THE ANATOMY

OF SOME

PROTOBRANCH MOLLUSKS

INTRODUCTION

Since the protobranchs appear among the earliest known fossils, and owing to the fact that their subsequent evolutionary history has been deciphered to a considerable degree, this group has been the subject of more or less intensive study on the part of numerous investigators. In the last analysis all of these investigations deal either tacitly or explicitly with the subject of relationships. Obviously the palaeontologist is limited to the examination of the shell alone, while others have considered the subject from the standpoint of development or the comparison of one or more systems of organs. As a result the members of this order are known to possess certain features, such as the gills, which appear to be archaic. The nervous system likewise is of a generalized type. According to Odhner ('12) the urogenital system represents a halfway stage between that of a hypothetical ancestor and the more complex species in the genus *Anodonta*, for example.

The foot, on the other hand, is operated by sets of muscles as complicated as in any other species of pelecypod. Kellogg ('15), after studying over thirty species of lamellibranchs, writes regarding *Yoldia limatula* (no nuculid was examined) that « it certainly possesses the most extraordinarly complex set of ciliary mechanisms in the group » of living bivalves. Also from the developmental standpoint the protobranchs exhibit certain features which appear to be far removed from a primitive condition. The gigantic test, as shown by the studies of Drew ('01), covers practically the entire embryo, and with the exception of the solenogastres (Pruvot '92) has no counterpart among the mollusks. Also the early cleavage stages appear to differ from the fundamental plan known to exist in the chitons, gastropods, scaphopods, annelids and flatworms.

The fact remains, however, that the protobranchs, or at least those genera represented in the present collection, constitute a closely related group; but to what extent they are primitive can be answered, if ever it can be answered, only by more detailed and more extended studies than we have at present. And, as Pelseneer and Odhner maintain, any attempts to solve the problem of relationships on the basis of a single system must, speaking generally, lead to erroneous conclusions. Only by a thoroughgoing study of all of the systems of organs in as many species as possible can we arrive at a satisfactory solution of this evolutionary problem. On such a principle the following investigation has been conducted.

MATERIAL

The material serving as the basis of the present study includes six genera and twenty-nine species. Their classification and the localities from which they were taken are detailed in the appended table. All of the specimens were killed in alcohol, and in some instances they have been preserved for more than half a century. Accordingly the major portion of the anatomical details described in the following pages has been determined by dissections.

TABLE I

SPECIES	LOCALITY	STATION	FATHOMS
Nucula « *cancellata* » Jeff.	Georges Bank, Behring Sea	Alb 2571	1356
» *nitidosa* Winckworth	Halland, Sweden		5–11
» *nucleus* L.	Bohuslän, Sweden		30–100
» *proxima* Say	Long Id. Sound		12.5
» *rugosa* Odhner	Madagascar		
» *sulcata* Bronn	Bohuslän, Sweden		13.5
» *taeniolata* Dall	Acapulco, Mexico	Alb 3417	493
» (*Ennucula*) *tenuis* Mont.	Behring Sea	Alb 3518	36
» (*Ennucula*) *tenuis* Mont.	Greenland		100–120
» (*Nucula*) *tumidula* Malm	Bohuslän, Sweden		125
Acila (*Truncacila*) *castrensis* (Hinds)	Monterey Bay, Calif.		60–80
» (*Truncacila*) *castrensis* (Hinds)	S. of Alaskan Peninsula	Alb 3210	483
» (*Acila*) *divaricata* (Hinds)	Off Honshu Id. Japan	Alb 3771	61
» (*Acila*) *fultoni* (Smith)	Bay of Bengal		200–300
Yoldia beringiana Dall	Behring Sea	Alb 3601	1044
» *ensifera* Dall	Bellingham, Washington	Alb 3612	11
» *limatula* Say	Long Id. Sound	FH 1765	37

TABLE I (CONTINUED)

SPECIES	LOCALITY	STATION	FATHOMS
Yoldia limatula (?)	Avatcha Village, Kamtchatka	Alb 3642	16
» *montereyensis* Dall	Montérey Bay, Calif.		382–58
» *sapotilla* Gould	Off Massachusets	FH 1161	45
» *scissurata* Dall	Captain's Bay, Alaska		
» (*Megayoldia*) *thraciaeformis* Sto.	Avatcha Village, Kamtchatka	Alb 3777	37
Yoldiella inflata V. et B.	Off Nantucket, Mass.	Alb 2706	1188
» *iris* V. et B.	Martha's Vineyard, Mass.	FH 1093	349
Malletia chilensis Desm.	Talchano, Chili		
» (*Pseudomalletia*) *obtusa* M. Sars	Österfjord, Norway		250–325
« *Leda* » *caudata* Donovan	Off Martha's Vineyard, Mass.	Alb 2528	479
» *extenuata* Dall	S. W. of Sitka Sound, Alaska	Alb 2859	1569
» *fossa* Baird	Behring Sea	Alb 3610	75
» *minuta* Müller	Upernivik Harbor, Greenland		13
» *pontonia* Dall	Off San Diego, California	Alb 2923	822
» (*Sacella*) *taphria* Dall	Monterey Bay, California		15

Alb., U. S. Fish Commission Steamer « *Albatross* ».
FH., U. S. Fish Commission Steamer « *Fisk Hawk* ».

All of the species listed in the table have been examined, and typical examples have been described and figured in considerable detail. In other instances where there is a departure from the usual type these differences have been noted and figured. In the genus *Nucula*, for example, the chief variations occur in connection with details of the musculature and configuration of the digestive tract. In *Yolda*, on the other hand, the digestive system in its general aspects is constructed throughout on the same fundamental plan, the chief differences between the various species being associated with the relative size and distribution of some of the smaller muscles chiefly in the region of the pericardium. In short, an attempt has been made, by description and figures, to afford data to those who may be interested in the evolutionary history of the group, and its relation to other pelecypods and mollusks in general (¹).

(¹) I am deeply indebted to Doctor Alexander Wetmore and Doctor Paul Bartsch of the U. S. National Museum for the major portion of the specimens described in the present work. My sincere thanks also are due to Doctor Nils Odhner who has

It is important to note that certain specimens dredged off Avatcha Village, Kamtchatka, are not certainly identified. Some of the experts to whom they have been submitted are convinced that they are *Yoldia limatula*. Dr. Paul Bartsch, on the other hand, in a written communication expresses the opinion that they may represent an undescribed species. Compared anatomically with Atlantic specimens the Kamtchatkan representatives appear to be very closely related if not identical. But whatever the exact relationships may be in this case, the important point is that both Atlantic and Pacific specimens are treated in the present account, and, furthermore, where the Pacific material is under consideration the name is followed by a query, *Yoldia limatula* (?).

Yoldia thraciaeformis is another example where differences exist between Atlantic and Pacific individuals. The western representatives are considerably smaller than the eastern (as 37 mm. to 53 mm. on the average) yet all are sexually mature. Furthermore, the larger specimens possess certain small muscles in the vicinity of the anterior adductor which appear to have no counterpart in the smaller individuals. This unlikeness may fall within the normal range of variation of the species, or it may be due solely to the difference in size. A comparison of specimens of the same length may be needed to settle this point.

Anatomically *Acila lyallii* appears to be identical with *A. castrensis*, as certain authors have maintained from the study of shell characters.

Nucula taeniolata Dall is not *Nucula, sensu stricto*, to judge from shell characters; anatomically it is unlike *Nucula nucleus* (Linné), the type species of the genus *Nucula*.

Finally, several species are referred to the genus « *Leda* ». Most modern taxonomists employé the generic name *Nuculana* Link, 1807, pointing out that it has priority over *Leda* Schumacher, 1817. Such nomenclatural matters are beyond the scope of this paper.

EXTERNAL FEATURES

Mantle Glands.

Upon the removal of the shell of all of the species of *Nucula* and *Acila* examined in connection with the present work the mantle was found to present an opaque, clouded appearance, the general appearance being illustrated in Pl. IV,

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supplied several species of *Nucula* as well as specimens of *Malletia obtusa*. To Doctor Hubert G. Schenck, who first interested me in the general problem of protobranch anatomy, I am obligated also for his council, literature and various specimens. *Acila fultoni* and *Malletia chilensis* were furnished respectivly by Doctor R. M. Kleinpell and Doctor R. A. Mc Lean. To both I extend my sincere thanks. It is a pleasure also to thank Doctor Paul Pelseneer for reprints of his various and valuable studies on molluscan anatomy and classification. And finally I am deeply indebted to my good friend Doctor G. Dallas Hanna for various specimens. literature and other favors too numerous to itemize.

fig. 29. Examples of several different species were sectioned, but in no case was the state of preservation sufficiently perfect to make it reasonably certain that this excessive thickening of the mantle is due to a pronounced development of gland cells rather than to an undue accumulation of blood in some of the mantle sinuses.

Stempell ('93) notes that in some of the protobranchs the gland cells characteristic of the mantle are more abundant and more prominent in the neighborhood of the mouth and palp tentacle. The same apparently is true of *Nucula sulcata, N. rugosa, N. proxima, N. nucleus* and *Acila castrensis.* At all events the areas in question appear to owe their thickening to high columnar cells with small nuclei and extremely delicate walls, which in most instances have been ruptured or macerated to a greater or less degree. What possibly may be the secretory product is abundant in quantity, but with the stains employed it exhibits the same reaction as the blood elsewhere in the body.

In this connection, however, it is a significant fact that in a carefully preserved specimen of *Yoldia ensifera,* kindly furnished by Doctor G. Dallas Hanna, sections show that the epithelium of the inner face of the mantle, from a point about opposite the anterior border of the anterior shell adductor to approximately the level of the mid section of the stomach, is characterized by a sharply defined area whose general appearance and location are represented in pl. VIII, fig. 67, g. The component cells are relativly high elements (Pl. VII, fig. 48) evidently derived entirely from the inner epithelial layer of the mantle.

As this paper was about to go to press, specimens of « *Leda* » *taphria* were kindly furnished by Dr. G. Dallas Hanna. These had been killed in Bouin's solution and sections of the mantle show conclusivly that in this species at least the excessive thickening of the mantle is due to the development of high columnar cells almost completely filled with a homogeneous secretion unaffected by Delafield's haematoxylin. The general appearance of these elements bears a fairly close resemblance to those of *Yoldia ensifera* (Pl. VI, fig. 48).

The function of these organs is problematical. Stempell suggests that the secretion of the gland cells of the mantle in general prevents an abrasive action on the part of detrital material; and while this indeed may be the case it does not preclude the possibility that the secretion may also serve to bind the food material, and thus facilitate its transport to the mouth. Years ago Kellogg ('15) demonstrated in *Yoldia* the fact that material, nutritive and otherwise, when deposited upon practically any spot on the body surface, may be conveyed to the mouth region by way of an intricate system of ciliated grooves. In experiments I have made upon several eulamellibranchs the conveyed material (carmine, india ink, silt, etc.) travels along these grooves in such a definite fashion, without any scattering, that evidently it is bound by the mucus which covers the general surface of the animal. Whether this is true of the protobranchs in general remains to be demonstrated.

In several species of *Nucula* and *Acila* the mantle cavity contained large quantities of a secretory product which under the coagulating influence of the original preservative had bound the detrital material to a greater or less degree. In *Acila fultoni* and *A. divaricata*, for example, the inner face of the mantle, especially in the region of the palp tentacle, was coated with compacted detritus as firm as sandpaper. Also in one specimen of *Nucula rugosa* the mantle cavity contained large quantities of a secretory product which also surrounded detrital material in the palp grooves, and extended for a considerable distance into the œsophagus. Hence, while it is possible that the secretion in question may prevent the abrasive action of material entering the mantle cavity, it likewise may serve to bind this same material and thus facilitate its transference to the mouth.

Siphons.

Members of the genus *Nucula* and *Acila* are entirely devoid of siphons. In the remaining protobranchs these organs are developed to a greater or less degree. Drew ('99) in his study of *Yoldia* writes as follows :

> « In development the exhalent siphon is formed first, apparently by a union of the margins of the mantle followed by a growth into a tube, and the withdrawal of the base of the tube into the mantle-chamber. A ridge on the inside of each mantle-lobe connects the base of the siphon with the margins of the mantle. This ridge seems to indicate the margin of the mantle that has been drawn in with the receding siphon. The inhalent siphon is formed ventral to the base of the exhalent siphon by the fusion of the ridges just described, accompanied by a dorsal arching of the ventral wall of the inhalent siphon, which now forms the dorsal wall of the inhalent as well. The line of fusion on the ventral side of the inhalent siphon remains distinct even in adult specimens. »

In *Yoldia, Malletia* and « *Leda* » the exhalent siphon is present, whereas the inhalent siphon may be complete or its formation may be arrested permanently at some intermediate stage corresponding to embryonic stages in the development of *Yoldia limatula* as determined by Drew. For example, in *Yoldia montereyensis* (Pl. VI, fig. 47) and *Y. beringiana* the folds of the inhalent siphon are not fused. In « *Leda* » *fossa* the same condition exists. In several other species of these genera in the present collection the fusion is more or less complete, the line of union being indicated by a notch followed by a faint ridge along the ventral face of the siphon.

In all of the specimens of *Yoldiella iris* and *Y. inflata* the posterior section of the mantle cavity was loaded with detritus bound solidly together with some glandular product. This not only macerated the tissues to some extent, but also made impossible by dissection or sections the careful examination of the arrangement of the siphons in these species.

Hypobranchial Gland.

Pelseneer ('91) has described an organ in the protobranchs which he terms a hypobranchial gland. It undoubtedly exists, is unquestionably a gland, and it is located dorsal to the branchiae. In this sense it is definitely a hypobranchial structure, although this does not commit us to the theory that it is the homolog of the same named gland in other mollusks.

As may be seen in the figures (Pl. II, fig. 16, hy), it is a paired body, each division extending from the pericardial cavity to the posterior shell adductor. Furthermore, it involves a modification of the dorsal portion of the mantle, the adjacent body wall and the outer face of the suspensory membrane of the gill. The component cells are pyriform or columnar and are relativly high, those of *Acila divaricata* attaining a height of 0,45 mm. Their secretion apparently differs in the various species, in some instances staining deeply in Delafield's haematoxylin, while in other cases it remains unaffected.

Byssus.

The so-called byssus gland, opening in the mid-line at the posterior border of the pedal disc, varies greatly in size in the different species. In *Nucula tenuis* it is a comparativly bulky organ (Pl. IV, fig. 34), and is but sligthly less so in *N. proxima* and *N. nucleus*. In *N. rugosa, N. sulcata* (Pl. V, fig. 42) and *Acila castrensis*, on the other hand, it is close to the vanishing point, and it is doubtful if it could be located without the aid of sections. All of these species were sexually mature, so there is no means of knowing at present whether the young individuals of these last-named species possess well developed glands in their early growth stages.

In *N. tenuis* the proximal half of this organ, presumably the equivalent of a duct, is lined with a thin epithelial layer essentially the same as that covering the foot in general. At the junction with the gland its lumen is narrowed somewhat, due to transverse muscle bundles whose fibers give no evidence of forming anything in the nature of a sphincter. The gland also is incompletely divided into a dorsal and ventral section due to the development of an inwardly directed fold invaded by muscle fibers. Histological details are not especially clear owing to the state of preservation, but it is certain that the gland cells are slender columnar elements containing darkly staining granules and basal nuclei.

In *Nucula rugosa*, which appears to be typical of those species with a relativly small byssus, the same two divisions are represented. The duct, as usual, is lined with the same low epithelium, but the glandular section is greatly reduced, and its lumen is exceedingly slender. Furthermore, the gland cells appear to have a more cubical form. In *N. sulcata*, on the other hand, the cells seemingly are more scattered, and at certain points appear to possess a pyriform shape, although this feature could not be determined with certainty. Their relation to the lumen likewise remains obscure, and in all probability the lumen itself would have escaped notice had it not been for the darkly staining secretion contained therein.

In *Yoldiella inflata* the byssus is a comparativly well-developed organ with the glandular portion distinctly bilobed as though in its development it had had a double origin. In *Malletia obtusa,* on the other hand, this gland is relativly small and short, and, as in the foregoing species, it manifests signs of a double origin.

MUSCULAR SYSTEM

The muscular system of the different species of *Nucula, Acila, Yoldia* and *Malletia* considered in the present account are constructed upon essentially the same plan, and bear witness to the close relationship of the group. The two species of *Yoldiella,* owing to their small size, were examined in a general fashion only, but the main features of their musculature bear a close resemblance to the other genera.

For the sake of clearness the muscular system may be considered under six heads : the shell adductors; the muscles of the mantle; the branchial muscles; those of the digestive tract; and those of the visceral mass and foot which are best treated in combination. In the present connection but little attention has been paid to the first beyond indicating their position and proportions. Also the musculature of the mantle and of the siphons has been traced in a general fashion only, since this field has been covered satisfactorily by various investigators.

Branchial muscles.

The musculature of the branchiae has been traced only partially owing to the fact that the secretion of the hypobranchial gland, after preservation in alcohol, masks the muscle fibers to a great degree. In *Yoldia montereyensis* a number of delicate strands extend from the visceral wall in the neighborhood of the pericardium to the branchiae. In several other species there are faint indications of a similar system. On the other hand, in practically every species treated in the present work a strong muscle (Pl. VII, fig. 6I) originates dorsal to the posterior shell adductor, and, extending anteriorly and spreading in a fanwise fashion, is attached to the dorsal border of the branchial leaves. It may function to remove detritus from the gills, and possibly may serve to regulate the blood flow to this organ.

Muscles of mouth region.

Owing to the small size of the various species of *Nucula* the muscles in the region of the mouth have been studied in large measure by means of sections, and these show that only slight variations occur within the genus. At least this is true of *N. tenuis, N. proxima, N. sulcata* and *N. rugosa*. *Yoldia limatula* was studied also by means of sections as well as by dissection.

In *Nucula* the ventral body wall, from the level of the mouth to a point about midway of the anterior border of the shell adductor, is provided with numerous small muscles which attach chiefly to the sheath surrounding the adductor. These are largely confined to the more lateral regions. Beyond attaching the body wall firmly during the vigorous movements of the foot it is difficult to ascribe any other function to this set of muscles.

Immediately anterior to the mouth and supra-oesophageal ganglion powerful muscles attach to the dorsal body wall near the midline, and ventrally are inserted fanwise in the ventral body wall (Pl. II, fig. 12). This state of affairs continues for a short distance posterior to the mouth, especially heavy muscle bands being inserted in the region of the palps. Owing to the fact that the intrinsic muscles of the oesophagus are comparativly weak, it is possible that these muscles, by their contraction, raise the mouth region from time to time, and thus push through the oesophagus the food which has accumulated in what may be termed the buccal cavity.

In *Yoldia limatula* the distribution of the muscles in the mouth region is essentially the same as in *Nucula,* although the individual bundles are fewer in number and larger. In the neighborhood of the mouth five muscles on each side attach to the ventral body wall and on the other hand are inserted in the dorsal wall of the body. The pair arising from the lateral borders of the mouth (Pl. VI, fig. 51, br) attach to the dorsal surface of the body internal to the anterior retractor of the foot. These muscles are not shown in some of the figures, but they appear to be a constant feature in *Yoldia.* In « *Leda* » *pontonia* these muscles are inserted close to the insertion of the anterior pedal protractor.

The muscles of the anterior section of the digestive tract are complicated, and have been traced to only a slight degree. They comprise circular muscles which doubtless act as an oral sphincter. Small dilators likewise are visible, extending from the buccal wall to the insertion of the palp or a short distance more laterally. In addition there are diagonal and longitudinal fibers in the anterior section of the digestive tract, but their exact distribution has not been determined.

Muscles of the Foot and Body Wall.

The other two divisions of the muscular system, those of the visceral mass and of the foot, are relativly extensive, and to a considerable degree merge into one another. This becomes more evident when we recall the fact that in cross section the walls of the visceral mass are roughly hemispherical in outline (Pl. I, fig. 7). The curved portion, that situated next to the shell, usually possesses no muscle fibers beyond a few delicate strands in the region of the attachment of the mantle to the body (as in Pl. V, fig. 39). On the other hand, the more or less horizontal floor of the visceral sac consists of a muscular layer, which is unbroken save at a more or less central point where the stomach and intestine unite, and the visceral sinuses communicate with those of the foot. This central depression may be termed provisionally the pedal pit. Furthermore, when the viscera have been removed (as in Pl. VIII, fig. 63) the exposed floor muscles are found to extend from the anterior shell adductor to the region of the pericardium and the anterior border of the hypobranchial gland, where in a more or less complicated fashion they reinforce the posterior body wall.

Anteriorly this ventral muscular wall is attached to the ventral surface of the sheath surrounding the anterior shell adductor beyond which a few strands extend into the mantle border (Pl. VII, fig. 57). Further anchorage is afforded by muscles, varying in number and size in the different species, which are attached to the shell along the posterior border of the anterior adductor. These are especially well developed in the larger more muscular species, such as *Acila divaricata* and *Yoldia thraciaeformis* (Pl. V, fig. 39, Pl. IX, fig. 78). Additional muscle bundles, likewise varying in number according to the species from two to ten, arise from the antero-lateral borders of the anterior pedal protractors. These clearly are evident in *Yoldia sapotilla* (Pl. IX, fig. 75) and *Acila divaricata* (Pl. X, fig. 89).

The lateral borders of the visceral floor also are attached to the shell, the scar in some species forming an extended streak from the anterior adductor to the pericardium and even beyond (See Schenck '34, Pl. III, fig. 4 of *Ennucula obliqua*). In various of the larger species the muscles are more distinct, and are responsible for several clearly defined scars to which Odhner has given the name « punctiform » (See Schenck '34, p. 21). In *Acila divaricata*, for exemple, radiating muscles (Pl. V, fig. 39) are imbedded in the wall tissue. In addition, there are other bundles which spring from the lateral body wall, and on the other hand are inserted in the floor a short distance within its margin (left side of Pl. V, fig. 39).

In the region of the pericardium the fibers derived from these various sources form various patterns as they extend into the formation of the posterior wall of the visceral cavity. In *Nucula rugosa* (Pl. II, fig. 14), for example, they constitute a comparativly simple sheet. In *Acila fultoni*, and to a greater extent in *A. divaricata* (Pl. V, fig. 39), they are grouped into several distinct bundles. The same is true of *Yoldia limatula* (?) as shown in Pl. VIII, fig. 63. In every instance, as they extend posteriorly and envelop the posterior wall, the resulting muscular layer reaches the dorsal surface in the region of the umbo. Elsewhere the dorsal surface of the visceral mass is devoid of muscle fibers.

Passing now to the great muscles responsible for movements of the foot, the posterior pedal retractor (Pl. X, fig. 83, rp) is usually larger than all of the protractors combined. As is indicated in the diagram, it extends from the postero-dorsal surface of the body to the pedal disc, forming what may be termed the core of the foot. Unquestionably it functions as a definite retractor.

Of the three pairs of large pedal muscles, located on each side of the oesophagus immediately behind the shell adductor, the most posterior one (Pl. X, fig. 83, r) also appears to function as a definite retractor. Its fibers extend into the foot chiefly in the neighborhood of the disc, forming more or less of a sheath about the strands of the posterior retractor.

The two remaining pairs (Pl. X, fig. 83, p, p) probably act, directly or indirectly, as protractors of the foot. The more anterior one, which for the lack of a better name may be termed Protractor A, in some species is situated immediately in front of Protractor B (Pl. VI, fig. 51), or it may hold a more lateral position (Pl. V, fig. 39). To a slight extent it contributes to the formation of the ventral body wall, but the great majority of its fibers extend into the foot, many of them being inserted in what may be termed the « heel », or that angular portion of the foot (Pl. X, fig. 83, h) located at approximately the same level as the pericardium. Muscle Pro. B also contributes to the formation of the ventral body wall, and some of its fibers enter the heel, but the major portion extends into the mid-pedal region between the heel and the disc.

In accounting for the function of these two pairs of muscles it is evident that the heel plays an important part. It is a highly compact portion of the foot, with small blood sinuses, and is marked by a high degree of rigidity. Obviously the contraction of the muscles attached to it will tend to protrude the foot — a direct action therefore.

The indirect action of these muscles is not so obvious. As noted previously, they tend to form a sheath about the central core formed by the posterior pedal retractor, so that to some extent they may be looked upon as circular muscles. In addition, there are numerous intrinsic circular pedal muscles. The combined result of the contraction of Pro. A, Pro. B and of the intrinsic circular muscles tends to decrease the diameter of the foot, and at the same time to force the blood supply into the disc region and thus protract the foot. This type of protraction, therefore, is to some extent indirect.

Among the various intrinsic pedal muscles, the most conspicuous are transverse bundles bridging the area between the anterior pedal retractors and the pericardium. Evidently they correspond to similar bands scattered throughout the deeper portions of the foot, but they are of larger size and greater length, in some instances extending entirely across the foot. A few strands from some of the bundles immediately posterior to the anterior retractors enter into the formation of the ventral visceral wall (Pl. V, fig. 39), but the greater number are deeper and more strictly pedal. In *Yoldia ensifera* (?), at least, some of these muscles in the neighborhood of the anterior retractors curve anteriorly and extend for varying, distances into the neighborhood of the pedal disc (Pl. X, fig. 86, tr).

The floor of the pedal pit consists of a sheet of these transverse muscles whose general position and arrangement are sufficiently illustrated (pl. V, fig. 39; Pl. VIII, fig. 63) to require no particular comment. It may be added, however, that they rest upon that section of the intestine immediately beyond the stomach, and that a very much thinner sheet of transverse muscles lies immediately beneath this same division of the gut (Pl. X, fig. 83, i).

Finally, there are two pairs of conspicuous muscles which appear to be a constant feature of the protobranchs in general. These occupy a lateral position at the same general level as the union of the auricles and branchial sinuses. The more dorsal pair (Pl. V, fig. 39, dm) frequently is responsible for a distinct shell scar which Odhner has termed the « median muscle scar » (see Schenck '34, p. 21). The ventral one (Pl. V, fig. 39, vm) is somewhat more diffuse, and usually forms a fainter scar which is termed by the same author the « central muscle scar ». In the following account the dorsal pair will be termed the dorso-median muscles, while the ventral pair will be called the ventro-median.

The dorso-median pair gives off a few fibers which, extending anteriorly, enter into the floor of the visceral cavity. Other fibers from its posterior border are distributed over the posterior wall of the visceral sac. The greater number of strands extend into the pedal tissue, and crossing the mid line are continuous with similar bundles from the opposite side. In other words, they form the transverse muscles bounding a portion of the posterior border of the pedal pit.

The ventro-median muscles likewise enter into the formation of the ventral wall of the visceral mass, giving off fibers anteriorly and posteriorly, the last named taking part in the formation of the hinder wall of the visceral sac. A few fibers attach superficially to the upper portions of the foot.

Several authors have described muscles in *Anodonta, Cardium,* etc. which are termed *levator pedis,* « Fussheber » or merely « Heber ». These are attached to the shell in the neighborhood of the umbo, but we have no detailed information as to their distribution. They possibly have their counterpart in one or both of these median muscles but their exact function is a matter of conjecture. In the case of the protobranchs they may reinforce the pedal retractors. At the same time it is possible that, during the vigorous movements of the foot, they may serve to more firmly anchor the pericardial region to the shell.

DIGESTIVE SYSTEM

The mouth, as in other pelecypods, occupies a ventral position between the anterior adductor and the foot. In the nuculids and *Malletia obtusa* it is situated immediately behind the adductor; in the other genera it is adjacent to the foot or in a more intermediate position. Its relation to the palps is shown in Pl. VII, fig. 57, m. Speaking generally, this first division of the digestive tract in the neighborhood of the supra-oesophageal ganglia remains comparativly narrow, after which it expands to a considerable degree before passing into the more distal section of the oesophagus proper. In every species examined on this point this expanded region is provided with ridges composed of high columnar ciliated cells, which may pass, without any marked change, into those characterizing the greater part of the oesophagus. On the other hand, the ridges may be few in number, and in marked contrast to those of the undoubted oesophagus. Also in *Nucula sulcata* there is a marked enlargement of the digestive tract, midway between the mouth and the dorsal body wall, which seemingly is produced by the contraction of attached muscles. Evidently each species has developed its own characteristic pattern.

Pelseneer ('91) considers that these ridges may be the homolog of the oesophageal glands of other mollusks. On the other hand Stempell calls attention to the fact that neither the ridges nor the intervening furrows present any evidence of glandular activity. This same author also raises the objection that there is an almost total lack of pharyngeal muscles characteristic of many other mollusks. Unfortunately the specimens of *Nucula sulcata* in the present collection are not sufficiently preserved to determine the finer details of this section of the digestive tract, but the muscles are more highly developed than in any other species of *Nucula* in hand, and are worthy of a more detailed examination.

In passing it may be suggested that, as others have maintained, this region of the body is in a highly undeveloped condition when compared to the gastropods, for example. Jaws and radulae are unnecessary, and while cilia within the digestive tract may aid in transfering food material from the palps into the digestive tube it appears probable that when this first section of the gut is filled, and the mouth is then closed, that the food is pushed along by the contraction of various muscles extending from the mouth region to the dorsal body wall.

In all of the protobranchs, apparently, the stomach comprises two divisions not especially distinct externally when this organ is distended with food, but differing markedly from each other when viewed internally. Furthermore, the dorsal section is provided with a coecum situated dorsally, and on the left face a fairly well-defined outpouching may be present. These likewise may become indistinct when charged with food material. The finer details of this entire organ have been described in detail by Stempell ('98), and in this account a few details only call for additional comment. It should be noted, however, that in all of the species here described the main features are constant, and the variations comparativly slight.

Upon opening the dorsal wall of the stomach, the most prominent structure appears as a thickening of the left lateralwall of the dorsal division of this organ (Pl. VI, fig. 54). The anterior face of this projection, approximately at right angles to the general gastric epithelium, extends to the mid body line. Posterior to this point it gradually decreases in height. Dissections and sections demonstrate that this ridge is covered with a relativly thick, flexible substance readily stripped off from the underlying cells. And the study of sections also discloses the fact that this same material not only covers the great ridge of the left gastric wall, but it also extends over the major portion of the posterior wall of the stomach, and is continuous over the fold separating the dorsal and ventral divisions (Pl. IX, fig. 81, sh). In every instance the underlying cells are high columnar elements, in some species containing a finely granular material.

Stempell considers that this cuticular lining to be the homolog of the gastric shield (flèche tricuspide) of other pelecypods, and there appears to be no serious objection to such a view. He also states that a crystalline stile is absent, which possibly is open to question. At all events, sections of *Nucula rugosa*, *N. tenuis*, *N. proxima* and *Acila castrensis* clearly show that a very short distance posterior to the left bile duct the dorsal coecum is continued as a short conical outgrowth (Pl. IX, fig. 81, s; Pl. III, fig. 26). Its exact relation to the cuticle of the shield has not been determined, but otherwise its general relations are shown in the figures. Unfortunately its state of preservation prevents an accurate description of the histological details. It most certainly is composed of high columnar cells, and cilia may be present. The lumen, however, is empty. Whether this structure represents a crystalline stile in a degenerate or rudimentary condition is an open question. It is not a constant feature, however, as is witnessed by the fact that in *Nucula nucleus* no trace of it has been discovered.

The epithelium, lining the dorsal division of the stomach and not covered by the gastric shield, is fashioned into ridges whose number and arrangement vary according to the species. A fairly typical example occurs in *Yoldia limatula* (Pl. VI, figs. 54, 55) where a prominent angular thickening is present on the right side, and from it numerous grooves extend over the entire right hand wall. In sections the component cells are seen to be comparativly high columnar elements bearing cilia. A slight exception occurs in *Nucula proxima* and *N. tenuis* where over a comparativly small area some of these ciliated ridges are separated by low columnar cells without cilia (Pl. IV, fig. 33).

The ventral section of the stomach presents the same general appearance in all of the species examined. Its walls are smooth or are provided with very low folds, and its cells do appear to be provided with bristles (Borsten) as Stempell maintains.

In all of the species of *Nucula* and *Acila* there are two bile ducts. The right one is considerably larger than the left, and it enters the stomach at the junction with the oesophagus. Its branches can be traced from the left side as well as the right. In one specimen of *Nucula tenuis* the right and left divisions of the duct enter the stomach by separate though closely approximated openings; in other cases they unite immediately before their union with the stomach. The left duct drains its secretion largely from the left postero-dorsal region of the body cavity. In *Yoldia limatula* the right duct has shifted to a greater degree, its opening into the stomach being slightly to the left of the oesophagus. The left duct lies slightly behind the right one, and is in a more dorsal position. In several species, figuring in the present account, the liver had become so closely attached to the stomach, due to the action of the preservative, that the position of the bile ducts can be determined only from sections. Hence these structures are omitted from some of the figures.

The digestive tract of *Malletia obtusa* presents a few unique features. The oesophagus, for example, upon reaching the posterior margin of the anterior pedal retractors, swings sharply to the left (Pl. VIII, fig. 65), and connects with the stomach at a considerable distance from the mid line. In the same figure the right bile duct passes dorsal to the distal half of the intestine, and opens on the anterior face of the stomach. The same arrangement of the ducts occurs in « *Leda* » *taphria* and apparently in « *L.* » *pontonia*. The left duct, shown in the figure, enters the stomach in the usual position.

In Pl. VIII, fig. 66 the stomach and a portion of the intestine are represented as viewed from behind. The dark brown nutritive material (represented by stipples in the figure) in two specimens carefully examined was distributed throughout the entire digestive tract with the exception of the coiled section adjacent to the stomach, which was utterly devoid of any foreign substance. The cells in this particular division are lined with high columnar cells, possibly glandular, although no definite secretion could be demonstrated after treatment with Delafield's haematoxylin.

The arrangement of the intestine finds its simplest expression in *Yoldia, Yoldiella, Malletia and* « *Leda* ». Here after leaving the stomach it extends along the right side of the body as far forward as the anterior adductor where in a wide loop it skirts the margin of the body cavity, and upon reaching the mid line extends to the posterior adductor.

In *Nucula* and *Acila* the configuration of the intestinal tract is more variable. The simplest type occurs in several species, for example *N. tenuis* and *N. nucleus*. The various species of *Acila* figuring in the present account also present essentally the same appearance. Evidently this is the basic and possibly the primitive plan from which more complicated types have evolved. In *Nucula taeniolata* (Pl. III, fig. 24), for example, the original loops are still recognizable but others have been added. The most extreme example occurs in *N.* « *cancellata* » (Pl. I, fig. 2) which has developed far beyond other protobranchs in this respect.

In this connection it is interesting to note that the various species of *Yoldia, Yoldiella, Malletia* and « *Leda* » in the present collection possess intestines of the same relative length along with the same arrangement. And this is independent of the fact that they occur at depths ranging from 11 to 1569 fathoms. In *Nucula* and *Acila*, on the other hand, the simplest types occur in comparativly shallow water between the limits of 5 and 125 fathoms. The more complicated *N. taeniolata* occurs at 493 fms., while *N.* « *cancellata* » was dredged at a depth of 1356 fms. There thus appears to be a correlation between length of intestine and depth. However, this may be merely a coincidence, since the known examples are too few to establish this fact definitely for other species. If such indeed is the case it may be that nutritive material diminishes according to the depth, and that the complete digestion and absorption of food demands correspondingly elongated intestines. Further observations are needed before this point can be settled. However the question may be decided, it is apparent that at the present time it is futile to attempt to determine which type of gut is the most primitive, and whether it bears a close resemblance to that of the ancestral protobranch.

The material included in the intestinal tract shows a characteristic arrangement (Pl. V, fig. 43). Whether this is due to to a typhlosole or to a varying number of ridges could not be determined. The epithelial lining does indeed vary in height in accordance with indentations in the included detrital material, but this may be merely the result of pressure due to shrinkage in the process of preservation. Moreover, it is evident that the grooves in the main intestinal tract bear no relation to those in the faecal matter common in marine sediments. The last named, obviously, are formed by folds characteristic of the rectal epithelium only.

CIRCULATORY SYSTEM

Since no attempt has been made to section the larger species of protobranchs, the relation of the heart to the intestine has not been determined in the case of the various species of *Yoldia* and « *Leda* ». In *Nucula* and *Acila* the intestine is ventral to the pericardium, as several authors have noted. In *Malletia obtusa* the heart is contracted to a considerable degree, and while it is expanded beneath the gut there is no clear evidence that the intestine actually penetrates the heart. Other features of the circulation, described in the following paragraphs, have been determined in a general fashion from the reconstruction of sections of *Nucula tenuis*, where heavy walls bound the closed portion of the system, and a contained coagulum at several points serves as an injection mass.

The anterior aorta arises from the heart slightly to the left of the mid dorsal line (as in *Acila castrensis*, Pl. IX, fig. 77), and coursing dorsally over the stomach supplies it with at least three branches. In this same region a few delicate twigs were found to pass between the follicles of the liver and gonad. Continuing forward, the aorta rests upon the dorsal surface of the oesophagus until it reaches a point approximately half way to the shell adductor where it passes to the right and ventrally, gradually sinking until it reaches the vicinity of the mouth opening. A short distance posterior to this point it originates a vessel which extends into the neighborhood of the pedal ganglia where it divides repeatedly and becomes lost to view. Also in the oesophageal region small branches pass from the aorta to the adjacent liver and gonad.

The details of the circulation in the region of the supra-oesophageal ganglia are illustrated in Pl. IV, fig. 31. Here it is seen that the dorsal aorta splits upon reaching the posterior borders of the mouth, each limb continuing forward to unite into a single median vessel anterior to the mouth and ventral to the shell adductor. For a short distance the pedal connectives are imbedded in the walls of this circular vessel, but anterior to their union with the supra-oesophageal ganglia the vessels pass beneath the commissure. In approximately the same plane as the origin of the pedal connectives a strong dorsally directed vessel arises and soon divides, one branch skirting the inner face of the gonad, while the other follows the pedal retractor to a point close to the dorsal body wall. Beyond this point they could not be traced. Slightly anterior to this point a strong ventrally directed vessel enters the palp.

The single vessel anterior to the mouth passes beneath the adductor and divides, after developing at least one pair of branches passing into the gonad. These paired vessels, extending in an antero-lateral direction, reach the anterior border of the adductor where each makes its way into the mantle. Beyond this point its connections could not be followed.

The posterior aorta, upon leaving the pericardium, courses along the dorsal side of the intestine and soon becomes lost to view. There are faint evidences that it develops branches which supply the kidney. In *Nucula rugosa* the same state of affairs exists, and while the aorta may supply the kidney no direct connection has been traced between it and a system of sinuses chargd with blood which are located between the outgrowths of the kidney. On the other hand they communicate with a blood space beneath the gut. The relation of this space to other vessels is unknown.

The efferent branchial sinus, as usual, supplies the heart with blood, and in addition there is an extensive supply coming in from a sinus located along the junction of the mantle and the body proper. It is possible that this is the blood space clearly visible in *Yoldia limatula* (?) (Pl. VIII, fig. 58) (1).

NERVOUS SYSTEM

In *Nucula rugosa*, where the nerves in the sections appear with unusual clearness, the supra-oesophageal ganglia are seen to originate two pairs of nerves whose general arrangement is shown in Pl. VIII, fig. 69. The more median pair courses over the superior surface of the adductor and enters the mantle. Beyond this point they could not be traced, but it is probable they unite with branches of the second pair of mantle nerves.

This second pair of mantle nerves arises at about the same level as the preceding, but more ventrally and after extending anteriorly for a short distance each member of the pair originates a delicate branch which ramifies throughout the

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(1) The efferent branchial sinuses in *Nucula rugosa* contain what evidently is an unknown species of a sexually mature trematode, six being located on the left side and eight on the right.

fibers of the adductor, and doubtless innervates them. The remaining ramus continues its forward course to the adductor where it divides, one branch proceding forward while the other extends laterally to the mantle border. This lateral division, extending anteriorly, forms a loop and anastomoses with the forwardly directed nerve. From the loop a small twig originates which innervates the anterior portion of the mantle. As may be seen in the figure (fig. 69), the laterally directed mantle nerve also continues along the mantle border to a point approximately opposite the middle of the branchia. Here it breaks up into a plexus whose subdivisions doubtless anastomose with those of the main mantle nerve from the visceral ganglia. This type of nervous system is duplicated almost exactly in *Acila castrensis*.

Nerves of the same origin have been discovered in *Nucula proxima* (Pl. VIII, fig. 70) and *N. nucleus* (Pl. X, fig. 91), but owing to the excessive development of the gonad their ultimate course could not be followed.

In a definitely identified specimen of *Yoldia limatula* from long Island Sound the supra-oesophageal ganglia and their main nerves appear as in Pl. X, fig. 85. Two pairs of nerves (*m*) supply the mantle. The more anterior one very soon gives rise to a small nerve (*a*) which innervates the adductor muscle. The remaining division may be seen in Pl. VII, fig. 58 to skirt the posterior border of the adductor, and extend to the mantle margin. The second pair of mantle nerves arises laterally a short distance posterior to the first. In fig. 58 it is seen to rest on the floor of the visceral cavity, and still more laterally to extend in a postero-lateral direction into the mantle. In « *Leda* » *pontonia* and « *L.* » *fossa* the same nerves exist, and this particular mantle nerve in *Yoldia montereyensis* was followed to a point about opposite to the middle of the branchia. Here, as in *Nucula rugosa*, it develops a plexus, and probably is continuous with the main mantle nerve from the visceral ganglia.

In this account it will be noted that no nerves have been discovered in *Yoldia* or « *Leda* » which extend over the adductor and into the mantle. In *Nucula*, it will be recalled, each of the remaining pair of mantle nerves springs from a single root, and divides some distance beyond their point of origin. In *Yoldia*, and probably in « *Leda* », the separation is much greater, so great in fact that the two divisions, emerge from the ganglia at a considerable distance from each other. Otherwise this portion of the nervous system is fundamentally the same in these genera.

In *Malletia obtusa* the nerves throughout are very delicate, and even in sections are very difficult to trace. As far as could be determined, there are two pairs of nerves arising from the supra-oesophageal ganglia and probably innervating the mantle. Pelseneer ('11) figures two distinct pairs of mantle nerves in *Malletia sibogai*. In *M. obtusa*, on the other hand, these nerves on each side are very close together. The smaller and more median one courses dorsally, and at approximately the same level as the posterior border of the adductor becomes lost among the follicles of the gonad. The remaining nerve procedes in an anterolateral direction, and two thirds of the distance to the mantle border divides, one branch extending anteriorly, while the other was lost to view in the posterior third of the body.

From the ventral surface of the supra-oesophageal ganglia, at approximately the same level as the mouth, the palp nerves originate. A short distance beyond their point of origin they pierce the body wall, and, coursing through the dorsal tissue of the palp, enter the muscle of the palp tentacle. This state of affairs exists in representatives of all of the genera considered in the present account. In *Yoldia limatula* this nerve, at several points throughout its course, was found to originate delicate twigs which entered the more ventral portions of the palp. In the palp tentacle muscle, near the point where it attaches to the body, the palp nerve enlarges to form a distinct ganglion from which a nerve originates that has been traced far toward the tip of this organ. This ganglion has been found in several species of Nucula. In *Yoldia limatula* there is a distinct enlargement, but the ganglion cells are relativly few. Otherwise its relation to the palp is essentially the same as in *Nucula.*

In *Yoldia limatula* a small nerve arises on each side of the mouth from the inner face of the supra-oesophageal ganglia, and passes directly to the buccal wall. Beyond this point it could not be followed. There are indications that a similar nerve exists in *Acila castrensis.* It is possible that this pair may form a plexus over the digestive tract as in the gastropods (Fisher ('02). If so it differs from *Mytilus,* as described by List ('02), where a branch from each cerebro-pedal connective innervates the intestine, liver and gonad. No mention was made of any other nerves supplying these organs.

At the present time it is by no means an assured fact that the supra-oesophageal nerve mass represents the closely fused cerebral and pleural ganglia. Theoretically it does, for there is no more conservative structure, one less subject to modification than the nervous system. Furthermore, these ganglia occur in the amphineurans, scaphopods, gastropods and even in the highly modified cephalopods as witnessed by von Ihering (see especially the work of L. Duthiers '56-7, Fisher '04, Heath '05 and von Ihering '80). If they have no counterpart in pelecypods this fact certainly throws the burden of proof on those who hold this opinion, but as the matter now rests neither side has presented any very convincing evidence.

List ('02), in his detailed account of *Mytilus* and related genera, designates the supra-oesophageal nerve mass the cerebral ganglia without making any comment. Pelseneer and Stempell, on the other hand, look upon it as the closely approximated cerebral and pleural ganglia; and in support of their belief they call attention to a distinct furrow which is believed to separate the two. Evidently this furrow is not a constant feature, however, since usually it shows but faintly or not at all in stained preparations of dissected material (Pl. X, fig. 85).

In this connection it may be mentioned that Fisher ('04) has shown that in the gastropod, *Lottia gigantea,* the cerebral ganglia, in addition to forming the usual commissure and the cerebro-pleural and cerebro-pedal connectives, innervates the eyes, tentacles, lips and otocysts. In the protobranchs the first two organs are absent. The lip or palp nerves emerge from the supra-oesophageal ganglia at a point posterior to the position of the furrow as this last named structure is shown in the figures by the above named authors. This, however is not a serious objection, since the nerves in question actually may originate in cells of true cerebral ganglia.

As is well known, the nerves supplying the otocysts branch off from the cerebro-connectives a short distance from the pedal ganglia. Sections of a few species of *Nucula,* for example *N. sulcata,* show that some of the otocyst fibers come from the supra-oesophageal ganglia. Others, equally distinct, curve in the opposite direction, and appear unquestionably to have a direct connection with the pedal ganglia. It is entirely possible that in the evolution of this group a departure from the gastropod type has occurred, but the question can be answered only after modern neurological methods have been employed.

In *Nucula* Pelseneer has discovered a double origin of each pedal connective, and Stempell has described essentially the same arrangement in « *Leda* » *sulculata.* Both of these investigators are in agreement that these represent the cerebro-pleural and cerebro-pedal connectives of other mollusks. Without attempting to decide upon the correctness of this view, it may be said that these nerves probably exist in all of the species of *Nucula* and *Acila.*

However, unlike « *Leda* » *sulculata,* as described by Stempell, these connectives frequently originate at essentially the same level, and are comparativly close together. But, after all, the emergence of the nerves from the ganglia is of little significance. The important question remaining to be solved relates to their cellular connections. The two roots actually may spring from cerebral and pleural ganglia respectivly; and even the single root occurring in *Yoldia,* for example, may likewise have the same double origin as Burne ('04) has shown to be the case in « *Solenomya* ». The problem is important, but at the present time the known facts are tantalizingly few, and certainly afford no definite answer, although the subject has received careful attention by Burne on the basis of the known facts.

Stempell also figures ('93, fig. 37) a fine nerve (x) which, as a branch of each pleuropedal connective, penetrates the pedal musculature, and ultimately fuses with the pedal connective in the neighborhood of the pedal ganglia. This same author considers this particular pair of nerves to represent dorsal components of the otocyst nerves. It is to be recalled, however, that since the original discovery by L. Duthiers several investigators have agreed that the otocyst is innervated by fibers from the cerebral ganglia. Hence, unless « *Leda* » represents an extreme modification in this regard its fibers must originate in cells apart from those giving rise to the pleural ganglia. But here again this problem, and the one regarding the constitution of the supra-oesophageal ganglia can only be settled after a thorough study of carefully preserved material.

The differences existing in the various species in connection with the visceral ganglia are comparativly slight. As has been noted by various authors, especially Pelseneer, the two ganglia in the nuculids are widely separated (Pl. VIII, fig. 69), whereas in the remaining genera they are closely appressed (Pl. X, fig. 90). Furthermore, since siphons are absent in the first named group, there obviously is no corresponding nerve. With this exception this portion of the nervous system is fundamentally the same in all of the protobranchs.

The remaining nerves comprise three pairs, one of which supplies the gills. Of the others, one is directed posteriorly, and extending ventral to the posterior adductor enters the mantle. Judging by sections there is evidence that it anastomoses with the main mantle nerve which, as in *Nucula rugosa* (Pl. VIII, fig. 69), extends in a wide arc to the mantle border where there is strong evidence that, after developing a plexus, it becomes continuous with a mantle nerve arising from the supra-oesophageal ganglia.

REPRODUCTIVE SYSTEM

As several authors have shown, and as the figures indicate (Pl. I, fig. 7), the gonad presents the form of a vault situated immediately beneath the dorsal and lateral body walls with its base supported by the ventral wall. In no species in the present collection does it extend into the mantle, nor is there any evidence of hermaphroditism. Its thickness in the adult condition is a variable, depending upon its relation to the breeding season. Nevertheless, even after the follicles have been freed of their sex products, they retain their position, judging by sections and dissections.

As is well known, the gonad in several species of pelecypods is known to be a distinctly paired organ throughout life. In many other species this presumably primitive as well as embryonic condition may be partially obliterated by the fusion of the follicles along the mid line. This appears to be the state of affairs in several species. For example, it is certain that the great anterior pedal protractors and retractors divide the gonad anteriorly in such species as *Nucula tenuis* and *N. sulcata*, and they appear to remain distinct throughout their entire extent. In *N. proxima*, on the other hand, sections and reconstructions seemingly demonstrate that there is a partial fusion of the original halves.

The gonoducts are comparativly short tubes, usually extending from the median muscles (Pl. V, fig. 39 dm, vm) to the external opening (k) where they communicate with the nephridia. Their more exact relations, as well as their histological details have been described by Drew, Odhner and more especially by Stempell.

NEPHRIDIUM

The protobranch excretory system has been the subject of investigation on the part of several workers, notably Pelseneer ('91, '98), Stempell ('98), Drew ('99) and Odhner ('12), and the results herewith presented are chiefly a confirmation of their findings. Furthermore, although the material in hand has been preserved in alcohol, and is not especially favorable for the study of the finer histological details, the main features of these organs are very well defined in *Nucula proxima*, *N. tenuis*, *N. sulcata* and *N. rugosa*.

In every instance each kidney roughly resembles an inverted U, the curved division extending to the branchio-auricular opening or a little beyond, while the two limbs terminate at about the same level as the posterior pericardial wall. In the smaller species the dorsal walls are comparativly smooth and the ventral surfaces possess but few outpouchings. In the larger species coeca occur throughout most of the glandular portion of these organs; to a somewhat greater extent, in fact, than is indicated in the figures. Furthermore, several authors have described a connection across the mid line between both nephridia. This certainly is the case in the larger species, *Nucula rugosa* and *N. sulcata*. Also it may occur in the other species named above, but the sections in hand give no clear evidence that such is the case, although it is certain that a few of the coeca of the two kidneys are in direct contact with each other.

About midway between the extremities of each kidney the reno-pericardial opening occurs to be followed by a comparativly short, ciliated canal which opens into the proximal limb of the organ. In approximately the same plane the gonoduct communicates with the exterior. Close to this opening the gonoduct is joined by the ureter, a relativly slender canal opening into the distal limb. In addition to these structures Stempell, for « *Leda* » *sulculata*, and Burne ('03), for *Nucula nucleus*, have described a small canal, uniting the ciliated funnel and the urogenital cloaca. This they term the gonopericardial duct. The material in the present collection gives inconclusive results, but in *Nucula sulcata* a small tube, partially imbedded in the body wall, courses alongside of the gonoduct from the region of the ciliated funnel to the urogenital opening to the exterior. It appears, therefore, to have the requisite connections required by the gonopericardial duct, but at present this is inconclusive. It is to be hoped that some investigator, with well preserved material, will settle this important point.

In *Malletia obtusa* the urogenital system is not especially favorable for study, but it is certain that in its main features it agrees with *Nucula*. For the most part the two kidneys are separated by a portion of the intestine, yet it is a significant fact that at the same level as the urogenital outlet a long finger-shaped outgrowth from each kidney is directed inwardly to the mid line where they come in contact with each other. The walls between the two appear to be intact, but the fact that they come in contact suggests that an opening may exist, and that a sphincter muscle may be present and be so contracted in preserved material that no actual communication can be demonstrated. Or, even though no definite opening exists, there may be an osmotic interchange for some unknown reason.

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PLATE I

EXPLANATION OF PLATE I

FIG. 1. — Side view of *Nucula nucleus*. Actual size, 10 mm.

FIG. 2. — Dorsal view of intestinal tract of *Nucula nucleus*. Coils spread somewhat for the sake of clearness.

FIG. 3. — Dorsal view of digestive system of *Nucula nitidosa*. Bile ducts (b) shown on left side.

FIG. 4. — Cross section of *Nucula* « *cancellata* ». b, byssus; g, gonad; i, intestine; l, liver; p, palp; pt, palp tentacle; s, stomach.

FIG. 5. — Side view of *Nucula cancellata*. Actual size, 4.5 mm.

FIG. 6. — Dorsal view of intestine of *Nucula nucleus*. Coils spread slightly.

FIG. 7. — Cross section of *Nucula proxima* close to the junction of stomach and intestine. p, palp; s, stomach.

FIG. 8. — View, from right side, of intestine of *Nucula nucleus*.

FIG. 9. — Lateral view of *Nucula nitidosa*. Actual length. 9.5 mm.

FIG. 10. — Lateral view of *Nucula tumidula*. Actual length, 6.5 mm.

PL. I.

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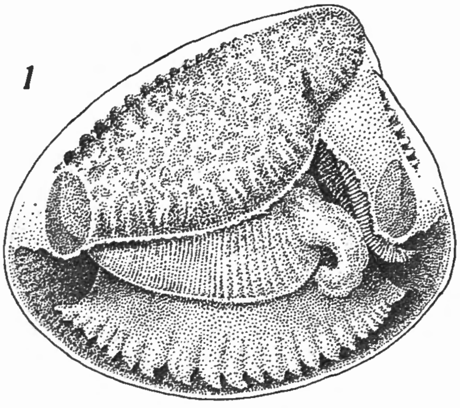

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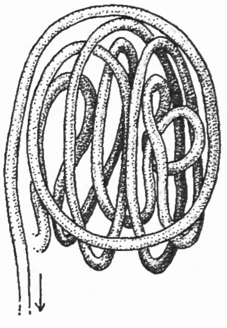

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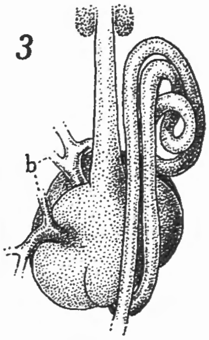

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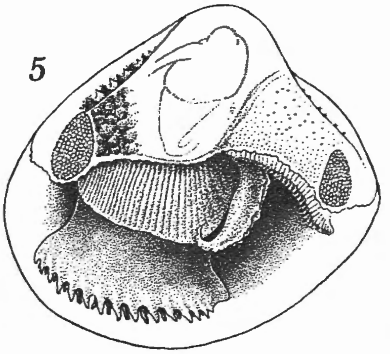

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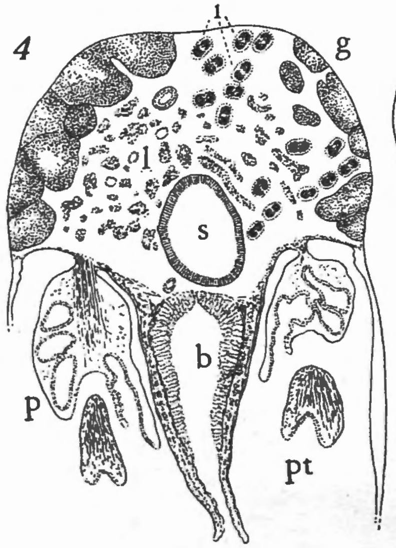

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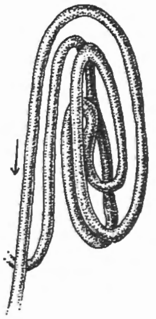

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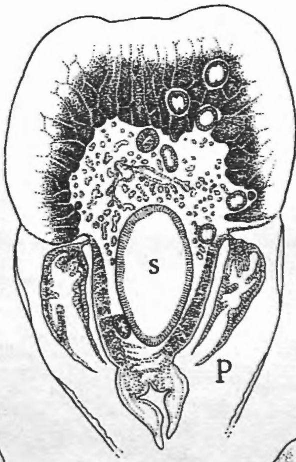

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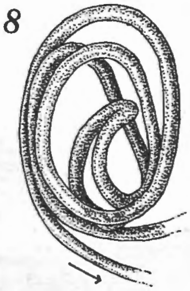

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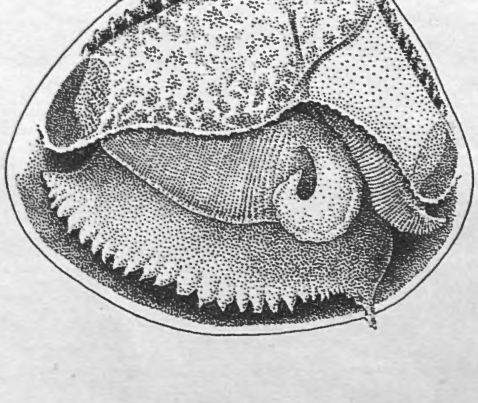

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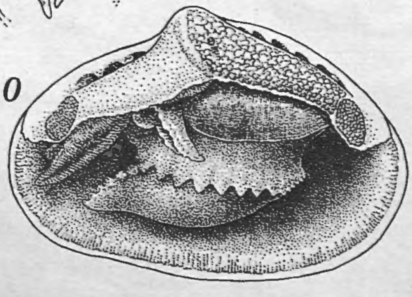

H. HEATH. — Protobranch Mollusks.

PLATE II

EXPLANATION OF PLATE II

Fig. 11. — Lateral view of *Nucula rugosa*. Actual length, 12 mm.

Fig. 12. — Cross section through mouth region of *Nucula rugosa*. g, gonad; n, supra-oesophageal ganglia; o, oesophagus; p, palp.

Fig. 13. — Dorsal view of digestive tract, liver, bile ducts and heart of *Nucula rugosa*.

Fig. 14. — Dorsal view of ventral floor of visceral cavity of *Nucula rugosa*.

Fig. 15. — Dorsal view of digestive tract of *Nucula proxima*.

Fig. 16. — Cross section of *Nucula proxima* through b, branchia; g, gonad; h, heart; hy, hypobranchial gland; k, kidney.

Fig. 17. — Lateral view of *Nucula proxima*. Actual size, 6 mm.

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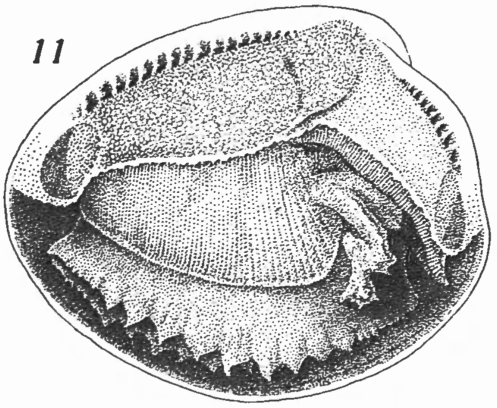

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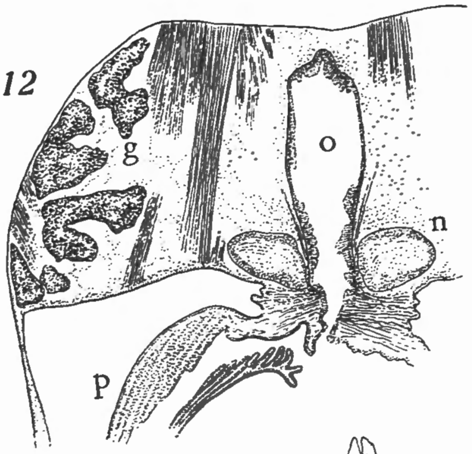

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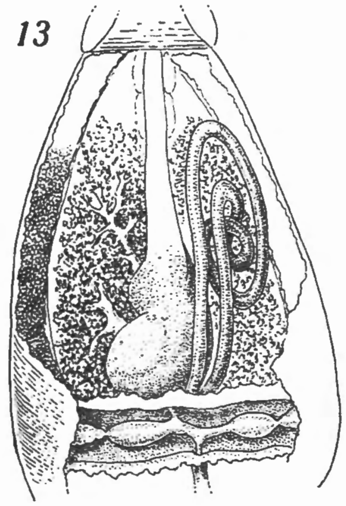

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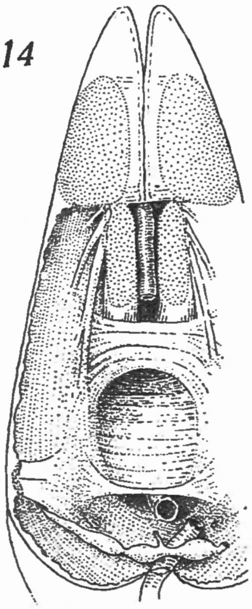

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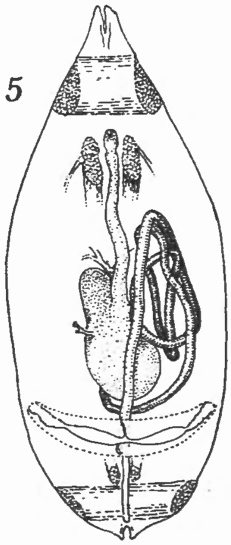

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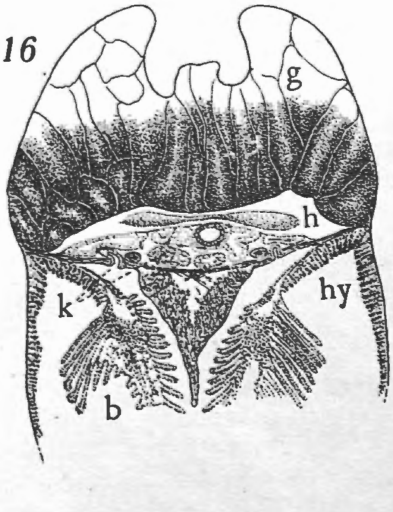

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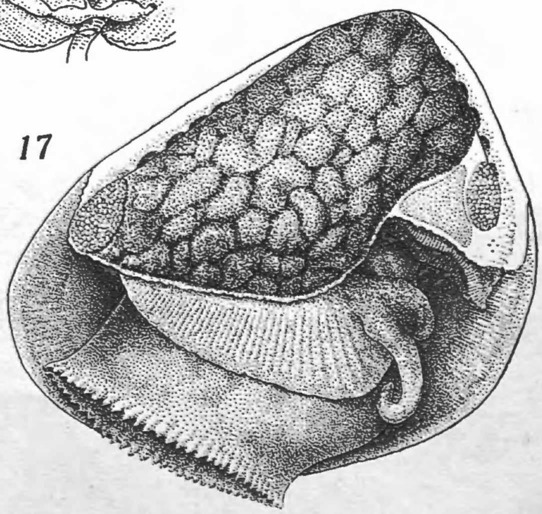

PLATE III

EXPLANATION OF PLATE III

FIG. 18. — Lateral view of *Nucula sulcata*. Actual length, 14 mm.

FIG. 19. — Lateral view of *Nucula tenuis*. Actual length, 11 mm.

FIG. 20. — Dorsal view of digestive tract and heart of *Nucula tenuis*. b, bile duct.

FIG. 21. — Ventral view of floor of visceral cavity of *Nucula tenuis*.

FIG. 22. — View, from right side, of intestine of *Nucula tenuis*.

FIG. 23. — View, from right side, of intestine of *Nucula rugosa*.

FIG. 24. — Dorsal view of digestive tract of *Nucula taeniolata*.

FIG. 25. — View, from right side, of intestine of *Nucula tumidula*.

FIG. 26. — Cross section of crystalline stile (?) of *Nucula tenuis*.

FIG. 27. – Side view of digestive tract and nervous system of *Nucula proxima*. A combination of dissection and reconstruction of sections.

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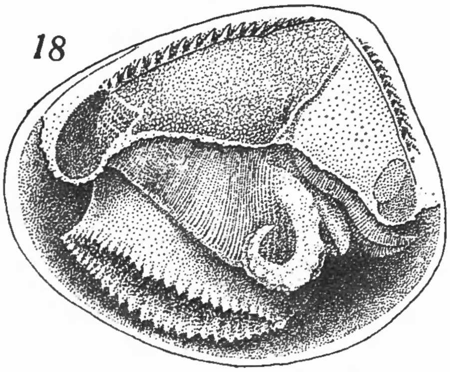

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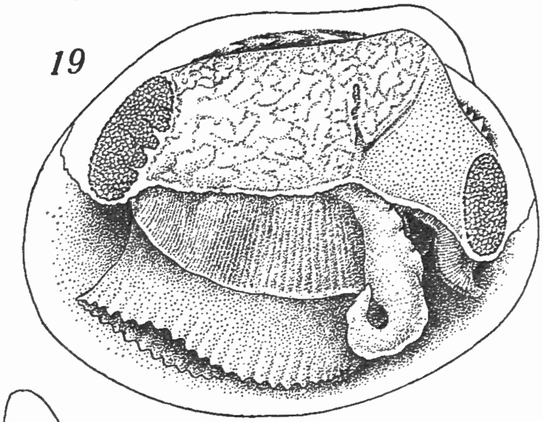

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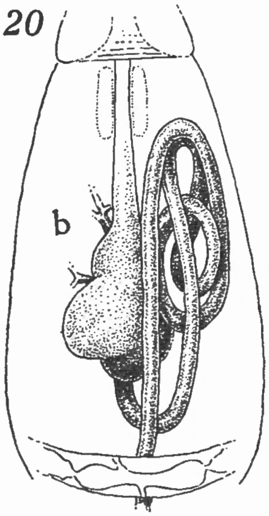

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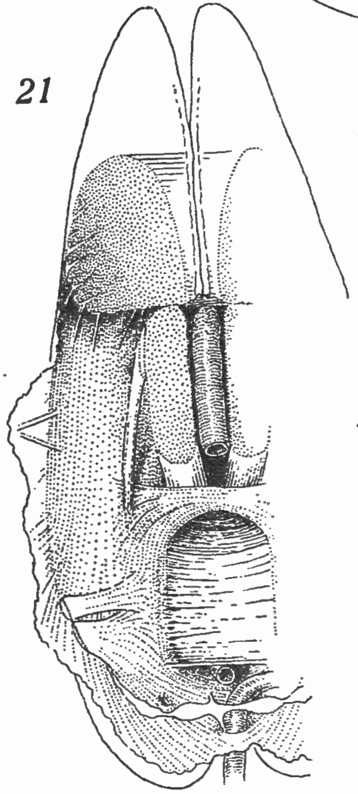

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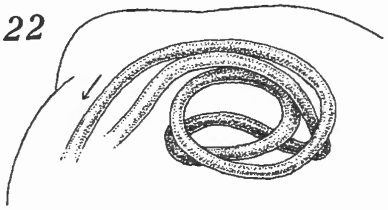

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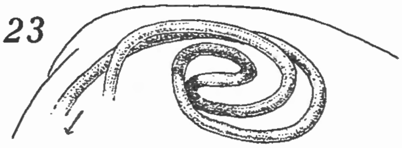

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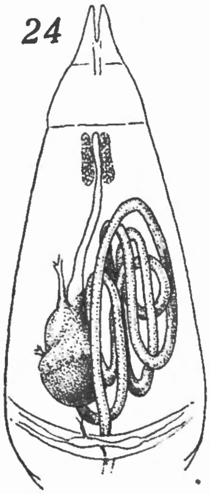

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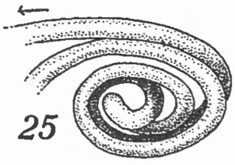

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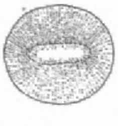

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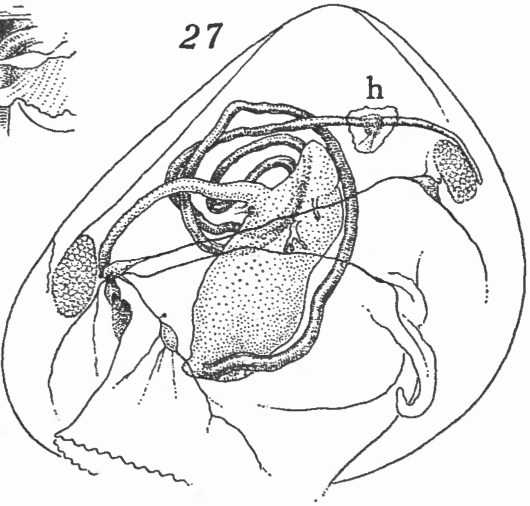

H. HEATH. — Protobranch Mollusks.

PLATE IV

EXPLANATION OF PLATE IV

Fig. 28. — Lateral view of *Nucula tumidula*. Actual length, 6.5 mm.

Fig. 29. — Lateral view of *Acila divaricata*, showing location of possible glandular thickening of the mantle. Actual length, 28 mm.

Fig. 30. — Dorsal view of intestine and ventral floor of visceral cavity of *Acila castrensis*.

Fig. 31. — Dorsal view of blood vessels of *Nucula tenuis* in region of supra-oesophageal ganglia. Vessels with heavy outlines.

Fig. 32. — Dorsal view of digestive tract and heart of *Acila divaricata*.

Fig. 33. — Gastric epithelium of *Nucula tenuis* from right hand wall of the upper division of the stomach.

Fig. 34. — Cross section of the byssus gland of *Nucula tenuis*.

Fig. 35. — Lateral view of digestive tract of *Acila divaricata*. h, heart.

Fig. 36. — Sagittal section of stomach and bile duct of *Acila castrentis*. h, heart; i, intestine.

Fig. 37. — Lateral view of *Acila divaricata*. Actual length, 28 mm.

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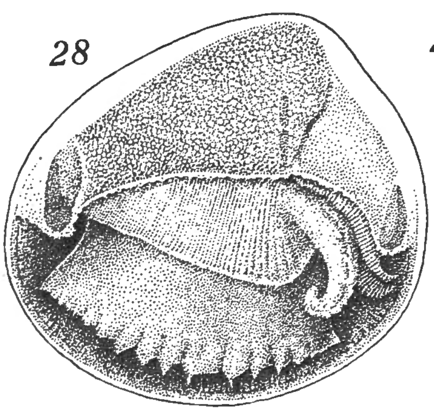

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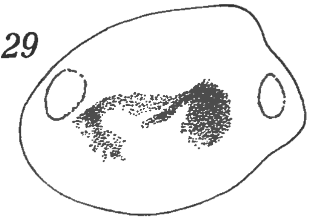

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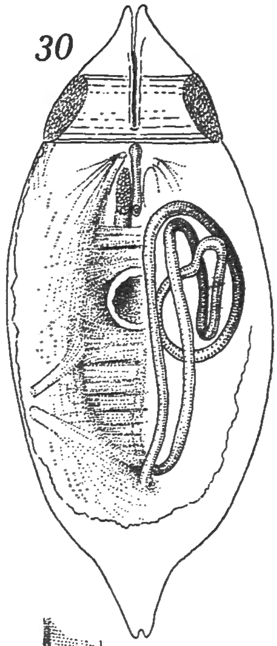

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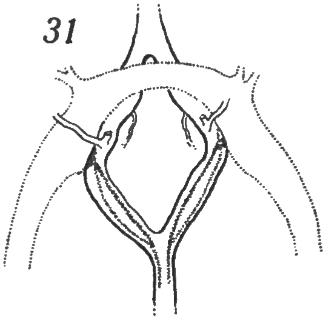

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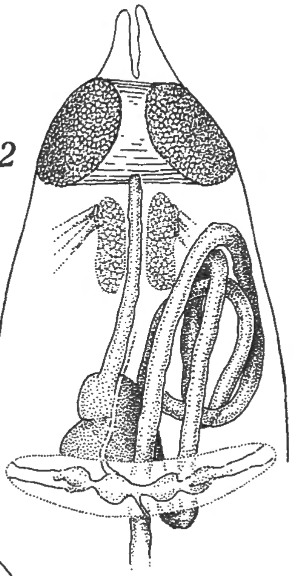

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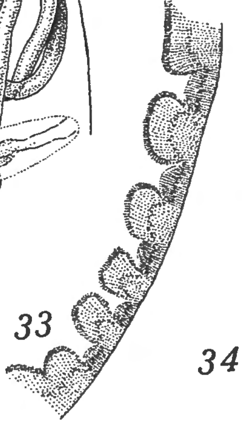

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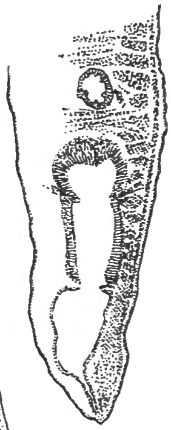

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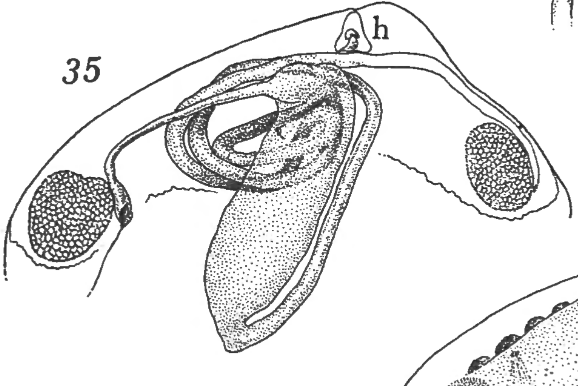

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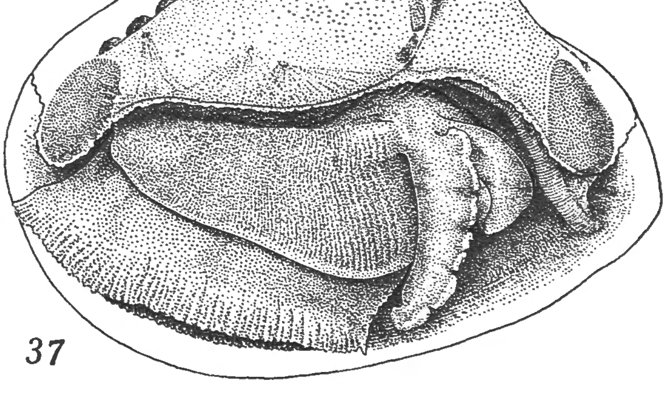

PLATE V

EXPLANATION OF PLATE V

FIG. 38. — Dorsal view of digestive tract and heart of *Acila fultoni*.

FIG. 39. — Dorsal view of floor of visceral cavity of *Acila divaricata*. dm, dorso-median muscle; h, opening of efferent branchial sinus into heart; k, external outlet of urogenital system; p, anterior pedal protractors; r, retractor; vm, ventromedian muscle.

FIG. 40. — Dorsal view of floor of visceral cavity of *Acila fultoni*.

FIG. 41. — Dorsal view of digestive tract and heart of *Nucula sulcata*.

FIG. 42. — Lateral view of byssus gland and duct of *Nucula sulcata*. Glandular portion somewhat macerated.

FIG. 43. — Cross sections of intestine of (a) *Nucula proxima*, (b) *N. sulcata* and (c) *N. tenuis*.

FIG. 44. — View, from right side, of intestine of *Nucula tenuis*.

FIG. 45. — Lateral view of *Acila fultoni*. Length of shell, 33 mm.

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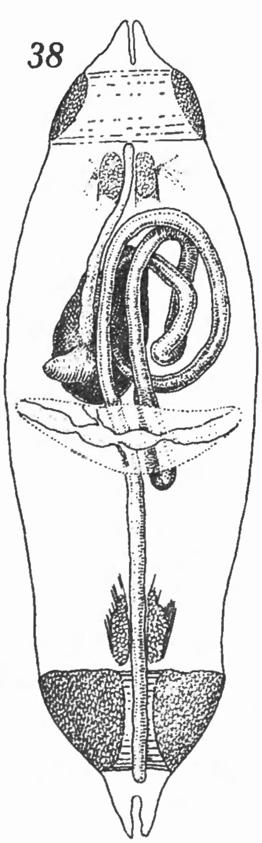

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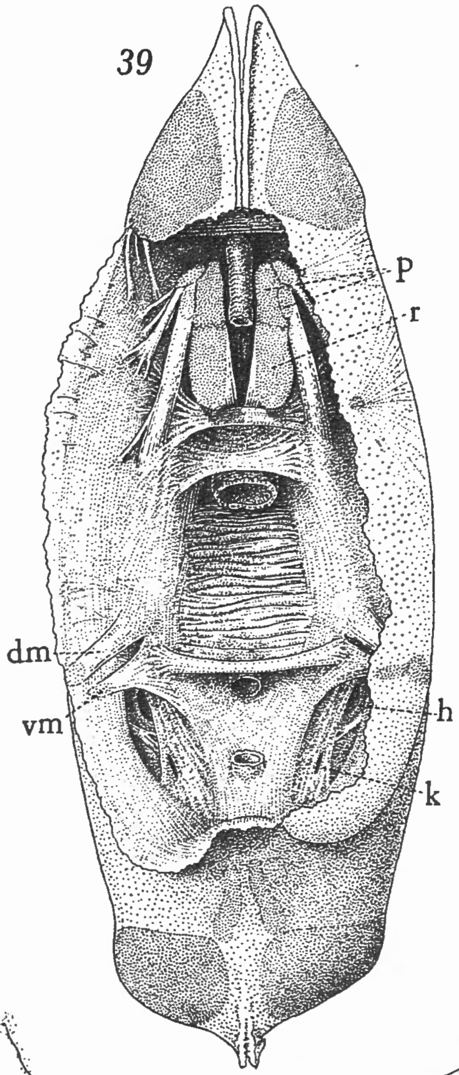

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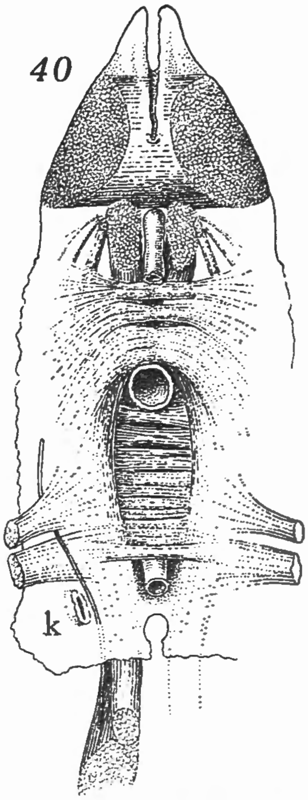

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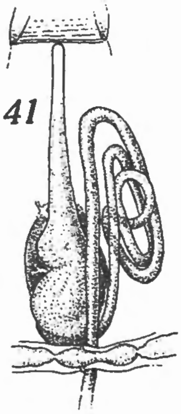

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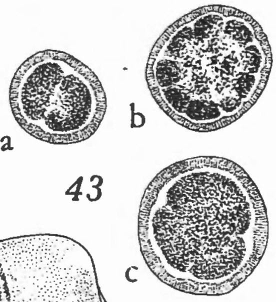

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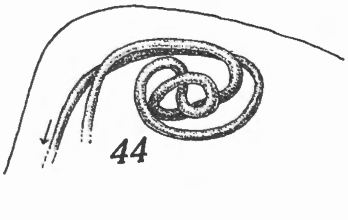

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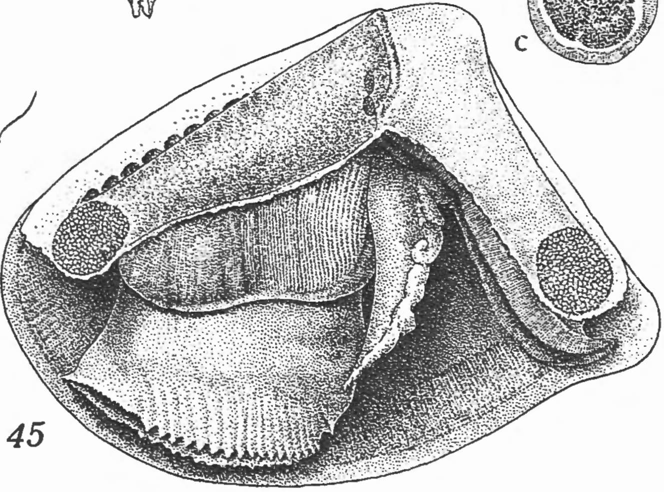


H. HEATH. — Protobranch Mollusks.

PLATE VI

EXPLANATION OF PLATE VI

FIG. 46. — Lateral view of *Yoldia sapotilla.* Actual length, 24 mm.

FIG. 47. — Ventral view of exhalent siphon of *Yoldia montereyensis.* b, branchia.

FIG. 48. — Modification of mantle, right side, of *Yoldia ensifera.* For its exact position see. Pl. VIII, Fig. 67, g.

FIG. 49. — Ventral view of exhalent siphon of *Yoldia limatula* (?). b, branchia.

FIG. 50. — Lateral view of *Acila castrensis.* Actual length, 11 mm.

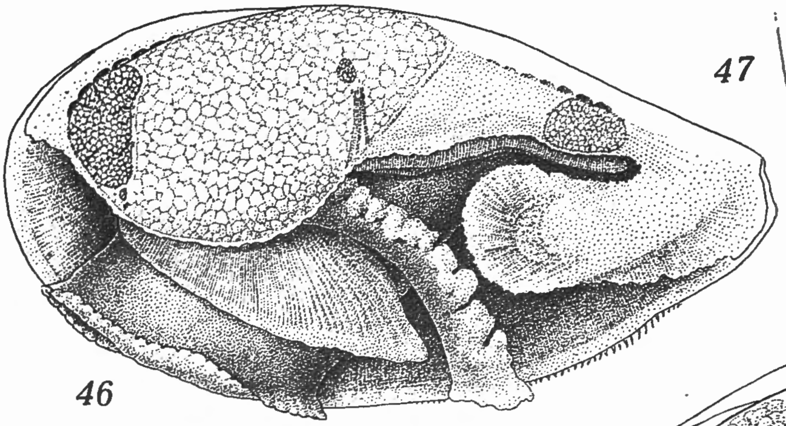
FIG. 51. — Side view of dorsal half of *Yoldia montereyensis* with gonad and liver removed.

FIG. 52. — View, from right side, of stomach of *Yoldia scissurata.* b, bile duct.

FIG. 53. — Lateral view of *Yoldiella inflata.* Actual length, 5.5 mm.

FIG. 54. — Inner surface of left half of stomach of *Yoldia limatula.* b, opening of bile duct.

FIG. 55. — Inner surface of right half of stomach shown in Fig. 54.



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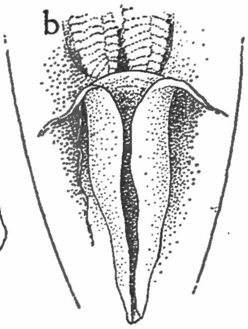

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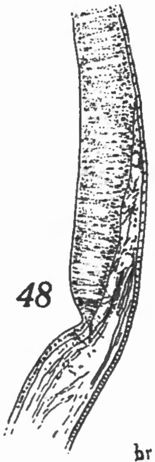

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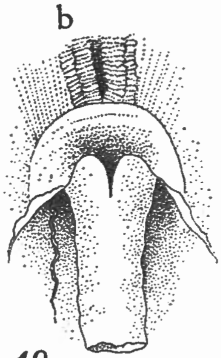

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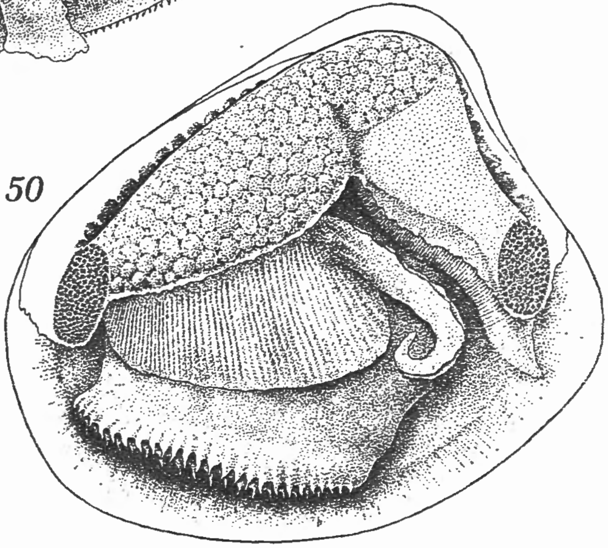

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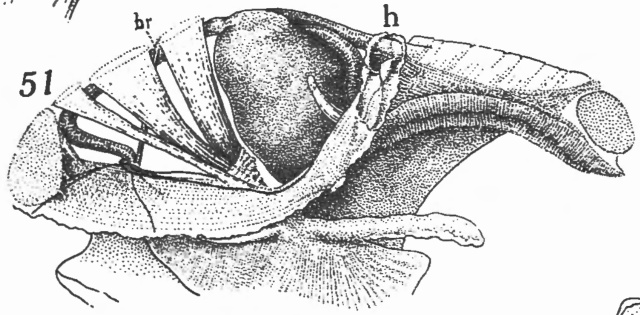

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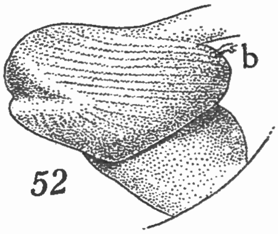

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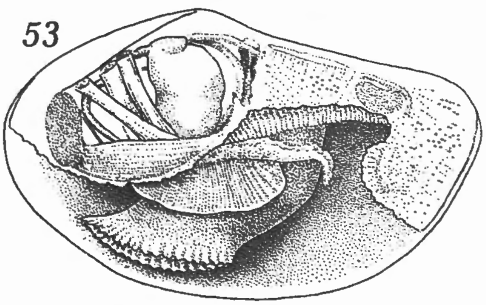

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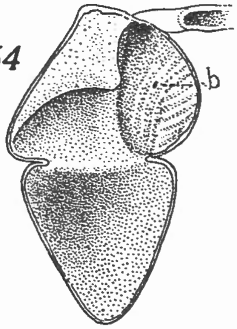

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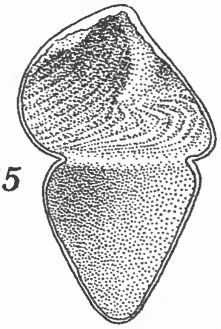

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PLATE VII

EXPLANATION OF PLATE VII

FIG. 56. — Lateral view of « *Leda* » *fossa*. Actual length, 25 mm.

FIG. 57. — *Yoldia montereyensis*. Ventral view of mouth (m), foot (f), and forward section of palps (p) whose anterior muscular attachment (a) is shown on left side of figure. (The entire attachement is shown in Pl. VIII, Fig. 73.)

FIG. 58. — Lateral view of *Yoldia limatula* (?). Actual length, 44 mm.

FIG. 59. — Lateral view of « *Leda* » *taphria*. Actual length, 19 mm.

FIG. 60. — Posterior end of branchia of « *Leda* » *taphria*, showing afferent (a) and efferent (e) sinuses, and the radiating gill muscles which are attached to the shell dorsal to the adductor.

FIG. 61. — Left face of stomach and bile duct of *Yoldia scissurata*.

FIG. 62. — Lateral view of *Malletia obtusa*. Developing reproductive follicles partially surround the liver dorsal to the palp.

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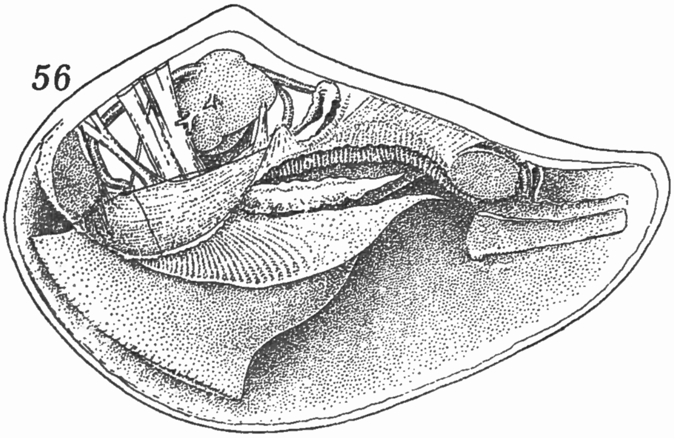

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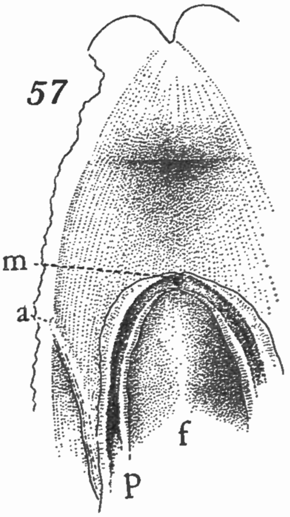

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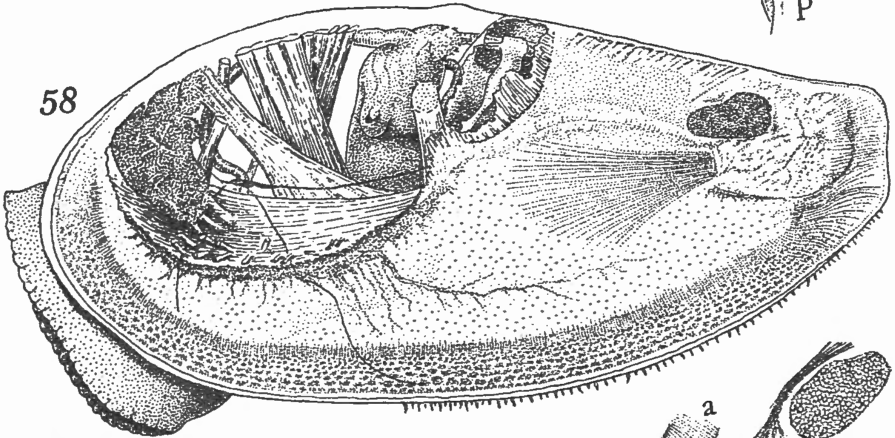

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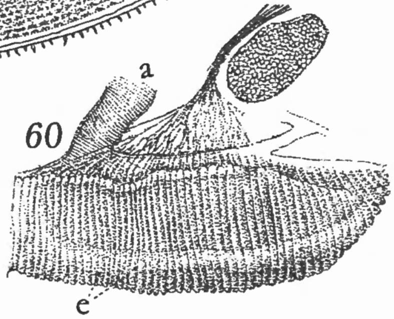

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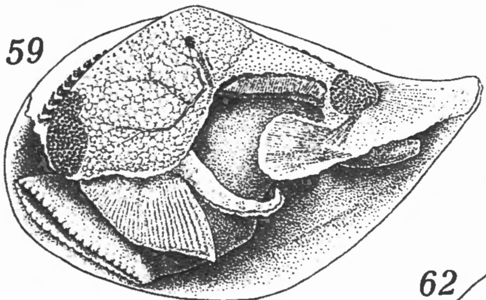

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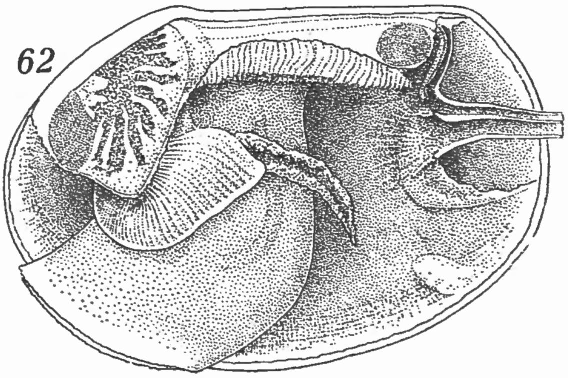

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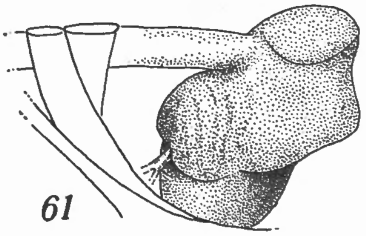


H. HEATH. — Protobranch Mollusks.

PLATE VIII

EXPLANATION OF PLATE VIII

FIG. 63. — Ventral floor of visceral cavity of *Yoldia limatula* (?). Shell length, 44 mm. d, dorso-median muscle; n, pallial connective; v, ventro-median muscle.

FIG. 64. — Dorsal view of digestive tract and heart of *Yoldia limatula.*

FIG. 65. — Dorsal view of digestive tract and heart of *Malletia obtusa.* d, right bile duct, opening through forward wall of stomach, while the left one is seen immediately behind the end of the oesophagus, o.

FIG. 66. — Lower portion of stomach and proximal section of intestine of *Malletia obtusa.* Food material is lacking in the non-stippled coils.

FIG. 67. — Cross section of *Yoldia ensifera* at level of mouth and mouth cavity (m) ventral to which are the palps with the supra-oesophageal ganglia occupying an intermediate position. f, foot; g, glandular (?) development of inner epithelial layer of mantle.

FIG. 68. — View of ventral floor of visceral cavity of « *Leda* » *fossa.* Actual length, 25 mm. d, dorso-median muscle; v, ventro-median muscle.

FIG. 69. — Diagram of nervous system of *Nucula rugosa* from dissection and the reconstruction of sections. The supra-oesophageal ganglia originate two pairs of mantle nerves, a small pair innervating the adductor, the pedal and pallial connectives, and a pair of palp nerves. The visceral nerves are the same as those shown in Fig. 90, omitting the pair supplying the siphon retractors.

FIG. 70. — Dorsal view of supra-oesophageal ganglia and nerves of *Nucula proxima* : a reconstruction. m, nerves to mantle; p, palp nerve; pe, pedal connective.

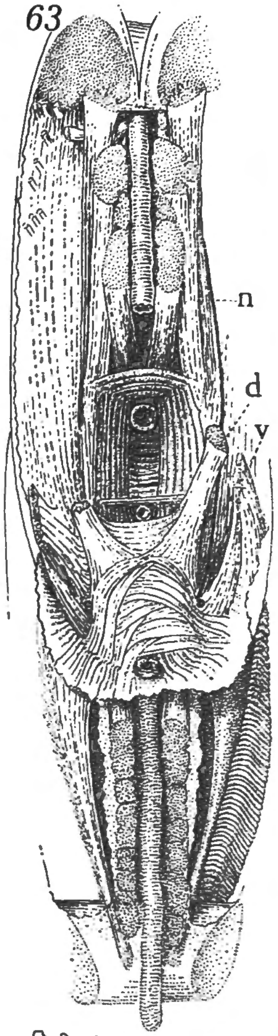
FIG. 71. — Left kidney of *Nucula proxima* : a slightly diagramatic reconstruction. g, gonoduct; p, reno-pericardial opening.

FIG. 72. — Slightly diagramatic reconstruction of left kidney of *Nucula sulcata.* g, gonoduct; p, reno-pericardial opening.

FIG. 73. — Lateral view of left palp and tentacle of *Yoldia montereyensis*, showing the extended muscular attachment to the body and shell.

FIG. 74. — Diagramatic reconstruction of left kidney of *Nucula nucleus.* g, gonoduct; p, reno-pericardial opening.

PL. VIII.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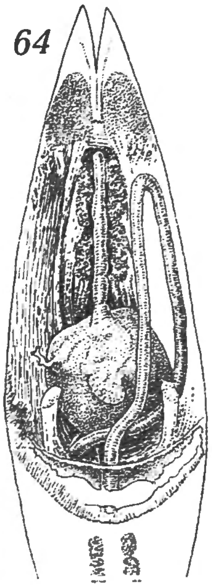
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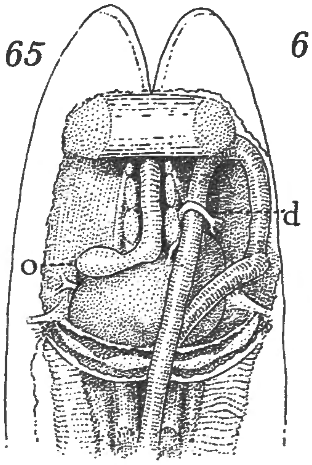
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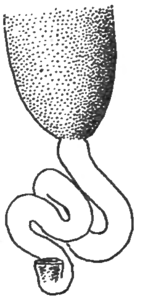
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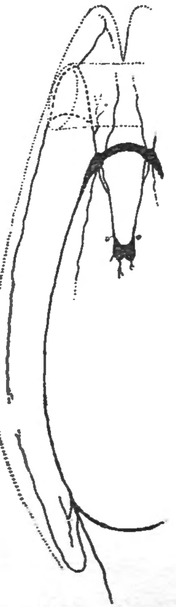
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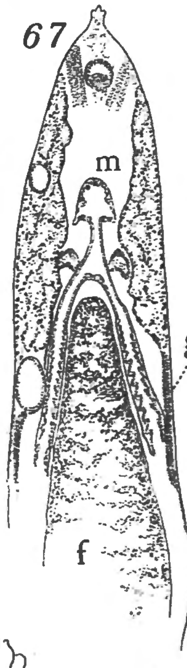
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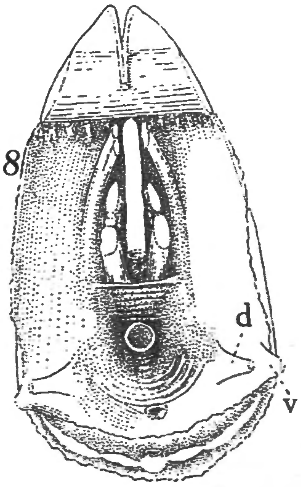
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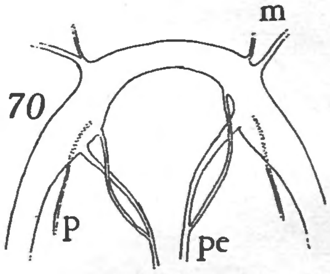
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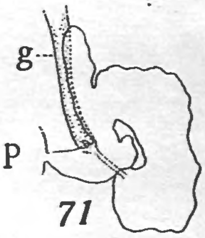
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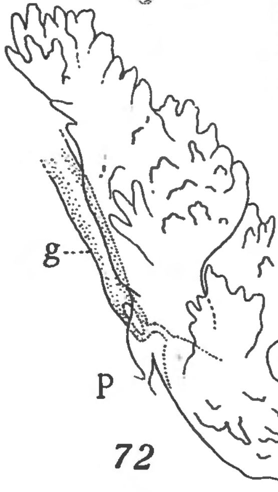
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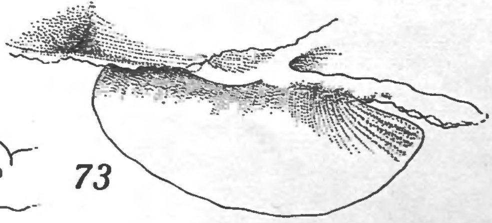
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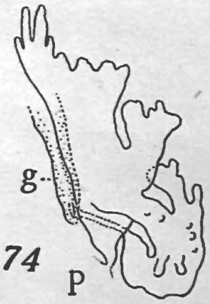
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H. HEATH. — Protobranch Mollusks.

PLATE IX

EXPLANATION OF PLATE IX

FIG. 75. — Lateral view of *Yoldia sapotilla*, showing the more important pedal muscles and their relation to the digestive system. Length of shell, 24 mm. h, heart.

FIG. 76. — Ventral floor of visceral cavity of *Acila castrensis*. Length of shell, 11 mm.

FIG. 77. — Diagramatic representation of heart, kidney and gonoduct of *Acila castrensis*.

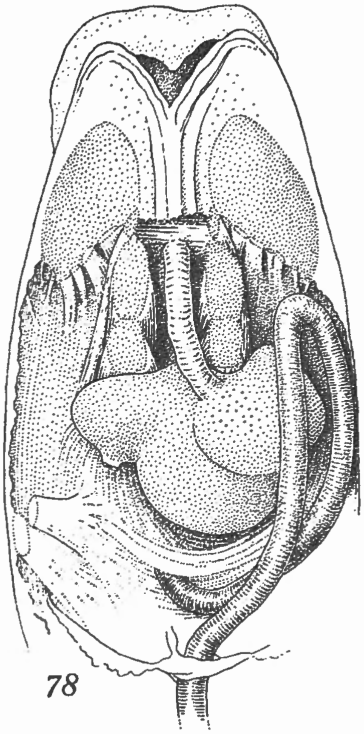
FIG. 78. — Dorsal view of digestive tract of *Yoldia thraciaeformis* (Casco Bay, Maine). Length of shell, 37 mm.

FIG. 79. — Posterior end of palp together with tentacle and « hood » of *Nucula sulcata*.

FIG. 80. — Transverse section through stomach of *Nucula proxima*, showing gastric shield and left bile duct, b.

FIG. 81. — Transverse section through stomach of *Nucula tenuis*, showing gastric shield, sh, and crystalline stile (?), s.

FIG. 82. — View, from left side, of digestive system of *Acila fultoni*. Length of shell, 33 mm.



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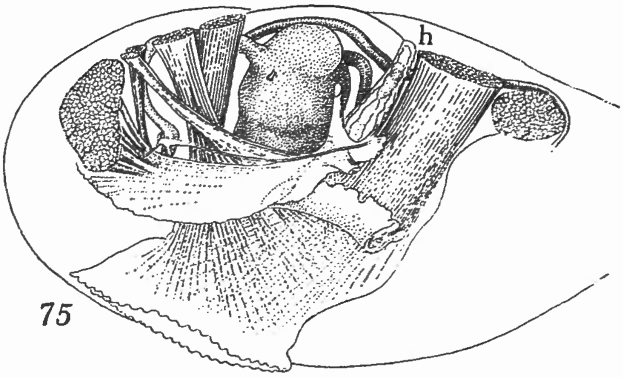

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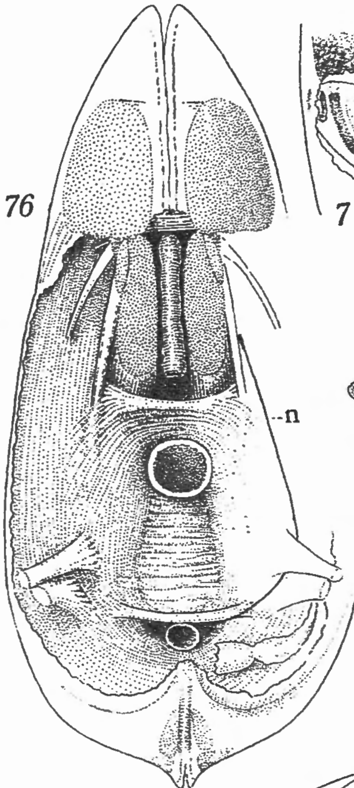

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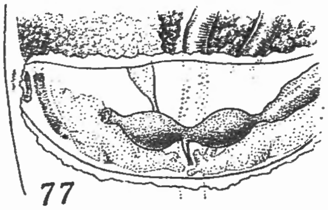

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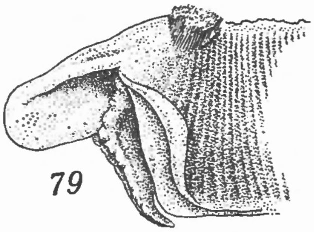

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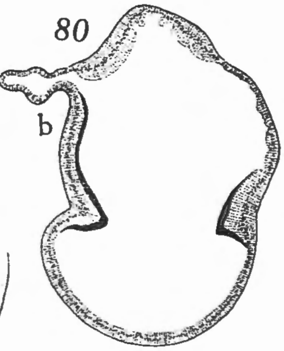

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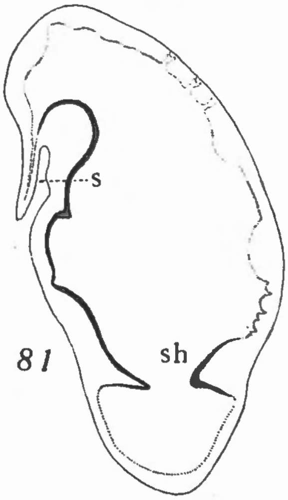

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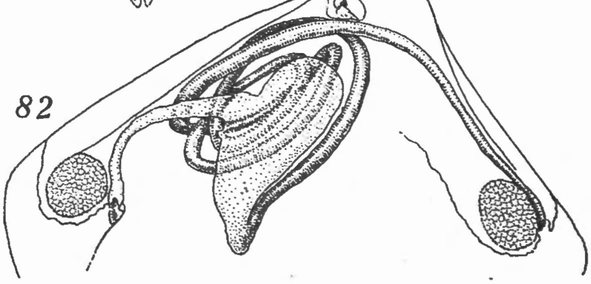

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PLATE X

EXPLANATION OF PLATE X

FIG. 83. — *Yoldia limatula* (?). This specimen has been cut longitudinally along the midline to show the arrangement of the principal pedal muscles. dm, dorso-median muscle; g, pedal ganglion; h, « heel » of foot; i, position of proximal section of intestine bounded above and below by transverse muscles; p, anterior pedal protractors; r, anterior pedal retractor; rp, posterior pedal retractor.

FIG. 84. — Reconstruction of left kidney of *Nucula rugosa*. g, gonoduct; p, reno-pericardial opening.

FIG. 85. — Dorsal view of supra-oesophageal ganglia of *Yoldia limatula* (?). Camera drawing of dissected specimen. m, mantile nerves; p, palp nerve; u, nerve with unknown destination.

FIG. 86. — *Yoldia limatula* (?). The main mass of transverse muscles shown in Fig. 83 has been removed to indicate the position of the more superficial protractors, pr; dm, dorso-median muscle; r, anterior retractor; t, transverse muscle bands derived from the dorso-median muscle; tr, the more dorsal transverse bundles which form the upper border of the pedal pit.

FIG. 87. — Posterior end of *Malletia chilensis*. Owing to slight maceration, the exact extent of the anal chamber, a, was not determined.

FIG. 88. — View, from left side, of the digestive and nervous systems of *Acila castrensis*. p, nerve to palp and tentacle.

FIG. 89. — Lateral view of *Acila divaricata*, showing chief muscles of foot and gill.

FIG. 90. — Visceral ganglia and main nerves of *Yoldia limatula*. g, nerves to gill; m, mantle nerves; s, nerve to retractor muscle of siphon.

FIG. 91. — Reconstruction of supra-oesophageal ganglia of *Nucula nucleus*. m, mantle nerves; p, palp nerve.

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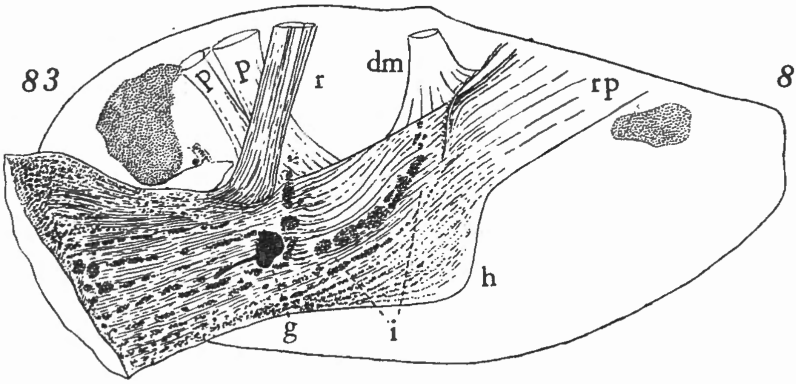

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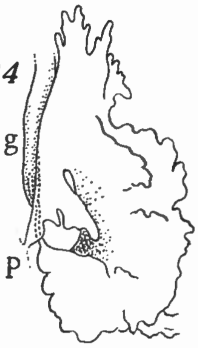

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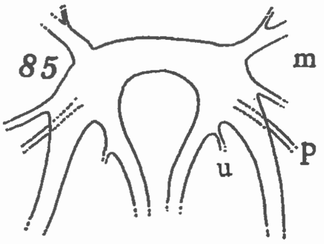

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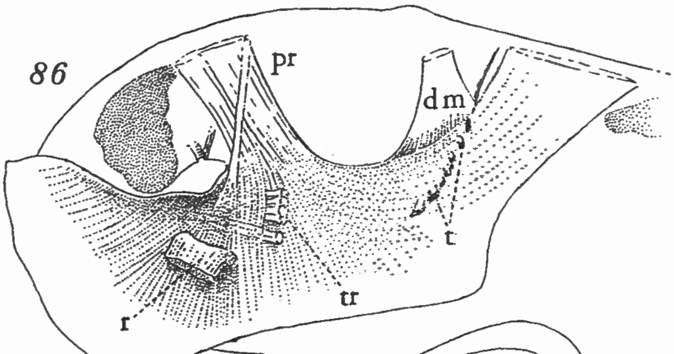

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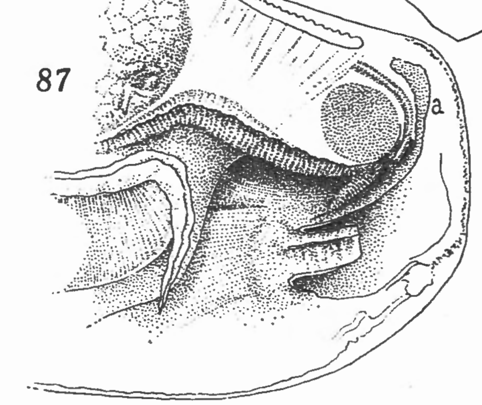

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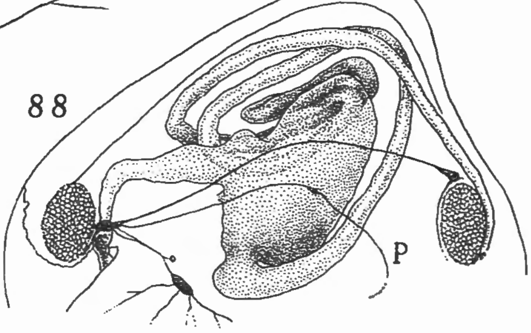

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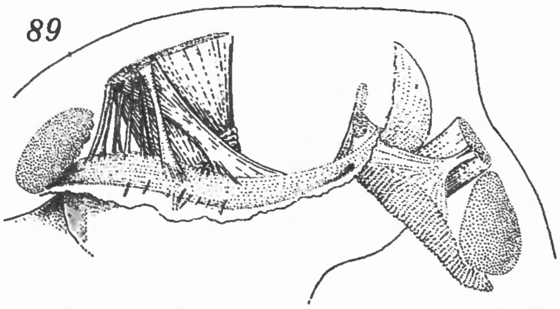

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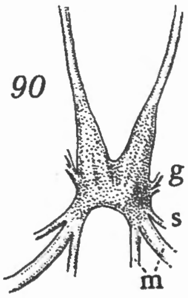

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