

1 UNCOVERING THE HOLES AND CRACKS: FROM ANECDOTE TO TESTABLE
2 HYPOTHESES IN PREDATION STUDIES

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7 **Abstract:** Biological interactions between organisms have long been believed to be very
8 important in structuring communities and, scaled up over geological time, in the evolution of
9 organisms. Investigations of palaeontological evidence for predator-prey interactions have
10 been popular pursuits and a number of attractive hypotheses have been proposed which link
11 increased predation pressure with a whole range of morphological and ecological changes
12 which are apparent over the course of the Phanerozoic. In particular studies of fossil drill
13 holes and repair scars in shelly prey have been common targets for research. However the
14 nature of some of our data has been rather anecdotal and restricted in range. Perhaps we
15 should be more concerned that we are not picking up the true range of natural variability.
16 This paper aims to highlight the sources of variability in our data and, going forward, to urge
17 the collection of quantitative data from many more samples and (palaeo)environmental
18 settings in order that we might properly be able to separate the intrinsic natural variability in
19 our data from robust temporal or spatial trends.

20 **Keywords:** predation, drill holes, repair frequency, palaeoecology, macroevolution
21

22 THE profound impact of biological interactions in modern communities (both marine and
23 terrestrial) is well known. While Taylor (2016) reviewed the importance of competition
24 between organisms, this contribution focuses on the importance of predatory interactions in
25 the marine realm.

26 At the level of the solitary organism the impact of predatory activity is clear; successful
27 predation is, of course, terminal resulting in loss of potential fecundity. Even an unsuccessful
28 predation attempt incurs costs on the fitness of the target prey organism through the
29 metabolic costs associated with both hard and soft tissue repair and the consequent re-
30 allocation of resources to this end. It is also likely that leakage of body fluids may make a
31 second attack more likely (Vermeij 1983). For colonial organisms, predation is more similar
32 to grazing and the case is less straightforward. Loss of individuals, although not terminal,

1 may reduce overall colony fitness through costs associated with induced defences or loss of
2 reproductive structures (Harvell 1986; Rotjan and Lewis 2009; Wang *et al.* 2015) but may be
3 beneficial in other ways by allowing removal of competitors or helping to create recruitment
4 opportunities where space is limited (e.g. Mumby 2009). At the community level, predators
5 are known to control the distribution and diversity of prey organisms by preventing
6 superabundance and domination by major space occupiers (Connell 1970; Paine 1974;
7 Menge and Sutherland 1987) and gradients in predation pressure are thought to influence
8 latitudinal species diversity (Freestone and Osman 2010; Freestone *et al.* 2011) .

9

10 **AN EVOLUTIONARY IMPORTANCE FOR PREDATION?**

11 It is perhaps a relatively easy step to scale up the importance of predation in modern
12 communities to an importance on evolutionary timescales and it is clear from the fossil record
13 that some organisms have been attacking others from at least the late Pre Cambrian
14 (Bengston and Zhao 1992). Many attractive hypotheses have been advanced that invoke
15 changes in either levels or styles of predation pressure to explain a range of
16 macroevolutionary phenomena (Jablonski 2008). From the evolution of hardparts during the
17 Cambrian explosion (Vermeij 1989; Knoll 2003) and set against a backdrop of the
18 intensification and increased sophistication of predation during the mid-Palaeozoic (Signor
19 and Brett 1984; Brett and Walker 2002) and Mesozoic marine revolutions (Vermeij 1977,
20 1978, 1987) a range of changes have been envisaged that might be attributable to increased
21 predation pressure. These include the appearance of morphological adaptations such as thick
22 or spiny shells, reduced exposed apertures (Vermeij 1977, 1987; Kelley 1989; Klompmaker
23 and Kelley 2015), the adoption of new life habits such as deep burrowing (Kier 1974,
24 Stanley 1977) and reduction of ‘exposed’ epifaunal habits, such as epibyssate attachment
25 (Skelton *et al.* 1990) and shifts in distribution with more susceptible taxa being restricted
26 particularly to refuges (Stanley 1977; Jablonski and Bottjer 1990; Baumiller and Gahn
27 2003).

28 In particular, Vermeij (1987) has been a driving force in generating a whole range of
29 hypotheses concerning the evolution of predators and their prey, introducing the notion of
30 escalation where the driving force behind predator-prey evolution is governed by the
31 predator’s own enemies rather than the classic arms race in which the prey ‘lead’, and
32 compiling the first real sets of data that might test these ideas. That seminal contribution
33 ignited a whole field; Vermeij (1987) has been cited over 1370 times (Googlescholar July

1 2016). Predation studies in the fossil record have become a hive activity as witnessed by the
2 proliferation of papers, particularly on molluscan subjects. However some of our data has
3 been rather anecdotal, often restricted to a few specimens or single localities. There are
4 obvious problems with trying to construct long term trends from very few data points. As a
5 result we have not managed to test the major ideas and hypotheses because we are as yet to
6 gain a good grasp of the complex variability of our data nor to grapple with the timescales
7 necessary (Jablonski 2008). The more we have looked the more complex, and therefore
8 interesting, the issues have become. Some of the very few large scale data-rich studies have
9 that been performed concern drilling predation on bivalve and gastropod prey from U.S. Gulf
10 Coast in the wake of the K-Pg mass extinction (summarised by Kelley *et al.* 2001, Kelley
11 and Hansen 1993, 2006). Those studies have revealed a complex series of escalation series
12 mediated by the K-Pg and later mass extinctions and a perplexing lack of evidence that mass
13 extinctions selectively remove more escalated prey (Hansen *et al.* 1999).

14 Clearly we need time to study the impact of predator-prey interaction on evolution but
15 we also need more focus on larger data sets and to understand variability over a range of time
16 and length scales. This contribution puts forward a very personal view point of the issues we
17 need to consider in order to be able to better interrogate the fossil record of predator-prey
18 interactions and to assess the generality of the conclusions we can draw. It underlines points
19 which may seem well known but which, in our haste to resolve grand hypotheses (a seeming
20 necessity for winning grants or writing high impact papers), are easily overlooked.

21 **WHAT CAN WE ACTUALLY MEASURE FROM THE FOSSIL RECORD?**

22 If we are to have any sense from the fossil record of changing predation levels over time or
23 between environments we require some measure of predation pressure. Yet such a simple
24 idea is actually rather difficult to measure, even in modern settings.

25 The fossil record has revealed a number of iconic specimens which seem to catch
26 predators in the act, or at least catch them 'red handed'. For example, Vannier (2012)
27 described the plentiful undigested skeletal remains of shell organisms (e.g. hyolithids and
28 brachiopods) in the guts of the many individuals of the Cambrian priapulid worm *Ottoia* and
29 Pollard (1968) described the occurrence of cephalopod hooks in guts of an ichthyosaur.
30 Such findings rely, however, on very exceptional preservation and still only tell us that a
31 particular style of predation was utilised at a particular geological time rather than giving us a
32 measure of this type of activity. As is well known, many predator groups have known

1 feeding methods that require neither fossilizable hardparts that we might recognise under
2 'normal' taphonomic conditions nor leave diagnostic damage on their fossilised prey
3 (Vermeij 1987; Harper 2006). Even where there might be some recognition that an organism
4 has predatory functional morphology (such as claw or jaws) which *might* provide us with the
5 suggestion that a particular group may have fed in a particular way this is not incontrovertible
6 evidence that they *did* or that the structure evolved for that specific function rather than being
7 co-opted for that function by subsequent exaptation (Vermeij 1982a). In short, observations
8 from the predators themselves do not offer the opportunity to collect systematic data and even
9 recognising that some may have fed in a particular way does not automatically allow us to
10 construct guilds by collating all taxa within a particular higher taxon as feeding in a particular
11 way (Chalcraft and Reserits 2003). These points render many seemingly attractive
12 hypotheses untestable. For example, Donovan and Gale (1990) suggested the post-Palaeozoic
13 decline in rhynchonelliform brachiopods might be attributed, at least in part, to the rise in
14 extra-oral feeding asteroids. Although that suggestion provoked a certain amount of lively
15 debate (Blake and Guensburg 1990; Vermeij 1990; Pratt 1991; Gale and Donovan 1992) it is
16 difficult to conceive of an adequate test.

17 Our best opportunity to collect data of sufficient quality and quantity to test
18 hypotheses is to use prey remains that can be recognised and counted. Automatically we are
19 then restricted to investigating only certain styles of predation, namely drilling and some
20 types of crushing.

21 *Drilling predation*

22 Of all the different styles of predation, drilling is the most easily and uncontroversially
23 recognised in dead shell material using the criteria of Baumiller (1990) (Fig. 1A). This has
24 opened up a whole range of avenues to explore the metrics of this behaviour including
25 frequency of attack, success rate, prey size preference and stereotypy of attack siting. It is not
26 my intention to review these here; thorough discussions already exist (Kitchell *et al.* 1981,
27 1986; Cortez *et al.* 1998; Kelley and Hansen 2003; Harper 2003). The relative ease with
28 which quantitative data can be extracted from drilled prey items has made them very popular
29 targets for research, requiring little or no sophisticated equipment and relatively little prior
30 training (Hattori *et al.* 2014). As a result in the last 30 years there have been a large number
31 of published studies, both in the peer-reviewed literature and as conference contributions.
32 However, there may be issues. Many studies are perhaps marred by very small data sets and

1 there may be problems of interpretation, for example in identifying the actual driller
2 (Bromley 1981; Dietl and Kosloski 2013) and it is known that some prey may be fed on
3 without completing their drill holes, at least in aquaria, thus giving the false impression that
4 the attack may have been incomplete (Ansell and Morton 1987; Kowalewski 2004) although
5 these may be artefacts of tank experiments where predators behave atypically or the health of
6 protagonists may be compromised (Visaggi *et al.* 2013). Additionally, there may be
7 taphonomic issues associated with the transportability or the mechanical strength of drilled vs
8 non drilled shells which might distort the relative numbers prey in any sample (Lever *et al.*
9 1961; Roy *et al.* 1994; Chattopadhyay *et al.* 2013; Molinaro *et al.* 2013; Tapanila *et al.*
10 2015). These are essentially issues that must be resolved at each locality where samples are
11 being analysed.

12 *Crushing predation*

13 The recognition and metrification of crushing predation has been much more problematic.
14 Although many predatory taxa crush open the shelly defences of their prey, the resultant
15 debris may be undiagnostic and very difficult to distinguish from damage caused by abiotic
16 or post mortem breakage. In some cases damage may appear distinctive, for example the
17 apparent bite marks on ammonites (Kauffman and Kesling 1960; Martill 1990) but even so
18 these may be equivocal as alternative suggestions have been made (Kase *et al.* 1994) and,
19 these are again, in one way or another 'exceptionally preserved'. Their value is largely to
20 tell us that a particular style of predation was happening to some degree at a particular
21 location and time, and do not provide absolute data that might be used to compare between
22 samples. The best metrics for crushing come from studies of the repair of failed crushing
23 predation which at least indicate that the damage was pre-mortem (Fig. 1B). Such studies
24 have dwelt particularly on molluscs and brachiopods (reviewed by Alexander and Dietl
25 2003)). Gastropods dominate such datasets because of the relative ease of with they are able
26 to repair (Vermeij 1983). Again, however, it may be difficult, particularly for single
27 specimens, unequivocally to discriminate between the repair of damage produced by
28 crushing predators and that caused by abiotic processes such as crushing by rolling clasts or
29 ice (Shanks and Wright 1986; Cadée 1999) or sustained during burrowing (Checa 1993).
30 This matter may be resolved where there are sufficient data by recognising patterns
31 (Kowalewski 2002; Harper *et al.* 2009; Harper *et al.* 2012) and, in some instances, it may be
32 possible to gain a sense of proportion of abiotically damaged specimens by examining levels
33 of breakage on shells known to have been killed by drilling (Stafford and Leighton 2011).

1 Perhaps counterintuitively, the uncertainty of identifying crushing predation and the attendant
2 need for more data to allow pattern recognition has meant that the literature is less full of
3 reports on single/few repairs than is the case for drill holes. However, the main concern with
4 these studies is actually the extent to which studies of repair frequency reflect predation
5 frequency; prey which is heavily attacked by highly efficient and effective predators may
6 have similar repair frequencies to those which are almost never attacked (Alexander 1981).
7 There is an extent to which these concerns may be exaggerated. Studies which have
8 investigated predation efficiency in natural environments have shown that failure is
9 commonplace (Vermei 1982a,b) and, comfortably, Stafford *et al.* (2015) in a study of
10 Recent gastropods from 6 sites in Canada show that repair frequency correlated best with
11 crab abundance, suggesting that *in this instance*, repair frequency is a good proxy for
12 crushing predation pressure although further studies are required to test whether this is
13 reliably so.

14 **HOW WELL CAN WE LINK PREDATORS AND THEIR PREY?**

15 Aside from the fact that we are measuring only some, perhaps relatively few, types of
16 predation, there are other concerns if we wish to attempt to link the acquisition of perceived
17 defensive adaptations or life habit or distributional shifts to a particular predation pressure
18 rather than a more generalised notion. Although some predators may be highly adapted to
19 feed on one prey taxon many are highly opportunistic eating a whole range of different prey
20 (including carrion). As such the influence of a particular predatory taxon may be quite diffuse
21 (Walker and Brett 2002). In the gastropods for example, members of the Mitridae and the
22 Cassidae are specialised for feeding on sipunculans and echinoderms respectively, whereas
23 members of the Muricidae and Buccinidae are generalists (Taylor *et al.* 1980; Taylor 1989)
24 although again specific species or even individuals may concentrate and be habituated on
25 particular prey items (Hughes and Dunkin 1984). In practice, many of the predatory taxa we
26 are interested in charting over evolutionary time are catholic in their diets and so we may be
27 faced with a situation where we are seeing and measuring only part of their activities as some
28 of their prey will had better preservation potentials than others; frequency tallies from the
29 fossil record may reflect taphonomy more than real vulnerability and preference. Also many
30 predators may feed in different ways on different taxa and so we may capture only part of the
31 repertoire of any particular predator. For example, Todd and Harper (2010) pointed out that
32 although the records of highly stereotyped drill holes in the bivalve *Venericor* from the
33 London Clay at Nursling (UK) are the only evidence we have of co-existing octopods in that

1 fauna, it is highly unlikely that these were their only prey. Octopods attack in a range of
2 different ways and only drill their more 'tricky' prey (McQuaid 1994; Steer and Semmens
3 2003).

4 From the point of view of the prey, it is important to accept that in recognising and
5 assessing predation from trace fossils we are, in most instances, collecting data for guilds of
6 predators and not for particular predatory species. Many of the prey taxa that we are often
7 interested in may have a wide range of predators and one of the well known paradoxes in
8 predation studies is that although it is often easy to identify styles of predatory damage it is
9 might not be possible to link those activities to a particular predatory taxon (Bromley 1981).
10 Different predators with different predatory strategies may result in different defensive
11 adaptations. For a prey taxon that is a 'common' food source for a variety of predatory
12 groups there may be trade-offs to make in adaptations, for example emphasis of armour by
13 thickening shells may compromise mobility

14 Where a number of different predatory taxa use similar attack methods the effects of
15 each will be difficult to disentangle if all we have is the damage of each. Although the
16 overall patterns may be similar, different predatory taxa will have their own preferences,
17 handling strategies and success rates. For example Kabat and Kohn (1986) reported
18 predation on 10 co-existing naticid taxa from the Pleistocene of Fiji. Of these, six taxa were
19 perforated by naticid-type drill holes. Although it was possible to look at size relationships
20 and patterns of drilling predation for each of the prey species it was not possible for them to
21 be matched with any, or all, of the 10 potential drillers in order to investigate their individual
22 strategies and preferences and so no prospect of addressing the interesting question as to any
23 were indulging in cannibalism. It is possible that large enough data sets might allow species-
24 attributed drill holes to be identified by their precise geometries or associated rasping traces
25 (Kowalewski 2004; Grey *et al.* 2005; Schiffbauer *et al.* 2008) but such 'finger
26 printing' determinations require a large amount of material and the variation, particularly in
27 outline and where the prey have different thickness and microstructures, and the need for
28 individual inspection by electron microscope may make such determinations sadly totally
29 impractical. Failure to be able to discriminate between the activities of confamilial predators
30 in a sample may be vexing but more critical where two unrelated predators may be at work.
31 Casey *et al.* (2015) re-examined the case of naticid-like holes from the Neogene Atlantic
32 Coastal Plain of the U.S. which has been extensively used in predator-prey studies. They
33 argued, based on understanding of stereotypy and prey size considerations for modern

1 naticids, that the large muricid gastropod *Ecphora* co-occurs may well have been responsible
2 for some of the drill holes and their activities may blur the signal proposed for naticid
3 predation.. However, there was no reliable way to distinguish between the two types of drill
4 holes created. Muricids and naticids drill by similar means but have very different ways of
5 handling their prey; naticids envelope and grapple with their prey using their large foot and
6 drill with an accessory boring organ (ABO) located in the proboscis whereas muricids
7 essentially perch on top of their prey and drill using an ABO in the foot (Carriker 1981). We
8 might expect these different handling strategies to result in different predator-prey size
9 relationships, levels of stereotypy and levels of success (as measured by complete drill holes)
10 (e.g. Casey *et al.* 2015) and similarly we might expect them evolutionarily to select for
11 different defensive adaptations in the prey.

12 **BLURRING THE BIOLOGICAL SIGNAL: MISSING THE NATURAL VARIATION**

13 Single specimens with predation damage, however fascinating, cannot provide us with the
14 kind of data we need to test hypotheses. Ideally we need multiple examples from a single
15 site; Vermeij *et al.* (1989) uses the figure of at least 10 drilled individuals in order to
16 calculate drilling frequency and 10 drill holes before calculating prey efficiency but it is clear
17 that in order to detect subtle differences we need much larger data sets. One of the criticisms
18 of earlier analyses has been that although lumping data from different species or genera into
19 higher taxon units provides larger sample sizes it might not be appropriate (Harper *et al.*
20 1999; Kowalewski 2002, Vermeij 2002). Although Kelley and Hansen (2006) found that
21 there were no significant differences in their drilling frequency analyses in Coastal Plain
22 drilling patterns over the Cenozoic when they analysed lower taxon units rather than by
23 assemblage level data (Kelley *et al.* 2001), there were significant difference in the results of
24 changes in success and failure rates. The importance of analysing data from lower taxonomic
25 units may vary from assemblage to assemblage but failure to do so runs the risk of lumping
26 taxa together which never shared a habitat in life and had no chance of interacting. Because
27 it is well known that many predators select their prey on the basis of size, as noted above, it
28 should also be important to examine patterns of predation within particular size classes in
29 order to standardise tests between sample sites (Ottens *et al.* 2012; Dietl and Kosloski 2013).
30 These requirements are very limiting for many studies as the numbers of individuals required
31 becomes prohibitively difficult to obtain without increasing fears of time and space
32 averaging.

33 Although single sites might show us a particular phenomenon or the first evidence of a
34 particular type of predation, they also may be used to chart changes at a very specific locality

1 over important or interesting time intervals, for example mass extinctions and their
2 aftermaths. However, if we are to pick up true patterns in predation pressure over
3 evolutionary change we need to examine different sample sites and to have some
4 understanding of the variability that might be expected either spatially or temporally. This
5 potential variability occurs over a range of different length scales;
6 predation pressure may vary over small distances or even short periods of time. The sources
7 of this variation may be due to some combination of primary biological signal and
8 taphonomic artefacts and the two need to be disentangled. If we sample over too coarse a
9 temporal or spatial range we risk a recording a meaningless average.

10 ***Small scale biological variation***

11 The seafloor is a complex mosaic of different habitats and consequently the availability of a
12 particular prey taxon maybe somewhat patchy. This patchiness may be persistent over long
13 periods but equally may be of short term duration modulated by seasonal changes and the
14 short spans of opportunistic fauna (Staff *et al.* 1986). Habitat complexity may also have a
15 significant impact on both local predator abundance and also predation intensity (Hereu *et al.*
16 2005). Where preferred prey is restricted either to habitat 'islands' or in time, predators may
17 have to show a certain amount of behavioural flexibility to cope with less desirable prey. The
18 impact of patchy prey distribution will be different on different sorts of predators. For
19 example highly mobile predators, such as fish, may be able to forage for their preferred prey
20 over large distances, whereas slow moving gastropods may be restricted to feeding on what is
21 in a relatively small area.

22 Cadée *et al.* (1997), following Schmidt (1989), highlighted high interspecific and
23 interhabitat variation in shell repair frequency in gastropods within a relatively small (10
24 km²) study area including tidal channels and flats with intervening salt marshes within a
25 modern Californian bay area. Whilst a survey such as that described can pick up variation in
26 a survey of a modern area where samples can be collected *in situ*, they identified a trio of
27 taphonomic problems which would hamper any palaeoecological study that attempted to
28 explore these patterns using the type of shelly deposit that a palaeontologist might usually
29 deal with: time averaging, habitat mixing and collection averaging. Cadée *et al.* (1997) make
30 the point that 'The fact remains that there is as much variation in repair frequency among
31 species and microhabitats at one time (the Recent) in the geological record as there is
32 throughout the record'(p, 76). This is a sombre message for anyone trying to establish long
33 temporal trends and patterns from relatively few sampling sites.

1 ***Broader scale biological variation***

2 On a much broader spatial scale we might expect large variations in primary pattern of
3 predation. Suggestions that predation pressure in the modern oceans decreases with both
4 increasing latitude (Paine 1966; MacArthur 1972; Freestone *et al.* 2011) and increasing water
5 depth are well known paradigms (Vermeij 1987; Aronson and Blake 2001). Perhaps
6 counterintuitively the empirical data to support these are surprisingly sparse (Schemske *et al.*
7 2009; Freestone *et al.* 2011) but this probably reflects the fact that studies of sufficient
8 magnitude and replicability, particularly outside shallow accessible water, are both time and
9 resource intensive. Alternative ways of studying such variation employ what are ostensibly
10 palaeontological techniques of looking at shell repair and damage (Vermeij *et al.* 1980;
11 Alexander and Dietl 2001a; 2003). Many studies have picked up a latitudinal increase in the
12 frequency of crushing predation, as judged from repair metrics, towards the tropics (Vermeij
13 1978; Vermeij *et al.* 1981), although as Alexander and Dietl (2003) point out, repair data for
14 boreal and polar gastropods are sparse. One reason for this, at least in the Southern Ocean, is
15 the absence of crushing crustaceans and restricted fish fauna (Aronson & Blake 2001;
16 Aronson *et al.* 2007). The pattern from drilling seems less clear. Some studies, for example
17 Alexander & Dietl (2001b) and Visaggi *et al.* (2015) have demonstrated an increase in naticid
18 drilling with decreasing latitude but others have not (Vermeij *et al.* 1989; Kelley and Hansen
19 2007). No comparable analysis has been published for muricids. Drilling is a time
20 consuming, and in itself risky, operation. Levels of drilling predation may be affected by
21 latitude in different ways. As it is primarily a chemical processes (Carriker 1981), penetration
22 rates will be faster at higher temperatures leaving less risk of disturbance by either abiotic
23 factors (such as waves or emersion with the resultant threats of desiccation or heat shock) or
24 by intraspecific competitors or their own predators (Vermeij 1993). Harper and Peck (2003)
25 reported the Antarctic muricid *Trophon longstaffi* taking 29 days to complete a bivalve meal
26 in aquaria, compared to a matter of hours in the tropics (Patterson *et al.* 1982). However,
27 competition and pressure from their own predators may be greater at lower latitude, as may
28 prey shell thickness to be penetrated (Vermeij 1993). These factors may influence both
29 frequency of drilling predation and the likelihood of recording failed (=incomplete drill
30 holes).

31 There have been few attempts to obtain data for modern predation at a range depths
32 and most studies have only sampled a modest depth range. Although Sander and Lalli (1982)
33 found no significant variability in drilling predation across the margin of the Bermudan

1 platform, Sawyer & Zuschin (2010) did discover differences between drilling frequency
2 between intertidal and sublittoral prey in the Adriatic. Harper and Peck (2016) examined
3 repair in rhynchonelliform brachiopods over a depth range of 4000m which showed a strong
4 negative correlation between the frequency of crushing repairs and increasing water depth.

5 Given the kind of variability that we might expect both local levels and broader
6 geographic zones it is not surprising that the levels of observed predation is very variable
7 indeed. The analysis by Harper and Peck (2016) for repair of crushing damage from
8 rhynchonelliform brachiopods from 112 shallow water sites across the southern hemisphere
9 and into low latitudes in the northern hemisphere clearly shows the variability in this metric.
10 The maxima in repair frequency shows a robust pattern of highs in the mid latitudes and lows
11 in the tropics and sub polar region but even in the mid latitudes there are a number of samples
12 which yield values of, or close to, zero. These data suggest that trying to extract
13 evolutionary patterns from effectively random single sites from the fossil record may fail to
14 show real patterns and, even where they do show anticipated patterns, replication should be
15 sought. Moreover, most single site studies (either neontological or palaeontological) are not
16 random. No one publishes this type of data if the frequency is, or is close to, zero. Instead
17 they are heavily biased towards sites with intense predation (Baumiller and Bitner 2004;
18 Baumiller *et al.* 2006). More modern baseline studies of the type of Alexander and Dietl
19 (2001a) and Harper and Peck (2016) are required to establish the true range of variation in
20 predation frequency. These will provide a better framework for understanding single
21 palaeontological study sites and also the variation that has been recorded in some Cenozoic
22 drill hole studies, for example Kelley and Hansen (1996) and Hoffmeister and Kowalewski
23 (2001).

24 **LONG TERM TAPHONOMIC ISSUES**

25 If one of the goals of predations studies is to pick up major temporal shifts in levels and
26 patterns of predation then it must be accepted that the signal may be blurred, or worse
27 modified, by taphonomic processes. There is a perennial concern of time and spatial
28 averaging in the fossil record; accumulated shell beds may record a mixture of individuals
29 over hundreds or even thousands of years (Kowalewski *et al.* 1998) thus presenting us with
30 difficulties in comparing results and a mismatch of scale with neontological data (Jablonski
31 2008). However, other taphonomic modifications may be particularly problematic if they

1 reflect changes in unrelated biological factors or secular variation in the physical environment
2 over long periods of geological time.

3 One particular factor to consider is the mineralogical and microstructural make up of
4 prey organisms and how their different preservation potentials impact how easily we can
5 recognise predation traces. Importantly do major shifts in potential influence our reading of
6 the reading of the predation record? It is striking that much of the evidence of Palaeozoic and
7 Mesozoic predatory activity is focussed on calcitic shelled prey such as brachiopods
8 (Alexander 1981, 1986) and echinoderms (Baumiller 1990, 1993, 1996; Baumiller and Gahn
9 2003), or those which biomineralised in calcium phosphate, such as inarticulate brachiopods
10 and ‘small shelly fossils’ (Chatterton and Whitehead 1987; Conway Morris and Bengston
11 1994). There are relatively few data for predation of Palaeozoic molluscs, most of which
12 were originally aragonitic with very low probability of preservation of original shell material,
13 and it seems unlikely that mouldic preservation will provide reliably recognizable predation
14 traces. It is difficult to believe that they were relatively immune from predation compared,
15 for example, to brachiopods. The only report known to me of damage repair from Palaeozoic
16 bivalves comes from Devonian pteriods in which the original outer shell mineralogy was
17 calcitic (Nagel-Myers *et al.* 2009), although repairs have been studied in Palaeozoic
18 pleurotomariid gastropods which were originally aragonitic (Lindström and Peel 2005). Even
19 in the Mesozoic, most molluscan predation trace fossils are reported most often in taxa which
20 are predominantly calcitic, such as oysters (e.g. Dietl *et al.* 2000) or in wholly aragonitic taxa
21 in which there has been exceptional preservation of the original mineralogy or microstructure
22 (Taylor *et al.* 1983; Fürsich and Jablonski 1984; Newton 1987; Harper *et al.* 1998, 1999).
23 Hoffmeister *et al.* (2004), report a small number of drill holes in silicified bivalves from the
24 Permian and it would be instructive to research silicified molluscan faunas elsewhere from
25 the Palaeozoic, such as those studied by Cherns and Wright (2000) to search specifically for
26 predation damage. As noted by Kidwell and Brenchley (1994), post-Palaeozoic shelly beds
27 are dominated by more durable molluscs and in particular bivalves which became thicker
28 shelled and tended to utilize lower organic shell structures when compared to thinner shelled
29 and more fragile brachiopods. These changes taken together may have conspired to play
30 down the importance of molluscan prey in the Palaeozoic, and also perhaps to suppress
31 evidence of predators that specialized in feeding upon them.

32 Another potential for causing apparent long term changes occurs in the record of
33 drilling predation. Vermeij *et al.* (1989) observed that the relative importance of drilling

1 predators could be exaggerated at sites where crushing predation was high because the
2 activities of those crushers removed undrilled dead prey items from any tally of drilled vs
3 undrilled dead. This might prove a problem when comparing any set of localities but could
4 prove especially problematic where there are major differences between the occurrences of
5 crushing predators between sample sites. For example, one of the predictions made by
6 Vermeij (1987) concerning mass extinctions is that frequencies of some types of predation
7 should increase after such events because well-defended prey are preferentially removed.
8 Examination of the changes in drill hole frequency in molluscan prey over mass extinction
9 intervals have been popular tests of this hypothesis (Kelley *et al.* 2001; Kelley and Hansen
10 2006) but those same extinctions may also have seen major guild changes in crushing
11 predators (Walker and Brett 2002).

12 **A PRESSING NEED TO EXPAND DATA SETS**

13 By far the majority of quantitative studies of predation in the fossil record have been
14 undertaken on gastropod and bivalve prey. This preoccupation is understandable as there is a
15 very extensive literature on modern predation in these groups which has been of great
16 assistance in interpreting the fossil data. It is worth stressing, however, that the data we have
17 on modern molluscs is largely limited to commercially important taxa such as scallops,
18 mussels, and clams and contemporary data are far fewer for other important bivalve clades
19 such as anomalodesmatans or protobranchs (Harper 2011). It is also worth noting that
20 although modern mussels are important prey items for a whole host of predatory taxa (Harper
21 2006), almost nothing has been reported for fossil mytilids probably because so many of their
22 predators leave little or no trace of their activities (Harper 2005). For other taxa, such as
23 brachiopods, bryozoans, crinoids there has been little impetus to study predation in modern
24 settings (Donovan and Gale 1990) and, for most of these examples, there are probably more
25 well known reports concerning predation evidence of fossil material than extant records.
26 Indeed much of the observation of extant members of these taxa has been undertaken by
27 palaeontologists rather than zoologists and much of it published in the palaeontological
28 literature (e.g. Meyer 1985; Oji 1996).

29 It is also worth underscoring the point that absence of *reported* evidence of predation is not
30 the same thing as a particular taxon suffering zero or insignificant predation. There is also a
31 nagging question as to how much predation is significant in either ecological or evolutionary
32 terms.

1 Twenty years ago it was easy to dismiss drill holes in fossil brachiopods as almost
2 entirely known from the Palaeozoic (e.g. Smith *et al.* 1985) or perhaps the records of some
3 predators making ‘mistakes’ (Kowalewski *et al.* 2005). Much more effort has now been made
4 to examine drilling in post-Palaeozoic and modern brachiopods (reviewed in Harper, 2011).
5 Shell damage and repair has been recorded in 70% of 112 large samples of rhynchonelliform
6 brachiopods from a range of latitudes and depths (Harper & Peck, 2016). Similarly, drilling
7 occurs in brachiopod samples from a wide variety of environmental and geographical
8 settings; Harper (2011, Table 2) compiled the drilling frequencies recorded for 29 samples of
9 Recent brachiopod single species from the literature varying from <1% to 35% and Harper *et al.*
10 *al.* (2011) presented evidence that gastropod drilling of several New Zealand brachiopod
11 populations appeared both regular and stereotyped. Palaeontological studies have shown that
12 at least at some sites in the geological past levels of drilling predation on brachiopods has
13 been high (Baumiller and Bitner 2004; Baumiller *et al.* 2006; Tuura *et al.* 2008; Hiller 2004).
14 It remains unclear whether predation has been important in the post Palaeozoic restriction of
15 brachiopods as suggested by Stanley (1977), but it remains a plausible factor (Jablonski
16 2008) and a matter which may be resolved with a greater body of data. Similarly, (Baumiller
17 and Gahn 2003) have described a paradigm shift in the way that predation might be perceived
18 in the evolution of crinoids and the restriction of many stalked taxa to refuge environments in
19 the modern oceans. As with brachiopods, a paucity of modern records combined with the fact
20 that they do live in low predation refuges had fuelled the notion that there was little
21 interaction between crinoids and predators in evolutionary time.

22 Research on recognising and quantifying predation on other potential prey taxa which
23 have good fossil records is at a very much earlier stage. Nevertheless, in the last few years
24 there has been a real expansion in the taxonomic targets of predation in fossils including
25 echinoids (Nebelsik and Kowalewski 1999), barnacles (Klompaker *et al.* 2015), crustaceans
26 (Klompaker *et al.* 2013), solitary corals (Webb and Yancey 2010), scaphopods
27 (Klompaker 2011), ammonites (Kerr and Kelley 2015; Takeda *et al.* 2016), cornulitids
28 (Vinn 2008) and tube worms (Klompaker 2012; Martinell *et al.* 2012). Nevertheless, it
29 takes time to develop an infrastructure for such research, and to establish what questions need
30 to be addressed and to assess what types of sampling strategy work. Baseline data for these
31 taxa are still some way away.

32 Just as there is a need to expand our repertoire of taxonomic target, much might be
33 gained from expanding away from concentration on North America and European fauna.
34 Again in recent years there has been a welcome expansion of horizons and new data are being

1 published from different regions such as India (Mallick *et al.* 2013, 2014), South America
2 (Martinelli *et al.* 2013; Visaggi and Kelley 2015) and Australasia (Tuura *et al.* 2008; Hiller
3 2014). Further expansion of these studies will provide an understanding of broader scale
4 spatial variation in predation pressure over evolutionary time. It is already postulated that
5 there are strong latitudinal gradients in modern predation and inter-oceanic differences in the
6 development of prey defence (Vermeij 1976, 1978, 1987). How have such differences and
7 gradients evolved?

8 We can often bemoan the lot of a palaeontologist and the incomplete and biased fossil
9 record. However, palaeontological methodologies and perspectives can offer real
10 opportunities to bridge some of the scale mismatches between palaeontological and
11 neontological data (Jablonski, 2008) by providing data collections of a type that can be
12 integrated together. Moreover, palaeontologists are able to routinely sample from sediments
13 deposited from a whole range of environments and depths which are not accessible to
14 neontologists for conventional large scale studies. For the Recent logistical difficulties of
15 hamper data collection from all but the shallowest water and even there direct observation is
16 limited to largely to either human or ROV dives or periods of tidal emersion. The
17 development of techniques to extract quantitative predator-prey interaction data from dead
18 shells allow palaeontologists to enhance our understanding on all time scales. But the key
19 will be gathering enough high quality data to be able to differentiate between real temporal
20 and spatial trends.

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20 Figure caption

21 Fig.1. Examples of recognisable predation from the fossil record. A. Successful predatory

22 drill hole (arrowed) through the valve of *Anadara lienosa* from the Pleistocene

23 Caloosahatchee Formation, Florida. B. Repaired apertural damage (arrowed) sustained by *Turritella*

24 *imbricateria* from the Eocene London Clay Formation, U.K. (CASM C58229). Both scale bars are 10

25 mm.

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1 Figure 1



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