COADAPTATION IN THE TRIGONIIDAE, A REMARKABLE FAMILY OF BURROWING BIVALVES

by STEVEN M. STANLEY

ABSTRACT. During the Mesozoic Era, the Trigoniidae became the dominant family of shallow-burrowing bivalves of near-shore marine habitats. Several bizarre morphological features make this the most unusual large family of burrowing bivalves ever to have existed. Forming a coadapted complex, these features enabled Mesozoic trigoniids to burrow with great efficiency, which largely accounts for their evolutionary success. Their adaptive zone included numerous niches in habitats characterized by coarse, shifting substrata. Enormous complex hinge teeth evolved to keep trigoniid valves aligned at wide angles of gape required by a large, muscular, cockle-like foot. The dentition and, by inference, the enormous foot evolved during the Triassic and ushered in a remarkable adaptive radiation. In many species, unusual arrays of knobs or ridges on the shell surface gripped the sediment to facilitate burrowing.

Trigoniids resemble cardiids and can be regarded as the cockles of the Mesozoic, but had less mobility, in part because of the friction of their complex hinge teeth. None the less, Mesozoic trigoniids were more advanced bivalves than are the Anadarinae, which have radiated in the Cenozoic. Had the trigoniids not suffered almost total extinction at the end of the Cretaceous, they would remain diverse today.

THE Trigoniacea represent one of the most unusual large fossil groups of burrowing bivalves. Study of the group was undertaken in the belief that its bizarre morphologic features should afford special opportunities for functional analysis. This has indeed turned out to be the case. Furthermore, the manner in which these structures have functioned elucidates the adaptive significance of morphologically distinct structures that perform comparable functions in other taxa. The remarkable role that the Trigoniacea played in the history of nineteenth-century science (Gould 1968) also evokes special interest. Thought to have been extinct since the Mesozoic, the superfamily was proven extant in 1802 with the discovery of a living species that Lamarck named *Trigonia margaritacea* (Pl. 1, figs. 1–11). *Neotrigonia*, the genus subsequently erected for this species (Cossman 1912), contains all known living trigoniacean species. The exact number of these, all of which live in the vicinity of Australia and New Zealand, is at issue. Deschet (1966) recently concluded that more than five living species of the genus and three or four fossil species can be recognized. Nineteenth-century debate issuing from the discovery of the living genus centered upon whether the phylogeny of the group was temporally disjunct, perhaps testifying to special creation. The debate was resolved in 1865, when *Eotrigonia subundulata* (Jenkins) (Pl. 1, figs. 12, 13) was described from the Tertiary of Australia. It was recognized that the ranges within Australia of *Eotrigonia* (Lower Eocene–Miocene) and *Neotrigonia* (Oligocene–Recent) document evolutionary continuity for the superfamily at very low diversities since the Mesozoic. In contrast, the Trigoniacea of the Jurassic and Cretaceous were highly diverse in form and taxonomic representation.

The taxonomy and phylogeny of Mesozoic trigoniaceans unfortunately remain rather poorly delineated. Lycett (1879) produced an immense monograph of the British Mesozoic taxa that remains useful, however, and Cox (1952 and Cox *et al.* 1969)

[Palaeontology, Vol. 20, Part 4, 1977, pp. 869–899, pls. 116–119.]

contributed valuable summaries of recognized genera. Although the following analysis will focus upon post-Triassic forms, the comprehensive account of early trigoniaceans presented recently by Newell and Boyd (1975) is of great value in providing a phylogenetic background, and the useful reviews of Fleming (1964) and Deschet (1966) of the relict trigoniids of the Cenozoic complement Newell and Boyd's work, to bracket the Mesozoic history of the group.

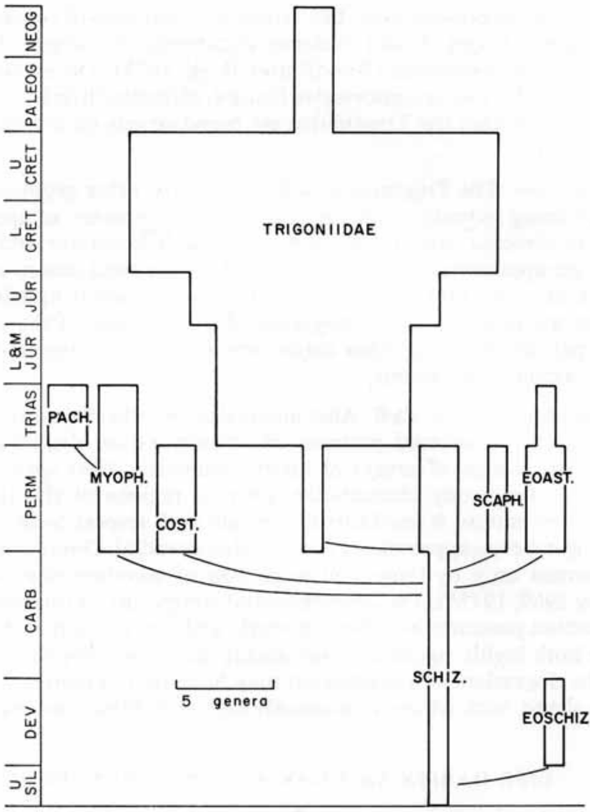
Traditional classifications (Cox, *et al.* 1969) recognize two principal trigoniacean families, the Myophoriidae (Upper Silurian–Upper Jurassic) and their descendants, the Trigoniidae (Middle Triassic–Recent). Newell and Boyd (1975), however, place the dominant Paleozoic genus *Schizodus* (Upper Silurian–Upper Permian) in a new monogeneric family, the Schizodidae, and also separate other taxa from the Myophoriidae (text-fig. 1). In their scheme, which places reduced emphasis upon grades of dentition, the Myophoriidae and Trigoniidae range back into the Permian. The trigoniids are not only more diverse and abundant in fossil occurrence than all earlier trigoniacean groups combined, but they are characterized by larger mean body size, more complex dentition, and more pronounced ornamentation of the shell surface. Indeed, although their occurrence is primarily Tethyan, the Trigoniidae are the most diverse and conspicuous group of shallow-burrowing bivalves occurring in rocks of Jurassic and Lower Cretaceous age. The early portions of this paper will treat the functional morphology of the trigoniids. Their great evolutionary success in the Mesozoic will be interpreted in a final section.

BIZARRE MORPHOLOGIC FEATURES

The unusual adaptations to which the evolutionary success of the Trigoniidae will be attributed are of four types. One of these is a fleshy organ, the foot, and the other three are skeletal features. As will become clear, these structures cannot be considered in isolation. Strong functional interrelationships have emerged that relate to a fundamental evolutionary theme of improved burrowing efficiency. Brief descriptions of the features follow.

The foot. Neotrigonia shares the ability to jump (Pl. 116, figs. 6–9) with rather few other bivalve genera (Ansell 1969; Stanley 1970). This legendary prowess of *Neotrigonia* was apparently first reported by Woodward (1851) from second-hand information. What permits *Neotrigonia* to jump is its possession of a foot bearing a strong resemblance to the typical muscular foot of the Cardiidae, the family of cockles. While in cockles the foot is typically L-shaped, in *Neotrigonia* a projecting heel gives the foot a shape more like an asymmetric T (Pl. 1, figs. 6–8). *Neotrigonia* is a burrowing animal and the present study, like the evaluation by Gould (1969), has uncovered no evidence that any trigoniacean has been anything other than a burrower.

Most clams burrow by means of rocking movements of the shell. Typically, the hinge axis is horizontal in the erect probing orientation, from which the shell rocks forward and back after the foot probes downward and obtains anchorage. In trigoniids, however, as in cardiids (Stanley 1970), the hinge axis is tilted forward in the erect probing orientation. This happens because, although the foot emerges from the shell opposite the hinge, the 'toe', which does the probing, is directed



TEXT-FIG. 1. Generic diversities of families of the Trigoniacea. Families represented by abbreviations: Pachycardiidae, Myophoriidae, Costatoriidae, Schizodiidae, Scaphellinidae, Eoastartidae, Eoschizodidae. Familial taxonomy from Newell and Boyd (1975). Generic data from Cox *et al.* (1969) and Newell and Boyd (1975).

anteriorly. The toe and heel together form an effective anchor. Though not itself fossilized, the unusual, muscular foot can be traced back through trigoniid phylogeny by indirect means because of its coadaptive relationship to certain skeletal features.

Newell and Boyd (1975) noted that the trigoniacean ligament has been a remarkably conservative feature of evolution, remaining as a simple C-shaped paravincular structure. It would seem that this simple ligament and that of the cardiids have sufficed because the muscular foot of each group has aided in valve opening, whereas the foot of most other groups of clam is too weak to perform such a function.

Hinge teeth. Trigoniid hinge teeth are large and distinctive, radiating from the beaks far into the interior of the shell (Pl. 116, fig. 4). They also project from each valve unusually far across the commissure. The articulating surfaces of the teeth bear well-developed transverse ridges. Fossil evidence documents the origin of this kind of dentition early in the Mesozoic (Newell and Boyd 1975). Once established, this specialized dentition became a conservative feature, changing little to the present day. Generic distinctions within the Trigoniidae are based largely on external shell shape and ornamentation.

Outline in lateral view. The Trigoniacea differ from most other groups of burrowing bivalves in containing virtually no strongly prosogyrous species, or species in which the umbones are directed very much anteriorly. The Schizodidae and many of the Myophoriidae are approximately orthogyrous. Of the trigoniid genera and subgenera recognized by Cox *et al.* (1969), about three-quarters are clearly opisthogyrous, and most of the rest are more or less orthogyrous. This incidence of the opisthogyrous condition is unparalleled among other major families of burrowing clams and will be shown to have special implications.

External ornamentation of the shell. Also unequalled in other families of burrowing clams is the variety of unusual patterns of ornamentation displayed within the Trigoniidae. These consist of arrays of knobs, tubercles, short spines, and ridges. Different patterns frequently characterize different regions of the shell. In many species, at least one pattern is markedly discordant with respect to the spiral growth of the shell, being not even approximately concentric or radial. Discordant ornamentation can be formed only by tangential migration of secretion sites at the mantle margin (Stanley 1969, 1975*b*). The developmental complexity of this process suggests that strong selection pressures have been at work, and the function of the ornamentation should be both highly significant and readily detectable. We might also suspect *a priori* that the discordant ornamentation may have been adaptively linked to the opisthogyrous shape, with which it commonly occurs in Mesozoic trigoniids.

LIFE HABITS AND HABITAT PREFERENCES

It would be extremely hazardous to rely solely on data from the living *Neotrigonia* in order to evaluate the modes of life and environmental occurrences of the diverse array of fossil trigoniids. *Neotrigonia* is not even a 'living fossil', if we restrict application of the phrase to extant taxa closely resembling geologically ancient forms. It ranges back only to the Oligocene and differs in form not only from Mesozoic taxa, but also from *Eotrigonia* (Pl. 116, figs. 12, 13). Over thirty living bivalve genera are considered to be much older than *Neotrigonia*, ranging back to the Late Paleozoic or Early Mesozoic (Stanley 1972). None the less, observations on *Neotrigonia* are of great value when judiciously applied to fossil forms in conjunction with related observations on the fossil taxa themselves. As part of the present study, living members of the species *N. margaritacea* (Lamarck) were studied in the laboratory. They were collected between French and Quail Islands in Westernport, a bay in Victoria, Australia.

Habitat preferences. At Westernport, *N. margaritacea* is found along the bottoms of large tidal channels at depths ranging from about 10 to 20 m, where normal tidal currents range up to 5 knots; it inhabits an area of approximately 200 km^2, commonly in densities as high as 60 individuals/m^2 (J. Watson, pers. comm. 1971). A general survey of environments and faunas of Westernport has been prepared by Watson (1971). The sediment from which the animals were collected for this study is a very poorly sorted fine sand which is representative of the substrata generally inhabited in Westernport. *Neotrigonia* is most commonly found in deeper habitats of the Australian continental shelf. It apparently extends into the harbour of Westernport because the natural tidal channels here are deep enough that their waters remain cool, the maximum summer temperature being about 16 °C. In these tidal channels *Neotrigonia* is subjected to periodic exposure by continual scour of the sediment it inhabits. Many individuals lie partly exhumed at the sediment-water interface.

The stratigraphic occurrence of trigoniids indicates that the group has included many species capable of withstanding strong water movements. A number of species clearly inhabited environments characterized by shifting substrata. My first field observation of a fossil trigoniacean was of *Pterotrigonia* sp. in the Albian Walnut Formation west of Austin, Texas, where this species occurs in a well-sorted calcarenite beneath an oolitic limestone. Both facies have been interpreted to have been formed by submarine bars in highly agitated, shallow water (Moore 1964). More recent collection in the present study of numerous trigoniid species from the Jurassic and Lower Cretaceous of England has revealed a frequent association of Jurassic species with oolitic deposits. Trigoniids were collected from sixteen stratigraphic units of the British Jurassic, and in twelve of these the beds in which trigoniids were found contained ooliths or were associated with oolitic facies. These units are the Upper *Trigonia* Grit, *Clypeus* Grit, Doulting Beds, and Anabacia Limestones of the Inferior Oolite; the Stonesfield Slate, Cotswold Slate, and White Limestone of the Great Oolite Series; the Corallian *Myophorella huddlestoni* and *M. clavellata* Beds; the Lower *Trigonia* Pebble Bed (McKerrow 1958, p. 17) and Upper *Trigonia* Bed (McKerrow 1958, p. 18) of the Corallian Berkshire Oolite Series; and the Portland Freestone Beds.

There is little evidence that trigoniids actually inhabited bars of shifting oolite. In the Bahamas today the only bivalve to occupy submarine oolite dunes is the very-rapid burrower *Tivela abaconensis* (Purdy, 1964). Indeed, some oolitic deposits of the Mesozoic formed in rather quiet water. Klein (1965) interpreted the oolitic Cotswold Slates, for example, as having a lagoonal or mudflat origin, and Wright (1974) concluded that units of the Gypsum Spring Formation of Wyoming that yield *Trigonia americana* formed in hypersaline lagoons. None the less, Mesozoic trigoniids tend to occur in grain-supported arenites, many of which, like the calcareous Walnut Formation described above, represent somewhat unstable habitats. In the present study trigoniids were collected from twenty-five Jurassic and Cretaceous units, and in twenty-one of these the shells were found in beds that thin-section analysis revealed to be of grain-supported arenitic lithology. This sample of occurrences is reasonably unbiased, in that it represents promising collecting sites recommended by palaeontologists familiar with much of the Jurassic and Cretaceous of England. This disposition toward coarse substrata may have had its origins in trigoniaceans of the mid-Paleozoic. Bowen *et al.* (1974) report that *Eoschizodus* tends to occur in sandstones in the Upper Devonian Sonyea Group of New York State. In North America, the ability of Mesozoic trigoniids to occupy unstable, sandy substrata is shown not only by the occurrence in the Walnut Formation described above, but also by the presence of *Scabrotrigonia emoryi* in what Scott (1974) has interpreted to be 'mid shoreface' deposits ('downslope from the wave break zone') in Lower Cretaceous deposits of the south-western United States.

The ability of a group of organisms to occupy coarse, somewhat unstable substrata need not preclude the adaptation of some of its representatives to more stable benthic settings. Some Mesozoic trigoniids occupied muds or muddy sands. Even these species, however, tended to inhabit shallow, near-shore settings. *Vaugonia*, found in life position in mudstones of the Peak Shales of Yorkshire, occurs with wood fragments (Pl. 117, fig. 3) in what are probably lagoonal deposits. In the Lower Greensand of the Isle of Wight, *Yaadia nodosa* and *Pterotrigonia mantilli* abound in beds of muddy sandstone that also contain abundant remains of land plants (Casey 1961). The Fuller's Earth of southern England, which yields species of *Trigonia* and *Myophorella* (Arkell, 1947), has been judged to be a lagoonal or mudflat deposit (Klein 1965). Units of the Sundance and Gypsum Springs Formations of Wyoming in which species of these same genera occur are also considered to be lagoonal (Wright 1974). Pliensbachian beds of Vancouver Island, British Columbia containing three trigoniid species also contain plant fossils and coal (Poulton 1976). Trigoniids abound in the near-shore facies of the British Chalk, but are virtually unknown from deep-water facies (W. J. Kennedy, pers. comm., 1970; Carter 1972). This sample of occurrences, in combination with the association of many other species with oolitic deposits, indicates that a large majority of Mesozoic trigoniids inhabit areas of the sea-floor no deeper than perhaps 10 or 15 m. Living populations of *Neotrigonia* live primarily in deeper waters, so that the occurrence of this genus is quite atypical for the family.

Life habits. We can predict the life positions of most trigoniids from their shell form. The typically flattened posterior region of the shell, where the inhalent and exhalent currents are located, should normally lie parallel to, and level with, the surface of the substratum (Seilacher 1954; Stanley 1970). This is, in fact, the life position of *Neotrigonia*, as observed by McAlester (1965). As among other non-siphonate burrowing bivalves, the posterior region of the shell is often exposed at the sediment-water interface. In some members of the population of Westernport, the exposed region is colonized by sponges and, less often, by hydrozoans (Pl. 116, figs. 10, 11). Comparable encrustation is frequently seen among fossil trigoniaceans, confirming the inferred life position (Pl. 117, figs. 7, 9). Growth of the serpulid along but not across the commissure of the animal shown in Plate 117, fig. 9 suggests that the worm colonized the shell while the clam was alive. Even more direct evidence confirming the inferred life position is *in situ* preservation of *Vaugonia* (*Vaugonia*) *literata* in the Toarcian Peak Shales (Pl. 117, fig. 3).

Even in the absence of behavioural observations, the large, muscular foot of *Neotrigonia* offers evidence that the genus is an adept burrower (McAlester 1965). This inference has been borne out by laboratory study of *N. gemma* by Tevesz (1975) and of *N. margaritacea* by the present author. Because a flowing sea-water system was not available in Melbourne, where burrowing observations were made, individuals were studied in aerated tanks of natural sea-water immediately after capture. Following procedures established in an earlier study (Stanley 1970), a burrowing rate index (B.R.I.) was calculated for *N. margaritacea*:

$$\text{B.R.I.} = \frac{{}^{3}(\text{mass (g.)})}{\text{burrowing time}} \times 100.$$

This index permits comparison of species of differing size. Using cube root of mass rather than a direct linear measurement removes the bias of shape. Burrowing time is the interval from erection of the shell to complete burial. Native sediment was used in the study of *Neotrigonia*, and the temperature was maintained at 16 °C., the maximum summer temperature at the Westernport habitat. The index averaged 0·44 for the three animals that were timed (Table 1). Tevesz (1975) calculated a mean burrowing rate index of 0·8 for ten individuals of the species *N. gemma* at about the same temperature. Burrowing time for a bivalve is related inversely to temperature, and the scale of comparison used in the earlier, more general study (Stanley 1970) was established for experiments at 18 °C. or above, where little effect of temperature is seen. Allowing a slight upward adjustment of the *Neotrigonia* indices on this count, *N. margaritacea* falls within the category of moderately rapid burrowers. *N. gemma* falls within this category even without such adjustment.

TABLE 1. Calculation of a burrowing rate index for *Neotrigonia margaritacea* (Lamarck) at 16 °C.

Length of shell	Weight of animal (g)	Burrowing time (sec.)	Burrowing rate index
3·45	15·2	525	0·47
2·84	7·1	390	0·49
2·6	5·5	470	0·37
		mean	0·44

A deficiency in the burrowing behaviour of *Neotrigonia* that is not revealed by the calculation of burrowing rate indices is the tendency of members of the genus in nature to lie partly exposed on the sediment surface for long periods of time without starting to rebury themselves. Encrustation by epibionts covers only the exposed posterior tip of many living Westernport animals, as described earlier, but other individuals have remained less deeply buried and reclining on one valve long enough for sponges to cover most of the upper valve. Its frequent failure to reburrow promptly, and its slightly lower burrowing rate index, show *Neotrigonia* to be a less efficient burrower than are most living cockles (Cardiidae), which more than any other extant family resemble the Trigoniidae in both gross shell and pedal morphology. None the less, *Neotrigonia* is a more rapid burrower than *Anadara* (Arcidae), *Glycymeris* (Glycymeridae), *Astarte* (Astartidae), *Eucrassatella* (Crassatellidae), *Venericardia* (Carditidae), or any other non-siphonate, suspension-feeding genus of marine bivalves that I have studied (Stanley 1970). The burrowing ability of the Trigoniidae, contributed primarily by the muscular foot, accounts for the fact that many of its Mesozoic representatives have successfully invaded coarse, somewhat unstable substrata from which periodic exhument by current scour was inevitable.

FUNCTIONAL MORPHOLOGY

Dentition. In all members of the Trigoniidae, the articulating surfaces of primary hinge teeth bear secondary grooves (Pl. 116, fig. 4), which have been termed striations (Newell and Boyd 1975). Because of the high relief produced by these features and the intervening ridges, I prefer instead to refer to the ridges as secondary dentition. As Newell and Boyd (1975) have noted, the function of the secondary dentition must be to keep the valves aligned. Indeed, it is the function of the primary dentition to keep the valves aligned, but less perfectly. The implication would seem to be that there has been some special utility in the Trigoniidae for a more effective alignment system than is found in most other bivalve families. In general, misalignment at closure leaves slight gapes between the valves in certain regions, rendering a clam vulnerable to predation or damage from unfavourable conditions of the physical environment.

The inferred problem of valve alignment in trigoniids clearly stemmed from the evolution of the muscular foot. When the foot is extended for burrowing, and especially for jumping, the valves of *Neotrigonia* gape quite widely. The jumping animal of Plate 116, fig. 3 has opened its valves to an angle of about 15°. The angle of gape required by *Neotrigonia* merely for burrowing greatly exceeds that observed for most other burrowing bivalves, in which the foot is a less muscular structure that is compressed into a sheet-like configuration where it passes between the valves. In venerids, for example, gaping of the valves during probing of the foot is barely perceptible from most vantage points. If valve closure has an accidental shearing component (i.e. a component of rotation parallel to the commissure), the degree of final misalignment will be proportional to the original angle of gape. Herein lies the special problem of the trigoniids. Cockles (Cardiidae), having a muscular foot like that of the trigoniids, share this problem. By means of photography, I have found maximum gaping of the valves in the normal burrowing behavior of *Trachycardium egmontianum* (Shuttleworth) to be about 13° (Pl. 118, fig. 1). In *Trachycardium* and other cockles, the problem of maintaining alignment has been solved by the deployment of prominent lateral hinge teeth that occur far from the beaks and project well across the commissure (Pl. 118, fig. 2). As one might predict, the anterior teeth, which lie further from the hinge axis than the posterior teeth, are especially long. Nothing resembling the remarkable lateral teeth of cockles is found among other bivalve taxa.

EXPLANATION OF PLATE 116

Figs. 1, 2. Anterior and left lateral view of a juvenile *Neotrigonia margaritacea* (Lamarck), × 1·15.

Fig. 3. Left lateral view of adult *N. margaritacea*, × 1·15.

Fig. 4. Dentition of *N. margaritacea*, × 2·1.

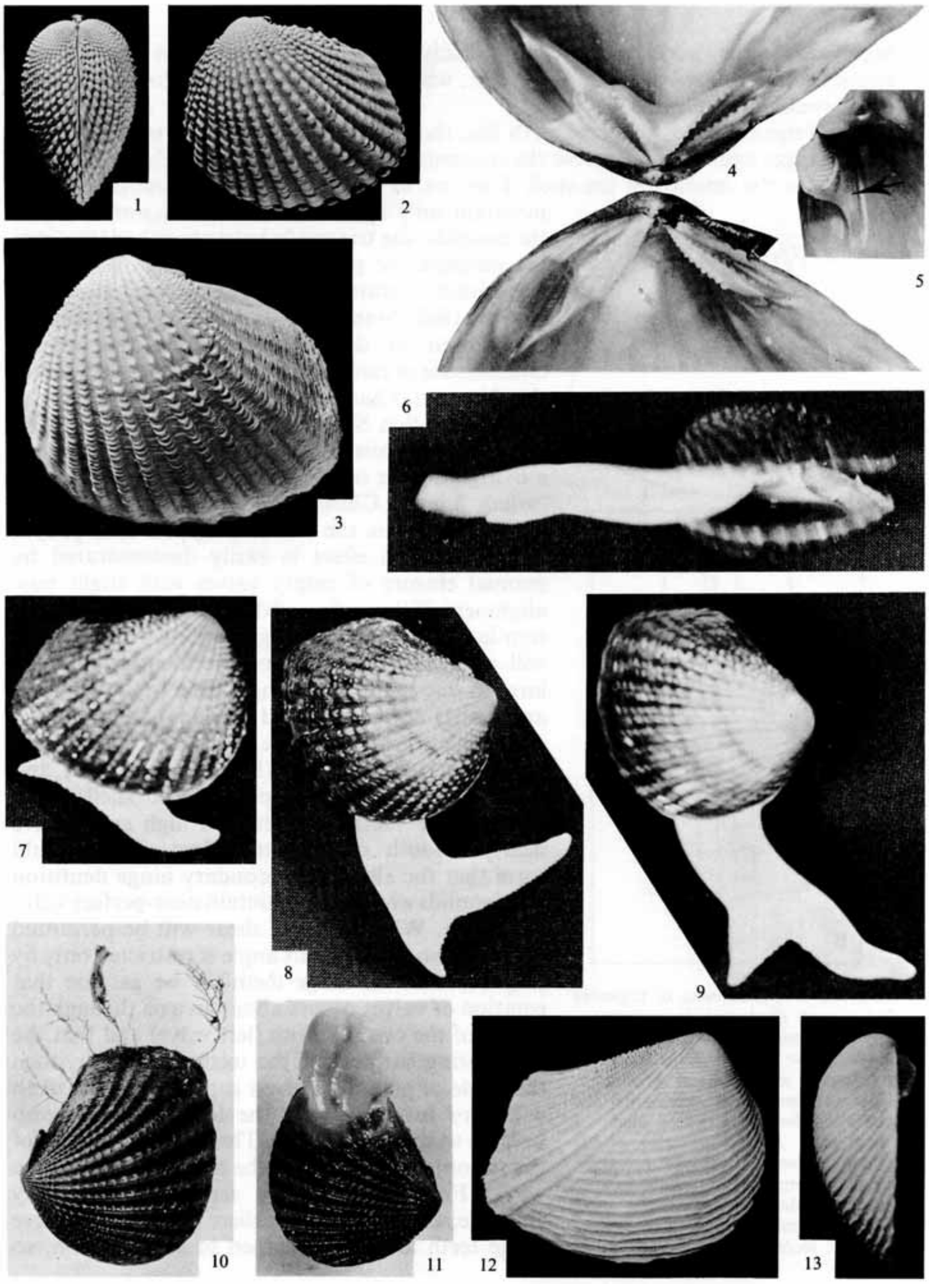
Fig. 5. Myophorous buttress (arrow) supporting the anterior hinge of the right valve of *N. margaritacea*, × 1·25.

Figs. 6–9. Pedal movements of *N. margaritacea* in the process of leaping, × 1.

Fig. 10. Hydroids attached to the posterior of a live specimen of *N. margaritacea* figured in living orientation. From Westernport, Victoria, Australia, × 0·9.

Fig. 11. Sponge attached to the posterior of a live specimen of *N. margaritacea* figured in living orientation. From Westernport, Victoria, Australia, × 0·85.

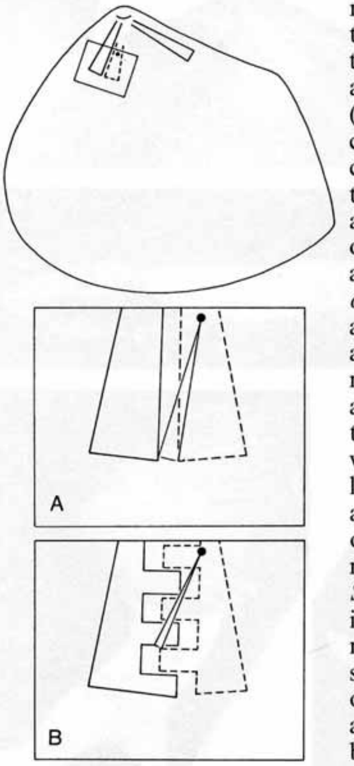
Figs. 12, 13. Right lateral and anterior views of *Eotrigonia subundulata* (Jenkins), × 1·4. BMNH L42330. The abbreviation BMNH stands for British Museum (Natural History).



STANLEY, trigoniid burrowing bivalves

Significantly, the lateral teeth are only weakly developed in the unusual living cardiid species *Papyridea soleniformis* Bruguière, which has a less muscular foot than most other cockles (Stanley 1970).

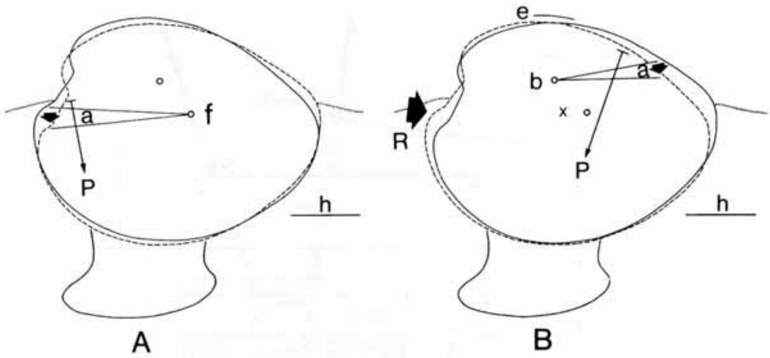
The Trigoniidae lack lateral teeth like those of cockles, but their primary hinge teeth project unusually far across the commussure and radiate unusually far from the beaks into the interior of the shell. Even so, at wide gapes simple dentition would maintain only approximate valve alignment. Like the cardiids, the trigoniids have special adaptations to complete the process as the valves come into apposition. Contrary to ideas expressed elsewhere (Carter 1968; Stanley 1970), it seems clear that the crenulation or denticulation along the ventral commissure of cardiids and certain other taxa serves this function. I have discovered this not intuitively, as it seems that Stenzel (1971) did earlier, but by observing the misaligned closure of the valves of a living member of the venerid species *Chione cancellata* Linné. Closure was completed with an audible click, as the valves snapped into proper alignment. The effect is easily demonstrated by manual closure of empty valves with slight misalignment. If the surface of denticulation or crenulation has a generally zig-zag or sine-wave profile, it will produce alignment from accidental offsets as large as one-half a wave length. The trigoniids have apparently never employed marginal denticulation or crenulation to complete the job of valve alignment. Even *Neotrigonia* (Pl. 116, figs. 1–3) and *Scabrotrigonia*, in which pronounced shell ridges intersect the ventral margin at a high angle, have nearly smooth commissures. Instead, it would seem that the elaborate secondary hinge dentition of trigoniids evolved to maintain near-perfect valve alignment. What angle of shear will be permitted between two valves if this angle is restricted only by play between the hinge teeth? If we assume that rotation of valves occurs about an axis through the centre of the central tooth (left valve) and that the articulating surfaces of the teeth are planar, then the angle of play for a given gap between the teeth will vary inversely with the length of the teeth parallel to the commissure. The unusual features of the trigoniid hinge reduce the angle of play in two ways. First, the primary teeth are unusually elongate, as mentioned earlier. Secondly, bivalve hinge teeth are wedge-shaped in cross-section, so



TEXT-FIG. 2. Functioning of trigoniid hinge teeth illustrated diagrammatically by consideration of hypothetical shells. *Above*: outline of shell showing rectangular area enlarged in A and B. Gap between teeth represents the condition for a particular angle of valve gape. Axis of shearing of the valves represented by solid dot. A, angle of play permitted by teeth lacking secondary dentition. B, smaller angle of play permitted by teeth possessing secondary dentition.

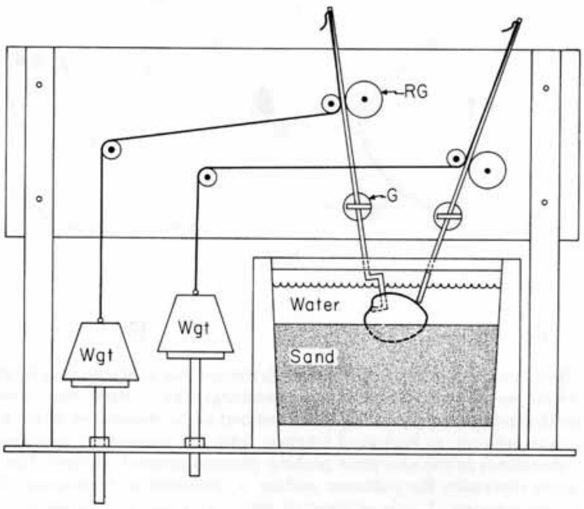
that simple teeth with smooth surfaces permit an increased angle of play parallel to the commissure with increased gape; the secondary dentition of the trigoniids must have arisen to maintain closer alignment at wide gapes, as illustrated in text-fig. 2. It is chiefly the first-formed and last-formed secondary teeth that function at any given time. The latter assume intermediate positions as new teeth are added during entogeny.

Shell profile. The unusually high incidence of opisthogyrous morphologies in the Trigoniidae is interesting in light of the general value of the prosogyrous condition to burrowing (Stanley 1975*b*). Because the prosogyrous condition is typical of burrowing bivalves, its function will now be briefly reviewed.



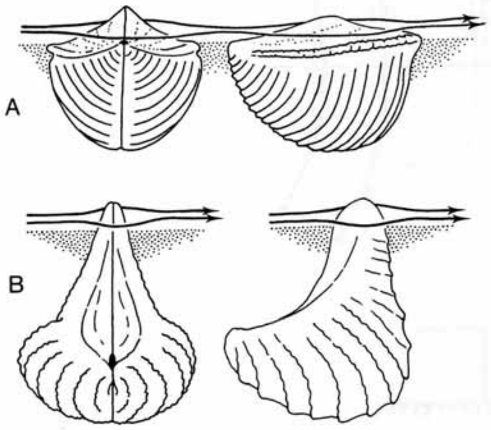
TEXT-FIG. 3. Burrowing mechanism of *Mercenaria mercenaria*, as shown by a single forward-and-back rocking movement documented by cinematography. A, partly buried shell rocking forward from the erect probing position (solid outline) to the position of maximum forward rotation (dashed outline); B, backward rotation from the position of maximum forward rotation (solid outline) to the next erect probing position (dashed outline). The dotted line in each diagram represents the sediment surface. P, direction of contraction of the pedal retractor causing rotation; f, axis of forward rotation; a, angle of rotation of the shell; h, horizontal line; b, axis of backward rotation; R, resistant force of sediment against the blunt anterior region of the shell; e, position of the dorsal shell margin in the previous erect probing position (solid outline of diagram A), showing downward progress.

Of geometric necessity a helically coiled, prosogyrous shape produces broad umbones and requires the presence of a lunule (Carter 1967). The umbones and lunules form a blunt anterior end of the shell. The function of this typical shape relates to the forward-and-back rocking movements of burrowing (Stanley 1975*b*). It has been demonstrated by analysis of ciné-photographs that the rocking movements of a typical species, *Mercenaria mercenaria* (Linneus), are purely rotational. The animal penetrates forward and downward by a series of 'walking' movements, because the axis of backward rotation lies anterior to the axis of forward rotation (text-fig. 3). The anterior pedal retractor muscles relax after rotating the shell forward. The axis of backward rotation is then determined chiefly by the direction of the force applied by the posterior pedal retractors and by the distribution of the resistant forces of sediment against the shell. In part because of the sizable forward component of the posterior retractor force, the blunt anterior end is jammed forward into the sediment during backward rotation, tending to lock in place because of its large surface area. Since the anterior end does not slip upward easily, the axis of backward rotation is shifted anteriorly so that a large downward step is taken. Using robots of *Mercenaria* made to burrow with a machine (text-fig. 4), this shift has been demonstrated, as has an increase in downward progress for a given number of rocking movements (Stanley 1975*b*). Robots were cast from a mould of a real shell. An unaltered robot burrowed about 20% deeper in twenty rocking movements than a robot altered by the addition of a discoid 'false front', which did not catch so effectively in the sediment (Stanley 1975*b*).



TEXT-FIG. 4. Machine used to make robots burrow. The robot is pushed into sand in an aquarium by two rods pulled downward by brass cables to which weights are attached via pulleys. Roller guides (one of which is labelled RG) and clasp guides (one of which is labelled G) hold rods in place. Guides and pulleys are all fixed in temporary positions to a vertical plate by magnets. Rods were moved manually in final experiments.

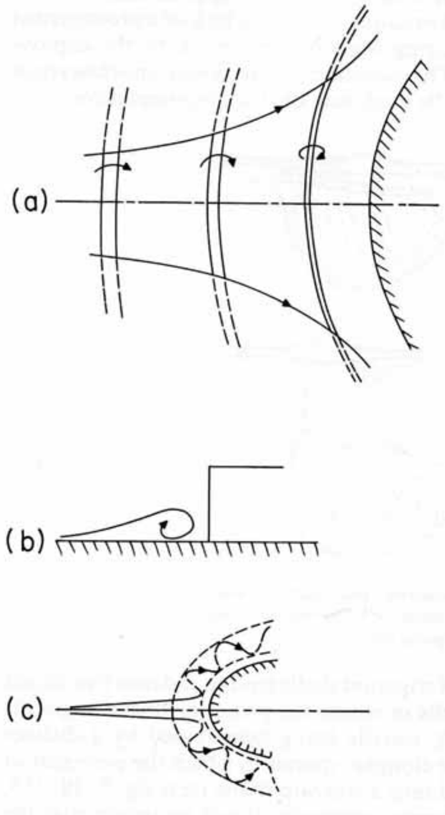
If a pronounced prosogyrous shape is useful in burrowing, why is this shape virtually absent from known species of the Trigoniidae, which did, after all, evolve in the direction of increased burrowing efficiency? The answer seems to be that the primitive morphology of the family made it very unlikely that a prosogyrous shape would evolve from the essentially orthogyrous shape of the ancestral Myophoriidae. The anterior adductor muscles of trigoniids lie unusually close to the beaks. Furthermore, in even the earliest trigoniids, the muscle attachment on each valve is located on a myophorous buttress that is tied to the anterior hinge tooth (Pl. 116, fig. 5). In fact, it seems likely that the origin of the buttress had nothing to do with the function of the muscle, but served to strengthen the elongated teeth. (The posterior teeth, lying closer to the valve margin, received adequate support without the buttress.) Thus, a large amount of umbonal space was required by (1) the huge teeth, which radiate from and are necessarily tied to the beak, (2) the pronounced myophorous buttress that was required to support the teeth, and (3) the anterior adductor that was attached to the buttress. Appreciable forward coiling of the beak, which requires a relatively low whorl expansion rate (Raup 1966), was therefore precluded. As will be described in the following section on shell ornamentation, the lack of a prosogyrous shape for efficient burrowing was offset during Mesozoic evolution by the deployment of special patterns of ornamentation. The evolution of a markedly opisthogyrous shape seems to have been associated with the evolution of this ornamentation.



TEXT-FIG. 5. Flow of bottom currents past partly exposed posterior margins of the shells of *Trigonia* (A) and *Scabrotrigonia* (B).

Morphologies of the posterior regions of trigoniid shells tend to fall into two broad categories. The first includes compact shells in which the posterior-dorsal region is pyramidal (text-fig. 5; Pl. 117, figs. 8–10), usually being demarcated by a distinct carina. The second category includes more elongate species in which the posterior of the shell has become curved and extended into a rostrate shape (text-fig. 5; Pl. 118, figs. 9–11; Pl. 119, fig. 12). The two categories intergrade. It will be shown that the morphology of each is an adaptation for reducing scour of sediment from around the shell in the life position.

It is quite common for currents or waves touching the sea-floor to scour sediment from around pebbles, shells, or other obstacles protruding above the bottom. This phenomenon is not well understood (Richardson 1968; see also Allen 1965 and Karcz 1968), but the general explanation is that because of drag, currents move more slowly near the sediment-water interface than higher in the water column. Flowing water can then be viewed as passing over the bottom with a rotational component of movement, known as vorticity. As a vortex approaches a protruding obstacle, it is stretched around the obstruction (text-fig. 6). Vorticity then increases because the product of vorticity times cross-sectional area must remain constant. Stretched vortex tubes that accumulate around an obstruction cause scour if a critical velocity is reached. If the flow of water in the environment is unidirectional, scour patterns tend to have a crescentic shape.



TEXT-FIG. 6. Illustration of the nature of vorticity: *a*, diagrammatic representation of the stretching of vorticity (curled arrows) in a flow (broadly curving arrows) that diverges around an obstacle (dashed line). The fluid in the vorticity tubes spins more rapidly with stretching. *b*, side view of path taken by a particle of fluid as it approaches an obstacle. *c*, top view of *b*. After Richardson (1968).

It is the posterior region of a living infaunal bivalve lacking long siphons that is often exposed above the sediment surface, making the animal vulnerable to crescentic scour. The flattened pyramidal posterior-dorsal region of many extinct trigoniids permitted passage of water currents over the tops of partly exposed animals, rather than diverting currents around the shell flanks, where scour would have resulted (text-fig. 5A). This effect of shape has been observed in experiments of the kind described in the following section. Similarly, the elongate, rostrate posterior of other trigoniids (text-fig. 5B) reduces scour because intensity of scour tends to decrease with obstacle size. In addition, the rostrate shape places the visceral portion of the animal at considerable depth, so providing protection against predation. Both pyramidal and rostrate morphologies also appear convergently in various non-trigoniid bivalve groups, but usually in association with the prosogyrous condition.

EXTERNAL ORNAMENTATION

When this study was initiated, it was postulated that certain types of trigoniid ornamentation might have aided burrowing, while other types might have reduced current scour of sediment adjacent to the shell. Both these hypothetical functions have been tested experimentally.

Adaptations for burrowing. It has been suggested that certain types of ridges on the shell surface, by virtue of their asymmetric cross-sectional shapes and discordant orientation, aid bivalves in burrowing (Stanley 1969). The Trigoniidae show very many examples of such ridges and other features of the shell surface that may have functioned in a similar way. Clear-cut examples of the ridges in question are seen, for example, in *Psilotrigonia* (Pl. 118, fig. 8), *Eotrigonia* (Pl. 116, figs. 12, 13), and *Vaugonia* (Pl. 117, figs. 1, 2). In each of these genera, the ridges are limited to the anterior portion of the shell. According to the hypothesis previously put forward, the gentle ventral slope of each rib slides easily through the sediment in the forward rotation of a burrowing movement, and the steep dorsal slope grips the sediment in the backward rotation that follows. Asymmetric ridges that are more nearly concentric, but can operate in the same way, are found in certain trigoniids, including *Rutitrigonia* cf. *dunscombensis* (Lycett), which was collected from the Basement Bed of the Wilmington Sands (Lower Cenomanian) and is figured in Plate 118, fig. 3. There happens to be a living venerid, *Anomalocardia brasiliana* (Gmelin), that is closely convergent with this species (Pl. 118, figs. 4–6). Experiments with this living species show that the ridges decrease the number of burrowing sequences required for burial by 15–20% (Stanley, in preparation).

Types of ornamentation other than asymmetric ridges were initially judged to have aided trigoniids in burrowing, but their function is neither obvious nor easily tested in the absence of living homeomorphs. Two examples will be considered here, the more or less concentric ornamentation of *Trigonia*, as exemplified by *T. papillata* Agassiz (Pl. 117, figs. 8–10), and the curved rows of knobs on the lateral surfaces of *Yaadia nodosa* (Pl. 117, figs. 4, 6, 7) and other species (Pl. 119, figs. 6–9). Both these extinct species have been studied using robots similar to those employed to test the function of the prosogyrous condition (Stanley 1975*b*) as mentioned above. Robots (Pl. 117, figs. 4, 5, 10–12) were made from aluminium-filled epoxy casts of real shells. Matching valves of *Trigonia* were cast individually but, in the absence of comparable fossil material, a double-valved specimen of *Yaadia* was cast in two parts, each of which was then hollowed out to approximately its original thickness. Each robot was fitted with rods used to simulate the downward forces of pedal retractor muscles, except that the rods pushed from above rather than pulling from below. In this way, the rocking motion of burrowing was simulated. The anterior rod was attached to a cylindrical sleeve rotating about a bolt holding the two valves together at the position of attachment of the anterior retractor muscles. The posterior rod was attached to an external flange located slightly posterior to the sight of posterior pedal attachment in order to increase leverage. This modification was required in the absence of ventral expulsion of water comparable to that used by living bivalves to loosen the sediment at the start of each rocking movement. With a comparable modification, robots of *Mercenaria mercenaria* entered the substratum at nearly the same angle as live animals of the species (Stanley 1975*b*). Appropriate orientations of the rods for the application of forces were estimated for the fossil trigoniids from shell-shape and muscle-scar location. Angles of rotation for the simulated burrowing movements were estimated from observations of unrelated living animals of comparable shapes. The same angle was used for forward and backward rotation (only under this condition will a shell maintain a consistent burrowing orientation, and cinematography shows that the condition does, in fact, hold for the living *Mercenaria*). Varying this angle of rotation and the orientation of the forces by moderate amounts was found in preliminary experiments to have little effect on the rate or direction of simulated burrowing motion.

Robots were made to 'burrow' using a machine depicted in text-fig. 4. The rods applying forces were held in place by guides and rollers attached by magnets to a vertical plate. The rods were shifted as burrowing proceeded and thus maintained at constant orientations with respect to the bivalve. Forces were applied by hand in final experiments, because preliminary experiments (Stanley 1975*b*) showed that such forces, if just great enough to overcome resistant forces, produced net downward walking movement virtually identical to those produced by a more intricate procedure using weights attached to cords.

EXPLANATION OF PLATE 117

Figs. 1, 2. Left lateral and anterior views of *Vaugonia* (*V.*) *literata* (Young and Bird) in living orientation, ×0·75.

Fig. 3. Oblique plan view of *V.* (*V.*) *literata* in life position adjacent to a piece of carbonized wood in the Peak Shales at Ravenscar, Yorkshire, ×0·7.

Figs. 4, 5. Left lateral views of robots of *Yaadia nodosa* (Sowerby) unaltered and with knobs ventral to the carina removed, ×0·5. Robot on right has a polyethylene boot shielding the aperture for the anterior rod used to produce forward rotation in 'burrowing'. Robot on left has the boot removed to display the rod. The anterior rod is attached to a sleeve about the more anterior of the two bolts holding the valves together. Posterior rods were attached to the rectangular flanges projecting from the siphonal region. Horizontal white stripes indicate position of sediment-water interface at the start of experiments.

Fig. 6. Anterior view of *Y. nodosa*, ×0·5. BMNH 47213.

Fig. 7. Left lateral view of *Y. nodosa*, ×0·6. BMNH 47213. The serpulid attached to the left valve seems to have grown downward along the exposed posterior portion of the shell until striking the sediment, at which point it turned and grew upward again.

Fig. 8. Oblique anterior view of *Trigonia papillata* (Agassiz), showing deflection and dorsal steepening of each rib where it passes from the flank of the valve onto the anterior surface, ×0·7. Mus. Nat. Hist. Naturelle (Paris) No. 1899-20.

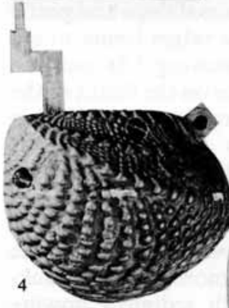
Fig. 9. Dorsal view of the specimen of *T. papillata* in fig. 8, showing restriction of an attached serpulid to the upper surface of the left valve, ×0·7.

Fig. 10. Left lateral views of three robots of *T. papillata*, one in an unaltered state, one with ornamentation of the lateral flanks removed, and one with all ornamentation ventral to the carina removed, ×0·55.


1

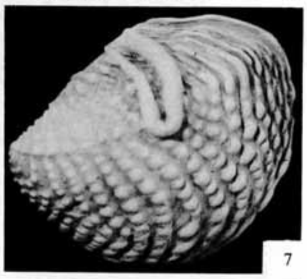

2

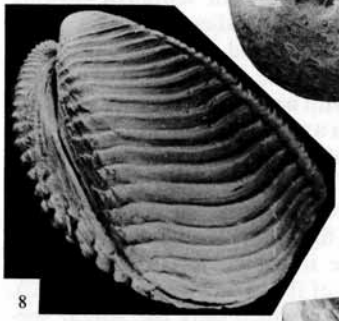

3

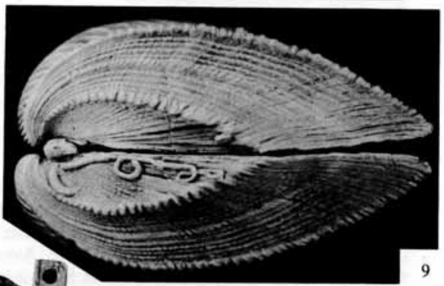

4

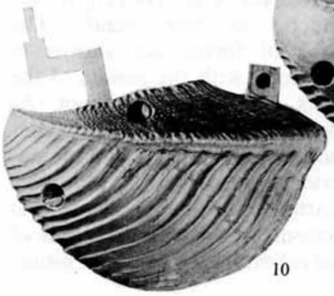

5


6


7


8

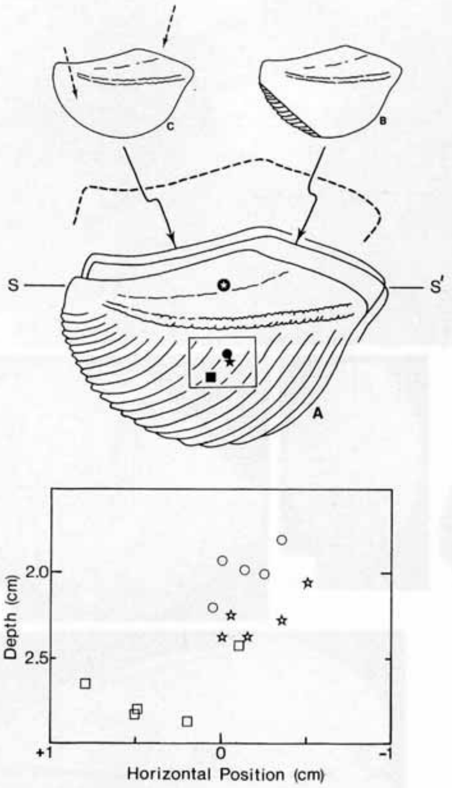

9


10


11


12

STANLEY, trigoniid burrowing bivalves



TEXT-FIG. 7. Results of experiments with robots of *Trigonia papillata* Agassiz. Original position of all robots with respect to the sediment-water interface (S–S′) is shown by dashed dorsal outline. Average final positions for robots A, B, and C in five trials are shown by solid outlines. Each trial consisted of ten simulated burrowing sequences. Relative final positions of 'homologous' points on the robots are shown by solid symbols within rectangle: square, robot A; star, robot B; circle, robot C. Rectangle is 2 cm wide. Position of 'homologous' point at the start of 'burrowing' shown by encircled star. Graph below is enlargement of rectangle, showing positions of 'homologous' points with respect to their original position (co-ordinates O, O) for five trials with each robot. Dashed arrows in C show application of forces. The anterior force moved its point of application 6 mm. The posterior force restored model to orientation shown.

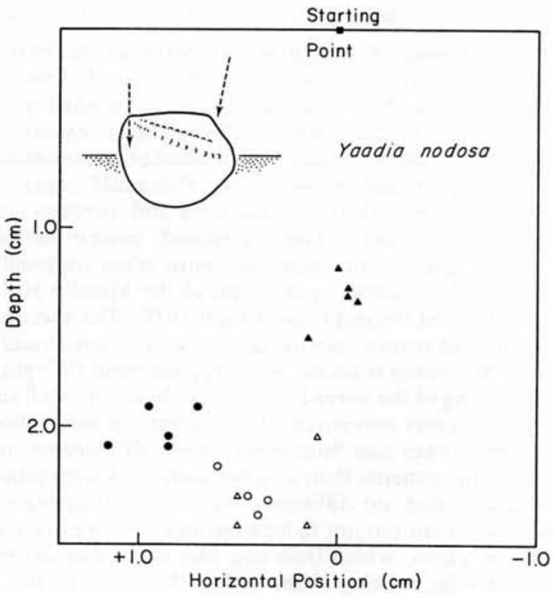
The ornamentation of *Trigonia* (Pl. 117, figs. 8–10) consists of nearly concentric ridges (costae). The ridges are deflected slightly where they pass around a shoulder of minimum convexity near the anterior end of the shell (Pl. 117, fig. 8). Anterior to this deflection, the ridges are asymmetrical, having the familiar steep dorsal slope and gentle ventral slope of the ridges found to aid *A. brasiliana* in burrowing. The question is whether the ridges on the flanks of the shell, which are roughly symmetrical in cross-section, also aid burrowing. It can be postulated that the concave side of a ridge tends to catch sediment when rotated forward, offering substantial resistance to movement, while the convex side slides more easily in backward rotation, with sediment flowing distally via the adjacent valley. (The principle invoked here is the one employed in the construction of current meters with hemispherical cups rotating about an axle to form an impeller.) The effects of the anterior and lateral segments of ridges were tested by comparing the burrowing progress of three robots (Pl. 117, figs. 10–12): an unaltered robot (A), one in which all ornamentation anterior of the carina was removed (C), and one in which only the lateral segment of ridges were removed (B). Starting from a position of partial burial, each robot was subjected to five experimental sequences of ten rocking movements each, in fine sand. The orientations of forces are shown in text-fig. 7, along with the results of the experiments. The unaltered robot (A) on the average 'burrowed' 37% deeper than robot C, in which all ornamentation anterior to the carina was removed. Robot B attained an average depth that was intermediate, but closer to that of the altered robot. By the Mann-Whitney

U-test, the difference between A and B is significant at the 99·6% level and the difference between B and C is significant at the 98·4% level. Thus, not only do the anterior asymmetrical segments of the ridges aid in burrowing, but the lateral, symmetrical segments have an even greater effect. Similar experiments comparing robots A and C in medium sand revealed a weaker effect of ornamentation (a difference of 23% for average depth attained in four runs). This result suggests that the ornamentation in question is more effective in fine sand and, perhaps other fine-grained sediments, than in coarse sediments. There is, indeed, some evidence that the genus *Trigonia* occurs in finer grained substrata than most other trigoniids. I have found it in the Fuller's Earth at the south-eastern end of the Mendip Hills, and it occurs in the Kimmeridge Clay and Oxford Clay (Lycett 1879). The specimen of Plate 117, figs. 8, 9 was also removed from a micritic matrix, and *T. americana* of the Gypsum Spring Formation of Wyoming is found in muddy sediment (Wright 1974).

The effect on burrowing of the curved rows of knobs on the shell surface of *Yaadia nodosa* (Pl. 117, figs. 6, 7) was also studied by experiments with robots. As shown in text-fig. 8, an unaltered robot had 'burrowed' about 50% deeper in fine sand after ten simulated rocking movements than a robot with the knobs removed. In similar experiments in medium sand, no difference was found. It appears that the knobs function in cohesive sediment but not in loose sediment. Cohesive sediment seems to pack against a row of knobs, which then acts like a rib, whereas loose sand slides readily between the knobs, making them useless. In fact, like the genus *Trigonia*, strongly nodose species seem to be found more commonly than other trigoniids in lithologies exhibiting a high percentage of mud-sized particles. The occurrence of *Y. nodosa* (Pl. 117, figs. 6, 7) in muddy units of the Lower Greensand is one example. Though largely grain supported, the *Myophorella clavellata* and *M. huddlestoni* Beds also have a substantial micritic matrix, and *Myophorella* occurs in the Kimmeridge Clay and Oxford Clay (Lycett 1879).

There can be little question that the trigoniids' widespread evolution of ornamentation as an aid in burrowing served to compensate for their lack of a prosogyrous shape. Only one recognized genus of the Trigoniidae is moderately prosogyrous and it is aptly named *Prosogyrotrigonia* (Krumbeck 1924). It is an early (Triassic) member of the family and, significantly, is also unusual in having simple concentric ornamentation that is symmetrical in profile and may not have aided in burrowing (Pl. 118, fig. 7). Thus *Prosogyrotrigonia* may be an exception supporting the rule that strongly discordant ornamentation evolved in the Trigoniidae to compensate for the absence of an opisthogyrous shape.

Adaptations for reducing current scour. It has commonly been assumed that certain kinds of ribs and spines of the shell surface may serve to stabilize bivalves in sediment (Carter 1968; Kauffman 1969; Stanley 1970). Implicit here has been the idea that such ornamentation should tend to prevent an animal from moving. In reality, as current velocity is increased, sediment begins moving long before a bivalve itself moves. Experiments using a wave tank have demonstrated that many types of ornamentation serve to reduce sediment scour (Stanley, in preparation), and it may be that no type of ornamentation functions *directly* to prevent a bivalve from moving. The wave tank is essentially a narrow, ten-foot long aquarium suspended from



TEXT-FIG. 8. Results of experiments with robots of *Yaadia nodosa* (Sowerby). In fine sand the unaltered robot (solid dots) 'burrowed' more deeply in five trials than the robot from which surficial knobs were removed (solid triangles). In medium sand the unaltered robot (open circles) burrowed to virtually the same average depth as the altered robot (open triangles). Diagram at upper left shows starting position for models in experiments. Arrows show application of forces. The anterior force moved its point of application 6 mm. The posterior force restored model to orientation shown. Depths and horizontal positions shown represent net movements from the starting-point produced by ten simulated burrowing sequences.

EXPLANATION OF PLATE 118

Fig. 1. Posterior view of *Trachycardium egmontianum* (Shuttleworth) with its valves at position of maximum gape in the movements of burrowing, ×1.

Fig. 2. Anterior view of *T. egmontianum* with valves spread to display lateral teeth projecting far across the commissure, ×1.

Fig. 3. Right lateral view of *Rutitrigonia dunscombensis* (Lycett) collected by the author at Hutchins Quarry (Waterworks Pit), Wilmington, South Devon, ×1·2.

Fig. 4. Oblique posterior lateral view of the Recent venerid *Anomalocardia brasiliana* (Gmelin) from Mayaguez, Puerto Rico, ×2. This species exhibits asymmetric ridges that resemble those of *R. dunscombensis* and that aid in burrowing.

Figs. 5, 6. Anterior and left lateral views of *A. brasiliana*, ×1·25.

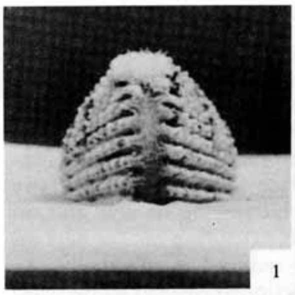
Fig. 7. Left lateral view of *Prosogyrotrigonia timorensis* (Krumbeck), ×0·82. From Krumbeck, 1924.

Fig. 8. Right lateral view of *Psilotrigonia beesleyana* (Lycett), ×1.

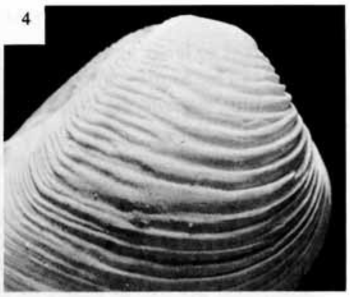
Figs. 9, 10. Dorsal and right lateral views of *Pterotrigonia etheridgi* (Lycett) in living orientation, ×0·6.

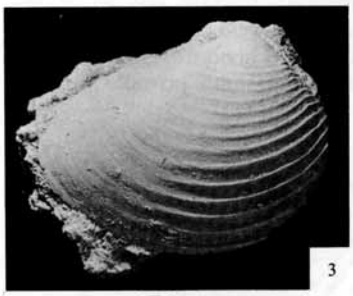
Fig. 11. Oblique posterior dorsal view of *P. etheridgi*, ×0·6.

PLATE 118


1

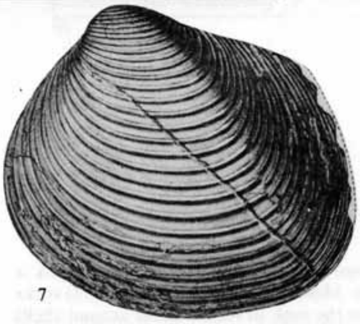

2

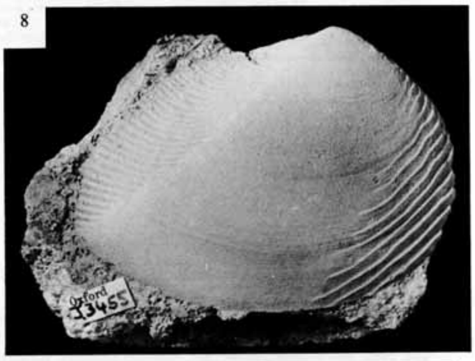

4

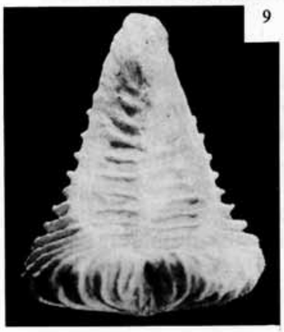

3


5

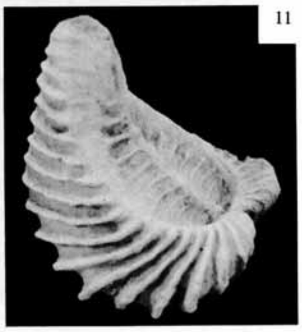

6


7


8


9

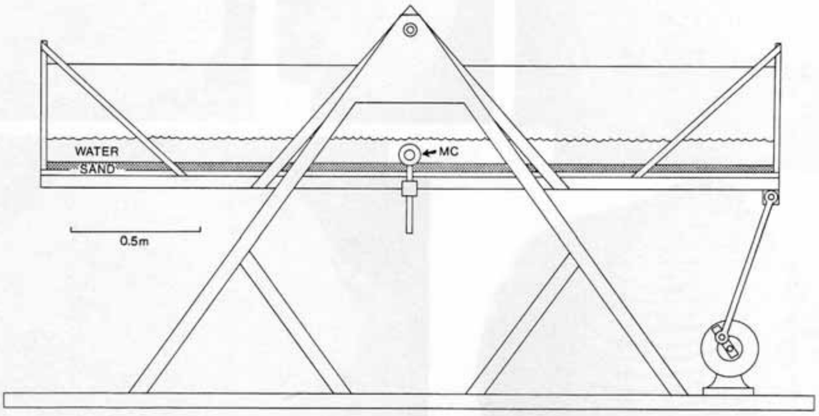

10


11

STANLEY, trigoniid burrowing bivalves

a central axle so as to rock when one end is cranked up and down by a motor (text-fig. 9). The angle and velocity of rotation and the depth of water in the tank are all variable, permitting control of the current velocities of water flowing back and forth.

Preliminary experiments with the wave tank showed that much of the ornamentation of fossil trigoniids could not have functioned to reduce sediment scour. Many trigoniid species are quite large compared to an average burrowing bivalve and, in nearly all of the large species, the zone of scour is very wide, extending too far beyond the reach of spines, ridges, or knobs for these to have reduced it effectively. As described above, in many of these the ornamentation functioned instead to increase burrowing efficiency. In smaller members of the Bivalvia, however, ridges and spines can reduce scour significantly (Stanley, in preparation). Certain species of the Veneridae, like *Mercenaria mercenaria*, exhibit strongly developed ornamentation at the juvenile stage, but little or none at the adult stage. This ontogenetic pattern seems to reflect the greater vulnerability to scour of the small juvenile bivalve. A juvenile's survival is further jeopardized by high vulnerability to drilling, opening, or breaking by a predator and to physical transportation to an unfavourable environment (Stanley, 1972). A similar ontogenetic pattern is displayed by various fossil trigoniids and also by the living *Neotrigonia margaritacea*, in which the juvenile has short spines emanating from distinct radial ridges (Pl. 116, figs. 1, 2). Beginning at a length of about 2 cm, however, new spines that are grown begin to become weaker and less regularly positioned. At larger sizes, even the ribs ultimately become faint.



TEXT-FIG. 9. Diagrammatic side-view of the wave tank used to study scour around shells. Tank is suspended by an axle near the apex of an A-shaped frame. Motor-driven crank (lower right) rocks the tank back and forth. MC-movie camera mounted on the tank to record scour around shells placed in centre of tank.

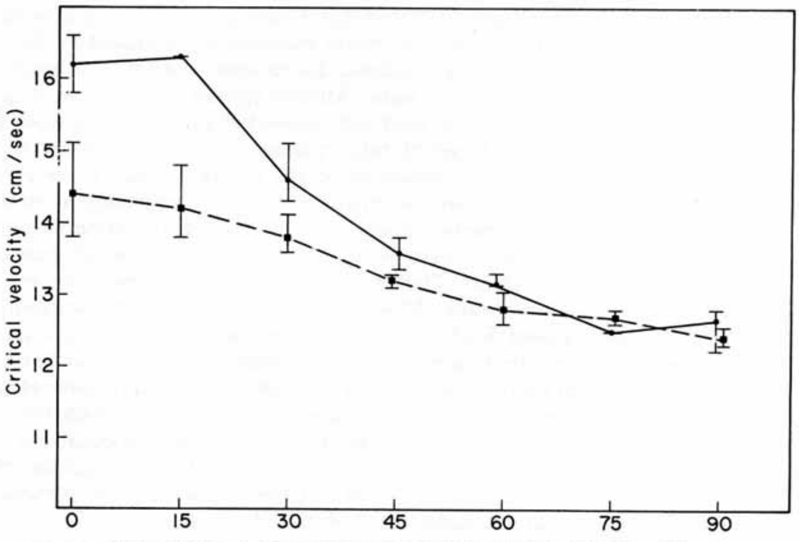
Using the wave tank described above, in a manner to be discussed elsewhere

(Stanley, in preparation), I have demonstrated that the spines of the young *Neotrigonia* (2·5 cm long) retard scour. The oscillating water movements produced in the wave tank imitate the back-and-forth flow produced by circular motion of a wave as it flattens out upon approaching the sea-floor. Models (epoxy casts) of *Neotrigonia* were placed at the centre of the wave tank and subjected to oscillating flow. Unidirectional flow such as that produced by tidal currents would yield similar results, except that scour would be more pronounced on the upstream side of the animal. In one kind of experiment, scour around an unaltered model of a juvenile *Neotrigonia* was compared to scour around the model that was made from the same mould but had its spines removed. The models were placed in a flat bed of fine sand resembling the native sediment of Westernport. They were positioned 4 cm apart, one on each side of the mid-line of the wave tank. Models were orientated in life positions but with 0·8 cm of the shell exposed. Such exposure is common for *Neotrigonia* in nature, as described above. In each experiment, the pair of models was subjected to a given number of oscillations and then photographed from above. No appreciable effect of the ornamentation was observed for orientations of the shell in which the commissure lay within 75° of the direction of current flow. In these orientations, very little ornamentation projects into the path of flowing water. For orientations of the commissure 0°–60° from the direction of current flow, however, the presence of ornamentation reduced scour markedly (Pl. 119, figs. 1–5).

In a second type of experiment, models were run individually in order to determine the critical velocity at which scour began. In each experiment, current velocity increased from a low value until scour was observed. This procedure was somewhat subjective, but the convention followed was to define the critical velocity as the one at which grains of sand began to move so consistently that grain movement was observed in five or more successive cycles over a viewing interval of twenty cycles. Each determination was checked by raising the velocity further and approaching the critical velocity from above. Results of a series of such measurements are presented in text-fig. 10. The ornamentation has no significant effect when the commissure is nearly perpendicular to current direction. As in photographic comparisons (Pl. 119, figs. 1–5), however, an effect is seen when the commissure is oriented at lower angles to the current direction, increasing to a maximum at 15°–0°. Experiments comparing smooth models with those for which spines were removed but the low radial ribs at their base were left intact, showed that the ribs have virtually no effect on the critical velocity of scour.

One may wonder if burrowing bivalves might have evolved the behavioural adaptation of orientating themselves preferentially with the commissure paralleling the prevailing current direction. Such behaviour, has, in fact, been observed for a few bivalve species (Stanley 1970; O'Gower and Nicol 1971), but many species do not live in areas where there is a strongly dominant direction of flow, and *Neotrigonia* has not been studied in this respect.

We can predict that the greater the elevation of the posterior end of a burrowing bivalve above the sediment surface, the more pronounced will be the scouring of sediment around it. The larger the surface area of the obstruction perpendicular to flow direction, the greater should be the volume of water diverted around the shell per unit time. A third type of experiment bore out this prediction. Critical velocity



TEXT-FIG. 10. Critical velocities at which scour began around models of a juvenile *Neotrigonia* shell (2·5 cm long) with 0·8 cm of the posterior end of the model exposed above fine sand. Squares: mean value of three measurements for model with spines removed. Dots: mean values for unaltered model. Bars depict ranges of values. See text for definition of critical velocity.

was found to decrease with an increase in height of exposure of the model shell (text-fig. 11).

I make no pretence of evaluating all types of trigoniid ornamentation in this analysis. Clearly, most ornamentation anterior to the carinas of trigoniid shells aided in burrowing, as discussed above. The margin of the carina itself corresponded in life to the ventral margin of the inhalent current opening (Gould and Jones 1974).

EXPLANATION OF PLATE 119

Figs. 1–5. Results of experiments in which models of a juvenile shell of *Neotrigonia margaritacea* in living orientation but exposed 0·8 cm above the sediment (fine sand) were subjected to scour by oscillating water current. In the full range of orientations shown, the right-hand model, from which spines were removed, suffered greater scour of peripheral sand. Number of cycles of oscillation and maximum velocity of flow during each oscillation were varied according to susceptibility to scour at each orientation, as follows: 1, 35 cycles, 16·1 cm/sec.; 2, 35 cycles, 16·3 cm/sec.; 3, 35 cycles, 14·8 cm/sec.; 4, 20 cycles, 14·8 cm/sec.; 5, 30 cycles, 14·6 cm/sec. All figures, × 0·75.

Fig. 6. Anterior view of *Laevitrigonia manseli* (Lycett), × 0·8. BMNH L6819.

Fig. 7. Left lateral view of *L. manseli*, × 0·7. BMNH L6819.

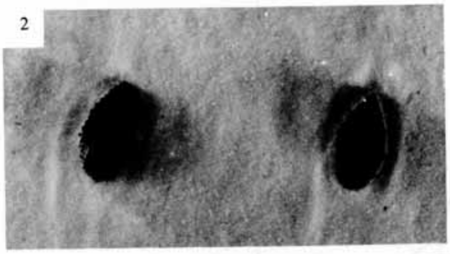
Figs. 8, 9. Oblique and anterior lateral views of *Myophorella clavellata* (Sowerby), × 0·6. BMNH 51029.

Figs. 10, 11. *Lyriomyophoria elegans* (Dunker), × 0·5. From Newell and Boyd (1975).

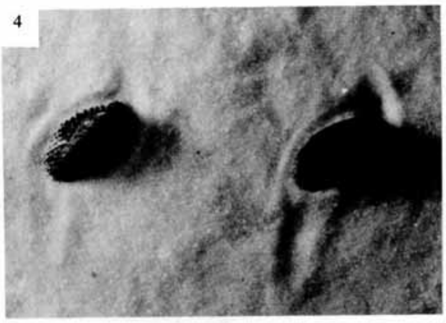
Fig. 12. Left lateral view of *Megatrigonia conocardiiformis* (Krauss) in living orientation, × 0·85. BMNH LL13601.

PLATE 119

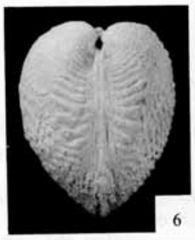

1

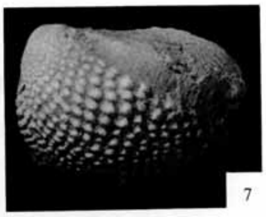

2


3

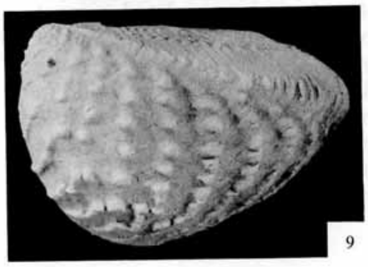

4


5


6


7


8

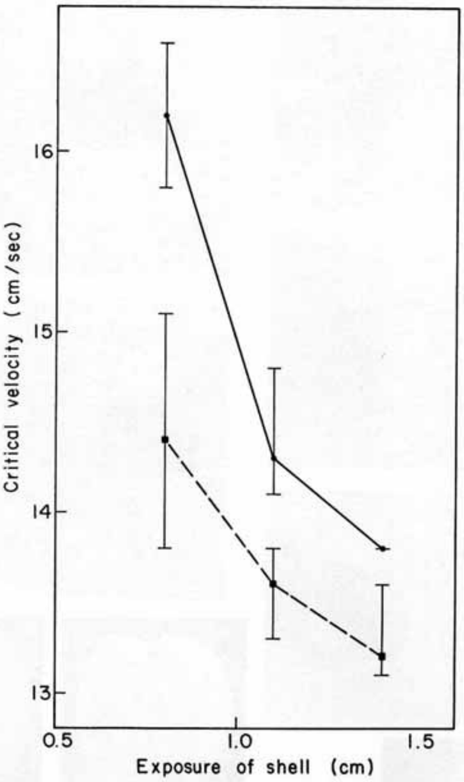

9


10


11


12

STANLEY, trigoniid burrowing bivalves



TEXT-FIG. 11. Critical velocities at which scour began for each of three elevations of the posterior tip of *Neotrigonia* models above the surface of fine sand. Symbols as in text-fig. 10.

The carina represents the trace of a minor deflection of the shell margin. The carinas of the two valves are offset so as to interlock at the margin, and perhaps aided in valve alignment at closure. The area dorsal to the carina is smooth or granulated in most species. The granulation (Pl. 117, fig. 9) may have served to camouflage an animal by trapping a thin layer of sediment when the surface of the shell was exposed. At any rate, the posterior dorsal region lacks pronounced ribs or spines of the sort found in certain cardiids. (Pl. 118, fig. 1). The reason may be that the trigoniids' lack of mantle fusion and discrete siphons required that the posterior mantle margins remain mobile to control water flow. Formation of permanent siphons in the Cardiidae may have freed the mantle lobes adjacent to the shell for secretion of more elaborate spines and ribs.

INTERPRETATION OF EVOLUTIONARY HISTORY

To summarize the foregoing analysis, the Trigoniidae, which seem to display a varied collection of bizarre morphological features, actually exhibit a remarkable degree of coadaptation, illustrating in an impressive way Cuvier's Principle of Correlation, or the tendency of arrays of morphologic features to operate in concert, or at least with compatability, fitting a taxon to a particular mode of life. Thus, evolution of the remarkable muscular foot, which was the adaptive breakthrough leading to the Mesozoic radiation of the trigoniids, required wide gaping of the valves, which led to the evolution of large, complex hinge teeth. The foot gave trigoniids the capacity to occupy shifting substrata on a large scale. Rapid burrowing would have been aided by the evolution of a prosogyrous shape, but this was apparently precluded by the early evolution of the huge central hinge teeth, the myophorous buttress required for support of the teeth, and the adductor muscle attached to the buttress. As an alternative to the prosogyrous shape, which is a common feature of other bivalve families, discordant patterns of ornamentation evolved to grip the sediment. Here, then, we have a chain of coadaptive relationships.

Partial adaptive analogy between the Trigoniidae and the Cardiidae offers additional insight. The cardiids are in various ways more advanced bivalves than the trigoniids. They have eulamellibranch rather than filibranch gills and well developed siphons with tentacles that often bear eyes (Charles 1966). Their muscular L-shaped foot resembles the trigoniid foot but moves more rapidly, and the cardiids are indeed more rapid burrowers (Stanley 1970). Having a more effective pedal system than the trigoniids, and being somewhat prosogyrous, the cardiids have had much less need for anterior ornamentation to aid in burrowing. Such ornamentation is found in only a few cardiid species (Stanley, in preparation). The two families arrived at quite different solutions to the problems of valve alignment imposed by large angles of gape. The trigoniid solution took the form of large, complex hinge teeth, which are highly specialized and evolved very little after arising in the Triassic. The hinge teeth apparently limited the group's mobility somewhat by introducing sizeable frictional forces opposing valve movement. These frictional forces can be easily examined by manipulation of empty valves. In the cockles, an alternative and less confining solution was made possible by certain ancestral features of the group: heterodont dentition and radial ribbing of the shell. Elongate, loosely articulating lateral teeth evolved as a mechanism for crude valve alignment at wide gapes, and the interlocking terminations of radial ribbing or fine-scale crenulation of the ventral valve margins arose to ensure accurate final closure. Not only can cardiids jump like trigoniids, but some can swim (Stanley 1970). Movements of the shell are very rapid here, as in burrowing. The condition of the Cardiidae is reminiscent of that of the swimming scallops, in which articulating structures of the hinge are weak and the valves move with little friction. It would seem that the complex dentition of trigoniids, which has borne the entire responsibility for valve alignment, has been one of the chief adaptive deficiencies of the group in comparison with the cardiids.

The excellent phylogenetic study by Newell and Boyd (1975) of the Paleozoic trigoniaceans that preceded the Trigoniidae reveals interesting aspects of the origins of trigoniid adaptations. As we would predict, the adaptations led to much greater success of the trigoniids, as measured by diversity (text-fig. 1), than was ever attained by their antecedents. Among Newell and Boyd's conclusions are the following. The early trigoniacean groups were not only of restricted generic diversity, they were of conservative morphology. All pre-Permian forms (Eoschizodidae, Schizodidae) had smooth shells. These gave rise to both smooth-shelled and ornamented taxa, but only certain of the latter diversified markedly and survived into the Jurassic as the Trigoniidae. Newell and Boyd (1975) have shown that the secondary dentition that characterizes the Trigoniidae arose polyphyletically within the more primitive members of the Trigoniacea. The oldest species displaying it is from the Early Triassic, and it also appears in incipient form in several Middle Triassic species. One of the striking discoveries of Newell and Boyd is that the appearance of secondary dentition was sporadic and variable, even within species. Some individuals of transitional species may lack any secondary dentition, while others have it along almost all articulating surfaces. The evolution of a full complement of secondary dentition in one or more ancestral groups, together with elongation of the primary teeth, rapidly led to the condition of the advanced Trigoniidae. The exact ancestry of the family is uncertain, but the oldest genus recognized by Newell and Boyd (1975) is *Lyriomyophoria* of the Permian (Pl. 119, figs. 10, 11). Its external morphology is much like that of *Trigonia*, but its hinge teeth are short and lack secondary dentition.

While it is quite likely that late Palaeozoic trigoniaceans were more adept burrowers than other contemporary taxa, we may infer that the modern trigoniacean foot underwent much of its evolutionary development during the origin of secondary dentition in the Triassic, opening one of the most remarkable chapters in the history of the Bivalvia. No Palaeozoic group of suspension-feeding infaunal bivalves compares to the Mesozoic trigoniids in morphologic diversity, including range of body sizes and variety of ornamentation patterns, and I doubt that any Palaeozoic group was their equal in adeptness at burrowing. It was no accident that the Trigoniidae became the most successful group of shallow burrowing bivalves occupying near-shore habitats of Mesozoic seas. Although they clearly remained more primitive than the Cardiidae in ways discussed above, we can, in a sense, view the trigoniids as the cockles of the Mesozoic. The almost total extinction of the family at the close of the Mesozoic certainly had little to do with any of the features discussed in the present study. Like contemporaneous mass-extinctions of other Tethyan groups, it remains a mystery. (The fact that a single recognized genus, *Eotrigonia*, remained in the early Cenozoic can be viewed as a statistical accident.) Hence, there is no apparent fossil evidence that trigoniids are rare today because they have been unable to meet the demands of the modern marine ecosystem. The Anadarinae (burrowing arcids), which are well represented in modern seas, have life habits that are somewhat similar to those of cardiids and trigoniids but are distinctly less adept burrowers than *Neotrigonia* (Stanley 1970).

Further evidence that remnant trigoniids have not performed poorly in the Cenozoic history of the Bivalvia comes from consideration of rates of diversification. New techniques for estimating rates of speciation show that marine Bivalvia have generally speciated at very low rates (Stanley 1975*a*, in press). For newly radiating taxa of the Cenozoic, the net rate of geometric increase (rate of speciation minus rate of extinction) has produced an average doubling time for number of species of about 11 my. *Neotrigonia* arose in the Oligocene and now contains about six or seven living species. These facts show that the net rate of geometric increase and doubling time for number of species in *Neotrigonia* are very close to the average for other genera and families of the Bivalvia that have been radiating simultaneously. Clearly *Neotrigonia* has been holding its own. It seems evident that, if trigoniids had been present in high diversity at the start of the Cenozoic, they would persist in high diversity today.

CONCLUSIONS

The Trigoniidae radiated early in the Mesozoic, to become the most abundant and diverse family of shallow-burrowing bivalves in shallow marine habitats of the Jurassic and early Cretaceous. The centre of trigoniid distribution was in the Tethyan Realm.

The adaptive zone of Mesozoic trigoniids included relatively unstable, sandy areas of the sea-floor. Most populations occupied substrata of grain-supported arenitic lithologies and nearly all lived nearshore, in water less than 10–15 m deep.

Trigoniidae of the Mesozoic were shallow burrowers that had life positions similar to that of *Neotrigonia*, the only living genus of the family. Though a relict, *Neotrigonia* is not truly a living fossil genus because it ranges back into only the Oligocene.

The initial radiation of the trigoniids was triggered by the evolution of a large, muscular, T-shaped foot that probably endowed them with better mobility than was possessed by any Palaeozoic group of suspension-feeding clams.

The enormous trigoniid hinge teeth with transverse striations (secondary dentition) evolved to maintain valve alignment at the wide angles of gape required for extrusion of the muscular foot. The appearance of these teeth in the early Mesozoic fossil record signals the origin of the muscular foot.

The so-called myophorous buttress of the Trigoniidae is actually a structural support for the large anterior hinge tooth.

Evolution of the bulky hinge teeth, myophorous buttresses, and associated anterior adductor muscle virtually eliminated the possibility for the Trigoniidae to evolve a prosogyrous shape from the orthogyrous shape of their ancestors.

The lack of a prosogyrous shape of the sort that assists many other bivalve taxa in burrowing was compensated for in the Trigoniidae by the evolution of various kinds of discordant ornamentation that aided in burrowing.

The seemingly curious suite of morphologic structures of the Trigoniidae formed a coadaptive system that represented an alternative to the sets of adaptations found in other groups of burrowing bivalves.

In their pedal morphology, behaviour, and gross shell form, the Mesozoic Trigoniidae resembled the Cardiidae. Despite being slightly less mobile than cardiids, they can be viewed as the cockles of the Mesozoic.

Neotrigonia and the rest of the Trigoniidae are not properly considered to be primitive bivalves. They are more advanced, for example, than the Anadarinae, which resemble them in gross form and life position and which have radiated in the Cenozoic despite being sluggish burrowers.

For unknown reasons, the Trigoniidae were nearly wiped out by the mass extinction at the end of the Cretaceous. The low present-day diversity of the Trigoniidae is largely a result of this mass extinction. *Neotrigonia* has actually flourished since arising in the Oligocene, having speciated at approximately the average rate of speciation for other radiating bivalve taxa of the Cenozoic.

Acknowledgements. Numerous individuals provided indispensable aid in the completion of this study. I am particularly indebted to W. J. Kennedy and H. S. Torrens, each of whom generously guided me in the field for several days. Others who kindly provided assistance or hospitality were R. J. Cleevely, A. Hallam, M. R. House, W. S. McKerrow, N. J. Morris, C. P. Nuttall, B. Sellwood, J. D. Taylor, and G. Townson in England; I. D. Hiscock, B. J. Smith, and J. Watson in Australia; S. Freniex and M. Rioult in France; and D. W. Boyd and N. D. Newell in the United States. The British Museum of Natural History and the French Musée National d'Histoire Naturelle lent numerous specimens for study. This research was undertaken with the support of the National Science Foundation (GB-26466).

REFERENCES

ALLEN, J. R. L. 1965. Scour marks in snow. *J. sedim. Petrol.* **35,** 331–338.

ANSELL, A. D. 1969. Leaping movements in the Bivalvia. *Proc. malacol. Soc. Lond.* **38,** 387–399.

ARKELL, W. J. 1947. The geology of the country around Weymouth, Swanage, Corfe & Lulworth. *Mem. geol. Surv. Gr. Brit.*

BOWEN, Z. P., MCALESTER, A. L. and RHOADS, D. C. 1974. Marine benthic communities of the Sonyea Group (Upper Devonian) of New York. *Lethaia,* **7,** 93–120.

CARTER, R. M. 1967. On the nature and definition of the lunule, escutcheon and corcelet in the Bivalvia. *Proc. malacol. Soc. Lond.* **37,** 243–263.

—— 1968. On the biology and palaeontology of some predators of bivalved Mollusca. *Palaeogeog., Palaeoclimat. Palaeoecol.* **4,** 29–65.

—— 1972. Adaptations of British Chalk Bivalvia. *J. Paleont.* **46,** 325–340.

CASEY, R. 1961. The stratigraphical paleontology of the Lower Greensand. *Palaeontology,* **3,** 487–621.

CHARLES, G. H. 1966. Sense organs (less cephalopods). *In* WILBUR, K. M. and YONGE, C. M. (eds.), *Physiology of the Mollusca.* Academic Press, London, 455–521.

COSSMAN, M. 1912. Sur l'évolution des trigonies. *Ann. Paléont. Fr.* **7,** fasc. 2.

COX, L. R. 1952. Notes on the Trigoniidae, with outlines of a classification of the family. *Proc. malacol. Soc. Lond.* **29,** 45–69.

—— *et al.* 1969. Superfamily Trigoniacea. *In* R. C. MOORE (ed.), *Treatise on Invertebrate Paleontology, part N, Mollusca 6, Bivalvia.* Geol. Soc. America and University of Kansas Press. Lawrence, Kansas, 471–489.

DESCHET, Y. 1966. Études sur des Trigoniidae Cenozoïques. *Trav. Lab. Paleont. Univ. Paris.* Université de Paris.

FLEMING, C. A. 1964. History of the bivalve family Trigoniidae in the south-west Pacific. *Austral. J. Sci.* **26,** 196–203.

GOULD, S. J. 1968. *Trigonia* and the origin of species. *J. History Biol.* **1,** 41–56.

—— 1969. The byssus of trigonian clams: phylogenetic vestige or functional organ? *J. Paleont.* **43,** 1125–1129.

—— and JONES, C. 1974. The pallial ridge of *Neotrigonia*: functional siphons without mantle fusion. *Veliger,* **17,** 1–7.

KARCZ, I. 1968. Fluviatile obstacle marks from the wadis of the Negev (southern Israel). *J. sedim. Petrol.* **38,** 1000–1012.

KAUFFMAN, E. G. 1969. Form, function, and evolution. *In* R. C. MOORE (ed.), *Treatise on Invertebrate Paleontology, part N, Mollusca 6, Bivalvia.* Geol. Soc. America and University of Kansas Press, Lawrence, Kansas, 129–205.

KLEIN, G. dev. 1965. Dynamic significance of primary structures in the Middle Jurassic Great Oolite Series, southern England. *Soc. econ. Paleont. Mineral. Spec. Publ.* **12,** 173–191.

KRUMBECK, L. 1924. Die Brachiopoden, Lamellibranchiaten und Gastropoden der Trias von Timor. 2. Palaeontologischer Teil. *Paläontologie von Timor*, **13,** 1–275.

LYCETT, J. 1879. A monograph of the British fossil Trigoniae. *Palaeontographical Society*. Adlard, London.

MCALESTER, A. L. 1965. Life habits of the 'living fossil' bivalve *Neotrigonia. Abstr. geol. Soc. Am.* **102,** 104.

MCKERROW, W. S. 1958. Geology around the university towns: the Oxford District. *Geol. Assoc. Guides*, **3,** 1–15.

MOORE, C. H. 1964. Stratigraphy of the Fredericksburg Division, South-Central Texas. *Rep. Invest. Bur. econ. Geol., Univ. Texas*, **52,** 1–48.

NEWELL, N. D. and BOYD, D. W. 1975. Parallel evolution in early trigoniacean bivalves. *Bull. Am. Mus. nat. Hist.* **154,** 53–162.

O'GOWER, A. K. and NICOL, P. I. 1971. Orientation of the bivalve *Anadara trapezia* (Deshayes) relative to water currents. *Veliger*, **13,** 275–278.

POULTON, T. P. 1976. Some Lower Jurassic trigoniid bivalves from southwestern British Columbia. *Bull. geol. Surv. Canada*, **256,** 41–53.

PURDY, E. G. 1964. Sediments as substrates. *In* J. IMBRIE and N. NEWELL (eds.), *Approaches to Paleoecology*. Wiley, New York, 238–271.

RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. *Jour. Paleont.* **40,** 1178–1190.

RICHARDSON, P. D. 1968. The generation of scour marks near obstacles. *J. sedim. Petrol.* **38,** 965–970.

SCOTT, R. 1974. Bay and shoreface benthic communities in the Lower Cretaceous. *Lethaia*, **7,** 315–330.

SEILACHER, A. 1954. Ökologie der triassischen Muschel *Lima lineata* (Schoth) und ihrer Epöken: *Neues Jb. Geol. Paläont. Monatsh.* **4,** 163–183.

STANLEY, S. M. 1969. Bivalve mollusk burrowing aided by discordant shell ornamentation. *Science*, **166,** 634–635.

—— 1970. Relation of shell form to life habits in the Bivalvia. *Mem. geol. Soc. Amer.* **125,** 1–296.

—— 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Jour. Paleont.* **46,** 165–212.

—— 1975*a*. A theory of evolution above the species level. *Proc. nat. Acad. Sci.* (*U.S.A.*), **72,** 646–650.

—— 1975*b*. Why clams have the shape they have: an experimental analysis of burrowing. *Paleobiology*, **1,** 48–58.

—— In press. Trends, rates, and patterns of evolution in the Bivalvia. *In* A. HALLAM (ed.), *Patterns of Evolution*. Elsevier, The Hague.

STENZEL, H. B. 1971. Oysters. *In* R. C. MOORE (ed.), *Treatise on Invertebrate Paleontology, part N, Mollusca 6, Bivalvia.* Geol. Soc. America and University of Kansas Press, Lawrence, Kansas, 954–1224.

TEVESZ, M. J. S. 1975. Structure and habits of the 'living fossil' pelecypod Neotrigonia. *Lethaia*, **8,** 321–327.

WATSON, J. 1971. *A Preliminary Account of the Benthic Flora and Fauna of Northwestern Westernport, Victoria.* Underwater Research Group of Victoria, Melbourne.

WRIGHT, R. P. 1974. Jurassic bivalves from Wyoming and South Dakota: A study of feeding relationships. *Jour. Paleont.* **48,** 425–433.

WOODWARD, S. P. 1851. *A Manual of the Mollusca*. John Weal, London.

STEVEN M. STANLEY

Department of Earth and Planetary Sciences
Johns Hopkins University
Baltimore, Maryland 21218
U.S.A.

Typescript received 1 September 1976