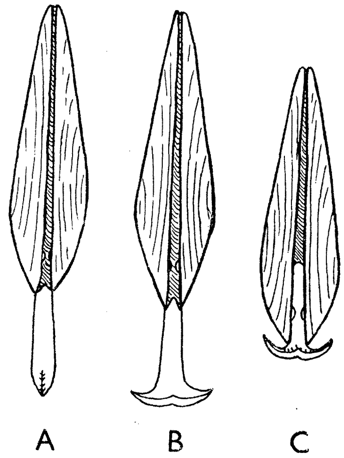

FIG. 7. *Yoldia limatula*, animals viewed from ventral side showing (A, B, C) operation of the foot in burrowing. × $1\frac{1}{3}$. After Drew (1900).

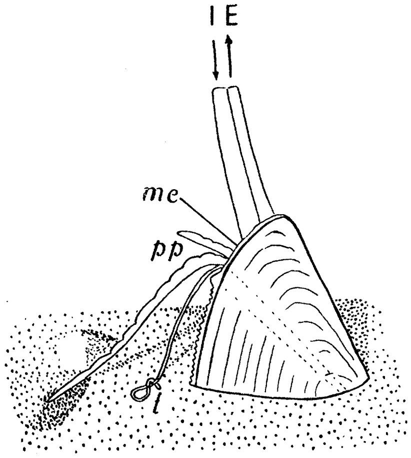

FIG. 8. *Yoldia limatula*, animal viewed from the right side when buried normally and both feeding and respiring. × $2\frac{1}{2}$. Lettering as before. After Drew (1901).

## 3. THE MANTLE CAVITY

### (*a*) *Nuculidae*

The nature of the organs and the currents in the mantle cavity is best described by reference to *Nucula hanleyi* (fig. 9). The mantle edges are free anteriorly, ventrally and posteriorly, there being no structural division into inhalant, exhalant and pedal openings. As in all Protobranchia (Stempell 1898 *a*) the mantle edge is thickened and divided into three folds having the same functions as those present in the other Lamellibranchia (see Yonge, 1936 *b*). The visceral mass is rounded and compact and the adductors (*aa*, *pa*) large and of about equal size. There is an obvious macroscopic difference in each between an outer opaque white region and an inner light brown and translucent region. The former constitutes the "quick" and the latter the "catch" muscle. The retracted foot (*f*) occupies the greater part of the ventral region of the mantle cavity. The ctenidia (*c*) extend from the postero-ventral border of the visceral mass diagonally downwards to the posterior margin of the mantle cavity. The terminal quarter is free, connected only by the membrane (*sm*) to the base of the posterior adductor. As shown in fig. 10 (*hg*), the hypobranchial glands cover the surface of the suprabranchial cavity on either side of, but not between, the ctenidial axes. They consist of elongated cells, swollen with secretion, which cover the outer surfaces of the suspending membrane and the dorsal surface of the pedal retractors (*pr*) and extend dorsally and then ventrally over the mantle as far as the upper surface of the outer leaflets of the ctenidia. Posteriorly they end blindly in a pocket dorsal to the posterior adductor not extending on to the surface of the suspending membrane attaching the posterior region of the ctenidia to the ventral surface of the adductor. There is no gland in the suprabranchial cavity bounded ventrally by the inner leaflets of the ctenidia. Pelseneer (1891) originally described and figured the glands as rounded masses projecting from the latero-dorsal walls of the mantle and almost filling the lateral suprabranchial cavities. He may have been misled by the mass of secretion (*sc*) which in sections occupies these regions.

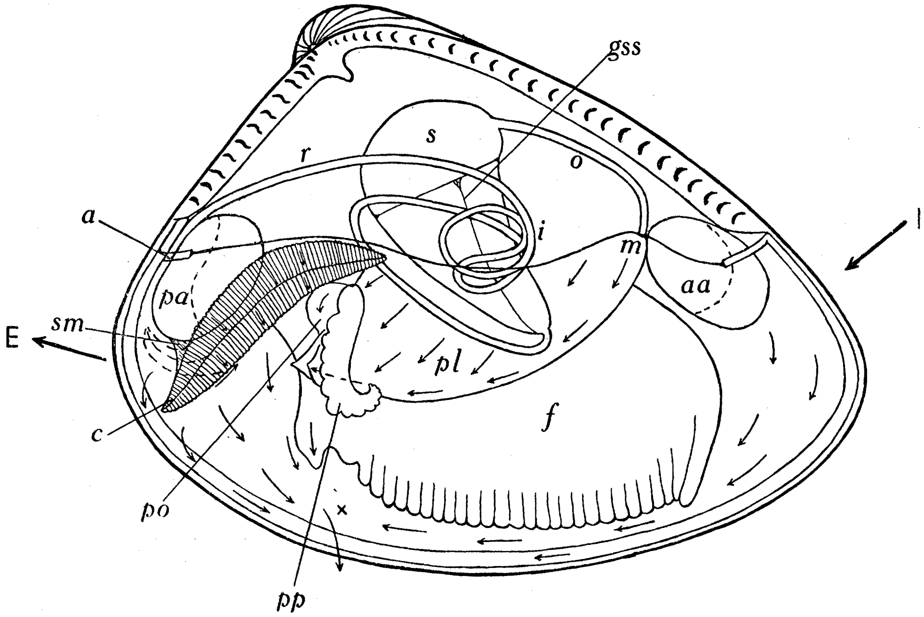

Fig. 9. *Nucula hanleyi*, organs in the mantle cavity and of the alimentary canal viewed from the right side. × $7\frac{1}{2}$. *a*, anus; *gss*, groove in "style-sac" region of stomach; *i*, intestine; *m*, mouth; *o*, oesophagus; *pl*, palp lamellae; *po*, palp pouch; *r*, rectum; *s*, stomach; *sm*, suspending membrane; *X*, region where material collected prior to ejection from mantle cavity. Other lettering as before. Arrows indicate direction of ciliary currents in mantle cavity.

The labial palps are very large, consisting on each side of flat, paired lamellae (fig. 9, *pl*), the opposed faces of which are grooved, and an unpaired, elongated palp proboscis (*pp*), shown withdrawn in fig. 9 but capable of extension far beyond the shell (see fig. 2), and a rounded palp pouch (*po*) at the point of union of the other two parts.

The respiratory currents are, when compared with those of Filibranchia or Eulamellibranchia, very weak. They are created by the lateral cilia on the gill filaments. Except when the foot is protruded, the mantle edges are opposed ventrally, but, following a slight relaxation of the adductors, the mantle edges separate anteriorly and posteriorly to form two slit-like openings extending from the point of union of the mantle edges to the beginning of the ventral surface both anteriorly and posteriorly. The former constitutes the inhalant, the latter the exhalant, aperture. The tips of the ctenidia are normally so placed that they just touch the mantle edges immediately anterior to the exhalant aperture (see fig. 9). In this way the mantle cavity is divided into a large inhalant cavity and a much smaller exhalant cavity consisting of the postero-dorsal region behind the ctenidia. The free tips of the ctenidia readily curl back when stimulated, to the extent indicated by the broken line in fig. 9; this probably takes place normally when the adductors contract and so permits of the sudden ejection of water and sediment posteriorly which invariably occurs when the shell closes. When the palp proboscides are extruded mid-ventrally, there is also possibly some intake of water in this region. The protrusion of the foot, by causing a universal separation of the mantle edges, apparently upsets temporarily the respiratory currents. It should be noted that when the animal is buried, water is taken from *beneath* the surface of the substratum (see fig. 2). This is possible owing to the limited extent to which the anterior margin is covered and to the porous nature of the substratum, but it probably curtails intake of water mid-ventrally when the palps are extruded. The very gentle nature of the currents prevents any excessive intake of sediment.

The direction of the respiratory currents in *Nucula* has not previously been observed, it having been assumed that the inhalant as well as the exhalant aperture is posterior. The full implications of the present findings, revealing what is clearly a primitive condition, will be discussed later.

Within the infrabranchial cavity, currents on the mantle cavity carry particles to the region "*X*", where they are carried over the mantle edge of the exterior. The foot is not ciliated except for the "heel" region, where there is a current directed ventrally. Currents on the outer surfaces of the palp lamella carry particles diagonally to the tip, whence they are transferred to the current on the foot. The region of extrusion lies immediately below this portion of the foot. Particles caught on the ventral (frontal) surface of the gill filaments are carried to the mid-line and then conveyed forward. Their fate will be discussed later. Owing to the relatively indifferent attachment of the ctenidial filaments to one another by ciliated disks (fig. 10, *cd*) a quantity of fine material is carried through the ctenidia, and this is massed together by the secretion of the hypobranchial glands (fig. 10, *sc*). The more powerful current created in the smaller cavity dorsal to the inner leaflets (see fig. 10) probably accounts for the absence of a hypobranchial gland in this region.*

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* Heath (1937) refers to glandular regions in the mantle near to the mouth in various species of *Nucula*. Although this region is often swollen with blood, no evidence of mucous glands has been found in any species here examined.

The hypobranchial gland in *Nucula* is thus strictly homologous with this structure in the prosobranch Gastropoda (Yonge 1937, 1938), where it is of universal occurrence with the exception of species in which the great development of the ctenidia for feeding purposes, as in *Crepidula* and *Capulus*, prevents particles passing between or beyond the filaments. The opinion of Stempell (1898*a*), who attempts to homologize the hypobranchial gland of *Nucula* with the pallial gland near the inhalant siphon in *Nuculana*, cannot be upheld. The gland has an accessory function in *Nucula delphinodonta*, where its secretion forms the brood-sac attached to the posterior end of the shell (Drew 1901). But this is a specialization not found in all species of *Nucula*, whereas the gland is of universal occurrence. It also occurs in *Acila* (Heath 1937).

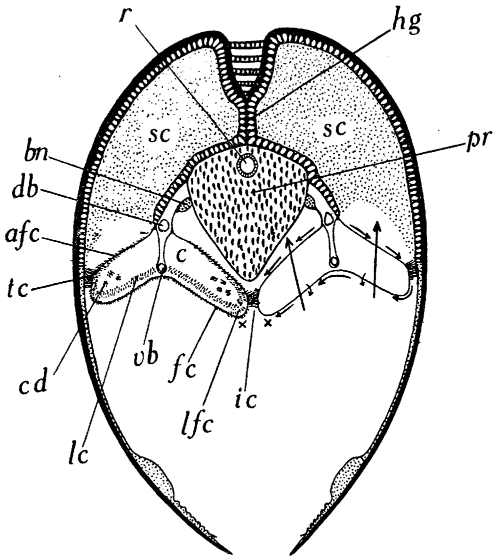

FIG. 10. *Nucula turgida*, semi-diagrammatic transverse section showing relations of organs in the region immediately anterior to the posterior adductor. × 22. *afc*, abfrontal cilia; *bn*, branchial nerve; *cd*, ciliated disks; *db*, dorsal blood vessel in ctenidial axis; *fc*, frontal cilia; *hg*, hypobranchial gland; *ic*, interlocking cilia between inner leaflets of ctenidial filaments; *lc*, lateral cilia; *lfc*, latero-frontal cilia; *pr*, posterior pedal retractor; *sc*, secretion from hypobranchial glands; *tc*, terminal cilia on dorso-lateral margins of outer leaflets of ctenidial filaments; *vb*, ventral blood vessel in ctenidial axis. Other lettering as before. Arrows on ctenidial filament shown on right indicate direction of beat of afrontal, lateral, latero-frontal and frontal cilia.

### (*b*) *Solenomyidae*

*Solenomya* differs in many respects from all other genera of the Protobranchia. The visceral mass is small and obscured by the ctenidia (fig. 11, *c*) which are so large as to occupy about half the mantle cavity. *Solenomya* resembles *Nucula* in the absence of siphons, but there is a posterior aperture separated from the pedal opening by a fusion of the mantle edges which extends half-way along the ventral side. The posterior aperture is fringed with tentacles (see fig. 11), but there is no division into inhalant and exhalant openings. Kellogg (1892) states that in *Solenomya velum* the sides of this aperture may approach one another, and Morse (1913) records similar observations, adding that the upper opening is always the larger. Owing to its small size it was impossible to make similar observations on *S. togata*. The pedal aperture extends around the anterior end from the centre of the mid-ventral line (figs. 11, 12, *mj*) to the anterior margin of the hinge dorsally. Tentacles fringe the antero-dorsal margin. The adductors are large and of about equal size. The foot (*f*) occupies, when withdrawn, practically all the mantle cavity anterior to the gills. The palps are very small, consisting mainly of an unpaired flap on each side. As stated by Pelseneer (1891), there is a pair of very large hypobranchial glands. As shown in fig. 13 they are divided into two portions, one extending over the morphologically inner (structurally ventral) surface of the suspending membrane ($hg_2$) and the other over the outer (dorsal) surfaces ($hg_1$). These dorsal glands also cover the surface of the visceral mass but, owing to the great dorso-ventral extension of the ctenidial filaments, which restricts the suprabranchial cavity as shown in fig. 13, they do not extend laterally over the mantle surface as in *Nucula.*

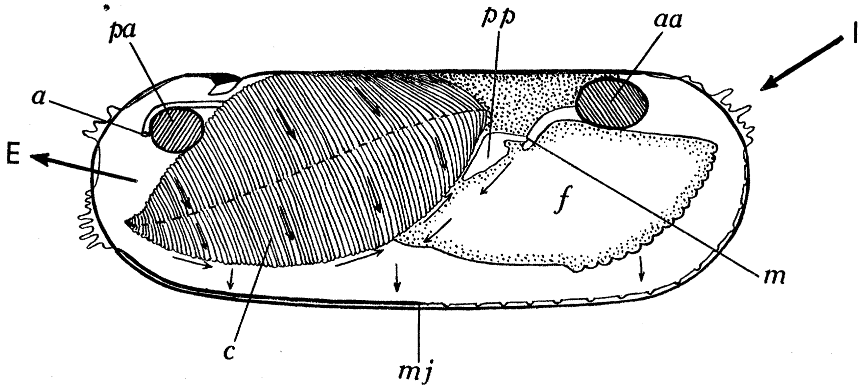

FIG. 11. *Solenomya togata*, organs in mantle cavity viewed from right side. × 14. *mj*, anterior end of ventral fusion of mantle edges. Other lettering as before. Arrows indicate direction of ciliary currents.

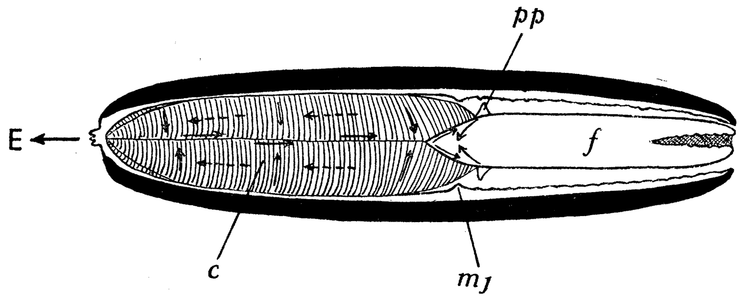

FIG. 12. *Solenomya togata*, animal viewed from the ventral aspect after cutting through the ventral fusion of the mantle edges. × 14. Lettering as before. Broken arrows indicate direction in which large particles or masses are carried over the surface of the ctenidia.

A series of complex, flask-shaped mucous glands is present in the middle fold of the mantle edges. These have been described microscopically in *Solenomya togata* by Stempell (1899) and macroscopically in *S. velum* by Morse (1913). Their secretion possibly lubricates the ventral region of the shell and prevents it cracking when it bends inwards; it may, incidentally, be responsible for the water-repellant characteristics of the periostracum. There are also glandular areas in the anterior region of the mantle which have been described and figured by Stempell (1899). Orton (1913) states that the inhalant current is drawn in antero-dorsally by way of the region fringed with tentacles, the posterior aperture being exclusively exhalant, the tips of the ctenidia being applied to the postero-ventral margin of the posterior aperture, i.e.

precisely as in *Nucula*. Unfortunately the specimens of *Solenomya togata* examined at Naples were so very small that exact determination of the inhalant current was difficult. But the presence of the antero-dorsal tentacles, the arrangement of the gills and the unique shape and habits of this Protobranch, all indicate the presence of this anterior inhalant current. Such a current would also explain Morse's observations on *S. velum* burrowing with the anterior end exposed. On the other hand, there are the observations of Kellogg (1892) and Morse (1919) that in *S. velum* the posterior opening is frequently divided into what appear to be exhalant and inhalant openings. Morse writes: "The sides of the siphonal opening are in constant motion in and out, though this motion is alternate and rhythmic." It appears possible that, on occasion, an inhalant current may be drawn in posteriorly. This would require only the adjustment of the very mobile tips of the ctenidia in the middle of the posterior aperture when the walls of this were drawn together.

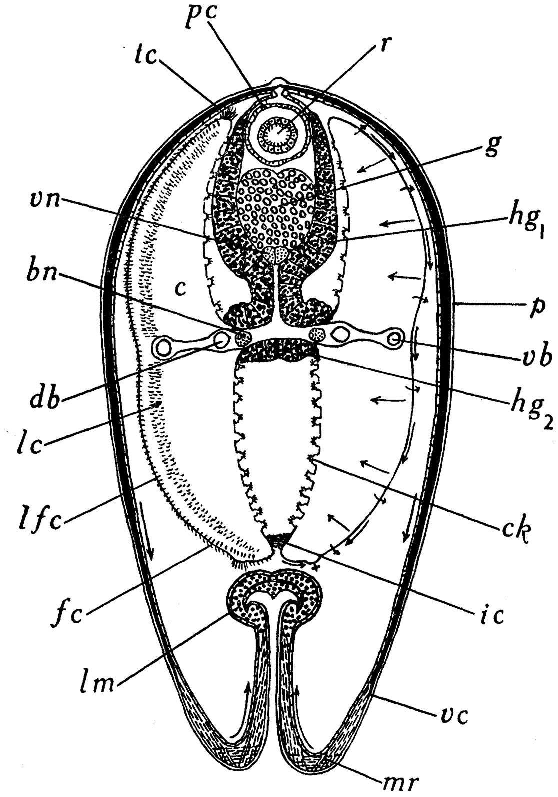

FIG. 13. *Solenomya togata*, semi-diagrammatic transverse section through the middle of the region occupied by the ctenidia, showing the relation of the organs and the ventral intucking of the shell; the ctenidial filaments are actually disposed obliquely as shown in fig. 11. × 11. *ck*, ciliated knobs on filaments; *g*, gonad; $hg_1$, $hg_2$, hypobranchial glands in outer and inner (topographically dorsal and ventral) regions of exhalant chamber respectively; *lm*, longitudinal muscle in fused, inner fold of mantle edge; *mr*, radial muscles in ventral region of the mantle responsible, in co-operation with the longitudinal muscles, for the ventral intucking of the shell; *p*, periostracum; *pc*, pericardium; *vc*, ventral extremity of calcified portion of shell (calcification shown in black dorsal to this); *vn*, visceral nerve. Other lettering as before. Arrows indicate direction of ciliary currents on ctenidial filaments and on mantle surface.

Cleansing currents are well developed. As in *Nucula*, particles are carried downward along the sides of the base of the foot (figs. 11, 12) and also on the mantle lobes (fig. 13). But there is no backwardly directed current mid-ventrally, and extrusion of waste material must be brought about by the contraction of the foot, aided by the intucking of the ventral region of the shell. The combined effect will be to expel material with great force through the ventral portion of the posterior aperture. This is, as already noted, the mechanism of the "swimming" motion, and the latter may therefore be regarded, as in the other cases of swimming in Lamellibranchs (Yonge 1936*b*), as an incidental result of the mechanism for extrusion of sediment from the mantle cavity. The mantle cavity of *S. togata* was frequently found almost blocked with material cemented together. In view of its habits, abnormally large amounts of material must enter the mantle cavity anteriorly; these are then apparently consolidated by secretion from the anterior mucous glands and expelled posteriorly by violent contractions of the foot. Ciliary currents alone would certainly be inadequate. Finally, there is, when much material is placed upon it, a backward passage of material over the surface of the ctenidia (indicated by the broken arrows of fig. 12). This is due to a bending over of the filaments, thereby exposing the latero-frontal cilia on the anterior side and obscuring the frontal cilia which, as Orton (1913) has noted, normally carry isolated particles to the ventral surface of the ctenidia.

Conditions in *Solenomya* are certainly very different from those in any other Protobranch, or indeed any other Lamellibranch. This genus appears unique in its capacity to live for a great part of, if not all, the time without direct contact with the water above the substratum in which it burrows.

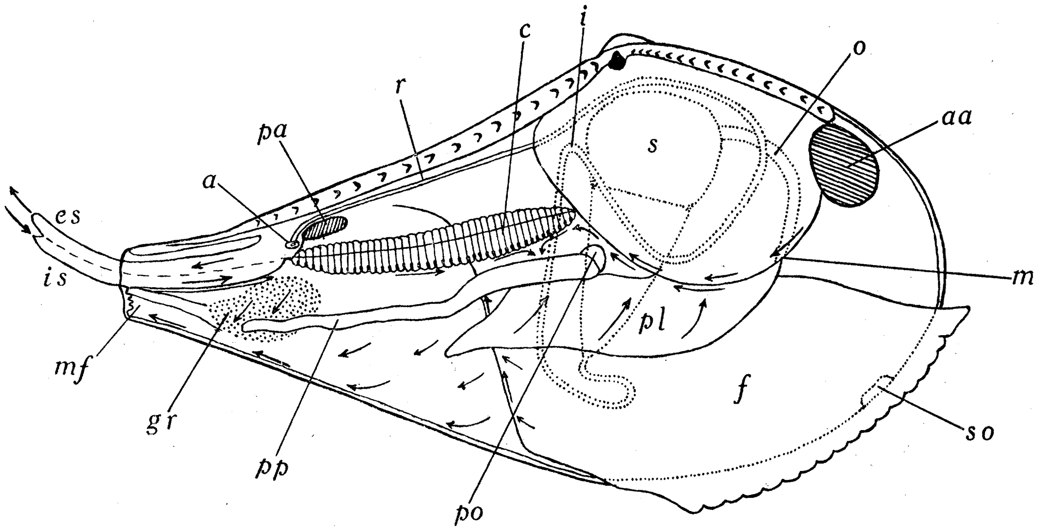

FIG. 14. *Nuculana minuta*, organs in the mantle cavity and of the alimentary canal (latter indicated by dotted lines) viewed from the right side. × 10. *gr*, glandular region in mantle. Other lettering as before.

### (*c*) *Nuculanidae*

The organs in the mantle cavity of *Nuculana minuta* and the nature of the currents have recently been admirably described and figured by Atkins (1936). The exhalant siphon (fig. 14, *es*) is a complete tube, but the shorter inhalant siphon (*is*) is incomplete, the under side being formed by the apposition of the two lateral folds, connexion being maintained by means of interlocking cilia (see fig. 18 B). It is therefore structurally, though not functionally, in communication with the extensive pedal opening which extends to the anterior margin of the hinge. The visceral mass is more elongated than in *Nucula* but otherwise similar; the anterior adductor is larger than the posterior. The foot (*f*) calls for no special comment. The ctenidia (*c*) are relatively smaller than in *Nucula* and extend directly backwards from the visceral mass to the base of the siphons. No trace of a hypobranchial gland has been found in this or any other species of the Nuculanidae. Pelseneer (1891) described one in *Lembulus pella*, but Stempell (1898*a*) states that this gland is absent in this species and in *Yoldiella sulculata*. But all workers have noted the presence of a glandular region of the mantle cavity (*gr*) in the infra-branchial chamber immediately ventral to the base of the siphons. This occurs in all species examined, except in *Malletia obtusata*, but is very slightly developed in *Yoldia limatula*. The palps are essentially similar to those of *Nucula*, but the proboscides (*pp*) extend directly backwards. They pass out of the shell immediately beneath the siphons by way of an opening bounded ventrally by prominent folds on the margins of the mantle (*mf*) which are, as already noted, particularly well developed in *Lembulus* (fig. 5) and also in *Malletia* (fig. 16). The presence of these folds is responsible for the original description by Deshayes (quoted by Pelseneer 1911) of a third siphon. Stenta (1909) described in "*Leda*" *commutata* a ciliated sense organ in the middle fold of the mantle edge near the anterior end. Sections reveal the presence of a similar organ in *Nuculana minuta* (fig. 14, *so*), and it appears to be of universal presence in the Nuculanidae. The mantle edges are invariably enlarged in this region (see figs. 5, 14, 15, 16, 17, *so*). On the other hand, the cephalic or adoral sense organ described by Stempell (1899) in *Solenomya togata* and by Vlès (1905) and Hirasaka (1927) in *Nucula* spp. is absent in the Nuculanidae.

As already noted, the respiratory currents on *Nuculana minuta* and of all other Nuculanidae are powerful but, for reasons to be discussed later, intermittent. Cilia on the mantle carry particles ventrally and then posteriorly, and they are rejected by way of the opening through which the palp proboscides project (i.e. essentially as in *Nucula*). The secretion from the glandular area (*gr*) probably assists in their consolidation. The mechanism is similar to that found in the other Lamellibranchia (e.g. *Mya*, Yonge 1923), except that particles are not rejected by way of the inhalant siphon. Ciliation on the foot is confined to the heel, but particles are carried *upwards* and thence on to the mantle surface. On the outer surfaces of the palp lamellae particles are carried diagonally upwards and forwards and transferred to currents running posteriorly along the base of the visceral mass. The absence of hypobranchial glands is certainly correlated, here and in all the Nuculanidae, with the compact nature of the ctenidia through which only the smallest particles can pass and also with the very powerful exhalant current which they produce.

Conditions in *Yoldiella lucida* (fig. 15) are not significantly different. The organs are more compactly arranged owing to the relatively shorter shell which has a very abbreviated posterior rostrum. The foot is relatively larger and so are the ctenidia (*c*), the filaments of which are broader and deeper. Less than half the filaments are united posterior to the foot, and this appears to be characteristic of the genus. The palps are very similar to those of *Nuculana minuta*. The animals are so small that examination of ciliary currents is difficult, but there is no doubt that the cleansing currents are the same as those in *N. minuta* and the muscular action of the ctenidia no less developed. The unpaired posterior tentacle (shown in fig. 4 but not in fig. 15), present in all species of the Nuculanidae examined other than *N. minuta*, has already been noted. The siphons are of particular interest in that the partition between the two siphons as well as the ventral surface of the inhalant siphon consists of opposed surfaces united by *ciliary* junctions only (see fig. 18 A).

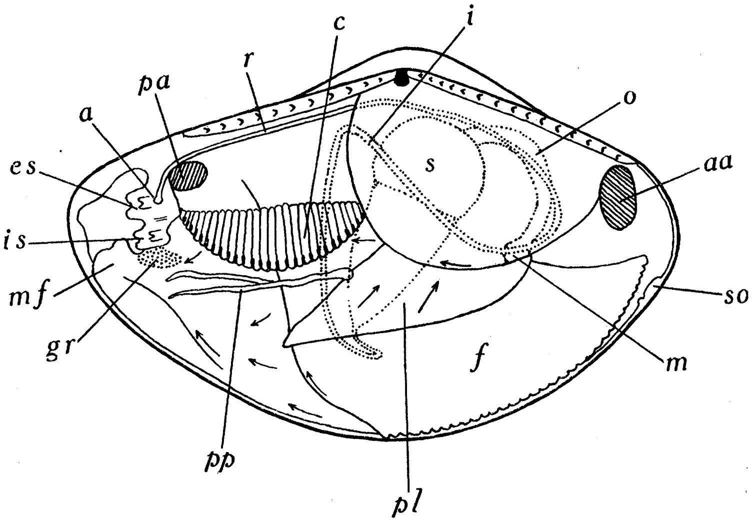

FIG. 15. *Yoldiella lucida*, details and lettering as for fig. 14. × 14.

The disposition of the organs in the mantle cavity and the direction of the cleansing currents in *Lembulus pella* are essentially the same as in the two preceding species. The two points of distinction are the lack of any connexion between the ctenidia of the two sides and the fusion of the tissues to form two complete siphonal tubes.

The flattened shape, transparency of the shell and of the tissues, combined with the relatively large size made *Malletia obtusata* ideal for examination of the living animal. The general arrangement for the organs is, as shown in fig. 16, very similar to that of the preceding species. The most notable differences are the large, fused siphons with the anus (*a*) projecting well into the base of the exhalant siphon, the greater length of the palp lamella (*pl*) and well-defined outlet for the palp proboscides (*pp*) bounded by enlarged folds on the mantle edge (*mf*). The anterior marginal sense organ (*so*), of the same structure as that present in the preceding species, is very large and situated in a prominence in the mantle edge. Finally, the ctenidia (*c*) are relatively even larger and the filaments closely compacted. The cleansing currents are similar to those in the two preceding genera with the exception of those on the outer faces of the palp lamella which carry particles to the tip and not to the base.

Conditions in *Yoldia limatula*, as shown in fig. 17, based on figures by Drew (1899) and Kellogg (1915), differ from those in *Malletia* only in details associated with its vertical as opposed to horizontal burrowing. The ctenidia (*c*) are relatively smaller but clearly, from Drew's statements, function in essentially the same manner. A well-developed marginal sense organ (*so*) occurs on a protuberance of the antero-ventral mantle edge. Kellogg (1915), in his account of this species, states that "there is a general ciliation of the mantle walls, with no distinct tracts, collections being carried ventralward and backward and leaving the mantle chamber at the point, just below the siphon, where the palp tentacles are extruded". There is a small glandular region in the postero-ventral region of the mantle not noticed by either Drew or Kellogg.

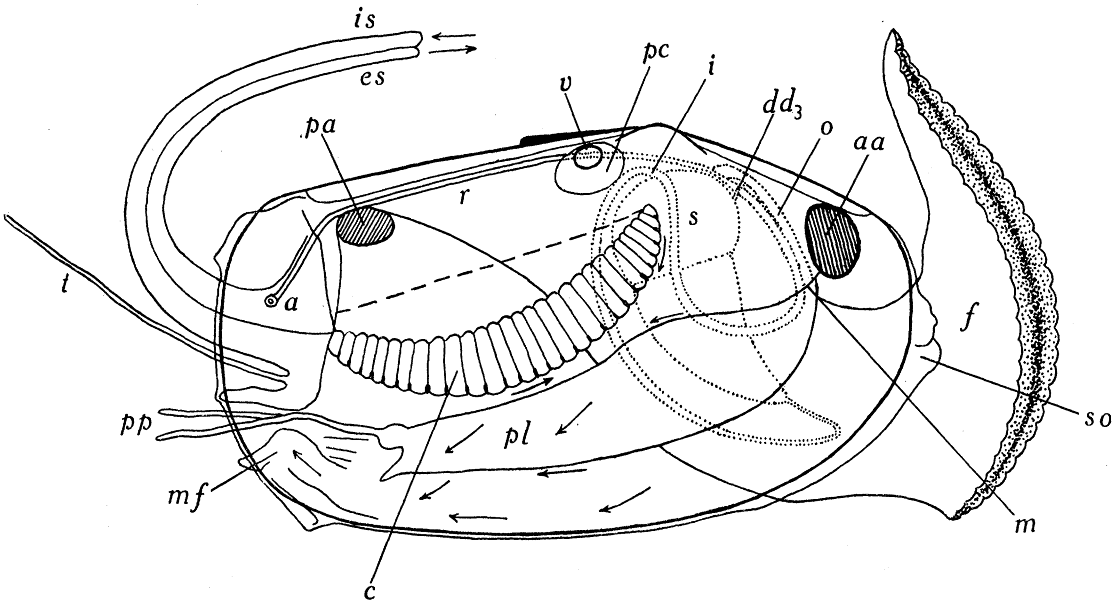

FIG. 16. *Malletia obtusata*, viewed from right side with shell intact. × 10. $dd_3$, duct of third mass of digestive diverticula; *v*, ventricle. Other lettering as before. Broken line indicates position of dorsal surface of ctenidium when pulled upwards during respiratory movements.

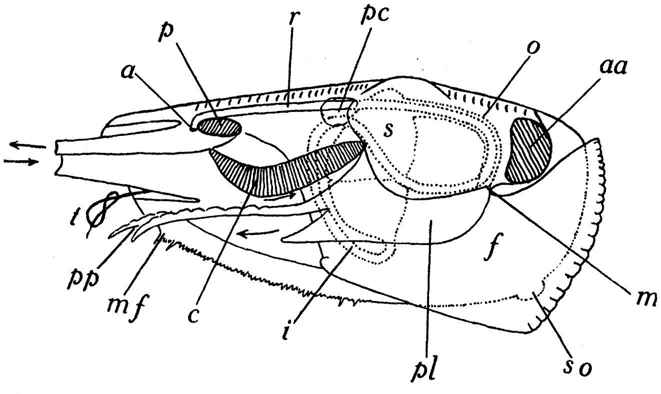

FIG. 17. *Yoldia limatula*, details and lettering as for figs. 15, 16. × 2. Modified after Drew (1899) and Kellogg (1915).

Observations on the Nuculanidae reveal that the constituent genera form a well-defined group with many features in common. The palps are similar in structure and the proboscides are protruded posteriorly. The ctenidial filaments are closely compacted and very muscular (see below), and correlated with these features is the absence of a hypobranchial gland. A posterior glandular region in the mantle occurs in most species. The siphons show an interesting series in the fusion of the walls of the two tubes. In *Yoldiella lucida* and *Y. sulculata* (Stempell 1898*a*) there is no fusion, contact being made by ciliary junctions only; in *Nuculana minuta* and also *Yoldia montereyensis*, *Y. beringiana* and "*Leda*" *fossa* (Heath 1937), the exhalant siphon is a fused tube, but the ventral edges of the inhalant siphon are united by ciliary junctions; while in *Lembulus pella*, *Malletia obtusata* and *Yoldia limatula* both siphons are fused tubes. The different conditions, which are shown diagrammatically in fig. 18, appear to be correlated with the length of the siphons. There would appear to be reason for thinking that in the Lamellibranchia siphons may have originated in this manner, ciliary junctions preceding tissue connexions. Parallel conditions occur in the ctenidia, the interfilamentary connexions of cilia found in the Protobranchia and the Filibranchia giving place in the Eulamellibranchia to tissue connexions between adjacent filaments.

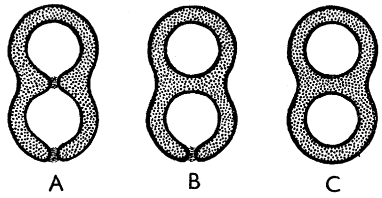

FIG. 18. Diagram indicating the different manner in which siphons may be formed in the Nuculanidae. A, with the partition between the siphons and the ventral surface of the inhalant (ventral) siphon both maintained by ciliary junctions; B, with the former consisting of a tissue junction; C, with both consisting of tissue junctions.

Finally, in the Nuculanidae a marginal sense organ is universally present. Its function is obscure. The cavity in which it lies will certainly be opened out when the foot is withdrawn, and the sense organ possibly possesses tactile properties concerned with the sediment brought in on the sides of the foot which are wiped against this region during withdrawal. Drew (1899) described the protuberance of *Yoldia* as ciliated, bearing a row of sense papillae and having branches of the anterior pallial nerve and enlarged pallial muscles passing into it. He failed to note the internal sense organ later described by Stenta (1909) in "*Leda*" *commutata*. Drew thought that the function was probably tactile in connexion with the foot.

## 4. FORM AND FUNCTION OF THE CTENIDIA

Knowledge concerning the primitive nature of the ctenidia of the Protobranchia dates from the descriptions by Mitsukuri (1881) of those of *Nucula proxima* and *Yoldia limatula*. In 1891 Pelseneer, on the basis of further examination of species of these genera and of *Leda* and *Solenomya*, instituted the order Protobranchia to include all Lamellibranchia in which the two demibranchs of the ctenidia each consist of a series of flattened leaflets more akin to those of the aspidobranch ctenidia of the zygobranchiate Gastropoda, such as *Haliotis* (Yonge 1939), than to the elongated, reflected filaments of the Filibranchia and Eulamellibranchia. The primitive nature of these ctenidia was further demonstrated by Ridewood (1903) who accepted Pelseneer's order Protobranchia. Wallengren (1905) first elucidated the nature and significance of the ciliation of the gills of the higher Lamellibranchia, while Orton (1912, 1913) showed that the ciliation of the gills of *Nucula* and *Solenomya* is essentially similar. Atkins (1936, 1937, 1938) has described these gills in further detail. The functioning of the much more specialized ctenidia of the Nuculanidae was first noted by Kellogg (1892) and Drew (1899), who described these organs in *Yoldia limatula* and drew attention to their pumping action. Kellogg (1915) later gave a very detailed account of the ciliary currents on the ctenidia of this species. Atkins (1936) is the only other worker to observe the living ctenidium in any species of the Nuculanidae. She has described the ctenidia of *Nuculana minuta* in detail and also noted their pumping action due to rhythmical contractions.

The gills of *Nucula* have been described and figured by Orton (1912) and Atkins (1936, 1938), and little further comment is necessary. The nature of the ciliation is shown in fig. 10. There are lateral (*lc*), latero-frontal (*lfc*), frontal (*fc*) and abfrontal (*afc*) cilia; ciliated disks (*cd*) serve to unite adjacent filaments, while long cilia (*ic*) on the inner margins of the leaflets interlock with each other and keep the two ctenidia in functional contact. Similar cilia (fig. 10, *tc*) on the outer tips of the leaflets are in contact with the mantle surface. Orton regarded these also as interlocking cilia, but there are no large cilia on the mantle surface with which they can effectively interlock. It is more probable, especially in view of conditions in the Nuculanidae, that these cilia, which beat upwards, serve to draw the ctenidia downwards. They will thus counteract the action of the water current created by the lateral cilia which will tend to push the ctenidia upwards.

The ciliation on the ctenidia of *Solenomya* is essentially the same as in *Nucula* but abfrontals are absent. Orton (1913) suggested that the ciliated knobs (fig. 13, *ck*) serve to unite the lower leaflets to one another and the upper ones to the sides of the visceral mass. But, as shown in fig. 13, this cannot be so and they actually unite adjacent filaments in the same manner as do the ciliated disks in *Nucula*. The long cilia (fig. 13, *ic*) on the inner sides of the tips of the inner (lower) leaflets interlock with each other and *not*, as Orton suggested, with the mantle. The long cilia (*tc*) on the tips of the upper filaments will serve, as do those of *Nucula*, to counteract the inward pressure of the respiratory current.

In both genera the frontal cilia carry particles to the inner (in *Solenomya* ventral) margins of the inner leaflets whence they are conveyed anteriorly. In *Nucula* (figs. 9, 19) this anterior current extends only as far as the posterior margin of the foot, in *Solenomya* it continues for some distance after the two ctenidia are separated by the foot, actually as far as the palp proboscis (fig. 11, *pp*). Attention should be drawn to the limited, but very definite, muscular action of the suspending membrane attached to the posterior end of the ctenidia in both genera, and previously recorded for *Nucula* by Drew (1901) and Atkins (1936). In both genera chitinous supporting rods (fig. 33, A, B) extend beneath the epithelium bearing the lateral cilia, i.e. along the entire ventral surface, and through the axis run dorsal and ventral longitudinal blood vessels (figs. 10, 13, *db*, *vb*). The remaining point of interest in connexion with these undoubtedly primitive ctenidia concerns their evolution and this will be dealt with in a later paper on the evolution of the molluscan ctenidium.

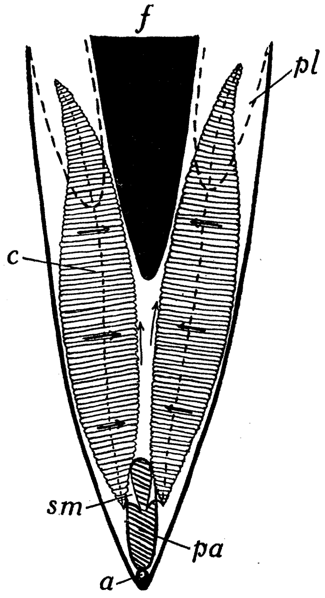

FIG. 19. *Nucula hanleyi*, ctenidia and adjacent organs viewed from the ventral aspect, the two ctenidia being separated owing to pulling apart of the shell valves. × 8. Lettering as before. Arrows indicate direction of ciliary currents on the ventral (frontal) surface of the ctenidial filaments and on their inner margins.

The ctenidia of the Nuculanidae have evolved along very different lines. All function in essentially the same manner. They create a respiratory current primarily by intermittent pumping actions due to muscular contractions and in a manner closely analogous to that found in the Septibranchia (Yonge 1928). The constituent genera may be divided into three groups in accordance with the degree to which their ctenidia are specialized. In *Nuculana*, *Yoldiella* and *Lembulus* the ctenidia are least specialized, in *Yoldia* they are probably somewhat more specialized but are certainly different in significant respects, while those of *Malletia* represent the final stage in the evolution of this type of "pumping" ctenidium.

The structure of the filaments of the first three genera is well exemplified by conditions in *Lembulus pella* (fig. 20). Each is composed of two leaflets, convex ventrally and separated by the concavity of the axial groove (*ag*). Dorsally they are also somewhat convex but upturned at the margins. They are attached, mid-dorsally, to a muscular suspending membrane (*sm*). There are two longitudinal blood vessels, dorsal and ventral (*db*, *vb*), the former running within the base of the suspending membrane and the latter just within the ctenidial axis above the axial groove. Strands of longitudinal muscle (*lm*) lie ventral to both blood vessels. Muscles extend down either side of the suspending membrane immediately below the epithelium and, ventral to the dorsal blood vessel, their fibres radiate out (*rm*) through the extent of each leaflet. All of these muscles are *striated.*

The ventro-lateral surfaces of the leaflets are laterally expanded and united with those of the next filament by ciliary junctions (*cj*). Adjacent filaments can, however, be easily separated in life and always become detached after fixation. The broad dorsal, and the much more restricted ventral, surfaces are not laterally expanded and those of adjacent filaments are free from one another.

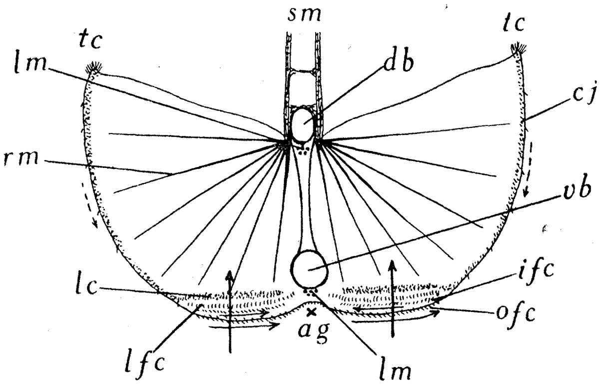

Fig. 20. *Lembulus pella*, lateral view of a single ctenidial filament, drawn from life. × 53 *ag*, axial groove; *cj*, ciliary junction around ventro-lateral margins; *ifc*, inner series of frontal cilia; *lm*, longitudinal muscle; *ofc*, outer series of frontal cilia; *rm*, radiating strands of muscle. Other lettering as before. Arrows indicate direction of beat of lateral and two sets of frontal cilia, broken arrows that of sparse cilia on lateral surfaces, cross the anteriorly directed current in the axial groove.

Lateral cilia (*lc*) are confined to the ventral region; they create a continuous but limited respiratory current. Beneath the epithelium which bears them extend the chitinous supporting rods (fig. 33, C). A line of latero-frontal cilia (*lfc*) bounds the edge of the ventral opening between the filaments. As described by Atkins (1936, 1937) for *Nuculana minuta*, there are two sets of frontal cilia on the ventral surface. Coarse cilia form an outer series (*ofc*) on the summit of the ventral convexity of the filaments. They beat inwards to the middle line between the ctenidia. The inner series (*ifc*), consisting of fine cilia on either side of the outer series, beat inwards towards the axial groove in each ctenidium. The nature of the beat of these cilia is indicated most clearly in fig. 21 which shows the appearance of the ventral region when flattened out under a cover-slip. Material carried to the mid-line between the two ctenidia by the outer series of cilia on the inner filaments is rotated by cilia on the margin and finally conveyed into the tracts of fine cilia and so into the axial groove. In addition to the ventral cilia there are sparse cilia, up to $20\,\mu$ long, on the expanded lateral surfaces of the filaments. These beat towards the ventral surface. On the latero-dorsal margins of the filaments are groups of very long cilia (*tc*) which beat in the opposite direction. They probably help to drive the ctenidia downwards after they have been pulled up in the pumping action.

The filaments are arranged alternately on either side of the axis as shown in fig. 21 and, for *Malletia obtusata*, in fig. 28, although not in figs. 22, 23, 24, 26 as it is not apparent when the ctenidia are stretched out. Kellogg (1892) shows this alternate arrangement in his figure of a horizontal section through the gills of *Yoldia limatula* and Ridewood (1903) in *Y. subaequilateralis*, but neither Drew (1899) nor Kellogg (1915) indicate it in their figures of the intact ctenidia of *Yoldia limatula*. It certainly occurs in all species of Nuculanidae here examined. It is probably primitive, being found also in aspidobranch Gastropoda, such as *Theodoxus* [*Neritina*] *fluviatilis* (Lenssen 1902), and in the Loricata. In the Nuculidae and Solenomyidae the filaments are opposite. This is probably a secondary condition due to the increased numbers of filaments in the ctenidia.

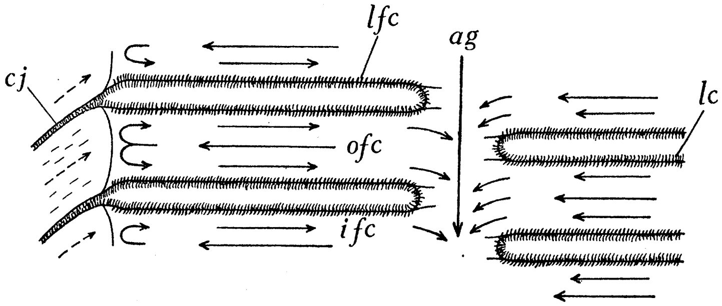

FIG. 21. *Lembulus pella*, portion of right ctenidium from the ventral aspect when flattened under a cover-slip with the inner leaflets shown complete but only the inner half of the outer leaflets, drawn from life. × 115. Lettering and arrows as before.

The filaments of *N. minuta* have been described and figured by Atkins (1936, 1937) and are very similar. The most notable differences are the straighter sides of the filaments and the presence laterally of interlocking cilia near the dorsal extremity of the lateral surfaces of the inner filaments. By this means the filaments of the two sides are united posterior to the foot. The filaments of *Yoldiella lucida* are too small to be easily examined, but they are essentially similar.

The appearance in life of the ctenidia of all three species when viewed from the ventral surface is shown in figs. 22–24, the arrangement of the pore-like ventral openings between the filaments being clearly shown. In *Lembulus pella* (fig. 22) each ctenidium consists of some forty-eight filaments, they are separated for the greater part of their extent by the foot and are not united posterior to this. In *Yoldiella lucida* (fig. 23) each consists of some twenty-six filaments of which the anterior fifteen are separated by the foot, but the remainder are united by ciliary junctions. In *Nuculana minuta* (fig. 24) each consists of about forty filaments of which only the anterior fourteen are separated by the foot, the remainder being united. In all, the frontal ciliation is similar. Material which is carried to the middle line by the outer series of frontal cilia tends to be carried back to the axial grooves by the inner series as indicated in fig. 21. Atkins (1936) states that in *N. minuta* material which collects in the mid-line posterior to the foot tends to be thrown forward from filament to filament by muscular and not ciliary action and so finally conveyed to the rejection tracts on the posterior margin of the foot. This was not observed in *Lembulus pella*. In other cases it drops off into the mantle cavity.

Material in the axial grooves is carried anteriorly over the greater part of the ctenidia, but posteriorly in the extreme anterior end. The two streams meet in the region of the fourteenth filament (counting from the anterior end) in *Lembulus pella* and at the eighth filament in *Nuculana minuta* and *Yoldiella lucida*. The ultimate fate of this material will be considered in the section devoted to feeding.

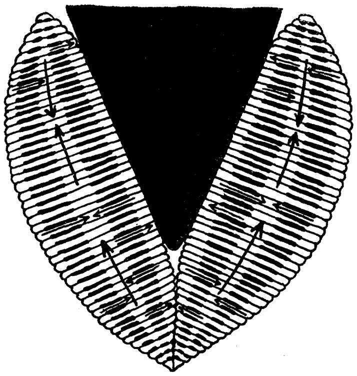

FIG. 22. *Lembulus pella*, ctenidia viewed from the ventral aspect after the shell valves have been pulled apart. × 8.

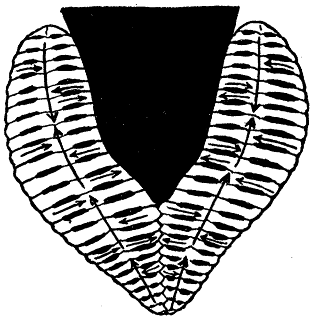

FIG. 23. *Yoldiella lucida*, ventral view of ctenidia. × 22.

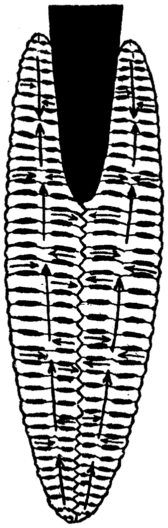

FIG. 24. *Nuculana minuta*, ventral view of ctenidia. × 16.

The ctenidia of *Yoldia limatula*, originally described by Mitsukuri (1881), have been examined from the functional aspect by Kellogg (1892, 1915) and Drew (1899). The essential features of the filaments are shown in fig. 33, D. They differ from those of the three genera just considered in their more rounded form, the lateral surfaces being extended dorsally and curling inward. Ciliary junctions (fig. 33) extend from the dorso-lateral margin to the middle of the lateral surface leaving wide ventral and ventro-lateral openings between the filaments. The extent of the lateral cilia and of the chitinous supporting rods (fig. 33) is correspondingly wide. Although not specifically mentioned by either Kellogg or Drew, sections reveal that latero-frontal cilia fringe the openings. According to Kellogg (1915), the frontal cilia beat exclusively towards the axial groove, cilia corresponding to the outer series in the three preceding genera being apparently absent. Although the ctenidia are only separated for half their length by the foot (see fig. 17), there appear to be no interlocking cilia uniting the filaments of the two sides but, although not previously described, long cilia (fig. 40, pl. 15, *tc*) do occur on the latero-dorsal margins. In this figure the ventral blood vessel (*vb*) and longitudinal muscles (*lm*) are clearly displayed. A unique feature is the modification of the third and fourth filaments of the inner side only of each ctenidium. They are swollen (Drew 1899) and allow particles of sediment to pass between them into the supra-branchial cavity (Kellogg 1915).

The ctenidia of *Malletia obtusata* were examined in great detail both in life and after sectioning. They have not previously been described and are of unusual interest owing to their high degree of specialization. They are relatively somewhat larger than in the other Nuculanidae and form two elongated rounded masses which extend for about half the length of the body (fig. 16, *c*). Each ctenidium is about 1 mm. wide in the middle of its length in an animal 1 cm. long. There are about fifty filaments (fig. 26) of the same general appearance as those of *Lembulus pella*. They are attached to a very muscular suspending membrane (fig. 25, *sm*) and the radiating (*rm*) and longitudinal muscles (*lm*) in the filaments are very well developed. As in all other species of Nuculanidae these muscles are striated. The two longitudinal blood vessels (*db*, *vb*) are notably wide.

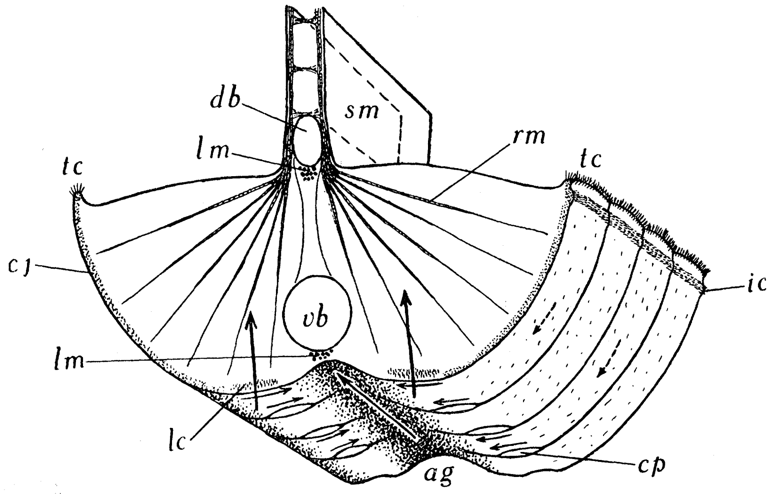

FIG. 25. *Malletia obtusata*, four filaments of the right ctenidium taken from the region posterior to the foot and viewed from the antero-ventral aspect showing the margins of the inner leaflets. × 65. *ic*, cilia on inner leaflets which interlock with those on the left ctenidium; *cp*, ciliated pores representing the small extent to which the filaments are not united ventrally. Other lettering as before. Arrows indicate direction of beat of lateral and frontal cilia and those in the axial groove, broken arrows that of sparse cilia on lateral surfaces of filaments.

As shown in fig. 25, the ventral and lateral surfaces of the filaments are laterally expanded, and, except for a very restricted pore-like region (*cp*) on the summits of the convexities on either side of the axial groove, united by ciliary junctions (*cj*). This union is so firm that the living ctenidia can be stretched tightly without the filaments separating. They only part after hard and repeated pulling with needles. The general impression gained of the living ctenidia is that of a delicate septal membrane perforated by four longitudinally arranged series of slit-like pores (see fig. 26). When touched the ctenidia react as a unit and not as a series of semi-independent filaments as do those of *Nucula*. The inner margins of the inner filaments of either side are united to one another in the region posterior to the foot by means of interlocking cilia (fig. 25, *ic*) situated on a low ridge near the latero-dorsal margin. These junctions in life are as firm as those between adjacent filaments of the same ctenidium. Their structure is shown in fig. 27.

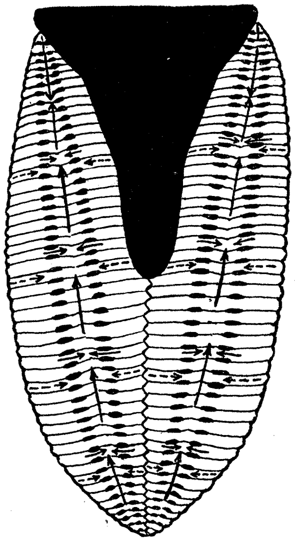

FIG. 26. *Malletia obtusata*, ventral view of ctenidia. × 16.

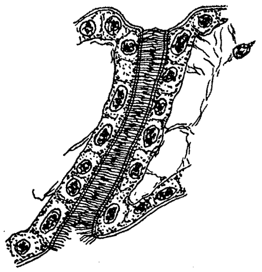

FIG. 27. *Malletia obtusata*, transverse section through ciliary junction uniting inner leaflets of filaments posterior to foot (see fig. 25, *ic*). × 516.

Groups of cilia, about 40 $\mu$ long, occur on the rounded latero-dorsal margins (fig. 25, *tc*). The probable function of these has already been discussed in the case of *Lembulus pella*. Contact with the mantle surface laterally and with the sides of the foot in the mid-line anteriorly is certainly maintained by the great distension of the filaments with blood. This is not obvious in fixed material when the filaments collapse (see figs. 30, 31), but is very marked in life. Dorsally the filaments are not expanded laterally and are free from one another. This is shown in fig. 28 which also clearly indicates the relative size of the ventral openings and their connexion with the wide space between the filaments dorsally.

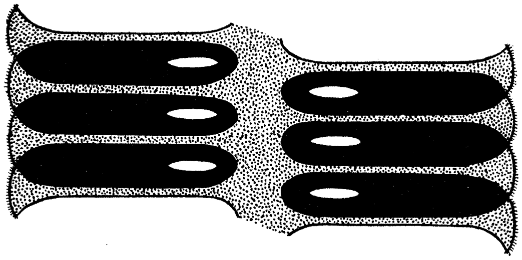

FIG. 28. *Malletia obtusata*, semi-diagrammatic representation of the appearance, from the dorsal aspect, of the ctenidial filaments. Axis and dorsal surface of filaments stippled, ventral ciliated pores between filaments (see fig. 25, *cp*) shown white. × 65.

The ctenidia are united anteriorly with the visceral mass by means of the axis, the dorsal vessel entering in this region and the ventral vessel leaving. Posteriorly the terminal filaments of each ctenidium are united to the base of the septum separating the two siphons. Union takes the form of yet another ciliated junction. This is more extensive than any of the others, the postero-dorsal surface of the filaments wrapping round the end of the siphonal septum as shown in section in fig. 29 and fig. 45, pl. 15 (*cjs*). In *Yoldia limatula* the terminal filaments do not wrap round the base of the siphonal septum but are applied to the morphologically dorsal surface of this which is bent at right angles ventrally. The very extensive ciliary junction so formed is shown in fig. 40, pl. 15. Less extensive ciliary junctions of the same type unite the ctenidia of *Lembulus pella* and *Nuculana minuta* to the siphonal septum. *Yoldiella lucida* is so small that the exact state of affairs is difficult to determine, but a ciliary junction exists. The strain that must be encountered in this region when the ctenidia are raised indicates the great efficiency of these ciliary junctions.

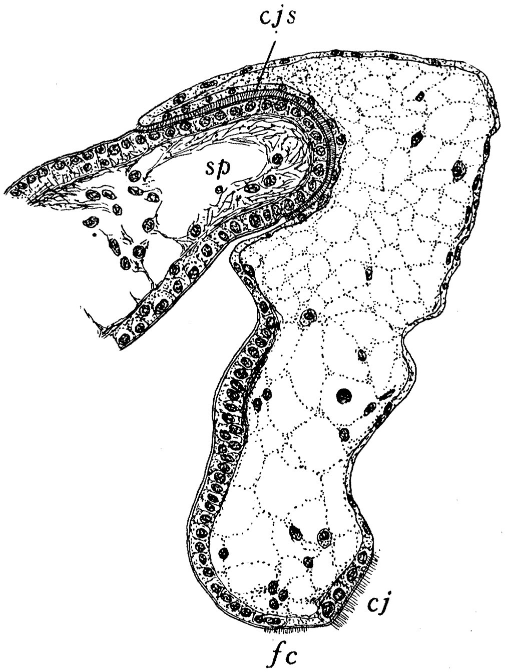

FIG. 29. *Malletia obtusata*, longitudinal section showing nature of the ciliary junction between the terminal ctenidial filament and the anterior end of the siphonal septum. × 387. *cjs*, ciliated junction between postero-dorsal surface of filament and siphonal septum; *sp*, siphonal septum. Other lettering as before.

The detailed structure of the filaments of *Malletia obtusata* can best be described by reference to transverse sections through one of the ventral pore-like openings (fig. 30) and through the region of ciliary junction lateral to this (fig. 31). In both regions columnar epithelium with numerous large nuclei bounds the frontal (ventral) surface and the lateral surface to the limited extent to which this is ciliated. The greater part of the lateral surfaces and the abfrontal (dorsal) surface is bounded by a very thin pavement epithelium with a few scattered nuclei. There is a very spacious internal cavity and this is occupied, apart from strands of striated muscle (*mu*) and connective tissue, with coagulated blood plasma and a few blood cells.

Frontal cilia (fig. 30, *fc*) are sparse and confined to the margins of the frontal regions

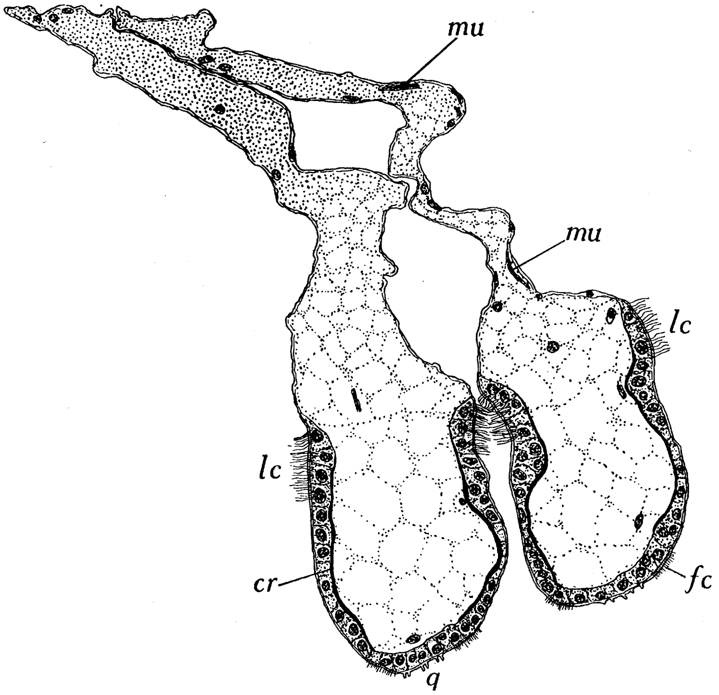

FIG. 30. *Malletia obtusata*, transverse section through two ctenidial filaments in the region of the ventral ciliated pores. × 387. *cr*, chitinous supporting rods; *mu*, strands of striated muscle; *q*, outgrowths on frontal surface. Other lettering as before.

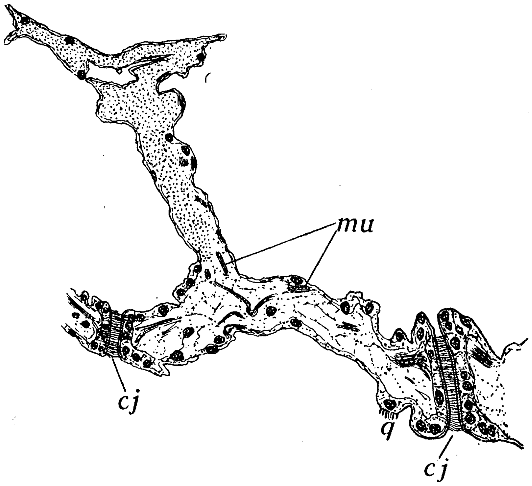

FIG. 31. *Malletia obtusata*, transverse section through a ctenidial filament lateral to that shown in fig. 30 and passing through ciliated junctions with the adjacent filaments. × 387. Lettering as before.

between the ventral pores and regions immediately adjacent to this (fig. 29, *fc*). Scattered frontal cilia seen in life on the lateral margins of the filaments (indicated in fig. 25) are not apparent in sections. There is *no* division into outer and inner series of frontal cilia as in *Lembulus pella* and *Nuculana minuta*. Small outgrowths of unknown function also occur on the frontal regions (figs. 30, 31, *q*). Long lateral cilia occur on the opposed faces of the leaflets on the sides of the pores (figs. 25, 30, *lc*), but they are restricted to an area only four or five cells in depth at the dorsal extremity of the columnar epithelium. The limited region occupied by lateral cilia is strengthened by chitinous supporting rods (fig. 30, *cr*) beneath the epithelium. The unusually short extent of these is indicated in fig. 33, E. Latero-frontal cilia are absent and also, as in all Nuculanidae, abfrontals. The ciliary junctions (fig. 31, *cj*) are similar to those between the filaments of the ctenidia of the two sides but the valve-like nature of their dorsal surfaces is noteworthy. It is strikingly reminiscent of the structure of the pores in the muscular septum of Septibranchia such as *Cuspidaria* (Yonge 1928).

Examination of the cilia in life revealed that the sparse frontal cilia carry particles exclusively into the axial groove (figs. 25, 26) where a weak ciliation is responsible for their passage forward except in the extreme anterior region where the current is posterior (see fig. 26). As in *Nuculana minuta* and *Yoldiella lucida*, the two currents meet at the eighth filament where material collects into small masses and then drops off on to the posterior surface of the foot or on to the mantle or is possibly removed direct by the palp proboscides. Only in the latter case (never actually observed) could it reach the palp lamella and so possibly the mouth.

The movements of the ctenidia were followed both in the intact animal (impossible in the other Nuculanidae owing to the opacity of the shell) and after one valve had been removed. After being drawn upwards by the contraction of the striated muscles they slowly descend owing to the combined effect, probably, of (1) relaxation of the muscles, (2) distension of the filaments with blood, (3) passage of water through the ventral pores owing to the action of the lateral cilia and (4) the beating of the long cilia (*tc*) on the latero-dorsal margins. They then assume the position shown in fig. 16 and, in diagrammatic transverse section, in fig. 32 (*c*). After a period of, on the average, 28 sec. after the last upward movement, the contraction of the longitudinal and radial muscles in the ctenidia aided by the muscles in the suspending membrane again causes a sudden raising which is accompanied by the sudden intake through the inhalant, and expulsion through the exhalant, siphon already described. The contraction of the longitudinal muscles will cause complete or almost complete closure of the ventral openings. The position of the ctenidia when drawn up is indicated by the broken line in fig. 16 and by the dotted outline ($c_1$) in fig. 32. The general form and remarkably compact nature of the ctenidia and the closeness with which they are applied, owing to distension with blood, to the surface of the mantle, to the sides of the foot and to each other posteriorly—as shown in fig. 32—together with the ciliary junction with the siphonal septum, combine to render them an admirable pumping septum.

The ctenidia of all of the Nuculanidae are thus modified to form delicate septal partitions perforated by slit-like ventral pores (see figs. 22, 23, 24 and 26) and completely separating the inhalant and exhalant chambers. The frequency of the pumping action varies in the different species, as stated in the section on habits, but it also varies from time to time in the same individual. The ctenidia of all species are characterized by a ventral and lateral flattening of the margins of the filaments, by highly developed ciliary junctions with consequent reduction of free cilia and by the presence of striated muscles. The latter have presumably been evolved, as have the striated muscles in the septum of *Cuspidaria* (Grobben 1892; Yonge 1928), in connexion with the repeated sudden movements of the ctenidia. In correlation with the loss of cilia is a conspicuous reduction in mucous glands. They are relatively numerous in *Yoldia* in correlation with the greater extent of free cilia. There is a copious blood supply, entering anteriorly by way of the dorsal (afferent) vessel and leaving, also anteriorly, by the ventral (efferent) vessel, as originally stated by Pelseneer (1891) for the ctenidia of *Nucula*. Circulation of blood in the ctenidia is thus essentially as it is in the ctenidia of the prosobranch Gastropoda, i.e. in the primitive condition. The ctenidia of *Nucula* and *Solenomya* are in respect of their blood supply unmodified, but in the Nuculanidae the blood space within the filaments is greatly increased. This represents specialization in connexion with the mode of action of these ctenidia, but it also indicates that they have retained to the full the primitive function of respiration. It is possible, as suggested originally by Drew (1899), that the pumping movements may assist in the circulation of the blood.

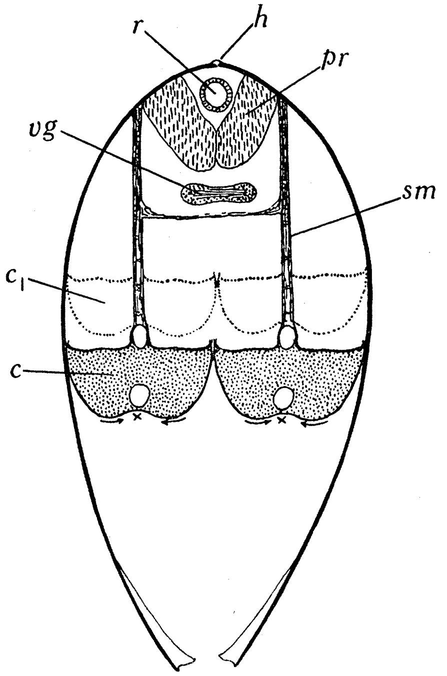

FIG. 32. *Malletia obtusata*, semi-diagrammatic cross-section through the region posterior to the foot showing the manner in which the ctenidia are raised. × 14. $c_1$, position of ctenidial filaments when fully raised; *h*, hinge; *vg*, visceral ganglia. Other lettering as before.

In fig. 33 the salient points of the ctenidial filaments of (A) *Nucula*, (B) *Solenomya*, (C) *Lembulus*, (D) *Yoldia* and (E) *Malletia*, are compared. In the two first the water current is created by lateral cilia exclusively, as in the primitive molluscan ctenidium. The area occupied by these cilia is indicated by the extent of the chitinous supporting rods (shown cross hatched). Adjacent filaments are united by indifferently efficient ciliated disks and knobs (both shown in black), while filaments of the two sides are united by interlocking cilia (*ic*) easily separated in life. In all Nuculanidae the filaments are united to a much greater extent by cilia which are with little doubt modified lateral cilia. Reduction in the area occupied by lateral cilia is indicated by the limited extent of the chitinous supporting rods, which are small in *Lembulus* (also *Nuculana* and *Yoldiella*), wide in *Yoldia*, but still smaller in *Malletia*. Ciliary junctions (*ic*) also unite the inner filaments of the two sides posterior to the foot in *Nuculana*, *Yoldiella* and *Malletia*, but not in *Lembulus* or *Yoldia* which rely on blood pressure exclusively for this union. Latero-frontal cilia occur in all Protobranchs examined with the exception of

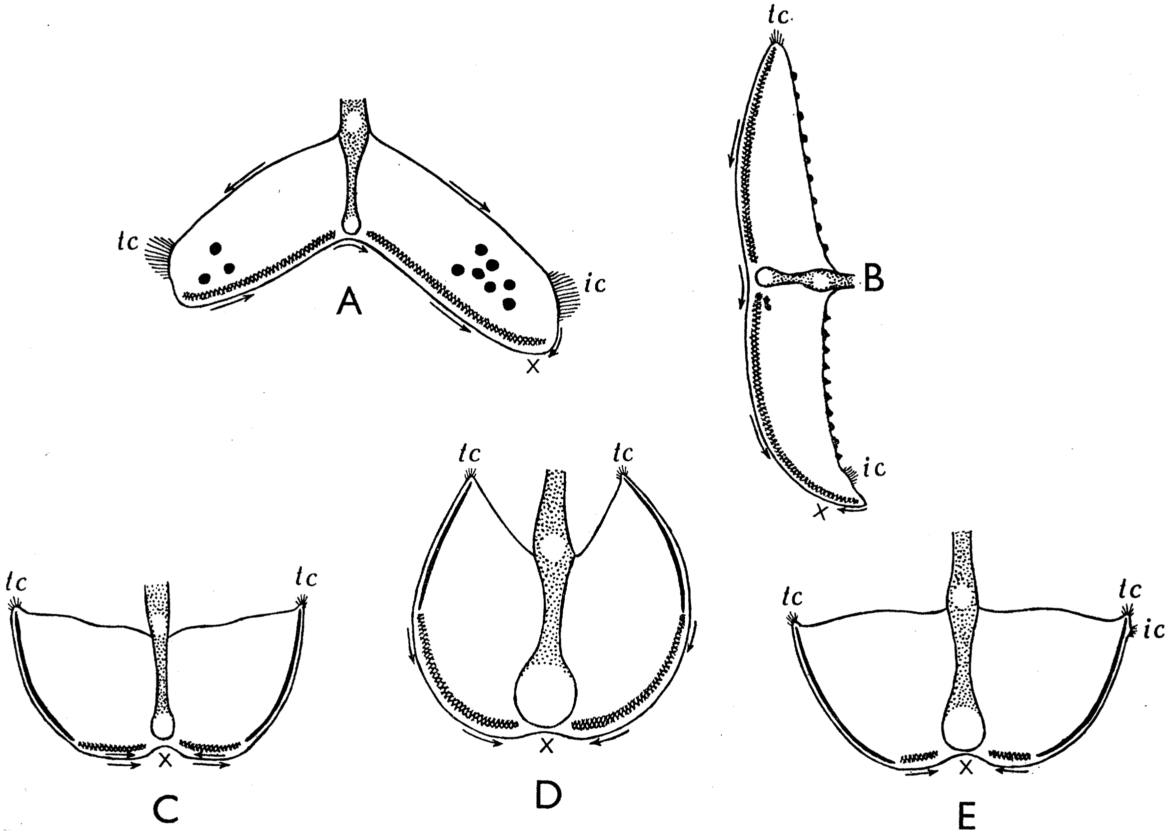

FIG. 33. Semi-diagrammatic representation of the ctenidial filaments in A, *Nucula*; B, *Solenomya*; C, *Lembulus pella*; D, *Yoldia limatula*; E, *Malletia obtusata*. Varying magnifications. *ic*, interlocking cilia between inner filaments of ctenidia of two sides; *tc*, terminal cilia. Ciliary junctions between adjacent filaments of same ctenidium shown black, extent of chitinous supporting rods (and so of lateral cilia) shown by cross hatching. Arrows indicate beat of frontal cilia only (and abfrontals in *Nucula*), crosses position of anteriorly directed ciliary currents.

*Malletia*. Here the ventral openings between the filaments are apparently too small to require the sieving action of these cilia for the prevention of particles passing through them into the suprabranchial chamber. Long cilia (*tc*) on the outer, and in the Nuculanidae also on the inner, latero-dorsal margins of the filaments probably in all cases assist in maintaining the ctenidia in a ventral position. In *Yoldia* the dorsal projections of the filaments probably aid in this. Drew (1899) states that "Pressure is insured by the pressure of the blood inside the plates, and by the soft dorsal projections of the plates. These projections must act like the leather on a plunger of a suction pump, making good contact when the pressure is from above and not hindering its descent."

In *Nucula* and *Solenomya* particles are carried by the frontal cilia to the inner margins of the ctenidia where they pass forward over the great extent of the ctenidia. The action of the coarse outer frontal cilia in *Lembulus*, *Nuculana* and *Yoldiella* has the same effect and these ctenidia may therefore be regarded as to some extent intermediate in character between those of *Nucula* and *Solenomya* on the one hand and those of *Yoldia* and *Malletia* on the other. The frontal cilia in the last two beat exclusively towards the axial groove as do the fine, inner cilia *Lembulus*, *Nuculana* and *Yoldiella*. In *Nucula* alone are the primitive abfrontal cilia retained.

In respect of their great reduction in free cilia and high development of ciliated junctions between adjacent filaments, filaments of the two sides and between ctenidia and siphonal septum, the ctenidia of *Malletia* may be regarded as representing the culminating stage in the evolution of the pumping ctenidia of the Nuculanidae. Those of *Yoldia* have clearly evolved on somewhat different lines. The filaments are less specialized in respect of ciliated junctions, but are more specialized in shape while the modified third and fourth filaments of the inner side are unique.

Although the ctenidia of the Nuculanidae function in a manner similar to the septum of the Septibranchia and striated muscle is present in both (excluding the less specialized septibranch, *Poromya*), there are important points of difference. When at rest the septum is in the dorsal position (Yonge 1928), but the ctenidia of the Nuculanidae are in the ventral position. The septum is attached to the shell by pairs of anterior and posterior septal muscles, modifications possibly of the original longitudinal muscles in the case of *Cuspidaria*, in the Nuculanidae by a suspending membrane. The current created by the septum is powerful enough to draw in the animal matter on which the Septibranchia feed, respiration being carried out primarily through the mantle; in the Nuculanidae feeding is by means of the palp proboscides, the ctenidae being exclusively, or almost exclusively, concerned with respiration. The resemblance between the two is the result of convergence, although both represent modifications of the same fundamental structures.

## 5. Labial palps and feeding

### (a) *Nuculidae*

Hirasaka (1927) has described both the structure and mode of functioning of the labial palps in *Nucula nucleus*. No significant differences have been observed in the other species examined. Each palp consists of a pair of relatively immense palp lamellae (fig. 9, *pl*), the opposed faces of which are ridged, and a single palp pouch (*po*) and palp proboscis (*pp*) (Hirasaka's terminology is used throughout). The proboscis is capable of great extension and is very mobile. The under surface is grooved and richly ciliated, the upper convex surface is unciliated but both surfaces have many mucous glands. The proboscis is attached to the postero-dorsal corner of the outer lamella, and its longitudinal muscle is continued through the side of the visceral mass forming a retractor (Pelseneer 1891). Functional contact is made between the proboscis and the internal faces of the lamella by means of the concave palp pouch which is attached immediately posterior to the base of the proboscis and hangs down with the inner margin lying between the opposed lamellae and the outer margin in the concavity of the proboscis. As noted by Drew (1901) and Morse (1919), as well as by Hirasaka, during feeding the palp proboscides are extruded between the opened shell valves on the ventral side immediately posterior to the heel of the foot (see fig. 2, *pp*). *Nucula* feeds beneath the surface, but occasional extrusions of the proboscides when the animal is not buried reveal their great extensibility and mobility. Material is collected by the tip and passes, by way of the ciliated groove, to the base of the proboscis. It is here transferred to the inner surface of the pouch which conveys it between the palp lamellae where it is sorted out by the action of complex series of ciliary tracts on the ridges and folds, aided by muscular action and mucous secretion. Excess material is carried to the free (ventral) margins of the palp lamellae by ciliated tracts on upper regions of the ridges, other material is conveyed into the lateral oral groove between the opposed lamellae by way of deeper currents (exactly as shown for *Yoldiella* in fig. 35). Hence it is carried towards the mouth. But there is also a passage of fine material, not observed by Hirasaka, over the surface of the ridges towards the mouth. The material carried to the free edges of the lamellae is conveyed to their tips which curl back and so transfer it to the mantle surface. The mechanism is essentially the same as that in the higher Lamellibranchia (Wallengren 1905; Kellogg 1915; Yonge 1923, 1926*b*), except that, in correlation with the nature of the food particles, larger particles and masses eventually reach the mouth.

As shown by Orton (1912, 1913), the frontal cilia on the ctenidia carry particles to the mid-line between the two ctenidia where they are passed forward in a common stream to the posterior margin of the foot. But at best this can be regarded as no more than an accessory means of food collection and for the following reasons:

(1) The ctenidia and palps are not directly connected, although Orton (1912) and Atkins (1936) have described some degree of co-operation between the two.

(2) A highly efficient mechanism for the direct collection of organic detritus exists in the palp proboscides.

(3) The ctenidia are relatively small and the lateral surfaces of the filaments restricted in area so that, as already stated, the current created—and hence the amount of material drawn in—is very much less than in the Filibranchia or Eulamellibranchia. For this reason observations, such as those of Atkins (1936), on the transference on to the palps of relatively large amounts of material placed on the ctenidia when one shell valve has been removed have probably little bearing on conditions in life.

(4) The relatively inefficient lateral attachments of the filaments by means of ciliated disks enable many of the finer particles to pass direct into the suprabranchial cavity. The presence of hypobranchial glands is an indication that material *does* pass in quantity into this region. Muscular action may also cause separation of the two ctenidia. The ctenidia of *Nucula* cannot be compared as strainers of food particles with those of the Filibranchia or Eulamellibranchia.

(5) All material collected by the ctenidia passes to the posterior region of the foot where currents will tend to carry it direct to the principal region of extrusion (see fig. 9).

While it is impossible to agree completely with Hirasaka's statement that "almost all particles on the gill fall into the mantle cavity" being later expelled, it is equally impossible to agree fully with Orton (1912, 1913) and Atkins (1936) who regard the ctenidia as feeding organs. They are better regarded as essentially organs of respiration with possibly some accessory function as collectors of food particles.

### (*b*) *Solenomyidae*

The palps of *Solenomya* are smaller and simpler in structure than in any other Lamellibranch. The only obvious portion is a single, small triangular flap (figs. 11, 34, *pp*) on either side which never extends more than half way down the side of the foot. It is *not* ridged in the inner face. Previous workers have been content to regard this as the entire palp but, as shown in figs. 11, 34, it is attached at its base to the outer of two thin ridges which enclose a narrow groove (fig. 34, *gp*). Those of the two sides run forward and meet anteriorly in the region of the mouth (*m*). As shown by Orton (1913) particles are collected on the relatively very large ctenidia and passed by frontal cilia to the mid-ventral line where they are carried forward and finally upwards on either side of the base of the foot (see figs. 11, 12). The mobile ends of the palps hang down and normally rest on the anterior edge of the ctenidia about the region where this anteriorly directed ciliary current ceases, as shown in fig. 11. Morse (1913) found that in *S. velum* particles are collected from the ctenidia by the very mobile palps and carried to the mouth. This has been confirmed in *S. togata*. Cilia on the under, somewhat concave, face convey particles into the narrow groove (fig. 34, *gp*) which communicates with the mouth (*m*). The ridges which bound the groove are richly ciliated, particles being carried upwards on both sides and so into the rejection tracts on the base of the foot (see figs. 11, 34). Only the particles deepest in the groove will actually reach the mouth.

There can be no question that in *Solenomya* the enlarged ctenidia are responsible for food collection as well as for respiration and that the palps merely serve, as in the Filibranchia and Eulamellibranchia, for the conveyance of this to the mouth and for its final sorting. Selection is very rigid. Not only are large masses of material conveyed posteriorly over the surface of the ctenidia as already described (see broken arrows in fig. 12) but the material which is carried forward is further selected in the grooves so that only the very finest particles or masses reach the mouth. Ridewood (1903) and Morse (1913) regarded the single triangular flap as representing the palp proboscis of other Protobranchia, and this may be accepted, but there can also be little doubt, from the standpoint alike of position and function, that the ridges bounding the groove leading from this to the mouth represent reduced, but still efficient, palp lamellae.

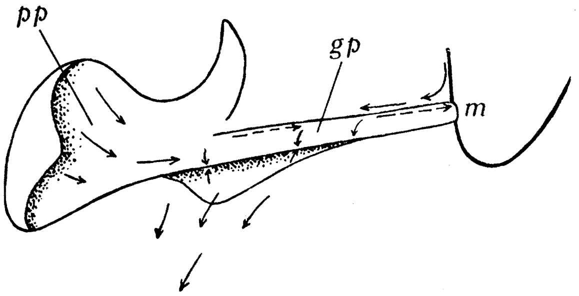

FIG. 34. *Solenomya togata*, labial palps of right side with proboscis turned back to show under surface. × 80. *gp*, position of groove bounded by ridges which represent reduced palp lamellae. Other lettering as before. Broken arrows indicate direction of ciliary currents in groove.

It may be deduced that in *Solenomya* bottom material is drawn into the mantle cavity anteriorly, by muscular rather than by ciliary action, and that, after rigorous sorting on the ctenidia and the palps, the finest particles are passed to the mouth. Conditions are therefore somewhat intermediate between those in the other Protobranchia, which feed on bottom deposits by means of the palp proboscis, and those in the Filibranchia and Eulamellibranchia which feed primarily on phytoplankton brought in with the inhalant current.

### (*c*) *Nuculanidae*

In all of the Nuculanidae the palp proboscis is very large and has essentially the same structure and mode of functioning as in the Nuculidae, i.e. is grooved and highly ciliated on the under side, and convex and unciliated on the upper side. It is attached to the base of the outer lamella and possesses a retractor muscle. Hirasaka (1927) states that the palp pouch occurs only in *Nucula* and neither Atkins (1926) nor Kellogg (1915) figure anything corresponding to it in *Nuculana minuta* or in *Yoldia limatula*. It is certainly absent in *Lembulus pella*, but does appear to be represented in *Nuculana minuta*, *Yoldiella* *lucida* and *Malletia obtusata* by a small flap (see fig. 35, *po*) which forms an extension of the inner palp lamella and which encircles the base of the proboscis. It is much better developed in *Nuculana minuta* than in the other two species (fig. 14, *po*). The palp lamellae have the same structure as in *Nucula*, the internal ridges being especially numerous in *Malletia obtusata*. Food material is collected by means of the palp proboscis, the tips of which in all cases project far beyond the posterior extremity of the shell, and is carried in along the grooves. The reduced palp pouch assists in all cases with the conveyance of material between the lamellae and there is therefore good reason for considering this homologous with the larger structure in the Nuculidae. Between the lamellae, as shown in fig. 35, particles are sorted out in the usual manner. Currents on the summits of the ridges carry fine particles across the lamellae towards the mouth, others, somewhat deeper, carry particles to the margins of the lamellae where they are carried back and eventually conveyed to the mantle surface. Currents still lower down carry material into the lateral oral groove (*log*) between the opposed lamellae. Here it is carried forward to the mouth, being there joined by material conveyed over the summits of the ridges. In *Nuculana minuta*, as previously described by Atkins (1936), the posterior tip of the outer lamella is elongated the better for disposing of waste material. This is also the case in *Lembulus pella*, but not in *Yoldiella lucida*, *Malletia obtusata* or in *Yoldia* (Kellogg 1915). There is no connexion between the palps and ctenidia. Indeed in *Nuculana minuta*, *Lembulus pella*, *Yoldiella lucida* or *Malletia obtusata*, as shown in fig. 35, currents on the intervening surface of the visceral mass carry particles posteriorly away from the palps. Any collection of material by the ctenidia must, therefore, if it is ever to reach the mouth, be conveyed direct from the gills by way of the palp proboscis. This was never observed, but it may possibly occur. In *Yoldia limatula*, Kellogg (1915) has described and figured a posterior extension of the lateral oral groove (representing, as noted by Atkins (1936), the posterior margins

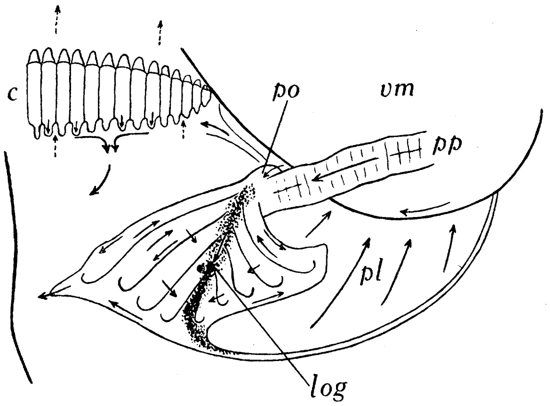

FIG. 35. *Yoldiella lucida*, labial palps of right side with part of outer lamella turned back. × 26. *log*, lateral oral groove; *vm*, visceral mass. Other lettering as before. Arrows indicate direction of currents on inner and outer faces of lamellae, under surface of palp proboscis, on the anterior end of the ctenidia and adjacent regions.

of the palp lamellae which are fused for some distance from their base in this genus) which "is often placed in such a position that it touches the lower surface of the anterior end of the gill...from time to time it receives the gill collections". No such mechanism exists in the other genera of the Nuculanidae. This fusion of the base of the posterior border of the lamellae explains the absence of anything corresponding to the palp pouch in *Yoldia*.

In the Nuculanidae, as in the Nuculidae, feeding is essentially the concern of the palp proboscis and the ctenidia play little, if any, part in this. Opinions have varied as to the significance of ciliary collections on the ctenidia. For *Y. limatula* Drew (1899) considered that food collection by the ctenidia was unnecessary and also that their pumping action "would seriously interfere with their normally performing such a function". Kellogg (1915), on the other hand, observed that particles were carried from the ctenidia to the palp lamellae by way of the extension of the lateral oral groove and states that the pumping action of the ctenidia does not disturb small collections. The extent of the frontal cilia is certainly greater than in any other genus of the Nuculanidae (see fig. 33). Atkins (1936) finds "it difficult to believe that the chief function of the gill of *Nuculana* is that of collecting food", and stresses the small extent of the possible food collecting surface. This is equally true of *Yoldiella* and *Lembulus*, while in *Malletia* food collection by the ctenidia is certainly negligible. It must be borne in mind that the presence of frontal cilia does *not* necessarily imply food collection, their primitive function being that of collecting and carrying away sediment brought in with the respiratory current, a function which they continue to possess in the prosobranch Gastropoda and the Loricata (Yonge 1938, 1939). With the exception of the Solenomyidae there is no definite evidence that they have taken over the function of food collection in any of the Protobranchia while in the Nuculanidae muscular activity has rendered even their cleansing function largely unnecessary.

## 6. ALIMENTARY CANAL

In general form the alimentary canal of the Protobranchia is similar to that of other Lamellibranchia. The course it takes in the majority of the species examined is shown in figs. 9 (*Nucula hanleyi*), 14 (*Nuculana minuta*), 15 (*Yoldiella lucida*), 16 (*Malletia obtusata*), 17 (*Yoldia limatula*) and 38 (*Solenomya togata*). The gut of *Lembulus pella* resembles that of *Nuculana minuta* in all essentials.

In all the mouth (*m*) opens in the mid-line ventrally some little distance behind the anterior adductor (*aa*). It leads into a short, relatively wide oesophagus (*o*) which in some cases, e.g. *Yoldiella lucida* and also *Lembulus pella* (Pelseneer 1891), bends anteriorly before passing dorsally and then posteriorly into the antero-dorsal region of the stomach (*s*). In all but the Solenomyidae this is a relatively enormous structure, by far the largest organ in the body. It is divided into two well-defined regions: a rounded dorsal region into which open the ducts of the digestive diverticula, and an elongated ventral region which tapers to a point ventrally where the intestine (*i*) emerges from it. This ventral region extends into the base of the foot and its position in the Nuculanidae varies with the movements of the foot, being directed posteriorly when the foot is withdrawn, as in figs. 14 and 15, ventrally when the foot is partly extruded (fig. 17), and anteriorly when the foot is fully extended (fig. 16). The intestine (*i*) runs on the right side of the body and, except in the Solenomyidae, describes a varying number of loops before passing dorsally and becoming median in position. Finally it merges into the rectum (*r*) which passes through the ventricle in all but the Nuculidae, where it runs ventral to the heart. The anus (*a*) opens behind the posterior adductor (*pa*) and in some species, notably *Malletia obtusata* (fig. 16), is not attached to this but extends into the base of the exhalant siphon.

Although most workers on the Protobranchia, especially Heath (1937) who has figured many species, have described the general anatomy of the alimentary canal, only Pelseneer (1891) and, in more detail, Stempell (1898*a*, 1899) have given any account of histology. But the value of this work is much reduced by lack of knowledge as to the physiology of the gut and consequent inability to correlate form and function. The alimentary canal is actually highly specialized for extracting nutriment from the particles of organic detritus mixed with fragments of sand and other inedible matter which are collected by the palp proboscides (with the exception of *Solenomya*), and, after rigorous sorting on the palp lamella (and ctenidia in *Solenomya*), are passed into the mouth. The structure of the various regions of the gut has been examined from the functional aspect, in most detail in the Nuculanidae and especially in the largest of these, *Malletia obtusata*. Conditions in this family will therefore be discussed first, significant differences in the Nuculidae and the Solenomyidae being recorded later.

### (*a*) *Nuculanidae*

#### (i) *Mouth and oesophagus.*

The mouth is a relatively wide opening leading into the oesophagus which, with the exception of the stomach, is the most capacious region of the alimentary canal. It is dilated in the region adjacent to the mouth, laterally in the majority of cases but also dorso-ventrally in *Lembulus pella* and *Yoldiella lucida* (see fig. 15). The epithelium consists of high columnar cells thrown into series of folds and richly ciliated except laterally where it is composed of flattened cells on which cilia cannot be seen in section (see fig. 41, *lg*, pl. 15). Pelseneer (1891) regarded this entire region as equivalent to the pharyngeal region in Gastropoda and the lateral areas, which are to some extent cut off from the lumen of the oesophagus by high epithelial folds at their margins, as oesophageal glands. Stempell (1898*a*) disagreed with Pelseneer. He is certainly correct; the lateral regions are not glandular and there is no reason for regarding this region as pharyngeal, the enlargement can probably be correlated with the relatively large particles or masses which may enter the mouth. Pelseneer (1891) claimed that a cuticular structure occurred on the ventral walls in *Lembulus pella* and he homologized it with the jaw of Gastropoda such as *Patella*. Stempell (1898*a*) pointed out that this is actually a close set layer of cilia and Pelseneer later (1911) withdrew his statement. Mucous glands are abundant here, and there is a well-developed layer of circular muscle as well as small dilators (Heath 1937).* Throughout the rest of the oesophagus the epithelium, everywhere ciliated, is composed of still higher cells, but there is less folding. Mucous glands and muscles are less abundant. The oesophagus is concerned with the transport of material to the stomach. Propulsion is primarily by cilia, assisted probably by muscles to some extent anteriorly. It is therefore intermediate in character between that of a typical Eulamellibranch, such as *Mya* or *Ostrea* (Yonge 1923, 1926*b*), where cilia are exclusively employed, and that of the Septibranchia where muscle is highly developed and peristalsis responsible for conveyance of the large food masses to the stomach.

(ii) *Stomach.*

The structure and functioning of this remarkable organ can best be described by particular reference to that of *Malletia obtusata*, which, owing to its size, was examined in greatest detail. The stomach in the other Nuculanidae is essentially similar.

The position of the stomach *in situ* is shown in fig. 16 (*s*). In an animal of shell length 1·4 cm. the stomach is about 3·5 mm. long and 1·5 mm. wide at the dorsal end. Unlike the stomachs of the Filibranchia and Eulamellibranchia those of the Protobranchs (excluding *Solenomya*) are but slightly attached to the surrounding organs and tissues and, in consequence, very easy to dissect out intact. The appearance of that of *Malletia obtusata*, when viewed from the right and left sides respectively, is shown in fig. 36 A, B. The rounded dorsal region is, in the main, dark brown in colour, clearly divided into different regions but with a smooth outer surface. The oesophagus (*o*) enters a little to the left of, and ventral to, the antero-dorsal surface. The three ducts ($dd_1$, $dd_2$, $dd_3$) which communicate with the brown mass of the digestive diverticula which surround the stomach in life, all enter this region of the stomach on the left side. The ventral region is sharply separated from the dorsal region by a transverse ridge. It is reddish brown, softer in texture, but with the same smooth external surface, and is cone-shaped. A well-defined groove (*gss*) with bounding ridges is clearly apparent through the tissues running down the anterior surface, turning a little to the right ventrally before merging into the intestine which in this region is twisted into a series of loops (*ti*).

The internal appearance of the stomach when cut open longitudinally along a line a little to the right of the mid-line posteriorly and laid out flat for inspection is shown in fig. 37. The dorsal region is composed of three distinct areas. There is a ciliated area composed mainly of a complicated series of fine grooves and folds (*sr*). It lies, as shown in fig. 36 A, mainly on the right side and is broadly crescentic in outline. The three ducts of the digestive diverticula ($dd_1$, $dd_2$, $dd_3$) open in this ciliated region. The re-

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* Heath also describes muscles extending from the mouth region to the dorsal body wall. He suggests that they may raise the mouth and assist in pushing food through the oesophagus.

mainder of this part of the stomach is lined with chitin. The greater part of this forms a broad girdle (*ch*) round the stomach (well shown in fig. 36 A, B) tapering towards the anterior margin and interrupted there to allow for the passage of the ciliated groove which connects the dorsal ciliated area with the groove (*gss*) in the ventral region. The chitin has an average thickness of $18\,\mu$, the epithelium which secretes it being raised into a conspicuous ridge, about $135\,\mu$ thick, around the ventral margin (see fig. 42, *rc*, pl. 15). Yellowish green granules, probably excretory in nature, occur in the cells which secrete the chitin. A little to the left of the anterior side a short caecum (figs. 36 B, 37, *ca*) extends beneath the chitinous epithelium. Attached dorsally to the wide posterior chitinous region is a much thicker area of chitin (*gs*) which bears a conspicuous tooth some 0·3 mm. thick. This, for reasons given below, is to be regarded as homologous with the gastric shield of the other Lamellibranchia.

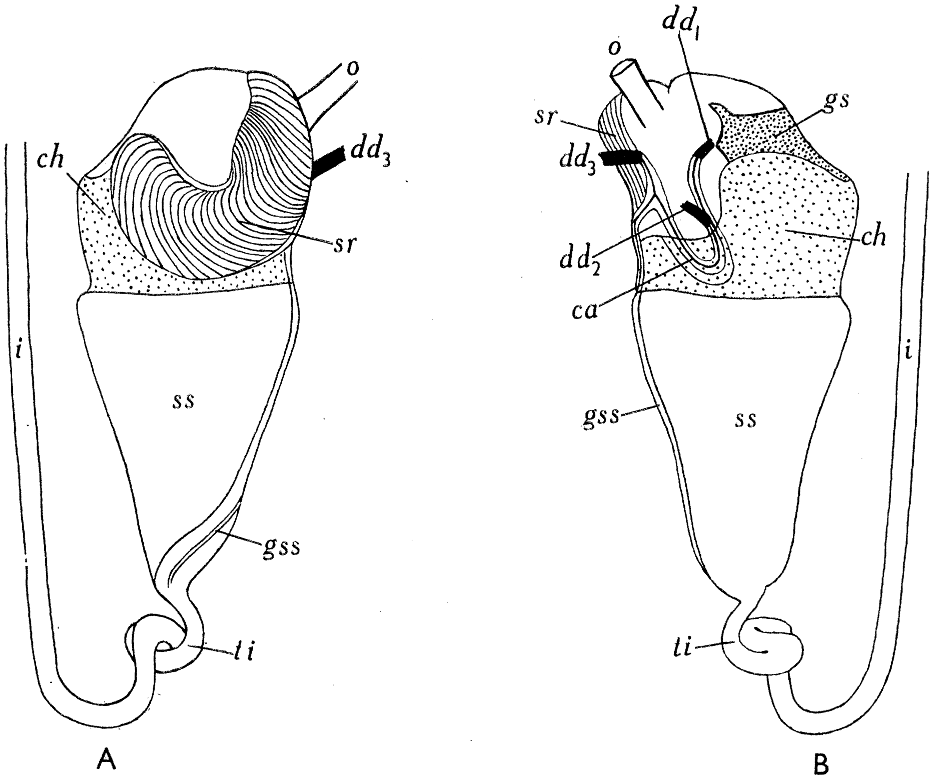

FIG. 36. *Malletia obtusata*, intact stomach, after removal of digestive diverticula, viewed from right (A) and left (B) sides, drawn from life. ×20. *ca*, caecum; *ch*, chitinous girdle; $dd_1$, $dd_2$, $dd_3$, ducts of three masses of digestive diverticula; *gs*, gastric shield; *gss*, groove in "style-sac" region; *sr*, sorting region; *ss*, "style-sac region"; *ti*, twisted region of intestine. Other lettering as before.

The ventral region (fig. 42, pl. 15) is ciliated throughout. The general surface consists of a smooth epithelium (*ess*), about $60\,\mu$ deep, bearing dense bristle-like cilia $15\,\mu$ long. The cells stain homogeneously and the nuclei are arranged in an even line some one-third of the distance from the base to the free edge of the cells. This epithelium corresponds in all respects to the very typical style-sac epithelium found in all other Lamellibranchia (Nelson 1918; Yonge 1923*b*) and also in the various style-bearing Gastropoda (Yonge 1923*a*, *b*). On either side of the anterior groove (*gss*) the cells are elongated and much narrower, resembling, on a reduced scale, the cells of the typhlosoles which bound the style-sac epithelium and separate it from the intestine in Lamellibranchia such as *Ostrea* (Yonge 1926*b*) in which the two are connected by a narrow longitudinal slit. The cells of the groove (fig. 42, *gss*, pl. 15) form an extremely low pavement epithelium only 4–5 μ deep but ciliated.

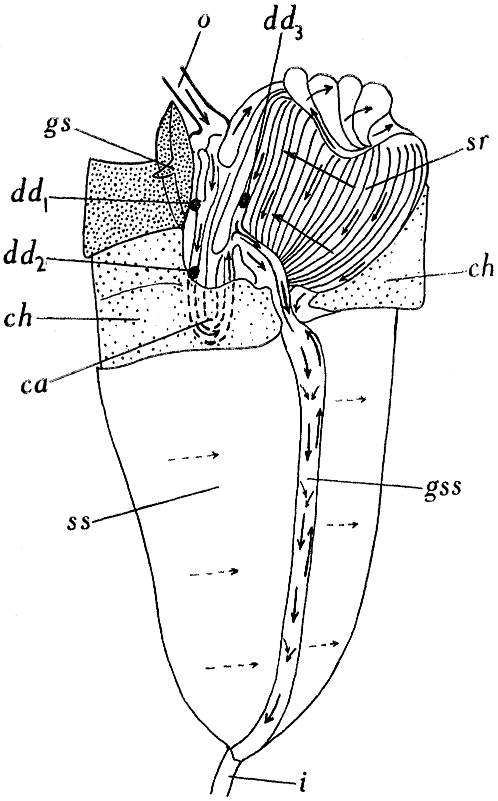

FIG. 37. *Malletia obtusata*, interior of stomach as seen after cutting longitudinally a little to the right of the mid-line posteriorly. × 20. Lettering as before. Arrows indicate direction of ciliary currents, broken arrows those on "style-sac" epithelium. Gastric shield region darkly stippled, chitinous girdle lightly stippled.

A well-developed investment of elastic connective tissue surrounds the outer wall of the stomach and accounts for the smoothness of the outer surface. In addition there are circular muscle fibres around the ventral region. When removed from a freshly caught animal the stomach is invariably distended with material which is clearly under pressure because when the stomach wall is punctured with a needle the contents burst out. They consist of fine particles, including diatom tests, fragments of plant material, spines, sand grains, etc., all compacted with mucus (see fig. 42, pl. 15). The entire stomach contents can actually be pulled out as an elongated mass if a needle is inserted into one end.

The nature of the ciliary currents within the stomach is indicated by the arrows in fig. 37. Material enters by way of the oesophagus (*o*) and is probably in the first place conveyed ventrally, passing the first and second openings into the digestive diverticula ($dd_1$, $dd_2$) into which some of the smaller particles probably pass. It is then carried in and out of the small caecum (*ca*) which penetrates under the chitinous girdle and so towards the sorting region (*sr*) and the opening of the third duct into the digestive diverticula ($dd_3$). Apart from this the functioning of the intact stomach must be deduced from its appearance when examined whole and after longitudinal incision. The greater part of the material which enters must certainly be compacted into the mucus-laden mass, the mucus being secreted, as in all style-bearing Mollusca, by the epithelium of the "style-sac" region. Berkeley (1935) has recently shown that the crystalline style is composed largely of mucin. This mass is rotated by the bristle-like cilia of the "style-sac" epithelium in an anticlockwise direction (see broken arrows in fig. 37). At the same time it is pushed forward into the dorsal region of the stomach by the beating of a line of cilia on the right side of the groove. The whole mechanism is essentially the same as that in the style-sac of *Ostrea* (Yonge 1926*b*). The anterior end of the mucous mass is wrapped round the tooth on the gastric shield and must be pressed tightly against this and against the chitinous girdle. It is therefore formed, rotated and pushed forward ventrally, and compressed against the chitinous regions dorsally, partly probably by the contraction of the circular muscle in the ventral region.

This dorsal compression will have two effects. It will bring about trituration of the comparatively large, and often hard and sharp, particles carried into the stomach and which may attain a diameter of over 100 $\mu$. In view of the nature of the food material this is clearly of importance because, as indicated below, there is no enzymatic action in the stomach. It will also tend to squeeze out fluid while fine particles will be carried to the periphery of the mucous mass owing to centrifugal action, as suggested by Barrington (1937) in *Amphioxus*, where analogous conditions prevail. These particles will be pressed against the sorting region (*sr*). Here cilia in the depths of the furrows carry larger particles ventrally and so into the groove which communicates, by way of the gap in the chitinous girdle, with the groove in the ventral region (*gss*). Cilia on the summits of the ridges beat at right angles to those in the burrows and carry the finest particles anteriorly and so towards the opening into the third and largest mass of digestive diverticula ($dd_3$). Actually most material which enters this duct must come from the sorting region. Probably other crushed particles squeezed out of the mucous mass enter the other two ducts ($dd_1$, $dd_2$). The larger particles and mucus-laden masses which are carried into the groove in the ventral ("style-sac") region are conducted rapidly along this and make their way finally into the intestine (*i*). Cilia on the sides of the groove beat downwards into this, carrying fresh particles into the groove from the ventral region and preventing those in the groove from escaping.

So far as the action of the sorting region is concerned the mechanism of the stomach is essentially the same as in Filibranchia and Eulamellibranchia such as *Modiolus*

(Nelson 1918), *Mya* (Yonge 1923), *Ostrea* (Yonge 1926*b*) and *Ensis* (Graham 1931). In all of these there is a complicated region of ridges and furrows which serve to sort out particles sending the finer ones into the ducts of the digestive diverticula and the coarser ones direct into the intestine. Only in *Tridacna*, where the food is unusually finely divided, is this region absent and all particles passed direct into the ducts (Yonge 1936*a*).

But there are certain fundamental differences between the stomach of *Malletia* and the other Protobranchia, and that of the higher Lamellibranchia. Although the gastric shield is similar in form and general function in both, the chitinous girdle occurs only in the Protobranchia. Its presence is to be correlated with the nature of the food which needs to be squeezed and crushed. This also explains the presence of the sheath of elastic connective tissue and muscle and also the absence of attachment between the stomach and the surrounding tissues which would impair its activity in this respect. Conditions are somewhat similar in the Septibranchia where the stomach acts as a crushing gizzard (Yonge 1928). Finally, although the "style-sac" secretes a mucous mass similar to that which forms the style, there are important differences. In the first place the food particles are mixed freely with this and not merely stirred by it as they are in the Filibranchia and Eulamellibranchia. In the second place it contains no amylase. This was demonstrated by experiments on *Nucula turgida*. The stomach contents of fifty large individuals were removed, shaken up with sea water to form an opalescent solution, and made up to 20 c.c. Half was boiled and to both halves added 5 c.c. of 2% soluble starch with a little toluol. Both were incubated for 8 days at 30° C. At the end of that period both were tested for glucose but no trace was found in either experiment or control. The stomach of the Protobranchia is thus devoid of any digestive action. It is concerned (*a*) with the trituration and sorting out of the particles passed into it from the oesophagus, sending small particles into the digestive diverticula and larger ones into the intestine, and (*b*) with the consolidation of faeces and the coating with mucus of hard particles which might otherwise perforate the delicate walls of the intestine and rectum.

### (iii) *Origin of the crystalline style.*

Apart from its interest as an organ highly specialized for the particular needs of the Protobranchia, the stomach in these animals gives some indication of the manner in which that unique and very remarkable structure, the crystalline style, may have evolved. As stated elsewhere (Yonge 1932*b*), this could only have appeared in a group of animals which makes widespread use of cilia and of mucus, the latter forming the material of the style (Berkeley 1935), the former serving to shape it, drive it forward into the stomach and to rotate it. Judging by conditions in the Protobranchia, it may well have been concerned in the first place with the mixing of the relatively large, and often hard and sharp, particles into a mucus-laden mass to permit of effective trituration in the stomach. This would have the important additional effect of consolidating the fragments after trituration into homogeneous faeces which would not damage the walls of the intestine and rectum. The supreme importance of faeces formation in Mollusca in which the anus opens into the mantle cavity has been emphasized in the case of Gastropoda by Graham (1932) for *Patella* and by Yonge (1937) for *Aporrhais*, and in Lamellibranchia by Yonge (1935). The chitinous areas on the walls of the stomach evolved in association with the need for trituration.

The great evolution in the Filibranchia and Eulamellibranchia of the ctenidia as organs for the collection of minute phytoplankton organisms rendered trituration unnecessary. But the mucous rod was retained. It became larger and firmer with the greater size attained by the style-sac and probably served originally to mix the food thoroughly in the stomach as well as to assist, to a smaller measure than formerly, with the formation of faeces. The chitinous area was reduced to the thicker gastric shield area against which the head of the style bears when it rotates. With the loss of the triturating action the stomach became firmly attached to the surrounding tissues.

The style must also, at some stage, have become an important organ of digestion owing to the added secretion by the style-sac epithelium of an amylase which was adsorbed on the mucus. The continual liberation of this enzyme in small quantities into the stomach owing to the lowered *p*H in that region (Yonge 1926*b*, 1932*a*) provided an ideal mechanism for enzyme liberation in animals which are continually passing small quantities of finely divided food, rich in carbohydrates, into the stomach. In many Eulamellibranchs, e.g. *Mya* (Edmondson 1920; Yonge 1923), *Ensis* (Graham 1931) and *Tridacna* (Yonge 1936*a*), the style-sac has become separated from the intestine and the style become a firm rod (attaining a length of 34 cm. in *Tridacna derasa*) which in *Mya* takes 74 days completely to regenerate if experimentally removed (Edmondson 1920). Finally, in the Septibranchia, where ciliary feeding mechanisms have been replaced by the muscular septum which draws in the carnivorous food of these animals, the stomach has been reconverted into a crushing gizzard, lined with chitin throughout and very muscular (Yonge 1928). The style is here reduced to a small rod, in a separate sac, and its only possible function is the original one of coating hard particles, formed when the exoskeleton of crustacean and other prey is crushed by the gizzard, and so protecting the delicate walls of the intestine and rectum.

It is interesting to note that, in the course of recently completed work on the style-bearing Gastropoda, Graham (1939) has found conditions very similar to those in the Protobranchia. He has shown that in *Diodora* (*Fissurella*), although what appears from histological evidence to be a style-sac is present, it secretes only an ill-compacted mass of mucus in which food particles, largely animal in nature, are embedded. There is *no* amylase and the stomach has an extensive investment of chitin. Similar conditions probably prevail in other of the more primitive Prosobranchia such as *Emarginula*, *Theodoxus* [*Neritina*] and *Ampullaria*. Since the style mechanism in Gastropoda such as *Crepidula* (Mackintosh 1925), *Aporrhais* (Yonge 1937) and *Pterocera* and *Strombus* (Yonge 1932*a*) is essentially the same as in the Filibranchia and Eulamellibranchia, it would appear that evolution of the style mechanism has followed similar lines in the two classes.

### (iv) *Digestive diverticula.*

In all the Nuculanidae the digestive diverticula consist of three brown lobular masses which communicate with the stomach by way of relatively long, undivided ducts. Like the stomach the diverticula are attached very slightly to surrounding tissues and the three masses can easily be dissected free, attached only by the narrow ducts to the dorsal region of the stomach. Although all three ducts open, as already described, on the topographically left side of the stomach, only the diverticula connected with the first and second ducts (figs. 36 B, 37, $dd_1$, $dd_2$) lie on the left side. Of these the first and smallest is posterior and the second anterior. The third duct ($dd_3$) leaves the stomach near the anterior side and passes anteriorly before turning to the right and, in *Malletia*, passing around the second ascending loop of the intestine as shown in fig. 16 (and figured from the dorsal aspect by Heath (1937), fig. 65, pl. viii). These diverticula are spread over the right side of the dorsal region of the stomach and form the largest of the three masses. There is an obvious macroscopic difference between the first mass and the other two, the former being paler in colour and the individual tubules larger.

Sections reveal that the ducts are similar histologically to the ciliated region of the stomach and that the diverticula of the second and third masses are essentially similar to those of the Filibranchia and Eulamellibranchia as described by Gutheil (1912) and Yonge (1926*a*). They are oval or rounded in cross-section (see fig. 41, pl. 15) with the free margin of the cells irregular in outline and the cells containing many vacuoles often with small, darkly staining inclusions. Here and there are crypts of smaller, darkly staining cells which, as previously shown (Yonge 1926*a*), are groups of young cells which by division make good the loss of older cells which are eventually liberated into the lumen. As in the diverticula of all other Lamellibranchia, there is no evidence of any secretion, but abundant evidence of ingestion and intracellular digestion of minute particles. Cilia are absent in sections but, as observed in the living diverticula of a variety of Lamellibranchia (Yonge 1926*a*), it is highly probable that long cilia do occur at the ends of the tubules in life and are responsible, by their beating, for the circulation of fluid within the diverticula. Muscles are absent.

The diverticula composing the first mass are about twice as wide in cross-section, with thicker walls and a wider lumen. The outline of the constituent cells cannot be determined owing to the great mass of ingested particles which, in *Nuculana minuta* which has proved the most satisfactory histological material, may attain a diameter of up to 90 $\mu$. The appearance of these diverticula is well shown in the microphotograph reproduced in fig. 43, pl. 15. They resemble most closely the diverticula in the septibranch *Cuspidaria* (Yonge 1928), into the wide lumen of which pass the food particles produced by the crushing action of the gizzard. In one specimen of *Yoldia* these diverticula were almost black in colour owing to the presence in the cells and in the lumina of numerous particles of black sand. It appears, therefore, that larger particles exclusively enter the first mass of diverticula. The position of the opening (fig. 37, $dd_1$) near to the oesophagus will permit of the entry of particles before they become incorporated in the mucous mass which occupies the general lumen of the stomach. Specimens of *Lembulus pella* were placed in water containing a suspension of the blood of a dogfish and, after periods of 6 and 12 hr., were fixed in Bouin's fluid. After sectioning, corpuscles were found in the stomach and a few ingested in the cells of the wide diverticula, but none in the cells or lumen of the second and third masses of diverticula. The corpuscles were about $12\,\mu$ long and are presumably either too large to enter the second and third ducts or else were unable to reach these openings before being incorporated in the mucous mass where they will be crushed. The presence of the wide diverticula is to be regarded as yet another specialization of the gut in correlation with the relatively large food particles.

### (v) *Digestion and absorption.*

Digestion is exclusively intracellular, even the style amylase, the only extracellular enzyme present in the gut of the other Lamellibranchia, being absent. Intracellular digestion is confined to the digestive diverticula. There are no wandering phagocytic blood cells in the epithelium and lumen of the stomach and adjacent regions such as occur in Filibranchia and Eulamellibranchia (Yonge 1926*a*, *b*). The employment of these cells is correlated with the very finely divided nature of the food, diatoms and similar phytoplankton organisms being frequently ingested whole by them, and they are absent from the gut of the carnivorous Septibranchia (Yonge 1928). In the Nuculanidae smaller particles are ingested in the cells of the second and third masses of diverticula and larger ones in the more capacious cells of the first mass. The restriction of ingestion (including absorption) to the diverticula in *Nucula* has been previously shown (Yonge 1926*a*) by feeding animals with iron saccharate and later determining the distribution of ingested material in sections. The same localization of ingestion has been determined by similar means in *Lembulus pella.*

In respect of digestion, therefore, the Protobranchia are a primitive group, but the retention of intracellular digestion exclusively is to be correlated with the action of stomach in grinding up the larger particles swallowed, and, in the Nuculanidae, with the presence of the modified wide diverticula.

### (vi) *Intestine.*

The first section of the intestine consists of a series of twisted loops (fig. 36 A, B, *ti*). This portion of the gut extends into the base of the foot and when the foot is protruded the coils are pulled out into a simple loop as shown in fig. 16. The intestine then runs dorsally parallel to the posterior wall of the stomach and then turns anteriorly and ventrally extending in most species as far forward as the mouth (see figs. 15–17) before passing dorsally again, this time in close association with the oesophagus. Except in *Yoldia* (fig. 17), it then extends dorsal to the stomach and finally merges into the rectum in the mid-line. In all cases the loops lie on the right side of the body. The groove in the ventral region of the stomach is continuous with the lumen of the intestine, while the elongated cells of the ridge which bounds the left side of the groove, and which broadens somewhat in the ventral end of the stomach, are continued as a prominent ridge along one side of the lumen of the intestine. This ridge is due entirely to the greater length of the epithelium which composes it and *not* to an intucking of the wall of the intestine, the outer surface being round in cross-section (fig. 44, pl. 15). The intestine having no power of absorption, this ridge is distinct both structurally and functionally from the typhlosole present in the absorbing gut of other invertebrates such as the Annelida. It decreases steadily in size throughout the course of the intestine.

The cells of the intestine are all ciliated throughout and mucous glands occur. When freshly caught animals of any species of the Nuculanidae are fixed and sectioned the intestine is invariably found to be filled with a homogeneous mass of very fine fragments embedded in mucus. The particles never attain the size of those present in the stomach, an indication of the effective trituration which occurs there. The function of the intestine is the same as that of other Lamellibranchia and of the coiled intestine of Gastropoda such as *Patella* (Graham 1932) or *Aporrhais* (Yonge 1937), namely the consolidation of faecal matter into compact pellets which will not foul the mantle cavity with fine fragments when extruded. The length of the intestine is due exclusively to this.

(vii) *Rectum.*

This region is straight and is narrower than the intestine. The ridge is reduced to a minute elevation mid-dorsally although in *Nuculana minuta*, *Lembulus pella* and *Yoldiella lucida* the epithelium in the anal region is raised into a series of low ridges. The epithelium is low, especially in *Malletia obtusata* and *Yoldia limatula*, densely ciliated and contains mucous glands. Circular muscle fibres surround the rectum and are especially well developed in *Malletia obtusata*, where they form an outer investment equal in thickness to the epithelium. In the anal region longitudinal muscles also occur, being again best displayed in *M. obtusata*. Both sets of muscles presumably aid in defaecation. Finally a mass of unicellular glands is present in the anal region. They were first identified by Stempell (1898*a*) and termed by him anal glands. As shown in Fig. 45, *agl*, pl. 15, they lie beneath the thin rectal epithelium. They appear to open by a series of fine ducts around the sides of the anal opening. This region is ciliated and, although not examined in life, it is possible that the cilia carry the secretion on to the sides of the faecal pellets, thereby providing for the lubrication of their passage through the exhalant siphon. The glands are certainly best developed in species with long siphons such as *M. obtusata*. The faecal pellets (fig. 45, *fa*, pl. 15) are extremely well compacted after their passage through the intestine and rectum. They emerge as short rods which never flake, even when torn with needles, and they were observed to pass lengthways through the exhalant siphon. The danger of fouling the mantle cavity is effectively met.

### (*b*) *Nuculidae*

It will be sufficient to mention the significant differences existing between the gut in this family and in the Nuculanidae. In *Nucula* the oesophagus opens anteriorly into the stomach which has the same general form and certainly functions in the same manner. Yellowish green inclusions are very abundant in the cells which secrete the chitinous investment and also in the epithelium of the ducts of the digestive diverticula. The nuclei of the cells of the ventral region are elongated, but the cilia form the same even, bristle-like covering and the function of this region is the same as in the Nuculanidae. The groove (fig. 9, *gss*) runs down the *right* side. The principal difference lies in the digestive diverticula. As noted by Heath (1937), there are only two ducts in *Nucula*, left and right. The former probably corresponds to the second duct in the Nuculanidae (see figs. 36, 37, $dd_2$), the latter to the third duct ($dd_3$). There is a ridged sorting region in the stomach and the ducts bear the same relation to this and to the opening of the oesophagus as do those of the Nuculanidae. The ducts are very short, branching repeatedly almost immediately after they leave the stomach. The diverticula are attached closely to the walls of the stomach and correspondingly difficult to dissect free. They all agree in structure with the narrow diverticula of groups two and three in the Nuculanidae and with the diverticula of the Filibranchia and Eulamellibranchia. For that reason the left duct in *Nucula* probably corresponds to the second duct in the Nuculanidae, and the first duct, with the wide diverticula, in that family represents an element in the digestive system added for the better digestion of the large food particles. It is clear from the observations of Heath (1937) that the stomach and gut of *Acila* are similar to those of *Nucula*.

There are no twisted coils of intestine adjacent to the ventral region of the stomach; this may be explained by the shorter distance to which the stomach extends into the base of the foot. The intestine does not extend so far anteriorly as in the Nuculanidae but the coiling, always on the right side, is more complex (see fig. 9). Heath (1937) has described and figured the condition in a variety of species of *Nucula* and *Acila*. The coiling is most elaborate in *Nucula* "*cancellata*". Heath produces evidence which indicates that the more complex coiling is typical of animals living in the greatest depths. In ignorance of the fact that in no Lamellibranch does the intestine absorb, he suggests that, as nutritive material diminishes with depth, a more elongated intestine is necessary for adequate digestion. The animals may certainly have to take in larger quantities of bottom material at these depths to obtain sufficient nutriment, but the added need for consolidation of the greater amount of waste material as faecal pellets seems the most reasonable explanation for the greater length of the gut.

The histology of the intestine and rectum calls for no comment; the latter possesses well developed circular muscle but, correlated no doubt with the absence of siphons, there is no anal gland in this family. The anus opens on the mantle edge immediately ventral to the point of fusion posteriorly (fig. 9, *a*). Species of *Nucula* were observed defaecating. The elongated faecal pellets are pushed out from between the shell valves by muscular contraction in the rectum and anus. Only after they have been expelled do the shell valves contract and create a current of water which carries the pellets away from the margin of the shell. Moore (1931 *a*, *b*) has described the faecal pellets in British species of *Nucula*. He describes them as consisting of rods, sculptured in longitudinal grooves, and breaking transversely into lengths of 0·2 to 1·0 mm. or more. The number of grooves varies in the different species—due to the different ridging of the rectum—and the pellets can be distinguished specifically. Their extremely compact nature, as a result of the united action here described of the stomach, intestine and rectum, is indicated by Moore's statement (1931 *a*) that they are "sufficiently firm to allow identification in muds laid down on the bottom for over fifty years".

### (*c*) *Solenomyidae*

As observed originally by Pelseneer (1891) the gut of *Solenomya* is noteworthy for its small size and the reduced condition of many of its parts. That of *S. togata*, which lies in the mid-line throughout, is shown in fig. 38. The small mouth (*m*) leads into a narrow oesophagus (*o*) with no oral dilation, which passes dorsally before turning posteriorly and gradually widening to merge into the stomach. This extends anteroposteriorly, bending ventrally to only a slight extent as shown in fig. 38. It is relatively

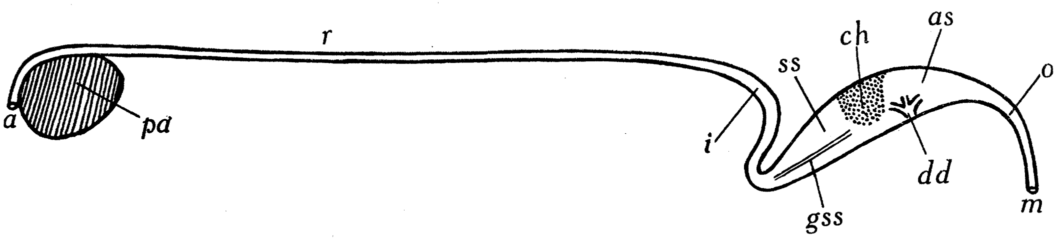

FIG. 38. *Solenomya togata*, semi-diagrammatic representation of the alimentary canal viewed from right side. × 37. *as*, anterior, ciliated region of stomach. Other lettering as before.

very much smaller than in the other Protobranchia and is divided into three regions. There is an anterior ciliated region (*as*) at the posterior end of which open, ventrally, the symmetrical paired ducts of the digestive diverticula (*dd*). The appearance in transverse section of this region is shown in fig. 46, pl. 15. The ducts (*dd*) branch immediately, merging into the diverticula (*dd*) which have relatively wide lumina in which old cells liberated from the epithelium are frequently found. The diverticula are few in number and confined to the immediate vicinity of the stomach. Posterior to this region lies the chitinous girdle (fig. 38, *ch*) which covers the dorsal and lateral walls of the middle region of the stomach, leaving a broad ciliated channel ventrally. There is nothing corresponding to a gastric shield bearing a chitinous tooth. The cells which secrete the chitin contain the usual yellowish inclusions. The posterior region corresponds to the ventral region in the other Protobranchia. It has a typical "style-sac" epithelium with a groove (*gss*) on the *right* side in communication with that in the chitinous region. It tapers into the intestine (*i*) which first bends dorsally and then merges into the long rectum (*r*) which, after passing through the elongated pericardium (see fig. 13, *pc*), opens at the anus (*a*) behind the posterior adductor (see figs. 11, 38). As in the Nuculidae, there is no anal gland.

The gut of *Solenomya* appears more primitive than that of the other Protobranchia, but actually represents a secondary simplification. This was maintained originally by Stempell (1899) who correlated its small size with the high organic content in the substratum in which the animal lives. More significant probably is the finely divided nature of the particles which enter the mouth owing to rigorous sorting on the enlarged ctenidia and the small, but very efficient, palps. Apparently *all* particles which enter the gut pass into the ducts of the digestive diverticula. There is no sorting region in the stomach, a condition similar to that in *Tridacna* (Yonge 1936*a*) where the food is also very finely divided. Only after rejection from the diverticula do particles come under the crushing action of the chitinous region and experience preliminary moulding into faeces here and in the posterior region, these regions of the stomach being concerned exclusively with this function. None but the most minute particles have been found in the gut. The limited extent of the diverticula may be due to the high organic content of the food, as suggested by Stempell, but also to the smaller, and so more easily digested, particles which enter them. The smaller size of the stomach is certainly due to the smaller food particles. The absence of lateral coiling in the gut is probably due to the relatively greater length of the animal posterior to the stomach in the Solenomyidae. The intestine and rectum are actually not much shorter in relation to the size of the animal than in the Nuculanidae. The effect of this on the arrangement of the ducts of the digestive diverticula is discussed below.

### (*d*) *Symmetry of the gut*

Pelseneer (1891) thought that the displacement to the right side of the intestine in the Nuculidae and Nuculanidae was primitive, an indication of a fundamental asymmetry he ascribed to the primitive Mollusca. Stempell (1898*a*), on the other hand, considered it to be secondary, a view which later found confirmation in the embryological work of Drew (1901) who showed that in *Nucula delphinodonta* the gut bends to the right during development. In the Nuculanidae this bending of the intestine has been accompanied by its extension anteriorly, with a consequent pushing of the oesophagus to the left which has produced a twisting round of the stomach in that direction. The oesophagus enters the stomach on the topographically left side, the morphologically right duct of the digestive diverticula being carried round to the topographically left side of the stomach although remaining, as shown in fig. 36 B (*dd*$_3$), on the right of the oesophagus. The groove in the ventral region which in *Nucula* and in *Solenomya* (figs. 9, 38, *gss*) lies on the right side has in the Nuculanidae become anterior owing to this twisting. Only near the ventral extremity does it come round to the right side (see fig. 36 A). The anterior regions of the gut in the Nuculidae remain symmetrical presumably because the animals are broader in proportion to their length. This has permitted the intestine to make even more extensive coils without extending far anteriorly and so affecting the position of the oesophagus, although in species of both *Nucula* and *Acila*, Heath (1937) shows that both stomach and posterior end of the oesophagus are pushed bodily to the left. The reason for the coiling of the intestine, and so indirectly for the displacement and twisting of the stomach in the Nuculanidae, lies in the need for effective consolidation of the faeces. In *Solenomya* where, owing to the smaller size of the food particles and the relatively greater length of the body posterior to the stomach, there is no need for coiling, the intestine remains in the midline and in consequence, despite the narrowness of the body, the oesophagus opens anteriorly into the stomach and the ducts of the digestive diverticula are symmetrically disposed.

## 7. Discussion

### (*a*) *Nature and evolution of the Protobranchia*

All species of the Protobranchia are specialized for burrowing into and moving through a soft substratum. Different species are adapted for life in different types of bottom material. In *Yoldia* alone is burrowing habitually vertical and horizontal movement absent. The foot, erroneously described by early workers as a primitive structure with a creeping sole similar to that of many modern prosobranch Gastropoda and of the Loricata (Amphineura), is a most highly evolved organ permitting relatively rapid movement into and through the substratum. It is controlled by an unusually large number of widely distributed pedal muscles. The functional significance of these was first realized by Drew (1899) in *Yoldia*, while the pedal muscles of many species have recently been described and figured in beautiful detail by Heath (1937). He distinguishes between a pair of very large posterior retractors, a pair of anterior retractors, two pairs of anterior protractors, a pair of dorso-median and a pair of ventro-median muscles which may reinforce the pedal retractors and possibly also anchor the pericardial region to the shell during vigorous movements of the foot, and finally transverse and circular intrinsic muscles in the foot. The opinion of Pelseneer (1891) that the wide distribution of these muscles is primitive cannot be upheld.

The Protobranchia feed by means of the labial palps on organic deposits within the bottom material. The most significant part of these structures are undoubtedly the proboscides which, except in the Solenomyidae, are the actual food collecting organs, the other regions being concerned with sorting and passage to the mouth. Except in the Solenomyidae, the ctenidia, although they may play a minor role in food collection, are *not* an essential part of the feeding mechanism. Conditions in the Protobranchia reveal that the evolution of the labial palps was the *essential preliminary* to the conversion of the ctenidia into feeding organs, a process which has resulted in the evolution of the highly successful Filibranchia and Eulamellibranchia.

The primitive mollusc possessed a pair of ctenidia in the posterior mantle cavity and had presumably a well-developed head with the mouth resting on the surface when feeding with the aid of the radula, probably in much the same manner as does *Patella*. In certain stocks evolution led to the forward extension of the mantle cavity on either side of the foot. In one group, which gave rise to the Loricata, the foot elongated and retained the creeping sole, the shell took the form of a series of plates and, owing to the restricted space on either side of the broad foot, the ctenidia were multiplied (Yonge 1939). In these animals the mouth remained in contact with the substratum and the radula was retained. In another group the body and foot became narrower, but extended dorso-ventrally, while a hinged bivalve shell evolved for its complete enclosure. The mouth necessarily lost contact with the substratum, but this can only have occurred *after* the appearance of elongated upper lips which took over the function of food collection. This involved a change in feeding habits because the animal could no longer rasp off particles from a hard substratum, but the change in form and function of the foot now permitted life on or in a soft substratum. Thus the apparently highly specialized foot of the Protobranchia may well be primitive for the Lamellibranchia.* Originally particles collected by the long upper lips, represented by the palp proboscides of the Nuculidae and Nuculanidae, were probably crushed up by the radula. But further evolution led to the appearance of the paired palp lamellae lateral to the mouth. Sorting of the particles collected by the proboscides occurred here and only the smallest particles passed into the mouth. The radula was finally lost and trituration confined to the stomach. Conditions in Gastropoda such as *Diodora* (Graham 1939) indicate that even when a radula is present final trituration may occur in the stomach.

It is along these lines that we may explain the evolution of animals similar to the modern Protobranchia with palp proboscides and palp lamellae but no buccal mass. The ctenidia extended somewhat anteriorly, but retained in essentials their primitive structure, relations and function. Latero-frontal cilia were acquired in correlation with the greater amount of sediment which entered the mantle cavity in the new environment and would tend to block the spaces between the filaments and also the exhalant cavity. Despite the statement of Atkins (1938) to the contrary, these cilia must

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* The so-called byssus gland present in all Protobranchia, although only conspicuous in the Solenomyidae, is a mucous gland probably homologous with pedal glands in the Gastropoda. It probably lubricates the surface of the foot, hence its greater development in the most active burrowers, the Solenomyidae. The true byssus gland possibly evolved from this and first appeared in Filibranchia which took to life in shallow waters where the bottom was hard and water movements great. But ciliary feeding mechanisms must have evolved before this change in habit could have taken place. Hence the byssus gland, regarded as an organ for producing attaching threads, cannot be regarded as a primitive structure in the Lamellibranchia.

only have become concerned with feeding later, although their presence in the ciliary feeding mechanisms of the Lamellibranchia—where alone they occur—is certainly one of the reasons why this group has developed this type of feeding with such outstanding success.

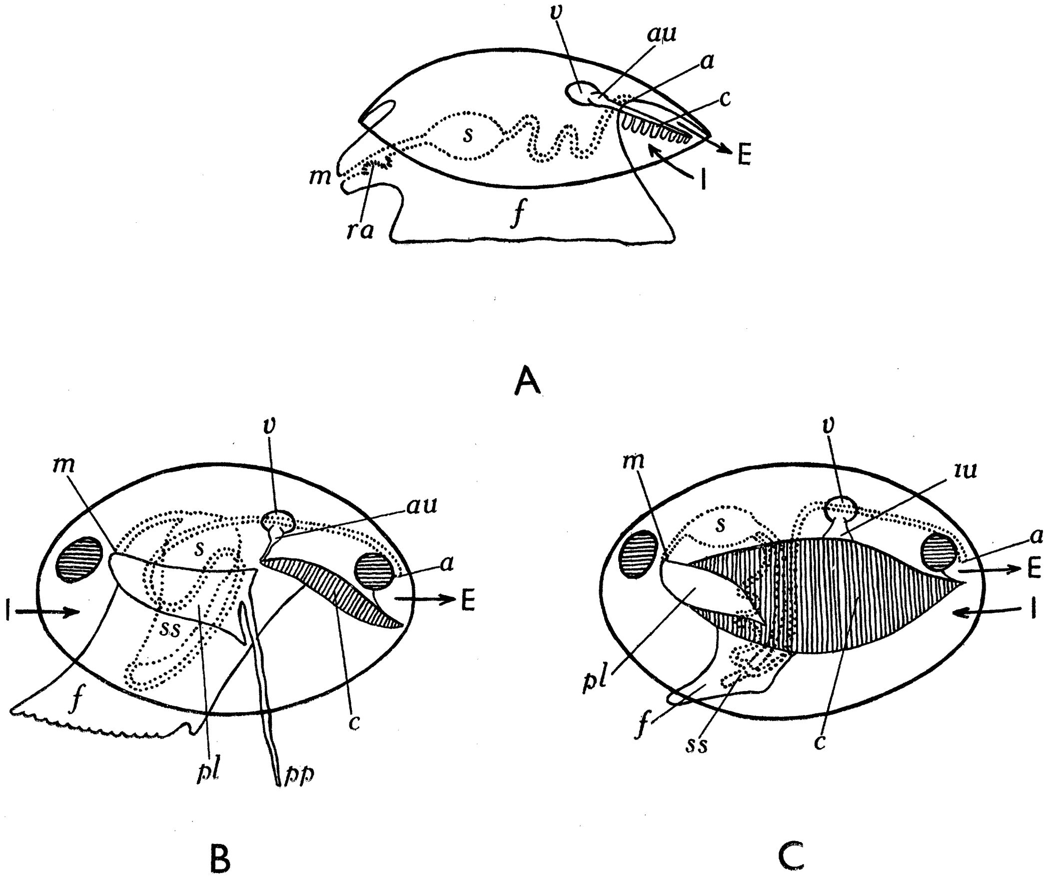

Fig. 39. Diagrams illustrating stages in the evolution of the Lamellibranchia, showing significant changes in the orientation of the body, form of the shell, foot, ctenidia and heart, alimentary canal (stippled) and labial palps. A, structure of hypothetical primitive Mollusca (modified after Pelseneer); B, protobranch stage; C, final condition in typical Eulamellibranch without siphons. *au*, auricle; *ra*, radula. Other lettering as before.

The further extension of the ctenidia in the long, deep mantle cavity continued until their anterior ends lay between the palp lamellae in close proximity to the mouth. The filaments were increased in number and converted from flattened leaflets into long, narrow filaments which eventually acquired the reflected form typical of those of the Filibranchia and, by further tissue fusion, those of the Eulamellibranchia. The great expanse of ciliated surface made possible the conversion of a limited respiratory current into one also adequate for feeding. The frontal ciliation, concerned in the primitive ctenidium with cleansing (and still so concerned in the Gastropoda; Yonge 1938, 1939), became a most efficient means of food collection. The latero-frontals prevented clogging. This transference of feeding from the palp proboscides to the ctenidia led to the loss of this primitive portion of the palps but the lamellae were retained, essentially unaltered in form and function, as the labial palps of these animals. But the presence of these organs indicates that the Lamellibranchia *must* have passed through an evolutionary stage corresponding to the condition exhibited by the modern Nuculidae. Although certain pectinibranch Gastropoda have, independently, adapted the ctenidia as ciliary feeding organs (Orton 1912; Yonge 1938; Graham 1938), they have *not* acquired palps and in all cases retain the radula. The three significant stages in this suggested evolutionary history of the Lamellibranchia are illustrated diagrammatically in fig. 39.

Conditions in the Solenomyidae are of great interest. Here the ctenidia have enlarged, the filaments increasing in number and extent but retaining the primitive features of those of the Nuculidae. Although the palps are no longer concerned with the direct collection of food, the reduced proboscides persist as essential intermediaries between the ctenidia and the mouth; they collect food from the ctenidia instead of from outside the shell. The animals remain essentially deposit feeders, but deal with this in suspension within the mantle cavity.

The structure of the gut is correlated with the nature of the food, being correspondingly reduced in the Solenomyidae. All trace of organs connected with the original buccal cavity have disappeared in all Protobranchia and so have digestive glands associated with the oesophagus. In the Loricata, on the other hand, the latter, in the form of "sugar glands", are retained and so are the radula and associated organs (Fretter 1937). No other source of extracellular enzymes has appeared in the Protobranchia, the "style" substance being concerned exclusively with assistance in trituration and in the formation of faeces. The digestive diverticula are organs of intracellular digestion exclusively, although in the Nuculanidae an additional mass of these has been acquired for dealing with larger particles. After effective trituration and mixing with mucus in the stomach, the particles are moulded into faecal pellets in the long intestine. This mechanism is primitive and is also retained in the Loricata, Fretter (1937) having described the very elaborate intestinal mechanisms concerned with the formation of faecal pellets in that group. In both form and manner of functioning the gut of the Nuculidae clearly foreshadows that of the higher Lamellibranchia. The possible mode of evolution of the style mechanism has been described while digestion of larger particles in these animals is carried out by wandering phagocytic blood cells which parallel in their action that of the enlarged diverticula in the more specialized Protobranchia comprised in the Nuculanidae.

In the primitive Mollusca the respiratory current must have entered the posterior mantle cavity ventrally (see fig. 39 A) and, after flowing upward between the gill filaments, passed out dorsally. When the mantle cavity and the ctenidia extended anteriorly, the inhalant opening eventually moved forward. It remains anterior in the Loricata (Yonge 1939). In the Protobranchia the original anterior inhalant current persists in the Nuculidae and Solenomyidae, but has been lost in the more specialized Nuculanidae. Although the latter are certainly not ancestral to the Filibranchia and

Eulamellibranchia, yet they indicate the manner in which the anterior inhalant current has been replaced by a posterior current entering ventral to the exhalant current. The possibly universal mode of formation of the siphons, by ciliary junctions replaced by tissue junctions (see fig. 18), is beautifully displayed in existing members of this family. The advantage of a posterior inhalant opening in animals which move into and through a soft substratum is clear. It enables the animals to keep the anterior end under the surface while still respiring freely and to move about without the sediment which will be stirred up entering with the inhalant current. It has enabled *Yoldia* to exist with the anterior end permanently buried. The Nuculidae have countered the difficulties inherent in the possession of an anterior inhalant current by moving about sparingly when once buried. The Solenomyidae which move about more freely have acquired the unique capacity of intucking the ventral margins of the shell and so clearing the mantle cavity of the great quantities of sediment which habitually enter. The evolution of the higher Lamellibranchia from forms such as the modern Nuculidae is indicated by the presence in the less specialized Filibranchia, *Glycymeris* and *Arca*, of a small interior inhalant current in addition to a much larger posterior current (Atkins 1936). But with these exceptions the inhalant current is exclusively posterior in the higher Lamellibranchia except in the Lucinacea ("Erycinacea", see Pelseneer 1911), where the animals have secondarily adapted the burrowing foot as a creeping organ and live either free on a hard surface like *Kellia* or, more usually as in *Montacuta*, in commensal relationship with other invertebrates (Leyborne Popham 1939).

The disposal of sediment which collects in the mantle cavity becomes a matter of the greatest importance in Mollusca which have taken to life in a soft substratum. Except in the Solenomyidae cleansing of the mantle cavity in the Protobranchia is by the agency of cilia which carry particles to the region where the palp proboscides are extruded, i.e. ventrally in the Nuculidae, posteriorly in the Nuculanidae. Final ejection is aided by contractions of the adductors. This mechanism foreshadows those in the higher Lamellibranchia, where material is extruded by way of the inhalant opening or siphon. In the Solenomyidae ejection is essentially muscular, the result of the intucking of the ventral margins of the shell. Anterior mucous glands in this family and posterior mucous glands in many of the Nuculanidae aid in the consolidation of the particles.

The ctenidia of the Nuculidae and Solenomyidae retain all essential primitive characteristics, and closely resemble those of zygobranchiate Gastropoda such as *Diodora* or *Haliotis* (Yonge 1939). They have the same leaf-like filaments and the same arrangement of dorsal (afferent) and ventral (efferent) blood vessels, and of lateral, frontal and (except in the Solenomyidae) abfrontal cilia with chitinous supporting rods under the epithelium carrying the first of these. They have extended further anteriorly owing to an increase in the number of filaments, but the blood supply still enters and leaves at the anterior end of the axis, as it does in certain Filibranchia such as *Pecten*. There are certain significant differences. There is the dorsal attachment, but this is represented in the Gastropoda by the short posterior dorsal attachment in *Haliotis* and *Diodora* and by the extensive dorsal attachment of the single ctenidium in the Trochidae (Randles 1904). The filaments are also united to some extent by interlocking cilia. Latero-frontal cilia have been acquired and act as strainers impeding the passage of particles between the filaments. They have a secondary function in the Solenomyidae where they assist in selection. The filaments are opposite instead of alternate. But although these developments in the ctenidia have brought about a more efficient division of the mantle cavity into inhalant and exhalant chambers, the still imperfect nature of this is indicated by the retention in these two families of hypobranchial glands in the exhalant chamber.

In the Nuculanidae the ctenidia have evolved along lines of their own, although the filaments are clearly modifications of those in the Nuculidae and the blood supply is identical. By the great development of ciliary junctions between adjacent filaments, those of opposite sides and between the terminal filaments and the siphonal septum, together with the flattening of the ventral margins of the filaments and great development of striated muscle and of internal blood spaces, the ctenidia have been converted into a delicate muscular septum perforated by four rows of delicate, ciliated pores. This remarkable development of the primitive ctenidium is paralleled only by an analogous modification of the eulamellibranch gill into the muscular septum of the Septibranchia. In the Nuculanidae, judging by the number of surviving species and genera and their wide distribution, the experiment has been more successful than in the Septibranchia. This is probably because they have not at the same time modified their feeding mechanisms which remain identical with those of the Nuculidae. But the Nuculanidae are a group in which extreme specialization in one set of organs has precluded further evolutionary advance.

### (*b*) *Interrelationships between the Protobranchia*

It follows from what has been said that the Nuculidae exhibit more primitive characters than any other existing family of the Lamellibranchia. In addition to the shell characters, with which this investigation is not specifically concerned, there are the open mantle cavity, the primitive ctenidia, the anterior inhalant current, the feeding mechanism and gut, and finally the foot and the habits which probably approximate most nearly to those of the primitive Lamellibranchia.

The Solenomyidae clearly derive from a common stock with the Nuculidae. Stempell (1899) listed the major differences in morphology from the Nuculidae and pointed out that the majority of these are to be correlated with the different mode of life. They are more obvious but less significant than the points of resemblance. The ctenidia, although certainly feeding organs and, as a result, greatly increased in number of filaments, and, owing to the shape of the body, differently orientated, are fundamentally similar and the hypobranchial glands are even better developed. There is the same anterior inhalant current. The palps, though modified in correlation with the change in size and function of the ctenidia, remain essentially the same. They are certainly not primitive as suggested by Morse (1913). The gut represents no more than a simplification due to the more finely divided nature of the food. The habit of burrowing deeply into the substratum has had the greatest effect in modifying structure. To this may be attributed the elongated, anteriorly directed foot with the absence of the anterior pedal protractors, the fusion of the posterior half of the mantle edges ventrally, and the great modifications of the shell. The ventral intucking due to absence of calcification is unique and so are the radiate folding of the shell and the presence of compound glands in the mantle edges, the secretion of which may be concerned in maintaining the flexibility of the ventral regions of the shell. The greatly modified, edentulous hinge, although possibly primitive if the Solenomyidae separated from the other Protobranchia before hinge teeth had been acquired, is functionally correlated with the need for sudden, repeated closures of the shell valves in connexion with movement and, more especially, the removal of sediment from the mantle cavity. The swimming Lamellibranchia, e.g. *Lima*, *Pecten* and *Amussium*, all lack hinge teeth and possess a powerful internal ligament. It has been emphasized elsewhere (Yonge 1936*b*) that the capacity for swimming is the result of further evolution of mechanisms concerned in the first instance with ejection of sediment from the mantle cavity. The length of the kidneys and of the pericardium and the modifications of the nervous system (described and figured by Stempell 1899), are also to be correlated with the elongation of the body. On the other hand, the absence of cross connexions between the kidneys and of sacculations on their walls and the opening of the gonoducts into the pericardial end of the kidney (Pelseneer 1891, 1899; Stempell 1899) are probably all primitive features.*

The Solenomyidae probably represent one of the first lines along which the early Lamellibranchia evolved. They are a very old group appearing in the Devonian and of the six genera recognized by palaeontologists only *Solenomya* persists. The species of this genus are widely scattered, occurring, according to Morse (1913), off the east and west coasts of North America, off West Africa and the Canaries, in the Mediterranean, around Australia and New Zealand, while *S. bartschi*, which attains a length of over eight inches, has been taken only off the Philippines. It is surprising that any species of a group which evolved so early along such specialized lines have survived.

The Nuculanidae, as indicated by the possession of relatively few, alternately disposed, ctenidial filaments, probably diverged earlier and so have evolved further from the primitive Protobranchia stock. This is best indicated by tabulating those features in which they differ from *both* the Nuculidae and the Solenomyidae.

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* Iredale (1939) separates the Solemyidae [=Solenomyidae] from the other Protobranchia and places them in a separate order Palaeobranchia. He states, in explanation of this, that "The edentulous hinge and weak shell contrast greatly with the multidentate hinge and stout shell of its associates elsewhere, the Nuculids, the only resemblance being the simple gill seen in the animals of both these groups. This, however, is of quite a different nature in each case, and is certainly not a sign of any relationship whatever." It is impossible, in the light of the work of Pelseneer (1891) and of Stempell (1899) and of the facts presented in this paper, to admit the truth of this statement.

TABLE I

| | *Nuculidae* and *Solenomyidae* | *Nuculanidae* |
|---|---|---|
| 1. | Ctenidial filaments richly ciliated and relatively unspecialized but opposite | Filaments with sparse free cilia and highly specialized but alternate |
| 2. | Ciliary junctions confined to simple disks and knobs | Ciliary junctions highly developed and very efficient |
| 3. | Respiratory current created by lateral cilia | Current created by muscular, pumping movements |
| 4. | Anterior inhalant current | Posterior inhalant current |
| 5. | Siphons absent | Siphons present |
| 6. | Hypobranchial glands present | Hypobranchial glands absent |
| 7. | Adoral sense organs present | Adoral sense organ absent |
| 8. | No marginal sense organ | Marginal sense organs present |
| 9. | No posterior unpaired tentacle | Tentacles present in all but *Nuculana minuta* |
| 10. | Mucous glands on mantle, if present, anterior | Mucous glands, if present, posterior |
| 11. | Oesophagus and stomach never twisted to left though may be displaced to that side | Oesophagus and stomach twisted to left |
| 12. | Two ducts into digestive diverticula and all diverticula the same | A third duct leading into a region of specialized diverticula |
| 13. | Visceral ganglia smaller than cerebral ganglia | Visceral ganglia about equal in size to cerebrals |

Despite some superficial differences, notably in respect of shell characters, the Nuculanidae are a very homogeneous group. They have improved on conditions in the Nuculidae by the acquisition of siphons and a posterior inhalant current and, although retaining the feeding mechanism unchanged, have added a specialized region of wide diverticula in the gut. They have exploited the possibilities of ciliary junctions to a unique degree. The enlarged visceral ganglia are probably due to the posterior extension of the body. But although the pumping ctenidia constitute one of the most interesting respiratory mechanisms in the animal kingdom, they have rendered further evolution impossible. Hence this family, established in the Silurian, has done little more than maintain itself while the higher Lamellibranchia have evolved their characteristic ciliary feeding mechanism and become widespread.

Such evolution as has occurred in the Nuculanidae has led to the appearance of animals with delicate and more flattened shells adapted for life in the deep seas where competition is slight. These genera include *Malletia*, *Tyndaria* and *Neilonella* which are included by Thiele (1934) in the Family Malletiidae. But the present study of *Malletia* has failed to reveal any structural differences sufficient to justify its separation from the other Nuculanidae. The external ligament and open statocysts mentioned by Thiele are not sufficient to outweigh the many points the two have in common. There is actually more reason for separating *Yoldia* from the other Nuculanidae, but this has never been suggested. The "Malletiidae" are Nuculanidae which have been modified, mainly in shell characters, to fit them for life in the soft mud of abyssal seas.

### (*c*) *Systematic position of the Protobranchia*

Pelseneer (1891) gave a list of characters in respect of which he claimed that the Protobranchia are more primitive than all other existing Lamellibranchia, and of five additional characters in which the Nuculidae (in which at that time he included the Nuculanidae) are more primitive than the Solenomyidae. Stempell (1898*a*) agreed that the Protobranchia are phylogenetically the oldest living Lamellibranchia. He disposed of Pelseneer's statements that a pharyngeal region and jaw is present, that the posterior aorta is absent, that the kidney sacs of the two sides do not intercommunicate and that the gonads open into the pericardial extremity of the kidneys. Pelseneer (1899, 1911) later accepted these corrections, but rightly continued to maintain that hypobranchial glands homologous with those of the Gastropoda occur which Stempell (1898*a*, 1899) had also contested. Stempell (1898*a*) added as primitive characters the simple relation of the soft parts to the shell and the primitive characters of the shell without prismatic layer and with unmodified hinge teeth and ligaments. Drew (1899) showed that both Pelseneer and Stempell were wrong with reference to the presence of a creeping sole and the primitive nature of the pedal muscles and also, as far as *Yoldia* was concerned, the presence of open statocysts. He also (1899, 1901) denied their further contention that pleural ganglia exist distinct from the cerebral. Burne (1904), after a study of *Nucula nucleus*, came to the same conclusion. Heath (1937) has reviewed the position and adopted a non-committal attitude, and the presence of separate pleural ganglia remains very doubtful. There is no reason for assuming that the primitive Mollusca had separate pleural ganglia.

The kidneys have been further studied by Burne (1903), Odhner (1912) and Heath (1937). They are certainly primitive in that the excretory lining is continuous. Odhner (1912) has shown that the configuration of the kidneys in the Nuculidae and Nuculanidae, where the external opening is directed posteriorly, agrees with that in some Filibranchia such as the Mytilidae, whereas the condition in *Solenomya*, where there is an anteriorly directed opening, agrees with that in other Filibranchia, such as the Arcidae, and in all the Eulamellibranchia and Septibranchia. He constructed a bifurcating phylogenetic tree on this basis with *Solenomya* as an offshot from the base of the larger branch. But, as Burne (1903) has pointed out, the configuration of the kidneys in the Nuculidae and Nuculanidae is probably affected by backward displacement due to the very large stomach. It appears unsound, therefore, to base any far-reaching conclusion on this point of difference. Pelseneer (1891) considered that the ventral passage of the rectum in relation to the heart was a primitive feature, but Drew (1901) showed that the rectum actually traverses the ventricle during development but subsequently, owing apparently to pressure from the growing kidneys, the heart is displaced dorsally.

There remain, of the primitive characters originally listed by Pelseneer and by Stempell, the following:

1. Posterior ctenidia with leaf-like filaments closely resembling those of the zygobranchiate Gastropoda. (Modified in the Nuculanidae.)

2. Hypobranchial glands. [Absent in the Nuculanidae, but present in *Monia* amongst the Filibranchia (Atkins 1936).]

3. Posteriorly situated heart with muscular auricles connecting with the efferent vessels leaving the anterior end of the gill axes. (This condition is also found in certain Filibranchia.)

4. Kidneys glandular throughout.

5. Visceral ganglia indifferently developed. (Except in the Nuculanidae.)

6. Mantle widely open. (Not in the Solenomyidae, but found also in many Filibranchia.)

7. Statocysts open to the exterior. (Except in certain Nuculanidae, but also open in various Filibranchia.)

8. Taxodont dentition. (Solenomyidae possibly secondarily edentulous, but Arcacea also taxodont.)

As a result of the work of Drew (1899, 1901) may be added:

9. Presence of a test round the embryo.

And as a result of the present work also:

10. Anterior inhalant current. (Except in the Nuculanidae.)

11. Labial palps with proboscis.

12. Gut with triturating stomach, mucus from "style-sac" region concerned with assisting trituration and with formation of faeces, but without amylase.

13. Digestion exclusively intracellular in the digestive diverticula. (Additional specialized digestive diverticula in the Nuculanidae.)

The Protobranchia constitute a natural group. Although certain of their primitive features, notably nos. 3, 6, 7, 8 and, to a minor extent, 2 and 10 in the above list, they share with some of the Filibranchia, the points of difference far outweigh these resemblances. The incorporation by Neumayr (1891) and Thiele (1934) of the Protobranchia with the Arcacea, although reasonable if only the taxodont dentition of the shell is considered, is revealed as untenable after the structure and physiology of the two groups has been adequately examined. Neumayr originally separated the Solenomyidae from the rest of the Protobranchia and included them, with other edentulous families from the early Paleozoic, in the Palaeoconcha. Although Thiele regrouped them with the other Protobranchia, Davies (1933, 1935), following Douvillé (1912), separated them again and regards them as broadly ancestral to the burrowing order Desmodonta which includes genera such as *Panope*, *Pandora* and *Mya* as well as the Teredinidae and the Septibranchia. But examination of the structure of *Solenomya* reveals not only its close association with the Nuculidae, but also its unique line of specialization involving both soft parts and the shell. It is impossible to regard it as even broadly ancestral to any of the higher Lamellibranchia. Odhner (1912), who fell into the same error, in this case on the basis of the form of the kidney, makes it broadly ancestral to quite a different group of the higher Lamellibranchia.

Shell characters alone can never provide a sound basis for the general classification of the Lamellibranchia, although they constitute the only criteria for extinct species. The shell may certainly be greatly modified in relation to habit and *Solenomya* provides an admirable example of this. On the other hand, Pelseneer's system, based on the ctenidia, has not been entirely successful. It has recently been subjected to an exhaustive analysis by Atkins (1938). The Filibranchia, as she points out, are certainly not a natural group, while the septibranchiate condition may have been acquired independently by the Poromyidae and the Cuspidariidae (Yonge 1928). Atkins (1938) has shown that the Lamellibranchia may be divided into two groups on the basis of the nature of their latero-frontal cilia. One group has large eu-latero-frontal cilia with subsidiary pro-latero-frontals. The other has very small micro-latero-frontal cilia. The former group includes the Protobranchia, some of the Filibranchia, the Eulamellibranchia and the Septibranchia; the latter the Pseudolamellibranchia (as re-established by Pelseneer in 1911) and the remaining Filibranchia. Atkins suggests that the second group is not derived from the same stock as the first and that the Nuculidae cannot therefore be regarded as ancestral to them. But she bases this on the assumption that "It seems very improbable...that such useful structures in the ciliary method of feeding as eu-latero-frontal cilia once possessed would be lost, so long as the method of obtaining food remained the same." But this statement disregards the fact that filtration of water through the gill is controlled by muscular action and blood pressure as well as by the latero-frontal cilia. This has been shown conclusively by Elsey (1935) in *Ostrea gigas* and *O. lurida.* It will be impossible to assess the value of Atkins' suggestions until the relative importance of these additional mechanisms controlling filtration have been determined in ctenidia with and without large eu-latero-frontal cilia. It is hoped to go into this matter with the attention that it deserves in a forthcoming paper on the evolution of the molluscan ctenidium.

There remains, therefore, Pelseneer's separation of the Protobranchia from the rest of the Lamellibranchia and this is certainly based on fundamental differences between the two groups. It is to be concluded that the order Protobranchia established by Pelseneer in 1891 is valid and that it represents the one unquestionably natural group within the class Lamellibranchia.

## 8. Summary

1. The habits, the structure and physiology of the organs in the mantle cavity, and the nature of the gut, have been examined in representatives of the Nuculidae, Solenomyidae and Nuculanidae, the three families which constitute the Protobranchia.

2. In all the foot is a large and highly specialized organ permitting movement into and through a soft substratum. *Solenomya* is adapted for life under the surface and the shell is greatly modified in correlation with this habit, *Yoldia* for life in vertically constructed burrows. Large and numerous pedal muscles operate the foot.

3. In the Nuculidae and Solenomyidae the inhalant current enters anteriorly, in the Nuculanidae posteriorly through siphons which in different species show interesting stages in the conversion of ciliary into tissue junctions.

4. Rejection of sediment from the mantle cavity is carried out by ciliary tracts leading ventrally in the Nuculidae and posteriorly in the Nuculanidae, in both cases to the region where the palp proboscides are extruded. In the Solenomyidae rejection is primarily the result of the intucking of the uncalcified, ventral regions of the shell causing an almost complete obliteration of the mantle cavity when the adductors contract. Anterior mucous glands are associated with cleansing in the Solenomyidae, posterior glands in many of the Nuculanidae.

5. The ctenidia of the Nuculidae and Solenomyidae are primitive with the addition of ciliary disks or knobs uniting the filaments and of latero-frontal cilia, and are essentially similar. Those of the Solenomyidae are feeding as well as respiratory organs and correspondingly increased in extent and number of filaments which are opposite. Those of the Nuculidae are primarily respiratory. Hypobranchial glands occur in these two families only.

6. The ctenidia of the Nuculanidae are highly specialized to form delicate septal membranes perforated by four rows of ciliated pores. Striated muscle in the suspending membrane, axis and in the filaments permits rhythmical upward movements which cause sudden intake of, and expulsion of, water. This modification is due to the flattening of the ventral margin of the filaments and to the intimate union of adjacent filaments, those of opposite sides (in some species), and of the terminal filaments with the siphonal septum, all by means of highly efficient ciliary junctions.

7. Ventral (efferent) and dorsal (afferent) blood vessels run through the ctenidial axes in all species. The former maintain their primitive connexion with the muscular auricles.

8. The palps consist of one pair of long, extensile palp proboscides and two pairs of grooved palp lamellae with an intermediate palp pouch in the Nuculidae and some Nuculanidae. The proboscides are the feeding organs in the Nuculidae and Nuculanidae, extending outside the shell and conveying material to the lamellae by way of ciliated grooves on their under sides. Sorting action on the lamellae prevents any but the smallest particles entering the mouth. In the Solenomyidae the reduced proboscides collect food particles direct from the ctenidia. Sorting, which is initiated on the ctenidia, is completed between the pair of low folds, which represent the palp lamellae, and only extremely fine particles enter the mouth. All of the Protobranchia are deposit feeders.

9. Except in the Solenomyidae, the oesophagus is dilated anteriorly, but this is for

the accommodation of the relatively large food particles and does not represent a modified pharynx.

10. The stomach, except in *Solenomya*, possesses a dorsal ciliated sorting region from which only the finest particles are sent into the ducts of the digestive diverticula. In all there is also a dorsal (or anterior) crushing region lined with chitin and a ventral (or posterior) "style-sac" region which secretes mucus. In this particles are embedded to assist in trituration and also in the formation of faeces. No amylase is secreted with this mucus.

11. The digestive diverticula in the Nuculidae and Solenomyidae consist of two symmetrically arranged masses communicating with the stomach by a right and a left duct. In the Solenomyidae all particles enter the diverticula, in the Nuculidae only those passed into them by the sorting region. In the Nuculanidae there is an additional mass of wide diverticula on the left side posterior to the original left mass. The duct opens near to the opening of the oesophagus into the stomach and much larger particles enter.

12. Digestion is exclusively intracellular and confined to the digestive diverticula there being no phagocytic blood cells in the epithelium or lumen of the gut.

13. The intestine and rectum are concerned exclusively with the formation of the very compact faecal pellets. In the Nuculidae the intestine is looped on the right side of the body sometimes displacing the stomach to the left; in the Nuculanidae the intestine extends further anteriorly and, by pushing the posterior region of the oesophagus to the left, twists the stomach round in that direction. In the Solenomyidae the gut runs in the middle line throughout.

14. The Nuculidae are the least specialized of the Protobranchia and represent the most primitive living Lamellibranchia. The Solenomyidae are specialized in one direction, notably in respect of habits which is reflected in the greatly modified shell, the Nuculanidae still further in another direction involving the evolution of the pumping ctenidia.

15. The structure and habits of the Nuculidae probably correspond fairly closely with those of the primitive Lamellibranchia from which the existing higher forms evolved. These must certainly have possessed the same type of ctenidia, an anterior inhalant current, and also palp proboscides the presence of which permitted the retreat of the mouth from the substratum and the enclosure of the body in a bivalve shell. The typical lamellibranch gut with the style mechanism could also have evolved from the gut of the Nuculidae. The foot of the Protobranchia, permitting life on a soft substratum, is probably also primitive, being correlated with the possession of palp proboscides used for collecting food from this type of bottom.

16. The "Malletiidae" are Nuculanidae specialized, especially in shell characters, for life on the soft mud of deep seas. There is no adequate reason for establishing a separate family for their inclusion.

17. The position of the Protobranchia in relation to the rest of the Lamellibranchia

is reviewed and the conclusion reached that they represent the one unquestionably natural group within the class Lamellibranchia.

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# EXPLANATION OF PLATE 15

## KEY TO LETTERING ON PLATE

*agl*, anal gland; *c*, ctenidium; *ch*, chitin lining dorsal region of stomach; *cjs*, ciliary junction between ctenidium and siphonal septum; *dd*, duct of digestive diverticula; *ess*, epithelium of "style-sac" region of stomach; *ex*, base of exhalant siphon; *fa*, faecal pellet ready for extrusion through anus; *gss*, groove in "style-sac" region of stomach; *lg*, lateral groove in oesophagus; *lm*, longitudinal muscle running through ventral surface of ctenidial axis; *rc*, epithelial ridge around ventral margin of dorsal region of stomach; *s*, lumen of stomach; *sp*, siphonal septum; *tc*, terminal cilia on dorso-lateral margins of ctenidial filaments; *td*, tubule of digestive diverticula; *vb*, ventral blood vessel in ctenidial axis.

FIG. 40. *Yoldia limatula*, longitudinal section through posterior region of a ctenidium and through the siphonal septum showing the nature and extent of the ciliary junction between the two. × 80.

FIG. 41. *Nuculana minuta*, transverse section through oesophagus close to the mouth and through a number of the third (right) mass of digestive diverticula. × 150.

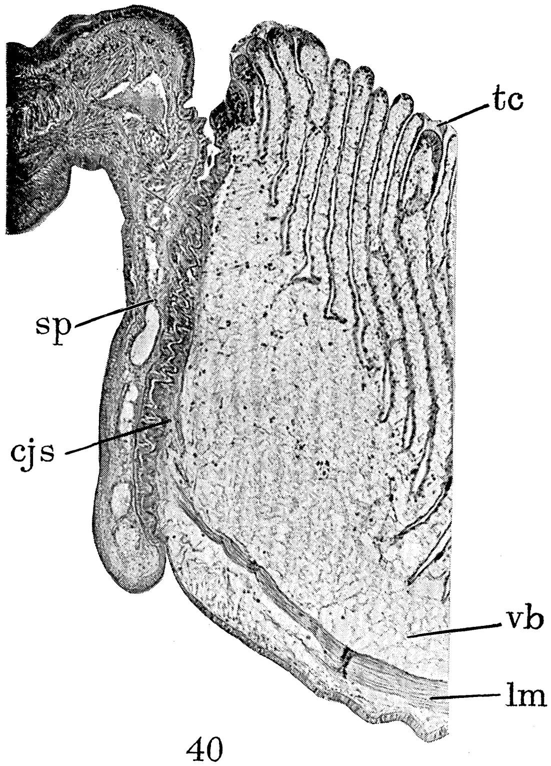
FIG. 42. *Malletia obtusata*, transverse (morphologically longitudinal) section through the stomach in the region of its greatest length showing dorsal and ventral ("style-sac") regions and nature of contents. × 40.

FIG. 43. *Nuculana minuta*, transverse section through a number of the first (left posterior) mass of digestive diverticula. The section, of the same magnification as fig. 41, shows the much greater width of these diverticula and the very large particles ingested within their cells. × 150.

FIG. 44. *Nuculana minuta*, transverse section through the intestine shortly after it has left the stomach and showing the epithelial ridge and finely divided contents massed together with mucus. × 150.

FIG. 45. *Malletia obtusata*, longitudinal section through the free, posterior end of the rectum and the anus. × 65.

FIG. 46. *Solenomya togata*, transverse section through the posterior end of the anterior, ciliated region of the stomach showing the symmetrically arranged ducts on right and left sides leading into the digestive diverticula. × 230.



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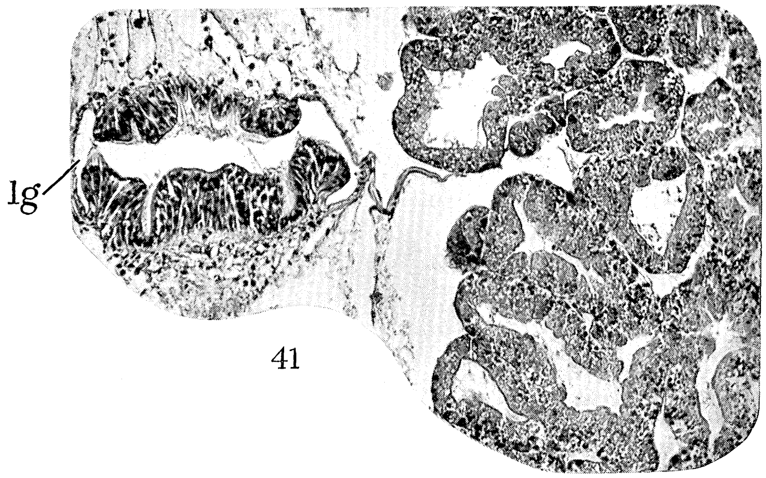

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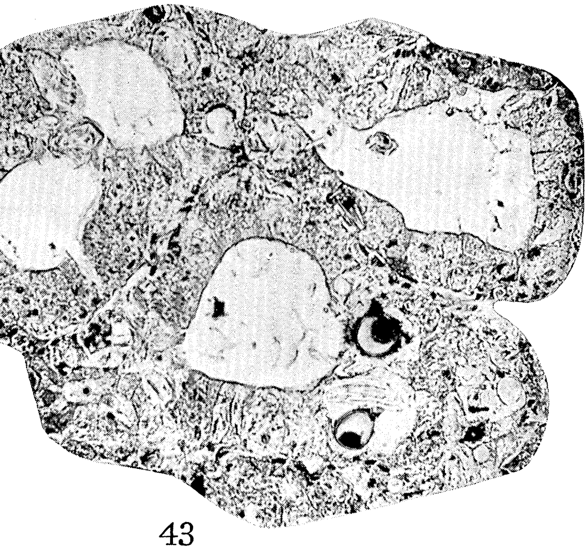

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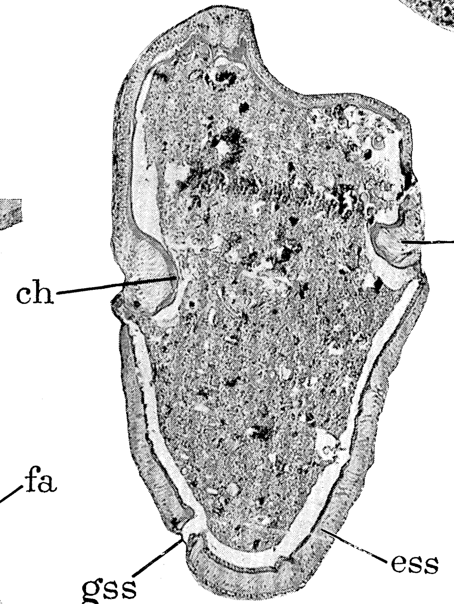

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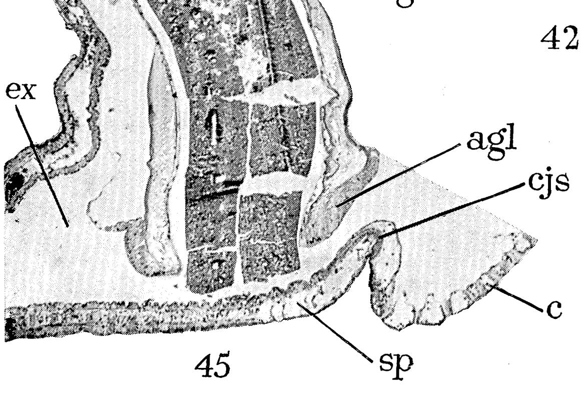

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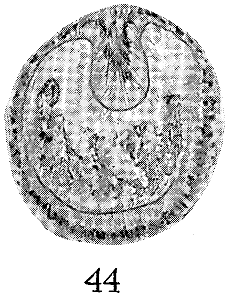

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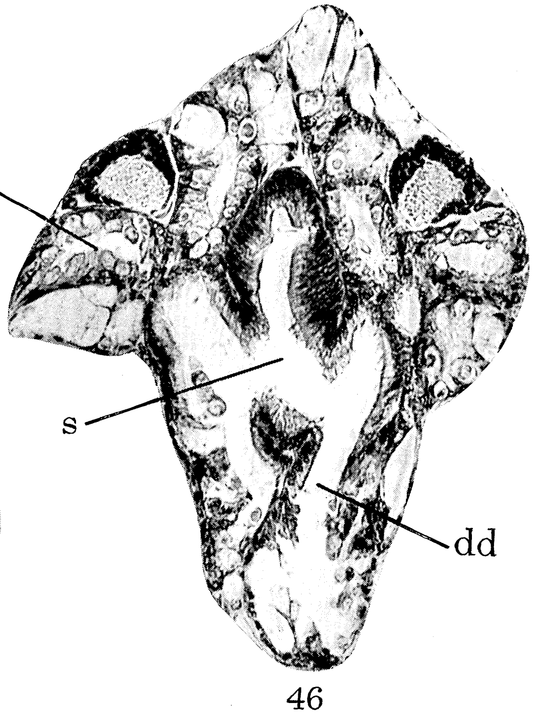

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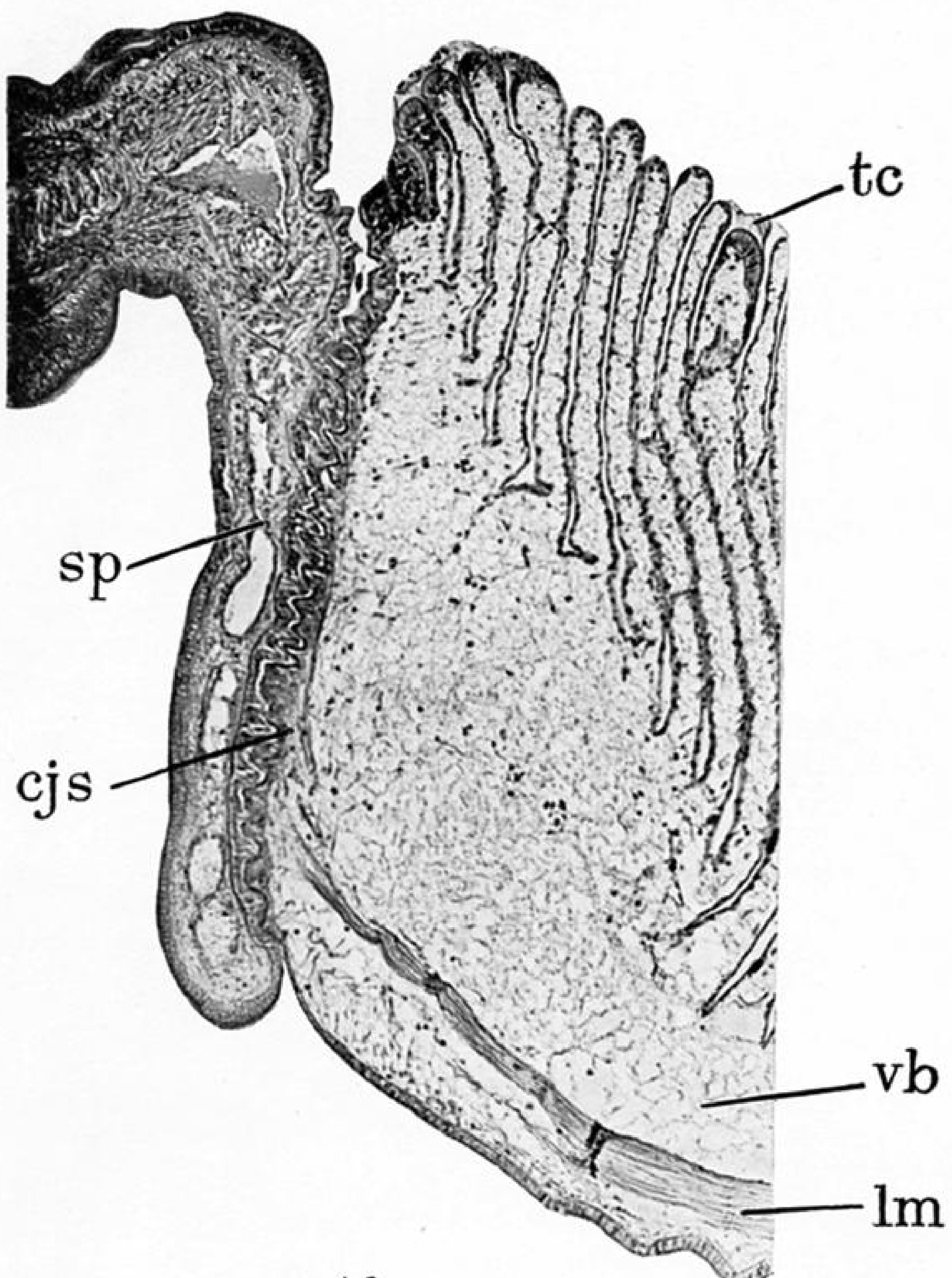

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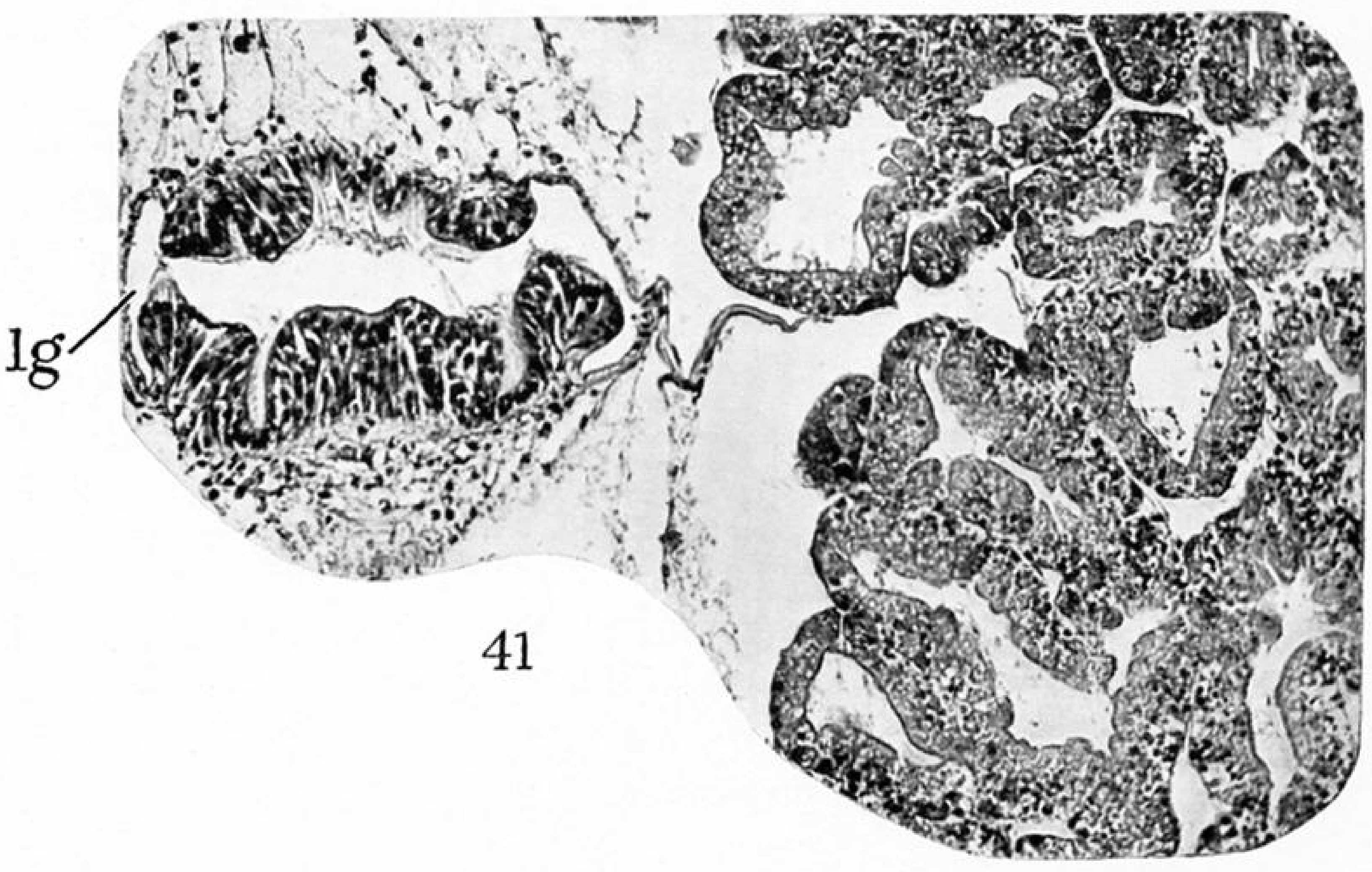

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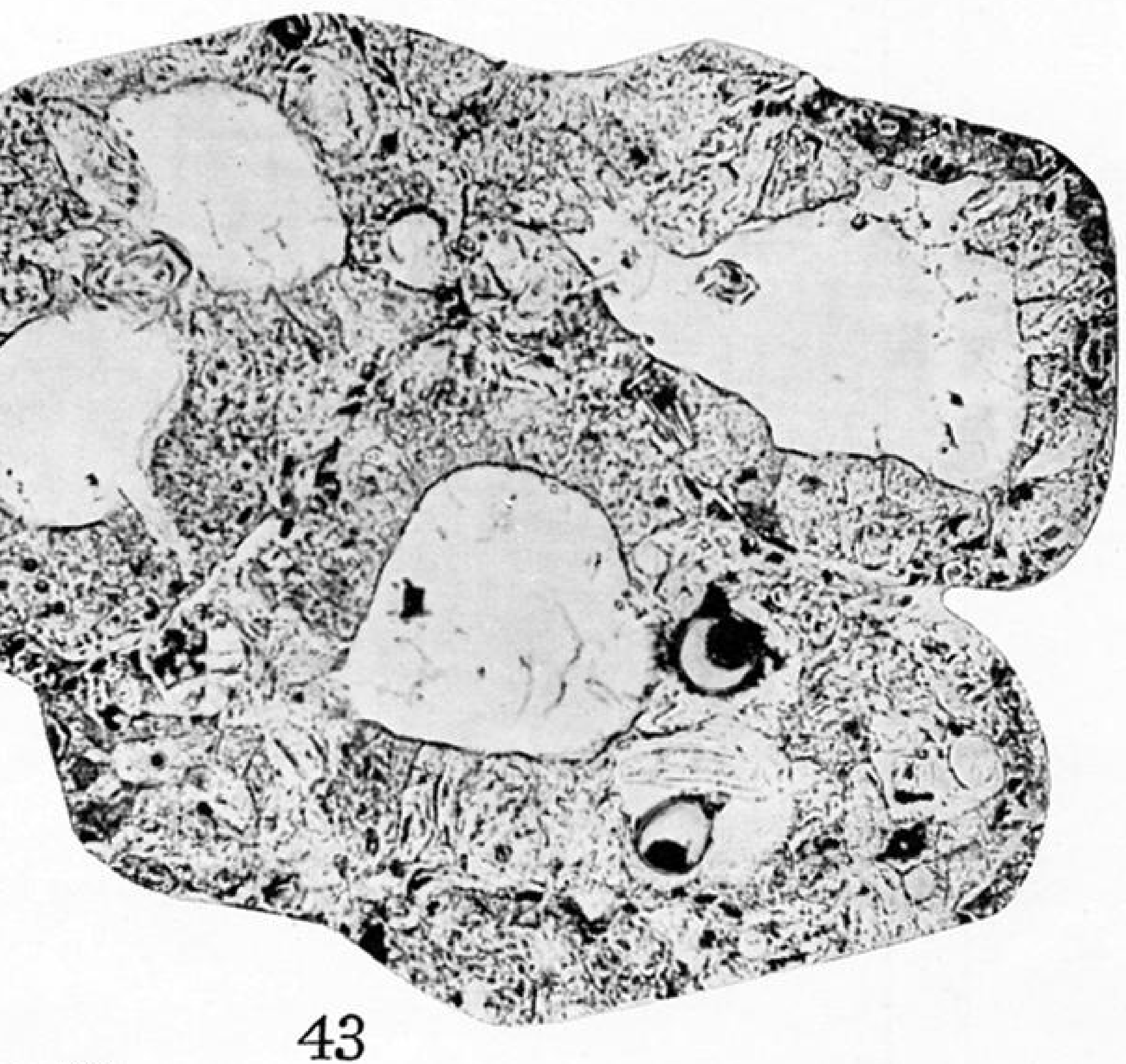

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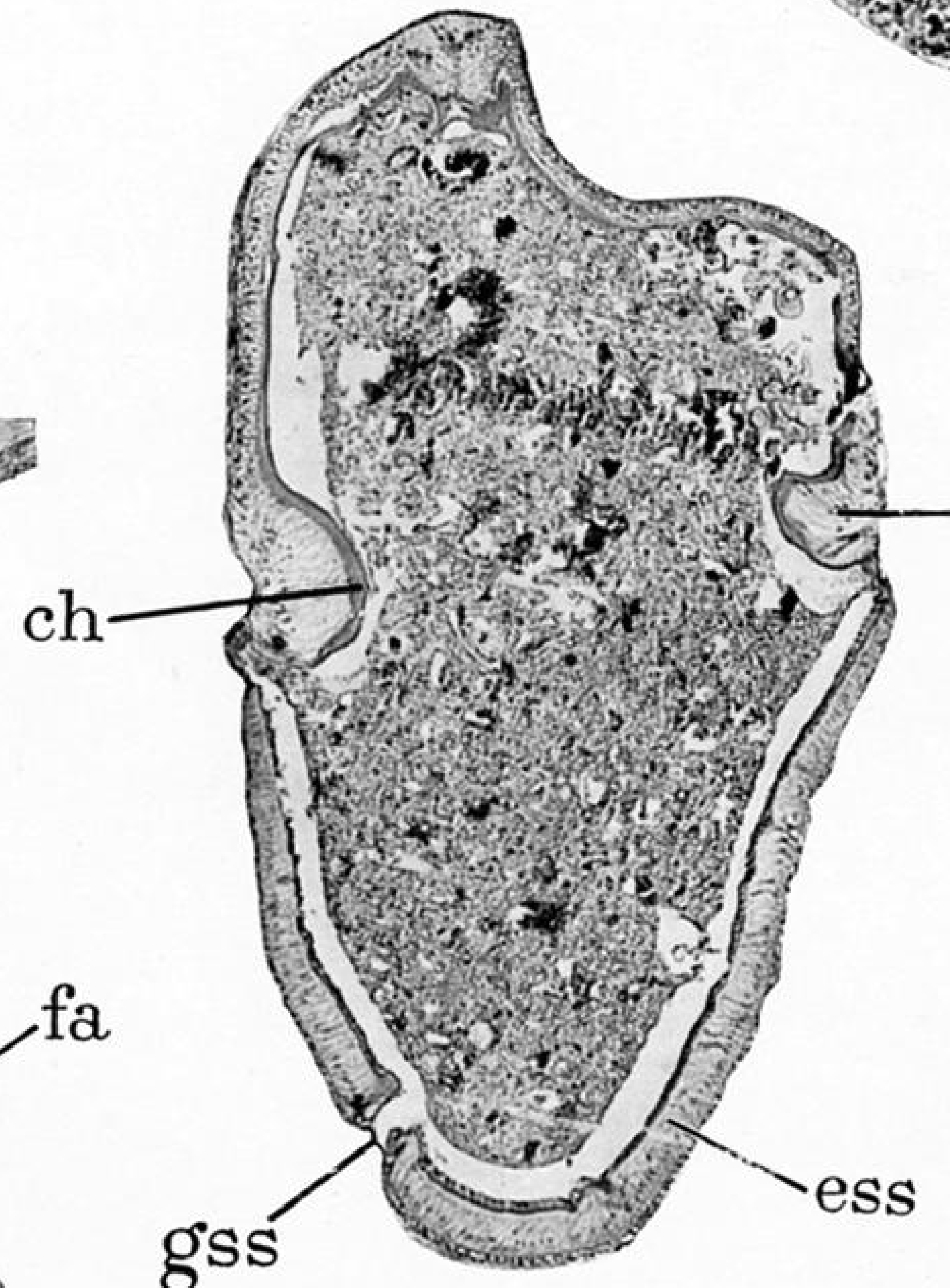

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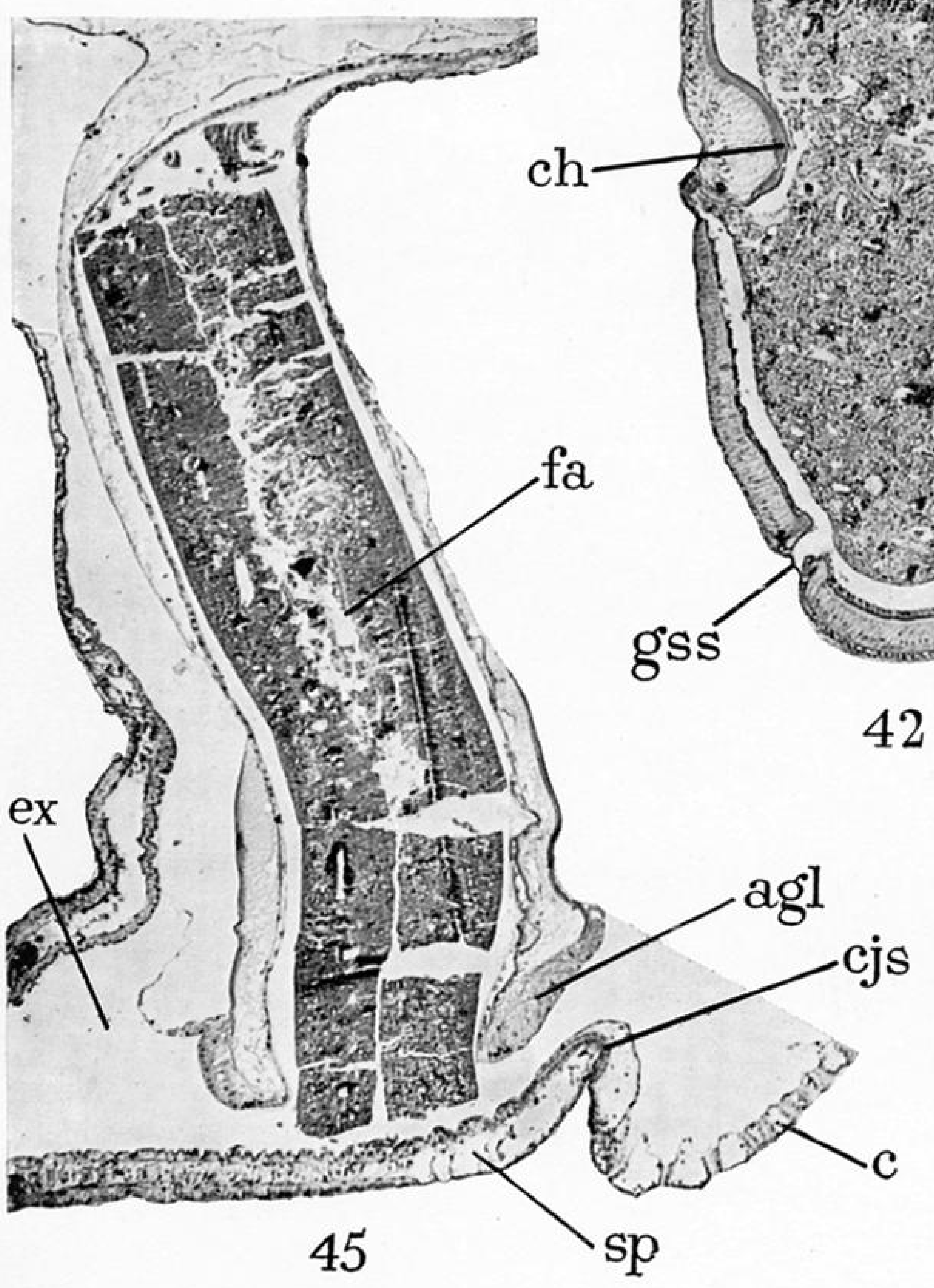

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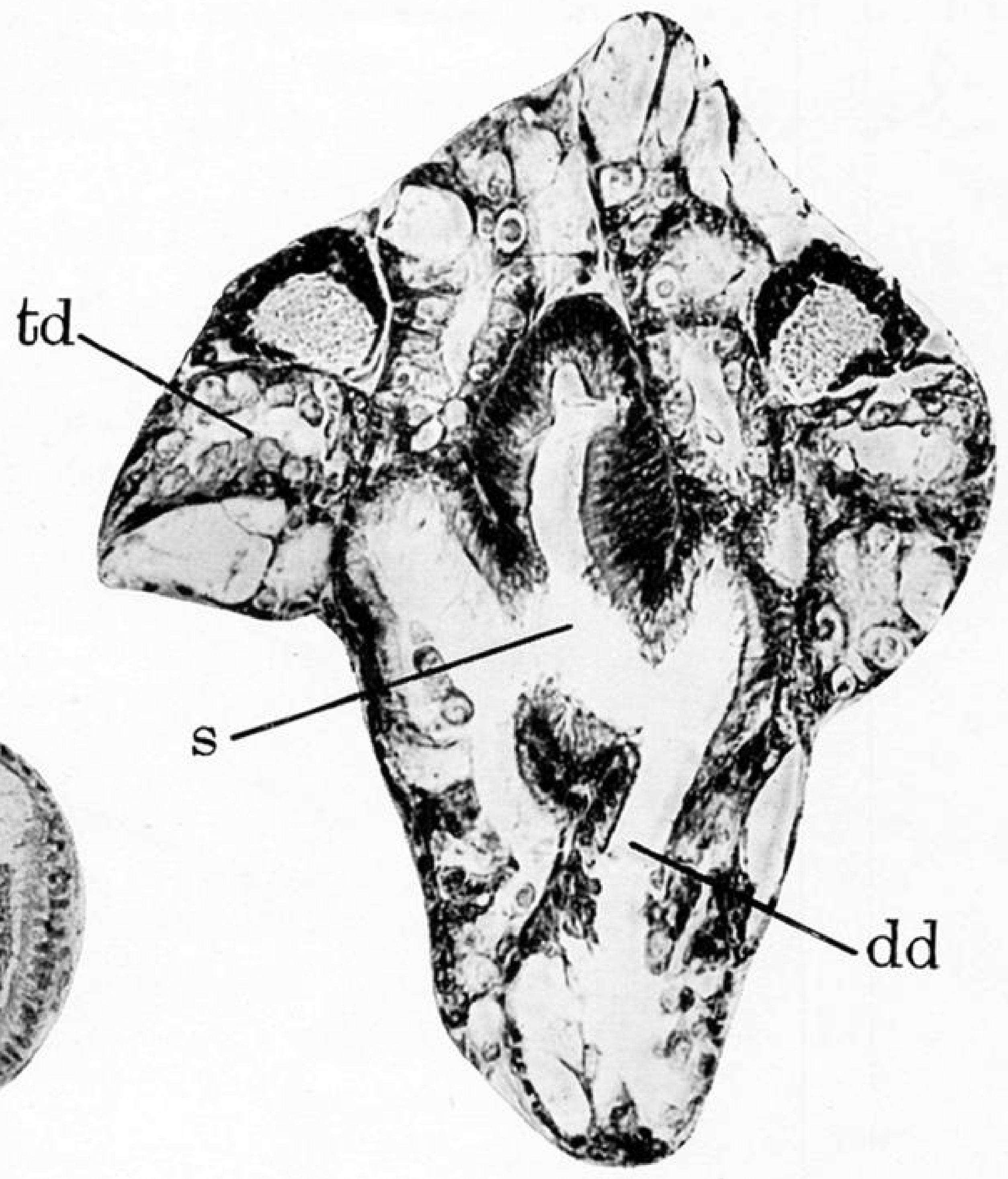

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