



Patterns and processes of shell fragmentation in modern and ancient marine environments

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Abstract

Shell fragments are important components of many Recent and fossil marine benthic ecosystems and can provide crucial information on past and present environmental conditions. Interpreting such fragments requires integrated knowledge in various fields and the information potential is therefore rarely optimally utilized. This paper uses the definition of a fragment as being a piece of shell having less than 90% of its original form. It then outlines the potential characteristics, pathways, and fates that shells and their fragments can have.

Fragmentation is a key factor shaping the shelly part of death assemblages, but it is difficult to interpret because it can be broadly caused by ecological, biostratigraphic or diagenetic processes and also depends on shell strength. Strength, in turn, reflects multifunctionality during ontogeny and depends on a complex set of skeletal and taphonomic factors. Therefore, no particular shell parameter clearly determines strength, but thickness, microstructure type and degree of organic matrix have the strongest influence on pre- and post-mortality strength. Size measurements are usually less important for shell strength than thickness, although ecologically complex size refuges from predation do exist. Similarly, shell shape, sculptural features and specific aperture types (in gastropods) provide various defence strategies rather than increasing strength per se.

Key ecological factors of fragmentation include predation due to crushing, peeling, along with mistaken predation, self-inflicted damage during predation and burrowing, and more physical aspects such as impacts by stones. Modern studies must consider damage by benthic commercial fisheries or dredging by scientific vessels. Key biostratigraphic factors include transport-induced abrasion (littoral zone of surf-washed beaches), bioerosion and dissolution (mainly sublittoral environments). Diagenetically, fragmentation during compaction mainly occurs when shells are in direct contact with one another or with coarser grains; taphonomic features (e.g., drillholes) have only minor influence.

A key step in interpreting fragments is to categorize breakage into repaired versus unrepaired, diagnostic versus non-diagnostic, and severe versus localized damage. Quantifying the above categories can then provide useful information on breakage patterns and underlying processes. Understanding the many characteristics of shells and their fragments is a significant interpretive tool in maximizing the information gain in palaeoecological and taphofacies analyses.

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1. Introduction

Palaeontologists deal with two types of material: complete fossils and fragments. In the past, most invertebrate palaeontologists were more interested in the former than in the latter (Seilacher, 1973; Bishop, 1975). In recent years, however, fragments have provided interesting evidence for ecological, taphonomic and evolutionary topics. Some of the most unusual molluscan taxa are nearly exclusively known from fragments (Yancey and Boyd, 1983; Yancey and Stanley, 1999) and for many taxa, fragments contribute to a better knowledge of their spatial distribution pattern (Nebelsick, 1992; Dulai, 1996) or their fossil record (Paul, 1998; Oyen and Portell, 2001) and extinction pattern (MacLeod and Ward, 1990).

Shell fragments are very common in modern death assemblages (Tauber, 1942; Hollmann, 1968; Pilkey et al., 1969; Yamaguchi, 1977; Vermeij, 1979, 1982; Staff and Powell, 1990; Cadée, 1968, 1994; Zuschin and Hohenegger, 1998) and fossil assemblages (Zuschin and Stanton, 2002; Zuschin et al., unpublished data from Grund formation, Miocene, Austria). The sources of fragmentation, however, differ strongly. In a bay in Panama, for example, bivalve fragmentation is not related to physical parameters (water energy, depth) or shell features (thickness); the type of death itself is probably more important than post-mortem processes (Best and Kidwell, 2000a). In contrast, the moderate fragmentation patterns observed in three generations of cheniers in Baja California is mostly related to physical processes (currents and waves generated by storms and tides) during the initial biostratinomic phase (Kowalewski et al., 1994). Distinct differences in fragmentation between two tidal flats (North Sea and Gulf of California) and shell-rich cheniers of the Colorado Delta plain are interpreted to reflect different hydrodynamic regimes (Kowalewski et al., 1995). A mixture is possible: in the intertidal environments at Provincetown Harbor (Massachusetts) the overall physical fragmentation patterns are obscured by gull predation on the bivalve *Mercenaria mercenaria* (Meldahl and Flessa, 1990). Mistaken predation, in which shell-crushing predators break empty shells (LaBarbera, 1981; Walker and Yamada, 1993), may also play a role, although this contribution is probably relatively low compared to the total amount of ingested shells (e.g., Cate and Evans, 1994, p. 261). Distinction is difficult:

based on the abundance of broken shells, nearshore high-energy environments are indistinguishable from outer shelf sediments, where fragmentation mainly results from biological processes (Pilkey et al., 1969).

Processes of breakage and fragmentation are therefore standard issues in taphonomic research (Müller, 1979; Powell et al., 1989; Kidwell and Bosence, 1991; Parsons and Brett, 1991; Martin, 1999) and palaeoecology textbooks (e.g., Boucot, 1981; Dodd and Stanton, 1990; Etter, 1994; Brenchley and Harper, 1998). Fragmentation is the only frequently investigated biostratinomic feature that is produced not only by biostratinomic processes but also by ecological interactions, during diagenesis, and by tectonics (Fig. 1). The taphonomic and palaeoecological value of fragments, however, is lessened by the fact that the various sources of breakage and fragmentation are difficult to distinguish (e.g., Vermeij, 1983a; Cate and Evans, 1994; Dodge and Scheel, 1999) and that shell-breaking predation is characterized by strong temporal and latitudinal gradients (e.g., Vermeij, 1983a,b). This is reflected in different estimations of the relative contributions of potential sources of fragmentation, which range from a predominance of predation (Powell et al., 1989; Boston and Mapes, 1991) to bioturbation in quiet offshore environments (Brenchley and Harper, 1998, p. 72, and to physical fragmentation (Parsons and Brett, 1991). Other potential causes are compaction (Hoffman, 1976; Kowalewski, 1990) and sample handling (Flessa et al., 1992).

The present review is the first attempt to summarize information from empirical and experimental studies and from observations of all potential sources of fragmentation (ecological interactions, biostratinomic processes, compaction, tectonic strain, and the sampling process). We discuss definitions of breakage and fragments, the methods to quantify fragmentation, the role of (mostly experimentally measured) shell strength and the relation of shell strength to shell parameters (size measurements, thickness, shape, microstructure, organic matrix, spines and varices) and taphonomic features (taphonomic grades, drillholes). We evaluate the importance of considering breakage patterns for recognizing the responsible underlying process and emphasize the role of fragmentation for taphofacies analysis (Fig. 1).

The information presented is mollusc-oriented because this group has been the primary target of

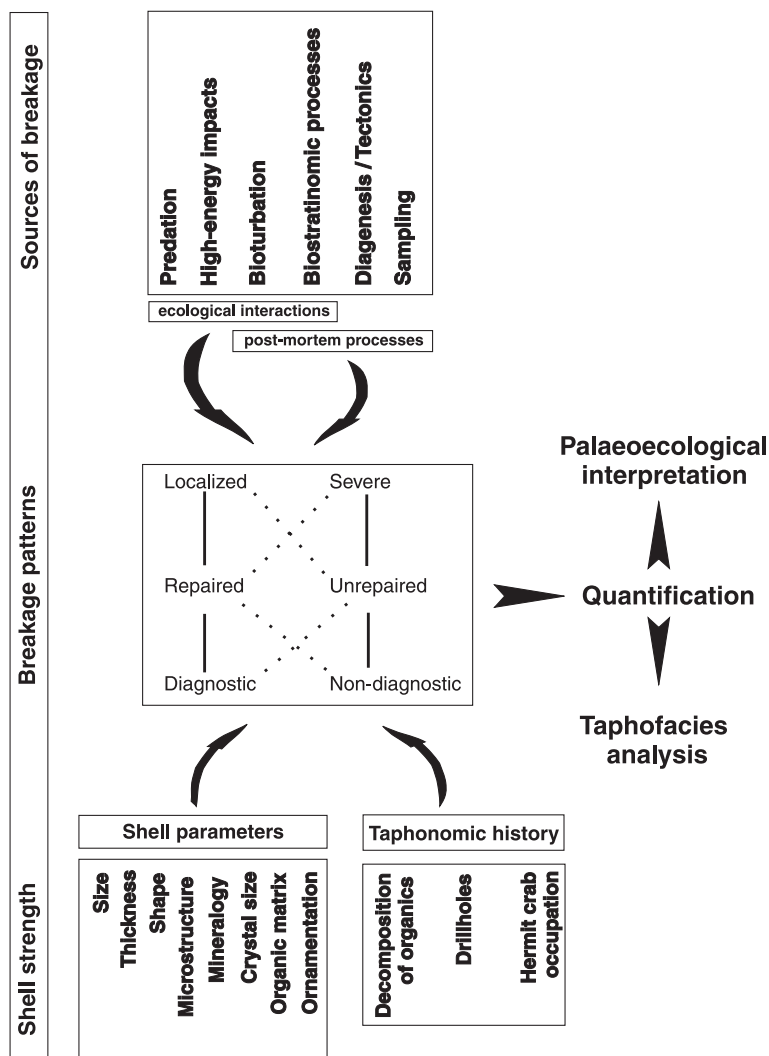


Fig. 1. The interplay of different sources of breakage and shell strength result in complex breakage patterns. Rigorously classifying breakage type and quantifying fragments increase the value of fragments for taphofacies analyses and palaeoecological interpretations.

taphonomic research. Additional studies on brachiopods, echinoderms, corals, ostracods, foraminifers and plants are considered, but mainly to supplement interpretations of the mollusc material.

2. Definitions of breakage and fragments

Fragmentation is the breakage of skeletons or skeletal elements without regard to natural joints

(Speyer and Brett, 1988). The question of how to define a fragment for taphofacies analysis is discussed in Powell et al. (1989) and Davies et al. (1990). The latter authors define a whole shell as any shell having >90% of the original form for which an anterior–posterior length in bivalves or a long-axis length in gastropods (usually the apex–base length) can be measured. Accordingly, each piece of shell not matching that definition is a fragment. This definition is very similar to approaches that differentiate between

partially destructive and totally destructive feeding processes (Cate and Evans, 1994), severe and localized damage (Alexander, 1981; Elliott and Bounds, 1987) and sublethal and lethal breaks (e.g., Vermeij, 1979). A problem exists in studies in which shells are regarded as broken only if the damage would have been sufficient to kill the original occupant because it may be difficult to differentiate lethal from sublethal breaks (Vermeij, 1983a). Such studies rely on an a priori assumption based either on expert judgement on lethality, or on laboratory experiments that fatally injured the same species (Vermeij, 1982). Moreover, “lethally” broken shells were often actually occupied by hermit crabs or broken when empty (Vermeij, 1982) (see also Section 3.1.1.3: Mistaken predation). Finally, non-lethal damage such as chipping of the outer lip of a gastropod may be very important for the taphofacies concept and for ecological interpretations.

The definition of Davies et al. (1990) is very useful because (1) it is numerical and it avoids speculation on the fragmentation process and the severity of the damage and (2) the quantitative 90% criterion provides a distinct baseline. Beyond the definition itself, information on the fragmentation process based on distinctive fragmentation patterns considerably increases the value of a fragment for taphofacies and other analyses. Disadvantages, in gastropods, are that the destruction of the apertural area may preclude accurate estimates of the original shell length. In large data sets, especially those which include small molluscs, percentage measurements are not feasible. Here, the 90% criterion has to be estimated visually (e.g., Zuschin and Hohegger, 1998), whereby the operator’s error is likely to be large.

Another problem is that distinctive breakage patterns can be observed most readily on “whole” shells with only localized damage (e.g., peeling predation); most fragments make up unidentifiable shell hash and the source of fragmentation cannot be recognized (Alexander, 1986a). Taphonomic grades for increasing degrees of fragmentation can help to overcome these problems (see also Section 6: Methods to quantify breakage). The concept of taphonomic grades was introduced by Brandt (1989) to facilitate comparisons between entire assemblages. Most other studies, however, used it to evaluate the condition of individual specimens (e.g., Feige and Fürsich, 1991; Kowalewski et al., 1994, 1995; Kidwell et al., 2001).

Some of them differentiate minor breakage and major breakage (more than 20% broken away) (Davies et al., 1989; Parsons, 1989); it might be appropriate to distinguish a third grade for those shells that are broken into two more or less equal parts.

Kidwell et al. (2001) chose a very different approach for bivalves and treated disarticulation as a state within fragmentation; they distinguished three grades (no damage: valves articulated; low damage: whole but disarticulated; high damage: large or small fragment).

In taphofacies analysis, many workers count, as fragments, only shell pieces containing apex or beaks in order to avoid counting the same individual more than once. Such fragments usually make up only a small part of the total fragments present in a death assemblage: because taphonomic disintegration rates are sufficiently high, this concern is usually unjustified. We therefore concur with Powell et al. (1989) that the entire fauna should be used. Moreover, fragments may bear substantially different taphonomic information (e.g., dissolution, edge rounding, encrustation) than whole individuals (Staff and Powell, 1990). For this reason it can be helpful to distinguish between whole individuals, identifiable fragments and unidentifiable fragments (after Kidwell et al., 2001).

3. Sources of breakage

Various processes give rise to fragments. Here, we distinguish a succession of partially overlapping processes, beginning with ecological interactions (predation, high-energy impacts and bioturbation), followed by the biostratinomic processes of bioerosion, dissolution and abrasion and, ultimately, diagenesis (compaction), tectonic stress (shear) and sample handling (Fig. 2).

3.1. Ecological processes

In accordance with the definition of ecology as the interaction between organisms and their environment, this section treats both interspecific interactions and environmental influences (e.g., rock, ice, wave impacts) on living shelled organisms. Anthropogenic influences are also subsumed under this heading.

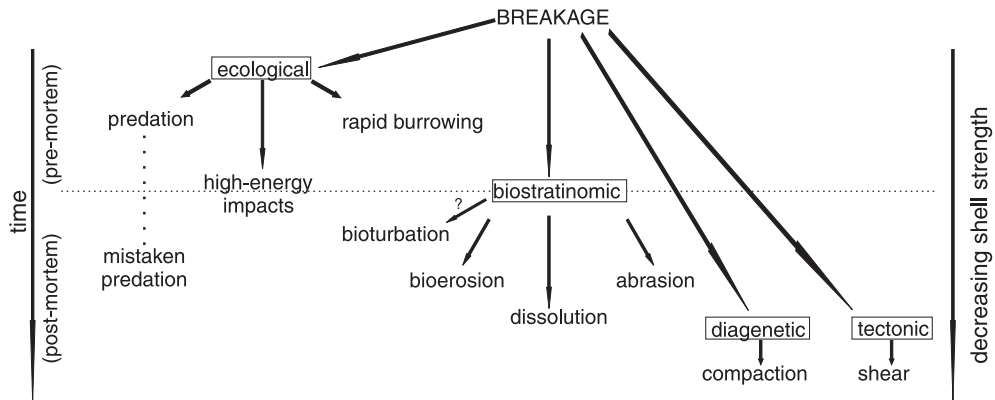


Fig. 2. Major categories of shell breakage and their temporal relationship. Shell strength decreases with time and sampling can lead to further breakage at each step. Predation is clearly an ecological interaction but mistaken predation refers to a predator's inability to distinguish live prey from empty shells. High-energy impacts of rocks, ice and waves may occur during an organism's life-time or post-mortem. Rapid burrowing to escape predators and readjustment after storms can result in self-inflicted damage of deep-infaunal bivalves. Bioerosion, dissolution and abrasion typically occur post-mortem but may already act on living shelled organisms. Bioturbation is frequently assumed to be a major source of breakage, but case studies are lacking. Compaction and shear are clearly post-mortem processes.

3.1.1. Shell-breaking predation and shell repair (=shell regeneration)

Predation is a complex interaction in which individuals of one species kill and are capable of consuming a significant fraction of the biomass of individuals of another species (Abrams, 2000), which should be interpreted in the light of optimal foraging theory (Hughes, 1980; Stephens and Krebs, 1986). Predators may contribute to the regional or global extinction of prey organisms (Schoener et al., 2001; Ozanne and Harries, 2002), they effectively control prey distribution and abundance (e.g., Beal et al., 2001) and they can also change prey size distributions (Kvitek et al., 1992; Ejdung and Elmgren, 2001). Crushing predators can even restructure a benthic community by discarding the shells of their prey and exposing high numbers of old buried shells, which in turn become colonized by hard substrata dependent epifauna (Kvitek et al., 1992).

For the purpose of the present study, predation is simply defined as the successful or unsuccessful attempt to eat living animals. In most cases, however, it is not possible to distinguish between traces of predation and those of scavenging (the eating of dead animals) (Bishop, 1975). Durophagy is the consumption of prey protected by a hard skeleton (Aronson, 2001).

3.1.1.1. Shell-breaking methods.

A predator must detect, recognize, locate and move toward and attack a potential prey (e.g., Endler, 1986). Most shell-crushing predators in search of food detect their prey by vision (fishes, birds, mammals, octopuses, stomatopods) or with chemical and mechanical receptors (in the antennae and hairs of claws of crabs for example) (Vermeij, 1993). If capture is successful, subjugation and then consumption of the prey follow (Bishop, 1975; Vermeij, 1983a,b). Among the five categories of methods of subjugation outlined by Vermeij (1987), only two—pre-ingestive breakage and drilling—leave consistent traces on a victim's skeleton. Organs used by shell-breaking predators to dismember shells in aquatic environments are jaws (Fig. 3A,B) (fishes, turtles, lizards, crocodiles, mammals), beaks (Fig. 3C,D) (birds, turtles, cephalopods), claws (Fig. 3E,F) (arthropods—mainly crabs and lobsters), mandibles (clawless lobsters), thoracopods (Fig. 3G) (stomatopods), pharyngeal bones and teeth in the throat (Fig. 3H) (e.g., labrids, cichlids and freshwater minnows), gizzards (Fig. 3I) (birds, opisthobranch gastropods) and shell lips (Fig. 3J,K) (some gastropods) (Bishop, 1975; Nielsen, 1975; Vermeij, 1993).

Predators break shells either by crushing, pounding, peeling, shaking or dropping (Bishop, 1975; Vermeij, 1978, 1983a, 1987; Cadée, 1989, 1995,

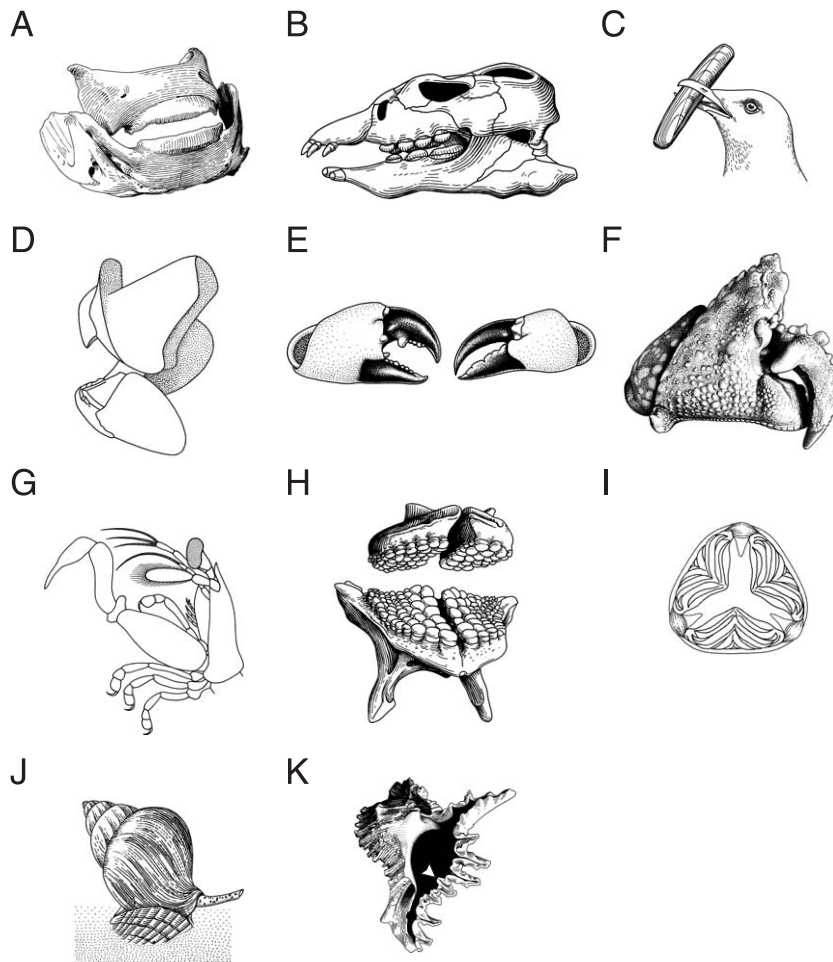


Fig. 3. Examples of shell-breaking organs of aquatic predators used to crush and dismember shells. (A) Jaws of *Diodon hystrix*, a porcupine fish (modified after Vermeij, 1993). (B) Jaws of *Placodus*, a placodont reptile (redrawn after Bishop, 1975). (C) Beaks of the herring gull *Larus argentatus* (redrawn after Cadée, 2000). (D) Beaks of *Nautilus* (redrawn after Saunders et al., 1978). (E) Crushing and cutting claws of the common mud crab *Panopeus herbstii* (redrawn after Bishop, 1975). (F) Specialized right peeling claw of the box crab *Calappa convexa* (redrawn after Vermeij, 1993). (G) Thoracopod of gonodactylid stomatopod (modified after McLaughlin, 1980; Geary et al., 1991; Stachowitsch, 1992). (H) Pharyngeal teeth of the black drum *P. cromis* (redrawn after Cate and Evans, 1994). (I) Cross-section of gizzard of opisthobranch gastropod (modified after Rudman, 1971, 1972; Alvarez et al., 1993). (J) Thin outer lip of the gastropod *Busycon* (redrawn after Nielsen, 1975). (K) Wedge-shaped tooth (arrow) of *M. fortispina* projects inwardly from the outer lip of the aperture (redrawn after Ankel, 1938).

2001). In crushing, the shell as a whole is compressed between two hard surfaces, e.g., the jaws of diodontid porcupine fishes (Vermeij, 1983a, p. 652) or the toothed inner surfaces of the fingers of a crab's claw (e.g., Behrens Yamada and Boulding, 1998; Taylor, 2001). Attacking crabs often load shells many times, and so-called fatigue fractures may occur after

repeated loading cycles that did not cause immediate failure (Elner, 1978; Boulding, 1984; Boulding and LaBarbera, 1986; Currey, 1988). Shell-crushing seabirds (e.g., eider and shelduck) and some opisthobranch gastropods ingest whole small molluscs and break the shells in their gizzard (Cadée, 1968, 1994, 1995; Trewin and Welsh, 1976). Similarly, many fish

use thickened pharyngeal bones or teeth in the throat to crack shells after swallowing (e.g., Liem, 1974; Cate and Evans, 1994).

A variation of the crushing method is hammering or pounding, in which the hardened dactyls of the second thoracopods (formerly termed maxillipeds) (the gonodactyloid “hammer” after Currey, 1990) of gonodactyloid stomatopods (e.g., Bertness, 1982; Geary et al., 1991) or the bill of birds (e.g., Drinnan, 1957) are brought down repeatedly on a victim’s shell. Sea otters as they float on their backs can use rocks or other hard objects to hammer open prey shells or beat shells against one another (Kvitek et al., 1992) and birds (e.g., gulls, ospreys and crows) can carry larger shells (which they cannot break in their gizzard) to high altitude and drop them onto rocks to crack them open (Siegfried, 1977; Zach, 1979; Kent, 1981a; Maron, 1982; Leshem, 1985; Mienis, 2000; Cadée, in press). In peeling, the growing edge of a shell is the only part of the shell that is grasped by the predator (e.g., spiny lobsters or calappid crabs) (Schäfer, 1962; Bertness, 1982; Lawton and Hughes, 1985).

Chipping is a similar process to peeling: The feeding process of bivalve-eating, non-drilling, stenoglossan gastropods (like the buccinid *Buccinum*, the melongenid *Busycon*, the fasciolarids *Fasciolaria* and *Pleuroplaca* and the muricids *Murex fortispina* and *Murex fulvescens*) involves the snail inserting its shell lip into the slit between the tightly fitting valves and wedging them apart so that the proboscis may be inserted (for review, see Nielsen, 1975). Among the above taxa, the more thick-shelled snails (some *Busycon* and *Murex*) press their shells so firmly against the bivalve that smaller or larger pieces become chipped off from the valves (e.g., Warren, 1916; Carriker, 1951; Wells, 1958; Paine, 1962). *M. fortispina* is reported to use a special wedge-shaped tooth which projects inwardly from the outer lip of the aperture and is used to force the valves apart (for references and discussion see Ankel, 1938; Schäfer, 1962). Herring gulls collect bivalves like *Ensis directus* (as well as shorecrabs) by repeatedly shaking the animals in their beak for several seconds; this treatment distinctly damages the middle part of the valve (Cadée, 2000).

3.1.1.2. The effects of shell-breaking predation. The effects of feeding activities can be non-destructive, shell-weakening, partially destructive or totally des-

tructive (Fig. 4) (modified after detailed information provided in Boucot, 1981; Cadée, 1994, 1995; Cate and Evans, 1994).

In non-destructive feeding activity, valves and shells remain undamaged: asteroids, fish (cunners), birds (oystercatchers, gulls) and mammals (walrus) may leave shells whole and even articulated. The shells can be opened externally without being destroyed (asteroids), ingested and in rare cases regurgitated whole (gulls), and may even pass the digestive tract alive and unaffected (cunners, shelduck). Note that even very fragile shells such as *Bulla* can be swallowed and digested by nudibranchs without any obvious sign of predation (Warme, 1971).

Shell-weakening feeding activities are mainly represented by drilling predation (see also Section 4.2: Shell strength in relation to taphonomic features).

In partially destructive feeding activities, marginal parts of shells are damaged by chipping, crushing, peeling and rasping as is reported for the gastropod *Busycon* spp., calappid crabs, spiny lobsters, fishes (tetradontids and ballistids) and birds (oystercatchers).

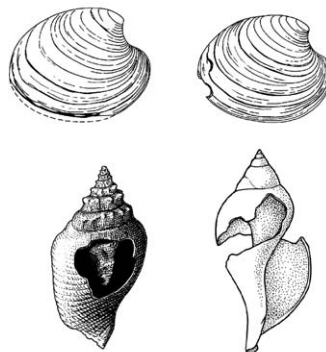
In totally destructive feeding activities, shells are damaged extensively. In contrast to Cate and Evans (1994), we include in this category also feeding processes that break one valve but leave the other one intact. This is based on the practical consideration that the distinction of whether one or both valves were broken is normally not possible after disarticulation and during time-averaging. Totally destructive feeding processes are reported by opisthobranch gastropods (*Philine*, *Scaphander*), crabs, lobsters, fish (rays, cunners, plaice, flounder), and birds (oystercatchers, eider duck, herring gull, knots). These organisms destroy shells in different ways: (1) they crush the shell externally and ingest only the soft parts (oystercatchers, crabs, lobsters, rays, cunners); (2) they break shells in their mouth and then pass the fragmented shell material through the digestive tract (fish with crushing-type teeth such as sciaenids, labrids); and (3) they ingest whole shells, crush them in the gizzard and defecate or regurgitate the fragments (e.g., *Philine*, *Scaphander*, flounder, eider duck, herring gull, knot shelduck). Therefore, damage will depend both on the predator and the prey species.

The partially and totally destructive feeding processes distinguished in the present contribution overlap with the categories of severe crushing and

A. Totally destructive



B. Partially destructive



C. Shell-weakening



D. Non-destructive



Fig. 4. The effects of feeding activities (predation) on shells. (A) Most durophagous predators shatter shells into several angular pieces and create shell hash; figured example is a crushed *Comus* shell from the Gulf of Aqaba, northern Red Sea. (B) Partially destructive feeding activities (= localized predation) yield fragments with the highest information content (= distinct breakage patterns). See Fig. 14 for more information on diagnostic unrepaired shell damage. (C) From the breakage point of view, drilling predation is the most common shell-weakening feeding activity; figured example is a *Dosinia* valve with a typical naticid drill hole from the northern Bay of Safaga, Red Sea. (D) In non-destructive feeding activities, valves and shells remain undamaged.

localized damage (Alexander, 1981; Elliott and Bounds, 1987) and potentially create large quantities of fragments: Cate and Evans (1994) suggest that each fish of the species *Pogonias cromis* contributes about 1.5 kg of fragmented shell material and disarticulated valves to Texas bay sediments annually (totaling thousands of tons). Similarly, Cadée (1995) estimates that about 70% of the annual shell carbonate production in the Dutch Wadden Sea (ca. 200 million kg) are fragmented by predators (birds, shorecrabs, fish).

Many modern shell-crushing predators, such as octopuses, consume prey in their shelters and discard the broken shells in middens (for review, see Walker, 1990). In the fossil record, for example, similar nests of crushed, angular rudist valves in the Santonian–Maastrichtian of the Pyrenees are interpreted as in situ remnants of predation (D. Sanders, personal communication, 2001).

3.1.1.3. Mistaken predation. The inability to recognize live prey from empty shells is reported for drilling predatory gastropods (Dietl and Alexander, 1995; Lescinsky et al., 2002) and for shell-breaking crabs (LaBarbera, 1981). According to Walker and Yamada (1993), mistaken predation by crabs biases the death assemblage toward peeled and fragmented gastropod shells because crabs attack more empty gastropods than empty bivalves. Cate and Evans (1994) reported that *P. cromis* also ingested minor amounts of dead shell material in Texas bays. Ingestion of such material is also common in shelducks and reported from many birds; like stones, it may help to break shells in stomachs (Trewin and Welsh, 1976; G. Cadée, personal communication, 2001).

3.1.1.4. Shell repair. Repaired skeletal injury (e.g., Figs. 3–5 in Savazzi, 1990; Fig. 11 in Savazzi, 1991) is the most easily interpreted evidence of breakage. It

is often considered as unsuccessful attack (predatory failure) (e.g., Ebbestad and Peel, 1997) and as a conservative measure of the potential for anti-predatory selection and of predation pressure (Vermeij, 1987). It is reported from many fossils including echinoderms, trilobites, brachiopods, polyplacophorans, scaphopods, gastropods, bivalves, cephalopods, bryozoans, cnidarians and foraminifers (for a review see Vermeij, 1983b; Brett, 1990; Lipps, 1988; Aronson and Blake, 2001; Baluk and Radwanski, 1977; Oschmann, 1989; Babcock et al., 1987) and also occurs in larval shells (e.g., Hickman, 2001). Shell repair has also been reported for drill holes in mussels (e.g., Dietl, 2000). Note that injuries other than those produced by predation, e.g., by boring organisms such as the polychaete *Polydora*, can also be repaired (Lauckner, 1983).

In molluscs, predation-related shell repair is expressed as a jagged scar that usually disrupts growth lines or ornamentation (Fig. 5) (Papp et al., 1947; Raffaelli, 1978; Robba and Ostinelli, 1975; Vermeij et al., 1981); in cross-section it is visible as an indentation in the normal growth line of the outer shell surface, which is evident across the entire shell margin and not only in the damaged area (Ramsay et al., 2001; Ramsay and Richardson, 2000). Sometimes scars are not visible superficially but can only be recognized in cross-sections (Ramsay et al., 2001). The presence of repair scars is usually used to make paleoecological inferences about shell-breaking predators (e.g., Kohn and Arua, 1999; Kowalewski and Flessa, 2000; Kröger, 2002), but is not directly correlated with predation intensity or rates (Schoener,

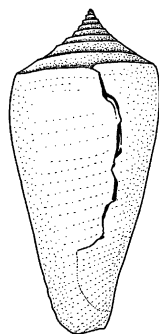


Fig. 5. Shell repair is mostly interpreted as unsuccessful predatory attack but can also result from ecological processes other than predation (redrawn after Kohn, 1999).

1979; Schindel et al., 1982). Repair frequency is influenced by the abundance and the strength of predators relative to the abundance and strength of the prey (Vermeij, 1982). If the strength of the former increases relative to that of the latter, the proportion of successful attacks also increases and the frequency of repaired damage decreases (Hughes and Elner, 1979; Elner and Raffaelli, 1980). Gastropod species that are rarely successfully predated have a high frequency of repair and a low percentage of lethally broken shells, and vice versa (Vermeij, 1982). As indicated by repair scars, gastropods frequently survive peeling predation, but large holes and fractures of the body whorl (e.g., those produced by gonodactyloid stomatopods) are usually fatal (Wagge and Mittler, 1953; Kohn, 1992). In contrast to gastropods, bivalves have very low frequencies of shell repair (e.g., Alexander and Dietl, 2001) because even minor damage of the valve margin increases the probability of detection by other predators due to metabolites leaching from the soft tissue (Vermeij, 1983b). Seasonal differences in predation (Peterson, 1982; Cote et al., 2001) can coincide with seasonal differences in percentage chipped and crushed shells (Beal et al., 2001) and in some circumstances can be recognized in fossil shelled organisms from periodically recurring repair scars along the growing edge (Kowalewski and Flessa, 2000).

Repair occurs also after non-lethal shell damage due to causes other than predation, e.g., impact by stones, self-inflicted damage during predation and burrowing, damage by beamtrawl fishery (see Cadée et al., 1997; Cadée, 1999 for short discussion), and intraspecific fighting (Saunders et al., 1978). Jones (1982) discusses sediment incursion into the shell and resulting damage to the epithelial cells as the most probable cause of shell repair in Silurian brachiopods. In certain instances the potential prey may use its shell as an offensive weapon and damage the shell of the predator (e.g., Branch, 1979). Shell repair may be absent either if predation intensity was zero or if predators were 100% efficient (Schoener, 1979), and the variation in repair frequency can be large between species as well as between habitats (Geller, 1983; Schmidt, 1989; Cadée et al., 1997; Walker, 2001). A significant increase through time in the frequency of repair scars was suggested by Vermeij (1987) for Mesozoic shallow-water gastropods in soft bottoms. Based on repaired injuries, however, turrilline gas-

tropods show an apparent stability in predation frequencies since the Late Cretaceous (Allmon et al., 1990), and a real, increasing trend in shell repair with time is questioned by Cadée (1999). In general, shell repair is much more rapid in terrestrial than in aquatic molluscs, is faster at the shell edge than in the central region, and is influenced by environmental parameters (for a review on the physiological aspects of shell regeneration, see Watabe, 1983). The presence of scars does not adversely affect crushing resistance (Blundon and Vermeij, 1983) and sometimes even seems to increase shell strength (Checa, 1993).

3.1.1.5. Anti-predatory strategies. The main anti-predatory strategies among fast-moving prey are behavioral avoidance, whereas camouflage or mimicry, communal, chemical or morphological defenses predominate among slow-moving or sessile organisms (Stanley, 1977; Kohn, 1999; Smith and Jennings, 2000). Certain molluscs (mainly gastropods) use their shell as a weapon against predators. Some limpets, for example clamp their shell down on the foot of predatory snails (Branch, 1979; see Vermeij, 1993 for more examples). Many molluscs receive protection from hosts, including cnidarians (e.g., epitoniids, architectonicids, ovulids, coralliophilids), sponges (triphorids, cerithiopsids, siliquariids), echinoderms (e.g., eulimids), mantis shrimps (*Caledoniella* and some leptonoids), ascidians (*Musculus*), and other molluscs (pyramidellids) (for details and more examples see Vermeij, 1993). Spatial refuges for prey are generally harsh physical environments outside the tolerance range of the predators (Seed and Hughes, 1995). Examples are the high intertidal zone, where prey organisms are safe from benthic marine predators (e.g., Beal et al., 2001; Hiddink et al., 2002) but not from birds (e.g., Sutherland et al., 2000), or any region with fluctuating or extreme salinity (Seed and Hughes, 1995). Other types of spatial refuges are structurally complex habitats such as seagrass meadows (see Peterson, 1982 for references) or mussel beds (e.g., Dolmer, 1998). Also, very low and very high population densities are an effective refuge for many infaunal molluscs (for references, see Seed and Hughes, 1995), and for infaunal bivalves, burrowing more deeply increases safety against predators (Blundon and Kennedy, 1982; Kvittek et al., 1988; Edelaar, 2000) but at the cost of reduced feeding efficiency (de

Goeij and Luttikhuisen, 1998). Morphological defenses are of primary interest for palaeontologists because they can be easily recognized in fossils. They are either constitutive or induced (Kohn, 1999), that is, they are either the result of selection among genetically determined, fixed phenotypes in the population (Vermeij, 1983a,b; Seeley, 1986) or are induced within an individual's lifetime (Havel, 1987; Stearns, 1989; Tollrian and Harvell, 1999; Leonard et al., 1999; Smith and Jennings, 2000). For details on morphological defenses, see Section 4: Shell strength and its role for fragmentation.

3.1.1.6. Spatial trends in predation. Large-scale geographical trends are evident. Shell-breaking predation is more common in marine than in freshwater environments. Among the latter, only Lake Tanganyika contains heavily armored gastropods and specialized shell-crushing crabs (West et al., 1991; Vermeij, 1993). Tropical intertidal and shallow subtidal faunas are more specialized for attack and defense than those in temperate and polar regions (for review, see Currey, 1988). For example, anti-predatory morphological features (spines, ribs, thick shells and narrow apertures) are increasingly common toward the tropics (Vermeij, 1978, 1993; Palmer, 1979; Vermeij and Currey, 1980; for Palaeozoic examples see Leighton, 1999; Dietl and Kelley, 2001). Moreover, compared to temperate snails, tropical snails move very little or hide when submerged because of more intense predation (Bertness et al., 1981). Crabs, teleosts and rajids are very important shell-crushing predators in the tropics, but unimportant or even absent from Antarctica. Durophagous predation is comparatively important in the arctic region for reasons that are probably very complex, including faunal isolation and seasonality in productivity (for review, see Aronson and Blake, 2001). Predation by birds seems to be more intense in temperate (see Bertness et al. 1981, for references) and polar areas (e.g., Cadée, 1999) than in the tropics. Repair frequency depends on the ability of the prey to survive an attack as well as on predation frequency (see Section 3.1.1: Shell repair). Based on shell repair, latitudinal gradients of shell-crushing predation can therefore only be assessed within a broadly distributed taxon, but not with assemblages of different species composition, as was outlined by Dietl and Kelley

(2001). In contrast, drilling intensity seems to increase with increasing latitude, albeit with very high spatial variability on the local and regional scale (Hoffmeister and Kowalewski, 2001), because the drillers themselves are less prone to shell-crushing predation in higher latitudes (for review, see Aronson and Blake, 2001).

Shells in the tropics are more robust and stronger because of higher predation intensities, although higher water temperature (Graus, 1974), which makes it energetically less costly to lay down shell than in cold water (Dawkins and Krebs, 1979), and higher evolution rates (Rosenzweig, 1995; Flessa and Jablonski, 1996) may also play a role. Vermeij (1979) speculates that on a regional scale, interspecific differences in vulnerability to breakage are related more to overall shape, whereas on a larger geographical scale, structure may be more important. Nacreous and other organic-rich shells are especially common today in polar regions, the deep sea, and fresh water, whereas energetically cheaper microstructures with highly mineralized shells predominate in warm seas (Vermeij, 1976, 1993). Beyond the above latitudinal trends, longitudinal differences may exist: several crab genera (*Carpilius*, *Eriphia*, *Ozius*), for example, have larger and more robust claws in the western Pacific and in the Indian Ocean than in the Eastern Pacific, which in turn contains more robust species than the Atlantic Ocean (Vermeij, 1976, 1993). It is difficult, however, to translate increasing size and robustness into greater crushing force, because maximum muscle stress declines with increasing claw size (see Taylor, 2001 for details and references).

The few studies of deep-water faunas initially led to the impression that predation is more common in shallow than in deeper environments. The deeper shelf to deep sea are frequently considered to provide a refuge for relicts of Palaeozoic faunal elements and for invertebrates lacking predatory defenses (for overviews, see Vermeij, 1987; Aronson and Blake, 2001). A potential onshore origination of Mesozoic durophagous predators eliminated epifaunal suspension-feeding communities from shallow-water soft-substratum habitats and replaced them by infaunal and mollusc-dominated communities (Jablonski and Bottjer, 1983, 1990; but see Smith, 1994 for a critique of this view). On a macroecological scale, for example, the Mesozoic marine revolution caused a global decline of

dense ophiurid and stalked crinoid associations in coastal habitats (see Aronson and Blake, 2001 for review). New data on shell repair, distinct breakage patterns and shell-crushing predators, however, suggest that deep-water communities are also strongly influenced by predation (Quetglas et al., 2001; Vale and Rex, 1988, 1989; Voight, 2000a, 2000b; von Rützen-Kositzkau, 1999; Walker, 2001; Walker and Voight, 1994; Walker et al., 2002).

3.1.1.7. Temporal trends in predation. Large- and small-scale temporal trends in durophagous predation can be differentiated. With increasing predation, gastropod shell morphology changes within a relatively short time (e.g., West et al., 1991). Three Phanerozoic trends provide evidence for an increase in predation-induced fragmentation during geological time: (a) the radiation of shell-breaking predators, (b) an increase of breakage-induced shell repair, and (c) an increase in morphological characteristics that resist breakage (e.g., Vermeij et al., 1981). In addition, increasing durophagous predation can lead to a reduction in prey abundance over geologic time (Aronson and Blake, 2001).

The oldest mineralized skeletons are of Ediacaran age and their widespread appearance at the base of the Cambrian can most probably be related to increasing predation pressure (for short discussion see Conway Morris, 2001). The increase in predation through the Phanerozoic (Papp et al., 1947; Hutchinson, 1961; Stanley, 1977; Vermeij, 1977; Signor and Brett, 1984) can probably be related to increasing nutrient supplies and productivity, either from an increase in diversity and biomass of vegetation on land or from submarine volcanism (Vermeij, 1995; Bambach, 1999). Shell-breaking predators probably existed in the Early Paleozoic, but the first rapid radiation of durophagous predators (placoderm and chondrichthyan fish and phyllocarid and eumalacostracan arthropods) occurred in the mid-Devonian (Signor and Brett, 1984). Triassic shell-breaking predators included placodont reptiles and cephalopods with calcified jaws. The second major episode of diversification, known as the Mesozoic marine revolution, began in the Jurassic and continued into the Palaeogene (Vermeij, 1977) and resulted in a marked decrease of dense ophiuroid populations, stalked crinoids and brachiopods in shallow-water environments (e.g., Aronson, 1989). The Jurassic was marked by the appearance of brachiuran

crabs, palinurid spiny lobsters, stomatopods, batoid rays, pycnodont holostean fishes and birds. In the Cretaceous, ichthyosaurs and mosasaurs developed the shell-crushing life habit and the Palaeogene was characterized by an explosive diversification of shell-breaking crabs and acanthopterygian teleost fishes (for reviews, see Vermeij, 1983a, 1987). Crabs and fish are probably the most important shell-breaking predators in modern marine environments (e.g., Vermeij, 1978; Palmer, 1979; Bertness and Cunningham, 1981; Cate and Evans, 1994). The above trend is also paralleled by a strong increase in drilling predation since the Cretaceous (Kowalewski et al., 1998) and corresponds well to a change from epifauna-dominated benthic assemblages in the Palaeozoic and early Mesozoic to infauna-dominated assemblages in the Cretaceous and Cenozoic (Signor and Brett, 1984; Vermeij, 1977). The increasing infaunalization in the Triassic, however, could be independent from the expansion of

major predatory groups. Instead, it might be related to other interconnected abiotic and biotic causes associated with the recovery after the end-Permian mass extinction (McRoberts, 2001).

3.1.2. High energy

Storm events are frequently suggested as a major source for fragments in the fossil record (e.g., Skelton et al., 1995; Sanders, 1996; Lukeneder and Harzhauser, 2002) and Seilacher (1973, Fig. 6) suggested that breakage on a rocky shore will largely follow radial and concentric shell structures (Fig. 6). Impact of rolling and water-borne rocks on shelled organisms is probably very common but has not been well documented (Strathman, 1981). The few reports do show that wave-borne rocks or ice blocks can produce strong fragmentation (Bulkley, 1968; Shabica, 1971; Raffaelli, 1978; Blankley and Branch, 1985; Shanks and Wright, 1986; Cadée, 1999) and may result in

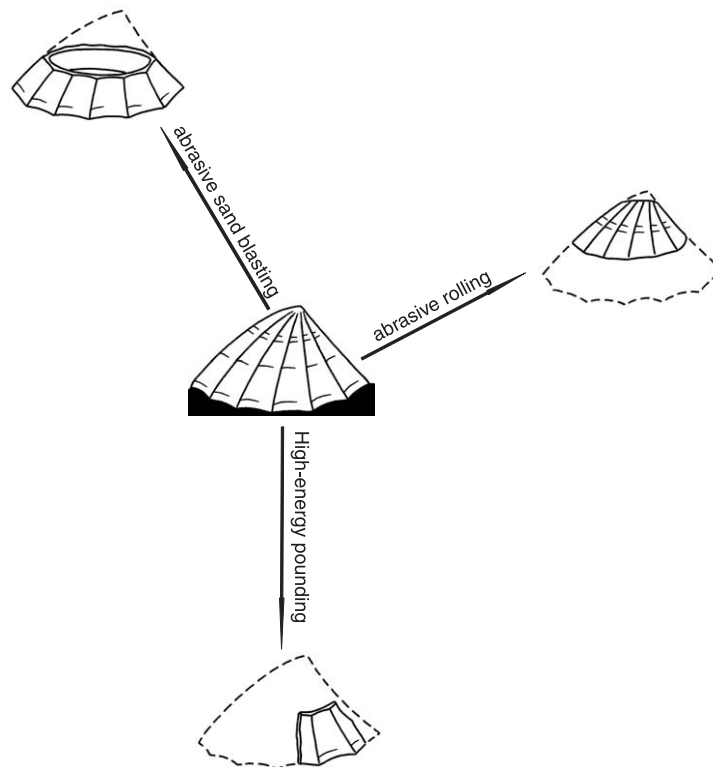


Fig. 6. Limpets as an example of shell breakage. Abrasion by sand blasting (shell remains fairly stable) affects the exposed shell parts. Rolling along the sediment surface will mainly abrade the free edges. Pounding on a high-energy rocky shore, in contrast, is assumed to follow radial and concentric shell structures (modified after Seilacher, 1973).

repaired damage that probably cannot be distinguished from breakage due to crushing predation (Cadée, 1999). Branching, reef-associated corals are typically affected by fragmentation, as commonly observed after storms (Lirman, 2000).

3.1.3. Bioturbation

Some authors (Parsons and Brett, 1991, p. 41; Brenchley and Harper, 1998, p. 72; Bradshaw and Scoffin, 2001, Fig. 1) suggest that in quiet, offshore environments fragmentation is correlated with, and presumably attributable to bioturbation; i.e., organismic activity that alters existing sediment structures and can produce traces. However, we were unable to find any case studies that would support this assumption.

Checa (1993) proposed that shell damage in deep-endobenthic bivalves occurs during rapid burrowing to escape predators and readjustment after storm-induced changes in the sediment column (Fig. 7). Similarly, Alexander and Dietl (2001) suggest that ventral repairs among deep infaunal bivalves such as *E. directus* may have been induced by sediment-loading stress during burrowing. Checa (1993) explicitly excludes a predatory origin for damage in these deep burrowers because breakage characteristics diagnostic of predation are absent and because the bivalves are not directly accessible to predators. In burrowing experiments with these bivalves, damage along the rims showed that chips were frequently retained by the periostracum (Checa, 1993). Burrowing experiments with (comparatively) thick-shelled *Glycymeris glycymeris* in sand did not result in shell damage, but this might be expected in coarser grained, gravelly sediment (Ramsay et al., 2001). Coarse-

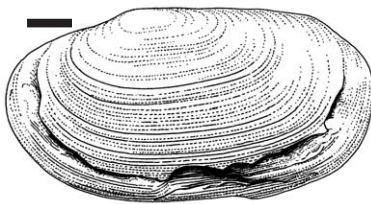


Fig. 7. Repaired breakage morphology in the deep infaunal bivalve *Lutraria lutraria*. Shell damage is interpreted to result from rapid burrowing to escape predators and readjustment after storm-induced changes in the sediment column. Scale bar is 1 cm (redrawn after Checa, 1993).

grained substrate is reported to cause fractures in *M. mercenaria*, which sometimes burrows in sediment rich in shell hash (Alexander and Dietl, 2001). Checa's (1993) results, however, are in strong contrast to those of Wainwright (1969), who concluded that there was no shell strain during the burrowing process, even under severe adduction, unless an object was placed between the valves.

3.1.4. Anthropogenic influences

In samples of living benthic communities and in actuopalaeontological studies, the influence of commercial fisheries on faunal structure and on the condition of shelly organisms should not be underestimated (e.g., Bergman et al., 2002; Pranovi et al., 2001). The problem may be compounded by the difficulty in differentiating between damages caused by fishing activities or natural disturbances (Ramsay et al., 2001). In the North and Irish Seas, for example, fishing intensities are high and the bottom may be trawled as much as 5–10 times per year (Ball et al., 2000). Beam and otter trawls are known to heavily impact macro- and megafaunal benthic populations (e.g., Ramsay et al., 2001). On the soft sublittoral sediment bottoms in the Northern Adriatic Sea, for example, trawling can crush *Pecten jacobaeus* shells and shears off the tops of the pen shell *Atrina pectinata* (Fig. 4 in Kollmann and Stachowitsch, 2000). Subsequent trawling tends to snag the serpulid tube worms that grow on the dead shells, dislodging and further damaging them severely (Fig. 8 in Stachowitsch and Fuchs, 1995). Elsewhere, contact with trawl doors and tickler chains led to high direct mortalities of bivalves, whereby more robust species (*Corbula*, *Astarte*) suffered less damage. The more vulnerable species were either fragile (*Macra corallina*) or lived in the uppermost layer of the sediment (*Spisula* sp.) (Bergman and van Santbrink, 2002). Discarded bivalves and gastropods or disturbed, damaged or moribund molluscs in the swath of fishing gear attract predators and scavengers (Groenewold and Fonds, 2000), no doubt further altering the natural proportion of damaged and undamaged shells.

Physical disturbances by ship groundings cause huge amounts of coral fragments (e.g., Bruckner and Bruckner, 2001; Riegl, 2001 for coral communities) but we are not aware of data for shelled organisms.

3.2. Biostratinomic processes

Biostratinomic processes (i.e., post-mortem, pre-burial processes) can either weaken or directly fragment shells (see also Section 4.2: Shell strength in relation to taphonomic features). Abrasion, bioerosion and dissolution are treated here, although they may already occur in living organisms (e.g., Cummins, 1994; Mao Che et al., 1996), and the latter also occurs during diagenesis (when total loss or replacement of the original shell is the rule) (e.g., Brachert and Dullo, 2000; Cherns and Wright, 2000). Experimental studies suggest that the above agents are more effective when acting together (Kotler et al., 1992), but the effects of mechanical abrasion, microboring, and corrosion (i.e., major degree of dissolution after Davies et al., 1989 that is evident from very soft shell surface, loss of sculpture and presence of many pittings) are difficult to distinguish in fossils. Therefore, the use of the term *corrasion* was suggested to indicate the general state of wear in shells resulting from any combination of these processes, and provides a general index of exposure time (Brett and Baird, 1986; Brett, 1990; Parsons and Brett, 1991). Experimentally deployed shells demonstrate that, during the first 2 years of exposure, biostratinomic fragmentation is quantitatively unimportant and primarily restricted to edge chipping (Callender et al., 2002; Lescinsky et al., 2002).

3.2.1. Abrasion

Several authors (Pratje, 1929; Schäfer, 1962, Fig. 98; Seilacher, 1973, Fig. 6; Cadée, 1999, Fig. 9) have proposed that abrasion by sand blasting and by rolling, each produces distinctive and diagnostic fragments which can be distinguished from high energy pounding (Fig. 6). Savazzi (1991, Fig. 11n), for example, suggested that the numerous small indentations along the outer lip of thin-shelled living (repaired) and dead (unrepaired) strombid shells were produced by storm events.

Experimental tumbling of regular echinoids completely breaks the corona into small fragments within a few days to weeks, depending on temperature (Kidwell and Baumiller, 1990). Driscoll and Weltin (1973) concluded from tumbling experiments that abrasive mollusc shell reduction (with “fragments” as end products of abrasion) is important only on surf-

washed beaches because even after simulation of hundreds of kilometers of transport many specimens were still identifiable to the species level (compare also Hollmann, 1966). An experiment by Kontrovitz (1967) with ostracod valves yielded similar results. In accordance with these laboratory studies, abrasion was much less important on experimentally deployed shells in Bahama (shelf to slope) and in the shallow-water Java Sea than dissolution and bioerosion (Callender et al., 2002; Lescinsky et al. 2002). The effectiveness of abrasion is controlled by grain size and sediment sorting (abrasion is inversely correlated with sorting and is greater in fine and coarse versus medium sand) (Driscoll and Weltin, 1973). Little is known about the resistance of the various shell microstructure types to abrasion: homogeneous structure seems to be most resistant, followed by crossed lamellar and nacreous microstructures (Carter, 1980; Gabriel, 1981; Currey, 1990).

3.2.2. Bioerosion and dissolution

In intertidal and shallow sublittoral environments, boring marine organisms are the primary agent of shell destruction (Driscoll, 1970; Cutler and Flessa, 1995); their importance increases with productivity and decreases with higher sedimentation (Lescinsky et al., 2002). In these shallow marine environments, the diversity of micro- and macroborers is usually high and includes cyanobacteria, fungi, sponges and bivalves (e.g., Cobb, 1969; Feige and Fürsich, 1991; Kleemann, 1996; Mao Che et al., 1996; Scoffin and Bradshaw, 2000; for many more references, see Radtke et al., 1997). Encrusting organisms, however, may strongly inhibit bioeroders (Henderson and Styan, 1982; Smyth, 1989; Cadée, 1999). Endolithic fungi are important bioeroders in the deep sea (e.g., von Rützen-Kositzkau, 1999) and constitute a potentially significant food source for scraping organisms, which enhance shell destruction (Poulicek, 1983). With increasing water depth and in higher latitudes, dissolution is also very important (Alexandersson, 1979; Cutler and Flessa, 1995) and is known to produce fragments in foraminifera (Stuut et al., 2002). Flessa and Brown (1983) and Callender et al. (1992) have proposed that for shells lying on the sea floor, dissolution reduces shell weight (carbonate loss) and shell sculpture and produces edge rounding. Dissolution and bioerosion were important tapho-

onomic processes affecting experimentally deployed shells on the Bahama shelf and slope, but varied significantly between environments and species, and affected different shell areas to different degrees (Callender et al., 2002; Staff et al., 2002). However, if fragmentation occurs, then the shells are maintained in recognizable condition only by the periostracum (Callender and Powell, 1992; Callender et al., 1994). In contrast, Walker et al. (1998) found that encrustation rather than bioerosion was a dominant pattern on gastropod shells bagged and tethered for 1 year on the Bahama shelf and slope.

3.3. Diagenetic processes and tectonic strain

Diagenesis and tectonic strain can result in flattening and shear deformation of fossils. Flattening is a consequence of compaction during sediment accumulation and diagenesis. Shear refers to distortions of shape caused by differential stresses due to tectonic movements, which include sedimentary folding and slumping (Hughes, 1999).

3.3.1. Compaction

Compaction affects mineralized skeletons in two ways and may markedly affect the morphology of fossils (Briggs, 1990; Hughes, 1999): Rigid exoskeletons fracture (“brittle fractures”) due to overburden pressure, confining pressure (from the adjacent sediments) and internal stresses, whereas plastic deformation occurs in skeletons that have lost rigidity through diagenesis, e.g., through loss of organic matrix (Fig. 8). Thus, the composite materials of shells (see Section 4.1.4: Microstructure) dramatically change their properties after the organic matrix has decayed away, yielding different levels of vulnerability to compaction. On the other hand, the great flexibility of prismatic layers in inoceramid bivalves enabled plastic deformation already during early biostratinomic phases, as interpreted from a puncture by a belemnite rostrum (Stilwell and Crampton, 2002).

Cracks in fossil skeletons indicate that the fossils accommodated compaction by brittle fracture, and such broken fossils are among the most common criteria for the recognition of compaction in limestones (Meyers, 1980; Flügel, 1982, p. 89; Clari and Martire, 1996; Grütznier and Mienert, 1999; Kendall, 2000; Gnoli, 2002; Melim et al., 2002, p. 41). Fracture

patterns, however, vary among fossil groups, but the effects of flattening have rarely been systematically studied (Hughes, 1999). Some studies analyzed the effects of flattening using bivariate comparisons between variables, for example length and width (e.g., Ferguson, 1962; Webster and Hughes, 1999). This approach allows the patterns of variation in this bivariate relationship to be referred to the a priori known direction of maximum deformation—usually in the vertical or *z*-dimension (Hughes, 1999). Few other studies on flattened fossils applied multivariate techniques to landmarks on fossils, mostly by analyzing their geometric relationships (e.g., Hughes, 1999). The multivariate approach allows to evaluate the overall effects of deformation on fossil form, both in the vertical dimension and in the bedding or *xy*-plane (Hughes, 1999). Hughes’ (1999) study on Silurian trilobites shows complex deformation patterns yielding very different patterns of fracturing among different specimens. Nevertheless, certain unifying themes are evident: (a) the degree of deformation is strongly related to size: smaller specimens suffered less deformation than larger ones and (b) some skeletal components tend to deform as integrated units (see Hughes, 1999 for a detailed discussion).

Shell fragmentation induced by compaction should be controlled by mechanical shell strength and by extrinsic factors such as sediment grain size, burial orientation, nature and timing of diagenesis, whether cavities within the shell are open or filled by sediment or cement (Müller, 1979; Briggs, 1990), and particularly by shell dissolution and cementation. Early cementation of the sediment prevents compaction and related fragmentation; concretions may either prevent fragmentation when they include the fossil (Fig. 8) (e.g., Anderson, 1997; Huggett et al., 2000), or enhance fragmentation and deformation when they underlie the fossil (Seilacher et al., 1976).

Experimental studies on breakage of shells and abiogenic components (mainly ooids) during compaction have been carried out in wet systems (Kontrovitz, 1967; Fruth et al., 1966; Bhattacharyya and Friedman, 1979, 1984; Shinn et al., 1977; Shinn and Robbin, 1983), dry systems (Rex and Chaloner, 1983; Zuschin and Stanton, 2001) and under air pressure (Brenner and Einsele, 1976). Even though some of the experimentally compacted sediments strongly resembled real rock, it is probably impossible to reproduce the effect

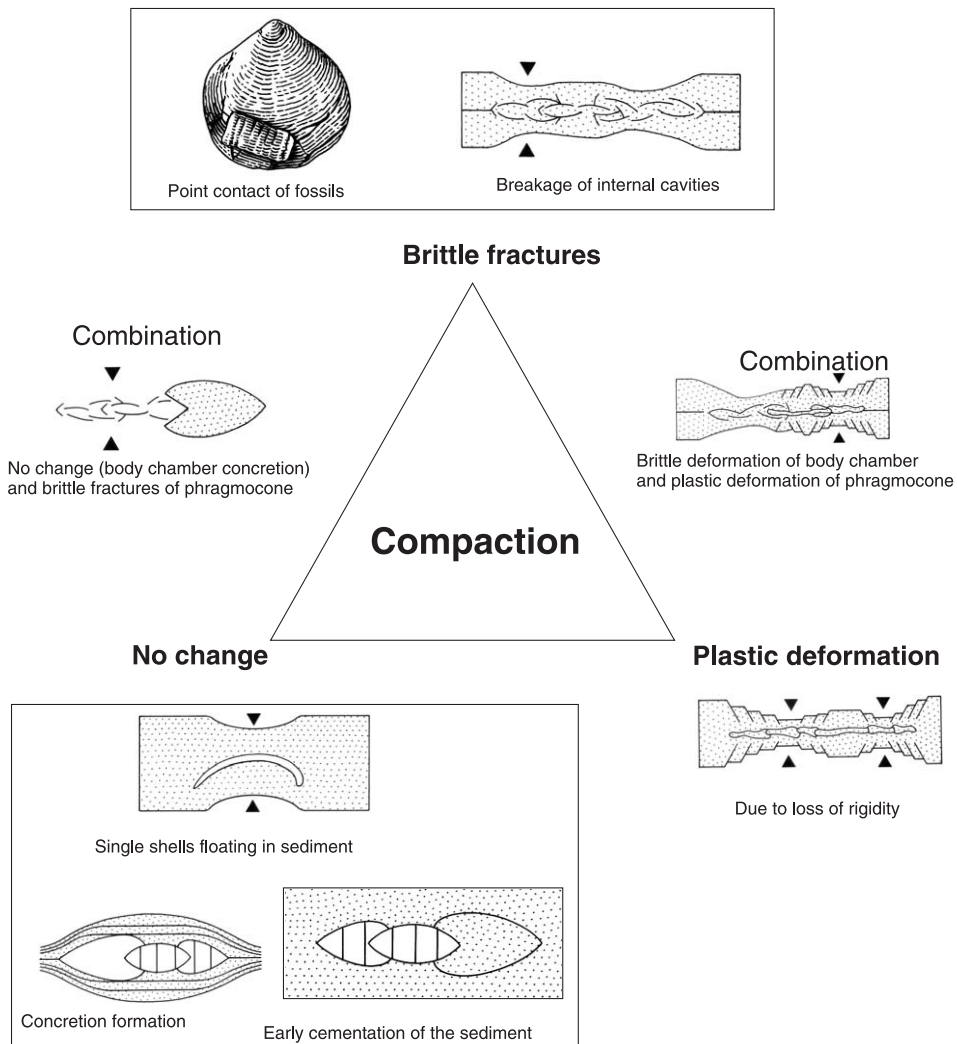


Fig. 8. The effects of compaction on the morphology of fossils. Morphology may remain unchanged in single shells floating in the sediment because the lack of point contacts prevents fragmentation. The fossil is still rigid and therefore does not respond to increasing pressure with plastic deformation. Early cementation of the sediment or concretion formation can leave shells unaffected by compaction, especially fossils with internal cavities (e.g., cephalopods). Brittle deformation occurs in rigid exoskeletons. Here, point contacts increase (e.g., crinoid element on brachiopod shell) the likelihood of fracturing, but single shells with internal cavities (e.g., cephalopods) may break without point contacts. Plastic deformation occurs in skeletons that have lost rigidity through diagenesis. Combinations of the above processes can occur in one and the same fossil and reflect the different strengths of various shell parts (e.g., early brittle deformation of the weaker body chamber and later plastic deformation of the stronger phragmocone of cephalopods) or selective diagenesis (e.g., early formation of body chamber concretion and brittle deformation of the phragmocone of cephalopods). Recombined after [Seilacher et al. \(1976\)](#) and [Elliott and Bounds \(1987\)](#).

of an overburden load of hundreds of meters of sediment on hard parts because the rate of experimental loading is orders of magnitude greater than the strain rate in nature ([Shinn and Robbin, 1983](#)). Another difficulty in experimental approaches is to determine the exact flow path of escaping fluids during compac-

tion (e.g., [Shinn and Robbin, 1983](#)). The experiments suggest that lateral expansion during compaction is generally limited due to constraint by the confining sediment ([Briggs and Williams, 1981](#); [Rex and Chaloner, 1983](#)). Most deformation related to flattening is therefore in the vertical dimension ([Hughes, 1999](#)).

The common view is that compaction-induced breakage is likely only when sediment grain size is large relative to shell size (Dodd and Stanton, 1990). The above experiments, however, show that this view fails to consider that coarse-grained sediments are more resistant to compaction because of the supporting effect of the grains and the lower pore-water volume (Briggs, 1990). Fine-grained sediments, in contrast, retain large amounts of water and compaction occurs as a result of water movement and related pore-volume reduction (Shinn and Robbin, 1983; Briggs, 1990). In experiments with wet and dry sand (<0.5 mm), embedded shells could not be broken by compaction unless they were buried less than about 3–5 mm deep (Klähn, 1931). This was mainly due to the strong adhesion between sand grains, but also to the edge effect at the margin of the cylinder, which prevented significant deformation of the embedded organisms (Klähn, 1931; Rex and Chaloner, 1983).

In contrast to sand samples, muddy sediments can be reduced in volume by 50% or more at pressures that simulate about 100 m of burial; higher pressure does not significantly increase compaction. During compaction, skeletal material rotated towards the horizontal plane as a response to stress, but remained largely intact, probably because mud and interstitial water act as a single fluid, effecting an isotropic force on a skeletal element. Deformation was rare and breakage mainly occurred when shells were in direct contact with each other or with coarser grains; smaller skeletal particles resisted compaction more readily than larger ones (Shinn et al., 1977; Shinn and Robbin, 1983). The importance of point contacts during compaction is emphasized in studies on lime mud compaction (Fruth et al., 1966; Bhattacharyya and Friedman, 1979) and is mirrored in crushing experiments, in that breakage patterns typically radiated from the point of loading. A perfect fit between artificially ground valves and the underlying surface after selectively removing irregularities (=point contacts) yielded extraordinarily strong shells (Zuschin and Stanton, 2001). In nature, this is supported by the compaction-induced breakage recorded from Pennsylvanian brachiopods that closely adjoin each other or other skeletal elements, such as of crinoids (Fig. 8, top left) (Elliott and Bounds, 1987). Similar features are frequently observed in microfacies analysis of limestones (see Fig. 16B) (Meyers, 1980; Flügel, 1982). Without specimen-to-specimen contact,

shell deformation during compaction tends to yield distorted shell forms accompanied by subtle fractures and corrugations that are most readily recognized in thin sections (Ferguson, 1962, Plate 22 and Fig. 1). Exceptions to this rule may include the ammonites. Here, fragments commonly develop along reinforced structures throughout the shell without specimen-to-specimen contact (e.g., keel fractures, umbilical fractures) (Seilacher et al., 1976; Alexander, 1986b). Strength differences in these shells result in two phases of compaction and breakage: phragmocones, which are supported by septa, are very strong, whereas the body chamber collapses easily. On the other hand, the body chamber may be selectively preserved if it is filled with sediment or within a concretion (Fig. 8). Compaction accompanied by shell dissolution results in wrinkling deformation (Seilacher et al., 1976). Compactional fragmentation of ostracod valves also indicates differences in resistance between taxa (Kontrovitz, 1967).

The lack of compaction-induced fragments is commonly interpreted as the lack of any compaction (see Shinn et al., 1977 for short discussion), but experiments clearly show that fragmentation can be minimal even when the sediment thickness is reduced by 50% or more (Shinn et al., 1977; Shinn and Robbin, 1983). Note that shells demonstrably broken by compaction are good evidence that sufficient compactional pressures were reached before the sediment was consolidated (Brenner and Einsele, 1976).

Because most reports on compaction-induced fragmentation are observational (e.g., Wignall and Myers, 1988) and because this process is a key factor in certain deposits, quantitative studies need to be performed. A case in point are the Miocene Korytnica Clays in Poland: fragmentation is fairly uniform throughout the basin and not restricted to the thinnest parts of valves (Hoffman, 1976; Kowalewski, 1990). These authors exclude environmental energy and transportation because the fragments are generally sharp edged; they consider breakage by scavengers or predators to be unimportant because the intensity of such biotic damage would have varied from sample to sample.

3.3.2. *Shear*

Rocks can undergo multiple tectonic phases, but fossils rarely survive more than a single phase of

shear-deformation. The direction of simple shear can be determined by the orientation of cleavage and from the shape of the deformed fossils (see Hughes, 1999 for overview). Deformed fossils are generally valuable tools for the tectonic interpretation of rocks (Ramsay and Huber, 1983; Lloyd and Ferguson, 1988; Cooper, 1990) but the major palaeontological application is the investigation of the taxa present within such samples (e.g., Bambach, 1973; Sadler, 1974; Hughes and Jell, 1992) and the restoration of their original form (Doveton, 1979; Briggs and Williams, 1981; Rushton and Smith, 1993; Motani, 1997; for review, see Hughes, 1999).

3.4. Sampling and post-collection fragmentation

Any sampling method, but especially bulk sampling, probably increases the numbers of fragments in modern death assemblages and fossil assemblages. Quantitative studies on this topic, however, are lacking. Samples used for taphofacies analysis should be taken with a uniform method to minimize the resulting biases.

Post-collection transport can increase the numbers of fragments considerably for fragile shells, whereas robust shells remain largely unaffected; shells stored at the bottom of a shipping box are more affected than those on the top (Flessa et al., 1992).

Powell et al. (1989) suggested that taphonomically altered shells are particularly prone to breakage during collection.

4. Shell strength

Strength is a crucial aspect of fragmentation (Wainwright, 1969). One can differentiate between inherently strong and inherently weaker shells, fragmentation along weakest (or most vulnerable) parts of strong shells, or decreased strength in taphonomically weakened shells.

Shell strength is an adaptation to stresses and the result of selection among genetically determined phenotypes in the populations (Vermeij, 1983a,b; Seeley, 1986); it can also be ecophenotypic, induced within an individual's lifetime (Havel, 1987; Stearns, 1989; Palmer, 1990b; Tollrian and Harvell, 1999; Leonard et al., 1999; Smith and Jennings, 2000; Reimer and

Harms-Ringdahl, 2001). Stress is a measure of the intensity of force (measured in Newtons) per unit cross-sectional area (Currey, 1990). Stresses are of two main types: (1) static, for instance sediment pressure and water movement and (2) dynamic, for instance impact loading by pebbles and rocks, or biogenic interactions (Taylor and Layman, 1972).

The resistance of a shell to breakage should depend to some extent on its strength, which can be divided into three major types and has been studied in taphonomic experiments.

1. Strength has been defined as maximum compressive force required to break a shell (Fig. 9) (Whatley et al., 1982; LaBarbera and Merz, 1992; Kidwell and Baumiller, 1990; Roy et al., 1994; Miller and LaBarbera, 1995; Zuschin and Stanton, 2001).
2. Toughness is the total physical work (in energy or time) necessary to break a shell (Fig. 9) (Kidwell and Baumiller, 1990; Miller and LaBarbera, 1995; Smith et al., 1999).
3. Toughness (sensu Currey, 1977, 1988) is a measure of the ability of a microstructure to stop cracks from forming or, if they have formed, to prevent them from extending (Fig. 10).

The first aspect is relevant to all causes of fragmentation; the second is especially important for

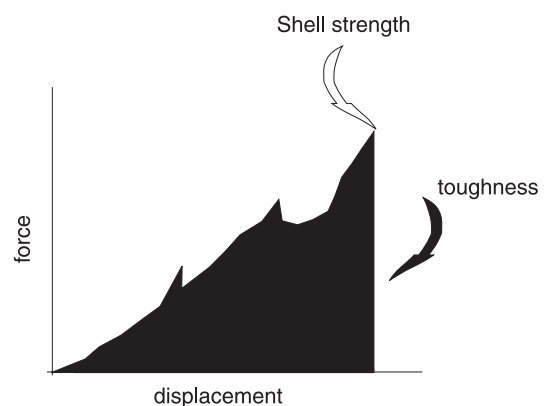


Fig. 9. Shell strength is measured as the maximum force at failure and is relevant to all causes of fragmentation. Shell toughness is the black area under the force–displacement curve and is a proxy for a predator's metabolic costs (modified after Kidwell and Baumiller, 1990).

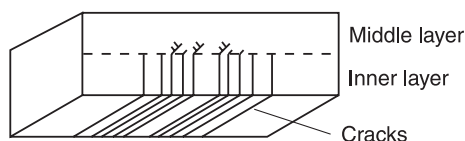


Fig. 10. Microstructure-toughness refers to the ability of a microstructure to stop cracks from forming or extending. Here, the cracks travel immediately to the junction of the inner and middle layer, but invade the middle layer only with difficulty (redrawn after Currey and Kohn, 1976).

predation-induced breakage and may be a useful and easily obtained proxy for the predator's metabolic costs (Miller and LaBarbera, 1995); the third aspect is relevant to the effects of skeletal microstructure on fracture propagation (see Currey, 1990 for detailed information).

Shell strength depends upon many shell features, such as size, microstructure, shape, thickness and ornamentation, whose individual contributions are extremely difficult to evaluate (Taylor and Layman, 1972; Whatley et al., 1982; Kontrovitz et al., 1998). Consequently, when measured experimentally it appears to be highly variable (Fig. 11) (see also Figs. 2 and 3 in Buckley and Ebersole, 1994; Fig. 6 in Pechenik et al., 2001; Fig. 3 in Zuschin and Stanton, 2001; Fig. 3 in Saunders and Wehmann, 1977; Figs. 1 and 2 in Roy et al., 1994; Table 1 in Alexander, 1990b; Fig. 1 in LaBarbera and Merz, 1992; Fig. 4 in Blundon and Vermeij, 1983; Fig. 5 in Daley, 1993; Fig. 6a in Cote et al., 2001). Similarly, resistance to mechanical force in reef corals is highly variable and can be related to colony morphology (colony height, branch thickness, branch spacing, colony area) (Fig. 3 in Marshall, 2000).

The great variability in the data sets no doubt reflects the multifunctionality of a shell (e.g., Savazzi, 1991; see also Whatley et al., 1982), which must not only be strong or stiff, but also encloses the soft tissue, bores into various substrata or acts as a buoyancy tank (Currey, 1988). Moreover, shells are seldom subject to a single type of predator or environmental stress (Sih et al., 1998) and therefore have to adopt diverse anti-predatory defenses. Bivalved animals for example can prevent shell-margin damage by (1) commissural protection through inequivalve condition or development of spines that project well beyond the line of contact between the valves, (2) mantle retraction, and

(3) globose shell form (for review, see Vermeij, 1983b). Rather than being the prime descriptor of a shell's resistance, strength is thus a compromise among a multitude of functions and can only be adequately evaluated for a species in relation to its life habit and ecological needs (Zuschin and Stanton, 2001). Vermeij (1993, p. 122), however, speculates that great variation of experimentally measured shell strength among shells of similar mass and thickness can be related to the (unpredictable) presence and frequency of tiny cracks in the shell wall (see also Klähn, 1931, p. 452; Whatley et al., 1982).

4.1. Shell strength in relation to shell parameters

Early point-load experiments already revealed a relation between resistance to breakage and shell thickness (Papp et al., 1947, p. 302) as well as highly variable within-taxon (e.g., Klähn, 1931) and between-taxon differences in crushing-resistance (e.g., Kontrovitz, 1967 for ostracods). Any attempt to quantify and interpret strength must consider physical shell parameters of the studied taxa. These can be metric dimensions such as size measurements (length, width, height, volume) and thickness, or nominal and ordinal categories such as shape, microstructure and sculptural

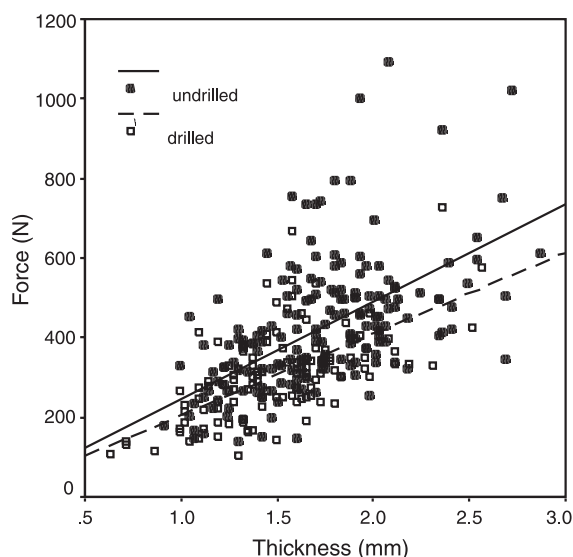


Fig. 11. Shell strength (= force) as a function of thickness for drilled and undrilled *Anadara*. Samples are significantly different (redrawn after Zuschin and Stanton, 2001).

features. Note that differences between left and right (or upper and lower) valves can occur (e.g., Daley, 1993 for brachiopods), and that drying or heating may influence a shell's resistance (Gaffey et al., 1991; Wainwright, 1969).

4.1.1. Size (length, width, height, volume)

One of the most commonly cited factors in the ecology and taphonomy of shelled organisms is shell size. This factor is typically expressed as length, width and height, or less frequently as volume or mass. This section focuses on shell size in general.

Although a shell's strength is typically correlated with its size (e.g., LaBarbera and Merz, 1992; Miller and LaBarbera, 1995; Cote et al., 2001), the correlation with its thickness is stronger, probably because thickness is a better defense against breakage (see Section 4.1.2: Thickness): it increases more with predation intensity than shell size (for discussion and references, see Smith and Jennings, 2000). Therefore, crushing experiments, which are not related to a particular predator–prey system, show that strength is better predicted by thickness than by size (Currey, 1988; Alexander, 1990b; Zuschin and Stanton, 2001).

In contrast, experimental and empirical studies that focus on particular predator–prey systems show that large size can be an effective anti-predatory defense and that the frequency of repaired injury increases with shell length (for review, see Vermeij, 1983a). Thus, for example, rapid growth to achieve a large size relative to predators is apparently a principal defense of strombid gastropods against peeling predation (Savazzi, 1991). This is also an example of a size refuge or critical size—the size above which an organism is safe from predation by a particular predator (e.g., Paine, 1976; Hughes and Elner, 1979; Jeffries and Lawton, 1984; Cadée, 1989). But ecological and behavioral considerations such as energy content, search time and handling time may supercede simple size–strength considerations, as is emphasized in optimal foraging theory (Hughes, 1980; Stephens and Krebs, 1986). In particular, the following aspects show that the concept of size refuges from predators can be difficult to interpret:

(1) For any given combination of predator and prey, there is some size at which the probability of

successful predation declines, but there is no sharp cut off (Palmer, 1990a).

- (2) Large prey is also very attractive because it provides more energy when eaten and in some cases the largest sizes are removed selectively (Peterson, 1982; Currey, 1988; Kvitek et al., 1992; Zwarts and Blomert, 1992). Larger prey size can be included in the diet as the predator grows (Juanes, 1994).
- (3) Paine (1963) pointed out that size differences between predator and prey per se are protective, not necessarily size increase of the prey, and that both very big and very small prey may be uninteresting to a given predator. Examples of the protective small size of gastropods are discussed in Kohn (1999). Similarly, selective preservation of small molluscs during destructive feeding occurs (Boucot, 1981; Chao, 1973; Cate and Evans, 1994; Cadée, 1995).
- (4) Many predators (e.g., fish, decapods, isopods) prefer molluscan prey well below the critical size that they could handle (Boulding, 1984; Juanes, 1992, 1994; Ejdung and Elmgren, 2001) because size selection is related to the optimal allocation of time or energy spent searching for and handling prey (Werner and Hall, 1974). In feeding experiments, crabs usually preferred size classes of molluscan prey that were far below this critical size, probably as a compromise between maximizing energy intake and minimizing handling time and the risk of claw damage (Seed and Hughes, 1995). For example, handling time increases, albeit unpredictably, with prey size (Boulding, 1984; Eggleston, 1990; Cote et al., 2001).
- (5) Prey may also have an effective refuge in size well below the critical size if alternative, more vulnerable species are simultaneously available to the predator (Seed and Hughes, 1995). As the optimal shell size becomes depleted, crabs choose progressively larger and smaller individuals than the optimal size (Elner and Hughes, 1979).
- (6) Predators may change their foraging strategy with increasing prey size (e.g., Eggleston, 1990, Schindler et al., 1994). For example, *Littorina littorea* which are small enough to fit within the gape of the claw of *Cancer pagurus* are crushed, whereas larger snails are peeled back from the

aperture (Lawton and Hughes, 1985). Similarly, small *M. mercenaria* are crushed by the crab *Neopanope texana*, whereas larger bivalves are chipped at the shell margin (Landers, 1954).

- (7) Shell sizes (modal size, median size, size range) of northeastern Pacific bivalves are invariant along a latitudinal gradient (Roy et al., 2000), although predation pressure increases towards the tropics (see Section 3.1.1: Spatial trends in predation).

4.1.2. Thickness

Shell thickness, which may be a constitutive (=genetically determined) or induced defense mechanism is probably the most reliable defense against crushing and peeling predators (Currey, 1988; Kohn, 1999; Zuschin and Stanton, 2001). Thickening may involve the entire shell, only the last whorl or only a terminally thick outer lip; a special type of thickening is the formation of projecting knobs and varices (Kohn, 1999).

A thick shell is an obvious defense against breakage because thicker shells are stronger, less likely to be dislodged, more difficult to be manipulated by predators and less likely to be attacked by a boring predator (Vermeij, 1983a, p.653; Currey, 1988; but see Dietl, 2000). Carter (1968) suggested that greater thickness inhibits predation by crabs, boring gastropods and crushing fish. For example, many predators selectively attack thinner-shelled prey. This is the case for the gastropod *Busycon* feeding on bivalves (Carriger, 1951; Paine, 1962), and for predatory fish feeding on bivalves (Blegvad, 1930) and on thin-shelled, more easily dislodged juvenile brachiopods (Rudwick, 1970, p. 161). Thickness is probably the factor that limits the ability of stomatopods to break or spear a shell (Geary et al., 1991; Pether, 1995) and thicker outer lips of gastropods prevent crabs from successfully breaking open the aperture (Papp et al., 1947; Vermeij, 1982). These observations are supported by a wealth of experimental case studies:

- Shell strength (in tension, compression, bending) increases with the square of its thickness (Currey, 1980; Currey and Hughes, 1982; Kohn, 1999). Although a shell's strength also increases with its size (see Section 4.1.1: Size), it is better predicted by its thickness (Currey, 1988; Alexander, 1989, 1990a,b; Zuschin and Stanton, 2001). Specifically:

A shell of a particular size increases its strength primarily by thickening the shell wall (e.g., Currey and Hughes, 1982; Cook et al., 1986), although predator-dependent trade-offs between increased thickness and size exist (Smith and Jennings, 2000; Trussel and Nicklin, 2002).

- Intense predation (e.g., by crabs or fish) yields stronger shells due to thicker walls or thicker lips for a given size, both on the ecological and evolutionary scale (Currey and Hughes, 1982; Cook et al., 1986; Palmer, 1990b; Reimer and Harms-Ringdahl, 2001). This is even true of those molluscs whose predators (e.g., sea stars) leave the shell largely unaffected (see Carter, 1968 for review). For example, *Mytilus edulis* develops larger adductor muscles and thicker, more rounded shells when raised in the presence of the sea star *Asterias rubens* (Reimer and Tedengren, 1996).
- Thickness also provides a defense against shell-boring predation because greater wall thickness increases the drilling time and the drillers' own risk of predation (for discussion and more references see Smith and Jennings, 2000). Therefore, for a given prey size, thicker specimens are less likely to be completely drilled than thinner ones by predators of the same size (Kitchell et al., 1981; Dietl and Alexander, 1995).

Many other examples support the role of shell thickness. In cephalopods, shell strength increases with increasing wall and septum thickness (Daniel et al., 1997). In general, repair following unsuccessful predation yields a thicker and stronger shell at the damaged site, which can be regarded as an individual adaptation (Checa, 1993). Shell stiffness is also proportional to thickness in scallops (Pennington and Currey, 1984). When crushed, the thicker posterior parts of brachiopod shells remain unfragmented (unpublished experimental data cited in Emig, 1990).

Nevertheless, shell strength as a function of thickness is highly variable and thickness therefore cannot simply be interpreted as an adaptation against breakage (Fig. 11). It may provide greater stability as indicated by the fact that epifaunal, attached bivalves are often thinner than their shallow-burrowing infaunal relatives, which may be susceptible to storm scour and transportation (Stanley, 1970; Wainwright et al., 1982).

4.1.3. Shape

Shell architecture must profoundly affect strength and a mollusc's resistance against lethal breakage. This factor is not well understood because comparing shells of distinctly different shapes is very difficult (Currey, 1988). On a regional scale, interspecific differences in vulnerability to breakage have been tentatively related to overall shape (e.g., Vermeij, 1979), and selection due to predation may create a bias towards origination of sturdier morphologies within a clade, e.g., aporrhaid gastropods (Roy, 1994). In gastropods, narrow or small apertures, well-developed apertural teeth, thickened varices and high-spired turreted shells appear to be good defenses against peeling predation, and globular compact shapes are more resistant against crushing than loosely coiled ones (Papp et al., 1947; Vermeij, 1983a; Palmer, 1990a,b; Savazzi, 1991). The presence of an umbilicus decreases strength because adjoining parts are unsupported by previous coils and are therefore susceptible to catastrophic breakage. The umbilicus is therefore frequently replaced by a callus or by the formation of high-spired shells (Vermeij, 1993, p.127). The latter often also have narrow apertures. Crabs large and strong enough to do so, however, break such shells across the spire (Zipser and Vermeij, 1978). Other effective defenses of the aperture include projections from the rim, folds at the columella and tightly fitting opercula (e.g., Stanley, 1982; Vermeij, 1993).

Experimentally measured strength in extant brachiopods is significantly correlated with valve-biconvexity (Alexander, 1990b). This may explain why biconvex Ordovician brachiopods were apparently stronger (low frequencies of repair and only localized damage due to unsuccessful predation) than concavo-convex forms, which showed extensive damage (Alexander, 1986a). In the bivalve *Anadara*, valves are strongly arched from dorsal to ventral margin and bear strong radial ribs. These architectural features may enhance crushing strength and thus reduce dependence on shell thickness and microstructure (Zuschin and Stanton, 2001). Limpet shapes provide protection only as long as the shell fits perfectly against the surface of the hard substratum (Lowell, 1987), and damage along the margin is frequent (Cadée, 1999).

Hinge teeth and serrations along the free margin of valves reduce shear. Projecting edges (in corbulids, some arcids and pectinids) can prevent damage of the

seal between valves, and interdigitating ribs across the slightly gaping valves (e.g., some cardiids) protect the soft parts. The risk of serious damage is strongly reduced by the ability to withdraw soft parts from the growing margin in most gastropods and scaphopods, and in a few bivalves. Very smooth and slippery gastropods without periostracum (e.g., Cypraeidae, Olividae, Marginellidae) appear to inhibit manipulation by some predators (mostly crabs) (Vermeij, 1993; Kohn, 1999).

Cephalopod shells can be interpreted as a series of domes, each supported by the junctions of the internal septa with the shell wall (Jacobs, 1990). The evolution of septal complexity has usually been regarded as an adaptive response to compressive stress imposed by hydrostatic pressure, with increasing complexity indicating greater habitat depth (e.g., Westermann, 1975; Hewitt and Westermann, 1987; Jacobs, 1990). Daniel et al. (1997), however, showed that complexly sutured forms were not better adapted to withstand high hydrostatic pressures (and therefore water depth) than forms with simple cap-shaped septa. Rather, complexly sutured forms were better able to compensate for abrupt changes in buoyancy, suggesting that this complexity may have been an adaptation to avoid predation by improving mobility and the ability to compensate for sudden shell loss due to predators (Daniel et al., 1997; Kröger, 2002).

4.1.4. Microstructure, organic matrix and crystal size

Molluscan shells have a variety of different microstructures that influence strength. They originally probably arose as a consequence of simultaneous calcium carbonate precipitation and the formation of the organic matrix. Subsequently the selective advantage—perhaps involving shell strength—stabilized this arrangement (Taylor, 1973). Mollusc shells are composite materials consisting of crystalline calcium carbonate, nearly exclusively in the crystallographic form of calcite or aragonite (the density of calcite being 7% lower than that of aragonite), together with a largely proteinaceous organic phase, the matrix. The matrix is a relatively minor component, rarely exceeding 5% by weight of the total shell (Currey and Taylor, 1974; Currey and Kohn, 1976; Carter, 1980; Palmer, 1983; Currey, 1990).

Microstructure strength is in part determined by the organic material content, which serves as an elastic,

strength-enhancing mortar (Currey and Taylor, 1974; Currey, 1988, 1990). This adhesive matrix holds the stiff components (the mineral fraction) together and also keeps them apart, preventing blocks large enough to contain dangerously long cracks (Currey, 1990; Smith et al., 1990). Organic material is comparatively abundant in nacreous shells (Taylor and Layman, 1972; Currey and Taylor, 1974) and also very expensive to produce (Palmer, 1983). Apart from the matrix, the periostracum and conchiolin layers are important organic shell components. The periostracum enhances shell flexibility and serves as a chip-retaining structure, minimizing shell loss (e.g., Checa, 1993; Callender et al., 1994; Cate and Evans, 1994). Thickened periostracum effectively protects against drilling predators in the Mytiloidea (Harper and Skelton, 1993), as do conchiolin layers in corbulid bivalves (e.g., Lewy and Samtleben, 1979; Harper, 1994). The conchiolin layers also increase strength and toughness by acting as crack stoppers (Kardon, 1998) and their decomposition weakens the shell mechanically after death (Lewy and Samtleben, 1979).

Shell microstructures are much stronger in compression than in tension: it is easier to break shells by pulling than by pushing (Vermeij, 1993). Organic matrix separates the crystallites so that cracks in the brittle crystallites have to expend energy passing through the presumably much more pliant matrix in order to propagate. Cracks in nacreous and prismatic structure travel either in the matrix (nacreous and prismatic) or between the matrix and the mineral (nacreous only). This probably absorbs considerable energy (Currey and Taylor, 1974; Currey, 1977). Crossed-lamellar structure is generally much weaker than nacreous structure although its strength is highly anisotropic and its arrangement of crystallite layers allows a certain degree of crack stopping (Kamat et al., 2000); homogeneous material is the weakest and very brittle due to its low organic content (Currey and Kohn, 1976; Currey, 1988). On the other hand, homogeneous and crossed-lamellar structures resist abrasion very well (Gabriel, 1981). The fracture characteristics of other structural types are less well known.

Foliated calcite, which occurs only in epifaunal bivalves, is relatively weak (Currey and Taylor, 1974) and has a very low resistance against drilling and abrasion (Gabriel, 1981). In compensation, however, it permits the construction of mechanically sturdy

arches and folds in pectinids (Waller, 1972). Oyster shells, which are almost entirely foliated and very weak, do not crack cleanly, but folia flake and splinter off (Currey and Taylor, 1974) and they are more likely to localize the area of damage resulting from strong point impacts (Taylor and Layman, 1972; Carter, 1980). Some calcitic shells of oysters, several sedentary Pectinacea and Hippuritacea have evolved cavities that may limit the spreading of incipient cracks (Carter, 1980), and pockets of crumbly chalky calcite are possibly very effective in absorbing the stress that would otherwise fracture the shell (Currey and Taylor, 1974).

The combination of prismatic and nacreous microstructure in pinnaceans deflects vertical fractures along the interlayer boundary; this results in extensive fracturing of the outer prismatic layer and a largely intact inner nacreous layer (Taylor and Layman, 1972, Fig. 4 in Carter, 1980). Prismatic material is weak but can be produced very quickly; combined with sufficient organic material it is very flexible (for example, at the shell margins of many pinnaceans and pteriacans) (Currey, 1990; Stilwell and Crampton, 2002). Moreover, prismatic microstructure effectively resists drilling predation (Gabriel, 1981).

Crystal size may have some influence on strength because thaidid gastropods with coarse, well-defined crossed-lamellar structure are significantly more resistant to crushing than those with fine, indistinct crossed-lamellar structure (Vermeij and Currey, 1980).

The anisotropic shell microstructure of strombid gastropods seems to preferentially propagate cracks parallel to the aperture rather than perpendicular to it, which is interpreted as a protection against peeling crabs (Fig. 11k in Savazzi, 1991).

Nacreous microstructure is the phylogenetically oldest and mechanically strongest of all microstructures (Taylor and Layman, 1972; Taylor, 1973; Currey and Taylor, 1974; Currey, 1976, 1977, 1988; Evans et al., 2001). Why, then, were any other structures evolved (Taylor and Layman, 1972; Taylor, 1973)? The seven separate evolutionary trends in bivalve shell structure (Taylor, 1973) indicate that a number of factors other than strength and stiffness are involved.

- (1) Multifunctionality: The shell serves to enclose the soft tissue, it bores into various substrata or may

act as a buoyancy tank (Currey, 1988). Correspondingly, the life habit of bivalves is correlated with microstructure (Taylor and Layman, 1972). Epifaunal (byssate, cemented) bivalves possess combinations of prismatic and nacreous or foliated structures. In contrast, most burrowing bivalves have combinations of crossed lamellar and complex crossed lamellar structures (for more detailed information see Taylor and Layman, 1972). Weaker crossed lamellar structures occur in bivalves with massive shells, whereas stronger crossed lamellar structures occur in burrowing bivalves (Currey and Taylor, 1974).

- (2) Cost: The shell has to be produced quickly and, metabolically speaking, cheaply (Palmer, 1983). This latter requirement is better met by the predominant but weak cross-lamellar structure than by nacre (Currey and Taylor, 1974). For example, gastropods with a higher fraction of skeletal organic matrix (e.g., nacreous structure) regenerate shells more slowly than do gastropods with a lower fraction (e.g., crossed-lamellar structure) (Palmer, 1983). As the cost of calcification is less than 1/7 to 1/30 that of protein synthesis, the evolutionary trend in molluscs (and brachiopods) to lose microstructures with high organic content seems reasonable (Palmer, 1983).

Moreover, most gastropods with shells rich in organic matrix belong to rather slow-moving species, which indicates a trade-off between high costs of organic-rich shells and high costs of locomotion. The presence of nacre is also mostly coincident with small individuals, which may be more susceptible to predation from a greater variety of would-be enemies than are larger individuals (Vermeij, 1983a,b).

Although microstructure is an important determinant of strength, other parameters may be equally or more important in resisting breakage. For example, nacreous microstructure (*Mytilus*) is mechanically much stronger than crossed-lamellar microstructure (*Anadara*), and homogeneous microstructure (*Mercenaria*) is the weakest and very brittle due to its low organic content (Taylor and Layman, 1972; Currey and Taylor, 1974; Currey and Kohn, 1976; Currey, 1976, 1977, 1988). These strength relations, however, are only partly reflected in shell-crushing experiments (Zuschin and Stanton, 2001). As expected, for a given

valve thickness, both *Mytilus* and *Anadara* are much stronger than *Mercenaria*, but *Mytilus* is weaker than *Anadara*. The *Anadara* valve, however, is more strongly arched from dorsal to ventral margin and possesses strong radial ribs, which probably enhances its crushing strength. This indicates that the primary importance microstructure can be overridden by gross morphological characteristics, as was also suggested by Vermeij (1979).

4.1.5. Sculptural features—spines and varices

Sculptural features influence the toughness aspect of strength (Fig. 9). The few studies on larval shells of planktotrophic gastropods show that apertural beaks, velar notches, peripheral angulations, and continuous spiral elements of shell sculpture retard mechanical breakage at the growing apertural margin and afford effective protection in predatory confrontations with zooplankton (Hickman, 1999, 2001). Most case studies, however, deal with adult shells.

In adult shells, spines have a variety of functions, including support on soft substrata, anchorage in shifting substrata, a sensory early warning system, and predator deterrence (for a short overview and references, see Leighton, 2000). As a predator deterrent, spines protect epifaunal bivalves and brachiopods from drilling predation by gastropods (Stone, 1998; Leighton, 2001) or may provide suitable sites for protecting/camouflaging epibionts (Vance, 1978; Feifarek, 1987). Probably more important, however, is the protection from durophagous predators. Experimental studies show that the spines, nodes and varices of bivalves and gastropods effectively thwart crushing predators, especially fish, by increasing the effective shell diameter, distributing stress over larger areas, localizing stress at the thickest parts, increasing the potential damage to a predator (Palmer, 1979) and greatly increasing the total work necessary to break a shell (Bertness and Cunningham, 1981; Miller and LaBarbera, 1995). Strombid shells possess varices reinforcing the early whorls, which are interpreted as a periodic strengthening of the aperture against peeling predators (Savazzi, 1991). Sculptural features counteract bending when a compressive force is applied to convex outer surfaces. Continuous bending increases the risk that the inner shell layer will fail under tension, before the outer shell layer does so in compression, because the shell as a whole is much

stronger in compression. Sculptural features that reduce bending therefore impart strength (Vermeij, 1993, p. 125).

Palmer (1979) regards spines as primarily, if not exclusively, effective against shell-crushing fish rather than crabs: spines would be effective in the latter only if the spiral distance between spine tips was distinctly less than the breadth of the molars of crushing claws. In fact, spines could even give crabs a better grip. Moreover, spines offer little defense against crabs that peel starting at the aperture (Palmer, 1979). In this context, strombid shells possess varices reinforcing the early whorls, which are interpreted as a periodic strengthening of the aperture against peeling predators (Savazzi, 1991).

Spines probably have an anti-predatory function in other groups as well: the dramatic increase of rugosity among Mesozoic nautiloids and ammonoids is suggested to help prevent breakage by predators (Ward, 1981; Bardhan and Halder, 2000). For extant brachiopods, Alexander (1990b) showed that strength is significantly correlated with ribbing and, in Devonian and Mississippian forms, that spines served more to protect against predation than for anchoring in soft substrate (Alexander, 1981; Leighton, 2000). Also, strong corrugations and/or plications apparently increased shell strength in Ordovician, Mississippian and Triassic brachiopods (Westermann, 1964; Alexander, 1981, 1986). In echinoids, spines may also protect the tests from impact failure by absorbing energy and spreading the impact over a broader area (Strathman, 1981). In star fish, spines and granules probably help protect against breakage by predation (Blake, 1990). Spines in bryozoans deter feeding by nudibranchs (e.g., Yoshioaka, 1982; Iyengar and Harvell, 2002).

The advantage of sculpture over thickness lies (1) in reduced metabolic costs: evenly distributing the material in the spines would probably not provide equal protection and (2) in more rapid growth: uniformly thick shells require more time to attain a given length than a thin-shelled animal of similar shape (Palmer, 1979; Pennington and Currey, 1984; Savazzi, 1991).

4.2. Shell strength and taphonomy

Taphonomic, i.e., post-mortem, processes reduce strength (Brenner and Einsele, 1976; Westermann and

Ward, 1980; Kaesler et al., 1993) and can promote fragmentation (Powell and Davies, 1990). As the post-mortem interval increases, the number of fragments can increase with the same energy input (see Daley, 1993 for experiments with brachiopods).

4.2.1. Decomposition of organic shell components

During a mollusc's life, the organic matrix acts as a template for mineralization and provides elasticity and strength; after death it protects the mineral components of the shell from diagenetic effects (Clark, 1999). Although the organic matrix initially protects crystallites, its progressive decomposition increases vulnerability to crystallite-by-crystallite disintegration; as a microbial substrate the organic content also appears to promote dissolution and microboring (Glover and Kidwell, 1993; Freiwald, 1995). This makes shells with very high matrix content extraordinarily resistant during the animal's lifetime, but also extremely vulnerable to fragmentation after death. For example, Zuschin and Stanton (2001) show experimentally that fresh *Mytilus*, which has an organic-rich nacreous inner layer, is resistant to fragmentation. The organic material rapidly degrades in seawater, however, markedly decreasing strength (compare also unpublished data of LaBarbera, cited in LaBarbera and Merz, 1992). In contrast, *Mercenaria* consists of brittle crossed lamellar and homogeneous shell layers, which are organic-poor (Currey and Kohn, 1976; Currey, 1988): exposure to seawater did not decrease strength (Zuschin and Stanton, 2001).

Post-mortem reduction in strength and toughness is more rapid in warm than in cold water because organic decomposition is temperature dependent (Kidwell and Baumiller, 1990). Anaerobic is slower than aerobic decomposition (Kristensen et al., 1995), but anoxia in itself does not prevent this decomposition (Plotnick, 1986; Allison, 1988; Kidwell and Baumiller, 1990). By excluding scavenging organisms, however, anoxia may indirectly reduce fragmentation rate. Matrix degradation is very slow after burial, even in fairly permeable sediments; it probably occurs largely before burial. Matrix preservation potential is illustrated by fossil mytilids, dating back as far as the Pennsylvanian, which have a better-preserved organic matrix than their modern counterparts (Clark, 1993, 1999). The specific style of disintegration of rudists (especially radiolitids) into fragment-like, radial fun-

nel plates (attached valve) and ostracal and hypostracal portions (free valve) was probably induced or aided by discontinuities in the shell structure, most importantly the presence of organic membranes that decomposed post-mortem (Sanders, 1996). These fragments in a broad sense are the major component of a widespread platform-margin facies (the “calcarei saccaroidi”) of the Upper Campanian to Maastrichtian of the Apennines (Mutti et al., 1996; Vecsei, 1998). Brachiopod valves with high amounts of organic components undergo rapid degradation and disappear completely within a few weeks to several months (e.g., *Lingula* and *Glottidia*) or disintegrate into crystalline calcitic fibers (*Terebratulina*). Only the thicker posterior parts of three-layered brachiopods (*Gryphus*) remain in the sediment for several years, whereas the thinner anterior parts fragment mechanically into small pieces (Emig, 1990).

There is a crucial difference between pre- and post-mortality resistance to breakage. At neither time does skeletal mineralogy clearly influence the resistance of skeletal materials to breakage and abrasion, but microstructure and disposition of organic matrix play a role: In living forms the organic matrix increases strength, whereas in dead shells, the loss of the matrix, through decay (Glover and Kidwell, 1993; Freiwald, 1995), lowers skeletal durability (e.g., Chave, 1964) and shell strength (Lewy and Samtleben, 1979; LaBarbera and Merz, 1992; Zuschin and Stanton, 2001) (see also Section 4.1.4: Microstructure).

4.2.2. Drill holes

Drilling predation by gastropods (for reviews, see Carriker, 1981; Kabat, 1990; Reyment, 1999) has been used to estimate post-mortem breakage because gastropods do not drill empty shells (but see Dietl and Alexander, 1995) or those occupied by hermit crabs (Vermeij, 1982). The latter author showed that less than 10% of “lethal breakage” can be related to post-mortem artifact. The underlying assumptions of this approach are that the preservation potential of drilled and undrilled shells is not significantly different (e.g., Dudley and Vermeij, 1978) or that taphonomic biases can be identified (Kornicker et al., 1963; Kowalewski, 1990).

Nevertheless, drill holes may significantly bias the fossil record in ways that are difficult to quantify: (1) differences in transportability and thus accumulation

of drilled and undrilled shells (Lever et al., 1961), (2) preferential destruction of undrilled shells by crushing predators (Vermeij et al., 1989), and (3) preferential loss of drilled shells by post-mortem breakage due to reduced strength (Fig. 9) (Roy et al., 1994; Pechenik et al., 2001; Zuschin and Stanton, 2001). Note, however, that drilled shells were significantly weaker than undrilled counterparts only in point load experiments but not under compactional load in a dry system, where contact between shells was recognized as the critical factor (Zuschin and Stanton, 2001). This is supported by studies which show that hermit crabs avoid damaged and drilled shells (Abrams, 1980; Pechenik and Lewis, 2000), probably because they are weaker and more vulnerable to crushing and peeling (Pechenik et al., 2001).

Patterns of drilling predation in fossil assemblages will in most cases therefore be taphonomically biased records of the original biological signal: they underestimate predation intensity (Roy et al., 1994). The proportion of drilled shells, however, can also be overestimated when shell-crushing predation is important but cannot be recognized, or when broken valves are specifically neglected (Vermeij et al., 1989).

4.2.3. The role of hermit crabs

Among the variety of secondary inhabitants (e.g., amphipod and tanaid crustaceans, octopuses, sipunculids) that potentially influence the palaeoecological and taphonomical information provided by gastropod shells, hermit crabs are by far the best studied (Walker, 1990). Experimental and empirical studies showed that hermit crab-inhabited shells are weaker than those occupied by the living snail (Rossi and Parisi, 1973; McLean, 1983; Walker, 1988; LaBarbera and Merz, 1992) because hermit crabs have no mechanism to repair or maintain their housings (LaBarbera and Merz, 1992). A great variety of crushing predators (e.g., spiny lobsters, crabs, stomatopods, bony fish, and elasmobranchs) feed both on shells inhabited by hermit crabs and living snails (for references, see LaBarbera and Merz, 1992). Therefore, the evolution of hermit crabs yielded not only more potential prey items for durophagous predators, but may also be responsible for the frequently observed attacks on shells too large for such predators to crush (e.g., Vermeij, 1977; Wainwright, 1987; LaBarbera and Merz, 1992). Hermit crabs, however, sometimes try

to minimize the risk and preferentially shun or exchange damaged or drilled housings (Abrams, 1980; McClintock, 1985; Pechenik and Lewis, 2000). Moreover, hermit crab-occupied shells are preferentially taphonomically altered (encrusted, bored) (Ehrenberg, 1931; Stachowitsch, 1977, 1980; Walker, 1992; Taylor, 1994; Zuschin and Piller, 1997; Creed, 2000). Note that encrustation may slow or compensate the decrease of shell strength (Stachowitsch, 1980) and that some epigrowth such as sea anemones protects against predation (McLean, 1983). At the same time, the presence of shell-boring organisms (e.g., endolithic algae, sponges, polychaetes) greatly reduces shell strength (Kent, 1981b; Fig. 3 in Buckley and Ebersole, 1994).

5. Breakage patterns

Not all shells fragment in the same manner and the resulting patterns can provide information about vulnerable parts and about specific breakage mechanisms. In this section we propose to distinguish various categories of fragmentation (repaired versus unrepaired and diagnostic versus non-diagnostic), to classify them descriptively according to their appearance, to record them in terms of location on the shell or to summarize fractures in sketches, and to relate breakage patterns to shell parameters; we then discuss the interpretative gain of this approach (Fig. 12).

5.1. Repaired and unrepaired injuries

Regardless of the fragmentation process, damaged valves can be sorted into repaired and unrepaired injuries (e.g., Alexander, 1981, 1986b). The former necessarily were caused by non-lethal damage and yield characteristic scars (e.g., Figs. 4 and 7 in Papp et al., 1947; Fig. 4 in Nielsen, 1975; Fig. 1 in Vermeij, 1983b; Figs. 3–5 in Savazzi, 1990; Fig. 11 in Savazzi, 1991) (see also Section 3.1.1.4: Shell repair). Unrepaired injuries, in contrast, represent both lethal and post-mortem damage, which are difficult to separate.

Unrepaired damage can be differentiated into diagnostic and non-diagnostic features. The latter can be sorted into severe crushing, involving large parts of the shell, and localized damage (Fig. 12) (Alexander, 1981; Elliott and Bounds, 1987).

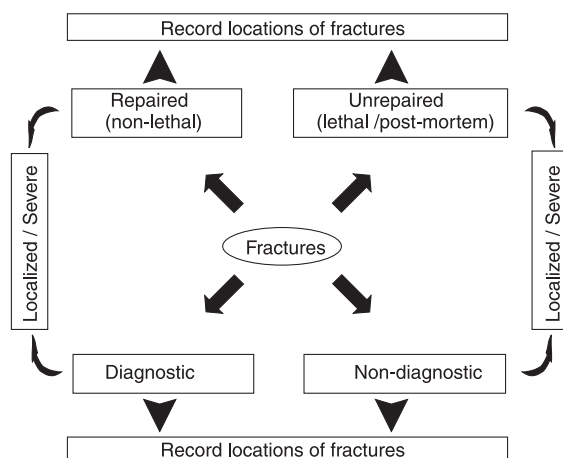


Fig. 12. Breakage patterns should be distinguished into repaired and unrepaired and into diagnostic and undiagnostic fractures. Any of these categories can consist of localized or severe damage and the location of the fractures should be recorded.

However, apart from repaired shells, fragmentation due to ecological processes (including predation, impact of rocks and ice blocks) is difficult to recognize in death assemblages/fossil assemblages: resistance to lethal damage by durophagous predators often cannot be assessed because the prey was fragmented and or digested beyond recognition in the preserved shell hash (Bishop, 1975; Alexander, 1981, 1986a). Therefore, fossil shells were probably broken by predators if:

- (1) the sediments indicate no physical disturbance (e.g., storms, turbidity currents) or diagenetic effects such as compaction (Kauffman, 1972; Vermeij, 1983a; Watkins, 1991),
- (2) there is good evidence for shell repair (see Section 3.1.1: Shell breaking predation and shell repair),
- (3) potential durophagous predators are present in the assemblage (e.g., Brunton, 1966; Sarycheva, 1949; Cadée, 1968; Kauffman, 1972; Bishop, 1975),
- (4) macro- or micro-scale predation scars can be detected on skeletal elements (Fig. 14G) (Norton, 1988; Checa, 1993; Neumann, 2000; Heithaus et al., 2002),
- (5) fragments are present in regurgitates, gastroliths and coprolites (Kauffman, 1972; Bishop, 1975; Trewin and Welsh, 1976; Watkins, 1991; Sato and

- Tanabe, 1998) or characteristic shell middens produced by octopus (Ambrose, 1983; Walker, 1990; Dodge and Scheel, 1999),
- (6) bivalves are found with one valve broken but with the ligament still present (Fig. 3L) (Cadée, 1968, 1995, 2000).

Compaction-induced breakage can be easily confused with fragmentation by predation. Good indirect evidence for a predominance of the former is a lack of repaired damage (e.g., Elliott and Bounds, 1987) and the co-occurrence of fragments in the rock approximately in their original relative position (Fig. 16) (Dodd and Stanton, 1990).

Case studies that successfully differentiated between several breakage processes for similar taxa are rare. For Miocene sand dollars, however, Nebelsick (1999a) was able to differentiate between lethal predation (hollowed out central areas), non-lethal predation (cusped irregularities of the ambitus) and compactional fragmentation (radial cracking and skeletal implosion) of the test.

5.2. Diagnostic unrepaired shell damage

Sources of breakage can be identified if they result in fragments with distinctive, source-dependent breakage patterns. In crushing experiments with *Littorina irrorata*, cracks typically spread along the suture and/or were parallel to growth lines (Blundon and Vermeij, 1983). Primary fractures in the brachiopod *Terebratalia transversa* followed the plane of maximum convexity (Daley, 1993). In other experiments, however, very heterogeneous breakage patterns result even if the force is applied consistently at the same location (Fig. 26 in Klähn, 1931; Fig. 4 in Kaesler et al., 1993; Fig. 7 in Zuschin and Stanton, 2001). Variation in breakage will clearly be even greater in nature because predators will not always apply forces at the same position and foraging strategy changes with prey size (crushing in small individuals versus peeling and chipping in larger individuals) (e.g., Landers, 1954; Lawton and Hughes, 1985). Ontogenetic changes in shell-crushing behaviour of predators can also be expected (compare Urrutia and Navarro, 2001). Recognizing the cause of fragmentation based on breakage patterns is therefore extremely difficult.

Small bite traces (diameters much less than 1 mm) with irregular outline are produced by the cottid fish *Asemichthys*, which is able to puncture shells (mostly of gastropods) with its morphologically specialized vomer (an element of the neurocranium) (Norton, 1988). Similar, but distinctly larger (diameters ranging from 2 mm to more than 2 cm) and more regular punctures preserved in the skeletons of various Pennsylvanian invertebrates (conularids, nautiloids and ammonoids) and in Cretaceous ammonoids are interpreted as bite traces of predatory cladodont sharks and mosasaurs, respectively (Mapes and Hansen, 1984; Mapes et al., 1989, 1995; Kauffman, 1990); such fossil finds are considered to be good indicators for crushing predation (Fig. 13) (e.g., Bishop, 1975). This view, however, was recently challenged. In point load experiments, mosasaur robots either fragmented *Nautilus* shells into many angular pieces or produced indistinct angular holes (Kase et al., 1998). Therefore, the round to oval perforations in the Cretaceous ammonites were reinterpreted as diagenetically modified limpet home scars (Kase et al., 1998; for discussion, see Tsujita and Westermann, 2001). Similarly, based on crushing experiments, distinctive crescentic margins (Fig. 13B) are rather unlikely to indicate fish predation as was suggested by Boyd and Newell (1972).

Nevertheless, some damage patterns are very distinct and are clearly attributable, sometimes even to a specific predator (Fig. 14) (traces of predation sensu

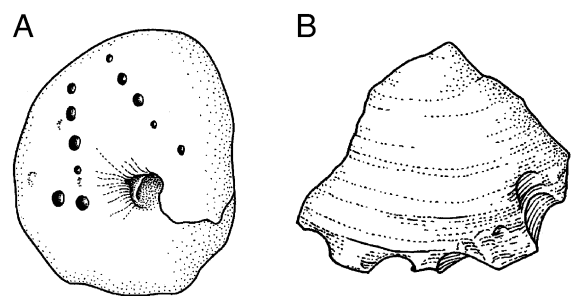


Fig. 13. Doubt has recently been cast on whether “bite traces” indicate predation because comparable point load experiments shatter shells (Kase et al., 1998). (A) Round to oval perforations found on Cretaceous ammonites were considered as direct evidence for mosasaur-predation but were recently reinterpreted as diagenetically modified limpet home scars (redrawn after Kauffman and Kesling, 1960). (B) Accordingly, distinctive crescentic shell margins are rather unlikely to indicate fish predation (redrawn after Boyd and Newell, 1972).

Bishop, 1975). Crabs, stomatopods, lobsters and crayfish peel back the apertural margin of gastropods in a characteristic way (Papp et al., 1947; Schäfer, 1962; Bertness, 1982; Vermeij, 1993). But seabirds, such as the eider duck, produce very similar breakage patterns in their gizzard (Schäfer, 1962), and similar patterns may even be caused by waves dashing shells against a rocky substrata (Fig. 239 in Schäfer, 1962). Smashing stomatopods produce very typical, subcircular to irregular holes (diameters 5–25 mm) with sharp edges, which are not accompanied by a scar or hole on the opposite side of the gastropod shell (Bertness, 1982; Geary et al., 1991; Kohn, 1992; Baluk and Radwanski, 1996). Vermeij (1993, p. 94), however,

reports identical damage inflicted by crabs on cowries. Spearing stomatopods prefer soft-bodied prey but may be responsible for small irregular punctures (diameters 0.2–1.5 mm) in mollusc shells (mostly thin-shelled tellinids) (Pether, 1995). Octopuses are important shell-crushing predators (Voight, 2000a) and are reported to produce distinct bite traces on legs of crabs (Fig. 4 in Dodge and Scheel, 1999); sometimes they leave characteristic scars on shells (Fig. 4 in Checa, 1993).

Some gastropods (e.g., *Busycon* and some species of *Murex*) attempt to pry or chip clams open with their relatively thin outer lip (Fig. 3J) (e.g., Carriker, 1951; Wells, 1958; Nielsen, 1975; Peterson, 1982). This

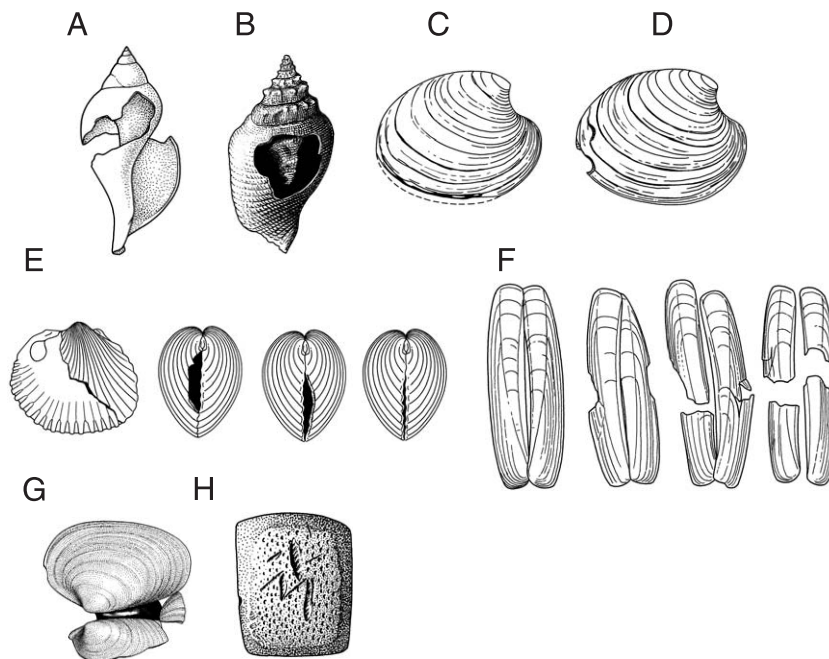


Fig. 14. Examples for traces of predation (sensu Bishop, 1975) resulting from partially destructive feeding processes. (A) Crabs, stomatopods, lobsters and crayfish peel back the apertural margin of gastropods in a characteristic way (redrawn after Bishop, 1975). (B) Gonodactyloid stomatopods (see Fig. 3G) produce very typical, subcircular to irregular holes with sharp edges, which are not accompanied by a scar or hole on the opposite side of the gastropod shell (redrawn after Geary et al., 1991). (C) *Busycon* and certain other gastropods pry open clams with their thin outer lip (see Fig. 3J), which may chip off small portions of the valves in a characteristic way (redrawn after Carriker, 1951). (D) Localized posterior damage in infaunal bivalves like *M. mercenaria* can result from siphon nipping or from crabs inserting their walking leg between the valves of the feeding clam (redrawn after Bishop, 1975). (E) When seabirds like oystercatchers rigorously hammer cockle shells open, characteristic localized damage at the anterior end occurs in moderate-sized shells, whereas smaller specimens show severe but non-diagnostic fractures that run from the ventral border to the umbo (redrawn after Drinnan, 1957). (F) Shaking of *E. directus* by herring gulls (see Fig. 3C) causes different grades of damage, all located in the middle part of the valves (redrawn after Cadée, 2000). (G) *Saxidomus* with typical sea otter breakage pattern leaves one valve intact and attached by the hinge ligament to the other partial valve. The break often more or less follows a growth line in the shell, leaving a much more even break line than crab or octopus predation (redrawn from a photo kindly provided by Rikk Kvitek). (H) Predation scars interpreted as teeth imprints of fish on asteroid ossicle (redrawn from Neumann, 2000).

process may chip off small portions of the valves in a characteristic way (Fig. 14C) (Warren, 1916), but often also severely cracks them (Figs. 3 and 4 on Plate 1 in Carter, 1968). This action may also chip the predator's shell lip (especially when the attacked bivalves close the shells with great force) and result in characteristic repair scars (Fig. 4 in Nielsen, 1975; see Fig. 1 on Plate 60 in Fagerstrom, 1961 for a potential fossil example). Crabs can produce distinct shell margin damage when trying to force open valves and chip off portions of the valves (Fig. 2 in Carriker, 1951; Landers, 1954; Bishop, 1975). Crabs can also leave small circular nicks on the commissure of shallow infaunal bivalve shells when they insert their walking leg between the valves of the feeding clam (Fig. 14D) (Moulton and Gustafson, 1956; Bishop, 1975). Identical small-scale and localized posterior damage in infaunal bivalves such as *M. mercenaria* can result from siphon nipping (Peterson and Quammen, 1982) (Fig. 3B in Alexander and Dietl, 2001). When cockle shells are rigorously pushed or hammered by seabirds (e.g., oystercatcher) until they open, the damage may depend on size: moderate-sized shells suffered characteristic localized damage at the anterior end; smaller specimens showed severe but non-diagnostic fractures that ran from the ventral border to the umbo (Fig. 14E) (Fig. 5 in Drinnan, 1957). Shaking of *E. directus* by herring gulls causes different grades of damage, all located in the middle part of the valves (Fig. 14F) (Fig. 2 in Cadée, 2000). Star fish usually leave shells unaffected (for review, see Carter, 1968), but some species chip the valve margin of clams in an attempt to open them (Mauzey et al., 1968).

Several authors (Pratje, 1929; Fig. 98 in Schäfer, 1962; Fig. 6 in Seilacher, 1973; Fig. 9 in Cadée, 1999) have proposed that abrasion by sand blasting produces diagnostic fragments (Fig. 15), and Savazzi (1991, Fig. 11n) suggested that the numerous small indentations along the outer lip of living (repaired) and dead (unrepaired) strombid shells are typically produced by storm events. Abrasion should be easily distinguishable from high energy impacts due to rocks or from shell-crushing predators by its associated loss of sculpture and progressive rounding (Pratje, 1929). It should also be possible to distinguish (at least using SEM) between abrasive features caused by transportation and the loss of sculpture

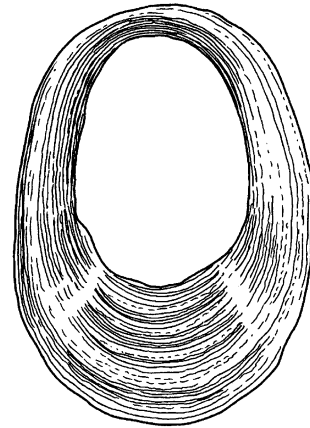


Fig. 15. Distinct fragment of the limpet *Nacella* produced by abrasive sand blasting (redrawn after Cadée, 1999).

and progressive edge rounding caused by bioerosion and dissolution (Brett and Baird, 1986; Parsons and Brett, 1991; Cutler and Flessa, 1995; Nebelsick, 1999b).

When fragments can be directly observed in the field or in thin sections of lithified sediments, compactional fragmentation should be distinct because damage is unrepaired and fragments should be together in the rock, approximately in their original relative position (Fig. 16) (e.g., Plate 22 in Ferguson, 1962; Figs. 2–4 and 6 in Meyers, 1980; Fig. 2d–p in Elliott and Bounds, 1987; Fig. 6 in Hughes and Cooper, 1999; Fig. 2 in Gnoli, 2002). Typically, however, the biogenic material used for taphofacies and palaeoecological analysis is from unconsolidated sieved sediments and this information is lost. This probably explains why compaction can be mistaken for predation (Briggs, 1990). For example, there is some debate as to whether unrepaired fractures in Paleozoic brachiopods are due to one or the other (see Elliott and Bounds, 1987 for details). Different fracture patterns on brachiopods, presumably resulting from compaction, were used to determine the orientation of shells when deposited: life-orientation was inferred for anterior–posteriorly crushed specimens and reorientation by currents for dorsoventrally flattened or laterally compressed specimens (Alexander, 1986b).

Breakage patterns of lower diagnostic power include damage to valve dentition: this is commonly

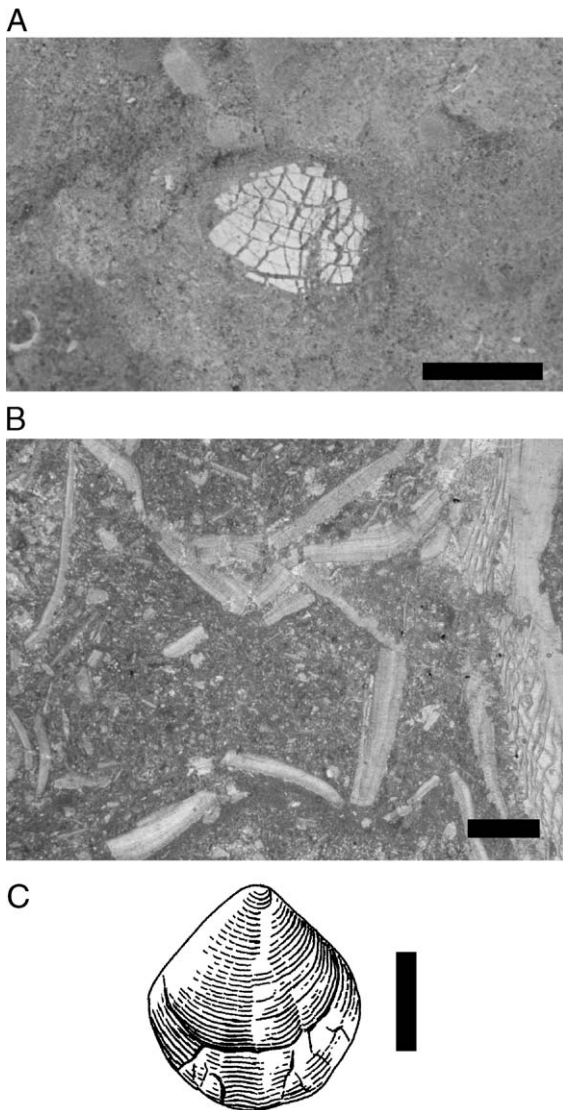


Fig. 16. Compactional fragmentation is unrepaired and fragments are together in the rock, approximately in their original relative position. (A) Unidentified bivalve from Kleinebersdorf, Miocene, Austria. Scale bar is 1 cm. (B) Thin section of radiolitid bivalve packstone, Cretaceous, Turkey. Scale bar is 1 mm. (C) Brachiopod *Composita subtilita* from the Pennsylvanian of Arizona. Scale bar is 1 cm (redrawn from Elliott and Bounds, 1987).

attributed to predation because it suggests that the damaging forces affected articulated valves and that the interlocking hinge features were sheared (Boyd and Newell, 1972). Sea otters for example can insert their canine into the space between the valves and use

it to pry the shells apart in two unbroken halves. This method usually leaves the valves intact, but tears the hinge ligament and breaks off one or more of the hinge teeth (Rikk Kvitek, personal communication, April 2002). Similarly, Boyd and Newell (1972) interpreted fractures across the thickest parts of valves as predation because water energy would preferentially break the thinnest parts. Tasch (1973, p. 295) recorded Mesozoic brachiopods with numerous minute injuries, which are interpretable as reptilian or fish bites. In echinoids, cross-plate fractures were used to discriminate between pre- and post-mortem breakage (Schäfer, 1962; Strathman, 1981; Smith, 1984). However, such fractures also can be produced after death up until the ligament decays, which is strongly temperature dependent (Kidwell and Baumiller, 1990). Sharp-edged molluscan fragments have been interpreted to stem from compaction or predation; at the least, they indicate the absence of transportation (e.g., Boyd and Newell, 1972; Hoffman, 1976). On the other hand, such long and straight margins have been reported to be transportation related (Hollmann, 1968), but this probably reflects sampling immediately after a storm (G. Cadée, personal communication).

Because drill holes can act as local stress concentrators (Wainwright et al., 1982), fractures created in point load experiments pass preferentially through these holes (Roy et al., 1994; Zuschin and Stanton, 2001). This pattern can be used to indicate preferential post-mortem loss of drilled shells: If fragments are rare or mostly contain intact drill holes, then the presence of drilled shells did not contribute significantly to shell breakage (Roy et al., 1994).

Specific characteristics of hermit crab-occupied shells (e.g., tube worms in the aperture) can help to determine whether breakage occurred during or after the life-time of the snail (Stachowitsch, 1980; Walker, 1992).

Many of the above examples are only diagnostic for some broken specimens in a shelly assemblage or only when specific methods are applied (e.g., study of compactional fragmentation in thin sections). In most cases, therefore, diagnostic unrepaired damages will help to identify the presence of a specific source of fragmentation (e.g., predation or compaction), but will not allow its rigorous quantification.

5.3. Non-diagnostic unrepaired shell damage

Most unrepaired damage is indistinct for several reasons:

- (1) Most durophagous predators shatter shells into several angular pieces (Fig. 4A) (e.g., Fig. 1 in Plate 1 in Carter, 1968; Fig. 4 in Trewin and Welsh, 1976; Fig. 5 in Cate and Evans, 1994; Plate 1 in Cadée, 1995; Table 1 in Voight, 2000a), creating shell hash (Alexander, 1986a; Geary et al. 1991) without predation scars. The fragmented material resulting from predation by the fish *P. cromis*, for example, showed remarkably little alteration (other than fragmentation) and commonly retained the periostracum. The size frequency distribution of the shelly material, however, is significantly altered by this predation (Cate and Evans, 1994).
- (2) Breaks tend to follow lines of weakness such as changes in skeletal structure and mineralogy, lines of ornamentation such as ribs and growth lines on molluscs, or sharp changes in convexity (Hollmann, 1968; Müller, 1979). In predation by fish or birds, fragment size and shape as well as the morphology of the broken surface appear to be largely a function of the original size and microstructure of the valve or of structural features such as growth lines, but are not related to predator size (Cate and Evans, 1994; Wilson, 1967).
- (3) With increasing taphonomic degradation, shell strength decreases (Brenner and Einsele, 1976; Kaesler et al., 1993) and the style of fracturing becomes less predictable (Kaesler et al., 1993; Hollmann, 1968). The importance of shell parameters on taphonomic features was already recognized by Kessel (1938), who tentatively related different states of preservation of various shell taxa prone to the same taphonomic processes to differences in shell shape, structure, mineralogy, crystal size, and organic matrix. Similarly, Schäfer (1962, Fig. 96) related the features of mechanical destruction of gastropod shells largely to their shape and sculpture. Hollmann (1968), finally, speculated that fragment shape and contours are chiefly determined by intrinsic shell features and are little influenced by the different transportation

processes (grinding, swinging, dragging, sliding or rolling) in the surf or in currents. Degradation in brachiopods depends on the amount of organic components and very little on environmental conditions (Emig, 1990).

- (4) Resistance against abrasion, which may ultimately lead to fragments, depends on thickness and ornamentation: thicker shells with stronger ornamentation are more resistant than thin counterparts (Driscoll and Weltin, 1973), and homogeneous structure (which breaks easily) has been shown to be very resistant against abrasion (Gabriel, 1981).

It is difficult to relate breakage patterns to shell parameters and shell strength. In general, fracture patterns differ considerably between and within taxa, and most attempts to correlate such patterns with measured shell variables or shell strength have failed (e.g., Zuschin and Stanton, 2001). Similarly, a factor analysis of shell variables and repair frequencies shows that no single variable has a dominant influence on the frequency of sublethal breakage and its likelihood of repair, and that influences on repair frequencies are complex (Alexander and Dietl, 2001).

6. Methods to quantify fragmentation and breakage

Quantifying breakage involves distinguishing between repaired shells and unrepaired fragments, calculating indices, graphically representing results and attempting to reconstruct individual numbers of shells from this material.

6.1. Recurrent breakage patterns and their quantification

One way to quantify breakage patterns and to recognize whether certain shell regions are more subject to breakage than others is to record the locations of the repaired and unrepaired fractures (Fig. 17) (Drinnan, 1957; Carter, 1968; Boyd and Newell, 1972; Alexander, 1981, 1986b; Elliott and Bounds, 1987; Kelley, 1988; Kelley, 1991a,b; Davies et al., 1989; Dietl, 2000; Ramsay et al., 2001); the adopted

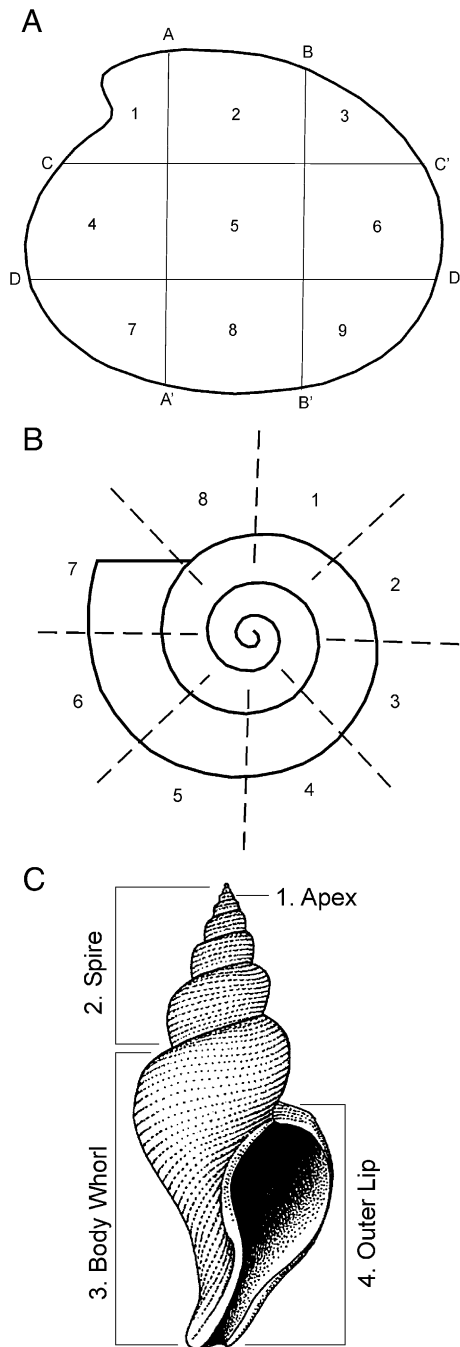


Fig. 17. Fractures should be recorded in terms of the affected shell regions. (A) Standard location scheme for bivalves (redrawn after Kelley, 1988). (B) Standard location scheme for low-spired gastropods (redrawn after Kelley, 1991a,b). (C) Standard shell areas for high-spired gastropods (redrawn after Davies et al., 1989).

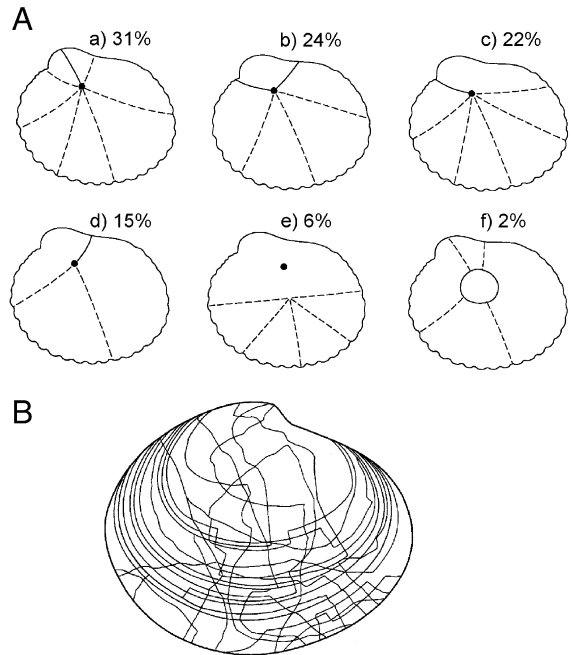


Fig. 18. Fractures can be summarized in sketches. (A) Simplified classification of breakage patterns of experimentally crushed *Anadara*; dot=point of loading, solid line=obligatory fracture type, dashed line=optional fracture for specific breakage type (redrawn after Zuschin and Stanton, 2001). (B) Summarized breakage patterns of beach-collected *Mactra* shells (redrawn after Hollmann, 1968).

scheme for shell regions will vary according to shell shape (Fig. 17B,C). Damage can also be summarized in sketches (Fig. 18) (Hollmann, 1968; Feige and Fürsich, 1991; Kaesler et al., 1993; Daley, 1993; Zuschin and Stanton, 2001). Percentage-frequencies of damage type and position can then be calculated and represented (e.g., as pie diagrams) to ascertain which type of damage is more likely to display which type of repair (Alexander and Dietl, 2001).

A descriptive categorization of fractures according to their appearance was suggested and discussed by Alexander and Dietl (2001) and can be used for repaired, unrepaired, diagnostic and non-diagnostic breakage patterns. In bivalves, a fracture's outline and its relative position to the shell margin enables distinguishing between scalloped injuries (breakage that subparallels commarginal growth lamellae), divoted shells (triangular to chevron-shaped depressions with a piece of the shell margin removed), cleft

shells (a shear in the valve, extending from the shell margin toward the beak), embayed shells (arcuate or horseshoe-shaped deformations where a large piece of the shell is removed and shows an irregular jagged fracture), and shells that show combinations of these damages (Boshoff, 1968; Alexander, 1986a; Checa, 1993; Dietl et al., 2000).

6.2. *Repaired shells*

Shell repair is not directly correlated with predation intensity and rates (Schoener, 1979; Schindel et al., 1982) but does provide evidence that shell-breaking ecological interactions may have occurred in the fossil record or in a specific habitat (e.g., Vermeij et al., 1981; Walker, 2001). Shell repair can be counted on 1, 2, or all whorls of a shell. In many species, only repairs of the last whorl can be identified with certainty, because earlier whorls are often too corroded, encrusted, or obscured by later whorls (Schmidt, 1989; Cadée et al., 1997). Repair frequency is defined as the average number of scars per individual or as the number of repaired shells divided by the total number of shells in a sample (e.g., Robba and Ostinelli, 1975; Raffaelli, 1978; Elner and Raffaelli, 1980; Vermeij, 1982; Alexander and Dietl, 2001; Walker, 2001). Comparisons between different taxa are difficult because shell parameters (see Section 4.1: Shell strength in relation to shell parameters) and molluscan life habits (see Section 7: Taphofacies analysis) strongly influence the likelihood of surviving high energy impacts or crushing predation. Shell repair frequencies of modern species may provide a benchmark for fossil assemblages (Alexander and Dietl, 2001) but should be formulated within the context of functionally and ecologically similar taxa through time (Vermeij, 1987); the anthropogenic influence on (sublethal) fragmentation also has to be considered (Ramsay et al., 2000).

6.3. *Unrepaired damage*

Most attempts to quantify fragmentation from death assemblages or fossil assemblages largely rely on counting numbers of whole and broken skeletons (e.g., Zuschin and Hohenegger, 1998). Some actuopalaeontological studies weighed fragments

and entire shells separately (e.g., Van Straaten, 1956; Cadée, 1994). A subdivision into major breakage (more than 20% broken away) and minor breakage was suggested (Davies et al., 1989; Parsons, 1989).

Results can be presented most simply as percentages of broken shells (Zuschin and Hohenegger, 1998) or as ratios of whole shells to fragments (Fürsich and Flessa, 1987). Fragmentation properties can also be described in terms of categories or “grades” (e.g., good, fair, poor), which can be presented as stacked bar graphs (Feige and Fürsich, 1991) or as ternary taphograms (Kowalewski et al., 1994, 1995): Stacked bar graphs have the advantage that any number of “grades” of fragmentation can be accommodated. Ternary taphograms are very effective graphically in capturing differences/similarities between samples or taxa, but have the disadvantage that only three states per variable are possible and that the statistically important confidence intervals of the frequency data cannot be presented (see Kidwell et al., 2001 for discussion). Results can also be presented as threshold damage profiles (histograms) that summarize the percentage of shells showing fragmentation (Best and Kidwell, 2000a; Kidwell et al., 2001). These damage profiles use only the highest damage grade of the variable (e.g., fragmentation), but visually emphasize its rank order importance and allow the calculation of confidence intervals (Kidwell et al., 2001).

6.4. *Individual numbers from fragments*

Reconstructing the original number of individuals from fragments generally relies on counting distinct fragments (e.g., beaks, umbos, columellas) (e.g., Cadée, 1968, Kowalewski et al., 1994), which yields a minimum estimate of individuals, or counting indistinct fragments as well (e.g., wall fragments) (e.g., Lozek, 1964; Davies et al., 1989; Voight, 2000a), which yields a maximum value. Powell et al. (1989) suggested to use the entire fauna because taphonomic turnover is usually sufficiently high to prevent an individual from being counted more than once. Indices provided by Lozek (1964) to reconstruct individual numbers from indistinct fragments are problematic because the approach is based on predefined relationships that are intuitive and not

based on experiments. Specifically, he proposed counting five indistinct fragments as one individual; in the case of very abundant fragments, the number of calculated individuals was to be reduced by increasingly higher, predefined percentages. However, such reconstructions are probably easier for single-valved than for bivalved organisms or animals with multi-element skeletons because disarticulation is not an issue (see Gilinsky and Bennington, 1994 for discussion).

7. Taphofacies analysis

Taphofacies analysis categorizes assemblages based on similar taphonomic features and has become a standard tool in reconstructing ancient depositional environments (Brett and Baird, 1986; Speyer and Brett, 1986, 1988). The basic tenet is that important taphonomic processes which biased the assemblage can be identified by examining the shells themselves and their position relative to one another (e.g., Tauber, 1942; Powell, 1992).

Fragments are of twofold interest in taphofacies analysis: (1) Fragmentation is a taphonomic feature per se, which may vary among different sedimentary environments (e.g., Zuschin and Hohenegger, 1998) and (2) fragments may contain other environmentally sensitive taphonomic signatures (e.g., abrasion, encrustation) (e.g., Nebelsick, 1999b; Bradshaw and Scoffin, 2001).

7.1. Generalizations

Shell strength as a function of shell parameters is highly variable, as are the respective breakage patterns. This corresponds to the high number of non-diagnostic damages in modern and ancient shelly assemblages and indicates that resistance to breakage is a compromise among a multitude of factors and can only be adequately evaluated for a species in relation to its life habit and ecological needs, along with individual taphonomic history. Nevertheless, a number of generalizations can be drawn:

- (1) Fragmentation is pervasive across most environments. In the Northern Red Sea for example, fragments make up more than 88% of the total mollusc remains >1 mm, but differences between environments are evident, with the most striking feature being a relatively low percentage of fragments in samples from mud (<70%) in contrast to >85% in muddy sand and coral-associated sands (Zuschin and Hohenegger, 1998).
- (2) Predation is a major source of breakage and fragments: Predation-induced fragmentation increased over geological time. Shell-breaking predation is more common in marine than in freshwater environments. Tropical intertidal and shallow subtidal faunas are more specialized for attack and defense than those in temperate and polar regions. Predation probably also strongly influences deep-water communities. Spatial refuges for prey include harsh physical environments outside the tolerance range of the predators, structurally complex habitats, very low and very high population densities, and increasing burrowing depth of infauna (see Section 3.1.1: Shell breaking predation and shell repair).
- (3) Apart from the environment, life habit (epifaunal versus infaunal) influences fragmentation because: (a) epifaunal shells are more susceptible to rapid deterioration (e.g., Callender et al., 1994) and show higher fragmentation frequencies (Best and Kidwell, 2000b), (b) deep burrowing protects fauna from shell-crushing predators (see Section 3.1.1.5: Anti-predatory strategies), and (c) epifauna is exposed to the impact of saltating clasts (see Section 3.1.2: High energy). (See, however Section 3.1.3: Bioturbation: Self-inflicted damage to deep and rapidly burrowing infauna.)
- (4) Biostratinomic fragmentation is quantitatively unimportant in field experiments and primarily restricted to edge chipping, at least during the first 2 years of exposure (Callender et al., 2002; Lescinsky et al., 2002) but may become more important with increasing time intervals (Powell and Davies, 1990). Differences in fragmentation are substrate-related and apparently greatest between hard and soft substrata: experimentally deployed shells were more often broken on hardgrounds than in soft sediments, where they were mostly undisturbed and covered by sediment (Parsons-Hubbard et al., 1999).
- (5) Fragments are a poor indicator for high water energy or transport: Breakage resulting from these

mechanisms generally cannot be distinguished from that caused by most crushing predation (Tauber, 1942; Cadée, 1999). Similarly, abrasion can produce fractures and fragmentation (Driscoll and Weltin, 1973), but fragments are an unreliable measure of this environmental factor. Rather, the effects of abrasion (loss of sculpture and progressive rounding (Pratje, 1929)), size frequency distributions, shell orientations and valve ratios can be used as independent features to recognize transportation (Salazar-Jiménez et al., 1982; Kornicker et al., 1963; Boyd and Newell, 1972). Transportation may also selectively accumulate shell fragments (Lever, 1958).

- (6) The proportion of fragments is sieve mesh-size dependent. Finer sediment fractions contain more fragments than coarser ones (Staff and Powell, 1990; Kidwell et al., 2001).
- (7) Taphonomic features of fragments (e.g., dissolution, edge-rounding, encrustation) differ from those of whole individuals (Davies et al., 1989; Staff and Powell, 1990; Callender and Powell, 1992; Callender et al., 1992; Pilkey et al., 1969) and may have a greater environmental sensitivity (Davies et al., 1989; Staff and Powell, 1990).

7.2. Future research considerations in taphofacies analysis

Taphofacies analyses using fragments have been severely restricted by different definitions of fragments, differences in quantification of fragmentation, differences in taxa regarded (whole assemblages versus target taxa) and differences in grain sizes considered. We therefore recommend the following.

- (1) Better standardizing the methods. The methods used to describe taphonomic characteristics of mollusc shells differ greatly among researchers (for short discussion see Davies et al., 1990). This problem is acute in the present context because fragmentation may result from ecological interactions or taphonomic processes and because definitions overlap. We suggest using the 90% criterion of Davies et al. (1990), followed by categorization into repaired versus unrepaired and diagnostic versus non-diagnostic damage. The quantification of all three types can then provide additional information on underlying patterns and

processes (see Section 6: Methods to quantify breakage and fragmentation).

- (2) Better resolving the highly different sources of fragmentation. The first step is to distinguish ecological (predation, high energy impacts) from physical (biostratinomic and diagenetic) sources. All repaired damages indicate non-lethal effects due to ecological interactions in a broad sense. Predators are involved if (a) there is no evidence in the sediments for physical disturbance (e.g., storms, turbidity currents) or diagenetic effects such as compaction, (b) certain characteristic repairs dominate (e.g., consistent lip damage), (c) characteristic unrepaired damages point to specific predators, (d) potential durophagous predators are preserved, (e) predation scars can be detected on skeletal elements, (f) fragments are present in regurgitates and coprolites, and (g) bivalves are found with one valve broken but with the ligament still present.

Loss of sculpture and rounding distinguish the influence of abrasion and corrosion from high energy impacts by rocks and from shell-crushing predators. Compaction-induced breakage can be easily confused with predation. Good indirect evidence for compaction is a lack of repaired damage and the co-occurrence of fragments in the rock, approximately in their original relative position.

Information can also be gained from the largest category, namely non-diagnostic unrepaired damage: both durophagous predators and physical destruction can lead to shell hash. Categories of severe and localized damage should be distinguished and breakage patterns quantified to determine underlying patterns and processes.

- (3) Considering grain-size sensitivity. Cross-study comparisons are difficult when different shell sizes are considered (Kowalewski et al., 1994; Best and Kidwell, 2000a), i.e., when different mesh-sizes are used: finer sediment fractions contain more fragments than coarser ones (Staff and Powell, 1990; Kidwell et al., 2001).

- (4) Considering large versus small-scale incompatibility. Taphofacies analyses can be undertaken across large-scale environments (with different shelly assemblages) that are equally distinguishable by sedimentological and biological criteria or within biologically and lithologically uniform environments, which may show subtle taphonomic differences (for a short dis-

cussion, see Kowalewski et al., 1994; Staff and Powell, 1990).

(5) Differentiating between target taxa and total assemblages. Fragmentation does not affect all taxa equally (Tauber, 1942). Therefore, taphofacies analyses considering all the specimens found in a sample (Davies et al., 1989a; Staff and Powell, 1990, Zuschin and Hohenegger, 1998) probably yield different results from those restricted to selected target taxa (Fürsich and Flessa, 1987; Meldahl and Flessa, 1990; Feige and Fürsich, 1991; Kowalewski et al., 1994). This is confirmed by a case study in which only one of the three target taxa was sensitive to the same suite of environmental differences as the total assemblage (Kidwell et al., 2001). Target taxa (those found across all studied environments), however, may be extremely helpful to overcome problems in large-scale studies, where the shelly assemblages change regionally (Parsons and Brett, 1991).

(6) Reconciling taphonomic versus evolutionary definitions of breakage and fragments. Evolutionary approaches consider shells as broken only if the damage would have been sufficient to kill the original occupant (e.g., Vermeij, 1979), although it is sometimes difficult to differentiate lethal from sublethal breaks (Vermeij, 1983a).

(7) Incorporating shell repair in taphofacies analysis. Repair is easy to determine and offers an opportunity to separate ecological interactions from post-mortem fragmentation.

(8) Considering the sample size problem. Cumulative sampling curves (= collection curves) should be generated to establish the adequate number of specimens for taphofacies analysis (Kidwell et al., 2001). Accordingly, samples smaller than 20 specimens are insufficient to determine taphonomic signatures and 120–150 specimens are needed to confidently establish damage profiles for taphonomic variables.

(9) Considering the operator problem. Data collected by a single operator are superior to those produced from multiple operators, and if multiple operators are involved the most reliable data are those based on a single, high threshold of damage (rather than several states of damage) (Kidwell et al., 2001).

(10) Considering taxonomic and evolutionary trends in predation. Durophagous predators seem to prefer thick-shelled molluscs over thinner brachiopods because the latter are repellent (e.g., Thayer, 1985).

Among molluscs, gastropods and bivalves have generally differed in their response to increasing predation during the Phanerozoic: The former have tended to emphasize armor, the latter, escape from and avoidance of predators (Vermeij, 1983b). For the few examples of gastropods that respond to predators with escape, see Kohn (1999). Vermeij (1982, 1983b, 1993) suggested that most bivalves (and a few gastropods such as *Ficus*) are unable to evolve armor because they are unable to survive attack and therefore responded by escape or avoidance strategies. This corresponds well to a change from epifauna-dominated benthic assemblages in the Palaeozoic and early Mesozoic to infauna-dominated assemblages in the Cretaceous and Cenozoic (Signor and Brett, 1984; Vermeij, 1977).

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