THE MESOZOIC MARINE REVOLUTION: AN OVERVIEW OF A BIOLOGICAL 'ARMS RACE'

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ABSTRACT

Vermeij (1977) in a brilliant introspection notices a sudden escalation of bloody battle between marine predators and their prey in Mesozoic. This rise of extensive predation set the evolutionary trend of many benthic groups, which continue even today. Though prey communities responded to a single cause, evolution followed diverse lines. Vermeij deals mainly with the different morphological trends of gastropods. We, here, in a preliminary investigation bring together subsequent case studies and notions ingrained in literature to see the impact of the Mesozoic marine revolution on other invertebrate groups. The effect appears to be quite stunning and holistic. It made the marine life wonderful for the second time in the history. Impact of the Mesozoic marine revolution was felt at different hierarchical levels and modes of evolution appeared punctuational, involving species selection. While intense predation pressure thoroughly reorganized the prey community, it did not ensue extinction at higher levels, like the mass extinction events caused by abiotic factors. Mass extinction events appear to have derailed the evolved trends of benthic communities by taking toll of the adaptive forms, which arose in response to the Mesozoic marine revolution. But, same antipredatory trends persist in the stragglers across the mass crisis boundaries, says K-T. This large-scale adaptive trend has puzzled Gould (1990).

INTRODUCTION

Life has two extremities – it originates and eventually dies. Between these two end points, life grows in case of an individual. At higher levels, i.e., species, genus or clade, life evolves. During evolution, life's progress may assume a direction known as evolutionary trend. Evolutionary trend may be defined as "persistent directional evolutionary changes" [see Glossary, Mc Namara (ed.), 1990, p. 353]. Various patterns of evolutionary trends emerge in lineages that are the artifacts of many factors. Palaeontologists, for example, debate continuously whether these trends are adaptive or not.

In the early days ever since Darwin, evolutionary trends were seen basically as an adaptationist programme. Organisms evolve and change in a particular direction because they gain advantage in which natural selection is the driving force. The great palaeontologist, Simpson (1953) proclaimed, "all long- and most short range trends consistent in direction are adaptively oriented." Against this view of panadaptation, many recent workers have advocated a non-adaptive explanation of the evolutionary trends. For example, Stanley (1975) envisaged that the evolutionary trends operate at many taxonomic levels (i.e., hierarchical) and that species selection instead of natural selection, is causally responsible for the large-scale macroevolutionary trend within any evolutionary lineage. Within-species change has nothing to do with the directionality of the lineage and microevoltuon is 'decoupled' from macroevolution. Gould (1990) suggested speciation and sorting as the source of

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evolutionary trends. According to him (Gould, 1988), changes of variance can explain many trends.

However, one biotically driven attribute appears to be the trend-setter for many groups. It is the Mesozoic marine revolution as envisaged by Vermeij (1977). The Mesozoic seas witnessed sudden appearance of a plethora of predatory taxa and this sent a red alert to the rival prey camp. Shallow marine benthic habitat was red with jaws and claws of fishes and crabs. Every new acquisition of weaponry of the offenders was countered by the victims by deploying various novel means of predatory avoidance. This protracted war resulted in a thorough organizational shake-up within the prey communities and many evolutionary trends quickly appeared, which Vermeij (1987) has called “escalation”, but all showed defensive strategies. However to Gould’s (1990, p.22) utter surprise, this hypothesis is based on adaptation and progression in Darwinian sense. Gastropods became mechanically sturdy, increasingly spinose and developed many other features as defensive measures against shell crushing. Bivalves and echinoids increasingly took refuge within the sediments and thereby becoming infaunas. Ammonites and nautiloids evolved shell rugosity to elude the jaws of death. Many other groups also responded to this great and sudden escalation of predation pressure. Does the Mesozoic marine revolution pertain to any single, sustained trend to every major group? No, it is rather the response of many taxa to a single cause (sudden rise of predators), but in their own ways. Therefore, while the Mesozoic marine revolution affected all organisms prone to predation, there appeared many directional trends with some even opposite in nature. It is not all pervasive, like Cope’s Rule (Stanley, 1973) showing a single, large-scale trend across many taxonomic groups.

THE MESOZOIC MARINE EVOLUTION

During Mesozoic especially in the Jurassic, there suddenly arose many groups of organisms in the seas as well as on the lands who were capable of killing efficiently other organisms, thus posed as formidable predators. Majority of marine predatory groups were small in size, but powerfully built and capable of destroying shells of prey communities. They adapted various feeding types – shell crushing, spearing, wrenching extracting of soft parts from shell etc. They mainly colonized in shallow water environments and adopted visually hunting strategies. Prey communities, which included mostly benthic organisms, were badly affected, and underwent a thorough shake up. Every morphological acquisition of the predators was countered by the development of characters, useful to predatory avoidance in prey communities. Powerful eyes capable of discerning colours and strong jaws capable of shell-crushing were disillusioned by the stunning mimicry, camouflage or infaunalization within sediments and “the increase in shell thickness and spinosity of snails matched with growing strength in the claws of crab predators” (Gould, 1990, p.22). This sustained hide-and-seek games between prey and predator led to the development of enormous pile of arsenal in both camps, which is uniquely coined as biological ‘arms race’ by Vermeij, (1977). The impact of sudden rise of predation was so far-reaching that many organisms crossed their ecological thresholds. Gastropods were forced to venture on land (i.e., Pulmonata) or remained afloat as nektoplanktons (Pteropoda) during the Jurassic since aquatic, especially benthic environments became inimical due to predation. Bivalves had to make excursion again to the fresh water bodies as shallow marine

Predators	Apperance	Mode of feeding
Asteroidea (including star fish)	Late Ordovician	Extraoral and intraoral digestion; molluscivore.
Dipnoi (fresh water lungfishes)	Devonian	Crushing; durophagous.
Heterodontidae (sharks)	Jurassic	Crushing; durophagous.
Batoidea (rays)	Jurassic	Crushing; durophagous.
Teleostei (Bony fishes)	Triassic	Crushing, wrenching, swallowing whole; durophagous.
Stomatopoda (Crustacean)	Jurassic	Hammering and spearing; durophagous.
Palinuridae (spiny lobsters) and Nephropidae (lobsters)	Jurassic	Crushing; durophagous.
Brachyura (crabs)	Jurassic	Crushing, apertural extraction; durophagous.
Aves (birds)	Late Jurassic	Crushing, swallowing whole, wrenching; molluscivores.
Cephalopoda (Ammonitina, Nautilina and Belemnites)	Jurassic	Crushing; durophagous.
Muricacea (gastropods)	Early Cretaceous	Drilling, apertural extraction.
Naticea (gastropods)	Triassic	Drilling.
Other Neogastropoda	Early Cretaceous	Apertural extraction; molluscivores.
Cynatidae (Mesegastropods)	Late Cretaceous	Apertural extraction; molluscivores.
Actinaria (sea anemones)	No fossil records	Swallowing whole.

Table 1. Appearance and mode of feeding of the predators which evolved during the Mesozoic (modified after Vermeij, 1977)

environments were infested with dreaded predators.

Vermeij (1977) in his seminal paper listed the origination of various kinds predators belonging to different taxonomic groups, which employ different feeding strategies (see Table 1).

He (1977) documented in detail the responses of the gastropods in the event of rapid increase in the intensity of predation pressure. He also briefly mentioned the reactions of other hapless preys. Since then, there is no serious and comprehensive attempt to evaluate the evolutionary trends within the other prey lineages except some well studied, but isolated case histories (e.g., Ward, 1981, for ammonites; Roy, 1994, for a subset of gastropods and Bardhan and Halder, 2000, for nautiloids). But, in literature, evidences of the effect of the Mesozoic marine revolution are implicit in other groups. Here, we shall assess the historical consequences of the bloody battles between the predators and the major marine prey communities.

GASTROPODA

Vermeij (1977) gave a detailed account of different solutions offered by the gastropods against predation since Jurassic. They developed diverse trends, exploited every opportunity to evade predation. Gastropods are preyed upon by various durophagous (shell crushing) animals and many of them appeared during the Jurassic (see Table 1). Besides, many extinct Mesozoic groups such as *Ichthyosaur*, mososaurid lizard and ptychodontoid sharks were also believed to be the important predators, which achieved durophagy by that time (see Vermeij, 1977 and references therein). Gastropods are hunted by the predators right from their early ontogeny and through out the phylogeny! Think of great internal asymmetry of gastropods, which is known as torsion. Torsion occurs at planktotrophic larval (valiger) stage and it brings the anus over the mouth, thus causing a great sanitation problem. This inherent disadvantage is borne by the gastropods since the Cambrian. But, at the same time the twist of the internal organs due to torsion enables gastropods to develop operculum at the posterior tip of foot. It allows mouth to first enter the shell when threatened by an approaching predator and the operculum comes last to conceal the aperture (see Stanley, 1975). Torsion thus protects the animal right from the valiger stage. A fortress is always vulnerable in the absence of doors. For the gastropod shell operculum is the fitting trap door! The most dominant evolutionary trend seen in the gastropod phylogeny from the Jurassic onward was against shell crushing. There was a decreasing trend of evolute, planispiral and umbilicate forms in archaeogastropods since the Jurassic. Non-umbilicate mesogastropods and neogastropods also greatly evolved in the later half of the Mesozoic (Vermeij, 1977). Open coiling, large umbilicus and high whorl expansion rate make gastropods more prone to shell crushing (Vermeij, 1976). These forms are even found today, mainly in fresh water or land where shell-crushing predators are lesser. Such forms, if present in marine environment are generally small in size, evidently to avoid durophagy. If the jaws (fishes) and claws (decapod crustacea) were the order of the Mesozoic seas, gastropods responded by developing mechanically more sturdy shells. Thick shell, strong nodes and elaborate spines appeared rapidly in post-Jurassic mesogastropods, neogastropods and neritaceans. Spines not only increase the effective size of a shell (thus small predators can be avoided), but also strengthen it against any breakage (Vermeij, 1974). Narrow, elongated aperture effectively restricts the entry of predators such as crabs, muricids and some other neogastropods which indulge in apertural extraction of soft parts of the victims as feeding mode. These novelties have been the predominant trends of many gastropods since Cretaceous. Vermeij (1977) noted apertural dentition as primarily an anti-crushing device, but it appears that dentition seems to provide some sort of a holdfast for the soft body parts against apertural extraction. Co-occurrence of slit-like aperture with denticulated lips in many groups e.g. *Cypraea* (Cowrie), *Cassis* (helmet shell) and cymatiids (tritons) or collumelar plica e.g. in *Turbinella* (the great Indian blowing conch, also used as bangles by married women) speaks for its additional function. External features being species specific and easily recognizable, were targeted extensively by the predators and therefore, there was a tendency to conceal it by a mantle envelope (e.g., *Cypraea*) or losing it altogether (e.g., nudibranchs) as seen in present day oceans. Remarkably, this trend also developed since Jurassic (see Portmann, 1967). This phenomenon has been interpreted as failure of the shell to act as a place of refuge. The shell loss is commonly associated with a great speed or development of an obnoxious and acidic secretion as a means of protection (Vermeij, 1977; Peel, 1987).

Subclass Pulmonata, include terrestrial gastropods or secondarily fresh water dwelling groups. They evolved and quickly diversified during the Mesozoic. They are detorted groups with mantle cavity vascularized to act as air breathing lung. This rapid change and ecological breakthrough in a molluscan group to become land dweller are significant. We believe that this is no coincidence that their origination took place in Mesozoic when intense predation pressure made the marine substrate nearly inimical for benthic groups and perhaps forced some of them to venture on land. It is worth noting that some prosobranchs and opisthobranchs also began to inhibit land and fresh water at the same time. It is evident that marine substrates became increasingly inhospitable as many predators although appeared in the Jurassic, achieved durophagy in the Cretaceous or later in the Early Tertiary. Besides, there were many grazers and browsers, e.g., teleostean (bony fish) or holostean (the pycnodonts), sea urchins (echinoids) and many gastropods. Majority of them continue even today. The fishes which feed on algae, have shearing dentition capable of breaking off the protruding parts or crushing the whole shell of smaller size. Sea urchins are chief destroyers of today's coral reef and associated fauna. Many opisthobranchs and prosobranchs are grazers and carnivorous, feeding on cniderians and other benthic animals. As a result benthic habitat became very stressful since the Cretaceous. The gastropod evolution reached its real acme in the Tertiary with the great diversification of siphonate neogastropods. Along with them evolved another new ecologic group i.e., pteropods in the early Tertiary. They were tiny, pelagic opisthobranchs found in great numbers in rock record as deep-water pteropod ooze. We speculate that evolution of pteropods took place as an escape reaction from benthic ecology in response to intense grazing. Many gastropods pass through different plankotrophic larval stages during ontogeny. In valiger stage of larval development when torsion occurs, they have a thin nucleus shell with a peculiar wing-like organ called velum. Velum, which is modified into foot during adult ontogeny of benthic gastropods, acts as a swimming device. It is studded with numerous cilia, which by means of continuous stirring helps in swimming. Pteropods retain all these larval features including pelagic life, but they are adult. This clearly indicates that they were paedomorphically, especially progenetically derived and thus escape benthic life mode during the late ontogeny of their ancestors. Intensity of predation was such that every order of opisthobranchs and prosobranchs had their pelagic representatives.

BIVALVIA

Bivalves, a major class of Mollusca, constitute the dominant benthic prey community of today's oceans. Scores of millions of dead bivalve shells litter the intertidal areas to suggest their great success. If we look closely, we shall see that majority of them are siphonate infaunas – a morphological as well as ecological novelty, which was not present right from their appearance in the Cambrian. Bivalves are headless, eyeless and retain many other characters of primitive molluscs. They are simple, yet they are ecologically specialized and diverse. If diversity and abundance are the measures of evolutionary success of any animal group, bivalves are the 'advanced' group and 'progressive' too (see also Gould, 1986).

Diversity at any hierarchic level (e.g. genus or family) in the bivalve phylogeny has increased ever since the Ordovician. Even the great mass extinction events could not perturb the ever-increasing trend. Sudden demise of many groups was quickly replenished by a burst of evolution, thereby restoring the background value (see Miller, 1990, fig. 6.1D). Therefore, it will not be understood from the diversity curve that what was the impact of the Mesozoic marine revolution in the bivalve community since the Jurassic. The effect lies elsewhere.

During Palaeozoic, especially after the great burst of radiation in the Ordovician, bivalves adapted to various modes of life and feeding strategies. These were mainly epifaunal, endobyssate and shallow burrowing groups, having adapted to both suspension and deposit feeding types. Throughout Palaeozoic, although relative diversity fluctuated, endobyssate group dominated the adaptive landscape of bivalves. After the Permian-Triassic boundary mass extinction episode and especially from Jurassic onwards, the relative percentage of the endobyssate group fell dramatically and diversity of free burrowing ecologic group increased greatly (Stanley, 1968, 1977). Earlier, the infaunal groups had included mainly mucous-feeding bivalves (e.g. Lucinaceae) or very shallow burrowers that lay near the sediment-water interface. It was in early Mesozoic times that the bivalves with true siphon flourished. Siphon is formed by the fusion of the posterior parts of the mantle and has a tubular and muscular extension. It allows the burrowing bivalves to communicate with the external world above the substrate. Stanley (1968) described the development of siphon as the key innovation of the Mesozoic bivalves. Siphon and the presence of strong, muscular foot enabled the bivalves to become deep infauna. Great number of bivalve superfamilies having characterized by heterodont and desmodont dentition evolved during the early Mesozoic. Clarkson (1999, p. 212) observed, “Indeed the second great expansion of the bivalves during the early Mesozoic and continuing through out the Cenozoic was directly due to the fact that they could burrow”.

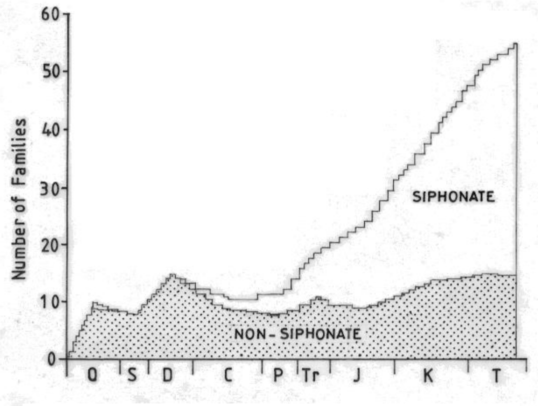

Fig. 1. Changes of diversity of siphonate and non-siphonate burrowing bivalves through ages (after Stanley, 1977).

But why did this great diversification wait for a long time (siphonate groups although many of them were mucous feeders, originated in the Late Palaeozoic, see Stanley, 1977, 1979) and take place only during the Jurassic (see Fig.1)? We have already mentioned that intense grazing and shell crushing by the predators that made life hard for the benthic preys during the Late Mesozoic. The sudden rise of predation sent a red alert to the whole benthic community and triggered a thorough reorganization of the earlier morphology and ecology. Many groups, for example, gastropod resorted to planktonic life or made excursion to fresh water or even to land. But the most dominant trend taken up by many unrelated groups, even different phyla, was the infaunalization during Jurassic and Createaceous times. Many gastropods even adapted infaunal life habit and underwent great diversification (Vermeij, 1977). An entirely new morpho-ecologic group, showing great diversity, evolved within the echinoids, i.e., Irregularia (Kier, 1974, 1987 and see below) and Stanley (1977) noted a dramatic rise of the siphonate, infaunal bivalves.

Both Stanley (1977, p.200) and Vermeij (1977, p. 225) were not certain to single out predation as the prime causal factor for bivalve diversity. Stanley (1979, p. 293) saw basically predation as a ‘braking mechanism’, which slows down the evolutionary rate of speciation and/or promote extinction. While explaining the gradual decline of the endobyssate bivalves during the Palaeozoic, he attributed predation as the sole cause. Many higher taxa according to him (Stanley, 1979, p. 293) radiated in the absence of predation. Again, elsewhere, he (p. 204) suggested that predation pressure of less intensity can accelerate diversification. However, concomitant rise of many predatory animals and great expansion of many benthic prey communities during the Jurassic deserve special notice. Moreover, many of these prey showed parallel evolutionary trends towards infaunalization at the same time. For gastropods and echinoids, it is convincingly shown that predation was the cause. Modern bivalves are devoured by the every predator that arose in the Jurassic (see Table1). They are killed by means of crushing, spearing, swallowing of the whole body and more importantly by drilling predators. Two important predatory drilling gastropods i.e, muricids and naticids achieved this capacity in Cretaceous. Many dead bivalve shells of the present day oceans bear characteristic boring marks made by these drilling gastropods.

Infaunalization includes invasion into two ecological regimes – soft sediments and hard substrates. In soft sediments digging is done by muscular foot. Hard bottom penetration is achieved through mechanical boring by shell rotation or acid secretion. It is not an accident that boring bivalves also appeared in the Jurassic (Pojeta, 1987).

CEPHALOPODA

Vermeij (1977) noted the existence of heteromorph (irregular coiling) shell within the Palaeozoic and the Mesozoic cephalopods and speculated that if these forms had continued today they would have been restricted to the deeper water, which is less frequented by the predators. But, many regular nautiloids and ammonites along with belemnites survived till the end of Cretaceous and faced the brunt of the sudden rise of predators during the Mesozoic. How did they respond to such hostility? We here examine all the major subclasses of the Mesozoic cephalopods.

Ammonidea:

Contoured frequency diagrams of Raup and Stanley (1985, fig8-2, 8-3) elaborated later by Ward (1981, fig. 2.6) show that the best-fit design adapted by ammonites throughout their career is an involute form with elliptical whorl section. Functionally, this streamlined shape is hydrodynamically more efficient, allowing ammonites a quicker movement in the water. In addition, it may appear that like in the gastropods, open coiling of cephalopods is vulnerable to predation. In contrast, involute shell, which protects the more fragile early whorls, might have been a defensive measure against predation during the Mesozoic. But older groups, such as the, Late Paleozoic order Goniatitina were more involute (see Raup and Stanley, 1985, fig. 8-3) than the true Mesozoic ammonites. Contemporary nautiloids were also more involute than the Jurassic-Cretaceous ammonites (see Ward, 1981, Fig. 7). Besides, many evolute ammonites persisted and diversified, and heteromorphs were abundant in the post-Triassic oceans. It seems that shifting of morphospace within ammonite phylogeny towards the optimally designed involute shape speaks for rather better hydrodynamic efficiency and distinction of adaptive peaks of nautiloids and ammonites was the result of the biotic competition (see also Ward, 1980). Ammonite's planispiral baüplan has a finite limit and is constrained mainly by growth. Variation in shell form occurs by the interplay of three Raupian parameters i.e., degree of involution (D, distance of generating curve), inflation (W, rate of whorl expansion) and shape of the generating curve (S) (Kennedy and Cobban, 1976) and the gross shell form shows homeomorphism, which is common place in phylogenetic history of the ammonites. Ward (1984), therefore, explored the possible counter measures taken up by the ammonites against predation in another line of investigation – shell sculpture. Ammonites are brilliantly ornamented by ribs, tubercles and spines and in the past they were the collectors' pride. Palaeontologists interpreted functional significance of ammonites shell sculpture in various ways ranging from hydrodynamic efficiency (Chamberlain and Westermann, 1976), withstanding ambient hydrostatic pressure (Spath, 1919), better buoyancy regulation (Teichert, 1967; Kennedy and Cobban, 1976), resistant against predation and impact with the substrate (Westermann, 1971, 1990), sexual display (Kennedy and Cobban, 1976) and camouflage (Cowen et al., 1973).

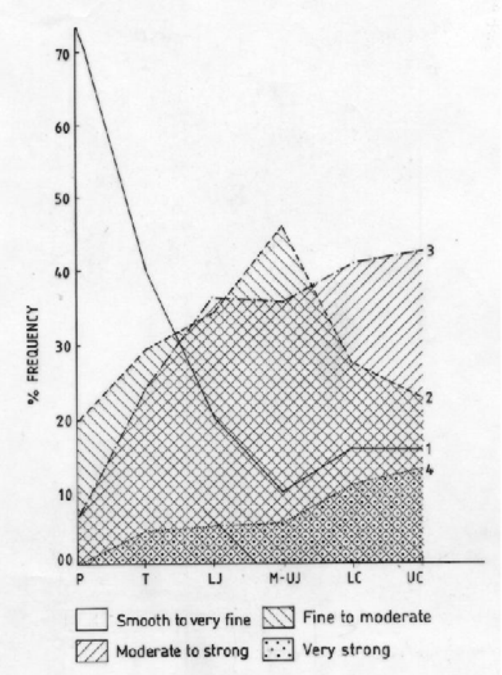

Fig. 2. Frequency distributions of categories of rib patterns of ammonites during Late Palaeozoic and Mesozoic (modified after Ward, 1981)

While all these functions of ammonite ornamentation are feasible, Ward (1981) has singled out predation as the sole cause for the increasing shell rugosity in the Mesozoic ammonites, which evolved as a defensive adaptation. Ribbing on ammonite shell increases resistance against shell breakage; for the same shell thickness, corrugated part would be stronger than smooth shell against the point-load exerted by toothed predator (Westermann, 1971). Kauffman and Kesling (1960) reported a famous case where a specimen of *Placenticeras mecki* of the Cretaceous was bitten several times by mosasaur reptile. The shell was punctured, but not crushed. Though genus *Placenticeras* has numerous species, except one species in Bagh, central India, none have their apertural margin preserved (see Klinger and Kennedy 1989; Gangopadhyay and Bardhan, 1998). This indicates perhaps that they had been suffered from extensive predation. Bagh Sea in India during the Coniacian was deep inland and placid in nature. This attributed to less hostility of the normal marine predators and a single species, i.e., *P. kaffrarium* almost monopolized the Bagh sea. It has many specimens having their peristome intact (see for detail, Bardhan *et al*, 2002).

Apertural breakage of ammonite shell by decapod crustaceans and repairing of the injuries have also been reported (Roll, 1935; Thiermann, 1964 in Ward, 1981). Many ammonite fossils have been found with shell injuries done by predators or by defensive efforts of their prey (Ward and Wicksten, 1980). The nature of ribbing during Mesozoic was mostly radial. This would align the brekage parallel to the peristome margin and cause less damage to the body chamber. Apertural thickening by internal ridges (i,e. pseudoconstriction, see Westermann, 1990) increased the mechanical strength against the shell crushing. Presence of spine at the peristome is primarily seen as either a mechanical protection against apertural extraction of the soft parts by the predators (Kennedy and Cobban, 1976) like that of gastropods (see Vermeij; 1977) or as a sensor because these spines are mainly hollow and delicate (Westermann, 1990). Ward (1981) has shown an evolutionary trend of the increasing strength of ammonoid shell-ribbing during the Mesozoic (Ward, 1981, present fig. 2) and highest incidence of nodose and spinose forms occur during the Cretaceous. His main argument was the timing of appearance of the increasing strength of shell rugosity. While ribs of varying strength were present since Palaeozoic, there was a dramatic increase of the ribbing strength in the Middle Jurassic, which continued with accelerated pace till the end of Cretaceous. He therefore, supported Vermeij (1977) and mentioned that the trend of shell rugosity in ammonites also orchestrated the trend in other invertebrate groups.

We have mentioned about the other usages of the ammonite shell sculpture and they appear to be also quite reasonable. Presence of ribbed shell might convert the nature of water flow from laminar to turbulent boundary layer flow, thereby increasing the "streamlining" and hydrodynamic efficiency (Chamberlain and Westermann, 1976). The prominent spines are hollow or even septate in some cases (see Kennedy and Cobban, 1976) to increase buoyancy. We believe that the ornamentation of ammonites initially evolved to serve various functions or it had multiple uses. The function of the same sculpture also differs from taxon to taxon (Westermann. 1990). But, due to the escalation of predation during the Mesozoic marine revolution, the current utilities were either suppressed or played a secondary role. The ornamental rugosity was channelised to serve only one function i.e., protection.

If the ratio between the rib width and the shell diameter of ammonites exceeds 0.05, the hydrodynamic efficiency of the shell decreases (Chamberlain in Ward, 1981). The coarsely ornate Jurassic and Cretaceous ammonites had greater magnitude than this critical value, and thus seemed to have sacrificed speed for protection. Many ammonites were thoroughly ornamented, but shell ornamentation on their phragmocones rather lowered the strength against the ambient hydrostatic pressure. A smooth shell with circular whorl section was the most adaptive design (Westermann, 1990). Yet, the ornamentation in young was crucial for survival against predation.

Ornamentation may also be an expression of the genetic variability within a population. Many ammonite species show great intraspecific variation. Often there is a positive correlation between the degree of inflation and strength of ornamentation (Westermann, 1966). The Coniacian *Placenticeras kaffrarium* of the Indo-Madagascan Faunal province shows stunning intraspecific variation – from smooth, slender and oxyconic *umkwelanense* variant to tumid *kaffrarium* variant with three rows of tubercles – leading to an ornamental polymorphism (Klinger and Kennedy, 1989; Bardhan *et. al*., 2002). The ornate variant here clearly had an extra adaptive edge over the smooth sympatric variant. Widely variable populations were not generally under strong selection pressure (Seilacher, 1972). But in later phylogeny of the family Placenticeratidae, a trend of increasing rugosity and body size (the youngest species during the Campanian attained diameter of about 1 m, see Emami *et. al*, 1984 in Klinger and Kennedy, 1989), which were hypermorphically derived (Kennedy and Wright, 1985), was set. In a well-developed sexually dimorphic species, microconch is generally strongly ornamented up to the end of the body chamber whereas the macroconchiate body chamber may be devoid of any ornament (Callomon, 1963, Jana, 2002). But this genetic character of microconch may be transmitted to descendant species, which has both sexual morphs thoroughly ornamented. In this way higher taxonomic group may appear through macroevolution (cf. Stanley, 1979). Such was the case for subfamily level transition from Macrocephalitiane to Eucycloceratinae during the Middle Jurassic (Jana 2002, Jana et al., in press). There are many similar instances where ornaments had appeared intrinsically, not as a product of natural selection. But, these sculptures were later co-opted as defensive measures against predation (Bardhan and Halder, 2000). Gould and Vrba (1982) decribed this phenomenon as "exaptation". Prominent and slender spines on body chamber might develop merely due to ontogenetic scaling (Checa, 1985). These spines as in productid brachiopods, then played a secondary role for protection and perhaps as camouflage (Westermann, 1990). Isolated mutations or developmental constraints (mainly heterochrony) initially induced important morphological changes and trends are 'exaptive expansion' (cf. Gould, 1990) guided by extrinsic factors (here biological, i.e, predation). Dommergues (1990) described such trends in many Jurassic ammonites.

Ammonite diversity patterns have a fluctuating history; after a sudden crush at Permo-Triassic boundary, the diversity roared to explosive adaptive radiation during the Mesozoic. The Palaeozoic goniatiids gave rise to Triassic ceratiids from which rapidly evolved the true ammonites (having ammonitic suture) after the end-Triassic mass extinction. Jurassic is often called the "Age of Ammonites" (more than 650 genera highest ever for any period). The great and sudden diversification of the new and last order Ammonitina was associated with many new novelties other than suture. One was the prevalence of strong and widespread sexual dimorphism. In sexual dimorphism, the sexes are not only separate, the males and the females differ from each other at least in size. This size dimorphism of ammonites is known as early as from the Devonian. However, from the Jurassic onward dimorphism is characterised by size, nature of coiling and ornamentation. The males that are smaller (called microconch) are not only more strongly ornamented than the larger females (called macroconch), they have bizarre structures like the rostrum, and lappets etc., at the aperture and are more aberrantly coiled. The disparity between two sexes is so great that palaeontologists took about 100 years to understand that they are the two sexual variants of same biological species. The microconchiate characters are variously interpreted as sexual characters, sexual display (see Kennedy and Cobban, 1976) or helps in mate recognition (Jana 2002; Jana et al., in press). Westermann (1990) believes that well developed dimorphism implies ecological niche partitioning. Majority of the ammonite groups are currently interpreted as having nectobenthic life mode in shallow water where they faced stiff competition for food. He mentions that the shallow water ammonites are strongly dimorph while the pelagic groups (e.g. phylloceratids and lytoceratids) have no or poorly developed dimorphism. Ammonites inhabited in the shallow water shelf environments since the Palaeozoic. Though there had been no ecological shift during the Jurassic, yet we get pronounced shell dimorphism in all Jurassic and Cretaceous families (Donovan et. al., 1981; Klinger and Kennedy, 1989).

Vermeij (1977, 1987) has shown that the great predation during the Mesozoic marine revolution did not act as an agent of death in the long run; instead, prompted great diversification of many new and existing groups in which sex prevails. Evolution of sex is primarily seen as a caterer of evolutionary radiation. It provides wide range of genetically derived intraspecific variation within a population upon which natural selection or drift can work. The Late Precambrian metazoan evolution is perhaps associated with the origin of sex (Schopf et. al., 1973) and so also the Cambrian explosion of all the modern day bisexual phyla (Stanley, 1979). The Mesozoic ammonites were not only diverse, they were characterised by rapid turn over and equally dominant evolutionary bursts, which made them “biological stopwatches”. Excellent biostratigraphic zonation of the Jurassic System of rocks is possible only because of the scores of short-lived, ephemeral ammonite species or genera. We believe that even within bisexuality, dimorphism has more evolutionary potential because here, outbreeding takes place between parents who are quite dissimilar, resulting more variation in the population. More ornamental rugosity of microconchs would play major role in the evolution within lineages and there would be a phylogenetic slant towards the increasing strength of the shell sculpture, if these were found to be resistant to crushing. This exactly happened during the Jurassic. Stanley (1979) stresses that sex plays more important role in macroevolution. Rapid origination of higher categories is only possible by quick speciation events, which again can only be accomplished by sexual taxa. The early Middle Jurassic times witnessed the appearance of many superfamilies showing evolutionary increase of shell sculpture. Nektobenthic habitats of the shallow water were for the first time infested with many rapidly rising predatory groups. Other molluscs solved it by various ways as discussed above. Ammonites responded by increasing the strength of ornament and great diversification. This was possible because ammonites adopted a new kind of reproductive strategy — strong, ornamental dimorphism. It is remarkable that records of the earliest sexual dimorphism in other cephalopods such as nautiloids (see Bardhan and Halder, 2000) and coleoids (Doyle, 1985) appeared in the Jurassic (see discussion below).

Did ammonites belong only to the prey community? The order Ammonitina that appeared only during the Jurassic had many novelties. These are widespread and elaborate sexual dimorphism just mentioned and the calcified jaw structure known as aptychi. Early ammonites had chitinous anaptychi from which the Jurassic aptychi evolved and eventually replaced it. This change over as well as the various types of strongly ornamented calcitic aptychi suggests a new kind of feeding strategy (Kennedy and Cobban, 1976). Structurally aptychi resemble jaws of present day *Nautilus* or octopuses which are active hunters of the bottom dwelling crustaceans. Crabs resist nautiloid predation by chelae and often break the peristome of the *Nautilus* in a manner much similar to that found in the ammonite shells. Ward (1981) has therefore reasons to speculate that the ammonites especially of the Cretaceous used to prey heavily on various and large size crustaceans. Claws in crabs, spines in lobsters and other armors arose primarily as defense adaptation and they later turned into formidable predators (for detail, see Crustacean section).

We also believe that ammonites being most diverse in the Jurassic park under the sea and having been equipped with prehensile tentacles, well developed jaws, eyes and a capacity to have extensive and complex courtship ritual (if lappets are a product of sexual selection), were intelligent and important predatory animals. They adopted visually hunting strategies like fish and occupied higher level at the food web. As it often occurs, the hunter becomes a victim of other group, ammonites took care of defense by increasing the shell rugosity. Many aptychus closely conform the apertural outline of the ammonites, but anaptychi never closely match. This led Kennedy and Cobban (1976) and others to believe that aptychi acted secondarily as an operculum to protect soft parts from any possible attacker (for different view see Lehmann, 1981).

Nautiloidea:

Among the post-Triassic nautiloids, many genera are characterized by transverse ornamentation, believed to have evolved independently in many families. Tintant and Kabamba (1983, 1985) and Tintant (1989) attributed this to adaptation. According to them ribbing evolved gradually in response to a change in the habitat. Bardhan and Halder (2000), on the other hand, believe that ribs were formed by crowding of growth lines, as a corollary to changes in body size during paedomorphic evolution. Initially the ribs had no direct functional significance. Detailed study of the origin and the nature of ribbing patterns in *Paracenocerous,* one of the earliest post-Triassic genera, led them to draw some general conclusions about the phylogenetic history of ribbing in nautiloids. These ribs appeared suddenly in a species, *P. jumarense* in the Late Bathonian of Kutch, Gujarat, in a manner compatible with the punctuational model of evolution (Gould and Eldredge, 1993). Some other contemporary genera are also found to have similar ribbing patterns. The ribs were initially weak and restricted to either the flanks or the venter of the adult body chamber. They evolved essentially as an evolutionary by product, perhaps serving no functional purpose. Subsequently, the nautiloid ribs became progressively stronger, extending all around the shell like those of the contemporary ammonites. The frequency of the ribbed taxa and the strength of ribbing increased in later nautiloids (fig.3), paralleling the trend in ammonites (Ward, 1981). This is believed to be an adaptive response to the Mesozoic marine revolution (Bardhan and Halder, 2000). Ribbing, though not adaptive at first in the nautiloids, was subsequently co-opted as a defensive adaptation. The evolution of this structure is a good example of exaptation (Gould and Vrba, 1982).

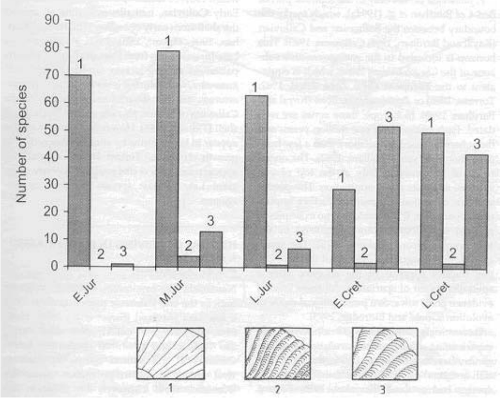

Fig. 3. Frequency distributions of categories of rib patterns, (1) fine, (2) moderate and (3) strong in species of Jurassic-Cretaceous nautiloids (after Bardhan and Haldar, 2000)

Coleoidea:

The subclass Coleoidea of Cephalopoda is represented in the present day seas by the squids, cuttlefishes and octopuses. They are dibranchiate, having internal shells. In octopus it is lost altogether. Except belemnites the fossil record of Coleoids is poor. Coleoids doubtfully appeared in Devonian (Engeser, 1990). Recently, Engeser and Bandel (1988) and Engeser (1990) revised the coleoid classification and subdivided them into two orders, extinct *Belemnoidea* and *Neocoleoidea* [it has two extant groups, the *Octopodifarmis* (eg. Octopus) and *Decapodifarmis* (squids, sepia etc)]. Belemnoidea were represented during the Paleozoic by aulacoceratids and phragmoteuthids. The Triassic aulacoceratids e.g., *Aulacoceras* and *Ausseites,* had covering, called guard or rostrum, on the tip of the phragmocone. The rest of the phragmocone along with the small guard was believed to be enclosed by the mantle as found in the endoskeleton of the present day coleoids. Aulacoceratids and phragmoteuthids continued up to the Early Jurassic (Engeser and Bandel, 1988). Belemnites sensu stricto suddenly appeared during the Jurassic and continued upto the end of the Cretaceous. In belemnites, body chamber was reduced to pro-ostracum and the guard became an enormously large, a massive, bullet-shaped cylinder of solid calcite. It resides at the posterior part and encloses the whole phragmocone. Phragmocone is a hydrostatic organ and is also present in other cephalopods such as nautiloids, ammonoids and orthocone cephalopods. Some workers believe that orthocone cephalopods were vertical migrants in water. Addition of external thickening as guard initially acted as a counter weight to maintain a horizontal disposition of the body while swimming. But, why the Jurassic-Cretaceous belemnites had massive guards covering the whole skeleton? It is conceived that the guard or the rostrum in the Triassic *Aulacoceras* was used not only to counterbalance the buoyant phragmocone but also to protect young shell (Swinnerton, 1950) — a step against high juvenile mortality owing to predation. So it can be considered to be a case of exaptation. To protect only young was not enough when predation pressure accelerates. Aulacoceratids became extinct in the early Jurassic. It is significant that belemnites being better equipped with the armour, i.e., their rostrum, evolved not only in the Ealy Jurassic, they also rapidly diversified. Predation on belemnites was perhaps intense. Rostra of many species bore injury marks those were subsequently repaired (Bandel and Kulicki, 1985). Holder (1973) found tooth scratches probably made by marine saurians on the live belemnite rostrum. They are believed to have been extensively predated by the Mesozoic marine reptiles such as *Icthyosaur* and large toothed fishes (Ager, 1976). Jurassic sharks were also eminently suited to a bellemnite diet. In a famous discovery from the Lias of Germany, a Mesozoic shark belonging to the genus *Hybodus*, has been found to contain more than 200 belemnite rostra in its stomach (Jordan *et al*., 1975) Belemnites were also active predators; they fed on smaller organisms (Morton, 1971; Young and thompson, 1976). Belemnites, equipped with hooks on all ten arms and eyes with lens (Engeser and Bandel, 1988; Engeser, 1990) were capable of visual hunting. All recent coleoids are active predators, feeding on bivalves, crustaceans and small fishes. It is, therefore, believed that the Mesozoic belemnites occupied an important position as carnivores in the trophic chain.

Since, they were also extensively predated by large fishes and reptiles, rostrum which enclosed phragmocone completely in belemnites, evolved rapidly as a defense mechanism. Significantly, the Jurassic belemnites were also found to be sexually diamorphic (Doyle, 1985). Like ammonites and nautiloids, they too seemed to employ sex as an adaptive strategy to diversify (Donovan and Harcock, 1967; Stevens, 1973). They continued with much vigor till the end of Cretaceous when, like many other taxa, they fell victim to the major mass extinction event. This catastrophy shifted the evolutionary trend within the phylogeny of Coleoidea. Neocolioidea which remained insignificant during the Cretaceous, suddenly went into great adaptive radiation at the beginning of Tertiary (Engeser, 1990). They quickly diversified, perhaps to exploit all the vacated niches left by the ammonites and belemnites, once their formidable competitors. Subsequently, evolution progressed mainly in two directions. One was the reduction of guard. The shell underwent rapid degeneration resulting in the total loss of the shell. Another trend led to the early loss of rostrum, decrease in phragmocone size and finally, the development of lanceolate pro-ostracum, which is still found in present day squid, *Loligo*.

Intensity of predation appeared not to have been stalled after the K-T boundary mass extinction since there arose different kinds of predators in the Tertiary marine waters (Vermeij, 1980). The reduction of shell or its internalization, also took place in many gastropod groups of the Tertiary, as a reaction against extensive predation on shelled prey. This loss has been interpreted as a de-emphasis of the shell as a protecting device. It is commonly associated with great speed (e.g., squids) or with toxicity and unpalatability.

BRACHIOPODA

What are the attributes that control diversity, evolutionary trends and dominance of a lineage? The great decline of brachiopods from the major shallow water benthic constituents of Palaeozoic to highly reduced ones in Late Mesozoic onwards, has been explained by causal factors, like their competition with bivalves, and the evolutionary consequence of their great dying because of the Permo-Triassic boundary mass extinction.

Brachiopods appeared during the Cambrian and then quickly diversified in to three subphyla, which still continue. By the Devonian, brachiopods were most diverse (see Rowell and Grant, 1987, present fig.4) and they dominated the entire shallow water community throughout Palaeozoic. The Permian brachiopods underwent a great adaptive radiation. They were not only diverse and the most abundant fossils of the shallow deposits of the world, they also made an important ecological breakthrough. Brachiopods are filter-feeder, sessile benthos. They have various life modes; majority employ pedicle as means of attachment. Many strophomenides and some spiriferides were free lying. Less common brachiopods are encrusted and epiplanktonic inhabits. During the Permian, productides crossed the previous ecological threshold to invade a new zone i.e., infaunal niches. Productides adapted to quasi- to fully infaunal life. The spines in adult pedicle valve helped them anchor firmly within sediments, and a concave brachial valve received sediments settling from above. In *Waagenoconcha*, a Permian genus, brachial valve developed small, delicate spines to prevent removal of sands from the surface by strong currents (Grant, 1966). Brachiopods thus would, become fully covered and be well camouflaged (Clarkson, 1999, fig.7.17e). This clearly indicates that productides adapted to infaunal life for protection and competed well with the nonsiphonate infaunal bivalves. Besides, other groups showed 'great evolutionary plasticity' and colonised in reef environment. Many of them looked bizarre, 'unbrachiopod-like', but all were highly adapted to their respective niches (Rudwick and Cowen, 1968).

Alas, brachiopods were worst hit by the great Permo-Triassic mass extinction and productides became completely extinct. Extinction thus removed the best-adapted taxa from the brachiopod phylogeny. Rhynchonellides, terebratulides and few others managed to straddle past the crisis boundary and subsequent brachiopod evolution was directed to their ways. They diversified during the Jurassic, and by the Cretaceous they were abundant in shelf environment including shallow waters, but were localized. Since then, the brachiopods lost their dominance in shelf habitat, which was instead successfully colonized by bivalves. Brachiopods are now found in deep and cold seas. While there were 4500 fossil genera, and they are currently restricted to only 100 living genera. This speaks for a great fall of their diversity and a shift of ecology from shallow to deep waters since the Mesozoic.

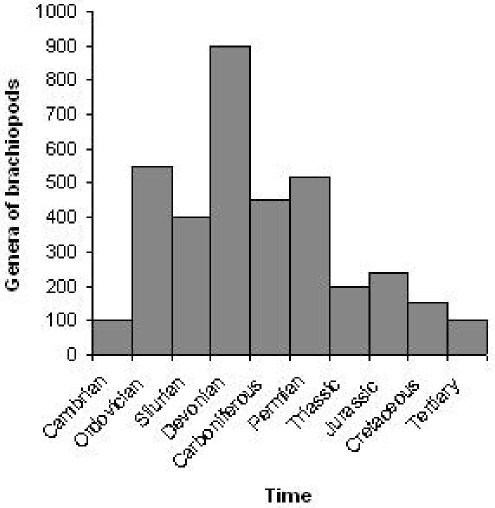

Fig. 4. Changes of diversity of Brachiopoda with time (after Rowell and grant, 1987)

Why did brachiopods fail to reestablish their supremacy in shallow water environments? Many hypotheses have been put forward to explain their dwindling and ecological exclusion from the shelf area. Competition with the bivalves, especially with infaunal siphonate groups, is considered to be the one of the likely causes. Siphonate bivalves are more efficient filter feeder and physiologically superior to brachiopods; a fierce fighting between them resulted in the ultimate community replacement (Steele-Petrovic, 1979). Gould and Galloway (1980) alternatively, attributed the bivalvian take over to another causal factor — the evolutionary aftermath of the end-Permian extinction crisis, which took the toll of majority of the brachiopods. The bivalves, however, were less severely affected (fig.1). Bivalves, the first among the survivors, then rapidly monopolized the vacated shallow water niches left by the Permian brachiopods. Benton (1983) also mentioned that competition as well as catastrophic demise might be responsible for such a large-scale faunal replacement.

During Palaeozoic, especially in the Permian, brachiopods were not only diverse and abundant, they also successfully competed with the bivalves for both infaunal and epifaunal habitats. "Brachiopods dominated the level-bottom nearshore and shelf habitats during Palaeozoic time, *but they were able to share a number of habitats (especially in the nearshore region) with bivalves* [italics ours] and a long-term equilibrium was set up"(Clarkson, 1999, p.50) In fact, living side by side with bivalves, the Mesozoic terebratulides and rhynchonellides were the commonest fossils in many shelf habitats, such as, in the classical Jurassic section of Kutch, India (personal observation). The dwindle of brachiopods actually started from late Mesozoic. We, therefore find no reason why won't the surviving brachiopods compete with bivalves to colonize the substrate? It was really a bad luck and not a bad gene (cf, Raup, 1991) that the productides were completely wiped out during the end Permian crisis. Had it not been the case, they could have been formidable competitors of the siphonate bivalves during the Mesozoic.

Stanley (1979) singled out predation as the likely cause for the decline of brachiopods. Clarkson (1999) considered that the rise of starfish in the Mesozoic might have been responsible for the decline of brachiopods. We, here, emphasize that many other predators which appeared due to the Mesozoic marine revolution, for example, drilling gastropods, also exerted much pressure on the epifaunal brachiopods (Grant,1987). Terebratulides were extensively predated and Ovcharenko (1969) reported from the Middle Jurassic of Pamir, a predation-driven evolutionary trend within a lineage i.e., *Kutchithyris.* We know that the punctate brachiopods can reduce predation of the boring organisms by means of the presence of various proteins and lipids in their cacae. But this ability to repel predators was not achieved by the punctate brachiopods in Palaeozoic (Grant, 1987)! We have already mentioned that bivalves overcame the danger by adapting more to infaunal life. The Mesozoic brachiopods were fixosessile (having strong pedicle attachment) and, thus, phylogenetically constrained (cf. Seilacher, 1972) not to develop the burrowing ability. They finally gave way shallow water areas to the bivalves and migrated to the placid deep and cold water as we find them today.

Look at the inarticulate *Lingula,* which is a living fossil since the Cambrian and has a wide ecological range covering shelf and basinal regions in the past (Cherns, 1979) to the present day brackish to intertidal environments (Craig, 1951). The modern level- bottom near shore habitat is infested with bivalves and *Lingula* survives! *Lingula* has “weathered the storm” of extinction, competition and predation better because of the fact that it could efficiently burrow.

ECHINOIDEA

It is the largest class within the Phylum Echinodermata that appeared during the Ordovician. All Palaeozoic taxa were regular echinoids (having pentameral symmetry; mouth and anus on opposite sides of a spherical test), dominated by cidaroids. They were ornamented with large tubercles, spines and simple ambulacral plates. They all were epifaunal, living on substrate since they could not burrow. During the great end-Permian mass extinction event, all Palaeozoic echinoid taxa died; only the genus, *Miocidaris* straddled past the P-T boundary. For the major part of the Triassic, echinoids remained small and less diverse. Then, in the Late Triassic-Early Jurassic, the stragglers went on a spectacular adaptive radiation and produced an entirely new stock that is known as noncidaroid regular echinoids (fig. 5). They are distinguished from Palaeozoic cidaroids in having compound ambulacral plates and more tuberculate interambulacral plates. They are also epifaunal. Soon, during the Early Jurassic, they gave rise to a new group, which lost pentameral symmetry of the primitive echinoids —the Irregularia.

The irregular echinoids were characterised by a dominant bilateral symmetry and migration of the periproct from the apical disc to the lower surface. These morphological innovations enabled the irregular echinoids to become infaunal, which subsequently gave the echinoid evolutionary history a slant towards this new group. Many taxa since the Jurassic independently became irregulars to adapt for an infaunal mode of life. They dominate the present day seas.

Echinoids have many predators like fishes, crabs, mammals and birds; even the man prefers their palatable eggs. Some echinoids devour other members. For example, in the present day ocean, large, regular echinoids eat sand-dollar (a type of asteroid) from the edges like a biscuit. The Post-Palaeozoic cidaroids are “improved regulars” being larger in size and more spinuous; they dominated the Triassic. But, during the Jurassic a major change took place. The noncidaroid regulars developed compound ambulacral

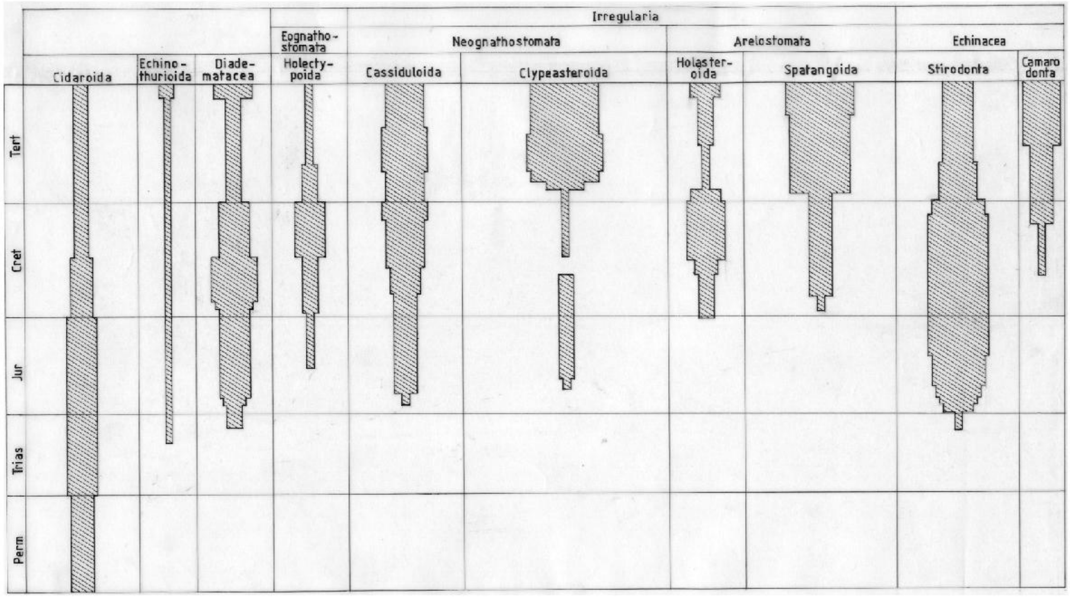

Fig. 5. The stratigraphic range chart of echinoderm classes. Note appearance of irregular echinoids during Jurassic.

enabling them to build up large spines attached to the ambulacra (Kier, 1987). Large spines in regular echinoids were primarily for protection from the predators and for locomotion. Even some used spines to bore within hard substrate to conceal themselves from predators. The regular echinoids of the tropics, where predation is more intense, employ poisonous spines as defense adaptation. Pedicellariae, nothing but modified spines, are the Jurassic acquisitions, consequent to the beginning of the “arms races”. The pincers, besides performing other functions, prevent small predators; some use poison to repel larger attacker, say, a starfish (Kier, 1987).

Kier (1987, p. 669) observed that, “ The most significant post-Palaeozoic development was the evolution of the irregular echinoids during the Early Jurassic”. Vermeij (1977) related the infaunalization of irregular echinoids as the reflection of intensification of predation at or above the sediment-water interface. It is interesting to note that the bivalves also solved the same predation pressure by increasingly adapting to an infaunal mode of life since the Jurassic. The true siphonate groups emerged during that time. Irregular echinoids superimposed bilateral symmetry over the pentamerous baüplan, native to old regulars. Periproct came out of the apical system and migrated towards posterior; likewise peristome shifted towards anterior. This made revolution as it offered better sanitation within the burrows. Like bivalves the echinoids had to take care of problems related to communication with the external world for food and respiration. The bivalves solved it by innovating siphon and the echinoids used their versatile tube feet, which among multiple uses, serve respiration and feeding. Other significant changes from epifaunal to infaunal life habit are the flattening and elongation of the test, decrease in size, but increase in number of tubercles and spines, development of petals and phyllodes and loss of teeth (see Kier, 1987 and present fig. 6). Burrowing echinoids scrape through sediments horizontally and assume the shape of a deep burrowing bivalve in profile (see fig.6, c) — a remarkable evolutionary convergence.

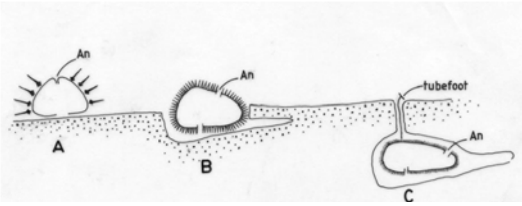

Fig. 6. Evolution of irregular echinoids showing major morphological changes to become infauna, during the Jurassic. An = anus. (modified after Kier, 1982)

OTHER TAXA

If the effects of the Mesozoic marine revolution are far reaching in the groups mentioned above, how did other taxa respond to these phenomenal biotic stresses? Even a casual reading of this fossil records, reveals their stunning reactions. The effects in some of the other marine invertebrate community are described in short details.

Corals:

Corals of the present day tropical oceanic waters are dominated by the taxa belonging to the order Sclerectinia. They evolved during the Middle Triassic and all post-Lower Triassic corals are included in the order. By the Middle Jurassic, corals became true reef builder and were present everywhere. Reefs are massive, wave resistant organic build up made by diverse genera of corals and other groups. The Great Barrier Reef of Australia is a recent example of a huge organically built structure made by the corals. It runs over several thousands of kilometers. More than 700 coral species live in the Indo-Pacific coral reefs. The success of scleractinians, ever since the Jurassic, is closely linked with their ability to make reefs. Reef formation involves presence of "groups of individuals structurally bound together in varying degree of skeletal and physiological integration" (Clarkson, 1999). Closely linked individuals act in a coordinated manner so that the whole reef can function as a single unit. It is a key physiological development. Massive and rapid growth of the coral reefs becomes possible for their one remarkable ecological breakthrough, that is a symbiotic association of corals with algae (dianoflagellate and zooxanthellae). Algae enable corals to secrete more calcium carbonate and provide oxygen and food. But, why do they build reefs? Reef communities appeared throughout the geological time and advantages of reef building are mainly stability and protection. Almost every predator of modern seas has a share of diet on the corals. Fishes (e.g., parrot fish), reptiles (turtles) and starfish (*Acanthaster*) are dreaded predators of corals. A massive coral colony is less vulnerable than solitary individuals. The ability to physically integrate them and to increase high carbonate productivity through algal symbiosis, appear to be the responses of the corals against rapid rise of many predators since the Jurassic.

Crinoidea:

Crinozoans are primitively stalked echinoderms (pelmatozoans)

Prey	Defensive adaptation	Appearance of antipredatory device	Function
Gastropoda	Decreasing trend of evolute, panispiral and umbilicate forms.	Jurassic	Against durophagy.
	Sturdy shells with strong nodes and spines.	Jurassic	Against durophagy.
	Narrow, elongated and denticulated aperture.	Cretaceous	Against apertural extraction.
	Internallisation or complete loss of shell.	Jurassic	De-emphasis of shells as protective device and to avoid species-specific predation.
	Development of detorted groups (Pulmonata), which made excursion to fresh water.	Mesozoic	Against marine predators.
	Development of siphonate gastropod and/or infaunalisation.	Diversification during Tertiary	To avoid intense grazing in benthic ecology.
	Size reduction to become tiny, pelagic opisthobranchs – pteropods.	Early Tertiary	To avoid intense grazing in benthic ecology.
Bivalvia	Infaunalisation of true siphonate group including burrowing and boring.	Originated in the Early Mesozoic	Intense predation in epifaunal benthic ecology.
Brachiopoda	Shift in ecology from shelf to deep and cold seas.	Mesozoic	To avoid intense predation in the shelf region.
	Punctate brachiopods having various proteins and lipids in cacae.	Mesozoic	To repel predators.
Echinoidea	Development of Irregularia, rapid infaunalisation and modification of tube feet that helped in respiration and feeding.	Early Jurassic	To avoid intense predation in epifaunal benthic ecology.
	Large spines attached to the compound ambulacra.	Jurassic	Providing mechanical protection & helping in locomotion and boring within hard substrate.
	Poisonous spines	Jurassic	Against tropical predators.
	Pedicellariae	Jurassic	Prevent small predators.
Coral	Reef building capacity by the symbiotic association with algae.	End of Middle Jurassic.	Defense adaptation against coral crushing predators.
Crinoidea	Appearance of first unstalked order commatulida.	Jurassic	To move freely and to choose suitable refuge.
Bryozoa	Appearance of Cheilistomata having calcified and integrated zooids.	Jurassic	To avoid predation by providing resistance.
Foraminifera	Appearance of planktonic foraminifera.	Middle Jurassic.	Avoiding bioturbation and intense benthic grazing.
Crustacea	Rigid carapace.	Jurassic	Armour against durophagy and drilling.
	Chelae	Jurassic	To avoid predation by providing resistance.
	Evolution of hermit crabs taking refuge in discarded gastropod shells.	Jurassic	To avoid predators who swallowed the whole.
Cephalopoda	Ammonides and nautiloids having increasing shell rugosity.	Jurassic	Protection against durophagy.
	Evolution of belemnites and development of massive guard or rostrum.	Jurassic	Against durophagy.

Table 2: Appearance and function of the defensive adaptation of different prey communities which evolved during the Mesozoic.

with long arms and normally lack complex respiratory structure. The comatulid crinoids have, however, lost their stalks and become secondarily free. It is only during Jurassic when the first unstalked order Comatulida evolved which broke free from their stalks in the early stages. They became capable of moving away from predators and can hide in crevices (Stanley, 1979). Their great subsequent diversification and dominance in the present day sea may be seen as a response to high intensity of predation that started taking place only during Jurassic (see also Ward, 1981).

Bryozoa:

Bryozoans, an important faunal constituent of present day marine environment, were more diverse during Paleozoic. After the great Permo-Triassic extinction event, only one group (Cyclostomata) managed to survive and flourished immediately in the absence of little competition. But a new group (Cheilistomata) arose in Jurassic; they were ecologically superior in having increasing calcification, integration of the zooids and capability to live on different habitats across the bathymetry. During the end of Mesozoic, Clyclostomata started declining when competed with the group, cheilostome. McKenney and Jackson (1989) believed that great diversity of the cheilostomes not only lies in their adaptation to different ecology but they considered cheilostome colony as a living mechanism to defend itself against the predators. They also believed that decreasing relative diversity of Post-Palaeozoic erect species is due to increased predation pressure.

The Planktons:

Theyar (1983) suggested that major diversification of planktic organisms took place during the Mesozoic and may be intimately related to the rise of bioturbating animals. Recently Signor and Vermeij (1994) demonstrated that the planktic ecology is a safe refuge from predation as well as bioturbation for both adult and larvae. It has been mentioned earlier, because of the sudden rise of predation especially on the benthic communities, many faunas took refuse within the sediments. The triumph of siphonate bivalves is a testimony of the occupation of this kind of new ecological niche. Many other groups also adapted the infaunal habit e.g., Irregular echinoids. Jurassic also witnessed the sudden increase in burrowing activities (Stanley, 1979). Because of intense grazing by the predators and the churning by infaunal preys, the marine substrate became very unstable and perhaps inimical to other benthic groups. During Mesozoic, many organisms, including the predators changed their early life mode strategy and adapted planktic larval stage e.g., brachyuran crabs and spiny lobster (Schram, 1982; Signor and Vermeij, 1994). It is remarkable that the undoubted fossil record of planktic foraminifera came from the Middle Jurassic (Tappan and Loeblich, 1988).

The Crustaceans:

Many crustaceans e.g., decapods (crabs, lobsters) and stomatopods, arose in the Jurassic and perhaps achieved durophagy by the Late Cretaceous (Vermeij, 1977 and references therein). Initially they showed a strong predator driven species selection (Stanley, 1979). The brachyuran crabs posses a rigid carapace, used as armour as well as a weapon like chelae. Hermit crabs are known from the Jurassic onwards. They solved the problem by taking refuge in discarded gastropod shells. This step, however, had other implications. This defense strategy extended the ecological life span of snail shell, thereby dramatically increasing the abundance of shelled prey. As a result, the predators that were familiar with crustacean diet, had to develop shell-crushing devices. This permitted the predators to specialise on shelled prey where such speciallisation would have been trophically unfeasible before the hermit crabs arose (Vermeij, 1977).

Being well equipped, lobsters both chelate and armoured like shrimps, they swim only at a slower speed. Shrimps developed morphologies for rapid propalsion as an escape mechanism. Lobsters show a distinct trend of strengthening the defensive devices, a move from buffer zone towards predatory camp. Recently Tsudy *et al* (1998) observed morphological changes in a lobster *Hoploparia* from the Late Cretaceous, Antactica. The spines of the older species had gradually become absent and delicately constructed claws have been modified to robust ones in the younger species. This perhaps suggests a gradual transformation of the ancestral prey community to a predatory descendant, since spines are basically produced as a defensive, adaptation whereas robust and coarsely ornate claws appear to be a predatory acquisition.

REMARKS

The above discussion suggests that the major organization of life, especially of the marine communities, had assumed a new look since Mesozoic onwards. Every major group, belonging to either prey or predator community, responded to the Mesozoic marine revolution. The prey communities, which evolved defense mechanism, underwent a great and rapid diversification (see Table. 2) and those, which failed to adopt effective resistance, dwindled slowly or excluded to placid areas where they became less diverse. One of the remarkable aspects of the Mesozoic marine revolution is that both the predator and the prey communities show sustained adaptive trends as if the evolutionary energy was concentrated on perfecting the acquired biomechanical designs for better efficiency. Modernisation and sophistication of arms and amours were the rules of the game. "……increasing strength and efficiency in crab claws matched by growing intricacy and sophistication of adaptive defenses in molluscan shells" (Gould, 2002, p.951).

One of the greatest fallout of the Mesozoic marine revolution was the 'escalation' of evolutionary tempo that fueled rapid origination of many taxa. Even in the human society (see the news paper clipping at the outset) "arms race" initiates not only a tit-for-tat policy, but also escalates piling up of huge armaments within a short period of time. Vermeij (1977) has demonstrated this fundamental change in the community reorganization, involve very brief geological time intervals, in comparison to a relative stasis of the morphological consistency that spanned for hundreds of millions of years. Gould (1990, 2002) admits that the Mesozoic marine revolution produced trends, which were biotically controlled and adaptive. He wonders that how could this trends be accomplished; whether it is supposedly gradual, involving anagenetic escalation or it demands a punctuational reinterpretation. He argued that this rapid modernization of the prey and the predator can be explained by " macroevolution as a process based upon geologically rapid production of high level individuals by punctuational speciation as the primary units of change" (Gould, 2002, p. 950). Jablonski and Bottjer (1990 a, b) demonstrated that the evolutionary innovations of the post-palaeozoic major benthic invertebrates took place on the shelf region. The major novelties at higher taxonomic level arose in the onshore areas (nearshore to inner shelf), which dramatically increased since the Jurassic. Vermeij (1977) stressed that the Jurassic predators mainly colonised in shallow water. He also envisioned that this rapid coevolution of the prey and the predator could be explained by macroevolutionary theory (Stanley, 1975, 1977). The driving force which Stanley called species selection, explains the long-term trends acquired by both the prey and the predators. Stanley (1979) also believed that the concomitant rise of the marine crabs, teleost fishes and carnivorous gastropods in Late Mesozoic had a great effect on the rapid evolution of modern bivalves. The large-scale adaptive trends of bivalves and other marine prey communities may be explained by the species selection, guided by predation, following Stanley (1979, p.200-202). Recently, Miller (1998) and Jablonsky (1999) reaffirmed that the escalation of arms race did take place "far more abruptly" and evolutionary trend is nothing but "a summation of punctuational events".

Why was Jurassic the time of life's great reorganization? Vermeij (1977) this time, sought answer not in the biotic factors but in a physical attribute and its aftermath – continental fragmentation. Valentine and Moore (1970) have correlated the diversity of marine invertebrate with the patterns of continental assembly and break up throughout Phanerozoic (see Condie, 1989, Fig. 11.26). Aggregation of continents reduces habitable space, thereby causing fall of organic diversity. On the other hand, continental fragmentation increases more habitable shelf areas and can promote rapid diversity. This is exactly what happened time and again in the Phanerozoic history of life. The formation of Pangea II in the end-Permean resulted in large-scale destruction of many shelf areas, and the life on the earth received the biggest jolt (about 97% of the marine species died). Conversely, since the Jurassic onwards continents started rifting and consequently there arose a bewildering array of taxa following the species-area effect. Hallam (1973) recognized that other factors such as increase of ecological niches, reproductive isolation between the population now separated by oceanic barriers and competition among organisms to occupy similar niches are responsible for the rapid increase in the diversity of the organisms during the continental fragmentation. The diversity curve (Condie, 1989, Fig. 11.26) also reveals the exponential rise of invertebrate families since the Jurassic. Vermeij (1977) also considered latitudinal steepening of the climatic gradient (note that the length of continents were longitudinally aligned) and the tropical settings of the Mesozoic continents as other causal factors. It is well recognized that the biotic diversity varies across latitude, attaining its widest range near the Equator. Besides, Jurassic heralded an age after one of the major mass extinction events, the end-Triassic. The mass extinction opened up ecological opportunities for the survivors, and the might account for the diversity and novelties (cf. Jablonski and Bottjer, 1990a).

POSTMORTEM

Defense is the self-right. What is significant is the "escalation" of the diversity of those who fought back. Those who failed did not go extinct but gradually lost diversity or slowly migrated to placid areas.

The Mesozoic marine revolution has shifted the emphasis from the traditional Darwinian competition to predation as the likely biotic agent of large-scale evolution, at least, since the Jurassic.

In ecological theory, predation may promote diversity in an organic community by relieving resource limitation (Paine, 1966). The Mesozoic marine revolution may be seen as a scaled-up and complex version of the ecological theory in spaciotemporal background.

The Mesozoic marine revolution did not pertain to any single, sustained trend to the prey communities, instead, there arose many trends which are sometimes opposite in nature.

Mass extinction event could not derail the antipredatory trends acquired by the prey. The large-scale trends have been explained by species selection and predation was the driving force.

Jurassic marks the “Bioevent par excellence” since it was the time of continental fragmentation which increased the shelf areas. Onshore was the site of major morphological innovation.

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