The Mesozoic Marine Revolution and epifaunal bivalves

E.M. Harper & P.W. Skelton

E.M. Harper, Dept. Earth Sciences, Downing St., Cambridge CB2 3EQ, UK; P.W. Skelton, Dept. Earth Sciences, The Open University, Milton Keynes MK7 6AA, UK.

Key words: Mesozoic Marine Revolution, epifaunal bivalves, defences.

The well documented dramatic increase in predation pressure which started during the early Mesozoic, termed the Mesozoic Marine Revolution (MMR), had an important impact on the evolution of prey organisms (Vermeij, 1983).

Epifaunal bivalves in particular are at considerable risk to predation. In this paper we consider the types of predation to which epifaunal bivalves are prone and outline the evolutionary history of the different modes of predation. We explore methods by which bivalves are known to evade these activities and chart the appearance of these defences in the fossil record. These sections involve both review of the massive existing literature on molluscivory and the presentation of new experimental data, in particular on the value of cementation and various types of valve ornament.

Many previously suggested adaptations have been based on rather anecdotal evidence. Such claims need to be validated by experimental evidence of the value of a specific adaptation against a specific mode of predation. Even so it may be difficult to demonstrate that such a defence is a primary adaptation rather than a fortuitous secondary benefit of a non-adaptive or otherwise selected character.

Inevitably certain taxa will be prevented from evolving particular defences by the constraints of their own body plans, whilst others will be preadapted for others. For example, obvious defensive adaptations, such as the possession of spines and thick shells are not uniformly distributed amongst the bivalve clades. In this survey we demonstrate that these defences are linked with basic features of valve secretion. Spines can only be created by bivalves which possess a very flexible periostracum, whilst thick shells are restricted to those utilising relatively inexpensive microstructures with a low organic content, for example foliated calcite. Mytiloids have been prevented from evolving such structural armour by these constraints and have, instead, resorted to a plethora of behavioural defences.

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Introduction

Avoidance of predation is of critical importance to any organism. Predation, along with competition, is important in the regulation of populations and therefore its rôle in shaping evolution is fundamental. Predation pressure in marine benthic communities has not been constant over geological time; it is well documented that after a sharp increase at the beginning of the Mesozoic there has been a continuous increase in the numbers and the adaptive diversity of predatory groups (Papp et al., 1947; Vermeij, 1977, 1978, 1987).

Amongst prey organisms the bivalved molluscs are potentially some of the most vulnerable. Vermeij (1983) noted that the bivalved form (of both molluscs and brachiopods) is very susceptible to marginal damage, which with the poor capacity of the animal for sealing and healing, is often fatal. This condition, argues Vermeij, has made it imperative that bivalves evolve defensive adaptations which allow them to evade their predators rather than by increasing their armour as in the case of the gastropods. It is this extreme vulnerability of the bivalves, coupled with a rich post-Palaeozoic fossil record and the high preservation potential of predator induced injuries, which make the bivalves ideal subjects for the study of the effects of increasing predation pressure.

The epifaunal bivalves, those exposed at the sediment-water interface, seem to have been particularly vulnerable to the increase in predation pressure over the Phanerozoic (Stanley, 1977; Skelton et al., 1990). This paper considers how predation may have affected this particular group of bivalves. We consider the types of predation to which epifaunal bivalves are prone and outline the evolutionary history of the different modes of predation. We explore methods by which bivalves are known to evade these activities and chart the appearance of these defences in the fossil record. Inevitably certain taxa were channelled towards some defensive adaptations and not others by the constraints and preadaptations of their own body plans: such evolutionary options are also discussed.

Epifaunal bivalves

The Bivalvia are primitively infaunal (Pojeta & Runnegar, 1985). However, the first epifaunal taxa appear early in the geological history of the class in the Ordovician e.g. pterineids and modiomorphids (Pojeta, 1971). Epifaunal bivalves may be divided into three broad ecological categories (see Table 1): (i) those which attach to the substratum (either soft or hard) by an organic byssus spun by the underside of the foot, (ii) those which attach by cementing one of the valves to a hard substratum and (iii) those which have cast off their attachment to become free-lying, some with the ability to swim. Table 1 also shows the taxonomic spread of boring bivalves. Although this habit should properly be considered as infaunal, many of the boring clades have evolved from epifaunal ancestors. From the information given in the table it is apparent that the only bivalve orders which have failed to produce any epifaunal members are the Nuculoida, Solemyoida, Lucinoida (although it does include some cryptobyssate forms), Actinodontoida, Trigonioida, and Myoida. The last order does contain many of the boring families.

Table 1. Division of bivalve orders which display(ed) an epifaunal mode of life into broad ecological categories. The dates of the earliest examples are given in brackets. It should be noted that in some orders the habit may be polyphyletic.

Bysally attached	Cemented	Free lying	Borer
Modiomorphoida (Arenig)	Pterioida (Liassic)	Pterioida (Llanvirn)	Mytiloida (Ordovician + Triassic)
Mytiloida (? Famennian)	Ostreoida (Triassic)	Ostreoida (Triassic)	Arcoida (Pliocene)
		Hippuritoida (Aptian)	
Praecardioida (L. Ordovician)	Veneroida (? Coniacian)		Pholadomyoida (Bajocian)
Arcoida (? Arenig)	Pholadomyoida (Oligocene)		Myoida (Eocene)
Pterioida (Llanvirn)	Hippuritoida (Oxfordian)		
Limoida (Caradoc)			
Ostreoida (Ludlow)			
Veneroida (Senonian)			
Hippuritoida (Eifelian)			
Lucinoida (Palaeocene)			

Most epifaunal bivalves fall into the byssally attached category and it is clear that the very earliest epifaunal bivalves adopted this habit. Byssate attachment is inferred from extinct taxa by the presence of a distinct anterior byssal notch, such as for the pteriacean *Pterinea*. Yonge (1962) recognised a byssally attached phase in the larval history of virtually all living bivalves and suggested that its retention as a mode of fixation in adult forms is the result of neotenous evolution. It is evident that this change occurred very early in bivalve phylogeny allowing members of the class to exploit the more exposed epifaunal life habits.

Predators on bivalves

The·identities of Recent bivalve predators have received much attention in the literature because of the devastating effect they have on commercial shellfisheries (e.g. Hancock, 1960). Carter (1968a) was the first to document the biology and palaeontology of bivalve predators and this work was significantly updated by Vermeij (1987) who gives a comprehensive review of the evolution of durivorous groups.

In studying the defensive adaptations of bivalves it is necessary to consider the methods used by their predators. Vermeij (1987) enumerates five general methods by which durivores subjugate and ingest their prey. We consider that four of these are important in relation to the bivalves:

1) Whole animal ingestion, where the bivalve is entirely enveloped or swallowed by the predator, digested within its body and then the hardparts are voided intact.

2) Extraction and Insertion, where either force or toxins are used to overcome the contractive power of the adductor muscle(s), allowing the valves to gape apart, thus enabling the removal of flesh through the open valves.

3) Pre-ingestive Breakage or Crushing, induced by the application of force by either jaws or 'claws'. This technique often involves substantial destruction of the valves.

4) Boring or Drilling; whereby the valve is punctured by means of a hole through which the flesh can be extracted.

Vermeij's fifth predatory method, which he terms 'transport', is a process by which the prey item is transported to an alien environment for consumption. Although in a very few cases, e.g. the transport of freshwater bivalves to dry land by the stork, *Anastomus lamelligerus* Temminck, 1823, as described by Root (1963), the transport is actually instrumental in forcing the bivalve to gape, most examples merely involve transfer to another site where one of the previously described methods is utilised. For example, Cadée (1989) describes predation of mussels by avian predators which transport their prey inland before crushing them.

Table 2 gives a brief review of the major molluscivore taxa which use each predatory method and indicates the first appearances of the major molluscivores which fed in each way. From this information it is clear that during the Palaeozoic the chief 'agents of bivalve death were those that fed by whole animal ingestion and crushing. The latter only really became important in the Devonian (Signor & Brett, 1984). The rôle of whole animal ingestion is rather difficult to gauge as it leaves no diagnostic traces on its prey and the ability to feed in this manner cannot be inferred from functional morphological studies of potential predators. However, Vermeij (1987) regards it as a very primitive feeding mode and the evidence that the Middle Cambrian priapulid worm *Ottoia prolifica* Walcott, 1911 fed in this manner on brachiopods and hyoliths (Conway Morris, 1977) suggests that such early worms might also have been capable of feeding on bivalves.

It is well documented that the early Mesozoic saw an increase in the numbers of crushing predators and also the introduction of other more advanced feeding methods: the Mesozoic Marine Revolution (Vermeij, 1977). Ability to feed by prising may be inferred from studies of predator functional morphology and it is now clear that the ability to feed extra-orally in starfish was acquired in the early Mesozoic (Gale, 1987). Although there are signs of boreholes in some Ordovician brachiopods (Carriker & Yochelson, 1968) and indeed in the very earliest hard-parted organisms (Bengston & Zhao, 1992), it is very difficult to determine whether these were predatory boreholes and they certainly do not constitute a major cause of death. Fürsich & Jablonski (1984) describe boreholes in bivalves of Triassic age which have the characteristic countersunk morphology of holes bored by naticid gastropods. However, these boreholes do not puncture epifaunal bivalves and Fürsich & Jablonski believe that the boring habit evolved in the Triassic 'naticids' but was subsequently lost again until the Early Cretaceous. Intense predation pressure from boring is not likely to have started until the evolution of the habit in the muricid gastropods in the Albian (Taylor et al., 1983).

It is the increased and escalating numbers of post-Palaeozoic predators which is

Table 2. Predatory methods used by the major molluscivore taxa and their first appearance in the fossil record. Based on Vermeij (1990).

Predatory methods	Predatory groups and timing of acquisition
Whole animal ingestion	- ?worms, Cambrian (e.g. Conway Morris, 1977)
	- intra-oral feeding starfish, Early Ordovician (Blake, 1981)
	- gastropods, e.g. olivids and volutes (Vermeij, 1987)
	- rays and skates, Devonian (Vermeij, 1987)
	- bony fish, Tertiary radiation (Vermeij, 1987)
Insertion and extraction	- arthropods, e.g. crustaceans and chelicerates, Devonian (Signor & Brett, 1984)
	- extra-oral feeding starfish, Early Jurassic (Blake, 1981; Gale, 1987)
	- wedging gastropods, e.g. Buccinidae (Vermeij, 1987)
	- birds, Neogene (Vermeij, 1987)
Breakage	- arthropods, e.g. crustaceans, Triassic (Vermeij, 1987)
	- fish, Devonian (Signor & Brett, 1984)
Boring	- unknown early borers, into late Precambrian *Cloudina* (Bengston & Zhao, 1992)
	- first definite gastropod borers (naticids and muricids) Cretaceous (Albian) (Taylor et al., 1983)

usually stressed in discussions of the MMR. Yet as far as evolving prey defences is concerned the important point is the diversification in feeding methods. No longer were bivalves faced with merely evading crushing predation but also boring and prising. Different methods of predation require different, and perhaps conflicting, defensive strategies. It is clear that many modern bivalves live in habitats where they may be attacked by a whole range of predatory methods. For example, Kitching et al. (1959) show that the mussels around Lough Ine (Ireland) are subject to predation by gastropods (boring), crabs (crushing) and starfish (prising apart). How then did post-Palaeozoic epifaunal bivalves react in response to this battery of threats?

Methods of study

Since the basic bivalve bodyplan is so simple and the range of predatory methods so great it is possible to interpret virtually any post-Palaeozoic change in shell morphology or life habit as defensive. Temporal coincidence of predator and prey is not sufficient evidence. The assertion that a given feature of a bivalve has evolved as a defensive adaptation postulates both that the feature reduces the costs to survivors-

hip exacted by predators, and that it has evolved as a consequence of that selective benefit. Testing the assertion thus requires both experimental tests (for postulated fitness advantage) and retrospective tests (for the association of the emergence of the feature in question with independent evidence for likely intensification in the relevant mode(s) of predation), as illustrated, for example, in Harper's (1991) study of the evolution of cementation in the bivalves. We have therefore attempted to extend the application of this dual approach of experimental and corroborative, retrospective testing to the study of other postulated adaptations. Such data have been gathered both from our own experimental and palaeontological investigations, and from those reported in the literature.

In some instances suitable data are practically unobtainable: for example, the fossil record may be virtually mute concerning many aspects of behaviour and physiology (as discussed later). In such cases only informed speculation is feasible for the time-being, though even this exercise can be useful for identifying issues worthy of further probing as new techniques of analysis and forms of data become available.

Defensive adaptations
Inhibitive and evasive life habits

Skelton et al. (1990) demonstrated that throughout the Mesozoic there was a pronounced decline in the frequency of bivalve families pursuing an exposed byssate life habit. However, this decline did not result in a parallel decrease in the overall frequency of epifaunal bivalve families (although there was a smaller decline); rather, there were adaptive radiations into other epifaunal and associated life habits, such as attachment by cementation, the ability to swim, adoption of cryptobyssate habits and boring into hard substrate. Although many of these life habits have had Palaeozoic exponents, for example the cementing pseudomonotids in the Carboniferous and Permian (Newell & Boyd, 1970) and the Ordovician borer *Corallidomus* (Pojeta & Palmer, 1976), they were restricted to only a very few genera. It was not until the Mesozoic that these other epifaunal life habits were exploited in any significant numbers as noted above. In the case of the cementers and the borers the habit has been acquired polyphyletically in several distinct higher taxa, particularly from the early Mesozoic (Vermeij, 1987; Harper, 1991; Carter, 1978). It is possible to demonstrate that all the cementing clades, and the boring lithophagids, hiatellids and tridacnids were derived from byssate ancestors, and indeed most living examples pass through a byssate phase early in ontogeny. Where habits have been polyphyletically acquired over a very short space of geological time there is compelling evidence for an extrinsic selective force (Skelton, 1991).

Several authors, e.g. Stanley (1977) and Palmer (1982) have remarked on this adoption of alternative epifaunal life habits and have suggested that the cause of this was the increased predation pressure. Stanley (1977) has also suggested that there was a similar effect on the infaunal bivalves with an increase in burrowing depth.

Cementation

Harper (1991) has experimentally shown that cemented bivalves are less vulnera-

Table 3. Results of experiments offering boring muricid predators the choice of byssate and artificially cemented mussels. The numbers of both prey types were always equal and hence, if the predators experience no differences between the prey, that they should be eaten in equal proportions (the null hypothesis).

Predators vs. prey	no. cemented eaten	no. byssate eaten	P
Thais luteostoma vs. *Septifer virgatus* I	17	27	>0.05
Thais luteostoma vs. *Septifer virgatus* II	19	23	>0.05
Thais clavigera vs. *Septifer virgatus* I	29	42	>0.05
Thais clavigera vs. *Septifer virgatus* II	35	30	>0.05
Nucella lapillus vs. *Mytilus edulis*	12	5	>0.05

ble from predatory starfish and crustaceans than similar byssate bivalves. This decreased vulnerabilty appears to result from the greater difficulty in manipulation of the former. Although it is still possible for predators to eat cemented forms they are more time- (and energy) consuming to subjugate and hence provide a lower energy yield. However, Harper goes on to suggest that cementation is likely to provide little protection from drilling muricid gastropods as these predators do not manipulate their prey. In order to test this hypothesis a number of experiments were run in Hong Kong where there is a large number of intertidal predatory gastropods. These feeding trials were similar in construction to the previous experiments, this time using the mussel *Septifer virgatus* (Wiegmann, 1835) as the prey item and the muricids *Thais luteostoma* (Holten, 1802) and *T. clavigera* (Kuster, 1858) as predators. A single experiment was repeated with temperate species in Oban (Scotland), using *Mytilus edulis* (Linnaeus, 1758) and *Nucella lapillus* (Linnaeus, 1758). The results of these experiments are presented in Table 3. In none of the trials was there any statistically significant difference between the vulnerability of artificially cemented and byssally attached prey. The case of drilling predation is interesting as it has been shown that it did not become an important threat to the bivalves until the Cretaceous (Taylor et al., 1983), some considerable time after many bivalves had evolved the cemented habit in the early Mesozoic. Although our experiments have shown no difference in the vulnerability of the attachment types it may be that true cemented bivalves are actually more vulnerable than the artificially cemented mussels employed in these experiments. Mussels have a wide range of behavioural defences (discussed later), many of which involve activity of the foot. Since most cemented bivalves either entirely lack or have a much diminished foot these defences are denied them. It may be that cemented taxa actually present sitting targets to their muricid predators and therefore have had to rely on alternative defensive adaptations.

Boring, nestling and cryptobyssate habits

Encasement in a hard substratum would seem to provide ample protection from a large number of predators. Indeed, many of the boring bivalves possess very thin and fragile shells. The ability to bore into hard substrates (both coral and hard grounds) has evolved at least nine times since the beginning of the Palaeozoic (see Vermeij, 1987). Of these the major clades of boring bivalve, the lithophagids, gastro-

chaenids, pholads, and hiatellids all have an Early Mesozoic origin. It is therefore tempting to speculate that boring, like cementation, evolved in response to the MMR. More specifically, boring bivalves seem to be able to evade intensive crustacean and fish predation. Our own preliminary experimental evidence suggests that mussels sunk into artificial boreholes are inaccessible to predatory *Cancer pagurus* Linnaeus, 1758 and *Carcinus maenas* (Linnaeus, 1758). However, experimental evidence fails to show that there is any defensive advantage against other predatory methods. Haderlie (1980) has experimentally shown that the asteroid *Pisaster* can feed on bivalves through the aperture of the bivalve's borehole and our own experiments have confirmed this for *Asterias*. Taylor (1976) has also provided evidence that predatory gastropods, with their long proboscides, can also feed on boring bivalves. Many of the boring bivalves do possess posterior structures, such as the 'igloos' in gastrochaenids (Carter, 1978), that may be interpreted as defensive, guarding the vulnerable aperture. Morton (1990a) suggests that the ability to bore live corals in some mytilids is a defensive adaptation from which the bivalve gains protection by being encircled by the stinging nematocyst cells of the host. He suggests that the evolution of this habit was a response to the rise of the predatory gastropods and therefore predicts an early Tertiary origin for the habit. There is some palaeontological support for this; Savazzi (1982) describes live boring in the solitary coral *Fungiacava* during the Eocene, whilst the first live boring into colonial corals has been identified in Miocene *Porites* (Harper & Wood, unpublished).

Some byssally attached bivalves live nestled in inaccessible locations, such as crevices, for example the Isognomidae and Arcidae. There is a clear defensive value to such a habit. We have run experiments where we have allowed pteriid bivalves, *Isognomon legumen* (Gmelin, 1791), to settle in artificial crevices with side walls angled at 30° and 80° to one another. Predatory muricids introduced into this system showed a statistically significant preference for boring those *Isognomon* in the wider crevices (80°). Analysis of predator behaviour showed that this preference was merely a reflection of crevice size relative to gastropod size. Narrower crevices deny access to broader whorled gastropods. Indeed we discovered that the higher spired form *Morula musiva* (Kiener, 1835) was more successful in narrower crevices than was the squatter *Thais clavigera*.

A special kind of byssate nestling, which frequently involves miniaturization, has allowed the exploitation of potentially protective small cavities, including those associated with the burrows of, or even within other organisms. Such 'cryptobyssate' habits (Skelton et al., 1990) characterise many of the leptonaceans, for example the parasitic *Entovalva*, which lives deep within holothurians (Yonge & Thompson, 1976). Another example is the malleid *Vulsella*, which lives embedded in sponges (Reid & Porteous, 1980). It seems likely that such habits reduce exposure to predators, although this assertion remains to be tested. Regrettably, however, the fossil record of these forms (many of which have fragile shells) is both patchy and inadequately studied, so retrospective testing for the evolution of cryptobyssate habits is also likely to be problematical.

Occupation of the intertidal refuge

Certain bivalves have gained protection by inhabiting the physiologically 'difficult'

intertidal zone. The superior ability of many bivalves to seal their valves (discussed later) has allowed them to overcome the problems of thermal stress and desiccation better than many predatory groups. Taylor (1990) has shown that the intertidal oyster *Saccostrea cucullata* (Born, 1778) in Hong Kong is subject to far fewer gastropod predators than the subtidal *Alectryonella haliotoidea* (Lamarck, 1836). Likewise Seed (1990) recognises a similar high intertidal refuge for the mussel *Brachidontes variabilis* (Krauss, 1848) from the portunid crab *Thalamita danae* Stimpson, 1858. The requirements for such tight sealing are identical to those which prevent the egress of body fluids, and thus bivalves which had evolved tight fitting valves to prevent being recognised by predators would have been preadapted for intertidal life.

Although there are few recognised rocky shore facies in the fossil record (Johnson, 1988), it is nevertheless clear that bivalves were capable of exploiting the intertidal zone at least since the Liassic (see Ager, 1986).

Occupation of the deep sea refuge

The deep sea also offers a similar refuge from high predation pressure. Morton (1990b) illustrates the range of bivalves inhabiting deep water. Although some of these taxa may be considered primitive 'relict' species (e.g. the arcoid *Bathyarca*), some, for example *Cuspidaria* and *Lyonsiella*, have become highly specialised scavengers and carnivores. Morton believes that these specialised pholadomyoideans had Palaeozoic ancestors which occupied the shallow waters and that the selection pressures of the MMR drove them into the deeper waters and facilitated their radiation. Although the most spectacular examples of these deep-sea bivalves are the infaunal pholadomyoids, the niche is exploited by the epifaunal arcoids and pectinoids.

Structural defences of the shell

The bivalve shell represents an important line of defence. It has long been argued that the acquisition of hardparts in a number of unrelated taxa during the Tommotian must have conferred some protection against predators (Vermeij, 1987). Variation in shell structure and thickness must affect the susceptibility of bivalves to forms of predation which involve destruction of the shell i.e. crushing and boring.

Shell microstructure

Within the Bivalvia there are several types of shell microstructure — prismatic and foliated calcite, and nacreous, prismatic, myostracal prismatic, homogeneous, crossed lamellar, and complex crossed lamellar aragonite. All valves are composed of at least two of these microstructural units. Using Carter (1990) and our own data we surveyed the microstructural make-up of the post-Palaeozoic epifaunal families. These fall into seven different arrangements shown in Fig. 1. It is clear that, once a superfamily has acquired a particular shell microstructure, it remains remarkably constant over evolutionary time. Only the rudists and a few chamids appear to have added a unit, in both cases an external prismatic shell layer, during their evolutionary histories. However, there may be evolutionary changes in the relative amounts of
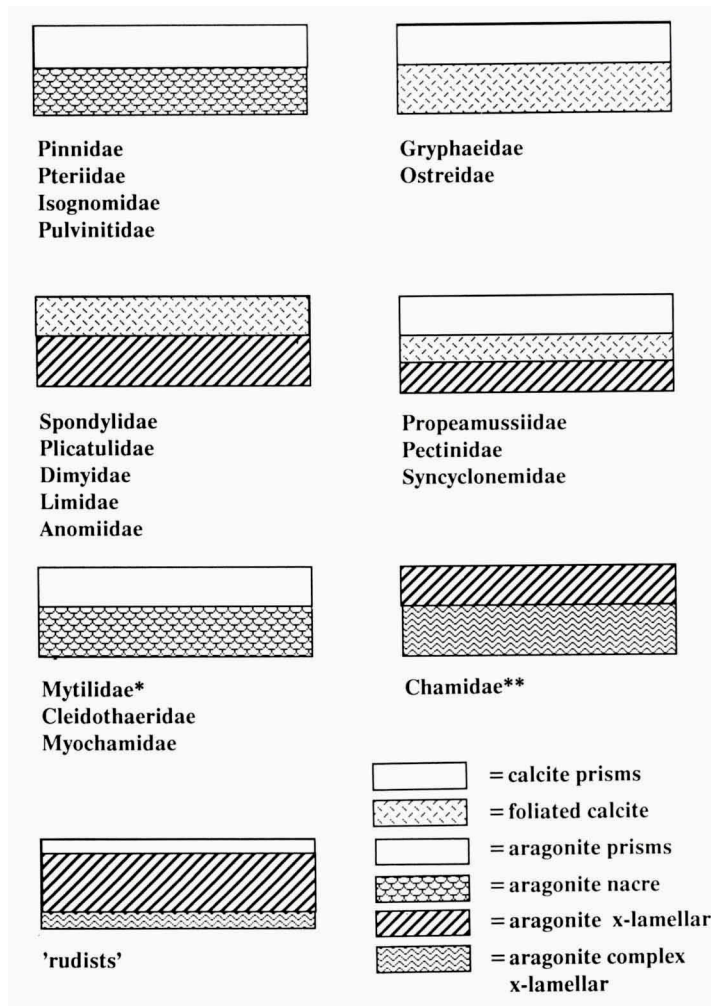
Fig. 1. Diagrammatic illustration of the shell microstructural arrangements displayed in epifaunal bivalves. Data was taken from Carter (1990) and our own observations. In each case the upper surface of the rectangle represents the upper surface of the valve. Adductor and pallial myostraca are not included. * = Some temperate Mytilacea have calcitic outer layers (Carter, 1990). ** = In two species, *Chama pellucida* Broderip, 1835 and *C. exogyra* Conrad, 1837 there is an outer shell layer of prismatic calcite.

each microstructure within the shell, for example an increase in the amount of foliated calcite in the Pectinacea (Waller, 1972)

Taylor & Layman (1972) have studied the mechanical properties of various microstructures and related these to life habits. They discovered that foliated calcite is restricted to epifaunal taxa. Somewhat paradoxically they found that the most primitive structural arrangement, aragonite prisms overlying nacre, from which all other micro-

structures ultimately evolved (Taylor, 1973), has the highest mechanical strength. Foliated calcite, particularly that of the oyster *Crassostrea gigas* Thunberg, 1793, was found to be extremely weak. Taylor & Layman suggest that this apparent anomaly of the evolution of a plethora of weaker shell microstructures may be explained by the fact that they appeared very early in bivalve history and may reflect selective forces other than those for shell strength.

All the families which possess foliated calcite are now placed within the pteriomorph order Ostreoida (Waller, 1978), except for the Limidae in which Carter (1990) describes the foliae as distinct from true foliated calcite structure. It would therefore appear that the anomalous change to foliated calcite is one of the synapomorphies for the order and hence characterises a monophyletic taxon. Waller (1972) suggested that the presence of foliated calcite in members of the Pectinoidea has allowed them to develop radial ribbing and fine micro-ornament, but there is no evidence that either can be construed as defensive. The importance of microstructure in controlling shell ornament is discussed in the next section.

Boring muricids make their holes by a combination of rasping with the radula and chemical attack by a secretion from the accessory boring organ (ABO) located in the foot. Gabriel (1981) studied the susceptibility of various shell microstructures to muricid attack by simulating the effects of various components of the ABO secretion and abrasion. She found that the microstructures could be ranked in the following list of decreasing resistance: calcite prisms > crossed lamellar > nacre > homogeneous > foliated calcite > oyster chalk. Susceptibility to ABO must be dependent upon a number of factors such as microhardness, solubility and organic content. It is the latter factor which is possibly of most relevance here. Taylor & Layman (1972) list the organic content of each of the microstructures that they examined. Although variable they discovered that the organic content was highest in prisms followed by nacre with lowest values for foliated and crossed lamellar structures. This trend corresponds reasonably well with Gabriel's data, with microstructures high in organic content being most resistant to simulated boring. Although the ABO secretion is known to contain enzymes capable of digesting organic matter (Carriker & Williams, 1978) it is clear from studying the bored surfaces of mussel shells illustrated by Carriker (1978) that the organic matrix is more resistant than the crystalline material.

Periostracum

The periostracum may also be considered as an integral part of the molluscan shell, even though in many bivalve taxa it is only transient and is absent from all but the valve edges. Although the primary function of the molluscan periostracum is considered to be of involvement in shell secretion (Taylor & Kennedy, 1969) it may also play a defensive rôle. In Harper & Skelton (1993) we describe experimental results which show that mytilid valves which have been stripped of their thick periostraca are more vulnerable to muricid drilling than valves in which the periostracal sheet remains intact. We suspect that this relative immunity is conferred by the inert nature of the periostracum, which retards penetration by the ABO secretion. Other epifaunal taxa with considerably thickened and persistent periostraca may also derive such benefit, for example arcoids. A similar defensive value has been demonstra-

ted for the intra-shell conchiolin sheets of *Saccostrea cucullata* (see Taylor, 1990) and also those of the infaunal corbulids (Lewy & Samtleben, 1978).

Shell thickness

Organic content may also have some bearing on possible shell thickness. It has been suggested that those microstructures with a high organic content are more meta-bolically expensive and time consuming to produce (Gabriel, 1981). It is therefore interesting to note that many of those bivalves which are (or were) capable of forming very thick shells, such as oysters and caprotinid and caprinid rudists have or had shells composed chiefly of microstructures which are very low in organic content — foliated and complex cross and crossed lamellar respectively. (However, other thick-shelled rudists, such as hippuritids, requieniids and radiolitids had a thick outer layer of organic rich fibrillar prismatic calcite, though this is probably itself associated with the sustained attachment of the adult shell in these taxa.) Boring is a time-consuming process and it appears intuitively obvious that bivalves with thicker shells will be less vulnerable to successful attack. Kelley (1989) has argued that an increase in shell thickness she records in Neogene infaunal bivalves is attributable to selection by increasing naticid predation. It should, however, be noted that many gastropods are nevertheless known to select a boring site in the thicker part of the valves.

Thickness is very difficult both to measure and quantify in many fossils, in partic-ular those which originally possessed aragonitic inner shell layers which are fre-quently lost during diagenesis. It is therefore difficult to amass evidence to support the notion that post-Palaeozoic bivalves have increased in shell thickness.

Bivalve size

Large bivalves are difficult to handle and manipulate, such that the benefits of an increased flesh yield of a larger prey item may be outweighed by the extra energy consumption of obtaining it and also the increased risk of an increased handling time during which the predator itself may be vulnerable to predation or physical stresses. There is now an impressive body of literature which shows that many predators feed optimally and take prey which conform in size to that which might be predicted, e.g. Elner & Hughes (1978). In certain cases there will be an upper limit to the size of prey that may be taken. For example, whole animal ingestion is only possible when the intended prey item can be fully ingested and bivalves may only be crushed when the shell fits into the open chelae or jaws. It therefore seems likely that some bivalves have gained some defence from large size. Seed (1990) has argued that the seemingly ill protected mussel *Perna viridis* (Linnaeus, 1758) is very vulnerable to predation by the crab *Thalamita danae*. However, rapid growth of the mussel allows it to reach a size refuge where it becomes difficult to manipulate and hence less vulnerable.

There is evidence for a phyletic size increase in many bivalves, e.g. Hallam (1978), and it is possible that one of the factors responsible for this phenomenon may be increasing predation pressure.

Hermetic valve closure

Hermetic valve closure may also be considered likely to provide some defence against predation (Vermeij 1983; 1987). In the first place, by arresting the leakage of biochemical cues into the surrounding water, it can be expected to lower the risk of detection by many predators (as noted earlier). Secondly, Vermeij (1987) has noted that this feature allows some small bivalves to pass unscathed through the guts of whole animal ingestors, even when they have been detected — a process which might be termed the sweetcorn effect. Experimental confirmation of such fitness benefits (with respect to individuals in which the seal has been artificially removed) is still needed, but the hypothesis is plausible on functional grounds.

Certain modifications of valve edge morphology can promote hermetic closure. The commonest device is that of thin, slightly flexible, projecting margins, which can be pressed together so as to provide a seal. Usually, such extended margins arise from an outer shell layer of some form of conchiolin rich, prismatic microstructure (Carter & Tevesz, 1978). The effectiveness of the seal depends on the area of flush contact between the adpressed margins. There are two constructional possibilities for enhancing this area. Where the valve margins remain symmetrical, lateral compression of the shell may enlarge the contact area by yielding a more acute angle of marginal incidence. Carter & Tevesz (1978) noted just such a morphocline, combining the increased prominence of an outer prismatic shell layer with lateral compression of the shell (and reduced dentition), passing from the paraphyletic cyrtodonts (e.g. the Devonian *Ptychodesma knappianum* Hall & Whitfield, 1872) to the derived pterioids. The flexible, and rapidly repaired nature of the valve margins in the latter (as in *Pteria* and *Pinna*) is well known (Vermeij, 1983). Harper (in press) has shown that the large area of marginal contact in the pteriid *Isognomon legumen* also provides defence against extra-oral feeding starfish. The large expanse of shell that needs to be parted before insertion of the stomach can be accomplished frequently means that the starfish has to exert great force (often resulting in harmless breakage of the flange) and may then give up.

The second means for increasing the area of mutual contact of the valve margins is the development of asymmetry, whereby the margin of one valve projects over and around the more or less recurved margin of the other — again providing a flush contact, even in globose shells. Such is the case with the flexible marginal flanges of oysters, and also the highly globose diceratid rudists (Fig. 2).

That such devices do provide effective sealing is readily demonstrated by the tolerance of intertidal exposure in some of the taxa which possess them. The question that remains to be answered, however, is whether or not the feature originally e-volved as a defensive adaptation, or whether it arose as an adaptation to some other function (such as the resistance to desiccation cited above), merely conferring the secondary benefit of evasion of predators. Nor need these different functions be mutually exclusive (as discussed earlier). In the case of the rudists, it is yet to be shown that the diceratids ever occupied an intertidal habitat, so underwater sealing of the closed valves does seem to have been selected for, rendering the hypothesis at least highly plausible.
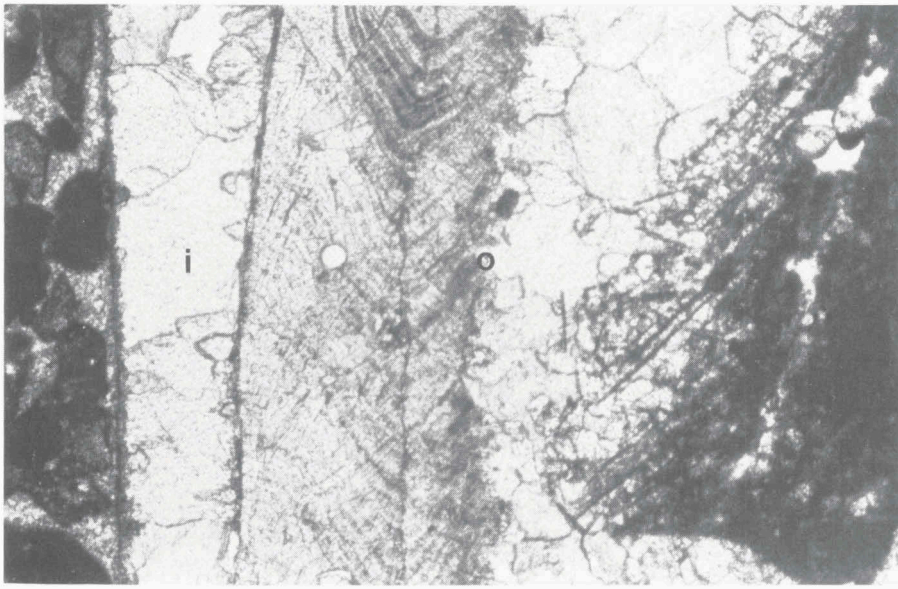
Fig. 2. Radial section of the ventral region of the left valve of *Epidiceras sinistrum* (Deshayes, 1824) from the Middle Oxfordian of Dompcerrix (Meuse), NE France. Shell interior (with lime grainstone fill) to the left; top is towards the commissure. The originally aragonitic inner shell layers (i) have been leached away and the resulting cavity reduced somewhat by inward collapse of the outer shell layer (o), and then filled by calcite spar cement. The outer shell layer consists of fibrous prisms of calcite orientated more or less normally to the growth lines, though part of the layer has been replaced by sparry calcite (at the right) and the outermost zone heavily infested by algal borings (filled with dark micrite). Note how the outer parts of the growth lines curve around asymptotically towards the commissure, where they would have lain flush against the recurved outer margin of the left valve (not shown). The photomicrograph is c. 3.5 mm across.

Spines and flanges

An obvious potential defensive adaptation is that of prominent spines and flanges; as seen in many modern epifaunal bivalves, such as spondylids, chamids and several oysters, (Kauffman, 1969; Stanley, 1970). Here we use the term spine very loosely to include any outgrowth from the valve surface. The spread of these spiny taxa has been recorded by Nicol (1965).

The actual value of spines and flanges is debatable, with several possible defensive rôles having been postulated. Logan (1974), in discussing the long spines of *Spondylus americanus* Hermann, 1781, suggests six possible functions of which three are defensive (the remainder deal with mode of attachment and anchorage). His defensive functions are as (i) supports of sensory mantle tissue to provide an 'early warning system', as has been postulated for the spines of the Jurassic brachiopod *Acanthothyris* by Rudwick (1965), (ii) promoting the growth of camouflaging epibionts, and (iii) protection of the soft parts by forming a sharp protective cage around the ventral

gape. Of these Logan favours the final option as a primary rôle but concedes that they may act in the others as secondary functions.

Spines are clearly multifunctional in many bivalves (Carter, 1968b). Certainly in many cementing taxa downward pointing rhizoid spines on the 'lower' valve are important either in attachment or in supporting the valve and serve no primary defensive function.

Vance (1978) and Feifarek (1987) have performed manipulative experiments to test the relative vulnerability of spiny *Chama* and *Spondylus*, respectively, and those from which the ornament had been removed. Both discovered that it was not the actual removal of the spines themselves which increased prey vulnerability but the consequential loss of the epibiota fouling those spines. There may be a number of explanations for these observations. The presence of effluent discharged by these foulers may mask the attractive 'odour' of the bivalves, or similarly they may disguise the prey from predators which use visual cues. Alternatively, a number of studies e.g. Forester (1979) and Pond (1992) have suggested that the presence of sponges encrusting scallop shells may prevent predatory asteroids from gaining a purchase on the valves with their tube feet.

A more direct defensive mechanism is supported by Logan (1974) from his functional morphological study of spondylid spines. He believes that the large ventrally-directed sharp pointed spines guard the gape and are important in deterring the major fish predators. Carter (1967) has experimentally demonstrated that the similar spines in the infaunal bivalve *Hysteroconcha* deter predatory starfish and gastropods.

Our own studies have investigated the spines of the oyster *Saccostrea cucullata*. *Saccostrea* is very common in the intertidal zone of rocky shores around Hong Kong. Here, as studied by Taylor (1990), they are chiefly preyed upon by the boring muricids *Thais clavigera* and *Morula musiva*. Taylor suggests that the dense hyote spines present on the upper valve may be anti-predatory devices. They are only infrequently encrusted by other epibionts and therefore can hardly be considered as camouflaging. They are also upward pointing and therefore do not guard the gape effectively. One of us (EMH) has performed preliminary experiments offering *M. musiva* the choice of feeding on oysters which are naturally spiny and those from which the spines have been removed. Of 23 oysters bored only 4 were spiny. These results suggest that the spines are indeed effective deterrents to these gastropods (P<0.01) These observations tally well with field observations which show that naturally bored specimens are frequently punctured in eroded areas of the shell. Indeed Taylor (1990) has identified a pronounced stereotypy of borehole positioning in the thicker parts of the shell, i.e. regions more likely to be denuded. We suspect that the inhibitory effect of the dense spine cover is simply from limiting the space available for applying both the radula and ABO.

Many bivalves bear flanges rather than spines. Ansell and Morton (1985) describe how the concentric flanges of the venerid *Bassina* sp. protect against boring naticids by providing decoy valve margins. They show that the majority of boreholes pass harmlessly through the flanges rather than the valve itself. We suspect that the concentric flanges of certain species of chamids may serve a similar function.

What is the geographic distribution of spiny taxa? Similar methods to those used by Vermeij & Veil (1978), in their study of the latitudinal pattern of shell gaping, have

Table 4. The distribution of spiny epifauna in the Recent malacofauna of North America.
See text for details.

| West coast US | | East coast US | |
province	% spiny species	province	% spiny species
Aleutian	18	Arctic	0
Oregonian	15	Boreal	16
Californian	27	Carolinian	29
Panamic	30	West Indies	26

been used to assess the geographical distribution of spiny bivalves in the Recent epi-faunal malacofauna of North America. Data were harvested from the faunal lists and shell descriptions of species of bivalves recorded in Keen (1971), Abbott (1974), and Humfrey (1975). The results, expressed as a percentage of the total number of epi-faunal species, are tabulated for each faunal province in Table 4. These results clearly show that on both coasts of North America there is a discernible trend for an increas-ing proportion of the fauna being spiny with decreasing latitude. These data concur well with Nicol's (1965) assertion that the spiny bivalve taxa are concentrated in warmer waters and are entirely absent from the polar regions.

Further analysis of our data shows that the equatorward increase in spiny taxa is largely due to the addition of higher taxa not present at higher latitudes, e.g. cha-mids and plicatulids. Only in the case of the Ostreacea is there any indication that within the superfamily there is a trend of increased spinosity with decreasing lati-tude.

There are at least two possible explanations for this geographical distribution. Ei-ther, as Nicol (1965) suggests, the increased solubility of calcium carbonate in colder waters prevents or retards the ability to form excessive ornamentation, or the forma-tion of spines reflects adaptation to the increased predation pressure in the tropics. Both alternatives are plausible and it is possible that they reinforce one another. However, a suitable test of the rôle of predation in favouring the acquisition of spines is to track the temporal distribution of spiny bivalves.

Very few Palaeozoic bivalves, either epi- or infaunal, are spiny. Vermeij (1987) states that the earliest spiny bivalves are the early Carboniferous Pseudomonotidae, but these are not extravagantly ornamented and indeed many of their outgrowths are concentrated on the 'lower' valve and may be interpreted as important in their cemented attachment. The only other spiny Palaeozoic bivalves appear to be mem-bers of the Aviculopectinidae, e.g. *Clavicosta* and *Girtypecten*. Indeed, all Recent taxa which are highly spinose have post-Palaeozoic origins.

We have collected data on the spinosity of various of the more overtly spiny post-Palaeozoic bivalves. In the case of the Spondylidae we have inspected the 'upper' left valves of a large number of fossil and Recent specimens in our own and museum collections searching for spines and flanges. These data have been supplemented by species descriptions provided by Zavarei (1973). Figure 3 shows the percentage of species in each period which bear outgrowths on the left valve. The vast majority of
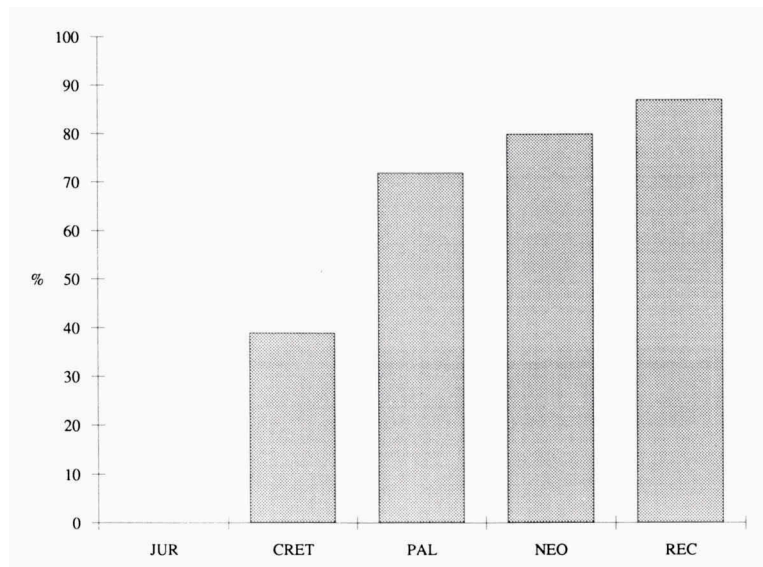
Fig. 3. The percentage of spiny species of the genus *Spondylus* over geological time. Numbers of species considered: Recent (31), Neogene (6), Palaeogene (21), Cretaceous (8), and Jurassic (6).

Recent species are extremely spinose with only five species being recorded lacking spines or flanges: *Spondylus tenuispinosus* Sowerby, 1847, *S. pacificus* Reeve, 1856, *S. coccineus* Lamarck, 1819, *S. microlepis* Lamarck, 1819, and *S. gussoni* da Costa, 1829. By contrast very few of the Mesozoic forms bear spines on the left valve, indeed none of the Jurassic species are thus ornamented, although most possess marked outgrowths on the attached right valve. Such spines which do occur on the left valve are often small and far shorter than is seen in Recent species. A similar survey of Mesozoic oysters reveals that both families have spiny representatives (Ostreidae, e.g. *Saccostrea* and Gryphaeidae, e.g. *Hyotissa*) but that the habit is not widespread and is restricted to late Cretaceous and younger genera. Of the rudists only advanced members of the Radiolitidae, which ranged from the Aptian to the Maastrichtian, became spinose, for example the bizarre Late Cretaceous genus *Pseudopolyconites*. Early chamids also appear less spiny than their Recent counterparts. By contrast members of the Plicatulacea show a reverse trend. Many of the Jurassic species are notably spiny, for example *Plicatula echinoides* Blake, 1880 (Portlandian) and *P. fistulosa* Morris & Lycett, 1853 (Bajocian), whilst many of the Tertiary and Recent species bear no spines at all. Apart from the exception of the Plicatulacea there appears to be a trend towards increased spinosity over geological time with a marked increase in spiny taxa in the Late Mesozoic. We do not believe this to be a taphonomic artefact. The coincidence of this temporal trend with the MMR lends support to the notion that predation pressure is an important selection pressure favouring this ornament. An interesting parallel to this study is that by Signor & Brett (1984) on spinosity in brachiopods. By contrast with the bivalves many of the Palaeozoic brachiopod genera bore spines and there was a pronounced increase in these during the Devonian. Signor & Brett believe that this increased spinosity coincides with the appearance

and radiation of durophagous placoderm and chondrichthyan fish and arthropods.

Spines thus seem to be important defensive adaptations. Yet there are some clades of epifaunal bivalves which have never possessed spines or flanges, most notably the Mytilacea and Arcacea. What are the constraints involved? Using data from Figure 1 we discover that there is no particular outer shell microstructure which favours spine formation and it is also not possible to argue that these bivalves inhabit waters too cold to allow the necessary calcium carbonate precipitation. There appear to be two fundamental requirements for spine formation (i) possession of a periostracum flexible enough to produce a template, and (ii) a mantle edge which is highly extensible in order to deposit shell material far from the valve edge. We suggest that both mytilids and arcs lack both these fundamental preadaptations. Both possess a very thick periostracum which Harper (in prep.) shows to be incapable of describing a template for fine ornament and also a mantle edge which is incapable of extending far. It is interesting that the preadaptations for spine formation are also some of those required for cementation (Harper, 1992) and lack of these attributes has also prevented these clades from exploiting that defensive habit. Yet the Mytilacea and Arcacea have perhaps evolved an alternative to spines. Many of their species possess hairy periostraca which Bottjer & Carter (1980) suggested might be defensive. Wright & Francis (1984) have experimentally demonstrated that the awns of the mytilid *Modiolus modiolus* (Linnaeus, 1758) discourage attachment, and therefore presumably boring, by muricids.

Behavioural and physiological defences

Defences are not restricted to those adaptations which can be recognised as either life habits or hardpart modifications. Ansell (1969) describes molluscan defences as either passive (morphological adaptations) or active (performed in direct response to predatory behaviour). Behavioural and physiological defences fall into the latter category. Although it is possible to demonstrate that many bivalve taxa utilise active defensive strategies, the ability is not reflected in the hardpart morphology and is therefore rather difficult to infer from the fossil record.

Active escape

Ansell (1969) describes the means by which some bivalves literally escape their foe. Many of these locomotory responses, such as rapid burrowing, autotomy and leaping are restricted to infaunal bivalves. Some epifaunal bivalves do, however, possess a swimming escape response, for example many pectinids and limids. In these forms rapid valve clapping is sufficient to propel the bivalve away from the predator. Swimming bivalves do display certain morphological adaptations, such as thin relatively unornamented valves and large centrally placed adductor scars. However, it is very difficult to infer when the ability to swim first appeared, although Hayami (1991) has documented a number of morphological features which produce an effective airfoil, which he sees as criteria to recognise fossil swimmers. It appears obvious that the ability to swim has arisen polyphyletically within the Pectinoidea and Hayami (1991) suggests that the habit evolved in direct response to the increased predation pressure

of the MMR. Although there is an undoubted defensive advantage to this type of flight it has not been shown conclusively that swimming is primarily a defensive adaptation. Waller (1978) presents evidence that the swimming habit was present in limoids as far back as the Ordovician. Indeed Morton (1980) believes that the swimming habit in *Amussium pleuronectes* (Linnaeus, 1758) is primarily involved with seasonal migration rather than for defence.

Assault

For bivalves with a tight byssate or cemented attachment flight is not possible. For many of these taxa reciprocal offense is a realistic defence. Stasek (1965) records offensive behaviour in the giant clam *Tridacna maxima* Röding, 1798 which repel predatory fish by accurately squirting them with fluid from their siphons.

The mytilids have a well developed behavioural defence system to cope with the threat of muricid borers. Wayne (1987) and Petraitis (1987) have both described the ability of *Mytilus edulis* to trap would be assailants in their byssal threads, and Day et al. (1991) describe a similar behaviour in *Choromytilus meridonalis* (Krauss, 1848) and *Mytilus galloprovincialis* Lamarck, 1819 in response to threats from predatory dogwhelks. Interestingly, these latter authors show that the response is very specific and is not activated by non-boring muricids. Wayne (1987) has also shown that *Mytilus edulis* also attempts to dislodge its muricid predators by valve flapping and foot flailing. In the course of our experiments a similar behaviour has been observed in *Septifer virgatus* and *Perna viridis*. Active valve movements are employed by other bivalves. Carriker & van Zandt (1972) have described valve flapping in *Crassostrea* which they interpret as an attempt to dislodge predatory muricids. During our experiments we have observed this behaviour in *Crassostrea gigas* which have been maintained with the asteroid, *Asterias rubens* Linnaeus, 1758. Occasionally starfish were found with one arm tightly trapped between the valves of a closed oyster (see Fig. 4). Several of these subsequently escaped with damage to the arm whilst in two instances the trapped individuals actually autotomised the arm. As yet we are uncertain as to whether this is a natural defensive strategy found in these oysters. However, this is not the only report of oysters trapping their predators; Burrell (1977) described an oyster which trapped a muricid eventually incorporating it into its own shell.

One of us (EMH) has also observed an individual of *Pinctada* sp., which was menaced by a muricid (*Morula musiva*), performing elaborate rocking motions, presumably to dislodge its assailant.

Clumping

Members of the Mytilacea also show a pronounced tendency to form clumps of individuals, and if separated individuals will rapidly regroup. Okumura (1986) and Lin (1991) have shown that individuals within these clumps, in particular those located in the middle, are less easy to extract and manipulate and are thus less vulnerable to crustacean predation.
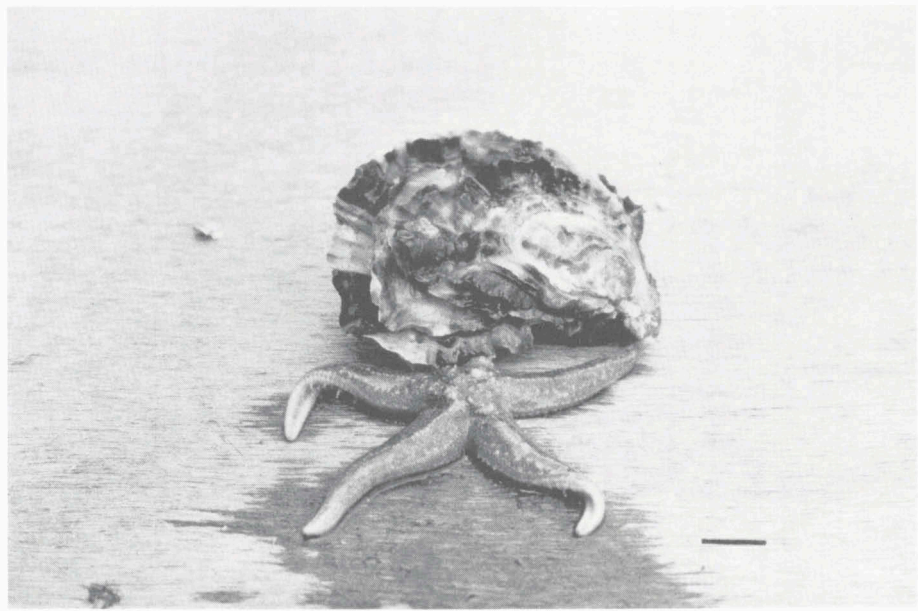
Fig. 4. *Asterias rubens* Linnaeus, 1758 trapped between the closed valves of a large individual of *Crassostrea gigas* Thunberg, 1793. Scale bar = 1 cm.

Distastefulness

Predators avoid prey which have an unpleasant taste or are toxic. In some cases, for example mussels which are vectors for paralytic shellfish poisoning, the nature of this toxicity is temporary and restricted to times of dinoflagellate blooms. Such toxicity can therefore not be described as adaptive. However, in some bivalves toxicity from dinoflagellates is more permanent, for example *Spondylus butleri* Reeve, 1856 (Harada et al., 1982).

The evolution of defensive adaptations: preadaptations and constraints

In this paper, we have reviewed experimental and other evidence for a wide variety of defensive adaptations in living epifaunal bivalves, variously effective against several different kinds of predator, and we have cited evidence from the fossil record that the majority of these adaptations evolved in concert with the marked proliferation of durivorous predators from early Mesozoic time onwards (the MMR of Vermeij, 1977). Yet none of the defences described in this paper is found in all epifaunal bivalves and no bivalve species possesses them all. However effective a given mode of defence, certain taxa will be prevented from evolving suitable adaptations by the constraints of their own body plans, including in some cases those imposed by conflicting demands of other defensive strategies. The variegated repertoire of defensive adaptations in bivalves can be analysed in Seilacher's (1985) terms of evolutionary
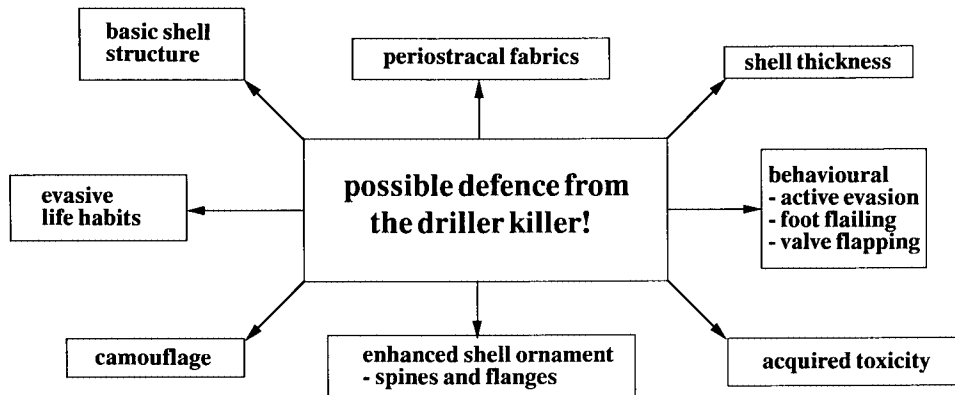
Fig. 5. Possible defensive adaptations which may be effective against boring muricid predators.

constraints and 'licences'.

Shell cementation provides a good illustration. This habit, as noted earlier, seems usually to have evolved in taxa derived from byssate ancestors. But a glance at Table 1 shows that certain major byssate taxa are notably absent from the list of those with cemented members, e.g. among extant taxa, the mytiloids and arcoids

The mussels (mytiloids) are, in general, an interesting group with apparently very few morphological defences. Harper (in prep.) argues that the group has been severely constrained by the thick inflexible periostracum which has prevented them from cementing and from forming elaborate spines and flanges. Instead the mussels have had to rely on a plethora of behavioural adaptations, as well as an ability to live intertidally and to grow rapidly, for their defence. This case may well be paralleled by the arcoids, the evolution of which Thomas (1978) has already argued has been constrained by their primitive and conservative bodyplan.

By contrast, cementation evolved several times in the pterioids (including at least five times in the pectinaceans; Harper & Palmer, 1993). The commonly thin periostracum in these forms was probably an important preadaptation for the cemented habit, in addition to their primitively byssate life habits.

A thick periostracum evidentally provided no such constraint on the evolution of the boring habits: these evolved in both the mytiloids and the arcoids (as well as in other, infaunal taxa: see Table 1). A thickened periostracum may be a vital preadaptation for the evolution of chemical borers in order that they do not erode their own valves. By contrast, again, however, the habit has seemingly never arisen amongst the pterioids. The pterioids all possess extremely thin periostraca but other possible constraints that may have excluded them from boring habits include their more or less compressed (and/or auriculate) shell form, itself associated with effective marginal sealing, as noted earlier, and, in many, a monomyarian condition.

An interesting case study is the means by which epifaunal bivalves defend themselves from attack by boring muricid gastropods. There are two features of muricid predation which make this an ideal study. Firstly, boring muricids (along with certain octopods) use a very different feeding technique to that used by other mollusci-

vores. The defensive strategies required to deter chemical dissolution of the shell are very different, and perhaps conflicting, to those required against prising and crushing. Secondly, the boring is a much more recent threat to bivalves, significantly postdating other predatory methods. Taylor et al. (1983) record the first muricid predation in bivalves from the early Cretaceous and it is likely that they did not become a major threat until much later. It is conceivable, therefore, that adaptations which evolved in response to predation pressure in the early MMR may have been unsuitable to meet this new menace. Today, however, boring gastropods are of enormous importance. Galtsoff (1964) describes them as 'the most deadliest enemy' of the oyster Crassostrea virginica Gmelin, 1791, whilst Jackson (1977) attributes over 50% of mortalities amongst chamids, dimyids and spondylids on a tropical reef to gastropod borers.

Faced with this onslaught, epifaunal bivalves have responded according to the constraints mentioned above. Mussels armed with only their thickened periostracum, have often retreated to such physiologically stressful refugia as the intertidal zone, and areas of fluctuating salinity, and have adopted a variety of behavioural defences, as discussed earlier. The cemented taxa have acquired additional defences, such as spines, flanges and intrashell conchiolin sheets, although many have also exploited the intertidal refuge, too (e.g. oysters).

Such evolutionary constraints and licences are not, of course, limited to the tradeoffs between different defensive strategies: other aspects of morphology and life habits can also be expected to have been affected. An interesting question, for example, is how photosymbiotic taxa such as Tridacna evolved their association with dinoflagellates in the first place. The case of Spondylus butleri, mentioned earlier, suggests one possible (speculative) pathway. The initial infestations of mantle tissues by freeliving dinoflagellates could readily have occurred as a (frequent) accident of gill suspension feeding. However, if the ingested dinoflagellates proved in any way distasteful or toxic to predators of ancestral tridacnids, then there would be an immediate fitness gain from possession of them. Adaptation of the valve's mantle margins for retaining and culturing the dinoflagellates is likely to have ensued. The metabolic benefits to the host of the photosynthetic activity of the dinoflagellates might have then emerged as a secondary consequence of the established endosymbiosis, which would then be preadaptation for the photosymbiosis.

Another series of licences may have initiated the even more bizarre evolutionary history of the extinct rudist bivalves. The first recorded rudists (family Diceratidae) already possessed the fibrillar prismatic calcite outer shell layer that is characteristic of the group (see Fig. 2). The ended asymptotic growth lines of that layer in one valve, reflect a highly extensible mantle margin, and this was evidently already employed in securing marginal growth-attachment to the substratum. Indeed, from the outset the valve of attachment appears to be fixed in different genera (e.g. by the right valve in Diceras and by the left valve in Epidiceras) - a taxonomic distinction confirmed by other details of the dentitions and sizes (Skelton, 1978). It is most parsimonious, therefore, to assume that attachment evolved independently in (at least) two stocks, in which the distinctive outer shell layer was already present. As noted earlier, the primary adaptive function of the latter was probably hermetic valve sealing. Once established, however, the rôle of the outer shell layer in attachment

became paramount, providing both literally and metaphorically the platform of the later adaptive radiation of the group (Skelton, 1978).

We suggest that this balance between constraint and preadaptation is a recurrent theme in the evolution of bivalve defences. Having identified the various defensive adaptations available to epifaunal bivalves, it is now necessary to determine the constraints and preadaptations which control their distribution amongst the bivalve clades.

Acknowledgements

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