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The Functional Morphology of *Neotrigonia margaritacea* (Bivalvia: Trigoniacea), with a Discussion of Phylogenetic Affinities

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ABSTRACT. *Neotrigonia margaritacea* is one of six living Australian species of the Trigoniacea, an otherwise extinct group of Mesozoic 'cockles' which dominated shallow inshore seas worldwide. The Trigoniacea have usually been grouped with the freshwater Unionacea, each within its own order, in the sub-class Palaeoheterodonta. This taxonomic decision is largely based on hinge and shell structure, but other morphological evidence does not support such a contention, *Neotrigonia* being characterised by a lack of mantle fusion and possession of 'filibranch' ctenidia, the Unionacea by well developed siphons and 'eulamellibranch' ctenidia. Such morphological discrepancies sustain lively debate in the literature, but seem to have been resolved when the ciliary pathways on the ctenidia of both groups were described to be uniquely similar.

This study re-examines living *N. margaritacea* and investigates the histology of the ctenidia in particular, and concludes that in terms of structure and ciliary pathways, *Neotrigonia* is unique, and that its affiliations lie not with eulamellibranch bivalves but with the filibranch bivalves of the Pteriomorphia.

The myophorid origin of the Trigoniacea is undisputed, as is the widely held view that the group is terminal, i.e. it has not given rise to other bivalve lineages. It is noted, moreover, that some palaeontologists regard the Palaeoheterodonta as an artificial assemblage and the conclusion of this study supports the view that the Trigoniacea and Unionacea are not closely related. I believe the Trigoniacea to represent another line of pteriomorph evolution: perhaps sharing some remote palaeotaxodont ancestor with the Unionacea, but in no greater sense than that the same ancestors are believed to be those of probably all living bivalve groups.

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The extant Trigoniacea are the living remnants of a once diverse and populous group of Mesozoic bivalves that were widely distributed in shallow seas throughout the world, and with a centre of distribution in the Tethyan realm (Stanley, 1977). Today, they survive only in the waters of the south-west Pacific and around Australia (Fleming, 1964). Six extant species are recognised (McMichael, 1956; Habe, 1985), all belonging to *Neotrigonia*. A systematic revision of the Caenozoic Trigoniidae by Darragh (1986) suggests that *Neotrigonia* evolved from *Eotrigonia* in the Oligocene or early Miocene while *Eotrigonia* evolved from *Trigonia* s.s. in the late Cretaceous or early Tertiary. A visit to southern Australia under the auspices of the Association of Commonwealth Universities Senior Travelling Fellowship Scheme allowed examination of *N. margaritacea* (Lamarck, 1804). Because they were the most diverse and conspicuous shallow-burrowing component of near-shore marine assemblages in the Mesozoic, the Trigoniacea have received much attention from past (e.g., Lycett, 1879) and contemporary palaeontologists, e.g., Cox (1952), Fleming (1964), Newell & Boyd (1975) and Stanley

(1977; 1978). The latter author has comprehensively described the adaptive morphology of the group and its evolution.

The trigoniid shell is well known (Cox, 1952; McMichael, 1956; Taylor *et al.,* 1969; 1973; Newell & Boyd, 1975; Stanley, 1977; 1978), perhaps being the most studied of all bivalves. A wide variety of other authors, e.g., Ridewood (1903), Pelseneer (1911), Atkins (1938), White (1942), Purchon (1957), Gould (1969), Gould & Jones (1974) and Tevesz (1975), have described many aspects of tissue morphology summarised by Boss (1982), although as far as I can discover only Tevesz (1975) appears to have investigated living individuals. For reasons which will later become obvious it was decided to reinvestigate the anatomy of *Neotrigonia.*

Palaeontologists have held long debates over the Trigoniacea (Trigonioidea) and today the order is linked with the extant Unionoida (Unionacea) and the extinct Modiomorphoidea in the Palaeoheterodonta (Newell, 1969). The reasons for linkage with the Unionacea have a long, tortuous, history.

The Schizodontida, as originally defined by Steinmann (1903), included only the Trigoniacea but was extended by Neumayr (1884; 1889) to include the Unionacea (Naiadida) on the common basis of a nacreous shell, striated, schizodont hinge teeth and an unfused mantle margin. Douville (1912), however, pointed out that the similarity between these two groups is delusive, for the trigoniid tooth is not originally double as in the Unionacea, but is formed by division of a primitively simple tooth. Douville derived the Trigoniidae from the Preheterodonta by way of the Myophoridae, and most modern authors accept this, e.g., Cox (1952; 1969), Newell (1969), Newell & Boyd (1975) and Stanley (1977; 1978). The Trigoniacea are considered to be a terminal group (Douville, 1912).

The evidence of shell structure and mineralogy (Taylor *et al.,* 1969; 1973) and dentition sustain the view of linkage between the Trigoniidae and Unionacea, prompting Morris (1978, p. 268) to state that "the Unionacea are the result of separate invasions by Trigoniaceans of the non-marine habit", and Gould & Jones (1974, p. 5) to state that "The freshwater unionids are the closest living relatives of trigoniids".

Students of anatomy however, have found little evidence in support of this view. Most important evidence comes from studies of the ctenidia. On the basis of ctenidial structure, Ridewood (1903) placed the Trigoniacea in his order Eleutherorhabda (Sub-order Mytilacea), Pelseneer (1911) placed them in his order Filibranchia (Sub-order Arcacea) while Atkins (1938, p. 396) concluded that the arrangements of the ciliary tracts in the Naiadacea and Trigoniidae are "entirely different" prompting her to place the Trigoniidae in her order Filibranchia. Notwithstanding the above evidence, however, Tevesz (1975) concluded that the Trigoniacea had a gill ciliation of type D (Atkins, 1937b), hitherto believed to be uniquely possessed by the Unionacea. Such an observation seems to end the argument: the Trigoniacea and Unionacea now being linked by similarities in shell and tissue morphology and function.

This study, however, re-examines the morphology of *Neotrigonia margaritacea,* disputes the conclusion of Tevesz (1975), re-opens the discussion on trigoniid affinity with the Unionacea and comes to a number of conclusions of its own.

Materials and Methods.

Living specimens of *Neotrigonia margaritacea* were studied, during January 1985, at the Marine Science Laboratories, Queenscliff, Victoria, of the Department of Conservation, Forests and Lands of the Victorian Government, Australia. Ciliary currents were elucidated using Carmine in sea water. Subsequently I received a collection of preserved specimens of the same species dredged from 10 m in the North arm of Western Port Bay, Victoria, during 13—14 Feb 1985. These specimens, preserved in vapour-suppressed, neutral formalin, were subsequently dissected and two of them, following removal from the shell, were serially sectioned transversely and sagittally at 6 μm.

Additionally, pieces of ctenidia were removed from other specimens and sectioned transversely at 4 μm. Alternate slides of the whole animals were stained in either Ehlich's haematoxylin and eosin or Massons' trichrome. Sections of the ctenidia were additionally stained in Heidenhain's haematoxylin and light green. Specimens of *Mytilus edulis* from Great Britain, and *Barbatia virescens* and *Anodonta woodiana* from Hong Kong, have been sectioned and stained as above for comparison of ctenidial ciliation.

Abbreviations used in the figures are listed below.

A-Anus, AA-Anterior adductor muscle (or scar), APP-Anterior pedal protractor muscle (or scar), APR-Anterior pedal retractor muscle (or scar), AS-Anterior socket, AU-Auricle, C-Cilia, CA-Ctenidial axis, CD-Ciliated disc, CFC-Coarse frontal cilia, CM-Circular muscle, CR-'Chitinous' rod, CT-Ctenidium, DOG-Distal oral groove, ELFC-Eulaterofrontal cilia, E'S'-Exhalant 'siphon', FC-Frontal cilia, FFC-Fine frontal cilia, FG-Food groove, F(H)-'Heel' of foot, F(T)-'Toe' of foot, GA-Gonadial aperture, GR-Groove, H-Haemocoel, HE-Heart, ID-Inner demibranch, ILP-Inner labial palp, IMF-Inner mantle fold, I'S'-Inhalant 'siphon', K-Kidney, L-Ligament, LC-Lateral cilia, LFC-Long frontal cilia, LFP-Lateral foot papillae, LIM-lips of mouth, LM-Longitudinal muscle, LP-Labial palp, MC-Mucous cell, MFP-Median foot papillae, MLFC-Microlaterofrontal cilia, MM-Mantle margin, MF-Middle mantle fold, OD-Outer demibranch, OM-Oblique muscle, OMF-Outer mantle fold, P-Pericardium, PA-Posterior adductor muscle (or scar), PAB-Posterior aortic bulb, Palid-Point of attachment of ascending lammella of inner demibranch to visceral mass, PE-Periostracum, PEM-Pedal elevator muscle (or scar), PG-Pericardial gland, PL-Pallial line, PLFC-Prolaterofrontal cilia, PP-Papilla, PPR-Posterior pedal retractor muscle (or scar), PR-Pallial ridge, PRM-Pallial retractor muscle, PS-Posterior socket, R-Rectum, RA-Renal aperture, RPA-Renopericardial aperture, TM-Transverse muscle fibres, V-Ventricle, VM-Visceral mass

FUNCTIONAL MORPHOLOGY

Shell. There are already many substantial descriptions of fossil and Recent trigoniids (Lycett, 1879; Fleming, 1964; Newell & Boyd, 1975) and interpretations of shell morphology (Stanley, 1977; 1978). It is, however, appropriate to briefly review important features. The shell (Fig. 1) is cockle-shaped with a small external, parivincular, opisthodetic ligament (L). As noted by Stanley (1977; 1978), the trigoniid shell is unusual in that the umbones are orthogyrous — an uncommon feature among other burrowing bivalves where typically the beaks are prosogyrous. The external surface of the shell is radially sculptured with pronounced pustulose ribs forming an interlocking, scalloped margin. Taylor *et al.* (1969) have shown the shell to be aragonitic and to comprise three layers. The outer is prismatic, the middle and inner layers of lenticular and sheet nacre respectively. The hinge teeth are relatively enormous and comprise, in the right valve, two diverging, blade-like teeth that interlock with two deep and narrow sockets (AS;PS) in the left valve. The articulating surfaces of both teeth and sockets possess well developed transverse ridges and grooves (Newell & Boyd, 1975) that serve to sustain valve alignment during those times when the valves gape widely, as during leaping (Stanley, 1977; 1978). This is because the angle of gape required for burrowing (or leaping) greatly exceeds that observed for most other bivalves (Stanley, 1977; 1978). The anterior tooth and socket are each supported by a strong buttress. The pallial line (PL) is entire, simple and deeply recessed from the valve margin. The positions and arrangements of major muscle scars will be described later. Smith (1983) has shown that representatives of the Margaritiferidae, alone among the Unionacea, possess small mantle-shell attachment scars. These also occur in members of the Trigoniacea, strengthening arguments for a link between the Unionida and Trigonioida.

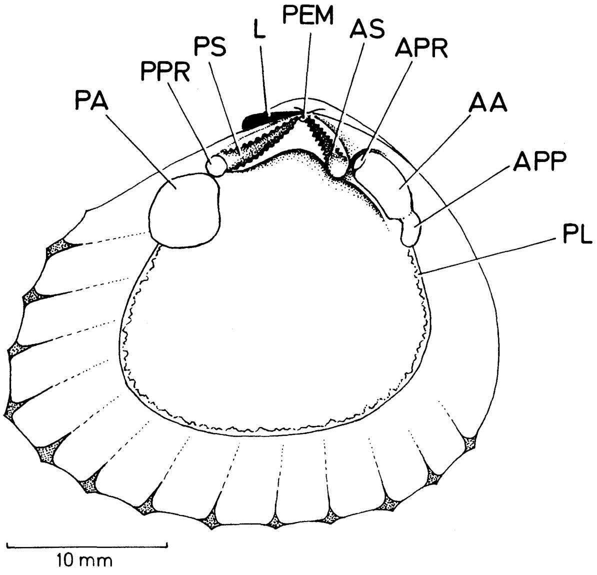

Fig. 1. *Neotrigonia margaritacea.* Internal view of left shell valve. (For abbreviations see 'Materials and Methods').

Mantle and siphons. The mantle is relatively featureless and Figure 2 shows the ventral mantle margin in transverse section. It is remarkably simple with the usual three folds (Yonge, 1957; 1982); inner (IMF), middle (MMF) and outer (OMF) — all small and of uncomplicated structure. There is an extensive haemocoel (H) between mantle epithelia. From the periostracal groove arises a thin (8 μm), single-layered periostracum (PE). The inner and middle folds possess small, presumably sensory, papillae (PP) that extend all the way around the unfused anterior, ventral and posterior margins of the mantle. The papillae of the middle fold are uniformly small and evenly distributed. Anteriorly, however, the papillae of the inner fold are modified to define two 'siphons', functionally but not morphologically delineated by pallial fusions (Fig. 3). Anteroventrally, the inner fold, demarcating the inhalant 'siphon' (I'S'), possesses three outwardly arranged rows of tentacles. In an adult specimen (i.e. of shell length 25—35 mm), there are usually seven large, ramose, tentacles. These are interspersed by a further array of eight smaller, but still ramose tentacles. Each tentacle alternates with the third, outermost, array of small papillae. This inhalant 'siphon' is functionally separated from the exhalant (E'S') by a pallial ridge (PR) (Gould & Jones, 1974). These authors conclude that when left and right mantle edges are applied to each other, the pallial ridges will be apposed, producing a firm division between inhalant and exhalant waters. The ridges are fed by branches from the posterior aorta and are probably inflated hydraulically by blood from the circulatory system — perhaps that contained within the pallial haemocoels described above. The exhalant 'siphon' is delineated by a dense array of smaller and larger papillae which extend along the anterodorsal edge of the inner folds, but also densely cover the outer surface of this fold. Anterior enlargement of the pallial retractor muscles

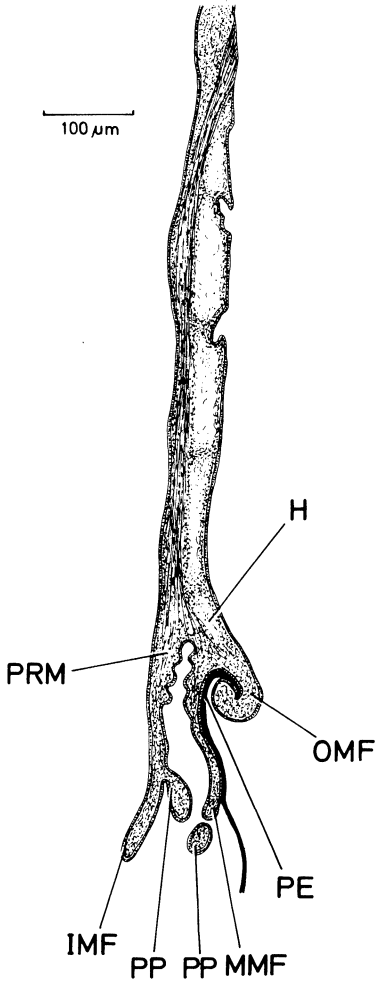

Fig. 2. *Neotrigonia margaritacea.* Transverse section through right mantle margin. (For abbreviations see 'Materials and Methods').

creates a siphonal musculature that is responsible for retracting the siphons, by inverting them, prior to valve closure.

Musculature and foot. There are anterior and posterior adductor muscles (Figs 1 and 4, AA; PA), the latter more rounded and somewhat larger than the former, which is dorsoventrally elongate. Both are located high up on the shell and internal to each is a large pedal retractor muscle (APR; PPR). The posterior is located anterodorsally to the posterior adductor; the anterior dorsally to the anterior adductor, being inserted on the anterior face of the buttress supporting the anterior hinge tooth or socket. In addition to these usual pedal muscles, there are two others. Paired anterior pedal protractor muscles (APP) are located ventral to the anterior adductor and send branches into the foot to pull it forwards. Paired pedal elevator muscles (PEM) arise from just beneath the umbones and extend into the posterior regions of the visceral mass to pull it upwards and backwards. These muscles were commented upon by Fleming (1964) and are characteristic of all Recent and extinct trigoniaceans. Fleming believed left and right pedal elevator muscles to be unequal, the left larger than the right. This, however, is not so, the illusion being created by the fact that the left muscle is more deeply inserted into the umbones behind the hinge teeth sockets of the left valve, whereas the insertion of the right is less deeply impressed by virtue of it being between the hinge teeth of the right valve.

The visceral mass and foot of *Neotrigonia* are most unusual, comprising a muscular, column-like, visceral mass which terminally expands into an anchor-like foot comprising a posterior 'heel' (Figs 4 and 5, F(H)) and an anterior 'toe' (F(T)). The anterior portion of the foot retracts closely against the visceral mass, the dorsal edge of the 'toe' fitting into a groove

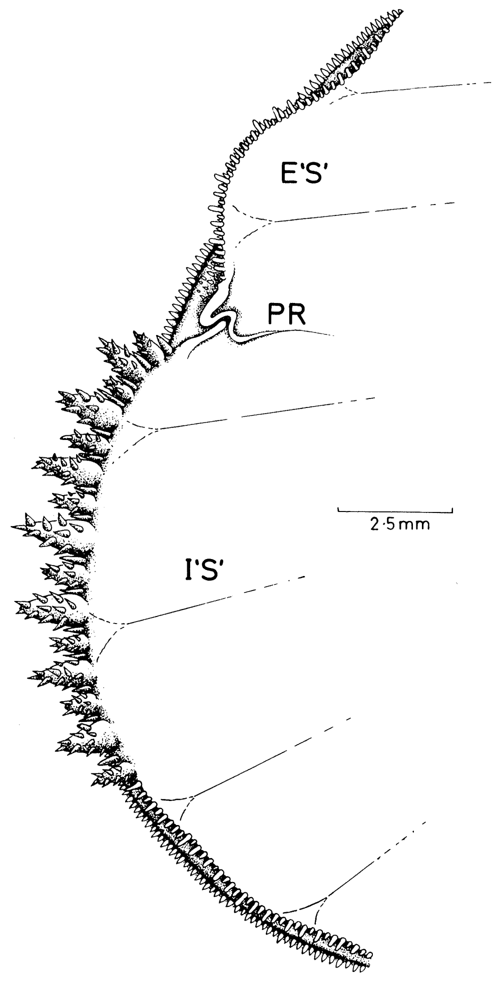

Fig. 3. *Neotrigonia margaritacea.* Left posterior mantle margin, showing inhalant and exhalant 'siphons'. (For abbreviations see 'Materials and Methods').

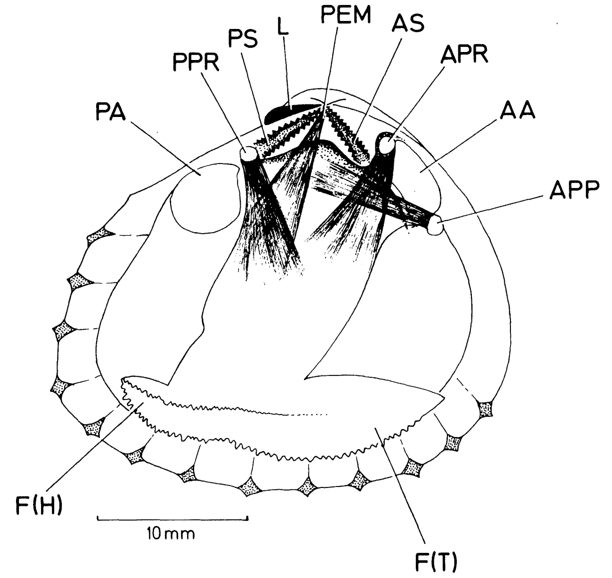

Fig. 4. *Neotrigonia margaritacea.* Visceral mass and foot, with musculature, as seen from right side. (For abbreviations see 'Materials and Methods').

(GR) on the anterior face of the visceral mass. From the posterior to the anterior, the foot is medially lined by a series of papillae (Fig. 6, MFP) which are possibly sensory. Similarly, from the posterior end a second series of lateral papillae (LFP) extend around each side of the foot to about halfway along its length. Apparently during leaping, the sole of the foot can be flattened to form a sucker-like disc, adhesion being aided by secretions from glands in the sole of the foot (Gould, 1969). Tevesz (1975) has described the burrowing sequence of *N. gemma.* Gould (1969) has described from the foot of *N. margaritacea* a small byssal apparatus which is functionless in the adult and represents the remnant of a juvenile organ, reduced by allometry.

The form of the foot in transverse section (Fig. 5) is trefoil, the medial (MFP) and lateral (LFP) series of papillae, creating this unusual shape. The musculature of the foot is complex and comprises a number of layers. Beneath the outer epithelium is a thick layer of longitudinal muscles (LM). Beneath is a layer of oblique muscles (OM) surrounding an extensive layer of circular muscles (CM) that sends fibres into the lateral and medial papillate ridges of the foot's sole. The central region of the foot, bounded by the circular muscles, is occupied by longitudinal muscles (LM) enclosing a capacious haemocoel (H). The two sides of the foot, but especially the central region of longitudinal muscles, are cross-connected by transverse muscle fibres (TM).

Such complexity of structure and, especially musculature, clearly point to an active, burrowing life style with the added capacity for leaping, possibly for defensive purposes.

Ciliary currents of visceral mass and mantle. The visceral mass is richly endowed with cilia that subserve a cleansing function (Fig. 6). Dorsally, ciliary currents sweep material forwards, but such material eventually passes downwards and then is turned posteriorly to contribute to a major rejectory tract on that region dividing visceral mass from foot. Material entering this tract passes posteriorly and eventually falls off, onto the mantle, from a point just above the 'heel' of the foot. The rejection tract is also contributed to by a few ciliary currents on the foot, but this organ is typically free of ciliary activity.

The ciliary currents of the mantle (Fig. 7) approximate those of the visceral mass. Dorsally, the currents sweep forwards but eventually material passes downwards and then is turned posteriorly to contribute to a major rejectory tract on each mantle lobe. Extending along the inner edges of the ventral mantle margins such tracts also receive material from the rejection tracts on the visceral mass. The accumulated waste material flows towards the inhalant siphon in these two streams and is expelled eventually as a pseudofaecal bolus from the ventral borders of the inhalant 'siphon'.

Ctenidia and currents. One of the most remarkable, indeed bafflingly odd, features of *Neotrigonia* are the 'filibranch' ctenidia (Ridewood, 1903; Pelseneer, 1911; Atkins, 1938). Most precisely, this refers to the fact that the individual filaments are not united ventrally with their neighbours except by opposing ciliary discs on the lateral bases of the filaments. The ctenidium is therefore filibranch, homorhabdic and

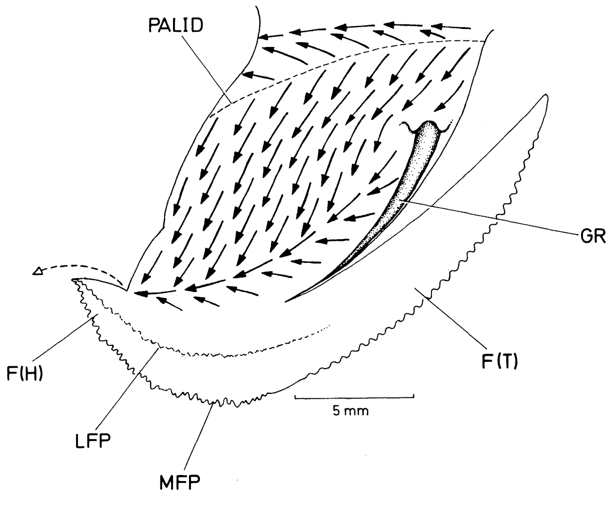

Fig. 5. *Neotrigonia margaritacea.* Transverse section through foot, showing the extensive musculature. (For abbreviations see 'Materials and Methods').

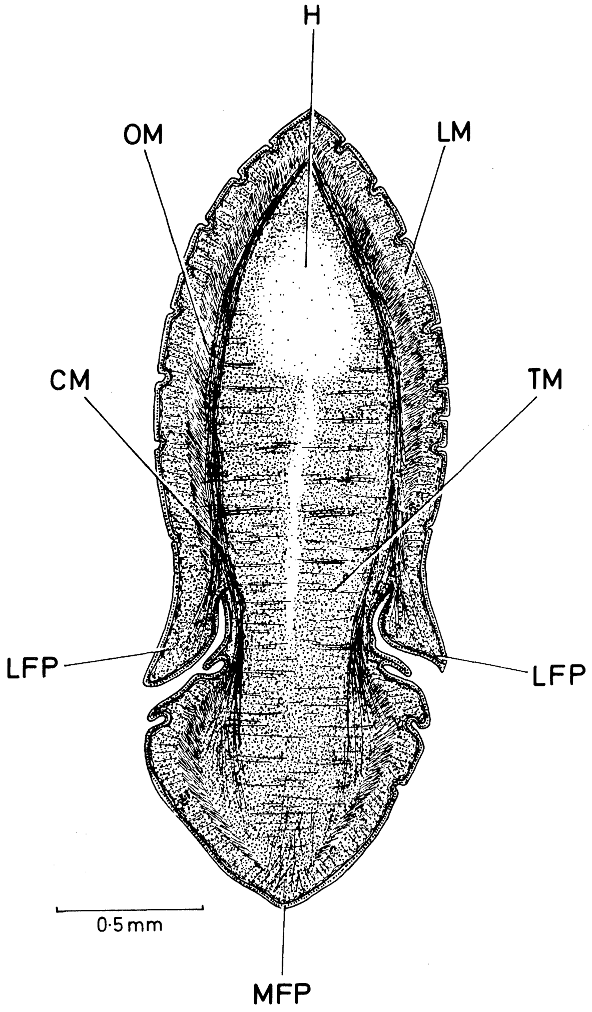

Fig. 6. *Neotrigonia margaritacea.* Visceral mass and foot, as seen from the right side and showing ciliary currents. (For abbreviations see 'Materials and Methods').

nonplicate. Each ctenidium comprises two demibranchs (Fig. 8), the outer (OD) of which is dorsoventrally shorter than the inner (ID). As in some other bivalve groups, e.g. the Arcacea, Anomiacea and Pectinacea, the ctenidia extend beyond the posterior border of the visceral mass, so that the posterior ends are free and broadly separate, with the pallial ridge separating supra- from infra-branchial chambers. The outer demibranchs are also slightly shorter anteroposteriorly than the inner so that, as will be explained, only the inner demibranchs extend into the distal oral grooves.

The upper margins of the ascending lamellae of the inner and outer demibranchs are only weakly attached to the visceral mass and mantle respectively (Fig. 9). This is the result of a delicate union of opposing cilia (C), 4—5 µm long. Such a situation is seen elsewhere only in members of the Palaeotaxodonta, Pteriomorphia (Grobben, 1900; Atkins, 1937a) the Anomalodesmata (Morton, 1985) and *Ensis* (Atkins, 1937c).

The structure of an individual ctenidial filament, first described by Ridewood (1903) and Atkins (1938), is illustrated in Figure 10. Its structure is unique in the Bivalvia with the frontal ciliation largely separated from the remainder of the filament. Closest structural similarities are with the palaeotaxodont *Nuculana* where "disposition of the cilia approaches the arrangement .... in *Trigonia* alone among Lamellibranchs" (Atkins, 1937a, p. 194). Thus, apically, the filament comprises in transverse section a rounded 'head' attached by a 'stalk' to the remainder. On the 'head' are three ciliary tracts: an apical series of cells with short (4 µm) coarse frontal cilia (CFC), flanked on either side by long (8 µm) frontal cilia (LFC). According to Atkins (1938), the 'stalk' too is ciliated with short (2—3 µm), fine frontal cilia (FFC). I, however, have had difficulty in deciding whether or not such structures are indeed cilia or microvilli, especially since the cells they arise from are not columnar, but comprise a flattened squamous epithelium. The central section of the filament comprises those cells concerned with filtration. The lateral cilia (LC) are long (12 µm) and create the flow of water between filaments. Apically from these are the cells bearing the eulaterofrontal cilia (ELFC) which are long (18 µm), with pronounced ciliary rootlets. Separating these two cell types is a mucous cell (MC). The basal component of the filament comprises cells which bear the cilia of the ciliated discs (CD). The filament is supported by distinctive 'chitinous' rods (CR), but it is significant

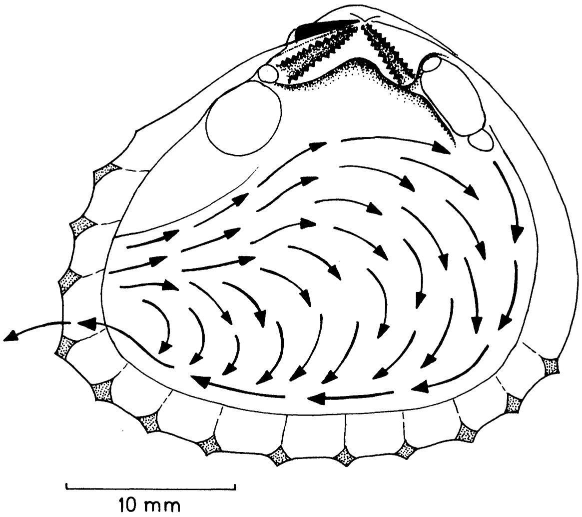

Fig. 7. *Neotrigonia margaritacea.* Mantle of left valve, showing ciliary currents. (For abbreviations see 'Materials and Methods').

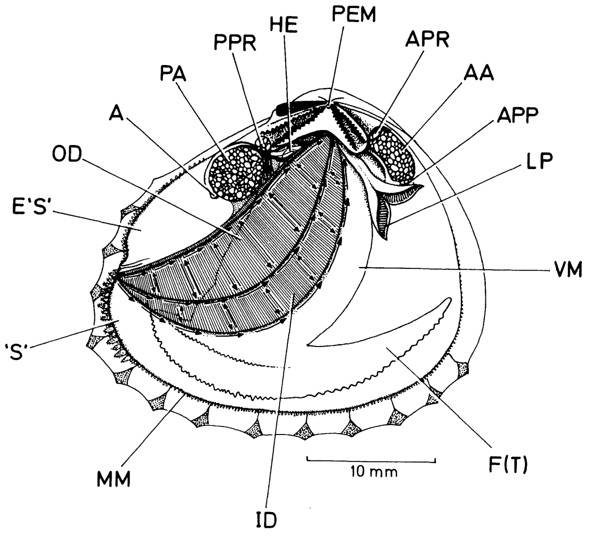

Fig. 8. *Neotrigonia margaritacea.* Internal view of organs of mantle cavity, as seen from right side and showing ciliary currents of right ctenidium. (For abbreviations see 'Materials and Methods').

that the major structural enlargement of the rods is basal, as in the Pteriomorphia (Fig. 16A and B) but not eulamellibranchs (Fig. 16C), and thus only flexibily support the central stalk and apical components of each filament. Atkins (1938) reports that the chitinous rods of *Neotrigonia* are calcified basally, as elsewhere seen only in species of the Unionacea (Ridewood, 1903). I can not differentiate such a structural difference between the 'chitinous' rods of *Neotrigonia* and other bivalves. The haemocoel that the filament encloses is richly endowed with leucocytes, and the chitinous rods are cross-connected by transverse fibres.

Importantly, Tevesz (1975) considers the ctenidial ciliation of *Neotrigonia* to be of Type D, as seen elsewhere only in the Unionacea (Atkins, 1937b). This is not so. Particles placed on the ctenidial surfaces move upwards and downwards, this being the differential function of the two types of frontal cilia on the apical 'head' of the filament. Oralward acceptance tracts are located in the ventral marginal grooves of both demibranchs, the ctenidial axis, and in the junctions of the ascending lamellae of the inner and outer demibranchs with the visceral mass and the mantle respectively. The gill ciliation (Fig. 11) is thus of Type B(1b) (ordinary filaments) and thus typical of most 'pseudolamellibranch' families, e.g. Pteriidae, Pectinidae, Limidae and Ostreidae. A similar condition defined as C(1a) (ordinary filaments) is seen in the Solenidae. In the majority of the above bivalves, however, the ctenidium is deeply plicate and up or down transfer of particles on the surface of the ctendium is the responsibility of different filaments. Only in the Arcacea and Anomiacea does the homorhabdic filament head possess differentiated ciliary tracts of coarse and fine frontal cilia resulting in the ctenidium fulfilling a particle sorting role. In these bivalves, however, the ventral marginal grooves pass material posteriorly for rejection as pseudofaeces. This type of ctenidium is defined as type B(1a) (Atkins, 1937b) and, but for the posteriorly directed ventral rejection tracts, most closely approximates the situation seen in *Neotrigonia.* Reversal of these ventral tracts, orally, would produce a ctenidium with a structure, ciliation and sorting function very reminiscent of *Neotrigonia.* Thus in terms of frontal ciliation, the ctenidium of *Neotrigonia* is most like the Arcacea and Anomiacea, but in terms of ciliary currents it is most like the Pseudolamellibranchia. I believe *Neotrigonia* to represent a unique condition, possibly intermediate between these groups of bivalves.

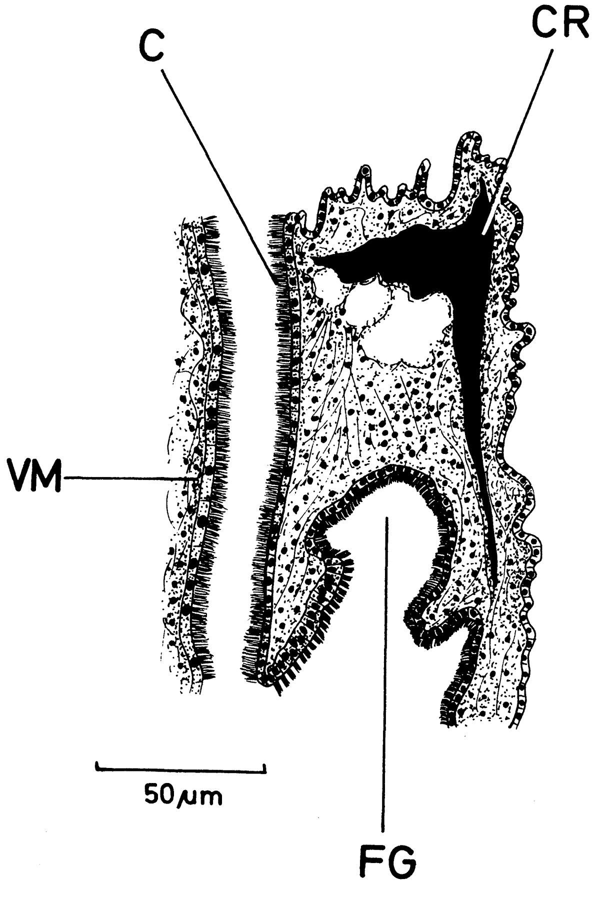

Fig. 9. *Neotrigonia margaritacea.* Transverse section through dorsal edge of right ascending lamella of inner demibranch with visceral mass showing ciliary union. (For abbreviations see 'Materials and Methods').

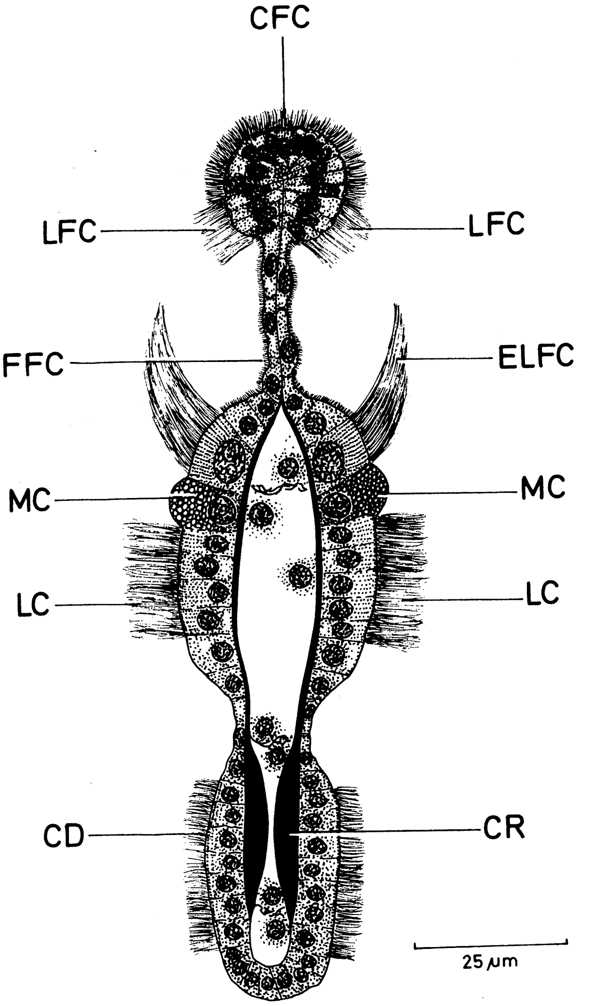

Fig. 10. *Neotrigonia margaritacea.* Transverse section through single ctenidial filament, showing arrangement of cilia. (For abbreviations see 'Materials and Methods').

Labial palps. Figure 12 is an enlarged view of the anterior end of the right ctenidium and associated labial palps. The anteriormost filaments of the inner demibranchs (ID) only extend into the distal oral groove (DOG) so that material arriving at the ctenidial terminus in the food grooves of the outer demibranch (OD) must pass onto the inner demibranch, if only briefly, before proceeding further. Such a ctenidial-labial palp junction is of Category 3, possessed by a number of other bivalve groups including members of the Pteriomorphia, Palaeoheterodonta (i.e. Unionacea), Heterodonta and Anomalodesmata (Stasek, 1963), while the forshortened outer demibranch is characteristic of the Mytilacea (Pteriomorphia) (Morton, 1987).

The distal oral grooves are long, and probably the ventral marginal food grooves of the inner demibranchs fit into them in life so that material is more effectively passed to the labial palps. The palps (ILP, OLP) are relatively small and extend as two triangular extensions of the distal oral grooves and lips of the mouth (LIM) on each side of the visceral mass just beneath the anterior adductor (AA) and anterior pedal protractor muscles (APP). Material passes down the distal oral groove and then passes onto the fused distal edges of the palps and thence between their inner faces. These comprise a series of ridges and grooves (Fig. 13) extending at right angles to the proximal oral grooves. Material reaching the inner faces either quickly passes over the crests of the ridges (if it is small and light enough) into the proximal oral groove and is accepted, or passes into the grooves between palp crests where it is subjected to a number of resorting currents and is thus either

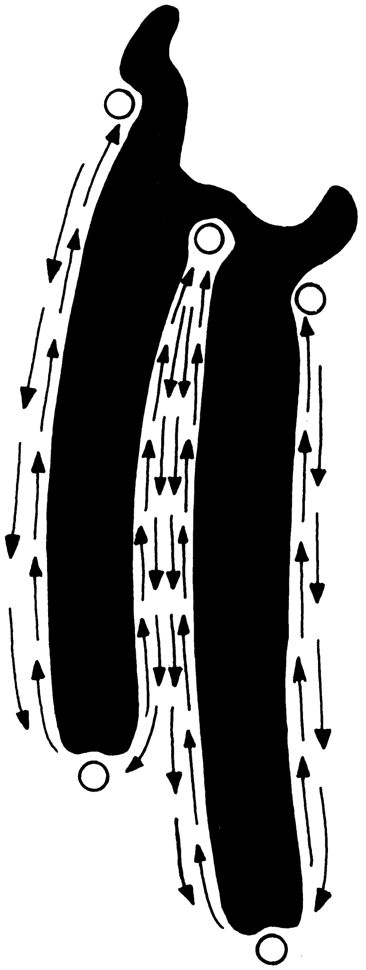

Fig. 11. *Neotrigonia margaritacea.* Diagrammatic transverse section through left ctenidium showing arrangement of ciliary currents on each lamella and the five oral food grooves (O).

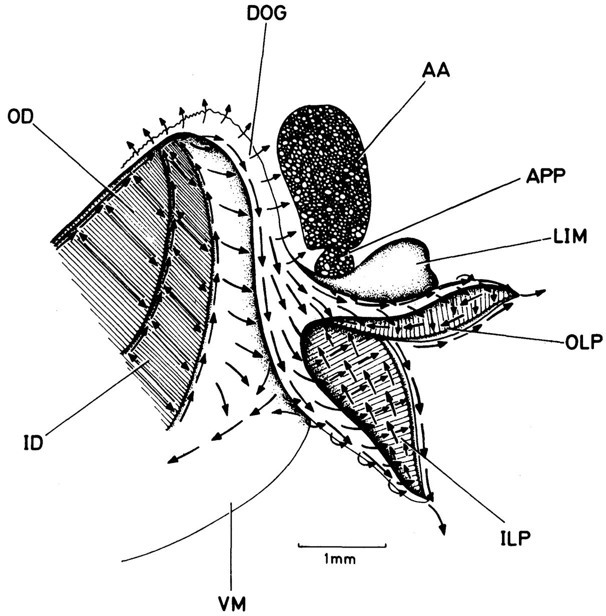

Fig. 12. *Neotrigonia margaritacea.* Detail of anterior end of ctenidium on right side and labial palps, with ciliary currents. (For abbreviations see 'Materials and Methods').

returned to the crests of the ridges or is rejected and falls into the depths of the grooves. The latter material is passed to the edge of each palp and is then transferred to the palp tip where it is rejected and becomes incorporated into the cleansing system of the visceral mass and mantle to be ultimately rejected as pseudofaeces. The palp ciliation is thus of the typical bivalve form, sustaining an important role in the sorting of material collected by the ctenidia.

Alimentary canal. The course of the alimentary tract in *Neotrigonia* has been illustrated by Gould (1969, Fig. 1), while Purchon (1957) has described the structure of the stomach and assigned it to Type 4, also possessed by representatives of the Pteriomorphia, Palaeoheterodonta (i.e. Unionacea), Heterodonta and Anomalodesmata (Purchon, 1957; 1958; 1960). Of importance are the facts that (1) the style sac and mid gut are conjoined, (2) the rectum is traversed by the ventricle of the heart, and (3) the stomach is characterised by the concentration of ducts to the digestive diverticula into three large embayments, extreme reduction of food-sorting caecum, the absence of a well developed tongue of the major typhlosole, the great development of the dorsal hood and its contained sorting areas, and the great development of the 'posterior sorting area' on the right wall of the stomach. On the basis of these structural features, Purchon (1957) considered the stomach of *Neotrigonia* to most resemble those of representatives of the Limidae, Pectinidae and Anomiidae (Pteriomorphia).

Organs of the pericardium. The structure of the pericardium of *Neotrigonia* has been briefly described by White (1942). The pericardium (Fig. 14, P) is located just beneath the posterior hinge tooth and socket. The heart comprises a single ventricle (V) with an anterior and a more pronounced, posterior aortic bulb (PAB) and is also traversed by the rectum (R). The lateral auricles (AU) are triangular and their walls and, to a lesser extent, those of the pericardium possess elements of the pericardial gland (PG). From the posteroventral margin of the pericardial cavity arise the paired renopericardial apertures (RPA) leading into the paired, light brown kidneys (K). The kidneys extend beyond the confines of the visceral mass within and above the ctenidial axis (CA). Pelseneer (1891) and White (1942) consider the kidney of *Neotrigonia* to most closely resemble that of the Arcidae.

From each kidney (Fig. 15, K) arises a renal aperture (RA) that discharges ventrally into the suprabranchial component of the mantle cavity. Just anterior to each of these is a gonadial aperture (GA) leading into the dorsally situated and paired gonads. *Neotrigonia* is dioecious.

Discussion

The Trigonioida, a group of Mesozoic 'cockles',

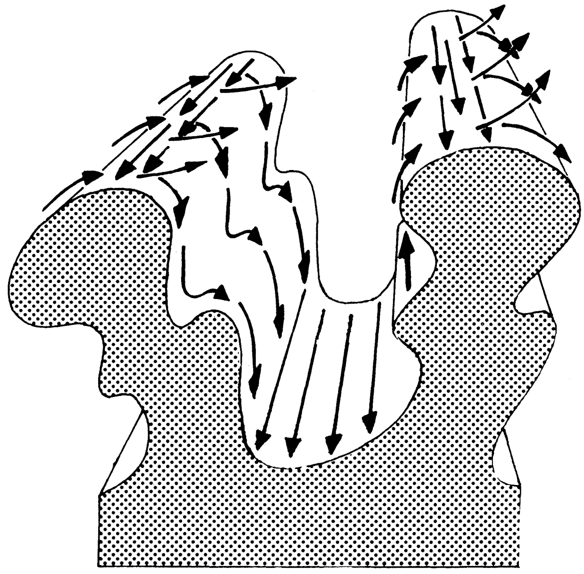

Fig. 13. *Neotrigonia margaritacea.* Diagrammatic transverse section through two palp ridges showing arrangement of ciliary tracts on various areas of their crests and grooves.

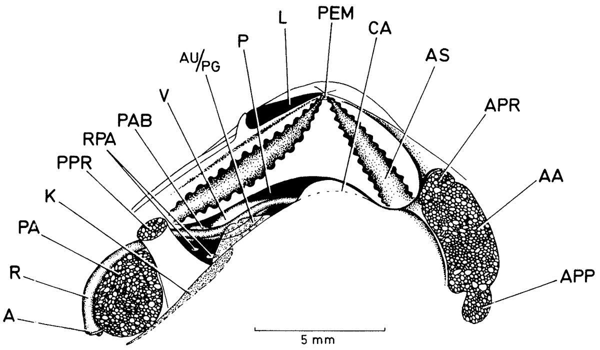

Fig. 14. *Neotrigonia margaritacea.* Detail of hinge region of the valve, showing structure of organs of pericardium. (For abbreviations see 'Materials and Methods').

survive today in Australian waters as living remnants of a once diverse and populous order and sustain lively debate in the literature. They have traditionally been located, along with the Unionoida and the extinct Modiomorphoida in the Palaeoheterodonta. Such conclusions, especially with regard to their affiliation with the Unionoida, arise because of the supposed common possession of schizodont hinge teeth (Cox, 1969), a similar shell mineralogy and microstructure (Taylor *et al.*, 1969; 1973), mantle-shell attachment scars (Smith, 1983) and similar gill ciliation (Tevesz, 1975). This relationship, especially in the light of this research, bears further discussion. First, it is worth quoting Cox (1969, p. 52) at length, with regard to the hinge teeth. "The term schizodont has little value. It was originally applied primarily to the type of dentition found in the family Trigoniidae, in which the median tooth of the left valve, one of a small number radiating from the beaks, is broad and bifid. This feature has no particular significance, as bifid teeth are found in many other groups, including many heterodonts. Forms belonging to the fresh-water superfamily Unionacea have been described as schizodont, as their dentition shows some similarity to that of the Trigoniacea, although not in this particular respect. The type of hinge found in these two superfamilies probably arose independently from the actinodont type." This argument strengthened the earlier views of Cox (1960) who thought that the Unionacea and Trigoniacea should be placed in separate orders, a view from which no student of the Trigoniacea has dissented. Newell (1969, p. 215) also believed that "The Palaeoheterodonta comprise(ing) the early actinodonts, unionaceans, and trigonaceans may be an artificial grouping". Newell concluded that the actinodonts, comprising the oldest known bivalves, may have given rise to the Pteriomorphia, Heterodonta and possibly other groups.

The second argument, that the Unionacea are more closely related to the Trigoniacea in comparison with other groups on the basis of shell mineralogy and microstructure (Taylor *et al.*, 1969; 1973), can also be questioned. These authors showed that such a shell structure is also possessed by the Anomalodesmata and, with slight variations in outer layer structure, i.e., aragonitic complex prisms or calcite simple prisms (instead of aragonitic simple prisms), by some superfamilies of the Palaeotaxodonta and Pteriomorphia respectively. Ben Mlih (1983), however, has re-examined shell structure in *Neotrigonia margaritacea* and shown that the outer layer comprises complex prisms, not simple as described for this species by Taylor *et al.* (1969). In such a case, shell structure is closest to the Palaeotaxodonta. The common possession by *Neotrigonia* and species of *Margaritifera* (Unionacea) of mantle-shell attachment scars has also been used to suggest common origins (Smith, 1983). Although the Margaritiferidae may be primitive (Smith, 1983), it is not known to what extent similar scars occur in older representatives of other phylogenies also. Third and finally, although most earlier authors (i.e. Ridewood, 1903; Pelseneer, 1911; Atkins, 1938) recognised that an important difference between the Trigoniacea and Unionacea was the filibranch and eulamellibranch ctenidia

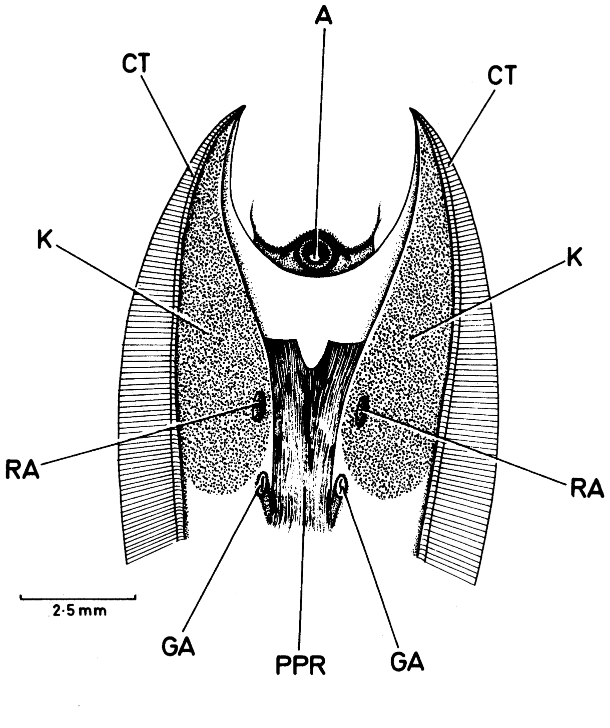

Fig. 15. *Neotrigonia margaritacea.* Ventral view of posterior ends of ctenidia, showing kidneys, anus and renal and gonadial apertures. (For abbreviations see 'Materials and Methods').

respectively, Tevesz (1975) concluded that both have a similar pattern of gill ciliation (Type D)(Atkins, 1937b). This study has shown that this is not true and that whereas ctenidial structure is most like that of *Nuculana* (Palaeotaxodonta) (Atkins, 1937a), the ctenidial currents most closely approximate type B(1b)I (characteristic of the Pteriomorphia) (Atkins, 1937b). This is not, however, because of heterorhabdy, as in many pteriomorphs, but rather because each filament has a frontal ciliation that effects sorting — a situation more reminiscent of other members of the Pteriomorphia (e.g., Arcacea and Anomiacea), albeit homorhabdic, macrociliobranch and non plicate — but nevertheless filibranch in general plan. The trigoniacean ctenidium is in fact unique in both structure and ciliation, but its affinities lie with 'filibranch' not 'eulamellibranch' grades or organization. Figure 16 compares filament structure in A, *Barbatia virescans* (Arcacea) B, *Mytilus edulis* (Mytilacea) and C, *Anodonta woodiana* (Unionacea) and from which (with comparison of Figure 10) it can be seen that *Neotrigonia* bears close similarities in terms of frontal ciliation with the Arcacea, but is macrociliobranch like *Mytilus*. The absence of inter-filamentar and inter-lamellar junctions, as in *Anodonta*, precludes close association with *Neotrigonia*, especially since all unions in the trigoniid are ciliary — features of the most primitive palaeotaxodont and pteriomorph ctenidia. In fact, Atkins (1938) thought the filament of *Neotrigonia* compared most clearly with that of *Nuculana minuta* (Palaeotaxodonta) (Atkins, 1938, p. 373, fig. 8), but to this author a more relevant comparison is with the situation in the Arcacea and Anomiacea (Type, B(1a)) but with the reversal, orally, of the currents of the ventral marginal grooves. Clearly these bivalves are reminiscent of primitive conditions in the Bivalvia, the ctenidia having a sorting function and unwanted particles being rejected from the ctenidia in the ventral marginal grooves. In all other bivalves, currents in these grooves are oral and it is clear that at some time an intermediate condition must have evolved. I believe *Neotrigonia* to be representative of such an evolutionary intermediate condition and forming a unique link between the more primitive ciliation of the Arcacea and Anomiacea and the remainder of the 'filibranch' bivalves. The importance of this, is that conditions in *Neotrigonia* are thus those which facilitated the enormous subsequent success of the modern suspension feeding Bivalvia in the Mesozoic and Caenozoic.

Importantly, Purchon (1978) has constructed a cladogram of bivalve relationships based on the multivariate analysis of nine character states. His results indicated affinity between the Trigoniacea,

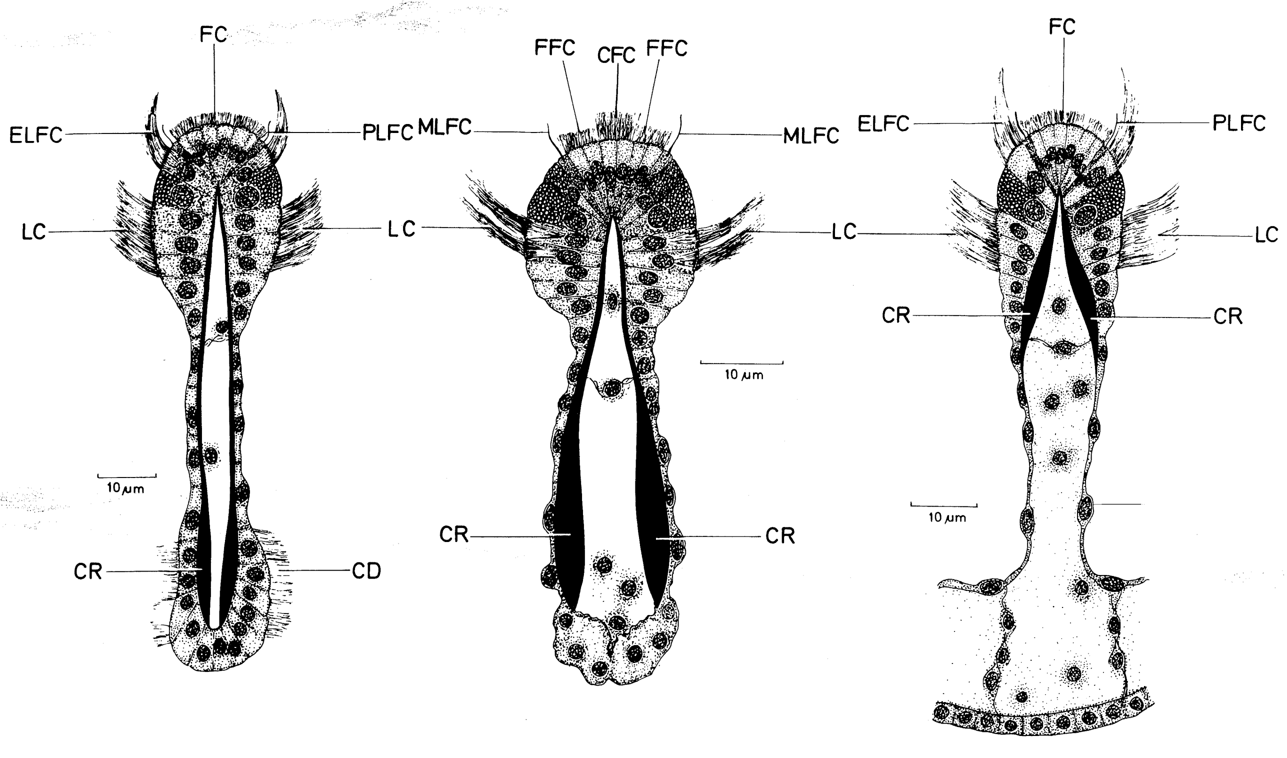

Fig. 16. Transverse section through gill filaments of **A,** *Mytilus edulis; B, Barbatia virescens* and **C,** *Anadonta woodiana.* A and C, from Hong Kong, B from Great Britain. These should be compared with Figure 10. (For abbreviations see 'Materials and Methods').

Unionacea, Lucinacea and Crassatellacea at about the 76 percentage similarity level. Despite this, Purchon (1978, p. 431) concluded that "the Unionacea and Trigoniacea should not be isolated in a subclass Palaeoheterodonta, but should be transferred into the subclass Heterodonta". Stanley (1977; 1978) has made a detailed study of the Trigoniacea and concluded that they arose from a schizodian grade ancestor (Schizodiidae) in the late Palaeozoic and radiated in the Mesozoic to produce a trigonian grade dentition via the intermediary of a myophorian grade dentition. The Trigoniacea therefore seem to represent a Mesozoic group of bivalves, related to the oldest bivalves and from which probably nearly all bivalve groups have subsequently arisen (Newell, 1969). Thus, the curious suite of morphological characters found in the Trigoniacea form a co-adaptive system that represents an alternative to the sets of characters found in other groups of burrowing bivalves (Stanley, 1977). Do the characters of *Neotrigonia* here further elucidated support this contention?

Table 1 compares *Neotrigonia* with other bivalve superfamilies on the basis of eight character states, with appropriate subcharacterisation. From this comparison it can be seen that it would be very difficult indeed to find a close living relation of *Neotrigonia.* The Trigoniacea seem to have affinities with representatives of virtually every bivalve order and if the term 'schizodont' is ignored, a close relationship with the Unionacea is not at all apparent. One wonders if the conclusions reached by Purchon (1978) would have been very different if the term 'schizodont' (a term considered delusive by Douville (1912)) had not been used in the analysis and if greater account was taken, instead, of ctenidial structure.

It is not suggested that the character states herein used all possess equal, if any, phylogenetic value. Indeed it is clear that althouth some are adaptive features (characteristic of the Trigoniacea when seen in concert (Stanley, 1977; 1978)), others are convergent and yet others simply 'bivalve' features. Thus, two adductor muscles are bivalve characters, the variation in size between groups being adaptive. Alternatively, the presence of pedal protractor muscles, but more importantly pedal elevator muscles, is an adaptive feature clearly indicative of an active foot, both for rapid burrowing and escape. This is amply exemplified by those bivalves which possess such features (e.g. the burrowing Heterodonta) which, with ventral mantle fusion, the formation of siphons and a eulamellibranch ctenidium, have greatly improved the efficiency of suspension feeding and permitted colonisation of the soft intertidal — a habitat from which the Trigoniacea, for converse reasons, were excluded (Stanley, 1968).

Generally, convergent features have been largely excluded from the analysis, there being little point in exposing similarities in overall shell form between the many 'cockle' groups (e.g. Arcacea and Cardiacea) and *Neotrigonia,* just as the triangular heteromyarian form has little significance in differentiating between those many epibyssate lineages that possess it.

Purchon (1960b) has argued that stomach structure has important phylogenetic meaning, but the similarities between that of *Neotrigonia* and a wide array of other bivalves (Table 1) suggest that structure, because the filtered material so obtained is most efficiently digested in a similar manner, may be highly adaptive too. Gill structure may also be adaptive, but nevertheless, grades of specialisation are well known (Atkins, 1938) and the clear relationship is between *Neotrigonia* and the Pteriomorphia (Table 1). Purchon (1978) confined his comparison of gill ciliation to macro- and microciliobranch conditions (Atkins, 1938). The evolution of eulaterofrontal cilia in the Bivalvia possibly has only limited phylogenetic value, being a highly adaptive character trait. Of much more value must be the combined character traits of the ctenidium, as discussed earlier.

Associated with simpler, filibranch, ctenidial ciliation is the lack of pallial fusions (Stanley, 1968) and this holds true for *Neotrigonia,* again with a clear relationship to the Pteriomorphia standing out.

The picture emerging from this study of *Neotrigonia,* therefore, is of a group of bivalves with similarities to representatives of almost every major bivalve subclass. They indeed appear to be living remnants of a myophorid stock from which probably all modern bivalve lineages arose (Newell, 1969). Just as important, however, they seem to be a group from which no other 'higher' forms have arisen (Douville, 1912). There is perhaps, in terms of shell structure, the lack of mantle fusions and gill structure, a closer relationship with the Palaeotaxodonta and Pteriomorphia. Certainly such a conclusion could not be countered by a lack of similarity in terms of shell structure or stomach structure. Almost just as certainly, a close affinity with the Unionacea becomes less convincing. This is especially significant if one accepts that the term 'schizodont' has "little value" (Cox, 1969). It is perhaps more significant than is currently realised that the secondary dentition on the hinge teeth of *Neotrigonia* were regarded by Stanley (1977; 1978) to be structures aiding valve alignment, in the absence of an extensive ligament, during wide valve gaping, perhaps during leaping. Perhaps if the term 'secondary' is applied more rigorously, i.e. that such serrations are truly secondary, adaptive features, then the already questionable argument of the significance of comparable striations on the schizodont dentition of the Unionacea becomes even less forceful. That is, this character in the Unionacea may also be adaptive, because of wide valve gaping.

Early students of the Trigoniacea, e.g. McMichael (1956), considered them to be "living fossils" as does Tevesz (1975). Stanley (1977; 1978) questioned the

Table 1. Comparison of eight *Neotrigonia* characters with those of other superfamilies of bivalves, representatives of which possess similar characters.

	Character	**Reference**	**Superfamily**	**Sub-class**	
1)	Shell structure Aragonitic, three layers Outer: Prismatic (Aragonitic simple prisms*) Middle: lenticular nacre Inner: sheet nacre *complex prisms	Taylor *et al.*, 1969; 1973.	Nuculacea	(outer layer = complex prisms)	Palaeotaxodonta
			Pandoracea Poromyacea Pholadomyacea		Anomalodesmata
		Ben Mlih, 1983	Mytilacea Pinnacea Pteriacea	(outer layer = Calcite simple prisms)	Pteriomorphia
			Unionacea	(outer layer = Aragonitic simple prisms)	Palaeoheterodonta
2)	Hinge teeth Schizodont	Cox, 1952; 1969; Newell, 1969; Newell & Boyd, 1975	Unionacea	Palaeoheterodonta	
3)	Ligament parivincular, opisthodetic	Trueman, 1969	Solemyacea	Cryptodonta	
			Mytilacea Pinnacea Pteriacea	Pteriomorphia	
			Unionacea	Palaeheteodonta	
			Lucinacea Crassatellacea Cardiacea Mactracea Solenacea Tellinacea Dreissenacea Glossacea Veneracea Myacea Pholadacea	Heterodonta	
			Poromyacea Verticordiacea Pholadomyacea Pandoracea Clavagellacea	Anomalodesmata	
4)	Musculature a) Equal adductors, pedal retractors + anterior pedal protractors	Various authors	Unionacea	Palaeoheterodonta	
			Arcacea	Pteriomorphia	
			Lucinacea Leptonacea Gastrochaenacea	Heterodonta	
	b) pedal elevator muscles	Pelseneer, 1911	Tellinacea Cardiacea Mactracea Solenacea Gastrochaenacea	Heterodonta	
5)	Mantle fusions None	Yonge, 1957; 1982	Nuculacea	Palaeotaxodonta	
			Arcacea Limopsacea Pinnacea Pteriacea Pectinacea Anomiacea Limacea Ostreacea	Pteriomorphia	

6) Ctenidia			
a) filibranch	Ridewood, 1903; Atkins, 1938	Arcacea	Pteriomorphia
		Limopsacea	
		Mytilacea	
		Pteriacea	
		Pectinacea	
		Anomiacea	
b) homorhabdic/non plicate	Atkins, 1938	Arcacea	Pteriomorphia
c) Posterior ends of ctenidia unattached	Various authors	Arcacea	Pteriomorphia
		Limopsacea	
		Pteriacea	
		Pectinacea	
		Anomiacea	
		Limacea	
		Ostreacea	
d) Ciliary fusion of dorsal edge of ascending lamellae to visceral mass or mantle	Atkins, 1937a,c; 1938	Nuculacea	Palaeotaxodonta
		Anomiacea	Pteriomorphia
		Pteriacea	
		Pinnacea	
		Arcacea	
	Morton, 1985	Pholadomyacea	Anomalodesmata
		Pandoracea	
		Thraciacea	
		Clavagellacea	
e) Gill ciliation, type B(1b)	Atkins, 1937b	Pteriacea	Pteriomorphia
		Pectinacea	
		Limacea	
		Ostreacea	
f) Macrociliobranchia	Atkins, 1938	Nuculacea	Palaeotaxodonta
		Nuculanacea	
		Solemyacea	Cryptodonta
		Mytilacea	Pteriomorphia
		Ostreacea	
		Unionacea	Palaeoheterodonta
		Lucinacea	Heterodonta
		Leptonacea	
		Crassatellacea	
		Cardiacea	
		Mactracea	
		Solenacea	
		Tellinacea	
		Dreissenacea	
		Arcticacea	
		Corbiculacea	
		Veneracea	
		Myacea	
		Gastrochaenacea	
		Hiatellacea	
		Pholadacea	Anomalodesmata
		Pandoracea	
		Thraciacea	
		Pholadomyacea	
		Clavagellacea	
7) Ctenidial/labial palp junction			
Category I	Stasek, 1983	Nuculacea	Palaeotaxodonta
		Mytilacea	Pteriomorphia
		Unionacea	Palaeoheterodonta
		Crassatellacea	Heterodonta
8) Stomach structure			
Type IV	Purchon, 1957; 1958; 1960a	Pectinacea	Pteriomorphia
		Anomiacea	
		Limacea	
		Unionacea	Palaeoheterodonta
		Carditacea	Heterodonta
		Crassatellacea	
		Gastrochaenacea	
		Hiatellacea	
		Pandoracea	Anomalodesmata
		Clavagellacea	
		Thraciacea	

validity of this term in defining a group of Mesozoic bivalves with living representatives, that would, but for unknown extinction forces, constitute an important ecological group in near shore habitats world wide. Semantics aside, however, it would seem to this author that the term 'living fossil' might be appropriately applied to the Trigoniacea, because as this study suggests they possess many remarkable characters which in combination must reflect very early bivalve features. Notable among these are the ctenidial ciliation and the lack of pallial fusions. So early, in fact, that their ancestors, the Myophoridae, have been viewed as the stem group for perhaps most of today's living members of the Bivalvia. If this is so, then the Trigoniacea are 'living fossils', closely allied with the extinct Myophoridae and Modiomorphida, sharing shell and ctenidial features with the Palaeotaxodonta, but just as importantly having a clear affiliation with the Pteriomorphia. The Unionacea, as Purchon (1978) points out, might be linked to the Heterodonta. This suggestion needs further investigation, but the essential conclusion this study reaches is that the Trigoniacea seem to represent another line of pteriomorph evolution, perhaps sharing some remote palaeotaxodont ancestor with the Unionacea, but in no greater sense than that the common ancestors of the two were probably also the ancestors of most other living bivalves.

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Errata

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Colour frontispiece: Caption C refers to Figure D.
Caption D refers to Figure C.

p. 283, Insert after 1st paragraph, Column 2: **Distribution.** Japan, South China Sea, north-western Australia to Queensland, Lord Howe Island, Malaysia, 55–270 m.

p. 330, 2nd column, ref. Wicksten & Mendez, last line read: the Eastern Pacific Ocean. Bulletin of the Southern California Academy of Sciences 8(3): 106–120.

p. 333, 1st column, line 4, Barker & Grigg, 1977 read: Grigg & Barker, 1977

p. 334, 1st column, line 17, Barker & Grigg, 1977 read: Grigg & Barker, 1977

p. 337, References, reference 2, Barker & Grigg, 1977 read: Grigg & Barker, 1977

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p. 343, figure caption Figure 5 refers to Figure 6 (p. 344)

p. 344, figure caption Figure 6 refers to Figure 5 (p. 343)