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A Freshwater Shell-less Mollusc from the Caribbean: Structure, Biotics, and Contribution to a New Understanding of the Acochlidioidea

Jessie J. Rankin

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NUMBER 116

JESSIE J. RANKIN

A Freshwater Shell-less Mollusc from the Caribbean: Structure, Biotics, and Contribution to a New Understanding of the Acochlidioidea

ROM

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A Freshwater Shell-less Mollusc from the Caribbean: Structure, Biotics, and Contribution to a New Understanding of the Acochlidioidea

Abstract

The detailed study of a new freshwater shell-less mollusc found on the island of St. Vincent, at an altitude of 411.5 m in the mud interstices of a spring-fed mountain marsh, has stimulated a reassessment of the problematical systematic status of the Acochlidioidea. A new classification of the order is given, based on fundamental anatomical characters. The relationship of the order to other groups is discussed.

The new animal, *Tantulum elegans*, gen. et sp. nov., is the first of this group to be found in the Caribbean and the first freshwater species from the Western Hemisphere.

Introduction

In July 1972, several specimens of a small, blind and shell-less mollusc were found by Dr. A. D. Harrison in a mountain marsh in the Golden Grove district of St. Vincent, West Indies. This area had been under constant surveillance for 14 months, during a detailed ecological survey of the fresh waters of the island (Harrison and Rankin, 1976), but these animals had not previously been noticed. Subsequent searches showed that they were restricted to one small portion of the grid, where one of the mountain springs bubbled up into the marsh through deep, soft mud.

Examination of living specimens revealed an external morphology with a few similarities to *Strubellia paradoxa*, as redescribed by Küthe (1935), but with a colourless, semitransparent integument that appeared white in reflected light, and through which much of the internal anatomy could be seen. Specimens were kept alive and studied in the field laboratory for several months; histological preparations were later made of some specimens and fundamental differences between this species and *S. paradoxa* were immediately apparent. Consequently, the specimens are here described as a species new to science, and a new genus and family within the Acochlidioidea are erected to contain it.

The detailed study of this new species revealed a number of previously unknown facts regarding acochlidioidean structure and physiology and gave a clearer understanding of classificatory characteristics within the group. This led to the development of the new classification of the order here presented.

Materials and Methods

Attempted narcotization of these tiny animals with chloral hydrate produced marked osmotic uptake of water, with consequent rupture before the point of anaesthesia. Therefore, untreated, actively moving, fully extended specimens were fixed by sudden application of hot AFA and preserved in 80 per cent alcohol. Subsequently, some specimens were stained with either Ehrlich's haematoxylin or acetocarmine, and mounted whole; others were cleared in cellosolve and embedded in glycol methacrylate. Transverse, longitudinal, and horizontal series of sections 3 μm thick were obtained and stained with methylene blue or haematoxylin-eosin. Fortunately this technique gives a clear, permanent staining, particularly of nervous tissue, without the hazards of mountants and permits the use of immersion oil without the intervention of a coverslip.

Reconstructions were built by transillumination of serial camera lucida drawings made with coloured permanent inks on 0.127 mm thick cellulose acetate film, spaced by glass plates.

For Key to Lettering of Figures see page 114.

Systematic Section

Tantulidae fam. nov.

Acochlidioideans with the characters of the Suborder Pharyngoneura (see definition in New Classification of the Acochlidioidea, p. 91) and with dorsal visceral sac not very distinctly different in appearance from the anterior hump; two pairs of similar cephalic appendages; digestive caecum saclike, broad, as long as visceral sac and undivided internally; radular plane very sharply bent with lower portion distinct from upper and half the length; nephridium large with single nephrostome and long renopericardial canal, small intrarenal flagellated pore, long looped nephric duct, ciliated nephridiopore; gonad discrete, gonoduct simple and without glands but with diverticulum and short anterior extension, gonopore opens in dextroventral pouch.

Tantulum gen. nov.

Diagnosis

With the characters of the family and with hollow rod and boomerang-shaped spicules, 75 μm or more in length, in the glandular integument; labial tentacles digitiform and broadened at base, posterior tentacles digitiform and shorter; foot long, thin, narrow, rounded at anterior end, tapering to posterior point; dorsal visceral sac longer than length of foot; eyes absent; branched cephalic and tentacular sense organs, large locular anterior (buccal-tube) sense organs, very large bilobed oral (=suprapedal) organ with tactile scoop-rim ventral to mouth; radular formula 1-R-1 or 1-R-2 with about 45 tooth rows and approximately one-fourth of these in lower portion of radula; nephridium with vacuolated nephrocytes, nephric duct with no

canalicular crossconnections; pharyngeal food canal cuticularized, pharyngeal salivary glands elongated and each emptying through spherical pump into highly contractile duct which enters modified reservoir in posterior pharyngeal wall; flagellate oesophagus and intestine.

Type Species

Tantulum elegans sp. nov.

Etymology

The generic name is from the Latin *tantulum*, meaning so small a thing, or such a trifle.

Tantulum elegans sp. nov.

Type Material

The type material (ROM Cat. no. 1118) consists of the following: (a) the holotype, as a whole mount; (b) a paratype series comprising several whole specimens (AFA fixed, alcohol preserved), 1 whole mount of radula, 1 set of transverse sections, 2 sets of longitudinal sections, 1 set of horizontal (frontal) sections. All material is in the collections of the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum.

Type Locality

Golden Grove, St. Vincent, W.I. (13°11'30''N, 61°11'30''W), at 411.5 m, in interstices of mud in spring pool of mountain marsh draining into Upper Yambou River. Specimens collected July 1972, and subsequently by Dr. A.D. Harrison and Dr. J.J. Rankin.

Etymology

The specific epithet is from the Latin *elegans*, meaning elegant or fine.

Diagnosis

With the characters of the genus. Living animal 2 mm in total length and 0.29 mm in breadth across broadest part of hump; colourless, appearing to be white in reflected light, semitransparent in transmitted light; small spicules in subepidermal layers of mantle and dorsum, large skeletal spicules extending into haemocoel walls and found in two main concentrations, one overlying anterior ganglionic complex and the other overlying pericardium and heart (Fig. 1). Radular formula 1-R-2, (1-R-1 in juveniles), $\frac{U\ 33}{L\ 12} = 45$ in adults, may be $\frac{U\ 25}{L\ 10} = 35$ in juveniles. Rachidian tooth 18 to 20 μm high and 16.3 to 17.6 μm broad, with four or five denticles on either side of median denticle. Right medial tooth-plate 25 to 26 μm wide and 5 μm long, curved, with 5 μm long spine on both anterior and posterior borders. Right outer tooth-plate 3 μm wide and 5 μm long. Left lateral tooth-plate 21 to 22 μm wide and 5 μm long, also curved and bearing spines similar to right medial tooth-plate. Posterior spine of

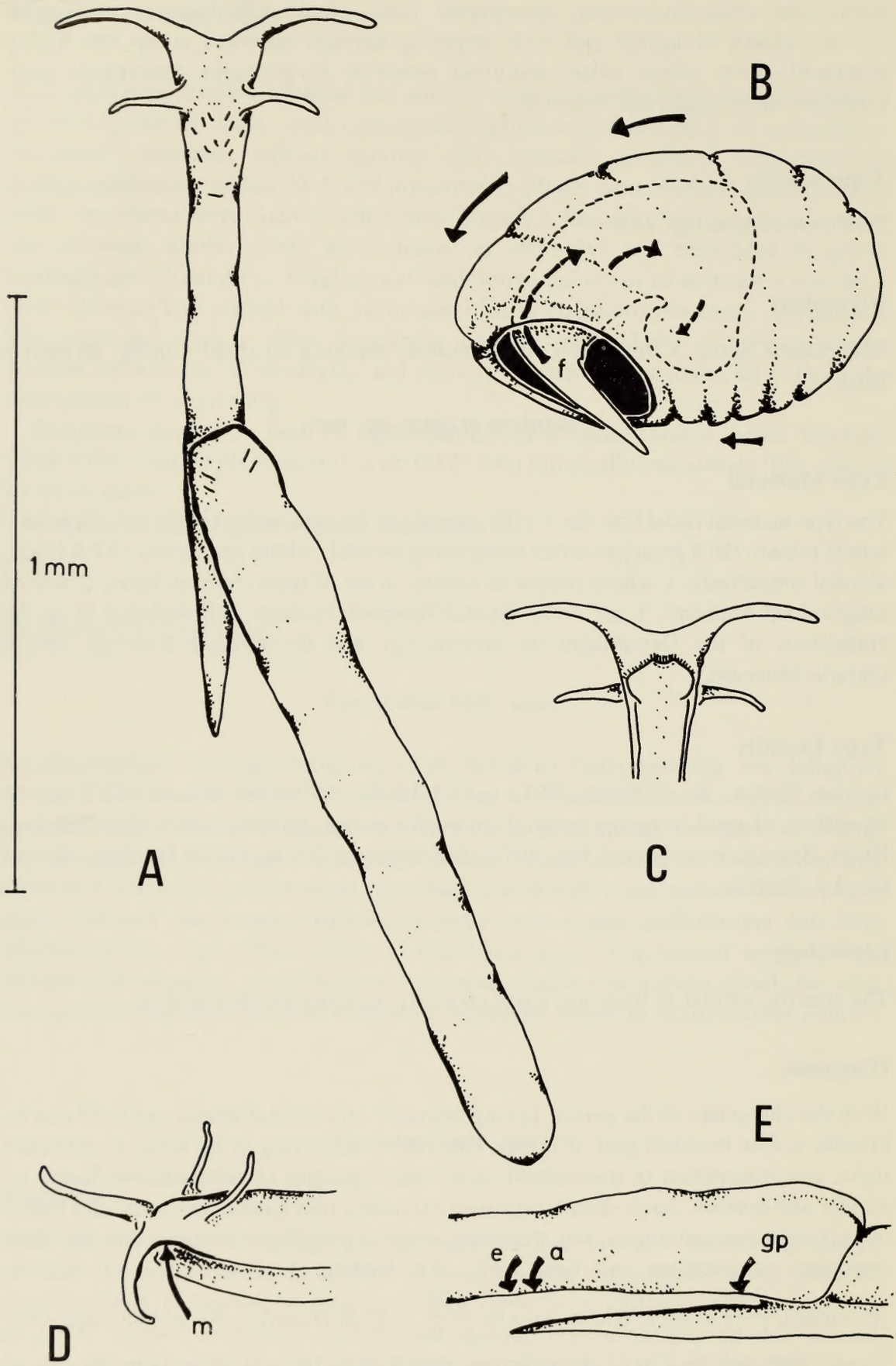


Fig. 1 *Tantulum elegans*. Drawings from life.

A Extended specimen, dorsal view.

B Rolled-in specimen.

C Head, ventral view.

D Head, lateral view.

E Mid-region, left lateral view.

one tooth-plate is very closely apposed to anterior spine of consecutive plate; spines are set at an angle, diagonal to long axis of radula, with points facing posteriorly.

Morphology and Anatomy

External Morphology

The living, fully extended animal is long and thin, with a posteriorly tapered foot and an elongated dorsal visceral sac which is freely movable (Fig. 1A). The head (Fig. 1C, D) bears two pairs of tubular tentacles; the anterior or labial is larger, slightly flattened near the head and moves mostly in the horizontal plane; the posterior or "rhinophores" is smaller and moves mostly in the vertical plane.

There is no shell or spicular pallial test and the animal is capable of rolling up (Fig. 1B) into a ball with only the tip of the foot protruding from the greatly contracted hump. In this process the head is curled over dorsally and tucked into what may be regarded as a temporary mantle cavity in the anterodextral part of the free hump, the integument of which rolls forward enveloping the whole of the anterior part of the animal.

The mouth (Fig. 1C, D) is situated anteriorly, between the head and the foot. The anus and the nephridiopore lie close to each other on a small ciliated patch of integument on the ventral (=morphogenetic posterior) surface of the dorsal visceral sac, at the level of the tip of the foot.

The main genital opening is anterior to the anus and nephridiopore, near the juncture of the foot with the hump (Fig. 1E) and lies within a shallow invagination or pouch which is described in the next section.

The body surface is slightly rugose owing to the presence of large gland cells in the integument but some of the spicules glisten through the body wall. The lateral surfaces of the foot are smoother than the hump but the sole is entirely ciliated.

Alimentary System

The mouth is surrounded dorsally and laterally by rounded lips (Fig. 2:ul) the epithelium of which carries a few minute chitinous hooks and contains clusters of small, darkly cyanophilic buccal chemoreceptor cells. Ventrally the mouth is bounded by the thickened ridge of a hemispherical and almost suckerlike scoop of the bilobed suprapedal, or oral, organ (Fig. 2:spg); the cells of the scoop are elongate and compressed, with stiff cilia, rather like sensory bristles. The faintly staining cells (Fig. 20:or) of the oral organ are supported by an irregular framework of darker staining basket cells and are filled with a secretion which is quite distinct from that of either the pharyngeal salivary glands or the integumental gland cells. The secretion does not show distinct granules or globules under the light microscope and tends to appear homogeneously grey with methylene blue and only faintly staining with eosin; it appears to be somewhat similar to that of the pedal glands, described later, but in the latter case granules have been noted.

The buccal cavity (Figs. 2, 3, 4:bc) is differentiated into two well-marked zones, the buccal tube and the pharynx. The buccal tube (called buccal or oral tube, and sometimes erroneously anterior oesophagus) is long with extremely thin walls which are nonciliated and highly extensile and mobile. Two pairs of distinct muscles, the dorsal (dbd) and ventral (vbd) buccal dilators (Figs. 2, 4:dbd, vbd), help in the

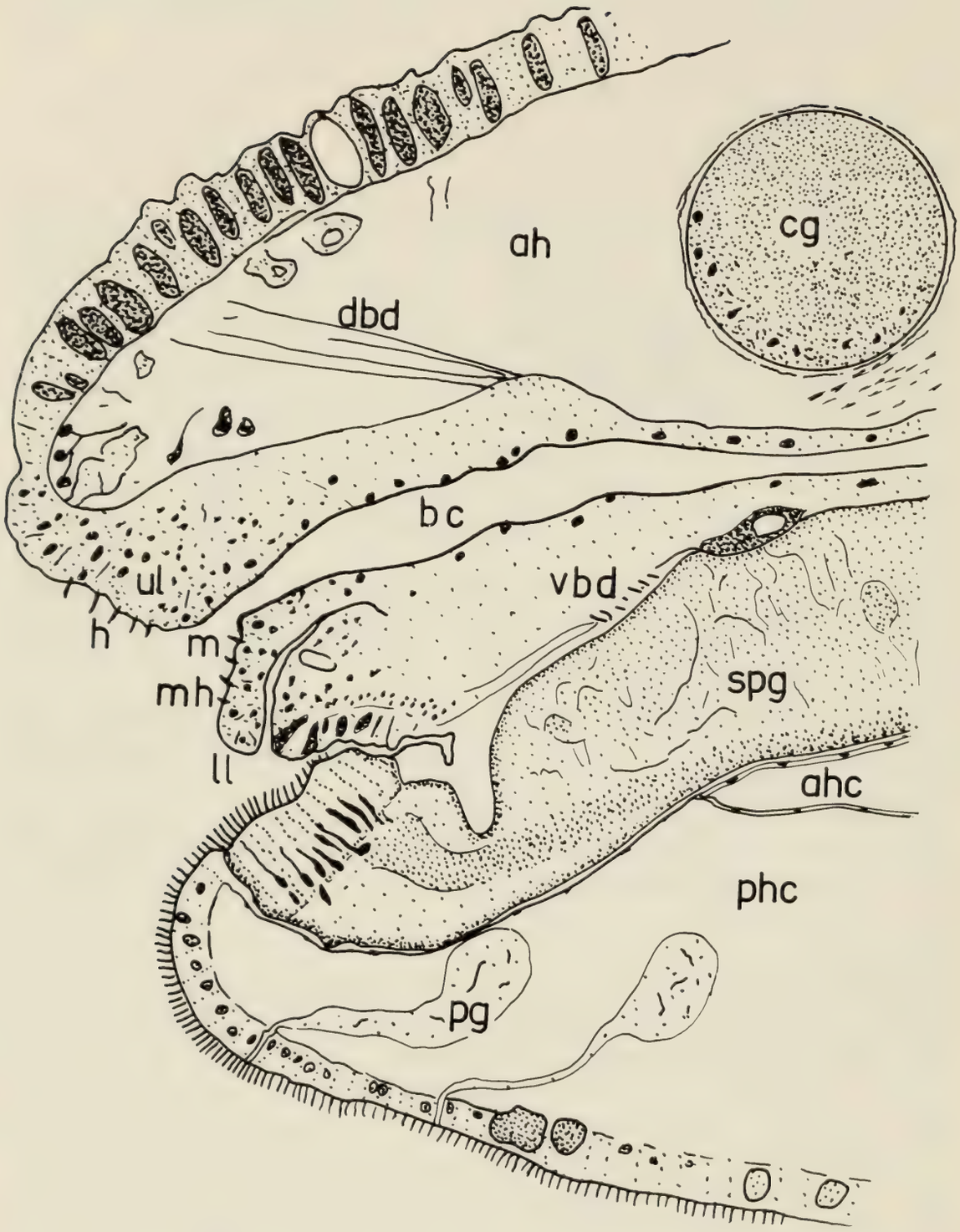


Fig. 2 *Tantulum elegans*. Camera lucida drawing of right paramedial section of head.

dilatation of this elongate structure and permit the "eversion" of the pharynx up to mouth level. For a description of this process see page 40. Immediately over the dorsolateral surface of the buccal tube lie the anterior sense organs, large, locular, highly innervated olfactory structures which are described later.

The buccal tube passes through the prepharyngeal nerve ring and turns immediately upward to widen and differentiate into a clearly distinguishable pharynx (Fig. 4). This is a complex structure with both extrinsic and intrinsic musculature and is composed

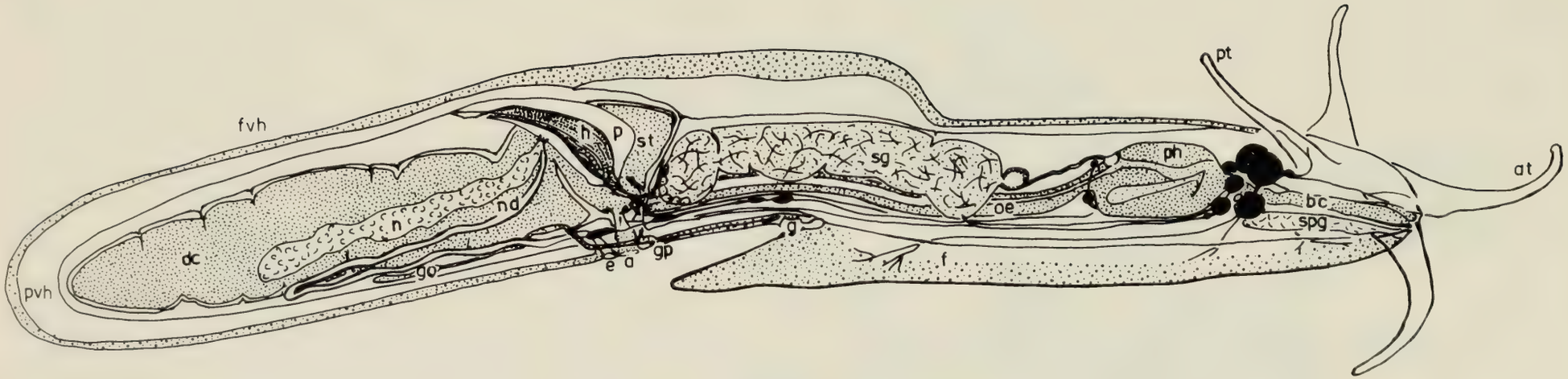


Fig. 3 *Tantulum elegans*. Lateral optical section.

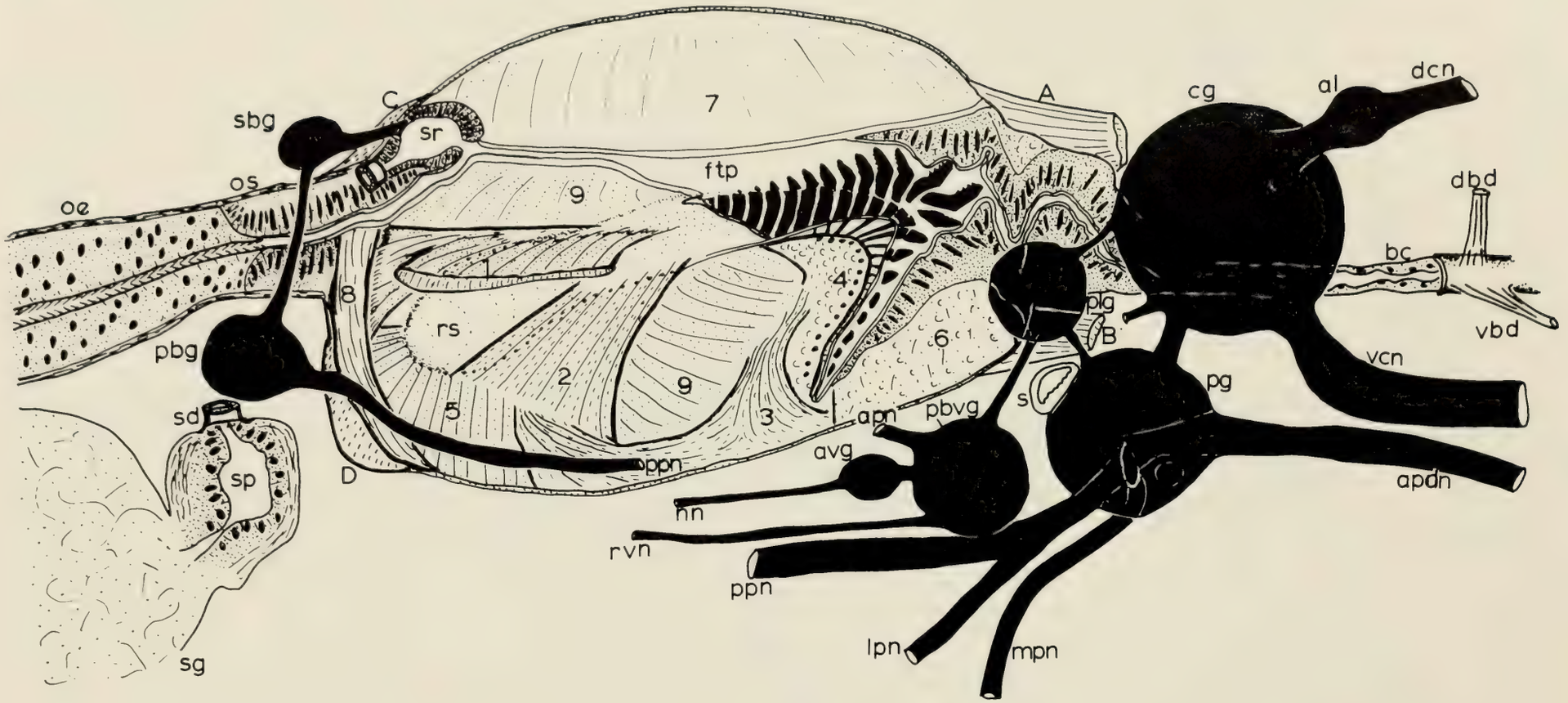


Fig. 4 *Tantulum elegans*. Pharynx in right paramedial section with superimposed nervous system.

1. Lateral tensor muscle.
2. Ventral depressor muscle.
3. Ventral radular protractor muscle.
4. Transverse tensor muscle.
5. Posterior radular retractor.
6. Anterior pharyngeal dilator.
7. Pharyngeal sphincter.
8. Posterior pharyngeal compressor.
9. Radial pharyngeal compressor.

A Anterolateral pharyngeal protractor muscle.
B Ventral pharyngeal protractor.
C Posterior pharyngeal retractor muscle.
D Ventral pharyngeal protractor muscle.

of several main parts: the region of the inner lips, the pharyngeal food canal (ftp), the radular sac or bulb (rs), the lingual cushion (9, 4), the lateral pouches, the subradular sac, the radula, and the pharyngeal reservoirs of the salivary ducts. The whole is bound together by sphincter muscles. Details are as follows: the pharyngeal food canal is laterally flattened and passes dorsally over the radular sac to enter the oesophagus through a pharnygeal sphincter (os). Immediately anterior to the sphincter the lumen of the canal is entered by two small chambers (sr), which serve as internal pharyngeal reservoirs for the salivary ducts. The anterior part of the food tube is flattened around the lingual tip and confluent with the central subradular pouch and the two lateral pouches. A large lingual cushion supports the radular sac and is a complex structure.

As the widening buccal tube passes through the nerve ring, its epithelial lining becomes thickened and cuticularized, merging with that of the pharynx to form a valvular structure capable of compression and friction. This bucco-pharyngeal thickening into internal lips operates as a jaw against the functional radular teeth. The toughened epithelium spreads itself around the whole of the anterior protruding end of the radular lingual cushion and merges with the cuticularized epithelium of the dorsal flattened portion of the pharyngeal food canal (Fig. 20A:fc) as it passes over the radular sac (rs). The toughened epithelium also merges with that of the lateral pharyngeal extensions (lpe) of the canal and the subradular sac (srp) and also with the anterior opening of the radular sac (Fig. 19A) which is a bifid slit.

The radular sac is clearly a diverticulum from the food canal. The sac floor lies over the lingual cushion, bending sharply over the tip to merge with the wall of the second diverticulum or subradular sac. The floor epithelium of the radular sac produces a subradular membrane which is extended at the tip into a broad area of clearly defined tensor strands (Fig. 19B:ts) connecting the epithelium proper with the cuticle of the radular ribbon. The outer wall of the radular sac is muscularized and forms a radular sheath to which muscles are attached, as mentioned below.

The proliferating zone of radular odontoblasts produces an inverted and narrow radular ribbon with a central row of rachidian teeth. At any one time the ribbon shows 45 transverse rows, 33 being placed in the upper portion and 12 in the downward hook. In juveniles the formula may be $\frac{U\ 25}{L\ 10} = 35$. As the tooth rows pass over the bending plane of the tongue tip, the ribbon opens flat and the rows splay out over the tip; teeth in the downward hook show considerable wear.

The tooth formula (Fig. 5) for each transverse row is 1-R-2. The single, large, median, rachidian tooth is subsymmetrical and triangular, with an apex that has a recurved margin bearing four or five small denticles on both borders; these denticles are not always evenly spaced. There is one main lateral, or pleural, tooth-plate on either side; this is a curved rectangular plate with a distally placed denticle on both anterior and posterior borders. The denticle of the posterior border of one lateral tooth-plate is closely adpressed to the anterior denticle of the tooth-plate in the following transverse row, the lateral tooth-plate of one side meets the corresponding lateral plate dorsally in the folded portion of the radula. On the right side there is an additional square outer lateral tooth-plate which appears to be imperfectly freed from the radular membrane; these extra plates may not be visible in juveniles.

The dental formula of 1-R-2 approximates the rachiglossate formula for stenoglossan (neogastropod) prosobranchs, which is a reduced taenioglossan (mesogastropod) form.

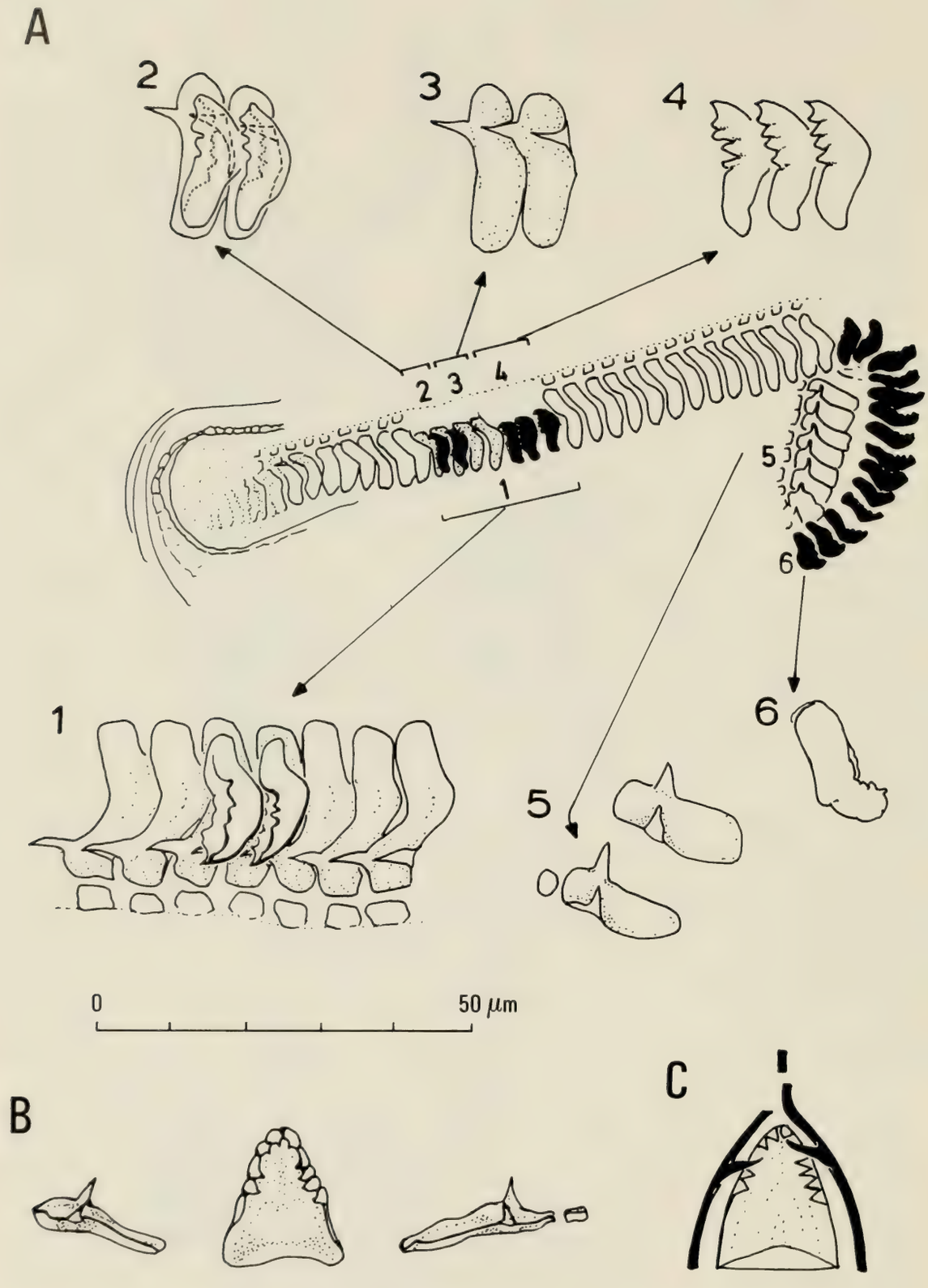


Fig. 5 *Tantulum elegans*. Camera lucida drawings of radula.

A Lateral view of teeth *in situ*: 1 Seven right outer and medial lateral tooth-plates opened out from radula, together with two rachidian teeth. 2 Two left lateral tooth-plates and two rachidian teeth. 3 Upper view of two left lateral tooth-plates showing postero-diagonal spines. 4 Rachidian teeth, right lateral view. 5 Left and right lateral tooth-plates from lower radular section. 6 Worn rachidian tooth.

B Posterior view of operative tooth-row.

C Diagram of folded radula, tooth-plates in solid black.

The sharp bending plane of the radula and its one currently operating row of denticulate teeth form an efficient radular grasping scoop. The pharyngeal food canal and radular bulb, composed of radular sac and lingual cushion, are all bound together by an overlying complete canopy of sphincter or circular muscles which I have called a "velarium"; there is therefore formed a united structure capable of being moved as a whole as well as showing movement of individual parts.

There are four pairs of strong extrinsic pharyngeal muscles (Fig. 4) which move the entire pharynx, two being protractors and two retractors. One pair (A) of protractors originate on the fascia of the pharyngeal sphincters at the anterolateral corners of the pharynx and run forward to their insertion on the head; one pair (B) originate more ventrally on the anterior wall and run forward alongside the buccal cavity to their insertion near the frontal cleft between the anterior tentacles. Both pairs of retractors originate on posterolateral corners of the pharynx and run laterally (C) and ventrolaterally (D) to their insertions on the lateral body wall.

The intrinsic musculature (Fig. 4), which alters the shape of the pharynx, is massive and enables it to act not only as a churning mechanism but also in great part as a suction bulb, sucking mud and detritus into the food canal. A thin fibrous sheet, (outer part of "velarium") surrounds the entire bulb, binding food canal and radular apparatus into an entity. No true cartilaginous odontophores or bolsters are present, but small, thin, irregular plates of cartilage cells are found in the radial pharyngeal muscles of the lingual cushion (Fig. 20A).

The following intrinsic muscles (Fig. 4) have been identified and labelled according to obvious functions; other small bundles may exist but it is difficult to delimit their boundaries in reconstructions:

1. *Lateral tensors* paired, fanshaped muscles originating on the dorsolateral walls of the radular sheath (rs) and inserted against the fibres of the posterior pharyngeal compressor muscles (8); they elevate and spread the radula.

2. *Ventral depressors* paired, fanshaped muscles originating on the lateral and ventral walls of the radular sheath and inserted on posterior muscles; they help to retract and close the radula.

3. *Ventral radular protractor* pulls down on the anterior end of the lingual cushion and helps to roll the radula forward and downward over the lingual tip.

4. *Transverse tensor* a large sheet of muscle forming the anterior part of the lingual cushion; it spreads the radula and operates the teeth via the dental tensor fibres of the anterior subradular membrane.

5. *Posterior radular retractor* a suspensor of the radular sac; acts also as a posterior retractor.

6. *Anterior pharyngeal dilators* paired; open and close the pharyngo-buccal junction and help to manipulate it against the operative teeth.

7. *Pharyngeal sphincters* or "velarium", paired dorsal muscle blocks, united mid-dorsally by a strong fascia and with sheetlike extensions which encircle the pharynx in its upper two-thirds; blocks have fibres running radially from central and lateral parts of food canal outward; contraction of blocks opens food canal and shortens pharynx; contraction of extensions compresses pharynx.

8. *Posterior pharyngeal compressor* an almost circular band, which compresses

the pharynx posteriorly, acting as a pharyngo-oesophageal sphincter and as an attachment for radular retractors.

9. *Radial pharyngeals* paired, massive lateral muscles forming the major part of the lingual cushion of the pharyngeal bulb and containing thin chondroid plates in their upper layers; depress the floor of the food canal, raise the radular sheath and, in general, act as a pharyngeal pump.

The two salivary reservoirs (sr) which lie dorsolaterally within the pharyngeal bulb each open into the posterior part of the food canal. They receive the ducts of the pharyngeal glands posteriorly. Just posterior to them there is a distinct oesophageal ''sphincter'' surrounding the cuticularized opening of the pharyngeal food canal into the oesophagus (oe). The cells of the sphincter are columnar and darkly staining, with a strong resemblance to those of the inner lips and ''jaws''.

The elongate pharyngeal salivary glands (Figs. 3, 4:sg) lie one on either side of the oesophagus and contain acinar secretory cells in all phases of activity. Each gland is tubular, with a very narrow central lumen surrounded by a regular, radiating framework of darkly cyanophilic basket cells. The acinar secretory units are tightly packed within this framework, their ductules often engorged with fully formed droplets (Fig. 11E:zg) which stain a deep, dark, nonpurplish blue with methylene blue and which appear to be zymogenic in character. The droplets find their way to the anterior apex of the gland for disgorgement into the pharyngeal salivary duct (sd). A sphincter controls this opening into the lower part of the duct which is here expanded into an almost cuboidal cisterna or ampulla (Figs. 4:sp; 11E), which is highly muscular. This structure is here termed ''pharyngeal pump'', as it apparently acts as a small pumping vestibule which can forcibly eject secretions from the gland through the duct into the salivary chamber of the pharynx thus into the food canal. Bergh (1895) mentions a spherical expansion or ampulla in this same region of the pharyngeal salivary duct in *Palliohedyle* (=*Acochlidium*) *weberi* but does not describe it further.

The pharyngeal pump (Fig. 11E) is lined with cuboidal cells, each with a very large nucleus. However, on the wall nearest to the gland, this single-layered epithelium is expanded into a mound of cells, the innermost cells of which are ciliated. It is into the centre of this mound that the salivary gland opens. Passage of secretory droplets through this mound obviously ruptures the thin membranes of these delicate vesicles and liberates their contents; no droplets are found in the pump.

The ducts are extensile and highly contractile. They tend to be almost fully contracted in even reasonably extended fixed animals; in the living animals, however, they can be seen to be clearly distinct from the ampullae and to be capable of contracting by themselves, coiling and uncoiling during movements of the pharynx. The whole apparatus resembles a pump-operated syringe, injecting secreted material as required.

At the posterior end of each pharyngeal gland is found a cuplike area which is formed of very large, lightly staining cells, of a totally different appearance from the secretory network seen in the rest of the gland; the function of these cells is at present unknown.

The oesophagus (Fig. 4:oe) is long, with a fairly thick and muscular wall and, posterior to the sphincter, is lined with ciliated epithelium, which has cuboidal cells with large central nuclei and cilia of from 10 to 15 μm in length (Fig. 11C). The entire

oesophagus is accompanied by very powerful longitudinal muscles (Fig. 7C), which pass along with it through the "septum" which separates the cephalic from the visceral haemocoels.

An elongate, but small, tubular gland (Figs. 12B, 13B) was found in one series of transverse sections; its histology differs from that of the pharyngeal glands. It lies ventral to the oesophagus but no opening has been observed. It is referred to later under Reproductive System.

The oesophagus (Figs. 7B, C, 11C) passes down through the anterior visceral haemocoel (Fig. 7A:avh) and into the posterior visceral, where it enters the stomach (Figs. 7B, C). The stomach (st) is wide and is demarcated from its digestive diverticulum (dc) or caecum by only a deep groove. Cilia are found in the oesophageal entry and the intestinal exit areas only. The cells of the endothelial lining are digestive and are similar to and contiguous with the cells of the digestive caecum.

The digestive diverticulum is a large, elongate sac lying in its own tubular haemocoelic space (Figs. 7A:chc; 16C) and filling the entire length of the free visceral hump, and half of the breadth (Fig. 16C). The lumen of the caecum is extensive and clearly visible in the living animal during the ingestive phase of digestion; it is completely unbranched and without internal partitions. The digestive cells (Fig. 21A,B) appear to be all of one type but may vary enormously in thickness and appearance depending on the physiological state of the digestion at any given time. These cells are clearly absorptive, the greater part, if not all of the caecal digestion taking place not in the lumen (Fig. 21A, B:lu) but intracellularly. They become enlarged with digestive products and secretions until the lumen is completely occluded (Fig. 21A:olu).

This occlusion seems to involve an actual breakdown of cell membranes and coalescence of products at some points at least, reminiscent of the condition reported by Westblad (1922) for turbellarians, where temporary fusion of gut walls across the lumen produces a sponge of digestive cells. Examination by electron miscroscopy is required to assess the extent of such fusion in *Tantulum elegans*.

In the posterior third of the diverticulum the digestive cells often are swollen with large vacuoles. It is noteworthy that great collections of giant amoebocytes are found in the posterior visceral haemocoel, in which lies the caecal haemocoelic "tube". They attach themselves to the haemocoelic membrane particularly in the region of the vacuolated gastric cells (Fig. 9A,B). There would therefore appear to be free passage of certain digestive products across two temporarily adjacent membranes and this material seems to attract the wandering cells. These large amoebocytes are described in the section on Free Cells (p. 33).

Free particles of ingested food material, mostly plant detritus and animal remains, can be seen in the lumina of the digestive diverticulum and stomach during the early ingestive phase. These particles are constantly churned, until absorbed or eliminated, by means of a rhythmic peristalsis which is independent of the general locomotory contractions of the body wall and which also appears to be independent of the digestive stage reached by the animal. This is discussed more fully under Physiology (p. 43).

Indigestible material is eliminated through a short, vertical, densely ciliated intestine (i) (Figs. 7B, C, 14A), which leads off from the stomach (st) directly opposite and very close to the entry of the oesophagus (oe). The intestine dilates into a rectal swelling (Figs. 7B,C,14B:r) which is bulbar but histologically similar. The rectum

emerges on to a small ciliated patch (Fig. 14C:cp) on the ventral surface of the free hump (=morphogenetic posterior) through an independent anus, which is found exactly in the median line of the animal (Fig. 14B:a).

Nervous System

The nervous system shows a considerable degree of cephalization, with most of the major ganglia concentrated into an almost double nerve ring around the anterior end of the pharynx (Figs. 4, 6). There is also some degree of cerebralization, fusion being particularly noticeable in the more posterior of these ganglia. A pharyngeal plexus is also present. Nerves tend to be greatly elongated because of the attenuation of the animal. There are no eyes, but exceedingly minute saccules that may be possible vestiges occur at the base of the posterior tentacles. Well-developed sensory structures occur in the head and tentacles.

GANGLIA

All ganglionic masses are discrete spheres, distinctly encapsulated with a thin inner perineurium and a thick, fibrous epineurium such as can be seen surrounding the cerebral ganglia (cg) in Figure 18A and B, and Figure 19A. They are characterized by the deeply cyanophilic staining of their peripheral neurons and central punkt substance. Large neurons are noticeable amongst the smaller ones and are found particularly around the posterior periphery of each ganglion; these large cells are not present in the ganglioniclike swellings found on the visceral and nephridial nerves.

The paired cerebral ganglia (Figs. 4, 6:cg) are very large, 70 μm in diameter, and lie close together, being linked by a very short, thin commissure which passes across dorsal to the posterior end of the buccal tube (Figs. 4, 19B:bc). Each ganglion is produced laterally into a small lobe (al) (see also Fig. 18A:cll, where right lobe is labelled) from which emerges the large dorsal cephalic nerve (dcn), which supplies the dorsum of the head, the dorsal lip, and the posterior tentacles. Each cerebral ganglion also gives off a large ventral cephalic nerve (vcn), which supplies the anterior tentacles, the anterior sense organ, and the oral organ. Posteriorly each cerebral ganglion gives off a lateral pharyngeal nerve (Fig. 6A, B:lphn). A small statocyst nerve is also given off laterally from each ganglion and a very fine nerve, discussed later, emerges from the base of each lateral lobe.

Vertical connectives link the cerebral ganglia to the pedal ganglia (pg); short, thin connectives also connect them to the pleural ganglia (plg).

The pedal ganglia are 60 μm in diameter and therefore almost as large as the cerebrals, but are more widely separated. They are connected to each other ventral to the buccal tube by a very thick commissure (Fig. 20B). Each ganglion gives off three main pedal nerve trunks which supply all regions of the foot.

The small, paired pleural ganglia lie posterior to the cerebrals to which they are joined by thin connectives. The right pleural ganglion is linked to the combined parietal-buccal-visceral ganglion (Fig. 4, 6A:pbvg) of that side and the left pleural is connected with the left parietal ganglion (Fig. 6B:pag), which has the left anterior buccal (bg) attached to it by a very short connective.

The large left visceral ganglion (Fig. 6B:vg) is not fused with any other ganglion but is connected by a short connective to the left parietal (pg) and by a very thick and strong visceral commissure to the enlarged and fused ganglion of the right side. The right ganglion (Figs. 4, 6:pbvg) of the visceral complex is fused with parietal and

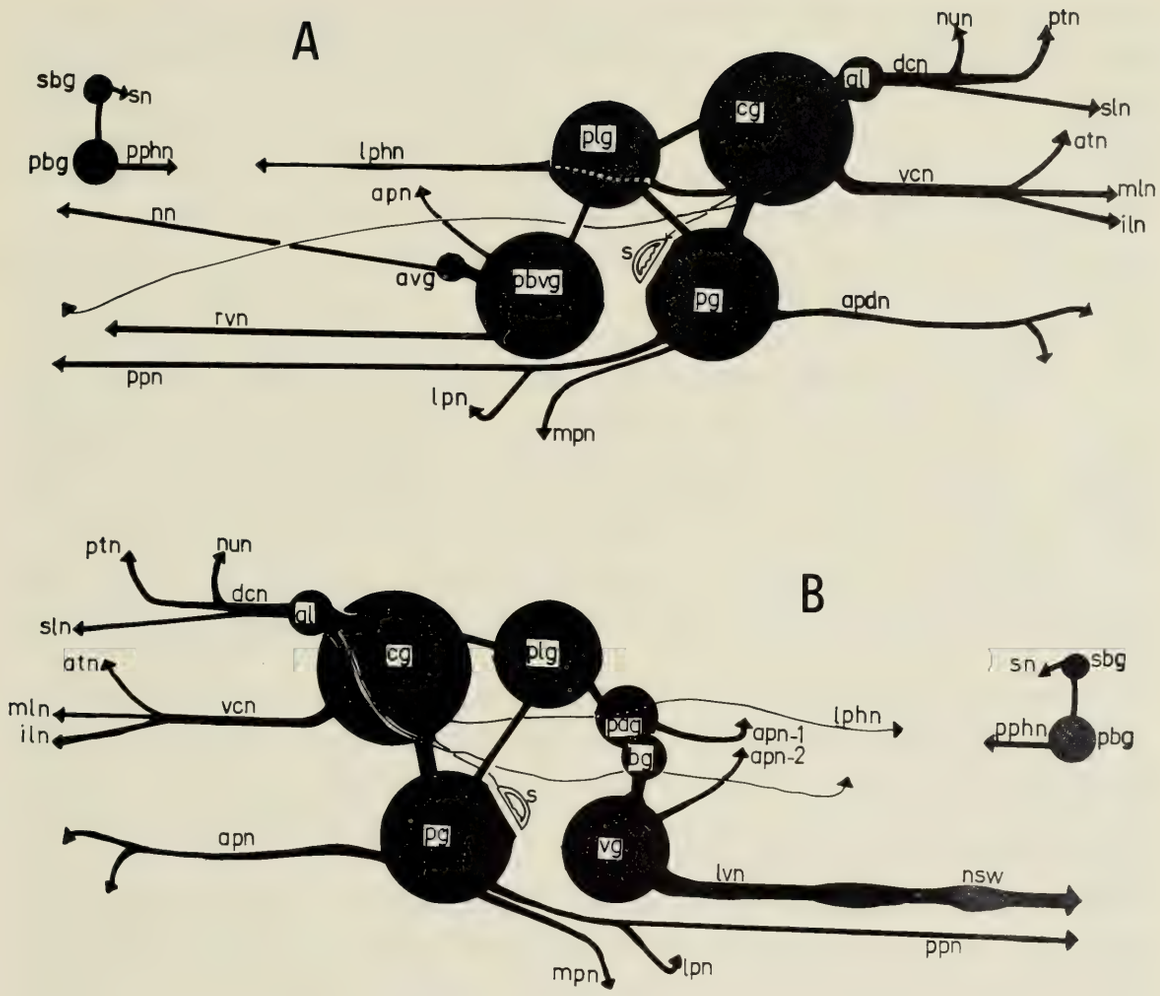


Fig. 6 *Tantulum elegans*. Plan of anterior nervous system.
A Right side.
B Left side.

anterior buccal elements and also has an accessory visceral ganglion (avg) closely attached to it. The nerves from the visceral complex are described below.

Small, paired posterior buccal (=posterior pharyngeal) ganglia (Figs. 4, 6A, B:pbg), 36 μm diameter, are situated on the ventrolateral surface of the oesophagus, just posterior to the pharynx and are connected to each other, ventral to the oesophageal sphincter, by means of a short but strong commissure. They are linked by fine, vertical connectives with the suprabuccals (sbg) (=oesophageals) and supply the posterior pharynx.

The very small, paired suprabuccal ganglia lie above the oesophageal sphincter (Fig. 4:os) and supply the salivary reservoirs of the pharynx and the pharyngeal salivary ducts. No connecting dorsal commissure could be found.

NERVES

Nerves tend to be not only long, but in many cases massive in size. Anteriorly a thick dorsal cephalic (Figs. 4, 6A, B:dcn) emerges from the anterior lateral lobe (al) of the cerebral ganglion (cg) with apparently most of its fibres originating in the ganglion. This nerve divides into two, the dorsal branch dividing almost immediately into a

small nuchal (nun), supplying the dorsum of the head, and a posterior tentacular (ptn), going to the ramifying cell masses under the epidermis which fill the haemocoel of the posterior tentacles. The ventral and small branch of the dorsal cephalic continues forward as the superior labial (sln) to supply the head and dorsal lip.

A large ventral cephalic nerve (vcn) leaves the cerebral ganglion anteriorly and dips downward ventrally, passing under the ventral pharyngeal protractor muscle and travelling forward to the head in close association with the clumped anterior sense organ and eventually branching into three. The anterior tentacular branch (Fig. 6A, B:atn) goes out into the tip of the labial tentacles, the median labial (mln) supplies the anterior surface of the head and the mouth with its buccal cells; both of these branches ramify to supply the same type of branching sensory cell masses as are found in the posterior tentacles. The third branch, the inferior labial (iln), supplies the oral organ with the funnel and scoop of the lower lip.

The statocyst nerve is very delicate and its distal part travels along in the epineurium of the pedal ganglion and emerges opposite the statocyst (Figs. 4, 6A, B:s).

From the left cerebral ganglion a very fine nerve of doubtful homology arises from the base of its anterolateral lobe (Fig. 6B) and eventually enters the mid-pharyngeal musculature; the comparable nerve from the right anterolateral lobe (Fig. 6A) is more difficult to trace, as it is even more delicate, but appears to run down the right side of the anterior haemocoelic wall.

From a common area of origin on the pedal ganglion (Figs. 4, 6A, B, 20:pg) three large nerves emerge. The anterior pedal (apdn) runs forward to supply the anterior part of the foot, including the pedal glands in that area. The middle pedal (mpn) travels out into the anterior haemocoel and passes through that membrane into the dorsal and lateral parts of the middle area of the foot. The posterior pedal divides (ppn), its lateral branch following the middle pedal into the anterior haemocoel but supplying the sole of the foot; the main branch runs parallel to the visceral haemocoelic tube to the level of the posterior border of the pharynx, where it dips into the pedal haemocoel, branching extensively in the posterior foot region.

Delicate pallial nerves run up laterally from the pleural ganglia (plg) to the body wall.

A pair of anterior pharyngeal nerves (Fig. 6A:apn) supply the first part of the pharynx, passing into the lateral musculature of either side. The right one originates from the fused parietal-buccal-visceral (pbvg) ganglion; the left (Fig. 6B:apn-1) arises from the parietal (pag), with attached buccal (bg), of the left side. In addition to these, a second left anterior pharyngeal nerve (apn-2) enters the pharynx, having originated in the left visceral ganglion (vg). All of these anterior pharyngeal nerves pass through the pharynx and are linked with the posterior ganglia by means of plexiform connections (Fig. 19A); many strong, longitudinally running nerve strands are seen within the instrinsic musculature.

The paired lateral pharyngeal nerves, the right one (Fig. 6A:lphn) being much sturdier than the left (Fig. 6B:lphn), enter the dorsolateral musculature of the pharynx, becoming linked with the pharyngeal nerve plexus. This pair of pharyngeal nerves is the equivalent of buccal connectives seen in other genera. (See p. 69 for further discussion of the buccal nervous system.)

The short, stout posterior pharyngeal nerves (Fig. 6A, B:pphn) run directly forward from their respective ganglia. Thus the buccal elements of the anterior buccal ganglia

are joined to the posterior buccal by means of only these internal connections. This extensive innervation is obviously correlated with the great size and differentiation of the pharynx.

On the right side, a long, thin nephridial nerve (Fig. 4, 6A:nn) which develops swellings along its length, emerges from the fused parietal-buccal-visceral ganglion, via the accessory visceral ganglion (avg), and travels backward laterally alongside the right pharyngeal salivary gland, through the cephalic-visceral "septum" and down to the nephridial duct.

The right visceral (rvn) emerges almost ventrally from the same ganglion and passes backward underneath the right pharyngeal salivary gland, supplying that gland and sending a few fibres, in a thin connection, to the left visceral nerve.

The left visceral nerve (Fig. 6B:lvn) is a very strong, thick nerve with numerous very large ganglionic-like swellings (nsw) throughout its length. It emerges from the left visceral ganglion (vg) and passes posteriorly directly ventral to the pharynx and oesophagus, and immediately lateral to the anterior ventral artery. It goes down into the posterior haemocoel to the level of the intestine where it swells out into two serially arranged "ganglia". These swellings are elongate but not discrete and sheathed as are the anterior ganglia; it is difficult to make out cells and therefore doubtful if they should be termed ganglia. However, because of their situation, the anterior has been termed "abdominal ganglion" and the posterior the "genital ganglion". The abdominal gives off the posterior visceral nerve that divides into two: the caecal, which supplies the digestive diverticulum and sends a minute branchlet to the nephrostome, and the cardiac, which supplies the pericardium and the heart. The genital ganglion gives off a genital nerve to the narrow genital duct, and a very long gonadial that goes down the side of the caecum to the gonad.

In addition to these main branches of the left visceral nerve in the posterior visceral haemocoel, there are also several small branches in the anterior visceral haemocoel; small branches go to the pharyngeal salivary gland on either side and several very short branches go to the curious swellings in the wall of the anterior ventral artery, which are described later. In addition, numerous small branches are given off to the longitudinal muscles which pass through to the posterior haemocoel and to their points of insertion on the caecum.

Sense Organs and Associated Structures

There are no functional eyes. However, in the subepidermal tissue of the body wall, close to the dorsolateral surfaces of the cerebral ganglia, there are what appear to be very minute spherical saccules, visible only under very high magnification. These structures may bear no relation whatsoever to eyes, but, because of their position (which is comparable to that in which the eyespots of *Microhedyle cryptophthalma* are found) there is the remote possibility that they are vestiges of eye remnants.

Two statocysts are present (Figs. 4, 6A, B:s), one on the posterior surface of each pedal ganglion, and innervated from the cerebral ganglion. Each statocyst is large, hemispherical, two-layered, maintaining its firm shape in all sectioned series.

In close association with the ventral cephalic nerves and lying over and alongside the buccal tube are large, branching clumps of mixed neural and secretory tissue, containing cyanophilic neurons and clear secretory vesicles, and here collectively termed the anterior sense organs (Fig. 18B:aso). These organs communicate with the oral end of the buccal cavity by means of many branching processes which look like

nerve endings and fine ductules, and which pass through the buccal membrane. It is suggested that these organs are olfactory in nature, having the usual sensory function, and having some form of secretion that somehow assists the sensory function, possibly by altering the pH.

There are also branched cephalic sense organs (Fig. 18A:cso) which are extensive in area, filling the cavities of both anterior and posterior tentacles and the anterior part of the cephalic haemocoel. These organs are highly innervated by ramifying branches of the anterior and posterior tentacular and the median labial nerves. Their sensory cells have long, fine tips which are extended through the epidermis to reach the body surface. These organs are associated with perception of tactile and possibly sonic stimuli, as confirmed by the obvious searching activity of the tentacles and their immediate response to external stimuli. It is suggested that it is by this organ that the animal is aware of the physical character of its surroundings, for example, size of mud interstices, depth of water, and movement of both the water and the mud substrate.

Chemoreceptor buccal cells are found concentrated in the lips; they are small, with tiny, deeply cyanophilic nuclei.

Some mention must be made here of two other structures, not primarily sense organs, but which may have some sensory functions. The first is the large oral or suprapedal gland (Fig. 2:spg), described previously, that contains in its mid-ventral region a massive array of nerve fibres forming a tract leading towards the scoop ridge. The projections of the cells of this ridge may be minute cirrilike sensory processes; the ridge is held stiffly (Fig. 1C) in the living animal, as can be seen readily when it is moving under the surface film in an inverted position.

The second of these structures is the foot gland which occurs in numbers in the pedal sole. Although each of these glands obviously fulfils its glandular function by opening to the exterior through the epidermis of the pedal sole, the body of the gland extends through the connective tissue into the haemocoelic space of the pedal haemocoel (Fig. 10C). It is therefore possible that they may be sensitive to changes in turgor pressure as the foot travels over the substrate; they are innervated directly by the anterior pedal nerves.

Circulatory System

The pericardium (Figs. 7A, B, C, 8A, 14B, C, 15A, B, C:p) is large, shaped somewhat like a brazil nut and situated diagonally on the right, immediately posterior to the dorsal haemocoel (dh) of the visceral hump (Fig. 7A, B, C, 8A). It is anchored (Fig. 8A) by numerous muscle strands (pam), which are attached to the subepidermal muscles, and steady it during the very active pulsation of the heart; presumably these strands provide the necessary state of controlled stretch required for adequate heart beat.

The wall of the pericardium is very thin, being composed of flattened epithelium and small muscle cells (Fig. 16A:mpw); posteriorly, in the vicinity of the nephrostome, it is only of one cell thickness, forming an extremely delicate membrane. There are three openings in the wall. On the posterior wall there is a two-flap (Fig. 16A:t-fv), or sinu-cardiac, valve (Fig. 8A:va) at the junction of the posterior visceral haemocoelic sinus with the heart. This valve is operated by numerous muscle strands which are inserted on the body wall muscles and on haemocoel walls (Fig. 8A:pvm); it provides direct access for body blood returning

particularly from the extended haemocoels of the enlarged visceral sac. Just beside this valve the curving tip of the pericardium is firmly anchored (Fig. 16C:ptp).

Also on the posterior wall of the pericardium there is a large nephrostome (Fig. 8B, C:ns; 16D:nf), described under Excretory System. On the lower part of the anterior pericardial surface is the large, balloon-valved aperture of the common aorta.

On the right side of the animal the pericardium tapers off towards the ventral body wall.

The heart (Fig. 7A, B, 15C, 16A:h) is an elongate, distinctly single-chambered structure which curves from the two-flap valve to the aorta without constriction or histological change in its muscular walls (Fig. 15B, C). At present there is no available embryological material from which to deduce the true homologies of this chamber, but, judging from the position of the valves and the character of the walls, the heart is all ventricle. The absence of an atrium is interesting in the light of Raven's (1958) statement that atria are not morphological parts of the heart, but derived embryologically from the branchial veins, secondarily joining the heart. Kowalevsky (1901) first reported a single-chambered heart in *Hedylopsis spiculifera*, but did not describe it further.

The myocardial cells are simple and tapering with long fibrils. There is no distinct epicardium although scattered squamous cells are present. There is no endocardial lining.

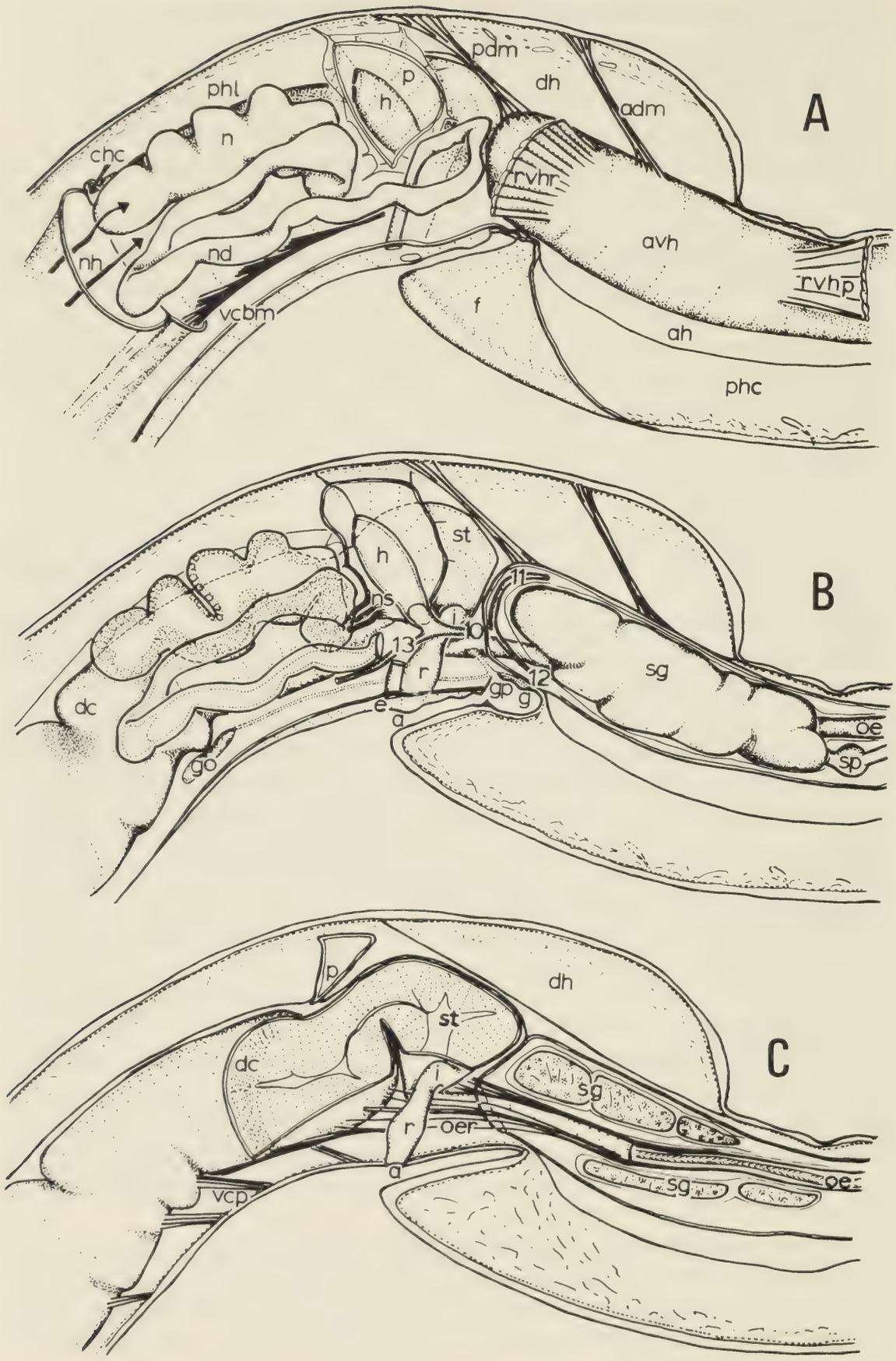
The common aorta (Fig. 14C:ca) emerges from the heart via the hemispherical balloon valve (Fig. 7B, 15A, 16D:bv) and has a structure (Fig. 14) similar to that of the heart with, in addition, a surrounding thick outer coat of longitudinal muscles. It divides into two aortae (Fig. 7B) as it passes vertically downward. The posterior visceral aorta (13) passes backward along the right side of the digestive caecum. The anterior cephalic aorta (Fig. 14:aca; Fig. 7B:10) passes forward and slightly upward and divides into two; one artery, the dorsal anterior (11), proceeds dorsally between the upper surfaces of the pharyngeal glands, and the other artery, the ventral anterior (12), passes forward ventral to the oesophagus. Both of these anterior arteries are distinguishable right up to the head region.

There is a specialized area in the wall of the anterior ventral artery, where some large cells bulge into the lumen of the artery, forming nodules (Fig. 11D); these nodules receive fibres from the adjacent visceral nerve and may be sensory, perhaps even constituting some form of pace-maker mechanism.

Well-defined haemocoelic spaces or sinuses are present. In the anterior region the gut with its associated glands is enclosed in a thin tube, the anterior visceral haemocoel (Fig. 7A:avh), which travels along with the gut during body movements and also during withdrawal of the head into the hump. This visceral tube lies concentrically within the anterior haemocoel (ah) and thus there are two forward haemocoels, one within the other.

In the foot there is a very large pedal haemocoel (Figs. 7A, B, 13A:phc), which in cross-sections through the mid region is shown to be divided by diagonal strands of tissue into three compartments (Fig. 12A, B). It should be noted that the oral or suprapedal organ is excluded from the pedal haemocoel (Fig. 2), although it appears to be pushed into the foot.

In the free hump region the haemocoels are complex (Fig. 7). In the anterior and upper part of the hump, where it bulges up from the anterior body and head, there is a large dorsal haemocoel (dh); this is the space into which the body wall invaginates to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engulf the head during the rolling-in process. Posteriorly the free hump is filled by the long, tubular posterior haemocoel (phl); this contains the pericardium (p) and two haemocoels. The first of these is the caecal haemocoel (chc), in which lie the stomach (st) and digestive caecum (dc), the gonad (go), and posterior nerves and blood vessels; the second is the nephridial haemocoel (nh), containing the long, bulging nephridium (n) and its looped duct (nd). Figure 7A shows the spatial relationships of these haemocoels; haemocoels may also been seen in the transverse series of sections (Figs. 12–17).

The curved surface where the anterior, caecal, and posterior haemocoelic walls impinge is termed for convenience the ''cephalic-visceral septum'', although it is clearly an oversimplification to call this structure either a septum or a diaphragm.

The blood cells are small, nucleate, and not particularly numerous (Fig. 9F, G, H). They are found chiefly in the heart and arteries and are more fully described in the section on Free Cells (p. 33).

In the living animal there is no sign of respiratory pigment in the haemolymph.

Excretory System

The single excretory organ or nephridium (Figs. 3, 7A, B, 8A:n) lies dorsally within its own haemocoelic cavity, towards the animal's right side and extends backward from the pericardium to more than half the length of the free visceral hump. It is capable of contraction both during and independent of body locomotory movements. It consists of a nephrostome (Figs. 7B, 8B, C, 16B:ns), renopericardial canal (Fig. 8B, C:rpc), elongate pouched nephridium proper, and looped tubular nephric duct (Fig. 7A:nd) opening through a nephridiopore (Fig. 14C:np) directly to the exterior, adjacent to, but quite separate from, the anus (a).

The nephrostome funnel (Figs. 8B, C:ns; Fig. 16D:nf) is approximately 48 μm in diameter and extends well into the lumen of the pericardium (p) (Fig. 8C). Each cell in the funnel bears a tuft of four very long flagella which curve around and down into the renopericardial canal. Individual, unbroken lengths of flagellum have been measured at 60 μm, so that the total length may exceed this figure. The kinetosomes of the flagella are situated near the proximal (lumen) border of the cell, the large, elongate nuclei being immediately distal to them (Fig. 8D).

The renopericardial canal (Fig. 8C:rpc) is continuous with the funnel and bears similar cells, whose flagellar tufts also pass backward towards the internal opening of the canal. The canal in longitudinal section is shaped like an elongate horseshoe (Fig. 8C), being about 74 μm long and 43 μm wide. It is circular in transverse section and shows a vortex in the centre of a mass of swirling flagella (Fig. 21B).

The canal opens by a fine exit tubule (Fig. 16D:et) into the nephridium proper, which is a long sac and is sinuously bent.

Fig. 7 *Tantulum elegans*. Optical dissections of middle region, from right side.

- A Integument removed, pericardium partially opened.
- B Haemocoels opened, nephric duct cut, pericardium fully opened.
- C Excretory system, heart, vessels, right pharyngeal gland, gonad, and most of pericardium removed; stomach and digestive caecum opened.
- 10 Anterior cephalic aorta.
- 11 Dorsal anterior artery.
- 12 Ventral anterior artery.
- 13 Posterior visceral aorta.

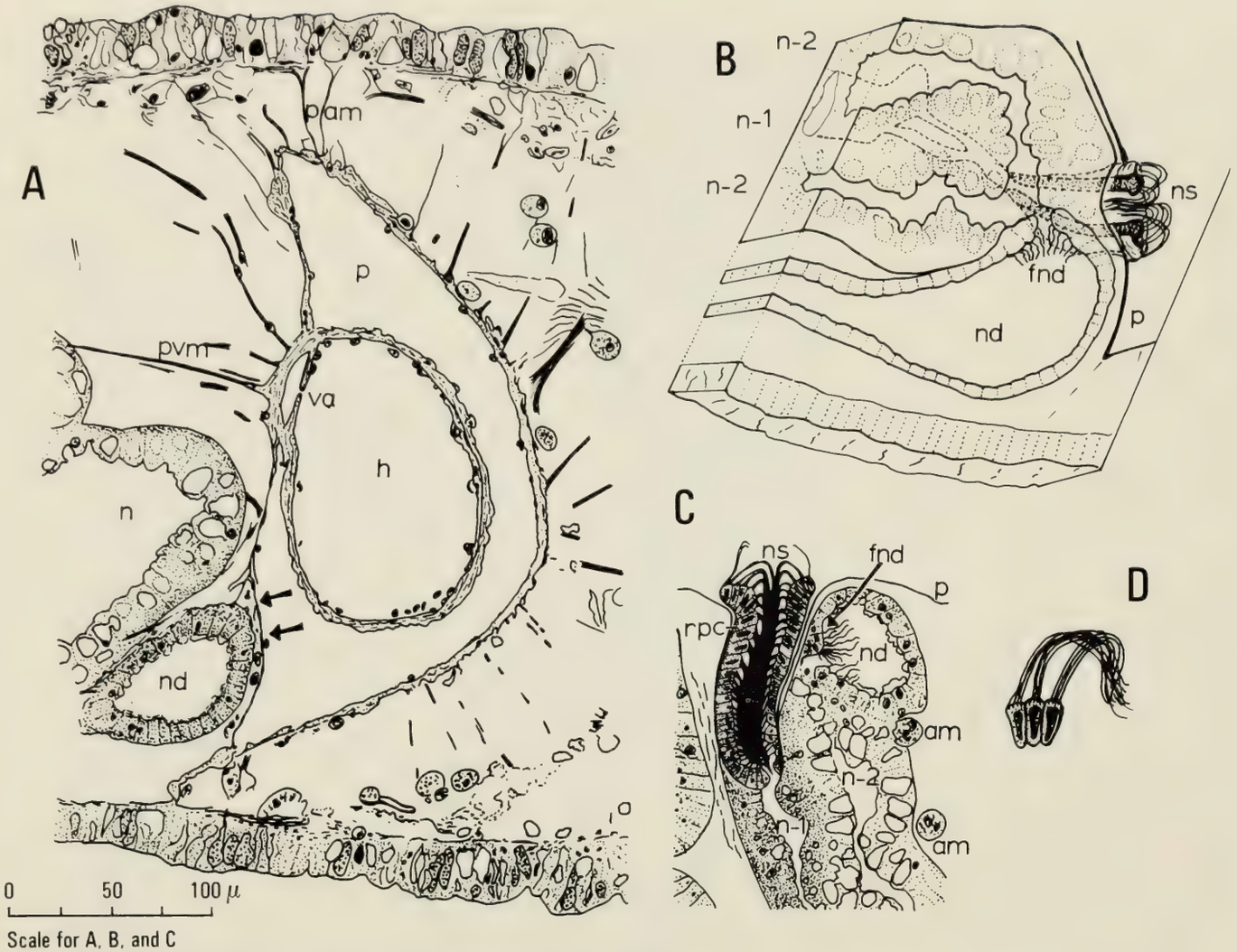


Fig. 8 *Tantulum elegans*. Pericardium and excretory system.

A Heart in pericardium, camera lucida drawing of three superimposed sections.

B Nephrostome and renopericardial canal, stereogram showing relations to nephridium and duct.

C Renopericardial canal, camera lucida drawing of two superimposed horizontal sections.

D Flagellated cells of renopericardial canal.

Internally, the sac is complex in character. The proximal part is composed of several layers of nephrocytes which surround the entry of the renopericardial canal. These cells have small vacuoles and are very granular in appearance; they continue down the mesial side of the nephridium, enclosing a small, irregular lumen (Fig. 8B, C, 17A, B:n-1) which widens near the tip. These cells merge with much larger nephrocytes, which each contain an enormous vacuole, occupying the greater part of the cell. Often the vacuoles of neighbouring cells appear to show very fine interconnecting ductules. The nucleus of the large nephrocyte is large, peripheral, and usually somewhat lateral to the vacuole. The large nephrocytes surround a very large lumen (Figs. 8B, C, 17A, B:n-2), which occupies the greater part of the nephridium, often forming only a single layer around the cavity. There are therefore two main parallel tubes surrounded by nephrocytes in the nephridium, one being very much wider than the other (Fig. 17B). The function of these kidney cells is discussed under Physiology.

The nephridium connects with the long, looped nephric duct (nd) which lies alongside it by a minute pore, with cells that bear delicate flagella 14 μm in length (Fig. 16B:fp). The pore is termed here the "inner flagellated pore" (Fig. 8B:fnd).

The two arms of the duct and the nephridium are held firmly together by the outer wall of the nephric haemocoel (Fig. 17A, B:nh) which forms a mesenterylike sheet.

The structure of the nephric duct suggests that it is more than a simple conduit or ureter, playing an important part in active excretory exchange. The walls contain muscle fibrils and are lined with small cuboidal epithelial cells (Fig. 11B), which show a densely cyanophilic peripheral area and a thin irregular inner portion towards the lumen (lu) of the duct. These thin portions curve and give the impression of temporary projections from the cells (Fig. 16D:cuc). The latter part of the duct dips down sharply alongside the intestine and rectum to open through the nephridiopore beside the anus in the small ciliated patch (Fig. 14C).

The innervation, mentioned previously, would indicate that the nephridial duct is innervated from the right side of the visceral loop, whereas the renopericardial canal and nephridium are innervated from the left side; this may possibly indicate either a double origin for the kidney or a separate origin for the duct.

Reproductive System

In all specimens examined the reproductive system presents a reduced appearance, which makes interpretation of the histology difficult. Until further material is available I wish to reserve my final opinion as to whether this animal is dioecious or hermaphrodite, protandrous or protogynous, and shall therefore simply describe the structures so far noted.

A small, narrow, tubular gonad (Figs. 3, 7B:go) is present in the caecal haemocoel (Fig. 14A:chc), ventral to the digestive caecum and half-way down its length. The cell boundaries within the gonad are somewhat indistinct, but there are at least two main types of cell present (Fig. 9G in right-hand tube), distinguishable largely by their nuclei. Cells with ill-defined borders and long, oval nuclei, containing evenly distributed chromatin, are found in clumps with the long axis of the nucleus usually parallelling the walls of the gonad. Large cells with round nuclei are tightly packed diagonally within the walls; the cytoplasm of these latter cells tends to show clear spaces, which in the transverse series of sections (Fig. 15D:go) show up distinctly as actual vacuoles, whereas each nucleus shows a curious central, densely staining

round nucleolus with stellar projections into a clear perinucleolar area which is surrounded by concentric rings of chromatin granules.

The gonoduct is long and very narrow with tiny cells each containing a round, darkly staining nucleus. The gonoduct proceeds without change in character as far foward as the rectum, where it is joined by a short vertical diverticulum (Fig. 13B:gdi) which lies against the wall of the rectum and intestine, and which is indistinguishable histologically from the gonoduct. The duct then continues forward to open into a slitlike groove, which is situated in the dorsal wall of what is here termed the "gonadial or genital pouch" (Fig. 7B:g). This pouch is a wide indentation of the ventral surface of the visceral sac integument and is situated on the animal's right side, extending slightly over the mid line towards the left, at the juncture of the hump with the foot. It is possible that this pouch is homologous with a mantle cavity.

There is no duct or ciliated groove visible between the gonopore and the head. There is, however, a structure whose affinities are not immediately definable; just posterior to the left posterior tentacle there is a small ridge (Fig. 18B:r), of nonglandular epidermis in which there is a small canalicular opening (co), leading inward to a thin-walled saccule (s). This saccule lies lateral to the cerebral ganglion (cg) and is not to be confused with the statocyst of the same side, which is ventral and posterior to it and near the pedal ganglion. Although it is unlikely, this structure with its small duct could be regarded as the remnants of a male intromittent apparatus. although it is more usual to find such structures behind the right, rather than the left, tentacle. If it is part of the male genitalia, then the animal must be regarded as either male or hermaphrodite, and consequently the gonad is either a testis or an ovotestis.

If the gonad is a testis, then the large cells with the round nuclei must be regarded as sperm mother cells, and the cells of indefinite outline and elongate nuclei as developing early spermatids. If, however, the gonad is to be regarded as an ovotestis, then the large cells might be oogonia and the clumps of elongate cells spermatogonia. Unfortunately no matured genital products were found in any series of sections. Similarly, the gonoduct is either a sperm duct, with storage diverticulum, or a common spermoviduct with a seminal receptacle in which self sperm from the protandrous male phase could be stored until needed.

It is however possible that the anterior sac is only a developmental stage in the formation of a true penial complex and that the plastic appearance of the gonadial cells is simply an indication of immaturity.

It is more likely that *Tantulum elegans* is a true hermaphrodite and protandrous, as populations composed entirely of males are not as common as either purely female or mixed populations amongst Gastropoda.

Musculature

Because of the elongated shape of this animal and the consequent lengthening and narrowing of body organs, the musculature shows a very noticeable development of shortening and retractor elements. In addition to the normal longitudinal muscles found in the walls of various structures, there are greatly thickened long strands at certain points throughout the body which obviously can act as locomotory and emergency retractors. There are relatively few protractor muscles, protraction being accomplished largely by relaxation of the retractors.

Every large structure, including nerves and blood vessels, is accompanied by long fibres, ensuring rapid rolling-in in response to adverse stimuli. There are both

longitudinal and circular strands in the subepidermal connective tissue but many of these fibres are tangentially arranged. The walls of the haemocoelic cavities, whose fluid maintains the turgor of the animal, are also supplied with thin muscle strands.

In the foot (Fig. 12A, B), the diagonal partitions, which divide the haemocoel into three compartments, contain muscle strands. These strands obviously aid in the contouring of the lubricated and gliding ciliated sole.

In the dorsal haemocoel (Fig. 7A, B) there are anterior (adm) and posterior (pdm) diagonal retractor muscles which run from the wall of the anterior visceral haemocoelic tube to the body wall; these are responsible for pulling the head end back dorsally so that it can be tucked into the hump. This movement may be assisted by the posterior and ventral pharyngeal retractors, the anterolateral pharyngeal protractors, and possibly also the visceral haemocoel retractors (rvhr); simultaneous contraction of these muscles would produce a withdrawal of the head. Forward movement of the anterior visceral haemocoel itself is assisted by paired lateral protractors (rvhp).

The whole pharyngeal complex, that is, pharynx, pharyngeal salivary ducts, and glands, together with the anterior part of the oesophagus, is in constant to-and-from movement within the body, as can easily be seen in the living animal. This movement is produced by the extrinsic pharyngeal muscles described under Alimentary System (p. 10).

The elongate oesophageal retractors (Fig. 7C:oer) which accompany the oesophagus, passing through the cephalic-visceral septum to attach to the stomach and anterior walls of the digestive caecum, can withdraw the latter part of the oesophagus during rolling-in; the oesophagus becomes looped over in this process, and the pharyngeal glands bunch up into two large clumps.

Powerful muslces also originate on the septum and posterior part of the oesophagus and are attached serially, by digitating fibres, onto the digestive caecum and ventrolateral body wall. They have been termed the ventral caecal bdelloid muscles (Fig. 7A:vcbm), as they are clearly used in major leechlike looping of the free visceral hump during locomotion.

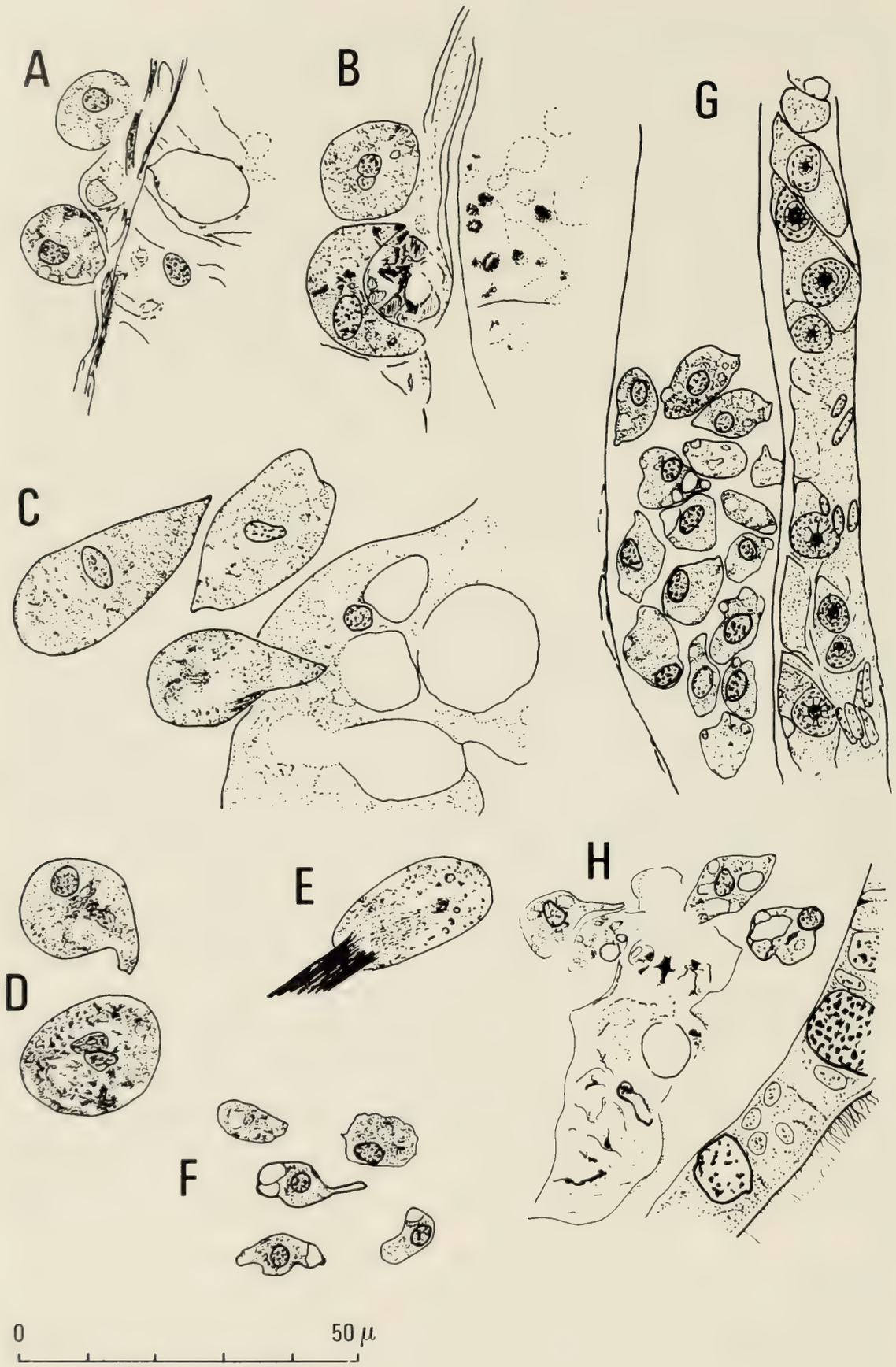
In the same anterior region of the caecum there are several serially arranged ventral caecal protractors (Fig. 7C:vcp), which may assist in initiating the reverse phase of peristaltic contraction of the intrinsic caecal muscles.

Muscle fibres may be arranged in loose bundles, as in the somatic muscles; they may also be found criss-crossing in thin sheets, as in the thin splanchnic muscular coats of various organs and in the subepidermal layers; they may also be arranged directionally in thick blocks and sheets, as described for the pharynx (Fig. 20A).

Muscle cells may also occur individually, such as those that anchor the pericardium (Fig. 8A:pam); they appear to be almost always binucleate, with fibres that are generally single at point of origin and with a bifurcate tip at place of insertion.

Integument

The integument consists of a single-layered epidermis, a thin muscular layer, and a zone of connective tissue of very variable thickness. The whole integument is glandular, with no specialized pallial zone or shell-forming areas, but with subepidermal spicules in certain places. Cilia are present only on the pedal sole and anterior curve of the foot. The integument is sturdy, except on the upper surfaces of the foot, where it is noticeably thinner.


A
B
G
C
D
E
H
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0
50 μ

The cells of the epidermis (Fig. 10) are large; on the dorsal surface (A, B) and tentacles they are columnar, but they tend to be more cuboidal on the ventral surface (D). On the sole of the foot they are smaller and distinctly cuboidal (E).

Several types of cells are distinguishable. The supporting cell has fine, lightly staining eosinophilic granules and an elongate nucleus with delicate chromatin; in the pedal sole the supporting cell is similar but ciliated, with a kinetosome clearly visible at the base of each cilium, and with a larger, more rounded nucleus. Interspersed among these cells are large, ovoid cells with very large granules; each has a small pore to the exterior, which because of the great size of these cells, is not visible in all sections. Their muco-polysaccharide granules stain deep purplish blue with metachromatic methylene blue and it is therefore easy to assess the cell distribution; the cells are very numerous over the dorsum as a whole, with slightly greater concentrations over the head and anterior hump, whereas they are more evenly distributed in the lower surface of the visceral sac. In the pedal sole they are fewer in number, tending to occur in small clumps and to be absent from the anterior tip.

Pyramidal cells are also seen, each with a large cavity leading to the exterior by a small neck and pore. Some of these cavities may not be entirely empty but contain granular debris near the base. As this debris is also purple in colour, it is suggested that these "goblet cells" are merely exhibiting the empty phase of the muco-polysaccharide-secreting cell.

Sensory cells as such cannot be clearly distinguished although it is suspected that they are present as thin, slender rods; nerve endings (Fig. 10G) have been noticed near such structures.

In the pedal sole there are also numerous ducts and openings of the subepidermal pedal glands (Fig. 10C). These are large glands whose lobular bodies extend well into the pedal haemocoel, where they appear to be freely movable. The interior of each gland contains an irregular meshwork with darkly staining small patches and a secretion which is smoothly homogeneous in most of the gland but which becomes at times finely granular near the duct.

Immediately under the very thin basement membrane of the epidermal cells lies the thin muscle zone, with its fibres arranged in several planes. Attachments of somatic muscles (Fig. 10F) may also be seen here.

The variable connective tissue zone is widest at the posterior end of the foot, the end of the trailing hump, and above the dorsal haemocoel (Fig. 10A). The main cells are very large, polygonal, extremely faintly staining and delicate, and form a loose parenchyma. Some more darkly staining smaller collagenous cells are found in this zone, together with transiting nerve and muscle fibres.

Spicule forming cells are found (Fig. 10A) in the connective tissue, always in the

Fig. 9 *Tantulum elegans*. Free cells. Camera lucida drawings.

- A Digestive giant amoebocytes near vacuolated cell of digestive caecum.
- B Digestive giant amoebocyte in active phagocytosis from caecal haemocoel.
- C Excretory giant amoebocytes near nephridium, one cell sending lobopod into nephrocyte.
- D Calciferous giant amoebocytes, upper cell beginning condensation of calcium, lower cell with more condensed calciferous material.
- E Spiculocyte pushing out calciferous striae.
- F Blood cells, central one shows large lobopod.
- G Blood cells clumping in posterior visceral aorta near gonad.
- H Blood cells clumping near pedal gland.

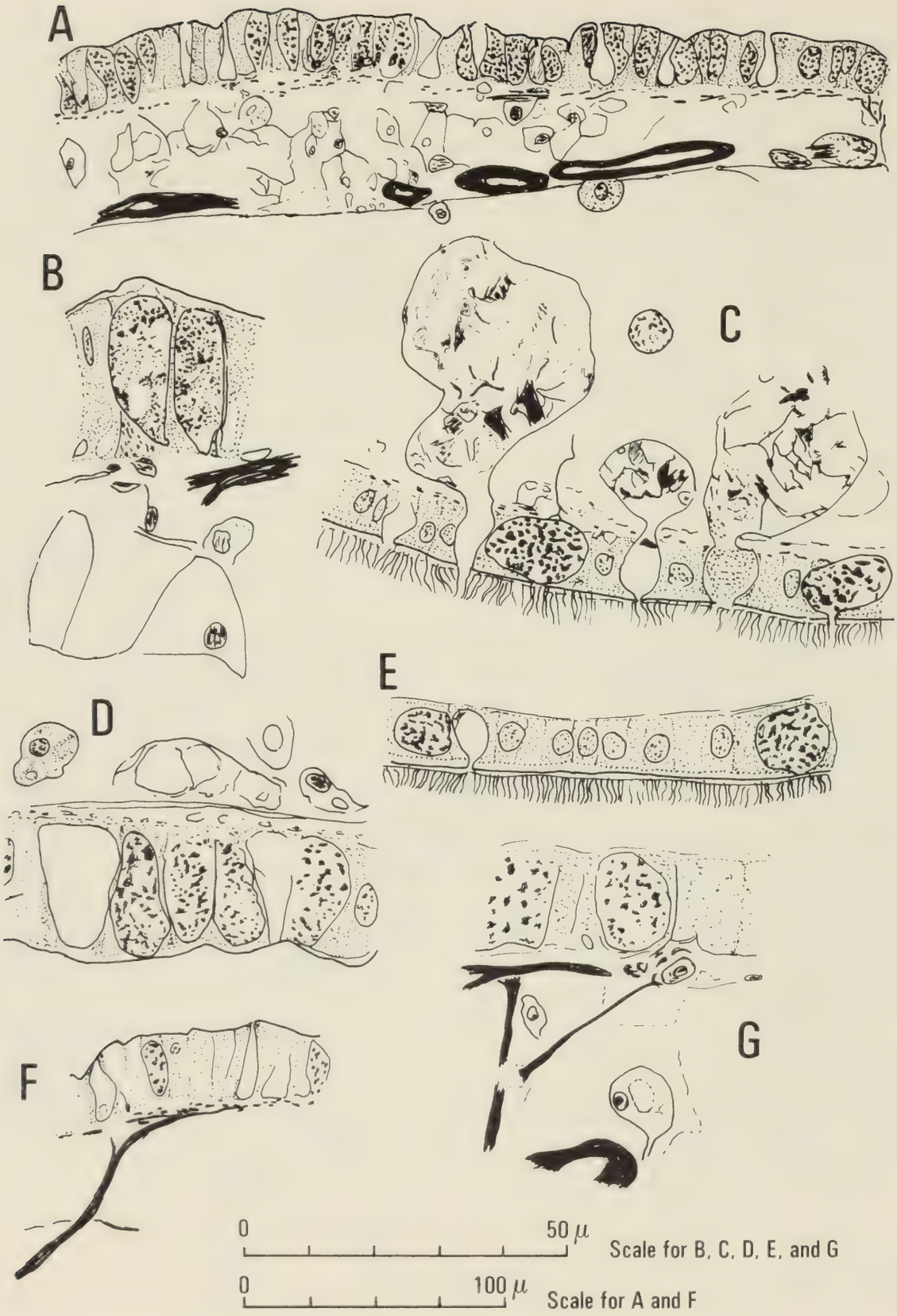


Fig. 10 *Tantulum elegans*. Integument. Camera lucida drawings.

- A Dorsal hump region, over dorsal haemocoel.
- B Cells from dorsal hump region, enlarged.
- C Pedal sole, mid-pedal region.
- D Ventral hump region, mid-region visceral sac.
- E Pedal sole, near anterior border.
- F Attachment of somatic muscle to subepidermal muscle layer.
- G Nerve with ending in epidermis.

area adjacent to a haemocoel. Formation of the spicule is described in the section on Free Cells. Spicules are elongate, hollow, curved rods or boomerangs with a definite distribution pattern and size range. Small integumental spicules, few in number, are found scattered over the hump; at the posterior tip of the hump they are more concentrated. Large skeletal spicules, however, may attain the length of 75 μm or more and are restricted to two zones in the animal, the cerebro-pharyngeal and the pericardial. A cluster of these giant spicules overlies the anterior ganglionic complex dorsally and some of the more lateral spicules are produced downward on either side of the complex and of the pharynx (Fig. 1A). Similarly, the pericardial region is protected dorsally and dorsolaterally. Thus the two most vulnerable and important areas of this mollusc receive girderlike support and coverage.

Free Cells

There are two distinctly recognizable categories of wandering cells, blood cells and giant amoebocytes.

Blood cells (Fig. 9F, G, H) are amoebocytic, being from 10 to 12 μm in length when at rest but capable of attenuating themselves to 15 μm or more. They are never rounded, and are irregularly ovoid or spindle-shaped at rest. The nucleus is oval, eccentric, and has a distinctly stained nuclear membrane and a few dense patches of chromatin. The finely granular cytoplasm is arranged in strands around small clear areas and also one or more true vacuoles or vesicles are always present. The latter give the characteristic frothy appearance to the cells.

Blood cells are comparatively few in number and are most easily found in the heart and major vessels. Clustering of cells, which does not appear to be explainable simply by reason of fixation during histological preparation, has been noticed both within a blood vessel (Fig. 9G left-hand tube) and in a haemocoel (Fig. 9H on left). In the first instance the blood cells are separated from the gonad by only the very thin vessel wall; in the second, blood cells may be seen pushing amoeboid processes into the tissue of a pedal gland.

Giant amoebocytes are spherical at rest, being from 15 μm to 20 μm or more in diameter but capable of extending themselves to 35 μm or more (Fig. 9C, D). They are characteristically found in the posterior, dorsal, and anterior haemocoels and never in the heart or blood vessels; they are most numerous around the posterior curve of the digestive caecum, near the genital opening and near the tip of the nephric haemocoel.

The giant cells are found in four main functional phases, at least one of which appears to be irreversible. These phases are digestive, nephridial, skeletal, and genital.

Digestive amoebocytes can be found in large numbers clinging to the regions of the posterior haemocoelic wall which are adjacent to the digestive caecum. In Figure 9A two cells may be seen near a recently discharged vacuole; although separated from the caecum by both posterior and caecal haemocoelic walls it can be seen that the cells are closely pushed in towards the gastric cells and that secreted material is being passed across the double membrane into the cytoplasm of the giant cell. This type of gastric vacuole is found chiefly in the posterior third of the caecum, in the region where the greatest number of giant cells is found. Figure 9B shows an amoebocyte actively engulfing secretory droplets from the double membrane; similar material is seen in the adjacent gastric cells.

At the posterior end of the nephridium, the adjacent haemocoelic walls are thin and

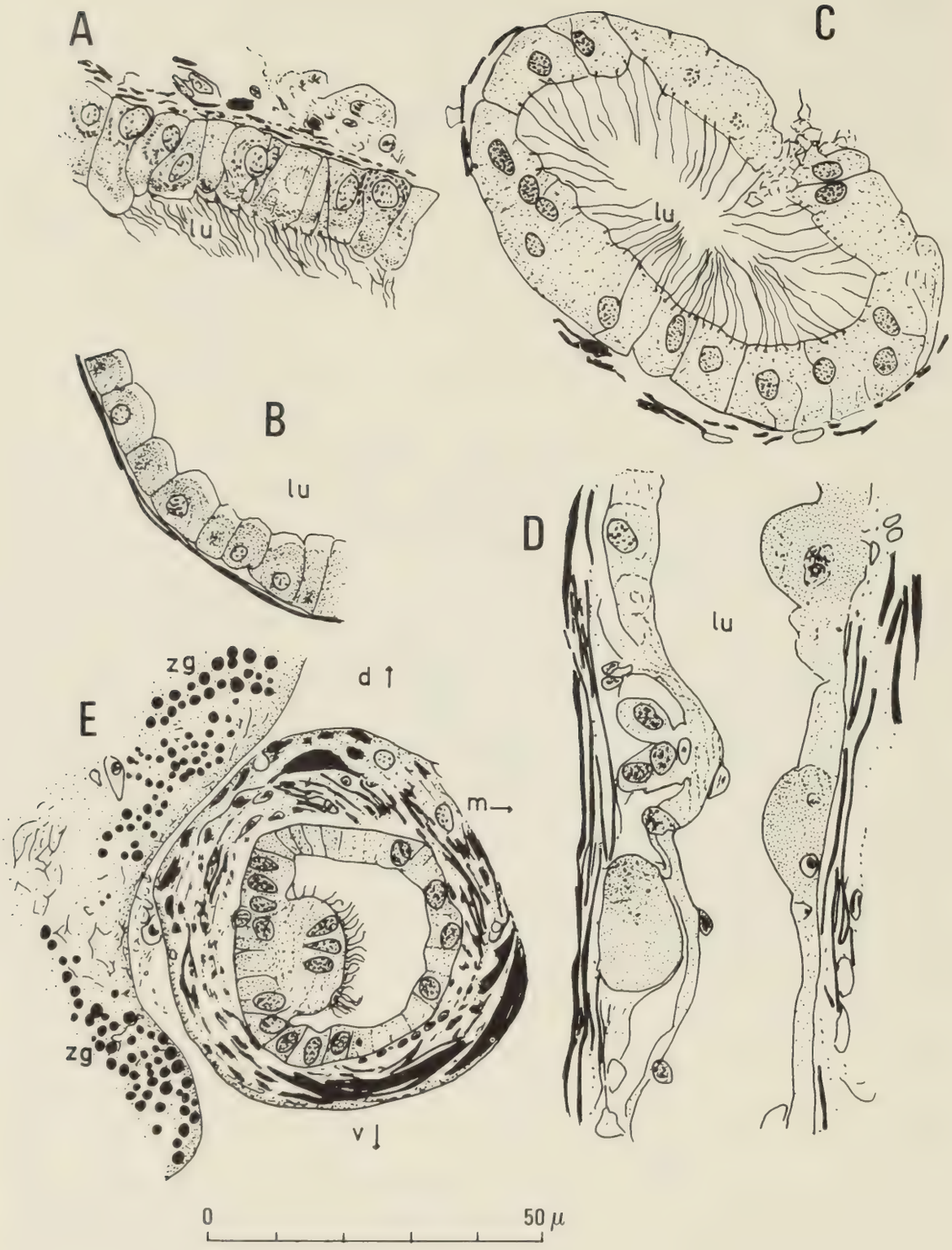


Fig. 11 *Tantulum elegans*. Histology. Camera lucida drawings.

A Intestine, longitudinal section showing bands of mitochondria around nuclei.

B Nephric duct, longitudinal section showing clear inner borders of cells.

C Oesophagus, transverse section showing long cilia.

D Anterior cephalic artery, longitudinal section showing nodules pushing into lumen.

E Pharyngeal pump, section through mound of ciliated cells, slightly to one side of pharyngeal gland opening.

closely adherent to the nephridium (Fig. 7A) and it is in this region that clusters of giant cells are found. Figure 9C shows active cells, one of them with a lobopod actually penetrating to a vacuole; the upper two cells appear more swollen as if recently engorged by substances carried by, or dissolved in, the nephric fluid. What we see here is obviously a selective reabsorption in process.

Giant amoebocytes may also exist as skeletal cells which become spiculocytes in connective tissue adjacent to haemocoels. Figure 9D shows skeletal amoebocytes as seen in the dorsal haemocoel just before they penetrate the very thin haemocoelic wall. In both, the beginnings of calcium deposition may be seen. Figure 9E shows the emergence of the spicule; even very long spicules may be found with their mother spiculocyte still attached and still apparently functioning. It is not known whether additional calcium cells may contribute to the formation of any one spicule, although the presence of adjacent cells (Fig. 10A) suggests this possibility. How these calcium layers are laid down is not known but it is possible that the process may be similar to the formation of calcium spherites discussed by Wilbur (1972).

The method of formation of spicules in *Tantulum* is clearly different from that found in the Aplacophora where the spicule is secreted by an epidermal cell (Hoffman, 1949), or the Polyplacophora where the spicule is formed by an epidermal cell packet, or even in Doridaceans (Prenant, 1924) where connective tissue scleroblasts secrete the spicule and persist as a thin film around it. Wagge (1951), however, reported the transfer in *Helix aspersa* of calcium from the digestive gland by amoebocytes to repair sites in the shell.

Ecology

Physical Environment

The totally freshwater marsh in which *Tantulum elegans* was found is one of many which form part of the Upper Yambou River drainage system. It is fundamentally a high level marshy basin approximately 16 by 20 m, formed on a steep slope by several springs which emerge directly from the mountainside (Fig. 22) and which eventually drain by one main channel into the river below. Most of the area of the marsh is naturally under sedge, *Fuirena umbellata* Rottb. but the central, deeper portion is planted out with *Colocasia esculenta* Schott, the edible dasheen, the term being a local corruption for *taro de Chine*. The leaves of the latter are cropped only occasionally in this particular marsh and therefore broad leafy shade, with water surface values of from 5 to 300 hectolux, is available. The aquatic, bulbous roots are dug out once, or perhaps twice a year, leaving the habitat undisturbed for most of the year.

The major part of the substrate, that is in the sedge section and in the channels, is a light covering of mud over gravel, but in the dasheen area there is only a thick deposition of soft, silty mud which is bound together by a tangled mat of rootlets. Within the dasheen portion of the swamp there are further very small springs of oxygenated water welling up from below the mud and it is the area above one of these that forms the microbiotope in which *T. elegans* was found. Surface water averages 3 to 4 cm in depth but the whole sampling site is merely a thin surface deposition on an elevated water table. Sampling in this area is therefore sometimes only possible by clinging to a raft of horizontally placed branches.

The flow of water through the marsh is slow but constant and the area is sheltered and not subject to heavy seasonal scouring by rain flow-off. Water temperature remains within the range 24.0°C to 28.0°C, but is usually 27.0°C to 28.0°C. Turbidity in the outflow channel rises to only 11–7 APHA units.

Chemical Environment

The average figures for water analysis from this marsh are given in Table 1. It will be noted that the chloride is low and the conductivity only moderate. The silicate is high but is a reasonable norm for volcanic islands. There is no marine influence, the marsh being over 411.5 m vertically up and approximately 3.75 km by road from the sea.

Diurnal fluctuation in ionic content is measurable but of a small order.

Biological Environment

The associated biota of *T. elegans* are given in Table 2. The number of species sharing the same microhabitat in close association is limited, but a few forms are found nearer the periphery of the dasheen area and in the sedge sections of the marsh. The latter have been included as there is no great physical barrier to movement for most species. *T. elegans* itself, however, does not move from its own little microbiotope. Similarly, the freshwater polychaete, *Lycastopsis hummelincki* Augener, previously recorded at a much lower altitude from the island of Curaçao in more brackish water, is also only found here in the dasheen area. Both of these species require high oxygen tension, hence their preference for highly oxygenated spring water.

Table 1 Water analysis of microhabitat of *Tantulum elegans*

pH	6.76
Conductivity	99.00 μmhos
HCO_3^-	82.35 mg/l
Ca^{++}	10.00 mg/l
Mg^{++}	3.75 mg/l
Na^{+}	10.00 mg/l
K^{+}	1.85 mg/l
Cl^{-}	20.63 mg/l
SO_4^{--}	2.50 mg/l
Sio_2^{--}	50.35 mg/l
P as reactive phosphorus	0.396 μg-at/l
N in nitrate form	21.20 μg-at/l
N in nitrate form	0.351 μg-at/l
Fe^{+++}	No trace
Mn^{++}	No trace
Ba^{++}	No trace
Arsenic	No trace
Copper	No trace
Zinc	No trace

The shelled amoeba *Centropyxis* sp. is abundant in the air-water interface and on other surfaces of the marshes of St. Vincent; the dead bodies of these amoebae fall to the mud surface to form an important part of the detritus.

The only other molluscs present are the common pelecypod *Pisidium punctiferum* (Guppy) and the St. Vincent pulmonate *Physa marmorata* Guilding.

Behaviour

T. elegans moves through the narrow interstices of loose mud by virtue of its finely streamlined shape, extreme flexibility, and lubricated body surface. In conditions of very high oxygen tension it may travel down to a depth of 10 cm or more, although it is usually found in the upper regions of the mud. When the oxygen content drops, it crawls rapidly up to the mud-water interface, often allowing itself to float upward to the water-air interface where it crawls upside-down under that film. In laboratory testing, oxygen depletion by withdrawal of an aerator bubbler will cause it to come to the mud surface within a few minutes.

Observation of movement is made relatively easy by the animal's small size and clear transparency in transmitted light. Locomotion is rapid, 1.5 mm per second or more, and is accomplished in several ways. Smooth, swift gliding is accomplished by means of the ciliary beat of the narrow pedal sole and is the usual means of progression on smooth substrates such as glass, finely divided mud, or the air-water interface. On coarser mud this ciliary gliding is accompanied by muscular movements of the sole, especially the edges.

In crawling over algal filaments, the ciliary and sole movements are assisted by other pedal muscles so that a central longitudinal groove is formed around the filament thus gripping it in the manner of a monorail train; at the same time the edges of the sole show irregular wavelike contractions until the animal finds more solid ground.

At intervals in all gliding movement, the free trailing hump loops under itself and gives a leechlike thrust to the animal. This bdelloid movement is noticed particularly on rough surfaces and precedes upward flotation to the water-air interface. The movement may be designed principally as an assistance to anal or excretal evacuation, or even to peristalsis, but it also appears definitely to assist in locomotion.

When crawling on an immersed and inverted glass plate, the contouring of the pedal sole may be observed without difficulty. The greater part of the sole is flattened against the glass but the centre is longitudinally raised off the plate, forming a narrow and shallow groove. In addition, whenever the animal stops moving, a central round and suckerlike hemisphere is raised, forming an adhesive disc. This movement appears to be accompanied by heavier secretion of mucus.

Turning movements are preceded by strong flexion of the head and curvature of the anterior tentacles; burrowing commences by backward movement of these tentacles until they form an arrowhead with the tip of the head. Apparently at this time the posterior tentacles are still used as sensing devices, assessing the quality of the surrounding medium. Although not so well structured for the purpose as those of *Hedylopsis spiculifera*, the anterior tentacles may also form a bulldozing shovel,

Table 2 Associated biota of *Tantulum elegans*

	Dasheen area	Sedge area
Algae	Unidentified spp.: Chrysophyta	*Spirogyra* sp.: Zygnematales
Graminae		*Fuirena umbellata* Rottb.
Araceae	*Colocasia esculenta* Schott	
Protozoa	*Centropyxis* sp.: Testacealobosa	*Centropyxis* sp.: Testacealobosa
Nemertea		*Prostoma rubra* (Leidy): Rhynchocoela
Turbellaria	*Stenostomum* sp.: Catenulida	Unidentified sp.: Neorhabdocoela
	Dugesia arimana Hyman: Tricladida	
Nematoda	*Dorylaimus stagnalis*: Dorylaimida	
Annelida	*Lycastopsis hummelincki* Augener: Nereidae, Polychaeta	*Ilyogenia* sp.: Megascolicidae, Oligochaeta
	Aelosoma sp.: Aelosomatidae, Oligochaeta	*Eukerria*-SV sp. 2: Megascolicidae, Oligochaeta
Crustacea	*Cyclops* sp.: Copepoda	
	Cypretta sarsi Brady: Cypridae, Ostracoda	*Cypretta infesta* Klie: Cypridae, Ostracoda
	Darwinula stevensoni (Brady & Robertson) Cypridae, Ostracoda	*Darwinula stevensoni* (Brady & Robertson): Cypridae, Ostracoda
Arachnida		*Hydrozetes* sp.: Oribatidae
Insecta	*Belostoma subspinosa subspinosa (Beauvois): Belostomatidae, Hemiptera*	*Mesovelia mulsanti*: Veliidae, Hemiptera
	Enallagma sp.: Libellulidae, Odonata	*Oxyethira janella* Denning: Hydrophilidae, Trichoptera
	Eristalis (=Tubifera) sp.: Syrphidae, Diptera	*Psychoda* sp.: Psychodidae, Diptera
		Bezzia-type larvae: Ceratopogonidae, Diptera
Mollusca	*Pisidium punctiferum* (Guppy): Sphaeridae, Pelecypoda	*Pisidium punctiferum* (Guppy): Sphaeridae, Pelecypoda
	Physa marmorata Guiding: Physidae, Gastropoda	*Physa marmorata* Guilding: Physidae, Gastropoda

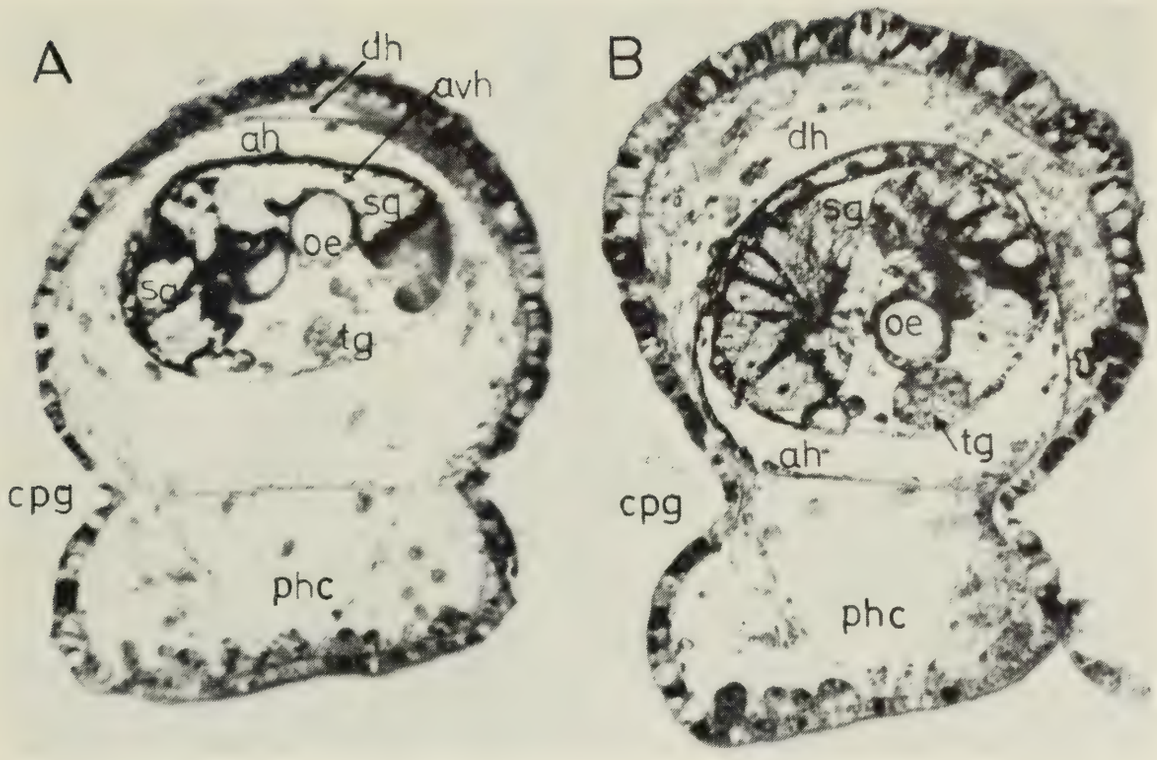


Fig. 12 *Tantulum elegans*. Transverse series.
A Through cephalo-pedal groove.
B Through dorsal haemocoel.

usually held fairly stiffly in an extended position; they may also push at and curve around lumps of detritus, rather like a feeding finger.

When tested in the laboratory, *T. elegans* showed a strongly negative phototaxis to a direct narrow beam of light; rapid circular gliding was produced by strong overhead cold light, especially when no mud surface was provided. No backward movement was observed, negative response being attained by turning, or attempts at burrowing. In nature, burrowing is obviously the preferred response to excessive light. No special areas of light-sensitivity have been observed, but the lack of definitive eyes and pigmented integumental areas suggest that the whole integument reacts strongly and evenly to light.

T. elegans is extremely sensitive to any movement of the environment, whether of the substrate or even of the surface film, reacting immediately with a positive and specific rolling-in reaction (Fig. 1B). The head initiates the rolling, turning back dorsally together with the anterior part of the foot. Almost immediately the mantle of the dorsal visceral sac contracts, the forward part of it wrinkling over the curved-over head which is still pushing in towards a temporary "mantle cavity" in the dorsal surface on the animal's right side. The rolling of the head continues until only the posterior tip of the foot remains outside the integument covering of the hump. The animal remains rolled up until the stimulatory movement of the water is over. It also appears to be capable of distinguishing between normal flowing movement, or even gentle circulatory movement produced by a bubbler, and that of a touch or knock such as may be given by a passing animal.

Feeding is by active and almost continual ingestion of finely divided, rich organic mud particles and biological detritus, and is accomplished by the combined action of a number of structures. Mud and detritus that have already been broken down during

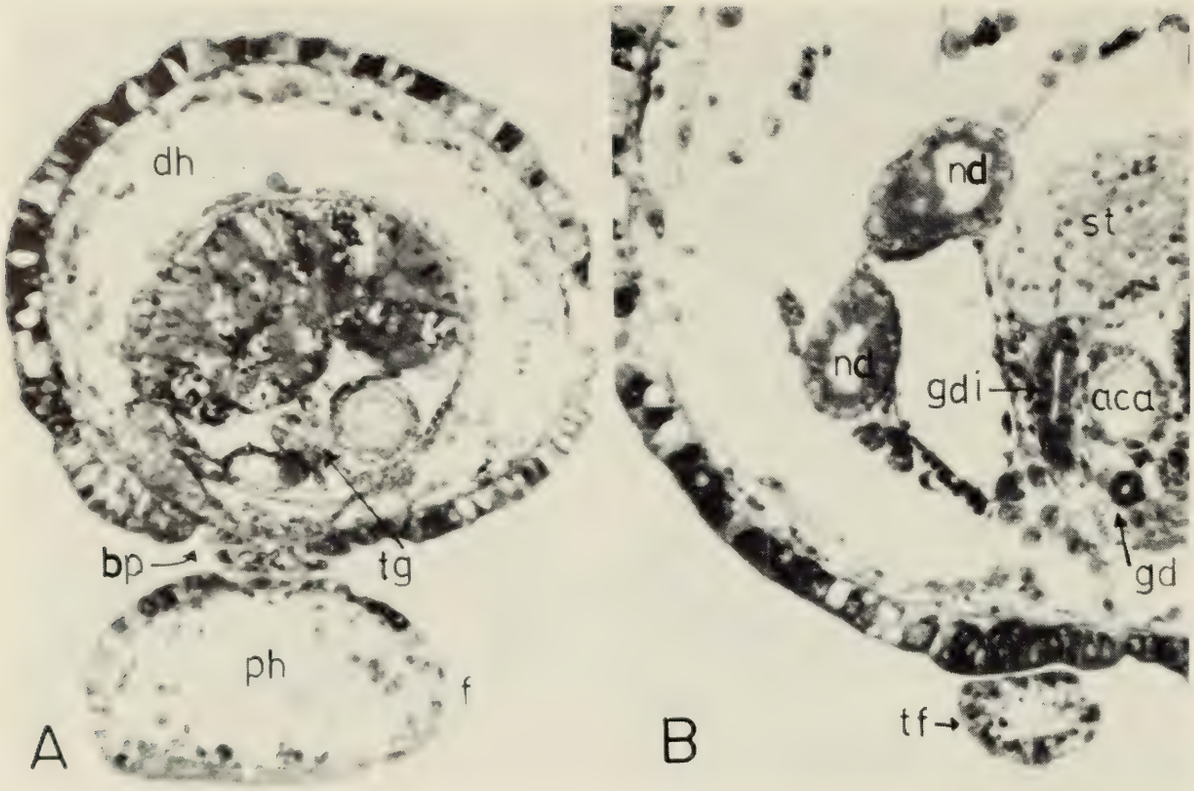


Fig. 13 *Tantulum elegans*. Transverse series.
A Through beginning of pouch (=mantle cavity).
B Through genital duct and its diverticulum.

the digestion of animals such as *Physa marmorata* and *Lycastopsis hummelincki* seem to be particularly useful to *T. elegans*. Some form of selection of food appears to be made by the chemotactic action of both pairs of tentacles and the upper and lateral lip areas, as mud and detritus is not indiscriminately ingested.

Physiology

T. elegans shows a limited temperature range, with an optimum at 24.0°C to 27.0°C. Elevation of temperature to 30°C produces death and lowering to below 22.0°C produces sluggish movement. However, a temperature of around 28.0°C produces increased rate of locomotion without apparent permanent damage. The animal can avoid hot and cold spots in its environment, usually by an initial rolling-in followed by exploratory extension and turning. Detailed controlled experiments were not possible on freshly captured animals, hence there are no further measurements.

As far as has been determined, feeding physiology is as follows: when suitable food presents, the pharynx moves rapidly forward, trailing the pharyngeal ducts and glands with it. This brings the radula towards the mouth; it is not possible actually to see the expansion and concertina folding of the buccal tube as the pharynx everts through it, although the muscular character of the thin walls suggests that this stretching and wrinkling occurs. As the pharynx moves forward it appears to contract, presumably exerting suction. There is no visible external extrusion of mucus from the mouth, so it is likely that mucous secretion produced by the massive oral organ is simply sucked in with the food material by the same pharyngeal action.

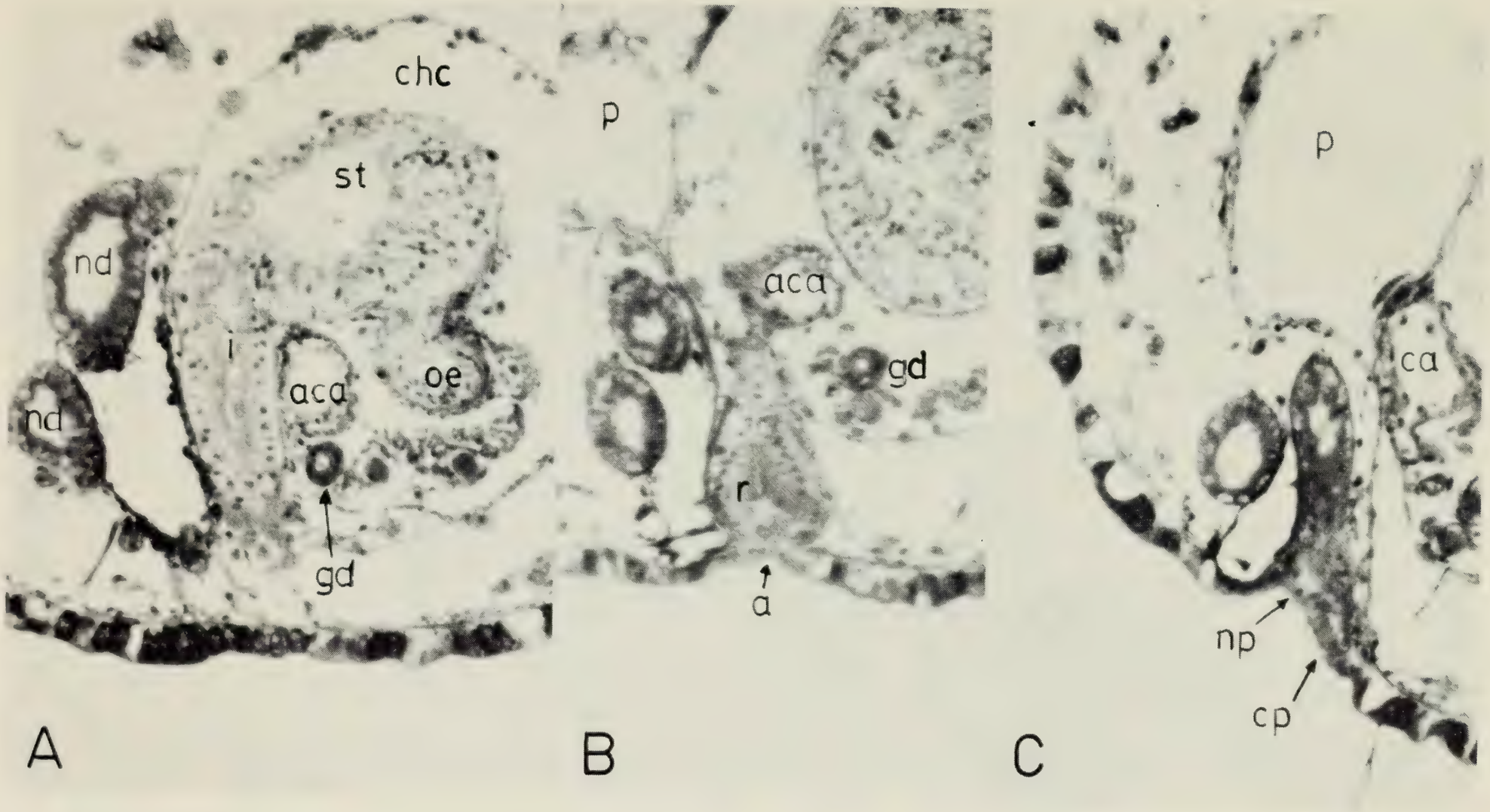


Fig. 14 *Tantulum elegans*. Transverse series.
A Through stomach and intestine. B Through rectum. C Through nephridiopore.

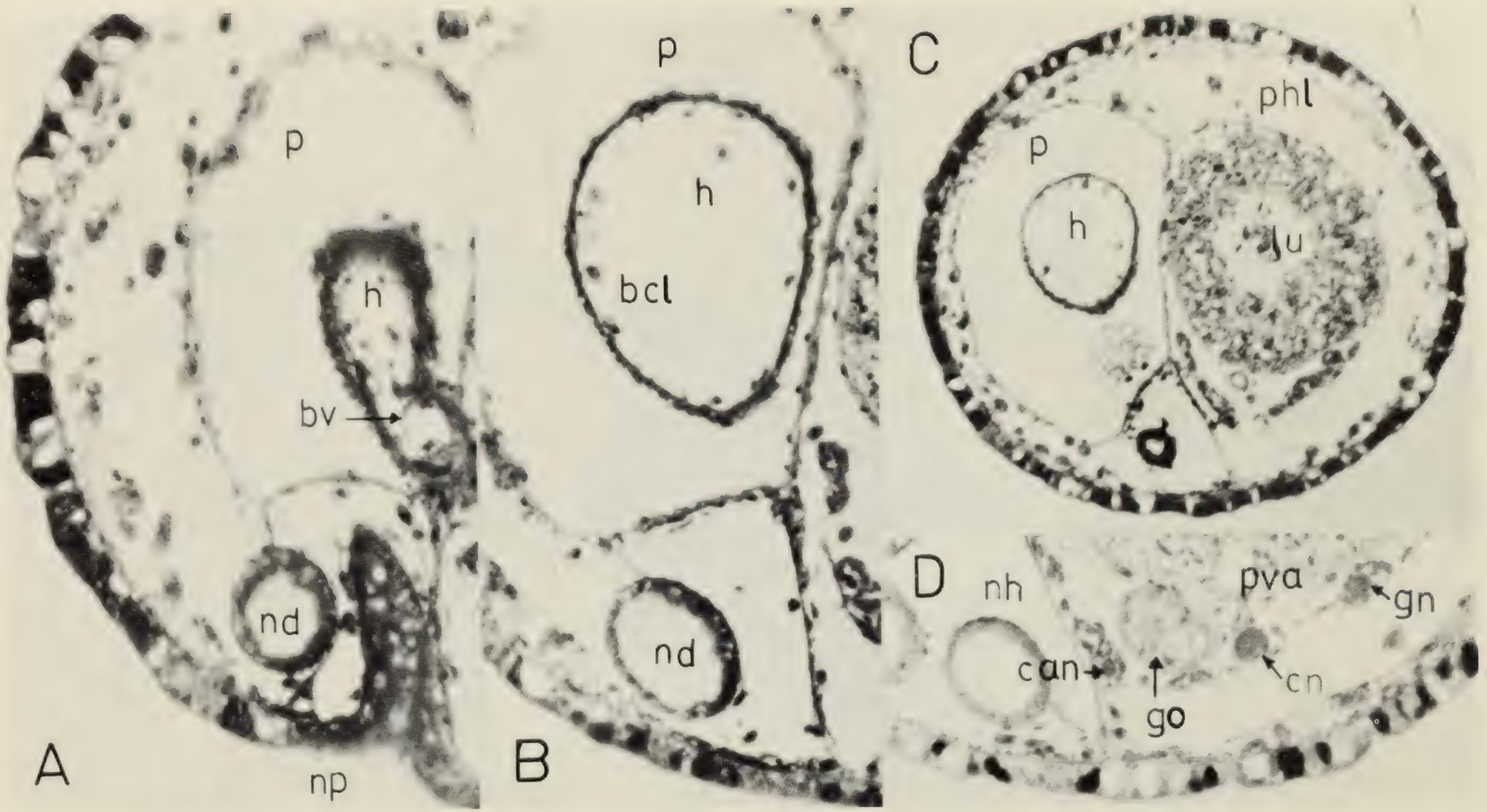


Fig. 15 *Tantulum elegans*. Transverse series.

A Through balloon valve of heart.
B Through heart.
C Through pericardium and caecal haemocoel.
D Through gonad.

As the pharynx begins to move backward the pharyngeal salivary ducts contract into a tight spiral and the pharyngeal pumps are pushed against the glands. This action could initiate the contraction of these cisterna, thus releasing the secretion into the salivary reservoirs of the pharynx, but it is more likely that it is the stretching of the duct as the pharynx moves forward again that produces this result. In the latter case, the entering food would find digestive juice already waiting for it within the food canal of the pharynx. Detailed histochemical tests were not possible on the animals available, but the size, staining characteristics, and method of production of the secretory vesicles all suggest that they are some form of zymogen granule, containing one or more digestive enzymes.

The intrinsic pharyngeal musculature appears to be in almost continual movement as the shape alters, so that the entering food is obviously being manipulated and perhaps, to a certain extent, crushed against the cuticularized epithelium. The next forward movement and major bulbar compression of the pharynx probably also has the effect of forcing out through the oesophageal sphincter this churned-up food paste composed of detrital mud, mucus, and enzymatic juice.

Movement of the food mass within the oesophagus appears to be attained by the ciliary action of the epithelium combined with jerky movements, especially of the more posterior part. The latter may form the looping that pulls the oesophagus back towards the stomach. A true smooth peristalsis has not been observed in the oesophagus.

Rhythmical bidirectional peristalsis does, however, occur in the stomach and digestive caecum. This movement produces a pulsating churning effect on the contents, particularly in the caecum, and is independent of other movements (Fig. 21B). The contraction wave passes from anterior to posterior, taking about two seconds to pass down, then there is a pause for another three to four seconds, and then the return wave, lasting for about two seconds, passes forward from the posterior tip to the stomach.

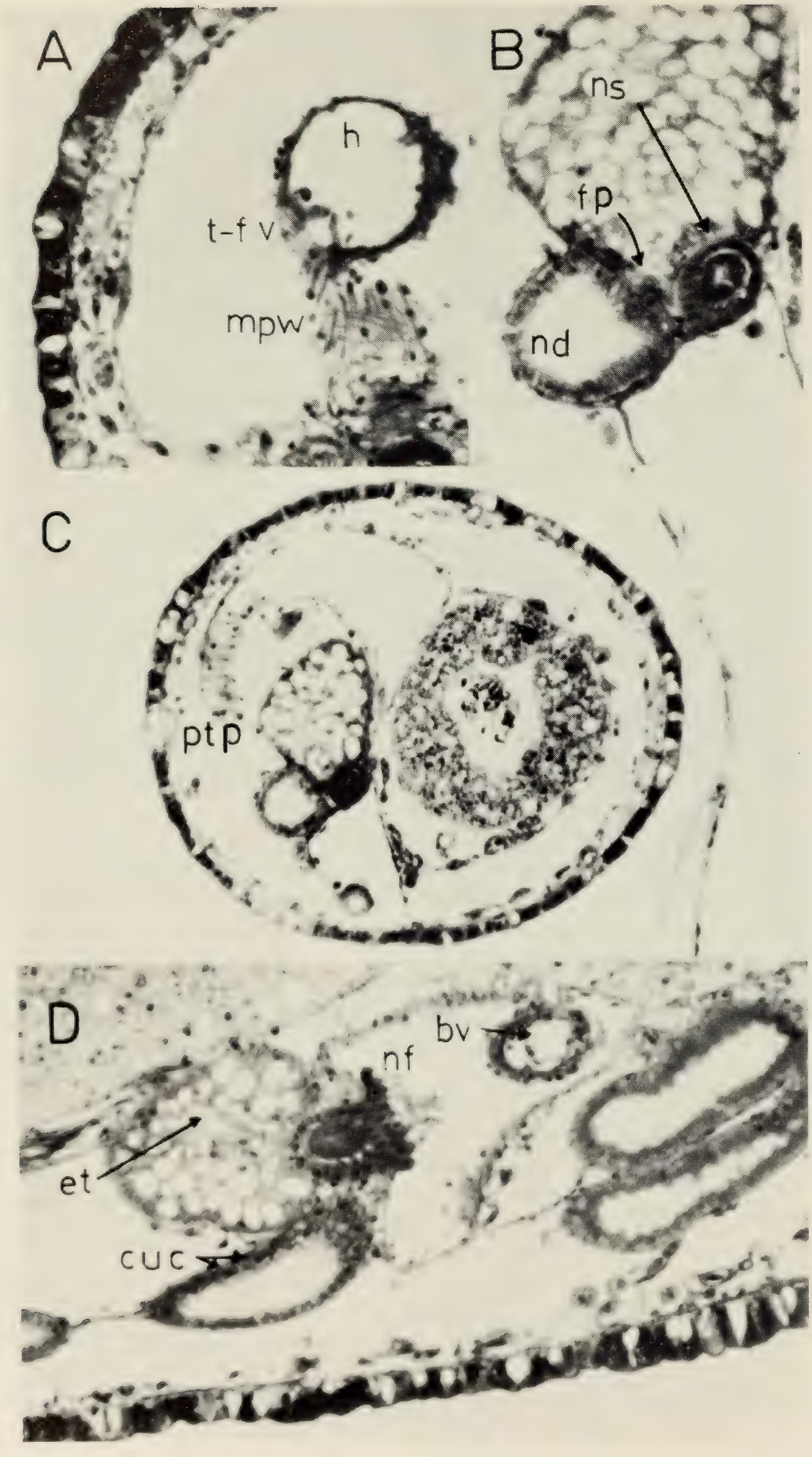
Such peristalsis is reminiscent of the pulsations reported for the cerata of *Alderia* (Schulz, 1936) and *Stiliger* (Marcus and Marcus, 1956), and possibly also of that briefly mentioned for the digestive caecum of *Stellaspina* (=*Microhedyle*) *lactea* by Hertling (1930) and later for *Mancohedyle* (=*Microhedyle*) *brasilensis* (formerly *milaschewitchii*) by Marcus and Marcus (1954).

The peristaltic pressure presumably also aids in the movement of digestive products across the membranes of the caecal cells into the lumen and also across the basement membranes of these cells into the haemocoel, and to the waiting phagocytic giant amoebocytes. There are also indications (Fig. 21A) that peristalsis occurs even when cell coalescence across the lumen may be taking place.

Production of formed faecal pellets has not been observed and all egested material appears diffuse and either flocculent or granular. The shortness and ciliation of the intestine and rectum would appear to preclude such compacting of the faeces. Egestion appears to occur at irregular intervals.

The beating heart is easily seen in the living animal; at a temperature of 24.0°C the rate of beat is approximately one per second. Casual observations suggest that the rate is affected by temperature and not by cold light. The stretched condition of the heart in the pericardium would provide a regular and constant stimulus for contraction; this has been suggested for *Dolabella* by Nomura (1963).

The microanatomy of the heart suggests that considerable pressure is built up and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that blood is forced to the extremities, returning in the haemocoelic spaces. The lack of a true atrium, or auricle, is interesting. The mechanism of diastolic refilling of the heart differs in degree from that suggested by Krijgsman and Divaris (1955). It would appear that a sufficiently constant "head" of blood is held in the haemocoels and that their structure is sufficiently constant, with true walls, so that they form distinct enclosures or sinuses rather than mere irregular spaces.

The pericardium and heart also play an important part in the excretory cycle of this animal. There are no specialized areas of secretion in the pericardial wall, suggesting that the pericardial fluid is a filtrate. The contraction of the heart not only forces the blood out through the aortic balloon valve but also provides negative pressure within the tensed pericardial cavity, thus producing a filtration through the pericardial wall from adjacent haemocoels. The greatest extent of such filtration would be through the posterior wall of the pericardium which is very delicate, thin, and flat. Ultrafiltration of this nature has been reported for *Octopus dofleini* (Harrison and Martin, 1965) and for *Haliotis rufescens* (Harrison, 1962).

Relaxation of the heart muscle would not only provide bulbar filling through the flap valves but would squeeze the pericardial fluid towards the nephrostome. The protrusion of the nephrostome funnel into the pericardium would ensure that the vortex, produced by the flagella of the renopericardial canal, was held away from the wall of the pericardium and that therefore maximum vortical suction was exerted on the pericardial fluid.

The opening of this renopericardial canal into the nephridium is very small and the pressure built up at this point must be considerable, sufficient, in fact, to cause ultrafiltration through the nephrocytes of the first part of the nephridium.

It is obvious from the microanatomy that the pericardial fluid has a fate that is at least threefold: some of its contents will pass directly through the cells of this spongy area to be reabsorbed into the adjacent haemocoel and in some cases picked up by giant cells; some contents are held for a time within these nephrocytes; but the bulk of the pericardial fluid is retained within the nephridium in the lumina for a longer period. It would appear that this nephric fluid filters across from lumen n-1 to lumen n-2 (Fig. 8B, C), which becomes greatly distended. The size of this distended sac (Fig. 17B), as well as its narrow wall of vacuolated cells, suggests that it is actively functional as an osmo-regulatory as well as an excretory organ.

It would appear that the renal product becomes fairly concentrated, as additional flagella are provided at the narrow exit of the nephridium into the nephridial duct to assist it through. The great length of the duct is surprising, suggesting even further ionic exchange as well as water reclamation; this condition is usually associated with terrestrial adaptation, especially in land Pulmonata (Martin and Harrison, 1966), but here it is found in a totally aquatic animal. The histochemistry and renal programme of these excretory structures in *Tantulum* would be of great interest.

The confusion regarding wandering cells in the Mollusca may be seen by references to the summaries of Owen (1964) on amoebocytes, and Hill and Welsh

Fig. 16 *Tantulum elegans*. A, B, and C, transverse series; D, longitudinal series.
- A Through sinu-cardiac (two-flap) valve.
- B Through nephric sponge and flagellated pore.
- C Through tapered end of pericardium.
- D Through nephrostome funnel, anterior part of renopericardial canal and part of exit tubule of canal.

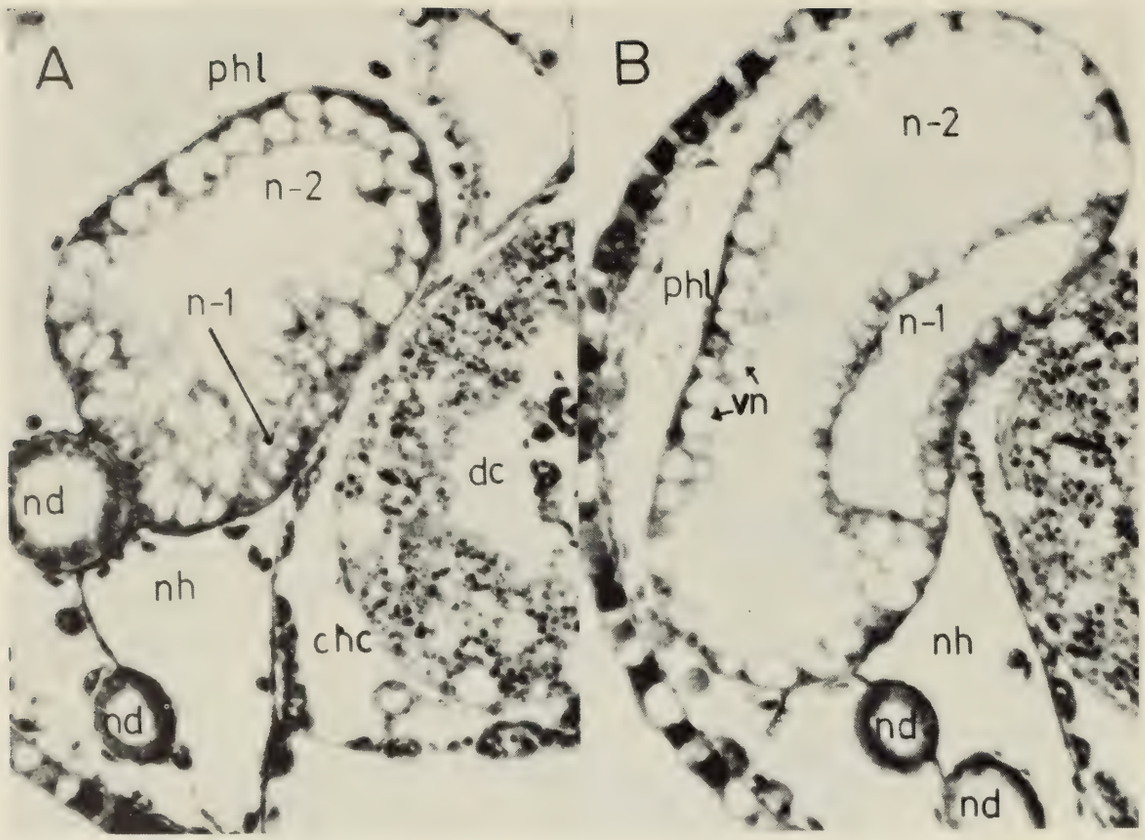


Fig. 17 *Tantulum elegans*. Transverse series.
A Through nephridium, showing beginning of division into first and second nephridial tubes.
B Region of expanded nephridial tubes.

(1964) on blood cells; it is obvious that much work remains to be done in this field. In *Tantulum elegans* there is a clear distinction between the main types of wandering cells. From cytological appearances and position it can be deduced that the giant amoeboid cells play extensive roles in digestion, excretion, and spicule formation, whereas the blood cells are associated with the rapid transport system and are probably therefore concerned largely with antibody production. It seems likely that the large amoebocytes are periodic, as suggested for *Helix* by Wagge (1955). No amoebocytes have been noticed in the gut lumen; indeed, it is hard to see how they could avoid being crushed in such a situation, especially during the absorptive phase of the digestive eptithelium.

Unfortunately nothing is as yet known of the reproductive physiology of this animal.

New Classification of the Acochlidioidea

In attempting to assess the systematic position of this interesting animal it became obvious that it did not fit naturally into any of the existing families of the Acochlidioidea, although it exhibited many of the basic features of the group. A new family, the Tantulidae, had to be created for its reception. This fact led to further consideration of the existing classification and in particular to the characters upon

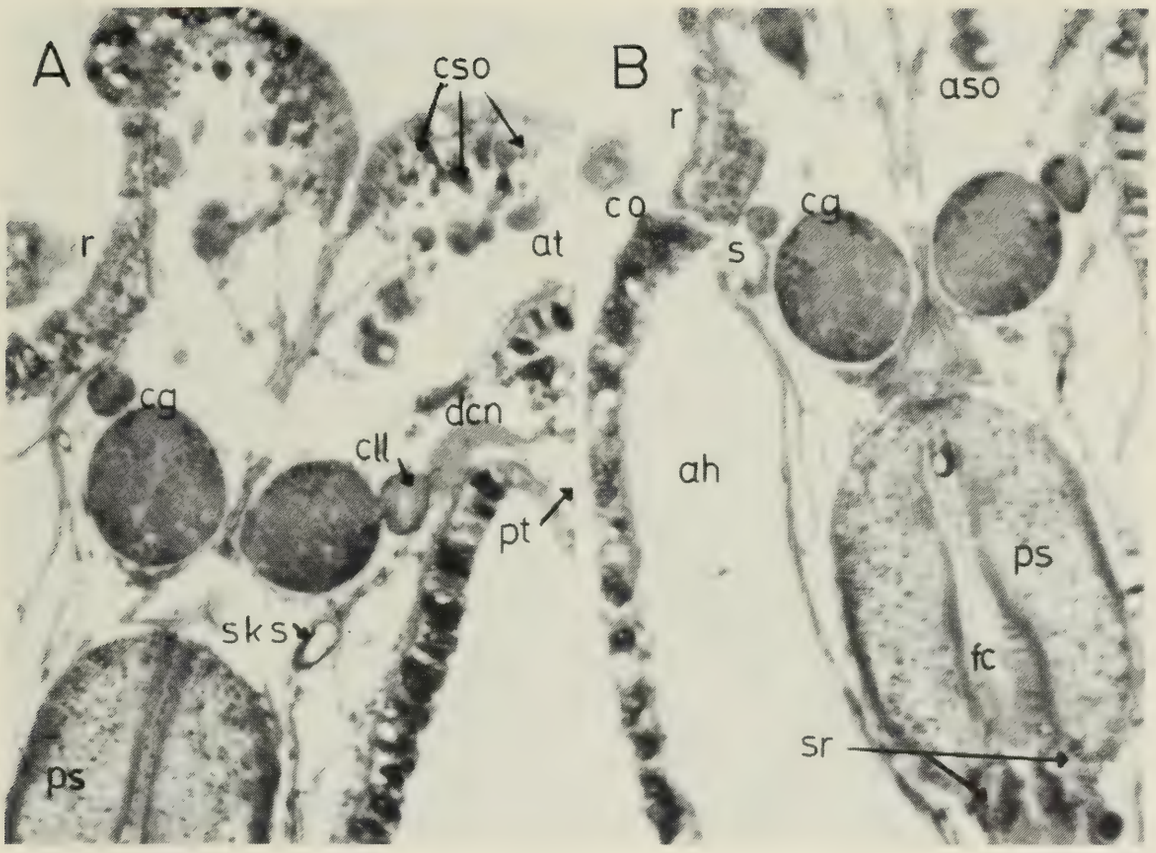


Fig. 18 *Tantulum elegans*. Horizontal series, specimen slightly tilted downward on left side. Anterior end.

A Through level of pharynx roof.

B Through canalicular opening and beginning of "reproductive" saccule.

which it is based. Division of the group into the three families at present recognized (Taylor and Sohl, 1962), the Acochlidiidae, Hedylopsidae, and Microhedylidae, is done solely on externalia, radular formulae, sexual characters, and the condition of the digestive caecum. Whereas it is useful to have a classification which may enable immediate identification on externally visible and other readily available signs, it is seldom sufficient to indicate phylogenetically true ordinal or familial relationships. Major body systems must be included before any proper assessment of groupings can begin.

As a result of these considerations a visual matrix analysis of all available information was made and a new classification devised which would fit these facts. This revision is discussed in the next section. It should be pointed out that it must of necessity be an interim classification as it is based partly on information gleaned from a scanty and not always thorough literature. I hope that it will serve to emphasize the great gaps in our present knowledge and to show the sort of questions we should be asking ourselves when attempting to place new species. An illustrated scheme of definitions has been given rather than a dichotomous key, as the latter could lead to false assumptions of relationships at this stage of limited knowledge.

Scope of the Group and its Position in the Gastropoda

Odhner's original (1937a) creation of the Acochlidioidea (=Hedylacea) as a separate order removed these molluscs from the Nudibranchia where they had been placed by

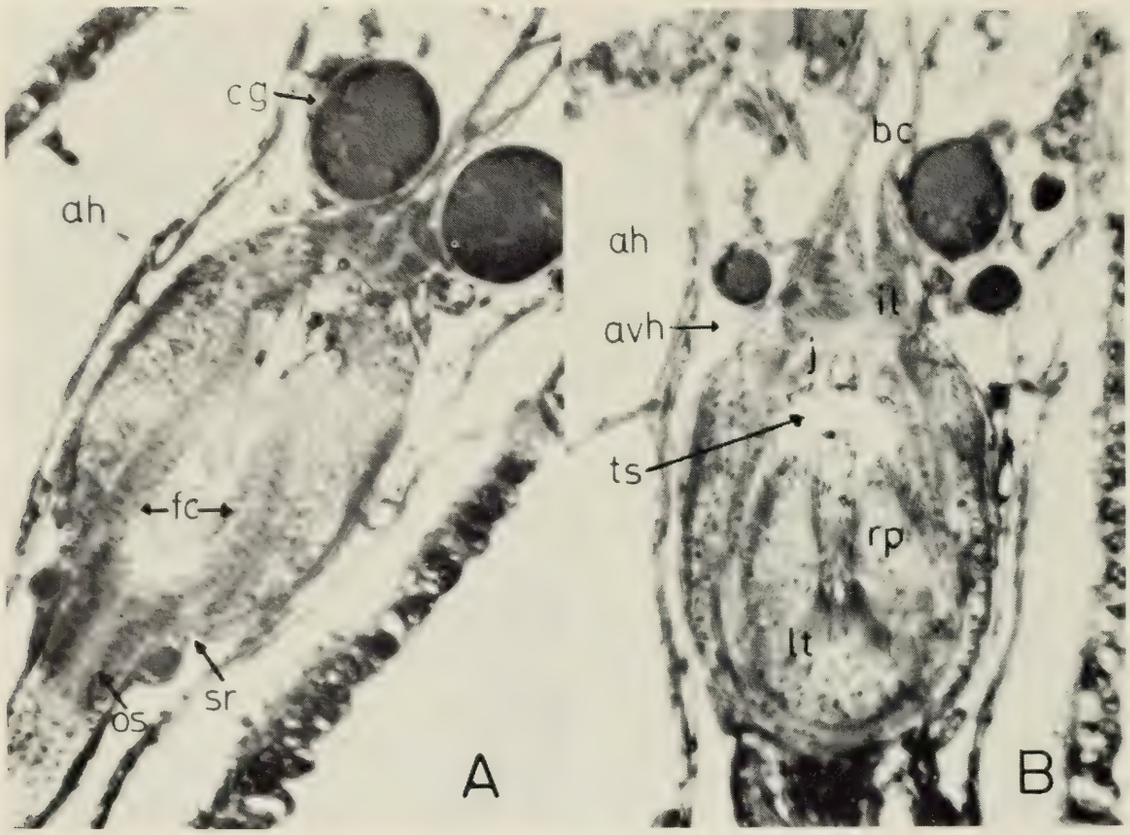


Fig. 19 *Tantulum elegans*. Horizontal series, specimen slightly tilted downward on the left side. Anterior end.

A Through level of food canal floor and pharyngeal nerve plexus.

B Through level of operative radular row.

Bergh (1895); he further suggested that they showed relationship to the diaphanid cephalaspids. Later Marcus (1953) widened Odhner's definition to accommodate two new genera, *Unela* and *Ganitus*. Boettger (1955), followed by Zilch (1959-60) reduced the order to familial rank and placed it in the Cephalaspidea. This position was again altered (Franc, 1968b, in accordance with a personal communication from Odhner) and a new form of the Order Acochlidiacea was erected, which contained two suborders, the Philinoglossacea and the Euacochlidiacea. Some subsequent authors, for example Salvini-Plawen (1973), continue to follow Boettger and Zilch, whereas others, such as Taylor and Sohl (1962) and Hyman (1967), regard the group as a separate order of the Opisthobranchia as originally conceived by Odhner (1937), and with more or less the scope of Marcus's (1953) definition.

It is felt that this return of the Acochlidiacea, termed Acochlidioidea by Taylor and Sohl (1962), from subordinal to full ordinal rank, separate from the Philinoglossoidea and the Cephalaspidea, is more than amply justified in the light of the essential unity and state of specialization it exhibits. (See definition of the Acochlidioidea in the classification, p. 83.) Thus we find that there are basic similarities of pattern and condition in both body form and body systems throughout the group and these similarities persist even in animals with greatly differing modes of life. Furthermore, certain surprisingly close sequences of pattern change may also be noted.

In Figure 23 an attempt has been made to formulate the way in which the basic pattern of form has been achieved and to compare it with the parallel groups

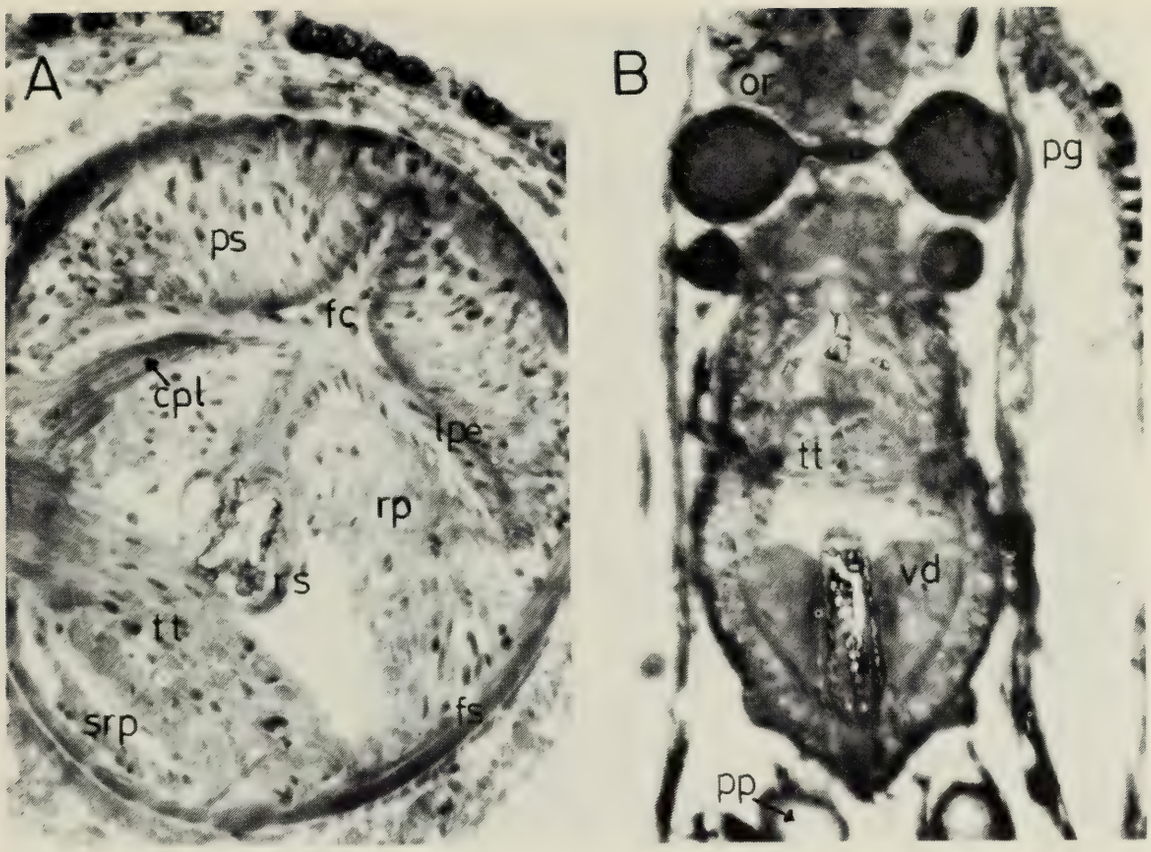


Fig. 20 *Tantulum elegans*

A Transverse section of pharynx through transverse tensor muscle.

B Horizontal section of anterior end through level of pedal commissure.

Philinoglossoidea and Platyhedyloidea (see pp. 55, 108). In addition, two main trends may be seen. The *first* trend involves modifications of what might be termed a suprasubstrate form towards life within the substrate. This process includes not merely the development of a capacity for burrowing down into the substrate but modification into a truly intra-substrate form capable of living within the aquatic interstices of a particulate environment of marine or freshwater gravels, sands, or muds. The *second* trend is towards freshwater existence. In an animal such as *Tantulum elegans* we see these two trends successfully merge and we have an animal which is not only an interstitial dweller but which is fully adapted for life in totally fresh water.

The first trend is concerned largely with alterations resulting from required changes in size, body form, and modes of life in relation to the demands of the new particulate environment, whereas the second is concerned with alterations arising from physiological adaptations to changes in salinity and oxygen tension in the environment. These latter changes are not simply those encountered in a direct move from sea to estuary to river to lake or to marsh, but obviously those found on other salt/fresh interfaces as for instance in zones of groundwater emergence within the sea beach where both horizontal and vertical stratification of salinity gradients may occur. Some of these changes are discussed further under the section Characters used in the Classification, page 55, but detailed discussion is not within the scope of this paper.

The modifications for interstitial dwelling, as seen in *Tantulum elegans*, are:

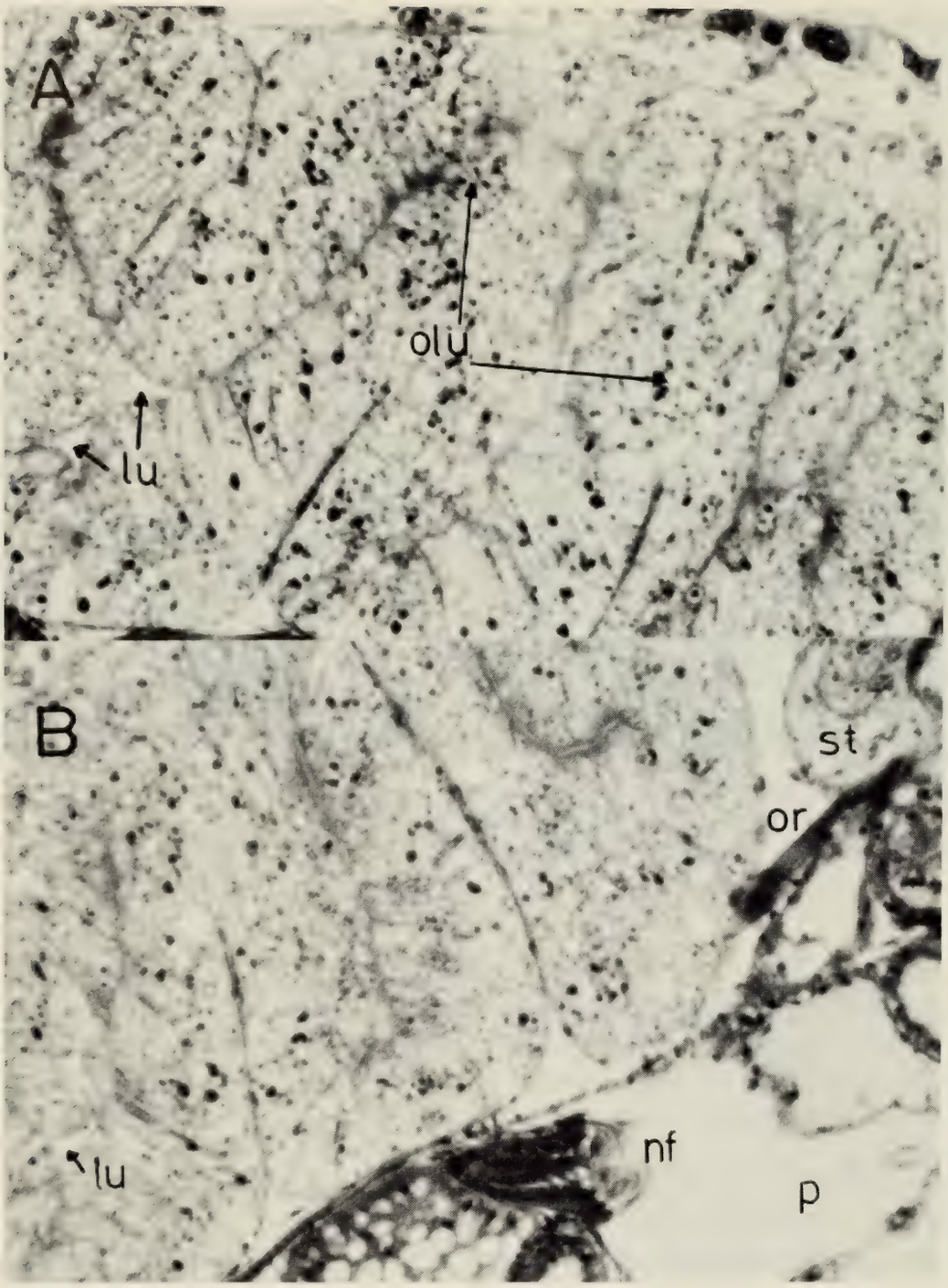


Fig. 21 *Tantulum elegans*. Longitudinal series.

A Caecum in peristalsis, showing phase of coalescence.

B Caecum, showing independence of peristaltic contractions from adjacent organs.

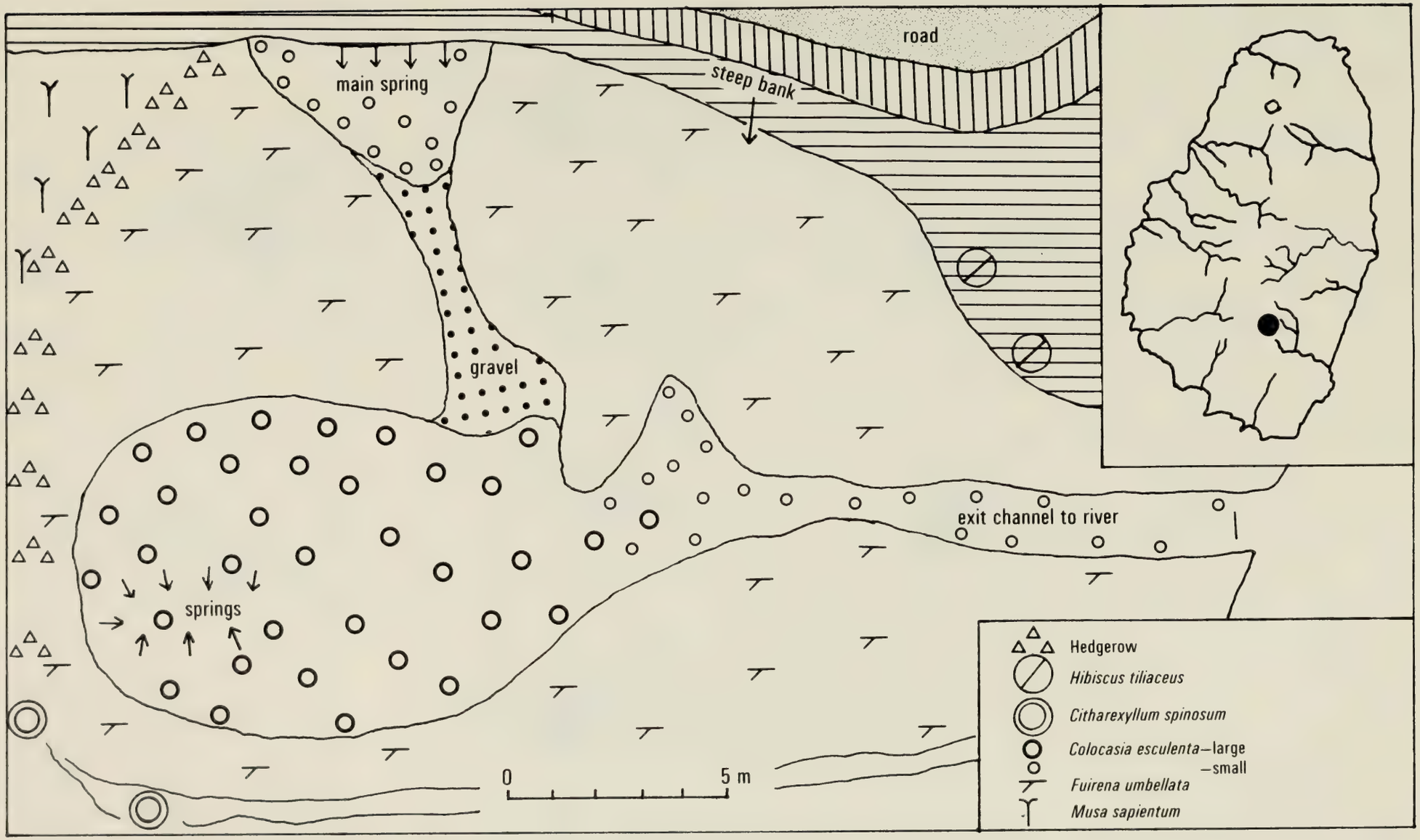
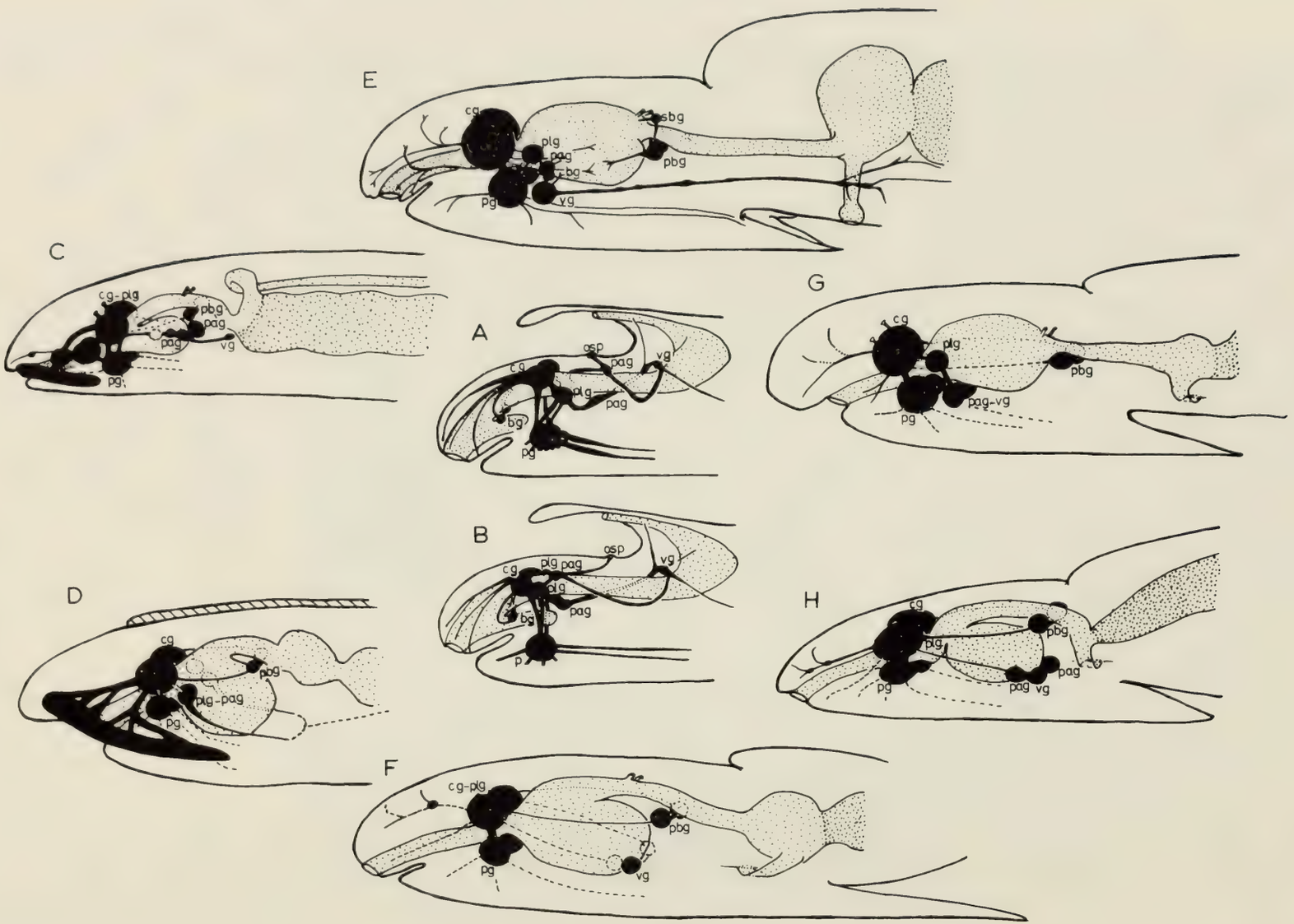


Fig. 22 Map of mountain spring marsh, habitat of *Tantulum elegans*. Inset: island of St. Vincent, West Indies.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reduction in size; loss of shell; streamlining and slenderizing of shape by detorsion and uncoiling, giving increased flexibility and mobility; definition of many haemocoelic spaces, giving increased control of turgor; concentration and forward placement of nervous system; loss of ctenidium with freedom of movement unhindered by either open, siphonal, or pulmonary mantle cavity; feeding differentiation of buccal region into a suctorial-scoop mechanism, with narrow, tubular buccal tube and highly muscular united pharyngeal region and with a narrowed radular ribbon containing strong scooplike triangular rachidian teeth; a long and large peristaltic digestive caecum; loss of pigment; loss of eyes.

The modifications for living in freshwater which are shown by *Tantulum* are: excretory system enlarged and modified for increased osmo-regulation and ionic reclamation; delicate integument almost totally available for respiration, with spicules restricted in number and position and with surface of visceral hump greatly extended.

The placement of the Acochlidioidea within the Gastropoda remains difficult. It embodies many features from all three of the existing major groups, Prosobranchia, Opisthobranchia, and Pleurobranchia (Pulmonata). Reversion to the older terminology of Streptoneura and Euthyneura does nothing to obviate this difficulty but rather seems to take us further from having to make any decisions regarding the true relationship of this group with other orders.

Resemblances to many groups exist, notably to the smaller Rissoacea, the Philinoglossoidea, some of the Cephalaspidea, the Cylindrobullacea, the Sacoglossa, and the Aeolidoidea. In fact, all of these groups would appear to have more in common with each other than with any of the other groups. It is possible that we should be considering a further major divergent grouping of molluscs from the main prosobranch stem near the Rissoacea. Fretter and Graham (1962) suggested that some rissoacean families, particularly the smaller forms, are artificially clumped in the prosobranchs and Ponder (1973) suggests that the "main stem" consists of several parallel lines, rather than being like the trunk of a branching tree. These "converging" anatomical resemblances require to be subjected to the rigorous testing of biochemical systematics, using, for instance, the techniques of immunological response of body fluids and muscle extracts (Wright, 1966; Wright and Klein, 1967; Davis, 1968). Working upward from the species level it should be possible to clarify greatly the relationships of these difficult taxa.

However, as the scope of this paper is limited to the Acochlidioidea, I would point

Fig. 23 Possible relationships of acochlidioidean nervous systems.

A Epiathroid condition (most monotocardians), after Fretter and Graham, 1962.

B Concentrated condition (Rissoacea, Stenoglossa, pyramidellids), after Fretter and Graham, 1962.

C *Philinoglossa* (Philinoglossacea), after Marcus and Marcus, 1954; variations seen in *Sapha*, Marcus, 1959 and *Pluscula*, Marcus, 1953.

D *Philine aperta* (Cephalaspidea), from drawings and text, Brown, 1934.

E *Tantulum elegans* gen. et sp. nov. (Tantulidae fam. nov.).

F *Palliohedyle weberi* (Palliohedylidae), from text, Bergh, 1895; *A. amboinense* with lobed pedals, double pedal commissure, and double cerebro-pedal/buccal connectives (Bücking, 1933).

G *Hedylopsis suecica* (Hedylopsidae), from drawings and text, Odhner, 1937a.

H *Unela* (Unelidae), after Marcus, 1953; *Microhedyle tyrtowii* (Microhedylidae) has cerebropleural ganglia united to pedals either side (Kowalevsky, 1901). Broken lines follow my suggestions. (See Note 1, page 123.)

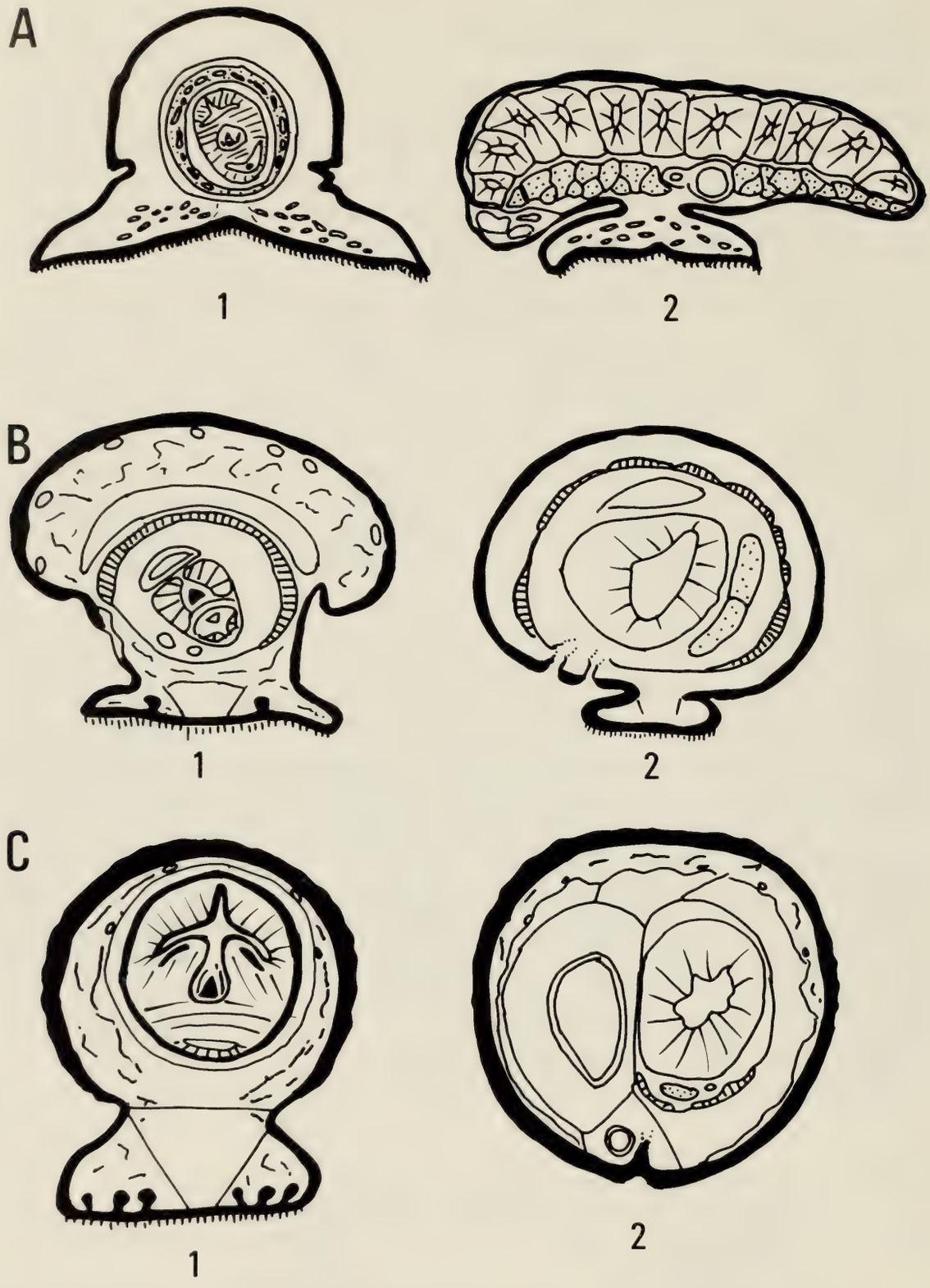


Fig. 24 Patterns of construction in the Acochlidioidea. Transverse sections through 1 pharyngeal region and 2 dorsal visceral sac.

A Pedoneura: *Acochlidium amboinense*, after Bücking, 1933.

B Proprioneura: *Hedylopsis spiculifera*, after Kowalevsky, 1901.

C Pharyngoneura: *Tantulum elegans*.

out merely that they share with the Philinoglossoidea and with families such as the Platyhedylidae (Salvini-Plawen, 1973) a number of characters that appear to be of more than ordinal value and which tend to set them all apart from the major groups. Whether or not these accumulated and distinctive tendencies are the result of parallel or linear or ramifying phylogenetic changes will remain speculative until further species are described. With the increasing interest in interstitial faunas we may confidently expect many new species to be discovered, and it is therefore felt that the delay in establishing new ordinal and family groups and even in creating new genera because of limited numbers of described species is no longer justified and may even lead to further complications in the synonymy. I would suggest therefore that we give serious consideration to the establishment of a new section of molluscs, perhaps called the **Ceratobranchia**, with the following definition:

> Freshwater or marine molluscs, often small and of interstitial habit, with shells reduced or totally absent and often replaced with a spicular pallial test or internal spicular skeleton or scattered integumental spicules, detorted, with no ctenidia or pulmonary chamber but with integumental respiration, with anterior nervous system concentrated in pharyngeal region, with the visceral hump uncoiled and either dorsoventrally compressed along the length of the extended foot with accompanying posterior extension of the intestine, or produced dorsally into a free dorsal visceral sac and retaining a short intestine, with radula reduced in numbers of tooth rows and teeth, with a tendency to reduction in the reproductive system and with sexes often temporarily or spatially separated, with the heart two-chambered, one-chambered, or missing, and with blood vessels often missing.

Such a grouping would include the Acochlidioidea, Philinoglossoidea, and Platyhedyloidea nov. ord. (see below p. 108); it is possible also that the other groups mentioned above may fit more naturally here than in their present insecure positions. Also it may prove necessary at a later date, when more species and genera have been discovered, to erect a new order for forms such as *Ganitus* with its differing pharyngeal construction. This was first tentatively suggested by Marcus (1953:173) on the basis of the entirely differing pharyngeal region. As shown later I have created a family Ganitidae and a superfamily Avelariacea but because of other features have retained at present their position in the Acochlidioidea.

Characters Used in the Classification

MORPHOLOGY

The degree of separation of the hump from the foot has been used as a classificatory character since its first mention by Kowalevsky (1901). Figures 24 and 25 illustrate the condition seen in the suborders. In this paper the anterior separation of head/hump from the foot is regarded as indicative of a different grade of total organization, and the presence of an anterior groove, called the cephalo-pedal groove, is therefore significant. In some forms, for example *Microhedyle tyrtowii*, where the pedal sole is merely a ciliated ventral band of the anterior hump, only a posterior viscero-pedal groove separating off the foot-tip is present; in other forms, for example *Tantulum elegans*, the cephalo-pedal groove is continued posteriorly merging indistinguishably with the posterior viscero-pedal groove; in *Asperspina* (=*Hedylopsis*) *brambelli* the latter groove (Swedmark, 1968:fig. 1A) extends forward a little. However, a strongly

Fig. 25 Patterns of construction in the Acochlidioidea. Cerebroneura.

A Velariacea: *Microhedyle tyrtowii*, transverse sections through 1 pharynx and 2 dorsal visceral sac; after Kowalevsky, 1901.

B Avelariacea: 1 *Ganitus evelinae*, reconstruction of transverse section through mid-pharynx from other sections and textual information, Marcus 1953; 2 *Paraganitus ellynnae*, transverse section through dorsal visceral sac, after Challis, 1968.

C Velariacea: *Unela remanei*, transverse section through dorsal visceral sac, after Marcus, 1953.

D Velariacea: *Sabulincola odhneri*, transverse section through dorsal visceral sac, after Marcus and Marcus, 1955.

developed foot is regarded here as one in which muscle fibres and internal haemocoels are readily seen; the foot of the Asperspinidae is not of this construction. It is quite clear from the transverse sections of *Antemnella* (=*Hedylopsis*) *loricata* (Swedmark, 1968:pl. II) that there is no cephalo-pedal groove present.

The breadth and anterior angling of the foot and the size and shape of its posterior end are also used as characters, as they are again indicative of differing modes of life. In Figures 24A and 26A we see the strong foot of *Acochlidium amboinense*, the suprasubstrate dweller; in Figures 24B and 27A the somewhat narrower foot of *Hedylopsis*, the gravel and shell-sand dweller; and in Figures 24C and 27D the foot of *Tantulum*, which is sufficiently narrow for interstitial living but broad enough for gliding over the surface of soft mud when necessary.

The size and condition of the two pairs of tentacles also are indicative of modes of life and hence important at the generic level. The anterior (labial) pair vary from lappetlike structures in *Palliohedyle* (=*Acochlidium*) *weberi* (Fig. 26B), to the long digitiform tentacles of *Tantulum* (Fig. 27D). The posterior pair when present are never true rhinophores and show flattening rarely.

Body size is also important, the suprasubstrate species being 10 times as large as the intrasubstrate forms. Attempts have been made (Poizat, 1971) to correlate size of species with habitat and with sizes of interstice and/or substrate particle.

The condition of the mantle is important, particularly the character and disposition of glandular cells and spicules, but this feature must be considered together with more fundamental body organization before placing a species. Thus both *Hedylopsis spiculifera* (Fig. 27B), and *Asperspina brambelli* (Fig. 29D), show spicular tests but differ organizationally.

There is no permanent open, siphonal, or pulmonary mantle cavity, but the method of formation of a temporary one during withdrawal caused by adverse stimuli is a diagnostic character (Figs. 26C, 27A, B, D, 28A, 29D, F).

ALIMENTARY CANAL

Foregut (Fig. 31)

Two basic types of foregut differentiations are recognized in the group for classification purposes.

The first type, found in the Ganitidae fam. nov. (Fig. 31, Type 1) consists of a buccal cavity organized into a short anterior buccal tube, a radular sac without operative musculature and without supporting lingual cushion, a subradular sac with large muscles operating between its chitinous end posteriorly and two chitinous plates ("jaws", Marcus, 1953) anteriorly, and with a short uniseriate radula composed of lanceolate rachidian teeth only. In this form the pharyngeal food tube portion of the foregut, between the "inner lips" and the entrance of the pharyngeal salivary ducts, is not bound with the radular and subradular sacs by a velarium of circular muscles.

The second type shows a sequence of variation from a poorly developed pharynx (Fig. 31, Type 2A), with small radular cushion and short velarium of circular sphincter muscles, to a complex structure (Fig. 31, Type 2C) with large radular cushion and complete binding to form an enlarged, highly muscular and unified bulbar pharynx. Thus Kowalevsky, 1901, page 12 (see also his fig. 21) for *Microhedyle tyrtowii*, states: "Sa structure est assez compliquée. . .on voit qu'il est toujours constitué par deux régions, une antérieure qui forme une sorte de couvercle ou

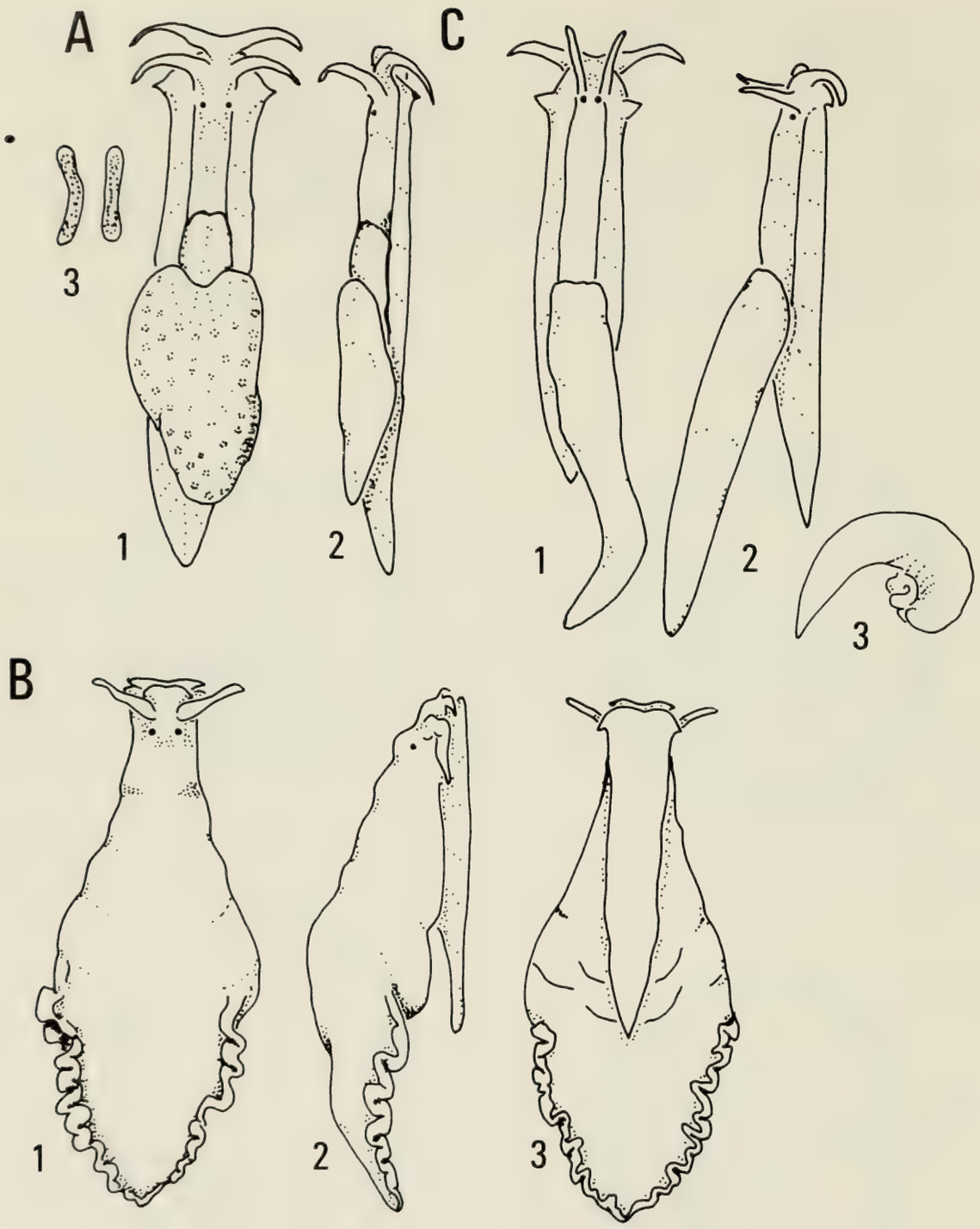


Fig. 26 Morphology of the Acochlidioidea. Pedoneura.

A *Acochlidium amboinense*, 1 dorsal view, 2 lateral view, 3 spicules; after Bücking, 1933.

B *Palliohedyle weberi*, 1 dorsal view, 2 lateral view, 3 ventral view; after Bergh, 1895.

C *Strubellia paradoxa*, 1 dorsal view, 2 lateral view, 3 curled specimen; after Küthe, 1935.

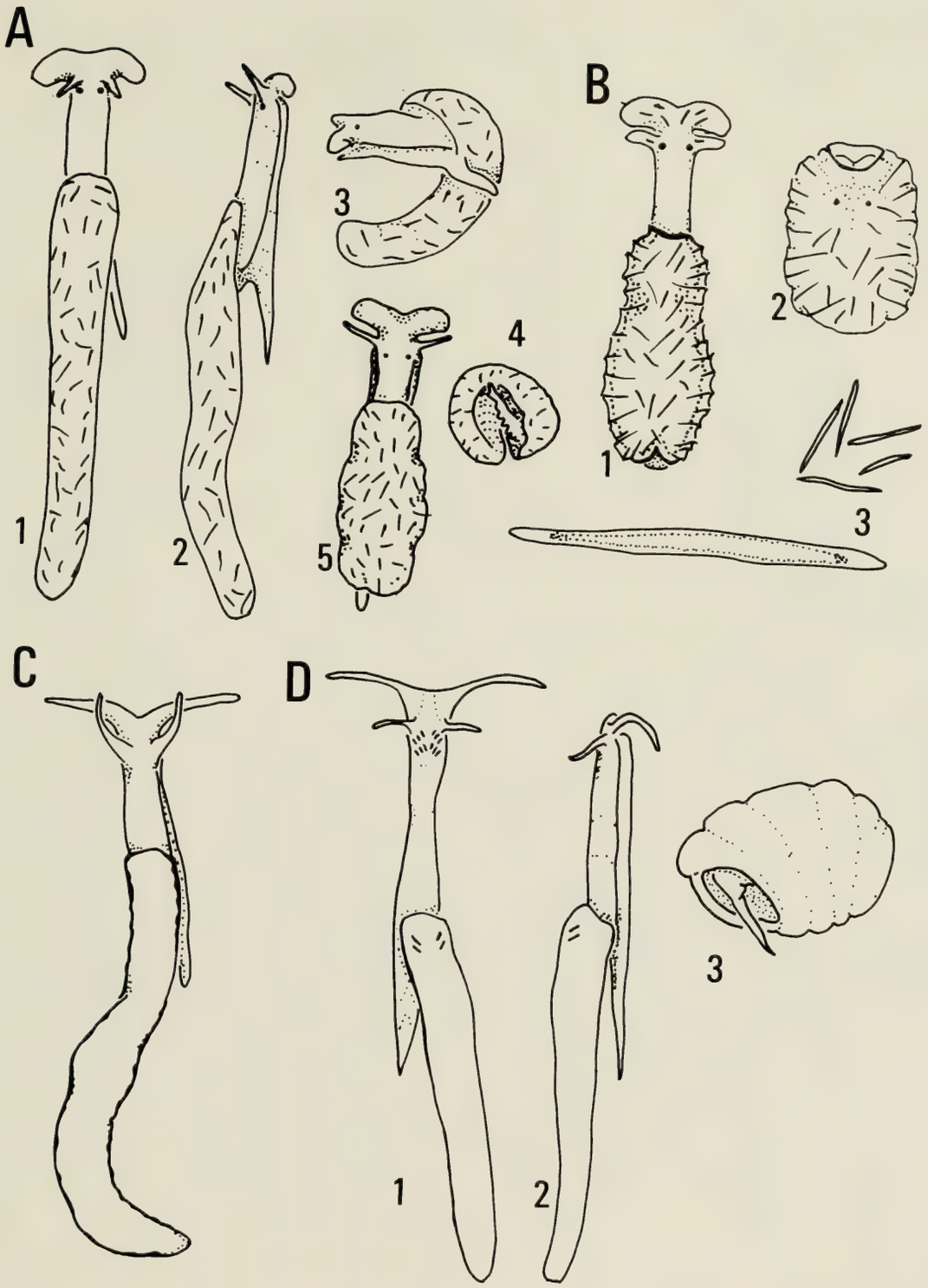


Fig. 27 Morphology of the Acochlidioidea. Proprioneura A–C, Pharyngoneura D.

A *Hedylopsis suecica*, 1 dorsal and 2 lateral views of body form extended for interstitial crawling, after Odhner, 1937a; 3 partially curled form, after Marcus, 1953; 4 fully curled form; and 5 normal surface-crawling attitude, after Odhner, 1939a.

B *Hedylopsis spiculifera*, 1 dorsal view, 2 withdrawn animal, 3 spicules; after Kowalevsky, 1901.

C *Pseudunela cornuta*, dorsal view, after Challis, 1970.

D *Tantulum elegans*, 1 dorsal view, 2 lateral view, 3 withdrawn animal.

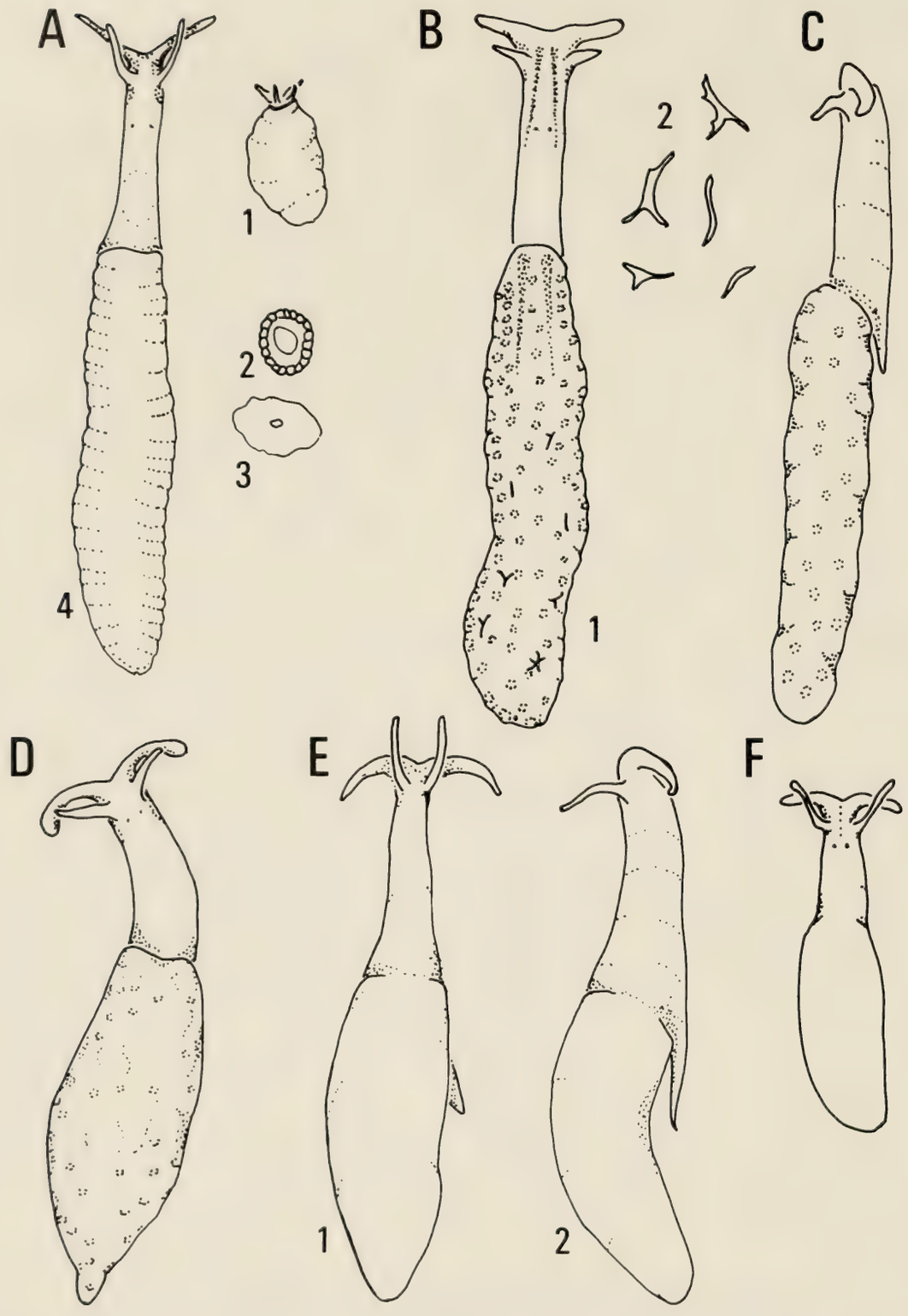


Fig. 28 Morphology of the Acochlidioidea. Cerebroneura. Microhedylidae A–D, Unelidae E, Sabulincolidae F.

A *Microhedyle tyrtowii*, 1 withdrawn animal, 2 ring spicular plate, 3 spicular plaque, 4 dorsal view; after Kowalevsky, 1901.

B *Stellaspina glandulifera*, 1 dorsal view, 2 spicules; after Kowalevsky, 1901.

C *Stellaspina lactea*, lateral view, after Hertling, 1930.

D *Microhedyle crypthophthalma*, dorsal view, after Westheide and Wawra, 1974.

E *Unela remanei*, 1 dorsal view, 2 lateral view; after Marcus, 1953.

F *Sabulincola odhneri*, dorsal view, after Marcus and Marcus, 1955.

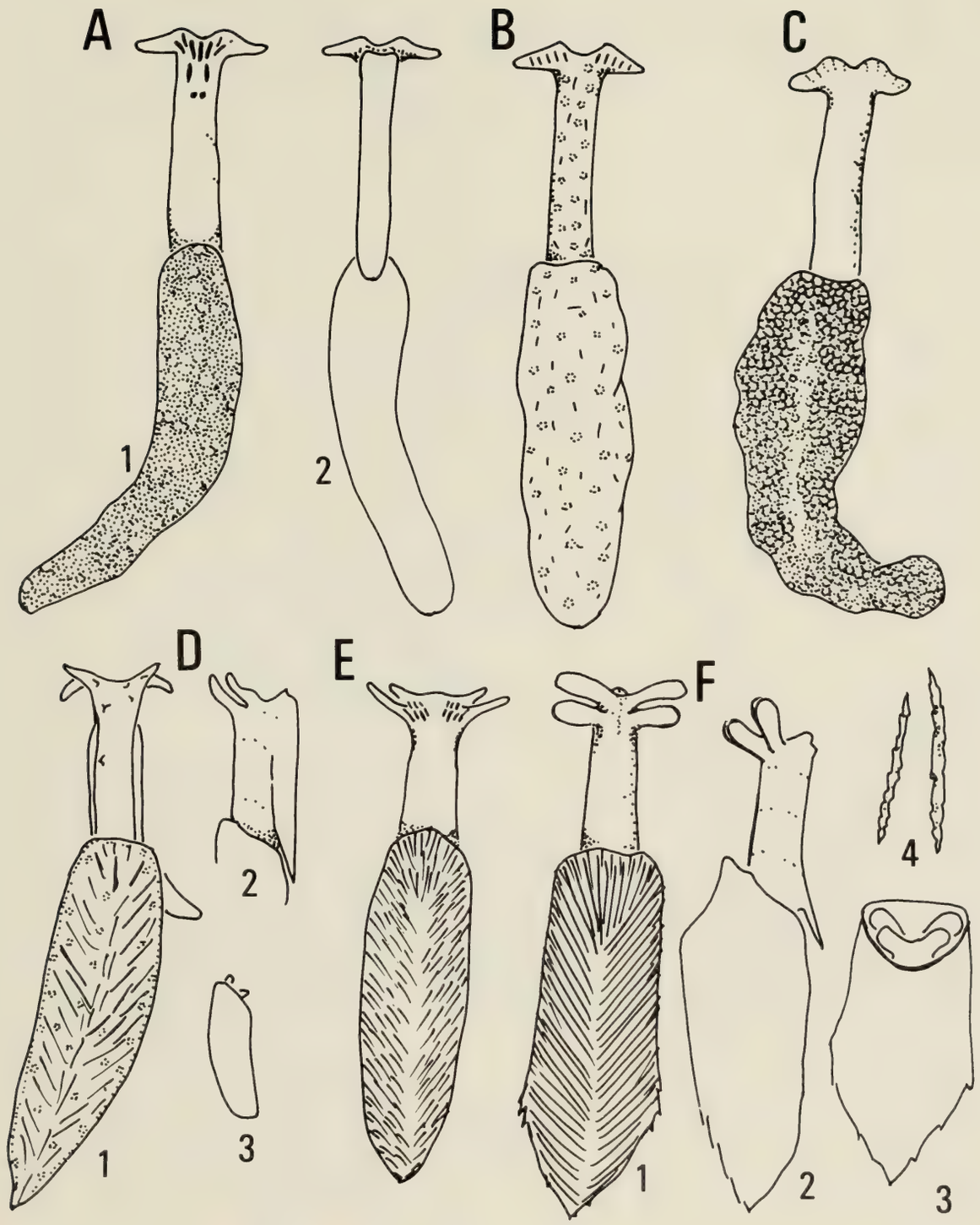


Fig. 29 Morphology of the Acochlidioidea. Cerebroneura. Mancohedylidae A–C, Asperspinidae D–G.

A *Mancohedyle milaschewitchii*, 1 dorsal view, 2 ventral view; after Kowalevsky, 1901.

B *Gastrohedyle brasilensis* , (=*milaschewitchii*: Marcus and Marcus, 1954), dorsal view, after Marcus and Marcus, 1954.

C *Maraunibina verrucosa*, dorsal view, after Challis, 1970.

D *Asperspina brambelli*, 1 dorsal view, 2 anterior of animal in lateral view, 3 withdrawn animal; after Swedmark, 1968.

E *Anademaria rhopalotecta*, dorsal view, after Salvini-Plawen, 1973.

F *Antemnella loricata*, 1 dorsal view, 2 lateral view, 3 withdrawn animal; after Swedmark, 1968; 4 spicules of *A. brambelli* and *A. rhopalotecta*, after Swedmark, 1968 and Salvini-Plawen, 1973.

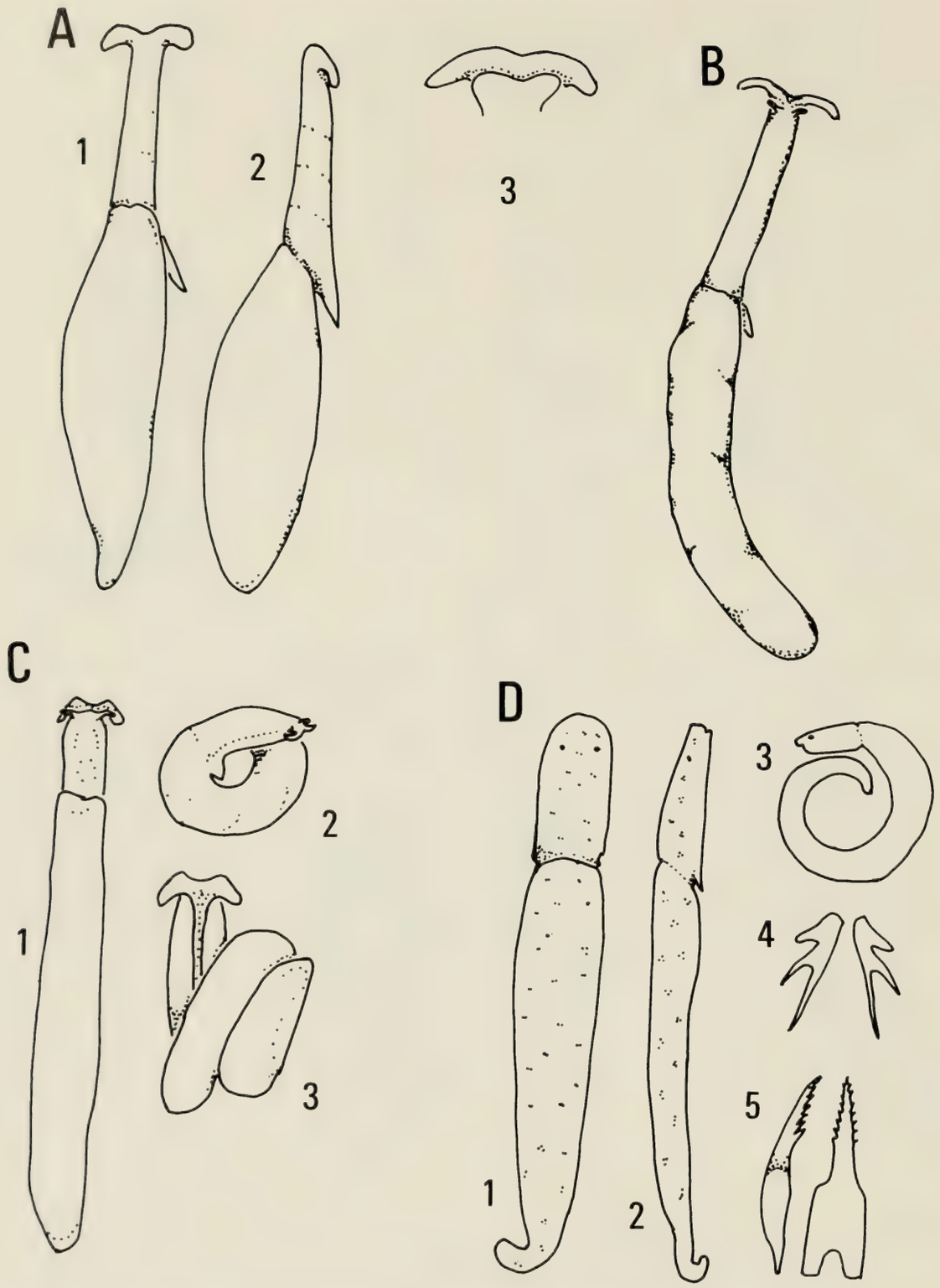


Fig. 30 Morphology of the Acochlidioidea. Cerebroneura: Ganitidae A and B. Visceroneura:Livorniellidae C. Morphology of the Platyhedyloidea D.

A *Ganitus evelinae*, 1 dorsal view, 2 lateral view, 3 ventral view of head; after Marcus, 1953.

B *Paraganitus ellynnae*, dorsal view, after Challis, 1968.

C *Livorniella glomerans*, 1 dorsal view, 2 lateral view, partially coiled specimen, 3 ventral view of fully coiled specimen; after Salvini-Plawen, 1973.

D *Platyhedyle denudata*, 1 dorsal view, 2 lateral view, 3 curled specimen, 4 "jaws", 5 tooth in anterior and lateral views; after Salvini-Plawen, 1973.

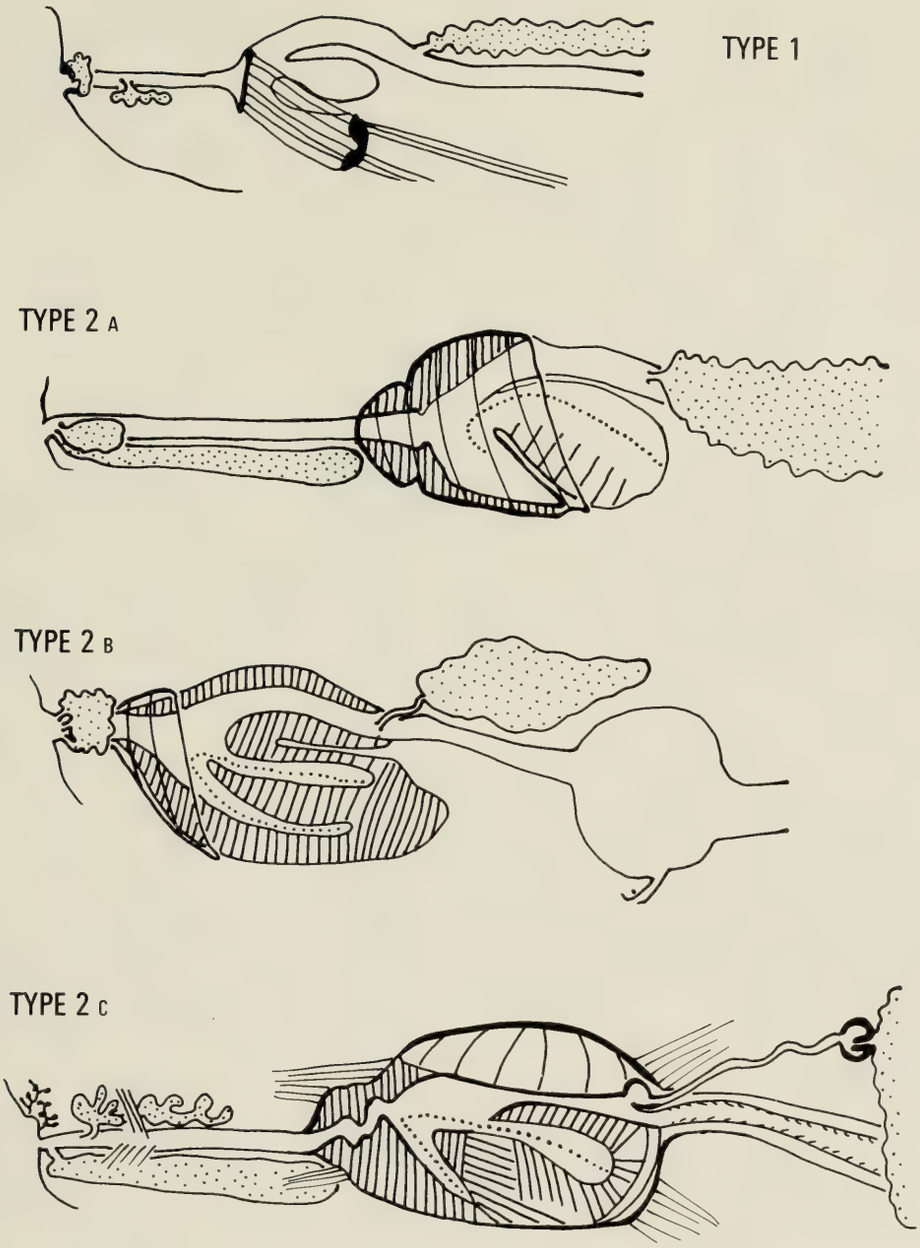


Fig. 31 The buccal cavity in the Acochlidioidea.
Type 1 *Paraganitus ellynnae*, after Challis, 1968.
Type 2 A *Microhedyle tyrtowii*, after Kowalevsky, 1901.
B *Acochlidium amboinense*, after Bücking, 1933.
C *Tantulum elegans*.

d'enveloppe externe, et l'autre interne . . . La région postérieure, contenant la radula, peut être regardée comme le bulbe radulaire.'' The condition for *Tantulum elegans*, Figure 4, is described on pages 13 to 16.

Bücking 1933, p. 557 says of *Acochlidium amboinense*: ''Der muskalöse Pharynx der in seinem Innern die Radula birgt, besteht äusserlich betrachtet aus einem oberen gewölbten und einem unteren Teil, der etwas breiter, aber mehr zusammengedrückt ist. Der vordere Teil des Pharynx ist durch Muskeln mit der Mundröhre verbunden und stellt eine Art Deckel oder äussere Hülle dar. Der intere Teil ist grösser und trägt innen auf der Mittellinie einer zungenartigen Muskel masse die Radula. Dieser verhältnismässig grosse Teil des Pharynx muss z. T. durch die enge Mundröhre hervortreten, wenn das Tier seine Radula benutzen will.''

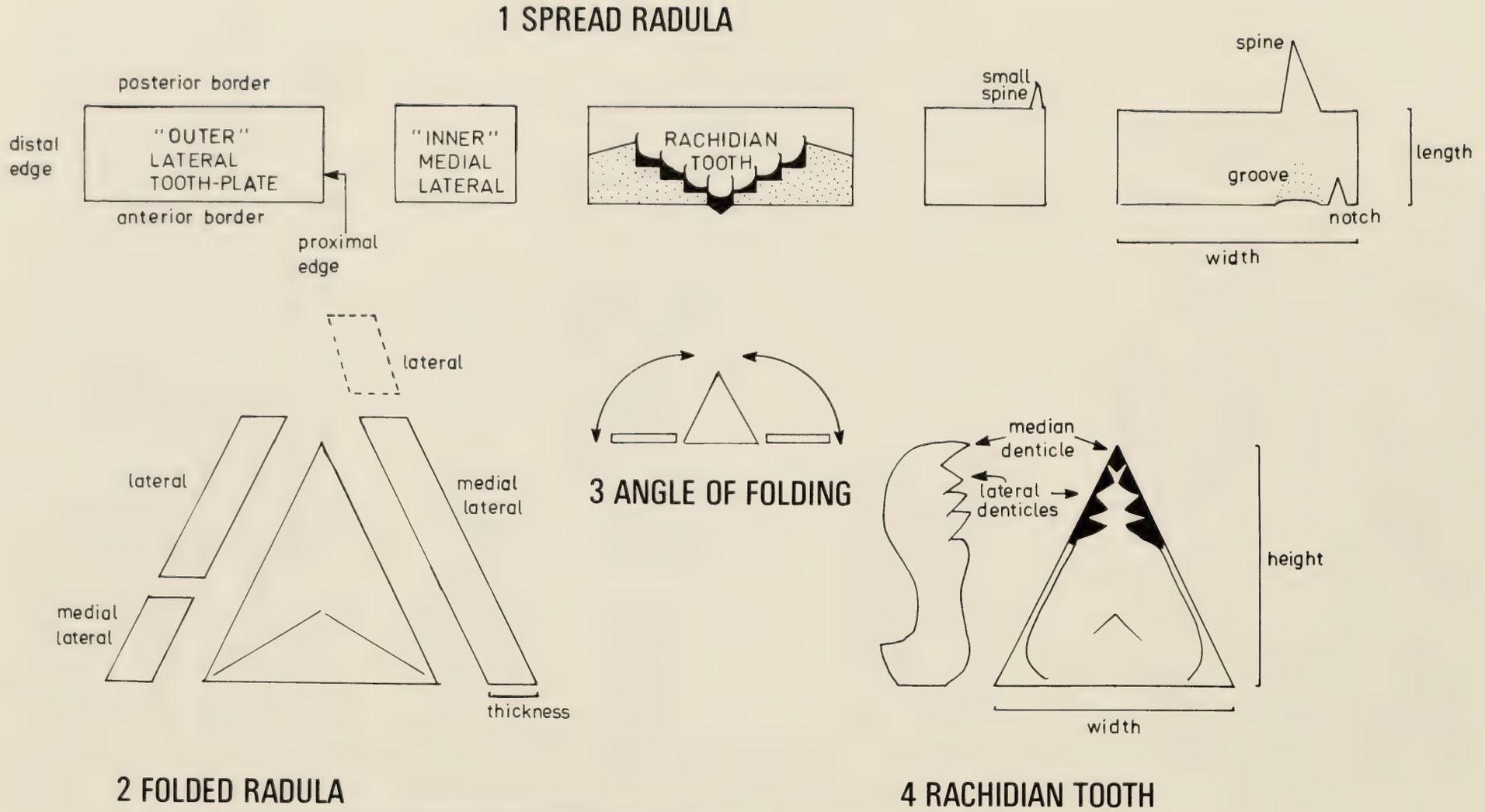


Fig. 32 Key characters for radular identification and measurement.

1. Spread radula in dorsal view.
2. Folded radula.
3. Angle of folding.
4. Rachidian tooth in lateral and dorsal views.

In all forms of the second type the basic radular formula is n-R-n, with n = 1 or 2 flattened lateral tooth-plates, and with R = 1 triangular, scooplike rachidian tooth which often possesses lateral denticles. Figure 32 shows the key characters for radular identification and Figures 33 to 37 show the tooth patterns for the various species in the group. Kowalevsky (1901:12-13) considers only the central rachidian tooth to be a true tooth, and the lateral "teeth" to be accessory plates; in this paper laterals, therefore, are referred to as tooth-plates. This view of Kowalevsky's is interesting especially when one remembers that the rachidian tooth is characteristically lost in the Philinoglossoidea (radular formula typically 3-0-3), whereas typical teeth are present laterally.

In the Pedoneura and the Proprioneura the radular ribbon is long and sharply angled anteriorly, the upper and lower portions being of almost equal length; in the Pharyngoneura the ribbon is sharply bent upward, the lower portion being about one-quarter the length of the upper; in the Cerebroneura the ribbon is curved anteriorly and the lower portion is one-third or less the length of the upper portion, except in the Ganitidae where there is no distinction possible between upper and lower zones.

Lining of gut

The gut is either ciliated throughout, as in *Unela*, or with only the oesophagus and intestine ciliated, as in *Tantulum*, or not ciliated throughout, as in *Microhedyle tyrtowii*. Cuticularization of the pharyngeal food canal, as in *Tantulum*, is clearly of functional and classificatory importance, but unfortunately information regarding other forms often has had to be obtained from authors' drawings of transverse sections and these are not always clear on this point.

Midgut (Fig. 38)

Differentiation of a stomach varies as the following examples show: it is absent in *Unela*, small and discrete in *Microhedyle* (see present definition), large and globular in *Gastrohedyle* and *Acochlidium*, and large and widely confluent with the digestive caecum in *Tantulum*.

The midgut diverticulum or caecum is usually single; in *Palliohedyle* (=*Acochlidium*) *weberi* a remnant of the left diverticulum is considered to be present. The digestive diverticulum shows branching (*Palliohedyle*), or lobulation (*Acochlidium*), or internal folding (*Strubellia*), or is a simple caecum which varies in length from the same length as the visceral sac (*Tantulum*), to longer (*Microhedyle*), to very much longer (*Livorniella*) (=*Microhedyle glomerans*).

The digestive cells (= "liver" or "digestive gland") are variously distributed; for example in *Palliohedyle* they are confined to the ends of the diverticular branches, in *Acochlidium* they surround the digitiform lobes, in *Tantulum* they are incorporated in the wall of the caecum and to a lesser extent in the stomach. Peristalsis of the caecum has only been reported for *Microhedyle lactea* (Hertling, 1930), *Gastrohedyle brasilensis* nov. sp. (= *Microhedyle milaschewitchii*: Brazil form) as given by Marcus and Marcus, 1954, and for *Tantulum elegans*.

Hindgut (Fig. 38)

The intestine may be ciliated or not, with or without a bulbar rectal swelling, fairly long and passing forward to a dextrolaterally situated anus, or short and passing

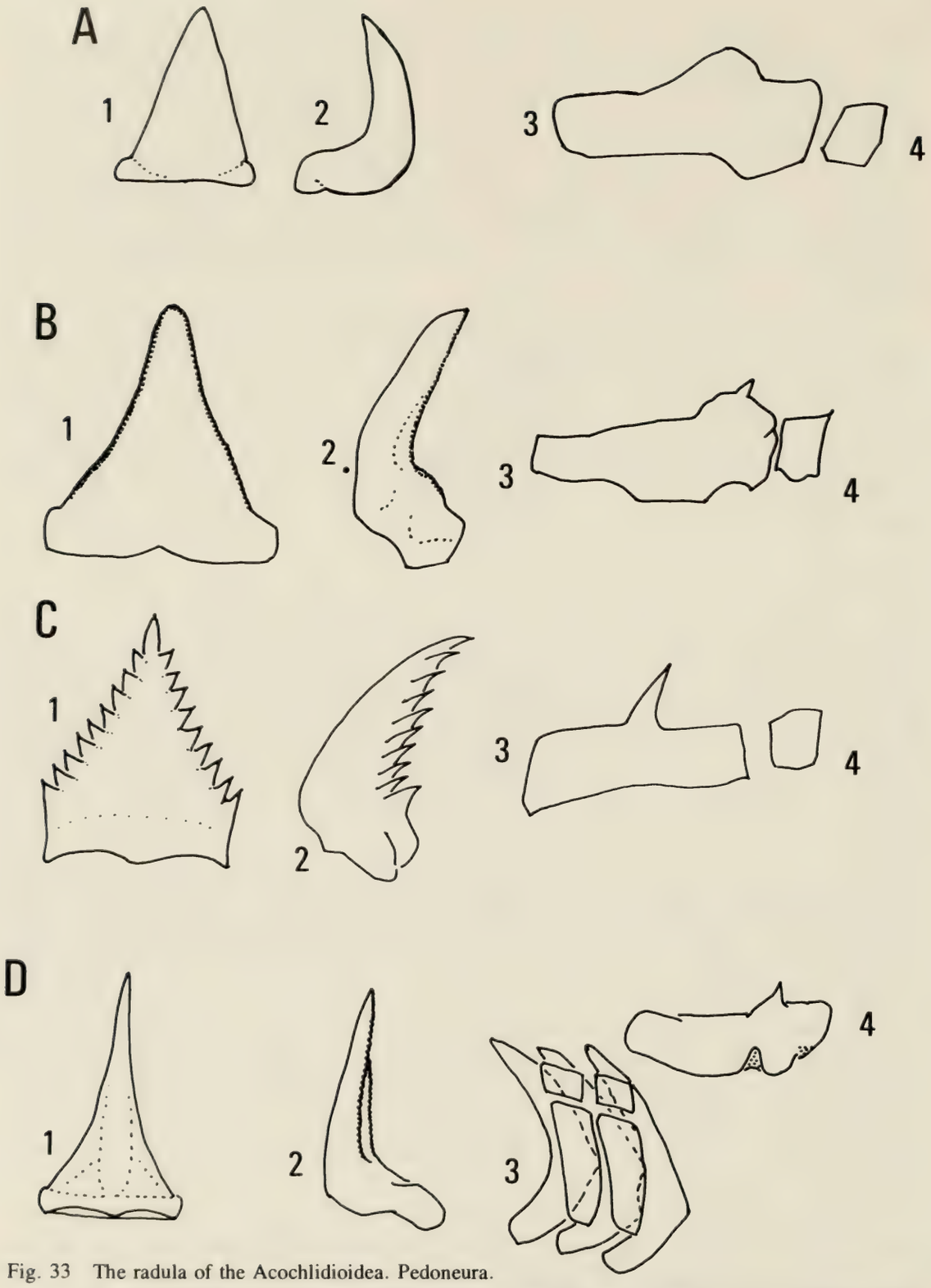


Fig. 33 The radula of the Acochlidioidea. Pedoneura.

A *Acochlidium amboinense*, Amboina form, 1 anterior and 2 lateral view of rachidian tooth, 3 right medial lateral tooth-plate, 4 right outer lateral tooth-plate; after Bücking, 1933.

B *Acochlidium amboinense*, Palau Islands form, 1 anterior and 2 lateral view of rachidian tooth, 3 right medial lateral tooth-plate, 4 right outer lateral tooth-plate; after Bayer and Fehlmann, 1960.

C *Palliohedyle weberi*, 1 posterior and 2 lateral view of rachidian tooth, 3 right medial lateral tooth-plate, 4 right outer lateral tooth-plate; after Bergh, 1895.

D *Strubellia paradoxa*, Amboina form 1, 2, and 3. 1 anterior and 2 lateral view of rachidian tooth, 3 portion of radula from right side, after Küthe, 1935; 4 Guadalcanal form, "outer" right lateral tooth-plate, after Wawra, 1974.

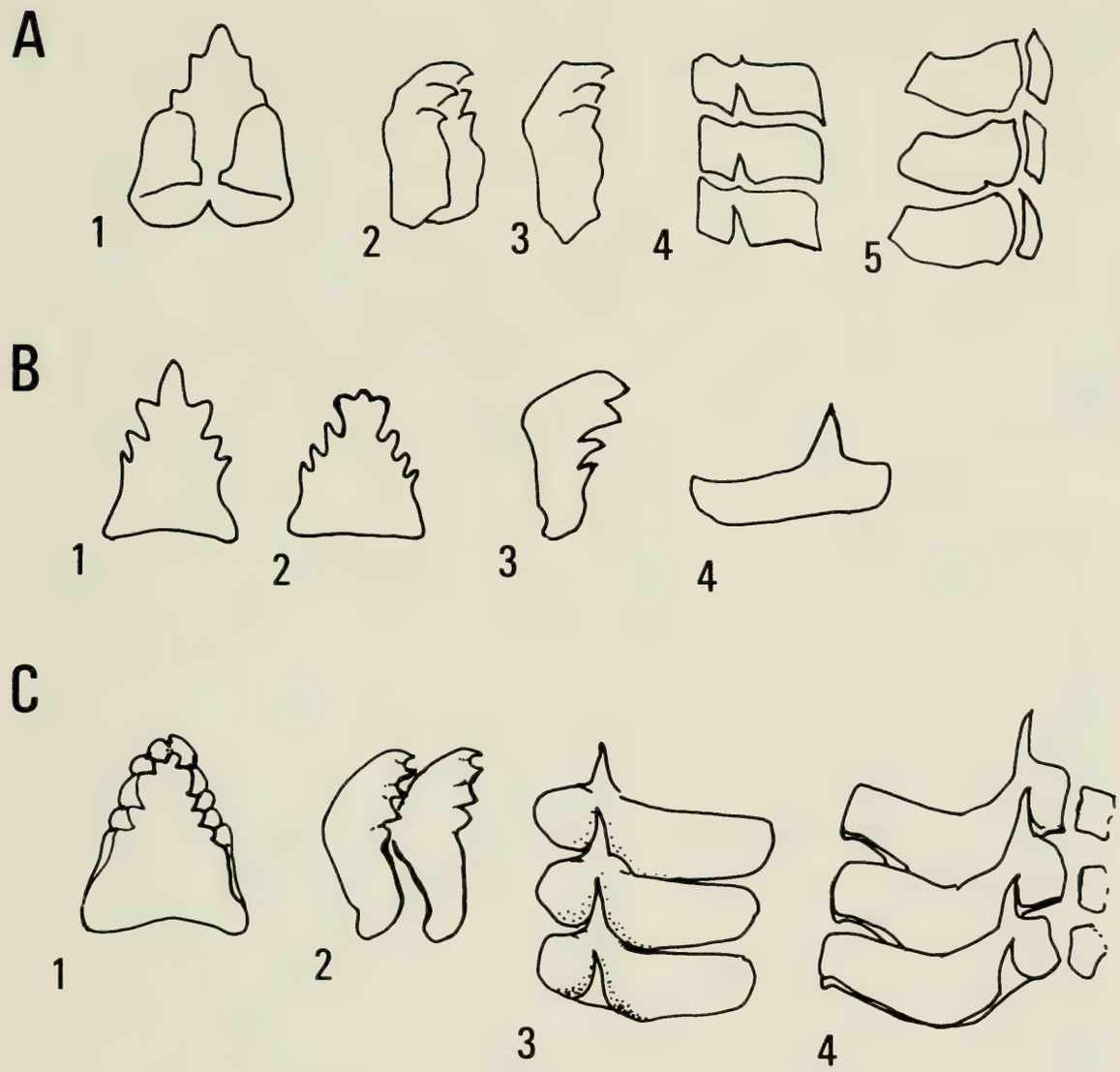


Fig. 34 The radula of the Acochlidioidea. Proprioneura A and B. Pharyngoneura C.

A *Hedylopsis suecica*, Banyuls-sur-Mer form, 1 anterior, 2 semilateral, and 3 lateral view of rachidian tooth, 4 left lateral tooth-plate, 5 right medial lateral and outer lateral tooth-plates; after Marcus, 1953.

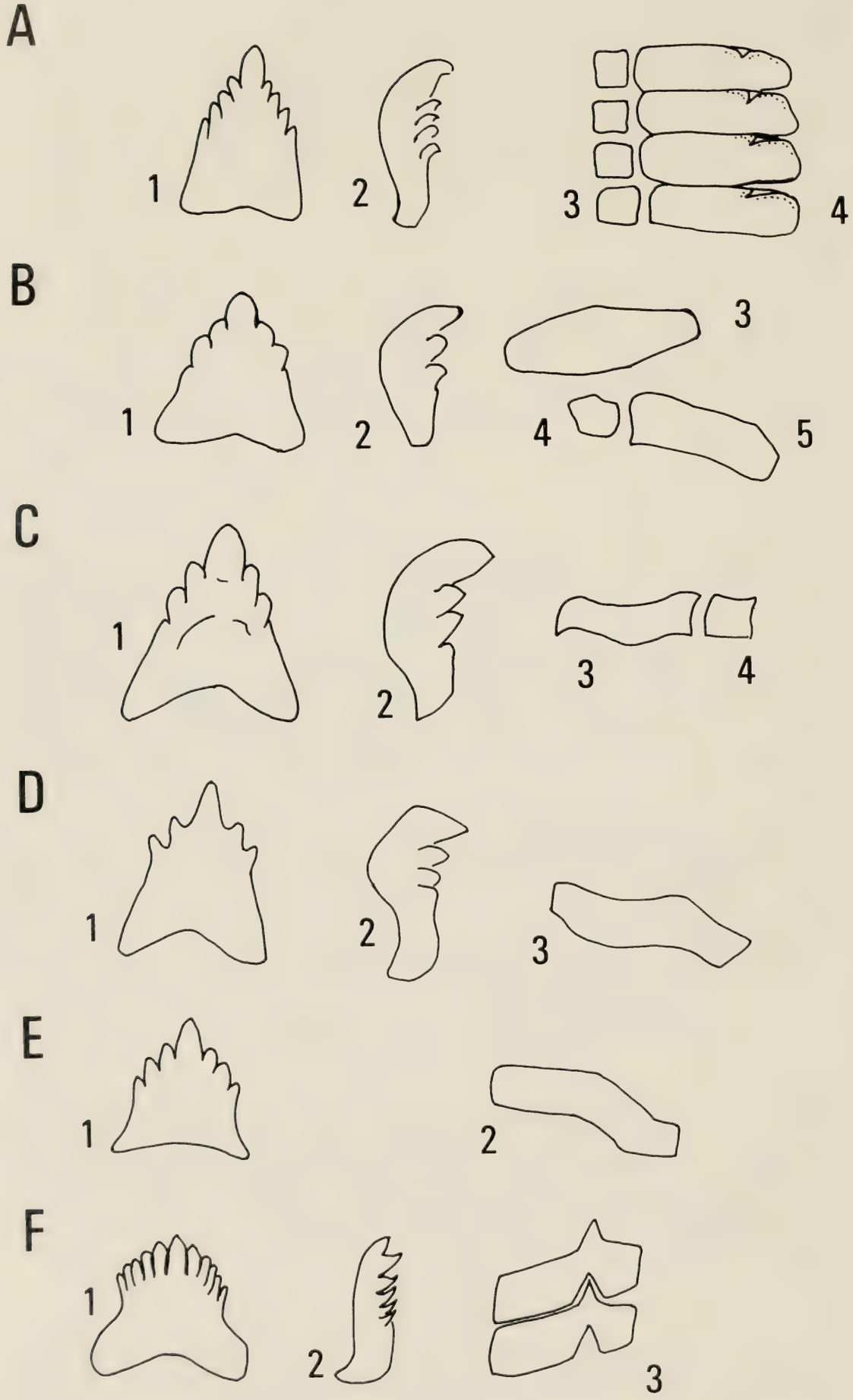
B *Pseudunela cornuta*, 1 anterior view of rachidian tooth, usual form, 2 anterior view of rachidian tooth, less common form, 3 lateral view of rachidian tooth, 4 left lateral tooth-plate; after Challis, 1970.

C *Tantulum elegans*, 1 posterior and 2 lateral views of rachidian teeth, 3 left lateral tooth-plates, 4 right medial and outer lateral tooth-plates.

vertically down to a ventral anus, or intermediate to the two latter conditions. The position of the anus with regard to nephridiopore and genital pore is considered to be very important as being indicative of the extent of detorsion and of the extent of freeing of the alimentary canal from the excretory and genital systems. Figure 38 shows the importance of this feature in distinguishing between the Acochlidioidea and the Philinoglossoidea.

NERVE GANGLIA, COMMISSURES, AND CONNECTIVES

The nervous system is detorted in all forms and shows a modified and concentrated epiathroid condition, with shortening and euthyneury of the visceral loop. There is a high degree of sensory development in head and tentacles which may be correlated


A
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with the anterior position of the nerve ring. The condition of the nervous system is also closely related to modifications seen in the alimentary canal. Thus the degree of development of the buccal nervous system and the degree of shortening of the visceral loop are correlated with the state of pharyngeal differentiation. The whole consideration of this point was greatly assisted by the excellent condition of the sectioned material of *Tantulum elegans* in which even the smallest nerves and connectives could be traced. Knowledge of this material was used as a basis for ascertaining the significance of various ganglia especially in cases where the literature was vague or misleading. Clearly we still need to know a great deal more of this system in other species. The three main distinguishing characters used here are (i) cephalization, or the extent of anterior placement of ganglia, (ii) cerebralization, or the degree of fusion of ganglionic elements, and (iii) the proportionate development of various ganglia.

Concentration of the nervous system is shown chiefly by cephalization in, for example, the Proprioneura, whereas cerebralization achieves this aim in, for example, the Cerebroneura. Figure 23 shows some of the modifications and concentrations of the basic epiathroid condition and Figures 39 and 40 show the various patterns achieved. The prepharyngeal positioning of the nerve ring in the Acochlidioidea is regarded here more as a functional corollary of a highly differentiated buccal cavity, (as was suggested by Franc, 1968a for the Oleacinidae, Pulmonata, and as seen in the benthic Amphiboloidea), rather than as a primitive opisthobranch condition. In all forms the visceral loop elements are anteriorly positioned either anterior to, immediately under, or just posterior to the pharynx, a condition that cannot be considered primitive.

The nerve ganglia are not equally developed in all forms. Thus, for instance, one can expect larger pedal ganglia and/or a stronger and perhaps even doubled pedal commissure in forms with a large foot (for example, *Acochlidium*).

Other characters used are lobulation and encapsulation. Encapsulation of ganglia is reported for *Palliohedyle* and *Tantulum* and is characteristic of pulmonates. Lobulation of ganglia is also a diagnostic character, for example the anterior lobes of the cerebral ganglia in *Tantulum*, and the anterior large lobes (?) of the pedal ganglia in *Palliohedyle*, but unfortunately this character is not always clearly described.

Commissures occur between members of paired ganglia, and connectives between

Fig. 35 The radula of the Acochlidioidea. Cerebroneura: Microhedylidae A–C, Unelidae D, Sabulincolidae E, F.

A *Microhedyle tyrtowii*, 1 anterior and 2 lateral view of rachidian tooth, 3 medial lateral tooth-plate, 4 outer lateral tooth-plate; after Kowalevsky, 1901.

B *Microhedyle cryptophthalma*, 1 anterior and 2 lateral view of rachidian tooth, 3 left lateral tooth-plate, 4 right medial lateral tooth plate, 5 right outer lateral tooth-plate; after Westheide and Wawra, 1974.

C *Stellaspina napolitana* (=*M. glandulifera*, Naples form), 1 posterior and 2 lateral view of rachidian tooth, 3 left outer lateral tooth-plate, 4 left medial lateral tooth-plate; after Marcus and Marcus, 1954.

D *Unela remanei*, 1 anterior and 2 lateral view of rachidian tooth, 3 lateral tooth-plate; after Marcus, 1953.

E *Sabulincola odhneri*, 1 anterior view of rachidian tooth, 2 lateral tooth-plate; after Marcus and Marcus, 1955.

F *Sabulincola gerlachi*, 1 anterior and 2 lateral view of rachidian tooth, 3 lateral tooth-plates; after Marcus and Marcus, 1959.

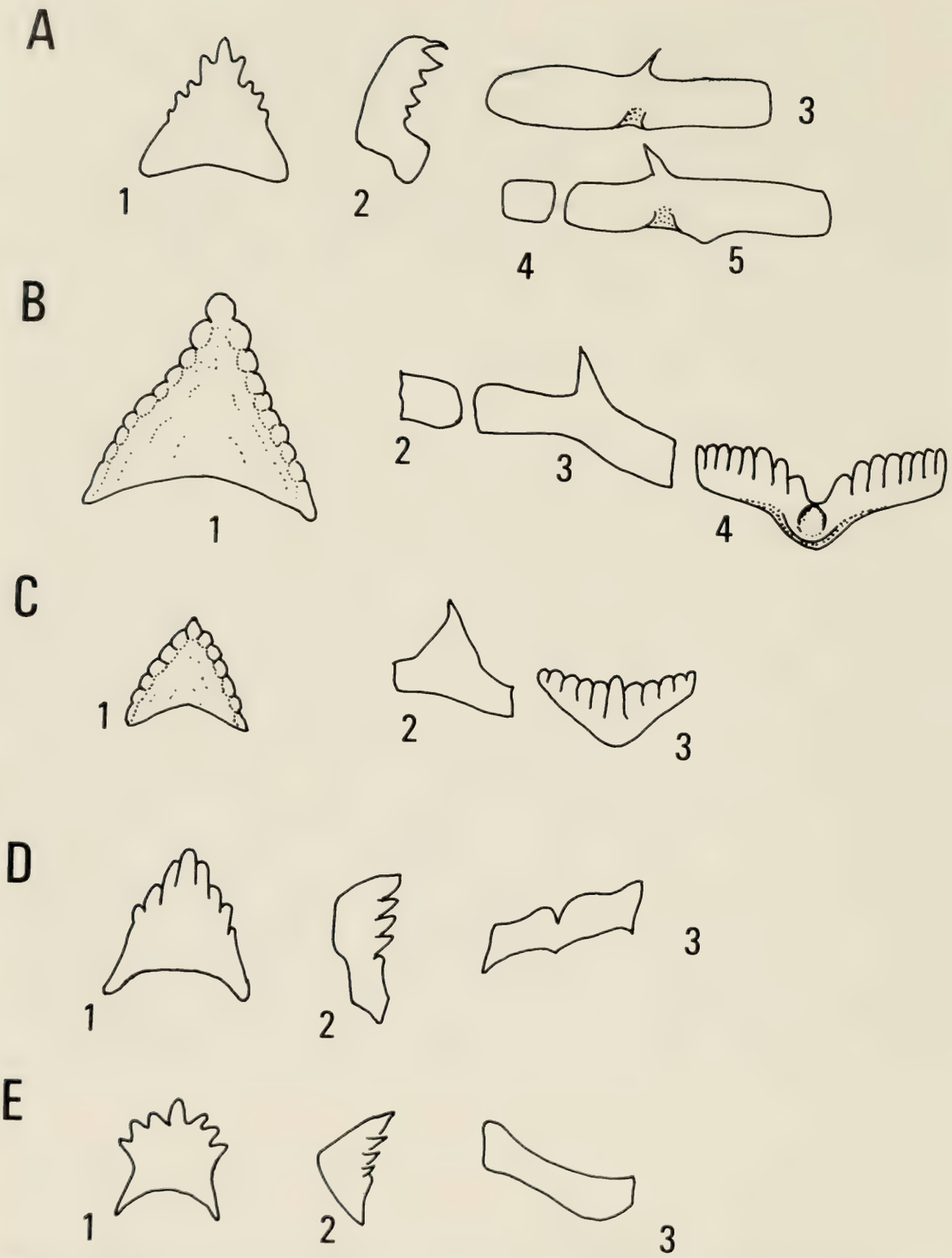

Fig. 36 The radula of the Acochlidioidea. Cerebroneura: Asperspinidae A–C, Mancohedylidae D, E.

A *Anademaria rhopalotecta*, 1 anterior and 2 lateral view of rachidian tooth, 3 left lateral tooth-plate, 4 right medial lateral tooth-plate, 5 right outer lateral tooth-plate; after Salvini-Plawen, 1973.

B *Asperspina brambelli*, 1 anterior view of rachidian tooth, 2 left outer lateral tooth-plate, 3 left medial lateral tooth-plate, 4 dorsal view of rachidian tooth; after Swedmark, 1968.

C *Antemnella loricata*, 1 anterior view of rachidian tooth, 2 left lateral tooth-plate, 3 dorsal view of rachidian tooth; after Swedmark, 1968.

D *Gastrohedyle brasilensis* 1 anterior and 2 lateral view of rachidian tooth, 3 lateral tooth-plate; after Marcus and Marcus, 1954.

E *Maraunibina verrucosa* 1 anterior and 2 lateral view of rachidian tooth, 3 lateral tooth-plate; after Challis, 1970.

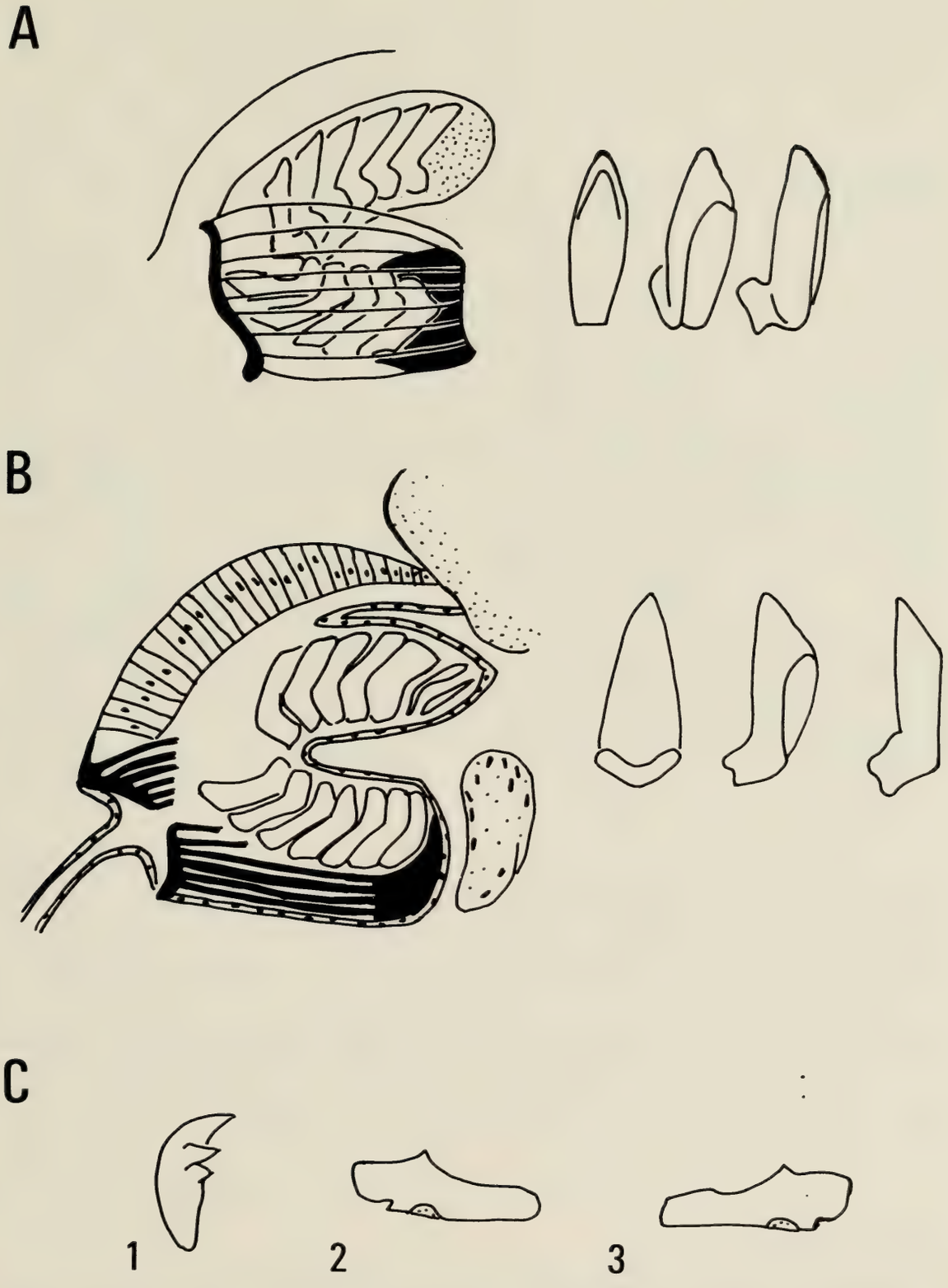

Fig. 37 The radula of the Acochlidioidea. Cerebroneura: Ganitidae A, B, Visceroneura: Livorniellidae C.

A *Ganitus evelinae*, entire radula in left lateral view, rachidian tooth in various views; after Marcus, 1953.

B *Paraganitus ellynnae*, entire radula in left lateral view, rachidian tooth in various views; after Challis, 1968.

C *Livorniella glomerans*, 1 lateral view of rachidian tooth, 2 left lateral tooth-plate, 3 right lateral tooth-plate; after Salvini-Plawen, 1973.

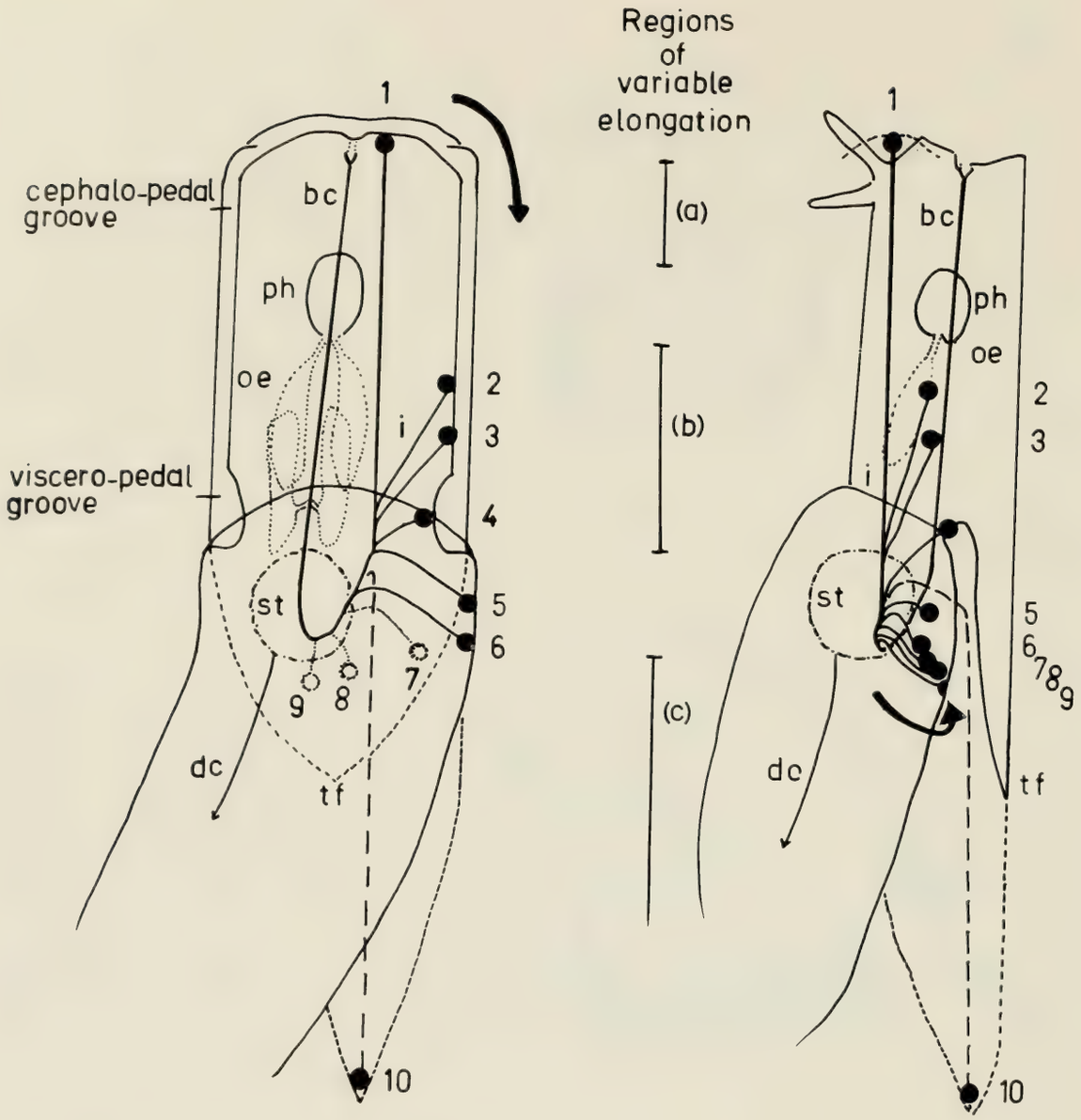

Fig. 38 Basic patterns of form and alimentary canal differentiation in the Acochlidioidea, Philinoglossoidea, and Platyhedyloidea. Numbers 1 to 10 indicate the position of the anus.

1. Fully torted position, hypothetical.
2. *Strubellia*
3. *Acochlidium*
4. *Unela, Asperspina, Antemnella, ?Ganitus, ?Paraganitus* (*Platyhedyle* also, but with shortened gut).
5. *Microhedyle*
6. *Hedylopsis*
7. *Pseudunela, Stellaspina*
8. *Sabulincola*
9. Fully detorted acochlidioidean position, *Tantulum*. Heavy black arrows indicate directions of detorsion, dashed line shows elongation of intestine and detorted position in the Philinoglossoidea (no free visceral sac); a = region of buccal tube, b = region of oesophagus, c = region of digestive caecum; broken lines indicate outlines of foot in Philinoglossoidea; dotted lines in region of oesophagus show positions of pharyngeal and oesophageal salivary glands.
10. *Philinoglossa*

differing ganglia. Basic terminology is used for all ganglia. Thus "pleural" refers to the previsceral loop ganglia that supply the mantle; "parietal" refers to the first pair in the visceral loop and the cumbersome, inaccurate and unnecessary "supra-" and "subintestinal" terms are discarded; "visceral" refers to the single, paired (or otherwise combined) posterior ganglion(a) in the visceral loop that give rise to the visceral nerves; "buccal" refers to ganglia (or parts of ganglia) that supply the buccal cavity, and which are generally connected to the cerebral ganglia. In *Tantulum* the buccal system or loop is not simple as, for example, in *Unela* but is extensively differentiated into "anterior buccal ganglia" supplying the buccal tube and anterior pharyngeal plexus, the "suprabuccals" supplying the salivary reservoirs within the pharynx, and the "posterior buccals" supplying the posterior part of the pharnygeal plexus and the pharyngeal salivary ducts and ampullae (Fig. 4). The term "accessory" when used in front of another name suggests that it is an additional ganglionic mass supplying the same structures as the main ganglion. Small accessory ganglia occurring on the dorsal cephalic nerve are omitted from the diagnoses as they are often described and labelled differently for the same animal by different authors; anterior sense organs, either bulbar, branched, or locular are also omitted from diagnoses in most cases for the same reason, especially as some authors have not distinguished secretory, neurosecretory, and neural structures.

Information on nerves is scanty but from scattered statements one gathers that the basic plan in the Acochlidioidea appears to resemble that worked out in detail for *Tantulum* in this paper; because of these omissions, nerves are not used in the classification as a character, although details if known, would provide an excellently suitable character.

SENSE ORGANS

Eyes are considered here to be well developed only if they show a structure with the complexity seen in *Acochlidium* and *Strubellia* (Fig. 41); moderately developed eyes are those showing an eye vesicle with definite pigment layer; poorly developed eyes or eyespots are tiny vesicles, often hidden, and containing only a few pigment grains.

Statocysts do not appear to be diagnostic and shape may be distorted in sectioned specimens; they are therefore not used here.

Nonvibratile tactile cilia, for example those on the head and tentacles of *Microhedyle tyrtowii*, are included where they are known to occur.

EXCRETORY SYSTEM

The terminology used here is in accordance with basic zoological standards and hence "nephrostome funnel" refers only to the ciliary- or flagellar-tufted funnel(s) between the pericardium and the nephridium; the "renopericardial canal" refers to the variously shaped, ciliated, or flagellated duct leading from the nephrostome into the nephridium; "internal flagellated (or ciliated) pore" refers to the opening by which the nephridium communicates with the nephric duct when present; a true "nephric duct" is a clearly distinguishable structure, (not merely a narrowed portion of the nephridium), leading from the nephridium to the external opening or "nephridiopore". The vertebrate term "cloaca" is held properly to belong only to a chamber into which anal, excretory, and genital products all discharge and hence does not apply to any known Acochlidioidean.

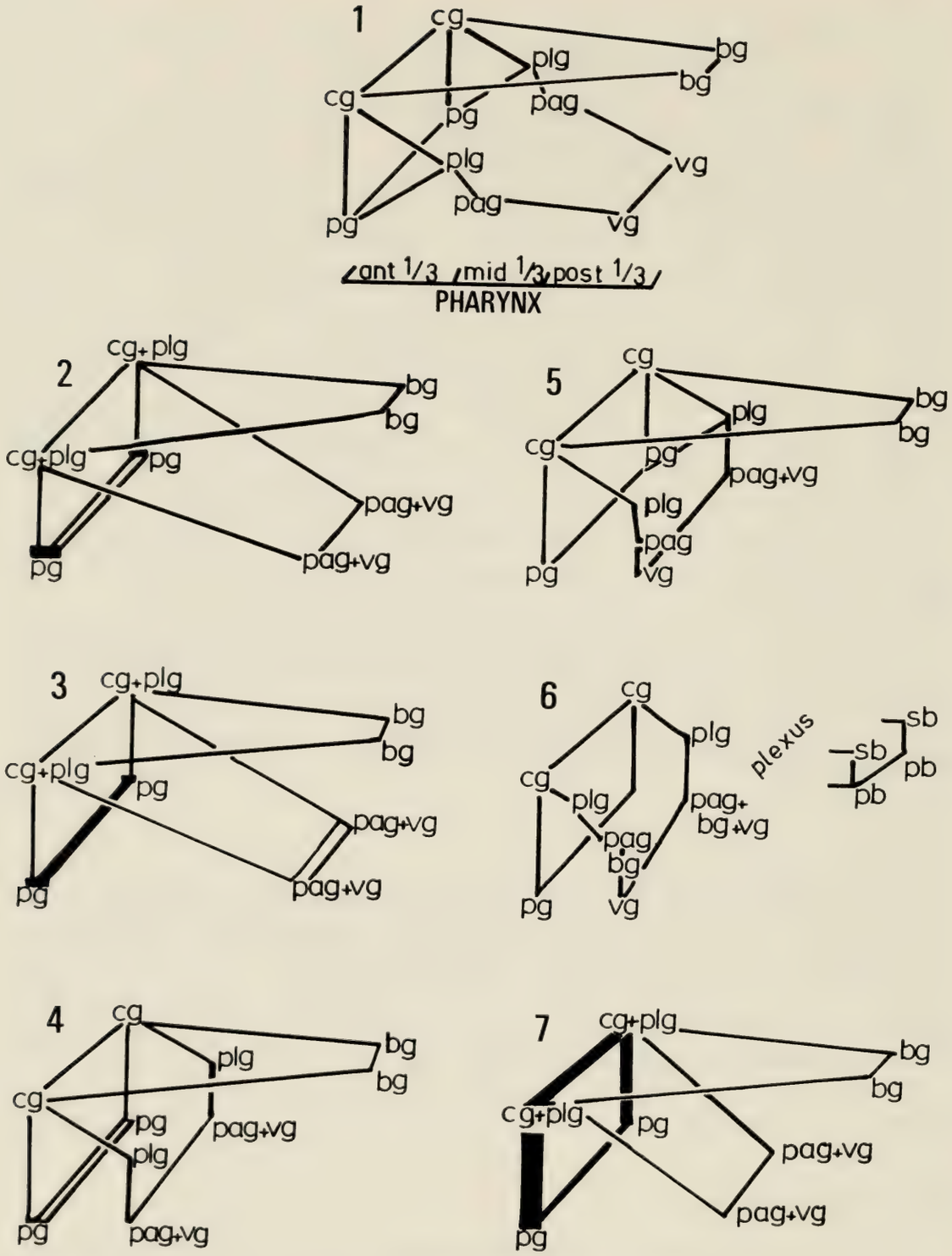

Fig. 39 Patterns of arrangement of neural ganglia in the Acochlidioidea.

1. Basic acochlidioidean pattern
2. *Acochlidium amboinense*
3. *Palliohedyle weberi*
4. *Hedylopsis suecica*
5. *Pseudunela cornuta*
6. *Tantulum elegans*
7. *Microhedyle tyrtowii*

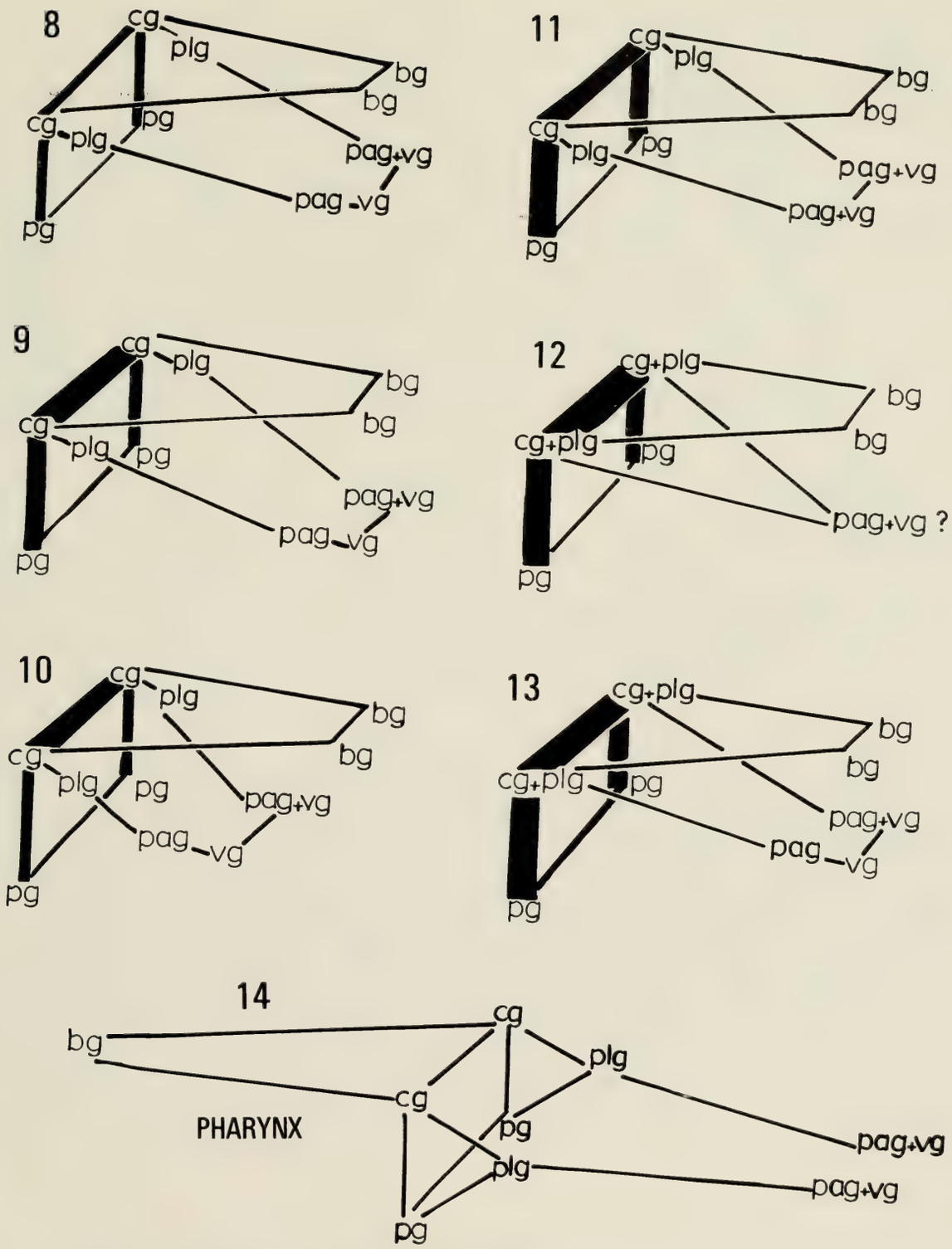

Fig. 40 Patterns of arrangement of neural ganglia, continued.

8. *Stellaspina lactea*
9. *Unela remanei*
10. *Gastrohedyle brasilensis*
11. *Asperspina brambelli*
12. *Antemnella loricata*
13. *Ganitus evelinae*
14. *Platyhedyle denudata* (Platyhedyloidea)

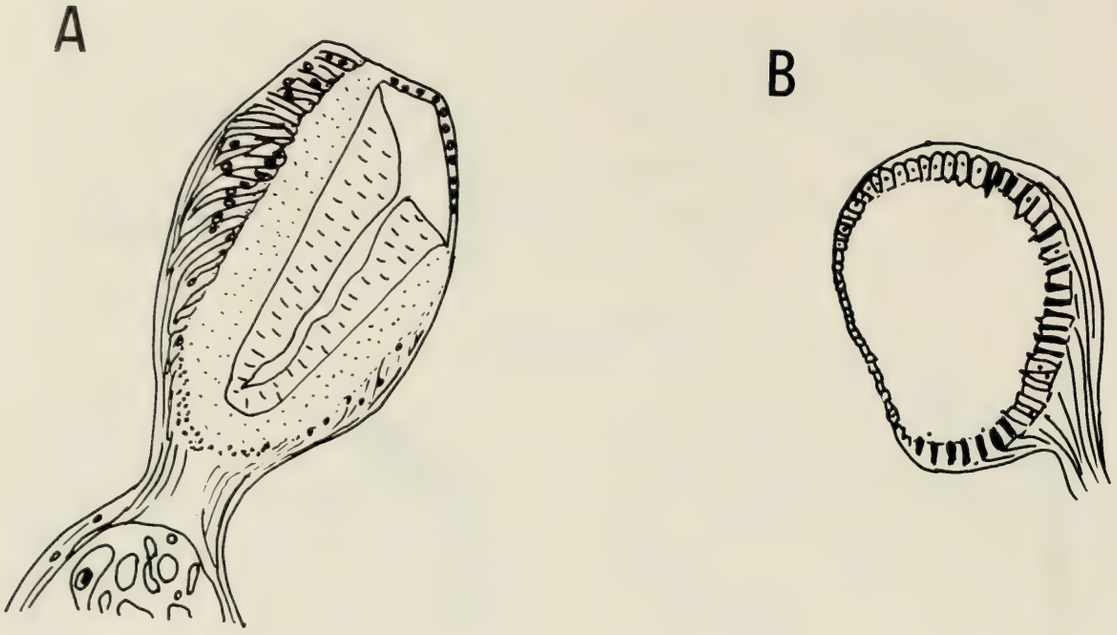

Fig. 41 Types of the well-developed acochlidioidean eye.
A *Strubellia paradoxa*, after Küthe, 1935.
B *Acochlidium amboinense*, after Bücking, 1933.

A nephridium may be a simple, contractile, semiporous sac without nephrostome, renopericardial canal, or nephric duct as in *Microhedyle tyrtowii*, or a voluminous sac with many nephrostomes and with a nephric duct as in *Palliohedyle weberi*, or a long, tubular structure with a very long looped and interconnected nephric duct as in *Strubellia paradoxa*, or a complex structure with two lumina surrounded by vacuolated nephrocytes and with a long looped nephric duct as in *Tantulum elegans*.

The position of the nephridiopore in relation to other body openings is diagnostic; it may be associated with the gonopore as in the Cerebroneura (for example, *Microhedyle*); or with the anus as in the Pedoneura (for example, *Acochlidium*), the Proprioneura (for example, *Hedylopsis*), and the Pharyngoneura (for example, *Tantulum*).

REPRODUCTIVE SYSTEM

The basic plans and terminology referred to in the classification are indicated in Figure 42. Male intromittent organs and anterior seminal ducts or ciliated grooves are found only in the Pedoneura and Proprioneura which all have a well-developed foot and cephalo-pedal groove; in other forms the reproductive system shows considerable reduction. The penis is considered to be armed and perforated when crowned with rows of chitinous hooks and internally traversed by a ductal anterior vas deferens bearing a chitinous tip (for example, *Acochlidium amboinense*, Fig. 42G). This perforate condition is shown also in some aeolids such as *Catriona* and *Phidiana* and also in some sacoglossans as *Stiliger, Limapontia,* and *Alderia* (Hyman, 1967). It is considered to be armed and valvular when it has ridged hook-bearing lips or flaps distally and contains only a channeled anterior vas deferens internally with no chitinous tip externally (for example, *Palliohedyle weberi*, Fig. 42H). It is considered

bimuscular and glandular when comprised of two main muscle masses, one operating the opening of the penial gland duct and bearing a large solid chitinous hook, the other controlling the opening of the prostate ducts into the tube of the penial stylet (for example, *Strubellia paradoxa*, Fig. 42D); in this form the ciliated seminal groove approaches the groove of the stylet externally, not through the penis. It is eversible when capable of total eversion and traversed by the anterior vas deferens (for example, *Hedylopsis suecica*, Fig. 42E). It is considered simple and glandular when it is comprised of only a muscular sac (with a hollow basal spine) and opens to the exterior by a short penial duct unprotected by any stylet; in this form the integumental anterior vas deferens and the prostate duct arrive independently at the external penial opening (for example, *Pseudunela cornuta* Fig. 42F).

The structure of spermatozoa and spermatophores is used where information is available.

HEART, BLOOD VESSELS, AND HAEMOCOELS

These structures are the most poorly described in the literature and diagnostic characters have therefore been confined to basics with details omitted. Thus the heart is either two-chambered as in the Pedoneura (for example, *Acochlidium*), or with a single chamber as in the Proprioneura (for example, *Hedylopsis*) and Pharyngoneura (for example, *Tantulum*), or absent as in the Cerebroneura (for example, *Microhedyle, Ganitus*).

Blood vessels have been described for *Acochlidium amboinense* (Bücking, 1933), for *Strubellia paradoxa* (Küthe, 1935), and now for *Tantulum elegans*. There is also the reported trace of one vessel-like structure in *Unela* (Marcus, 1953). In the definitions of the new classification blood vessels are indicated simply as absent or present, where the latter is substantiated.

The number and condition of haemocoelic spaces present unfortunately could not be used as a character, again owing to incomplete information; in some cases only two spaces, the cephalic and visceral, are mentioned when camera lucida drawings clearly show other haemocoels. No doubt the original mention of the badly named "diaphragm" (Kowalevsky, 1901:10) has been responsible for this confusion. Internal circulation and control of turgor obviously depend on the construction and comparmentalization of the "body cavity" hence it is to be hoped that more information along these lines will soon be available for this group.

MUSCULATURE

The condition of the muscle strands at various situations in the body has been used as a diagnostic character where information is clear and names used are self-explanatory. This is another area where more detailed study is required.

FREE CELLS

Description of these is confined to a few species such as *Microhedyle tyrtowii* and *Tantulum elegans* but it is obvious that major differences must exist in view of the differing methods of excretion, circulation, and spicule formation in the Acochlidioidea.

A
nephridium
duct
gonad
B
mucous gland
albumin gland
seminal vesicle
ejaculatory duct
C
D
E
bursa copulatrix
seminal vesicle
penis
F
prostate
penial
G
H
?
?

Notes on the New Definitions

All suborders are new, with accompanying definitions. Definitions of all existing families are clarified in terms of the type genus and species in each. This has necessitated the removal of some species from existing genera and the creation of some new genera. All available information has been used in arriving at these definitions. For instance, in some cases where existing definitions have not included all pertinent facts, these have been culled from visible features in illustrations, from other textual sources, or from personal observations.

The classification presented here, with a number of monogeneric families and monotypic genera, may appear to be too complicated for this small group of molluscs. However, the few acochlidioidean species so far described come from widely separated biogeographic regions leaving most of the coastlines of the world unsampled. None has been collected as yet from the sea-shores of western North America, Africa, continental Asia, Australia, and Pacific South America. It is hoped that this scheme will form a useful skeletal classification for the large number of species yet to be discovered.

Acochlidium weberi (Bergh, 1895) (Fig. 26B) has been removed from the genus on obvious grounds such as the number and condition of the head appendages, the size of the foot and its relationship to the hump, the size and character of the dorsal visceral sac, the radula, the digestive caecum, and the reproductive and excretory systems. A new genus *Palliohedyle* (L.: palliolum = a little Greek cloak or mantle) has been erected for its reception. The differences between *A. amboinense* (Fig. 26A) and *P. weberi* are considered to be more than merely generic and the latter has therefore been placed in a separate family, the Palliohedylidae.

Strubellia paradoxa (Strubell, 1892) (Fig. 26C) has been removed from the Hedylopsidae and placed in a new family, the Strubelliidae, which is now grouped together with the Acochlidiidae and the Palliohedylidae in a new suborder, the Pedoneura. The reasons for this are very obvious from the clarified definitions of the existing families of Acochlidiidae and Hedylopsidae, even although we still await Wawra's (1974) promised redescription of the nervous system of *Strubellia*.

Hedylopsis suecica Odhner 1937a (Fig. 27A) is retained as a separate species instead of as a local form of *H. spiculifera* (Kowalevsky, 1901) (Fig. 27B) as suggested by Swedmark (1971), because the two are clearly distinguishable in their own niches (Poizat, 1971) and are separable as indicated in the classification.

The newer species *H. brambelli* Swedmark 1968 (Fig. 29D), *H. rhopalotecta* Salvini-Plawen 1973 (Fig. 29E), and *H. loricata* Swedmark 1968 (Fig. 29F) do not belong in the genus *Hedylopsis* in spite of their spicular pallial tests, as they totally

Fig. 42 Basic plans of reproductive systems and types of penial structure encountered in the Acochlidioidea. Plans A, B, and C without penis; types D to H hermaphrodite.

- A *Microhedyle*, male or female.
- B *Paraganitus*, male and female
- C *Tantulum*, male and/or female?
- D *Strubellia*, male and female, penis bimuscular and glandular.
- E *Hedylopsis*, penis eversible and evaginable.
- F *Pseudunela*, penis simple and glandular.
- G *Acochlidium*, penis armed and perforated.
- H *Palliohedyle*, penis armed and valvular.

lack many basic characters of the Hedylopsidae including the following: cephalization of the visceral loop ganglia to an anterior position while maintaining separation of anterior ganglia, penis, pericardium, heart, blood vessels, and complex nephridium. Although some of the detailed structure of the pharyngeal region is not known for these forms, they have been placed in a new family, the Asperspinidae, in a new superfamily Velariacea, in the new suborder Cerebroneura; they are clearly closer to the microhedylids in most anatomical features than to any other acochlidioidean group. Three new genera, *Asperspina, Antemnella,* and *Anademaria*, have been erected for these forms because of basic differences in structure that prevent them being placed in the same genus.

The subgenus *Pseudunela* of Salvini-Plawen 1973 (Fig. 27C) has been elevated to full generic rank, removed from the Microhedylidae, and placed in a new family, the Pseudunelidae, which is considered to be near the Hedylopsidae in the new suborder Proprioneura. The Pseudunelidae differ structurally from the Hedylopsidae in features such as the ventrolateral position of the anus and its closer relationship to the genital pore, in general morphology, and in arrangement of the nervous system.

The status of the genus *Microhedyle* has been altered recently out of all recognition so that the present expanded genus bears little resemblance to the type species. In 1930 Hertling erected this genus for *Hedyle tyrtowii, H. milaschewitchii,* and *H. intermedia* (= *glandulifera*), all described by Kowalevsky (1900 and 1901), and for his own *M. glandulifera lactea*. Of these four species, put into the new genus at one time, we must use the one that has historical precedence as the type species for the genus *Microhedyle*. *Microhedyle tyrtowii*, (Fig. 28A) was the first species described by Kowalevsky (1900) and in addition he designated this species later (1901:14) as showing marked differences from *Acochlidium* (= *Hedyle*). In fact, he suggests that *M. tyrtowii* not only belongs to a new genus, but to a new family although he does not give it a name. Fortunately, he describes this species in some detail (1901) and uses it as a basis of comparison for all his other species. The subsequent creation of the junior synonym *Parhedyle* Thiele 1931 is, as pointed out by Westheide and Wawra (1974), both invalid and unnecessary. Hence *M. tyrtowii* remains the type species of the genus *Microhedyle*, forming the basis of the family Microhedylidae.

The subgenus *Mancohedyle* Salvini-Plawen 1973 has been elevated here to full generic status to accommodate *Microhedyle milaschewitchii* (Kowalevsky) 1901 (Fig. 29A); this species forms the basis of a new family, the Mancohedylidae, created for it and for two new genera *Gastrohedyle* and *Maraunibina*. *Gastrohedyle* has been erected for the Brazilian form of *M. milaschewitchii* described by Marcus and Marcus (1954) which is regarded here as not only a separate species but also a separate genus; it therefore becomes *G. brasilensis*, (Fig. 29B), using the Marcus and Marcus description as the definition for the new species and genus. Although in the same family, the species *Microhedyle* (*Mancohedyle*) *verrucosa* Salvini-Plawen 1973 is considered to differ at the generic level and a new genus *Maraunibina* (Fig. 29C) erected for its reception.

The species *Microhedyle glandulifera* (Kowalevsky) 1901 was originally mentioned by him in a preliminary note in 1900 as *M. intermedia*; however, I have not been able to trace this 1900 reference and cannot therefore tell whether it gives sufficient information to constitute a valid description. We may later have to revert to the earlier name of *intermedia*, although this would be unfortunate as it is less descriptive and not so commonly used in the literature. It is considered here as

belonging to a separate genus on the basis of anatomical differences (see classification) and *Stellaspina* has therefore been created for it. *S. glandulifera* (Fig. 28B), *S. lactea* (Fig. 28C), and the Naples form (Marcus and Marcus, 1954) are considered as separate species for structural reasons and because they are found in waters with differing salinities (Kowalevsky, 1901). The Naples form has been given the name *S. napolitana*. Because of the possibility that additional species may have been included wrongly under the names of *S. glandulifera* and *S. lactea*, any reported findings of these species in waters distant to the type localities have been omitted from the lists until such time as they may be confirmed on the basis of the additional facts brought to light in this new classification.

Unela remanei Marcus 1953, (Fig. 28E), is retained in the genus *Unela* instead of being demoted to a subgenus of Microhedyle, as suggested by Salvini-Plawen (1973), for the following basic reasons: the nephridiopore is anterior to the genital pore, there are no spicules, the radula has more rows of teeth and a formula of 1-R-1, the gut is internally ciliated, and the recorded size, 5 mm, is much greater than that of any species of *Microhedyle*.

Unela odhneri Marcus and Marcus 1955, (Fig. 28F) is mentioned by name only by Delamare DeBoutteville (1953a and 1953b), being listed simply as "*Microhedyle odhneri* (in litteris)"; this species differs from both *Unela* and *Microhedyle* in a number of essential characteristics and I have therefore created a new genus for it, called *Sabulincola*.

The species *Microhedyle glomerans* (Fig. 30C) does not belong with the genus *Microhedyle*, nor even to the suborder Cerebroneura, for important reasons such as the complete separation of the anterior ganglia, the strongly developed visceral loops and visceral nerve, the general morphology with grooved pedal sole, and the totally different method of contraction of the long dorsal visceral sac. *M. glomerans* has therefore been placed in a new genus *Livorniella* (L.; *livornius* = a little Livornian, named after its coast of origin), and given a new family, the Livorniellidae, to accommodate it. It has been placed tentatively in a new suborder, the Visceroneura.

Ganitus evelinae Marcus 1953, (Fig. 30A) and *Paraganitus ellynnae* Challis 1968, (Fig. 30B) have been placed in a new family, the Ganitidae, created as a type family of the superfamily Avelariacea, on the basis of very strong structural evidence. As can be seen from the definitions of this family and superfamily, these two genera differ fundamentally from the Velariacea, which comprises the Microhedylidae, Mancohedylidae, and Asperspinidae.

Platyhedyle denudata Salvini-Plawen 1973 (Fig. 30D) is an important new find; Salvini-Plawen has placed it tentatively in what he terms the Cephalaspidea-Acochlidioidea but suggests that it may in fact belong in a parallel but separate group. *P. denudata* differs from any acochlidioidean in the following characters: flattened form with broad head bearing no cephalic appendages and with very elongate dorsal visceral sac, partially coiled when disturbed; animal cannot retract into visceral hump; postpharyngeal nerve ring; anteriorly placed buccal ganglion, indicating entirely different type of pharyngeal differentiation; no cephalization of visceral loop ganglia to pharyngeal region; salivary? glands lie on either side of stomach (point of entry into gut not yet determined but may be mid-gut glands); monoseriate radula with sharply pointed, denticulate, narrowly hemiconical, large-based rachidian teeth and no lateral plates; reduced oesophagus; (buccal cavity unfortunately as yet undescribed). I propose therefore an Order Platyhedyloidea, as defined at the end of

the classification, to accommodate this family, and suggest, as mentioned previously, that it be placed within a new broader grouping, the Subclass Ceratobranchia.

Outline of Classification

Order Acochlidioidea
- Suborder Pedoneura subord. nov.
  - Family 1. Acochlidiidae rev.
    - *Acochlidium amboinense* Strubell 1892
  - Family 2. Palliohedylidae fam. nov.
    - *Palliohedyle weberi* (Bergh) 1895
  - Family 3. Strubelliidae fam. nov.
    - *Strubellia paradoxa* (Strubell) 1892
- Suborder Proprioneura subord. nov.
  - Family 1. Hedylopsidae rev.
    - *Hedylopsis spiculifera* (Kowalevsky) 1901
    - *Hedylopsis suecica* Odhner 1937a
  - Family 2. Pseudunelidae fam. nov.
    - *Pseudunela cornuta* (Challis) 1970
- Suborder Pharyngoneura subord. nov.
  - Family 1. Tantulidae fam. nov.
    - *Tantulum elegans* gen. et sp. nov.
- Suborder Cerebroneura subord. nov.
  - Superfamily I. Velariacea superfam. nov.
    - Family 1. Microhedylidae rev.[1]
      - *Microhedyle tyrtowii* (Kowalevsky) 1900: revised Kowalevsky 1901
      - *Microhedyle cryptophthalma* Westheide and Wawra 1974
      - *Microhedyle nahantensis* (Doe) 1974
      - *Stellaspina glandulifera* (Kowalevsky) 1901
      - *Stellaspina lactea* (Hertling) 1930
      - *Stellaspina napolitana* sp. nov.
    - Family 2. Sabulincolidae fam. nov.
      - *Sabulincola odhneri* (Marcus and Marcus) 1955
      - *Sabulincola gerlachi* (Marcus) 1959 incertae sedis
    - Family 3. Unelidae fam. nov.
      - *Unela remanei* Marcus 1953
    - Family 4. Mancohedylidae fam. nov.
      - *Mancohedyle milaschewitchii* (Kowalevsky) 1901
      - *Gastrohedyle brasilensis* nov. sp.
      - *Maraunibina verrucosa* (Challis) 1970
    - Family 5. Asperspinidae fam. nov.[2]
      - *Asperspina brambelli* (Swedmark) 1968
      - *Antemnella loricata* (Swedmark) 1968
      - *Anademaria rhopalotecta* (Salvini-Plawen) 1973
  - Superfamily II. Avelariacea superfam. nov.

[1] See note 1, page 123.

[2] See note 2, page 123.

Family 1. Ganitidae fam. nov.
Ganitus evelinae Marcus 1953
Paraganitus ellynnae Challis 1968
Suborder Visceroneura subord. nov.
Family 1. Livorniellidae fam. nov.
Livorniella glomerans (Salvini-Plawen) 1973

Order Platyhedyloidea ord. nov.
Family 1. Platyhedylidae Salvini-Plawen 1973
Platyhedyle denudata Salvini-Plawen 1973

Definitions and Synonymy

Please see pages 55 to 77 and Figures 24 to 42 for identifying characters and Figure 32 for methods of radular measurement.

Order Acochlidioidea def. nov.

Hedylacea Odhner 1937
Acochlidiacea Odhner 1939
Acochlidiacea: Marcus 1953
Acochlidioidea: Taylor and Sohl 1962
Euacochlidiacea: Franc 1968
Cephalaspidea, Acochlidiacea: Salvini-Plawen 1973
Acochlidiacea: Westheide and Wawra 1974

Molluscs with the characters of the Ceratobranchia (see p. 55). Hump uncoiled and produced into a free dorsal visceral sac which is carried posteriorly. Foot either well developed and set off from the anterior hump by a cephalo-pedal groove, or merely forming a ciliated ventral band on the hump and with the posterior end of the foot freed by a viscero-pedal groove. Animal capable either of retracting into temporary mantle cavity of dorsal visceral sac or of coiling the dorsal visceral sac temporarily. Anterior ganglia (cerebral and pedal) always cephalized to form a prepharyngeal nerve ring, with pleural ganglia often included in this ring. Visceral loop ganglia always cephalized at least as far forward as the posterior end of the pharynx and often linked with anterior ring. Cerebralization (= fusion) of ganglia variable. Anus either dextrolateral, ventrolateral, or ventral. Buccal cavity differentiated into buccal-tube and pharyngeal regions, with pharynx variably developed. Radula with central rachidian tooth and either one or two flattened lateral tooth-plates on either side, may show asymmetry; tooth rows comparatively few. Either hermaphrodite or with sexes separate, spermatophores may be formed.

Suborder Pedoneura subord. nov.

Freshwater, riverine or estuarine, but not interstitial acochlidioidean molluscs of moderate size (20 to 30 mm in length). Foot large, muscular, and demarcated by deep and fusing cephalo-pedal and viscero-pedal grooves from the anterior hump. Anus dextrolateral. Pedal nervous system well developed, with ganglia enlarged or lobular, with large or doubled commissure. Cerebralization of anterior ganglia marked. Visceral loop ganglia cephalized to mid-pharyngeal position. Buccal system simple.

Well-developed eyes occur. Pharynx of moderate size with velarium, small lingual cushion, curved radular bending plane, and distinct lower portion of radula. Rachidian tooth pointed, triangular and with finely denticulate (serrate) or adenticulate lateral margins. Digestive caecum usually single (if paired, left duct is very reduced), either branched or with internal divisions. Heart two-chambered (one atrium and one ventricle), pericardium and blood vessels well developed. Excretory system well developed with large nephridium, renopericardial nephrostome(s), and nephric duct present; nephridiopore opens near anus. Reproductive system well developed, with genital glands forming distinct masses not intimately bound in with digestive diverticulum. Penis and accessory glands present, anterior vas deferens may be intraepidermal duct or surface groove.

Family Acochlidiidae rev.

Hedylidae Bergh 1895
Hedylidae: Hertling 1930, in part
Hedylinae: Thiele 1932, in part
Acochlidiidae: Odhner 1937a, in part

Riverine animals with the characters of the Pedoneura. Two pairs of similar cephalic appendages present. An internal spicular skeleton present. Stomach globular. Digestive caecum a single diverticulum with long, digitiform, glandular lobes bound together by thin muscle sheath. Radula with lower recurved portion as long as upper. Nephridium a broadened sac widely attached to pericardium with numerous small interconnecting nephrostomes, nephric duct short. Penis armed and perforated.

Genus *Acochlidium* Strubell 1892

Acochlidium Strubell 1892
Hedyle: Bergh 1895 (not *Hedyle* Guenée 1857; not *Hedyle* Malmgren 1865)
Acochlidium: Odhner 1937a; in part

With the characters of the family and with skeletal spicules occurring as tubular, laminate rods up to 500 μm in length. Anterior and posterior tentacles almost equal in size, broad at base, tapering into digitiform tips. Foot broader than anterior hump and with angled anterior corners. Dorsal visceral sac as broad as foot and extending posteriorly to level of tip of foot. Mantle smooth, with no convoluted lateral borders. Eyes well developed and more posterior than bases of posterior tentacles. Radula with about 54 tooth rows and approximately one-half of these in lower portion. Digestive caecum with 14 lobes bearing glandular areas along their length. Twenty to 25 renopericardial nephrostomes. Hermaphrodite. Common genital duct divides into two. Penis posterodextral to pharynx, chitinous stylet is short and hollow and opens on right just posterior to pharynx. Oviduct passes over surface of penis and opens near male opening.

Type Species

A. amboinense Strubell 1892

Acochlidium amboinense Strubell 1892

Acochlidium amboinense Strubell 1892
Hedyle amboinensis: Bücking 1933
Acochlidium amboinense Bücking: Odhner 1937a

With the characters of the genus. Living animals 25.0 to 35.0 mm in length. Colour olive-green flecked with white, with head and anterior body slightly paler, anterior mantle darker green. Radular formula 2-R-2, $\frac{U\ 28\text{-}32}{L\ 24\text{–}25}$ = Max. 52-56. Rachidian tooth 200 to 270 μm in height, 150 μm broad with lateral borders plain or very finely serrate. Medial lateral tooth-plate 40 μm long, 110 μm broad, with a a blunt process bearing zero to three denticles on distal part of upper margin and with lower edge of following plate recessed to accommodate this process. Outer lateral tooth-plate small, subquadrangular, 20 μm long, 25 μm broad, often with a tiny denticle at the two posterior corners. Spicules in ring around oesophagus and in tissue of foot, not in dorsal visceral sac. Penis of moderate size, about 2 mm long with about 15 large and eight or nine smaller chitinous hooks on crown and a chitinous stylet up to 1 mm in length at end of vas deferens.

Type Locality

Stream in Ambon Island, Moluccas, Indonesia.

Other Localities

Arakitaoch Stream in Babelthuap Island, Palau Islands, Carolines at 46 to 58 m above sea level in basaltic cascade zone.

Family Palliohedylidae fam. nov.

Hedylidae Bergh 1895
Hedylidae: Hertling 1930, in part
Hedylinae: Thiele 1932, in part
Acochlidiidae: Odhner 1937a, in part

Estuarine animals with the characters of the Pedoneura. Two pairs of dissimilar cephalic appendages present. Integumental spicules present in head. Foot only moderately large. Stomach globular. Digestive caecum basically paired but left duct much reduced and right duct branched with glandular areas confined to tips of branches. Radula with lower recurved portion much shorter than upper. Nephridium attached to pericardium, structure not fully known. Penis armed and valvular.

Genus *Palliohedyle* gen. nov.

Hedyle Bergh 1895 (not *Hedyle* Guenée 1857; not *Hedyle* Malmgren 1865)
Acochlidium: Odhner 1937a, in part
Palliohedyle (L.: *palliolum* = a little Greek cloak or mantle)

With the characters of the family and with integumental spicules occuring as laminate rods up to 25 μm in length. Anterior cephalic appendages broad at base and small,

forming supralabial lappets rather than tentacles, posterior tentacles rounded, tapering to digitiform tips. Foot narrower than anterior hump and with angled anterior corners. Dorsal visceral sac voluminous, extending posteriorly greatly beyond level of tip of foot. Mantle smooth, with convoluted lateral borders. Eyes well developed and near bases of posterior tentacles. Radula with more than 100 tooth rows and approximately one-third of these in lower portion. Left digestive caecum very small, right divided into two main longitudinal branches, each with sequential short bifid branchlets bearing glandular areas at their tips. Spherical or spindle-shaped ampulla on salivary duct. Renopericardial nephrostome apparently single. Hermaphrodite. Penis dorsal to pharynx. Subintegumental anterior vas deferens present.

Type Species

P. weberi (Bergh) 1895

Palliohedyle weberi (Bergh) 1895

Hedyle weberi Bergh 1895
Acochlidium weberi: Odhner 1937a

With the characters of the genus. Living animals 30.0 mm in length and 15.0 mm broad across the dorsal visceral sac. Colour muddy white or brownish grey with a faint reddish shimmer in parts, reddish pigment cells present in head. Radular formula 2-R-2, $\frac{U\ 75}{L\ 24}$ = Max. 113. Rachidian tooth 120 μm high, 90 μm broad and with nine sharply pointed denticles on either side of median denticle. Medial lateral tooth-plate 75 μm broad, with spine in middle of posterior border. Outer lateral tooth-plate 20 μm broad, with no spines or denticles; right outer lateral tooth-plates imperfectly freed from radular membrane. Spicules restricted to bundles in head. Penis enormous, up to 8 mm in length, pear-shaped, with about 37 small chitinous hooks in double left ridge and 14 larger hooks on medial border of "lip".

Type Locality
Estuary near Bari, Flores Island, Indonesia. No other localities on record.

Family Strubelliidae fam. nov.
Riverine animals with the characters of the Pedoneura. Two pairs of similar cephalic appendages present. Spicules may be absent. Stomach not distinct. Digestive caecum large and long, with internal longitudinal folds. Radula with lower recurved portion as long as upper. Nephridium complex with single nephrostome, nephric duct long. Penis bimuscular and glandular.

Genus *Strubellia*: Odhner 1937b

Acochlidium Strubell 1892, in part
Hedyle: Bücking 1933, in part
Acochlidium: Küthe 1935, in part

With the characters of the family and with no spicules. Anterior tentacles digitiform and slightly broadened at base, posterior tentacles also digitiform and slightly smaller. Foot narrower than anterior hump and with angled anterior border. Dorsal visceral sac narrower than foot and extends well beyond its posterior tip. Mantle smooth, with no convoluted lateral borders. Eyes well developed and at base of posterior tentacles. Radula with about 54 tooth rows and approximately half of these in lower portion of radula. Digestive caecum as long as visceral sac and fills nearly half of its width, with internal longitudinal glandular folds. One renopericardial nephrostome. Sexes separate. Testis lie under digestive caecum, vas deferens and seminal vesicle open separately on genital papilla anterior to anus, integumental ciliated sperm groove leads from genital papilla to anterior tip of penis. Penis posterodextral to pharynx, chitinous penial stylet very long and contains both tube and gutter, opens to exterior on head between anterior and posterior right tentacles. In female, oviduct opens anterior to anus.

Type Species
S. paradoxa (Strubell) 1892

Strubellia paradoxa: (Strubell) 1892

Acochlidium paradoxum Strubell 1892
Strubellia paradoxa: Odhner 1937b

With the characters of the genus. Living animals 20 to 30 mm in length. Colour muddy yellow on head and anterior body, with little white spots indicating the position of glands, dorsal visceral sac reddish brown. Radular formula 2-R-2, $\frac{\text{U } 28\text{–}32}{\text{L } 24\text{–}45}$ = Max. 52–56. In Solomon Islands specimens, rachidian tooth 103 μm high and 75 μm broad, with lateral borders very finely serrate, medial lateral tooth-plate approximately 67 μm broad with spine on distal third of posterior margin and corresponding groove on anterior margin, outer lateral tooth-plate approximately 17 μm broad with no spines. Renopericardial canal flagellate, nephridium a long double sac, nephric duct looped with a few canalicular connections between arms of loop. Penis about 1.3 mm in length with chitinous stylet, (0.5 mm, Ambon form; 0.9 mm, Guadalcanal form), and basal spine.

Type Locality
Stream in Ambon Island, Moluccas, Indonesia.

Other Localities
Matanikau River (4.8 km up from mouth), Guadalcanal Island, Solomon Islands.

Suborder Proprioneura subord. nov.

Marine, littoral or infralittoral, interstitial acochlidioidean molluscs, found in gravel or sand. Size 3.0 to 4.0 mm in length. Foot moderately well developed, with muscle fibres and internal haemocoelic spaces, demarcated by cephalo-pedal and viscero-

pedal grooves from anterior hump. Anus either dextrolateral or ventrolateral. Anterior ganglia characteristically separated or with very slight cerebralization. Visceral loop ganglia cephalized to anterior pharynx; buccal system simple. Eyes either well developed or poorly developed. Pharynx of moderate size with velarium, small lingual cushion, curved radular bending plane and distinct lower portion of radula. Rachidian tooth subtriangular with margins bearing a few large denticles. Digestive caecum single, tubular, with neither branches, lobes, nor internal divisions; as long as dorsal visceral sac. Heart one-chambered, pericardium and blood vessels present. Excretory system well developed with large nephridium, renopericardial nephrostome, and nephric duct present; nephridiopore opens near anus. Reproductive system well developed, with genital glands forming distinct masses not intimately bound in with digestive diverticulum. Penis present, anterior vas deferens may exist partly as open ciliated groove and partly as intraepidermal duct. Large, paired oral (= suprapedal) glands present.

Family Hedylopsidae rev.

Microhedylidae, Subfamily B. Odhner 1937a
Hedylopsidae Odhner 1952
Hedylopsidae: Marcus 1953

With the characters of the suborder Proprioneura. Two pairs of dissimilar cephalic appendages present. Pallial spicules large and forming a stiffening of the mantle (= pallial test). Stomach small, straight, and indistinct. Radula with lower recurved portion as long as upper. Nephridium large with single renopericardial nephrostome, nephric duct very long, nephridiopore closely associated with anus. Anus dextrolateral. Cerebralization of anterior ganglia slight. Hermaphrodite genital pore anterior to anus and opening separately, large bursa copulatrix present, anterior integumental ciliated groove present. Penis eversible. Spermatozoon with large pear-shaped head and long flagellum.

Genus *Hedylopsis* Thiele 1931

Hedyle Bergh 1895 (not *Hedyle* Guenée 1857; not *Hedyle* Malmgren 1865)

With the characters of the family and with spicules fusiform and slightly irregular. Anterior cephalic appendages very broad and flat, posterior tentacles small and digitiform. Integument of dorsal visceral sac distinctly different from that of anterior body, either slightly or greatly stiffened by irregularly placed long spicules, retraction of head and anterior hump into mantle is linear not curved. Eyes are well developed. Radula with about 40 to 45 tooth rows and approximately one-half of these in lower portion. Nephridium elongate, nephric duct looped. Protandric hermaphrodite. Penis anterodorsal to pharynx, stylet tip small and hollow, opens at base of right posterior tentacle. Hermaphrodite pore dextrolateral on dorsal visceral sac near tip of foot. Ciliated groove closes to form subintegumental anterior vas deferens. Seminal vesicle and bursa copulatrix present.

Type Species

H. spiculifera (Kowalevsky) 1901

Hedylopsis spiculifera (Kowalevsky) 1901

Hedyle spiculifera Kowalevsky 1901
Hedylopsis spiculifera: Thiele 1931

With the characters of the genus. Living animals 4 mm in length. Colour brownish. Dorsal visceral sac broad, disclike, extending to near foot-tip, mantle greatly stiffened. Small spicules occur on head and anterior tentacles. Vibratile cilia occur on head and anterior tentacles. Radular formula 2-R-2, $\frac{U\ 20}{L\ 18} = 38$. Rachidian tooth with two large denticles on either side of median denticle. Medial lateral tooth-plate with spine on posterior border. Outer lateral plate subquadrangular. Penis undescribed for this species.

Type Locality
Sea of Marmara, Turkey.

Other Localities
Lesbos (Mytilene), Aegean Sea, Greece.

Hedylopsis suecica Odhner 1937a

With the characters of the genus. Living animals 4 mm in length. Colour opaque white, often with light brownish tinge on undersurface of dorsal visceral sac. Dorsal visceral sac not much broader than anterior hump, extending posteriorly well beyond tip of foot, mantle slightly stiffened, pallial spicules 250 μm in length. No spicules on head and anterior tentacles. Radular formula 2-R-2, $\frac{U\ 21–26}{L\ 20–23} = 41–49$. Rachidian tooth with two large denticles on either side of median denticle. Medial lateral tooth-plate without spine. Outer lateral tooth-plate irregularly subquadrangular on right side, imperfectly freed sometimes from medial lateral tooth-plate on left side (Marcus, 1953) in specimens from Banyuls-sur-Mer. Penis 0.4 mm in length, tiny basal spine present.

Type Locality
Kristineberg, Gullmar Fjord, Skagerrak, Norway.

Other Localities
Banyuls-sur-Mer, France.

Family Pseudunelidae fam. nov.

With the characters of the suborder Proprioneura. Two pairs of similar cephalic appendages present. Spicules or spicular pallial test characteristically absent. Stomach a flexed tube. Radula with lower recurved portion much shorter than upper. Nephridium large (further information lacking). Anus ventrolateral. Cerebralization

of anterior ganglia absent. Hermaphrodite genital pore associated with anus in antrum (= ''cloaca''), short bursa copulatrix present, anterior intraintegumental vas deferens present. Penis simple and glandular. Spermatozoon undescribed.

Genus *Pseudunela* subgen. elev.

Microhedyle (*Pseudunela*): Salvini-Plawen 1973

With the characters of the family. Anterior tentacles flattened at base, digitiform distally. Posterior tentacles digitiform, shorter than anterior. Integument of dorsal visceral sac not distinctly different from that of anterior body. Eyes poorly developed. Radula with about 50 tooth rows and approximately one-fourth of these in lower portion. Hermaphrodite, not protandric. Penis approximately dorsal to pharynx and oesophagus, no stylet, penial duct opens at base of right posterior tentacle. Hermaphrodite duct branches into very short oviduct and vas deferens; vas deferens travels to integument and there becomes enclosed and ciliated subintegumental vas deferens; oviduct widens into vestibule which also receives bursa copulatrix and intestine. Seminal vesicle not recorded. (The ''odontophore'' of Challis, 1970, p. 35 may be the lingual cushion of the pharynx.)

Type Species
P. cornuta (Challis) 1970

***Pseudunela cornuta* (Challis) 1970**

Microhedyle sp. 1 Challis 1969
Hedylopsis cornuta Challis 1970
Microhedyle (*Pseudunela*) *cornuta*: Salvini-Plawen 1973

With the characters of the genus. Living animals 2.5 mm in length. Colour translucent white, dorsal visceral sac opaque creamy yellow. Dorsal visceral sac narrow, almost twice as long as length of pedal sole, often held in curved position. Radular formula 1-R-1, $\frac{U\ 37}{L\ 13} = 50$. Rachidian tooth 15 μm high, 12 μm broad, with three (occasionally four) large denticles on either side of median denticle. Lateral tooth-plate with spine on proximal third of posterior border. Penis calculated as 0.3 mm long plus penial duct which is also 0.3 mm long, basal spine 100 μm in length near large disclike eminence.

Type Locality
Maraunibina Island, off Guadalcanal, Solomon Islands.

Other Localities
Guadalcanal; Banika Beach, Russel Islands, Solomon Islands.

Suborder Pharyngoneura subord. nov.

Freshwater, semilentic, interstitial acochlidioidean molluscs of very small size (ca 2 mm). Foot moderately well developed, with muscle fibres and internal haemocoelic spaces, demarcated by moderate cephalo-pedal and viscero-pedal grooves from anterior hump. Anus ventral. Pharyngeal nervous system complex, with additional buccal ganglia and with intrapharyngeal plexus connecting posterior to anterior buccal ganglia. Pleural and visceral loop ganglia cephalized to anterior pharynx. Cerebralization of anterior ganglia slight, ganglia encapsulated. Eyes may be absent. Pharynx large with complete velarium of sphincter muscles, sharply angled radular bending plane, large lingual cushion. Rachidian tooth subtriangular, scooplike, with margins bearing a few large denticles. Digestive caecum single, tubular, with neither branches, lobes, nor internal divisions; as long as dorsal visceral sac. Heart one-chambered (ventricle); pericardium, blood vessels, and many haemocoelic spaces present. Excretory system very well developed with nephridium, renopericardial nephrostome, renopericardial canal, and nephric duct present; nephridiopore opens near anus. Reproductive system not fully known, apparently simplified, with genital glands forming distinct masses not intimately bound in with digestive caecum. Penis, accessory glands, and anterior extension of genital duct not reported.

Family Tantulidae fam. nov.

Mountain spring-marsh animals with the characters of the Pharyngoneura. Two pairs of similar cephalic appendages present. Internal spicular skeleton and integumental spicules present. Stomach large and widely confluent with digestive caecum. Radula with lower portion distinct and in large subradular sac. Nephridium large, renopericardial nephrostome single, renopericardial canal long, nephric duct very long, nephridiopore closely associated with anus. Gonopore a ventral slit in a dextroventral pouch in region of viscero-pedal groove.

Genus *Tantulum* gen. nov.

With the characters of the family and with hollow rod and boomerangshaped spicules 75 μm or more in length. Anterior tentacles digitiform and broadened at base, posterior tentacles digitiform and shorter. Dorsal visceral sac not very distinctly different in appearance from the anterior hump. Foot long, thin, narrow, rounded at anterior end, tapering to posterior point. Eyes absent. Radula with about 45 tooth rows and approximately one-fourth of these in lower portion of radula (35 rows, and one-third in juveniles). Branched cephalic and tentacular sense organs, large locular anterior (buccal-tube) sense organs, and very large bilobed oral (=suprapedal) organ with tactile scoop-rim present. Nephridium complex, with two internal lumina and with vacuolated nephrocytes; communicating by internal flagellated pore with long, looped nephric duct which shows no cross-connections between arms of loop. Pharyngeal food canal cuticularized. Pharyngeal salivary glands elongated with highly contractile ducts, each having a spherical pump and emptying into modified reservoir in posterior pharyngeal wall. Oesophagus flagellate. Diverticulum present on genital duct.

Type Species

T. elegans sp. nov.

Tantulum elegans sp. nov.

With the characters of the genus. Living animals 2 mm in length and 0.29 mm in breadth across broadest part of dorsal visceral sac. Colourless, appearing white in reflected light, semitransparent in transmitted light. Dorsal visceral sac long, extending well beyond foot-tip. Small spicules occur in subepidermal layers of mantle and dorsum. Large skeletal spicules extend into haemocoel walls and occur in two main concentrations, one overlying and lateral to anterior ganglionic complex and the other overlying cardiopericardial region. Radular formula 1-R-2, (1-R-1 in juveniles), $\frac{U\ 33}{L\ 12} = 45$ in adults, may be $\frac{U\ 25}{L\ 10} = 35$ in juveniles. Rachidian tooth 18 to 20 μm high and 16.3 to 17.6 μm broad, with four or five denticles on either side of median denticle. Right medial lateral tooth-plate 25 to 26 μm wide and 5 μm long; right outer lateral tooth-plate 3 μm wide and 5 μm long. Left lateral tooth-plate 21 to 22 μm wide and 5 μm long. Right medial and left lateral tooth-plates both curved and with 5 μm long spine on both anterior and posterior borders, spines closely apposed to those of adjacent tooth-plates in series.

Type Locality

Spring-fed mountain marsh (411.5 m), Yambou River system, St. Vincent Island, West Indies. No other localities known as yet.

Suborder Cerebroneura subord. nov.

Marine, littoral or infralittoral, interstitial acochlidioidean molluscs, found in gravel or sand at variable depths. Size very small (0.5 to 2.7 mm in length). No cephalo-pedal groove present. Viscero-pedal groove either simple and shallow or extended forward laterally. Foot therefore either simply a longitudinally placed ciliated ventral bandlike zone of anterior hump with free posterior tip of variable length, or partially set off from anterior hump. Foot neither muscular nor with internal haemocoelic septa. Cerebral ganglia large. Cerebralization of anterior ganglia either marked or (more rarely) absent. Visceral loop ganglia cephalized either to posterior end of pharynx or to midpharynx. Buccal system simple. Eyes either moderately developed, or simple pigmented eye-spots often not easily distinguishable, or absent. Pharynx small, with or without small velarium, lingual cushion either small or absent. Radular bending plane curved with lower portion either moderately distinct or merging indistinctly with upper. Digestive caecum single, tubular, narrow and either straight and as long as dorsal visceral sac, or variously bent and longer than sac. Heart absent, pericardium absent or reduced, blood vessels absent. Excretory system poorly developed with small nephridium, renopericardial nephrostome and canal absent or very reduced, no differentiated nephric duct, nephridiopore either associated with or near gonopore, or absent. Reproductive system tends to show simplification, with genital glands intimately bound in with digestive diverticulum. Either hermaphrodite, simultaneous or protandric, or with separate sexes. Penis absent, anterior vas deferens absent or very reduced, an open ciliated groove sometimes present in female. Integument characterized by moderate or large glands.

Superfamily Velariacea superfam. nov.

(L.: *velarium* = canopy.) With the characters of the Suborder Cerebroneura. Radular

formula 1-R-1, (1-R-2), or 2-R-2, with more than 20 tooth rows. Recurved lower row of radula with about one-fifth to one-half the number of tooth rows in the upper. Rachidian tooth either triangular, subtriangular, or semilunar in shape, with margins either smooth, serrate, or denticulate. Radular sac with operative musculature and with lingual cushion, subradular sac small. Short velarium present, pharynx partially bound, no chitinous bars ("jaws").

Family Microhedylidae rev.

Microhedylinae Hertling 1930
Parhedylinae Thiele 1932, in part
Microhedylidae Odhner 1937a
Microhedylidae: Marcus 1952
Microhedylidae: Challis 1968
Microhedylidae: Swedmark 1971

With the characters of the Superfamily Velariacea. With two pairs of tentacles, more or less similar, often delicately digitiform, anterior tentacles either rounded or slightly flattened. Either vibratile or nonvibratile stiff tactile cilia may be present on head and both pairs of tentacles. Dorsal visceral sac longer than length of anterior hump plus foot-tip. Foot merely a ventral ciliated band of anterior hump and free only posteriorly. Anus dextrolateral on dorsal visceral sac. Genital pore dextrolateral in viscero-pedal groove. Nephridiopore opens immediately adjacent to genital pore, sometimes in common genito-nephric atrium. Nephridium a thin-walled contractile sac with no nephrostome. Eyes primitive or moderately developed or absent. Pleural ganglia either close to cerebral ganglia or fused with them. Gut not internally ciliated or partially ciliated. Digestive caecum either longer than length of dorsal visceral sac and markedly bent or twisted and fairly narrow, or as long as dorsal visceral sac and slightly bent or twisted and fairly broad. Ventral and lateral longitudinal retractor muscle blocks situated along body wall throughout their length; ventrals may occur as separated bundles. Either with very long ventrolateral oral (=suprapedal) glands and smaller dorsal cephalic glands, or with small ventrolateral buccal glands and sometimes very long pigmented dorsal cephalic glands. Integumental glands either of moderate or very large size. Spicular structures either absent, or small and present either as plaques and beadlike rings, or as uni- or multiaxonic rods (usually triaxonic). Sexes separated (protandric hermaphrodites). Integumental anterior vas deferens or male external ciliated groove absent; short, reduced ciliated furrow may occur in female form. Ovocyte vitelline and large. Spermatozoon flagellate, with long, narrow, spiralled head. Integumental fertilization by attached spermatophores occurs.

Genus *Microhedyle* rev.

Hedyle Bergh 1895, in part
Microhedyle: Hertling, 1930
Microhedyle (Parhedyle): Thiele 1931, in part
Parhedyle: Odhner 1952, in part
Microhedyle (Microhedyle): Salvini-Plawen 1973, in part
Microhedyle: Westheide and Wawra 1974, in part

With the characters of the family (revised). Two pairs of digitiform tentacles, anterior pair showing some degree of flattening. Radular formula 2-R-2 or 1-R-2, or 1-R-1 with about 30 to 40 tooth rows and approximately one-fifth to one-third of these in recurved portion of radula. Rachidian tooth triangular, with two to four denticles on either side of median denticle. Pleural ganglia fused with or touching cerebrals. Digestive caecum longer than length of dorsal visceral sac, fairly narrow and markedly bent or twisted. Eyes primitive or absent. Spicular structures if present, found both as irregular plaques, each with or without a central hole, and as beadlike rings and egg-shaped refractive bodies. Long ventrolateral suprapedal glands and small dorsal cephalic glands present. Integumental glands of moderate size.

Type Species
M. tyrtowii (Kowalevsky) 1900

Microhedyle tyrtowii (Kowalevsky) 1900

Hedyle tyrtowii Kowalevsky 1900; expanded description 1901
Microhedyle tyrtowii: Hertling 1930
Microhedyle (Parhedyle) tyrtowii: Thiele 1931
Parhedyle tyrtowii: Odhner 1952
Microhedyle tyrtowii: Westheide and Wawra 1974

A long, thin species, 1.8 mm in length, with the characters of the genus. Anterior tentacles fused at base to form upper lip. Foot zone of anterior hump semicircular anteriorly, with pointed free posterior tip. Radular formula 2-R-2, $\frac{U\ 27–29}{L\ \ 6–8}$ = Max. 35. Rachidian tooth an isosceles triangle with four large denticles on either side of median denticle. Medial lateral tooth-plate small and square. Outer lateral tooth-plate rectangular with spine on posterior border. Pleural ganglia broadly fused with cerebrals.

Type Locality
Sevastopol, Black Sea, USSR.

Microhedyle cryptophthalma Westheide and Wawra 1974

With the characters of the genus and 1.6 mm in length, 0.46 mm in breadth across the dorsal visceral sac. Anterior tentacles slightly flattened and longer than posterior pair. Radular formula 1-R-2, $\frac{U\ 22–27}{L\ \ 4–9}$ = 26–36. Rachidian tooth 6 μm high, 3 μm broad, with two denticles on either side of median denticle. Right medial lateral tooth-plate 6 μm broad, 3 μm long, outer right lateral tooth-plate 9 μm broad, 3 μm long. Left lateral plate (=outer + medial) is 13 μm broad, 3 μm long. Tooth-plates are without spines. Spicular platelet rings measure 8 to 9 μm and include 15 to 20 platelets: irregularly rounded or oval plaques measure 10 to 18 μm in diameter; smoothly egg-shaped refractive bodies measure about 20 μm along long axis. Spermatophores

spindle-shaped, 80 to 187 μm in length and 17 to 30 μm in breadth, enclosing 200 to 300 spermatozoa. Vitelline ovocytes 450 μm, one mature and two immature occurring simultaneously.

Type Locality
Canet Plage, France.

Other Localities
Amilcar and Insel Djerba, Tunisian coast; Nabeul and Hammamet, Gulf of Hammamet, Tunisia; Arco Felice and Castel Volturno, Italy.

Microhedyle nahantensis (Doe) 1974

Unela nahantensis Doe 1974

With the characters of the genus and 2.7 mm in maximum length and 0.35 mm in maximum width across dorsal visceral sac. Anterior tentacles moderately flattened and longer than posterior pair. Foot-tip about one-third length of dorsal visceral sac. Radular formula 1-R-1, $\frac{U\ 30(22–35)}{L\quad 5–9} = 39(34–56)$ (adult). Rachidian tooth 10 to 12 μm broad, 10 to 12 μm high, with three denticles on either side of median denticle. Lateral tooth-plate with no spines and 15 μm broad and 4 μm long. Pleural ganglia touching cerebrals. Short ciliated furrow present in female form. Spermatophores about 0.26 to 0.46 mm in length. Spicular platelet rings up to 20 μm in diameter, with about 18 squared platelets 1.0 to 2.0 μm in diameter.

Type Locality
Canoe Beach, Marine Science Institute, Nahant, Massachusetts, USA.

Genus *Stellaspina* gen. nov.

Hedyle Bergh 1895, in part
Microhedyle: Hertling 1930, in part

(L.: *stella* = star; *spina* = spicule.) With the characters of the family (revised). Tentacles digitiform, anterior pair moderately flattened. Radular formula 2-R-2, with about 40 tooth rows and approximately one-fifth to one-fourth of these in recurved portion of radula. Rachidian tooth subtriangular with two or three denticles on either side of median denticle. Outer lateral tooth-plate broad and without spine. Pleural ganglia close to, but separate from cerebrals. Digestive caecum as long as length of dorsal visceral sac, fairly broad and only slightly bent or twisted. Eyes either moderately developed or absent. Spicules present as mon- or polyaxonic rods (usually triaxonic and starlike). Small ventrolateral buccal glands and very long dorsal cephalic glands present. Integumental glands are of very large size.

Type Species

S. glandulifera (Kowalevsky) 1901

Stellaspina glandulifera (Kowalevsky) 1901

Hedyle intermedia Kowalevsky 1900b (? if valid description)
Hedyle glandulifera Kowalevsky 1901
Microhedyle glandulifera glandulifera: Hertling 1930

With the characters of the genus. Living animals about 1.8 mm in length. Colour brownish on head and dorsal cephalic glands, either colourless or faintly brownish on anterior body and dorsal visceral sac. Eyes moderately developed. Kowalevsky (1901) reports the radula and teeth to be like *Microhedyle tyrtowii*, therefore the rachidian tooth must have about four lateral denticles on either side of median denticle and the formula must approximate $\frac{U\ 26–27}{L\ \ 6–8}$ = Max. 34–35 with the lateral tooth-plates occurring as small medial and wide outer structures. Vibratile cilia on tentacles.

Type Locality
Sea of Marmara, Turkey.

Other Localities
See section Notes on the New Definitions, page 81, comment on new species *S. napolitana*.

Stellaspina lactea (Hertling) 1930

Microhedyle glandulifera lactea Hertling 1930
Microhedyle lactea: Odhner 1937a

With the characters of the genus. Living animals about 2.0 to 2.7 mm in length. Colourless and with colourless dorsal cephalic glands. Eyes moderately developed. Radular formula 2-R-2, $\frac{U\ 31}{L\ 8–13}$ = 38–44. Rachidian tooth with two lateral denticles on either side of median denticle.

Type Locality

Helgoland Island, North Sea, West Germany.

Other Localities
Banyuls-sur-Mer, France.

Stellaspina napolitana sp. nov., ex Marcus and Marcus 1954

Microhedyle glandulifera (Kowalevsky 1901): Marcus and Marcus 1954

With the characters of the genus and with the coloration of *S. glandulifera*. Size of

living animals unrecorded. Eyes absent. Radular formula 2-R-2, $\frac{U\ 24}{L\ 7} = 31$. Rachidian tooth with two lateral denticles on either side of median denticle.

Type Locality

Naples, Italy.

Other Localities

? Banyuls-sur-Mer, France.

Family Sabulincolidae fam. nov.

(L.: *sabulo* = sand, gravel; *incola* = dweller.) With the characters of the Superfamily Velariacea. With two dissimilar pairs of tentacles. No cilia on head and tentacles. Foot a ciliated ventral band of anterior hump, freed posteriorly by viscero-pedal groove. Anus ventrolateral on dorsal visceral sac and adjacent to nephridiopore. Genital pore not associated with anus or nephridiopore. Nephridium simple, nephrostome not reported. Eyes moderately well developed. Gut not internally ciliated. Digestive caecum very broad, as long as length of dorsal visceral sac. Independent muscles well developed, with long ensheathed dorsolateral and ventral retractors. Spicules present as monaxonic rods. Mature reproductive system unknown as yet. Anterior vas deferens or external ciliated groove absent. Integumental glands very numerous and either moderately large or very large. Position and state of pleural ganglia and visceral loop ganglia not described.

Genus *Sabulincola* gen. nov.

Unela Marcus 1953, in part

With the characters of the family. With anterior pair of tentacles flattened, posterior pair digitiform and smaller than anterior tentacles. Radular formula 1-R-1, with about 40 to 50 tooth rows and proportionate number in lower part of radula unknown (see *S. gerlachi*). Rachidian tooth triangular, with three (to six, see *S. gerlachi*) lateral denticles. Digestive caecum with thick, glandular wall. Spicules small. Integumental glands moderately large.

Type Species

S. odhneri (Marcus and Marcus) 1955

***Sabulincola odhneri* (Marcus and Marcus) 1955**

Microhedyle odhneri (listed name only, Delamere Deboutteville 1953a and b)
Unela odhneri Marcus and Marcus 1955 (first description)

With the characters of the genus and about 1.8 mm in length. Dorsal visceral sac twice the length of the anterior hump plus foot tip. Radular formula 1-R-1, $\frac{U\ ?}{L\ ?} =$ 39–48. Rachidian tooth an equilateral triangle 10 μm in width at base, with three

denticles on either side of median denticle. Lateral tooth-plate 12 μm broad and 2.5 μm long, with no spines.

Type Locality

North of Banyuls-sur-Mer, near Le Racou and Canet Plage, France; in gravel and coarse sand, littoral zone.

Sabulincola gerlachi (Marcus and Marcus) 1959
(In genus incertae sedis)

Microhedyle gerlachi Marcus and Marcus 1959

(Description of this form is incomplete and based on retracted, preserved specimens; it does not belong in the genera *Microhedyle* or *Stellaspina* or *Unela*, and until the condition of the pedal region and the internal anatomy is better known I have placed it in this genus.) Extended length of living animal unknown, preserved length about 0.55 mm. Anterior tentacles flat, posterior tentacles digitiform and very small. Eyes moderately well developed. Radular formula 1-R-1, $\frac{U\ 32}{L\ 18} = 50$. Rachidian tooth triangular with five or six denticles on either side of median denticle. Lateral tooth-plates with spine on posterior border and with deep corresponding notch on anterior border. Integumental glands very large.

Type Locality

Addu Atoll, Maldive Islands, in coarse sand at depth of 10 m.

Other Localities

Fadiffolu Atoll, Maldive Islands, in coarse sand in outer reef in depth of 6 m.

Family Unelidae fam. nov.

With the characters of the Superfamily Velariacea. With two pairs of dissimilar tentacles. Nonvibratile stiff tactile cilia present on anterior tentacles. Foot extensively set off posteriorly from hump by forward extensions of pedo-visceral groove. Dorsal visceral sac not longer than length of anterior hump plus foot-tip. Anus dextrolateral in viscero-pedal groove. Genital pore anterior to groove and adjacent to nephridiopore. Nephridium a small sac with a small nephrostome. Eyes may be absent. Pleural ganglia separate from cerebrals. Visceral loop ganglia cephalized to posterior end of pharynx. Gut internally ciliated. Digestive caecum fairly broad. Longitudinal retractor muscles simple strands and retain their close relationship to body wall throughout their length. Small ventrolateral buccal glands present, but neither long dorsal cephalic glands nor true suprapedal glands present. Sexes separate. Either integumental anterior vas deferens or ciliated spermatic groove present. Spermatozoon threadlike, with short, straight head not sharply marked off from flagellum.

Genus *Unela* Marcus 1953

Unela Marcus 1953
Microhedyle (Unela): Salvini-Plawen 1973

With the characters of the family. Anterior tentacles a little flattened, posterior tentacles shorter and each expanded into a bulbar basal swelling. Radular formula 1-R-1, with about 50 tooth rows and approximately one-fourth of these in recurved portion. Rachidian tooth triangular with about two lateral denticles on either side of strong median denticle. Pleural ganglia separate from cerebrals. Digestive caecum wide and not longer than length of dorsal visceral sac. Eyes absent. Spicules absent. Small ventrolateral buccal glands present, neither long dorsal cephalic glands, nor true suprapedal glands present.

Type Species
U. remanei Marcus 1953

***Unela remanei* Marcus 1953**

Unela remanei Marcus 1953
Microhedyle (Unela) remanei: Salvini-Plawen 1973

With the characters of the genus. Living animals 3.0 to 5.0 mm in length. Posterior tentacles with groove demarcating bulbar base from head. Colourless. Radular formula 1-R-1, $\frac{\text{U } 37\text{–}42}{\text{L } 9\text{–}14} = 51$. Rachidian tooth 12 μm high and 12 μm broad with two denticles on either side of median denticle. Lateral tooth-plate 14 μm wide, with small spine proximally on anterior border. Integumental anterior vas deferens present in male. Anterior ciliated groove of unknown function present in female. Spermatophores occur.

Type Locality
São Sebastião Island, Brazil, in coarse sand, lower tidal zone.

Family Mancohedylidae fam. nov.

Microhedylidae Odhner 1937a, in part

With the characters of the Superfamily Velariacea. With the anterior tentacles flattened throughout into oral lappets and fused in mid-line to form upper lip over mouth, posterior tentacles absent. No cephalo-pedal groove present. Viscero-pedal groove either small and shallow or very faintly marked. Foot-tip either very small or barely visible. Cilia either present or absent on head and appendages. Dorsal visceral sac much longer than length of pedal sole. Anus dextrolateral, either in viscero-pedal groove or on dorsal visceral sac, and posterior to nephridiopore and gonopore, female genital pore may open anterior to pharynx. Eyes either absent or moderately well developed. Pleural ganglia either close to cerebrals or fused with them. Visceral loop ganglia cephalized under anterior third of pharynx. Digestive caecum longer than

length of dorsal visceral sac and either bent, or peristaltic, or convoluted. Integumental glands of moderate size, usually very numerous in dorsal visceral sac. Spicules either absent or large, fusiform, smooth, and tending to show concentration in head and lappets with either few or none in mantle of dorsal visceral sac. Small oral glands either present or absent. Sexes separated. Neither integumental anterior vas deferens nor external ciliated groove present.

Genus *Mancohedyle* gen. nov. (elev. subgen. of Salvini-Plawen 1973)

Hedyle Bergh 1895, in part
Microhedyle: Hertling 1930, in part
Ganitus: Marcus 1953, in part
Microhedyle: Marcus and Marcus 1954
Microhedyle (Mancohedyle): Salvini-Plawen 1973, in part
Microhedyle: Westheide and Wawra 1974, in part

With the characters of the family. Anterior lappets curved into the form of a bow. Spicules large, fusiform, and smooth; found in bundles on head and lappets, and scattered on dorsal visceral sac. Cilia absent on head and lappets. Eyes moderately well developed. Viscero-pedal groove only a shallow indentation, foot-end rounded. Radular formula 2-R-2, with about 34 tooth rows and one-third to one-quarter of these found in the recurved portion of the radula. Female genital pore anterior to pharynx. Buccal-tube long, with no buccal glands entering it. Stomach absent. Pharyngeal salivary glands paired, well separated, long, thin, and tapering. Digestive caecum narrow and bent posteriorly. Pleural ganglia fused with cerebrals (Kowalevsky, 1901:figs. 46, 48). Ovary tubular with long oviduct.

Type Species
M. milaschewitchii (Kowalevsky) 1901

***Mancohedyle milaschewitchii* (Kowalevsky) 1901**

Hedyle milaschewitchii Kowalevsky 1901
Microhedyle milashewitchii: Hertling 1930
Ganitus milaschewitchii: Marcus 1953
Microhedyle milaschewitchii: Marcus and Marcus 1954
Microhedyle (Mancohedyle) milaschewitchii: Salvini-Plawen 1973
Microhedyle milaschewitchii: Westheide and Wawra 1974

With the characters of the genus. Living animals 1.8 mm in length. Colourless, with bright green digestive caecum (Kowalevsky, 1901:20). Radular formula 2-R-2, $\frac{\text{U } 26\text{–}28}{\text{L } 6\text{–}8} = 34$. Integumental glands show through as small white patches. A slower moving species than *Microhedyle tyrtowii*.

Type Locality
Sevastopol, Black Sea, USSR, in coarse sand.

Other Localities

Princes Islands, Sea of Marmara, Turkey, in very fine sand; Lesbos (Mytilene), Aegean Sea, Greece.

Genus *Gastrohedyle* gen. nov.

Hedyle Bergh 1895, in part
Microhedyle: Hertling 1930, in part
Microhedyle (Mancohedyle): Salvini-Plawen 1973, in part
Microhedyle: Westheide and Wawra 1974, in part

(Gk.: *gaster* = stomach). With the characters of the family. Anterior lappets flat, triangular, with edges straight and angled. Spicules large, fusiform, smooth, numerous, set in parallel in head and lappets, fewer and irregularly arranged in anterior hump and dorsal visceral sac. Cilia present on head and lappets. Eyes moderately developed. Viscero-pedal groove faint, rounded hind-end of foot coalesced with dorsal visceral sac. Radular formula 1-R-1, with about 44 tooth rows and one-half of these found in the recurved portion of the radula. Anus on dorsal visceral sac, nephridiopore and (male) genital pore near viscero-pedal groove. Buccal-tube long with no buccal glands entering it. Stomach very large and spherical. Pharyngeal salivary glands short, thick, bound into one structure. Digestive caecum narrow and showing peristalsis. Pleural ganglia close to but not fused with cerebrals (Marcus and Marcus, 1954:fig. 13). Visceral loop ganglia well forward under pharynx. Testis a winding duct with irregular grapelike swellings. Seminal vesicle present.

Type Species
G. brasilensis sp. nov. (see below).

***Gastrohedyle brasilensis* sp. nov.**
(with description Marcus and Marcus 1954)

Microhedyle milaschewitchii (Kowalevsky) 1901: Marcus and Marcus 1954
Microhedyle sp.?: Challis 1970
Microhedyle (Mancohedyle) milaschewitchii: Salvini-Plawen 1973, in part

With the characters of the genus. Living animals 1.5 mm in length. Colourless, with bright green digestive caecum. Radular formula 1-R-1, $\frac{U\ 29}{L\ 15} = 44$. Rachidian tooth subtriangular, 8 μm broad and 4 μm high, with three lateral denticles on either side of median denticle. Lateral tooth-plate 8 μm broad and 2 μm long, with very small spine midway on anterior border, and deep notch midway on posterior border.

Type Locality

Ilhabela, near São Paulo, Brazil, eulittoral zone.

Genus *Maraunibina* gen. nov.

Microhedyle (Mancohedyle): Salvini-Plawen 1973, in part

With the characters of the family and with anterior lappets curved into form of a "classical bow". Spicules absent. Cilia absent on head and lappets. Eyes absent. Foot-tip pointed and free with small viscero-pedal groove present. Radular formula 1-R-1, with about 43 tooth rows and one-third of these found in the recurved portion of radula. Genital pore and nephridiopore close together and anterior to anus (exact position in body unknown). Buccal tube short with buccal glands opening into it. Stomach absent. Oesophageal(?) salivary glands present, paired, voluminous. Pleural ganglia close to, but not fused with cerebrals. Visceral loop ganglia very close to pedals (see Challis, 1970:fig. 5 I, where pedals seem to include posterior ganglia, perhaps difficult to distinguish).

Type Species

M. verrucosa (Challis) 1970

Maraunibina verrucosa (Challis) 1970

Microhedyle verrucosa Challis 1970
Microhedyle (Mancohedyle) verrucosa: Salvini-Plawen 1973

With the characters of the genus. Living animals 1.5 mm in length. Translucent white with bright green digestive caecum. Radular formula 1-R-1, $\frac{U\ 33}{L\ 10} = 43$. Rachidian tooth subtriangular, 6 μm broad and 5 μm high, with three denticles on either side of median denticle. Lateral tooth-plate curved, 8 μm broad and 2 μm long, with neither spines nor notches.

Type Locality
Maraunibina Island, Marau Sound, East Guadalcanal, Solomon Islands.

Other Localities
Guadalcanal Island, Solomon Islands; Banika Beach, Russell Islands, Solomon Islands.

Family Asperspinidae fam. nov.

Hedylopsidae Odhner 1952, in part
Hedylopsidae: Marcus 1953, in part

With the characters of the Superfamily Velariacea. With two pairs of tentacles, both pairs either rounded or showing some degree of flattening. Dorsal visceral sac characterized by formation of spicular "test" with spicules long, rod-shaped, or fusiform, with rough irregular surface, and arranged in definite pattern. Smaller spicules may occur on head and tentacles. Short cilia found on head and anterior tentacles. Dorsal visceral sac much longer than length of anterior hump plus foot-tip. No true cephalo-pedal groove but with foot marked off in varying degrees by forward extension of viscero-pedal groove. Anus, nephridiopore, and gonopore dextrolateral in viscero-pedal groove. Eyes may be absent. Pleural ganglia either close to cerebrals

or fused with them. Visceral loop ganglia posterior to pharynx. Digestive caecum as long as length of dorsal visceral sac. Integumental glands of large size on dorsal visceral sac. Buccal-tube with two "callosities" or "longitudinal dorsolateral protruberances" (Swedmark, 1968:179, 184). Velarium of pharynx short. Hermaphrodite. External ciliated groove(s) present. Ducts of pharyngeal salivary glands united before entering posterior end of pharynx.

Genus *Asperspina* gen. nov.

Hedylopsis Odhner 1937a: Swedmark 1968

(L.: *asper* = rough; *spina* = spicule.) With the characters of the family and with both pairs of tentacles rounded and short. Posterior tentacles carried forwardly over anterior pair. Spicules small and occasionally triaxonic on head, tentacles, and anterior body; very long on dorsal visceral sac and arranged diagonally to main axis, but not densely packed together to form distinct spicular test. Foot-tip small and bluntly pointed. Dorsal visceral sac broad and posteriorly pointed. Eyes absent. Radular formula 2-R-2, with about 40 tooth rows and up to one-third of these found in the recurved portion of the radula. Hermaphrodite pore very close to both anus and nephridiopore (exact position unknown). Gut ciliated. Buccal tube and oesophagus short. Small stomach present. Digestive caecum broad and straight. Pleural ganglia close to large cerebrals, cerebro-pedal connectives very broad. Visceral loop ganglia (parietal + visceral) close to pharynx posteriorly (Swedmark, 1968:182 misprint "pleural"). Hermaphrodite gland closely bound to digestive caecum. External ciliated sperm groove present.

Type Species

A. brambelli (Swedmark) 1968

***Asperspina brambelli* (Swedmark) 1968**

Hedylopsis brambelli Swedmark 1968

With the characters of the genus. Living animals 2.3 mm in length. Colourless or slightly pink or brownish. Radular formula 2-R-2 (occasionally 1-R-2), $\frac{U\ 24}{L\ 17} = 41$. Rachidian tooth 18 μm broad and 19 μm high, with eight denticles on either side of median denticle. Inner lateral tooth-plate 22 μm broad, with median spine of 2.5 μm length on posterior border. Outer lateral tooth-plate subquadrangular; indefinite outer border (Swedmark, 1968:fig. B, pm) suggests it is imperfectly freed from radular membrane. Spicules of dorsal visceral sac attain 225 μm in length.

Type Locality
Menai Bridge, Wales.

Other Localities
Ellskär, Kristineberg, Gullmarsfjord, Skagerrak, Norway. (The form reported from

Ellskär shows a basic difference in the radula and may prove to be another genus. Radular formula is 2-R-2, $\frac{U\ 34}{L\ 5\text{–}6}$ = 38–45, with only one-seventh of the tooth rows being found in the recurved lower portion of the radula, rather than one-third as in the Menai Bridge specimens. Further information as to internal anatomy is required for the proper classification of this form.)

Genus *Antemnella* gen. nov.

Hedylopsis Odhner 1937: Swedmark 1968

(L.: *antemna* = a sail-yard; in reference to form and method of carrying of tentacles.) With the characters of the family and with both pairs of tentacles flattened, broadened, and carried anterodorsally like four small sails. Spicules rough; small and fusiform on head and tentacles; long, tightly packed diagonally and evenly formed into an angular spicular test of dorsal visceral sac, with consequent loss of contractility. Foot not offset by cephalo-pedal groove (Swedmark, 1968:plate II, figs. 1, 2, 3); foot-tip short and offset by small pedo-visceral groove. Eyes absent. Radular formula 1-R-1, with about 60 tooth rows and one-quarter of these found in the recurved portion of the radula. Cilia present on anterior pair of tentacles. Gut ciliated, except stomach. Buccal-tube small and with small structures similar to *Asperspina brambelli* (see note on "callosities" p. 103). Oesophagus short. Stomach small. Digestive caecum straight. Intestine short. Anus, nephridiopore, and hermaphrodite pore very close together, situated in viscero-pedal groove. Hermaphrodite gland shows single very large (150 μm) vitelline ovocyte at one time, and may show active spermatogenesis simultaneously. Considerable cerebralization of anterior ganglia, with cerebral fused to pleural on either side and broadly connected. Visceral loop ganglia (parietal + visceral) posterior to pharynx (Swedmark, 1968:185; pl. II, fig. 5, misprint "pleural").

Type Species
A. loricata (Swedmark) 1968

***Antemnella loricata* (Swedmark) 1968**

Hedylopsis loricata Swedmark 1968

A small species. Living animals 0.9 mm in length when fully mature. Colourless. Radular formula 1-R-1, $\frac{U\ 48}{L\ 12}$ = 60. Rachidian tooth 8 μm high and 8 μm broad, with five denticles on either side of median denticle. Lateral tooth-plates of similar breadth (Swedmark, 1968:fig. 3D), and with a large medial spine on posterior border. Spicules of dorsal visceral sac attain 180 μm in length.

Type Locality
Submarine dune of Trezen ar Skoden, Roscoff, Finistère, France, in shell sand at 50 m depth.

Genus *Anademaria* gen. nov.

Hedylopsis Odhner 1937: Salvini-Plawen 1973

(Gk., L.: *anadema* = ornament for head.) This definition is provisional, pending further anatomical information. With the characters of the family and with both pairs of tentacles rounded, short, and carried forwardly aloft. Posterior tentacles longer than anterior and inclined forwardly dorsal to them. Spicules rough; small and arranged in a bundle on each side of head near bases of tentacles; moderately long in visceral sac, arranged diagonally and somewhat irregularly into distinct spicular test. Viscero-pedal groove extends forward laterally, setting off a small foot from hump. Dorsal visceral sac rounded. Eyes absent. Radular formula 1-R-2, with about 40 tooth rows, proportion in recurved part of radula unknown. Internal anatomy unknown.

Type Species
A. rhopalotecta (Salvini-Plawen) 1973

Anademaria rhopalotecta (Salvini-Plawen) 1973

Hedylopsis rhopalotecta Salvini-Plawen 1973

With the characters of the genus. Living animals 2 mm in length. Colour milky grey, with delicately reddish brown digestive caecum. Radular formula 1-R-2, $\frac{U\ ?}{L\ ?}$ = 38–43. Rachidian tooth semilunar, 8 μm high and 10 μm broad, with four denticles on either side of median denticle. Left lateral tooth-plate 14 μm broad and 2.5 μm long with a median spine on its posterior (?) border and a corresponding groove on its anterior (?) border. Left medial lateral tooth-plate 10 μm broad and 2.5 μm long, also with spine and groove. Left outer lateral tooth-plate 3 μm broad and 2.5 μm long. Spicules of dorsal visceral sac attain 120 to 160 μm by 8 to 15 μm.

Type Locality
Secche della Meloria (Livorno), in medium coarse shell sand, in 3 to 4 m depth.

Superfamily II. Avelariacea superfam. nov.

(L.: *a-* = without; *velarium* = canopy.) With the characters of the Suborder Cerebroneura. Radular formula 0-R-0, with less than 20 tooth rows. Radular bending plane a wide curve, with upper and lower portions not clearly distinguished. Rachidian tooth lanceolate and slightly concave, with a broad base and without lateral denticles. Radular sac without operative musculature or lingual cushion. Subradular sac with large muscles operating between its chitinous end posteriorly and chitinous plates ("jaws") anteriorly. No velarium present and therefore pharyngeal food canal, radular sac, and large subradular sac with its muscles are not bound together by any sphincter.

Family Ganitidae fam. nov.

Microhedylidae: Marcus 1952, in part

With the characters of the Superfamily Avelariacea. With one or two pairs of tentacles, posterior tentacles reduced or missing, anterior pair may show a little flattening. Dorsal visceral sac much longer than length of anterior hump plus foot-tip. Cephalo-pedal groove absent. Viscero-pedal groove small and not extending forward. Anus, nephridiopore, and genital pore open near each other dextrolaterally anterior to viscero-pedal groove. Nephridium either a thin-walled sac with small nephrostome and with nephridiopore opening immediately above gonopore, or with wall showing inner infoldings, with no nephrostome and with nephridiopore (Challis, 1968:195, fig. 3C, "nephrostome") opening along with gonopore into vestibule. Eyes absent. Pleural ganglia fused with cerebrals. Gut not internally ciliated. Buccal-tube short, buccal glands present. Oesophagus narrow. Stomach absent. Digestive gland longer than length of dorsal visceral sac and may show coiling or twisting. Intestine continues with and is histologically similar to oesophagus. No dorsal cephalic glands present. Integument very glandular. Spicules absent or spicular "shadows" present. Sexes may be separate. Gonads tubular. Integumental anterior vas deferens either absent or very reduced in length. Females may show abortive right ciliated groove of unknown function. Spermatophores occur. Spermatozoon threadlike, with short head not markedly set off from flagellum.

Genus *Ganitus* Marcus 1953

With the characters of the family. Anterior tentacles show flattening, posterior tentacles absent. Spicular "shadows" present. Radular formula 0-R-0, with 10 to 14 tooth rows and no lateral tooth-plates. Dorsal visceral sac approximately same length as pedal sole and almost indistinguishable from anterior hump dorsally. Stiff tactile cilia occur on anterior border of labial tentacles. Nephridium a thin-walled sac with ciliated nephrostome, and with nephridiopore separate from gonopore. Digestive caecum only slightly longer than dorsal visceral sac. Sexes separate. Integumental anterior vas deferens absent. Female abortive ciliated groove present.

Type Species
G. evelinae Marcus 1953

Ganitus evelinae Marcus 1953

With the characters of the genus. Living animals 2.2 mm in length. Colour white, with brown digestive caecum. Foot-tip pointed. Dorsal visceral sac fusiform or sausage-shaped. Radula with usually 11 teeth, size of tooth not recorded.

Type Locality
Ilhabela, São Sebastião, in Brazil, in coarse sand, sheltered lower tidal zone.

Genus *Paraganitus* Challis 1968

With the characters of the family. Anterior tentacles slender and digitiform, posterior pair reduced in size. Spicules absent. Dorsal visceral sac slender and about twice as long as length of pedal sole, slightly broader than anterior hump. Radula with about 12 tooth rows. Tactile and/or vibratile cilia not reported on head and tentacles.

Nephridial wall shows inner infoldings, no nephrostome, nephridopore opens along with gonopore in small ciliated vestibule. Digestive caecum much longer than length of dorsal visceral sac, convoluted. Integumental anterior vas deferens very reduced in length. No female abortive ciliated groove present. Sexes separate.

Type Species
P. ellynnae Challis 1968

Paraganitus ellynnae Challis 1968

With the characters of the genus. Living animals 1.8 mm in length. Colour translucent white, digestive caecum visible as indistinct brown line. Foot-tip moderately pointed. Dorsal visceral sac sausage-shaped. Radula with 10 to 14 tooth rows, size of tooth not recorded.

Type Locality
Komimbo Bay, Guadalcanal Island, Solomon Islands, in sand, lower intertidal zone.

Other Localities
Maraunibina Island off Guadalcanal Island, Solomon Islands; Banika Beach, Russell Islands, Solomon Islands; Pango Beach, Ile Efate, New Hebrides.

Suborder Visceroneura subord. nov.
(preliminary and incomplete diagnosis)

Marine, interstitial molluscs with the characters of the Acochlidioidea. Size very small. No cepahlo-pedal groove present. Viscero-pedal groove shallow and small, sets off very reduced foot-tip. Ciliated pedal sole characterized by median longitudinal groove. Dorsal visceral hump shows elongation. Anus dextrolateral. No cerebralization of anterior ganglia. Visceral loop ganglia cephalized to posterior third of pharynx. Visceral nervous system well developed. Buccal nervous system simple. Pharynx of moderate size (details not known). Radular bending plane curved anteriorly, with recurved lower portion distinct from upper. Rachidian tooth may have large denticle present on margin. Lateral tooth-plates are present. Digestive caecum single, tubular, very much longer than length of dorsal visceral sac. Blood system not described. Excretory system well developed although not fully described, appears to differ from other Acochlidioidea. Nephridium large and contains a densely granular substance. Reproductive system undescribed. Integument without moderate or large glands. Spicules may be absent.

Family Livorniellidae fam. nov. (preliminary diagnosis)

Microhedylidae: Swedmark 1971: Salvini-Plawen 1973

With the characters of the Suborder Visceroneura. With two pairs of dissimilar tentacles. Dorsal visceral sac elongated and capable of coiling into whorls. External ciliated groove present. Cerebral ganglia show lobulation. Radular formula may be 1-R-1, with about 38 tooth rows with one-fourth of these in recurved portion of

radula. Rachidian tooth triangular. Paired oral glands present. No very large integumental glands.

Genus *Livorniella* gen. nov.

Microhedyle (*Microhedyle*) Salvini-Plawen 1973
Microhedyle: Westheide and Wawra 1974, in part

(L.: *Livorniella* = a little Livornian, from place of origin of type species.) With the characters of the family and with anterior tentacles flattened and downwardly curved, posterior tentacles very short and digitiform. Radular formula 1-R-1, with 38 tooth rows and one-fourth in recurved portion. Rachidian tooth with few denticles. Globular stomach present. Digestive caecum very long and S-shaped.

Type Species
L. glomerans (Salvini-Plawen) 1973

***Livorniella glomerans* (Salvini-Plawen) 1973**

Microhedyle (*Microhedyle*) *glomerans* Salvini-Plawen 1973

With the characters of the genus. Living animals 2.3 mm in length. Colour unknown. Anterior tentacles short and formed into shape of a bow. Radular formula 1-R-1, $\frac{U\ 28}{L\ 10}$ = 38. Rachidian tooth equilateral, 9 μm high, with two large denticles on either side of median denticle. Lateral tooth-plate 12 to 13 μm broad and 5 μm long with hooklike spine on posterior border, and corresponding groove on inner surface of anterior border, also with small notch distally on anterior border, and with "optically clear band" on outer surface (= lower surface when radula is spread). Histology unknown.

Type Locality
Secche della Meloria, Livorno, Italy, in medium-coarse sand at 5 m depth.

Order Platyhedyloidea ord. nov.

Marine molluscs, interstitial, with the characters of the Ceratobranchia. Shell absent (spicules also absent). Partially detorted. With hump largely uncoiled and produced into a free dorsal visceral sac which is carried posteriorly. Cephalo-pedal groove absent: viscero-pedal groove tends to be shallow, setting off a rudimentary foot-tip. Anterior ganglionic ring cephalized only to posterior region of pharynx. Visceral loop ganglia not cephalized; associated with stomach. Buccal ganglion(a) anterior to pharynx. Short intestine proceeds posteriorly to dextrolateral anus. Blood system not described. Excretory system not described.

Family Platyhedylidae Salvini-Plawen 1973

With the characters of the order. Animals show dorsoventral flattening. Animal contracts by dorsoventral curling (in pill-bug fashion), not by coiling nor by

withdrawal into temporary mantle cavity. No cerebralization (=fusion) of anterior ganglia (cerebral, pleural, and pedal). Sexes separated. Pharynx shows anterior cuticular bars.

Genus *Platyhedyle* Salvini-Plawen 1973

With the characters of the family. Radula uniseriate, with very few tooth rows and these are equally divided between upper and lower portions. Rachidian tooth with very large bifid base and long hemiconical pointed tip bearing spinose posterior margins. Cephalic appendages absent. Eyes well developed. Stomach large, globular, with adjacent paired glands (? mid-gut salivary glands). Digestive caecum single, tubular, broad, and bent. Anus in viscero-pedal groove. Large cepahlic glands present.

Type Species
P. denudata Salvini-Plawen 1973

***Platyhedyle denudata* Salvini-Plawen 1973**

Marine animals, interstitial in sand, with the characters of the genus. Living animals 4.5 mm in length. Colour grey brownish, with olive-green digestive caecum. Head blunt and broad. Foot-tip a minute ridge. Spicules absent. Digestive caecum looped, twice the length of dorsal visceral sac. Radular formula 0-R-0, $\frac{U\ 9}{L\ 9} = 18$. Rachidian tooth 37 μm high, with base plate 12 μm high and 8 μm broad, and with sharp point 25 μm in height and bearing six or seven lateral spines (=sharp denticles) on either side of very small median tip. Ovary, near end of recurved portion of digestive caecum, contains three large vitelline ovocytes at once.

Type Locality
Secche della Meloria, Livorno, Italy, in medium-coarse shell sand at 3 to 4 m depth.

Summary

In the first portion of this paper a new genus, species, and family, *Tantulum elegans*: Family Tantulidae, is created for the reception of the first freshwater Acochlidioidean to be found in the Western Hemisphere. Methacrylate-embedded material has made possible a detailed microanatomical study from various series of sections cut at 3 μm thinness. Some of the interesting points emerging from this study and from observations of the living animals are as follows:

1. The pharyngeal zone of differentiation of the buccal cavity is complex, with two diverticula, the radular sac and the subradular sac, and a well-developed musculature operative mainly on the radular sac and innervated by an extensive nerve plexus supplied from an extended buccal ganglionic system.

2. The ducts of the very large pharyngeal salivary glands are highly contractile and each bears a bulbar contractile ampulla with internal ciliated mound, for the controlled propulsion of salivary secretions into a pair of small reservoirs opening into the posterior end of the cuticularized pharyngeal food canal.
3. Traces of asymmetry persist in the arrangement of the lateral accessory tooth-plates of the folding, and basically uniseriate, radular ribbon, and in the lateral tilting of the whole pharynx.
4. The large and simple digestive caecum shows active and independent and bidirectional rhythmical peristalsis, with intracellular digestion and luminal occlusion.
5. Major neural ganglia are cephalized to the anterior end of the pharynx, some cerebralization being noted in the more posterior of these ganglia; ganglionic masses are large, discrete, and encapsulated; nerves are numerous.
6. Both anterior and posterior pairs of tentacles are of identical microanatomical structure; the term "rhinophore" is here a misnomer.
7. Branched cephalic sense organs are extensive and found in head and tentacles; locular and neurosecretory anterior sense organs also are present; chemoreceptor buccal cells are concentrated in the lips.
8. The large bilobed oral or suprapedal gland contains a large nerve tract.
9. The heart is single-chambered, with valves at either end, and maintained in a stretched condition within an anchored pericardium; true blood vessels and haemocoelic sinuses are present.
10. The excretory system is complex with vortical suction exerted on the pericardial fluid by the long flagella of the renopericardial canal, and ultrafiltration, with some reabsorption into the adjacent haemocoel, through the vacuolated nephrocytes of one nephridial lumen to variable retention and concentration in an enlarged second lumen with consequent osmo-regulation; an extremely long true nephric duct provides further ionic exchange and water reclamation, a feature that is surprising in a fully aquatic form.
11. In all specimens examined the reproductive system is simple, with small discrete gonad, long and narrow gonoduct bearing a short diverticulum just prior to the gonopore, which opens as a slit within a wide indentation of the dorsal visceral sac which has been termed the "gonadial pouch". No anterior duct or grooves or intromittent organs were found.
12. Musculature is extensive and well developed; muscle cells appear to be almost always binucleate.
13. Numerous small integumental and a few large skeletal spicules are present; they are formed by giant amoebocytes. Other giant cells are excretory or digestive. Blood cells are amoebocytic, smaller than giant cells, and have vacuolated cytoplasm.
14. The habitat of *Tantulum elegans* is a high-level mountain spring marsh devoid of marine influence.
15. Locomotion is rapid, by ciliary gliding and muscular movements of the pedal sole and dorsal visceral sac; a specific "rolling in" reaction occurs.

In the second portion of this paper a new classification of the Order Acochlidioidea is proposed; this has been based on a visual matrix analysis of forms found to 1974

and has included a study of major body systems in an attempt to arrive at true familial relationships. The Acochlidioidea are regarded as a separate order which, together with other groups such as the Philinoglossoidea, show tendencies that suggest they may belong outside the Opisthobranchia and form with these groups a cohesive section of Mollusca in which respiration is not ctenidial or pulmonary but integumental; the shell is absent or replaced by spicules; the visceral hump is carried uncoiled and extended either as a free dorsal visceral sac or adpressed along a lengthened foot; and in which separation of sexes and spermatophoral integumental fertilization often occurs. It is suggested that consideration be given to the establishment of a new section of Mollusca, bearing these characteristics and termed the **Ceratobranchia.** The Acochlidioidea have been divided into five suborders and 13 families (p. 82). All genera and species have been redefined in comparable terms and major points of difference have been indicated in the illustrations.

Résumé

Dans la première partie du présent article, un genre, une espèce et une famille—*Tantulum elegans*: Famille Tantulidae—sont crées pour inclure le premier Acochlidioidea d'eau douce trouvé dans l'hémisphère ouest. Le matériel enrobé dans le méthylacrylate a rendu possible l'étude microanatomique détaillée à partir de diverses séries de coupes de 3 μm d'épaisseur.

Voici quelques faits intéressants suite à cette étude et à des observations sur des animaux vivants:

1. La zone pharyngienne de différentiation de la cavité buccale est complexe, avec deux diverticules, un sac radulaire, et un sac subradulaire ainsi qu'une musculature bien développée actionnant principalement le sac radulaire et innervée par un vaste plexus nerveux en provenance d'une extension du système ganglionnaire buccal.
2. Les conduits des très grosses glandes salivaires sont extrêment contractiles et chacun porte une ampoule bulbeuse contractile avec une protubérance interne ciliée pour l'expulsion contrôlée des sécrétions salivaires dans une paire de petites poches s'ouvrant à l'extrémité postérieure de la partie pharyngienne, recouverte de cuticule, du tube digestif.
3. Il subsiste des traces d'asymétrie dans l'arrangement, fondamentalement unisérié, des plaques dentaires accessoires de la courbure de la radula et du ruban radulaire et aussi dans l'inclinaison latérale de tout le pharynx.
4. Le caecum digestif, grand et simple, présente un péristaltisme actif, indépendant, rythmique, et bidirectionnel avec digestion intracellulaire et occlusion de la lumière.
5. Les ganglions nerveux majeurs sont céphalisés à la partie antérieure du pharynx et on peut noter une certaine cérébralisation dans la partie plus postérieure de ces ganglions; les masses ganglionnaires sont grosses, discrètes, et encapsulées; les nerfs sont nombreux.
6. Les deux paires de tentacules, antérieure et postérieure, ont une structure microanatomique identique; le terme "rhinophore" est ici une fausse appellation.
7. Les organes sensitifs céphaliques ramifiés sont étendus et se trouvent dans la tête et les tentacules; les organes sensitifs loculaires et neurosécréteurs antérieurs sont

aussi présents; les cellules buccales chimioréceptrices sont concentrées dans les lèvres.

8. La grande glande orale bilobée ou glande suprapédiaire contient un gros cordon nerveux.
9. Le coeur a une chambre simple, avec des valvules à chaque extrémité et est maintenu tendu à l'intérieur d'un péricarde ancré; de véritables vaisseaux sanguins et des sinus hémocéliens sont présents.
10. Le système excréteur est complexe avec une succion en spirale excercée sur le fluide péricardique par le long flagelle du canal rénopéricardique; l'ultrafiltration se fait avec une certaine réabsorption dans l'hémocèle adjacent à travers les néphrocytes vacuolés et la lumière néphrétique à rétention variable et la concentration a lieu dans une seconde lumière élargie, d'où résulte l'osmorégulation; un véritable conduit néphrétique extrêmement long assure un échange ionique et une récupération d'eau supplémentaires, ce qui est surprenant chez une forme pleinement aquatique.
11. Chez tous les spécimens examinés, le système reproducteur est simple avec de petites gonades discrètes, un gonoducte long et étroit portant un petit diverculum juste avant le gonopore qui s'ouvre comme une fente à l'intérieur d'un large repli du sac viscéral dorsal que l'on a appelé "poche gonadiale". On n'a trouvé aucun canal antérieur, aucun sillon ou organe d'intromission.
12. La musculature est étendue et bien développée; les cellules musculaires semblent presque toujours binuclées.
13. De nombreux petits spicules intégumentaires et quelques grands spicules squelettiques sont présents; ils sont formés par les amibocytes géantes. Les autres cellules géantes sont excrétrices ou digestives. Les cellules sanguines sont amiboïdes, plus petites que les cellules géantes et ont un cytoplasme vacuolé.
14. L'habitat de *Tantulum elegans* consiste en des étangs de haute montagne alimentés par des sources, donc sans aucune influence marine.
15. La locomotion est rapide par action ciliaire et par action musculaire de la sole et du sac viscéral; parfois la tête se replie dorsalement dans une cavité temporaire formée par l'enroulement du sac viscéral.

Dans le seconde partie de cet article on propose une nouvelle classification de l'ordre Acochlidioidea; on s'est basé sur l'analyse d'une matrice visuelle des formes trouvées jusqu'en 1974 et on a aussi inclus l'étude des systèmes importants afin d'arriver à de véritables affinités familiales. Les Acochlidioidea sont considérés comme un ordre séparé qui, avec d'autres comme les Philinoglossoidea, montrent une tendance suggérant qu'ils puissent appartenir à un groupe à l'extérieur des Opisthobranchia et former avec ces groupes une section cohérente de Mollusques chez lesquels la respiration n'est pas cténidiale ou pulmonaire mais intégumentaire; la coquille est absente ou remplacée par des spicules; la masse viscérale est portée nonspiralée et prolongée comme un sac viscéral dorsal libre ou est appressée sur un pied allongé; et chez ces animaux il y a séparation des sexes et la fertilisation est intégumentaire. On suggère de tenir compte de l'établissement d'une nouvelle section de Mollusques présentant ces caractéristiques et portant le nom de **Ceratobranchia.** Les Acochlidioidea ont été divisés en cinq sousordres et 13 familles (p. 82). Tous les genres et espèces ont été redéfinis en termes comparables et les différences majeures sont indiquées sur les illustrations.

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Key to Lettering of Figures

a	anus
aca	anterior cephalic aorta
adm	anterior diagonal muscle
ah	anterior haemocoel
al	anterolateral lobe
am	giant amoebocyte
ant	anterior
apdn	anterior pedal nerve
apn	anterior pharyngeal nerve
apn-1	upper left anterior pharyngeal nerve
apn-2	lower left anterior pharyngeal nerve
aso	anterior sense organ
at	anterior tentacle
atn	anterior tentacular nerve
avg	accessory visceral ganglion
avh	anterior visceral haemocoel
b	posterior
bc	buccal tube
bcl	blood cell
bg	buccal ganglion
bp	beginning of gonadial pouch
bv	balloon valve (cardio-aortic)
ca	common aorta
can	cardiac nerve
cg	cerebral ganglion
chc	caecal haemocoel
cll	anterolateral lobe of right cerebral ganglion
cn	caecal nerve
co	canalicular opening
cp	ciliated patch
cpg	cephalo-pedal groove
cpl	cartilaginous lingual plates
cso	cells of the branched sense organ
cuc	cuboidal cells of nephridial duct
d	dorsal
dbd	dorsal buccal dilator muscle
dc	digestive caecum
dcn	dorsal cephalic nerve
dh	dorsal haemocoel
e	nephridopore
et	exit tubule of renopericardial canal
f	foot
fc	food canal (dorsal portion) of pharynx, showing cuticularization

fnd	flagellated pore into nephric duct
fp	small cells of flagellated pore between nephridium and nephric duct
fs	fibrous envelope of pharynx
ftp	food canal or tube of pharynx
fvh	free dorsal visceral hump
g	genital pouch
gd	genital duct
gdi	genital diverticulum
gn	gonadial nerve
go	gonad
gp	gonopore
h	heart
i	intestine
il	inner lip of buccal cavity
iln	inferior labial nerve
j	fibrous "jaw", pressing medially against rachidian tooth and posteriorly against lateral tooth
lb	lower border
ll	lower lip
lpe	lateral pouch extension of food canal
lphn	lateral pharyngeal nerve
lpn	lateral pedal nerve
lt	lateral tensor muscles of radular sheath
lu	lumen
lvn	left visceral nerve
m	mouth
m	medial (Fig. 11E)
mh	mouth hooks
mln	median labial nerve
mpn	middle pedal nerve
mpw	muscle strands in pericardial wall
n	nephridium
n-1	lumen of first nephridial tube
n-2	lumen of second nephridial tube
nd	nephric duct
nf	flagellated funnel cells of nephrostome protruding into pericardium
nh	nephric haemocoel
nn	nephridial nerve
np	ciliated cells of nephridiopore merging with ciliated patch
ns	nephrostome
nsw	neural swelling
nun	nuchal nerve

oe	oesophagus
oer	oesophageal retractor muscles
olu	caecal lumen occluded by coalescence
or	glandular cells of oral organ (suprapedal) (Fig. 20B)
or	oesophageal retractor muscles (Fig. 21B)
os	oesophageal sphincter
p	pericardium
pag	parietal ganglion
pam	pericardial anchoring muscles
pbg	posterior buccal ganglion
pbvg	parietal-buccal-visceral ganglion
pdm	posterior diagonal muscle
pg	pedal ganglion
pgl	pedal gland
ph	pharynx (in Fig. 13 ph = pedal haemocoel)
phc	pedal haemocoel
phl	posterior visceral haemocoel
plg	pleural ganglion
pnp	pharyngeal nerve plexus
pp	lumen of pharyngeal pump
pphn	posterior pharyngeal nerve
ppn	posterior pedal nerve
ps	pharyngeal sphincter muscle, dorsal block (part of velarium)
pt	posterior tentacle
ptn	posterior tentacular nerve
ptp	tapered posterior end of pericardium
pva	posterior visceral aorta
pvm	cardio-haemocoelic valve muscle strand
r	rectum (in Fig. 18A, B, r = subtentacular ridge)
rp	radial pharyngeal muscle
rpc	renopericardial canal cells
rs	radular sheath of radular sac
rvhp	right visceral haemocoel protractor muscle
rvhr	right visceral haemocoel retractor muscle
rvn	right visceral nerve
s	statocyst (in Fig. 18B, s = saccule)
sbg	suprabuccal ganglion
sd	pharyngeal salivary duct
sg	pharyngeal salivary gland
sks	skeletal spicule cut transversely
sln	superior labial nerve
sn	salivary nerve
sp	pharyngeal pump
spg	oral organ (suprapedal)
sr	salivary reservoirs of pharynx

srp	subradular pouch (sac)
st	stomach
tf	posterior tip of foot
t-fv	two-flaps of cardio-haemocoelic valve
tg	tubular "gland"
ts	tensor strands of subradular membrane
tt	transverse tensor muscle
ul	upper lip
v	ventral
va	cardio-haemocoelic valve (Fig. 8)
vbd	ventral buccal dilator muscle
vcbm	ventral caecal bdelloid muscle
vcn	ventral cephalic nerve
vcp	ventral caecal protractor muscles
vd	ventral depressor muscle
vg	visceral ganglion
vn	vacuolated nephrocytes
zg	zymogenic droplets

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Note 1 A new eyeless, aspicular species of *Microhedyle* has been found in the littoral of the Bay of Fundy and is being described.

Note 2 Addition in proof. Morse (1976) describes a new species of acochlidioidean that appears to belong not with the Hedylopsidae but rather with the Asperspinidae, close to *Asperspina brambelli* (Swedmark) because of the following: very simple nephric system, lack of a true cephalo-pedal groove with internally marked haemocoelic divisions as in *Hedylopsis spiculifera*, structure of radula, and lack of an eversible penis.

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