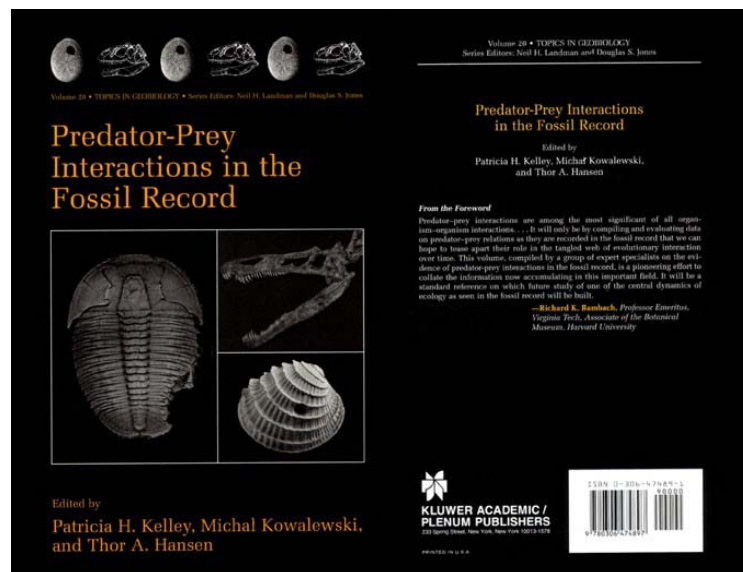


Kelley, P.H., M. Kowalewski & T.A. Hansen. eds. 2003. **Predator-prey interactions in the fossil record.** – New York, Kluwer Academic /Plenum Publishers (Topics in Geobiology 20)

Book review by F.P. Wesselingh



What on earth makes some palaeontologists enthusiastic about holes, scars and other irregular damages to otherwise nice fossils? A growing number of scientists is dedicated to research in these areas, and the reasons why are well covered in a nice book about predator-prey interactions in the fossil record. There are two main motives for the study of predatory traces and anti-predatory behaviour or characteristics. The first motive is to gain insight in the evolution of adaptations ranging from individual specimens to whole ecosystems. This line of research has gained momentum with the formulation of the escalation theory of Vermeij (1987). Vermeij's theory postulates that the interchange between predators and prey has resulted in an increasing robustness and morphological and behavioural complexity of (marine) biota, both in prey and predator groups. The second line of research, reconstructing food webs, has been especially advanced in archaeological and archaeo-zoological research since the 1980's. Here, the main objective has been to reconstruct the functioning of ecosystems and predator-prey relationships in terrestrial fossil biota that are usually characterised by their very low fossilisation potential.

The book is divided into two parts. The first part, covering 15 chapters, is a taxonomic review of the fossil record of predation. These 15 chapters are concerned with a review of predation or prey potential of a variety of groups, ranging from Foraminifera to dinosaurs. This section of the book shows very well the large differences that exist in the research on predator-prey relationships from the fossil record for each group. For example, comparatively little is known about these processes in ancient reef biota and bryozoans, whereas the large amount of data and knowledge from fossil molluscs is represented in three chapters. Other well-studied groups include trilobites and vertebrates. The chapters in this book show considerable advances that are currently being made in the study of predator-prey relationships in groups such as brachiopods and echinoids. Whenever possible attention is paid to knowledge of predator-prey relationship and their marks in hard parts in the recent biota, and then turn to the fossil record to assess patterns in a prey-predator context. Both potential predatory marks/traces on fossil biota, as well as their remains in gut-contents and coprolites (whenever available) add to the insight of past processes. Also, many of the morphological characteristics that evolved in groups give insight into their role as prey or predator. As can be expected with so many contributions, the style and readability differs between the chapters, but most of the book is pretty well readable for the general palaeontologist. Most of the chapters are adequately illustrated, though chapters 13-15 (predation on and by vertebrates) lack illustrations that can give a non-specialist some idea about what the scars look like on fossils.

Several things struck. In chapter 1 (predation on and by Foraminifera) a photograph of an *Orbulina universa* consuming a calanoid copepod (figure 5) is of outstanding beauty. In this chapter the figure captions of figures 9 and 10 are changed, causing some confusion. This chapter and the second chapter (ancient reef builders) give a good overview of (potential) predators. I was struck that predation on reef biota is relatively poorly studied, though it seems highly significant in order to understand the evolution of reef biota. Chapter 3 (trilobites) is a very well illustrated overview. Strangely enough predation incidences on trilobites is (strongly) skewed towards the right margins, which is linked to right-left behavioural asymmetry in trilobites. In chapter 4

(predation on ostracods) the authors remind us of the relationship between the abundance of ostracods and incidence of (gastropod) predation from core data. Chapters 5 and 6 (drilling predation and shell breaking predation on gastropods and bivalves respectively) illustrate the advanced state of this type of research on molluscs. With their abundance in the fossil record and the accretionary mode of documenting history, molluscs have been a major group on which Vermeij (1987) based his escalation theory. However, a straightforward thickening and increasing ornamentation in time as well as from cold to warm habitats within time, as should be expected from this theory, is usually but not always evident from the fossil record. This is partly due to analytical problems that are treated in both chapters. The largest difficulty is that no mechanism has been found to assess predator success from the fossil record, since many successful events have led to the total destruction of prey shells. This is a very important process, which has been quantified by Cadée (1995). This overlooked paper estimates that in a temperate tidal environment about one third of the yearly mollusc production is fragmented by birds and possibly a similar amount by crabs, adding to an incredible destruction rate of 60-70% of shell production by predators. The uselessness of sublethal damage for estimates of predator levels is also acknowledged in chapter 7 (predation on cephalopods). This chapter is an elegant combination of biological and palaeontological documentation of the process. Insight into predation on brachiopods (chapter 8) is increasing fast. This chapter neatly addresses questions such as 'Why would anything eat a brachiopod?', 'What ate Palaeozoic brachiopods?' and whether predation was important during the Palaeozoic. In figure 3 of this chapter, covering an ornamentation index for Silurian to Mississippian brachiopods and incidence of drill holes, the latter is very high around 380 Ma ago, and directly followed by assemblages that are much more ornamented. As a bystander, this implicates that increasing predation may have triggered a revolution in ornamentation, a conclusion that is not drawn by the author himself. Chapter 9 summarises knowledge of predation on bryozoans. With its excellent illustrations it provides scientists with a very good starting point for further research in this theme, which has hardly been studied in bryozoans so far. Predation on echinoderms has received far more attention, as is reflected in chapters 10 (crinoids) and 11 (echinoids), both with excellent illustrations of predation scars on fossils and recent taxa. The ability to regenerate damage in (several) crinoids adds to their utility in this sort of studies. Strangely enough, neontological observations of predation are actually very rare. This contrasts with clues from Palaeozoic fossils that show considerable predation pressure at the time. For the echinoids, the authors make clear that it is difficult to distinguish between marks from predators and parasites that complicate the life of sea urchins, but that incidence is increasing especially in the Cenozoic.

Chapters 12-15 deal with vertebrate predation in the fossil record (fishes, dinosaurs, small mammals and early humans respectively). The dinosaur chapter yields an impressive illustration of a predatory attack of a Mongolian *Velociraptor* on a *Protoceratops*, fossilised in the act. Such an exceptional fossil teaches us much about actual predation in past times. The author (and authors of later chapters) point to the difficulty to distinguish between scars from predation and scavenging, though other indirect evidence is very illuminating. Both in small mammal and archaeo-zoological research, careful documentation of scars and coprolites, as well as observations on the recent biota have greatly improved insight in past communities, that are generally characterised by their poor fossilisation potential. The human style of predation, targeting prey far larger than the predator, evolved about 2,5 Ma ago, and increasingly complex behaviour related to hunting practices evolved since then. Evolution of hunting appears to be driven more by social demands rather than the need for larger prey in itself.

The second part, consisting of three chapters, treats major macro-evolutionary episodes in the history of predation. The three chapters deal with the origin and early evolution of predators, predation during the Palaeozoic and the Mesozoic marine revolution respectively. The three chapters are nice contributions combining all kinds of data sources in order to draw a larger picture of the evolution of predation and the implications for ecosystem evolution. Chapter 16 deals with the rise of predation in the Cambrium. The origin of macroscopic predation is linked to the decline of Ediacaran biota, the skeletonization of Cambrian metazoans as well as their diversification. A mathematical model (the ecotone model) explores how in the very brief lower Cambrium interval predation had a very profound impact on the biota. It suggests (p. 396) "the introduction of a single macropredator species in the late Proterozoic marine biosphere induced a paleoecological phase shift accomplished by predator-induced spread of the predatory lifestyle". Although some of the assumptions remain to be tested, the model gives plausible explanations as to the very rapid evolution during the Early Cambrian, and provides some very interesting new venues for research into this 'Cambrian explosion'. Chapter 17 deals with durophagy during the Palaeozoic. Durophagous predators became common only in the Devonian and afterwards. The chapter neatly reviews all sort of indications for Palaeozoic predator-prey relationships and reviews possible predator groups. The increase of these groups is matched by (1) increasing spinosity in brachiopods and echinoderms, (2) increase of gastropod genera lacking an umbilicus (that makes snails vulnerable to attack) and (3) the loss of disjunct coiling in gastropods. These indications are taken together to argue for a mid Palaeozoic increase of durophagous predation, in an escalatory sense. Chapter 18 deals with the Mesozoic marine revolution. Here, a good overview of the first onset of predator groups during the Mesozoic is

summarised and discusses evolution of prey responses. In this second part I missed a chapter devoted to where we stand in respect with the escalation theory of Vermeij (1987), which is the central paradigm of most of the workers of this book.

As a whole, the book is obligatory reading for those palaeontologists working with predator-prey relationships, as well as taphonomists interested in the explanation of scars, holes and other irregularities on otherwise nice fossils. The many different groups treated by specialists can make the reading at times somewhat difficult, though most chapters are well summarised and illustrated, thus enhancing the accessibility for the general palaeontologist.

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