PREDATORS AND PREDATION IN PALEOZOIC MARINE ENVIRONMENTS

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ABSTRACT—*The Paleozoic body fossil record of potential benthic predators includes nautiloid and ammonoid cephalopods, phyllocarids, decapods, and several lineages of gnathostomes. The latter group, in particular, radiated rapidly during the Devonian. In the pelagic realm, predator-prey interactions involving cephalopods and some nektonic arthropods probably appeared in the Ordovician. Again, evidence indicates intensification of pelagic predation, much of it by arthrodires and sharks on other fishes, during the Devonian radiation of gnathostomes.*

Trace fossils provide direct evidence of predatory attack from the Ediacarian and Early Cambrian onward, but with a substantial increase in the Siluro-Devonian. Brachiopod and molluscan shells and trilobite exoskeletons show evidence of healed bite marks and peeling from the Cambrian onward, but with an increased frequency in the Devonian. Predatory drill holes with stereotypical position and prey-species preference are found in brachiopods (Cambrian onward) and mollusks (Ordovician onward); boreholes also show increased frequency in the middle Paleozoic. Certain of these boreholes are tentatively attributable to platyceratid gastropods.

Hard-shelled benthic organisms with thicker, more spinose skeletons may have had a selective advantage as durophagous predators increased. Brachiopods, gastropods, trilobites, and crinoids show an abrupt increase in spinosity beginning in the Siluro-Devonian. But spinosity decreases after the early Carboniferous. Late Paleozoic benthos may have taken refuge in smaller size and resistant, thick-walled skeletons, as well as endobenthic and cementing modes of life. Conversely, in the pelagic realm, external armor was reduced, while more efficient, fast-swimming modes of life (e.g., in sharks) increased in the post-Devonian.

INTRODUCTION

PREDATION, THE KILLING and ingestion of one animal by another carnivorous organism, has undoubtedly been an important interaction in marine environments throughout Phanerozoic history (see Connell, 1970; Paine, 1974; Vermeij, 1977, 1987; Signor and Brett, 1984; Brett, 1992, in press; Bambach, 1993, for reviews). Arguably, predation is a key driving force in evolution. However, documentation of ancient predation is difficult. Not surprisingly, despite compilations (e.g. Vermeij, 1987), many questions regarding the pattern of evolution of predator-prey interactions remain unanswered. How rapidly did predation develop, and through what stages? Was the rise of predators gradual and steady, or episodic? Is there evidence for replacement in particular predatory guilds following mass extinctions?

In this paper, the varied types of Paleozoic marine predators are reviewed in chronological order. Both pelagic and benthic ecosystems are considered. The latter are more thoroughly documented, and thus they are afforded more discussion. Basic lines of evidence for ancient predator-prey interactions include: a) evidence for predatory adaptation, and b) evidence of predation. A key line of evidence for predation is the body fossil record of organisms in which morphology (e.g., claws, jaws, teeth) or phylogenetic relationship indicates a durophagous carnivorous habit (Signor and Brett, 1984). Inference of predatory behavior, obviously based on analogy with living organisms, becomes more tenuous in ancient, extinct fossil organisms. Direct evidence of predation, as documented in the fossil record, includes those rarely preserved body fossils showing predator-prey interactions as well as other direct evidence in the

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form of trace fossils (e.g., shell repair, drilling, and coprolites; see Figs. 4, 5).

This paper also reviews evidence for response of potential prey organisms to various phases in the evolution of predators in marine ecosystems through the Phanerozoic. We consider the predicted evolutionary consequences of intensified attack on hard-shelled prey, and compare these to the actual record of changes in skeletal morphology. Finally, we discuss several ecologically significant correlations of change in marine ecosystems that may reflect predator-prey co-evolution.

CAMBRIAN RISE OF PREDATORS

Record of Marine Predators.—There is evidence of marine predation as early as the latest Proterozoic (Conway Morris and Jenkins, 1985;
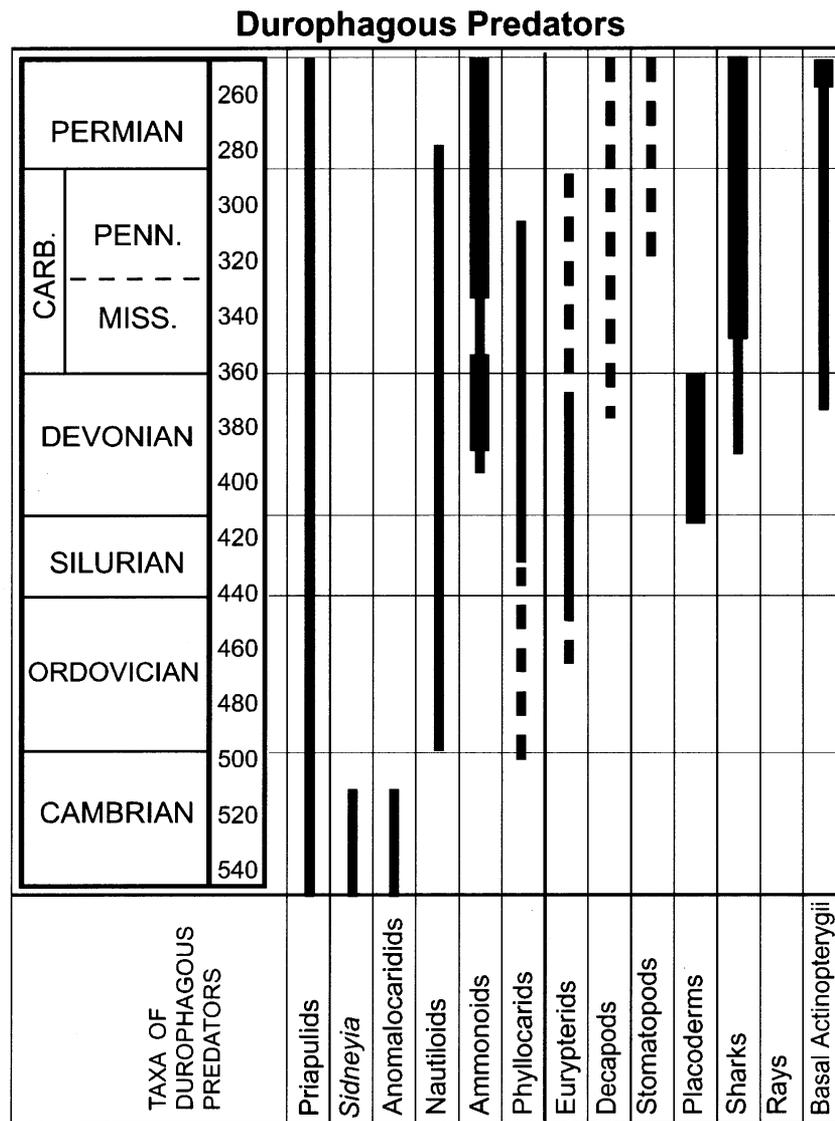

FIGURE 1—Ranges of various taxa of Paleozoic durophagous (hard shell feeding) predators. Thin lines: present, but minor; thick lines: abundant; broken lines: possibly present but rare. Carb: Carboniferous; Miss: Mississippian: Penn: Pennsylvanian.

Bengtson, 1994). Certainly, by the Early Cambrian, predators were impacting the marine shelly benthos (Fig. 1) (Babcock and Robison, 1989; Babcock, 1993; Conway Morris and Bengtson, 1994), although predation styles were less sophisticated than during the rest of the Paleozoic (Conway Morris, 2001). Nevertheless, for the Cambrian Burgess Shale communities at least, the predatory guild was fully functioning (Conway Morris, 2001).

Anomalocaridids.—Among the oldest large (up to 1 m) predators were the anomalocaridids, an enigmatic but widely distributed Cambrian taxon, with a circular slicing oral ring (Fig. 2). Bite marks on Cambrian trilobites have been attributed to these large predators (Conway Morris and Jenkins, 1985). Nedin (1999) postulated that trilobites were captured by the large anterior appendage of the anomalocaridids and then forced into the mouth, where the victim was repeatedly flexed to crack its exoskeleton. Consequently, among the earliest lines of irrefutable evidence for predation are trilobites that show healed divots or scalloped areas removed from portions of the dorsal exoskeleton (Fig. 3.1). Some of these bite marks in Cambrian trilobites have been attributed to anomalocaridids (Nedin, 1999). Many of these bite marks occur on the posterior right pleural lobes of trilobites (Babcock and Robison, 1989; Babcock, 1993). The consistent location of bite marks implies either that much predation occurred from the rear, or that anterior attacks were more commonly fatal. It further suggests left-right asymmetries (lateralization) in mode of attack by visual predators, or in behavioral response of the attacked trilobites, or both (Babcock, 1993).

Trilobites.—Trilobites themselves (Fig. 3.1) have been cited as primitive predators on soft-bodied organisms. Trace fossil assemblages from the Cambrian show numerous instances of trilobite-produced *Rusophycus* and *Cruziana* intercepting *Planolites* or *Teichichnus* traces attributable to infaunal worms. These interception traces have been interpreted as evidence for foraging and hunting behavior in trilobites (Bergström, 1973; Fortey and Owens, 1999).

Other Predators.—Trilobite sclerites, ostracodes, and hyolithids have also been found in gut traces of other large Cambrian arthropods, including *Sidneyia* (Briggs, et al., 1994) and *Utahcaris* (Conway Morris and Robison, 1988); the enigmatic arthropods *Yohoia* and *Branchiocaris* also may have been durophagous predators
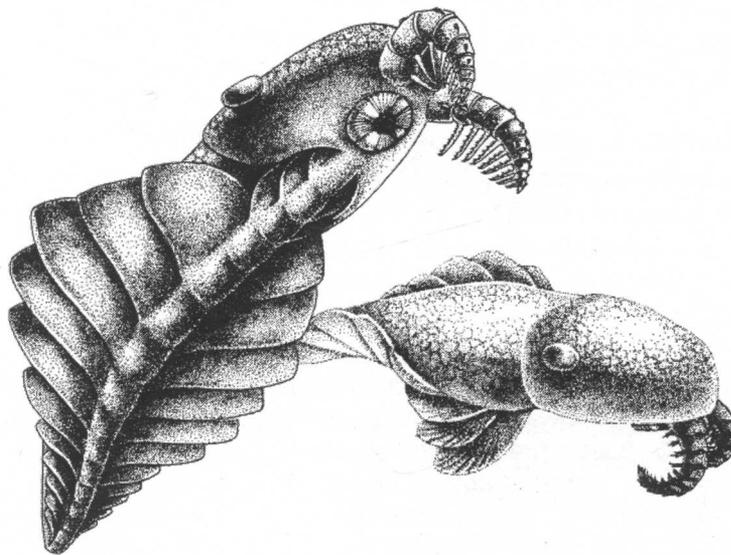

FIGURE 2—*Anomalocaris;* reconstruction based on material from Middle Cambrian, Burgess Shale, ×0.5. Drawing by Marianne Collins, from Gould (1989); reprinted by permission.
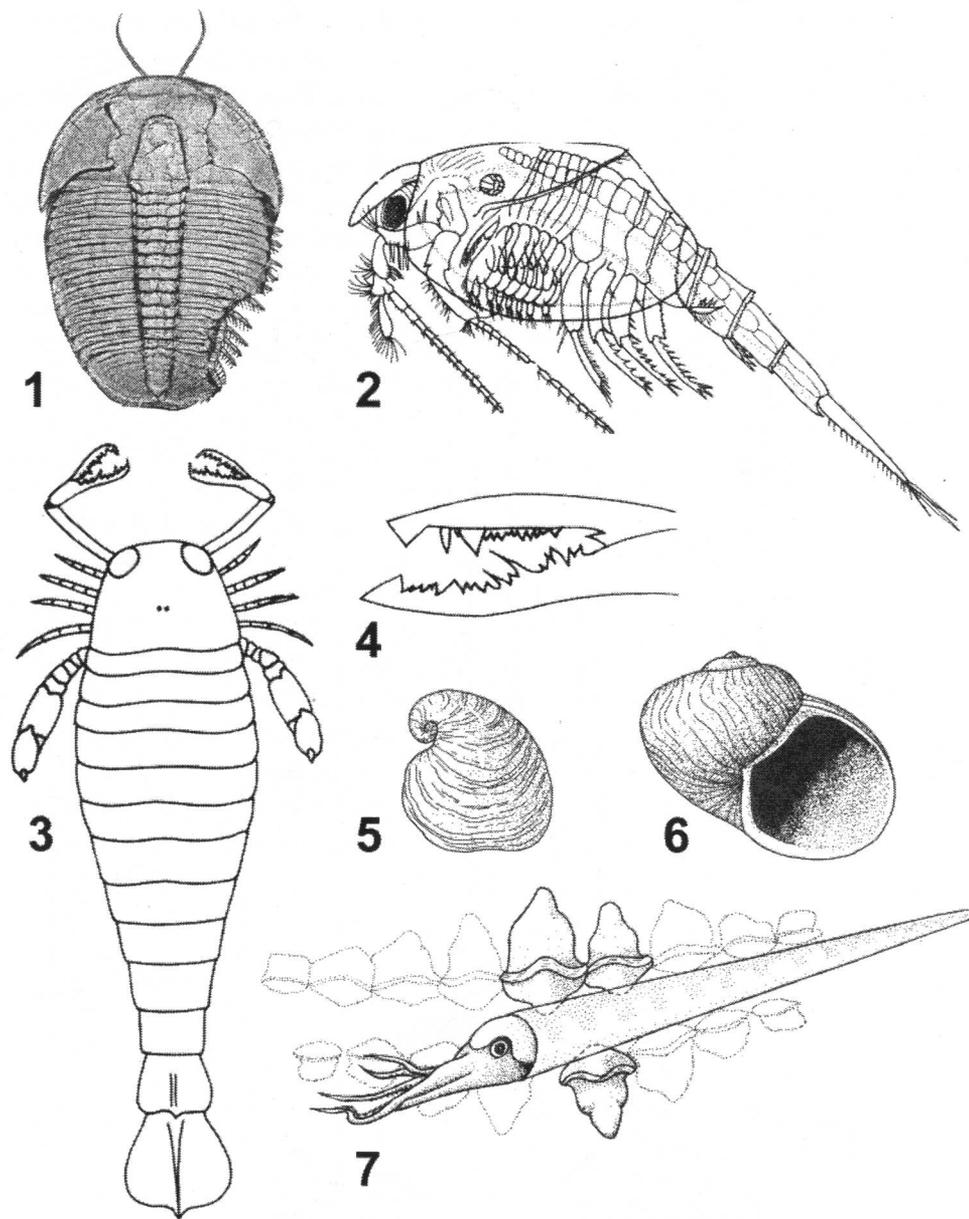
FIGURE 3—Examples of Paleozoic marine predators. 1—Reconstruction of trilobite *Elrathia kingi* with appendages, showing a divot in the lower right pleuron probably from an anomalocaridid; ×1. 2—The Recent phyllocarid *Nebalia*. 3—Large predaceous eurypterid *Pterygotus;* ×0.25. 4—Enlargement of chelicera of *Pterygotus* showing serrated cutting edges; ×0.5. 5, 6—Platyceratid gastropods: 5—*Platyceras;* Devonian; 6—*Naticonema;* Silurian-Devonian; ×1. 7—Nautiloid cephalopod, reconstructed with outlines of dental arcade of the shark *Petalodus*, based on specimen with rows of punctures from Pennsylvanian of Kentucky. 1, based on specimen illustrated by Babcock (1993); 2, from Clarkson (1996); 5, 6, from Tasch (1980); 7, from Mapes and Hansen (1984).

(Vermeij, 1987). In addition, specimens of priapulid worms from the Burgess Shale have been found with hyolithids in their gut trace (Conway Morris, 1977; Briggs et al., 1994, their fig. 73). The earliest report of cannibalism is also known from the Burgess Shale. One specimen of *Ottoia*, a priapulid, had a proboscis of another *Ottoia* preserved in its gut (Briggs et al., 1994). Modern priapulids are also known to be cannibals. Thus, priapulid feeding behavior has remained remarkably similar for 530 million years (Fig. 1).

Nautiloid cephalopods appear late in the Cambrian, but they only attain abundance and large size during the ensuing Ordovician Period. All known living cephalopods are carnivorous, but early forms were small, poor swimmers that may have been bottom-feeding scavengers (Bandel, 1985; Lehmann, 1988), and only later did nautiloids develop as major predators.

Trace Fossils.—Circular borings made by putative predators that are 0.1 mm to 4 mm in diameter occur on shells from the Early Cambrian onward (Bengtson and Zhao, 1992; Conway-Morris and Bengtson, 1984; Miller and Sundberg, 1984). Minute pits are reported in the enigmatic phosphatic shell of the Early Cambrian *Moburgella* (Bengtson and Zhao, 1992; Conway Morris and Bengtson, 1994). These borings were evidently produced by an organism capable of drilling phosphatic shells. This borer may have persisted into the middle Paleozoic. Chatterton and Whitehead (1987) reported similar cylindrical drill holes on about 10% of the valves of a lingulate brachiopod from the Silurian of Oklahoma.

Putative predator borings are also known to occur in the exoskeletons of agnostoid trilobites (Babcock, 1993). Some of these tiny pits have pearl-like plugs, evidently secreted by the trilobites in response to the predatory action of the predator (or parasite). These ancient pits resemble borings made by modern nematodes (Sliter, 1971) and provide circumstantial evidence for the existence of boring nematodes as far back as the Early Cambrian.

Häntschel et al.'s (1968) compendium on coprolites cites only 25 reports of pre-Devonian coprolites; most of these are small and phosphatic.

Subsequently, there have been several reports of Cambrian coprolites containing trilobite sclerites, echinoderm ossicles, and fragments of inarticulate brachiopods (Sprinkle, 1973; Conway Morris and Robison, 1986, 1989; Babcock, 1993; Nedin, 1999).

Pelagic Predators?—Seemingly, there was little to no development of a pelagic predator-prey system during the Cambrian, as there are relatively few definite pelagic forms. Cephalopods remained small benthic forms, and open swimming vertebrates, other than possible conodont animals, had yet to appear. It is possible that large nektonic arthropods, such as *Sidneyia*, may have preyed upon each other or on conodont animals.

CAMBRIAN RESPONSE: EARLY PALEOZOIC MARINE PREDATOR REVOLUTION

In many ways, the Cambrian revolution of predators was the first major episode of escalation in marine ecosystems, although the effect of newly evolved groups of biting and drilling predators is so pervasive that it might be overlooked. With the exception of tiny boreholes in some of the earliest small calcareous shelly organisms, *Cloudina* (Bengtson and Zhao, 1992), there is, as yet, no evidence of predators in the latest Proterozoic (Vendian). This observation led to the scenario of a nearly predator-free, early "Garden of Ediacara" phase in Earth's history (McMenamin, 1986; McMenamin and McMenamin, 1990).

The first wave of predation may have instigated the acquisition of hard skeletons by numerous taxa during the Cambrian explosion (Bengtson, 1994; Conway Morris, 2001). The apparently "explosive" development of phosphatic and calcitic sclerites, valves, and armor in the Early Cambrian may well have been driven by biting organisms. The early and evolutionarily critical rise in Cambrian predators is reviewed by Babcock (in press), who proposes to call this the "early Paleozoic marine revolution."

The appearance of skeletons was geologically rapid, probably encompassing no more than ten million years, and was one of the most dramatic episodes of convergent evolution in the history of

metazoans. Some nine phyla of animals, as well as algae (receptaculitids), almost simultaneously acquired skeletal coverings of varied physiological origins and compositions, including protein, chitin, silica, apatite, calcite, and aragonite.

Babcock (1993) notes that the frequency of healed bite marks in trilobites actually *declines* in the Late Cambrian and Early Ordovician; moreover, the proportion of right posterior bite marks declines. This trend apparently coincides with the disappearance of anomalocaridids. However, a host of new organisms appearing in the middle Paleozoic ushered in a new wave of predation: the "Middle Paleozoic Revolution".

MIDDLE TO LATE PALEOZOIC MARINE PREDATORS

The Ordovician brought on a further phase of predator escalation, but one that remained somewhat subdued until the middle Paleozoic. While large predators were present from Cambrian times onward, a number of new marine predators appeared by the Middle Ordovician, including asteroids, varied arthropods, larger cephalopods, and probably drilling gastropods. Subsequently, durophagous predators showed an abrupt increase in the Devonian (Fig. 1). These included crustaceans and, most notably, several fish groups.

Arthropods and their Traces.—Arthropods no doubt continued to occupy predator guilds in the middle to late Paleozoic. Further examples of trilobite "hunting burrows" have been described (e.g. Brandt et al., 1995), and the morphology of endites in larger trilobites, such as *Isotelus* and phacopids, suggests that these appendages served to grasp and perhaps masticate weakly skeletonized organisms.

Durophagous arthropods of the early to middle Paleozoic include eurypterids and phyllocarid crustaceans (Figs. 3.2–3.4). Eurypterids appear in the Ordovician in marine environments and, during the Silurian, included some of the largest arthropods that have ever lived. Pterygotids with estimated lengths in excess of four meters were also equipped with formidable chelate chelicerae (Selden, 1984, 1992) (Fig. 3.4). There seems little doubt that these

claws were used in seizing and slicing prey. However, it is unlikely that these organisms dwelled in open marine environments. Indeed, these eurypterids are most commonly associated with brackish estuarine facies, suggesting that they inhabited marginal marine environments (Selden, 1984). Fossil associations suggest that other eurypterids, and perhaps non-marine vertebrates, may have formed a part of their diet.

Phyllocarid crustaceans (Fig. 3.2) appeared in the Cambrian, but diversified in the Devonian (Signor and Brett, 1984). Stout, molariform, and calcified gastric teeth may have been utilized in prey mastication. Unlike eurypterids, the phyllocarids were relatively common in open marine environments, and may have preyed upon shellfish.

Decapod crustaceans with claws for crushing prey appeared in the Devonian and diversified in the later Paleozoic, but they were mainly small and uncommon. The ancestors of stomatopods probably diverged from the rest of the malacostracans in the Devonian (Schram, 1982, 1984; Hof, 1998); paleostomatopods occupied nearshore habitats and are known from North America and Europe (Schram, 1977; Jenner et al., 1998). Primitive stomatopods that do not smash their prey, such as hemisquillids, can eat solitary corals, crabs, bivalves, and fish (Basch and Engle, 1989).

Scalloped fractures of the outer lips of Paleozoic gastropod shells (Fig. 4.1) resemble marks made by modern predatory crustaceans that "peel" gastropod shells to reach the body of the snail (Vermeij et al., 1981; Schindel et al., 1982; Ebbestad and Peel, 1997; Ebbestad, 1998). However, these peeled shells are not attributed to durophagous crabs (which do not appear until mid Mesozoic times; see Walker and Brett, this volume) and, at present, the predator remains unknown. This type of probable arthropod peeling trace is known in shells from the Middle Ordovician (Peel, 1984) onward, but is rare—generally < 7% of shells—in the early to middle Paleozoic (Schindel et al., 1982; Peel, 1984).

The middle Paleozoic appears to have been a time of intensification of this type of interaction. Devonian and Carboniferous gastropod and ammonoid shells show increased frequencies of

shell repair, though slightly lower frequencies than those recorded for snails of comparable size in the later Mesozoic (Vermeij et al., 1981; Schindel et al. 1982; Brett and Cottrell, 1982; Bond and Saunders, 1989).

Cephalopods.—Large nautiloids, endoceratoids, and actinoceratoids, some exceeding five meters in length, were abundant in marine benthic assemblages from the Early Ordovician onward (Fig. 3.7). All known cephalopods are carnivorous (Nixon, 1988). By analogy with modern *Nautilus*, these nautiloids probably possessed chitinous beaks capable of shearing skeletons (Alexander, 1986a; Saunders and Ward, 1987). The oldest known cephalopod jaws are Carboniferous in age and are similar to Recent coleoid jaws (Lehmann, 1988). Radulae of cephalopods date back to the Silurian (Mehl, 1984), and are also similar to Recent coleoid radulae, suggesting stasis in feeding morphology from the middle Paleozoic to the Recent for these groups.

Alexander (1986a) attributed divots and crescentic healed breakages in Ordovican brachiopod shells, especially strophomenides, to nautiloids; and Rudkin (1985) described a specimen of the Late Ordovician trilobite *Pseudogygites* with crescentic bite marks, which he attributed to an endoceratoid. Brunton (1966) and Elliot and Brew (1988) also noted predatory fractures preserved on Carboniferous brachiopods that they attributed to nautiloid predation.

Possible crop residues from large nautiloids in the Ordovician contain abundant trilobite fragments (Brett, unpublished data). Kloc (1987) described a pyritized coprolite from the Late Devonian that he attributed to a nautiloid, and Zangerl et al. (1969) reported possible nautiloid coprolites.

In addition to nautiloids and ammonoids, coleoids first appeared in the Early Devonian (Lehmann, 1976), and recently a Carboniferous "octopod" has been reported from the Mazon Creek fossil Lagerstätte (Kluessendorf and Doyle, 2000). Because of their soft-bodied construction these cephalopods have a very poor fossil record and their impact as predators is not known.

Gastropods and Drilling Predation.—Modern gastropods of several families are voracious predators that use a combination of chemical and mechanical radular drilling to penetrate the shells of their prey (Carriker and Yochelson, 1968; Carriker, 1969, 1981; Kabat, 1990), forming distinctive bore holes termed *Oichnus* by Bromley (1981). For many years it was assumed that this type of drilling was confined to meso- and cenogastropods, and *Oichnus* in Paleozoic shells was ascribed to another type of unknown predator (Carriker and Yochelson, 1968; Smith et al., 1985). However, recent discoveries suggest that platyceratid archaeogastropods were also predatory drillers. Baumiller (1990) and Baumiller et al. (1999) documented gastropod-like drill holes beneath the shells of attached platyceratid gastropods on a crinoid and on a brachiopod shell. These intriguing cases, although possibly recording parasitism, prove the capacity for radular drilling among platyceratids.

The family Platyceratidae spans the period from the Middle Ordovician to the Late Permian (Bowsher, 1955); highly modified genera, such as *Platyceras* itself (Fig. 3.5), were clearly commensal/ parasitic on pelmatozoan echinoderms. However, others, notably *Cyclonema* (Ordovician-Silurian) and *Naticonema* (Ordovician-Devonian) (Fig. 3.6), retained unspecialized shells and may have been facultatively free-living scavengers and predators.

Predatory drill holes provide direct evidence for carnivory. It is important to use specific criteria to recognize drill holes in the fossil record, since substrate borers or pressure dissolution can make holes similar to drillings (Richards and Shabica, 1969; Lescinsky and Benninger, 1994) (Figs. 4, 5). Kowalewski et al. (1998) used specific criteria to recognize predatory borings. First, completed drill holes are generally single and unhealed; second, drill hole position is consistently located over a food-rich area of the prey; third, there should be no attachment scars—such scars would indicate that the drill holes were made by parasitic, rather than carnivorous, organisms. Kowalewski et al. (1998) also suggested that the ratio of inner to outer diameter of successful beveled borings should exceed 0.5, as in most modern predatory drill holes. However, this criterion does not apply to cylindrical

borings of the type made by muricid gastropods.

Drill holes of at least two distinctive types occur in middle to late Paleozoic shells (Ausich and Gurrola, 1979). These were termed Type A and Type B boreholes and they are morphologically similar to the later muricid and naticid gastropod drill holes, respectively (see Figs. 4.3, 4.4). Type A drill holes (Figs. 5.1, 5.2) are smaller, cylindrical, and may penetrate shells from below; they may
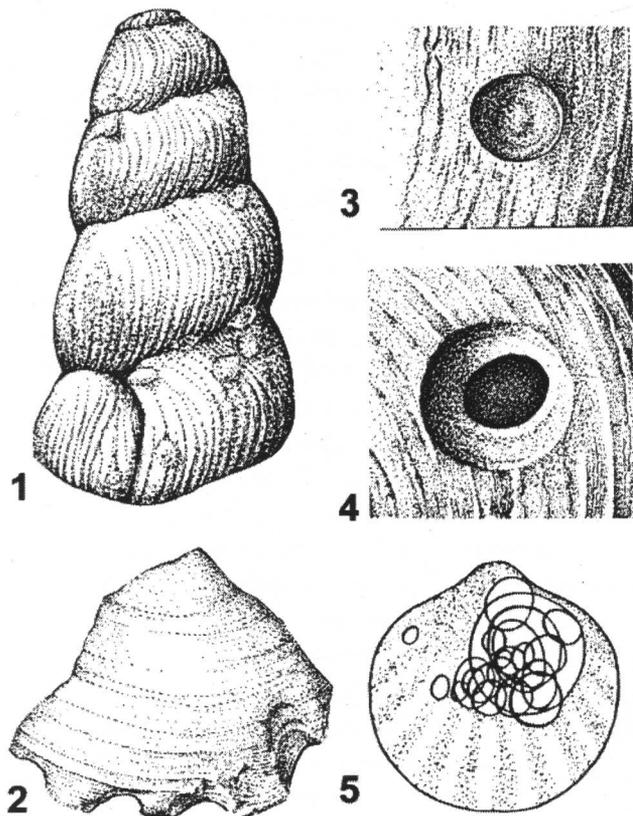

FIGURE 4—Traces of predation, in fossil and Recent shells. 1—Shell of Devonian gastropod *Palaeozygopleura* with sublethal healed fracture of the outer lip. 2—Permian bivalve shell with healed crescentic fractures along valve margin; probably the result of attempted predation by a fish. 3—Incomplete bore hole of *Polinices duplicata;* note raised boss at center. 4—Complete drill hole of *Natica severa;* note beveled outer margin. Redrawn from photographs in the following sources: 1, Brett and Cottrell (1982), 2, Boyd and Newell (1972); 3, 4, Carriker and Yochelson (1968). Figure modified from Brett (1992).

record attacks by parasitic organisms (Ausich and Gurrola, 1979). However, Type A drill holes occur as a single drill hole per shell and display a non-random stereotyped pattern characteristic of carnivores (Fig. 5.6) (Smith et al., 1985; Leighton, 2001a, b). Cylindrical holes are known from Late Ordovician (Cincinnatian) brachiopods (Bucher, 1938; Cameron, 1967). Some of these have proven to be domichnial borings (*Trypanites*) made in dead shells (Carriker and Yochelson, 1969; Richards and Shabica, 1969). But Kaplan and Baumiller (2000) argued recently that at least some of these holes show non-random positioning, and hence were probably produced by predatory organisms.

Rohr (1976) observed prey and site selectivity of small boreholes in Silurian orthid brachiopods. Liljedal (1985) also noted Type A borings in silicified Silurian bivalves. Similarly, Type A borings occur in about 11% of the Early Devonian brachiopod *Discomyorthis* and show evidence of size and site selectivity on the prey shells (Sheehan and Lespérance, 1978). Buehler (1969) reported a low frequency (2.25%) of cylindrical borings in Middle Devonian shells, as did Rodriguez and Gutschick (1970). However, the jury is still out on the issue of whether these were predatory or merely parasitic in nature (Leighton, 2001a, b).

Type B boreholes are parabolic, 1–3 mm in diameter, and display a chamfer or bevel; incomplete boreholes possess a central raised knob or boss (see Figs. 4.3–5.5). These most closely resemble drillings of modern naticid gastropods. These boreholes first become common in Devonian brachiopods (Fenton and Fenton, 1931, 1932; Smith et al., 1985; Kowalewski et al., 1998); earlier possible examples are known from Ordovician brachiopods (S. Felton, pers. comm.) but have not been documented in the literature. Brunton (1966) reports frequencies of up to 30% of brachiopods drilled with this type of hole in assemblages of late Carboniferous age. Relatively few typical Type B borings are reported from the Upper Carboniferous to Permian (see Kowalewski et al., 2000). However, a series of papers document small (< 2 mm) boreholes with chamfering, which should perhaps be assigned to a third category; these occur
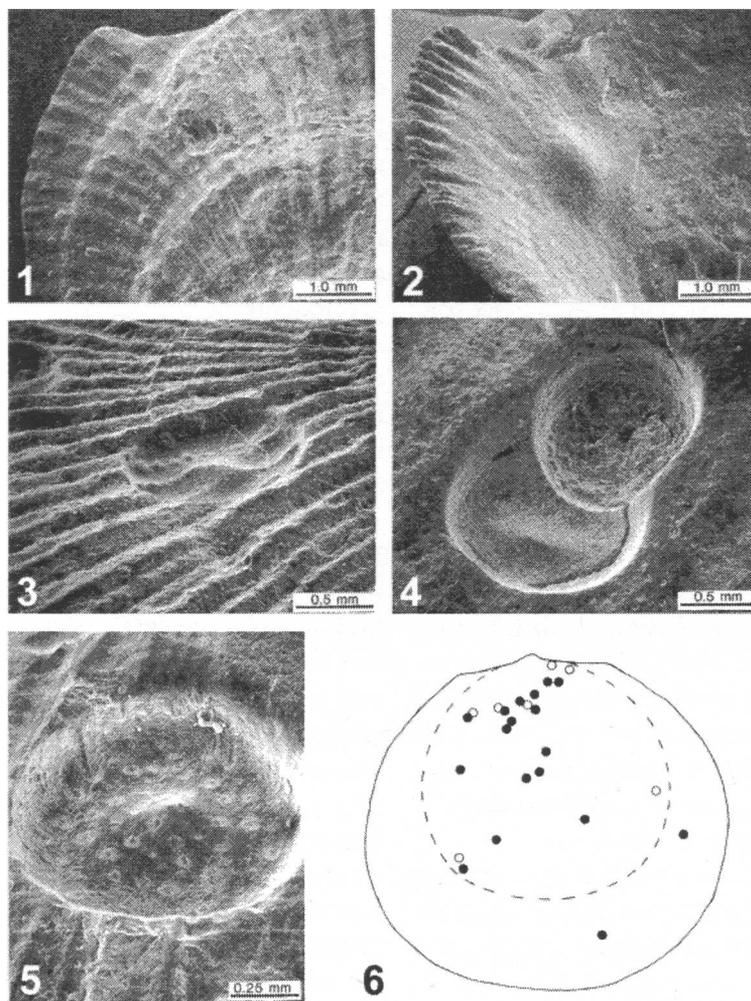
FIGURE 5—Gastropod-like boreholes in brachiopods from the Middle Devonian Hamilton Group of New York State. Note scale bars. 1, 2—Type A borehole on the brachiopod *Rhipidomella;* 1 shows exterior view, 2, with negative reversed for comparison, shows blister of healed shell on interior of the shell. 3—Incomplete hole in *Rhipidomella* showing central boss. 4—Two overlapping sediment-filled boreholes on *Parazyga;* upper hole is complete; note chamfer (bevel) well displayed on lower hole. 5—Incomplete borehole in *Douvillina* showing central raised boss; note truncated pseudopunctae of shell. 6—positions of drill holes on the brachiopod *Rhipidomella* showing stereotypy of positioning over main visceral mass of brachiopod. Modified from Smith et al. (1985).

primarily in diminutive brachiopods belonging to the family Cardiarinidae (Cooper, 1956; Bassett and Bryant, 1993; Grant 1988; Morris, 1994). Hoffmeister et al. (2001a) report drilling frequencies of up to 33% in *Cardiarina.* The boreholes show stereotypy with respect to valves and preferred site on shells.

Until recently, it was quite unclear what organisms were responsible for Type B boreholes, but the discovery of platyceratid gastropods in direct association with this type of drill hole on Lower Carboniferous crinoids suggests that these snails were among the culprits (Baumiller, 1990, 1996; Baumiller et al., 1999). Several studies have shown that Type B hole-drillers display a distinct preference for particular prey taxa, notably athyrid and certain strophomenid brachiopods. They also show

stereotypical positioning on valves (see Fig. 4.5), as is typical for predatory gastropods (Ausich and Gurrola, 1979; Smith et al., 1985; Leighton, 2001a).

As with durophagous predation, there is evidence for intensification of shell drilling in the Devonian (Kowalewski et al., 1998), although the fossil record of platyceratids shows relatively little increase during this time. Initially, it was thought that the frequency of drilling declined in the late Paleozoic (Kowalewski et al. 1998), and this seems to be supported in some cases (Kowalewski et al., 2000; Hoffmeister et al., 2002). However, for individual species data, drilling frequencies can be similar to those reported for the Late Cretaceous to Cenozoic—which can exceed 30% per species examined (Ausich and Gurrola 1979; Hoffmeister et al. 2001a, b).

Asteroids.—Asteroids evidently developed their notoriously predaceous habits early in their history (Blake and Guensburg, 1992). Middle Ordovician starfish have been found with gastropod shells in their gut cavities (Spencer and Wright, 1966). Still older possible examples of starfish predation are known from as early as the Whiterockian (Middle Ordovician; G. C. Baird, pers. comm.).

There is controversy as to whether or not starfish developed extraoral digestion in the Paleozoic (see Donovan and Gale, 1990). However, Blake and Guensburg (1994) describe an Ordovician *Promopalaeaster* in apparent feeding position on a bivalve, a characteristic behavior related to extraoral digestion. Similarly, Clarke (1921) illustrated probable examples of starfish predation from the Devonian of New York, where specimens of *Devonaster* apparently were overwhelmed by sediment while in feeding position on bivalves.

Gnathostomes.—The earliest well-known predatory gnathostome fishes are Silurian acanthodians, although possible acanthodian spines and chondrichthyan (shark) denticles are known from the Middle Ordovician (Benton, 1997). These fishes and their later Paleozoic descendants possessed sharp teeth with cutting plates adapted for predation on soft to chitinous invertebrates and other fishes.

The earliest major radiation of durophagous (shell-crushing) fishes undoubtedly occurred in the Early to Middle Devonian. Varied placoderms, including rhenanids with blunt crushing plates and ray-like benthic adaptation, and ptyctodonts with hypermineralized tritors, also evolved during the Devonian. The ptyctodonts and rhenanids may have been important crushers of hard-shelled prey (Figs. 5.1, 5.2), although their remains are uncommon in most marine invertebrate-rich assemblages. Nonetheless, there are reports of ptyctodonts in normal marine shell beds (Moy-Thomas and Miles, 1971). Ptyctodonts, in fact, are most commonly associated with fragmentary remains of arthrodires. Their blunt, crushing teeth may have been adapted for cracking the armor of arthrodires during scavenging.

Placoderms became extinct by the end of the Devonian (Moy-Thomas and Miles, 1971), but were replaced by varied sharks (Fig. 6). Especially during the Carboniferous and Permian, many types of sharks evolved, including the symmoriaformes, hybodontids, and ctenacanthoids, some of which developed broadened teeth and were durophagous (Moy-Thomas and Miles, 1971; Mapes and Benstock, 1988) (Fig. 6). For example, Boyd and Newell (1972) report a high percentage of Permian bivalves with divots in the shells probably produced by sharks (see Fig. 4.2). Chimaeras or holocephalans (e.g., helodontoids, cochliodontoids, and petalodontids) possessed autostylic (fused) skulls and hypermineralized, crushing dentition analogous to that of earlier ptyctodonts (Fig. 6.4). Certain Carboniferous chimaeras, such as *Helodus*, have been implicated as producers of distinct crush marks in Carboniferous and Permian brachiopod and bivalve shells (Brunton, 1966; Boyd and Newell, 1969; Alexander, 1981). Hansen and Mapes (1990) also reported crush marks in Upper Carboniferous nautiloids that they attributed to the shark *Petalodus* (Fig. 3.7). Chimaeroids underwent a five-fold increase in taxonomic richness in the Carboniferous relative to the Devonian (Mapes and Benstock, 1988). However, durophagous holocephalans also underwent a major decline in the Upper Carboniferous and Permian (Mapes and Benstock, 1988).

In addition, during the Carboniferous, deep-bodied chondrostean fishes of the Doryopteridae developed well-defined tooth plates for crushing
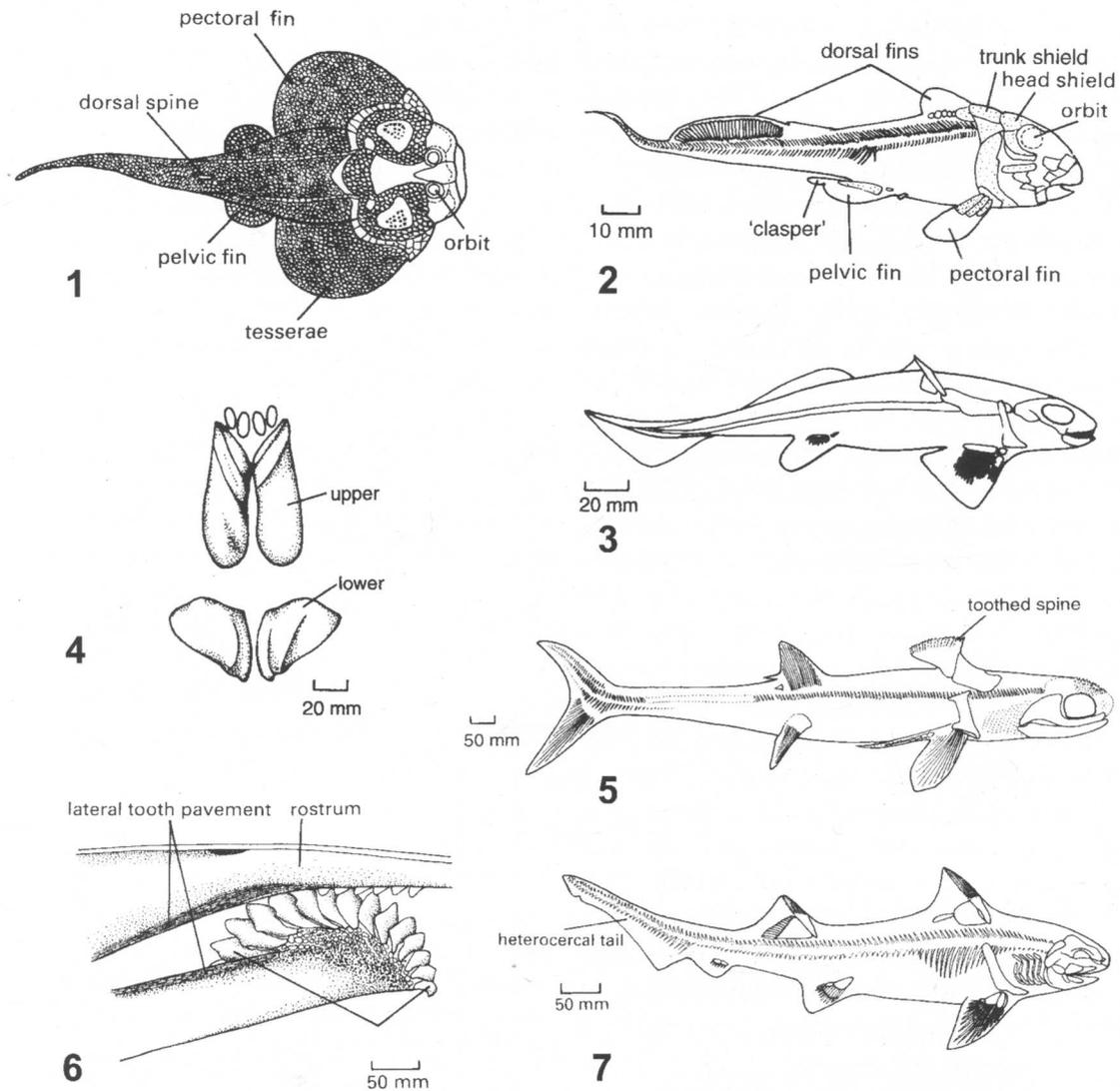
FIGURE 6—Middle Paleozoic predatory fishes. 1—Rhenanid, ray-like placoderm *Gemuendina,* Early Devonian. 2—Ptyctodont placoderm *Ctenurella*, Devonian. 3—Upper and lower dentition of holocephalan *Deltoptychius*, showing hypermineralized tritor grinding gnathal plate. 4—Holocephalan *Helodus*, Pennsylvanian. 5—*Stethacanthus;* note toothed brush structure, Mississippian. 6—Eugeneodontiforme shark *Sarcoprion;* tooth whorl in lower jaw opposes pavement in rostrum, Pennsylvanian. 7—*Hybodus*, hybodont shark. 1, from Moy Thomas and Miles, 1971; 2, 3, from Stensiö, 1969; 4, from Patterson, 1965; 5, 6, from Moy-Thomas and Miles, 1971; 7, from Zangerl, 1981.

hard-shelled prey. These reef-dwelling fishes show many similarities to specialized reefal teleost fishes of the Cenozoic (Moy-Thomas and Miles, 1971; Benton, 1997).

There is limited information concerning the coprolites or gut contents of the shark group. However, the few trace fossils available reveal that benthic organisms formed a food source for some of these predatory sharks. For example, coprolites and gut contents of Carboniferous-Permian holocephalans, sharks, and other fish contain fragmented brachiopods and crinoid ossicles (Zangerl and Richardson, 1963; Malzahn, 1968; Moy-Thomas and Miles, 1971).

Pelagic Predators.—Although pelagic predation by swimming arthropods or cephalopods may have occurred as early as the Cambrian, the first direct evidence for predator-prey relationships among nektonic organisms is from the Devonian (Fig. 7). The rise of goniatite ammonoids in the Devonian may have impacted the pelagic ecosystem. These presumably predatory cephalopods are commomly found in settings in which there is little or no benthic fauna (e.g., black shales recording anoxic sea floors). Hence, these organisms may have fed on pelagic organisms, such as swimming crustaceans, other cephalopods, conodont animals, and perhaps small fish (Lehmann, 1976, 1988).

Many of the arthrodires, with sharp shearing gnathal plates, were undoubtedly piscivorous. Hlavin

(1973, 1990) reports on an articulated specimen of the arthrodire *Holdenius*, from the Upper Devonian Cleveland Shale, preserved adjacent to the remains of its prey: a ctenacanth shark, which had been bitten in half (Fig. 8). This is direct evidence for predation—although *failed* predation in this case: an anterior dorsal spine from the ctenacanth was found lodged in the palate and extending into the braincase of the *Holdenius*. The arthrodire was probably killed instantly when it was impaled on the spine of its prey (a lose-lose situation!).

Other groups, such as cladodont sharks, with sharp, cusped teeth, clearly had an impact on fish and on certain probably pelagic invertebrate prey. Williams (1990) provides an excellent summary of evidence for cladodont predation from fecal
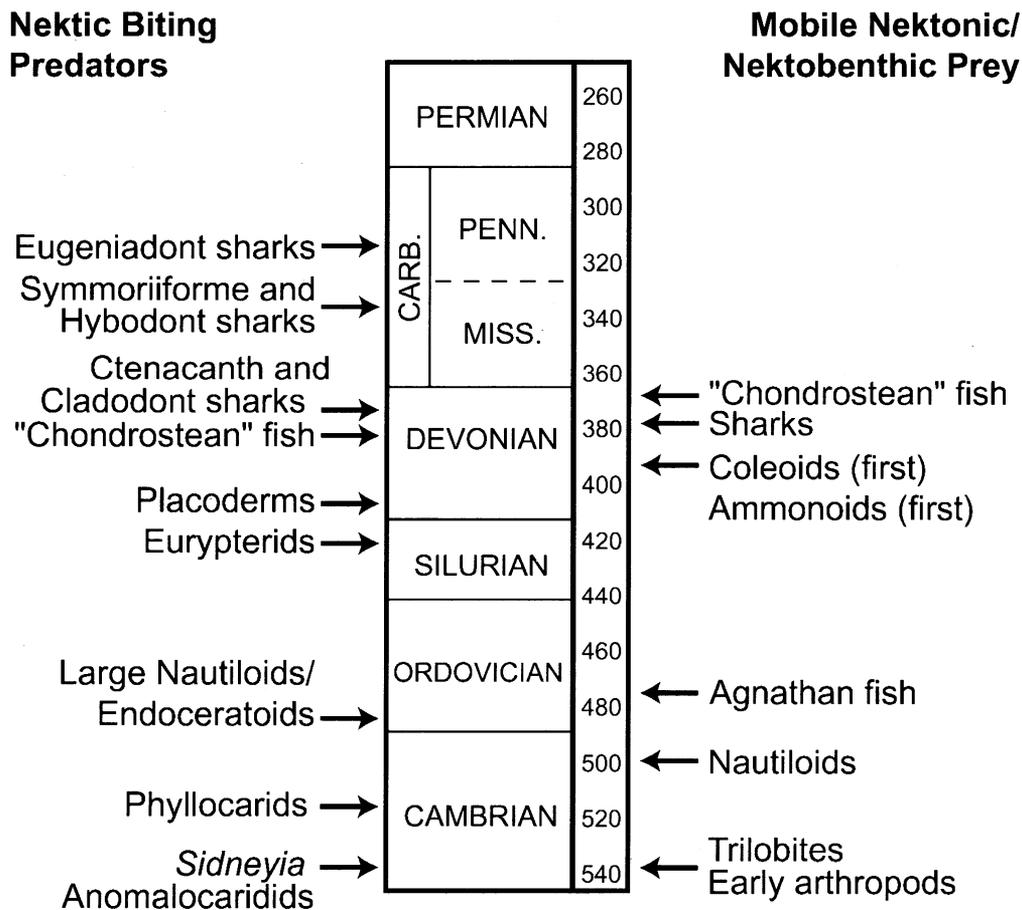

FIGURE 7—Time-line of appearance of major groups of Paleozoic pelagic predators and prey.
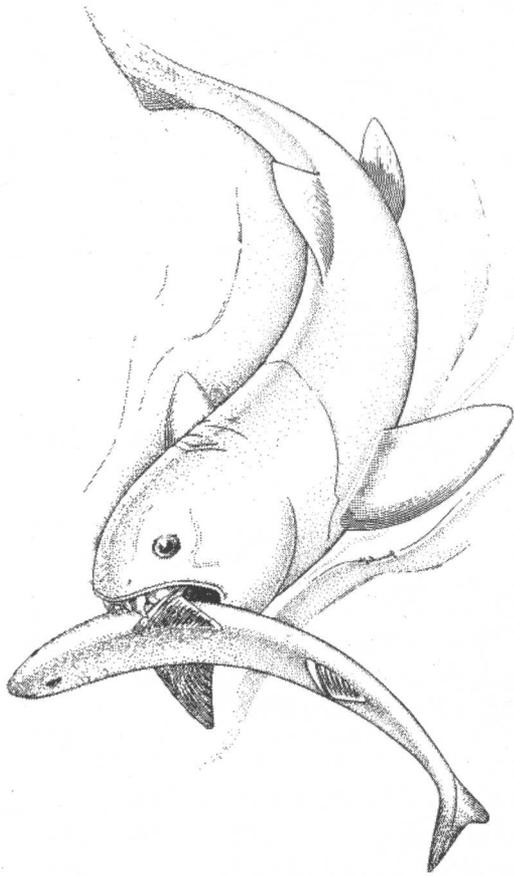
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FIGURE 8—Reconstruction of the arthrodire *Holdenius* attacking a ctenacanth shark; based on specimen from Upper Devonian Cleveland Shale, northern Ohio. Drawing by J. P. Lufkin; from Hlavin (1990).

masses and gut residues in the body cavities of more than 50 well-preserved cladoselachid sharks from the Upper Devonian Cleveland Shale in Ohio. The most commonly preserved ingesta are scales and bones of palaeoniscoid fishes (present in 64% of shark specimens)—with a few showing both head-first and tail-first swallowing orientations—followed by remains of the crustacean *Concavicaris* (found in 28%). One unidentified cladoselachid had two ctenacanth shark spines embedded in its jaw and at least two *Cladoselache* have smaller specimens of *Cladoselache* in the gut cavity, indicating cannibalistic behavior in this pelagic predator. About 5% of the *Cladoselache*

contained conodonts, and all of the conodont-bearing sharks (including one in the body cavity of a larger shark!) are small individuals, which further suggests size partitioning of food resources. Ctenacanth sharks have been found with small arthrodires in the gut cavity. In turn, the larger palaeoniscoid osteichthyan fishes of the Cleveland Shale also show evidence of pelagic predatory behavior. Ironically, these osteichthyans have small sharks and arthrodires in their gut cavities.

Trace fossil evidence of attacks by the shark *Symmorium* is also known from shells of Upper Carboniferous coiled nautiloids (Mapes and Hansen, 1984; Hansen and Mapes, 1990). Shells of the nautiloid *Domatoceras* show punctures that match the spacing of tooth files in the associated shark (Fig. 9). Zangerl and Richardson (1963) and Zangerl et al. (1969) also report abundant evidence from coprolites, regurgitates, and gut contents for shark predation on other fishes preserved in the Upper Carboniferous Mecca Quarry Shale in Illinois.

The Cleveland Shale and Upper Carboniferous shark-bearing shales generally lack benthic body or trace fossil assemblages, and were evidently deposited in anoxic bottom waters. Hence, these complex food webs involved an entirely pelagic community. Many of these early shark, osteichthyan, and arthrodiran predators may have had little impact on marine benthic communities.

DEVONIAN-PERMIAN: MIDDLE PALEOZOIC MARINE REVOLUTION

Signor and Brett (1984) explored several Paleozoic adaptive trends that served to strengthen invertebrate skeletons or make them more difficult to attack. They inferred that these trends were, at least in part, a response to increased predation intensity during the middle Paleozoic "precursor" to the Mesozoic marine revolution. This term is perhaps inappropriate as it implies a preliminary build-up to the later revolution. In fact, we argue that the two actually involved separate radiations of predators and were separated by a major reorganization of predator-prey interactions and
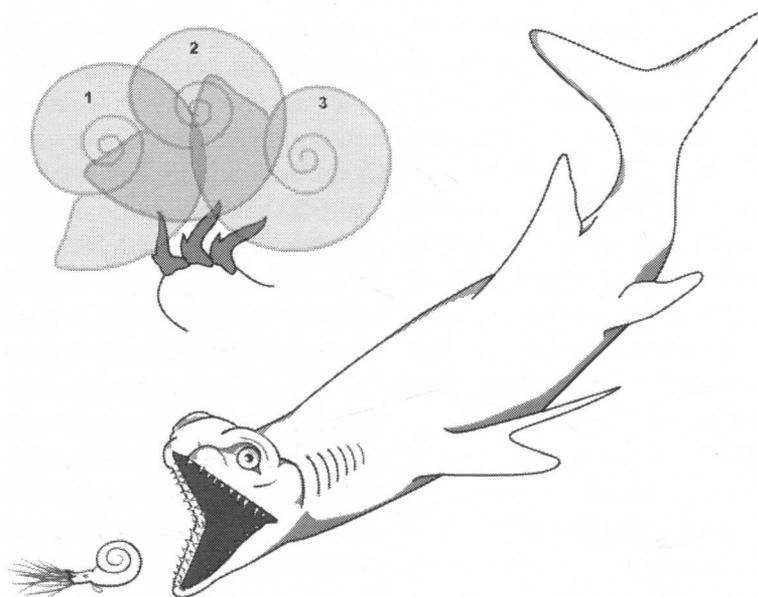
FIGURE 9—Shark predation on Pennsylvanian nautiloids. Bottom—reconstruction of shark *Symmorium* shown attacking a small coiled nautiloid. Top—sequence of events involved in producing punctures in a nautiloid shell rotated over tooth row; adapted from Mapes and Hansen (1990).

other aspects of ecology as a consequence of the Permo-Triassic extinction. Hence, we herein refer to the purported middle Paleozoic escalation phase simply as the "Middle Paleozoic Revolution."

Possible responses (aptations sensu Gould and Vrba, 1982; Vermeij, 1987; Gould, 2002) to predation pressure may follow two patterns: a) changes in behavior and mode of life, and b) changes in morphology. Both types of aptations can be inferred for middle to late Paleozoic organisms. These responses may represent direct adaptations to increased predation pressure, such as the preferential survival of spiny organisms, as well as exaptions that spring from pre-existing skeletal features that can be co-opted for a different function (Gould and Vrba, 1982; Gould, 2002). In a majority of cases it is not possible to distinguish between these modes of origin.

Micro-architecture.—One such exaptation that may impede predation is shell micro-architecture. For example, micro-architecture such as pseudopunctae in brachiopod shells may help to prevent propagation of shell fractures (Alexander, 1986a, 2001). Perhaps the advantage of this micro-architecture provides

one of the reasons that pseudopunctate brachiopods, especially productids and chonetids, become dominant in the late Paleozoic.

Shell Architecture.—In some groups of gastropods, the presence of an open umbilicus weakens the shells and makes them more easily crushed (Vermeij, 1983, 1987). Therefore, one might predict a decline in umbilicate forms in the face of increasing predation pressure. In a sample of some 60 genera of bellerophontids, Signor and Brett (1984) found a substantial decline in umbilicate forms, beginning in the Silurian Period (Fig. 10).

Ribbing and fluting also render shells more resistant to crushing; again Signor and Brett found an increased incidence of sculpture in post-Silurian nautiloids. Alexander (1986b) observed a parallel decrease in the incidence of smooth implicate shells and increase of coarse ribs in post-Silurian brachiopods. Similarly, he observed a declining proportion of rectimarginate shells in favor of stronger uniplicate and strongly ribbed shells. Such morphological features could aid in the resistance to shell breaking and crushing predators. Strongly plicate brachiopods, such as

rhynchonellides, also appear to have been avoided by shell boring organisms, at least in the Devonian (Bordeaux and Brett, 1990).

Fluted margins may also give shells tighter closure against the prying action of starfish, as does interlocking hinge dentition, and central placement of adductor muscles (Alexander, 2001). Later Paleozoic brachiopods and bivalves show increased frequency of fluting, interlocked hinge teeth, and centralization of adductor muscle scars.

Greater shell thickness could also have been advantageous during a time of increased durophagous predation, drilling predation, or
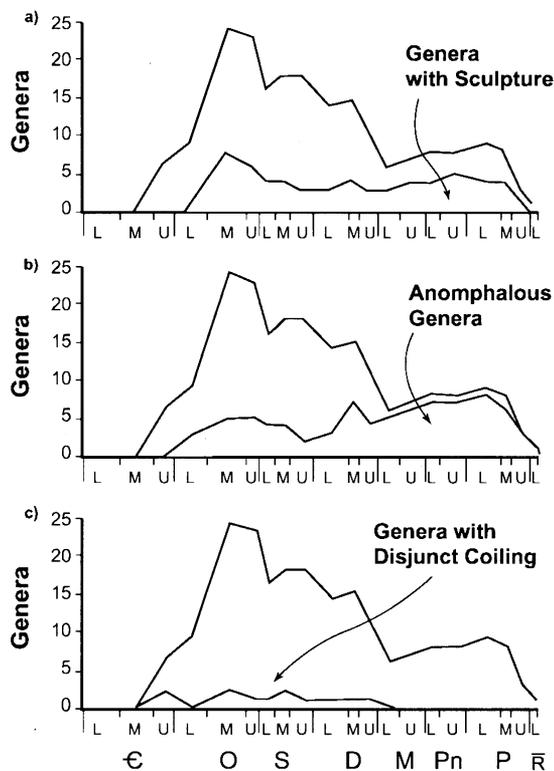

FIGURE 10—Morphological trends in bellerophontid mollusks. Upper curve shows total number of genera; area under lower curve represents proportion of total genera that show indicated feature: (a) presence of sculpture; (b) anomphalous (lacking umbilicus); (c) disjunct coiling. Note loss of genera with disjunct coiling and increase in proportion of genera with sculpture and lacking an umbilicus. Redrawn from Signor and Brett (1984).

parasitism. Leighton (2001b) also notes a tendency for brachiopods to develop thickened muscle platforms in the most drill-prone centrally located shell areas. A trend toward increased plate thickness is evident in late Paleozoic crinoids. Certain Permian taxa are extraordinarily thickly plated (Signor and Brett, 1984).

Spinosity.—Spinose skeletons may deter both durophagous and drilling predators. An increase in the frequency of taxa with skeletal spines during the Paleozoic is documented by Signor and Brett (1984); spines may also increase in length and sharpness. Articulate brachiopods show a strong increase in the presence of spines on both the pedicle and brachial valves, reflected in the rise to dominance of the productides, in the later Paleozoic (Signor and Brett, 1984). Although the spines on the deeply convex pedicle valve of productides may have served as "rooting" spines for these semi-endofaunal brachiopods (Grant, 1966; Rudwick, 1970) (Fig. 10), they may also have been functional in preventing predatory attack, particularly from below by infaunal predators. Leighton (2001a) showed that among Late Devonian brachiopods the spinose *Devonoproductus* had a much lower frequency of completed boreholes than either contemporaneous atrypids or *Douvillina*.

Among gastropods, relatively few Paleozoic genera (~5%) show spines; however, here the exceptions may prove the rule. No spinose genera are known from the lower Paleozoic and spinose forms first appear in the Silurian. Moreover, all of the spinose gastropods are inferred to have been relatively sedentary. Notably, several species of spinose platyceratids appear in the Devonian. A permanently sessile commensalistic/parasitic lifestyle (Bowsher, 1955; Rollins and Brezinski, 1988; Baumiller, 1990; Boucot, 1990) may have rendered these gastropods particularly vulnerable to predatory attack, and conferred a selective advantage to species that evolved spines.

Trilobites also show an abrupt, but short-lived, burst of spinosity during the Devonian. The well known and highly diverse trilobites from the Emsian-Eifelian of Morocco and North America show a high frequency of spinose genera in several

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lineages (Kloc, 1992). Kloc (1992, 1993) has also documented the occurrence of possible camouflage strategies in the Early Devonian selenopeltid trilobite *Dicranurus*. The elongate cephalic spines are typically heavily bored and encrusted. Kloc suggests that these encrusted spines served to obscure the image of the trilobite from visual predators in a strategy analogous to that of decorator crabs.

Long spines on the calyces and tegmens of crinoids are reasonably interpreted as a deterrent to would-be predators. Therefore, it is significant that no crinoids display spinose calyces prior to the Wenlock (Silurian), when *Calliocrinus* displays large tegminal spines (Signor and Brett, 1984). Both camerate and cladid crinoids in several families show a substantial increase in the proportion of spinose genera commencing in Early Devonian time (Fig. 11). The proportion of spinose genera increases to a maximum in Visean time and then declines in the late Paleozoic in concert with the decline of camerate crinoids during the Chesterian crisis identified by Ausich et al. (1994).

Other crinoids, primarily Devonian-Lower Carboniferous camerates, but also a few late Paleozoic cladids, developed elongate spines on the calyx (Fig. 12). A few genera developed spinose
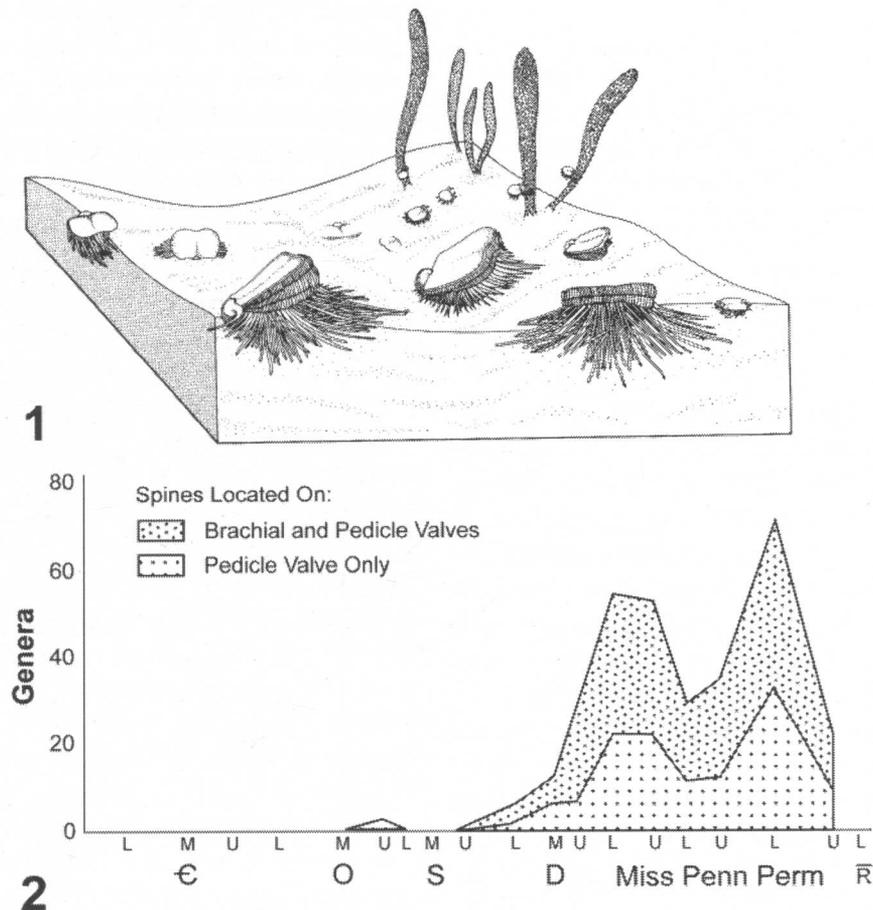

FIGURE 11—Spinosity in brachiopods. 1—Reconstruction of the productid brachiopod *Waagenoconcha* from the Permian of Russia; note juveniles attached to algae by "clasping spines," and quasi-infaunal mode of life, with "rooting" spines in adults, ×1; from Grant (1966). 2—Brachiopod genera, primarily productides, with spines on the pedicle or both valves. Both show consistent trends; from Signor and Brett (1984).

plates on the axillaries of the arms. *Arthroacantha*, a very common and widespread Devonian camerate, possessed articulated spines on the calyx, as well as spines on the arms (Fig. 12.1) (Kesling and Chilman, 1975). Within this genus there is also a trend of increasing spine length into the Late Devonian (G.C. McIntosh, pers. comm., 2001).

Aronson (1991) argued that if predation pressure were a significant factor in crinoid communities a major decline in crinoid thickets would be expected between pre-Devonian and Carboniferous benthic assemblages. This prediction was based in part on evidence that

stalked crinoids migrated offshore in the face of the Mesozoic marine revolution of predators (Meyer, 1985). Aronson made corrections for differences in rock volume of various ages and predicted the frequency of dense crinoid assemblages for each age. He found that dense crinoid thickets did not, in fact, show a decline during this interval. This provides negative evidence for the escalation hypothesis and might suggest that predation pressure was not, in fact, a major factor in controlling crinoid density. Alternatively, Aronson suggested that the general lack of reefs in the Lower Carboniferous caused a
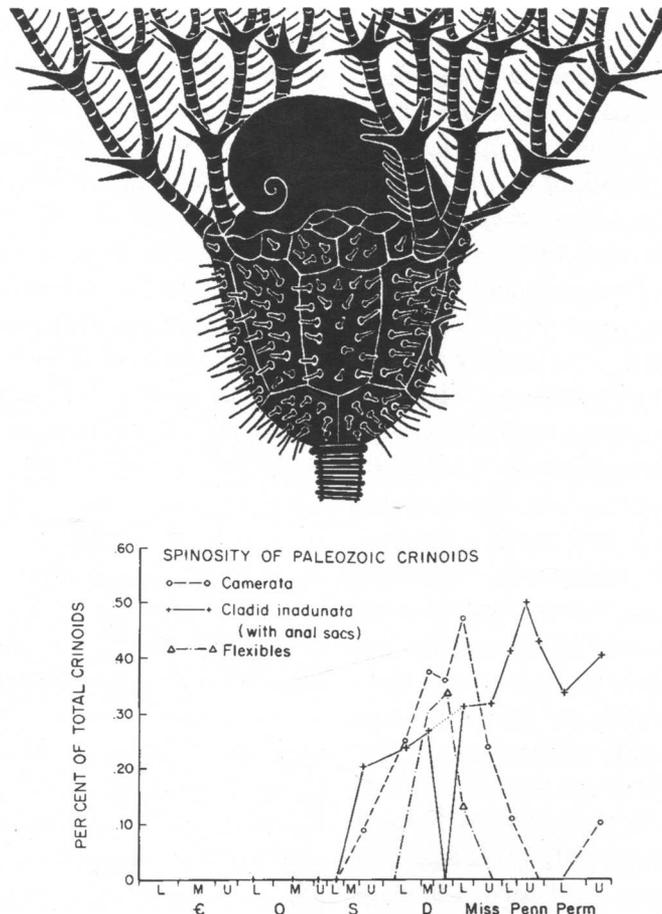

FIGURE 12—Spinosity in Paleozoic crinoids. 1—Reconstruction of Devonian crinoid *Arthroacantha* with attached (coprophagous) *Platyceras* gastropod, ×2; note jointed spines on calyx and spines on axillaries of arms. 2—Percentages of spinose genera in three subclasses of crinoids through the Paleozoic Era. 1, Modified from Kesling and Chilman (1975); 2, from Signor and Brett (1984).

decline in specialized reef-dwelling fish predators. This is questionable since most known Devonian gnathostome fish fossils are not associated with reefs, but occur rather in open marine settings. One might, alternatively, suggest that crinoids were able to adjust, up to a point, to the increased pressure of grazing by sharks, holocephalans, and other fishes. The rise in spinosity and plate thickness may have been effective temporarily in preventing decimation by predators.

Surprisingly, all crinoid subclasses exhibit *decreased* spinosity in the late Paleozoic, following a Lower Carboniferous high (Signor and Brett, 1984). Waters and Maples (1991) suggest that predators were able to "keep up" with the armaments of their prey and that spinose plates became ineffective as a defensive strategy; smaller size and compactness of the calyx may then have been more effective strategies. This trend toward smaller sizes may have other meanings, such as declining food resources, although no correlations are obvious.

A majority of the common Devonian platyceratid host crinoids were spiny, and nearly all spiny crinoids were at least occasional hosts of platyceratids. In contrast, none of the common Ordovician or Silurian crinoid or cystoid hosts were spiny. Obviously, the spines were *not* a deterrent to platyceratids. *Arthroacantha*, the most widely cited host genus (with populations showing up to 70% individual infestation by *Platyceras*) possessed both movable spines on the calyx and axillary spines on the arms. Intriguingly, *Platyceras dumosum,* one of the common symbionts, also possessed long spines. Brett (in press) suggests that the development of spines in crinoids was an anti-predatory adaptation mediated by the presence of gastropods. Even if crinoids were not tasty prey (as has been suggested by some modern studies: Meyer and Ausich, 1983), gastropods may have been. If gastropod-bearing crinoids were frequently "targeted" by durophagous predators, they may have experienced a higher selection pressure to evolve spines (as did the gastropods themselves) than did non-host crinoids.

Life Habit Changes.—Vertebrates typically show a pattern of *decreasing* skeletal armor during the late Paleozoic. Early agnathan "ostracoderms" and placoderms were heavily encased in dermal bone. Dermal bone may have served non-defensive functions, such as areas for muscle attachment and phosphate sinks. However, it is also probable that this armor deflected predatory attack, especially from contemporary invertebrate predators. Ironically, it may be the preference of these early vertebrates for marginal marine environments that fostered escalation, as these environments were also home to large predaceous eurypterids.

Subsequently, the rise of gnathostome fishes must have placed additional predation pressure on other vertebrates. It is perhaps surprising that some of the largest predators of the Devonian—the arthrodires—had heavily armored heads. This may reflect the evolution of still more effective, faster-swimming sharks, or it may merely reflect another type of adaptation—possibly for phosphate exchange—unrelated to predation. In any case, heavy dermal armor was largely lost with the extinction of placoderms. The successful predators of the later Paleozoic probably reduced armor as an adaptation for increased maneuverability and rapid swimming. This apparently was a highly successful tradeoff. The appearance of varied fin spines in sharks and peculiar spine and brush "headgear" in the stethacanthids (Fig. 6.5) may represent anti-predatory or sexually selective adaptations (Zangerl, 1981).

Life habit changes among Paleozoic organisms include the development of endobenthic and cemented modes of life. Semi-endofaunal (frequently termed quasi-infaunal in earlier literature) habits were adopted by many orthide and strophomenide brachiopods as early as Early Ordovician time, but the proportion of semi-endobenthic brachiopods increased in the late Paleozoic with the rise to dominance of productides and chonetid brachiopods (Thayer, 1983) (Figs. 11, 13). This change coincides with the middle to late Paleozoic revolution of predators.

Bottjer (1985) related increasing intensity of predation to the progressive occupation by bivalves of successively deeper endobenthic tiers (Ausich and Bottjer, 1982). Endobyssate and shallow-

burrowing bivalves occupied an upper endofaunal tier, 0 to -6 cm (i.e., at and up to 6 cm below the sediment–water interface), from Cambrian times onward. Invasion of an intermediate (-6 to -12 cm) tier by venerid and pholadomyid bivalves occurred later during the Devonian; pholadomyids pushed downward into the deep, -12 to -100 cm, tier slightly later in the Lower Carboniferous. Bottjer (1985) attributes this increased tiering to the mid-Paleozoic escalation of predators. Deep endobenthic modes of life were limited during the Paleozoic by the absence of mantle fusion and lack of true siphons in most bivalve clades (Stanley, 1970, 1977) (Fig. 13).

Cementation of shells to hard substrates also makes them harder to dislodge by durophagous predators (Harper, 1991). Alexander (2001) notes that two major groups of brachiopods (productides and orthotetaceans) show an increased frequency of cemented forms during the later Paleozoic (Fig. 13). During the Carboniferous, pseudomonotid bivalves also adopted a cemented mode of life and evolved shell spines, presumably in response to increased predation pressure.

SUMMARY

There is a growing body of evidence that predation on hard-shelled marine organisms intensified during the middle Paleozoic (Fig. 13). The direct fossil record of potential predators shows a substantial increase in durophagous shell-crushing predators, as well as pelagic pursuit and ambush piscivorous predators. Trace fossil evidence provides a strong case for the existence of predatory attack on shelled organisms as early as the Cambrian.

Predation in marine environments evolved through several phases of intensification with minor setbacks following mass extinctions (Fig. 13). The first phase might be termed the Cambrian Revolution. In this phase, large predators, such as anomalocaridids, other enigmatic arthropods, and perhaps trilobites, first had an impact on marine communities.

A middle Paleozoic phase of predation intensification, emphasized by Signor and Brett (1984), involved the rise of nautiloid and ammonoid cephalopods, phyllocarids, asteroids, and several lineages of gnathostome fishes. The latter group in particular radiated rapidly during the Devonian to produce diverse durophagous and piscivorous placoderms and sharks. Major Late Devonian extinctions terminated the placoderms, but their guilds were rapidly replaced by evolving sharks, holocephalans, and bony fishes.

Brachiopod and molluscan shells and trilobite exoskeletons show evidence of healed bite marks and peeling from the Cambrian onward, but with a marked increase in frequency in the later Paleozoic. Predatory drill holes with stereotypical position and prey-species preference are found in brachiopods (Cambrian onward) and mollusks (Ordovician onward), but boreholes also show increased frequency in the middle Paleozoic.

The Permo-Triassic extinction crisis constituted a major setback for all marine communities. This certainly included many predatory taxa (e.g., many ammonoids, nautiloids, phyllocarids, predatory archeogastropods). However, it is likely that certain active predatory organisms (e.g., fishes) were not as strongly affected as others. Studies by Knoll et al. (1996) note that many sedentary benthic organisms (e.g., brachiopods, echinoderms) have a lower capacity for controlling CO_2 concentrations than do some "high energy" organisms, including active predatory arthropods and vertebrates. These authors postulate preferential extinction of many filter-feeding invertebrates during an interval of hypercapnial stress.

Drilling predation appears to have been common in the Paleozoic (Kowalewski et al., 1998). The evolution of Paleozoic drilling actually occurs in two phases: a Precambrian to Silurian stage, and a Silurian to Carboniferous phase (Kowalewski et al., 1998, their figure 3). Drilling was globally widespread in the Permian, but the frequency of drilling bivalve or brachiopod prey was relatively low (Kowalewski et al., 2000). As more data are added to our knowledge of drilling predation, it appears that there is not an ever-increasing escalatory trajectory through the

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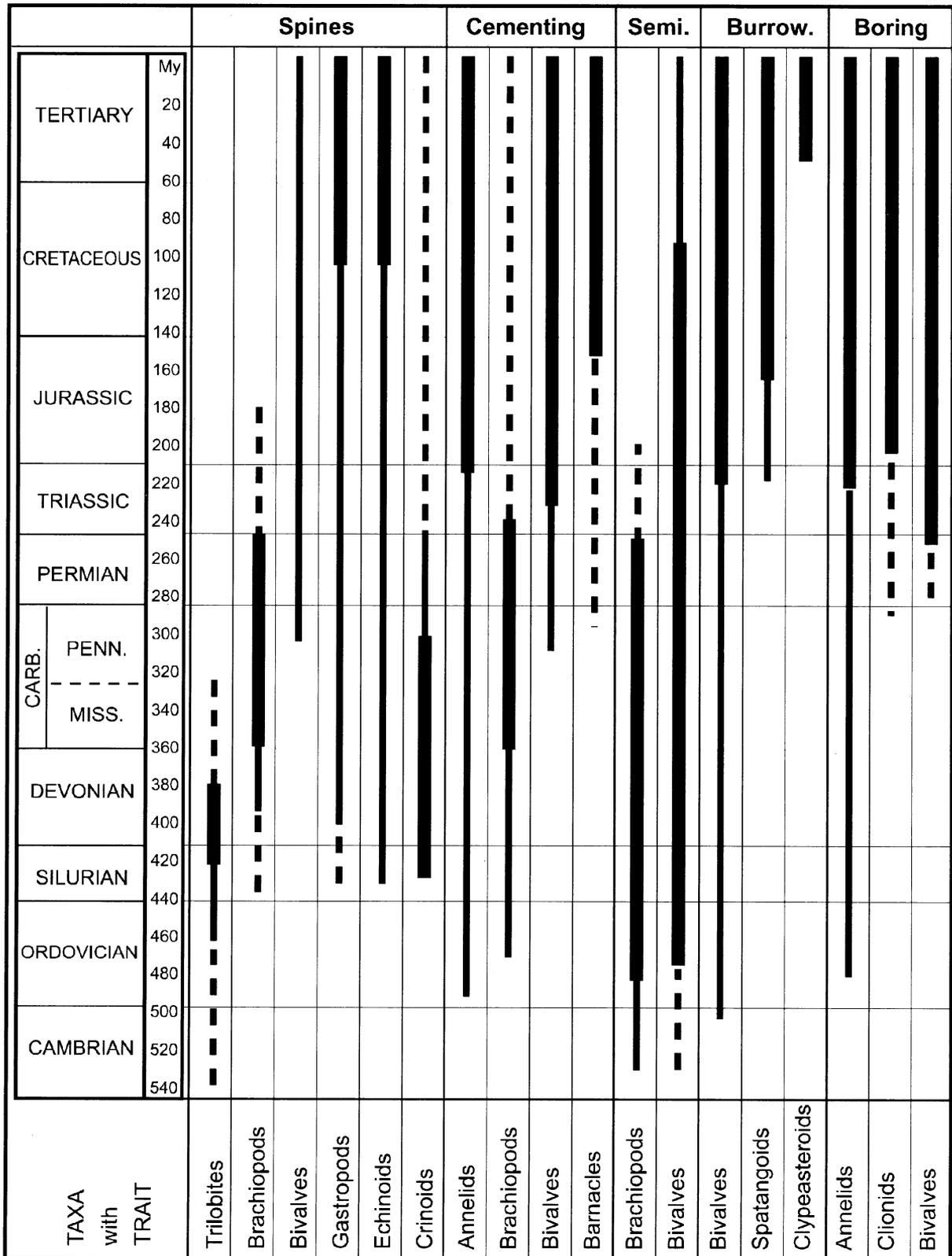
Phanerozoic of drilling predation (as depicted in Vermeij, 1987); rather, it appears in phases related to the predators that evolved during that time.

Predator-prey interactions were probably of fundamental importance in shaping and directing long-term trends by evolutionary adaptation and cooptation (Vermeij, 1977, 1987). The response of benthic organisms to the Cambrian rise of predators may be one of the most significant events in the history of life: the nearly synchronous evolution of sclerotized and biomineralized armor and the appearance of an abundant skeletal fossil record.

Brachiopods, gastropods, trilobites, and crinoids, among others, show an abrupt increase in spinosity in the Middle Devonian and Lower Carboniferous. There are also possible patterns of increased spinosity along latitudinal gradients in the Carboniferous. But spinosity decreases after the early Carboniferous. Late Paleozoic forms may have taken refuge in smaller size and resistant, thick-walled skeletons.

Hard-shelled organisms may have responded to crushing and drilling predation by evolving a variety of thicker, more spinose skeletons. Although escalation is sometimes cast as an ongoing "arms race," in actuality, escalation of predator-prey relationships may have developed in a series of incremental steps during episodes of abrupt biotic reorganization punctuating longer interludes of relative stability.

ACKNOWLEDGMENTS

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FIGURE 13—Ranges of possible anti-predatory traits in various benthic marine invertebrates. Thin lines: present, but minor; thick lines: abundant; broken lines: possibly present, but rare. Abbreviations: Burrow: burrowing; Carb: Carboniferous; Miss: Mississippian; Penn: Pennsylvanian; Semi: semi-endobenthic.

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