

Effect of Extrinsic Factors on Biofabric and Brachiopod Alteration in a Shallow Intraplatform Carbonate Setting (Upper Triassic, West Carpathians)

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Upper Triassic assemblages containing the terebratulid brachiopod Rhaetina gregaria from a shallow, intraplatform carbonate setting of the Fatra Formation are classified according to biofabric, geometry, and internal structure into 6 deposit types, which are interpreted as: (1) autochthonous primary biogenic, (2) autochthonous winnowed or sediment starved, (3) parautochthonous storm-wave, (4) parautochthonous storm wave/flow, (5) amalgamated storm-reworked, and (6) allochthonous (long-term current/wave) deposits. Their distribution on the bed scale correlates with depth-related environmental gradients in regard to the position of fair-weather wave base, average storm wave base, and maximum storm wave base. The biofabric, geometry, and internal structure of brachiopod deposits were predominantly influenced by: (1) storm activity, related to variations in sedimentation rates and water energy; and (2) original variations in composition and spatial distribution of life associations. Fossil assemblages preserved in brachiopod deposits have a wide range of temporal resolution, ranging from census to environmentally condensed types. Brachiopod assemblages in the storm-reworked deposits probably were affected by catastrophic mortality. The distinction of brachiopod deposit types based on deposit-level criteria does not wholly correspond to the classification of taphofacies types based on intensity of shell alteration. The biofabric and associated deposit-level properties reflect final depositional processes (i.e., the rate and permanence of burial), whereas shell alteration of brachiopods reflects mainly variation in the nature of pre-burial environmental conditions. The lowest degree of alteration (i.e., low levels of bioerosion, micritization, encrustation, and disarticulation) is associated with deposits that were affected by storm-induced sudden burial. In general, settings with high proportions of micritic mud (associated with mixed brachiopod-bivalve associations) are characterized by relatively low alteration of brachiopods. These settings are in sharp contrast to hard-bottom settings (associated with coral associations), in which bioerosion and micritization are high. This difference in shell alteration is the effect of extrinsic factors related to lower turbidity, higher proportion of hardparts and higher storm reworking in latter settings.

Autochthonous/parautochthonous benthic associations dominated by the short-looped terebratulid Rhaetina gregaria are typical of settings below the fair-weather wave base, with background low-energy condition. This is in contrast to high-energy/hard-bottom occurrences of this association from other regions. The difference in preservation

potential of brachiopods due to differential extrinsic factors (e.g., between hard- and soft-bottom settings) can substantially bias the understanding their ecology and temporal shifts in environmental preferences. Data about substantial bioerosion/micritization of brachiopods in some deposit types indicate their higher durability and inherently higher preservation potential in contrast to actualistic data about the poor resistance of modern brachiopods to destruction.

INTRODUCTION

In actualistic studies of death assemblages, quantitative analyses based on taphonomic signatures (the measures that detect intensity and magnitude of shell alteration) have been used to define taphofacies types that are well correlated with environmental gradients (Powell et al., 1989; Meldahl and Flessa, 1990; Staff and Powell, 1990; Kowalewski et al., 1994; Nebelsick, 1999). In addition to taphonomic signatures, deposit-level properties related to biofabric, geometry, and internal structure of deposits are used to define taphofacies of fossil assemblages (Brett and Baird, 1986; Speyer and Brett, 1988, 1991; Olóriz et al., 2002; Wani, 2003) because they help incorporate effects of background and episodic processes, such as bioturbation, long-term wave activity, or episodic storm activity. The term shell concentration often is used in taphonomic analyses of fossil assemblages (Kidwell et al., 1986). Definitions of shell concentrations are similarly based on both their deposit-level properties (biofabric, geometry, internal structure) and the taphonomic signatures (Parsons et al., 1988; Kidwell, 1991a; Fürsich and Oschmann, 1993; Abbot, 1997; Simões and Kowalewski, 1998; Fürsich and Pandey, 1999; Mandic and Piller, 2001; Nebelsick and Kroh, 2002; Zuschin and Stanton, 2002). A comparative approach based on combining both of these data types can be used to provide a high-resolution tool for interpretation of paleoenvironment.

Although there is a lot of actualistic information about the variation of taphonomic signatures of molluscs (see Kidwell et al. 2001), there are few actualistic studies concerning alteration of articulate brachiopods across environmental boundaries. Because articulate brachiopods are characterized by a unique shell structure and composition, further study concerning their alteration patterns and preservation potential is needed. Some taphonomic signatures are relatively straightforward. For example, an abundance of articulated shells nearly excludes the possibility of long-term mechanical reworking. However, shell

resistance to disarticulation when exposed on the seafloor, as well as the role of organic-matrix decay on rates of disarticulation, are poorly known (e.g., Daley, 1993). Rather than use taphonomic signatures as unambiguous evidence of environmental conditions in taphofacies analyses of fossil assemblages, their resolution potential for paleoenvironmental interpretation should be tested independently in taphonomic analyses.

Therefore, these two types of taphonomic data (deposit-level properties and taphonomic signatures), potentially reflecting different processes operating at different scales (Davies et al., 1989a, b; Fürsich, 1995; Behrensmeier et al., 2000), are analyzed separately in this study of brachiopod assemblages. Two specific aspects are addressed here: (1) the variation in biofabric (i.e., three-dimensional arrangement of skeletal elements), geometry, and internal structure of brachiopod deposits with respect to environmental gradients; and (2) the effect of extrinsic environmental factors on brachiopod shell alteration. The first aspect provides the basic framework for genetic interpretation of brachiopod deposits. The second aspect provides detailed insights into taphonomic pathways (i.e., the rates, selectivity, and importance of particular destructive and constructive processes) during the formation of death assemblage (Meldahl and Flessa, 1990; Kowalewski et al., 1994; Macchioni, 2000; Wani, 2001). This aspect is very important because it enables testing of differences in preservation potential of brachiopod associations among settings and addressing of questions related to its compositional fidelity (i.e., the quantitative faithfulness of the record of population-community-level features to the original biological signal; Behrensmeier et al., 2001). In addition to addressing the role of extrinsic factors in alteration and preservation potential of brachiopod associations at this local scale, this taphonomic analysis provides new insights into the relatively poorly known preservation potential of brachiopods, information that is relevant to the interpretation of brachiopod distribution patterns at all scales.

In the first part of this work, deposit-level properties are analyzed and interpreted in terms of environmental gradients. In the second part, the variation of taphonomic signatures is evaluated with respect to: (1) previously defined brachiopod deposit types, (2) benthic association types, and (3) deposit types with different packing density. Correlation of taphofacies types based on taphonomic signatures with the classification of brachiopod deposit types based on their deposit-level properties also is examined.

GEOLOGIC SETTING

Paleogeography

During the Upper Triassic, the West Carpathians were situated on the extensive epeiric carbonate platform on the northwestern margin of the Tethys Ocean in the subtropical climatic belt (Fig. 1A). The Rhaetian Fatra Formation, which displays considerable facies variation both horizontally and vertically, was deposited in the shallow-water, intraplatform, marine, predominantly carbonate setting of the Fatric Unit (Central West Carpathians; Michalík, 1982; Fig. 2). Carbonate deposition is characterized by reduced terrigenous input and low subsidence re-

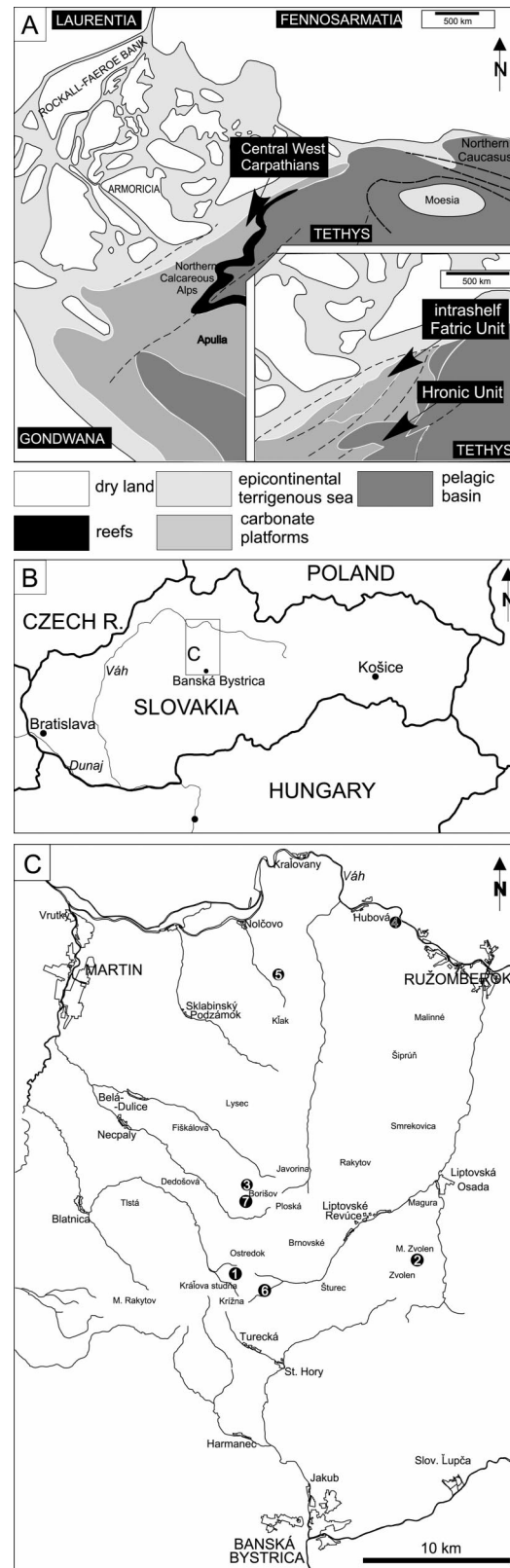


FIGURE 1—Paleogeographic and geographic maps of the study area. (A) General paleogeographic position of the Fatric Unit (Central West Carpathians) in the Upper Triassic (Norian/Rhaetian; modified after Michalík (1994). (B) Regional map with location of the study area. (C) Geographic location of sections in the Vel'ká Fatra Mts. 1—Dedošova; 2—Malý Zvolen; 3—Borišov; 4—Bystrý potok; 5—Ráztoky; 6—Krizna; 7—Belianska.

regime. At the beginning of the Jurassic, the depositional regime in the Fatric Unit was replaced abruptly by terrigenous sedimentation of the Kopianec Formation (Hettangian–Early Sinemurian). The scale of observation in this study includes only a small portion of the intraplatform setting of the Fatric Unit, preserved in a 40-km-long transect in the Veľká Fatra Mountains (central Slovakia). Here, the Fatra Formation is formed by four large-scale, 6–15-m-thick, shallowing-upward sequences bounded by laterally extensive unconformities (Tomašových, 2004).

Brachiopods and Benthic Associations

Brachiopods are represented most commonly by the dielasmatid terebratulid *Rhaetina gregaria* (Suess), which is characterized by middle-sized to moderately large (15–25 mm long in adult stage), ovate-subpentagonal, smooth bi-convex shells (Michalík, 1975; Pearson, 1977). The shell structure of relatively thin valves (0.25–0.4 mm) is punctate. The second common species is represented by middle-sized (20 mm in length), ribbed, semipyramidal spiriferinid *Zugmayerella uncinata* (Schafhäütl), with punctate shell structure and 0.3–0.5 mm thick valves. Both taxa have cyrtomatodont (interlocking) hinges, which indicates lower susceptibility to disarticulation. However, *Zugmayerella* is characterized by the presence of a strophic hinge line and relatively poor development of interlocking characters (socket ridges, teeth morphology; Pearson, 1977; Siblík, 1998). The shell structure of both species is characterized by the presence of organic-rich primary and secondary layers only; a tertiary layer is not developed. The punctate *Rhaetina pyriformis* (Suess), impunctate rynchonellid *Austrirhynchia cornigera* (Schafhäütl), and inarticulate *Discinisca suessi* (Gümbel) are much less common.

Four brachiopod associations have been recognized primarily by the taxonomic composition and relative abundance of taxa (Tomašových, 2002). Brachiopods occur either in (1) level-bottom benthic associations, predominantly with soft substrata and dispersed hard (shelly) substrata, including (1a) *Rhaetina* and (1b) *Rhaetina-Zugmayerella* associations; (2) benthic associations on the transition between level-bottom and patch-reef structures with higher proportions of hard microsubstrata and high small-scale spatial variability (*Rhaetina-Retiophyllia*-solenopora-ceans association); or (3) as subordinate components in patch-reef/biostrome associations with dominant retiophyllid corals providing the highest proportion of hard substrata (*Retiophyllia* association). It is important to note that this distinction does not incorporate any taphonomic data, and should reflect primary ecologic subdivision of non-random recurrent community relicts. Therefore, the same type of benthic association can occur in various types of brachiopod deposits, which are defined according to their taphonomic properties. In the following text, the first two types are designated as brachiopod-bivalve associations, and the latter two as coral associations. The term assemblage refers here to any group of organisms from a sample or locality, with no ecologic meaning (Fürsich, 1990).

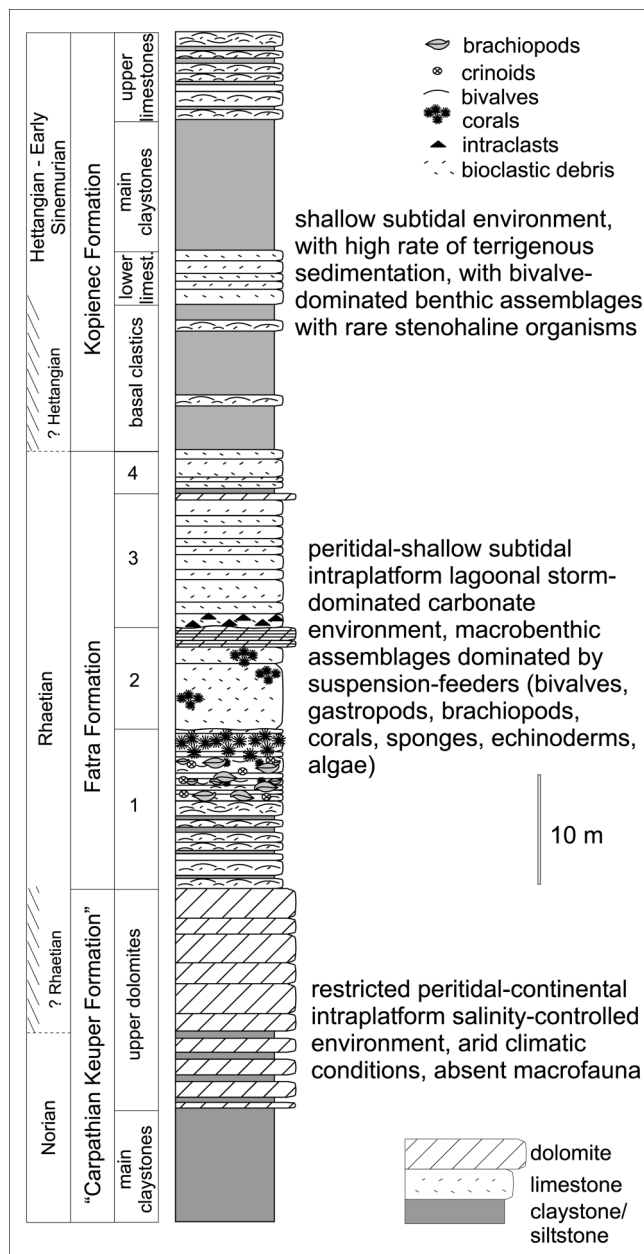


FIGURE 2—Basic lithostratigraphic scheme of the Uppermost Triassic–Lowermost Jurassic strata in the Fatric Unit, Central West Carpathians. The subdivision of the Fatra Formation corresponds to four large-scale shallowing-upward sequences.

METHODS

Sedimentologic, taphonomic, and paleobiologic data of deposits with brachiopod remains were described in the field, from 7 sections (Dedošova, Ráztoky, Malý Zvolen, Bystrý potok, Krížna, Belianska, and Borišov, Figs. 1B–C, 3). The term shell concentration is used here to denote deposits of any geometry containing a relatively dense accumulation of biogenic hardparts larger than 2 mm (Kidwell, 1991a; Fürsich, 1995). In order to trace the taphonomic pathways of the brachiopods, it is also necessary to compare samples in which brachiopods are not the dominant component. Therefore, the general descriptive term bra-

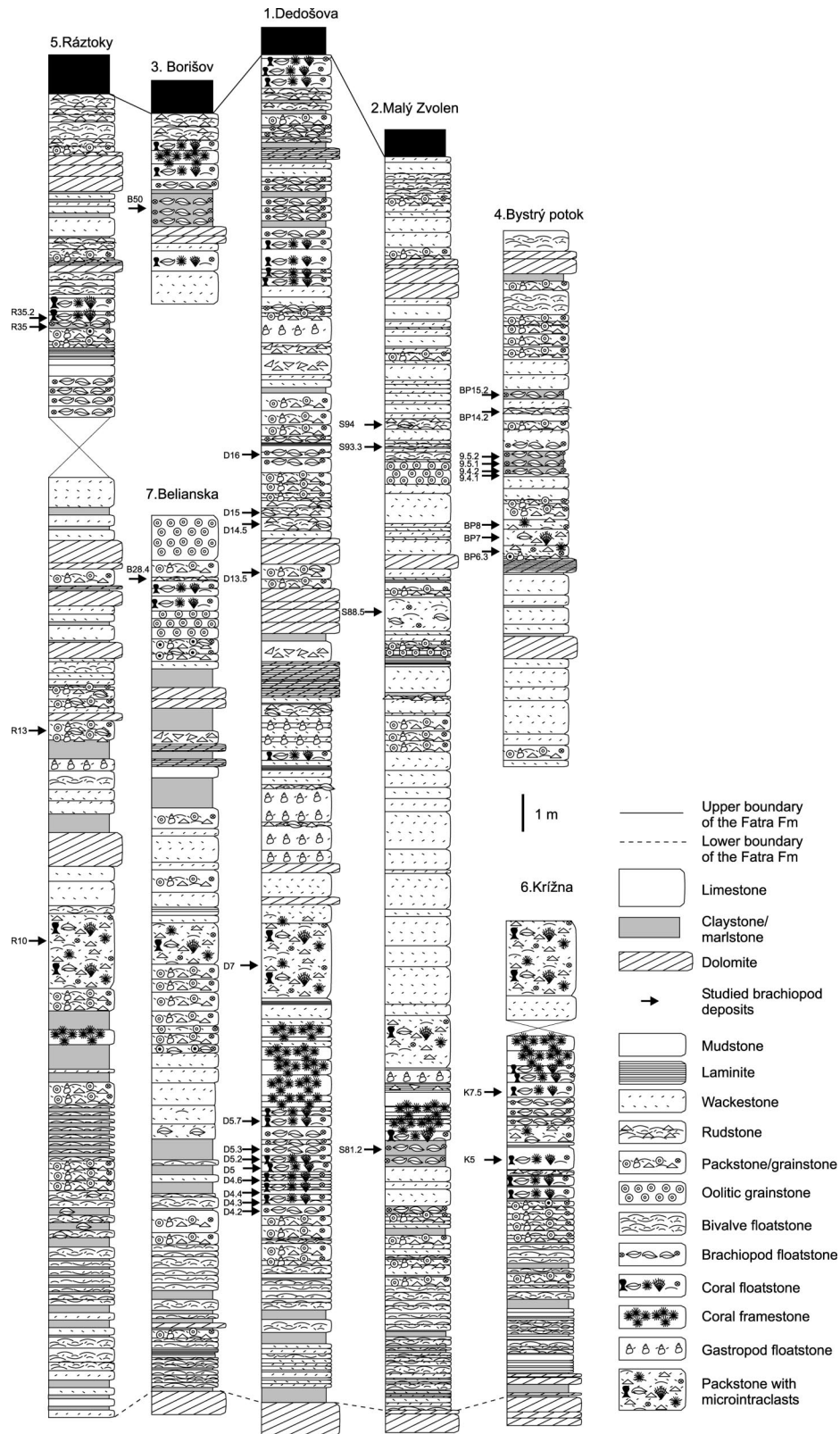


FIGURE 3—Sections of the Fatra Formation with brachiopod deposits. Arrows point to brachiopod deposits that were studied in detail (Table 1). From Tomašových (2004), with permission of Springer-Verlag.

chiopod deposit is used here to refer to any brachiopod-bearing deposit. Brachiopod deposits have been classified into several types on the basis of bed-level properties (sorting, packing, orientation, geometry, internal structure, and thickness). Microfacies types of Dunham (1962) and Embry and Klovan (1972) and bed geometry/internal structure have been used for this classification of brachiopod deposit types.

The biofabric and geometry of deposits were described using the scheme of Kidwell et al. (1986) and Kidwell and Holland (1991). Allochem abundance was estimated using the comparative method of Baccelle and Bosellini (1965) and Schäfer (1969). In addition to brachiopods, deposits contain other common benthic components, such as bivalves, echinoderms, corals, sponges, and calcareous algae. Because these taxa are characterized by differences in shell structure and mineralogy, only the taphonomic signatures of the most common terebratulid brachiopod *Rhaetina*, which occurs in all types of brachiopod beds, have been compared. Although the resolution of taphofacies types based on a single target taxon may be different from that based on the total assemblage (Kidwell et al. 2001), variation in intrinsic factors is minimized, and differences between taphofacies types can be related more directly to extrinsic environmental factors. For some samples that contain other brachiopod taxa, additional data are included for the spiriferinid *Zugmayerella*. For all samples, the proportion of disarticulation and type of shell infilling were determined in the field and the degree of fragmentation, micritization, bioerosion, and encrustation were scored using thin sections. Within-sample variation in preservation (pedicle/brachial valve ratio, disarticulation of *Rhaetina* versus *Zugmayerella*) was obtained from hand sampling of specimens. The proportion of disarticulated specimens and presence of sparitic infillings were scored qualitatively. If no articulated shells were observed, disarticulation was scored as high. When there was a mixture of articulated shells and disarticulated valves, disarticulation was designated as medium. In the case of dominance by articulated shells, disarticulation was scored as low. Shell sparitic infillings were recorded as abundant or rare. Forty-four beds were studied at this scale (Table 1).

For quantitative study of the degree of fragmentation, bioerosion, micritization, and encrustation, 32 thin sections of selected beds were investigated. All brachiopod remains above 2 mm were scored from thin sections using 50x magnification under a light binocular microscope. Due to differences in packing density and the limited size of thin sections, the number of brachiopod remains ranges from a low of 10 to a high of 87 specimens. These relatively small sample sizes may cause the alteration frequency distributions to be unstable (see Kidwell et al., 2001). Consistent scoring of the taphonomic variables bioerosion and encrustation in compact and lithified carbonate deposits often is difficult because the outermost shell layers frequently fall away from specimens, and the outer and inner surfaces are often covered by an early-diagenetic microsparitic calcite layer. Due to intrastratal pressure solution, stylolites also often dissolve the surface of brachiopod shells. This signature of late-diagenetic origin is easily recognized in thin sections, can be confused with corrosion or bioerosion in specimens sampled by hand. In addition to

this, the taphonomic analysis of thin sections allows recognition of the preservation of signatures that are not visible on the bioclast surfaces, thus distinguishing multiple taphonomic events (Brachert et al., 1998; Nebelsick and Bassi, 2000) and excluding the collecting bias due to selective hand sampling.

For the degree of micritization, bioerosion, and encrustation, a taphonomic grade of good (alteration absent), fair (alteration moderately present), or poor (alteration dominant) has been assigned to each of the brachiopod remains (Fig. 4). Micritization corresponds predominantly to the destructive type, characterized by an altered and irregular bioeroded brachiopod surface in contact with a micritic rim. Bioclasts entirely covered by thick micritic rims were scored as poor. Micritic rims developed only on a limited portion of the surface were scored as fair. A grade of good corresponded to the absence of destructive micritization. Similarly, in the case of bioerosion and encrustation, specimens that were bioeroded/encrusted around the whole surface were designated as poor, only on some parts as fair, and unaffected as good. In order to pool samples into taphofacies types according to their taphonomic signatures and compare these groupings with the classification of deposit types, a Q-mode hierarchical cluster analysis using the squared Euclidean distance measure and the Ward method as the clustering technique was performed.

RESULTS

Brachiopod Deposits

Based on the deposit-level properties (biofabric, geometry, and internal structure), 6 types of brachiopod deposits are defined: (1) bio-floatstones, (2) pavements of bio-packstones, (3) bio-floatstones with complex internal structure (CIS), (4) biointra-packstones with CIS, (5) thick biointra-packstones, and (6) biointra-rudstones. These properties are summarized in Table 2.

(1) *Bio-floatstones*: These deposits contain 10–30-cm-thick bioturbated beds with dispersed to loosely packed, poorly sorted, randomly oriented bioclasts (Fig. 5B, D). Two brachiopod-bivalve associations occur in this type. In the first, the brachiopod *Rhaetina gregaria* is dominant (Fig. 5C) and bivalves (*Atreta*, *Chlamys*, *Rhaetavicula*, *Plagiostoma*) are subordinate. The second consists of a moderately diverse association (Fig. 5A) composed predominantly of the terebratulid *Rhaetina gregaria*, the spiriferinid *Zugmayerella uncinata*, and the bivalve *Atreta intusstriata*. Other brachiopods (*Discinisca*, *Austrirhynchia*) and bivalves (*Actinostreon*, *Modiolus*, *Pteria*, *Antiquilima*, *Rhaetavicula*, *Plagiostoma*, *Liostrea*) are less abundant. In both types, brachiopods constitute about 15–25% of rock volume. Locally, *Rhaetina* forms small-scale clusters (10–20 cm in length), 1–2 shells thick, with pedicle openings oriented predominantly downwards (Fig. 5D). In coral associations, the significant component is formed by dispersed coral colonies of *Retiophyllia* and *Astraeomorpha*, calcareous sponges, and solenoporacean algae; brachiopods (*Rhaetina*) are less common (5% of rock volume). Dispersed coral colonies are usually preserved in life orientation. Disarticulated crinoid ossicles, echinoid spines, gastropods, and ostracodes are common. This type typically alternates with the second deposit type.

TABLE 1—Database of brachiopod deposits of the Fatra Formation (Vel'ká Fatra Mts.), with their characteristic features (rand. = random; mod. = moderate).

Sample	Thickness	Packing	Sorting	Orientation	Internal structure	Base	Facies	Disarticulation	Sparitic infilling
DD4 (1)	12 cm	dispersed	poor	random	simple		wackestone	medium	rare
BP9.4.1a	17 cm	loose	poor	random	simple		floatstone	medium	rare
BP9.4.2	14 cm	loose	poor	random	simple		floatstone	medium	rare
BP9.4.3a	7 cm	loose	poor	random	simple		floatstone	medium	rare
BP9.4.4	8 cm	dispersed	poor	random	simple		floatstone	low	rare
BP15.2	25 cm	loose	poor	random	simple		floatstone	medium	rare
DD5.7 (1)	12 cm	loose	poor	random	simple		floatstone	medium	
DD16	25 cm	dispersed	poor	random	simple		floatstone	medium	
B50	25 cm	loose	poor	random	simple		floatstone	low	rare
S81.2	30 cm	loose	poor	random	simple		floatstone	medium	rare
R35	10 cm	loose/dense	poor	random	simple		floatstone	medium	rare
BP9.4.1b	1 cm	dense	moderate	concordant	simple		packstone	high	rare
BP9.4.3b	1 cm	dense	moderate	concordant	simple		packstone	high	rare
BP9.5.1b	1 cm	loose/dense	poor/mod.	concordant	simple		packstone	high	rare
DD4.2 (1)	15 cm	loose/dense	poor	rand./nesting	complex	erosional	floatstone	low	abundant
DD4.6a (2)	15 cm	loose	poor	random	complex	erosional	floatstone	low	abundant
DD5.2 (1)	18 cm	loose/dense	moderate	rand./nesting	complex		floatstone	low	abundant
DD4 (3)	25 cm	loose/dense	poor	rand./nesting	complex		floatstone	medium	
DD4.2 (3)	20 cm	loose	poor	rand./nesting	complex		floatstone	medium	
B28.4	10 cm	loose/dense	poor	random	complex	erosional	floatstone	low	abundant
BP9.5.1	5 cm	loose/dense	poor	rand./nesting	simple		floatstone	low	
BP9.5.2	5 cm	loose/dense	poor	rand./nesting	simple		floatstone	low	
DD4.3 (3)	15 cm	dense	moderate	concordant	complex	erosional	packstone	high	
DD4.4 (3)	20 cm	dense	good	concordant	complex	erosional	packstone	high	
DD4.6b (2)	13 cm	dense	good	concordant	complex	erosional	packstone	high	
DD5 (1)	25 cm	dense	moderate	concordant	complex	erosional	packstone	medium	
DD5.3 (1)	30 cm	loose/dense	moderate	random	complex		packstone	medium	abundant
S88.5	30 cm	loose/dense	moderate	concordant	complex		packstone	high	
S93.3	4 cm	loose	moderate	concordant	simple		wackestone	high	
R35.2	20 cm	dense	moderate	random	complex		packstone	medium	
DD7	200 cm	dense	bimodal	random	simple	erosional	packstone	high	
BP6.3 (1)	30 cm	loose/dense	bimodal	random	simple	erosional	packstone	high	abundant
BP7	42 cm	loose/dense	bimodal	random	simple	erosional	packstone	high	
BP8	28 cm	dense	bimodal	random	simple	erosional	packstone	high	
R10	200 cm	loose/dense	bimodal	random	simple	erosional	packstone	high	
R13	52 cm	dense	bimodal	random	simple		grainstone	high	
DD13.5	40 cm	dense	good	random	simple		packstone	high	
K5	30 cm	dense	good	random	simple		grainstone	high	
DD14.5	25 cm	dense	good	concordant	simple	erosional	rudstone	high	
DD15	20 cm	dense	good	random	simple	erosional	rudstone	high	
BP6.3 (2)	30 cm	dense	good	random	simple	erosional	rudstone	high	
BP14.2	10 cm	dense	good	concordant	simple	erosional	rudstone	high	
S94	28 cm	dense	good	concordant	simple	erosional	rudstone	high	

(2) *Bio-packstone (Pavements)*: Pavements less than 1 cm thick on the bedding planes of limestone beds are characterized by loose/dense packing, poor/moderate sorting, and predominantly concordant orientation of bioclasts (Fig. 6A–F). Microstylolites and residual-clay seams are common; thin Fe-crusts are preserved locally. Bedding planes are locally completely covered by small clusters of cementing bivalves (*Atreta*, Fig. 6C) or well-preserved crinoidal ossicles (Fig. 6D). Mixed brachiopod-bivalve associations are of moderate diversity and consist of the brachiopods *Rhaetina gregaria*, *Zugmayerella uncinata*, and *Austrirhynchia cornigera*, and the bivalves *Atreta intusstriata*, *Rhaetavicula contorta*, *Palaocardita austriaca*, and *Chlamys valoniensis*.

(3) *Bio-floatstones with Complex Internal Structure*: 5–25-cm-thick beds or lenses of this type commonly contain densely/loosely packed and poorly sorted brachiopods (Fig. 7B, C). Three-dimensional clusters with randomly orient-

ed brachiopods, several dm in length, are typically present in this type. Locally, nesting and stacks of convex-down disarticulated valves are observed. The typical feature is a complex internal structure (CIS) within a single limestone bed, where this bio-floatstone alternates with thin (2–5 mm), well-sorted, allocthonous calcarenitic packstones with erosional bases (Fig. 7A, D). The matrix consists either of calcilutite (micrite) or well-sorted calcisiltite (unidentifiable bioclastic debris). The brachiopod *Rhaetina gregaria* forms almost monospecific concentrations (15–35% of rock volume, Fig. 7E). Other components (*Atreta intusstriata*, echinoderms, algae) are less common. This deposit type is rather discontinuous laterally and often passes into or alternates with the biointra-packstones with CIS.

(4) *Biointra-packstones with Complex Internal Structure*: 4–30-cm-thick beds of this type commonly display a biofabric ranging from moderately/bimodally sorted and

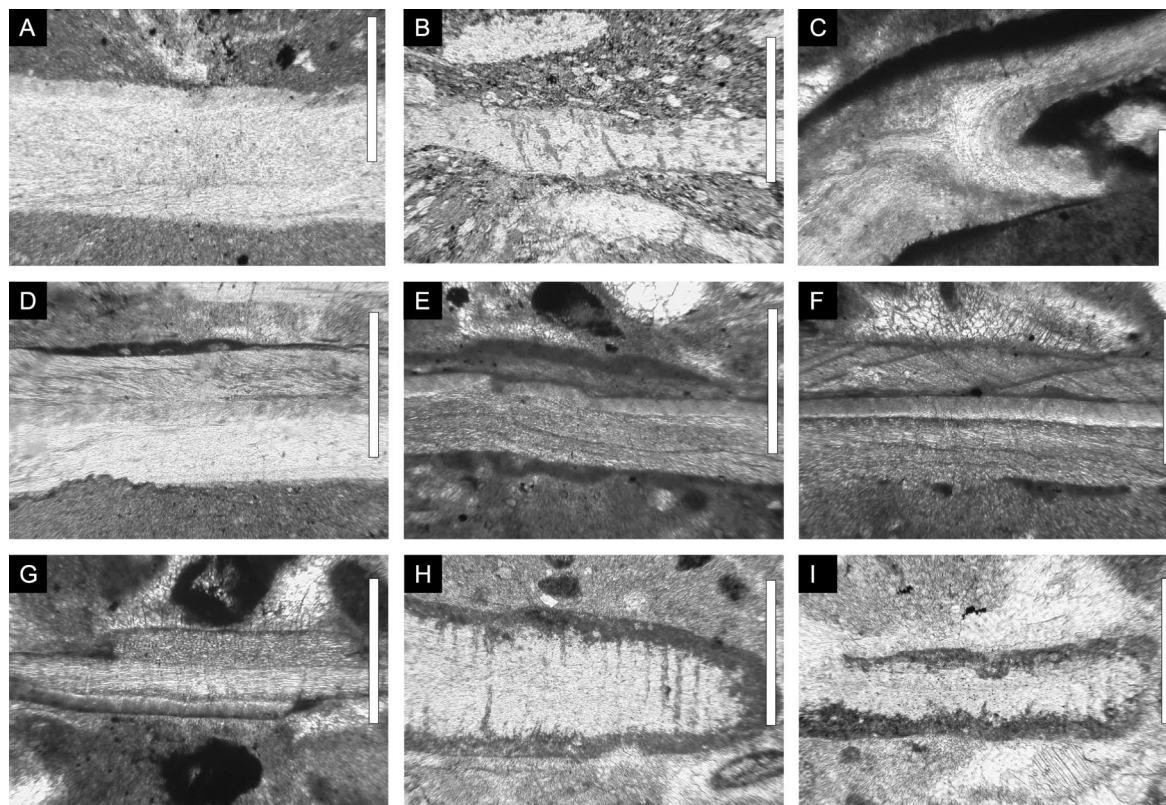


FIGURE 4—Taphonomic grades of brachiopods in thin-sections; scale bars = 0.5 mm. (A) Good, without any taphonomic alteration. (B) Bioerosion: poor (intense penetration). (C) Micritization: poor (valve covered by thick micritic rims). (D) Encrustation: fair (some portion is encrusted by foraminifers). (E, F) Encrustation: poor (cementing bivalves and foraminifers). (G) Bioerosion and micritization: fair. (H) Micritization: poor (valve completely covered by destructive micritic rims). (I) Poorly preserved, rounded fragment with high degree of micritization and bioerosion.

TABLE 2—Deposit-level taphonomic properties and signatures of 6 basic deposit types and their basic interpretation (concord. = concordant; hab. = habitat; NSWB = normal storm wave base; FWWB = fair-weather wave base).

Taphonomic signatures and bed-level properties	Bio-floatstones	Bio-packstone-pavements	Bio-floatstones with complex internal structure	Biointra-packstones with complex internal structure	Thick-bedded biointra-packstones	Biointra-rudstones
Disarticulation	medium	high	low	medium-high	high	high
Fragmentation	53.3–100%	81.8%	10–80.4%	85.5–100%	74.7–100%	83.9–100%
Bioerosion	11.8–93.4%	2.6%	0–25%	15.9–100%	78.9–100%	64–97.2%
Micritisation	0–73.3%	18%	0–22.5%	18.3–58.3%	65.4–93.3%	16.4–94.2%
Encrustation	0–16.6%	7.7%	0–12.2%	4.9–18.4%	0–12.2%	1.6–23.1%
Spartic infillings	rare	rare	abundant	abundant	abundant	abundant
Assemblage	pauci/poly-specific	pauci/poly-specific	paucispecific	polyspecific	polyspecific	polyspecific
Packing	dispersed-loose	loose-dense	loose-dense	dense	loose-dense	dense
Sorting	poor	poor-moderate	poor-moderate	moderate-good	bimodal	good
Orientation	random	concordant	random	random-concord.	random	concordant
Geometry	bed	pavement	bed-lense	bed	bed	bed
Internal structure	simple	simple	complex	complex	simple	simple
Interpretation	within-habitat	within-habitat	within-hab./census	within/out of hab.	multiple-hab.	multiple/out of hab.
Depositional process	minor reworking/bioturbation	winnowing/starvation	storm-reworking-storm wave	storm-reworking-storm wave/flow	storm-reworking-amalgamation	long-term wave/current
Setting	below NSWB	below NSWB	above NSWB	above NSWB	above NSWB	above FWWB

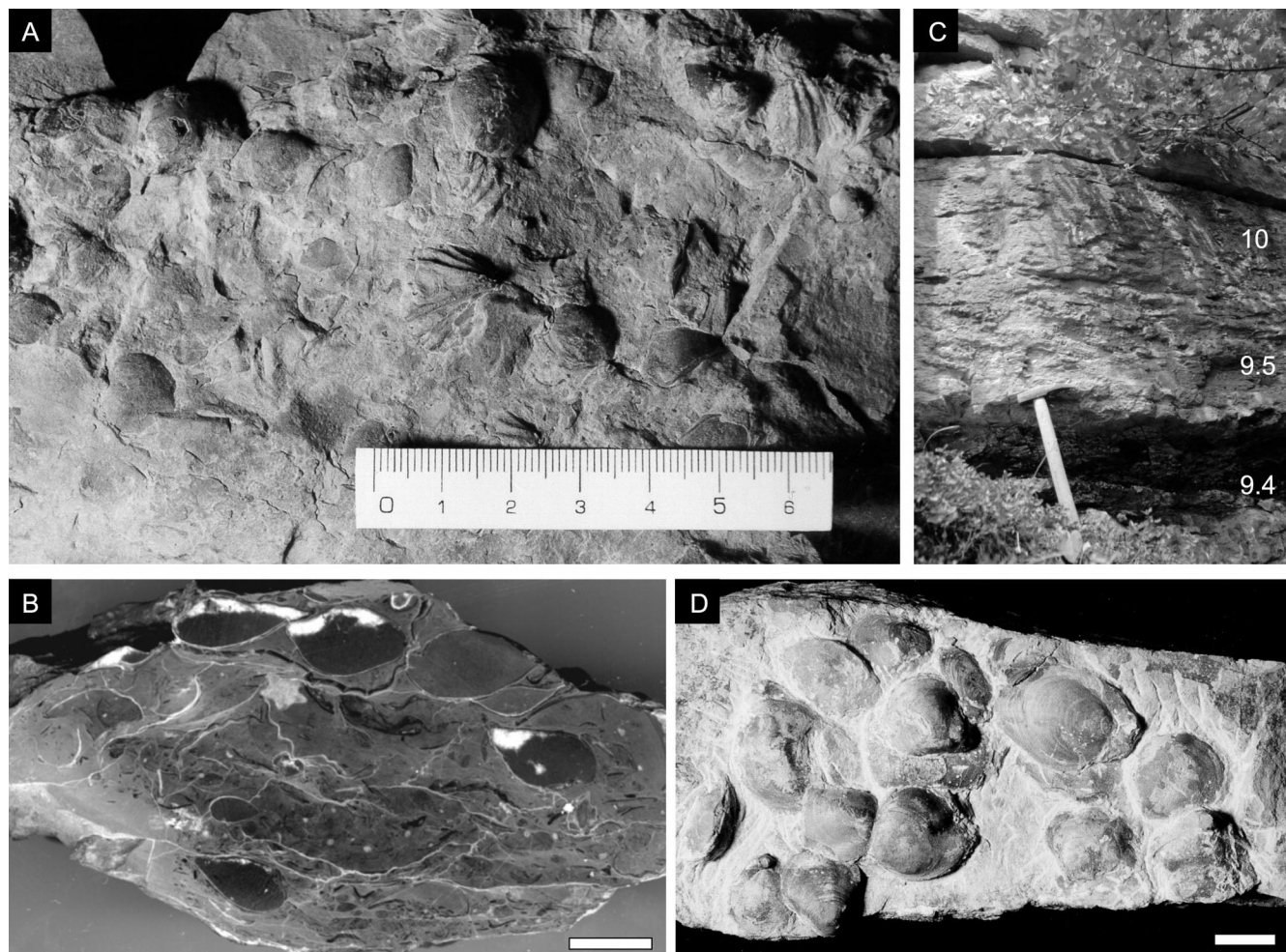


FIGURE 5—Bio-floatstone deposits. (A) Upper surface view of bio-floatstone with *Rhaetina gregaria* and *Zugmayerella uncinata* (Bystrý potok III-9.4.2); lighting from lower left. (B) Side-view of polished section of bio-floatstone with *Rhaetina gregaria* (Bystrý potok II-9.4). (C) Outcrop appearance of brachiopod bio-floatstone (bed 9.4) overlain by bio-floatstone with CIS (beds 9.5–10) (Bystrý potok II). Scale bar = 1 cm. (D) Upper surface view of nest with *Rhaetina gregaria* shells (Malý Zvolen 81.2); lighting from lower left. Scale bar = 1 cm.

loosely packed type without preferred orientation (concordant, oblique, or nested) to well-sorted and densely packed type with predominantly concordant orientation of bioclasts (Fig. 8A, B). The biofabric changes rapidly both horizontally and vertically. The micritic matrix contains loosely/densely packed calcarenitic allochems (shell debris, intraclasts, peloids, and ooids). Beds are characterized by sharp, irregular, erosional bases, and fining-upward grading (Fig. 8C). A complex internal structure is represented by alternation of several cm-thick packstone interbeds with basal erosional surfaces and different levels of sorting and packing. Benthic associations, which are represented mostly by a patch-reef *Rhaetina-Retiophyllia*-solenoporaceans association, and less commonly, by level-bottom (*Rhaetina* ass.) types, consist of brachiopods (abundant *Rhaetina gregaria*, less common *Zugmayerella uncinata*), bivalves (*Atreta intusstriata*, oysters, pectinids), gastropods, echinoderms, calcareous sponges, corals (*Retiophyllia*, *Astraeomorpha*), solenoporacean algae, and cyanobacteria (*Cayeuxia*).

(5) *Thick-bedded Biointra-packstones*: This deposit type is characterized by thick bedding (30–200 cm), clast-sup-

ported fabric, bimodal sorting of allochems (well-sorted calcarenitic bioclastic-intraclastic debris and poorly sorted ruditic bioclasts of variable alteration), and random orientation (Fig. 9A, B). Locally, internal bedding planes are distinguishable on the basis of shaly intercalations. This deposit passes laterally into the 4th or 6th deposit types. The micritic matrix is absent locally. Well-sorted, angular, and oval peloids are common; ooids also may be present. Brachiopods represented by *Rhaetina gregaria* (5–15% of rock volume) are not the main component in the diverse spectrum of benthic taxa. Recrystallized bivalve fragments are dominant; gastropods, coral fragments or whole coral colonies, red algae, echinoderm ossicles, and foraminifers are common.

(6) *Biointra-rudstones*: 10–30-cm-thick, very well-sorted beds are characterized by densely packed bioclasts that are mainly concordantly and convex-up oriented (Fig. 9C, D). The lower boundary is sharp (although overprinted by stylolites), and signs of grading of size and density of allochems are locally present. Intraclasts, ooids, and peloids are present in variable amounts. Brachiopods (7.5–25% of rock volume) are represented by *Rhaetina gregaria* only.

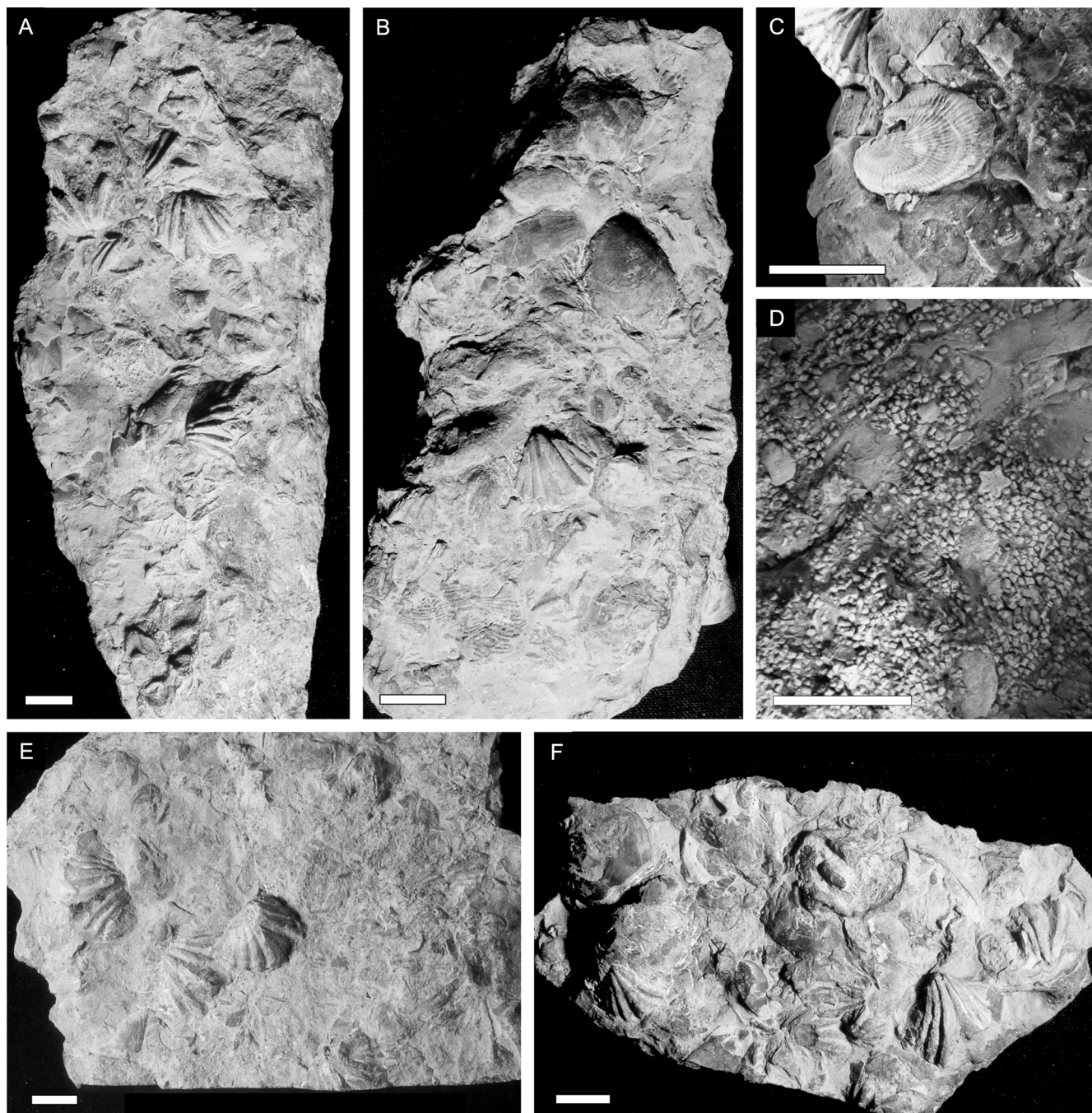


FIGURE 6—Bio-packstone—pavements; scale bars = 1 cm. (A) Upper surface view of bio-packstone pavement with disarticulated *Zugmayerella* valves and bivalve *Atreta* (Bystrý potok I-12.3); lighting from bottom. (B) Upper surface view of pavement with disarticulated brachiopods (Bystrý potok III-9.4.1); lighting from bottom. (C) *Atreta intusstriata*, a cementing bivalve typical of this deposit type. (D) Upper surface view of crinoidal pavement (Bystrý potok III-9.5.1). (E) Upper surface view of pavement with disarticulated *Zugmayerella* valves (Bystrý potok III-9.4.1); lighting from left. (F) Upper surface view of pavement with disarticulated brachiopods (Bystrý potok III-9.4.1); lighting from right.

Taphonomic Signatures

Quantitative data on the degree of micritization, bioerosion, fragmentation, and encrustation are presented and compared using alteration frequency histograms of individual samples (Fig. 10), deposit types (Fig. 11A), benthic-association types (coral and brachiopod-bivalve associations, Fig. 11B), and with respect to the proportion of al-

lochems (below 30%, 30–60%, and above 60%, Fig. 11C). In the latter three histograms, the taphonomic grades of fair and poor were pooled together. The level of significance was estimated using a 95% confidence interval. The distinction of sample groupings (taphofacies types) based on taphonomic signatures and their relationship to the classification of deposit types based on deposit-level properties were explored using a cluster analysis (Fig. 12). Qualita-

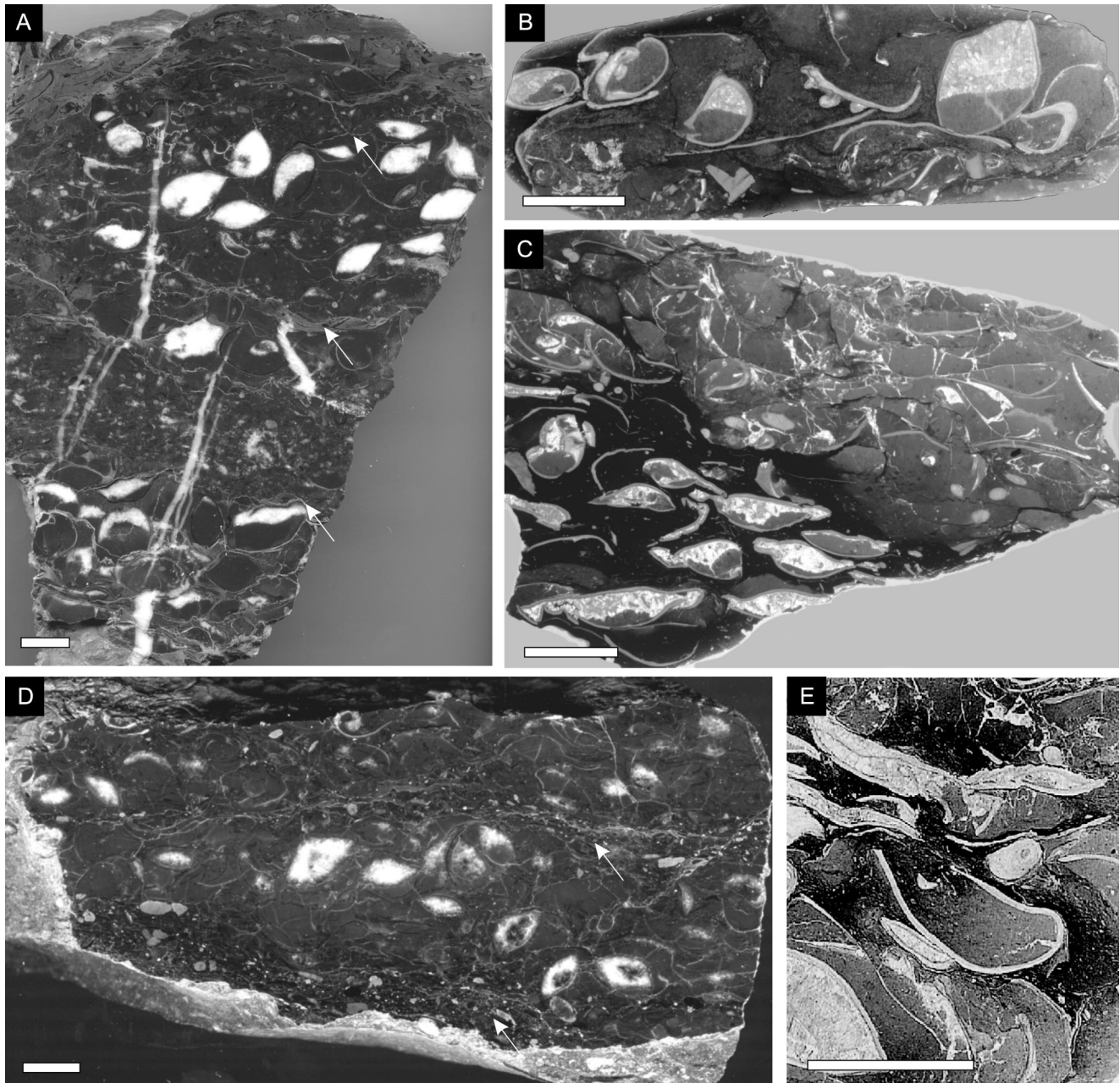


FIGURE 7—Bio-floatstones with CIS; scale bars = 1 cm. (A) Side view of polished section with complex internal stratification (CIS) formed by interlayering of bio-floatstones with articulated shells with geopetal fills and thin well-sorted biointra-packstones with erosional bases (arrows point to erosional boundaries, Dedošova 4.2). (B) Side view of Bio-floatstone with calcisiltic matrix and floating shells with geopetal infillings (Bystrý potok II-9.5). (C) Side view of thin-section with bio-floatstone with articulated *Rhaetina gregaria* shells (Dedošova 4.6a). (D) Side view of polished section with complex internal stratification formed by alternation of well-sorted calcarenitic interbeds (arrows) with parautochthonous *Rhaetina* coquinas (Belianska 26.4). (E) Side views of thin-sections with dominant articulated shells (Dedošova 4.2 and 4.6).

tive data on disarticulation and shell infilling are presented in Table 1. The distinction of brachiopod-bivalve and coral association is applied only to supposedly autochthonous and parautochthonous deposit types (Bio-floatstones, Pavements, Bio-floatstones with CIS, Biointra-packstones with CIS; see discussion). There is a close correspondence between the type of benthic association and its allochem content. Most of the brachiopod-bivalve associations fall into the category with low allochem content (below 30%), whereas deposits containing coral associa-

tions are characterized by higher allochem content (35–62.5%).

Disarticulation: The proportion of disarticulation is low to medium in Bio-floatstones (Table 1). In this deposit, the proportion of articulated nonstrophic shells of *Rhaetina* is higher (50%) in comparison to that of specimens of *Zugmayerella* (10–30%). A low proportion of disarticulated shells is typical of Bio-floatstones with CIS. Disarticulated valves are more common in Pavements (90–95% in *Zugmayerella*, 50–75% in *Rhaetina* counted from hand-sam-

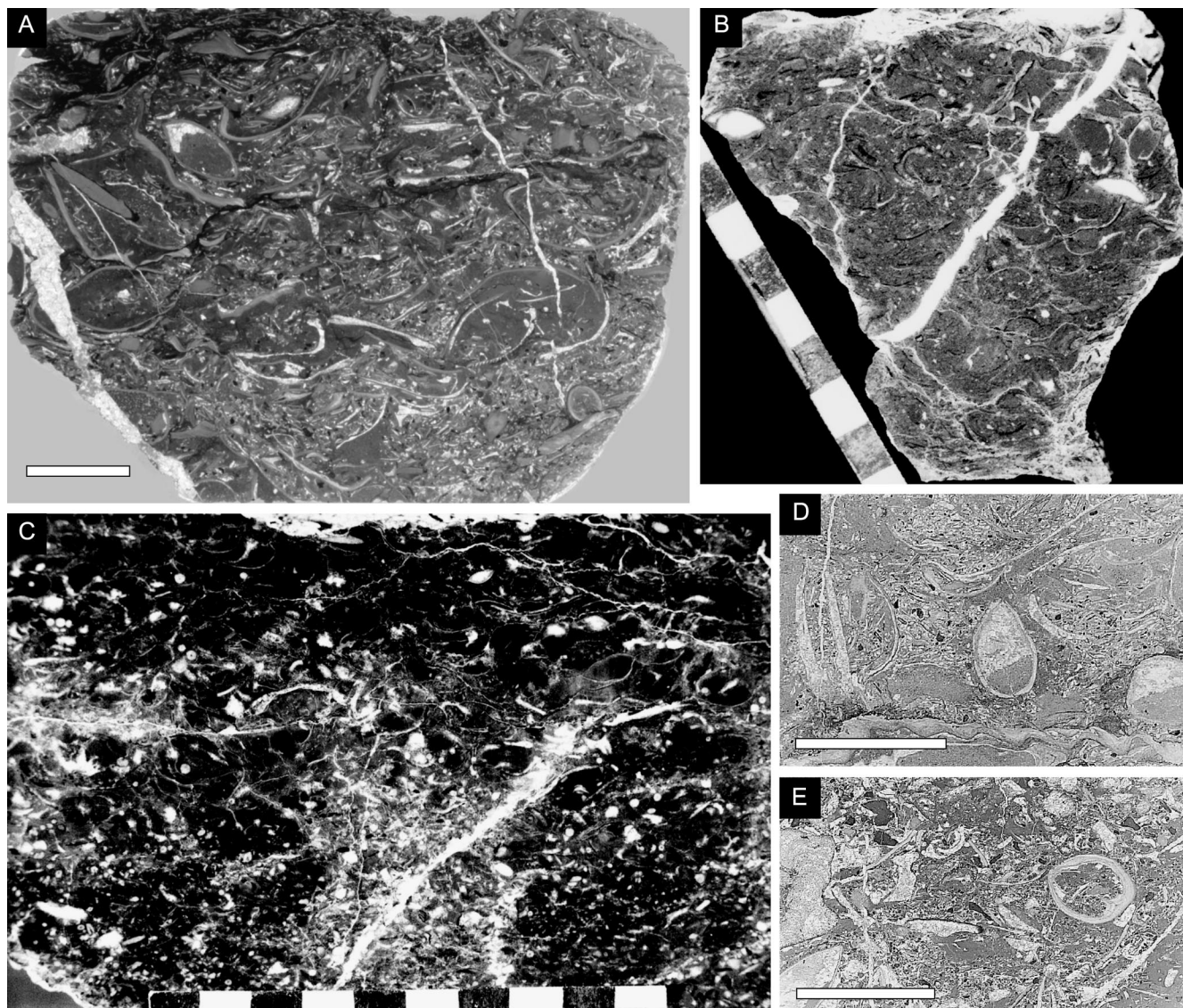


FIGURE 8—Biointra-packstones with CIS; scale bars: 1 portion = 1 cm. (A, B) Side views of thin-section and polished section, respectively (Dedošova 4.6b). (C) Side view of polished section with erosional base and grading (Dedošova 4.4). (D) Side view of thin section, with higher proportion of articulated shells, nesting, and concave-up orientations (Dedošova 5.2b). (E) Plane view of thin-section (Dedošova dolina 5).

pled specimens), and Biointra-packstones with CIS. Thick-bedded biointra-packstones and Biointra-rudstones show a scarcity or total absence of articulated shells.

Shell Infillings: The type of shell infilling varies substantially among individual deposit types. Obviously, only deposits with preserved articulated shells were compared. Biofloatstones and Pavements contain articulated shells predominantly with homogenous micritic infilling. Biofloatstones and Biointra-packstones with CIS are characterized by dominance of complete or partial sparitic infillings (Table 1). The micritic parts of shell infilling are micritic or peloidal. Although consistent data on the preservation of delicate internal structures (loops) are not available from all deposit types, it is interesting to note that in Biofloatstones with CIS, loops are preserved in most of the shells.

Bioerosion: Variation in the degree of bioerosion in Biofloatstones is very high (Figs. 10, 11A). In Pavements and

Biofloatstones with CIS, the degree of bioerosion is very low (0–25% per sample, Fig. 11A). Variation in the degree of bioerosion is very high in Biointra-packstones with CIS (15.9–100% per sample). The degree of bioerosion is also high in Thick-bedded biointra-packstones (78.9–100% per sample) and Biointra-rudstones (64–97.2% per sample). In brachiopod-bivalve associations, 17.4–43.8% of specimens are affected by bioerosion (Fig. 11B). In coral associations, taphonomic alteration is higher, but more variable, reaching up to 93.4% of bioeroded specimens. Although boring frequency in other taxa has not been quantified, bivalve macroborings (*Lithophaga* sp.) are very abundant in retio-phyllid corals, *Astraeomorpha*, and solenoporacean algae in coral associations. The difference between the degree of bioerosion of brachiopod-bivalve and coral associations is significant in terms of non-overlapping 95% confidence intervals. Samples with low packing density (below 30%) are characterized mostly by lower degrees of bioerosion (0–

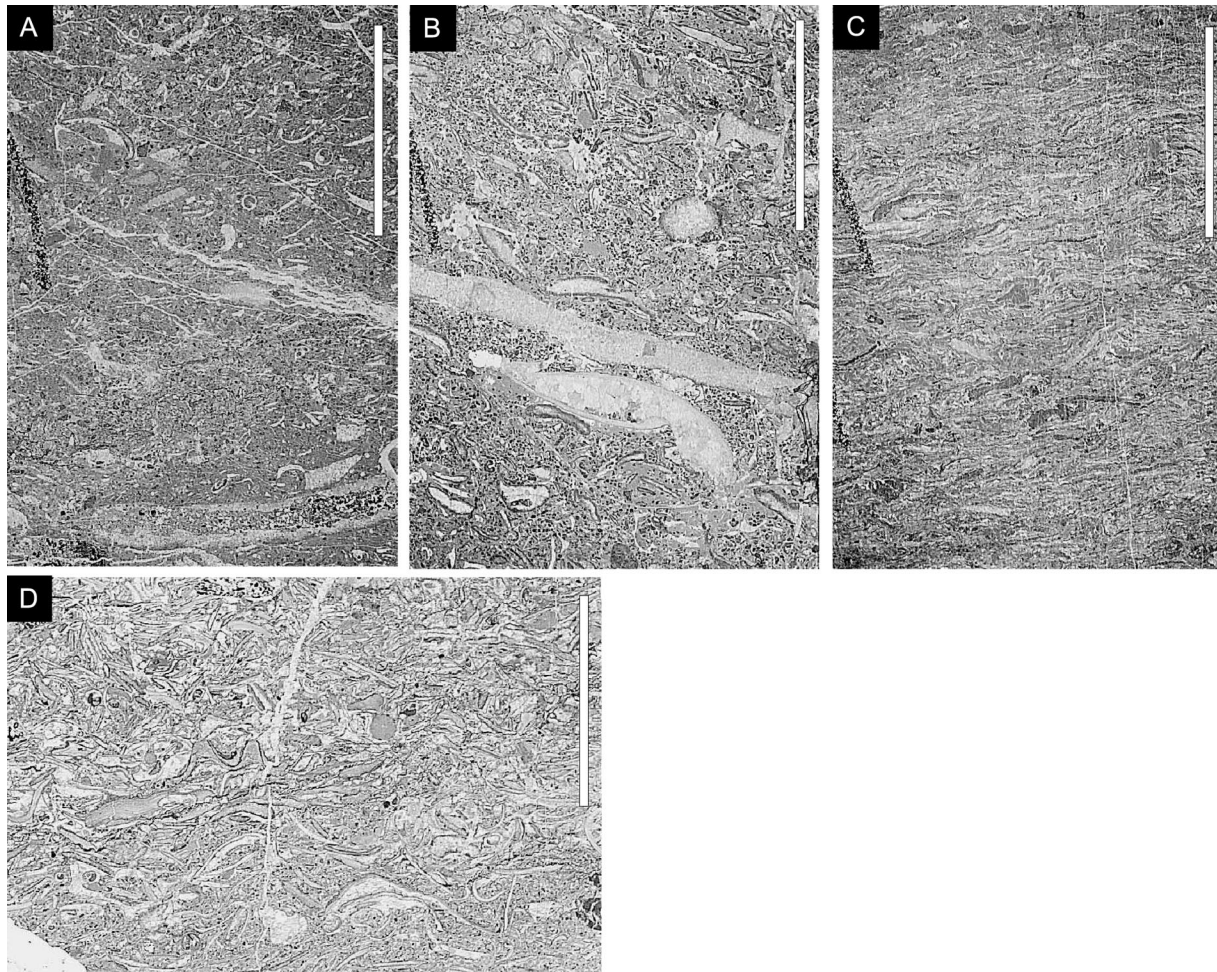


FIGURE 9—Thick-bedded biointra-packstones; scale bars: 1 portion = 1 cm. (A, B) Side views of thin-sections with bimodal sorting and high preservational variation (Bystrý potok 8; 6.3); Biointra-rudstones. (C, D) Side views of thin-sections with concordantly oriented and highly degraded bioclasts (Bystrý potok 14.2, Dedošova 14.5).

43.8%) in comparison to samples with higher packing density (Fig. 11C).

Micritization: The degree of micritization is typically uniform and very low in the Bio-floatstone deposits with CIS (0–22.5%, Fig. 10). Thick-bedded biointra-packstone deposits are mostly highly affected by micritization (65.4–93.3%). The degree of micritization in Biointra-rudstones is more variable (16.4–94.2%). The degree of micritization in Bio-floatstones with CIS is significantly different than in Biointra-packstones with CIS, Thick Biointra-packstones, and Rudstones (Fig. 11A). There is a significant difference between brachiopod-bivalve and coral associations (Fig. 11B). Micritization in the latter type is more variable and mostly higher (18.3–77.3% per sample), in contrast to the former (0–22.5% per sample). The degree of micritization is significantly lower in deposits with lower packing density (Fig. 11C).

Encrustation: Encrustation is mostly very low on brachiopods and is characterized by cementing bivalves (*Atrypa intusstriata*) or sessile foraminifers (*Tolypammina*, *Planinvoluta*). Although not quantified, qualitatively it seems that more robust taxa, such as corals or red algae, are more heavily affected by encrusting and boring for-

minifers (*Baccinella irregularis*, *Lithocodium aggregatum*) and serpulids. In general, the degree of encrustation on brachiopods is very low and relatively uniform in all deposit types (below 25% per sample, Fig. 10). Encrustation is mostly absent or very scarce in Bio-floatstone deposits with CIS (0–10%). In the coral associations, the degree of encrustation (5–17% per sample) is higher in comparison to those in brachiopod-bivalve associations (Fig. 11B). The highest degree of encrustation is reached in deposits with higher packing density (23% per sample), although there is no significant difference in confidence intervals (Fig. 11C).

Fragmentation: Levels of fragmentation are mostly high across all samples and deposit types (Figs. 10, 11). The proportion of fragmentation in Bio-floatstone deposits is variable, ranging from 53.3–82.6% in brachiopod-bivalve and 76.5–100% in coral associations. The difference between means of these associations is significant at $p=95\%$. The variation also is high in Bio-floatstone with CIS (10–80% per sample). The confidence intervals of mean value of this deposit type do not overlap with those of Biointra-packstones with CIS, Thick-bedded biointra-packstones, and Biointra-rudstones. These latter types are character-

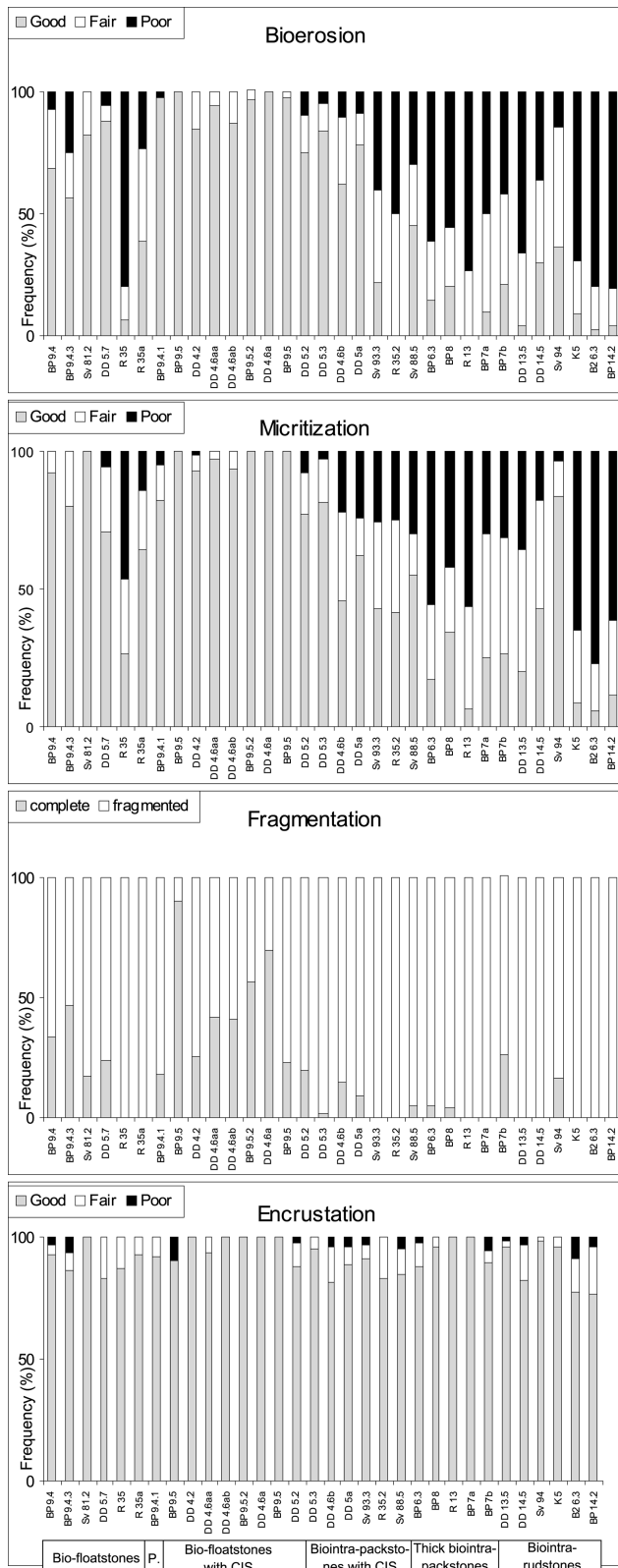


FIGURE 10—Levels of taphonomic signatures (bioerosion, micritization, fragmentation, encrustation) in individual samples. The assignment of samples to particular deposit types is given at the bottom of figure (P. = Pavements).

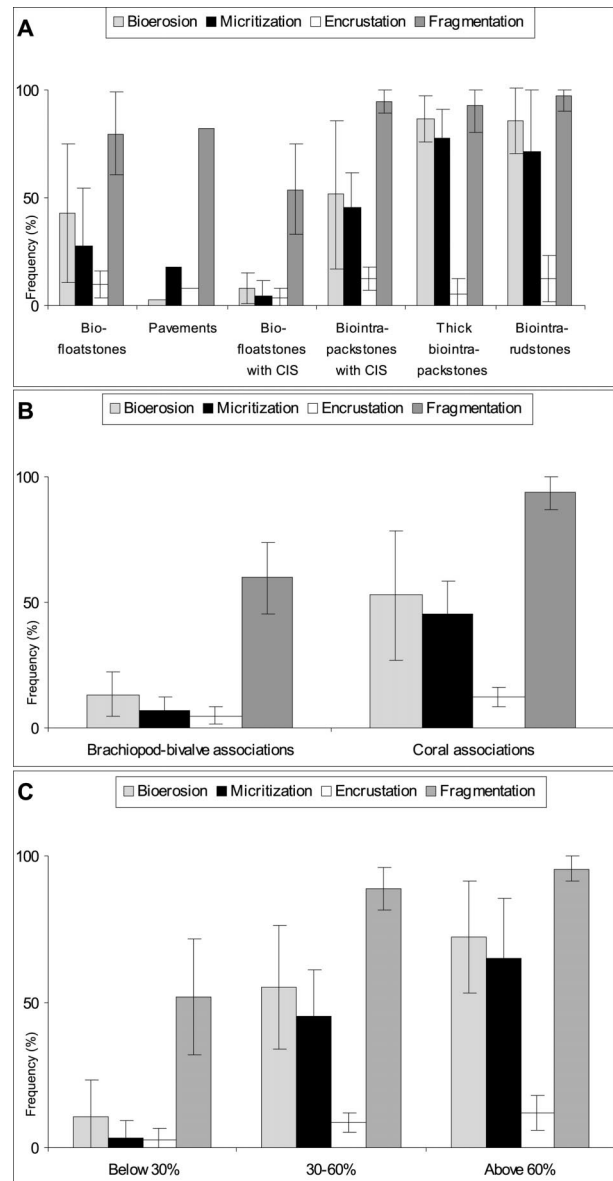


FIGURE 11—Alteration frequency histograms of mean values of taphonomic signatures. (A) Deposit types; for pavements, only data from one sample were available. (B) Benthic associations. (C) Allochem content (packing density).

ized by uniformly high proportions of fragmentation (74.7–100%). The levels of fragmentation in deposits with high packing density (above 30% and 60% of allochems) are higher and more uniform (66.8–100%) in comparison to deposits with lower packing density (10–82.6%).

Taphofacies Types Based on Taphonomic Signatures: In order to compare the classification of brachiopod-deposit types based on deposit-level properties with different taphofacies types based on taphonomic signatures, cluster analysis was used for basic distinction of taphofacies types (Fig. 12A). Three clusters with substantial differences in mean values of particular taphonomic signatures were recognized (Fig. 12B). When clusters 1 and 3 were subdivided further into subclusters, differences in the mean values were very small (not shown). Therefore, three tapho-

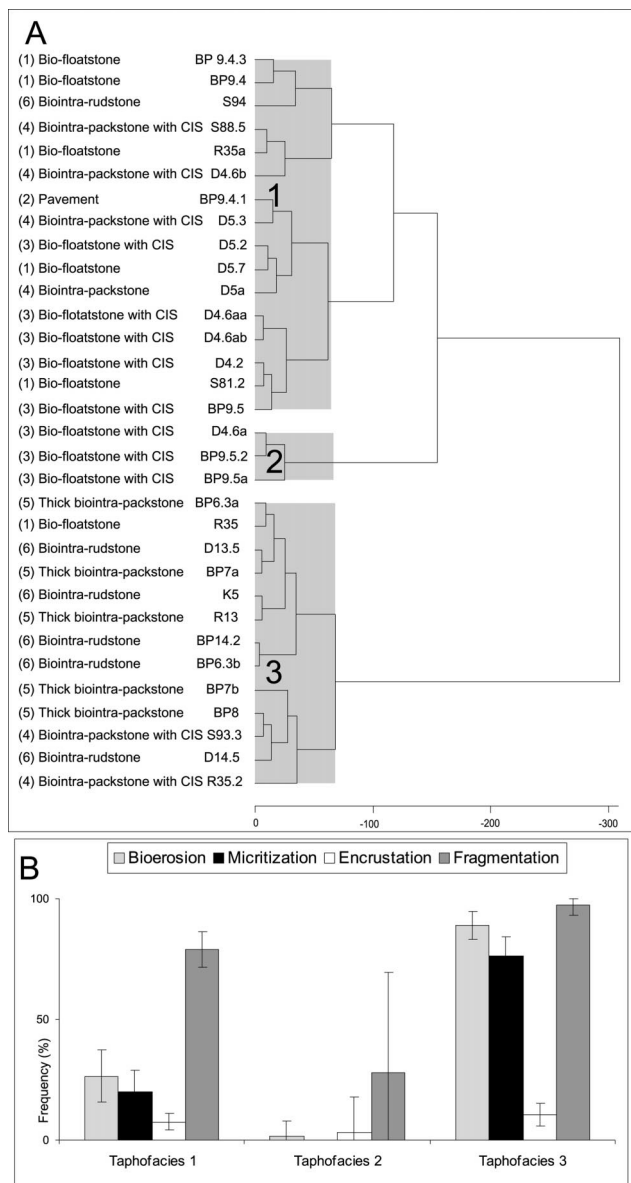


FIGURE 12—(A) Cluster analysis of 32 samples with taphonomic signatures (bioerosion, micritization, encrustation, and fragmentation) as the variables. On the left side, corresponding deposit types based on deposit-level properties are shown. (B) Alteration frequency histograms of 3 clusters recognized by the cluster analysis.

facies types based on taphonomic signatures can be distinguished: (1) Taphofacies 1, characterized by moderate degree of bioerosion/micritization (Cluster 1); (2) Taphofacies 2, with the lowest degree of bioerosion/micritization (Cluster 2); and (3) Taphofacies 3, characterized by the highest degree of bioerosion/micritization (Cluster 3). The rank order of individual categories in histograms is mostly similar. Fragmentation is the highest, bioerosion and micritization follow, and the proportion of encrustation is the lowest. The proportion of bioerosion and micritization is substantially lower in the first two taphofacies in comparison with Taphofacies 3. In addition, the proportion of bioerosion and micritization is substantially higher in Taphofacies 1 in comparison with Taphofacies 2.

As can be seen from the taphofacies composition (Fig. 12), samples within particular taphofacies types correspond to several deposit types, and particular deposit types can be present in two taphofacies types. However, thick biointra-packstones and biointra-rudstones are consistently characterized by high alteration (Taphofacies 3). Bio-floatstones with CIS are consistently present in Taphofacies 1 and 2 only, characterized by the lowest alteration. Bio-floatstones and biointra-packstones with CIS are present in Taphofacies 1 and 3. In summary, the correspondence between the assignment of particular samples either to the deposit types or to the taphofacies types is relatively poor, although some deposit types are consistently characterized by relatively stable levels of taphonomic alteration.

DISCUSSION

Brachiopod-deposit Types

In the following text, the genesis of the brachiopod-deposit types is interpreted and classified (genetic terms in parentheses) according to a process-related approach used in classification of shell concentrations (see Speyer and Brett, 1991; Fürsich and Oschmann, 1993; Fürsich, 1995).

(1) *Thin-bedded Bio-floatstones*: The fabric of brachiopods, together with the absence of high-energy sedimentary structures, indicates an environment below storm wave base, suggesting that these deposits probably underwent only minor post-mortem reworking. The lithologic homogeneity of this deposit type, co-occurrence of benthic taxa that are characterized by similar ecological requirements, and the absence of evidence for census, environmental, or biostratigraphic condensation (Kidwell, 1998) allow an interpretation as autochthonous within-habitat time-averaged assemblages. The high abundance of brachiopods can be linked to their relatively high productivity and/or the low rate of destruction of their dead shells (primary biogenic deposit). Small-scale brachiopod clusters probably are preserved in original position. Close spatial association with Pavements indicates the proximity of maximum storm wave base.

(2) *Bio-packstone—Pavements*: The restriction of microbial rims and sessile foraminifers to the upper surfaces of bioclasts indicates a stable position on the seafloor. This, along with the absence of sorting and rounding, suggests that disturbance of the sea floor was minor. The origin of this biofabric may be due to episodic distal storm flow winnowing (winnowed deposit) and/or periodically reduced background rates of sedimentation (sediment-starved deposit). Microstylolites indicate a significant diagenetic overprint, leading to the enrichment of fossil hardparts.

(3) *Bio-floatstones with Complex Internal Structure*: The complex internal structure indicates episodic high-energy events, most probably of storm origin. Nesting in various directions and convex-down orientation of valves indicate the presence of turbulent/vortical flow and suspension settling (Middleton 1967; Futterer, 1982). Because brachiopod shells are oriented inconsistently with respect to the antero-posterior axis, it is improbable that they are conserved in their life orientation. The features typical of this deposit type (laterally restricted monospecific assemblage of concentrated, predominantly articulated shells, closely

associated with erosional surfaces) are comparable with a catastrophic mortality model proposed by Tsujita (1995) for the origin of bivalve shell clusters in the Late Cretaceous Bearpaw Formation. The main mechanism is related to a combination of a clustered or gregarious life habit of shell producers and storm-induced sea-floor scouring and subsequent filling, preferentially localized around topographic irregularities produced by clusters of live shells (Johnson, 1957; Aigner and Futterer, 1978; Goldring and Aigner, 1982). Therefore, simple-event mechanical reworking and rapid *in-situ* burial of living brachiopod clusters in a scour-generated depression could be responsible for the origin of this deposit type in environments with low-energy background conditions. Therefore, time-averaging is minimal and the deposits represent census assemblages produced by catastrophic mortality (e.g., Brett, 1990). Waves generated by storms may be the best explanation (storm wave deposit).

(4) *Biointra-packstones with Complex Internal Structure*: As in the previous deposit, complex internal structure with internal erosional boundaries suggests episodic storm activity. Moderate or bimodal sorting, loose packing, absence of preferred orientations or nesting, and convex-down orientations indicate more storm wave influence, whereas well-sorted and densely packed bioclasts with predominantly concordant and convex-up orientations are more indicative of storm flow activity. In the latter case, some exotic allochems (ooids, oncoids, or intraclasts) indicate short-term transport in storm-induced currents and deposition of suspended material in graded bedding (Aigner, 1979). In addition to different intensity of storm reworking, the original difference in the species composition (i.e., higher proportion of corals, sponges, and algae) probably also affected the difference in biofabric between Bio-floatstones with CIS and Biointra-packstones with CIS. High spatial heterogeneity in the species distribution across short distances indicates that the transport of benthic remains was not significant. Rapid lateral changes in biofabric are attributable to the irregular topography of patch-reefs and faunal patchiness, leading to localized storm-induced scour-and-fill mechanisms. This storm wave/flow deposit thus probably contains both parautochthonous and allochthonous bioclasts (mixed assemblage).

(5) *Thick-bedded Biointra-packstones*: Paleocologic and sedimentologic data suggest a composite origin of multiple-habitat, environmentally condensed assemblages. This represents an amalgamated storm-reworked deposit with the compounded effects of background and episodic processes. Locally, large overturned and complete branching coral colonies indicate the absence of prolonged transport. The microintraclastic, well-sorted matrix, and local absence of micritic mud points to long-term effects of a relatively higher-energy setting close to normal wave base or frequent multiple storm-reworking. The presence of complete and overturned branching coral colonies indicate periods with lower background energy and episodic storm burial. However, amalgamation and homogenization of deposits led mostly to the destruction of original features such as bedding or superposition of individual events.

(6) *Biointra-rudstones*: Good sorting, absence of fine matrix, dense packing, and rounding indicate long-term high-energy influence. Predominantly convex-up orientations,

in some cases, indicate higher current activity. The brachiopods and other bioclasts are probably mostly allochthonous or can represent residual *in-situ* components when the local setting changed from low- to high-energy conditions. Fossil assemblages are strongly biased toward the more resistant shelly remains. This long-term current/wave deposit was generated and accentuated by long-term, fair-weather high-energy and episodic storm-flow processes, as is indicated by its spatial association with peritidal and shoal facies (skeletal sand banks).

Processes Leading to the Origin of Brachiopod Deposits: Based on the interpretation of taphonomic properties of deposits, a process-related concept of classification of taphofacies or shell concentrations of epicontinental seas is appropriate (Speyer and Brett, 1991; Fürsich and Oschmann, 1993; Fürsich, 1995). Thus, fossil assemblages with the terebratulid brachiopod *Rhaetina gregaria* are classified into six basic deposit types: (1) autochthonous primary biogenic, (2) autochthonous winnowed or sediment/starved, (3) parautochthonous storm wave, (4) parautochthonous storm wave/storm flow, (5) amalgamated storm reworked, and (6) allochthonous long-term current/wave type. Described types of brachiopod deposits can be arranged on a short-term scale according to the degree of mechanical reworking and transport of bioclasts (Fig. 13) as simple event deposits in a simplified chart, with the exception of amalgamated storm-reworked deposit. In addition to this aspect, brachiopod deposits differ in relative degrees of time-averaging, ranging from census and within-habitat time-averaged to environmentally condensed types (Kidwell and Bosence, 1991). The differences in extrinsic factors reflect mainly variations in the degree of reworking and net rate of sedimentation.

Three groups of brachiopod deposits, corresponding to three main bathymetric settings with respect to position of fair-weather, storm, and maximum storm wave bases, can be distinguished according to the degree of reworking, internal microstratigraphy and the original composition of the benthic associations occupying the sea-floor.

(1) Relatively undisturbed deposits originating under long-term low-energy conditions (primary biogenic and winnowed or sediment-starved types) occur in environments between maximum and average storm wave base, with prevailing background taphonomic processes (bioturbation, background burial rate, net rate of sedimentation). This setting was inhabited mainly by moderately diverse brachiopod-bivalve associations (level-bottom *Rhaetina-Zugmayerella* and *Rhaetina* associations). Coral associations on the transition to patch reefs with dispersed coral colonies and algae rarely occurred in this zone. Due to poor storm influence, brachiopods did not experience complex burial/exhumation histories. The distinction between loosely (primary biogenic) and densely packed (winnowed or sediment starved) deposit types can be explained by changes in the net rate of sedimentation, leading to a different degree of time-averaging of two deposit types. Similar control on the preservation of autochthonous terebratulid shell beds is known from the Upper Muschelkalk of Germany (Aigner et al., 1978; Hagdorn and Mundlos, 1982), indicating that the changes in the net rate of sedimentation are the dominant taphonomic factor shaping biofabric of autochthonous brachiopod deposits.

(2) Storm-reworked deposits, with conflicting effects of

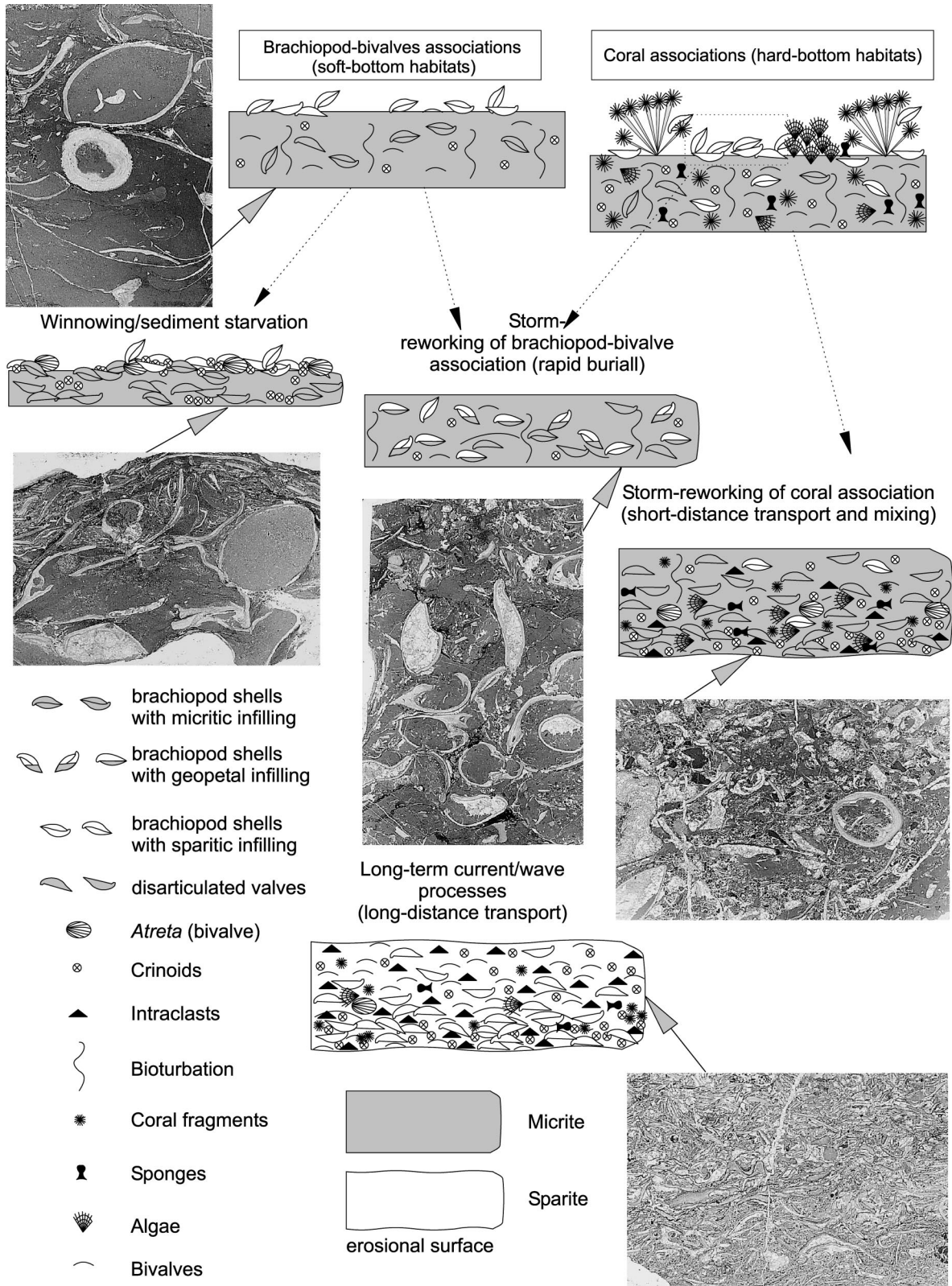


FIGURE 13—An idealized sequence of taphonomic events during the formation of brachiopod deposits, from autochthonous origin to allochthonous reworking.

background and episodic taphonomic processes, are represented by storm-wave and storm-flow types with CIS, deposited below fair-weather wave base, and amalgamated storm-reworked type, affected by storm reworking of higher intensity (e.g., Aigner, 1982; Norris, 1986; Parsons et al., 1988; Johnson, 1989; Drummond and Sheets, 2001) deposited nearer to the fair-weather wave base. They originated in settings above the normal storm wave base. These settings were predominantly inhabited by the coral associations (*Rhaetina-Retiophyllia*-solenoporaceans and *Retiophyllia* associations) or paucispecific brachiopod-bivalve associations (*Rhaetina* associations). They are preserved as parautochthonous storm-reworked deposits. Because coral associations were more common in this setting than brachiopod-bivalve associations, they had a higher probability of reworking. The presence of well-defined, centimeter-scale interbeds in Bio-floatstones with CIS and Biointra-packstones with CIS indicates that storm activity was less intense than in amalgamated Thick-bedded biointra-packstones. In addition to the differential storm-induced reworking and burial, original differences in composition of the benthic associations and patchy distribution of live brachiopod populations led to the differential biofabric between Bio-floatstones with CIS and Biointra-packstones with CIS. The storm activity probably caused burial-induced catastrophic mortality of brachiopod populations in this setting.

(3) Deposits originating under long-term high-energy conditions, in environments above fair-weather wave base, are represented by long-term current/wave type with compounded signatures of destructive background and episodic taphonomic processes. Transport out of habitat or gradual shallowing might lead to the origin of these deposits, where preservation of brachiopods has been overprinted by long-term higher energy conditions.

Taphonomic Signatures

Disarticulation: The highest proportion of articulation is present in deposit types that are interpreted as storm-wave deposits associated with rapid burial. The medium proportion of disarticulation in Bio-floatstone deposits, interpreted as an autochthonous primary biogenic deposit, points to higher activity of disturbing biota and/or higher intrinsic rate of destruction. In autochthonous pavements, the higher proportion of disarticulation indicates relatively longer residence times on the sea-floor compared to thin-bedded bio-floatstones. The difference in the proportion of disarticulation between *Rhaetina* and *Zugmayerella* reflects the differences in hinge strength. In deposits affected by transport, complex burial/exhumation history, and long-term high-energy influence, the proportion of disarticulation is high, thus, the proportion of disarticulation can be positively correlated with residence time on the sea floor, which is directly related to the reduced rate of sedimentation and higher intensity of episodic or long-term high-energy events.

Shell Infillings: A high proportion of articulated shells, completely or partially filled with sparitic calcite, is typical of the Bio-floatstones with CIS. The interpreted storm-wave origin associated with rapid burial suggests that penetration of the mud was inhibited. The association of sparite-filled brachiopod shells with higher rates of sedi-

mentation also has been documented in Middle Triassic shell beds (Aigner et al., 1978; Török, 1993). In contrast, the shell fillings in Bio-floatstones are mostly micritic. If the interpretation of these deposits as that of an autochthonous primary biogenic type holds, shells were not buried rapidly by storm events (i.e., they were exposed for at least some time on the sea-floor). The residence time was sufficient to completely fill the articulated shell with micritic mud. The process of filling of brachiopod shells is usually explained simply by infiltration of sediment, draft filling (draft stream created by external turbulence, Seilacher, 1971), or sediment traps, which are characterized by narrow gaps (e.g., pedicle opening) and overhangs (e.g., high valve convexity). In the latter case, due to the difference in density gradient of suspended sediment on the sea floor and within the shell, there is a higher input of sediment into the sediment trap (shell), which consequently is overtrapped with fine sediment (Gardner, 1980a, b). The type of shell infilling thus reflects mainly the rate of burial/residence time on sea/floor.

Bioerosion / micritization: Levels of bioerosion and micritization are closely associated, as evinced by vacant microborings that have been filled with micritic cement; although other biologically mediated precipitation processes may influence micritization (Kobluk and Risk, 1977). Low degrees of bioerosion and micritization in brachiopod-bivalve associations in Bio-floatstone deposits, interpreted to represent an autochthonous deposit unaffected by episodic storm burial, point to some intrinsic or extrinsic factor(s) inhibiting microboring organisms from brachiopods exposed on the sea floor. High net rate of sedimentation is improbable because of the ecological structure of benthic associations dominated by epifaunal suspension-feeders (Tomašových, 2002). Light limitation can be excluded because of green algae are common. Other ecological factors, such as levels of nutrient supply, may control the distribution of bioeroders (Hallock and Schlager, 1986; Hallock, 1988; Lescinsky et al., 2002). The intrinsic cause can be related to valve thinness and/or relatively high rate of destruction of brachiopod shells when they are exposed on the sea floor. It is known that boring organisms exhibit highly selective settlement behavior for thicker and more durable shells (Best and Kidwell, 2000b). High rates of shell destruction due to organic matrix breakdown (shell maceration), which occur rapidly in modern temperate settings, could lead to the effect that when exposed on the sea-floor, brachiopod shells decomposed rapidly and thus provided poor substrates for boring organisms (Daley, 1993).

The association of low degrees of bioerosion with deposits with low allochem content (i.e., high proportion of micritic mud) agrees with results of other studies (Vogel et al., 1987; Best and Kidwell, 2000a, b). In soft-bottom environments, the scarcity of microborings can be explained by unstable conditions at the sediment-water interface, due to higher turbidity and mud re-suspension. Therefore, environmental factors related to fine-grained sediment accumulation can have both ecological and taphonomic effects on observed levels of bioerosion. On one hand, high turbidity and unstable substrate can primarily decrease the ecological abundance of borers, and on the other hand, fine-grained sediment has a relatively high potential to bury shells and protect them from taphonomic destruction

related to bioerosion. There is probably a complex relationship between several inter-related factors controlling the activity of boring organisms, so the interpretation of bioerosion intensity is not always straightforward.

In coral associations, the degree of bioerosion of brachiopods is relatively high. Here, environmental factors can be explained in terms of higher proportions of hard and stable substrata and reduced turbidity/sedimentation rates (Pandolfi and Greenstein, 1997). Scattered brachiopod shells preserved in life positions in inter-corallite voids are often micritized and encrusted by foraminifers and serpulids, suggesting different taphonomic pathways in patch-reef/biostrome associations in comparison to level-bottom associations.

Encrustation: The degree of encrustation is interestingly very low. In general, Triassic level-bottom encrusting associations are not very common, although encrusting associations known from Rhaetian Hybe Formation (Hronic Unit of the Central West Carpathians) are highly diverse (Taylor and Michalík, 1991). Restricted diversity of encrusters is probably also the effect of environmental instability and habitat restriction of depositional setting of the Fatric Unit (Michalík, 1982; Tomašových, 2002). Another explanation can be related to the lowered productivity regime, which seems to be negatively correlated with encrustation intensity in modern seas (Birkeland, 1977, 1989; Lescinsky et al., 2002). The abundance of *Retiophyllia* coral patch-reefs should indicate the absence of eutrophic conditions. Shell orientation, size, and ornamentation are significant factors determining the proportion and composition of encrusting communities (Kesling et al., 1980; Spjeldnaes, 1984; Alvarez and Taylor, 1987; Alexander and Scharf, 1990; Powers and Ausich, 1990). For example, Bordeaux and Brett (1990) observed that smooth punctate terebratulids were relatively free of encrusters in contrast to other brachiopods. However, it is also possible that the encrusting communities were dominated by non-preserved taxa with low preservation potential, leading to the substantial decrease of encrustation in the fossil assemblages (Lescinsky, 1993).

Overall Taphonomic Alteration: The significant differences between the intensity of taphonomic alteration among particular samples pooled either according to their deposit-level properties (Fig. 11A) or according to their taphonomic signatures (Fig. 12) indicate inherent variations in taphonomic pathways related to extrinsic environmental factors. Variation of taphonomic signatures in samples can be very high and does not strictly follow the distinction of deposit types based on their deposit-level properties (Fig. 12). This is probably due to the fact that biofabric primarily reflects final depositional processes (the rate and permanence of burial), whereas some taphonomic signatures reflect variation in the nature of pre-burial environmental conditions (Davies et al., 1989a; Fürsich, 1995). For example, sorting, packing, and geometry of a deposit can be formed during one short-term high-energy event. In contrast, the degree of bioerosion or encrustation will depend on more long-term ecologic/taphonomic conditions. The lowest brachiopod alteration, associated with low levels of bioerosion/micritization, encrustation, and disarticulation, is associated with the deposit type that was affected by sudden burial (Bio-floatstones with CIS). Thick-bedded Biointra-packstones and

Biointra-rudstones are consistently characterized by high proportion of bioerosion, micritization, and fragmentation. This indicates that deposits originating near fair-weather wave base and characterized by long-term or repeated short-term reworking were affected by the highest brachiopod alteration.

In regard to the intensity of brachiopod alteration caused by bioerosion/micritization in autochthonous and parautochthonous deposit types, two different patterns can be recognized, related to the difference in composition of benthic association types (brachiopod-bivalve versus coral). In brachiopod-bivalve associations, bioerosion and micritization are absent or scarce, whereas coral associations with small-scale patch-reefs/biostromes, bioerosion/micritization, and fragmentation are more common (Fig. 11B). Higher alteration of brachiopods in coral patch-reefs/biostromes probably is related to several inter-related factors, including the intrinsically high proportion of hard substrata and increased effect of taphonomic feedback (higher shelliness, lower proportion of soft sediment, increased bioerosion; see Kidwell, 1991b), bottom-water quality suitable for borers and encrusters, and frequent storm-reworking (burial-exhumation), leading to longer residence time on the sea-floor. Similarly, the difference between deposits with low- and high-packing density (Fig. 11C) can reflect the importance of several inter-related factors, such as substrate type, rate of sedimentation, and turbidity. Therefore, due to between-setting variation in rates of taphonomic destruction, it seems that Upper Triassic brachiopods exhibited a difference in preservation potential between high-/low-energy and hard-/soft-bottom settings, which means that their compositional fidelity can differ substantially. The depth-/substrate-related distribution pattern of brachiopod fossil associations is probably biased due to this extrinsic difference in their preservation potential. Such bias potentially can be detected when there are significant between-setting differences in taphonomic alteration within one taxonomic group characterized by similar intrinsic preservation properties (i.e., durability).

IMPLICATIONS FOR UPPER TRIASSIC BRACHIOPOD DISTRIBUTION PATTERNS

Only a few local studies exist on the pattern of brachiopod distribution from the Triassic–Jurassic boundary (Michalík et al., 1991; Sandy, 1995; Dulai, 2001, 2003; Tomašových, 2001). The evaluation of brachiopod distribution patterns before and after the end-Triassic event and the study of their survival and recovery inevitably depend on understanding the taphonomic processes controlling their preservation in fossil assemblages. It has been suggested that the distribution patterns of Upper Triassic brachiopod associations can be correlated with depth-related environmental gradients (Golebiowski 1991, Sandy, 1995). According to Sandy (1995), based mainly on brachiopod distribution in the uppermost Norian–Rhaetian Kössen Formation of the Eastern Alps, short-looped terebratulids (represented by *Rhaetina gregaria*) show a strong preference for shallower water, transgressive portions of the sequence, which represent high-energy environments. Although the Rhaetian Fatra Formation does not contain deep subtidal or offshore deposits (character-

ized in the Kössen Formation by dominance of rhynchonellids, athyrids and long-looped terebratulids, it seems that the complete bathymetric range of *Rhaetina gregaria* is preserved. However, taphonomic analysis suggests that although a *Rhaetina*-dominated association is present in the uppermost part of the environmental gradient in the West Carpathians, autochthonous/parautochthonous occurrences are restricted to settings below the fair-weather wave with background low-energy conditions, often in association with soft macrosubstrata (*Rhaetina* and *Rhaetina-Zugmayerella* associations), or in coral associations. Fragments or disarticulated valves of *Rhaetina* also are preserved in coarse-grained high-energy deposits originating near or above the fair-weather wave base (Thick-bedded biointra-packstones and Biointra-rudstones), but the statement about their original presence in this habitat remains inconclusive. On one hand, high-energy, hard-bottom settings are characterized by a higher rate of destruction, which leads to higher alteration of brachiopods (see discussion), even if they are preserved in their original habitat. On the other hand, transport out of habitat or environmental condensation (e.g., Jeram model, see Seilacher, 1985) may result in brachiopods being preserved in such high-energy deposits.

Sedimentologic and deposit-level taphonomic properties give more support to the latter view. Although an onshore-offshore distribution pattern of brachiopod associations is not disregarded, the resolution of the habitat preference of *Rhaetina gregaria* is substantially enhanced in this study. Nevertheless, when Upper Triassic and Early Jurassic brachiopod associations are compared in time-environment diagrams (Sandy, 1995), this difference is more important, because habitats with originally different depths can be incorrectly considered as bathymetrically equivalent. Based on the dominant occurrence of rhynchonellids in shallow, high-energy habitats in the Early Jurassic, in contrast to the dominance of short-looped terebratulids in the Upper Triassic, Sandy (1995) hypothesized that rhynchonellids replaced short-looped terebratulids in this habitat after the end-Triassic mass extinction. Therefore, confirmation of this habitat replacement hypothesis must first be tested by assessing the degree of taphonomic overprint on distribution of Upper Triassic short-looped terebratulid-dominated associations, originally interpreted as inhabiting shallow, high-energy settings in the Eastern Alps and other regions. If there are temporal shifts in environmental preferences of particular taxa (e.g., before and after mass extinction), it is necessary to test if occurrences in onshore settings (mostly associated with high-energy/hard-bottom conditions) are substantially overprinted by taphonomic processes.

PRESERVATION POTENTIAL OF BRACHIOPODS

In addition to variations in extrinsic environmental factors (e.g., rate of burial, water chemistry, bioturbation, activity of boring organisms), another factor influencing the preservation potential of dead organisms is their inherent resistance to destruction (Kowalewski, 1996a). The inherent potential to preserve articulated brachiopods in the fossil record is positively influenced by their stable low-magnesium calcitic mineralogy, type of hinge, lack of ligament, macroscopic body size, gregarious settlement, and

lower predation susceptibility (Kidwell, 1990; Copper, 1997). However, the high organic content of brachiopod shells (Curry et al., 1989) may increase the rate of shell breakdown significantly due to decomposition of organic matrix (shell maceration) and thus decrease the preservation potential during processes in the taphonomic active zone (Alexandersson, 1979; Kidwell, 1990; Glover and Kidwell, 1993; Kidwell and Brenchley, 1994, 1996). Although actualistic data about the rate of destruction of modern brachiopods are derived mostly from temperate siliciclastic settings, studies show brachiopods decompose very rapidly due to the breakdown of organic matrix (i.e., on the scale of several months, see Collins, 1986; Gaspard, 1989, 1996; Emig, 1990; Daley, 1993). However, the durability of articulate brachiopods in carbonate environments is poorly known. The data presented here provide some implications about taphonomic pathways and preservation potential of articulate brachiopods in an Upper Triassic carbonate setting.

Relatively complex alteration patterns of brachiopods in Biointra-packstones with CIS, Thick-bedded biointra-packstones, and Biointra-rudstones indicate that brachiopods were affected by substantial destruction due to bioerosion and micritization (associated with cement precipitation), suggesting that they could withstand long-term exposure to destructive agents. Therefore, this supports the idea that in carbonate settings some other taphonomic pathways (e.g., cement precipitation in inter-fiber voids) can exclude rapid shell maceration and increase shell durability. This is especially supported by the fact that terebratulids (*Rhaetina*) and spiriferinids (*Zugmayerella*) with very thin and punctate valves should be more susceptible to rapid shell maceration than brachiopods with impunctate valves (see Emig, 1990). Relatively lower rates of destruction are probable also for modern terebratulid brachiopods from the SW Brazilian tropical carbonate shelf (Kowalewski et al., 2002). These data point to the possibility that inherent resistance to destruction also is environment-dependent and distribution patterns of brachiopods in siliciclastic and carbonate settings can be biased due to different taphonomic pathways (e.g., variations in rate of organic-matrix breakdown and cement precipitation due to differences in pore-water chemistry and concentration and type of organic matrix, see Mitterer and Cunningham, 1985). Although this is intuitive (e.g., decrease in the durability of aragonitic shell due to undersaturation of calcium carbonate), it is important to note that due to cement precipitation in inter-crystalline voids, the resistance to destruction potentially can be increased during taphonomic processes (Alexandersson, 1972; Cutler and Flessa, 1995).

Reduced thickness of brachiopod shell beds is supposed to represent additional evidence for lower durability/lower degree of time-averaging of brachiopods (Kidwell and Brenchley, 1996). In the framework of long-term trends in shell-bed thickness, the described brachiopod deposit types of the Fatra Formation that can be considered as shell concentrations (i.e., characterized by dense packing of brachiopods) are typical of archaic shell-bed types with low thickness (mostly up to 50 cm, Table 1). This confirms the idea that the limited physical scale and low taphonomic complexity of brachiopod shell beds can be related to their organic-rich shell microstructure and life habits (rel-

atively low fecundity and limited distribution in high-energy environments, see Kidwell and Brenchley, 1994, 1996; Simões et al., 2000).

However, some of the brachiopods in this study exhibited substantial shell alteration in some deposit types, in contrast to typical Paleozoic brachiopod shell beds. In most samples, dense packing (i.e., shelliness, Cummins et al., 1986; Davies et al., 1989b) can be explained either by sudden burial by storm waves (leading to catastrophic mortality and rapid escape from the taphonomic active zone; Bio-floatstones with CIS) or by secondary enrichment by storm currents (Pavements and Biointra-packstones with CIS). Therefore, presented data indicate that preservation potential/durability of Upper Triassic brachiopods in carbonate settings was relatively higher in comparison to that of modern brachiopods from siliciclastic settings, which can exhibit substantial taphonomic alteration and show signs of cement precipitation in borings, although reduced thickness can indicate the presence of some other factors limiting their durability/potential to form thick shell beds.

The inherent durability of brachiopods has important implications for the quality of their fossil record. Unaltered and relatively uniform preservation of fossil brachiopods typically is explained by a low rate of taphonomic destruction and completeness of brachiopod assemblage is supposed to be relatively good. However, if brachiopods disintegrate into calcitic fibers faster than they accrue post-mortem alteration due to bioerosion/micritization (see Kidwell and Brenchley, 1996), then a fossil assemblage of well-preserved brachiopods must have been briefly exposed on the sea-floor, and had a relatively rapid escape from the taphonomic active zone (e.g., burial due to bioturbation). For example, Fürsich and Pandey (2003) described an Upper Jurassic siliciclastic shell bed with well-preserved terebratulid brachiopods, interpreted as part of a maximum flooding zone deposit, which originated under reduced net rate of sedimentation. Therefore, they assumed that assemblages are highly time-averaged. This can have important implications for the durability of brachiopods (i.e., they did not decompose very rapidly in the described setting). However, because taphonomic destruction in terms of disarticulation, fragmentation, or bioerosion is low, the reverse interpretation can be supposed (i.e., they degraded so rapidly that they could not accrue any substantial bioerosion). This distinction in interpretation of brachiopod durability is important, since the quality of resulting fossil assemblage will be substantially different (see Kowalewski, 1996b, 1997). In the case with a low rate of shell destruction, the probability of a higher degree of time-averaging is greater. In the case with a higher rate of shell destruction, the temporal resolution of the brachiopod assemblage probably will be higher (i.e., it will be characterized by more limited time-averaging and higher compositional fidelity). For example, in spite of high rate of destruction of punctate brachiopods in the Pacific Northwest (Daley, 1993), their rank abundances and size-frequency distributions can be represented faithfully in the death assemblages (Kowalewski et al., 2003; Tomašových, in press, a).

CONCLUSIONS

(1) Uppermost Triassic fossil assemblages with the terebratulid brachiopod *Rhaetina gregaria* from shallow in-

traplatform carbonate settings of the Fatra Formation were classified according to the fabric criteria of whole assemblages into 6 deposit types, which are interpreted as: (1) autochthonous (primary biogenic and winnowed or sediment-starved); (2) parautochthonous storm-reworked (storm wave, storm wave/flow and amalgamated storm reworked); and (3) allochthonous (long-term current/wave) deposits. Their distribution on the bed scale correlates with a depth-related environmental gradient with respect to the positions of fair-weather wave base, average storm wave base, and maximum storm wave base, and thus provides high-resolution information for paleoenvironmental reconstruction. Extrinsic variation contributing to the different fabric, geometry, and internal structure is related to: (1) rate of sedimentation; (2) water energy related to reworking and burial; and (3) original differences in distribution and composition of life associations. Because coral associations were more common above normal storm wave base, they had a higher probability of reworking than the brachiopod-bivalve associations. Fossil assemblages preserved in brachiopod deposits record a wide range of temporal resolutions, ranging from census to environmentally condensed types. In storm-reworked types, brachiopod populations commonly were affected by catastrophic mortality due to rapid burial and have limited time-averaging.

(2) Based on taphonomic signatures, three taphofacies types were recognized. This distinction, which does not strictly follow the distinction based on the fabric criteria, probably is because the biofabric primarily reflects final depositional processes (the rate and permanence of burial), whereas some taphonomic signatures reflect variation in the nature of pre-burial environmental conditions. The lowest degree of alteration, associated with low levels of bioerosion, micritization, encrustation, and disarticulation, is uniformly linked to deposits that were affected by sudden storm-induced burial. In respect to the type of benthic association and substrate type, the lowest alteration is present in deposits containing brachiopod-bivalve associations and deposits with large proportions of micritic mud. Settings with higher proportions of micritic mud (associated with brachiopod-bivalve associations) are characterized by very low degrees of bioerosion and micritization, in contrast to hard-bottom settings (associated with coral associations). This probably results from mainly extrinsic factors related to lower turbidity, higher proportion of hardparts, and higher storm reworking in the latter habitats. This effect can lead to differential between-habitat alteration of brachiopods.

(3) Autochthonous/parautochthonous occurrences of benthic associations dominated by the short-looped terebratulid *Rhaetina gregaria* are typical of settings below the fair-weather wave base, with background low-energy conditions, in contrast to high-energy/hard bottom occurrences of this association type from other regions. The difference in preservation potential of brachiopod assemblages due to extrinsic factors (e.g., between hard- and soft-bottom settings) can bias substantially understanding of their ecology and temporal shifts in their environmental preferences.

(4) Substantial taphonomic alteration of brachiopods due to bioerosion/micritization in some deposit types provides the evidence that they can resist certain levels of destruction. Actualistic data about very rapid destruction of

brachiopods are probably adequate only for some taphonomic pathways (e.g., in siliciclastic settings).

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REFERENCES

- ABBOTT, S.T., 1997, Mid-cycle condensed shell beds from mid-Pleistocene cyclothems, New Zealand: implications for sequence architecture: *Sedimentology*, v. 44, p. 805–824.
- AIGNER, T., 1979, Schill-Tempestite im Oberen Muschelkalk (Trias, SW-Deutschland): *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 157, p. 326–343.
- AIGNER T., 1982, Calcareous tempestites: storm-dominated stratification in Upper Muschelkalk limestones (Middle Triassic, SW-Germany): in Einsele, G., and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer-Verlag, Berlin, p. 180–198.
- AIGNER, T., and FUTTERER, E., 1978, Kolk-Töpfe und -Rinnen (pot and gutter casts) im Muschelkalk—Anzeiger für Wattenmeer?: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 156, p. 285–304.
- AIGNER, T., HAGDORN, H., and MUNDLOS, R., 1978, Biohermal, biostromal and storm-generated coquinas in the Upper Muschelkalk: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 157, p. 42–52.
- ALEXANDER, R.R., and SCHARF, C.D., 1990, Epizoans on late Ordovician brachiopods from southeastern Indiana: *Historical Biology*, v. 4, p. 179–202.
- ALEXANDERSSON, E.T., 1972, Micritization of carbonate particles: processes of precipitation and dissolution in modern shallow-marine sediments: *Bulletin of the Geological Institutions of the University of Uppsala N.S. 3*, v. 7, p. 201–236.
- ALEXANDERSSON, E.T., 1979, Marine maceration of skeletal carbonates in the Skaggeerak, North Sea: *Sedimentology*, v. 26, p. 845–852.
- BACCILLE, L., and BOSELLINI, A., 1965, Diagrammi per la stime viva della composizione percentuale nelle rocce sedimentaire: *Annali dell'Università di Ferrara, Scienze Geologiche e Paleontologiche*, v. 1, p. 59–62.
- BEHRENSMEYER, A.K., KIDWELL, S.M., and GASTALDO, R.A., 2000, Taphonomy and paleobiology: in Erwin D.H., and Wing S.L., eds., *Deep Time: Paleobiology*, Supplement to v. 26, p. 103–147.
- BEST, M.M.R., and KIDWELL, S.M., 2000a, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. I. Environmental variation in shell condition: *Paleobiology*, v. 26, p. 80–102.
- BEST, M.M.R., and KIDWELL, S.M., 2000b, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. II. Effect of bivalve life habits and shell types: *Paleobiology*, v. 26, p. 103–115.
- BIRKELAND, C.E., 1977, The importance of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits: *Proceedings of the Third International Coral Reef Symposium*, Miami, v. 1, p. 15–21.
- BIRKELAND, C.E., 1989, Geographic comparisons of coral-reef processes: *Proceedings of the Sixth Coral Reef Symposium*, v. 1, p. 211–220.
- BORDEAUX, Y.L., and BRETT, C.E., 1990, Substrate specific associations of epibionts on Middle Devonian brachiopods: implications for paleoecology: *Historical Biology*, v. 4, p. 203–220.
- BRACHER, T.C., BETZLER, C., BRAGA, J.C., and MARTIN, J.M., 1998, Microtaphofacies of a warm temperate carbonate ramp (uppermost Tortonian/lowestmost Messinian, Southern Spain): *PALAIOS*, v. 13, p. 459–475.
- BRETT, C.E., 1990, Ostrution deposits: in Briggs, D.E.G., and Crowther, P.R., eds., *Palaeobiology. A Synthesis*: Blackwell Science, Oxford, p. 239–243.
- BRETT, C.E., and BAIRD, G.C., 1986, Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation: *PALAIOS*, v. 1, p. 207–227.
- COLLINS, M.J., 1986, Post mortality strength loss in shells of the recent articulate brachiopod *Terebratulina retusa* (L.) from the west coast of Scotland: in Racheboeuf, P.R., and Emig, C.C., eds., *Les Brachiopodes Fossiles et Actuels, Biostratigraphique du Paléozoïque*, v. 4, p. 209–218.
- COPPER, P., 1997, Articulated brachiopod shellbeds: Silurian examples from Anticosti, Eastern Canada: *Geobios, Mémoire Spécial*, v. 20, p. 133–148.
- CUMMINS, H., POWELL, E.N., STANTON, R.J., JR., and STAFF, G., 1986, The rate of taphonomic loss in modern benthic habitats: how much of the potentially preservable community is preserved?: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 52, p. 291–320.
- CURRY, G., ANSELL, A.D., JAMES, M., and PECK, L., 1989, Physiological constraints on living and fossil brachiopods: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 80, p. 255–262.
- CUTLER, A.H., and FLESSA, K.W., 1995, Bioerosion, dissolution and precipitation as taphonomic agents at high and low latitudes: *Senckenbergiana Maritima*, v. 25, p. 115–121.
- DALEY, G.M., 1993, Passive deterioration of shelly material: a study of the recent Eastern Pacific articulate brachiopod *Terebratalia transversa* Sowerby: *PALAIOS*, v. 8, p. 226–232.
- DAVIES, D.J., POWELL, E.N., and STANTON, R.J., JR., 1989a, Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 72, p. 317–356.
- DAVIES, D.J., POWELL, E.N., and STANTON, R.J., JR., 1989b, Relative rates of shell dissolution and net sediment accumulation—a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor: *Lethaia*, v. 22, p. 207–212.
- DRUMMOND, C., and SHEETS, H., 2001, Taphonomic reworking and stratal organization of tempestite deposition: Ordovician Kope Formation, Northern Kentucky, U.S.A.: *Journal of Sedimentary Research*, v. 71, p. 621–627.
- DULAI, A., 2001, Diversification of Mediterranean Early Jurassic brachiopods after the end-Triassic mass extinction—new results from Hungary: in Brunton, H., Cocks, R., and Long, S., eds., *Brachiopods: Past and Present: The Systematic Association Special Volume Series*, v. 63, p. 411–423.
- DULAI, A., 2003, Taxonomic composition of Mediterranean Early Jurassic brachiopod faunas from Hungary: niche replacement and depth control: *Fragmenta Palaeontologica Hungarica*, v. 21, p. 43–50.
- DUNHAM, R.J., 1962, Classification of carbonate rocks according to depositional texture: *Memoirs of the American Association of Petroleum Geologists*, v. 1, p. 108–121.
- EMBRY, A.F., and KLOVAN, J.E., 1972, Absolute water depth limits of Late Devonian paleoecological zones: *Geologisches Rundschau*, v. 61, p. 672–686.
- EMIG, C.C., 1990, Examples of post-mortality alteration in Recent brachiopod shells and (paleo)ecological consequences: *Marine Biology*, v. 104, p. 233–238.
- FÜRSICH, F.T., 1990, Fossil concentrations and life and death assemblages: in Briggs, D.E.G., and Crowther, P.R., eds., *Palaeobiology. A Synthesis*: Blackwell Science, Oxford, p. 258–263.
- FÜRSICH, F.T., 1995, Shell concentrations: *Eclogae Geologicae Helveticae*, v. 88, p. 643–655.

- FÜRSICH, F.T., and OSCHMANN, W., 1993, Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India: *Journal of the Geological Society*, London, v. 150, p. 169–185.
- FÜRSICH, F.T., and PANDEY, D.K., 1999, Genesis and environmental significance of Upper Cretaceous shell concentrations from the Cauvery Basin, southern India: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 145, p. 119–139.
- FÜRSICH, F.T., and PANDEY, D.K., 2003, Sequence stratigraphic significance of sedimentary cycles and shell concentrations in the Upper Jurassic–Lower Cretaceous of Kachchh, western India: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 193, p. 285–309.
- FUTTERER, E., 1982, Experiments on the distinction of wave and current influenced accumulations: *in* Einsele, G., and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer-Verlag, Berlin, p. 175–179.
- GARDNER, W.D., 1980a, Field assessment of sediment traps: *Journal of Marine Research*, v. 38, p. 41–52.
- GARDNER, W.D., 1980b, Sediment trap dynamics and calibration: a laboratory evaluation: *Journal of Marine Research*, v. 38, p. 17–39.
- GASPARD, D., 1989, Quelques aspects de la biodégradation des coquilles de brachiopodes; conséquence sur leur fossilisation: *Bulletin de la Société Géologique de France* (8), t. V, p. 1207–1216.
- GASPARD, D., 1996, Taphonomy of some Cretaceous and recent brachiopods: *in* Copper, P., and Jin, J., eds., *Brachiopods: Proceedings of the 3rd International Brachiopod Congress*: A.A. Balkema, Rotterdam-Brookfield, p. 95–102.
- GLOVER, C.P., and KIDWELL, S.M. 1993, Influence of organic matrix on the post-mortem destruction of molluscan shells: *Journal of Geology*, v. 101, p. 729–747.
- GOLDRING, R., and AIGNER, T., 1982, Scour and fill: the significance of event sedimentation: *in* Einsele, G., and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer-Verlag, Berlin, p. 354–362.
- GOLEBIEWSKI, R., 1991, Becken und Riffe der alpinen Obertrias—Lithostratigraphie und Biofazies der Kössener Formation: *Exkursionen im Jungpaläozoikum und Mesozoikum Österreichs, Österreichische Paläontologische Gesellschaft*, Vienna, p. 79–119.
- HAGDORN, H., and MUNDLOS, R., 1982, Autochthonschille im Oberen Muschelkalk (Mitteltrias) Südwestdeutschlands: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 162, p. 332–351.
- HALLOCK, P., 1988, The role of nutrient availability in bioerosion: consequences to carbonate buildups: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 275–291.
- HALLOCK, P., and SCHLAGER, W., 1986, Nutrient excess and the demise of coral reefs and carbonate platforms: *PALAIOS*, v. 1, p. 389–398.
- JOHNSON, M.E., 1989, Tempestites recorded as variable *Pentamerus* layers in the lower Silurian of southern Norway: *Journal of Paleontology*, v. 63, p. 195–205.
- JOHNSON, R.G., 1957, Experiments on the burial of shells: *Journal of Geology*, v. 65, p. 527–535.
- KESLING, R.V., HOARE, R.D., and SPARKS, D.K., 1980, Epizoans of the Middle Devonian brachiopod *Paraspirifer bownockeri*: their relationship to one another and to their host: *Journal of Paleontology*, v. 54, p. 1141–1154.
- KIDWELL, S.M., 1990, Phanerozoic evolution of macroinvertebrate shell accumulations: preliminary data from the Jurassic of Britain: *Paleontological Society Special Publications* No. 5, p. 309–327.
- KIDWELL, S.M., 1991a, The stratigraphy of shell concentrations: *in* Allison, P.A., and Briggs, D.E.G., eds., *Taphonomy: Releasing the Data Locked in the Fossil Record*: Topics in Geobiology 9, Plenum Press, New York, p. 115–129.
- KIDWELL, S.M., 1991b, Taphonomic feedback (live/dead interactions) in the genesis of bioclastic beds: keys to reconstructing sedimentary dynamics: *in* Einsele, G., Ricken, W., and Seilacher, A., eds., *Cycles and Events in Stratigraphy*: Springer-Verlag, Berlin, p. 268–282.
- KIDWELL, S.M., 1998, Time-averaging in the marine fossil record: overview of strategies and uncertainties: *Geobios*, v. 30, p. 977–995.
- KIDWELL, S.M., and BOSENCE, D.W.J., 1991, Taphonomy and time-averaging of marine shelly faunas: *in* Allison, P.A., and Briggs, D.E.G., eds., *Taphonomy: Releasing the Data Locked in the Fossil Record*: Topics in Geobiology 9, Plenum Press, New York, p. 115–209.
- KIDWELL, S.M., and BRENCHLEY, P.J., 1994, Patterns in bioclastic accumulation through the Phanerozoic: changes in input or destruction?: *Geology*, v. 22, p. 1139–1143.
- KIDWELL, S.M., and BRENCHLEY, P.J., 1996, Evolution of the fossil record: thickness trends in marine skeletal accumulations and their implications: *in* Jablonski, D., Erwin, D.H., and Lipps, J.H., eds., *Evolutionary Paleobiology*: The University of Chicago Press, Chicago, London, p. 290–336.
- KIDWELL, S.M., FÜRSICH, F.T., and AIGNER, T., 1986, Conceptual framework for the analysis and classification of fossil concentrations: *PALAIOS*, v. 1, p. 228–238.
- KIDWELL, S.M., and HOLLAND S.M., 1991, Field description of coarse bioclastic fabric: *PALAIOS*, v. 6, p. 426–434.
- KIDWELL, S.M., ROTHFUS, T.A., and BEST, M.M.R., 2001, Sensitivity of taphonomic signatures to samples size, sieve size, damage scoring system, and target taxa: *PALAIOS*, v. 16, p. 26–52.
- KOBLUK, D.R., and RISK, M.J., 1977, Micritization and carbonate-grain binding by endolithic algae: *Bulletin of the American Association of Petroleum Geologists*, v. 61, p. 1069–1082.
- KOWALEWSKI, M., 1996a, Time-averaging, overcompleteness, and the geological record: *Journal of Geology*, v. 104, p. 317–326.
- KOWALEWSKI, M., 1996b, Taphonomy of a living fossil: the lingulide brachiopod *Glottidia palmeri* Dall from Baja California, Mexico: *PALAIOS*, v. 11, p. 244–265.
- KOWALEWSKI, M., 1997, The reciprocal taphonomic model: *Lethaia*, v. 30, p. 86–88.
- KOWALEWSKI, M., CARROLL, M., CASAZZA, L., GUPTA, N., HANNISDAL, B., HENDY, A., KRAUSE, R.A., JR., LABARBERA, M., LAZO, D.G., MESSINA, C., PUCHALSKI, S., ROTHFUS, T.A., SÄLGEBAK, J., STEMPIEN, J., TERRY, R.C., and TOMAŠOVÝCH, A., 2003, Quantitative fidelity of brachiopod-mollusk assemblages from modern subtidal environments of San Juan Islands, USA: *Journal of Taphonomy*, v. 1, p. 43–65.
- KOWALEWSKI, M., FLESSA, K.W., and AGGEN, J.A., 1994, Taphofacies analysis of Recent shelly cheniers (beach ridges), Northeastern Baja California, Mexico: *Facies*, v. 31, p. 209–242.
- KOWALEWSKI, M., SIMÕES, M.G., CARROLL, M., and RODLAND, D.L., 2002, Abundant brachiopods on a tropical upwelling-influenced shelf (southeast Brazilian Bight, South Atlantic): *PALAIOS*, v. 17, p. 277–286.
- LESCINSKY, H.L., 1993, Taphonomy and paleoecology of epibionts on the scallops *Chlamys hastata* (Sowerby 1843) and *Chlamys rubida* (Hinds 1845): *PALAIOS*, v. 8, p. 267–277.
- LESCINSKY, H.L., EDINGER, E., and RISK, M.J., 2002, Mollusc shell encrustation and bioerosion rates in a modern epeiric sea: taphonomy experiments in the Java Sea, Indonesia: *PALAIOS*, v. 17, p. 171–191.
- MACCHIONI, F., 2000, Bioeroded and/or encrusted ammonite moulds and their taphonomic implications: *Rivista Italiana di Paleontologia e Stratigrafia*, v. 106, p. 337–352.
- MANDIC, O., and PILLER, W.E., 2001, Pectinid coquinas and their palaeoenvironmental implications—examples from the early Miocene of northeastern Egypt: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 172, p. 171–191.
- MELDAHL, K.H., and FLESSA, K.W., 1990, Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment: *Lethaia*, v. 23, p. 43–60.
- MICHALÍK, J., 1975, Genus *Rhaetina* Waagen, 1882 (Brachiopoda) in the uppermost Triassic of the West Carpathians: *Geologický Zborník—Geologica Carpathica*, v. 26, p. 47–76.
- MICHALÍK, J., 1982, Uppermost Triassic short-lived bioherm complexes in the Fatic, Western Carpathians: *Facies*, v. 6, p. 129–146.
- MICHALÍK, J., 1994, Notes on the paleogeography and paleotectonics of the Western Carpathian area during the Mesozoic: *Mitteilungen der Österreichischen Geologischen Gesellschaft*, v. 86, p. 101–110.
- MICHALÍK, J., IORDAN, M., RADULOVIC, M., TCHOUMATCHENCO, P., and VÖRÖS, A., 1991, Brachiopod faunas of the Triassic–Jurassic

- boundary interval in the Mediterranean Tethys: *Geologica Carpathica*, v. 42, p. 59–63.
- MIDDLETON, G.V., 1967, The orientation of concavo-convex particles deposited from experimental turbidity currents: *Journal of Sedimentary Petrology*, v. 37, p. 229–232.
- MITTERER, R.M., and CUNNINGHAM, R., JR., 1985, The interaction of natural organic matter with grain surfaces: implications for calcium carbonate precipitation: *SEPM Special Publication*, v. 36, p. 17–31.
- NEBELSICK, J.H., 1999, Taphonomy of *Clypeaster* fragments: preservation and taphofacies: *Lethaia*, v. 32, p. 241–252.
- NEBELSICK, J.H., and BASSI, D., 2000, Diversity, growth-forms and taphonomy: key factors controlling the fabric of coralline algae dominated shelf carbonates: in Insalaco, E., Skelton, P.W., and Palmer, T.J., eds., *Carbonate Platform Systems: Components and Interactions*: Geological Society of London, Special Publication, v. 178, p. 89–107.
- NEBELSICK, J.H., and KROH, A., 2002, The stormy path from life to death assemblages: the formation and preservation of mass accumulations of fossil sand dollars: *PALAIOS*, v. 17, p. 378–393.
- NORRIS, R.D., 1986, Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California: *PALAIOS*, v. 1, p. 256–270.
- OLÓRIZ, F., REOLID, M., and RODRÍGUEZ-TOVAR, F.J., 2002, Fossil assemblages, lithofacies, taphofacies and interpreting depositional dynamics in the epicontinental Oxfordian of the Prebetic Zone, Betic Cordillera, southern Spain: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 185, p. 53–75.
- PANDOLFI, J.M., and GREENSTEIN, B.J., 1997, Taphonomic alteration of reef corals: effects of reef environment and coral growth form: I. The Great Barrier Reef: *PALAIOS*, v. 12, p. 27–42.
- PARSONS, K.M., BRETT, C.E., and MILLER, K.B., 1988, Taphonomy and depositional dynamics of Devonian shell-rich mudstones: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 109–139.
- PEARSON, D.A.B., 1977, Rhaetian brachiopods of Europe: *Neue Denkschriften des Naturhistorischen Museums in Wien*, v. 1, p. 1–70.
- POWELL, E.N., STAFF, G.M., DAVIES, D.J., and CALLENDER, W.R., 1989, Macrobenthic death assemblages in modern marine environments: formation, interpretation, and application: *Reviews in Aquatic Sciences*, v. 1, p. 555–589.
- POWERS, B.G., and AUSICH, W.I., 1990, Epizoan associations in a lower Mississippian paleocommunity (Borden Group, Indiana, U.S.A.): *Historical Biology*, v. 4, p. 245–265.
- SANDY, M., 1995, Early Mesozoic (Late Triassic–Early Jurassic) Tethyan brachiopod biofacies: possible evolutionary intra-phylum niche replacement within the Brachiopoda: *Paleobiology*, v. 21, p. 479–495.
- SCHÄFER, K., 1969, Vergleichs-Schaubilder zur Bestimmung des Alchemehalts bioklastischer Karbonatgesteine: *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, v. 1969, p. 173–184.
- SEILACHER, A., 1971, Preservational history of ceratite shells: *Palaeontology*, v. 14, p. 16–21.
- SEILACHER, A., 1985, The Jeram model: event condensation in a modern intertidal environment: in Bayer, U., and Seilacher, A., eds., *Sedimentary and Evolutionary Cycles*: Springer-Verlag, Berlin, p. 336–341.
- SIBLÍK, M., 1998, A contribution to the brachiopod fauna of the “Oberrhätalkalk” (Northern Calcareous Alps, Tyrol-Salzburg): *Jahrbuch der Geologischen Bundesanstalt*, v. 141, p. 73–95.
- SIMÕES, M.G., and KOWALEWSKI, M., 1998, Shell beds as paleoecological puzzles: a case study from the Upper Permian of the Parana Basin, Brazil: *Facies*, v. 38, p. 175–196.
- SIMÕES, M.G., KOWALEWSKI, M., TORELLO, F.F., GHILARDI, R.P., and MELLO, L.H.C., 2000, Early onset of modern-style shell beds in the Permian sequences of the Parana Basin: implications for the Phanerozoic trend in bioclastic accumulations: *Revista Brasileira de Geociências*, v. 30, p. 495–499.
- SPEYER, S.E., and BRETT, C.E., 1988, Taphofacies models for epeiric sea environments: Middle Paleozoic examples: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 225–262.
- SPEYER, S.E., and BRETT, C.E., 1991, Taphofacies controls. Background and episodic processes in fossil assemblage preservation: in Allison, P.A., and Briggs, D.E.G., eds., *Taphonomy: Releasing the Data Locked in the Fossil Record*: Topics in Geobiology 9, Plenum Press, New York, p. 501–545.
- SPJELDNAES, N., 1984, Epifauna as a tool in autecological analysis of Silurian brachiopods: *Special Papers in Paleontology*, v. 32, p. 225–235.
- STAFF, G.M., and POWELL, E.N., 1990, Local variability of taphonomic attributes in a parautochthonous assemblage: can taphonomic signature distinguish a heterogeneous environment?: *Journal of Paleontology*, v. 64, p. 648–658.
- TAYLOR, P.D., and MICHALÍK, J., 1991, Cyclostome bryozoans from the late Triassic (Rhaetian) of the West Carpathians. *Czechoslovakia: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 182, p. 285–302.
- TOMAŠOVÝCH, A., 2001, The distribution of rhynchonellid brachiopods after the T–J boundary in Europe: Abstracts of the SW England field workshop (IGCP 458—Triassic/Jurassic Boundary Events), Taunton, p. 19–22.
- TOMAŠOVÝCH, A., 2002, Benthic assemblages and depositional environment in the Uppermost Triassic (Rhaetian) of the West Carpathians (Fatric Unit, Vel'ká Fatra Mts.): Unpublished M.S. Thesis, Comenius University, Bratislava, 136 p.
- TOMAŠOVÝCH, A., 2004, Microfacies and depositional environment of an Upper Triassic intra-platform carbonate basin: the Fatric Unit of the West Carpathians (Slovakia): *Facies*, v. 50, p. 77–105.
- TOMAŠOVÝCH, A., in press, a, Postmortem durability and population dynamics affecting the fidelity of brachiopod size-frequency distributions: *PALAIOS*, v. 19, no. 5.
- TSUJITA, C.J., 1995, Origin of concretion-hosted shell clusters in the late Cretaceous Bearpaw Formation, southern Alberta, Canada: *PALAIOS*, v. 10, p. 408–423.
- TÖRÖK, A., 1993, Brachiopod beds as indicators of storm events: an example from the Muschelkalk of southern Hungary: in Pálffy, J., and Vörös, A., eds., *Mesozoic Brachiopods of Alpine Europe*, Hungarian Geological Society, Budapest, p. 161–172.
- VOGEL, K., GOLUBIC, S., and BRETT, C.E., 1987, Endolith associations and their relation to facies distribution in the Middle Devonian of New York State, U.S.A.: *Lethaia*, v. 20, p. 263–290.
- WANI, R., 2001, Reworked ammonoids and their taphonomic implications in the Upper Cretaceous of northwestern Hokkaido, Japan: *Cretaceous Research*, v. 22, p. 615–625.
- WANI, R., 2003, Taphofacies models for Upper Cretaceous ammonoids from the Kotanbetsu area, northwestern Hokkaido, Japan: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 199, p. 71–82.
- ZUSCHIN, M., and STANTON, R.J., JR., 2002, Paleocommunity reconstruction from shell beds: a case study from the Main Glauconite Bed, Eocene, Texas: *PALAIOS*, v. 17, p. 602–614.

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