The functional morphology of *Propeamussium lucidum* (Bivalvia: Pectinacea), a deep-sea predatory scallop

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(With 18 figures in the text)

The abyssal propeamussiid *Propeamussium* is well known from studies of shell structure and is believed to be representative of a relict lineage, sister to the group which gave rise to all shallow-water pectinaceans.

From analyses of stomach contents, species of *Propeamussium* have been reported to be predators. This study confirms this and shows that small meiobenthos or epibenthic planktonic larvae and crustaceans constitute the diet. Prey is thought to be caught by an inrush of water to the mantle cavity and pushed into the mouth with the foot. The stomach is small, secondarily simplified and adapted for the digestion of small creatures. It is convergent with the stomachs of similarly predatory, abyssal anomalodesmatans. Palps are vestigial. The ctenidia are of a new type (B(4)), perhaps derivable from the dimyid ctenidium by the loss of the ascending lamellae of all four demibranchs and the ventral fusion of inner and outer descending lamellae on each side of the body to create a gill where the apices of the filaments are internal. Filter feeding is thus impossible, the ctenidia now wholly subserving a respiratory function.

Aspects of shell structure, adductor muscle arrangement and form of the pallial margin suggest that *P. lucidum* is a proficient swimmer. It is concluded, however, that prey is not caught during swimming, and that the two activities are mutually incompatible. Probably swimming is used only for escape.

Ctenidial structure forges links with the Plicatulacea (Dimyidae, Plicatulidae), shell structure with the Pectinacea (Pectinidae, Spondylidae) and it is concluded that the Propeamussiidae is indeed a relict group with links back to more primitive plicatulaceans and with the modern shallow-water Pectinacea, but evolving, in the isolation of the abyss, remarkable adaptations for a predatory mode of life. The Propeamussiidae also demonstrate striking convergence with the abyssal predatory Anomalodesmata.

Contents

Introduction

The Pectinacea, comprising the Pectinidae, Spondylidae and Propeamussiidae, have attracted much attention, the Pectinidae in particular, because of their economic importance. The scallops also exhibit quite remarkable morphological adaptations, in particular the evolution of the monomyarian form (Yonge, 1953) and an associated ability to swim (Yonge, 1936; Gould, 1971; Thayer, 1972; Morton, 1980). Most scallops, e.g., *Chlamys* (Moore & Trueman, 1971) are poor swimmers, and this facility is essentially an escape response, whereas in *Placopecten* and *Amusium* (Caddy, 1968; Morton, 1980) swimming skills are remarkable. Probably these genera are the only true epifaunal swimming bivalves; reports of swimming abilities in representatives of other groups, e.g. the Limidae (Gilmour, 1967), Solemyidae (Reid, 1980) and Solenidae (McMahon & McMahon, 1983) result from their recessing or highly proficient burrowing abilities. A report of *Limaria fragilis* being able to swim continuously for 15 min (quoted in Baldwin & Lee (1979)) needs further clarification. Conversely, the Spondylidae are cemented, species of *Spondylus* being most obvious in tropical reef habitats (Yonge, 1973). By contrast, little of detail is known about the Propeamussiidae, largely because they occupy abyssal depths from 150 to > 5000 m (Knudsen, 1967; Waller, 1971, 1984). Allen (1983), in his review of the deep sea Mollusca, makes no mention of them although an earlier review by Knudsen (1979) recognized their importance. Waller (1971, 1978) considers that, on the basis of shell structure, the Propeamussiidae are primitive scallops, living relics of a group otherwise thought to have become extinct at the end of the Palaeozoic and a sister group to that which gave rise to all other extant Pectinacea. No propeamussiid has ever been observed alive and only tantalizing pieces of information about their morphological adaptations are available. Apparently, the mantle margin is much simplified (Waller, 1971), there is a post-rectal muscle (Bernard, 1978), there are no pedal retractor muscles (Waller, 1971) and the ctenidia lack any unifying junctions (Yonge, 1981). Such morphological simplifications of the basic scallop plan could represent an essential primitiveness or they could be adaptations facilitating occupation of the abyss. Knudsen (1967, 1970), however, has examined deep water propeamussiids in more detail and suggests, on the basis of stomach content analyses, not only that the Propeamussiidae are predators, but that they catch their prey whilst swimming. This view (Allen, 1983) has been largely accepted by other authors (Yonge, 1981) but never confirmed. The only other known bivalve predators are members of the anomalodesmatan Verticordiidae (Allen & Turner, 1974; Morton, 1984, 1987), Parilimyidae (Morton, 1982), Poromyidae (Yonge, 1928; Morton, 1981) and Cuspidariidae (Yonge, 1928; Reid & Reid, 1974; Allen & Morgan, 1981), all confined to deep water. Representatives of these families are, however, sedentary predators and possess remarkable adaptations that facilitate unusual feeding modes (Morton, 1987). Were species of *Propeamussium* to be swimming predators, one would anticipate even more remarkable adaptations and yet the suggestion of Knudsen (1967, 1970) has elicited little further study. During a research visit by BM to the Institute of Oceanographic Sciences of the United Kingdom in 1987, the opportunity was taken to examine samples of *Propeamussium lucidum* (Jeffreys, 1879) obtained

during I.O.S. sampling programmes. In addition, comparative information on *P. permirum* (Dautzenberg, 1925) and *P. hypomeces* (Dautzenberg & Fischer, 1897) has been obtained, but this study is concerned principally with *P. lucidum*. Information on propeamussiid anatomy is sparse and scattered widely in the literature. This study of *P. lucidum* thus investigates the anatomical evidence for the suggestion of Knudsen (1967) that these scallops are swimming predators.

Taxonomy

Newell (1969) considered the Pectinacea Rafinesque, 1815 to comprise four extant families: Pectinidae, Plicatulidae Watson, 1930, Spondylidae Gray, 1826 and Dimyidae P. Fischer, 1886. *Propeamussium* De Gregorio, 1884 was included in the *Amusium* Roding, 1798 group of the Pectinidae (Hertlein, Cox & Newell, 1969).

Waller (1978) amended this classification, elevating the Dimyidae and Plicatulidae to superfamilial status and relocating them in the Ostreina Férussac, 1822, with the Ostreacea Rafinesque, 1815. This left only three extant families within the Pectinacea: Propeamussiidae (Abbott, 1954), Pectinidae and Spondylidae.

Removal of the Dimyidae and Plicatulidae from the Pectinacea had been proposed by Yonge (1975) on the basis of differences in ligament structure. Yonge, however, opted to retain familial status for the Dimyidae and Plicatulidae, placing them in the Plicatulacea rather than utilizing the older available name Dimyacea, arguing that use of the latter would confuse the status of the monomyarian Plicatulidae.

Waller (1978) separated the Propeamussiidae from the Pectinidae on the basis of shell structure (Waller, 1971, 1972) and suggested that the Propeamussiidae were a relict group with links to the ancestors of all modern shallow-water scallops.

Materials and methods

Specimens of *Propeamussium lucidum*, *P. hypomeces* and *P. permirum* were obtained from hauls taken with a variety of epibenthic sledges (Aldred, Thurston, Rice & Morley, 1976; Rice, Aldred, Darlington & Wild, 1982), made under the auspices of the I.O.S. Deep Benthic Biology Programme and housed in the Institute of Oceanographic Sciences, Wormley, Surrey, U.K. Some specimens were collected in the eastern Tropical and North Atlantic Ocean at bathyal and abyssal depths between 1970 and 1979 (Table I). Material was fixed in borax-buffered formalin on shipboard and preserved in 80% alcohol. Specimens of *Propeamussium* were separated during initial sorting prior to fixation or removed from residues in the laboratory. Some specimens were dissected. Others were decalcified and, following routine histological procedures, sectioned at 6 μm both transversely and horizontally. Alternate slides were stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

Biology

Species of *Propeamussium* have been recorded from the North Atlantic Ocean, the Indian Ocean, the Western, Central and Eastern Pacific Ocean and the Pacific sector of the Southern Ocean (Knudsen, 1970).

The most comprehensive account of the Propeamussiidae is based largely on the collections of the John Murray Expedition (Knudsen, 1967). Of the eight species reported upon, seven were considered to be bathyal, with minimum and maximum depth ranges between 183–710 m for *P. sibogai* (Dautzenberg & Bavay, 1905) and 914–2160 m for *P. watsoni* (Smith, 1885). Minimum and

TABLE I

*List of stations yielding **Propeamussium** species*

Station	Date	Position Start N	Start W	End N	End W	Gear	Depth (m)
7432	26.10.70	38°45·1′	28°35·6′	38°44·0′	28°33·4′	BN2·4	1233–1227
7711#62	28.5.71	52°50·0′	20°02·8′	52°49·9′	20°03·8′	BN2·4	2727–2720
7975	19.7.72	26°23·6′	14°51·1′	26°25·5′	14°50·2′	BN2·4	785–834
8524#1	28.6.74	20°45·5′	22°42·5′	20°46·6′	22°42·0′	BN1·5/5	4412
8524#6	28.6.74	20°44·3′	22°44·4′	20°44·9′	22°44·3′	BN1·5/5	4414–4416
8582#5	7.2.75	25°33·6′	16°40·1′	25°34·1′	16°40·4′	BN1·5/5	2999
8976	5.8.76	32°54·6′	11°40·4′	32°54·4′	11°38·5′	BN2·4	3610–3646
9035	23.8.76	34°06·0′	11°55·5′	34°06·2′	11°54·8′	BN2·4	4457–4453
9131#9	19.11.76	20°18·3′	21°43·4′	20°17·9′	21°42·3′	BN0·5/5	4015–4006
9131#10	19.11.76	20°15·1′	21°35·5′	28°14·5′	21°34·6′	BN1·5/5	3952–3950
9131#11	20.11.76	20°09·0′	21°40·0′	20°08·7′	21°39·3′	BN1·5/5	3921
9131#12	20.11.76	20°07·0′	21°26·0′	20°06·6′	21°25·1′	BN1·5/5	3861 3856
9541#1	15.4.77	20°07·0′	21°25·3′	20°07·7′	21°25·1′	BN1·5/5	3850–3854
9541#3	15.4.77	20°08·1′	21°41·2′	20°08·6′	21°40·8′	BN1·5/5	3910 3912
10111#8	9.9.79	49°32·6′	13°07·1′	49°33·5′	13°05·9′	BN1·5/3M	1630–1640
10141#1	3.10.79	24°33·8′	19°48·6′	24°34·8′	19°40·7′	BN1·5/3M	3460–3470
10143#1	4.10.79	24°43·6′	20°03·7′	24°44·5′	20°04·5′	BN1·5/3M	3780 3810

maximum temperature ranges for these species were 6·5–12·0 °C to 2·0–6·9 °C respectively. *Propeamussium meridionale*, on the other hand, was considered to be abyssal, with a depth range between 1893 and 4810 m and a temperature range of 1–4 °C. *P. meridionale* was found to be widely distributed in the Indian and Central Pacific Oceans. *P. meridionale* is dioecious and was considered by Knudsen (1970) to have an egg diameter of 110–130 μm and a larval shell (prodissoconch) length of 230–250 μm and thus to demonstrate lecithotrophic development with a short pelagic larval stage. The prodissoconch of *P. lucidum* is of a similar size.

In a later paper, reporting on the abyssal Bivalvia obtained by the Galathea Expedition, Knudsen (1970) provided further information on other species of the Propeamussiidae, e.g., *P. octodecim-liratum* (Melvill & Standen, 1907), *P. permirum* (Dautzenberg, 1925), *P. solitarum* (Smith, 1894) and *P. watsoni*. These species were shown to be abyssal. The depth range of *P. meridionale* was given as 1900–4800 m and the temperature range from 0·8–4·0 °C. The depth range for *P. permirum* was 4400–4900 m and a mean temperature of 2·8 °C was identified.

Propeamussium lucidum has been reported from many localities in the eastern North Atlantic Ocean, from the area off south-west Ireland (Jeffreys, 1879) south to the Azores (Dautzenberg & Fischer, 1897; Locard, 1898) and Canary Islands (Soot-Ryen, 1966). A single specimen from the Mediterranean (Gulf of Taranto, 367 m) has been assigned to this species (Di Geronimo & Panetta, 1973), but, on the grounds of shallow depth of occurrence and much higher ambient temperature, must be queried. Early records of *P. lucidum* from the Caribbean area have been referred to *P. pourtalesianum* (Dall, 1886). All of the material attributed to *P. lucidum* by Smith (1885), including that from off Pernambuco, has 13 or more internal ribs so must be excluded from this species, in which the rib count is almost invariably 11. The bathymetric range in the Atlantic Ocean is 1019 m (Jeffreys, 1879) to 4255 m (Locard, 1898). Material used in this study extends the

latitudinal range of *P. lucidum* south to 20°N and north to 53°N, and the bathymetric range to at least as shallow as 834 m (Station 7975).

Because of shell form and adductor muscle arrangement, Thayer (1972), Knudsen (1967, 1970) and Yonge (1981) all considered species of *Propeamussium* to be highly efficient swimmers. Species of *Propeamussium* are considered to be predators (Knudsen, 1967, 1970). Knudsen (1970) believed that capture takes place by means of valve movements such that the prey is sucked into the mantle cavity. Yonge (1936) suggested that the swimming habit in the Pectinidae arose from a mantle-cleansing mechanism, prompting Knudsen (1970) to suggest that feeding, i.e. prey capture, could result from a further development of the swimming habit. Yonge (1981) then concluded that prey was possibly entrapped during swimming.

Functional morphology

The shell

Shell structure of the Propeamussiidae has been described by Waller (1971, 1972, 1984) and Newell & Boyd (1985), while Yonge (1975) has described the ligament and shown it to be of the typical pectinacean type and thus distinct from that of the Dimyidae and Plicatulidae (Plicatulacea). In addition, *P. meridionale* has been described in general terms by Knudsen (1967, 1970).

The shell of *P. lucidum* is typically scallop-shaped, i.e. approximately circular and somewhat inequivalve (Figs 1, 2 and 6). The valves are semitransparent, thin and easily damaged. Each valve has a small convexity which reaches a maximum at an approximately central point (Figs 3, 4 and 5). External sculpture is very weak and dissimilar on the two valves. Contrary to the observation of Yonge (1981), there is a byssal notch (Fig. 2, BN) on the anterior auricle (AU) of the right valve.
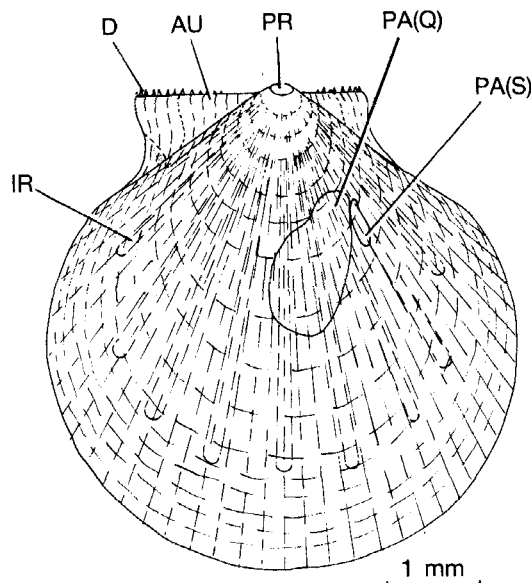

FIG. 1. *Propeamussium lucidum.* An external view of the left shell valve. (For abbreviations see p. 496.)
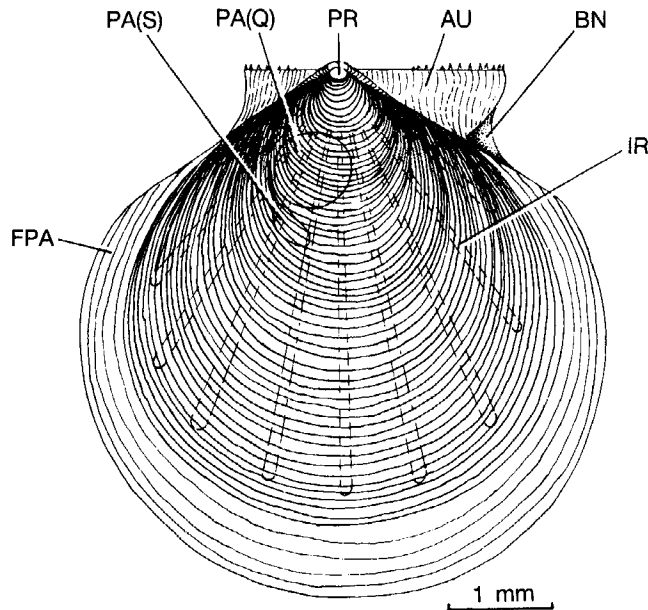
B. MORTON AND M. H. THURSTON

FIG. 2. *Propeamussium lucidum.* An external view of the right shell valve. (For abbreviations see p. 496.)

This does not possess a ctenolium (Waller, 1984) to separate byssal threads, so it is unlikely that *P. lucidum* is ever attached byssally, except perhaps as a newly-settled juvenile. Both antero- and postero-dorsal margins are emarginated and upturned to allow the unrestained exit and separation of mantle fluids during valve adduction (Fig. 3). The posterior auricle is a little smaller than the anterior and the dorsal margin possesses numerous small spines or denticles. *P. lucidum* is monomyarian and distinctly inequilateral, although adoption of the scallop form creates a superficially equilateral individual, except for the dissimilar anterior and posterior auricles. This makes the umbo appear to be off centre (Fig. 3) when in fact it is not. The prodissoconch (Figs 1 and 2, PR) is distinct and about 200–230 μm in length. Adult specimens examined herein ranged up to about 14 mm in diameter, although damage to valve margins makes this figure an approximation only. The species exhibits an allometric change, becoming relatively deeper and shorter with increasing size (Thurston & Morton, In prep.).

The left valve (Figs 1 and 6) comprises an outer layer of foliated calcite (Waller, 1972) (retermed fibrous prismatic by Newell & Boyd, 1985) and an inner layer of crossed lamellar aragonite. The
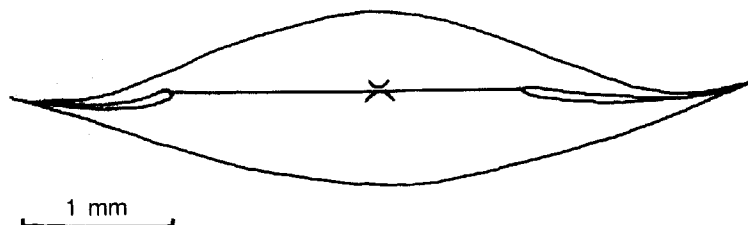

FIG. 3. *Propeamussium lucidum.* A dorsal view of the shell to illustrate the aerofoil shape, with the right valve uppermost.
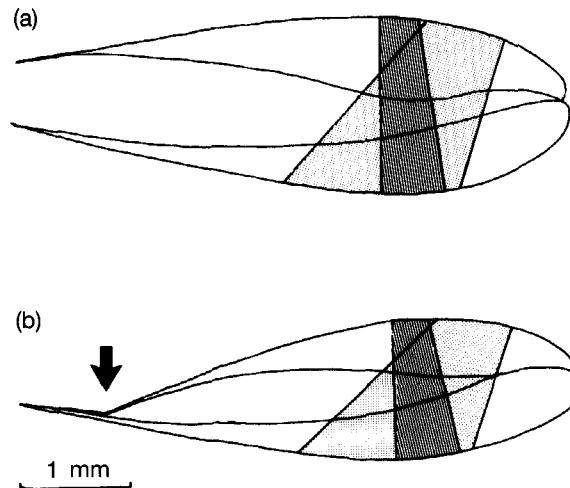
FIG. 4. *Propeamussium lucidum*. Lateral views of the shell (a) open and (b) closed to illustrate flexure of the right valve marginal apron during adduction (arrow), and the arrangements of the 'quick' (light stipple) and 'slow' (dark stipple) components of the posterior adductor muscle drawn accurately to scale. The right valve is uppermost.

right valve (Figs 2 and 6) comprises a thin outer layer of short simple calcite prisms which extend beyond the inner non-prismatic, crossed lamellar layer to create a broad, flexible, prismatic, extracostal apron (FPA). The outer surface of the left valve is basically smooth, but may show a varying though small degree of surface ornamentation (Fig. 6a). Faint radial striae may be present, usually near the mid line rather than anteriorly or posteriorly. In addition, irregular concentric corrugations may be present. These are always weak and few in number. The outer part of the valve, where the prismatic layer is not underlain by crossed lamellar aragonite, has a finely striate appearance under transmitted light due to the organization of the very small prisms of which it is
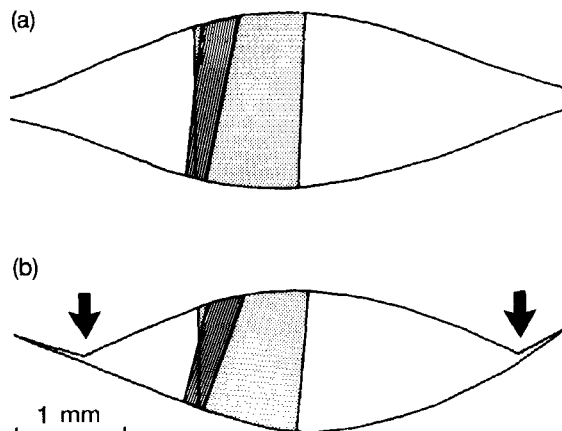

FIG. 5. *Propeamussium lucidum*. Ventral views of the shell (a) open and (b) closed to illustrate flexure of the right valve marginal apron during adduction (arrows), and the arrangements of the 'quick' (light stipple) and 'slow' (dark stipple) components of the posterior adductor muscle drawn accurately to scale. The right valve is uppermost.
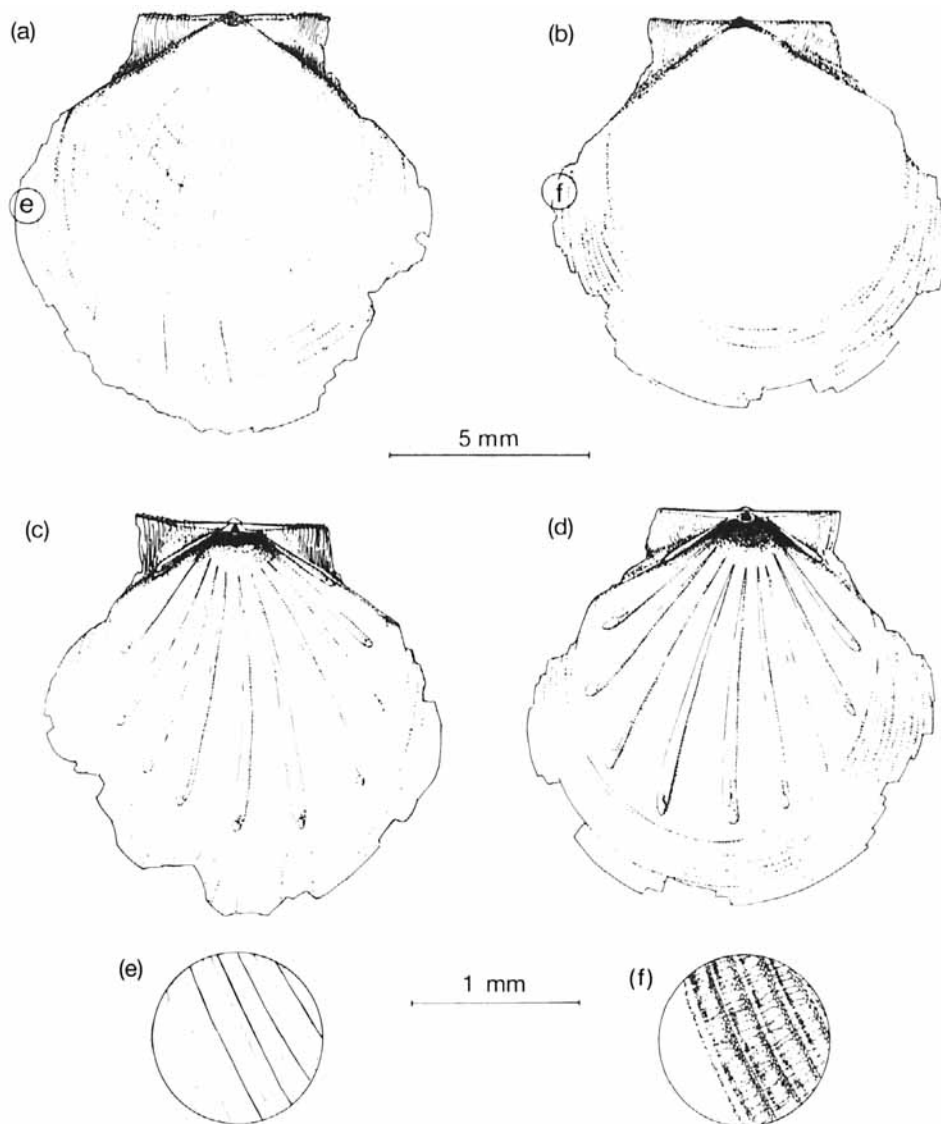
FIG. 6. *Propeamussium lucidum.* (a, b) External views of left and right shell valves. (c, d) Internal views of left and right shell valves. (e, f) Detail of marginal shell sculpture of left and right valves.

constituted (Fig. 6e). The outer surface of the right valve is marked with a faint, regular, concentric ornamentation deriving from the organization of its constituent prisms (Fig. 6b, f). This consists of concentric arrays of large prisms (115–130 μm in length) which alternate with smaller prisms (20–45 μm in length) arranged in bands three or four prisms wide (Fig. 7). The organic matrix between prisms is very thin. Each shell valve is strengthened internally by 11 (rarely 10 or 12) radial ribs or costae (Fig. 6c, d), including the two auricular costae which are always present. The ribs appear first in individuals 1 mm, or more usually 2 mm, long. The ribs gradually increase in breadth
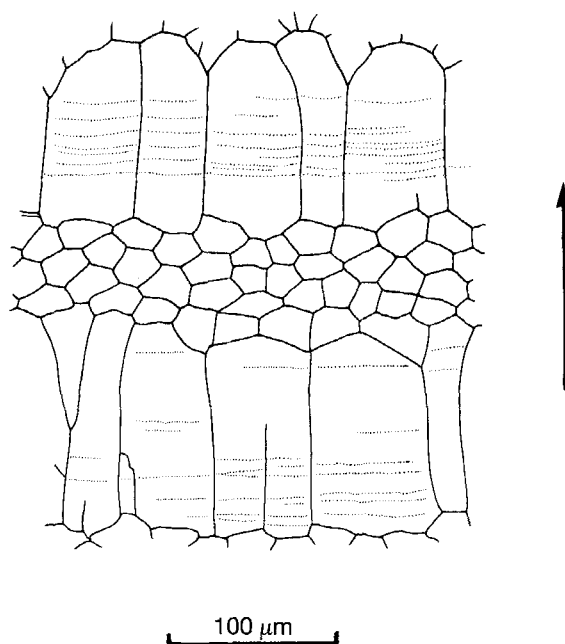
100 μm

FIG. 7. *Propeamussium lucidum*. Arrangement of calcite prisms in the flexible prismatic apron of the right valve. The arrow points towards the umbones.

towards the edge of the inner crossed lamellar layer, but do not extend on to the fragile, prismatic, extracostal apron. This area of the right valve in particular is often damaged and repaired.

The hinge complex of *P. lucidum* is fragile and most of the specimens available for study were incomplete. Sufficient details can, however, be made out to provide an insight into hinge function. The central, pad-like, inner ligament layer is small and provides the opening thrust when compressed (Yonge, 1978*a*). It is situated symmetrically relative to the shell, but just posterior to the centre of the hinge line owing to the slightly longer anterior auricles. Lateral to the internal inner ligament layer are long stretches of anterior and posterior outer ligament layers, the function of which is to hold the edentulous inner dorsal margins of the valves firmly in alignment. The ligament thus conforms to the basic pectinacean plan (Trueman, 1953; Yonge, 1978*a*). Flat areas with minutely roughened surfaces occur on the inner face of the auricles, immediately ventral to the outer ligament layer. Each valve has two such areas separated by the inner ligament layer (Fig. 8a, b). The width of these areas is approximately constant close to the inner ligament layer, but tapers almost to nothing at the extremities of the auricles. The outer ligament layer is straight, and for most of its length coincides precisely with the dorsal edge of the auricles. At the distal end of the posterior auricle, however, and to a lesser extent the anterior auricle of the left shell valve, it comes to lie just inside the valve edge, which curves over the margin of the right auricle (Fig. 8c, d). The corresponding margin of the right auricle is simple (Fig. 8e, f).

As will be seen, the striated (quick) element of the adductor muscle is very oblique in *P. lucidum* and is attached to the shell valves in a position posterior to the vertical axis through the inner ligament layer. The tendency of stresses imposed during adduction would be to rotate the right valve in a clockwise direction relative to the left valve when viewed from the right side, with the
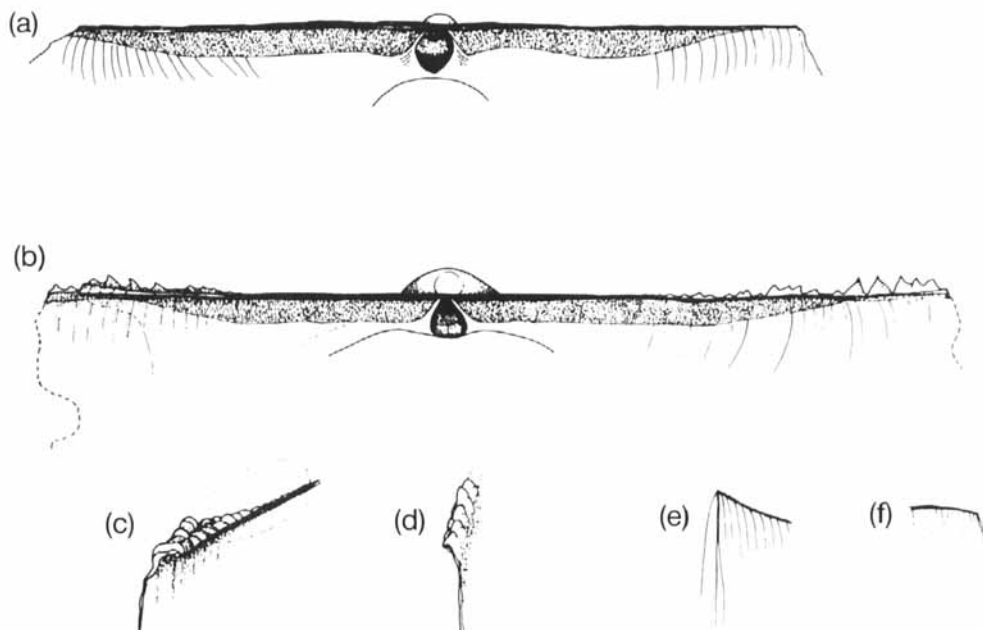
FIG. 8. *Propeamussium lucidum*. (a, b) Internal surface of hinge line of left and right auricles. (c, d) Posterior and anterior ends of left auricle. (e, f) Posterior and anterior ends of right auricle.

inner ligament layer acting as pivot. This contrasts with the situation in *P. dalli* (Smith, 1885) as figured by Thayer (1972; fig. 4A) in which the adductor muscle is (apparently) attached symmetrically ventral to the inner ligament layer. In *P. dalli*, adduction stresses would be of a shearing rather than a rotational nature. In *P. lucidum*, the rotational forces would be reduced when the valves are closed, by friction between the roughened areas on the internal faces of the auricles, and limited by the overlapped extremities of the left auricles. The outer ligament layer would prevent valve separation, align them and thus stop the right auricle overriding the hooked margin of the left.

When the shell is tightly closed, the marginal extracostal apron of the right valve is flexed and adpressed against the more rigid and radially strengthened margin of the left valve. Seen from different viewpoints (Figs 4 and 5), it is clear that the shell of *P. lucidum* is modified to improve swimming efficiency particularly when, during valve adduction, the flexibility of the right valve margin recesses this valve within the left. The thin, light shell, smooth outer shell surface, internal ribbing, small valve convexity which raises the fineness chord, central point of maximum convexity, emarginated anterior and posterior shell margins and aerofoil shape suggest strongly that *P. lucidum* is an effective swimmer. Exactly similar adaptations equip *Amusium pleuronectes* for efficient swimming (Morton, 1980).

The musculature

The musculature of *P. lucidum* is much simplified and comprises a single enlarged posterior adductor which is divided into two components (Fig. 9): a smaller component of smooth or 'slow'
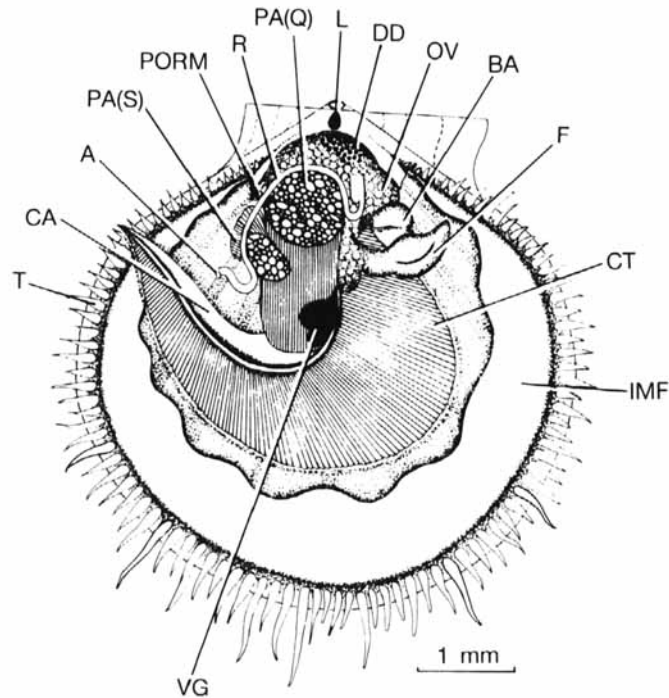
FIG. 9. *Propeamussium lucidum*. The organs of the mantle cavity after removal of the right shell valve, mantle lobe and ctenidium. (For abbreviations see p. 496.).

fibres (PA(S)) which functions to sustain adduction of the valves and a larger component of striated or 'quick' fibres (PA(Q)) that is thought to be responsible for the rapid adduction of the valves, as for example during swimming (Thayer, 1972; Morton, 1980). As in other scallops, both the orientation of these two muscle blocks and the position and size of the insertion on the left and right valves is different. This arrangement creates a muscle obliquity that serves not only to enhance the potential for sustained adduction and the capacity of the 'quick' muscle for work, but also to reduce the effects of shear at the hinge line (Thayer, 1972; Morton, 1980). Thus, on the right valve, the insertion of the quick component of the adductor muscle is small, close to the umbo and located on the posterior face of the shell (Figs 4 and 5). The insertion of the slow component of the adductor muscle on the right valve is postero-ventral to the quick component. On the left valve the insertion of the quick component of the adductor muscle is longer dorso-ventrally, but narrower antero-posteriorly and further away from the umbones. This muscle is thus strongly oblique in the dorso-ventral axis of the shell and therefore highly characteristic of a strong swimmer. Similarly, the insertion of the slow component of the adductor muscle on the left valve is more extensive dorso-ventrally, narrower antero-posteriorly, and has the insertion further posteriorly but closer to the umbones. The orientation of this component of the adductor muscle is thus in opposition to that of the quick component, particularly in the dorso-ventral plane, and thereby plays a role in preventing shear. The arrangement of the two muscle blocks fits the definition of an efficient swimmer (Thayer, 1972) and is closely comparable to *Amusium pleuronectes*, the most efficient swimming scallop so far reported (Morton, 1980). In *P. lucidum*, as in other propeamussiids, e.g.

Cyclopecten argenteus, C. knudseni and *C. squamiformis* (Bernard, 1978), there is a small post-rectal muscle, arching between the valves, dorsal to the rectum (Figs 9 and 11, PORM). For other propeamussiids, Bernard (1978) reports there to be an abdominal sense organ associated with this muscle, but this has not been detected in *P. lucidum*. As in other propeamussiids, *P. lucidum* possesses no pedal retractor muscles, a further feature seeming to indicate a proficiency in swimming (Gould, 1971).

The mantle

The general mantle under the valves is thin, the two epithelia comprising simple squamous cells (Fig. 10, M). The mantle margin is of the typical pectinid plan (Morton, 1980) but much simplified.
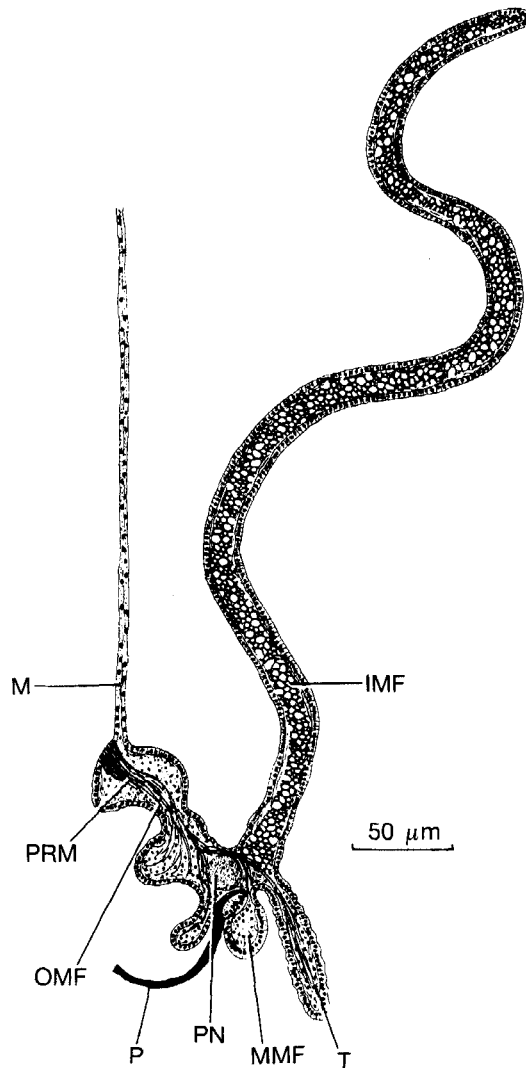

FIG. 10. *Propeamussium lucidum.* A transverse section through the left mantle margin. (For abbreviations see p. 496.).

It comprises the usual three folds (Yonge, 1982). The outer (OMF) is small, secreting the shell from its outer surface and the periostracum (P) from its inner. The middle fold (MMF) is also small and bears on its inner surface a series of tentacles that circumscribe both lobes (Fig. 9, T). The inner fold (IMF) is in the form of an enormous velum that is extensively muscularized. So large is the velum, that when retracted it can be up to 50% of the dorso-ventral length of the shell. Unlike other pectinids, e.g. *Amusium* (Morton, 1980), the velum does not possess tentacles nor does the middle fold possess pallial eyes. The pallial line lies well inside the borders of the inner crossed-lamellar layer of the shell and from it arises a large pallial retractor muscle (Fig. 10, PRM) which sends branches into all folds. There is also a large pallial nerve (PN).

The ctenidia

The left and right ctenidia of *P. lucidum* are large (Fig. 9, CT) and curve around the posterior adductor muscle (PA(Q); PA(S)), from the anterior to the posterior. The posterior ctenidial axes (CA) are free, so that in life, the posterior ends of the ctenidia project between the posterior mantle and shell margins. In all dissected specimens, ctenidial structure was hard to distinguish because the filaments all appear unconnected. Such a situation is well known; Bernard (1978) reported upon the same situation in *Cyclopecten knudseni* and considered them 'damaged' by entry of mud into the mantle cavity, presumably when the scallop was first caught. Transverse and horizontal sections of the ctenidia have, however, clarified their structure.

The ctenidia of representatives of the Pectinidae have been studied by Ridewood (1903), Atkins (1936), Owen & McCrae (1976) and Yonge (1981). They report a pseudolamellibranch structure of conventional form. This is not so in *Propeamussium*. In transverse section (Fig. 11), left and right ctenidial axes (CA) can be identified easily, the former finding attachment below the posterior adductor muscle (PA(Q)), the latter to the mantle. Casual observations suggest that there is but one demibranch on each side, with ascending and descending lamellae. This is not the case. Close examination reveals that the apices of the ctenidial filaments, which in every bivalve hitherto described face to the outside of the lamella, in the case of *P. lucidum* face internally. The bases of the filaments point outwards. Examination of the filament using oil immersion, i.e. at a magnification of 1000 ×, demonstrates another remarkable feature: the apical ciliation comprises only frontal cilia (Fig. 12, FC) and lateral cilia (LC). There are no eulatero-frontal cilia which in many bivalves constitute the filtering mechanism, nor are there microcilia on the apex which in other pectinids, for example, also serve to assist in particle selection (Atkins, 1938). Finally, there are no food grooves on the ctenidia, either on the ventral margins or in the dorsal junctions with muscle or mantle. The ctenidia of *P. lucidum* are incapable of filtration or of any food gathering, transporting and sorting functions.

We will leave discussion on the functioning of the *P. lucidum* ctenidium to later, but it is here necessary to suggest how such a structure may have evolved. In the typical bivalve (Fig. 13a), the suprabranchial chamber is separated from the infrabranchial by paired ctenidia. The ctenidia comprise inner and outer demibranchs, each, in turn, with inner descending (DLID; DLOD) (from the ctenidial axis) and outer ascending lamellae (ALID; ALOD). The latter unite with the visceral mass (inner demibranch) or mantle (outer demibranch). Ridewood (1903), however, described for *Anomia aculeata* a situation in which all ascending lamellae are lost. Separation of the suprabranchial from the infrabranchial chamber is by fusion of the left and right descending lamellae of the inner demibranchs and by the union of the ventral edges of the descending lamellae of the outer demibranchs with the left and right mantle lobes (Fig. 13b). Yonge (1977) described a
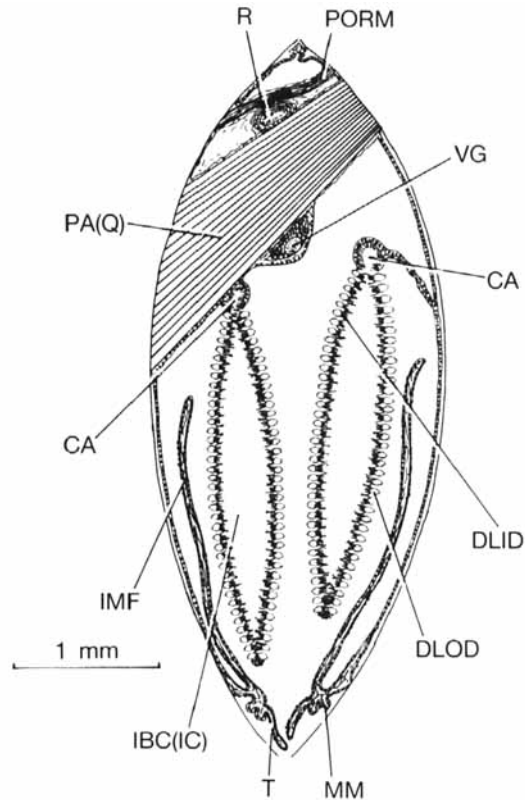
B. MORTON AND M. H. THURSTON

FIG. 11. *Propeamussium lucidum*. A transverse section through the animal in the dorso-ventral axis of the body to illustrate the remarkable arrangement of the ctenidia. (For abbreviations see p. 496.)
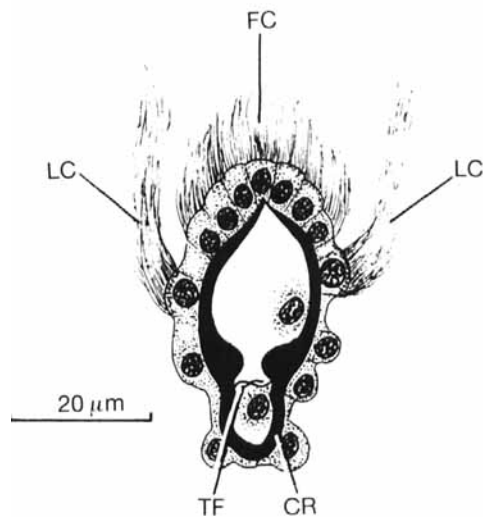

FIG. 12. *Propeamussium lucidum*. A transverse section through a single ctenidial filament. (For abbreviations see p. 496.).
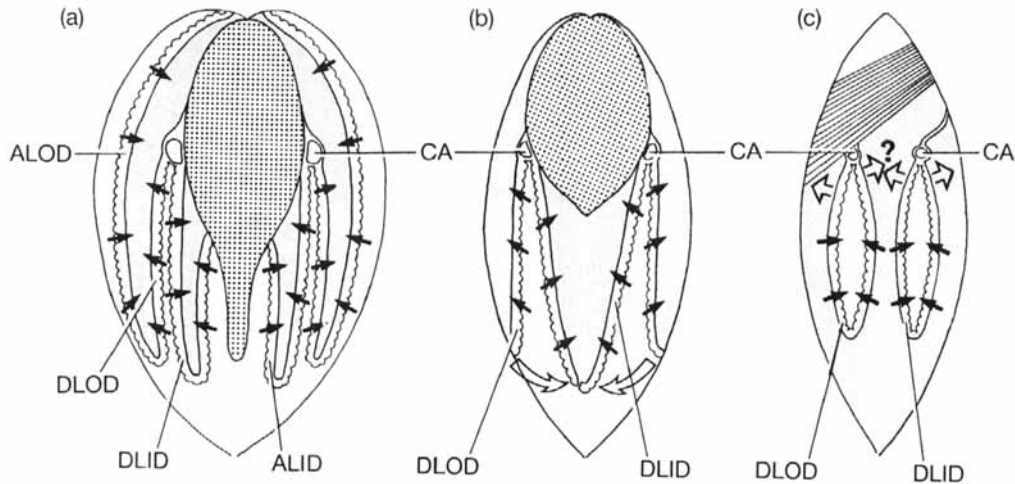
FIG. 13. Transverse sections through the bodies of (a) a 'typical' lamellibranch; (b) a representative of the Dimyidae (after Yonge, 1978*b*) and (c) *Propeamussium lucidum*. In all, dark arrows indicate the direction of movement of water through the ctenidia. In (b), the large open arrows show how the situation in *Propeamussium* (c) has been formed, by ventral fusion of descending lamellae of inner and outer demibranchs. Open arrows with a question mark in (c) relate to the question of how water circulates through such a ctenidium (see text p. 492). Light stippling indicates the extent of the suprabranchial chamber. Note how in (c), unlike (a) and (b), the suprabranchial chamber surrounds the ctenidia which, in turn, enclose the infrabranchial chamber. (For abbreviations see p. 496).

similar situation in *Heteranomia squamula* and for species of *Dimya* (Yonge, 1978*b*: fig. 10). For the unusual case of *P. lucidum* there can be one explanation only. The ventral margins of the descending lamellae of the inner and outer demibranchs of the left side have fused, and so have those of the right. As a consequence, the suprabranchial chamber surrounds the ctenidia, the filament apices of which are internal as are the left and right remnants of the infrabranchial chamber (Fig. 13c). In effect, the reduced ctenidia of *P. lucidum* have been turned inside out. The ctenidia can function only for respiration.

The labial palps, lips and mouth

The labial palps of *P. lucidum* are much reduced and extensively fused to the buccal lips (Figs 14 and 15). The lips of a typical, filter-feeding bivalve are provided with a series of pronounced ciliary ridges and grooves that effect particle sorting. This is not the case in *P. lucidum* where the remnants of the palps (ILP; OLP) have a series of faint ridges only, lateral to the mouth, that can play no role in particle sorting. The lips of the mouth are large. The outer (OL) in particular comprises a large, centrally projecting, flap that overarches the inner lip to form a capacious buccal sac (Fig. 14). Pulling back the outer lip (Fig. 15) reveals a wide mouth (MO). The foot (F) was often observed stuck between the buccal lips.

The visceral mass and foot

The visceral mass is small and a component of it is located on the anterior face of the 'quick' portion of the posterior adductor muscle (Fig. 9, PA(Q)). It extends dorsally to fill the sub-
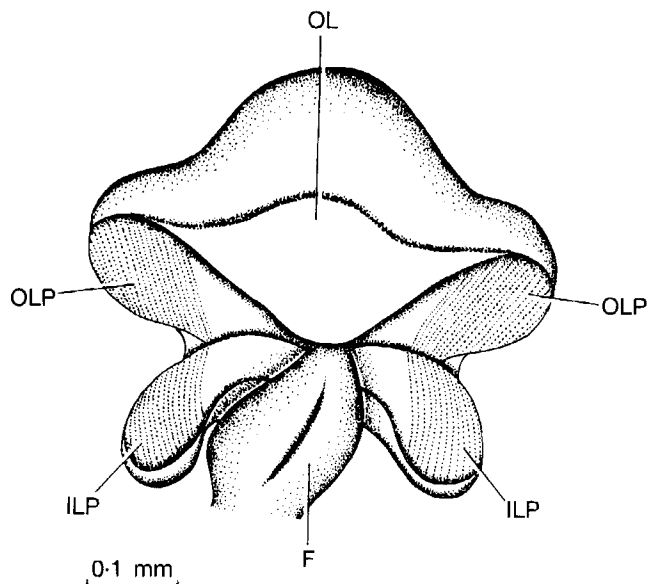
FIG. 14. *Propeamussium lucidum.* A ventral view of the labial palps, foot and outer lip of the mouth forming a buccal pouch. (For abbreviations see p. 496.)
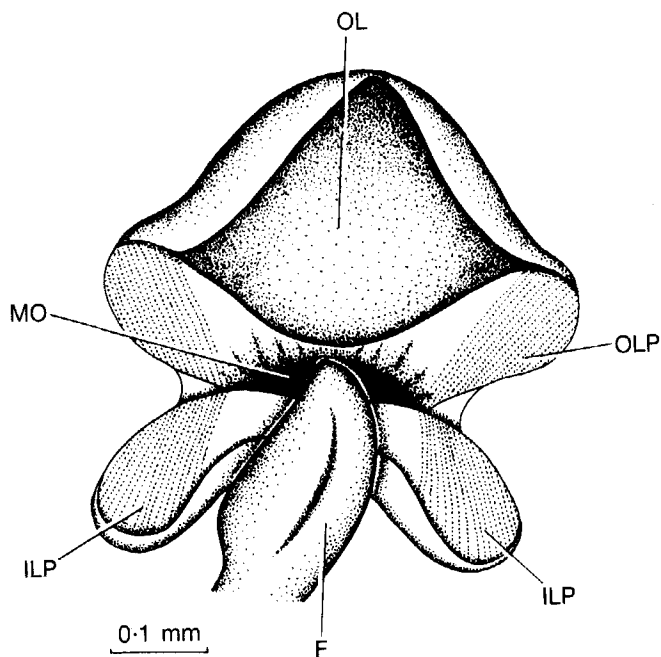
FIG. 15. *Propeamussium lucidum.* A ventral view of the labial palps and foot, with the outer lip pulled back to expose the buccal pouch and mouth. (For abbreviations see p. 496.).
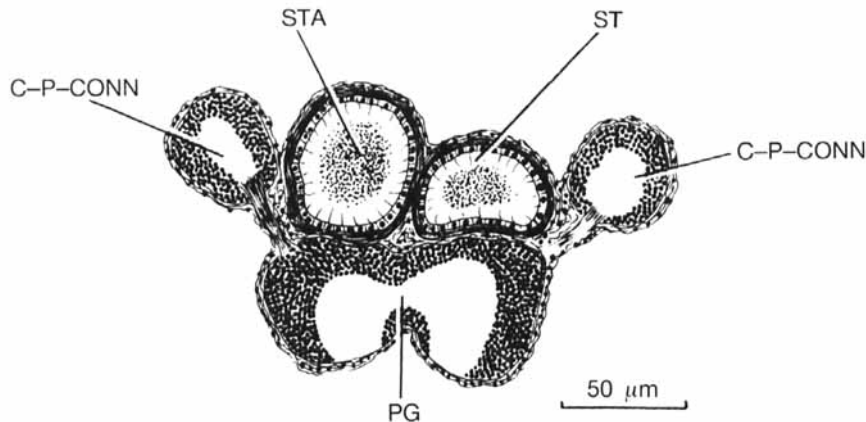
FIG. 16. *Propeamussium lucidum*. A transverse section through the pedal ganglia and the paired statocysts. (For abbreviations see p. 496.).

umbonal spaces of each valve, beneath the hinge line. From the anterior component arises the foot (F) which is a relatively large stalk-like structure with a bulbous, pointed end. On the ventral surface of the bulb, there is a byssal groove, but no byssus was found, at least not in the adults examined. Yonge (1981) concluded that the propeamussiid foot 'assists in cleaning; it can have no other function'.

Waller (1984) points out that, contrary to the widely held view that propeamussiids are free-living, most species have a persistent byssal notch throughout ontogeny and therefore probably are byssate. *Cyclopecten* is byssally attached (Yonge, 1981; Waller, 1984). *Propeamussium lucidum*, despite possessing a byssal notch, is not byssally attached as an adult, though it may be as a juvenile.

At the base of the foot lie the paired pedal ganglia (Fig. 16, PG). Dorsal to these are paired statocysts (ST) each of which is some 70 μm in diameter. Each statocyst comprises a capsule of cuboidal cells possessing a few cilia. The statocyst cavity is occupied by many hundreds of tiny (< 1 μm) crystalline statoconia (STA). The statocysts are surrounded by a fibrous capsule.

Both components of the visceral mass accommodate elements of the gonads and the dorsal component contains the alimentary canal. *P. lucidum* is dioecious.

The alimentary canal

The wide oesophagus (Fig. 17, 0) is directed dorsally and opens into the anterior face of the stomach. The conjoined mid gut (MG) and style sac (CSS) arise from the floor of the stomach and pass ventrally. The style sac is short and below it the mid gut undertakes a short turn to pass dorsally and loop over the 'quick' component of the posterior adductor muscle (PA(Q)). As the rectum (R), the intestine now passes under the post-rectal muscle (PORM), over the 'slow' component of the posterior adductor muscle (PA(S)) to open at an anus (A) that is free from all attachments and discharges into the postero-dorsal region of the mantle cavity (Fig. 9, A).

The stomach is small and wholly unlike the capacious sac of the typical filter feeding bivalve. In a specimen of *P. lucidum* some 10 mm in diameter, the stomach would be less than 1 mm long. The stomach is seen in external view in Fig. 17 and as a transparent object in Fig. 18. Basic structural elements of the stomach have been determined by dissection, but details have been elucidated by

B. MORTON AND M. H. THURSTON

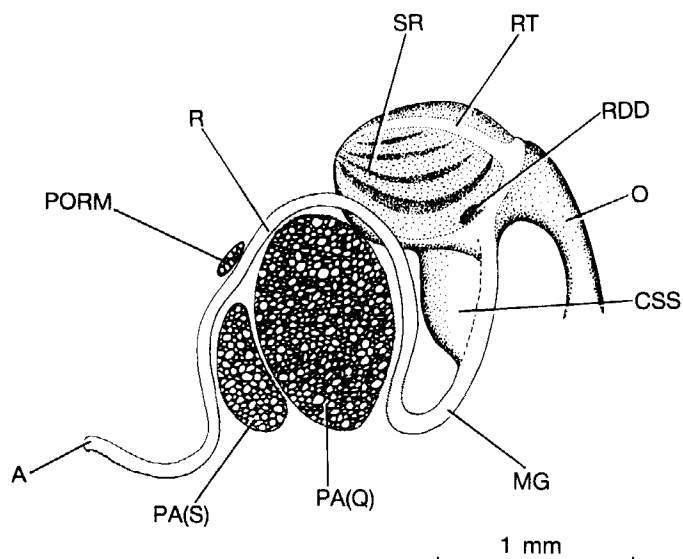FIG. 17. *Propeamussium lucidum*. A general illustration of the alimentary canal with the stomach seen in right lateral view. (For abbreviations see p. 496.).
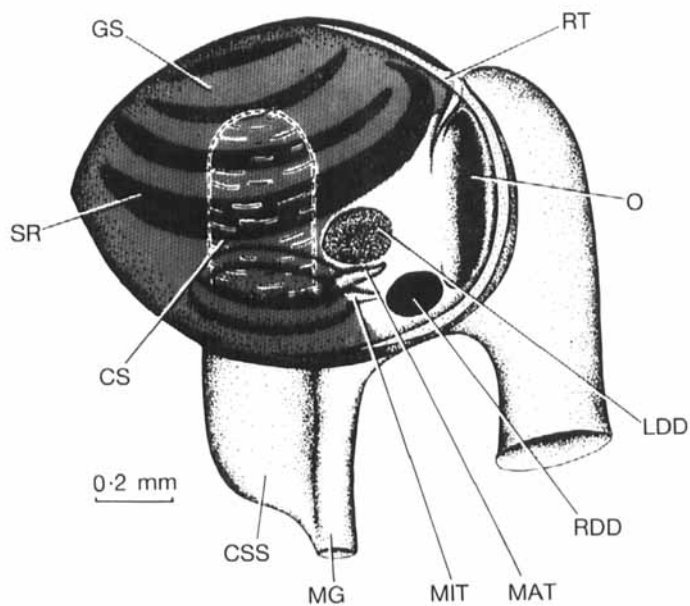
FIG. 18. *Propeamussium lucidum*. The stomach seen as a transparent object from the right side. Reconstructed from dissections and transverse sections. The stippling demarcates the extent of the gastric shield. (For abbreviations see p. 496.).

means of serial sections. Its structure is exceedingly simple. Most of the postero-dorsal and lateral surfaces of the stomach are covered by a chitinous cuticle which is the greatly enlarged gastric shield (Fig. 18, GS). Beneath this, and seen as structurally darker areas on the right side of the stomach, are a series of ridges (SR). The gastric shield borders the opening to the conjoined style sac (CSS) and mid gut (MG) and a single large opening to the digestive diverticula on the left side (LDD). Because of this latter arrangement, the opening is designated the left pouch. A second opening on the right side of the stomach (RDD) is unflanked by the gastric shield and is termed the right caecum in view of the fact that probably it represents the food-sorting caecum of the more typical pectinid. Thus, as in other pectinids (Graham, 1949; Purchon, 1957), there is no left caecum. Arising from the conjoined style sac and mid gut are two small typhlosoles both of which soon terminate on the floor of the stomach. These are the major (MAT) and minor (MIT) typhlosole remnants, each possessing a short intestinal groove which, in other bivalves, transports unwanted material to the mid gut. Passing above the opening of the oesophagus (O) into the stomach and along its right side, but also sending branches to the left and posterior aspects of the stomach, are lightly defined tracts. These are thought to be rejectory tracts (RT) that collect unwanted material and would take it to a position on the right floor of the stomach and thus into proximity with the typhlosoles and the mid gut. A small crystalline style (CS) projects into the stomach from the style sac.

Analyses of stomach contents

Twenty-six specimens of *P. lucidum* were dissected. The stomach of each was isolated and cut open and the contents were removed with a fine-bore Pasteur pipette and examined under high-power microscopy. Contents are identified in Table II. Of the 26 stomachs, nine were empty and 17 contained tissues of one kind or another. Seven individuals contained foraminiferans, five had harpacticoid copepods, two had bivalve veligers and one had eggs while five individuals had unidentified tissue in the stomach. Of the 23 identifiable prey items, 13 (57%) were foraminiferans, six (26%) were harpacticoids and four (17%) were eggs and larvae.

Comparative studies have been made on *Propeamussium permirum* and *P. hypomeces*. Twenty-six individuals of *P. permirum* provided only a single foraminiferan, but only seven out of 26 *P. hypomeces* had empty stomachs. Of the remaining 19, 12 contained benthic and planktonic foraminiferans and one radiolarian, four contained crustacean (copepod) remains, one an egg, two had bivalve veliger larvae, and another a juvenile bivalve while one had a Pentactula larva and three had unidentifiable larvae. In a total of 32 prey items, 17 (52%) were foraminiferans, seven (22%) were bivalve and other larvae, four (13%) were crustaceans, and four (13%) other categories. Sizes of these prey items were in the range 60–250 μm. One bivalve larva of 250 μm filled the stomach of the scallop which had eaten it.

Propeamussium lucidum and *P. hypomeces* are micropredators with similar diets; the former depend upon foraminiferans, harpacticoid copepods, larvae and eggs and the latter on foraminiferans, larvae and small crustaceans. Although direct evidence from stomach contents is lacking for *P. permirum*, this species shows the same adaptations for processing prey as do the other two species, suggesting that it, too, is a micropredator. It seems clear that prey items are captured individually and processed. In some cases, individual prey items occupied almost all of the stomach volume. No detritus was found in any stomach examined.

B. MORTON AND M. H. THURSTON

TABLE II

The diets of **Propeamussium lucidum**, **P. permirum** *and* **P. hypomeces**

	P. lucidum		*P. permirum*		*P. hypomeces*	
	Station	Stomach contents	Station	Stomach contents	Station	Stomach contents
1.	9131#11	Tissue remains	8976	—	10111#8	2 Foraminifera (100 μm) 2 radiolarians (60 + 80 μm)
2.	9131#11	—	8524#1	1 Foraminifera	10111#8	—
3.	9131#11	2 Foraminifera (1 benthic: 1 planktonic)	8524#1	—	10111#8	1 Foraminifera (120 μm)
4.	7975	2 Foraminifera (1 benthic: 1 planktonic)	9131#11	—	10111#8	1 egg (100 μm) 1 copepod abdomen
5.	7975	1 planktonic Foraminifera	9131#11	—	10111#8	—
6.	7975	1 bivalve veliger 1 harpacticoid	9035	—	10111#8	Crustacean remains
7.	7975	2 Foraminifera	9035	—	10111#8	Crustacean remains
8.	9541#1	—	10143#1	—	10111#8	—
9.	7432	1 harpacticoid cephalothorax	10143#1	—	10111#8	3 Foraminifera (100 μm) Crustacean remains
10.	7432	Tissue remains	10143#1	—	10111#8	1 Foraminifera (100 μm) 1 bivalve veliger (100 μm)
11.	7432	Tissue remains	10143#1	—	10111#8	1 Foraminifera (80 μm)
12.	7432	—	10143#1	—	10111#8	—
13.	10141#1	—	10143#1	—	10111#8	—
14.	10141#1	2 Foraminifera 1 allogromiid	10143#1	—	10111#8	2 ciliated larvae (160 μm) (half digested) 1 Foraminifera (60 μm)
15.	10141#1	—	10143#1	—	10111#8	1 Foraminifera (80 + 100 μm) 1 larva (half digested)
16.	10141#1	—	10143#1	—	10111#8	
17.	7711#62	—	10143#1	—	10111#8	1 Foraminifera (100 μm)
18.	8682#5	Setae	10143#1	—	10111#8	1 Foraminifera (80 μm) 1 larva (120 μm) (half digested)
19.	8682#5	Harpacticoid cephalothorax + thorax	9541#3	—	10111#8	1 Foraminifera (80 μm)
20.	8682#2	Tissue remains	9131#10	—	10111#8	—
21.	9541#3	1 harpacticoid	9131#12	—	10111#8	2 Foraminifera (200 μm)
22.	9541#3	—	9131#9	—	10111#8	2 Foraminifera (80 + 100 μm)
23.	9541#.	—	9131#9	—	10111#8	—
24.	9541#1	1 harpacticoid	9131#9	—	10111#8	1 bivalve juvenile (1000 μm)
25.	9131#12	1 bivalve larva 2 Foraminifera	8524#6	—	10111#8	1 Pentactula larva (200 μm)
26.	9131#12	1 Foraminifera 2 eggs	9035	—	10111#8	1 bivalve veliger (250 μm)

Discussion

The anatomy of the Propeamussiidae has received piecemeal attention. Shell structure is well known (Waller, 1971, 1972; Newell & Boyd, 1985) and Waller (1971) suggests that *Propeamussium* and its allies are living relicts of a group thought to have become extinct at the end of the Palaeozoic and that this group is sister to the stock which produced all other extant Pectinacea (Waller, 1978). The significance of the external prismatic layer of the right valve extending beyond the inner non-prismatic layer as a broad flexible apron, however, has not been discussed. This study suggests a number of functional roles for such a structural arrangement. First, with adduction, the marginal prismatic apron will be closely adpressed to the rigid margin of the lower valve. This creates a tight seal and offers protection against predation. A predator, biting this (and many shells show evidence of repaired marginal damage) would not obtain access to the tissues further in, as the pallial line is deeply recessed. Secondly, the flexible margin allows a smaller 'residual volume', i.e. that volume remaining at full adduction, than would two rigid valves of similar shape and size. Thayer (1972) has pointed out that for a swimming monomyarian, the critical factor governing efficiency is the volume of water which can be discharged per unit time (V/t). For maximum efficiency of a jet system, V must be increased and t reduced. The marginal seal increases 'vital capacity', i.e. the volume which can be expelled from the 'propulsion chamber' by full adduction, at the expense of residual volume, thereby enhancing propulsion. This feature, in combination with the externally smooth shell, the hydrodynamically more efficient edge-upward aerofoil shape (Thayer, 1972; Morton, 1980), and the obliquely oriented 'quick' striated portion of the adductor muscle which increases the closing velocity of the valves, suggests strongly that *P. lucidum* is a highly efficient swimmer. The extensive pallial velum further attests to this. However, the aerofoil shape of *P. lucidum* created when the right valve is adpressed against the left is the opposite of the situation found in the swimming Pectinidae, e.g. *Amusium pleuronectes* (Morton, 1980), where the right valve is the lower. Similarly in the Dimyidae (Yonge, 1978*b*), Spondylidae, Plicatulidae and *Hinnites* in the Pectinidae, cementation is by the lower right valve (Yonge, 1975). *Propeamussium* is thus quite different from all other plicatulaceans and pectinaceans in that the right valve is uppermost. Thirdly, the slow relaxation of the adductor will, with a sustained marginal seal, create a suction device within the mantle cavity, so that when the seal is broken there will be an inrush of water. This may constitute the mechanism by which *P. lucidum* feeds. Further, with prey captured, adduction will reduce the effective volume of the mantle cavity, restricting the movement of the prey and making ingestion easier. If prey capture is by the slow relaxation of the adductor muscle, it is clear that this deliberate action is incompatible with swimming, for the rapid valve movements necessary to achieve the latter would flush out captured prey.

From the evidence of Knudsen (1967), who after examining seven abyssal and bathyal propeamussiids concluded that all fed on small crustaceans (copepods, ostracods, cumaceans and isopods), and with the additional information on *P. lucidum, P. permirum* and *P. hypomeces* here examined, it seems clear that species of *Propeamussium* are predators of the meiobenthos and small epibenthic organisms (Knudsen, 1967; this study). In particular, *P. meridionale* and other propeamussiids seem to feed principally on harpacticoid copepods (Knudsen, 1970; Hicks & Marshall, 1985). Hitherto, however, no morphological evidence of predation has been found. Yonge (1981) concluded that absence of a lip apparatus in *Propeamussium* would enable small animals to enter the mouth, implying passive ingestion. This is not so. Much like the predatory verticordiid *Lyonsiella formosa* (Allen & Turner, 1974; Morton, 1984), the lips of *P. lucidum* are

formed into a capacious buccal pouch into which, we believe, captured prey is stuffed by the foot. A similar function for the foot of the Verticordiidae has been suggested by Morton (1987). In *Poromya* (Poromyidae), greatly extendable palps carry prey to the mouth (Morton, 1981). This cannot be true of *P. lucidum* where the palps are vestigial. In addition, the palps can play no role in sorting, selection and rejection of filtered food, their usual function in the Bivalvia. This possible mode of feeding is further negated by the fact that *P. lucidum* has no means of collecting such food.

Superficially, the large ctenidia seem typical structures, except that the filaments are little united one with the other and there are no interlamellar junctions. Dall (1883, 1886) thought each demibranch comprised only one row of filaments. Ridewood (1903) corrected this, but then proceeded to suggest that there was little of interest in the gills except that the ascending lamella extended only half-way up the descending lamella. This also is not true, but no one, it appears, has investigated propeamussiid ctenidial structure in further detail. As described earlier, ascending lamellae are absent and, on each side of the body, the descending lamellae of inner and outer demibranchs fuse ventrally, to create, in effect, an inside-out gill. As a consequence, the infrabranchial chamber is split into left and right remnants enclosed by the ctenidia, which in turn are surrounded by a greatly enlarged suprabranchial chamber. No filament possesses filtering cilia. The gill can have only a respiratory function. In the absence of living animals it is unknown how such a gill functions. If, in life, the filaments are functionally united, the lateral cilia will create an inward flow. This may billow or leak out. If, as seems more likely, however, the filaments and lamellae are so disunited that there is no pattern to flow, water may be circulated around each filament in a disorganized way and exchanged as a result of valve adduction. Such a structure makes it clear, however, that *P. lucidum* is not a filter feeder.

Most species of *Propeamussium* are bathyal or abyssal (Knudsen, 1967, 1970), and in these environments sediments frequently are mobile and easily resuspended. The sucking in of meiofaunal prey under these circumstances almost inevitably will be accompanied by an intake of sediment. The unique organization of the ctenidia would result in the ciliated tracts being removed from direct contact with prey organisms and sediment samples. Once the prey has been ingested, cleansing of the mantle cavity is probably not by ciliary means but by valve adduction.

Members of the Verticordiidae and Parilimyidae (Allen & Turner, 1974; Morton, 1982, 1984, 1987) are also predators, but possess normal functional ctenidia. It is thus possible that they might filter out material which could serve as additional food. This is not so in *Propeamussium*. As noted by Knudsen (1967) for the propeamussiids examined by him, and as confirmed in this study, there is never any detritus in the stomach. *Propeamussium* is a highly specialized micropredator. Final proof of this is revealed by stomach structure. The tiny stomach bears no similarity to the capacious stomachs of other pectinids or other filter-feeding bivalves (Purchon, 1957). Most of the inner surface of the stomach is covered with a chitinous gastric shield, the style is small and there are only two large openings into the digestive diverticula. Ciliary pathways are reduced to a few anterior tracts, presumably rejectory in function. Superficially there is no reason to assign the stomach of *Propeamussium* to the pectinid Type IV of Purchon (1957). It is most similar to Type II, characteristic of the septibranch anomalodesmatans (Purchon, 1956, 1960). It is probable that stomach Type II of these anomalodesmatans results from simplification of another type (IV), as a consequence of the change from filter-feeding to a predatory mode of feeding (Morton, 1982). The same applies to *Propeamussium*, in which the stomach is simplified from the pectinid plan which Purchon (1957) classifies as Type IV, and so is also of Type II. It is thus similar by convergence to that of the carnivorous Anomalodesmata, and the Type II stomach cannot have the phylogenetic significance attributed to it by Purchon (1956, 1960).

Waller (1971) has pointed out that the Propeamussiidae are primitive and perhaps related to the stock that has given rise to all other pectinaceans. This study of *P. lucidum* broadens this argument, especially with regard to ctenidial structure. As explained, the remarkable ctenidium of *P. lucidum* can be derived from the simpler conditions found in the Dimyidae and in *Heteranomia* (Anomiidae) (Ridewood, 1903; Atkins, 1936, 1937; Yonge, 1978*b*) and which Yonge designated Type B(3). The unique gill of *Propeamussium* should thus be designated Type B(4). The essential interest of this similarity, however, is that the ctenidium of *Propeamussium* creates a morphological bond not with its superficially most similar allies, the Pectinacea, but with a much more primitive group, the Dimyidae. Yonge (1975) has shown that the Dimyidae and Plicatulidae are sufficiently different from the families of the Pectinacea in terms of ligament structure to warrant erection of a new superfamily, the Plicatulacea. Indeed, the ctenidium of *Plicatula* (Yonge, 1973: fig. 16) is also dimyid-like (Yonge, 1978*b*: fig. 10). If one accepts this argument, then it is clear that *Propeamussium*, though possessing a unique ctenidium, has close links with both the Plicatulacea (in terms of gill structure) and the Pectinacea (in terms of shell form and ligament structure). Waller (1971) also points out that propeamussiid shell structure is similar to that of plicatulids, spondylids, limids and many Mesozoic pectinids. The Propeamussiidae can be regarded as the link between the superficially quite dissimilar Plicatulacea and Pectinacea, but with obvious affinity to the latter.

Propeamussium must be regarded therefore in the light of both its primitive and its highly advanced characters. The carnivorous anomalodesmatans have posed the same problem (Morton, 1987) in the possession of apparently highly specialized character traits in what are generally considered to be ancient lineages. The evidence from *Propeamussium*, however, now seems, by virtue of convergence, to support the claims of Morton (1987) with regard to the predatory families of the Anomalodesmata. These and the Propeamussiidae both seem to be descendants of primitive stocks, which have survived in the deep seas as relict groups, but which have, in adopting a predatory mode of life, evolved marvellously contrived adaptations that make them some of the most specialized and extraordinary of bivalves.

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Abbreviations used in the figures

A	Anus	MIT	Minor typhlosole
ALID	Ascending lamella of inner demibranch	MG	Mid gut
ALOD	Ascending lamella of outer demibranch	MM	Mantle margin
AU	Auricle of shell	MMF	Middle mantle fold
BA	Buccal apparatus	MO	Mouth
BN	Byssal notch	O	Oesophagus
CA	Ctenidial axis	OL	Outer lip
C-P-CONN	Cerebropleural-pedal connective	OLP	Outer labial palp
CR	'Chitinous' rod	OMF	Outer mantle fold
CS	Crystalline style	OV	Ovary
CSS	Crystalline style sac	P	Periostracum
CT	Ctenidium	PA(Q)	'Quick' (striated) component of posterior adductor muscle (or scar)
D	Denticle		
DD	Digestive diverticula	PA(S)	'Slow' (smooth) component of posterior adductor muscle (or scar)
DLID	Descending lamella of inner demibranch		
DLOD	Descending lamella of outer demibranch	PG	Pedal ganglia
F	Foot	PN	Pallial nerve
FC	Frontal cilia	PORM	Post-rectal muscle
FPA	Flexible prismatic apron	PR	Prodissoconch
GS	Gastric shield	PRM	Pallial retractor muscle
IBC(IC)	Infra-branchial chamber (internal component)	R	Rectum
		RDD	Right opening to digestive diverticula (right caecum?)
ILP	Inner labial palp		
IMF	Inner mantle fold	RT	Rejectory tract
IR	Internal rib of shell	SR	Stomach ridge
L	Ligament	ST	Statocyst
LC	Lateral cilia	STA	Statoconia
LDD	Left opening to digestive diverticula (left pouch?)	T	Tentacle
		TF	Transverse fibres
M	Mantle	VG	Visceral ganglia
MAT	Major typhlosole		