Differential taphonomy of modern brachiopods (San Juan Islands, Washington State): effect of intrinsic factors on damage and community-level abundance

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The differences in shell structure and population turnover between organic-poor, impunctate (*Hemithiris*) and organic-rich, punctate brachiopod (*Terebratalia*) in a mixed-bottom, siliciclastic setting (San Juan Islands, WA) lead to different taphonomic damage and fidelity with respect to community-level abundance in death assemblages. In comparing shell interiors of similar-sized specimens, *Terebratalia* is predominantly affected by fibre detachment and shows almost no microbioerosion at the SEM scale; whereas, *Hemithiris* shows less marked fibre detachment at the SEM scale and is more intensely affected by microbioerosion both at SEM and light microscope (LM) scales. Fibre detachment related to rapid, microbially-induced organic matter decay appears to be the main destructive process acting on *Terebratalia*. Higher bioerosion levels in *Hemithiris* at SEM and LM scales are probably related to a combination of a low maceration rate and a preferential settlement by borers. From their vastly different abundances in life assemblages it can be deduced that *Terebratalia* produces dead shells at a much higher rate than *Hemithiris*. Therefore, the proportion of altered *Terebratalia*, relative to *Hemithiris*, is expected to be decreased due to its higher production of recently dead cohorts. That *Terebratalia* is also characterized by high damage levels shows that differential population turnover alone is not responsible for the differences in taphonomic damage. This shows that organic-rich and organic-poor shells are characterized by differential post-mortem durability. Although very few *Hemithiris* are present in the life assemblages, high durability ensures its relative over-representation in death assemblages. *Terebratalia* is not strongly under-represented in death assemblages, despite its high destruction rate, because of large production of recently dead shells. Even with the biasing effect of differential durability, the good fidelity reported in previous live-dead studies can be enhanced by higher population turnover of numerically dominant taxa, leading to constant input of recently dead shells into death assemblages. □ *Actualistic taphonomy, bioerosion, durability, fidelity, maceration, palaeoecology.*

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Introduction

Taphonomic processes are important in controlling how faithfully the biological signal of a life assemblage will be captured in a fossil assemblage (Fürsich & Aberhan 1990; Kidwell & Flessa 1995; Olszewski 1999; Behrensmeyer *et al.* 2000; Bush *et al.* 2002; Alin & Cohen 2004). If community level characteristics of a fossil assemblage are to be interpreted, it is essential to understand the taphonomic pathways which have altered the original signal. The preservation potential of a fossil assemblage is influenced by *extrinsic* and *intrinsic* factors (Kowalewski 1996; Best & Kidwell 2000a, b). The *extrinsic* factors (e.g. rate of burial and reworking, substrate type, temperature, pore-water chemistry, bottom water oxygenation etc.) are relatively well explored, and often predictably covary with depth-, substrate- or latitude-related environmental gradients (Parsons & Brett 1991). The concept of taphofacies and their usage for palaeoenvironmental interpretation is based on understanding this covariance (Brett & Baird 1986; Brett & Speyer 1990; Kowalewski *et al.* 1994; Nebelsick 1999; Callender *et al.* 2002; Staff *et al.* 2002; Oloriz *et al.* 2002; Cózar 2003; Nielsen & Funder 2003; Wani 2003; Yesares-Garcia & Aguirre 2004). Additionally, most generalizations about fidelity patterns in the fossil record are phrased in terms of different extrinsic factors (Kidwell & Bosence 1991; Kidwell & Flessa 1995; Zuschin *et al.* 2000; Kidwell 2001; Zuschin & Oliver 2003).

The role of the *intrinsic* factors in controlling the preservation of a fossil assemblage, such as inherent

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shell *durability* and *population dynamics*, have become increasingly appreciated in the last ten years (Allmon 1993; Greenstein 1993, 1995; LeClair 1993; Pandolfi & Greenstein 1997a; Best & Kidwell 2000b; Powell *et al.* 2002; Greenstein & Pandolfi 2003; Zuschin *et al.* 2003; Nielsen 2004; Lazo 2004; Tomašových 2004a). Short-term experimental data indicate that taxon-specific variations in mineralogy and/or shell microstructure result in differential shell destruction rates (Henrich & Wefer 1986; Smith *et al.* 1992; Glover & Kidwell 1993; Perry 1998). Differences in the durability and population dynamics (i.e. dynamics of dead shell production) of component taxa within a fossil assemblage can skew its community-level abundances (Pandolfi & Greenstein 1997b; Pandolfi & Minchin 1995; Cherns & Wright 2000; Wright *et al.* 2003). In addition to the effect on fidelity, these differences influence damage patterns (i.e. taphofacies). Best & Kidwell (2000b) concluded that extrinsic factors exerted a dominant qualitative effect on the rankings of taphonomic variables in bivalve death assemblages from mixed siliciclastic-carbonate settings, while intrinsic factors (related to life habits and shell structure/mineralogy) affected only the intensity of the taphonomic variables. While this is a good beginning, the relative effects of intrinsic factors still need further exploration in other depositional systems. In addition, the role of intrinsic factors in controlling preservation potential is still poorly known for several important fossil groups, including rhynchonelliformean brachiopods (Emig 1990; Tomašových 2004a).

Minimizing variation in extrinsic factors, any differences in taphonomic damage should be caused by variation in intrinsic factors. Therefore, to understand the role of intrinsic factors and to test their importance, within-habitat preservation and fidelity with respect to the community-level abundance of two brachiopod species (*Terebratalia transversa* and *Hemithiris psittacea*) are assessed in this comparative study. Based on field and experimental data (Glover & Kidwell 1993; Daley 1993; Kidwell & Brenchley 1994, 1996; Simon *et al.* 1994), it has been hypothesized that organic-rich shells have lower post-mortem durability than organic-poor shells, leading to differences in their taphonomic destruction rates. Brachiopods with organic-rich, punctate and organic-poor, impunctate shell structure derived from a single habitat can provide a potential test of such hypothesis (i.e. are differences in shell structure correlated with damage patterns?). An initial null hypothesis begins with the assumption that extrinsic factors are constant and variations in intrinsic factors related to life habit, shell mineralogy and thickness are minimized. Therefore, if shell structure and organic content do not differentially affect rates of destruction (i.e. postmortem durability), there should be no difference in damage patterns between the punctate organic-rich (*Terebratalia transversa*) and impunctate organic-poor (*Hemithiris psittacea*) brachiopods.

In this paper, the damage patterns of two brachiopod species are compared and evaluated in terms of differential postmortem durability. Dead-shell production rate, as related to population turnover is another intrinsic factor, and while not explicitly examined here, its potential effects on damage patterns and community-level abundance are also discussed. Abundance data of live and dead brachiopods derived from the same samples, give some indication of population turnover, and have already been partially examined (Kowalewski *et al.* 2003). Based on taphonomic scoring and sample-level abundances, it is shown that these two taxa are characterized by differences in durability and population turnover. This causes their distinct taphonomic damage and differences in fidelity pattern in terms of their abundance in death assemblages.

Methods

The data used in this study were produced by students in the 2002 Taphonomy class at the Friday Harbor Laboratories, Washington State, and include 446 specimens of *Terebratalia transversa* (bulk samples of four sites – 1-5-D, 3-3-D, 4-1-D, 6-2-D, see Kowalewski *et al.* 2003) and 167 specimens of *Hemithiris psittacea* (bulk and non-bulk samples of 3 sites – 1-5-D, 3-3-D, 6-2-D). All samples represent relatively deep, mixed-bottom settings (between 64 and 84 m in depth) with a high proportion of fine silty/sandy sediment (the 0.0063–1 mm sediment fraction accounts for 0.7–2.4 kg in each 20 l sample), and dispersed cobbles/pebbles. Samples 1-5-D and 6-2-D are derived from a moderately steep slope on the eastern side of the San Juan Channel (Fig. 1) near Rock Point. Samples 3-3-D and 4-1-D are from the western side of the San Juan Channel. All samples examined here primarily are derived from low/moderate-energy conditions and are influenced by tidal currents. The tidal range in Puget Sound is about 3.3 m, which generates strong tidal currents in the sounds and narrows (Lie 1974), leading to good circulation and relatively stable water temperatures (7–13°C) together with normal marine salinity throughout the whole year (Thomson 1981).

Although differing with respect to pedicle muscle activity and reorientation ability (Thayer 1975; LaBarbera 1977, 1978), *Terebratalia transversa* (order Terebratulida) and *Hemithiris psittacea* (order Rhynchonellida) are both epifaunal, and attached to

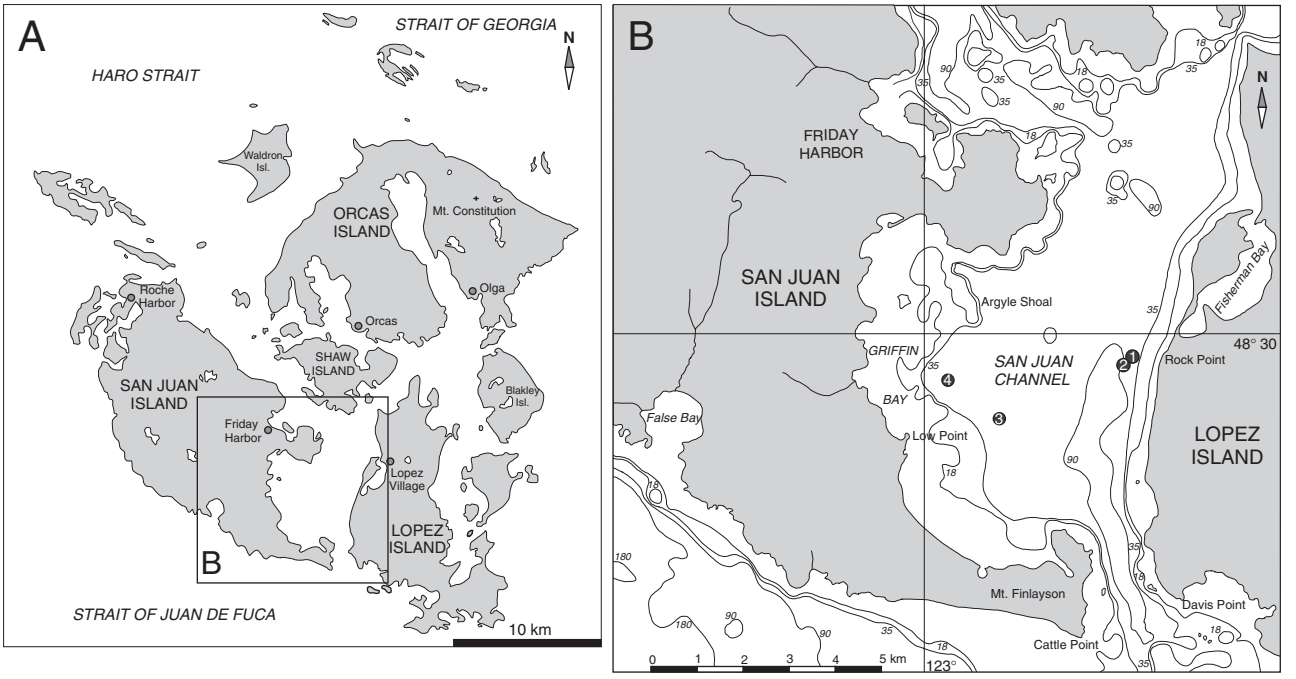


Fig. 1. Geographic map of the study area with dredged localities. □A. San Juan Archipelago. □B. Detailed view of the San Juan Channel with four samples (1 – Sample 6-2-D, 2 – Sample 1-5-D, 3 – Sample 3-3-D, 4 – Sample 4-1-D).

the substrate with a pedicle throughout their life. They represent two typical groups of rhynchonelliformean brachiopods (i.e. terebratulids and rhynchonellids) which have dominated brachiopod communities since the Triassic and remain the most common groups of rhynchonelliformean brachiopods in modern seas.

Both brachiopod species possess low-magnesium calcitic, biconvex, slightly inflated valves, with a cyrtomatodont (interlocking) hinge. The shell thickness of adult *Terebratalia* (measured near anterior edge) ranges from 0.4–0.95 mm, and that of adult *Hemithiris* from 0.35–0.85 mm. Pedicle valves of adult *Terebratalia* are 20–35 mm long, while *Hemithiris* is smaller, around 16–20 mm in length. *Terebratalia* is characterized by a high morphologic variation with respect to shell outline, convexity and ornamentation (Schumann 1991; Krause 2004). Both species are characterized by a two-layered shell microstructure consisting of a very thin, primary granular layer and a thicker secondary layer formed by calcitic fibres bounded by organic sheaths. The difference between the species is that valves of *Terebratalia* are punctate, with perforations (punctae) occupied by caecal prolongations of outer mantle epithelium and a relatively high organic content when compared to the impunctate valves of *Hemithiris*.

Taphonomic damage for all specimens was scored as presence/absence data under light microscope (LM) magnification up to 10×. Among the taphonomic variables scored were: disarticulation, fragmentation, internal fine-scale surface alteration, internal non-predatory macrobioerosion and internal encrustation. External surfaces are not discussed here in order to minimize the effect of pre-mortem processes on shell preservation. At the LM scale, fine-scale surface alteration denotes any microscopic dulling, chalkiness, pitting, or erosion of the original surface. Using the LM no secondary precipitation was observed. Mean values of taphonomic variables with 95% confidence intervals are used for comparison of damage levels. The confidence intervals were derived from the bootstrapped mean-frequency distribution (resampled with replacements, corresponding to the number of specimens in the sample/sieve, and iterated 1000 times; the code is available on request). Non-metric multidimensional scaling (NMDS) based on Manhattan distances was used to compare overall taphonomic damage of *Hemithiris* and *Terebratalia*, using five taphonomic variables. NMDS based on Bray-Curtis dissimilarities was performed for ordination of life and death assemblages, with species abundances as the variables.

Internal surfaces were observed under the scanning electron microscope (SEM) in order to determine possible qualitative differences in type and intensity of fine-scale surface alteration. Nine *Terebratalia* specimens and six *Hemithiris* specimens of comparable size (below 10 mm) were selected for SEM analysis (Table 1). Under 500–1000× magnification, the following taphonomic damage types were scored for

Table 1. Taphonomic scoring of nine *Terebratalia* and six *Hemithiris* specimens selected for SEM analysis. Explanations: 1 – presence, 0 – absence. The first letter of the specimen ID indicates the sample (E – Sample 1-5-D, J – Sample 3-3-D, D – Sample 6-2-D).

						Light microscope (10×):				*SEM scoring (500–1000×):*						
Specimen ID	ventral valve length (mm)	dorsal valve length (mm)	width (mm)	maximum fragment dimension (mm)	Valve (v = ventral, d = dorsal)	Fragmentation	Internal alteration	Internal bioerosion	Internal encrustation	fibre detachment	intra-fibre fragmentation	small-scale dissolution	micro-borings (1–10 µm)	nanno-borings (0.25–0.5 µm)	sample	species
E305	—	4.2	4.48	—	d	1	1	0	0	1	1	0	0	1	1-5-D	*T. transversa*
E306	—	3.36	—	—	d	1	1	0	0	1	1	0	0	1	1-5-D	*T. transversa*
E332	1.64	—	1.5	—	v	1	1	0	0	1	1	1	0	1	1-5-D	*T. transversa*
E334	2	—	1.8	—	v	1	1	0	0	1	0	1	0	1	1-5-D	*T. transversa*
J410	2.8	—	—	—	v	0	1	0	0	1	0	1	0	1	3-3-D	*T. transversa*
D326	—	1.36	1.26	—	d	0	1	0	0	1	1	0	0	0	6-2-D	*T. transversa*
D333	1.96	1.5	1.64	—	d	0	0	0	0	0	0	0	0	0	6-2-D	*T. transversa*
D346	1.32	1.08	1.18	—	v	0	0	0	0	0	0	1	0	0	6-2-D	*T. transversa*
D524	—	—	—	9.7	?	1	1	1	1	1	1	0	0	1	6-2-D	*T. transversa*
J421	—	2	1.8	—	d	1	1	0	1	1	1	1	1	1	3-3-D	*H. psittacea*
E359	2.52	2.01	2.01	—	d	0	0	0	0	0	0	0	0	0	1-5-D	*H. psittacea*
D525	—	—	—	4.1	v	1	1	1	0	1	0	0	1	1	6-2-D	*H. psittacea*
D526	—	2.87	—	—	d	1	1	1	0	1	1	1	1	1	6-2-D	*H. psittacea*
D527	3.07	—	—	—	v	1	1	0	0	1	0	0	1	1	6-2-D	*H. psittacea*
D528	3	—	—	—	v	1	1	0	0	1	1	1	1	1	6-2-D	*H. psittacea*

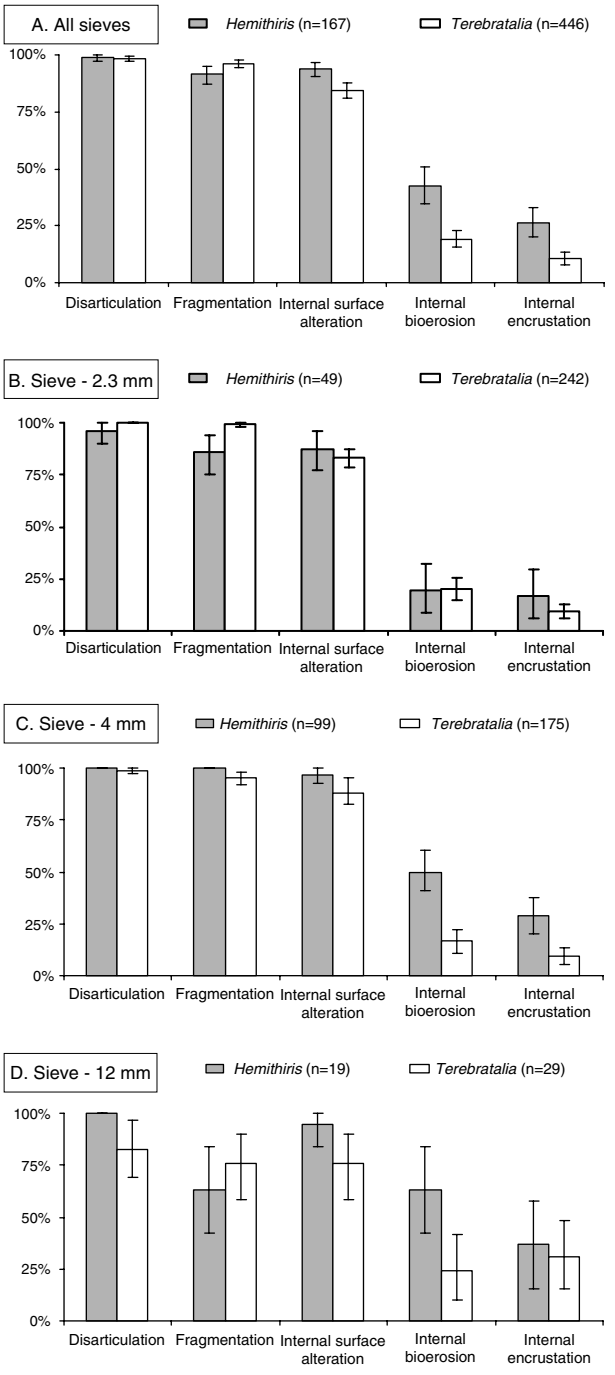


Fig. 2. Relative proportions of taphonomic variables with bootstrapped 95% confidence intervals. □A. All sieves. □B. 2.3 mm sieve size. □C. 4 mm sieve size. □D. 12 mm sieve size.

presence/absence: (1) detachment of fibres from internal surface, (2) intra-fibre fragmentation, (3) small-scale dissolution, (4) simple dispersed circular nannoborings (0.25–0.5 μm in diameter), and (5) microborings formed by a complicated network of borings (2.5–10 μm in diameter). For closer inspection, higher magnifications (2000–5000×) were used. The specimens are deposited at the Paleontological Institute in Würzburg (PIW2005I-1–15). The first letter of the specimen ID indicates the sample (E – Sample 1-5-D, J – Sample 3-3-D, D – Sample 6-2-D).

Results

Damage levels in Terebratalia and Hemithiris

Taphonomic variables of the samples were compared pairwise in all sieves and individual sieve sizes (2.3 mm, 4 mm, and 12 mm, Fig. 2). Ranks of individual taphonomic variables are similar in both species (Fig. 2), with disarticulation having the greatest frequency (82–100%), followed by fragmentation (63.1–100%) and surface alteration (75–96%). The proportions of macrobioerosion (16–63%) and encrustation are lower, with the latter consistently attaining the lowest levels (9–36%). The proportion of disarticulated and fragmented specimens is very high in all sieve sizes. In the 4 and 12 mm sieve size, there are no articulated *Hemithiris* specimens (in the 2.3 mm sieve, several articulated juveniles are present). In pooled samples, there are no significant differences (in terms of bootstrapped 95% confidence intervals) between the two species with respect to disarticulation and fragmentation. *Hemithiris* (87–96%) shows higher surface alteration than *Terebratalia* (75–88%), although this is significant in the pooled samples only. *Hemithiris* is significantly more bioeroded (50–63%; except for the 2.3 mm sieve size) than *Terebratalia* (16–24%). In the 4 mm and pooled samples, *Hemithiris* is also significantly more affected by encrustation. Macroborings are mainly represented by *Reticulina* (curved, branched borings larger than 10 μm in diameter produced by green algae *Ostreobium*). *Entobia* traces produced by sponge *Cliona* are very rare (A. Hendy 2003: personal communication).

Fragmented specimens of *Terebratalia* are significantly more altered with respect to surface alteration, macrobioerosion and encrustation than complete specimens (Fig. 3A). While this may seem trivial, note that complete *Terebratalia* specimens are not affected by any macrobioerosion and encrustation. In contrast, there are no significant differences in surface alteration between complete and fragmented *Hemithiris*. Disproportionate distribution of specimens in the smaller fractions can be seen in Fig. 3B. In *Hemithiris*, the 4 mm class is more frequent than the 2.3 mm size class, in contrast to *Terebratalia*. The differential damage levels are supported also by multivariate analysis. Q-mode NMDS based on five taphonomic variables and including individual samples and samples pooled after the sieves show that with the

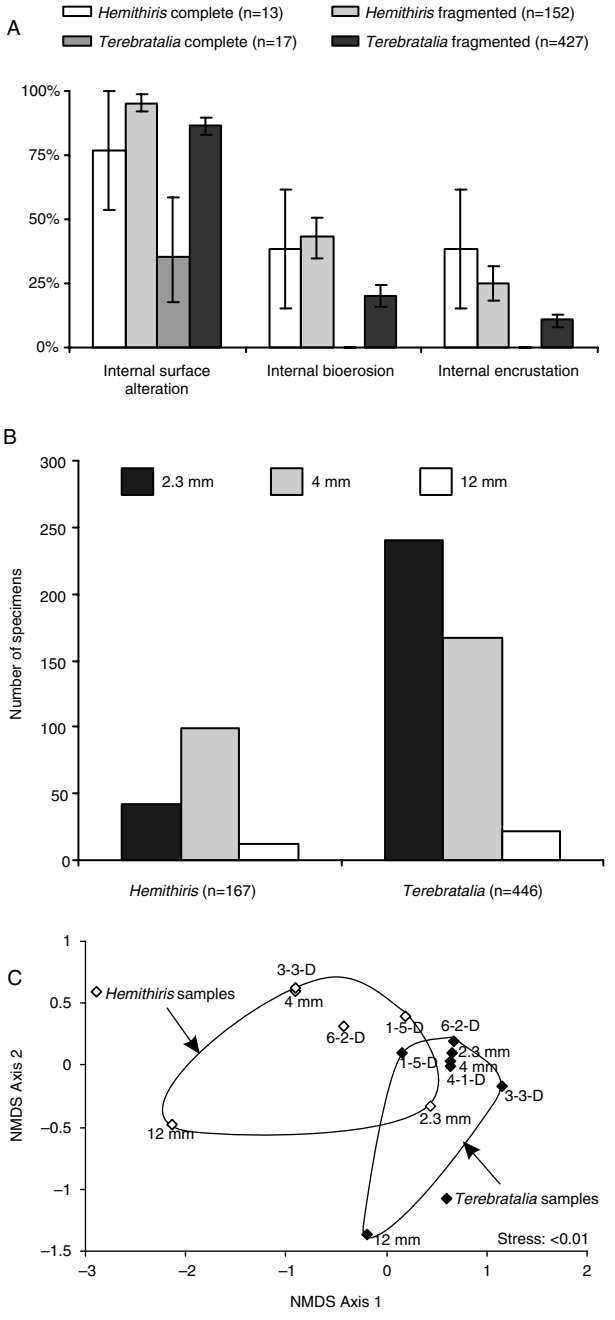


Fig. 3. □A. Comparison of fragmented and complete *Hemithiris* and *Terebratalia*, with respect to the internal surface alteration, macrobioerosion and encrustation (bootstrapped 95% confidence intervals). □B. Size-frequency distribution of specimens in three size classes. Note substantially higher proportion of the 2.3 mm class in contrast to the 4 mm class in *Terebratalia*. □C. Non-metric multidimensional scaling (NMDS) of individual samples and samples pooled according to sieves, based on five taphonomic variables.

exception of the 2.3 mm sieve size, *Hemithiris* and *Terebratalia* samples are segregated (Fig. 3C). The smaller size classes are differentially preserved than larger size class above 12 mm.

Internal surface fine-scale alteration

Based on SEM observations, fine-scale surface alteration is of complex origin and includes: (1) fibre detachment from shell surface, (2) intra-fibre fragmentation, (3) microbioerosion, and (4) small-scale dissolution (Table 1). The main reason for including microbioerosion under this category is that *Hemithiris* specimens scored as *altered* and *unbored* under the LM show high levels of microbioerosion under the SEM. This means that under the LM, this type of damage was not recognized as macrobioerosion but as fine-scale surface alteration (Table 1).

Terebratalia. – Internal surfaces of specimens scored as unaltered under the LM are similarly pristine under the SEM (Fig. 4A), although in a few cases show subtle local dissolution (Figs 4B–D). In D346, for example, the outer surfaces of fibres are slightly dissolved at the anterior valve margin only, and always in association with abundant bacteria (Fig. 4C, D).

Fibre detachment is a very pronounced feature, and is represented either by a large-scale exfoliation of whole sheets of secondary fibres (typically creating jagged appearance, Figs 5A, 6C), or by loosening of individual fibres from the internal surface of the valve (Figs 4G, 5A, F). As a result of fibre detachment, the whole internal surface can become densely covered by microscopic fragments of calcitic fibres (Figs 5F, 6E). Intra-fibre fragmentation involves 'in situ' breakage of secondary fibres which remain present within the valve surface (Figs 6B, D, F).

In specimens J410 and E332, small-scale dissolution is preferentially localized in areas affected by either incomplete shell secretion or dissolution of previously secreted fibre (e.g. muscle scars) during the life of the individual (Figs 4H, 5B–C). In specimen E334, localized surficial dissolution is present on the margin of the valve (Fig. 4E–F). In some cases, dispersed pyrite grains are present on the internal shell surface, while in others the punctae contain pyritic aggregates (Fig. 5E).

Microbioerosion typical of *Hemithiris* was not observed. Specimens scored as altered under the LM always show simple scattered nannoborings under the SEM (Fig. 5G–H). In addition, specimen D524 which was scored as bored under the LM showed sinuous branched macroborings, 20–30 μm in diameter (Fig. 6H).

Hemithiris. – Specimens scored as unaltered when observed at the LM scale show relatively pristine internal surfaces (Fig. 7A). In specimens scored as altered using a LM, fibre detachment is qualitatively less pronounced compared to that of *Terebratalia*, and is restricted to the loosening of individual fibres from the valves surface (Fig. 7E). In contrast, microbioerosion under SEM is substantially more intense

and mainly represented by densely spaced networks of linear or sinuous unbranched microborings, commonly 1–2.5 μm in diameter (Fig. 7B–H). Locally, larger tubular or spherical borings occur, 5–10 μm in diameter (Fig. 7B–D). Specimens scored as bored under the LM show both micro- and macroborings, as in specimen D525.

Abundances of brachiopods in life and death assemblages

Kowalewski *et al.* (2003) analyzed fidelity of life and death assemblages from the studied samples. Due to the small species number in the samples (including Samples 1-5-D, 3-3-D, 4-1-D and 6-2-D), quantitative fidelity indices were conclusive for *pooled* life and death assemblages only. These displayed a significant Spearman rank correlation ($r = 0.41$, $p = 0.0001$), suggesting that the rank abundances of species in the life communities are at least partly preserved in the death assemblages. However, the pooled samples included several depth habitats with compositionally variable assemblages which could obscure between-habitat differences in taphonomic pathways.

To minimize between-habitat variation due to the pooling of samples and specifically address the fidelity with respect to the rank and relative abundances of the two brachiopods, all life and death assemblages analyzed by Kowalewski *et al.* (2003) are re-plotted here in NMDS (Fig. 8). To demonstrate the effect of the inclusion of fragments, both exhaustive (EDA, with fragments and without correction for disarticulated elements) and restrictive (RDA, without fragments and with correction for disarticulated elements, for details see Kowalewski *et al.* 2003) death assemblages are shown. NMDS shows compositional segregation between the life assemblages (LA), EDAs and RDAs. This is supported by significant pairwise differences among them (ANOSIM, Table 2). This means that the average of rank dissimilarities within the RDAs (or EDAs) is smaller than the average of rank dissimilarities between the RDAs (or EDAs) and LAs. The difference in community-level abundances of live and dead brachiopods is shown by bubble plots (Fig. 8). *Hemithiris psittacea* was *not* found in the LAs. However, several live *Hemithiris* juveniles were found in non-bulk samples from the same sites. This indicates that they are rare but nevertheless present in the larval pool. In terms of relative and rank abundance, *Hemithiris* is over-represented in the EDAs and missing or rare in the RDAs. *Terebratalia* can be over-represented in the EDAs but mostly under-represented in the RDAs (Fig. 8).

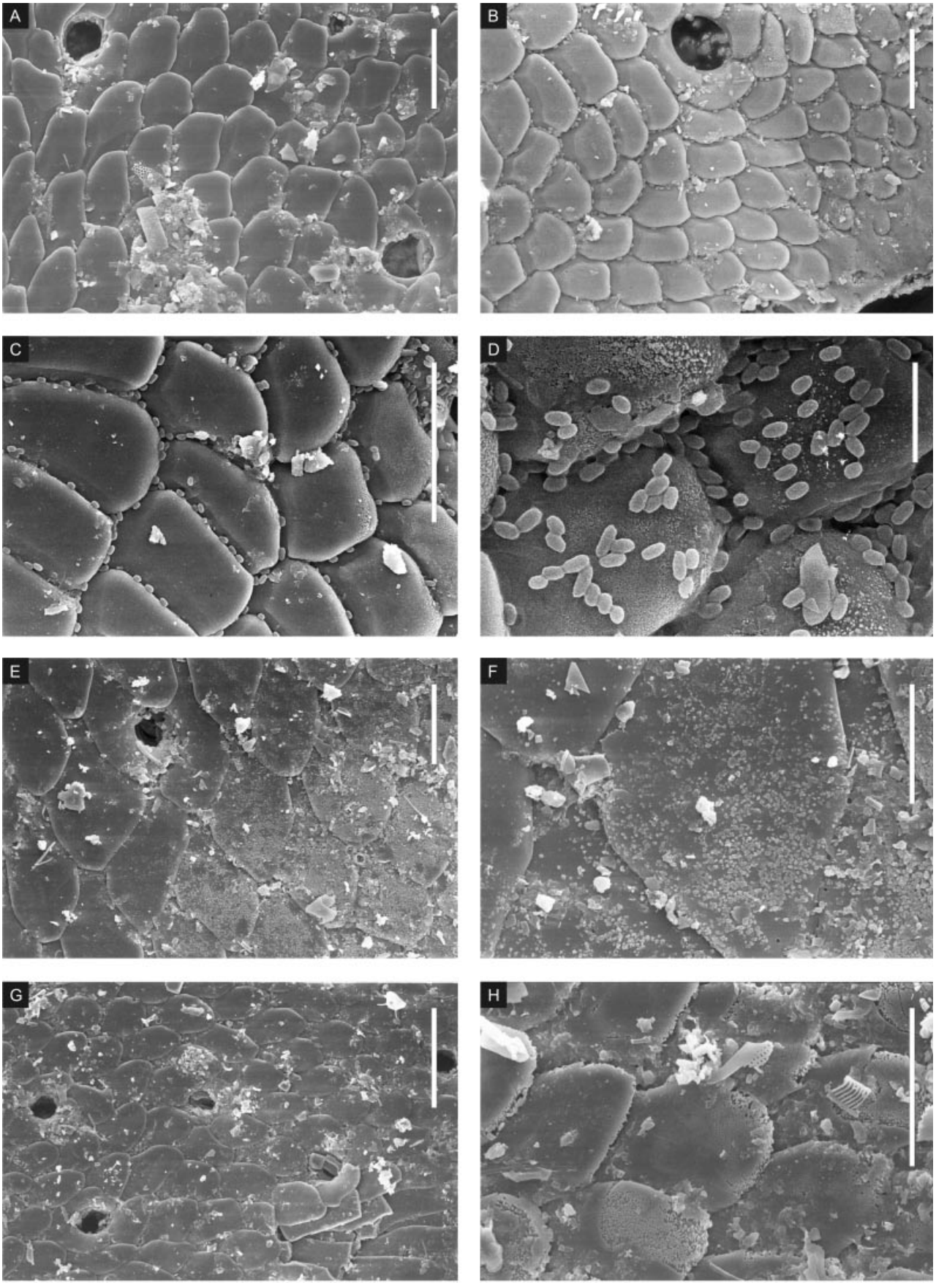
Four samples analyzed in this paper are shown separately in Figure 9. *Terebratalia* is relatively common in the life assemblages and can be one of the most abundant species (Samples 1-5-D and 6-2-D). In the EDAs, *Terebratalia* consistently occupies higher rank position than in the LAs. *Hemithiris* is present in all four samples and belongs to the common species in Samples 3-3-D and 6-2-D (Fig. 9). Interestingly, it can be even more abundant than *Terebratalia* (Sample 3-3-D). In contrast, in the RDAs, relative and rank abundances of *Terebratalia* are substantially lower than in the LAs. The only exception is Sample 3-3-D which has a small sample size.

Discussion

Differences in damage between Terebratalia and Hemithiris

Disarticulation and fragmentation. – The high proportion of disarticulated specimens of both species is surprising as their interlocked hinge should provide high resistance against destruction (Brett 1977; Sheehan 1978; Brett & Baird 1986; Holland 1988). However, given experimental data describing the poor mechanical strength of dead terebratulid shells (Collins 1986; Daley 1993), disarticulation can probably proceed rapidly as a result of organic matter decay in modern temperate settings. Collins (1986) observed the rapid decrease in the resistance of *Terebratulina* against the point loading force during 218 days. Daley (1993) demonstrated that with increasing time since death, the mean gape angle and the degree of fragmentation significantly increased in *Terebratalia*. Although intense dredging and locally high-energy bottom currents may cause high levels of physical disturbance, the high proportion of fine sediment in our samples indicates low energy conditions during background sedimentation rates. This indicates that high disarticulation and fragmentation rates may not require substantial physical transport or reworking.

Intuitively, with increasing time since death, fragmentation will positively correlate with other destructive processes (Fig. 10). Kidwell *et al.* (2001) observed that fragments yield consistently higher frequencies of all types of damage in comparison to whole shells. Nevertheless it is interesting to compare the preservation differences between complete and fragmented specimens when they are exposed to the same extrinsic factors (e.g. Davies *et al.* 1989; Staff & Powell 1990; Zuschin *et al.* 2003). Comparisons of complete and fragmented specimens of *Hemithiris* indicate that complete valves can sustain similar levels of surface alteration, macrobioerosion and encrustation as fragmented valves. This is in contrast to the pattern observed in complete and fragmented


A
B
C
D
E
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G
H

Terebratalia in which complete valves display much less damage, possibly indicating its higher rate of fragmentation; i.e. *Terebratalia* valves are fragmented more rapidly than *Hemithiris*. Complete *Terebratalia* valves thus do not accrue much damage in terms of surface alteration, macrobioerosion or encrustation.

Internal fine-scale surface alteration. – The high proportion of specimens with fine-scale surface alteration suggests that this pattern is related to an important post-mortem destructive process which acts on the internal valve surface of both species. Although the between-species differences in the proportion of fine-scale alteration are very slight at the LM scale (Fig. 2), they are much more substantial when analyzed at SEM scales. This points to the importance of using high-resolution (SEM) tools in detecting damage patterns (Cutler 1995; Cutler & Flessa 1995; Nielsen 2004).

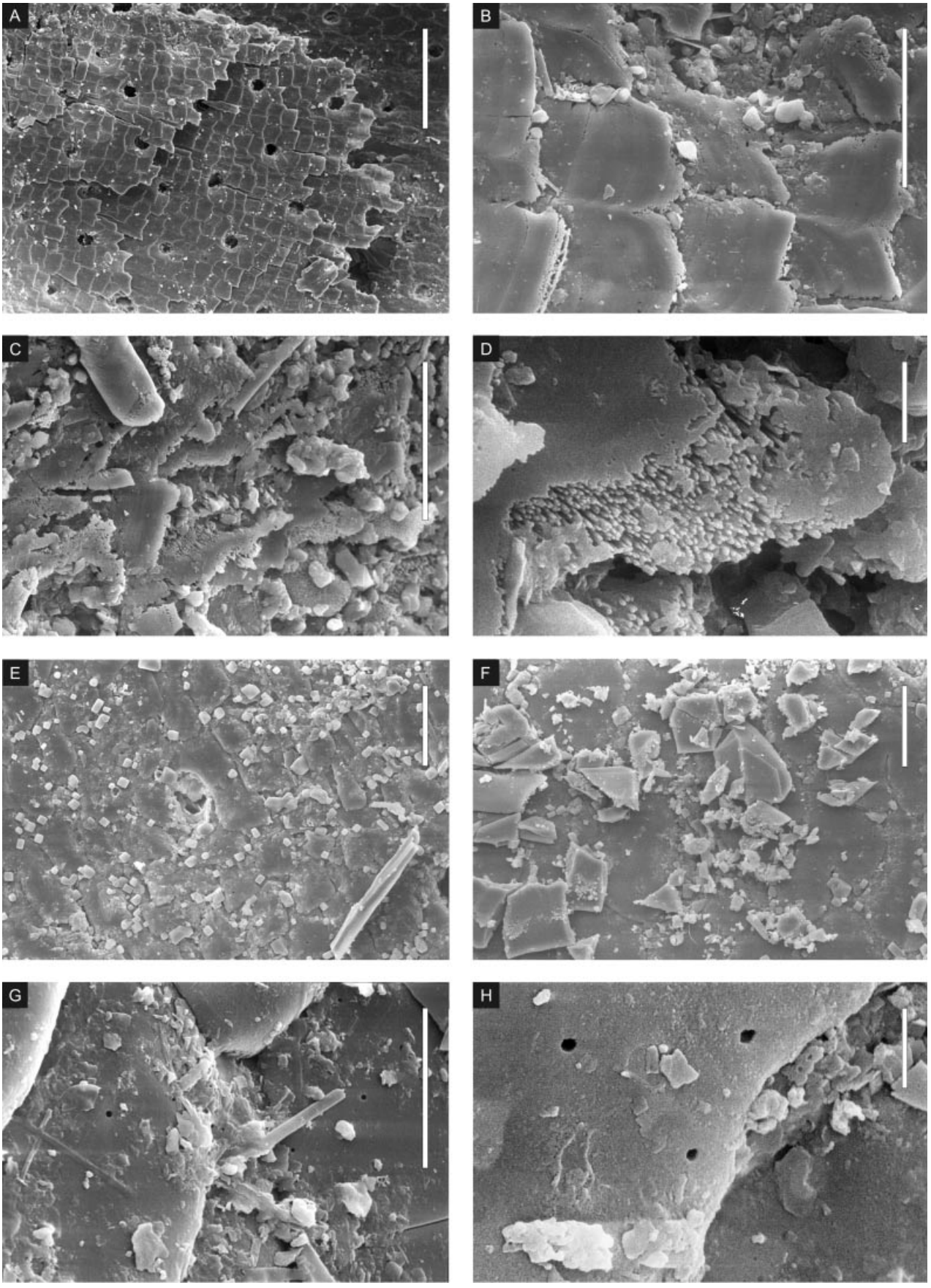
Detachment of fibres from the internal surface can be assigned to the degradation of organic matrix, most probably by bacterially-induced decay, and is more commonly known as shell maceration (Alexandersson 1979; Freiwald 1995, 1998). This is indicated by the presence of bacteria on the fibre surfaces and between fibres (original position of intercrystalline organic matter, Fig. 4B–D) and the exfoliation/loosening of fibres which are preferentially in the position of the organic sheaths (Fig. 5A). The free space left by degraded organic matter is not infilled with newly precipitated carbonate material, leading to the large-scale detachment of fibre sheets and individual fibres giving a jagged appearance to the shell surface. Based on the high proportion of fine-scale alteration at the LM scale and intense fibre detachment at the SEM scale, it seems that shell maceration is the main destructive process acting on *Terebratalia*. This agrees with other published reports in which shell maceration is commonly reported as a distinct damage type in modern punctate brachiopods from shallow, temperate siliciclastic or deep slope/basinal settings (Stewart 1981; Collins 1986; Emig 1990; Gaspard 1989, 1993, 1996a, b).

In contrast, fine-scale alteration as a result of higher intensity microbioerosion appears to be a very important destructive process operating on *Hemithiris* (Fig. 7). Although resin casts are needed for identification of borers, nannoborings 0.25–0.5 μm in diameter can indicate activity of bacteria or fungi. Elongate microborings typical for *Hemithiris*, 1–2.5 μm in diameter, could possibly correspond to fungi or blue-green algae (Young & Nelson, 1988). Fibre detachment also affects *Hemithiris*, but to a lesser degree (probably related to lower proportion of shell organic matter and more limited access by microorganisms). With no other evidence, it is difficult to assess if the rate of maceration of *Terebratalia* is higher than the rate of microbioerosion of *Hemithiris*. However, the between-species difference in preservation of complete specimens (Fig. 3A) indicates that *Terebratalia* breaks up more rapidly and thus has a higher rate of shell destruction. Also, the mode in the 2.3 mm class is indicative of a higher tendency to disintegrate into fragments in *Terebratalia* (Fig. 3B).

Internal macrobioerosion. – Rare occurrence of macrobioerosion in the 2.3 mm size fraction may indicate a lower frequency of macroborers attacking very small brachiopod fragments. This is in accordance with results of Hannisdal (2004) who observed low levels of macrobioerosion in brachiopods compared to bivalves in sieve fractions under 1 mm. It is known that fine sieve size fractions consistently yield lower damage frequencies compared with coarse sieve sizes (Kidwell *et al.* 2001).

In addition to the higher intensity of microbioerosion at the SEM scale, higher levels of macrobioerosion at the LM scale in the *Hemithiris* death assemblage can be related to preferential attack by borers known for their selective settlement behaviour (Young & Nelson 1988; Kiene *et al.* 1995; Perry 1998), or to greater exposure time (longer time exposed to borers), or to some combination of these factors. For example, shells with relatively low porosity are more susceptible to boring activity (Best & Kidwell 2000b). High organic content can be unpalatable for some microboring organisms (Rooney & Perkins 1972), thus making a shell less susceptible to bioerosion. On the other hand, it may also attract boring organisms as it provides the food source for them (e.g. fungi, Simon *et al.* 1994). A greater exposure time can also result from a low rate of *Hemithiris* destruction in comparison to *Terebratalia* (leading to longer exposure of *Hemithiris*). The relationship between a higher durability of *Hemithiris*

Fig. 4. Fine-scale alteration of *Terebratalia* on SEM scale. □A. Unaltered specimen (D333D) with pristine shell surface. Scale: 20 μm. □B. Anterior edge of unaltered specimen with pristine surface with abundant bacteria (D346). Scale: 20 μm. □C. Bacteria are preferentially present in inter-fibre boundaries (D346). Scale: 20 μm. □D. Abundant bacteria are associated small-scale surficial dissolution of fibre surfaces. Scale: 5 μm. □E. Specimen E334 with pristine secondary fibres on the left and altered fibres on the right. Scale: 20 μm. □F. Detail of Fig. 7E, with visible localized small-scale dissolution on the fibre surfaces. Scale: 10 μm. □G. Altered specimen (J410) with initial detachment of individual fibres from internal surface. Scale: 50 μm. □H. Same specimen as in G. Shell mosaic is formed by incompletely secreted fibres. This is caused by incomplete coalescence of calcitic granules and leading to relatively high proportion of organic matter within fibres. Those fibre parts are preferentially fragmented/dissolved. Scale: 20 μm.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and preferential attack by borers does not have to be mutually exclusive as boring taxa selectively infest more durable shell substrata (Young & Nelson 1988; Best & Kidwell 2000b).

Because it is known that the rate of colonization by boring organisms proceeds very rapidly (on the scale of few weeks/months) in modern settings (Tudhope & Risk 1985; Vogel *et al.* 2000), high destruction rate of *Terebratalia* alone is probable not sufficient for explaining the absence of microbioerosion in *Terebratalia* at SEM scale. Active microbial deterioration of punctate shells and the by-products of microbial activity would probably also initially inhibit settlement by borers (Collins 2005: personal communication). Some combination of lower susceptibility to bioerosion and a shorter exposure time of *Terebratalia* in contrast to *Hemithiris* is probably needed.

Effect of intrinsic factors on taphonomic damage

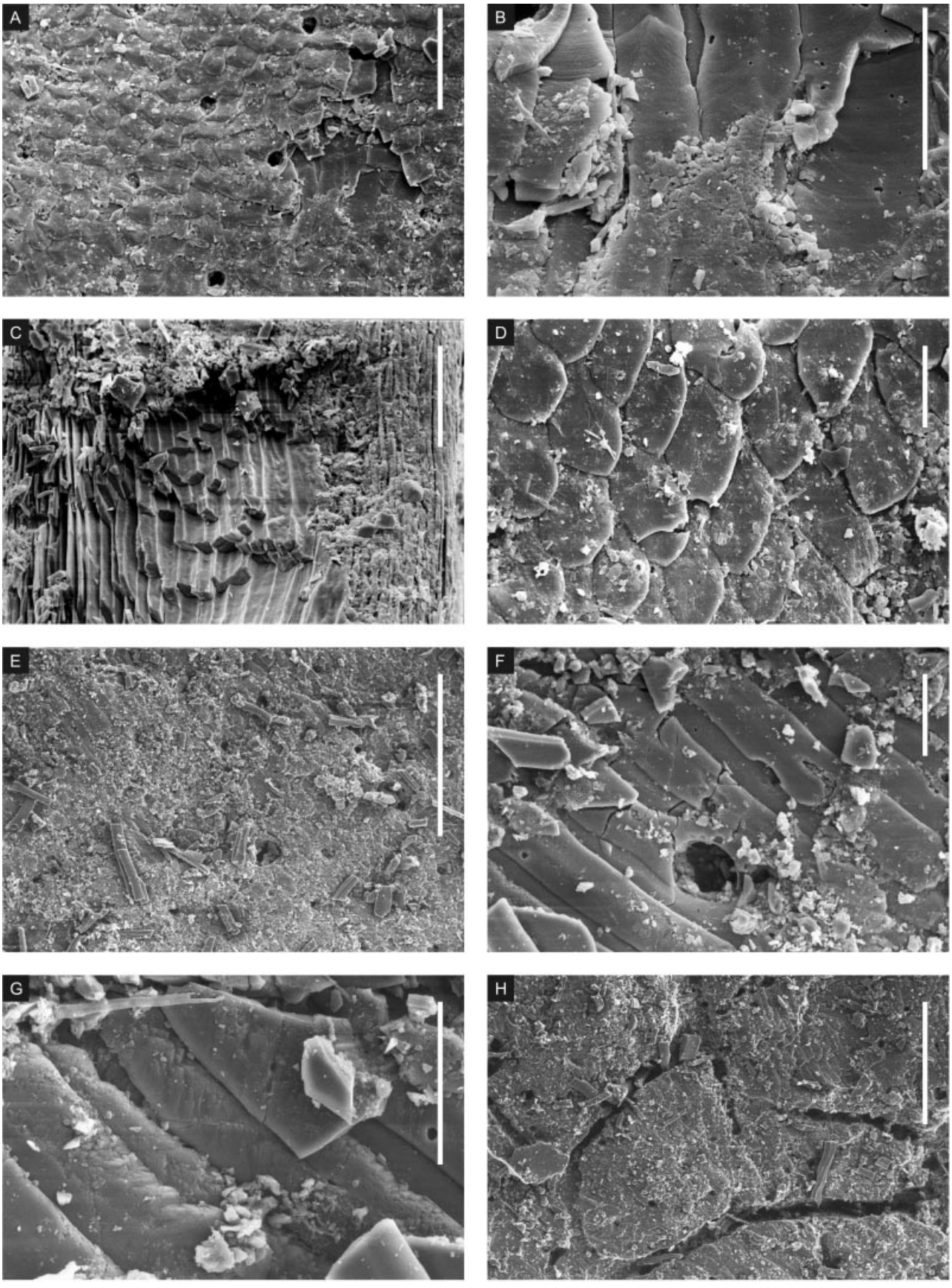
Shell destruction rate. – Under the hypothesis of differential skeletal durability, it is expected that there will be a significant difference in the relative proportion of taphonomic damage between taxa with higher and lower susceptibility to destruction. An implicit assumption is that the rate of destruction is higher for more susceptible taxon, and given the same residence time at the sediment-water interface, more susceptible taxa will suffer higher weight/volume loss than less susceptible taxa (Fig. 10A; Driscoll 1967; Simon *et al.* 1990, 1994; Glover & Kidwell 1993).

However, there is no simple relationship between a rate of taphonomic damage (e.g. in terms of bioerosion) and the rate of shell weight/volume loss. For example, if bioerosion is the main destructive process, the more susceptible taxon will be affected by higher degree of bioerosion after the same amount of time in contrast to less susceptible taxon (Fig. 10A). On the other hand, if rate of weight/volume loss is influenced predominately by maceration, and it occurs more rapidly than the rate of accrual of damage by bioerosion (Fig. 10B), the taxon more susceptible to maceration (i.e. with less durability) will suffer a lower degree of bioerosion (Best & Kidwell 2000b). In Figure 10B (bioerosion rate is the same for both taxa), the less durable taxon can maximally attain a grade of 2 (point A) on the bioerosion scale. In contrast, the more durable taxon, less susceptible to maceration, is exposed longer and therefore can attain a higher degree of bioerosion (point B). Hence, when evaluation of post-mortem durability is based on bioerosion levels only, higher levels of bioerosion may be associated either with less durable (Fig. 10A) or more durable taxon (Fig. 10B). Therefore, perceived patterns of taphonomic damage in terms of taphonomic variables are not simply linked to rates of shell weight/volume loss and moreover are limited by several biasing methodologic factors (e.g. Kidwell *et al.* 2001).

As SEM analysis provides a sensitive tool for detecting differences in intensity of fibre detachment (comparing specimens of similar size and comparable damage scored at the LM scale), the difference in fibre detachment due to microbial degradation can be taken as initial evidence for differential shell maceration rates in *Hemithiris* and *Terebratalia*. Higher bioerosion in *Hemithiris* is probably related to its higher durability combined with preferential attack by borers. This suggests that the rate of destruction due to bioerosion in *Hemithiris* is lower than the rate of destruction due to maceration in *Terebratalia*. Therefore, the null hypothesis regarding no significant difference in damage between organic-rich and organic-poor brachiopods can be rejected. This supports the idea about higher post-mortem susceptibility of organic-rich brachiopods to destruction.

In addition to the higher organic content (Curry & Ansell 1986), higher destruction rates of *Terebratalia* can be related to the punctate shell structure and the type of organic matter. The presence of punctae has a consequence for different architecture (e.g. higher porosity and higher surface area/weight ratio) and therefore potentially higher susceptibility to destruction (Flessa & Brown 1983; Henrich & Wefer 1986). Another difference which potentially leads to differential rates of destruction is the types of organic matter used by terebratulids and rhynchonellids (Jope 1965; Cusack *et al.* 1997). The differences are related to the absolute and relative abundances of amino acids in both intercrystalline and intracrystalline organic matter (Curry *et al.* 1991; Walton *et al.* 1993). In

Fig. 5. Fine-scale alteration of *Terebratalia* on SEM scale. □A. Large-scale detachment of whole sheets of fibres from internal surface, leading to a typical jagged appearance (E332). Scale: 100 μm. □B. Detail of Fig. 5A showing fibre surfaces with incompletely secreted and preferentially fragmented microgrowth increments. Scale: 20 μm. □C. Detail of intra-fibre fragmentation and small-scale dissolution (E332). Scale: 20 μm. □D. Detail of incompletely secreted fibre overprinted by small-scale dissolution (E332). Scale: 2 μm. □E. Altered surface covered with dispersed pyritic grains (E306). Scale: 20 μm. □F. Altered surface with delaminated and fragmented individual fibres (E306). Scale: 20 μm. □G. Altered surface covered with algal filaments and dispersed nannoborings (E305). Scale: 20 μm. □H. Detail of Fig. 5G showing nannoborings. Scale: 2 μm.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addition, the shell proteins of rhynchonellids are probably more resistant to the oxidative effect of the exposure to sodium hypochlorite than the shell proteins of terebratulides (Collins *et al.* 1991: Walton *et al.* 1993).

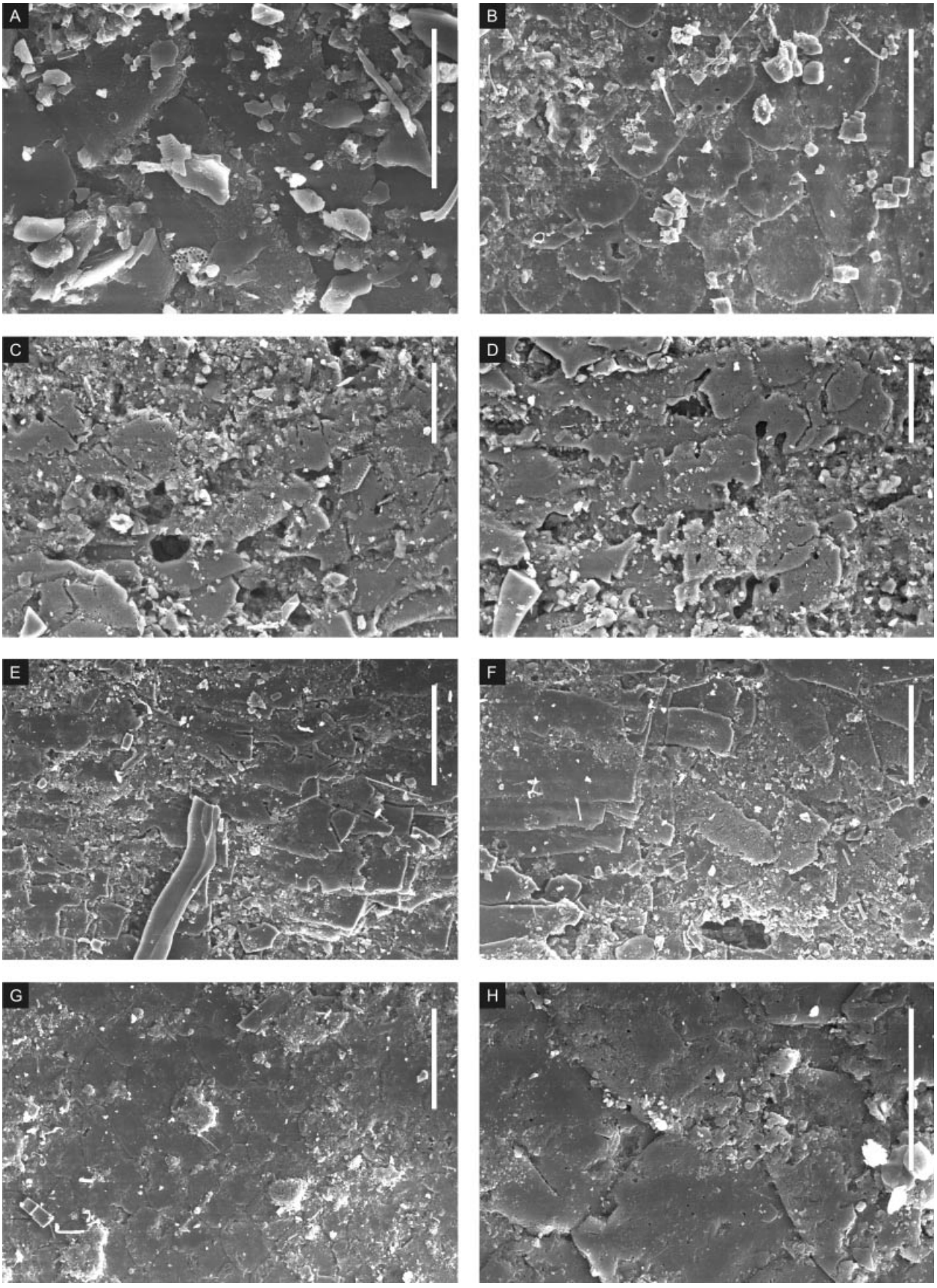
Dead-shell production rate. – A simple consequence of Figure 10C is that, in a time-averaged death assemblage, the same damage patterns of two taxa can be related to differential exposure times of differentially durable taxa. This is related to the equifinality principle – the same preservation may result from different pathways (Lyman 1994). Therefore, phrasing the null hypothesis, regarding post-mortem susceptibility to destruction, in terms of differential damage may be 'too null' when specimens are compared which do not have the same exposure time. If taxa fluctuate in population density in time and certain taxa are added to a death assemblage at a greater rate than other taxa at some intervals, their lower taphonomic damage may be a consequence of the greater abundance of more recently dead cohorts. For example, Pandolfi & Greenstein (1997a) demonstrated this effect in the preservation of branching corals from the Great Barrier Reef. They assumed that a lower damage of branching corals, in contrast to massive and free-lying corals, can be the consequence of a greater abundance of more recently dead branching corals.

It is known that fluctuations in population density (i.e. inconstant dead-shell production rates) may bias the relative abundance of species (Kidwell 2002, Vermeij & Herbert 2004) or its size classes (Tomašových 2004a). However, because differences in age (time since death)-frequency distributions can result from differential production of long and recently dead cohorts, population turnover may also overprint relative proportions of taphonomic variables of death assemblages.

In a setting with no burial and reworking, or when the probability of reworking and burial is the same for each species, age-frequency distribution of dead shells can be characterized as a function of differential shell destruction rates and differential population turnover [see Olszewski (2004) for modeling the effects of reworking and burial]. The effect of shell destruction rates is obvious as it sets limits to exposure time. In an extreme case when dead shells belong to a species which is absent from the living community (e.g. due to a change in ecologic conditions), its dead-shell production rate is zero. In this case, it means that long-dead cohorts with long exposure times will be dominant in a species' death assemblage. Therefore, temporal fluctuations in population density, leading to inconstant rate in production of dead shells, can determine the relative proportions of long and recently dead cohorts. This will thus influence the damage pattern of a death assemblage. Theoretically, this indicates that taxa with the same durability but differential population turnover can be characterized by differential taphonomic damage. Therefore, the null hypothesis concerning the effect of differential durability on damage patterns needs to take into account the potential effect of differential population turnover.

Available data regarding the abundance of *Terebratalia* and *Hemithiris* in life assemblages (Figs 8, 9) allow one to evaluate possible effects of population turnover on their taphonomic damage patterns. The abundance data show a great difference in the relative and absolute abundances between *Terebratalia* and *Hemithiris* and indicate a recently high production of dead shells by *Terebratalia*. A high number of *Terebratalia* added into the death assemblage in the recent periods would lead to a high abundance of recently dead cohorts with shorter exposure times and thus should decrease the proportion of altered *Terebratalia* specimens. This makes the null hypothesis of differential durability for *Terebratalia* and *Hemithiris* more conservative, because the high proportion of recently dead *Terebratalia* should decrease its assemblage-level damage. If *Terebratalia* would show lower damage than *Hemithiris*, the difference in taphonomic damage could be theoretically caused by differential population turnover. This is in contrast to the higher damage of *Terebratalia* predicted by the hypothesis that organic-rich brachiopods have lower durability. The higher intensity of fibre detachment related to maceration observed in *Terebratalia* is in accord with the latter hypothesis. Therefore, the previous interpretation that *Hemithiris* and *Terebratalia* have differential post-mortem susceptibilities to destruction is not discredited. It would be violated if high proportion of altered *Terebratalia* would be associated with low proportion of recently dead cohorts, but this is not the case.

Fig. 6. Fine-scale alteration of *Terebratalia* on SEM scale. □A. Altered surface with delaminated and fragmented individual fibres (E305). Scale: 50 μm. □B. Detail of Fig. 6A, with newly exposed fibre surfaces and with visible intra-fibre fragmentation. Scale: 20 μm. □C. Large-scale exfoliation of fibres leads to freshly exposed fibre surfaces (E305). Scale: 50 μm. □D. Altered shell mosaic covered by algal filaments and formed with loosened fibres and initial intra-fibre fragmentation. Scale: 20 μm. □E. Altered surface covered by detached and fragmented fibres (D524). Scale: 200 μm. □F. Intra-fibre fragmentation and detachment of fibres from the surface (D524). Scale: 20 μm. □G. Exposed fibre surfaces with signs of initial recrystallization (D524). Scale: 20 μm. □H. Sinuous macroborings within highly altered internal surface (D524). Scale: 200 μm.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Theoretically, both dead-shell production and shell destruction rates have thus effects on damage patterns in death assemblages. This is schematically shown in Fig. 11. The highest assemblage-level damage (i.e. shell condition-frequency distribution is dominated by altered shells) is expected in taxa with a high shell destruction rate and a recently low production of dead shells. In contrast, the lowest damage (i.e. shell condition-frequency distribution is dominated by unaltered shells) is expected in taxa with a low destruction rate and a recently high dead-shell production rate. In this respect, the interplay of the two intrinsic factors (i.e. durability and population turnover) typical for *Terebratalia* and *Hemithiris* cause both taxa to be highly altered, although the damages are qualitatively different and due to different taphonomic pathways.

This relationship between shell destruction and dead-shell production rates is conceptually similar to the 'taphograms' (frequency distributions of shell condition) of Fürsich & Flessa (1991). They predict that the taphonomic damage pattern of the whole assemblage will depend on the difference between shell production and destruction. Fürsich and Flessa (1991) were interested in how differential damage patterns can provide a taphonomic clock for time averaging (or rather length of exposure time), depending on different burial and reworking rates (for discussion of taphonomic clock see Flessa 1993; Kidwell 1993, 1998; Martin *et al.* 1996; Meldahl *et al.* 1997). In contrast to those taphograms, the emphasis in this paper is that taphonomic damage patterns are not only a function of extrinsic conditions, but are also influenced by intrinsic taxon-specific shell destruction and dead-shell production rates. This means that differential damage patterns can be produced in the same environment, because of differences in inherent shell durability and population turnover.

Effect of intrinsic factors on community-level abundances

The differences in population turnover and shell destruction rates have an important impact on fidelity patterns (Cummins *et al.* 1986; Staff *et al.* 1986; Nebelsick 1996; Kidwell 2002). High destruction rates of *T. transversa* are somewhat counterintuitive when considering the over-representation of this species in the exhaustive death assemblages (Figs 8, 9). One explanation may be related to the higher maceration/fragmentation rate itself combined with easy identification of even the very small fragments. Kowalewski *et al.* (2003) discussed in detail how fragments can affect fidelity indices. The higher destruction rate can produce a higher proportion of fragments and thus inflate the numerical abundance in the death assemblages. This becomes a problem due to the relatively easy of identification of punctate fragments compared with many bivalve and gastropod fragments of comparable size which cannot be determined at the specific level. Indeed, if fragments are excluded from the death assemblages (RDA), dead rank and relative abundances of *Terebratalia* decline in the RDAs (Figs 8, 9). This indicates that observed over-representation of *Terebratalia* in the EDAs is the consequence of the inclusion of fragments. In addition, the absence of correction for disarticulated elements also inflates the abundance of brachiopods in the EDAs. With the exception of the sample 3-3-D, *Terebratalia* occupies in the RDAs consistently lower ranks and lower relative abundances in comparison to the LAs. Note that Kowalewski *et al.* (2003) did not analyze sample-level abundances of the RDAs because number of species was too small for evaluating Spearman rank correlation. If rank and relative abundances in the RDAs would be biased due to the small number of specimens, the RDAs should not be compositionally segregated from the LAs and EDAs by chance (Table 2). It seems that the slight under-representation of relative and rank abundance of *Terebratalia* in the RDAs is consistent. However, as a constant production of dead shells opposes a very low durability of *Terebratalia*, the high proportion of recently dead shells guarantees that *Terebratalia* is not strongly under-represented in the death assemblages. Similar reasoning was used to explain the fidelity of rank abundances in death assemblages with obviously differentially durable taxa. Kowalewski *et al.* (2003) thus supposed that the relatively good fit of rank abundances of the pooled life and death assemblage (for brachiopods and molluscs) is due to the dominance of the most recent dead cohorts in the death assemblages [see Kidwell (2002) for generality of this hypothesis].

Fig. 7. Fine-scale alteration of *Hemithiris* on SEM scale. □A. Internal surface of unaltered specimen (E359) with microscopic shell debris. Some portions are covered by organic linings. Scale: 20 μm. □B. Altered shell mosaic with dispersed microborings (J421). Scale: 50 μm. □C. Altered specimen with intense microbioerosion and intra-fibre fragmentation (D525). Scale: 20 μm. □D. Altered specimen with intense microbioerosion formed by borings of various diameter and shape (D525). Scale: 20 μm. □E. Detachment and fragmentation of individual fibres associated with high intensity of microbioerosion (D526). Scale: 50 μm. □F. Intense microbioerosion and small-scale dissolution of fibre surfaces (D526). Scale: 50 μm. □G. Altered surface affected by bioerosion. Punctae are infilled by pyritic aggregated (D527). Scale: 50 μm. □H. Detail of Fig. 7G. Scale: 20 μm.

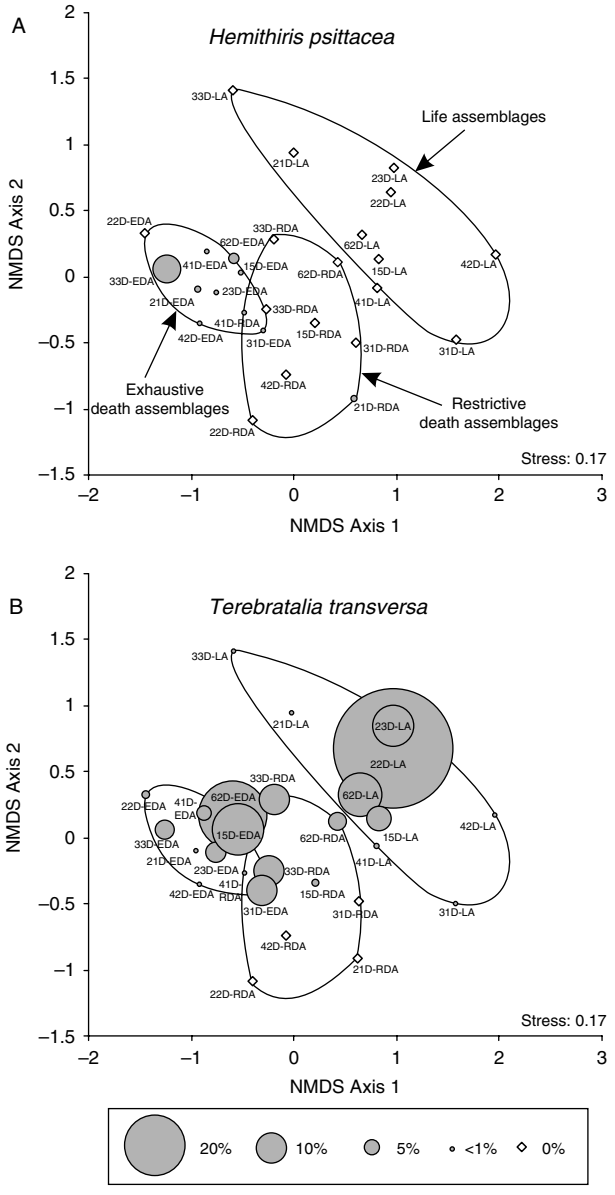


Fig. 8. Non-metric multidimensional scaling (NMDS) ordination of life, exhaustive death (including fragments) and restrictive (without fragments and with correction for disarticulated elements) death assemblages. □A. Bubble plots showing relative proportions of *Hemithiris psittacea*. Note the absence of *Hemithiris* in the life assemblages. □B. Bubble plots showing relative proportions of *Terebratalia transversa*.

In contrast, even though *Hemithiris* is nearly absent in the life assemblage, a high durability ensures its relatively high abundance in the death assemblages. Exclusion of fragments also decreases the relative abundances of *Hemithiris*, but because there are simply no living specimens, they are still over-represented in the death assemblages. This demonstrates that the death assemblages are characterized by disharmonious time-averaging (Kowalewski 1996), i.e. punctate brachiopods represent more recent time periods than impunctate brachiopods. This pattern is comparable to Kidwell's model (2002) of a low destruction rates for rare taxa and a higher destruction rates for abundant taxa. Higher destruction rates of *Terebratalia* can be a general feature of punctate brachiopods characterized by the specific shell structure/organic matter content. If not opposed by high production of dead shells, it may lead to under-representation of rank abundances of punctate brachiopods in death and fossil assemblages in temperate, siliciclastic settings (the durability of punctate brachiopods in carbonate settings is probably higher, see Carroll *et al.* 2003 and Tomašových 2004b). This shows how the delicate interplay of durability with population turnover determines the fidelity of community-level abundance (Fig. 11). As a high population turnover is generally typical of numerically abundant taxa, such taxa have a high probability to be abundant in a death assemblage even when characterized by a low durability. This is because high population turnover can ensure that recently dead cohorts will be still well represented in a death assemblage.

Conclusions

1. At the light microscope scale, there are significant differences in the relative proportion of macrobioerosion between punctate *Terebratalia* and impunctate *Hemithiris* (with exception of the 2.3 mm sieve size fraction). In addition,

Table 2. Results of analysis of similarities (ANOSIM) testing the difference in composition between the LAs, RDAs and EDAs. The *p*-value with asterisk shows the adjusted level of significance after the Bonferroni correction.

	R Statistic	*p*-value (*<0.016)	Actual Permutations	Number of permuted R higher or equal to observed R
Global test	0.56	<0.0001	10000	0
Pairwise comparisons				
Restrictive vs. exhaustive death assemblages*	0.54	<0.0001	10000	0
Life vs. restrictive death assemblages*	0.45	<0.0001	10000	0
Life vs. exhaustive death assemblages*	0.73	0.0001	10000	1

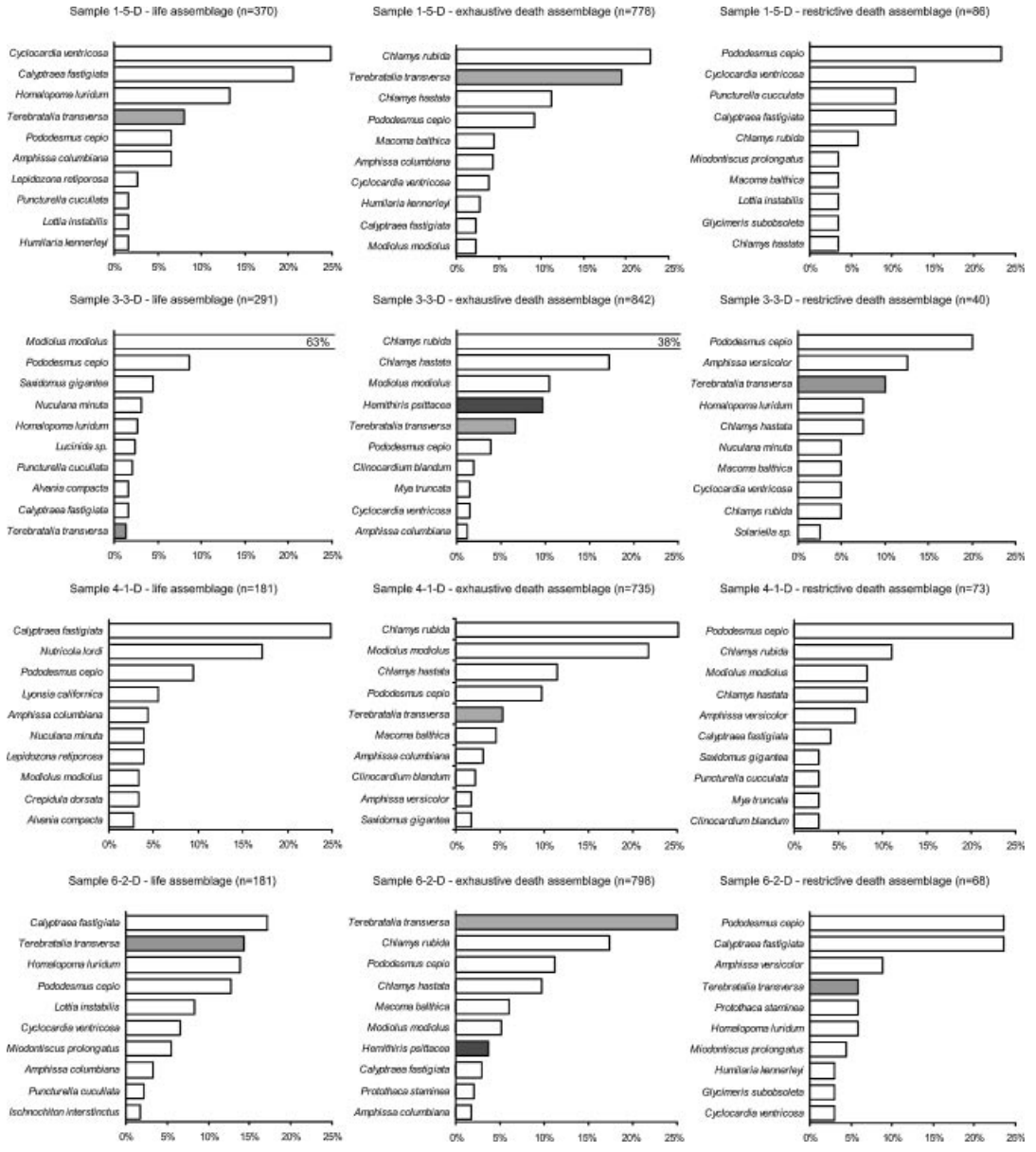
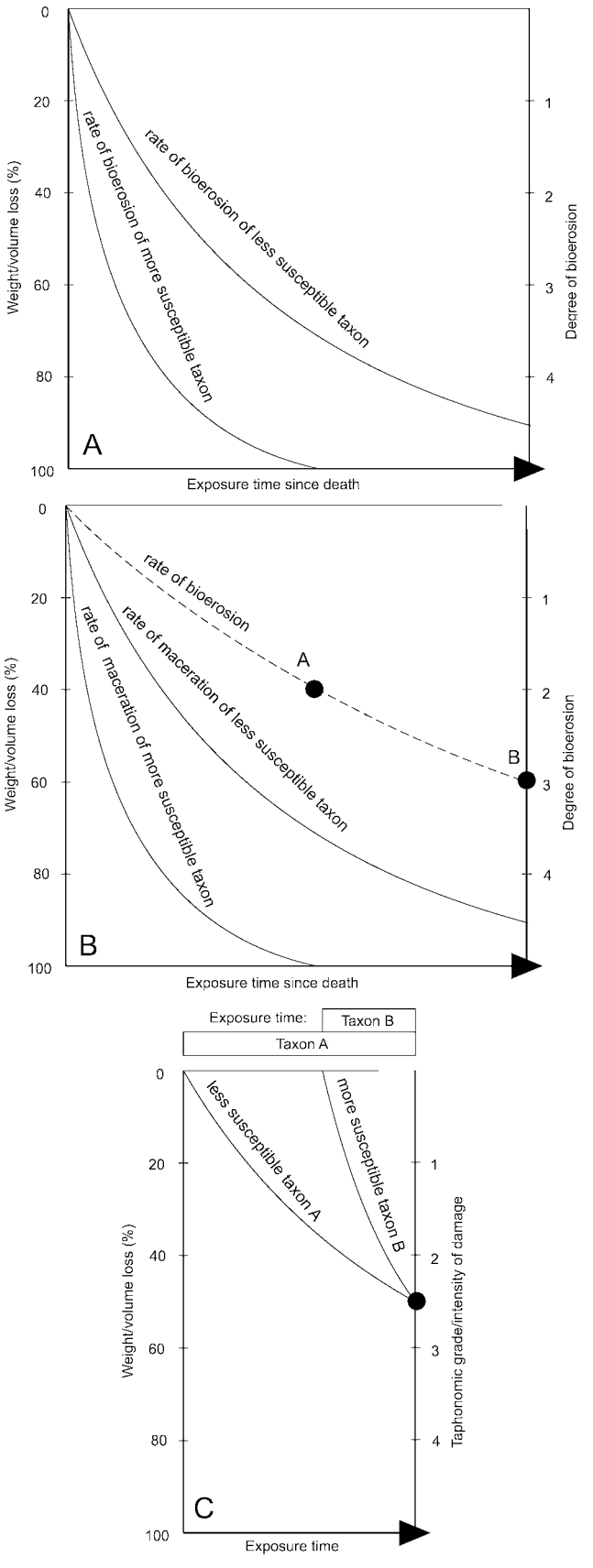


Fig. 9. Relative abundances of *Terebratalia* and *Hemithiris* in life, exhaustive (including fragments) and restrictive (without fragments and with correction for disarticulated elements) death assemblages from four sites. Only the 10 most common species are shown. *Hemithiris* is absent in all life assemblages. In the life assemblage of Sample 4-1-D, *Terebratalia* occupies the 17th rank (1.7%). In the exhaustive death assemblages of Samples 1-5-D and 4-1-D, *Hemithiris* occupies the 16th rank (1.6%) and the 23rd rank (0.5%), respectively.

there is a significant difference in preservation between complete and fragmented *Terebratalia* fragments, in contrast to *Hemithiris*. Fine-scale surface alteration is the taphonomic variable affecting the most specimens of both species and is obviously related to the main destruction process of impunctate *Hemithiris* and punctate *Terebratalia*. Microbioerosion contributes substantially to fine-scale surface alteration in *Hemithiris* at SEM scale. In contrast, fibre detachment is more intensive in *Terebratalia*. Although taphonomic variable rankings at the LM scale are similar in both brachiopods, the differences in macrobioerosion at the LM scale and the consistent difference in the qualitative pattern of fine-scale alteration at SEM scale indicate differences in their taphonomic pathways. Therefore, taphonomic damage of punctate and impunctate brachiopods within one habitat is governed, at least in part, by their difference in shell structure/organic matter content.



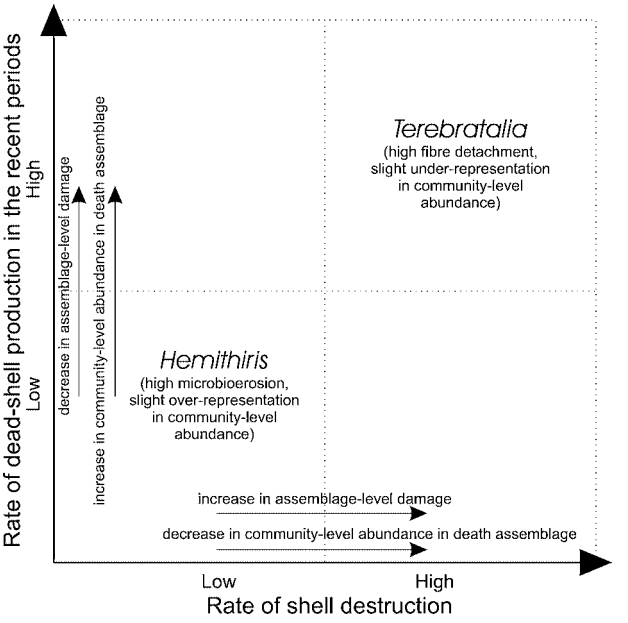


Fig. 11. Schematized effect of a rate of shell destruction (related to postmortem durability) and a rate of production of dead shells in the recent periods, on assemblage-level damage levels and community-level abundance in death assemblages. *Hemithiris* is characterized by high durability but minimal production of dead shells in the recent periods. In contrast, *Terebratalia* is characterized by low durability but constant input of dead shells in the recent periods.

2. The difference in damage is not enhanced by the difference in population turnover because a high turnover rate of *Terebratalia* should result in recently dead cohorts dominated by non-altered *Terebratalia* with a very short exposure time. A probable scenario leading to differential damage pattern is thus related to a lower shell destruction rate of more durable, organic-poor *Hemithiris*, leading to a greater exposure time, probably positively correlated with preferential settlement by borers. The high intensity of fibre detachment in *Terebratalia* suggests its higher rate of microbially-induced shell maceration due to higher shell organic matter content.

Fig. 10. □A. Schematic comparison of two taxa with differential durability. Bioerosion is the main destructive process. The more susceptible taxon is affected by higher degree of bioerosion after the same amount of time in contrast to more durable taxon. □B. Maceration is the main destruction process. Bioerosion rate is slower than maceration rate and is constant for both taxa. The less durable taxon can maximally attain a grade of 2 (point A) on the bioerosion scale. The more durable taxon with lower maceration rate is longer exposed and therefore can attain higher degree of bioerosion (point B). □C. The same damage pattern of two taxa with differential durabilities can be caused by their differential dead-shell production rates.

3. Low destruction rates of *Hemithiris* are responsible for its over-representation in the death assemblages. The constant input of abundant dead shells, related to high abundances in the life assemblages, explains that rapidly macerating *Terebratalia* is not strongly under-represented in the death assemblages. Its community-level abundance would be poorer if the low durability is not opposed by constant input of recently dead shells.

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Appendix 1

Absolute abundances of *Terebratalia* and *Hemithiris* specimens with particular taphonomic damage in four samples and three sieve classes. The first letter of a sample or a sieve indicates its assignment to *Terebratalia* (T) or *Hemithiris* (H).

Samples	H-15D	H-33D	H-62D	T-15D	T-33D	T-41D	T-62D
Disarticulation	14	82	29	150	55	38	196
Fragmentation	14	82	29	148	51	37	193
Internal alteration	12	80	29	141	49	34	151
Internal bioerosion	2	43	8	37	4	7	37
Internal encrustation	4	23	8	19	0	4	24
Total number of specimens	14	82	29	151	56	39	200

Sieve sizes	H-2.3 mm	H-4 mm	H-12 mm	T-2.3 mm	T-4 mm	T-12 mm
Disarticulation	47	99	19	242	173	24
Fragmentation	42	99	12	240	167	22
Internal alteration	42	95	18	199	154	22
Internal bioerosion	9	49	12	49	29	7
Internal encrustation	8	28	7	22	16	9
Total number of specimens						
Disarticulation	49	99	19	242	175	29
Fragmentation	49	99	19	242	175	29
Internal alteration	48	98	19	240	175	29
Internal bioerosion	47	98	19	240	175	29
Internal encrustation	47	98	19	240	175	29

Appendix 2

Absolute, relative and rank abundances of *Terebratalia* and *Hemithiris* in the life, exhaustive and restrictive death assemblages of the samples which were analyzed by Kowalewski *et al.* (2003) and used in this paper.

	Life assemblage – absolute abundance	Exhaustive death assemblage – absolute abundance	Restrictive death assemblage – absolute abundance	Life assemblage – relative abundance	Exhaustive death assemblage – relative abundance	Restrictive death assemblage – relative abundance	Life assemblage – rank	Exhaustive death assemblage – rank	Restrictive death assemblage – rank
Terebratalia transversa									
Sample 1-5-D	30	151	2	8.1	19.4	2.3	4–6	2	11–16
Sample 2-1-D	2	4	0	1.0	0.7	—	13–14	18	—
Sample 2-2-D	32	23	0	39.5	3.6	—	1	4	—
Sample 2-3-D	27	40	4	13.6	6.7	5.6	2	4	6–7
Sample 3-1-D	1	13	0	0.4	2.2	—	22–36	10	—
Sample 3-3-D	4	56	4	1.4	6.7	10	10	5	3
Sample 4-1-D	3	39	1	1.7	5.3	1.4	15–17	5	12–27
Sample 4-2-D	3	8	0	0.5	1.2	—	19–21	14–15	—
Sample 6-2-D	26	200	4	14.4	25.1	5.9	2	1	4
Hemithiris psittacea									
Sample 1-5-D	0	14	0	—	1.8	0	—	12	—
Sample 2-1-D	0	12	1	—	2.0	1.9	—	12	9–17
Sample 2-3-D	0	4	0	—	0.7	0	—	22	—
Sample 3-1-D	0	8	0	—	1.3	0	—	16	—
Sample 3-3-D	0	82	0	—	9.7	0	—	4	—
Sample 4-1-D	0	3	1	—	1.4	1.4	—	20–23	12–27
Sample 4-2-D	0	3	0	—	0.4	0	—	21–23	—
Sample 6-2-D	0	29	0	—	3.63	0	—	7	—