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## Aspects of the Adaptive Morphology and Evolution of the Trigoniidae [and Discussion]

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## Aspects of the adaptive morphology and evolution of the Trigoniidae

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[Plates 1 and 2]

During the Jurassic and Early Cretaceous, the Trigoniidae were the dominant family of shallow-burrowing bivalves of warm, shallow seas. *Neotrigonia* is the only genus that survives today.

Judging from the biology of *Neotrigonia* and the functional morphology and occurrence of extinct genera, the Trigoniidae represent an advanced family of burrowing Bivalvia. The family has been characterized by efficient locomotion, owing in large part to the presence of an unusually muscular foot, resembling that of the living Cardiidae. Other unusual features of the Trigoniidae relate to the presence of the foot. Complex hinge teeth with secondary dentition evolved to maintain valve alignment at the wide angles of gape required for extrusion of the foot. Myoporous buttresses evolved to support the large anterior hinge teeth. These anterior features seem to have obstructed the evolution of a prosogyrous shape of the kind that facilitates burrowing within many other bivalve taxa. Alternatively, there evolved in the Trigoniidae various kinds of external shell ornamentation that aided in burrowing. Thus, the many unusual morphological features of the Trigoniidae have been strongly coadaptive.

The Mesozoic Trigoniidae seem to have been more advanced animals than any shallow-burrowing, suspension-feeding bivalves of the Palaeozoic and also than certain successful living groups with similar modes of life. Though slightly less advanced than the Cardiidae, they can be regarded as the cockles of the Mesozoic. Had the group not suddenly been decimated by environmental deterioration at the end of the Mesozoic, it would undoubtedly flourish today. *Neotrigonia* has, in fact, speciated at a high rate in comparison with other living genera of bivalves. A relatively recent origin and lack of primitive features disqualify *Neotrigonia* from status as a living fossil genus. It is the sole survivor of its family, but an advanced and modern animal nonetheless.

### INTRODUCTION

The Trigoniidae, formerly grouped within the single genus *Trigonia*, have long held great interest for the palaeontologist and malacologist, in part because the group exhibits unusual morphological features, and in part because in 1802 a living species of trigoniid was found, proving the group to be extant when it had long been considered to have died out at the end of the Cretaceous Period.

In the present contribution, which is in part a summary of a more detailed analysis (Stanley 1977*a*), I will focus upon two aspects of the evolutionary history of the Trigoniidae. The first is the significance of the unusual morphological features of the group. It will be shown that these structures represent a unique coadaptive complex: a peculiar set of interlocking adaptations that differ from adaptations that perform similar functions in other taxa. The second matter to be emphasized is related to the first. It will be argued that the trigoniids, though primarily Mesozoic in temporal distribution, are not a primitive group of bivalves; the

designation of *Neotrigonia* as a genus of 'living fossils' is inappropriate. It will be concluded that *Neotrigonia* in particular and the Trigoniidae in general are quite advanced taxa that would flourish today had they not suffered an untimely mass extinction.

#### UNUSUAL FEATURES OF THE TRIGONIIDAE

All living species of the Trigoniidae are assigned to the genus *Neotrigonia* – (figures 1–8†). While *Neotrigonia* is in certain ways atypical of the Trigoniidae, it displays certain features that offer insight into the evolution of the family. The number of valid species within *Neotrigonia* is a matter of debate, but Deschet (1966) judged that there are more than five living species and three or four currently recognized extinct ones.

The remarkable ability of *Neotrigonia* to leap was noted long ago (Woodward 1851). This behaviour is clearly made possible by the large muscular foot. This foot resembles that of the cockles, which leap in a similar manner (Stanley 1970), but has a distinct posterior 'heel' (figures 6–8) not present in cockles. The unusual foot also endows *Neotrigonia* with the capacity for efficient burrowing. In comparison with other burrowing bivalves (Stanley 1970) *Neotrigonia* is a moderately rapid burrower (Tevesz 1975; Stanley 1977). This is unusual for a filibranch animal lacking siphons. All other non-siphonate suspension-feeding genera whose habits I have studied are more sluggish burrowers. These include *Anadara* (Anadarinae), *Noetia* (Noetiidae), *Glycymeris* (Glycymeridae), *Astarte* (Astartidae), *Eucrassatella* (Crassatellidae), and *Venericardia* (Carditidae).

Another distinctive feature of *Neotrigonia*, shared by all members of the Trigoniidae but a few early species, is massive hinge dentition in which transverse ridges lie along the articulating surfaces of the primary teeth (figure 2). These ridges will be referred to herein as secondary dentition.

*Neotrigonia* also differs from typical burrowing bivalves in being essentially orthogyrous (having beaks that point neither appreciably forward nor appreciably backward). The forward-directed (prosgyrous) beaks of most burrowing bivalves produce a blunt anterior region

#### DESCRIPTION OF PLATE 1

FIGURE 1. Left lateral view of *Neotrigonia margaritacea* (Lamarck).

FIGURE 2. Hinge teeth of *N. margaritacea* (magn.  $\times 2.1$ ).

FIGURE 3. Myophorous buttresses (arrows) of *N. margaritacea* (magn.  $\times 1.25$ ).

FIGURE 4. Hydroids attached to the posterior end of a live specimen of *N. margaritacea* figured in life orientation. Collected at Westernport, Victoria, Australia (magn.  $\times 0.9$ ).

FIGURES 6, 7 AND 8. Pedal extrusion and leaping of *N. margaritacea* (natural size).

FIGURES 9 AND 10. Right lateral and anterior views of *Eotrigonia subundulata* (Jenkins). B.M.N.H. ‡ L42330 (magn.  $\times 1.4$ ).

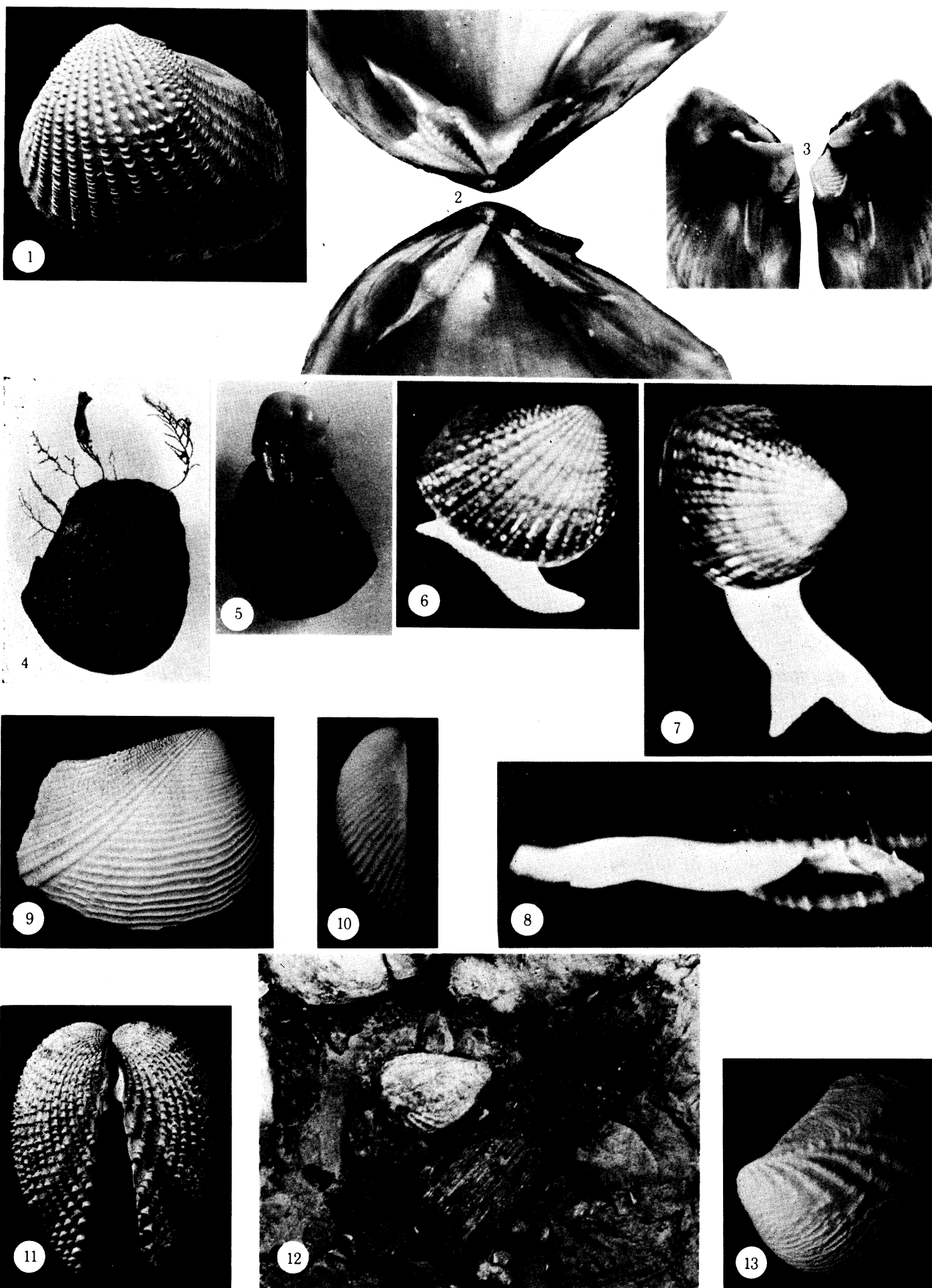
FIGURE 11. Anterior view of gaping valves of the cardiid *Trachycardium egmontianum* (Shuttleworth), showing lateral teeth (natural size).

FIGURE 12. Bedding surface of the Peak Shales at Ravenscar, Yorkshire, showing oblique dorsal view of *Vaugonia* (*V.*) *literata* (Young & Bird) preserved in life position, adjacent to a piece of carbonized wood (magn.  $\times 0.7$ ).

FIGURE 13. Left lateral view of *V. (V.) literata* in life orientation (magn.  $\times 0.75$ ).

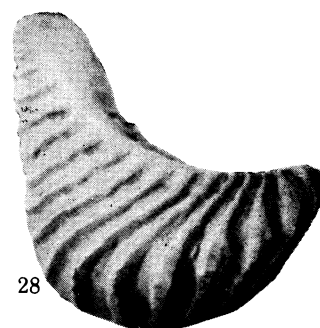
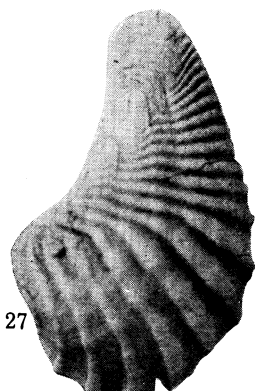
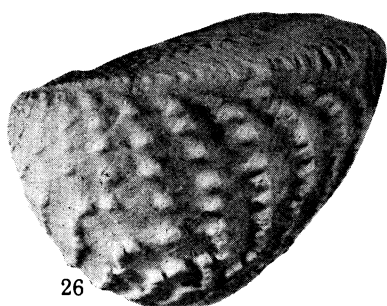
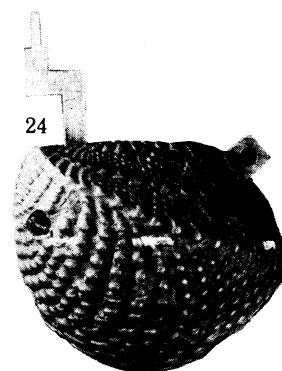
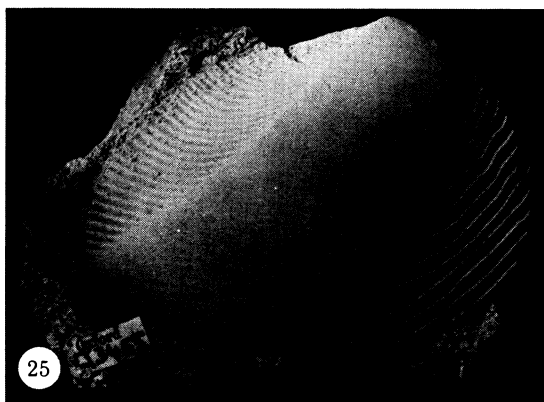
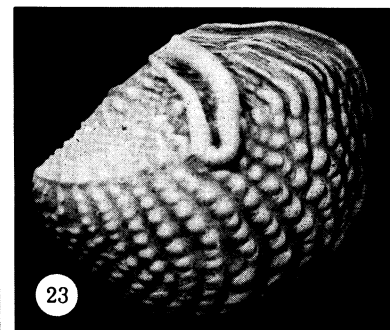
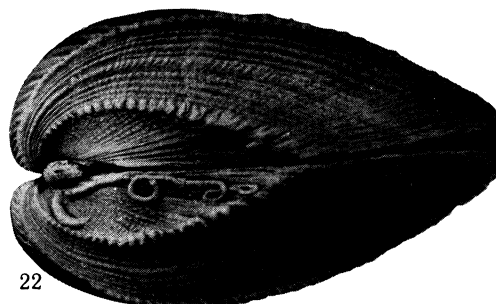
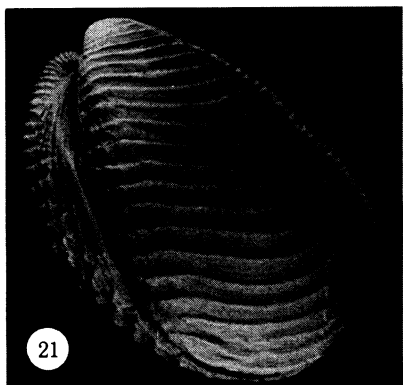
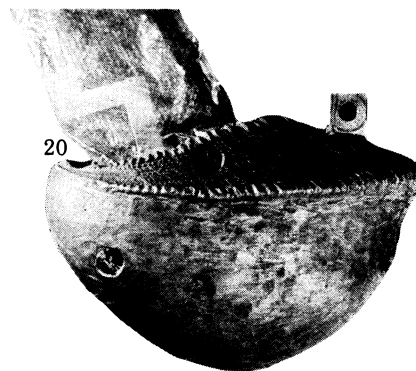
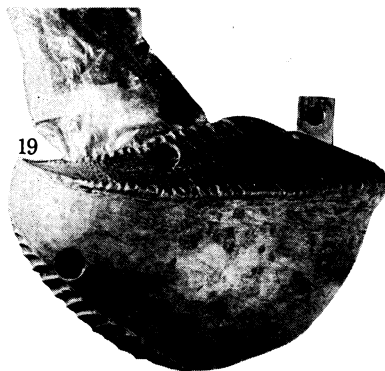
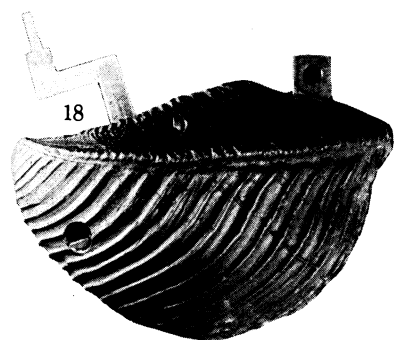
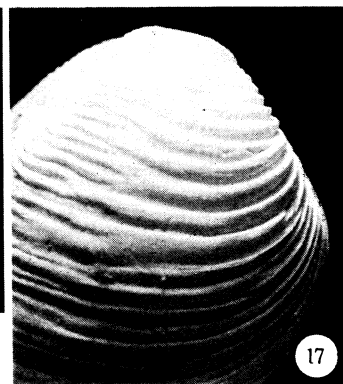
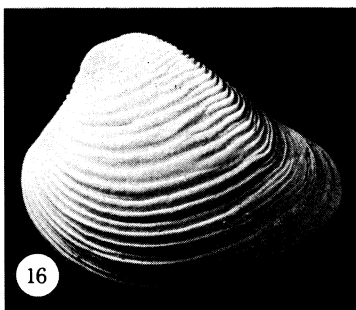
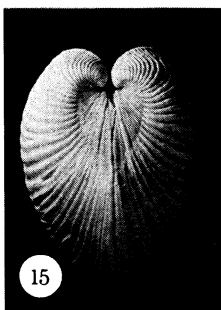
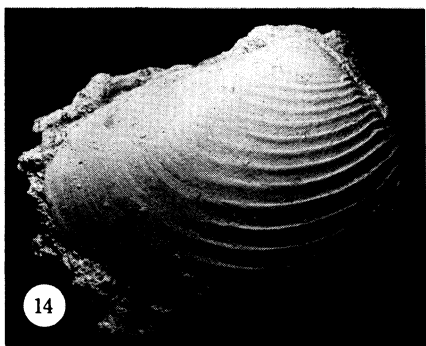
† Figures 1–13 appear on plate 1 and figures 14–28 on plate 2.

‡ British Museum (Natural History).



FIGURES 1-13. For description see opposite.

(Facing p. 248)



FIGURES 14–28. For description see opposite.

consisting of broad umbones and a central lunule. When forced against the sediment during backward rotation of the shell in burrowing, this region tends to lock in place instead of slipping upward. The result is a larger downward step than would be taken in the absence of the blunt anterior. Thus the prosogyrous condition aids a typical bivalve in burrowing (Stanley 1975). Nearly all fossil genera of the Trigoniidae are either orthogyrous, like *Neotrigonia* (figure 1), or opisthogyrous, having beaks that are directed posteriorly (figures 18, 27 and 28). In fact, the incidence of the opisthogyrous shape in the Trigoniidae is unequalled within any other major family of burrowing bivalves. This anomalous condition deserves evaluation.

The variety of bizarre patterns of external ornamentation on trigoniid shells is also unparalleled in other large families of burrowing bivalves. Many of the patterns are markedly discordant with respect to concentric and radial features of trigoniid shells. Some consist of ridges, some of knobs or short spines, and others of combinations of these structures (figures 13, 16, 18, 23, 25, 26, 27 and 28).

#### BRIEF EVOLUTIONARY HISTORY

For the most part, the Trigoniidae represent a Mesozoic taxon (figure 29). They arose from Palaeozoic trigoniaceans that generally possessed small, externally smooth shells with hinge teeth of moderate size that lacked secondary dentition. Traditionally, the Trigoniidae were defined on the basis of complex dentition, but Newell & Boyd (1975) concluded that the secondary dentition of trigoniids arose polyphyletically (figure 30). They concluded that dentition cannot be used as a key feature in classification, and they relied instead upon gross shell

#### DESCRIPTION OF PLATE 2

- FIGURE 14. Right lateral view of *Rutitrigonia dunscombensis* (Lycett) collected from the Cenomanian Wilmington Sands at Hutchins Quarry (Waterworks Pit), Wilmington, South Devon (magn.  $\times 1.2$ ).
- FIGURES 15 AND 16. Anterior and left lateral views of the venerid *Anomalocardia brasiliana* (Gmelin), from Mayaguez, Puerto Rico (magn.  $\times 1.25$ ).
- FIGURE 17. Oblique posterior view of *A. brasiliana*, showing asymmetric ridges resembling those of *Rutitrigonia* (magn.  $\times 2$ ).
- FIGURES 18, 19 AND 20. Left lateral views of three aluminium-filled epoxy robots of *Trigonia papillata* (Agassiz), one in the unaltered state, one with ornamentation removed from the flanks, and one with all ornamentation ventral to the carina removed (robots of figures 18 and 19 retain polyethylene boots that excluded sand from dorsal openings from which rods projected for application of forces). (magn.  $\times 0.55$ ).
- FIGURE 21. Oblique anterior view of *T. papillata* showing dorsal steepening of ribs where they pass from the flank to the anterior of the valve. Mus. Nat. Hist. Nation. (Paris) 1899–20 (magn.  $\times 0.7$ ).
- FIGURE 22. Dorsal view of the specimen of figure 21, showing the tube of a serpulid worm that apparently grew along the exposed commissure of the living bivalve (magn.  $\times 0.7$ ).
- FIGURE 23. Left lateral view of *Yaadia nodosa* (Sowerby) showing the tube of a serpulid worm that seems to have grown from the posterior of the partly buried living bivalve downward to the sediment surface and then upward again. B.M.N.H. 47213 (magn.  $\times 0.5$ ).
- FIGURE 24. Left lateral view of robot of *Y. nodosa* with original ornamentation intact (magn.  $\times 0.5$ ).
- FIGURE 25. Right lateral view of *Psilotrigonia beesleyana* (Lycett) (natural size).
- FIGURE 26. Left lateral view of *Myophorella clavellata* (Sowerby) in inferred living orientation. B.M.N.H. 51029 (magn.  $\times 0.6$ ).
- FIGURE 27. Left lateral view of *Megatrigonia conocardiiiformis* (Krauss) in inferred living orientation. B.M.N.H. LL13601 (magn.  $\times 0.85$ ).
- FIGURE 28. Right lateral view of *Pterotrigonia etheridgi* (Lycett) in inferred living orientation. B.M.N.H. 83698 (magn.  $\times 0.6$ ).

form and pattern of external ornamentation, which seem to be conservative evolutionary features within particular clades. In their new classification, one Permian genus, *Lyroschizodus*, is assigned to the predominantly Mesozoic family. This genus and a small number of Triassic genera lack what Newell & Boyd (1975) term the trigonian grade of dentition, characterized by large primary teeth bearing secondary dentition. All lineages of the Trigoniidae that made the transition into the Jurassic, however, seem to have possessed dentition of the trigonian

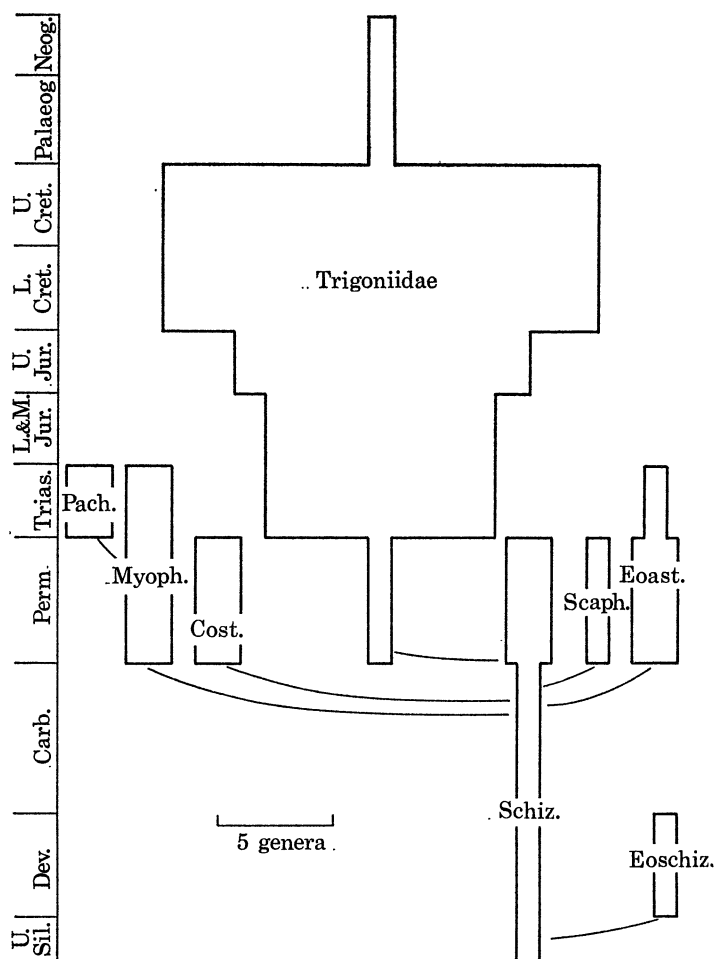


FIGURE 29. Changes in diversity of the Trigoniidae at the genus level. Families represented: Pachycardiidae, Myophoriidae, Costatoriidae, Schizodiidae, Scaphellinidae, Eoastartidae, Eoschizodidae. Familial taxonomy from Newell & Boyd (1975). Generic data from Moore (ed. 1969) and Newell & Boyd (1975).

grade. During the Mesozoic, the trigoniids radiated to become the dominant family of shallow-burrowing clams in nearshore habitats of Jurassic and Early Cretaceous Tethyan seas. In the Late Cretaceous the family suffered a mass extinction so severe that there survived perhaps only a single lineage, consisting of or giving rise to the Cainozoic genus *Eotrigonia* (figures 9 and 10). Apparently *Neotrigonia* diverged from *Eotrigonia* in the mid-Cainozoic. Both *Eotrigonia* and *Neotrigonia* are distinct in form from nearly all Mesozoic genera. Of currently recognized Mesozoic forms, *Mesotrigonia* from the Upper Cretaceous of New Caledonia seems most similar to *Eotrigonia* and may be an immediate ancestor or close relative (Frencix 1958).

A few years ago I suggested that typical Mesozoic trigoniids were more adept in locomotion

than virtually all suspension feeding, burrowing bivalves of the Palaeozoic and that their radiation represented part of a general post-Palaeozoic expansion of the bivalve adaptive zone into habitats characterized by shifting substrata that were inaccessible to sluggish burrowers of the Palaeozoic (Stanley 1972). This conclusion was based in part on personal collection of British trigoniids from 25 Jurassic and Cretaceous sedimentary units, 21 of which consist of grain-supported sediments dominated by particle sizes in the sand range (Stanley 1977a).

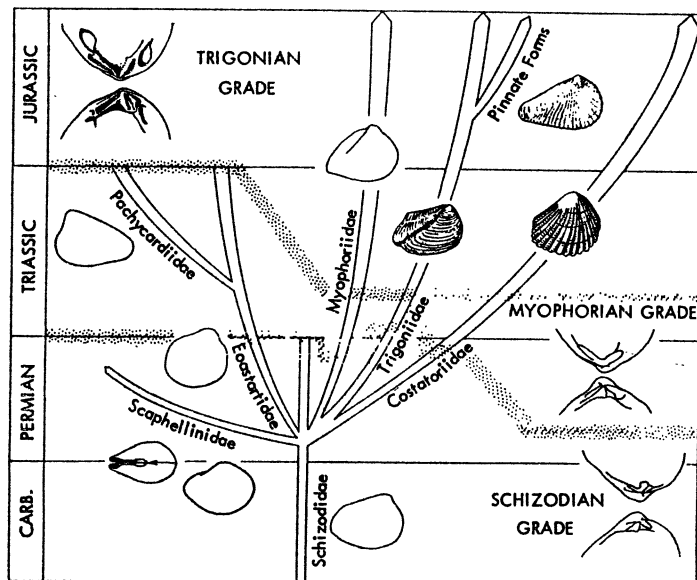


FIGURE 30. Morphological divergence of the Trigoniacea, showing polyphyletic origin of advanced grades of dentition. The trigonian grade, representative of post-Triassic members of the Trigoniidae, is shown as having arisen in three separate lines of descent. From Newell & Boyd (1975).

Nearly all of the occurrences are in substrata that clearly accumulated at water depths no greater than 10–15 m. The conclusion, based on work in Britain, that Mesozoic trigoniids were restricted to shallow water, is corroborated by reports of occurrences in North America (Scott 1975; Wright 1974; Poulton 1976; Stanley 1977a). In contrast, populations of *Neotrigonia* commonly occur at depths ranging from 70 m to more than 100 m (McAlester 1965; Deschet 1966; Tevesz 1975). Thus the habitat of *Neotrigonia* is unrepresentative for the family. As noted by various workers (McAlester 1965; Tevesz 1975; Stanley 1977a) the posterior margin of the shell of *Neotrigonia* in life position lies horizontal, at or above the sediment surface. That this orientation typified extinct trigoniids as well is suggested by the flattened shape of the posterior margin of the shell (Seilacher 1954; Stanley 1970), by attachment of epibionts to this region of the shells of both *Neotrigonia* and extinct species (figures 4, 5, 22 and 23), and by preservation of animals *in situ* (figure 12).

#### COADAPTIVE FEATURES

Given the observation that *Neotrigonia* is an adept burrower and that Mesozoic trigoniids occupied coarse, shifting substrata, I suggested that the Mesozoic adaptive radiation of the family was triggered by the origin of the kind of muscular foot that persists in *Neotrigonia* (Stanley 1972). This idea can be tested by the study of trigoniid dentition.



It seems evident that the complex hinge teeth of *Neotrigonia* function to accommodate the foot by maintaining alignment of the valves at the wide angles of gape required for its extrusion. Typical burrowing bivalves, such as most members of the Veneridae, have a sack-like foot that passes between the valves as a thin sheet. During extrusion of this kind of foot, gaping of the valves is almost imperceptible. The relatively wide gape of *Neotrigonia* is illustrated in figure 8. The primary teeth of *Neotrigonia* project radially into the interior of the shell a great

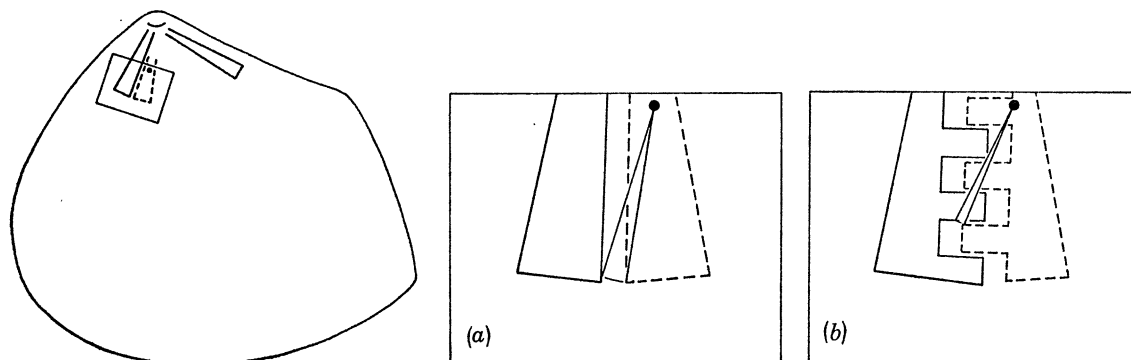


FIGURE 31. Diagrams illustrating the functioning of the hinge teeth of post-Triassic trigoniids. The rectangular area in the drawing on the left is enlarged in the other figures. The gap between the teeth represents the condition for a particular angle of gape. The axis about which the valves shear is indicated by solid dots. The angle of shear is smaller in a hypothetical animal lacking secondary dentition (a) than in one possessing it (b).

distance from the beak. Their unusual length limits the angle of play, or shearing motion, parallel to the commissure. Hinge teeth, however, are wedge-shaped in a plane perpendicular to the commissure, so that the angle of play between the valves normally increases with angle of gape. The wide gape of *Neotrigonia* would allow for considerable play and valve misalignment at closure were it not for the presence of the secondary hinge teeth. Orientated with their long axes perpendicular to the commissure, these structures prevent the angle of play between the valves from increasing appreciably with an increase in gape (figure 31).

The idea that the large, complex dentition of the trigoniids relates to the presence of the foot can be tested by consideration of the Cardiidae, which have a similar foot. In this family the cardinal teeth are neither large nor equipped with secondary dentition. They are, however, complemented by widely separated lateral teeth that project well across the commissure (figure 11). These lateral teeth are loosely articulated at wide gapes, but maintain approximate valve alignment until, as the valves close, the shorter cardinal teeth mesh with little play. The cardinal teeth and crenulations at the valve margin bring the valves into precise alignment at closure. Thus the lateral teeth of cardiids serve a function equivalent to the secondary dentition on the primary teeth of *Neotrigonia*. The presence of analogous structures in the Cardiidae supports the idea that the presence of the secondary dentition in the Trigoniidae relates to the presence of a muscular foot. This relation, then, permits us to test the idea that the origin of the muscular foot triggered the Mesozoic adaptive radiation of the Trigoniidae. The question to be asked is whether the complex dentition, which is readily preserved in the fossil record, evolved just before the radiation began. In an exemplary study mentioned above, Newell & Boyd (1975) have documented the simultaneous enlargement of the primary dentition and polyphyletic origin of the secondary dentition. These changes occurred during the Early and

Middle Triassic, in fact, when the radiation began. This temporal coincidence of the complication of dentition and the onset of adaptive radiation seems to confirm the idea that musculation of the foot was the adaptive breakthrough that triggered the radiation.

The opisthogyrous shell form of trigoniids, and at least some patterns of external ornamentation of the trigoniid shell, can be shown also to have been adaptively linked. Judging from the utility of the prosogyrous shape to burrowing (Stanley 1975), the opisthogyrous shape of trigoniids represented a deficiency. Most Palaeozoic members of the Trigoniacea were more or less orthogyrous, but being laterally compressed, they presumably were moderately efficient burrowers. With the evolution of the muscular foot, however, it seems that efficient locomotion was being selected for, and it might therefore seem strange that a prosogyrous shape did not develop. The reason that it did not develop will be considered later.

What arose in the Mesozoic Trigoniidae in place of a prosogyrous shape were various patterns of ornamentation that served to aid in burrowing. Some of these (figures 13, 14, 21, 25 and 27) took the form of asymmetric ridges of the type postulated to grip the sediment during backward rotation of the shell in burrowing, while sliding through it with little friction during forward rotation (Stanley 1969). This alleged function has been tested by study of the living venerid *Anomalocardia brasiliensis* (Gmelin) (figures 15, 16 and 17) which is convergent in form with the British Cretaceous trigoniid *Rutitrigonia* cf. *dunscambensis* (Lycett) (figure 14). Experiments were conducted in which the ridges of the venerid species were rendered inoperable by filling of the intervening valleys with neutrally buoyant wax. The ridges were found to decrease by 15–20% the number of burrowing sequences required for burial of the shell in the animals' native sand (Stanley 1977a).

Other patterns of ornamentation of the Mesozoic Trigoniidae are without counterpart in the Recent Bivalvia. One of these consists of concentric ridges that are symmetrical in cross section. Such ridges typify the genus *Trigonia sensu stricto*. In considering the function of these ridges it was postulated that they might aid in burrowing by gripping the sediment in backward rotation of the shell, while sliding through it with less resistance in forward rotation. An analogy can be made with a current meter in which cups rotate about an axle because resistance to flow against the concave side of a cup is greater than resistance to flow against the convex side. This idea was tested by experimentation with robots of the genus *Trigonia* that were cast in aluminium-filled epoxy from moulds of fossil shells (figures 18, 19 and 20). Rotational movements of natural burrowing were simulated by applying downward forces to rods attached to the robots in such a way as to simulate the forces of pedal retractor muscles. Details are presented elsewhere (Stanley 1977a). Three robots were tested in fine sand: one (robot *A*) in which natural ornamentation was left intact (figure 18), one (robot *B*) from which all ornamentation ventral to the carina was removed (figure 19), and one (robot *C*) from which ornamentation was removed only from the flanks of the shell (figure 20). The third robot was employed because the natural shell possesses anterior ridges that are asymmetrical in cross section and that were presumed to aid in burrowing (figure 21). The aim was to distinguish between the effect of this ornamentation and the effect of the symmetrical ornamentation on the flanks of the shell. The results of the experiments are presented in figure 23. In ten rocking movements, the unaltered robot 'burrowed' on the average 37% more deeply than robot *B*, in which all ornamentation ventral to the carina was removed. Robot *C*, in which the asymmetrical anterior ridges were left intact, attained an intermediate depth. The difference in depth attained by *A* and *B* is significant by the Mann-Whitney *U*-test at the 99.6% level. The

difference for *B* and *C* is significant at the 98.4% level. The anterior ridges aid in burrowing, as assumed, but the flank ridges provide even more assistance. In medium sand, experiments yielded a smaller disparity between robots *A* and *C* in depth attained, suggesting that the ridges function most effectively in fine-grained sediment. In fact, *Trigonia* seems to inhabit fine-grained substrata more frequently than most other members of the family (Stanley 1977a).

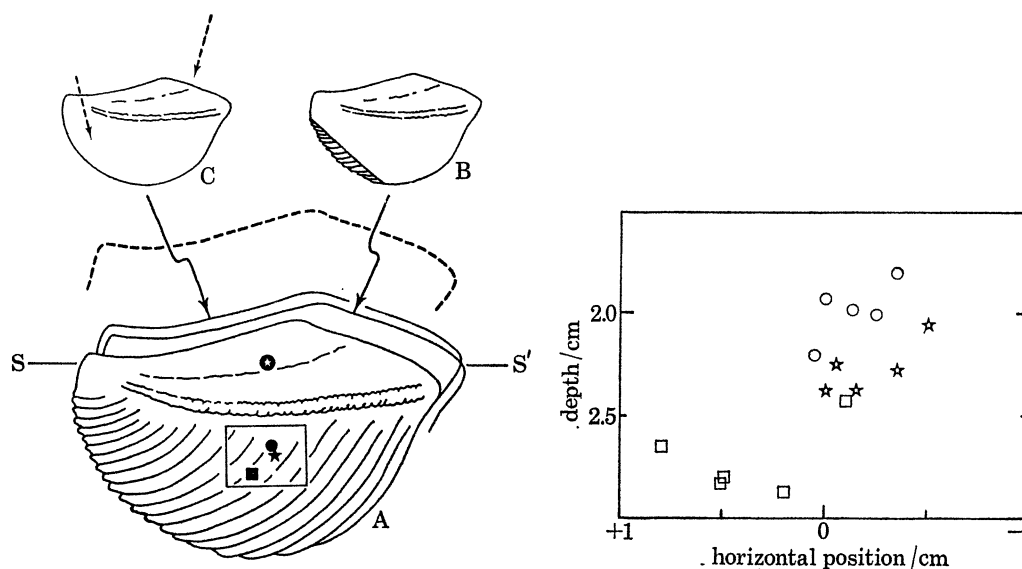


FIGURE 32. Results of experiments in which robots were used to simulate the burrowing of *Trigonia papillata* Agassiz. Three robots (*A*, *B*, and *C*) were employed (see text). Each experiment was initiated with a robot in the position of the dashed dorsal outline with respect to the sediment/water interface (*S-S'*). Average final positions for each robot in five trials is shown by a solid outline. Each trial consisted of ten simulated burrowing sequences. 'Homologous' points on the robots at the start of 'burrowing' were positioned at the point of the encircled star. Final positions of the 'homologous' points are shown by solid symbols within the small rectangle: square, robot *A*; star, robot *B*; circle, robot *C*. Enlargement of the rectangle alongside shows the positions of the 'homologous' points with respect to their original position (coordinates 0, 0) for five trials with each robot. Dashed arrows in *C* show orientation of forces applied. The anterior force moved its point of application 6 mm, and the posterior force restored the robot to its original orientation (the orientation figured).

Robots were also used to test the effect on burrowing of ornamentation consisting of curved rows of knobs. An unaltered robot of *Yaardia nodosa* (figure 24) was found to burrow about 50% more deeply by ten simulated rocking movements in fine sand than a robot with the knobs removed. The knobs were found to have no significant effect in medium sand, however. It seems likely that cohesive sediment packs against the knobs as if they were a rib, whereas loose sand passes readily between them. In fact, nodose fossil populations of *Yaardia* and *Myophorella*, like those of *Trigonia*, seem to occur more frequently in muddy sediments than do populations of other trigoniid genera (Stanley 1977a).

While not all patterns of external ornamentation of the shells of Mesozoic trigoniids functioned as aids to burrowing, many of them did. Thus, many lineages possessed an alternative to a prosogyrous shape, which in more typical burrowing bivalves facilitates burrowing. The ornamentation of trigoniids, in fact, operated in much the same way as the blunt anterior of prosogyrous bivalves, catching the sediment to prevent upward slippage of the anterior end of the shell during backward rotation. Why did the Mesozoic Trigoniidae not instead evolve

a prosogyrous condition? The answer may well lie in the complex nature of the structures that evolved within the anterior region of the shell. The feature known as the anterior myophorous buttress (figure 3) clearly serves to support the elongated anterior hinge tooth, which is a brittle structure projecting far into the interior of the shell. The posterior hinge tooth, which lies along the dorsal margin of the shell, needs no comparable supporting structure. The anterior hinge tooth, myophorous buttress, and anterior adductor represent a bulky complex of structures. The evolution of these massive features was apparently permitted by the orthogyrous shape and high whorl expansion rate (Raup 1966) of Palaeozoic trigoniaceans. The hinge teeth must radiate from the beak, and yet in the Trigoniidae these teeth have been tied to the anterior adductor muscle by the myophorous buttress. These linkages may not have rendered impossible the evolution of distinctly prosogyrous shape, but they would seem to have made the evolution of such a shape unlikely. The evolution of a prosogyrous shape would of necessity have been accompanied by a decrease in whorl expansion rate of the conical shell. This change and helical coiling would have reduced the space available for the hinge teeth and related structures. This may explain why the Trigoniidae evolved ornamentation that aided burrowing rather than evolving a prosogyrous shape. Phylogenetic details remain to be worked out, but the pathway to sediment-gripping ornamentation was clearly polyphyletic.

In summary, the array of unusual morphologic features of the Mesozoic Trigoniidae composed an integrated functional system. The overall evolutionary theme was one of efficient burrowing. The evolution of the muscular trigoniid foot required increased gaping of the valves and was therefore accompanied by two morphological changes that ensured the maintenance of valve alignment: enlargement of the primary hinge teeth and evolution of secondary dentition. The so-called myophorous buttress evolved as a support for the anterior dentition. Probably because of the evolution of these bulky umbonal features, discordant ornamentation rather than a prosogyrous shell shape evolved as an aid to burrowing.

#### SUCCESS AND EXTINCTION: WERE TRIGONIIDS OUTMODED?

Though different from the Cardiidae (cockles) in certain respects, extinct genera of the Trigoniidae resemble this group sufficiently that they may reasonably be viewed as the cockles of the Mesozoic: they were compact, shallow burrowers with an unusually muscular foot that served both for burrowing and for leaping. Like the cockles, their greatest diversity was in sandy habitats of warm, shallow seas. There seems little question that the coadaptive system of the Mesozoic trigoniids that permitted effective locomotion was less efficient than the alternative solution of the cardiids. There is a large amount of friction in the intricate hinge system of *Neotrigonia*, and it may be that the muscular foot of *Neotrigonia* aids the ligament significantly in opening the valves. Cockles, as described above, have a compound system of valve alignment. At wide angles of gape, loosely fitting lateral teeth that offer little friction maintain approximate alignment (figure 11). Small, weak cardinal teeth and marginal denticulation, also offering little friction, bring the valves into proper apposition at closure. As might be expected, the valves of cockles move much more rapidly during locomotion than do the valves of *Neotrigonia*, and, in fact, most cardiids burrow somewhat more rapidly than *Neotrigonia*. In addition *Neotrigonia*, which can presumably be taken to represent the Trigoniidae in general, has filibranch gills and lacks siphons, making it more primitive than the eulamelli-branch, siphonate cardiids. It is not at present clear when the muscular foot of the Cardiidae

evolved, but it seems likely that, as in the Trigoniidae, the origins of this organ and co-adaptive features providing for efficient locomotion ushered in the adaptive radiation of the family.

Being more primitive than the Cardiidae, however, by no means doomed the Trigoniidae to failure in modern seas. As mentioned earlier, I know of no other living genus of non-siphonate suspension feeding bivalves that is as efficient in locomotion as *Neotrigonia*. Judging from shell form, no Palaeozoic group of suspension-feeding bivalves is likely to have equalled Mesozoic trigoniids in locomotory efficiency. In addition to the Cardiidae, a living taxon resembling the Trigoniidae in general shell form and life position is the Anadarinae. Though slow burrowers (Stanley 1970) the Anadarinae have diversified quite successfully since arising in the Cretaceous. Given the evidence for the adaptive superiority of trigoniids over nearly all suspension-feeding burrowing bivalves of the Palaeozoic and over certain successful groups of Recent seas, it seems evident that the trigoniids are not primitive clams ill-fitted to the modern world.

Fleming (1964) noted that Late Cretaceous trigoniid faunas of Australia exhibit some endemism, which apparently foreshadowed the total isolation of the family in the Cainozoic. Today *Neotrigonia* is distributed around most of the circumference of Australia. Perhaps because of the presence of several other relict taxa in the vicinity of Australia, it has become customary to view this region as a general refugium for outmoded organisms. Certainly *Neotrigonia* is a relict genus, but the sudden extinction of its forebears by no means identifies these taxa as archaic creatures.

In examining extinction within a taxon it is important to distinguish between normal rates of extinction and pulses of termination known as mass extinctions. Clearly portions of the world ecosystem collapsed near the end of the Cretaceous Period and, for reasons that are not entirely clear, certain taxa like the trigoniids suffered especially high rates of extinction. Some taxa disappeared altogether. The Trigoniidae hung on by a thread, perhaps a single lineage. No particular genus or species of the family is actually known to have crossed the Cretaceous–Tertiary boundary. The documented record of *Eotrigonia* commences in the Eocene. *Neotrigonia* (Late Miocene–Recent) is the only other recognized genus of Cainozoic trigoniids.

The history of *Neotrigonia* actually suggests that this genus has been thriving in an evolutionary sense. During perhaps no more than 10 Ma of existence, *Neotrigonia* has produced a standing diversity of at least six species. Its mean rate of diversification, or fractional increase per unit time ( $R$ ) can be obtained from the exponential equation

$$N = N_0 e^{Rt}, \quad (1)$$

where  $N$  is present diversity,  $N_0$  is the original number of species (one, assuming monophyly),  $t$  is time since origination, and  $e$  is the base of natural logarithms. The conservative assumption that only six species now exist gives a value for  $R$  of 0.18. Setting  $N/N_0 = 2$  in equation (1), we obtain average doubling time:

$$t_2 = \ln(2)/R. \quad (2)$$

For *Neotrigonia*,  $t_2 = 3.85$ , which is relatively high for the marine Bivalvia, (Stanley 1977*b*). For most modern radiating bivalve groups  $t_2$  is in the neighbourhood of 11 Ma. Even if *Neotrigonia* were found to extend back to the mid-Oligocene, its average doubling time would be about 11 Ma.

Net rate of increase ( $R$ ) equals rate of speciation minus rate of termination of lineages, and  $t_2$  varies inversely with  $R$ . Obviously *Neotrigonia* has speciated at a high rate and has fared well

against extinction. It may be that high rates of speciation have resulted from the linear distribution of populations around the perimeter of Australia. It hardly seems possible that the success of *Neotrigonia* has been fostered by a dearth of predators or competitors; especially in the north, the seas of Australia are teeming with life. Rather, what we seem to have is an illustration of the generally sluggish nature of speciation in the marine realm (Day 1963). Even after 20 Ma of existence, an average Cainozoic family of marine bivalves has achieved a standing diversity of only three or four species (Stanley 1977*b*). Exponential increase accounts for the pinched tail at the base of most balloon diagrams representing diversity within higher taxa (Stanley 1975). For bivalves, and for many other invertebrate taxa, the tail tends to be exceedingly long and thin. Recovery from a mass extinction as severe as the Cretaceous decimation of the Trigoniidae is expected to be very slow.

The record of diversification of *Eotrigonia* is quite incomplete (Fleming 1964; Deschet 1966). The fact that only a single genus seems to have descended from it is perhaps a matter of chance. A family of bivalves represented by only a single species is highly vulnerable to catastrophic extinction. Similarly, a family represented by two or three species is vulnerable to catastrophic reduction to a single species, which will considerably delay subsequent diversification. These considerations hold whether the small number of species in question represents an incipient family or the remnant of a once diverse family, as was the case with *Eotrigonia*. Chance factors tend to play a major rôle in the history of small clades.

What we can see from direct evidence is that *Neotrigonia* diversified quite successfully. This fact supports the conclusion, based on comparative morphology and ethology, that *Neotrigonia* in particular and the Trigoniidae in general have represented an advanced level of adaptation endowing them with the potential to thrive in the modern world.

An analogy with the dinosaurs is appropriate. Once considered to have been archaic, lumbering beasts, dinosaurs are now recognized to have been endothermic and highly mobile animals (Bakker 1971) that intergrade with birds (Ostrom 1975). As Bakker (1975) has argued, there is no reason to believe that Mesozoic dinosaurs were ill-adapted by modern standards. No argument is made that in behavioural complexity or ecological versatility the dinosaurs were fully equivalent to modern mammals, but their level of adaptation was for many years underestimated. Traditionally the dinosaur has been belittled simply because it went extinct. Even the dinosaurs' status as an extinct group disappears if birds are classified with them (Bakker 1975).

Another example is provided by the rudist bivalves, which apparently outcompeted scleractinian corals to dominate tropical reefs of Cretaceous age (Kauffman & Sohl 1974). Like the trigoniids, they were largely confined to the Tethyan region, and they too suffered mass extinction (in their case, total extinction) at the end of the Cretaceous. Scleractinian corals rebounded to dominate tropical reefs of the Cainozoic era. Had the rudists survived into the Cainozoic, there is no reason to believe that they would not still hold dominance.

Thus resistance to mass extinction is not necessarily a measure of success in a biological context: success against competitors and predators. *Neotrigonia* has been viewed as an archaic genus simply because nearly all members of its family died out catastrophically. If species of *Neotrigonia* and, for that matter, of Jurassic and Cretaceous trigoniid genera were somehow transplanted into warm shallow seas around the modern world, I have no doubt that they would flourish and speciate at least as successfully as the less highly adapted Anadarinae.

The traditional labelling of *Neotrigonia* as a 'living fossil' seems unjustified. I would agree

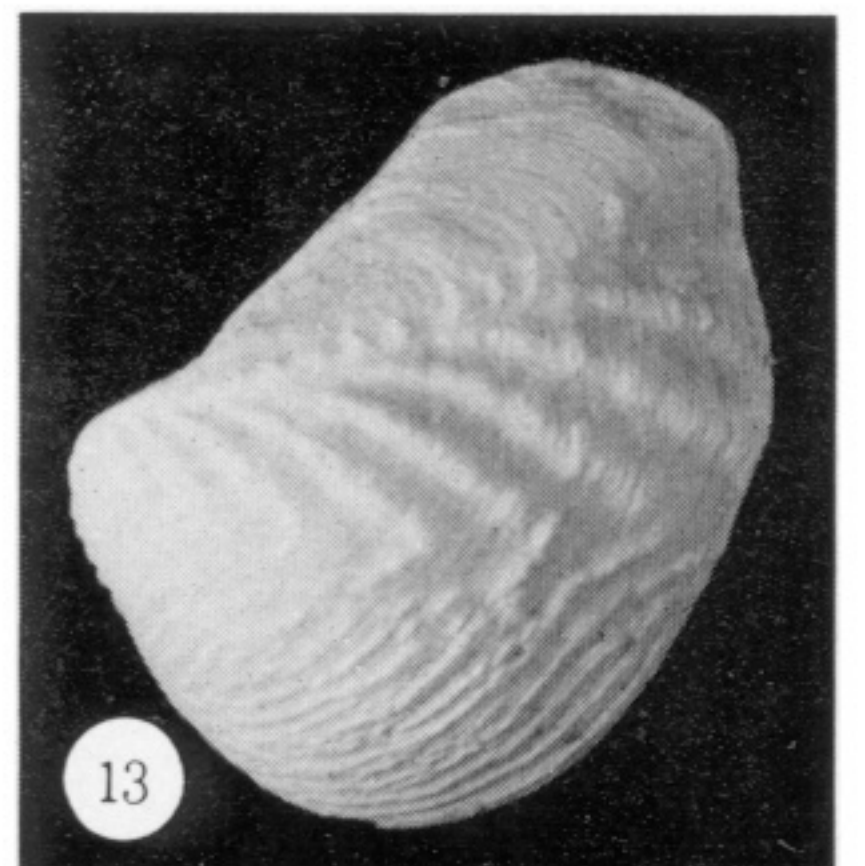
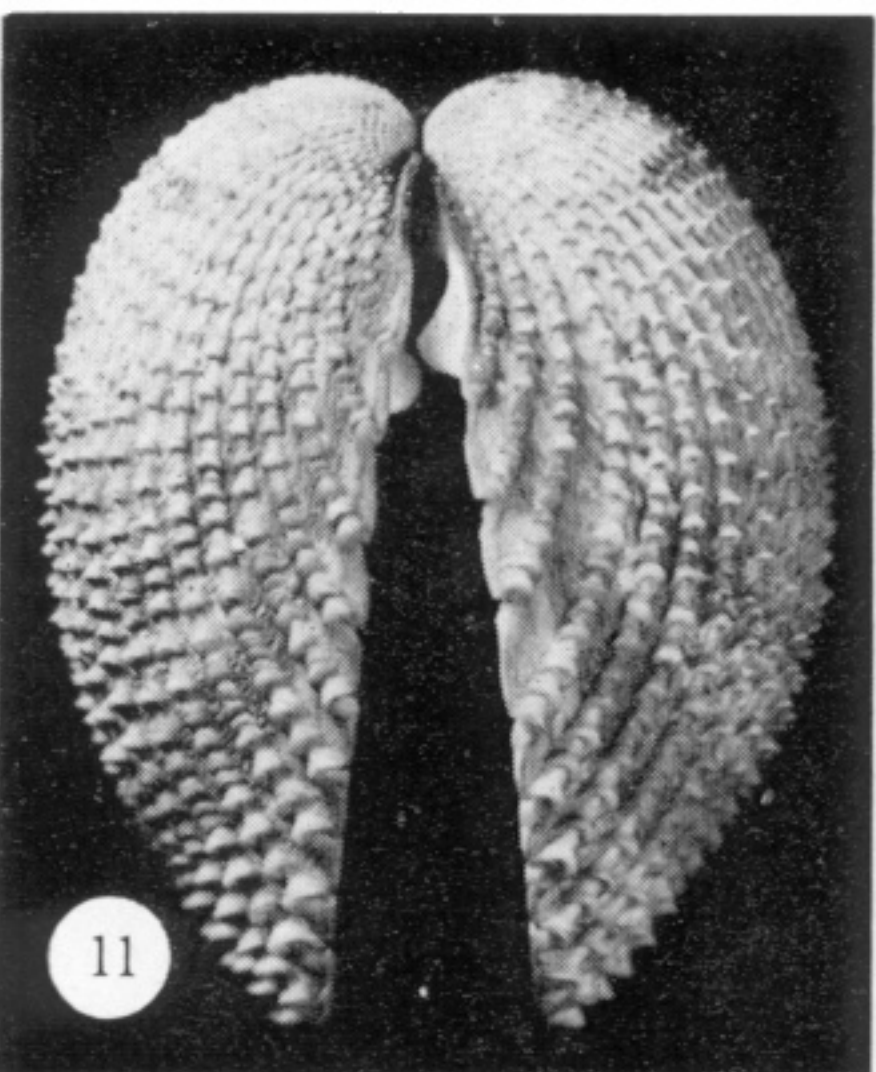
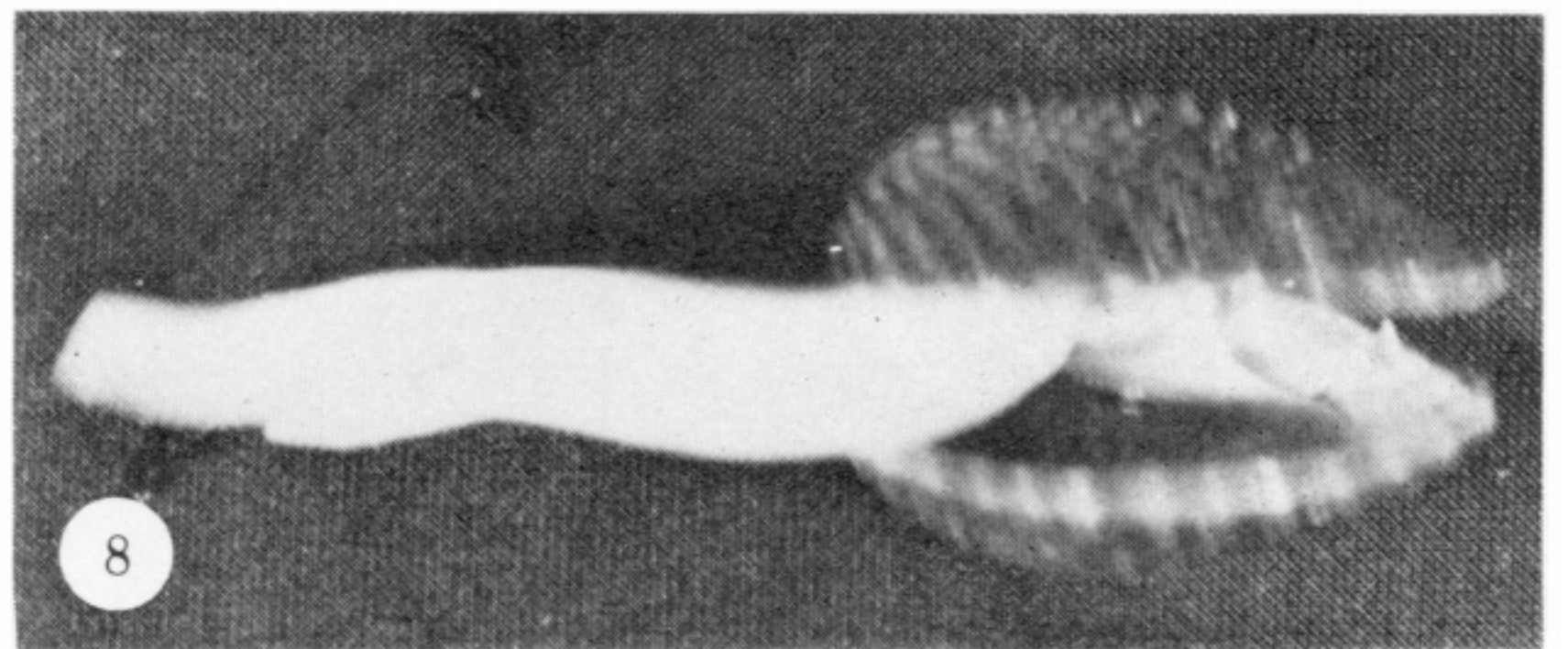
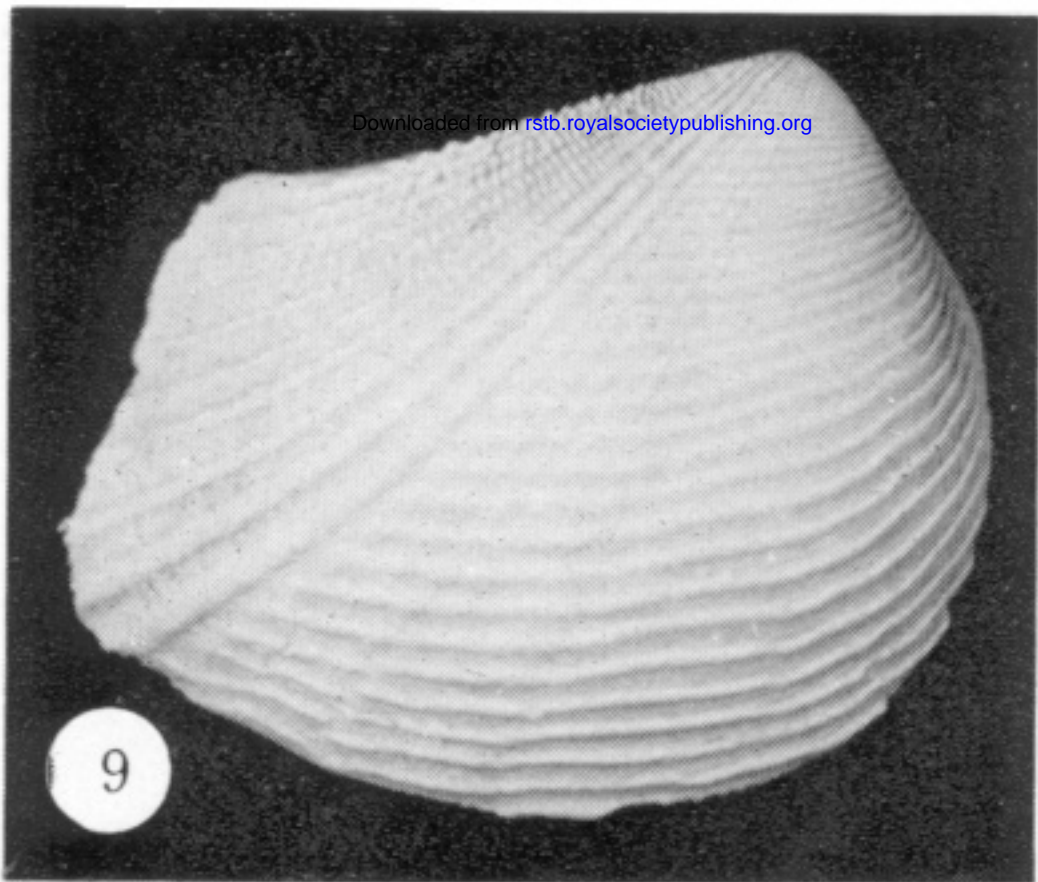
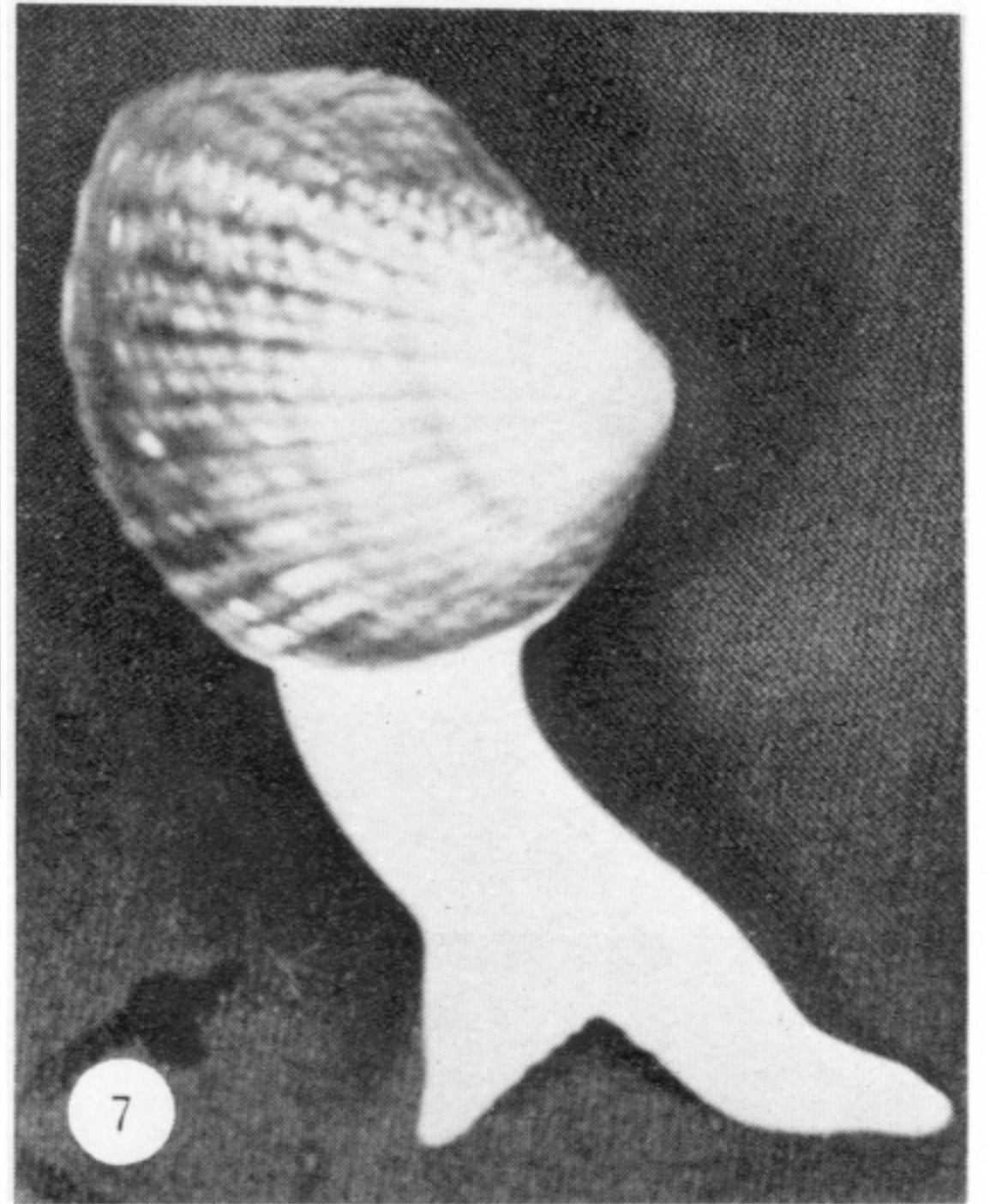
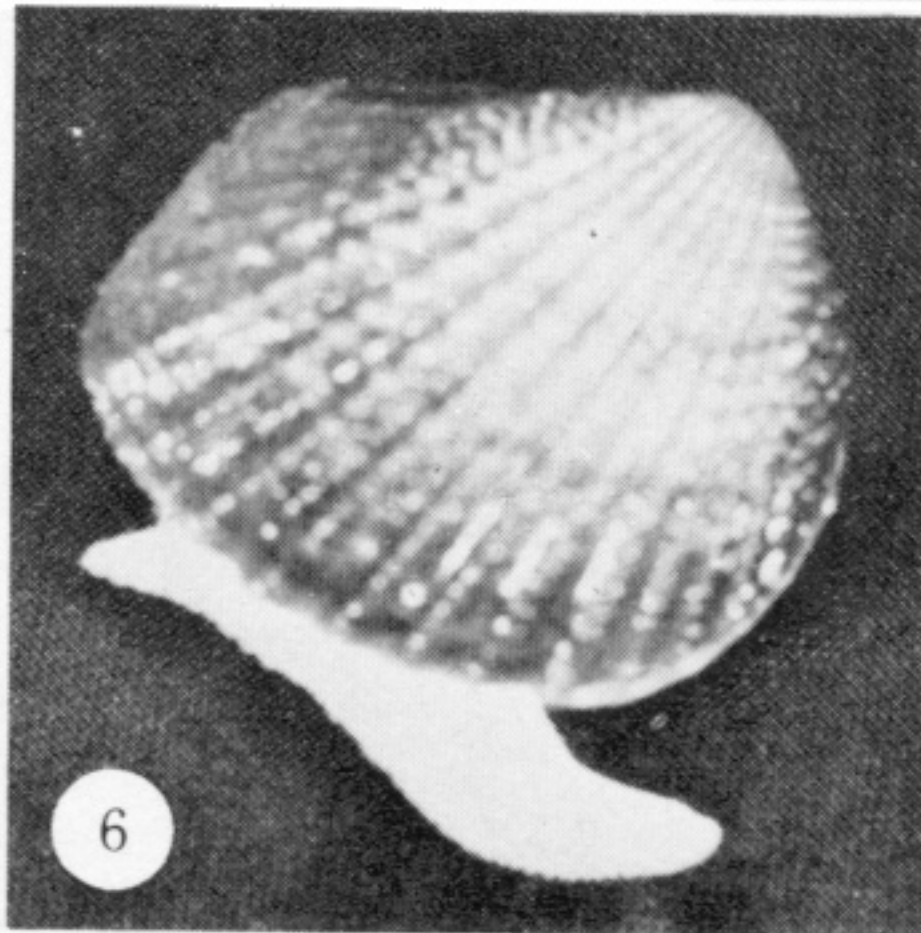
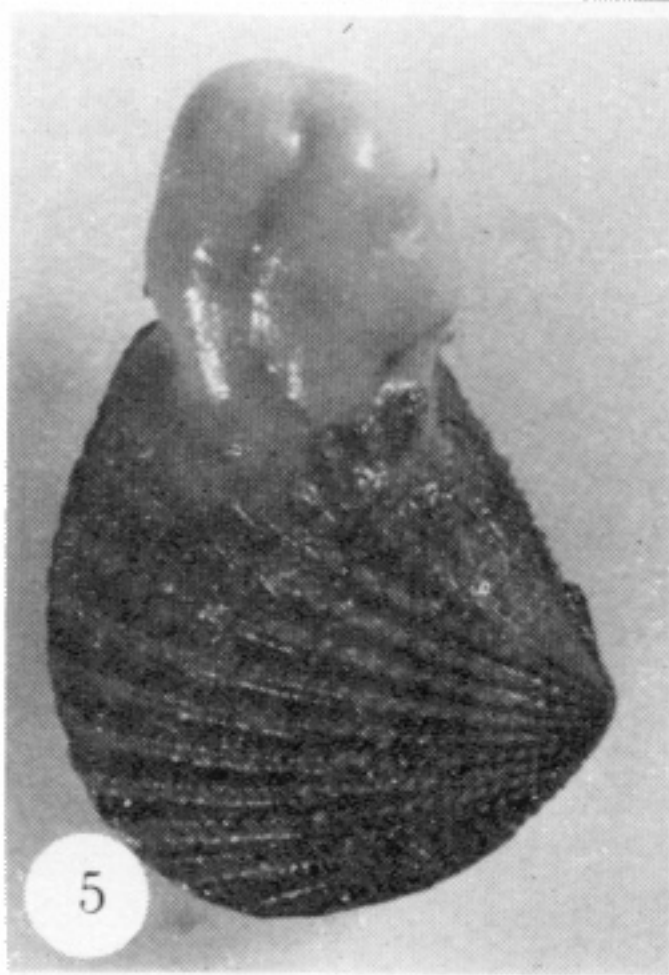
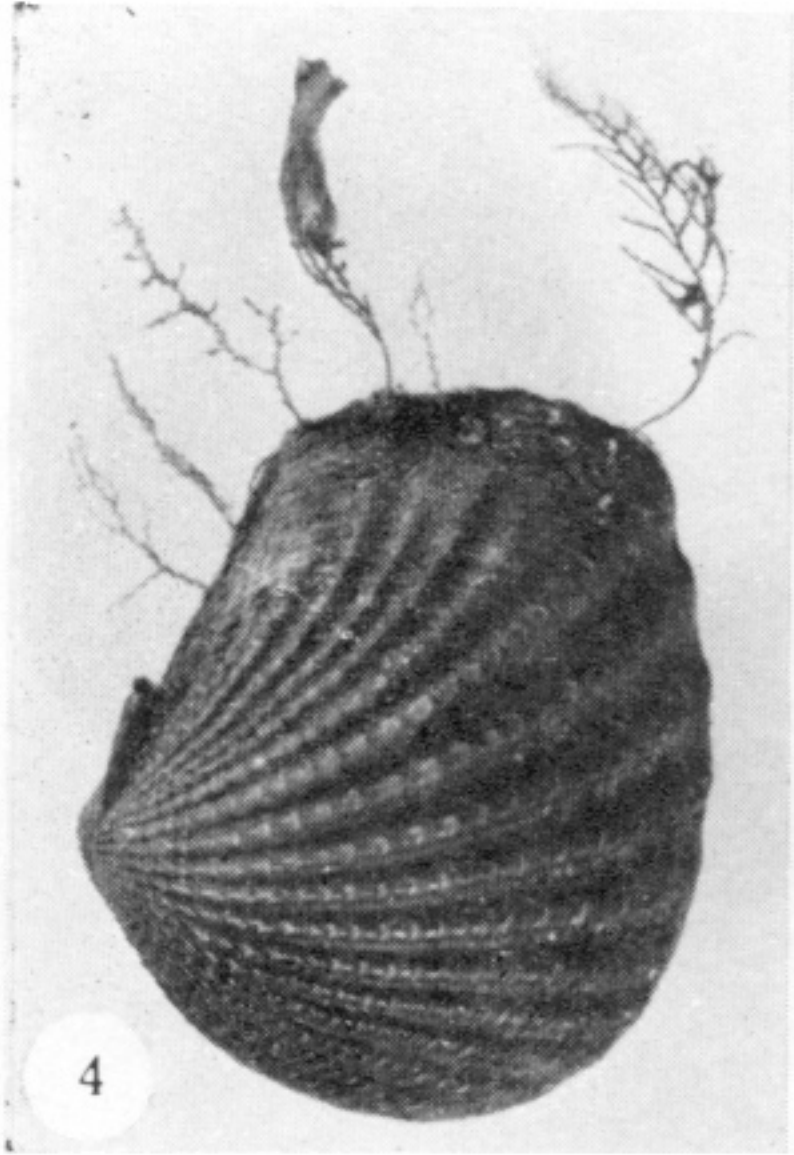
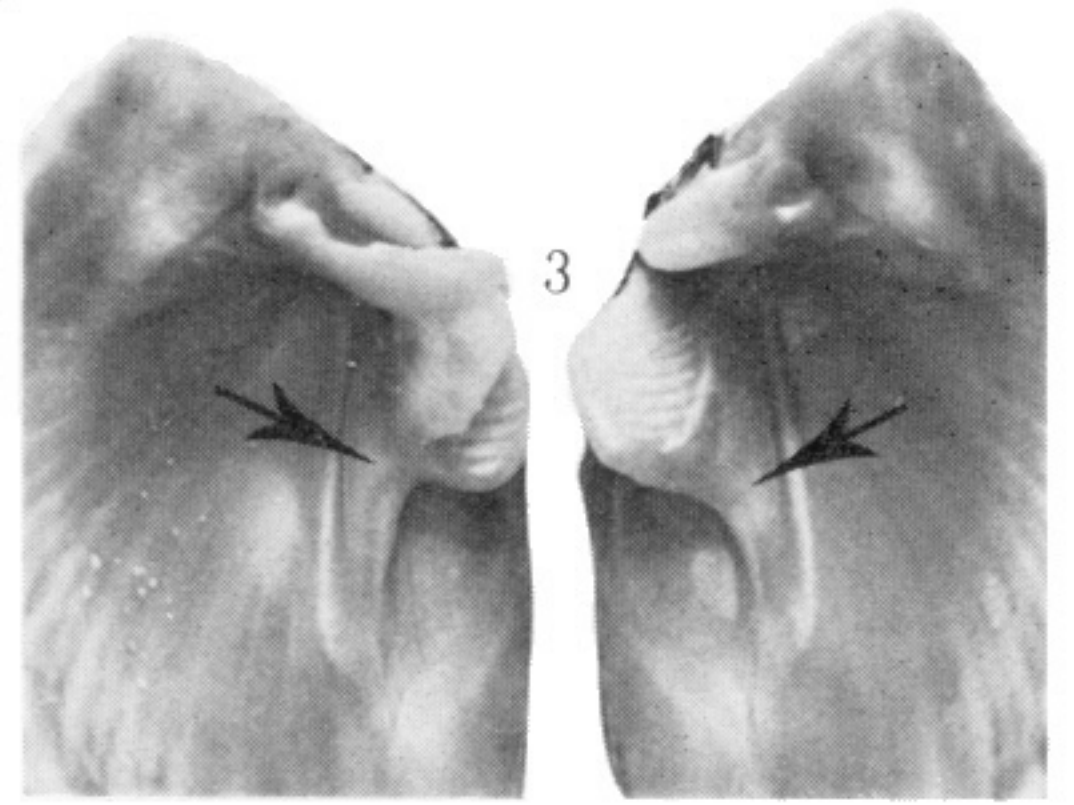
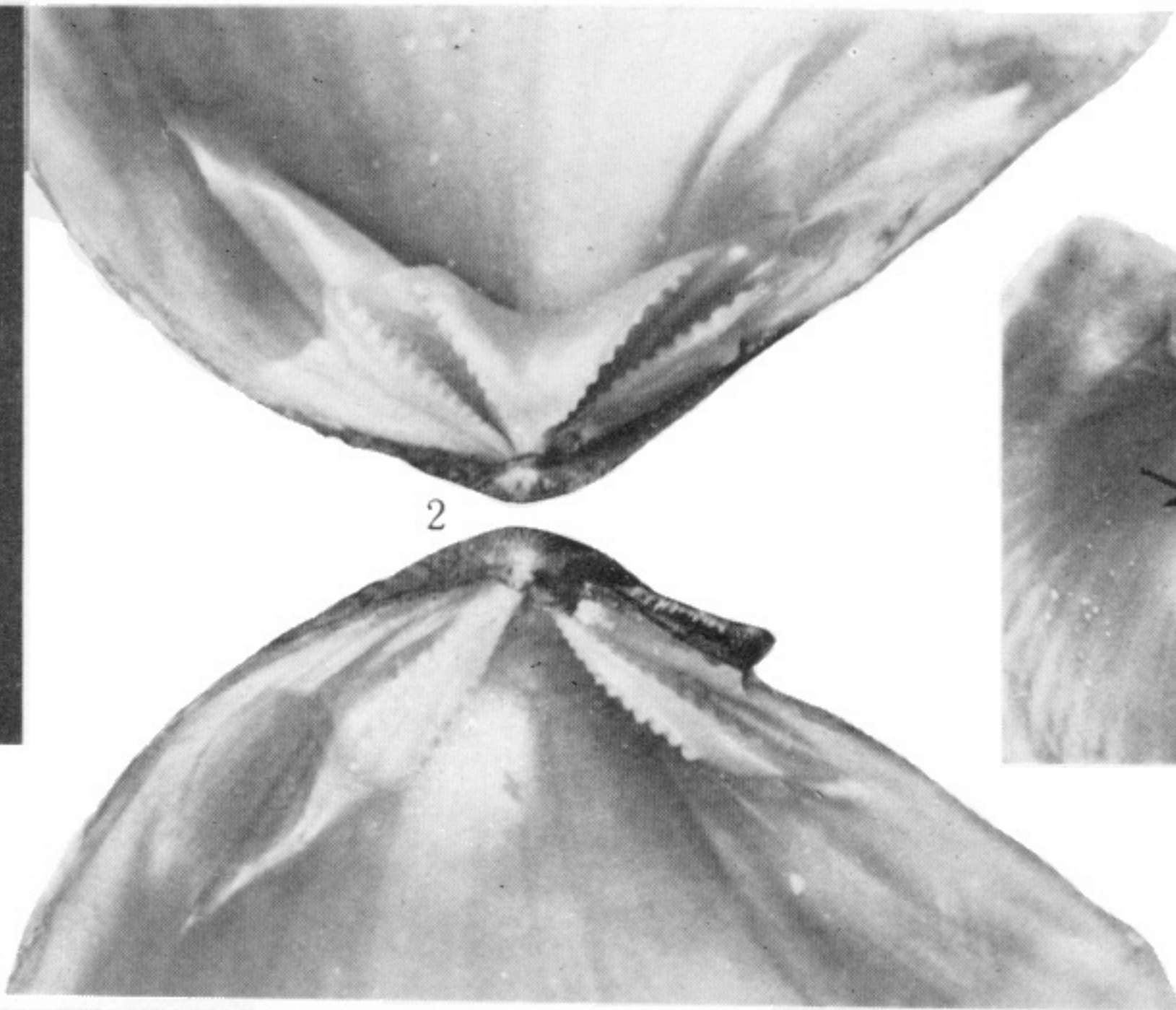
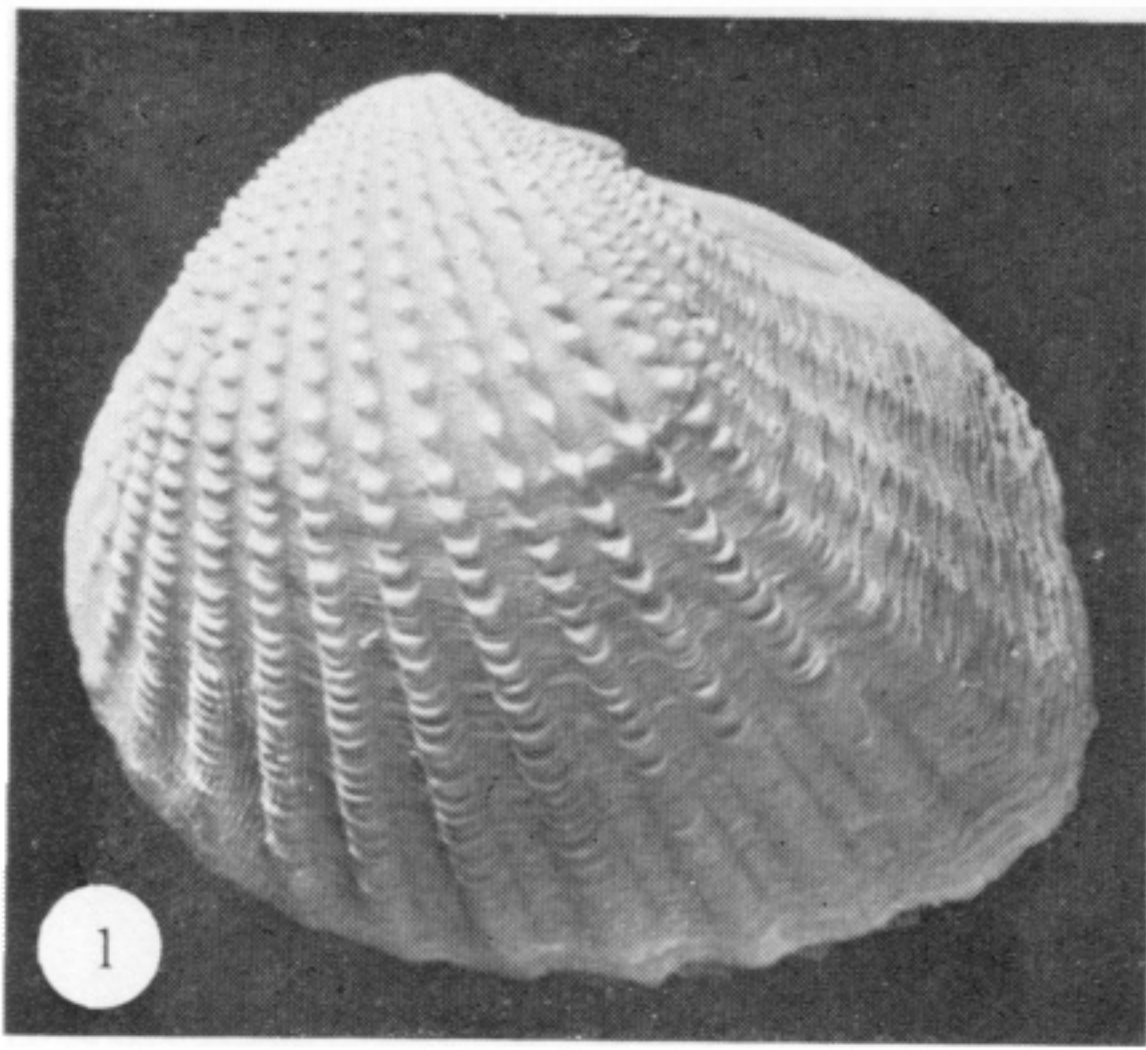
with the restriction by Eldredge (1975) of the phrase 'living fossil' to taxa that have persisted for long intervals of time with little evolutionary change and that are primitive or archaic in comparison with living taxa of the same class or phylum. Eldredge also suggests that to qualify as a living fossil group a taxon should have persisted at low diversity within a small geographic area. Many people have described *Neotrigonia* as a living fossil taxon (McAlester 1965; Tevesz 1975; Eldredge 1975), apparently because it is the sole survivor of a previously flourishing group. Neither the genus nor the family, however, is relatively old. *Neotrigonia* has only existed for about 10 Ma, while more than 35 living genera of bivalves originated more than 150 Ma ago (Moore (ed.) 1969). Several families of living bivalves are older than the Trigoniidae. Not only does *Neotrigonia* fail to meet the age requirement for status as a genus of living fossils but the 'living fossil' label tends to carry the implication that *Neotrigonia* is a primitive or archaic member of its class. As amply documented above, this implication is misleading. It therefore seems best that the label be dropped.

## REFERENCES (Stanley)

- Bakker, R. T. 1971 *Evolution* **25**, 636–658.  
 Bakker, R. T. 1975 *Scient. Am.* April, 58–77.  
 Day, J. H. 1963 *System. Ass. Publ.* **5**, 31–49.  
 Deschet, Y. 1966 *Trav. Lab. Paleont. Univ. Paris*.  
 Eldredge, N. 1975 *Nat. Hist.* **84**, 60–69.  
 Fleming, C. A. 1964 *Aust. J. Sci.* **26**, 196–203.  
 Freneix, S. 1958 *Sci. Terre* **4**, 153–207.  
 Kauffman, E. G. & Sohl, N. F. 1974 *Verh. Naturf. Ges. Basel* **84**, 399–467.  
 McAlester, A. L. 1965 *Geol. Soc. Am.*, abstracts 102. Boulder, Colo.  
 Moore, R. C. (ed.) 1969 *Treatise on invertebrate paleontology*, part N, Mollusca 6 (Bivalvia). Lawrence, Kansas: University of Kansas and Geological Society of America.  
 Newell, N. D. & Boyd, D. W. 1975 *Bull. Am. Mus. nat. Hist.* **154**, 53–162.  
 Ostrom, J. H. 1975 *A. Rev. Earth planet. Sci.* **3**, 55–77.  
 Poulton, T. P. 1976 *Bull. geol. Surv. Can.* **256**, 41–53.  
 Raup, D. M. 1966 *J. Paleont.* **40**, 1178–1190.  
 Scott, R. 1975 *Lethaia* **8**, 241–252.  
 Seilacher, A. 1954 *Neues Jb. Geol. Palaont. Monatsch.* **4**, 163–183.  
 Stanley, S. M. 1969 *Science, N.Y.* **166**, 634–635.  
 Stanley, S. M. 1970 *Mem. geol. Soc. Am.* **125**, 1–296.  
 Stanley, S. M. 1972 *J. Paleont.* **46**, 165–122.  
 Stanley, S. M. 1975 *Paleobiology* **1**, 48–58.  
 Stanley, S. M. 1977a *Palaeontology*. (In the press.)  
 Stanley, S. M. 1977b In *Patterns of evolution* (ed. A. Hallam). Amsterdam: Elsevier. (In the press.)  
 Stanley, S. M. 1977 *Palaeontology* **20**, 869–899.  
 Tevesz, M. J. S. 1975 *Lethaia* **8**, 321–327.  
 Woodward, S. P. 1851 *A manual of the Mollusca*. London: John Weal.  
 Wright, R. P. 1974 *J. Paleont.* **48**, 425–433.

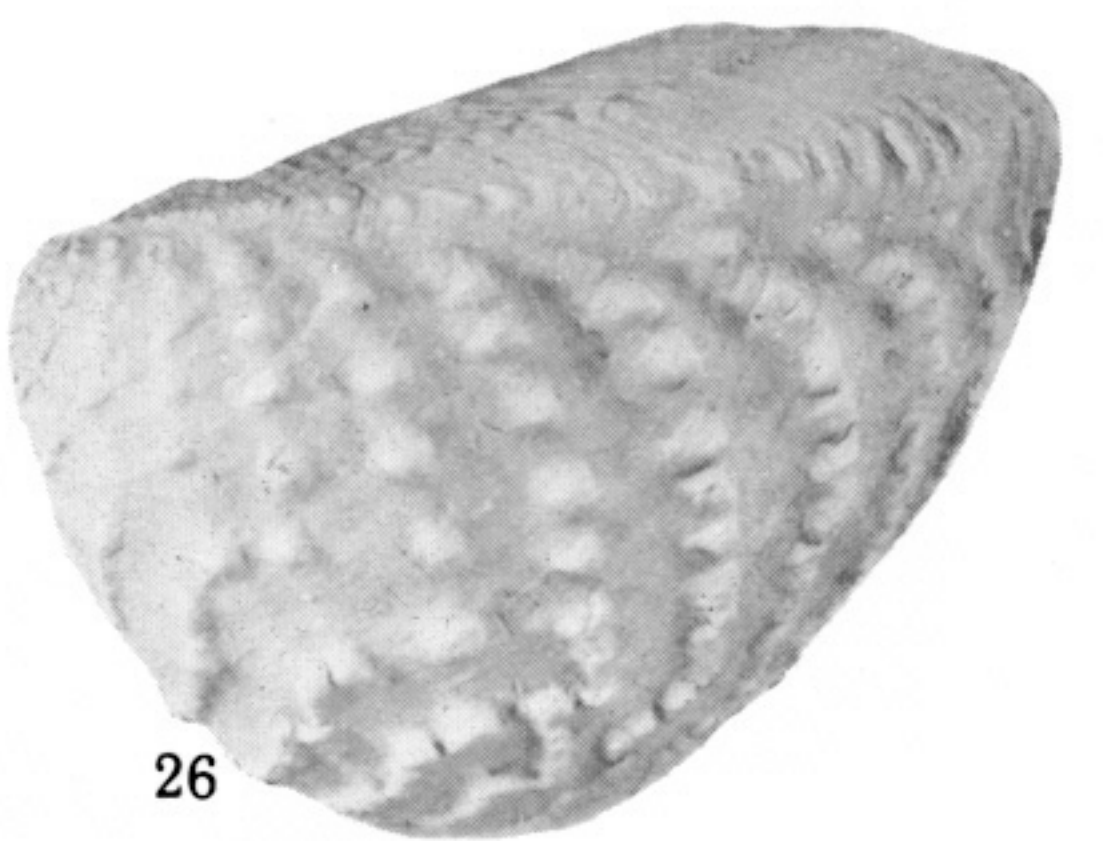
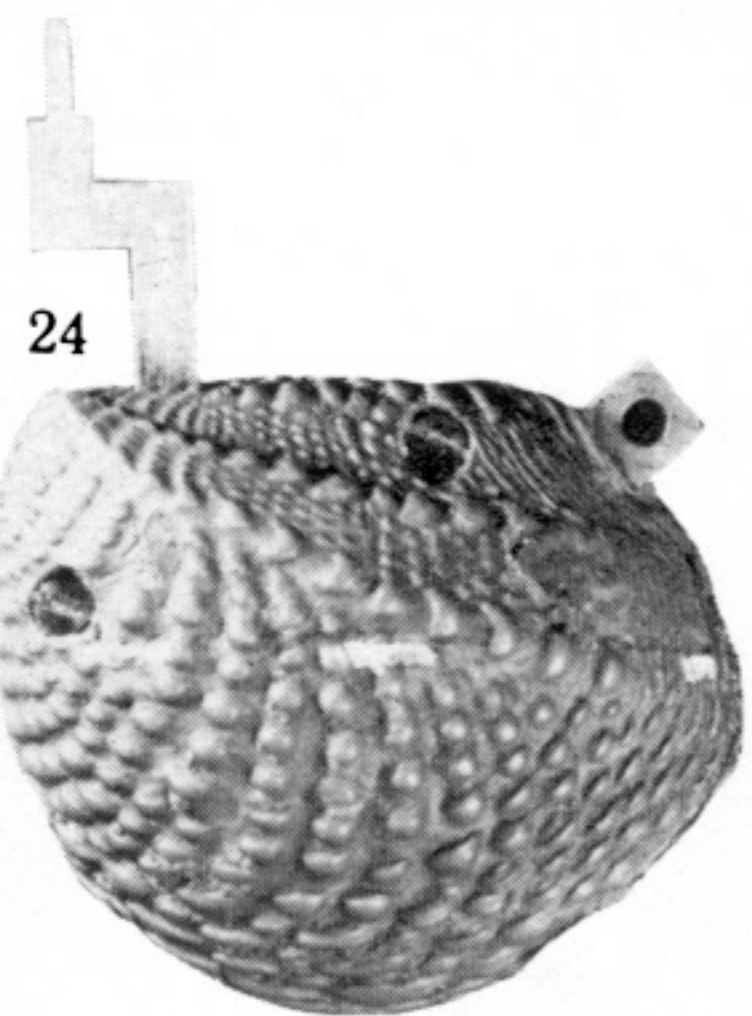
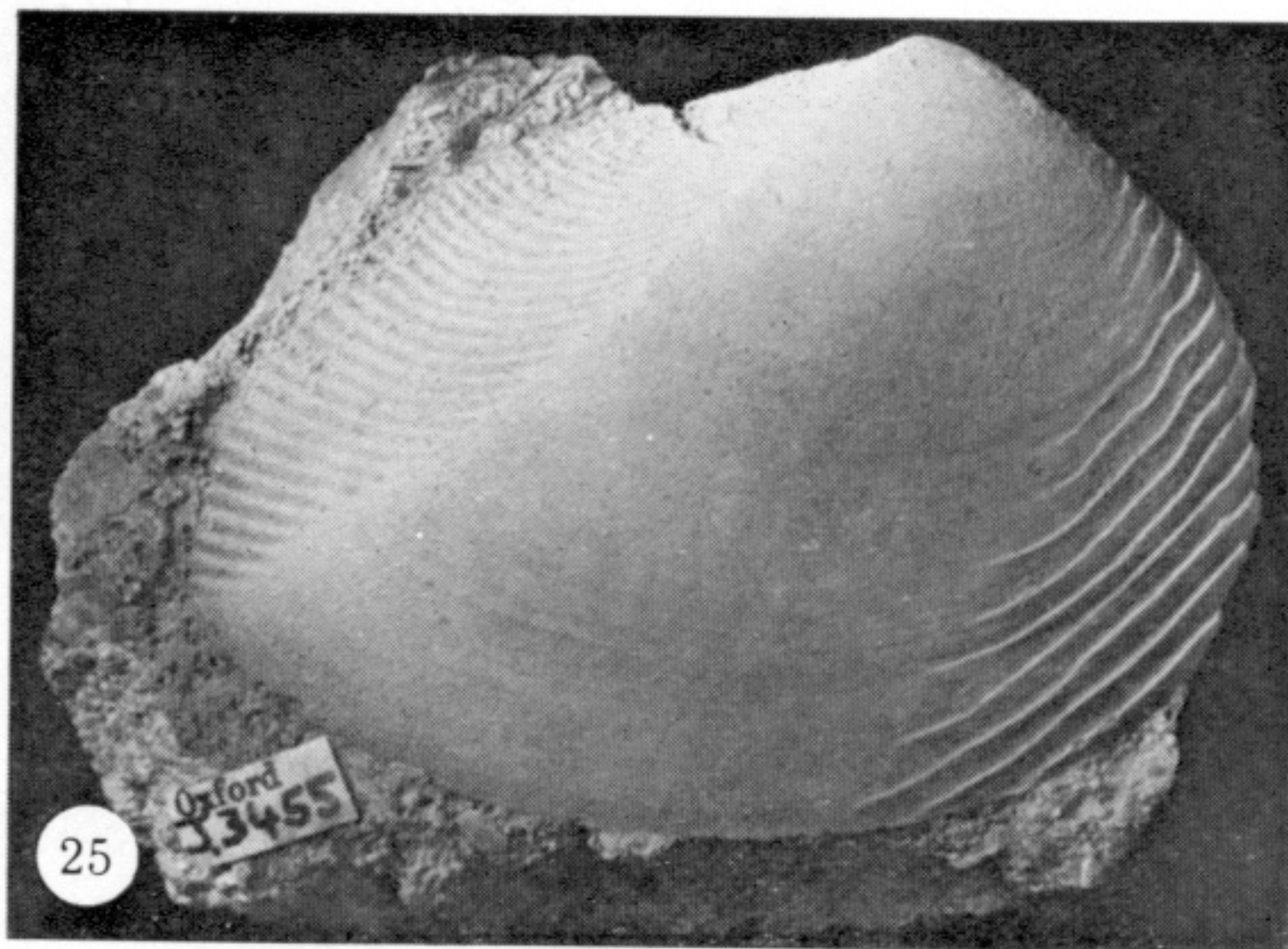
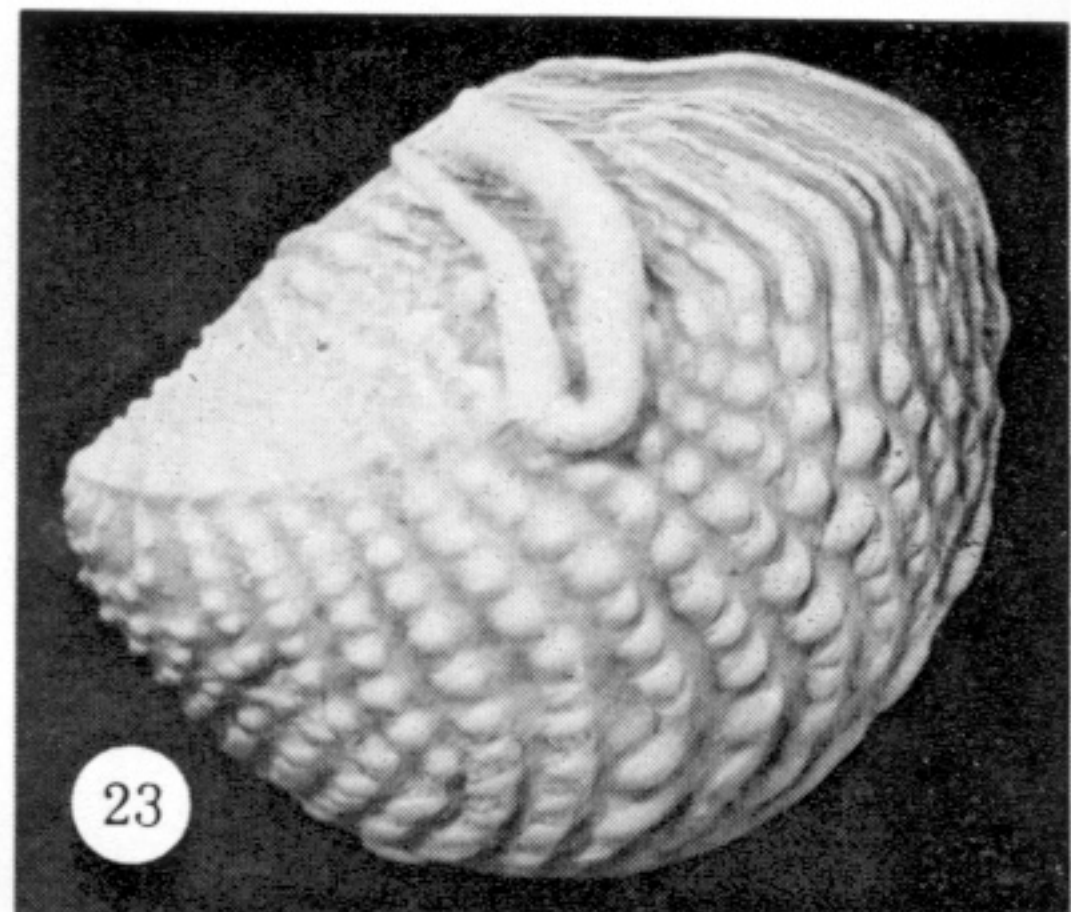
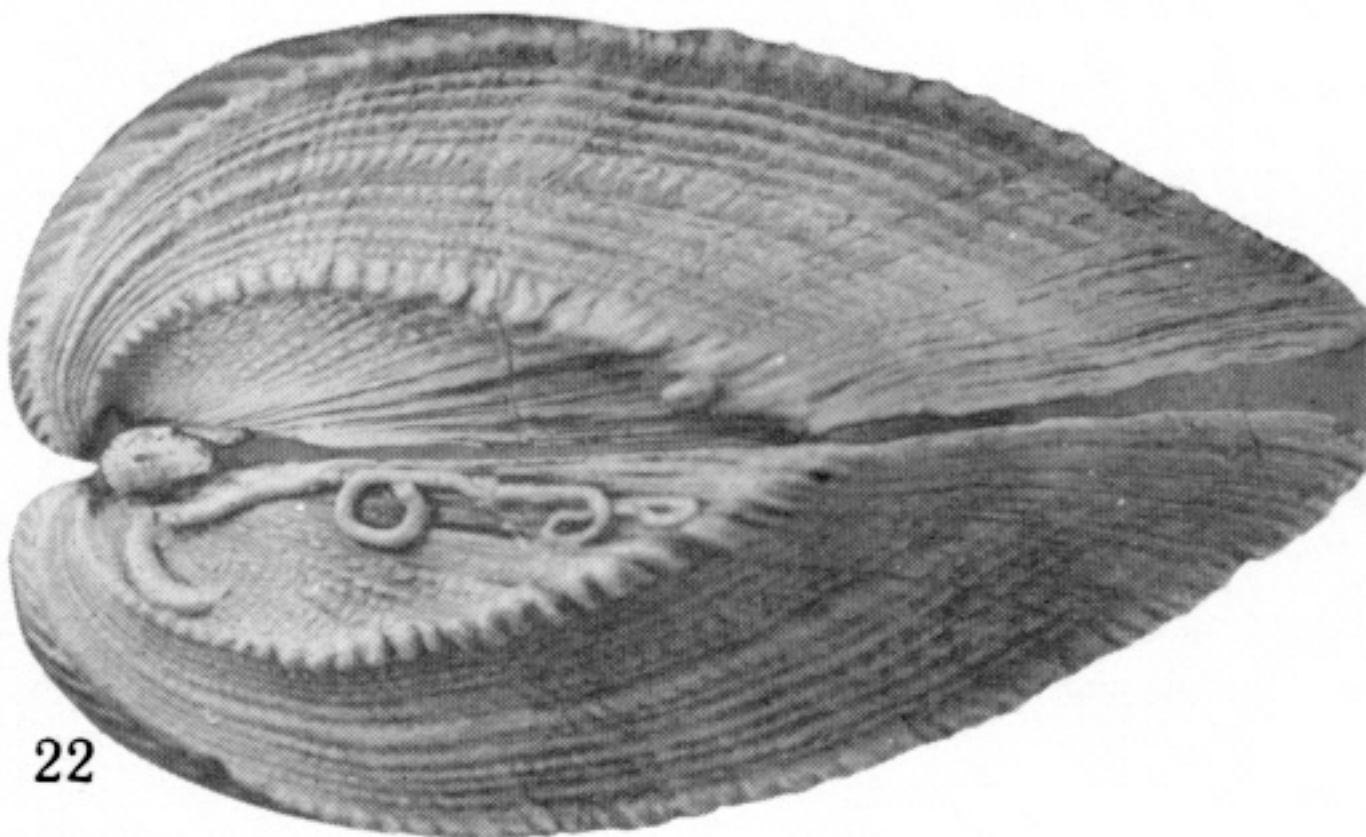
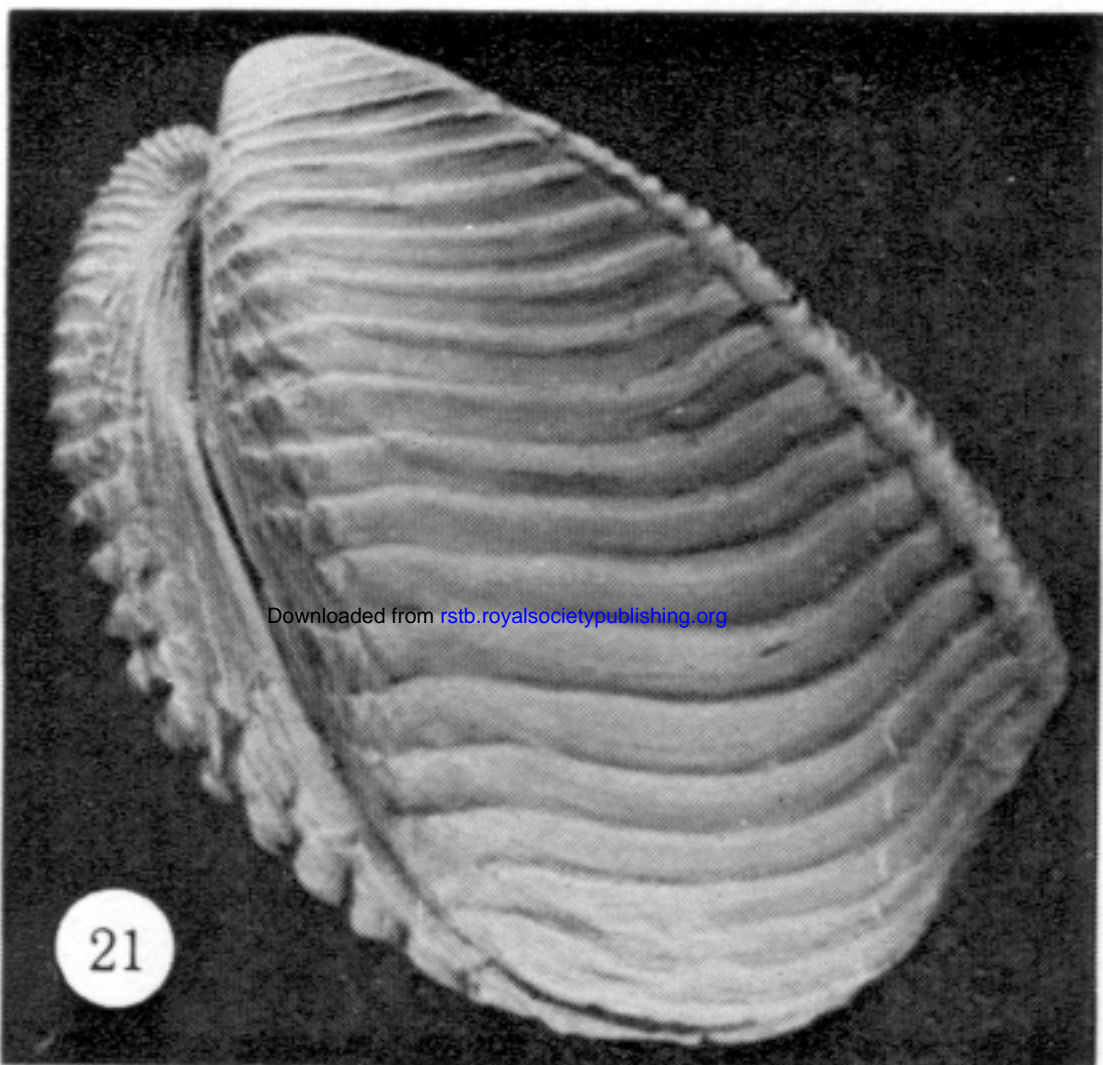
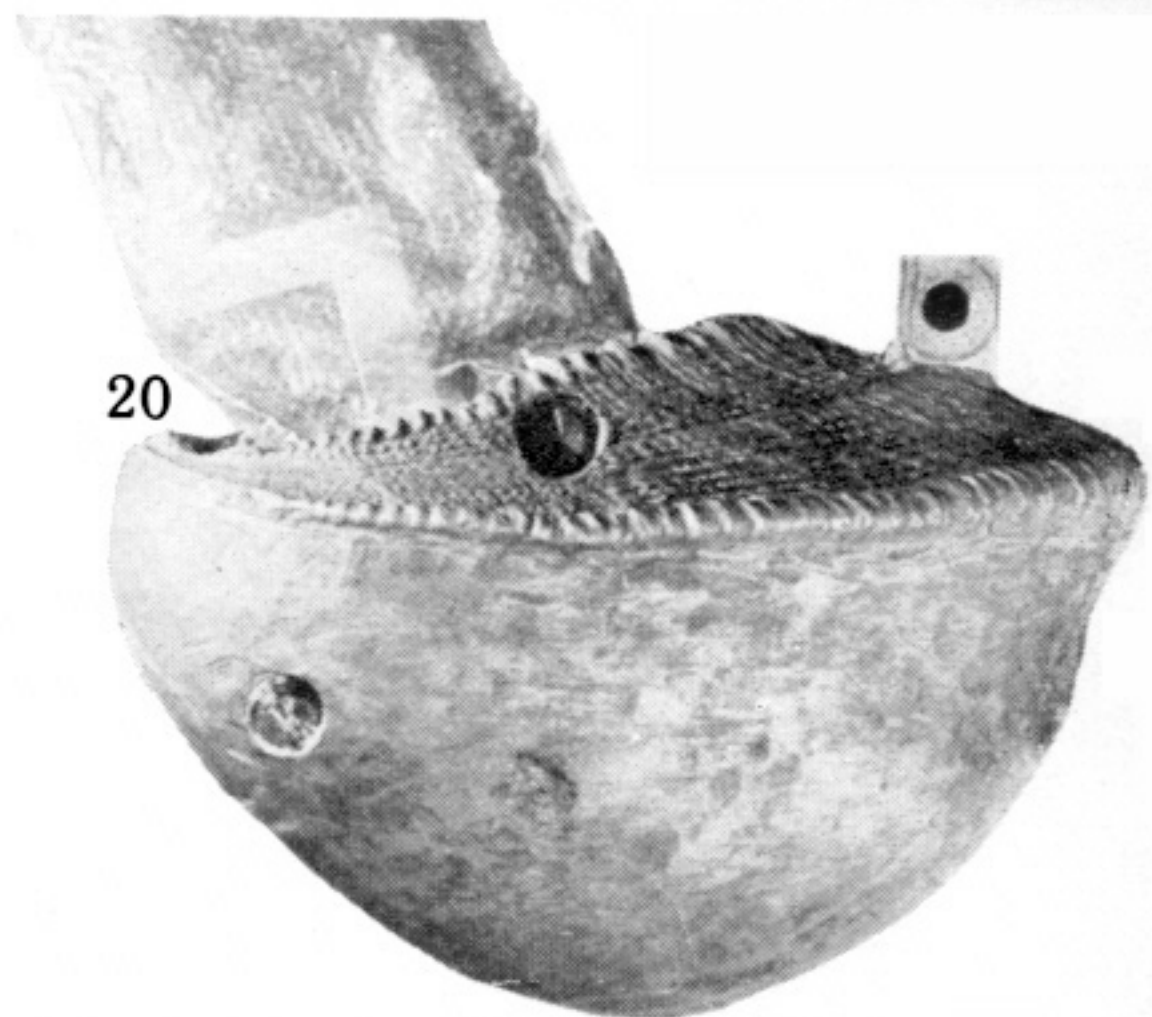
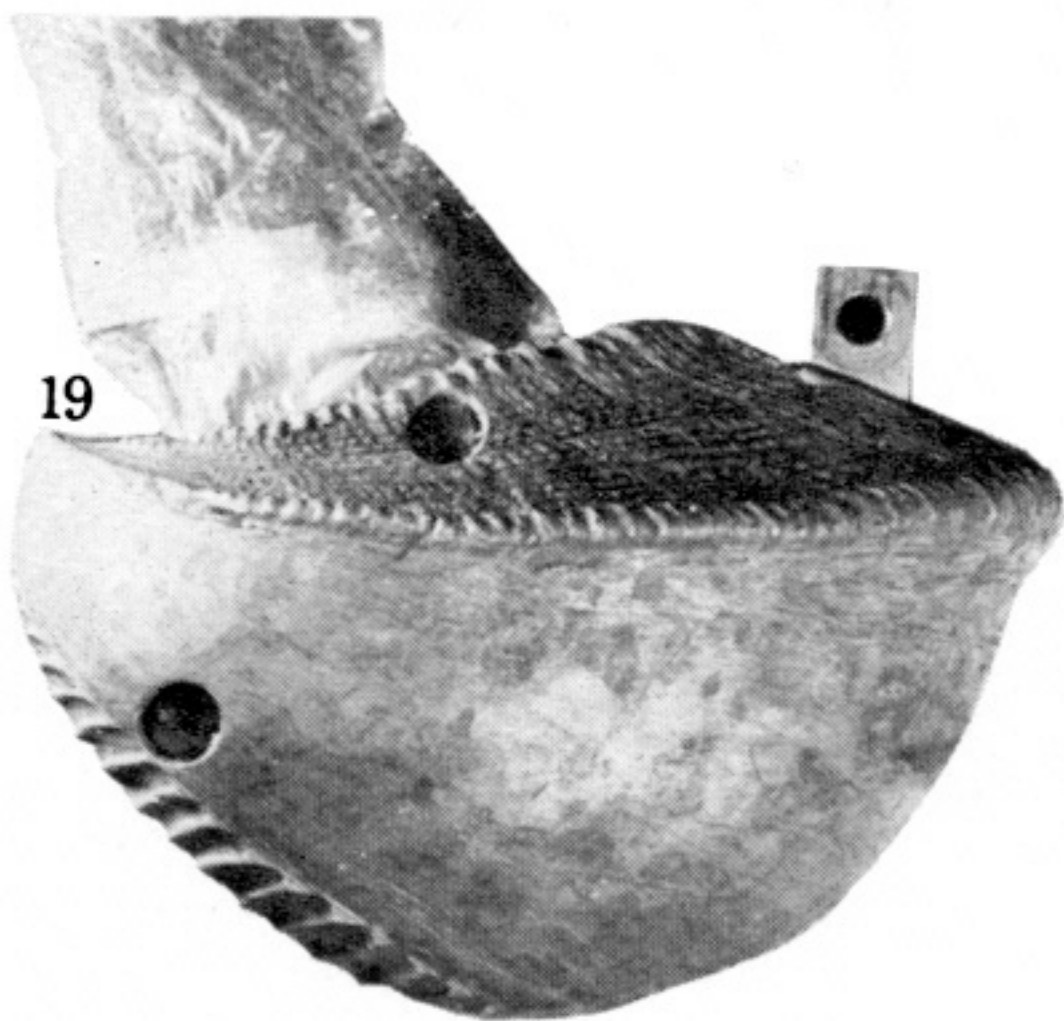
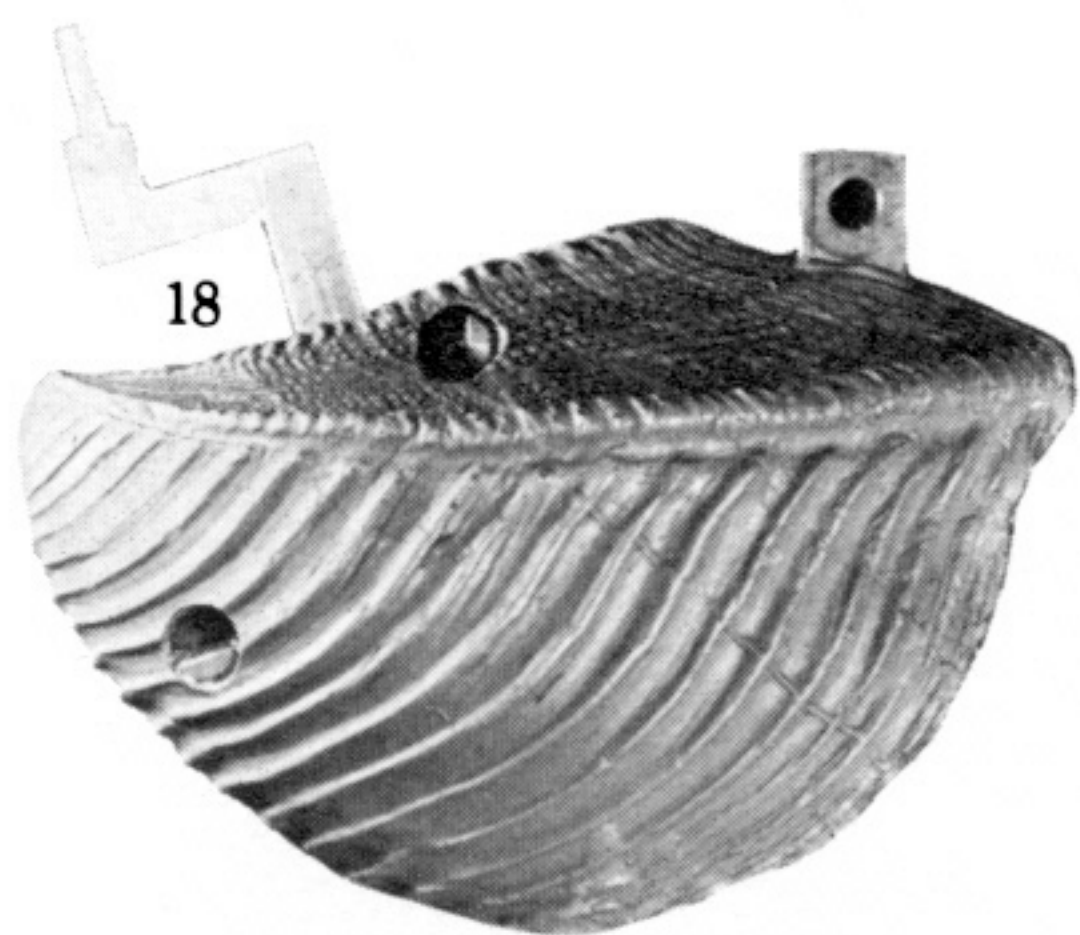
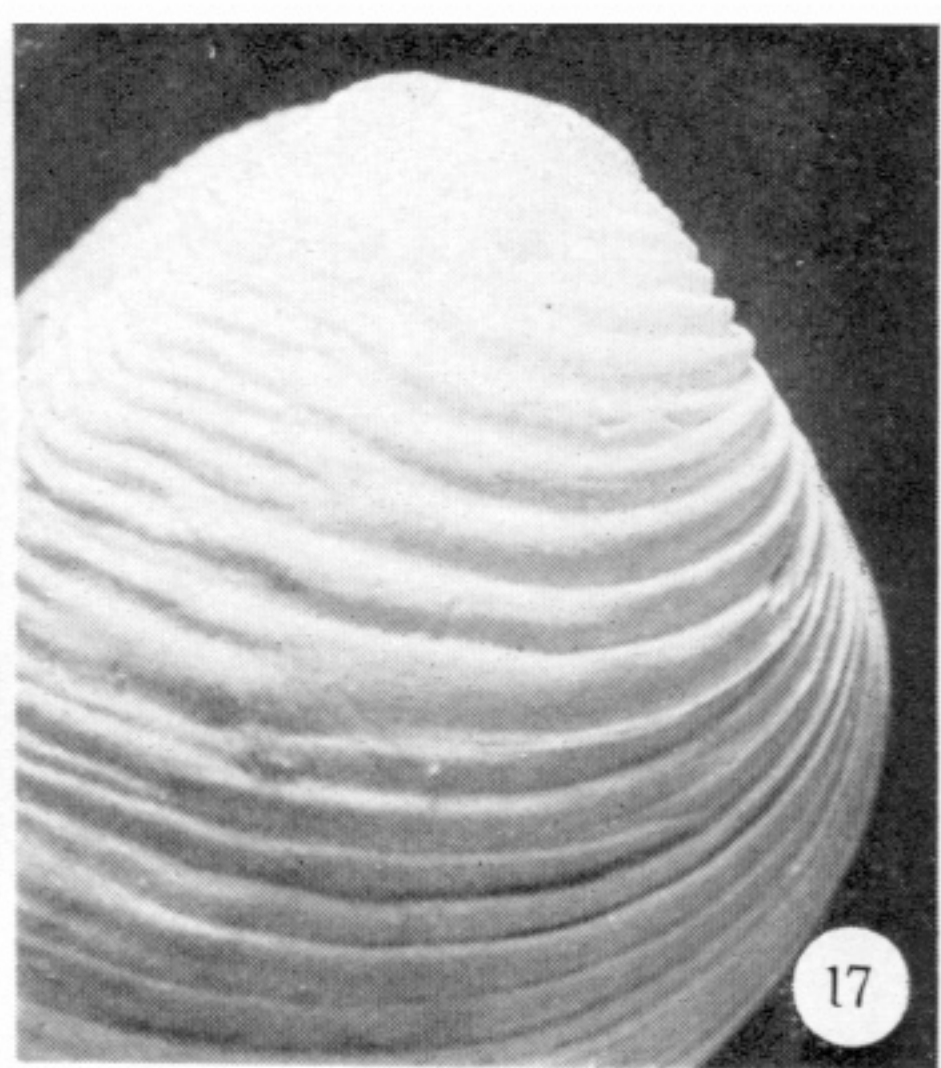
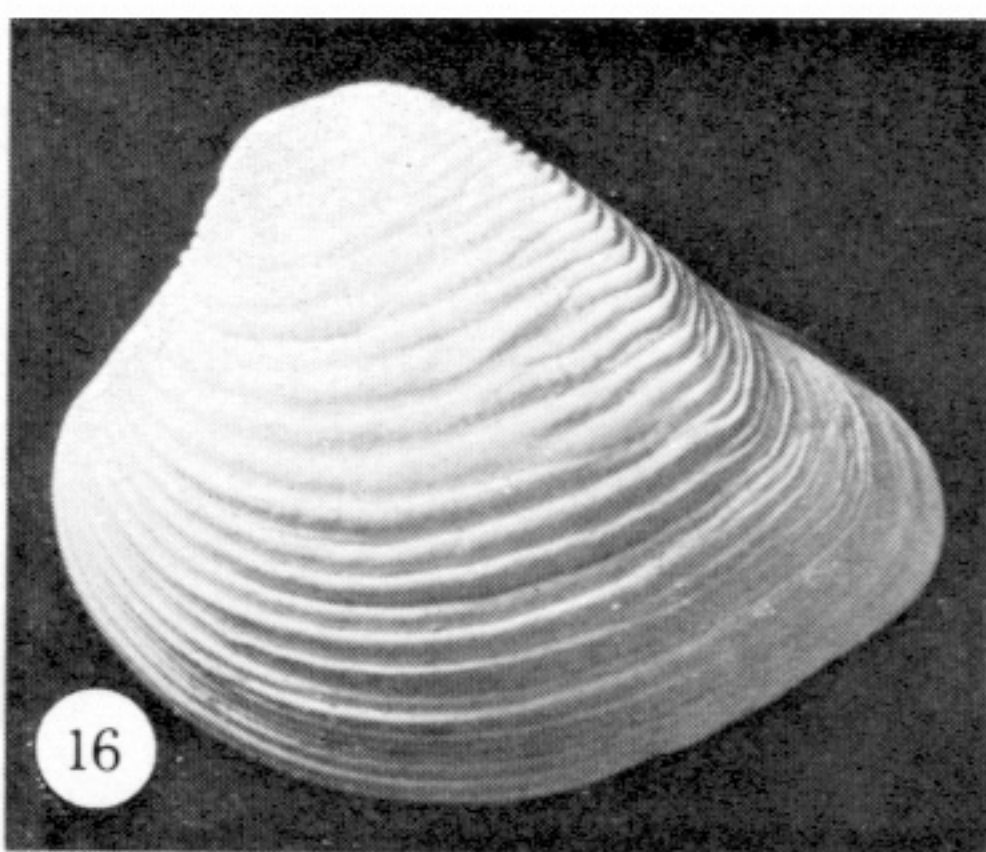
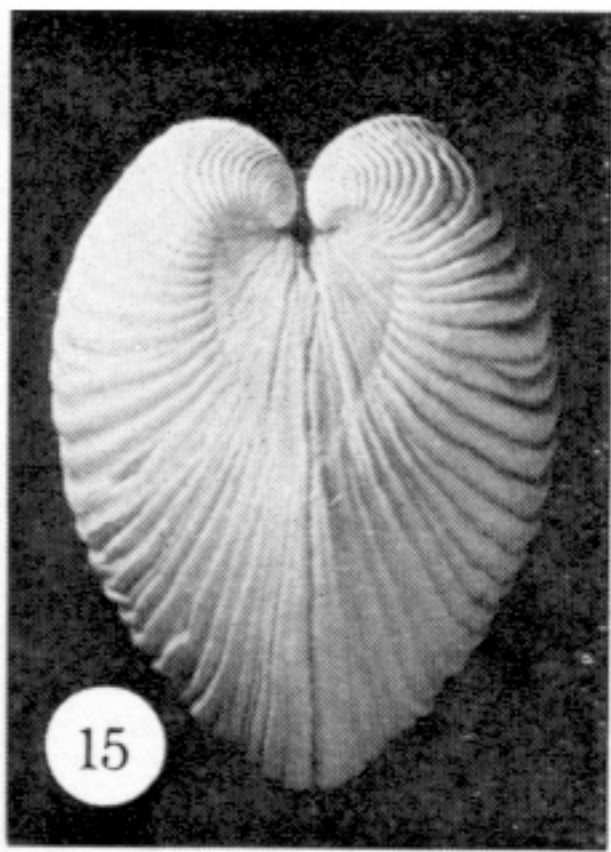
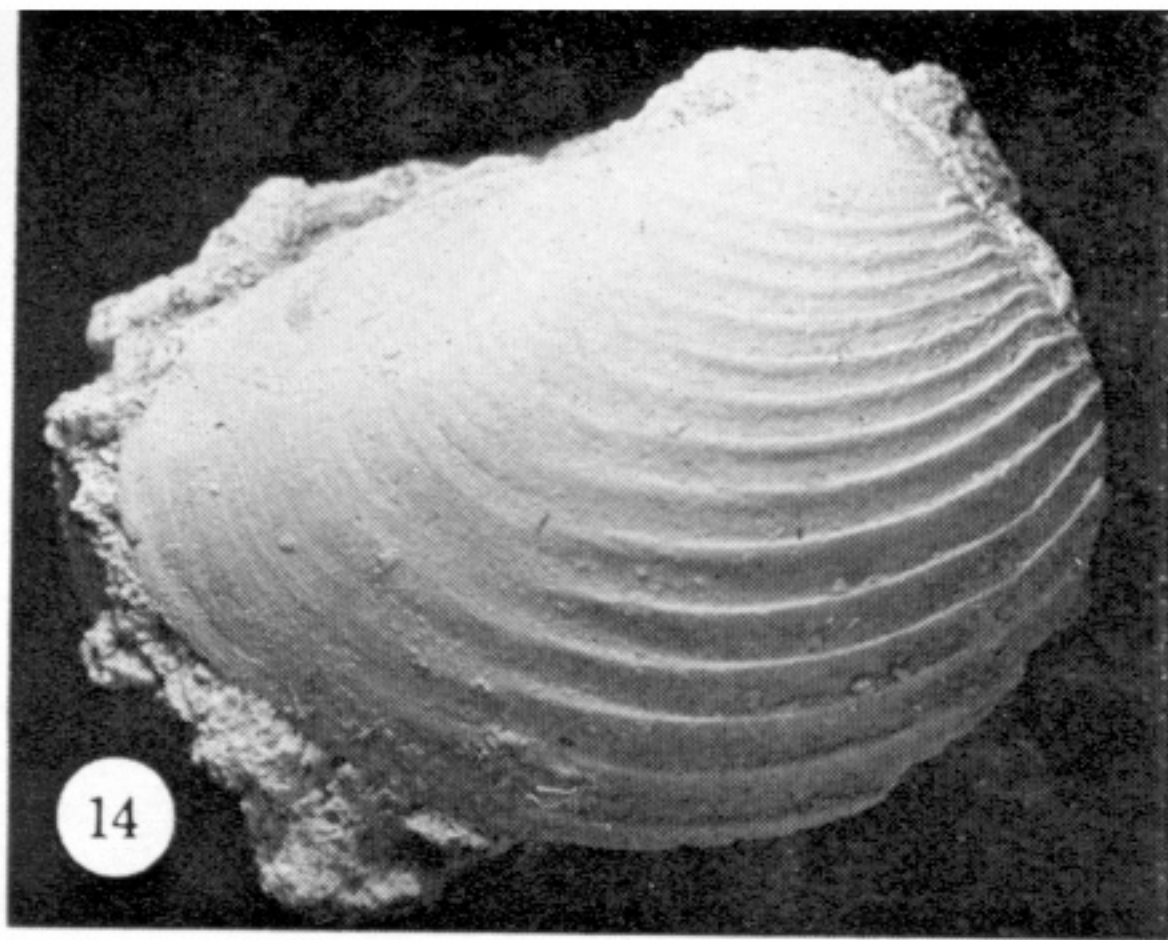
## Discussion

T. R. WALLER (*Department of Paleobiology, Smithsonian Institution, Washington, D.C. 20560, U.S.A.*). Professor Stanley's idea that the transverse ridges on hinge teeth minimize shear on the hinge of shells which must gape widely is neatly supported by evidence from larval bivalves. In the larval stage, the valves of the prodissoconch must gape widely to allow protrusion of the velum and its basal mass, which are large relative to the size of the shell. In the case of *Mytilus edulis* and *Ostrea edulis*, and perhaps in many other bivalves, the larval hinge teeth have prominent transverse ridges which minimize shear on the hinge.



FIGURES 1-13. For description see opposite.





FIGURES 14-28. For description see opposite.