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PART N, REVISED, VOLUME 1, CHAPTER 22: PREDATION OF BIVALVES

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INTRODUCTION

Most bivalves provide an excellent flesh yield, in particular those with well-developed adductor musculature or a large foot. Their only potential drawback as a food source is the bivalve's strong and rapid response to disturbance by shutting the valves, locking the tissue away within the confines of the protective shell. However, once the shell is breached, the meat is immediately available and is free from indigestible matter such as spicules; relatively few species have been found to be toxic. These factors, together with the widespread occurrence of bivalves, often in high abundance in many marine and freshwater communities, make them prime prey targets, and they figure prominently in the diets of many different predatory (and scavenging) taxa. Somewhat inevitably, most of what we know about the predation of modern bivalves is heavily biased by studies of commercially important species, such as oysters, mussels, and scallops. Little is known about predation on taxa such as the protobranchs, arcoids, lucinids, or anomalodesmatans.

Few predators are fully specialized only for bivalve prey, and, in practice, most predators that take bivalves have catholic diets. However, in some habitats where a particular bivalve is very abundant, they may form the bulk of a predator's diet. For example, Hughes and Dunkin (1984) showed that the dogwhelk *Thais lapillus* may become habituated to taking the blue mussel *Mytilus edulis*. Conversely, any particular bivalve species may have a wide range of predators that use very different predatory techniques to attack them. For example, Harper (2006, fig. 4C) illustrated a partial food web for *Mytilus edulis* showing eight higher taxa of potential predators.

Predators may use a number of techniques to access their bivalve prey, and some may use different methods on a single prey species, depending on the size of the individual tackled (McQuaid, 1994; Steer & Semmens, 2003). These techniques may be broadly categorized, for ease of discussion, as swallowing, grazing, prising, pre-ingestive crushing, and drilling (see also Vermeij, 1987; Alexander & Dietl, 2003, for a slightly different classification). Each technique is practiced by a range of different taxa and in different ways. Below, we outline each of these methods and consider whether they provide diagnostic evidence for use in inferring the activities of particular predatory groups for death or fossil assemblages of bivalves. We also provide an indication of the known fossil record of predatory behavior on bivalves. We then examine the ways in which predation is believed to have influenced bivalve evolution, before suggesting avenues for future research.

SWALLOWING

A number of predators feed simply by swallowing bivalves whole. These include a variety of worms, including the nemerteans (Bourque, Miron, & Landry, 2001) and polychaetes (Emson, 1977); intra-oral feeding starfish, e.g., *Pycnopodia* (Mauzey, Birkeland, & Dayton, 1968) and *Luidia* (McClintock & Lawrence, 1981); and a wide variety of chondrichthyan and osteichthyan fish, such as rays (Yamaguchi, Kawahara, & Ito, 2005); cod (Arntz, 1978); wrasse (Denny & Schiel, 2001); and, in freshwater, roach (Prejs, Lewandowski, & Stanczykowska-Piotrowska, 1990); and carp, catfish, and freshwater drum (Thorp & Covitch, 2001; Magoulick & Lewis, 2002). Many of these fish are equipped

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with powerful pharyngeal mills that crush the shells once ingested. A number of marine ducks (e.g., eider feeding on cockles and mussels; CADÉE, 1994) swallow their prey whole and, in freshwater ecosystems, diving ducks such as scaup and tufted ducks feed extensively this way on zebra mussels (HAMILTON, ANKNEY, & BAILEY, 1994). In these instances, again, ingested shells are macerated by the action of a muscular gizzard.

Predators that feed in this way may be extremely important: LAPPALAINEN, WESTERBOM, and HEIKINHEIMO (2005) argued that roach are important in structuring bivalve communities in the Baltic Sea, and their activities produce a significant proportion of skeletal debris within the sediment; for example, CADÉE (1994) estimated that the activities of eider and shelduck feeding on mussels and cockles in the Wadden Sea contribute at least 75% by weight of the carbonate fragments, and that physical fragmentation is rather unimportant.

Simply swallowing prey whole is a basic form of predation, requiring no specialization of feeding apparatus, and the size and type of prey are limited to small individuals that fit through the mouth and throat of the predator. It is virtually impossible to identify diagnostic damage in dead or fossil shell material in order to attempt to recognize this type of predation, particularly where whole shells are voided by the predator (Fig. 1). Where a pharyngeal mill or gizzard is employed to macerate shells, the resulting angular debris (Fig. 2) may be recognizable as distinct from the more rounded debris produced by abrasion during postmortem transport (OJI, OGAYA, & SATO, 2003), although identification of the culprit(s) and quantification of their importance may be difficult. Similarly, the lack of specialization of predator functional morphology also means that it is difficult to identify with certainty which extinct predators fed in this way. However, discrete accumulations of angular shell debris, including that of trigoniid bivalves, have been found in otherwise fine-grained facies from the Middle Jurassic of Poland. ZATOŃ and SALAMON (2008) interpreted these as regurgitates of durophagous predators, probably fish. It seems highly likely, however, that earlier examples exist. Such problems of predator identification also make it difficult to assess the relative importance of this type of predation over geological time.

GRAZING

Other predators, chiefly fish (e.g., rays, flatfish, sculpins), crabs, and birds (gulls and waders), are able to feed on larger prey by effectively grazing the soft parts of bivalves, most often the tips of the siphons (PETERSON & QUAMMEN, 1982; KVITEK, 1991; MOREIRA, 1995, 1996; ANSELL, HARVEY, & GÜNTHER, 1999; ARRIGHETTI, LIVORE, & PENCHASZADEH, 2005) but also the foot (SALAS, TIRADO, & MANJÓN-CABEZA, 2001; MOURITSEN & POULIN, 2003) and mantle lobes (TODD, LEE, & CHOU, 2009). Such grazing may be acute; MOREIRA (1995) cited individual black-headed gulls taking up to 17 *Scobicularia plana* siphons per minute in winter. Walruses feed by exposing deep burrowing bivalves (e.g., *Mya arenaria*) using their flippers and by generating powerful water jets with their snouts and then either stripping the tissue from the intact shells by suction or by simply biting off the siphons (OLIVER & others, 1983; WELCH & MARTIN-BERGMANN, 1990; GINGRAS & others, 2007).

Prey subjected to grazing may often survive the attack and regenerate tissue, although at a cost to the bivalve's fitness as evidenced by slower growth (COEN & HECK, 1991), particularly where the cropping also damages the shell edge. The costs of siphon nipping may also involve increased vulnerability to other predators; for example, DE GOEIJ and others (2001) showed that, following siphon nipping by flatfish, individuals of *Macoma balthica* are able to burrow less deeply and thus are more prone to predation by shorebirds, such as oystercatchers. Few studies have focused on identifying grazing predation from dead or fossil shell

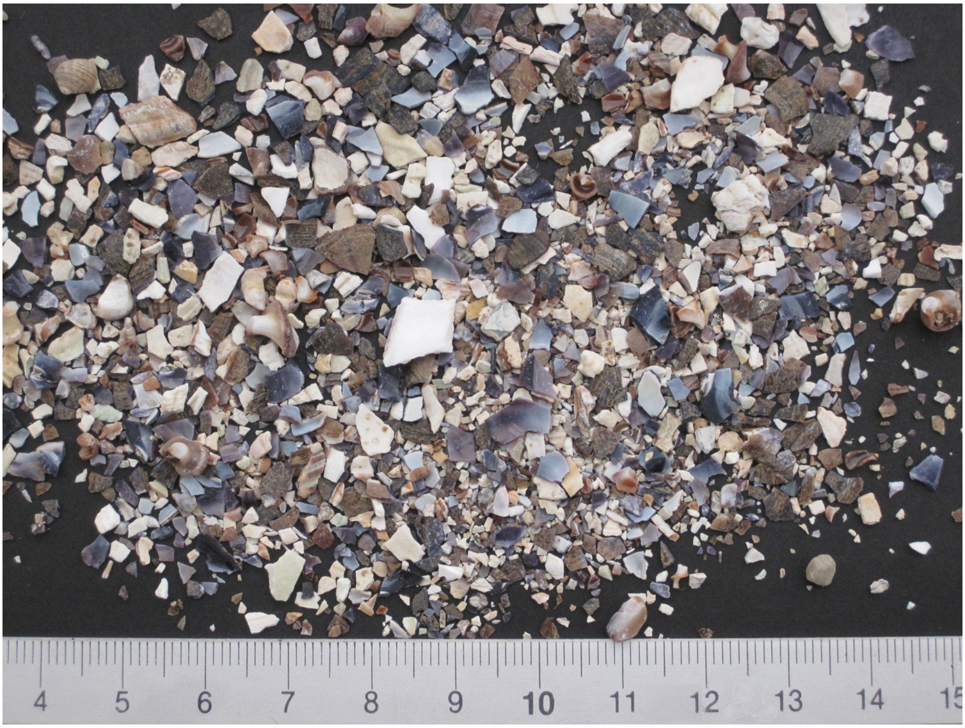

FIG. 1. *Cerastoderma edule* fragments regurgitated by a herring gull, Texel, The Netherlands. Note that some cockles remain unbroken, and one is even still articulated; scale in cm (new; photograph courtesy of Gerhard Cadée).

assemblages. Siphon nipping may be inferred from concentration of damage (repaired or unrepaired), often as triangular divots, at the posterior shell margin of burrowing bivalves (PETERSON & QUAMMEN, 1982; CADÉE, 1999; ALEXANDER & DIETL, 2001; KRAEUTER, 2001). The extensive feeding activity of walrus herds in Pleistocene beds around Washington (United States) has been inferred from distinctive trace fossils intersecting bivalve burrows (GINGRAS & others, 2007).

PRISING APART VALVES

Another broad set of techniques for feeding on bivalves involves prising apart the two valves and feeding through the gape produced. Key exponents of this method are the extra-oral feeding starfish, which use their suckered tube feet to overcome the strength of the adductor muscle(s) to create a gap between the valves just large enough to insert the stomach lobes to commence digestion (FEDER, 1955; MAUZEY, BIRKELAND, & DAYTON, 1968). Starfish are known to be voracious predators of shellfish, causing enormous damage to shellfisheries (MENGE, 1982), and are an important determinant of the natural distribution of mussel beds (SEED & SUCHANEK, 1992). It is unfortunate that this type of predation leaves no diagnostic trace fossils; this factor, combined with the poor body fossil record of asteroids, makes it difficult to assess the importance of extra-oral feeding over geological time. There is disagreement over when the ability to feed in this way evolved because of different interpretations of the limited body fossils (see HERRINGSHAW, SMITH, & THOMAS, 2007); however, exceptional preservation may provide evidence of starfish

FIG. 2. Angular fragments of largely *Mytilus edulis* and *Cerastoderma edule* from the feces of eider duck,Texel, The Netherlands; scale in cm (new; photograph courtesy of Gerhard Cadée).

caught in the act of feeding in this manner on an Ordovician bivalve (BLAKE & GUENSBERG, 1994). Despite this evidence, it may be that extra-oral feeding in asteroids did not become widespread until the Jurassic radiation of forcipulate-solasteroid starfish in the Jurassic (BLAKE, 1993). In addition to starfish, some octopods use their suckered arms to pull apart bivalves (STEER & SEMMENS, 2003). As with starfish, little evidence of such behavior in the fossil record can be expected.

Another type of predation within the broad category of prising is shell wedging. Some groups of predators are specially adapted for wedging apart the valves of bivalves by inserting a lever between them to force them apart. These include members of the gastropod superfamily Buccinoidea (i.e., the families Buccinidae, Melongenidae, Fasciolariidae), in which the apertural lip of the shell is used (NIELSEN, 1975; DIETL, 2003a, 2003b), and some crustaceans, for example, slipper lobsters, which use their dactyli (LAU, 1987).

Wedging may cause inadvertent breakage of the valve edges of the prey, and these predation traces may be sufficiently distinctive to allow for their confident identification in dry shell material (Fig. 3) (ALEXANDER & DIETL, 2003; DIETL, 2003a, 2003b). Furthermore, in the case of buccinoid gastropods, this type of predatory activity may inflict damage on the predator, where the apertural lip is itself damaged and later repaired. Such scars are distinct from those inflicted by the snail's own predators; for instance, DIETL, DURHAM, and KELLEY (2010) demonstrated that scars on *Fasciolaria (Cinctura) lilium hunteria* produced by wedging predation on the oyster *Crassostrea virginica* were distinct from damage induced by crab predation on *Fasciolaria.* Recognition of these repairs in buccinoid shells at

FIG. 3. Feeding scar produced by a busyconine whelk; scale bar approximately 10 mm (new; photograph courtesy of Greg Dietl).

least may be used to infer that they fed in this manner (DIETL & ALEXANDER, 1998; DIETL, 2003a, 2003b; DIETL, DURHAM, & KELLEY, 2010).

PRE-INGESTIVE BREAKAGE

A wide range of predators tackle relatively large, rewarding, bivalve prey by smashing the shell before ingesting the flesh. Many use jaws or claws to break open the shell to access the flesh within, for example malacostracan crustaceans (crabs, lobsters, crayfish, stomatopods; SEED, 1992), xiphosurids (BOTTON, 1984), birds (waders such as oystercatchers; HULSCHER, 1996), fish (e.g., rays; GRAY, MULLIGAN, & HANNAH, 1997), and octopods (HARTWICK, TULLOCH, & MACDONALD, 1981). SEED and HUGHES (1995) showed the variety of different chela morphologies displayed by different crustacean taxa as specializations for opening different prey types, whereas other small individuals and nonchelate crustaceans instead use their mandibles to chip away the valve margins of bivalve prey (LAU, 1987; MORTON & HARPER, 2008). Other predators have alternative methods to break open shells that do not require specialist jaws or appendages. For example, the sea otter uses a variety of tools, such as stones, to smash open the shells of its bivalve (and echinoid) prey (KVITEK, BOWLBY, & STAEDLER, 1993). In the case of gulls (e.g., *Larus argentatus*), breakage of the shells of large mussels and cockles is achieved by dropping them onto hard surfaces during flight (CADÉE, 1989) or, in the case of the razor shell, shaking it vigorously (CADÉE, 2000).

Damage resulting in death caused by crushing predators is at least potentially recognizable in either dead modern or fossil individual material (ALEXANDER & DIETL, 2003), but it may be extremely difficult to distinguish between shell debris produced by predators and that produced by other destructive processes, before or after death. Alternative, nonpredatory causes of fatal damage to live shells include percussion by rolling stones or ice (SHANKS & WRIGHT, 1986; CADÉE, 1999) and, in modern material, dredging activities (GASPAR, RICHARDSON, & MONTEIRO, 1994) or, in the intertidal zone, human trampling (CINTRA-BUENROSTRO, 2007). A variety of criteria

FIG. 4. Angular debris produced by the shore crab *Carcinus maenas* feeding on *Mytilus edulis;* scale bar, 10 mm (new).

that may be used to discriminate between predatory and nonpredatory damage have been discussed by KOWALEWSKI (2002), who highlighted the repetitive nature of damage, complementary scars on both valves that have been attacked by scissorlike weapons, and indication of stereotypy and size selection. Nonetheless, where damage is severe, such tests may be hard to apply. OJI, OGAYA, and SATO (2003) showed that shell fragments produced by postmortem transport tend to be rounded and abraded rather than sharp and angular, as occurs in predatory attacks.

Once it has been established that breakage was caused by a predator, the identity of the attacker may in some cases be determined. Some predators leave rather distinctive marks (ALEXANDER & DIETL, 2003) but many do not (Fig. 4). The challenge remains to catalog and understand damage by known predators so that comparison can be made with fossil material.

As with other methods of predation, crushing predators are not always successful (see YAMADA & BOULDING, 1998, for an example), allowing the injured prey to repair its shell. Failure to complete an attack may be the result of effective defense by the prey, or because the predator has been disturbed by another organism (including its own predators), or a change in the physical conditions in the environment. In the former case, failure is a very important selection agent in the evolution of defensive traits (VERMEIJ, 1987): a predator that is 100% successful will not cause such adaptation. Similarly the prey may also survive other forms of shell breakage, including self damage during burrowing (CHECA, 1993; ALEXANDER & DIETL, 2001).

Repairs may be identified by careful inspection of shell surfaces where normal growth lines are disrupted and there is clear evidence of a ragged scar where shell material has been lost before normal shell secretion resumes (Fig. 5). Disruption of growth lines alone, with no jagged scar, may simply reflect growth of the shell in confined spaces. Some repaired breaks show evidence of broken pieces of shell having been incorporated into

FIG. 5. Scalloped repaired marginal damage in *Pycnodonte vesicularis,* British Chalk, Sedgwick Museum (Cambridge University), SM. B.6534; scale bar, 10 mm (new).

the newly formed shell. Subsequent shell growth often appears to bulge out beyond the scar, and, in instances where the mantle has been badly damaged, shell growth in that region of the shell remains retarded relative to adjacent sections.

The terminology applied to different types of shell repair was originally developed in the study of Paleozoic brachiopods (ALEXANDER, 1981, 1986), and its application to bivalves is discussed in detail by ALEXANDER and DIETL (2001, 2003). Examination of repaired specimens may alleviate some of the problems of trying to discriminate between predatory and nonpredatory damage, because it is easier to recognize particular patterns and size relationships. However, the significance of the levels of repair seen in any population is difficult to interpret (ALEXANDER, 1981; KOWALEWSKI, 2002; LEIGHTON, 2002; ALEXANDER & DIETL, 2003): low repair frequencies in a given species may indicate either infrequent attack on an unfavorable prey or high success rates of a highly efficient predator. In order to circumvent such problems in interpreting repair scars, STAFFORD and LEIGHTON (2011) tested a method, initially proposed by VERMEIJ (1982a), for estimating frequency of crushing predation. They used shells with predatory drillholes (for which cause of death is known) to establish a taphonomic fragmentation baseline within an assemblage. Although the method was only tested on gastropods, STAFFORD and LEIGHTON (2011) stated that it should also be applicable to bivalves.

A number of different durophage groups (placoderm and chondrichthyan fish and phyllocarid and eumalacostracan crustaceans) appear to have radiated during the middle Paleozoic (see SIGNOR & BRETT, 1984; BRETT & WALKER, 2002; BRETT, 2003). SIGNOR and BRETT (1984) argued that

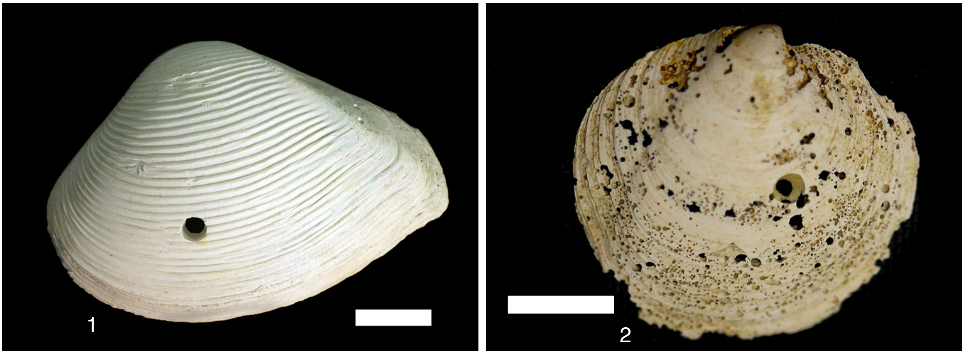

FIG. 6. *1,* Drillhole in crassatellid from the Sarasota Formation, Florida; *2,* drillhole in *Stewartia anodonta* from the Caloosahatchee Formation, La Belle, Florida; scale bars, 10 mm (Kelley, 2008; photograph courtesy of Timothy Kelley).

the activities of these durophages produced a selection pressure favoring spinosity in brachiopod and crinoid prey. Little research has yet been done on Paleozoic bivalves, but NAGEL-MYERS, DIETL, and BRETT (2009) have shown relatively high levels of marginal repair in Middle Devonian pterineid bivalves. Similarly, repaired marginal breakages attributed to predatory activity have been reported in Mesozoic inoceramids (KAUFFMAN, 1971; OZANNE & HARRIES, 2002) and oysters (DIETL, ALEXANDER, & BIEN, 2000) and linked to escalation of durophagous predation in the Cretaceous.

DRILLING

A more subtle way of getting through the valves is practiced by predators that drillholes in shells, through which they feed, or as a way of delivering toxins in order to force the bivalve to gape. The principal culprits in modern seas are muricid and naticid gastropods, which attack (largely but not invariably) epifaunal and infaunal shelly organisms respectively, including bivalves. These gastropods use chemical dissolution by acidic secretions from their accessory boring organs (located in the proboscis and foot respectively in naticids and muricids) in combination with mechanical rasping by the radula, in order to drill through their prey shells (ZIEGELMEIER, 1954; CARRIKER, 1981; CARRIKER & GRUBER, 1999). The distinctive round holes thereby produced have been referred to the ichnogenus *Oichnus* BROMLEY (1981). Generally the two different groups produce holes of different morphology: those drilled by muricids are generally straight sided (*Oichnus simplex*) and those drilled by naticids are countersunk with the outer borehole diameter being greater than the inner diameter (*O. paraboloides*; BROMLEY, 1981; CARRIKER, 1981) (Fig. 6). Recognition of these morphological differences can, therefore, be used to distinguish between the activities of these predators in shell accumulations (e.g., ADEGOKE & TEVESZ, 1974; TAYLOR, CLEEVELY, & MORRIS, 1983; KABAT, 1990; KOWALEWSKI, 1993; ALEXANDER & DIETL, 2001; KELLEY & HANSEN, 2006), although some caution must be exercised (BROMLEY, 1981). It is clear that discrimination based on drillhole shape alone is not always accurate: the muricids *Trophon, Chicoreus*, and *Phyllonotus* produce holes that might well be assigned to *O. paraboloides* (GORDILLO, 1998; HARPER & PECK, 2003; DIETL, HERBERT, & VERMEIJ, 2004), requiring the use of additional characteristics, such as drillhole size or position to distinguish the driller. Other modern gastropods, for example some marginellids, are also known to drill into bivalves (PONDER & TAYLOR, 1992), leaving small holes similar to those made by naticids.

Drillholes produced by predatory octopods are small and often (but not invariably) of a distinctive oval or teardrop

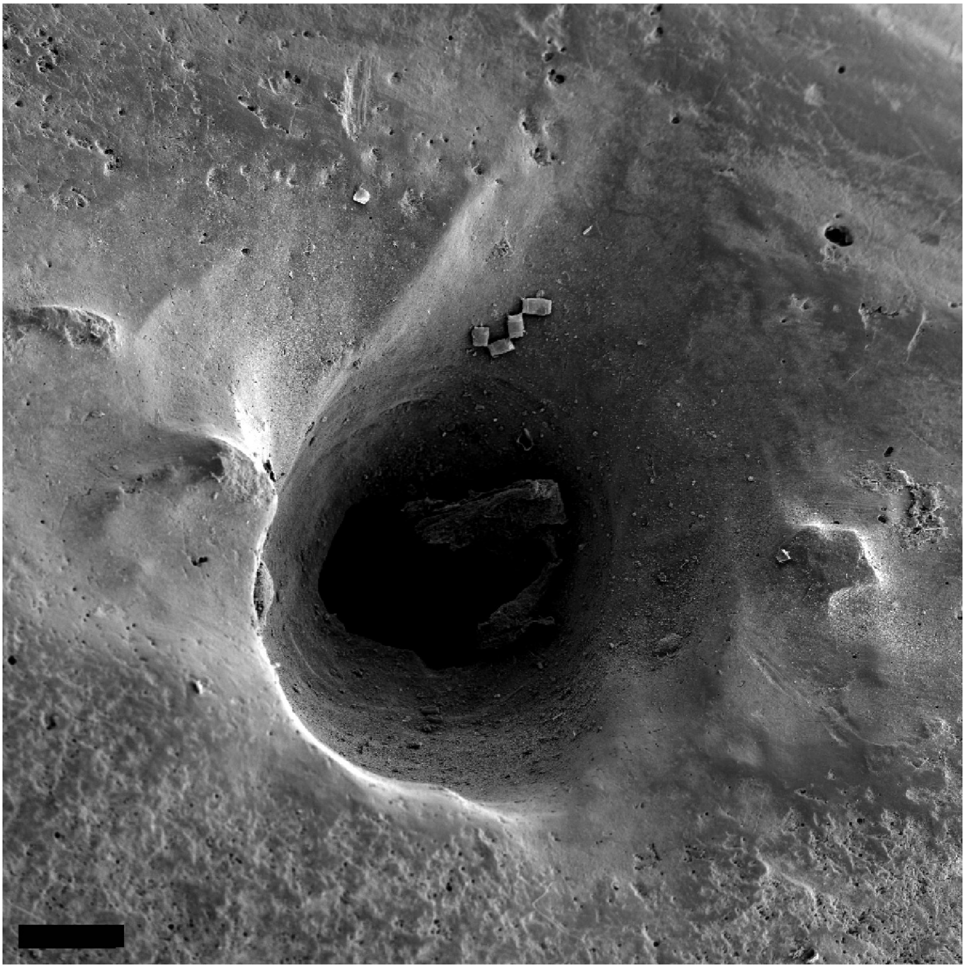

FIG. 7. Scanning electron micrograph of *Oichnus ovalis* drilled by *Octopus vulgaris* in Recent *Perna perna,* South Africa; scale bar, 200 µm (new).

shape (NIXON, 1980; BROMLEY, 1993) (Fig. 7). They frequently show a high degree of stereotypic placing over the victim's adductor muscles, thus allowing rapid delivery of the toxins to the muscle system (BROMLEY, 1993; CORTEZ, CASTRO, & GUERRA, 1998).

Drillholes in shell material represent perhaps the easiest form of predation to infer, and, as a result, there have been numerous studies of drilling predation. The distinctive morphology of fossil drillholes and the recognition of established ichnotaxa means that, with caution (see BROMLEY, 1981; KOWALEWSKI, 1993), at least the higher taxon (i.e., family) of the predator can be identified. Approaches to identifying the drilling predator below the family level have been proposed using microstructural characteristics of drillholes (SCHIFFBAUER & others, 2008) or the ratio of inner and outer borehole diameters (GREY, BOULDING, & BROOKFIELD, 2005), but have not yet been demonstrated to be reliable (see DIETL & KELLEY, 2007). The body fossil record of naticid and muricid gastropods dates to the Early Cretaceous (Albian); it is apparent that they have been active drillers of bivalves since then and particularly so since the beginning of the Cenozoic (TAYLOR, CLEEVELY, & MORRIS, 1983; KELLEY & HANSEN, 1993, 2003, 2006; HARPER, 2003). However, given the multiple evolution of drilling within gastropods, it is possible that other, extinct taxa may have also drilled bivalves. Indeed, drillholes in Lower Jurassic infaunal bivalves (HARPER, FORSYTHE, & PALMER, 1998) and Permian bivalves (HOFFMEISTER & others, 2004) predate the known body fossil record of extant drilling gastropods. Octopod drillholes, despite their distinctive morphology and distribution, seldom have been reported in the fossil record (BROMLEY, 1993; HARPER 2002), with most examples coming from Pliocene scallops, and the oldest recognized examples being from the Eocene (TODD & HARPER, 2011).

In addition to identifying predators, detailed study of drillholes may provide a wealth of other data. Drillhole diameter is generally thought to be related to predator size (KITCHELL & others, 1981; CARRIKER & GRUBER, 1999), which permits examination of predator–prey size selection, for instance by correlating prey size and drillhole size (e.g., ANSELL, 1960; KITCHELL, 1986; KELLEY & HANSEN, 1996b). Many drilling predators display amazing constancy in drillhole location, suggesting a well-developed behavioral stereotypy. This site selectivity is particularly evident in naticid gastropods, which tend often to drill in the umbonal or central region (THOMAS, 1976; KELLEY, 1988; KINGSLEY-SMITH, RICHARDSON, & SEED, 2003), and for octopods, which target the adductor and pallial musculature (CORTEZ, CASTRO, & GUERRA, 1998). The basis for selecting particular regions may relate to minimizing drilling time by drilling thinner areas of the shell (KITCHELL, 1986), ease of handling (THOMAS, 1976), or gaining direct access to calorically rewarding tissue (HUGHES & DUNKIN, 1984). Similarly, for this form of predation, it is relatively easy to quantify successful and unsuccessful drilling attempts by the recognition of complete holes (which penetrate the entire thickness of the valve) and incomplete (or repaired, see DIETL, 2000) drillholes, respectively. Some caution must be used in interpreting incomplete holes. Successful attacks by naticids, in which the prey suffocated during drilling, may yield incomplete holes (see ANSELL & MORTON, 1987, for a laboratory example), and when multiple muricids attack a prey simultaneously, they may abandon a partially completed hole once the prey is breached and feed through the gape (TAYLOR & MORTON, 1996). Nonetheless, study of drillhole size and positioning and also success rate, and in particular changes in them over geological time, has indicated evolution of particular behavioral traits on the part of the predator (e.g., selectivity of prey species or size and drillhole site on the prey; KELLEY, 1988, 1989; KELLEY & HANSEN, 1996b) or of defensive adaptations by the prey (KELLEY, 1989, 1991; KELLEY & HANSEN, 2001; KELLEY & others, 2001).

PREDATION AND BIVALVE EVOLUTION

There can be little doubt that predation has been an important force in the evolution of marine communities (VERMEIJ, 1987; STANLEY, 2008). The fossil record provides good evidence for radiations of durophagous predators during the middle Paleozoic (SIGNOR & BRETT, 1984; VERMEIJ, 1987; BRETT & WALKER, 2002; BRETT, 2003), and as part of the Mesozoic Marine Revolution (STANLEY, 1977; VERMEIJ, 1977, 1987; WALKER & BRETT, 2002; HARPER, 2003).

Because bivalves are such cosmopolitan organisms, and they appear to be a favored prey by such a wide range of different predatory groups, we might anticipate that these great radiations of predatory activity must have had an impact on their evolution. We could predict that those individuals or taxa that are in some way less vulnerable to predation (for example, in terms of life habit, behavioral, or morphological traits) will survive better than those that are more susceptible. As long as not all predatory attempts are successful, we might predict the evolutionary selection of particular traits (Vermeij, 1982b).

Defensive adaptations of bivalves have been discussed by a number of authors (Carter, 1968; Ansell, 1969; Vermeij, 1987; Harper & Skelton, 1993a), and it is clear that the adaptive responses of particular taxa may be shaped by factors that are various and complex, involving the need to defend against different types of predator. Defenses against one predator may make the species more susceptible to other predators, however (Dietl & Kelley, 2002). In addition, different taxa may be either preadapted to, or constrained from, evolving particular defensive features (De Angelis, Kitchell, & Post, 1985; Harper & Skelton, 1993a).

The bivalve form is very susceptible to damage. Failed predation that breaks the valve margins is difficult to seal, and the resulting opening leaks metabolites and/or blood, which may weaken the bivalve and attract secondary predation (Vermeij, 1983). As a result, repair is rather less frequently seen in bivalves than it is in gastropods, which are more able to withstand such damage. Vermeij (1983) suggested that bivalves have consequently responded to increased predation pressure over the Phanerozoic not by emphasizing armor (as gastropods have done; Vermeij, 1977) but by evading capture (and the threat of damage) by changes in life habits and behavior. Various life habits have been described as providing safety from predators and may have evolved in response to increased predation pressure, including deep burrowing (Stanley, 1968), cementation (Harper, 1991), boring into hard substrates (Stanley, 1977; Palmer, 1982), and traits such as ability to swim (e.g., scallops and limids) and leap (e.g., cockles and trigoniids) when threatened (Ansell, 1969; Hayami, 1991; Donovan, Elias, & Baldwin, 2004). It is of interest that these life habits are considered derived and are largely post-Paleozoic innovations. Skelton and others (1990) pointed out that among epifaunal bivalves, these new habits have evolved at the expense of diversity of the exposed byssate taxa. Furthermore, other vulnerable life habits, such as free reclining, exploited so successfully by gryphaeid and exogyrid oysters in the Mesozoic, also declined over a similar time frame (LaBarbera, 1981).

Whereas the predominant form of defense in bivalves is thought to be flight rather than fight, some taxa have been reported to show active responses to predatory attack. Most well documented are the responses of mussels to drilling muricids; the offending gastropods are captured and trapped by byssal threads or dislodged by active movements of the foot or valves (Petraitis, 1987; Wayne, 1987; Day, Barkai, & Wickens, 1991). Stasek (1965) and Wilkens (1986) reported *Tridacna maxima* deterring fish predators by accurately squirting them with a jet from the siphons. There are also more anecdotal accounts of would-be predators becoming trapped by their prey snapping shut on them (e.g., Burrell, 1977; Harper & Skelton, 1993a).

Few bivalves have been shown to be toxic and, where such reports occur, the toxicity is usually secondary, being acquired from dinoflagellates or diatoms rather than secretions by the bivalve. Nonetheless, there is evidence that such acquired toxicity may have definite value in deterring the bivalve's predators. For example, sea otters and wading birds have been shown to modify their prey choices to avoid bivalves that have been especially affected by toxic algal blooms (Kvitek, 1991; Kvitek & Bretz, 2004, 2005).

Bivalves may also evade capture by using camouflage. Cryptic coloration in the hypertrophied mantles of tridacnids may inhibit fish that use visual cues (Todd, Lee, & Chou, 2009), whereas scallops, spondylids, and chamids acquiring a coating of sponges and other epibionts may confuse predators that hunt using both visual and chemosensory information (Vance, 1978; Feifarek, 1987). These bivalves may promote the growth of camouflaging epibionts by virtue of their spiny ornaments. Several authors suggest that the sponge coatings of certain scallops may also inhibit attack by extra-oral feeding asteroids by interfering with the attachment of their tube feet (Bloom, 1975; Marin & López Belluga, 2005; Farren & Donovan, 2007). Epibionts may also provide a chemical defense to their bivalve hosts (Laudien & Wahl, 2004).

Despite the importance of avoiding capture, there are a number of morphological traits in bivalves that may offer defense against predators. Such traits may be considered using the nomenclature of Gould and Vrba (1982) as those that are adaptive (i.e., traits that have been selected for by predation pressure) or those that are exaptive (i.e., traits for which defensive value is secondary or incidental to the primary selective advantage). However, such distinctions may be extremely difficult to determine (e.g., Harper, 1994; Kardon, 1998).

Many predators are limited in the size of prey that they are capable of handling, either because of the additional time required to manipulate larger prey items (Elner & Hughes, 1978) or because of absolute limits to predator abilities. For example, prey size is limited by the size of the mouth for predators that swallow their prey, or by the size of the foot for naticid gastropods that envelope their prey within their foot for drilling. Particularly rapid growth in some taxa may mean that potential prey reach a size as refuge from predation (De Angelis, Kitchell, & Post, 1985; Seed, 1990).

Proposed morphological defenses include protection against the acids secreted by drilling gastropods by either thickening the outer periostracum or incorporating organic layers within the shell in corbulids, ostreids, and lucinids (Lewy & Samtleben, 1979; Taylor, 1990; Harper & Skelton, 1993b; Kardon, 1998; Ishikawa & Kase, 2007). De Angelis, Kitchell, and Post (1985) argued, based on modeling, that increasing shell thickness should be an evolutionary strategy of bivalves experiencing naticid gastropod predation. Such thickening of the shell was reported by Kelley (1989, 1991) and Kelley and Hansen (2001) for several Eocene and Miocene bivalve lineages of the United States Coastal Plain in response to naticid predation. Harper and Skelton (1993a) noted that taxa with thicker shells generally employ shell microstructures, such as foliated calcite and crossed lamellar aragonite, that are known to be low in organic matrix and consequently may be cheaper to secrete (Palmer, 1992); such microstructures, although mechanically weaker in terms of resistance to bending, impact resistance, and compression, are harder, and crossed-lamellar structures may be more resistant to abrasion (Taylor & Layman, 1972). It is also notable that shell thickening may be induced in some species by exposure to predators (Trussell & Smith, 2000; Cheung & others, 2004). Such induced defenses may be favored when pressure from the predator is variable and unpredictable but sometimes strong, when cues are available to trigger the defense, and when the defense is effective but costly or involves tradeoffs.

Shell ornamentation has been postulated to serve as an antipredatory adaptation (Thomas, 1978; Kelley & Hansen, 1996a). Bivalve ornamentation that may protect against predation includes radial or concentric costae or folds, as well as spines. For instance, Dietl, Alexander, and Bien (2000) found that radial costae increased in Cretaceous exogyrine bivalves as an evolutionary response to durophagous predation. Radial folds are also more common in Recent tropical bivalves exposed to intense predation than in cooler water faunas (Alexander & Dietl, 2003). The antipredatory function of such ornamentation may represent an exaptation, as Stanley (1988) interpreted many cases of bivalve sculpture as facilitating burrowing and/or stability within the substrate.

The occurrence of elaborate spiny ornament in bivalves appears to increase over geological time and with decreasing latitude (Harper & Skelton, 1993a). Spines may have a multitude of defensive (and other) functions, including increasing the effective size of the bivalve (and thereby defending against predators that swallow their prey whole), providing direct defense, and encouraging epibiont settlement (Feifarek, 1987; Stone, 1998; Han & others, 2008). Spines are a prime example, however, of an adaptation that, however effective, is restricted to taxa with particular preadaptations, for example the thin, flexible periostraca necessary to describe their templates (Harper & Skelton, 1993a). Interestingly, although mytiloids and arcoids are unable to form calcareous spines, some have long flexible processes attached to the periostacum, which provide some defense (e.g., Wright & Francis, 1984). These processes are not periostracal in origin but are pedal secretions onto outer surface of the periostracum (Ockelmann, 1983).

Flexible valve margins, as seen, for example, in pterioids and ostreoids, may provide defense against attack by creating a hermetic seal that prevents the escape of cues that attract chemosensory predators (Vermeij, 1983, 1987; Esteban-Delgado & others, 2008) and also by excluding predators that chip at the shell margins, by promoting sealing following unsuccessful attack (Carter & Tevesz, 1978). Dietl and Alexander (2005) showed that repair frequencies are higher in pinnoids than in bivalves with more rigid margins, suggesting that the former are better able to survive unsuccessful predation attempts. Overlapping valve margins (as in corbulid bivalves) may have a similar effect of sealing the valves (as well as resisting compressive forces generated by shell-crushing predators; Vermeij, 1987). The need to seal gaps between the valves, which may allow the egress of chemical cues, seems to be underscored by the reduction of taxa with permanent gapes at lower latitudes (where presumably predation pressure is more intense; Vermeij & Veil, 1978). Some bivalves (e.g., scallops and cockles) have crenulated margins, which have been suggested to provide protection by either enhancing the hermetic seal or by preventing shearing between the valves (Reif, 1978; Vermeij, 1987).

The evolutionary mechanisms involved in the evolution of bivalve defenses against their predators remain an active area of research. In particular, debate has concerned whether such evolution can be characterized as involving escalation or coevolution (and which model of coevolution might be involved). A key question concerns the extent to which prey influence the evolution of their predators (Dietl & Kelley, 2002). In coevolution, two or more species (i.e., predator and prey) evolve in response to one another; adaptation is reciprocal. In contrast, escalation represents evolution in response to enemies (Vermeij, 1994). Escalation recognizes asymmetry in selection; typically the selective pressures imposed by predators on prey are stronger than those imposed by prey on their predators (the so-called life-dinner principle, in which failure by the prey causes loss of life but failure by the predator only means loss of a meal; Dawkins & Krebs, 1979, p. 489).

Both coevolution and escalation could account for response of bivalve prey to their predators (as predators represent enemies to their prey), but escalation views the effect of prey on their predators as unimportant unless the prey are dangerous (and therefore enemies) to their predators. When escalation occurs between predators and dangerous prey, responses can be reciprocal (and thus considered coevolution). Evolution of antipredatory defenses by bivalves in response to naticid gastropod predation has been considered to represent escalation; Kelley (1992) found that Miocene naticids did not evolve offenses to counter the evolution of their bivalve prey but instead responded evolutionarily to their own predators. However, the bivalve *Mercenaria* was considered dangerous to its busyconine gastropod predator because the predator frequently breaks its shell while chipping open the prey (Dietl, 2003a). The evolution between *Mercenaria* and its busyconine predator can thus be considered an example of coevolution.

In evaluating the importance of processes such as escalation and coevolution on a predator-prey system, consideration must be given to the role of other species affecting the interaction; such species may impose selection pressure that either reinforces or opposes selection due to the interaction of interest (Dietl & Kelley, 2002). The presence of multiple predators may have emergent effects on a prey, in which the effect of a particular predator on its prey is either lessened or intensified by the additional predators (Sih, Englund, & Wooster, 1998). In other words, the effect of multiple predators need not be additive. Both risk enhancement and risk reduction have been observed due to the presence of multiple predators. For instance, if a prey's defenses against one predator increase its vulnerability to another predator, predation frequency may be increased more than would be expected based on the effect of either predator alone. Conversely, if predators interfere with or prey upon one another, the presence of multiple predators may reduce risk to their prey.

Attention must also be paid to the geographical and temporal scale of the interaction. For instance, the geographic structure of populations has been considered to contribute significantly to potential causes of long-term evolutionary stasis and short-term evolutionary dynamics (Eldredge & others, 2005). The geographic mosaic theory of coevolution explicitly considers the role of spatial variation in the outcome of interspecific interactions in coevolution (Thompson, 1994, 2005). Thompson's view recognizes a geographic mosaic of hot spots in which interacting species have reciprocal effects on each other's fitness and reciprocal adaptation occurs, and cold spots in which reciprocal selection is not occurring (for example, because other interactions exert stronger selective pressure or because one species is too rare). Although coevolution may generate novelty in local areas, spatial variation in selection is likely to produce stasis on a larger geographic and temporal scale (Eldredge & others, 2005).

Thompson (2005) proposed a process of coevolutionary alternation with escalation in which natural selection favors predators that preferentially attack the least defended prey, leading to evolution of improved defenses in those prey. At the same time, selection should favor the loss of defenses in unattacked prey species. Geographic variation in selection should thus produce geographic variation in prey defenses and predator preferences. Dietl and Kelley (2007) tested this hypothesis of coevolutionary alternation with escalation by examining spatial variation in morphological defenses of bivalve prey and in predator preferences indicated by naticid gastropod drilling frequencies in the Miocene Calvert Formation of Maryland. Results did not support the hypothesis of coevolutionary alternation with escalation. Predators did not prefer the least defended (thinnest) prey species, nor did prey defenses and preference rankings by the predator vary geographically as predicted. Dietl and Kelley (2007) concluded that the discrepancy may occur because the hypothesis of coevolutionary alternation focuses on evolution of local, highly specialized adaptations, whereas the bivalve defense examined (shell thickness) is a more general response to classes of enemies. Further work is needed to determine whether the hypothesis of coevolutionary alternation with escalation can explain more complex evolutionary patterns of defenses and counterdefenses found in the fossil record.

OPPORTUNITIES FOR FUTURE RESEARCH

The above examples show the wide range of adaptive responses suspected or demonstrated to have resulted from predation pressure. In fact, a great many of them rely principally on rather anecdotal evidence. There is great scope for testing putative defensive adaptations, both in terms of demonstrating that they do truly have the benefit commonly ascribed to them, but also demonstrating unambiguously that there are plausible coincidences between the onset of a particular style of predation pressure with the evolution of particular traits. The matter is, however, complicated by the fact that many bivalve taxa may have a multitude of different predators using a wide range of techniques upon them. No single defensive adaptation is effective against all types of attack and, importantly, there may be trade offs required between particular strategies.

Further understanding of the impact of predators on the evolution of bivalves requires more data from both modern and fossil faunas. There is much scope for refining our knowledge of when particular predatory methods evolved and quantifying their impact over geological time. Such work will certainly involve utilizing novel methods for recognizing particular modes of predation.

Much of the quantitative data collected to date concerns drilling predation, and in particular, the activities of naticid gastropods. It would be beneficial to gain further understanding of other predator groups, including novel ways of recognizing their activities from dead or fossil shell material. Moreover, understandably, most published research on predation of modern bivalves has concentrated on commercially important species; data for other taxa would be welcome. Furthermore, studies that report predation frequencies (both modern and fossil) are understandably focused on sites where levels are significant, but there is a need to further understand variability in levels across a range of environmental scales.

There is also a notable bias in our data toward North America and western Europe (Harper, 2006). There is a clear need to further evaluate hypotheses with data on the impacts of other types of predators and from a wider range of geographic areas and environments. Predation studies that incorporate current ecological theory (e.g., various processes of coevolution and/or escalation; inducible defenses; emergent effects of multiple predators) would also be welcome.

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