

# Composition of Hettangian brachiopod communities in the Western Carpathians: implications for recovery after the end-Triassic mass extinction event

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The Lower–Middle Hettangian post-extinction brachiopods in the Western Carpathians occur in micrite-rich limestones with sponge spicules and peloids that represent carbonate-rich, mixed-bottom habitats below a maximum storm wave base. *Lobothyris* is the first brachiopod appearing in a succession and locally occurs in monospecific, autochthonous or paraautochthonous shell beds. *Lobothyris* was less disarticulated and fragmented and attained a larger size in shell beds than in shell-poor beds. Uniform size modes of adults in shell beds indicate that the high shell density of *Lobothyris* was not a result of opportunistic bursts. The increase in shell density thus might be more related to a decrease in adult mortality rate and increase in mean adult size. The *Lobothyris* community was stratigraphically replaced by a community dominated by oysters, and higher by a community dominated by the terebratulid *Zeilleria*, the multicostate rhynchonellid *Jakubirhynchia* and oysters. Compositionally, similar brachiopod communities dominated either by (1) *Lobothyris* or (2) *Zeilleria* and multicostate rhynchonellids inhabited also other western Tethyan regions during Hettangian. *Lobothyris* occupied shallower habitats or habitats more proximal to shoreline than *Zeilleria* and multicostate rhynchonellids. Distinct habitat preferences of *Lobothyris*, *Zeilleria* and rhynchonellids reflect an increase in between-habitat variation in composition of brachiopod communities in the western Tethys after the end-Triassic mass extinction. □ *Jurassic, mass extinction, palaeoecology, taphonomy, Triassic, Western Carpathians.*

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In spite of some discussion about duration of the end-Triassic mass extinction, i.e. whether it was stepwise or catastrophic (Hallam 2002), this event records genus and family extinction rates that were substantially higher than those typical of most other Phanerozoic stages (Sepkoski 1997). This event strongly affected distribution and abundance of brachiopods (Dagys 1990; Sandy 1995) and bivalves (McRoberts & Newton 1995; McRoberts *et al.* 1997; Hautmann 2004). An increase in predation and competition intensity is one of the explanations accounting for the general decrease in abundance and diversity of brachiopods through the Mesozoic (Vermeij 1987). Alternatively, effects of relatively sudden global or regional extrinsic disturbances might also govern this brachiopod decline, and can thus provide opposite or complementary explanations of their Mesozoic ecologic and evolutionary history (Jablonski 2001). Evaluating response of brachiopods to extensive extrinsic disturbance at the end of the Triassic is thus essential for understanding their distribution pattern during the Mesozoic (Pálffy 2003).

The recovery of Hettangian brachiopods in NW Europe was slow and characterized mainly by monospecific occurrences of the rhynchonellid

*Calcirhynchia calcaria* Buckman (Hallam 1960; Alméras & Hanzo 1991). In contrast, Hettangian brachiopods were characterized by a higher taxonomic diversity in the Tethyan area (Dulai 2001). The aim of this study is to evaluate the composition and temporal replacement of Lower–Middle Hettangian brachiopod communities in the Western Carpathians, to assess whether brachiopod shell beds reflect bursts of post-extinction opportunists, and to compare them with other brachiopod communities known from Hettangian deposits of the western Tethys area.

Although the presented data are derived from one section only, it is the only known site in the Western Carpathians where post-extinction Hettangian brachiopods occur in high abundance. This site thus provides a unique opportunity to study the composition of post-extinction brachiopod communities in the Western Carpathians.

## Methods

Six hundred fifty-two incompletely silicified specimens of brachiopods and bivalves were collected or counted

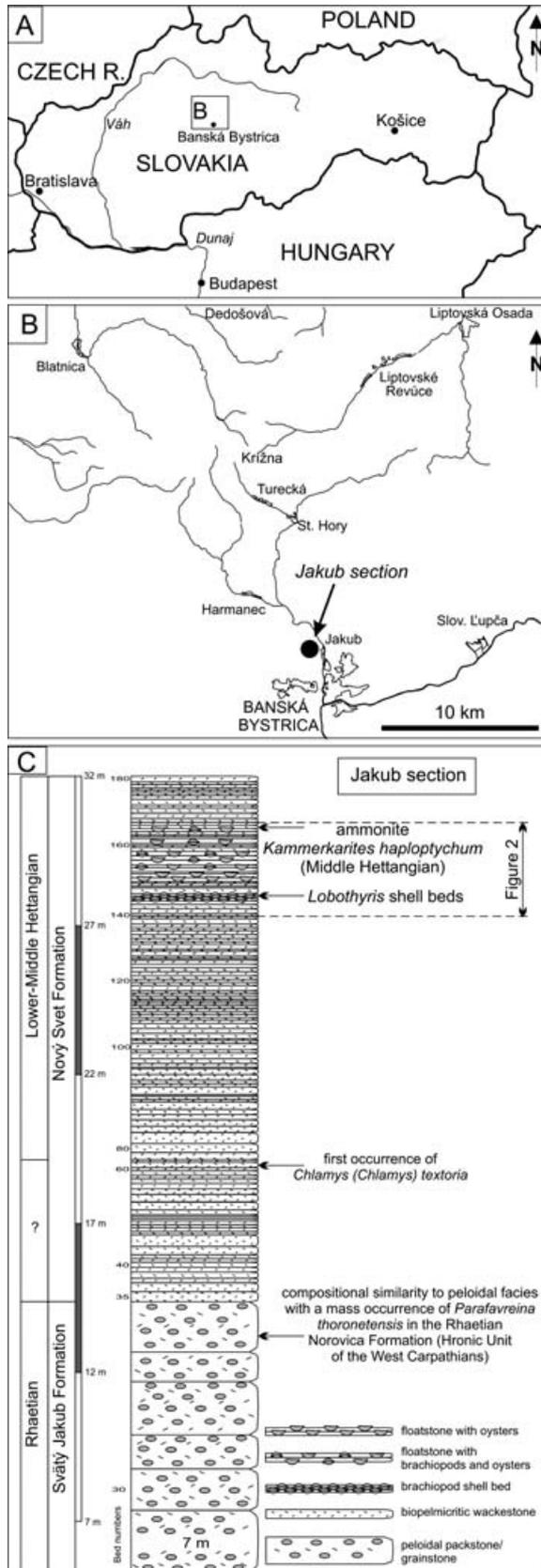


Fig. 1. □A, B. Geographic location of the Jakub section in Slovakia. □C. Stratigraphic section showing its basic subdivision into the Svätý Jakub and Nový Svet formations.

in a stratigraphic section near the Jakub village (Fig. 1A–B, Tomašových & Michalík 2000). The section is situated in the southern part of the Veľká Fatra Mountains in central Slovakia (Fig. 1) and belongs to the Fatric Unit. Absolute abundances were counted as the sum of shells and valves and transformed to relative abundances (Table 1). The relationship among samples and among taxa was evaluated with a Bray-Curtis similarity coefficient and analyzed with a cluster analysis (group-average linking method) and non-metric multidimensional scaling (NMDS). The evenness of samples was computed with the probability of an interspecific encounter (PIE, Hurlbert 1971). PIE is one of the few evenness indices that is unbiased by sample size (Gotelli & Graves 1996). Size-frequency distributions (SFDs) of specimens > 5 mm were computed for evaluating between-sample differences in size modes of adults of three brachiopod species. Proportions of articulated and complete specimens were calculated from the sampled specimens.

### Geographic setting

The Western Carpathians were situated on the northwestern margin of the Tethys Ocean during the Hettangian. In this area, marine deposits of the Hettangian age continuously overlie Rhaetian deposits in the Fatric Unit only. The Hettangian deposits in the Fatric Unit mostly belong to the Kapienec Formation. This formation consists of claystones, siltstones and sandy limestones and may contain abundant bivalves (Kochanová 1967). Brachiopods are rare (Gaździcki *et al.* 1979). In the southernmost part of the Fatric Unit, isolated tectonic blocks show a quite different succession of the Hettangian deposits. These deposits contain minor siliciclastic admixture and belong to the carbonate-rich Nový Svet Formation (Fig. 1C, Tomašových & Michalík 2000; Tomašových 2006). In contrast to the Kapienec Formation, this formation contains Hettangian communities dominated by brachiopods.

### Stratigraphic section

The Nový Svet Formation overlies peloidal limestones of the Svätý Jakub Formation with rare macrofauna (Fig. 1C). Based on compositional similarities with the Rhaetian Norovica Formation in the Hronic Unit, the Svätý Jakub Formation is most probably of Rhaetian age. The Nový Svet Formation is formed by dark grey, well-bedded biopel-wackestones and floatstones with common peloids and sponge spicules.

Table 1. Sample-level absolute abundance data of brachiopods and bivalves. Abundances of *Gryphaea* sp. in beds 151–153 are based on counts on bedding planes that were stopped when the first 30 specimens were recorded in each bed. Abundance data from beds 143, 154 and 157 were not used in multivariate analyses.

Sample (bed)	<i>Lobothyris andleri</i>	<i>Zeilleria perforata</i>	<i>Jakubirhynchia latifrons</i>	<i>Gryphaea</i> sp.	<i>Chlamys (Chlamys) textoria</i>	<i>Camptonectes</i> sp.	<i>Plagiostoma</i> aff. <i>punctatum</i>	Pteriomorphid indet	Heterodont indet
143	4	0	0	0	0	0	0	0	0
144	85	0	0	0	0	0	0	0	0
145	102	0	0	0	0	0	0	0	0
146	98	0	0	3	0	0	0	0	0
147	16	0	0	1	0	0	0	0	0
151	0	0	0	30	0	0	0	0	0
152	0	0	0	30	0	0	0	0	0
153	0	0	0	30	0	0	0	0	0
154	0	1	1	1	0	0	0	0	0
155	0	53	27	8	1	0	0	0	0
156	0	8	4	4	0	0	0	1	0
157	0	6	1	1	0	0	0	0	0
158	1	16	3	5	0	1	0	1	1
161	0	8	0	14	1	0	0	0	0
167	0	50	38	8	2	1	1	0	0

The bedding planes of wackestones and floatstones are enriched in silt-sized quartz, locally forming 0.5–1 cm thick, poorly lithified layers or pavements. The proportion of sponge spicules slightly increases and peloids slightly decreases upwards, implying a deepening-upward trend towards the Middle Hettangian part of the section. Macrofauna is relatively rare in the lower part of the Nový Svet Formation, represented by bivalves (*Chlamys (Chlamys) textoria* (Schlotheim), *Plagiostoma* aff. *punctatum* (J. Sowerby), *Gryphaea* sp.) and echinoids. In the upper part of the Nový Svet Formation, shell-rich floatstones with abundant macrofauna alternate with bioturbated biopel-wackestones with rare macrofossils (Fig. 2). Microfacies differences between shell-poor and shell-rich limestone beds are minor. In beds 144–146, the terebratulid *Lobothyris andleri* (Opell) forms a 20-cm thick interval of three shell beds (Fig. 1C). An ammonite *Kammerkarites haploptychum*, which marks the Middle Hettangian, was found in the upper part of the Nový Svet Formation (bed 168). The fossil assemblages described here are supposed to be of Early–Middle Hettangian age.

## Benthic communities

A cluster analysis based on Bray-Curtis (BC) similarities discriminated three groups of samples (Fig. 3A). They include (1) four samples dominated by a short-looped terebratulid *Lobothyris andleri*, (2) four samples dominated by *Gryphaea* sp., and (3) four samples with a long-looped terebratulid *Zeilleria perforata* (Piette), a multicostate rhynchonellid

*Jakubirhynchia latifrons* (Geyer), and *Gryphaea* sp. These sample groups are termed as communities here. The *Lobothyris* community is replaced stratigraphically by two other communities (Fig. 2). Q-mode NMDS shows that the *Gryphaea* and *Zeilleria-Jakubirhynchia* communities are more similar in composition to each other than to the *Lobothyris* community (Fig. 3B). R-mode NMDS indicates that *Zeilleria*, *Gryphaea* and *Jakubirhynchia* have similar sample-level abundances and coexist more commonly with each other than with *Lobothyris* (Fig. 3C). BC similarities among *Lobothyris* and other taxa are invariably very low (BC < 5). In contrast, BC similarity between *Zeilleria* and *Jakubirhynchia* is substantially higher (BC = 58). BC similarities between *Gryphaea* and *Zeilleria* (BC = 28), and between *Gryphaea* and *Jakubirhynchia* (BC = 19) are relatively low. The guild structure is simple, dominated by epifaunal, poorly mobile suspension-feeders represented by pedunculate brachiopods, free-lying bivalves and epibyssate bivalves.

### The *Lobothyris* community

This is the first brachiopod community that appears in the section. It is represented by 305 individuals and occurs in a 73-cm thick bedset of wackestones and floatstones that alternate with thin poorly lithified layers or pavements (beds 141–147). *Lobothyris andleri* (97.8%) dominates and *Gryphaea* sp. is rare (2.2%). The evenness (PIE) is extremely low (0–0.12).

Wackestones and floatstones contain sponge spicules (10 to 15%), ostracods, echinoderm fragments and variable amounts of dispersed peloids (Fig. 4A).

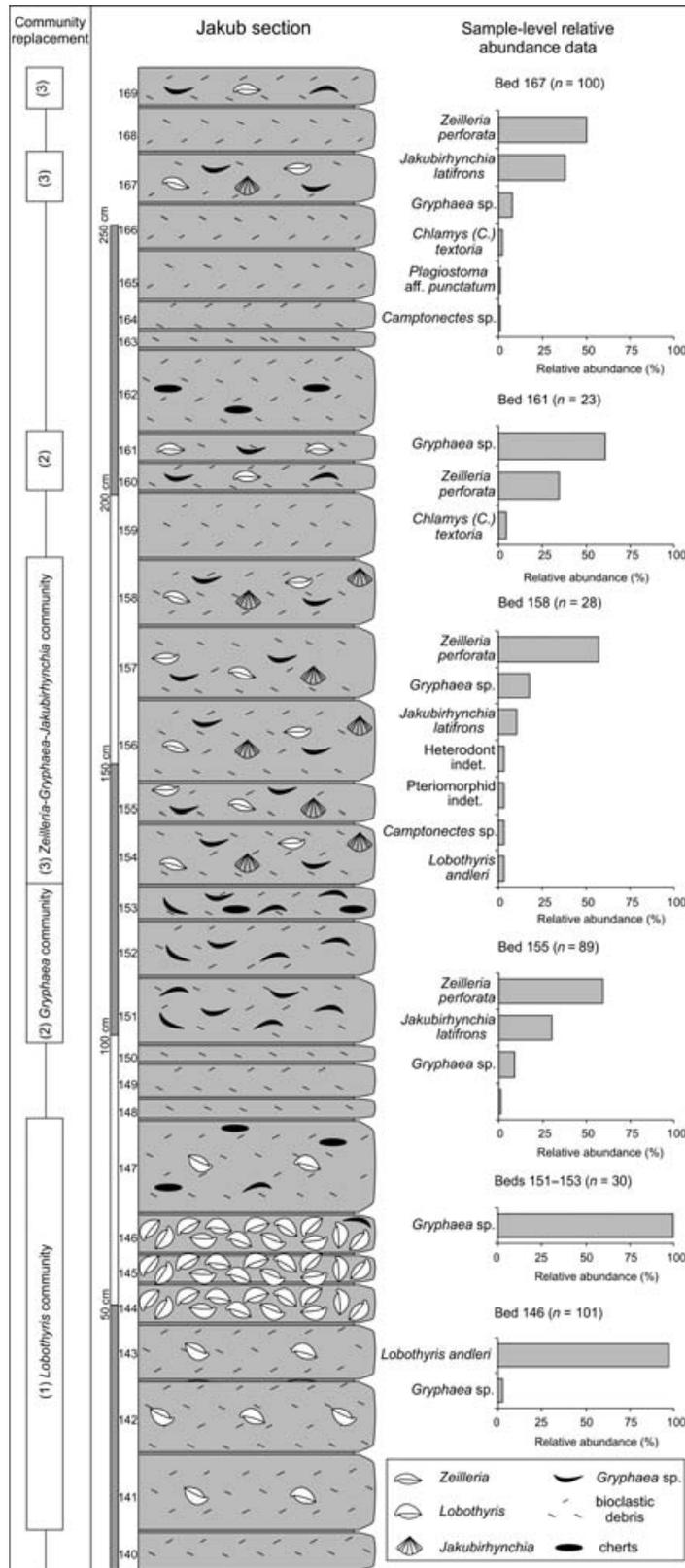


Fig. 2. The upper part of the Nový Svet Formation (Lower-Middle Hettangian) showing alternation of shell-rich and shell-poor beds and community replacement.

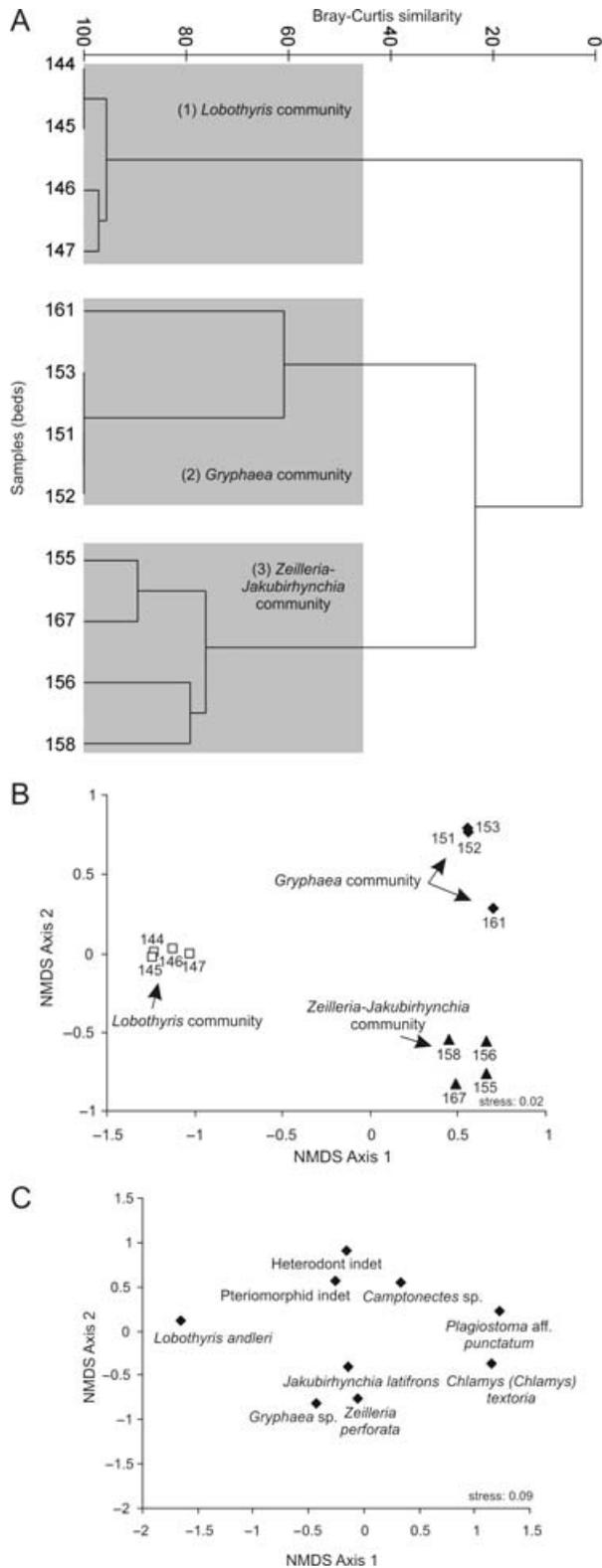


Fig. 3. □A. Q-mode cluster analysis discriminating three benthic communities. □B. Q-mode NMDS showing compositional relationship among samples and corresponding communities. □C. R-mode NMDS indicating similarity in abundance patterns among species. The scaling and orientation of axes in NMDS are arbitrary. The configurations are rotated to have the greatest variation along the first axis for visual convenience.

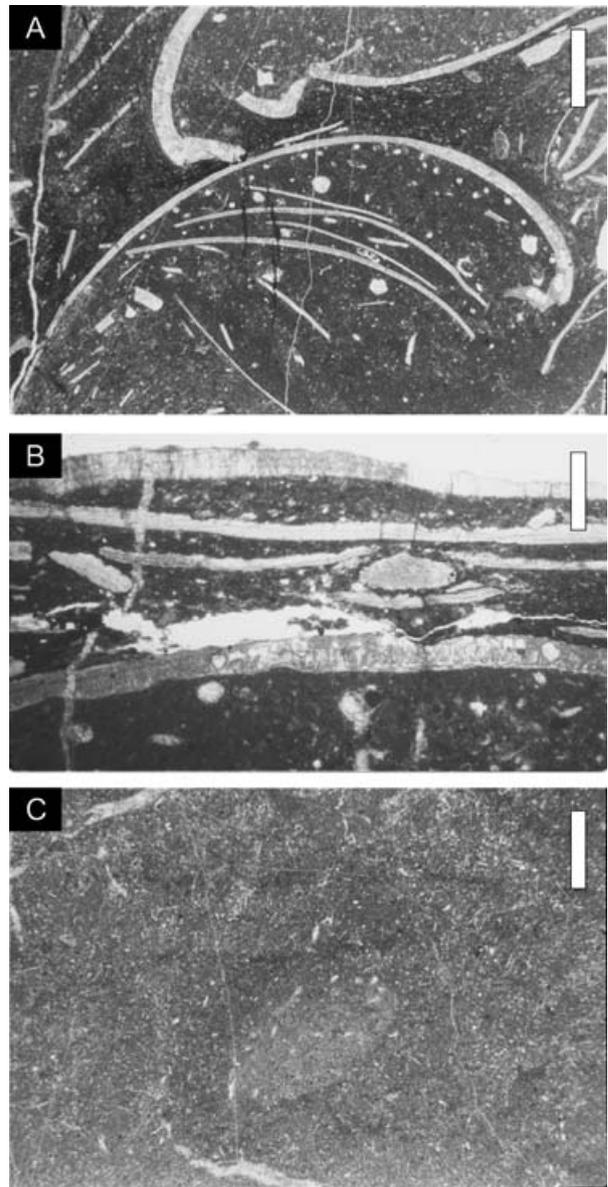


Fig. 4. □A. Floatstone with *Lobothis andleri* (bed 146) (scale bar = 0.5 mm). □B. Fragmented and disarticulated valves of *L. andleri* forming pavement enriched in quartz admixture (bed 146) (scale bar = 2 mm). □C. Shell-poor, bioturbated wackestone (bed 148) (scale bar = 0.5 mm).

Intraskelatal cavities are filled with micrite. Bioclasts are rarely encrusted, bored or coated with crusts. Shell density varies substantially within the bed set. In its lower (beds 141 to 143) and uppermost part (bed 147), brachiopods are dispersed, poorly sorted and randomly oriented. A 20-cm thick group of beds of loosely or densely packed brachiopod shell beds (beds 144–146) is present in its middle part. Here, brachiopods are poorly sorted, commonly in nested and stacked orientations and form approximately 15% to 35% of rock volume (Fig. 5A–C). In contrast

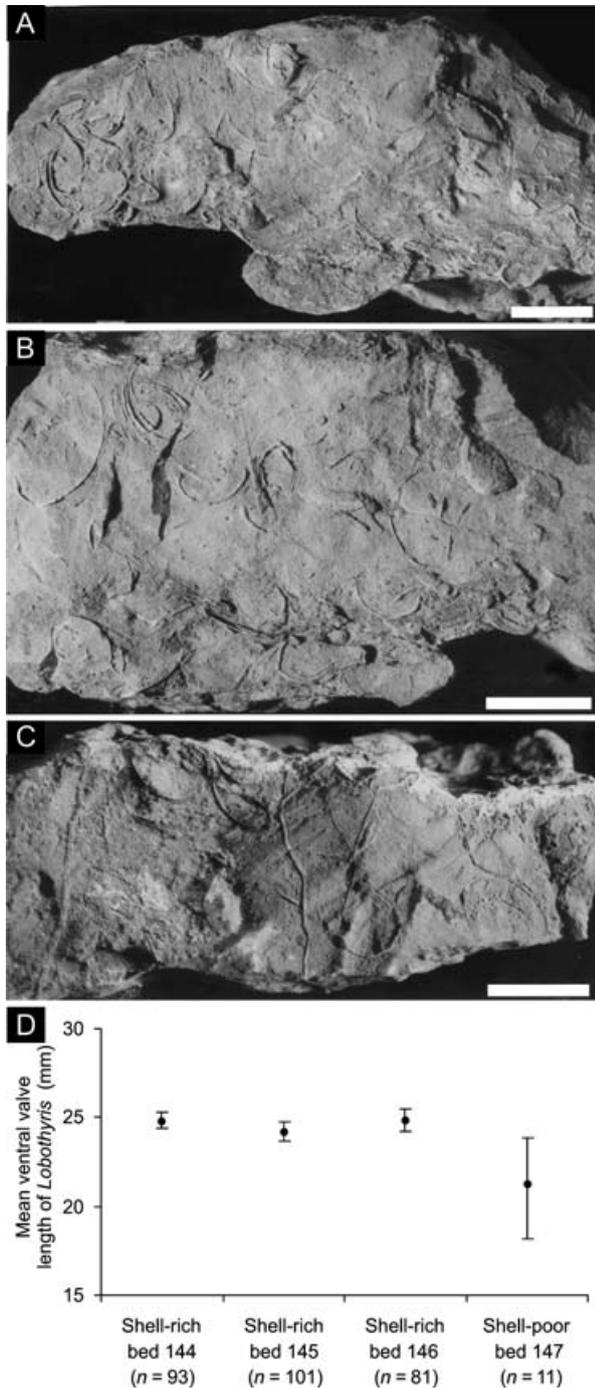


Fig. 5. Side views of the *Lobothis* shell beds. □A. Bed 146. □B. Bed 145. □C. Bed 144 (scale bars = 2 cm). □D. Differences in mean length of ventral valves of *Lobothis* between shell beds 144–146 and shell-poor bed 147 (with bootstrapped 95% confidence intervals).

to higher fragmentation and disarticulation in shell-poor beds (about 40%), brachiopods exhibit low proportions of disarticulation (3–12%) and fragmentation (1–8%) in shell beds. Mean sizes of ventral valves from three shell beds are higher (24.2–24.9 mm) than

in shell-poor beds (21.3 mm). Bootstrapped 95% confidence intervals indicate that this difference is probably significant (Fig. 5D). SFDs of *L. andleri* demonstrate that a size mode attains uniformly 27 mm in each of the three successive shell beds (Fig. 6). Pairwise comparisons show no significant differences in shape of SFDs (Kolmogorov Smirnov test, Fig. 6A) and in their medians among three shell beds (Mann-Whitney U test, Fig. 6A).

The pavements enriched in siliciclastic admixture consist mainly of bioclastic material and peloids. Shell density can be high, resulting in densely packed fabric (Fig. 4B). Brachiopods are predominantly disarticulated and fragmented, poorly sorted and mainly concordantly oriented. Bioclasts are locally encrusted with sessile foraminifers and coated with thin micritic crusts. Signs of truncation or grading are missing.

### The *Gryphaea* community

It is represented by 113 individuals and is typical of beds 151–153 where *Gryphaea* sp. forms a monospecific assemblage in bioturbated biopelmicritic floatstones. In bed 161, *Gryphaea* sp. (60.9%) is accompanied by *Zeilleria perforata* (34.8%) and *Chlamys* (*Chlamys*) *textoria* (4.3%), and the evenness (PIE) is higher (0.53). Sponge spicules, ostracodes and silt-sized bioclastic debris are common. Oysters are dispersed or loosely packed (10% to 15%), poorly sorted, and randomly oriented. The proportions of disarticulated and fragmented valves are moderate. In the thin sections, oysters are rarely bored or encrusted.

### The *Zeilleria-Jakubirhynchia* community

It is represented by 234 individuals and its sample-level species richness (4–7) and evenness (PIE = 0.55–0.71) are higher in comparison to two other communities. *Zeilleria perforata* prevails (53.4%), and the multicostate rhynchonellid *J. latifrons* (25.7%) and *Gryphaea* sp. (14.6%) are common. *Lobothis andleri*, regular echinoids and other bivalves are rare (below 2.5%). SFDs of *Z. perforata* from beds 155–158 and 167 are similar and show comparable size modes of about 20–21 mm (Fig. 6B). Differences in SFDs of *J. latifrons* between beds 155 and 167 are also minor (Fig. 6C) and show similar size modes (14–15 mm). Wackestones and floatstones are bioturbated and contain sponge spicules, ostracods, echinoderm ossicles and gastropods. Bioclasts are dispersed or loosely packed (10% to 15%), poorly sorted, randomly oriented and locally form small clumps. The intraskeletal cavities are mostly filled with micrite. Proportions of disarticulation (38–44%) and fragmentation (27–35%) are moderate.

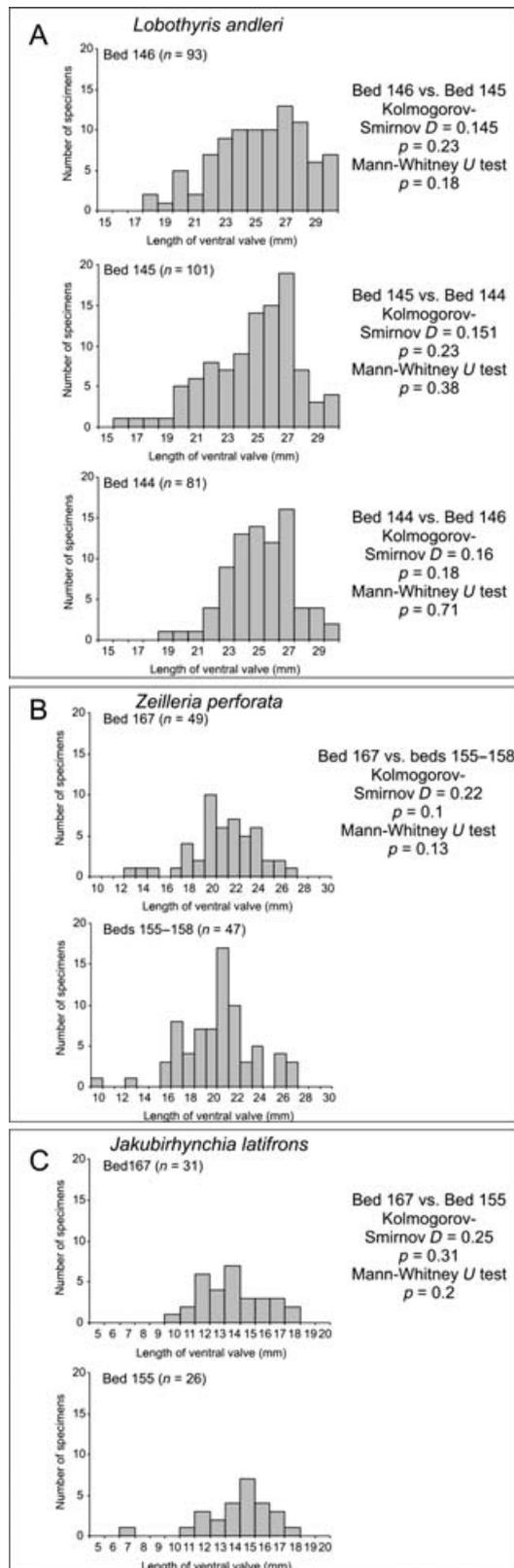


Fig. 6. Size-frequency distributions of three brachiopod species and between-sample Kolmogorov-Smirnov and Mann-Whitney  $U$  tests. □A. *Lobothyris andleri*. Three samples correspond to shell beds 144–146. □B. *Zeilleria perforata*. □C. *J. latifrons*.

Juvenile or sub-adult oysters locally encrust large bioclasts. Encrusters, borers and coatings are rare.

## Taphonomy

### Wackestones and floatstones

High or moderate proportions of articulated and complete specimens and poor sorting suggest minor post-mortem disturbance. Rarity of sparitic shell infills and absence of internal stratification indicate that the fossil assemblages were not rapidly buried. Low levels of bioerosion and encrustation might be related to presence of thin sediment veneer covering dead shells in environments rich in micrite. The *Lobothyris* shell beds can thus be classified as primary biogenic concentrations (Fürsich & Oschmann 1993). Small-scale irregularities in shell density and preferential stacking or nesting can be explained by bioturbation. Any signs of varying sedimentation rate between shell beds and shell-poor beds are missing, implying that higher shell density was not primarily related to lower sedimentation rate. Higher proportions of articulated and complete adult specimens and their higher mean size in shell beds than in shell-poor beds imply that the origin of the *Lobothyris* shell beds resulted from a combination of increased dead-shell production rate and/or decreased shell destruction rate.

Although fragments or recrystallized, originally aragonitic bivalves are locally present in the thin-sections, it is not clear whether the observed rarity of aragonitic taxa is caused by dissolution and lithification bias or whether it reflects their real rarity. Presence of gastropods and ammonites and high shell density of brachiopods may indicate that although the rarity of aragonitic taxa can be taphonomically enhanced, the community structure dominated by calcitic taxa might correspond to the original community composition.

### Pavements

Pavements probably reflect reduced rate of sedimentation because higher fragmentation, disarticulation and local presence of encrusters and coatings in shell-rich pavements indicate longer exposure on sea floor (Kidwell 1986). This could be owing to low supply of carbonate mud and selective winnowing of fine particles, which increased the likelihood of destruction and alteration by processes operating near the sediment–water interface. The high-frequency alternation of wackestones/floatstones with pavements can thus reflect subtle variations in the rate of sedimentation.

## Brachiopod habitats and community replacement

Sedimentologic and taphonomic evidence indicate a habitat below a maximum storm wave base, with background low-energy conditions, reduced or absent siliclastic supply, and substrate formed by micrite or mixture of micrite and shell debris. The abundance of sponge spicules hints at the presence of siliceous sponges in the original benthic community. In spite of the compositional segregation of the three communities in Q-mode NMDS, they are uniformly preserved in micrite-rich limestones with minor microfacies variations. The trend in the decrease in abundance and size of peloids up-section may indicate a deepening upward trend and thus subtle habitat differences between the *Lobothyris* community and two other communities replacing this community higher in the section. The compositional differences between communities might be related to factors that negatively correlated with increasing depth such as decreased nutrient supply, flow velocity or sediment input. In this case, *Lobothyris* preferred shallower habitats, and *Zeilleria* and *Jakubirhynchia* preferred deeper habitats. Uniform size modes of *Lobothyris* in three successive shell beds indicate a rather stable mortality rate in adult stages. The peak in shell density in beds 144–146 thus does not reflect episodic bursts of opportunists that may dominate in benthic communities during survival intervals after mass extinctions (Harries *et al.* 1996). The differences in mean size of *Lobothyris* between shell-rich and shell-poor beds indicate that the increased shell density was rather related to higher survival and/or higher growth rate of adults.

## Hettangian brachiopod communities in the western Tethys

Note that the described Hettangian brachiopod communities share no common species with brachiopods that occupied Late Triassic habitats in the western Tethys (Michalík & Jendrejáková 1978; Michalík 1993). With the exception of zeillerioids, Rhaetian brachiopod communities were also dominated by different clades such as dielasmatooids, hemithiridoids, athyridoids or spondylospirooids. Brachiopod communities dominated by *Zeilleria* and multicostate rhynchonellids occur in the Hettangian deposits of the Eastern Alps (Siblík 1993a, b; Böhm *et al.* 1999), Transdanubian Central Range (TCR, Dulai 2003) and Southern Alps (Gaetani 1970). Similarly, brachiopod communities dominated by *Lobothyris* inhabited

several regions of the western Tethys during Hettangian. The Early Hettangian habitats of the Eastern Alps (Golebiowski & Braunstein 1988; Siblík 1999) were dominated by *Lobothyris andleri* and *L. delta* (Neumayr). *L. ovatissimaeformis* (Böckh) dominated in the Southern Alps (Gaetani 1970) and TCR (Dulai 1993a, b). *Lobothyris* occurs in various deposit types, ranging from oosparites/biointrasparites (Southern Alps), oomicrites and oncomicrites (TCR), biointramicritic packstones (Eastern Alps) up to biopelmicritic wackestones (Western Carpathians). This distribution indicates variable conditions with respect to energy level and substrate stability and thus a generalistic life habit of *Lobothyris*. Within-basin comparisons suggest that *Lobothyris* dominated in habitats that were shallower or more proximal to shoreline than habitats occupied by other brachiopods (Dulai 2003). In addition to the Western Carpathians, stratigraphic replacement of the *Lobothyris* community by communities dominated by zeillerioids and multicostate rhynchonellids was recorded in the Southern Alps (Gaetani 1970) and Eastern Alps (Siblík 1993b, 1999). This replacement consistently correlates with a deepening upward trend. Because the differentiation of Hettangian brachiopod communities into those dominated either by *Lobothyris* or *Zeilleria* and multicostate rhynchonellids was typical of several distinct basins, different habitat preferences of these brachiopods reflect a specific aspect of the recovery in the western Tethys as a consequence of increased between-habitat variation in community composition.

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