



Hunting evidence for the Mesozoic Marine Revolution: progress and challenges

Elizabeth M. HARPER

E.M. Harper, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK; emh21@cam.ac.uk

KEY WORDS - Biotic interactions, predation, drilling, crushing, damage repair.

ABSTRACT - The 1970's saw a stream of papers that crystallised the notion of a "Mesozoic Marine Revolution" during which the pace and intensity of biotic interactions (predation, competition and substrate disturbance by grazing and bioturbation) increased and had a marked effect on benthic marine communities. The tantalizing ideas and hypotheses which have stemmed from this time have had a lasting effect on the course of palaeoecological studies. Of all the interactions, predation has been most amenable to study but even then, only a subset has been interrogated; the field has been dominated by the study of drilling predation in largely molluscan prey. However, there has been considerable progress in broadening our data gathering activities in terms of prey taxa and styles of predatory evidence, ecosystems and geographic regions investigated. This review concentrates on findings since 2000, identifying areas where great progress has been made and describing locations, such as the northern high latitudes and Tropics and the deep sea, intertidal zone and freshwater ecosystems, where information is lacking but probably tractable. Nevertheless, it is imperative that even for well-studied systems we collect more fossil data from any setting or geographic region in order to take account of the variability seen in the patchwork mosaic of modern marine habits, even in shallow water.

INTRODUCTION

All living organisms interact with others, whether members of their own species or those that share their living space. All interactions may have costs and benefits to one party, or both. The scope of these interactions is very broad but the most widespread include competition for resources, predation, parasitism and disturbance, for example by grazing activity. Two facts are apparent: 1) biological interactions are extremely important in the modern world in terms of community structure and diversity (Paine, 1966, 1974; MacArthur, 1972; Menge & Sutherland, 1987; Stanley, 2008), and 2) many, but not all, involve protagonists which have fossil records suggesting the possibility of such interactions in the geological past. As such, it seems likely that biological interactions will have played a role in evolutionary processes. The relative importance of that role may be hotly debated, firstly regarding the relative role of the physical environment (e.g., Jablonski et al., 1985; Clarke & Johnston, 2003; Barnes & Conlon, 2007) and secondly, the relative importance of different biological interactions (Stanley, 2008) and it is vital to acknowledge that in different environments or habitats the balance between these may be different (see Voje et al., 2015).

Organisms have been interacting for billions of years (Petroff et al., 2010). By the Cambrian explosion (541 Ma) predation was in full swing and may have been an important selection pressure favouring the evolution of shells and other protective hardparts (see Wood, 2011). No one denies that biotic interactions were many and varied throughout the Palaeozoic (Brett & Walker, 2002; Nanglu & Caron, 2021; Vinn et al., 2021), but the emphasis of this contribution is on post-Palaeozoic biotic interactions, the dramatic changes that occurred, in particular in shallow marine communities,

and their potential role in establishing the Modern Fauna, during a phenomenon that has been termed the Mesozoic Marine Revolution (MMR) (Vermeij, 1977).

Palaeontologists have long appreciated the ubiquity and importance of biological interactions. This is obvious in the frenetic activity shown in Henry de la Beche's "Duria Antiquior (A more ancient Dorset)" (Fig. 1). Originally drawn in 1831, it reconstructed the Jurassic seascape of Dorset (UK) based on the finds of the famous fossil collector and dealer Mary Anning (1799-1847) (Rudwick, 1992). Early literature, for example Buckland (1835), Fenton & Fenton (1931) and Brunton (1966) explicitly reported predation in the marine fossil record, but it was later in the 1970's when the evolutionary importance of such interactions was posited (Stanley, 1968, 1974, 1977; Kier, 1974; Vermeij, 1975, 1976; Meyer & Macurda, 1977). The concept of the MMR was formalised in a wide-ranging paper by Vermeij (1977) showing an increase in gastropod shell defences (changes in thickness, enhanced ornament, coiling patterns) occurred during the Mesozoic, at a time coincident with the major evolutionary radiation of durophagous (shell breaking) fish and crustaceans. This, he noted, was coincident with an increase in substrate disturbance from the activities of grazers (such as regular echinoids and fish), a shift in some major taxa, e.g., bivalves (Stanley, 1968, 1977) and echinoids (Kier, 1974), towards deep infaunalization, and the marginalisation of other taxa, for example brachiopods (Stanley, 1974, 1977) and stalked crinoids (Meyer & Macurda, 1977) away from the shallow shelf seas. Major, example-rich syntheses followed (Vermeij, 1978, 1987), with the development of the ideas of "escalation", whereby evolution is a top-down process driven by an organism's own predators or competitors, and the notion that, although biotic interactions have become increasingly exigent over the course of the Phanerozoic,



Fig. 1 - *Duria Antiquior*: a reconstruction of “a more ancient Dorset” based on the Jurassic fossils collected by Mary Anning, originally painted by Henry de la Beche in 1831. A number of copies were made, and the image shown here, on a canvass 2440 x 1660 mm, was produced by Robert Faren in around 1851 for Adam Sedgwick to use for his undergraduate lectures at the University of Cambridge (UK). It is currently on public display at the Sedgwick Museum of Earth Sciences. © 2022 Sedgwick Museum of Earth Sciences, University of Cambridge. Reproduced with permission.

their influences have been mediated by changes in physical environment such as climate, tectonic events and relate also to primary productivity (Vermeij, 1987, 1998, 1999).

These ideas have launched a rich and varied field of research which aims to collect evidence and test these ideas. Emphatically the MMR was an interplay of predation, competition and substrate disturbance. Research has heavily focussed on the first, not because the others are less important, but they are more difficult to recognise and quantify in the fossil record (but see Radley [2010], Buatois et al. [2016] and Taylor [2016] for examples). It is for this reason that this review concentrates mainly on predation.

The problem with studying the MMR is that, even confining the discussion to predation, it is a complex mosaic of different organisms and environments. It should not be thought of as a single event; indeed, the term itself means different things to different researchers. The original notion was very much of a rising crescendo starting in the later part of the Mesozoic towards the present. Now we can identify phases within that with different guilds of predators becoming important at different times, for example the rise of several crushing vertebrates in the Late Triassic (Tackett, 2016) and the two episodes (Late Triassic-Early Jurassic and Middle to Late Cretaceous), associated with the rise of defensive

adaptations, recognised by Vermeij (2008). We should expect the course of the MMR to play out differently amongst various prey taxa and in different environments and habitats. This is an important point because some authors have sought to test the importance of predatory interactions using diversity curves at the global scale (e.g., Gould & Calloway, 1980; Aberhan et al., 2006; Madin et al., 2006). However, I strongly share the belief that lists of taxa occurring in any time slice are not sufficient, they are not an adequate test of the importance of biotic interactions over coarse spatial or temporal scales as they conflate different biotic and abiotic effects and provide no reassurance that the compared taxa interacted in any meaningful way (or even lived in the same biogeographic region or habitat) (Dietl & Vermeij, 2006). In seeking to understand and test the hypotheses associated with the MMR we need to use data that demonstrate genuine biological interactions between taxa at the local scale (Dietl, 2003; Dietl & Vermeij, 2006; Vermeij, 2008). However, this is not a trivial task. Even for the Recent, exploring ecological patterns is both difficult and far from complete and data are patchy across a complex mosaic of environments (e.g., Estes & Peterson, 2000; Thyrring & Peck, 2021). Trying to extract data over geological time, recognising and sampling disparate habitats, amongst changing sea levels, shifting global climates and changing

“cast lists” (many with no suitable modern analogues), not to mention the vagaries of the fossil record, is much more challenging.

My standpoint is to accept the importance of biotic interactions in the modern fauna and to recognise that these processes must have some part in deeper evolutionary history but also to emphasise the absolute imperative to test this. The aim of this particular contribution is not to provide yet another review of marine biotic interactions and their recognition in the fossil record. There have been many examples of these (e.g., Vermeij, 1987; Harper & Skelton, 1993; Brett & Walker, 2002; Walker & Brett, 2002; Taylor, 2016), most recently and comprehensively Klompmaker et al. (2019). Instead, it is my purpose to highlight areas where new information has been added to the debate since 2000 and where active research might be fruitful within the next decade or so. The focus is predominantly post-Palaeozoic. Although it is necessary (and right) to quote older literature, I have deliberately chosen to include a large proportion of new literature. Inevitably this is a personal viewpoint, biased by my own interests.

WHERE DO OUR DATA COME FROM?

It is well known that predator-prey interactions recognised in the fossil record are hugely biased towards certain types of prey and predators. That record cannot be regarded as representative of the total history of predation or even of all durophagous predation because there are so many durophages which have almost no body fossil record or which leave no discernible evidence of their activities.

Prey targets

Klompmaker et al. (2019) provided an assessment of 350 predation studies that have dealt with fossil material from the marine fossil record which have been published since 1860; they also logged a further 105 records from recently dead modern material. This database is assuredly incomplete; many studies and valuable data lie hidden or scattered within other publications, for example regional treatises or monographs whose focus is elsewhere. However, the finding that most information is available for particular prey or predator taxa is undoubtedly true. Molluscs in particular are very well-represented; Klompmaker et al. (2019) found that of 3,380 instances of identified prey occurrences in the marine record, 77% were molluscan.

These are not reasons why we should stop collecting molluscan data but rather that we should exploit it and collect more. In particular molluscan prey have been major “workhorses” in the Cenozoic explosion in drilling predation by naticid and muricid gastropods (see Kelley & Hansen, 2003, 2006 and references therein). But not all molluscan preys are equally exploited by research. Most studies involve bivalve or gastropod prey and even within those classes the coverage is far from even. We have comparatively good knowledge of certain lower taxa. Within the fossil bivalves our knowledge is chiefly focussed on certain pteriomorphs (particularly oysters and arcoids) and euheterodonts (principally veneroid clams). Even in the neontological literature these groups

predominate, with the addition of mytiloid mussels, and are principally represented even within those groups by taxa which are commercially important. There are very few reports of predation in either living or fossil protobranchs, palaeoheterodonts or anomalodesmatans (Harper, 2011). Major extinct clades such as the rudists appear to lack any records of predation whatsoever and there are few in inoceramids (e.g., Harries & Schopf, 2003); despite both large taxa appearing to offer inviting sources of meat, Skelton (1979) hypothesised the secretion of a noxious mucus as a possible explanation for rudists to inhibit predators. The gastropods are similarly incompletely covered, with particular groups such as the naticoids, turritellids and buccinoids being far better represented than others, though welcome new studies by Lindström & Peel (2005, 2010) have focussed on the shell repair in fossil pleurotomariids.

Despite their preponderance, bivalves and gastropods, of course, are not the only potential prey targets to have good fossil records from which data might be extracted. There are many reports of predation on non-molluscan prey in the fossil record (including markedly the brachiopods discussed later), but in the last 20 years there has been an acceleration in studies which have reported data from other target taxa. Excellent new studies highlighting recognisable predation damage include those in the smaller extant molluscan classes, such as scaphopods (Klompmaker, 2011; Mallick et al., 2017; Gordillo & Malvé, 2021) and chitons (Rojas et al., 2014) or extinct molluscan taxa such as ammonites (Klompmaker et al., 2009; Andrew et al., 2010, 2015; Kerr & Kelley, 2015; Takeda et al., 2016) or fossil specimens of decapods (Klompmaker et al., 2013), echinoids (Grun et al., 2017; Farrar et al., 2020; Petsios et al., 2021), serpulid worms (Martinell et al., 2012; Villegas-Martin et al., 2016; Harper et al., 2018), ostracods (Villegas-Martin et al., 2019) and barnacles (Gordillo, 2013; Donovan & Novak, 2015; Klompmaker et al., 2015).

Although records exist for fossil bryozoans (e.g., Taylor, 1982; Berning, 2008), it is perhaps surprising that there are not more. Lidgard (2008) found evidence of 399 predatory species, from a wide range of higher taxa, feeding on modern bryozoans, but little is yet known about any diagnostic damage they might leave aside from the recognition of drill holes (Taylor, 2020). Given the general tractability of bryozoans to produce large amounts of data (Taylor, 2016) and the fact that bryozoans are colonial and so predation of individual zooids is akin to grazing (Taylor, 2020), whereas most predation studies focus on solitary organisms, it would clearly be of great interest to further this research. Foraminifera are another surprisingly poorly covered taxa. Records do exist (e.g., Hageman & Kaesler, 2002; Culver & Lipps, 2003) but given the huge number of large samples with extremely good spatial and temporal data from various deep-sea drilling programmes there is huge scope to undertake very detailed studies.

There may be much to learn for little-studied taxa. All predator-prey studies in the fossil record follow an “evolutionary trajectory”, which there is very little opportunity to short-circuit. Initial studies appear often as rather disparate observations made by a small number of dedicated individuals before going on to build comparative data from different localities and time frames while

gaining a mature methodological framework and accepted metrics which can be applied by a wider community of researchers.

That it is possible to gather momentum to improve the corpus of data on less studied prey taxa, with dramatic changes in our understanding in the evolution of predator-prey systems, is emphasised by the changes made in the study of crinoids. Baumiller & Gahn (2003) charted a “paradigm shift” in our understanding of the importance of predation to the evolution of crinoids from an era when crinoid predation was scarcely recognised. These authors credited this shift to the publication of the seminal paper by Meyer & Macurda (1977), which hypothesised that the apparent restriction in the distribution of modern stalked crinoids to “deeper” waters, in stark contrast to the Palaeozoic when it is evident that they inhabited a range of depths and to the free-living comatulids which occur regularly in shallow water, might be due to the rise of predators, in particular teleost fish. Since then, there have been multiple papers collecting data on arm injuries and bite marks which have gathered a mass of evidence on interactions between crinoids, fish and echinoid predators which have supported the basic hypothesis and identified a number of behavioural and morphological adaptations which appear to be defensive (e.g., Baumiller et al., 2008, 2010; Gorzelak et al., 2012).

A similar tale has unfolded in the study of post-Palaeozoic brachiopods. Although records of predation damage in Palaeozoic brachiopods have long been known, largely fuelled by the work of the late Richard Alexander (e.g., Alexander, 1981, 1986 a, b; Leighton, 2003), there were very few examples known from younger strata and a general lack of reports from living brachiopods leading to a general consensus that predation is not a major cause of mortality (Thayer, 1985; James et al., 1992; Kowalewski et al., 2005). However, recognition of scattered records and concerted searches of collections has yielded both living and fossil data that suggest that in shallow water brachiopods have been subjected to both drilling and crushing predation (Baumiller & Bitner, 2004; Baumiller et al., 2006; Tuura et al., 2008; Harper, 2011; Harper et al., 2011, 2019a; Tyler et al., 2013; Harper & Peck, 2016; Gordillo et al., 2019).

Predatory taxa or methods

Many predators and their activities are invisible to the “normal” fossil record. Predators or prey, which themselves have a low preservation potential, and/or prey, which may themselves have high preservation potentials, that show no diagnostic damage go unrecorded. Instances of chance exceptional preservation, such as the gut contents of middle Cambrian priapulid *Ottoia prolifica* Walcott, 1911 from the Burgess Shale Lagerstätte, which demonstrates a generalist predatory diet dominated by hyolithids (Vannier, 2012), provide valuable data. However, they cannot be used to undertake quantitative analyses over more than short temporal or local spatial scales. Furthermore, they document only those elements of the diet which had hard-parts which were not digested. There are many taxa which are known to be predators, for example sea anemones and various worms, whose activities are scarcely documented even in Recent times let alone in the fossil record. And asteroids which are

important durophages and cause enormous damage to commercial shellfisheries; for example, Gallagher et al. (2008) estimated that in the Menai Straits (Wales, UK) *Asterias rubens* Linnaeus, 1758 was responsible for the deaths of 20,000 mussels per hectare per day, but these activities are invisible in the fossil record and surprisingly controversial (Blake & Guensburg, 1990; Donovan & Gale, 1990; Vermeij, 1990; Gale & Donovan, 1992). It is necessary that we should be clear for which predators we can meaningfully collect quantitative data; not all durophages, but rather a smaller group of them and even then, only activities for some of their prey taxa.

Realistically, we are forced to concentrate on two broad modes of predation: crushing and drilling (Vermeij, 1987). However, recognising the actual predators can still be very challenging. For crushers this means identifying predator morphology, such as jaws or claws, though in doing so we do not know that predation was their primary function (rather than being exaptive) and so have no guarantee that possession of these traits truly demonstrates crushing predators (Vermeij, 1982; Chalcraft & Reser, 2003), while for drillers there is no manifestation on the hardparts that reveals the ability to drill. Our best source of data is to recognise diagnostic damage (or repaired damage) on prey hardparts, which may be used to infer a particular style of predation has been employed, and to link this to higher taxa or guilds of predators rather than specific predatory species. Of course, our chance of recognising damage is greatest where there are still extant taxa and where comparative data are available.

DRILLING PREDATION - The study of drill holes has been the mainstay of palaeontological research on predation. They make up not only the majority of recognised predation traces in the fossil record (over 75% in the analysis in Klompmaker et al., 2019), but have also been the source of most quantitative analyses. There is a strong literature both on criteria needed to recognise such holes over those caused by other biotic (e.g., parasitic or endolithic attack) or abiotic causes and their analyses (see Klompmaker et al., 2019 for an up-to-date review). Much of the attention has been focussed on shelly prey (mostly themselves molluscs) from Cretaceous to Recent which are apparently drilled by predatory gastropods mostly inferred to be the work of two important extant clades, the Naticidae and Muricidae (Carriger, 1981). Naticids and muricids were both diverse and abundant in shallow water communities throughout the Cenozoic and their drill holes are relatively easy to recognise by their morphologies (but see Bromley, 1981). Other extant drilling gastropods, the Cassidae and Eulimidae, are primarily associated with echinoderms and similarly have distinctive drill holes and behaviours which have been well recognised in the fossil record (Petsios et al., 2021).

Drilling predation is, however, not confined to gastropods. In modern oceans octopods are important and sophisticated marine predators (Ambrose, 1986; McQuaid, 1994; Steer & Semmens, 2003; Villanueva et al., 2017). They have a broad repertoire of predatory techniques which either leave no trace (pulling with the arms) or lack distinctive features (biting with the beak), but it has long been known that octopods can drill holes in shelly prey through which to deliver a paralysing toxin (e.g., Pilson & Taylor, 1961; Nixon, 1979; Nixon &

Young, 2003). Recognition of these small, often ragged or oval holes in the fossil record was initially limited, but the first report of them appears to be from the Pliocene of Italy (Robba & Ostinelli, 1975). However, in recognising a specific ichnotaxon *Oichnus ovalis*, Bromley (1993) formalised the distinctness of at least some examples. With this increased awareness, systematic searching has massively increased their known record in both living and fossil molluscan assemblages (Harper, 2002; Todd & Harper, 2010; Klompmaker & Landman, 2021; Gordillo et al., 2022), fossil decapods (Pasini & Garassino, 2012; Klompmaker et al., 2013), barnacles (Klompmaker et al., 2014, 2015) and ostracods (Villegas-Martin et al., 2019). At present most records contain few drill holes, largely based on the novelty of finding fossil octopod holes rather than analyses of behavioural patterns, and most are from relatively young sediments (Pliocene-Recent), though it is not yet clear if this is an artefact of not looking deeper into time. The oldest yet recognised examples are from three bivalve shells from the Late Cretaceous (Campanian) of the USA (Klompmaker & Landman, 2021). There remains the problem that octopod holes may have been mistaken for those made by small muricid gastropods in the past. However, such is the pace of discovery, that we may expect considerable improvement in this coverage and the opportunity to explore the evolution of this highly complex and stereotyped predatory behaviour.

Despite the enthusiasm for drill hole research in the fossil record, several areas are problematic. Of these there are two which are of particular interest: 1) comparative poverty of muricid drill hole data and 2) the identity of earlier Mesozoic (and Palaeozoic) drillers.

Although it is well known that both naticid and muricid gastropods are drilling predators and have been since at least the Middle Cretaceous, the vast majority of quantitative research has been done on naticids, for example on their temporal and spatial distribution (Kelley & Hansen, 2006; Visaggi & Kelley, 2015) and on detailed behavioural predator-prey selection models (Kitchell et al., 1981, 1986; DeAngelis et al., 1985). This is perhaps surprising in that probably the most detailed study of any driller and its behaviour was undertaken on the muricid “oyster drill” *Urosalpinx cinerea* (Say, 1822) (Carriker & Van Zandt, 1972) and classic work on the European dogwhelk *Nucella lapillus* (Linnaeus, 1758) (e.g., Hughes & Dunkin, 1984). The reasons are not clear but several points may be made. One is the general lack of distinctiveness of muricid drill holes which are typically cylindrical and straight-sided, ichnotaxon *Oichnus simplex* Bromley, 1981 (Carriker, 1981). This means that surveys may be compromised by a mixture of genuine muricid holes and those drilled by other taxa (e.g., octopods), but also fail to recognise some modern muricids drill holes which appear countersunk and more similar to those drilled by naticids (e.g., Gordillo & Amunátegui, 1998; Harper et al., 2011). Secondly, many muricids have catholic diets within even a single species utilising a wide range of prey taxa, not all of which have high preservation potentials (e.g., Taylor & Morton, 1996), and may use drilling on only some of their prey (Gordillo & Archuby, 2012); on the other hand naticid taxa tend to have a much narrower prey base, principally of molluscs (Kabat, 1990), meaning that only part of muricid activity is captured

from fossil assemblages. Thirdly, naticids manipulate their prey to a much greater extent than muricids. Since naticids envelope the prey in their foot in order to apply the accessory boring organ (ABO) located in the proboscis, there tends to be a pronounced stereotypy both in drill hole positioning and size selectivity (Carriker, 1981; Kabat, 1990), which is far less apparent in muricids which crawl over the surface of their prey and apply the ABO, located in the foot (Carriker, 1981).

The distinctive form of muricid and naticid drill holes and their occurrence is so widespread in modern seas that it is eminently reasonable to recognise similar holes in the fossil record, particularly where they co-occur with body fossils of these taxa. In an analysis of the stratigraphic occurrence of drill holes throughout the Phanerozoic, Kowalewski et al. (1998) concluded that there were two phases of moderate to high frequency (Cambrian-Carboniferous and Late Cretaceous-Recent) separated by a period of low frequency (Permian-Early Cretaceous). Whilst the final phase can almost certainly be attributed to the muricid and naticid gastropods, it is usually accepted that neither group existed prior to the Early Cretaceous and the best-known earliest examples of drill holes of both taxa remain the Albion Blackdown Greensand of the UK (Taylor et al., 1983). Although the nature of the Palaeozoic drillers is equally unclear, for any discussion of the MMR the culprits for the Permian-Early Cretaceous is of key interest. It is undoubtedly true, fewer holes are reported in this interval and it is relatively easy to dismiss isolated early reports as aberrations (Sohl, 1969, p. 729). However, there have been increasing numbers of reports, fuelled perhaps by increasing awareness (e.g., Fürsich & Jablonski, 1984; Harper et al., 1998; Harper, 2003; Bardhan et al., 2012; Klompmaker et al., 2016; Tackett & Tintori, 2019; Karapınar et al., 2021; Saha et al., 2021). More recent reports are frequently larger samples with evidence of size selectivity and stereotypic drill hole siting (e.g., Karapınar et al., 2021), which demonstrate the experience level of the unknown predator.

The identity of these Mesozoic drillers is a discussion point. The size and general circular appearance of the holes is highly suggestive of gastropods. Most reported Mesozoic drill holes are countersunk, conforming to the ichnogenus *Oichnus paraboloides* described by Bromley (1981), which are usually associated with those made by naticid gastropods. Early studies recognising such holes from the Triassic were interpreted as the result of a “failed experiment” in naticid feeding on the grounds that it was summarised that these holes were produced by co-occurring ampullinids which were then recognised as an early subfamily within the Naticidae (Sohl [1969] used the now synonymised Ampullospiridae) (Sohl, 1969; Fürsich & Jablonski, 1984). However, the naticid status of the ampullinids has been called into question (e.g., Bandel, 1993 who regarded them as neritimorphs) and they are now recognised as members of the caenogastropod superfamily Campaniloidea (Bouchet & Rocroi, 2005). As such, there is no particular reason to implicate ampullinids in drilling pre-Cretaceous holes, and indeed observations on the only extant ampullinid species, *Cernina fluctuata* (G.B. Sowerby I, 1825), by Kase & Ishikawa (2003) revealed that it is an herbivore rather than a predator. Nonetheless, positive recognition of fossil Naticidae is

made difficult by their featureless globular shells, the most definitive characters of which come from the protoconch (Bandel, 1993) and thus easily lost by poor preservation. Recently, Saha et al. (2021) claimed that Upper Jurassic drill holes from Kutch in India co-occur with naticids that had been recognised in these beds by Das et al. (2019). This would indeed be interesting as the first recently claimed Jurassic naticids known, perhaps opening the way for other Jurassic drill holes to be recognised. However, Karapınar et al. (2021) expressed caution noting the unfortunate combination of generally poor preservation and the lack of distinctive shell characters. Karapınar et al. (2021) considered several possible candidates for drill holes which they described in thysirid bivalves from the Early Jurassic of Germany but find no likely candidates, except perhaps the enigmatic neritomorph/caenogastropod *Hayamia reticulata* (Münster in Goldfuss, 1844).

A point which is repeatedly made in the recent literature is that the ability to drill is well known to have arisen multiple times even within the extant gastropods and as drill holes are not uncommon in the Palaeozoic, particularly in brachiopod prey (Kowalewski et al., 1998), there is no reason to believe that extinct taxa might not also have done so (e.g., Fürsich & Jablonski, 1984; Harper et al., 1998; Karapınar et al., 2021), leaving us with the frustrating conclusion that we may never actually know the drillers.

CRUSHING PREDATION - Crushing predators are very widespread and important in modern seas and involve a range of vertebrates (fish, reptiles, birds and mammals) and invertebrates (principally decapod crustaceans but also chelicerates, gastropods and cephalopods) (see Vermeij, 1987). Despite this, and the likelihood of many extinct taxa (e.g., the large marine reptiles, fish and possibly ammonoids) also being important, crushing predation is more difficult than drilling to recognise and to quantify in the fossil record.

Lethal damage is difficult to differentiate from post-mortem damage because of the lack of distinctiveness. Nonetheless some predators do leave recognisable damage, most obviously apertural peeling by crabs on gastropod prey which has been a key target for collecting data on predation frequency (e.g., Vermeij, 1976; Vermeij et al., 1981; Alexander & Dietl, 2003; Dietl & Kosloski, 2013). However, it is worth emphasizing that many crustaceans do not leave such diagnostic damage (Lau, 1987). Basic natural history observations have been made on other groups, for example stingray damage on a spatangoid echinoid (Grun, 2016) and apertural spine insertion damage in bivalves by muricids (Gordillo, 2001), but more similar studies would be most welcome. Although such observations may seem piecemeal, they provide the search image necessary to uncover new data sources in the fossil record.

More opaque, however, are the activities of predators which crush their shelled prey into multiple pieces which may appear very difficult to differentiate from damage caused during transport, particularly on an individual level. This is particularly important, as this seems to introduce a bias against recognising the activities of large, mobile predators (in particular vertebrates). However, a significant paper by Oji et al. (2003) demonstrated that it might be possible to pick up temporal changes in

crushing predation in the fossil record by surveying the proportion of angular fragments in beds. Using tumbling barrel experiments as a proxy for sedimentary transport on mollusc shells they showed that these processes produce abraded debris. These authors then analysed the damage seen in shell debris in shallow-marine beds from the Triassic to the Late Pleistocene of Japan, showing that angular debris was virtually absent during the Mesozoic, but then became widespread; evidence they interpreted as demonstrating the activities of the rapidly diversifying teleost and decapod taxa during the Cenozoic. A similar approach has been used by Salamon et al. (2014), who used an analysis of Palaeozoic (Ordovician-Mississippian) shell debris from 57 European localities to demonstrate an increased in crushing predation following the end Devonian Hangenberg extinction, which they attributed to the radiation of durophagous fish at that time (Sallan et al., 2011).

WHOLE ANIMAL INGESTION - Although it is traditional to bemoan the lack of evidence for predators that primarily engulf their prey, this is not strictly true. “Bromalites”, i.e., coprolites, regurgitates and gut contents, are a potential rich source of data concerning both crushing and wholesale ingestion methods. However, notwithstanding early work by Buckland (1835), these trace fossils have been difficult to work with because of a myriad of problems, such as recognition and attribution (Klompaker et al., 2019); also, their comparatively low preservation potential makes such discoveries useful “snap shots” rather than a source of quantitative data.

The most direct, but rare, evidence come from stomach (gastrolites) or intestine (cololite) contents that occur in situ within the remains of a fossilised organism providing incontrovertible evidence of ingestion by a predator which may itself be identified with high confidence (e.g., echinoid spines and molluscs within Jurassic pycnodont fish in Kriwet, 2001; fish in pterosaurs in Witton, 2018). But even so there may be problems in interpretation (see Witton, 2018), and it is also true that stomach contents do not necessarily reflect the full diet of a predator; the recognisable remains of different prey taxa/parts may have different residence times within the gut. This is beautifully illustrated by experiments to interpret the stomach contents of modern walrus (Sheffield et al., 2001), whereby evidence of much of the prey ingested is “lost” by rapid digestion.

While in situ gut contents can only provide evidence of a last meal, regurgitates and coprolites are rather more widespread being the result of normal body functions although not definitively linked to their producer.

Regurgitates have received renewed interest and are well reviewed by Klug & Vallon (2019), but they require low energy conditions to prevent dispersion (Hoffmann et al., 2020). They essentially also must be noticed at point of collection and are less likely to be spotted in surveys of museum collections of material collected for other purposes. However, despite the difficulties of identifying the detailed taxonomy of their producers, they provide good definitive proof of ingestion and processing of well constrained prey by certain predatory guilds, in particular large vertebrate groups for which the feeding and dietary evidence is surprisingly rare. For example, a Middle Jurassic site in Poland has yielded regurgitates

(presumably of fish) containing molluscs and echinoderms (Zatoń et al., 2007; Borszcz & Zatoń, 2013) and indeed, as noted by Borszcz & Zatoń (2013) the oldest yet known evidence of predation on echinoid prey. Another recent work has recognised Late Devonian regurgitates, attributed to gnathostome fish, containing ammonoid shells (Klug & Vallon, 2019).

Coprolites may be more recognisable and possibly more taphonomically robust, but as ever it may be difficult to recognise the producer. Most of the published instances concern coprolites produced by vertebrates but a significant paper by Knaust (2020) revealed the wealth of invertebrate coprolites that might be recognised; for example, the very architecture of microcoprolites associated with galaethid crabs suggests that these might have been active predators back to the Oxfordian (Senowbari-Daryan et al., 2007).

GEOGRAPHIC PATTERNS

One of the most widely touted paradigms associated with global patterns of biotic interactions in modern seas is that concerning latitudinal patterns, in particular the presumption that these are strongest at lower latitudes, though universality of this has not been demonstrated (Kelley & Hansen, 2007; Schemske et al., 2009; Freestone & Osman, 2010; Freestone et al., 2011). There are difficulties in gaining adequate and comparable data from all latitudes and environments. For example, most marine organisms live at depths beyond easy access for direct observation, hence the preponderance of studies on organisms from the intertidal zone or coral reefs (Estes & Peterson, 2000). But even in these “easy” environments there may be problems achieving a good geographic coverage, for example Thyrring & Peck (2021) pointed out that most intertidal studies are from the mid latitudes. These problems are also compounded by the need to recognise regional differences, such as differences between ocean basins as highlighted by Vermeij (1976), who showed that gastropod defences are better developed in the Pacific and Indian Oceans than those of the Atlantic.

To chart the existence and evolution of global patterns in the fossil record requires sufficient geographic distribution of data from each of the time frames involved. If such patterns are difficult to establish in the Recent then the problems are many times magnified for the fossil record. The problems split into two types: 1) lack of accessible exposure of a particular age in the required region and 2) lack of research to date. The first problem is insurmountable and real. For example, the past distribution of the continents and ages of rocks exposed now are such that it is actually very difficult to collect low latitude shallow water data for much of the Mesozoic, for example the Cretaceous of the South and Central American region (Rojas & Sandy, 2019). The second problem is centred on the fact that the geographic coverage of palaeo-predation studies has historically been biased towards localities in Western Europe and North America (Harper, 2016; Klompmaker et al., 2019). This is rectifiable and there have been significant avenues made into developing data from other geographic regions in the last 20 years, though clearly there is a long way to go. Most successful

have been a series of data-rich studies from India which have completely transformed our knowledge in that region, largely by collecting data on drilling predation on molluscan prey, from the Jurassic to the Recent, including highly interesting studies specifically considering the impact of the K-Pg mass extinction (e.g., Bardhan et al., 2012, 2014; Chattopadhyay & Dutta, 2013; Mallick et al., 2013, 2014, 2017; Das et al., 2019; Goswami et al., 2020; Mondal et al., 2021; Saha et al., 2021).

Similar focus has been directed towards the higher latitudes of the Southern Hemisphere with research around Antarctica (Jonkers, 2000; Aronson & Blake, 2001; Aronson et al., 2009; Brezina et al., 2016; Dietl et al., 2018; Harper et al., 2018, 2019b), the Magellanic region (Gordillo & Archuby, 2012; Gordillo, 2013; Martinelli et al., 2013) and New Zealand (Jonkers, 2000; Hiller, 2014). Compared to the attention given to sites in the Southern Hemisphere, there is less research in comparable high latitudes in the Northern Hemisphere although Neely et al. (2021) is a welcome addition for the Pliocene-Pleistocene of Iceland. However, it should also be noted that there are also fewer comparative neontological data and Aristov & Varfolomeeva (2019) suggested that Arctic predation patterns are probably underestimated.

The palaeotropics are surprisingly poorly surveyed. Given the extraordinarily high biodiversity of the modern Indo-Pacific shallow water fauna (Bouchet et al., 2002; Sanciango et al., 2013), it is particularly vexing that there is a near total absence of data here, despite evident exposure of Cenozoic and Mesozoic strata (see Peters et al., 2005, fig. 3).

Without good data from the high and low latitudes, and across a range of time slices, it is impossible to contribute to any discussion of the evolution of latitudinal trends in predation pressure.

ENVIRONMENT OR HABITAT SPECIFIC DATA

The seafloor is very patchy and there are, of course, marked gradients such as depth and temperature; moreover, there are different types of communities, for example those that dwell on hard or soft substrates, and those that live at different depths within the water column. Although there may be some overlap between these different ecospace, there is a pressing need also to explore biotic interactions from different environments and habitats. Indeed, Klompmaker et al. (2019, p. 473) criticised that “relatively little attention has been paid to environmental gradients in predation in deep time”.

Intertidal zone

A disproportionate amount of data that we have for modern marine biotic interactions come from the intertidal zone; including some of the classic work on predator-prey interactions (Paine, 1974). This is, of course, perfectly understandable given the ease of accessibility and familiarity of the taxa involved, though even here the coverage is biased towards the activities of slow-moving predators which are active over multiple tidal cycles and tends to exclude fish and birds. Yet the intertidal may itself be an important refuge and it would be interesting to chart the evolution of its fauna (Harper & Skelton, 1993). But

the narrow, ephemeral intertidal zone is extremely rarely preserved in the rock record let alone allowing study of predator-prey interactions. However, some data exist, most famously from the Cretaceous Ivö Klack fauna (Campanian) of southern Sweden where there is evidence of both sponge predation (Bromley, 1970) and drilling in brachiopods (Schroeder et al., 2018).

Deep water

There is a prevailing theme that over time, and particular during the MMR, “primitive” taxa have moved progressively offshore, coupled with the idea of the deeper sea being a refuge from biotic interactions (Jablonski et al., 1983; Vermeij, 1987; Jablonski, 2005, 2008; Klompmaker et al., 2019); this has been invoked for different taxa, e.g., stalked crinoids (e.g., Meyer & Macurda, 1977; Oji, 1996; Aronson & Blake, 2001). The fact remains, however, that predation levels in deeper waters are little understood both in modern and ancient settings. For the Recent, data are much more difficult to acquire in deeper water beyond the reach of SCUBA diving; direct observation is limited to those made from deep submersibles and remotely operated vehicles. One way around this is to use a “palaeontological” approach by using recognisable damage (both fatal and repaired) on shell material collected either dead or alive in trawl or grab samples. Using this method Harper & Peck (2016) analysed shell repair in 112 bulk samples of modern rhynchonelliform brachiopods collected from a wide range of depths (0 to 4,000 m) from all latitudes. They showed a strong inverse relationship between crushing predation pressure and increasing depth, with most shell repair recorded from water depths of less than 200 m, and very little from either continental shelf or deep-sea habitat. Similar higher repair frequencies in shallower water have also been uncovered in more regional studies using death assemblages (Kropp, 1992) or tethered shell experiments (Walker et al., 2002). However, a study of large deeper water gastropods of the genus *Gaza* from a range of bathyal sites around North, South and Central America showed surprisingly very high repair frequencies (Walker & Voight, 1994) demonstrating our failure to understand the variability which occurs in the very large and massively under-sampled habitat.

Many of the difficulties of sampling modern deep-sea faunas are alleviated in the palaeontological record where faunas are conveniently exposed on land (Walker & Voight, 1994), but, as they remarked, collection of predation data from fossils from deeper water lithologies has been generally overlooked and there is little sign that this has been rectified in the intervening period. An important exception is Walker (2001), who recorded relatively high rates of both repaired damage and drilling predation in a wide range of gastropod prey taxa from Pliocene turbidite slope deposits from Ecuador, again underlining that there have perhaps been higher levels of predation in such settings than has generally been appreciated.

Vent and hydrocarbon seep sites

Despite the general suggestion that deep sea communities show low levels of predation, the situations at vents or seeps appear to be rather different. In contrast

to the vast tracts of abyssal plains, vent and seep sites have received relatively more attention. These sites often host very specialised thriving communities of organisms (see Kiel, 2010) with complex trophic relationships from producers (in association with bacterial symbionts), grazers, suspension feeders, predators, scavengers, and parasites. A variety of vent “mussels”, siboglinid tubeworms, gastropods and ghost shrimps (see Voight, 2000a) are prey items to a whole host of predatory taxa, including zoarcid fish (Sancho et al., 2005), crabs of various families (e.g., Bythograeidae, Galatheidae) (Martin & Haney, 2005; Dittel et al., 2008), octopods (Voight, 2000b) and various gastropods (e.g., buccinids, turrids) (Warén & Bouchet, 1993). Long term field-based experiments, which have excluded large predatory fish and molluscs, have shown that biological interactions (both predation and disturbance) exert a strong control of benthic community structure on the East Pacific Rise (Micheli et al., 2002). Direct observations are clearly limited and even the creative use of isotopes can be confusing (Voight, 2000a), so, again, the most data-rich studies involve the collection of repair scar frequencies. For example, Rhoads et al. (1982) described damage on the 24% of 139 sampled shells of *Bathymodiolus thermophilus* Kenk & B.R. Wilson, 1985 on the Galapagos Rift which they attributed to the crab *Bythograea thermydron* Williams, 1980 and indicated that this mussel reached a size refuge after which it was immune to such attacks. Voight & Sigwart (2007) studied the shells of the vent limpet *Lepetodrilus fucensis* J.H. McLean, 1988 from three sites on the Juan de Fuca Ridge noting higher levels of repair from sites with more predators and linking damage specifically to the buccinid gastropod *Buccinum thermophilum* Harasewych & Kantor, 2002.

There have been interesting discussions as to whether vent and seep communities might be seen as refuges from high levels of predation, perhaps in part defended by the peculiarly toxic nature of their environment, or whether they are oases of opportunity (Sandy, 2010). The foundations of modern vent fauna, as determined by molecular genetics, appear to have Mesozoic roots, with the Cretaceous particularly implicated (see review in Kaim et al., 2021). However, there are very few fossil vents recognised and their preservation is usually poor (Little et al., 1998; Kaim et al., 2021), so the recognition of biotic interactions would be difficult. The specialised faunas associated with hydrocarbon seeps, by contrast, have been recognised throughout the last 420 million years and have been well studied in the fossil record. Although brachiopods are infrequent at modern seeps, there has been a particular interest in the large “dimerelloid” brachiopods which dominate many seep deposits from the Devonian to Cretaceous (Campbell, 2006; Sandy, 2010) and these brachiopods show frequent repaired shell damage over this entire period (e.g., Biernat, 1957; Baliński & Biernat, 2003; Sandy, 2010). Indeed, Sandy (2010) estimated that 10% of *Sulcirostra* from a Jurassic seep in Oregon (USA) showed repaired damage, which he contended was higher than the general “non-seep” brachiopods. Likely culprits were cephalopod or crustacean predators, with Sandy favouring galatheid crabs, which are important predators at modern vents and seeps, and encouraging further investigation into the distribution of their microcoprolites (Senowbari-Daryan et al., 2007).

Repaired damage to fossil bivalves at seeps has less frequently been investigated. However, Kiel et al. (2016) described such damage (and drill holes) in three taxa from Oligocene seeps in Japan and attempted to use differential rates between the taxa to infer sulphide tolerances of the prey, suggesting that those with fewer repairs may inhabit more sulphide rich habitats which are less attractive to visit from potential predators.

Although drill holes in fossil seep brachiopods have not yet been recorded, there are a number of records from Cenozoic bivalves from Eocene to Miocene chemosymbiotic communities associated with cold seeps and whale falls from Japan (Amano, 2003; Amano & Jenkins, 2007; Amano & Kiel, 2007 a, b; Kiel et al., 2016). These drill holes resemble those made by naticid gastropods. However, the recent recognition of the oldest known drill holes at seeps, in lucinid bivalves from cold methane seeps in the Western Interior Seaway (USA) during the Late Cretaceous (Campanian), are attributed to octopus rather than gastropods (Klompaker & Landman, 2021), opening up the possibility of finding similar holes at other seep sites.

Freshwater systems

Although research on the MMR has been understandably focussed on marine organisms, their freshwater counterparts have also come under some scrutiny. There are fewer durophagous predators in freshwater relative to the sea; entire major durophage groups are totally absent (e.g., asteroids) and others, for example fish and crustaceans, although very active, have rather lower diversity. An important near absence is the Neogastropoda, which have been hugely important marine predators since the Early Cretaceous (Taylor et al., 1980), though the buccinids (themselves an important marine predatory group; e.g., Yamakami & Wada, 2021) are represented in freshwater by the Assassin snails (Strong et al., 2017). The total absence of the neogastropod Muricidae (along with the littorinomorph Naticidae) means that there are no predatory drill holes to be recognised, robbing us of a valuable source of data.

There are, nonetheless, a range of durophagous predators which are known to attack molluscan prey and so may be potential sources of data (both Recent and fossil). They include most obviously aquatic taxa, such as a multitude of vertebrates, notably fish but also waterbirds (Leeuw, 1999), turtles, otters and muskrats (Zahner-Meike & Hanson, 2001), and crustaceans, such as crayfish and crabs (Covich et al., 1981; Czarnoleski et al., 2011), but also land-based predators such as rats (Gordon et al., 2016). Nearly all Recent studies have focussed on gastropod prey (e.g., Vermeij & Covich, 1978; West & Cohen, 1994; DeWitt et al., 2000). Some Recent freshwater gastropods show morphological defences such as shell thickening, enhanced ornamentation, narrowing apertures of the types seen in marine taxa (Vermeij & Covich, 1978; Vermeij, 2015; Davis et al., 2020). However, in general, freshwater gastropods show disproportionate numbers of “weaker” shelled forms (planispiral and open coiling) (Vermeij & Covich, 1978; Vermeij, 2015). Putative defences in freshwater bivalves have not been explored in detail. Aside from their evident thick shells in some taxa, there is little ornamentation

though in a few taxa, such as *Etheria* hollow spines may develop (see Yonge, 1962).

In systems where shell thickening and spinosity in gastropods have been detected, suggestions have been made of co-evolution (that is the reciprocal evolution of prey and predators, as opposed the top-down processes described by escalation) between the prey and both fish and crustacean predators, for example Lake Tanganyika (West & Cohen, 1994), Lakes Poso and Malili in Sulawesi (von Rintelen et al., 2004) and Lake Ohrid in the Balkans (Albrecht & Wilke, 2008). Similarly, Stelbrink et al. (2020) found that viviparid snails with thick shells and coarse ornamentation are almost exclusively found in lentic environments, predominantly from a Bellamyinae clade inhabiting ancient lakes in South Asia (e.g., Yunnan, Myanmar, Indonesia Philippines) and not in lotic habitats. It has been noted that these lake systems have two notable features: 1) they are “ancient” permanent lake systems and 2) they are relatively warm water settings; by contrast snails living in Lake Baikal, a very ancient but cold-water lake, are lacking in such defences. Freshwaters are typically more undersaturated with respect to calcium carbonate than most marine waters. Although the carbonate chemistry of freshwater is hugely variable and complex (Kelts & Hsü, 1978), the solubility of aragonite (from which all freshwater mollusc shells are composed) is inversely proportional to temperature. Adaptations that require heavy shell investment are likely to be more energetically costly “solutions” than in marine waters. An interesting question, surrounding the apparent poor development of shell adaptations in freshwater gastropods, therefore, might be whether other “cheaper” strategies such a defensive behaviour might be favoured. Covich (2010) reviewed a range of behavioural responses by thin shelled gastropods to their predators, including active burrowing and shaking, along with more responses such as suddenly dropping off the substrate, while Czarnoleski et al. (2011) described different behavioural responses of zebra mussels to fish and crayfish predators.

Most studies of defensive attributes in freshwater molluscs result from limited ecological and aquarium studies (Weigand et al., 2014; Davis et al., 2020) and there appear to be few systematic baseline studies for predation damage and repair in various modern freshwater taxa or habitats. This is, perhaps, less of a surprise for bivalves, given the fact that drilling predators are yet unknown from their habitats and their poor ability to repair non-lethal crushing damage (Vermeij, 1983), although their fragments have been recorded from rat middens (Gordon et al., 2016). But the lack of quantitative investigations in gastropods, where repair is more easily measured, is striking. Nonetheless, a recent study by Cadée (2015) documented the occurrence of repaired apertural breakage (15.5% of a sample of 400 adults) in the modern freshwater gastropod *Bithynia tentaculata* (Linnaeus, 1758) from a death assemblage from The Netherlands. Cadée tentatively ascribed this damage to failed fish predation by Roach (*Rutilus rutilus* [Linnaeus, 1758]). There is a clear need for other similar studies from different parts of the world and different freshwater ecosystems to establish useful comparative modern and fossil data.

Molluscs have existed in freshwater settings since at least in the Devonian (Gray, 1988). The fossil record is

harder to interrogate than for marine faunas; taphonomic problems abound (Gray, 1988), a major problem being rapid dissolution of carbonate shells which may differentially affect different taxa in an assemblage (e.g., Kotzian & Simões, 2006; Cristini & Francesco, 2019). At present the records of predation of fossil freshwater molluscs are very sparse with putative bitemarks recognised by Kear & Godthelp (2008) and Gorzelak et al. (2010) and shell fragments preserved in coprolites (Yates et al., 2012). A notable study by Rasser & Covich (2014) documented the occurrence of perforations in planorbis and hydrobiid gastropod shells from a Miocene lake deposit in SW Germany. Although the definitive culprit was unknown, the lack of known drillers, the lack of co-occurring crustaceans, together with the match between the size of the holes with the dimensions of pharyngeal teeth of fish, implicate the latter. It seems highly likely that the comment by Rasser & Covich (2014, p. 531) that “Researchers in palaeolimnology may have overlooked the scars and holes in their shell samples previously” is correct and that studies deliberately focussed on search for predation damage in palaeontological material would be highly desirable.

LOOKING BACKWARDS TO THE PALAEOZOIC

Although the ideas of marine revolutions driven by biotic interactions were initially centred on the Mesozoic, quite rapidly a similar precursor was identified during the middle Palaeozoic (Signor & Brett, 1984; Brett & Walker, 2002). Damage and other evidence of predation have now been confidently reported from earlier in the Palaeozoic, see Bicknell & Paterson (2018) for a review of Cambrian evidence and Alexander (1986a), Lindström & Peel (2005) and Ebbestad et al. (2009) for other lower Palaeozoic examples. The rapid radiation in the Middle Devonian of durophages, principally various gnathostome fish, but potentially also nautiloids, goniatites and phyllocarids, has been linked to various forms of damage in shelly invertebrates after that time (e.g., Alexander, 1981, 1986b; Nagel-Myers et al., 2009). Along with drill holes in echinoderms and brachiopods, perhaps linked to platyceratid gastropods (e.g., Baumiller, 1990, 1996; Baumiller et al., 1999), this suggests an increase in predation pressure at that time. These observations have been linked with changes in prey morphology, which may be interpreted as defensive (e.g., increase in spinosity in brachiopods and crinoids), or the ability for regeneration (Signor & Brett, 1984; Brett & Walker, 2002; Brett, 2003; Thomka & Eddy, 2018).

Although the end Permian mass extinction wiped out many predatory taxa and reset the composition of benthic communities of potential prey (Gould & Calloway, 1980) and the Triassic is seen as a period of generally low predation intensity (Kowalewski et al., 1998; Tackett & Tintori, 2019), the Palaeozoic and Mesozoic should not be seen as two hermetically sealed eras. In fact, it is striking that there are very few papers recording Permian predation (Kowalewski et al. [2000] and Hoffmeister et al. [2004] are notable exceptions) and records throughout the Triassic and Jurassic continue to be sparse. It is as yet unclear if this is a genuine gap, a lack of concerted research

effort, a taphonomic problem or a failure of recognition of damage. Most of the important modern predatory groups whose activities we recognise in the fossil record have later Mesozoic origins but there may have been extinct predators which were active at that time.

ENERGY BUDGETS: THE COST OF DEFENCE

From the outset, studies of the evolutionary responses to increased predation pressure have focussed on successful adaptations being metabolically expensive. These might include increasing armour by growing thicker or more ornamented shells, employing active escape responses such as swimming or leaping, or manufacturing toxins. This may explain why some low metabolic rate taxa fare badly and move into refugia where resources are few (e.g., Stanley, 1977; Vermeij, 1977, 1987). Vermeij (1977, 1998) linked the onset of the MMR with major events of submarine volcanism, starting with the breakup of Pangea, causing conditions which favoured diversification and enhanced productivity by causing global warming, increased sea level, expanding the areas of shallow shelf sea and injecting nutrients into the biosphere. Vermeij (1998) argued that this extrinsic tectonic control was amplified by positive feedbacks as increasingly metabolically demanding life-styles took off. These are very interesting ideas. Although metabolic rate is difficult to assess for extinct organisms, there have been interesting contributions using organism size as a proxy, for example Payne et al. (2014) and Strotz et al. (2018), or growth rate established by sclerochronology (Dietl et al., 2002). Payne et al. (2014) determined that the metabolic activities of marine bivalves have increased by up to two magnitudes over the last 465 Ma and that one possible explanation is the exploitation of new food sources. The idea that food available for benthic suspension feeders increased during the Mesozoic, with the rise of major phytoplankton groups (e.g., mixotrophic dinoflagellates, diatoms and coccoliths), has been explored by Martin & Quigg (2012), Knoll & Follows (2016), Wiggan et al. (2018) and Fantasia et al. (2022). It opens the way for interesting discussions as to the effect this increase in nutrients and the link with tectonic events may have in particular regions at different times during the course of the MMR. For example, Crame (2018) identified one of the repercussions of the final separation of South America from Antarctica (Maldonado et al., 2014) was the strengthening of the Antarctic Circumpolar Current system which enhanced upwelling and nutrient upwelling which has in turn been linked to a diversification of phytoplankton within the last 15 Ma (Lazarus et al., 2014). He went on to note that this, not only increased the amount of organic material arriving for benthic organisms, but also temporally corresponds with the major radiations of large vertebrate whale, fish and seal predators.

FINAL THOUGHTS

The recognition that something changed to increase the intensity of biotic interactions starting during the Mesozoic and that this might have some large part to

play in the shaping of modern marine communities was itself a polyphyletic event (Stanley, 1968, 1974, 1977; Kier, 1974; Vermeij, 1975, 1976; Meyer & Macurda, 1977), was brought sharply into focus by Vermeij (1977, 1987). The resulting recognition of a Mesozoic Marine Revolution has been the catalyst for an enormous amount of scientific data gathering and debate. Although much has been achieved, the sheer enormity of the task of documenting appropriate data and seeking to unravel the course and impact of change over the 250 million years leaves us with much to do. To test whether the MMR has been a major impact in the evolution of life we need gain a firm understanding of the phenomenon on a range of temporal and spatial scales (Harper, 2016). If we were designing this as an experiment, we would want well-distributed, dense data-rich sampling of a wide range of interacting taxa, from all environments and over the full 250 Ma period. However, the vagaries of taphonomy and the limited geological control of available outcrops and exposures rob us of this opportunity.

The MMR is emphatically not a uniform or single process. We must expect complex patterns with the emergence of different predators or predatory methods becoming important in different ecosystems and prey taxa at different times. We must anticipate a cascade of events, which will again happen at different rates and ways across ecosystems and regions. We must also not forget the other biotic interactions, which are usually less easy to observe and quantify in fossil record. Although there is a general impression that predation is the key interaction (Stanley, 2008), there is little to indicate that this is universal and again there is a pressing need to be able to develop methods of gaining a better understanding of competition and the impact of grazing and bioturbation amongst particular taxa or in specific environments.

Our data will probably always be dominated by certain taxa, most obviously molluscs, but also brachiopods and echinoderms. Even so there is much we must still determine. Although for these taxa and their predators there is a wealth of published data and a strong mature understanding of analytical methodologies, there is more yet to be done. It is well known that there is huge variation in predation metrics across even small spatial scales; Cadée et al. (1997, p. 76) remarked “The fact remains that there is as much variation in repair frequency among species and microhabitats at one time (the Recent) in the geological record as there is throughout the record”. There is a particular problem for palaeontological studies: where there are sites or prey taxa with no or little predation data despite good sampling numbers, these data almost never get published (unless part of a much broader study which does include notable intensities) and so the full range of variability of predation is never reported (Harper, 2016). This should spur palaeontologists to collect more samples and data and to resist the temptation to publish ideas on large scale trends or processes from few sampling sites or time intervals.

The study of well-known prey taxa tells us only part of the story. Since 2000 there has been a steady increase in interest in other taxa, of habitats other than the shallow shelf sea, and most importantly from regions other than Western Europe and North America. These contributions are enormously welcome. Although it is a relatively

straightforward task to collect more data on well-known predator-prey systems in new geographic regions or different environments, establishing new methodologies and analytical methods for little studied prey taxa takes more effort and time to mature.

In short, there is much yet to do.

ACKNOWLEDGEMENTS

I am grateful to Gaia Crippa for inviting this contribution and Patricia Kelley for a generous and constructive review.

REFERENCES

- Aberhan M., Kiessling W. & Fürsich F.T. (2006). Testing the role of biological interactions in the evolution of Mid-Mesozoic marine benthic ecosystems. *Paleobiology*, 32: 259-277.
- Albrecht C. & Wilke T. (2008). Ancient Lake Ohrid: biodiversity and evolution. *Hydrobiologia*, 615: 103-140.
- Alexander R.R. (1981). Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulate. *Journal of Paleobiology*, 55: 192-203.
- Alexander R.R. (1986a). Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods. *Journal of Paleobiology*, 60: 273-285.
- Alexander R.R. (1986b). Frequency of sublethal shell-breakage in articulate brachiopod assemblages through geologic time. *Biostratigraphie Paléozoïque*, 4: 150-166.
- Alexander R.R. & Dietl G.P. (2003). The fossil record of shell-breaking predation on marine bivalves and gastropods. *Topics in Geobiology*, 20: 141-176.
- Amano K. (2003). Predatory gastropod drill holes in Upper Miocene cold-seep bivalves, Hokkaido, Japan. *Veliger*, 46: 90-96.
- Amano K. & Jenkins R.G. (2007). Eocene drill holes in cold-seep bivalves of Hokkaido, northern Japan. *Marine Ecology*, 28: 108-114.
- Amano K. & Kiel S. (2007a). Drill holes in bathymodiolin mussels from a Miocene whale-fall community in Hokkaido, Japan. *Veliger*, 49: 265-269.
- Amano K. & Kiel S. (2007b). Fossil vesicomyid bivalves from the North Pacific Region. *Veliger*, 49: 270-293.
- Ambrose R.F. (1986). Effects of octopus predation on motile invertebrates in a rocky subtidal community. *Marine Ecology Progress Series*, 30: 261-273.
- Andrew C., Howe P. & Paul C. (2015). Fatally bitten ammonites from septarian concretions of the ‘Marston Marble’ (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy. *Proceedings of the Geological Association*, 126: 119-129.
- Andrew C., Howe P., Paul C.R.C. & Donovan S.K. (2010). Fatally bitten ammonites from the lower Lias Group (Lower Jurassic) of Lyme Regis, Dorset. *Proceedings of the Yorkshire Geological Society*, 58: 81-94.
- Aristov D. & Varfolomeeva M. (2019). Moon snails *Amauropsis islandica* can shape the population of Baltic clams *Limecola balthica* by size-selective predation in the high-latitude White Sea. *Polar Biology*, 42: 2227-2236.
- Aronson R.B. & Blake D.B. (2001). Global climate change and the origin of modern benthic communities in Antarctica. *American Zoologist*, 41: 27-39.
- Aronson R.B., Moody R.M., Ivany L.C., Blake D.B., Werner J.E & Glass A. (2009). Climate change and trophic response of the Antarctic bottom fauna. *PLoS One*, 4: e4385.
- Baliński A. & Biernat G. (2003). New observations on rhynchonelloid brachiopod *Dzieduszyckia* from the Famennian of Morocco. *Acta Palaeontologica Polonica*, 48: 463-474.
- Bandel K. (1993). Caenogastropoda during Mesozoic times. *Scripta Geologica*, Special Issue, 2: 7-56.

- Bardhan S., Chattopadhyay D., Mondal S., Das S., Mallick S., Chanda P. & Roy A. (2012). Record of intense predatory drilling from Upper Jurassic fauna of Kutch, India: Implications for the history of biotic interaction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 317-318: 153-161.
- Bardhan S., Mallick S. & Das S. (2014). Palaeobiogeographic constraints on drilling gastropod predation: a case study from the Miocene Khari Nadi Formation in Kutch, Gujarat. *Special Publication of the Palaeontological Society of India*, 5: 205-213.
- Barnes D.K.A. & Conlan K.E. (2007). Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society of London B*, 362: 11-38.
- Baumiller T.K. (1990). Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. *Palaeontology*, 33: 743-748.
- Baumiller T.K. (1996). Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 123: 343-351.
- Baumiller T.K. & Bitner M.A. (2004). A case of intense predatory drilling of brachiopods from the Middle Miocene of southeastern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 214: 85-96.
- Baumiller T.K., Bitner M.A. & Emig C.C. (2006). High frequency of drill holes on brachiopods from the Pliocene of Algeria and its ecological implications. *Lethaia*, 39: 313-320.
- Baumiller T.K. & Gahn F.J. (2003). Predation on crinoids. *Topics in Geobiology*, 20: 263-278.
- Baumiller T.K., Leighton L.R. & Thompson T.R. (1999). Boreholes in Mississippian spiriferide brachiopods and their implications for Paleozoic gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 147: 283-289.
- Baumiller T.K., Mooi R. & Messing C.G. (2008). Urchins in the meadow: paleobiological and evolutionary implications of cidaroid predation on crinoids. *Paleobiology*, 34: 22-34.
- Baumiller T.K., Salamon M., Gorzelak P., Mooi R., Messing C.G. & Gahn F.J. (2010). Benthic predation drove early Mesozoic crinoid radiation. *PNAS*, 107: 5893-5896.
- Berning B. (2008). Evidence for sublethal predation and regeneration among living and fossil ascophoran bryozoans. *Virginia Museum of Natural History Special Publication*, 15: 1-5.
- Bicknell R.D.C. & Paterson J.R. (2018). Reappraising the early evidence of durophagy and drilling predation in the fossil record: implications for escalation and the Cambrian Explosion. *Biological Reviews*, 93: 754-784.
- Biernat G. (1957). On *Peregrinella multicastrata* (Lamarck) (Brachiopoda). *Acta Palaeontologica Polonica*, 2: 19-50.
- Blake D.B. & Guensburg T.E. (1990). Predatory asteroids and the fate of brachiopods – a comment. *Lethaia*, 23: 429-430.
- Borszcz T. & Zatoń M. (2013). The oldest record of predation on echinoids: evidence from the Middle Jurassic of Poland. *Lethaia*, 46: 141-145.
- Bouchet P., Louzouet P., Maestrati P. & Heros V. (2002). Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, 75: 421-436.
- Bouchet P. & Rocroi J.-P. (2005). Classification and nomenclature of gastropod families. *Malacologia*, 47: 1-397.
- Brett C.E. (2003). Durophagous predation in Paleozoic marine benthic assemblages. *Topics in Geobiology*, 20: 401-432.
- Brett C.E. & Walker S.E. (2002). Predators and Predation in Paleozoic Marine Environments. *Paleontological Society Papers*, 8: 93-118.
- Brezina S.S., Cech N., Martin Serralta D. & Casadio S. (2016). Cannibalism in Naticidae from the La Meseta Formation (Eocene, Antarctica). *Antarctic Science*, 28: 205-215.
- Bromley R.G. (1970). Predation and symbiosis in some Upper Cretaceous clonid sponges. *Bulletin of the Geological Society of Denmark*, 19: 398-405.
- Bromley R.G. (1981). Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geologica Hispanica*, 16: 55-64.
- Bromley R.G. (1993). Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. *Bulletin of the Geological Society of Denmark*, 40: 167-173.
- Brunton C.H.C. (1966). Predation and shell damage in a Viséan brachiopod fauna. *Palaeontology*, 9: 355-359.
- Buatois L.A., Carmona N.B., Curran H.A., Netto R.G., Mángano M.G. & Wetzel A. (2016). The Mesozoic Marine Revolution. *Topics in Geobiology*, 40: 19-134.
- Buckland W. (1835). On the discovery of coprolites, or fossil feces, in the Lias of Lyme Regis, and in other Formations. *Transactions of the Geological Society of London*, 3: 223-236.
- Cadée G.C. (2015). Shell repair in the freshwater gastropod *Bithynia tentaculata* (Linnaeus, 1758). *Vita Malacologica*, 13: 31-34.
- Cadée G.C., Walker S.E. & Flessa K.W. (1997). Gastropod shell repair in the intertidal of Bahia la Choya (N. Gulf of California). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 136: 67-78.
- Campbell K.A. (2006). Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past developments and future research directions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232: 362-407.
- Carriker M.R. (1981). Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, 20: 403-422.
- Carriker M.R. & Van Zandt D. (1972). Predatory behaviour of a shell-boring muricid gastropod. *Behaviour of Marine Animals Current Perspectives in Research*, 1: 157-244.
- Chalcraft D.R. & Reseratis W.J. Jr (2003). Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology*, 84: 2407-2418.
- Chattopadhyay D. & Dutta S. (2013). Prey selection by drilling predators: a case study from Miocene of Kutch, India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 374: 187-196.
- Clarke A. & Johnston N.M. (2003). Antarctic marine benthic diversity. *Oceanography and Marine Biology: An Annual Review*, 41: 47-114.
- Covich A.P. (2010). Winning the biodiversity arms race among freshwater gastropods: competition and coexistence through shell variability and predator avoidance. *Hydrobiologia*, 653: 191-215.
- Covich A.P., Dye L.L. & Mattice J.S. (1981). Crayfish predation on *Corbicula* under laboratory conditions. *American Midland Naturalist*, 105: 181-188.
- Crame J.A. (2018). Key stages in the evolution of the Antarctic marine fauna. *Journal of Biogeography*, 45: 986-994.
- Cristini P.A. & Francesco C.G.D. (2019). Taphonomic field experiment in a freshwater shallow lake: alteration of gastropod shells below the sediment–water interface. *Journal of Molluscan Studies*, 85: 403-412.
- Culver S.J. & Lipps J.H. (2003). Predation on and by Foraminifera. *Topics in Geobiology*, 20: 7-32.
- Czarnoleski M., Müller T., Kierat J., Gryczkowski L. & Chybowski Ł. (2011). Anchor down or hunker down: an experimental study on zebra mussels' response to predation risk from crayfish. *Animal Behaviour*, 82: 543-548.
- Das S.S., Mondal S., Saha S., Bardhan S. & Saha R. (2019). Family Naticidae (Gastropoda) from the Upper Jurassic of Kutch, India and a critical reappraisal of taxonomy and time of origination of the family. *Journal of Paleontology*, 93: 673-684.
- Davis A.R., Rees M.R., Rashni B. & Haynes A. (2020). Are spine-bearing freshwater gastropods better defended? *Ecologies*, 1: 3-13.
- De Angelis D.L., Kitchell J.A. & Post W.M. (1985). The influence of naticid predation on evolutionary strategies of bivalve prey: conclusion from a model. *The American Naturalist*, 126: 817-842.

- DeWitt T.J., Robinson B.W. & Wilson D.S. (2000). Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evolutionary Ecology Research*, 2: 129-148.
- Dietl G.P. (2003). The escalation hypothesis: one long argument. *PALAIOS*, 18: 83-86.
- Dietl G.P., Kelley P.H., Barrick R. & Showers W. (2002). Escalation and extinction selectivity: morphology versus isotopic reconstruction of bivalve metabolism. *Evolution*, 56: 284-291.
- Dietl G.P. & Kosloski M.E. (2013). On the measurement of repair frequency: how important is data standardization. *PALAIOS*, 28: 394-402.
- Dietl G.P., Nagel-Myers J. & Aronson R.B. (2018). Indirect effects of climate change altered the cannibalistic behaviour of shell-drilling gastropods in Antarctica during the Eocene. *Royal Society Open Science*, 5: 181446.
- Dietl G.P. & Vermeij G.J. (2006). Comment on "Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates". *Science*, 314: 925.
- Dittl A.I., Perovich G. & Epifanio C.E. (2008). Biology of the vent crab *Bythograea thermydion*: a brief review. *Journal of Shellfish Research*, 27: 63-77.
- Donovan S.K. & Gale A.S. (1990). Predatory asteroids and the decline of the articulate brachiopods. *Lethaia*, 23: 77-86.
- Donovan S.K. & Novak V. (2015). Site selectivity of predatory borings in Late Pliocene balanid barnacles from south-east Spain. *Lethaia*, 48: 1-3.
- Ebbestad J.O.R., Lindström A. & Peel J.S. (2009). Predation on bellerophonitiform molluscs in the Palaeozoic. *Lethaia*, 42: 469-485.
- Estes J.A. & Peterson C.H. (2000). Marine ecological research in seashore and seafloor systems: accomplishments and future directions. *Marine Ecology Progress Series*, 195: 281-289.
- Fantasia A., Ferreira J., Thibault N., Krenker F.-N. & Bodin S. (2022). The middle-late Aalenian event: a precursor of the Mesozoic Marine Revolution. *Global and Planetary Change*, 208: 103705.
- Farrar L., Graves E., Petsios E., Portell R.W., Grun T.B., Kowalewski M. & Tyler C.L. (2020). Characterization of traces of predation and parasitism on fossil echinoids. *PALAIOS*, 35: 215-227.
- Fenton C.L. & Fenton M.A. (1931). Some small borings of Paleozoic age. *American Midland Naturalist*, 12: 522-528.
- Freestone A.L. & Osman R.W. (2010). Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. *Ecology*, 92: 208-217.
- Freestone A.L., Osman R.W., Ruiz G.M. & Torchin M.E. (2011). Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology*, 92: 983-993.
- Fürsich F.T. & Jablonski D. (1984). Late Triassic naticid drillholes: carnivorous gastropods gain a major adaptation but fail to radiate. *Science*, 224: 78-80.
- Gale A.S. & Donovan S.K. (1992). Predatory asteroids and the fate of brachiopods: a reply. *Lethaia*, 25: 346-348.
- Gallagher T., Richardson C.A., Seed R. & Jones T. (2008). The seasonal movement and abundance of the starfish, *Asterias rubens* in relation to mussel farming practice: a case study from the Menai Strait, UK. *Journal of Shellfish Research*, 27: 1209-1215.
- Goldfuss A. (1844). Petrefacta Germaniae, Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angrenzenden Länder, Teil 3. Molluscorum Gasteropodum Reliquiae. Einkammerige Schnecken der Vorwelt. 128 pp. Arnz & Comp., Düsseldorf.
- Gordillo S. (2001). Marcas de la depredación de *Acanthina* Fisher von Waldheim, 1807 (Gasteropoda: Muricidae) sobre Bivalvia. *Ameghiniana*, 38: 55-60.
- Gordillo S. (2013). Muricid boreholes in Pleistocene acorn barnacles from the Beagle Channel: trophic interactions during the Last Interglacial in southern South America. *Alcheringa*, 37: 479-486.
- Gordillo S. & Amunátegui S. (1998). Estrategias de depredación del gastrópodo perforador *Trophon geversianus* (Pallas) (Muricoidea: Trophonidae). *Malacologia*, 39: 83-91.
- Gordillo S. & Archuby F. (2012). Predation by drilling gastropods and asteroids upon mussels in rocky shallow shores of southernmost South America: paleontological implications. *Acta Palaeontologica Polonica*, 57: 633-646.
- Gordillo S., Bayer M.S., Aranzamendi M.C., Taverna A. & Morán G.A. (2019). The ecological role of brachiopods in the Namuncurá MPA/Burdwood Bank, off southern South America. *Marine Biodiversity*, 49: 1667-1681.
- Gordillo S. & Malvé M.E. (2021). Drilling predation on Antarctic tusk shells: first records on Recent scaphopods from the Southern Hemisphere. *Antarctic Science*, 33: 344-348.
- Gordillo S., Morán G.A. & Malvé M.E. (2022). Octopuses and drilling snails as the main suspects of predation traces on shelled molluscs in West Antarctica. *Polar Biology*, 45: 127-141.
- Gordon T.A.C., Wilding E.L. & Aldridge D.C. (2016). Predation of freshwater gastropods (*Viviparus viviparus*) by brown rats (*Rattus norvegicus*). *Journal of Molluscan Studies*, 82: 457-463.
- Gorzela P., Niedźwiedzki G. & Skawina A. (2010). Pathologies of non-marine bivalve shells from the Late Triassic of Poland. *Lethaia*, 43: 285-289.
- Gorzela P., Salamon M.A. & Baumiller T.K. (2012). Predator-induced macroevolutionary trends in Mesozoic crinoids. *PNAS*, 109: 7004-7007.
- Goswami P., Das S.S., Bardhan S. & Paul S. (2020). Drilling gastropod predation on the lower Miocene gastropod assemblages from Kutch, western India: spatiotemporal implications. *Historical Biology*, 33: 1504-1521.
- Gould S.J. & Calloway C.B. (1980). Clams and brachiopods-ships that pass in the night. *Paleobiology*, 6: 383-396.
- Gray J. (1988). Evolution of the freshwater ecosystem: the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62: 1-214.
- Grun T.B. (2016). Echinoid test damage by a stingray predator. *Lethaia*, 49: 285-286.
- Grun T.B., Kroh A. & Nebelsick J.H. (2017). Comparative drilling predation on time-averaged phosphatized and nonphosphatized assemblages of the minute clypeasteroid echinoid *Echinocyamus stellatus* from Miocene offshore sediments (Globigerina Limestone Formation, Malta). *Journal of Paleontology*, 91: 633-642.
- Hageman S.A. & Kaesler R.L. (2002). Fusulinids: predation damage and repair of tests from the Upper Pennsylvanian of Kansas. *Journal of Paleontology*, 76: 181-184.
- Harasewych M.G. & Kantor Y.I. (2002). *Buccinum thermophilum* (Gastropoda: Neogastropoda: Buccinidae), a new species from the Endeavour vent field of the Juan de Fuca Ridge. *Journal of Molluscan Studies*, 68: 39-44.
- Harper E.M. (2002). Plio-Pleistocene octopod drilling behavior in scallops from Florida. *PALAIOS*, 17: 292-295.
- Harper E.M. (2003). Assessing the importance of drilling predation over geological time. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 201: 185-198.
- Harper E.M. (2011). What do we really know about predation on modern rhynchonelliforms? *Memoirs of the Association of Australasian Palaeontologists*, 41: 45-57.
- Harper E.M. (2016). Uncovering the holes and cracks: from anecdote to testable hypothesis in predation studies. *Palaeontology*, 59: 597-609.
- Harper E.M., Crame J.A. & Pullen A.M. (2019b). The fossil record of durophagous predation in the James Ross Basin over the last 125 million years. *Advances in Polar Science*, 30: 199-209.
- Harper E.M., Crame J.A. & Sogot C.E. (2018). 'Business as usual': drilling predation across the K-Pg mass extinction event in Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 498: 115-126.
- Harper E.M., Forsythe G.T.W. & Palmer T. (1998). Taphonomy and the Mesozoic Marine Revolution: preservation state masks the importance of boring predators. *PALAIOS*, 13: 352-360.

- Harper E.M., Lamare M.D. & Lee D.E. (2019a). Patterns of unrepai red shell damage in Recent brachiopods from Fiordland (New Zealand). *Rivista Italiana di Paleontologia e Stratigrafia*, 125: 669-677.
- Harper E.M. & Peck L.S. (2016). Latitudinal and depth gradients in marine predation pressure. *Global Ecology and Biogeography*, 25: 670-678.
- Harper E.M., Robinson J.H. & Lee D.E. (2011). Drill hole analysis reveals evidence of targeted predation on modern brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 305: 162-171.
- Harper E.M. & Skelton P.W. (1993). The Mesozoic Marine Revolution and epifaunal bivalves. *Scripta Geologica, Special Issue*, 2: 127-153.
- Harries P.J. & Schopf K.M. (2003). The first evidence of drilling predation in Inoceramids. *Journal of Paleontology*, 77: 1011-1015.
- Hiller N. (2014). Drill holes and shell repair in brachiopods from a Late Cretaceous (Maastrichtian) oyster reef, North Canterbury, New Zealand. *Cretaceous Research*, 49: 83-90.
- Hoffmann R., Stevens K., Keupp H., Simonsen S. & Schweigert G. (2020). Regurgitalites – a window into the trophic ecology of fossil cephalopods. *Journal of the Geological Society of London*, 177: 82-102.
- Hoffmeister A.P., Kowalewski M., Baumiller T.K. & Bambach R.K. (2004). Drilling predation on Permian brachiopods and bivalves from the Glass Mountains, west Texas. *Acta Palaeontologica Polonica*, 49: 443-454.
- Hughes R.N. & Dunkin S.B. (1984). Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.) feeding on mussels, *Mytilus edulis* L. in the laboratory. *Journal of Experimental Marine Biology & Ecology*, 77: 45-68.
- Jablonski D. (2005). Evolutionary innovations in the fossil record: the intersection of ecology, development and macroevolution. *Journal of Experimental Zoology*, 304B: 504-519.
- Jablonski D. (2008). Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution*, 62: 715-739.
- Jablonski D., Flessa K.W. & Valentine J.W. (1985). Biogeography and paleobiology. *Paleobiology*, 11: 75-90.
- Jablonski D., Sepkoski J.J., Bottjer D.J. & Sheehan P.M. (1983). Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science*, 222: 1123-1125.
- James M.S., Ansell A.D., Collins M.J., Curry G.B., Peck L.S. & Rhodes M.C. (1992). Recent advances in the study of living brachiopods. *Advances in Marine Biology*, 28: 175-387.
- Jonkers H.A. (2000). Gastropod predation patterns in Pliocene and Recent pectinid bivalves from Antarctica and New Zealand. *New Zealand Journal of Geology and Geophysics*, 43: 247-254.
- Kabat A.R. (1990). Predatory ecology of naticid gastropods with a review of shell boring. *Malacologia*, 32: 155-193.
- Kaim A.J., Little C.T.S., Kennedy W.J., Mears E.M. & Anderson L.M. (2021). Late Cretaceous hydrothermal vent communities from the Troodos ophiolite, Cyprus: systematics and evolutionary significance. *Papers in Palaeontology*, 7: 1927-1947.
- Karapınar B., Werner W., Fürsich F.T. & Nützel A. (2021). Predatory drill holes in the oldest thyasirid bivalve, from the Lower Jurassic of South Germany. *Lethaia*, 54: 229-244.
- Kase T. & Ishikawa M. (2003). Mystery of naticid predation history solved: evidence from a 'living fossil' species. *Geology*, 31: 403-406.
- Kear B.P. & Godthelp H. (2008). Inferred vertebrate bite marks on an Early Cretaceous unionoid bivalve from Lightning Ridge, New South Wales, Australia. *Alcheringa*, 32: 65-71.
- Kelley P.H. & Hansen T.A. (2003). The fossil record of drilling predation on bivalves and gastropods. *Topics in Geobiology*, 20: 113-139.
- Kelley P.H. & Hansen T.A. (2006). Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 236: 302-320.
- Kelley P.H. & Hansen T.A. (2007). Latitudinal patterns in naticid gastropod predation along the east coast of the United States: a modern baseline for interpreting temporal patterns in the fossil record. *SEPM Special Publication*, 8: 287-299.
- Kelts K. & Hsü K.J. (1978). Freshwater Carbonate Sedimentation. In Lerman A. (ed.), *Lakes*. Springer, New York, NY: 295-323.
- Kenk V.C. & Wilson B.R. (1985). A new mussel (Bivalvia, Mytilidae) from hydrothermal vents, in the Galapagos Rift zone. *Malacologia*, 26: 253-271.
- Kerr J.P. & Kelley P.H. (2015). Assessing the influence of escalation during the Mesozoic Marine Revolution: shell breakage and adaptation against enemies in Mesozoic ammonites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 440: 632-646.
- Kiel S. (2010). *The Vent and Seep Biota: aspects from microbes to ecosystems*. Topics in Geobiology 33. 487 pp. Springer, Heidelberg.
- Kiel S., Amano K. & Jenkins R.G. (2016). Predation scar frequencies in chemosymbiotic bivalves at an Oligocene seep deposit and their potential relation to inferred sulfide tolerances. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 453: 139-145.
- Kier P.M. (1974). Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *Memoir of the Paleontological Society*, 5: 1-95.
- Kitchell J.A., Boggs C.H., Kitchell J.F. & Rice J.A. (1981). Prey selection by naticid gastropods: Experimental tests and application to the fossil record. *Paleobiology*, 7: 533-552.
- Kitchell J.A., Rice J.A., Kitchell J.F., Hoffman A. & Martinell A. (1986). Anomalies in naticid predatory behavior: a critique and experimental observations. *Malacologia*, 27: 291-298.
- Klomp maker A.A. (2011). Drilling and crushing predation on scaphopods from the Miocene of the Netherlands. *Lethaia*, 44: 429-439.
- Klomp maker A.A., Karasawa H., Portell R.W., Fraaije R.H. & Ando Y. (2013). An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *PALAIOS*, 28: 599-613.
- Klomp maker A.A., Kelley P.H., Chattopadhyay D., Clements J.C., Huntley J.W. & Kowalewski M. (2019). Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior. *Earth Science Reviews*, 194: 472-520.
- Klomp maker A.A. & Landman N.H. (2021). Octopodoidea as predators near the end of the Mesozoic Marine Revolution. *Biological Journal of the Linnean Society*, 132: 894-899.
- Klomp maker A.A., Natascha A., Waljaard R. & Fraaije H.B. (2009). Ventral bite marks in Mesozoic ammonoids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 280: 245-257.
- Klomp maker A.A., Nützel A. & Kaim A. (2016). Drill hole convergence and a quantitative analysis of drill holes in mollusks and brachiopods from the Triassic of Italy and Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 457: 342-359.
- Klomp maker A.A., Portell R.W. & Karasawa H. (2014). First fossil evidence of a drill hole attributed to an octopod in a barnacle. *Lethaia*, 47: 309-312.
- Klomp maker A.A., Portell R.W., Lad S.E. & Kowalewski M. (2015). The fossil record of drilling predation on barnacles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 426: 95-111.
- Klug C. & Vallon L.H. (2019). Regurgitated ammonoid remains from the latest Devonian of Morocco. *Swiss Journal of Palaeontology*, 138: 8797.
- Knaust D. (2020). Invertebrate coprolites and cololites revisited. *Papers in Palaeontology*, 6: 385-423.
- Knoll A.H. & Follows M.J. (2016). A bottom-up perspective on ecosystem change in Mesozoic oceans. *Proceedings of the Royal Society B*, 283: 20161755.

- Kotzian C.B. & Simões M.G. (2006). Taphonomy of Recent freshwater molluscan death assemblages, Touro Passon Stream, Southern Brazil. *Revista Brasileira de Paleontologia*, 9: 243-260.
- Kowalewski M., Dulai A. & Fürisch F.T. (1998). A fossil record full of holes: The Phanerozoic history of drilling predation. *Geology*, 26: 1091-1094.
- Kowalewski M., Hoffmeister A.P., Baumiller T.K. & Bambach R.K. (2005). Secondary evolutionary escalation between brachiopods and enemies of other prey. *Science*, 308: 1774-1777.
- Kowalewski M., Somoos M.G., Torello F.F., Mello L.H.C. & Ghilardi R.P. (2000). Drill holes in shells of Permian benthic invertebrates. *Journal of Paleontology*, 74: 532-543.
- Kriwet J. (2001). Feeding mechanisms and ecology of pycnodont fishes (Neopterygii, Pycnodontiformes). *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe*, 4: 139-165.
- Kropp R.K. (1992). Repaired shell damage among soft-bottom mollusks on the continental shelf and upper slope north of Point Conception, California. *Veliger*, 35: 36-51.
- Lau C.J. (1987). Feeding behavior of the Hawaiian slipper lobster *Scyllarides squammosus*, with a review of decapod crustacean feeding tactics on molluscan prey. *Bulletin of Marine Science*, 41: 378-391.
- Lazarus D., Barron J., Renaudie J., Diver P. & Turke A. (2014). Cenozoic planktonic marine diatom diversity and correlation to climate change. *PLoS One*, 9: e84857.
- Leeuw J.J. (1999). Food intake rates and habitat segregation of tufted duck *Aythya fuligula* and scaup *Aythya marila* exploiting Zebra mussels *Dreissena polymorpha*. *Ardea*, 87: 15-31.
- Leighton L.R. (2003). Predation on Brachiopods. In Kelley P.H., Kowalewski M. & Hansen T.A. (eds), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology, 20, Springer, Boston, MA: 215-237.
- Lidgard S. (2008). Predation on marine bryozoan colonies: taxa, traits and trophic groups. *Marine Ecology Progress Series*, 359: 117-131.
- Lindström A. & Peel J.S. (2005). Repaired injuries and shell form in some Palaeozoic pleurotomarioid gastropods. *Acta Palaeontologica Polonica*, 50: 697-704.
- Lindström A. & Peel J.S. (2010). Shell repair and shell form in Jurassic pleurotomarioid gastropods from England. *Bulletin of Geosciences*, 85: 541-550.
- Linnaeus C. (1758). *Systema Naturae per Regna tria Naturae, Secundum Classes, Ordines, Genera, Species cum characteribus, differentiis, synonymis, locis. editio decima, reformata*. 824 pp. L. Salvii, Holmiae.
- Little C.T.S., Herrington S., Maslennikov V.V. & Zaykov V.V. (1998). The fossil record of hydrothermal vent communities. *Geological Society, London, Special Publications*, 148: 259-270.
- MacArthur R.H. (1972). *Geographical ecology: patterns in the distribution of species*. 288 pp. Princeton University Press, Princeton, NJ.
- Madin J.S., Alroy J., Aberhan M., Fürsich F.T., Kiessling W., Kosnik M.A. & Wagner P.J. (2006). Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates. *Science*, 312: 897-900.
- Maldonado A., Bohoyo F., Galindo-Zaldivar F.J., Hernandez-Molina F.J., Lobo F.J., Lodolo E., Martos Y.M., Pérez L.F., Schreider A.A. & Somoza L. (2014). A model of oceanic development by ridge jumping: Opening of the Scotia Sea. *Global and Planetary Change*, 123: 152-173.
- Mallick S., Bardhan S., Das S.S., Paul S. & Goswami P. (2014). Naticid drilling predation on gastropod assemblages across the K-T boundary in Rajahmundry, India: new evidence for escalation hypothesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 411: 216-218.
- Mallick S., Bardhan S., Paul S., Goswami P. & Das S.S. (2017). Record of naticid predation on scaphopods (Mollusca) from the Latest Maastrichtian of Rajahmundry, India. *Ichnos*, 24: 37-50.
- Mallick S., Bardhan S., Paul S., Mukherjee S. & Das S.S. (2013). Intense naticid drilling predation on turritelline gastropods from the Indian subcontinent from the K-T boundary at Rajahmundry, India. *PALAIOS*, 28: 683-696.
- Martin J.W. & Haney T.A. (2005). Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005. *Zoological Journal of the Linnean Society*, 145: 445-522.
- Martin R. & Quigg A. (2012). Evolving phytoplankton stoichiometry fueled diversification of the marine biosphere. *Geosciences*, 2: 130-146.
- Martinell J., Kowalewski M. & Domenech R. (2012). Drilling predation on serpulid polychaetes (*Ditrupa arietina*) from the Pliocene of the Cope Basin, Murcia region, southeastern Spain. *PLoS One*, 7: e34576.
- Martinelli J.C., Gordillo S. & Archuby F. (2013). Muricid drilling predation at high latitudes: Insights from the southernmost Atlantic. *PALAIOS*, 28: 33-41.
- McLean J.H. (1988). New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea I. Systematic descriptions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 319: 1-32.
- McQuaid C.D. (1994). Feeding behaviour and selection of bivalve prey by *Octopus vulgaris* Cuvier. *Journal of Experimental Marine Biology and Ecology*, 177: 187-202.
- Menge B.A. & Sutherland J.P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, 130: 730-757.
- Meyer D.L. & Macurda D.B. (1977). Adaptive radiation of the comatulid crinoids. *Paleobiology*, 3: 74-82.
- Micheli F., Peterson C.H., Mullineaux L.S., Fisher C.R., Mills S.W., Sancho G., Johnson G.A. & Lenihan H.S. (2002). Predation structures communities at deep-sea hydrothermal vents. *Ecological Monographs*, 72: 365-382.
- Mondal S., Chakraborty H., Saha S., Dey S. & Sarkar D. (2021). High biogeographic and latitudinal variability in gastropod drilling predation on molluscs along the eastern Indian coast: Implications on the history of fossil record of drillholes. *PLoS One*, 16: e0256685.
- Nagel-Myers J.J., Dietl G.P. & Brett C.E. (2009). First report of sublethal breakage-induced predation on Devonian bivalves. *PALAIOS*, 24: 460-465.
- Nanglu K. & Caron J-B. (2021). Symbiosis in the Cambrian: enteropneust tubes from the Burgess Shale co-inhabited by commensal polychaetes. *Proceedings of the Royal Society B*, 288: 20210061.
- Neely S.H., Kelley P.H. & Friedman M.M. (2021). Predator-prey interactions among Pliocene molluscs from the Tjörnes Peninsula, Iceland, across the trans-Arctic invasion. *Lethaia*, 54: 643-663.
- Nixon M. (1979). Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia*, 18: 431-443.
- Nixon M. & Young J.Z. (2003). *The Brains and Lives of Cephalopods*. 392 pp. Oxford University Press, Oxford.
- Oji T. (1996). Is predation intensity reduced with increasing depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution. *Paleobiology*, 22: 339-351.
- Oji T., Ogaya C. & Sato T. (2003). Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology*, 29: 520-526.
- Paine R.T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100: 65-75.
- Paine R.T. (1974). Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15: 93-120.
- Pasini G. & Garassino A. (2012). Naticid gastropod and octopodid cephalopod predatory traces: evidence of drill holes on the leucosid crab *Ristoria pliocaenica* (Ristori, 1891), from the Pliocene of the "La Serra" quarry (Tuscany, Italy). *Atti della*

Società Italiana di Scienze Naturali del Museo Civico di Storia Naturale di Milano, 153: 257-266.

- Payne J.L., Heim N.A., Knoppe M.L. & McClain C.R. (2014). Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years. *Proceedings of the Royal Society B*, 281: 20133122.
- Peters S.G., Nokleberg W.J., Doebrich J.L., Bawiec W.J., Orris G., Sutphin D.M. & Wilburn D.R. (2005). Geology and Non Fuel Mineral Deposits and Resources of Asia and the Pacific. *U.S. Geological Survey Open File Report*, 2005-1294c.
- Petroff A.P., Sim M.S., Maslov A.M., Krupenin M., Rothman D.H. & Bosak T. (2010). Biophysical basis for the geometry of conical stromatolites. *PNAS*, 107: 9956-9961.
- Petsios E., Portell R.W., Farra L., Tennakoon S., Grun T.B., Kowalewski M. & Tyler C.L. (2021). An asynchronous Mesozoic marine revolution: the Cenozoic intensification of predation on echinoids. *Proceedings of the Royal Society B*, 288: 20210400.
- Pilson M.E.Q. & Taylor P.B. (1961). Hole drilling by Octopus. *Science*, 134: 1366-1368.
- Radley J.D. (2010). Grazing bioerosion in Jurassic seas: a neglected factor in the Mesozoic marine revolution? *Historical Biology*, 22: 387-393.
- Rasser M.W. & Covich A.P. (2014). Predation on freshwater snails in Miocene Lake Steinheim: a trigger for intralacustrine evolution? *Lethaia*, 47: 524-532.
- Rhoads D.C., Lutz R.A., Cerrato R.M. & Revelas E.C. (1982). Growth and predation at deep-sea hydrothermal vents along the Galapagos Rift. *Journal of Marine Research*, 40: 503-513.
- Robba E. & Ostinelli F. (1975). Studi paleoecologici sul Pliocene figure, I. Testimonianze di predazione sui molluschi Plioceni di Albenga. *Rivista Italiana di Paleontologia e Stratigrafia*, 81: 309-372.
- Rojas A. & Sandy M.R. (2019). Early Cretaceous (Valanginian) brachiopods from the Rosablanca Formation, Colombia, South America: biostratigraphic significance and paleogeographic implications. *Cretaceous Research*, 96: 184-195.
- Rojas A., Verde M., Urteaga D., Scarabino F. & Martinez S. (2014). The first predatory drillhole on a fossil chiton plate: an occasional prey item or an erroneous attack? *PALAIOS*, 29: 414-419.
- Rudwick M.J.S. (1992). Scenes from deep time. 280 pp. University of Chicago Press, Chicago.
- Saha R., Paul S., Mondal S., Bardhan S., Das S.S., Saha S. & Sarkar D. (2021). Gastropod drilling predation in the Upper Jurassic of Kutch, India. *PALAIOS*, 36: 301-312.
- Salamon M.A., Gorzelak P., Niedźwiedzki R., Trzesiok D. & Baumiller T.K. (2014). Trends in shell fragmentation as evidence of mid-Paleozoic changes in marine predation. *Paleobiology*, 40:14-23.
- Sallan L.C., Kammer T.W., Ausich W.I. & Cook L.A. (2011). Persistent predator-prey dynamics revealed by mass extinction. *PNAS*, 108: 8335-8338.
- Sancho G., Fisher C.R., Mills S., Micheli F., Johnson G.A., Lenihan H.S., Peterson C.H. & Mullineaux L.S. (2005). Selective predation by the zoarcid fish *Thermarces cerberus* at hydrothermal vents. *Deep Sea Research I*, 52: 837-844.
- Sanciangco J.C., Carpenter K.E., Etnoyer P.J. & Moretzsohn F. (2013). Habitat availability and heterogeneity and the Indo-Pacific Warm Pool as predictors of marine species richness in the Tropical Indo-Pacific. *PLoS One*, 8: e56245.
- Sandy M.R. (2010). Brachiopods from ancient hydrocarbon seeps and hydrothermal vents. In Kiel S. (ed.), *The Vent and Seep Biota*, Topics in Geobiology, 33, Springer, Dordrecht: 279-314.
- Say T. (1822). An account of some of the marine shells of the United States. *Journal of the Academy of Natural Sciences, Philadelphia*, 2: 221-248; 2(2): 257-276, 302-325.
- Schemske D.W., Mittelbach G.G., Cornell H.V., Sobel J.M. & Roy K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Reviews in Ecology, Evolutionary Systematics*, 40: 245-269.
- Schroeder A.E., Sørensen A.M. & Surlyk F. (2018). Morphological adaptations of the brachiopods from a Late Cretaceous rocky shore, Ivö Klack, southern Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 514: 785-799.
- Senowbari-Daryan B., Gaillard C. & Peckmann J. (2007). Crustacean microcoprolites from Jurassic (Oxfordian) hydrocarbon-seep deposits of Beauvoisin, southeastern France. *Facies*, 53: 229-238.
- Sheffield G., Fay F.H., Feder H. & Kelly B.P. (2001). Laboratory digestion of prey and interpretation of walrus stomach contents. *Marine Mammal Science*, 17: 310-330.
- Signor P.W. & Brett C.E. (1984). The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology*, 10: 229-245.
- Skelton P.W. (1979). Preserved ligament in a radiolitic rudist bivalve and its implication of mantle marginal feeding in the group. *Paleobiology*, 5: 90-106.
- Sohl N.F. (1969). The fossil record of shell boring by snails. *American Zoologist*, 9: 725-734.
- Sowerby G.B.I. (1825). A catalogue of the shells contained in the collection of the late Earl of Tankerville: arranged according to the Lamarckian conchological system: together with an appendix, containing descriptions of many new species. vii + 92 + xxxiv pp. London.
- Stanley S.M. (1968). Post-Paleozoic adaptive radiation of infaunal bivalve molluscs: a consequence of mantle fusion and siphon formation. *Journal of Paleontology*, 42: 214-229.
- Stanley S.M. (1974). What has happened to the articulate brachiopods? *Geological Society of America Abstracts with Programs*, 6: 966-967.
- Stanley S.M. (1977). Trends, rates, and patterns of evolution in the Bivalvia. In Hallam A. (ed.), *Patterns of Evolution*, as illustrated by the fossil record: 209-250.
- Stanley S.M. (2008). Predation defeats competition on the seafloor. *Paleobiology*, 34: 1-21.
- Steer M.A. & Semmens J.M. (2003). Pulling or drilling, does size or species matter? An experimental study of prey handling in *Octopus dierythraeus* (Norman, 1992). *Journal of Experimental Marine Biology and Ecology*, 290: 165-178.
- Stelbrink B., Richter R., Köhler F., Riedel F., Strong E.E., Van Bocxlaer B., Albrecht C., Hauffe T., Page T.J., Aldridge D.C., Bogan A.E., Du L.-N., Manuel-Santos M.R., Marwoto R.M., Shirokaya A.A. & Von Rintelen T. (2020). Global diversification dynamics since the Jurassic: low dispersal and habitat-dependent evolution explain hotspots of diversity and shell disparity in river snails (Viviparidae). *Systematic Biology*, 69: 944-961.
- Strong E.E., Galind L.A. & Kantor Y.I. (2017). Quid est *Clea helena*? Evidence for a previously unrecognized radiation of assassin snails (Gastropoda: Buccinoidea: Nassariidae). *PeerJ*, 5: e3638.
- Strotz L.C., Saupe E.E., Kimmig J. & Lieberman B.S. (2018). Metabolic rates, climate and macroevolution: a case study using Neogene molluscs. *Proceedings of the Royal Society B*, 285: 20181292.
- Tackett L.S. (2016). Late Triassic durophagy and the origin of the Mesozoic Marine Revolution. *PALAIOS*, 31: 122-124.
- Tackett L.S. & Tintori A. (2019). Low drilling frequency in Norian benthic assemblages from the southern Italian Alps and the role of specialized durophages during the Late Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 513: 25-34.
- Takeda Y., Tanabe K., Sasaki T. & Landman N.H. (2016). Durophagous predation on scaphitid ammonoids in the Late Cretaceous Western Interior Seaway of North America. *Lethaia*, 49: 28-42.
- Taylor J.D., Cleavelly R.J. & Morris N.J. (1983). Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology*, 26: 521-533.
- Taylor J.D., Morris N.J. & Taylor C.N. (1980). Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology*, 23: 375-409.

- Taylor J.D. & Morton B. (1996). The diets of predatory gastropods in the Cape d'Aguilar marine reserve, Hong Kong. *Asian Marine Biology*, 13: 141-166.
- Taylor P.D. (1982). Probable predatory borings in Late Cretaceous bryozoans. *Lethaia*, 15: 67-74.
- Taylor P.D. (2016). Competition between encrusters on marine hard substrates and its fossil record. *Palaeontology*, 59: 481-497.
- Taylor P.D. (2020). *Bryozoan Paleobiology*. 320 pp. Wiley Blackwell, Hoboken, NJ.
- Thayer C.W. (1985). Brachiopods versus mussels: competition, predation and palatability. *Science*, 228: 1527-1528.
- Thomka J.R. & Eddy D.B. (2018). Repeated regeneration of crinoid spines in the Upper Pennsylvanian of eastern Ohio: evidence of elevated predation intensity and significance for predator-driven evolution of crinoid morphology. *PALAIOS*, 33: 508-513.
- Thyrring J. & Peck L.S. (2021). Global gradients in intertidal species richness and functional groups. *eLife*, 10: e64541.
- Todd J.A. & Harper E.M. (2010). Stereotypic boring behaviour inferred from the earliest known octopod feeding traces. *Lethaia*, 44: 214-222.
- Tuura M.E., Baumiller T.K. & McNamara K.J. (2008). Drill holes in Australian Cainozoic brachiopods. *Historical Biology*, 20: 203-212.
- Tyler C.L., Leighton L.R., Carlson S.J., Huntley J.W. & Kowalewski M. (2013). Predation on modern and fossil brachiopods: assessing chemical defences and palatability. *PALAIOS*, 28: 724-735.
- Vannier J. (2012). Gut contents as direct indicators for trophic relationships in the Cambrian marine ecosystem. *PLoS One*, 7: e52200.
- Vermeij G.J. (1975). Evolution and distribution of left-handed and planispiral coiling in snails. *Nature*, 254: 419-420.
- Vermeij G.J. (1976). Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature*, 260: 135-136.
- Vermeij G.J. (1977). The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology*, 3: 245-258.
- Vermeij G.J. (1978). *Biogeography and adaptation: patterns of marine life*. 332 pp. Harvard University Press, Harvard.
- Vermeij G.J. (1982). Unsuccessful predation and evolution. *The American Naturalist*, 120: 701-720.
- Vermeij G.J. (1983). Traces and trends in predation, with special reference to bivalved animals. *Palaeontology*, 26: 455-465.
- Vermeij G.J. (1987). *Evolution and escalation: an ecological history of life*. 527 pp. Princeton University Press.
- Vermeij G.J. (1990). Asteroids and articulates: is there a causal link? *Lethaia*, 23: 431-432.
- Vermeij G.J. (1998). Volcanoes, and Phanerozoic Revolutions. *Paleobiology*, 21: 125-152.
- Vermeij G.J. (1999). Inequality and the directionality of history. *The American Naturalist*, 153: 243-253.
- Vermeij G.J. (2008). Escalation and its role in Jurassic biotic history. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 263: 3-8.
- Vermeij G.J. (2015). Gastropod skeletal defences: land, freshwater, and sea compared. *Vita Malacologica*, 13: 1-25.
- Vermeij G.J. & Covich A.P. (1978). Coevolution of freshwater gastropods and their predators. *The American Naturalist*, 112: 833-843.
- Vermeij G.J., Schindel D.E. & Zipser E. (1981). Predation through geological time: evidence from gastropod shell repair. *Science*, 214: 1024-1026.
- Villanueva R., Perricone V. & Fiorito G. (2017). Cephalopods as predators: a short journey among behavioral flexibilities, adaptations, and feeding habits. *Frontiers in Physiology*, 8: 598.
- Villegas-Martin J., Ceolin D., Fauth G. & Klompmaker A.A. (2019). A small yet occasional meal: predatory drill holes in Paleocene ostracods from Argentina and methods to infer predation intensity. *Palaeontology*, 62: 731-756.
- Villegas-Martin J., Rojas-Consuegra R. & Klompmaker A.A. (2016). Drill hole predation on tubes of serpulid polychaetes from the Upper Cretaceous of Cuba. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 455: 44-52.
- Vinn O., Ernst A., Wilson M.A. & Toom U. (2021). Symbiosis of cornulitids with the cystoporate bryozoan *Fistulipora* in the Pridoli of Saaremaa, Estonia. *Lethaia*, 54: 90-95.
- Visaggi C.C. & Kelley P.H. (2015). Equatorward increase in naticid gastropod drilling predation on infaunal bivalves from Brazil with paleontological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 438: 285-299.
- Voight J.R. (2000a). A review of predators and predation at deep-sea hydrothermal vents. *Cahiers de Biologie Marine*, 41: 155-166.
- Voight J.R. (2000b). A deep-sea octopus (*Graneledone* cf. *boreopacifica*) as a shell-crushing hydrothermal vent predator. *Journal of Zoology*, 252: 335-341.
- Voight J.R. & Sigwart J.D. (2007). Scarred limpets at hydrothermal vents: evidence of predation by deep-sea whelks. *Marine Biology*, 152: 129-133.
- Voje K.L., Holen Ø.H., Liow L.H. & Stenseth N.C. (2015). The role of biotic forces in driving macroevolution: beyond the Red Queen. *Proceedings of the Royal Society B*, 282: 20150186.
- von Rintelen T., Wilson A.B., Meyer A. & Glaubrecht M. (2004). Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in ancient lake on Sulawesi, Indonesia. *Proceeding of the Royal Society of London Series B*, 271: 2541-2549.
- Walcott C.D. (1911). Cambrian geology and paleontology. Middle Cambrian annelids. *Smithsonian Miscellaneous Collections*, 57: 109-144.
- Walker S.E. (2001). Paleoeology of gastropods preserved in turbiditic slope deposits from the Upper Pliocene of Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166: 141-163.
- Walker S.E. & Brett C.E. (2002). Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Paleontological Society Paper*, 8: 119-193.
- Walker S.E., Parsons-Hubbard K., Powell E. & Brett C.E. (2002). Predation on experimentally deployed molluscan shells from shelf to slope depths in a tropical carbonate environment. *PALAIOS*, 17: 147-170.
- Walker S.E. & Voight J.R. (1994). Paleoeologic and taphonomic potential of deepsea gastropods. *PALAIOS*, 9: 48-59.
- Warén A. & Bouchet P. (1993). New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seep. *Zoologica Scripta*, 22: 1-90.
- Weigand A.M., The Volkswagen Foundation Lake Malawi Field School 2012 Consortium & Plath M. (2014). Prey preferences in captivity of the freshwater crab *Potamonautes lirrangensis* from Lake Malawi with special emphasis on molluscivory. *Hydrobiologia*, 739: 145-153.
- West K. & Cohen A. (1994). Predator-prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. *Archiv für Hydrobiologie, BeiheftErgebnisse der Limnologie*, 44: 267-283.
- Wiggin N.J., Riding J.B., Fensome R.A. & Mattioli E. (2018). The Bajocian (Middle Jurassic): A key interval in the early Mesozoic phytoplankton radiation. *Earth Sciences Reviews*, 180: 126-146.
- Williams A.B. (1980). A new crab family from the vicinity of submarine thermal vents on the Galapagos Rift (Crustacea: Decapoda: Brachyura). *Proceedings of the Biological Society of Washington*, 93: 443-472.
- Witton M.P. (2018). Pterosaurs in Mesozoic food webs: a review of fossil evidence. *Geological Society, London, Special Publications*, 455: 7-23.
- Wood R. (2011). Paleoeology of early skeletal metazoans: insights into biomineralization. *Earth Sciences Reviews*, 106: 184-190.
- Yamakami R. & Wada S. (2021). Prey utilization by *Neptunea arthritica* (Caenogastropoda: Buccinidae): predation on gastropods and size-related variation. *Journal of Molluscan Studies*, 87: eyab016.

- Yates A.M., Neumann F.H. & Hancox P.J. (2012). The earliest Post-Paleozoic freshwater bivalves preserved in coprolites from the Karoo Basin, South Africa. *PLoS One*, 7: e30228.
- Yonge C.M. (1962). On *Etheria elliptica* Lam. and the course of evolution. including assumption of monomyarianism. in the family Etheriidae (Bivalvia: Unionacea). *Philosophical Transaction of the Royal Society, Series B*, 244: 423-458.
- Zahner-Meike E. & Hanson J.M. (2001). Effect of muskrat predation on naiads. *Ecological Studies (Analysis and Synthesis)*, 145: 163-184.
- Zatoń M., Villier L. & Salamon M.A. (2007). Signs of predation in the Middle Jurassic of south-central Poland: evidence from echinoderm taphonomy. *Lethaia*, 40: 139-151.

Manuscript received 10 January 2022
Revised manuscript accepted 15 March 2022
Published online 29 April 2022
Editor Gaia Crippa



Elizabeth M. Harper is a palaeobiologist at the University of Cambridge (UK) where she is Professor of Evolutionary Malacology and Honorary Curator of Invertebrate Palaeontology in the Sedgwick Museum of Earth Sciences. She is also an Honorary Fellow of the British Antarctic Survey. She received her BA degree from the University of Cambridge (1986) and a PhD from the Open University (1990). She returned to Cambridge University in 1992. Her research work has concentrated on the evolutionary biology of molluscs and brachiopods with major strands in biomineralization, predator-prey relationships and phylogenetic relationships. She has strong focus on using neontological material and data to elucidate evolutionary questions.