

TRACES AND TRENDS OF PREDATION,  
WITH SPECIAL REFERENCE TO  
BIVALVED ANIMALS

*by* GEERAT J. VERMEIJ

**ABSTRACT.** Predation is an ecological interaction which has had a profound impact on the course of organic evolution. Full understanding of this impact can come only when fossil traces of predation are interpreted properly and catalogued systematically. The most reliable traces are those left after unsuccessful attempts by predators to subjugate their prey.

Although predation seems to have increased in evolutionary importance through the course of the Phanerozoic, gastropods and bivalved animals have generally differed in their response to it. Gastropods have tended to emphasize armour, whereas the chief defences of bivalved animals have been escape from and avoidance of predators. The reason for this difference in evolutionary response is hypothesized to lie in the consequences of shell damage. For gastropods, non-lethal damage probably does not increase susceptibility to other causes of death, but for many bivalved animals marginal valve damage increases detectability of the prey because metabolites leach from the soft tissues even when the valves are shut. Accordingly, most pelecypods have very low frequencies of shell repair, and their potential for evolving resistance to breakage is much smaller than that of gastropods.

**PREDATION** is an ecological interaction which has had a profound impact on the course of organic evolution. Although probable traces of predation date back to the early Cambrian (Pocock 1974), the anecdotal nature of most of the data on these traces has precluded a quantitative understanding of the importance of predation as a component of selection through the course of Phanerozoic time. Moreover, the traces have frequently been misinterpreted, or they have been attributed to non-biological causes. Accordingly, it is appropriate to clarify the meaning of the various traces, to call for more systematic surveys of the traces, and to outline hypotheses about predation over time. These are the aims of this paper.

Predation consists of three more or less distinct phases: the detection or recognition phase, the pursuit or escape phase, and the subjugation or resistance phase (Holling 1966). Predators and prey may show adaptations to each of these phases, but typically adaptation to one phase is better than to the others.

The evolutionary pathways taken by different groups against predators vary. Some groups, like the gastropods, emphasized armour, whereas unshelled cephalopods came to depend chiefly on escape. Pelecypods are conservative and seem to have evolved less conspicuous armour than have gastropods. Their defence lies chiefly in escape or avoidance (Vermeij 1978).

Two important and largely unexplored questions arise from these initial impressions. 1. Does evolutionary emphasis on one form of defence preclude or usurp other types of defence? 2. How are the various pathways of defence determined? I discuss these questions here with special reference to bivalves, whose functional morphology is perhaps better understood than that of any other group of invertebrates. I shall argue that, although adaptation to all phases of predation has increased through time, bivalved animals have had to rely more on escape and avoidance than on armour because of the detrimental consequences of shell damage.

## TRACES OF PREDATION

Palaeontologists have available to them three types of evidence of predation. These are: (1) the presence of identifiable remains in faeces (coprolites) or in the stomachs of fossil predators; (2) fossils which have been attacked and killed in a characteristic way by predators; and (3) scars left as the result of unsuccessful attacks by predators. Functional morphology can provide a fourth, less direct, form of evidence. Characters associated in living species with avoidance, escape, or resistance may be interpretable in fossils as antipredatory adaptations if there is some independent evidence that the predator to which the prey had a defence co-occurred with the prey.

Evidence of type 1 provides a direct connection between predator and prey, but it cannot usually yield data on the ecological or evolutionary impact of predation. Although hard parts can be recognized in the coprolites or stomachs of predators, many soft-bodied prey cannot be detected, so that the relative contribution of preserved prey to the overall diet cannot be established. Moreover, the diet of many large, living predatory species is catholic and varies considerably among individuals and from place to place. Accordingly, not too much weight can be placed on the contents of one or a few coprolites or fossil stomachs. Finally, the absence of diagnostic hard parts in preserved faeces or stomachs does not prove that the predator in question did not feed on hard-bodied prey. Crabs, rays, and many other shell-breaking predators ingest only a small fraction of their prey's hard parts, and spit out most of the diagnostic pieces before swallowing the flesh.

Type 2 evidence is difficult to distinguish from postmortem alteration in many cases, but there are exceptions. Drilling predators (gastropods and octopods) leave unambiguous evidence of their activity in the form of holes through the skeleton of their prey. The ecological importance of drilling as a cause of death can be inferred by estimating the proportion of a population of 'dead' shells that has been drilled. The inferred importance of drilling will be overestimated if shell fragments (resulting from lethal breakage) are ignored and if breakage is an important cause of death; it will be underestimated if the prey are sometimes killed without drilling (Vermeij 1980).

The importance of breakage as a cause of death can be inferred if (1) a given break can be recognized as having been lethal; (2) broken and unbroken prey were preserved with equal probability; and (3) breakage was not postmortem (Vermeij 1982a). The first criterion is difficult to satisfy in fossils because it requires that non-lethal damage be distinguished from lethal breakage. Normally, this distinction is possible only after living prey are placed with and damaged by known predators in the laboratory. Differences between prey species may be profound. Destruction of the body whorl, for example, is lethal for short-spined gastropods such as *Conus* and *Strombus*, but is not lethal for such high-spined genera as *Terebra* (Vermeij *et al.* 1980; Vermeij 1982a). The second criterion is likewise difficult to satisfy. Probably the most reliable samples in which to estimate the incidence of lethal breakage are those consisting of uneroded shells in fine sediments where waves or currents are unlikely to have effected large-scale transport. Restriction to samples of this kind also minimizes problems associated with the third criterion. The frequency of postmortem 'lethal' breakage can be estimated in populations in which drilling is a common cause of death. Because drilling gastropods appear to drill chiefly living molluscs and to shun hermit crabs and other secondary shell inhabitants, a drilled 'lethally' broken shell can usually be inferred to have been broken after the mollusc's death. In studies of Recent gastropods (Vermeij 1982a), I have found postmortem breakage to be of relatively minor importance; it inflates estimates of the ecological impact of breakage by no more than 10%. In summary, reliable estimates of the incidence of lethal breakage are unlikely to be obtained for fossil prey species, and difficult to achieve even for Recent species.

The third type of evidence for predation is unsuccessful attack. The incidence of predatory failure provides no information about the ecological importance of predation, but instead permits an evaluation of the role of predation in selection. In principle, selection for antipredatory traits is possible when predators always detect, catch, and subdue their prey. If predators sought out, pursued, and attempted to kill only prey which they could eat, vulnerable individuals would quickly be removed from the prey population and only undesirable or insuperable prey would be left behind to reproduce. Most predators, however, show very high rates of failure during one or more stages of

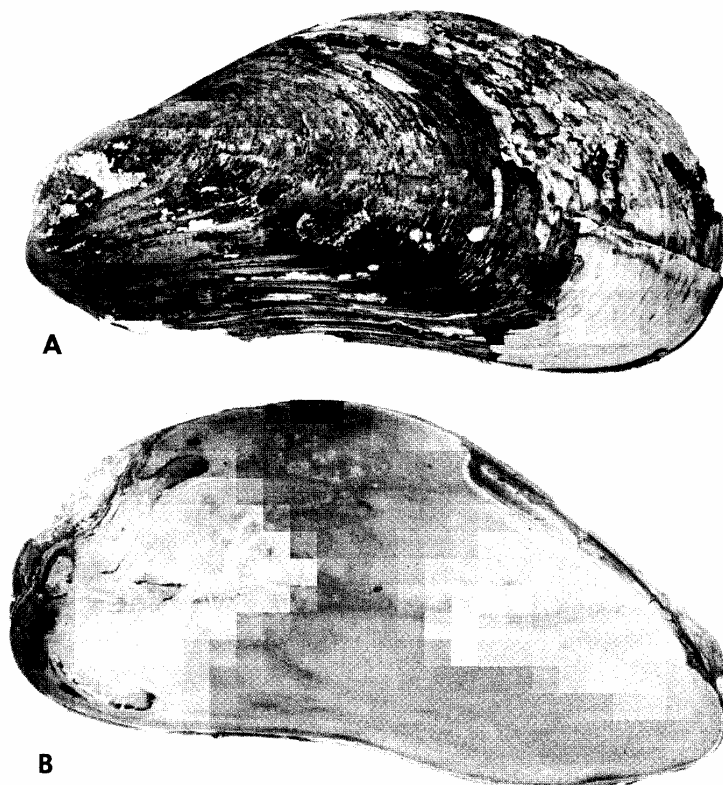
predation (Vermeij 1982b). Although many predators are capable of learning to recognize unsuitable prey and to avoid pursuing or subduing them, learning is accomplished by trial and error, the error being an attempt to acquire unsuitable prey. Moreover, many predators regularly attack unsuitable prey. For all practical purposes, therefore, antipredatory aptation can occur only when predators are frequently unsuccessful in detecting (or encountering), pursuing, or subduing prey (Vermeij 1982b). The prey which evade, escape, or resist predation successfully may differ in subtle ways from prey which are killed. The incidence of unsuccessful attack therefore provides a conservative measure of the potential for antipredatory selection.

It is important to recognize that only certain types and certain phases of predation can be inferred in fossils. Many types of predation leave no diagnostic marks on the prey. When prey are swallowed whole, for example, the predator usually leaves the skeleton intact or disarticulated in unbroken pieces. Even unsuccessful attempts at swallowing may leave no traces. Most predators that attack molluscan tissues by way of the aperture or commissure also leave the skeleton intact, although some damage to the growing edge may occur in some instances. Only predation by skeletal breakage or drilling can leave traces in externally shelled fossils. Unsuccessful predation can be inferred confidently in fossils only for the final (subjugation) stage of predation. Failure to detect or catch the prey may engender strong selection for antipredatory features, but it remains unrecorded in the fossil record.

Repaired skeletal injury is probably the most commonly preserved form of non-lethal predation in fossils. The capacity to repair the skeleton after damage appears to be universal in animals, although the rates of this repair vary widely according to taxon and habitat. Skeletal repair is known in echinoderms (Ebert 1968; Zinsmeister 1980), trilobites (Ludvigsen 1977; Snajdr 1981; Pocock 1974), corals (Loya 1976; Bak *et al.* 1977), brachiopods (Paine 1963; Brunton 1966; Alexander 1981; Jones 1982), and the extant classes of molluscs: Polyplacophora (Tucker and Giese 1959), scaphopods (Papp *et al.* 1947), gastropods (Andrews 1935; Boekschoten 1967; Bulkley 1968; Currey and Kohn 1976; Geller 1982; and many other references reviewed by Vermeij 1978, 1982b, in press), pelecypods (see text-fig. 1) (many reports including Baker 1901; Sykes 1905; Warren 1916; Magalhaes 1948; Yonge 1953; Boshoff 1968; Kauffman 1972; Richardson *et al.* 1980; Savazzi 1981), and cephalopods (Westermann 1971).

The interpretation of shell repair in gastropods is usually straightforward (Vermeij 1982a, b). Most features of armour (thick shell, narrow aperture, capacity to withdraw the soft tissues far into the shell) are associated with a high frequency of non-lethal repaired shell damage. This type of damage results when the outer lip is attacked, broken, and subsequently repaired by the retractable mantle margin of the gastropod. The only type of armour which is not associated with a high frequency of repair is a thickened outer lip. The latter often remains intact even after a vigorous attack. Nevertheless, the frequency of repair serves as a minimal estimate of the importance of shell breakage as a component of selection, and gives an indication of the importance of the shell as an effective fortress.

Shell repair in bivalved animals is somewhat more difficult to interpret than in gastropods. Non-lethal injury of the lip of a gastropod shell does not expose the soft tissues, because the injury does not usually extend beyond the operculum of the retracted animal. Even in species without an operculum, the typical lip injury does not result in exposure of the retracted soft tissues. If it did, the prey would probably be eaten by the attacker. The same applies to injury in scaphopods. For many bivalved animals, however, an injury to the commissure of the valves results in a temporary breach through which metabolites could pass even when the valves are completely adducted. This could be detrimental, because the metabolites released into the environment of an unprotected animal attract potential predators (Christensen 1970; Carriker and Van Zandt 1972; Palmer *et al.* 1982). The capacity to isolate soft tissues temporarily from the outside world is an effective way of avoiding detection by would-be predators which depend on chemoreception. Accordingly, a high frequency of non-lethal marginal injury in bivalved animals indicates not only that the shell and other defences were sufficient to resist subjugation by a predator, but also that the victim was capable of tolerating temporary incomplete closure of the adducted valves. For pelecypods with a permanent anterior or



TEXT-FIG. 1. *Modiolus modiolus* in dorsal (A) and ventral (B) views, showing a remarkable repaired injury. Specimen dredged alive at six to seven fathoms depth off St. Andrews, New Brunswick, Canada, September 1982.

posterior gape, such as many temperate deep-burrowing mactrids, myacids, and solenids (Vermeij and Veil 1978), marginal damage might not be very detrimental because it does not substantially increase the prey's detectability, but for species which can normally seal off the soft tissues completely a marginal injury could increase susceptibility to other causes of death.

There seem to be at least two fundamental ways in which bivalved animals can prevent marginal damage from breaking the seal between the adducted valves. First, the edges of one or both of the valves may extend beyond the line of contact between the valves. The commissure lies in a furrow between the slightly projecting valve edges in some venerid and fimbriid pelecypods, and is tucked in beneath the projecting edge of either the right or left valve in the Corbulidae and some Arcidae. This latter protection of the commissure is associated with an inequivalve condition (Nicol 1958; McGhee 1978; Lewy and Samtleben 1979). It is extremely rare in brachiopods; only some Permian richthofeniids, oldhaminids, and lytoniaceans had the brachial valve recessed within the pedicle valve (Rudwick 1961; Rudwick and Cowen 1967; Williams and Hurst 1977). Another variation on the theme of commissural protection is the development of spines or scales which project well beyond the line of contact between the valves, as in spondylid and some chamid pelecypods and in some

upper Palaeozoic strophomenide brachiopods (Stanley 1970; Rudwick 1970). The second mechanism preventing marginal damage from being lethal is mantle retraction. A highly retractable mantle edge coupled with a thin, flexible prismatic distal portion of the valves is characteristic of pinnacean and pteriacean pelecypods (Yonge 1953; Carter 1980). When the valve edges are bitten or chipped, the mantle can be withdrawn and the break temporarily sealed between the remaining flexible surfaces of the opposing valves. Valve flexibility does not seem to have evolved in articulate brachiopods (Carter 1980), but some strophomenides had the anterior edges of their valves extended with very little space between the adducted valves (Rudwick 1970). The hypothesis that these methods of commissural protection indeed permit non-lethal marginal damage and the eventual evolution of breakage-resistant armour has not been tested.

Some pelecypods and brachiopods may have overcome the problem of marginal damage by evolving globose shells in which the seam between the closed valves blends in with the smooth contour of the shell as a whole. When a potentially shell-breaking predator attacks, the edge is no more vulnerable than are other parts of the shell. If the attack is unsuccessful, the shell remains undamaged. Smoothly contoured globose shells are present among some arcid, corbulid, and shallow-burrowing lucinid pelecypods and among many rhynchonellide brachiopods. Again, the suggested protective function of globosity in preventing marginal damage requires experimental confirmation.

If the soft tissues were toxic or repellent to an intruder, a marginal break would not necessarily increase risk of death to the victim, even if more animals were able to detect the metabolites diffusing from the animal. I know of no documented examples of intrinsic toxicity in pelecypods, although temporary toxicity due to infestation by dinoflagellates is widespread. C. W. Thayer has unpublished data suggesting that articulate brachiopods from Puget Sound may be repellent to predaceous crabs, fishes, asteroids, and gastropods. The apparent rarity of toxicity in pelecypods is surprising, but it is consistent with the edibility of most pelecypods to humans.

Because non-lethal shell damage may increase the detectability of bivalves to potential predators, the geographical and temporal patterns in the incidence of shell repair in bivalved animals may be quite different from those in gastropods. Both the development of breakage-resistant shell armour and the frequency of non-lethal shell injury in gastropods increase from the temperate zones to the tropics, from fresh to salt waters, from the tropical Atlantic to the tropical Pacific and Indian Oceans, and through time from the Palaeozoic to the late Mesozoic and Cenozoic (Vermeij 1978, 1982*b*; Vermeij *et al.* 1980; Vermeij and Currey 1980; Palmer 1979; Bertness *et al.* 1981). In pelecypods, the incidence of permanently gaping species, which typically burrow deeply into unconsolidated sediments, declines from high to low latitudes (Vermeij and Veil 1978), while the incidence of tight closure (as reflected in the incidence of crenulate valve margins) increases toward the tropics (Vermeij 1978). These patterns suggest the following hypotheses: (1) predation by animals which penetrate between the valves becomes evolutionarily more important toward the tropics; and (2) detection by predators is more strongly selected against at low latitudes than at higher latitudes. Moreover, temperate bivalves may be able to sustain greater injury than their warmer-water counterparts. Accordingly, the incidence of non-lethal marginal breaches may be greater at higher latitudes than in the tropics. Marginal damage which does not expose the soft tissues when the valves are shut should be more common in the tropics, as is lip damage in gastropods.

A preliminary analysis of my unpublished data on mussels (*Mytilidae*) shows frequencies of repair in this family to be extremely low and not to change with latitude. Yet mussels are frequently attacked by crabs, birds, and other potential shell-breakers which often fail to kill their prey (Ebling *et al.* 1964; Harger 1972; Elner 1978; Griffiths and Seiderer 1980).

Other work in progress suggests that the incidence of marginal repair in fresh-water unionid pelecypods is very high. Nearly every shell of some thick-shelled species from the central and southern United States bears scars. In some respects, this might be expected if chemoreceptive predators are rare in fresh waters, but the observation of high frequencies of marginal repair in fresh-water clams leads to a curious paradox. Unionids may often be exposed to stronger selection in favour of breakage-resistant armour than are marine pelecypods, in which the threat of chemical

detection may be very much greater. This situation contrasts strongly with that in gastropods, where armour and repair are both much more common in marine species. If these patterns are borne out, they point to the possibility that selection for one form of defence often depends on the importance of other selective factors.

#### PREDATION THROUGH TIME

It has been suggested that armour in gastropods increased in incidence and in degree of expression through the course of the Phanerozoic (Papp *et al.* 1947; Vermeij 1975, 1977). During the middle and late Palaeozoic, gastropods with mechanically weak features (umbilici, loose coiling) comprised more than 25% to 30% of the species in most local assemblages, whereas forms with breakage-resistant features (narrow aperture, thick outer lip, strong tuberculate sculpture) were rare or absent. Beginning in the middle Jurassic, a shift took place in gastropod architecture, so that gastropods with breakage-resistant traits and with the capacity to withdraw the body far into the shell expanded in numbers at the expense of mechanically weak forms. By the late Cenozoic, species with apertural modifications comprised more than 20% of most tropical assemblages, whereas umbilicate forms were found in fewer than 10% of species (Vermeij, in press). The hypothesis that breakage became an increasingly important component of selection after the Triassic is supported by data showing that the frequency of predator-induced shell repair increased after that time (Vermeij *et al.* 1981). P. Signor suggests that early Palaeozoic gastropods were even less well armoured than were their middle and late Palaeozoic descendants, and that the Devonian was a time of architectural change as important as the Jurassic. Armour also increased in ammonoids, in which the frequency of strong sculpture and of complexly fluted sutures increased gradually, if not constantly, from the Devonian to the late Cretaceous (Ward 1981).

It may be possible to make a similar case for increasing armour through time in bivalved animals, but critical experiments linking specific shell features to breakage-resistance have not been done, and temporal patterns in these features have not been documented in detail. At the microstructural level, several groups of pelecypods have evolved shells of foliated calcite, which permits the development of strengthening radial plications, as in Mesozoic and Cenozoic Pectinidae (Waller 1972). Oysters (mostly post-Permian Ostreacea) and several sedentary Pectinacea and Cretaceous Hippuritacea have evolved calcitic shells in which cavities may limit the spreading of incipient cracks (Carter 1980). On the other hand, it has been shown that nacre is typically stronger (with respect to compression) than are other types of molluscan microstructure (Currey and Taylor 1974; Currey 1976, 1977), yet nacre is also the primitive microstructure in pelecypods and gastropods (Taylor 1973; Carter 1980). The evolutionary abandonment of nacre in favour of prismatic, foliated, crossed-lamellar, and other microstructures in many lineages argues strongly against an increase in shell strength over time at the microstructural level. Palmer (in press) has now shown that gastropods with nacreous structure, in which the organic content is higher than in other microstructural types, regenerate shell more slowly than do gastropods with crossed-lamellar structure.

Radial and concentric sculptures thicken and perhaps sometimes buttress the shell of pelecypods and brachiopods. In infaunal forms, these types of ornament also promote anchorage or burrowing in the sediment. Among infaunal pelecypods, external ornament was rare during the Palaeozoic (e.g. *Astartella*), but it became widespread with the rise to dominance in the Triassic and Jurassic of the Trigonicea and the hegemony of the heterodonts in the Cenozoic (Stanley 1977a, b, 1981). Thick shells are another obvious defence against shell-breakers, but I have no data on changes in the occurrence of thick-shelled bivalved taxa over time.

Stanley (1970) remarked with justifiable surprise that epifaunal pelecypods are often thinner-shelled than their shallowly burrowing infaunal relatives. This is evident, for example, in the Carditacea and Arcacea of the modern world ocean. The only epifaunal taxa that have distinctly thick shells are cemented forms (Ostreacea, Chamacea), large byssally attached giant clams (Tridacnidae), and some small Arcacea and Carditacea living under stones; but many shallow-burrowing infaunal taxa have shells that are as thick as or thicker than those of species from beneath

boulders. These observations highlight the paradox that, although attached epifaunal pelecypods would be readily available targets for attack by shell-breakers, many of these animals have not adopted exceptional armour as their chief defence.

I believe that the explanation for this paradox lies in the poor capacity of bivalved animals to sustain even slight marginal damage. In order to evolve armour, animals must survive episodes of damage-inducing attack (Vermeij 1982*b*). In bivalved animals, however, marginal damage often invites predators or other potential agents of death to a damaged individual. Accordingly, it may be difficult in general for bivalved animals to sustain and survive shell damage. As pointed out above, exceptions may occur among taxa with highly retractable mantle margins and flexible valve margins, and among species in which the valves project beyond the commissure. Armour would be expected to evolve only among taxa with these attributes, at least as a defence against shell breakage.

Initial support for this hypothesis comes from data on the incidence of repaired marginal breaks in Recent pelecypods. In temperate and tropical mytilids, donacids, and venerids I have examined, the frequency of repair is typically extremely low, almost never rising above 0.15 scars per shell. Many samples show no repair. The only species I have encountered so far with plentiful repaired damage is the shallow-burrowing venerid *Anomalocardia flexuosa* from Brazil, in which I have found frequencies of up to 0.70 scars per individual. In their survey of six common pelecypods from the Pliocene of Albenga, Italy, Robba and Ostinelli (1975) found repair in only two species, *Anadara diluvii* (0.07) and *Corbula gibba* (0.35). The latter species is characterized by a thick shell of which the right valve ventrally overlaps the smaller left valve.

The underlying assumption that marginal damage is detrimental to bivalved animals still requires confirmation. I know of no data in the literature bearing on this point.

Those who are sceptical of the above arguments will counter that many epifaunal pelecypods are, after all, thick-shelled and therefore well armoured. Examples include many cemented forms, giant clams, and a few very large mytilids. In this connection it is important to remember that thickened valves are advantageous for many reasons. One advantage is protection against muricacean drilling gastropods, whose attempts to drill are frequently unsuccessful (see Vermeij 1982*b*, for a review). Unsuccessful drilling can lead to strong selection for thick shells. Although drilling predation is known throughout most of the Palaeozoic and Mesozoic eras, it did not become quantitatively important until the late Cretaceous (Vermeij 1977; Sohl 1969; Vermeij and Dudley 1982). It may therefore prove difficult to separate drilling from breakage as a cause for the evolution of thick-shelled pelecypods.

If many pelecypod groups did not emphasize armour as a defence, they did respond to increasing selection from predators by escaping or avoiding their enemies. Stanley (1970, 1975, 1977*a, b*, 1981), who has studied shell features which promote burrowing, notes that these features were rare during the Palaeozoic, but became widespread during the Mesozoic and Cenozoic. Sculpture of the ratchet type, in which the anterior and ventral flanks of ribs are less steep than the posterior and dorsal flanks, aids some venerids, cardiids, trigoniids, and tellinids in burrowing and in gripping the sediment (Stanley 1977*b*, 1981). Ribs of this morphology appeared for the first time in Mesozoic Trigoniacea, and are common today in tropical, shallow-burrowing pelecypods and infaunal gastropods (see also Signor 1982). Pelecypods with smooth, glossy, streamlined shells, which are associated with rapid burrowing, are known only in Cretaceous to Recent families such as the Veneridae, Donacidae, Tellinidae, and Mesodesmatidae (Stanley 1977*a*). Runnegar (1974) points out that deep-burrowing late Palaeozoic anomalodesmatans had the umbones placed anterior to the shell's midline, whereas many deep-burrowing post-Palaeozoic members of this group have the umbones in a more posterior position. He interprets this change as reflecting an increase in the size of the foot and a change from a ventral to an anterior position of the pedal gape. These changes in relative foot size and orientation may mean that post-Palaeozoic Anomalodesmata from deep sediments are better burrowers than were their late Palaeozoic counterparts (Runnegar 1974). Modern cockles (Cardiidae) are typically faster burrowers than *Neotrigonia*, a relict living representative of the functionally equivalent but chiefly Mesozoic family Trigoniidae (Stanley 1977*b*). Sedentary epifaunal pelecypods and brachiopods on unconsolidated bottoms were very common in the Palaeozoic, but these types of animals

waned after the Permian except in deep waters, where inoceramids remained important until the late Cretaceous. Animals of this type are essentially absent from the Recent fauna. The only pelecypods that live on the surface of unconsolidated sediments are very large (the tridacnid *Hippopus*), byssally attached, or mobile (Pectinacea, *Placuna*) (Stanley 1977a; Thayer, in press). These trends suggest that mobility, especially burrowing, became increasingly important to the survival of pelecypods through time. I interpret this increased emphasis on mobility to be a response to an increase in the importance of predation as a component of selection in pelecypods.

Thayer (in press) interprets the rise of mobile suspension-feeders at the expense of sedentary reclining forms as a reflection of the increasing importance of sediment disturbance (bioturbation) over the course of the Phanerozoic. Certainly this possibility cannot be discounted; indeed, it is likely that both predators and bioturbation were responsible for the increased emphasis on mobility in pelecypods. It may be that increased bioturbation is itself a manifestation of an increase of predation at and above the sediment surface.

Another theme which runs through the evolutionary history of pelecypods is that of predator avoidance. Stanley (1972, 1977a) noted that semi-infaunal byssally attached pelecypods were widespread during the Palaeozoic, but today survive chiefly in sediments which are stabilized by the roots of marine angiosperms. Predators in such vegetated sediments are much less effective at finding prey than they are in unvegetated sands (Peterson 1979, 1982; Heck and Thoman 1981). The increased emphasis on tight closure and the largely post-Palaeozoic occupation of deep sediments by pelecypods may be other expressions of the increasing emphasis on predator avoidance by pelecypods. With respect to the latter trend, Blundon and Kennedy (1982) have shown that deeply burrowing clams stand a greater chance of remaining undetected by burrowing crabs than do clams which are buried more shallowly.

Another possible evolutionary response of bivalved and other animals to predation is a reproductive one. Some species may have no morphological or behavioural defences against predators, but instead may have fecundities that are so high that the prey population is maintained even in the face of intense predation on adults. Whether this response can legitimately be classified as an antipredatory aptation in the sense of Vermeij (1982b) is a matter of personal opinion, but in any case little can be said about its incidence in the modern fauna or about its evolutionary history.

Although analysis of groups other than gastropods and bivalved animals is beyond the scope of this paper, increasing emphasis on armour or escape through the course of the Phanerozoic seems to characterize most groups of animals. I interpret these patterns to mean that predation in general has become increasingly important in determining the morphology and distribution of marine invertebrates. Groups which, for one reason or another, have been unable to evolve effective armour or methods of escape survive today only in physiologically marginal habitats where predators are slow or rare (Vermeij 1978). I believe that the gradual occupation of such environments, including deep sediments and the cold deep sea, was one consequence of the increasing evolutionary impact of predation through the Phanerozoic.

Predation is by no means the only, or even the primary, cause for the observed architectural and ecological changes through time. Competition for scarce resources probably also intensified over the course of the Phanerozoic, and indeed may be fundamental to the evolution of enhanced predatory capabilities in many groups (Vermeij, 1982b). The importance of predation is often easier to assess than that of interactions such as competition, parasitism, or mutualism, but this does not mean that these other relationships were less important.

One of the unique contributions that palaeontologists can make to the study of evolution is the documentation of trends or of the lack of trends through time. This documentation will require large-scale surveys of the occurrence of architectural traits in groups from different periods, the incidence of traces of predation, and the importance of other biological relationships between organisms. These surveys should encompass all species in the community, not just those in which a given phenomenon is particularly common. Studies of interactions between a few chosen species from one formation in one period are interesting and often important, but in the context of the documentation of long-term trends they are anecdotal and therefore potentially misleading. Further-



more, it is important to compare spatial variation with temporal variation. Inevitably, there is much variation in the incidence of unsuccessful predation and in almost every other aspect of biological interaction from place to place, even when the habitats are much the same (Vermeij *et al.* 1981). Without an awareness of such variation, it is difficult to evaluate the reality of purported temporal trends.

Many questions remain to be answered. How did the major episodes of mass extinction influence the observed trends? Were the trends temporarily reversed, or was the pattern of selective extinction such that the trend toward greater antipredatory aptation was accentuated? Was the increase in gastropod armour during the mid-Mesozoic stimulated or accelerated by the breakup and dispersal of the continents? More generally, is the increase in defence to be expected from first principles of evolution, as suggested by Darwin (1872), or were the trends driven by extrinsic historical factors of geography, climate, and crisis? These questions will challenge palaeontologists for years to come.

## REFERENCES

- ALEXANDER, R. R. 1981. Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulate. *J. Paleont.* **55**, 192-203.
- ANDREWS, E. A. 1935. Shell repair in the snail, *Neritina*. *J. exp. Zool.* **70**, 75-107.
- BAK, J. P. M., BROUNS, J. J. W. M. and HEYS, F. M. L. 1977. Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. *Proc. Third Intern. Coral Reef Symp.* **1**, 144-148.
- BAKER, F. C. 1901. Some interesting molluscan monstrosities. *Trans. Acad. Sci. St. Louis*, **11**, 143-146.
- BERTNESS, M. D., GARRITY, S. D. and LEVINGS, S. C. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution*, **35**, 995-1007.
- BLUNDON, J. A. and KENNEDY, V. S. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. exp. mar. Biol. Ecol.* **65**, 67-81.
- BOEKSCHOTEN, G. J. 1967. Palaeoecology of some Mollusca in the Tielrode Sands (Pliocene, Belgium). *Palaeogeogr., Palaeoclimat., Palaeoecol.* **3**, 311-362.
- BOSHOFF, P. H. 1968. A preliminary study on conchological physio-pathology, with special reference to Pelecypoda. *Ann. Natal Mus.* **20**, 199-216.
- BRUNTON, H. 1966. Predation and shell damage in a Visean brachiopod fauna. *Palaeontology*, **9**, 355-359.
- BULKLEY, P. T. 1968. Shell damage and repair in five members of the genus *Acmaea*. *Veliger*, **11** (suppl.), 64-66.
- CARRIKER, M. R. and VAN ZANDT, D. 1972. Predatory behavior of a shell-boring muricid gastropod. In WINN, H. E. and OLLA, B. L. (eds.). *Behavior of marine animals. Vol. I: Invertebrates*, 157-244. Plenum, New York.
- CARTER, J. G. 1980. Environmental and biological controls of bivalve shell mineralogy and microstructure. In RHOADS, D. C. and LUTZ, R. A. (eds.). *Skeletal growth of aquatic organisms; biological records of environmental change*, 69-113. Plenum, New York.
- CHRISTENSEN, A. M. 1970. Feeding biology of the sea-star *Astropecten irregularis*. *Ophelia*, **8**, 1-134.
- CURREY, J. D. 1976. Further studies on the mechanical properties of mollusc shell material. *J. Zool., Lond.* **180**, 445-453.
- 1977. Mechanical properties of mother of pearl in tension. *Proc. R. Soc. Lond. B*, **196**, 443-463.
- and KOHN, A. J. 1976. Fracture in the crossed-lamellar structure of *Conus* shells. *J. Material Sci.* **11**, 1615-1623.
- and TAYLOR, J. D. 1974. The mechanical behaviour of some molluscan hard tissues. *J. Zool., Lond.* **173**, 395-406.
- DARWIN, C. 1872. *The origin of species by natural selection or the preservation of favoured races in the struggle for life*, 6th edn., reprinted 1962. Colliers, New York.
- EBERT, T. A. 1968. Growth rates of a sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology*, **59**, 1075-1091.
- EBLING, F. J., KITCHING, J. A., MUNTZ, L. and TAYLOR, C. M. 1964. The ecology of Lough Ine. XIII Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J. anim. Ecol.* **33**, 73-83.
- ELNER, R. W. 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia (Berlin)*, **36**, 333-344.
- GELLER, J. B. 1982. Microstructure of shell repair materials in *Tegula funebris* (A. Adams, 1855). *Veliger*, **25**, 155-159.

- GRIFFITHS, C. L. and SEIDERER, J. L. 1980. Rock-lobsters and mussels—limitations on preferences in a predator-prey interaction. *J. exp. mar. Biol. Ecol.* **44**, 95–109.
- HARGER, J. R. 1972. Competitive co-existence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. *Veliger*, **14**, 387–409.
- HECK, K. L. Jr. and THOMAN, T. A. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. exp. mar. Biol. Ecol.* **53**, 125–134.
- HOLLING, C. S. 1966. The functional response of invertebrate predators to prey density. *Mem. ent. Soc. Can.* **47**, 3–86.
- JONES, B. 1982. Paleobiology of the Upper Silurian brachiopod *Atrypa*. *J. Paleont.* **56**, 912–923.
- KAUFFMAN, E. J. 1972. *Ptychodus* predation upon a Cretaceous *Inoceramus*. *Palaentology*, **15**, 439–444.
- LEWY, Z. and SAMTLEBEN, C. 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia*, **12**, 341–351.
- LOYA, Y. 1976. Skeletal regeneration in a Red Sea scleractinian coral population. *Nature*, **261**, 490–491.
- LUDVIGSEN, R. 1977. Rapid repair of traumatic injury by an Ordovician trilobite. *Lethaia*, **10**, 205–207.
- MAGALHAES, H. 1948. An ecological study of snails of the genus *Busycon* at Beaufort, North Carolina. *Ecol. Monogr.* **18**, 377–409.
- MCGHEE, G. R. 1978. Analysis of the shell torsion phenomenon in the Bivalvia. *Lethaia*, **11**, 315–329.
- NICOL, D. 1958. A survey of inequivalve pelecypods. *J. Washington Acad. Sci.* **48**, 56–62.
- PAINE, R. T. 1963. Ecology of the brachiopod *Glottidia pyramidata*. *Ecol. Monogr.* **33**, 187–213.
- PALMER, A. R. 1979. Fish predation and the evolution of gastropod shell defense: experimental and geographic evidence. *Evolution*, **33**, 697–713.
- (in press). Relative cost of organic matrix in calcium carbonate skeletons: evidence from marine gastropods. *Mar. Biol.*
- SZYMANSKA, A. and THOMAS, L. 1982. Prolonged withdrawal: a possible predator evasion behavior in *Balanus glandula* (Crustacea: Cirripedia). *Ibid.* **67**, 51–55.
- PAPP, A., ZAPPE, H., BACHMAYER, F. and TAUBER, A. F. 1947. Lebensspuren mariner Krebse. *K. Akad. Wissensch. Wien, Mathem. Naturwiss. Kl., Sitzber.* **155**, 281–317.
- PETERSON, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In LIVINGSTON, R. J. (ed.). *Ecological processes in coastal and marine systems*, 233–264. Plenum, New York.
- 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar. Biol.* **66**, 159–170.
- POCOCK, K. J. 1974. A unique case of teratology in trilobite segmentation. *Lethaia*, **7**, 63–66.
- RICHARDSON, C. A., CRISP, D. J. and RUNHAM, N. W. 1980. Factors influencing shell growth in *Cerastoderma edule*. *Proc. R. Soc. B*, **210**, 513–531.
- ROBBA, E. and OSTINELLI, F. 1975. Studi paleoecologici sul Pliocene Ligure I. Testimonianze di predazione sui molluschi Pliocenici di Albenga. *Riv. Ital. Paleont.* **81**, 309–372.
- RUDWICK, M. J. S. 1961. The feeding mechanism of the brachiopod *Prorichthofenia*. *Palaentology*, **3**, 450–471.
- 1970. *Living and fossil brachiopods*, 199 pp. Hutchinson & Company Limited, London.
- and COWEN, R. 1967. The functional morphology of some aberrant strophomenide brachiopods from the Permian of Sicily. *Boll. Soc. paleont. Ital.* **6**, 113–176.
- RUNNEGAR, B. 1974. Evolutionary history of the bivalve subclass Anomalodesmata. *J. Paleont.* **48**, 904–940.
- SAVAZZI, E. 1981. *Barbatia mytiloides* and the evolution of shell torsion in arcid pelecypods. *Lethaia*, **14**, 143–150.
- SIGNOR, P. W. III. 1982. Constructional morphology of gastropod ratchet sculpture. *Neues Jb. Geol. Paläont. Abh.* **163**, 349–368.
- SNAJDR, M. 1981. Bohemian Proetidae with malformed exoskeletons (Trilobita). *Palaentologie*, **24**, 37–61.
- SOHL, N. F. 1969. The fossil record of shell boring by snails. *Am. Zool.* **9**, 725–734.
- STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Mem. geol. Soc. Am.* **125**, 1–296.
- 1972. Functional morphology and evolution of byssally attached bivalve molluscs. *J. Paleont.* **46**, 165–212.
- 1975. Why clams have the shape they have: an experimental analysis of burrowing. *Paleobiology*, **1**, 48–58.
- 1977a. Trends, rates, and patterns of evolution in the Bivalvia. In HALLAM, A. (ed.). *Patterns of evolution, as illustrated by the fossil record*, 209–250. Elsevier, Amsterdam.
- 1977b. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Palaentology*, **20**, 869–899.
- 1981. Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology*, **7**, 384–393.

- SYKES, E. R. 1905. Variation in Recent Mollusca. *Proc. malac. Soc. Lond.* **6**, 253-271.
- TAYLOR, J. D. 1973. The structural evolution of the bivalve shell. *Palaeontology*, **16**, 519-534.
- THAYER, C. W. (in press). Sediment-mediated biological disturbance and the evolution of marine benthos. In TEVESZ, M. J. S. and MCCALL, P. L. (eds.). *Biotic interactions in Recent and fossil benthic communities*. Plenum, New York.
- TUCKER, J. S. and GIESE, A. C. 1959. Shell repair in chitons. *Biol. Bull.* **116**, 318-322.
- VERMEIJ, G. J. 1975. Evolution and distribution of left-handed and planispiral coiling in snails. *Nature*, **254**, 419-420.
- 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245-258.
- 1978. *Biogeography and adaptation: patterns of marine life*, 332 pp. Harvard University Press, Cambridge.
- 1980. Drilling predation of bivalves in Guam: some paleoecological implications. *Malacologia*, **19**, 329-334.
- 1982a. Gastropod shell form, repair, and breakage in relation to predation by the crab *Calappa*. *Ibid.* **23**, 1-12.
- 1982b. Unsuccessful predation and evolution. *Am. Nat.* **120**(b), 701-720.
- (in press). Shell-breaking predation through time. In TEVESZ, M. J. S. and MCCALL, P. L. (eds.). *Biotic interactions in Recent and fossil benthic communities*. Plenum, New York.
- and CURREY, J. D. 1980. Geographical variation in the strength of thaidid snail shells. *Biol. Bull.* **158**, 383-389.
- and DUDLEY, E. C. 1982. Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the southeastern United States. *Cretaceous Res.* **3**, 397-403.
- SCHINDEL, D. E. and ZIPSER, E. 1981. Predation through geological time: evidence from gastropod shell repair. *Science*, **214**, 1024-1026.
- and VEIL, J. A. 1978. A latitudinal pattern in bivalve shell gaping. *Malacologia*, **17**, 57-61.
- ZIPSER, E. and DUDLEY, E. C. 1980. Predation in time and space: peeling and drilling in terebrid gastropods. *Paleobiology*, **6**, 352-364.
- WALLER, T. R. 1972. The functional significance of some shell microstructures in the Pectinacea (Mollusca Bivalvia). *Intern. Geol. Congr., 24th Session, Montreal, Canada. Sec. 7*, Palaeontology, 48-56.
- WARD, P. 1981. Shell sculpture as a defensive adaptation in ammonoids. *Paleobiology*, **7**, 96-100.
- WARREN, S. 1916. The feeding habits of *Busycon Nautilus*, **30**, 66-68.
- WESTERMANN, G. 1971. Form, structure and function of shell and siphuncle in coiled Mesozoic ammonoids. *Contr. Life Sci. Div. R. Ont. Mus.* **78**, 1-39.
- WILLIAMS, A. and HURST, J. M. 1977. Brachiopod evolution. In HALLAM, A. (ed.). *Patterns of evolution, as illustrated by the fossil record*, 79-121. Elsevier, Amsterdam.
- YONGE, C. M. 1953. Form and habit in *Pinna carnea* Gmelin. *Phil Trans. R. Soc. B*, **237**, 355-374.
- ZINSMEISTER, W. J. 1980. Observations on the predation of the clypeasteroid echinoid, *Monophoraster darwini*, from the Upper Miocene Entrerios Formation, Patagonia, Argentina. *J. Paleont.* **54**, 910-912.

GEERAT J. VERMEIJ

Department of Zoology  
University of Maryland  
College Park, Md. 20742  
U.S.A.

Manuscript received 22 November 1982

Revised manuscript received 20 December 1982