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THE FOSSIL RECORD OF PREDATION: METHODS, PATTERNS, AND PROCESSES

The papers assembled in this volume show compellingly the methodological, topical, and conceptual richness of paleontological research on predation. Such studies span a broad spectrum of organisms and a wide range of observational scales, from individual interactions to global-scale secular trends. The fossil record offers us diverse and provocative evidence of predator-prey interactions through time, ranging from predation traces to functional morphology and phylogenetic affinities. In recent years, these diverse data have become a base for posing increasingly sophisticated questions and for testing increasingly complex hypotheses.

As clearly demonstrated in this volume, predation can be defined in a variety of ways. A predator can be defined very broadly as "an organism killing another organism for nutritional purposes" (Bengtson; see also Labandeira; Lipps and Culver; Brett and Walker), or the definition may be restricted behaviorally by excluding organisms that kill by passive filter-feeding, so that predators are only "those organisms that hunt or trap, subdue, and kill individual animals that have some capacity for either protection or escape" (Bambach; see also Kowalewski). Predation as a concept may be restricted to macro-carnivory—with a predator then defined as "a large animal or sometimes a plant consuming part or the whole of another animal" (Vermeij)—or can be expanded to include tiny organisms, like foraminifera subduing and eating larger animals (Lipps and Culver), or even behaviors that involve the killing of plants (e.g., seed predation; Labandeira). Thus, the definition of predation varies significantly among researchers. The term predation may also include related behaviors along a spectrum from active predation to scavenging, from lethal predation to partial (sublethal) predation, parasitism, and amensalism (see Baumiller and Gahn; Labandeira; Kowalewski; Vermeij).

METHODS

The chapters included in the first part of the volume review a variety of methods that can be applied to study the fossil record of predation. Various direct and indirect indicators of predation are available to paleontologists, including trace fossils, coprolites, gut contents, exceptional preservational events, taphonomic patterns, and indirect evidence provided by functional morphology and phylogenetic affinities (Kowalewski). Because of the highly disparate nature of the data itself, variable research goals, and even personal idiosyncrasies, the methods used to study ancient predator-prey interactions are very diverse.

Among various lines of evidence, trace fossils left by predatory activity offer a particularly rich source of quantifiable data (Kowalewski; see also Haynes; Lipps and Culver; Brett and Walker; Walker and Brett; Baumiller and Gahn; Farlow and Holtz; Bengtson; Dietl and Kelley; Vermeij); and various analytical approaches for studying trace fossils can be fruitful depending on the nature of the material and the scientific goals of paleontological projects (Kowalewski). Coprolites and stomach contents also provide a wealth of direct data on ancient predator-prey interactions and are widely used for studying the diet of ancient predators, from marine invertebrates to terrestrial vertebrates (Chin; see also Brett and Walker; Walker and Brett; Labandeira; Farlow and Holtz). In addition to the predation traces studied by paleontologists, anthropologists have developed a distinct set of qualitative and quantitative methods for studying the hunting behavior of hominids, not only to distinguish between scavenging and predation, but also to draw the much more subtle distinctions among different butchering behaviors, such as skinning, meat-stripping, or sectioning of animal carcasses (Haynes).

The methods part of this volume shows that the methodological dimension of research on the fossil record of predation is a rapidly growing field of study, with many promising future research directions—particularly through laboratory experiments, observations in present-day ecosystems, and numerical modeling. Clearly, we need to continue improving our statistical tools and analytical strategies and to work together on erecting some general methodological guidelines for studying the fossil record of predation.

PATTERNS

The chapters included in the second part of this volume impressively document the range of evidence related to predator-prey interactions that has been amassed by paleontologists. However, these studies also point to the numerous temporal and taxonomic gaps in our current knowledge.

The fossil record of microorganisms provides insights into primary producers and secondary consumers in marine ecosystems over the last 3.8+ billion years, and points to a long-term increase in the complexity of trophic structures of marine ecosystems through the history of life (Lipps and Culver). In particular, the trophic strategy of endosymbiosis between animals and microbes, especially photosynthesizing algal eukaryotes, seems to have long played an important role in marine ecosystem development and the evolution of organisms (Lipps and Culver).

The marine invertebrate fossil record offers a spectacular wealth of evidence relating to predator-prey interactions, including trace fossils, coprolites, and functional morphology of prey and predators (Brett and Walker; Walker and Brett). These predatory records suggest that long-term evolutionary changes in predation pressure are linked to episodes of abrupt biotic reorganization during and after mass extinctions, punctuating longer interludes of relative stability (Brett and Walker; Walker and Brett). Moreover, the evolution of predation in the pelagic realm may have been largely decoupled from its evolution in benthic ecosystems. The data from the marine fossil record make a strong case for the existence of predatory attack on shelled organisms as early as the latest Precambrian and the early Cambrian—with a further intensification of predation during the middle Paleozoic paralleled by increases in spinosity and other potentially defensive traits of the prey skeleton (Brett and Walker). In contrast, late Paleozoic forms may have taken refuge in smaller size and resistant, thicker-walled skeletons (Brett and Walker). Following the end-Permian mass extinction, the data suggest episodic, but generally increasing, predation pressure on marine organisms through the Mesozoic-Cenozoic interval. Predation in benthic communities may have intensified substantially in the Late Cretaceous–Early Cenozoic with the evolution of neogastropods, varied crustaceans, and durophagous fish. In the early to mid-Mesozoic, large-predator guilds were filled predominantly by varied marine reptiles; whereas neoselachian sharks, teleosts, and marine mammals dominated in similar roles throughout the Late Cretaceous to Cenozoic (Walker and Brett).

The marine invertebrate record also supplies evidence relating to parasite-host interactions, with a nearly even distribution of reported cases through the post-Cambrian Phanerozoic (Baumiller and Gahn). However, in few of the reported examples can we explicitly distinguish parasitism from predation, commensalism, or mutualism; and only in exceptional cases (such as interactions involving platyceratids and crinoids) is the evidence for parasitic interactions sufficiently compelling (Baumiller and Gahn).

Terrestrial and freshwater invertebrates also provide a diverse fossil record of predation, parasitoidism, and parasitism—with evidence for carnivory (i.e., taxonomic affiliation, fossil structural and functional attributes, organismic damage, gut contents, coprolites, and mechanisms indicating predator avoidance) occurring from the mid-Paleozoic to the Recent (Labandeira). However, only 12 invertebrate phyla have become carnivorous in the continental realm and only the two most diverse groups (nematodes and arthropods) left behind a comparatively good fossil record (Labandeira).

Major groups of amniote predators such as theropod dinosaurs and carnivorous synapsids offer a continuous fossil record of predator-prey interactions in the terrestrial realm. The fossil record of predatory theropod dinosaurs suggests that the taxonomic composition of dinosaurian predator-prey systems varied notably as a function of time and geography (Farlow and Holtz). Details regarding diet and hunting behavior of theropods can be inferred from their functional morphology, supported by evidence from taphonomic associations with likely prey species, bite marks, gut contents, coprolites, and trackways (Farlow and Holtz). Following the K-T extinction, carnivorous birds (the direct descendants of theropods) remained prominent predators throughout the Cenozoic Era (Farlow and Holtz).

The fossil record of synapsids points to significant parallels between the diversification of non-mammalian synapsid predators in the Late Carboniferous–Triassic and the Cenozoic radiation of mammalian predators: both groups evolved sabertooth forms as well as short-snouted, powerful biting forms (Van Valkenburg and Jenkins). Both radiations are characterized by repeated patterns in which one or a few clades evolved large size and dominated the carnivore guild for several million years, but then declined and were replaced by new taxa (Van Valkenburgh and Jenkins). Both non-mammalian and mammalian synapsid clades show trends toward increasing body size and hypercarnivory over time (Van Valkenburgh and Jenkins).

PROCESSES

The last part of this volume includes chapters that provide an introduction to some major models regarding the origin and history of predation as well as the evolutionary role of predator-prey interactions through time.

Although data on early life are understandably scarce, existing data and theoretical considerations suggest that predation may have played an important role in some of the major transitions in evolution, including the origin of eukaryotic cells, the origin of multicellularity (as a means of acquiring larger size), the decline of stromatolites, the diversification of acritarchs, and the Cambrian explosion (Bengtson; see also Lipps and Culver). Predation may have been a decisive selective force behind the transition from simple, mostly microbial, ecosystems to those with complex food webs and higher-order consumers (Bengtson; Lipps and Culver). Following the Cambrian explosion, the diversity of predators and the proportion of the total fauna represented by predators have both increased throughout the Phanerozoic, implying that ecosystems have increased their ability to support either more predators or more specialization among predators (Bambach). This pattern may be linked to a secular increase in diversity and biomass of primary producers, and changes in the composition of prey taxa (Bambach).

The evolutionary importance of predation remains a hotly debated topic. Arms races between predators and prey may be driven by two related processes: escalation—enemy-driven evolution, in which the role of prey in the evolution of the predator is downplayed—and coevolution—in which two or more interacting species respond reciprocally to one another; prey are thought to drive the evolution of their predator, and vice versa (Dietl and Kelley; Vermeij). In the fossil record, the two processes are distinguished most reliably when the predator-prey system is viewed within the context of the other species that may influence the interaction, thus allowing for a relative ranking of the importance of selective agents (Dietl and Kelley). Scale is also important in evaluating the role of escalation and coevolution in the development of species interactions: prey are likely to exert some selective pressure on their predators over ecological time scales, but predators may still exert primary "top-down" control in directing evolution over evolutionary timescales. In the long term, predators have two principal effects: they influence prey phenotypes and they restrict prey to environments where predators are rare (Vermeij). Predators likely control overall directionality in evolution because of the inequalities of predator and prey in control of resources (Vermeij; Dietl and Kelley). Indeed, predators have the evolutionary upper hand over the long run, especially in the expression of sensory capacities, locomotor performance, and the application of force; and only in passive defenses (armor, toxicity, large body size) does escalation favor the prey (Vermeij). The evidence provided by the fossil record points to increases over time in both predator power and prey defenses. These escalatory increases have proceeded episodically (Brett and Walker; Walker and Brett; Vermeij) against a backdrop of generally increasing productivity (Bambach) and increasing top-down evolutionary control by high-energy predators (Vermeij).

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