

The fossil record of durophagous predation in the James Ross Basin over the last 125 million years

Elizabeth M. HARPER^{1*}, J. Alistair CRAME² & Alice M PULLEN¹

¹ Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK;

² British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Received 5 January 2019; accepted 18 February 2019; published online 30 March 2019

Abstract We review the evidence for predation of shelly benthic prey over 125 million years of earth history in the James Ross Basin, Antarctica (~65°S). Although poor in the Early Cretaceous lower parts of the sequence, which represent essentially deeper water facies, evidence for both potential crushers and drillers becomes more apparent in the Santonian–Campanian Santa Marta Formation, and by the Maastrichtian López de Bertodano Formation there is an extensive fossil record of drill holes attributable to naticid gastropods, and some evidence of crushing by decapods crustaceans and possibly other taxa too. This continues at a similar level of intensity across the K/Pg boundary into the Danian Sobral Formation, but is less well constrained in the latest Paleocene–Early Eocene. The most extensive record of predation occurs in the Middle Eocene section of the La Meseta Formation on Seymour Island which also records the highest levels of benthic diversity within the entire basin. This key section is providing some important new evidence to suggest that the rate of acceleration of benthic predation intensity through the Late Mesozoic–Early Cenozoic in the polar regions may be similar to that seen in lower latitude regions. Predator–prey interaction was a key factor in the evolution of polar marine faunas too.

Keywords drilling, crushing, molluscs, escalation, Seymour Island

Citation: Harper E M, Crame J A, Pullen A M. The fossil record of durophagous predation in the James Ross Basin over the last 125 million years. *Adv Polar Sci*, 2019, 30(3): 199-209, doi: 10.13679/j.advps.2019.0001

1 Introduction

Interactions between organisms are thought to be key factors driving diversity and community structure in recent habitats and also long term changes in diversity and adaptive responses in organisms over evolutionary timescales (Vermeij, 1987; Jablonski, 2008; Taylor, 2016). Of these, predator-prey interactions are arguably most important (Stanley, 2008). Changing levels of predation pressure and repertoire of attack methods has long been associated with the evolution of particular morphological defences (e.g. robust shells or spines), particular life habits (e.g. deep or active burrowing) and behavioral (e.g. swimming or leaping to evade capture) or physiological

responses (e.g. production of toxins) (see Vermeij, 1987, 1993; Skelton et al., 1990; Harper and Skelton, 1993). It also follows that prey taxa that are unable to defend themselves may be forced either to extinction or to live in refuge environments where the predation pressure is less (Vermeij, 1987; Jablonski and Bottjer, 1990). This scenario has been proposed to account for the current distributions of sclerosponges (Jackson et al., 1971), articulate brachiopods (Stanley, 1977) and stalked crinoids (Baumiller and Gahn, 2003) which are generally found to flourish in deeper, colder or more cryptic habitats.

Testing such ideas effectively needs good sources of quantitative data which account for local and regional variability on a range of temporal scales (Harper, 2016). Many forms of predation, such as those where prey is swallowed whole or where either or both of predator and

* Corresponding author, E-mail: emh21@cam.ac.uk

prey are totally soft-bodied, are not possible to study from death assemblages of modern organisms. Instead we must rely on direct observation which limits the amount of data obtainable, and obviously offers no possibility of study in ancient fossilized communities. However, durophages (predators which attack organisms with hard parts either by crushing or drilling through their exoskeletons) do have the potential to produce recognisable damage which may allow the collection of robust data sets on predator-prey interactions from the fossil record (see Harper, 2016 for discussion).

There are a number of different reasons why there might be interest in understanding predator-prey interactions from the fossil record around Antarctica.

(1) Despite the acceptance of the paradigm that predation intensity decreases with increasing latitude, studies demonstrating this are few, and data from genuinely high latitudes (both for modern and fossil sites) are generally lacking.

(2) Major changes in biotic interactions occurred in the Mesozoic, collectively known as the Mesozoic Marine Revolution (MMR) (Vermeij, 1977, 1987). Those changes included an increase in the sophistication of durophagous feeding methods and the radiation of key modern predator groups (such as the neogastropods, fish and decapod crustaceans). Yet the MMR is a complex phenomenon which doubtless played out in different ways in different geographic regions, niches and environments (Vermeij, 2008; Harper, 2003a). Thus far, there have been no studies of the appearance of particular predatory strategies at high latitude.

(3) Although there has been some evidence to suggest that the effects of the K/Pg event were less severe in the high latitudes (Zinsmeister et al., 1989; Keller, 1993; Raup and Jablonski, 1993), a recent re-evaluation of the event in Antarctica indicates that the benthic molluscan fauna suffered a 61% extinction, thus putting it well within the global average of 40%–75% (Witts et al., 2016). There have been a number of studies of the effect of the K/Pg and Eocene/Oligocene extinctions on predator-prey relationships at a number of low latitude sites (Gulf Coast [Kelley and Hansen, 1993, 1996a, 1996b, 2006; Hansen and Kelley, 1995; Hansen et al., 1999; Kelley et al., 2001; Hansen et al., 2004; Reinhold and Kelley, 2005] and India [Mallick et al., 2013, 2014]) but unfortunately far fewer at high latitudes.

(4) The modern Antarctic Fauna is dominated by sessile suspension feeding taxa such as sponges, brachiopods, bryozoans, ascidians and some echinoderms, and relatively few prominent active predators. In particular, sharks, rays and decapod crabs are missing, with few teleosts or skates (Clarke and Crame, 1992; Aronson and Blake, 2001; Hall and Thatje, 2011; Griffiths et al., 2013). This loss of important predatory groups from shallow water communities is believed to result from the Late Eocene global cooling events and loss of shallow-water habitats.

This in turn has been used to infer reduced benthic predation pressures in the Antarctic and the dominance of 'primitive' suspension feeding communities (Aronson and Blake, 2001; Aronson et al., 2007, 2009).

(5) If this reduction of active durophagous predators due to cooling has promoted the development of a poorly defended shallow marine community, it follows that such a fauna may be very susceptible to global warming, allowing re-invasion by active predators (Aronson et al., 2007). Indeed, there is already concern about the effect of lithodids (anomuran King Crabs) on the continental shelf of the western Antarctic Peninsula (Aronson et al., 2015).

In this study we test some of these ideas and principles using the extensive fossil record of the James Ross Basin (JRB). A series of intensive investigations by a variety of research teams over the last forty years has revealed that this is one of the best, and most complete, Late Mesozoic–Early Cenozoic marine sedimentary records at a high paleolatitude (~65°S) in either hemisphere (Crame, this volume). In total, the sedimentary succession is approximately 7 km in thickness and ranges in age from Aptian–Late Eocene. The rocks are of volcanoclastic origin throughout and in general show a broad-scale fining-upwards trend from conglomerates, breccias, and coarse-grained sandstones in the Early Cretaceous to much finer-grained sandstones, siltstones and mudstones in the Late Cretaceous and Paleogene (Crame, this volume, and references therein).

The Early Cretaceous deposits represent the accumulation of a deep marine clastic wedge close to the fault-bounded basin margin. There are some indications of shallowing to shelf depth in the Turonian Brandy Bay Member of the Whisky Bay Formation (Crame, this volume). Further shallow-water facies are recorded from the Coniacian Hidden Lake Formation, but they do not really become extensive until the Santonian–Campanian Santa Marta Formation. Shallow-water facies then predominate throughout the great part of the Late Campanian–Eocene record (Marambio and Seymour Island Groups) within the JRB, and form the main focus of this study. These faunas are of relatively low taxonomic diversity but high abundance.

The geological record of the JRB also includes a very small outcrop of Cockburn Island Formation occurring on the north-eastern tip of Cockburn Island, immediately to the north of Seymour Island (Crame, this volume, Figure 1). This comprises an approximately 10 m thickness of coarse-grained sandstones and pebbly sandstones bearing an extremely shallow-water molluscan fauna of earliest Pliocene age (Jonkers, 1998; Jonkers et al., 2002).

2 Methods

The aim of this contribution is to examine the fossil record of predation in the JRB over the last 125 million years. It necessarily focuses on types of predators that have a

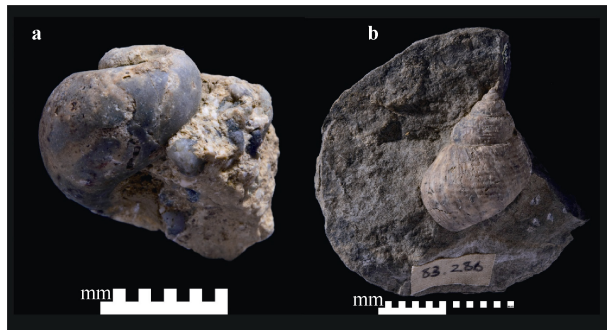


Figure 1 Earliest examples of probable naticid gastropod body fossils from the JRB. **a**, Internal mould from the Whisky Bay Formation (Seymour Island) BAS Collections; **b**, Snow Hill Island Formation (Seymour Island). BAS Collections DJ 83.286.

functional morphology that is easily recognisable in the body fossil record indicating how they fed, or those which leave recognisable evidence on their prey. We concentrate on identifying instances which have, or have the potential to provide, useful data for giving insights into the

evolution of the modern Antarctic fauna. We have surveyed the evidence of durophagous and drilling predation in the geological record of the JRB. Our database for this work was established using a combination of studying all published records of the geological record of the JRB (whether they explicitly recorded predation or not), together with a full examination of all molluscan and worm material in the reference collections housed in both the British Antarctic Survey (BAS), Cambridge UK, and the W. J. Zinsmeister collection in the Paleontological Research Institution (NPI), Ithaca, N.Y. (USA). In all we have screened over 11000 specimens for potential predation damage. Wherever possible we have located specimens to measured stratigraphic sections within each of the principal sedimentary formations as defined in Crame (this volume, Figures 1 and 2). Further details as to the principal sections, lithologies, lithofacies and depositional environments within these formations can be found in the following sources: Scasso et al., 1991; Crame et al., 2004, 2014; Olivero, 2012.



Figure 2 Predatory drill holes, believed to be made by “*Vanikoropsis*” *arktowskiana*, in a variety of shelly prey from the Maastrichtian LBF of Seymour Island. **a**, *Struthiochenopus hurleyi*; **b**, *Cucullaea raea* (DJ.959.141, Klb 7 and 8); **c**, *Leonucula nova* (Number to be obtained, La Meseta); **d**, *Rotularia* sp. (DJ.952. A2, Klb 9); **e**, “*Vanikoropsis*” *arktowskiana* (DJ.951.28, Klb 8) and **f**, *Pycnodonte vesicularis* (DJ.953.627, Klb 9). All specimens in BAS collections.

2.1 Drilling predation

The occurrence of neat drill holes in shelly prey taxa is a very well-known phenomenon which has been often studied in both Recent and fossil assemblages. A number of different taxa are known to be able to drill holes through the shells of their prey (Kabat, 1990) but the major drillers in

modern oceans are gastropods (principally members of the Naticidae and Muricidae, but also Cassidae) (Carriker and Williams, 1978; Hughes and Hughes, 1981; Kelley and Hansen, 2003).

The study of drilling predation is in many respects easier than that of any other form of predation because the resulting drill holes are, with practice, easy to recognise and

distinguish from post mortem damage. Drill hole morphology tends to be reasonably distinctive and thus allow assignment to at least predator clade (e.g. the straight sided holes of muricids, countersunk holes of naticids, or small elliptical holes of octopods) (Carriker, 1981; Bromley, 1993), although some caution is required in making all these identifications (Bromley, 1981). Confidence may increase where drill holes of a particular morphology occur together with body fossils of a candidate driller. Such confidence is less well placed with the reverse situation, that is where body fossils exist of possible drillers but without confirmatory co-occurring drill holes; the presence of adaptations required for drilling (chiefly the accessory boring organ) is not reflected in the shell characters and in any case assigning extinct gastropod species to higher taxa is not necessarily straight forward (Bouchet and Rocroi, 2005). Drill holes may be far more abundant in any bed than the body fossils of the makers which means that they can provide sufficient data for robust quantitative studies. Such data might include the frequency of drilling predation, prey preferences, percentage of incomplete (failed) drill holes, preferential drill hole siting and possible relationship between drill hole diameter (as a proxy for predator size) and prey size (see Kowalewski, 2002; Kelly and Hansen, 2003; Harper, 2003b for reviews of methods).

There is excellent evidence for drilling predation in the JRB, recognising both trace fossil evidence of the drill holes and body fossils of likely drillers. Naticid-like body fossils occur in the BAS collections from the Whisky Bay and Snow Hill Island formations (Figures 1a, 1b, respectively; Crame, this volume, Figures 1 and 2). Scasso et al. (1991) report the occurrence of naticid body fossils throughout the Santa Marta Formation where they co-occur with an abundant bivalve and gastropod fauna, with locally abundant serpulid worms, although they did not record drill holes in these potential prey.

The first definite evidence of drilling predation in the JRB is the abundant presence of countersunk drill holes in the Maastrichtian López de Bertodano Formation (LBF) in a range of bivalves (including *Pycnodonte* [Figure 2f], *Lahillia*, *Cucullaea* [Figure 2b], *Eselaevitrigonia* and *Oistotrigonia*), gastropods (*Struthiochenopus* [Figure 2b], *Taioma*, “*Cassidaria*” [Figure 3a] and “*Vanikoropsis*” [Figure 2e]) and serpulid worm (*Rotularia*) [Figure 2d] prey (Harper et al., 2018). Although in Harper et al. (2018) we chose not to calculate the frequency of drilling predation, the large number of drill holes observed (759 in total; 715 in LBF and 44 in succeeding Sobral Formation) show that such attacks were not uncommon. These circular drill holes were large (up to 6.41 mm in diameter) and, in the time period studied (informal mapping units K1b 8 to Kplb 10 of the LBF and the Sobral Formation; Crame, this volume), holes occurred in a wide selection of prey (15 species of bivalves, 8 species of gastropods and 1 genus of serpulid worm) indicating that the predator was catholic (= including a wide variety) in its diet and differences between taxa in

the prey list at different stratigraphic levels probably reflected availability rather than genuine choice. This was particularly clear after the K/Pg mass extinction event where many of the common prey taxa became extinct locally (trigoniid bivalves and *Rotularia*) while a few ‘disaster taxa’, such as the bivalves *Lahillia larseni* and *Cucullaea ellioti* and gastropod *Struthiochenopus hurleyi*, are abundant in the ‘Recovery Unit’ Kplb 10 (Witts et al., 2016; Crame, this volume). Despite the broad range of prey selected, at all stratigraphic levels there was good evidence that for the commonly eaten taxa there was consistency in drill hole siting and often a significant correlation between drill hole diameter and prey size, indicating familiarity and experience. All drilled taxa were typically soft-bottom dwellers and either sedentary or slow moving. The scale of these drill holes suggests a gastropod driller, and since many of the prey were shallow burrowers, including the semi-infaunal gryphaeid oyster *Pycnodonte* (where most individuals were drilled in the lowermost left valve) the suggestion is that the driller was also infaunal. The only plausible candidate is “*Vanikoropsis*” *arkowskiana*, which Crame et al. (2014) suggest should be placed within a new genus of the Naticidae. Assuming that “*V.*” *arkowskiana* is the driller we also have evidence that it is a cannibal (Figure 2e).

Body and trace fossils of naticid gastropods are also abundant in the Eocene La Meseta Formation (LMF) on Seymour Island (Crame, this volume, Figures 1 and 2). A number of different naticid taxa, including the tropical *Polinices*, have been recognised by earlier authors (e.g. Stilwell and Zinsmeister, 1992) but it seems more likely that they should be referred to the modern Antarctic genus *Falsilunatia* Powell, 1951 (Beu, 2009; Crame et al., 2014). *Falsilunatia* is an important predator in modern Antarctic shallow water settings (Dell, 1990) and which extends the drilling activity of this predatory taxon back into the Middle Eocene. The predatory activities of this naticid are clear in the form of large drill holes (up to 6 mm in diameter) with the classic countersunk (*Oichnus paraboloides*) morphology in a range of molluscan prey, principally the bivalves *Retrotapes*, *Leionucula* (Figure 2c) and also conspecifics (Aronson et al., 2009). This latter cannibalism has also been studied in detail by Brezina et al. (2016) and Dietl et al. (2018). The general results of these studies have been to show that *Falsilunatia* showed familiarity with its prey, exhibiting preference for both prey size classes and drill hole siting. Interestingly, Aronson et al. (2009) found that there was no change in the frequency of drill holes in the abundant venerid bivalve *Eurhomalea* (perhaps more correctly identified as *Retrotapes*) over a pronounced cooling event in the uppermost LMF, and Dietl et al. (2018) showed no change in the frequency of cannibalism over the same interval. Additionally, naticid drill holes have been found in LMF in the burrowing lingulid brachiopod, *Glottidia antarctica* (Wiedman et al., 1988; Bitner, 1996; Emig and Bitner, 2006; Figure 1b).

In contrast to the good record of drilling predation by naticids in the JRB, that by muricid gastropods is much sparser. The earliest drill holes attributable to this family appear to be those in pedunculate terebratulide brachiopods (*Liothyrella* sp. and *Macandrevia cooperi*) from the LMF (Bitner, 1996). These small (0.6–1.4 mm in diameter) cylindrical drill holes (referable to *Oichnus simplex*) in epifaunal prey are typical of muricids (Carriker, 1981). The holes are coincident with the occurrence of two muricids, *Trophon radwini* (Stilwell and Zinsmeister, 1992) and *Eupleura suroabditia* (Stilwell and Zinsmeister, 1992), which occur in the LMF (Beu, 2009; Crame et al., 2014). It is of note that Aronson et al. (2009) found no drill holes in their study of the LMF epifaunal brachiopods *Bouchardia*, perhaps, they suggest, because they were unattractive prey items or because they did not share the same habitat as *Falsilunatia*.

In the younger Pliocene Cockburn Island Formation, which is only exposed on Cockburn Island (Crame, this volume, Figures 1 and 2), numerous large drill holes (1.0 to 6.3 mm) in the large epifaunal scallop *Zygochlamys andersonni* are attributed to muricids by Jonkers (2000) on the basis of similar drilling patterns in modern *Zygochlamys* from New Zealand and the co-occurrence of *Trophon* in the sediments. It is worth noting that they are similar in morphology and size to holes drilled in modern Antarctic bivalves and brachiopods by *Trophon shackletoni* (Harper and Peck, 2003) and from trophonids preying on bivalves in the Beagle Channel (Gordillo, 1998; Gordillo and Amunastegui, 1998; Martinelli et al., 2003).

Although the above studies show that it is possible to demonstrate a fossil record of drilling predation of both naticids and muricids in the JRB, it is difficult to get a sense of how important drilling predation was at any one site. It is a well-known problem that studies which aim to assess drilling frequency by calculating the proportion of drilled versus non-drilled prey items may drastically exaggerate the importance of drilling if crushing predators have removed ‘undrilled’ shells or tubes from the assemblages (Vermeij et al., 1989; Smith et al., 2019). This problem may be particularly acute in situations, such as in the Late Mesozoic–Early Cenozoic of the JRB, where large vertebrates could have been responsible for an unknown amount of predation (see next section; Harper et al., 2018). This problem is also compounded by the fact that our 125 million year time frame covers both the K/Pg mass extinction, when there may have been major shifts in the guilds of crushing predators, and also Late Eocene global cooling, which coincides with the loss of major crushing clades from the modern Antarctic fauna. Both of these events could have had significant effects on drilling frequency calculations (Aronson et al., 2009; Dietl et al., 2018).

Aside from naticid and muricid gastropods, other potential drillers of shelly prey are worth considering for sediments of the JRB age range. Although some faunal lists suggest that the Maastrichtian LBF contains body fossils of

“*Cassidaria*” *mirabilis* Wilckens, 1910, which would be of interest because modern cassids are known to be specialist drillers of echinoderm prey (Hughes and Hughes, 1981), Crame et al. (2014) rejected this tonnoid assignment, suggesting rather that the prominent anterior canal and distinctive pattern of ornament of the shell strongly indicate that it is a neogastropod instead. Octopods are important top predators in modern seas and many of them drill distinctive holes, often exquisitely accurately sited into major muscles in their prey, through which to inject a paralysing venom (Bromley, 1993). The modern Southern Ocean has a rich octopod fauna (Collins and Rodhouse, 2006) and although little appears to have been published on their feeding behaviour and no drill holes are yet reported, their ability to secrete venom is well established (Undheim et al., 2010). Elsewhere, drilling octopods have a trace fossil record that dates at least to the Lower Eocene (Todd and Harper, 2011) and although there are no instances currently recognised in the JRB strata they might be anticipated.

2.2 Crushing predation

In modern oceans organisms that crush the hard parts of their prey (e.g. sharks, teleost fish and a variety of crustaceans) are important predators of a whole variety ‘shelly’ prey, and the mode of feeding has a long evolutionary history (see Vermeij, 1987; Walker and Brett, 2001; Kelley and Hansen, 2003). However, the modern Antarctic Fauna is well known to be impoverished in such crushing groups; sharks, decapod crabs and stomatopods are entirely absent, and skates and teleosts play only a minor role. Their decline has been attributed directly to the Late Eocene global cooling event, onset of glaciation, and loss of shallow-water habitats (Clarke and Crame, 1992; Aronson and Blake, 2001, 2009).

The study of the fossil record of predators which smashed their way into ‘shelly’ prey is much more problematic than that of drillers. The occurrence of body fossils with functional morphologies, either claw or jaws, may suggest that certain taxa were capable of skeletal damage but give little evidence that either were used in this way, rather than for their own defence (Vermeij, 1982). Even if they were so used, there may be few clues to what they were attacking. Recognition of ‘crushed’ prey may be difficult, particularly if the resultant debris is hard to distinguish from either abiotic damage, for example moving rocks or ice (Shanks and Wright, 1986; Cadée, 1999; Harper et al., 2012), or even post mortem breakage. However, the fragmentation patterns seen in shell beds may be indicative; shell breakage caused by predators tends to produce sharp jagged fragments rather than the abraded damage that is caused by breakage during post-mortem transport (Oji et al., 2003; Zatoñ and Salamon, 2008). Indeed, Oji et al. (2003) suggest that there is an increase in fragmentation in shell beds from the Late Cretaceous onwards which relates to the rise in teleost and decapod crustacean predation. However, the most secure evidence of

the biotic nature of shell damage may come from individuals which have suffered unsuccessful attack and subsequently repaired. Such specimens prove that the damage is pre-mortem and allows the recognition of styles of damage and size relationships which may indicate predator behaviour, as is evident in damage repair in a study of modern Antarctic and Falkland Islands brachiopods (Harper et al., 2009).

There is evidence for crushing predation in the JRB, recognising two major groups of potential predators; decapod crustaceans and 'large vertebrates'. The body fossil record of crustaceans has been well studied and it is evident that a range of crustaceans occur throughout the section (e.g. Feldmann and Wilson, 1988; Tshudy and Feldmann, 1988; Feldmann et al., 2003). Trace fossils of their feeding activity exist but have not yet been studied quantitatively. The oldest recorded trace of crustacean durophagy in the JRB is a repaired apertural break in the gastropod *Taioma* by Aguirre-Urreta and Olivero (1992, Figure 3a) from the Santa Marta Formation. Figure 3a shows similar repaired damage in "*Cassidaria*" *mirabilis* from the LBF, and we have recorded repaired breaks in two individuals of *Falsilunatia* (out of a total of 659 individuals) from the Eocene LMF.

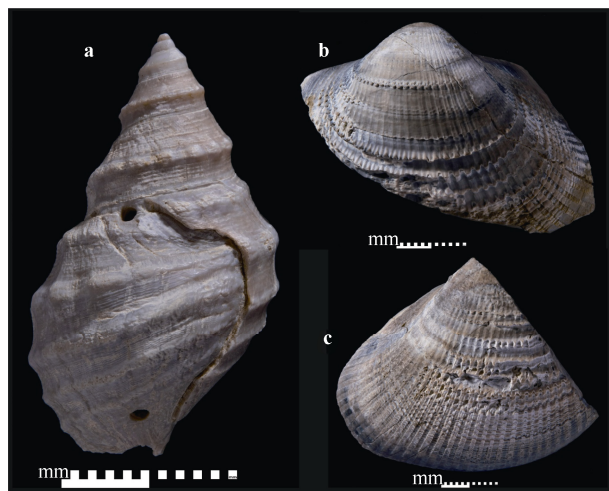


Figure 3 Evidence of crushing predation from Seymour Island. **a**, Repaired apertural damage (and predatory drill holes) in "*Cassidaria*" *mirabilis* from the Maastrichtian LBF; **b** and **c**, Conspicuous damage tentatively recognised as unrepaired predation damage in *Cucullaea raea* from the Middle Eocene La Meseta Formation. All specimens in the BAS collections.

It seems likely that large vertebrates, equipped with crushing or piercing jaws, were important predators in the JRB. They fall into two guilds; marine reptiles and fish. There are several groups of large marine reptiles represented in the Mesozoic sediments of the JRB. O'Gorman (2012) reviews the presence of plesiosaurids throughout the Marambio Group and although we have no direct evidence of their diets, and they may be thought to

predominantly have fed on pelagic fish and cephalopods (Chatterjee and Small, 1989), stomach contents from the Cretaceous of Australia demonstrate that at least some elasmosaurids fed on benthic shelly invertebrates such as bivalves and gastropods (McHenry et al., 2005). Similarly, mosasaur remains are known from the LBF (Martin and Crame, 2006) and again while there is no direct evidence in these sediments of their diets, stomach contents from elsewhere also show that some mosasaurs were capable of scooping up and eating benthic invertebrates (Martin and Fox, 2007). Damage caused by such large reptile predators would be difficult to recognise with any confidence, but it is worth noting that the Kotink Formation yields what appear to be fragmented inoceramids (Ineson et al., 1986).

Although such crushing reptiles became extinct in the K/Pg mass extinction, other guilds of durophagous vertebrates either appeared or radiated afterwards. There is a rich shark fauna recorded from the LMF (Long, 1992; Engelbrecht et al., 2017) and skate teeth have been recorded at one locality (Long, 1994). As with the large reptile predators, confidently identifying predated material proves impossible but it is striking that some of the large arcoid bivalves, *Cucullaea raea*, from the LMF have unusual breaks (Figures 3b and 3c) which are difficult to reconcile with post-mortem transport damage. Although it is far from clear what caused this damage, it is a strong possibility that this is the result of durophagous predation perhaps by some large fish or rays?

3 Discussion

3.1 The history of predation in the JRB

There is an extensive 125 million year history of both durophagous predators and their styles of predation on shelly benthos at this unique high latitude site. It should be reiterated at the outset that poor preservation potential means that soft bodied predators, such as nemerteans, starfish and sessile anemones, which are very important in the modern Antarctic Fauna (Aronson and Blake, 2001; McClintock et al. 2008; Peck and Brockington, 2013), cannot be routinely tracked, nor can the activities of various neogastropod groups (e.g. buccinids and conoideans) which leave no diagnostic damage on their prey. However, starfish from the JRB are well known, with four species from the LMF of Seymour Island (Blake, 1988). Blake (1988, p.491) points out that their presence in a fauna which also contains a rich molluscan fauna is highly suggestive; nevertheless, the details of their participation, and that of other soft bodied predators, in food webs are unknown and are likely to remain so.

It is notable that there is no direct evidence for durophagous predation in the Gustav Group, the stratigraphically oldest in-situ sediments in the JRB which date from the Aptian to Coniacian (Crame, this volume), and the only body fossil evidence of possible predators are

scant shark teeth and vertebrae in the Kotick Point Formation, possible crushed inoceramids, and a single internal mould of a probable naticid gastropod from the Whisky Bay Formation (Figure 1a). At first sight, this lack of signs of predators and their activities is interesting as elsewhere in the world there are comprehensive records of drilling activity in the Early Cretaceous, such as in the Albion Blackdown Greensand of the UK (Taylor et al., 1983). But records are generally uncommon elsewhere until the Later Cretaceous (Kowalewski et al., 1998), and the Gustav Group is interpreted as predominantly sediments from deeper water settings, with inoceramid and oxytomid bivalves (Crame, this volume), and it is known that predation intensity decreases dramatically with increasing water depth (see Harper and Peck, 2016). Nonetheless, both drilling and crushing predation are known in Late Cretaceous inoceramids, for example from the Western Interior Seaway of the US (e.g. Harries and Ozanne, 1998; Ozanne and Harries, 2002; Harries and Schopf, 2003) and Speden (1971) reported apparent faecal masses/regurgitates containing inoceramid debris from the Late Cretaceous of New Zealand. Although these reports may come from shallower water deposits they do indicate that inoceramids were attractive to at least some predators and it might be that the fragmented inoceramids from the Gustav Group would repay further study for evidence of shell damage and or repair.

In a similar way there is potential for predation-focused studies on the Santonian–Campanian Santa Marta Formation, the lowest unit of the Marambio Group. These shallower water deposits have an abundant and diverse body fossil fauna, largely comprising bivalves and gastropods (Scasso et al., 1991), which shows a broad-scale shallowing upwards trend to reveal the first trigoniid bivalve facies in its Beta Member (Crame, this volume). Trigoniid bivalves are demonstrably common prey items in other Jurassic and Cretaceous faunas, e.g. drillholes in Jurassic from India (Bardhan, 2012) and the Early Cretaceous (Albian) Blackdown Greensand of UK (Taylor et al., 1983), as well as higher up in the Marambio Group in the LBF of Seymour Island (Harper et al., 2018). They are also the victims of crushing predation in the Jurassic of Poland (Zatoń and Salamon, 2008). Similarly, arcoid bivalves and aporrhaid gastropods are also drilled frequently in the Blackdown Greensand (Taylor et al., 1983), as well as the LBF (Harper et al., 2018). However, despite the occurrence of naticids (yet to be formally described) in the Santa Marta Formation (Scasso et al., 1991), there have been no drill holes reported and only one record of a *Taioma* with a repaired break (Aguirre-Urreta and Olivero, 1992). It would be instructive to know if this absence of documented trace fossil evidence of predation is genuine or the result of it not having been recognised.

The fossil record of the latest part of the Marambio Group (i.e. the LBF) and the Eocene LMF provide excellent evidence for both the occurrence of taxa likely to have been

durophagous and trace fossil activity of drilling and crushing predation. The first certain JRB naticid drill holes occur in Unit K1b 5 of the LBF and these then occur plentifully throughout the LBF, including over the K/Pg mass extinction horizon and into the Sobral Formation (Harper et al., 2018), and then throughout the Eocene LMF. Although there have been several reports of cannibalism within the LMF naticids (Brezina et al., 2016), comparatively little is known about other aspects of their behaviour. A conference abstract by Kelley et al. (1997) does suggest that the frequencies of drilling predation observed in the LMF are not substantially different to those of the same age from the tropical/subtropical US Gulf Coast (Kelley and Hansen, 1993; Hansen and Kelley, 1995). There is scope, perhaps, to test and extend these observations with more data and also to compare results with other broadly coeval data from the Calcaire Grossier Formation (Lutetian, France) (Taylor, 1970) and Ameki Formation (Middle Eocene, Nigeria) (Adegoke and Tevesz, 1974), both of which have plentiful records of drilling predation.

In contrast to the long and excellent record of naticid drill holes, there are no certain muricid records from the diverse gastropod fauna of the LBF. The first recognised muricid holes occur in brachiopods within the Middle Eocene Telms 2–5 of the LMF, and even there the data are relatively sparse, perhaps largely because these are soft-bottom faunas which are less associated with muricid gastropods but also recognising that the Paleogene precedes the major Neogene radiation of the group (Vermeij, 1996). Nevertheless, muricid gastropods are today the second most important neogastropod group in the Antarctic at the present day (i.e. after Buccinidae) (Dell, 1990; Harper and Peck, 2003).

The record of crushing predators for both the LBF and LMF are good, but it is notable that the guilds involved have changed, most notably over the K/Pg mass extinction with the loss of marine reptiles and the subsequent radiation of fish and sharks. Our failure to be able to link any of these vertebrate crushers with specific trace fossils, however, makes any kind of quantitative analysis of frequency of attack or changing behaviours impossible to assess. This is particularly vexing as this seriously impacts our ability to understand the relative importance of the more easily quantified drilling predation. Crushing crustaceans are easier to track as the damage, at least for some of them, are more easily recognised and suitable for quantitative studies (Alexander and Dietl, 2003; Dietl and Kosloski, 2013). However, thus far there have been no systematic collections of data for shell repair of this type.

3.2 Changes in predatory activity over time

The above synthesis indicates that the Late Mesozoic–Early Cenozoic evolution of benthic predation patterns in the polar regions is essentially similar to that seen at the more familiar lower latitude localities. Predation intensity

increases significantly in the Late Cretaceous and continues unabated across the K/Pg boundary into the Early Cenozoic. It is noticeable that as predation intensity increases up-section so too does taxonomic diversity. The Middle Eocene section of the LMF records the highest level of species richness in the entire JRB (Crame, this volume). Evolutionary escalation, whereby a predator–prey ‘arms race’ accelerates evolutionary diversification (Vermeij, 1987), may also be an important process in the polar regions.

Although we now know that the K/Pg mass extinction event in Antarctica was just as intense as elsewhere in the world (Witts et al., 2016), there is very little recorded change in the styles of predator–prey relationships across this key boundary. The types of predator may have changed but the intensity of their interaction with the benthos remained essentially similar (Harper et al., 2018). A further interesting feature to have emerged recently is the retrograde character of the current Antarctic shallow marine fauna, with its distinct “Paleozoic” appearance, and it is thought that the elimination of important shell crushing predators following Late Eocene cooling (which is recorded in the very highest levels of the Seymour Island sedimentary succession) is very largely responsible for this (Aronson et al., 1997, 2007, 2009; Aronson and Blake, 2001; Eastman 2005; Ivany et al., 2008). Cooling in turn may have had an interesting effect on drilling predation in the region. Drilling in both muricid and naticid gastropods is a largely chemical process (Carriker and Williams, 1978) and it might be expected that this would be slow in the very cold waters; indeed, Harper and Peck (2003) found that in aquarium studies the muricid *Trophon longstaffi* took up to 29 d to drill and feed on *Laternula elliptica* and up to 20 d to despatch *Liothyrella uva*. It might be anticipated that such long feeding times, where the predator is prone to disturbance by either environmental changes or competitors and attack by their own predators (Kelley and Hansen, 2003; Hutchings and Herbert, 2013) would deter this type of predation. In fact naticids are key elements of the modern Antarctic fauna (Dell, 1990) and their intensive activity can be traced back to the Middle Eocene LMF and the Maastrichtian LBF and Snow Hill Island formations. Muricids are prominent in the modern Antarctic fauna too (Dell, 1990), despite the apparently very slow rates of drilling in cold water (Harper and Peck, 2003). Their predominantly Neogene global radiation is less conspicuous in the southern high latitudes, although there are records from the Early Miocene Cape Melville Formation of King George Island, South Shetland Islands (Beu, 2009).

The backdrop of changing predator–prey interactions in the fossil record of the JRB is perhaps best viewed as a combination of water depth change and global cooling. However, further work is needed to identify any subtleties which might accompany shorter term climatic events within this timeframe (e.g. Huber et al., 2018). There is also the interesting observation from outside the JRB there is

evidence for decapod groups in close association with diamictite and dropstones as late as the Miocene Cape Melville Formation (Whittle et al., 2014) which suggest perhaps that their general exclusion from the modern Antarctic Fauna is not due only to the Eocene cooling event. Finer scale data, linked with detailed environmental data will surely shed further light on these issues.

Acknowledgments We are grateful to the NERC grant NE/I005803/1 and various colleagues who have been worked in the field to collect the many samples on which our studies are based. We thank both Greg Dietl and Judith Nagel-Myers for allowing us access to the PRI collections. We are also grateful to Peter Bucktrout (BAS) and Sharon Stewart (Cambridge Earth Sciences) for help with the figures.

References

- Adegoke O S, Tevesz M J S. 1974. Gastropod predation patterns in the Eocene of Nigeria. *Lethaia*, 7: 17-24.
- Aguirre-Urreta M B, Olivero E B. 1992. A Cretaceous hermit crab from Antarctica: predatory activities and bryozoan symbiosis. *Antarc Sci*, 4: 207-214.
- Alexander R R, Dietl G P. 2003. The fossil record of shell-breaking predation on marine bivalves and gastropods//Kelley P H, Kowalewski M, Hansen T A. Predator–prey interactions in the fossil record. Kluwer, 141-176.
- Aronson R B, Blake D B. 2001. Global climate change and the origin of modern benthic communities in Antarctica. *Am Zool*, 41: 27-39.
- Aronson R B, Blake D B, Oji T. 1997. Retrograde community structure in the late Eocene of Antarctica. *Geology*, 25: 903-90.
- Aronson R B, Moody R M, Ivany L C, et al. 2009. Climate change and trophic response of the Antarctic bottom fauna. *PLoS ONE*, 4(2), e4385.
- Aronson R B, Smith K E, Vos S C, et al. 2015. No barrier to emergence of bathyal king crabs on the Antarctic shelf. *PNAS*, 12 (42): 12997-13002.
- Aronson R B, Thatje S, Clarke A, et al. 2007. Climate change and the invasibility of the Antarctic benthos. *Annu Rev Ecol Evol Syst*, 38: 129-154.
- Bardhan S, Chattopadhyay D, Mondal S, et al. 2012. Record of intense predatory drilling from Upper Jurassic bivalves of Kutch, India: implications for the history of biotic interaction. *Palaeogeog Palaeoclim Palaeoecol*, 317: 153-161.
- Baumiller, T K, Gahn F J. 2003. Predation on crinoids//Kelley P H, Kowalewski M, Hansen T A. Predator–prey interactions in the fossil record. Kluwer, 263-278.
- Beu A G. 2009. Before the ice: Biogeography of Antarctic Paleogene molluscan faunas. *Palaeogeog Palaeoclim Palaeoecol*, 284: 191-226.
- Bitner M A. 1996. Encrusters and borers of brachiopods from the La Meseta Formation (Eocene) of Seymour Island, Antarctica. *Pol Polar Res*, 17: 21-28.
- Blake D B. 1988. Eocene asteroids (Echinodermata) from Seymour Island, Antarctic Peninsula. *Mem Geol Soc Am*, 169: 489-498.
- Bouchet P, Rocroi J-P. 2005. Classification and nomenclator of gastropod families. *Malacologia*, 47: 1-397.

- Brezina S S, Cech N, Martin Serralta D, et al. 2016. Cannibalism in Naticidae from the La Meseta Formation (Eocene, Antarctica). *Antarc Sci*, 28: 205-215.
- Bromley R G. 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geol Hisp*, 16: 55-64.
- Bromley R G. 1993. Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. *Bull Geol Society Denmark*, 40: 167-173.
- Cadée G C. 1999. Shell damage and shell repair in the Antarctic limpet *Nacella concinna* from King George Island. *J Sea Res*, 41: 149-161.
- Carriker M R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, 20: 403-422.
- Carriker M R, Williams L G. 1978. The chemical mechanism of shell dissolution by predatory boring gastropods: a review and a hypothesis. *Malacologia*, 17: 143-156.
- Chalcraft D R, Reseratis W J. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology*, 84: 2407-2418.
- Chatterjee S, Small B J. 1989. New plesiosaurs from the Upper Cretaceous of Antarctica//Crame J A. Origins and evolution of the Antarctic biota. *Geol Soc Lond Spec Pub*, 47: 197-215.
- Clarke A, Crame J A. 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Phil Trans Roy Soc B*, 338: 299-309.
- Collins Ma, Rodhouse P G K. 2006. Southern Ocean cephalopods. *Adv Mar Biol*, 50: 191-265.
- Crame J A. 2019. Paleobiological significance of the James Ross Basin. *Adv Polar Sci*, 30(3): 186-198, doi: 10.13679/j.adyps.2018.0047.
- Crame J A, Beu A G, Ineson J R, et al. 2014. The early origin of the Antarctic marine fauna and its evolutionary implications. *PLoS ONE*, 9: e114732.
- Crame J A, Francis J E, Cantrill D J, et al. 2004. Maastrichtian stratigraphy of Antarctica. *Cret Res*, 25: 411-423.
- Dietl G P, Kosloski M E. 2013. On the measurement of repair frequency: how important is data standardization. *Palaaios*, 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. *Roy Soc Open Sci*, 5: 181446. <http://dx.doi.org/10.1098/rsos.1>.
- Eastman J T. 2005. The nature of the diversity of Antarctic fishes. *Polar Biol*, 28: 93-107.
- Emig C, Bitner M A. 2006. *Glottidia* (Brachiopoda: Lingulidae) from the Eocene La Meseta Formation, Seymour Island, Antarctica. *Palaeontology*, 48: 423-431.
- Engelbrecht A, Mörs T, Reguero M A, et al. 2017. New carcharhiniform sharks (Chondrichthyes, Elasmobranchii) from the early to middle Eocene of Seymour Island, Antarctic Peninsula. *J Vert Pal*, 37: 6, doi: 10.1080/02724634.2017.1371724.
- Feldmann R M, Wilson M T. 1988. Eocene decapod crustaceans from Antarctica. *Mem Geol Soc Am*, 169: 465-488.
- Feldmann R M, Tshudy D M, Thomson M R A. 1993. Late Cretaceous and Paleocene Decapod Crustaceans from James Ross Basin, Antarctic Peninsula: Memoir of the Paleontological Society, 28: 1-41.
- Feldmann R M, Schweitzer C E, Marensi S A. 2003. Decapod crustaceans from the Eocene La Meseta Formation, Seymour Island, Antarctica: a model for preservation of decapods. *J Geol Soc*, 160: 151-160.
- Förster R, Gaździcki A, Wrona R. 1987. Homolodromiid crabs from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica. *Palaeontol Pol*, 49: 147-161.
- Gaparini Z, Del Valle R, Goñi R. 1984. Un elasmosaurio (Reptilia, Plesiosauria) del Cretácico Superior de la Antártida (An elasmosaurid [Reptilia, Plesiosauria] from the Upper Cretaceous of Antarctica). *Contribuciones del Instituto Antártico Argentino*, 305: 1-24.
- Gordillo S. 1998. Trophonid gastropod predation on Recent bivalves from the Magellanic region//Johnston P A, Haggart J W. Bivalves: an eon of evolution Paleobiological Studies honouring Norman D. Newell. Calgary University Press, Calgary, 251-254.
- Gordillo S, Amunátegui S. 1998. Estragias de depredación del gastrópodo perforador *Trophon geversianus* (Pallas) (Muicoidea: Trophonidae). *Malacologia*, 39: 83-91.
- Grande L, Chatterjee S. 1987. New Cretaceous fish fossils from Seymour Island, Antarctic Peninsula. *Palaeontology*, 30: 829-837.
- Griffiths H J, Whittle R J, Roberts S J, et al. 2013. Antarctic crabs: invasion or endurance? *PLoS ONE*, 8, e66981.
- Hall S, Thatje S. 2011. Temperature-driven biogeography of the deep-sea family Lithodidae (Crustacea: Decapoda: Anomura) in the Southern Ocean. *Polar Biol*, 34: 363-370.
- Hansen T A, Kelley P H. 1995. Spatial variation of naticid gastropod predation in the Eocene of North America. *PALAIOS*, 10: 268-278.
- Hansen T A, Kelley P H, Haasl D M. 2004. Paleocological patterns in molluscan extinctions and recoveries: comparison of the Cretaceous–Paleogene and Eocene–Oligocene extinctions in North America. *Palaeogeogr Palaeoclimatol Palaeoecol*, 214: 233-242.
- Hansen T A, Kelley P H, Melland V, et al. 1999. The effect of climate-related mass extinctions on escalation in molluscs. *Geology*, 27: 1139-1142.
- Harper E M. 2003a. The Mesozoic marine revolution//Kelley P, Kowaleski M, Hansen T. Predator-Prey interactions in the fossil record. New York: Kluwer Academic, 433-455.
- Harper E M. 2003b. Assessing the importance of drilling predation over the Palaeozoic and Mesozoic. *Palaeogeogr Palaeoclimatol Palaeoecol*, 201: 185-198.
- 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, Sogot C E. 2018. 'Business as usual': drilling predation across the K-Pg mass extinction event in Antarctica. *Palaeogeogr Palaeoclimatol Palaeoecol*, 498: 115-126.
- Harper E M, Clark M S, Hoffman J I, et al. 2012. Iceberg scour and shell damage in the Antarctic bivalve *Laternula elliptica*. *PLoS ONE*, 7(9): e46341.
- Harper E M, Peck L S. 2003. Predatory behaviour and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biol*, 26: 208-217.
- Harper E M, Peck L S. 2016. Latitudinal and depth gradients in marine predation pressure. *Glob Ecol Biogeogr*, 25: 670-678.
- Harper E M, Peck L S, Hendry K R. 2009. Patterns of shell repair in articulate brachiopods indicate size constitutes a refuge from predation. *Mar Bio*, 156: 1993-2000, doi: 10.1007/s00227-009-1230-1.
- Harper E M, Skelton P W. 1993. The Mesozoic marine revolution and epifaunal bivalves. *Scripta Geol Special Issue*, 2: 127-153.
- Harries P J, Ozanne C R. 1998. General trends in predation and parasitism upon inoceramids. *Acta Geol Pol*, 48(4): 377-386.

- Harries P J, Schopf K M. 2003. The first evidence of drilling predation in inoceramids. *J Paleont*, 77 (5): 1011-1015.
- Huber B T, Macleod K G, Watkins D K. 2018. The rise and fall of the Cretaceous Hot Greenhouse climate. *Glob Planet Change*, 167: 1-23.
- Hughes R N, Hughes H P I. 1981. Morphological and behavioural aspects of feeding the Cassidae (Tonnacea; Mesogastropoda). *Malacologia*, 20: 385-402.
- Hutchings J A, Herbert G S. 2013. No honor among snails: Conspecific competition leads to incomplete drill holes by a naticid gastropod. *Palaeogeogr Palaeoclimatol Palaeoecol*, 379-380: 32-38.
- Jablonski D. 2008. Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution*, 62: 715-739.
- Jablonski D, Bottjer D J. 1990. The origin and diversification of major groups: environmental patterns and macroevolutionary lags//Taylor P D, Larwood G P. Major evolutionary radiations. Systematics Association Special Volume, 42, Oxford University Press, 17-57.
- Jackson J B C, Goreau T F, Hartman W D. 1971. Recent brachiopod-coraline sponge communities and their paleoecological significance. *Science*, 173: 623-625.
- Jonkers H A. 1998. The Cockburn Island Formation, Late Pliocene interglacial sedimentation in the James Ross Basin, northern Antarctic Peninsula. *Newsl Stratigr*, 36: 63-76.
- Jonkers H A. 2000. Gastropod predation patterns in Pliocene and Recent pectinid bivalves from Antarctica and New Zealand. *NZ J Geol Geophy*, 43: 247-254.
- Jonkers H A, Lirio J M, Del Valle R A, et al. 2002. Age and depositional environment of the Miocene–Pliocene glaciomarine deposits, James Ross Island, Antarctica. *Geol Mag*, 139: 577-594.
- Kabat A R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia*, 32: 155-193.
- Keller G. 1993. The Cretaceous-Tertiary boundary transition in the Antarctic Ocean and its global implications: *Mar. Micropaleontol*, 21: 1-45.
- Kelley P H, Hansen T A. 1993. Evolution of the naticid gastropod predator-prey system: an evaluation of the hypothesis of escalation. *PALAIOS*, 8: 358-375.
- Kelley P H, Hansen T A. 1996a. Naticid gastropod prey selectivity through time and the hypothesis of escalation. *PALAIOS*, 11: 437-445.
- Kelley P H, Hansen T A. 1996b. Recovery of the naticid gastropod predator-prey system from the Cretaceous-Tertiary and the Eocene-Oligocene extinction. *Geol Soc Spec Publ*, 102: 373-386.
- Kelley P H, Hansen T A. 2003. The fossil record of drilling predation on bivalves and gastropods//Kelley P, Kowalewski M, Hansen T A. Predator–prey interactions in the fossil record, Springer, 113-139.
- Kelley P H, Hansen T A, Graham S E, et al. 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States coastal plain. *Palaeogeogr Palaeoclimatol Palaeoecol*, 166: 165-176.
- Kelley P, Thomann C, Hansen T, et al. 1997. A world apart but not so different: Predation by naticid gastropods in Antarctica and the U.S. Gulf Coast during the Eocene (abstract). *Geol Soc Am Abst Prog*, 29: A107.
- Kellner A, Simões T, Riff D, et al. 2011. The oldest plesiosaur (Reptilia, Sauropterygia) from Antarctica. *Polar Res*, 30: 1-6, doi: 10.3402/polar.v30i0.7265.
- Kowalewski M. 2002. The fossil record of predation: an overview of analytical methods. The fossil record of predation. *Pal Soc Sepcial Papers*, 8: 3-42.
- Kowalewski M, Dulai A, Fürsich F T. 1998. A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology*, 26(12): 1091-1094.
- Long D R. 1992. Sharks from the La Meseta Formation (Eocene), Seymour Island, Antarctic Peninsula. *J Vert Paleont*, 12: 11-32.
- Long D R. 1994. Quaternary colonization or Paleogene persistence? Historical biogeography of skates (Chondrichthyes: Rajidae) in the Antarctic ichthyofauna. *Paleobiol*, 20: 215-228.
- Mallick S, Bardhan S, Paul S, et al. 2013. Intense naticid drilling predation on turrilline gastropods from the Indian subcontinent from the K-T boundary at Rajahmundry, India. *PALAIOS*, 28: 683-696.
- Mallick S, Bardhan S, Das S S, et al. 2014. Naticid drilling predation on gastropod assemblages across the K-T boundary in Rajamundry, India: new evidence for escalation hypothesis. *Palaeogeogr Palaeoclimatol Palaeoecol*, 411: 216-228.
- Martin J E, Crame J A. 2006. Palaeobiological significance of high-latitude Late Cretaceous vertebrate fossils from the James Ross Basin, Antarctica. *Geol Soc Spec Publ*, 258: 109-124.
- Martinelli J C, Gordillo S, Archuby F. 2013. Muricid drilling predation at high latitudes: insights from the southernmost Atlantic. *PALAIOS*, 28: 33-41.
- Martin J E, Fox J E. 2007. Stomach contents of *Globidens*, a shell-crushing mosasaur (Squamata), from the Late Cretaceous Pierre Shale Group, Big Bend area of the Missouri River, central South Dakota. *Geol Soc Amer Special Pap*, 427: 167-176.
- McClintock J B, Angus R A, Ho C, et al. 2008. A laboratory study of behavioral interactions of the Antarctic keystone sea star *Odontaster validus* with three sympatric predatory sea stars. *Mar Biol*, 154: 1077-1084.
- Mchenry C R, Cook A G, Wroe A. 2005. Bottom-feeding plesiosaurs. *Science*, 310: 75.
- O’Gorman J P, Gasparini Z, Reguero M. 2010. *Aristonectes parvidens* Cabrera (Sauropterygia, Plesiosauria) from Cape Lamb, Vega Island (Upper Cretaceous), Antarctica. The Fourth Scientific Committee on Antarctic Research Open Science Conference, 36 August, Buenos Aires, Argentina.
- O’Gorman J P. 2012. The oldest elasmosaurs (Sauropterygia, Plesiosauria) from Antarctica, Santa Marta Formation (upper Coniacian? Santonian–upper Campanian) and Snow Hill Island Formation (upper Campanian–lower Maastrichtian), James Ross Island. *Polar Res*, 31: 1-10.11090, doi: 10.3402/polar.v31i0.11090.
- Oji T, Ogaya C, Sato T. 2003. Increase of shell crushing predation in fossil shell fragmentation. *Paleobiol*, 29: 520-526.
- Olivero E B. 2012. Sedimentary cycles, ammonite diversity and palaeoenvironmental changes in the Upper Cretaceous Marambio group, Antarctica. *Cret Res*, 34: 348-366.
- Ozanne C R, Harries P J. 2002. Role of predation and parasitism in the extinction of the inoceramid bivalves: an evaluation. *Lethaia*, 35: 1-19.
- Peck L S, Brockington S A. 2013. Growth in the Antarctic octocoral *Primnoella scotiae* and predation by the anemone *Dactylanthus antarcticus*. *Deep Sea Res II*, 92: 73-78.
- Pirrie D, Crame J A, Riding J B. 1991. Late Cretaceous stratigraphy and sedimentology of Cape Lamb, Vega Island, Antarctica. *Cret Res*, 12: 227-258.

- Pirrie D, Feldman R M, Buatois L A. 2004. A new decapod trackway from the Upper Cretaceous, James Ross Island, Antarctica. *Palaeontology*, 47: 1-12.
- Raup D M, Jablonski D. 1993. Geography of end-Cretaceous marine bivalve extinctions. *Science*, 260: 971-973.
- Reguerro M A, Marsenssi S A, Santillana S M. 2012. Weddellian marine/coastal vertebrate diversity from the basal horizon (Ypresian, Eocene) of the *Cuccullaea* I Allomember, La Meseta Formation, Seymour (Marambio) Island, Antarctica. *Rev Peru Biol*, 19: 275-284.
- Reinhold M E, Kelley P H. 2005. The influence of antipredatory morphology on survivorship of the Owl Creek Formation molluscan fauna through the end-Cretaceous extinction. *Palaeogeogr Palaeoclimatol Palaeoecol*, 217: 143-153.
- Richter M, Ward D J. 1990. Fish remains from the Santa Marta Formation (Late Cretaceous) of James Ross Island, Antarctica. *Antarc Sci*, 2: 67-76.
- Scasso R A, Olivero E B, Buatois L A. 1991. Lithofacies, biofacies, and ichnoassemblage evolution of a shallow submarine volcanoclastic fan-shelf depositional system (Upper Cretaceous, James Ross Island, Antarctica). *J S Am E Sci*, 4(3): 239-260.
- Shanks A L, Wright W G. 1986. Adding teeth to wave action: the destructive effects of wave-born rocks on intertidal organisms. *Oecologia*, 69: 420-428.
- Skelton P W, Crame J A, Morris N J, et al. 1990. Adaptive divergence and taxonomic radiation in post-Palaeozoic bivalves//Taylor P D, Larwood G. Major evolutionary radiations. Systematics Association Special Volume 42, Oxford University Press, 91-117.
- Smith J A, Dietl G P, Handley J C. 2019. Durophagy bias: The effect of shell destruction by crushing predators on drilling frequency. *Palaeogeogr Palaeoclimatol Palaeoecol*, 514: 690-694.
- Speden I A. 1971. Notes on New Zealand fossil Mollusca, 2: Predation on New Zealand Cretaceous species of *Inoceramus* (Bivalvia). *NZ J Geol Geophy*, 14: 56-60.
- Stanley S M. 1977. Trends, rates, and patterns of evolution in the Bivalvia//Hallam A. Patterns of evolution, as illustrated by the fossil record. Elsevier, 209-250.
- Stanley S M. 2008. Predation defeats competition on the seafloor. *Paleobiol*, 34: 1-22.
- Stilwell J D, Zinsmeister W J. 1992. Molluscan systematic and biogeography. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *Ant Res Ser*, 55: 192.
- Taylor J D. 1970. Feeding habits of predatory gastropods in a Tertiary (Eocene) molluscan assemblage from the Paris Basin. *Palaeontology*, 13: 254-260.
- Taylor J D, Cleavelly R D, Morris N J. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology*, 26: 521-553.
- Taylor P D. 2016. Competition between encrusters on marine hard substrates and its fossil record. *Palaeontology*, 59: 481-497.
- Todd J A, Harper E M. 2011. Stereotypical boring behaviour inferred from the earliest known octopod feeding traces: Early Eocene, southern England. *Lethaia*, 44: 214-222.
- Tshudy D M, Feldmann R M. 1988. Macrurous decapod crustaceans, and their epibionts, from the López de Bertodano Formation (Late Cretaceous), Seymour Island, Antarctica. *Mem Geol Soc Am*, 169: 291-301.
- Undheim E A B, Georgieva D N, Thoen H H, et al. 2010. Venom on ice: First insights into Antarctic octopus venoms. *Toxicon*, 56: 897-913.
- Vermeij G J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiol*, 3: 245-258.
- Vermeij G J. 1982. Unsuccessful predation and evolution. *Am Nat*, 120: 701-720.
- Vermeij G J. 1987. Evolution and escalation: an ecological history of life. Princeton University Press, 527.
- Vermeij G J. 1993. A natural history of shells. Princeton University Press, 207.
- Vermeij G J. 1996. Marine biological diversity: muricid gastropods as a case study//Jablonski D, Erwin D H, Lipps J H. Evolutionary paleobiology. Chicago: University of Chicago Press, 355-375.
- Vermeij G J. 2008. Escalation and its role in Jurassic biotic history. *Palaeogeogr Palaeoclimatol Palaeoecol*, 263: 3-8.
- Vermeij G J, Dudley E C, Zipser E. 1989. Successful and unsuccessful drilling predation in Recent pelecypods. *Veliger*, 32: 266-273.
- Walker S E, Brett C E. 2002. Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Pal Soc Special Papers*, 8: 119-193.
- Wiedman A, Feldmann R M, Lee D E, et al. 1988. Brachiopoda from the La Meseta Formation (Eocene), Seymour Island, Antarctica. *Mem Geol Soc Am*, 169: 449-457.
- Whittle R J, Quaglio F, Griffiths H J, et al. 2014. The Early Miocene Cape Melville Formation fossil assemblage and the evolution of modern Antarctic marine communities. *Naturwissenschaften*, 101: 47-59.
- Whitham A G, Ineson J R, Pirrie D. 2006. Marine volcanoclastics of the Hidden Lake Formation (Coniacian) of James Ross Island, Antarctica: an enigmatic element in the history of a back-arc basin//Francis J E, Pirrie D, Crame J A. Cretaceous–Tertiary high-latitude palaeoenvironments: James Ross Basin, Antarctica. *Geol Soc Lond Spec Pub*, 258: 21-47.
- Witts J D, Whittle R J, Wignall P B, et al. 2016. Macrofossil evidence for a rapid and severe Cretaceous–Paleogene mass extinction in Antarctica. *Nat Comms*, 7: 11738.
- Zatoń M, Salamon M Z A. 2008. Durophagous predation on Middle Jurassic molluscs, as evidenced by shell fragmentation. *Palaeontology*, 51(1): 63-67.
- Zinsmeister W J, Feldmann R M, Woodbourne M O, et al. 1989. Latest Cretaceous/earliest Tertiary transition on Seymour Island, Antarctica. *J Paleontol*, 63: 731-738.