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The Mesozoic marine revolution: evidence from snails, predators and grazers

Geerat J. Vermeij

Abstract.—Tertiary and Recent marine gastropods include in their ranks a complement of mechanically sturdy forms unknown in earlier epochs. Open coiling, planispiral coiling, and umbilici detract from shell sturdiness, and were commoner among Paleozoic and Early Mesozoic gastropods than among younger forms. Strong external sculpture, narrow elongate apertures, and apertural dentition promote resistance to crushing predation and are primarily associated with post-Jurassic mesogastropods, neogastropods, and neritaceans. The ability to remodel the interior of the shell, developed primarily in gastropods with a non-nacreous shell structure, has contributed greatly to the acquisition of these antipredatory features.

The substantial increase of snail-shell sturdiness beginning in the Early Cretaceous has accompanied, and was perhaps in response to, the evolution of powerful, relatively small, shell-destroying predators such as teleosts, stomatopods, and decapod crustaceans. A simultaneous intensification of grazing, also involving skeletal destruction, brought with it other fundamental changes in benthic community structure in the Late Mesozoic, including a trend toward infaunalization and the disappearance or environmental restriction of sessile animals which cannot reattach once they are dislodged. The rise and diversification of angiosperms and the animals dependent on them for food coincides with these and other Mesozoic events in the marine benthos and plankton.

The new predators and prey which evolved in conjunction with the Mesozoic reorganization persisted through episodes of extinction and biological crisis. Possibly, continental breakup and the wide extent of climatic belts during the Late Mesozoic contributed to the conditions favorable to the evolution of skeleton-destroying consumers. This tendency may have been exaggerated by an increase in shelled food supply resulting from the occupation of new adaptive zones by infaunal bivalves and by shell-inhabiting hermit crabs.

Marine communities have not remained in equilibrium over their entire geological history. Biotic revolutions made certain modes of life obsolete and resulted in other adaptive zones becoming newly occupied.

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Introduction

When we view the history of life from its beginnings some three billion years ago, we seem to witness a pattern of comparatively sudden revolutions interspersed with long intervals of relative quiescence. The most notable revolutions, the development of hard parts in the Early Paleozoic and the marine events of the Late Mesozoic, are not the instantaneous take-overs or inventions with which we identify revolutions in human history, but lasted tens of millions of years; yet, these episodes are short relative to the hundreds of millions of years when comparatively little fundamental change took place in community organization.

In the Early Cambrian, diverse marine groups developed skeletons of calcium phosphate, calcium carbonate, and silica. Some groups were earlier in this development than others (for a review see Stanley 1976a), but by the Middle Cambrian most groups which were to play an important role in the fossil record had become skeletonized. By early Ordovician time, marine communities had acquired fundamental characteristics which they would retain for more than three hundred million years during the remainder of the Paleozoic and Early Mesozoic. During this period, reefs came and went (for reviews see Newell 1971; and Copper 1974), and groups diversified and declined; but most marine benthic communities were dominated by epifaunal

(surface-dwelling) or semi-infaunal elements (Stanley 1972, 1977).

Then, inexplicably, things began to change. Beginning in the Jurassic and continuing at an accelerated pace in the Cretaceous, changes in life habits took place which fundamentally altered relationships among organisms in shallow-water marine communities. These currents of change were unaffected by, or only temporarily delayed, by episodes of extinction, including the crisis at the end of the Cretaceous (Maastrichtian-Danian transition). Stanley (1977) and Meyer and Mc-Curda (1977) have already treated some aspects of this reorganization, and I have speculated on some curious changes in shell geometry which affected gastropods in the Mesozoic (Vermeij 1975). The consensus reached from these investigations is that the intensity of predation has increased substantially since the Middle Mesozoic.

In this paper, I shall expand upon this theme. From further evidence of skeletal geometry and other data, I shall argue that predation as well as grazing has intensified and become more destructive to skeletons; and I shall ask, mostly in vain, what triggered this Mesozoic reorganization.

Trends in Gastropod Morphology

Tertiary and Recent marine gastropods differ from Mesozoic and especially from Paleozoic snails in many architectural ways and include in their diverse ranks a complement of mechanically sturdy forms quite unknown in earlier times. First, the incidence of shells possessing an umbilicus (cavity in the base of the cell created by the incomplete overlap of adjacent whorls) has significantly decreased in the course of geological time (Vermeij 1975). Paleozoic gastropod faunas were heavily dominated by archaeogastropods and by bilaterally symmetrical bellerophontaceans. (For the purposes of this paper, I shall here regard Bellerophontacea as belonging to the class Gastropoda, and follow for convenience the classificational scheme of Taylor and Sohl (1962). Runnegar and Pojeta (1974) have presented arguments in favor of transferring the bellerophonts to the Monoplacophora; see also Golikov and Starobogatov (1975) for further discussion.) I have estimated that 74%

of the genera in the largely Paleozoic and Early Mesozoic superfamily Pleurotomariacea had umbilicate shells, while only 58 to 60% of the genera in the Mesozoic and Cenozoic Trochacea possess umbilici (Vermeij 1975). Non-umbilicate shells with often relatively high spires, placed by Knight et al. (1960) in the Murchisoniacea, Subulitacea, and Loxonematacea, were present from Late Cambrian or Early Ordovician time onward; but the great expansion of the largely non-umbilicate mesogastropods and neogastropods did not take place until the latter half of the Mesozoic. Thus, archaeogastropods still predominated in Triassic faunas, but Jurassic and Cretaceous assemblages already contained a large diversity of mesogastropods. Siphonate neogastropods and higher mesogastropods constitute the majority in some Late Cretaceous and nearly all Cenozoic gastropod assemblages (Sohl 1964).

The trend in the reduction in frequency of umbilicate shells seems to reflect an overall increase in the mechanical resistance of shells to crushing (Vermeij 1976). The large umbilicus and high whorl expansion rate (W) render the West Indian trochid *Cittarium pica* vulnerable to predation by crabs at larger shell diameters than the taxonomically and ecologically related western Pacific *Trochus niloticus*, which has a lower W and a smaller umbilicus (Vermeij 1976).

Several additional features of gastropod shell architecture support the thesis that predation intensity due to crushing enemies has increased since the Middle Mesozoic. The diversity, and especially the size, of bilaterally symmetrical (usually umbilicate) coiled shells among the gastropods has dramatically decreased since the Late Cretaceous (Vermeij 1975). Today, such planispiral shells are found principally in fresh water and on land, where they may still attain diameters as much as 5 cm. In the sea, however, all planispirally coiled snails are small (usually less than 0.5 cm in diameter), and most are found among algae, under stones, or in the plankton. Predation by shell crushing seems to be unimportant for very small snails (see e.g. Hobson 1974; Stein et al. 1975) and is likely to be of greater consequence for snails living on exposed rock surfaces than for those living among algae or under rocks (Vermeij 1974). In the latter two habitats, constraints on rapid locomotion and

visual detection limit the activities of such potential crushing predators as fishes and crabs. Planispiral coiling among planktonic gastropods may be related to their swimming mode of life and seems to be associated with rapid locomotion. Most planktonic predators, moreover, do not appear to use crushing as a means of prey capture.

Pre-Cretaceous seas, in contrast, often supported large planispiral or near-planispiral snails (Macluritacea, Euomphalacea, Bellerophontacea, Pleurotomariacea, etc.), most of which were probably members of the benthic epifauna (Vermeij 1975). At least in some macluritaceans and euomphalaceans, the planispiral geometry was not associated with rapid locomotion but rather with a sedentary mode of life on quiet bottoms (Yochelson 1971).

Rex and Boss (1976) have summarized the taxonomic distribution of the 15 Recent species of gastropods exhibiting open coiling. Open coiling is defined by Rex and Boss (1976) as regular coiling based on the logarithmic spiral, in which adjacent whorls do not touch one another; thus, such groups as *Vermicularia*, *Siliquaria*, and Vermetidae, whose coiling is irregular and non-logarithmic, are excluded. Of the 15 Recent species, only 8 are marine, 3 are found in fresh water, and 4 are terrestrial. From estimates of Recent molluscan species numbers given by Boss (1971), I calculate that open coiling is found in about 1 out of every 2,200 marine gastropod species, 1 out of every 1,000 fresh-water species, and 1 out of every 3,750 terrestrial species of shelled gastropod. The fresh-water forms with open coiling all occur in cold lakes, where crushing predation is rare (Vermeij and Covich 1977). Most of the marine open-coiled snails are found either in very deep water (*Lyocyclus*, *Epitonium*) or in sand associated with cnidarians (*Spirolaxis*, *Epitonium*). The habits of *Extractrix* and *Callostracum* are not known but are probably sandy or muddy, judging from the distribution of other members of their respective families (Cancellariidae and Turritellidae). Predation through crushing is probably relatively uncommon in most of these environments. Bright (1970), for instance, found few shelled invertebrates in the diet of 81 deep-sea fish individuals he examined from the Gulf of Mexico, and these were ingested whole. Cnidarians often give associated animals a measure of protection from potential predators (see for example McLean and Mariscal 1973).

Open coiling was apparently much commoner in the Paleozoic and Early Mesozoic than now. From various sources (Knight et al. 1960; Wanberg-Eriksson 1964; Yochelson 1971), I have counted some 18 to 20 genera of Paleozoic, and 2 genera of Triassic gastropods with open coiling. Some of these, such as the Paleozoic *Macluritella* and various euomphalids, may have rested on soft muds (Yochelson 1971), while others (e.g. the Platyceratidae and the Late Devonian and Triassic Tubinidae) may have been sedentary reef-associated forms (Bowsher 1955; Knight et al. 1960).

Paleozoic nautiloids and Mesozoic ammonoids also included in their ranks many shells with open and sometimes irregular coiling, which could not have been well suited for rapid swimming (Kummel and Lloyd 1955). The only Recent externally shelled cephalopod (genus *Nautilus*) has rather tight coiling, and the only living cephalopod with open coiling (*Spirula*) lives at moderate depths and has an essentially internal shell. It is very likely that the fragile open coiling of fossil cephalopods would, if these animals were alive today, restrict them to great depths or to other marginal habitats where shell-destructive predation is rare.

The ability to remodel the interior of the shell has contributed greatly to the increased sturdiness of Late Mesozoic and especially Cenozoic gastropods (Mesogastropoda, Neogastropoda, and Neritacea). Carriker (1972) has suggested that the external spines of many muricid shells are resorbed by the left edge of the mantle as the exterior of the shell is obliterated from view by the encroaching inner lip during spiral growth. Spines of this type serve to increase the effective size of the shell, and often strengthen it against crushing or other destruction (Vermeij 1974 and references therein). Without resorption or remodeling, these spines and other collabral sculptural elements (those parallel to the outer lip) would protrude into the aperture and, if large enough, might interfere with retraction of the body into the shell. Although such protrusions are actually known in some fresh-water shells (e.g. *Biomphalaria*) and land snails (*Helicodiscus* and other genera),

they are apparently exceedingly rare among marine gastropods. In the archaeogastropods (excluding Neritacea), where resorption appears to be poorly developed or altogether absent, this problem can be avoided by either (1) covering the sculpture with a thick inductural glaze, or (2) producing shells with reduced whorl overlap so that interference with previously built sculpture is minimal (see also Vermeij 1973). The first solution demands a relatively broad aperture and would restrict the sculptured surface to the body whorl. Examples of the second solution, which implies a tall spire that can often be cracked by predators, are provided by the sometimes open-coiled, strongly ribbed mesogastropod *Epitonium* and by the trochid archaeogastropod *Tectus*, which is sculptured with one or more spiral rows of knobs on the upper face of the whorls and is further characterized by a spire unusually high for an archaeogastropod (apical half-angle of Palauan *T. triseriata* is 26.3°).

In view of these and other limitations imposed by general shell geometry on sculpture (see also Vermeij 1971, 1973), it is perhaps not surprising that few Paleozoic snails had shells in which nodes, spines, or strong collabral ridges were the dominant sculptural elements. Examples of periodically produced collabral lamellae are known in some bellerophonts (the Middle to Upper Ordovician *Phragmolites*, the Middle Ordovician to Silurian *Temnodiscus*, and the nearly open-coiled Middle Silurian *Pharetrolites*). Collabral threads often associated with nodes or even spines were developed in the Lower to Middle Permian portlockiellid *Tapinotomaria* and by various Upper Devonian open-coiled Tubinidae. The high-spired Pseudozygopleuridae of the Carboniferous and Permian were usually characterized by evenly spaced collabral ridges.

In the pre-Cretaceous Mesozoic we see a larger number of gastropods with collabral sculpture: some Triassic and Jurassic Helicotomidae (Macluritacea); Triassic Porcelliidae, Zygitidae, and Jurassic Pleurotomariidae (Pleurotomariacea); open-coiled Triassic Tubinidae (Oreostomatacea); some Turbinidae (Trochacea), Middle Triassic and younger Cirridae and Amberleyidae (Amberleyacea); high-spired Triassic and Jurassic Zygopleuridae (Loxonematacea), Middle

Jurassic and younger Neritidae (Neritacea); and Jura-Cretaceous high-spired nerineaceans. Yet, it is primarily the Cretaceous and Cenozoic mesogastropods and neogastropods in which nodes, spines, and collabral ribs have been most elaborately developed. Some contemporaneous trochid, turbinid, and cyclostrematid archaeogastropods have also produced such sculpture (recall the trochid *Tectus*, for example), but their numbers are less impressive.

Similarly, extensive development of protective dentition on the inner face of the outer lip is predominantly a post-Jurassic innovation which, in such groups as Neritidae, Muricidae, and many other mesogastropods and neogastropods would be impractical if it could not be secondarily resorbed as the position of the growing edge moves in a spiral direction. Without remodeling, teeth restricting accessibility into the aperture could be developed only in the adult stage of species with determinate growth, when spiral growth has ceased. Indeed, such teeth are commonly seen in cowries (Cypraeidae), helmet shells (Cassidae), and many tritons (Cymatiidae), as well as in many Paleozoic nautiloids and Mesozoic ammonoids. These molluscs forfeited the luxury of apertural defense during the active spiral phase of growth, when most gastropods are particularly vulnerable to predation.

The first snail with outer-lip dentition seems to be the Middle Permian subulitid *Labridens* (Knight et al. 1960). The only other gastropod with labial teeth to have evolved before the Late Cretaceous is the Upper Jurassic to Upper Cretaceous trochid *Chilodonta*. Within the internally resorbing Neritidae (Woodward 1892), which arose during the Triassic, the first genera to show dentition on the outer lip (*Myagrostoma*, *Velates*, and *Nerita*) date from sediments of Late Cretaceous age, when most of the higher mesogastropods and neogastropods also differentiated or expanded.

In *Conus*, *Olivella*, *Bullia*, Ellobiidae, and possibly other snails with markedly narrow and elongate apertures, extensive internal resorption of whorl partitions (Fischer 1881; Crosse and Fischer 1882; Morton 1955) secondarily widens the shell cavity to accommodate the visceral mass while at the same time effectively restricting entry into the aperture. Before the Cretaceous, relatively long, nar-

row apertures are known in but a few isolated genera: the Lower Carboniferous opistho-branch *Acteonina*, the Lower Carboniferous to Lower Permian *Soleniscus* and Middle Permian *Labridens* (Subulitiidae), and the Lower Jurassic to Upper Cretaceous neritid *Pileolus* (see Knight et al. 1960). The greatest diversity of snails with slit-like apertures is found in the post-Jurassic cypraeids, vexillids, conids, mitrids, olivids, columbellids, marginellids, and even strombids.

It may thus be concluded that Neritacea, mesogastropods, and especially neogastropods have, by evolving and taking advantage of the capacity to remodel the shell interior, significantly broadened the range of shell types that were available to earlier archaeogastropods. In particular, remodeling has enabled these snails to acquire combinations of short spires, narrow apertures, strong external sculpture, and apertural dentition which render the shell relatively impervious to predation by crushing or other shell-destructive modes of attack. In most archaeogastropods, possession of one architectural antipredatory attribute compromises another, so that the shell is rarely as well defended (in a geometrical sense) as in many post-Jurassic siphonate snails.

In passing, it is worth noting that all the gastropods in which internal remodeling has been employed extensively have a non-nacreous shell structure. Currey and Taylor (1974) have shown that nacre is in many ways mechanically tougher and stronger than other types of shell microarchitecture, yet nacre appears to be the primitive condition in most molluscan classes (Taylor 1973). The intriguing possibility that the advantages of remodeling in non-nacreous shells could have contributed to the replacement through time in many lineages of the nacreous type of structure with other forms of microarchitecture deserves further investigation.

Portmann (1967) and many others have pointed out that the external shell has been internalized or entirely lost in a large number of gastropod and cephalopod lineages. This loss is interpreted by these authors as a de-emphasis of the shell as a protective device. It is, of course, impossible to know how widespread this loss was in the course of Paleozoic and Mesozoic history; but it does seem that shell loss in Recent molluscs is associated either with great speed (cephalopods, heteropod gastropods) or with toxicity or unpalatability (many nudibranchs, onchidiids, perhaps some fissurellids?). Even in cowries (Cypraeidae), in which the well-developed shell is often covered during life with the mantle, Thompson (1969) demonstrated the existence of acid-secreting cells which may discourage predation by fishes. (See also Thompson 1960). Thus, internalization and loss of the shell may have been alternative solutions to the problem of increased predation intensity on molluscs.

Gastropod Predators

There is good reason to believe that the increase in snail-shell sturdiness beginning in the Cretaceous and continuing through the Tertiary has accompanied, and was perhaps in response to, the evolution of powerful, relatively small, shell-destroying (durophagous) predators. Table 1 summarizes the geological origins of the major groups of present-day molluscivores, and shows that most of these are in the Mesozoic era. Within the majority of durophagous groups (for example, in the teleosts, brachyurans, birds, and drilling gastropods), the ability to destroy or penetrate shells was not perfected until Late Cretaceous time or even later (Sohl 1969; Vermeij 1977), long after these groups first arose. The Asteroidea (sea stars) are the only group of important Recent molluscivores with a known pre-Mesozoic history, and they do not employ crushing or other shell-destructive methods to obtain their molluscan prey. Sea stars interpreted to have employed extraoral digestion co-occur with intraorally digesting sea stars in Upper Ordovician rocks (see Carter 1968).

There were, of course, durophagous predators which affected shelled molluscs in Paleozoic and Mesozoic communities but are no longer with us today. Several Late Devonian arthrodires and arthrodire relatives (e.g. *Mylostoma* and the ptyctodonts) had jaw dention in the form of a crushing pavement, as did a number of Late Devonian to Permian hybodont sharks. Some of the latter were apparently quite small fishes (e.g. *Chondrenchelys* and *Helodus*) (Romer 1966). Hybodont sharks may have been responsible for the disarticulation and shell breakage observed

TABLE 1. Origins and modes of predation used by recent molluscivores.

Asteroidea; extraoral and intraoral digestion; arose and became molluscivores Late Ordovician; Carter (1968)

Dipnoi (fresh-water lungfishes); crushing; arose and became durophagous in Devonian; Thomson (1969)

Heterodontidae (sharks); crushing; arose and became durophagous in Jurassic; Romer (1966)

Batoidea (rays); crushing; arose Jurassic, became durophagous in Cretaceous; Bigelow and Schroeder (1953)

Stomatopoda (crustaceans); hammering and spearing; arose Jurassic, may have achieved durophagy by late Cretaceous; Holthuis and Manning (1969)

Palinuridae (spiny lobsters) and Nephropidae (lobsters); crushing; arose Jurassic, date of acquisition of durophagy uncertain; George and Main (1968)

Brachyura (crabs); crushing, apertural extraction; arose Jurassic, achieved durophagy by Latest Cretaceous or Paleocene; Glaessner (1969), Stevčić (1971), Vermeij (1977)

Aves (birds); crushing, swallowing whole, wrenching; arose Late Jurassic, were molluscivorous by Late Eocene; Cracraft (1973)

Muricacea (gastropods); drilling, apertural extraction; arose Albian (Early Cretaceous), drilling by Campanian (Late Cretaceous); Sohl (1969)

Naticacea (gastropods); drilling; arose Triassic, drilling by Campanian (Late Cretaceous); Sohl (1969)

Other Neogastropoda; apertural extraction; arose Early Cretaceous, molluscivory certainly established by Late Cretaceous; Sohl (1964, 1969)

Cynatiidae (Mesogastropoda); apertural extraction; arose and became molluscivorous Late Cretaceous; Sohl (1969)

Actinaria (sea anemones); swallowing whole; nothing known of fossil record

Teleostei (bony fishes); crushing, wrenching, swallowing whole; arose Triassic, durophagy by Late Cretaceous or earliest Tertiary; Schaeffer and Rosen (1961)

among some thick-shelled trigoniacean, heterodont, and taxodont-hinged bivalves in the Park City Formation of the Lower Permian of Wyoming (Boyd and Newell 1972). Earlier in the Paleozoic, cephalopods may have been important molluscivores, but no record of their activities remains.

Probable Mesozoic durophages include the remarkable Triassic marine placodont reptiles (von Huene 1956), the Triassic ichthyosaur *Omphalosaurus*; the Late Cretaceous mososaurid lizards, especially the genus *Globidens* (see Kauffman and Kesling 1960); and the Cretaceous ptychodontoid sharks (Romer 1966). Kauffman (1972) believes ptychodonts to have been important predators on

inoceramid bivalves (see also Speden 1971) and has described some suggestive tooth-marks on these large shells. Tooth-marks on the rostra of Jurassic belemnites from southwest Germany are also thought to have been made by various fishes (Riegraf 1973).

It is, of course, difficult to assess the impact of extinct predators; yet, the large number of taxa which have perfected durophagy in the Cenozoic suggests that shell-crushing has become a relatively more important form of predation on molluscs over the course of time. Westermann (1971) noted that the frequency of repaired shell injuries among Mesozoic ammonoids was less than the 19% frequency reported by Eichler and Ristedt (1966) for juvenile Recent *Nautilus pompilius*. Preliminary results from studies on repaired injuries in high-spired Cretaceous and Cenozoic gastropod shells (Vermeij, Zipser, and Dudley, in preparation) point to the same conclusion.

Moreover, drilling appears to be a relatively new form of predation invented by gastropods and octopods in the Late Cretaceous (Sohl 1969). Problematical perforations in Paleozoic shells, especially brachiopods, seem in most cases to have been made after death of the affected animal and therefore did not constitute predation (Carriker and Yochelson 1968; Sohl 1969). Even if the boreholes observed by Rohr (1976) in Silurian brachiopods of the genus *Dicaelosia* were made during the life of the brachiopod, they occur in less than 3% of the population, and were thus extremely rare compared to the holes made in Tertiary shells.

Infaunalization and Grazing

Stanley (1977) has summarized additional changes in the composition and structure of marine benthic communities through geological time. Foremost among the long-term trends recognized by him is what may be labeled an infaunalization of soft-bottom benthic animals, which becomes particularly noticeable during the Late Cretaceous. In the Paleozoic, many brachiopods and stalked crinoids lived on the surface of, or were partially buried in, subtidal muds. In the Mesozoic, the epifaunal reclining habit is commonly seen in inoceramid bivalves. From the Late Cretaceous onward, however, these epifaunal and semi-infaunal elements have been largely

replaced by infaunal forms (see also Rhoads 1970). Among bivalves, for example, there has been a relative decrease in the diversity of endobyssate (byssally attached semi-infaunal) forms since the Ordovician, and a corresponding dramatic increase in infaunal siphonate bivalves since the Paleozoic and especially the Late Mesozoic (Stanley 1968, 1970, 1972, 1977). Gastropods and echinoids exhibited a similar, disproportionate infaunal diversification in the Jurassic and Cretaceous (Kier 1974; Stanley 1977). All these changes may reflect intensification of predation or other sources of mortality at and above the sediment-water interface.

A further indication of this comes from architectural changes in the epifauna itself. Waller (1972) noted that most Paleozoic pectinacean bivalves (scallops) were characterized by prismatic shell structure; sculpture consisted of radial thickenings (costae). During the Mesozoic, shallow-water pectinaceans leading to the present-day Pectinidae became increasingly characterized by a foliated calcitic structure, which permitted the development of radial crinkles or folds (plicae). These, in turn, permit the necessarily thin shell of these swimming bivalves to be buttressed against what Waller (1972) believed to be an ever increasing number of shell-destroying predators.

Brachiopods today are found mostly in cryptic temperate and deep-sea environments but in the Paleozoic and pre-Cretaceous Mesozoic were dominant elements of hard- as well as soft-bottom epifaunal assemblages. C. W. Thayer has pointed out to me that, when a brachiopod which normally lives attached by a peduncle becomes dislodged by some external agent, it cannot reattach itself and is therefore far more likely to die than is a byssally attached bivalve, which can in principle re-establish itself after being torn loose. It is these byssally attached bivalves, together with the post-Permian oysters and other bivalves cemented with one valve to the underlying substratum, that have come to predominate in Mesozoic and Cenozoic epifaunal assemblages. In the same way, stalked crinoids are today restricted to the deep sea but were important constituents of Paleozoic shallow-water bottom communities. They probably cannot reattach once dislodged and gave way to other organisms in the Mesozoic. The only

surviving crinoids in shallow water are post-Permian comatulids which can change their position at will and are able to attach themselves facultatively by means of the cirri (see also Meyer and McCurda 1976).

Increased epifaunal predation may well be partly responsible for these far-reaching changes in benthic community structure (Stanley 1977; Meyer and McCurda 1977), but I am inclined to think that heavier grazing pressures have had a more profound influence (see also Garrett 1970). Two groups which today contain quantitatively important grazers, the teleostean fishes and echinoid echinoderms, have apparently been significant forces in shallow-water community structure only since the Late Mesozoic. Teleosts arose in the Triassic, but the critical morphological breakthroughs permitting them to browse algae, nip coral polyps, and scrape hard surfaces were not perfected until the Cretaceous (Schaeffer and Rosen 1961). The pycnodonts, an early (Jura-Cretaceous) holostean experiment in grazing and browsing, had teeth perhaps adapted for breaking off protruding parts of invertebrates (Romer 1966). (In a reinterpretation of pycnodonts, Thurmond (1974) suggests that the Jura-Cretaceous Gyrodus group was characterized by a shearing dentition, while the European Tertiary Pycnodus group had strictly crushing teeth adapted for feeding on small shelled invertebrates.) However, the scarids, acanthurids, kyphosids, and other typical grazers and browsers of tropical reefs are apparently of latest Cretaceous or, more probably, of earliest Tertiary extraction (see Hiatt and Strassburg 1960; Romer 1966; Hobson 1974). These fishes have a profound impact not only upon the algae which they eat, but equally on other epifaunal organisms which are scraped or sheared off the rock along with the algae (see, for example, Stephenson and Searles 1960).

Sea urchins (Echinoidea) arose no later than the Late Ordovician but were not common in intertidal or shallow-water communities until the latter half of the Mesozoic (Kier 1974; Bromley 1975). For example, they were not the important destroyers of reef limestone in the Paleozoic that they are in reefs of the present day (Newell 1957; Copper 1974). Like grazing fishes, echinoids scrape rocks bare of macroscopic algae and epifaunal animals and are known to have a profound in-

fluence on the composition and architecture of tropical as well as temperate hard-bottom communities (see e.g. Sammarco et al. 1974; Dayton 1975). The Aristotle's Lantern, with which hard surfaces are scraped by the urchin, began its development as the perignathic girdle in the Permian but was not perfected until shortly before the Maastrichtian in the Late Cretaceous, at which time the pentaradial traces characteristic of modern echinoid grazing first became common in shallow-water communities (Bromley 1975).

Grazing chitons and gastropods, which today have less impact on the epifauna than do sea urchins and teleosts (Stephenson and Searles 1960; Dayton 1975), have probably been present in shallow-water and intertidal communities since the Early Cambrian. Although certain deeply scouring limpets (post-Permian Acmaeidae and Patellidae) may be able to graze the algal turf to a lower height than can other gastropods, I doubt that grazing gastropods have contributed materially to the demise of the brachiopods and stalked crinoids, or to their restriction to cryptic or deep-water environments. The relative impact of other, post-Paleozoic and usually post-Cretaceous, grazers among crabs, mammals, birds, and reptiles has not been investigated thoroughly even in Recent communities and cannot be evaluated for ancient assemblages.

Other Mesozoic Changes

Reefs have developed at various times in the Phanerozoic, but post-Jurassic reefs differ in many important ways from all earlier versions of this community. Not only were rock-destroying fishes and echinoids absent or unimportant in Paleozoic reefs, but the structure of modern reefs is far more cavernous than that of Paleozoic and perhaps even Late Cretaceous rudist reefs (Jackson et al. 1971; Kauffman and Sohl 1974). Copper (1974) has noted that such fast-growing palmate or highly branched reef builders as the present-day acroporid and pociloporid corals were unknown in Paleozoic reefs. Skeletons of this type probably contribute heavily to the creation of caves and other interstices and did not arise among corals until later in the Cretaceous. Possibly they reflect more intense competition for light than was typical of reef builders in earlier epochs.

Two ecologically important communities, the sea-grass bed and the mangrove swamp or mangal, were not present before Late Cretaceous time (see Brasier 1975). The flowering plants which give these communities their names possess roots which stabilize and baffle the sediment, thus providing a habitat for a great diversity of marine organisms.

In benthic communities as a whole, many groups (echinoids, gastropods, bivalves, crustaceans, fishes) seem to have diversified dramatically beginning in the Middle Jurassic and continuing through the Cretaceous and Tertiary periods. This diversification is so widespread and pervasive that I am inclined to concur with Valentine (1969) that it is a real phenomenon and not merely the consequence of preservational biases (see Raup 1972 for a careful discussion on this point).

The alterations which affected marine communities during the Mesozoic were not limited to the benthos. Beginning in the Jurassic, there was a marked expansion in the diversity of marine microplankton, including the appearance of the first planktonic Foraminfera and Coccolithophorida; planktonic diatoms joined the assemblage in the Cretaceous (for a review see Lipps 1970).

Events on land are more spread out over geological time than were those in the sea. With the evolution of endothermy among therapsid reptiles in the Permian and probably dinosaurs in the Triassic came important alterations in trophic energy transfer which were to persist, with a short exceptional period in the Paleocene, to the present day (Bakker 1972, 1975). Dinosaurs evolved cursorial (fast-running) habits by Middle or Late Triassic time, and large cursorial vertebrates were important constituents of terrestrial communities throughout the rest of the Mesozoic and Cenozoic, again excepting the Paleocene (Bakker 1975). The only events on land which coincide in time with the Late Mesozoic marine reorganization are the evolution in the Early Cretaceous of angiosperms, their rapid rise to dominance in the Late Cretaceous and Cenozoic (Muller 1970), and the unprecedented radiation of insects which pollinated their flowers and ate their leaves (Ehrlich and Raven 1964). The diversification of birds may also be related to the rise of angiosperms and insects (Morse 1975).

Not all groups were, however, affected by

the Mesozoic reorganization. S. A. Woodin has pointed out to me that, judging from the meager fossil record, most polychaete families were established in the Early Paleozoic and that no significant or detectable morphological changes have taken place among the worms since then. Nuculacean bivalves, inarticulate brachiopods, and other groups characteristic of physiologically stressed or marginal environments seem also to have remained much the same morphologically through time. Although further, more detailed studies are required, it seems that the most profound changes affected communities in physiologically favorable environments.

Discussion

Throughout geological time, there has been a tendency in many skeletonized groups for morphologically simple, unadorned forms to give rise to, or to be replaced by, types with more elaborate skeletons. These elaborate forms are then largely obliterated in the major episodes of extinction, and the process begins anew. Thus, Valentine (1973) has commented that the skeletons of Lower Cambrian brachiopods, trilobites, and molluscs are often simple ("grubby," in his terminology), while Permian representatives often have elaborately sculptured or otherwise highly "specialized" skeletons. After the Permo-Triassic extinctions, Early Triassic fossils are once again simple, while Cretaceous skeletons are often bizarre and, in the case of ammonoids with complex sutures or irregular coiling, even a bit rococo. The frequent extinctions which have ravaged the planktonic world have affected primarily the elaborate and the adorned forms, and it is generally the morphologically conservative types which survive and rediversify after an episode of extinction (Lipps 1970; Cifelli 1976; Fischer and Arthur 1977).

Is this gradual process of skeletal elaboration and specialization comparable to the revolutionary events in the Early Paleozoic and Late Mesozoic? I believe not. The long-term skeletal specialization may be one expression of a continuing process of coevolution or coadaptation, in which predators increase their prey-capturing efficiency, while the prey are continually seeking ways to evade, repel, or otherwise thwart their enemies. Species less well adapted to the constantly changing biotic scene are more likely to become extinct or to be pushed into marginal habitats than are those which can successfully coexist with predators and competitors. In other words, the process which Stanley (1975, 1977) has called species selection may well account for the long-term trend toward greater predator-prey and competitor-competitor coadaptation. If this same species selection is to account for the Late Mesozoic community reorganization (Stanley 1977), then it is surprising that the various seemingly independent events contributing to it did not take place at widely different times but rather took place more or less in concert; and we must wonder why the critical adaptive breakthroughs either came so late in time or lay dormant for tens to hundreds of millions of years before spawning a major diversification. In other words, the Mesozoic revolution, recognized by the preferential survival of powerful consumers and well-armed prey over species less well adapted to predation, reflects unusually intense species selection; it upset the status quo which had been established since the Early Paleozoic. The species selection which prevailed during this long interval of "equilibrium" produced more powerful or more elaborate variations on a few adapted themes but produced very few new themes. Thus, I envision one of a few physical or geographical events as having permitted a degree of speciation and coevolution that would not have been possible under earlier conditions.

In the Early Paleozoic, we can point to several events which could have triggered, or at least greatly speeded up, the diversification of the Metazoa and the development of hard parts in many of their lineages. Skeletonization in the Cambrian is broadly correlated with the demise of stromatolites and with the greater activity of grazers, small burrowers, and perhaps predators (Garrett 1970; Awramik 1971; Stanley 1973). Rhoads and Morse (1971) have conjectured that these developments were made possible when the dissolved oxygen concentration exceeded about 1 ml O_2 per liter of water, since calcification at lower dissolved oxygen concentrations would have unacceptably compromised other competing functions involving calcium (see also Towe 1970). Stanley (1976b) has further suggested that the invention of sex late in the Precambrian promoted both speciation and

adaptive radiation, diversifying what by modern standards must have been a monotonous biota.

What features made the Middle Mesozoic earth so special that skeletal destruction developed or became more important among both predators and grazers in shallow benthic environments? In attempting to account for the concomitant burst of biotic diversification in the Middle and Late Mesozoic, Valentine (1969) and Valentine and Moores (1970) pointed to the breakup of continents beginning in the Jurassic and to the gradual steepening of the latitudinal climatic gradient during the Tertiary. These tectonic and climatic events created biogeographical provinces where only one or a few had existed before and thus promoted geographical isolation and subsequent speciation. Moreover, the resulting constant raising and lowering of geographical barriers would have led to even more isolation, differentiation, and eventual contact with species which had previously evolved under different biological regimes. This continual biological rearrangement and opportunity for speciation could promote coevolution and coadaptation and speed up the spread of a major adaptive breakthrough.

Speciation would have been even more favored if ocean circulation (and thus planktonic larval dispersal) were reduced during periods of high diversity (polytaxic episodes), as has been suggested by Fischer and Arthur (1977). Slow circulation and high diversity, moreover, were generally associated with high stands of sea level and, therefore, with large areas available for occupation by benthic and planktonic marine life (Fischer and Arthur 1977; Valentine and Moores 1970). It is important to remember, however, that episodes of provinciality had occurred in earlier epochs —the Late Ordovician and Permian, for example—without resulting in the kind of reorganization of communities witnessed in the Mesozoic.

The events which shaped the Mesozoic revolution probably took place in a tropical setting, since some of the most characteristic symptoms (intense grazing by teleosts, predation by crushing) are today predominantly warm-water phenomena (Earle 1972; Vermeij 1977). Hence, one could argue that the perhaps unusually benign climate during much of the Mesozoic (at least in polytaxic times)

created conditions favorable to the revolution (for a review of climate see Cracraft 1973). Again, however, it must be recalled that mild climatic episodes may have characterized the Devonian and perhaps other Paleozoic epochs without initiating major upheavals in marine community organization. Furthermore, intense grazing and predation by crushing are typical of Recent tropical marine assemblages despite a steep latitudinal gradient in climate and the large extent of temperate and polar oceanic waters.

In short, continental breakup and long-lasting favorable climate may have created conditions favorable to the evolution of skeleton-destroying predators and well-armored prey and had far-reaching consequences for benthic marine communities as a whole. Whether the Mesozoic era differed fundamentally from the Paleozoic in these respects remains to be determined, and the problem of dormant adaptive breakthroughs is not yet satisfactorily solved.

Lipps and Mitchell (1976) and Fischer and Arthur (1977) have independently pointed to the diversification of very large open-ocean predators during Mesozoic and Tertiary polytaxic episodes. During these times of high diversity and reduced oceanic circulation, the prey populations upon which the very large predators depended must have been large enough and stable enough to permit exploitation by a specialized animal. Many of the gigantic consumers became extinct during oligotaxic episodes (periods of low diversity and more rapid oceanic circulation) and were therefore only ephemeral elements in the community. In this way, they differ importantly from the benthic products of the Mesozoic revolution, since these animals persisted in spite of the periodic crises that beset the biotic world as a whole. The resources upon which the new predators depended were therefore more permanent and more reliable through time.

The gradual occupation of new adaptive zones may have contributed to the evolution of new and more specialized predators. Stanley (1968) has documented the invasion of deep sediments by shelled bivalves. Though this invasion began in the Early Paleozoic, it was primarily a Mesozoic phenomenon associated with the evolution of siphons through mantle-lobe fusion. This ecological expansion

may have led to an overall increase in the availability and abundance of prey protected by a hard shell. Whether such an expansion was independent of, or correlated with, the appearance of more specialized predators remains an open question.

Another example of a possible increase in shelled food supply, and of the occupation of a new adaptive zone, is the evolution and diversification of hermit crabs (Paguridea). These crustaceans, which are known from the Jurassic onward (Glaessner 1969), normally live in the discarded shells of snails but do not usually feed on the previous adult inhabitants of their domiciles. As a result, hermit crabs could have enormously extended the ecological life-span of the average snail shell, thereby dramatically increasing the number and abundance of shelled prey. This effect, which would be particularly strong in the tropics (where most hermit crabs live today), could permit predators to specialize on shelled prey where such specialization would have been trophically unfeasible before the hermit crabs arose. The propensity of shell-crushing fishes, crabs, and other predators (which take both hermit crabs and snails) to attack living gastropod prey too large for them to crush, a common phenomenon today (Vermeij 1976; Miller 1975), would be encouraged if attacks on hermited shells of equal size are sometimes successful. In such cases, the hermited shell may have been weakened by boring organisms, or the crab may be somewhat too large for its shell, thus being more vulnerable to successful attack than is the living snail which built the shell. Indeed, Rossi and Parisi (1973) have shown that hermited shells are more vulnerable to crushing by the crab *Eriphia verrucosa* than are conspecific shells inhabited by living snails. Shell characteristics promoting resistance to predators might become more strongly selected for as more predators assault the living shelled snail.

Just how much hermit crabs have added to the ecological life-span of a given gastropod shell may be difficult to assess in the fossil record, but it may be possible to show whether a given fossil shell was inhabited by a hermit crab before being preserved in the sediment. If, in any assemblage, most fossils bear evidence of having been carried by a hermit crab, it may be concluded that the ecological life-span of the shell is relatively long. If reliable criteria for hermit-crab occupation would be established, then the proportion of hermited shells in a given fossil assemblage may give some relative indication of the extent to which the supply of shelled prey is constituted by hermit crabs.

The evolution of hermit crabs would not explain why drilling was developed among predatory gastropods and octopods, since at least gastropods do not normally drill hermited shells. However, the adaptive expansion of the bivalves may possibly be connected with the development of this new method of predation.

Finally, the consequences of the Mesozoic community reorganization underscore the fact that what ecologists perceive as long-term equilibria in communities may from time to time be fundamentally shaken by revolutionary events. Not only is the functional architecture of component species in a community affected by these events but so are such community properties as species diversity and trophic structure. Certain modes of life become obsolete or restricted to a small number of marginal environments, while other adaptive zones are newly occupied and previously untapped resources are newly exploited. From present evidence, it seems that periods of equilibrium have been interrupted by destabilizing revolutions and that these revolutions are not strictly connected with the major biotic crises.

Acknowledgments

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