

## ON THE BIOLOGY AND PALAEOONTOLOGY OF SOME PREDATORS OF BIVALVED MOLLUSCA

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### SUMMARY

A summary is given of the feeding habits of known predators on bivalve molluscs, including birds, fish, Pinnipedia, Mollusca, Arthropoda and Asterozoa. The fossil record of these groups, and of other possible extinct predators, is discussed in relation to the fossil record of the bivalves. It is concluded that asteroids are, and were, probably the most important of all predatory groups, and their ethology is presented in some detail. The relationship between the earliest Asterozoa and coextant Bivalvia in the Ordovician is discussed, and it is concluded that both intraoral and extraoral types of asteroid feeding were established at an early stage in the Palaeozoic. The known escape responses of Recent mollusca are described. It is postulated that several types of protective adaptation may have been important in the evolution of the Bivalvia: in particular, it is suggested that the primary significance of many types of radial ribbing lies not in the ribs themselves, but in the interlocking of the commissure that gave rise to them.

### INTRODUCTION

It is becoming increasingly difficult for the palaeontologist to keep abreast of the enormous accumulation of literature on the biology of Recent representatives of his selected group of animals. Yet today, more than ever before, it is imperative that palaeontological work be based on a sound understanding of the living animal, and of the community that it inhabits. A considerable amount of research has now been done on the anatomy and functional morphology of the Bivalvia. Most of this is well known and readily located with bibliographic aids. Somewhat less easy to track down are the many scattered papers which deal, perhaps incidentally, with the mode of life and Recent ecology of the group. Whilst working on the interpretation of various features of bivalve morphology from a functional point of view, I have found it useful to gather the available



published information on the habits of known predators of bivalves—a topic which receives scant attention in modern palaeoecology texts. There have been important advances in the knowledge of relationships between bivalves and particular predators, especially with respect to the Asterozoa. It is the aim of this paper to summarise these recent advances in the hope that this information may be useful as a basis for further studies on the functional morphology and palaeoecology of the Bivalvia.

#### BIVALVE PREDATORS

Amongst the Recent animals that are known to feed on bivalves are birds, fish, various other vertebrates, crustacea, echinodermata, cephalopoda and gastropoda. Certain other predators, especially parasites such as the flatworm (WOELKE, 1957), may also take a considerable toll of bivalves, but discussion here will be restricted to those major animal groups which have, at least potentially, an important palaeontological role. It will be convenient to consider each of these groups of animals separately, to summarise what is known about their modern ethology, and to note when they first appeared in the fossil record (Fig.1). The possibility of certain extinct groups of animals having fed on the Bivalvia will also be considered.

##### *Birds*

Many species of wader include shellfish in their diet. The early papers of DEWAR (e.g., 1908) drew attention to the most destructive of these waders in England—the common oystercatcher, *Haematopus ostralegus* L.—and described its method of feeding on *Mytilus edulis* L. *Haematopus* was also noted to feed on *Tapes*, *Modiola* and *Pholas*. Later papers by HEDLEY (1915) and TOMKINS (1947) confirmed this report for the Australian and American species of oystercatcher respectively. The Australian bird was noted to prey particularly on *Plebidonax deltoides* (LAMARCK), whilst the American species preferred feeding on oysters. Many other species of bird have been reported as frequenting shellfish beds, including gulls, knot, dunlin, carrion crow, duck etc. (HANCOCK and URQUHART, 1965).

Two more modern studies have described in detail the method of feeding of the oystercatcher and have given valuable quantitative estimates of the amount of depredation it causes amongst a known population of the cockle *Cerastoderma edule* (L.) (DRINNAN, 1957; HANCOCK and URQUHART, 1965).

If the birds are feeding in shallow water, the cockles are located primarily by sight, only rarely by probing with the beak. When a cockle is located the beak is driven smartly between the valves whilst they are still open. This ap-

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Fig.1. Generalised stratigraphic ranges of important molluscan predators.

parently disables the animal, perhaps by severance of one or both of its adductors, for the shells of cockles killed in this fashion rarely show signs of damage or chipping.

If the birds are feeding on uncovered sand when the tide is out, then probing is necessary to locate the cockles. When a cockle is found it is levered out of the sand with the bill and then usually carried to a suitable spot for opening. This is often a slight rise, or an area of harder sand, where the shell is vigorously pushed or sharply hammered until it opens; if the cockle should be buried in the sand by the force of the blows, it is moved a short distance and then attacked again.

Drinnan found that in Morecambe Bay during the two winters 1953–1954 and 1954–1955 the birds were strongly selective as to the size, and hence the age group, of the cockles on which they were feeding. In the winter of 1953–1954 the birds were feeding predominantly on cockles 20–30 mm in length (inferred to be of the 1951 spatfall). Pressure thrusts, rather than blows, were used for opening the shells. In a sample of 215 opened shells, 211 showed that access to the shell had been gained by the breakage of the anterior end (Fig.2b). In the winter of 1954–1955 the birds were feeding on cockles 25–35 mm in length (again inferred to be of the 1951 spatfall). This time, of a sample of 1,515 opened shells, 1,478 showed the morphological damage to be confined to the site of siphon extrusion, i.e., the place where the shell has a small though persistent gape (Fig.2a).

Drinnan concluded from this data and from his field observations that cockles were opened by random application of pressure by the bill to the valve margins. In smaller cockles this results in a fracture running from ventral border to umbo; in larger shells the increased thickness would demand a much greater force to achieve such a fracture and so “entry is gained by forcing the valves apart, with much less extensive damage, at the persistent gape”.

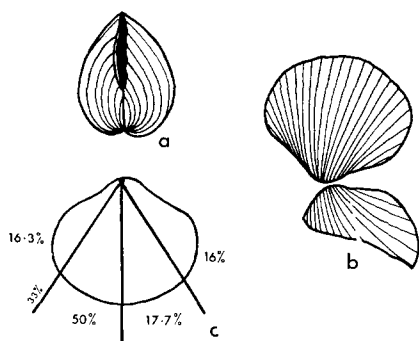


Fig.2. Damage to the shell of *Cerastoderma edule* (L.) by oystercatchers; a. moderate sized shell opened with little morphological damage at the site of the permanent posterior gape; b. smaller shell opened by breakage of the anterior end; c. analysis of shell fractures, figures indicate percentage fractures in the various quadrants and (33%) at the point of posterior gape. (After DRINNAN, 1957, fig.5; HANCOCK and URQUHART, 1965, pl.9.)

Using estimates based on sampling counts for the bird population (30,000 oyster catchers), the cockle density (109/sq. yard), and the feeding rate (214 cockles/bird/day), Drinnan showed that for the period the birds were present—roughly September–March—the mortality due to oyster-catcher feeding was 21.9% of the total cockle population. The fact that the birds were selectively feeding on the 1951 spatfall resulted in a 33.15% mortality for that age group. These figures may be contrasted with the total known mortality of 73.8% and 80.2% for the whole population and for the 1951 age group, respectively.

The work of HANCOCK and URQUHART (1965) in the Bury Inlet, southern Wales, confirmed most of these observations and provided additional convincing evidence that oyster catchers were responsible for the heavy mortality of cockles during their second winter.

The *Haematopus*–*Cerastoderma* relationship is summarised in some detail because well documented accounts of these particular animals are available. There can be no doubt that other scattered references contain evidence that a large variety of intertidal bivalves are preyed on by many different species of bird. Brachiopods are also eaten by shore birds (PAINE, 1962). However, the critical point is that it is indisputable that birds are capable of exercising considerable selective pressure favouring those intertidal bivalves that have some method of resisting their particular type of predation.

Birds of essentially the same type as the modern waders were well established by the Eocene (Charadriiformes and Gruiformes both represented). The family Haematopidae has its first representative, *Paractiornis perpusillus* WETMORE, in the Miocene of Nebraska. It would thus appear that bird predation may have been an important selective pressure throughout the Tertiary.

The morphological damage caused to bivalves by bird predation is characteristic (Fig.2), and the recognition of this damage in fossil bivalves could lead to stimulating inferences as to the presence or absence of avian predators in fossil environments.

### *Fish*

In Recent seas there are two main groups of fish that account for significant amounts of predation amongst bottom-dwelling invertebrates.

The first includes mostly large fish, many of them belonging to the shark family, which feed on bivalves of all sizes. The bivalve prey is scooped or plucked off the bottom and then crushed by the strong teeth, or grinding palate, that these fish invariably possess. A certain amount of broken shell must inevitably pass to the stomach along with the soft parts of the bivalve, but most of it is presumably selectively discarded from the mouth. Fish of this type are able to cope with even the massive shells of large bivalves. For instance, one of the rays is a serious predator in the pearly oyster beds of Ceylon (RUSSELL and YONGE, 1947):

*Pinctada* commonly attains a length of 7 inches. Amongst this ethological group may also be included certain smaller fish, like the wrasse and the wolfish with its "very remarkable tooth armature" (RAYMONT, 1963), which also have specialised teeth in the mouth or throat.

The second group of fish predators are some of the common teleosts. Most important are the various types of flatfish (plaice, dab, long rough dab, flounder) which account for significant depredation amongst bivalved mollusca (RUSSELL and YONGE, 1947; BLEGVAD, 1925). The flatfish can only cope with small bivalves; BLEGVAD (1915) concluded that the maximum size that can be swallowed by plaice is ca. 3 cm. The flatfish either swallow the bivalve whole and digest it in the stomach, or they bite off the exposed fleshy parts such as siphons.

Because of their commercial importance, especially in Europe, these common benthic flatfish have been the object of particularly close study. BLEGVAD (1925) concluded that the common forms of flatfish, and the eel and haddock, were significant predators of bivalved mollusca. The small lamellibranch species of *Abra*, *Solen*, *Nucula*, *Tellina*, *Macoma*, *Mactra*, and juveniles of *Mya*, *Mytilus*, *Cyprina* and *Scrobicularia* were all rated as first class fish food, i.e., wherever they occur they are eaten by fish of all ages from about 1 year old (BLEGVAD, 1930). Blegvad also drew attention to the fact that the common thick shelled *Astarte* spp. were not consumed, and only the very smallest of the thick shelled *Venus gallina*. The larger bivalves such as *Mya*, *Mytilus* and *Cyprina* are also not eaten as adults, though eel and cod have been observed to bite off the siphons of large *Mya*; *Corbula* is only eaten by fish when no other food is available.

More recently the plaice has been studied in some detail by DAWES (1931) and BUCKMAN (1952). They conclude that during the warm half of the year, a normally growing plaice that has to "hunt" to find its food will eat 3–5% of its own living weight of *Mytilus* flesh per day. These figures are much reduced in cold weather and feeding ceases below about 10°C.

### *Fossil fish*

It is relevant to record here the first appearance of major fish groups in the fossil record.

Like the birds, the teleost fishes underwent a vast expansion at the beginning of the Tertiary, and all the major groups including forms related to modern flatfish (Heterosomata), can be traced back at least that far. Their habits of bivalve predation have presumably been operative throughout Tertiary time.

The ancestral shark line was derived from the Devonian cladoselachians, and became widespread in the Carboniferous and Lower Permian. However, later in Permian and Triassic rocks fish remains are very scarce and the shark stock "seems only to have survived by adopting a varied diet, including invertebrate food" (J. Z. YOUNG, 1950). The Triassic heterodont sharks (of which the north Australian *Heterodontus* is a Recent survivor) possessed pointed teeth in front

and flattened crushing teeth further back in the jaw, and presumably lived at least partly on invertebrates, including Bivalvia. Later still with the advent of the modern type of sharks and rays in the Jurassic, many different forms became adapted to living on the abundant shell life to be found on the shallow sea floors (*Hybodus*, *Rhinobatis*). Another important group of Jurassic fish, the pycnodonts, possessed a dentition of massive rounded teeth and "were restricted by their feeding habits to ... waters with a rich shelly fauna" (RAYNER, 1958).

The interpretation of the earliest fossil vertebrates is still very much under discussion, but it would seem unlikely that any of the pre-Carboniferous forms known at present were markedly specialised towards predation on hard-shelled marine mollusca, though COLBERT (1955) has suggested that the Upper Devonian antiarchs were becoming adapted to a bottom living and feeding mode of life.

In one of the few studies of morphological damage to fossil invertebrates and its relation to possible predators, SARYCHEVA (1949) suggested that certain types of lesion on the shells of Carboniferous productids of Moscow were caused by fish belonging to the Brachyodonti, the teeth of which (*Petalodus*) are common in Russian Carboniferous rocks.

The reason for the lack of literature on this topic is probably because of the difficulty of unequivocally recognizing damage caused by fish predation. One of the few common examples in Recent seas is the extensive damage often caused to *Pinna* by fish bites. This genus, by virtue of its mode of life, is peculiarly exposed to such predation, and it is significant that this has resulted in major morphological adaptations. These include the ability to retract the mantle edge far back into the shell, and the ability to secrete new shell over any damaged area at a remarkably fast rate. In addition there is a special organ developed (the pallial organ as defined by YONGE, 1953), apparently for the purpose of clearing the mantle cavity of debris after attack by fish. The power of this animal to resist the attacks of predators is shown by the fact that its shell may carry twelve or more zones of major damage.

#### *Relative importance of fish predation*

It is clear that fish predation may reach significant proportions; for example E. J. Perkins (quoted in HANCOCK and URQUHART, 1965) found that 27 flounders of length 25–35 mm contained 751 *Macoma*, 543 *Cerastoderma* (all under 18 mm) and 9 *Hydrobia*, and estimated that in the Solway area cockles comprise 36% of the diet of plaice and 18% of flounders. Nevertheless, it would seem that this pales into insignificance when compared with the enormous havoc wreaked by invertebrate predators.

THORSON (1958) summarised most available data on predation in benthonic communities and introduced new estimates on the rate of feeding per body weight per day for various groups of animals. He concluded that "on an average, growing invertebrate predators seem to consume four times as much food per day and unit

weight as bottom dwelling fishes". But PETERSEN (1915) calculated that in the Kattegat area of Denmark during 1910 approximately a million tons of potential fish food (molluscs, polychaetes, crustaceans) was competed for by 5,000 tons of flounders and 75,000 tons of invertebrate predators. Therefore, as Thorson points out, "we must recognise the amazing fact that only 1-2% of the "fish food" on the sea bottom is actually eaten by fish; the rest is taken by invertebrates". Admittedly, these estimates are gross approximations, but even if they should prove to be considerably in error it would not effect the general conclusion to be drawn from this work.

### *Other vertebrates*

Several of the larger mammals of Recent seas include benthonic invertebrates in their diet; for example the harbour seal (*Phoca vitulina* L.) feeds on "many kinds of fishes, shellfishes, and squids" (SCHEFFER, 1958), and another pinnipede, the walrus *Odobenus rosmarus* (L.), has become highly specialised to a diet that "consists almost entirely of bivalve molluscs" (HARRISON and KING, 1965).

The walrus finds its food by stirring the shallow, gravelly substrate with its tusks and sorting the shellfish so obtained with its sensitive lips and whiskers. Stomach contents very rarely contain pieces of shell but are full of the fleshy parts of bivalves, whilst heaps of undamaged shells are often found around walrus breathing holes. Presumably the animals must occasionally crush molluscs, for their cheek teeth get well worn, but on the whole it "seems very likely that they [the bivalves] are sucked out of their shells". It is possible that the bearded seal (*Erignathus barbatus* (ERXLEBEN)) also obtains much of its food by a sucking technique (HARRISON and KING, 1965).

The present world population of walruses is estimated at between 45,000 and 90,000 (SCHEFFER, 1958), so it might be said that they are relatively minor predators on bivalves as a whole. However, the fact that the stomach of an adult walrus may weigh as much as 109 lb. (i.e., contain the remains of some 600 bivalves), makes it plain that they must be regarded locally as serious predators.

### *Fossil forms*

More detailed knowledge of the feeding habits of Recent Pinnipedia might be of great value in interpreting the possible habits of extinct groups of marine vertebrates. The Pinnipedia themselves have a fossil record back to the Miocene (KELLOGG, 1922).

In the Early Triassic, a group of marine reptiles, the placodonts, became specialised for life in shallow marine waters. The teeth in the front of the skull were protruding and peg like (Fig.3), whilst the maxillary teeth and the palatine bones in the back portion of the lower jaw were reduced in numbers and broadened. They formed "huge, blunt grinding mills, which when brought together by the strong jaw muscles must have been capable of crushing tough sea shells.





Fig.3. The skull of Triassic placodont reptiles. a. *Placodus*, original skull about 10 inches long (after Romer, fig.161). b. *Cyamodus*, view of plate with crushing teeth. (After SWINTON, 1954, fig.31.)

Evidently *Placodus* swam along slowly, plucking various mussels and other shells off the sea floor and crushing them with strong jaws and teeth" (COLBERT, 1955). It seems likely that this group occupied much the same ecological niche as the walrus does today; indeed COLBERT (1966) has recently commented that "Placodonts are fossil walruses".

Other groups of extinct animals that have been suggested to prey on molluscs include the rhyncosaurs, Triassic reptiles with specialised crushing beak and jaws (J. Z. YOUNG, 1950), and *Desmostylus*, a specialized Miocene subungulate mammal. Some of the dinosaurs might also have supplemented their diet with molluscan food.

## *Mollusca*

### *Gastropods*

Many gastropods are carnivorous and the bivalve mollusc is an important and common prey; "hundreds and possibly thousands of species of predatory gastropods drill holes through the shells of other molluscs and extract the meat" (DEMORAN and GUNTER, 1956). Although this feeding method has been known for many years, and is used by gastropods of widely separated families (Naticidae, Muricidae, Thaisidae, Cassidae), there has been a large measure of disagreement as to the exact technique employed. Some authors have suggested that mechanical rasping is the most important (FISCHER, 1922; PELSENEER, 1925), others have favoured a chemical secretion of some type (SCHIEMENZ, 1891; ANKEL, 1937). However, following the work of CARRIKER (1951, 1959) and ZIEGELMEIER (1961), it is now generally agreed that both mechanical and chemical activity are involved in the act of drilling. For example, *Urosalpinx* and *Eupleura* (Muricidae) alternate a few minutes of active rasping with the radula with longer periods of up to an hour of softening the site of boring by close application of secretions from an

accessory gland located in the anterior part of the foot.

Although the exact nature of the chemical secretion remains undetermined, it is *not* acid, as has so often been suggested. It may be an enzyme which digests the conchiolin matrix, or it might perhaps release chelating agents which form water soluble compounds with the calcium of the shell (CARRIKER, 1959).

The experiments of DEMORAN and GUNTER (1959) demonstrate the extreme hardness of a typical borer, *Thais haemostoma*. Excision of the odontophore (a long cephalic extension bearing the radula distally) resulted in its regeneration in 3 weeks in those individuals that survived the operation. The regenerated odontophore was morphologically and functionally entirely normal.

The different groups of predatory gastropods utilise slightly different methods of boring, and it is often possible to recognise the family of gastropods responsible for a particular boring. ZIEGELMEIER (1961) has clearly described how the odontophore in the Naticidae rotates on its long axis during rasping, resulting in the characteristic neatly circular, smoothly bevelled hole. The muricids (e.g., *Nucella*) may make a hole morphologically similar to that of naticoid's though generally less bevelled, but an uncompleted boring is readily distinguished by its lack of a central boss (Fig.4).

Several workers have sought to establish a preferential boring site for

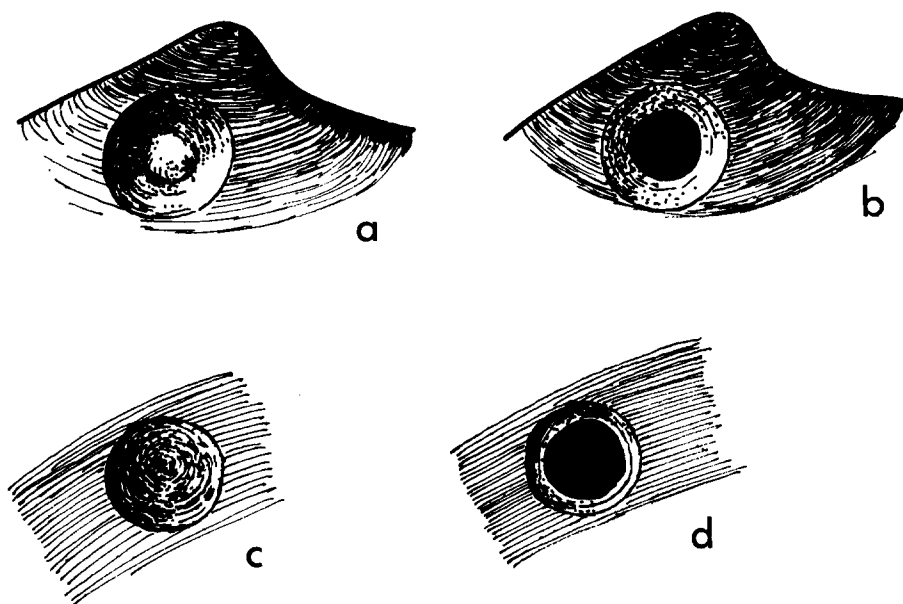


Fig.4. Bivalves bored by gastropods. a. Shell incompletely bored by *Natica*; note the prominent boss. b. Shell perforated by *Natica*. c. Shell incompletely bored by *Nucella*; note absence of boss. d. Shell perforated by *Nucella* bevelled shelf not as wide as in *Natica*. (After FRETTER and GRAHAM, 1962, fig.129.)

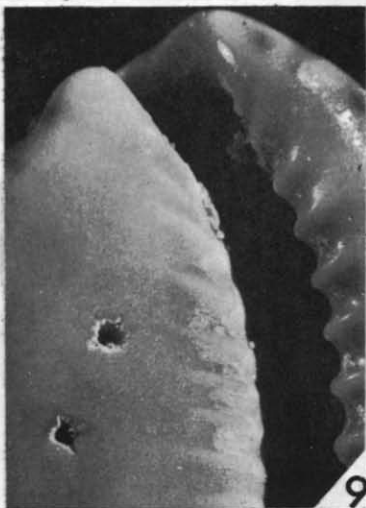
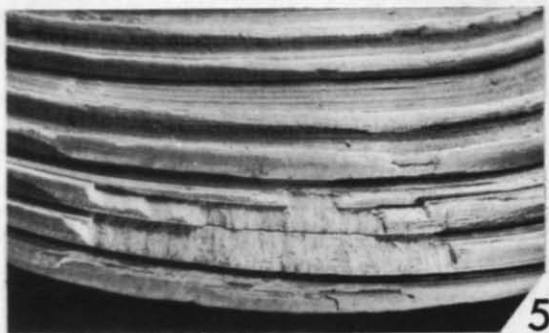
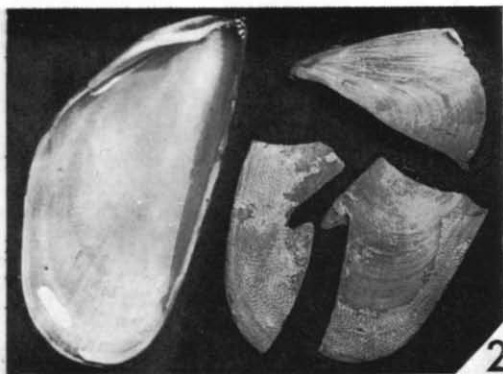
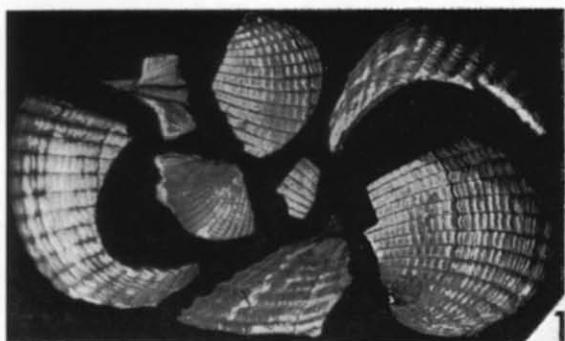
particular predatory species; the results are somewhat inconclusive, and even conflicting. Thus ANSELL (1960) finds that *Natica alderi* (FORBES) tends to preferentially attack *Venus striatula* (DA COSTA) round the margin of the shell, where it is thinnest. But BELDING (1930) found that most shells were bored towards the posterior end of the valves, and yet other authors have found a virtually random distribution of bored holes (HAYASAKA, 1933). Muricids are reputed to selectively attack the junction of the two valves.

Because of the readily recognisable, often characteristic, morphological damage, this is one of the few types of predation that has received consistent attention from the palaeontologist. The literature is scattered but common; recent papers noted include those of HAYASAKA (1933), FISCHER (1963, 1966), and SILER (1966). The feeding habit appeared at least as early as the Upper Ordovician (CLARK, 1908; BUCHER, 1938), and recently GRANT (1965) has figured probable gastropod borings from an Upper Cambrian fauna from North America. In all these cases the prey were brachiopods.

Another method of predation is perhaps less generally known to the palaeontologist; some gastropods, including the common American *Busycon* and European *Buccinum*, use the edge of their shell to force an entry between the shells of a bivalve (Plate I, 3, 4 and 7). Early authors (COLTON, 1908; WARREN, 1916; MAGALHAES, 1948) expressed conflicting opinions as to whether these animals were serious predators of shellfish. CARRIKER (1951) therefore undertook a series of experiments on the feeding habits of *Busycon*, and concluded that it was indeed an active predator of bivalve molluscs, consuming up to 4.5 bivalves, mainly *Mytilus* and *Venus*, per animal per week. Predation of *Urosalpinx* and *Polinices* was also studied, and it was shown that both these predators and *Busycon* had a marked tendency to select and attack the thinner shelled bivalves first.

Of the feeding habits of *Busycon*, Carriker writes: "in an aquarium conchs creep at a relatively fast rate, 6 to 12 seconds per centimeter, attracted by water pumped from the exhalent siphon of buried bivalves. Even deeply buried quahogs [*Venus mercenaria* L.] are readily dug out and attacked ... *Busycon* mounts the quahog and holds it ... so oriented that the ventral edges of the quahog lie directly under the outer lip of the conch shell. Then the snail, by very slowly and strongly contracting the columellar muscle, brings the margin of its own shell to bear on the slight depression at the junction of the two quahog valves, and presses against the edge of the valve farthest from it. Such force is generally sufficient to chip off a portion of the quahog shell (Plate I, 7). The gastropod then slowly relaxes, drawing its shell away from the quahog valves. This slow chipping is continued until an opening of sufficient size is effected to permit the conch to wedge its shell margin between the quahog valves". It is apparently quite common for one or both of the valves to become badly cracked in this process (Plate I, 3). Consumption of the soft parts after entry has been gained is accomplished by "a physical rasping off and swallowing of bits of the mollusk flesh".

PLATE I



A more recent study (PAINE, 1962) has supported Carriker's contention that there is a tendency for thinner shelled bivalves to be selectively attacked—*B. contrarium*, when offered an equal number of *Lucina* and thick shelled *Chione*, ate 2.5 times as many of the former. It also transpires that amongst the many American species of *Busycon* there is a clear morphological division into species with a thick shell lip (e.g., *B. contrarium*), and those with a thin shell lip (e.g., *B. spiratum*). The forms with thick shell lips selectively prey on tightly closed bivalves, such as *Chione*, *Cardita*, *Mercenaria* and *Crassostrea*, whilst those with thin shell lips tend to attack thin shelled slightly gaping genera (*Ensis*, *Mactra*) or forms such as *Aquiptecten* which can only remain shut for limited periods of time. In every known case of two sympatric *Busycon* species, one is of each morphological type.

Finally, a third method of taking prey has been developed by sand-living gastropods such as cassids and volutes. These animals are equipped with a large fleshy foot with which they are said to "take prey by smothering" (MORTON, 1958).

### *Cephalopods*

Observations on octopuses have shown that these animals may feed dominantly on bivalves when such food is available. The common method of opening the shell is by pulling it apart with the suckers (MACGINITIE and MACGINITIE,

### PLATE I

Morphological damage to Recent Mollusca inflicted by known predators. All of these specimens, except 1, 2, and 6, were kindly provided by Dr. R. T. Paine, who also provided the comments quoted.

1. *Cerastoderma edule* (L.), ×1. Specimen successfully opened and eaten by a large blue lobster, *Homarus vulgaris* (MILNE-EDWARDS). Note the complete shattering of the valves into angular fragments.
2. *Mytilus edulis* (L.), ×1. Specimen successfully opened, but not eaten, by the same lobster.
3. *Lucina* sp., ×2. Specimen successfully attacked and eaten by *Busycon contrarium* CONRAD. Shell badly smashed rather than ground (cf. 4).
4. *Chione cancellata* L., ×3. Specimen opened and eaten by *B. contrarium* CONRAD. Note the ground valve edges, usually situated between the siphons or at one end of the valve.
5. *Humiliaria kennerleyi* REEVE, ×2. Specimen pulled open, with minor damage to the mid-ventral margins, by *Orthasterias*. This type of damage (flaking off of concentric ridges adjacent to commissure) usually occurs over the siphons (cf. 6).
6. *Venerupis pullastra* (MONTAGU), ×1. A dead specimen baited with *Mytilus*, and held together by rubber bands, that was attacked and broken by a large *Asterias* that settled in feeding position over the posterior end of the shell (the anterior and antero-ventral margins were protected by a PVC sheath).
7. *Mytilus californianus* CONRAD, ×2. Specimen attacked by chipping of the valve margins by *Muricanthus nigritus* (PHILIPPI). These two species are normally allopatric, but although predation was aquarium induced the chipped margins are characteristic of attack by this species.
8. *Lunatia lewisi* GOULD, ×4. Successfully drilled by *Octopus dolfini*.
9. *Cypraea* sp., ×4. Specimen inferred to have been predated by *Octopus* sp.

1949), but recently PILSON and TAYLOR (1961) have reported that octopuses sometimes use the radula to bore holes in the shell of their prey. They then inject venom through these holes, which are of characteristic oval shape and much smaller than the typical hole bored by carnivorous gastropods (Plate I, 8, 9). *Haliotis*, *Tegula*, *Chione*, *Mytilus* and *Nassarius* have all been attacked in this way in the aquarium. Further evidence of the feeding habits of octopuses comes from the observation that it is commonly possible to locate octopus lairs under water by means of the pile of empty shells and debris outside them (LANE, 1957).

In view of the abundance and diversity of Mesozoic ammonoids, and Palaeozoic nautiloids, it is as well to bear in mind the possibility that certain specialised groups of these fossil cephalopods fed on Bivalvia. In the paper referred to above (see the section on fossil fish), Sarycheva recognised two types of morphological damage in her fossil productids. That entailing extensive damage to both valves was attributed to fish; that entailing localised damage to one valve was attributed to orthocerid type nautiloids. Sarycheva attributed the lack of fossil cephalopod "beaks", in spite of common fossil cephalopods, to the same factor that governs their distribution in Recent sediments: by virtue of their chitinous composition, the beaks do not stand up well to the rigours of fossilisation.

Whilst not doubting Sarycheva's interpretation of nautiloid predation, the fact that this type of damage is so rare, and has so seldom been noted on fossil invertebrates, suggests that nautiloids are perhaps not a major cause of bivalve predation.

### *Arthropoda*

The numerous shallow-water species of crab have been described as "ubiquitous omnivores to whom little comes amiss" (YONGE, 1949), and it is well known that these animals are highly efficient scavengers. Less well known is the fact that they are sometimes a serious pest to bivalves.

NELSON (1916) was one of the first to call attention to the possibility that crabs might be held responsible for damage to oyster beds. ORTON (1926) carried out field experiments on the growth of *Cardium* and concluded that the common British shore crab is a great enemy of small cockles; and LUNZ (1947) showed that the American blue crab was locally perhaps the most serious of all oyster pests. ATKINS (1960) has reported the predation of crabs on the small brachiopod *Megathiris*.

The extent of predation may be inferred from reports such as CARRIKER's (1951), that a 12 cm crab cracked open and consumed six *Venus* (of 3–4 cm in length) in 7 days. The common method of attack on bivalves is for the crab to break away the margins of the shell with the claws and then pick out the flesh (YONGE,

1960). Lobsters, on the other hand, just crush the whole shell in their pincers (Plate I, 1, 2).

The fossil record of the Decapoda (crabs, lobsters and related forms) is fairly good. They first appear in the Triassic, with crabs becoming important in the Jurassic and remaining a major constituent of Tertiary faunas up to the present day. ROLL (1935) attributed morphological damage to *Haploceras* and *Oppelia*, from the Malm of Germany, to attack by a large crustacean. It is conceivable that certain chelicerates were carnivorous predators of benthonic molluscs, though current opinion would hold that the largest of these, the eurypterids, were adapted to a brackish water regime, and would thus have been restricted in their choice of bivalve prey.

### *Asterozoa*

Much of the large amount of literature on this group of echinoderms contains at least passing reference to the relationships between asteroids and their common food sources. Some of these works include extensive bibliographies (e.g., HYMAN, 1955). Conspicuous amongst asterozoan foods are all types of mollusca, but especially Bivalvia. I shall concentrate on important recent papers that provide up-to-date information on the ethology of the asteroids. Fossil asteroids, and their relationship with fossil bivalves, are discussed later in the paper.

Sea stars are exclusively marine benthonic animals. They may be found on almost any type of bottom, but are particularly common in the littoral zone where they feed voraciously on most available slowly moving or sessile animals, particularly molluscs and other echinoderms (HYMAN, 1955). Although most species are of moderate size for invertebrates (about 12 cm in diameter), some forms attain a diameter of over 2 ft. (VERRILL, 1909). They search for prey by moving slowly over the surface of the substrate, using their tube feet (Fig.5); recognition of food

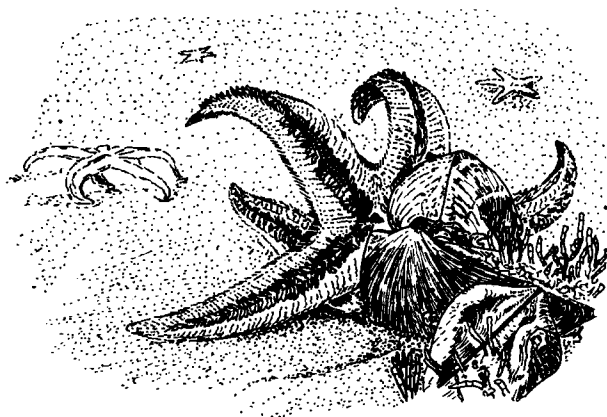


Fig.5. *Astropecten irregularis* attacking an *Arca*. (After HYMAN, 1955, fig.169.)

is primarily by touch, though chemo-sensory recognition has been suggested for some species (e.g., MILLIGAN, 1915). *Pisaster brevispinus*, a sub-tidal inhabitant of sandy gravel in Puget Sound, has been observed to locate itself accurately over the top of burrowed clams (especially *Saxidomus* and *Protothaca*) which are then dug out by the use of somewhat specialised tube feet (SMITH, 1961). Other genera like *Astropecten* have species with specialised tube feet for burrowing and ploughing through the sandy substrate just below the surface (SCHIEMENZ, 1896).

In experiments carried out with stained starfish in eastern Canada, G. F. M. SMITH (1940) found that the maximum distance travelled by *Asterias vulgaris* was 211 m in 4 months; the average distance travelled by any individual of the group of starfish studied was only about 21 m. Chemo-sensory ability was suggested by the tendency to move directly towards food, that was up to 12 m distant, at a rate of 6 m per day. However, most authors seem to agree with GALTISOFF and LOOSANOFF (1939) that feeding of asteroids is consequent upon location of prey after a period of random wandering on the substrate, and that starfish can pass within a few inches of food without apparently recognising it.

One of the reasons for the success of the asteroids is their remarkable lack of enemies and their durability. Although vast numbers of bipinnarate pelagic larvae are consumed by other benthic predators, the adult starfish has almost no enemies (COE, 1912; BLEGVAD, 1915). Starfish are able to fast for several months with no visible ill effects other than growth being completely checked until feeding recommences (COE, 1912).

#### *Feeding habits*

That certain starfish feed predominantly, and many starfish at least partly, on bivalved mollusca has been stressed by many authors (SCHIEMENZ, 1896; MEAD, 1900; VERRILL, 1909; COE, 1912; HUNT, 1925; CLARK, 1934; G. F. M. SMITH, 1940; REESE, 1942; RICKETTS and CALVIN, 1949). Amongst their prey have been noted *Arca*, *Ostrea*, *Mytilus*, *Venus*, *Dosinia*, *Mactra*, *Pecten*, *Corbula*, *Cultellus*, *Lutraria*, *Syndosmya*, *Montacuta*, *Saxidomus* and *Protothaca*. In short, nearly all the major groups of bivalves are known to be preyed on by asteroids. Other common molluscan foods are gastropods and cephalopods, while M. YOUNG (1926) has reported that the common New Zealand *Coscinasterias calamaria* will feed on the brachiopod *Neothyris lenticularis*. Barnacles, *Pectinaria*, other echinoderms and even fish (JENNINGS, 1907; BLEGVAD, 1915) may also be eaten.

Within the asteroids, two broad types of feeding behaviour may be distinguished. Generally speaking, neither inflicts consistent morphological damage on the prey animal, though two examples of damage due to extraoral feeding are figured (Plate I, 5, 6).

The first is characterised by those species with short inflexible rays and very distensible mouths. These forms feed by eating large numbers of small animals whole. The fleshy parts are digested by the sea star and the empty shells



and other exoskeletons are ejected later through the mouth (HYMAN, 1955). This is termed the *intraoral* method of feeding. Interestingly, this group of asteroids is dominant in deeper water (HYMAN, 1955), and this may perhaps be correlated with the fact that the bivalves found in such locations are generally small and thin shelled. EICHELBAUM (1910) found that *Astropecten irregularis* ate mainly bivalves, snails, young asteroids and ophiuroids: one specimen contained nineteen identifiable bivalves in its stomach, besides numerous fragments of other bivalves. HAMANN (1885) recorded a specimen of *Astropecten auranciaceus* that had swallowed ten scallops, six *Tellina*, five scaphopods, and several snails. A deeper water form, *Psilaster andromeda*, was dredged from 210 m and found to feed mainly on bivalves, one specimen containing 24 (EICHELBAUM, 1910).

The second broad group comprises those forms with longer flexible arms; they have evolved the remarkable technique of extruding the stomach into the animal on which they are preying. In the case of bivalves, of course, they must first gain access to the interior of the shell. Such a feeding method is termed *extraoral*, and is a particularly important and versatile technique. The size of food that can be digested by intraorally feeding asteroids is restricted by the size of their mouth; extraoral feeders, on the other hand, are able to digest animals of any size, provided always that they can first gain access.

There can be no doubt that asteroids are able to penetrate into even large bivalves. For example, HUNT (1925) reported that *Asterias rubens* of 14 cm size opened a *Cyprina* 12 cm long; and GALTISOFF and LOOSANOFF (1939) maintain that "the most common food of the starfish consists of comparatively large animals and molluscs well protected by heavy shells". Similarly, REES (1957) writes that "the chief enemy of the scallop is the starfish. As soon as one comes near, it will attempt an immediate escape by swimming".

#### *Behavioural observations on feeding*

It is important, therefore, to determine how asteroids gain access to the interior of large bivalve shells. Among the less likely suggestions that have been proposed are that the sea star might take the bivalve by surprise before it had time to close its shell; that it might hypnotise the mollusc; that it might make an opening in the shell by the use of acid secretion; or that it might suffocate the bivalve by enveloping the edge of the shell. A large amount of research has now been done on this question, most of it neatly summarised by CHRISTENSEN (1957).

The two methods which are currently regarded as most probable are those involving the use of either force or poison.

The efficacy of the latter method has been questioned. It has been shown that certain Recent asteroids do not normally secrete any poison or narcotic agent into the shell of their prey (e.g., *Pisaster ochraceus*, FEDER, 1955). On the other hand, extracts of the juices of other starfish have been shown to have highly toxic effects on various invertebrates (FÄNGE, 1963). It seems possible

that access to the interior of bivalve shells may sometimes be aided by the toxic effects of fluids secreted by the starfish, but this method may be of minor importance.

The earliest convincing evidence that starfish use force for opening their prey was presented in a now classic paper by SCHIEMENZ (1896). Schiemenz established that it was possible for *Asterias* to open its prey by adopting a humped up feeding attitude over the prey and by pulling with its tube feet. Using experimental apparatus he was able to demonstrate that sea stars were capable of exerting with their tube feet a momentary force of at least 1,350 g. Since the estimates that were then available of the force with which bivalve adductors contracted indicated forces of the order of 1,000 g (it is now known that large bivalves can exert forces considerably in excess of this), it seemed that starfish could indeed open their prey by force alone.

Although much was written in the interim, some supporting this theory (COE, 1912) and some critical of it (REESE, 1942), it was not until the work of FEDER (1955) that it could be established beyond doubt that seastars could open their prey by force alone. Feder severed the adductors in mussels and bound their valves together with strong rubber bands. He measured the gape caused by *Pisaster ochraceus* when it attacked the doctored mussel, and then determined the force necessary to duplicate this gape. He showed that a *Pisaster* of 30 cm diameter was capable of exerting forces of up to 4,000 g. Feder's work was followed closely by a similar paper by LAVOIE (1956). In this case the technique was slightly different, the adductors being replaced by steel or plastic springs, but essentially the same conclusions were reached, that forces of up to 3,000 g could be exerted.

It seems to me necessary to quote other parts of the work of these authors in full, for it has most important implications for the study of bivalve morphology. Feder writes: "Early in the study an important question was raised: does *Pisaster* really have to pull open a bivalve mollusc in order to feed on it? An examination of mussels, *Mytilus californianus*, being fed upon in the field has indicated that the larger mussels frequently remain closed during a great part of the feeding process and that they often do not gape until considerable digestion has taken place. In fact, a number of mussels have been observed with their valves closed even though a starfish had digested practically all of the soft parts except the posterior adductor muscle. In these cases the starfish were feeding with their oral regions pressed tightly against the ventral valve edges of the mussel. A close inspection of this region reveals an important point. The shells are not perfectly sealed here but instead have a permanent opening where the byssus threads protrude between the two valves. This slit may measure as little as 0.5 mm in width in the smaller mussels ...". Feder continues: "*Tivela stultorum* is considered to be a tightly sealed mollusc, and yet it also has an opening between the valves both anteriorly and posteriorly, measuring between 0.1 mm and 0.6 mm. Fourteen additional species of Pacific coast clams have been examined, and it has been found that they all have an opening in the shell posteriorly that is large enough for the

insertion of a *Pisaster* stomach. Although these openings in both the mussel and the Pismo clam are partially blocked by the pliable periostracum, it has been found that the starfish can readily peel this back in the feeding process".

And Lavoie records a striking example of the same phenomenon: "A mussel whose valves were bolted together very firmly so that no space could be discerned between them under  $9\times$  magnification was loosened forcibly from the grasp of a sea star that had humped over it for several hours. The asteroid's stomach was mostly inside the shell and it did not slip out again during the next hour while the sea star dragged the shell along the bottom of the aquarium".

Feder also showed that it was not necessary, as Schiemenz had supposed, for the starfish to assume the humped up pose in order for it to feed, and that even one-, two-, and three-armed starfish are able to feed on mussels "even though they are generally unable to orient their arms in a pulling position". Further, LAVOIE (1956) and later CHRISTENSEN (1957) showed that the classical theory of the starfish outlasting the bivalve in pulling power, even though a momentary application of its maximum force is insufficient to open the valves, is in all probability wrong. It seems more likely that "the opening of the valves is a rapid process involving overwhelming, continuous forces, so that the predator may be considered to relax its pull upon the valves at intervals and to allow its stomach to be compressed between the valves until it pulls them apart again".

HANCOCK (1965) is the only author to have considered this from the bivalve's point of view, and to attempt to ascertain what defence the bivalve might have against predation by these ruthlessly efficient carnivores. In laboratory experiments the rate of feeding of *Asterias rubens* L. was consistently higher on British mussels (*Mytilus edulis* L.) than on specimens of the Danish race of the same species. As Danish mussels possess larger adductors than British mussels of the same shell length, it is probable that the former were more difficult for the starfish to open, and hence larger adductor muscles may be interpreted as a defensive adaptation against starfish predation.

#### *The mechanism of stomach intrusion*

At first sight it would seem that the extraoral and intraoral feeding habits are fundamentally different. For this reason it is interesting and important to note that *both* habits involve the same fundamental process: that of the insertion of the stomach lobes *into* the prey (D.A. Hancock, personal communication, 1966). Obviously this must be so for the extraoral feeding habit; but the fact that, with intraoral feeding, penetration of the interior of the prey by discrete stomach lobes takes place after ingestion sheds much light on the possible evolution of the extraoral habit.

Unfortunately little work has been done on the actual mechanism of stomach extrusion, though ANDERSON (e.g., 1954) has dealt in some detail with the anatomy of the cardiac stomach of *Asterias forbesi*. He found that the outer

surface of the stomach has a complex system of muscle fibres inserting to muscular and connective tissue in the stomach wall, and originating from five nodules at the points of attachment to the stomach of the paired retractor strands in the arms. Eversion of the stomach is preceded by opening of the mouth and relaxation of the muscles in the wall of the stomach and the intrinsic retractor strands. Eversion then takes place by contraction of the muscles in the body-wall which increases the intracoelomic pressure against the relaxed walls of the stomach, which are then forced out through the mouth as fluid filled vesicles.

It is highly significant that CHRISTENSEN (1957) has found that during normal feeding "each of the five stomach lobes is inserted as deeply into the different cavities of the prey as possible", and when it is not possible to insert all the lobes into the prey, the efficiency and speed of feeding is very much reduced.

### *Distribution*

Temperature and salinity appear to be important factors controlling the distribution of Recent asteroids (HYMAN, 1955). The group reaches its maximum faunal diversity and numerical representation in uniformly cold coastal waters, but has a cosmopolitan distribution—occurring in arctic, antarctic and tropical seas. Asteroids reach their maximal development in shallow waters, but range down through all depths to 6,035 m. Many genera are eurythermous; others are tolerant of a wide range of salinity. For instance, *Asterias rubens* can tolerate salinities ranging from 8 to 35 parts per thousand.

Asteroids inhabit many different types of bottom; the same species may be found on rocky, sandy or soft bottoms, and their distribution appears to be controlled primarily by the abundance of bivalves. GALTISOFF and LOOSANOFF (1939) report: "During the three surveys, 4,998, or approximately 99 % of starfish, were collected at stations where shells were present, as compared with only 65 starfish found at stations located on other types of bottom".

### *Abundance*

Because of the damage caused to the shellfish industries, there have been many papers contributed on the distribution of particular asteroids. Unfortunately few of these contain accurate data on the density of asteroid populations, but their qualitative estimates leave us in no doubt as to the enormous abundance of asteroids in certain areas. A typical statement reads thus: "This fish is certainly an ill and evil star to the oyster and its cultivators. At times covering the bottom to a depth of 18 or 20 inches and extending in solid bunches or masses over considerable areas of ground, they are capable of blanketing entire beds of oysters in their slow but sure advance, leaving not a living bivalve behind" (B. F. Wood, quoted in COE, 1912). Subjective impression this may be, but no-one could doubt that starfish are locally abundant in the light of such a statement. Such quantitative estimates that I have been able to find support this impression.

GALTSOFF and LOOSANOFF (1939) report that in 1931 as many as 6,987,650 starfish were removed from 1,500 acres of oyster beds, and the same company "caught and destroyed almost twice as many in 1929". G. F. M. SMITH (1940) estimated that the density of starfish on oyster beds varied from 1,800 to 60,000 per acre (0.4 to 15/m<sup>2</sup>) and noted that the individuals tended to be smaller in areas of high population density.

#### KNOWN ESCAPE RESPONSES OF MOLLUSCS

Recent work has brought to light fascinating data on complicated escape responses engendered in certain gastropods by asteroids (BULLOCK, 1953; FEDER, 1963).

If the body fluids of *Pisaster* are allowed to drip into a small rock pool containing common intertidal gastropods (*Tegula*, *Littorina*), most of the gastropods will climb up the side of the pool directly away from the inferred predator, those nearest being the first affected (FEDER, 1963). If a roving starfish should contact the shell edge of a limpet then, far from clamping its shell in its normal "danger reaction", the limpet undergoes the most extraordinary series of gyrations (termed mushrooming by BULLOCK, 1953) to free itself, and then glides rapidly away, easily out-distancing its predator. Other known escape responses include a dramatic leaping motion reported for *Nassarius*, and the tube feet of *Asterias* provoking *Natica* to draw a fold of mantle over its shell, thus preventing the tube feet of the asteroid from gaining an attachment (SCHIEMENZ, 1896).

The important thing about these escape reactions is that they are specific to asteroids: they are not evoked by other foreign objects such as crab claws, sea weeds, snail shells or soft parts, rocks, human fingers or implements. Bullock tested many common species of gastropod for escape responses to asteroids; particularly striking is the behaviour of two closely related species of limpet, living respectively high and low on the beach. In the former species application of starfish tube feet to the mantle edge provokes no reaction; this correlates with the rarity of starfish in the upper beach zone. In the latter case, there is a violent response, correlating with the common occurrence of asteroid predators in the lower beach zone. In fact, this behaviour is so decisive that it produces a clear differentiation of the two species! Unfortunately palaeontologists have to rely on less refined criteria for recognising their fossil taxa.

Such studies demonstrate that starfish tube feet provoke striking and highly specific escape responses in many species of gastropod; and chemical sensory perception is also well developed in some forms.

Lamellibranchs have not been so intensively studied, though the escape mechanism of pectinids by swimming has been known for many years. RAY (1959) has demonstrated that *Clinocardium nuttalli* (CONRAD) leaps vigorously, using the

tip of the foot somewhat like a pole vaulter, in order to escape from *Pisaster ochraceus* (Fig.6). It would seem likely that most mobile bivalves also have some sort of escape reaction. There are few examples of this in the literature, but this probably reflects the lack of critical observations rather than a widespread lack of such behaviour. Lamellibranchs being on the whole sedentary, it would be surprising if they had not evolved some means of countering the threat posed to them by asteroid predation. A bivalve that is permanently fixed to the sea floor (*Mytilus*, arcids), or even one that lives only partly buried (venerids, cardiids), is obviously far more vulnerable than a form that can move readily (*Pecten*, gastropods).

#### PROTECTIVE ADAPTATIONS

It is clear that the bottom-dwelling bivalves, ever since their appearance on the geological scene, have been a convenient food source for varied types of animal. It is a reasonable a priori assumption that the selection pressure thereby brought to bear on different populations of bivalves will have resulted in the perpetuation of those morphological variants best suited to counter predation. The following are suggested as some of the more important protective adaptations against predation that have arisen during the phylogeny of the Bivalvia:

(1) The assumption of a streamlined, smooth shell enabling burrowing to be carried out quickly and efficiently. This will confer a degree of protection against

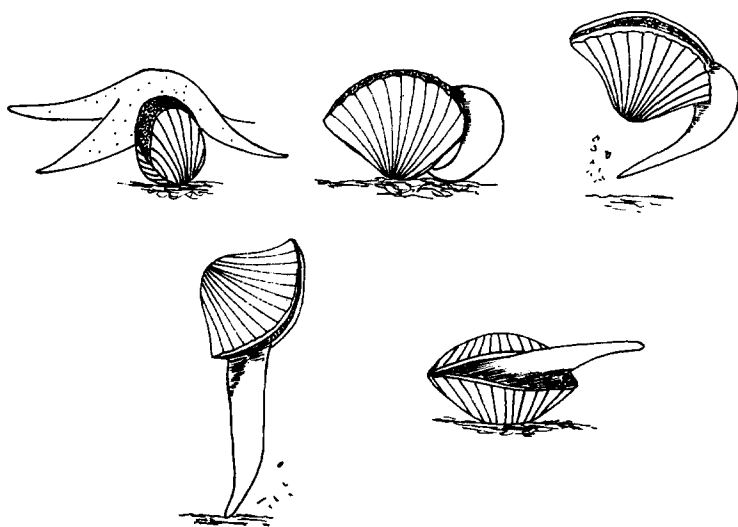


Fig.6. *Clinocardium nuttali* (Conrad) leaping to escape from attack by *Pisaster ochraceus* (BRANDT). (After RAY, 1959, pl.2.)

all predators except those (certain gastropods and asteroids) that plough through the substrate in search of food.

(2) An increase in size will protect epifaunal forms, or shallow burrowers, from predation by small teleost fish and intraorally digesting asteroids. When taken to the extremes of *Tridacna* such a size increase obviously offers considerable protection against other carnivores as well, but bivalves as large as this are very rare. However, the part that size relationships play in faunal communities is by no means simple; it is often advantageous to be small, as well as big. PAINE (1963) has given a clear example of this, noting that the large carnivorous gastropod *Pleuroploca* will not attack "such small morsels as *Nassarius*, *Chione* and *Cardita*." He concludes that it is size differences that are protective, not necessarily size increase on the part of the prey animal alone.

(3) An increase in shell thickness will help to combat predation by crabs, boring gastropods, and crushing fish.

(4) The assumption of a tightly closing shell with an interlocking commissure will provide a measure of protection against most predators including gastropods, birds and cephalopods. In particular, the acquisition of an interlocking commissure may form a protection of great importance against the attacks of extra-orally feeding starfish.

#### *Postulated function of interlocking*

The first three of the suggestions made above are, of course, by no means original. The fourth is certainly debatable and must stand or fall by future experiments on the selective habits of asteroids. Meanwhile, I suggest tentatively that the primary function of commissure interlocking is to ensure as close and snug a fit as possible between the opposing valve edges.

OLIVER (1923) stressed that all intertidal animals have to cater for the basic problem of conserving moisture during the period of low tide; many animals do this by the adoption of a closely fitting and precisely closing external shell. Oliver went on to suggest that the degree of perfection with which the two valves of a lamellibranch fit together might be related to the position of the animal in the intertidal belt, and he concluded that "though the pelecypod shell is primarily a weapon of defence, it is essential as a conserver of moisture to those animals regularly left dry by the tide".

It might be postulated from this that interlocking valve margins, because of their close fit, are adaptations for the retention of moisture by intertidal bivalves. Though this may be partly true, it cannot be the sole explanation of interlocking, for many subtidal and deeper water bivalves possess shells with tightly interlocking margins.

However, while agreeing with Oliver's basic contention that the shell is primarily defensive, I would include in the "shell" the property of marginal

interlocking. It is necessary to consider what animals marginal interlocking might serve as a defence against.

It is possible that the possession of interlocking might confer some advantage on those bivalves, such as *C. edule*, that are subject to predation by birds. On the other hand, many bivalves with closely interlocking commissures live subtidally in several feet of water where bird predation does not take place.

Crabs gain access to bivalve shells by breaking away the margins of the shell. Any adaptation towards preventing this would be expected to take the form of shell thickening, or of smooth flush shell margins to prevent the crab from gaining a grip. The possession of marginal denticulation might even be disadvantageous with respect to such predators.

Gastropods of the *Busycon* type force the edge of their shell between the valves of a pelecypod and often chip pieces off. Obviously in this case thickening of the valve edge and the adoption of close marginal interlocking will both be advantageous.

Asteroids of the extraoral feeding type are able to insert their stomachs through openings as small as 0.1 mm in breadth. It is extremely doubtful whether even the closest fitting of smooth bivalve commissures fit with this degree of precision, especially when it is remembered that two layers of periostracum issue from between the valve edge. Even if it be admitted that the assumption of flush fitting valve edges confers a degree of protection on the owner, there is no doubt that many different modern asteroids are capable of exerting enough force on normal sized bivalves to gain entry to their shells. And in the case of smooth commissures, once entry has been gained, it is mechanically a simple matter for the stomach to spread laterally all around and into the commissure in much the same way that one would slit a shell open with a knife. But if the commissure should be closely denticulate, it is very much more difficult, if not impossible, to slit the shell open in such an efficient manner. In the case of the asteroid, although initial penetration of the stomach would not be prevented by close marginal denticulation, the subsequent spreading of the stomach lobes might be severely inhibited (unless, of course, the bivalve was forced to gape widely). At every point on the commissure at which the asteroid wished to penetrate, it would have to insert a discrete stomach lobe.

It has been shown in the first half of this paper that when asteroids cannot penetrate readily with all five of their stomach lobes, digestion is radically slowed. It is also well established that asteroids will leave bivalves that are difficult to open or digest, and crawl away in search of "easier meat" (GALTSOFF and LOOSANOFF, 1931; CHRISTENSEN, 1957). Although requiring further rigorous support, in the light of observations such as these it is surely a reasonable postulate that marginal interlocking is capable of being an efficient defence against asteroid predation. Such a postulate has the merit of explaining the following observations:



(1) Interlocking commissures structurally similar to those of modern bivalves first appeared in the uppermost Ordovician or lowest Silurian; fish, birds and advanced crustaceans and gastropods were not at that time available as predators of bivalve molluscs. If interlocking commissures do represent protective adaptation against predation by some group of animals, the only likely groups of predators are the nautiloids or the Asterozoa.

(2) Once acquired, interlocking commissures would have conferred concomitant protection against other groups of predators that were only to evolve later.

(3) Interlocking has the advantage that it causes the valves to be sealed tightly—perhaps an important factor in intertidal survival.

(4) Essentially equivalent interlocking, though of different morphological detail, occurs in the Arcidae, Veneridae, Cardiidae, Lucinidae, Carditidae and Nuculacea (Plate II, 3–7, 10). These bivalves inhabit many different ecological zones and ways of life; no previously postulated function for interlocking valve edges, or for radial ribs, can help to explain their presence in all these contrasted groups of bivalves.

(5) Current interpretations of radial ribbing in the Bivalvia (e.g., that they are for strengthening the shell, or for aiding the animal to grip the sand while burrowing), though perhaps true in certain specific instances, are unconvincing as generalisations. For many bivalves in which interlocking is well developed, the generation of radial structures on the valve surface becomes an inevitable consequence of this interlocking; the radial ribs do not necessarily need to have a function in themselves.

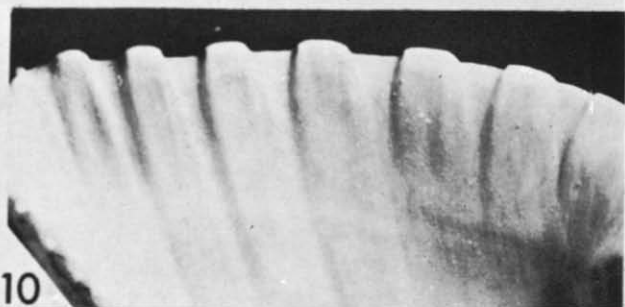
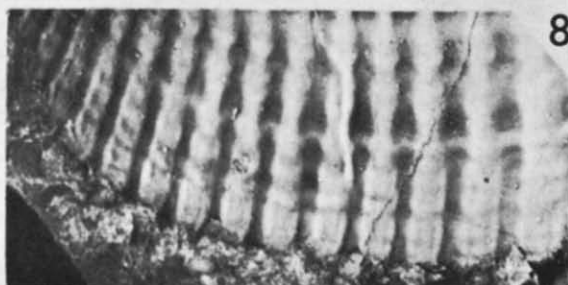
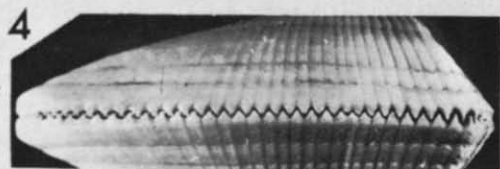
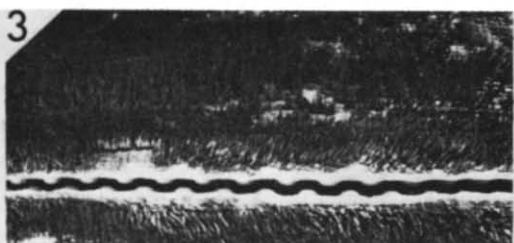
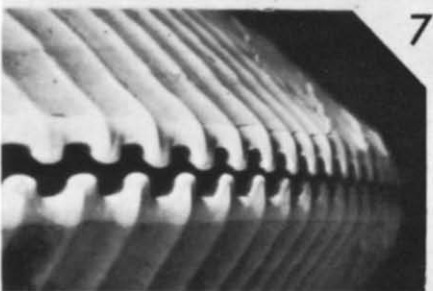
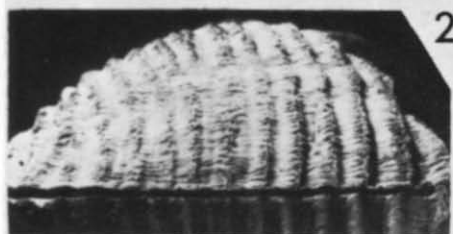
(6) Asteroids inhabit all bivalvian ecological habitats except fresh water. In the only fresh water bivalve to possess radial ribs (*Castalia ambigua* Lk.) the ribs are irregular, only developed in the juvenile, and their interlocking is rudimentary (Plate II, 2). EISMA (1965) has shown that “salinity, or some other factor dependant on salinity, determines the number of ribs on a cockle shell”.

(7) Very few of the deeper burrowing bivalves possess interlocking commissures. Conversely, most of the forms that are adapted to a shallow infaunal life, lying buried at or just below the surface of the substrate, possess strong interlocking of the two valves. And these forms are those that are most likely to fall prey to roving predators.

(8) Gastropods are known to have highly specific reactions to asteroid predation. Limpets will actually run away from an asteroid predator. Bivalve molluscs are comparable to gastropods in antiquity, abundance, diversity, ecology and mode of life, yet generally lack their advantage of mobility. It is surely inherently likely that bivalves would develop some defence against such a common predator as asteroids.

(9) It is virtually impossible for a bivalve to shut its valves tightly enough to prevent the intrusion of extraorally feeding asteroids. Can it be coincidence that

PLATE II



so many bivalves have a structural adaptation which, though not preventing the insinuation of an asteroid stomach, might reduce the amount of penetration and digestion possible?

## FOSSIL ASTEROZOA

The early phylogeny of the Asterozoa has been the subject of much intensive research, and some controversy, in the last few years, mainly stimulated by the discovery by FELL (1962, and other papers) of a living species of Somasteroid—a group of primitive Asterozoa hitherto thought to be restricted to the Lower Palaeozoic.

## PLATE II

1. *Castalia ambigua* LMK,  $\times 2$ . The only fresh water lamellibranch to possess radial ribs, this specimen shows the ribs still being formed at the ventral margin, and is not fully adult. Note the irregularity of ribs, especially anteriorly.
2. *C. ambigua* LMK.,  $\times 2.5$ . There is an almost complete lack of interlocking around the ventral valve margins. (Specimen from the McAndrew Collection, Cambridge University Zoology Department.)
3. *Glycymeris* sp., Recent,  $\times 2.5$ . Strong interlocking of the ventral margins without denticulation of the actual valve edge. Radial ribs are therefore not generated on the valve surface. (Sedgwick Museum collection of Recent Mollusca.)
4. *Donax punctatostratus* HANLEY, Recent,  $\times 2.5$ . An example of the strong ventral interlocking characteristic of the group; the trace of this interlocking during growth takes the form of incised radial striae on the valve surface. (Sedgwick Museum collection of Recent Mollusca.)
5. *Aulacomya* cf. *magellanicus* CHEMNITZ, Recent, Cape of Good Hope,  $\times 2.5$ . Characteristic weak marginal interlocking by gentle folding of the valve edge. (Sedgwick Museum collection of Recent Mollusca.)
6. *Chione* cf. *californiensis* BRODERIP, Recent, America,  $\times 5$ . View of tight marginal interlocking just anterior to the escutcheon on the posterior ventral valve margins; the interlocking is typical of the genus and results in characteristic radial structures on the valve surface. (Sedgwick Museum collection of Recent Mollusca.)
7. *Discors lyratum* (SOWERBY), Recent, Zanzibar,  $\times 5$ . The cardiids are nearly all characterised by strong interlocking of the ventral margins. Many different types of interlock occur and are partly responsible for the great range of morphological form shown by this family. *Discors* is unusual in that a marginal "tooth" corresponds to a rib on the valve surface; it is more normal for it to correspond to an interspace between ribs. (Sedgwick Museum collection of Recent Mollusca.)
8. *Slava interrupta* (BRODERIP), Silurian, Listice, Czechoslovakia,  $\times 6$ . Latex cast of internal mould of the ventral margins. Note the similarity of interlocking style to 10. (British Museum (Natural History), PL 4012.)
9. *Dualina tenuissima* BARRANDE, Silurian, Dworetz or Lochkow, Czechoslovakia,  $\times 6$ . Latex mould of a steinkern; well developed strong interlocking on the ventral margin (British Museum (Natural History), PL 4252.)
10. *Lunulicardia subretusa* (SOWERBY), Recent, Pacific,  $\times 4$ . Interlocking of the ventral margin structurally similar to Early Palaeozoic types. (Sedgwick Museum collection of Recent Mollusca.)

For the purposes of this paper it is obviously important to make such reliable inferences as are possible on the early feeding habits of the Asterozoa, and on their relationship with coeval Bivalvia.

HYMAN (1955) maintained that extraoral feeding in the asteroids is dependant upon their possession of long flexible arms equipped with specialised suction type tube feet. In the light of more recent work showing that asteroids can insinuate their stomach into prey without gripping with the arms, both these criteria become a little suspect. Nevertheless, they would still seem to be reasonable adaptations necessary for *efficient* extraoral feeding.

The earliest asterozoans (Fig.7) are Tremadocian (SPENCER, 1950) and occur in faunas from southern France and Czechoslovakia. In these early faunas there is already a differentiation into two recognisable groups: the somasteroids (*Villebrunaster*, *Chinianaster*) and certain primitive ophiuroids.

The somasteroids have a slightly later Upper Arenig representative in *Archegonaster*, and an Upper Ordovician form in *Arcophiactis*. Then the group is not known again in the fossil record, but it is represented in Recent seas, by the genus *Platasterias*. *Platasterias* has two distinct methods of feeding: (a) microphagous ciliary feeding; and (b) selective detrital feeding in which small prey, primarily amphipods, are captured by the tube feet and passed to the mouth. FELL (1962) has concluded that the fossil somasteroids fed by the same methods, but perhaps it should be mentioned that HYMAN (1955) noted that the fossil somasteroids must have been very flexible forms, and it would seem that they were at least structurally *capable* of extraoral feeding. In this respect it should be noted that *Chinianaster* is associated with the Arenig bivalves *Ctenodonta* and *Babinka* (THORAL, 1935). However, it is clear that modern opinion is against postulating an extraoral feeding habit for the somasteroids, though it would seem possible that they took some bivalve prey, perhaps in the course of detrital feeding.

The primitive ophiuroids continue into the Middle and Upper Ordovician as a distinctive and circumscribed morphological group. Their Recent representatives are mainly suspension feeders, though some carnivorous forms will take small prey, and there is no reason to doubt that the fossil ophiuroids fed in a similar way. They are therefore not discussed further.

The first true asteroid, albeit a primitive form, appears in the fossil record a little later than the somasteroids or ophiuroids in beds of early Arenig age on Ramsey Island, Pembrokeshire. Here there is a rich invertebrate fauna including *Petraster ramseyensis* (HICKS), which NICHOLS (1962) has termed the first true phanerozone starfish. In beds of the same age in France and Czechoslovakia there is a continuation of the somasteroids and primitive ophiuroids (*Palaeura*), and it is not until the Upper Arenig that the faunas of these areas contain any true asteroids (*Bohemaster*, *Protopalaeaster* as well as *Petraster*).

By the Middle Ordovician the fauna has become much more modern in appearance, and the somasteroids have largely disappeared (SPENCER, 1950).

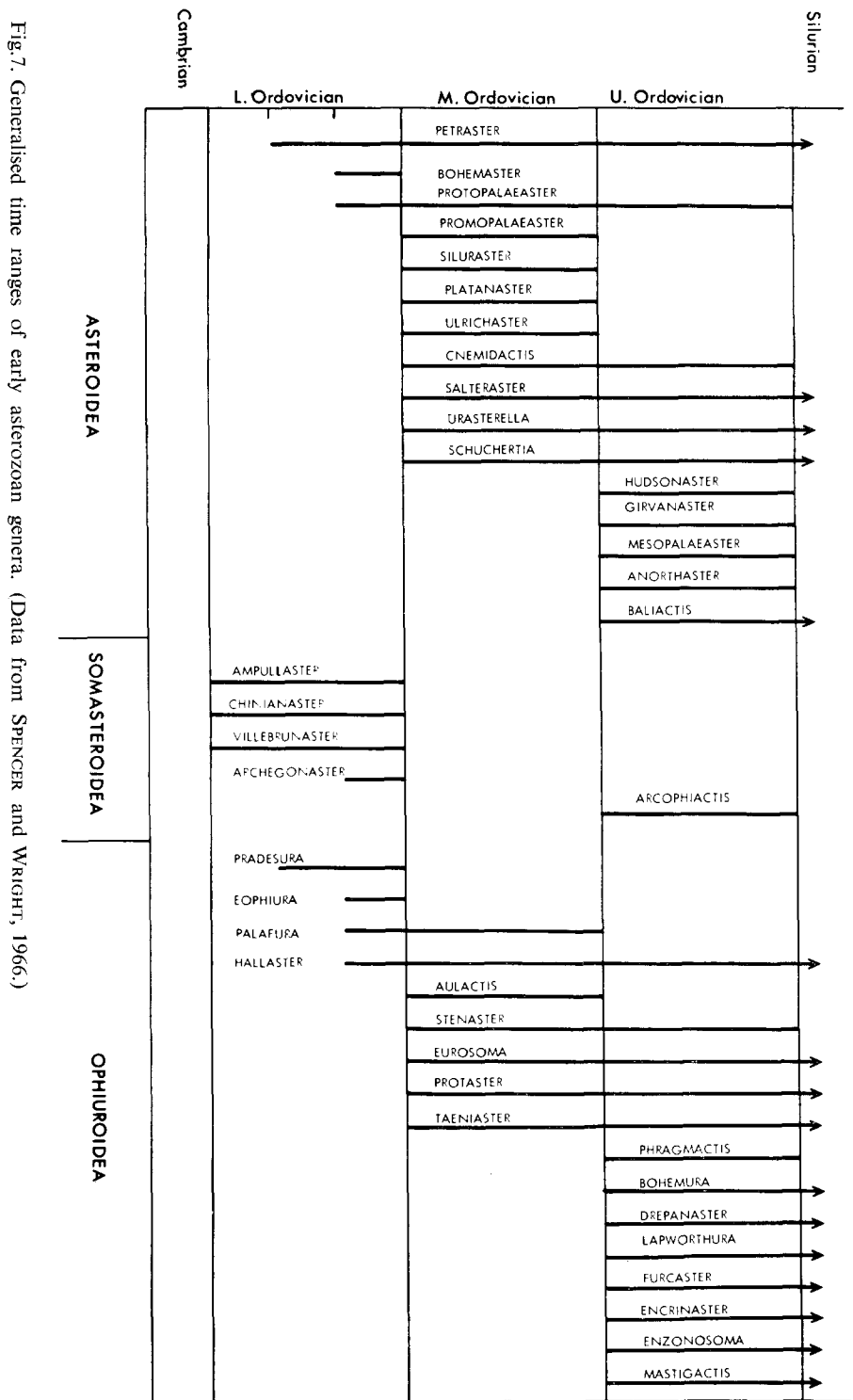


Fig.7. Generalised time ranges of early asterozoan genera. (Data from SPENCER and WRIGHT, 1966.)

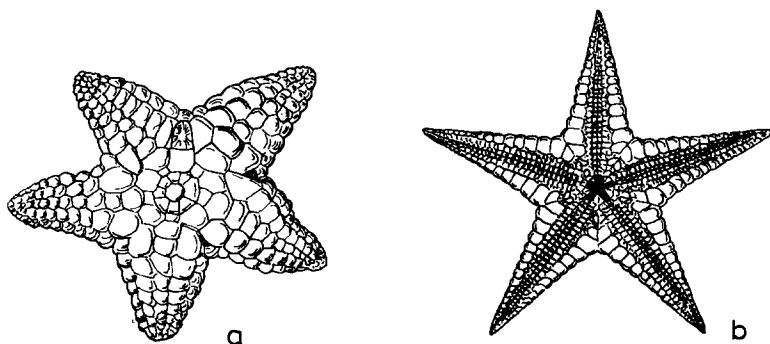


Fig.8. Possible Palaeozoic extraorally feeding asteroids. a. *Hudsonaster*, Upper Ordovician,  $\times 3$ . b. *Xenaster*, Lower Devonian,  $\times \frac{2}{3}$ . (After MOORE et al., 1952.)

The genera *Stenaster*, *Protopalaeaster*, *Petraster* and *Salteraster* have much the appearance of Recent starfish and occur in widely separated localities in Turkestan, Canada, Czechoslovakia, Ireland and Wales. And in *Hudsonaster* (Fig.8) "we have reached a condition of skeleton more of less common to all subsequent asteroids" (NICHOLS, 1962).

That these numerous Ordovician asteroids fed at least partly on Mollusca is certain. Intraoral feeding on gastropods is established as early as the Upper Ordovician, for specimens of *Girvanaster* from the starfish bed of Scotland have been found so full of small gastropods that their upper surface is dilated (SPENCER

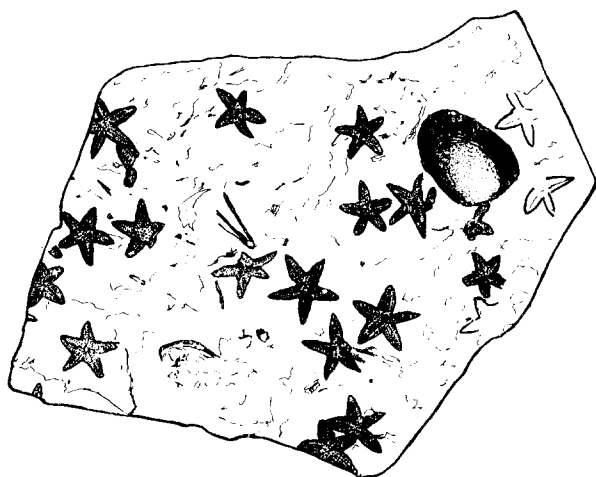


Fig.9. *Grammysia* surrounded by predatory *Devonaster eucharis* (HALL). An average example of the abundance of starfish at this Devonian locality. Approximately  $\times 0.25$ . (Drawn from pl.XIV of CLARKE, 1912b.)

and WRIGHT, 1966). It is significant also that LAMONT (1934) has recorded that the associated bivalves and brachiopods in this fauna are invariably sharply ribbed species, i.e., possessed strong interlocking.

For convincing evidence of extraoral feeding we have to consider somewhat younger faunas. The discovery of a large bed of Devonian starfish by CLARKE (1912b) must rank as one of the most remarkable palaeontological finds ever made. From an exposed surface of 200 sq.ft. of sandstone, 400 specimens of *Devonaster eucharis* (HALL) were collected, and these starfish were in intimate association with a fauna of bivalves of the genera *Grammysia* and *Pterinea* (Fig.9).

"Nearly every *Grammysia* or *Pterinea* found ... has a star in or on it, sometimes several about its edges suggestive of attack" (CLARKE, 1912a). "There is little doubt that the field was the proper feeding ground and habitat of these clams, and the evidence indicates that this being so, it was invaded by the starfish which congregated in these vast numbers in order to feed on the clams" (CLARKE, 1912b).

It remains to point out that from the relative size of the two animals (Fig.9) it is obvious that the starfish could not have been feeding intraorally. It can thus be considered as established that as early as the Devonian asteroids were present in large numbers and fed at least partly on bivalve mollusca by extraoral digestion.

*Meopalaeaster*, a genus closely related to *Devonaster* and included in the same subfamily, is known from the Upper Ordovician and almost certainly fed extraorally. And there is no doubt that other early asteroid genera were structurally capable of utilising this method of feeding. In the light of Hyman's criteria for efficient extraoral feeding, it is interesting to note that FELL (1963) has tentatively estimated that *Hudsonaster* (Fig.8) was the first starfish to acquire suctorial tube feet. It seems reasonable, then, to suggest that extraoral feeding was established early in the phylogeny of the asteroids, probably some time during the Lower or Middle Ordovician. It is a tempting thought that this new feeding habit might have been a factor in the immediate success and subsequent expansion of the group.

#### FOSSIL BIVALVIA

The close relationship between asteroids and bivalves is well established in the Recent fauna. It is far too striking to be coincidental that a similar relationship occurs in many early fossil faunas.

Apart from very rare Middle and Upper Cambrian occurrences (e.g., Montagne Noire, southern France, THORAL, 1935; Spain, VOGEL, 1962) the earliest bivalves are Ordovician. They occur in quartzose beds of Arenig age, mainly in Spain and France (Armorica Sandstone), and are small unornamented forms belonging to genera such as *Tancrediopsis*, *Redonia*, and *Ctenodonta*.

The Ramsey Island fauna referred to above, which is also of Arenig age,

is one of the few examples in the Lower Ordovician of fossilisation of an actual faunal community including lamellibranchs. Although not strictly biocoenotic, the fauna is numerically and biologically so rich that it undoubtedly represents a community of animals that lived together in closely knit ecological dependence. The fossils are well preserved, though a little distorted by tectonic movement, and occur strewn on bedding planes in very great abundance (e.g., Sedgwick Museum A44310). HICKS (1873) noted that the fauna was "exceedingly rich in Lamelli-branchiata, no less than twelve species, belonging to five genera, having been found", and orthid brachiopods are also abundant. The comparative morphology of these two invertebrate groups is most striking: the Bivalvia are small plain shells (typical length 5 mm) without either external radial ornament or interlocking commissures (*Glyptarca primaeva* HICKS, *Ctenodonta menapiensis* (HICKS)); but the brachiopoda are not only larger (typically 15 mm long), they also possess very strong interlocking of the ventral shell margins ("*Orthis*" *menapiensis* (HICKS), "*O*". *carausii* SALTER). I would suggest that neither these morphological characters, nor the faunal association, are coincidence, but that the associated asteroid (*Petraster*, diameter approximately 25 mm) was feeding on the Bivalvia by intraoral digestion, the brachiopods being protected mainly by their size. However, in view of the refined interlocking of the brachiopods, the possibility cannot be excluded that *Petraster* had already started to feed extraorally.

With the onset of the Middle Ordovician bivalves become somewhat more common and new forms start to appear in the faunas. At this stage we can consider the superb stratigraphic column of Czechoslovakia, for it is at this level (the (the Šárka Beds, stage *d1*, of Barrande, approximately Llanvirnian) that the first bivalves are known there. They belong to the genera *Babinka*, *Ctenodonta*, *Trancrediopsis*, *Redonia* and *Syneke*, and the fauna thus has much in common with the other European Early Ordovician bivalve faunas. However, in the ensuing Middle and Upper Ordovician beds the composition of the fauna changes steadily (beds *d2* to *d5* of Barrande) and at level *d5* the first radially ribbed bivalves start to appear. These belong to genera such as *Slava*, *Dualina*, *Praelucina*, and *Maminka*. Specimens of these fossils examined in the British Museum (Natural History) show clearly that the radial ribs on the external surface of the shell correspond to marginal interlocking of the commissure. Further, this interlocking is of structural types that are closely similar to those present in many other bivalves throughout the geological column, and in Recent faunas (see Plate II, 3–10).

In the Silurian beds (beds *e1*, *e2*, etc., of Barrande) there is a veritable explosion of bivalve evolution, particularly in bed *e2*. Whereas a total of only twenty genera of Bivalvia are known from the Ordovician beds of Czechoslovakia, from level *e2* of the Silurian alone 767 species belonging to 43 genera (BARRANDE, 1881) are known. These include new species of genera already occurring in the Ordovician faunas, and also a variety of new genera. Many of these new forms have



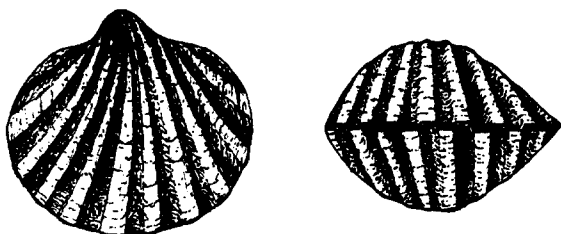


Fig.10. *Praecardium primulum* BARRANDE, stage e2 (Silurian), Czechoslovakia. (Drawn from pl.285 of BARRANDE, 1881.) Approximately  $\times \frac{1}{2}$ .

interlocking commissures resulting in radial ribs on the shell surface, and some of them are strikingly like modern cockles (Fig.10).

Undoubtedly part of this apparent major faunal change is due to facies control, and more of it is related to outdated systematics, but one may doubt whether this is the whole answer. It will be remembered (cf. Fig.7) that there was a large expansion of the asteroid fauna in the Middle and Upper Ordovician, and this was particularly true of Czechoslovakia. This asteroid expansion, perhaps significantly, predates the major change in the bivalve fauna. I would postulate that it was about this time that extraoral feeding became important in the asteroids, and that the morphological innovation of interlocking commissures in bivalves in the uppermost Ordovician and Lower Silurian is perhaps partly connected with predation by extraorally feeding asteroids.

It is likely that brachiopods formed a significant part of the diet of Palaeozoic asteroids. SCHUCHERT (1915, pl.13, fig.1) has illustrated a specimen of *Promopalaeaster wilsoni* (RAYMOND) preserved associated with a rich fauna of brachiopods from the Middle Ordovician of Canada. It is interesting that in Czechoslovakia brachiopods, like bivalves, also reach their apogee in numbers in the e2 horizon with 293 species. RUDWICK (1958) has commented on the morphological similarity between the marginal interlocking of bivalves and certain Palaeozoic orthides.

Finally, it must also be borne in mind that nautiloids may also have been important predators at this time. Specimen 80233 of *Slava*, in the British Museum, is on a small slab and almost entirely surrounded by orthocone nautiloids.

## CONCLUSIONS

Reference to Fig.1 will show that of the bivalve predators considered in this paper only two, the cephalopods and the asteroids, have a long Palaeozoic record. None of the vertebrates, crustacea or gastropods are likely to have been important pre-Devonian predators. Little is known of the ecology and feeding habits of Early Palaeozoic nautiloids, apart from the fact that they occur in enormous

numbers in certain faunas; it would seem unwise in this state of knowledge to regard them as major predators. One may conclude tentatively that the asteroids were the most important of early bivalve predators.

The additional suggestion, that certain features of bivalve morphology can be interpreted as protective against this group of carnivores, certainly requires experimental verification, but it is apparent that a credible circumstantial case can be established for this. Whilst I am aware that this paper is almost entirely a summary of other workers' findings, I feel that it will be of value even if only to draw attention to the great importance of ecological faunal studies in invertebrate morphological interpretation.

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