THE FOSSIL RECORD OF PREDATION: AN OVERVIEW OF ANALYTICAL METHODS

MICHAL KOWALEWSKI
Department of Geological Sciences, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24060 USA

ABSTRACT—*Paleontological research on predation has been expanding rapidly in scope, methods, and goals. The growing assortment of research strategies and goals has led to increasing differences in sampling strategies, types of data collected, definition of variables, and even reporting style. This methodological overview serves as a starting point for erecting some general methodological guidelines for studying the fossil record of predation. I focus here on trace fossils left by predators in the skeleton of their prey, arguably one of the most powerful sources of direct data on predator-prey interactions available in the fossil record. A critical survey of sampling protocols (data collecting strategy, sieve size, and sample size) and analytical approaches (predation intensity metrics, strategies for evaluating behavioral selectivity of predators, and taphonomic tests) reveals that various approaches can be fruitful depending on logistic circumstances and scientific goals of paleoecological projects. Despite numerous caveats and uncertainties, trace fossils left by predators on skeletons of their prey remain one of the most promising directions of research in paleoecology and evolutionary paleobiology.*

INTRODUCTION

IN RECENT YEARS, paleontological research on predation has become increasingly sophisticated in terms of complexity of tested hypotheses, intricacy of sampling designs, and quality of analytical methods. Moreover, its thematic scope has expanded abruptly as we now collect much more diverse data for a much broader spectrum of organisms over a much wider range of observational scales, from individual interactions to global-scale secular trends. Unfortunately, albeit perhaps inevitably, our data are collected in various, often disparate ways, so our research efforts are contaminated with methodologically undesirable idiosyncrasies. The irreconcilable differences in sampling strategies, types of collected information, definition of variables, and even reporting style make it difficult to compare directly many otherwise valuable data sets, and hamper meta-analytical attempts to explore hoards of data amassed in the rapidly growing literature on the fossil record of predation.

The methodological overview presented in this chapter and the two subsequent contributions included in this volume (Chin, 2002; Haynes, 2002) bring together a diversity of methods used for studying the fossil record of predation. These reviews should help us in collecting and reporting future data in a more congruent manner so as to avoid the confusion that we often encounter when communicating our research.

This chapter focuses primarily on trace fossils found on skeletons of marine invertebrate prey. Such fossilized traces of predation provide arguably the richest source of quantifiable data on prey-predator interactions available in the fossil record (see especially Kitchell, 1986) and have been widely used in paleontological research to date. Other important lines of evidence for studying predator-prey interactions are discussed here only briefly. The subsequent methodological contributions included in this volume review the methods employed to investigate coprolites (Chin, 2002) and the distinct strategies used to study hominids and other vertebrate predators and prey (Haynes, 2002).

Following Bambach (2002), predators are defined here as organisms that "…hunt or trap, subdue, and kill individual animals that have some capacity for either protection or escape." The word "individual" serves to distinguish predators from passive filter feeders, such as crinoids and some whales, which represent a distinct type of ecological interactions. However, even direct lines of evidence of predation (e.g., trace fossils, stomach contents, coprolites) rarely provide unambiguous means to distinguish predators from scavengers or even parasites (e.g., Baumiller et al., 1999; Kowalewski et al., 2000). Thus, paleontological research on "predation" is broader than indicated by the above definition. This is not necessarily a bad thing considering how closely those behaviors are related to predation. In fact, continuous behavioral spectra span from predation to scavenging, from lethal predation to partial (sublethal) predation (e.g., Nebelsick and Kampfer, 1994; Lawrence and Vasquez, 1996; Wood, in press; Vermeij, 2002), from predation to parasitism, or even from parasitism to amensalism or commensalism (Baumiller, 2002; Baumiller and Gahn, 2002). Moreover, in cases of confamilial predator-prey interactions, the attacker may end up being a prey (e.g., Dietl and Alexander, 1995, 2000). For all those reasons, and except for a few places where these terms are contrasted, the words "predator" and "prey" are used here broadly to denote predator/parasite/scavenger and prey/host/carrion, respectively.

MAJOR TYPES OF PREDATION INDICATORS

Various direct and indirect indicators of predation are available to paleontologists (Table 1):

1. *Trace fossils* left by predators on skeletons of their prey (drill holes, repair scars, tooth marks, gnawing, fracture, and other structural damage) are the most common and widely studied direct indicators of biotic interactions (e.g., Kauffman and Kessling, 1960; Brunton, 1966; Reyment, 1967; Hoffman et al., 1974; Thomas, 1976; Rohr, 1976; Sheehan and Lespérance, 1978; Vermeij et al., 1980, 1981; Alexander, 1981, 1986a, 1986b; Bromley, 1981, 1996; Smith et al., 1985; Allmon et al., 1990; Boucot, 1990; Martill, 1990; Babcock, 1993; Lyman, 1994; Hirsch et al., 1997; Nedin, 1999; Dietl et al., 2000; Neumann, 2000). Moreover, they often yield a variety of quantitative data (e.g., Kitchell, 1986) that can be used to test rigorously various hypotheses on predator-prey interactions (e.g., Babcock and Robinson, 1989;

TABLE 1—Major types of predation indicators.

Indicator	Type of Evidence	Examples
Trace Fossils	Direct	A predatory drill hole in a bivalve shell, a repair scar
Coprolites and Stomach Contents	Direct	A theropod coprolite with identifiable prey remains, a spiral coprolite
Exceptional Preservational Events	Direct	A parasitic/amensal snail preserved attached to a crinoid calyx, a fish buried alive while eating smaller fish
Taphonomic Patterns	Indirect	A localized accumulation of shell or bone (e.g., midden), skeletal fragmentation patterns
Functional morphology and phylogenetic affinities	Indirect	Heavily armored prey skeleton, powerful appendages designed for crushing prey skeleton, behavior of the nearest living relative

Kelley and Hansen, 1993; Alexander and Dietl, 2001; Dietl and Kelley, 2002).

2. *Coprolites and stomach contents* with identifiable prey remains consumed by predators are a direct indicator (e.g., Bishop, 1977; Sohn and Chatterjee, 1979; Stewart and Carpenter, 1990, 1999; Coy, 1995; Becker et al., 1999; Richter and Baszio, 2001; Carrion et al., 2001) that is particularly widely used in studying the fossil record of terrestrial vertebrates (e.g., Chin et al., 1998; Andrews and Fernandez Jalvo, 1998). Coprolite-based research is discussed later in this book (Chin, 2002). A source of direct evidence, similar to coprolites, is provided by stomach contents. Although rarely preserved in the fossil record, instances of prey remains found in the digestive system of a predator are known for a wide range of predator-prey systems (e.g., Spencer and Wright, 1966; Moy-Thomas and Miles, 1971: Alpert and Moore, 1975).

3. *Exceptional Preservational Events* (EPE), in which two or more individuals are preserved together while interacting (e.g., Baumiller, 1990; Carpenter, 2000), also represent a direct indicator of biotic interactions. Trace fossils left by interacting organisms can also be included here (e.g., trails left by predators chasing their prey; Lockley and Madsen, 1992; Pickerill and Blissett, 1999). Although such indicators can be an insightful source of information on biotic interactions, they are very rare and thus of limited use in quantitative analyses or any large-scale studies that require multiple records through time or space.

4. *Taphonomic patterns* offer a wide range of indirect evidence such as the degree and characteristics of shell and bone fragmentation, preservation of predators and prey in close spatial association, midden deposits, or some other distinct biostratinomic characteristics in the arrangement of prey skeleton fragments (e.g., Wilson, 1967; Cadée, 1968, 1994, 2000; Mayhew, 1977; Stallibrass, 1984, 1990; Wilson, 1987; Todd and Rapson, 1988; Van Valkenburgh and Hertel, 1993; Cate and Evans, 1994; Lyman, 1994; Brandt et al., 1995; Chin, 1997; Stewart et al., 1999; Merle, 2000). However, these indicators are often limited to unique taphonomic settings and their interpretation tends to be ambiguous. For example, fragmentation may occur due to various causes other than direct biotic interactions (although breakage of biotic origin may be admittedly a dominant factor; e.g., Cadée, 1968; Cate and Evans, 1994; Oji et al., 2001). Other taphonomic lines of evidence are also debatable. The close spatial association of presumed predators and prey may reflect unique preservational circumstances (e.g., taphonomic traps such as tar pits) and accumulations of abiotic origin may be so similar to middens that their differentiation requires a careful statistical analysis (e.g., Henderson et al., 2002).

5. *Indirect evidence* is also provided by inferring predatory or defensive behaviors from *functional morphology* of fossils and *phylogenetic affinities* of studied groups, including ecology and ethology of their nearest living relatives. There are obvious dangers of interpretations based on functional morphology and phylogeny. Organisms may change their behavior, but, due to exaptations or various constructional constraints, may still retain morphological characters reflecting their previous ecology and behavior. Also, a morphology that can be interpreted as serving a particular function (e.g., prey defensive traits) may have evolved due to abiotic factors, and distinguishing between the two causes may be difficult (e.g., Wood, in press). Phylogenetic affinities are also a dangerous tool given the arguably high evolutionary plasticity of ecology and behavior of organisms. Moreover, feeding ecologies may be non-randomly distributed within and across metazoan clades, as is suggested by the derived nature of herbivory observed at many scales of phylogenetic analysis (Vermeij and Lindberg, 2000). Even more discouragingly, indirect strategies based on phylogeny or functional morphology typically provide information about only one component of the biotic interaction (e.g., a particular predator, a given prey clade, etc.), but tell us next to nothing about types of organisms with which the studied group may have interacted. Moreover, such indicators offer no quantifiable paleoecological data on the frequency of predatory attacks, prey selectivity, size refuge, and other aspects of predator-prey interactions (see also Leighton, 2002). Thus, they offer limited interpretive

power relative to trace fossils or coprolites, especially for detailed paleoecological analyses. Despite those caveats, these indirect indicators represent a valuable source of data because functional morphology can be applied to nearly all fossil specimens, and interpretations based on phylogenetic affinities can be postulated for virtually any lineage. Not surprisingly, the approach has proven a powerful tool in numerous studies, especially in large-scale studies of temporal and spatial gradients (e.g., Vermeij, 1977, 1987, 2002; Signor and Brett, 1984; Leighton, 1999; McRoberts, 2001; Dietl and Kelley, 2001; Van Valkenburgh and Jenkins, 2002; Bambach, 2002; and references therein).

VIRTUES OF TRACE FOSSILS AS PREDATION INDICATORS

I focus here on the most common quantifiable indicator of predation in the fossil record: trace fossils. These direct indicators have numerous virtues:

1. Traces of predation are common across various depositional environments. For example, drill holes and repair scars of predatory origin occur not only in a wide spectrum of marine environments (see Vermeij, 1987, for numerous references) but also can be found on skeletons of terrestrial prey (e.g., Vermeij, 1987, 2002; Ørstan, 1999; Gittenberger, 1999). Similarly, vertebrate tooth and gnawing marks can be found in both terrestrial (Lyman, 1994; Haynes, 2002) and marine prey (Kauffman and Kesling, 1960; Stewart and Carpenter, 1999; Tsujita and Westermann, 2001; but see Kase et al., 1998).

2. Traces of predation are found on skeletons of a wide spectrum of prey—from protists (e.g., Sliter, 1971, 1975; Lipps, 1988; Culver and Lipps, in press; Lipps and Culver, 2002; Hageman and Kaessler, 2002) through virtually all groups of metazoans with biomineralized skeletons, including marine invertebrates (see especially Vermeij, 1987; Brett and Walker, 2002; Walker and Brett, 2002; Brett, in press; Alexander and Dietl, in press; Kelley and Hansen, in press), terrestrial invertebrates (LaBandeira, 2002), and terrestrial vertebrates, including hominids (e.g., Lyman, 1994; Haynes, 2002).

3. Traces of predation are ubiquitous in the geological record and span virtually the entire fossil record of metazoan organisms with biomineralized skeletons. Starting with enigmatic tubes of the Late Precambrian *Cloudina* (Bengtson and Yue, 1992; Bengtson, 2002) and followed by diverse trace fossils found in Cambrian prey (e.g., Alpert and Moore, 1975; Miller and Sundberg, 1984; Jensen, 1990; Conway Morris and Bengtson, 1994; Nedin, 1999), drill holes, punch holes, repair scars, and other traces left by predators litter the fossil record of marine invertebrates (see reviews and data compilations by Vermeij, 1983, 1987; Signor and Brett, 1984; Alexander, 1986b; Kabat, 1990; Kowalewski et al., 1998; Brett, in press; Brett and Walker, 2002; Walker and Brett, 2002). Trace fossils left in terrestrial invertebrate (Labandeira, 2002, and references therein) and especially vertebrate prey (e.g., Jacobsen, 1997, 1998; Farlow and Holtz, 2002; Haynes, 2002; and references therein) are also well documented.

4. Trace fossils left by predators are made in biomineralized skeletons. Consequently, such traces have as good, or almost as good (see below), potential for preservation as the skeletons of their prey.

5. Finally, and perhaps most importantly, traces of predation provide direct evidence of biotic interaction and thus offer a rich array of quantifiable data on predator-prey interaction. Drill holes offer a particularly spectacular example of the incredible wealth of data that can be retrieved from traces left by predators in the skeletons of their victims (Fig. 1).

CRITERIA FOR IDENTIFYING AND INTERPRETING PREDATION TRACES

Trace fossils that may record predatory activity are often controversial in terms of their origin and need to be assessed rigorously. I advocate here a three-phased evaluation approach.

First, the biotic nature of the traces needs to be demonstrated. Chemical and physical agents can also create marks on shells and bones. For example, Lescinsky and Benninger (1994) documented a

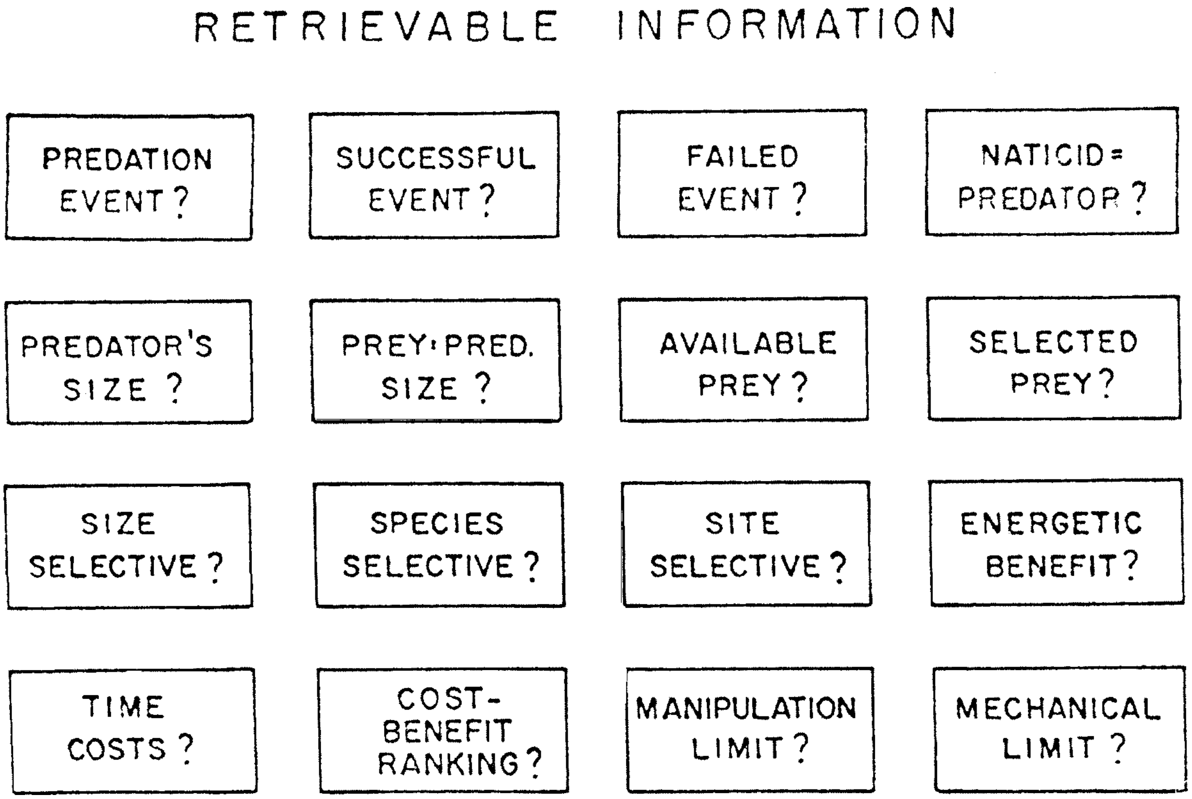

FIGURE 1—The wealth of ecological and behavioral information that may be obtained by analysis of just one type of trace fossils left by predators: drill holes (after Kitchell, 1986). Whereas many lines of evidence included on this diagram involve debatable assumptions, the figure illustrates the interpretive potential of the paleontological record provided by trace fossils left by predators on skeletons of their prey.

number of diagenetic alterations in marine invertebrate shells that could be potentially misidentified as traces of biological activity. Various abiotic processes, ranging from impacts of wave-borne stones to compaction, can result in fractures (or even repair scars in case of pre-mortem damage) and be mistaken for records of biotic interactions.

Second, demonstrating biotic origin is not enough. Not all biotic traces represent interactions between two living organisms. For example, substrate borings or substrate attachment scars can be postulated for structures interpreted as traces of predation or parasitism (see discussions in Carriker and Yochelson, 1968; Richards and Shabica, 1969; Kase et al., 1998; Kaplan and Baumiller, 2000, 2001; Wilson and Palmer, 2001; Tsujita and Westermann, 2001) and self-inflicted damage of burrowers can be misinterpreted as records of an encounter with a predator (Checa, 1993; Cadée et al., 1997). Thus, before attempting any analysis, it is necessary to demonstrate that the studied traces record contacts between living organisms (i.e., live-live rather than live-dead interactions).

Third, the specific ecological nature of the interaction needs to be identified. For example, many traces are ambiguous in that they may have been formed by predators, scavengers, parasites, amensals, or commensals. There are also cases when trace fossils represent self-inflicted damage suffered by a predator during an attack on its prey as in the case of predatory attacks by *Busycon* (Dietl, pers. comm., 2001). Thus, it is even possible incorrectly to attribute self-inflicted damage to a predator as a record of an attack by another predator (although this error can be often avoided by careful examination of the damage; Dietl, pers. comm., 2002). Finally, it is also useful to try to differentiate traces that represent sublethal damage (e.g., repair scars, healed drill holes, etc.) from lethal traces (e.g., extensive breakage, complete drill holes). It is noteworthy that sublethal damage may record two different types of events. First, it may represent failed lethal predation; for example, unsuccessful attacks of crabs that failed to kill and eat their mollusk prey. Second, sublethal damage may record successful partial predation by carnivores that only partially consume their prey. Such victims often recover, even though the attempt was *successful* from the perspective of the attacker. Examples of prey that are frequently subjected to partial predation in present-day ecosystems include, among others, echinoderms (e.g., Kowalewski and Nebelsick, in press), corals (e.g., Wood, in press), and bivalves (e.g., Vermeij, 2002).

Numerous lines of evidence can be used to recognize trace fossils produced by biotic interactions (see also Carriker and Yochelson, 1968; Bishop, 1975; Chatterton and Whitehead, 1987; Rohr, 1991; Lyman, 1994; Bromley, 1996; Baumiller et al., 1999; Alexander and Dietl, in press):

1. Traces have distinct geometric shape (e.g., drill holes, double punctures, peeling, tooth marks). This criterion helps to rule out abiotic origin of traces.

2. Traces show a relatively narrow size range. This pattern also suggests biotic origin of traces, as abiotic traces tend to be more variable in size.

3. The nature of traces suggests that they were made to gain access to the inside of the protective armor of the prey or host. This type of evidence includes, for example, holes and punctures that penetrate external skeletons from outside and do not go through the opposite side of those skeletons (traces that go through are likely to represent substrate borers; see Richards and Shabica, 1969; Kaplan and Baumiller, 2000).

4. Traces are distributed non-randomly across taxa. Such species-selectivity is strong evidence that traces are biotic in origin, especially if taxa are comparable in mineralogy, microstructure, and physical durability of skeletons, as it is hard to imagine that destructive abiotic (physical and chemical) processes would be highly selective among taphonomically comparable fossils.

5. Biotic traces made by predators or parasites are often non-random in their distribution on prey skeletons. Drill holes made by snails may concentrate in a particular area of the shell (e.g., Reyment, 1971; Negus, 1975; Berg, 1976; Kelley, 1988; Leighton, 2001) and vertebrate predators such as owls may preferentially break or otherwise damage only certain types of bones (Dodson and Wexlar, 1979; Kusmer, 1990; Lyman, 1994). This type of site-selectivity can not only help us to demonstrate the biotic origin of traces but may also allow us to postulate the specific type of behavior recorded by these traces. For example, traces may be distributed to give optimal access to muscle tissues, suggesting predatory rather than parasitic behavior (e.g., Hoffmeister et al., submitted).

6. Traces may occur preferentially in a particular size class of fossils. This pattern suggests size-selective behavior and thus points to biotic interactions. For example, Hoffmeister et al. (submitted) demonstrated that drill holes in Pennsylvanian brachiopods are restricted to a narrow size range of prey specimens.

7. Traces made by predators tend to be singular whereas parasitic traces are often multiple. For example, echinoid tests drilled by cassid snails typically bear one hole only (e.g., Nebelsick and Kowalewski, 1999) whereas those drilled by parasitic eulimid snails often contains several holes (e.g., Wáren et al., 1994; Kowalewski and Nebelsick, in press). However, there are exceptions. For example, predatory octopods tend to drill two or more holes to inject the venom more effectively (Bromley, 1993); and even textbook predators such as naticids and muricids are known to drill multiple successful holes in some prey (e.g., Dietl and Alexander, 2000; Dietl, 2000).

8. The presence of complementary scars on opposite sides of the skeleton suggests that these traces were made by a scissor-like weapon such as a crab claw or bird beak (e.g., Kowalewski et al., 1997).

9. The correlation between size of traces and size of fossils that contain them can also support predatory/parasitic origin of traces (but see discussion of taphonomic biases below).

10. Attachment scars can sometimes be observed in association with trace fossils, suggesting that the trace maker was attached to its victim for a prolonged period of time. Such attachment scars are typically interpreted as evidence for parasitic origin of traces (e.g., Matsukuma, 1978; Baumiller, 1990).

Typically, because of the nature of available data, only some of the above criteria are applicable in any given case study. Many of those criteria are insufficient when applied alone and, ideally, multiple lines of evidence should be applied to make a convincing case. The criteria can be supplemented with indirect lines of evidence such as the repeated co-occurrence of possible trace makers with their victims in many fossil assemblages through time and space, or such spatio-temporal changes in frequency of traces that are more likely to reflect changes in intensity of biotic interactions rather than changes in the intensity of taphonomic and other abiotic processes.

It is dangerous to assume, however, that all traces were made by the same type of organisms (e.g., naticid snails), or even represent a single behavior (e.g., predation) (see Gibson and Watson, 1989 for a convincing example). In fact, given a wide variety of origins that can be postulated for any given type of trace fossil (see below), it seems likely that trace fossil assemblages often contain a mix of records representing a whole spectrum of behaviors, including even abiotic traces. Ausich and Gurrola (1979) made a case for simultaneous presence of drill holes of parasitic and predatory origin in the same fossil assemblage, whereas a lively discussion between Kaplan and Baumiller (2000, 2001) and Wilson and Palmer (2001) offers a good example of methodological and practical difficulties in dealing with this issue. Ultimately, Bayesian statistical approaches may be needed to deal with those issues in a formalized way, but methodological strategies for dealing with this problem are still in their infancy.

CAN WE IDENTIFY THE CULPRIT?

Once the behavioral origin of the traces is demonstrated, one may attempt to pinpoint the biological identity of the culprit. However, as with any trace fossil (see Bromley, 1996), the identification of a predator from traces is a risky business (see especially Bromley, 1993). Different clades of predators often produce similar traces. For example, even the most morphologically distinct and informative traces such as drill holes can be made by a whole spectrum of organisms including as many as 14 different groups of predatory or parasitic invertebrates (Table 2; see also Vermeij, 1987; Kabat, 1990; Kowalewski, 1993; Brett and Walker, 2002; and Walker and Brett, 2002). Moreover, the same species of predator can produce traces that vary notably in morphology (e.g., Wodinsky, 1969; Bromley, 1970). In fact, even the same individual preying on a single prey type can make traces that vary greatly in shape and size, as demonstrated for single specimens of *Octopus vulgaris* preying on strombid gastropods (Arnold and Arnold, 1969).

In addition to these problems, the morphology of traces is not just a function of the anatomy and behavior of predators but may also vary greatly depending on prey morphology and many other factors. For example, at least seven additional factors are known to affect the geometry of a drill hole (Table 3). Because drill holes are widely considered to be one of the most unambiguous sources of information on predator-prey interactions in the fossil record (e.g., Kitchell, 1986), Table 3 is likely to be the best-case scenario. Arguably, other less distinct and inherently more variable traces such as repair scars, fractures, chewing marks and so on are an even more capricious source of information on the predator's identity, although exceptions certainly exist. For example, distinct double punctures made by stomatopods may be possible to identify in the fossil record (Geary et al., 1991; Bauk and Radwaski, 1996; but see Alexander and Dietl, in press).

In sum, different organisms can make similar traces, the same organisms can make different

TABLE 2—Drill hole producers reported in the biological and paleontological literature (expanded and updated after Kowalewski, 1993).

Drilling Organism	**Selected References**
NEMATODS	Sliter 1971, 1975; Arnold et al., 1985
FLATWORMS	Yonge, 1964; Woelke, 1957
GASTROPODS	
Nudibranchs	Zilch, 1959; Young, 1969; Taylor et al., 1983
Pulmonates	Wächtler, 1927; Degner, 1928; Carriker and Yochelson, 1968; Mordan, 1977
Platyceratids	Baumiller, 1990, 1993, 1996, 2002; Baumiller and Macurda, 1995; Baumiller et al., 1999
Naticids	Fischer, 1922-1966; Ziegelmeier, 1954; Carriker, 1961, 1981; Sohl 1969, Reyment, 1963-1967; Berg and Nishenko, 1975; Berg, 1976; Wiltse, 1980; Taylor et al., 1980; Savazzi and Reyment, 1989
Muricids	Fischer, 1922-1966; Carriker, 1943-1981; Reyment, 1963-1967; Sohl, 1969; Carriker and Van Zandt, 1972a,b; Matsukuma, 1977; Taylor et al., 1980, 1983
Cassids	Hirsch, 1915; Roughley, 1925; Day, 1969; Sohl. 1969; Hughes and Hughes, 1971, 1981; Nebelsick and Kowalewski, 1999; Kowalewski and Nebelsick, in press
Eulimids	Warén, 1980, 1981; Warén and Crossland, 1991; Crossland et al., 1991; Rinaldi, 1994; Warén et al., 1994; Kowalewski and Nebelsick, in press
Capulids	Orr, 1962; Kosuge and Hayashi, 1967; Matsukuma, 1978; Bromley 1981
Nassarids	Fisher, 1922, 1962a; Reyment, 1967; Morton and Chan, 1997
Marginellids	Ponder and Taylor, 1992
Buccinids	Peterson and Black, 1995; Harper et al., 1998
OCTOPODS	Fuijta, 1916; Arnold and Arnold 1969; Nixon, 1979; Ambrose, 1986; Guerra and Nixon, 1987

traces, and traces may also vary in morphology for reasons unrelated to the identity of a trace maker. Thus, with few exceptions, trying to identify the specific organism responsible for traces found in the fossil record is difficult. In fact, such identification efforts can only distract us from the real strength of trace fossils: their informative value as records of interactions that affected populations of an *identifiable* prey.

DATA COLLECTION

At least six strategies have been used to acquire data on traces of predation:

1. *Outcrop Surveys* rely on visual screening of outcrops for fossils with traces of predation, including accidental discoveries of such specimens by researchers collecting fossils for other reasons (e.g., Kowalewski and Flessa, 1994). Outcrop

TABLE 3—Confounding factors that may hamper reliable identification of the taxonomic identity of a drill hole maker; based on review by Kowalewski (1993).

Confounding Factors	Morphological Consequences	References
Site of the drill hole on the prey shell	Holes with an imperfectly developed form are produced when drilling is localized at the edge of the shell.	Vermeij, 1980
Thickness of the bored shell	The vertical shape of the hole is imperfectly developed if shells are too thin.	Ziegelmeier, 1954; Kitchell et al., 1981; Taylor et al., 1983; Yochelson et al., 1983
Structure of bored material	The stepped appearance of drill holes can result from the effect of the presence of the hard conchiolin layer in the shell of the prey (e.g., corbulid bivalves).	Ziegelmeier, 1954; Fischer, 1963; Taylor et al., 1983; Cauwer, 1985
Hardness of bored material	Changes in size and shape of drill holes may depend on the hardness of drilled skeleton, even when all holes were made by the same drilling predator.	Nixon, 1979
Ornamentation of prey shell	Drill hole geometry also can be controlled by ornamentation. For example, the drill hole morphotype "F" (sensu Arua and Hoque, 1989) always occurs between the ribs of ribbed shells (see Table 5 in Arua and Hoque, 1989).	Arua and Hoque, 1989
Geometry of prey shell	The unusual oval shape of the drill holes bored in scaphopod shells is an effect of the cylindrical geometry of the shell.	Yochelson et al., 1983
Taphonomic alteration	Taphonomic processes can affect drill hole morphology from subtle alteration of its outline to major modifications that completely change the shape of the drill hole. Whereas detailed studies exploring this issue are lacking, marginal remarks can be found in many previous works.	Vermeij and Dudley, 1982; Taylor et al., 1983; Allmon et al., 1990

surveys represent a highly uncontrolled sampling strategy that has limited use in quantitative analyses. However, they are an effective method for maximizing the chances of finding evidence of predation when such evidence is not expected to be common (e.g., in pilot projects that focus on time intervals, depositional environments, or prey types known to be a poor source of data on predation).

2. *Direct Bulk Sampling* provides quantitative data of highest quality by offering a full control on sampling design and data acquisition strategies. This method has been widely used to study predation (e.g., Hoffman and Martinell, 1984; Kelley and Hansen, 1993, 1996; Hagadorn and Boyajian, 1997; Stewart et al., 1999; Dietl et al., 2000). Although arguably superior to other sampling strategies, bulk methods suffer some drawbacks. First, bulk samples are limited spatiotemporally and, consequently, may offer a nonrepresentative estimate of the sampled fossil assemblage. Second, bulk samples are limited volumetrically and very large specimens may be

severely under-sampled (see also Dietl et al., 2000). Finally, a high time demand is involved in bulk sampling. Thus, typically, such studies are limited to few sites with a narrow stratigraphic and geographic coverage (e.g., Colbath, 1985; Kowalewski, 1990). However, large scale research programs that apply direct bulk sampling strategies are feasible and can yield some of the most comprehensive insights into the history of predation, as demonstrated by efforts of Kelley, Hansen, and their students and collaborators (e.g., Kelley and Hansen, 1993, 1996, in press; Hansen and Kelley, 1995; Kelley et al., 2001).

3. *Indirect Bulk Sampling* is based on reusing previously collected, either processed or—better yet—unprocessed, bulk materials. For example, despite highly constrained spatial, temporal, and environmental scopes of their study (north-central Europe, early middle Miocene, marine clastic epicontinental facies), Kowalewski et al. (2002) obtained numerous, high-quality bulk samples from museums, university collections, individual researchers, and private collectors. Hoffmeister and Kowalewski (2001) used the resulting dataset in a detailed quantitative analysis of drilling predation patterns and produced data comparable to those obtained when direct bulk sampling strategies are employed. Although the indirect bulk sampling method does not offer full control on selection of sampling sites and sample processing procedures, the resulting data can be of comparable quality and their acquisition can be much less time consuming, thus permitting studies with much broader spatial and/or temporal scopes.

4. *Museum Surveys* are a widely used method based on revisiting existing collections of fossils stored in museums and research collections (e.g., Hoffman et al., 1974; Allmon et al., 1990; Baumiller, 1993, 1996; Harper et al., 1998; Harper and Wharton, 2000; Hoffmeister, 2002; Hoffmeister et al., submitted). These types of projects can be particularly effective when traces of predation are rare and large collections need to be examined to achieve quantitative data (e.g., Hoffmeister, 2002). Museum collections may be biased by removal of "imperfect" specimens by overzealous curators (Walker, 1989) or by paleoecologists interested in studying specimens with trace fossils (Baumiller, pers. comm., 1999). Kowalewski (1990) showed that bulk samples of Miocene mollusks from the Korytnica Clays (central Poland) yielded similar estimates of drilling predation intensity for most (but not all) taxa that were analyzed previously by Hoffman et al. (1974; see also Zlotnik, 2001). However, some museum collections can offer materials that are comparable to bulk materials for individual taxa (Harper et al., 1998) or even for entire assemblages (Hoffmeister, 2002), providing suitable materials for quantitative studies.

5. *Monograph Surveys* represent a lamentably underutilized research strategy. Monographs provide thousands of photographs and thus allow us to examine quickly large numbers of specimens already identified and documented in terms of sampling site and stratigraphy. Such surveys are a great tool for pilot studies in exploring understudied groups of prey or geological time intervals known to have limited records of predation. Moreover, despite many obvious drawbacks, monographs can yield data that provide useful information on predator-prey interactions, and can go beyond mere pilot studies. Kowalewski et al. (2000) examined the series of monographs of Cooper and Grant (1972-1976) and were able not only to show that drilling predation (or parasitism) was continuously present in the Permian, but also to explore some quantitative patterns regarding behavioral stereotypy of the drillers. Even the quantitative estimates obtained by Kowalewski et al. (2000) were not unreasonable, as demonstrated in a subsequent study (Hoffmeister, 2002) of a brachiopod collection housed in the Smithsonian Institution (the collection is a nearly complete representation of bulk materials processed by Cooper and Grant during the preparation of their monographs).

6. *Meta-Analytical Literature Compilations* combine data assembled in previous qualitative and quantitative studies and provide a powerful tool for large-scale analyses of global secular trends in predation (e.g., Vermeij, 1987; Kowalewski et al., 1998). Although such studies are admittedly

hampered by methodological differences among case studies, they can provide first-order approximations for long-term trends that are otherwise difficult to access (but see Harper et al., 1999).

The six categories represent end members in a spectrum of possible approaches. Also, the data obtained with different approaches can be combined to broaden the scope of the study (e.g., Allmon et al., 1990; Hagadorn and Boyajian, 1997; Dietl et al., 2000). The numerous case studies cited for each strategy illustrate that all of the above approaches can be fruitful depending on logistic circumstances and research goals.

DATA PROCESSING

Numerous decisions are made when designing any research project. These decisions, often forced by pragmatic aspects of a particular investigation, can influence the quality and informative value of the data. Sieve size, sample size requirements, tallying strategies, and styles of data reporting are particularly important.

Sieve Size.—In many cases, paleoecological samples are processed with sieves to separate fossils from the enclosing sediment or rock. Sieve sizes can vary greatly among case studies, even for projects that target the same type of fossils. It is intuitively obvious that the choice of the mesh size used can greatly affect any quantitative paleoecological estimates derived from the analyzed residue. Because predators may be size selective (either directly by selecting certain size classes of prey or indirectly by selecting preferentially species from certain size classes), the sieve effect can be severe. To illustrate this problem, I re-analyze here a large dataset of mollusks from the Miocene of Europe (Hoffmeister and Kowalewski, 2001). The data include over 3500 specimens that were measured in terms of size and analyzed for presence of drill holes. A series of computer simulations was used to randomly sub-sample the database while mimicking the sieve effect (Fig. 2). The results indicate that, in this particular case, the drilling intensity rises as the mesh size is incrementally increased from 1mm to 10mm (the frequency of holes increases roughly by half: from ca. 15% for 1mm mesh to 23% for 10mm mesh). This simple example shows that the mesh size can influence the estimates of predation. Because small specimens can be excluded analytically, the compatibility of a study with previous studies is increased when the mesh size is small: the finer is the sieve, the more comparable will be the resulting data in future meta-analytical studies.

The above exercise shows how the exclusion of small specimens may affect the analysis. The exclusion or under-sampling of large specimens, which may be associated with bulk sampling (see above), may introduce similar types of biases into the analysis.

Sample Size Requirements.—Because traces of predation do not occur in all collected specimens and some specimens may bear more than one trace fossil, the sample size can be computed in three ways as (1) number of specimens; (2) number of trace fossils; and (3) number of specimens with traces fossils. Depending on the target of our analysis and frequency of traces, different sampling requirements may apply. For example, if the intensity of predation is the primary parameter of interest and traces are common, individual samples of 30 to 50 specimens may be sufficient to evaluate the analyzed patterns in a meaningful way. Note that maximizing the number of samples by reducing their size is a statistically advantageous tradeoff in quantitative paleoecological analyses (see Bennington and Rutheford, 1999). On the other hand, if the spatial distribution of traces is of primary interest and traces are rare, several thousand specimens may be required to obtain data that are statistically meaningful (e.g., Hoffmeister, 2002). Finally, the sample size also may be predetermined by demands of statistical tests (e.g., contingency tables [goodness of fit tests] require a certain number of observations per cell), although this issue can be partly alleviated by applying computer-intensive methods.

Tallying Strategies.—When processing samples, specimens and trace fossils can be tallied in several ways. First, data entry may be limited to

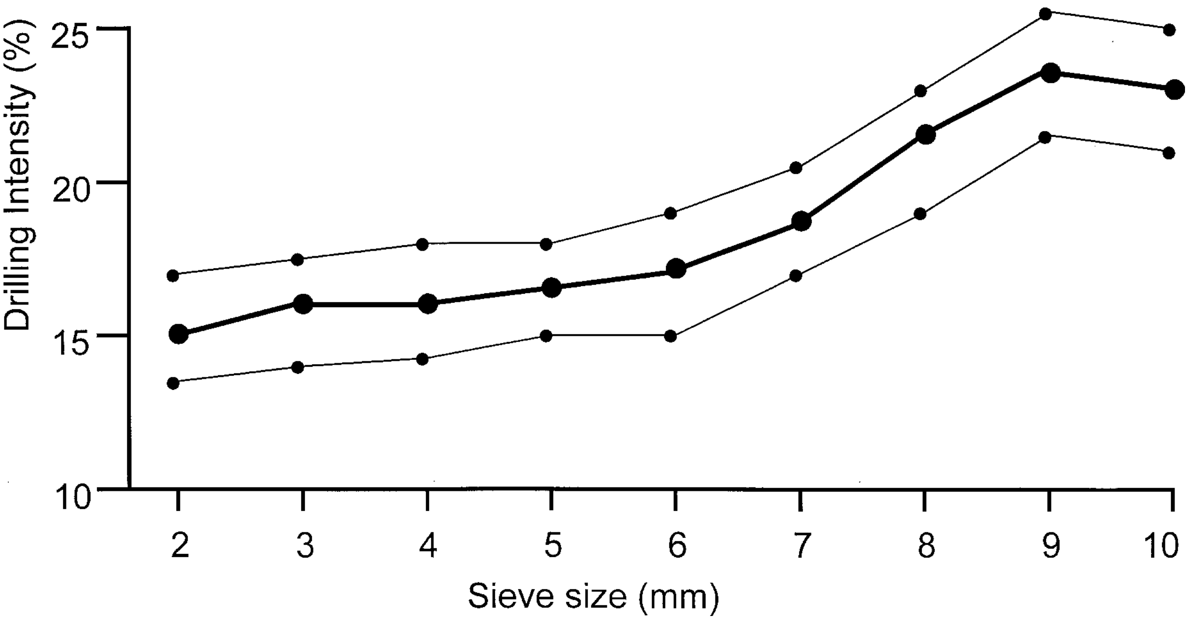

FIGURE 2—An empirical example of the effect of sieve size on the estimates of drilling intensity. A large dataset of Miocene mollusks (> 3500 gastropod and bivalve shells) was obtained by processing bulk samples using fine sieves with mesh below 1mm (Hoffmeister and Kowalewski, 2001; Kowalewski et al., 2002). An effect of sieve size was then mimicked in a computer simulation by removing from the database all specimens below a given mesh size. For each sieve size, 1000 subsamples of 100 specimens were randomly selected and assemblage frequencies (*AF*; see Equation 1) were computed, including mean drilling frequencies (large solid points) and 95% confidence intervals around them (small solid points). The confidence intervals are based on 2.5 and 97.5 percentile of 1000 *AF* values obtained for each mesh size.

only specimens with traces. This is usually not desirable because such data do not allow us to compute frequency of traces in bulk samples, and many other types of analyses (see below) cannot be conducted. However, this method may be effective in extracting some quantitative data, when very large collections are screened for traces of predation. Preferably, a data entry table should include at least one row per specimen (multiple rows per entry are recommended if multiple traces are found on the same specimens).

Data Reporting.—With increasing use of online repository systems, many journals allow for electronic publication of raw data tables. This is the most desirable way of reporting data that gives other researchers full access to all information collected in a project. Because the posting of repository materials may be delayed (authors may rightly feel it premature to disclose their data), it is also important to report clearly the results of the study, so the reader is able to distinguish, for example, counts of trace fossils from counts of fossils with traces and counts of valves of bivalves from counts of shells of bivalves.

ANALYSES OF PREDATION INTENSITY (FREQUENCY)

The frequency of traces is arguably the most important and widely used metric in quantitative analyses of the fossil record of predation that estimates the frequency of predator-prey interactions and may serve as a proxy for predation intensity (but see below). Four different, albeit related, methods have been used for estimating the frequency of predator-prey interactions in the fossil record.

1. Lower Taxon Frequency (*LTF*) aims to estimate the frequency of interactions for a given lower taxon of prey (typically species, genus, or family). Examples of *LTF* estimates include the frequency of drill holes in turittellid gastropods (e.g., Allmon et al., 1990) or the frequency of fractures in hominid bone assemblages (e.g., Villa and Mahieu, 1991). *LTF* is computed as follows:

$$\text{Equation 1:}\ \ LTF = D_K/N_K\ ,$$

where *K* is a lower taxon target in the analysis, D_K is the number of specimens of that taxon that contain at least one successful predation trace and N_K is the total number of specimens of that taxon in the sample. Similarly, *LTF* can be used to compute the frequency of failed attacks (e.g., frequency of repair scars in gryphaeid oysters), although the interpretation of such estimates tends to be more complicated (e.g., Dietl et al., 2000).

2. Assemblage Frequency (*AF*) aims to estimate the overall frequency of predator-prey interactions recorded by a fossil assemblage. In practice, this metric typically estimates frequency of traces in a higher taxon targeted by the bulk sampling protocol (e.g., all mollusks or all brachiopods). Examples include frequency of drilling in all mollusks found in bulk samples (e.g., Robba and Ostinelli, 1975; Hoffman and Martinell, 1984; Colbath, 1985; Kowalewski, 1990; Kelley and Hansen, 1993) or frequency of cut marks found in a survey of bones for all types of small or large bovids (e.g., Bunn and Kroll, 1986). *AF* is computed as follows:

$$\text{Equation 2:}\ \ AF = \Sigma D_i/\Sigma N_i\ ,$$

where D_i is the number of specimens of *i*-th species with at least one predation trace and N_i is the total number of specimens of *i*-th species in the sample.

3. Highest Lower Taxon Frequency (LTF_{MAX}) aims to estimate the highest frequency of traces observed among lower taxa. LTF_{MAX} is computed as follows:

$$\text{Equation 3:}\ \ LTF_{MAX} = D_{MAX}/N_{MAX}\ ,$$

where *MAX* is a lower taxon with the highest frequency of traces in the assemblage, D_{MAX} is the number of specimens of that species that contain at least one successful predation trace, and N_{MAX} is the total number of specimens of that species in the sample. This metric can be derived only from bulk materials when the data on frequency of traces for the entire sampled assemblage are available.

4. Assemblage Taxon Frequency (*ATF*), proposed by Vermeij (1987; see also Hansen and Kelley, 1995), is comparable to *AF* in that it also aims to estimate the overall predation intensity in a fossil assemblage. However, unlike the *AF* metric, the *ATF* metric uses a proportion of lower taxa rather than the proportion of specimens to derive an estimate of the overall predation intensity. *ATF* is computed as follows:

$$\text{Equation 4:}\ \ ATF = D_T/N_T\ ,$$

where D_T is a number of common taxa that frequently bear traces of predation and N_T is the total number of taxa in the sample. The terms “common” and “frequently” are defined *a priori* numerically. Vermeij (1987, p. 308), when analyzing drilling intensity for bivalved organisms through the Phanerozoic, defined “common species” as those represented by at least 20 valves and “frequently attacked” as those with $LTF > 10\%$. However, if traces are rare we may decide to define as “frequently attacked” lower taxa with as few as one specimen with traces of predation (i.e., $LTF > 0$) (e.g., Hoffmeister, 2002).

Except for *ATF*, all of the metrics listed above use some estimate of the number of specimens with traces of predation versus some estimate of the number of specimens. It is important to stress two caveats here. First, the number of specimens with traces of predation [D_K] is *not* synonymous with the total number of traces found in those specimens unless all specimens bear singular traces (i.e., multiple traces are completely absent). When computing predation intensity we should always use the number of prey specimens attacked (i.e., the number of specimens with traces) and not the number of attacks (i.e., the number of traces). Second, the strategies for computing the total number of specimens may vary greatly depending on the number of unique elements, degree of disarticulation of those elements, and statistical and taphonomic assumptions made in the course of a study (see especially Gilinsky and Bennington, 1994 and references therein). These equations are thus directly applicable only to specimens with single-element skeletons and may require modifications when applied to multi-element skeletons (see also below).

Discussion of Metrics.—LTF provides a metric system that offers the best chance for a biologically meaningful analysis of predator-prey interaction in the fossil record (see also Leighton, 2002; Vermeij, 2002). This is because lower taxa are more likely to represent a single behavioral and ecological type of prey, which may interact with a similar suite of predators through time and space. Also, potential taphonomic biases associated with differential preservation of taxa are not as severe when the analysis is restricted to a single genus or family (see also Leighton, 2002).The fact that the estimate is restricted to one prey type also decreases the chances for variable behavior of the trace maker, which may change its behavior depending on prey type (e.g., drilling predation may be obligatory for bivalve prey that are able to shut their valves tightly and facultative for prey with valves that allow a predator to insert its proboscis without drilling; e.g., Frey et al., 1986).

In contrast, the *AF* metric, by combining prey with a wide range of morphological and ecological characteristics, is less reliable both in terms of biologic interpretations and potential taphonomic biases. However, *AF* offers a significant pragmatic advantage: it can be computed for any fossil sample and thus provides a metric that is comparable analytically (if not biologically) throughout the fossil record. In contrast, few lower taxa are continuously abundant through long intervals of geological time and virtually none can be used to study very long secular trends: an *LTF* study encompassing the entire Phanerozoic cannot be done, except perhaps for such extremely conservative, long-lived lower taxa like Lingulidae. Thus, in the case of comprehensive long-term studies, *AF* is the lesser of two evils: it makes more sense to compare overall assemblage frequencies between the Paleozoic and the Cenozoic than to compare a specific family of Permian bivalves with a different family of Cenozoic bivalves. *AF* can be a useful indicator as long as we recognize that it is not likely to provide estimates for specific predator-prey interactions but rather represents a proxy for the overall predation pressure in the ecosystem. Whereas the credibility of *AF* has been recently debated (e.g., Leighton, 2002; Vermeij, 2002), it is worth pointing out here that assemblage-level metrics also provide an important baseline for the overall intensity of a particular behavior (e.g., drilling) through time. This baseline can provide an important reference standard against which specific lineages can be compared. Also, as shown below, the metrics tend to correlate highly (they are obviously dependent) so it may actually not matter that much which one is used. Thus, although *AF* may be a misleading metric when applied to test a specific model such as the Hypothesis of Escalation (this is yet to be demonstrated empirically), we should not discard it entirely.

LTF_{MAX} resembles *AF* in that it does not focus on specific interactions of a particular lineage of prey, but rather tries to estimate the overall intensity in the assemblage by targeting the most frequently drilled taxon. *AF* should tend to be more reliable because a maximum is a highly volatile parameter both in a statistical as well as biological sense.

Although *ATF* is akin conceptually to *AF*, it does differ fundamentally from *AF* in that it provides an estimate for how widespread predation was across prey taxa rather than across prey specimens. *ATF* may also provide an indirect proxy for behavioral, ecological, and maybe even taxonomic diversity of predators. Thus, in the best-case scenario, and notwithstanding all caveats listed above and below, *AF* may tell us how intense was the overall predation pressure ecologically (what proportion of biota was being killed by predators), and *ATF* can tell us how intense was predation pressure macro-evolutionarily (what proportion of phylogenetic lineages was affected by predators).

All four estimates are expected to show some correlation with one another: as frequency of traces increases the metrics all should go up. This is especially so in the case of *AF, LTF*, and LTF_{max} , which can become nearly synonymous when the analyzed fossil assemblages are close to monospecific, which happens occasionally especially in Paleozoic marine fossil assemblages (e.g., Chatterton and Whitehead, 1987). However, the extent to which the metrics approximate each other may vary notably, as exemplified in Figure 3 for these three metrics (*AF, LTF, ATF*). In the Paleozoic brachiopod assemblages from Texas, all metrics correlate tightly; whereas in the Miocene mollusk assemblages from Europe, the correlation is much poorer.

I do not advocate any of these metrics as necessarily superior to the others, as they all have advantages and drawbacks and all may be applicable depending on logistic circumstances and research goals. However, four recommendations seem appropriate here. First, researchers should make sure that they explicitly and precisely define the intensity metric up front. Second, whenever possible, data should be collected to make it possible to compute all metrics. Third, as suggested recently by Leighton (2002), the intensity metrics can be enhanced by combining these variables with population and size-class data, both within and across species. Finally, when the required data are available, multiple metrics should be computed so we can evaluate their relative volatility and interpret them jointly. As of now, only a few studies have used more than one type of metric when studying the intensity of predation (e.g., Hansen and Kelley, 1995; Hoffmeister, 2002).

Complicating Factors.—Regardless of the methods used, there are general complicating factors that need to be considered. Traces of predation represent a record of specific predator-prey interaction and there are many predators in ecosystems that kill without leaving any evidence because they feed by whole-animal ingestion or access soft tissue without damaging the prey skeleton. There are also many predators that destroy prey skeletons entirely. For all these reasons the assemblage-level estimates such as *AF* and *ATF* are likely to underestimate the overall predation pressures. The interpretation becomes even more ambiguous for specific predator-prey systems because frequencies of traces recorded in lower taxa (especially the *LTF* metric) can both underestimate and overestimate the intensity of predation. For example, a given frequency of tests of echinoids drilled by cassid snails may underestimate the importance of cassid-echinoid interactions because cassids are facultative drillers that occasionally access the soft tissues of their prey via peristomal or periproctal membranes (Hughes and Hughes, 1981), and because drillings of cassids may be mistakenly attributed to parasitic eulimid gastropods (see Kowalewski and Nebelsick, in press). On the other hand, the drilling frequency may overestimate the importance of cassids because many other predators of echinoids tend to destroy prey tests (e.g., Nebelsick, 1999; Kowalewski and Nebelsick, in press), resulting in too high a percentage of preserved tests killed by drilling predators. The importance of cassids may also be overestimated because eulimid drillings can be mistakenly attributed to cassids (e.g., Kowalewski and Nebelsick, in press).

A unique host of problems affects repair scars, healed drill holes, and other traces that record unsuccessful predation events. Such traces are inherently difficult to interpret (see also Schoener, 1979; Schindel et al., 1982; Vermeij, 1983; Walker and Voight, 1994; Cadée et al., 1997; Kowalewski et al., 1997; Leighton, 2002) because they cannot be used directly to estimate predation intensity: a prey population with a repair scar frequency of 20% may be preyed upon at much higher rates by an efficient predator or at much lower rates by a clumsy predator. In fact, some predators are known to repeatedly attack unsuitable prey (e.g., Vermeij, 1982), and thus it is feasible that a “prey” with frequent repair scars is never subjected to successful predation. Also, if a predator is (at least occasionally) successful, the repair scars represent only a subsample of all attacks. Unless the unsuccessful and successful attacks are statistically indistinguishable in their ecological and behavioral aspects (e.g., prey size, site of attack), a quantitative analysis of repair scars may provide misleading insights into predation.

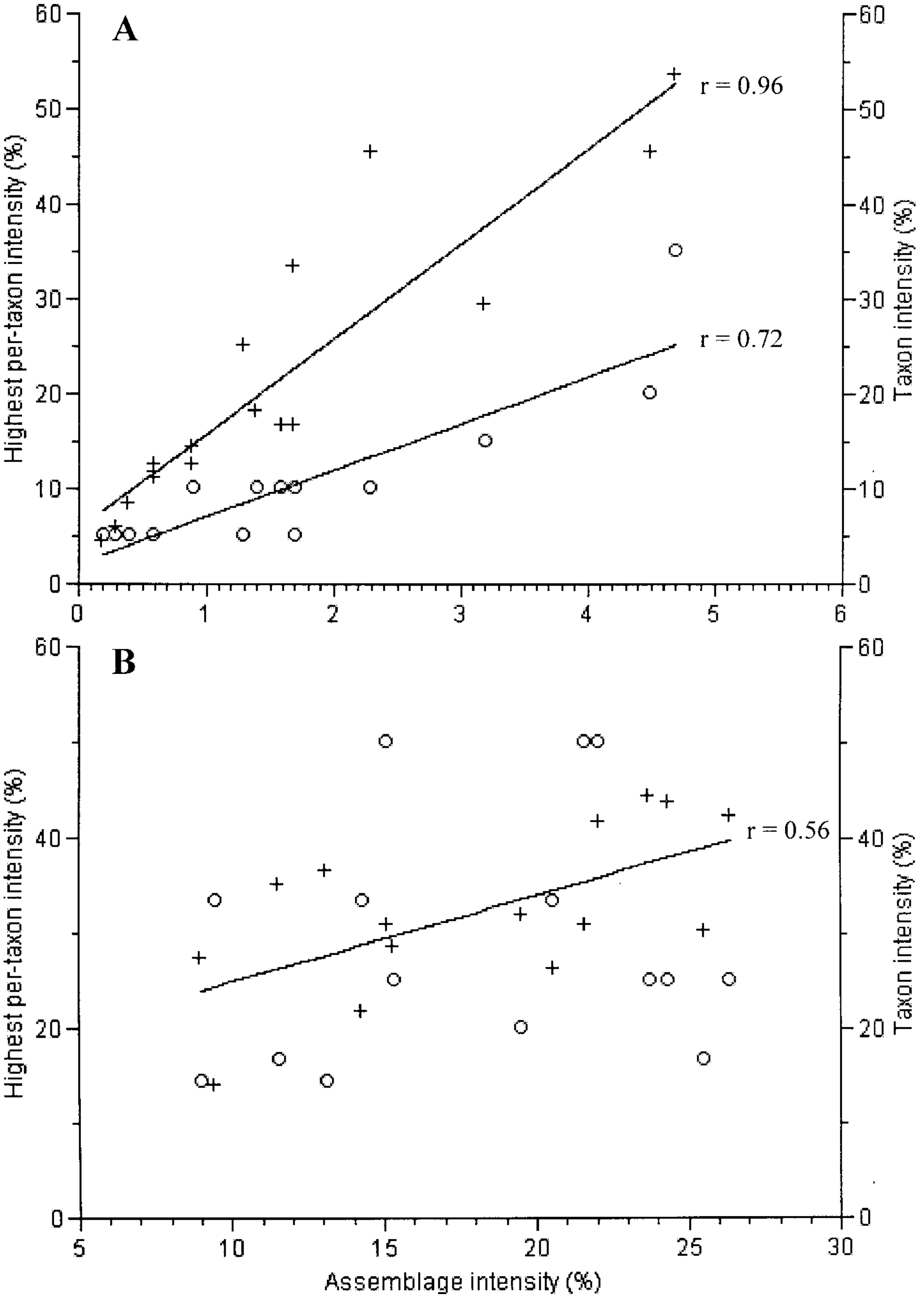

FIGURE 3—Comparison of three different metrics to estimate intensity of predation for the same sets of samples. Each point represents one sample. Symbols: + – highest per-taxon estimates plotted against assemblage estimates, o – taxon estimates plotted against assemblage estimates, *r* – Spearman rank correlation coefficient (reported only if $p < 0.05$). A. Drilling predation estimates for 21 museum samples of Permian brachiopods of West Texas (data from Hoffmeister, 2002). B. Drilling predation estimates for 15 bulk samples of Miocene mollusks of central Europe (data from Hoffmeister and Kowalewski, 2001).

Finally, traces of predation may both decrease and increase the preservational potential of the prey skeleton, biasing quantitative estimates based on frequency of specimens with traces (e.g., Roy et al., 1994; Hagstrom, 1999; Zuschin and Stanton, 2001; see also below for a discussion of taphonomic biases).

How to Correct Predation Frequency Estimates for Disarticulated Elements.—The equations discussed in the above section can be applied directly to taxa with single-element skeletons (gastropod shells, foraminiferan tests, etc.). However, many prey animals possess skeletons that consist of two or more elements that tend to disarticulate after death. If a predation event is recorded on one of those elements only, then the probability of finding evidence of predation (preserved by only one disarticulated element) is smaller than the probability of finding prey (represented by any of its elements). Consider, for example, a bivalve mollusk killed by a predator that drilled a hole in one of its valves. Assuming that both valves have the same preservational potential, the probability of finding one of the two valves of the prey is two times more likely than finding specifically the valve that was drilled. Thus, a correction by a factor of 2 is required. It is worth stressing here that, regardless of whether the sampling domain is infinite and all sampled valves are unique or the sampling domain is finite and some valves come from the same individuals (see Gilinsky and Bennington, 1994), this correction is required (see also Bambach and Kowalewski, 2000; Hoffmeister and Kowalewski, 2001).

The issue of correction may appear trivial but it turns out that there are two ways of making this correction and both of them are used in the literature.

$$\textit{Equation 5: } f_d = d/0.5n$$

$$\textit{Equation 6: } f_d = 2d/n,$$

where f_d represents the estimate of drilling frequency, d is the number of valves in the sample that contain at least one successful drill hole, and n is the total number of valves in the sample. These two equations may appear synonymous but, from a statistical perspective, they are not. Equation 6 produces an estimate with a sample size that is two times higher than an estimate produced by Equation 5. Consequently, Equation 6 offers much more power than Equation 5. Table 4 shows a hypothetical example of two samples of bivalves. If Equation 6 is employed all statistical tests used indicate that the two samples differ significantly in drilling frequency. If Equation 5 is used none of the tests rejects the null hypothesis that the two samples came from a single underlying population. Which equation is correct?

The answer to this question is not intuitively obvious. Whereas Equation 6 doubles the

TABLE 4—A hypothetical example illustrating differences in statistical power of the two equations used to correct frequency estimates for drill holes in bivalved fossils. Symbols: N – total number of valves, D – number of drilled valves, R – drilling frequency, P_{chi}, P_G, and P_{Fisher} – The probability estimates (Chi-square, Log-likelihood G, and Fisher's Exact tests, respectively) for the null hypothesis that the two samples came from a population with the same drilling frequency. All tests are significant at alpha=0.05 level for Equation 6, but none is significant for the more conservative Equation 5. Computer simulations (Fig. 4) show that Equation 5 yields correct estimates of Type I Error.

Sample 1	**Sample 2**	**Drilling Intensity**	
		Equation 5	Equation 6
N_1=30	N_2=40	N_1=15, N_2=20; D_1=11, D_2=5	N_1=30, N_2=40; D_1=22, D_2=10
D_1=11	D_2=5	R_1=73.3%, R_2=25%	R_1=73.3%, R_2=25%
R_1=36.7%	R_2=12.5%	P_{Chi}=0.09, P_G=0.08, P_{Fish}=0.13	P_{Chi}=0.02, P_G=0.01, P_{Fish}=0.02

observations in the numerator, increasing the power of the test, Equation 5 halves the number of observations in the denominator, decreasing the power of the test. A simple computer simulation can resolve this issue. If we draw random samples from a known underlying distribution and use a=5% to reject the null hypothesis, *which we know to be correct in this case,* we should reject incorrectly 5% of the tests. Results show that, regardless of sample size, when Equation 5 is used ca. 5% of tests are rejected and if Equation 6 is used over 11% of tests are rejected (Fig. 4). This simulation indicates that Equation 5 performs correctly and should be employed in future studies whereas Equation 6 clearly is too powerful and should not be used to correct for disarticulated elements.

Note here that the example considered above assumes the following: (1) the two opposite valves are equally likely to be preserved; (2) the predator always produces a trace in one valve only; (3) the trace does not weaken the skeleton; and (4) the predator does not show valve selectivity. All these assumptions are questionable, and more complex corrective strategies (most likely, based on the Bayesian approach) should be developed in the future.

Escalation parameters.—Escalation parameters are estimates that provide some measure of the predator's failure. A relative frequency of failed attacks (often referred to as "prey effectiveness"; e.g., Vermeij, 1987; Alexander and Dietl, in press; Kelley et al., 2001), as recorded by traces documenting unsuccessful attacks (e.g., repair scar

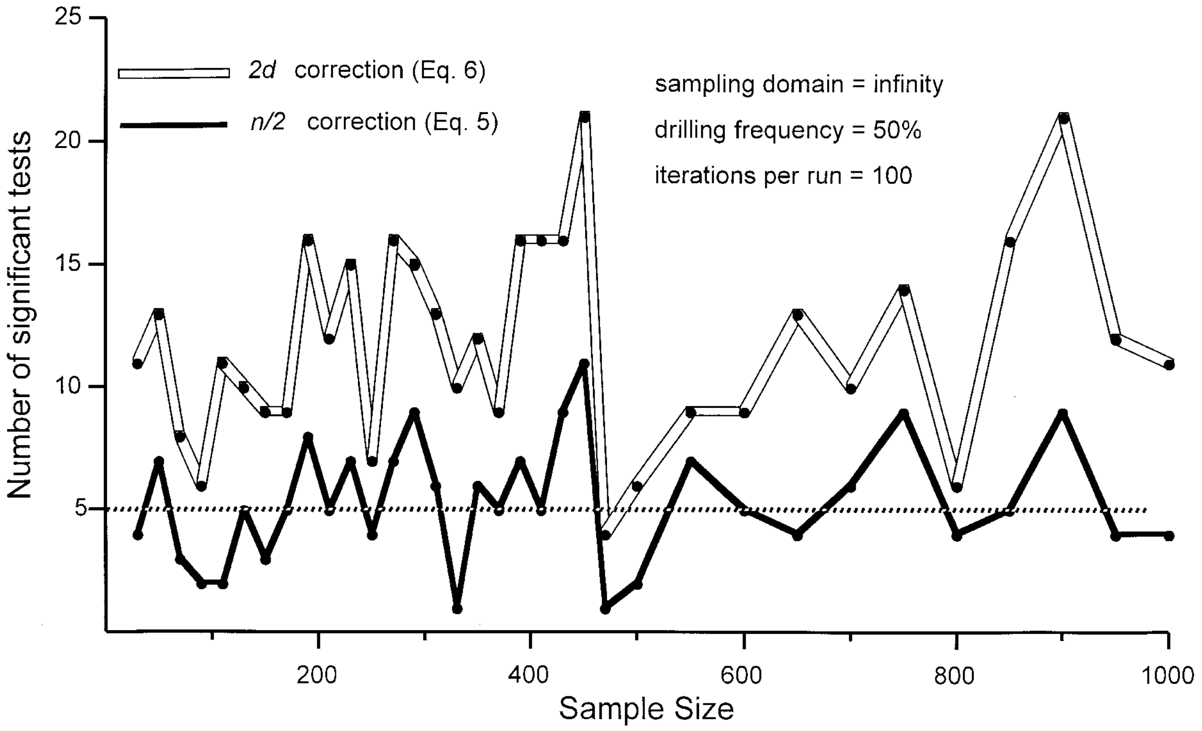

FIGURE 4—A series of computer simulations testing the statistical power of Equations 5 and 6. In the simulation, samples of specimens are drawn randomly from an infinite population of disarticulated valves of bivalve mollusks with a predefined drilling frequency of 50%. The correct null hypothesis (drilling frequency = 50%) is then tested for each random sample using Fisher's Exact Test and alpha=0.05. When Equation 5 is used the Type Error I (the erroneous rejection of the correct null hypothesis) varies around 5% (mean=5.32) indicating that this test performs correctly. When Equation 6 is used over 11% of tests are significant indicating that Equation 6 offers over two times more statistical power than it should.

or healed drill hole), is the most frequent metric of escalation. It is typically computed as follows:

$$\textit{Equation } 7: \; P_E = T_F/T_T \,,$$

where P_E denotes prey effectiveness computed as T_F, the number of a particular trace fossil of predatory origin that records failed attacks (e.g., the number of incomplete and healed drill holes), divided by T_T, the total number of these trace fossils (e.g., the total number of drill holes). Note that, unlike for the intensity metrics above, the numbers are computed using the number of traces and *not* the number of specimens with traces (if a predator left two repair scars on a single prey, the prey survived twice, not once, and the predator failed twice, not once).

As intensity metrics, escalation parameters and escalation tests are not without problems. For example, in a case of repair scars, numerous confounding factors need to be considered (based partly on Alexander and Dietl, in press):

1. No single method for quantifying shell breakage can be applied when prey include a wide range of taxonomy and morphology (e.g., highly ornamented forms provide many more indications of repair than do smooth forms) (see also Schindel et al., 1982; Cadée et al., 1997).

2. Repairs may accumulate on skeletal parts that are less readily preserved (e.g., opercula but not the shell of a gastropod; see Alexander and Dietl, in press).

3. Lethal shell damage is often unrecognizable and thus the denominator of Equation 7 is underestimated and the prey effectiveness is overestimated.

4. Predators may mistakenly attack a skeleton of a dead prey. Consequently, post-mortem attacks can be confused with successful attacks, the denominator of Equation 7 is overestimated, and the prey effectiveness is underestimated (see especially Walker and Yamada, 1993).

5. Prey skeletons are often completely destroyed by predators (e.g., Alexander and Dietl, in press).

6. Frequency of attacks can be severely underestimated in the case of prey that experience ecdysis. For example, if a trilobite molted 5 times and survived one unsuccessful attack, the frequency of repairs will be underestimated five-fold.

7. Different morphs of species that display sexual dimorphism or developmental polymorphism may be preyed upon with different intensity and/or different predatory success.

8. Spatial variability in escalation patterns may obscure temporal trends (e.g., Hoffmeister and Kowalewski, 2001).

9. Ambiguities in distinguishing failed and successful attacks can confuse the computation of the prey effectiveness (see above and Alexander and Dietl, in press).

10. Disarticulation may complicate computing the prey effectiveness (e.g., Alexander and Dietl, 2001).

Despite this depressingly long list of problems, there are exceptions when the complicating factors can be partly or entirely eliminated (e.g., Kohn and Arua, 1999; Alexander and Dietl, in press).

It is noteworthy that, very much as was the case for the intensity metrics above, Equation 7 can be computed at various scales—from specific lower taxa affected by a single type of trace fossil up to entire assemblages of prey including various higher taxa and a wide range of trace fossil types. All of the above factors complicating the prey effectiveness analysis are increasingly likely to mask or distort the patterns when the taxonomic resolution is decreased. Thus, the prey effectiveness is best applied to specific lineages (see also Vermeij, 2002). However, as in the case of intensity metrics and for similar reasons, we should not discard assemblage estimates completely. In this case again they may serve as an important reference baseline and overall proxy of failure rates. The assemblage approach is again more debatable when used to test specific causative hypotheses (although, again, it is yet to be demonstrated beyond reasonable doubt that the problems above render these assemblage tests completely invalid).

ANALYSES OF SELECTIVITY

The second major analytical focus of research on predation traces deals with selectivity patterns revealed by non-random distribution of traces (1) across prey taxa (taxon selectivity), (2) on prey skeletons (site selectivity), and (3) among prey with different sizes (size selectivity). This type of analysis is routinely included in detailed quantitative studies of predation traces and can provide many important insights into the nature of predator-prey interactions.

Taxon Selectivity.—Predators are often highly selective in choosing the species (or lower taxon) of their prey. In the most general terms, taxon selectivity simply means that a given taxon is attacked more frequently than is expected by chance. Based on the work of Botton (1984), Alexander and Dietl (in press) suggested that this type of evaluation can be performed using the Strauss Index, which can be defined as follows:

$$\text{Equation 8: } L_I = R_I — P_I,$$

where R_I is the percentage of specimens with traces belonging to taxon *i* computed relative to all specimens with traces found in the assemblage, and P_I is the percentage of taxon *i* in the assemblage. This index can help us to detect prey taxa with unusually high or low proportion of traces.

Another possible strategy is to apply computer simulations to evaluate how likely it is to obtain the observed distribution of traces across lower taxa for a given sampling design. In an example shown in Fig. 5, all common genera of silicified brachiopods from the Permian of West Texas (4452 specimens from 37 genera; data from Hoffmeister, 2002) are plotted and the frequency of traces of predation (drill holes) is marked by black parts of the bars. Notice that holes are generally rare (overall predation rate *AF* = 1.1%) so many genera do not include any specimens with traces (the

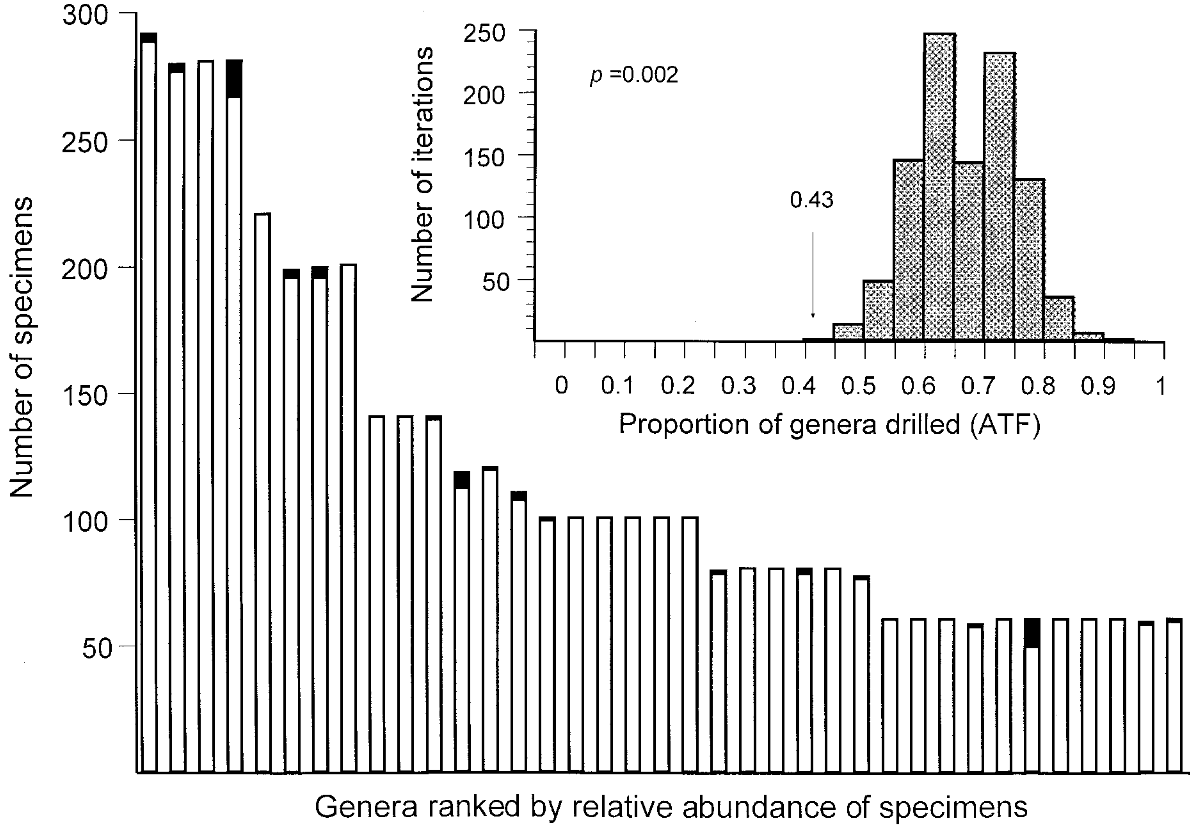

FIGURE 5—Evaluation of genus selectivity in drilling on Permian brachiopods from West Texas (data from Hoffmeister, 2002 and in prep.). See text for details. The SAS/IML code for the Monte Carlo model shown in the inset plot is provided in Appendix 1.

proportion of drilled brachiopod genera *ATF* = 43.6%). It is difficult to assess visually if the distribution of traces is random or not. A Monte Carlo model (see Appendix 1 for SAS/IML code) was therefore used to draw random samples of 4452 specimens assigned to 37 genera of brachiopods, mimicking the actual sample sizes for those genera. The simulated specimens were then "drilled" by the computer with an *a priori* assigned probability of 1.1%. The inset plot shows the result of the simulation. Only one time in 999 iterations was the simulated *ATF* value lower than or equal to 43.6%, demonstrating that drill holes are distributed non-randomly (i.e., if drilling was random, significantly more genera should contain holes than is observed in the data). The reported p=0.002 includes 999 random values and the actual sample (see Manly, 1995).

One should be careful in interpreting taxon selectivity, especially in the case of paleontological data. Because of time-averaging, the assemblage may contain prey taxa that never encountered the predator even though they are preserved in the same assemblage; so the "selectivity" may have nothing to do with active selection by predators but may simply reflect the fact that predators never had a chance to encounter some of their "contemporary" prey. Also, and this problem applies to neontological studies as well, the lack of traces may mean that the predators failed in their attacks, and not that they did not try.

Leighton (2002) points to another serious problem of selectivity analyses related to the sequential nature of many predator-prey interactions. Because marine benthic predators tend to encounter one prey at a time, the frequency of attacks may reflect the frequency of prey encounters, and not a preferential selection by an optimally foraging predator. If, as Leighton (2002) argues, the "zero-one rule" is in effect (i.e., any prey type that is ever taken will always be taken), then differences in frequency of drill holes or repair scars observed across prey taxa may reflect the relative abundance and/or accessibility of those prey taxa. Although the zero-one rule may be questioned—many models postulate that the behavior of individual organisms varies through time so any prey type that is ever taken does not have to be always taken (e.g., Evolutionarily Stable Strategy; see Dawkins, 1976 for an excellent review)—the sequential nature of encounters makes selectivity analyses based on relative frequencies of predation traces questionable (see Leighton, 2002 for more details).

Site Selectivity.—The location of trace fossils left by a predator on skeletons of its prey may provide useful information about the behavior of that predator and its interaction with its prey. Many predators, parasites, or amensal organisms are behaviorally stereotyped in showing a preference for a particular location for their attack or attachment site. Consequently, biotic traces often display non-random patterns in terms of their spatial distribution on prey or host skeletons. The evaluation of such site selectivity is useful for several reasons. First, the presence of site selectivity provides strong evidence for the biotic origin of traces (see section above on criteria for identifying traces of predation). Second, the specific nature of site selectivity may provide clues as to the nature of biotic interactions recorded by traces (e.g., drill holes located around areas that give direct access to muscle tissues of victims are more likely to represent predation than parasitism). Third, changes in site selectivity through time may offer a good tool for evaluating various evolutionary models (e.g., Hagadorn and Boyajian, 1997; Dietl and Alexander, 2000). In exceptional circumstances, multimodal patterns in distribution of trace fossils along the growth axis of its prey may be used to detect seasonality of predation and growth curves of the prey (e.g., Kowalewski and Flessa, 2000).

Although the evaluation of site selectivity can be applied to various types of traces, including fractures, repair scars, cut marks, and tooth marks (e.g., Babcock and Robinson, 1989; Lyman, 1994; Kowalewski et al., 1997; Kowalewski and Flessa, 2000), most of the studies in the marine fossil record have focused on drill holes in invertebrate shells (e.g., Reyment, 1971; Negus, 1975; Kelley, 1988; Kowalewski, 1990; Anderson, 1992; Roopnarine and Beussink, 1999; Dietl and Alexander, 2000; Hoffmeister and Kowalewski, 2001; and many

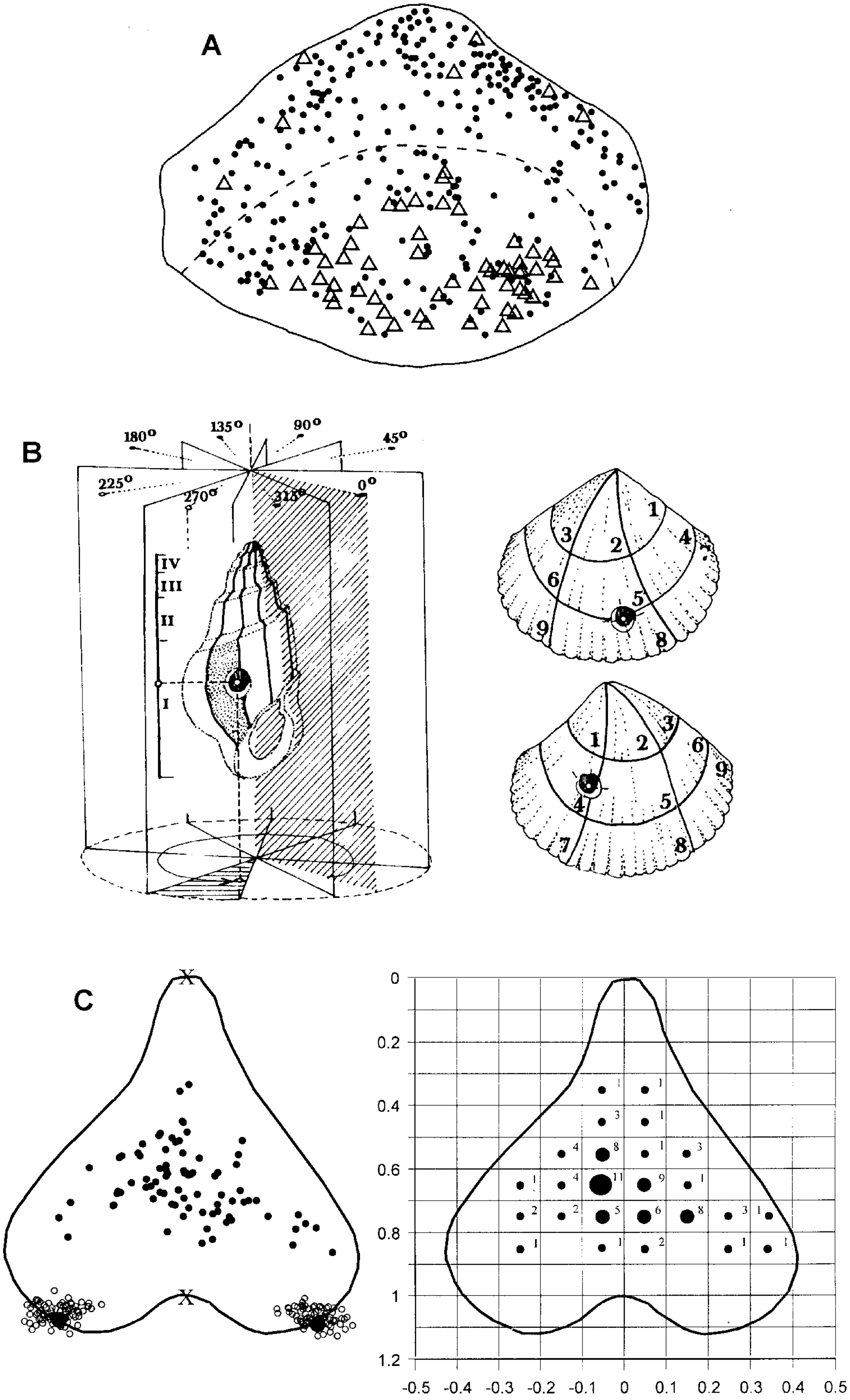
A
B
180°
135°
90°
45°
225°
270°
315°
0°
IV
III
II
I
1
2
3
4
5
6
8
9
1
2
3
4
5
6
7
8
9
C
X
X
0
0.2
0.4
0.6
0.8
1
1.2
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5

FIGURE 6

references therein). This is not surprising considering that drill holes are highly localized traces (i.e., attack sites can be unambiguously determined) that often represent a uniform record of a single behavior and are frequent enough to make statistical analyses possible.

The strategies used to study site selectivity are dependent on prey type and scale of analysis. They include two general approaches: (1) among-element selectivity and (2) within-element selectivity.

Among-element tests for selectivity are based on evaluating distribution of traces across different skeletal elements or symmetry axes. Naticids may prefer to drill a left rather than a right valve of a bivalve mollusk prey, or a carnivore may preferentially gnaw and chew particular types of bones (e.g., Dodson and Wexlar, 1979; Kusmer, 1990; Lyman, 1994). The evaluation methods are straightforward analytically (although biological interpretations may not be—see especially Kaplan and Baumiller, 2000; Wilson and Palmer, 2001; Kaplan and Baumiller, 2001) and typically involve a comparison of expected frequency of traces (given the relative frequency of elements) against their observed frequencies. The Fisher's exact test can be applied for cases when two elements are involved, and Homogeneity (G-test, Chi-square) and/or Kolmogorov-Smirnov tests can be applied for multiple elements. If elements vary in their preservational potential, a more complicated analysis can be considered: Kaplan and Baumiller (2001) combined trace fossil distribution patterns with taphonomic information in a way somewhat akin to Bayesian statistical methods.

Within-element methods test for non-randomness in the spatial distribution of trace fossils on a particular type of skeletal element: for example, distribution of repair scars on brachiopod valves along the growth axis (e.g., Kowalewski et al., 1997), angular distribution of drill holes on snail shells (e.g., Dietl and Alexander, 2000), or spatial distribution of attack sites across the symmetry axis of a bilateral organism (e.g., Babcock, 1993). Numerous analytical strategies have been developed over the years. The five main types can be distinguished here:

1. *Qualitative Approach* is based on superimposing all traces on a single "standard" element (Fig. 6a). This method is highly imprecise (because of the high potential operator error and morphological and allometric variability among specimens) and produces data that cannot be converted to data usable in other approaches listed below. On the other hand, the approach allows us to define sectors that are biologically meaningful, and it can be used to test very specific hypotheses about the nature of traces (see especially Leighton, 2001; Zlotnik, 2001).

2. *Sector Approach* is based on partitioning the prey skeleton into sectors and tallying the frequency of traces in each sector. The resulting distribution can then be evaluated statistically using homogeneity tests (e.g., Reyment, 1971; Kowalewski et al., 1997), the Shannon-Weaver Evenness Index (Dietl et al., 2001), or computer-intensive methods (e.g., Kowalewski et al., 1997). The sector-based approaches include two variants. *Uneven-sector* approach is a widely used strategy (e.g., Kelley, 1988; Kowalewski, 1990; Anderson, 1992; Hoffmeister and Kowalewski, 2001) based on

←

FIGURE 6—Examples of strategies for evaluating site selectivity of predation. All examples are based on drill holes in marine invertebrate prey. A. Qualitative approach based on plotting drill holes on a standardized prey skeleton. The diagram shows distribution of large (>1mm) (triangles) and small (<1mm) (dots) naticid holes in the right valve of the Miocene bivalve *Corbula gibba* (Korytnica Clays, Central Poland) (modified after Zlotnik, 2001). B. A scheme of uneven sectors based on Kelley (1988) and modified after Kowalewski (1990). C. Bookstein (shape) coordinates of drill holes in pedicle valves of the Pennsylvanian brachiopod *Cordiarina cordata* (left diagram). These data can be readily converted into even-sector data (right diagram). Both diagrams modified after Hoffmeister (2002) and Hoffmeister et al. (submitted).

partitioning a skeleton into a small number (typically <10) of sectors of uneven size (Fig. 6b). Because the sectors are of uneven size, data analyses are somewhat complicated as the sectors need to be corrected for differences in the area they represent. *Even-sector* approach, based on subdividing shells into sectors of equal area, is analytically more elegant because it makes all sectors statistically comparable (e.g., Reyment, 1971; Kowalewski et al. 1997); but it produces a biologically arbitrary grid system.

3. *Angular Approach* can be applied to skeletal surfaces that can be quantified using angles (e.g., snail or ammonite shells). The position of traces can be quantified using continuous variables measured in radians or degrees. Parametric tests for circular data (see Zar, 1999) can be applied but are not recommended because of the unrealistic assumptions of normality and, especially, unimodality. An example of a computer-intensive method that can be used to avoid these assumptions is provided in Appendix 1.

4. *Sclerochronological Approach* can be employed for repair scars in organisms with clearly defined growth axes. A distribution of traces along the growth axis of an organism can provide information about the distribution of unsuccessful attacks across prey age/size classes. In some exceptional circumstances this approach can be used to detect seasonality of predation (Kowalewski and Flessa, 2000), although this strategy is most applicable to living populations where time-averaging and several other complicating factors can be ignored.

5. *Landmark Approach* (Fig. 6c) was proposed in a clever analysis by Roopnarine and Beussink (1999), who treated drill holes as two-dimensional landmarks. This strategy allows us to apply modern morphometric techniques (e.g., Bookstein, 1991; Marcus et al., 1996; Dryden and Mardia, 1998) to compute the position of drill holes in relation to homologous landmarks and pseudolandmarks on the prey skeleton (Roopnarine and Beussink, 1999; Hoffmeister et al., submitted). This is one of the most effective ways of quantifying the position of predation traces (in fact, it can be viewed as a quantitative version of the qualitative approach discussed in point 1 above) that allows for rigorous integration of behavioral data on predators with morphological information about their prey. The analyses can be further enhanced by superimposing additional information such as trace size on the resulting plots (this last enhancement can also be exploited when other site-selectivity methods are used).

Size Selectivity.—Size of prey may be an important factor in many predator-prey interactions, as many prey become less vulnerable to predation as they grow bigger (see Vermeij, 1987 and references therein); and the cost-benefit ratio for predators may also vary considerably with prey size (e.g., Kitchell et al., 1981; Pyke, 1984; Kitchell, 1986). For all these reasons traces of predation may be non-randomly distributed across size classes of prey and, depending on the predator-prey system, may reflect size selectivity for smaller, intermediate, or larger individuals in a prey population (see examples in Alexander and Dietl, in press). Such non-random patterns may mean that the predator preferred attacking particular size classes. In the case of repair scars, the interpretation is more ambiguous because such a pattern may mean that the predator failed more frequently when attacking a given size range.

A simple analytical way to evaluate for size selectivity is to compare, within samples or collections, the size-frequency distributions (SFD) of drilled specimens of a given prey against the SFD of undrilled specimens of that prey. The statistical difference can be evaluated using non-parametric tests such as the Kolmogorov-Smirnov test (evaluating the significance of the overall shape differences) and the Wilcoxon test (evaluating the significance of the difference in central tendency as estimated by median specimen size).

Because some trace fossils such as drill holes may be used as a proxy for relative size of the predator (e.g., Kitchell, 1986; but note that this claim is based on one case study for one naticid species), there may even be a way to evaluate if prey size correlates with the size of its predator. Such correlation may also indicate size selectivity by the attacker. The approach involves a simple bivariate correlation analysis in which the size of a trace is evaluated against the size of a prey specimen that contains that trace (e.g., Kitchell et al., 1981; Kowalewski, 1990; Anderson, 1992; Harper et al., 1998). The standard correlation tests can be applied here. However, size data tend to be non-normally distributed and rarely represent continuous variables (e.g., drill holes may vary by as little as 1 mm so even if the measurement precision is 0.1 mm the resulting variable is discrete in practice: we group holes in 10 or so size categories). Consequently, Spearman rank correlation rather than Pearson correlation should be employed for analysis. The size estimate is typically based on the maximum dimensions of a skeleton. However, Centroid Size (CS) is preferred here because this landmark-based measure tends to be isometric (e.g., Dryden and Mardia, 1998). CS is especially convenient to use when geometric morphometric methods are applied to quantify prey shape and trace fossil position (see above).

In the case of drill holes, several studies integrated size selectivity with cost-benefit analysis (e.g., Kitchell et al., 1981; Kelley, 1988; Anderson et al., 1991; see recent review by Kelley and Hansen, in press, for more examples). In such analyses the cost-benefit analysis is used to estimate the expected size class of prey that should be preferred by the predator, and the resulting prediction is contrasted against the observed pattern estimated from the distribution of traces across all size classes of prey (but see Leighton, 2002).

Size analysis is prone to various biases. In the case of repair scars, the larger specimens tend to have more scars for two reasons that have nothing to do with size selectivity. First, the larger prey are often more likely to survive predatory attacks; and second, the larger prey lived longer and therefore had a higher chance of encountering predators (e.g., Vermeij and Dudley, 1982; Vermeij, 1987; Kowalewski et al., 1997; Alexander and Dietl, in press). Size analysis may also be particularly sensitive to taphonomic problems. A large trace made in a small skeleton may substantially weaken that skeleton and make its preservation less likely. Notice that typically a positive correlation is expected intuitively (larger predators eat larger prey), but such correlation can be enhanced because the skeleton of a small prey attacked by a large predator is less likely to be preserved than a skeleton of a large prey attacked by a large predator.

TESTING FOR TAPHONOMIC BIASES

Traces of predation may weaken prey skeletons or affect their hydrodynamic properties. Even if traces do not affect the skeleton notably, post-mortem processes may obscure or remove traces left by predators. Consequently, taphonomic filters ranging from pre-burial processes to compaction and diagenesis may bias quantitative patterns preserved in the geological record. For example, in the case of drill holes, Lever et al. (1961) demonstrated that drilled specimens were transported farther up the beach than undrilled valves (note that most fossil samples used in paleoecological studies are from deposits that accumulated in more offshore settings, for which the results of the Lever et al. (1961) study may not apply directly). Such post-mortem sorting may distort quantitative estimates of drilling intensity (see also Kornicker et al., 1961). Roy et al. (1994) used an experimental approach to show that drilled valves of the mactrid bivalve *Mulinia* were weaker under point-load compression than were undrilled valves. On the other hand, sediment compaction experiments indicate that drilled specimens of the bivalve *Anadara* break less frequently than comparable undrilled valves from the same genus (Zuschin and Stanton, 2001; see also Kaplan and Baumiller, 2000); and Hagstrom (1996) showed that the point-load weakening observed by Roy et al. (1994) may be a serious problem only in high-energy environments.

Many other taphonomic processes may distort the data. Post-mortem encrusters may veneer over a repair scar left by a predator, and incomplete drill holes can become “complete” through subsequent removal of their thin bottoms (e.g., the translucent, ultra-thin flooring of incomplete drill holes observed commonly in *Spisula solidissima* [R.R.

Alexander, pers. comm., 2002] can easily be removed by taphonomic processes).

The evaluation of paleoecological data on predation can involve both experimental and indirect taphonomic approaches. An experimental approach is exemplified by the work of Kaplan and Baumiller (2000), who performed a series of experiments with casts mimicking the morphology of the studied prey (the brachiopod *Onniella*) and used the results of their experiment to evaluate for taphonomic biases.

Taphonomic data can also be used indirectly to evaluate biases. Roy et al. (1994) suggested a set of simple questions to assess for taphonomic bias in drill holes. Do fragments of prey skeleton frequently show partial traces? Frequent partial traces indicate that most of the fractures pass through the trace fossils and may have been initiated by those traces. This pattern suggests that a bias exists. Are fragments generally common in the fossil assemblage? If they are rare, the fragmentation bias cannot be severe.

Nebelsick and Kowalewski (1999), in a study of drilling predation on echinoids, proposed a simple taphonomic model to test for bias. They argued that, if drill holes have no taphonomic effect, their distribution should be independent of the taphonomic alteration of drilled tests (i.e., uniform across taphonomic grades); if drill holes affect the preservation potential of echinoids by substantially weakening their tests, the proportion of drilled tests should decrease with the increase in taphonomic alteration; and, finally, if drill holes are of taphonomic (post-mortem) origin (i.e., they are pseudo-drillings), a proportion of drilled tests should increase with the increase in taphonomic alteration. Nebelsick and Kowalewski (1999) then showed that drilled specimens are as common among tests severely altered by taphonomic processes as among tests that are still pristine; that is, the proportion of drilled tests does not decrease or increase with the increase in taphonomic alteration of the tests (Fig. 7). They concluded that drill holes are unlikely to have a serious taphonomic effect even for the small, thin tests of the clypeasteroid echinoids used in their study. They noted, however, that the neontological material they studied, unlike most of the fossilized tests, was unaffected by compaction, during which preferential breakage of drilled tests would be more likely to occur. Finally, in a daring study, Kaplan and Baumiller (2000) proposed the use of taphonomic data to correct for biases in a quantitative way. This approach, specifically designed for bivalved organisms, estimates the magnitude of the differential bias in the preservation of opposite valves of an organism and uses the resulting estimate to correct the frequency data of trace fossils found in those valves.

METHODOLOGICAL RECOMMENDATIONS

It is clear from the above review that there is a multitude of approaches for collecting traces of predation, processing and tabulating the resulting materials, analyzing the resulting data, and interpreting the analytical outputs. It is also clear that interpretations are rarely unambiguous because of the complexity of ecological interactions, the confounding effects of abiotic factors, and the obscuring and biasing effects of taphonomic processes.

It would be foolish to suggest at this point (or perhaps at any point in the development of a scientific discipline) that we should erect strict guidelines regarding how to collect, analyze, or interpret the data (see also Feyerabend, 1978). Consequently, whereas I do propose here some general methodological recommendations, they are primarily geared toward making our data more compatible and readable (i.e., more useful to other researchers).

1. Given a wide range of data collecting and processing strategies, a method that maximizes the compatibility of resulting data with future comparative analyses should be preferred. For example, if possible, fine mesh size should be used in sieving the samples because that way data can be compared (by eliminating analytically small specimens) to other datasets that were processed with coarser meshes.

2. Results should be reported in a clear manner so that future researchers can combine the reported

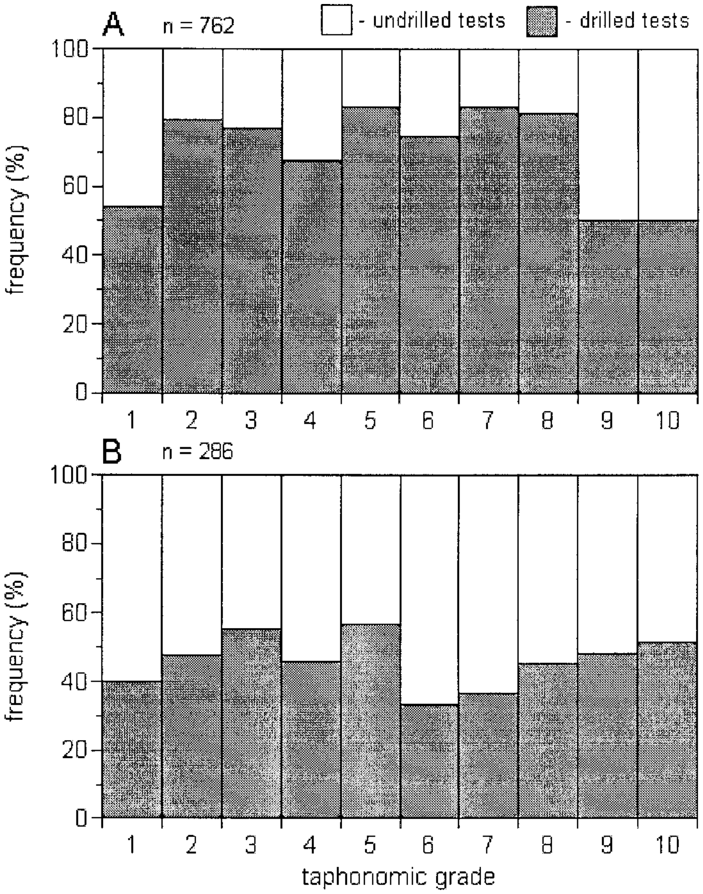

FIGURE 7—Taphonomic comparison of drilled and undrilled tests of clypeasteroid echinoids from the Northern Bay of Safaga, Red Sea. A. *Fibularia ovulum*. B. *Echinocyamus crispus*. Symbols: n – sample size. Modified after Kowalewski and Nebelsick (in press). Taphonomic Grade is a semi-quantitative rank variable that varies from 1 for the least altered echinoid tests to 10 for the most heavily altered tests.

data with other datasets or compute different indices than those computed in an original study. Also, one should not restrict her/his reports to processed/corrected results from which raw data cannot be recomputed. We should follow Stuckenrath's (1977, p. 187) plea not to correct raw data because "…eventually these corrected [data] will have to be uncorrected in order to be recorrected in order to be correct…".

3. When faced with different tabulating and analytical strategies, a method that makes the resulting data usable in the widest possible range of analytical approaches should be preferred. For example, if possible, data should be collected in a way that allows one to compute various measures of predation intensity rather than only one metric. A particular metric may indeed be the most useful and appropriate for a specific case study, but others may want to use the data for other reasons (even the authors may, perhaps, agree retrospectively that their preferred metric does not work for these new research goals).

4. When faced with a multitude of analytical choices, one should keep in mind that the choice of the method may not always be important. If possible, a comparison of different metrics may help us to resolve the issue (if all correlate highly the approach may not matter, but if they vary a lot

one needs to make an explicit claim as to why one of them is selected for the analysis).

5. Various protocols and analytical methods can be fruitful depending on the logistic circumstances and scientific goals of a paleoecological project.

6. The most fruitful analyses are based on relative comparative approaches. Latitudinal changes in predation intensity or temporal shifts in behavioral stereotypy are more insightful than a given absolute frequency of predation or a specific degree of stereotypy. Comparative analyses can also help avoid various biases. For example, taphonomic bias or spatial/environmental overprint can be minimized if comparisons are done for samples from similar taphonomic settings and comparable depositional environments (the "isotaphonomic approach" of Behrensmeyer and Hook, 1992).

7. Finally, regardless of the above points, it seems particularly useful to provide raw data (either as repository data or appendices) so that future researchers can re-analyze these data in new ways. Consider all the data on predation traces that have been collected over the last 40 years and cannot be accessed. At best, a few succinct tables and graphs are all that remain. This is the one mistake we need not repeat in our future efforts.

CLOSING REMARKS

The methodological dimension of research on predation traces is a rapidly growing field of study. Based on current activities, the future methodological themes that are likely to benefit our discipline include (1) laboratory experiments that should help us in dealing with various taphonomic biases, (2) neontological analyses that provide reference baselines and should further help us to understand various confounding factors that need to be accounted for before proposing any interpretation (e.g., spatial gradients in predation), and (3) numerical modeling that should continue to improve our arsenal of statistical tools and analytical strategies.

Despite all caveats and problems, distinct traces of predation such as drill holes offer one of the best sources of quantitative data in paleoecology. Such traces provide unusually favorable research conditions for testing new methodologies and for pushing our interpretive powers to the highest possible limits. Research on predation traces can thus be viewed as one of the foremost areas for testing the scientific limits of our discipline—by examining traces of predation we can examine the limits, strengths, methods, and assumptions of paleoecology.

ACKNOWLEDGMENTS

This project was supported by the NSF grant EAR-9909225. I thank Richard Alexander, Greg Dietl, Thor Hansen, Alan Hoffmeister, Patricia Kelley, and Lindsey Leighton for numerous comments and suggestions that improved this manuscript considerably.

REFERENCES

ALEXANDER, R. R. 1981. Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulates. Journal of Paleontology, 55:192–203.

ALEXANDER, R. R. 1986a. Resistance to repair of shell breakage induced by durophages in Late Ordovician brachiopods. Journal of Paleontology, 60:273–285.

ALEXANDER, R. R. 1986b. Frequency of sublethal shell-breakage in articulate brachiopod assemblages through geologic time. *In* P. R. Racheboeuf and C. C. Emig (eds.), Les Brachiopodes Fossiles et Actuels, First International Brachiopod Congress Proceedings, Biostratigraphie du Paleozoique, 4:159–166.

ALEXANDER, R. R., AND G. P. DIETL. 2001. Shell repair frequencies in New Jersey bivalves: a recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners. Palaios, 16:354–371.

ALEXANDER, R. R., AND G. P. DIETL. In press. The Phanerozoic history of shell-breaking predation on marine bivalves and gastropods. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Topics in Geobiology Series, Plenum Press/Kluwer, New York.

ALLMON, W. D., J. C. NIEH, AND R. D. NORRIS. 1990. Drilling and peeling of turritelline gastropods since the Late Cretaceous. Palaeontology, 33:595–611.

ALPERT, S. P., AND J. N. MOORE. 1975. Lower Cambrian trace fossil evidence for predation on trilobites. Lethaia, 8:223–230.

AMBROSE, R. F. 1986. Effects of *Octopus* predation on motile invertebrates in a rocky subtidal community. Marine Ecology Progress Series, 30:261–273.

ANDERSON, L. C. 1992. Naticid gastropod predation on corbulid bivalves: Effects of physical factors, morphological features, and statistical artifacts. Palaios, 7:602–620.

ANDERSON, L. C., D. H. GEARY, R. H. NEHM, AND W. D. ALLMON. 1991. A comparative study of naticid gastropod predation on *Varicorbula caloosae* and *Chione cancellata*, Plio-Pleistocene of Florida, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology, 85:283–290.

ANDREWS, P., AND Y. FERNANDEZ JALVO. 1998. 101 uses for fossilized faeces. Nature, 393:629–630.

ARNOLD, A. J., F. D'ESCRIVAN, AND W. C. PARKER. 1985. Predation and avoidance responses in the Foraminifera of the Galapagos hydrothermal mounds. Journal of Foraminiferal Research, 15:38–42.

ARNOLD, J. M., AND K. O. ARNOLD. 1969. Some aspects of hole-boring predation by *Octopus vulgaris.* American Zoologist, 9:991–996.

ARUA, I., AND M. HOQUE. 1989. Fossil predaceous gastropod borings from Nigeria. Palaeogeography, Palaeoclimatology, Palaeoecology, 73:175–183.

AUSICH, W. I., AND R. A. GURROLA. 1979. Two boring organisms in a Lower Mississippian community of southern Indiana. Journal of Paleontology, 53:335–344.

BABCOCK, L. E. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. Journal of Paleontology, 67:217–229.

BABCOCK, L. E., AND R. A. ROBINSON. 1989. Preferences of Palaeozoic predators. Nature, 337:695–696.

BAUK, W., AND A. RADWASKI. 1996. Stomatopod predation upon gastropods from the Korytnica Basin, and from other classical Miocene localities in Europe. Acta Geologica Polonica, 46:279–304.

BAMBACH, R. K. 2002. Supporting predators: Changes in the global ecosystem inferred from changes in predator diversity. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

BAMBACH, R. K., AND M. KOWALEWSKI. 2000. How to count fossils. Geological Society of America Abstracts with Programs, 32:A-95.

BAUMILLER, T. K. 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. Palaeontology, 33:743–748.

BAUMILLER, T. K. 1993. Boreholes in Devonian blastoids and their implications for boring by platyceratids. Lethaia, 26:41–47.

BAUMILLER, T. K. 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. Palaeogeography, Palaeoclimatology, Palaeoecology, 123:343–351.

BAUMILLER, T. K. 2002. Multi-snail infestation of Devonian crinoids and the nature of platyceratid-crinoid interactions. Acta Palaeontologica Polonica, 47:133–139.

BAUMILLER, T. K., AND F. GAHN. 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interactions. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

BAUMILLER, T. K., AND D. B. MACURDA, JR. 1995. Borings in Devonian and Mississippian blastoids (Echinodermata). Journal of Paleontology, 69:1084–1089.

BAUMILLER, T. K., L. R. LEIGHTON, AND D. THOMPSON. 1999. Boreholes in brachiopods of the Fort Payne Formation (Lower Mississippian, central USA). Palaeogeography, Palaeoclimatology, Palaeoecology, 147:283–289.

BECKER, M. A., J. MEIER, AND W. SLATTERY. 1999. Spiral coprolites from the Upper Cretaceous Wenonah-Mt. Laurel and Navesink formations in the northern coastal plain of New Jersey. Northeastern Geology and Environmental Sciences, 21:181–187.

BEHRENSMEYER, A. K., AND R. W. HOOK. 1992, Paleoenvironmental contexts and taphonomic modes, p. 15–136. *In* A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H. D. Sues, and S. L. Wing (eds.), Terrestrial Ecosystems through Time. The University of Chicago Press, Chicago.

BENGTSON, S. 2002. Origins and early evolution of predation. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

BENGTSON, S., AND Z. YUE. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. Science, 257:367–369.

BENNINGTON, J. B., AND S. D. RUTHEFORD. 1999. Precision and reliability in paleocommunity comparisons based on cluster-confidence intervals; how to get more statistical bang for your sampling buck. Palaios, 14:506–515.

BERG, J. C. 1976. Ontogeny of predatory behavior in snails (Prosobranchia: Naticidae). Nautilus, 90:1–4.

BERG, J. C., AND S. NISHENKO. 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. Paleobiology, 1:258–260.

BISHOP, G. A. 1975. Traces of predation, p. 261–281. *In* R. W. Frey (ed.), The Study of Trace Fossils. Springer-Verlag, New York.

BISHOP, G. A. 1977. Pierre feces: A scatological study of the *Dakoticancer* assemblage, Pierre Shale (Upper Cretaceous) of South Dakota. Journal of Sedimentary Petrology, 47:129–139.

BOOKSTEIN, F. L. 1991. Morphometric Tools for Landmark Data. Cambridge University Press, New York, 435 p.

BOTTON, M. L. 1984. Diet and food preference of the adult horseshoe crab *Limulus polyphemus* in Delaware Bay, New Jersey, USA. Marine Biology, 81:199–207.

BOUCOT, A. J. 1990. Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam, 725 p.

BRANDT, D. S., D. L. MEYER, AND P. B. LASK. 1995. *Isotelus* (Trilobita) "hunting burrow" from Upper Ordovician strata, Ohio. Journal of Paleontology, 69:1079–1083.

BRETT, C. E. In press. Predation in Paleozoic marine communities. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Topics in Geobiology Series, Plenum Press/ Kluwer, New York.

BRETT, C. E., AND S. E. WALKER. 2002. Predators and predation in Paleozoic marine environments. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

BROMLEY, R. G. 1970. Borings as trace fossils and *Entobia cretacea* Portlock, as an example. Geological Journal Special Issue, 3:49–90.

BROMLEY, R. G. 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. Acta Geologica Hispanica, 16:55–64.

BROMLEY, R. G. 1993. Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. Geological Society of Denmark Bulletin, 40:167–173.

BROMLEY, R. G. 1996. Trace Fossils; Biology, Taphonomy and Applications. Chapman and Hall, 361 p.

BRUNTON, H. 1966. Predation and shell damage in a Visean brachiopod fauna. Palaeontology, 9:355–359.

BUNN, H. T., AND E. M. KROLL. 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai George, Tanzania. Current Anthropology, 27:431–452.

CADÉE, G. C. 1968. Molluscan biocoenoses and thanatocoenoses in the Ria de Arosa, Galicia, Spain. Zoologische Verhandelingen, Leiden, 95:1–121.

CADÉE, G. C. 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea; palaeoecological implications. Palaeontology, 37:181–202.

CADÉE, G. C. 2000. Herring gulls feeding on a Recent invader in the Wadden Sea, *Ensis directus*. *In* The Evolutionary Biology of the Bivalvia. Geological Society Special Publications, 177:459–464.

CADÉE, G. C., S. E. WALKER, AND K. W. FLESSA. 1997. Gastropod shell repair in the intertidal of Bahia la Choya (N.Gulf of California). Palaeogeography, Palaeoclimatology, Palaeoecology, 136:67–78.

CARPENTER, K. 2000. Evidence of predatory behavior by carnivorous dinosaurs. Gaia, 15:135–144.

CARRIKER, M. R. 1943. On the structure and function of the proboscis in the common oyster drill, *Urosalpinx cinerea* Say. Journal of Morphology, 73:441–506.

CARRIKER, M. R. 1957. Preliminary study of behavior of newly hatched oyster drills *Urosalpinx cinerea* (Say). Journal of the Elisha Mitchell Scientific Society, 73:328–351.

Carriker, M. R. 1961. Comparative functional morphology of the boring mechanisms in gastropods. American Zoologist, 1:263–266.

Carriker, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. Malacologia, 20:403–422.

Carriker, M. R., and D. Van Zandt. 1972a. Predatory behavior of a shell-boring muricid gastropod, p. 157–244. *In* H. E. Winn and B. L. Olla (eds.), Behavior of Marine Animals: Current Perspectives in Research, Vol. 1 Invertebrates. Plenum Press, New York.

Carriker, M. R., and D. Van Zandt. 1972b. Regeneration of the accessory boring organ of muricid gastropods after excision. Transactions of American Microscope Society, 91:455–466.

Carriker, M. R., and E. L. Yochelson. 1968. Recent gastropod boreholes and Ordovician cylindrical borings. U.S. Geological Survey Professional Paper, 593-B:1–26.

Carrion, J. S., J. A. Riquelme, C. Navarro, and M. Munuera. 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. Palaeogeography, Palaeoclimatology, Palaeoecology, 176:193–205.

Cate, A. S., and I. Evans. 1994. Taphonomic significance of the biomechanical fragmentation of live molluscan shell material by a bottom-feeding fish (*Pogonias cromis*) in Texas coastal bays. Palaios, 9:254–274.

de Cauwer, G. 1985. Gastropod predation on corbulid bivalves; paleoecology or taphonomy? Annales du Société Zoologique de Belgique, 115:183–196.

Chatterton, B. D. E., and H. L. Whitehead. 1987. Predatory borings in inarticulate brachiopod *Artiotreta* from the Silurian of Oklahoma. Lethaia, 20:67–74.

Checa, A. 1993. Non-predatory shell damage in Recent deep-endobenthic bivalves from Spain. Palaeogeography, Palaeoclimatology, Palaeoecology, 100:309–331.

Chin, K. 1997. What did dinosaurs eat? Coprolites and other direct evidence of dinosaur diet, p. 371–382. *In* J. O. Farlow and M. K. Brett-Surman (eds.), The Complete Dinosaur. Indiana University Press, Bloomington.

Chin, K. 2002. Analyses of coprolites produced by carnivorous vertebrates. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

Chin, K., T. T. Tokaryk, G. M. Erickson, and L. Calk. 1998. A king-sized theropod coprolite. Nature, 393:680–682.

Colbath, S. L. 1985. Gastropod predation and depositional environment of two molluscan communities from the Miocene Astoria Formation at Beverly Beach State Park, Oregon. Journal of Paleontology, 59:849–869.

Conway Morris, S., and S. Bengtson. 1994. Cambrian predators: Possible evidence from boreholes. Journal of Paleontology, 68:1–23.

Cooper, G. A., and R. E. Grant. 1972–1976. Permian brachiopods of West Texas, I–V. Smithsonian Contributions to Paleobiology, 14:1–231; 15:233–793; 19:795–1298; 19:1300–1921; 21:1923–2285; 21:2288–2607; 24:2609–3159.

Coy, C. E. 1995. The first record of spiral coprolites from the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) southern Alberta, Canada. Journal of Paleontology 69:1191–1194.

Crossland, M. R., R. A. Alford, and J. D. Collins. 1991. Population dynamics of an ectoparasitic gastropod, *Hypermastus* sp. (Eulimidae), on the sand dollar, *Arachnoides placenta* (Echinoidea). Australian Journal of Marine and Freshwater Research, 42:69–76.

Culver, S. J., and J. H. Lipps. In press. Predation on and by foraminifera. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Topics in Geobiology Series, Plenum Press/Kluwer, New York, in press.

Dawkins, R. 1976. The selfish gene. Oxford University Press, New York, 224 p.

Day, J. A. 1969. Feeding of the cymatiid gastropod, *Argobuccinum argus*, in relation to the structure of the proboscis and secretions of the proboscis gland. American Zoologist, 9:909–919.

Degner, E. 1928. Über das Fleisch und Kalkbeddurfnis von *Cepaea nemoralis.* Archiv für Molluskenk., 60:209–213.

Dietl, G. P. 2000. Successful and unsuccessful predation of the gastropod *Nucella lapillus* (Muricidae) on the mussel *Mytilus edulis* from Maine. Veliger, 43:319–329.

Dietl, G. P., and R. R. Alexander. 1995. Borehole site and prey size stereotypy in naticid predation on *Euspira* (*Lunatia*) *heros* Say and *Neverita* (*Polinices*) *duplicata* Say from the southern New Jersey coast. Journal of Shellfish Research, 14:307–314.

Dietl, G. P., and R. R. Alexander. 2000. Post-Miocene shift in stereotypic naticid predation on confamilial prey from the Mid-Atlantic shelf: Coevolution with dangerous prey. Palaios, 15:414–429.

DIETL, G. P., AND P. H. KELLEY. 2001. Mid-Paleozoic latitudinal predation gradient: Distribution of brachiopod ornamentation reflects shifting Carboniferous climate. Geology, 29:111–114.

DIETL, G. P., AND P. H. KELLEY. 2002. The fossil record of predator-prey arms races: Coevolution and escalation hypotheses. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

DIETL, G. P., R. R. ALEXANDER, AND W. F. BIEN. 2000. Escalation in Late Cretaceous–early Paleocene oysters (Gryphaeidae) from the Atlantic Coastal Plain. Paleobiology, 26:215–237.

DIETL. G., R. R. ALEXANDER, P. H. KELLEY, AND T. A. HANSEN. 2001. Stereotypy of naticid predation on bivalves since the Cretaceous: trends, controlling factors, and implications for escalation. PaleoBios 21(supplement to number 2):78.

DODSON, P., AND D. WEXLAR. 1979. Taphonomic investigations of owl pellets. Paleobiology, 5:279–284.

DRYDEN I. L., AND K. V. MARDIA. 1998. Statistical Shape Analysis. Wiley, New York, 347 p.

FARLOW, J. O., AND T. R. HOLTZ. 2002. The fossil record of predation in dinosaurs. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation, Paleontological Society Special Papers, 8 (this volume).

FEYERABEND, P. K. 1978. Against method: Outline of an Anarchistic Theory of Knowledge. Verso, London, 339 p.

FISCHER, P. H. 1922. Sur les gastéropodes perceurs. Journal de Conchyliologie, 67:1–56.

FISCHER, P. H. 1962a. Perforations de fossiles Pré-Tertiaries attribuées a des gastéropodes prédateurs. Journal de Conchyliologie, 102:68–78.

FISCHER, P. H. 1962b. Action des gastéropodes perceurs sur des Mesalia de L'Étage Lutétien. Journal de Conchyliologie, 102:95–97.

FISCHER, P. H. 1963. Corbules fossiles perforées par des gastéropodes prédateurs. Journal de Conchyliologie, 103:29–31.

FISCHER, P. H. 1966. Perforations de fossiles Tertiaires par des gastéropodes prédateurs. Journal de Conchyliologie, 106:66–96.

FREY, R. W., J. D. HOWARD, AND J. S. HONG. 1986. Naticid gastropods may kill solenid bivalves without boring: Ichnologic and taphonomic consequences. Palaios, 1:610–612.

FUJITA, S. 1916. On the boring of pearl oyster by *Octopus (Polypus) vulgaris* Lamarck. Dobytsugaku Zasshi, 28:250–257.

GEARY, D. H., W. D. ALLMON, AND M. J. REAKA-KUDLA. 1991. Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. Journal of Paleontology, 65:355–360.

GILINSKY, N. L., AND B. BENNINGTON. 1994. Estimating numbers of whole individuals from collections of body parts: A taphonomic limitation of the paleontological record. Paleobiology, 20:245–258.

GITTENBERGER, E. 1999. Predatory bore-holes in shells of terrestrial snails: Roth has priority. Basteria, 63:164.

GIBSON, M. A., AND J. B. WATSON. 1989. Predatory and non-predatory borings in echinoids from the Upper Ocala Formation (Eocene), north-central Florida, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology, 71:309–321.

GUERRA, A., AND M. NIXON. 1987. Crab and mollusc shell drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Ria de Vigo (north-west Spain). Journal of Zoology, London, 211:515–523.

HAGADORN, J. W., AND G. E. BOYAJIAN. 1997. Subtle changes in mature predator-prey systems; an example from Neogene *Turritella* (Gastropoda). Palaios, 12:372–379.

HAGEMAN, S. A., AND R. L. KAESSLER. 2002. Fusulinids: Predation damage and repair of tests from the Upper Pennsylvanian of Kansas. Journal of Paleontology, 76:181–184.

HAGSTROM, K. M. 1996. Effects of compaction and wave-induced forces on the preservation and macroevolutionary perception of naticid predator-prey interactions. Unpublished Master's Thesis, 63 p.

HANSEN, T. A., AND P. H. KELLEY. 1995. Spatial variation in naticid gastropod predation in the Eocene of North America. Palaios, 10:268–278.

HARPER, E. M., G. T. W. FORSYTHE, AND T. PALMER. 1998. Taphonomy and the Mesozoic marine revolution: Preservation state masks the importance of boring predators. Palaios, 13:352–360.

HARPER, E. M., G. T. W. FORSYTHE, AND T. PALMER. 1999. A fossil record full of holes: The Phanerozoic history of drilling predation: Comment. Geology, 27:959.

HARPER, E. M., AND D. S. WHARTON. 2000. Boring predation and Mesozoic articulate brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology, 158:15–24.

HAYNES, G. 2002. Archeological methods for reconstructing human predation on terrestrial vertebrates. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

HENDERSON, W. G., L. C. ANDERSON, AND C. R. MCGIMSEY. 2002. Stratigraphic, taxonomic, and taphonomic criteria to distinguish shell-rich chenier and archaeological deposits of the Louisiana chenier plain. Palaios, in press.

Hirsch, G. C. 1915. Die Ernährungsbiologie fleischfressender Gastropoden (*Murex*, *Natica*, *Pterotrachea*, *Pleurobranchea*, *Tritonium*). I Teil. Makroskopischer Bau, Nahrungsaufnahme, Verdauung, Sekretion. Zoologische Jahrbuch, 35:357–504.

Hirsch, K. F., A. J. Kihm, and D. K. Zelenitsky. 1997. New eggshell of ratite morphotype with predation marks from the Eocene of Colorado. Journal of Vertebrate Paleontology, 17:360–369.

Hoffman, A., and J. Martinell. 1984. Prey selection by naticid gastropods in the Pliocene of Emporda (Northeast Spain). Neues Jahrbuch für Geologie und Paläontologie, Monatshaft, 1984:393–399.

Hoffman, A., A. Pisera, and M. Ryszkiewicz. 1974. Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica Clays. Acta Geologica Polonica, 24:249–260.

Hoffmeister, A. P. 2002. Quantitative analysis of drilling predation patterns in the fossil record: Ecological and evolutionary implications. Unpublished Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg, 293 p.

Hoffmeister, A.P., and M. Kowalewski. 2001. Spatial and environmental variation in the fossil record of drilling predation: A case study from the Miocene of Central Europe. Palaios, 16:566–579.

Hoffmeister, A. P., M. Kowalewski, R. K. Bambach, and T. K. Baumiller. Submitted. Intense drilling predation on the brachiopod *Cardiarina cordata* Cooper 1956 from the Pennsylvanian of New Mexico. Lethaia.

Hughes, R. N., and P. I. Hughes. 1971. A study on the gastropod *Cassis tuberosa* (L.) preying upon sea urchins. Journal of Experimental Marine Biology and Ecology, 7:305–314.

Hughes, R. N., and H. P. I. Hughes. 1981. Morphological and behavioural aspects of feeding in the Cassidea (Tonnacea, Mesogastropoda). Malacologia, 20:385–402.

Jacobsen, A. R. 1997. Tooth marks, p. 738–739. *In* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Jacobsen, A. R. 1998. Feeding behavior of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. Historical Biology, 13:17–26.

Jensen, S. 1990. Predation by Early Cambrian trilobites on infaunal worms; evidence from the Swedish Mickwitzia Sandstone. Lethaia, 23:29–42.

Kabat, A. R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. Malacologia, 32:155–193.

Kaplan, P., and T. K. Baumiller. 2000. Taphonomic inferences on boring habit in the Richmondian *Onniella meeki* epibole. Palaios, 15:499–510.

Kaplan, P., and T. K. Baumiller. 2001. A misuse of Occam's Razor that trims more than just the fat. Palaios, 16:525–528.

Kase, T., P. A. Johnston, A. Seilacher, and J. B. Boyce. 1998. Alleged mosasaur bite marks on Late Cretaceous ammonites are limpet (patellogastropod) home scars. Geology, 26:947–950.

Kauffman, E. G., and R. V. Kesling. 1960. An Upper Cretaceous ammonite bitten by a mosasaur (South Dakota). Contributions from the Museum of Paleontology, University of Michigan, 15:193–248.

Kelley, P. H. 1988. Predation by Miocene gastropods of the Chesapeake Group: Stereotyped and predictable. Palaios, 3:436–448.

Kelley, P. H., and T. A. Hansen. 1993. Evolution of the naticid gastropod predator-prey system: An evaluation of the hypothesis of escalation. Palaios, 8:358–375.

Kelley, P. H., and T. A. Hansen. 1996. Naticid gastropod prey selectivity through time and the hypothesis of escalation. Palaios, 11:437–445.

Kelley, P. H., and T. A. Hansen. In press. The fossil record of drilling predation on bivalves and gastropods. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Topics in Geobiology Series, Plenum Press/Kluwer, New York.

Kelley, P. H., T. A. Hansen, S. E. Graham, and A. G. Huntoon. 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. Palaeogeography, Palaeoclimatology, Palaeoecology, 166:165–176.

Kitchell, J. A. 1986. The Evolution of predator-prey behavior: naticid gastropods and their molluscan prey, p. 88–110. *In* M. H. Nitecki and J. A. Kitchell (eds.), Evolution of Animal Behavior: Paleontological and Field Approaches. Oxford University Press, New York.

Kitchell, J. A., C. H. Boggs, J. F. Kitchell, and J. A. Rice. 1981. Prey selection by naticid gastropods: Experimental tests and application to the fossil record. Paleobiology, 7:533–552.

Kohn, A. J., and I. Arua. 1999. An Early Pleistocene molluscan assemblage from Fiji: Gastropod faunal composition, paleoecology and biogeography. Palaeogeography, Palaeoclimatology, Palaeoecology, 146:99–145.

Kornicker, L. S., C. D. Wise, and J. M. Wise. 1961. Factors affecting the distribution of opposing mollusk valves. Journal of Sedimentary Petrology, 33:703–712.

Kosuge, S., and S. Hayashi. 1967. Notes on the feeding habits of *Capulus dilatatus* A. Adams, 1860 (Gastropoda). Scientific Reports of Yokosuka City Museum, 13:45–54.

Kowalewski, M. 1990. A hermeneutic analysis of the shell-drilling gastropod predation on mollusks in the Korytnica Clays (Middle Miocene; Holy Cross Mountains; Central Poland). Acta Geologica Polonica, 40:183–213.

Kowalewski, M. 1993. Morphometric analysis of predatory drillholes. Palaeogeography, Palaeoclimatology, Palaeoecology, 102:69–88.

Kowalewski, M., and K. W. Flessa. 1994. A predatory drillhole in *Glottidia palmeri* Dall (Brachiopoda; Lingulidae) from Recent tidal flats of northeastern Baja California, Mexico. Journal of Paleontology, 68:1403–1405.

Kowalewski, M., and K. W. Flessa. 2000. Seasonal predation by migratory shorebirds recorded in shells of lingulid brachiopods from Baja California, Mexico. Bulletin of Marine Science, 66:405–416.

Kowalewski, M., and J. H. Nebelsick. In press. Predation and parasitism on recent and fossil echinoids. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Topics in Geobiology Series, Plenum Press/Kluwer, New York.

Kowalewski, M., K. W. Flessa, and J. D. Marcot. 1997. Predatory scars in the shells of a Recent lingulid brachiopod: Paleontological and ecological implications. Acta Palaeontologica Polonica, 42:497–532.

Kowalewski, M., A. Dulai, and F. T. Fürsich. 1998. A fossil record full of holes: The Phanerozoic history of drilling predation. Geology, 26:1091–1094.

Kowalewski, M., M. G. Simões, F. F. Torello, L. H. C. Mello, and R. P. Ghilardi. 2000. Drill holes in shells of Permian benthic invertebrates. Journal of Paleontology, 74:532–543.

Kowalewski, M., K. Gürs, J. H. Nebelsick, W. Oschmann, W. Piller, and A. P. Hoffmeister. 2002. Multivariate hierarchical analyses of Miocene mollusks of Europe: Paleogeographic, biostratigraphic, and paleoecological implications. Geological Society of America Bulletin, 114:239–256.

Kusmer, K. D. 1990. Taphonomy of owl pellet deposition. Journal of Paleontology, 64:629–637.

LaBandeira, K. 2002. Paleobiology of predators, parasitoids, and parasites: Death and accommodation in the fossil record of continental invertebrates. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

Lawrence, J. M., and J. Vasquez. 1996. The effects of sublethal predation on the biology of echinoderms. Oceanologica Acta, 19:431–440.

Leighton, L. R. 1999. Possible latitudinal predation gradient in middle Paleozoic oceans. Geology, 27:47–50.

Leighton, L. R. 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. Palaeogeography, Palaeoclimatology, Palaeoecology, 165:53–69.

Leighton, L. R. 2002. Inferring predation intensity in the marine fossil record. Paleobiology, 28: in press.

Lescinsky, H. L., and L. Benninger. 1994. Pseudo-borings and predator traces; artifacts of pressure-dissolution in fossiliferous shales. Palaios, 9:599–604.

Lever, J., A. Kessler, P. Van Overbeeke, and R. Thijssen. 1961. Quantitative beach research, II, The 'hole effect': A second mode of sorting lamellibranch valves on sandy beaches. Netherlands Journal of Sea Research, 1:339–358.

Lipps, J. H. 1988. Predation on foraminifera by coral reef fish: Taphonomy and evolutionary implications. Palaios, 3:315–326.

Lipps, J. H., and S. J. Culver, 2002. The trophic role of marine microorganisms through geologic time. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation, Paleontological Society Special Papers, 8 (this volume).

Lockley, M. G., and J. Madsen, Jr. 1992. Permian vertebrate trackways from the Cedar Mesa Sandstone of Eastern Utah: Evidence for predator-prey interaction. Ichnos, 2:147–153.

Lyman, R. L. 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge, 524 p.

Marcus, L. F., M. Corti, A. Loy, G. J. P. Naylor, and D. E. Slice (eds.). 1996. Advances in Morphometrics. NATO ASI Series A: Life Sciences, 284, Plenum, New York, 587 p.

Martill, D. M. 1990. Predation on *Kosmoceras* by semionotid fish in the Middle Jurassic lower Oxford Clay of England. Palaeontology, 33:739–742.

Matsukuma, A. 1977. Notes on *Genkaimurex varicosa* (Kuroda 1953) (Prosobranchia: Neogastropoda). Venus, 36:81–88.

Matsukuma, A. 1978. Fossil boreholes made by shell-boring predators or commensals, Part I: Boreholes of capulid gastropods. Venus, 37:29–45.

Mayhew, D. F. 1977. Avian predators as accumulators of fossil mammal material. Boreas, 6:25–31.

McRoberts, C. A. 2001. Triassic bivalves and the initial marine Mesozoic revolution; a role for predators? Geology, 29:359–362.

Merle, D. 2000. Premiere étude taphonomique de la predation affectant de grands mollusques benthiques dans l'Eocene de Gan (Pyrenées-Atlantiques, France). Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes, 330:217–220.

Miller, R. H., and F. A. Sundberg. 1984. Boring Late Cambrian organisms. Lethaia, 17:185–190.

Mordan, P. B. 1977. Factors affecting the distribution and abundance of *Aegopinella* and *Nesovitrea* (Pulmonata: Zonitidae) at Monks Wood National Nature Reserve, Huntingdonshire. Biological Journal of the Linnean Society, 9:59–72.

Morton, B., and K. Chan. 1997. The first report of shell-boring predation by a representative of the Nassariidae (Gastropoda). Journal of Molluscan Studies, 63:476–478.

Moy-Thomas, J. A., and R. S. Miles. 1977. Palaeozoic Fishes, 2nd ed. Saunders, Philadelphia.

Nebelsick, J. H. 1999. Taphonomic legacy of predation on echinoids, p. 347–352. *In* M. D. Candia Carnevali and F. Bonasoro (eds.), Echinoderm Research 1998. Balkema, Rotterdam.

Nebelsick, J. H., and S. Kampfer. 1994. Taphonomy of *Clypeaster humilis* and *Echinodiscus auritus* from the Red Sea, p. 803–808. *In* B. A. David, A. Guille, J. P. Féral, and M. Roux (eds.), Echinoderms through Time. Balkema, Rotterdam.

Nebelsick, J. H., and M. Kowalewski. 1999. Drilling predation on Recent clypeasteroid echinoids from the Red Sea. Palaios, 14:127–144.

Nedin, C. 1999. *Anomalocaris* predation on nonmineralized and mineralized trilobites. Geology, 27:987–990.

Negus, M. 1975. An analysis of boreholes drilled by *Natica catena* (Da Costa) in the valves of *Donax vittatus* (Da Costa). Proceedings of the Malacological Society of London, 41:353–356.

Neumann, C. 2000. Evidence of predation on Cretaceous sea stars from northwest Germany. Lethaia, 33:65–70.

Nixon, M. 1979. Hole boring in shells by *Octopus vulgaris* in the Mediterranean. Malacologia, 18:431–444.

Oji, T., C. Ogaya, and T. Sato. 2001. Shell fragments in fossil shell beds as a result of durophagous predation: Results from field observation and tumbling experiments. Geological Society of America Abstracts with Programs, 33:A307.

Orr, V. 1962. The drilling habit of *Capulus danieli* (Crosse) (Mollusca Gastropoda). Veliger, 5:63–67.

Ørstan, A. 1999. Drill holes in land snail shells from western Turkey. Schriften zur Malakozoologie aus dem Haus der Natur, 13:31–36.

Peterson, C. H., and R. Black. 1995. Drilling by buccinid gastropods of the genus *Cominella* in Australia. Veliger, 38:37–42.

Pickerill, R. K., and D. Blissett. 1999. A predatory *Rusophycus* burrow from the Cambrian of southern New Brunswick, eastern Canada. Atlantic Geology, 35:179–183.

Ponder, W. F., and J. D. Taylor. 1992. Predatory shell drilling by two species of *Austroginella* (Gastropoda; Marginellidae). Journal of Zoology, 228:317–328.

Pratt, B. R. 1998. Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. Lethaia, 31:73–88.

Pyke, G. H. 1984. Optimal Foraging Theory: A critical review. Annual Reviews of Ecology and Systematics, 15:523–575.

Reyment, R. A. 1963. Bohrlöcher bei Ostrakoden (sowie einige paläoethologische Bemerkungen). Paläontologische Zeitschrift, 37:283–291.

Reyment, R. A. 1966a. Preliminary observation on gastropod predation in the western Niger Delta. Palaeogeography, Palaeoclimatology, Palaeoecology, 2:81–102.

Reyment, R. A. 1966b. Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda, Part 3: Stratigraphical, paleoecological and biometrical conclusions. Stockholm Contributions in Geology, 14:1–151.

Reyment, R. A. 1967. Paleoethology and fossil drilling gastropods. Transactions of the Kansas Academy of Science, 70:33–50.

Reyment, R. A. 1971. Introduction to Quantitative Paleoecology. Elsevier, Amsterdam, 226 p.

Richards, R. P., and C. W. Shabica. 1969. Cylindrical living burrows in Ordovician dalmanellid brachiopod beds. Journal of Paleontology, 43:838–841.

Richter, G., and S. Baszio. 2001. Traces of a limnic food web in the Eocene Lake Messel; a preliminary report based on fish coprolite analyses. Palaeogeography, Palaeoclimatology, Palaeoecology, 166:345–368.

Rinaldi, A. C. 1994. Frequency and distribution of *Vitreolina philippi* (De Rayneval and Ponzi, 1854) (Prosobranchia, Eulimidae) on two regular echinoid species found along the southern coast of Sardinia. Bolletino Malacologia, 30:29–32.

Robba, E., and F. Ostinelli. 1975. Studi paleoecologici sul Pliocene Ligure, I: Testimoniaze di predazione sui molluschi Pliocenici di Albenga. Rivista Italiana Paleontologia Stratigraphia, 81:309–372.

Rohr, D. M. 1976. Silurian predator borings in the brachiopod *Dicaelosia* from the Canadian Arctic. Journal of Paleontology, 50:1175–1179.

Rohr, D. M. 1991. Borings in the shell of an Ordovician (Whiterockian) gastropod. Journal of Paleontology, 65:687–688.

Roopnarine, P. D., and A. Beussink.1999. Extinction and naticid predation of the bivalve *Chione* von Mühlfeld in the Late Neogene of Florida. Palaeontologia Electronica, 2(1), 24, 719 KB.

Roughley, T. 1925. The perils of the oyster. Australian Museum Magazine, 2:277–284.

Roy, K., D. J. Miller, and M. LaBarbera. 1994. Taphonomic bias in analyses of drilling predation: Effects of gastropod drill holes on bivalve shell strength. Palaios, 9:413–421.

Savazzi, E., and R. A. Reyment. 1989. Subaerial hunting behavior in *Natica gualteriana* (naticid gastropod). Palaeogeography, Palaeoclimatology, Palaeoecology, 74:355–364.

Schindel, D. E., G. E. Vermeij, and E. Zipser. 1982. Frequencies of repaired shell fractures among the Pennsylvanian gastropods of North-Central Texas. Journal of Paleontology, 56:729–740.

Schoener, T. W. 1979. Inferring properties of predation and other injury-producing agents from injury frequencies. Ecology, 60:1110–1115.

Sheehan, P. M., and P. Lespérance. 1978. Effects of predation on the population dynamics of a Devonian brachiopod. Journal of Paleontology, 52:812–817.

Signor, P. W., III, and C. E. Brett. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. Paleobiology, 10:229–245.

Sliter, W. V. 1971. Predation on benthic foraminifers. Journal of Foraminiferal Research, 1:20–29.

Sliter, W. V. 1975. Foraminiferal life and residue assemblages from Cretaceous slope deposits. Geological Society of America Bulletin, 86:897–906.

Smith, S. A., C. W. Thayer, and C. E. Brett. 1985. Predation in the Paleozoic: Gastropod-like drillholes in Devonian brachiopods. Science, 230:1033–1035.

Spencer, W. K., and C. W. Wright. 1966. Asterozoans , p. U4–U107. *In* R. Moore (ed.), Treatise on Invertebrate Paleontology, Pt. U, Echinodermata 3, Vol. 1. Geological Society of America and University of Kansas Press, New York.

Sohl, N. F. 1969. The fossil record of shell boring by snails. American Zoologist, 9:725–734.

Sohn, E. G., and S. Chatterjee, 1979. Freshwater ostracodes from Late Triassic coprolites in Central India. Journal of Paleontology, 53:578–586.

Stallibrass, S. 1984. The distinction between the effects of small carnivores and humans on post-glacial faunal assemblages, p. 259–269. *In* C. Grigson and J. Clutton-Brock (eds.), Animals and Archaeology: 4. Husbandry in Europe. British Archaeological Reports International Series, 227.

Stallibrass, S. 1990. Canid damage to animal bones: Two current lines of evidence, p. 151–165. *In* D. E. Robinson (ed.), Experimentation and Reconstruction in Environmental Archaeology. Oxbow Books, Oxford.

Stewart, J. D., and K. Carpenter. 1990. Examples of vertebrate predation on cephalopods in the Late Cretaceous of the Western Interior, p. 203–207. *In* A. J. Boucot (ed.), Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam.

Stewart, J. D., and K. Carpenter. 1999. Examples of vertebrate predation on cephalopods in the Late Cretaceous of the Western Interior. Bulletin of the Southern California Paleontological Society, 31:66–73.

Stewart, K. M., L. Leblanc, D. P. Matthiesen, and J. West. 1999. Microfaunal remains from a modern East African raptor roost; patterning and implications for fossil bone scatters. Paleobiology, 25:483–503.

Stuckenrath, R. 1977. Radiocarbon: Some notes from Merlin's diary. Annals of the New York Academy of Sciences, 288:181–188.

Taylor, J. D., N. J. Morris, and C. N. Taylor. 1980. Food specialization and the evolution of predatory prosobranch gastropods. Palaeontology, 23:375–409.

Taylor, J. D., R. J. Cleevely, and N. J. Morris. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. Palaeontology, 26:521–553.

Thomas, R. D. K. 1976. Gastropod predation on sympatric Neogene species of *Glycymeris* (Bivalvia) from the eastern United States. Journal of Paleontology, 50:488–499.

Todd, L. C., and D. J. Rapson. 1988. Long bone fragmentation and interpretation of faunal assemblages; approaches to comparative analysis. Journal of Archaeological Science, 15:307–325.

Tsujita, C. J., and G. E. G. Westermann. 2001. Were limpets or mosasaurs responsible for the perforations in the ammonite *Placenticeras*? Palaeogeography, Palaeoclimatology, Palaeoecology, 169:245–270.

Van Valkenburgh, B., and F. Hertel. 1993. Tough times at La Brea: Tooth breakage in large carnivores of the Late Pleistocene. Science, 261:456–459.

Van Valkenburgh, B., and I. Jenkins. 2002. Evolutionary patterns in the history of Permo-Triassic and Cenozoic synapsid predators. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

Vermeij, G. J. 1977. The Mesozoic marine revolution: Evidence from snails, predators, and grazers. Paleobiology, 3:245–258.

Vermeij, G. J. 1980. Drilling predation of bivalves in Guam: Some paleoecological implications. Malacologia, 19:329–334.

Vermeij, G. J. 1982. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. Malacologia, 23:1–12.

Vermeij, G. J. 1983. Traces and trends of predation, with special reference to bivalved animals. Palaeontology, 26:455–465.

Vermeij, G. J. 1987. Evolution and Escalation. Princeton University Press, Princeton, New Jersey, 527 p.

Vermeij, G. J. 2002. Evolution in the consumer age: Predators and the history of life. *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

Vermeij, G. J., and E. C. Dudley. 1982. Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the Southeastern U.S.A. Cretaceous Research, 3:397–403.

Vermeij, G. J., and D. R. Lindberg. 2000. Delayed herbivory and the assembly of marine ecosystems. Paleobiology, 26:419–430.

Vermeij, G. J., E. Zipser, and E. C. Dudley. 1980. Predation in time and space: Peeling and drilling in terebrid gastropods. Paleobiology, 6:352–364.

Vermeij, G. J., D. E. Schindel, and E. Zipser. 1981, Predation through geological time: Evidence from gastropod shell repair. Science, 214:1024–1026.

Villa, P., and E. Mahieu. 1991. Breakage patterns of human long bones. Journal of Human Evolution, 21:27–48.

Wächtler, V. W. 1927. Zür biologie der Raublungenschnecke *Poiretia (Glandina).* Algira Brug. Zoologischen Anzeiger, 72:191–197.

Walker, S. E. 1989. Hermit crabs as taphonomic agents. Palaios, 4:439–452.

Walker, S. E., and C. E. Brett. 2002. Post-Paleozoic patterns in marine predation: Was there a Mesozoic and Cenozoic marine predatory revolution? *In* M. Kowalewski and P. H. Kelley (eds.), The Fossil Record of Predation. Paleontological Society Special Papers, 8 (this volume).

Walker, S E., and S. B. Yamada. 1993. Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. Palaeontology, 36:735–741.

Walker, S. E., and J. R. Voigt. 1994. Paleoecologic and taphonomic potential of deepsea gastropods. Palaios, 9:48–59.

Warén, A. 1980. Revision of the genera *Thyca, Stilifer, Scalenostoma, Mucronalia* and *Echineulima* (Mollusca, Prosobranchia, Eulimidae). Zoologica Scripta, 9:187–210.

WARÉN, A. 1981. Eulimid gastropods parasitic on echinoderms in the New Zealand region. New Zealand Journal of Zoology, 8:313–324.

WARÉN, A., D. R. NORRIS, AND J. T. TEMPELADO. 1994. Description of four new eulimid gastropods parasitic on irregular sea urchins. Veliger, 37:141–154.

WARÉN, A., AND M. R. CROSSLAND. 1991. Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), two genera parasitic on sand dollars. Records of Australian Museum, 43:85–112.

WILTSE, W. I. 1980. Predation by juvenile *Polinices duplicatus* (Say) on *Gemma gemma* (Totton). Journal of Experimental Marine Biology and Ecology, 42:187–199.

WILSON, J. B. 1967. Palaeoecological studies on shell-beds and associated sediments in the Solway Firth. Scottish Journal of Geology, 3:329–371.

WILSON, M. V. H. 1987. Predation as a source of fish fossils in Eocene lake sediments. Palaios, 2:497–504.

WILSON, M. A., AND T. J. PALMER. 2001. Domiciles, not predatory borings: A simpler explanation of the holes in Ordovician shells analyzed by Kaplan and Baumiller, 2000. Palaios, 16:524–525.

WOELKE, C. E. 1957. The flatworm *Pseudostylochus ostreophagus* Hyman, a predator of oysters. Proceedings of the National Shellfisheries Association, 47:62–67.

WOOD, R. In press. Predation in ancient reef-builders. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Topics in Geobiology Series, Plenum Press/Kluwer, New York.

WODINSKY, J. 1969. Penetration of the shell and feeding on gastropods by *Octopus*. American Zoologist, 9:997–1010.

YOCHELSON, E. L., D. DOCKERY, AND H. WOLF. 1983. Predation on sub-Holocene scaphopod mollusks from southern Louisiana. United States Geological Survey Professional Paper, 1282:1–13.

YONGE, C. M. 1964. Rock borers. Sea Frontiers, 10:106–116.

YOUNG, D. K. 1969. *Okadaia elegans*, a tube-boring nudibranch mollusc from the central and west Pacific. American Zoologist, 9:903–907.

ZAR, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, 663 p.

ZIEGELMEIER, E. 1954. Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda Prosobranchia). Helgoländer wissentschaftliche Meeresuntersuchungen, 5:1–33.

ZILCH, A. 1959. Euthyneura, p. 1–701. *In* O. H. Schindewolf (ed.), Handbuch der Paläozoologie, 6. Berlin.

ZOTNIK, M. 2001. Size-related changes in predatory behaviour of naticid gastropods from the middle Miocene Korytnica Clays, Poland. Acta Palaeontologica Polonica, 46:87–97.

ZUSCHIN, M., AND R. J. STANTON, JR. 2001. Experimental measurement of shell strength and its taphonomic interpretation. Palaios, 16:161–170.

APPENDIX 1—A SAS/IML and SAS/STAT program to test for non-random distribution of traces across taxa. The program generates four outputs: (1) frequency of traces for each taxon and each iteration; (2) Null proportion of taxa expected to contain traces sorted by iteration; (3) Null highest per-taxon frequency of traces sorted by iteration; and (4) Null highest per-taxon frequency of traces by iteration and taxon. Written by M. Kowalewski.

```
    %let prob=0.011; * - assemblage-level drilling frequency (AF);
    %let times=999; * - number of iterations;
    PROC IML;
    X={292,280,280,280,220,200,200,200,140,140,140,120,120,100,
    100,100,100,100,100,100,80,80,80,80,80,80,60,60,60,60,60,60,60,60,60,60,60};
* - enter the specimen numbers for all taxa here;
    START drill(X,fin);
      Z=X; a=1-&prob; b=&prob; k=nrow(Z);
      DO i=1 to k;
       new=shape(i,Z[i],1);
       size=shape(Z[i],Z[i],1);
       newsize=new||size;
       new2=new2//newsize;
      END;
      out1=new2; k2=nrow(out1);
      DO j=1 to k2;
        c=rantbl(0,a,b); c1=c-1;
        c2=c2//c1;
      END;
      out2=c2; out3=out1||out2;
      fin=out3;
    FINISH drill;
    START simul(X,out);
      do i=1 to &times;
      run drill(X,fin);
      fin2=fin||shape(i,nrow(fin),1);
      fin3=fin3//fin2;
      end;
      out=fin3;
    FINISH simul;
    RUN simul(X,out);
    CREATE new from out;
    APPEND from out;
    CLOSE new;
    RUN;
    DATA output;
      set new; taxon=col1; nspec=col2; drill=col3; iter=col4;
    PROC sort; by iter taxon nspec;
    PROC univariate noprint;
      by iter taxon nspec; var drill;
      output out=final n=n mean=mean sum=sum;
    title1*Simulation Output for &times iterat & drilling prob &prob*;
    title2'Total output';
    PROC print;
      var iter taxon nspec mean sum;
    DATA new2;
      set final;
      if sum>0 then sum=1;
    PROC univariate noprint;
      by iter; var sum;
      output out=final2 mean=mean;
    title2'Proportion of taxa drilled by iteration';
    PROC print;
    PROC univariate data=final noprint;
      by iter; var mean;
      output out=final3 max=max;
    title2'The highest per-taxon drilling frequency by iteration';
    PROC print;
    PROC sort data=final; by iter nspec;
    PROC univariate noprint;
      by iter nspec; var mean;
      output out=final4 max=max;
    DATA new3;
      set final4; keep iter nspec max;
    title2'The highest drilling frequency by taxon sample size by
iteration';
    PROC print;
    QUIT;
```

APPENDIX 2—A SAS/IML and SAS/STAT program for a two-sample bootstrap test for difference in means for circular (azimuth) data. The algorithm for the Watson-Williams two-sample test is based on equations from Zar (1999, p. 626, Example 27.8). F statistic is not corrected (i.e., K=1; see Zar, 1999, Equation 27.11). The correction is not needed here because the probability density function for F is established empirically through bootstrap simulation. Bootstrap probability [p] is calculated as follows: p=s+1/i+1, where s is the number of bootstrap values larger than or equal to actual F and i is the number of iterations (this equation includes the actual samples in computing p; see Manly, 1995). Written by M. Kowalewski. Note: This code was used recently by Dietl and Alexander (2000) to analyze changes in site selectivity of drilling on Cenozoic gastropods.

```
    %let TIMES=999;      *—number of times to randomize;
    %let DATA1='ang1.dat';   *—file containing first variable;
    %let DATA2='ang2.dat';  *—file containing second variable;
    Title1'2-sample bootstrap for circular data (Watson-Williams
test)';
    Title2'written by Michal Kowalewski, October 11, 1999';
    DATA data1;    infile &DATA1; input var1;
    DATA data2;    infile &DATA2; input var2; RUN;
    PROC IML; %let pi=3.1415926535;
    USE data1; READ all var{var1} into X1;
    USE data2; READ all var{var2} into X2;
    START RANVEC(in,v_out); k=nrow(in); v_index=in;
    DO i=1 to k; rand=floor((k-i+1)*ranuni(0) + 1);
v_ran=v_ran||v_index[rand]; v_index=remove(v_index,rand); END;
v_out=v_ran; FINISH RANVEC;
    START MIXUP(X,times,template);
    n=nrow(X); template=t(1:n)*j(1,times,1);
    DO i=1 to times; run ranvec(template[,i],out);
template[,i]=t(out); END; DO i=1 to n; run
ranvec(t(template[i,]),out); template[i,]=out; END; FINISH MIXUP;
    START WATSON(D1,D2,F);
    Y1=D1/(180/&pi); Y2=D2/(180/&pi); Y=Y1//Y2;
    C1=sum(COS(Y1))/nrow(Y1); S1=sum(SIN(Y1))/nrow(Y1);
    R1=sqrt(C1**2+S1**2)*nrow(Y1); a1=arcos(C1/(R1/
nrow(Y1)))*(180/&pi);
    C2=sum(COS(Y2))/nrow(Y2); S2=sum(SIN(Y2))/nrow(Y2);
    R2=sqrt(C2**2+S2**2)*nrow(Y2); a2=arcos(C2/(R2/
```

```
nrow(Y2)))*(180/&pi);
    C=sum(COS(Y))/nrow(Y); S=sum(SIN(Y))/nrow(Y);
    R=sqrt(C**2+S**2)*nrow(Y);   mean_a=arcos(C/(R/
nrow(Y)))*(180/&pi);
    Fstat=((nrow(Y)-2)*(R1+R2-R))/(nrow(Y)-R1-R2);
    F=a1||a2||mean_a||Fstat; FINISH WATSON;
    START BOOT(X1,X2,times,dist);
    RUN  watson(X1,X2,aF);  X=X1//X2;  k=nrow(X1);
j=nrow(X2);
    RUN mixup(X,times,template);
    Do   i=1   to   times;   Y1=X[template[1:k,i]];
Y2=X[template[(k+1):(k+j),i]];
    RUN watson(Y1,Y2,F); rF=rF//(i||F); END; rand=rF;
act=shape(aF,nrow(rand),ncol(aF)); dist=rand||act; FINISH BOOT;
    RUN BOOT(X1,X2,&times,dist);
    CREATE OUT from DIST [colname={‘i’ ‘r1’ ‘r2’ ‘mean-r’ ‘rF’
‘a1’ ‘a2’ ‘mean_a’ ‘aF’}];
    APPEND from DIST; CLOSE OUT;
    DATA report; set OUT; if i=1; keep a1 a2 mean_a aF;
    DATA count; set OUT; if rF>=aF then p=1; else p=0;
    PROC univariate noprint; var p; output out=last sum=s N=n;
    DATA prob; set last; n=n+1; p=(s+1)/n; keep p n;
    DATA final; merge prob report;
    PROC print data=final noobs split=’*’;
    label a1=’mean angle for the first sample’; label a2=’mean
angle for the second sample’; label mean_a=’mean angle for pooled
data’; label aF=’Waston-Williams Stat. without K-factor correction’;
label n=’number of random samples (# iterations + 1)’; label
p=’probabil. that 2 samples have the same mean angle’; RUN; QUIT
```