GALATHEA REPORT

Volume 3

GALATHEA REPORT

Volume 3

Scientific Results
of The Danish Deep-Sea Expedition
Round the World 1950-52

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FOREWORD

The present volume is Number Three of the series which will contain the scientific results of the deep-sea work carried out by the Galathea Expedition 1950-1952.

All results of studies on collections, etc. which were obtained either pelagically close to the surface or in shelf areas (down to a depth of some 400 m) will be published elsewhere. For reference a current list of such papers will be given in each new volume of the Galathea Reports. A full list of papers (up to 1958) was published in the Introduction to vol. 1 of the present series (1959, pp. 18-19).

The publication of a special Galathea Report has been made possible by a grant from Statens Almindelige Videnskabsfond (The Danish State Research Foundation). On behalf of the Galathea Committee, the Editors extend their warmest thanks to the Foundation for this support.

THE EDITORS

THE ANATOMY OF *NEOPILINA GALATHEAE* LEMCHE, 1957

(Mollusca Tryblidiacea)

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INTRODUCTION

A living representative of the molluscan order Tryblidiacea, captured by the Galathea Expedition, has been described by LEMCHE (1957a) under the name of *Neopilina galatheae*. An account of its anatomy was presented to the XVth International Congress of Zoology in London (LEMCHE and WINGSTRAND 1959), and the phylogenetical implications were discussed by LEMCHE (1959a, 1959b). Several other comments have been published but do not record new facts about the original material (BEKLEMISHEV 1958, GLASS 1957, KNIGHT and YOCHELSON 1958, 1959, LEMCHE 1957b, c, 1958a, b, YONGE 1957a, b, 1958). A chapter summarizing the more important features has been prepared for the "Traité de Zoologie".[1]

The preliminary note on the find aroused so considerable interest among zoologists, and the animal proved to be of such importance for the interpretation of fossil forms, that it was decided to lay special stress on a detailed description. As, however, the uniqueness of the find made it most important to distinguish very clearly between the facts observed and their theoretical implications, whether systematical or phylogenetical, it was decided to publish the mere facts about the structure of *Neopilina* in the Galathea Reports at the very first date possible, whereas the discussion of its consequences in phylogeny and systematics should be reserved for papers to follow elsewhere.

In order to present a prompt and extensive report on the anatomy of *Neopilina* the present authors joined in its preparation. But, as we found ourselves entangled in comparisons and phylogenetical speculations as soon as we left the level of pure description, we soon decided to exclude from our paper almost every reference to the literature.

The authors are highly indebted to the Carlsberg Foundation for granting support towards the investigations. The presentation of this paper has been greatly facilitated through the enthusiastic cooperation of the staff of the Institute for Comparative Anatomy and Zoological Technique. The painstaking work of preparing the illustrations for printing is due to Miss J. TESCH and Mr. A. ØYE. Some drawings have been made by Mr. P. WINTHER, whereas most of the originals have been produced by the authors themselves. Comparison with the fossil material was made possible through the courtesy of Prof. E. STENSIÖ of the Museum of Natural History, Stockholm, and Mr. E. YOCHELSON of the National Museum in Washington, both of whom have sent us rubber squeezes of fossil Tryblidians. Prof. STENSIÖ has also placed the beautiful photograph of *Pilina unguis* (Fig. 134) at our disposal. The English text has been revised by Mr. N. HAISLUND. To all those who have helped us in these various ways, we wish to extend our most cordial thanks.

MATERIAL AND METHODS

The material was obtained from station 716, 9° 23′ N., 89°32′ W.[2], 3,570 m depth (corrected), "dark, muddy clay, herring otter trawl", on May 6th, 1952. The sample contained 10 specimens with the soft parts preserved but more or less damaged, and three empty shells. The specimens were washed out of the muddy content of the trawl by means of surface water at a temperature of 28°C., which must have killed the animals immediately, if they did not die already during the transport to the deck of the ship from the abysses with its temperature of only 2°C. After lying some time on the deck and in the sieves, the animals were preserved in 70% ethyl alcohol (8 specimens) or 2% formaldehyde (2 specimens). Later, all of them were transferred to one jar with 70% ethyl alcohol. Originally, the empty shells were kept in the same jar with alcohol as the other specimens, but unfortunately an attempt was made afterwards to dry the shells, with the result that all of them broke to pieces.

When in the autumn of 1956 the specimens came to be investigated and their importance was realized, it was decided very soon to give them individual Roman numbers for easier registration, and to keep them apart from each other. Since then, the specimens have been treated as shown in Table 1.

The main part of the investigation has been carried out on the two sectioned specimens (III and IV). These were refixed for three days in 80%

1. After our manuscript was sent to the printer, a new species of *Neopilina* was described (CLARKE and MENZIES 1959).
2. In the Proceedings of the Zoological Congress (LEMCHE & WINGSTRAND 1959) a misprint occurred in the longitude record.

Table 1. The state of preservation and the use of the specimens of *Neopilina galatheae*.

Spec. No.	Length × breadth × height, mm.	State of preservation	Use
I	33 × 30 × 10	Intact shell and intact soft parts.	Holotype, untreated.
II	35 × 33 × 12	Well preserved. Formalin fixation?	Paraffin embedding attempted. Animal did not stand treatment with acids. Practically lost.
III	29 × 25 × 9	Mature ♀. Apex preserved in spite of rupture in the apical region. Larval shell present. Probably formalin fixation.	Cut into transverse sections. See text! Larval shell preserved in a block of celloidin in alcohol.
IV	29 × 27 × 9	Mature ♂. Apex preserved, but slightly damaged.	Cut into horizontal sections. See text!
V	36 × 34 × 12	Apical region destroyed, liver collapsed, radula emerging from the hole. Ventral side relatively well preserved.	Kept untreated. Used for exhibitions.
VI	ab. 25 × 22 × 9	Shell broken lengthwise, the right side of the animal slightly damaged along the margin.	Studies on gill position.
VII	37 × 35 × 13	A large hole in the apical region. Anterior end much damaged.	
VIII	37 × ? × 12	Apical region present, but the whole right side of the animal and shell crushed.	Additional studies on the radula.
IX	ab. 29 × 25 × 8	Broken lengthwise and folded almost like a bivalve.	Shell removed from the left side for studying muscle insertions. Pieces of right side mantle used for detailed studies.
X	?	Mature ♀. Loosened from the shell which was kept among the dried ones and afterwards broke to pieces. Animal much damaged in front.	Preliminary studies of the intestinal content and of the radula. Studies of muscles.
XI-XIII	?	Empty shells, afterwards broken to pieces.	Crystallographical studies. Trace elements, etc.

alcohol : 40 % formalin : glacial acetic acid (90 : 5 : 5 per volume). They were washed in 90 % alcohol and decalcified in 90 % alcohol with 2 % (per volume) of concentrated hydrochloric acid. Continuous 50 μ celloidin sections were prepared from both specimens. Spec. III was cut transversally, Spec. IV horizontally. The slides were stained in Mallory's phosphortungstic acid hematoxylin without dissolving the celloidin (WINGSTRAND 1951, p. 15).

The examination of the slides was supplemented by direct observations on the other specimens. Graphic as well as wax-plate reconstructions have been made whenever suitable, using lines of reference derived from photographs of the whole animals taken before sectioning. Careful search has been carried out throughout both series for detecting all possible structures present. The drawings as here given are of three kinds: graphic reconstructions as mentioned above, semi-diagrammatical ones to illustrate our ideas of the structures as based on the sum total of all our observations and, finally, descriptive ones made as naturalistic as possible to show just how much (and not more) it has been possible for us to observe on the material present. Hence, whereas the two first types of illustrations have been made as clear as possible, the last type is meant to be no clearer than the material allows, interpretation being kept down to a minimum. Finally, unretouched photographs have been used to provide documentation in a number of cases.

Although a considerable amount of facts could be derived from the available material, the following report will emphasize the need of getting living and well-fixed material, if possible even of larval stages, for the solution of many structural and functional problems.

GENERAL DESCRIPTION

The animals are bilaterally symmetrical. Small asymmetries are visible in some of the shells (Fig. 7), whereas those seen in the position of the anal opening, of the foot, and of the mouth in the preserved specimens are not constant in degree and perhaps may depend upon muscle contractions at the moment of fixation.

The whole dorsum is covered by a single, almost circular, cap-shaped shell, hiding the soft parts when the animal is viewed from all sides except the ventral one (Figs. 1-7).

The ventral side of the animal is soft, the epithelial surface almost everywhere being naked and often ciliated. There is a continuous pallial fold of almost uniform size and structure all round the animal (Figs. 1, 7). In the preserved specimens this fold is detached from the shell margin, whereas in the living animal it certainly underlies the peripheral part of the shell out to the very edge. This fold covers a likewise continuous pallial groove, surrounding the mouth region and the centrally placed, almost circular foot, the radius of which is about half that of the shell. The ventral surface of the foot is flat. Its muscular marginal parts are somewhat thickened, protruding, and irregularly folded (Figs. 9, 12). In the membranous central parts of the foot, the viscera are shining faintly through.

The mouth is situated approximately half-way between the anterior margins of the foot and of the shell. It is surrounded by an anterior lip and a small posterior one (Figs. 66, 67, 74). The anterior lip is closely associated with a preoral transverse fold dilating into broad ciliated flaps on each side, the "velum" of the present paper. The posterior lip is fused to a pair of ridges protruding from the ventral body wall, each carrying a fan-like tuft of tentacular appendages. The ventral body wall between the foot, the tentacle ridges, and the mouth forms a smooth, triangular propodial area. A small, thumb-like preoral tentacle is situated on each side of the mouth in the furrow between the velum and the anterior pallial fold.

Laterally to the foot, five pairs of gills are placed at regular intervals in the pallial groove, their original shape having been much disturbed during capture and preservation (Figs. 7, 12). The first pair of gills is situated at a slightly greater distance from the tentacle tufts than from the second pair of gills. A nephridial pore is present postero-medially to each gill base, visible only in microscopical sections. Still another pair of nephridial openings is found more anteriorly in the pallial groove without any traces of gills in the corresponding positions.

Posteriorly the anus is placed on a distinct papilla almost in the median line, half-way between the hind border of the foot and that of the mantle (Fig. 7).

The main arrangement of the interior organs is as follows. The anterior body region is occupied by a large blood space surrounding the pharynx, the radular apparatus, the subradular organ, the salivary gland, and the oesophagus, all of which organs are more or less median, and by a large number of muscles. Just under the shell in this region, ramifications from the dorsal coelomic cavities extend forwards associated with the paired pharyngeal diverticula (Fig. 11).

Further back, in the large peri-intestinal blood sinus, the stomach is found, surrounded by the paired liver (Figs. 8, 9, 167). Laterally, the large dorsoventral muscles pass down to the foot margin, and still more laterally the pallial folds contain the kidneys. More caudally the coils of the voluminous intestine occupy most of the space in the peri-intestinal blood sinus together with the ventral gonads (visible through the central parts of the foot). The paired dorsal coelomic cavities extend under the whole dorsal body wall. The last, medially placed part of the intestine is accompanied on each side by a pericardial cavity containing the paired heart (Fig. 10). Almost all parts of the nervous system are situated in or in close contact with the ventral body wall.

THE OUTER EPITHELIA

For the sake of completeness a description of the appearance of the outer epithelia is here given, in spite of their admittedly poor state of preservation. It may be mentioned already here that no single subepithelial gland cell has been discovered in the whole body in spite of intense search, and that no true invaginated glands occur in the body wall. Furthermore, most of the glandular areas show little specialization of the slender, ciliated interstitial cells between the secretory ones. In other molluscs, these ciliated cells usually appear only as minute triangular bodies facing the surface with their ciliated side and thinning out proximally between the secretory cells, so that their basal attachment is extremely difficult to recognize. In *Neopilina,* however, they are nearly always rather easy to trace down to the basement membrane.

SLIGHTLY SPECIALIZED EPITHELIA

Under this heading we describe those epithelia in which no particular specialization has been discovered.

(a) *The predominant pallial-groove epithelium* (Fig. 20) consists of cells 20-30 μ high and about 5 μ broad, with nuclei measuring 6 × 4 μ. The latter are scattered somewhat irregularly although mainly placed in the basal half of the cells. Most of the cells contain a granulated cytoplasm with its greatest staining property in the region distal to the nuclei. In the area around the foot base the epithelium differs slightly in being a little lower and less intensely stained. A peculiar feature in the latter area is the presence of indistinct large globules (or rolls) attached to the basement membrane. (Fig. 14). Cilia have been observed on the surface of some of the cells.

(b) *The epithelium on the sides of the foot* is about 40 μ high. It differs from the one just described in containing numerous granules of a yellowish-brownish substance (at least after staining), which might be either a pigment or a secretory substance (Fig. 15). Lighter cells or interspaces are seen between the normal cells. There is a cover of moderately long cilia which may arise only from the normal epithelial cells and not from the lighter parts.

(c) *The epithelium on the sides of the branchial lamellae* would appear to be the lowest unprotected one in *Neopilina,* being only 15-20 μ high. The cells carry cilia, but the destruction in these areas is such that it is very difficult to state their presence (Fig. 61).

(d) *The epithelium of the tentacle tufts* is rather typical, 15-35 μ high, and its cells contain some finely granular substance. Some cells carry long cilia. (Fig. 22).

(e) *The epithelium of the velar base* is very similar to that of the tentacle tufts, 30-40 μ high, although the granular matter seems to be somewhat coarser and more abundant. The surface is covered by cilia of moderate length (Fig. 17).

SPECIALIZED CILIATED EPITHELIA

(f) *The epithelium of the ventral foot surface* is a monolayer of 50 μ high and very narrow cells (Figs. 16, 26). The nuclei are situated at different levels. Close to the basement membrane a somewhat irregular layer of rounded nuclei of 3 μ size is found. The cells to which belong these nuclei soon reach their full width of 6-8 μ and keep this size almost to the distal end with some tendency to attenuate a little (Fig. 16). These cells appear to be glandular since they are filled up sometimes with indistinct yellow granules. Between the glandular cells other and still more slender ones are inserted with a darker cytoplasm and more elongate nuclei placed about half-way up the cells. Many of the supposed secretory cells appear to bulge out a little at the surface, whereas the interstitial cells are covered by 6-8 μ long cilia.

(g) *The epithelium of the tips of the gill lamellae.* The very tip of each gill lamella (with the possible exception of the longest ones) is covered by a short streak of strongly staining cells, 35 μ high and 3-10 μ broad (Fig. 18). No secretory cells are found between them, in contrast to the other areas of the gills. The nuclei are oblong and placed in the basal half of the cells. On the outer surface a dense cover of long cilia (up to 20 μ) is present, gradually decreasing in size to both sides of the tip.

(h) *A dense, ciliated columnar epithelium* is found on the more distal parts of the velum, on the swollen medial ends of the stems of the tentacle tufts, and also in a narrow zone on the middle marginal fold of the pallium (Figs. 19, 24, 32, 75). The thickness of this epithelium amounts to 90 μ. The cells are extremely narrow, their cytoplasm stains densely so that the whole epithelium looks rather dark. Most

of the long and slender nuclei are situated in the basal half of the cells, although none of them reach down to the basement membrane. The surface carries a dense cover of about 10-15 μ long cilia. A certain number of glandular cells are present. They contain in their outer part an oblong secretory mass of the same appearance as in the pedal gland cells. The structure of the basal parts could not be made out.

GLANDULAR EPITHELIA

(i) *Epithelia with scattered mucous cells.* On the ventral pallial surface, in the region just above the gills, the usual columnar epithelium contains many scattered goblet cells, which appear as light, empty spheres (Fig. 29). All nuclei are placed in the basal half of the cells, but it has not been possible to distinguish those belonging to the goblet cells. The interstitial cells seem to be covered by cilia. Quite a similar type of epithelium is present along both edges of the gill lamellae (Figs. 61, 64).

(k) *The marginal mucous gland* is a narrow zone along the inner side of the innermost marginal fold all round the body. In fact, it could be regarded as merely an extreme development of an epithelium like that just described, but the preponderance of the mucous cells justifies its being regarded as a distinct gland. The ciliated interstitial cells are elongate, but are distinct all the way to the basement membrane. The epithelium is almost 100 μ high (Figs. 31, 47).

(l) *The hypobranchial gland* epithelium forms one of the most highly developed secretory tissues in the outer epithelia, placed at the bases of the gills in the vicinity of the renal pores. It is formed by enormously swollen mucous cells with very few ciliated interstitial ones between them (Fig. 30). The height of the epithelium is 100-110 μ. The nuclei of the interstitial cells are often placed rather near the surface or at least half-way up the epithelium. The peripheral parts of these cells form more or less triangular patches of unchanged cytoplasm, whereas their lower parts are more or less difficult to trace down to the basement membrane. This tissue, therefore, constitutes almost an exact parallel to what is the usual type of secretory epithelia in molluscs.

(m) *The dark-staining, granulate gland cells.* On the anterior side of the preoral tentacle, a small group of very peculiar glandular cells is found (Fig. 28). The secretion stains strongly and is concentrated into large, sausage-shaped or pear-shaped drops, each filling the interior of one of the secretory cells. Each large drop consists of numerous small globular droplets lying densely together. Such droplets are also found distally to several of the gland cells in such a way that they may perhaps indicate the secretion to be given off continuously. The nuclei are difficult to observe, but seem to be rounded and of double the size of the usual epithelial ones. They appear to be placed near the lower end of the larger drops. In all, hardly more than 25 such secretory drops are found in each preoral tentacle. Scattered cells of the same type are present in the glandular zone along the anterior margin of the gill stems.

(n) *The pedal gland epithelium* covers the ventral side of the anterior foot margin. The thickness of this epithelium exceeds that found anywhere else on the outer surface, being up to 120 μ (Fig. 23). Two distinctly different types of cells occur in that region, viz. (1) normal slender ciliated interstitial cells with their very elongate nuclei placed at the usual distance from the surface (at the same level as in the neighbouring epithelium), but with very narrow basal ends, and (2) secretory cells having basally placed, rounded nuclei with a diameter from 3 to 5 μ. Single nuclei of large size (up to 8 μ) are found at different levels. Most of the cytoplasm of the glandular cells is placed below the level of the nuclei of the interstitial ones, so that the lower third of the epithelium almost looks as if consisting solely of secretory cells lying close together. The cytoplasm in the most basal 10 μ around the nuclei stains distinctly darker. Farther up in the epithelium the secretory cells are much narrowed in order to pass between the broader parts of the interstitial cells, but especially in the uppermost, rather unstained layer the secretory cells are sometimes seen to broaden once more, containing an oblong drop of some homogeneous secretory matter which stains rather slightly with a dull brown in the sections.

In many places at least the cilia are well developed on the interstitial cells, being both abundant and long, and the secretion is often found to form irregular globules or masses between the bases of these cilia.

CUTICLE-CARRYING EPITHELIA

(o) *The epithelium of the lips.* The upper lip is strongly folded in the preserved specimens. Both lips are covered by an epithelium (Fig. 27) looking much like the other high and dense ones (cf. Fig.

19), but it differs in being covered by a strong and continuous cuticle. The cells are about 90 μ high and their elongate nuclei are more distinct than those of the ciliated epithelia. The cuticle increases in thickness from the outer surfaces of the lips (being less than 10 μ in these areas) into the mouth, inside which the cuticle suddenly increases in thickness to form the "jaws". In some places there is an apparent stratification of the cuticle, but its importance is not too well understood.

The different kinds of epithelia associated with shell formation, such as

(p) *the periostracum gland cells,*
(q) *the prism-forming epithelium,*
(r) *the sterile shell epithelium,*
(s) *the nacre-forming epithelium,* and
(t) *the muscle attachment cells*

will be described in the immediately following chapter.

THE SHELL AND THE PALLIAL FOLD

The pallium forms a wide and strong circular fold all round the body. Its structure and shape is the same anteriorly, laterally, and posteriorly. For convenience the proximal limit of the pallial fold is taken to be along the lateral surfaces of the big dorso-ventral foot retractors, i.e. at the periphery of the foot base. Anteriorly the limit is taken to be along the base of the velum.

The outermost part of the pallial fold carries on its ventral side two smaller circular folds, both pointing ventrally, perpendicular to the mantle surface (Figs. 33, 45, 47). These two smaller folds are here mentioned as the middle and the inner marginal folds, respectively, whereas the part of the pallial fold lying distally to the middle fold is called the outer marginal fold.

The pallial fold is covered by two epithelia, the dorsal one with the shell, and the ventral one, which seems covered by cilia in most places. The ventral epithelium is the seat of two distinctly marked glandular areas, viz. the hypobranchial glands under the gill bases in close connection with the renal pores, and the marginal mucous gland forming a continuous strip of glandular epithelium all round the animal on the proximal side of the inner marginal fold.

The interior of the pallial fold is occupied by blood spaces, muscles, and connective tissue, with few viscera other than the kidneys which are found in the thicker proximal parts of the fold (Fig. 157). Ventrally, below the kidneys the ctenidia are inserted. Just centrally to the gill bases, the lateral nerve cord is placed closely inside the ventral epithelium, separated from the basement membrane only by a thin layer of muscle fibres.

The peripheral parts of the mantle are thin and contain almost only muscle fibres, connective tissue, and blood spaces with blood cells (Fig. 47). Also, an astonishingly rich nerve supply is found running out to the very marginal parts, most of the nerves continuing even into the outer marginal fold, although it is completely surrounded by the periostracum of the shell.

The shell, as seen from above, is a rather flat cap of almost circular outline (Fig. 2) the diameter of which is slightly larger longitudinally than transversely. The largest specimen measures 37 × 35 × 13 mm, the smallest one about 25 × 22 × 9 mm, whereas the type specimen is 33 × 30 × 10 mm. The thickness of the shell rarely exceeds 0,3 mm. Mostly it is below 0.2 mm. It would seem to be only in fully grown shells that the greater thickness occurs, and always only in a narrow belt rather near to the shell margin – as will be explained in more detail below.

Lines of growth are closely set on the shell surface, they are very fine but distinct (Figs. 36, 37). About every fifth of them is stronger than the others and protrudes somewhat over the next younger part of the shell. The lines of growth are crossed by 30-60 narrow and slightly elevated ribs radiating from the apical region (Fig. 36). Their distinctness diminishes with increasing distance from the apex, and they almost disappear in the outer, younger parts of the shell.

The apex is situated in the median plane almost vertically over the front margin of the shell, the anterior side of which is concave (Fig. 3, 4). As seen from the side, the dorsal surface of the shell forms a spiral so that, in the more apical part, about $^2/_3$ of a full exogastric coil is produced. The small apical prominence points obliquely downwards and forwards. In the largest specimen this point is found some 8 mm. above the anterior shell margin. The posterior slope of the shell becomes less and less convex caudally. It is very difficult to trace any asymmetry in the adult shell, the general appearance of which is one of bilateral symmetry.

A larval shell has been found in one of the specimens captured, evidently having been lost in all of the others, where only the slightest traces of an impression from the larval shell margins may be detected (Fig. 35). The larval shell (Figs. 34, 49) is peculiar in being dextrally coiled in a manner imitating that of prosobranch protoconchs, but the pronounced asymmetry disappears almost at once at the transition to the first part of the adult shell formed beneath the larval one. When, therefore, the larval shell becomes lost – as in most specimens – the remaining surface of the shell appears almost undisturbed (Fig. 35). The orientation of the larval shell is such that it opens into the morphologically posterior direction. In the actual, adult specimen the opening points upwards and forwards because of the coiling of the shell (Fig. 163 A).

The colour of the adult shell is a dull brown which grows darker towards the apex until it appears almost black, most of the black pigment being concentrated on the ribs and lines of growth. Towards the margin the shell shows a more uniform light brown, almost straw-coloured. Mostly, the surface of the shell is irregularly corroded, apparently through the action of sessile organisms.

As seen in our sections, the adult shell is composed of three layers, the outermost of which is a rather thin periostracum with more or less pigment (Figs. 39, 46). The middle layer is a thick prismatic one, on the inside of which the lamellate nacreous layer is found (Fig. 48). The thickness of the periostracum is nearly the same all over (3-5 μ). The two calcareous layers have proved to vary so regularly as to indicate the manner in which the shell substance is formed, and by which areas of the mantle (Fig. 33).

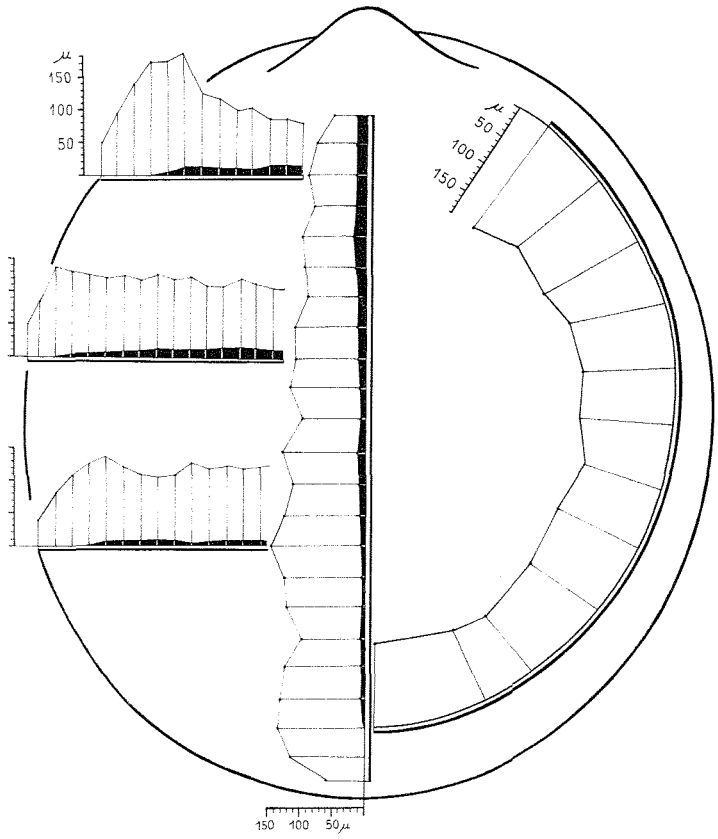
Of the three layers the periostracum is the only one bending round the outer edge of the shell and the underlying outer marginal fold to continue inwards on the ventral side thereof until – some millimeters from the margin – it reaches the periostracum gland. This gland forms a narrow circular band all round the animal at the base of the outer marginal fold. It consists of some 30 columnar epithelial cells in each cross section (Figs. 32, 50). Each cell appears as if delimited from its neighbours by a light interspace which may be artificial. Some of the nuclei of the epithelial cells are placed half-way up, but others seem to be placed more basally, although the presence of the latter cannot be proved because of the inadequate fixation. The glandular cells increase in height from the two or three low ones on the medial side of the strip to the most lateral ones, which are almost ten times as long as broad.

In the sectioned specimens the periostracum has broken along the very shell edge, owing to the contraction of the radial muscle fibres in the outer part of the pallium (Fig. 45). In fresh specimens the periostracum on the ventral side of the pallium forms an iris-like membranous ring inside the edge, especially distinct anteriorly.

As soon as the periostracum has bent round the margin to the dorsal side of the pallium, lime substance begins to be added to its interior surface. To get an impression of the places in which new substance is added, measurements have been taken on Spec. III, in which the thicknesses of the prismatic and the nacreous layers were measured along the median line of the shell and along three transverse sections. The prismatic one was also measured approximately over the periostracum gland (i.e. in the area where it was found to be thickest). The results are given in Text-fig. 1.

As seen in the diagram (Fig. 33), no nacreous substance is found in a zone immediately inside the margin, where, on the other hand, the prisms increase in height. Thus the prismatic layer must be formed by the dorsal epithelium of the outer marginal fold. As growth proceeds, new parts of the periostracum must bend up over the margin from the ventral side and new prisms must be initiated distally, at the same time as more and more substance is added to the more proximal prisms. Hence, the height of these prisms increases from the margin on to the region above the periostracum gland. When the height of the prisms decreases medially to this line, it means that no more substance is added. The larger the animal, the higher will be the prisms before they eventually come to lie inside their secretory area. Thus the younger parts of the shell are thicker than the older, more apical ones. In the diagram (Text-fig. 1) this fact is borne out by the measurements along the median line, showing a gradual increase in thickness from the apical region caudally. The diagram also shows that the maximum thickness of the shell is found laterally near the anterior end.

In a few places it is possible to see a fine dark line running through the prismatic layer almost parallel to the formative surface (Figs. 33 and 51). Such a line, when crossing the boundaries between the individual prisms, widens a little to form a small dark dot. The length of such a line, as measured



Text-fig. 1. The thickness of the shell (nacreous layer black, prismatic layer white) along the median line, along three transverse sections (left), and along the zone of maximum thickness inside the margin (right). The double line at the bottom of each graph indicates the line along which the measurements were taken in the celloidin sections. The scale is the same in all cases.

along a radius, is about 8-10 times the height of the prisms in the area in question. The same relation is found to exist between the width of the prism-forming marginal zone, and the height of the fully developed prisms just inside. Hence, there would seem to be little doubt that the said lines indicate temporary stops of growth. It is rather strange, however, to find so extremely few of these lines, none of our sections showing more than a single one each.

The nacreous substance makes its first appearance above the region of the periostracum gland and increases in thickness until reaching its definite thickness of approximately 12 μ just centrally to the insertions of the pedal retractors. Little increase of this layer is found in the central parts of the shell (Fig. 33 and Text-fig. 1). This means that the formative zone of the nacreous substance is the same as that in which muscles attach to the shell. The nacreous substance consists of quite a number of extremely thin lamellae.

The crystallographical properties of the shell are treated by W. J. SCHMIDT in a separate paper of this volume.

The prism-forming epithelium covers the dorsal surface of the outer marginal fold, but as this fold has been detached from the shell by the strong contraction at death, the epithelium is so greatly deformed that it is difficult to describe. As now seen in transversal sections (Fig. 38), this epithelium forms a rather narrow band – about 50 cells broad – centrally continuous with the one forming the nacre (Fig. 33).

Apparently the epithelium is built up of high columnar cells, but it should be remembered that lateral compression caused by the said contraction of the fold has increased the relative height of the cells. The number of prisms in a cross section through the marginal area of the shell is similar (about 50) to that of the number of cells in a section through the epithelium here described. It is probable, therefore, that each prism is formed by a single cell, which means that the epithelium must have covered the whole of the five times broader formative zone of the prismatic layer when the animal was alive. These considerations indicate the original epithelium to have been rather low, in appearance much like the nacre-forming one. The amount of cytoplasm is not very large, and the nuclei are placed almost centrally.

The sterile shell epithelium. The central part of the dorsum is covered by an extremely flat epithelium, the only outer one known to be squamous in this

animal. As the shell shows a strong tendency to detach from the epithelium beneath, this delicate membrane is rarely undisturbed. In some few places, however, over the hindmost parts of the intestine, this epithelium is visible as a much flattened layer, less than 5 μ thick. Flattened nuclei are scattered in it without visible cell walls between, and with no special cytoplasmatic structures to be seen (Figs. 33, 41).

The nacre-forming epithelium is much higher than the preceding one although still rather low (Figs. 43, 52, 55). The height is about 15 μ and the width of the cells is about 8-10 μ. The nuclei are correspondingly more globular or – often – slightly flattened, not elongate as in most other epithelia, and most of them are placed rather close to the outer surface. The cytoplasm is poorly preserved. The epithelium as seen in the present sections varies considerably in height in different places, but it has not been possible to find out whether this phenomenon is natural or artificial.

The muscle attachment cells. The zone of the nacre-forming epithelium on the dorsum is the only area in which muscles attach themselves to the shell (Fig. 130). This attachment takes place through specialized cells much larger than their neighbours and penetrated by a number of tonofibrils. These cells are found either scattered between the normal epithelial cells (Fig. 52) or concentrated into groups with no other cells interspersed (Figs. 44, 48, 53). When seen in tangential sections, the bulk of each cell consists of a circumscribed bundle of tonofibrils surrounded by some unchanged cytoplasm, with the nucleus situated at the surface of the bundle. In a few places, several nuclei have been observed lying inside their respective fibril bundles (Fig. 54). The preparations were not good enough for a detailed description of the tonofibrils, but it is evident that they are placed almost in parallel, having a direction that corresponds to that of the pull produced by the muscle fibre(s) attached.

In cross section the plates containing tono-fibrils appear as darker bodies separated from each other by ovate cavities corresponding to the interspaces as found in the tangential sections (Figs. 42, 44, 48). There is some tendency for the nuclei in some areas to be placed to the medial side of their respective fibre bundles.

The marginal folds. The outer edge of the pallium is enclosed within the *doublure* formed by the periostracum as it turns over from the dorsal to the ventral side. Immediately centrally (or proximally) to the periostracum gland two other folds appear on the ventral pallial surface. These three folds are termed the outer, the middle, and the inner marginal folds, respectively (Figs. 33, 45).

The outer marginal fold is covered on its dorsal side by the prism-forming epithelium described above. The ventral epithelium consists of cells which, although contracted almost to the degree of being distorted, still show signs of having been no higher than cubical. Apparently the ventral epithelium is devoid of gland cells. Towards the edge the cells enlarge and become narrower, and the edge itself would seem to carry high and narrow columnar cells. As mentioned above, the whole outer marginal fold is strongly contracted. It has been detached from the shell, and the periostracum has broken at the shell margin in the preserved specimens. Just beneath the prism-forming epithelium a layer of muscle cells is placed (Fig. 38). Probably these muscle strands are responsible for much of the pull which has torn away the outer marginal fold from its original attachment to the shell.

The interior of the outer marginal fold is occupied by a mixture of Leydig cells, blood cells, and crossing myofibres, all bathed as usual in the body fluid present. The whole fold appears to have been very flat, attenuating distally, but without any very strong attachment to the shell. The strong innervation along the ventral epithelium should be especially noticed. No sense organs have been detected there, but the nerves are far too strong and abundant to be without specific function. It is strange to find such a strongly developed innervation under an epithelium covered by a strong periostracum.

In every section fine muscle fibres are seen to attach to the basement membrane of the periostracum gland situated at the base of the outer marginal fold. These fibres run straight in an obliquely inward and upward direction, inserting to the shell above the innermost part of the marginal fold region (Fig. 33). They contribute to the formation of a pallial line all the way round the shell – almost as in bivalves.

Just proximally to the periostracum gland a thick ventral fold arises, large enough to appear very distinctly to the naked eye in preserved specimens (Figs. 32, 33, 45, 47). This middle marginal fold might well have become more pronounced through contraction, but there is good evidence that a thickening in this place is natural. The distal side of this fold is covered by closely set, very high and narrow columnar cells with a strong ciliation (cf. p. 13). In

cross sections the cells of this ciliated band are arranged in a fan-like manner. Those nearest to the periostracum gland have a lighter cytoplasm and probably no cilia. They would seem to form merely a covering of the newly formed edge of the periostracum, which, therefore, is well protected within an invagination of the epithelium.

No glandular cells are found on the strongly ciliated distal side of the middle marginal fold, but at its ventral edge the epithelium becomes lower, and the first globular mucous cells appear. This type of epithelium with scattered mucous cells continues down the proximal side of the said fold and up along the distal side of the inner marginal one.

The inner marginal fold (Figs. 25, 31, 33, 47) is less constant in shape than the other two. On the medial side it carries the marginal mucous gland (cf. p. 14). Farther proximally, on the ventral side of the pallial fold proper, the height of the epithelium diminishes again, the glandular activity becoming less and less pronounced, so that when reaching the base of the gills the epithelium is of the usual type with scattered mucous cells (as in Fig. 29).

Branches of the marginal pallial nerves supply not only the outer, but also the middle and the inner marginal folds, the interior of which is mostly occupied by connective tissue, scattered muscle fibres, and small blood spaces.

THE GILLS

Five pairs of well-developed gills are situated in the pallial groove lateral to the foot (Figs. 1, 7, 57). In the preserved specimens they appear as being far apart, with no relationships to each other. Their normal shape, however, is much disturbed, partly through contraction, and partly through the large amount of mud which, during dredging, had been pressed into the pallial groove. Fortunately one of the specimens had been laterally compressed in such a way as to simulate a bivalve, and in this specimen what is believed to be the original position of two successive gills could be studied. The results thus obtained were used as a control of – and have corroborated – the views reached from the examination of other specimens, especially the wax-plate reconstructions of Spec. III and the few remains of the destroyed Spec. II.

Each gill consists of an elongate stem and a series of 7-8 lamellae on one side (Figs. 58, 59). Sometimes there is an additional rudimentary series on the other side. The stem is compressed and slightly tapering, inserting dorsally in the pallial groove. The anterior end of the elongate insertion area points antero-laterally (In the present description of the gills, the direction of the pallial groove is regarded as longitudinal). The renal pores are placed close to the rear – postero-medially – of the respective gill bases. The stem of the gill immediately bends strongly, sweeping latero-posteriorly along the roof of the pallial groove, at an angle of 30-40° to the margin of the foot (Figs. 1, 57).

Seven or eight lamellae arise from the ventral (morphologically anterior) side of the stem, each lamella being as long as or somewhat longer than the part of the stem which is distal to the base of the lamella in question – only that the innermost two or three lamellae are still somewhat longer (Figs. 58, 59). Arising at almost equal intervals along the stem, the lamellae bend backwards and twist sufficiently to let the originally anterior margin become ventro-lateral, and the originally posterior one dorso-medial (Figs. 58, 59). The tips of many of the outer lamellae almost touch the roof of the pallial groove, but at present we cannot decide whether this is a natural position. The innermost two or three lamellae would seem to be long enough to touch the foremost parts of the gill behind with their tips. On each gill the innermost lamella arises in such a way that it might be more correct to state that it originates directly from the pallial roof close to the base of the true gill.

Although the stem – as mentioned above – is placed rather close to the roof of the pallium, a series of additional, very short lamellae are present on the dorsal side of the stem. These rudimentary lamellae have been seen with certainty in the three anterior pairs of gills, alternating with the much larger ventral lamellae (Figs. 56, 59). Hence, the structure of the gills in *Neopilina* does not prevent a comparison with the biserial gills of other molluscs.

For the description of the structure of each lamella it is suitable to distinguish between the epithelial and the subepithelial tissues.

The marginal areas lining the ventral and dorsal edges of the lamellae are covered by a ciliated epithelium with many globular mucous cells (Figs. 61, 64). The nuclei of the latter are either rounded or somewhat flattened on the side facing the secre-

tory drop. They are placed rather far basally. Quite a number of other nuclei are found at the same level in the epithelium, many of them being more elongate. Similar, elongate nuclei are scattered at almost any higher level. Most of the latter belong to the ciliated cells which form the greater part of the surface of the epithelium. Because of the presence of the globular cells many of the ciliated ones are somewhat curved and expand towards the surface. The cilia do not appear to be very long.

The flattened sides of the lamellae (often vaulted through the contraction of the muscle fibres inside) are covered by another type of epithelium. Because of contraction it is difficult to obtain any definite idea about the normal shape of these cells (Figs. 13, 63). The epithelium consists of two kinds of cells, slender ones with elongate nuclei and strong ciliation and broader cells with more rounded nuclei. The latter may perhaps be secretory, as they contain inclusions in their plasm. The bases of the cells have a stronger affinity to the stains than the rest of the cytoplasm. Probably this epithelium is the lowest unprotected one in *Neopilina,* but in the contracted state it is as high as the marginal one, 20–30 μ, in a few apparently undisturbed places only 15-20 μ. The cilia appear to be relatively long, perhaps about 10 μ.

Almost the whole of the gill surface – on the stem as well as on the lamellae – is covered by the two types of epithelia described above. A third type is found on the very tip of the lamellae, spreading out a little more on their ventral side than on their dorsal one. This epithelium (Fig. 18) consists almost solely of very dense, strongly staining columnar cells with very long and powerful cilia, measuring at least 20 μ. No mucous globular cells appear there, but very scattered dark granulated cells may be present.

As to the interior gill tissues, the same approximate symmetry is found as in the epithelia (Figs. 61, 63, 64). In every lamella each of the marginal secretory areas surrounds a nerve which is placed very close to the basement membrane of the epithelium, with very few and slender muscle fibres running peripherally around the nerve. These nerves give off again and again very small branches scattering in the more central part of each lamella, always very close to the epithelium. On each side of the nerve or a little more centrally in the lamella, some strong muscle fibres are found, running longitudinally in the lamella and tending to form two distinct, although close-set, bundles.

The remaining parts of the interior of each lamella are filled with a tangle of fibres of muscular and perhaps also connective tissue fibres, which, in the contracted lamellae, appear to cross abundantly in all directions in the centre (Figs. 61, 118). It would seem, however, that this condition is artificial, and that the functioning lamella is flat, with fibres running obliquely across from the epithelium of one side to that of the other. Almost no fibres have been found running obliquely proximo-distally. Therefore, the crossing fibres cause the lamella to become narrower and to thicken in the mid-line, but they do not shorten it. It must be the strong double pair of longitudinal muscles (gill retractors) that shorten the gills and their lamellae.

The crossing fibres do not, however, fill the whole of the interior of the lamella, small spaces containing body fluid and blood cells occurring everywhere although concentrating into two vessel-like blood sinuses, one inside the ventral and one inside the dorsal margin. In general these two main sinuses are placed immediately centrally to and sometimes between the double longitudinal retractors (Figs. 61, 63). A comparison with the vessels and blood spaces in the body proper has shown that the dorsal sinus is the afferent one, communicating with the large peri-intestinal blood sinus, whereas the more ventral and lateral sinus in the gill carries the oxygenated blood away from the gill past the kidney towards the auricle (Fig. 143).

In some cases elongate nuclei have been observed which presumably belong to the muscle fibres in the central tissues, whereas other, rounded nuclei certainly belong to the blood cells. It is not possible to make out whether there may be additional types of cells involved, either Leydig cells or cells of fibrous connective tissue. No trace of any skeletal (cartilaginous) tissue has been observed.

All of the said longitudinal nerves, muscles, and blood sinuses appear stronger on the afferent (dorsal) side than on the ventral side. Also, all these structures decrease in size with increasing distance from the base of the lamella. At the very tip first the blood space, then the muscles, and finally the nerve disappear, indicating that none of these structures continue around the tip.

The structure of the stem is in the main the same as that of a single lamella (Figs. 59, 62). The epithelium of the flattened sides looks very similar to that of the lamellae. The anterior and posterior margins of the stem also carry a similar epithelium with many interspersed globular mucous cells as found on the lamellae. There is a distinct difference, how-

ever, between the development of the two margins of the stem, the glandular elements being comparatively fewer and exclusively of the globular mucous type on the posterior margin. Anteriorly the globular gland cells are also the predominant cell element, but between them dark-staining granulate cells are common, particularly on the first and last gills. This secretory area on the stem of the gill with both kinds of glandular cells continues a little on the nearest part of the pallial epithelium, just antero-laterally to the gill base.

The internal structure of the gill stem also shows a picture similar to that of the lamellae. The efferent vessels along the ventral side of the lamellae fuse to form a longitudinal vessel along the anterior side of the stem, which, therefore, is the efferent or arterial side. The venous blood is distributed in quite a similar way along the opposite margin to the dorsal side of the lamellae. The nerves are arranged in exactly the same manner, lying between the vessels and the epithelium. As to the retractor muscles, they take a very similar course, but the presence of two separate bundles along each margin of the stem is not always as distinct as in the lamellae (Figs. 59, 60, 62, 65).

The comparative and functional implications of the investigations of the gills of *Neopilina* will be discussed on page 65.

THE FOOT

The circular foot occupies the central parts of the ventral side of the animal (Fig. 7). Being strongly contracted in the preserved specimens, its diameter is about half that of the shell. For descriptive purposes the foot is here regarded as the ventral body wall underlying the large peri-intestinal blood sinus (Figs. 8, 9, 10). Its central part forms a circular membranous disc which, at places, is little more than 0.1 mm thick and therefore somewhat transparent even in the preserved material. The periphery of the foot is developed as a prominent muscular foot margin all round the organ. The anterior foot margin is thickened by the presence on its ventral surface of the high pedal gland epithelium. All the other parts of the margin decrease in thickness towards a very sharp edge. The free margin is strongly folded because of contraction. Numerous deep circular folds on the vertical sides of the foot indicate that this organ has been subjected to a strong retraction. This is evident also from the fact that the foot has to be extended considerably from its position in the preserved specimens to reach the horizontal level of the shell margin (Figs. 8, 9).

The ventral surface of the foot – except along the anterior margin – is covered by a ciliated epithelium with many glandular cells (Figs. 16, 26) forming a creeping sole. The epithelium of the vertical sides of the foot differs in being less strongly ciliated and in containing coarse granules in many of its cells (Fig. 15). The change from one kind of epithelium to the other at the edge of the foot margin is very abrupt.

Ventrally along the anterior foot margin, just inside the edge, a transverse strip of thickened glandular epithelium is found, constituting a pedal gland (Figs. 23, 73). This epithelium extends laterally to a point just inside the first gill and does not transgress the edge of the foot anteriorly. It is separated from the epithelium of the side of the foot by a narrow zone of epithelium similar to that of the ventral surface proper (Fig. 73). In preserved specimens, a slight swelling of the tissue indicates the place of the pedal gland (Fig. 74). The whole area in question is folded in the preserved and contracted specimens, but there is no true invagination involved (Fig. 12). On the analogy of conditions in other molluscs it is suggested that the function of the pedal gland is the production of the mucus necessary for creeping. The presence of such a well-developed gland in this place, therefore, is an indication that the living animal is not quite sessile.

The interior of the foot is occupied by a tangle of connective tissue and muscular fibres. The latter form a delicate loose reticulum in the membranous centre of the organ (Fig. 117). The margins of the foot are highly muscular, containing two different circular muscle systems and also the ramifications of the large dorso-ventral pedal retractors (Fig. 119). These retractors consist of lateral and medial portions. The lateral ones (mm. latero-pedales) spread like fans into the margin of the foot and appear to have caused its retraction in the preserved specimens. The fibres of the medial portions (mm. mediopedales) spread in a central direction in close contact with the peri-intestinal blood sinus and are soon lost in the reticulum of fibres in the membrane forming the centre of the foot. The combined actions of both portions seem to have caused the lifting up of the foot as a whole.

Blood spaces are present particularly in the more interior parts of the foot, but are scarce near the brim and close to the sole. The pedal nerve cord on each side lies within a blood sinus just inside the base of the free brim of the foot, fusing posteriorly with the one from the other side. There is a strong inter-pedal commissure basal to the anterior foot margin, i.e. above the pedal gland. This means that there is a continuous circular nerve cord all round the foot (Fig. 135).

Certainly the living animal must be able to extend the foot below the level of the shell margin. The circular muscles along the sides of the foot (Figs. 119, 121) would seem to be able to constrict the "stalk" of the extended foot, and the big dorso-ventrals to retract it. The broad marginal parts of the foot can probably be extended to reach almost to the pallial margin, thus closing off more or less completely the pallial groove from the ventral side.

Superficially, the foot of *Neopilina* looks very much like a sucker. But no muscles attach to the central foot membrane in such a way that they could possibly lift it efficiently, thereby producing the necessary under-pressure below the centre of the foot. The medial portions of the foot retractors only spread in the peripheral parts of the large membrane. Thus it appears that the organ cannot function efficiently as a sucker. This is in accordance with the fact that *Neopilina* was found on soft bottom and that the trawl did not contain hard objects with smooth surfaces suitable for a sucker. The undamaged state of some of the specimens indicates that the animals have hardly adhered to any hard substratum left in the depths, from which the animals could have been torn off by the trawl. Moreover, the presence of three empty shells in the trawl shows that *Neopilina* lives on the spot and has not been attached to some drifting objects which, by accident, failed to come into the trawl, and from where the animals dropped off.

THE MOUTH REGION

The position of the mouth is definitely ventral. It is placed about half-way between the frontal edge of the shell and the anterior foot margin. Between the mouth and the foot there is a distinct, smooth triangular area, the propodial area (Figs. 66, 67). On all other sides the mouth region is surrounded by the anterior part of the pallial fold.

The mouth itself is delimited by the anterior lip in front and a small posterior lip behind (Figs. 66, 67, 74). In front of the anterior lip there is a low transverse fold which on each side forms a broad flap-like appendage. This entire structure is called the velum, because we regard it as a homologon of the larval velum of other molluscs. A small preoral tentacle is situated on each side anterior to the lateral part of the velum. The propodial area is delimited anteriorly and laterally by a strong ridge on each side, ending postero-laterally in a number of tentacles, the postoral tentacle tuft.

THE PREORAL TENTACLES

Antero-laterally to the base of the velum, in the furrow between this organ and the roof of the pallial groove, there is on each side a thumb-like, about 0.3 mm long appendage, the preoral tentacle (Figs. 69, 71). Each tentacle is lined by a ciliated epithelium, which at the base is continuous with and similar to the common epithelial covering of the pallial groove. From an average height of some 15 μ near the base the epithelium increases more or less stepwise in height to reach a thickness of 80-90 μ on the tip. Conversely, the ciliation seems to be densest and the cilia longer at the base (15-20 μ). As mentioned on p. 14, a group of some 25 dark granulate gland cells appears on the anterior side of the basal part of the tentacle (Fig. 70). Scattered light-staining secretory cells similar to those found in the pedal gland are present in the higher epithelia covering the outer parts of the tentacle. The high epithelium on the tip consists of several cell types, ciliated epithelial cells, secretory cells, and undetermined ones, corresponding to at least three kinds of nuclei. More precise correlation of the types of nuclei with those of the cells could not be carried out, but the rich innervation indicates that the tip epithelium is a sensory one.

The interior of the tentacle inside the basement membrane is occupied by a mixture of branching nerves, connective tissue, and muscle fibres. A thick nerve from the cerebral ganglion enters the tentacle almost axially, giving off small branches all the way towards the epithelium. The main part of the nerve continues to the tip region, forming a plate-like plexus just below the high, presumably sensory epithelium. The plexus contains several small dark

nuclei not found further inwards in the tentacle. The nature of the cells to which these nuclei belong, could not be ascertained, nor could the sensory cells be identified with certainty in the epithelium.

THE VELUM

Immediately in front of the anterior lip a low transverse crest, the anterior velar ridge, forms the anterior limit of the mouth region (Figs. 66, 67, 74). Just laterally of the mouth this ridge increases in height and bends latero-caudally on each side for some three millimeters, gradually growing higher and higher. At the level of the posterior lip the ridge loses its contact with the body wall and forms the broad and thick, almost quadrangular flaps. The whole structure is ciliated and corresponds to the velum of mollusc larvae. The ventral border except on the anterior ridge, from the point where the velum begins to increase in height and a little up the distal border, appears more whitish than the rest in the preserved specimens and is somewhat thicker than the other parts (Fig. 74). Probably the whole velum is much contracted and distorted in shape in the preserved specimens.

As to the histology the whitish marginal zone is formed by a very high epithelium (Figs. 19, 24) with strong ciliation, whereas the basal part of the medial side and almost the whole outer side is covered by a lower epithelium (Figs. 17, 21) with a less dense and shorter ciliation (Fig. 78).

The interior of the velum is occupied by an inner parenchyma in which connective tissue elements, muscle fibres, and small nerves are present. All these nerves are branches of the numerous nervi velares, which come from the cerebral commissure and from the cerebral ganglia (see Fig. 136). These nerves enter the velum close to its inner surface and spread in all directions, usually following along the basement membrane of the epithelium at a distance equalling the height of the epithelial cells. Around most of these nerves shrinkage or blood sinuses produce empty spaces sufficiently broad to demonstrate that the interior is occupied by an interstitial substance looking rather solid and homogeneous. Its exact character could not be made out from the available preparations. The muscle fibres are partly ramifications of the velum retractors (See p. 38), partly fibres crossing the velum in other directions. The impression is that of an organ of great flexibility, but rigid enough to be capable of being moved intentionally and efficiently in many directions.

THE POSTORAL TENTACLE TUFTS

Immediately behind the posterior lip there is a strong transverse fold or ridge interrupted by a deep median notch. This notch indicates that we have to do with a truly paired structure (Figs. 66, 67, 74). Laterally the ridge bends sharply in a latero-caudal direction (Fig. 68) and becomes thinner. Two to three millimetres further back it bends laterally once more in a curve which ends in pointing antero-laterally or even anteriorly (Figs. 66, 136). The curved part of the ridge carries a number of slightly branching tentacles on its free margin. Since the tentacles are present right up to the point where the free margin joins the ventral body wall, and because of the curvature of the attachment of this part of the ridge, the tentacles form a large fan-like structure behind the velum (Figs. 66, 68). This description is based on a careful study of sections and dissected specimens. Most of the specimens do not show the said arrangement very clearly. They often show the tentacles disordered so as to appear merely as simple tufts (Figs. 67, 74). Even in the specimen where the tentacles are least contracted, they do not by far reach the base of the first gill, but whether they are able to do so in the living animal is an open question. However, since they appear poorly ciliated, they can hardly serve as efficient organs for transportation of food from the gills – in the manner of the labial palps in the lamellibranchs.

The tentacles themselves are covered by an epithelium of rather ordinary-looking columnar cells, measuring 15-35 μ in height and containing some finely granular substance. Rather few scattered cells carry distinct cilia, whereas the other cells hardly do so (Fig. 22). The whole surface is strongly folded because of the contraction of the longitudinal muscular elements in the interior (Fig. 79). An epithelium of an entirely different type is present on the transverse part of the tentacle ridge behind the mouth. The tip of the lateral corner of this ridge is covered by an epithelium almost identical to that of the whitish marginal zone of the velum with high, narrow cells and a strong ciliation. The more medial parts have a little lower and broader cells in the epithelium which has been folded by the contraction of the animal, whereas the higher one of the corner has kept smooth (Figs. 72, 75). The folded parts do not seem to be ciliated, but may perhaps be covered by a very thin cuticle.

The interior of the tentacles proper looks like a fairly dense connective tissue containing quite a

number of muscular fibres which tend to keep along the surface. Towards the base the muscle fibres join to form big bundles which eventually form the retractor muscles (Fig. 80). Several small nerves pass down into the tentacles. They are branches from the second latero-pedal commissure, from the pedal nerve cord, and (the transverse part of the ridge) almost directly from the cerebral ganglion (Fig. 136).

Because of their situation and innervation the tentacles and the ridge upon which they are placed must be regarded as postoral structures.

THE FEEDING FURROW

Between the bases of the velum and of the tentacular ridge a deep and rather wide furrow leads into the mouth from each side (Figs. 66, 67, 71). This furrow in the contracted specimens at hand is almost closed ventrally by overhanging parts of the said appendages, but above these it forms a rather wide canal filled with bottom material. This filling might be accidental, as matter intruded during dredging would not easily be washed out again, but it might also mean that this furrow is the main feeding tract, being the natural course for the bottom material to follow when it has been picked up by the velum or tentacles or both.

The epithelium in the furrow is irregularly folded, probably because of contraction, and its state of preservation is poor. However, it appears much like that of the adjacent parts of the velum and of the tentacles. Scattered ciliated cells are present as on the tentacles, but it has not been possible to find any place with a stronger ciliation within this furrow proper. However, attention should be paid to the strong ciliation on the velum proper and on the corner of the tentacular ridge bordering on the furrow ventrally (Fig. 72).

THE LIPS

The lips are unpaired structures and surround the mouth from the anterior and posterior side, respectively. On each side there is a cleft between the anterior and the posterior lip, through which the mouth cavity communicates with the feeding furrow (Figs. 66, 67, 71).

The anterior ("upper") lip is crescent-shaped and appears strongly contracted in the preserved specimens, being highly folded transversally. From the anterior ridge of the velum this lip is separated by a shallow furrow only, so that its median parts are almost directly continuous with the preoral body wall (Fig. 81). The lateral corners of the lip project to form free points on each side of the mouth medially to the bases of the velar flaps (Fig. 66). The anterior lip consists of a parenchyma rich in muscle fibres and covered by a high, columnar epithelium. On the inner (oral) side of the lip this epithelium is covered by a cuticle about 15 μ thick. More deeply inside the mouth the thickness suddenly increases to 50-100 μ, thereby forming a cuticular plate covering the ventral ("anterior") wall of the pharynx (Figs. 76, 81, 90). This thick cuticular plate continues posteriorly on each side along the wall of the oral cavity, forming a strip of strengthened cuticle about 50-70 μ thick. These strips end up in jaw-like projections covering the lateral points of the anterior lip (Figs. 66, 71, 77). Externally the anterior lip is covered by a cuticle only 3-10 μ thick. This thin external cuticle is soft, as is also that of the median parts of the oral side, for the median part of the lip is strongly folded transversely. The highly cuticularized parts inside the mouth and in the pharynx form a kind of upper jaw, completely separated from the cuticularized parts of the posterior lip.

The posterior ("lower") lip is only a narrow shelf on the oral side of the transverse part of the tentacular ridge (Figs. 66, 67, 74), forming a sort of anteriorly placed bridge across the median notch of the latter (Fig. 71). It is marked off laterally from the tentacular ridge by a distinct furrow. The lip is covered by a cuticle about 40 μ high in the central parts, the thickness decreasing to 5-10 μ laterally. This cuticular plate of the posterior lip – or lower jaw – continues inwards along the posterior wall of the oral cavity into the subradular sac (Fig. 81).

COMPARATIVE REMARKS

Although we shall not enter into any detailed discussion, some homologies appear so evident that they can hardly be left uncommented on.

The preoral tentacles in *Neopilina,* being preoral sense organs innervated directly from the cerebral ganglia, are obviously homologous to the tentacles of prosobranch gastropods.

The velum, being a preoral, transversal, ciliated fold, is evidently a homologon of the velum of mollusc larvae. Consequently, the lateral flaps of the velum in *Neopilina* should be homologous to the outer labial palps in bivalves. The upper lip in the

latter, however, could be either corresponding to the anterior velar ridge or to the anterior lip in our animal.

Similarly, the postoral tentacles must be equivalents to the inner labial palps of bivalves, being postoral and connected with the posterior lip in both groups. The innervation and ontogenetic development of the arms of cephalopods and of the captacula of scaphopods would seem to indicate that these organs have the same origin.

The cuticularized parts in front of and behind the mouth in *Neopilina* have been called jaws in the above because they seem to be homologous to the jaws in so many other molluscs. A strengthening of both jaws in *Neopilina* could easily transform this whole structure into something like the beak of cephalopods. A reduction of the lower lip and of the medial part of the upper lip would produce paired jaws as e. g. in opisthobranch gastropods, and the reduction of the lateral parts of the upper jaw would result in the unpaired ones of many other gastropods.

THE DIGESTIVE SYSTEM

THE ORAL CAVITY AND THE SUBRADULAR SAC

The oral cavity may be defined as the space inside the mouth opening, but its lumen is rather narrow and the space not very well delimited. The anterior and posterior walls are formed by the respective lips. Laterally, the cavity receives the feeding furrow (Figs. 66, 71). The dorsal wall of the cavity looks different in the two sectioned specimens because of the different position of the radula and the subradular organ. In Spec. IV the radula is protracted so as to form part of the roof of the cavity, and the subradular organ is retracted into a blind sac opening through a narrow slit just at the base of the posterior lip (Fig. 81). In Spec. III the radula is retracted so that it does not reach into the oral cavity, but ends in front of it in the roof of the pharynx. In this specimen the subradular sac is more everted and the subradular organ lies uncovered in the roof of the oral cavity.

The lining of the oral cavity is a columnar epithelium covered by a cuticle on the anterior and posterior lips as described above. The roof of the cavity can be invaginated into the subradular sac as seen in Fig. 81. It is a naked, single-layered epithelium with numerous glandular cells. Their secretory material is visible as a string of granules extending from the cell base almost to the surface to end in a bigger oblong droplet.

The subradular sac is a broad pouch opening into the dorso-posterior part of the oral cavity. If retracted as shown in Fig. 81, it is partially subdivided into two sacs by a transverse fold which contains the unpaired subradular ganglion and the subradular nerves (Fig. 136). If protracted, the anterior wall of the sac may form the roof of the oral cavity as in Spec. III. Then the subradular organ is exposed towards the oral cavity, and the transverse fold subdividing the organ is not so distinct (Fig. 82).

The lumen of the subradular sac is lined by a single layer of high columnar epithelial cells. These cells are particularly high (more than 200 μ) in the part regarded as the subradular organ (Fig. 81), so identified by us because it is closely connected with the subradular ganglion. Admittedly, however, the sensory cells in this organ could not be identified in the material at disposal. The cuticle of the posterior lip continues along the posterior wall of the oral cavity on to the posterior wall of the subradular sac. This sac is immediately surrounded by the blood sinuses of the anterior body region (Figs. 11, 129).

THE PHARYNX AND THE RADULA APPARATUS

The pharynx. From the oral cavity the pharynx runs anteriorly towards the frontal shell wall, then turning dorsally and finally dorso-caudally to continue into the oesophagus near the apical region of the shell. Throughout, the lumen of the pharynx has its greatest extension in the transverse direction, in contrast to the oesophagus, which is strongly compressed and has a vertical, cleft-like lumen. The pharynx, as defined in this way, corresponds to the part called pharynx in chitons, but we do not intend to enter into any discussion here as to whether it contains entodermal elements as in the latter group (HAMMARSTEN and RUNNSTRÖM 1925). For descriptive purposes the horizontal part of the pharynx may be distinguished from its vertical part.

The former, horizontal part of the pharynx is dorso-ventrally flattened. Laterally, the dorsal and ventral walls lie in direct contact with each other

(Fig. 90, right). The dorsal wall is lined with the broad subradular membrane, which, in its median part, carries the teeth of the radula. These structures will be described separately below. The ventral ("anterior") wall is connected with the preoral body wall by means of numerous small muscular strands (Fig. 127). Its median parts are covered by a 50-90 μ thick epithelium, carrying the strong cuticular plate which is continuous with the covering of the anterior lip. This plate must be the counterpart against which the radula acts. Laterally, the ventral wall is soft, without a cuticle, and the epithelial cells decrease in height down to 8-12 μ most laterally. Apparently this soft part of the ventral wall makes the subradular membrane movable in relation to the ventral ("anterior") cuticular plate.

The vertical part of the pharynx has a broad lumen which is crescent-shaped in cross sections (Figs. 89, 129). The wall consists of a connective tissue membrane and a high columnar epithelium, with a very distinct row of basal granules under the free surface (Fig. 102). These, together with a very distinct striation in the peripheral part of the cells, indicate the presence of a ciliation. Actually, long cilia have been observed in a few places. The nuclei with very distinct nucleoles are placed basally in the cells.

There are three kinds of structures connected with the pharynx of *Neopilina* (Fig. 81), viz. the *anterior salivary gland* opening into the antero-ventral bend of the pharynx between the horizontal and the vertical part, the *radular sheath* lying dorsally to the oral cavity and the subradular sac and opening into the vertical part of the pharynx, and the *pharyngeal diverticula* joining the pharynx from each side just before it turns into the oesophagus.

The anterior salivary gland is an unpaired structure, situated in the pallial fold in front of the mouth (Fig. 81). The term has been chosen because of the apparent homology with the so-called salivary gland in chitons (FRETTER 1937). The gland projects as a diverticulum from the anterior wall of the antero-ventral bend of the pharynx. The gland is broad and its lumen is in open communication with that of the pharynx (Fig. 92). The posterior ("ventral") wall of the diverticulum is even and smoth, covered by a high columnar epithelium with a cuticle, continuous with that of the ventral wall of the pharynx (Fig. 81). The anterior wall forms several strong vertical folds. Its high columnar epithelium seems secretory, the basal parts of the cells staining much more intensely than the distal parts. Two kinds of cells are present, viz. narrow ciliated ones broadening only at the surface, and slender secretory ones appearing as lighter interspaces with indistinct contents.

The radula sheath is a very large posteriorly directed diverticulum arising from the vertical part of the pharynx (Fig. 81). In both specimens, the distal end is irregularly coiled (Fig. 84). The coils are placed mainly to the left in one specimen and to the right in the other one sectioned. The sheath is approximately cylindrical, a little depressed "dorso-ventrally". Its diameter is 0.4-0.5 millimetres. Only, the proximal part of the sheath, opening into the pharynx, is a broad plate-like structure as in chitons. There is a very sudden change from the cylindrical part to the inflated one, the latter having a constant width of 2.6 millimetres down to the junction with the equally broad pharynx (Fig. 83). In the inflated part we may, for descriptive purposes, distinguish a central lumen containing the radula, from the two lateral wings called the radula diverticula.

The radula sheath is suspended in the blood sinuses of the anterior body region. Just distally to the inflated part, a small transverse muscle appears to stabilize the proximal parts of the cylindrical sheath in a median position, whereas the more distal parts are allowed to coil up irregularly (Figs. 83, 84). The sheath is surrounded by a hardly detectable membrane of connective tissue, which measures about 1 μ only. Inside this membrane the sheath consists of an epithelium which in the distal part secretes the radula. The arrangement of the cells in the distal part of the sheath is tolerably distinct (Fig. 91). That side of the tube which, further down, becomes the ventral side, has a lower and smooth epithelium. Dorsally, the epithelium is very high, forming several longitudinal ridges which tend to fill up the lumen. When the teeth are formed in the remaining clefts of the original lumen, they are at first slightly stainable only, but further downwards in the sheath they stain darkly with hematoxylin. Still further down their own yellow-brown colour can be seen. As soon as the teeth have appeared, the arrangement of the epithelium becomes less distinct. There is still a smooth basal epithelium with almost cubical cells under the teeth, but the space between these is filled by a complicated mass of cells hanging down from the dorsal wall. Soon after the teeth have appeared, a fairly thick subradular membrane can be seen between their basal parts, apparently secreted by the smooth ventral epithelium.

Peculiar features are the large number of almost invisible, colourless rows of teeth contained in the distal half of the sheath, and the absence of even rudimentary teeth in the first quarter of a millimetre, together with the enormous numbers of cells apparently involved in the formation of the single teeth (Fig. 91).

A cross section of the sheath (Fig. 93) just behind the transition to the inflated part shows the smooth basal epithelium of its bottom and sides to be covered by a hyaline subradular membrane. The teeth are situated on this membrane, the lateral ones being placed high up on the side walls. The lumen is filled with the invaded epithelial cells of the dorsal wall, but the arrangement of these cells could not be made out in the available material.

The picture changes abruptly at the transition to the inflated part. In the latter the wall of the sheath extends into a broad and flat diverticulum on each side (Fig. 94). The radular teeth and the original subradular membrane are situated in a 0.5 millimetre broad median groove in which the median teeth occupy the bottom, whereas the lateral ones are placed along the sides (Figs. 95, 99). The subradular membrane rests on a low epithelium of cubical cells, which continues laterally to cover the smooth ventral wall of the radula diverticula. This epithelium secretes the secondary subradular membrane, which is continuous with the primary one but much broader, so that it reaches the lateral extremities of the diverticula (Figs. 83, 94). The dorsal wall of the inflated part has a higher and highly folded epithelium.

When the dilated part of the radula sheath opens into the vertical part of the pharynx, the subradular membrane with the radular teeth bends first ventrally and then caudally, following the dorsal ("posterior") wall of the pharynx (Fig. 81). All the way the epithelium under the subradular membrane consists of cubical cells.

The radula is a very strong structure, 14 millimetres long in the rather small Spec. VI, occupying almost the whole width of the primary subradular membrane. Each of the 45 rows forms a V-shaped figure with the tip of the V pointing towards the mouth (Fig. 88). The oldest 10-11 rows are placed in the part of the radula to which the broad secondary subradular membrane is attached, whereas the remaining rows are contained in the cylindrical radula sheath. The youngest 10 rows are more hyaline than the others and seem to be in a state of formation, and even the next 5 rows might not be quite finished. The following 20 rows seem to be fully formed, but not yet involved in the actual feeding function, which apparently is confined to the oldest 10 rows, where denudation is more or less distinct.

Each row has the formula 5-1-5 (Fig. 88), its lateral teeth varying much in shape. The median tooth is a slender, rod-like structure with almost no hook at all. From its somewhat broadened base a median, rounded keel arises, increasing gradually in width and height until most orally it takes up the whole width of the tooth. The whole median tooth measures 0.15 × 0.02 mm. Close to the median tooth the first lateral one is placed. It is somewhat larger, but of almost the same shape, with the exception that the oral end forms a rudimentary hook. The size of this first lateral tooth is 0.2 × 0.03 mm.

The second lateral tooth is a strong and broad hook with a blunt free end. Its base is almost 0.1 mm broad and 0.35 mm long exclusive of the free hook. This hook seems to project about 0.1 mm from the subradular membrane. Its tip is almost at the same level as that of the first lateral tooth.

The third lateral tooth is of almost the same shape, still more aboral in position, and with a much more prominent hook. It is the largest tooth in the radula. It is followed immediately by a membranous tooth, the comb-tooth or 4th lateral, which is of almost the same length and projects equally far into the lumen. The base of the comb-tooth, however, is narrow and rhomboidal, placed closely along the outer side of the base of the 3rd lateral. From this small and rather weak base the tooth itself extends inwards aborally or laterally to the 3rd one. Instead of a hook, the comb-tooth ends up in a transversely cut margin, slit up into some 40 long and curved denticles pointing aborally (Fig. 87). Only the outermost lateral denticles decrease in size, the inner about 20 ones being of almost equal length.

The fifth lateral tooth has a triangular base of the same, not very impressive thickness throughout, and a rudimentary hook indicated merely as an elongate and slightly curved, gently rounded elevation of the same height from one end to the other. The width of this rudimentary hook is almost the same as that of the second and third lateral.

In the pharynx the central parts of the subradular membrane carrying the radular teeth is 30-100 μ thick, whereas the lateral wings formed in the radula diverticula are 10-12 μ, or still less towards the margin. The membrane consists of a hyaline layer of considerable thickness, and a thin stainable layer at the surface. The latter layer, which stains blue with

the phosphortungstic acid hematoxylin, measures 5-15 μ in the central part and about 2 μ in the lateral parts of the membrane.

The deep median groove formed by the subradular membrane in the inflated part of the radula sheath is straightened out in the roof of the pharynx. In transverse sections the groove has a fairly flat bottom bordered laterally by almost vertical walls (Fig. 95). The really hook-like teeth, viz. the median and the three inner laterals, are all placed on the plane bottom of this radular groove. The fourth, comb-like lateral is situated right in the angle between the bottom and the sides, and the 5th lateral tooth sits on the side wall (Fig. 99). Since the groove is so distinct in the inflated part of the sheath, but is straightened out when bent down into the pharynx, the comb-like teeth must make some transverse movements when the radula is used. Although we cannot analyze in detail the function of the radula, attention should be called to the position of the two big hooks immediately behind each other, so that all the big hooks together form two symmetrically placed rows all along the radula (Fig. 100). Hereby a suitable arrangement for food transport up along the pharynx is established. The sweeping movements of the comb-teeth may in some unknown way assist in this transport. Observations on the freshly dissected radulae as well as on the sections revealed quite an amount of bottom material lying aborally of each hook, including the comb.

The supportive mechanism of the radula is very similar to that of chitons. In the angle between the pharynx and the radula sheath there is a transverse bar consisting of a median, unpaired muscle and a pair of short, rod-like cartilages over which the subradular membrane can slide (Figs. 81, 82, 95). The cartilaginous ends of this bar are intimately connected with a pair of radula vesicles, which are fixed and apparently also moved by a number of muscles as described on page 41 (Figs. 83, 90, 128).

The medial ends of the paired cartilages are connected over the mid-line by the above-mentioned m. impar radulae, and their lateral ends partly surround the radula vesicles. The tissue of the cartilaginous rods looks vesicular, with intercellular walls between the numerous bladders which contain the cell bodies (Fig. 96). This tissue appears to be a kind of primitive cartilage, corresponding to that found in the radula apparatus of gastropods and chitons, although admittedly no specific cartilage stains have been used for proving this statement.

The radula vesicles are fairly slender, spindle-shaped structures. The antero-medial end of each sticks in the cartilage of the transversal bar. The other end points postero-laterally and is fixed to the ventral body wall by several muscles (Fig. 83). The vesicle also serves as an insertion point for the big retractors of the radula and for some other muscles (pp. 39-40). Certainly, these radula vesicles must be rigid in the living animal to serve as a kind of skeleton. The walls of the vesicles are about 25 μ thick and consist of several lamellae of connective tissue. However, the vesicles have collapsed in both of the sectioned specimens (Fig. 94). The walls appear wrinkled and the connective tissue lamellae are no longer closely attached to each other. Probably these vesicles in the living animal are filled with a fluid, the pressure of which distends them to make them rigid. In chitons, the homologous radula vesicles have been said to be filled with gas (PLATE 1898, p. 40), but this cannot hold good in *Neopilina,* which lives at a depth of 3600 m. in the ocean, where gas secretion would be more than difficult. So we reexamined the contents of these vesicles in a living chitonid, *Lepidopleurus asellus,* from Danish shallow waters. No gas was present, but the vesicles were hard and distended by their fluid contents.

These bladders – like those in chitons – must serve as a kind of skeleton to which attach muscles mainly with the following two functions. Some are concerned with the movements of the radula membrane, others move and fix the vesicles in different positions. Since the vesicles are stiff and firmly connected with the radula cartilage, their movements will be transferred immediately to the transverse bar, thus assisting in the manipulation of the radula.

The pharyngeal diverticula. The pharynx is broad and flattened in the region above the radula sheath, but high up under the shell and immediately in front of the oesophagus the pharyngeal walls push out into a pair of extensive sacs. These pharyngeal diverticula (Figs. 81, 85, 86, 89, 129) extend closely below the dorsal shell epithelium in the anterior part of the animal, and their frontal pouches reach almost to the apex. The lumen of these diverticula is narrow and cleft-like in some places in the sectioned specimens. Unfortunately both of these are somewhat damaged in the apical region, a fact which together with the fairly complicated morphology of these organs makes the reconstruction in Fig. 86 less reliable in some details.

The pharyngeal diverticulum on each side is a flattened sac communicating with the pharynx just

behind the apex. It has several secondary pockets, but there are three main pouches on each side (Fig. 86), namely (1) a caudal one lying like a flattened tube above the liver and the intestine, just under the shell, and continuing to the level of the stomach, (2) an anterior pouch on each side from the frontal margin of the primary pharyngeal diverticulum. The two anterior pouches meet in the mid-line in front of the pharynx just below the apex. (3) A pair of dorsomedial pouches starting from the dorsal surfaces of the primary diverticula. They meet in the mid-line above the oesophagus.

The epithelium of the pharyngeal diverticula is quite different from that of the pharynx proper and the oesophagus, being a low columnar one, or even cubical, and 10-30 μ high (Fig. 103). This epithelium is very similar to that of the dorsal coelomic cavities, but it does not contain pigment. It was not possible to detect structurally different parts of this badly preserved epithelium. However, the openings of the diverticula into the pharynx are lined with an epithelium very similar to that of the pharynx proper, but its cells contain big granules in their distal half (Fig. 104).

THE OESOPHAGUS

The oesophagus is compressed so much that its lumen forms a vertical slit (Fig. 8). From its point of junction with the pharynx immediately behind the openings of the pharyngeal diverticula (Fig. 85) the oesophagus passes almost straight caudally and a little downwards, gradually withdrawing from the vicinity of the shell. It is covered by the dorsomedial pouches of the pharyngeal diverticula, and it is surrounded on both sides by the liver. Passing above the propodial area it runs ventrally of the intestinal loops and becomes separated from the ventral body wall only by some lobules of the liver. In the region above the anterior foot margin the oesophagus opens into the stomach.

The wall consists of a very thin membrane of connective tissue and a very high epithelium, the cells of which are about 60 μ high and 4 μ broad (Fig. 101). Basally in the cells a 10 μ high zone of a more stainable cytoplasm is found. Next, the nuclei are found, followed by a light-staining granulated zone occupying the middle half of the cells. The distal end looks almost exactly like that of the pharyngeal cells with strong striation and very dark basal granules. A dense ciliation has been clearly observed in the oesophagus, the cilia being half as long as the cells themselves.

THE STOMACH AND THE LIVER

The stomach is median, situated above the anterior foot region, partly in contact with the ventral body wall (Fig. 98). It is surrounded latero-ventrally by the gonad, laterally by the liver, and dorsally by the intestinal loops. The stomach is roughly triangular in shape, the broad posterior wall forming the base of the triangle (Fig. 85). The oesophagus opens at the opposite, anterior angle. The paired liver opens through long, slit-like openings along the two sides of the triangle. The intestine starts from the posterior wall near the mid-line. Dorsally to its exit there is a blind pocket in which a crystalline style is formed.

The epithelial lining of the stomach, inside a thin connective tissue membrane, is very like that of the oesophagus. The broad connections with the liver on each side (Fig. 98) makes it necessary to define the stomach as the part which is lined by the oesophageal type of epithelium, as indicated in Fig. 85. Only, the stomach epithelium does not reach as far laterally on the ventral side as on the dorsal one shown in the figure.

The crystalline style is very distinct in Spec. III, but poorly preserved in Spec. IV. Its position is dorso-median in the stomach. The posterior end sticks in the blind pocket above the exit of the intestine, and the anterior end extends to the vicinity of the entrance of the oesophagus. Probably the style is formed in the blind pocket, the strongly ciliated epithelium of which differs from that of the stomach proper merely in being somewhat lower (about 40 μ high) and with somewhat broader cells (5-6 μ). The strong ciliation in the pocket would seem to be sufficient to rotate the crystalline style in the usual manner.

In transverse sections the style appears to consist of several concentric layers (Fig. 97), which, however, are only cross sections of cornet-shaped membranes sticking in each other with the points directed caudally. The point of the final cornet sticks in the blind pocket above the intestine. All this indicates that the style is formed in the blind pocket and is continuously pushed forwards towards the aperture of the oesophagus, but it seems to be dissolved before reaching this point. At any rate it does not enter the oesophagus. We have failed to find any plate anteriorly in the stomach against which the style could work. The facts give little support to the idea that the structure should instead be a mucous string from the oesophagus, like the one present in some

other molluscs, for then it would enter the intestine (See discussion following the paper of LEMCHE and WINGSTRAND, 1959). Moreover, the orientation of the cornet-shaped membranes indicates that the style is formed caudally. A mucous string coming from the oesophagus would hardly show this structure.

The liver (hepatopancreas) is paired and opens into the stomach by a long, slit-like opening on each side. Each liver is extensively ramified, much more than shown in Fig. 85, in which only the most apparent lobules are indicated. The position of the liver is lateral to the stomach and the oesophagus (Figs. 8, 89). Caudally it covers the anterior part of the gonad and is itself covered by the intestinal loops. It extends to the segmental muscles in a lateral direction, and big lobules reach forwards almost to the pharynx. The anterior parts of the liver are separated from the dorsal body wall only by the inflated pharyngeal diverticula (Fig. 86).

The epithelium of the liver consists of cells which are 80-130 μ high and 10-15 μ broad. The cells have a very stainable basal part, whereas peripherally they contain several big granules each (Fig. 107). A yellowish-brown colour may perhaps indicate that the granules contain pigment. The size of these spheroid granules is usually between 7 and 10 μ, but some smaller granules are also present. Usually 5-10 granules form a single row in the peripheral part of each cell (Fig. 108). The small granules, when present, are all situated in the basal part of the row, i.e. near the stainable part of the cell. The peripheral end of the cell often projects like a tongue into the lumen. Often the spherules have dark centres and light peripheral zones, but their nature could not be established with certainty.

There is little content in the lumen of the liver whereas the stomach is well filled.

THE INTESTINE

The exit of the intestine from the stomach is situated in the mid-line near the ventral body wall below the blind sac of the crystalline style (Fig. 85). From there, the intestine immediately turns to the left to coil up in an anti-clockwise direction (as seen from above). There are six coils, arranged so as to form a flattened cone with the small coils dorsally (Figs. 9, 86, 157). The first two coils are the widest, the following ones becoming successively smaller and situated more dorsally, but the arrangement is somewhat irregular. The last (6th) coil forms the top of the cone ending in the rectum which runs straight caudally near the median line to the anal opening. The rectum, like other dorsally situated parts of the intestine, lies close to the dorsal body wall, separated from it by the dorsal coelomic cavity.

The coils of the intestine occupy most of the space above the foot and inside the segmental muscles. They are suspended in the peri-intestinal blood sinus (Figs. 9, 157, 167). Ventrally the coils rest directly on the ventral body wall or are separated from it by the gonads, anteriorly also by the stomach, the liver, and the oesophagus.

Histology of the intestine. The lumen of the intestine is circular or oval in cross sections, and there are no folds of any kind. The wall consists of a thin membrane of connective tissue directly bordering on the hemocoelic body cavity, and an epithelium lining the lumen. The connective tissue membrane is very thin (1-5 μ), but may be stratified in places. The histology changes gradually in a characteristic manner along the intestine. Just behind the exit from the stomach, the epithelium is very high and is similar to that of the stomach. The cells are about 45 μ high and 4-5 μ broad. The nuclei are distinct with prominent nucleoles contrary to conditions in the stomach. The surface is probably ciliated since basal granules are easily seen.

Already after half a coil the epithelium is only 25-35 μ high, decreasing still more through the 1st and 2nd coils, so that it reaches the final height of 10-15 μ in the 3rd to the 6th coils (Figs. 105, 106). The cells also become a little broader. They are 10-15 μ broad in some places in the 3rd coil, and 6-10 μ in the 4th to 6th coils. The basal granules are very distinct all over, and cilia have been observed with certainty.

The two last coils differ in that granules appear in the plasm of the cells. In the 5th coil the granules are rather sparse, becoming numerous in the 6th one. They are very dark and look like pigment. Usually they form a small group in the middle of the cell (Fig. 106).

The rectum has an epithelium similar to that of the last coiled part of the intestine. The dark-staining granules are numerous in the cells, which are a little higher than before (15-30 μ). Ciliation is distinctly present (Fig. 108 A).

Above, we have only described the predominant ciliated cells of the intestine, but this should not be taken to mean that no other cell types are present. Some observations in the poorly preserved material made us suspect the presence of some sort of secretory cells – as would, of course, be expected.

The anal opening is situated on a low papilla in the pallial groove behind the foot. The epithelium of the rectum is very uneven and variable in height just before the anal opening (15-60 μ). The very lips of the opening are covered by a ciliated epithelium, about 100 μ high (Fig. 109).

COMPARATIVE REMARKS

The oesophagus, the stomach, the liver, and the intestine of *Neopilina* is of the ordinary mollusc type. The distinctly paired and symmetrical liver recalls conditions in bivalves. In the presence of a crystalline style *Neopilina* differs from the recent polyplacophorans and is similar to many bivalves and some gastropods feeding on finely dispersed matter. The presence of such a style in the three molluscan groups Gastropoda, Bivalvia, and Tryblidiacea may indicate that this structure is a phylogenetically old feature in molluscs, although lost in a number of lines.

The pharyngeal apparatus, including the pharynx proper, the subradular organ, the anterior salivary gland, the radula apparatus, and the pharyngeal diverticula, shows much the same development in *Neopilina* and chitons (Compare figs. 81 and 169). Features common to *Neopilina* and chitons, but absent or problematic in other molluscs, are the presence of radula vesicles, the anterior position of the salivary glands, the great development of the pharyngeal diverticula, and the morphology of the subradular organ. On the other hand, *Neopilina* differs from chitons in having a coiled, not a straight radula sheath, and a symmetrical liver (cf. FRETTER 1937).

The morphology of the radula teeth is such as to allow a comparison with at least both polyplacophorans and gastropods. The median tooth, the big lateral hooks, and the triangular 5th lateral are very similar to teeth present in the radula of chitons. The comb-like 4th lateral of *Neopilina* is of a type indicated also in the development of the 5th lateral in *Nuttalochiton* and *Tonicella* (PLATE 1899). On the other hand, each row in the chitonid radula contains 8 + 1 + 8 teeth.

Comparison with gastropods suggests that the docoglossan type of teeth are related to the type represented by the median and three inner laterals of *Neopilina,* being hooked rods firmly fixed to the subradular membrane. Comparison with the typical rhipidoglossan radula opens up the possibility that the comb of slender marginal teeth in the latter corresponds to the single comb-like tooth in *Neopilina.* Both are situated on the sides of the radula furrow and are moved transversely when the radula functions. On this assumption it must be supposed that each of the denticles of the 4th lateral of *Neopilina* has become independent in the Rhipidoglossa, but there is another – and just as plausible – interpretation. In *Pleurotomaria* numerous bristles are present on the tips of some of the many lateral or marginal teeth (WOODWARD 1901), a development which might not be too different from that of the 4th lateral of *Neopilina.* So we leave the problem open.

THE MUSCULAR SYSTEM

This account of the muscular system is based mainly on the sectioned specimens (III and IV), but we have made quite a number of comparisons, particularly with the dissected Spec. X. The state of preservation of the muscles in the sections is excellent, although they have been fixed in a more or less contracted state. So we did not hesitate to carry out the examination in as much detail as ever possible, feeling that the muscular system is of fundamental importance in any discussion of the segmentation of this animal, and for its comparison with the fossil tryblidians. The presence of two series of sections, one horizontal and one transversal, facilitated the study of the different muscles considerably, because fibres difficult to trace in one series could often be clearly followed in the other. The two specimens are almost exactly alike in their myology which, of course, indicates that the structures described are typical of the species. Some differences between the two specimens in a few small muscles were noticed and will be mentioned in the text.

The complexity of the muscular system made it necessary to apply particular methods. First, the gross anatomy of the muscles was laid down by means of wax-plate reconstructions including the muscles, the wall of the pallial groove, the foot, and some other organs to which muscles attach (oesophagus, radula apparatus, etc.). The entire animal was reconstructed in 25 times enlargement from the horizontal series (IV), and the left side of the other specimen (III) again in 50 times enlargement. In both cases the orientation of the wax-plates was

based on photographs of the intact specimen, taken when it had been embedded in celloidin.

The diagrams illustrating this chapter are graphic reconstructions based on the transversal series (III), but the presence and course of the muscles shown have been checked on Spec. IV and on the wax-plate reconstructions.

For descriptive purposes the musculature is here divided into two main parts, viz. that of the body proper and that of the anterior region. The musculature of the body consists of three major subdivisions, viz. (1) the big pedal retractors, (2) the three circular (longitudinal) systems in the mantle and the foot, and (3) the gill muscles and some other small ones in the mantle fold and the foot.

In the anterior region we can distinguish three major subdivisions, viz. (1) the anterior continuation of the subepithelial circular muscle system, (2) the retractors of the velum, of the tentacles, and of the mouth region, and (3) the radular and other buccal muscles.

In most cases the nomenclature used is plainly descriptive, and only in a few cases have we ventured to use the terms of polyplacophoran anatomy. We have done this when the homology with chitonid muscles was evident, each time commenting on this in the text.

The lettering is made so that the big segmental muscles of the body proper are called A, B, C, ... H, whereas the smaller ones attaching to the shell in their neighbourhood are called A_1, B_1, A_2, B_2, etc. (Fig. 121). The three groups of muscle attachments to the shell in the anterior region are called X, Y, and Z (Fig. 84) in order to avoid any figures which could suggest segmental numbers, as we do not wish here to enter into any speculation about head segmentation.

HISTOLOGICAL REMARKS

In all the different kind of muscle fibres, the fibrils are packed together into a dense central bundle surrounded by a narrow sheath of sarcoplasm. There are fairly few nuclei, and it is our general impression that there is only one nucleus present in each fibre. These nuclei are more or less elongate in the direction of the muscle and are situated in the superficial sarcoplasm. Nuclei situated in the centre of the bundles of fibrils have not been observed. The length of the fibres varies as usual with the length of the muscle itself. The diameter of the fibres varies considerably, from 0.3 to 15 μ, and can be used, together with other histological details, for a rough classification.

(1) *The buccal musculature,* including all muscles connected with the radula apparatus and the pharynx, has the thickest fibres with a diameter of 6-15 μ, considerable variation occuring within one and the same muscle. The fibres are characterized by the presence in their plasm of small granules which, in the celloidin sections stained with phosphotungstic acid hematoxylin, assume a blue black colour similar to that of the nuclei (Fig. 115). Some buccal musculature shows a cross striation which is particularly distinct in the radula retractors (Fig. 116), but it has been observed in other buccal muscles as well, when their orientation and plane of sectioning was suitable. We do not know for certain whether all or only some of the buccal muscles are striated.

(2) *The big somatic muscles,* including the pedal retractors, the large circular muscles of the foot, and those associated with the gills, the velum, etc., consist of very closely packed fibres measuring 4-8 μ in diameter (Figs. 112, 113). Their bundles of fibrils stain a deep red and are highly refringent, much more so than in the buccal muscles. In spite of careful search, cross striation could not be detected.

(3) *Subepithelial and diffuse muscles fibres* in the foot and in the mantle are from 0.3 to 3 μ broad. The bigger of these fibres have a central bundle of fibrils and show the same staining properties as those mentioned above, so that their interpretation seems to be reasonably well founded. From such fibres there seems to be a continuous series of thinner ones down to the very smallest. It is doubtful whether all the thinnest ones are truly contractile, or whether some of them are connective tissue elements. A dense, continuous layer of parallel, definitely muscular elements is present beneath the epithelium of the inner part of the pallial groove (Fig. 114). Similar fibres form a diffuse system in the peripheral part of the mantle and in the margin of the foot. The central parts of the latter contain a fairly thin plate of straight muscle fibres in a horizontal, criss-cross arrangement (Fig. 117). Branched muscle fibres have been observed with certainty in the gills (Fig. 118) and may well occur elsewhere, too.

Arrangement of the fibres in the muscles. The material is not particularly suitable for studies of the associated connective tissue. In the big pedal retractors, etc., the fibres are closely packed with rather few connective tissue nuclei present. The latter are either round or elongate at right angles to

the direction of the muscles. Similarly, the connective tissue fibres appear to be transversely orientated, the superficial ones thus surrounding the entire muscle. The buccal muscles have a looser structure and contain considerably more connective tissue.

The attachment of the muscles to the shell is the one usual in molluscs. In the big somatic muscles the stainable part of the fibres ends at a considerable distance from the shell and is continued to the epithelium at the point of attachment by a fibrous tendon staining only slightly in our preparations (Fig. 110). The epithelium involved has been described on page 18. It is traversed by tono-fibrils placed as continuations of the fibrils of the tendon.

The smaller muscles attaching to the shell, and also the buccal muscles, have only very short or no tendinous parts, but the appearance of the mantle epithelium with its tono-fibrils is the same as that described above (Fig. 111).

THE MUSCLES OF THE BODY PROPER

The three main systems of musculature of the body proper will be dealt with separately here, as follows: (1) the eight pairs of big, segmental foot retractors, (2) the three circular systems with their branches to the shell, and (3) the gill muscles, the small pallial muscles, and the diffuse muscle fibres of the foot and mantle.

Since, like most other molluscs, *Neopilina* has a single continuous shell, it is not surprising that it completely lacks the complex system of dorsal muscles characteristic of the Polyplacophora, which system, in the latter group, serves only to move the shell pieces relative to each other.

The Segmental Foot Retractors

The 8 pairs of foot retractors attaching to the shell are a most conspicuous feature (Figs. 121, 126). The first three pairs attach to the shell a little higher up on the sides (Fig. 89) than the following five pairs (Figs. 11, 123). The points of attachment of the former are in front of the transversal plane through the anterior margin of the foot. They are also placed a little closer together than the next ones and therefore can be said to form a group of three on each side. The other five pairs follow in regular sequence to the hindmost one, which is situated just laterally to the rectum (Figs. 121, 130).

Each retractor consists of two different portions clearly homologous with the *m. latero-pedalis* and *m. medio-pedalis,* respectively, in chitonids (cf. HOFFMANN 1930 pp. 222-224) (Figs. 166-167). When reaching the foot the m. medio-pedalis becomes the more dorsal one. It runs dorsally to the m. obliquus anterior of the following segment (Figs. 110, 119) and, when passing above the foot margin, ramifies dorsally to the m. circularis pedis to spread in the space between the wall of the peri-intestinal blood sinus and the pedal nerve cord (Figs. 120, 122).

The m. latero-pedalis spreads more ventrally and laterally in the foot. It runs ventrally to the obliquus anterior of the following segment and of the majority of bundles belonging to the m. circularis pedis, ramifying partly in the muscular margin of the foot, partly more medially but always ventrally to the pedal nerve cord (Figs. 119, 122).

When reaching the foot margin the fibres of the m. latero-pedalis fan out to intermingle with the fibres from the same muscle of the neighbouring segments (Fig. 120). A horizontal section at a more ventral level, therefore, shows a continuous zone of retractor fibres passing down to the foot margin with no indication of the segmentation (Figs. 11, 123). The mm. medio-pedales behave similarly, forming a continuous ring of centrally directed fibres in the periphery of the foot, along the bottom of the peri-intestinal blood sinus (Fig. 120).

Since, in some fossil tryblidians, there are double muscle insertions on the shell corresponding to each foot-retractor portion as here described, the insertions of these muscles in *Neopilina* were analyzed thoroughly (Fig. 130). It was found that the m. medio-pedalis and m. latero-pedalis insert separately on the shell, but the two areas of attachment are confluent, and there may be some mixing of fibre bundles from the two portions. The areas of insertion are indicated in Fig. 130. In Muscle A, the two areas are well separated and distinct, the medio-pedalis inserting caudally to the latero-pedalis. In each of Muscles B-F the said areas are confluent, but the medio-pedalis inserts caudally of the latero-pedalis. Muscle G is remarkable on both sides of both of the sectioned specimens in that the medio-pedalis is double with one head inserting antero-laterally and the other caudo-medially to the latero-pedalis. In Muscle H the two portions are very difficult to follow and it is by no means certain that the areas marked in Fig. 130 are correct.

Whereas Muscles B-F are all very similar and differ only slightly from G and H, the first retractor (A) looks considerably different (Figs. 84, 120, 121). The m. latero-pedalis A behaves typically and ram-

ifies in the anterior margin of the foot. The m. medio-pedalis A has one portion running caudo-medially to the anterior part of the foot, ramifying dorsally to the pedal nerve cord like the typical medio-pedalis muscles, but another portion (m. oralis posterior) runs medially or antero-medially and acts as a retractor in the mouth region. One small band (m. transversalis A) branches off from the m. oralis posterior to form an unpaired transverse muscle in an inner ridge of the body wall above the propodial area (Figs. 84, 129). Another strong portion of the m. oralis posterior turns antero-medially and constitutes the main retractor of the velum (Figs. 127, 129). Other ramifications run to the body wall of the mouth region, and one small string passing down into the tentacle ridge seems to act as a tentacle retractor (Fig. 127).

As to the function, it is apparent that the mm. latero-pedales act as retractors of the foot margin and, together with the mm. medio-pedales, retract the foot as a whole. The opposite movements must be brought about by blood pressure as in other molluscs. The mm. medio-pedales A-C may also act as protractors and the medio-pedales F-H may similarly move the base of the foot caudally.

The Circular (Longitudinal) Systems

There are three distinct circular muscle systems in the body proper, viz. (1) the m. circularis pedis, forming an internal muscular ring in the peripheral part of the foot, (2) the m. circularis intermedius, a broad muscle band along the base of the foot near the bottom of the pallial groove, and (3) the m. circularis pallii, which forms a subepithelial membrane of circular fibres under the wall of the pallial groove (For orientation see Figs. 119 and 121). All these systems give off bundles attaching to the shell in different ways.

The m. circularis pedis forms a circular system of loosely packed, but strong muscle bundles in the peripheral part of the foot (Figs. 121, 126). The muscle does not give any immediate impression of being an anatomical unit and can be confused with ramifications of the foot retractors when the scattered muscle bands are seen in cross section. However, in horizontal sections and dissected specimens the fibres reveal their strict circular course and can be seen to form a system of their own, independent of the foot retractors (Fig. 121). The muscle separates the m. latero-pedalis from the m. medio-pedalis, but its dorsal and ventral fibres may intermingle with those of the said muscles (Fig. 119). The entire muscle is situated laterally to the pedal nerve cord which it follows all round the foot. Posteriorly, the muscle is continuous over the mid-line below the rectum, but at the anterior margin of the foot there is no or little such continuity. It is true that some fibres of the m. circularis pedis pass over to the other side anteriorly, but the greater number continue to the shell and do not merge with the circularis pedis of the other side (Figs. 121, 127).

In general the m. circularis pedis inserts on the shell by means of a great number of small muscle bands which are strictly segmentally arranged, but may show some variation in the anterior and posterior ends of the body. In addition some of the retractors of the buccal region seem to contribute to this muscle. In the typical segments, i.e. E and F, we find two shell insertions of branches connected with the m. circularis pedis. Because of their oblique antero-lateral or postero-lateral course they are called the m. obliquus anterior and m. obliquus posterior, respectively (Fig. 121). The majority of shell insertions of the m. circularis pedis appear to be referable to one or other of these categories. In addition a posterior retractor of the tentacles and of the velum (The m. cruciatus) fuses with the m. circularis pedis. This will be dealt with on p. 38 (Fig. 127).

The mm. obliquii anteriores are present in all segments from A to H, although that of Segment A differs a little from the following ones. A typical obliquus anterior in the middle body region inserts latero-caudally to the foot retractor, runs antero-medially under the latter to be flattened out as a broad and thin band along the wall of the pallial groove (Figs. 119, 121). Then it passes on antero-medially to the preceding segment, running between the latero-pedalis and medio-pedalis to fuse with the bundles of the m. circularis pedis. When the obliquus anterior is in contact with the wall of the pallial groove it gives off some fibres to the subepithelial circular muscle there (the m. circularis pallii). It can be very clearly seen that the m. obliquus anterior fuses with the m. circularis pedis and runs for at least some segments anteriorly as part of this muscle, but how far each fibre extends could not be stated.

The mm. obliquii anteriores of Segments B to H are all very similar and fit the above description very closely, disregarding the fact that the first two (B and C) are very small, and that the obliquii anteriores of B-D seem to lack connections with the m. circularis pallii. The so-called m. obliquus anterior

A differs considerably, and its interpretation is somewhat hypothetical. This muscle is considerably stronger than those of Segments B and C, and its point of insertion is not postero-lateral but antero-lateral to the corresponding foot retractor (A). Furthermore, its fibres take a more postero-medial, not antero-medial course, and cross over to the other side in front of the foot to fuse with the circularis pedis of that side (Figs. 127, 129). On the other hand, the obliquii anteriores B and C form a kind of transition from the typical obliquus muscles to the obliquus anterior A, as can be seen in the diagram. Also, the latter muscle is connected with the m. circularis pedis as are the typical members of this series. Therefore it would not seem hazardous to interpret this muscle as done here, accepting it as the first member of the series of obliquii anteriores.

The mm. obliquii posteriores are typical only in Segments E and F. The insertion is antero-lateral in relation to the corresponding foot retractor. From this insertion the muscle runs postero-medially beneath the foot retractor, crosses the obliquii anteriores of the two following segments in somewhat variable ways (Fig. 121) and passes along the wall of the pallial groove into the m. circularis pedis. Connections with the m. circularis pallii have not been seen with certainty. In the transversal series (Spec. III) the obliquii posteriores of the segments E and F are the only typical ones present. In the Spec. IV there is a small but typical obliquus posterior on each side also in Segment C. It attaches antero-laterally of the foot retractor C and runs postero-medially, but its very fusion with the circularis pedis could not be traced because the muscle is too small.

Another muscle which may be regarded as an obliquus posterior is the one called Y_1, which inserts far anteriorly, but runs caudally along the ventral body wall to fuse with the m. circularis pedis of the same side (Figs. 71, 121, 127). It might be an obliquus posterior A, but its attachment together with typical buccal muscles in the preoral region makes this interpretation somewhat doubtful.

The whole m. circularis pedis is supposed to be a constrictor of the foot base. Probably the obliquii anteriores and posteriores serve mainly to fix the system firmly, but of course they may also help partly to move the foot, partly to rotate it relatively to the shell.

The m. circularis intermedius is situated along the bottom of the pallial groove, ventrally to the foot retractors (Fig. 119). It is not immediately in touch with the epithelial basement membrane, but runs as a plate of discrete bundles of fibres, at some distance from the strongly folded wall of the foot base, into the longitudinal folds of which the bundles tend to dive down further caudally. The muscle consists of rather thick fibres of the usual somatic type (Fig. 113), which make it easily distinguishable from the m. circularis pallii, the very thin fibres of which are located in contact with the basement membrane of the epithelium (Fig. 114). Posteriorly, the m. circularis intermedius is directly continuous with the same muscle of the opposite side, the crossing of the midline taking place within the transverse folds at the base of the foot beneath the rectum. Anteriorly there seems to be an interruption of the ring (Fig. 121), since the fibres of this muscle attach to the shell.

The m. circularis intermedius is connected with the shell through two pairs of muscles, one anterior and one posterior. The anterior head inserts laterally to the foot retractor A and is a muscle of considerable strength (Fig. 127). It runs almost straight caudally under the anterior three foot retractors and flattens out to form a membrane near, but not in contact with, the bottom of the pallial groove. This muscle is the direct anterior continuation of the m. circularis intermedius, which therefore embraces the foot base like an U with the opening directed anteriorly.

The other insertion of the m. circularis intermedius is situated beside the anus, latero-caudally to the foot retractor H. A muscle runs antero-medially from the said point of insertion, ventrally to the retractor H and the corresponding obliquus anterior. The muscle crosses its counterpart from the other side and gives off some fibres to the m. circularis pallii. After reaching the opposite side the muscle fuses with the m. circularis intermedius (Fig. 121).

The details of the function of this whole muscle remain obscure, but it is supposed to assist the m. circularis pedis in constricting the foot base, and it may also help in pulling the whole foot forwards.

The m. circularis pallii is particularly interesting, since it is a typical cutaneous muscle situated inside the epithelium of the pallial groove. Laterally it reaches the base of the gills (or the lateral nerve cord, which means the same). Thus it is absent from the peripheral part of the mantle. Medially it extends approximately half-way down the sides of the foot, but it is lacking in the lower part of that organ (Fig. 119). It consists of a single layer of very thin, parallel muscle fibres lying in contact with the base-

ment membrane of the epithelium. Consequently it is folded in the same way as the epithelium. The muscle is not so impressive in transverse sections, but as seen from the surface in horizontal sections it shows up as a distinct membrane of closely packed, parallel muscle fibres (Fig. 114).

Posteriorly the muscle is directly continuous with that of the other side (Fig. 121). The crossing of the median line takes place along the transversal parts of the pallial groove and of the foot side in front of the anus. Anteriorly there is also some direct contact from one side to the other in the propodial region and along the surface of the foot, but a considerable portion of the muscle passes forwards laterally to the velum and to the mouth to form the more diffuse subepithelial muscle of the anterior body region (Fig. 127).

In the body proper there are no separate shell insertions of the m. circularis pallii, but some of the previously described mm. obliquii anteriores give off fibres spreading over the surface of the pallial groove (Fig. 121). It could not be decided with certainty whether these fibres only attach to this wall, or whether they really share in the formation of the circular pallial muscle. The question is hardly of fundamental importance, for their function will be the same whatever the case may be. Such pallial fibres have been seen to arise from the mm. obliquii anteriores D-H, but not from the obliquii anteriores A-C (Fig. 121). Likewise, the muscles Y_1 and the posterior head of the m. circularis intermedius give off some fibres to the circular pallial muscle, whereas the mm. obliquii posteriores E and F could not be seen to do so, although for some distance they run closely along the wall of the pallial groove. In the anterior region this muscle system inserts on the shell at several places (Fig. 127).

Since the shape of the living animal is not exactly known, it is difficult to suggest a function for the m. circularis pallii. The muscle may help keeping the pallial groove open, or it may influence the pressure of the body fluid. At all events this pressure must be essential in the movements of the animal, since the muscles mainly act as retractors and constrictors, whereas extension must be effected by blood pressure.

The Smaller Muscles of the Gills, Mantle and Foot

The different components assembled under this heading are probably of heterogeneous origin. The muscles of the gills and pallium show some anatomical similarities in so far as they insert on the shell and run to pallial structures, i.e. to the gills and to the epithelium of the pallial groove, respectively. The diffuse musculature of the gills, mantle, and foot may well be of quite different origin.

The mm. branchiales. As mentioned in the description of the ctenidia (pp. 20-21) each gill stem contains two double muscles, one external along the arterial side and one internal along the venous side. Both muscles give off branches into the lamellae of the gills (Figs. 60, 65). The m. branchialis externus is accompanied by the external gill nerve and the efferent gill vessel, the m. branchialis internus runs along the afferent gill vessel and the internal gill nerve. Both muscles pass between the nephridial lobules and through the blood sinuses of the mantle fold upwards to their insertion on the shell (Fig. 125).

The internal gill muscle is always well developed and emerges from the postero-medial corner of the gill base (Fig. 59). Its course is more or less dorsomedial from the gill base to the shell, where it inserts behind (or, in Segments D and E, posteromedially to) the foot retractor (Figs. 121, 130). The first gill (in Segment C) is exceptional in that its m. branchialis internus inserts laterally to the foot retractor. The external gill muscle is always present, but it is smaller than the internal one and is almost vestigial in the first two gill-bearing segments. It is present in the gills proper, but its continuation up to the shell consists of a few fibres, only. The insertion on the shell lies antero-laterally to that of the other muscle and is situated just outside the insertion of the foot retractor. (The lettering of these muscles is purely descriptive and should not be taken to involve any interpretation as to segmental limits).

Contraction of the entire system of the mm. branchiales must result in a withdrawal of the whole gill. In the stem the contraction of the double internal muscle alone will probably swing the stem backwards, the external one working antagonistically. Similarly, the single lamellae may be moved up and down by their respective rami of the same muscles. On the other hand, the two bundles present along each edge may perhaps be able to cause bending at right angles to the flattened surfaces of either the stem or the single lamellae (Figs. 59, 60).

The diffuse interior musculature of the gills is the only one in which branching of the single muscle cells has been observed with certainty in this animal (Fig. 118). Its arrangement has already been dealt with in detail on p. 20.

The mm. pallii dorsoventrales. The small muscles

inserting on the shell and running to the epithelium of the pallial groove are collected under this heading. They seem to be fairly variable, as considerable differences have been found between the two sectioned specimens. Such a muscle is constantly found just caudally to the foot retractor of each segment, with which it has a more or less confluent area of insertion, sometimes including that of the internal gill muscle. From the insertions the dorso-ventral pallial muscles pass vertically down to the epithelial lining of the pallial groove. In the reconstruction (Fig. 121) they are shown only in Segments B and C, but they are present in all segments although hidden under the respective foot retractor (see Fig. 130). They may reasonably be supposed to help maintaining the depth of the pallial groove.

Small muscle strands are also common, running from the base of the gills upwards to the shell, but since they only consist of a few scattered fibres each, they have not been included in Fig. 121.

The diffuse muscles of the mantle. The peripheral parts of the mantle fold, from the nephridial area to the margin, are occupied by a loose meshwork of scattered fibres not assembled into distinct muscles. Some of these fibres take a circular course and others a radial one. Among the latter there are some forming a more regular pattern of a m. retractor marginalis pallii to be found all around the animal. The fibres in question arise from a circular line on the interior surface of the shell outside the larger muscle insertions (Figs. 33, 130). They run outwards – at least partly – into the outermost parts of the outer marginal fold. Other fibres from almost the same area of insertion run to the base of the periostracum gland.

The diffuse muscles of the foot. The discrete muscles, i.e. foot retractors and m. circularis pedis, are restricted to the thickened periphery of the foot, from which the margin protrudes. The central parts of the foot is a comparatively thin plate forming the wall beneath the peri-intestinal blood sinus. This membrane is externally covered by the foot epithelium, but its main part is a parenchyma in which there is a meshwork of fibres, many of which appear muscular although partly of a very small calibre and mostly extending in the horizontal plane (Fig. 117). Some of them may originate in the mm. mediopedales. Also, the interior of the foot margin is traversed by scattered fibres, many of which connect the lowermost lateral wall of the foot with its ventral surface, apparently serving to maintain the foot edge as such.

THE MUSCLES OF THE ANTERIOR BODY REGION

The musculature of the anterior body region includes three fairly distinct parts, viz. (1) the subepithelial muscles of the body wall and their insertions on the shell, (2) the retractors of the oral region, of the tentacles, and of the velum, and (3) the buccal muscles, i.e. those of the radula apparatus and of the other parts of the digestive system.

The Subepithelial Muscles of the Body Wall

The subepithelial muscles of the anterior body region are direct extensions of the m. circularis pallii. Like this muscle they are situated in the body wall, forming thin membranes of densely packed parallel fibres close to the basement membrane of the epithelium. All these fibres are very thin.

When, coming from behind, the m. circularis pallii reaches the level of the anterior margin of the foot, some of its fibres pass over to the other side (Fig. 127). The remaining fibres continue cranially to become concentrated into a powerful band in the body wall just lateral to the tentacles and the velum. When arriving in front of the mouth, some of its fibres cross over to the other side as a preoral transverse muscular membrane, which, however, is not very strong.

Other fibres form a postoral muscular membrane with transversal fibres in the propodial area between the tentacle ridges. They complete the sphincter-like subepithelial muscular system around the mouth.

The peripheral part of the pallial fold in the anterior region is devoid of subepithelial muscular membranes, but there are some scattered fibres running more irregularly. The musculature of the mantle edge does not differ from that of the body proper, as described above.

The subepithelial muscular membrane receives fibres not only from Muscle Y_1 but also from two powerful muscles of the anterior region, viz. the m. praeoralis and the m. oralis anterior (Figs. 121, 127). The latter attaches to the shell within the insertion area named Y and consists of several portions. The most lateral one comes into close contact with the body wall at the level of the lateral parts of the velum (Fig. 127). At the same time it becomes flattened and divides into many small bundles. Further caudally the fibres of these bundles are lost among those of the subepithelial muscle.

The m. praeoralis belongs exclusively to the preoral body wall (Fig. 127). It inserts on the shell just laterally to the pharynx in the insertion area called X (Figs. 84, 132) and runs almost straight posteriorly down to the preoral body wall. Some of its fibres bend laterally to intermingle with the subepithelial muscle, but the majority turn medially, partly diving down into the preoral velar ridge and into the upper lip and partly forming a preoral transverse muscle. The latter, however, is only subepithelial to a small extent, as most fibres are situated deeper in the thickened body wall present in this region. Apparently the muscle serves as a protractor of the mouth region, and as a retractor of the upper lip and velar ridge.

Probably the main function of the subepithelial muscle is to support the ventral body wall of the anterior region. Also, it may act as a constrictor of the mouth region.

Retractors in the Mouth Region

Of the five retractors of the mouth region the three major ones attach to the shell (m. praeoralis, m. oralis anterior, and m. oralis posterior). The other two lack such a connection (m. cruciatus and m. tentacularis transversus).

The *m. praeoralis* was described above as a protractor of the mouth region and as a retractor of the anterior lip and the anterior velar ridge.

The *m. oralis anterior* is a fairly complex muscle, inserting on the shell within the area Y and running in a medio-posterior direction to divide into 5 or 6 more or less distinct portions (Fig. 127). The most medial portion turns straight medially to attach to the sides of the pharynx. The next portion runs down to the body wall, also in a medial direction, its fibres spreading into the anterior lip. The third portion passes downwards more posteriorly to the body wall behind the mouth. Its fibres continue as a transverse muscle in the posterior lip and in the transverse part of the tentacle ridge. The next portion, which is the most compact one, dives down into the lateral parts of the velum and seems to be an important anterior velum retractor. The most lateral portion bends caudally, passes down to the body wall, and flattens out, finally merging with the subepithelial muscle laterally to the velum, as described above.

M. oralis posterior. The m. medio-pedalis A gives off a very strong muscle, the m. oralis posterior, appearing as the most important of all retractors of the mouth region. From its insertion this muscle turns medio-anteriorly, the major portion diving down into the lateral parts of the velum as the main velum retractor (m. retractor veli posterior) (Figs. 72, 127, 129). Smaller branches are given off to the region of the lateral corners of the mouth, and one small portion dives down into the lateral parts of the tentacle ridge. The typical m. medio-pedalis A turns more postero-medially to the foot, but it gives off a branch, m. transversalis A, passing across the animal to join its counterpart on the other side (Fig. 129).

M. cruciatus, the crossed retractor, consists of two branches, one coming from the lateral parts of the velum and another from the tentacle ridge. On each side these two branches fuse and then cross over to the other side in close contact with the body wall (Figs. 121, 127). They continue postero-laterally along the body surface, ventrally to all other muscles, to fuse with the m. circularis pedis.

The *m. tentacularis transversus* almost joins the m. transversalis A in passing across the median line within the postoral internal fold of the propodial area. On each side the fibres dive down into the posterior part of the tentacle ridge to spread into the tentacles (Figs. 80, 127).

The subepithelial muscles of the anterior region, together with the different retractors just described, seem responsible for all the movements of the lips, the velum, and the tentacles. Probably contraction of the m. praeoralis, the m. oralis anterior, and the m. oralis posterior retracts the entire mouth region. Extension of the same region would seem to be caused by pressure of the body fluid, possibly in combination with movements of the radula apparatus. The subepithelial muscle, which, in combination with the postoral portion of the m. oralis anterior, forms a kind of sphincter of the mouth, may close this opening, whereas the m. praeoralis, the m. oralis posterior, and some portions of m. oralis anterior may widen the mouth. The velum retractors are derived from the m. oralis posterior, the m. oralis anterior, and the lateral portion of the m. cruciatus (lateral portion of velum), and from the m. praeoralis (anterior velar ridge). The tentacle retractors come from the m. oralis posterior and the m. cruciatus and are supplemented by the m. tentacularis transversus. Selective contraction of isolated components of this whole complex may cause horizontal movements of the tentacles and velum.

The Buccal Muscles

Under this heading we treat the muscles which obviously have to do with the movements of the radula apparatus, and also the few muscles concerned with the fixation and movements of the pharyngeal region. A certain knowledge of the anatomy of these parts is therefore a necessary prerequisite for the understanding of the morphology and function of the buccal muscles. This is the reason why we have dealt with the anatomy of the digestive system before that of the musculature.

The Muscles of the Radula Apparatus

The study of the radula muscles presented some difficulties, partly because the muscles in some regions are strongly contracted in the material available, and partly because of the bad state of preservation of the radula vesicles on which many muscles insert. However, the muscles of the radula apparatus can be clearly seen to insert in a way not very different from that of chitons, i.e.

(1) On the postero-lateral tip of the radula vesicles,
(2) On the subradular membrane in the radula diverticula,
(3) On the transverse cartilaginous rods of the radular support,
(4) On the radula sheath proper, and
(5) In the body wall only, but acting on the radula apparatus.

Muscles Inserting on the Tip of the Radula Vesicles

Quite a number of muscles insert on each radula vesicle, all of them restricted to its postero-lateral tip (Fig. 128), whereas the anterior end of the vesicle is firmly connected with the cartilaginous substance of the radula support. The said muscles appear to belong to two functional groups, viz. the muscles fixing and moving the vesicles as such, and those using the vesicles as a fixed base from which, by their contractions, they move the subradular membrane.

(a) The *m. retractor radulae* almost surrounds the radula vesicle as a muscular sac (Figs. 90, 94, 129). The muscle originates on the tip of the vesicle, passing forwards as three partially separate portions, all of which attach ventrally on the posterior and lateral edges of the radula diverticulum (Fig. 128), i.e. that the muscle inserts on the epithelium carrying the secondary subradular membrane in such a way that its pull retracts this membrane.

One portion of the muscle inserts far rostrally on the lateral edge of the subradular membrane, close to the m. tensor radulae, to run laterally to the vesicle on to its tip.

A series of other bundles of the same muscle attach beneath the edge of the subradular membrane along the lateral half of the posterior margin. Partly, these bundles turn obliquely sidewards above the vesicle to its lateral side before they attach to the tip. Others behave similarly without passing over to the lateral side.

A third portion inserts under the medial part of the posterior edge of the subradular membrane, close to the radula sheath proper. Although situated more ventrally this portion, too, runs postero-laterally to the tip of the vesicle, but it attaches from a ventral direction.

All the three portions form an almost continuous muscular sac round the radula vesicle, the lateral wall of the sac being completed by the m. protractor vesicae major, which comes from the shell (Figs. 84, 90). Apparently this complex muscle pulls the subradular membrane caudally. At the same time it may press the radula vesicles and the entire radula support forwards, making the radula approach still more closely to the underlying transversal bar.

(b) The *m. protractor vesicae major* inserts laterally to the pharynx on the anterior part of the shell, within the area X (Figs. 128, 132). The insertion is near the anterior mantle edge, the most rostral part of the muscle passing through a vascular channel in the mantle (Fig. 124). Then the muscle runs straight caudally above the ventral body wall to insert on the posterior tip of the radula vesicle. It participates in the formation of the muscular sac formed by the m. retractor radulae (Figs. 84, 128).

(c) *M. protractor vesicae minor* inserts more dorsally within the area X, together with the m. praeoralis (Fig. 132). When passing caudally it follows closely along the protractor major to its point of attachment (Fig. 128).

(d) *M. vesicae antero-lateralis* is small and fairly short. Inserting on the tip of the vesicle, it runs in an antero-lateral direction down to the ventral body wall in front of the retractor veli posterior (Figs. 83, 128).

(e) *M. vesicae antero-medialis* inserts on the tip of the vesicle and runs antero-medially to spread into the upper lip, passing just medially to the cerebral ganglion (Figs. 83, 128).

(f) *M. vesicae postero-lateralis* passes latero-posteriorly as a thin band from the tip of the vesicle,

closely following the m. transversalis anterior above the dorsal (medial) surface of the m. retractor veli posterior, behind which it attaches to the ventral body wall (Figs. 83, 128).

(g) *M. vesicae postero-medialis* passes from the same attachment medio-posteriorly above the velum retractor, diving down into the body wall in the region of the postoral tentacles to spread just medially of the statocyst (Figs. 83, 128).

(h) *M. vesicae ventralis* runs almost directly from the tip of the vesicle downwards to the body wall, spreading into the tissues immediately behind the velum retractor (Figs. 83, 128).

Altogether, the muscles b-h may be expected to move the vesicle in all directions except the dorsal one. Acting separately, the two protractors seem to pull the tip of the vesicle forwards, thus helping to press the radula apparatus anteriorly or ventrally. The antero-medial muscle may assist in the same movement, but may also pull the vesicle down towards the body wall. The postero-lateral and postero-medial muscles apparently retract the vesicle, the medial one also moving the tip medially, whereas the lateral one acts in the opposite way. The chief function of all these muscles must be to keep the tip of the vesicle fixed as a fundament for the movements of the radula. In addition the antero-medial muscle may function as an accessory retractor of the upper lip.

The Muscles of the Subradular Membrane

As mentioned on p. 27, the radula diverticula are flat, lateral expansions of that part of the radula sheath which opens into the pharynx. Inside, their ventral wall is covered by (probably secretes) the secondary subradular membrane to which are transferred the actions of the muscles described in this chapter. These muscles act particularly on those parts which lie within the radula diverticula, attaching along both the lateral and the posterior edges. In addition some muscles attach to the oral end of the membrane in the pharyngeal wall proper.

((a) *M. retractor radulae.* Although described above, this muscle is mentioned again here because it inserts under the posterior and postero-lateral edges of the subradular membrane, passing to the tip of the radula vesicle and functioning as a strong radula retractor).

(b) *M. protractor radulae* attaches from beneath to the lateral margin of the radula membrane at the oral end of the diverticula and in the adjacent part of the pharynx. Since the membrane probably functions by gliding over the radula skeleton, the position of the insertion area in the animal depends upon the state of contraction. The muscle passes straight anteriorly and is divided into a number (about ten) of different portions, the area of attachment to the shell being horseshoe-shaped (Figs. 11, 84, 128, 129, 132).

The muscle seems to pull the subradular membrane forwards, i.e. rolling the membrane into the mouth, whereas the retractor radulae acts antagonistically.

(c) *M. tensor radulae* is a fairly long and slender muscle inserting beneath the edge of the radula diverticula on each side, approximately between the big retractor and the big protractor (Fig. 128). It passes straight laterally to its insertion on the shell within the area Z (Fig. 132). The combined action of the two muscles in this pair may be either to flatten the membrane transversally or, simply, to stabilize it.

(d) *M. radulae longus.* This muscle consists of two parts, originating medially and caudally to Muscle C high up on the shell (Figs. 84, 130). It passes antero-medially downwards between the liver lobules to the pharyngeal region.

The *pars ventralis* gives off some small branches functioning as retractors of the subradular sac (Fig. 82). The main part closely follows along the dorsal wall of the pharynx to insert on the oral edge of the secondary subradular membrane (Figs. 90, 94).

The *pars dorsalis* originates on the shell a little antero-medially to the ventral part. It closely follows the pars ventralis downwards and forwards, but then swings off in a more dorsal direction to the oral end of the tubular radula sheath (Figs. 128, 129). It attaches ventrally on this sheath, but some fibres continue into the diverticular region. Hence, the pull exerted by the pars dorsalis would seem to act almost directly on the secondary subradular membrane. The muscle is kept in its proper position by two small muscular bands, viz. the m. radulae minor and the m. transversalis posterior (See below) (Fig. 128).

The two portions acting together are supposed to retract the entire radula apparatus into the body. Although the two portions, inserting on either end of the secondary subradular membrane, would appear able to act antagonistically in rolling the radula over the skeletal bar, we doubt that this is their main function. The big protractor radulae and retractor radulae described above are much more powerful, and at least the retractor is cross-striated, which

indicates strong activity. Hence, we suppose those big muscles to be the main ones for the usual feeding movements of the radula.

(e) *M. pharyngeus marginalis* attaches to the oral edge of the subradular membrane, laterally to the m. radulae longus pars ventralis, running caudally along the dorsal side of the pharynx near its lateral edge (Figs. 82, 90). Behind the mouth it dives down into the ventral body wall, then following closely along and lateral to the pedal nerve until disappearing among the fibres of the foot musculature. This muscle may assist in pulling the subradular membrane into the mouth, thus in some way collaborating with the m. protractor radulae.

The Muscles of the Radula Cartilages

A pair of cartilaginous rods, united medially by an unpaired muscle, forms a transverse bar over which the subradular membrane with the radula glides (Figs. 81, 82). The following muscles attach to these cartilages.

(a) *M. impar radulae* is a thick, median cushion, the fibres of which run transversely, connecting the medial ends of the two cartilages. Contracted, as in the sections, it bulges out all around (Figs. 82, 95). The muscle seems to be able to regulate the distance between the radula cartilages and, possibly, by separate action of single bundles to tilt them relatively to each other.

(b) *M. protractor cartilaginis dorsalis* attaches ventro-rostrally to the lateral end of the cartilage, passing straight anteriorly to the shell within the insertion area X. Immediately before the insertion a branch is given off, bending medio-dorsally to join the ventral part of the m. protractor radulae (Figs. 83, 128). The muscle would seem to pull the cartilages forwards.

(c) *M. protractor cartilaginis profundus* attaches to the lateral end of the cartilage near the radula vesicle. It passes antero-ventrally into the vascular channel of the mantle, which is also used by the more laterally placed protractor vesicae major (Fig. 124). Inserting far ventrally within the area X (Figs. 83, 128, 132), the present muscle pulls the cartilage anteriorly or ventrally and thus seems to play an important role in the protrusion of the radula.

(d) *M. cartilaginis antero-lateralis* attaches to the ventral surface of the end of the cartilage between the two muscles mentioned above (paragr. b and c) (Fig. 83). It passes straight antero-laterally to the shell, inserting within the area Y (Figs. 84, 132). Probably the muscle stabilizes the skeleton, which it may also retract from its lowest positions. Perhaps the muscle also straightens the angle between the two halves of the transverse bar.

(e) *M. protractor subradularis* is a small muscle originating on the lower surface of the cartilage near the point of junction with the radula vesicles. The muscle runs medio-caudally or medially to spread in the anterior wall of the subradular sac (Figs. 82, 83). When the subradular sac is protracted as shown in the figures, the function of the muscle is less obvious. It may be a protractor of the sac, working antagonistically to the subradular branches of the m. radulae longus pars ventralis.

The Muscles of the Radula Sheath Proper

The m. radulae longus pars dorsalis, which is rather intimately connected with the radula sheath, has been mentioned above (p. 40).

M. radulae minor attaches to the ventral surface of the radula sheath just behind the m. radulae longus. From this point the present muscle runs dorsally to the one mentioned, then turning more ventrally and somewhat posteriorly to spread in the ventral body wall in front of the velum retractor, just below the tip of the radula vesicle (Figs. 83, 128). The muscle seems to stabilize the radula transversely.

Other Muscles of the Radula Apparatus

Two muscles belong to the radula mechanism without inserting on it. They form transverse bands over the entire apparatus, apparently serving to keep it in its proper position. The anterior muscle is stabilized by some accessory ones.

(a) *M. transversalis anterior* forms a broad unpaired band across the posterior part of the radula diverticula (Figs. 88, 94, 128). Laterally the muscle runs over the dorsal surface of the muscular sac around the radula vesicles, then turning caudally and ventrally to pass as a thin membrane over the dorso-medial surface of the retractor veli posterior. Finally its fibres spread in the ventral body wall between the latter muscle and the true m. mediopedalis A. From the turning-point to the region of the velum retractor, the muscle runs in the mediodorsal edge of – and is kept in position by – a connective tissue membrane. This *membrana lateralis* is attached laterally to the ventral body wall along the muscle Y_1 and is stretched by two minor muscles described below.

Judging from the firm fixation of the muscle by the membrana lateralis, it stabilizes the radula ap-

paratus by keeping it down in the ventral part of the anterior body region.

(b) *M. tensor membranae lateralis* is extremely short. It comes from the body wall in front of the retractor veli posterior, running dorsally and medially to the membrana lateralis, which it seems to stretch in a lateral direction (Figs. 99, 128).

(c) *M. tensor membranae anterior* is long and slender, inserting on the shell near the mantle edge together with the protractor vesicae major (Figs. 124, 128). Thus, it is found in the vascular channel in the mantle fold together with the latter muscle and with the protractor cartilaginis profundus. It passes caudally along the protractor vesicae major to the anterior edge of the membrana lateralis, along the anterior margin of which it spreads, to stretch the whole membrane in an anterior direction. In this way the membrane seems to be prevented from gliding caudally when the m. transversalis anterior contracts.

(d) *M. transversalis posterior* forms a thin transverse band over the tubular part of the radula sheath and over the pars dorsalis of the m. radulae longus (Figs. 83, 128). Laterally it bends downwards and then caudally between the two parts of the said muscle, spreading its fibres into the ventral body wall just medially to the statocysts. Although the muscle certainly keeps down the proximal part of the tubular radula sheath, its main function would rather seem to be keeping the m. radulae longus pars dorsalis in the proper angle of attack.

Concerning the position of the whole radula apparatus, it is interesting to note the strictly median position of the proximal part up to the point of insertion of the m. radulae minor just behind the radula diverticula. Then, only the m. transversalis posterior keeps down loosely the immediately following part of the tubular sheath. Farther back, the sheath coils up irregularly.

The Muscles of the Pharynx

This part of the chapter contains the description of a number of small muscles attaching to the soft parts of the pharynx, not referable to any of the groups described above.

(a) *Mm. pharyngei praeorales*. The most oral part of the pharynx, which passes anteriorly from the mouth, is fixed to the preoral ventral body wall by a great number of small muscular strands, as indicated in Fig. 127.

(b) *M. protractor diverticulorum dorsalis* takes a complex course, originating in the ventro-lateral part of the area X, together with the m. protractor vesicae major, branching off from this muscle when it emerges from the vascular channel in the mantle fold (Fig. 124), and immediately turning medially between the other muscles in this area (Fig. 128). Then it turns dorsally to pass through the angle between the pharynx and the radula diverticula to the dorsal side of the latter. In this region some fibres pass transversely to the muscle of the opposite side, whereas the majority pass caudo-medially for some distance to fuse with those from the opposite side into an unpaired muscular band before they attach to the dorsal wall of the sheath in the region beneath the m. transversalis anterior (Figs. 94, 128).

Presumably the muscle maintains the correct position of the soft parts of the diverticula. Its transverse anterior part may be responsible for the acute angle between the posterior pharyngeal wall and the soft dorsal one of the radula diverticula. The longitudinal, caudal part may protract the latter wall when the underlying subradular membrane is pulled forwards.

(c) A number of very delicate muscular strands originate in the region of the transverse part of the preceding muscle, i.e. in the dorsal wall of the radula diverticula, passing dorsally to insert on the posterior wall of the pharynx.

THE INSERTION PATTERN ON THE SHELL

No real muscle scars are visible on the shell of *Neopilina*, probably because it is too thin, but a careful analysis has been made of the pattern of muscle insertions in order to provide the best possible basis for a comparison with the fossil forms. This was carried out by plotting in graphic reconstruction the distribution of the typical muscle attachment cells (p. 18) in the dorsal epithelium. The results are shown in Figs. 130 and 132.

There is a continuous zone of scattered attachment cells all around the animal, apparently constituting the equivalent of the pallial line in other molluscs. In the most anterior body region, to somewhere off the first pairs of pedal retractors, the zone only contains very scattered attachment cells among the common, nacre-forming ones. In all other parts the zone contains an almost continuous band of closely packed attachment cells along its medial limit, the remaining parts of the zone showing only scattered cells of this kind. A most interesting and unexpected fact appeared from this re-

construction, viz. that the inner boundary of the pallial line shows septa-like medial extensions off the pedal retractors C to H, accentuating the metamerism of the body. The muscle fibres inserting within the pallial line zone are the more or less scattered ones traversing the outer part of the pallial fold lateral to the nephridia.

The insertions of the more well-defined muscles – those being of particular interest to palaeontologists because they are potential sources of muscle scars in fossils – are arranged as follows, beginning with the most anterior ones.

One set of muscles is distinctly separate from all others in inserting through a vascular channel on the anterior shell wall close to the mid-line and peripherally in the pallial line zone below the insertion area X, to which it has been referred above (Figs. 128, 132). The inner half of this "potential scar" constitutes the insertion area of the m. protractor cartilaginis profundus. The lateral one is formed by three muscles, viz. m. protractor vesicae major, m. diverticulorum dorsalis, and m. tensor membranae anterior.

The insertion area X proper is situated just above the pallial line latero-ventrally to the apex (Fig.132). Its most prominent component is the complex, semilunar insertion of the m. protractor radulae. In contact with the pallial line insert the m. praeoralis and the main head of the m. protractor cartilaginis dorsalis. The smaller head of the latter muscle, and the m. protractor vesicae minor insert more centrally in the area.

The area Y, placed a little more laterally, contains potential scars of three muscles only (Figs. 84, 132). These are the m. oralis anterior, the m. cartilaginis antero-lateralis, and – in contact with the pallial line – the muscle Y_1.

The area Z contains only one muscle, the m. tensor radulae, the most lateral component of the buccal musculature (Fig. 84, 132).

Two buccal muscles remain to be treated, viz. the two portions of the m. radulae longus, inserting inside the pedal retractors C and D (Figs. 84, 130). These buccal muscle insertions are definitely more central in position than the girdle of body muscles now to be treated.

The potential scars of the well-defined body muscles group themselves round the eight pairs of pedal retractors (A-H). The groups A to C are placed more centrally (higher up on the shell) than the remaining ones, but this is hardly visible in Fig. 130 in which everything is projected on a horizontal plane, whereas it appears distinctly from a comparison between Figs. 11 and 89. The two portions of the big pedal retractors insert close together, the m. medio-pedalis lying posteriorly to the m. latero-pedalis with the exception of the retractors G and H. In G, the potential scar of the m. medio-pedalis is divided into two portions, one of which is anterior to the m. latero-pedalis. In H, the m. medio-pedalis inserts centrally to the m. latero-pedalis. It should be mentioned that the potential scar of the m. medio-pedalis A, as drawn in the Fig. 130, also includes the m. oralis posterior.

The smaller muscles group themselves round the big pedal retractors in a fairly constant pattern, allowing for some irregularities in the smaller pallial muscles (Fig. 131). The mm. obliquii anteriores insert in a regular manner peripherally or a little behind each of the eight pedal retractors. The mm. obliquii posteriores, however, are present only in the "genital segments", D and E, and insert in front of the respective pedal retractors.

The mm. branchiales externi (the outer gill retractors) have their potential scars immediately outside those of the pedal retractors C to G. The four hindmost mm. branchiales interni (inner gill retractors) insert behind or slightly centrally to the pedal retractors D to G, always in close contact with a pallial muscle. In the area C, however, the two gill retractors are situated close together immediately peripherally to the pedal retractor – and apparently without any relation to a pallial muscle.

The m. circularis intermedius has two big insertion areas, one off the pedal retractors A and B, and one off H (Figs. 121, 130). The dorso-ventral pallial muscles, passing from the wall of the pallial groove to the shell, are more irregular, but one such muscle is constantly present behind each pedal retractor, its scar being continuous with that of the m. branchialis internus in D to G. Another pallial muscle is attached just outside the anterior part of the pedal retractors A and C to G, and may therefore be regarded as a fairly constant feature.

COMPARATIVE REMARKS

The almost total lack of metamerism in the musculature of most molluscs makes a comparison difficult between them and *Neopilina*. A detailed homologization of the different muscles is possible only when dealing with the polyplacophores and the fossil tryblidians.

Comparison with the fossil tryblidians. The trybli-

dians are characterized by their multiple pairs of large complex muscle scars, inviting a direct comparison with the insertion pattern in *Neopilina* as described above.

Pilina unguis (LINDSTRÖM, 1884). We are much indebted to Professor E. STENSIÖ, for his kind permission to reproduce the photograph shown in Fig. 134 and for other valuable help which allowed us to study this beautifully preserved specimen in detail (cf. also the interpretation in Fig. 133). First, the size of the muscle scars in this fossil shows that the entire musculature was very much stronger than in the recent deep-sea species, a fact which together with the thickness of the shell is easily understandable in view of its occurrence in shallow water deposits. The pallial line area is not very distinctly delimited, but seems to be represented by a shallow groove at some distance outside the big muscle scars.

The five posterior paired sets of muscle scars are rather uniform as far as the evidence of the fossil goes. Each set consists of a large central scar, undoubtedly corresponding to that of the big foot retractor of *Neopilina*. Some of these central scars show indications of being subdivided into two almost equal parts, suggestive of the medio-pedalis and latero-pedalis portions of the corresponding muscles in *Neopilina*. Postero-medially to each big scar a distinct smaller one is present. In the corresponding place *Neopilina* shows two confluent muscle insertions, viz. those of the m. branchialis internus and of a small pallial muscle (Figs. 130, 131). Laterally to the big scars, the shell of *Pilina* shows a continuous series of – apparently four – more or less distinct scars. These are more difficult to interpret individually, but certainly correspond to the series of smaller muscle insertions in *Neopilina*, viz. m. obliquus posterior (most anteriorly), a pallial muscle, m. branchialis externus, and m. obliquus anterior (most posteriorly). It is tempting to suppose that the mm. obliquii are those placed at the ends of this series in the fossil, but it is impossible to say which of the middle ones is the branchial muscle. It might be noted that all the scars are placed very close together in this fossil, much more so than in *Neopilina,* where the muscles are reduced in size.

More anteriorly a large complex of scars is present in *Pilina*. Of these the more medial ones can be identified as belonging to the mm. radulae longus, partly because they are placed medially to the anterior continuation of the series of foot retractor scars, and partly because of certain features observed in chitons. In the latter the homologon of the m. radulae longus (PLATE 1898, Tafel 3, Fig. 23, retr') is subdivided into many small portions inserting separately to the shell. In *Pilina* we find a similar pattern of discrete insertions composing the big scars described above. A comparison with *Neopilina* shows that the mm. radulae longus in the recent species are very much reduced in size, indicating that the withdrawal of the radula apparatus in *Neopilina* affords much less muscular strength than in the littoral chitons and fossil tryblidians, which probably used their radula for browsing.

The series of three scars immediately lateral to the m. radulae longus would seem to be the anterior continuation of the series already described for the posterior part of the body, and would then correspond to the pedal retractors, etc., A to C in *Neopilina*. However, the interpretation of the most anterior scars as corresponding to A is somewhat uncertain, and most of the details are far from clear. The small muscle situated laterally to C might be a gill retractor, internal or external or both; cf. the strange situation of the m. branchialis internus in the "segment" C in *Neopilina*. The elongate scar outside B might be the insertion area of the m. circularis intermedius.

From the medial end of the scar A in *Pilina,* a very distinct ridge runs antero-medially to a point near the mid-line. Evidently this ridge constitutes a muscle scar, but there seems to be no counterpart in *Neopilina*. Comparison with chitons, however, indicate that this structure is associated with the presence of a diaphragm of the type drawn by PLATE (1898, Tafel 3, Fig. 25) and attaching dorsally at the boundary between the first and second shell piece.

Finally, there are some rough surfaces on the anterior shell wall of *Pilina*, to the sides and a little below the apex. These areas might easily correspond to the insertion areas X and Y in *Neopilina,* where several buccal muscles attach.

Tryblidium reticulatum LINDSTRÖM, 1880. The material available is not quite so excellent as that of *Pilina;* so the analysis could not be carried out in such detail. The big paired groups of muscle scars seem to be essentially similar to those of *Pilina* (Fig. 162E). The paired furrows interpreted as insertions of a diaphragm in *Pilina* are represented in *Tryblidium* by shallow, but broader transverse marks almost reaching each other in the mid-line. The impressions of the mm. radulae longus are present, but less distinct and apparently not subdivided.

Archaeophiala antiquissima (HISINGER, 1837). The general arrangement of the scars seems to be quite the same as in *Tryblidium* (Fig. 162H). We have had no access to any specimen of this species and therefore are unable to say what the so-called shadow scars stand for (KNIGHT, 1952). They may represent either pallial muscle insertions or scars of branchial muscles. The big anterior scars have medial lobes obviously corresponding to the mm. radulae longus. The medially directed, narrow anterior lobes suggest a comparison with the diaphragm furrows as e.g. in *Tryblidium,* but we cannot exclude the possibility that they are directly equivalents of the muscles A.

The genus *Drahomira* KNIGHT, 1952 is more aberrant, although undoubtedly belonging to the same group of fossils (See HORNY, 1956). There are seven pairs of distinct muscle scars. The hindmost one on each side is very irregular and difficult to interpret. The other scars with the exception of the first pair are regular and radially elongate. Some of HORNY's figures (his Figs. 2, 5, and 6) indicate that each scar is subdivided lengthwise into two narrow parts which we are inclined to interpret as the insertions of the two portions of the pedal retractors. In addition some of his figures (his Table II, Figs. 1 and 3) show a small scar immediately lateral to each elongate one, corresponding in position to the group of small scars in *Pilina*. The anterior scar on each side in *Drahomira* is remarkably different from that of the above-mentioned genera. No diaphragma scar is visible, and we are unable to identify even the scar of the long radula muscle.

Proplina cornutaeformis (WALCOTT, 1879). In the genus *Proplina* KOBAYASHI, 1933, distinct scars have been described only in *P. cornutaeformis*. In this species, YOCHELSON (1958) found "six sets of paired muscles, anterior muscle scars located about one-third of the distance from apex to posterior of margin, and relatively high in the cup; the first scar consisting of a sharp short depression in shell trending near 45 degrees to the margin of the aperture and a posteriorly elongated slight swelling located behind the depression." This anterior "scar" would seem to cover the anterior scar complex around the pedal retractors A, B (and, possibly, C) in *Neopilina*. The following scars are rather closely set, somewhat farther down towards the shell margin. A peculiar feature described by YOCHELSON is "the sixth set of scars on the posterior slope, somewhat wider than the others, widening and dying out towards the posterior margin, but continuing as faint furrows up along the dorsum above the general level of the other scars for some two-fifths of the length of the shell." In *Neopilina,* nothing comparable has been found.

Bipulvina croftsae YOCHELSON, 1958. In this fossil any diaphragm scar is hardly visible, but inside the first pedal retractor scars a pair of very shallow, elongate, and indistinct depressions might be the insertion areas of the m. radulae longus. The pedal retractor scars are peculiar in being subdivided by some transverse lines, the nature of which remains obscure. They can hardly – as proposed by YOCHELSON – correspond to growth lines as they are not parallel to the shell margin. In the anterior portion of the shell several sets of scars are described by YOCHELSON. These seem to be the insertions of buccal muscles and of the retractors of the oral region, but the detailed analysis of these interesting scars cannot yet be carried out.

Comparison with the Polyplacophora. The system of 8 pairs of large pedal retractors appears directly comparable in chitons and in *Neopilina*, and in both groups each retractor is subdivided into a m. mediopedalis and a m. latero-pedalis, characterized by their distribution in the foot and by their relations to the pedal nerve cord (Figs. 166, 167). In chitons the insertions of these muscles are in the regions of the boundaries between the consecutive shell pieces, so that each muscle is subdivided into an anterior and a posterior portion (PLATE 1898). The oblique muscles in chitons might perhaps be homologous with those described in *Neopilina*, but they pass between the two portions of the corresponding pedal retractors dorsal to the crossing of the latter, i.e. right under the shell. In chitons the gill retractors insert on the shell close to the pedal retractors, but as the arrangement of the gills does not accord with the eight foot retractors, the gill muscles have a segmental rhythm of their own.

Some of the buccal muscles in chitons may be directly compared with those of *Neopilina,* although we have hesitated to make an extensive comparison. The m. radulae longus is homologous with the radula retractor called "retr'" (PLATE 1898) in chitons, although in the latter this muscle is larger. The m. retractor radulae, passing from the radula vesicle to the radula diverticulum of the same side in *Neopilina*, has its direct counterpart in the muscle designated "lat" by PLATE (1898, Tafel 2, Fig. 19). The m. protractor vesicae major of *Neopilina* corresponds to the muscle "protre" of chitons (PLATE 1898, Tafel 4, Fig. 34). The small muscles fixing the tip of the radula vesicle to the ventral body wall are

present in both forms, and so is the unpaired m. impar radulae between the radula cartilages ("m" in PLATE 1898, Tafel 4, Fig. 35). Furthermore, the m. tensor radulae of *Neopilina* can be compared with the muscle marked "5" by PLATE (1898, Tafel 3, Fig. 23).

Some points of difference should be noted, first, the considerable strength of the m. radulae longus ("retr'") in chitons, which is weak in *Neopilina* and, secondly, the absence in the former of any muscles corresponding to the m. protractor radulae. This difference may be correlated with differences in function. In chitons, the radula apparatus is pushed down into the oral cavity and again retracted for each rasping movement, by which the strong m. radulae longus is supposed to be active. In *Neopilina*, the muscles moving the subradular membrane (m. protractor radulae and m. retractor radulae) are particularly well developed, thus indicating that the radula carries the food inwards by simply moving to and fro, without being protruded through the mouth for real rasping movements.

THE NERVOUS SYSTEM

The following account is based mainly on the two sectioned specimens, of which the transversal series (Spec. III) has been used for the graphic reconstructions, Spec. IV serving as a control. For unknown reasons the nervous system stands out much clearer in the sections of Spec. III. It has been difficult to establish the innervation of the smaller muscles because, before entering, the nerves usually divide into separate fibres which are invisible with the technique used. On the other hand, the gross anatomy of the nervous system and the relations to the other organs were easily observable.

GENERAL ANATOMY

The anterior part of the nervous system forms a *circum-oral nerve ring* consisting of a cerebral commissure in front, a pair of big cerebral ganglia laterally, and a subcerebral commissure behind the mouth (Figs. 135, 136). This ring emits caudally two main pairs of cords, viz. the *lateral* (viscero-pallial) *nerve cords* into the pallial fold, and the *pedal nerve cords* into the foot. Both pairs are continuous across the mid-line ventrally of the rectum. In the main, (1) the pedal cords innervate the foot, (2) the cerebral commissure and the lateral cords supply the pallial fold, (3) the organs of the mouth region are innervated mainly from the circum-oral nerve ring, (4) the gills receive segmentally arranged nerves from the lateral cords, and (5) strictly metameric latero-pedal connectives are present in each segment.

The terms as here applied have been borrowed from the anatomy of the polyplacophorans which have a very similar nervous system, the outlines of which have been described in the monograph by PLATE (1898).

HISTOLOGY

As in chitons and primitive gastropods the cords have a continuous layer of nerve cells along most of their surface, whereas the fibres form a central bundle (Fig. 138), but there is some tendency towards a concentration into ganglia anteriorly. The cerebral commissure seems to be devoid of nerve cells, and the same applies to the subcerebral commissure and to the proximal parts of the lateral and pedal cords. Distinct accumulations of nerve cells into ganglia are found in the lateral parts of the circum-oral ring, where great and complex cerebral ganglia are formed. Other distinct ganglia are the buccal ones, and the subradular ganglion on the dorsal wall of the subradular organ (Fig. 136). Graphic reconstructions and dissection did not reveal distinct accumulations of nerve cells or swellings in the pedal and lateral cords (Figs. 135, 140). The material does not allow detailed observations of the cytology of the nerve cells. These are small (about 10 μ) throughout, each with a nucleus measuring about 5 μ in diameter.

THE CIRCUM-ORAL NERVE RING

The circum-oral ring is situated on the inner surface of the ventral body wall, in which it is partly buried. The cerebral commissure lies in front of the mouth between the ventral body wall and the ventral ("anterior") wall of the pharynx (Fig. 81). The cerebral ganglia occupy the lateral parts of the ring, each ganglion being more or less tripartite with swellings at the base of the pedal cord, the lateral cord, and the cerebral commissure (Fig. 136). The subcerebral commissure, like the cerebral one, seems to be devoid of ganglionic cells. It forms a transverse string

behind the mouth, ventrally to the subradular sac and inside the transverse part of the tentacle ridge (Figs. 135, 136). The nerves emitted from these parts are as follows:

(a) *The nerves to the preoral part of the pallial fold* originate from the cerebral commissure and ganglion (Fig. 135). In Spec. III, there is a median nerve and three pairs of symmetrically arranged lateral ones. Like the mantle nerves of the postoral region they are strictly subepithelial, attached throughout their course to the basement membrane of the pallial epithelium.

(b) *The nerves to the velum and the anterior lip.* The cerebral commissure and ganglion emit a series of about ten richly branched ventral or ventromedial nerves on each side (Fig. 136). Some of these nerves pass to the anterior lip, but the majority dive down into the velum. The main nerves to the velar flaps are the lateral ones arising directly from the cerebral ganglia, which lie over the bases of the flaps.

(c) *The buccal connective and ganglion.* The buccal connective is emitted on each side from the caudomedial part of the cerebral ganglion, i.e. from the swelling giving rise to the pedal cord (Fig. 136). The connective passes rostrally above the cerebral commissure laterally to the pharynx to form a distinct buccal ganglion (Fig. 135). Immediately before reaching this ganglion the connective gives off a nerve towards the pharyngeal wall. From the opposite end of the ganglion the buccal commissure runs up to the dorsal side of the radula diverticulum, over the surface of which it passes caudally and then medially to meet its counterpart from the other side. Smaller nerves are given off both from the ganglion and from the commissure, but the analysis of these branches has not been carried out in detail because of their rather poor state of preservation.

(d) *The subradular nerve* is emitted from the caudo-medial part of the cerebral ganglion near the origin of the pedal nerve cord. The nerve passes to the dorsal side of the oral cavity to run through the lateral part of the furrow between the pharynx and the subradular sac (Fig. 136). It gives off a small branch to the anterior wall of the latter sac, then turning dorso-medially to end in the unpaired subradular ganglion in the transverse fold of the subradular sac (Figs. 81, 136).

(e) *A nerve to the posterior lip and to the transverse part of the tentacle ridge* arises from the cerebral ganglion close to the origin of the subcerebral commissure. The nerve passes medially in the body wall, giving off several branches to the posterior lip and to the transverse part of the tentacle ridge (Fig. 136).

(f) *The nerve to the preoral tentacle* comes from the cerebral ganglion and passes straight ventrally. (Since the tentacle is exactly ventral to the ganglion, the nerve cannot be seen in Fig. 136, but the site of the tentacle has been indicated by a dotted circle).

(g) *The first latero-pedal connective,* in fact, originates from the lateral part of the complex cerebral ganglion (Fig. 136). The nerve passes dorsally to the m. retractor veli posterior (Fig. 137) although it does not follow the surface of this muscle, but flattens out to penetrate between its most dorsal fibres – which makes the nerve most difficult to trace. It seems to innervate the velum retractor, but some of the nerve fibres pass through that muscle and could be followed postero-medially until they reach the pedal cord. In most of its course the nerve runs in close contact with the epithelium.

(h) *The lateral cord* originates from the lateral part of the cerebral ganglion (see below).

(i) *The pedal cord* is emitted from the postero-medial part of the cerebral ganglion (see below).

THE LATERAL NERVE CORDS

The lateral cord takes its origin from the lateral corner of the cerebral ganglion, to continue backwards close to the basement membrane of the epithelium of the pallial groove (Figs. 119, 148) and to pass medially to the gill bases until, in the region behind the foot, the cords of the two sides meet ventrally to the rectum. Hence, if the cerebral commissure is included, a nerve cord in contact with the epithelium is found all the way round in the pallial groove, even in front of the anus (Fig. 135). The lateral cord has an external layer of nerve cells, but no distinct ganglionic swellings. Only, the most anterior part of the cord, close to the cerebral ganglion, seems to lack nerve cells, as may also be the case with some parts of the commissure below the rectum, where details have been difficult to make out.

Nerves from the lateral cord:

(a) The medially directed nerves of the lateral cord are all segmental *latero-pedal connectives,* which will be dealt with below.

(b) *The external (anterior) gill nerves* are emitted from the lateral cord a little in front of each of the five gills, and the basal part may or may not be in common with that of a nerve to the pallial margin (Fig. 135). The external gill nerve turns caudally to enter the base of the gill together with the efferent

(arterial) gill vessel and the external gill muscle (Fig. 59), accompanying these structures along the anterior side of the gill stem and giving off branches along the ventral margin of each lamella (Fig. 61).

(c) *The internal (posterior) gill nerves.* Approximately at the level of each gill base a nerve arises from the lateral cord (Fig. 135), passing directly into the gill together with the internal gill muscle and the afferent gill vessel (Fig. 59). The nerve follows the posterior edge of the gill stem, branching out along the dorsal margins of the lamellae. The base of the internal gill nerve may also be connected with that of a pallial nerve.

(d) *The pallial nerves* are emitted more irregularly from the lateral cord. The number found between two subsequent gills varies from two to five, and there are some such nerves also in front of the first gill, as well as behind the last one laterally to the rectum (Fig. 135). In all, about 26 pallial nerves of different sizes are found on each side, including those from the cerebral ganglion and commissure. Like the other laterally directed nerves from the lateral cord the pallial nerves are closely attached to the basement membrane of the mantle epithelium. Most of the pallial nerves branch several times, the larger branches running to the outer and middle marginal folds of the pallium. Those to the outer fold often turn caudally to pass for a considerable stretch along the margin, but there is no true circular nerve in this region.

(e) *The renopore nerves* are very small and difficult to detect. They originate from the lateral cord between the anterior and posterior gill nerves of each segment to pass along the epithelium to the region of the renopore.

THE PEDAL NERVE CORDS

The pedal cords start from the caudo-medial part of the cerebral ganglia, taking at first a medio-caudal course so that the two cords run fairly close together through the propodial area (Fig. 135). Then, they turn more laterally to enter the musculature of the foot. All the way in front of the foot the pedal cords are in close contact with the ventral body wall. When entering the foot, the cords pass dorsally to the first latero-pedal muscle while keeping ventrally to the medio-pedal one. Inside the foot the cords are situated in a blood sinus, lying at a considerable distance from the ventral epithelium fairly close to the peri-intestinal blood sinus (Fig. 138). The cords are connected by a strong interpedal commissure in the base of the anterior foot margin. From there they turn laterally to run parallel to the periphery of the foot until, in the region in front of the anus, they are continuous with each other across the midline, ventrally to the rectum. This transverse connection is imbedded in the foot musculature at some distance in front of the posterior foot margin. The anterior interpedal commissure, the pedal cords, and the posterior connection actually form a nerve ring inside the circular, muscular foot margin (Fig. 135). All the way these cords are placed ventrally to the extreme ramifications of the medio-pedal muscles and dorsally to those of the latero-pedal ones (Figs. 119, 122).

Histologically the pedal cords consist of a central bundle of fibres and an external layer of ganglionic cells. Segmental swellings were sought for in vain by means of dissections of Spec. X (Fig. 140) and of graphic reconstruction of the sectioned Spec. III. Nor could any swellings be seen in the horizontal series (Spec. IV). The most anterior parts of the pedal cords, in front of the first latero-pedal connective, seem to be devoid of nerve cells.

The nerves given off from the pedal cords are:

(a) *Nerves to the postoral tentacles* (Fig. 136). Two small nerves are emitted from the pedal cord between the cerebral ganglion and the first latero-pedal connective on each side. These nerves leave the medial side of the pedal cord to pass down into the posteriorly directed part of the tentacle ridge. The posterior nerve gives off branches also to the body surface and probably to some of the muscles.

(b) *The medial foot nerves* (Fig. 135) arise medially from the pedal cords to spread in the central membraneous part of the foot. They are small and occur at irregular intervals. Metameric arrangement was not found in these nerves. Perhaps the anterior interpedal commissure might be regarded as an enlarged nerve of this kind, but careful examination showed that the medial foot nerves do not cross the midline in this way.

(c) *The latero-ventral foot nerves* (Fig. 135) are fairly big and numerous. They leave the pedal cord to pass latero-ventrally down between the fibres of the mm. latero-pedales to the free margin of the foot. On the way they give off numerous branches to the wall of the foot. Whether they also innervate some musculature could not be established. Usually, there are two such latero-ventral pedal nerves between two successive latero-pedal connectives in the region of the foot.

(d) *The latero-pedal connectives* have a strictly metameric arrangement in accordance with that of the muscles and gills. In Spec. III ten pairs of latero-pedal connectives are present. In addition there is in this specimen a similar, but very small nerve on the right side in the anterior foot region (marked x in fig. 135), situated like a typical connective, but ending without connection with the lateral cord.

The first two pairs of latero-pedal connectives are situated in the propodial region and have rather complex relations to the numerous surrounding muscles. The remaining eight connectives are distinctly metameric, with constant relations to the eight pairs of pedal retractor muscles (Figs. 137, 167). The third connective joins the pedal cord in front of the foot, whereas the last seven pairs join inside this organ. The lateral ends of the connectives meet the lateral cord proper at almost regular intervals. Only, the first connective differs in entering the lateral portion of the cerebral ganglion.

The relations of the latero-pedal connectives to the gill nerves are as follows. Nos. 6 to 9 lie in front of the two respective gill nerves, whereas connective No. 5 enters the lateral cord between the corresponding external and internal gill nerves.

The typical latero-pedal connectives (Nos. 4-10) leave the pedal cord to run straight laterally, passing dorsally to the m. latero-pedalis, but ventrally to the m. medio-pedalis and the m. circularis pedis (Fig. 137). Sometimes they pass between the ventral fibres of the circular muscle. On the way towards the side of the foot, i.e. approaching the wall of the pallial groove, the connective runs closely along the anterior surface of the m. latero-pedalis. In the region of the innermost part of the pallial groove, the nerve is often found to be curled because of the strong contraction of the foot muscles. Then, the nerve passes straight outwards to the lateral cord, running closely along the roof of the pallial groove inside the m. circularis pallii.

In the peripheral part of the foot some branches are given off to the foot muscles and to the wall of the pallial groove, including probably the two circular muscles of that region.

The 3rd latero-pedal connective is similar to the following ones, innervating the pedal retractor A. It connects with the pedal cord just in front of the anterior foot margin.

The two first connectives will be discussed separately because their relations to the muscles are different (Fig. 137). No typical pedal retractors are present in this region. The first connective leaves the lateral parts of the cerebral ganglion, passing medio-caudally to connect with the pedal cord. Immediately after leaving the cerebral ganglion the connective passes above (i.e. in front of) the m. retractor veli posterior. However, the nerve passes through some of the superficial bundles of this muscle, forming a flat membrane of nerve fibres. The nerve seems to innervate the muscle mentioned, but in addition gives off a branch of unknown destination.

The second connective passes ventrally (behind) the m. retractor veli posterior and does not seem to be related to any particular muscle. It gives off nerves to the statocysts and to the tentacles as described below.

THE NERVES TO THE POSTORAL TENTACLES AND TO THE STATOCYSTS

The nerves of the post-oral tentacles come from three different directions (Fig. 136). As mentioned above, a tentacle nerve is emitted from the postero-medial corner of the cerebral ganglion and passes medially to the transverse part of the tentacle ridge just behind the mouth. The next two tentacle nerves come from the pedal cord and pass down into the posteriorly directed part of the tentacle ridge. The main part of the innervation, however, seems to come from the 2nd latero-pedal connective, which gives off some small branches (about three) down into the latero-posterior part of the tentacle ridge. These small nerves could not be followed into the tentacles proper, but they definitely pass in that direction.

The statocyst nerves are important for the understanding of the morphology of the nervous system since in all other molluscs the statocysts are innervated from the cerebral ganglion. The statocyst nerve has been traced on both sides in both Spec. III and Spec. IV. It originates mainly from the ventral side of the statocyst to take a strictly anterior course (Fig. 136), all the way in close contact with the epithelium of the roof of the pallial groove. For some distance the nerve runs just medially to the duct connecting the statocyst with its point of origin in the epithelium. Then the nerve fuses with the 2nd latero-pedal connective. In the horizontally sectioned Spec. IV it can be distinctly seen that the fibres from the statocyst nerve, after fusion with the connective, pass antero-laterally out to the lateral nerve cord.

COMPARATIVE REMARKS

A primitive feature in the nervous system of *Neopilina* is the almost uniform distribution of the nerve cells along the main cords. Among other molluscs such absence of concentration is found only in chitons and in some primitive prosobranchs, as well as in the Solenogastres. The chitons may be said to be even more primitive than *Neopilina* in their uniform circum-oral nerve ring without distinct cerebral ganglia.

The general morphology of the nervous system is much like that of chitons, but there are some interesting differences. The lateral cords meet posteriorly, ventrally to the rectum in *Neopilina*, but dorsally to the rectum in chitons. In this respect *Neopilina* agrees with bivalves and gastropods (disregarding torsion) with their sub-rectal visceral commissure, provided that the visceral loop is homologous with the lateral cords.

Another difference relates to metamerism. In *Neopilina* the segmental rhythm is the same in all organ systems, including the gill nerves and the latero-pedal connectives. In chitons, however, the distribution of the nerves is much less regular and at any rate there is no correspondence in the rhythms of the gill nerves and the latero-pedal connectives.

Furthermore, the nervous system of *Neopilina* is closely associated with the ventral body wall, much more so than in other molluscs. This would seem to be a primitive feature.

The ganglion situated laterally to the mouth in *Neopilina* has been called the cerebral ganglion, but apparently corresponds to the cerebro-pleural ganglion in bivalves and scaphopods. In gastropods this ganglionic mass is subdivided into a cerebral and a pleural ganglion. The course of the statocyst nerve is particularly important for the interpretation of these relationships. In other molluscs the statocyst nerve is said to originate (or to end!) in the cerebral ganglion, although the statocysts are situated near the pedal ganglion, and the statocyst nerve can be closely associated with other connectives. In *Neopilina* the statocyst nerve joins the second latero-pedal connective. However, the differences may be more apparent than real. In primitive bivalves (HAAS 1935, Fig. 502) two connectives from the cerebro-pleural ganglionic mass pass down to the pedal ganglion on each side. Probably these connectives correspond to the proximal part of the pedal cord and to the first latero-pedal connective in *Neopilina*. In bivalves the statocyst nerve might be supposed to represent the remains of a connective corresponding to the 2nd latero-pedal one in *Neopilina*, if all the fibres except those from the statocyst have disappeared.

A similar discussion might obtain also in comparisons with gastropods, if it is remembered that the single ganglionic mass on each side has been subdivided into a cerebral and a pleural ganglion emitting the cerebro-pedal and pleuro-pedal connectives, respectively. These would then correspond to the proximal part of the pedal cord and to the first latero-pedal connective, respectively, in *Neopilina*, whereas the statocyst nerve would correspond to the vestigial 2nd latero-pedal connective. The latter, then, must have shifted its position in gastropods from the base of the visceral cord just behind the pleural ganglion to the cerebral ganglion proper.

SENSE ORGANS

Only three kinds of distinct, localized sense organs have been discovered in *Neopilina*, viz. (1) the paired preoral tentacles, (2) the unpaired subradular organ, and (3) the paired statocysts. It is reasonable to assume the velum and the postoral tentacle tufts to contain sensory cells, but probably their chief functions are not sensory. The same holds good of the marginal pallial fold and of the foot surface. In the pallial groove, sense organs of the type found in chitons have been searched for in vain, nor have osphradia been observed, but the absence of these organs cannot be established with full certainty. Aesthetes are definitely not present.

The preoral tentacles. The tip of each preoral tentacle with its high epithelium and rich innervation evidently serves as a sensory organ (chemoreceptor?). Its histology is described in some detail on p. 22 (Fig. 70).

The subradular organ is described as part of the oral cavity on p. 25. It is innervated from the subradular nerve and ganglion (p. 47, Fig. 136), and is characterized by its extremely high epithelial cells (Fig. 81).

The statocysts. The paired, well-developed statocyst is present in the ventral body wall behind the tentacle tuft, in front of the pedal retractor A but

behind the m. retractor veli posterior (Figs. 129, 137). It is found in the square formed by the pedal and the lateral nerve cords, together with the 2nd and the 3rd latero-pedal connective (Fig. 136).

Each statocyst is a flattened epithelial vesicle connected with the pallial groove by a long duct. From the vesicle the duct runs in an antero-lateral direction, but its connection with the mantle epithelium is still within the square formed by the said four nerves (Fig. 136).

The largest diameter of the vesicle is the transversal one (215μ), the minimum one being vertical (90μ). The height of the epithelium in the ventral wall of the bladder is 16μ or more, increasing in the side wall and decreasing again to about 11μ in the dorsal wall. The epithelial cells are high, columnar, and their basal ends are attached to a thin fibrous membrane. The nuclei are situated in the basal parts of the cells. It was not possible clearly to recognize the sense cells supposed to be present at least in the ventral part of the vesicle. This ventral wall, like the lateral ones, contains high cells with distinctly chromophilic plasm (Fig. 139), whereas the cells in the roof are lower and stain lightly. The opinion that the sense cells are situated in the ventral wall of the vesicle is supported by the manner in which the nerve originates. When traced back from its junction with the 2nd latero-pedal connective, the nerve can be seen to bend ventrally just in front of the statocyst, spreading over its ventral wall like a fibrous membrane. Apparently most of the nerve fibres originate in the ventral wall, as it was not possible to trace any of them up to the dorsal side of the vesicle. Sensory hairs are indistinctly indicated on the ventral epithelium.

Hence, the study of the statocysts seems to show that the animal rests on the bottom, foot downwards, thus disproving the hypothesis proposed in the preliminary note (LEMCHE 1957a).

The lumen of the statocyst is filled with debris without definite structure. If the statoliths consisted of calcium carbonate, they could not have escaped being destroyed by the acid used for re-fixation and decalcification.

The duct is approximately 0.6 mm long and 0.02 mm in diameter. It passes from the statocyst in an antero-lateral direction closely along the epithelium of the pallial groove. The walls are epithelial and the lumen narrow but distinct. The duct ends in contact with the mantle epithelium and probably its lumen opens into the pallial groove, but unfortunate circumstances made it impossible to establish whether or not there is any open communication.

Comparative remarks. In the structure and situation of the subradular organ *Neopilina* agrees almost entirely with the Polyplacophora, but in the other sense organs it is more like the other molluscs. *Neopilina* has no aesthetes, and the statocysts, absent in the polyplacophores, are present in *Neopilina* as in all other mollusc groups. The preoral tentacles of *Neopilina* would appear to be homologous with the preoral tentacles in gastropods. Osphradia or other sense organs have not been found in *Neopilina*, but, the negative evidence not being too reliable, we do not dare to draw any far-reaching conclusion on this basis.

CONNECTIVE TISSUE AND BLOOD CELLS

The subepithelial tissues in many parts of the body contain non-staining fibrils in great numbers. Although details could not be made out, it is apparent that most of these fibrils are connective tissue elements. The other parts of the connective tissue cells are indicated only by the presence of scattered nuclei. This type of connective tissue is present particularly in the foot, in the marginal parts of the pallium, in the velum, and in the postoral tentacles. In the latter organs and, less pronounced, in the velum the interstitial fluid has been precipitated as a fairly dense, hyaline substance. Maybe this sort of interstitial substance is viscous in life and adds to the rigidity of these organs. A similar precipitate was not found in other parts of the body (Figs. 78, 79). Whereas, owing to the state of preservation, the fibrous connective tissue could not be studied in detail, it was possible to observe typical Leydig cells and to distinguish them from the blood cells.

The Leydig cells are well developed. They are distinctly delimited, oval in shape, and contain an eccentric, spherical nucleus in a reticulate cytoplasm (Fig. 142). The presence of numerous dark-staining granules in the cytoplasm seems to be typical of these cells. The maximum diameter of the cell body is 13-15 μ, that of the nucleus being 3.5 μ. These cells are particularly abundant in the foot between the ramifications of the pedal retractor muscles and in the proximal part of the pallial fold. More scattered Leydig cells are found all over in the

foot, in the pallial fold, and in the ventral body wall of the mouth region. Similar cells occur also in the basal part of the velum, although in our preparations they look more vesicular in that place.

The blood cells. Most vessels in the sections are filled with a precipitate which is coarser or finer depending on the conditions of fixation. In this precipitate, free cells are often found, here interpreted as circulating cells of the blood. In places such cells are present in considerable numbers, usually attached to the walls of the vessels, e.g. in the heart and in the ventral, venous sinus of the pallial fold. As far as could be observed, the cells are of one type only. They are round or slightly oval with a maximum diameter of 7-10 μ (Fig. 141). Their plasm is faintly stainable and almost hyaline, sometimes containing a few granules of a slightly basophilic substance. The nucleus is round and small with a diameter of about 3 μ, looking completely compact and staining blackish with the hematoxylin.

At the first glance the blood cells may be confused with the Leydig ones, but they are smaller than the latter, more rounded, and possess more hyaline plasm. The blood cells are found in the vascular spaces and in addition also in the pericardial cavity.

THE VASCULAR SYSTEM

The present account of the vascular system will deal particularly with the heart and with the vessels immediately connected with this organ and with the gills. These vessels are well-defined by fairly distinct walls and could be studied in both section series. The remaining parts of the vascular system consist of big irregular sinuses surrounding the internal organs. Since these sinuses are difficult to treat morphologically, they will be mentioned only briefly.

Wax-plate reconstructions of the heart were made from both section series. The graphic reconstructions illustrating the arterial part of the system (Fig. 144) and its relation to the coelomic cavities (Fig. 146) were made from Spec. III.

GENERAL MORPHOLOGY

The general organization of the vascular system in *Neopilina* is the one common to all molluscs (Fig. 143), with the exception that the ventricle is paired. The dorsal heart, attached to the sides of the rectum in the posterior body region, receives the arterial blood from the efferent gill vessels via the atria. From the heart the dorsal aorta passes forwards, ending in the big hemocoelic space in the anterior body region. From there the vascular sinuses are continuous throughout most parts of the body. Particularly big hemocoelic spaces extend around the inner organs such as the radula apparatus, etc., and the complex formed by the intestine, the gonads, and the liver. This latter, peri-intestinal sinus is continuous laterally with a longitudinal venous one in the pallial fold just medially to the lateral nerve. From there the gills receive the venous blood via afferent gill vessels.

THE EFFERENT GILL VESSELS AND THE ARTERIAL MANTLE SINUSES

An efferent vessel drains each gill along its anterior edge (Figs. 59, 143). When this arterial gill vessel has entered the pallial fold at the base of the gill stem, it continues as a sinus between the lobules of the neighbouring nephridium upwards to the overlying dorsal body wall (Fig. 125), then inflating to form an arterial pallial blood sinus (Fig. 148). The pallial sinus is lateral in relation to the insertion areas of the pedal retractors and dorsal to the nephridium. The arterial pallial sinus formed by the last (5th) gill vessel on each side is directly drained by the last atrium, whereas those belonging to gills 1-4 on each side are interconnected to form a big longitudinal sinus above the bases of these gills (Fig. 144). This big sinus is drained by the more anterior atrium with which its posterior end is continuous.

The arterial pallial sinuses have very thin membraneous walls visible only in a few places. Usually the sinuses are bordered directly by the dorsal body wall and by the nephridial lobules (Fig. 148).

THE ATRIA

There are two pairs of atria in both specimens sectioned. The posterior one on each side opens into the hindmost part of the ventricle, draining the arterial pallial sinus of the last gill (Fig. 144). Therefore, this atrium seems to be a strictly segmental one, belonging to the last (5th) gill-bearing segment. In addition the last atrium receives some sinusoid vessels from the posterior part of the preceding nephridium, and a small vein from the pallium just

laterally to the rectum (Fig. 144). The segmental character of this atrium is emphasized by its position between the segmental foot retractors G and H. The more anterior atrium on each side is connected with the lateral corner of the corresponding ventricle (Fig. 144). The atrium is situated between the pedal retractors F and G, and thus should be regarded as the atrium of the 4th gill-bearing segment. However, when the atrium is followed laterally, it is seen to fuse with the above-mentioned longitudinal arterial pallial sinus. Thus it does not only drain the gill of its own segment (the 4th), but also gills 1-3. The drainage of gills 1-4 is therefore similar to the arrangement found in chitons, in which the single atrium on each side receives blood from all the gills by means of a similar longitudinal pallial sinus.

Both pairs of atria being directly continuous laterally with the respective pallial sinuses, it becomes necessary to define what is meant by the term atrium. We use this term for that part of the vessel which is in contact with the pericardial cavity, although not always completely surrounded by it (Figs. 146, 147).

The shape of the atria is tubular, but the tube flattens towards the junction with the pallial sinus. The walls are thin (1-3 μ), consisting of a membrane which contains longitudinal muscle fibres and probably connective tissue. A number of cells looking like blood cells attach to the inner and outer side of the wall, but it is not possible to see the endothelial lining supposed to exist.

THE VENTRICLES

There is one pair of ventricles, situated each on either side of the rectum above the posterior margin of the foot. When seen from above, each ventricle appears triangular with the long medial side attached to the wall of the rectum (Fig. 144). The opposing angle, projecting laterally, is connected with the anterior atrium. Caudally the ventricle ends in a short blunt diverticulum, the posterior atrium opening through its ostium in the hind part of the postero-lateral wall. The anterior corner of the triangular ventricle is prolonged as an aorta on each side of the rectum. In transverse sections the medial wall of the ventricle appears concave, being closely attached to the sides of the rectum (Figs. 143, 147).

Communications between the two ventricles have been intensively looked for both above and below the rectum, but in vain. The collapsed state of many vessels makes it difficult to arrive at safe conclusions of this kind, but as far as intercommunications between the ventricles are concerned, this negative statement should be fairly reliable. In many places the medial wall of the ventricle was observed to turn over directly into the dorsal and ventral walls, as shown in Fig. 143, which certainly speaks against the presence of communications across the mid-line. The presence of paired aortas in front of the ventricles supports this view.

The medial walls of the ventricles are directly attached to the connective tissue membrane of the rectum. Sometimes the connection is less intimate and there may be some meshwork of connective tissue between the two walls. The other walls of the ventricle are surrounded by the pericardial cavity.

The ventricular wall attaching to the rectum is very thin (1-2 μ). The free walls, i.e. those surrounded by the pericardial cavity, are thicker (4-5 μ) (Fig. 151). In the latter there is a distinct membrane of connective tissue together with numerous smooth muscle fibres, which are distinct in tangential sections, and which are present on both sides of the membrane. The inner side of the wall appears devoid of endothelial lining, but numerous blood cells stick to the wall. The outer (pericardial) surface of the wall is lined by a distinct layer of cells, which looks like an endothelium.

Many of the muscle fibres in the ventricular wall appear to be about 5 μ broad. Thicker fibres with a diameter up to 10 μ are present in the ostia (see below) and spread from there along the inner side of the ventricular wall. The muscle fibres are predominantly longitudinal, reaching from the posterior part of the ventricle forwards to insert on the dorsal body wall. Some of the fibres arising in the region of the ostia have been found to run transversally to insert on the wall of the rectum, but the majority turn anteriorly to follow the antero-lateral margin of the ventricle to the region of the aorta. With the said exception there are few or no transverse muscular elements in the ventricular wall.

THE ATRIO-VENTRICULAR OSTIA

As described above, there are two pairs of atrio-ventricular ostia in the heart (Fig. 144). They have almost the same diameter as the atria, at least as concerns the external contour (Fig. 147). However, the communication through the ostium is partly blocked by a distinct atrio-ventricular valve (Fig. 151), which looks like a fold from the inner surface of the tube. Its exact shape could not be made out,

because the valve is wrinkled and looks distorted, but it is not ring-shaped. The valve consists of a central lamella of connective tissue, lined on both sides by a layer of thick circular muscle cells similar to those of the buccal muscles. They are very broad (7-15 μ) and contain numerous basophilic granules, which tend to collect into lumps or plates, often simulating mitotic metaphase plates (Fig. 152). Muscle fibres of this same type are present also as a distinct constrictor on the outside of the wall round each ostium.

THE AORTA

Each ventricle continues forwards into an aorta attached to the side of the rectum in the same way as the ventricle (Fig. 144). Similarly the pericardium continues forwards as a narrow duct on each side, closely attached to the lateral wall of the aorta (Figs. 146, 153, 167). The wall of the aorta appears as only a thin membrane, but it contains a distinct longitudinal muscle bundle in its lateral wall bordering on the pericardial diverticulum.

In the central body region only one aorta is found, situated in the narrow median space above the rectum and below the dorsal body wall (Fig. 144). This unpaired aorta can be traced without difficulty caudally straight into the right paired aorta. The foremost part of the left paired aorta has completely collapsed so as to be very difficult to trace in the sections, but apparently it turns to the right to fuse with the right aorta in the manner shown in Fig. 144. One of the reasons for this interpretation is that the muscle band in the wall between the aorta and the pericardial diverticulum can be observed to turn to the right and to fuse with the corresponding one from the right side, thus forming an unpaired band. At the point where the two aortae fuse to form the unpaired one, the muscle band mentioned lies ventrally to the vessel and forms a ventral mesocardium-like membrane between the aorta and the rectum, thus separating the two pericardial diverticula which now lie beneath and somewhat laterally to the aorta (Fig. 167).

In the more caudal part the unpaired aorta runs along the dorsal mid-line of the rectum, but at the point where the rectum anteriorly bends to the right into the last intestinal coil, the aorta continues forwards in a strictly median position in close contact with the dorsal body wall (Fig. 144). Anteriorly the aorta extends to the region above the anterior foot margin. Then it widens like a funnel, probably to open directly into the blood sinuses of the anterior body region, but details could not be studied because of some damage to Spec. III, nor could it be decided whether branches are given off along the course of the aorta.

THE BLOOD SINUSES

The arrangement of the blood sinuses could not be made out in detail because of difficulties in tracing their delicate walls. However, most of the inner organs are surrounded by an extensive system of blood sinuses. The organs of the anterior region, such as the radula apparatus, the pharynx, and the oesophagus, are surrounded by a single big anterior blood sinus (Figs. 90, 129). Another big sinus occupies the spaces around the stomach, the liver, the intestinal loops, and the gonads (Figs. 8, 9, 167). There is a distinct but narrow perineural blood sinus around the pedal nerve cord on each side (Fig. 138). Between the lobules of the nephridia in the pallial fold numerous small spaces probably belong to the blood-sinus system. In addition the pallial fold contains two main longitudinal sinuses. One of them is the arterial pallial sinus dorsal to the nephridia, collecting the arterial blood from the gills before it passes further to the heart (See above). The other one is the longitudinal venous pallial sinus placed ventrally to the nephridia and giving off the afferent gill vessels (Figs. 143, 148). This sinus lies in close contact with the wall of the pallial groove, medially to the lateral nerve cord and laterally to the big segmental muscles. It is continuous from the anterior blood sinus in front to the region of the last gill, communicating extensively also with the peri-intestinal blood sinus (Fig. 143). In each gill-bearing segment this venous pallial sinus gives off an afferent gill vessel along the wall of the pallial groove ventrally to the nephridial lobules, but dorsally to the lateral nerve cord, to enter the gill (Fig. 167).

COMPARATIVE REMARKS

The vascular system of *Neopilina* is of a generalized molluscan type, but some of its features may be regarded as particularly primitive, viz. the slight differentiation of the sinuses into true vessels and the indications of metamerism. The paired state of the ventricle and of the posterior part of the aorta could be taken to support the view that this organization is the ancestral one in molluscs. Although this hypothesis makes it easy to explain the varying position of the ventricle in relation to the rectum within

the different groups, the embryonic development of the molluscan heart indicates a somewhat different interpretation of the variations. Embryologically the ventricle is part of the continuous hemocoelic space of the body, enclosed between the pericardial sacs to form a tube. If the hemocoelic space involved surrounds the rectum, as e. g. in *Neopilina* and many bivalves, the result will either be that the rectum passes through the ventricle tube or that it divides the hemocoelic space into two separate ventricles as in *Neopilina.*

In the vascular system of *Neopilina,* metamerism is indicated in the repetition of the afferent and efferent gill vessels, and in the presence of two pairs of atria, the hindmost one being a typical segmental atrium of the 5th gill-bearing segment (Fig. 165). Two pairs of atria are present also in *Nautilus,* but we have no means of deciding whether they represent the "same" segments as in *Neopilina.*

Neopilina is similar to the polyplacophorans in the presence of longitudinal pallial sinuses supplying the gills.

THE COELOMIC SYSTEM

In addition to the lumen of the gonads, which may be regarded as part of the coelom. there are two distinct sets of coelomic cavities in *Neopilina,* viz. the paired pericardial sacs, and the dorsal body coelom, which is likewise paired. Both kinds of cavities are situated immediately beneath the dorsal body wall, the pericardial sacs on either side of the rectum in the heart region, and the dorsal body coelom over most parts of the body in front of the heart. Communications between these two kinds of coelomic cavities have not been seen, but their possible existence cannot be definitely excluded.

THE PERICARDIAL SACS

The morphology of the pericardial sacs could be reconstructed satisfactorily from Spec. III (Fig. 146). The two sacs are symmetrically placed laterally to the rectum. Each surrounds the corresponding ventricle and the two atria, except medially, where the ventricle borders directly on the rectum (Figs. 143, 147). As far as observation goes, there are no connections between the pericardial sacs of the left and the right side.

In a caudal direction the pericardium extends a little beyond the posterior end of the ventricle along the side of the rectum. Laterally the pericardium shows one diverticulum along the posterior and another along the anterior atrium (Fig. 146). Medially the pericardium extends above and below the ventricle, attaching directly to the wall of the rectum. The pericardium continues anteriorly as a narrow tube, which lies laterally of the paired and unpaired aortas. It was not possible to establish how the tube ends anteriorly, because it is partially collapsed. It could be traced approximately to the point where the unpaired aorta inflates to open into the anterior blood sinus.

When the paired aortas have fused to form the unpaired dorsal aorta, the left and right pericardial tubes surround the aorta and meet ventrally to form the median aortic septum connecting the aorta with the rectum – and containing the muscle band mentioned under the description of the aorta (Fig. 167).

The lumen of the pericardial cavity looks empty, but several cells attach to the wall. These cells are rounded or elliptical with a blackish nucleus and appear to be identical with the blood cells.

The walls of the pericardial cavity are thin membranes of connective tissue. A regular endothelial lining could not be discovered. The dorsal wall is closely attached to the body wall, the ventral one borders on the blood sinuses and on the intestinal loops, most laterally also on the nephridia.

THE DORSAL BODY COELOM

The dorsal body coelom, too, is situated immediately beneath the dorsal body wall and is distinctly paired. Its character of a coelom is indicated by its contact with the nephridia. In most places its lumen is very narrow, either cleft-like or sometimes totally collapsed (Fig. 157). In such cases only the two characteristic epithelial walls indicate the extension of the coelom. Presumably the contraction of the animal when killed has contributed to this partial obliteration of the coelomic lumina. This collapsed state, together with some damage to the specimen dorsally, makes it very difficult to find out details about the coelom. The question whether it is segmentally divided or not must therefore be left open. However, the extension of the coelom under the body surface could be safely reconstructed because of the characteristic appearance of the epithelium lining the cavity (Fig. 146).

The dorsal coelomic cavity begins just in front of

the heart on either side, extending anteriorly as a big flattened sac beneath the dorsal body wall and reaching from near the mid-line out to the pedal retractor muscles. The medial margin extends above the intestine, the pericardial tubes, and the aorta so as almost to reach its contralateral partner (Figs. 153, 167). Just in front of the heart, but not farther anteriorly, another medially directed fold of the coelom is developed more ventrally, extending below the pericardium and the rectum. In Spec. III, at least, this ventral fold is better developed on the right side, in some places reaching to the left side, ventrally to the intestine, but it does not really fuse with its contralateral partner, so there is no communication between the two.

The anterior extension of the body coelom is of particular interest, but unfortunately the reconstruction of these parts is somewhat incomplete because of the damage to the dorso-medial area behind the apex.[1] However, the lateral contour of the coelom can be traced with certainty to the very anterior end of Spec. III (Fig. 146). Furthermore, it is certain that no coelom is present over the medial parts of the anterior body region. A comparison between Spec. III and IV definitely shows the coelomic cavities to extend forwards as a pair of lateral diverticula in the anterior body region. These diverticula pass medially to the pedal retractors A to C to contact each other in front of the pharynx (Fig. 146), where they are separated only by a median septum (Fig. 89). The lateral contours of these anterior coelomic parts show two deep indentations corresponding to the pedal retractors A and C, whereas B has not caused a deep notch.

In both section series the anterior part of the body coelom is seen to expand into wide lumina in the interspaces between the pedal retractors (These lumina are not visible in Fig. 146, which shows the outline of the whole coelom only). The foremost lumen lies between the preoral region and the retractor A (Fig. 129), the next between A and B, and the 3rd between B and C (Fig. 149). In the suitably sectioned Spec. IV, a tendency to a similar rhythmical cavity formation was observed also between the next pedal retractors. These cavities may perhaps be interpreted as segmental coelomic sacs, but it should be emphasized that the compressed state of the walls between the cavities makes it impossible to see whether true dissepiments are present, i.e. whether we have to do with real coelomic segments or not. On the other hand, the compressions between the cavities might be a direct effect of the contraction of the pedal retractors when the animal was killed. The question of the segmental subdivision of the coelom must therefore await further investigation on fresh material.

The walls of the body coelom consist of a thin fibrous membrane and an epithelium of a characteristic appearance (Figs. 103, 150). The epithelial cells are 12-15 μ high and 4-5 μ broad. The nuclei have not taken the stain, thus being difficult to see. Almost every cell contains some very characteristic, irregular granules, which in the preparations have a brownish or brownish green colour. Their size is about 3 μ, and usually 5-6 such granules are present in each individual cell. We regard these granules as a kind of pigment, as their colour cannot come from the stain used. Since they are present in very few other epithelia, these granules make the coelomic epithelium easily recognizable. The pigment-containing cells are strikingly similar to the chloragogen cells of annelids, but they seem to have been completely unknown in the coelom of molluscs. Some cells have a row of distinct basal granules along the surface, indicating the presence of cilia.

The body coelom seems to be in open connection with most of the nephridia, and there are also some slight indications of connections with the gonads – as described below.

COMPARATIVE REMARKS

In *Neopilina*, the coelomic system consists of three probably separate parts, viz. the paired pericardial sacs, the paired dorsal body coelom, and the two pairs of gonads. In this respect *Neopilina* could be said to represent a more advanced stage than *Nautilus* and some other cephalopods, in which the different parts of the coelom communicate.

The pericardium in *Neopilina* is developed in the way well known from other molluscs, with the exception of its being paired. The paired condition is a primitive feature as indicated by the paired rudiments in the embryos of other molluscs, and at the same time helps to explain the different positions of the pericardium in relation to the rectum. Moreover, if the pericardium is to be derived from paired coelomic sacs, it must be an originally paired structure.

The diverticula extending forwards along the

1. Distinct connections between the pharynx and the anterior parts of the dorsal body coelom are present in *N. ewingi*. The interpretation of these cavities will therefore be reconsidered in the report on the Vema material.

aorta in *Neopilina* have no counterparts in other adult molluscs. However, the anteriorly directed "Zellzapfen" from the pericardium in the embryo of *Acanthochiton* (HAMMARSTEN and RUNNSTRÖM, 1925, Fig. Q) might be a structure in point, even if the gonads proliferate from its ventral side as described by these authors.

The interpretation of the dorsal body coelom in *Neopilina* is more easily achieved if the conditions in chitons are used for comparison. The dorsal body coelom in *Neopilina* appears homologous with the gonads of chitons, both being situated immediately below the shell in contact with the dorsally placed aorta (Figs. 166, 167). A difference is that the gonad in chitons is restricted to the postoral region, whereas the dorsal body coelom in *Neopilina* extends even preorally. In *Neopilina* the dorsal coelom is distinctly paired, whereas the paired gonad rudiment in polyplacophorans usually fuse during the development (except in *Nuttallochiton* – PLATE 1898 and *Notochiton* – THIELE 1906).

The ventral gonad in *Neopilina* seems to have no counterpart in adult chitons (Figs. 166, 167). An outgrowth from the coelom extending ventrally to the intestine was described by KOWALEWSKY (1883) in embryos of *Chiton polii*. This part of the coelom might be taken to represent a homologon of the gonad in *Neopilina,* but it was not found in *Acanthochiton discrepans* by HAMMARSTEN and RUNNSTRÖM (1925).

If the gonad in bivalves, gastropods, and scaphopods is regarded as strictly homologous to that of chitons, it would correspond to the dorsal body coelom of *Neopilina* as well. In spite of the fact that the gonad in all cases arises from the pericardial wall, we do not feel convinced that this homology holds good in all cases, especially as regards bivalves, some of which show a most striking ventral position of the adult gonad. The rather apical position of the gonads in gastropods would seem to correspond much better to that of the dorsal body coelom of *Neopilina.*

Finally attention should be called to the unexpected presence of pigment granules in the epithelium of the dorsal body coelom in *Neopilina.* No other mollusc is known to possess anything similar in its coelom, but a coelomic epithelium of almost identical appearance is well-known from annelids as chloragogen tissue. In some molluscs (e.g. *Anodonta* – FERNAU 1914), similar inclusions have been found in the excretory epithelium of the kidneys.

THE NEPHRIDIA

The nephridia occupy most of the interior in the proximal half of the pallial fold laterally to the pedal retractor muscles (Fig. 157). These organs repeat themselves in the same rhythm as do the pedal retractors, the gills, the latero-pedal nerve connectives, etc. The problems of segmentation of the coelom, however, is far from having been finally solved (see above) and the segmental limits could not be established. Consequently we prefer in this place not to enter into any interpretation of the theoretical belongings of the different nephridia to specified segments. Instead, we choose to refer preliminarily to each nephridium simply by way of its topographical situation off (lateral to) the nearest pedal retractor.

Five pairs of nephridia open at the bases of the five pairs of gills, but in addition there is on each side a nephridial complex off the muscles A and B (Fig. 145). This complex opens through a single renopore in the pallial groove well anteriorly to the first gill and off the muscle B. The foremost portion of the complex may perhaps be regarded as a distinct nephridium off the muscle A, but it has no renopore of its own and its interpretation remains very doubtful. Thus, the number of safely identified nephridia on each side is six, and they are placed off the muscles B-G, respectively. Two pairs of nephridia – those off the muscles D and E – also serve as gonoducts in both sexes, but without showing any distinct specialization for this purpose.

THE STRUCTURE OF A NEPHRIDIUM

The two pairs of nephridia serving also as gonoducts are those most easily analyzed. They start from the body coelom with a – probably ciliated – funnel. From this funnel a short narrow duct leads into a nephridial gland constituting the excretory part of the kidney. This part consists of a central sac projecting into numerous lobules (Figs. 145, 167). The sac opens almost directly through a renopore into the pallial groove postero-medially to the base of the respective gill. The connections to the gonad will be discussed in the following chapter.

The nephrostome and duct. At one particular point each nephridium approaches the lateral margin of the dorsal coelom, to which it is connected by a string of cells which we interpret as a nephrostomic duct. In such places in the preparations the coelomic wall shows several irregularly placed openings leading into what appears as small pouches or short blind ducts (Fig. 155). Only a single one seems to continue into the nephridium (Fig. 156), thus forming the true nephrostomic duct. Some of the remaining structures may perhaps turn out to be parts of a sort of folded nephrostomic funnel, but observations on this point are most uncertain, the material being unsuited for such a refined histological examination.

The cells of the nephrostome and of the short adjoining duct are light-staining, much smaller than those of the functional nephridium, but containing similar large vacuoles, which makes it very difficult to see whether a lumen is present or not. The nephrostome cells may contain minute pigment granules, but they differ from the coelomic epithelial cells in staining much lighter (Fig. 155). Cilia have not been observed with full certainty, but basal granules have been observed in the nephrostome cells exactly as in the coelomic ones. The duct proper appears as a very thin string of cells – with or without a traceable lumen – which very soon joins the excretory part of the nephridium.

The nephridial gland. The central sac of the nephridium is situated above the renopore posteriorly or postero-medially to the gill base. Its contour is indistinct, as it gives rise to numerous lobules projecting in all directions and extending even laterally to the gill base. In the reconstruction (Fig. 145) only the contour of the kidney is given, with no regard to the individual lobules.

The walls of these lobules as well as of the central lumen consist of a thin basement membrane and an epithelium of a characteristic appearance very much like that in other molluscs (Fig. 125). The cells are 25-50 μ high, with slightly staining plasm containing numerous large vacuoles. These are larger near the lumen which, therefore, often is indistinctly delimited. The fixation is rather poor.

The renal duct and pore. The duct leading to the renopore is extremely short, leading directly from the central sac through the body wall into the pallial groove (Fig. 154) immediately inside or medio-caudally to the afferent gill vessel and above the innermost lamella of the gill (Fig. 59). The short duct is lined by a columnar epithelium of rather chromophilic cells, but no indication of any papilla is present around the renopore.

MUTUAL CONNECTIONS OF THE NEPHRIDIA

The series of nephridia in the pallial fold on each side appears fairly continuous, as the lobules from two successive nephridia intermingle. Considerable attention was paid to the question whether the lumina of the different nephridia communicate or whether they are separate. Detailed graphic reconstruction of the critical regions were made from Spec. III, showing that the nephridia off the muscles D, E, F, and G on the right side and those off E, F, and G on the left are separate (Fig. 145). Those off the muscles A to C may possibly intercommunicate. The picture, however, is very confused through extensive intermingling of the lobules, and our conclusions are correspondingly uncertain. It is evident at least that the most anterior diverticulum, off the muscle A, communicates with the nephridium off the muscle B. This diverticulum runs first medially and then anteriorly under the muscle A and in front of this muscle, extending forwards to a level lateral to the mouth in the narrow space between the ventral body wall and that of the preoral coelomic cavity. The base of the diverticulum is dilated so as to form a kind of central sac just in front of the muscle A, but as far as observation goes, there is no renopore from this sac. The diverticulum is continuous with the typical nephridium off the muscle B through the renopore of which it probably discharges its products.

CONNECTIONS WITH THE COELOM

In the sections the connections with the coelom are difficult to find and could be studied only in the better preserved Spec. III. The fragile and slender nephrostomic ducts are sometimes pressed between other organs, and in one case the duct has apparently been torn off (the nephridium off the muscle C left). Connections with the dorsal coelom through nephrostomes of the kind described above have actually been observed from the nephridia off the muscles D and E, but they are strongly indicated also off C (Figs. 145, 146). The nephridium off the muscles A to B shows intimate contact between its lobules and the body coelom in three places on each side, but the presence of nephrostomes could not be demonstrated. The nephridia off the muscles F and G be-

long to the region where the dorsal body coelom is substituted by the pericardial cavity. On the left side a distinct cellular strand from the nephridium off the muscle F passes dorsally to the atrium to connect with a corner of the pericardial cavity. No distinct lumen was observed, but because this strand connects the nephridium with the pericardium as described, it is believed to be a homologon of the nephrostomic duct. A similar strand on the right side is partially preserved, only. Another one can be indistinctly seen to run from the last nephridium on the left side to the pericardium, whereas the nephridium off the muscle G on the right side is completely crushed.

COMPARATIVE REMARKS

In having six pairs of nephridia *Neopilina* differs strikingly from all other recent molluscs, in which one pair is the rule and the two pairs in *Nautilus* an exception. The two pairs in *Nautilus* have sometimes been explained as being the result of secondary duplication, but now the conditions in *Neopilina* indicate them to be parts of a primitive metameric series.

In *Neopilina* each of the six pairs of complete renal organs connects with the coelomic system, the anterior 4 pairs with the dorsal body coelom (demonstrated for 3 pairs only), and the posterior 2 pairs with the pericardial sacs. In other molluscs the renal organs either connect with the pericardial sac (most cephalopods, gastropods, bivalves, and polyplacophorans) or have secondarily lost this connection (*Nautilus,* scaphopods). As in other molluscs the renal organs of *Neopilina* have proliferated to form highly lobulated "nephridial glands" with light-staining vacuolated cells, and they open at the base of the gills. No doubt, therefore, *Neopilina* possesses the same type of renal organs as do other molluscs.

A comparison with the single pair of kidneys in chitons (Figs. 166, 167) reveals that these organs have the same relation to the lateral nerve cord, but that there is a striking difference in the position of the nephridial gland proper. In chitons the gland of the individual, posteriorly situated nephridium extends far forwards *medially* to the pedal retractor muscles. In *Neopilina,* the several nephridial glands are placed *laterally* to the pedal retractors in the proximal parts of the pallial fold.

It might be surprising to find that some nephridia in *Neopilina* are actually connected with the pericardial sacs, whereas the more anterior ones start from the dorsal body coelom, but it should be remembered that both cavities are supposed to be parts of the original, paired coelomic sacs. Conversely, these facts could be taken to support the idea of the common origin of the pericardium and the dorsal coelomic cavities. The extensive communications between the various coelomic compartments found in many cephalopods illustrate the same point.

The term nephridium as used in this paper for the renal organs will be discussed in the next chapter.

THE GENITAL ORGANS

The sexes are separate, there being no indication whatsoever of hermaphroditism in the sectioned female (Spec. III) or in the male (Spec. IV).

The structure of the organs is most simple. The gonads are lobulated sacs situated in the perintestinal blood sinus, ventrally to the intestine and liver, and medially to the pedal retractor muscles (Figs. 165, 167). The extensive lobulation makes it difficult to see whether there are one or two pairs of gonads, but at least they extend over two segments, and in the male a separation into two pairs could be definitely observed.

The two pairs of short gonoducts are alike in both sexes, connecting the gonads with the nephridia off the muscles D and E on each side (Fig. 165). From the gonoducts the genital products pass through the respective nephridia and the renopore into the pallial groove. No copulatory organs are present.

THE FEMALE ORGANS

The ovaries are large, flat, and lobulated bodies, the contour of which is drawn in the Fig. 145. They are situated in direct contact with the ventral body wall (Fig. 157) above the more anterior region of the foot, from the level of the muscles C to that of E. However, since the oviducts are connected with the nephridia D and E only, the ovaries seem to belong to these two segments, secondarily extending forwards and backwards. Transversely the ovaries extend to the pedal retractors and, medially, almost to the median line (Fig. 9). They are covered dors-

ally by the intestinal loops, the stomach, and the liver, their lateral edges being in some places in direct contact with the dorsal coelomic epithelium.

Each ovarian lobule has a rather wide lumen which sometimes is almost empty, but usually contains free egg cells or oocytes protruding from the wall (Figs. 158, 159). Towards the peri-intestinal blood sinus the wall consists of a membrane, about 1 μ thick, which ventrally attaches directly to the body wall. Inside the membrane there is – in places – a distinct germinal epithelium with cubical cells, some of which have developed into oocytes. In quite large areas the epithelium seems to be absent, which may mean that eggs have recently been detached.

The germinal epithelium consists of almost cubical cells with a height of 10-15 μ. Their nuclei are about 4 μ in diameter. In our preparations these undifferentiated cells have an almost hyaline cytoplasm. The oocytes are scattered between these cells. The larger the oocytes, the greater is the content in their plasm of a substance staining dark red with the hematoxylin of MALLORY. The red-staining substance is always concentrated to that side of the cell which is turned away from the body surface, indicating that an artificial dislocation of the material has taken place as a consequence of the penetration of the fixation fluid (Fig. 159). When the cells approach their final size, distinct dark blue granules stain in their plasm, and the mature egg cells are filled with this dark bluish matter (Fig. 158).

Usually the mature eggs have an oblong cell body 220-320 μ long and 130-190 μ broad. Some eggs are extremely elongate (350 μ × 100 μ). The nucleus is eccentrically placed (Fig. 158) and has a diameter of about 60 μ. It contains a nucleole about 15 μ in diameter. In addition there are sometimes a few bodies or lumps of a chromophilic substance in the nucleus, but they may be artefacts. Because of this risk for artefacts we do not give any account of nuclear changes in the developing oocytes. No follicle cells are present.

The plasm of the egg cells is crowded with small granules staining a bluish black with hematoxylin, so that the egg cells look almost black in the sections (Fig. 158). The outer cell surface is only faintly indicated and there is no secondary egg shell of any kind. Immediately below the cell membrane a narrow granule-free zone is found. Even the eggs found in the nephridia near the renopore are quite naked without any indication of shells or secondary membranes. Thus, the eggs of *Neopilina* must be deposited without any shells or protective structures, a conclusion also supported by the absence of specialized glandular cells in the nephridia through which the eggs pass. The naked eggs suggest that fertilization takes place in the water outside the animal, as shown also by the absence of sperm in the female organs – and by the lack of copulatory organs.

During their growth the oocytes and immature egg cells remain attached by a broad base to the wall of the ovarian lobules (Fig. 159). The lumina near the oviduct are full of mature eggs which definitely are detached from the wall and lie free in the fluid. The walls of the lobules are smooth and even, so that the oocytes must be nourished from the surrounding peri-intestinal blood sinus, there being no internal ovarian vessels of the complex kind described e. g. in chitons. In the preparations, many egg cells are surrounded by some curious empty bladders. After careful consideration, however, we arrived at the conclusion that these bladders probably are the residues of lipoid droplets formed at the moment of fixation or during the subsequent treatment.

The oviducts. Two short ducts on each side run close behind the pedal retractors D and E (Fig. 145). Each starts from an ovarian diverticulum filled with ripe eggs, and leads into a nephridial sac (those off the muscles D and E, respectively). Every such communication, at any rate, deserves the name of a true oviduct. Its lumen is rather narrow (about 120 μ) in some places, but it is obviously strongly contracted. The walls of the oviduct are thin, consisting of an outer membrane of connective tissue about 2 μ thick, and a rather low epithelium, the cells of which are ciliated and cubical. Some of the epithelial cells are 10-12 μ high and seem to form longitudinal ridges in the (collapsed) oviduct, whereas the other cells are only about 5 μ high.

The nephridium proper constitutes the next – and final – part of the genital passage, but we do not like to include this part of the outlet tube into the term oviduct, as these nephridia are unmodified and like the others. Each oviduct opens into the central sac of the nephridium through a short zone some hundred μ in length, in which the cells are intermediate in appearance between those of the oviduct and of the nephridium and contain some stainable matter next to the lumen of the duct. A few egg cells are present in the central sacs of the nephridia off the muscles D and E, some being found even close to the renopore (Fig. 157).

Connections between the ovaries and the dorsal body coelom. In the medial parts of the body there

are no connections between the dorsal body coelom and the ovaries, the two being far apart. Above the anterior part of the foot there is sometimes a close contact between the coelomic epithelium and the lateral part of the ovaries. In some places the coelomic epithelium pushes out into diverticula obtaining a contact with the wall of the ovary which is so intimate that the existence of a real communication between the lumina cannot be excluded. However, the available sections do not allow final decision on this point. At any rate there is no such communication in the posterior part of the ovaries, where the coelom and the ovary are always far apart.

THE MALE ORGANS

The male organs are very similar to the female ones, but since the male has been sectioned horizontally, the female transversally, the two specimens offered somewhat different possibilities for the study of details. The testes are present in two pairs, each single one opening through a spermoduct into the nephridial sac of the respective segment (Fig. 167). The sperm is liberated through the renopore. There are no traces of copulatory organs.

The testes are situated approximately as are the ovaries in the female. Anteriorly they reach into the foremost foot region. Laterally, they extend to the pedal retractors. The two testes of each pair overlap near the median plane without fusing. Caudally the testes reach the level of the posterior foot margin. Those of the right side extend along the bottom of the peri-intestinal blood sinus across the median line, whereas the left ones are restricted to the left side. Dorsally the testes border on the intestinal loops, the dorsal body coelom, the stomach, and the liver. Whereas the ovaries are restricted to the very bottom of the peri-intestinal blood sinus, several lobules of the testes are found between the lower intestinal loops (Fig. 89).

Thanks to a suitable plane of section, it could be distinctly seen that there are two pairs of testes connected with the nephridia off the muscles D and E (Fig. 165). The lobules from a testis intermingle with those from the other on the same side, but the irregular cleft separating them could be followed from the most ventral section to the most dorsal one (Figs. 11, 123).

Each testis consists of small lobules, which are much smaller and more numerous than those of the ovaries (Fig. 160). All the ramifications meet at a point just behind and medially to the corresponding pedal retractor, from which point arises the spermoduct. Each lobule is surrounded by a 1-2 μ thick wall of connective tissue, inside which is found a compact mass of sperm cells and their developmental stages, of which only the nuclei are distinct in our preparations. The periphery of each lobule is occupied by larger nuclei with a diameter of 2-3 μ, probably representing spermatogonia and spermatocytes I. Farther inwards a layer of smaller nuclei is found, supposed to represent the spermatocytes II and spermatides (Fig. 161). Centrally each lobule contains a dense mass of small-sized nuclei, little more than 1 μ in diameter, which must belong to ripe spermatozoa since their tails can be observed as a striation in some small lumina between them. The rounded shape of the spermatozoan heads strongly indicates that fertilization takes place in the free water and not within the female (cf. FRANZÉN 1956), a conclusion arrived at also from other evidence. The parts of the testis nearest to the spermoduct are practically filled with ripe sperm.

The spermoducts. There are two spermoducts on each side, corresponding to the two testes and leading to the nephridial sacs off the muscles D and E, respectively. The tube as a whole measures about 1.3 mm in length and 150-650 μ in breadth (the variations depending on the degree of distension). The wall consists of a thin connective tissue membrane (1-2 μ thick) and an epithelium, the cells of which bulge out 12-15 μ into the lumen. This epithelium appears to be ciliated, as the external zone of its cells has a distinct striation perpendicular to the surface.

The whole spermoduct is filled with sperm, and this is also the case with the central sacs of the two pairs of nephridia in question (Figs. 11, 123). Even many of the lobules branching off from the central sac contain sperm. The walls of these lumina show the normal nephridial epithelium. The sperm can be seen also in the short tube connecting the nephridial sac with the renopore, and in the pallial groove around this urogenital opening. Thus, there is no doubt that the sperm is liberated directly into the water.

COMPARATIVE REMARKS

The gonads in *Neopilina* as in other molluscs are simple lobulated sacs lined by a germinal epithelium. No trace of hermaphroditism has been observed. *Neopilina* is as primitive as are the bivalves in the absence of follicle cells and egg membranes, in the rounded heads of the spermatozoa, as well as in the

absence of copulatory organs and the consequent liberation of the genital products directly into the water.

The intricate problem whether the gonads of *Neopilina* have been formed from the same parts of the coelomic system as in other molluscs has been discussed on page 57.

In the presence of two pairs of gonads *Neopilina* differs definitely from all other recent molluscs, so that we have to turn to annelids for finding a similar organization. The same holds true of the gonoducts, which appear in two pairs corresponding to the gonads. The gonoducts pass to the nephridial sacs of the respective segments and must be regarded as true coelomoducts, the primary function of which is to serve as outlets for the gonads (GOODRICH 1945).

The organization of the gonoducts and kidneys in *Neopilina* invite a consideration of their homologies in general among molluscs. In *Neopilina* the kidneys of the fertile segments have double connections with the coelomic system, viz. (1) by a gonoduct with the gonads and (2) by a nephrostome with the dorsal body coelom. A similar organization is well-known from other molluscs, the excretory organ usually starting from the pericardium, whereas the gonoduct may grow out to the body surface independently, or may open into the excretory duct in some way. Thus, the adult anatomy indicates that we have to do with two distinct tubular connections between the coelomic system and the outer body surface – which is in fact supported by the separate embryonic rudiments of these two ducts. A comparison with annelids strongly indicates that the gonoduct is homologous to an annelid coelomoduct, and the excretory organ to an annelid metanephridium. This homology is particularly evident when we consider the long series of nephridial organs in *Neopilina*, some of which combine with a gonoduct. This is the reason why, in the above description, we have considered the excretory organs of *Neopilina* as true nephridia.

Another interpretation was suggested by GOODRICH (1945 and earlier), who considered both the kidney and the gonoduct as coelomoducts, reasoning as follows. Early in molluscan phylogeny the single coelomoduct, originally serving as a gonoduct, has taken over the excretory function, whereas the true nephridium became reduced to the larval protonephridium. Secondarily, the coelomoduct divided into a tube serving as a gonoduct and another serving as an excretory organ. According to GOODRICH this is the state reached in recent molluscs, which exhibit different stages in the separation of the two ducts. However, it would appear much simpler to regard the kidney as a homologon of an annelid metanephridium and the gonoduct as an annelid coelomoduct as above suggested. This interpretation does not imply any hypothetical combination and re-separation of the functions.

GOODRICH bases his views on two main criteria:

(1) Both the gonoduct and the kidney in molluscs develop embryologically as outgrowths from the coelomic epithelium like typical coelomoducts.

(2) GOODRICH regards the molluscs as consisting of one segment only, i.e. he regards the indications of metamerism in *Nautilus* and chitons as secondary duplications. Then, the larval protonephridium becomes the true nephridium of this single segment, the other openings to be interpreted as coelomoducts.

The second criterion is immediately spoiled by *Neopilina*, which indicates a metameric tendency in ancestral molluscs (See pp. 66-67). If the ducts present in this animal are true coelomoducts and true nephridia, conditions are almost identical with those in annelids. The possible (or probable) presence of a larval protonephridium will not prevent this homology, the more so as such a protonephridium is present also in larval annelids.

The first criterion is difficult to discuss as far as *Neopilina* is concerned, because we do not know the embryonic development, but the strength of this criterion in general might be questioned. The embryonic development of typical metanephridia may vary, as e.g. in Oligochaeta, where they develop centrifugally instead of centripetally. Moreover, we are dealing with ducts which connect one epithelial surface (the ectoderm) with another (the coelomic epithelium), which both may contribute to the duct (e.g. in *Paludina*). Therefore, we cannot accept even the first criterion of GOODRICH's as conclusive in itself. It must be weighed against other evidence.

So we return to the direct comparison with the annelid metanephridium and coelomoduct, realising, however, that this view implies that the embryonic development of the metanephridium has changed more than hitherto observed in any recent annelid. Some knowledge of the embryonic development of *Neopilina* is urgently needed.

In other molluscs the single nephridium is connected with the pericardium, whereas the gonoduct comes from the gonad which – at least in *Neopilina* and chitons – is a pre-pericardial structure. Hence, the two ducts seem originally to belong to different segments, the nephridium being a component of a

pericardial segment and the gonoduct of a pre-pericardial one. This is obviously true of chitons, but whether it holds good of other molluscs is open to some doubt. The nephridium of chitons starts from the pericardium and opens into the pallial groove at the corresponding transversal level, whereas the gonads and the gonoduct are pre-pericardial. The latter opens into the pallial groove in front of the nephridial opening. The two ducts are situated on either side (anteriorly and posteriorly, respectively) of one of the pedal retractor muscle complexes. Since these complexes are homologous with the segmental pedal retractors of *Neopilina* the two pairs of ducts must belong to different segments.

Referring to the discussion on the coelom on page 57, we want to point out a difficulty in the homologization of the gonoducts in *Neopilina* and in chitons. In *Neopilina* it comes from a ventral gonad, whereas in chitons it has a dorsal origin (Figs. 166, 167).

ECOLOGICAL REMARKS

The facts actually known about the ecology of *Neopilina galatheae* are very few, but some additional information can be deduced from the morphological studies. The present chapter will be confined to a few points because of the old experience that ecological studies have to be made on the living animals.

As to the habitat, we know only the records given for the haul in question (See p. 10). The animals have been taken in truly abyssal surroundings (3570 m. depth) on dark, muddy clay which does not seem to contain hard objects suitable for the animal to creep on. So, *Neopilina* seems to be a true soft-bottom animal. The haul was a rich one, as will be seen from the following list taken from the original notes in Galathea's diary (depth record corrected in the notes):

St. 716. Acapulco-Panama. 89°32′ W. 9°23′ N. 6.V. 1952. Hour 11.30 a.m. Depth 3570 m. Surf. temp. 28.4 °C. Gear: Herring otter trawl. Wire out 8000 m, incl. of wire 39-43°, speed knots 2,3. Dur. of haul 120 min. Length of haul in sm. 4.5, direction of haul 287. Bottom: dark muddy clay.

Content of trawl (All determinations preliminary only):

PISCES: 5 *Bassogigas*, 3 *Bassogigas*, 26 *Bassozetus*, 15 *Mixonus* ?, 5 *Porogadus*, 1 juv. Brotulid, 3 *Nematonurus*, 4 Alepocephalidae, 1 cfr. *Bathytroctes*, 1 *Serrivomer*, 1 Nemichthyidae, 1 Stomiatidae, 1 *Stomias colubrinus*, 5 *Scopelengus*, 1 Myctophidae, 1 bit of an egg capsule of a shark?

ECHINODERMATA: a bit of a stalked crinoid.

4 species of Ophiuroidea (many specimens).

6 species of Asteroidea (many Porcellanasteridae, 1 *Hymenaster*, 1 Brisingidae, 1 *Pentagonaster*, several indeterminate large orange specimens).

3 species of Echinoidea (many *Plesiodiadema*, fragments of an irregular species and of a spatangid).

ab. 15 species of Holothurioidea (ab. 500 specimens) comprising *Scotoplanes*, *Oneirophanta*, *Benthodytes*, *Psycropodes*, Aspidochirotae, Molpadidae, and Dendrochirotae.

PANTOPODA: 3 Colossendeidae, yellow-orange.

1 *Colossendeis* with a thick proboscis.

ab. 10 Nymphonidae.

CRUSTACEA: 3 pale Homolidae, 5 *Munida* sp., 1 big *Munidopsis*, 17 Galatheidae, ab. 10 Crangonidae, a few *Hymenopenaeus*, ab. 300 Caridea (Hoplophoridae etc.) and Penaeidae in about 10 species, 31 *Scalpellum*, 2 big Arcturidae, 3 smaller Arcturidae, 3 middle-sized Munnopsinae, 34 Parasellidae, 2 big bathypelagic Parasellidae, 1 bathypelagic Amphipod, 6 bottom Amphipods, 1 ditto, 11 ditto, 2 ditto, 1 bottom-Cumacea, 3 Harpacticidae.

MOLLUSCA: 5 *Chaetoderma*, 10 Capulidae [= *Neopilina*] + 3 shells, ab. 140 *Dentalium* (big size), 2 Fusidae, 4 other Gastropods, 3 egg capsules of Gastropods, 32 haired-shelled bivalves, 2 *Leda*, 2 thick-shelled bivalves.

VERMES: 1 Hirudinea on *Bassozetus*, several species of Gephyrea, ab. half a litre of Polychaetes, several long tubes.

COELENTERATA: *Stephanoscyphus*, a hydroid species, 2 species of Actinians, several feather-shaped Anthipatharia, 1 small *Umbellula*, pieces of a Virgulariid, Zoantharia on *Hyalonema*-stalks.

PORIFERA: many specimens of a flat, leaf-like species. 2 species of *Hyalonema*.

Such richness is characteristic of the waters west of Central and South America, and it is possible that the presence of *Neopilina* depends on the high production of organic matter in these areas.

The intestines of the specimens of *Neopilina* were all filled with material looking quite similar to the bottom material adhering to the outer surfaces (Fig. 168). The intestinal content includes a high proportion of radiolarians, scattered centric diatoms, etc., mixed up with much undefined detritus matter. These facts, together with the appearance of the organs around the mouth, indicate that the animal is a deposit feeder. The food-collecting organs seem to be the postoral tentacles together with the velum. The only parts which could possibly function as a filter are the postoral tentacles, but it is impossible to guess how they actually work. Some specializations for this particular kind of food have been mentioned in the morphological chapters (pp. 24, 28 and 29).

The sexes are separate in *Neopilina* and the ani-

mals seem very little mobile, so fertilization would seem impossible if the animals are too widely scattered on the bottom. Therefore, the populations must be fairly dense in places and this is exactly what was found by the Galathea expedition, which got the 10 specimens in one single out of several hauls in the region. This all indicates that *Neopilina* has a patch-wise distribution on the bottom.

The lack of copulatory organs and of egg membranes, and the rounded heads of the spermatozoa all indicate that fertilization takes place in the free water masses. Moreover, there can hardly be any membranes of importance around the developing embryo. These facts together with the presence of a true protoconch on the adult shell show that there must be a free larval stage. The volume of the eggs is of the same order as that of the larval shell, which indicates that the larval life is short and the nutrition lecitotrophic.

After all, the whole reproduction takes place under such conditions that, in theory, it should be possible to fertilize the eggs and to rear the larvae under fairly simple laboratory conditions – the problem is only to get the living material.

CONCLUDING REMARKS

THE PROTOCONCH

Although apparently very much like a gastropod protoconch, the larval shell of *Neopilina* has not been subject to any torsion. This is apparent from the fact that the aperture of the larval shell faces posteriorly (Figs. 34, 163). Only, the protoconch is tilted over so as to rest on its originally right side. This tilting seems to correspond exactly to what happens to gastropod shells when the larvae are metamorphosing, and thus is a process quite different from torsion and occurring much later (Fig. 163). In the end, of course, this must mean that there is some asymmetry in the larva. The adult *Neopilina,* however, does not show any definite asymmetry. The slightly stronger development of the right gonads may or may not be significant in this respect.

THE ADULT SHELL

The adult shell of *Neopilina* is similar to that of *Nautilus* in being single, bilaterally symmetrical, and exogastrically coiled, but it differs from the latter in the absence of septa. The shells of other cephalopods are too reduced to be suitable for a comparison, and that of *Spirula* differs in being coiled endogastrically. The gastropod shell is similar to that of *Neopilina* in being single and exogastrically coiled, although the latter characteristic is concealed by the torsion, and the shell is asymmetrical (Fig. 163). The shell in scaphopods differs in being closed ventrally to form a tube, and that of bivalves shows slight indications of an exogastric coiling in the anterior bending of the umbo, but the shell is divided along the median line into two subequal halves. This latter fact does not prevent a derivation of a bivalve shell from a univalve one, however, for a similar division of shell plates has taken place in the polyplacophoran *Schizoplax,* whose shell plates are divided into right and left halves by a median ligament. The 8 shell plates of chitons differ completely from the single shell of *Neopilina.* Cuticular spines of the type present in chitons and in the Solenogastres are absent in *Neopilina.*

The microscopic structure of the shell of *Neopilina* with a prismatic and a nacreous layer beneath a periostracum looks very similar to that of primitive bivalves. Also, the way of formation of these three layers is much the same in both groups, with a periostracum gland situated on the ventral side of the pallial margin. This appears to be the primitive structure of the shell and of the pallial margin in the univalve and bivalve molluscs. In chitons the middle pallial fold is enormously developed and carries spicules (Figs. 166, 167), and in the Solenogastres the spicules cover the whole body. The chitons are different also in their several transverse growth zones across the back, and in the differentiation of the shell into an articulamentum and a tegmentum. The latter contains the aesthetes which are not present in *Neopilina,* a fact that might perhaps be explained as an adaptation to the conditions of life in the abysses, since indications of the presence of aesthetes in some fossil Tryblidians have been reported (KNIGHT & YOCHELSON, 1958).

Altogether, the shell of *Neopilina* might very well be regarded as primitive among the so-called conchiferous molluscs (Bivalvia, Scaphopoda, Gastropoda, Cephalopoda). It is more difficult to establish the relations between the polyplacophoran exoskeleton and that of *Neopilina.* The gross structure of the original exoskeleton would seem to have differentiated rather independently in these two groups.

THE FOOT AND THE PALLIAL GROOVE

In the structure of the foot and of the pallial groove *Neopilina* is almost identical with the polyplacophorans. In both, the foot is a broad sole, and the pallial groove is uniformly developed all around the body. In other molluscs the pallial groove is specialized in different ways, enlarged to a pallial cavity posteriorly in gastropods and cephalopods, extended to enclose the entire body also from the ventral side in bivalves. The latter development is carried still further by the ventral fusion of the pallial margins in Scaphopods. In the Solenogastres both the foot and the pallial groove are very much reduced.

STRUCTURES AROUND THE MOUTH

With respect to the structures around the mouth, *Neopilina* shows affinities to very different mollusc groups, more distinctly perhaps to the bivalves, whose lips and labial palps compare well with the complex constituted by the lips in connection with the velum and the postoral tentacles (See pp. 24-25). On the other hand, the preoral tentacles are certainly the homologues of the gastropod preoral ones. It is probable that the postoral tentacles of *Neopilina* are homologous to the captacula of scaphopods and of the arms of the cephalopods. Chitons are fairly different, but their oral disc may include the lips and the velum as seen in *Neopilina*. A furrow between the „velar part" of the disc and the very lips in some chitons (*Lepidopleurus* – HOFFMANN 1930, p. 146) supports this assumption. Living specimens of *Lepidopleurus* showed this velar part very distinctly; it is pressed against the substratum when the animal is creeping (own observations).

THE GILLS

The presence in the gills of *Neopilina* of two alternating series of lamellae (although unequal), each on either side of the stem, the course of the vessels, nerves, and muscles, and the structure of the epithelium agree closely with what we find in other molluscs, especially in the Polyplacophora. No doubt, therefore, the gills of *Neopilina* must be regarded as true ctenidia. This homology is supported by the identical situation of the gills in relation to the lateral nerve cords and to the renopores. Whereas *Neopilina galatheae* has five pairs of gills, one pair is the rule in other molluscs. Only, *Nautilus* has two pairs, which, with respect to their situation in relation to the heart, correspond to the two posterior gill pairs in *Neopilina*. In chitons there are many gills on each side, their number being independent of the repetition of most other organs.

In molluscs in general the ctenidia are in some way placed as a perforated wall separating a chamber which receives the inhalant water current, from another delivering the exhalant current. A similar arrangement might therefore be expected in *Neopilina*. Our observations on the dead specimens, combined with the information given by YONGE (1939) on conditions in the chitons, open a possibility of understanding the main features of the respiratory mechanism in *Neopilina*. In both there is a continuous pallial groove all the way round the body between the pallial fold and the extended foot margin. Laterally to the foot, this groove is divided by a vertical perforated wall formed by the gills, separating an outer (lateral) inhalant chamber from a medial, exhalant one lying close along the foot side. In chitons the anterior and posterior lamellae from two successive gills meet and are linked together by their apical cilia. In *Neopilina* the posterior row of lamellae is vestigial, and the anterior row on each gill bends ventrally and backwards (Fig. 164). When extended, the innermost and strongest lamellae are long enough to touch the next gill with their apical cilia, thus forming the necessary perforated wall between the two respiratory chambers. The outer shorter lamellae on each gill stem cannot reach the next gill, but our observations indicate that they bend dorsally and touch the pallial wall in the way shown in fig. 57 (Compare the similar contact in some bivalves!).

In a preliminary note based on the very incomplete information available at that time, YONGE (1957a) made some valuable suggestions for the further study of the gills. Partly because of his considerations we have paid special attention to the structure and possible function of these organs. Our main conclusion, however, is that they must be homologous to, and are able to function in a similar way as, the true ctenidia of the other molluscs. The many similarities in structural details between the gills of *Neopilina* and of the chitons appear to exclude the possibility that the former are secondary structures. The simplicity of structure common to the single gills in these two groups – a. o. the lack of skeletal bars – might indicate that we are here dealing with the primitive type of ctenidium from which other mollusc ctenidia might be derived. YONGE

(1947) makes the opposite derivation, but comes up against the difficulty that the gill skeleton is placed differently in cephalopods and primitive gastropods, which latter he regards as ancestral in respect to gill structure.

INTERNAL ORGANS

The comparative anatomy of each of the internal organ systems is discussed in the respective chapters. Here, only such points will be briefly mentioned as have any bearing upon the question of molluscan interrelationships. The similar body shape and the metamerism distinctly indicated both in *Neopilina* and in the polyplacophorans, invite a comparison between these two groups first. Even in many details conformity has been found in the pharyngeal apparatus, the muscles, the nerves, and the vascular system. However, the sensory organs, the coelom, and the uro-genital organs are all very different in the two groups. Especially, the chitons have developed their gonad in a place where *Neopilina* has a paired dorsal body coelom lined by an epithelium similar to the chloragogen cells of annelids.

Obvious similarities to the various other mollusc groups are the presence of a crystalline style in *Neopilina,* in many bivalves and in some prosobranchs; the presence of statocysts in all groups except chitons; the lack of differentiation of the cerebro-pleural ganglion in *Neopilina,* in bivalves, and in scaphopods, and the presence of two pairs of atria in *Neopilina* and in *Nautilus*.

The coelom and the uro-genital system of *Neopilina* is unique and probably primitive in many respects, but the continuous coelomic cavity in *Nautilus* and some other cephalopods would appear still more primitive than the divided coelom in *Neopilina*. On the other hand, *Neopilina* is on a line with all other molluscs except the cephalopods mentioned (and the Solenogastres) in the presence of a pericardial sac separated from the main coelomic cavity.

THE METAMERISM

With the exception of the preoral region the whole body of *Neopilina* shows a more or less pronounced metameric repetition of many organs (Fig. 165). The highest number of repeated units is found in the 10 pairs of latero-pedal nerve connectives, the first situated immediately behind the subcerebral commissure, the last posteriorly to the side of the rectum. Next in number are the large pedal retractor muscles, 8 pairs in all, corresponding to the hindmost 8 latero-pedal connectives. The mm. obliquii anteriores are correspondingly repeated, whereas the other smaller muscles are less constant in occurrence (Fig. 121). The six pairs of nephridia are placed outside the pedal retractors B to G, the foremost kidney extending anteriorly past A. The five pairs of gills with their nerves and muscles correspond beautifully to the five last pairs of nephridia. Further indications of a metamerism are present in the two pairs of gonads connected to the two middle pairs of nephridia, and in the two pairs of atria belonging to the two last gills.

Thus, disregarding the lack of gonads or atria in some segments, the metameric repetition of the organs follows a constant pattern in the posterior body region forwards to (and including) the pedal retractor D (Fig. 165). In the region of the muscle C, the only irregularity is a slight dislocation of the gill nerves in relation to the respective latero-pedal connective (Fig. 135). In front of C, the metamerism fades out gradually so that it becomes impossible to state any definite number of segments in the anterior body region. The group of organs around the muscle B is still rather complete, although the gill is lacking. A latero-pedal connective and a somewhat aberrant pedal retractor (A) is present in the next anterior segment, but the gill is absent and so is the renopore. It is impossible to state whether the nephridial lobules present off the muscle A represent a separate nephridial rudiment. The two most anterior latero-pedal connectives are not accompanied by any other metameric structure. Such fading out of a metamerism at the ends of the series is not uncommon in other metameric animals.

The metamerism of *Neopilina* is so regular and is present in so many organ systems that there is no reason to regard it as different from that of annelids and arthropods (Fig. 165). We do not know whether the dorsal coelom is metamerically subdivided or not, but a metameric tendency is present in the gonads which may be regarded as part of the coelomic system. Furthermore, arthropods and annelids often show a metameric subdivision of the ectodermal skeleton. Such segmentation is not present in *Neopilina,* but the eight shell plates present in the polyplacophores might be mentioned in this connection. They correspond to the metameric foot retractors which are homologous to those of *Neopilina*. Thus, the rhythm of repetition of the shell plates of chitons is the same as that found in the metamerism of *Neopilina*.

Annelids, arthropods, and molluscs have long been regarded as related, mainly because of the spiral type of cleavage and the trochophora larva found in both annelids and molluscs, and because of certain similarities in the metamerism, in the nervous system, the heart, and the excretory organs in annelids and arthropods. The affinity of the molluscs to the two other groups was sometimes doubted, mainly because the molluscs were regarded as non-metameric. This cleft is efficiently bridged by *Neopilina*. The only general feature which still remains as a sharp criterion for molluscs is the restriction of the ectodermal cuticular skeleton to the dorsal side of the animal, the development of the soft ventral surface into a muscular foot and a pallial groove with gills. In contrast, the cuticular skeleton of annelids and arthropods is present all around the body. *Neopilina* does not help us in bridging this gap, but the contrast is reduced by some annelids, which have ciliated ventral areas. Moreover, we do not know for certain whether the most primitive trilobites had a cuticle on the ventral side or not. The anatomy of *Neopilina* facilitates a comparison with annelids and arthropods also in some other respects. The entire urogenital system of *Neopilina* is very similar to that of a primitive annelid, and the extensive coelomic cavities in *Neopilina,* partly containing chloragogenic cells, combined with our knowledge of the coelom in *Nautilus,* also point in the direction of annelids. It would seem that the find of *Neopilina* forces us to reconsider the relations between annelids, arthropods, and molluscs.

For a comparison with other molluscs it is essential to observe that the metamerically subdivided portion of the body of *Neopilina* extends from the non-metameric oral region into the posteriorly situated heart region typical of all molluscs. The complete organization and the presence of a heart in the last segment makes it very different from an arthropod or annelid telson, indicating that the metameres in *Neopilina* are not formed by a rhythmic activity of a terminal growth centre. The more probable explanation would seem to be that the mesoderm in the body region of *Neopilina* is simultaneously subdivided in the manner characteristic of the most anterior segments in annelids and arthropods.

Whereas in the polyplacophores the metamerism is almost as strongly developed in some organs as it is in *Neopilina,* matters are different in the other molluscs. In *Nautilus* there is a body region with two pairs of gills, nephridia, atria, etc., which is very similar to the most posterior region with its two segments in *Neopilina*. In front of this region *Nautilus* shows no further segments in its body. In gastropods and bivalves as well as in the remaining cephalopods, and probably also in scaphopods, the heart region can be said to comprise only one such segment with its one pair of gills, atria, etc. In front of this part, slight indications of additional segments may be found in the subdivision of the pedal retractor in bivalves, and possibly in the subdivision of the columellar muscle in opisthobranchs (LEMCHE 1956, THOMPSON 1958), and also in the symmetrically arranged pairs of muscle fibres in larval prosobranchs (CROFTS 1955). An attempt at homologizing these more or less spurious anterior segments with regard to segment number would seem to be of doubtful value at present. That the conditions are complex is shown in patellids by their symmetrically placed and subdivided, horseshoe-shaped foot retractor, combined with strong and symmetrical pedal cords. This looks very much like the primitive condition as described above, but the position – almost above the head – of the anus and of the other organs of the originally posterior end contradicts such an interpretation.

RELATIONS TO THE FOSSIL TRYBLIDIANS

Neopilina galatheae should undoubtedly be included as a recent representative of the Tryblidiacea WENZ, 1938, which has hitherto comprized only fossil species from Cambro-Silurian deposits. This is born out by the similar shape of the shell and, particularly, by the almost identical appearance of the pattern of muscle insertions (see p. 44 and Figs. 130-134, 162). It is also characteristic of the whole group that the shells are approximately bilaterally symmetrical with the apex situated above the anterior shell margin (Compare Figs. 3, 4, 162).

NEOPILINA AND THE SYSTEMATICS OF MOLLUSCS

The presence in *Neopilina* of a metamerism similar to that of annelids and arthropods shows that the molluscs together with the annelids and arthropods can be derived from common ancestors with more or less distinct segments. Also, the homologies in the muscular system of *Neopilina* and the polyplacophores force us to accept the incomplete metamerism of the latter as being of this same kind. In all other molluscs, except *Nautilus* with its two distinct

body segments, the metamerism is but faintly indicated. The old concept of an original metamerism in molluscs (PELSENEER 1899, HEIDER 1914, SÖDERSTRÖM 1925, NAEF 1926) thus gains strong support from the structure of *Neopilina*. It is of course impossible to postulate any definite number of segments in the ancestral form, but from the present evidence it is unnecessary to suppose more than the number present in *Neopilina*. Nor is it necessary that the segmentation should have expressed itself very much in the external features.

The single shell, the different appearance of the pallial margin, and the absence of spicules in *Neopilina* prevent its incorporation in the polyplacophores. The contrast is emphasized also by the different position of the gonads (Figs. 166, 167). The tryblidians must therefore be put into a mollusc class of their own: the class of Monoplacophora (ODHER in WENZ 1938, KNIGHT 1952).

The subdivision of the molluscs, as often found in text-books, into Amphineura and Conchifera cannot be upheld after the finding of *Neopilina*, which is an amphineuran in its nervous system and a conchiferan in its exoskeleton. *Neopilina* has bridged the gap which was the basis of this subdivision. For systematic purposes it would seem more appropriate to treat the groups of Cephalopoda, Gastropoda, Scaphopoda, Bivalvia, Monoplacophora, Polyplacophora, and Solenogastres as classes of equal rank, which have evolved out of a common stem in very remote times, probably in the earlier part of the Cambrian, as indicated by the fossil record.

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INDEX

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Plate 1

Fig. 1. Ventral view of Spec. I (the holotype).
Fig. 2. Dorsal view of Spec. I.
Fig. 3. Spec. I from the right.
Fig. 4. Detail of Spec. I, showing the apical region from the right.
Fig. 5. Spec. I, anterior view.

an = anus
ap = apex
f. m = foot margin
gi = gills
m = mouth
pa. g = pallial groove
pa. m = pallial margin
po. t = postoral tentacles
sh. m = shell margin
vel = velum

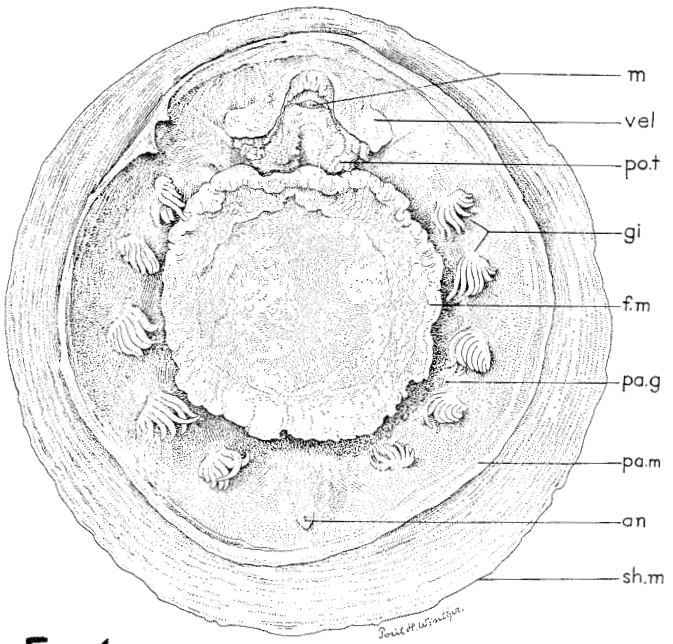


Fig.1

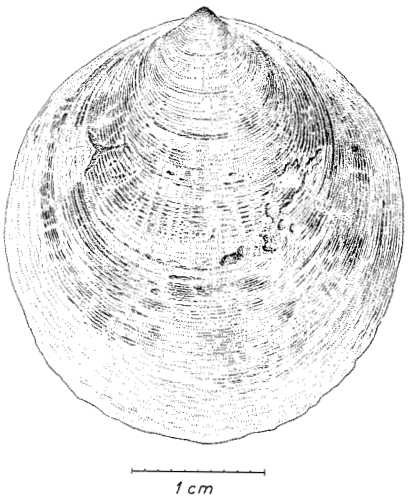
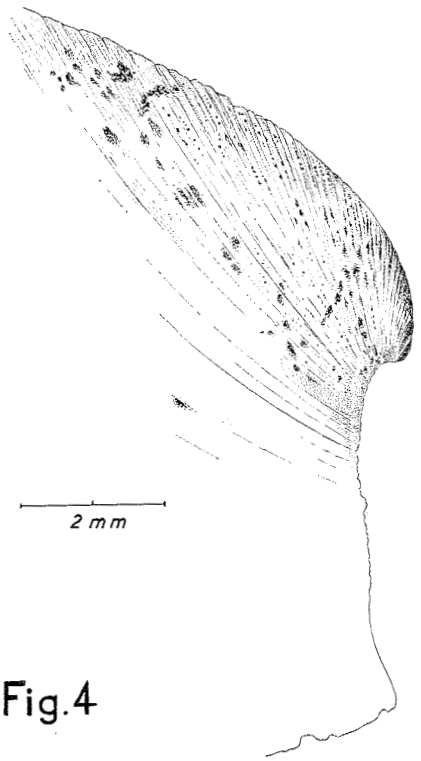


Fig.2



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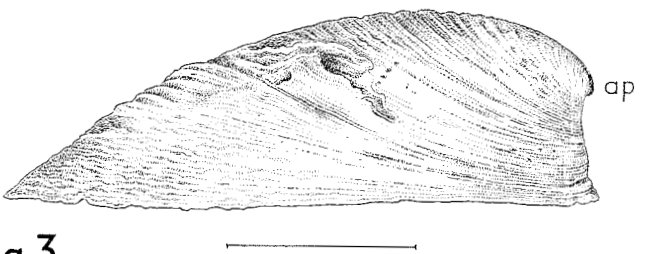

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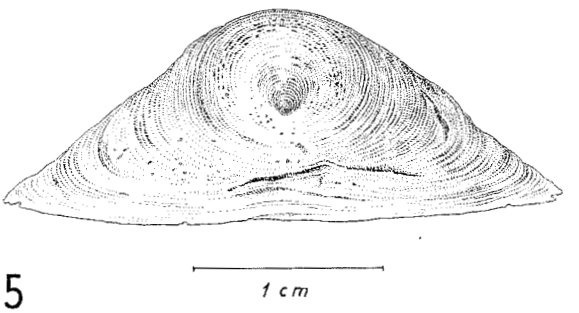
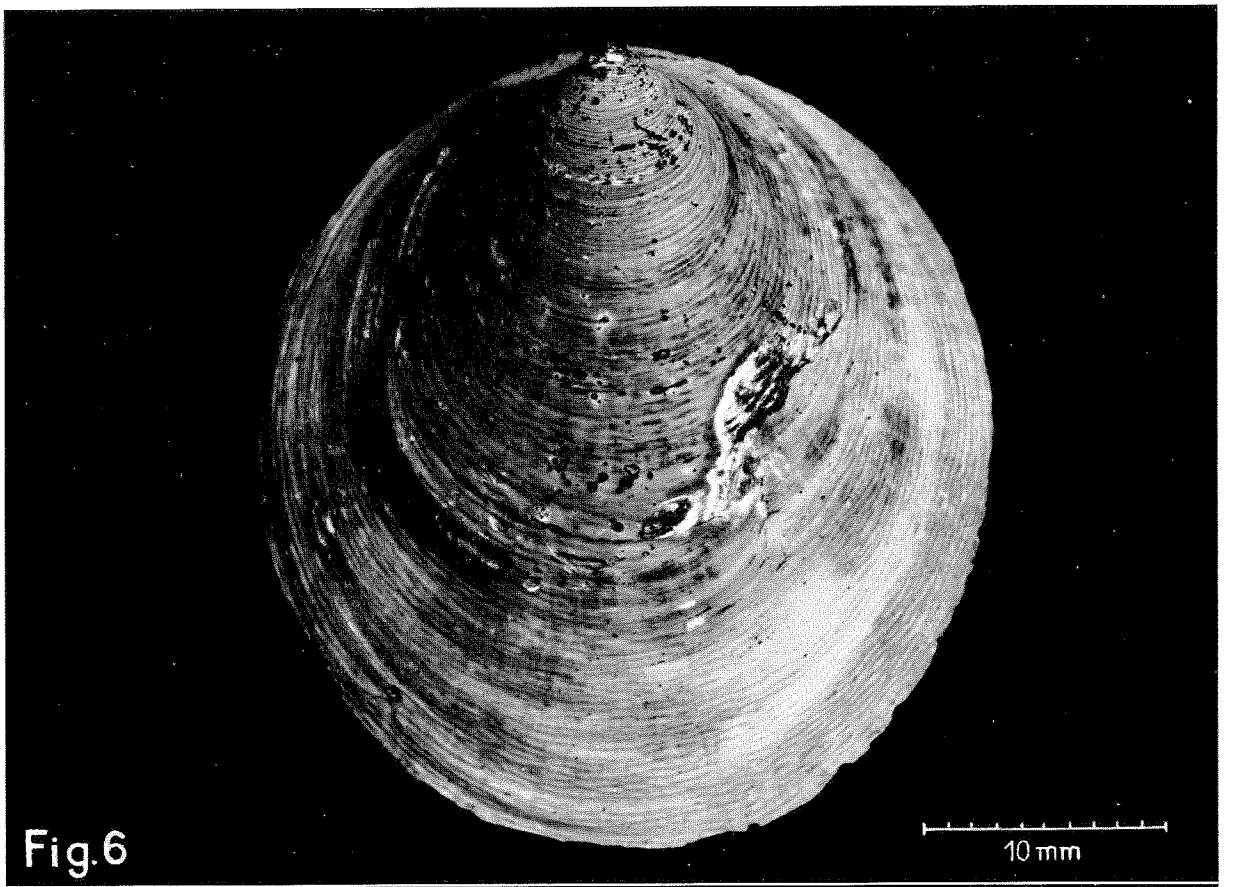


Fig.5

PLATE 2

Fig. 6. Photograph of Spec. I (holotype), dorsal view.
Fig. 7. Photograph of Spec. IV, ventral view.

For explanations see Plate 1.



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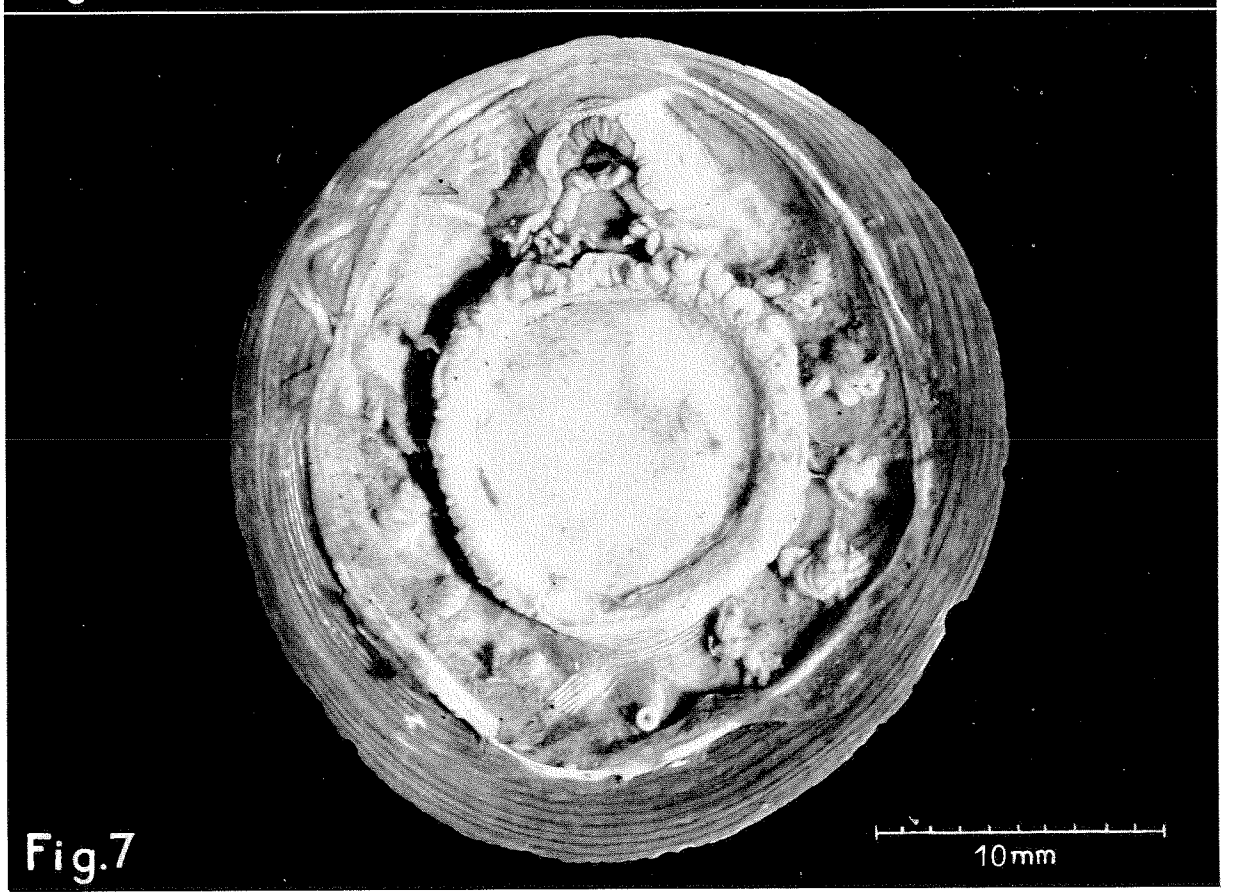


Fig.7

PLATE 3

Fig. 8. Transversal section through the anterior foot margin. Spec. III.
Fig. 9. Transversal section through the posterior end of the stomach. Spec. III.
Fig. 10. Transversal section through the heart region. Spec. III.

at_1 = atrium of heart, 1st pair
at.-ve. v = atrio-ventricular valve
d. coe = dorsal coelom
E = segmental foot retractor E
f. c = membranous foot centre
f. m = foot margin
gi_1 and gi_4 = gills, 1st and 4th pair, resp.
int. c 1-6 = intestinal coils 1-6
li = liver
ne = nephridia
oe = oesophagus
ov = ovaries
pa. g = pallial groove
pa. m = pallial margin
re = rectum
sh. m = shell margin
st = stomach
ven = ventricle of heart

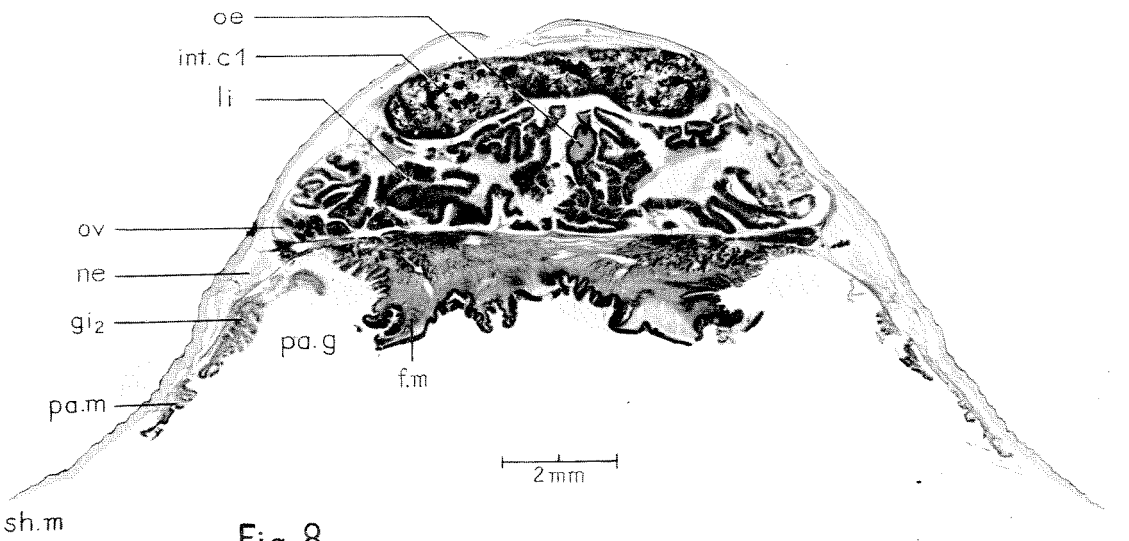


Fig.8

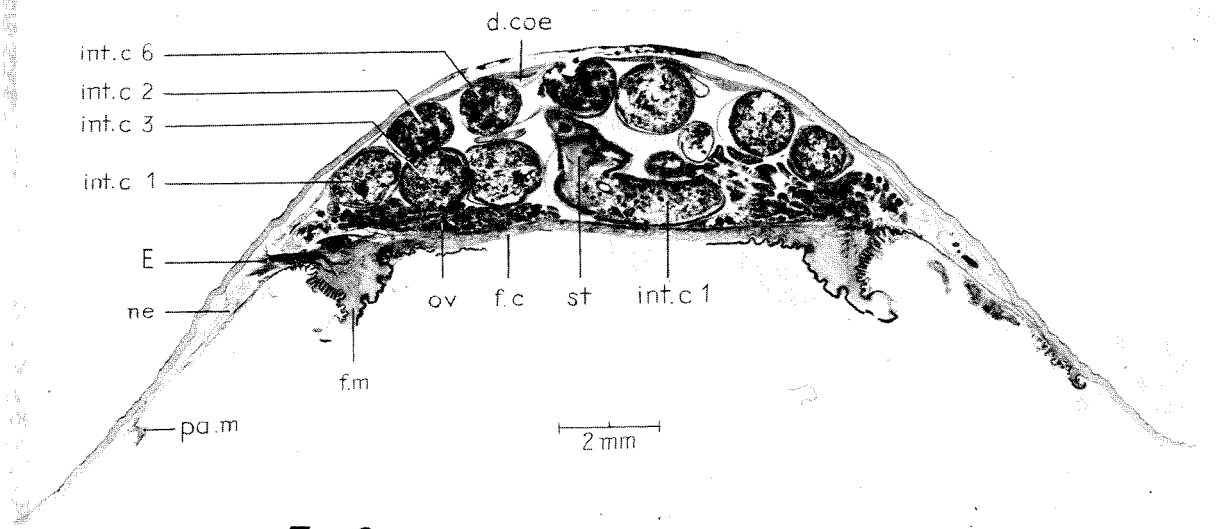


Fig.9

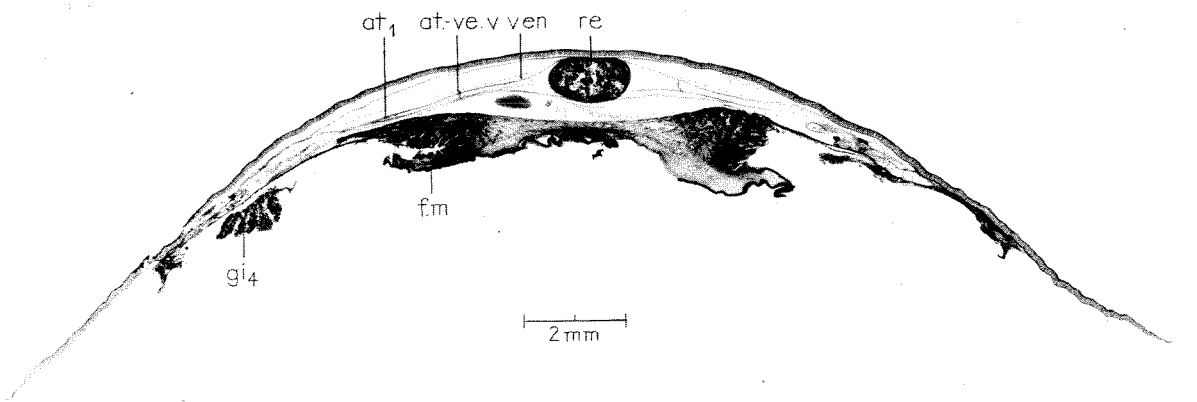


Fig.10

PLATE 4

Fig. 11. Horizontal section through the gonad and the segmental foot retractors. Spec. IV.

A_1 = m. obliquus anterior A
at_2 = atrium of heart, 2nd pair
D-H = segmental foot retractors D-H
d. coe = dorsal coelom, two pairs of anterior cavities shown
f. m = foot margin with ramifications of the pedal retractors A-C
m. ra. l = musculus radulae longus
m. re. ra = musculus retractor radulae
m. re. ve = musculus retractor veli posterior
m. pr. ra = musculus protractor radulae
m. t. A = musculus transversalis A
ne = nephridia
pa. g = pallial groove
ph = pharynx
re = rectum
s-r. o = subradular organ
te_1 and te_2 = testes, 1st and 2nd pair, resp.

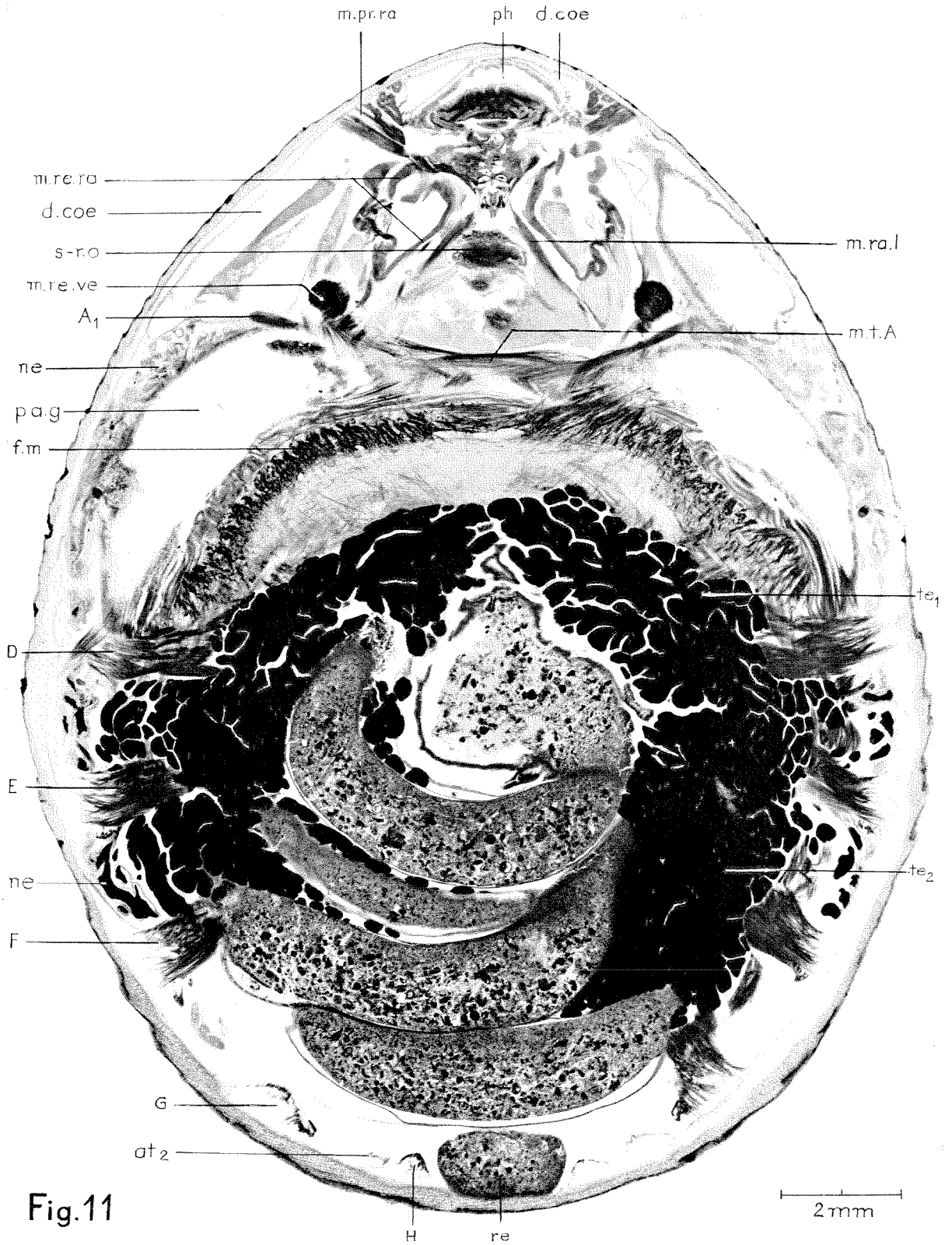

m.pr.ra
ph
d.coe
m.re.ra
d.coe
s-r.o
m.re.ve
A1
ne
p.a.g
f.m
m.ra.l
m.t.A
te1
D
E
ne
F
te2
G
at2
H
re
2 mm

Fig.11

PLATE 5

Fig. 12. Horizontal section of Spec. IV, at the level of the gills and the foot margin.

fe. f = feeding furrow
f. m = foot margin with ramifications of pedal retractor muscles
gi_1-gi_5 = gills, 1st to 5th pair, resp.
m. pr. ca. d = musculus protractor cartilaginis dorsalis
m. pr. v. m = musculus protractor vesicae major
ne = nephridia
or. c = oral cavity
pa. g = pallial groove
pe. g = pedal gland (i. e. the secretory epithelium of the anterior foot margin)
po. t = postoral tentacles
pr. t = preoral tentacle
re = rectum
sal. g = anterior salivary gland
sr. m = subradular membrane
tr. p. t. r = transversal part of tentacle ridge, associated with the posterior lip
ve = velum
Y_1 = the muscle Y_1

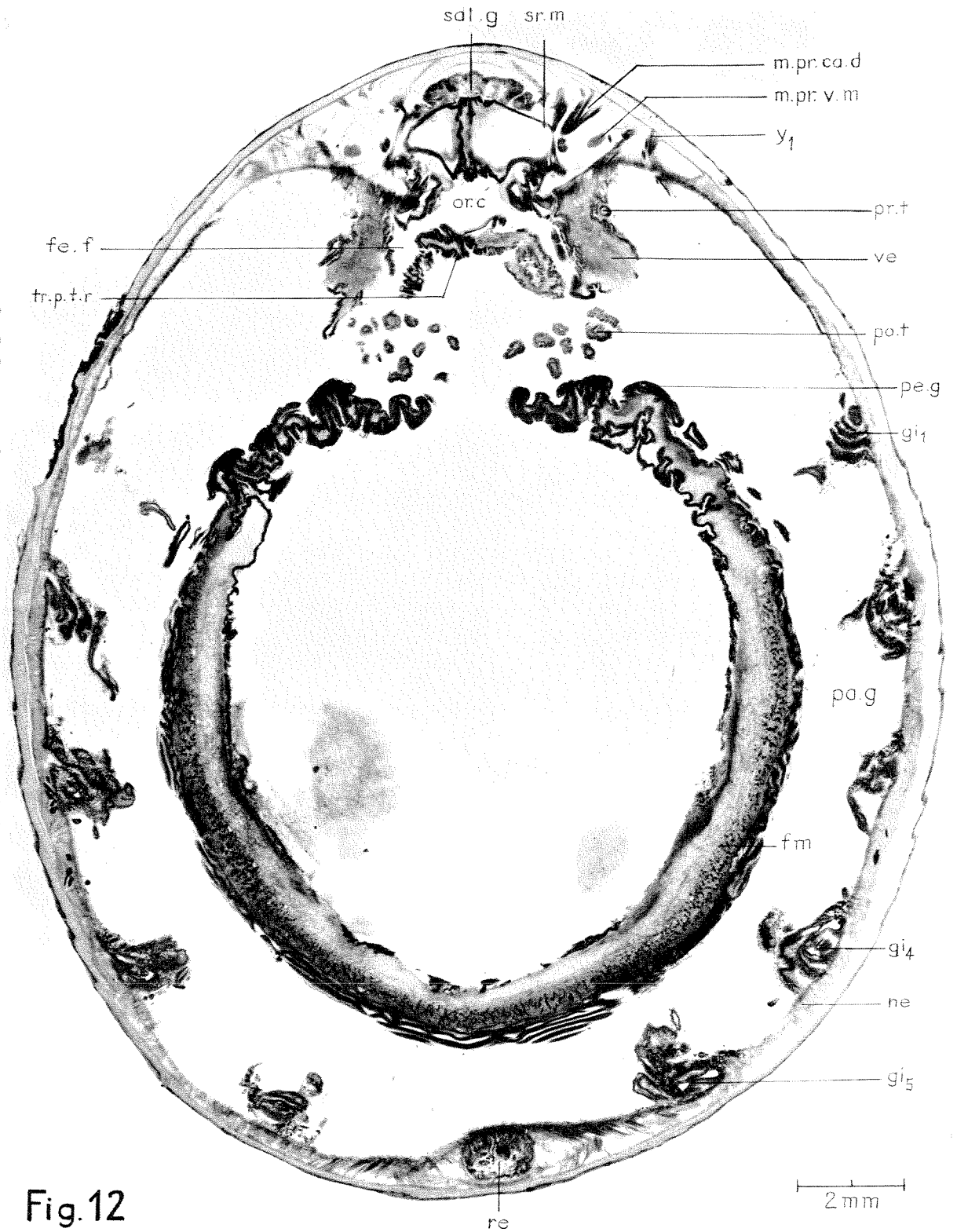

sal.g
sr.m
m.pr.ca.d
m.pr.v.m
y_1
or.c
pr.t
fe.f
ve
tr.p.t.r
po.t
pe.g
gi_1
pa.g
fm
gi_4
ne
gi_5
re
2 mm

Fig. 12

PLATE 6

Fig. 13. Ciliated epithelium on the side of a gill lamella. Spec. IV.
Fig. 14. Epithelium of the pallial groove, just inside the gills. Note the "globules" (gl) close to the basement membrane. Spec. III.
Fig. 15. Epithelium of the foot sides. Spec. III.
Fig. 16. Epithelium of the ventral foot surface. Slender, ciliated interstitial cells (in. ce) alternate with glandular cells (se. ce). Spec. III.
Fig. 17. Epithelium of the lateral, basal surface of the velum. Spec. III.
Fig. 18. Ciliated epithelium on the tip of a gill lamella. In the lower part of the figure transition to common gill-edge epithelium with goblet cells (mu. ce).
Fig. 19. Strongly ciliated, high epithelium on the free edge of the velum. Spec. III.

bl. ce = blood cells
gl = globules of unknown significance
in. ce = interstitial (ciliated) cells
mu. ce = mucous glandular cells
n = nerve
se. ce = secretory cells

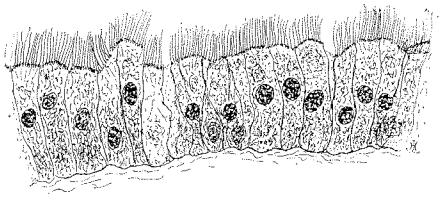


Fig.13

10μ

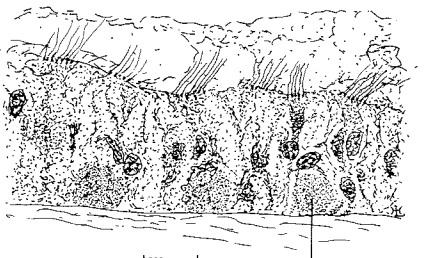


Fig.14

10μ

gl

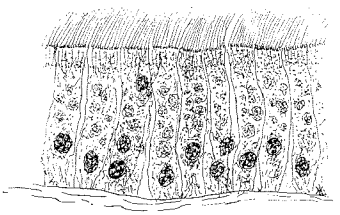


Fig.15

10μ

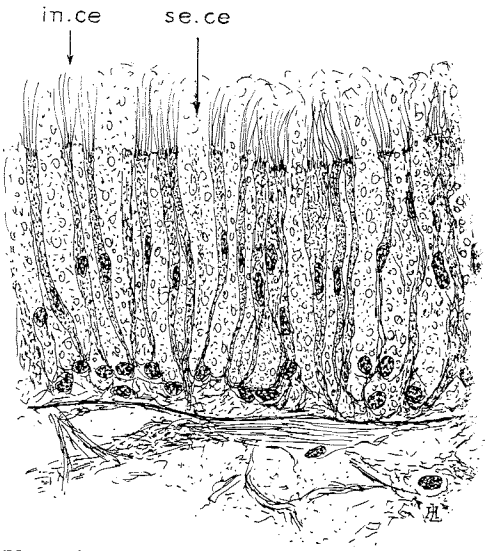


Fig.16

10μ

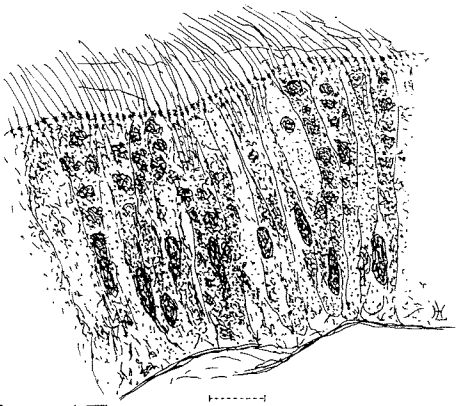


Fig.17

10μ

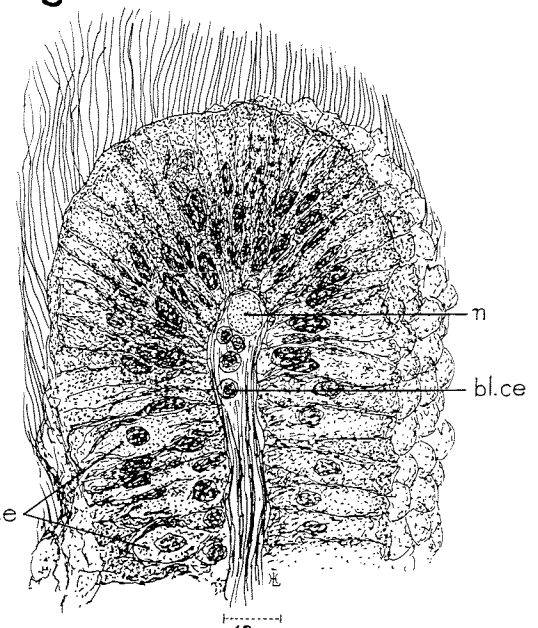


Fig.18

10μ

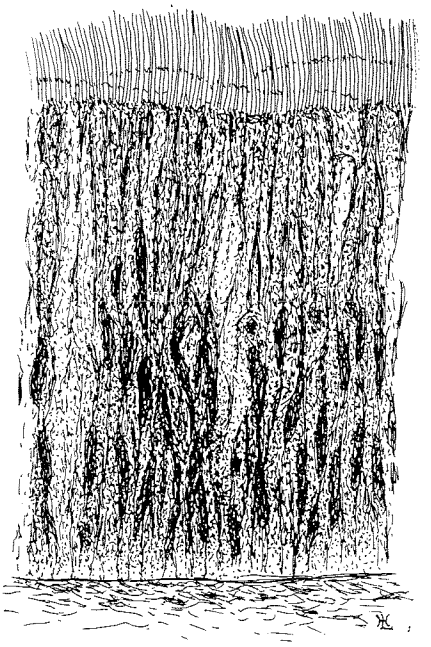


Fig 19

10μ

Plate 7

Fig. 20. Epithelium of the preoral pallial groove. Microphotograph. Spec. III.
Fig. 21. Ciliated epithelium on the lateral, basal surface of the velum. Note the big granules. Microphotograph, Spec. III.
Fig. 22. A single ciliated cell (ci. ce) in the epithelium of the postoral tentacles. Microphotograph, Spec. IV.
Fig. 23. Pedal gland epithelium with the two distinct layers of nuclei. Microphotograph, Spec. IV.

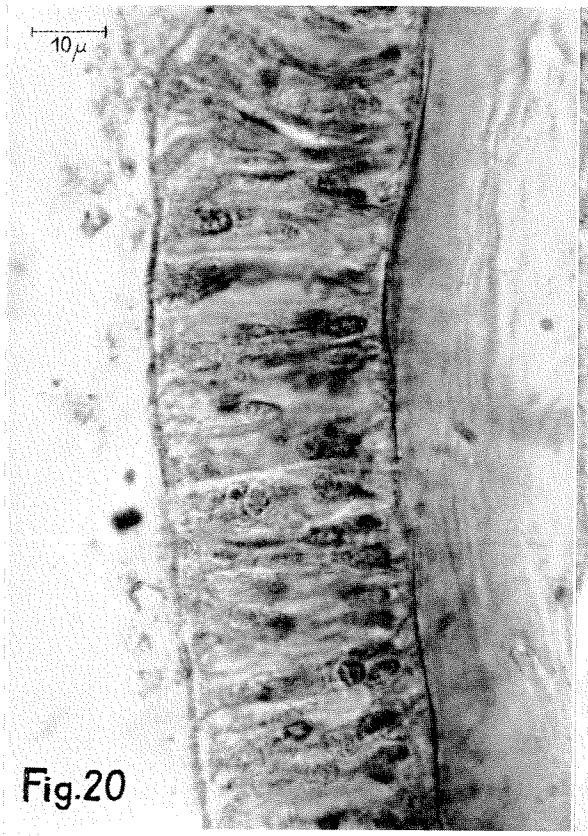
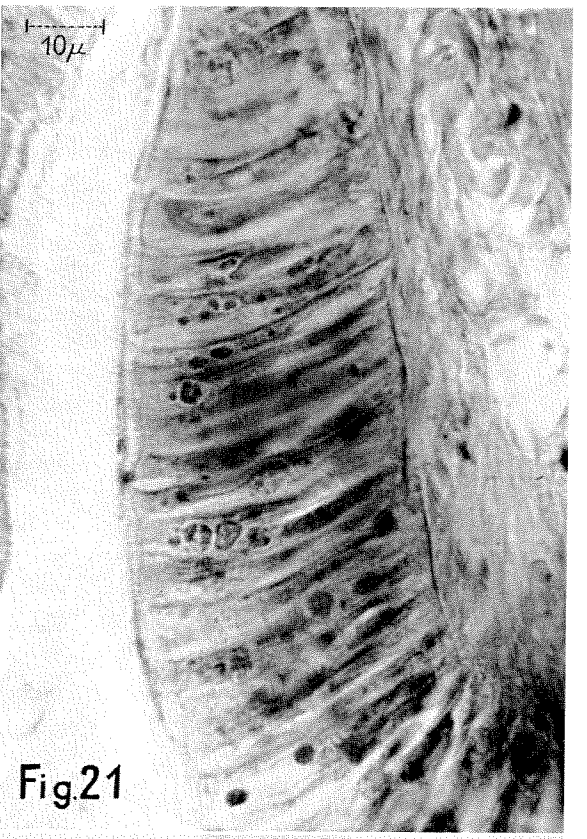


Fig.20



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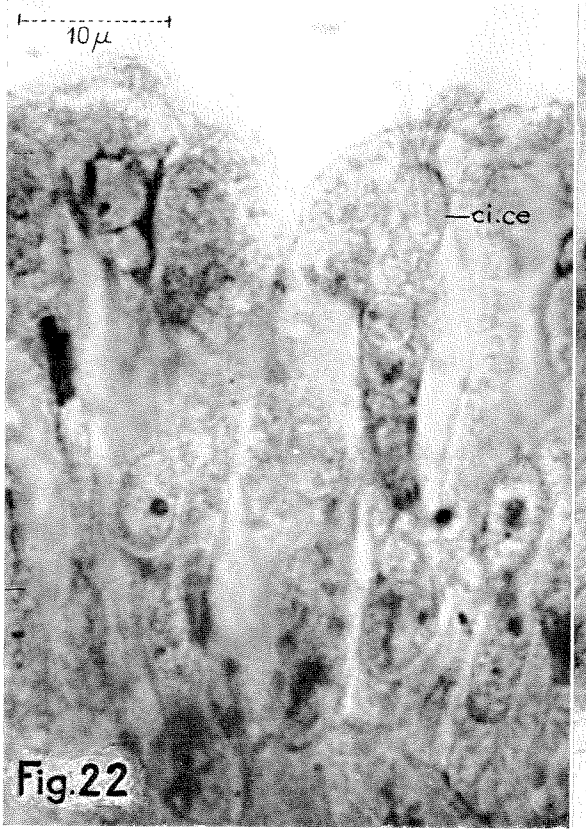


Fig.22

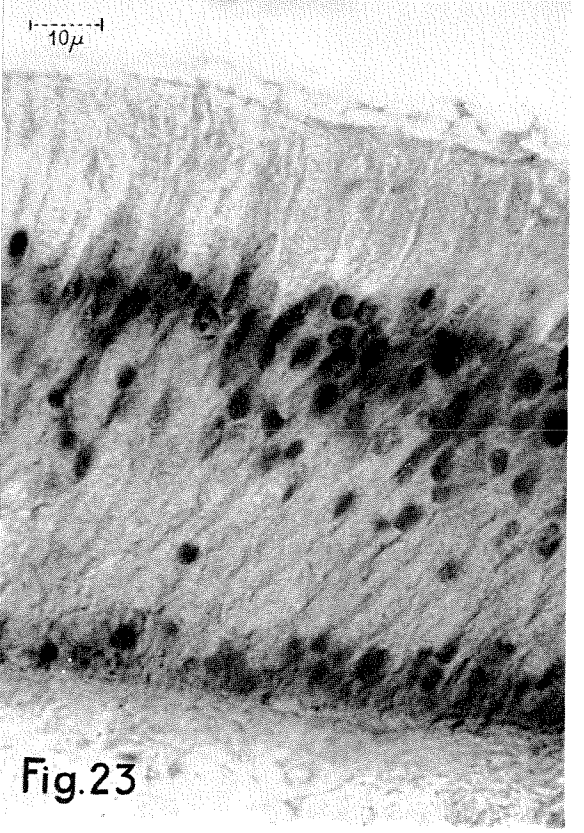


Fig.23

Plate 8

Fig. 24. Ciliated epithelium on the free edge of the velum. The vesicles under the surface are probably artificial. Microphotograph, Spec. III.

Fig. 25. Epithelium with goblet cells (mu. ce) and interstitial cells (in. ce) on the outer side of the inner marginal fold. Microphotograph, Spec. III.

Fig. 26. Ciliated epithelium on the ventral foot surface. Note the two layers of nuclei. Microphotograph, Spec. IV.

Fig. 27. Epithelium with cuticle on the inner side of the anterior lip. The vesicles under the cuticle may be artefacts. Microphotograph, Spec. III.

mu. ce = mucous (goblet) cells
in. ce = interstitial, ciliated cells

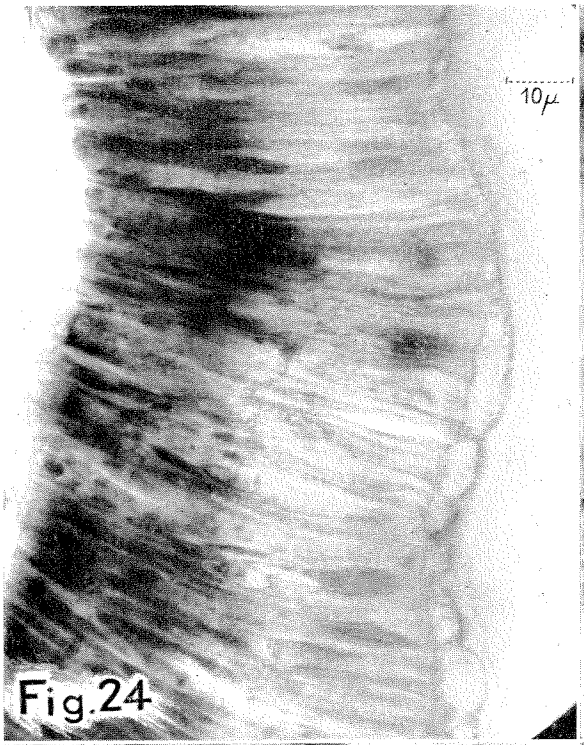


Fig.24

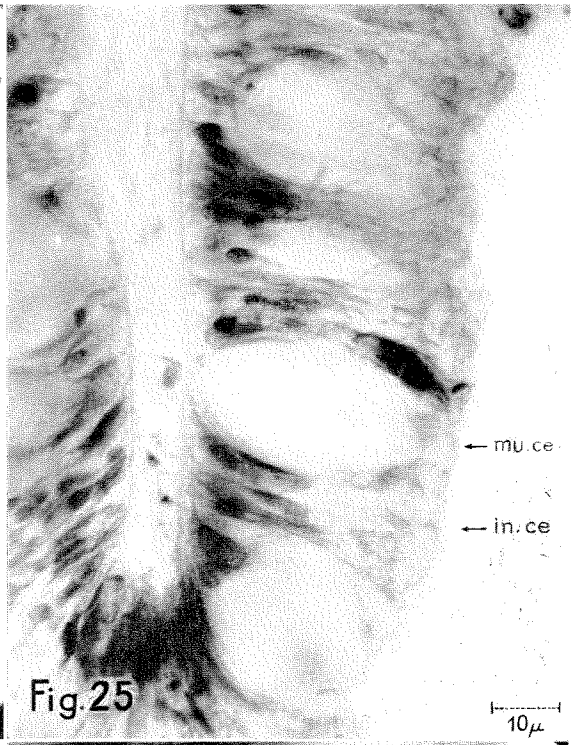


Fig.25

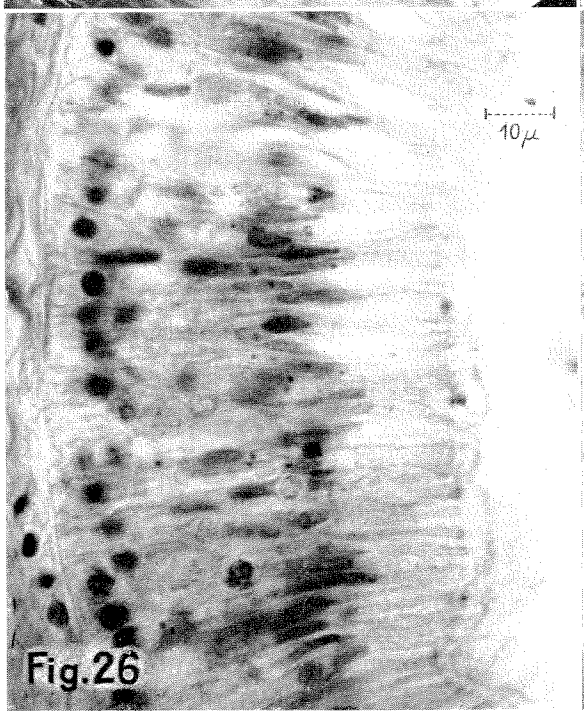


Fig.26

Fig.27

PLATE 9

Fig. 28. The dark-staining granulate gland cells in the basal part of the preoral tentacle. Spec. IV.

Fig. 29. Epithelium with scattered goblet cells (mu. ce) between the common, ciliated interstitial cells (int. ce) in the epithelium of the pallial groove above the gill. Spec. III.

Fig. 30. Epithelium of the hypobranchial gland, consisting of crowded glandular cells and a few, ciliated interstitial cells (in. ce). Spec. III.

Fig. 31. Inner marginal fold (in. ma. f) and marginal mucous gland (ma. mu. gl). Central direction to the left. Spec. III.

Fig. 32. Middle marginal fold (mi. ma. f) and periostracum gland (per. gl). Note the high, strongly ciliated epithelium on the outer (right) surface of the fold. Central direction to the left. Spec. III.

con. t = connective tissue
in. ce = interstitial (ciliated) cells
in. ma. f = inner marginal fold
m. pal = pallial muscle
ma. mu. gl = marginal mucous gland
mi. ma. f = middle marginal fold
mu = muscle fibres
mu. ce = mucous cells
per = periostracum
per. gl = periostracum gland

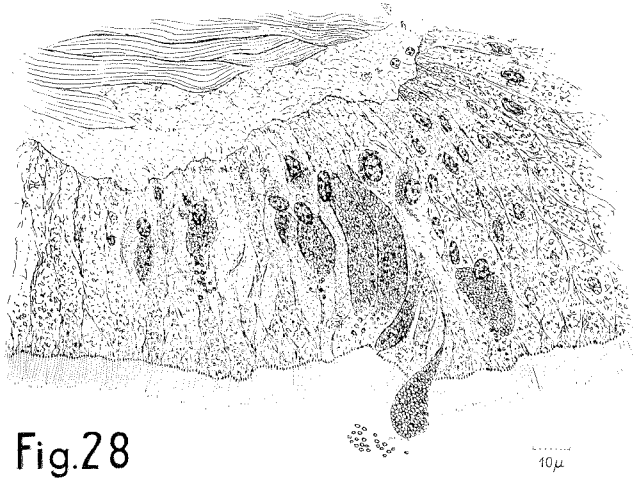


Fig.28

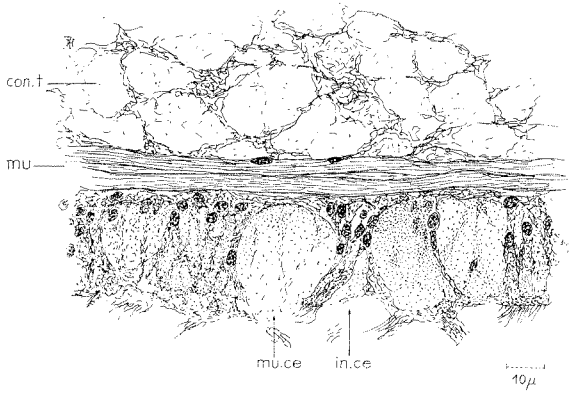


Fig.29

Fig.30

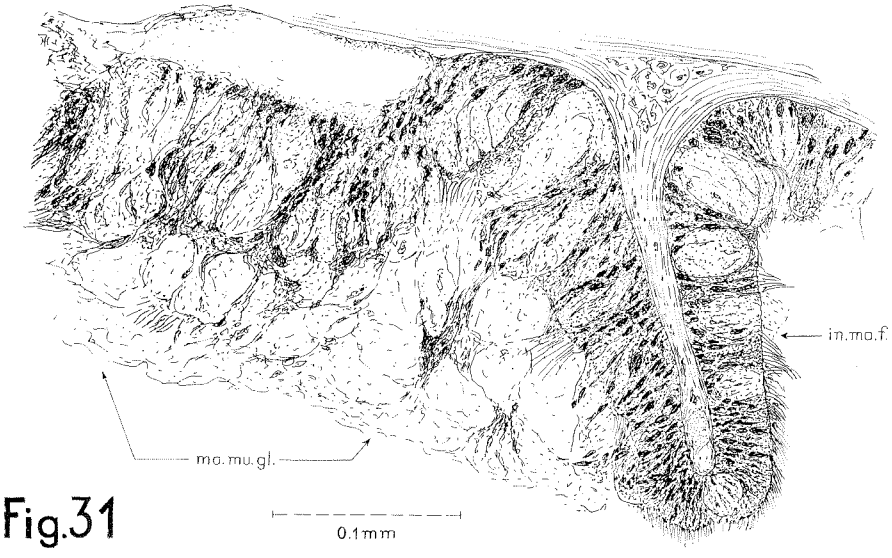


Fig.31

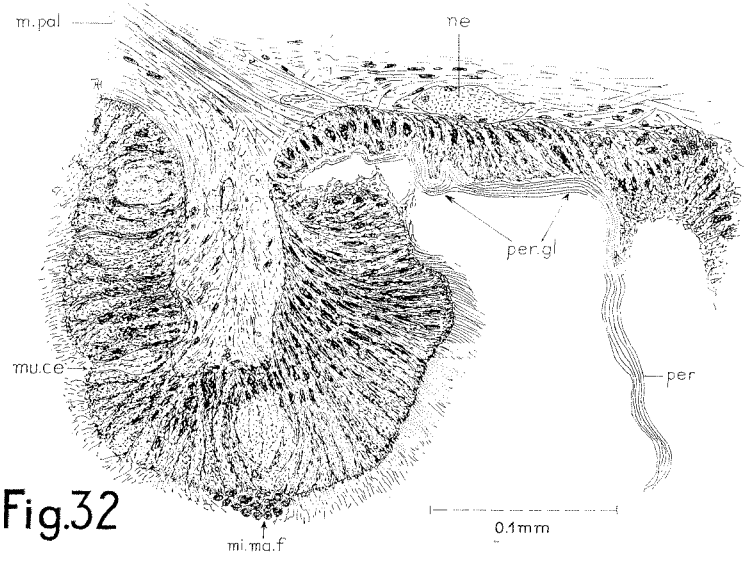


Fig.32

PLATE 10

Fig. 33. Diagram illustrating the formation of the shell and the structure of the pallial margin. The thickness of the shell has been increased several times in proportion to the other structures. The attachment of the outer marginal fold to the shell has not been observed in the sections. Compare Fig. 45.

Fig. 34. Sketch of the apex with the protoconch in Spec. III, drawn before the decalcification. The anterior wall of the animal is upwards in the figure. Compare Fig. 49.

Fig. 35. The apex of Spec. IV. The same orientation as Fig. 34. Slight impressions indicate the place of the lost protoconch.

Fig. 36. The outer surface of the shell with concentric growth lines and radial ribs. Spec. IV.

Fig. 37. Detail of the outer shell surface showing its puncture. Spec. IV.

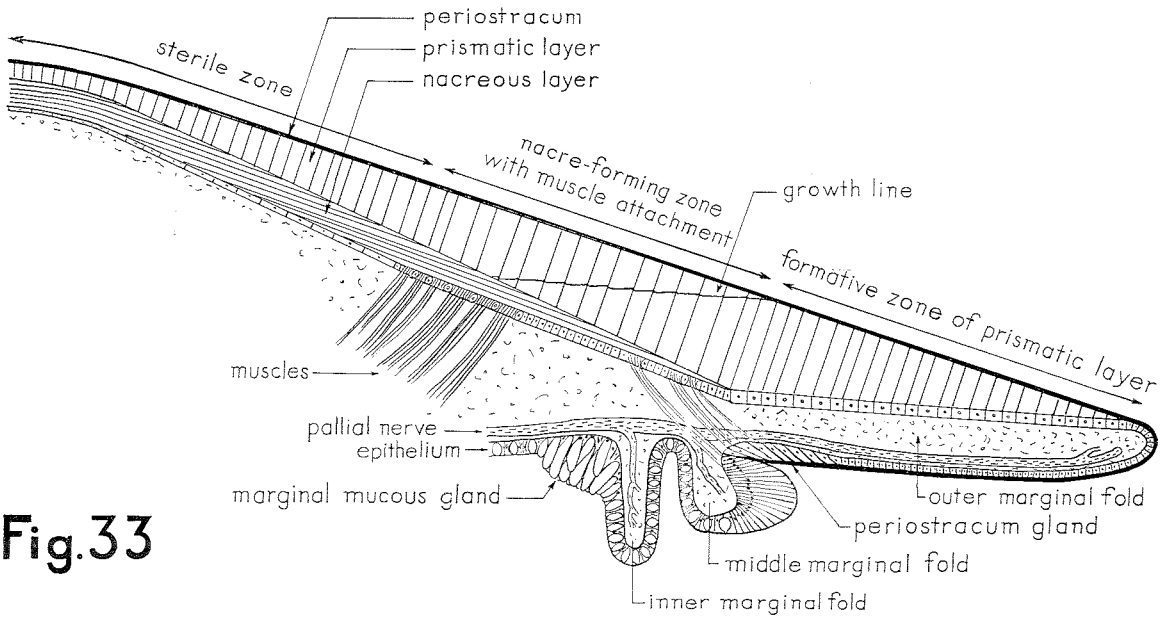


Fig.33

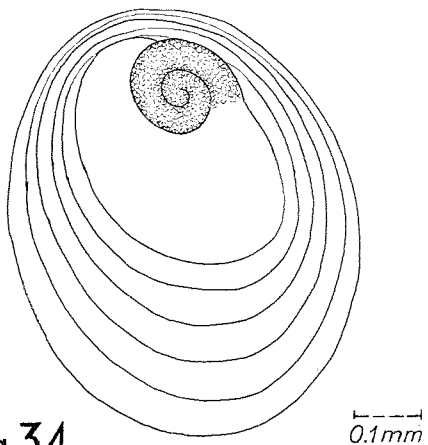


Fig.34

Fig.35

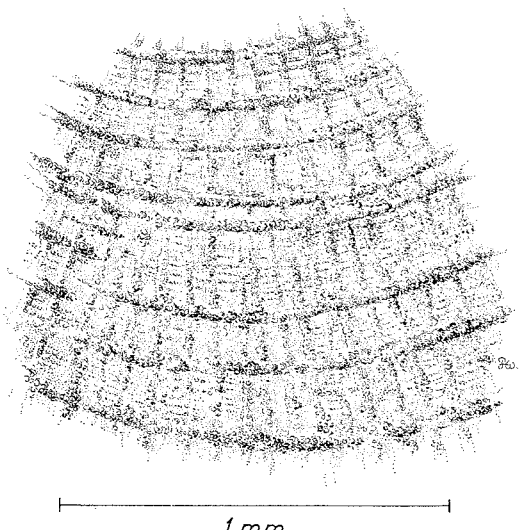


Fig.36

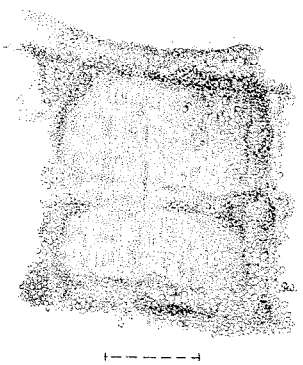


Fig.37

PLATE 11

Fig. 38. Prism-forming epithelium on the dorsal surface of the outer marginal fold. X marks the probable edge of this epithelium which, in the living specimens, underlies the edge of the shell. Compare Figs. 33 and 45. Spec. III.

Fig. 39. Shell and nacre-forming epithelium. Spec. III.

Fig. 40. Muscle attachment epithelium, tangential section. Spec. III. The tono-fibrils are collected in bundles, on the surface of which the nuclei are situated.

Fig. 41. Sterile shell epithelium between the nacreous layer and the wall of an intestinal loop. Spec. III.

Fig. 42. Muscle attachment epithelium in the region of insertion of the pedal retractors. Spec. III.

Fig. 43. Nacre-forming epithelium. Spec. III.

Fig. 44. Muscle attachment epithelium, showing the bundles of tono-fibrils and the position of the nuclei. Spec. III.

ep = epithelium
int. ep = intestinal epithelium
int. l = intestinal lumen
L. ce = Leydig cells
mu = muscle fibres
na. l = nacreous layer
per = periostracum
pr. l = prismatic layer
x = probable site of the edge of the outer marginal fold

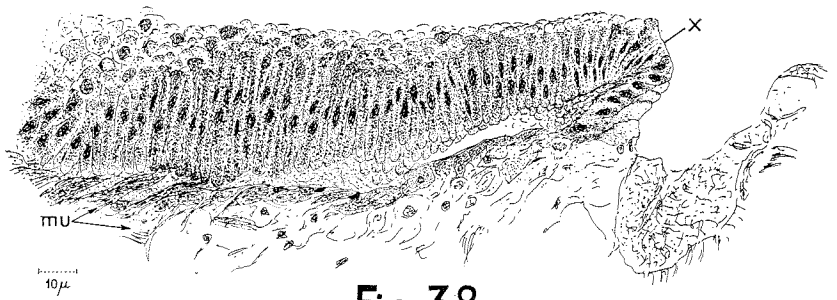


Fig.38

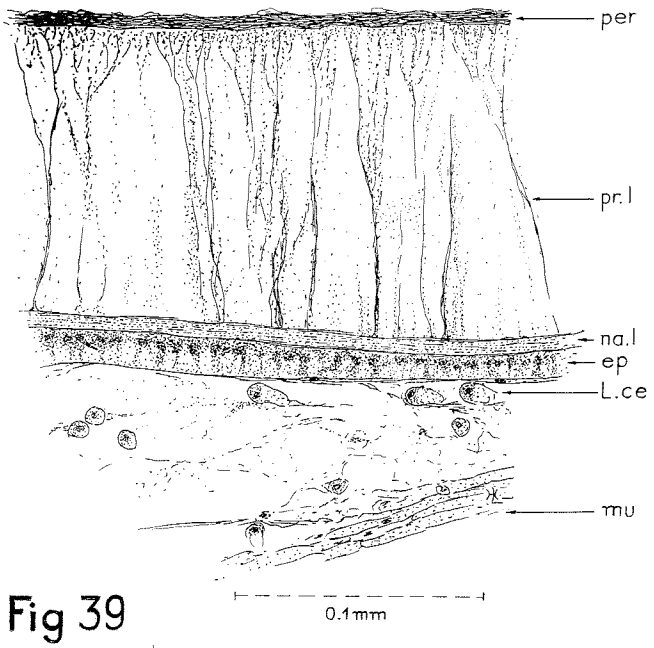


Fig 39

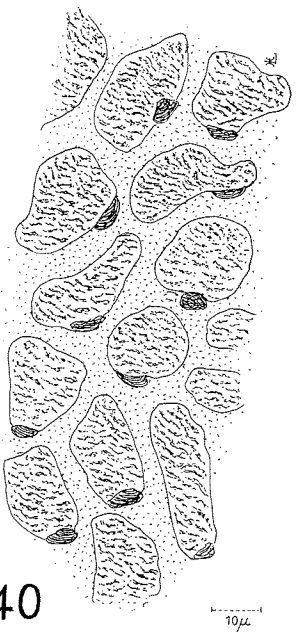


Fig.40

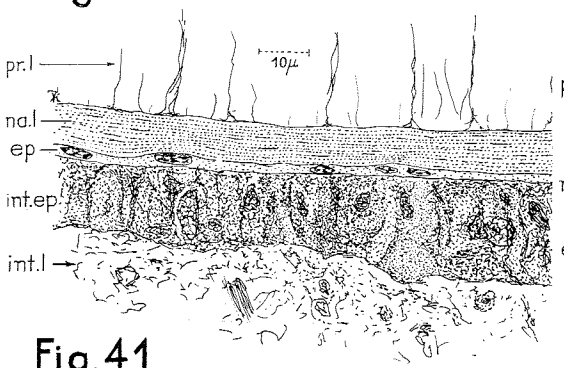


Fig.41

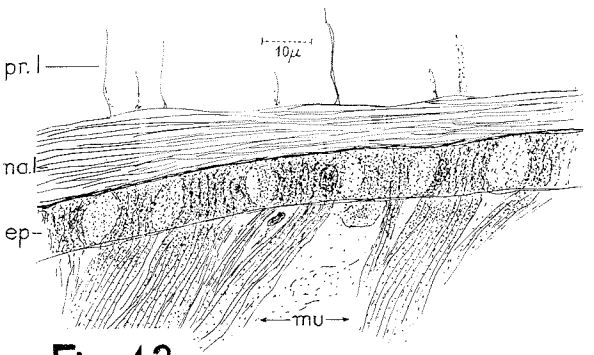


Fig.42

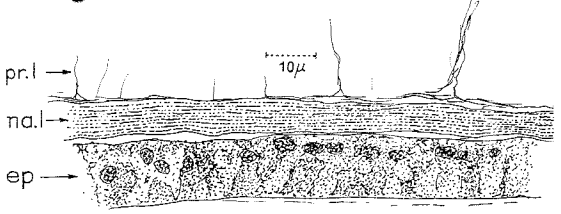


Fig.43

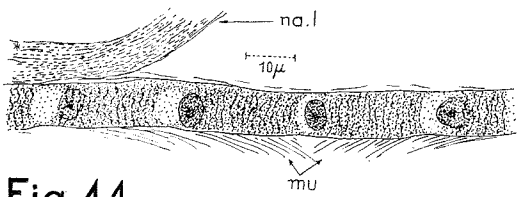


Fig.44

PLATE 12

Fig. 45. Section through the peripheral part of the shell and mantle. The latter must be strongly contracted since, in living specimens, the outer marginal fold (ou. ma. f) must reach the edge of the shell. The periostracum (per) has broken over at the shell edge. Microphotograph. Spec. III.

Fig. 46. The structure of the shell in the region of insertion of the pedal retractor muscles. Microphotograph. Spec. III.

Fig. 47. Section through the pallial fold, showing the marginal mucous gland (ma. mu. gl), the inner and middle marginal folds, and the periostracum gland (per. gl). Microphotograph. Spec. III.

Fig. 48. Muscle attachment epithelium with tono-fibrils (ep) underlying the lamellate nacreous layer in the region of the pedal retractors. Microphotograph. Spec. III.

ep = epithelium
in. ma. f = inner marginal fold
ma. mu. gl = marginal mucous gland
mi. ma. f = middle marginal fold
mu = muscles (tendinous part)
mu. a. ce = scattered muscle attachment cells
na. l = nacreous layer
ou. ma. f = outer marginal fold
per = periostracum
per. gl = periostracum gland
pr. l = prismatic layer

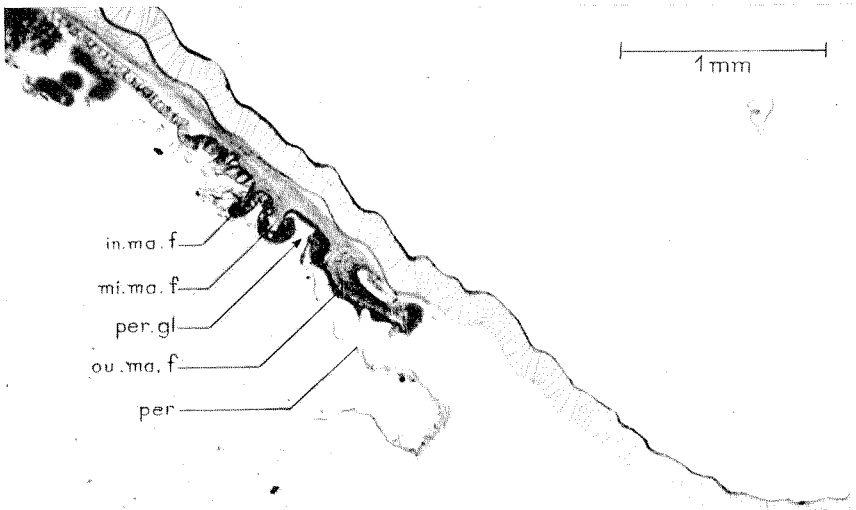


Fig.45

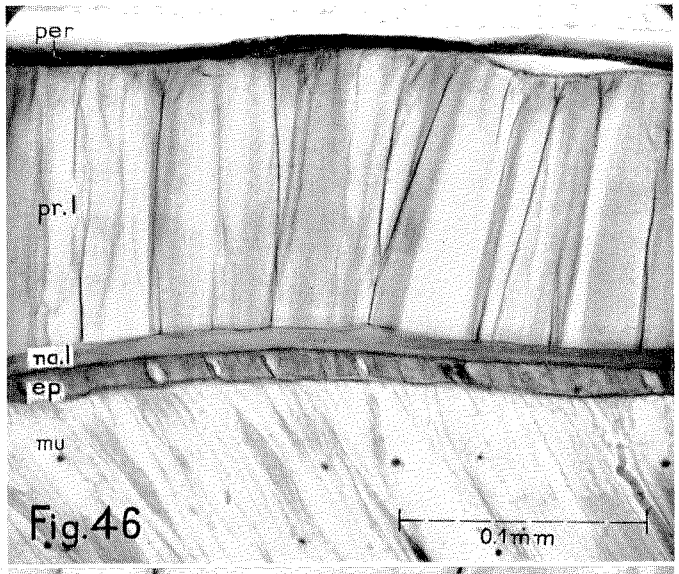


Fig.46

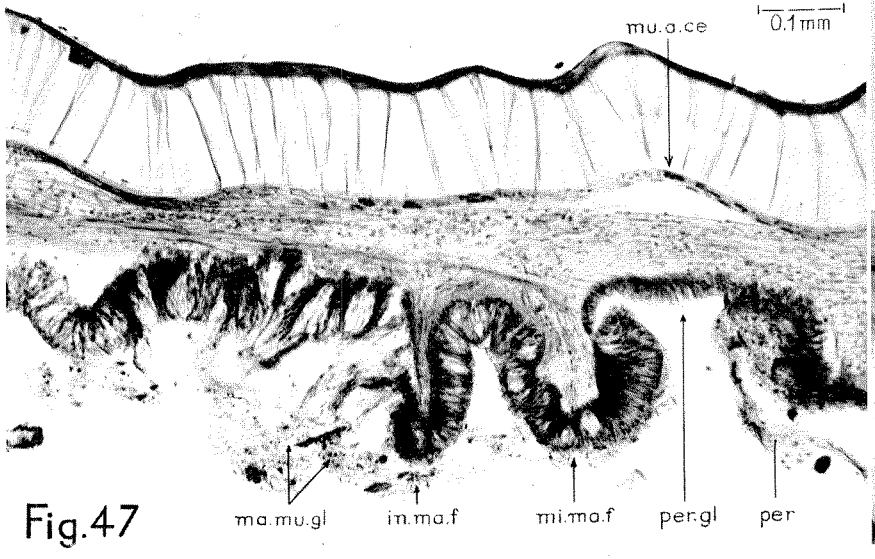


Fig.47

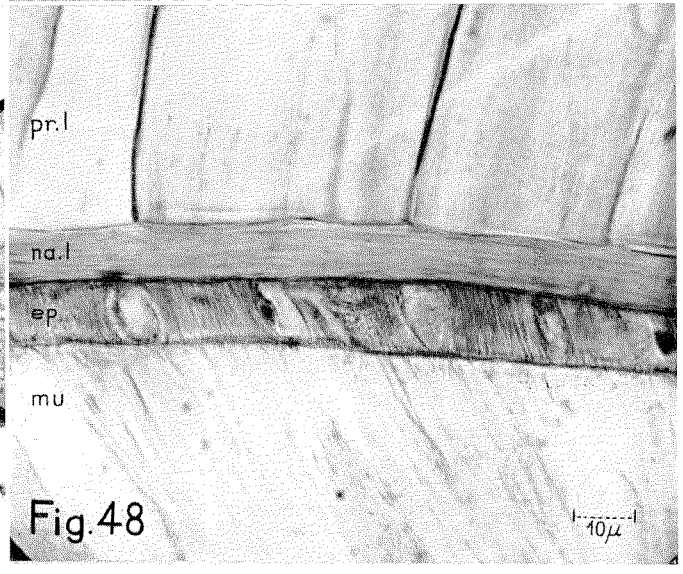


Fig.48

PLATE 13

Fig. 49. Apex with protoconch of Spec. IV after decalcification and imbedding in celloidin. Compare fig. 34. Microphotograph.

Fig. 50. Periostracum gland with the periostracum on the surface. Note the dark fibrils in the basal part of the cells. Central direction to the left. Microphotograph. Spec. III.

Fig. 51. Section through shell with a growth line (gr. l). Microphotograph. Spec. III.

Fig. 52. Nacre-forming epithelium (ep), with a single muscle attachment cell (mu. a. ce). Microphotograph. Spec. III.

ep = epithelium
gr. l = growth line
L. ce = Leydig cells
mu = muscle fibres
mu. a. ce = muscle attachment cells
na. l = nacreous layer
per = periostracum
per. gl = periostracum gland
pr. l = prismatic layer

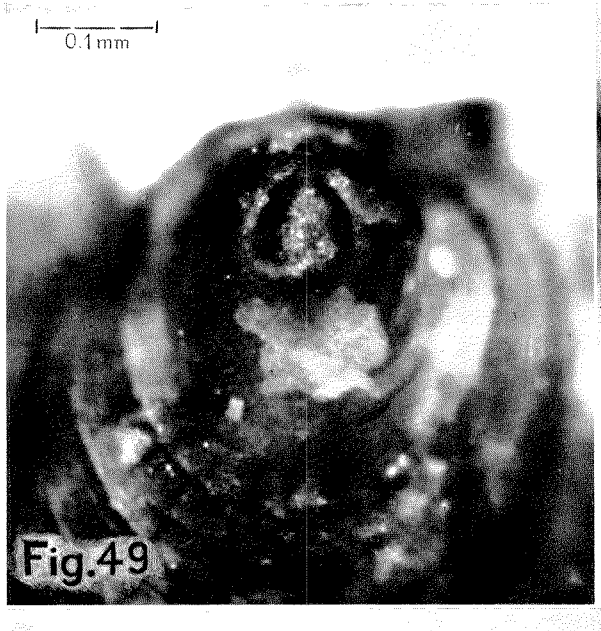


Fig.49

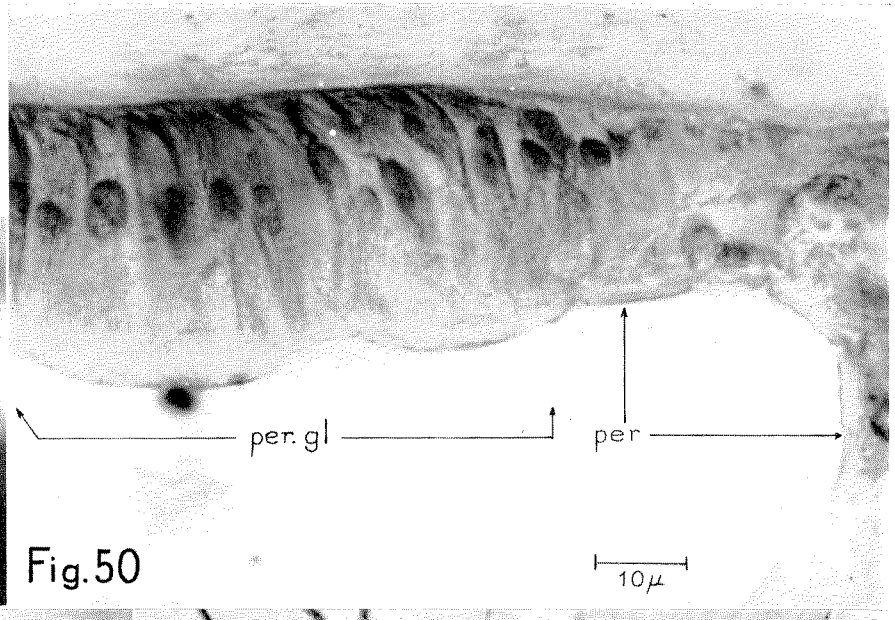


Fig.50

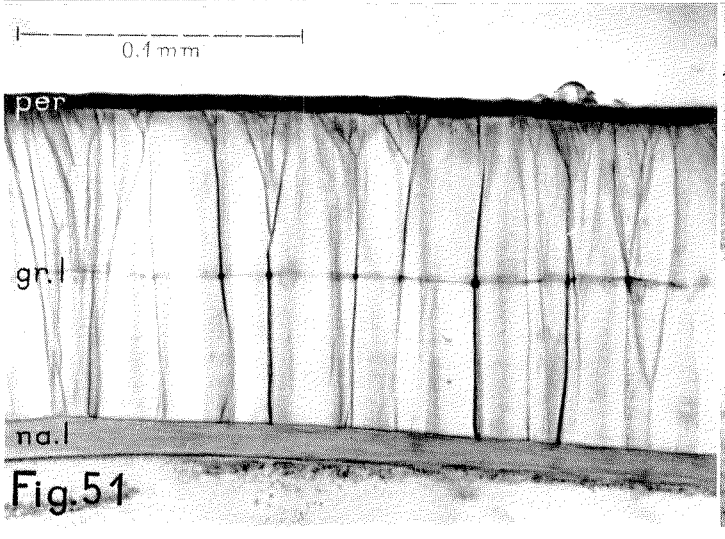


Fig.51

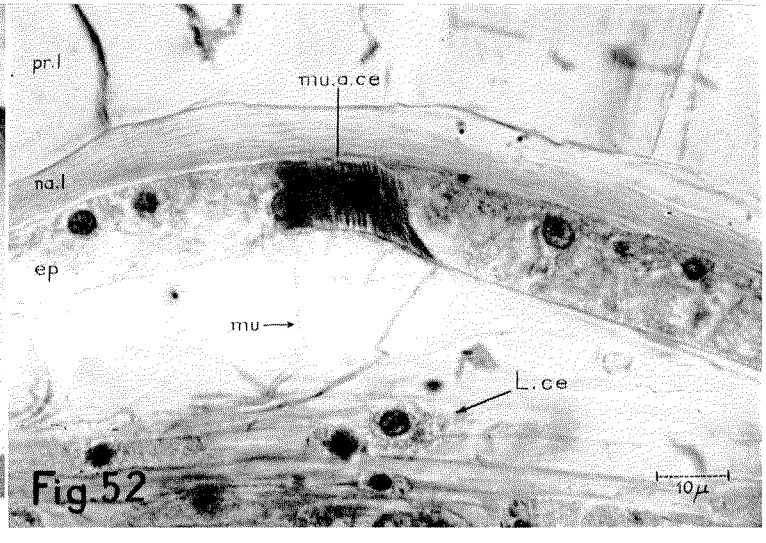


Fig.52

PLATE 14

Fig. 53. Muscle attachment epithelium, seen in tangential section. In the place shown, the nuclei are situated on the surface of the bundles of tono-fibrils. Microphotograph. Spec. III.

Fig. 54. Muscle attachment epithelium of a buccal muscle. The nuclei are situated inside the bundles of tono-fibrils. Microphotograph. Spec. III.

Fig. 55. Nacre-forming epithelium, seen in tangential section. Microphotograph. Spec. III.

Fig. 56. Longitudinal section through the stem of the 2nd left gill, showing the alternation of dorsal and ventral lamellae. Microphotograph. Spec. III.

do. la = dorsal lamellae
ne = nephridia
nu = nucleus
pa. w = wall of pallial groove
to.-fi = bundles of tono-fibrils
us. p = unspecialized plasm
ve. la = ventral lamellae

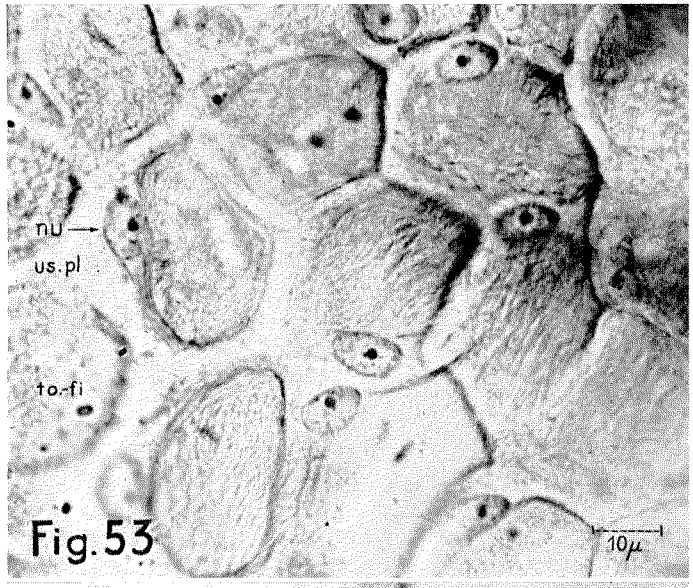


Fig.53

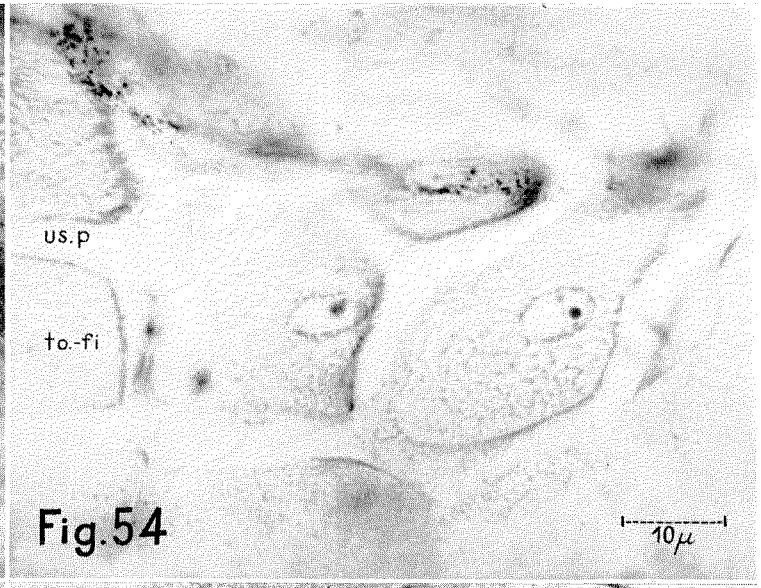


Fig.54

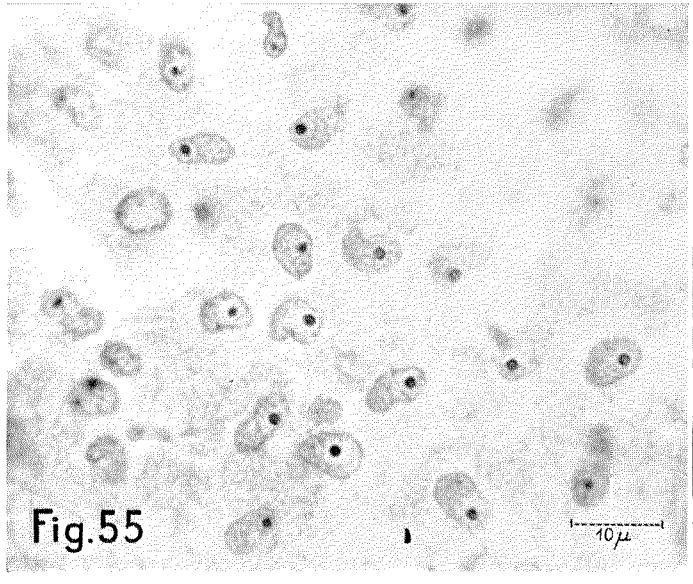


Fig.55

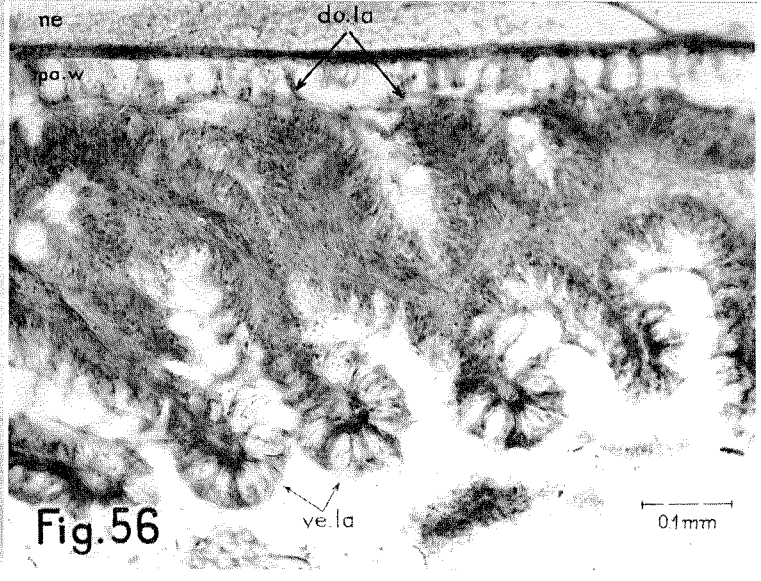


Fig.56

PLATE 15

Fig. 57. Ventral view of *Neopilina* showing diagrammatically the arrangement of the gills. The arrows indicate the probable course of the water currents. The foot margin is removed to the left in the figure.

an = anus
f. m = foot margin
gi_1-gi_5 = gills number 1 and 5, resp.
in. ma. f = inner marginal fold of mantle
m = mouth
mi. ma. f = middle marginal fold
ou. ma. f = outer marginal fold
pa. g = pallial groove
po. te = postoral tentacles
pr. te = preoral tentacle
vel = velum

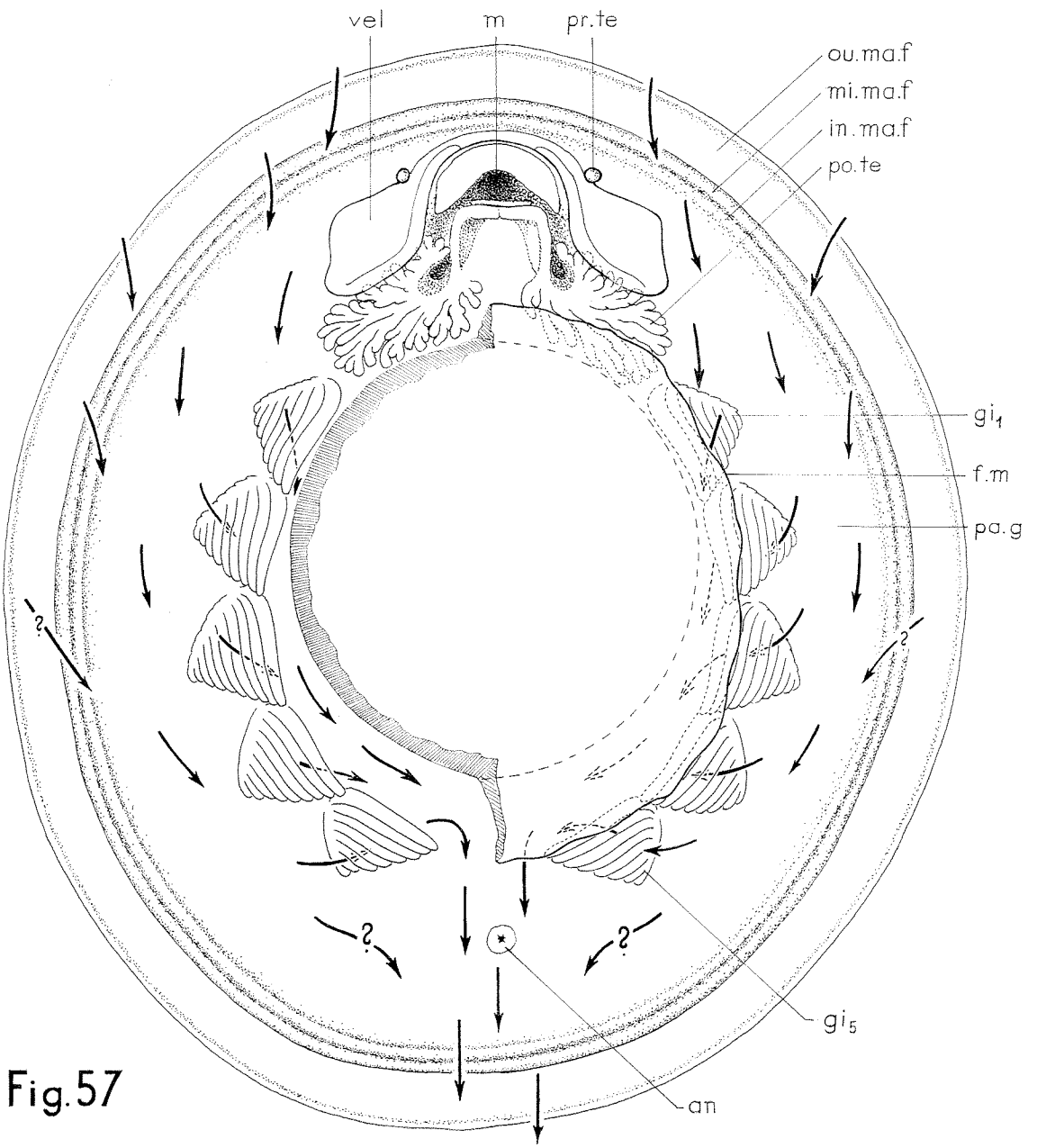


Fig.57

PLATE 16

Fig. 58. Diagrammatical drawing of a gill, seen from the ventral side. The lamellae are partly disarranged in the specimens but they have been drawn in what is believed to be the natural position. The different kinds of epithelia are indicated.

Fig. 59. The same gill, seen from the dorsal side. The position of the renopore is shown, and the longitudinal direction of the pallial groove is indicated by the orientation of the lateral nerve cord. Both figures are based on wax-plate reconstructions.

aff. g. v = afferent gill vessel
an. e. st = anterior edge of gill stem
do. e. la = dorsal edge of lamellae
do. la = dorsal gill lamellae
do. si. st = dorsal side of gill stem
eff. gi. v = efferent gill vessel
ext. gi. n = external gill nerve
int. gi. n = internal gill nerve
lat. n. c = lateral nerve cord
m. br. ext = musculus branchialis externus
po. e. st = posterior edge of gill stem
ren. p = renopore
si. la = sides of lamellae
tip la = tip epithelium of lamellae
ve. e. la = ventral edge of lamellae
ve. si. st = ventral side of gill stem

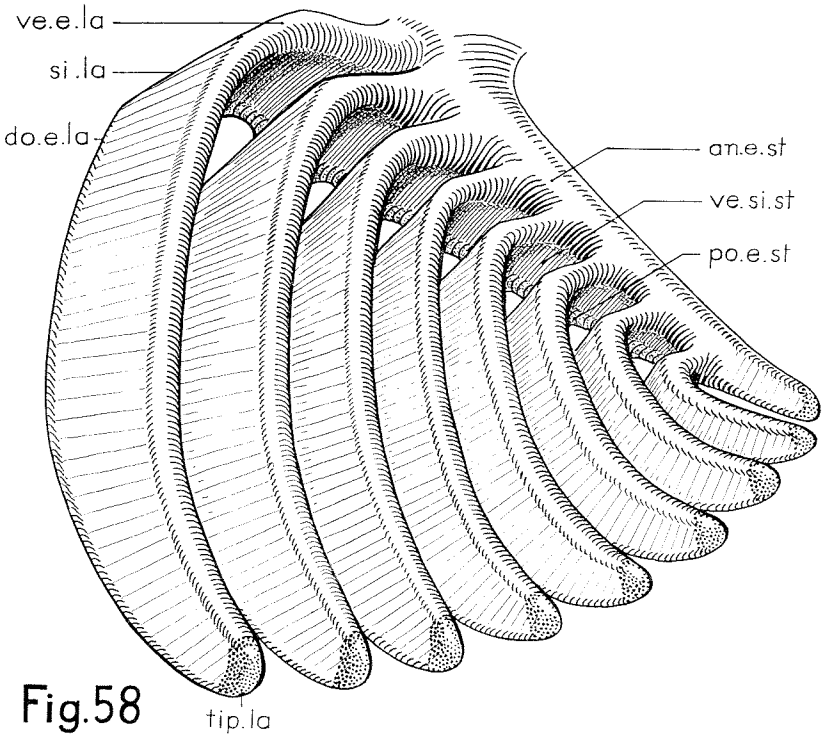

ve.e.la
si.la
do.e.la
an.e.st
ve.si.st
po.e.st
tip.la

Fig.58

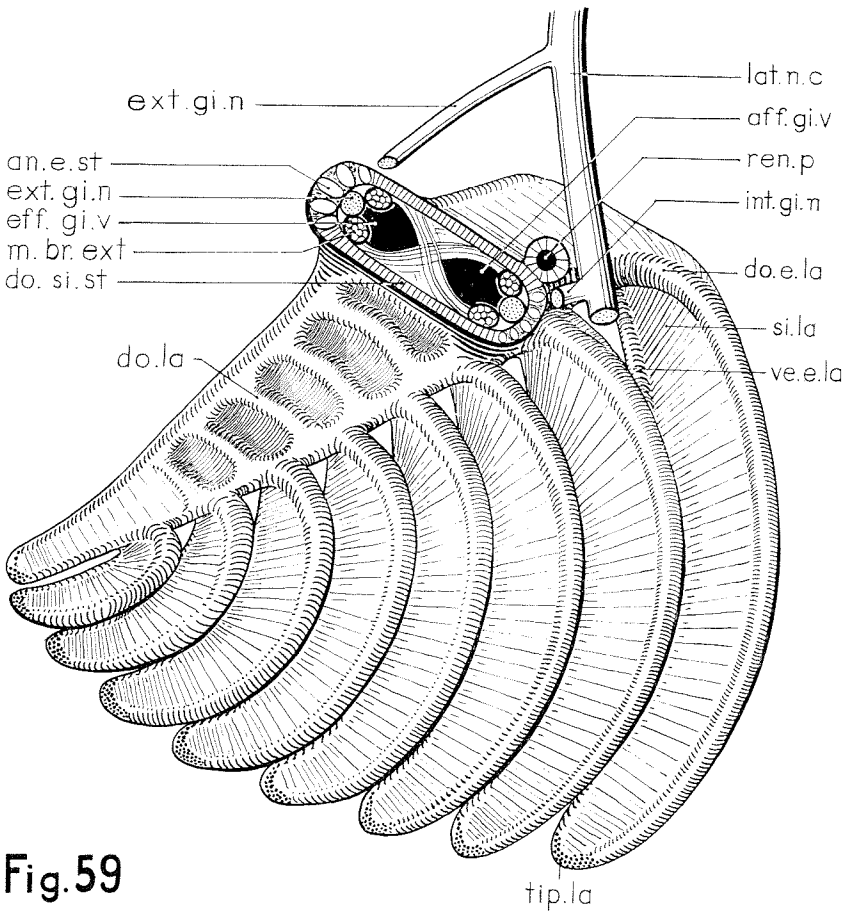

ext.gi.n
lat.n.c
aff.gi.v
an.e.st
ext. gi.n
eff. gi.v
m. br. ext
do. si. st
ren.p
int.gi.n
do.e.la
si.la
ve.e.la
do.la
tip.la

Fig.59

PLATE 17

Fig. 60. The course and ramifications of the gill retractors, shown diagrammatically in a simplified gill. Ventral view.

Fig. 61. Cross section of a gill lamella (1st right gill of Spec. III). Camera lucida drawing. Dorsal edge to the right.

aff. gi. v = afferent (venous) gill vessel
an. e. st = anterior edge of gill stem
do. e. la = dorsal edge of lamella
eff. gi. v = efferent (arterial) gill vessel
ext. gi. n = external gill nerve
in. ce = interstitial (ciliated) cells
in. gi. m = inner gill muscles
int. gi. n = internal gill nerve
lat. si. la = lateral side of lamella
m. br. ext. d = musculus branchialis externus dorsalis
m. br. ext. v = musculus branchialis externus ventralis
m. br. int. d = musculus branchialis internus dorsalis
m. br. int. v = musculus branchialis internus ventralis
mu. ce = mucous (goblet) cells
ve. e. la = ventral edge of lamella

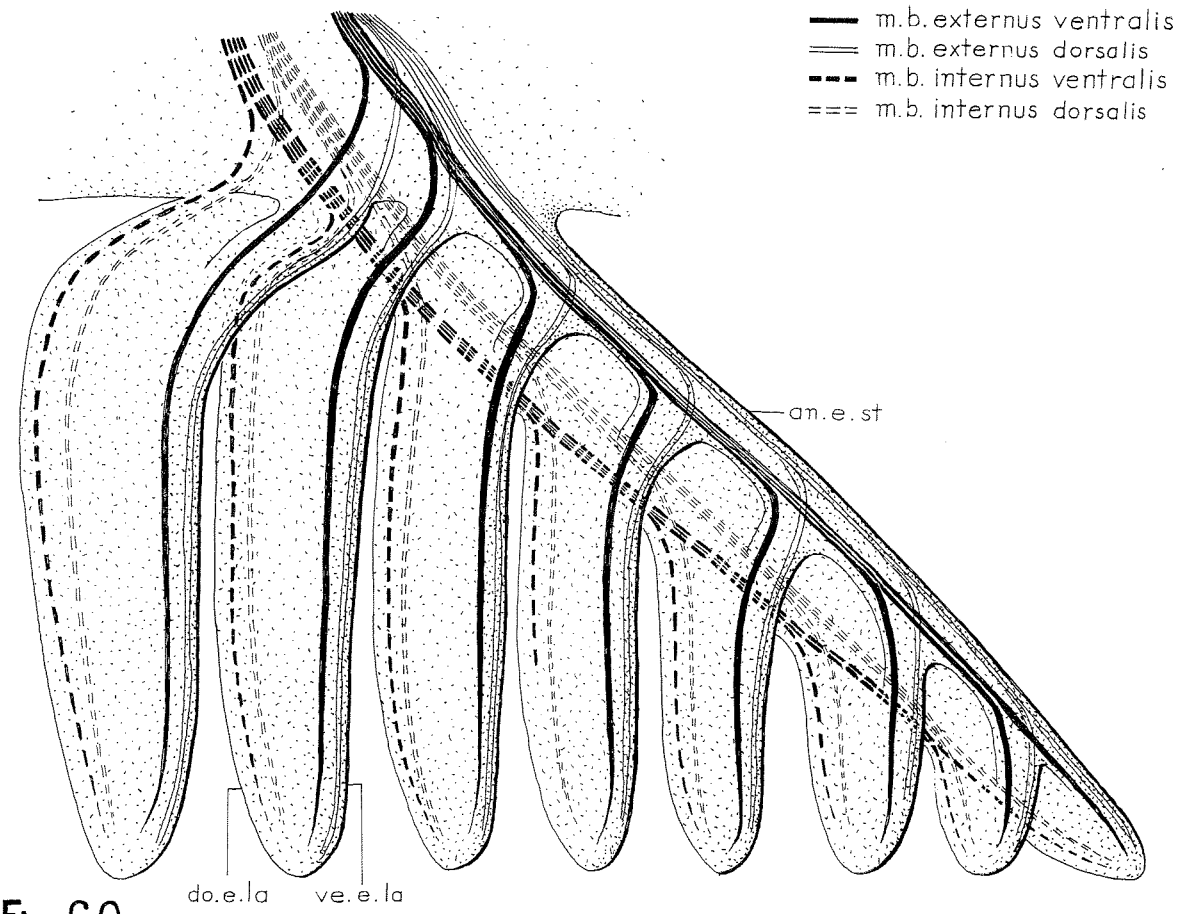

m.b. externus ventralis
m.b. externus dorsalis
m.b. internus ventralis
m.b. internus dorsalis
an.e.st
do.e.la
ve.e.la

Fig.60

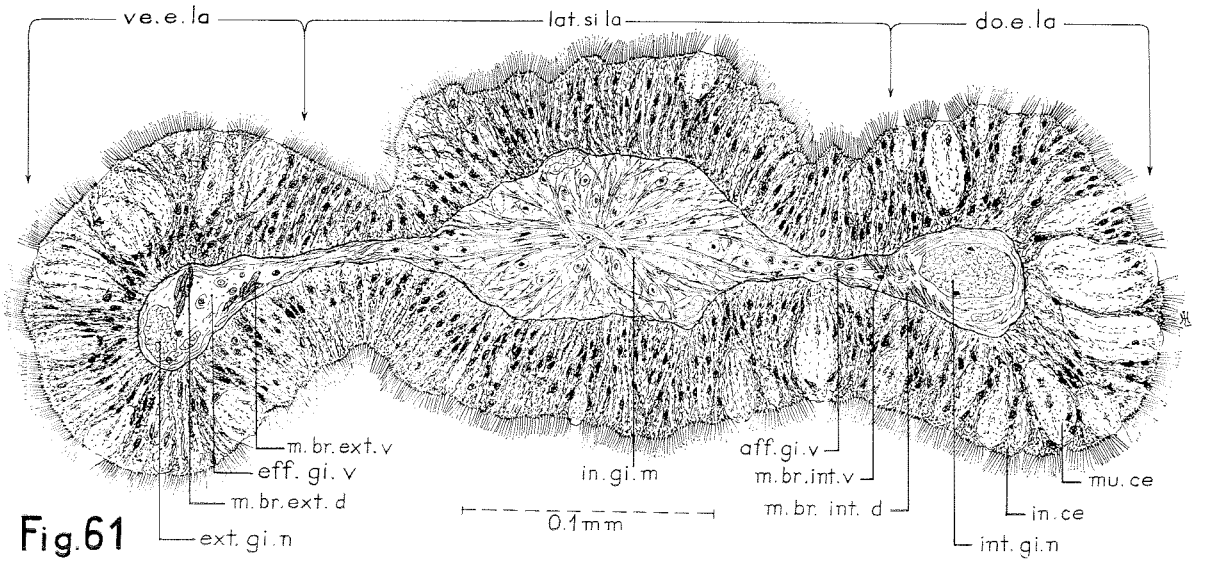

ve.e.la
lat.si la
do.e.la
m.br.ext.v
eff. gi. v
m.br.ext. d
ext. gi.n
in.gi.m
0.1mm
aff.gi.v
m.br.int.v
m.br. int. d
mu.ce
in.ce
int. gi.n

Fig.61

PLATE 18

Fig. 62. Cross section through the stem of the 5th left gill. Central direction to the left. Microphotograph. Spec. III.

Fig. 63. Cross sections of the lamellae of the 2nd right gill. Central direction to the right. Microphotograph. Spec. III.

Fig. 64. The dorsal edge of a gill lamella, showing ciliated interstitial cells (in. ce) and goblet cells (mu. ce). Microphotograph. Spec. III.

Fig. 65. Longitudinal section through the gill stem and the base of the lamellae, showing the ramification of the musculus branchialis internus (m. br. int). Microphotograph. Spec. III.

aff. gi. v = afferent (venous) gill vessel
ant. e. st = anterior edge of gill stem with dark granulate cells and mucous cells
do. e. la = dorsal edge of lamellae
eff. gi. v = efferent (arterial) gill vessel
ext. gi. n = external gill nerve
in. ce = interstitial (ciliated) cells
int. gi. n = internal gill nerve
m. br. ext = musculus branchialis externus (double)
m. br. int = musculus branchialis internus (double)
mu. ce = mucous (goblet) cells
pa. ep = pallial epithelium
ve. e. la = ventral edge of lamellae
ve. la = ventral lamella

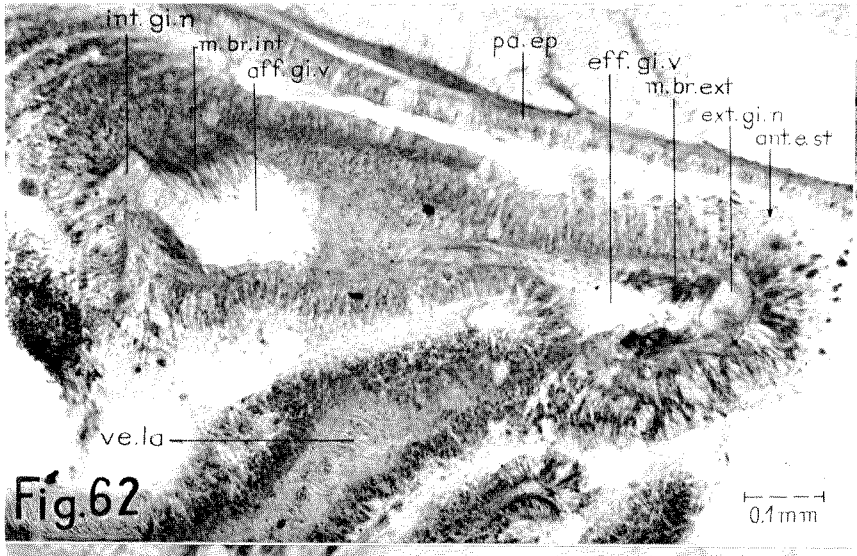


Fig.62

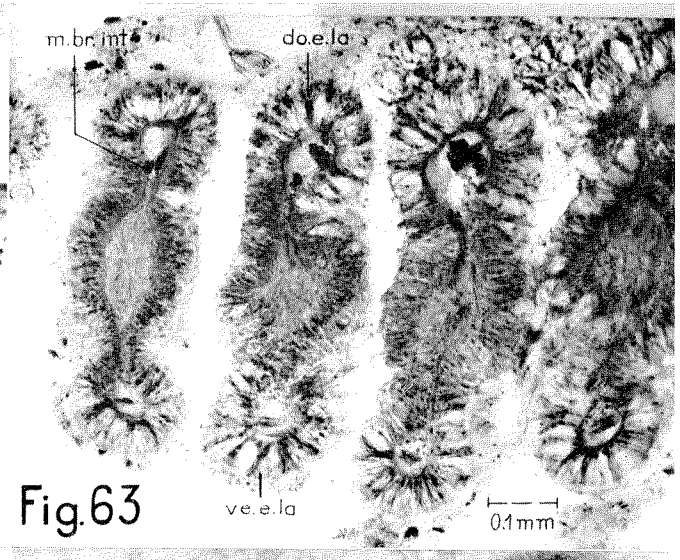


Fig.63

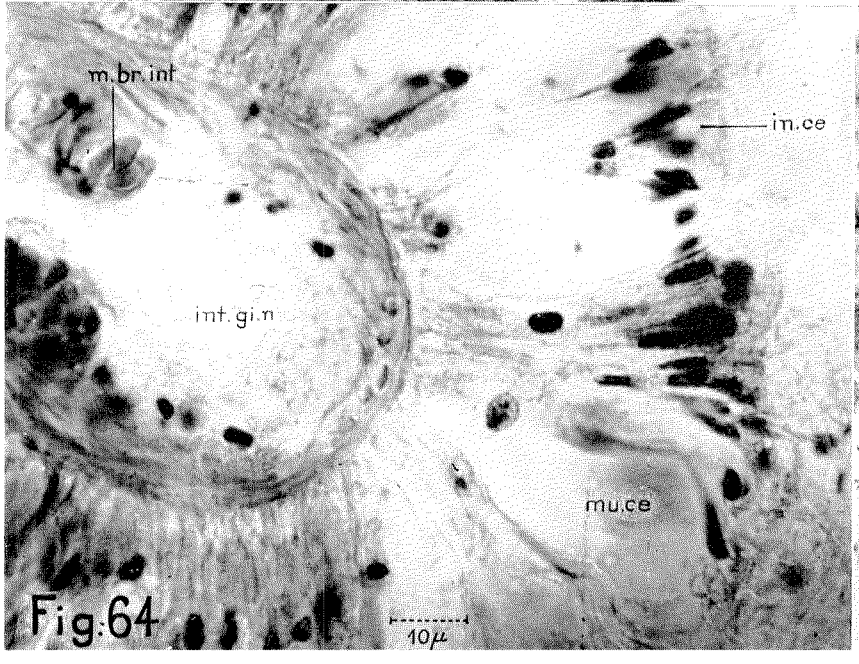


Fig.64

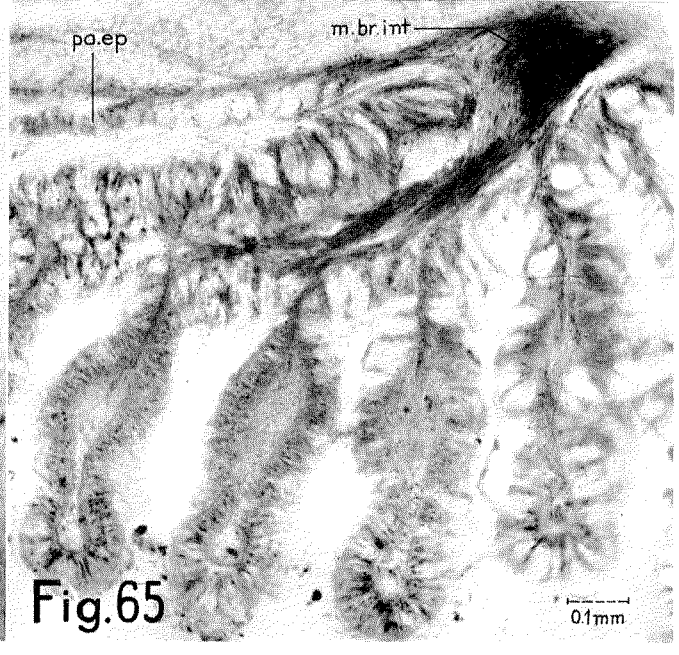


Fig.65

PLATE 19

Fig. 66. Diagrammatical drawing of the mouth region, based on Spec. IV but simplified and changed so as to show the morphological relationships indicated by the sections. Cuticle black.

Fig. 67. Drawing of the mouth region of Spec. IV in situ. For explanations see fig. 66.

Fig. 68. The appearance of the left tentacle tuft in Spec. VII, in which it is believed to be preserved in a natural position. The dislocated pallial fold (pa. m) covers part of the area.

Fig. 69. The preoral tentacle of the left side. Spec. VI.

Fig. 70. Longitudinal section through the preoral tentacle. Spec. III.

ant. l = anterior lip
ci. ep = ciliated epithelium on the transverse part of the tentacle ridge
co. ant. l = cuticularized corner of anterior lip
cu. ant. l = cuticular plate on the anterior lip and in the ventral wall of the pharynx
da. gr. ce = dark granulate cell
fe. f = feeding furrow
f. m = foot margin
m = mouth
me. ve. ri = median velar ridge
n. fi = nerve fibres
pa. ep = pallial epithelium
pa. m = pallial margin
po. l = posterior lip with cuticle
po. te = postoral tentacles
pp. a = propodial area
pr. te = preoral tentacle
ra = radula
te. ri = tentacle ridge
ve. e. vel = ventral, strongly ciliated edge of velum
vel = velum

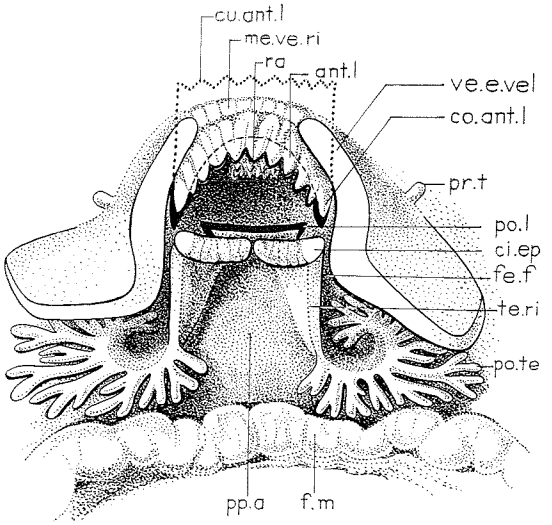


Fig.66

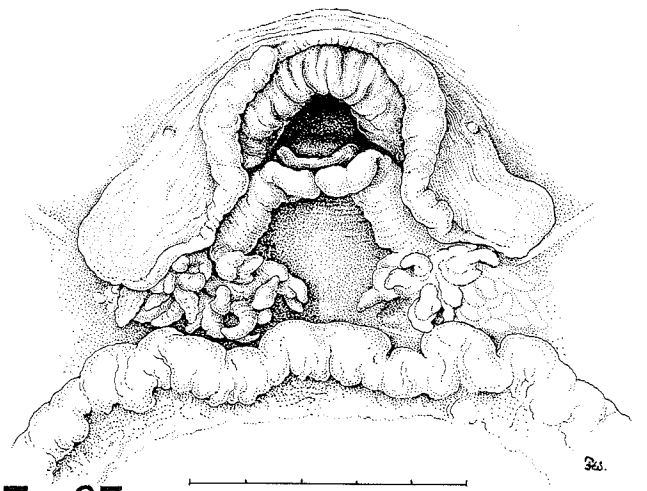


Fig.67

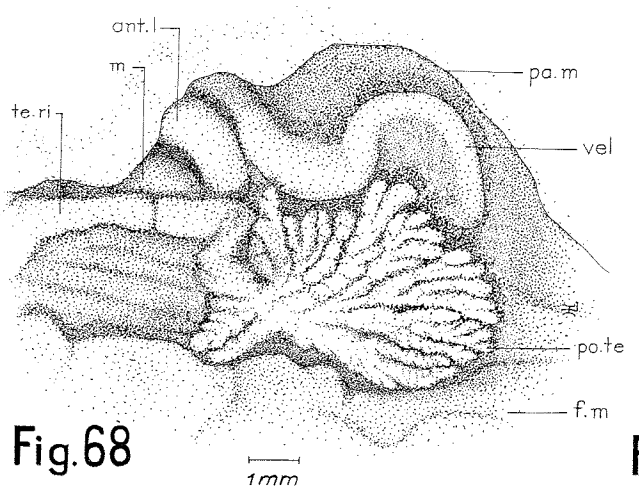


Fig.68

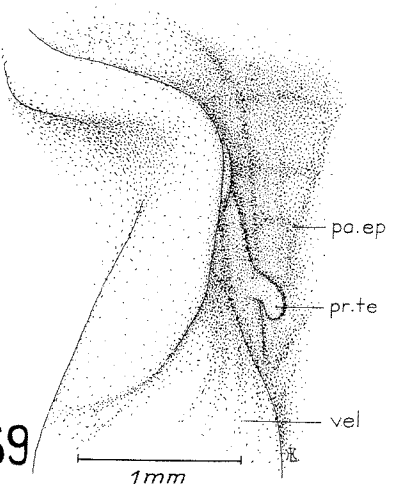


Fig.69

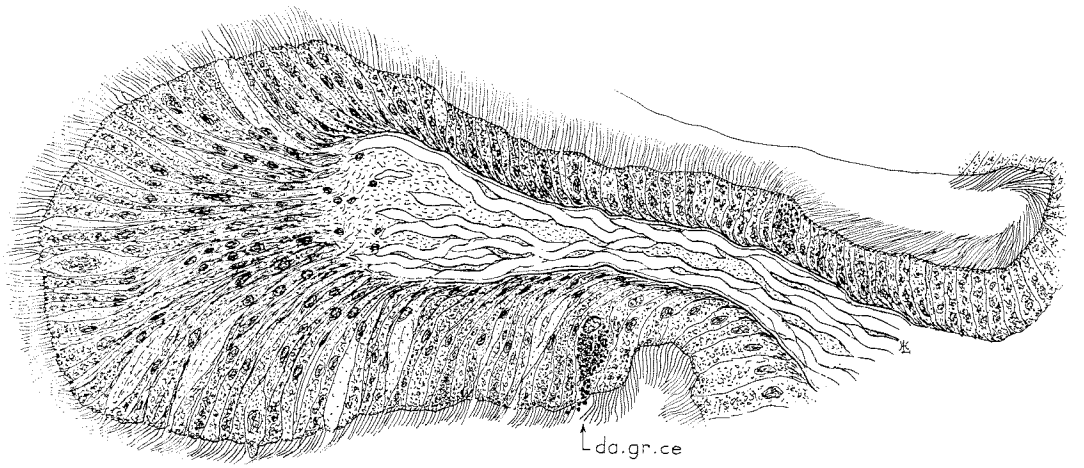


Fig.70

PLATE 20

Fig. 71. Horizontal section through the anterior body region at the level of the oral cavity. Microphotograph. Spec. IV.

Fig. 72. Transversal section just behind the mouth. Microphotograph. Spec. III.

bu. c = buccal connective
ci. ep = strongly ciliated epithelium on the tentacle ridge and on the ventral edge of the velum
cu. ant. l = cuticle on the anterior lip
d. coe = parts of the dorsal coelom
fe. f = feeding furrow
m. ca. a-l = musculus cartilaginis antero-lateralis
m. pr. ca. p = musculus protractor cartilaginis profundus
m. pr. ra = musculus protractor radulae
m. pr. v. ma = musculus protractor vesicae major
m. ra. l. d = musculus radulae longus, pars dorsalis
m. re. v = musculus retractor veli posterior
m. tr. a = musculus transversalis anterior
no. te. ri = median notch of the tentacle ridge
pe. g = pedal gland epithelium
po. l = posterior lip
po. te = postoral tentacles
pr. te = preoral tentacle
ra. sh = radula sheath
sal. g = "anterior salivary gland"
sr. m = subradular membrane
sr. o = subradular organ
te. ri = tentacle ridge
vel = velum
Y = insertion area Y
Y_1 = the muscle Y_1

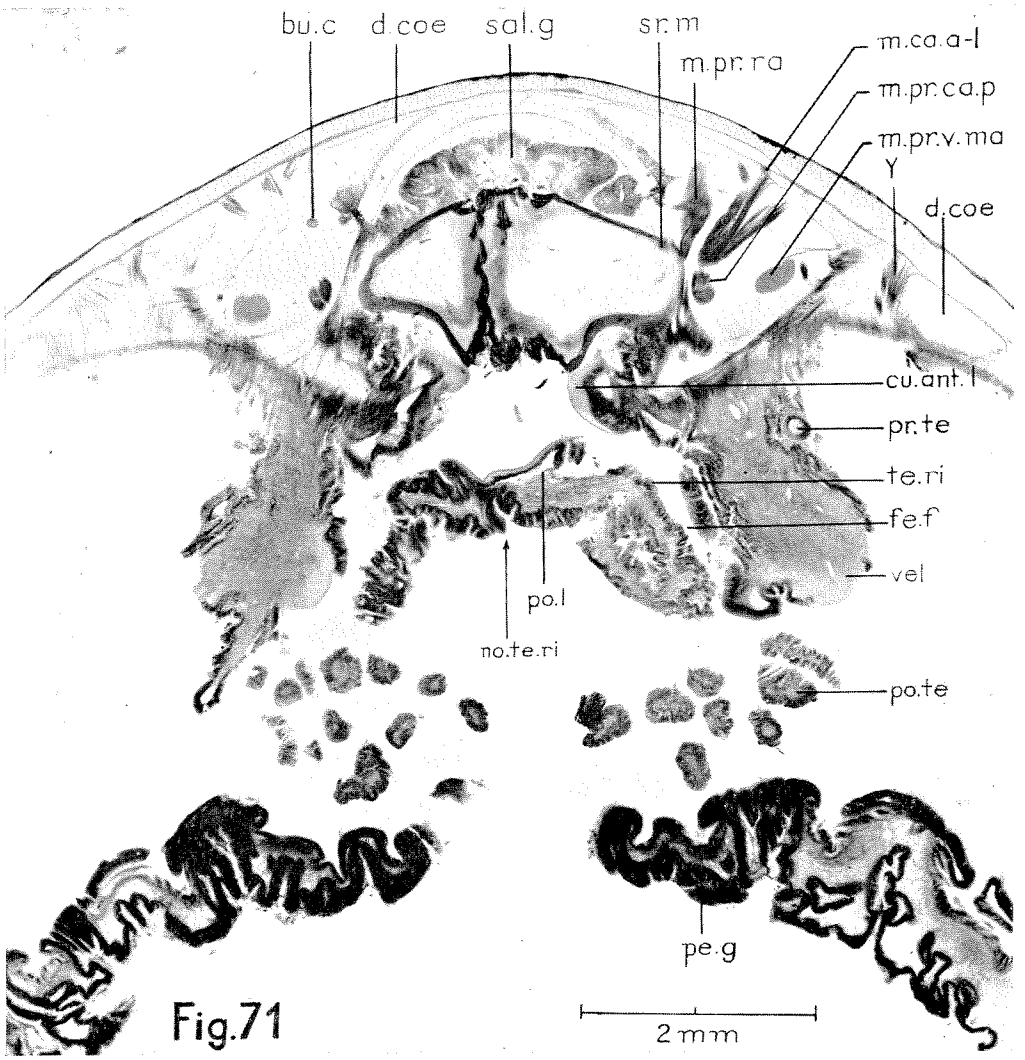

bu.c
d.coe
sal.g
sr.m
m.pr.ra
m.ca.a-l
m.pr.ca.p
m.pr.v.ma
Y
d.coe
cu.ant.l
pr.te
te.ri
fe.f
vel
po.l
no.te.ri
po.te
pe.g
2 mm

Fig.71

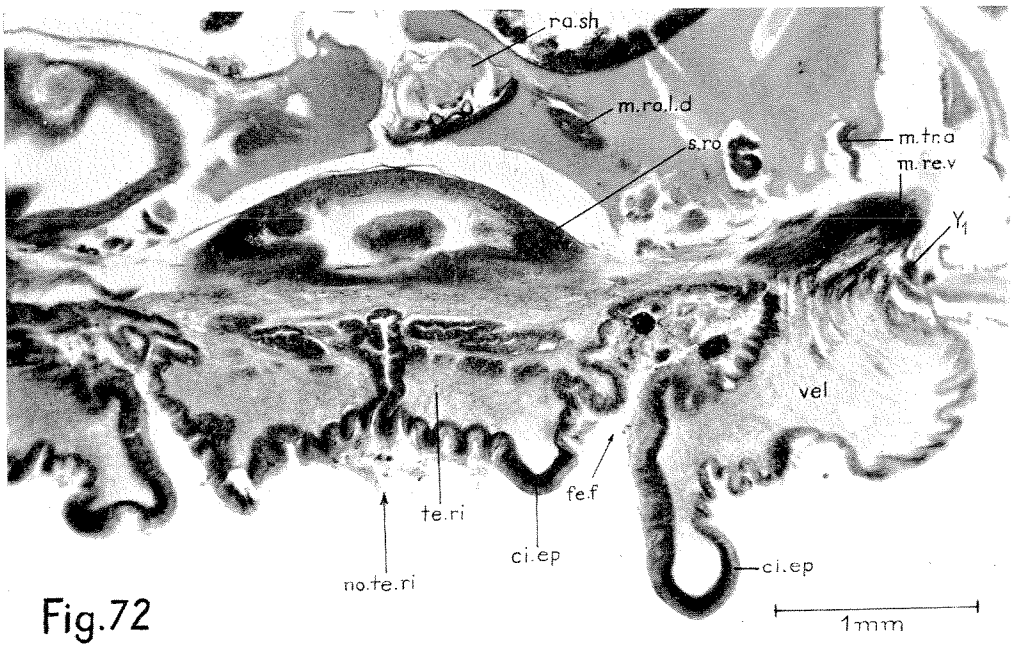

ra.sh
m.ro.l.d
s.ro
m.tr.a
m.re.v
Y_1
vel
te.ri
fe.f
ci.ep
no.te.ri
ci.ep
1mm

Fig.72

PLATE 21

Fig. 73. Horizontal section through folds of the anterior foot margin, showing the zone of "ventral foot epithelium" (ve. f. ep) separating the pedal gland epithelium (pe. g. ep) from the epithelium of the foot side (f. s. ep). Microphotograph. Spec. IV.

Fig. 74. The oral region of Spec. IV. For explanation compare Figs. 66 and 67. Photograph.

Fig. 75. Transversal section through the transverse, postoral part of the tentacle ridge, showing the cushion of ciliated epithelium next to the feeding furrow (ci. ep), and the origin of the posterior part of the ridge (po. te. ri). Microphotograph. Spec. III.

Fig. 76. High epithelium with cuticle on the inner side of the anterior lip. Microphotograph. Spec. III.

ci. ep = cushion of ciliated epithelium on tentacle ridge
cu. ep = non-ciliated epithelium (with cuticle?) on tentacle ridge
f. s. ep = foot side epithelium
pe. g. ep = pedal gland epithelium
po. te. ri = base of the posterior part of tentacle ridge
ve. f. ep = ventral foot epithelium

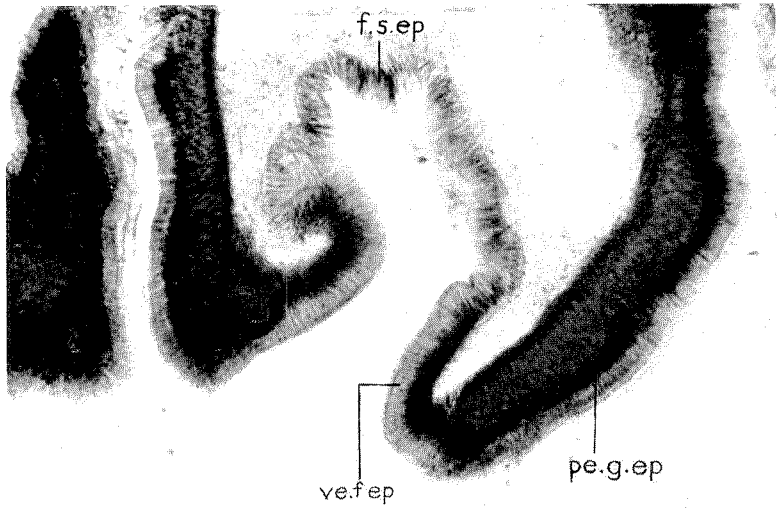


Fig.73

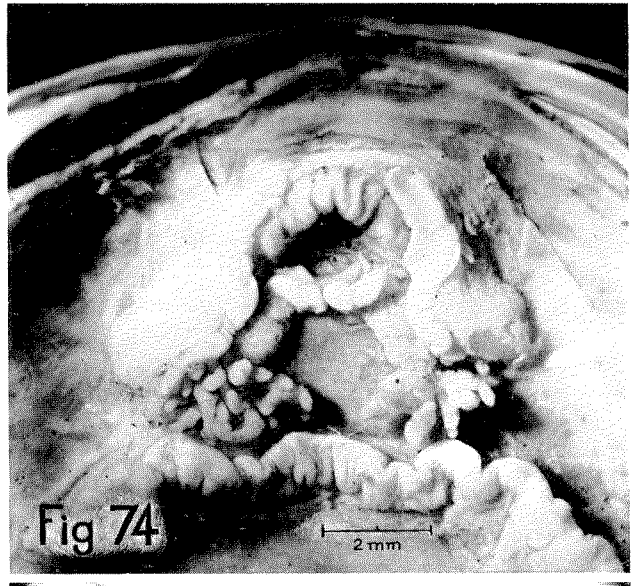


Fig 74

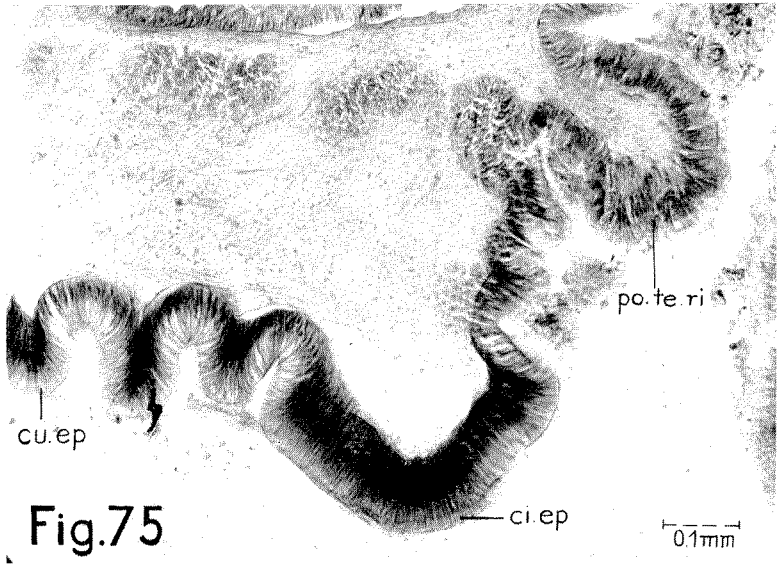


Fig.75

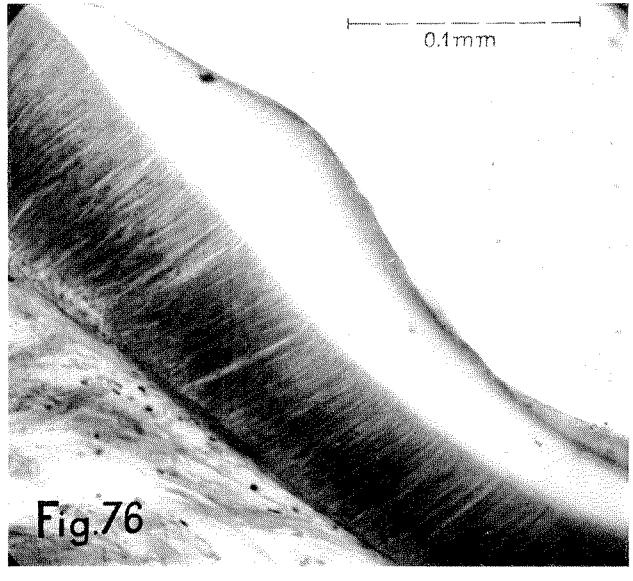


Fig.76

PLATE 22

Fig. 77. Transversal section of the anterior lip, showing the thin cuticle on the peripheral part (th. cu) and the strong one, which forms a bar along the inner side (cu. b). Microphotograph. Spec. III.

Fig. 78. Transversal section of the velum showing the two kinds of epithelia. Microphotograph. Spec. III.

Fig. 79. Branching postoral tentacles. Note the folded epithelium indicating strong contraction, and the dense appearance of the connective tissue. Microphotograph. Spec. IV.

Fig. 80. The entrance of the m. tentacularis transversus into the postoral tentacles. Microphotograph. Spec. III.

cu. b = cuticular bar along the inner side of the lip
L. ce = groups of Leydig cells
m. te. tr = musculus tentacularis transversus
si. ve = epithelium of the sides of the velum
th. cu = thin cuticle on the peripheral part of the lip
ve. e. ep = strongly ciliated epithelium on the ventral edge of the velum

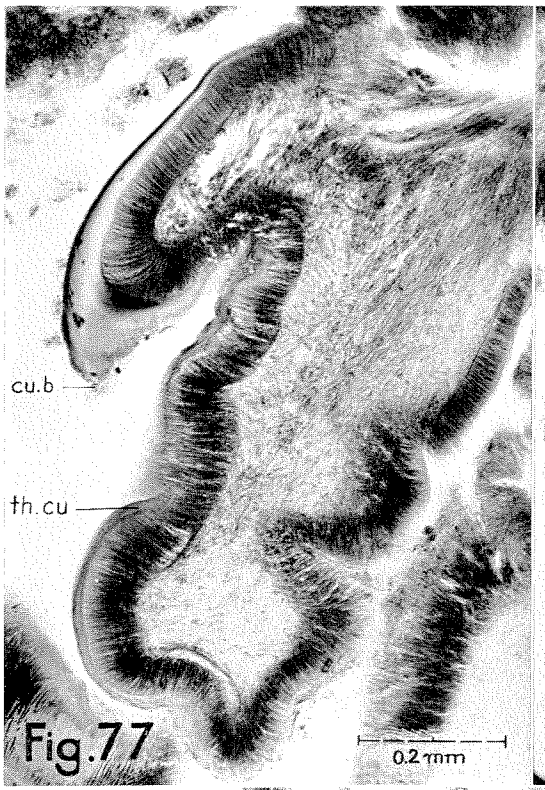


Fig.77

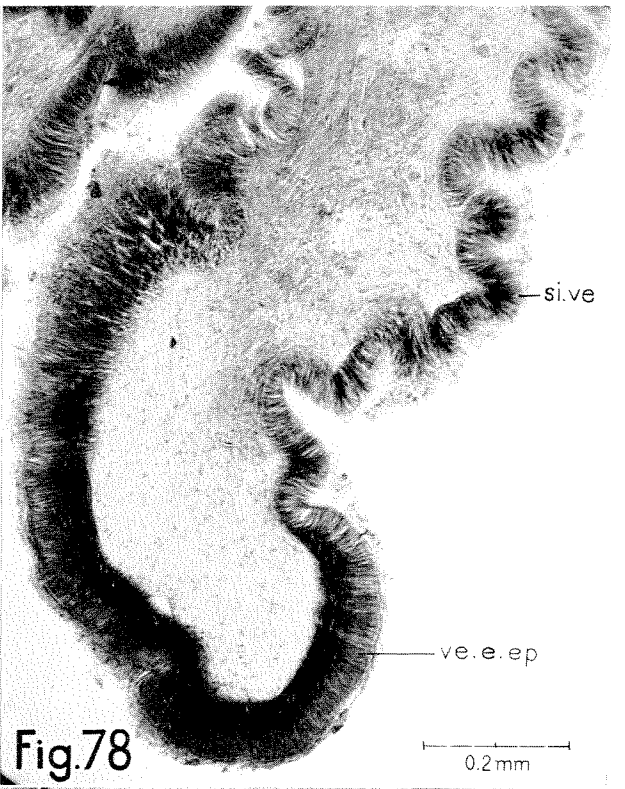


Fig.78

Fig.79

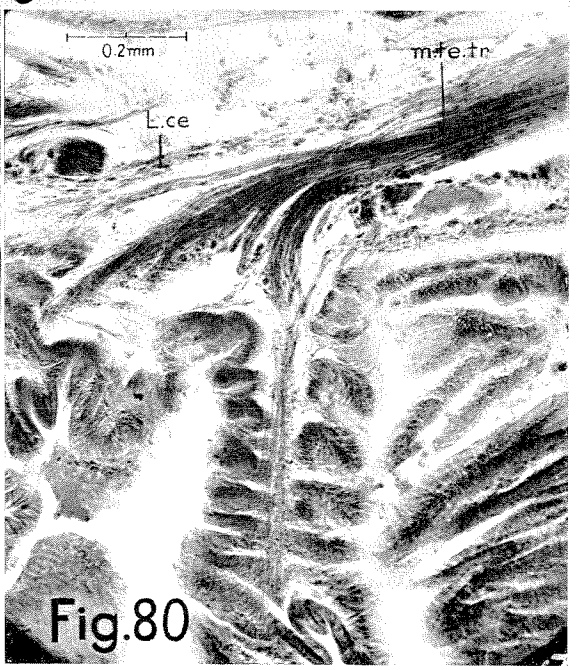


Fig.80

PLATE 23

Fig. 81. Median section of the oral region. Graphic reconstruction from Spec. IV.
Fig. 82. Dorsal view of the oral cavity, the horizontal part of the pharynx, and the radula support. Most of the radula cartilage is removed on the left side. The subradular membrane is only shown up to the region where it enters the radula diverticula. Graphic reconstruction from Spec. III.

A_1 = m. obliquus anterior A
ant. l = anterior lip
bl. s = blood sinus
cer. co = cerebral commissure
f. m = foot margin
lat. m. ph = lateral margin of pharynx
m. cru = musculus cruciatus
m. i. ra = musculus impar radulae
m. pr. sr = musculus protractor subradularis
m. ph. m = musculus pharyngeus marginalis
m. ra. l. d = musculus radulae longus, pars dorsalis
m. ra. l. v = musculus radulae longus pars ventralis
m. tr. A = musculus transversalis A
m. tr. ant = musculus transversalis anterior
oe = oesophagus
op. ph. d = opening into pharyngeal diverticula
or. c = oral cavity
or. e. sr. m = oral end of subradular membrane
ph = pharynx
po. l = posterior lip
ra = radula
ra. ca = radula cartilage
ra. sh = radula sheath
ra. ve = radula vesicle
re. sr. s = retractors of subradular sac
sal. g = "anterior salivary gland"
sce. co = subcerebral commissure
sh = shell
sr. g = subradular ganglion
sr. m = subradular membrane
sr. o = subradular organ
sr. s = subradular sac
te. ri = postoral part of tentacle ridge

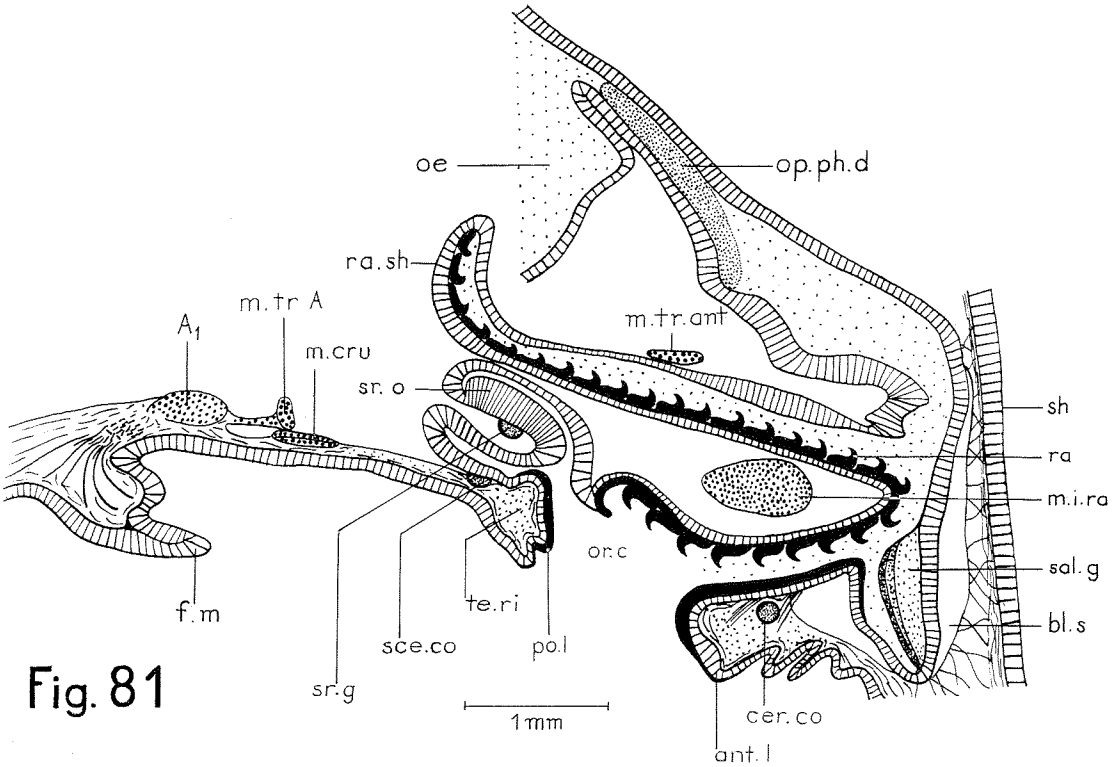

oe
op.ph.d
ra.sh
m.tr A
A1
m.cru
m.tr.ant
sr. o
sh
ra
m.i.ra
or.c
sal.g
bl.s
f.m
te.ri
sce.co
po.l
sr.g
1 mm
cer.co
ant.l

Fig. 81

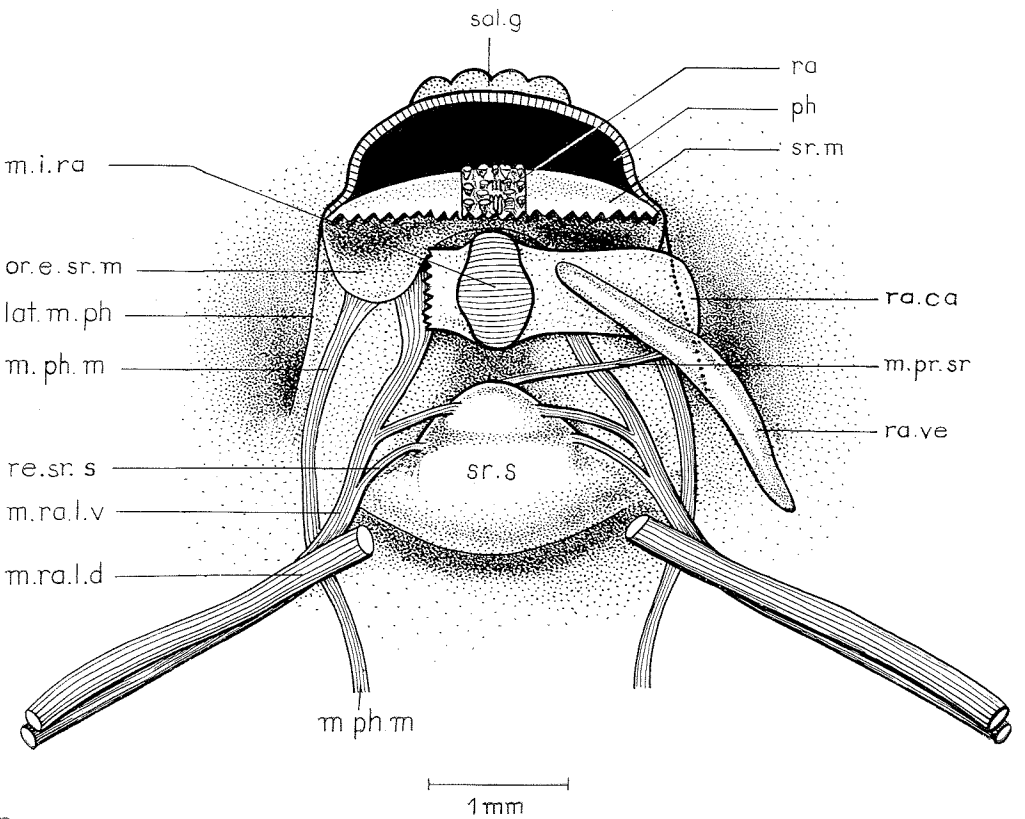

sal.g
ra
ph
sr.m
m.i.ra
or.e.sr.m
lat.m.ph
m.ph.m
ra.ca
m.pr.sr
ra.ve
re.sr.s
sr.s
m.ra.l.v
m.ra.l.d
m ph m
1 mm

Fig. 82

PLATE 24

Fig. 83. Dorsal view of the radula apparatus with some of the muscles. The dorsal epithelium of the radula diverticula is removed, and the subradular membrane is cut away on the right side. Graphic reconstruction from Spec. III.

Fig. 84. Dorsal view of the anterior body region, showing the radula apparatus and the more important muscles. Graphic reconstruction from Spec. III.

A-C = pedal retractors A to C
A_1-C_1 = mm. obliquii anteriores A to C
m. ca. a-l = musculus cartilaginis antero-lateralis
m. ci. int = musculus circularis intermedius
m. ci. pe = musculus circularis pedis
m. cru = musculus cruciatus
m. div. d = musculus protractor diverticulorum dorsalis
m. l-p. C = musculus latero-pedalis C
m. m-p. C = musculus medio-pedalis C
m. or. ant = musculus oralis anterior
m. or. po = musculus oralis posterior
m. pr. ca. d = musculus protractor cartilaginis dorsalis
m. pr. ca. d^1 = the small dorso-medial head of the musculus protractor cartilaginis dorsalis
m. pr. ca. p = musculus protractor cartilaginis profundus
m. pr. ra = musculus protractor radulae
m. pr. sr = musculus protractor subradularis
m. pr. v. ma = musculus protractor vesicae major
m. pror = musculus praeoralis
m. ra. l = musculus radulae longus
m. ra. mi = musculus radulae minor
m. re. ra = musculus retractor radulae
m. te. ra = musculus tensor radulae
m. te. tr = musculus tentacularis transversus
m. tr. A = musculus transversalis A
m. tr. ant = musculus transversalis anterior
m. tr. po = musculus transversalis posterior
m. ve. a-l = musculus vesicae antero-lateralis
m. ve. a-m = musculus vesicae antero-medialis
m. ve. p-l = musculus vesicae postero-lateralis
m. ve. p-m = musculus vesicae postero-medialis
m. ve. v = musculus vesicae ventralis
ph = pharynx
ra = radula
ra. ca = radula cartilage
ra. div = radula diverticula
ra. sh = radula sheath
ra. ve = radula vesicle
sal. g = "anterior salivary gland"
sr. m = subradular membrane
sr. s = subradular sac
Y_1 = the muscle Y_1
X, Y, Z = insertion areas X, Y, Z (see text!)

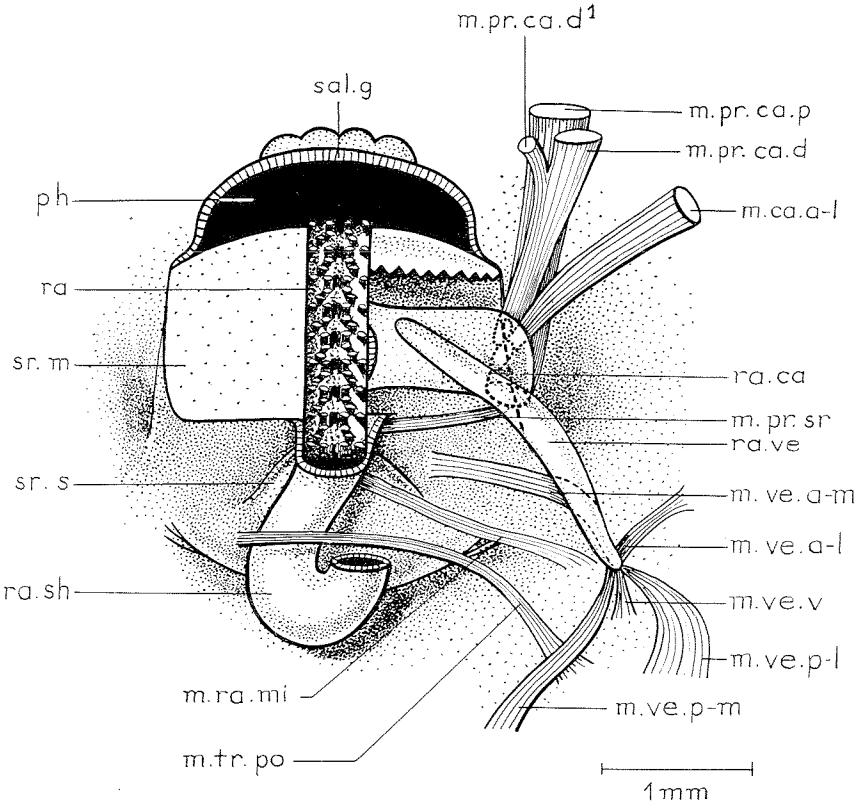

m.pr.ca.d¹
sal.g
m.pr.ca.p
m.pr.ca.d
ph
m.ca.a-l
ra
sr.m
ra.ca
m.pr.sr
ra.ve
sr.s
m.ve.a-m
m.ve.a-l
ra.sh
m.ve.v
m.ve.p-l
m.ra.mi
m.ve.p-m
m.tr.po
1mm

Fig.83

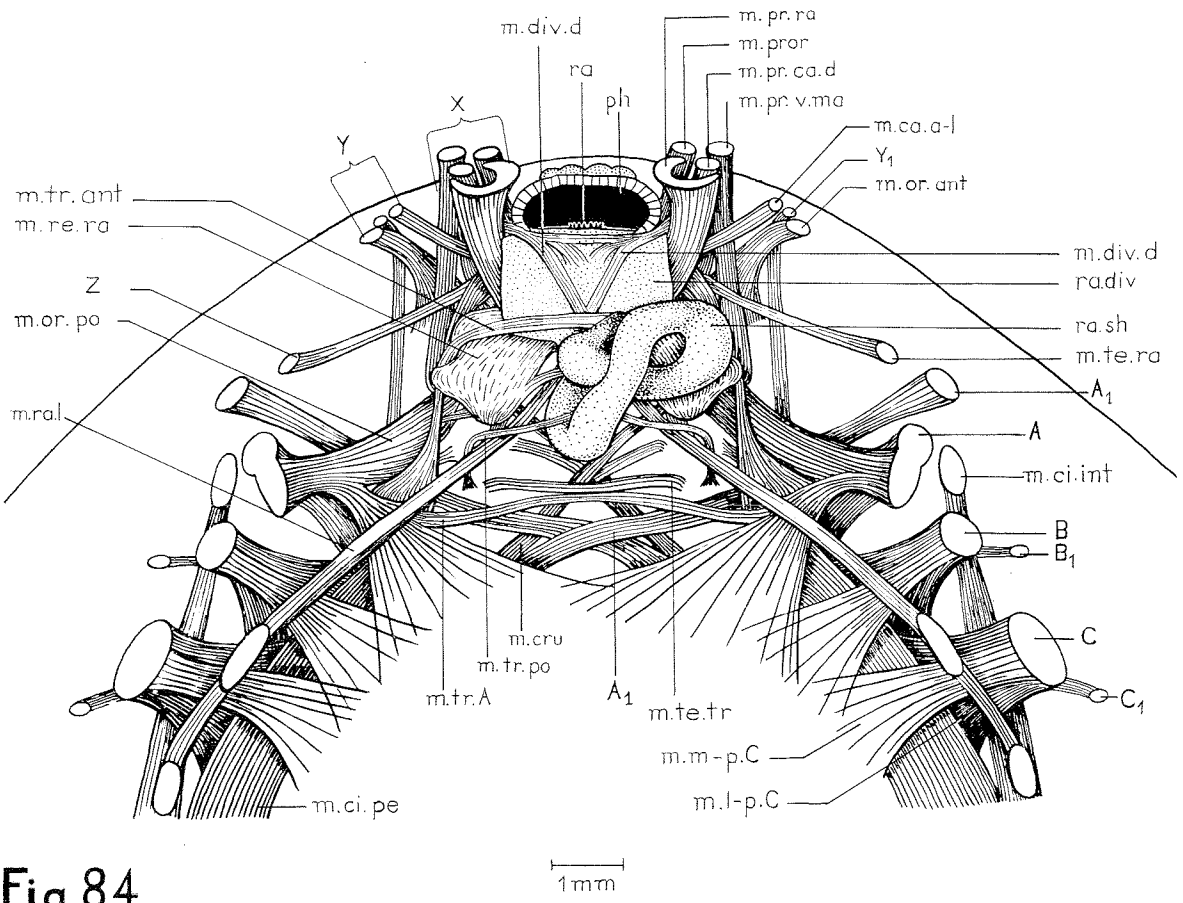

m.div.d
m.pr.ra
m.pror
ra
m.pr.ca.d
ph
m.pr.v.ma
X
Y
m.ca.a-l
Y₁
m.tr.ant
m.or.ant
m.re.ra
m.div.d
Z
ra.div
m.or.po
ra.sh
m.te.ra
A₁
m.ra.l
A
m.ci.int
B
B₁
C
m.cru
m.tr.po
m.tr.A
A₁
m.te.tr
C₁
m.m-p.C
m.l-p.C
m.ci.pe
1mm

Fig.84

Plate 25

Fig. 85. The digestive tract seen from above after removal of the pharyngeal diverticula and most of the intestine. The extension of the stomach epithelium is indicated by short strokes. The crystalline style is drawn as if visible through the wall. Graphic reconstruction. Spec. III.

Fig. 86. The digestive tract seen from above, the appearance of the postero-medial parts of the pharyngeal diverticula being uncertain because of damage to the specimen. Graphic reconstruction. Spec. III.

Fig. 87. Fourth lateral tooth of the radula showing the denticles. Spec. VI.

Fig. 88. Radular teeth of Spec. VI. One of the V-shaped rows is stippled. Oral direction upwards in the figure.

I-VI = Intestinal coils 1 to 6
an = anus
an. ph. d = anterior pouch of pharyngeal diverticula
ba. L_4 = base of 4th lateral tooth of radula
cr. st = crystalline style
int. c. 1 = intestinal coil 1
L_1-L_5 = 1st to 5th lateral
li = liver
M = median tooth of radula
me. ph. d = medial pouch of pharyngeal diverticula
oe = oesophagus
op. ph. d = opening into pharyngeal diverticula
po. ph. d = posterior pouch of pharyngeal diverticula
re = rectum
st = stomach

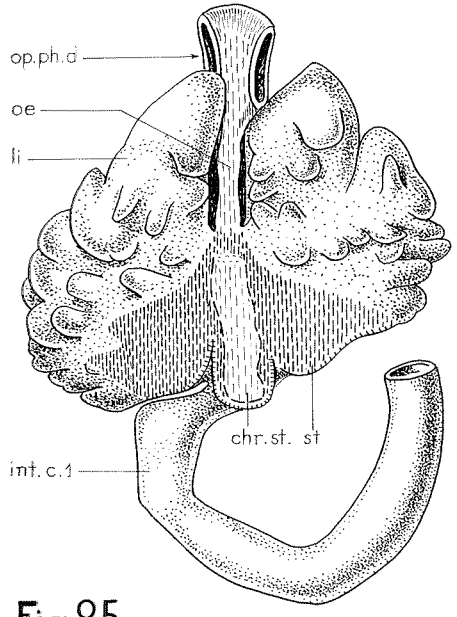


Fig.85

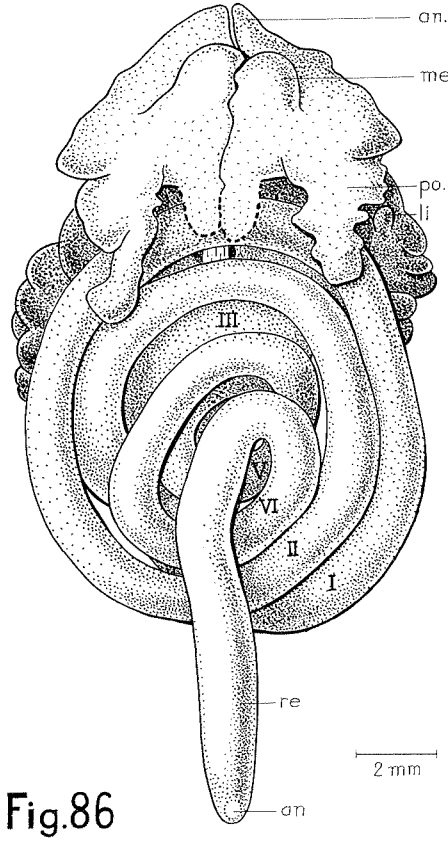


Fig.86

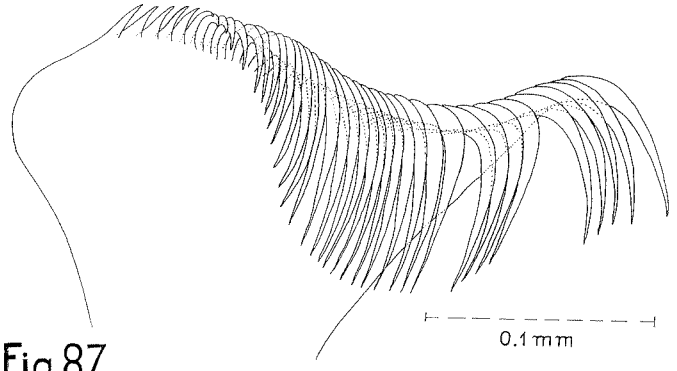


Fig.87

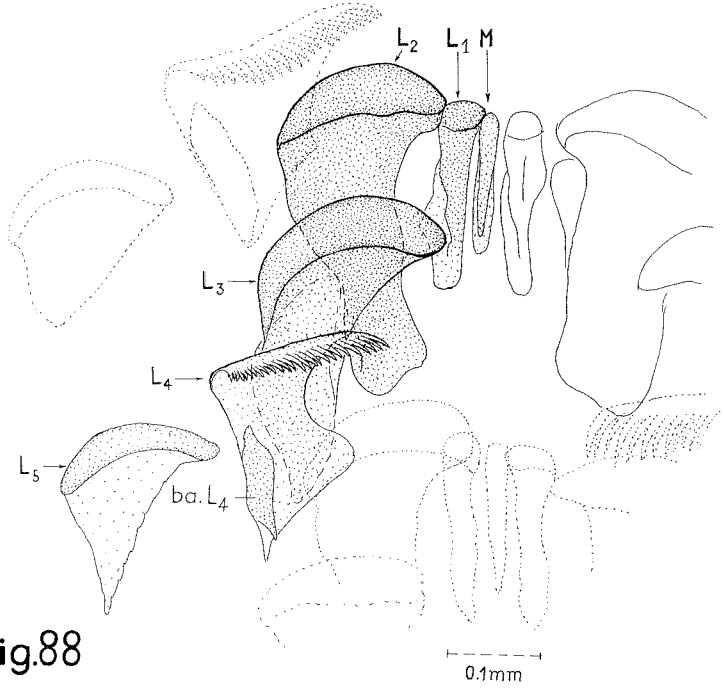


Fig.88

PLATE 26

Fig. 89. Horizontal section through the body above the level of most muscle insertions. Microphotograph. Spec. IV.

A-C = pedal retractors A to C
bl. s = blood sinus of the anterior body region
cl. te = cleft between the two testes
d. coe = dorsal coelom
li = liver
m. or. po = musculus oralis posterior
ne = nephridia
ph = pharynx
ph. d = pharyngeal diverticula
ra. sh = radula sheath
ra. ve = tip of radula vesicles with muscles
re = rectum
st = stomach
te_1-te_2 = testes, 1st and 2nd pair

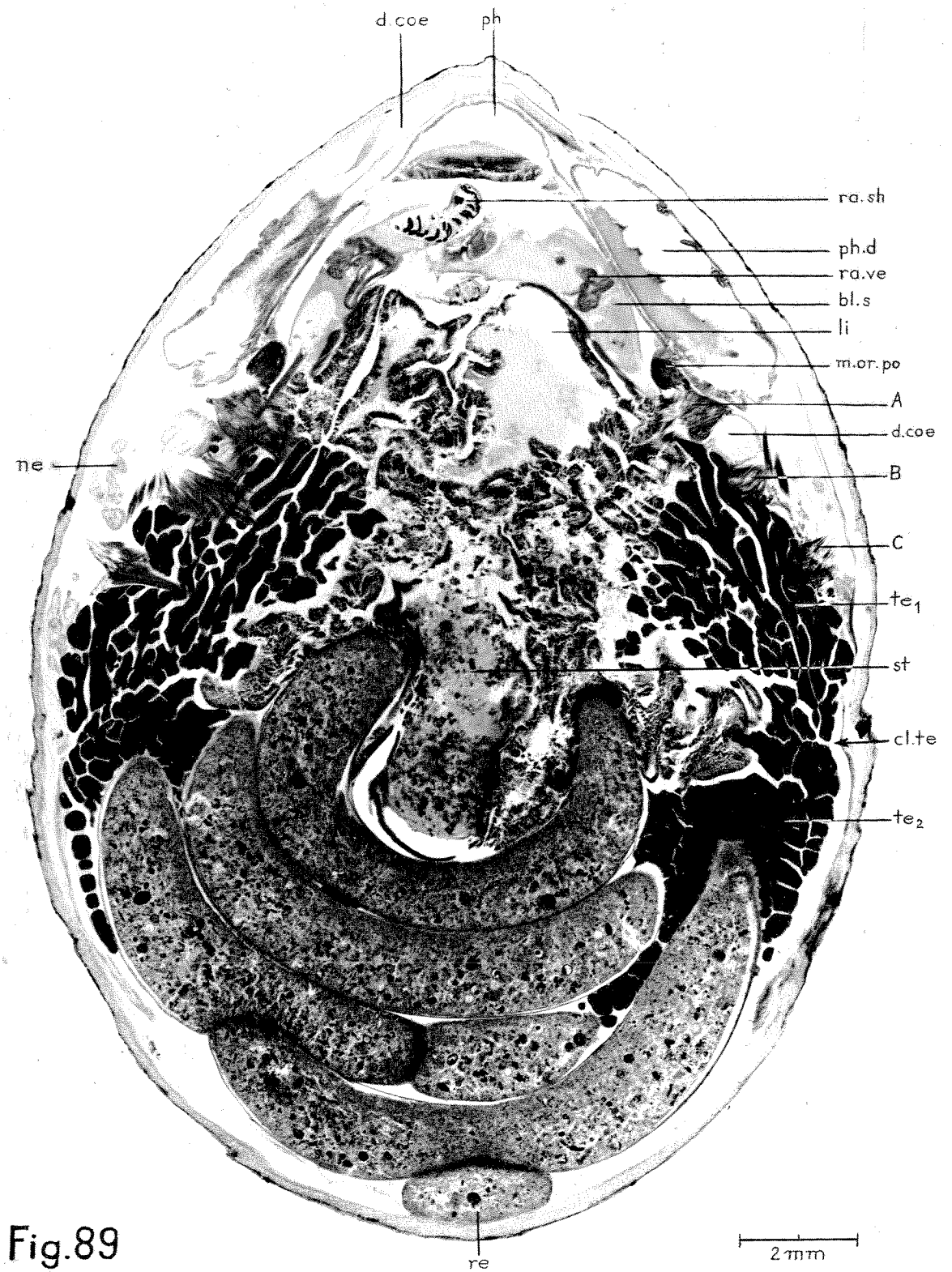

d.coe
ph
ra.sh
ph.d
ra.ve
bl.s
li
m.or.po
A
d.coe
ne
B
C
te1
st
cl.te
te2
re
2 mm

Fig.89

PLATE 27

Fig. 90. Transversal section just in front of the mouth, showing the pharynx and the radula sheath. Microphotograph. Spec. III.

Fig. 91. Cross section through the inner end of the radula sheath ("the radula gland"). The dorsal epithelium is folded into the lumen, whereas the ventral wall is smooth. Microphotograph. Spec. III.

Fig. 92. Horizontal section through the anterior end of the animal showing the salivary gland (sal. g) and the pharyngeal lumen (lu. ph). Microphotograph. Spec. IV.

Fig. 93. Cross section of the middle part of the radula sheath. Microphotograph. Spec. III.

bl. s = blood sinus
bu. c = buccal connective
cu. ph = cuticle of the ventral pharyngeal wall
d. coe = anterior diverticula of the dorsal coelom
L_2-L_4 = 2nd to 4th lateral teeth of the radula
lu. ph = lumen of pharynx
m. or. ant = musculus oralis anterior
m. ph. m = musculus pharyngeus marginalis
m. pr. c. p = musculus protractor cartilaginis profundus
m. pr. v. ma = musculus protractor vesicae major
m. pr. v. mi = musculus protractor vesicae minor
m. ra. l. v = musculus radulae longus, pars ventralis
m. re. ra = musculus retractor radulae
ra. sh = radula sheath
ra. ve = radula vesicles
sal. g = salivary gland
sr. m = subradular membrane
te. ri = tentacle ridge
ve. ep = ventral epithelium of radula sheath
vel = velum

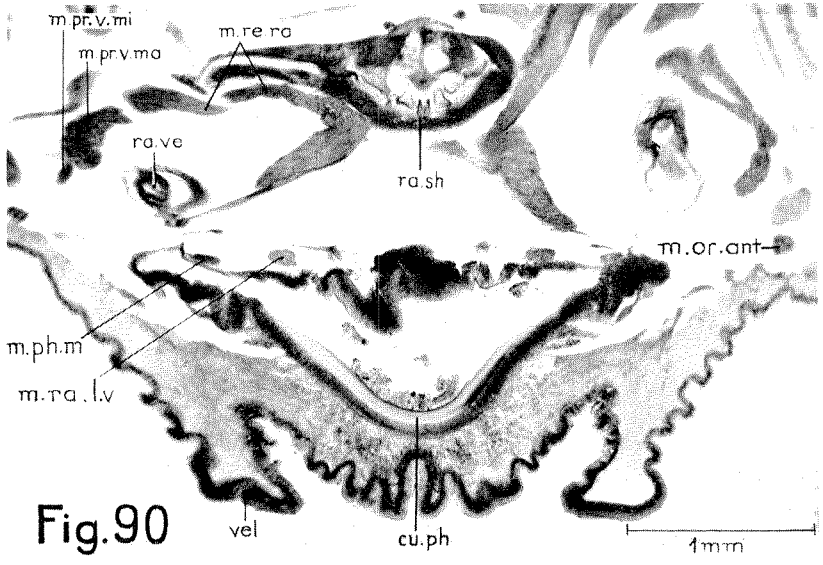


Fig.90

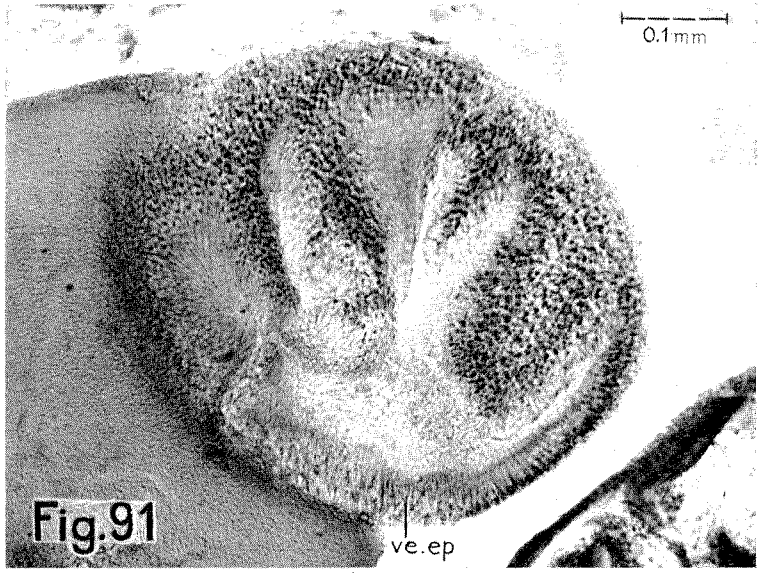


Fig.91

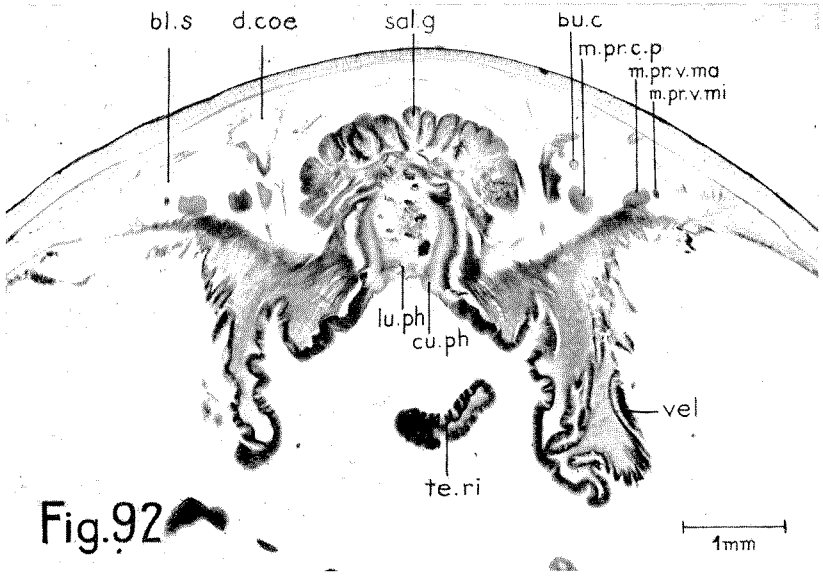


Fig.92

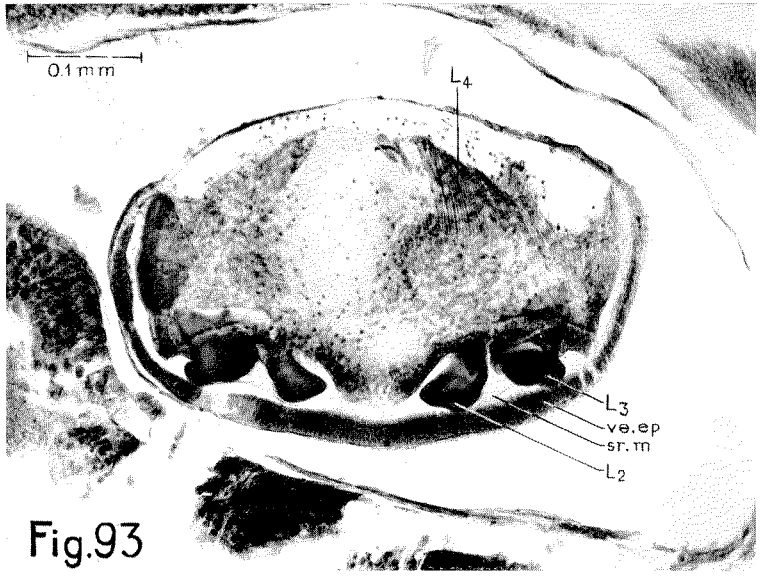


Fig.93

PLATE 28

Fig. 94. Transversal section of the pharyngeal region just in front of the oral cavity. Microphotograph. Spec. III.

Fig. 95. Transversal section of the radula furrow in the region of the radula diverticula. Microphotograph. Spec. III.

Fig. 96. The structure of the radula cartilage. Some cell nuclei are visible. Microphotograph. Spec. III.

cu. ph = cuticle of the ventral pharyngeal wall
ll = liver lobules
m. i. ra = musculus impar radulae
m. ph. m = musculus pharyngeus marginalis
m. pr. d. d = musculus protractor diverticulorum dorsalis
m. pr. ve. ma = musculus protractor vesicae major
m. pr. ve. mi = musculus protractor vesicae minor
m. ra. l. v = musculus radulae longus, pars ventralis
m. re. ra = musculus retractor radulae (different portions)
m. te. l = musculus tensor membranae lateralis
m. tr. a = musculus transversalis anterior
me. ve. ri = median velar ridge
oe = oesophagus
ra = radula
ra. ca = radula cartilage
ra. div = radula diverticula
ra. sh = radula sheath
ra. ve = radula vesicles
sr. m = subradular membrane; sr. m_1 and sr. m_2 indicate the stainable and non-stainable parts, resp.
Y_1 = the muscle Y_1

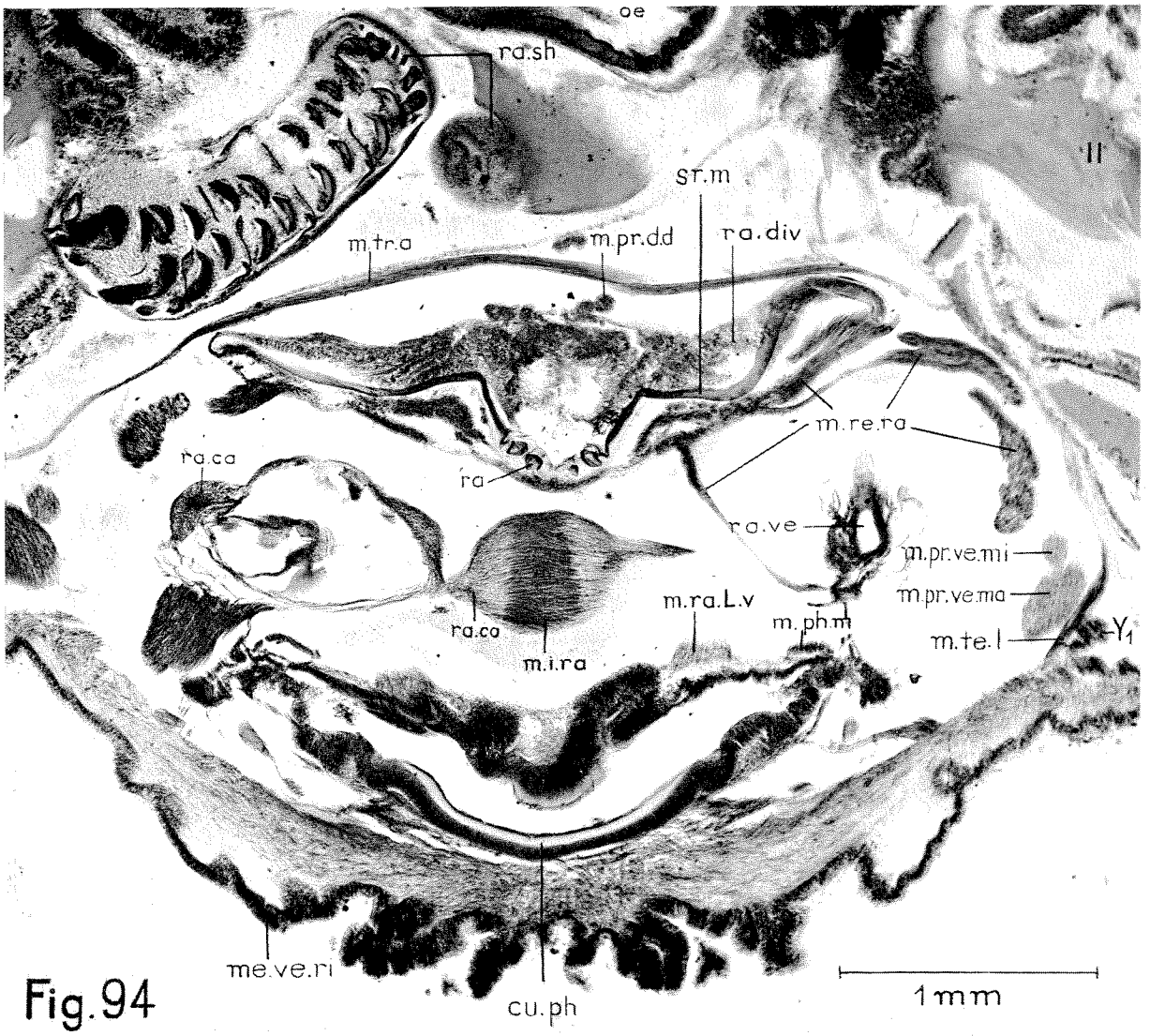


Fig.94

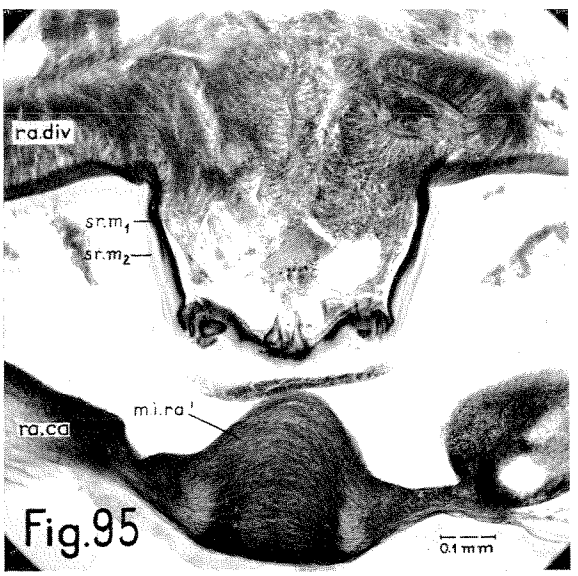


Fig.95

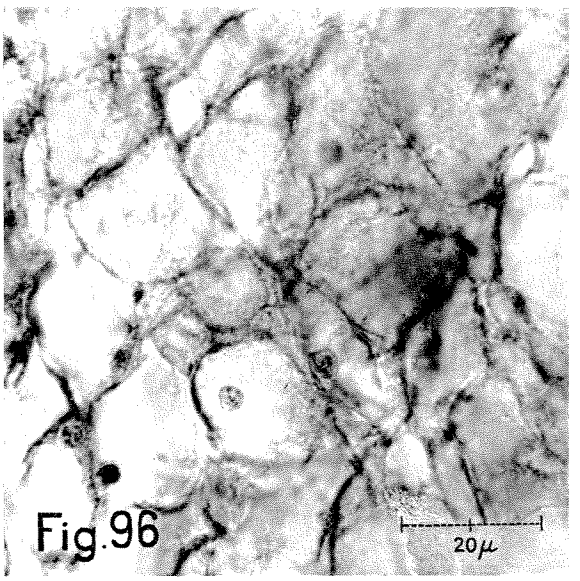


Fig.96

PLATE 29

Fig. 97. Cross section of the crystalline style lying just beneath the dorsal wall of the stomach. Microphotograph. Spec. III.

Fig. 98. Transversal section, showing the connection between the stomach (st) and the liver (li). Note that the stomach epithelium spreads far into the liver region in the dorsal wall. Microphotograph. Spec. III.

Fig. 99. Cross section of the radula furrow in the region of the radula diverticula to show the situation of the teeth. Microphotograph. Spec. III.

Fig. 100. Horizontal section through the tubular part of the radula sheath showing the arrangement of the teeth. Microphotograph. Spec. III.

chr. st = crystalline style
conn = connection between stomach and liver
L_1-L_5 = lateral teeth 1-5
ll = liver lobules
ov = ovary
sr. m = subradular membrane
st = stomach

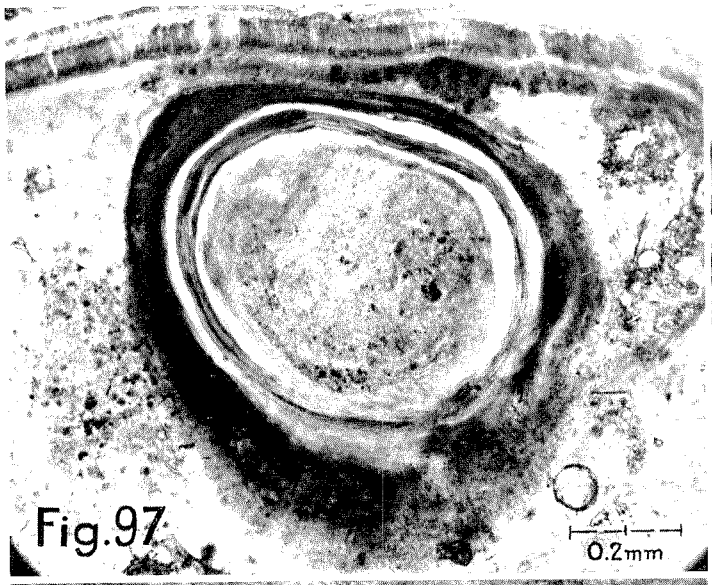


Fig.97

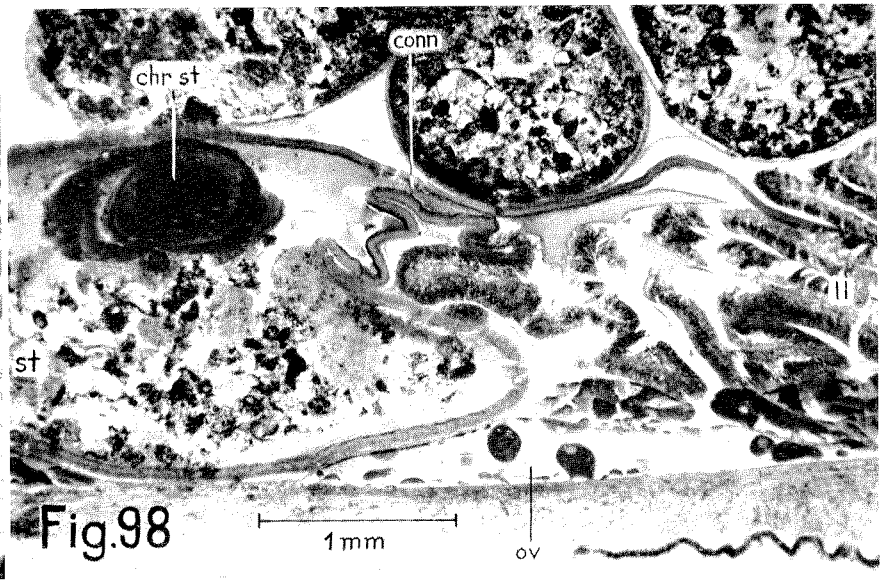


Fig.98

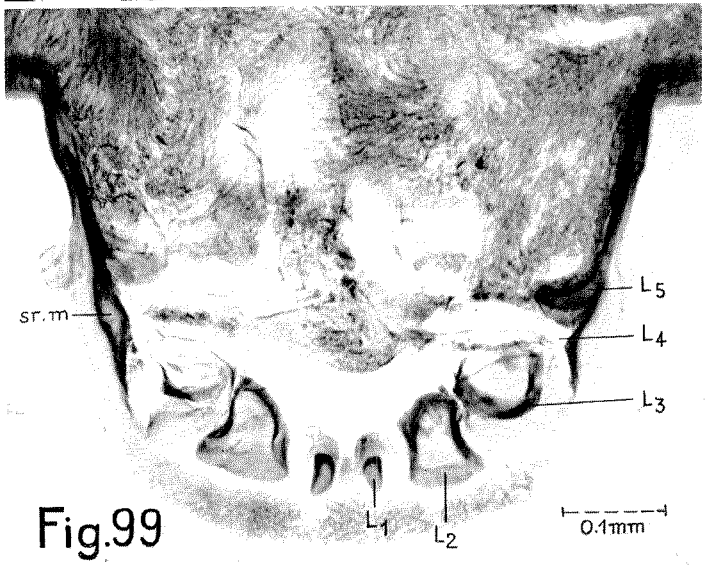


Fig.99

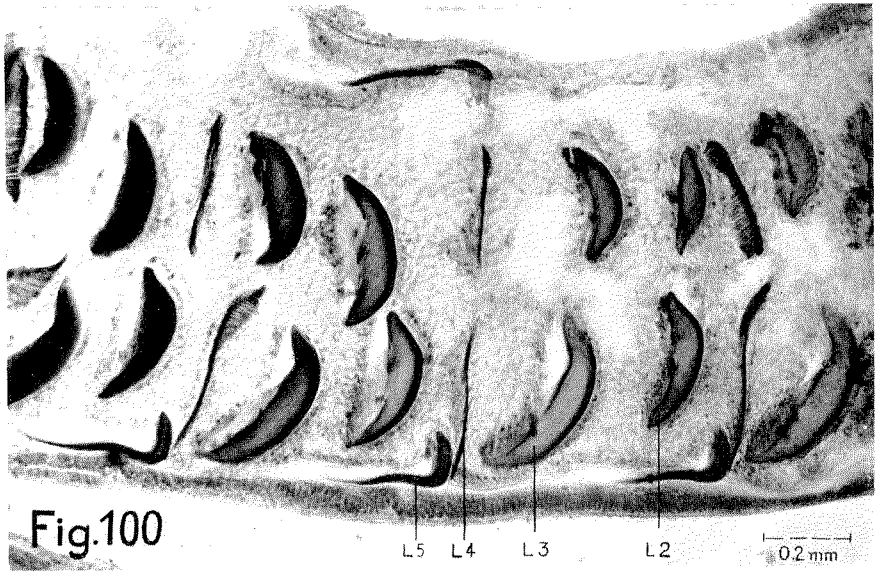


Fig.100

PLATE 30

Fig. 101. Ciliated epithelium of the oesophagus. The cells have a dark-staining base, a granulate middle part, and a striated peripheral one. The dark line of basal granules next to the lumen is distinct. Microphotograph. Spec. III.

Fig. 102. Detail of the pharyngeal epithelium, showing the basal granules and the ciliar roots in the peripheral end. Microphotograph. Spec. III.

Fig. 103. Walls of the pharyngeal diverticulum (left) and the dorsal coelom (right), the former with basal granules along the distal surface of some cells, the latter with pigment granules. Microphotograph. Spec. III.

Fig. 104. Epithelium of the pharynx near the pharyngeal diverticula. Basal granules, ciliar roots, and big dark-staining granules are distinct. Microphotograph. Spec. III.

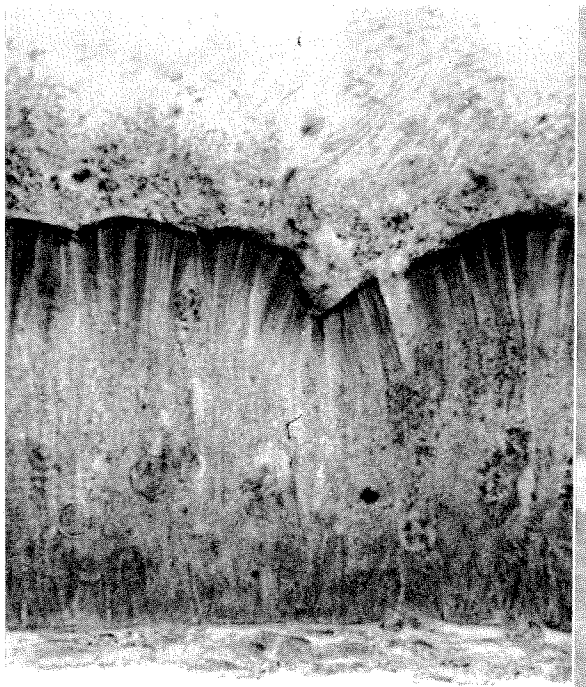


Fig.101 10μ

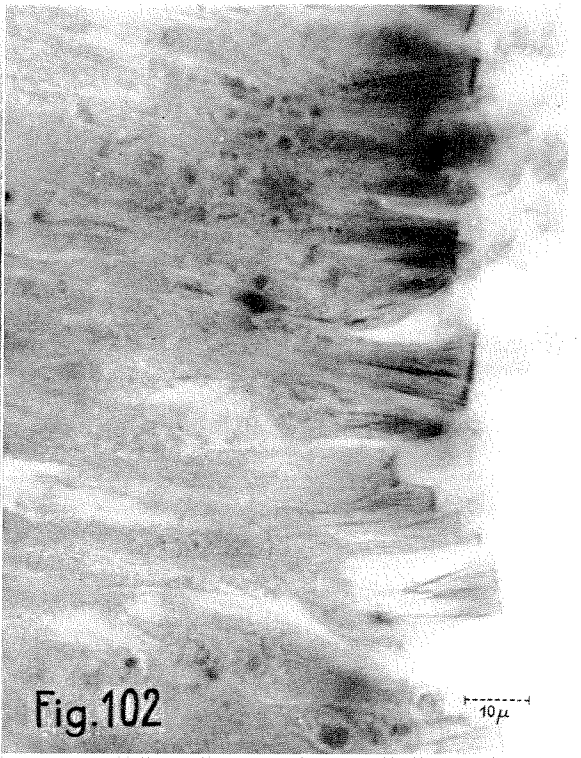


Fig.102 10μ

Fig.103 10μ

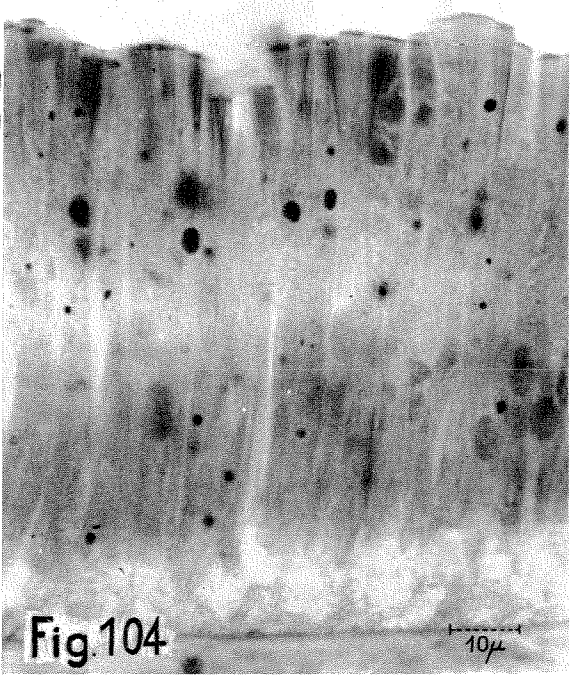


Fig.104 10μ

PLATE 31

Fig. 105. Walls of intestinal coils 4 (top) and 1 (bottom). Microphotograph. Spec. III.
Fig. 106. Wall of intestinal coil 6 showing pigment granules in the epithelial cells. Microphotograph. Spec. III.
Fig. 107. Wall of liver lobule. The basal parts of the cells (right) are dark, the peripheral parts contain the big granules. Microphotograph. Spec. III.
Fig. 108. Granules of the liver epithelium. Note the concentric structure. Microphotograph. Spec. III.

int. c. 1-6 = lumina of intestinal coils 1-6

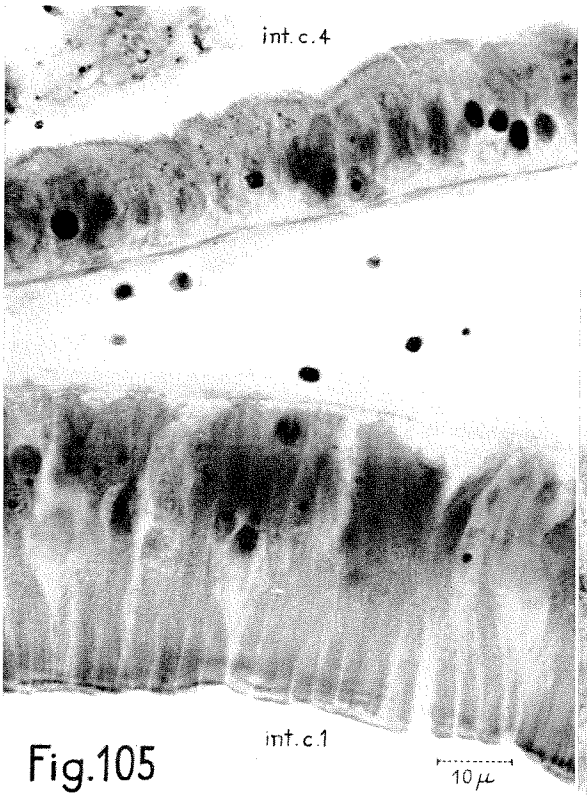


Fig.105

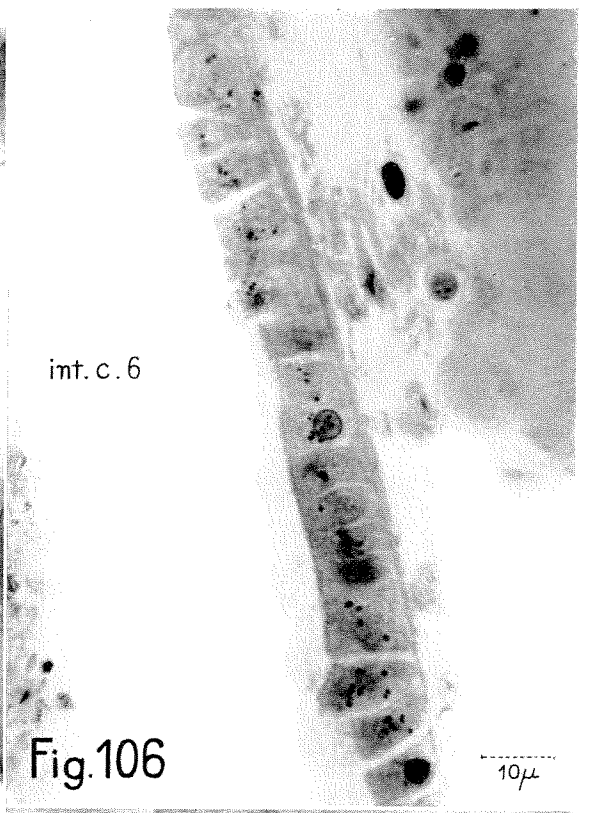


Fig.106

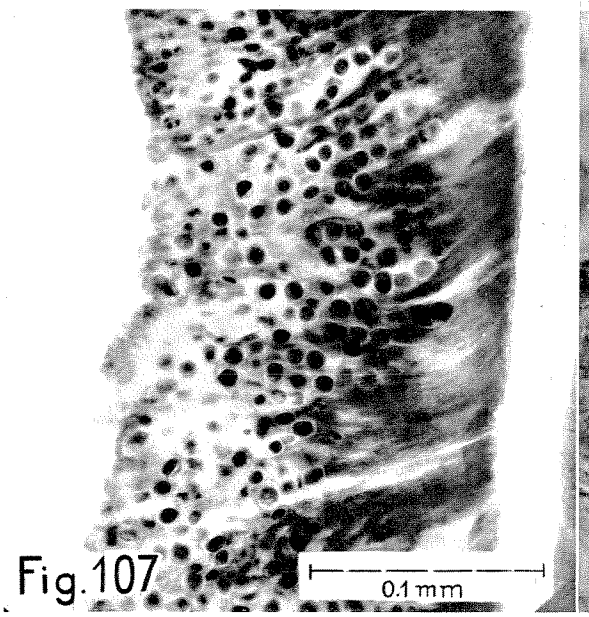


Fig.107

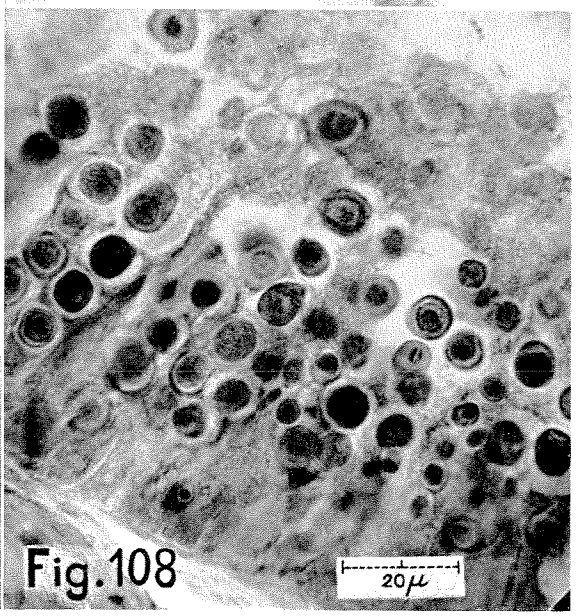


Fig.108

PLATE 32

Fig. 108 A. Epithelium of the rectum, not far from the anus, with high, ciliated cells. Microphotograph. Spec. III.

Fig. 109. Cross section of the anal papilla, showing the folded epithelium. Microphotograph. Spec. IV.

Fig. 110. Detail of a transversal section showing the pedal retractor E and the adjacent muscles. Microphotograph. Spec. III.

Fig. 111. Detail of a horizontal section, showing the insertion of the musculus protractor radulae (m. pr. ra). Note the absence of tendineous parts.

Fig. 112. Muscle fibres of a pedal retractor sectioned longitudinally. Note the position of the nucleus on the surface of the bundle of fibrils. Microphotograph. Spec. IV.

Fig. 113. Muscle fibres of the m. circularis intermedius. Microphotograph. Spec. IV.

Fig. 114. The thin muscle fibres of the m. circularis pallii, seen in a longitudinal section. Microphotograph. Spec. IV.

d. coe = dorsal coelom
$E_1 + E_2$ = crossing of the mm. obliquii E
F_1 = m. obliquus anterior F
fi = fibrils of the muscle fibre
m. ci. int = musculus circularis intermedius
m. ci. pa = musculus circularis pallii
m. lp = musculus latero-pedalis
m. mp = musculus medio-pedalis
m. pr. ra = musculus protractor radulae
mu. a. ep = muscle attachment epithelium
na. l = nacreous layer
nu = nucleus of muscle cell
ov = ovary
per = periostracum
pr. l = prismatic layer
sar = sarcoplasm
ten = tendineous part of muscle

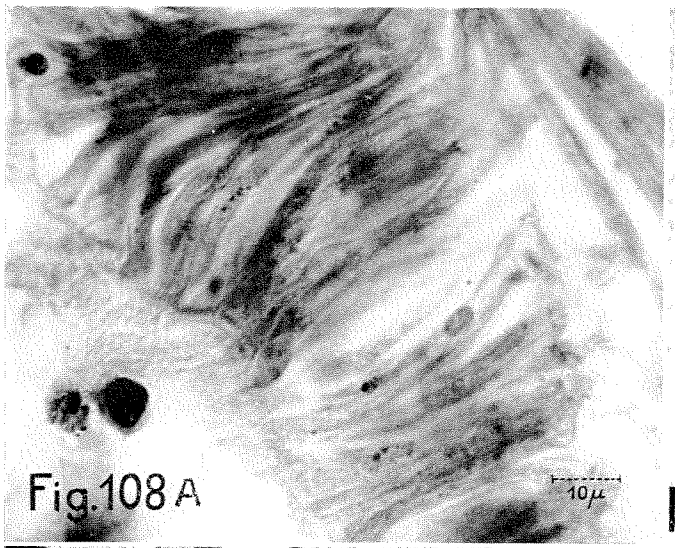


Fig.108 A

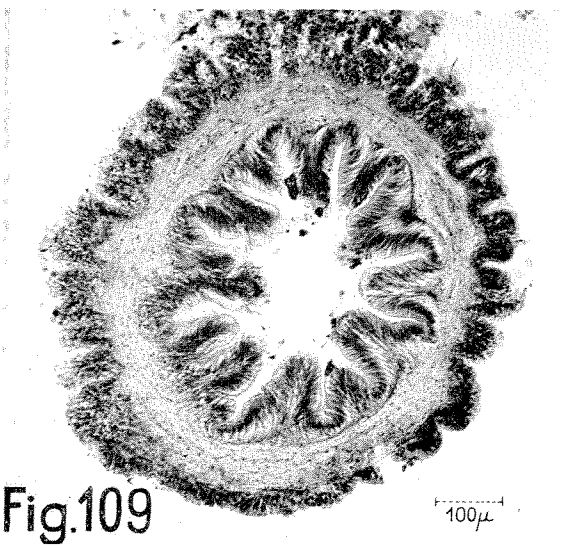


Fig.109

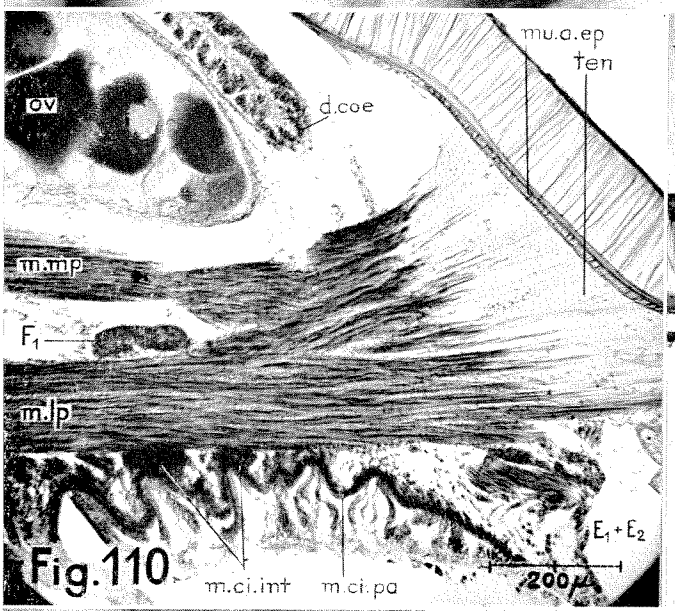


Fig.110

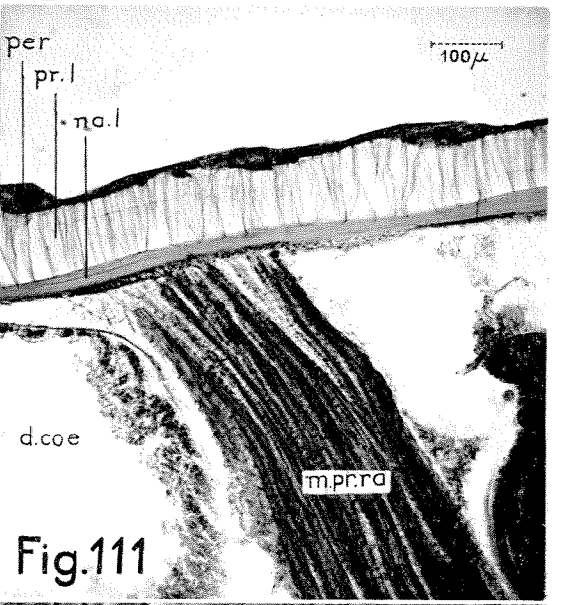


Fig.111

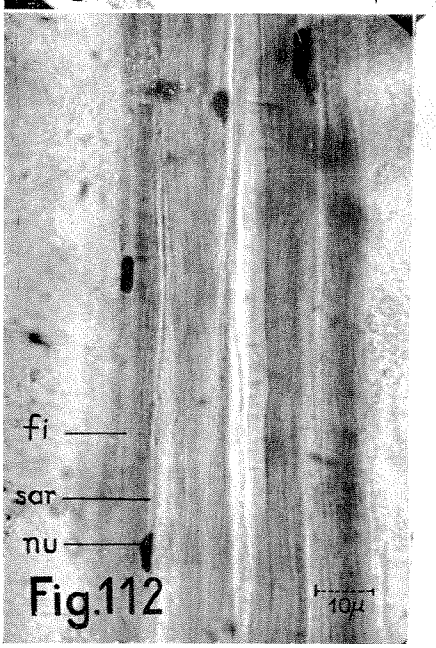


Fig.112

Fig.113

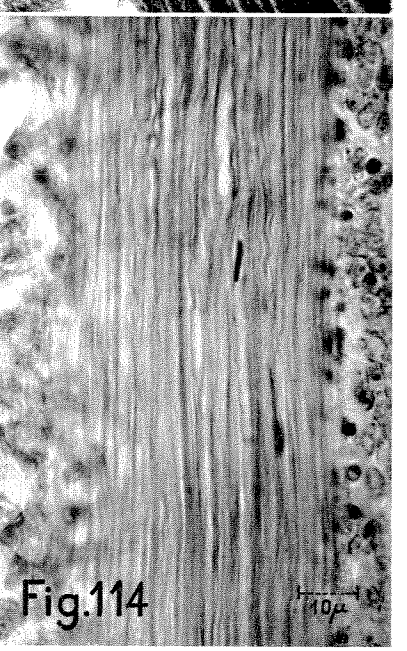


Fig.114

PLATE 33

Fig. 115. Fibres of the m. radulae longus with abundant basophilic granules. Microphotograph. Spec. IV.

Fig. 116. Fibres of the m. retractor radulae, showing cross striation. Microphotograph. Spec. III.

Fig. 117. The muscle fibres of the membranous foot centre, seen in a horizontal section. Microphotograph. Spec. IV.

Fig. 118. The central part of a gill lamella showing the crossing muscle fibres. Some ramifying fibres are visible. Microphotograph. Spec. III.

bl. v = blood vessel
ep = epithelium of gill lamella
nu = nucleus of muscle cell

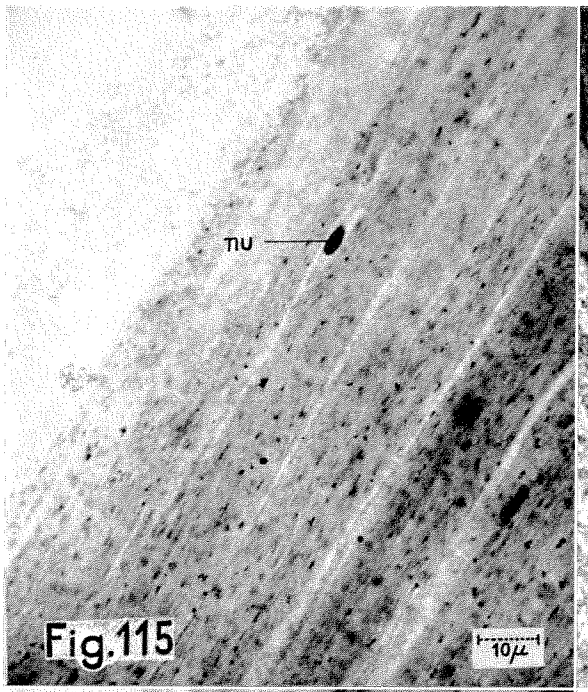


Fig.115

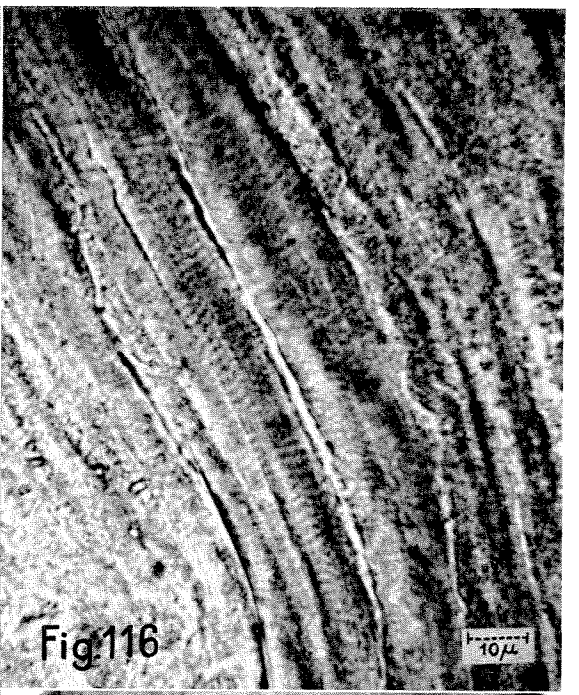


Fig.116

Fig.117

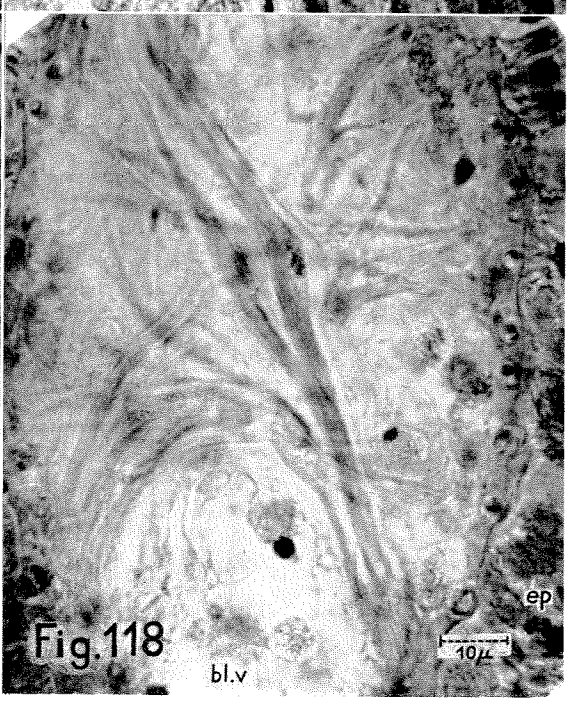


Fig.118

PLATE 34

Fig. 119. Camera lucida drawing of a transversal section through the body, at the level of the pedal retractor E. Only the left side is shown.

Fig. 120. Diagrammatical drawing, showing the origin and distribution of the fibres of the mm. medio-pedales (left) and the mm. latero-pedales (right). The insertion area within the big, complex scar is indicated by short streaks.

A-H = pedal retractors A to H
an = anus
art. pa. s = arterial pallial sinus
d. coe = dorsal coelom
f. c = foot centre
f. m = foot margin
int = intestine
la. n. c = lateral nerve cord
m = mouth
m. br. e_3 = musculus branchialis externus of 3rd gill
m. ci. int = musculus circularis intermedius
m. ci. pa = musculus circularis pallii
m. ci. pe = musculus circularis pedis
m. lp. E = musculus latero-pedalis E
m. mp. E = musculus medio-pedalis E
m. obl. a. F = musculus obliquus anterior F
m. or. po = musculus oralis posterior
m. re. te A = tentacle retractor from A
m. tr. A = musculus transversalis A
mm. obl. E = crossing of the mm. obliquii E
ne = nephridia
ov = ovary
pe. n. c = pedal nerve cord
ve. bl. s = venous pallial sinus

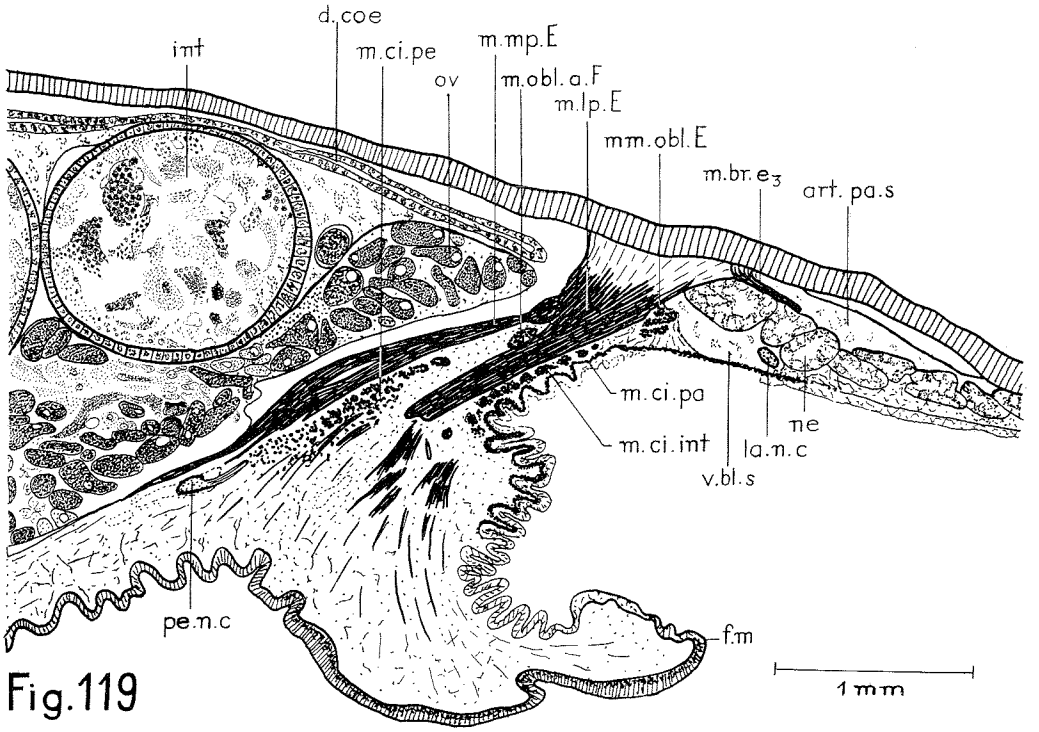


Fig.119

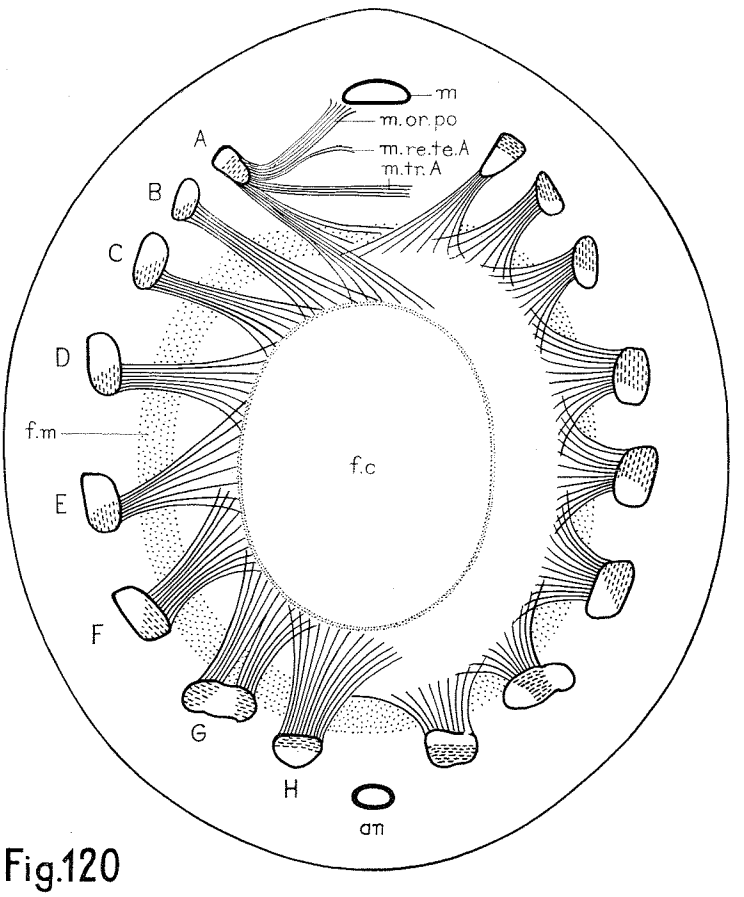


Fig.120

PLATE 35

Fig. 121. Graphic reconstruction of the body musculature of *Neopilina*, dorsal view. On the right side the circular systems only are drawn. Some critical points were confirmed by studies of wax models and by dissection of Spec. X.

A-H = pedal retractors A to H
A_1-H_1 = musculus obliquii anteriores A to H
E_2-F_2 = musculus obliquii posteriores E to F
C_3-G_3 = musculus branchiales interni C to G
C_4-G_4 = musculus branchiales externi C to G
Y_1 = the muscle "Y_1"
an = anus
m. ci. int = musculus circularis intermedius
m. ci. pa = musculus circularis pallii
m. ci. pe = musculus circularis pedis
m. cru = musculus cruciatus
m. lp = musculus latero-pedalis
m. mp = musculus medio-pedalis
m. or. a = musculus oralis anterior
m. or. p = musculus oralis posterior
m. pa = pallial muscles
m. pro = musculus praeoralis

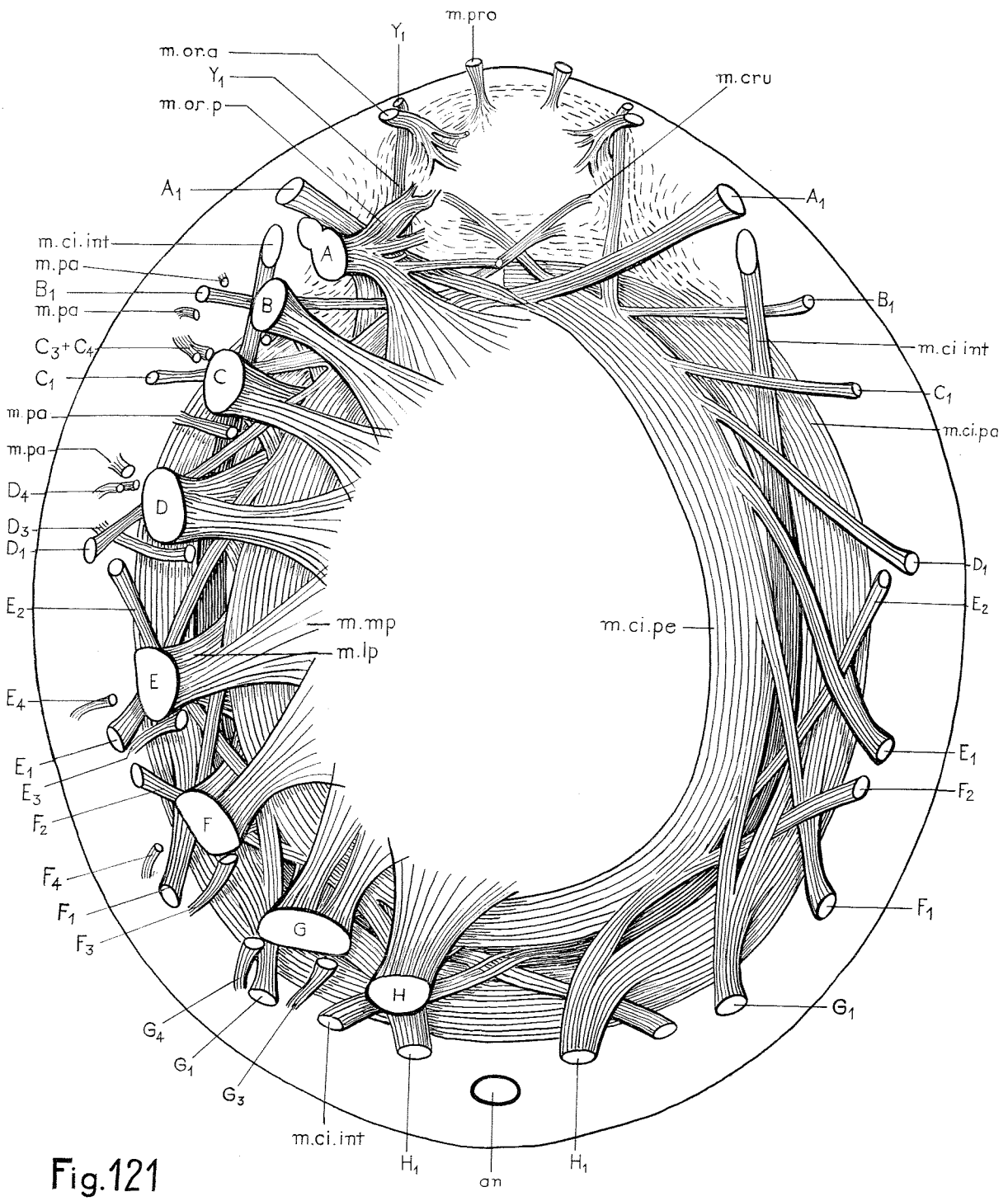

m.pro
Y1
m.or.a
Y1
m.or.p
m.cru
A1
A1
m.ci.int
m.pa
B1
m.pa
B1
m.ci.int
C3+C4
C1
C1
m.pa
m.ci.pa
m.pa
D4
D3
D1
D1
E2
E2
m.mp
m.lp
m.ci.pe
E4
E1
E3
F2
E1
F2
F4
F1
F3
F1
G4
G1
G3
G1
m.ci.int
H1
an
H1
A
B
C
D
E
F
G
H

Fig.121

PLATE 36

Fig. 122. Transversal section through the middle body region at the level of the pedal retractor E. Microphotograph. Spec. III.

art. p. s = arterial pallial sinus
d. coe = dorsal coelom
f. c = membraneous foot centre
f. m = foot margin
la. n. c = lateral nerve cord
m. ci. pa = musculus circularis pallii
m. ci. pe = musculus circularis pedis
m. lp. E = musculus latero-pedalis E
m. mp. E = musculus medio-pedalis E
m. obl. a. F = musculus obliquus anterior F
m. br. e = musculus branchialis externus
mm. obl. E = crossing of the mm. obliquii E
ne = nephridia
ov = ovary
pa. m = pallial margin
pe. c = pedal nerve cord
per. bl. s = peri-intestinal blood sinus
ve. p. s = venous pallial sinus

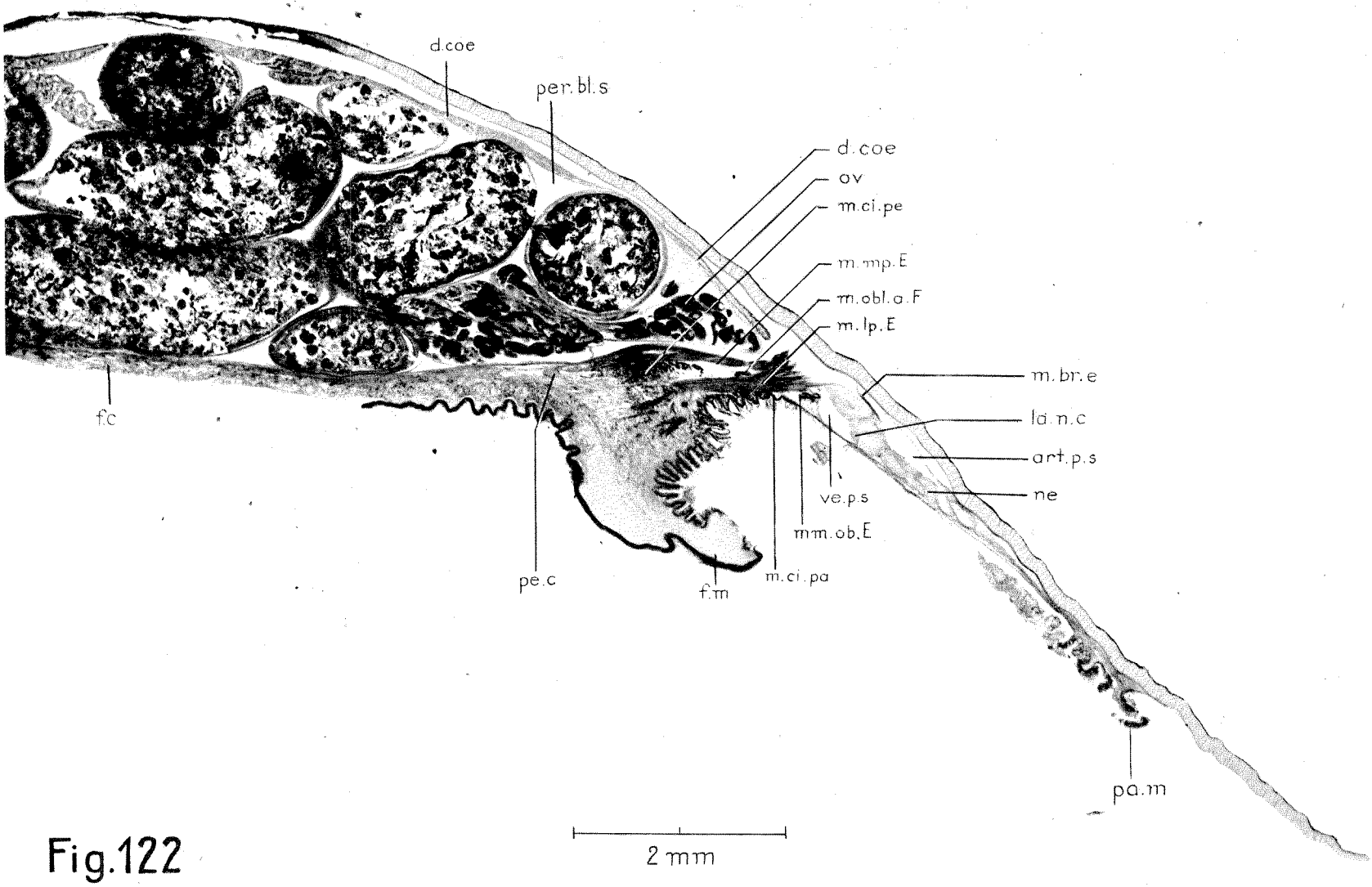

d.coe
per.bl.s
d.coe
ov
m.ci.pe
m.mp.E
m.obl.a.F
m.lp.E
m.br.e
la.n.c
art.p.s
ne
ve.p.s
mm.ob.E
m.ci.pa
f.c
pe.c
f.m
pa.m
2 mm

Fig.122

PLATE 37

Fig. 123. Horizontal section through the body at the level of the muscle insertions. Posterior part of left side shown. Microphotograph. Spec. IV.

at_2 = left posterior atrium
cl. te = cleft between the two testes
D-H = foot retractors D-H
f. m = foot margin with ramifications of the mm. latero-pedales
m. br. i_{3-5} = mm. branchiales interni of 3rd to 5th gill
m. ci. pa = musculus circularis pallii (visible at several places)
mm. br_1 = mm. branchiales of 1st gill
ne = nephridia
ne. sp = nephridia with sperm
re = rectum
te_1, te_2 = anterior and posterior left testes

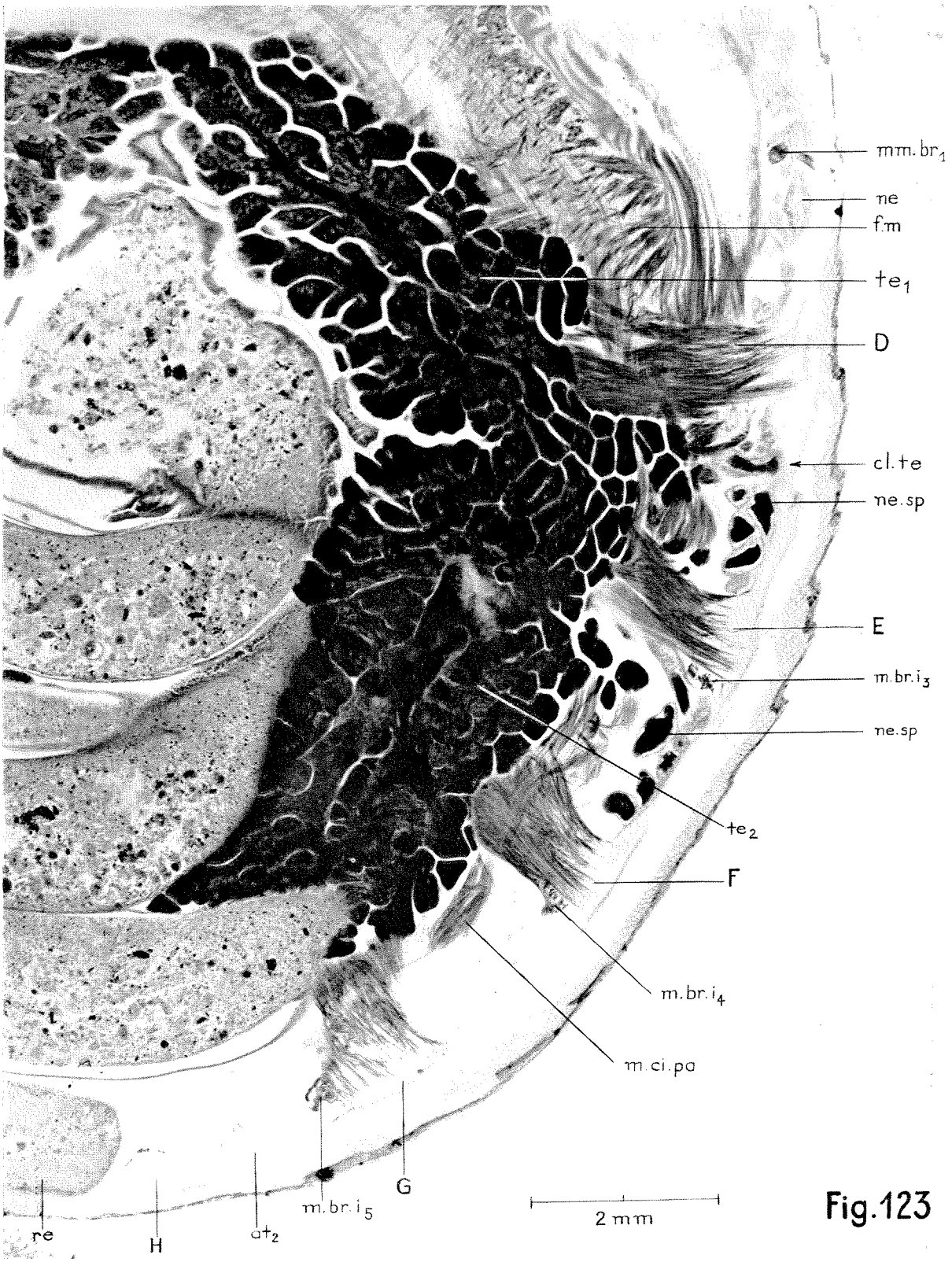

mm.br1
ne
f.m
te1
D
cl.te
ne.sp
E
m.br.i3
ne.sp
te2
F
m.br.i4
m.ci.pa
G
m.br.i5
2 mm
re
H
at2

Fig.123

PLATE 38

Fig. 124. Horizontal section through the anterior end with the salivary gland and the muscles lying in the anterior pallial fold. Microphotograph. Spec. IV.

Fig. 125. Transversal section through the region of the 1st gill showing the internal gill retractor. Microphotograph. Spec. III.

Fig. 126. The inner side of the ventral body wall of the dissected Spec. X, showing the m. circularis pedis and the foot retractors. Photograph.

ant. l = anterior lip
a. pa. s = arterial pallial sinus
a. ve. ri = anterior velar ridge
bl. s = blood sinus, lodging the muscles
D-F = pedal retractors D-F
E_1-F_1 = mm. obliquii anteriores E and F
gi = gill
m. br. i = musculus branchialis internus
m. ci. pe = musculus circularis pedis
m. pro = musculus praeoralis
m. pr. ca. p = musculus protractor cartilaginis profundus
m. pr. di = musculus protractor diverticulorum dorsalis
m. pr. ve. ma = musculus protractor vesicae major
m. te. me. a = musculus tensor membranae anterior
ne = nephridia
pe. n. c = pedal nerve cord
pr. l = prismatic layer of shell
sal. g = salivary gland

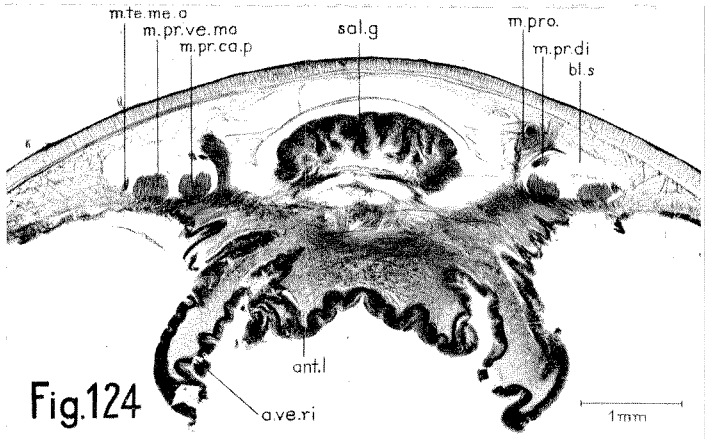


Fig.124

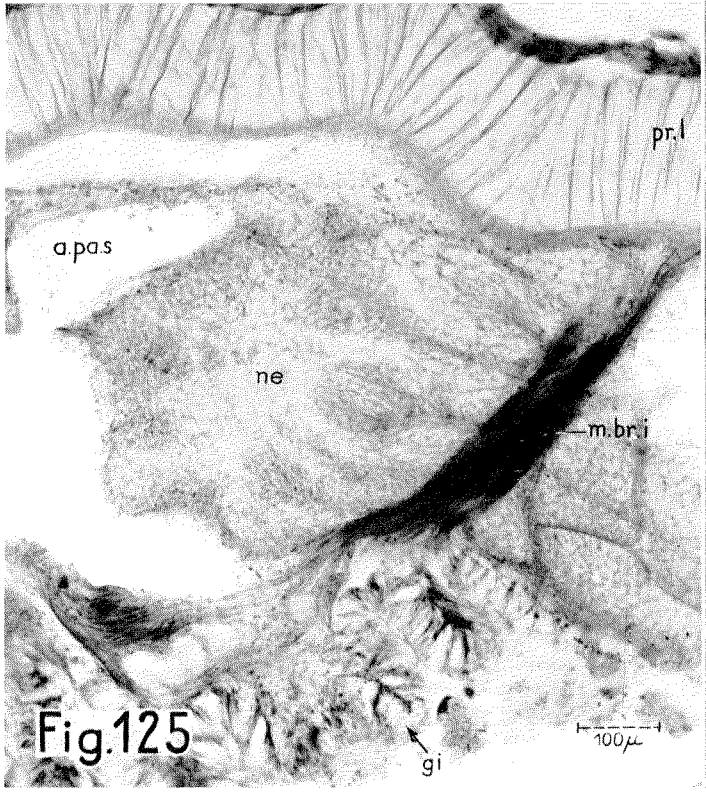


Fig.125

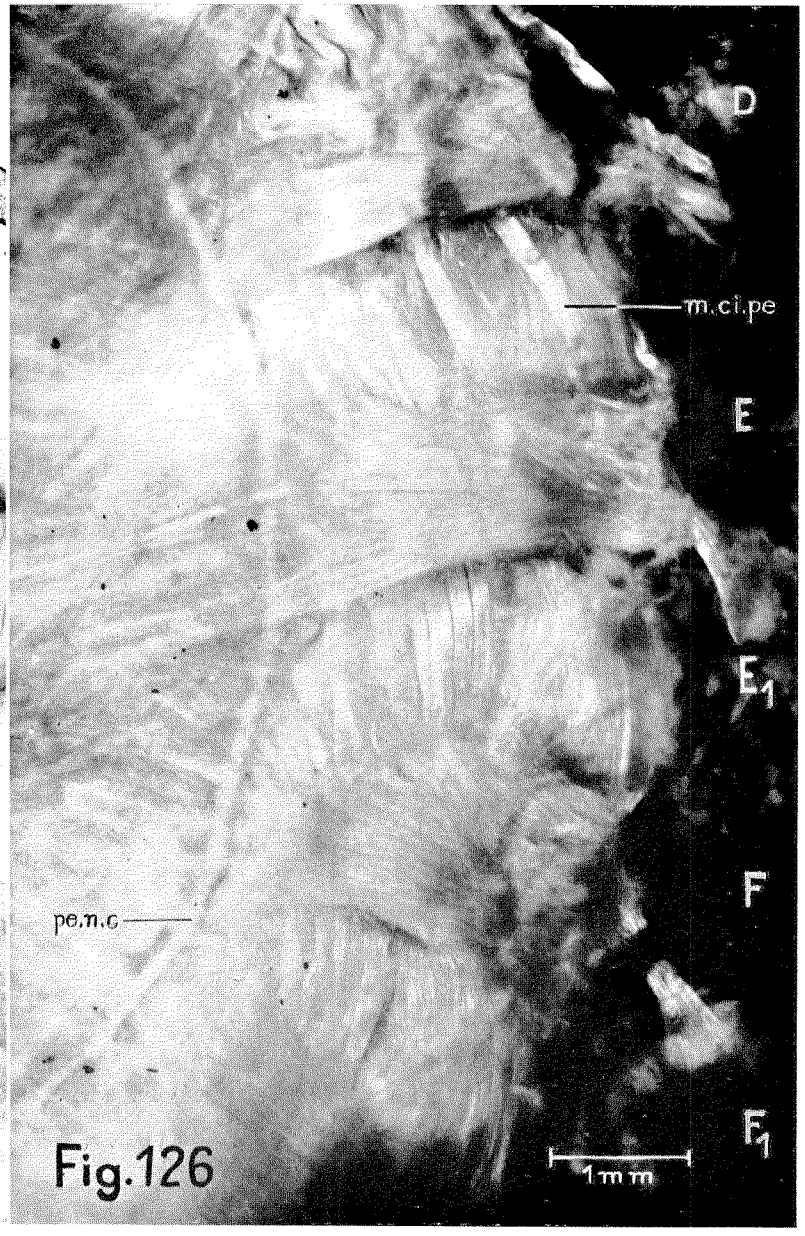


Fig.126

PLATE 39

Fig. 127. Muscles associated with the ventral body wall of the anterior body region. Dorsal view. The bases of the anterior lip (ba. a. l), the velum (ba. ve), and the tentacle ridge (ba. te. ri) are indicated by stippling. Graphic reconstruction from Spec. III.

Fig. 128. The muscles of the radula apparatus, dorsal view. Graphic reconstruction from Spec. III.

A-C = pedal retractors A to C
A_1-D_1 = mm. obliquii anteriores A to C
ba. a. l = base of anterior lip
ba. ve = base of velum
ba. te. ri = base of tentacle ridge
m. ca. a-l = musculus cartilaginis antero-lateralis
m. ca. a-m = musculus cartilaginis antero-medialis
m. ca. p-l = musculus cartilaginis postero-lateralis
m. ca. p-m = musculus cartilaginis postero-medialis
m. ca. v = musculus cartilaginis ventralis
m. ci. int = musculus circularis intermedius
m. ci. pa = musculus circularis pallii
m. ci. pe = musculus circularis pedis
m. cru = musculus cruciatus
m. or. ant = musculus oralis anterior
m. or. po = musculus oralis posterior
m. pha = pharyngeal muscles
m. pr. ca. d = musculus protractor cartilaginis dorsalis
m. pr. ca. d' = small dorsal head of same
m. pr. ca. p = musculus protractor cartilaginis profundus
m. pr. di = musculus protractor diverticulorum dorsalis
m. pr. ra = musculus protractor radulae
m. pr. ve. ma = musculus protractor vesicae major
m. pr. ve. mi = musculus protractor vesicae minor
m. pro = musculus praeoralis
m. ra. l = musculus radulae longus
m. ra. mi = musculus radulae minor
m. re. ra = musculus retractor radulae
m. re. ve = musculus retractor veli
m. sep = subepithelial muscle membrane
m. te. m. a = musculus tensor membranae anterior
m. te. m. l = musculus tensor membranae lateralis
m. te. tr = musculus tentacularis transversus
m. te. ra = musculus tensor radulae
m. tr. A = musculus transversalis A
m. tr. a = musculus transversalis anterior
m. tr. p = musculus transversalis posterior
m. ve. a-l = musculus vesicae antero-lateralis
m. ve. a-m = musculus vesicae antero-medialis
m. ve. p-l = musculus vesicae postero-lateralis
m. ve. p-m = musculus vesicae postero-medialis
m. ve. v = musculus vesicae ventralis
me. lat = membrana lateralis
ph = pharynx
p. d = pars dorsalis of the m. radulae longus
p. v = pars ventralis of the m. radulae longus
ra = radula
ra. div = radula diverticula
ra. sh = radula sheath
ra. ve = radula vesicle
sal. g = "anterior salivary gland"
Y_1 = the muscle Y_1

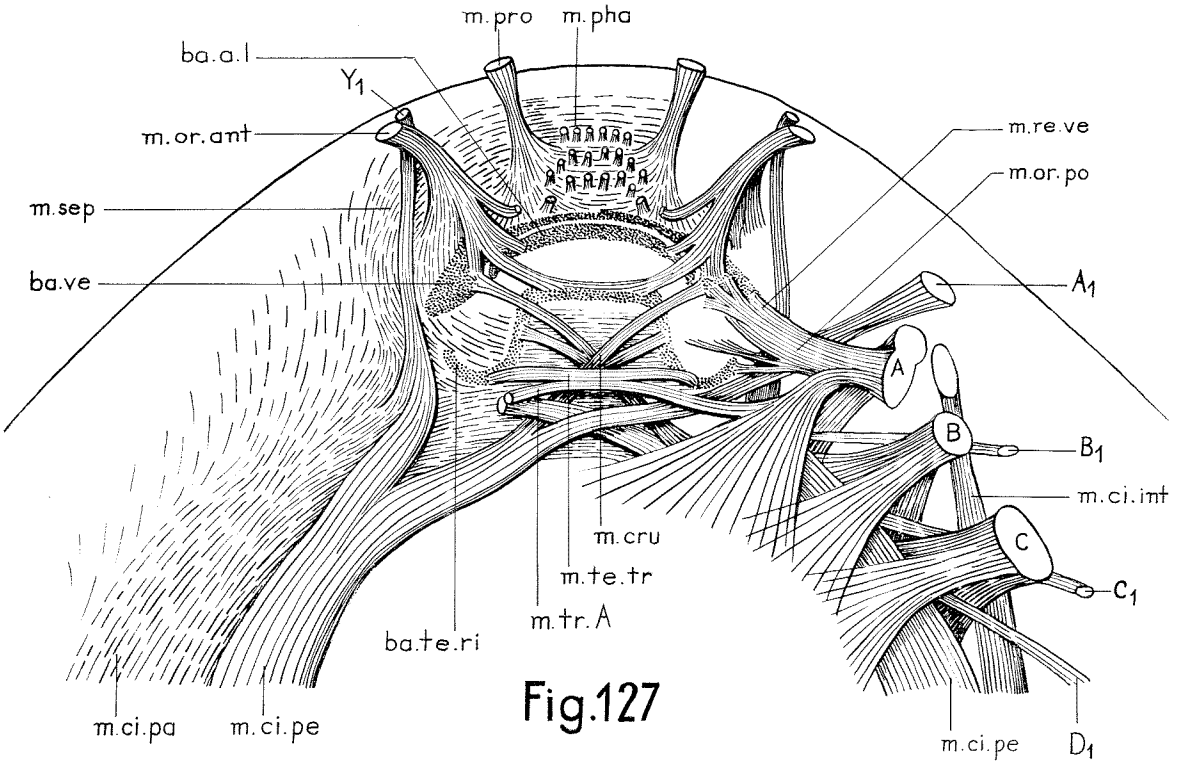


Fig.127

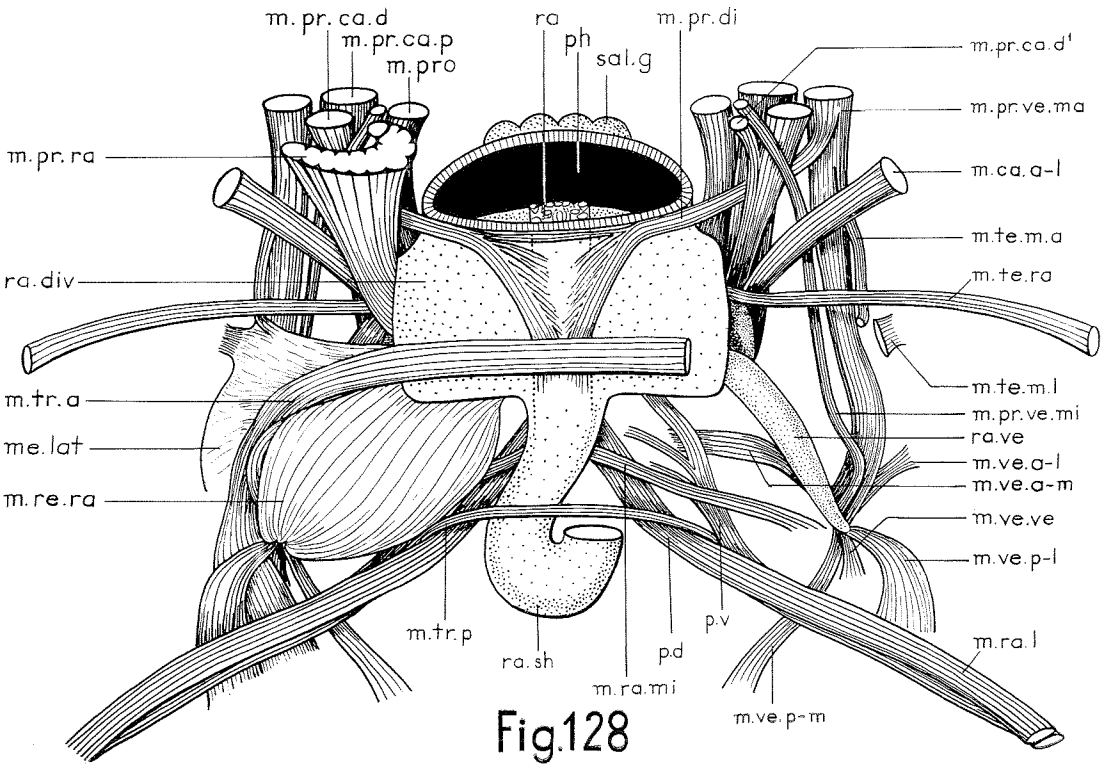


Fig.128

Plate 40

Fig. 129. Horizontal section through the anterior body region at a level just touching the pallial groove (pa. g). Microphotograph. Spec. IV.

d. coe = dorsal coelom
d. coe′ = pre-pharyngeal diverticula of dorsal coelom
m. lp = musculus latero-pedalis
m. obl. A = musculus obliquus anterior A
m. or. p = musculus oralis posterior
m. pr. ra = musculus protractor radulae
m. ra. l = musculus radulae longus
m. re. ra = musculus retractor radulae
m. te. tr = musculus tentacularis transversus
m. tr. a = musculus transversalis anterior
m. ve. p-l = musculus vesicae postero-lateralis
ne = nephridia
pa. g = pallial groove
ph = pharynx
ph. d = pharyngeal diverticulum (visible on the right side)
ra. sh = radula sheath
ra. ve = radula vesicle
sr. o = subradular organ
st = statocyst
te = testis

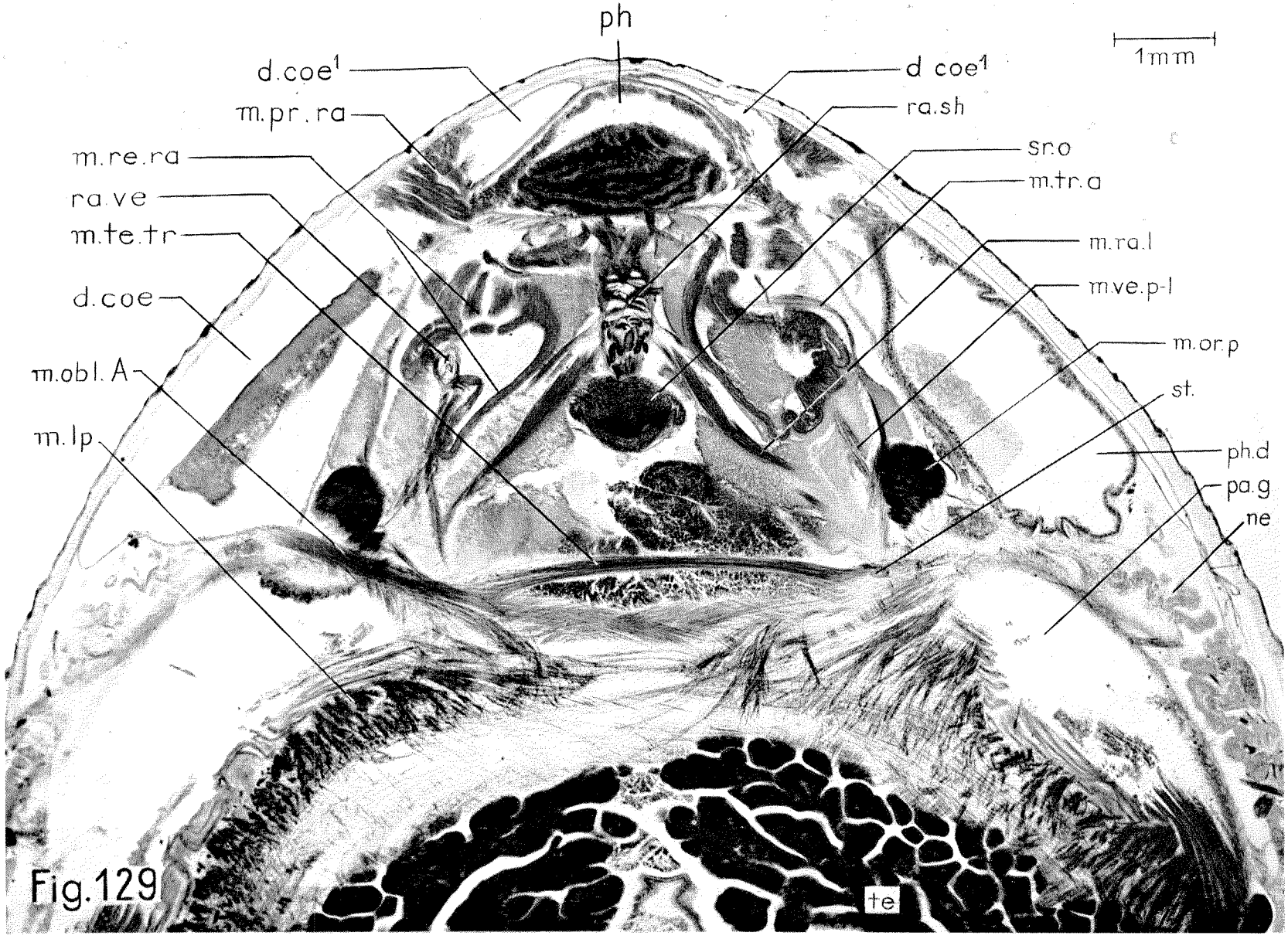

ph
d.coe¹
m.pr.ra
m.re.ra
ra.ve
m.te.tr
d.coe
m.obl.A
m.lp
d coe¹
ra.sh
sr.o
m.tr.a
m.ra.l
m.ve.p-l
m.or.p
st.
ph.d
pa.g
ne
1mm
te

Fig.129

PLATE 41

Fig. 130. Graphic reconstruction of the muscle insertion pattern on the left side of the shell in Spec. III. The areas with muscle insertion cells were projected on a horizontal plane. For explanations compare Fig. 131.

Fig. 131. Diagram of the insertion pattern of a typical muscle group in *Neopilina*, showing at the same time the meaning of the designations used in Fig. 130.

Fig. 132. Insertion pattern on the anterior shell wall of Spec. IV. The areas with muscle attachment cells have been projected on a transversal plane. The insertion areas of muscles related to the ventral body wall are hatched, those of the radula muscles are black.

Fig. 133. The pattern of muscle scars on the inner side of the shell of *Pilina unguis*, drawn on the basis of the specimen shown in Fig. 134, and completed in agreement with KNIGHT (1941). The present authors' interpretations have been introduced.

A-H = muscle attachment groups A to H
A_1 = musculus obliquus anterior A
ap = apex
di. sc = "diaphragm scar"
m. br. ex = musculus branchialis externus (white, double contour)
m. br. i = musculus branchialis internus (black, double contour)
m. ci. int = musculus circularis intermedius (black, white dots)
m. lp = musculus latero-pedalis (black)
m. mp = musculus medio-pedalis (large black dots)
m. obl. a = musculus obliquus anterior (horizontal streaks)
m. obl. p = musculus obliquus posterior (vertical streaks)
m. ra. l = musculus radulae longus
pa. l = pallial line
pa. m = pallial muscles (small dots)
X = insertion area X
X_1 = musculus protractor radulae
X_2 = musculus protractor cartilaginis dorsalis (the small head)
X_3 = musculus protractor cartilaginis dorsalis (the large head)
X_4 = musculus protractor vesicae minor
X_5 = musculus praeoralis
X_6 = musculus protractor cartilaginis profundus
X_7 = musculus protractor vesicae major, including also the heads of m. tensor membranae anterior and m. protractor diverticulorum dorsalis
Y = insertion area Y
Y_1 = the muscle Y_1
Y_2 = musculus oralis anterior
Y_3 = musculus cartilaginis antero-lateralis
Z = musculus tensor radulae
1-7 = the different parts of the muscle scar complexes in *Pilina* (Fig. 133), interpreted as:
1 = musculus latero-pedalis
2 = musculus medio-pedalis
3 = musculus obliquus posterior
4 + 5 = musculus branchialis externus and a pallial muscle
6 = musculus obliquus anterior
7 = musculus branchialis internus and (or) a pallial muscle

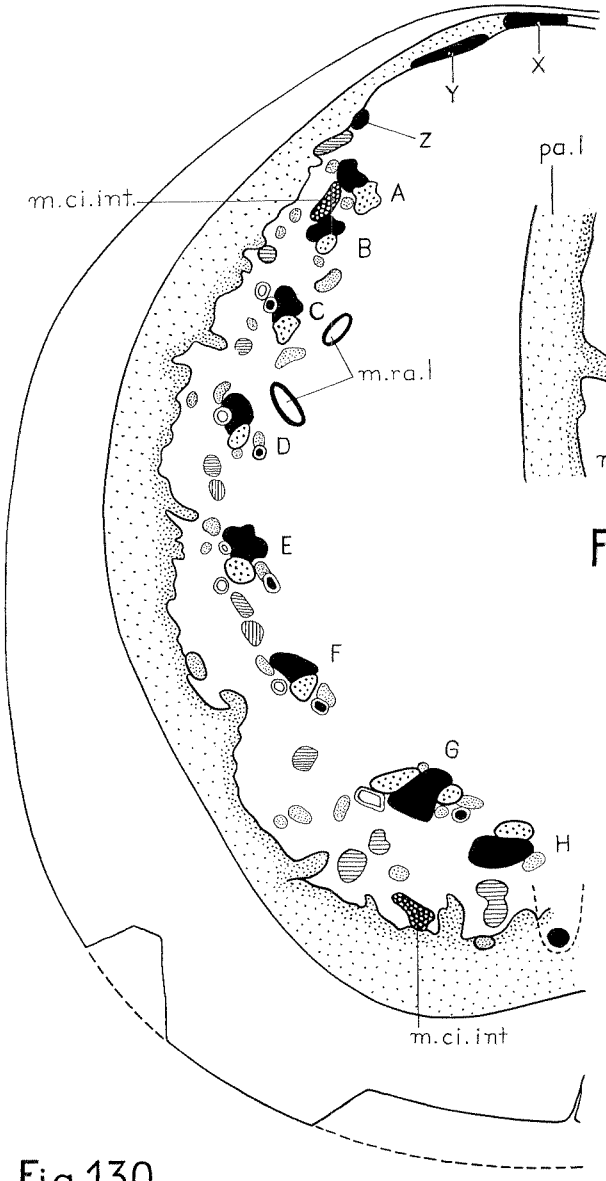


Fig.130

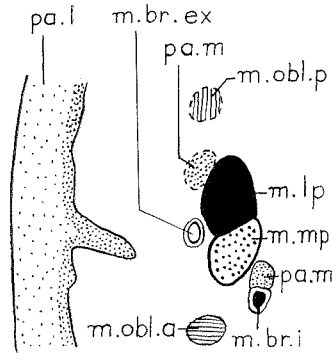


Fig.131

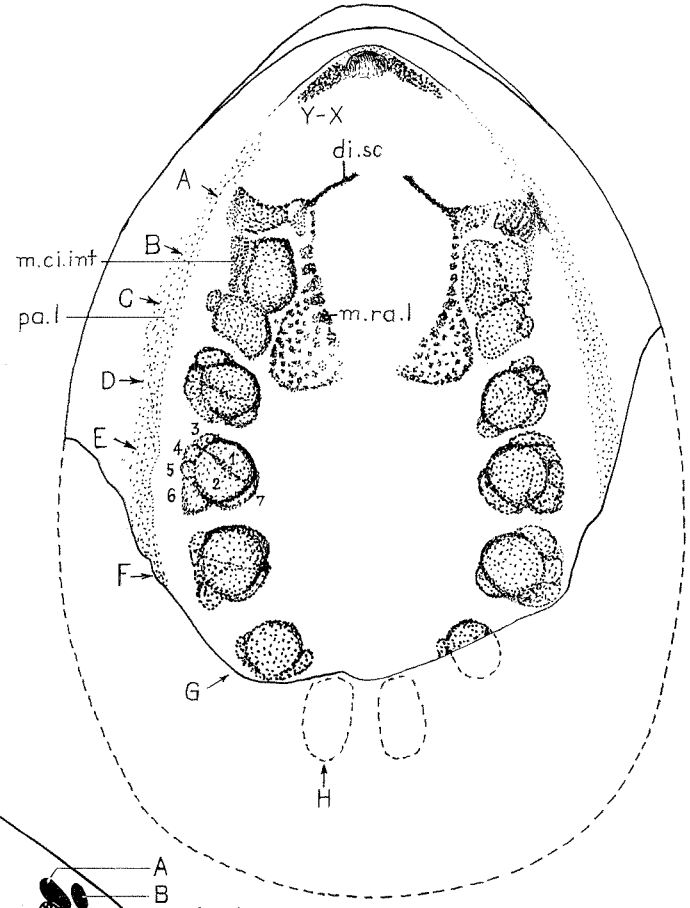


Fig.133

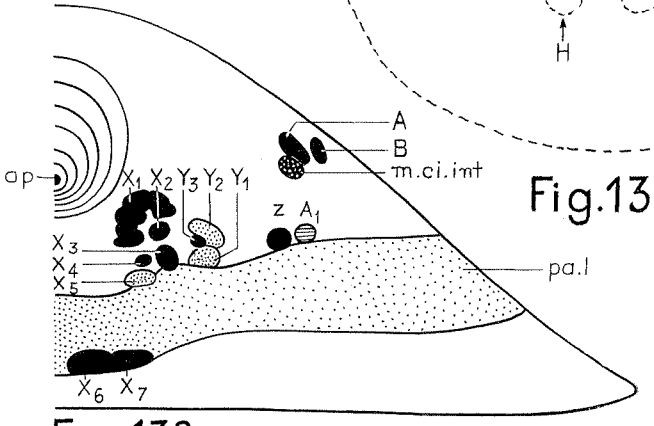


Fig.132

PLATE 42

Fig. 134. *Pilina unguis* (LINDSTRÖM), from the Silurian of Gotland (Compare LINDSTRÖM, 1884, pl. 19, fig. 2). Inner side of shell, smoked with ammonium chloride to make the muscle scars distinct. For interpretation see Fig. 133.

Specimen and photograph from the Paleozoological Department of the Swedish Museum of Natural History, Stockholm (Director, Prof. ERIK STENSIÖ).

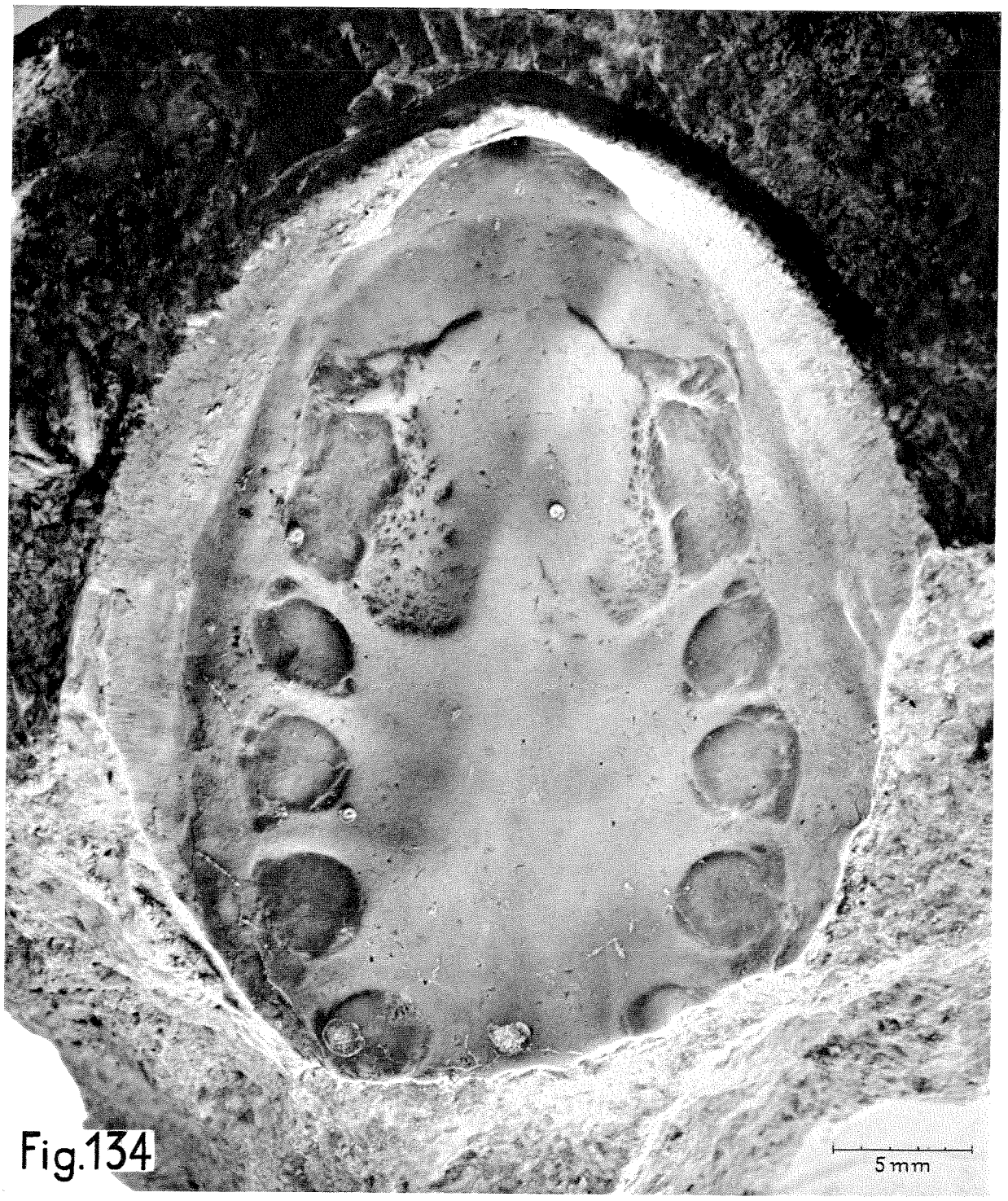


Fig.134

PLATE 43

Fig. 135. The nervous system, projected on a horizontal plane by means of graphic reconstruction. The right side includes all the traceable branches, the left one shows the latero-pedal connectives and the gill nerves only. Spec. III.

4-10 = latero-pedal connectives 4 to 10
bu. co = buccal connective
bu. g = buccal ganglion
cer. co = cerebral commissure
cer. g = cerebral ganglion
ex. g. n = external (anterior) gill nerve
f. m = foot margin
G = gills
i-p. co = inter-pedal commissure
in. g. n = internal (posterior) gill nerve
la. n. c = lateral nerve cord
la. pe. n = lateral pedal nerves
l-p. co_4 = latero-pedal connective 4
me. pe. n = medial pedal nerves
pa. n = pallial nerves
pe. n. c = pedal nerve cord
rp. n = nerve to the renopore

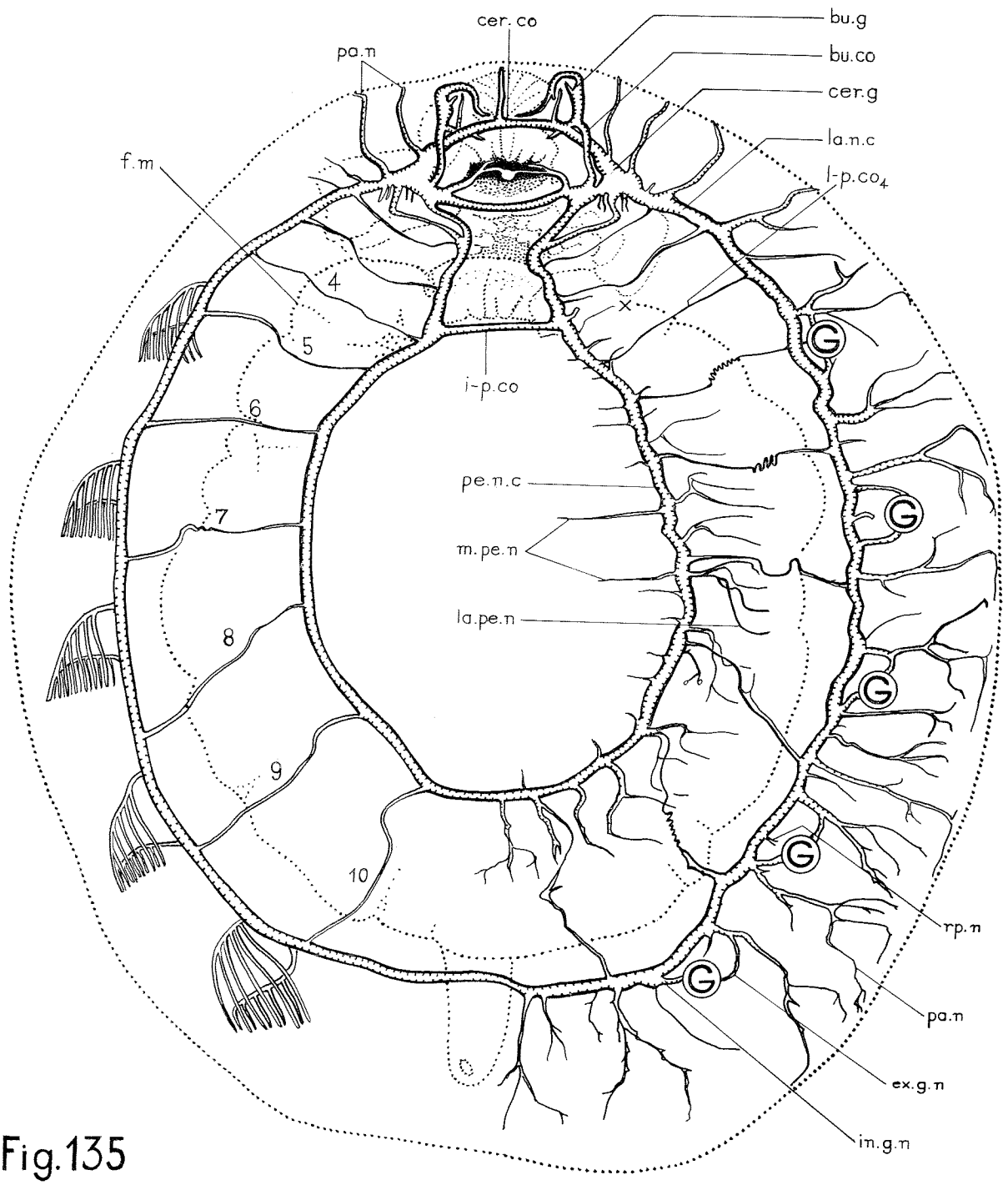

cer. co
bu.g
pa.n
bu.co
cer.g
la.n.c
f.m
l-p.co4
4
5
i-p.co
6
pe.n.c
7
m.pe.n
la.pe.n
8
9
10
rp.n
pa.n
ex.g.n
im.g.n

Fig.135

PLATE 44

Fig. 136. Anterior part of the nervous system, seen from above. The pharynx and the subradular organ are drawn to the left only. The base of the velum, the anterior lip, and the tentacle ridge is indicated by stippling, and the nerves passing to these organs are not particularly marked. Graphic reconstruction. Spec. III.

Fig. 137. The relation between the nervous system and the musculature in the anterior body region. Only muscles associated with the ventral body wall are shown. Graphic reconstruction. Spec. III.

1-6 = latero-pedal connectives 1 to 6
A-D = pedal retractors A to D
b. ant. 1 = base of anterior lip
b. te. ri = base of tentacle ridge
b. ve = base of velum
bu. co = buccal connective
bu. g = buccal ganglion
ce. co = cerebral commissure
ce. g = cerebral ganglion
ex. gi. n_1 = external (anterior) nerve of 1st gill
i-p. co = inter-pedal commissure
in. gi. n_1 = internal (posterior) nerve of 1st gill
la. n. c = lateral nerve cord
m. ci. pe = musculus circularis pedis
m. cru = musculus cruciatus
m. obl. A = musculus obliquus anterior A
m. or. a = musculus oralis anterior
m. or. p = musculus oralis posterior
m. pro = musculus praeoralis
m. te. tr = musculus tentacularis transversus
m. tr. A = musculus transversalis A
pa. n = pallial nerves
pe. n. c = pedal nerve cord
ph = pharynx
pr. te = base of preoral tentacle
sce. co = subcerebral commissure
sr. g = subradular ganglion
sr. n = subradular nerve
sr. s = subradular sac
st = statocyst
st. d = statocyst duct
st. n = statocyst nerve
ve. n = velar nerves and branches to anterior lip
Y_1 = the muscle Y_1

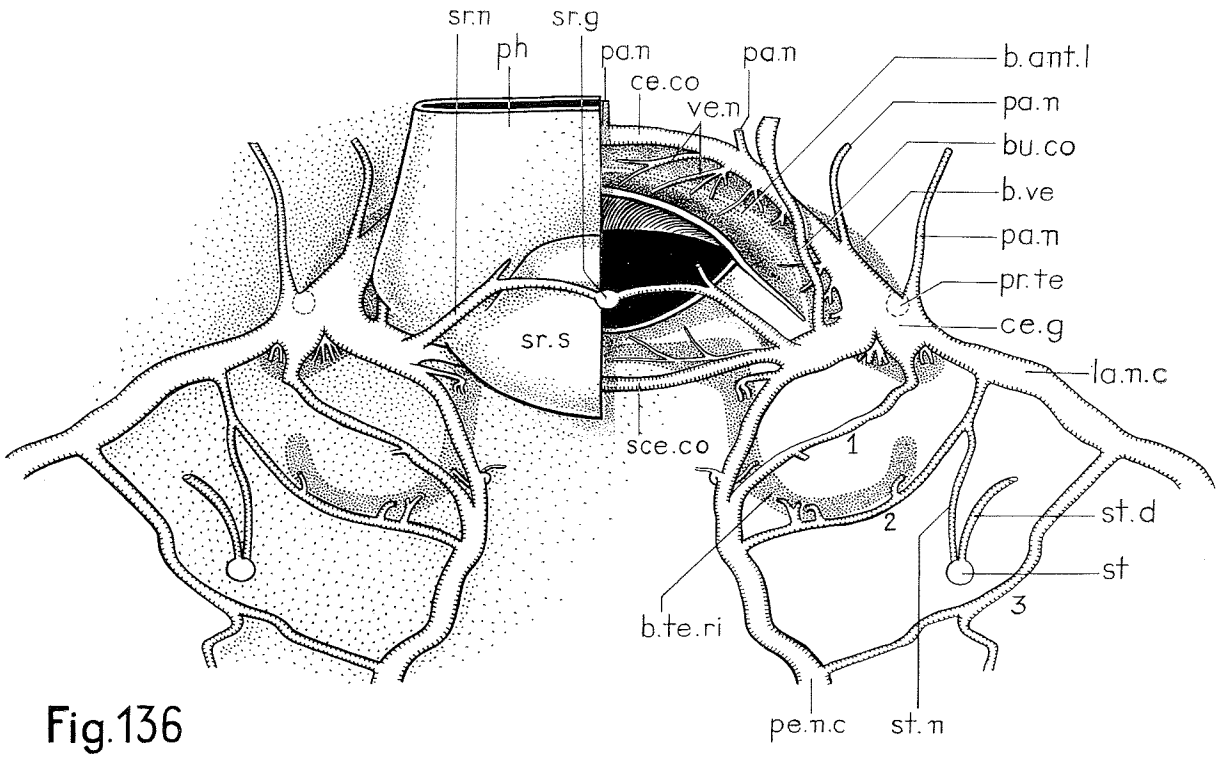


Fig.136

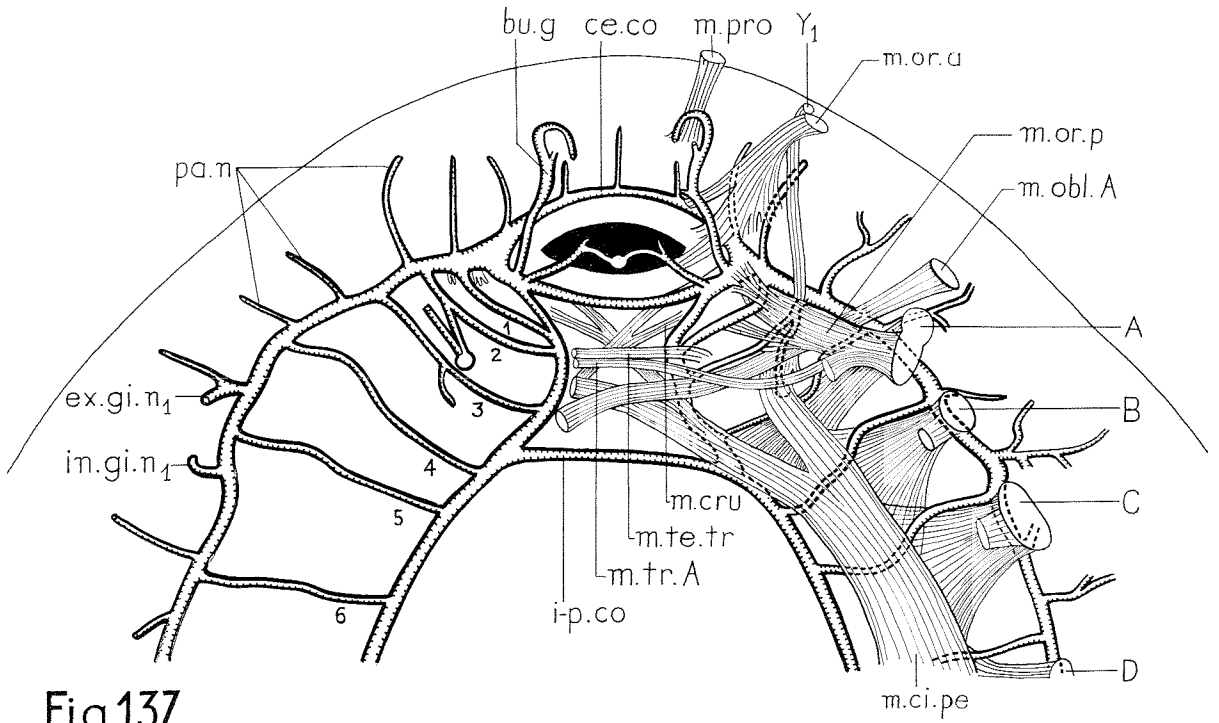


Fig.137

Plate 45

Fig. 138. Transversal section through the ventral body wall just inside the foot margin, showing the pedal nerve cord with its superficial layer of nerve cells. Microphotograph. Spec. III.

Fig. 139. Transversal section through the statocyst. Note the high and dark epithelium forming the bottom and the sides. Microphotograph. Spec. III.

Fig. 140. Part of the ventral body wall and of the foot of a dissected specimen, seen in transmitted light. The pedal nerve cord and the regularly spaced latero-pedal connectives are distinct. Photograph. Spec. X.

Fig. 141. Blood cells in a pallial blood sinus. Microphotograph. Spec. III.

Fig. 142. Leydig cells in loose connective tissue from the inner part of the pallial fold. Microphotograph. Spec. III.

bl. s = blood sinus
l-p. co = latero-pedal connective
ov = ovary
pe. n. c = pedal nerve cord

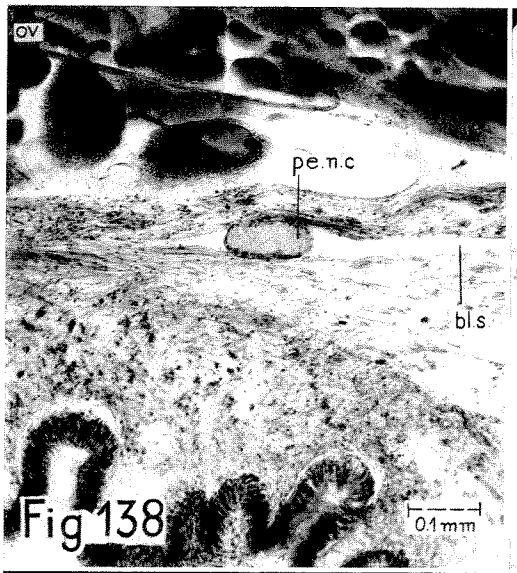


Fig.138

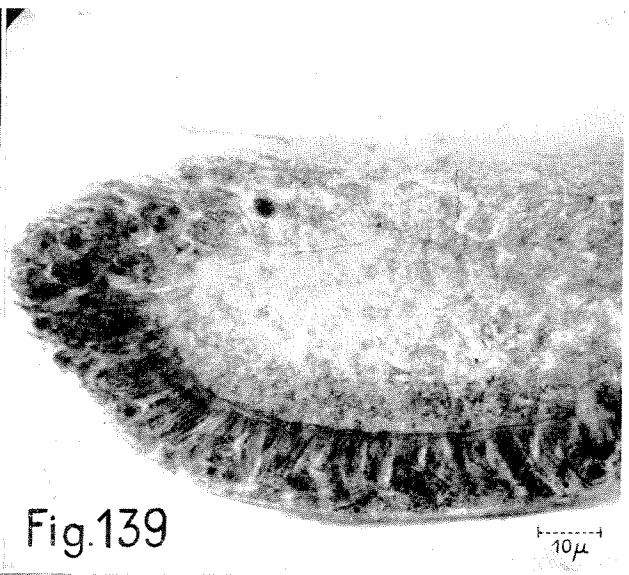


Fig.139

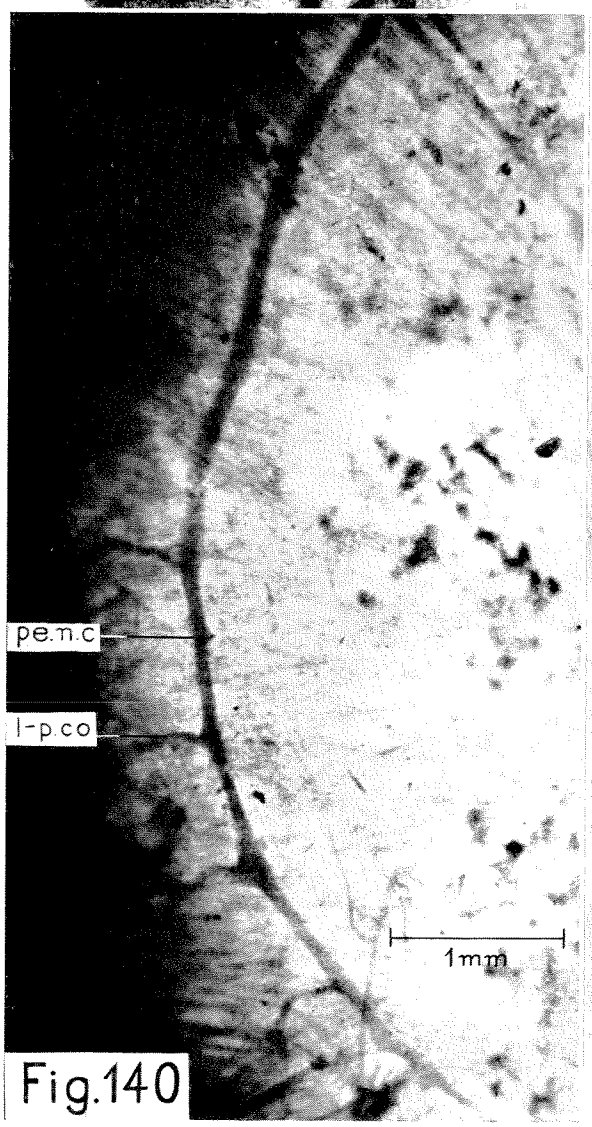


Fig.140

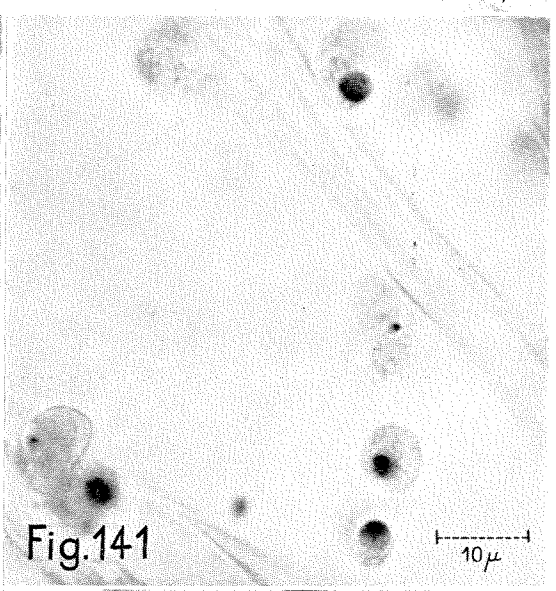


Fig.141

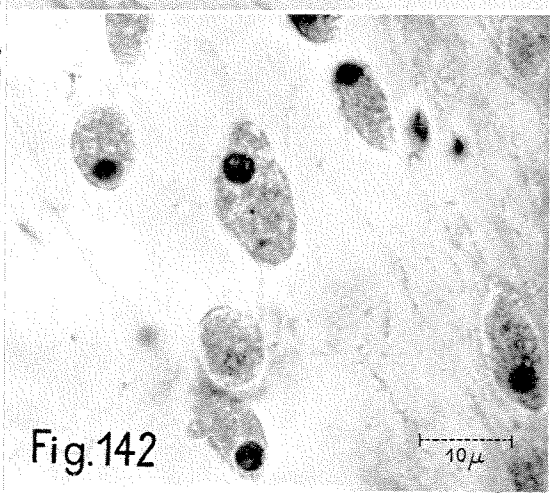


Fig.142

PLATE 46

Fig. 143. Diagrammatical section through the heart region, showing the heart and its connection with the gill circulation. Arrows indicate the supposed direction of the blood stream and of the water current through the gills.

Fig. 144. Graphic reconstruction of the arterial part of the vascular system, superimposed on the urogenital system. For explanations see also Fig. 145. Spec. III.

A-H = position of the pedal retractors A to H (not drawn)
an = anus
ao = aorta
a. pa. s = arterial pallial sinus
ar. cl = artificial cleft between pericard and dorsal epithelium
art. g. v_{1-5} = entrance of arterial vessels from 1st to 5th gill
atr = atrium, 1 and 2 indicates 1st and 2nd pair resp.
a-v. v = atrio-ventricular valves
gi. st = gill stem
m = mouth
ne = nephridia
od_2 = second oviduct
ov = ovary
per. bl. s = peri-intestinal blood sinus
perc = pericard
po. f. m = posterior foot margin
re = rectum
rep_{1-2} = renopores 1 and 2
ve. h = ventricle of heart
ve. pa. s = venous pallial sinus

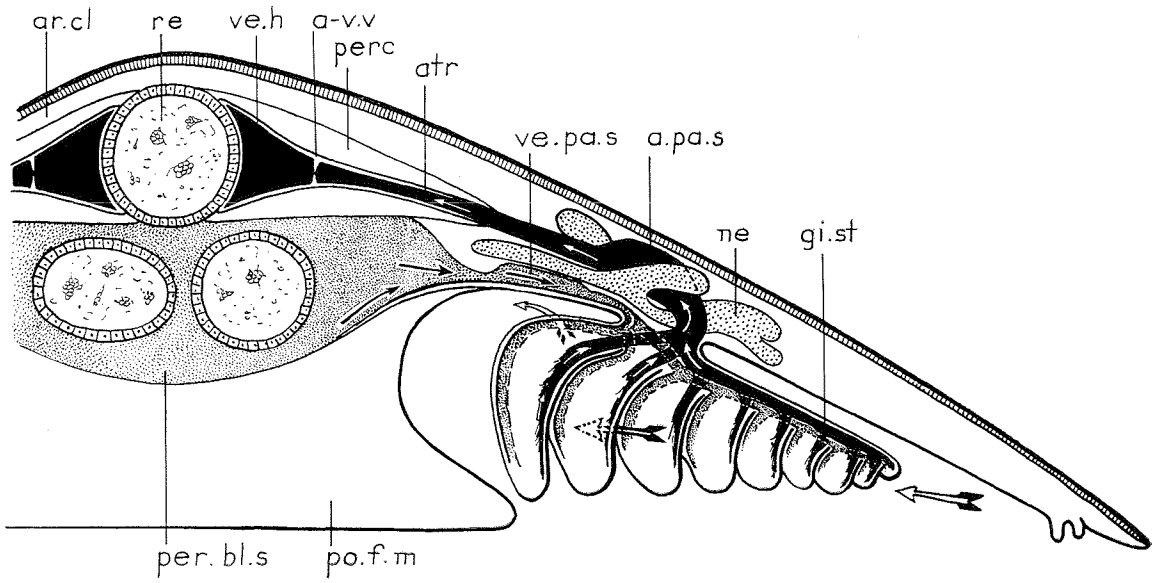


Fig.143

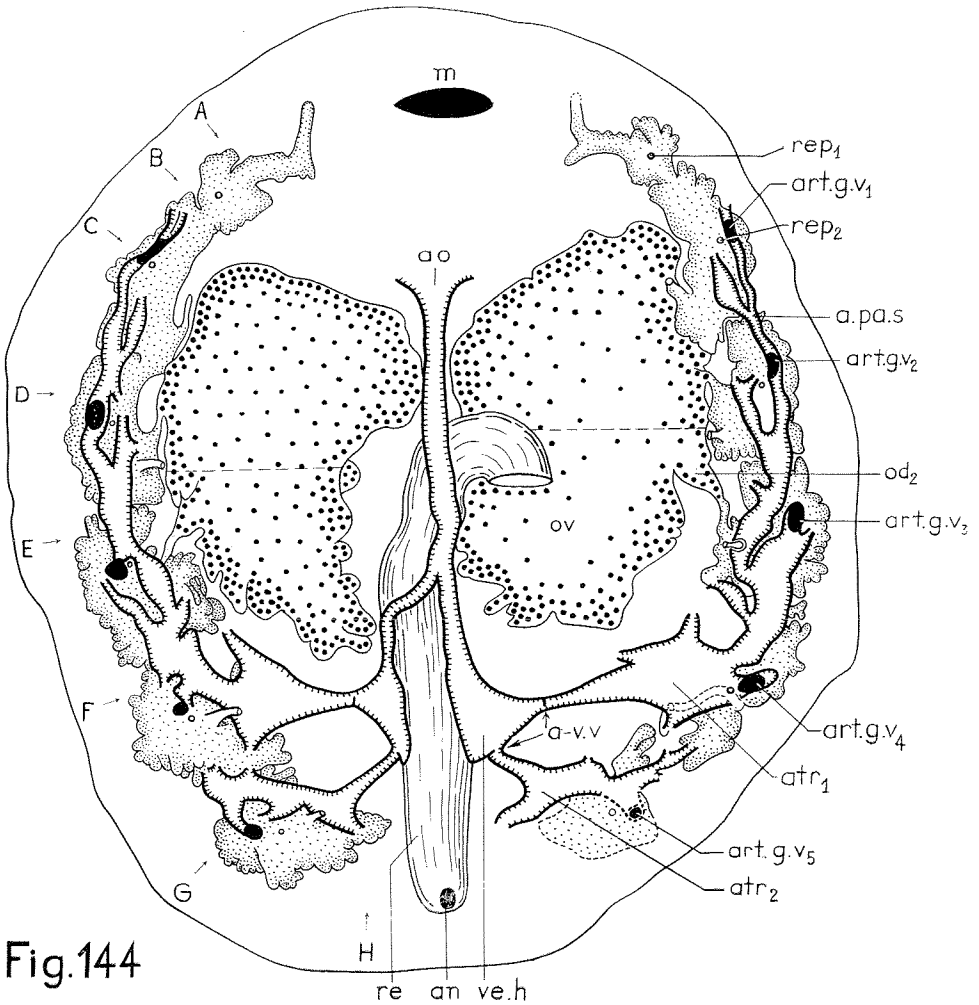


Fig.144

PLATE 47

Fig. 145. Graphic reconstruction of the urogenital system. Dorsal view. Spec. III. The posterior right nephridium is damaged in the preparations. Some of the nephrostomes are difficult to trace (compare text!).

Fig. 146. Graphic reconstruction, including the urogenital system, vessels, and coelomic cavities. Spec. III. For explanations compare Fig. 145 and 144. Some damage made the reconstruction of the dorsal coelom uncertain in the medio-dorsal region in front of the aorta.

A-H = position of pedal retractors A to H (not drawn)
a. pa. s = arterial pallial sinus
ant. ne. d = anterior nephridial diverticula
an = anus
ao = aorta
art. g. v_{1-5} = entrance of arterial vessels from 1st to 5th gill
d. coe = dorsal coelom (with crosses)
m = mouth
$nest_{2-6}$ = nephrostomes, corresponding to 2nd-6th renopore
od_{1-2} = oviducts, 1st and 2nd, resp.
ov = ovaries (two pairs probably present)
perc = pericard (short vertical strokes)
perc. d = pericardial diverticula along the aorta (interrupted lines)
pro. coe = preoral diverticula of dorsal coelom
rep_{1-6} = renopore 1-6

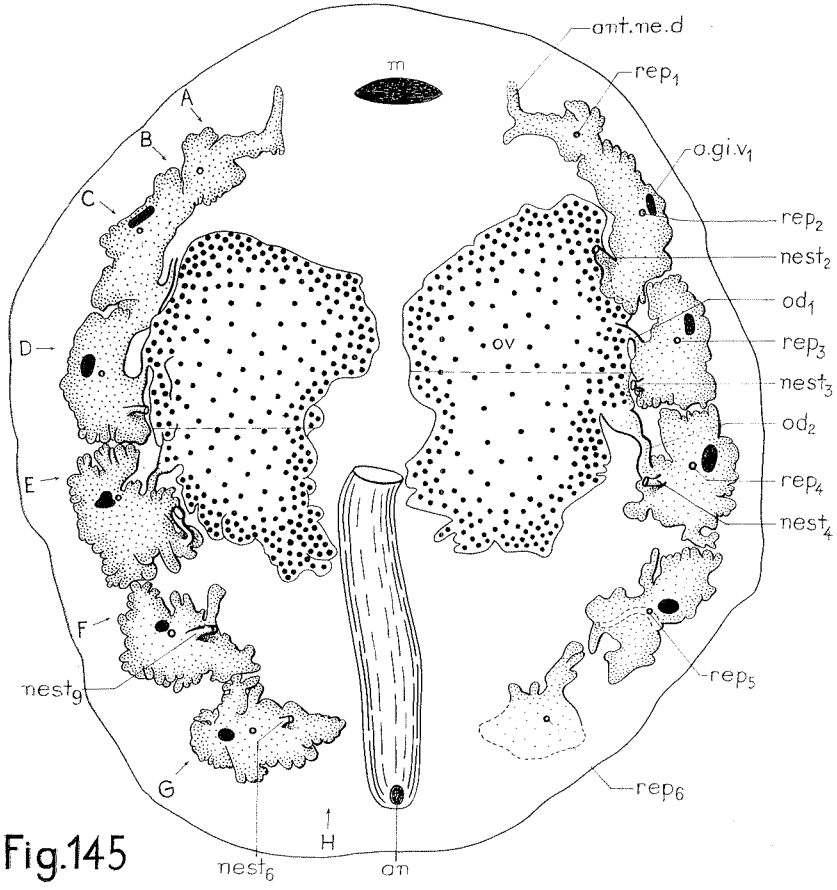


Fig.145

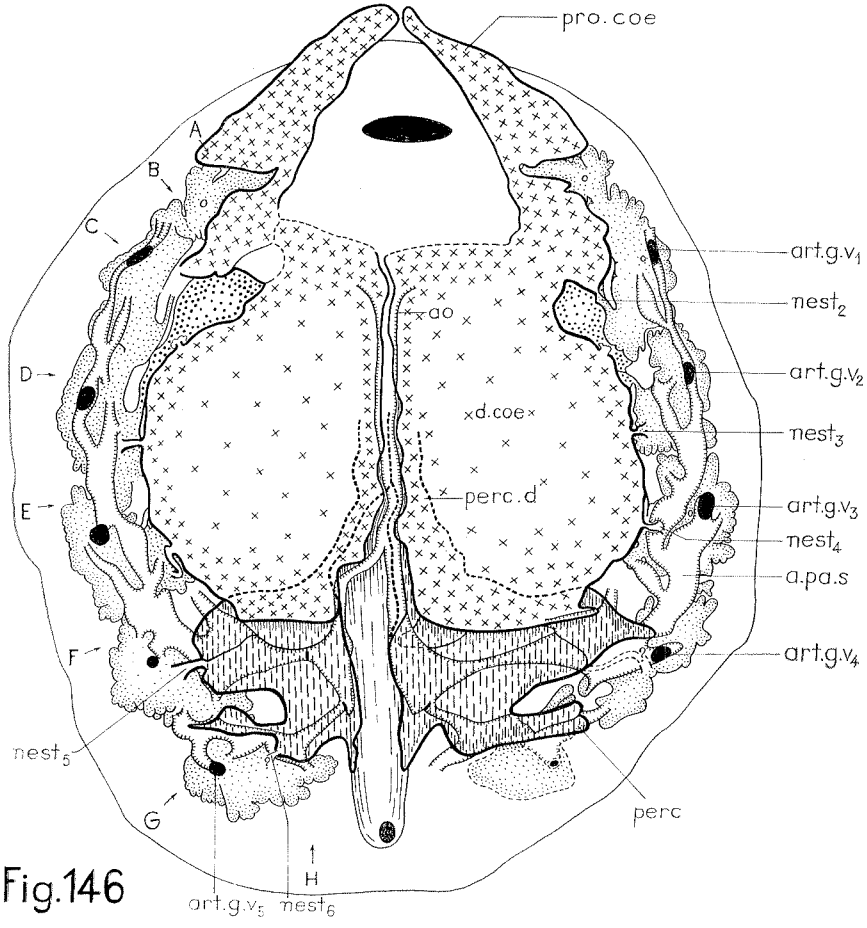


Fig.146

PLATE 48

Fig. 147. Transversal section through the heart region. Microphotograph. Spec. III.
Fig. 148. Transversal section through the middle body region, showing the blood sinuses in the pallial fold. Microphotograph. Spec. III.

a-v. v = atrio-ventricular valve
art. pa. s = arterial pallial sinus
atr_1 = atrium, anterior pair
do. coe = dorsal coelom
f. m = foot margin
f. s. ep = foot side epithelium
gi = gill
la. n. c = lateral nerve cord
m. lp. E = musculus latero-pedalis E
m. obl. a. E = musculus obliquus anterior E
ne = nephridia
ov = ovary
perc = pericard
re = rectum
ve. f. ep = ventral foot epithelium
ve. h = ventricle of heart
ve. pa. s = venous pallial sinus

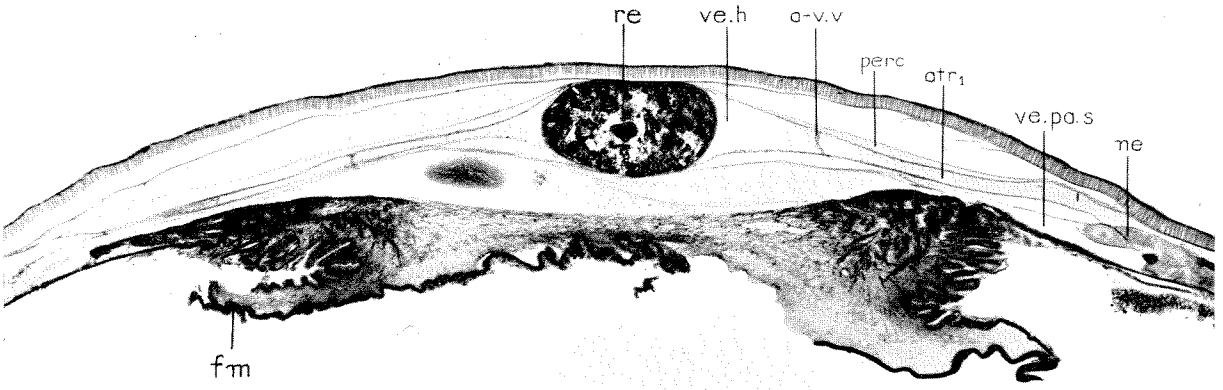


Fig.147

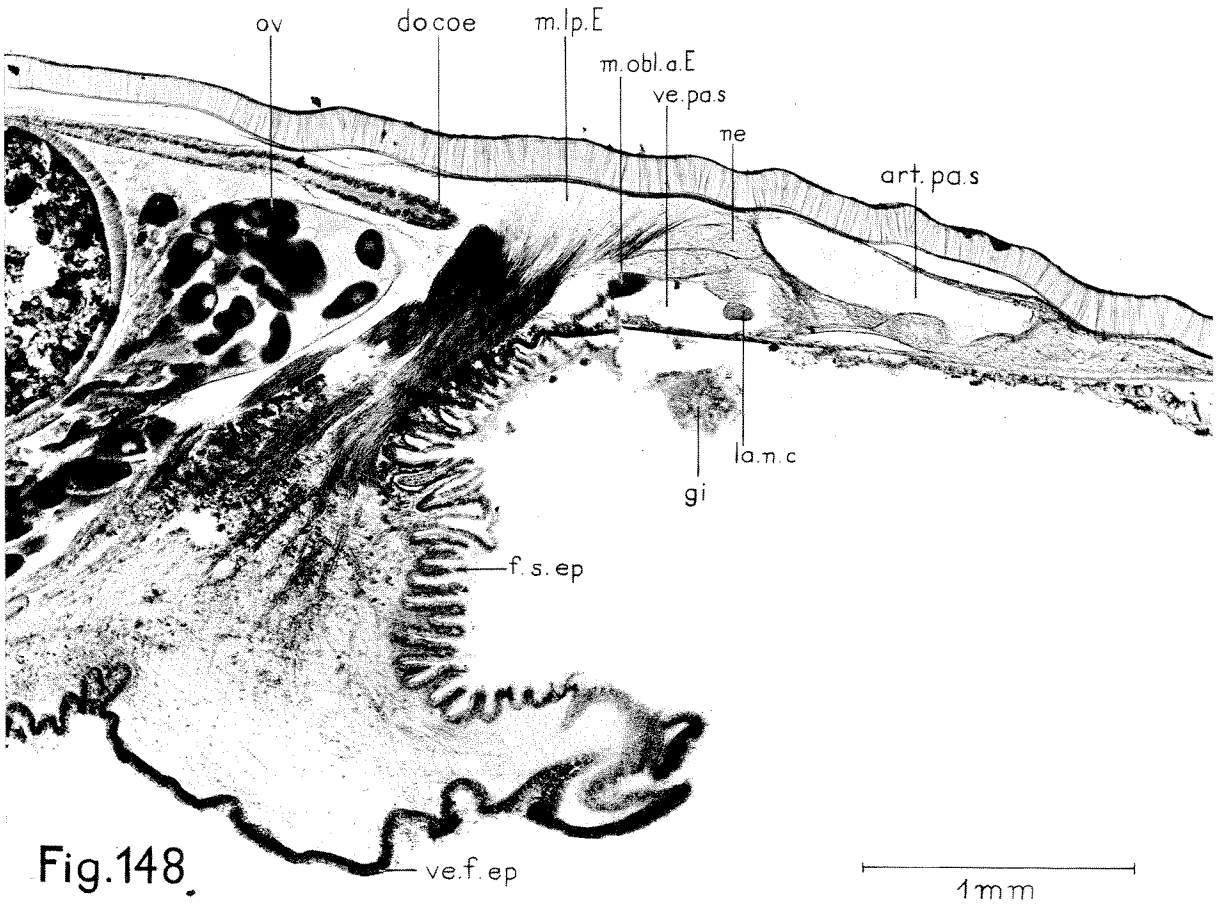


Fig.148

PLATE 49

Fig. 149. The sac-like dilatations of the dorsal coelom between the foremost pedal retractor muscles. Horizontal section. Anterior direction to the right. Microphotograph. Spec. IV.

Fig. 150. Epithelium of the dorsal coelomic cavity with pigment granules. Microphotograph. Spec. III.

Fig. 151. Detail of transversal section showing the thin walls of the ventricle, the atrium, the pericard, and the atrio-ventricular valve. The empty space above the pericard is an artefact. Microphotograph. Spec. III.

Fig. 152. Section through the atrio-ventricular valve. The membrane is covered on both sides by a layer of large (cross-sectioned) muscle cells, in which metaphase-like lumps of basophilic granules can be seen. Microphotograph. Spec. IV.

A and B = pedal retractors A and B
at = atrium of heart
a-v. v = atrio-ventricular valve
coe = coelom
coe. ep = coelomic epithelium
li = liver
na. l = nacreous layer
ne = nephridia
perc = pericard
ph. d = pharyngeal diverticula
pr. l = prismatic layer
st. p = sterile epithelium of pallium
te = testis
ve. h = ventricle of heart

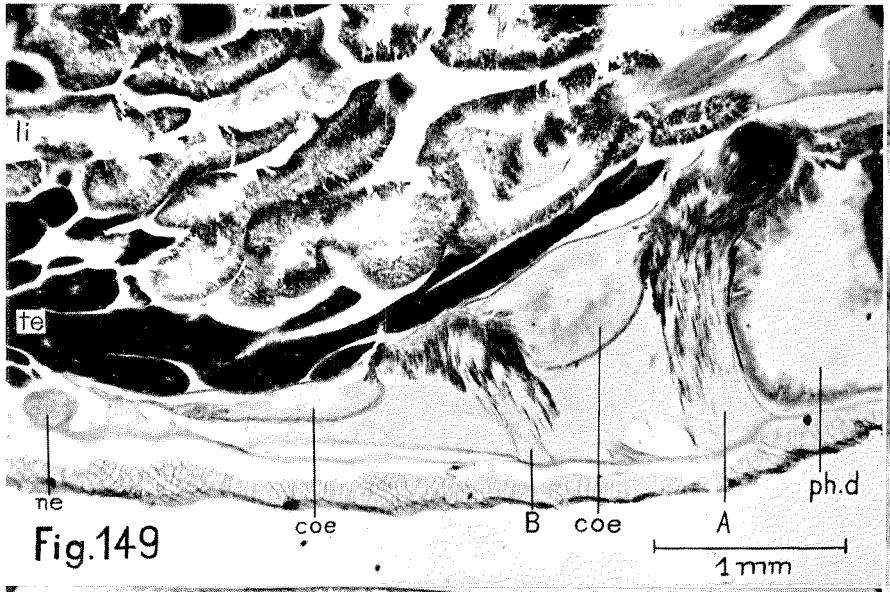


Fig.149

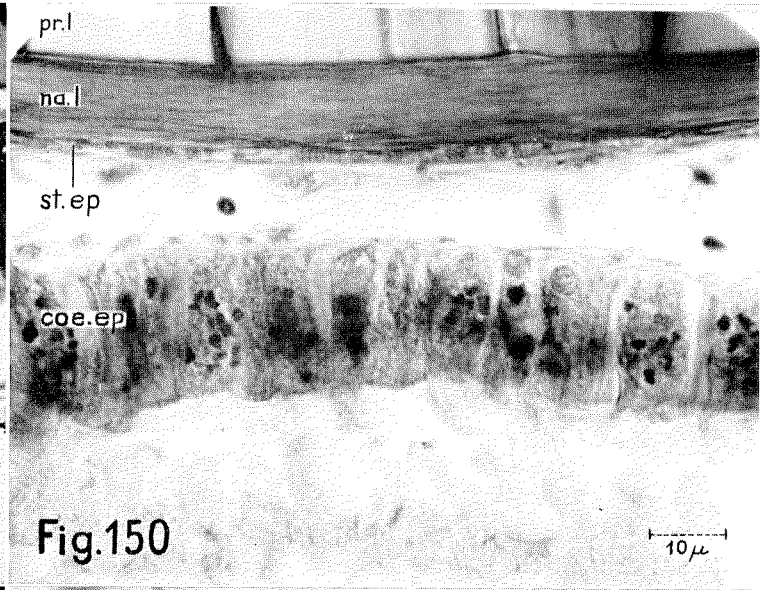


Fig.150

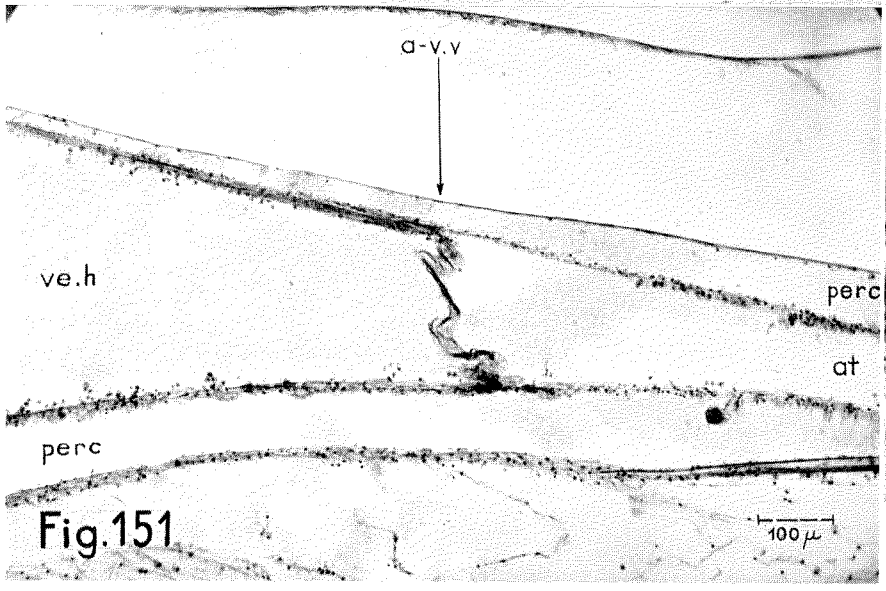


Fig.151

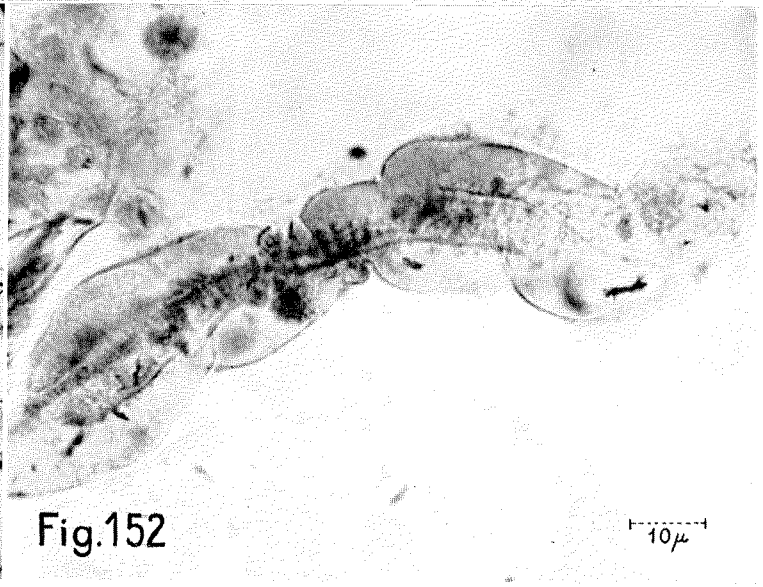


Fig.152

Plate 50

Fig. 153. Detail of transversal section, showing the aorta and its relation to the rectum, the dorsal coelom, and the pericard. Microphotograph. Spec. III.

Fig. 154. Transversal section, showing the pallial fold with the base of the gill and the renopore. Microphotograph. Spec. III.

Fig. 155. Transversal section through the lateral margin of the dorsal coelom, showing one of the nephrostome-like pouches (nest). Microphotograph. Spec. III.

Fig. 156. The connection between the dorsal coelom and the nephridium. Microphotograph. Spec. III.

ao = aorta
d. coe = dorsal coelom
gi = gill lamellae
la. n. c = lateral nerve cord
ne = nephridium
nest = nephrostome-like pouch from the coelom
ov = ovary
pa. w = epithelium of the pallial groove
perc = pericardial diverticulum
re = rectum
rep = renopore

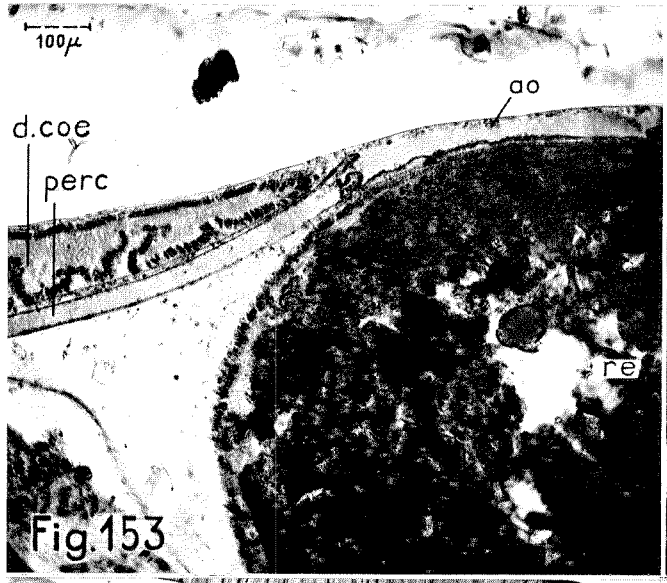


Fig.153

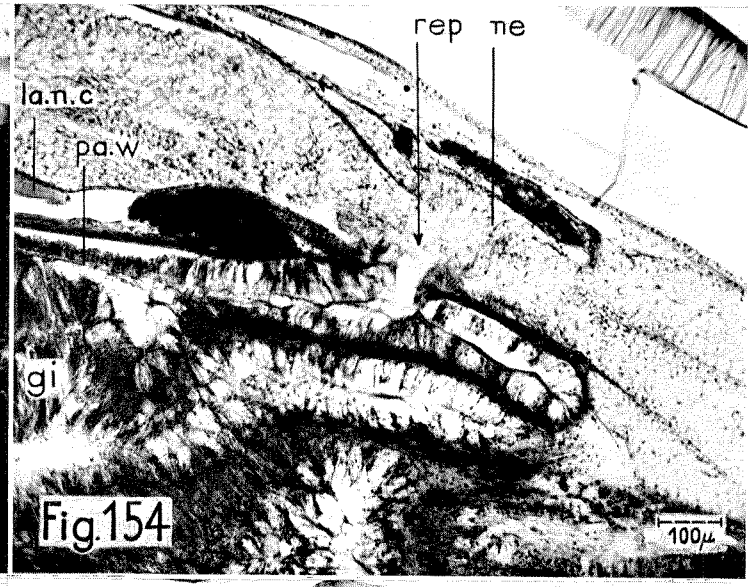


Fig.154

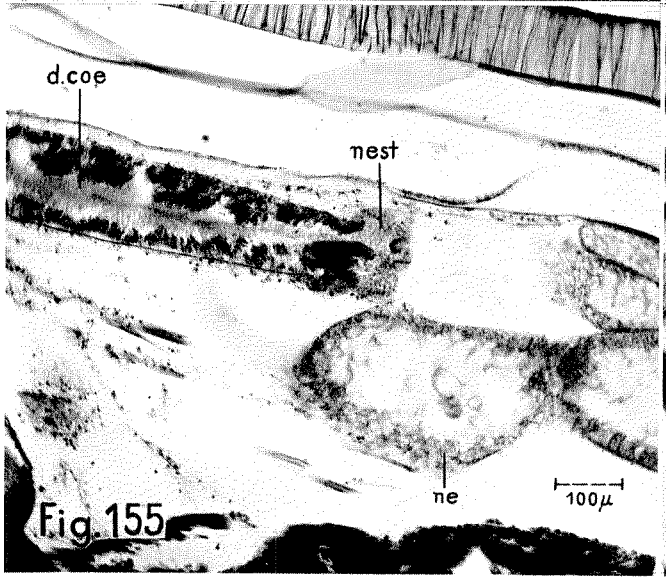


Fig.155

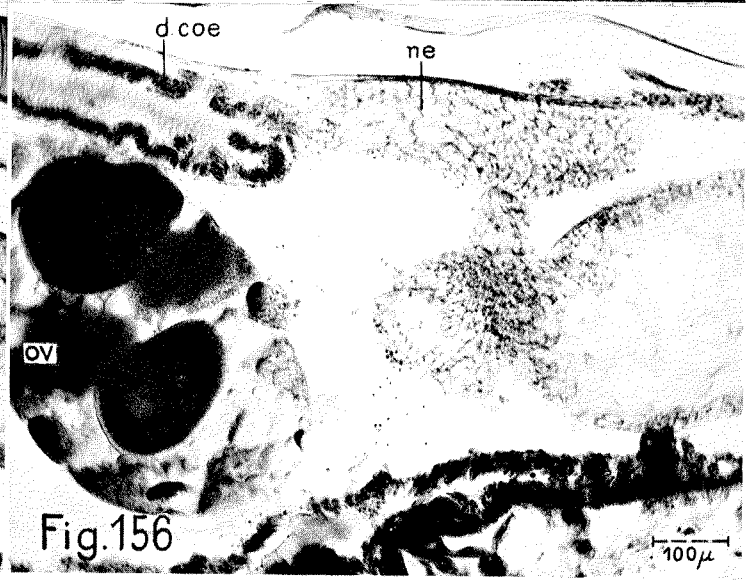


Fig.156

PLATE 51

Fig. 157. Transversal section through the middle body region, showing the relations of the uro-genital system. Microphotograph. Spec. III.

d. coe = dorsal coelom
egg ne = egg in the nephridium
f. m = foot margin
gi = gill
int. c_{1-6} = intestinal coil 1 to 6
la. n. c = lateral nerve cord
mi. ma. f = middle marginal fold
ne = nephridium
ou. ma. f = outer marginal fold
ov = ovary
pa. g = pallial groove
per = periostracum, detached from the shell margin
pe. n. c = pedal nerve cord
re = rectum

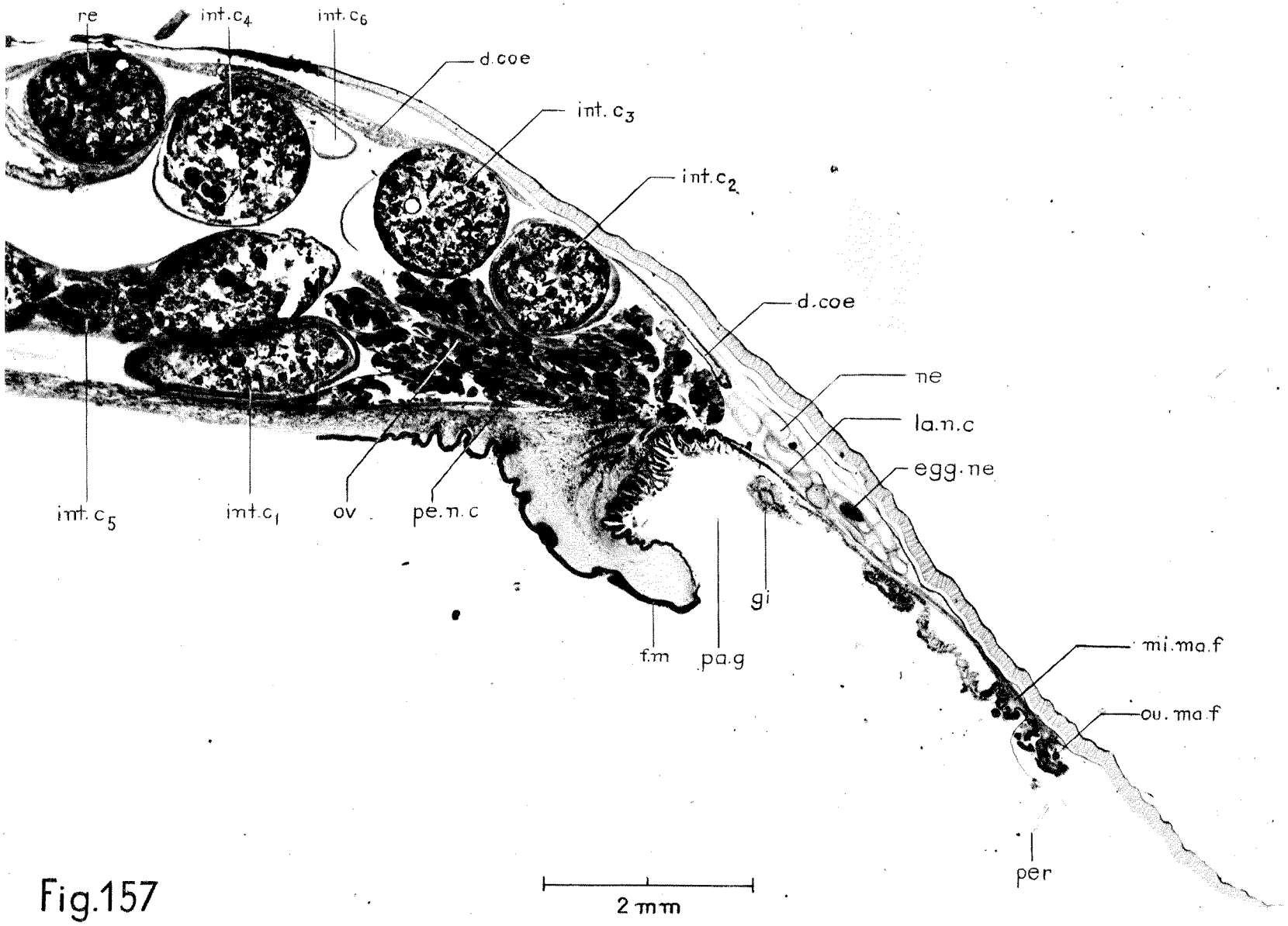

re
int.c4
int.c6
d.coe
int.c3
int.c2
d.coe
ne
la.n.c
egg.ne
int.c5
int.c1
ov
pe.n.c
gi
f.m
pa.g
mi.ma.f
ou.ma.f
per
2 mm

Fig.157

PLATE 52

Fig. 158. Section through an ovarian lobule with mature eggs. Microphotograph. Spec. III.

Fig. 159. Section through on ovarian lobule with developing oocytes. Microphotograph. Spec. III.

Fig. 160. Section through the testis showing the numerous and small lobules. Microphotograph. Spec. IV.

Fig. 161. The wall of a testicular lobule, with spermatogonia near the outer membrane (left). The lumen (right) is filled by ripe sperm, the tails of which can be seen as a striation in the light spaces. Microphotograph. Spec. IV.

int. c_1 = first intestinal coil
lu. ov = lumen of ovary
ooc = oocytes
r. sp = ripe sperm
spc = spermatocytes
spg = spermatogonia

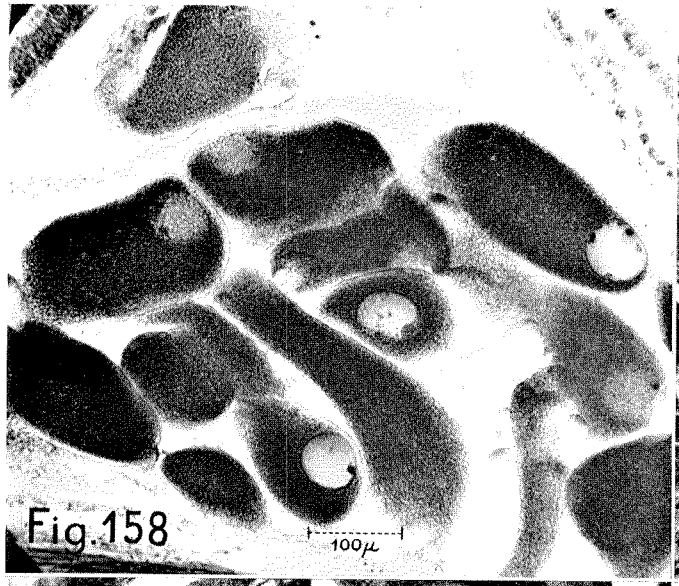
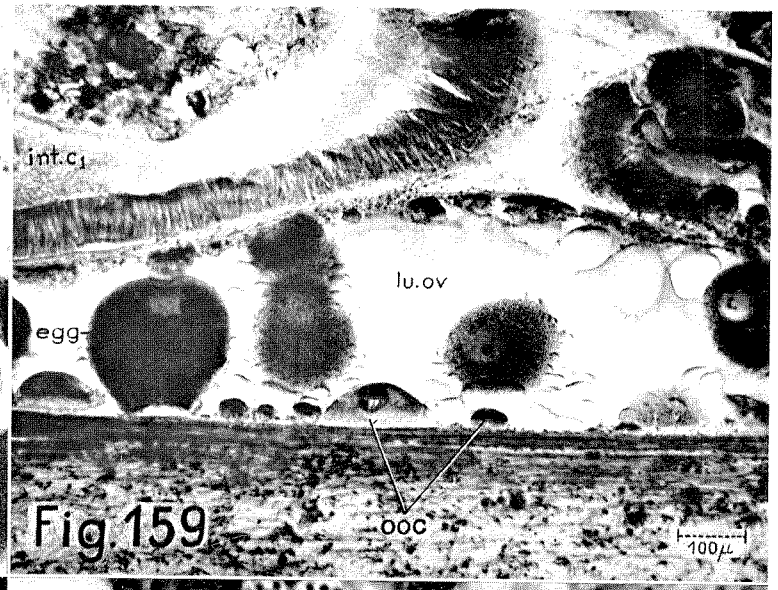


Fig.158
100μ


int.c1
lu.ov
egg
ooc
Fig.159
100μ

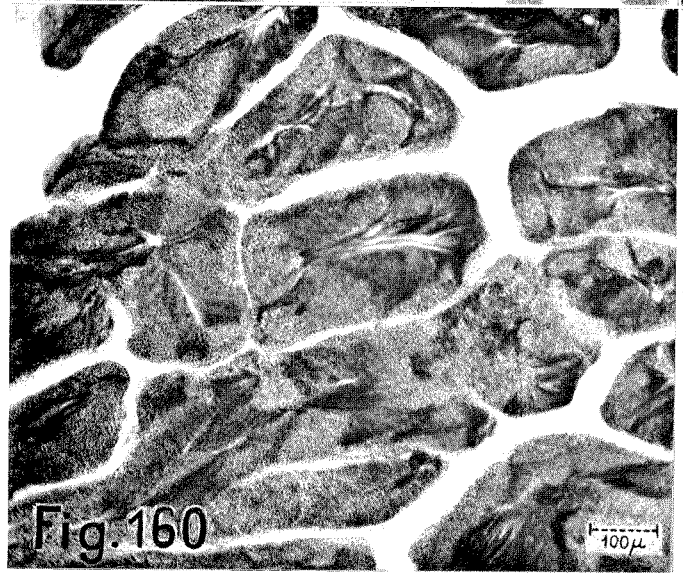


Fig.160
100μ

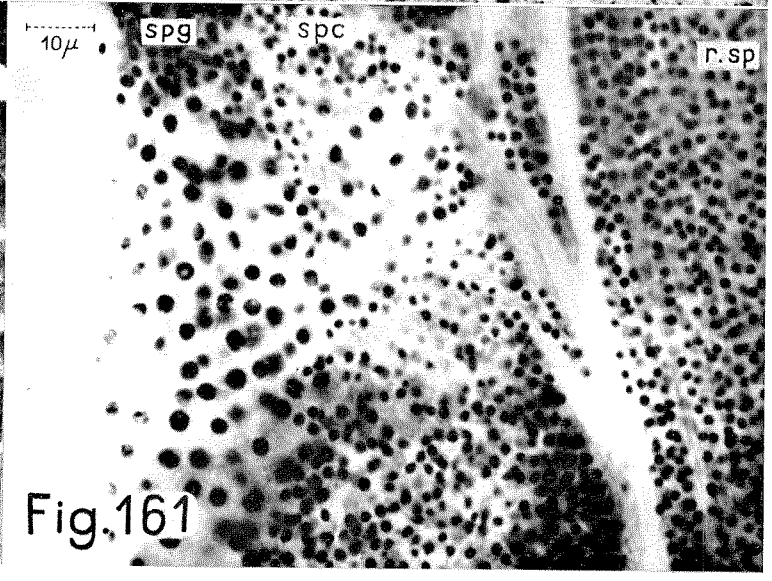

10μ
spg
spc
r.sp
Fig.161

PLATE 53

Fig. 162. Fossil tryblidians. A-D = *Pilina unguis* (Lindström) in ventral, lateral, anterior, and dorsal view. E-F = *Tryblidium reticulatum* Lindström in ventral and dorsal view. G-H = *Archaeophiala antiquissima* (Hisinger), in lateral and ventral view. Drawn after KNIGHT (1941, plate 3 and 4, and 1952, plate 1).

Fig. 163. Diagram of a young *Neopilina* (A), a young gastropod (B), and a *Nautilus*-like cephalopod (C) to show the differences in the orientation of the protoconch.

Fig. 164. Diagram of the gills of chitons (A) and of *Neopilina* (B). The gills are seen from the side, attached to the wall of the pallial groove and reaching down to the foot margin. It appears that the big, ventral lamellae of *Neopilina* correspond to the anterior lamellae of chitons.

m. s = muscle scars
sh. s = "shadow scars"
protc = protoconch

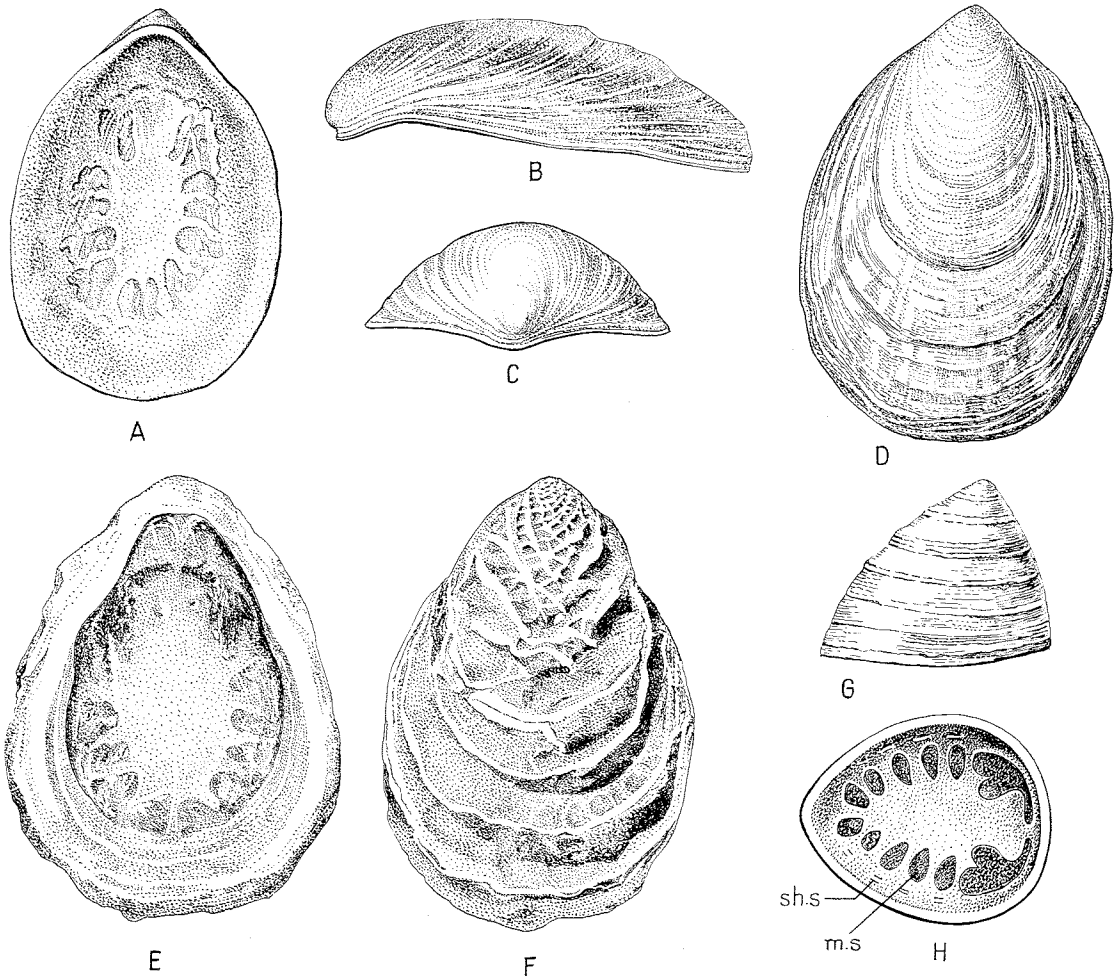


Fig.162

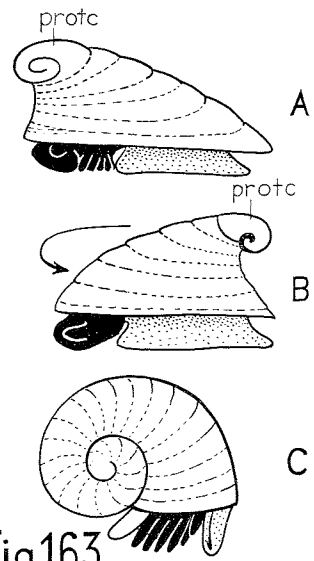


Fig.163

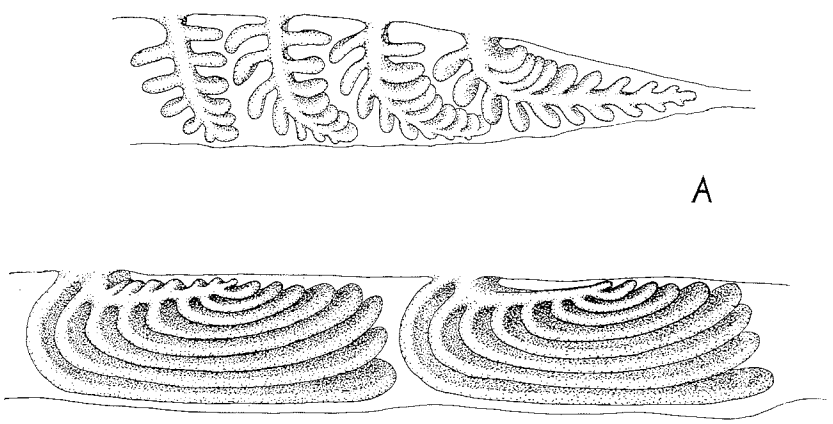


Fig.164

PLATE 54

Fig. 165. Diagram of the relations between the segmented organ systems in *Neopilina*. The gill nerves, the gill vessels, and many smaller muscles are strictly metameric but could not be included in the drawing.

A-H = foot retractor muscles A to H
an = anus
ao = aorta
at_2 = 2nd atrium of heart
ce. co = cerebral commissure
gi_5 = 5th gill
go = gonads
i-p. co = interpedal commissure
la. n. c = lateral nerve cord
lp. co_{10} = 10th latero-pedal connective
m = mouth
ne = nephridia
pe. n. c = pedal nerve cord
pr. te = preoral tentacle
st = statocyst
ve = velum
ve. h = ventricle of heart

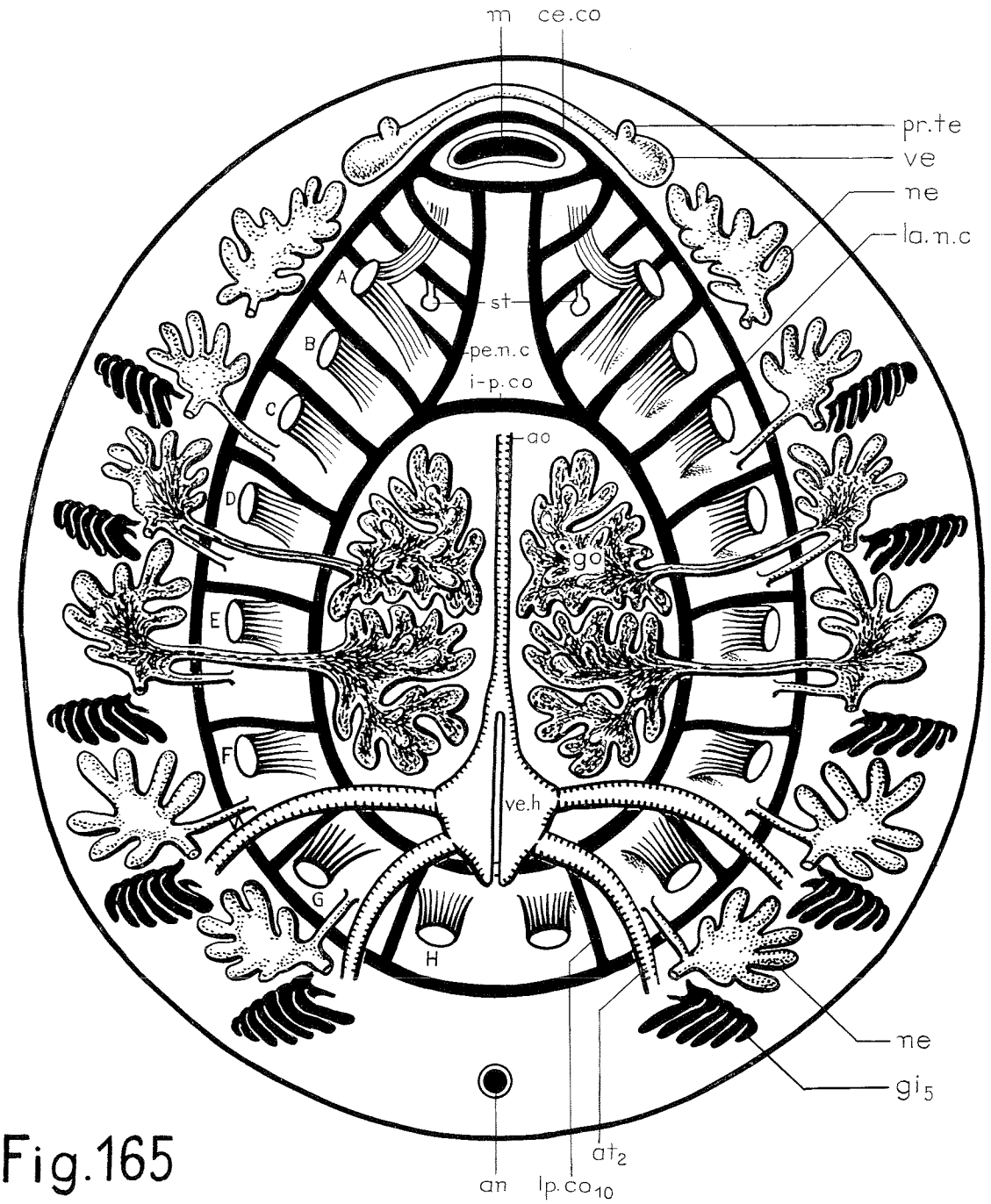

m
ce.co
pr.te
ve
ne
la.m.c
A
st
B
pe.m.c
i-p.co
C
ao
D
go
E
F
ve.h
G
H
ne
gi5
at2
an
lp.co10

Fig.165

PLATE 55

Fig. 166. Diagrammatic cross section through the middle body region of a *Chiton*. Partly after PLATE (1898).

Fig. 167. Diagrammatic cross section through the middle body region of *Neopilina*.

a. pa. s = arterial pallial sinus
ao = aorta
art = articulamentum
ci. i = musculus circularis intermedius
ci. pa = musculus circularis pallii
ci. pe = musculus circularis pedis
do. coe = dorsal coelom
f. m = foot margin
gi = gills
i. ma. f = inner marginal fold
la. n. c = lateral nerve cord
m. l. l = musculus longitudinalis lateralis
m. lp = musculus latero-pedalis
m. mp = musculus medio-pedalis
m. r = musculus rectus (longitudinal)
mi. ma. f = middle marginal fold
na. l = nacreous layer
ne = nephridia
ou. ma. f = outer marginal fold
ov = ovary
pa. m = pallial margin
pe. n. c = pedal nerve cord
per = periostracum
per. bl. s = peri-intestinal blood sinus
per. g = periostracum gland
perc = pericardial diverticula
pr. l = prismatic layer
tem = tegmentum

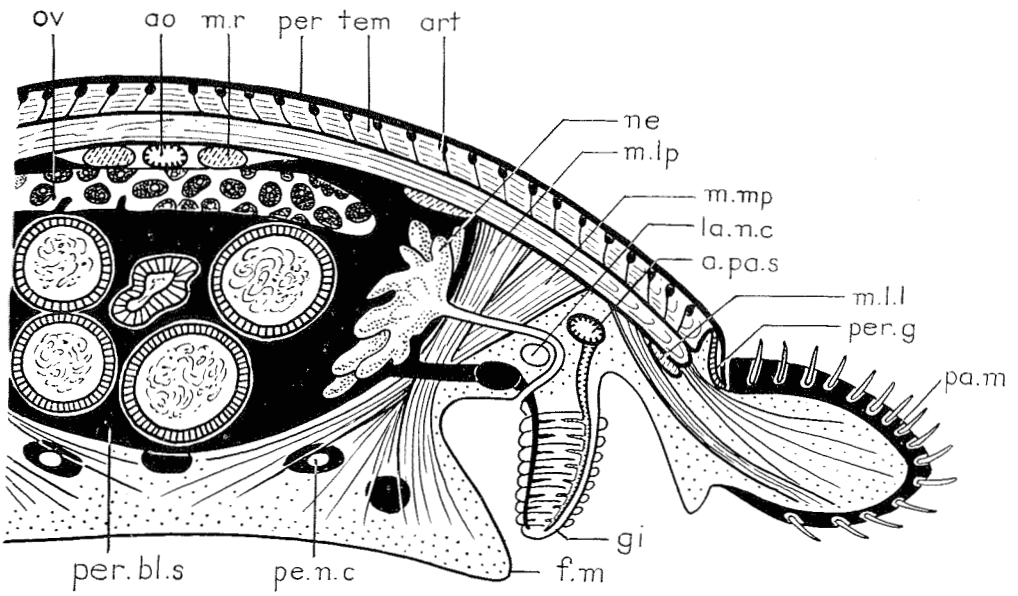


Fig.166

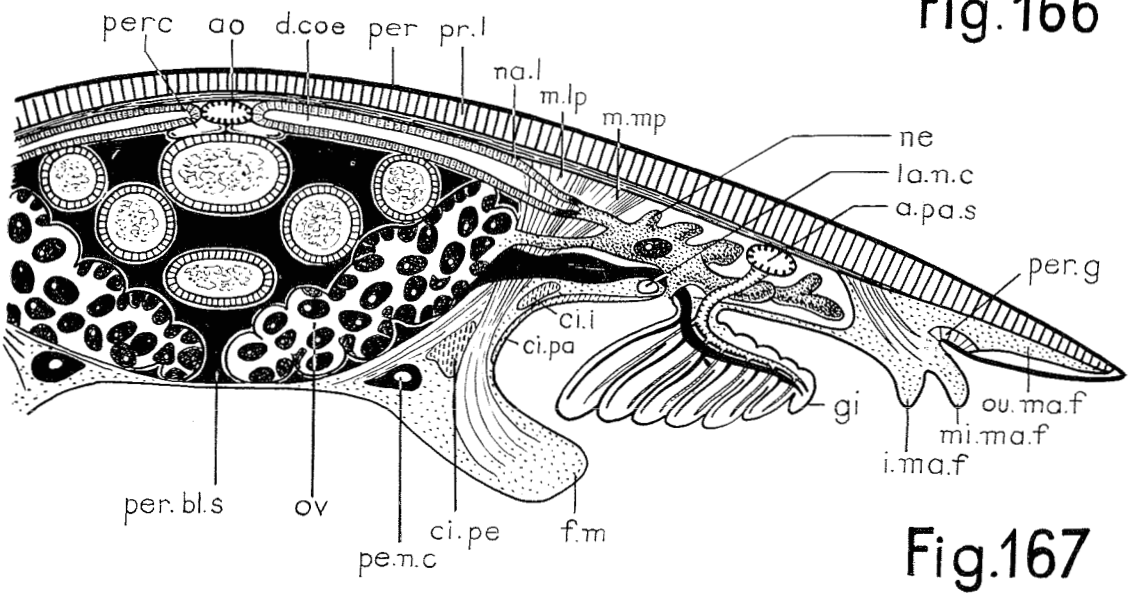


Fig.167

PLATE 56

Fig. 168. Cross section through the first intestinal coil. Radiolarians are common in the contents. Microphotograph. Spec. III.

Fig. 169. Median section through the anterior body region of a polyplacophoran, *Lepidopleurus asellus*. Microphotograph.

ae = aesthetes
ant. l = anterior lip
ce. co = cerebral commissure
f. m = foot margin
m = mouth
m. im. ra = musculus impar radulae
m. pl = mouth plate ("Mundscheibe"), the "velar" part
m. ra. l = musculus radulae longus ("retr'")
pa. m = pallial margin
ph. d = pharynx in the region of the diverticula
ra = radula
ra. ca = radula cartilage
ra. sh = radula sheath (partly damaged)
sal. g = salivary gland
sr. g = subradular ganglion
sr. o = subradular organ
ssc. co = subcerebral commissure

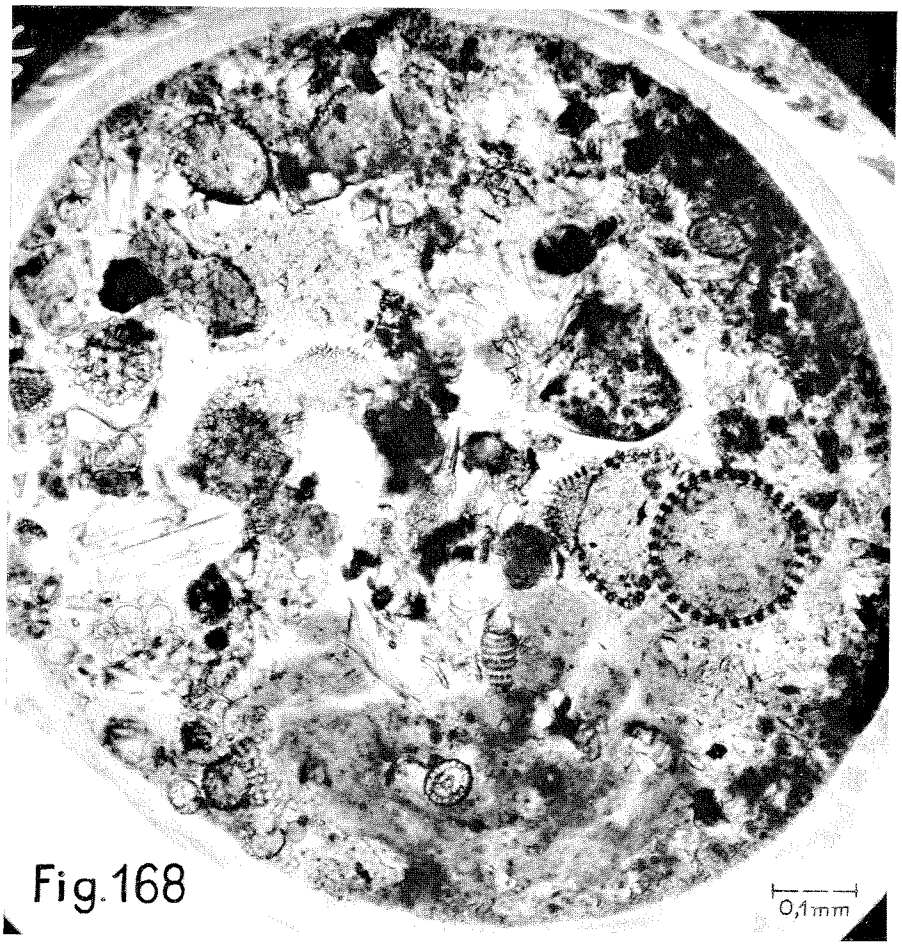


Fig.168

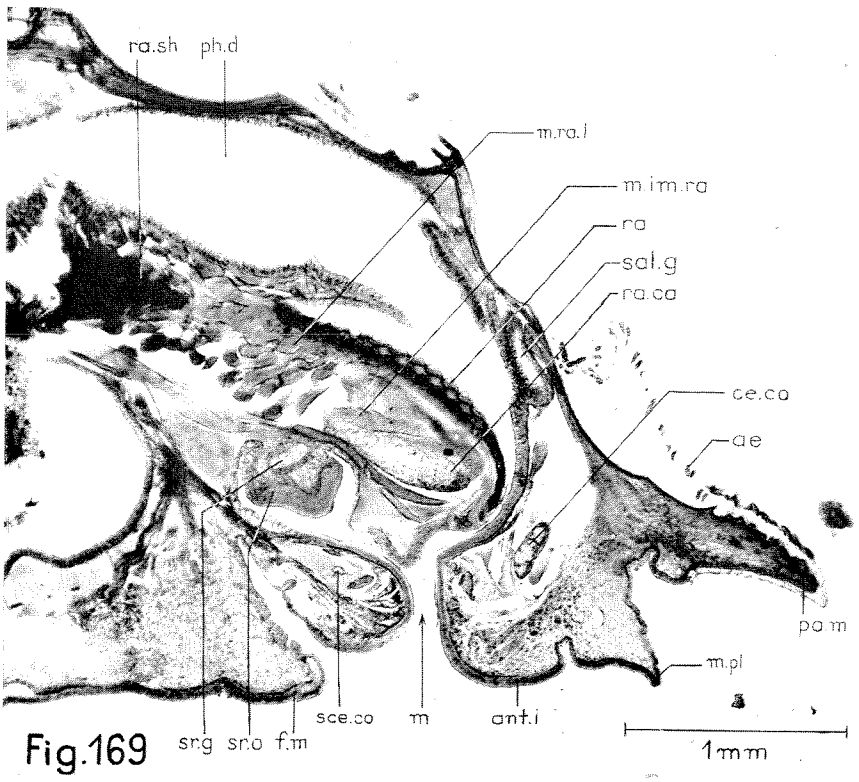


Fig.169

BEMERKUNGEN ZUR SCHALENSTRUKTUR VON *NEOPILINA GALATHEAE*

Von W. J. SCHMIDT
Giessen, Zoologisches Institut der Universität

Der freundlichen Anregung des Herrn Dr. H. LEMCHE, Kopenhagen, folgend, der mir einige Splitter von *Neopilina*-Schalen zugänglich machte, möchte ich im folgenden meine Ergebnisse betreffend deren feinere Struktur mitteilen, um womöglich auch auf diesem Wege einen Beitrag zur näheren Einordnung dieser Form im System der Mollusken zu liefern.

Zur allgemeinen Orientierung sei zunächst das Wesentliche aus den Angaben von LEMCHE (1957) betreffend die *Neopilina*-Schale vorausgeschickt: Sie ist löffelförmig, sehr dünn, zerbrechlich, zerspringt beim Trocknen, hat fast kreisförmigen Umriss ohne Einschnitte oder Unregelmäßigkeiten und mißt bei den größten Stücken 37 mm in der Länge und 35 mm in der Breite. Der Apex liegt vorne, schräg abwärts in die Medianebene hineingekrümmt und steht 8 mm über dem frontalen Rand. Die Schalenaussenfläche zeigt dicht gestellte Wachstumslinien, überkreuzt von 30-50 sehr dünnen dicht stehenden leicht erhabenen Rippen, die vom Apex ausgehen. Etwa jede 5. Wachstumslinie erscheint etwas stärker ausgebildet und erhebt sich ein wenig über die Oberfläche des nachfolgenden Schalenteils. Die geschilderten Strukturen sind in der apicalen Region deutlich, schwinden aber allmählich, je mehr man sich der Schalenperipherie nähert. Die Schaleninnenfläche bietet eine weich ausgebildete Wellung dar, kombiniert mit einem gestreckten Netzwerk.

Ein *Periostracum,* am Apex schwärzlich, auf dem übrigen Teil der Schale hellbraun, bedeckt die ganze Aussenfläche und setzt sich auf der Innenseite im Mantelrand fort bis zur periostracalen Schalendrüse, ungefähr 2 mm vom freien Mantelrand gemessen. Unter dem Periostracum folgt eine wohl ausgebildete Lage von *Kalkprismen;* an diese schließt eine Innenlage aus wenigen äusserst dünnen Lamellen, möglicherweise von *Perlmutter* an.

Neopilina besitzt eine rechts gewundene *Larvenschale* – wie sie für pelagisch lebende Prosobranchier-Larven bezeichnend ist – von ungefähr 0,15 mm Durchmesser mit eineinhalb Windungen; sie geht ziemlich unvermittelt in die adulte Schale über. Nur bei einem der 13 vorliegenden Stücke (10 vollständige Tiere und 3 Schalen) war die larvale Schale vorhanden; jedoch kündeten die Apices der übrigen Schalen durch leichte Vertiefungen an, daß auch sie eine solche trugen.

Die mir vorliegenden Schalenteile der *Neopilina* sind nur wenig gewölbt, zeigen keine deutlichen Rippen und ihr Periostracum ist gelblichbraun, so daß die Fragmente der Peripherie angehören dürften. Abb. 1 a (Taf. 1) gibt ein solches Stück von der Aussenseite mit den scharf hervortretenden Zuwachslinien wieder, Abb. 1 b das gleiche Stück von der Innenseite mit den Wellenzügen parallel dem Schalenrand. Hier und dort finden sich kleinere und größere halbkugelige Erhabenheiten auf der Innenfläche, wohl auf Fremdkörper zu beziehen, die zwischen Mantel und Schale gerieten und in die Schalenmasse eingeschlossen wurden.

Am besten geben Aufschluß über das Schalenrelief Schnittansichten, wie man sie durch Zerbrechen der mürben Schalenstücke erhalten kann, sowohl parallel als auch senkrecht zu den Anwachslinien. Die ersten (Abb. 2 a), aussen und innen eben, halten an den auf die Kante gestellten Schalenstück geradlinigen Verlauf ein, bei gleichbleibender Dicke. Die zweiten (Abb. 2 b) erscheinen unregelmäßig gewellt und zwar ist das Profil aussen etwas schärfer geprägt als innen. An solchen Präparaten sieht man bereits angedeutet die Prismen, am Bruch parallel den Wachstumslinien (Abb. 2 a) wie eine zarte Streifung senkrecht zur Schalenfläche; auf dem Bruch senkrecht zu den Anwachslinien stehen die Prismen zwar auch in jedem kleinsten Bereich senkrecht zur Schalenfläche aber im Großen gesehen pendeln sie entsprechend dem Auf und Ab der Wellen hin und her.

Durch fortschreitendes Zerdrücken kleiner Scha-

lenstücke in Canadabalsam mit dem quer abgestutzten flachen Stielende eines stählernen Skalpells erhält man Gruppen von wenigen zusammenhaftenden Prismen, die in der Richtung senkrecht zur Prismenachse dünner sind als beste Schliffe und daher mehr strukturelle Einzelheiten als solche zutage treten lassen.

Eine solche *Prismengruppe* (Abb. 3a) zeigt zunächst, wie die meisten Prismen durch die ganze Dicke dieser Schicht hindurchreichen, dabei im Wesentlichen den Querdurchmesser einhalten. Jedoch verjüngen sie sich im ältesten, an das Periostracum anschliessenden Viertel ihrer Länge kegelartig und enden abgerundet. Die dadurch zwischen den Prismenköpfen entstehenden Lücken füllen kleinere Prismen, die gleich den anderen abgerundet am Periostracum beginnen, dann aber alsbald spitz auskeilen; Abb. 3a läßt zwischen den beiden mittleren Prismen ein auskeilendes erkennen. Das jüngste Prismenende, das an die innere Schalenschicht anstößt, ist quer abgestutzt, manchmal auch ganz leicht vorgewölbt.

An den Prismen lassen sich zweierlei Strukturen wahrnehmen, *Faserung* und *Wachstumsschichtung*. Die erste geht in dem etwa $^4/_5$ der Gesamtlänge umfassenden unteren Teil der Prismen annähernd ihrer Achse parallel; im äusseren Fünftel dagegen konvergiert die Faserung gegen den Bildungspunkt der Prismen am Periostracum. Die Wachstumslinien zeigen sich am oberen Prismenende scharf ausgeprägt als parallele abwechselnd hellere und dunklere gekrümmte Zonen, die in jedem Prisma konzentrisch zu dessen Bildungspunkt verlaufen, also ihre Konkavität diesem zukehren (Abb. 3b); in benachbarten Prismen korrespondieren sie und künden so das gleichmäßige Wachstum der Schicht an. In den tieferen Anteilen der Prismen verschwindet allmählich die Durchbiegung der Wachstumslinien und sie verfließen zu einer einheitlichen Streifung senkrecht zur Prismenachse.

Die Durchsichtigkeit der Prismen ist in ihrem mittleren Teil am geringsten, weil hier die Schalenmasse von einer Art Körnung durchsetzt ist, die sich den übrigen Strukturen überlagert und wohl auf feinsten Hohlräumen beruht. Diese getrübe Mittelzone leuchtet im Dunkelfeld milchig auf.

Die Struktur der Prismen wird wesentlich erhellt durch ihre Untersuchung im *Polarisationsmikroskop*, die am besten an isolierten vorzunehmen ist, wie sie in den durch Zermalmen von Schalenstücken gewonnenen Präparaten nicht selten sich finden. Die Längsfaserung, jetzt durch unterschiedliche Polarisationsfarben der einzelnen Elemente hervorgehoben, erweist sich als ein Aufbau des Prismas aus *nadeligen*, an ihren beiden Enden zugeschärften Kristallen, die nach dem Bildungspunkt des Prismas konvergieren (Abb. 4); selbst im unteren Teil des Prismas ist manchmal die Konvergenz als eine Art *fiedrige* Anordnung der Elemente an der Oberfläche des Prismas noch kenntlich.

In keiner Stellung löschen die Prismen zwischen gekreuzten Polars aus; jedoch zeigt sich geringste Helligkeit, wenn sie mit ihrer Achse parallel der Schwingungsrichtung des Polarisators oder des Analysators stehen; eine dunkle Mittellinie, wie sie den ähnlich aufgebauten Aragonitprismen von Unioniden zukommt, ist aber in dieser Stellung nicht ausgeprägt.

Beobachtung eines Prismas mit seiner Länge einmal parallel und dann senkrecht zur Schwingungsebene des allein eingeschalteten Polarisators lehrt, daß die Schwingungsrichtung kleinerer Brechzahl längs im Prisma verläuft, also sein Vorzeichen als negativ inbezug auf diese Richtung zu bezeichnen ist. Alsdann ist die Lichtbrechung ein wenig größer als die von Canadabalsam, während das Prisma für das quer zu seiner Länge brechende schwingende Licht bedeutend höheren Brechungsindex als dieses hat; dieses Verhalten spricht für Aragonit.

Am Flachschliff der Schale (Abb. 5a) sieht man die polygonalen meist fünf-bis sechseckigen Querschnitte der Prismen, durch feine Trennungslinien gesondert, und entsprechend den Wachstumslinien in Reihen gestellt; ihre Umrisse erscheinen meist in radialer Richtung gestreckt. Doch wechseln mit Reihen solcher Polygone (Abb. 5c) mehr isometrische ab. Dies hängt mit der Wellung der Schale (vgl. Abb. 2b) zusammen: im Aufblich darauf erscheinen die Prismen in unterschiedlicher perspektivischer Verkürzung.

Zwischen den gewöhnlichen Prismen eingeschaltet und zwar innerhalb der gleichen Reihe oder zwischen benachbarten finden sich andere von viel kleinerem Querschnitt, vereinzelt oder zu mehreren beisammen, die im Vergleich zur Umgebung dunkel sich darbieten (Abb. 5b), sofern der Schliff seine äussere an das Periostracum grenzende Fläche dem Beschauer zukehrt. Dieses Verhalten beruht auf der mehr oder minder vollständigen Reflexion des durchgehenden Lichtes an spitzkegelförmig auslaufenden (»auskeilenden« s. o.) Prismen. Kehrt man den Schliff um, so verschwindet die Dunkelheit der kleinen Prismen.

Vor allem nach dem Anätzen der Schliffe mit

5 %iger Salzsäure macht sich insbesondere zwischen gekreuzten Polars auf dem Prismenquerschnit der Aufbau aus den dicht gefügten kristallinen Elementen bemerkbar, freilich bei weitem nicht so auffallend wie in der Längsansicht der Prismen (Abb. 4). Die Doppelbrechung der Prismen auf dem Flachschliff der Schale ist schwach. Stellt man auf den Bildungspunkt eines Prismas am Periostracum ein, so erscheint ein verwaschenes BERTRAND'-sches Polarisationskreuz von negativem Vorzeichen, wie es für tangentiale Anschnitte eines Sphärokristalls bezeichnend ist. Es ist der Ausdruck der Konvergenz der nadeligen Kristallelemente eines Prismas gegen dessen Bildungspunkt.

Nach vollständigem Entkalken der Prismenschicht (Abb. 5b) hinterbleibt ein wabiges Fachwerk aus organischer Substanz (Conchyolin), das die Gestalt der Prismen wiedergibt; hier und dort springen von seinen Wänden kurze Septen in die Wabenräume vor.

Die *innere Schicht* zeigt sich am Querschnitt (Querbruch der Schale, Abb. 3a) undeutlich lamelliert, aus kleinen plattigen Elementen aufgebaut, die wie zu einem etwas unregelmäßigen Ziegelmauerwerk miteinander verfugt sind. Stücke dieser Schicht (Abb. 6a) lassen in Flächenansicht am Rande die Lamellierung in stufenartigem Abfall erkennen. Unter starker Vergrößerung (Abb. 6c) nimmt man an der Flächenansicht eine Art Punktierung wahr, die auf Grübchen oder Kanälchen zu beziehen ist. Gelingt es, die innere Schicht von der Prismenlage zu trennen, so gewahrt man auf ihrer Haftfläche die Abdrücke der Prismen.

Zwischen gekreuzten Polars bietet die innere Schicht im Flächenbild, bei schwächerer Doppelbrechung als auf dem Querschnitt, eine Zusammensetzung aus größeren und kleineren unregelmäßig zum Teil zackig umrissenen Elementen dar, die unterschiedlich auslöschen (Abb. 6b). Am Querbruch (Abb. 3a) dagegen erfolgt die Auslöschung der inneren Schicht gleichmäßiger und zwar parallel der Lamellierung bei gleichem Vorzeichen (negativ zur Flächennormalen) und gleicher Lichtbrechung wie die Prismenschicht.

Da die Bestimmung des *Aragonit-* oder *Calcitcharakters* des Schalenkalkes weder auf polarisationsoptischem Wege noch an Hand der MEIGEN'-schen Reaktionen (die eher für Calcit zu sprechen schienen) befriedigend gelang, bin ich den Herren Dr. H. MAHL und Diplomphysiker E. KIRSTE bei der Firma CARL ZEISS, Oberkochen, zu großem Dank verpflichtet, daß sie auf meine Anregung an Hand des *Elektronenbeugungsbildes* das Schalenmaterial der *Neopilina* mit Calcit- und Aragonitproben verglichen. Dazu wurden die drei Materialien in einem Achatmöser gepulvert und dem Objektträger trocken aufgerieben. Es ergab sich, daß das Diagramm der *Neopilina*-Schale mit dem von *Aragonit* übereinstimmt (Tafel 2, a und b).

Angesichts der aragonitischen Natur des Schalenkalkes und der sehr viel schwächeren Doppelbrechung der Prismen und der inneren Schicht in Flächenansicht (Doppelbrechung des Aragonits in Richtung der I Mittellinie = 0,004) als am Querschnitt (Doppelbrechung längs der optischen Normale = 0,156, längs der II Mittellinie = 0,152) ist der Schluß berechtigt, daß die I Mittellinie des Aragonits in beiden Schichten senkrecht zur Schalenfläche steht, also annähernd der Länge der nadeligen Elemente der Prismen parallel geht, bzw. auf den plattigen Elementen der inneren Schicht senkrecht steht. Damit ist die *innere Schicht* als *Perlmutter* gesichert: als ein Aggregat tafelig nach der Basis ausgebildeter Aragonitkristalle (sog. Perlmutterblättchen), die unter meist allotriomorpher Begrenzung in einfacher Schicht durch Conchyolin zu den Elementarlamellen der Perlmuttermasse verkittet sind, die ihrerseits in meist großer Zahl übereinander gelegen, durch dünne Conchyolinschichten verbunden werden (W. J. SCHMIDT 1923; 1927) – was auch CH. GRÉGOIRE (1957) an prächtigen elektronenmikroskopischen Bildern dargetan hat. – Das Wesen der Prismenschicht wird unten näher erörtert.

Dem *Periostracum,* im Auflicht gelblich, auf der Aussenseite hier und da mit rotbraunen Flecken (anscheinend von aussen stammende eisenhaltige Fremdsubstanzen – die Schale gibt im ganzen schwache Eisenreaktion mit Ferrocyankalium und Salzsäure! –) haften beim Ablösen von der Kalkschale auf der Innenseite manchmal Reste der Prismenköpfe an, in denen undeutliche negative Polarisationskreuze sich wahrnehmen lassen. Unter stärkeren Vergrößerungen erkennt man am Periostracum eine enge zarte Streifung parallel den Anwachslinien, unterbrochen von hellen radialen Zügen (wohl entsprechend den Rippen der Schale). Stellenweise gewahrt man auch den Wachstumslinien entlang rundliche Abdrücke, viel kleiner als die der Prismen, die vielleicht auf Ausprägung der Stirnflächen der Mantelepithelzellen im Periostracum zu beziehen sind. Auf dem Querbruch bietet das Periostracum schwache Doppelbrechung dar.

Wenden wir uns nun der Frage zu, ob und welche Folgerungen sich aus der Schalenstruktur der *Neo-*

pilina hinsichtlich ihrer systematischen Stellung ziehen lassen. Gemäß der Gesamtorganisation dieses Monoplacophors (s. LEMCHE 1957) liegt es nahe, zunächst einen Vergleich mit der *Schalenplattenstruktur* der *Placophoren* zu versuchen. Bekanntlich finden sich auf dem Rücken der »Käferschnecken« acht hintereinander liegende Schalenstücke, jedes in eine äussere schwach verkalkte Schicht, das Tegmentum, und eine innere stark verkalkte, das Articulamentum, gegliedert. Das Tegmentum wird von schlauchartigen Fortsätzen des Epithels durchdrungen, welche die sog. Ästheten liefern. Es handelt sich also um eine hoch und spezifisch differenzierte Schale, die als ganzes gewiss keinerlei Vergleich mit der *Neopilina*-Schale erlaubt.

Nach HAMMARSTEN & RUNNSTRÖM (1925: *Acanthochiton*), COUVREUR (1929: großer exotischer Chiton) und BØGGILD (1930: Chiton spec., recent) findet sich in Tegmentum und Articulamentum »Gastropodenstruktur« (KESSEL) = »crossed lamellar structure« (BØGGILD). Wie zuletz und besonders eindringend KESSEL (1933 für *Viviparus*) dargelegt hat, sind bei Gastropoden *aragonitische Fibrillen* die letzten Bauelemente der Schale. Sie bilden (zu Balken zusammengefasst), zunächst *Lamellen*, die, mit ihren Flächen aneinandergefügt, senkrecht auf der Schalenfläche stehen, so daß man im Aufblick auf die Schale das sog. »*Bänderbild*« wahrnimmt, d.h. die parallel verlaufenden manchmal verzweigten und dann ineinander verfugten Lamellenscheitel. Auf dem Querschnitt der Schale parallel den Lamellen zeigt sich das »*Gitterbild*«, indem die Fibrillen hintereinander stehender Lamellen von einer zur anderen sich kreuzen; der Querschnitt senkrecht zu den Lamellen aber erscheint als »*Palisadenbild*«, weil die Durchschnitte der auf der Kante stehenden Lamellen säulenartig nebeneinander stehen. Solche Schichten liegen in der Schale zu mehreren übereinander, wobei die Lamellen benachbarter sich rechtwinkelig überschneiden und die Fibrillen sich kontinuierlich durch alle Schichten fortsetzen.

Solche aus Fasern aufgebaute, senkrecht zur Schalenfläche stehende Lamellen mit Kreuzung der Fibrillierung wurden nun von den oben genannten Autoren bei Chitonen nachgewiesen. HAMMARSTEN & RUNNSTRÖM (1925) heben bei *Acanthochiton* hervor, daß die Lamellen des Tegmentum mit denen des Articulamentum sich rechtwinkelig überschneiden, so wie bei den auf einander folgenden Schalenschichten von Gastropoden; BØGGILD (1930 – Taf. VIII, fig. 5) bezeichnet die auffallende *Feinheit* der Lamellen als ein Kennzeichen der Chitoniden. Es besteht also kein Zweifel, daß die Schalenstücke der Placophoren Züge von »crossed lamellar structure« aufweisen.

Bei *Neopilina* jedoch kommt diese typische lamellierte »Struktur« offensichtlich *nicht* vor und es mag also zunächst so scheinen, als ob überhaupt keine Beziehungen der Schalenstruktur von *Neopilina* zu jener der Placophoren bestünden.

Nun hat aber KESSEL (1936; 1950) überzeugend dargetan, daß die Lamellen der »Gastropodenstruktur« *Abwandlungen sphäritischer Anlagen* darstellen. Bei *Buccinum* z. B. besteht die äussere Schalenschicht aus »*gefiederten Prismen*« von polygonalem Querschnitt, deren Fibrillen in die darunter gelegene Schicht – mit typischer Gastropodenstruktur – übertreten und dort in Richtung der Balken weiter laufen. Ähnliche Verhältnisse liegen bei einigen *Turbo*-Arten vor. Schon früher hat KESSEL (1936) darauf hingewiesen, daß in den tieferen Schichten der Schale die »Gastropodenstruktur« sich zunehmend auflockert, bis sie schließlich in eine ausgesprochen sphäritische Bauweise übergeht. Weiter aber ist bekannt (KESSEL 1933), daß bei der Schalenregeneration (von *Viviparus)* statt der typischen Gastropodenstruktur – nachdem zunächst polyedrische Kristalle, Nadelbüschel und Sphärokristalle aufgetreten sind – senkrechte dicht gestellte Säulen entstehen, ähnlich den oben genannten gefiederten Prismen von *Buccinum* und *Turbo;* wie diese bieten sie auf dem Querschnitt Polarisationskreuze dar.

Es geht also die »Gastropodenstruktur« auf einen *sphäritischen Bauplan* zurück. Indem die Kalkfibrillen der gefiederten Prismen fächerartig in eine Ebene (die Plattenebene) auseinanderstreben und sich darin parallelisieren, entstehen die Lamellen, wobei jede derselben einer Reihe von Sphäriten ihren Ursprung verdankt (KESSEL 1950, für *Turbo).*

In die Nähe solcher Vorstufen der »crossed lamellar structure« möchte ich die gefiederten Aragonitprismen der *Neopilina* stellen, obwohl ihre kristallinen Elemente nicht so feinfaserig sind, wie in den von KESSEL beobachteten Fällen. Damit käme in der *Prismenschicht* der *Neopilina* ein weit verbreiteter und vielleicht primitiver Zug im Aufbau der Schale zum Ausdruck, über den die Placophoren bereits hinausgehen. Man darf aber auch nicht vergessen, daß *Neopilina* im Gegensatz zu den Placophoren, die meist in seichtem Wasser vorkommen, eine Tiefseeform ist und im Zusammenhang damit vielleicht eine *Rudimentation* der Schale eintrat und es dann ähnlich wie bei der Regeneration von Gastropodenschalen *nicht mehr* zur Entwicklung der

typischen Lamellenstruktur kommt, sondern das Produkt auf der Stufe der gefiederten Prismen stehen bleibt.

Einen übertriebenen Wert für Aufhellung systematischer Zusammenhänge wird man freilich weder dem Auftreten von gefiederten Prismen noch der »crossed lamellar structure« beilegen dürfen; denn die letzter Struktur findet sich auch bei zahlreichen *Muscheln* (s. z. B. bei BØGGILD 1930) und bei Unionidenperlen sah ich sie aus deren Aragonitprismen hervorgehen (noch unveröffentlicht), während sie in der *Schale* der Najaden unbekannt ist. Es sind also anscheinend für die Entstehung der kreuzstreifigen Lamellenstruktur bestimmte physikochemische Umstände maßgebend – ähnlich wie für das Auftreten von Calcit oder Aragonit (TRUEMAN 1942) – die bei sehr verschiedenen Gruppen gegeben sein können.

Perlmutter findet sich bei Süßwasser- und Meereslamellibranchiern, Gastropoden (z. B. *Turbo*, *Trochus)*, Cephalopoden (*Nautilus*, *Spirula*, vgl. AHRBERG 1935), ohne daß für diese Gruppen bezeichnende Unterschiede ihrer Struktur aufgewiesen werden könnten. Immerhin verweist das Vorkommen von Perlmutter die *Neopilina*-Schale eher zu Gastropoden als zu Placophoren, denen diese Schalenmasse fehlt.

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Erklärung der Abbildungen auf Tafel 1: *Neopilina*-Schale.

Abb. 1. Stück aus dem peripherischen Teil der Schale, 10 : 1. a) von aussen gesehen: scharf ausgeprägte Wachstumslinien, b) dasselbe Stück von innen gesehen: weiche Wellung.

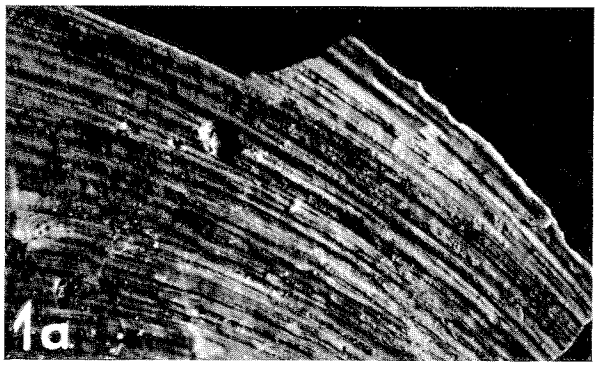
Abb. 2. Bruchkante einer Schale im Auflicht, a) parallel, b) senkrecht zu den Anwachslinien, 10 : 1.

Abb. 3. Querbruchpräparat der Schale, a) oben die Prismenschicht, unten die Innen-(Perlmutter-)lage; b) oberer Teil der Prismen mit konzentrischer Wachstumsstreifung, 450 : 1.

Abb. 4. Drei isolierte Prismen, Pol. +, 380 : 1.

Abb. 5. Prismenschicht in Flächenansicht, a) Totalpräparat etwas angeätzt, 150: 1; Aussenfläche nach oben: die auskeilenden Prismen dunkel; b) Schliff, Pol. ×, 380: 1; Struktur der Prismen; c) Totalpräparat von innen gesehen, 150: 1; Abhängigkeit des Prismenumrisses von der Wellung der Schale; d) Totalpräparat der entkalkten Schale, 150: 1; interprismatisches Fachwerk aus organischer Substanz, 150 : 1.

Abb. 6. Innen-(Perlmutter-)lage der Schale in Flächenansicht, a) gewöhnliches Licht, b) Pol. ×, 370 : 1; c) Kanälchen der Innenlage im optischen Schnitt (punktartig) 830 : 1.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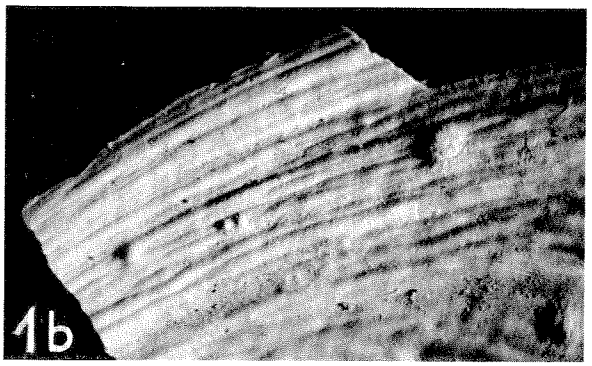
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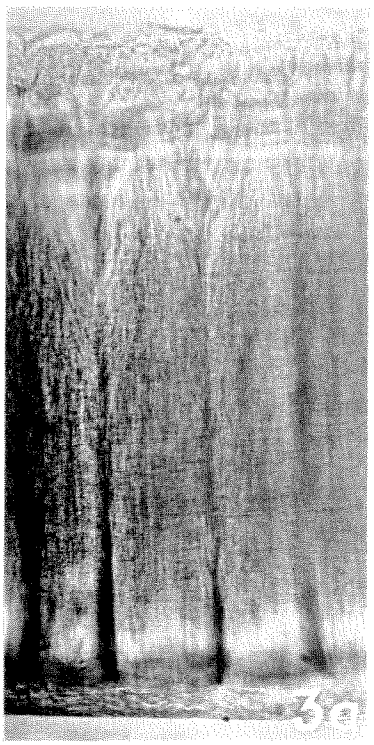
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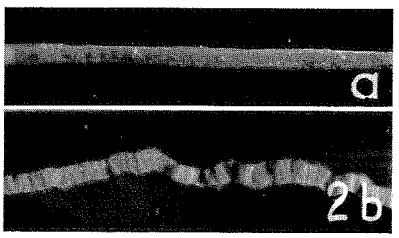
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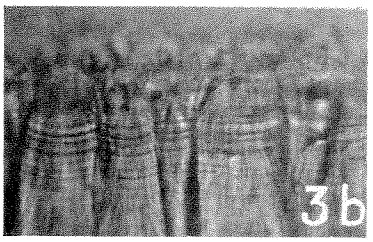
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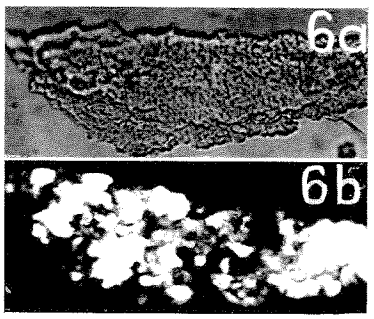
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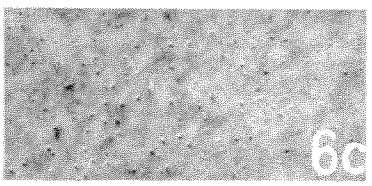
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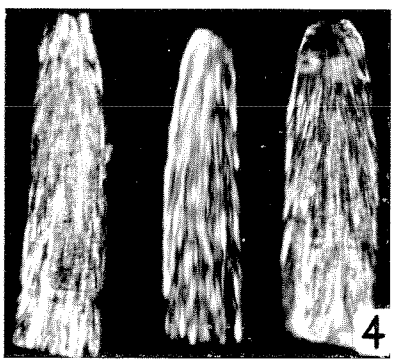
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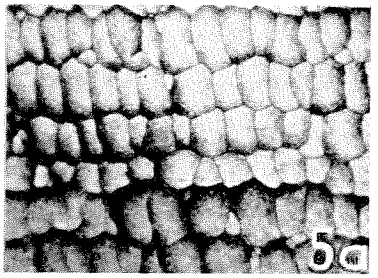
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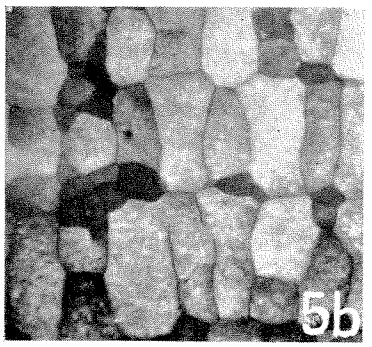
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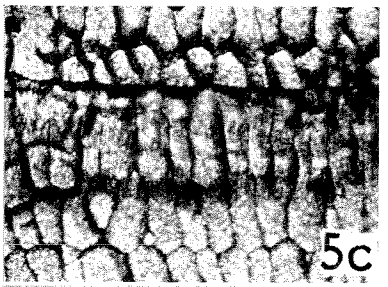
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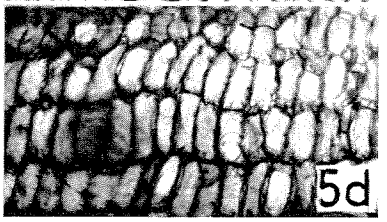
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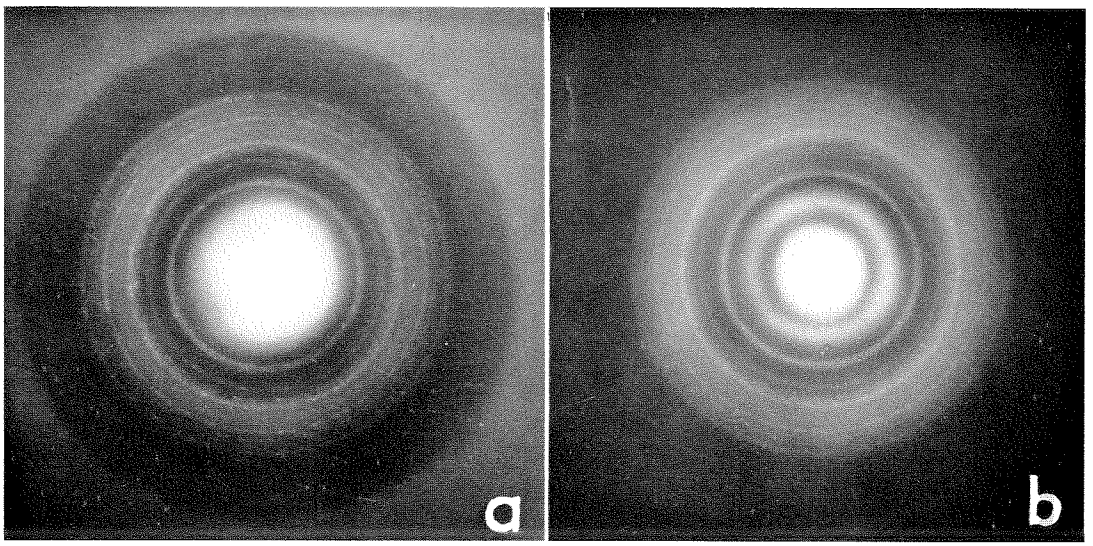

Tafel 2. Elektronenbeugungsdiagramme a) von der *Neopilina*-Schale, b) von Aragonit: Übereinstimmung der Ringdurchmesser.

THE EYES OF *IPNOPS MURRAYI* GÜNTHER, 1878

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INTRODUCTION

According to the literature *Ipnops* is the only vertebrate in which both the eyes and the optic nerves are completely missing. The present investigation has however shown, beyond doubt, that the peculiar organs on the head of *Ipnops*, which are generally held to be phosphorescent organs, are in reality modified eyes.

Like REGAN (1911), PARR (1928) places the genus *Ipnops* in the family Sudidae (Ordo Iniomi), by PARR divided into 4 subfamilies: Chlorophthalmini, Notosudini, Bathypterini and Paralepidini. Bathypterini, which is characterized i. a. by having very small eyes or no eyes at all, comprises the genera *Benthosaurus* GOODE and BEAN, 1886, *Bathypterois* GÜNTHER, 1878, *Bathymicrops* KOEFOED, 1927, and *Ipnops* GÜNTHER, 1878. PARR writes about Sudidae that "... in the series: *Chlorophthalmus – Bathysauropsis – Benthosaurus – Bathypterois – Ipnops* we recognize a continuous series of differentiations characterized by a gradual reduction of the eyes, depression of the head and elongation of the tail." BERG's classification of the iniomous fishes is in accordance with that of PARR (BERG 1940).

PREVIOUS INVESTIGATIONS

The first specimens of *Ipnops (I. murrayi)* were caught by the "Challenger"-Expedition, and from the very beginning much uncertainty has prevailed as to the function of the peculiar cephalic organs. In his description of the genus GÜNTHER (1878) writes among other things: "Head depressed, with broad, long, spatulate snout, the whole upper surface of which is occupied by a most peculiar organ of vision (or luminosity), longitudinally divided into two symmetrical halves." Later on the same author (GÜNTHER 1880) writes about the same organs: "The eye seems to have lost its function of vision and assumed that of producing light." In 1885 GÜNTHER described the cephalic organs of *Ipnops* as modified eyes and in the same place there is a description of the eyes by MOSELEY (pp. 239-240); according by MOSELEY each eye is covered by a transparent membrane, most likely representing the cornea. Under the membrane and separated from this by a shallow chamber filled with liquid, is the retina, which solely contains rods. Between the rods and the chamber is a very thin layer of nerve fibres. The chorioidea is subdivided into hexagonal areas which are concave towards the eye, and the rods seem to be aggregated in corresponding bundles, the rods resting on the concave inside of the hexagonal areas. About the function of the organ MOSELEY writes: "It is not improbable that these curious expansions of the recipient surface of the eye and its retina are a device for detecting the presence of very small quantities of light, at the expense of all apparatus for forming an image." Later, however, MOSELEY forms the opinion that the organs must be regarded as phosphorescent organs, and that any trace of eyes and optic nerves is missing (Appendix A in GÜNTHER 1887), and as this opinion is prevailing in most of the recent literature, MOSELEY's paper will be briefly recorded.

The symmetrical organs extend from an area a little behind the nasal capsules to an area dorsally of the hindmost part of the brain, and are situated in a pair of oblong cavities dorsally of the cranial cavity; the cavities are separated by a median septum, in front consisting of hyaline cartilage (a median crista on the cartilaginous plate which is situated in the roof of the mouth; cf. GÜNTHER 1887, pl. LXVIII) which is dorsally completed by connective tissue. According to MOSELEY the organs are covered by the dorsal cranial wall, which,

corresponding to the deepest part of the cavities, has a pair of convex cornea-like prominences, while the cranial wall in front and laterally of these is flat and provided with concentric striae (cf. text-fig. 1). Where the cranial wall covers the organs it is very thin and completely transparent. On the medial part of the organs a closed canal is situated. It contains partly a mucous canal, partly a nerve running to the nasal capsule, according to MOSELEY probably the nasal branch of the fifth cranial nerve. Corresponding to the anterior part of the brain the canal slants laterally. MOSELEY is of the opinion that the deepest part of the cavities, which is in the centre of the organ, corresponds to the place where previously the orbits were situated, just as the median septum should correspond to the interorbital septum. Seen from the dorsal side in reflected light the organs seem to be composed of a mosaic of light, hexagonal areas, each being about 40 microns in diameter.

Histologically the organs are of a quite uniform structure in their whole extent (cf. text-fig. 2); they are said to consist of hexagonal columns resting on a pigmented layer of connective tissue. Each hexagonal column, which is about 40 microns high, is composed of 30-40 transparent, hexagonal rods, the bases of which rest on the concave inside of a large, bowl-shaped hexagonal pigment cell containing a clearly marked nucleus. Distally each rod carries a hexagonal, nucleated cell. A few of the transparent rods, the longitudinal axis of which is at right angles to the surface of the organ, contain, according to MOSELEY, a small nucleus near the basis. The hexagonal columns are entangled in a reticulum of pigmented strings, the ramifications of which also traverse in between the rods. Furthermore, the organs contain capillaries. The hexagonal columns correspond to the light, hexagonal areas which are seen on the intact animal in reflected light. Moreover, MOSELEY states that both the pigmented reticulum and the capillaries can be seen on the intact animal in transparent light (optic section). Under the organs there is connective tissue with pigment cells, blood-vessels, and nerves. The organs get ample blood supply through a pair of vertical branches from the carotids.

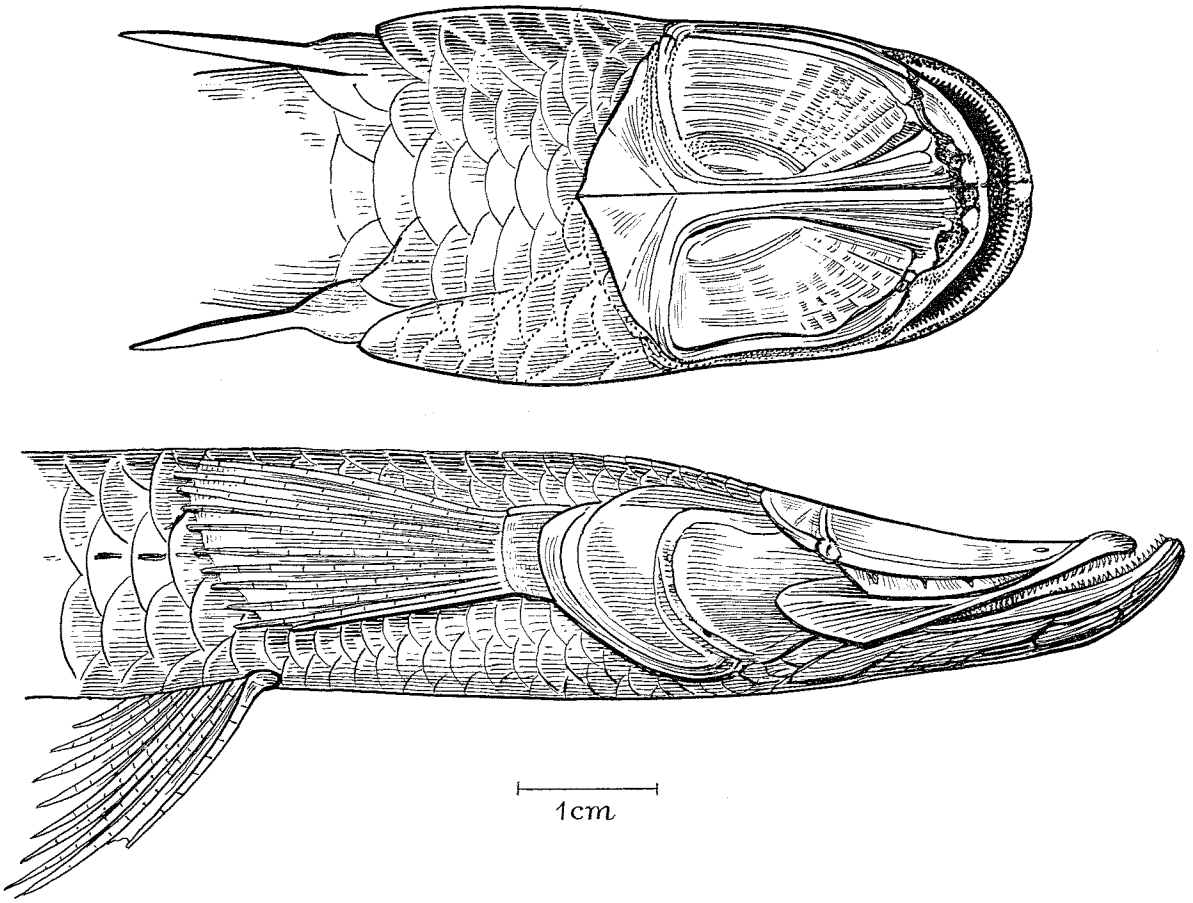
MOSELEY states that he has traced nerve fibres from the layer of connective tissue under the organ to the area with the pigmented hexagonal cells, but that it has been impossible to ascertain any actual connection between the nerve fibres and the elements of the organ. According to MOSELEY the nerve fibres no doubt originate from the fifth cranial nerve. MOSELEY concludes: "The phosphorescent organs can hardly be sense-organs, since they appear to be supplied with no special nerves but only by ordinary nerves. They are certainly not modified eyes. The richness of their blood supply is in favour of their being phosphorescent organs, as is also the extreme transparency of the portion of the roof of the skull covering them." He supposes that the phosphorescent organs in *Ipnops* are homologous with the phosphorescent organs on the head of other Scopelidae, being formed by fusion of their supranasal and subocular phosphorescent organs on either side of the head, resulting in complete obliteration of the eyes (by GÜNTHER *Ipnops* was placed in the family Scopelidae, cf. GÜNTHER 1878, 1880, and 1887). As in the Scopelidae the organs are internally delimited by pigmented connective tissue made of the corium.

Apparently, no later histological examination of the cephalic organs of *Ipnops* has been made, and MOSELEY's view is adopted in most of the later literature (e. g. GOODE and BEAN 1895, GOODRICH 1909, REGAN 1911, BARNARD 1925, PARR 1928, NORMAN 1939, WALLS 1942, FOWLER 1943, MARSHALL 1954, THINES 1955, and BERTIN 1958). Certain authors, however, have regarded the organs as eyes (JORDAN and EVERMANN 1896, JORDAN 1925). For the sake of completeness it ought to be mentioned that two authors have held the opinion that the organs function both as visual organs and as phosphorescent organs. Thus AGASSIZ (1888) writes about the modifications of the eyes of deep sea fishes: "In some cases the eyes have not been specially modified, but in others there have been modifications on the one hand to phosphorescent organs more or less specialized, or on the other to such remarkable structures as the eyes of *Ipnops*, intermediate between true eyes and specialized phosphorescent plates." GARMAN (1899) expresses a similar opinion: "Eyes (of *I. agassizii)* excessively differentiated, as visual organs, reflectors, and flash lights, occupying nearly half of the top of the head...".

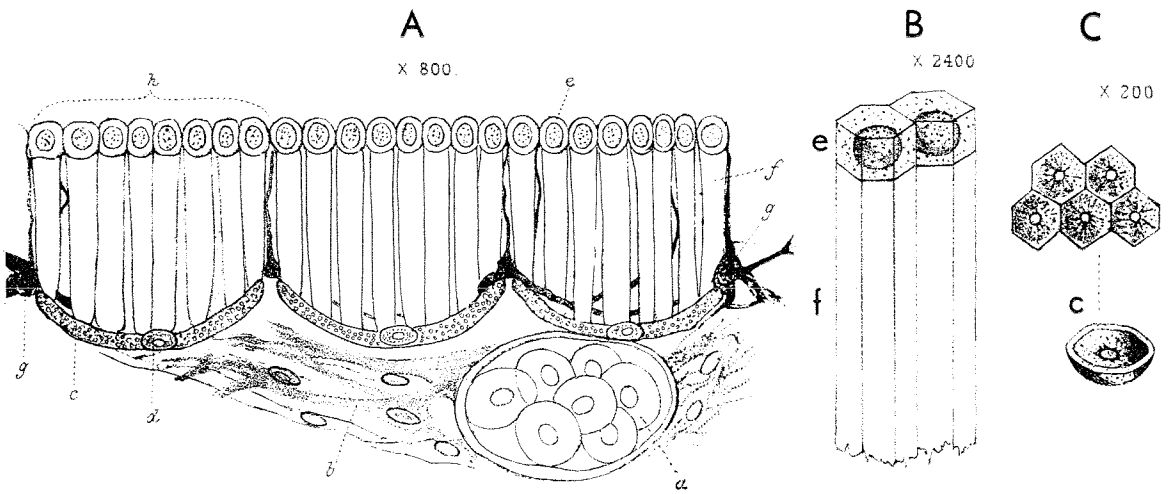
THE PRESENT INVESTIGATION

Material and Methods. Dr. A. F. BRUUN, of the Zoological Museum of Copenhagen, has been so kind as to place 3 specimens of *I. murrayi* GÜNTHER, 1878 from the collection of the "Galathea"-Expedition at the present author's disposal. The length of the fishes was about 9 cm. One specimen was fixed in Bouin's fluid; the head was embedded in paraffin, cut into 8 micron sections (transverse sections) and stained with hematoxylin-eosin. The two other specimens were fixed in formalin; the head of one of those was embedded in celloidin, cut into 50 micron sections (transverse sections) and stained with the phosphotungstic acid hematoxylin of MALLORY, while the other specimen was stained with alizarin.

The investigation clearly showed that the cephalic organs of *Ipnops* are modified eyes, the structure of which in the main is in accordance with MOSELEY's first description (MOSELEY in GÜNTHER 1885). This result follows partly from the fact that positively

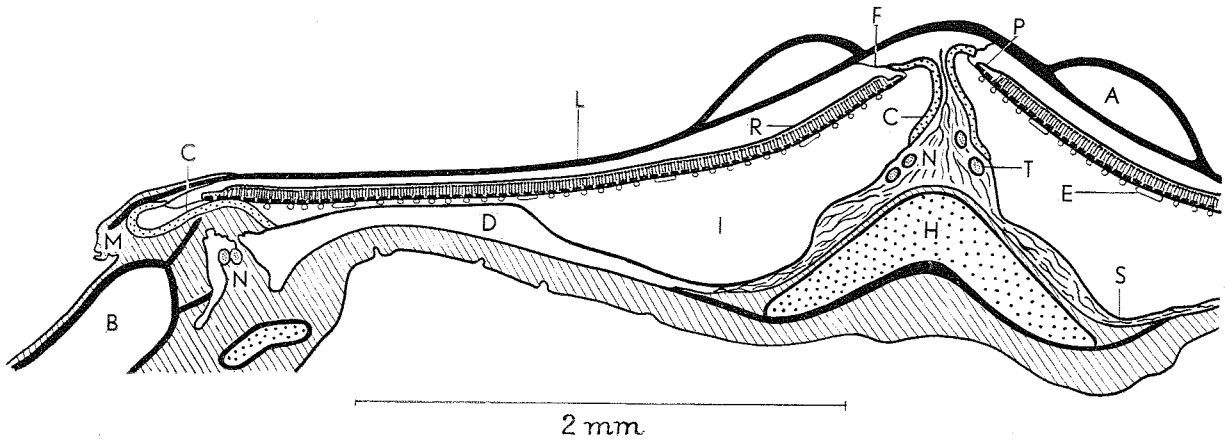


Text figure 1. Dorsal and lateral view of the head of *Ipnops murrayi*. Re-drawn from fig. 97, p. 239 in GÜNTHER 1885.



Text figure 2. The histological structure of the cephalic organs of *Ipnops murrayi*, as regarded by MOSELEY (from GÜNTHER 1887, pl. LXVIII, fig. 6, 7 and 10; H. N. MOSELEY del.). Fig. 2A shows a transverse section of the organ, fig. 2B shows the rods highly magnified, and fig. 2C shows the pigment cells. The letters on fig. 2B and C are added by the present author.

a: erythrocytes
b: pigment cell in the connective tissue under the organ
c: hexagonal pigment cell
d: nucleus of hexagonal pigment cell
e: hexagonal, nucleated cell
f: hexagonal rod
g: pigmented strings
h: a group of rods forming together a hexagonal column



Text figure 3. Diagram based on a photo showing a transverse section of the head of *Ipnops murrayi*, corresponding to the foremost half of the eyes (cf. pl. 1, fig. 2).

A: supraorbital canal
B: infraorbital canal
C: the sclera (cartilaginous part)
D: subbulbar fissure
E: choriocapillaris
F: peripheral part of scleral cornea (?)
H: hyalin cartilage
I: intraocular blood sinus
L: transparent membrane (the frontals ?)
M: lateral edge of transparent membrane
N: nerve(s)
P: pars coeca retinae
R: pars optica retinae
S: sclera (fibrous part)
T: olfactory tract

identified optic nerves, running to the organs, are present, partly from the structure of the organs, which have a retina with typical rods. The lense and its suspensory apparatus (including the retractor muscle) is missing. The iris (in the shape of a transverse diaphragm) is missing. The eyes are flattened and directed upwards. Since the optic nerves and the retina are of decisive importance for the understanding of the function of the organs, they will be dealt with first in the following.

The Optic Nerves. The papilla of the optic nerve (pl. 2, fig. 1) is situated a little behind and somewhat medially to the centre of the eyes The optic nerve is directed medio-caudally and perforates the sclera medially to the papilla of the optic nerve, so that a greater part than usual of the optic nerve is situated in the chorioidea. After the perforation of the sclera the direction of the two optic nerves is medio-caudal and dorsal, till they meet in the median plane, and for the rest of their course to shortly before the entrance into the mesencephalon they lie in contact with each other. The two optic nerves run parallel caudally, and in the chiasma, which is situated ventrally to the olfactory tracts, one of the optic nerves crosses the other (pl. 1, fig. 3-4). In the one specimen the left optic nerve, in the other the right optic nerve was lying on the top of the other in the chiasma. The optic tracts can be followed to the tectum opticum.

The Retina. The eyes of *Ipnops* may quite hypothetically be derived from typical laterally situated eyes by a turn of the bulbus of about 90°, so that the anatomical axis has been directed dorsally, while at the same time it must be imagined that the curvature of the retina has been straightened out and the iris reduced (text-fig. 3. Pl. 1, fig. 1-2). How the ontogenetic development really takes place is of course impossible to decide on the basis of the present material. Yet it seems reasonable to suppose that the region around the papilla of the optic nerve of *Ipnops* corresponds to the fundus.

According to BRAUER (1908) the retina of deep sea fishes is characterized partly by the lack of cones, partly by the fact that the pigment is in constant dark position; the processes of the cells of the pigment epithelium have been retracted into the cell body and cannot be re-formed. As regards these two features the retina of *Ipnops* makes no exception.

It is possible to distinguish between a pars optica and a pars coeca retinae. The latter is very narrow. The thickness of the retina in the anterior and posterior parts of the eye is about 35 microns, gradually tapering towards the ora terminalis retinae. In the central part of the retina the thickness is about 45 microns, and the thickness only diminishes close to the ora terminalis. Hyaloid vessels are not to be found.

The Pigment Epithelium. The cells are low, with-

out processes (pl. 2, fig. 1-4). Pigment is only to be found in the outer part of the cell (i. e. towards the chorioidea) where also the nucleus is placed (pl. 2, fig. 2 and 3). The outer part of the cell is frequently convex (pl. 2, fig. 3-4) and since only this part is pigmented, the pigment of each cell stands out as a crescent-shaped figure in the sections. No doubt these correspond to the bowl-shaped, hexagonal pigment cells, described by MOSELEY. According to MOSELEY the hexagonal rods rest on the inside of the bowl-shaped pigment cells. However, the pigment cells are not bowl-shaped, and the rods do not reach farther out than to the inner, unpigmented part of the cells. Now and then fragments of the rods are seen in the pigment cells, but this is obviously an artefact (pl. 2, fig. 3-4). The convex form of the outer part of the pigment cells, however, seems to be an artefact too. In the specimen fixed in Bouin the convex form was most frequently found in the fundus, where the bulbus is deepest. In the peripheral regions of the retina the outer part of the cells is plane (pl. 2, fig. 2). In the specimen fixed in formalin the pigment of all the cells in the pigment epithelium stands out as crescent-shaped figures, and the unpigmented part of the cells cannot be seen at all or only with difficulty. Supposing that MOSELEY had only a specimen fixed in formalin at his disposal, this may be the reason why he did not notice the inner, unpigmented part of the pigment cells. Thus the convex form of the outer part of the cells is probably due to a shrinking of the entire retina. In the specimen fixed in Bouin's fluid the shrinking is less marked; it is more pronounced in the fundus, the deeper part of the bulbus, as might be expected.

Thus the pigment cells are certainly not bowl-shaped, pigmented connective tissue cells, as described by MOSELEY, but retinal pigment epithelium cells without processes.

The retina s. str. contains only rods that are not hexagonal (pl. 2, fig. 1-4). Not the slightest trace of the hexagonal columns described by MOSELEY is to be found. The pigmented reticulum which, according to MOSELEY, is found in the layer of rods is an artefact.

The outer segments of the rods show the cross-lamination which is characteristic of visual cells. The inner segment is very short and contains no ellipsoid. The outer nuclear layer contains only a single layer of nuclei. In his first description (in GÜNTHER 1885), MOSELEY states that the retina ". . . is composed of a layer of remarkably long rods". The length of the visual cells in the eyes of teleosts is, as a rule, between 60 and 80 microns (ROCHON-DUVIGNEAUD 1943). DETWILER (1943) states that the length of the rods in the light-adapted eye of *Ameiurus* is 92-93 microns, in the dark-adapted eye 33,8 micron. BRAUER's survey of the length of the rods of some deep sea fishes (BRAUER 1908, p. 222) comprises several species the rods of which have about the same small length as those of *Ipnops*.

Immediately inside the outer nuclear layer there is a layer consisting of nerve fibres. The layers of nuclei, the inner nuclear layer and the ganglion cell layer, which are normally found inside the outer nuclear layer, are apparently lacking in *Ipnops*. However, some scattered nuclei are to be found inside the outer nuclear layer; they can be distinguished from the nuclei of the rods partly by their position, partly by means of their greater nuclear diameter. The nuclei of the rods are oval; the nuclei which are situated inside the outer nuclear layer possibly comprise three different nuclear types, two of which are shown on pl. 2, fig. 3 (X and Y). One of these (X) is almost spherical, the other type (Y) is oval. It is possible, however, that these two nuclear types represent a transverse section (X) and a longitudinal section (Y) of the same oval nuclear type, partly because the diameter of the spherical type corresponds to the width of the oval type, partly because the chromatin granules show the same arrangement in the two nuclear types. Besides these two (?) types, there is an oval nuclear type which is more flattened than type Y. The number of the nuclei, which certainly do not belong to the rods, is of the magnitude of 5-6000 in each retina. The number of optic fibres is about 500 (538 axons were counted in the right optic nerve, 496 axons in the left optic nerve in the specimen fixed in Bouin's fluid). None of the above mentioned nuclear types exists in a number corresponding to the number of nerve fibres in the optic nerves. The count, however, clearly shows that other cells than ganglion cells exist inside the outer nuclear layer, but neither these nor the ganglion cells can be identified. Yet it seems reasonable that the nerve fibres of the optic nerves represent the third neuron of the visual pathway, as in other vertebrates.

The membrana limitans externa could not be established conclusively. The membrana limitans interna exists. The falciform process is missing.

The thickness of the retina showe greater variation among the bony fishes than within other groups of vertebrates, from less than 100 to more than 500 microns (WALLS 1942). Its small thickness in *Ipnops*

(35-45 microns) is of course partly due to the shortness of the rods and partly to the reduction of the layers inside the outer nuclear layer. The number of rods in each retina is of the magnitude of 250000. Consequently, there is a very considerable summation (about 500 rods per optic nerve fibre). The total number of rods per retina is amazingly small compared with the numbers given by BRAUER (1908, p. 222). According to BRAUER the number of rods *per sq. mm* ranges from 115600 *(Cyclothone microdon)* to 20 millions *(Macrurus pumiliceps)* in the species examined by him. BRAUER calls attention to the fact that the numbers are not accurate, the varying thicknesses of the sections and the varying diameters of the nuclei not having been taken into account; nevertheless there are considerably more rods than in *Ipnops*.

The pars coeca retinae is quite narrow, 25-30 microns, and consists of two layers of cells in which only the cells belonging to the outer layer are pigmented. Unlike the pigment epithelium cells in the pars optica the whole cell body is pigmented. In some sections only one cell is seen in the outer layer. An accurate description of the morphology of these cells, however, cannot be given, as the cell limits are not visible on account of the pigment. The inner layer of cells consists of low, unpigmented cells. Evidently, no epithelial muscle cells exist in the pars coeca.

The pars coeca retinae is connected with the inside of the scleral cartilage near the upper edge of this by means of connective tissue cells in the inner layer of the chorioidea.

The Chorioidea. Immediately outside the retinal pigment epithelium the choriocapillaris follows, which consists of relatively few, rather wide capillaries (pl. 2, fig. 1-2). In this inner layer of the chorioidea there are locally many pigmented cells. The rest of the chorioidea is constituted by a very large, blood-filled sinus (text-fig. 3. Pl. 1, fig. 2) the extent of which corresponds to that of the retina, and which has its greatest depth in the region of the fundus. The argentea is missing. The corpus vasculari chorioideae is missing. As it is now and then claimed in the literature that the corpus vasculari is only to be found in species with pseudobranchs (e.g. WALLS 1942), it should be pointed out that *Ipnops* lacks pseudobranchs. There is no tensor chorioideae. WALLS (1942) maintains that this muscle is found only in fishes which are able to accomodate.

The Sclera. Corresponding to the peripheral parts of the eye the sclera consists of cartilage, while the remaining part is fibrous and very thin (text-fig. 3. Pl. 1, fig. 2-3), thus agreeing with the structure of the sclera of most other bony fishes, in which the sclerotic coat as a rule is fibrous and thin in the fundus, while in the anterior segment of the eye it is cartilaginous to a greater or smaller extent; in most of the species this cartilage forms an unbroken cartilaginous ring in the anterior segment of the eye. No ossicles have been found in the sclera of Ipnops. The cartilage of the sclera is connected with the transparent membrane that covers the eyes by means of a thin, fibrous membrane, which unites with the inside of the transparent membrane. Most likely this fibrous membrane represents the peripheral part of the scleral cornea (text-fig. 3. Pl. 1, fig. 2).

Under the lateral part of the sclera a subbulbar fissure is seen in the sections (text-fig. 3. Pl. 1, fig. 2). Below the anterior and the posterior part of the eye it is quite narrow and situated under the scleral cartilage, while below the central part of the eye its extent fairly corresponds to the breadth of the lateral half of the eye. As regards position this cavity corresponds to the lower of the two retrobulbar sinuses found in many bony fishes.

The transparent membrane (text-fig. 3. Pl. 1, figs. 1-2) which covers the eyes lies in the corium and appears in the sections as a uniform, non-cellular lamina. The membrane is unpaired and in extention slightly greater than that of the bulbus. The specimen stained with alizarin shows that the membrane consists of lamelliform bone. Corresponding to the hindmost part of the eyes, the membrane is on the inside provided with a short, low, median bony crista. The cornea-like prominences and the concentric striae described by MOSELEY (cf. text-fig. 1) were not found in any of the specimens which the present author had at his disposal; probably they are artefacts.

The two canals on the transparent membrane, one on either side of the median line, contain partly a nerve, partly lateral line organs; no doubt they are supraorbital canals. Under the lateral edge of the transparent membrane there is on either side another canal (text-fig. 3. Pl. 1, fig. 2) of which the delimitation, with the exception of the lateral wall, is osseous. Probably, they are infraorbital canals. The supraorbital as well as the infraorbital canals communicate with the surface in several places and they are both of them open in front and behind. As the supraorbital canals are situated on the transparent membrane, it is probable that this represents

the frontals, as also suggested by PARR (1928) in his characterization of the genus *Ipnops*.

Rudimentary Eye Muscles. Several rudimentary eye muscles were found, partly under the fundus region of the eye, partly antero-laterally and antero-medially. The muscles of the fundus region originate from a thin osseous lamina, which is situated ventrally to the sclera; they insert in the fibrous part of the sclera. That they are eye muscles is shown by the fact that they are innervated by the nervus oculomotorius. Since the muscle rudiments were found at intervals in many of the 8 micron sections, it is probable that there are several muscles (they may be m. rectus inferior, superior and anterior). Unfortunately, it was impossible to verify the number of muscle rudiments in the fundus region on the celloidin sections, because in these thick sections the pigment of the surrounding connective tissue concealed them completely. The m. rectus posterior is probably missing, since all the muscles of the fundus region seem to be attached to the n. oculomotorius, and since it has been impossible to find the n. abducens.

Antero-laterally there is a rudimentary muscle which inserts in the cartilage of the sclera, probably the m. obliquus inferior; it is innervated by the n. oculomotorius.

Antero-medially there is a muscle rudiment as well, inserting in the scleral cartilage, probably the m. obliquus superior. It has been impossible to follow the nerve of the muscle, and the present author has not been able to find the n. trochlearis in the isthmus region of the mesencephalon; the nerve is probably lacking.

All the rudimentary muscles are rather small; the muscle rudiments of the fundus region are about 30 microns wide, the m. obliquus superior and inferior are only about 18 microns wide.

The Innervation of the Eye. Ventro-laterally of the optic nerves and slightly in front of the chiasma there is on each side a ciliary ganglion. The ganglion lies in contact with the n. oculomotorius. The ganglion receives a branch from the ganglion Gasseri (there is no separate profundus ganglion). No separate radix sympathica is to be found. From the ganglion two ciliary nerves lead to the bulbus. Where they leave the ganglion both of them lie slightly laterally of the n. oculomotorius. One ciliary nerve runs rostro-dorsally and medially, crossing over the n. oculomotorius, and perforates the sclera medially on the boundary between its chondral and fibrous part; then it crosses the intraocular sinus and runs dorsally along the choriocapillaris to the region immediately medially of the pars coeca retinae; here it is divided into two branches, one leading forward, one backward. The nerve innervates the vessels of the choriocapillaris.

The second ciliary nerve runs medially too, crossing over the n. oculomotorius. It perforates the sclera together with the optic nerve and can be followed for a short distance on the inside of the sclera, where it runs laterally. There are also nerve fibres in the innermost layer of the chorioidea, immediately laterally of the pars coeca retinae at the lateral edge of the eye. These nerve fibres innervate the vessels of the choriocapillaris and are probably branches of the ciliary nerve which perforates the sclera together with the optic nerve, but it has not been possible to follow the intraocular course of this nerve. No separate long ciliary nerve has been found.

The n. oculomotorius runs forward ventrally of the bulbus and innervates the muscle rudiments which insert in the fibrous part of the sclera corresponding to the fundus region of the eye. Then it turns medially and runs forward along the scleral cartilage. Medially of the foremost part of the eye it joins a branch of the n. trigeminus for a short distance before it turns laterally and runs under the scleral cartilage to the antero-lateral edge of the bulbus; then the n. oculomotorius turns caudally and runs to the m. obliquus inferior.

DISCUSSION

The present investigation clearly shows that the cephalic organs of *Ipnops murrayi* are modified eyes. MOSELEY's first short description of the organs (in GÜNTHER 1885) is on all essential points correct. MOSELEY's second description of the histological structure of the organs (in GÜNTHER 1887), however, is erroneous and in the main seems to be based on artefacts. The most amazing discrepancy between his first and second description is that the layer with nerve fibres inside the layer of rods is completely neglected in his second description. This layer does not appear in any of MOSELEY's figures (GÜNTHER 1887, pl. LXVIII. Text-fig. 2). The only basis for the opinion that the rods consist of two separate components (transparent, hexagonal, non-nucleated rods and hexagonal, nucleated cells) seems to be MOSELEY's statement that an artificial fissure was often found in the layer of rods, separating the nucleated cells from the transparent rods. That MOSELEY was unable to see the cross-lamination of the outer segments of the rods, may either be due to the poor fixation of his material, or to the fact that his sections were too thick, probably both. In his second description MOSELEY states that an artificial fissure is to be found between the pigmented connective tissue under the rods (i.e. the innermost part of the chorioidea) and the bottom of the cavity in which the cephalic organs are situated. This fissure, however, is not artificial, it is the intraocular blood sinus.

That the cephalic organs of *Ipnops* are modified eyes is primarily shown by the positively identified optic nerves and by the structure of the organs, because they have a retina with typical rods. Furthermore, it has been emphasized that certain structural features, which are characteristic of the eyes of the teleosts, are present also in *Ipnops:* the structure of the sclera and the subbulbar sinus (?). The retina is in accordance with that of other deep sea fishes in lacking cones and in having a constant dark position of the retinal pigment. The eyes are directed upwards, which is to be expected in a benthonic fish. The reduction of the eye muscles is naturally connected with the form and position of the entire eye. No doubt the eye is immobile and thus the eye muscles have hardly any function in the adult animal.

The eyes of *Ipnops* must be regarded as specialized visual organs. The reduction of the retinal layers which are situated inside the outer nuclear layer is a natural consequence of the great summation. There is nothing at all in the structure of the organs to suggest that they should function both as visual organs and as phosphorescent organs as supposed by AGASSIZ (1888) and GARMAN (1899). As so clearly expressed by MOSELEY, it must be supposed that the structure of the organs with the flat retina is ". . . a device for detecting the presence of very small quantities of light, at the expense of all apparatus for forming an image."

SUMMARY

The paper deals with the peculiar cephalic organs of *Ipnops murrayi* GÜNTHER, 1878, which have been described as phosphorescent organs (MOSELEY 1887). In the literature *Ipnops* is ordinarily said to be the only vertebrate in which every trace of eyes as well as optic nerves is lacking. On the basis of the present investigation it can be positively stated that the cephalic organs of *Ipnops* are modified eyes. Positively identified optic nerves are to be found, and the organ has a retina with typical rods. The lens and its suspensory apparatus are lacking. The iris is reduced. The processus falciformis and hyaloid vessels are missing. Several rudimentary eye muscles exist, some of which are innervated by the n. oculomotorius. Nervus trochlearis and n. abducens are apparently missing. There is a ciliary ganglion, lying in contact with n. oculomotorius, and from where two ciliary nerves lead to the bulbus, where they innervate the chorioidea (choriocapillaris). The flattened and upwards directed eyes are covered by a transparent, unpaired bony membrane, which is supposed to represent the frontals, because two canals, probably supraorbital canals, are lying on the membrane, one on either side of the median line. Under the lateral edges of the membrane there are two more canals, supposed to be infraorbital canals.

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Pl. 1, fig. 1. Dorsal view of the head of *Ipnops murrayi*.

A: nasal capsule
B: anterior part of the supraorbital canal
C: the lateral edge of the transparent membrane
D: the lateral edge of the retina

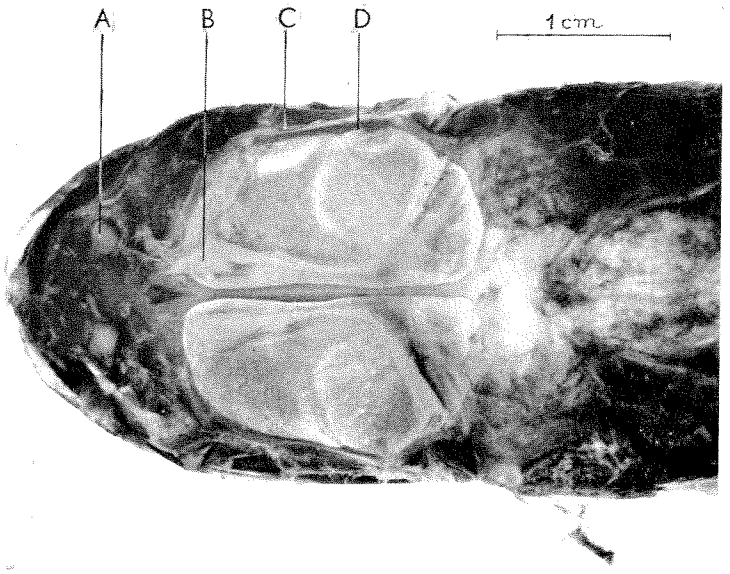
Pl. 1, fig. 2. Transverse section of the head of *Ipnops murrayi* corresponding to the foremost half of the eyes (cf. text-figure 3). 50 micron section. MALLORY's phosphotungstic acid hematoxylin. A. Øye photo.

A: supraorbital canal
B: infraorbital canal
C: sclera (cartilaginous part)
D: subbulbar fissure
H: hyaline cartilage
I: intraocular blood sinus
L: transparent membrane (the frontals?)
M: the edge of the transparent membrane
R: the retina (pars optica)
S: the sclera (fibrous part)

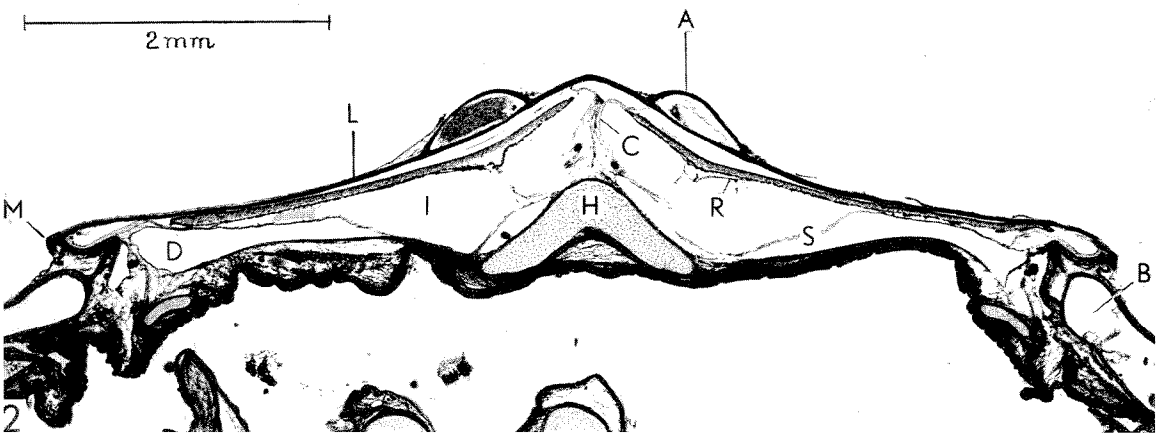
Pl. 1, fig. 3. Transverse section of the head of *Ipnops murrayi* through the chiasma. 8 micron section. Hematoxylin-eosin. NA: 0,25.

C: the chiasma
D: the dura
E: the epiphysis
I: intraocular blood sinus
H: the hypophysis
R: the retina
S: the sclera (cartilaginous part)
T: olfactory tract
V: vessel

Pl. 1, fig. 4. The same section as in fig. 3 at higher magnification to show the chiasma clearly. The meaning of the letters is the same as in fig. 3. NA: 0,25.



1



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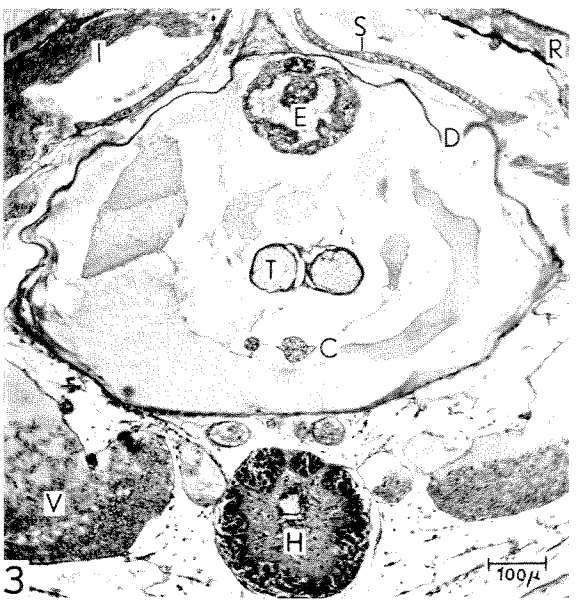

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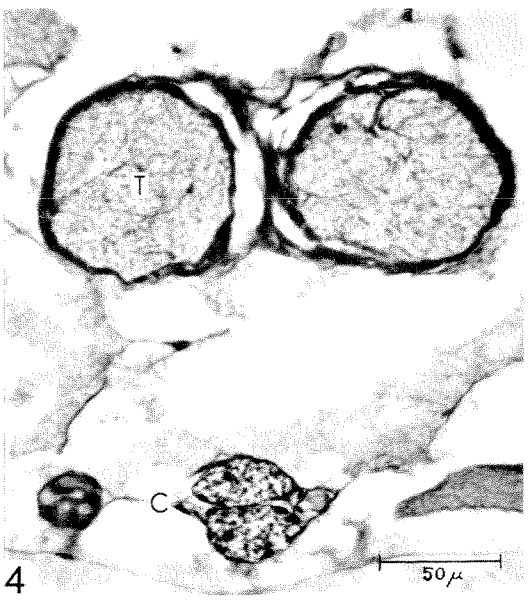

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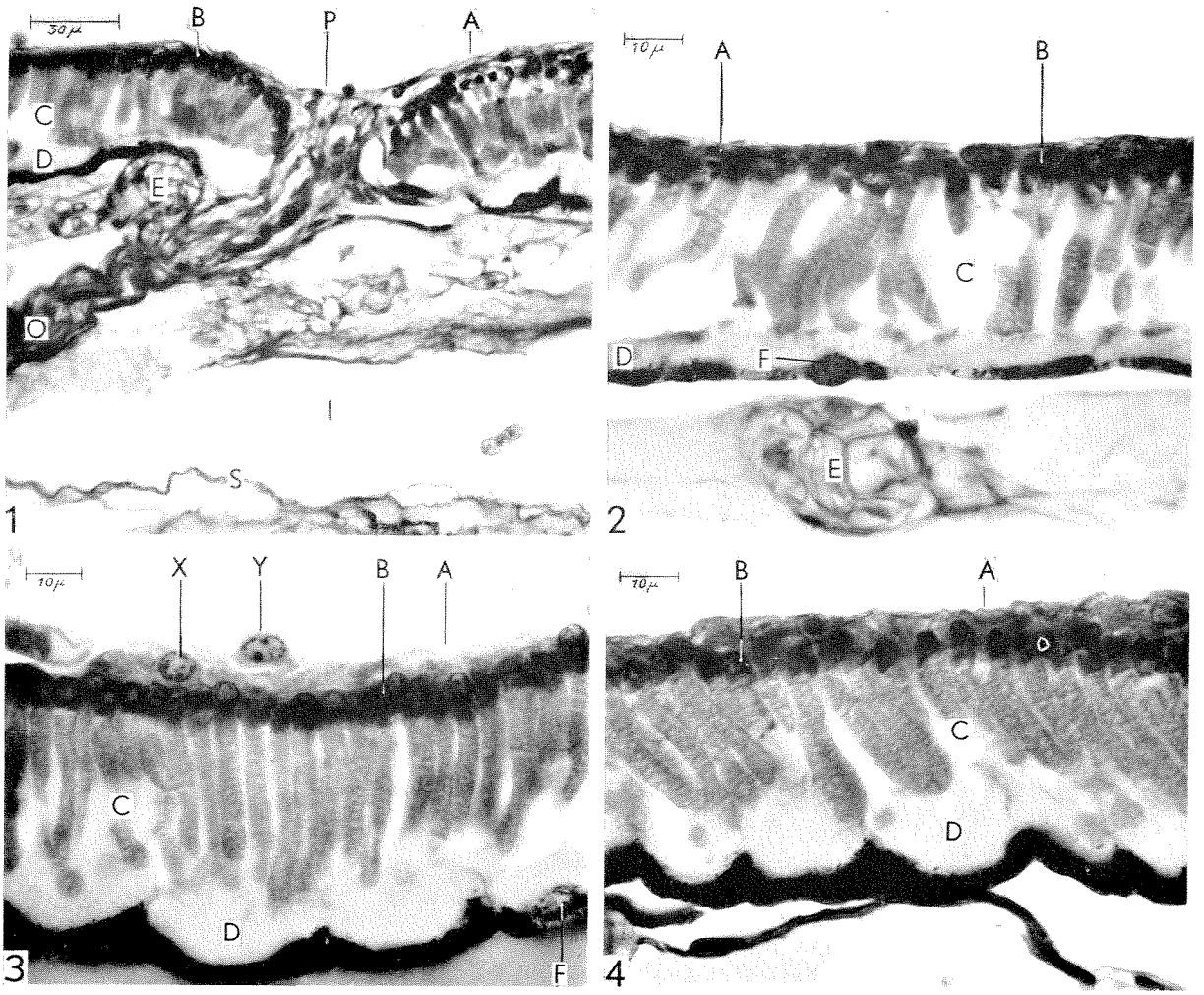

Pl. 2, fig. 1. The papilla of the optic nerve (left eye). 8 micron section. Hematoxylin-eosin. NA: 0,65

Pl. 2, fig. 2. Transverse section of the peripheral part of the retina. 8 micron section. Hematoxylin-eosin. NA: 1,30

Pl. 2, fig. 3. Transverse section of the retina in the fundus region. 8 micron section. Hematoxylin-eosin. NA: 1,30

Pl. 2, fig. 4. Transverse section of the retina in the fundus region. 8 micron section. Hematoxylin-eosin. NA: 1,30

A: layer with nerve fibres
B: outer nuclear layer
C: outer segment of the rods
D: the pigment epithelium
E: vessel in choriocapillaris
F: nucleus in retinal pigment cell
I: intraocular blood sinus
O: optic nerve
P: papilla of the optic nerve
S: sclera (fibrous part)
X and Y: nuclei inside the outer nuclear layer