POST-PALEOZOIC PATTERNS IN MARINE PREDATION: WAS THERE A MESOZOIC AND CENOZOIC MARINE PREDATORY REVOLUTION?

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ABSTRACT—Mesozoic and Cenozoic evolution of predators involved a series of episodes. Predators rebounded rather rapidly after the Permo-Triassic extinction and by the Middle Triassic a variety of new predator guilds had appeared, including decapod crustaceans with crushing claws, shell-crushing sharks and bony fish, as well as marine reptiles adapted for crushing, smashing, and piercing shells. While several groups (e.g., placodonts, nothosaurs) became extinct in the Late Triassic crises, others (e.g., ichthyosaurs) survived; and the Jurassic to Early Cretaceous saw the rise of malacostracan crustaceans with crushing chelae and predatory vertebrates—in particular, the marine crocodilians, ichthyosaurs, and plesiosaurs. The late Cretaceous saw unprecedented levels of diversity of marine predaceous vertebrates including pliosaurids, plesiosaurs, and mosasaurs. The great Cretaceous-Tertiary extinction decimated marine reptiles. However, most invertebrate and fish predatory groups survived; and during the Paleogene, predatory benthic invertebrates showed a spurt of evolution with neogastropods and new groups of decapods, while the teleosts and neoselachian sharks both underwent parallel rapid evolutionary radiations; these were joined by new predatory guilds of sea birds and marine mammals. Thus, although escalation is sometimes cast as an ongoing "arms race," in actuality the predatory record shows long interludes of relative stability puncturated by episodes of abrupt biotic reorganization during and after mass extinctions. This pattern suggests episodic, but generally increasing, predation pressure on marine organisms through the Mesozoic-Cenozoic interval. However, review of the Cenozoic record of predation suggests that there are not unambiguous escalatory trends in regard to antipredatory shell architecture, such as conchiolin and spines; nor do shell drilling and shell repair data show a major increase from the Late Mesozoic through the Cenozoic. Most durophagous groups are generalists, and thus it may be that they had a diffuse effect on their invertebrate prey.

"As evolutionists, we are charged, almost by definition, to regard historical pathways as the essence of our subject. We cannot be indifferent to the fact that similar results can arise by different historical routes." —Gould and Vrba, 1982

"This is not to say that selection is not important, but that its invocation is not justified until the role of chance in the operation of a basically stochastic universe is ruled out." —Schram, 1986

"A science grows only as it is willing to question its assumptions and expand its approaches." —Hickman, 1980

INTRODUCTION

THE CONCEPT OF predator-prey escalation is, in large measure, an outgrowth of the extensive studies of Vermeij (1977, 1987) on the so-called "Mesozoic Marine Revolution." This term might seem to imply that a dramatic development of marine predators was initiated at the Triassic; a continuous intensification of predator-prey relationships has been envisaged. In actuality, the Mesozoic and Cenozoic evolution of predators involved a series of episodes. In this paper we document the diverse predatory guilds of the Mesozoic and Cenozoic, especially vertebrates that putatively devoured invertebrate prey, with comments on their modes of feeding and possible impact on potential prey, focusing on benthic invertebrates. Predator guilds (e.g., marine reptiles) during the Mesozoic are surprisingly similar to those in the Cenozoic (e.g., marine mammals), except that the players have changed. Despite the setbacks of mass extinctions, the diversity of predators remained at a nearly constant proportion from the Late Triassic to mid-Cretaceous (Bambach and Kowalewski, 1999). However, during the last 110 million years (Late Cretaceous–Neogene), predators diversified faster than the rest of the fauna (Bambach and Kowalewski, 1999).

We also examine the patterns of predation in post-Paleozoic shell structure (e.g., conchiolin and spines), shell repair, and shell drilling. However, data from drilling and shell repair thus far do not show unambiguous escalatory trends. For the sake of argument, escalation is not a continual trend from the Mesozoic to the Cenozoic; rather, within each era it is dependent on the suite of predators and prey.

In the final section of the paper we reconsider the Mesozoic Marine Revolution hypothesis proposed by Vermeij (1977, 1978, 1987), and ask questions that may guide future research: Is the pattern of putative armor in invertebrates strictly related to predation, or might there be other hypotheses that could explain armor in organisms? Is there evidence that most predators are specialists on particular prey and thus might cause extreme selection in invertebrates who then respond with various escalating strategies (e.g., spines, chonchiolin) to mitigate the increased predation pressure? Does diffuse selection from generalist predators cause antipredatory armor to arise in a number of groups of invertebrates? If most predators are generalists, as appears to be the case based on the evidence amassed herein, then perhaps there was not a sufficiently intense selective force to produce a major "sea change" in antipredatory armor in any one group of marine invertebrates, especially in post-Paleozoic organisms. Thus, for example, durophagy may not necessarily mean that a predator ate molluscs; durophagous dentition could also indicate the eating of crustaceans, other hard-shelled prey, or even soft prey (e.g., Plotkin et al., 1993; Wilga and Motta, 2000). Perhaps also, as Gould and Vrba (1982) have recognized, there are a number of historical and non-adaptive routes by which specific aptations may ultimately arise in organisms, and such may also be the case with certain antipredatory strategies.

Despite its length, this paper is not an exhaustive review. However, we did strive both to provide a broad overview of Mesozoic and Cenozoic predators and their potential prey, and, perhaps more importantly, to demonstrate that there are alternative ways to think about these predatory patterns.

TRIASSIC PREDATORS AND PREDATION

All marine benthic ecosystems were profoundly altered by the Permo-Triassic extinction (Fig. 1). Many Paleozoic predators were eliminated, including most phyllocarids, platyceratid gastropods, goniatite ammonoids, and many primitive lineages of sharks. Other active predatory groups preferentially made it through this bottleneck, including the hybodontid sharks and the root-stocks of Mesozoic crustaceans and ammonoids (Knoll et al., 1996).

Gastropods and Bivalves.—Varied archaeo- and mesogastropod taxa rediversified in the Triassic. Nonetheless, records of gastropod drilling predation are surprisingly rare in this period (Kowalewski et al., 1998). However, in a few instances, drillers seem to have had a significant impact (Fürsich and Jablonski, 1984; Kowalewski et al., 1998). The first naticid-like mesogastropods (*Ampullina*) are known from this time (see Fig. 7) (Fürsich and Jablonski, 1984; Newton, 1983; Kowalewski et al., 1998). Given the rarity of naticid-like boreholes from the Late Triassic to the mid-Cretaceous (Albian), it has been suggested that predatory drilling was relatively ineffective and largely lost during the Triassic, only to be evolved again, successfully, during the Cretaceous (Kowalewski et al., 1998). Predatory septibranch bivalves also originated at this time (Skelton et al., 1990).

Ammonoids.—Ammonoids were nearly extinguished by the Permo-Triassic crises. However, the ceratitic ammonoids staged a rapid rediversificiation in the Triassic. Like other

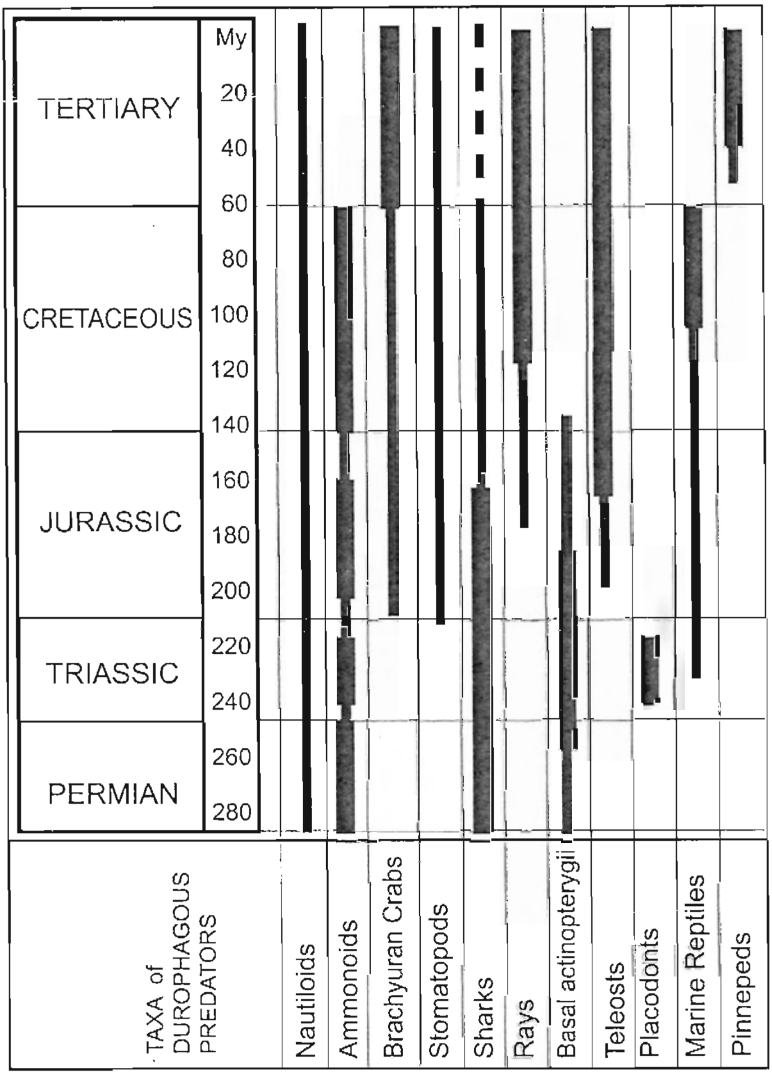


FIGURE 1—Ranges of various taxa of Mesozoic and Cenozoic durophagous (hard-shell crushing) predators. Thin lines: present, but of limited abundance; thick lines: abundant; broken lines: possibly present but rare as fossils.

ammonoids, the ceratites are assumed to have been predaceous, although data are very sparse. Stomach or crop contents of ammonoids are very rare, but when they are found provide important evidence for trophic relationships. One specimen of an Early Triassic ammonoid (*Svalbardiceras*) had ostracodes and foraminiferans among its gastric contents and may have been a predatory nektonic carnivore (Westermann, 1996, p. 675).

Crustacea and Ostracodes.—The most important post-Paleozoic groups of decapod, isopod, and amphipod crustaceans appeared in the Late Paleozoic, but they did not diversify significantly until the Jurassic (Briggs and Clarkson, 1990). Four out of 27 Paleozoic families survived into the Mesozoic, and only a few groups are known from the Triassic (Briggs and Clarkson, 1990). Various lobster groups evolved in the Triassic (Table 1). Their appendages indicate that they were durophagous, but modern lobsters feed on a wide variety of prey and are not specialists on molluscan prey. Ostracodes are known to be predators on

TABLE 1—Geographic and temporal ranges and feeding preferences of crustacean predators.

Taxon **Geologic Range**	**Geographic range and depth range (shallow, < 70 m; deep, > 70 m)**	**Specialist feeders on specific invertebrate prey?**	**Geologic range of durophagous anatomical features (molariform claws, mouth parts, etc.)**
Infraorder Brachyura Family Portunoidea Carcininae Portuninae Cretaceous (Maastrichtian)–Recent	Boreal to temperate	Generalists (bivalves, like oysters and mussels; scavengers; fish, plants, benthic invertebtrates, jellyfish, epibionts on Zostera, tunicates)	Unknown
Family Xanthidae Cretaceous–Recent (Schram, 1986)	Temperate to tropical	Generalists (mangrove detritus, other plants and detritus, small crustaceans, oysters, barnacles; *M. mercenaria* eats molluscs, like oysters, polychaetes, barnacles and other crustaceans)	*Menippe mercenaria* is the most famous shell-crusher of this group; the genus *Menippe* originated in the Middle to Upper Eocene (Glaessner, 1969), and *M. mercenaria* is known only from the Pleistocene (Rathbun, 1935)
Family Calappiidea Eocene–Oligocene to Miocene; Recent (Glaessner, 1969); Cretaceous–Recent (Schram, 1986)	South Pacific, Caribbean, North America, Europe	Generalists	The shell-peeling *Calappa flammea* is known from the Oligocene (Rathbun, 1930; Ross et al., 1964)
Decapod crustaceans (Order Decapoda) (earliest decapod is *Palaeopalaemon,* Schram, 1986) Late Devonian to Recent (Schram, 1986); Permo-Triassic to Recent (Williams, 1996)		Generalists	Unknown
Stomatopods (Order Stomatopoda) Extant: 350 spp, 66 genera,12 families Devonian to Recent	Chiefly tropical shallow to deep water; rare in temperate zones, none in polar regions	Specialists	Raptorial mouthparts, Devonian–Recent; folding raptorial thoracopods, in paleostomatopods, Carboniferous; gonodactyloid shell smashers, ?Cretaceous, Upper Miocene to Recent; Squillids, ?Cretaceous to Recent

(Table 1, cont.)

Family Cancridae Eocene to Recent (Schram, 1986)	Chiefly boreal and temperate; shallow and deep water	Generalists (sea urchins, polychaetes, scavengers, molluscs)	Molariform teeth and shell-crushing claws (Miocene to Recent)
Family Parthenopidae Eocene to Recent (Schram, 1986)	Temperate to tropical	Generalists, omnivores, detritivores; one species known as a shell-crusher (*Parthenope horrida*)	Gore and Soto (1979, p. 67) state that parthenopids are omnivores and detritivores; Debelius (1999, p. 259) figures *Parthenope horrida* eating a pufferfish; Vermeij 1978, p. 40, states that *Parthenope* (*Daldorfia*) *horrida* is a shell-crusher in the lab
Family Majidae Eocene to Recent (Schram, 1986)		Generalists	
Family Grapsidae Eocene to Recent (Schram, 1986)	Boreal, temperate to tropical	Generalists (sea urchins)	
Infraorder Palinuroidea Family Palinuridae (Lobsters) ?Lower Triassic, Mid-Triassic to Recent (Williams, 1996)	Temperate to tropical; deep and shallow water	Generalists (mollusks, sea cucumbers; Williams, 1984)	
Superfamily Nephropidae Family Nephropidae (Clawed marine lobsters) Permo-Triassic to Recent (Williams, 1996)	Temperate zones, North Atlantic, Europe; shallow and deep water (many migrate)	Generalists (molluscs, hydroids, crustaceans, lobsters, polychaetes, brittle stars, mussels, limpets, lobster molts, chitons, bryozoans, scallops, oysters, sea urchins, seaweeds; Williams, 1984; Lawton and Kavalli, 1995)	Molariform teeth on major crusher claw as in *Homarus* (Cretaceous to Recent; Glaessner, 1969)
Family Scyllaridae (Spanish Lobsters) ?Lower Cretaceous; ?lower Eocene to Recent (Williams, 1996)	Temperate to tropical	Generalists? (?scyphozoan medusae; Williams, 1984)	

polychaete annelids, and scavengers on dead polychaetes, fish, and squid (Vannier et al., 1998). They have serrated appendages that act like knives (or sandpaper) to abrade their food. Based on their feeding appendages, the Early Triassic cypridinids (and possibly the Late Ordovician myodocopids) may have been predators or scavengers on cephalopod carcasses (Vannier et al., 1998).

Chondricthyes.—The long-lived hybodontids flourished in the Triassic and became the dominant Jurassic sharks (Maisey, 1982). Hybodonts possessed varied dentition, ranging from high-cusped impaling teeth to low-crowned crushers, indicating rather generalized predatory diets (Maisey, 1982); they gave rise to swimming, piscivorous sharks, as well as pavement-toothed forms. The hybodont sharks may have arisen in the Devonian, but they underwent strong adaptive radiation during the Triassic (Maisey, 1982).

Sauropterygian clade.—The sauropterygian clade (Figs. 2, 6; Table 2) contains the Triassic stem groups such as placodonts, pachypleurosaurs, nothosaurs, and pistosaurs, and the Jurassic-Cretaceous crown groups known as plesiosaurs, pliosaurs, and elasmosaurs (Rieppel, 1999). Very little is known about the feeding mechanics of Triassic stem-group sauropterygians, which secondarily became aquatic from their terrestrial ancestors (see Rieppel, 2002). Feeding underwater, as the stem-group sauropterygians did, required a suite of anatomical and behavioral adjustments that had to allow for their adaptive radiation into early Mesozoic seas (Rieppel, 2002). Suction feeding appears to be the most efficient hydrodyamic way to solve the underwater feeding dilemma (Lauder, 1985); however, "quick snapping bites" at the air-water interface (or underwater) are also used, especially by crocodilians (Rieppel, 2002). Triassic sauropterygians covered all styles of feeding, and thus have little overlap in hypothesized feeding strategies. The varied nearshore habitats in the Middle Triassic, with lagoonal basins interspersed among reef habitats, may have accounted for the trophic-functional diversity of stem-group sauropterygians (Rieppel, 2002).

Placodonts.—During the Middle Triassic, the placodonts (Figs. 1, 2.1–2.3) evolved from unknown diapsid reptilian ancestors (Benton, 1993, 1997). The Triassic placodonts, sister group to all other Sauropterygia, have members that are interpreted to have been benthic predators on hard-shelled invertebrate prey. *Placodus*, for example, had pachyostosis (complete covering of the cheek by dermal bone), which added weight to the jaw and thus may have functioned as an adaptation for durophagy (Rieppel, 2002). Additionally, the procumbent and chisel-shaped premaxillary and dentary teeth may have functioned to pick off invertebrates from their substrate, which were then crushed with the posterior tooth plates before they were swallowed (Westphal, 1988). Biomechanically, the tooth plates of *Placodus* were positioned in such a way as to enhance crushing, but not increase load to the jaw (Rieppel, 2002). The basal stock of *Placodus* already had large crushing tooth plates and procumbent premaxillary teeth (Rieppel, 2002), indicating that durophagy was an ancestral condition in this group. The few durophagous taxa of placodonts may have had an impact on the rediversifying molluscan communities of the Triassic, but they became extinct in the major crises toward the end of that period.

Not all placodonts had dentition indicating that they ate benthic hard-shelled prey. More derived cyamodontids (*Placochelys* and *Psephoderma*) lack premaxillary and anterior dentary teeth, and may have picked up benthic soft-substrate invertebrates (like crustaceans) through suction action (Rieppel, 2002). Another basal cyamodontoid, *Henodus*, has much reduced crushing dentition, and may have had baleen that was used in sieving benthic invertebrates. *Henodus* is thus interpreted to have been a bottom-feeder—perhaps an herbivore or omnivore—but it was not durophagous (Rieppel, 2002).

Pachypleurosauria.—Pachypleurosaurs (Fig. 2.7) were swimming reptiles with long heads and interlocking lower and upper sharp teeth presumably for the capture of fish (Benton, 1997). Pachypleurosauria are considered to be the sister group of the Nothosauroidea, or the sister taxon to all other Eusauropterygia (composed of nothosaurs and plesiosaurs; Rieppel, 2002). Pachypleurosauria

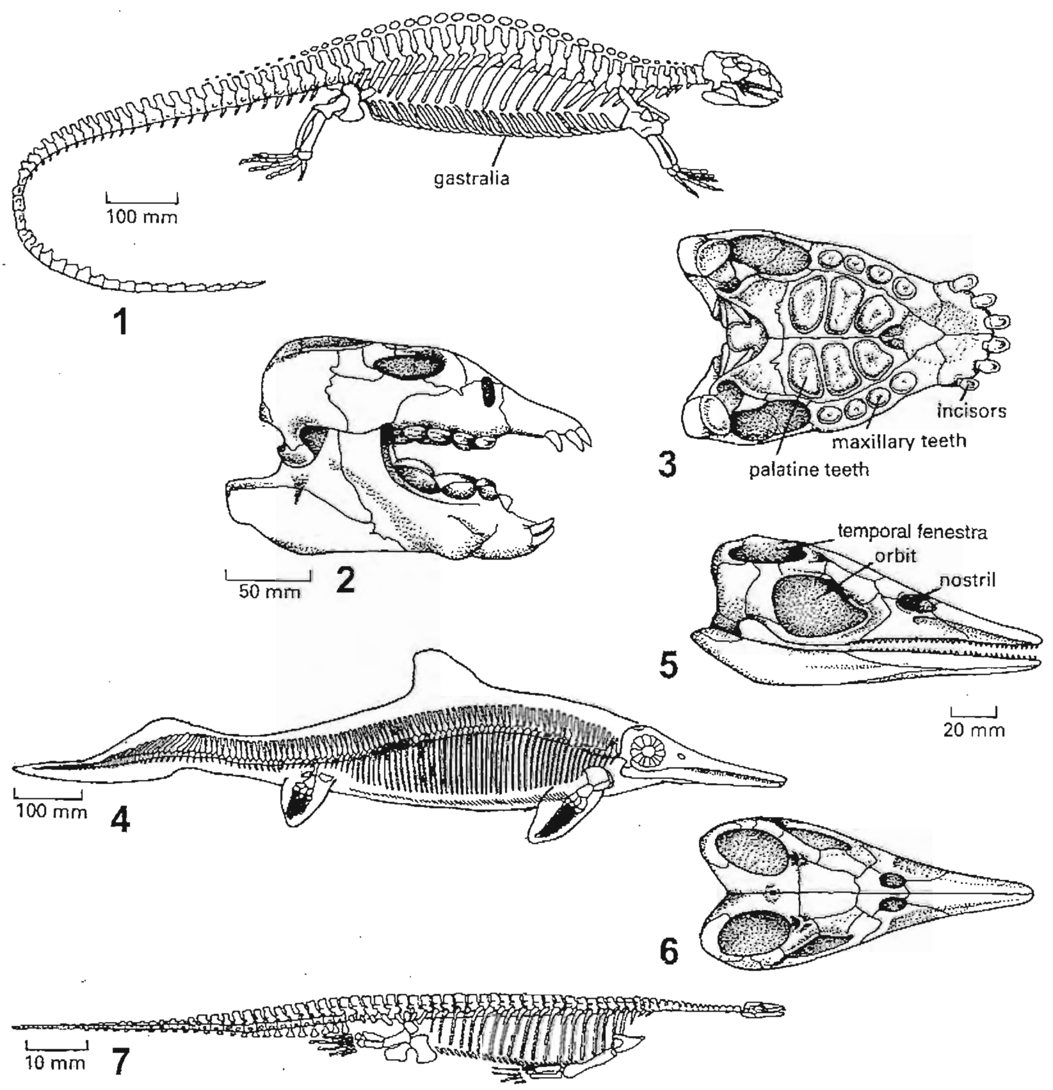


FIGURE 2—Triassic predatory reptiles. 1–3, Placodont reptile *Placodus*. 2, 3, Lateral and palatal views of skull; note spatulate incisors and broad "pavement" teeth in maxilla and palate. 4, Ichthyosaur *Mixosaurus*. 5, 6, Ichthyosaur *Grippia;* lateral and dorsal views of skull. 7, Nothosaur *Pachypleurosaurus*. Adapted from figures in Benton (1997).

are among the smallest of the sauropterygians: most attain a length of 50 cm; few attain lengths of 120 cm (Carroll and Gaskill, 1985; Rieppel, 2002). Based on a relatively large tympanic membrane and limited bone ballast, these marine reptiles may have inhabited shallow, coastal, and estuarine waters (Taylor, 2000). Pachypleurosauria (e.g., *Neusticosaurus*) had delicate jaws with homodont dentition; loading conditions of the jaw indicate that they were not efficient in subduing vigorous prey (Rieppel, 2002). Pachypleurosaurs probably were pelagic predators that used suction and rapid closure of the jaws to subdue soft-bodied cephalopods and small fish (Sander, 1989; Rieppel, 2002).

Nothosaurs.—The Middle Triassic Nothosauroidea (up to 4 m in length) are a major clade of the Eusauropterygia, members of which may have eaten fish, other sauropterygians, and

TABLE 2—Cenozoic marine vertebrate predator guilds.

Marine Reptile	**Geologic Range; Biogeography**	**Feeding Realm**	**Feeding Type**	**Putative Prey**	**Gastric Evidence or other evidence**	**Reference**
Placodontia	Middle Triassic (chiefly); late Lower to Upper Triassic of Europe, North Africa, Middle East; distribution restricted to western periphery of Triassic Tethys (Lucas, 1997)	Benthic	Durophagous (basal and derived cyamodontoids) to suction and sieving (*Henodus*); crush guild of Massare, 1997	Hard-shelled sessile to non-sessile invertebrates (cyamodonts); soft shelled invertebrates to plants (*Henodus*)		Rieppie, 2002; Massare, 1997
Pachypleurosaurs	Middle Triassic	Pelagic	Suction feeding	Soft-shelled invertebrates, cephalopods		Rieppie, 2002
Nothosaurs	Middle Triassic (chiefly); late Early Triassic to Upper Triassic; endemic to European/Asian continent (Lucas, 1997)	Pelagic	Suction feeding to fish-trap dentition	*Simosaurus* : hard-shelled invertebrates; all others fish, soft-shelled invertebrates	Juventile placodont in *Lariosaurus* stomach	Rieppie, 2002; Sanders, 1989; Tschanz, 1989
Pistosauroidea	Middle Triassic	Pelagic	Puncturing dentition	Soft-shelled invertebrates; fish		Rieppie, 2002
Plesiosaurs	Late Triassic (Rhaetian) to Late Cretaceous; global distribution in the Jurassic and Cretaceous, but had high endemism (Lucas, 1997)	Pelagic	Needle-shaped teeth; pierce I and II guilds of Massare, 1997	Soft-shelled invertebrates or fleshy prey; some may have strained small prey from water (*Cryptoclidus*)	Jurassic forms with cephalopod hooklets; gastroliths; ?regurgitates thought to be from plesiosaurs with ammonoid larvae and shells of *Baculites*	Rieppie, 2002; Massare, 1997; Pollard, 1968; Martill et al., 1994; Wetzel, 1960
Pliosaurs	Cretaceous	Pelagic	Pursuit predators; Cut and Pierce II guild of Massare, 1997; shake feeding	Large, fleshy prey: other reptiles, fish, and cephalopods	Cephalopod hooklets in *Peloneustes*	Rieppie, 2002; Massare, 1997; Martill et al., 1994
Elasmosaurs	Cretaceous	Pelagic	Robust teeth, pierce I and II guild of Massare, 1997			Rieppie, 2002; Massare, 1997
Ichthyosaurs	Early Triassic to late Cenomanian (Late Cretaceous); achieved global distribution by the Middle Triassic (Lucas, 1997)	Nearshore (Triassic) to Pelagic (Jurassic to Cretaceous); some were deep divers to a depth of 600 m to the mesopelagic layer of the ocean (*Ophthalmosaurus*); *Shonisaurus* (Upper Triassic, Nevada) was outer shelf or basinal in distribution (Hogler, 1992)	Cut, pierce, smash, crunch, and crush guilds of Massare (1987, 1997) Triassic icthyosaurs had heterodont dentition suggesting ambush, generalist predators in nearshore habitats; in Jurassic, mostly homodont dentition suggesting pelagic pursuit predators that specialize in a certain type of prey (Massare and Callaway, 1990)	Large, fleshy prey; soft prey; soft prey with internal hardparts; prey with bony scales or hard, thin exoskeleton; prey with a very hard exterior Large, rear teeth of Middle Triassic icthyosaurs *(Phalarodon, Omphalosaurus)* are suggestive of mollusc-crushing (Massare and Callaway, 1990), however this type disappeared by the Late Triassic; the Lower Triassic *Grippia* may also have been durophagous (Lingham-Soliar, 1999)	Gastric mass with cephalopod hooklets, most likely from belemnites or other types, in many ichthyosaur skeletons; coprolites indicate fish remains such as the Liassic nectonic or necto-benthic fish, *Pholidophorus;* ?Jurassic cuttle-fish; ?marine reptiles; wood; none found with ammonoid or belemnite shells in gastric contents	Massare, 1987, 1997; Pollard, 1968; Keller, 1976; Motani et al., 1999

(Table 2, cont.)

Mosasaurs	Late Cretaceous (Cenomanian to end Cretaceous); most were endemic to one region (Lucas, 1997)	Pelagic, ?Benthic	Ambush predators; most mosasaurs occupied the Cut guild; Crush and Pierce II guilds also occurred (Massare, 1997) Opportunistic generalists (Massare, 1997)	Large, fleshy prey, prey with hard exterior; *Globidens* was cosmopolitan in distribution and is thought to be durophagous (Lingham-Soliar, 1999)	Stomach contents indicate ammonoids, birds, fish, smaller mosasaurs; *Clidastes*, had a marine shark and a diving marine bird *Hesperomis* in gastric contents (Martin and Bjork, 1987)	Kauffman and Kesling, 1960; Martin and Bjork, 1987; Massare, 1997
Crocodiles	Early Jurassic to Recent	Benthic	Ambush predators; generalists, occupying the Cut, Pierce I and II, Crunch, and Crush guilds of Massare, 1997; *Globidens* only crush guild marine reptile since Triassic (Massare, 1997)	Teleosaurids (teleosaurs): fish, turtles, and ammonites; Metriorynchids (geosaurs): ammonites, belemnites, pterosaurs, and giant fish *Leedsichthys*	Crocodile tooth associated with turtle scutes in a teleosaurid; *Metriorhynchus* with abundant cephalopod hooklets; associated scales of *Lepidotes* associated with skeletal elements of *Steneosaurus; Metriorhynchus* tooth embedded in giant fish *Leedsichthys*	Martill, 1985, 1986; Hua and Buffetaut, 1997; Martell et al., 1994
Sea Turtles	Jurassic to Recent	Benthic to pelagic	Generalists to specialists	One form today feeds on molluscs (*Caretta*); one form in the Late Cretaceous may also have fed on molluscs (Hirayama, 1997); Others feed on sea grass, jellyfish, and crustaceans	No fossil evidence	Hirayama, 1997
Hybodont sharks		Benthic; necto-benthic	scavengers to predators; *Asteracanthus* had durophagous dentition (Jurassic)	Predators on surface-living ammonoids	Belemnites; one specimen (*Hybodus*) with over 250 rostra in gastric contents	Pollard, 1968
Chimaeras	Jurassic	Benthic				Martill et al., 1994
Neoselachian sharks	Jurassic	Benthic	some with durophagous dentition			Martill et al., 1994

hard- and soft-shelled invertebrates in the pelagic realm (Rieppel, 1998). Teeth of some nothosaurs, such as *Simosaurus*, have a bulbous shape which may have had a somewhat durophagous function (Rieppel, 2002). Anatomical evidence indicates that *Simosaurus* had strong neck muscles and was capable of rapid jaw opening; suction also may have been used to round up shelled ammonoids or fish (Rieppel, 2002). *Nothosaurus mirabilis* had specialized jaw adductor muscles, heterodont dentition with procumbent fangs, and a very narrow and elongate skull (Rieppel, 2002). The heterodont dentition suggests most nothosaurs ate fish, although the gastric contents of one nothosaurid (*Lariosaurus*) contained placodonts and small pachypleurosaurs (Sander, 1989; Tschanz, 1989; Rieppel, 2002). They may also have eaten soft-bodied invertebrates, such as cephalopods. *Simosaurus* may have eaten hard-shelled prey (Rieppel, 2002). Some nothosaurs, because of their large size, may have been at the top of the food chain.

Pistosauroidea.—The Triassic Pistosaruoidea gave rise to the plesiosaurs that were common in the Jurassic and Cretaceous seas. Some pistosaurians had jaws similar to those of the putatively fish-eating nothosaurids (e.g., *Nothosaurus*), and others, such as *Pistosaurus,* had narrow and elongated pincer-type jaws, that had less numerous and widely-spaced heterodont dentition with maxillary fangs (Rieppel, 2002). Puncturing prey, rather than suction feeding, may have been the modus operandi of these creatures, and they may have fed on soft-shelled pelagic invertebrates and fish (Rieppel, 2002).

Ichthyosauria.—Ichthyosaurs (Order Ichthyosauria) (Figs. 2.4–2.6; 4) are known from the Lower Triassic to Cenomanian (Bardet, 1994), but they have only recently been studied in detail (Callaway, 1997a). Triassic ichthyosaurs were nearly as diverse and widespread as Jurassic ichthyosaurs, but are notoriously affected by preservational bias (Callaway, 1997b; Sander, 1997). Because of this preservational bias, little is known about the evolution of dentition in Triassic ichthyosaurs. Most of them likely had heterodont dentition, indicating that they were generalist feeders in nearshore waters (Massare and Calloway, 1990).

Some Middle Triassic ichthyosaurs with large rear teeth may have been molluscivorous (Massare and Callaway, 1990). In the Jurassic and Cretaceous, the dentition became homodont, indicating that they may have become specialized on pelagic prey (Massare and Callaway, 1990). Perhaps they were specialists on fish and/or soft-bodied cephalopods (Sander, 1997; Massare and Callaway, 1990). Gastric contents indicate that they may have fed on belemnite cephalopods, although no belemnite or ammonoid shells have ever been found in ichthyosaurian stomach contents. Based on body form, by the end of the Triassic, ichthyosaurs were hydrodynamically advanced and were very fast-swimming animals (Lingham-Soliar, 2001).

Pterosaurs.—The appearance of pterosaurs in the middle of the Triassic Period (Benton, 1993) may have increased predation pressure on near-surface nektonic organisms, including fish and cephalopods. The long jaws and impaling spike-like teeth of rhamphorhynchids and many pterosauroids suggests a piscivorous diet in these flying reptiles.

TRIASSIC BENTHIC ORGANISMS: ANTIPREDATORY RESPONSES?

Varied morphological and behavioral features of benthic invertebrates have been interpreted as antipredatory adaptations (Fig. 3), although many of these features may be merely exaptations (*sensu* Gould and Vrba, 1982). Triassic benthic faunas are decidedly "no frills" relative to those of the late Paleozoic (Valentine, 1973). Shells are relatively thin and mainly lacking in spines. In addition, several groups of cemented bivalves—the ostreids, gryphaeids, plicatulids, and terquemids—first became abundant on hard substrates in the Triassic. Harper (1991) has demonstrated experimentally that predators avoid cemented bivalves when given a choice.

The evolutionary breakthrough of mantle fusion in bivalves led to the rapid development of infaunal clades in the early Mesozoic (Stanley, 1977). Mud- and rock-boring bivalves also first became common during this time (Seilacher, 1985;

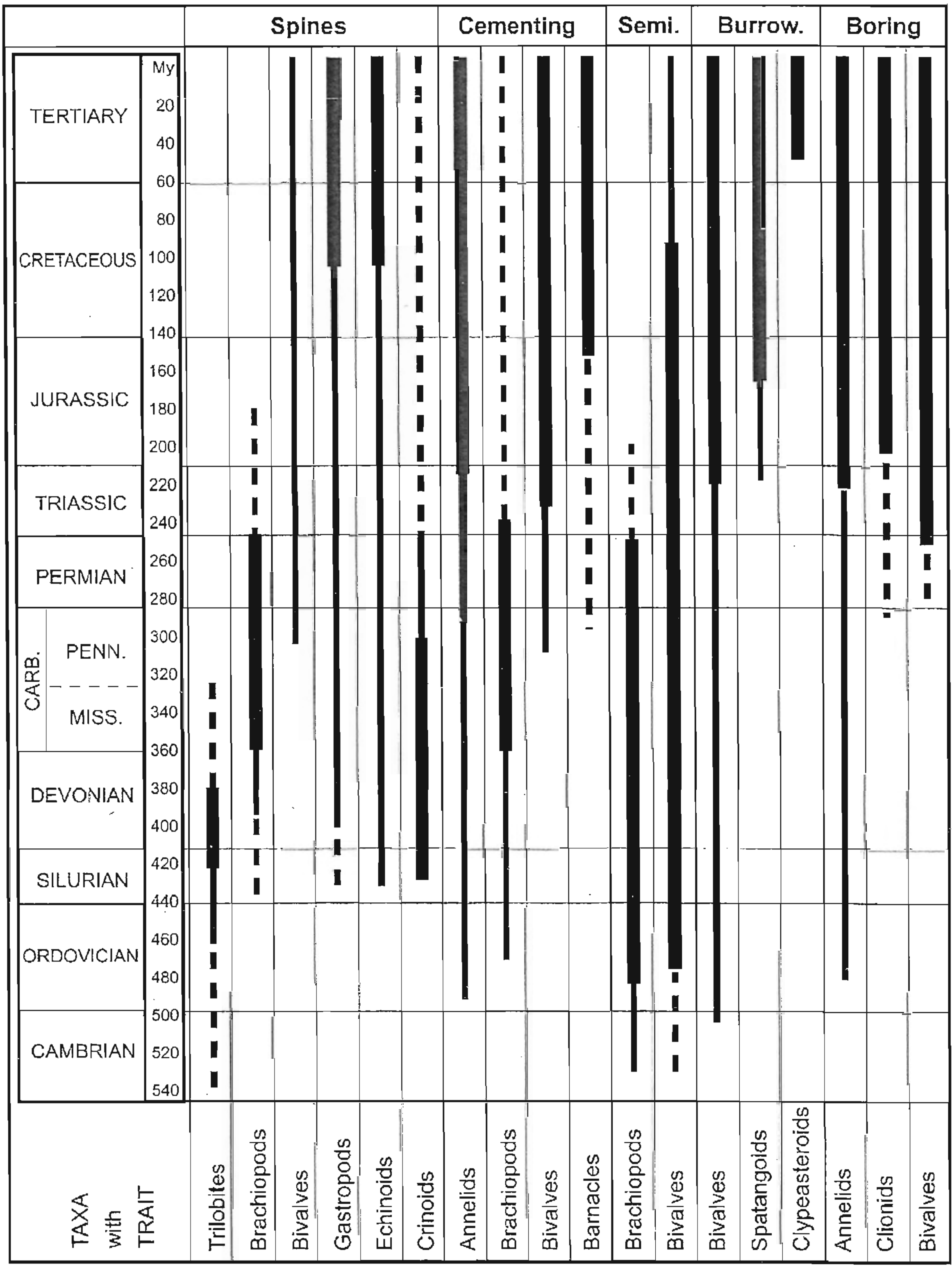


FIGURE 3—Temporal ranges of various potential anti-predatory adaptive or exaptative strategies in various invertebrate groups; semi: semi-endobenthic (quasi-infaunal); burrow: burrowing endobenthic organisms. Thin lines: present, but of limited abundance; thick lines: abundant; broken lines: possibly present but rare as fossils.

Bottjer, 1985). Deep burrows and endolithic crypts may have been particularly effective protection from grazing predators, such as placodonts. The near-synchronous development of this strategy in at least three independent lineages of venerid (Skelton et al., 1990) and myoid bivalves, as well as the great increase in endobenthic and endolithic anomalodesmatans—all during the Early Triassic—suggests intensification of some selective pressure (Fig. 3). Bottjer (1985) and Skelton et al. (1990) drew attention to the coincidence of this downward push with the Mesozoic Marine Revolution. However, McRoberts (2001) has recently argued that durophagous predators may not have been sufficiently abundant or widespread during the Triassic to account for the early radiation of endobenthic strategies. It is possible that the antipredatory advantages of living cryptically were merely a side-benefit of adaptation driven by other pressures, such as competition (McRoberts, 2001).

The overall frequency of shell repair, due either to predators or to physical factors in the environment (see Cadée et al., 1997; Cadée, 1999; Ramsay et al., 2001) is also low during this time interval, with repair frequencies evidently even lower than those of the late Paleozoic, as recorded by Vermeij et al. (1982) (Table 3).

Ammonoids.—Vermeij (1987) drew attention to the fact that surveys of ammonoid shell architecture and traces of predation on cephalopods are critically needed for the whole Phanerozoic. A general view of ammonoids suggests that their morphology is related to their pelagic, demersal, or planktic lifestyle (Westermann, 1996, p. 689), rather than to antipredatory features.

Early Triassic ceratitic ammonoids from platform environments are considered to have been chiefly nektonic in habit, although some planktonic and demersal forms occurred (Westermann, 1996). Offshore bituminous limestones of the Middle and Upper Triassic in Europe, North America, and China also contained coarsely costate to smooth ammonoid morphotypes, all of which were interpreted to be pelagic (including some with planktonic lifestyles). In the Late Triassic (Norian), however, most highly sculpted evolute ammonoid morphotypes disappeared, whereas smooth involute forms survived, and the first heteromorphs appeared.

Deep outer-shelf and upper-slope environments from the Early Triassic of China contained both smooth and costate ammonoids; deep basin ammonoids were smooth-shelled, some with fine sculpture, many of which are interpreted to have been pelagic (Westermann, 1996). Coarse sculpture, however, is thought to be commonly associated with basin-slope habitat.

Large pelagic predators, such as ichthyosaurs, plesiosaurs, placodonts, and turtles had evolved by the Late Triassic, and many are thought to have eaten ammonoids; ceratitic ammonoids do not seem to show classic antipredatory defenses. However, the temporal trends, if any, of ceratite shell injuries remain to be studied.

Echinoderms.—Echinoderms went through an evolutionary bottleneck after the Permian extinction, with at least five classes surviving into the Early Triassic (Simms, 1990). From low diversity in the Triassic, echinoids and crinoids diversified in the Middle Triassic, but some clades went extinct during the mid-Carnian. A second diversification occurred in the Norian and the Early Jurassic for both groups. Triassic crinoid forms re-evolved "passive" filtration systems like their Paleozoic forebearers. Most post-Paleozoic crinoids are thought to be anatomically similar to their Paleozoic ancestors; however, Donovan (1993) and Oji (2001) provide evidence that the Mesozoic crinoids (especially the Jurassic forms) were agile and could actively relocate—this may have provided a selective advantage as predation pressure increased (Meyer, 1985). Pseudoplanktic pentacrinitids, paracomatulids, and the true comatulids evolved in the Late Triassic and occupied niches altogether different from their Paleozoic counterparts (Simms, 1990). These new modes of life probably do not reflect escalation; overall, predation on these echinoderms is deemed to have been relatively low during the Triassic (Schneider, 1988).

The two main clades of echinoids, the Diadematacea and Echinacea, diversified in the Late Triassic and Early Jurassic, but still retained their mid-Paleozoic diversity levels (Simms, 1990).

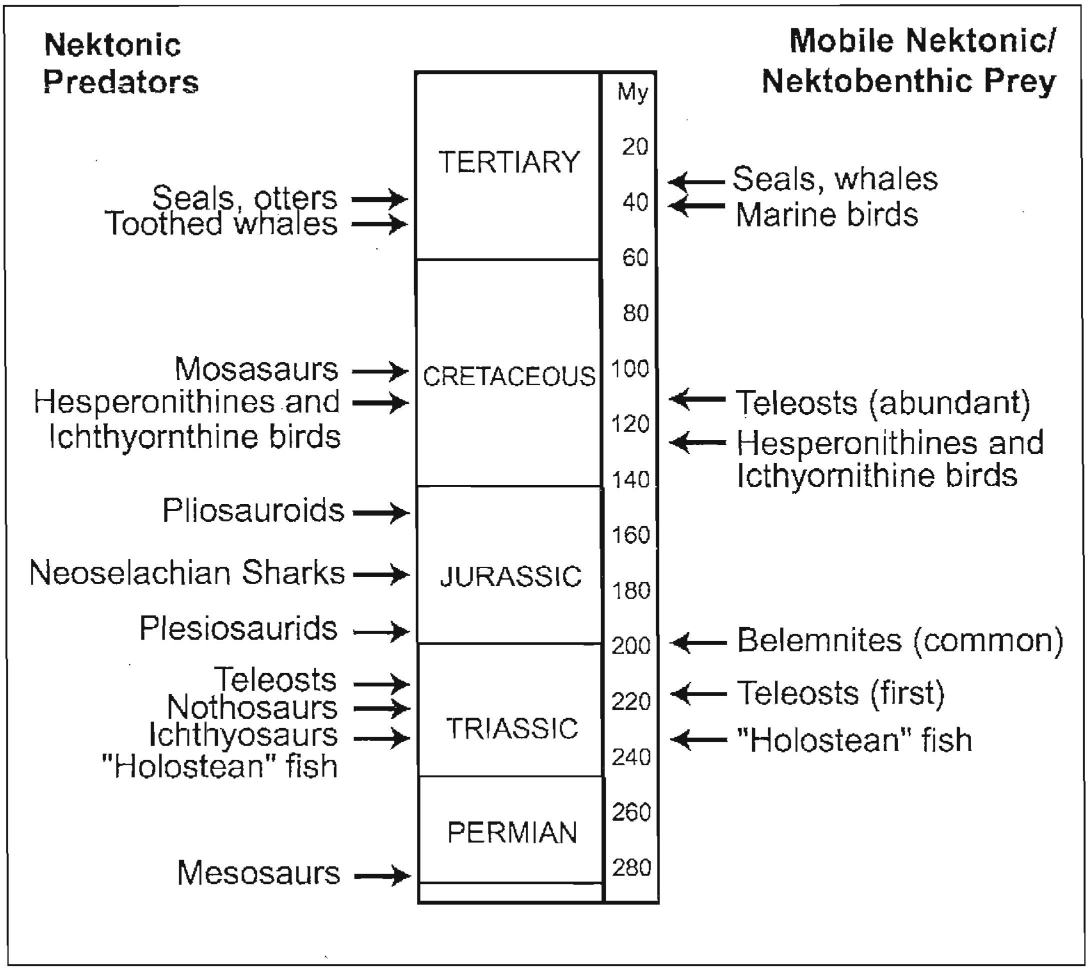


FIGURE 4—First appearances of major groups of Mesozoic and Cenozoic pelagic predators and potential prey. Arrows point to approximate time of first appearance of taxa.

The echinaceans developed carnivorous and herbivorous habits, and others started to bore into rock substrates. As noted, this latter could reflect an antipredation strategy, but there is little information available on predation-related injuries in these organisms during the Triassic.

JURASSIC PREDATORS

Much more is known about Jurassic predators chiefly because of the greater extent of epicontinental sea deposits compared to the Triassic. There are also many significant Lagerstätten from the Jurassic. Still, information concerning predator-prey relationships for the Jurassic is limited. Much of the evidence for vertebrate predation on Jurassic prey is circumstantial, based on overlapping faunal compositions of predator and prey, interpretation of tooth form, and attempts to match dental form with putative bite marks. Nevertheless, there is tantalizing evidence of predation. Fish (including sharks), ichthyosaurs and plesiosaurs are considered the dominant vertebrate predators (Figs. 1, 4; Tables 1, 2). These organisms could function as both pelagic and benthic predators, so their predatory activities cannot be exclusively tied to either of these realms (see Martill, 1990). Alternatively, some interpretations suggest that the dominant marine reptiles at this time were all pelagic predators

TABLE 3—Shell repair in bivalves and gastropods from Mesozoic and Cenozoic Localties. Only papers that cite their raw data, or semblance of such, are included in this table. According to Vermeij (1982, p. 233), the higher the frequency of scars, the greater is the role of the shell in protecting the gastropods against lethal breakage; if selection for armor is weak, then the frequency of repair should be low. The exceptional preservation required to detect shell repair is rare, especially in Paleozoic and Mesozoic gastropods (Vermeij et al., 1981).

Taxonomic Group; Age/Locality; Reference	**Evidence of Shell Repair**	**Calculation of Shell Repair Frequency**	**Range/Mean/median frequency**
Gastropods Upper Triassic; Northern Italy, St. Cassian Group, dolomites; species described Vermeij et al.(1982)	Broken edge is repaired; tiny chips ignored; some had only body whorls exposed, so not all shell areas were examined; small shells examined (<19mm)	Number of scars per shell	0.00–0.28/0.095*/no median n=558 indivs, 11 spp. *SEW calculated; differs from 0.08 reported in Vermeij et al., 1981. If 2 spp. were excluded that had zero shell repair, then the mean frequency would be 0.12.
Gastropods Cretaceous Ripley; species not described Vermeij et al. (1981)	Jagged trace of the outer lip where the latter has been damaged and subsequently repaired	Number of scars per shell	no range/0.35*/no median* *Their Note 5 states that median frequencies are reported in table 1; text states mean frequencies are recorded. SEW is assuming these are mean frequencies here. 24 species
Gastropods Miocene, all species, (Gatun 1–3); species not described. Vermeij et al. (1981)	As for Cretaceous Ripley	Number of scars per shell	0.19–0.33/0.40*/no median *SEW calculation of 0.29; this is based on mean frequency for all spp. from Gatun 1–3. 19 species
Gastropods Recent, all species (Panama, New Guinea, Mindanao, Hamahera, Guam) Vermeij et al. (1981)	As for Cretaceous Ripley	Number of scars per shell	0.08–0.44/0.28*/no median *SEW calculation: 0.28 is correct based on data presented.

(Table 3, cont.)

Bivlaves: Osteids, *Exogyra, Pycnodonte* Late Cretaceous (North Atlantic Coastal Plain, New Jersey) Dietl et al. (2000)	Repair scars that divert or cut across the normal concentric growth lamellae (including: scallops, meandering clefts, divoted repairs, and more extensive repairs including irregular fractures)	Total number of repair scars on left valves divided by the total sample size of repaired and uninjured valves	No median recorded. *Exogyra:* 0.00–1.11*/0.40; *Pycnodonte:* 0.12–0.38/0.23 Combined (*Exogyra* and *Pycnodonte*) mean frequency: 0.34 *Because more than one repair per shell was used, the frequency can exceed 1.0. x, Campanian: 0.11; x, Maastrichtian: 0.44 n =?528 or ?525 *Exogrya* spp., ?460 or ?450 *Pycnodonte* spp. for Cretaceous localities, total ~?988; they state n = "> 1600 indivs," 7 spp. (Paleocene + Cretaceous)
Bivalves: Ostreids, *Pycnodontes* early Paleocene Dietl et al. (2001)	As for bivalves	As for bivalves	0.07–0.09/0.08; for all size classes, mean = 0.10 (from their table 5) n = ?77, 1 sp. *Pycnodonta dissmilaris*
Gastropods lower Pliocene; Albenga, Italy Robba and Ostinelli (1975)	Jagged repair scars on shells	Number of individuals with one scar/total individuals of that species	Excluding samples with 1 individual: 0.03–0.59/0.29/no median (their table 10, p. 349–350) n = 3090 indiv.; 21 spp.
Bivalves: *Anadara* and *Corbula* only lower Pliocene; Albenga, Italy Robba and Ostinelli (1975)	Jagged repair scars on shells	As for gastropods	0.07–0.35/0.21 n=896, 2 spp. (corbulids had the highest shell repair frequency at 0.35)
Gastropods: Terebrids Eocene–Recent; tropical to subtropical Vermeij et al. (1981)	Repairs were recorded only if they extended 20% or more of the whole in a spiral direction or if they involved subjectively substantial breakage; excludes minor lip breaks	Number of repaired injuries divided by the total number of shells in the sample; frequency of repair is loosely correlated with the number of species of shell-peeling calappids	Median frequency reported (their table 1)*: Recent: n= 5735, 0.54; Pleistocene: n =110, 0.55; Pliocene, n = 314, 0.54; Miocene, n = 549, 0.57; Paleogene, n = 136, 0.47 * n must equal number of samples, but it is not clear; stated that samples with ten or more individuals were used; frequencies of repair have remained unchanged from the Eocene to Present
Gastropods: Littorinids Recent; cold temperate Rafaelli (1978)	No information; appears to be large, jagged repair scars (his fig. 1)	Frequency of snails with damaged shells estimated for each population	Many localities, here totaled together: 0.00–0.48/0.11 n = 4593

(Massare, 1987). Importantly, the range in tooth form and function in Jurassic (and Cretaceous) marine reptiles was at least as great as that of modern marine mammals (Massare, 1987).

Gastropods.—Although naticid mesogastropods (Fig. 6.4) existed in the Jurassic, boreholes are quite rare. However, recent discovery of drilled shells proves that the capacity for drilling predation did exist (Kowalewski et al., 1998).

Nautiloids.—Nautiloids were very diverse in the Paleozoic, but there were few nautiloids in the Mesozoic (House and Senior, 1981). Nautiloids are thought to have continued with their Paleozoic predatory mode of life, perhaps scavenging or preying on crustaceans (Fig. 1). A nautiloid with a complete jaw apparatus (rhyncolites) is known from lithographic limestone, Upper Jurassic of southwestern Germany (Dietl and Schweigert, 1999). Modern nautiloids can repair their shells (Meenakshi et al., 1974), although little is known about shell repair in Mesozoic nautiloids.

Ammonoids.—Shell shape in ammonoids is sometimes used to infer directly whether or not they were predatory. For example, large macroconchs of oxyconic forms are interpreted to be mobile predators (Westermann, 1996). Shell shape, sculpture (Fig. 6.1), and size (especially for macro- and microconchs) can also be explained by sexual dimorphism (Westermann, 1996). In terms of direct evidence, there is only one Early Jurassic example of an ammonoid (*Hildoceras*) with aptychi of juvenile ammonids within its body chambers (Westermann, 1996).

Middle Jurassic ammonoids appeared to occupy a number of trophic functional groups, from planktonic to demersal forms that presumably fed on ostracodes and microgastropods in algal mats (Westermann, 1996), although there is no data on gastric contents to confirm this. The lower Toarcian Posidonia shale (northwestern Europe) is known to have clusters of fragmented harpoceratine ammonoids, presumably from cephalopod predation (Lehmann, 1975). In turn, the stomach contents from a harpoceratine indicate that it preyed on small or juvenile ammonoids (Lehmann, 1975).

Finally, Late Jurassic ammonoids had trophically complex functional groups similar to those in the Middle Jurassic. Some ammonites may have fed on both the plankton and the benthos, depending on food availability and benthic anoxia. Ammonoid forms at this time had costae or nodose macroconchs, and microconchs with horns on some species; smooth shelled ammonoids were also common. Numerous records of ammonoid aptychi are reported from the body chambers of haploceratid ammonites, indicating predation; and specimens of the Late Jurassic ammonoid, *Neochetoceras*, have aptychi of conspecific juveniles within their body chambers, indicating cannibalism (Westermann, 1996, p. 676). A rare find of a *Saccocoma* crinoid among the stomach contents of *Physodoceras* is known from the Solnhofen Limestone (Milson, 1994). *Saccocoma* is variously interpreted as either planktic or benthic in habit (Milson, 1994), and depending on the interpretation of the life mode for *Saccocoma*, the ammonoid is interpreted as either a planktic or a benthic feeder (the latter interpretation is favored by Westermann, 1996).

Echinoderm Predators.—Living families of asteroids (e.g., Forcipulatida and Notomyotida) have their roots in the Early Jurassic (Hettangian) of Germany and Switzerland (Blake, 1993). Complete asteroids are exquisitely preserved in pelletoidal calcarenite from this time period. Modern forcipulatids are known to prey on other echinoderms, molluscs, barnacles, and many other types of invertebrates. The presence of many arms in asteroids (e.g., solasteroids) suggests that they were predators of active prey, such as other asteroids. Predation on active prey by solasteroids most likely evolved in the Jurassic (Blake, 1993).

Asteriids, in contrast, continued to feed on molluscs and other benthic prey as their Paleozoic ancestors did. During the Jurassic, asteriids had prominent adambulacral spines that their modern descendants no longer have; it is thought that these spines functioned to trap prey (Blake, 1993).

Decapods.—Despite the common assumption that shell-crushing crabs evolved during the Jurassic, in reality, only one group of lobsters (the Nephropidae) is known to have evolved during this time. All other groups evolved during either the

Paleozoic, Triassic, or Cenozoic (Table 1). Hermit crabs evolved in the Jurassic (Glaessner, 1969), and while they may crush mollusc shells (Vermeij, 1987), it is difficult to assess their overall importance as predators on molluscan groups. Hermit crabs can be scavengers, carnivores, filter feeders, or detritivores (Schram, 1986).

Chondricthyes.—The rapid radiation of sharks and marine reptiles (Figs. 1, 4) in the middle Mesozoic may have been triggered by the rise of vast numbers of squids and actinopterygian fishes, including semionitids and basal teleosts (Theis and Reif, 1985). The advances of increased swimming efficiency and maneuverability, and sensory ability enabled the neoselachians to pursue fast-swimming thin-scaled fishes and squids in nearshore environments (Packard, 1972).

Hybodont sharks of the Triassic (Fig. 5.4) were largely supplanted by the expanding neoselachian sharks during the Late Jurassic. The evolution of highly flexible, hyostylic jaws clearly marked a new level of sophistication in shark predation (Maisey, 1996). In hyostylic suspension the upper jaw is loosely articulated to the braincase and can by swung downward and forward on the hyomandibular bone. This enables sharks to thrust the jaws forward and gouge out large chunks of flesh from prey. This adaptive breakthrough fomented an adaptive radiation of sharks, which continued through the present day. Modern sharks show varied feeding modes, including grasping and swallowing, suction feeding, cutting, gouging, and crushing (Moss, 1977). One strongly modified clade from within the neoselachian shark lineage is the highly successful Batomorpha: rays and skates. These first appeared in the Late Jurassic but diversified in the Cretaceous. The dental plates of rays and chimaeroids of this type may be used for digging up shelled invertebrate prey, and then crushing them, leaving only fragments.

Osteichthyes.—Among the Jurassic bony fishes there is evidence for common piscivorous habits; for example, the famed Upper Jurassic Solnhofen Limestone provides many instances of predator-prey interactions (Voihl, 1990). Most "fossilized interactions" involve fish carcasses containing partially ingested smaller fish. Jurassic pycnodont reef fish developed deep-bodied morphologies. For example, *Daepedium* (Fig. 5) was a deep-bodied Jurassic marine fish with heavy ganoid scales, but with pebble-like teeth for crushing. Jurassic pycnodonts evolved batteries of rounded, shell-crushing teeth, plus specialized nipping teeth. A few pycnodontids even developed stout pavement teeth possibly for crunching corals; rare specimens have been found with coral fragments in the gut (Viohl, 1990). The general morphology of these fishes overlaps with that of deep-bodied platysomids of the Paleozoic and many reef-dwelling Cenozoic teleosts.

Fish with durophagous dentition, such as Semionotidae (*Lepidotes*, *Heterostrophus*), Pycnodontidae (*Mesturus*), as well as hybodont sharks (*Asteracanthusare*) and chimaeroids (*Brachymulus*, *Pachymylus*, *Ischyodus*), are thought to have been predators of ammonoids from the Middle Jurassic of the Lower Oxford Clay of England (Martill, 1990). Many well-preserved ammonoid fragments are thought to be the result of fish predation rather than physical factors (Martill, 1990). One ammonite specimen, a *Kosmoceras*, was found to have bite marks that were similar to the dental battery of the semionotid fish, *Lepidotes macrocheirus* (Martill, 1990).

Sea turtles.—Turtles are the only living reptiles that are fully adapted to a marine existence (except for egg laying). Many fossil sea turtles are only known from their plastron and carapace (Nicholls, 1997). The earliest sea turtles are the Plesiochelyidae, possible predators that lived in shallow, coastal waters.

Sauropterygians: *Plesiosaurs and pliosaurs*.—The plesiosaurs are thought to have diversified into two major grades during the Jurassic (Fig. 5; Table 2): the short-necked forms as fast-swimming pursuit predators (pliosaurs), and the long-necked forms as lurking ambush predators (plesiosauroids and elasmosaurids). O'Keefe (2002), however, has called this an oversimplified view of their actual morphological diversity.

A cladistic analysis revealed that plesiosaurs present a spectrum of body forms, and do not

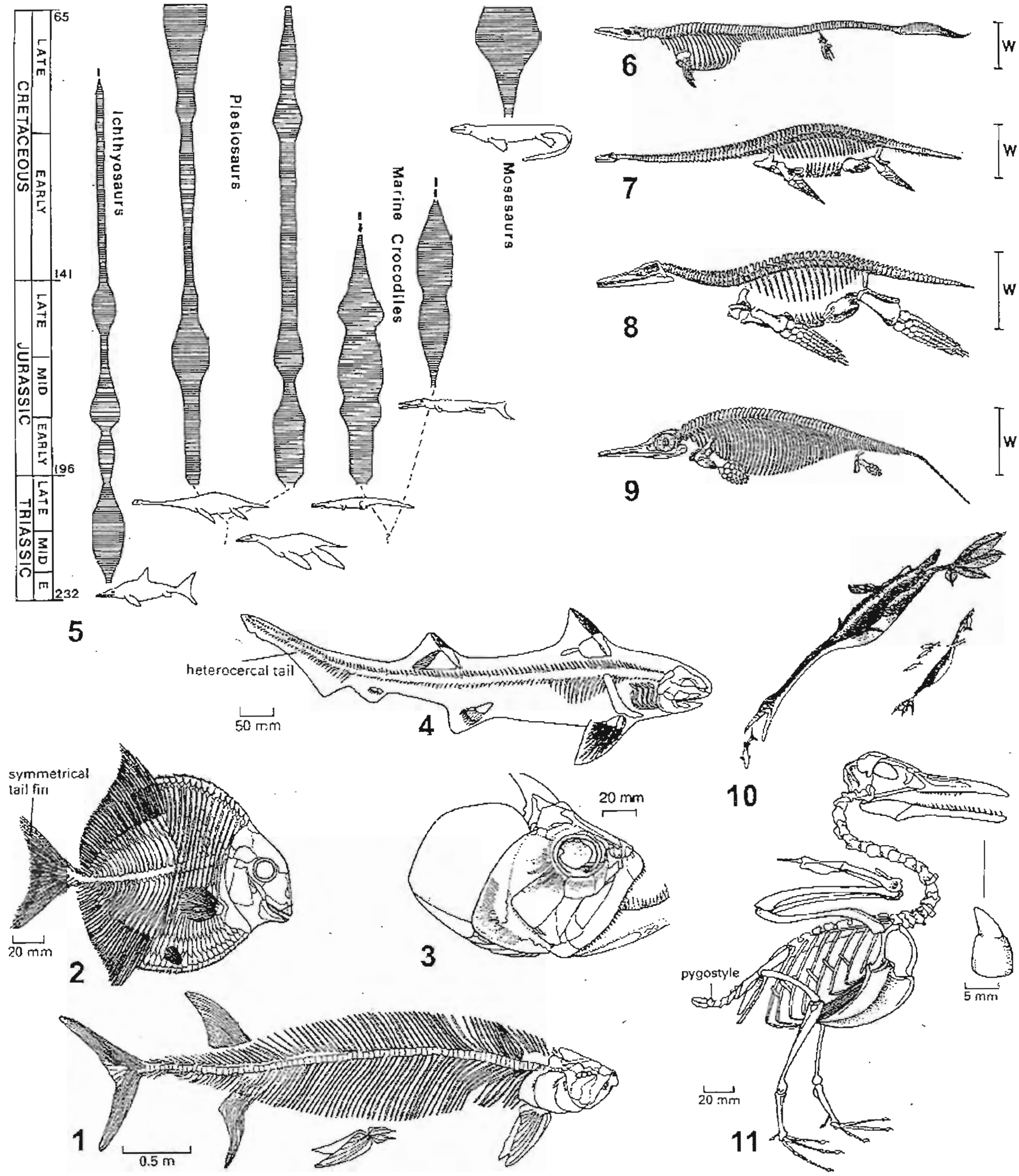


FIGURE 5—Mesozoic predatory marine vertebrates. 1, Cretaceous ichthyodectid teleost *Xiphactinus*. 2, Skeleton of the pycnodontid fish *Proscinetes*, Jurassic. 3, Skull of ichthyodectid teleost fish *Cladocyclus*, Cretaceous; Late Cretacous. 4, Hybodid shark, *Hybodus*. 5, Geologic distribution of marine reptiles, from left to right: ichthyosaurs, plesiosauroids, pliosauroids, teleosaurs, metriorhynchids, and mosasaurs. 6–9, Skeletons of Mesozoic marine reptiles: 6, Mosasaur *Plotosaurus*, Late Cretaceous. 7, Plesiosauroid *Muraenosaurus;* Jurassic. 8, Pliosauroid *Peloneustus;* Late Jurassic. 9, Ichthyosaur *Ophthalmosaurus;* Early Jurassic. 10, Cretaceous foot-propelled diving bird *Hesperornis*. 11, Skeleton of Creaceous marine bird *Ichthyornithyes*. Figures 1–4, 10, 11 adapted from Benton (1997); Figures 5–9 from Massare (1987).

discretely fall into two basic shapes: from the long-necked, small-headed elasmosaurs to the short-necked, large-headed pliosauromorphs (O'Keefe, 2002). By the Late Cretaceous, these pelagic marine reptiles were globally distributed (Rieppel, 1997). But the taxonomy of this group is still poorly known because of the inadequacy of type material, and preservational problems such as skull-less skeletons (Carpenter, 1997).

The plesiosaurs (clade Plesiosauria) were among the most diverse, geologically long-lived, and widespread of the Jurassic to Cretaceous marine reptiles, with a fossil record extending from the Triassic-Jurassic boundary to the Late Cretaceous (Figs. 5.5, 5.7) (Carroll and Gaskill, 1985; Rieppel, 1997). These large reptiles (up to 15 m long) had long paddle-shaped limbs (considered hydrofoils), short tails, long necks, needle-shaped conical teeth, and may have swam like modern sea lions (Godfrey, 1984; Carroll and Gaskill, 1985). Plesiosaurs are the only marine animals in which both forelimbs and hindlimbs performed as lift-based appendicular locomotion (i.e., as hydrofoils; Storrs, 1993). Pliosaurs had large skulls (up to 3 m) and jaws with large fang-like teeth (Taylor, 1992), and were capable of dismembering their prey (Taylor and Cruickshank, 1993).

The small relative skull size and neck length of plesiosaurs, in addition to their dentition, suggests that many of them may have fed on small fish and soft-bodied cephalopods; some may have also strained the water for prey (Massare, 1987; Rieppel, 1997). Their evolution may have been stimulated by the new abundance of larger actinopterygian fishes and sharks in offshore marine environments. Plesiosaurs from the Middle Jurassic of the Oxford Clay also are thought to have been specialists on soft-bodied cephalopods and fish (Martill, 1990). The gastric contents of one Late Jurassic plesiosaur, *Pliosaurus brachyspondylus*, included cephalopod hooklets (Tarlo, 1959). Wetzel (1960) has reported small ammonites in coprolites attributed to plesiosaurs.

Case studies from the Middle Jurassic Oxford Clay, United Kingdom, provide a window into the marine trophic relationships of this time period. The carnivorous plesiosaurs (*Liopleurodon*, *Pliosaurus*) were considered to be at the top of the Middle Jurassic food chain, presumably feeding on fish and "naked" (without a shell) cephalopods (Martill, 1990). The ichthyosaur *Ophthamosaurus* was thought to be a specialist on naked cephalopods, while marine crocodilians (*Metriorhynchus*, *Steneosaurus*) presumably fed on fish and naked cephalopods (Martill, 1986a, 1986b, 1990). Massare (1987) examined the conical pointed teeth form of some Jurassic ichthyosaurs and plesiosaurs, and concluded that the teeth functioned to pierce soft prey. Fish from these deposits were either plankton feeders or fed on smaller fish, indicating that the Middle Jurassic had a highly complex marine food web (Martill, 1990).

Ichthyosaurs.—Lower Jurassic localities from Europe (e.g., Lyme Regis, England; Holzmaden, Germany) indicate that marine reptile guilds at this time were dominated by a diverse array of ichthyosaurs (Figs. 5.5, 5.9) (Massare, 1987). Gastric contents from ichthyosaurs are known from Lower Jurassic localities in Europe (Pollard, 1968; Keller, 1976; Massare, 1987). The majority of preserved food remains were cephalopod hooklets (Massare, 1987, her table 1, p. 128). For example, preserved cephalopod hooklets (interpreted to be from belemnites), fish remains, and wood were present in the gastric contents from the small (< 3 m) Lower Jurassic ichthyosaur *Stenopterygius* (Keller, 1976). Putative phragmoteuthid cephalopods also were preserved in the stomach contents of the small Lower Jurassic icthyosaur, *Ichthyosaurus* (Pollard, 1968). No belemnite hardparts (besides hooklets) have been reliably found in ichthyosaur gut contents (Massare, 1987; but see Pollard, 1968). In contrast to the Lower Jurassic, Middle to Late Jurassic assemblages indicate a number of changes in the vertebrate predatory ensemble (Massare, 1987). Although the same functional feeding types (based on tooth form and wear) were present, the reptile groups were different, with pliosauroids and crocodiles dominating the assemblages, and with reduced ichthyosaur diversity (Massare, 1987). The Middle Jurassic cephalopod-eating ichthyosaur, *Ophthalamosaurus* (Fig. 5.9) is inferred to have dived to depths of 600 m, based on an analysis of its eyes and bone condition (Motani et al., 1999). Ichthyosaurs are also thought to have regurgitated hardparts of indigestible food. In the Peterborough quarry in England, Peter Doyle (unpublished, 2002) discovered "ichthyosaur regurgitates" of 160 million-year-old acid-etched juvenile belemnites. The acid-etched fossils indicate that they were once within the ichthyosaur stomach.

Marine Crocodiles.—Little is known about the fossil history of marine crocodiles (Suborder Mesosuchia) compared to other marine reptiles (Hua and Buffetaut, 1997). The earliest crocodiles (Teleosauridae) are known from the Early Jurassic. This group shows little adaptation for marine life, and it is only because they are found in shallow marine deposits that they are inferred to have been marine crocodilians (Hua and Buffetaut, 1997). Later in the Jurassic, these forms showed anatomical features that were more characteristic of life in marine conditions (e.g., streamlined skull, reduction in bony armor, and reduction of the forelimb). Some forms (*Steneosaurus*) had long, slender teeth and may have been piscivorous. Other teleosaurids had blunt teeth, and more robust jaws, and are thought to have been durophagous predators on ammonoids or sea turtles (Hua and Buffetaut, 1997).

The Early Jurassic to Early Cretaceous Metriorhynchidae include crocodilians with both long (longirostrine) and short (brevirostrine) snouts that may reflect dietary differences (Hua and Buffetaut, 1997). This group, because of its more streamlined body form and a skull similar to mosasaurs, is thought to have been pelagic. The stomach contents of a brevirostrine form (*Metriorhynchus*) contained ammonites, belemnites, pterosaurs (*Rhamphorhynchus*), and the large fish *Leedsichthys* (Martill, 1986b). *Metriorhynchus* and their ilk were probably lunging ambush predators that captured their prey by sudden bursts of swimming (Massare, 1987).

Two other groups of marine crocodiles, the Pholidosauridae (Lower-Upper Cretaceous boundary) and Dryosauridae (Upper Createceous to late Eocene) had fresh- and salt-water members (Hua and Buffetaut, 1997). The marine species of Pholidosauridae (*Teleorhinus*) are thought to have been piscivorous. Two groups of marine dryosaurids (Phosphatosaurinae and Hyposaurinae) are known: the phosphatosaurins had blunt teeth and robust jaws, and are thought to have preyed upon turtles and nautiloids; the hyposaurins, most common in the Paleogene, had long slender jaws and pointed teeth and were probably piscivorous (Hua and Buffetaut, 1997). Crocodilians are known to undergo rapid changes in dental morphology in response to environmental change related to dietary modification. It is thought that the piscivorous mode of life became more common after the Cretaceous mass extinction, when ammonoids and hard-shelled marine reptiles were not as common (Denton et al., 1997). However, the extinction of the dryosaurids in the Eocene is thought to have resulted from the expansion of whales, which may have competed with them for food (Hua and Buffetaut, 1997). Crocodiles also regurgitate their prey and such remains have been reported from the Paleocene of Wyoming (Fisher, 1981a, 1981b) but not from the Cretaceous.

CRETACEOUS PREDATORS

The Early Cretaceous marked the beginnings of a major reorganization of marine predators, including the rise of neogastropods, numerous cephalopod predators, and several new vertebrate predatory guilds (Figs. 1, 4–6). The Early Cretaceous saw the radiation of large teleost fish (> 3 m in length) and sharks, and the non-dominance of marine reptiles (Massare, 1987). Massive shell-crushing mosasaurs (e.g., *Globidens*) did not evolve until the Late Cretaceous. This major specialized functional feeding type had been essentially absent throughout most of the Mesozoic, since the extinction of Triassic placodonts (Massare, 1997). Late Cretaceous marine reptiles were dominated by ambush predators, such as mosasaurs; marine fish (including sharks) were much more common at this time and became more dominant components of the predator functional feeding guild than ever before in the Mesozoic. Marine reptiles such as plesiosaurs and ichthyosaurs were minor components of the Cretaceous predatory

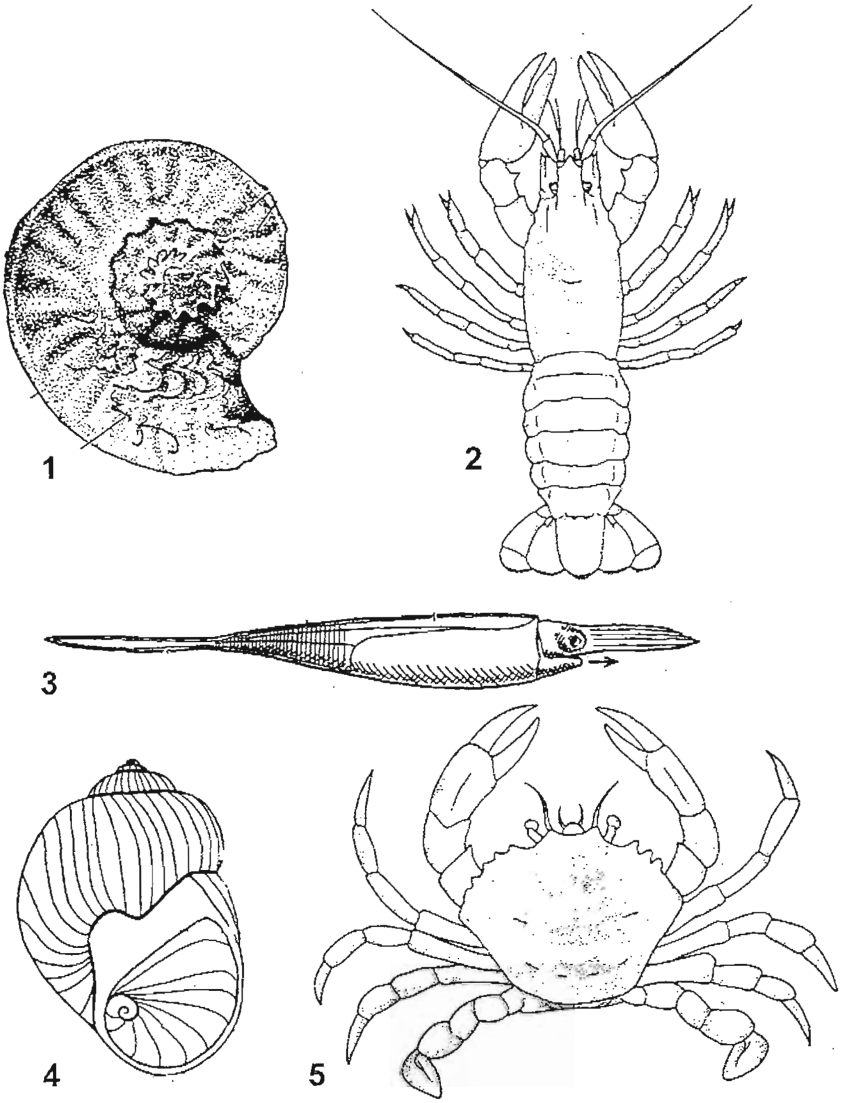


FIGURE 6—Representative Mesozoic marine invertebrate predators. 1, Ammonoid; note fluted ornamentation. 2, Homarid lobster. 3, Belemnite; *Belemnitella.* 4, Naticid gastropod. 5, Brachyuran crab. 1, 3 from Tasch (1980); 2, 4, 5 from Robison and Kaesler (1987).

food webs. In fact, ichthyosaurs and the pholidosaur marine crocodiles became extinct in the Early Cretaceous, and pliosaurids were rare (Massare, 1997). Ichthyosaur extinction may have been associated with the Cenomanian-Turonian boundary events, following a severe depletion in their putative belemnite prey (Bardet, 1992). During the Cretaceous and Tertiary, the offshore movement of fast-moving fishes and coleoids may have stimulated evolution of offshore hunting among the neoselachian sharks (Benton, 1997).

Gastropods.—The Cretaceous marks an important time of evolution in the predaceous shell-drilling gastropods. Several groups appeared and/or diversified during the Late Cretaceous and their distinctive drilling traces (*Oichnus*) become common at this time (Kowalewski et al., 1998). Naticids (Figs. 6.4, 7, 8.3) become abundant in the Late Cretaceous as do their diagnostic boreholes (Fig. 8.4) (see reviews by Kabat, 1990; Kowalewski, 1993). The drilling frequencies in some Cretaceous samples equal or exceed those observed in early Cenozoic samples from the Gulf Coastal Plains (Kelley and Hanson, 1993, 2001; Kelley et al., 2001; see discussion below). These studies are possible because naticids leave a unique type of countersunk drillhole in scaphopod, bivalve, gastropod, and conspecific gastropod prey, as well as other organisms (Carriker and Yochelson, 1968; Sohl, 1969; reviewed by Kabat, 1990; Kowalewski, 1993).

Muricids (Neogastropoda) also evolved in the Late Cretaceous; predaceous muricids produce characteristic cylindrical, non-chamfered boreholes (Fig. 8.3). Muricids form an ecletic gustatory group, ranging from herbivores to carrion feeders; however, most are shell drillers (Kabat, 1990). Shell drilling is most likely a pleisomorphic behavioral trait within the Muricidae, although not all muricid genera bore through hard exoskeletons (Vermeij and Carlson, 2000). In contrast to naticid

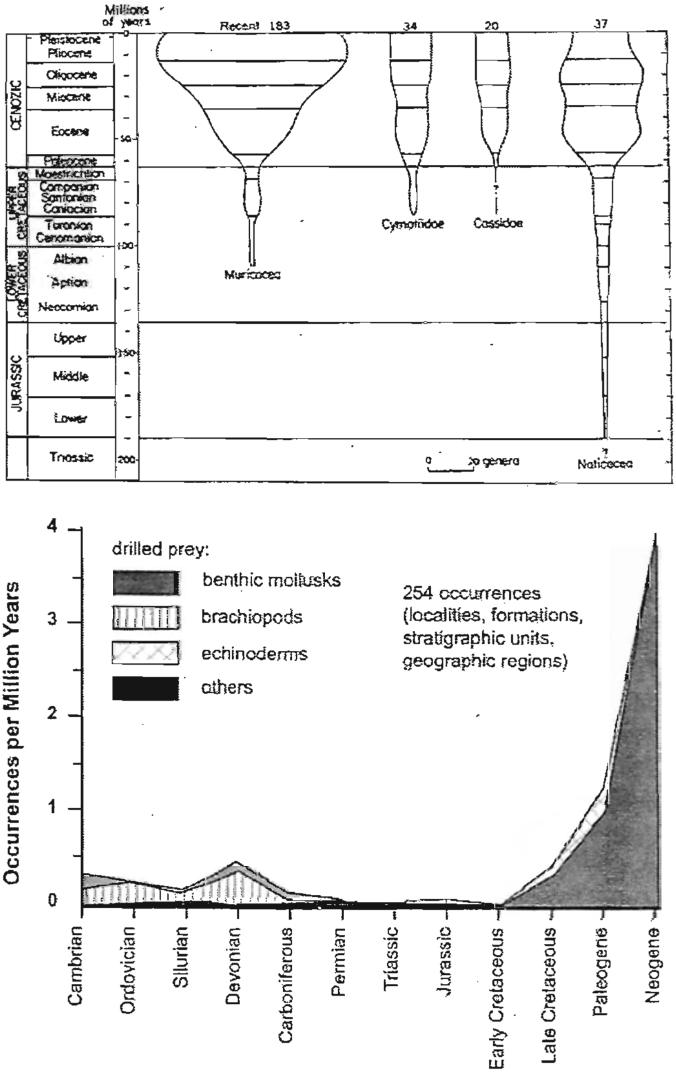


FIGURE 7—Diversification patterns of shell drilling through time: upper figure shows diversity of drilling gastropod clades through the Mesozoic and Cenozoic eras; lower figure shows frequency of drilled prey per million years through the Phanerozoic. Adapted from Sohl (1969) and Kowalewski et al. (1998).

boreholes, holes drilled by muricids are considerably less frequent in the Cretaceous than in most Eocene and younger samples (Vermeij, 1987).

Cephalopods.—As in the Jurassic, there were a host of belemnoids, ammonoids and nautiloids present in the Cretaceous (Fig. 6). All of these were probably nektonic predators, though their food may have ranged from zooplankton and larvae to other cephalopods (Packard, 1972). Cretaceous octopi are also known. While modern nautiloids appear to be extensively drilled by octopods (Saunders et al., 1991), no data exists for drilling predation on Mesozoic nautiloids. As in the Jurassic, Cretaceous ammonoids are thought to have been carnivorous. However, many species are thought to have eaten zooplankton (Ward, 1986).

Stomatopods.—Stomatopods are known to have extreme specialization in their limbs that is related to their predatory activities; no other major extant malacostracan group has such specialization (Kunze, 1983). All stomatopods are obligate carnivores (Table 1)—they eat only live prey—and use their large raptorial second maxillipeds for prey capture (Kunze, 1983). These folding raptorial thoracopods can be used in two ways: as either smashing or spearing appendages. Folding raptorial thoracopods are known from the Carboniferous palaeostomatopods (Schram, 1969), and within the Mesozoic forms. The extant superfamilies of stomatopods are thought to have originated in the Cretaceous (approximately 100 Ma; Ahyong and Harling, 2000); however, the true fossil record of this group begins in the Cenozoic, and will be discussed in that section.

Based on fossil mouthparts, specialization for the stomatopod's zealous carnivorous life style evolved very early, by the Late Devonian or Early Carboniferous, and the trend continued into the Mesozoic (Schram, 1979). Mouthparts shred the prey, and food is stuffed into the mouth, not unlike the way an energetic, hungry teenager feeds. Undigestible shell and cuticular material is regurgitated. The regurgitated remains have not been examined from a taphonomic perspective.

Decapods.—In contrast, to stomatopods, decapods are not obligate carnivorous predators; most are scavengers (Schram, 1986). The majority of the durophagous forms evolved in the Cenozoic, with just a few forms evolving in the Cretaceous (Table 1). The portunids and xanthids evolved in the Cretaceous, and today are generalist and opportunistic feeders, occasionally eating hard-shelled prey like molluscs. The slipper lobsters may have evolved in the Late Cretaceous, and they are thought to feed on scyphozoans (Table 1).

Chondricthyes.—The neoselachian sharks radiated during the Cretaceous. Cartilaginous shark skeletons do not fossilize well, and consequently, their teeth are used to infer their feeding behavior (Shimada, 1997). Despite popular accounts that Cretaceous sharks were some of most voracious of all predators, it is still not clear whether their attacks were on live or scavenged organisms. Healed injuries are usually taken to be attacks on live prey, but these are rare in the fossil record. Necrosis around bite marks is also used to infer predatory shark attacks (Schwimmer et al., 1997). Additionally, animals associated with shark remains are usually interpreted as the shark's last meal or as associative potential prey. For instance, in the Late Cretaceous Niobrara Chalk, a lamniform shark (*Cretoxyrhina mantelli*) is accompanied by well-preserved cartilagenous skeletal elements presumably from its last meal, the fish *Xiphactinus audax* (Shimada, 1997).

Late Cretaceous lamniform sharks (*Cretoxyrhina*) up to 6 m in length attacked or scavenged mosasaurs and perhaps plesiosaurs, and, in turn, were themselves possibly attacked or scavenged by other sharks (anacoracids; Shimada, 1997). Dental arcades of *Cretoxyrhina* are similar to those of modern predatory mako sharks, and, not surprisingly, they belong to the Family Lamnidae that includes the mako (*Isurus*), great white (*Carcharodon*), and salmon shark (*Lamna*) (Shimada, 1997). Although shark taxa are different through geologic history, Late Cretaceous sharks' functional feeding capabilities in ecosystems show parallels to modern sharks (Shimada, 1997).

Direct evidence of shark predation on mosasaurs is very rare. Shimada (1997) discusses several reports of putative shark attacks on mosasaurs, either

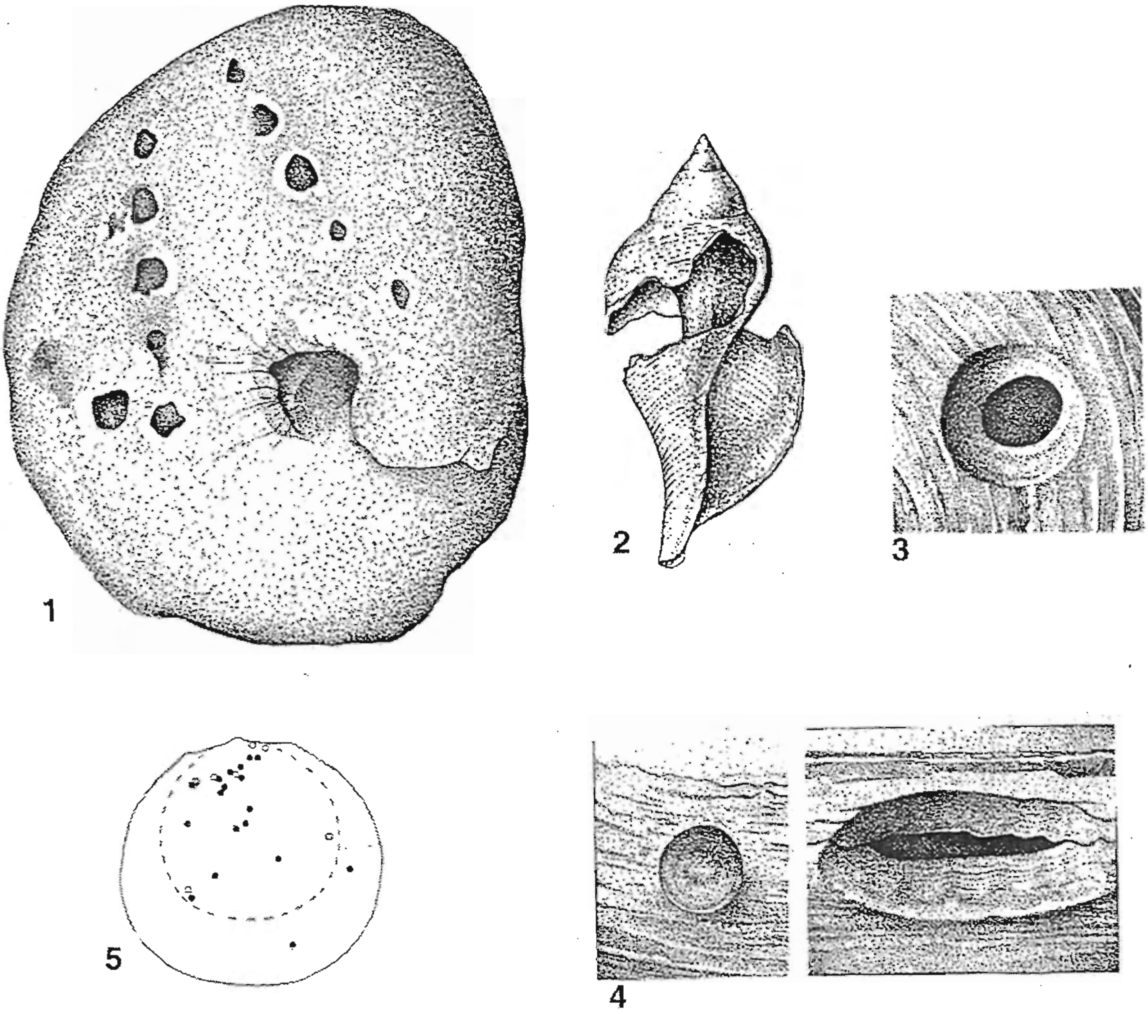


FIGURE 8—Traces of predation in fossil and Recent shells. 1, Shell of Cretaceous ammonite *Placenticeras* with rows of punctures, probably made by a mosasaur. 2, Recent gastropod shell (*Fasciolaria*) exhibiting peeling damage inflicted by a callapid crab, ×1. 3, 4, Profile views of incomplete and complete gastropod drill holes in cross sections of bivalve shell: 3, cylindrical muricid drill holes; 4, typical naticid holes; note parabolic cross section and central boss in incomplete borehole. 5, Locations of most frequent drill holes in Recent bivalves from the Niger Delta. Redrawn from photographs in the following sources: 1, Kauffman and Kesling (1960); 2, Bishop (1975); 3, Reyment (1971); 4, Sliter (1971). Figure modified from Brett (1990).

with shark teeth embedded in bone, tooth marks slashed into the bone, or evidence of gastric-acid etching on putative prey items. Rothchild and Martin (1990) report on a shark tooth embedded in mosasaur (*Clidastes*) bone, which subsquently was repaired and ultimately caused spondylitus. Bite marks on mosasaurs without evidence of healing are also reported (Hawkins, 1990). Shark bite marks are also known from elasmosaurid plesiosaur bones (Williston and Moodie, 1917; Welles, 1943).

Late Cretaceous galeomorph selachian sharks (*Squalicorax*) are thought to have been scavengers par excellence in the eastern Gulf Coastal Plain and Western Interior of the United States (Schwimmer et al., 1997). All living neoselachian sharks are carnivores, while galeomorph sharks may prey on mollusks, crustaceans, and vertebrates; *Squalicorax* is also thought to scavenge many types of prey (see table 1 of Schwimmer, et al., 1997). Evidence of scavenging may include embedded teeth which do not show evidence of wound healing or tissue necrosis, and shark teeth associated with putatively scavenged remains (Schwimmer et al., 1997). *Squalicorax*, a moderately sized shark at 3.5 m, had serrated dentition of the "cutting type," which may indicate relatively diverse feeding strategies. Isolated *Squalicorax* teeth, sometimes with associated bite marks, were reported embedded in a decayed mosasaur vertebra and a juvenile hadrosaur metatarsal (Schwimmer et al., 1997). Putative gut contents from *Squalicorax* include mosasaur limb bones (Druckenmiller et al., 1993).

Even fewer examples are known of shark attacks on benthic invertebrates. Molluscan shells, such as those of inoceramid bivalves, are known to have marginal edge fragmentation, and frequently are preserved as fragmented remains sometimes associated with the putative shell-crushing shark, *Ptychodus* (Kauffman, 1972). One inoceramid specimen, *Inoceramus tenuis*, is described as having shell injuries on its left valve perhaps directly stemming from *Ptychodus* predation (Kauffman, 1972). The right valve is uninjured, and Kauffman (1972) explains that this lack of injury is compatible with the life habits of the inoceramid, as the left valve was more exposed. Speden (1971) interprets aggregations of fragmented inoceramid shells from Late Cretaceous sites in New Zealand as evidence of regurgitated or fecal material from vertebrate predators. Inoceramids are usually found in quiet, deep-water settings, either in chalks or black shales (Kauffman, 1972)—thus, any information on their potential predators would illuminate the little-known paleoecology of deep-water fauna in the Late Cretaceous.

The batoid rays and skates first appeared in the Early Jurassic and diversified during the Late Jurassic and Cretaceous (Benton 1997; see also Vermeij, 1987). These specialized elasmobranchs were adapted in large part for durophagous benthic predation. Rays evolved stout hypermineralized pavement plates for crushing hard-shelled prey, such as crustaceans and molluscs (Fig. 9). Ray dentition is thus similar to the pavement teeth of Devonian ptyctodonts and rhenanids, and late Paleozoic holocephalans, Triassic–Jurassic semionotid fish, and Triassic placodonts. In all cases, crushing of hard-shelled prey is inferred, but of these groups certainly the batoid rays have been most successful. Many rays, exemplified by the cow nose rays, are capable of excavating shallow pits in sandy substrates in pursuit of infaunal bivalve, gastropod, polychaete, and other prey (see Fig. 12). Possible ancient ray pits have been reported from deposits as old as Late Cretaceous (Howard et al., 1977).

Osteichthyans.—The neoselachian radiation saw its counterpart in the Cretaceous osteichthyan teleost fishes (Fig. 5.1–5.3). The achievement of improved buoyancy via swim bladders, development of deep bodies, and anterior placement of pectoral and pelvic fins, represent coordinated adaptations for increased swimming efficiency and maneuverability during the Jurassic Period. During the Late Cretaceous, the development of hinged maxillae-premaxillae and highly protrusible mouths further gave rise to a new mode of suctorial predatory feeding. These adaptations in turn fostered a major adaptive radiation of neoteleost predators in the sea and in fresh water.

In the Cretaceous, large basal teleosts clearly dominated in the intermediate- to large-sized fish-eating predator guild. Many specimens of the large *Xiphactinus* (Fig. 5.1) from the Cretaceous of North America have been found with ingested fish in the body cavity. These include specimens from Kansas with as many as ten fish in the stomach and a 4.5-meter specimen with a 1.6-meter related ichthyodectid fish inside (Benton, 1997). Specimens of the pavement-toothed *Tribodus* from the Cretaceous Santana Formation of Brazil had stomach contents that included shrimp and fragmentary molluscan shells (Maisey, 1996).

Advanced acanthomorph teleosts evolved

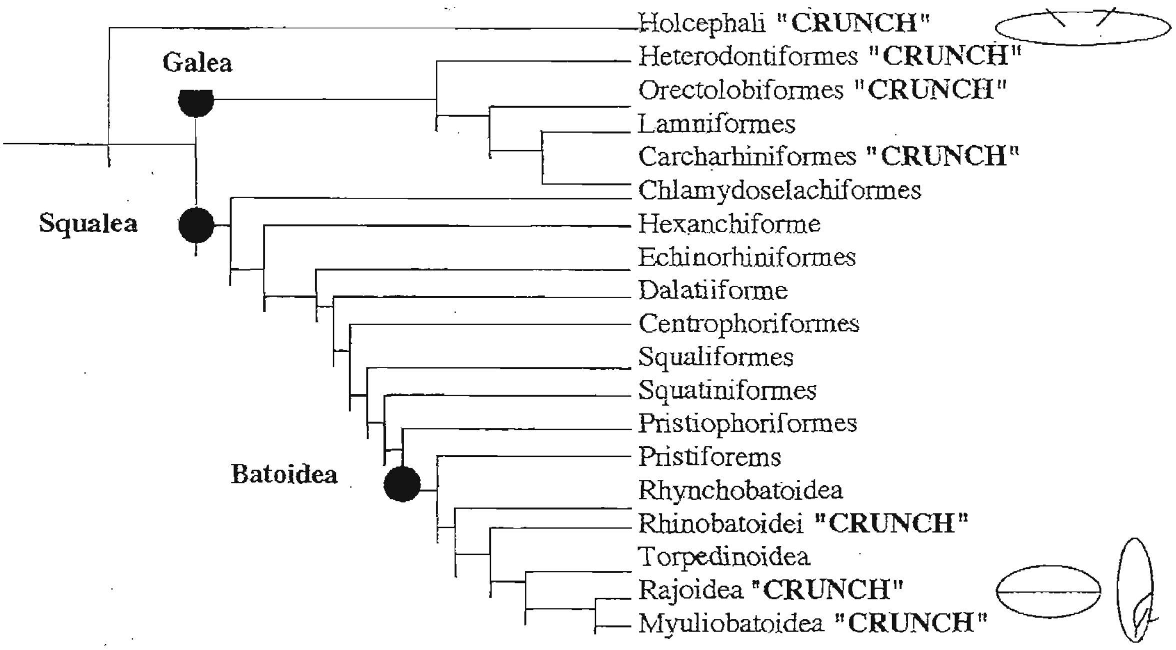


FIGURE 9—Cladogram of chondrichthyes (sharks) showing the repeated evolution of durophagy (indicated by "CRUNCH"; after Wilga and Motta, 2000).

further defense in the Late Cretaceous–Tertiary, without substantial loss of mobility, in the form of erectile fin spines. These adaptations may indeed have made the swallowing of whole prey sufficiently difficult that individuals possessing longer, sharper fin spines were frequently spared and/or avoided by experienced predators, thus driving adaptive trends in neoteleosts (Patterson, 1994).

Sea turtles.—Although modern turtles are all morphologically similar, Mesozoic sea turtles were far more disparate (Hirayama, 1997). There were up to three separate radiations of sea turtles in the Mesozoic (Nicholls, 1997). The Plesiochelyidae evolved in the Jurassic. The second group (Pelomedusidae) is presently restricted to fresh water, but in the Late Cretaceous and Early Tertiary, members of this group were present in shallow marine environments (Nicholls, 1997). The third group (Chelonioidea) first appeared in the late Early Cretaceous and includes the Dermochelyidae, Cheloniidea, and the Protostegidae (Hirayama, 1997). Of these, the jellyfish-eating stock (Dermochelyidae) arose in the Santonian and is still extant, and the other omnivorous and herbivorous groups (Cheloniidae) arose in the Aptian and are still extant, having reached a diversity peak during the Late Cretaceous (Hirayama, 1997). The Protostegidae were restricted to the Late Cretaceous. The Chelonidae and Dermochelyidae survived the mass extinction at the end of the Cretaceous, while most other marine reptiles, with the exception of the crocodiles, went extinct. The skull of Late Cretaceous Protostegidae turtles is similar to that of the modern freshwater molluscivorous turtle (*Malayemys*). Based on this similarity, it may have fed on pelagic ammonoids (Hirayama, 1997). The Protostegidae were the largest sea turtles known, characterized by massive heads, like that of the late Campanian *Archelon*. This gigantism was short-lived, as the Protostegidae went extinct before the end of the Cretaceous (Hirayama, 1997). The skulls of the Dermochelyidae are imperfectly known; however, it appears that the narrow lower jaw and other skeletal features suggest that the jellyfish-eating mode was developed during the Cenozoic (Hirayama, 1997).

Plesiosaurs.—Plesiosaurs are thought to have been top predators of Mesozoic seas, but there has been little evidence to support this claim (Sato and Tanabe, 1998). The oldest firm evidence of predator-prey associations between ammonoids and plesiosaurs is from a Late Cretaceous (Upper Cenomanian) outcrop from Hokkaido, Japan. From this locality, Sato and Tanabe (1998) describe gastroliths, 30 isolated and disarticulated ammonoid jaws, a shark tooth, and molluscan shells from the putative gastric contents of a polycotylid plesiosaur. While the head of the plesiosaur was missing, comparable teeth in other polycotylids suggest that they were poorly adapted to crush ammonite shells, and may have swallowed their prey whole. Plesiosaur gastric contents from the Early Cretaceous are known to include cephalopod jaws in association with gastroliths (Sato and Tanabe, 1998). Gastric residue from other Late Cretaceous plesiosaurs, however, had fish vertebrae, pterodactyl bones, and thin-shelled ammonites (Massare, 1987, her table 1, p. 128).

Mosasaurs.—Mosasaurs originated and diversified worldwide in less than 25 million years during the Late Cretaceous (Fig. 10), but met their untimely demise during the end-Cretaceous extinction event (Lingham-Soliar, 1999). By the time of their origin, the ichthyosaurs had gone extinct, and only a few plesiosaur families were still extant (Lingham-Soliar, 1999). Not since the Triassic placodonts, had a reptile group so dominated the durophagous functional lifestyle (Massare, 1987). Mosasaurs, with elongated snouts and elongated, fusiform bodies, include the largest marine reptiles ever known (e.g., *Mosasaurus hoffmanni* at over 17 m in length; Lingham-Soliar, 1998a). Because the Late Cretaceous sea levels were the highest recorded during the Mesozoic, these giant reptiles were more likely to be preserved than were other Mesozoic marine reptiles, and so we have a better understanding of their habits.

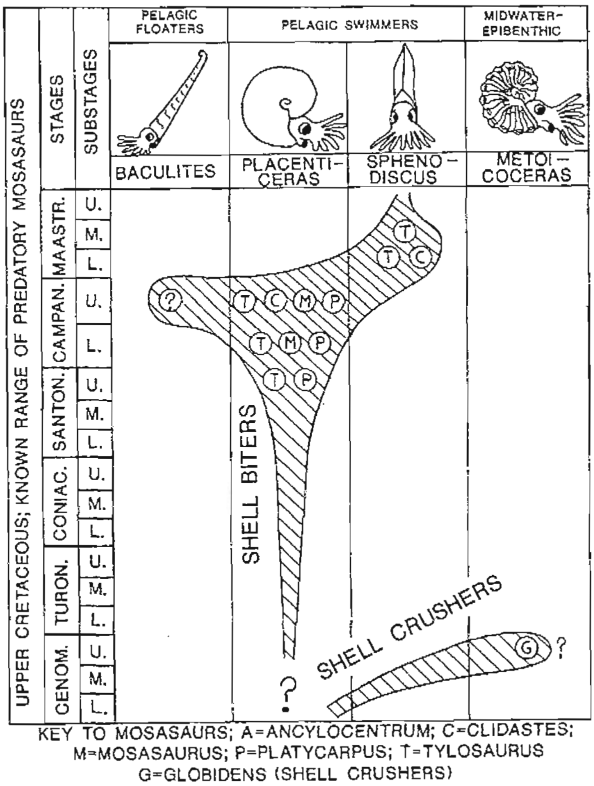


FIGURE 10—Temporal distribution of several genera of mosasaurs (indicated by letters and their apparent ammonite prey, based on bite/crush marks from Cretaceous deposits of the Western Interior Seaway. From Kauffman (1990).

Bone microstructure and bone density are used to infer the ecological distribution of mosasaurs in the water column (Sheldon, 1997). Reduced bone density of two common mosasaurs (*Clidastes* and *Tylosaurus*) indicates that they lived at great depth (Sheldon, 1997). Thus, even deep-water Late Cretaceous ammonoids that were thought to use depth as a refuge against predation (Westermann, 1996) may not have been immune to their attacks, which may have fragmented the shells completely. Evidence of deep diving in mosasaurs comes from avascular necrosis of their bones, indicating the "bends"—decompression syndome (Martin and Rothschild, 1989; Taylor, 1994). Some mosasaurs, however, had pachyostosis (bone thickening), which required that they increase lung volume to remain neutrally bouyant; in turn, increased lung volume means a larger rib cage, and thus more drag on the animal, making it a slow swimmer (Sheldon, 1997).

Mosasaurs with pachyostosis (e.g., *Platecarpus*) usually lived in shallow waters, but even these forms could dive to deeper depths as suggested by avascular necrosis in their bones. Similarly, skeletal elements of modern *Belgula* whales have pachyostosis, and consequently these whales spend most of their time in shallow water. However, *Belgula* whales also are susceptible to the bends if they dive too deeply, and this is recorded in their bones (Sheldon, 1997). Most deep-diving animals usually do not suffer the bends, although some turtles may show skeletal evidence of having had decompression syndrome (Motani et al., 1999).

Consequently, considering evidence from dentition, body form, thickness of skeletal elements, and avascular necrosis of the bones, mosasaurs are interpreted to have been top ambush predators that once foraged in lagoonal to open-ocean environments. Prey were swallowed whole, crushed, pierced, rammed, and shredded to name but just a few means of prey demise (Lingham-Soliar, 1998a, 1998b, 1999). The dentition of mosasaurs was so diverse that dentition patterns fit all five of Massare's (1987) functional predatory groups for Mesozoic marine reptiles (i.e., cut, pierce, smash, crunch, and crush guilds), a functional feat accomplished in just a short evolutionary time period (Lingham-Soliar, 1999). Because of these varied feeding modes, mosasaurs most likely fed on an array of benthic and pelagic organisms (Lingham-Soliar, 1999).

The West African *Pluridens walkeri*, for example, had broad-based and short tooth crowns that are speculated to be powerful enough to have crushed thin-shelled invertebrate exoskeletons (Lingham-Soliar, 1998b). *Globidens*, from the Upper Cretaceous of Belgium, had rounded and deeply wrinkled mushroom-shaped teeth that are thought to be specialized for crushing thick-shelled molluscs (Lingham-Soliar, 1999). In fact, *Globidens*, along with another coeval mosasaur, *Carinodens*, shows the most remarkable durophagous crushing dentition since the demise of the placodonts (Lingham-Soliar, 1999). While the biomechanical importance of such dentition was discussed (Lingham-Soliar, 1999), it still remains to be independently verified using experiments whether the many varieties of mosasaur teeth were capable of crushing ammonite shells or other putative prey, as well as how they crushed the shells.

Such biomechanical studies would be beneficial at least in coming to some conclusion as to how some ammonites received large holes in their shells; and indeed, Kase et al. (1998) performed such tests using modern *Nautilus* shells and a "mosasaur robot" modeled after a putative mosasaur predator of ammonites (*Prognathodon overtoni*). Seilacher (1998) also performed biomechanical tests using steel pliers and nautiloid shells. While it can be argued that *Nautilus* shells are not analagous to ammonite shells with respect to biomechanical loading (Tsujita and Westermann, 2001), it is still important to experimentally test the predatory hypothesis.

Numerous specimens of the ammonite, *Placenticeras*, from the Late Cretaceous Pierre Shale and Bearpaw Formation of the western interior of North America, show putative mosasaur tooth marks (Fig. 8.1) (Kauffman and Kesling, 1960; Kauffman, 1990; Hewitt and Westermann, 1990) that have been reinterpreted to be limpet homing scars that were enhanced by diagenesis (Kase et al., 1998). Kase et al.'s biomechanical tests indicated that robot bite marks on live *Nautilus* typically had jagged edges that did not show the concentric cracks characteristic of putative bite marks in *Placenticeras*. The innermost nacreous layer was shattered in the experiment, whereas internal shell layers under the putative mosasaur bite marks on *Placenticeras* were not (Kase et al., 1998). They also found few examples of *Placenticeras* with holes corresponding to mosasaur jaw shape. Consequently, they concluded that the holes in ammonites were limpet home scars, and not mosasaur predatory bite marks.

Tsujita and Westermann (2001) rejected the findings of Kase et al. (1998) and provided further observations in support of the mosasaurian origin of the holes. In fact, they pointed out that some of the experimental robot-induced holes that Kase et al. (1998) figured (e.g., their fig. 3b, p. 948) resembled those of putative mosasaurian bite marks on *Placenticeras meeki* (Tsujita and Westermann, 2001, fig. 3a,b, p. 251). Further, they argued that the biomechanical loading was oversimplified, and needs to be reanalyzed using various ammonite models in addition to testing various loading functions attributed to the jaws of mosasaurs. The lack of exact matching between jaw shape and putative bite marks is explained by the fact that like most marine reptiles, mosasaur jaws were not perfectly occluded; the lower jaw was loose enough to pivot laterally. Further, while well-preserved limpet fossils are found in the Pierre Shale, they have yet to be found in the Bear Paw Formation of Alberta. Thus, Tsujita and Westermann conclude that putative predatory holes on ammonites may be only rarely associated with limpet home scars, and the vast majority are from mosasaur predation. No one has done a quantitative comparision of the size of the bite marks, the size of the limpet home scars, the diameter of the preserved limpets, and related it to the range of tooth sizes found in contemporaneous mosasaurs.

Gastric contents from mosasaurs include cephalopod hooklets, fish, belemnites, turtle bones, and birds (Massare, 1987, her table 1, p. 128). For example, gastric contents from a single specimen of the mosasaur *Clidastes* included a marine shark and a diving marine bird, *Hesperornis* (Martin and Bjork, 1987). At least one squid gladius from the Pierre Shale exhibits bite marks attributable to a mosasaur (Stewart and Carpenter, 1990). Dollo (1913) reported a broken test of the echinoid, *Hemipneustes*, between the teeth of the mosasaur *Carinodens;* and numerous ammonites have tooth marks, presumably from mosasaur predation (Kauffman and Kesling, 1960; Kauffman, 1990). Some of these tooth marks, however, may also be limpet homing scars on some specimens (Kase et al., 1998). To date, no ammonites are known from mosasaur gastric contents (Martin and Bjork, 1987; Massare, 1987), and this may be due to taphonomic bias against the preservation of aragonitic ammonites in gastric contents (Tsujita and Westermann, 2001).

Sea and Shore Birds.—Finally, in the Late Cretaceous, two orders of marine diving birds evolved: the flightless, foot-propelled Hesperornithiformes and the swimming-winged Ichthyornithiformes. Both taxa had elongate beaks with rows of sharply pointed teeth, presumably for fish capture. Fish remains have been found in coprolites associated with *Hesperonis* (Benton, 1997, p. 273). Presumably, these taxa filled the guild presently occupied by diving sea birds, although the Cretaceous orders were evolutionary dead ends. One mosasaur specimen also contains ingested *Hesperonis* skeletal elements

JURASSIC–CRETACEOUS BENTHIC PREY AND THEIR POSSIBLE ANTIPREDATORY RESPONSES

Possible Behavioral Responses of Invertebrates.—During the Jurassic and Cretaceous, a host of organisms from sponges to worms, barnacles, and bivalves independently evolved an ability to bore into stiff mud, rock, carbonate, hardgrounds, shell substrates, and wood (Palmer, 1982; Seilacher, 1985; Wilson and Palmer, 1990, 1992). Submarine crypts and caverns seemingly provided a refuge for certain primitive groups, such as sclerosponges, many bryozoans, sedentary tube-dwelling polychaetes, and pediculate brachiopods (Palmer, 1982; Wilson and Palmer, 1990). A number of sedentary invertebrate groups persisted on exposed hard substrata during the Mesozoic. But these, in particular, show allegedly strong antipredatory skeletal adaptations (Fig. 3): they are strongly cemented (oysters, corals, barnacles), have thick, heavy shells (e.g., rudists, oysters), camouflage, and spines/spicules or toxins.

A major decline in free-resting benthic invertebrates occurred in the Mesozoic (relative to the Paleozoic). Quasi-infaunal forms, such as grypheid and exogyrid oysters, remained common on Mesozoic soft substrates, but these organisms were partially hidden and evolved thick, robust shells (Fig. 3). Exposed epifaunal brachiopods, corals, and crinoids were greatly reduced or absent from shallow marine soft-substrate settings during the Mesozoic (Thayer, 1983; Vermeij, 1987). Thayer (1983) argued that this decline in epifaunal suspension feeding may have been fostered by the rise of deeply burrowing infaunal "bulldozers," especially siphonate bivalves, during the Mesozoic. Moreover, predator grazing may be a further cause for the decline of epifaunal suspension feeders (Stanley, 1977).

Vermeij (1977) hypothesized that shell-breaking predation became a more important cause of mortality and was a driving force in evolution from the Mesozoic to Cenozoic. He termed this postulated major escalation of predator-prey interactions the "Mesozoic Marine Revolution" (MMR); in fact, most of the trends he described in adaptive morphology continued from the Mesozoic to the Recent, so the present discussion combines evidence from both eras.

Gastropods.—Gastropods show a number of trends, probably in response to shell crushing/drilling predation pressure (Vermeij, 1977, 1983, 1987). These include a further decrease in umbilicate and loosely coiled shells. The few remaining loosely coiled gastropods lived within sponges (sillquarids), or were cemented (vermetids), the latter sometimes forming large aggregates, or "reefs" (Vermeij, 1983). Other trends among Mesozoic gastropods include increased proportions of thick-lipped shell apertures, slit-like apertures, varices, and spines or knobs. The simultaneous increase in these features suggests a common evolutionary pressure, presumably the increase in durophagous predation (Vermeij, 1983, 1987). However, as this review shows, most of these durophagous predators are generalist feeders, feeding on a variety of hard-shelled prey, and not just molluscs. More work must be done to determine whether shell ornamentation really reduces successful predation. Shell sculpture and varices have been shown to decrease predation by sea stars and durophagous crustaceans in laboratory experiments (Donovan et al., 1999). Fish predation is also deterred by shell sculpture (e.g., stout spines) on gastropods (Palmer, 1979). However, field experiments demonstrate that shell sculpture may not always be a deterrant to predation for some gastropods (Ray and Stoner, 1995). For queen conch (*Strombus gigas*), living in aggregations and attaining large overall size was found to be more important in deterring predation than was shell sculpture (Ray and Stoner, 1995). Longer spines and heavier shells do not necessarily reduce predation mortality in queen conch, especially when predators attack through the aperture, as do crustaceans and predatory molluscs (Ray and Stoner, 1995).

Bivalves.—Much of the literature concerning bivalve shell ornamentation in relation to predation has been based on largely circumstantial evidence (Fig. 3) (Harper and Skelton, 1993). Spondylid bivalves provide an interesting example. These spiny epifaunal bivalves appear in the Middle Jurassic and show increasingly spinose shells up to the present day (Harper and Skelton, 1993). However, these spines apparently do not increase shell strength (Stone, 1998; Carlson, pers. comm., 2000), but do increase effective size and make shells more difficult to attack. Spines are also commonly worn off, and it is not known how this affects the survival of these cemented groups (see Logan, 1974).

Shell microstructures and the development of spines in some groups of bivalves may have originated in their Paleozoic ancestors (Table 5). Additionally, changes in thickness and arrangement of shell microstructure may also be primarily controlled by water chemistry and temperature, rather than by predation. Some microstructures, however, may secondarily function to reduce crack propagation, such as cross-lamellar structures, and increase abrasion resistance (Currey and Kohn, 1976). However, there are many ways to build cross-lamellar structures (Schneider and Carter, 2001). Shell microstructure such as spines, thickness of particular shell layers, and types of shell layers may reflect a phylogenetic constraint. Thickening of shell margins through extensive inductural deposits may be related to photosymbiosis, and not directly to predation (Schneider and Carter, 2001).

Cardiid (Jurassic to Recent) bivalve shell microstructure exhibits several evolutionary trends that may not be related to predation (Table 5). Some Cretaceous cardiids evolved stronger reflection of the shell margins, and increased thickness or secondary loss of the ancestral prismatic outer shell layers. However, these changes appear to be related to water chemistry and temperature. For example, microstructural convergences may be directly or indirectly tied to ocean chemistry and temperature:

cool climate may lead to thicker prismatic outer shell layers in some cardiid bivalves, similar to those of venerid bivalves (Schneider and Carter, 2001).

Cardiid bivalves are known for their spines. Cardiid spines can be formed in different ways: 1) by a mantle that is strongly reflected over exterior shell surfaces; 2) by extensions of the normal outer, or outer and middle shell layers; or 3) by the periostracum (formed on the undersurface of the periostracum, and cemented to the shell exterior). Cemented periostracal granules or spines in Carboniferous astartids, and in three subfamilies of cardiids (i.e., colpomyid and mytilid pteriomorhians and trigonioid palaeoheterodonts), suggest that periostracal mineralizing is plesiomorphic for the bivalvia, and is merely retained by many anomalodesmatans (Schneider and Carter, 2001). Thus, some spine forms in these Mesozoic and Cenozoic groups may be partly or largely the result of phylogenetic and physical environmental contraints.

Ammonoids as Prey.—Ammonoids are known to have sublethal injuries from the Mesozoic that may not have affected their bouyancy as much as sublethal injuries in nautiloids (Kröger, 2002). Unfortunately, little quantitative data exists for shell repair in ammonoids during this time. Westermann (1996) suggests that ammonoids lived in deeper-water areas to avoid predators, especially in the Cretaceous. However, there is now extensive evidence that marine reptiles were able to dive to deep depths during this time.

Vermeij suggests that shell repair increases in ammonoids during the Mesozoic, although he makes a plea that more data be accumulated in order to really assess this claim (Vermeij, 1987, p. 283–284). To date, little if any data exist to analyze antipredatory features and predation on Mesozoic ammonoids. Because shallow-water and deep-water forms were abundant, and because ammonoids occupied many different habitats within those settings during the Jurassic and Cretaceous, they would be ideal organisms by which examine environmental records of predation.

Ward (1986, p. 818) states that there is "abundant evidence…suggesting that predation by shell-breaking predators commonly occurred, for break marks are common in Jurassic and Cretaceous ammonites," but he does not provide data to support this statement. Data are needed on the number of ammonoid shells with evidence of healed injuries, and on whether this varies by environment of deposition, and on shell ornamentation through the Mesozoic. Equally important would be a comparative examination of healed scars on microconchs versus macroconchs, and on demersal versus more planktonic forms of ammonoids.

A few direct records of predation on ammonoids have been reported. Several examples of ammonoids with smaller ammonoid shells in their body chambers are cited above. Ammonite shell fragments are known from fish feces from the Solnhofen Limestone in Germany (Schindewolf, 1958). An unknown marine reptile apparently left twenty possible bite marks on a specimen of the Middle Jurassic ammonoid *Kosmoceras gulielmi* from the Middle Oxford Clay, England (Ward and Hollingworth, 1990). The bite marks are surrounded by an inclined ring of fractured shell, and because there was no sign of healing, the bites are considered to have been fatal to the ammonoid (Ward and Hollingworth, 1990). It is also thought, because of the diversity of predatory marine reptiles, fish, and belemnites, that ammonoids may have lived in deeper, slightly more oxygen-deficient waters at this time (Westermann, 1996). Vermeij (1987, p. 283) reviewed the limited anecdotal information concerning shell repair on ammonoids and suggested that the incidence of shell repair was low in Early and Middle Jurassic ammonoids.

If benthic durophagous predators were preying on ammonoids, the ammonoid prey should show a trend in antipredatory ornamentation and shell repair through the Mesozoic in accordance with the Mesozoic Marine Revolution theory of Vermeij (1977, 1987). As is the case for the Triassic, little is known about antipredatory effects of ammonoid shell shape and sculpture, although shell crushing marine reptiles, fish, and other cephalopods were quite diverse in the Jurassic and Cretaceous. Costae and spines in ammonoids have been considered to be antipredatory (Logan, 1974;

Westermann, 1996). Costae presumably strenthened the shell against predators (Checa and Westermann, 1989; Westermann, 1990), yet there are numerous examples of smooth-shelled ammonoid groups living contemporaneously in similar habitats. Spines and spine-like antipredatory features of adult ammonoids include spines on ancyclocone ammonoids, and protuberances such as lappets, rostra, and horns on microconchs (Westermann, 1996).

Ward (1981) argued, based on figures in the Treatise of Invertebrate Paleontology, that many of the highly sculptured Cretaceous ammonoids evolved primarily as a defense against shell crushing predators. Ammonites showed limited trends in shell ornamentation during the Mesozoic relative to their Paleozoic counterparts (Ward, 1981). Ward documented trends toward increased fluting and ribbing in ammonite shells during the Jurassic and Cretaceous.

There is only a slight increase in fine-to-moderate shell ornament in Middle to Late Jurassic ammonoids compared to Early Jurassic ammonoids (Ward, 1981, his fig. 2, p. 98). Additionally, there is no difference in moderately coarse to very coarse shell ornamentation between Early Jurassic and Middle to Late Jurassic ammonoids (Ward, 1981). The proportion of ammonoids with very coarse ornamentation stays the same through the Jurassic; moderate to strong ornamentation does increase by about 10%, but then changes little throughout the rest of the Mesozoic. Vermeij (1987) surmised from this data that armor in ammonoids was no longer a successful anti-predation strategy after the Turonian. Some long-lived groups of ammonoids, such as the Lytoceratidae and Phylloceratidae, remain morphologically similar through their geologic range, while other long-lived ammonoid families are morphologically diverse (Ward and Signor, 1983). It is not known what causes morphological stasis in some forms but not in others.

Ward (1981) found that 40% of Lower Cretaceous, and approximately 42% of Upper Cretaceous ammonoids had moderate to strong ribbing on their shells (his fig. 2, p. 98); all other shell surface types (i.e., no ornamentation, fine to moderate ribbing, and very strong ribbing) appeared to be similar for both time periods. Essentially, there appears to be no difference in ornamentation between the Lower and Upper Cretaceous ammonoids, despite the origin and evolution of durophagous mosasaurs in the Upper Cretaceous. Ward did not differentiate between benthic, planktonic, and pelagic ammonoids.

Ammonoid shell shape was also examined from the Berriasian to Maastrichtian, and little change was noted for coarsely ornamented ammonoids (Ward, 1986, his fig. 3, p. 9). Non-streamlined (non-ornamented) forms stay roughly the same through time, with slightly more in the Berriasian. Thus, it appears that shell ornamentation in ammonoids is not a direct result of predation.

A great deal of work remains to be done on testing various ammonoid shell forms in relation to predation. For example, it would still be beneficial to examine benthic versus pelagic ammonoids to determine if there is a difference in shell ornamentation between these two types.

A shift to more offshore ammonoid faunas in the Late Cretaceous, and the extinction of nearshore North Pacific forms prior to the Maastrichtian (Ward, 1986), may have resulted from increased competition and/or predation. However, there were numerous offshore, deep-diving predators in the Late Cretaceous (e.g., globally distributed mosasaurs, sharks, and other fish) that may have preyed on pelagic ammonoids and other pelagic invertebrate fauna.

The last ammonoids of the Late Cretaceous are best known from continental slope deposits, and include nektonic and planktonic forms (Ward, 1987); curiously, it is the durophagous nautiloids that survived the Cretaceous-Tertiary extinction event, and not the pelagic, perhaps chiefly planktivorous ammonoids of that time. This extinction may not be directly related to their planktic habit, but rather to the fact that that ammonoids had a planktic part of their early life cycle, whereas nautiloids had a benthic stage (Ward, 1986). However, nautiloids are dependent on other invertebrates for food, including crustacea, which have a planktonic period in their life cycle

Coleoids.—Other nektonic organisms gave up armor in exchange for more efficient swimming during the Mesozoic and Cenozoic (Vermeij, 1983). Soft-bodied coleoid cephalopods traded off external armor for increased speed and mobility and evasive defenses, such as sepia ink for camouflage (Packard, 1972; Lehmann, 1975). The majority of gastric contents preserved in marine reptiles, however, consist of hooklets from belemnites, and few from naked cephalopods. While the belemnites did not survive the Cretaceous mass extinction, the soft-bodied coleoids did. They faced a renewed group of predators in the Cenozoic—the marine mammals. Despite two revolutions in their predators, their morphology has remained remarkably static.

Decapods and Ostracodes.—Little is known about predation on decapods during the Cretaceous. Evidence of drilling predation in Cretaceous to Recent ostracode assemblages from Texas includes drillholes from juvenile naticid gastropods (Maddocks, 1988). It is not known if ostracodes developed antipredatory armor, although the incidence of drilling appears to increase from the Cretaceous into the Tertiary, but then declines in the Holocene (Maddocks, 1988). It is thought that smooth shells may be preferentially drilled, or at least may make drillholes more discernable to the paleontologist (Maddocks, 1988). Because of their abundance and worldwide distribution in a variety of environments, ostracodes would provide an important database from which to test the various marine revolutions; but they remain little studied.

Echinoderms.—Regional large deposits of crinoid grainstones and packstones (encrinites) are not present after the Jurassic (Ausich, 1997). The presence of regional encrinites since the Ordovician illustrated the domination of many shallow-shelf environments by crinoids and other stalked echinoderms perhaps for millions of years up to the Jurassic (Ausich, 1997). Comatulid crinoids evolved rapidly from the stalked forms during the Late Triassic–Early Jurassic (Meyer and Macurda, 1977), but their diversity remained fairly low (five species) during the Jurassic. Modern comatulids are known to be preyed upon by reef fishes (Meyer and Ausich, 1983; Meyer, 1985). There is also limited information concerning predation on crinoids during the Jurassic (Schneider, 1988). The offshore retreat of "primitive" groups, such as stalked crinoids, has been suggested to be a general trend that might be related to increased predation pressure (Jablonski et al., 1983; Vermeij, 1987; Bottjer and Jablonski, 1988; Jablonski and Bottjer, 1990). For example, Meyer and Macurda (1977) documented an offshore migration of stalked crinoids during the Jurassic. This onshore-offshore pattern in crinoid distribution needs to be re-examined in light of new data.

Most isocrinids (except for Pentacrinitidae) lived in shallow waters until the Mid-Cretaceous, whereas in the Cenozoic these forms inhabited deeper water (Bottjer and Jablonski, 1988).

In the Early Jurassic, the biggest evolutionary innovation in echinoderms appeared with the advent of irregular echinoids (Simms, 1990). The flattened tests of these creatures are thought to have been an aptation that provided greater stability within the substrate. At the same time, the periproct moved away from the apex of the test, in accord with their sediment-eating habits. By the Middle Jurassic, endobenthic irregular echinoids had evolved and rapidly diversified. Today, their descendants comprise nearly half of all extant echinoids (Simms, 1990). The aboral spines and the anal sulcus of these creatures (e.g., Galeropygidae) were consistent with their endobenthic lifestyle (Simms, 1990). The evolution of pencillate tube feet in these groups allowed them to pick up finer sedimentary particles via mucous adhesion (Simms, 1990). A peri-oral tube foot also allowed them to expand into new trophic realms. Was this endobenthic lifestyle provoked by predation, or merely by the opportunity for better feeding conditions? It should be noted that epibenthic echinoids were also diversifying at this time, with the Cassiduloids and their offshoots.

Fish are the dominant predators of modern ophiuroids (Aronson, 1988). Little is known about predation on Mesozoic ophiuroids, although the rate of arm regeneration appears to be low for Jurassic compared to Recent ophiuroids (Aronson, 1987, 1991). However, there is no clear evidence that ophiuroids developed antipredatory armor, as their morphology has remained relatively the same since their origin in the Ordovician (Aronson, 1991). It is possible that they developed better autotomization of their arms, like some crinoids; or maybe they developed into distasteful prey (Aronson, 1991). The evolutionary radiation of the spatangoids (and holasteroids) in the Cretaceous may have been the result of the Jurassic innovation of pencillate tube feet, a feature shared with no other echinoid group (Simms, 1990). Early Cretaceous spatangoids (*Hemiaster elegans washitae*) are reported to have drillholes from parasitic gastropods (Kier, 1981). Parasitic drillings are commonly associated with deformation of the echinoid ossicles where the parasite housed itself. Fish bite marks are well preserved on complete asterioids and asteroid ossicles from the Late Cretaceous White Chalk of northwestern Germany (Neumann, 2000). On some specimens, serrated tooth marks may be related to galeoid shark predation. Regurgitate pellets are also common in the White Chalk, and indicate that predation by these durophagous fish may have been size selective (Neumann, 2000).

Vertebrates.—As with late Paleozoic fish, armor does not appear to have been a significant part of the response to escalation among Mesozoic marine vertebrates. With the exception of relatively slow-moving placodonts and marine turtles, none of the marine vertebrates developed any unusual armor during the Mesozoic. Indeed, within actinopterygian fish there is a distinct trend toward reduction of ganoid scales in favor of lighter and less protective cycloid and ctenoid types (Patterson, 1994; Benton, 1997). Presumably, this scale reduction reflects the ineffectiveness of dermal armor against large predators, which demonstrably swallowed prey whole (Voihl, 1990). This further reduction in armament is clearly coordinated with the development of improved swimming speed, buoyancy control, and maneuverability in the Cretaceous teleosts. In turn, this increased mobility may well have triggered adaptations for improved speed, maneuverability, and/or stealth among larger predators, such as the neoselachian sharks, plesiosaurs, ichthyosaurs, and mosasaurs.

CENOZOIC PREDATORS

The Cretaceous-Tertiary extinction had a devasting impact on pelagic ecosystems. Ammonites and belemnoids, as well as large vertebrate predators, were decimated by this event. All of the marine reptilian predator guilds, except sea snakes and sea turtles, became extinct during this crisis—including mosasaurs, plesiosaurs, and ichthyosaurs, in addition to the flying pterosaurs. This left only the highly successful neoselachian sharks and teleost fishes in the vertebrate predator realm. Marine mammals emerged in the Eocene to essentially take over the ecological void left by Mesozoic marine reptiles (Table 4). In fact, tooth dentition in marine mammals closely parallels that of the Mesozoic marine reptiles (Massare, 1987, 1997).

Conversely, many benthic invertebrate predators, such as naticid and muricid gastropods and various decapod crustaceans, were seemingly little affected by the terminal Cretaceous extinctions. Several groups of shell-drilling predators evolved or diversified within the Cenozoic (for review, see Vermeij, 1987); some groups, such as the neogastropods, evolved in the Late Cretaceous. Prosobranch gastropod predators, the dominant drillers, were much more common in the Cenozoic than at any other time, though the Mesozoic record needs to be more throughly examined (Kowalewski et al., 1998). The record of octopod shell drilling is chiefly Cenozoic, with the soft-bodied octopod fossil record primarily within the Cretaceous to Paleogene (Engeser 1988; Harper, 2002).

Several major groups of vertebrate shell-crushing and shucking predators that may have seriously impacted benthic and pelagic marine biotas evolved or diversified during the Cenozoic: shell-crushing sea turtles (i.e., the single genus *Caretta*), the coral reef teleost fishes and other teleosts, rays and skates, diving marine and shore birds, pinnipeds, sea otters, gray whales, and humans. Among mammals, the origination of pinnipeds (seals and walruses), the cetaceans (especially the gray whale) in the Eocene, and sea otters (Carnivora; Family Mustelidae) in the late Miocene also potentially impacted Cenozoic

TABLE 4—Cenozoic marine vertebrates and their functional feeding groups.

Taxonomic Group	**Functional Feeding Group**	**Prey**	**Forensic Evidence (potentially traceable in the fossil record)**
Mustelidae (Sea otters)	Generalist carnivores	Abalone (*Haliotis*); sea urchins (*Strongylocentrotus franciscanus, S. purpuratus*); kelp crabs (*Pugettia*); rock crabs (*Cancer*); turban snails (*Tegula*); octopus (*Octopus*); bivalves (*Tivela, Saxidomus, Tressus*); sea stars (*Pisaster*)	Shell damage consisted of: fractured middle sections of shells as a result of being hit with stones by sea otter; larger shells may have fractured middle sections; edge damage may be due to otter gnawing on the edges of the shell or chipping with a stone
Cetaceans	Generalists	Krill, whales, dolphin, squid, callianassids, small bivalves; no specialists	Gray whales suck pits in the benthos to gather food; pits may be ephemeral, but may be preserved; no other information available
Pinnipeds	Generalist	Two genera are specialists on molluscs and crustacea	Walruses may leave marks on shells, but no record of this as yet
Sea Turtles	Generalist	One genus (*Caretta*) specialist on molluscs	*Caretta* may leave marks on molluscan prey, but no record of this as yet
Sea Snakes	Generalists		Crush prey, but no record of their predatory prowess as yet
Diving Marine Birds	Generalists	Eat crustacea, molluscs, fish; one genus appears to specialize on molluscs	Extensive literature on birds and how they forensically alter prey
Marine Crocodiles	Generalist	Birds, fish, turtles, humans, golf balls, etc.	No forensic information available

benthic invertebrate prey. Vermeij (1987) reviewed the molluscivorous habits of some of these groups, and here we discuss their more generalist feeding behavior, add or update several other groups, and suggest possible alternative scenarios to his escalatory hypothesis.

Stomatopods.—Stomatopod crustaceans are obligate carnivores and vicious predators. Stomatopods that crush the shells of their prey by pounding them with blunt expanded segments of their maxillipeds (e.g., Burrows, 1969) did not evolve until the Cenozoic (Hof and Briggs, 1997; Hof, 1998). Two major groups of stomatopods exist today: the squilloids and the gonodactyloids, which have very different means of feeding. The squilloids either attack prey with their dactylar spines, or grasp prey between the toothed margins of their propodus and dactylus (Kunze, 1983). Squilloids typically prey on fish, polychaetes, and very small crustaceans (Schram, 1986). In gonodactyloids, the propodus is swung from an anterioventral position, and prey is "smashed" on the lower part of the dactylus (Kunze, 1983). Gonodactyloids feed typically on hard-shelled prey like molluscs and large crustaceans (Schram, 1986). Both types, however, can also scoop up prey from the benthos with their maxillipeds.

The gonodactyloids can smash small to large holes in molluscan prey (Hof, 1998; Ahyong and Harling, 2000). Stomatopods can also shear gastropod shells in half and break the outer lip (Geary et al., 1991). Additionally, small puncture wounds in molluscan prey, called ballistic traces (e.g., the trace fossil *Belichnus*), are attributed to stomatopods (Pether, 1995). Most of the extant groups have an actual fossil record extending back only to the Eocene, with the shell-smashing gonodactylid group originating in the Miocene (Hof and Briggs, 1997; Hof, 1998). Approximately 400 living stomatopod species are recognized (Manning, 1995).

Despite their long history, only a few examples of gonodactylid shell-breaking predation are known from the Neogene fossil record. Geary et al. (1991) described a few cases of putative stomatopod shell damage from Pliocene localities in Florida. Baluk and Radwanski (1996) also documented stomatopod damage on diverse gastropods from Miocene localities in Europe. Stomatopod predatory damage should be easily recognized, and documentation of this damage in more assemblages would enhance the paleoecological picture of these creatures.

Brachyuran crabs and lobsters.—The second major wave of crustacean adaptive radiation occurred in the Paleogene. Brachyuran crabs had appeared in the Mesozoic, but new families of crabs such as the Portunidae, Cancridae, Grapsidae, and Ocypodidae arose in the Eocene (Table 1). Most brachyuran crabs are generalist and opportunistic feeders, and few are durophagous (Table 1). Brachyurans with heavily toothed claws apparently evolved in the Paleocene (Vermeij, 1983), but this has not been studied in detail. Crushing claws are a formidable tool for peeling and crushing molluscan shells and also for crushing other crustacea or hard-shelled prey. The distinctive peeling of calappid crabs has been documented in fossil and recent shells (Bishop, 1975; Vermeij, 1982, 1987). The parthenopid crabs, which originated in the Late Cretaceous, are known to eat molluscs only in the laboratory (Vermeij, 1978), and the few reports available show them eating puffer fish or non-molluscan invertebrates (Table 1). Clearly more work needs to be done on the parthenopid crabs. Durophagous cancrid crabs (*Cancer* spp.) eat a diversity of prey, such as polychaetes, squid, crustaceans, fish, and echinoderms, following the dominant macro-invertebrates in the habitat; whereas Ovalipid crabs may predominantly eat molluscs (Stehlik, 1993).

Lobsters also crush shells, but usually only fragments are left (Cox et al., 1997). In modern seas, rock lobsters are known to prey extensively on molluscs, such as abalones and turban snails in some localities (Van Zyl et al., 1998; Branch, 2000), and echinoderms in others (Mayfield et al., 2001). Very little is known about lobster foraging and how it would affect the fossil record of invertebrate hard-shelled prey (reviewed in part by Walker et al., 2002).

Gastropods.—Gastropod predators that chip and wedge open molluscan prey (e.g., Buccinidae, Fasciolaridae, and Melongenidae) originated in the Late Cretaceous, but diversified in the Cenozoic; however, the shell-chipping record in prey shells is known only from the Pliocene (Vermeij, 1987). Buccinid gastropods chip their outer lips in the process of preying on other mollusks, and then subsequently repair their self-inflicted breakage (Carriker, 1951; Nielsen, 1975). Dietl and Alexander (1998) noted that this type of lip damage occurs in buccinids as old as Miocene. Older buccinids, which range back to the Late Cretaceous, have not yielded evidence of this distinctive lip damage. Hence, the shell-prying habit of buccinids may have evolved within the Neogene.

The best evidence for predation in the Cenozoic fossil record comes from predatory drillholes preserved in prey ranging from protists, such as foraminifera, to many phyla of invertebrates, such as bryozoans, molluscs, brachiopods, and echinoderms (Carriker and Yochelson, 1968; Sohl, 1969; Taylor, 1970; Sliter, 1971; Bishop, 1975; Boucot, 1981, 1990; Bromley, 1981; Vermeij, 1987; Kabat, 1990; Kowalewski, 1993; Kowalewski and Flessa, 1997). Prosobranch gastropods are the primary shell drillers in marine environments, although nudibranchs (Vayssiereidae), flatworms, nematodes, and the protist foraminiferans have also evolved drilling apparatuses (Woelke, 1957; Sliter, 1971; Carriker, 1981; Hallock and Talge, 1994).

Eight families or superfamilies of molluscs have evolved drilling behavior. Naticids are the best studied, but the other groups of shell drillers were reviewed by Kabat (1990). Gastropods, in particular, have evolved a variety of means to prey upon hard-shelled prey, and one major family (Cassidae) and two little known groups (Marginellidae and Nassariidae) of shell drillers originated in the Cenozoic; the naticids and muricids persisted from the Mesozoic into the Cenozoic (Fig. 7). In drilling gastropods (e.g., muricids, naticids), the small rasping organ (the radula) and the accessory boring organ are used to drill holes in prey shells (Carriker, 1969). Predatory cephalopods, such as the octopus, also use the radula to bore into mollusc shells.

Capulids (Capulidae, Mesogastropoda) are specialized ectoparasites on molluscs and echinoderms (Kabat, 1990). Capulids drill their prey to extract nutrients from the host's feeding currents. They drill sharp-sided cylindrical holes and leave an attachment scar on their host's shell (Matsukama, 1978; Kabat, 1990). Capulid-host associations date back to the Late Cretaceous, where capulids are known to associate with inoceramid bivalves (Hayami and Kanie, 1980). Drilled inoceramids, however, are not reported for this assemblage. Capulid attachment scars and shell morphology that conforms to their host are reported in modern and middle Pleistocene assemblages (Orr, 1962; Grant-Mackie and Chapman-Smith, 1971). Such associations should be highly reliable, and could potentially be found in the fossil record (Boucot, 1990). Actual evidence of capulid drilling, however, is known only from one report from the late Pleistocene of Japan (Matsukama, 1978). Thus, very little is known about this intriguing parasitic drilling behavior in the fossil record.

Cassid (Tonnoidea, Mesogastropoda) predatory holes (not true drillholes, but rather rasped areas) in echinoderms date back to the Early Cretaceous, but have been little studied despite their ubiquity in Cenozoic and modern echinoids (Hughes and Hughes, 1981; Nebelsick and Kowalewski, 1999). Cassids use sulfuric acid from their proboscis gland and the radula to cut out (rather than drill) an irregular hole in echinoderm tests (Kabat, 1990); however, most workers use the term "drillhole" for their predatory traces. Although the earliest drilled echinoderm dates back to the Early Cambrian, most drilling predation on echinoids is known only from the Cretaceous and Cenozoic (Sohl, 1969; Beu et al., 1972; Nebelsick and Kowalewski, 1999). The earliest drillholes attributed to cassids were described from the Early Cretaceous (Albian) of Texas, but the cassid drilling record is much more extensive in the Cenozoic, especially from the Eocene to present (Hughes and Hughes, 1981; McClintock and Marion, 1993; Nebelsick and Kowalewski, 1999).

Muricids (Neogastropoda) diversified greatly in the Paleogene, occurring primarily in tropical to subtropical waters, although they are found in temperate and cooler regions as well (Vokes, 1971, 1990; Vermeij, 1996; Vermeij and Carlson, 2000). During times of reduced food, muricids may drill conspecifics (Spanier, 1986, 1987). An increase in such cannibalistic boring in muricids has been associated with sea level changes in the Red Sea (Spanier, 1987). Rarely, some muricids drill their own opercula or bore into dead empty shells (Prezant, 1983). While increasing drillhole size can be correlated with increasing size of muricid predator for some species, this does not hold for others (Urrutia and Navarro, 2001). Muricids may also change their drilling behavior and preferred drilling location on the prey with ontogeny (Urrutia and Navarro, 2001). Drillholes in inarticulate brachiopods are rare but reported in Recent communities, and may be due to muricid predation (Paine, 1963; Kowalewski and Flessa, 1997). Similar drillholes in fossil inarticulate brachiopods reported from the Tertiary of Seymour Island, Antarctica, and the eastern United States (Cooper, 1988; Wiedman et al., 1988; Bitner, 1996) may be attributed to a muricid predator.

The record of naticid predatory drillholes has been used extensively to examine the evolution of predatory behavior, escalation hypotheses, and cost-benefit analyses in modern and fossil assemblages (Taylor et al., 1980; Kitchell et al., 1981; Kitchell, 1986; Kelley, 1988; Kabat, 1990; Anderson et al., 1991; Kelley and Hansen, 2001; see below). The naticid subfamily Polinicinae diversified greatly in the Cenozoic, and the polinicid body fossil and predatory trace fossil record is extensive, especially after the Oligocene (Sohl, 1969; Taylor et al., 1983).

The Nassariids (Neogastropods) are carnivores or scavengers, and until recently, their predatory drilling habits were in question (Kabat, 1990; Kowalewski, 1993). Kabat (1990), in fact, suggested that drilling did not occur in this group, although the possibility of nassariid drilling was mentioned by Fischer (1963). Recently, Morton and Chan (1997) have shown unequivocally that some nassarids can drill prey. A few (8 of 30 individuals) laboratory-reared juveniles of *Nassarius festivus* were found with stereotypically-sited boreholes on the ventral surface of their main body whorl (Morton and Chan, 1997, their fig. 1). The boreholes varied in morphology, from elongate, irregular drillholes to spherical countersunk borings that were clearly rasped with the radula and aided by chemical dissolution. It is thought that drilling may be a juvenile behavior that is lost in the adults, as no adult nassariids have unequivocally been found to drill prey.

To date, two species (*Austroginella johnsoni* and *Austroginella muscaria*) of marginellid gastropods from southeastern Australia are known to drill into molluscan prey (Ponder and Taylor, 1992). Parabolic in sectional shape and circular to subcircular in outline, the studied drillholes range in length from 1.13 mm to 3.1 mm. Additionally, marginellid drillholes are countersunk with a very small inner diameter relative to the outer diameter. This inner opening may have an irregular shape that can be used to distinguish these borings from those of other predatory gastropods such as naticids. Naticids make larger drillholes (see Kowalewski, 1993). However, marginellid drillholes are similar to octopus drillings (Ponder and Taylor, 1992), and thus may be difficult to distinguish in the fossil record. Like octopods, marginellids may only use the drillhole for injecting toxins to relax the prey, rather than feeding through the hole. Under SEM, the calcareous microstructure is seen to be greatly etched, suggesting a dominant solutional mechanism for drilling.

Cephalopods.—Shell-crushing and crustacean-crushing nautiloids diversified after the Cretaceous-Tertiary extinction, and remained relatively abundant into the Miocene, when nautiloids were quite diverse and abundant in continental shelf habitats across the globe (Ward, 1987). The earliest *Nautilus* is known from the Eocene–early Oligocene, but no fossils are known from the upper Oligocene to Pleistocene (Teichert and Matsumoto, 1987). In modern seas, nautiloids extend from Fiji in the east to the Indian Ocean in the west, and from New Caledonia to Japan (Ward, 1987). Natiloids forage for prey or crustacean molts across great depth ranges. There may be up to seven species of nautiloids in modern oceans, but several of the species designations are debated (Saunders and Ward, 1987; Ward, 1987).

The prey of *Nautilus* is seemingly quite different from that of the Mesozoic ammonoids. Unfortunately, the feeding ecology of *Nautilus* is poorly known, but it is thought to be both a predator and a scavenger (Ward, 1987). While direct observations of predation are lacking, evidence from crop dissections suggests that nautiloids eat crustaceans, especially crabs (Saunders and Ward, 1987; Ward, 1987; Nixon, 1988). The crop of *Nautilus macromphalus*, for example, has often been found to contain many hermit crabs of one species (Ward, 1987). However, this dietary finding may be biased in that nearly all *Nautilus* studied are caught in traps, which also attract crustaceans. Additionally, nautiloids have been directly observed by divers to eat molts from lobsters and slipper lobsters. With their large, chitinous jaws tipped with calcium carbonate, nautiloids shred their prey or scavenged items into very small pieces of about 5 mm^3 (Nixon, 1988). Predators of *Nautilus* include sharks, triggerfish, humans, octopods, and perhaps other nautiloids (Ward, 1987).

Ammonites and nearly all belemnoids became extinct during the Cretaceous-Tertiary crisis. However, other coleoid cephalopods, such as the cuttlefish *Sepia*, the squids (*Loligo*), and *Nautilus,* are common in the Cenozoic (Nixon, 1988). The Sepiida, in particular, diversified greatly in the Cenozoic. Benthic sepiids and cuttlefish mainly feed on small crustacea, such as prawns (Nixon, 1988).

Drillholes in molluscan prey from Recent octopods are well known (Fugita, 1916; Pilson and Taylor, 1961; Wodinsky, 1969; Nixon, 1980; Bromley, 1981; Kowalewski, 1993). Octopuses use secretions and abrasion from an accessory salivary papilla in the drilling process (Nixon, 1979, 1980). Their drillholes are distinctly irregular or oval, with a very small inner borehole diameter (Kabat 1990). Despite their ubiquity in modern habitats, their ability to select particular prey, and their shell-collecting habits, few of their borings (trace fossils of *Oichnus* spp.) have been reported in the fossil record (Bromley, 1993; Harper, 2002). Robba and Ostinelli (1975) first reported octopod drillings from the Pliocene of Italy. Bromley (1993) reports octopus drillings from the Pliocene of Greece. Walker (1991, 2001) reports octopod drillings from the late Pleistocene of the Galápagos Islands, and for the late Pliocene of Ecuador. Harper (2002) records octopus drillings from the Plio-Pleistocene of Florida. Octopods may also drill nautiloids, many shells of which have multiple drillholes (Saunders et al., 1991). Octopods also make "kitchen middens" of their favored prey type which can be found outside their den; the shells are commonly drilled (Walker, 1990).

Echinoderms.—Evidence for the rise of asteroid predation in the Cenozoic is reviewed by Vermeij (1987). Gastropods were found within the oral disc of the sea star, *Ctenophoraster* in Eocene–Oligocene deposits from Antarctica (Blake and Zinsmeister, 1979). This type of *in situ* predation has a long fossil history dating back to the Paleozoic, but is rarely reported from Cenozoic localities. It is important to note that many Cenozoic predators that ingest their prey whole, such as sea stars, don't leave an imprint on their prey (see Vermeij, 1987). These predators are still abundant in the Cenozoic, and some have evolved to prey on reef corals (such as *Acanthaster plancii*).

Regular echinoids have emerged as a major predatory group. Using the jaws of their Aristotle's lanterns, echinoids are able to graze corals and even nibble on the tests of distantly related clypeasteroid "sand dollars" (Kier, 1977). An unusual modern predatory interaction between deep-water cidaroids and crinoids was documented by Baumiller et al. (1999): the cidaroid, *Calcocidaris micans,* devours the stalked isocrinoid, *Endoxocrinus parrae*. Another cidaroid, *Histocidaris nuttingi*, also contained crinoids in its gut (Baumiller et al., 1999).

Chondrichthyes.—Most sharks are opportunistic predators, with limited exceptions such as the planktivorous whale sharks (Cortés, 1999). Intriguingly, both sharks and bony fishes have evolved similar suites of prey capture strategies, including suction, grasping, biting, gouging, and filter feeding (Motta et al., 2002). Inertial suction feeding is thought to be ancestral in bony fishes, while the ancestral condition of sharks most likely involved grasping the prey and dismembering it with little upper jaw protrusion (Lauder, 1985; Motta et al., 2002). Some sharks, especially durophagous forms, use an inertial suction prey capture method similar to the bony fish. Suction feeding has arisen many times within the shark group, chiefly in relation feeding on benthic prey (Motta et al., 2002). Specializations for suction feeding include rapid jaw opening, a round terminal mouth, reduced dentition, and the ability to produce large suction pressures (Motta et al., 2002). Whale sharks (*Rhincodon*) possess these features, but are planktivorous. Thus, durophagy may be an exaptation from a primarily adaptive form of suction feeding in sharks.

Few shark groups are known to have evolved durophagous members, and thus durophagy is considered a rare form of feeding. Seven species of chimaerids (Holocephali), one species of horn shark (Heterodontidae), one species of nurse shark (Orectolobiformes), two species of the classically predatory Carcharhiniformes, and seven species of rays (Rhinobatoidea, Rajoidea, Myliobatioidea) are known to be durophagous. Stout, flattened teeth and robust jaws are the hallmarks of durophagy. Durophagy in sharks, however, does not necessarily mean that they eat molluscs; many

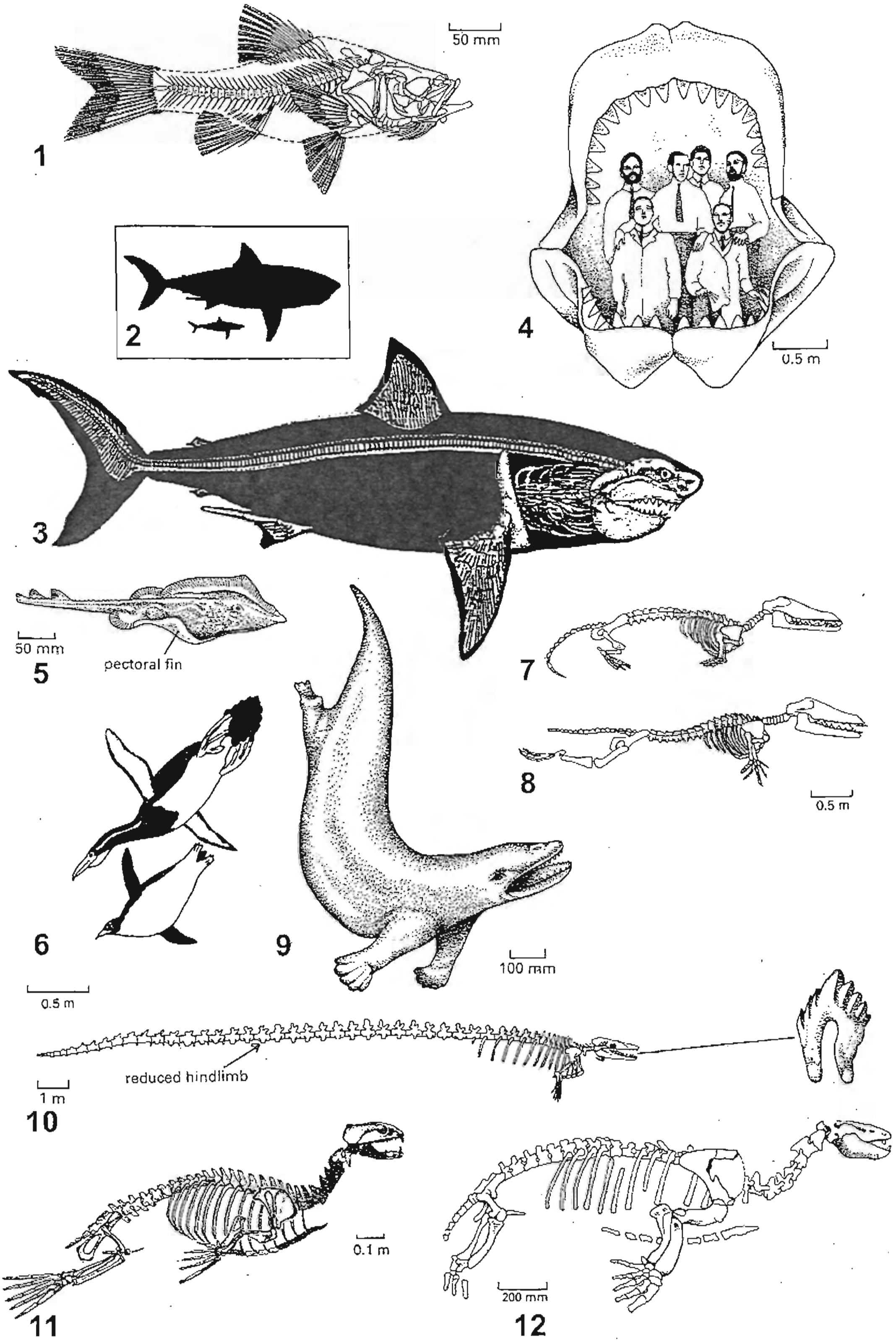

50 mm
1
2
4
0.5 m
3
50 mm
pectoral fin
5
7
8
0.5 m
6
9
100 mm
0.5 m
reduced hindlimb
1 m
10
0.1 m
11
200 mm
12

Figure 11

durophagous sharks eat crustaceans and/or fish (Wilga and Motta, 2000). For example, the chimaeroids have pavement tooth structures like the myliobatids, and feed primarily on molluscs and crabs (Di Gaincomo and Perier, 1996). Horn sharks feed primarily on limpets, bivalves, and blue crabs (Smith, 1942; Wilga and Motta, 2000). The nurse shark, *Ginglymostoma cirratum,* eats fish and crustaceans (Motta et al., 2002). The bonnethead (Carcharhiniformes) shark, *Sphyrna tiburo*, has molariform teeth and modified jaw structures that function in crushing hard-shelled crustaceans, but it can also eat fish (Wilga and Motta, 2000). Another member of Carcharhiniformes, the smoothhound or dogfish, *Mustelus*, has cusped teeth and also feeds primarily on crustaceans (Russo, 1975; Yamaguchi and Taniuchi, 2000). Some skates (Rajoidea), guitarfish (Rhinoboidei), and rays (Myliobatoidea) have crushing and grinding dentition for crunching crustacean or molluscan prey but they can also feed on polychates (Gregory et al., 1979; Wilga and Motta, 2000).

Neoselachian sharks became the top predators in the Cenozoic seas. During the Paleogene Period the successful galeomorphs (Galea) radiated into several clades, including the dogfish and gray sharks that feed on crustaceans and molluscs, the basking and whale sharks that strain krill from sea water, and the white sharks that eat fish, seals, and cetaceans (Benton, 1997). Members of the latter group attained large size, culminating with *Carcharodon megalodon* (Fig. 11.2–11.4) in the Miocene and Pliocene, a 10–20-meter-long shark with teeth up to 17 cm long. This giant shark may have been specialized for feeding upon whales (Gottfried et al., 1996). Shark teeth were found embedded in a whale jaw preserved in Pliocene sediments, suggesting a potential shark attack on the whale (Demere and Cerutti, 1982).

The radiation of deep-water Neoselachian-Squaliformes sharks, to which most of the modern forms belong (e.g., Somniosinae, Centrophorinae, most Etmopterinae, Oxynotinae), began in deep waters with demersal forms originating after the Cenomanian-Turonian anoxic event; the second radiation of Squaliformes sharks (most of the Dalatiidae) began in the Early Tertiary after the Cretaceous mass extinction, and these epipelagic sharks radiated into shallow waters (Fig. 9; see also Adnet and Cappetta, 2001, their fig. 4, p. 241). The dentition of most of these groups is quite varied, but most are heterodont. Most squaliformes dine on fish and cephalopods (Cortés, 1999).

All major living families of durophagous rays were established by the middle Eocene (Vermeij, 1987 after Maisey, 1982), but their effect on the resultant fossil record of molluscs and other prey is not known. It is clear that despite their pavement type dentition, rays eat a wide variety of food that is not necessarily hard-shelled prey. Some prey items ingested, however, may be incidental to their foraging for larger prey items. Modern bat rays, such as *Myliobatis californica,* feed on bivalves, crustaceans, and polychaetes; bivalves are the dominant food item for most size classes, except for the adults (Gray et al., 1997). Prey items within

←

FIGURE 11—Cenozoic marine vertebrate predators. 1, Teleost paracanthopterygian fish, *Mcconichythes*. 2, Silhouettes of modern great white shark *Carcharodon carcharias* and Neogene *C. megalodon*. 3, Outline and skeleton of *C. megalodon*. 4, *Carcharodon megalodon;* reconstructed jaws of *C. megalodon* (perhaps overestimated). 5, Batoid sting ray *Raja*. 6, Reconstruction of flightless marine, wing-propelled swimming birds drawn at same scale in swimming posture: lower figure is modern Emperor penguin; upper shows reconstruction of extinct pelecaniforme plotopterid. 7, 8, Early whale with limbs, *Ambulocetus* in two postures; Middle Eocene. 9, Reconstruction of oldest known whale *Pakicetus* (Early Eocene). 10, Early large whale *Basilosaurus;* note tiny head with distinctive, multi-cusped teeth; Late Eocene. 11, Early (Oligocene–Miocene) pinniped *Enalioarctos*. 12, Desmatophocid seal *Allodesmus*, Miocene. Figures adapted from Benton (1997).

Myliobatis stomach contents vary ontogenetically and with the sex of the ray (Gray et al., 1997). In the study by Gray et al. (1997), juvenile bat rays fed on small clams (≤ 5 mm clam siphon diameter), benthic shrimp, and polychaetes. Adult rays predominately fed on polychaetes, large clams (> 5 mm clam siphon diameter), and *Cancer* crabs. The largest rays preferred large clams and *Cancer* crabs. Large clams and crabs were eaten by adult female rays, whereas subadult and adult male rays fed primarily on polychaetes and burrowing shrimp. In other studies, large females also predominantly fed on echiuran worms (Karl and Obrebski, 1976).

Rays and skates excavate shallow pits in soft sediments in search of prey (Fig. 12) (Gregory et al., 1979). The cownose ray (*Rhinoptera bonasus*) and possibly other batoids repeatedly inhale sediments and water through the mouth and vent it out the gill slits; the pectoral fins act to move the sediment away and to enlarge the burrow (Gray et al., 1997). Similar shallow pits are present in Pleistocene localities, and are indicative of ray feeding activities (Fig.12) (Howard et al., 1977). These pits could be correlated with associated fragmented mollusc deposits, but, to date, this has not been examined

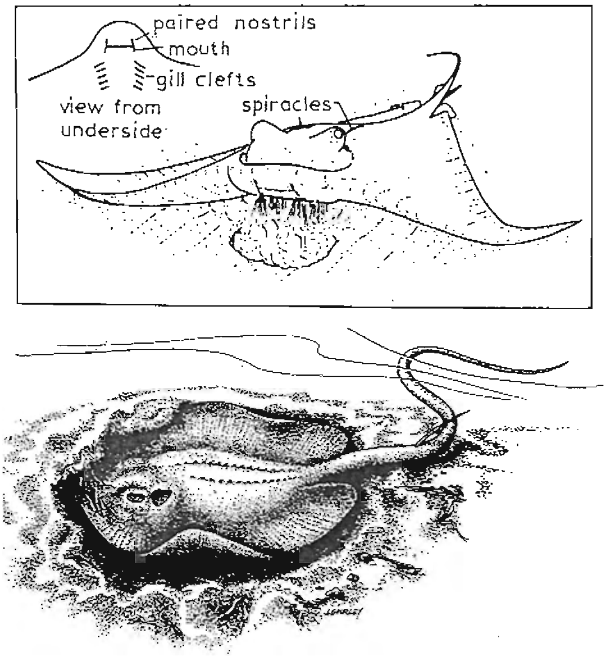


FIGURE 12—Benthic feeding by batoid rays. Upper figure, diagram of eagle ray *Myliobatis* jetting water through gill slits to excavate circular feeding depression. Lower figure, drawing of ray in feeding position on excavated pit. From Gregory et al. (1979) and Howard et al. (1977).

Pods of deep-water gastropods attributed to either fecal masses or regurgitated remains from shell-eating sharks or other predators, were described from bathyal Pliocene deposits from Ecuador (Hasson and Fischer, 1986, p. 35). However, a recent analysis of these shell "nests" revealed that they are not related to predation (Walker, 2001).

Osteicthyes.—The diversification of teleosts (Fig. 11.1) in the Cenozoic is unprecedented among vertebrates: presently some 23,670 species are assigned to 38 orders and 425 families (Patterson, 1994). This is largely the result of development of two clades during the Cenozoic, the Ostariophysi in fresh water and the very successful Acanthomorpha (over 21,000 extant species) in all environments (Maisey, 1996). Teleosts, ranging from tarpons to tunas, became the most common piscivorous open-water predators during the Cenozoic. Certain fast-swimming large predatory teleosts, such as swordfish, seemingly filled a part of the fast-swimming piscivorous predator guild held by ichthyosaurs and primitive teleosts (e.g. *Xiphactinus*) during much of the Mesozoic.

Ray-finned teleosts with molluscivorous habits originated and diversified in the Eocene, a few other groups in the Oligocene and Miocene (Vermeij, 1987). Additionally, a major evolutionary radiation occurred in the tropical reef fish fauna of the Eocene. Most of the fossil record of reef fish comes from Late Cretaceous to Miocene Tethyan reef deposits of southern Europe (Rosen, 1988; Choate and Bellwood, 1991). The best reef fish fossils, however, are from the Eocene of Monte Bolca, Italy (Blotte, 1980; Choate and Bellwood, 1991; Bellwood, 1996). These fossils are excellently preserved—some retain pigmentation—and represent mass mortality events, probably related to poisonous algal blooms (Choate and Bellwood, 1991).

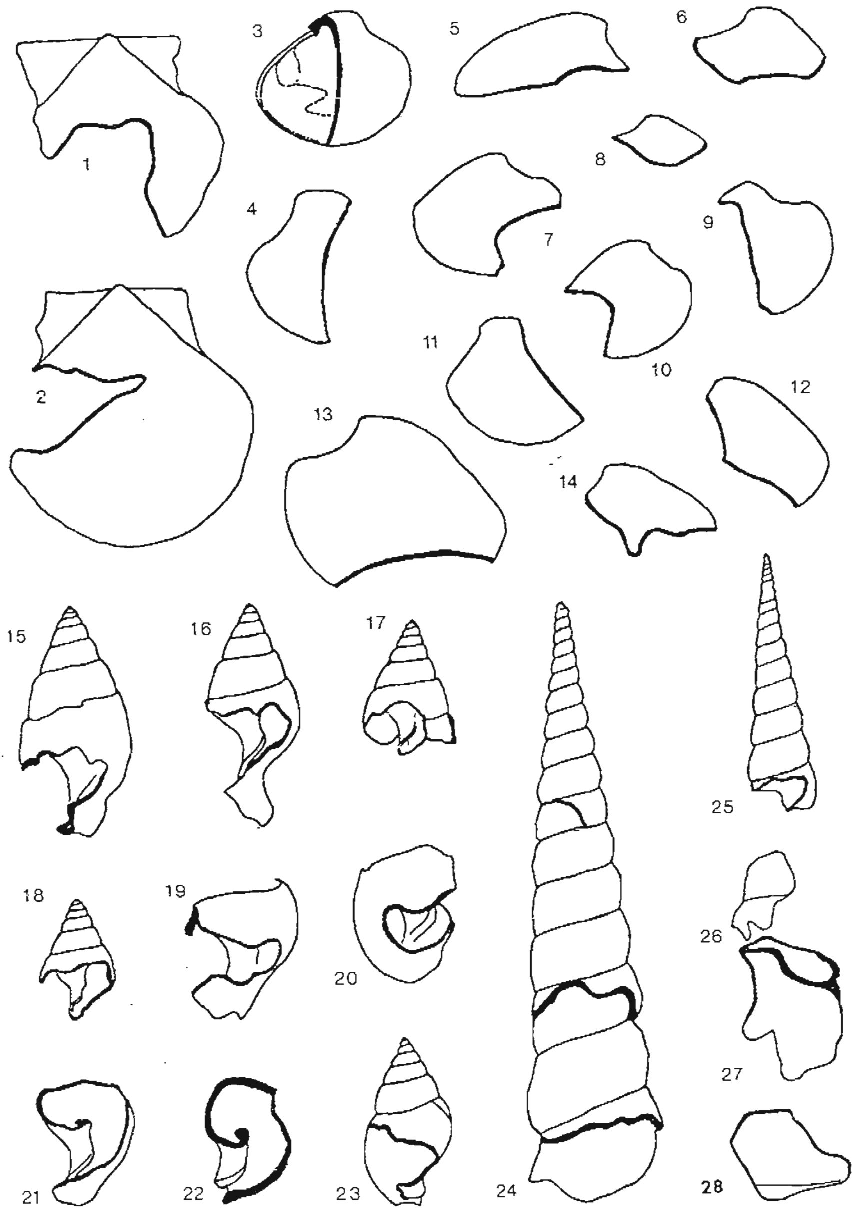
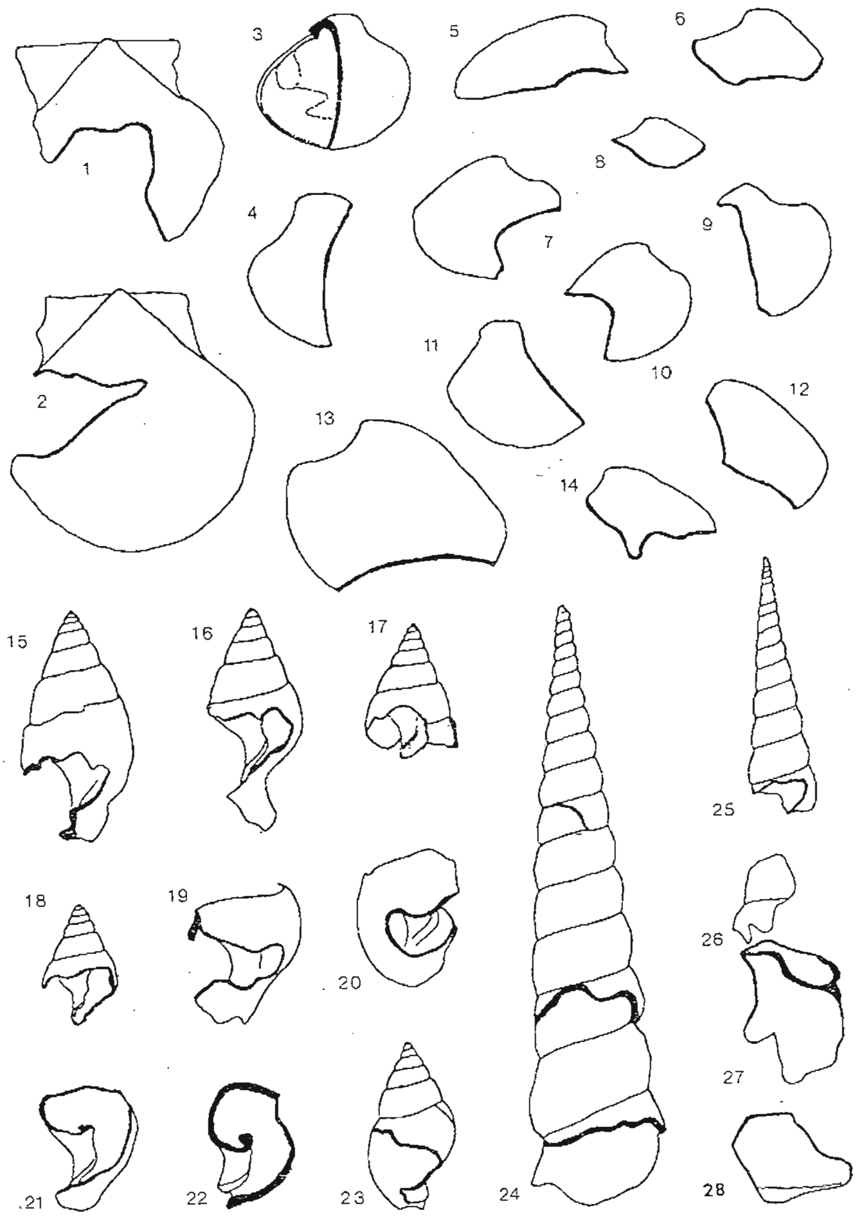


FIGURE 13—Recent shells dredged from Ria de Arosa, Galicia, Spain, showing healed (2, 23, 24) and unhealed fracturing attributable to crustaceans. 1, 2, Fragmented bivalve *Chlamys*. 3–14, Fragments of bivalve *Venus*. 15–23, Gastropod *Nassarius*. 24–28, *Turritella*. From Cadée (1968).

This extraordinary group of reef teleosts evolved rapidly, coinciding with the evolution of the coral taxa that dominate reefs today (Rosen, 1988; Choate and Bellwood, 1991). Within a 20-million-year period, most teleost families that occur in modern reefs had appeared, with the exception of the durophagous Sparidae, which evolved in the Miocene (Choate and Bellwood, 1991). Thus, with the evolution of the scleractinian coral species in the Eocene (*Acropora*, *Porites*, and *Pocillopora*), the reef fishes evolved as well. Since that time, reef fish morphology has remained relatively stable



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Today, predatory and grazing reef fish in the Indo-Pacific alone comprise over 4000 species of fish, representing 18% of all living fishes (Choate and Bellwood, 1991). The triggerfish (Tetraodontidae, Balistidae) are known to crush prey in their jaws. Triggerfish durophagous specializations include the loss of jaw protrusion, enlarged jaw adductor muscles, and stout teeth. Sparidae (parrot fish) also crush corals and other hard prey.

Fish other than tropical reef fish can fragment shell material (Cadée, 1968; Cate and Evans, 1994; Norton, 1995); although they may be responsible for a majority of fragmented shelly remains in the fossil record, direct evidence linking them to the scene of the crime is lacking. Alternatively, fish that puncture shelly hardparts are known (Norton, 1988), and it would be possible to trace this specific type of shell damage in the fossil record, although this has not been attempted.

Sea snakes.—Sea snakes evolved from varanid ancestors (as did mosasaurs) in the mid-to-Late Cretaceous, and diversified greatly in the Cenozoic (Caldwell and Lee, 1997; Lee and Caldwell, 2000). From the Late Cretaceous to Eocene, there were several genera of marine snakes representative of the booidean family Palaeophidae (Hecht et al., 1974; Heatwole, 1987). Early Tertiary fossils of sea snakes are very abundant and globally widespread. However, the Palaeophidae are not the direct ancestors of modern sea snakes; rather, the Family Elapideae (terrestrial, venomous snakes of the cobra family) is thought to have given rise to the extant sea snake fauna between 35 and 25 million years ago, in the Oligocene to Miocene.

However, the modern genera are not well known as fossils (Heatwole, 1987). The modern fauna of sea snakes, Laticaudinae and Hydrophiinae, are comprised of 12 genera and approximately 48 species (Hecht et al., 1974) distributed chiefly in subtropical to tropical oceans. A few saltmarsh and estuarine snakes also occur in temperate North America. Most sea snakes are nearshore creatures (within the 100 m isobath; Hecht et al., 1974). Although they not particularly well studied, it is thought that most sea snakes are piscivorous, with a few species that are "generalists"—that is, that feed on both fish and invertebrates such as crustaceans and molluscs (McCosker, 1975; Glodek and Voris, 1982; Voris and Voris, 1983; Heatwole, 1987). Saltmarsh snakes (natricines) eat small fish and fiddler crabs; the granulated file snake (*Acrochordus granulatus*) eats fish, crustaceans, and snails (Heatwole, 1987). Sea snakes swallow their prey whole, but it would be very useful to know what the taphonomic quality of the invertebrates are once they pass through the gut of the sea snake. That is, what size fragments? Is there any indication of gastric acids on the fragments? How much do they eat of varying prey items?

Sea turtles.—Cenozoic fossil turtles are known from a number of localities dating from the Paleocene (Weems, 1988). The Chelonoidea first appeared in the late Early Cretaceous and the Cenozoic fauna includes the survivors of the Cretaceous-Tertiary mass extinction: Dermochelyidae and Cheloniidea (Hirayama, 1997). Of these, the Dermochelyidae, with their thin shells and fontanellization, are poorly preserved; chelonids are better preserved, and are slightly better known (Weems, 1988). Despite this taphonomic problem, no catastrophic terminal Cretaceous event is evident in the record of sea turtles (Weems, 1988). Sea turtles had declined in diversity by the late Campanian, and were low in diversity during the Maastrichtian and Danian, but recovered in the Thanetian and Ypresian stages of the early Cenozoic (Weems, 1988). The cheloniids underwent a major diversification in the late Paleocene (Weems, 1988). This pattern of diversity matches the global pattern of oceanic cooling and warming in Late Cretaceous to early Tertiary time (Weems, 1988, p. 143, his fig. 27). The later Tertiary sea turtles are too poorly known to allow us to extrapolate diversity at this time, but in general, diversity declined from the Eocene to the five cosmopolitan species remainig today (Weems, 1988).

Although modern turtles are morphologically similar, their feeding preferences differ: the Cheloniidae are omnivorous, and herbivorous (Hirayama, 1997) adult green turtles (*Chelonia* *mydas*) eat sea grasses and algae; the hawksbills (*Eretmochelys imbricata*) eat sponges, and Kemp's ridley (*Lepidochelys kempii*) eats crustaceans. The Dermochelyidae are rather fond of jellyfish.

Caretta has massive jaws with a triturating surface; this genus is most common in temperate waters, and the present distribution of this sea turtle dates back to the early Pliocene (Dodd and Morgan, 1992; Parris et al., 2000). *Caretta* eats sea pens, crustaceans, and molluscs among many other prey items (Hendrickson, 1980; Plotkin et al., 1993; Nicholls, 1997). One species, *Caretta caretta*, the loggerhead turtle, is known to eat a variety of prey (Mortimer, 1982; Bjorndal, 1985). *Caretta* off the Texas shelf feed primarily on sea pens in the spring, and benthic crabs in the summer and fall (Plotkin et al., 1993). They can also eat molluscs, anthropogenic debris (e.g., fishing line, plastic trash bags), *Diopatra* tube worms, barnacles, fish, seaweed, whip coral, sea pansies, sea anemones, stomatopods, shrimp, and jellyfish (Plotkin et al., 1993). The small bivalve molluscs present in their stomachs may come from the digested tubes of *Diopatra*, and perhaps may not have been directly fed upon. Scavenging gastropods that feed on dead fish or crabs, such as *Nassarius acutus*, may have been eaten accidently as the turtle went after decaying fish (Plotkin et al., 1993).

Caretta populations from different geographic areas feed on different types of prey. In the western Mediterranean, *Caretta caretta* eat fish and tunicate salps, although they can also eat benthic crustaceans and molluscs (Tomas et al., 2001). However, the fish may be from scavenged by-catch that is thrown overboard by fisherman. *Caretta* can also forage on jellyfish at the ocean surface (Plotkin et al., 1993). The variety of prey that these loggerheads eat is impressive, denoting a generalist (Plotkin et al., 1993). Of all the sea turtles that exist today, *Caretta* is the only generalist.

Sea and Shore Birds.—The extinction of pterosaurs and early toothed diving birds in the Late Cretaceous left open another important niche for marine piscivorous predators. It seems that this void was filled rapidly by the evolution of neognathan sea birds (Fig. 11.6). Aquatic birds are included among the oldest fossils of the Division Neognathae, with Late Cretaceous records for the transitional shore birds (Feduccia, 1995). Several orders of marine birds have fossil records extending at least to the early Paleogene; these include Anseriformes (ducks), Gaviiformes (loons), and Charadriformes (shore birds).

Foot-propelled loons (O. Gaviiformes; Late Cretaceous(?) to Recent) and grebes (O. Podicepiformes; Miocene to Recent) appear highly convergent on the Cretaceous ichthyornithines and hesperornithines, but are not closely related (Chiappe, 1995). Contrastingly, gliding albatrosses (O. Procellariformes; Eocene to Recent), some with wingspans exceeding 3.5 m, gulls (O. Charadriformes; Eocene to Recent), and pelicans and cormorants (O. Pelicaniformes; Eocene to Recent) seemingly fill a guild similar to the Mesozoic sea-going, piscivorous pterosaurs. Finally, the penguins (O. Sphenisciformes; Eocene to Recent) (Fig. 11.6), including some 25 genera, have an excellent fossil record, primarily in the Southern Hemisphere (Simpson, 1975); diverse fossils are especially common in the Eocene to Miocene of New Zealand and Seymour Island. These amphibious birds have become specialized for rapid underwater flight even as they have lost aerial flying ability. Interestingly, an extinct clade of flightless pelicaniform birds, the Plotopteridae (Eocene to Miocene), convergently evolved elongate paddle-like wings for underwater flight. Some of the Pacific plotopterids attained lengths of 2 m (Olson and Hasegawa, 1979). All of these birds are primarily piscivores and their abundance attests to the proliferation of small teleost fish in near-surface seawater.

The diversification of diving and other coastal marine birds also may have greatly impacted the fossil record of crustaceans and molluscs (Vermeij, 1977, 1987). Although several groups originated in the Late Cretaceous, the diversification of shore birds and diving marine birds took place chiefly in the Paleogene (Vermeij, 1987). Oyster catchers, however, originated in the Neogene (Olson and Steadman, 1978). Diving marine birds catch fish that had previously preyed on molluscs; the molluscs are then transported to nests often far from their original habitat (Teichert and Serventy, 1947; Smith, 1952; Lindberg and Carlton, 1969; Lindberg and Kellogg, 1982). Coastal birds such as the oyster catchers and eiderducks can prey directly on large numbers of molluscs and other invertebrates (Schäfer, 1972; Cadée, 1989,1995). Oyster catchers penetrate molluscan prey by stabbing slightly gaping valves with their beaks, resulting in broken mollusc shells (Drinnan, 1957; Carter, 1968; Cadée, 1995). Oyster catcher predation often produces distinctive shell damage, with one valve fragmented and the other untouched (Drinnan, 1957). However, at least half of the prey shells may be left intact as these birds also insert their beak between the valves, supposedly without harming the shells.

The diet of herring gulls may consist of up to 70% marine molluscs. Prey are directly scooped up by the gull from the marine environment and transported to the shore where the shells are dropped over tidal flats or other hard surfaces, which fragments the shells so that the meat can be extracted (Cadée, 1995). Often, birds select particular sizes of prey, which can affect the resultant fossil record of coastal molluscan assemblages (Cadée, 1989). Cadée (1995) has estimated for the Dutch Wadden Sea that shell-crushing shore birds may fragment up to 35% of the annual shell carbonate production. Because the Dutch Wadden Sea benthos has up to 75% shell fragments, many of these fragments may be of biological rather than physical origin (Cadée, 1995). Thus, in shallow Cenozoic seas, coastal and sea birds would have been important agents of shell fragmentaion (Cadée, 1995). These fragments must occur in the fossil record (Trewin and Welsh, 1972), but it is generally impossible to pinpoint exactly who fragmented the shells.

Shore birds may also leave benthic feeding traces in soft sediment. For example, gulls such as *Larus ridibundus* may make troughs up to 3 m long, 15 cm wide, and 3 cm deep in soft shore sediments as they forage for food (Cadée, 1990). Shelducks make smaller pits (60 cm in diameter and 10 cm deep). These feeding traces are similar to those produced by foraging rays and flatfish (Cadée, 1990). However, rays excavate sand around the circumference of the foraging pits, whereas shelducks excavate to only one side (Cadée, 1990). These distinguishing characteristics could be obliterated by the tides, and therefore it may be difficult to distinguish bird foraging pits from those of benthic fish predators. Foraging pits of aquatic birds are known only from the Holocene.

Pinniped Mammals.—Pinnipeds—seals, sea lions, and walruses (Fig.11.11)—in modern seas have a global distribution, occur in enormous numbers in some regions of the world, and are able to dive to great depths in the ocean in search of food (Table 4). Therefore, some forms must have had a significant impact on hardshelled communities, although many eat fish. Some of the pinnipeds evolved molar crowns with hyper-mineralized cutting edges for crushing and piercing the hard exoskeletons of crustaceans and molluscs (Haley, 1986). Pinnipeds evolved in the Eocene, and thus have had over 40 million years to affect the evolutionary history of molluscs and arthropods; however, there is no indication that they did so.

Walruses (Family Odobenidae) feed mainly on benthic invertebrates, and have a peculiar feeding style: they suck out the siphon or foot of bivalves using their piston-like tongue while their mouth works as a vacuum pump (Muizon, 1993). Walruses have large and deep palates, a wide, blunt snout with strong muscular insertions, and a reduction of maxillary dentition (Muizon, 1993). The tusks are thought to have a primarily social, rather than foraging function. Walruses also leave long, narrow feeding tracks or small excavated pits that can be seen in side-scan sonar (Oliver et al., 1983; Nerini, 1984, her fig. 3).

All known odobenine odobenids (walruses) are bottom feeders and are first known from the Miocene (Repenning, 1976). Several extinct species from the Pliocene are known to have been molluscivorous (Repenning, 1976) and were widespread at that time in the northern hemisphere (Muizon, 1993). However, the modern walrus (*Odobenus*) has a fossil record only from the Pleistocene (Repenning, 1976). There is no direct fossil record of pinniped predatory behavior, with the possible exception of putative coprolites packed with crab parts, attributed to seals (Glaessner, 1960; Boucot, 1990).

Sea otters.—Sea otters (Table 4) evolved during the cooling period of the late Miocene, and are restricted to temperate regions (Van Blaricom and Estes, 1988). Otters occur in shallow coastal areas, where they eat a variety of invertebrate prey (Haley, 1986; Van Blaricom and Estes, 1988). In soft-sediment habitats, they are known to prey upon endobenthic bivalves (Kvitek et al., 1992, 1993). Sea otters ingest copious amounts of echinoderm and molluscan prey—taking in up to 35% of their body mass in invertebrate prey every day (Hines and Pearse, 1982)—but their predatory effects in the fossil record remain unknown. Hines and Pearse (1982) used the size, structure, and breakage characteristics of empty abalone shells to document the selectivity of the predator and the source of abalone mortality in a rocky subtidal habitat off of central California. Gormand sea otters prefer abalones in California, and can consume about ten abalones a day (Costa, 1978). Similarly, cracked shells were used to infer otter predation on bivalve prey in southeastern Alaska (Kvitek et al., 1992). In this area, sea otters substantially impacted the population of endobenthic bivalves and epibenthic urchins (Kvitek et al., 1992, 1993). Additionally, foraging pits dug by otters attracted predatory sea stars, which then ate any exposed molluscs. Otters digging for clams also exhumed buried shells (Kvitek et al., 1992), suggesting that biological remainie is common in these areas. The reworked shells then become settling sites for epibenthic invertebrates. Curiously, sea otter populations may be controlled by paralytic shellfish poisoning in these areas (Kvitek et al., 1993).

The predatory record of these creatures should be discernible because sea otters have peculiar carnassial teeth that are flat and rounded for crushing prey, and their lower incisors are used to scoop meat out of shells. One thing is certain, however: where sea otters occur, their effects on populations of their favored food items should be great. Sea otter predation on sea urchins has a considerable effect on nearshore community structure (Estes and Palmisano, 1974; Estes et al., 1982). It is also known that where humans have preyed on sea otters for their furry pelts, the resultant fossil record is skewed toward herbivorous limpets and sea urchins; where sea otters are not preyed upon, the stratigraphic record shows abundant kelp beds and fish populations (Simenstad et al., 1978).

Cetaceans.—Cetaceans (whales and dolphins) originated from land-dwelling artiodactyls in the early to middle Eocene (Gingerich et al., 2001; Thewissen et al., 2001). Early forms such as *Ambulocetus* (Fig. 11.7–11.9) probably were amphibious and may have behaved like seals (Thewissen et al., 2001). It is not known what these ancient toothed whales fed on. By the late Eocene the gigantic (20 m) and fully marine *Basilosaurus* seems to have occupied the guild of large Mesozoic marine reptiles, such as mosasaurs (Fig. 11.10). Its sharp, multiply cusped, undifferentiated teeth were apparently adapted to fish capture, although a relatively small head limited prey size (Benton, 1997). The toothed whales (Suborder Odontoceti) diverged in the Oligocene and radiated during the Miocene into a large number of smaller, dolphin-like lineages (Barnes, 1984). These whales evolved highly sensitive echolocation and fast-swimming behaviors. They are well adapted for chasing down and capturing fish, sharks, and, in some cases, other whales. Apparently, these odontocetes re-evolved many of the adaptations of Mesozoic pursuit predators, specifically the ichthyosaurs (see Massare, 1987, 1997). The largest toothed whales, sperm whales, are of uncertain origin, but molecular studies of Milinkovitch (1995) suggest that they may actually have been derived, in the Oligocene Epoch, from the baleen whales rather than the odontocete whales. Sperm whales are well adapted for deep diving in pursuit of squid prey and perhaps occupy the guild of some Cretaceous mosasaurs.

An unprecedented find of a walrus-like whale skull from the Pliocene of Peru indicates that one rare form of whale may have been durophagous on molluscs and/or crustaceans (Muizon, 1993). *Odobenocetops peruvianus* did not have an elongated rostrum, but had large ventrally directed premaxillary tusks, a deep-vaulted palette without teeth, and strong muscle scars on the premaxillae, which indicate durophagy (Muizon, 1993). Its morphology is similar to the Beluga and narwhal whales (Monodontidae).

The Suborder Mysticeti (baleen whales) originated in the Oligocene (Whitmore and Sanders, 1976) and developed sheets of horn- or hair-like baleen for sieving water to collect pelagic organisms, especially krill—a form of predation previously evolved by certain bony fish (e.g., Mesozoic pachycormids, and whale sharks) and perhaps by a Triassic marine reptile, the placodont *Henodus*. All of these organisms attained large size, and mysticete whales include the largest known organisms.

While a number of cetaceans may eat some benthic fauna, it is only the gray whale (Mysteceti, Eschrichtiidae, *Eschrichtius robustus*) that consistently raids the benthos in search of invertebrates (e.g., tubiculous amphipods and callianassid shrimp) to complement its fare of pelagic prey such as squids, mysid shrimp, and fish (Norris et al., 1983; Nerini, 1984). Gray whales are also known to skim eelgrass mats for both crustaceans and sea grass/algae, and sandy muddy habitats for gastropods, bivalves, and tube-building polychaetes (e.g., *Diopatra* and *Onuphis;* Nerini, 1984, her table 2). Buccinids, neptunids, thaids, and naticids are just a few of the gastropods that have been found among gray whale stomach contents; *Macoma, Mya*, and *Mytilus* are some of the ingested bivalves. The gray whale is able to sieve sediments through its thick baleen plates, which have coarser hairs than other baleen whales (Nemoto, 1970).

Gray whales leave very large feeding pits in shallow, nearshore to intertidal mudflats that are often the only record of their feeding behavior (Nerini, 1984, her fig. 1). On one benthic foraging dive, it is possible for one whale to make a series of shallow pits that are usually arrayed in a slight curve and range from 1 to 3 m long and from 0.5 to 1.5 m wide. Gray whales are known to commonly feed in Baja California lagoons, along their migratory range from the Bering Sea to Baja California (a 6000-km range), and in the northern Bering, Chukchi, and Beaufort Seas (Nerini, 1984). An entire population of gray whales (estimated in 1984 at 15,500 whales) could turn over 3,565 km^2/yr of sea bottom while feeding, considerably impacting the benthic communities where they feed (Nerini, 1984).

Gray whale fossils, however, are only known from the late Pleistocene, although several closely related groups are known from the Miocene of North America (Barnes and McLeod, 1984). The obligate barnacle parasite of gray whales, *Cryptolepas*, is also only known from the late Pleistocene (Barnes and McLeod, 1984). It is known that there were two allopatric populations of the gray whale in the early Holocene, one in the North Pacific and one in the North Atlantic, which is now extinct.

Order Sirenia (sea cows).—Sea cows date from the Eocene, and are a very small group of mammals that feed chiefly on sea grasses, algae, or water hyacinths (Domning, 1976; Savage, 1976). One particular fossil Sirenian, however, may have fed on benthic molluscs. *Miosiren* from the late Miocene of Belgium displays thickened tooth enamel and cusp modifications, which indicate that it may have fed on molluscs (Savage, 1976).

Other mammals that forage for marine invertebrates.—Raccoons (*Procyon*) forage for crustaceans in temperate to subtropical tidepools and salt marshes (Ricketts et al., 1985; Walker, pers. obs., 1997). The first known *Procyon* is from the upper Pliocene; there are several Pleistocene fossil species as well (Arata and Hutchison, 1964). Fossils of *Procyon* are known from all over the continental United States, as well as Baja California and Canada (Arata and Hutchison, 1964). Coyotes and other mammals also can feed in the intertidal zone of temperate regions (Ricketts et al., 1985). Rats, in particular, can prey on over 40 different types of intertidal organisms, especially key hole limpets, porcellanid crabs, and cancrid crabs (Navarrete and Castilla, 1993).

Humans.—Lastly, the origination of humans in the late Pleistocene added to the potential for coastal foraging and selection of particular invertebrate food items as evidenced by abundant kitchen midden sites around the world, as well as tools embedded in late Pleistocene coral reefs (see Walter et al., 2000). Humans have been using sea creatures for food and ornamentation for many thousands of years based on archaeological shell middens (e.g., Speed, 1969; Avery and Siegfried, 1980; Jerardino et al., 1992). For example, in Chile, the rocky coast has been exploited by humans for food for at least 8,500 years (Moreno, 2001). This foraging was tied closely to settlement of the Pacific region of South America, and has only recently been recognized as a force that affects the resultant ecological community structure of an area (Moreno et al., 1984). Ecological shifts in seafood biota directly or indirectly caused by humans are known from the present day (Castilla and Duran, 1985; Castilla, 1999) and from the stratigraphic record (Simenstad et al., 1978; Kirch, 1983).

EVOLUTIONARY VIGNETTES: SELECTED PATTERNS OF PREDATION FROM THE CENOZOIC

The Mesozoic Marine Revolution hypothesis (Vermeij, 1977, 1987) has been subjected to many tests, from several sources of evidence, chiefly to determine: (1) if shell armor increases through time; (2) if shell predators increase through time; and (3) if lethal shell injuries increase through time (see also Vermeij, 1983). In the following sections we review and critique some of the primary lines of argument. Most of the putative durophagous functional groups re-evolved in the Cenozoic, and, one could argue, became more common during this time than in the Mesozoic. However, some of this apparent increase may represent biases such as the Raupian "pull of the Recent" and the better record of well-preserved fossils. It is also well known that aragonitic Mesozoic invertebrates, especially molluscs, are not as well preserved as calcitic forms (except for ammonoids in black shales); whereas in the Cenozoic more aragonitic forms are preserved, giving us a more detailed picture of the potential predatory panorama. Shell repair, drilling, and other features can be distinguished on Cenozoic hardparts much more easily than on older ones. This is not a gloom-and-doom scenario, just a realistic one.

Examples of prey in coprolites or regurgitated remains, predation preserved *in situ*, and prey organisms in stomach contents are rare in Cenozoic deposits just as they are rare in Mesozoic and Paleozoic assemblages (Häntzschel et al., 1968; Boucot, 1990; Brett, 1990). While there is an extensive literature on coprolites, most studies focus on terrestrial and vertebrate remains; few if any coprolites in marine environments can be tied with reliability to a specific predator (Bishop, 1975; Boucot, 1990).

Echinoderms.—In many localities, not least in the Danish basin, the Cretaceous-Tertiary extinction greatly affected the invertebrate biota. However, several echinoderm groups do not appear to have been greatly affected by this extinction event, and show an increase in diversity directly above the boundary in the Danish basin (Kjaer and Thomsen, 1999). There are several examples of shallow-water stalked crinoids from the early Cenozoic (Oji, 1996); and further movement offshore of isocrinid (stalked) crinoids occurred in the Miocene in the Caribbean region (Bottjer and Jablonski, 1988; Donovan, 2001). Deeper-water crinoids have a relatively constant generic composition from the Miocene to the Recent; the Plio-Pleistocene regional extinction had little effect on this group (Donovan, 2001). Shallow water areas remain populated by stem-less comatulid crinoids (Donovan, 2001). This suggests that mobility and cryptic habitats may have enabled this group to survive in the face of high predation in shallow water.

Arm autotomy is common in stalkless crinoids, but has not been well documented in stalked crinoids (Oji, 1986). The ability to autotomize crinoid arms dates back at least to the Triassic (Oji and Okamoto, 1994). It is thought that autotomy acts as a "lizard-tail" defense (after Baumiller et al., 1999): arms can be dropped quickly into the mouths of predators, while the main body of the crinoid is left to regenerate new arms. It is possible that isocrinids exploited this ability and that this is what allowed them to survive the putative increased fish predation in the late Mesozoic (Oji and Okamoto, 1994). Modern crinoids from bathyal depths have more regenerated arms than crinoids from deeper depths (Oji, 1996).

Stalk shedding is also a common occurrence in isocrinoids, and may be a deterrent to predators. Baumiller et al. (1999) hypothesize that crinoids have evolved various antipredatory strategies since the Devonian: a planktonic (e.g., *Uintacrinus*) or pseudoplanktonic (e.g., *Seirocrinus*) lifestyle, stalk-shedding abilities (e.g., in isocrinids, comatulids), short-bursts of swimming (e.g., comatulids), and life in cryptic habitats (e.g., comatulids).

Kier (1977) plotted global diversity of echinoids through the Cenozoic, and showed limited diversity in the Paleocene and Oligocene Epochs, with peaks in echinoid diversity in the Eocene and Miocene–Pliocene Epochs; the record of regular echinoids was not as good as that of irregular echinoids. Regular echinoids are commonly fragmented, and their fragments usually are not studied by taxonomists (Greenstein, 1993) or are not collected (Oyen and Portell, 2001). Clypeasteroids evolved in the Paleocene and diversified rapidly, aided by the evolutionary innovation of numerous small tube feet and spine-free branching food grooves. Flattening of the test meant that only the top fraction of the sediment could be sieved for food particles (Kier, 1982).

Records of predation on Cenozoic echinoids are rare, even though in modern seas predation on echinoids is well documented (Nebelsick, 1995, 1999). Drilled echinoid tests are known from the Eocene Upper Ocala Formation in North Central Florida (Gibson and Watson, 1989). Some of these drillholes were predatory; others were parasitic. Parasitic eulimids are known to drill the aboral sides of echinoids; commonly an echinoid displays multiple drillholes made by parasitic gastropods (Berry, 1956). Cassid drillings on irregular echinoids are known from the Eocene of the Atlantic Coastal Plain (Woodcock and Kelley, 2001) and elsewhere (see Cassid review, this paper). Sand dollars (*Parascutella hobarthi*) from the lower Miocene of the Austrian Molasse Zone displayed repaired scallop-shaped areas on their tests resulting from predation, possibly by regular echinoids (Nebelsick, 1999). Lethal predation was indicated by large round holes cutting through the echinoid test or by bite marks penetrating the oral surface (Nebelsick, 1999). Fish bite marks on clypeasteroid echinoids are also reported from the upper Miocene of Argentina (Zinsmeister, 1980).

In the modern Atlantic and Gulf region, there are 95 asteroid species in 56 genera, with a depauperate (because of lack of work) record in the Cenozoic Caribbean region dating to the early Paleocene (Donovan, 2001). Asteroids are known from the Eocene to Pleistocene in Florida, and in some horizons their fragments are very abundant (Oyen and Portell, 2001). Amazing preservation of complete specimens of *Heliaster microbranchius* is known from the Pliocene of Florida (Oyen and Portell, 2001).

Ophiuroids are one of the most diverse extant echinoderm groups in the Caribbean region, but have a "poor" fossil record because of their easily disarticulated skeletons and a lack of work on these creatures (Donovan, 2001; Oyen and Portell, 2001). Nonetheless, a number of dense stalked crinoid-ophiuroid associations are known from before the Jurassic; a near absence of these dense assemblages after the Jurassic was postulated to be due to predation pressure (Aronson, 1987, 1991). Intriguingly, however, the Tertiary La Meseta Formation, Antarctic Peninsula, contains localized dense assemblages of autochthonous ophiuroids and crinoids representing shallow-water facies (Aronson et al., 1997). The incidence of sublethal arm injuries was low in this assemblage, suggesting that predation was rare; possibly in high latitude cool-water areas predation is suppressed.

Molluscs.—Molluscs provide the most important Cenozoic database for examining evolutionary questions regarding the fossil record of predation because they are globally widespread, very abundant, well preserved, and present in many different facies. Therefore, most studies have focused primarily on escalation in marine molluscs. Shell repair and shell drilling in molluscs have provided the database by which to examine Phanerozoic predatory trends. Shell repair data has not been applied with as much success as drilling predation, most likely because shell repair can be a consequence of a variety of physical and biological destructive factors. Shell repair may show an increase in the Cretaceous and Cenozoic, or it may not, and a closer examination of shell repair during this time is warranted (Table 3). Little work has been done for Cenozoic localities to examine shell repair with respect to habitat, species, and stratigraphic interval.

Do lethal shell injuries (or shell repair) increase through late Mesozoic-Cenozoic time?— Traces of non-fatal peeling in molluscs are evident as scars on the shell (Figs. 8.2, 13; Table 4) that result from repair of the outer shell lip by the mantle edge (Robba and Ostinelli, 1975; Raffaelli, 1978; Elner and Raffaelli, 1980; Vermeij et al., 1982; Vermeij, 1982; Allmon et al., 1990; Cadée et al., 1997). Frequency of shell repair is often cited in order to compare temperate with tropical and deep-sea with shallow-sea habitats, as well as to examine within- and between-habitat predation, and the temporal dynamics of shell repair. It appears that shell repair may increase through the Phanerozoic, with higher incidence of shell repair in the Cenozoic—indicating that durophagous predators become more of a threat to molluscan prey (e.g., Vermeij et al., 1980, 1982; Vermeij, 1983, 1987; Dietl et al., 2000). But analysis of the data on shell repair (Table 3) illustrates that there are no real differences in shell repair frequency between the Mesozoic and Cenozoic, despite the better record of marine durophagous predators at this time.

Shell repair must be interpreted with caution, as researchers use different methods and interpretations in analyses of shell repair data. Two methods are used to estimate shell repair frequencies. First, shell repair frequencies can be estimated by dividing the number of shells with one major repair (jagged scar) by the total number of shells in the sample (after Robba and Ostinelli, 1975; Raffaelli, 1978; Elner and Raffaelli, 1980; Geller, 1983; Vale and Rex, 1988, 1989; Cadée et al., 1997; Walker, 2001). This is the more conservative estimate for shell repair, as snails can survive injury more than once. If the snail is older, it may display more instances of shell repair. Second, shell repair frequency has also been calculated as the total number of scars in all shells divided by the total number of shells in the sample (Table 3) (Vermeij et al., 1980, 1982; Vermeij, 1982). This method does not take into account the fact that older shells may have more shell repair than younger shells, and thus can result in an overestimate of shell repair for an assemblage (although Vermeij has recognized this problem). Further, more instances of shell repair than actual sample size are commonly reported which makes the data difficult to interpret. Therefore, it is important to determine which method is most useful in examining the fossil record of shell repair and to be consistent with that method. Comparing papers that use different methods is difficult and tenuous at best.

Interpretations of shell repair must be carefully evaluated especially in regard to equating frequency of shell repair with intensity of predation (Cadée et al., 1997; Cadée, 1999). There are several factors that complicate the interpretation of shell repair. First, it is difficult to distinguish repair that may have been provoked by physical factors, such as burial or crushing between stones (e.g., Raffaelli, 1978; Cadée, 1999). Self-inflicted wounds resulting from the process of predation that are then subsequently repaired can also inflate estimates of shell repair. For example, buccinid gastropods chip their outer lips in the process of preying on other molluscs and then repair their self-inflicted breakage (Nielsen, 1975). Second, shell repair frequencies do not directly correlate with the intensity of predation, as a total absence of scars may mean either that predation did not occur or that predators were 100% efficient (Schoener, 1979). Third, the incidence of repair on a shell needs to be tied to the age of the organism, as older snails may exhibit more shell repair than younger ones. This may be especially true for deep-sea snails that may exhibit slower growth rates and increased longevity with depth (Vale and Rex, 1988). Fourth, certain life history traits (slow growing vs. fast growing, particular behavior) and feeding mode may affect whether and when a shell is exposed to predation. Fifth, some species may be more prone to predation than others in an assemblage (Hoffmeister and Kowalewski, 2001; Kelley and Hansen, 2001; Walker, 2001); and, using the metric of only one species' repair frequencies can bias the results for an entire assemblage. Lastly, for a time-averaged assemblage, shell repair frequencies might be higher than what would be found in the living population at any one time because of the patchiness of predation (and associated physical factors).

The consensus is, however, that conspicuous shell repair (i.e., conspicuously peeled shells with subsequent repair) is most likely the result of predation. That is, only deeply peeled injuries that are subsequently repaired can reliably be used in the analysis of shell repair, whereas repaired nips or edge chippings may not be indicative of predation (Walker and Voight, 1994; Walker, 2001). Consequently, although shell repair is not a good indicator of predation intensity, it is instrumental in providing a record of predators within a habitat when body fossils of the predators are missing.

Shell Drilling through Time.—Shell drilling frequency is less ambiguous in interpretation: a completed drillhole signifies prey mortality. Also, particular borehole morphologies may be associated with specific gastropod or octopod predators (Carriker and Yochelson, 1968; Kabat, 1990; Kowalewski, 1993; Kowalewski et al., 1998). Nonetheless, certain caveats also apply to the study of drilling predation.

Escalation studies of drilling predators and their prey have not generally taken into account the particular facies and associated biota of analyzed assemblages (with the exception of Hoffmeister and Kowalewski, 2001). Essentially, all assemblages are treated as if they were the same facies (e.g., onshore and offshore assemblages are grouped). Environmental differences between assemblages, however, can affect the morphology of the taxa—some species are larger in nearshore environments than they are in offshore environments (or vice versa). This gradient in morphology may not be related to predation.

Sedimentary facies could also have taphonomic effects. For example, assemblages deposited above storm wave base may sort drilled and undrilled shells differently compared to offshore assemblages. Drilled and undrilled shells can be differentially transported in nearshore settings and thus there may be a bias toward an overabundance of drilled shells in some localities. Additionally, drilled shells are more prone to taphonomic breakage than undrilled shells, and such breakage may be more common in some localities than others (Roy et al., 1994). Left vs. right valves of bivalves and pedical vs. brachial valves of brachiopods are also differentially transported and/or preserved (Brett and Allison, 1998). Thus, it would be important to know the valve frequencies of an assemblage, and whether they are biased. It would also be important to know if drilling predators were actually found in the same assemblage as the drillholes (e.g., Hansen and Kelley, 1995), but not all papers that examine drilling predation discuss this issue.

It is also important to examine more than one locality within a time period, as the record of predation is strongly controlled by habitat (Vermeij et al., 1981; Geller, 1983; Hansen and Kelley, 1995; Cadée et al., 1997; Hoffmeister and Kowalewski, 2001). Location within a sequence may also affect the density of drilled shells, as transgressive lag deposits formed after a major sequence boundary (e.g., extinction?) commonly contain more biotic information as a result of longer time averaging (Brett, 1995; Holland, 2000). Therefore, one must be careful in interpreting the pattern and process of drilling through the Phanerozoic, as it is not as simple as merely counting drilled taxa per temporal stratigraphic sequence. As Boucot said, "Nature does not take place within an ecological vacuum"; nor should evolutionary interpretations using the fossil record be decoupled from facies studies.

Given these caveats, based on an analysis of over 150,000 gastropod and bivalve shells from the Gulf and Atlantic Coastal Plain (GACP), Kelley and Hansen (2001) suggested that the interaction between naticid drilling predators and their prey does not necessarily show escalation from the Cretaceous to Oligocene. After examination of a number of localities, they found that there is an episodic pattern to drilling frequency, with mass extinctions resetting the "arms race" for faunas. Drilling within the most of their Cretaceous localities was greater than several of their late Eocene localities and similar to early Oligocene localities (their table 8.1, p. 153). This is a significant finding given that previously Vermiej (1987) had used naticid drilling as one line of evidence illustrating escalation in Cretaceous to Eocene faunas. In the Cretaceous Vermeij (1987) found limited drilling, but by the Eocene, drilling had reached modern levels.

Kelley and Hansen (1993), in contrast, did not find an ever-increasing trend in naticid drilling frequencies from the Cretaceous to Eocene for GACP molluscs. Escalation could also mean that a predator gets better at selecting prey; however, Kelley and Hansen (1993) did not find any temporal trends toward increased drillhole site stereotypy in naticids. Molluscan prey were found to have more incomplete drillholes and multiply drilled shells, indicating that prey effectiveness may have escalated, but Kelley and Hansen's (2001) data did not show a trend for most of the periods examined.

Kelley and Hansen (2001) also examined differences in morphology within molluscan genera that may be related to escalation. Although many genera were examined, four particularly long-ranging Miocene genera from the GACP—two gastropod predators (*Euspira heros* and *Neverita duplicata*) and two frequently drilled naticid prey (*Bicorbula idonea* and *Stewartia anodonta*)—were analyzed for different morphological charateristics (their table 8.3, p. 159). In this case, however, the gastropod predators are also cannibalistic. Results showed that shell size (height) did not change for either *E. heros*, *B. idonea*, or *S. anodonta* (no data are reported for *N. duplicata*), indicating that these prey species found no size refuge from predation over time. Shell thickness (which would make a prey item more difficult to drill) did not change for *E. heros*, decreased for *N. duplicata*, slightly increased for *B. idonea* and increased greatly for *S. anodonta*. Internal volume (an indicator of the amount of food a predator can take in) did not change within the Miocene. Thus, it appears that most prey characters deemed to be directly related to predatory escalation did not demonstrably change within the Miocene (except for shell thickness in *S. anodonta*). It would be interesting to know whether drilling frequency increased or stayed relatively the same across the various assemblages examined.

Escalated species are thought to be more sensitive to changes in primary productivity because maintaining heavy armor or high speeds to avoid predators requires high metabolic rates and thus an uninterrupted food source (Vermeij, 1987). Therefore, Hansen et al. (1999) tested whether purported escalated species (those with antipredatory adaptations such as heavy armor) were more vulnerable to extinctions caused by climate change and associated environmental changes. Ten shell characters deemed important for predator resistance were evaluated for GAPC molluscs across various mass extinction events associated with climatic cooling and/or a decline in primary productivity (e.g., Cretaceous-Paleocene; Eocene-Oligocene; middle Miocene; Pliocene-Pleistocene). Importantly, all these assemblages were deposited in relatively shallow shelf environments with roughly similar grain sizes; all but one assemblage was a bulk collection. Hansen et al. (1999) found that escalated species, overall, were not more vulnerable to climate-related mass extinction. Only ornamented Pliocene gastropod species were more susceptible to extinction than their weakly ornamented counterparts. In another study, Kelley et al. (2001) found that recovery faunas after a mass extinction event were not more vulnerable to enhanced drilling pressure, contrary to hypothesized predictions. Additionally, no overall trend in unsuccessful drilling was seen from the late Cretaceous to Pleistocene.

Spatial trends in drilling predation vary by environment in fossil studies. Hansen and Kelley (1995) used 27,554 specimens of GACP molluscs from the Eocene and found a statistically significant difference in drilling frequency between the inner- to middle- shelf Moodys Branch Formation and the outer-shelf Yazoo Formation, the deeper site having a higher frequency of drilling predation. However, for the five other assemblages examined from the Moody's Branch, there was no significant bathymetric trend. Drilling frequency was also highly correlated with the percentage of naticids and their preferred prey within each assemblage. Hoffmeister and Kowalewski (2001) examined spatial and environmental variation in drilling predation in the middle Miocene of Central Europe. The sampling methodology allowed for comparisons within provinces, between provinces (Boreal vs. Paratethys), and between facies (fine-grained vs. coarse-grained siliciclastics). They found that unsuccessful and multiple drillholes occurred more frequently in the Boreal province than the Paratethys province; the same facies also included molluscs with different drilling frequencies—with as much as a three-fold difference between samples collected in adjacent sites from the same facies! They concluded unequivocally that spatial variation should be evaluated independently before any large-scale temporal trends are inferred for predation. Clearly multiple collections with emphasis on facies need to be included in the temporal analysis of escalatory predation hypotheses.

Shell ornamentation (spines).—Spine development requires extra amounts of calcium carbonate in seawater, and shallow tropical marine waters meet this requirement (Nichol, 1965; Stanley, 1970). Spines have inspired varied hypotheses concerning their function as antipredatory architecture (Table 5). Few studies, however, have focused on alternative hypotheses such as whether spines are phylogenetic legacies of shell building (as in cardiid bivalves), non-aptive constructional artifacts, exaptations, or adaptations. Few workers have endeavored to apply such philosophical rigor, and many have created adaptive scenarios. Another important possible function of spines could be to increase surface area for the settlement of epibionts, and for trapping debris that camouflages the shells (Vance, 1978; Feifarek, 1987; Stone, 1998). Stone (1998) has shown that spines on epifaunal bivalves deter the attack of muricid shell-drilling predators, but muricids can still bore in areas where spines are absent. In the same study, spines were found not to deter predatory attacks by sea stars that engulf their prey. The rise of spinose ornamentation in bivalves predates the radiation of the predatory Muricidae in the Albian, and actually extends back to the late Paleozoic in the superfamily Pectinoidea (Stone, 1998).

Molluscan conchiolin layers: Are they antipredatory?—Conchiolin is the organic component of molluscan shells composed of proteins, polysaccharids, and glycosaminoglycans (Table 6) (Wilber and Simkiss, 1968; Gregoire, 1972; Wainwright et al., 1982). The periostracum and non-calcareous operculae are composed chiefly of conchiolin, while the nacreous layers and other shell microstructures contain various quantities of conchiolin. Thus, conchiolin has a very old history, putatively stemming from the oldest shelled mollusc in the Cambrian Period. What is puzzling, however, is that only a few groups of molluscs—chiefly the freshwater bivalves (e.g., Margaritiferidae, Unionidae, Mutelidae), estuarine to marine bivalves (Corbiculidae and Solenidae), and a few marine species—have conchiolin represented as separate sheets within their shells (Taylor et al., 1969; Anderson, 1992; Harper, 1994). Conchiolin, as a protein, is thought to form at a high metabolic cost to the organism—and, perhaps because of this, there appears to be an evolutionary tendency to lose conchiolin layers (references in Kardon, 1998). Thus, there must be some evolutionary reason for maintaining conchiolin in molluscan shells despite its high metabolic cost of production (Table 6). It has long been hypothesized that the conchiolin sheets deterred predation by drilling molluscan predators, such as naticid (Lewy and Samtleben, 1979) or muricid gastropods (Taylor, 1970,1981), and most of the work done to test this hypothesis has focused on the corbulid bivalves (Fischer, 1963; Lewy and Samtleben, 1979; De Cauwer, 1985; Anderson et al., 1991; Anderson, 1992; Harper, 1994). The corbulids (Family Corbulidae) are small, inequivalved bivalves with a globose shell form, a single byssus thread, and shallow burrowing habits (e.g., Stanley, 1970). They first appeared in the Middle Jurassic, with the greatest diversification taking place in the Cretaceous and Eocene (e.g., Hallam, 1976).

There appear to be three contrasting temporal "trends" related to whether conchiolin reduces predation. The first is that conchiolin does effectively reduce predation on corbulids through their evolutionary history. Fischer (1963), for

TABLE 5—Hypotheses for the origin of skeletal spines in marine invertebrates.

Hypothesis	**Evidence**	**Examples**	**Reference**
Spines develop in calcium carbonate supersaturated sea waters; most common in tropics	Less energetically costly to make spines in tropical waters	*Spondylus americanus*	Stanley, 1970
Spines are antipredatory	Primary spines that project outward may protect mantle edge	*Spondylus americanus*	Logan, 1974
Hollow spines and keels are for pelagic/planktonic existences	Economy of mass	Ammonoids	Birkelund, 1981
Spines have no function	Constructional artifact?	Alternative hypothesis for any invertebrate	Carter, 1967; Kauffman, 1969
Spines function in filter-feeding	Spines cover opening to animal	Poricthophenid brachiopods	Rudwick, 1970
Spines are an ancestral condition; phylogenetic constraint	Spines form in various ways, even within closely related families	Cardiid bivalves; anomalodesmatans	Schneider and Carter, 2001
Spines vary with environmental conditions of the substrate	Various spine types depending on substrate the larvae attach to	*Spondylus americanus* (Jurassic–Recent)	Logan, 1974
Attachment to substrate	Spines act as attachment mechanisms	Cemented bivalves like *Spondylus* whose right valve is attached to substrate; this hypothesis does not function for the left valve	Logan, 1974
Spines discourage epibionts	Spines and pedicellaria in some echinoderms discourage biont settlement; perhaps barbed secondary spines of *Spondylus americanus* reduce biont settlement	Sea urchins; the bivalve *Spondylus americanus*	Logan, 1974
Spines acts as supports for sensory mantle tissue; "mantle outposts" to give early warning signals of danger	--	Brachiopods (Jurassic *Acanthothirus*)	Rudwick, 1965; Logan, 1974
Spines serve a camouflagic function, breaking up distinctive outline of shell	Hair-like barbed spines typical of the neanic stage of the left valve of *Spondylus* which get covered with algae and sediment; spines are thickly encrusted with epiboints	Late Paleozoic productoid brachiopod, *Waagenoconcha;* *Spondylus americanus*	Grant, 1966; Logan, 1974
Spines stabilize the shell on a shifting substrate		The Cretaceous *Spondylus spinosus*	Logan, 1974; Carter, 1972
Spines keep the feeding margins of the shell above the substrate	--	--	Logan, 1974

TABLE 6—Evolutionary findings concerning whether conchiolin serves an anti-predatory function against drilling predators for corbulid bivalves. Alternative hypotheses are discussed in text.

Evolutionary conclusion	Evidence	Reference
Adaptation	Conchiolin arises at the same time as drilling predators in the Cretaceous	Harper (1994)
Exaptation*	Conchiolin arises in the Middle Jurassic, well before origin of drilling naticids; *however, no temporal trend in drilling predation	Kardon (1998)
Not Anti-predatory	No temporal trend in drilling predation	Anderson et al. (1991); Anderson (1992)
Phylogenetic Constructional Artifact	Conclusions drawn from synthesis of the literature	This paper

example, suggested that Recent corbulid species were less likely to be completely drilled than fossil species. Kardon (1998, p. 73) also suggests that in temporally and spatially separated fossil samples of corbulid bivalves, conchiolin layers are effective deterrents of naticid predation. The second is that drilling predation actually increased in corbulids over their evolutionary history. For example, although using a limited data set, Taylor et al. (1983) suggested that corbulids showed enhanced predation from the Late Cretaceous to Eocene. And lastly, others suggest that there is no spatial or temporal trend in drilling predation in corbulids. For example, in Late Cretaceous to Pliocene corbulid fossils from Europe and North America, De Cauwer (1985) found no trend toward increased complete drilling was found. Similarly, for Miocene to Pleistocene fossil corbulids from the Dominican Republic and Florida, there appears to be no spatial or temporal pattern in complete or incomplete drilling, strongly indicating that conchiolin layers are not effective deterrents to naticid predation (Anderson, 1992). Likewise, Harper (1994) reported that there was no significiant difference in drilling frequency among almost all geological samples examined from the Cretaceous to Plio-Pleisotocene. Further, Harper (1994) found that there was no significant difference in possession of conchiolin sheets between temperate and tropical localities. Given these contrasting findings, it is important to examine some of the salient evolutionary hypotheses regarding conchiolin as an antipredatory deterrent, such as cost-benefit analyses and whether conchiolin is an adaptation or exaptation (or neither) against predation.

Corbulids have small size and effective valve armor (i.e., relatively thick valves with conchiolin sheaths), and thus, according to Kitchell et al.'s (1981) cost-benefit model, would represent a high drilling investment with low benefits (De Cauwer, 1985). For example, Kelly (1988) found that predation on corbulids was lower than would be predicted by the cost-benefit model (but see Anderson, 1992). Yet corbulids are heavily drilled in many localities, and this may be a result of their tendency to cluster, their shallow burrowing depths, and their sluggishness (De Cauwer, 1985). Perhaps drilling predators may mistakenly drill empty shells in the presence of chemical attractants in the exhalant water of the corbulid associations (Carriker, 1981; De Cauwer, 1985); or there may be hydrodynamic and taphonomic reasons for the preponderence of drilled corbulids in some localities (De Cauwer, 1985).

Anderson et al. (1991) tested the cost-benefit model of Kitchell et al. (1981), and showed that a corbulid bivalve (*Varicorbula caloosae*) was no more likely to be drilled by a naticid predator than by a venerid bivalve (*Chione cancellata*), among Pleistocene fossils from Florida. Anderson (1992) examined many species of corbulids from the Miocene and Pliocene of the Dominican Republic and from the Pliocene and Pleistocene of Florida and found that the incidence of drilled, incompletely drilled, and multiply drilled valves was highly variable in space and time. This result was similar to other studies on drilled bivalves, and therefore indicates that conchiolin was generally not part of the antipredatory arsenal. Rather, alternative evolutionary hypotheses, such as conchiolin as a retardant of shell dissolution or a deterrent to crab-crushing predation (Anderson, 1992; Kardon, 1998), for example, need to be advanced and tested. The main evolutionary question, as Harper (1994) pointed out (paraphrasing Gould and Vrba, 1982), is whether conchiolin layers are a beneficial trait that is enhanced by natural selection (adaptation), or whether conchiolin layers are an exaptation, a beneficial trait that is secondarily co-opted for another function. Experimental testing is required to determine if a trait is truly beneficial; and there should also be a temporal correspondence between the evolution of the trait and the proposed selective agent (Harper, 1994).

Accordingly, Kardon (1998) tested three hypotheses concerning the evolutionary importance of conchiolin: 1) it retards shell dissolution; 2) it increases shell strength and thus deters crushing predation; and 3) it inhibites shell drilling by naticid gastropods. She also examined the fossil record of naticid drilling predators, and compared it to that of conchiolin-bearing corbulids (which hail from the Middle Jurassic; but see Harper, 1994) to examine the evolution of the trait in association with its putative selective agent (the naticids). Her experimental results show that conchiolin did retard shell dissolution, although—as she clearly pointed out—the majority of corbulids live in calcium carbonate–saturated regions, and have done so for most of their geologic history.

The most promising line of research concerning conchiolin, however, stems from the finding of mechanical tests that the conchiolin in corbulids may function to inhibit crack propagation, which in turn may be a deterrent to shell-crushing predation (Kardon, 1998). It remains to be tested whether conchiolin layers do inhibit shell-crushing predators. Biomechanical tests using corbulid bivalves, in addition to feeding experiments with live durophagous crustaceans, are needed to address this hypothesis. An historical analysis of shell repair in corbulids through time is warranted.

Lastly, Kardon (1988) found that naticid drilling rates were not significantly slowed by conchiolin layers. Further, although Kardon (1998) states that conchiolin has acted as an effective deterrent against drilling predation in the corbulid fossil record (p. 73, but see her p. 76), her data do not support this claim (p. 75, her table 2). Her results, in fact, support the findings of Anderson et al. (1991) and Anderson (1992) that there is temporal variation in drilling through time in corbulids, with no apparent trend. It would also be important to know from which facies these corbulids came, and whether taphonomic (hydrodynamic or biotic) conditions affected their preservation.

Although Kardon (1998) suggests that conchiolin is an exaptation, and Harper (1994) suggests that conchiolin is an adaptation, a review of the data to date indicates that conchiolin may be an artifact of construction. Of course, this statement needs to be refuted by scientific tests. That is, without further tests with shell-crushing predators, we cannot know if conchiolin is indeed a beneficial trait, either co-opted or evolved by the organism against predation. Other hypotheses were discussed by Harper (1994), such as protection against nonpredatory borers or assistance with hermetic sealing, and these could be rigorously tested as well (see Table 6). The oldest corbulids (Jurassic *Corbulomima*) were marine organisms, and had conchiolin before the evolution of naticid drilling during the Early Cretaceous (Kardon, 1998), further suggesting that conchiolin was not evolved as a deterrent to drilling predation. However, it would be very important to know the environmental conditions of the origin and diversification of corbulids; also, for those corbulids with more than one conchiolin layer, whether they are from "physiologically" more stressful environments, such as brackish water or anoxic environments. It would also be important to know their cladistic relationships with respect to their environment and conchiolin form.

SUMMARY DISCUSSION: AN EPISODIC HISTORY OF PREDATION

Predation in marine communities evolved through several phases of intensification with minor setbacks following mass extinctions (Fig. 14). The Permo-Triassic extinction crisis formed a major setback for all marine communities. This certainly included many predatory taxa (e.g., many ammonoids, nautiloids, phyllocarids, predatory archeogastropods). However, certain marine predators, notably bony fishes and sharks, seem to have been less strongly affected by this major extinction than were many benthic invertebrates (Knoll et al., 1996). Thus, predators seem to have rebounded rather rapidly and by the Middle Triassic a variety of new predator guilds had appeared, including decapod crustaceans with crushing claws, and shell-crushing sharks and bony fish. However, data from the Triassic regarding shell repair and drilling predation are almost non-existent. New groups of carnivorous marine reptiles also appeared in the Triassic, including durophagous placodonts, and piscivorous and perhaps cephalopod-eating pachypleurosaurs, nothosaurs, ichthyosaurs, and the first plesiosaurs.

Ceratite ammonoids and some marine reptiles (e.g., placodonts, nothosaurs) became extinct during Late Triassic crises. However, other lineages (e.g., ammonites, ichthyosaurs, plesiosaurs) survived to form the stem groups for new Jurassic radiations. The Jurassic to Early Cretaceous saw the rise of malacostracan crustaceans with crushing chelae and predatory vertebrates—in particular, the marine crocodilians, ichthyosaurs, and plesiosaurs. Following a setback in the Late Triassic, predators made a major re-advance in the mid-Mesozoic with the evolution of new groups of decapods, ammonites, neogastropods, and teleost fishes, as well as neoselachian sharks and marine reptiles. Some of these groups are thought to have been durophagous, but that does not mean they ate exclusively molluscan prey. Limited data from this time indicates that drilling predation existed, but occurred at low very frequencies.

The Late Cretaceous saw unprecedented levels of diversity of marine predaceous vertebrates including pliosaurs, plesiosaurs, and mosasaurs. The great Cretaceous-Tertiary extinction decimated marine reptiles. Drilling and shell peeling frequencies pick up in the Late Cretaceous corresponding to the evolution of new durophagous and shell-drilling groups. The drilling frequencies from this time are no different from those reported from Cenozoic localities; indeed, drilling and shell repair data from the later Cretaceous and Cenozoic show no apparent trends.

The Cretaceous-Tertiary mass extinction eliminated all large marine predators, including the mosasaurs, plesiosaurs, and many sharks and fish. Additionally, pterosaurs and early marine birds were eliminated. However, many benthic invertebrate and fish predatory groups survived; and during the Paleogene, predatory benthic invertebrates showed a spurt of evolution with neogastropoda and new groups of decapods, while the teleosts and neoselachian sharks both underwent parallel rapid evolutionary radiations; these were joined by new predatory guilds of sea birds and marine mamals. Ultimately, many of the large vertebrate predator guilds were refilled by newly evolved groups of marine mammals (cetaceans, pinnipeds) and birds (gulls, albatrosses, penguins). Despite the fact that a new suite of predators evolved in the Cenozoic, there are no apparent escalatory trends in durophagous predation.

All of this would seem to suggest episodic, but generally increasing predation pressure on marine organisms through the Mesozoic–Cenozoic interval. Theoretically, there should have been a

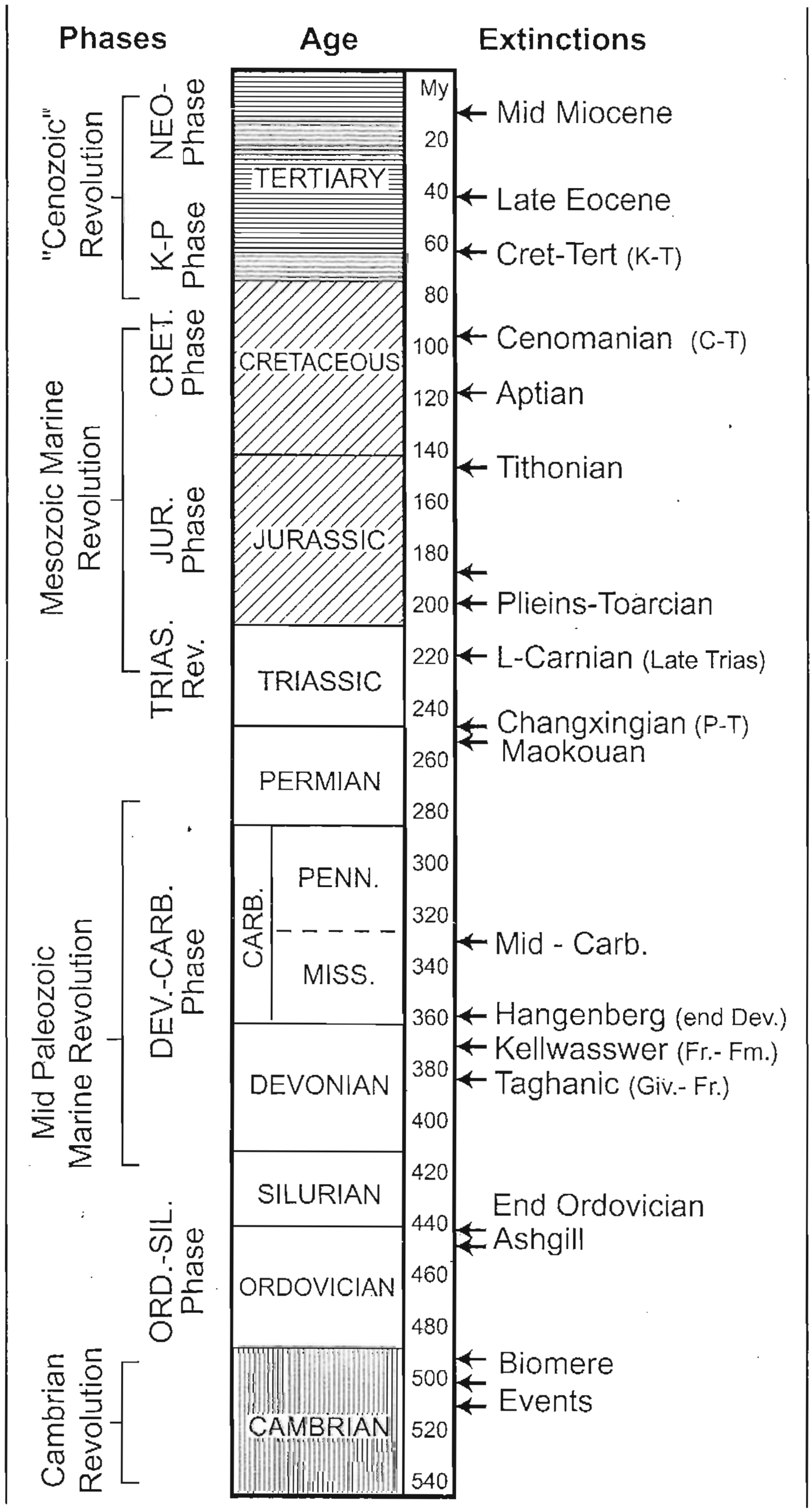

FIGURE 14—Summary diagram, showing phases of escalation in marine predator-prey systems and major extinction events.

Paleogene marine revolution in the molluscan realm, because of the increased abundance of drilling neogastropods, the first real records of durophagous stomatopods and decapod crustaceans, and the evolution of specialized bird and mammalian predators. However, most of these durophagous groups are generalists, and it may be that they had a diffuse effect on their invertebrate prey.

Finally, several new groups of carnivorous marine mammals and birds originated in the Miocene. Walruses, gray whales, and humans arose in the Neogene and affected the coastal hard-shelled biota in the areas where they foraged or settled. Thus, a Neogene phase of further predator intensification is also suggested. However, there is no direct evidence that prey were selectively affected (except for the widespread decimation of species by humans and their alteration of marine habitats).

The Cenozoic record seems to provide an excellent window into predation and its effects, but few have examined the temporal trends in predation during this time (except for naticid molluscan drillers; e.g., Hansen et al., 1999; Kelley et al., 2001). Given that many predators leave their signature on shells and other prey, it is just a matter of re-examining the fossil record with the specific intent to look for predation. More work needs to be done in this area, especially on drilling records from other gastropod groups, and on putative shell repair records that allow a comparison of Paleogene with Neogene localities. Additionally, in the Cenozoic, vast deep-sea (bathyal and deeper) fossil deposits of molluscs are well preserved in uplifted terraces in tectonically active regions of the world, allowing for comparisons of predation (shell repair, shell drilling) between shallow benthic and deep sea fossil assemblages (Walker and Voight, 1994; Walker et al., 2002).

Although escalation is sometimes cast as an ongoing "arms race," in actuality the predatory record shows episodes of abrupt biotic reorganization during and after mass extinctions, punctuating longer interludes of relative stability (Brett et al., 1996). Some clades may retain the historical legacy of the Paleozoic predatory revolutions, as could be argued for the stalked crinoids in modern oceans; other clades may continuously evolve new predators, as Vermeij (1987) has argued based on the gastropod fossil record. Schneider and Carter (2001) show that cardiid spine forms in Mesozoic and Cenozoic groups appear to be a Paleozoic ancestral condition, and appear not to be related to the putative Mesozoic Marine Revolution. Thus, a clade-by-clade analysis of predation would be most useful, as the different groups each have their own evolutionary histories and ecological constraints.

This review shows that not all morphology in benthic organisms need be directly related to predation. Additionally, most durophagous predators do not prey specifically on molluscs. They also prey on hard-shelled crustaceans, a major group of organisms deemed to have caused selective pressure toward escalated armor in gastropods (Vermeij, 1987). We also must strive to examine predation in assemblages spatially across different environments, mindful of taphonomic bias, if we are to derive evolutionarily and paleoecologically meaningful interpretations. The Phanerozoic record of predation is there, but it has not been fully explored; it is especially important to consider multiple working hypotheses about Phanerozoic predation as we seek to interpret this record.

Vermeij (1987) reviewed the record of molluscivorous predators, and their multifarious methods of predation in the Phanerozoic. He made a plea for more data on the responses of prey species in Mesozoic and Cenozoic assemblages (Vermeij, 1987, p. 239). Fifteen years later, his plea still stands.

ACKNOWLEDGMENTS

We dedicate this second entrée to Richard Bambach for his pioneering work concerning seafood through time. We greatly appreciate M. Kowalewski and P. Kelley for commissioning us to produce this synthesis. We thank L. Anderson, R. Feldmann, C. Hickman, A. Hoffmeister, G. Storrs, H. Greene, O. Rieppel, J. S. Pearse, R. Portell, and J. Voight for their thoughtful comments concerning numerous predation-related queries. A. Hoffmeister, W. Miller III, and two anonymous reviewers greatly improved the first draft of this paper. E. Reitz graciously allowed access to her zooarchaeology collections at the Georgia Museum of Natural History, Athens, Georgia. We also wish to thank Ruth Mawson and Peter Cockle, of Macquarie University, Australia, for facilitating the international editing of this manuscript. This is not an exhaustive treatment, and any predatory comments regarding this paper need to be addressed to the first author who will bristle with delight!

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