

Evaluating compositional turnover of brachiopod communities during the end-Triassic mass extinction (Northern Calcareous Alps): Removal of dominant groups, recovery and community reassembly

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Abstract

This study highlights the role of large-scale physical perturbations in mediating biotic replacements and shows that an environmental disturbance at the Triassic/Jurassic (T/J) boundary correlates with abrupt and substantial changes in the composition of brachiopod communities. Disturbance changed the phylogenetic structure of Early Jurassic brachiopod communities owing to a removal of higher taxa that were abundant in the Late Triassic. A replacement of brachiopod communities through the Rhaetian in the Kössen Basin (Northern Calcareous Alps), related to a combination of habitat tracking and immigration/local extinction events, indicates a high compositional turnover. This turnover is of local nature only because Early Rhaetian communities migrated or tracked their habitats beyond the Kössen Basin and persisted through to the Late Rhaetian in other regions. A siliciclastic interval that is several meters thick with rare brachiopods dated as the earliest Hettangian marks the extinction–survival interval. This interval is coeval with a negative carbon isotope anomaly, implying a correlation with global perturbation of carbon cycle. A rapid brachiopod recovery is indicated by a presence of several distinct communities in late Early and Middle Hettangian that show onshore–offshore differentiation and beta diversity comparable to pre-extinction levels. Analyses of similarities demonstrate that (1) the compositional turnover of brachiopod communities on generic level at the T/J boundary ($R=0.83$) is substantially higher than turnovers between the Rhaetian zones ($R=0.28–0.57$) and between the Hettangian zones ($R=0.28–0.53$), and (2) the turnover at superfamily level at the T/J boundary accounts for differential composition of Rhaetian and Hettangian communities. A global extinction of athyridoid, spondylospiroid and dielasmatoid superfamilies characterized by high-community level abundances during the Late Triassic led to a new assembly of Jurassic brachiopod communities from surviving superfamilies. In addition to persisting rhynchonellids and zeillerioids, Hettangian brachiopod communities were dominated by terebratuloids, spiriferinoids and pennospiriferinoids. These superfamilies were characterized in the Late Triassic by low community-level abundance. We argue for tracking the phylogenetic structure of communities across mass extinction events because a measurement of the turnover in community-level abundance of higher taxa can be highly relevant for estimating the ecologic impact of mass extinctions. Taxonomic extinction rate metrics or diversity measures can be depressed by surviving taxa that do not re-attain their pre-extinction community-level abundance.

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1. Introduction

One of the main interests in analysing variations in diversity, extinction rates, extinction selectivity, community attributes and morphologic disparity across mass extinctions is to assess the effects of environmental disturbances on evolutionary pathways and ecology, and to understand how ecosystems respond to large-scale environmental perturbations (Erwin, 2001). In the last years, a strong emphasis has been placed on ecologic changes during mass extinctions (Jablonski and Raup, 1995; McRoberts and Newton, 1995; Harries et al., 1996; Droser et al., 1997; Harries and Little, 1999; Lockwood, 2003; Hansen et al., 2004; Kiessling and Baron-Szabo, 2004; McGhee et al., 2004; Twitchett et al., 2004). These analyses indicate that effects of mass

extinctions are more diverse and complex than indicated by taxonomic extinction metrics at boundary intervals (Jablonski, 2002). One of the most profound effects is that mass extinctions remove successful incumbents (Rosenzweig and McCord, 1991; Jablonski, 2001). Extensive environmental perturbations leading to mass extinctions thus have a strong impact on evolutionary trajectories because taxonomic survivorship may differ from that operating during “background” times.

In this study we analyze a compositional turnover – the change in species composition and relative abundances – to evaluate the effects of environmental perturbation on brachiopod ecology at the end of the Triassic and across the Triassic/Jurassic boundary. To exclude biogeographic effects, the study area is restricted to the intra-platform Kössen Basin (Northern Calcareous

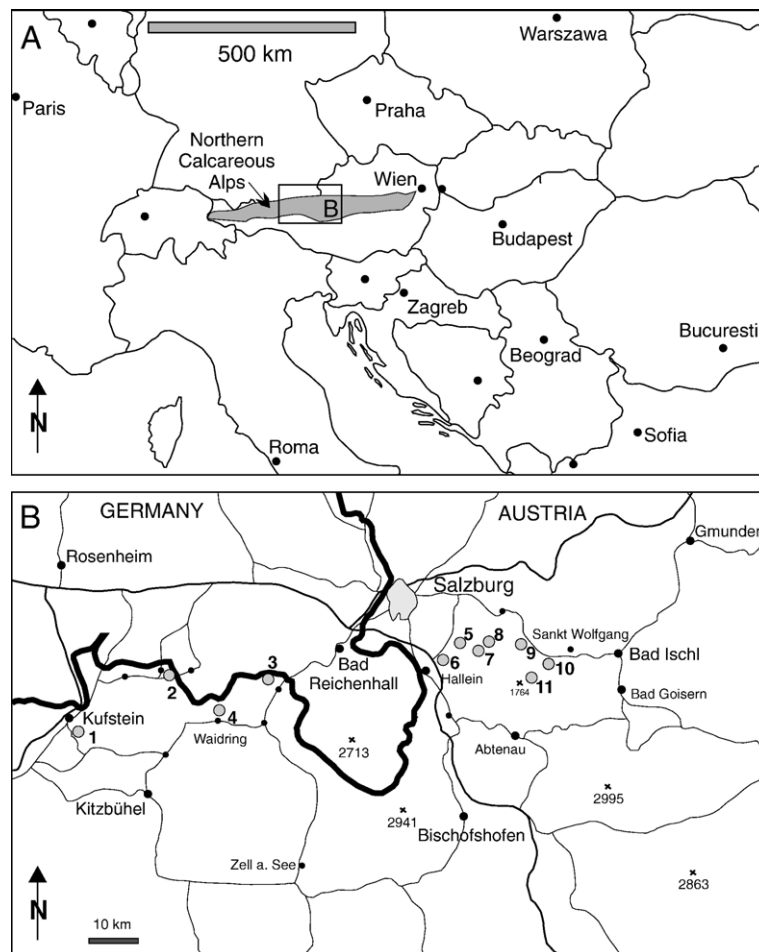
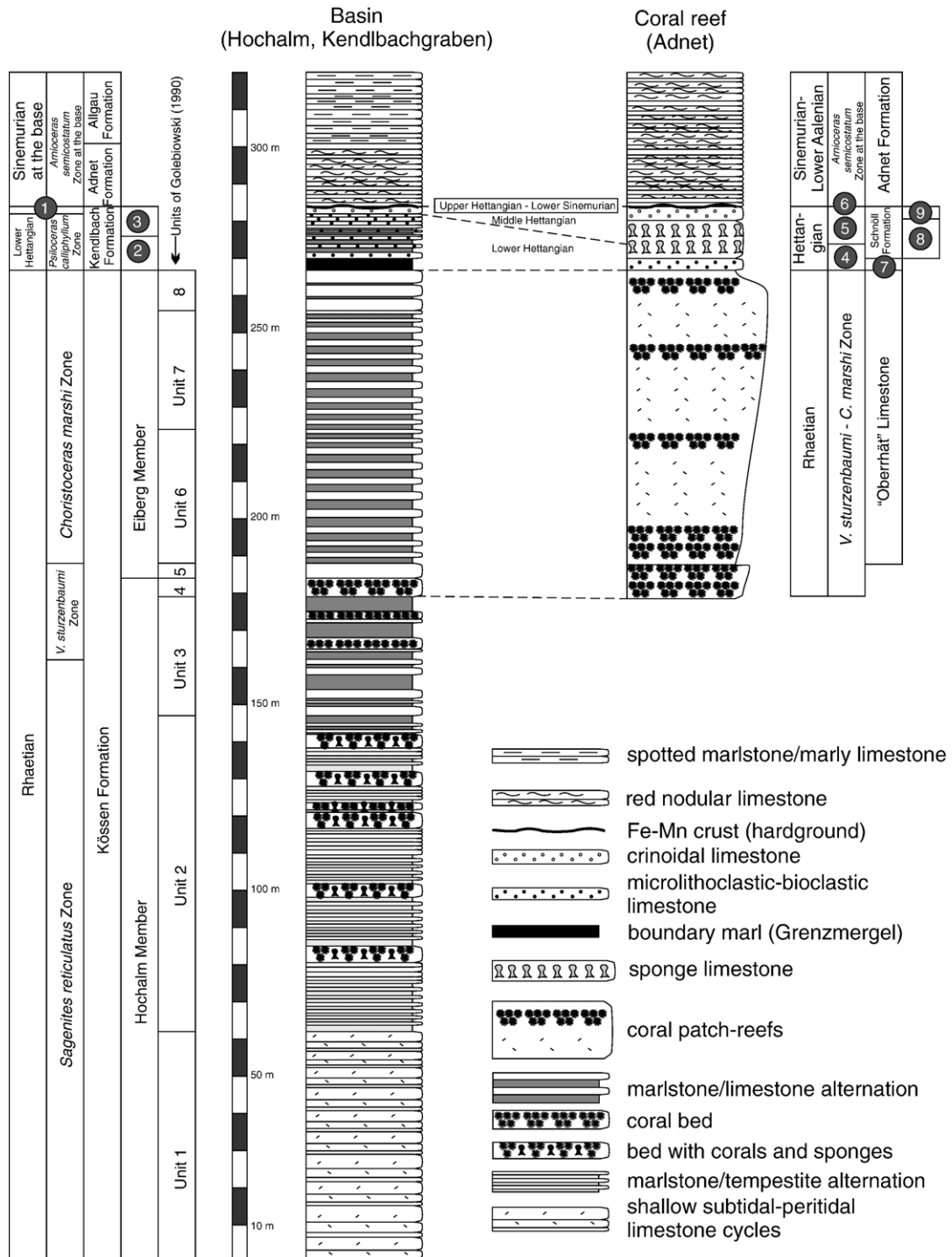


Fig. 1. (A) Geographic position of the Northern Calcareous Alps. (B) Geographic position of Rhaetian and Hettangian sections between Kufstein and Bad Ischl. Some of these sections are shown in Figs. 4 and 6. 1 — Eiberg (Rhaetian–Hettangian), 2 — Kössen–Weissloferbachgraben (Rhaetian), 3 — Hochalm–Sonntagshorn (Rhaetian), 4 — Steinplatte (Rhaetian–Hettangian), 5 — Gaissau–Mörtlbachgraben (Rhaetian), 6 — Adnet (Rhaetian–Hettangian), 7 — Hochleitengraben (Hettangian), 8 — Rötelswand (Rhaetian), 9 — Saubachgraben (Hettangian), 10 — Breitenberg (Hettangian), 11 — Kendlbachgraben (Rhaetian–Hettangian).

Alps, NCA). This basin was situated in the western margin of the Tethys Ocean in the Late Triassic (Fig. 1). The area of the NCA is one of the few places in the world where both Rhaetian and Hettangian brachiopods are numerically common. In addition, biostratigraphic correlation of Rhaetian and Hettangian sections is

constrained by ammonites and conodonts in the NCA, allowing their subdivision up to the zone levels. This study is of dual significance. First, because the Mesozoic represents a transition interval when the ‘Paleozoic’ evolutionary fauna was replaced by the ‘Modern’ evolutionary fauna (Sepkoski, 1996; Alroy, 2004),



distinguishing the role of mass extinctions in forcing this replacement compared to background times is of high importance (Miller, 1998; Chen et al., 2005). Second, this study is one of the first attempts to assess the impact of the end-Triassic mass extinction on Rhaetian and Hettangian brachiopods in terms of their distribution patterns and environmental preferences on zone level.

Two inter-related hypotheses are tested here. First, there is a difference in the composition of pre- and post-extinction brachiopod communities in terms of community-level abundance of brachiopod taxa. In order to avoid bias due to habitat tracking, local immigration/extinction and pseudo-extinction, this hypothesis is evaluated within a spatial framework and on several taxonomic levels. Second, environmental preferences of pre- and post-extinction brachiopod taxa are different. This second hypothesis is related to a proposal of Sandy (1995). He compared distribution patterns of Middle to Late Triassic and Early Jurassic brachiopods and suggested that there had been a change in environmental preferences of brachiopod suborders/orders at the T/J boundary.

2. Rhaetian and Hettangian brachiopod-bearing units in the NCA

2.1. Rhaetian deposits

Brachiopods analysed in this study are derived from the Kössen Formation, which consists of the Hochalm Member and the Eiberg Member, from the 'Oberrhät' Limestone, and from the Starhemberg Limestone. In the Frankenfels Nappe of the Bajuvaric Unit, the upper part of the Kössen Formation is represented by the Restental Member (Golebiowski, 1990).

Golebiowski (1990) subdivided the Kössen Formation into eight stratigraphic units (Fig. 2). The general environmental history of the Kössen Basin is interpreted as a response to a relative sea level rise (i.e., from a shallow lagoon in the Early Rhaetian up to an intra-platform basin at the end of the Rhaetian, Kuss, 1983; Golebiowski, 1991; Holstein, 2004). The lowermost part of the Hochalm Member (Unit 1) is formed by carbonates of shallow subtidal and peritidal origin. It contains no brachiopods.

The oldest brachiopods occur in Unit 2 which consists of small-scale sequences composed of siliciclastic and carbonate intervals (Fig. 3A; Golebiowski, 1990; Satterley, 1996; Tomašových, 2006a). Monospecific brachiopod assemblages of *Rhaetina gregaria* are limited to the carbonate intervals and lowermost part of the siliciclastic intervals (Fig. 3A). Signs of storm reworking represented by high-energy sedimentary features and shell beds indicate habitats between fair-weather wave base and maximum storm wave base (MSWB). In Unit 3, a thick, laterally extensive marlstone interval onlaps onto the carbonate platform and marks the maximum deepening event in the Early Rhaetian (Golebiowski, 1990). A regular alternation of biomicritic limestones and marlstones is typical of this unit. Unit 4 is characterized by a widespread development of coral beds and initial formation of large-scale patch-reefs (Fig. 3B). The Eiberg Member is characterized by a cyclic alternation of marlstones, marly limestones and micritic limestones, which record habitats below MSWB (Fig. 3C).

The Restental Member is a stratigraphic equivalent of the Eiberg Member. It originated in a shallow restricted basin with uniform, siliciclast-rich deposition. Importantly, taxa and some communities typical of the Hochalm Member (e.g., *Zugmayerella* community) persist here through to the Upper Rhaetian strata (Golebiowski, 1990). The 'Oberrhät' Limestone is formed by patch-reefs with scleractinians, sphinctozoans and diverse bioclastic debris (Stanton and Flügel, 1989). The patch-reefs corresponding to habitats above MSWB laterally replace the Eiberg Member. They are either in intra-basinal or in marginal, basin-platform boundary position. The Starhemberg Limestone forms layers within the Dachstein Limestone in the Tirolic and Juvavic units.

2.2. Hettangian deposits

The Hettangian deposits are represented by two formations (Fig. 4). The Kendlbach Formation consists of deposits originating in the former Kössen Basin. The Schnöll Formation is formed by deposits originating at places of the former patch-reef production. The upper boundary of the Kendlbach and Schnöll formations is

Fig. 2. A composite section across the Triassic–Jurassic boundary (T/J boundary) in the Northern Calcareous Alps. Biostratigraphic and lithostratigraphic subdivisions of Rhaetian and Hettangian follow Golebiowski (1990), Böhm (2003) and Böhm et al. (1999). Note that lithostratigraphic units within the Kössen Formation were re-numbered from 1 to 8 (in contrast to four units within the Hochalm Member and four units within the Eiberg Member). 1 — The condensed zone encompasses the Middle-Late Hettangian (*K. megastoma* and *A. marmoreum* zones) and earliest Sinemurian. 2 — The Tiefengraben Member, at the base with the boundary marl (Grenzmergel). 3 — The Breitenberg Member, in the uppermost part with the Enzesfeld Limestone. 4 — *P. calliphylum* Zone (Early Hettangian). 5 — *K. megastoma* Zone (Middle Hettangian). 6 — The condensed zone encompassing most probably the Late Hettangian and earliest Sinemurian (*A. marmoreum* Zone). 7 — The Kendlbach Formation. 8 — The Langmoos Member. 9 — The Guggen Member. The simplified section of the Kössen Basin is based on the Hochalm (Rhaetian part) and Kendlbach sections (Hettangian part). The simplified section of the Adnet is based on the Schnöll Quarry.

marked by Fe–Mn crusts or by the Enzesfeld Limestone (Late Hettangian to earliest Sinemurian age).

The Kendlbach Formation starts with the boundary marl at the base, followed by the siliciclastic Tiefengraben Member, and terminated by the carbonate-rich Breitenberg Member (Fig. 4; Golebiowski and Braunstein, 1988). A boundary marl that is several metres thick has low carbonate content and contains layers which are locally enriched in organic matter, pyrite, quartz and mica (Golebiowski and Braunstein, 1988). In the western part of the NCA, the lower parts of the boundary marl are represented by red marlstones and siltstones (Schattwald Shale). Although there are no ammonites, the boundary marl does contain rare lingulids, bivalves of Hettangian affinity and palynomorphs. The only known rhynchonelliform brachiopods are rhynchonellids from the Karwendelmunde section (Axel von Hillebrandt, pers. comm., 2005). The Tiefengraben Member is characterized by a relatively uniform alternation of micritic limestones and marlstones with rare bivalves (Fig. 4). The Breitenberg Member is formed by microintraclastic–bioclastic packstones and grainstones with bivalves and brachiopods of Early Hettangian age. In some sections, the boundary between the Tiefengraben and Breitenberg Member is more gradual, represented by alternation of marls and bioclastic limestones (Fig. 4). The deposits of the Middle Hettangian *K. megastoma* Zone are thin or missing in the Breitenberg Member (Kment, 2000).

In the areas of Triassic coral reefs, the time interval represented by the deposition of the boundary marl and Tiefengraben Member is mostly represented by a hiatus. The Early–Middle Hettangian deposits are represented by cross-bedded limestones of the Breitenberg Member and by the Schnöll Formation (Böhm et al., 1999; Böhm, 2003). The Schnöll Formation starts with the Langmoos Member, which is formed by bioclastic wackestones/floatstones with common *in situ* silicisponges (Delecat and Reitner, 2005), stromatolites, crinoids and brachiopods (Fig. 4). The Langmoos Member passes upward into the Guggen Member, which is represented by crinoidal–oncoidal wackestones (Fig. 4).

The Breitenberg or Guggen members pass upward into red nodular limestones of the Adnet Formation (Fig. 4). At their boundary, the Enzesfeld Limestone formed by biomicritic wackestones, packstones and Fe–Mn crusts contains brachiopods of the *Angulaticeras marmoreum* Zone (Böhm et al., 1999; Kment, 2000).

3. Methods

Two datasets based on new field data and literature compilations are analysed. The first one consists of 62

samples and 2861 brachiopod specimens from the Kössen Formation, patch-reefs ('Oberhät' Limestone) and the Starhemberg Limestone of Rhaetian age (Golebiowski, 1989; Siblík, 1998; Turnšek et al., 1999; and 25 unpublished samples). The second dataset is formed by 15 samples and 975 brachiopod specimens from the Hettangian Kendlbach and Schnöll formations, and the Enzesfeld Limestone (Siblík, 1993a,b, 1999; Böhm et al., 1999; and 4 unpublished samples). The samples correspond either to one bed or to a group of beds of similar lithology. With the exception of the Enzesfeld Limestone that can be biostratigraphically condensed, they represent census or within-habitat time-averaged relicts of local communities. The samples come from the central and eastern part of the NCA. The westernmost part of the NCA (e.g., Vorarlberg, McRoberts et al., 1997), the Restental Member and the Zlambach Formation are not represented in our datasets. However, species and generic composition of the communities of the Kössen Basin should be representative of the northern Tethyan margin.

Due to taxonomic inconsistencies, all analyses are performed on a generic level with two exceptions. (1) *Rhaetina gregaria* and *Rhaetina pyriformis* are treated separately during exploratory multivariate analyses because of their different stratigraphic and environmental distribution. However, they are pooled into one genus when differences between habitats and time intervals are tested. (2) Due to taxonomic inconsistencies, absolute abundances of Rhaetian rhynchonellids *Fissirhynchia fissicostata* (Suess, 1854), *?Calcirhynchia subrimosa* (Schafhäütl, 1851) and rhynchonellid sp. A (corresponding to '*Rhynchonella*' *subrimosa* of Suess, 1854) are pooled into 'rhynchonellids'. Although the generic assignments of *?C. subrimosa* and rhynchonellid sp. A are not resolved, it is probable that they represent genera other than *Fissirhynchia* and do not occur in the Hettangian. These three rhynchonellids are assigned to the family Cyclothyrididae and superfamily Hemithiridoidea because they possess canalifer crura. Taxonomic classification above the generic level follows Carter et al. (1994) and Savage et al. (2002).

Genus level abundance data are summarized in the Supplemental Information. Genera that are represented in the whole dataset by one or two specimens only were omitted (including *Bactrynum*, *Thecospira*, *Securithyris*, *Bakonyithyris*, *Securina*, "*Rhynchonella*" aff. *paolii* and "*Terebratula*" *juvavica*). The generic assignments follow the published determinations with an exception of one revised rhynchonellid genus (Tomašových, 2006b). Absolute numbers of brachiopod specimens were

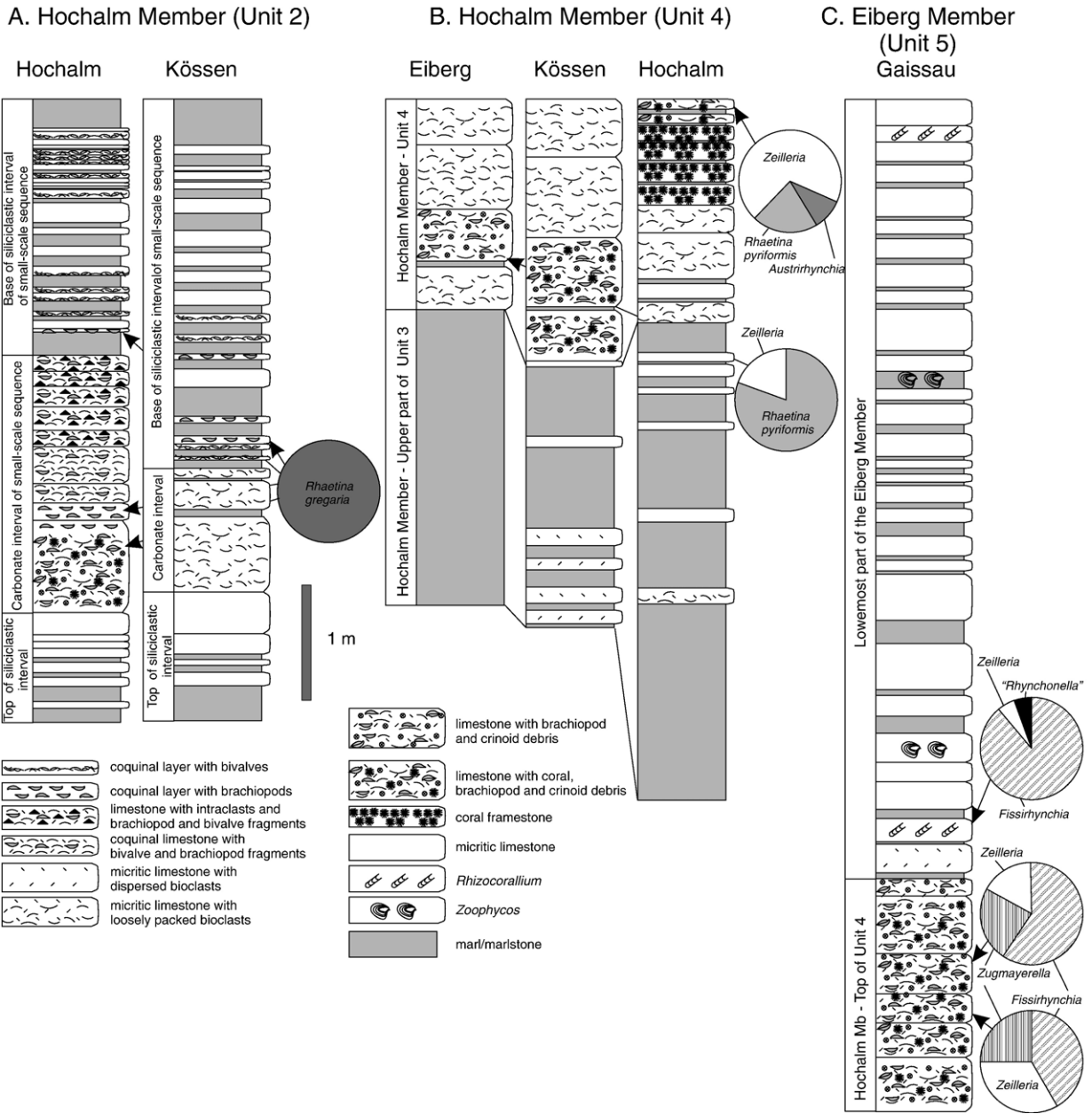


Fig. 3. Stratigraphic intervals within the Kössen Formation showing facies associations with sample-level abundances of brachiopod genera. Based on our field data. (A) Middle parts of the Hochalm Member with samples dominated by *Rhaetina gregaria*. (B) Uppermost part of the Hochalm Member in three sections showing transition into coral beds with scleractinian *Retiophyllia*. Samples are characterized by common *Zeilleria* and *Rhaetina pyriformis*. (C) Boundary between the Hochalm and Eiberg members showing transition into deep-water facies represented by alternation of marlstones and micritic limestones. Rhynchonellids and *Zugmayerella* are common here.

converted to relative abundances. Three types of multivariate methods are used, including cluster analysis based on Bray–Curtis similarity and group average clustering method, non-metric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA). NMDS is explicitly based on rank-order, Bray–Curtis dissimilarity matrix, and makes no assumptions about the

shape of species response to environmental gradient. In Q-mode NMDS analyses, if Bray–Curtis similarity is 100, two samples have identical composition. If it is 0, two samples have no species in common. In R-mode NMDS analyses, if Bray–Curtis similarity is 100, abundances of two genera are the same in all samples; if it is 0, the two genera have no samples in common.

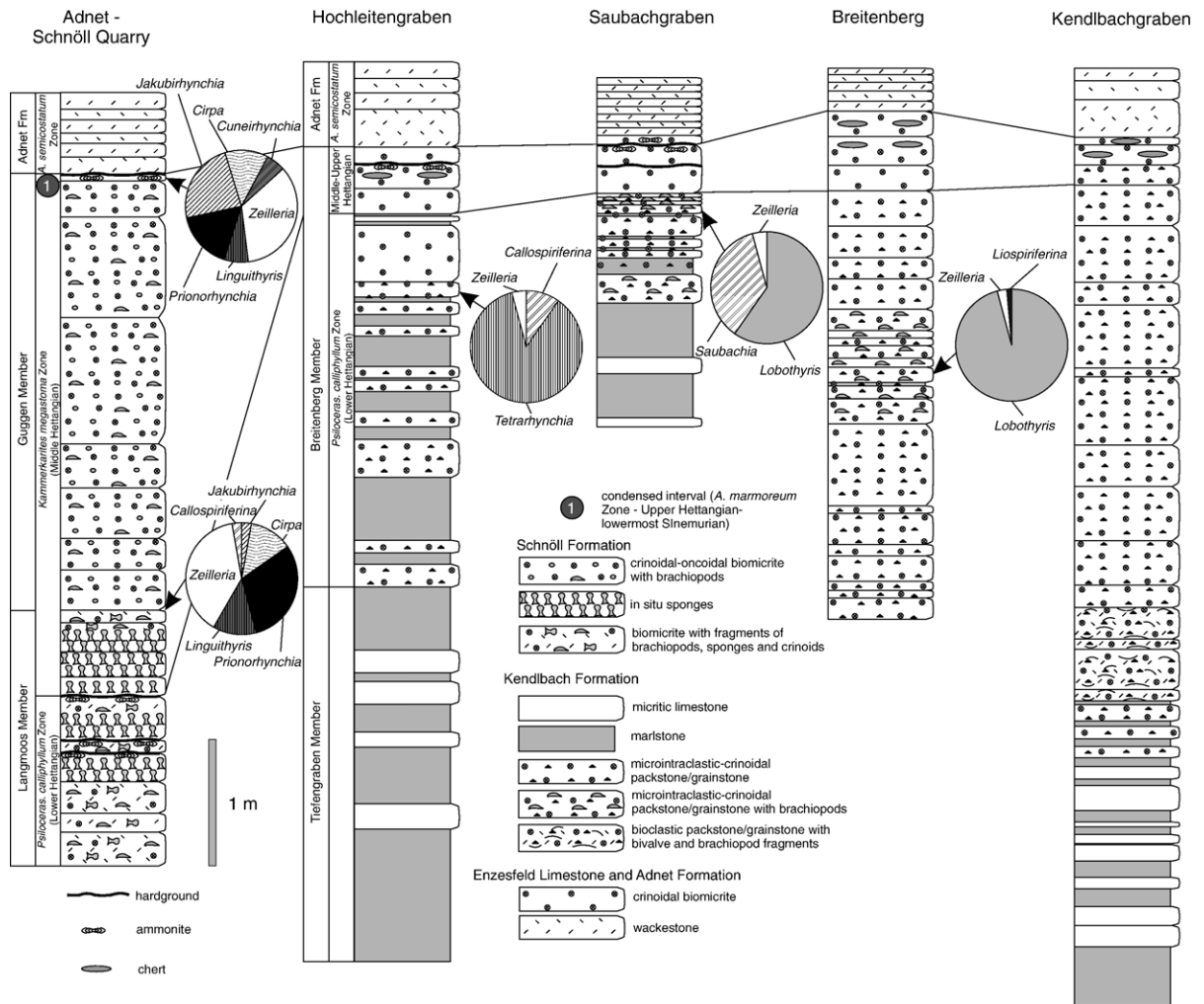


Fig. 4. Facies associations of the Hettangian deposits in the area of Osterhorngruppe (SE of Salzburg) shown in four sections with the Kendlbach Formation, and one section with the Schnöll Formation. Sample-level abundances of brachiopod genera illustrate compositional differences between formations and between stratigraphic zones. Based on our field data. The correlation is based on biostratigraphic data in [Suess and Mojsisovics \(1868\)](#), [Blind \(1963\)](#), [Plöching \(1975\)](#), [Blau and Grün \(1996\)](#) and [Böhm et al. \(1999\)](#). The *P. calliphylum* Zone is restricted to the Breitenberg Member.

NMDS is used here for visualizing of between-sample differences in taxonomic composition ([De'ath, 1999](#)). In this study, NMDS with three pre-specified dimensions was repeated twenty times with different random positions of samples or taxa in starting configurations. DCA is implicitly based on Chi-square distance matrix and assumes the unimodal response of species distributions along an environmental gradient. Detrending procedure creates artefactual diamond-shaped or triangle-shaped patterns ([Kenkel and Orlóci, 1986](#); [Minchin, 1987](#)). However, sample scores along the first axis might be highly correlated with environmental gradients ([Holland et al., 2001](#); [Scarponi and Kowalewski, 2004](#);

[Holland, 2005](#)). Sample scores along the first DCA axis will be used here as an approximate measure of beta diversity. The first DCA axis is re-scaled in standard deviation (S.D.) units. A 50% change in sample composition is approximately recorded as 1–1.4 S.D. units and a complete turnover correspond to about 4 S.D. units ([Hill and Gauch, 1980](#)).

One-factorial analysis of similarities (ANOSIM) is used for testing if average rank dissimilarity within habitats or stratigraphic zones, based on Bray–Curtis coefficient, is significantly lower than average rank dissimilarity between habitats or stratigraphic zones ([Clarke and Green, 1988](#)). If the null hypothesis (e.g.,

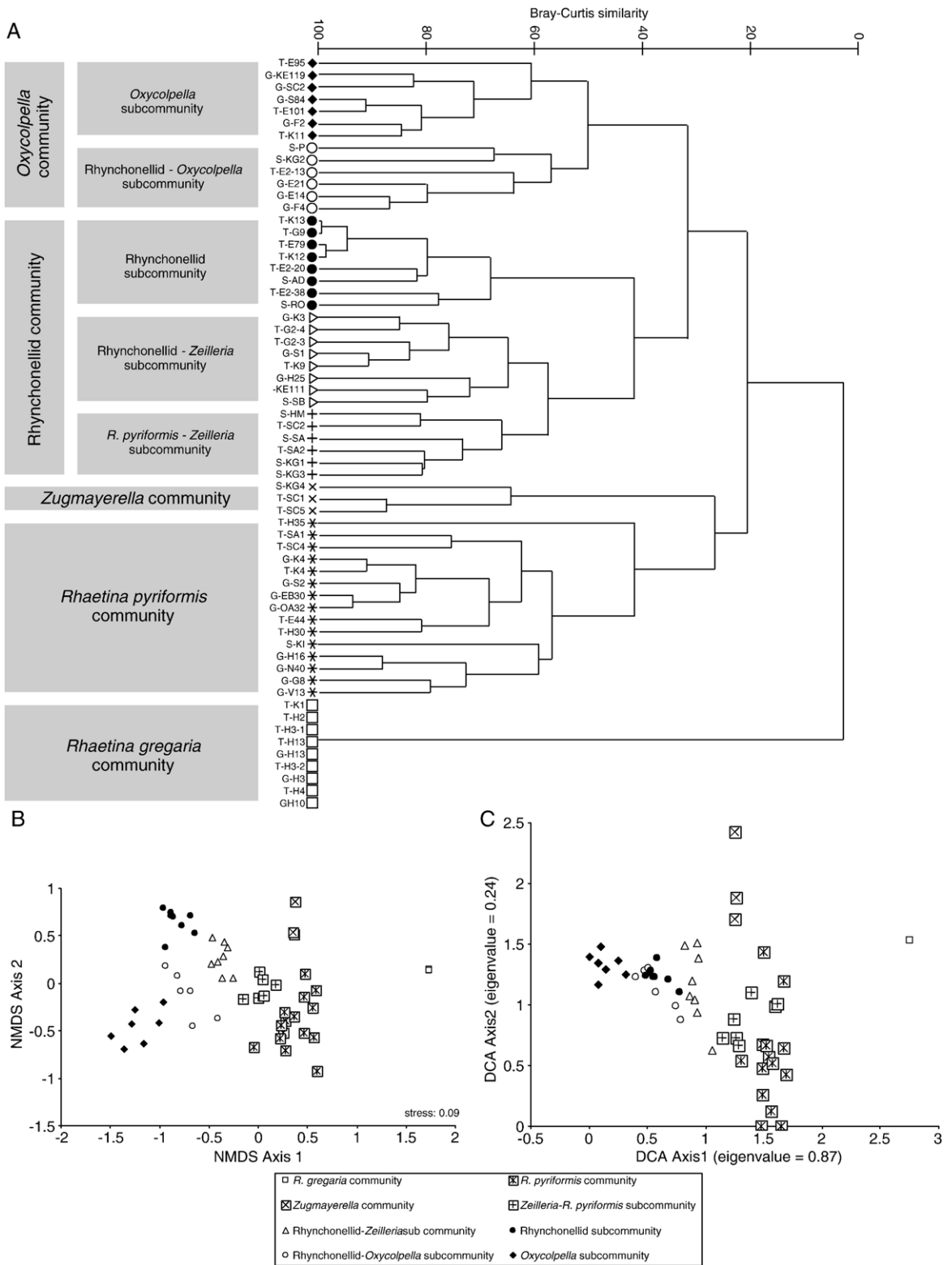


Fig. 5. Rhaetian communities. (A) Q-mode cluster analysis. (B) Q-mode non-metric multidimensional scaling (NMDS). Note that the scaling and orientation of axes in NMDS are arbitrary. The configuration is rotated to have the greatest variation along the first axis for visual convenience. (C) Detrended correspondence analysis of samples (genera are shown in Fig. 7). Note that nine samples of the *Rhaetina gregaria* community correspond to one point in NMDS and DCA plots.

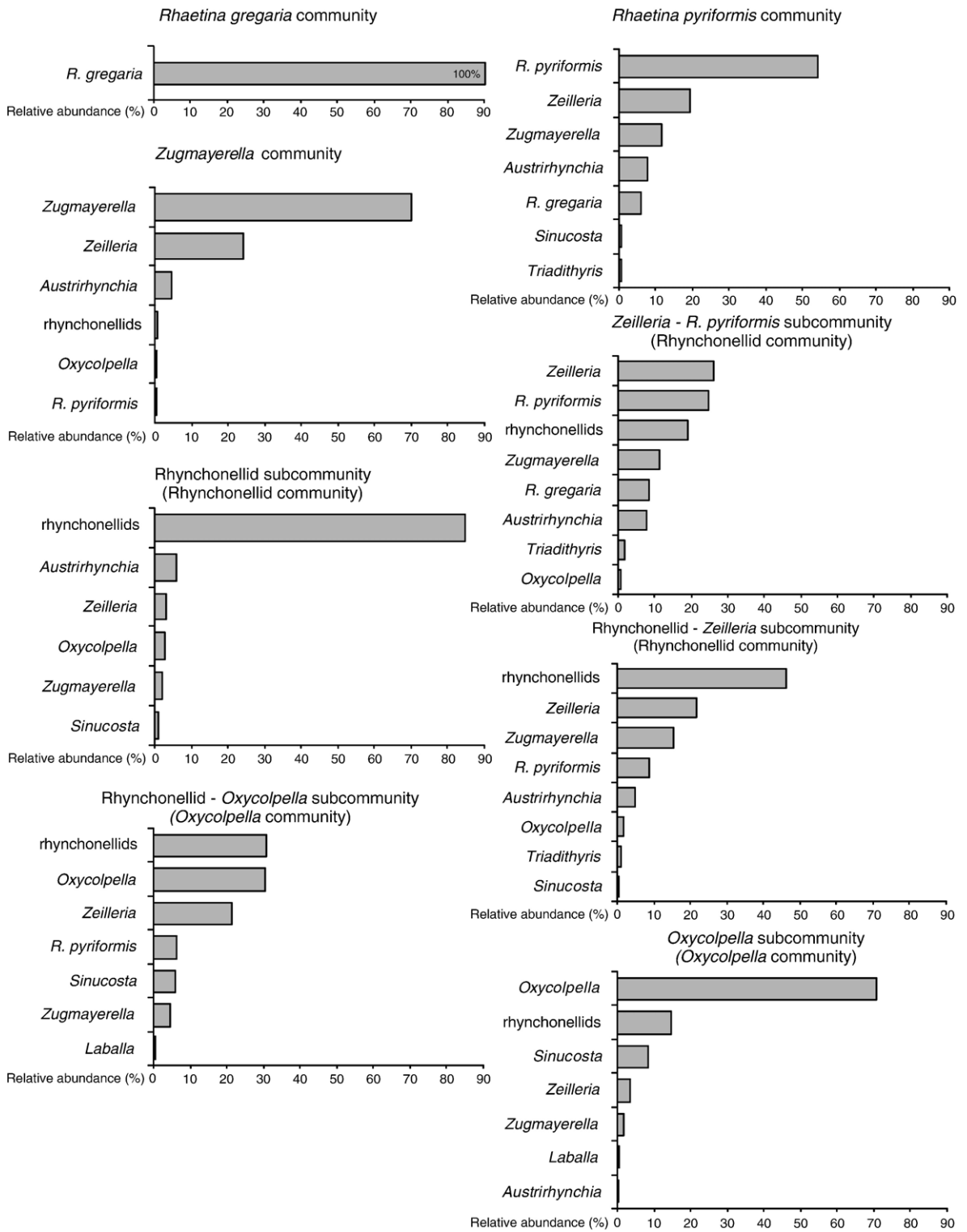


Fig. 6. Relative abundances of brachiopods in five Rhaetian communities with five subcommunities.

there are no differences in composition among habitats or zones) is rejected, the pattern that average rank dissimilarities within habitats are smaller than those between habitats cannot be produced by a chance. Test statistic (R) attains the values from -1 to 1 . It is approximately zero if the null hypothesis is true, so average of rank dissimilarities between and within habitats will be more or less the same. Large values close to one are indicative of complete compositional separation of habitats or zones. Significance levels are computed with a general randomization Monte Carlo approach. All analyses were done using the PRIMER software (Clarke and Warwick, 2001), with the exception of DCA (PAST software, Hammer et al., 2001).

Based on a geological time scale of Gradstein et al. (2004), the Rhaetian has a duration of about 4 Ma and the Hettangian about 3 Ma. Therefore, the Rhaetian and Hettangian zones have approximately comparable average duration (i.e., ~ 1 Ma). The stratigraphic units of the Kössen Formation defined by Golebiowski (1991) are also used in some analyses. Three habitats are distinguished, including (1) habitats above normal storm wave base (NSWB) with signs of frequent storm disturbance (e.g., amalgamation of storm-reworked beds and signs of sorting and wave or current preferred orientation), (2) below NSWB with signs of rare storm disturbance (e.g., thin layers of storm-reworked bed embedded between marlstones or micrite-rich limestones), and (3) below maximum storm wave base (MSWB) with missing signs of storm disturbance. The habitats above fair-weather wave base (FWWB) are not represented in our dataset. The habitats were either directly scored in the field or the habitat assignments were based on published sections (Golebiowski, 1989; Böhm et al., 1999).

Analyses of Rhaetian and Hettangian datasets are divided into two parts. First, the communities are discriminated with cluster analyses, relationship between samples and genera is evaluated with NMDS, and beta diversity is assessed in DCA. Second, ANOSIM is used for testing whether there is a significant difference in composition between stratigraphic zones and between habitats. The first hypothesis, testing the differences in composition between Rhaetian and Hettangian communities, is evaluated with ANOSIM by comparing (1) the Rhaetian and Hettangian stages, and (2) the Rhaetian and Hettangian zones on genus, family, superfamily, suborder, and order levels. The second hypothesis tests the differences in environmental distribution of suborders and orders with time-environment diagrams (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985).

4. Rhaetian

4.1. Rhaetian brachiopod communities

Q-mode cluster analysis of 62 samples discriminated five sample groups at Bray–Curtis similarity corresponding to 40 (Fig. 5A). They are termed as communities in this paper (palaeocommunity types in terms of Bambach and Bennington, 1996). At Bray–Curtis similarity of 50, the Rhynchonellid community can be further subdivided into three subcommunities and the *Oxycolpella* community into two subcommunities. This subdivision into subcommunities is adopted here because the pooling of samples into the communities obscures their sample-level relative abundances (Fig. 6). Q-mode NMDS (Fig. 5B) and DCA (Fig. 5C) indicate that with the exception of the *R. gregaria* community, the communities show gradual transitions in terms of their composition. The *R. pyriformis* community is compositionally replaced by the *Zugmayerella*, Rhynchonellid and *Oxycolpella* communities. The maximum sample score is 2.8 along the first axis, implying the gradient length of 2.8 SD units and relatively moderate beta diversity. However, the *R. gregaria* and the *Oxycolpella* communities do not share any species in common, indicating almost complete turnover along the gradient.

The *Rhaetina gregaria* community is represented by nine samples with 315 specimens. *R. gregaria* commonly occurs in shell concentrations, associated with less common bivalves (*Atreta*, *Rhaetavicula*, *Gervillaria*, *Chlamys*, *Liostrea*). This community occurs in the *Sagenites reticulatus* Zone only. It occurs either in coral debris or bioclastic floatstones in the carbonate intervals, or in marly floatstones in the lower parts of the siliciclastic intervals (Fig. 3A).

The *Zugmayerella* community is represented by three samples with 193 specimens. *Zugmayerella* (mainly *Z. koessenensis*, 70%) dominates, followed by less common *Zeilleria* (24%) and rare *Austrirhynchia* (5%). Rhynchonellids, *Oxycolpella* and *R. pyriformis* are very rare (below 1%). Epifaunal bivalves (*Chlamys* and *Plagiostoma*) are common. The community is limited to coral–bioclastic limestones or bioclastic marlstones near patch-reefs in the *Vandaites sturzenbaumi* Zone.

The *Rhaetina pyriformis* community is represented by 15 samples and 351 specimens. *R. pyriformis* is dominant (54%); *Zeilleria* (19%), *Zugmayerella* (12%), *Austrirhynchia* (8%) and *R. gregaria* (6%) are less common. From bivalves, *Chlamys*, *Plagiostoma*, *Gervillaria*, *Atreta* and *Actinostreon* are present. It occurs

in coral debris floatstones and coral framestones of the *V. sturzenbaumi* Zone (Fig. 3B).

The Rhynchonellid community consists of three subcommunities. The *Zeilleria*–*Rhaetina pyriformis* subcommunity represented by six samples with 351 specimens occurs in bioclastic marlstones and coral beds of the *V. sturzenbaumi* Zone. *Zeilleria* (26%) and *R. pyriformis* (24%) are abundant; rhynchonellids (19%), *Zugmayerella* (11%), *R. gregaria* (9%) and *Austrirhynchia* (8%) are less common. *Triadithyris* is rare (2%). Bivalves are mainly represented by *Gervillaria* and *Actinostreon*. The Rhynchonellid–*Zeilleria* subcommunity is represented by eight samples with 254 specimens and occurs in coral debris floatstones and marly limestones and marlstones of the *V. sturzenbaumi* and *Choristoceras marshi* zones. Rhynchonellids dominate (46%); *Zeilleria* (21%), *Zugmayerella* (15%) and *R. pyriformis* (9%) are less common. *Austrirhynchia* (5%) and *Oxycolpella* (1%) are rare. Bivalves *Atreta*, *Plagiostoma* and *Oxytoma* can occur in this subcommunity. The Rhynchonellid subcommunity is represented by eight samples with 721 specimens. It occurs in biomicritic limestones and marlstones in the *V. sturzenbaumi* and *C. marshi* zones. Rhynchonellids strongly dominate (85%). *Austrirhynchia* (6%), *Zeilleria* (3%), *Oxycolpella* (3%), *Zugmayerella* (2%) and *Sinucostra* (1%) are rare. Bivalves *Chlamys*, *Oxytoma* and *Atreta* typically occur in this subcommunity.

The *Oxycolpella* community consists of two subcommunities. The Rhynchonellid–*Oxycolpella* subcommu-

nity is represented by six samples with 407 specimens and occurs mainly in biomicritic limestones and marlstones of the *V. sturzenbaumi* and *C. marshi* zones. Rhynchonellids and *Oxycolpella* are equally abundant (30%); *Zeilleria* (22%) is less common. *R. pyriformis* (6%), *Sinucostra* (6%) and *Zugmayerella* (5%) are rare. Bivalves (*Chlamys*) are very rare. The *Oxycolpella* subcommunity consists of seven samples formed by 269 specimens and is limited to biomicritic limestones and marlstones of the *C. marshi* Zone. *Oxycolpella* is dominant (71%); rhynchonellids (15%) and *Sinucostra* (9%) are less common. Other brachiopods as *Zeilleria* (3%) and *Zugmayerella* (2%) are rare. Bivalves (*Chlamys*, *Oxytoma* and *Cassianella*) are rare.

4.2. Co-existence patterns of Rhaetian brachiopod genera

In R-mode NMDS, *R. gregaria* is distinctively separated from all other genera and has the highest Bray–Curtis similarity with *R. pyriformis*. *R. pyriformis* have higher Bray–Curtis similarities with *Zugmayerella* and *Zeilleria* than with rhynchonellids (Fig. 7A). Finally, *Oxycolpella*, *Sinucostra* and rhynchonellids form the group of closely co-existing taxa with similar abundance patterns. *R. gregaria* is strongly segregated from other brachiopods in DCA (Fig. 7B). The ordination of genera along the first axis in DCA is comparable to the compositional replacement in R-mode NMDS (i.e., *R. pyriformis* is replaced by *Zugmayerella*, *Zeilleria*, rhynchonellids and *Oxycolpella*).

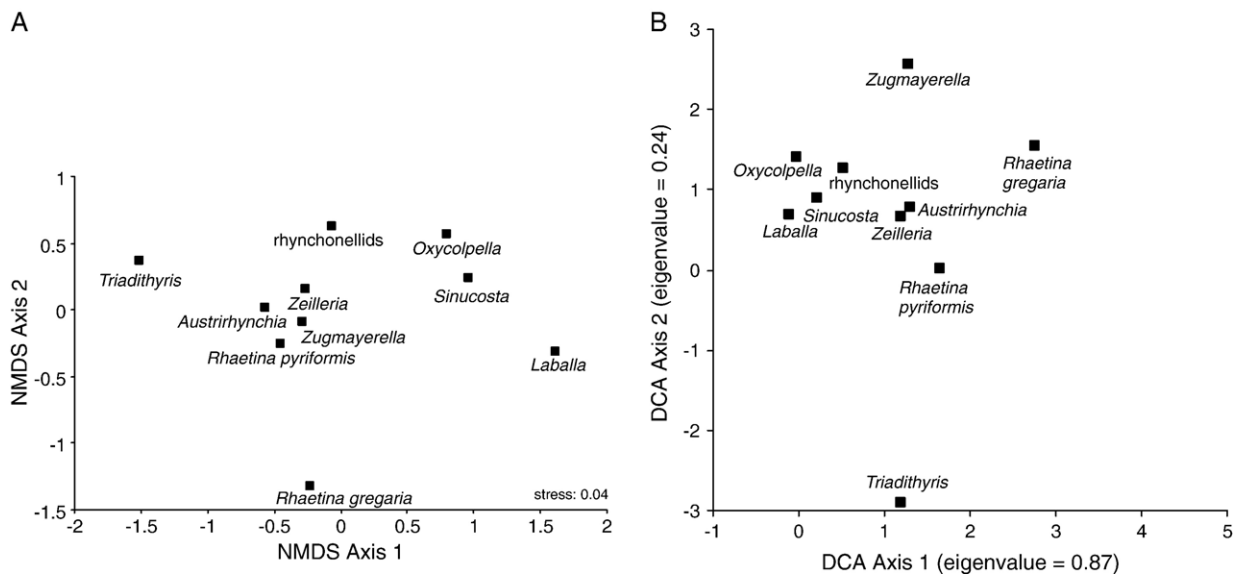


Fig. 7. Abundance patterns of Rhaetian brachiopods. (A) R-mode non-metric multidimensional scaling (NMDS). The configuration is rotated to have the greatest variation along the first axis for visual convenience. (B) Detrended correspondence analysis of genera and two species of *Rhaetina*.

Table 1

Results of ANOSIM showing differences in composition among Rhaetian zones and among Hettangian zones

Stratigraphic zones	<i>R</i> statistic	<i>p</i> -value	Permutations	Number of permuted <i>R</i> ≥ observed <i>R</i>
Rhaetian — global test	0.57	<0.0001	10000	0
Rhaetian — pairwise tests:				
<i>S. reticulatus</i> Zone vs. <i>V. sturzenbaumi</i> Zone	0.28	0.004	10000	35
<i>V. sturzenbaumi</i> Zone vs. <i>C. marshi</i> Zone	0.57	<0.0001	10000	0
<i>S. reticulatus</i> Zone vs. <i>C. marshi</i> Zone	0.99	<0.0001	10000	0
Hettangian — global test	0.42	0.007	10000	69
Hettangian — pairwise tests:				
<i>P. calliphylum</i> Zone vs. <i>K. megastoma</i> Zone	0.53	0.007	1287	9
<i>A. marmoreum</i> Zone vs. <i>K. megastoma</i> Zone	0.28	(0.24)	21	5
<i>P. calliphylum</i> Zone vs. <i>A. marmoreum</i> Zone	0.31	(0.11)	45	5

Pairwise comparisons between the Unit 2 and all other units are not shown as they are always significant at $p < 0.0001$ (*R* is mostly close to one). The alpha value in pairwise comparisons is 0.016 (0.05/3) after the Bonferroni correction. The *p*-values in parentheses are inconclusive due to low number of permutations.

4.3. Linking Rhaetian brachiopods to stratigraphy

The global ANOSIM and pairwise comparisons among three zones demonstrate significant differences in community composition ($R=0.57$, $p < 0.0001$, Table 1). The difference between the *S. reticulatus* and *V. sturzenbaumi* zones corresponds to the replacement of the *R. gregaria* community by the *R. pyriformis*, *Zugmayerella* and Rhynchonellid communities (Fig. 8). The difference between the *V. sturzenbaumi* and *C. marshi* zones corresponds to the disappearance of the *R. pyriformis* and *Zugmayerella* communities and the appearance of the *Oxycolpella* community in the *C. marshi* Zone (Fig. 8). This test indicates a substantial taxonomic turnover among stratigraphic zones within the Kössen Basin. The communities dominated by *Zugmayerella* in the Hochalm Member are missing in the middle and upper parts of the Eiberg Member in the Kössen Basin. However, they occur in siliciclastic, shallow habitats of the *C. marshi* Zone in the Frankenfels Nappe (Bajuvaric Unit, Golebiowski, 1991). In addition, the *R. gregaria* and *R. pyriformis* communities persist to the Late Rhaetian in the West Carpathians (Michalík, 1973; Michalík et al., 1979).

4.4. Linking Rhaetian brachiopods to environment

The differences in community composition among three habitats are significant with global ANOSIM ($R=0.396$, $p < 0.0001$). Pairwise comparisons show that the difference between habitats below and above MSWB is significant only (Table 2). Due to the high compositional turnover between stratigraphic zones, testing among habitats is restricted to four stratigraphic levels (Table 2).

Monospecific assemblages with *R. gregaria* in Unit 2 of the Hochalm Member occupied habitats above NSWB and below NSWB. They occur in coral patch-

reefs, shell-rich floatstones and packstones, micrite-rich floatstones and marly mudstones.

Habitats above and below NSWB in units 3 and 4 of the Hochalm Member are significantly different in community composition ($R=0.258$, $p=0.007$). Habitats below NSWB associated with coral beds or bioclast-rich bottom were inhabited by the *R. pyriformis* or the *Zugmayerella* community (Fig. 9A). Habitats above NSWB associated with coral patch-reefs were inhabited by the *R. pyriformis* community, and the *Zeilleria*—*R. pyriformis* and Rhynchonellid—*Zeilleria* subcommunities. They were occupied by more common rhynchonellids in contrast to the habitats below NSWB (Fig. 9A). Note that siliciclastic, soft-bottom habitats below MSWB are represented by marlstones that contain rare brachiopods.

The difference between habitats above and below MSWB in units 5–7 of the Eiberg Member is of borderline significance ($R=0.3$, $p=0.042$). Habitats below NSWB with bioclastic micritic substrate were occupied mainly by the *Zugmayerella* and Rhynchonellid communities (Fig. 9B). Habitats below MSWB with marly micritic substrate were inhabited by the Rhynchonellid and *Oxycolpella* communities. Habitats above NSWB are not represented in our dataset.

Habitats above and below MSWB in Unit 8 of the Eiberg Member show also differences in community composition ($R=0.593$). Patch reefs above MSWB (habitats above and below NSWB are not differentiated in this case) were inhabited by the Rhynchonellid and Rhynchonellid—*Oxycolpella* subcommunities (Fig. 9C). Marly micritic habitats below MSWB were dominated by *Oxycolpella*.

The depth- and substrate-related distribution patterns demonstrate that the particular habitats were differentially inhabited by brachiopods at each stratigraphic level (Fig. 9). The habitats between NSWB and MSWB were

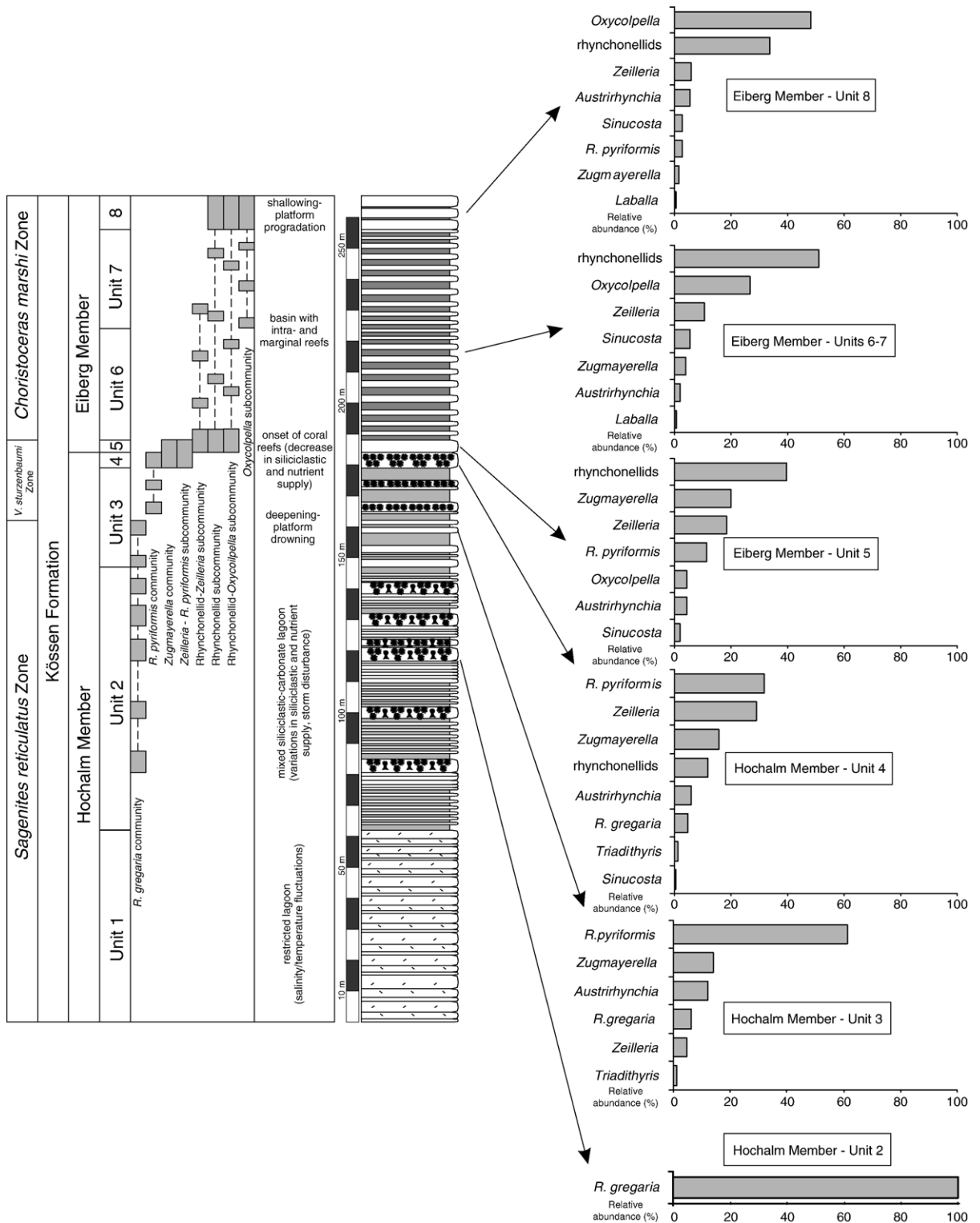


Fig. 8. Stratigraphic distribution of Rhaetian communities and pooled compositions of eight stratigraphic units of the Kössen Formation. Note that the changes in environmental history of the Kössen Basin correlate with the community replacement. Explanations are in Fig. 2.

Table 2
Results of ANOSIM showing differences among Rhaetian habitats and among Hettangian habitats

	<i>R</i> statistic	<i>p</i> value	Actual permutations	Number of permuted <i>R</i> ≥ observed <i>R</i>
<i>Rhaetian — all samples</i>				
Global test	0.4	<0.0001	10000	0
Pairwise tests:				
Above NSWB vs. below NSWB	0.02	0.21	10000	2191
Below NSWB vs. below MSWB	0.71	<0.0001	10000	0
Above NSWB vs. below MSWB	0.41	<0.0001	10000	0
<i>Rhaetian — stratigraphic levels</i>				
Hochalm				
Member (units 3–4)				
Above NSWB vs. below NSWB	0.26	0.007	10000	70
Eiberg Member (units 5–7)				
Below NSWB vs. below MSWB	0.31	0.042	10000	252
Eiberg Member (unit 8)				
Below NSWB vs. below MSWB	0.59	(0.029)	35	1
<i>Hettangian — all samples</i>				
Global test	0.89	<0.0001	10000	0
Pairwise tests:				
Above NSWB vs. below NSWB	0.53	(0.095)	21	2
Below NSWB vs. below MSWB	0.95	(0.022)	45	1
Above NSWB vs. below MSWB	0.98	0.001	1287	1

The alpha value in pairwise comparisons is 0.016 (0.05/3) after the Bonferroni correction. The *p*-values in parentheses are inconclusive due to low number of permutations.

inhabited by the *R. gregaria* community in Unit 2, by the *R. pyriformis* community in units 3–4, by the *Zugmayerella* community in units 5–7 and by the Rhynchonellid community in Unit 8. Habitats below MSWB were dominated by the Rhynchonellid community in units 5–7 and by the *Oxycolpella* community in Unit 8.

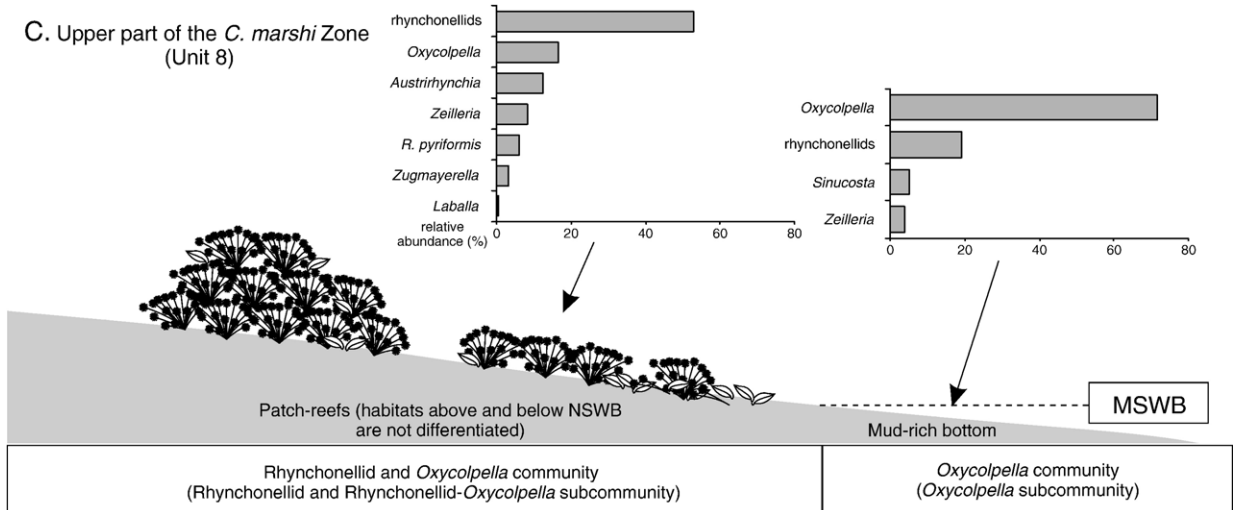
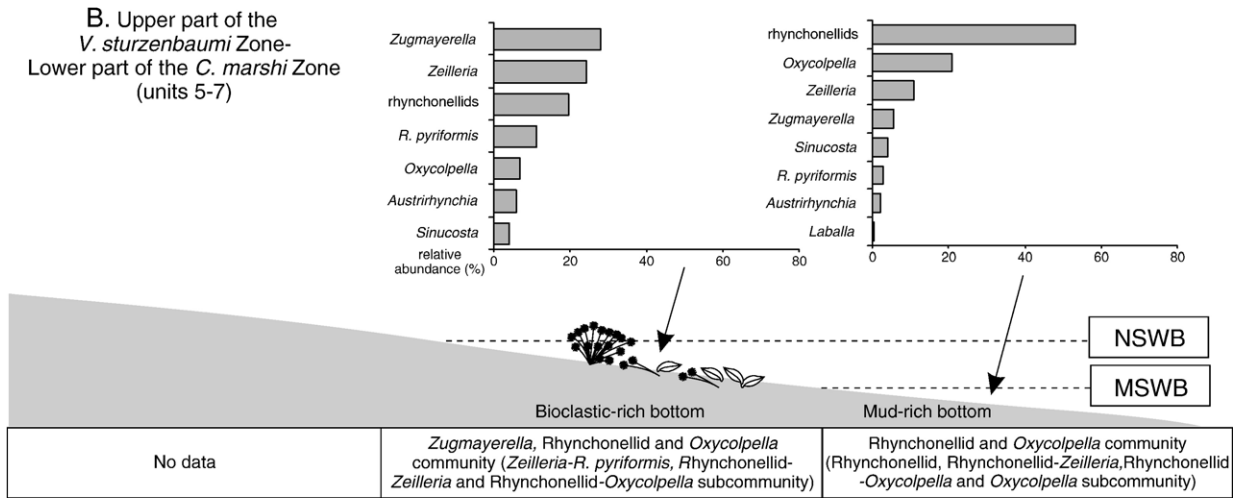
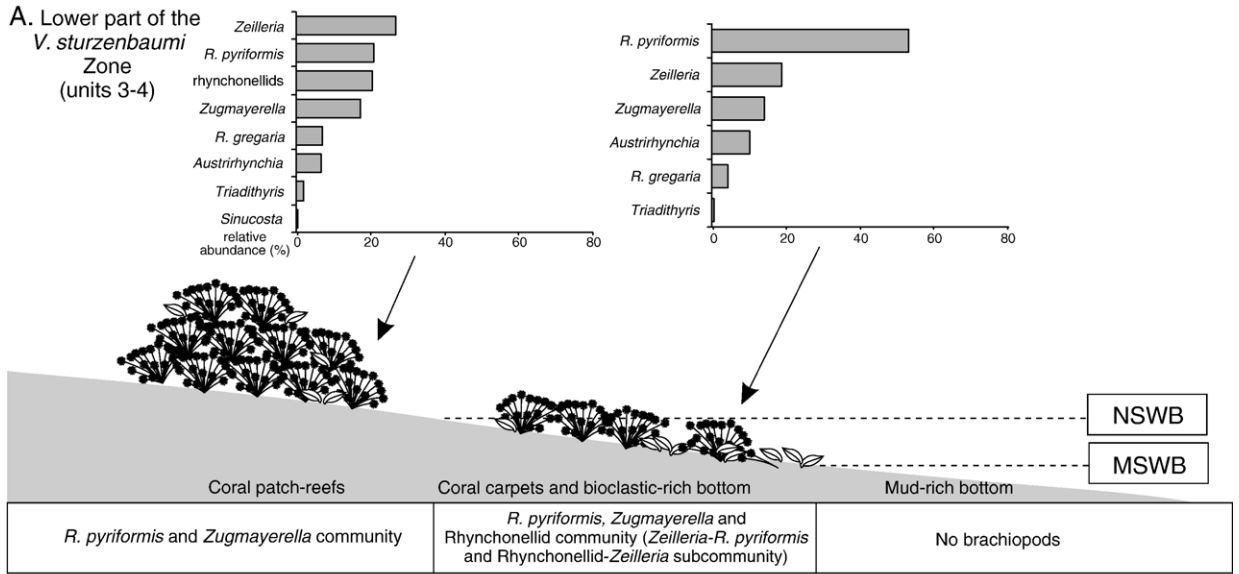
On one hand, some genera preferred particular habitats along the bathymetric transect. *Zugmayerella* was most abundant in habitats between NSWB and MSWB, *Rhaetina* was most common above MSWB, and *Oxycolpella* was most common below MSWB. On the other hand, *Zeilleria* was a generalist in terms of substrate and depth distribution because it occurred across the whole onshore–offshore transect. Rhynchonellids were also generalists in terms of their depth distribution. They were more common in shallow than in deep habitats in units 3–4 and in Unit 8; in contrast, they were more common in deep habitats in units 5–7.

4.5. Discussion

Although the compositional differences between stratigraphic zones are significant, they are biased by spatial coverage of the analysed samples, and do not represent large-scale turnover caused by extinctions of dominant taxa during the Early Rhaetian. All communities and their dominant taxa persisted in the Western Tethys up to the younger part of the *C. marshi* Zone, indicating that their compositional variation and between-habitat differentiation were relatively stable during the Rhaetian. Brachiopods migrated or tracked their habitats into areas more proximal to the shoreline during this time. The disappearance of the *R. gregaria*, *R. pyriformis* and *Zugmayerella* communities during the Late Rhaetian was a local feature of the Kössen Basin.

With the exception of the *R. gregaria* community, the compositional overlaps indicate that the communities were not discrete and were composed of taxa with broadly overlapping habitat preferences. The effects of depth and substrate on environmental separation of brachiopods are demonstrated by between-habitat differences in community composition at each stratigraphic level. For example, effects of substrate can reflect the differences between coral beds and coral patch-reefs in the Hochalm Member, or the differences between micritic and coral substrates in the Eiberg Member.

The overlap in the depth distribution between *R. gregaria* and *R. pyriformis* is in contrast to their supposed depth differentiation as suggested by Golebiowski (1991). However, although *R. gregaria* and *R. pyriformis* both occupy habitats above MSWB, their replacement coincides with the decrease in the frequency and thickness of storm-reworked beds, indicating a net increase in relative sea level (Golebiowski, 1990). In the Fatic Unit of the West Carpathians, *R. gregaria* occupied habitats above MSWB. This species persisted through to the latest Rhaetian in habitats which were very proximal to the shoreline (Michalík et al., 1979; Michalík, 1982;



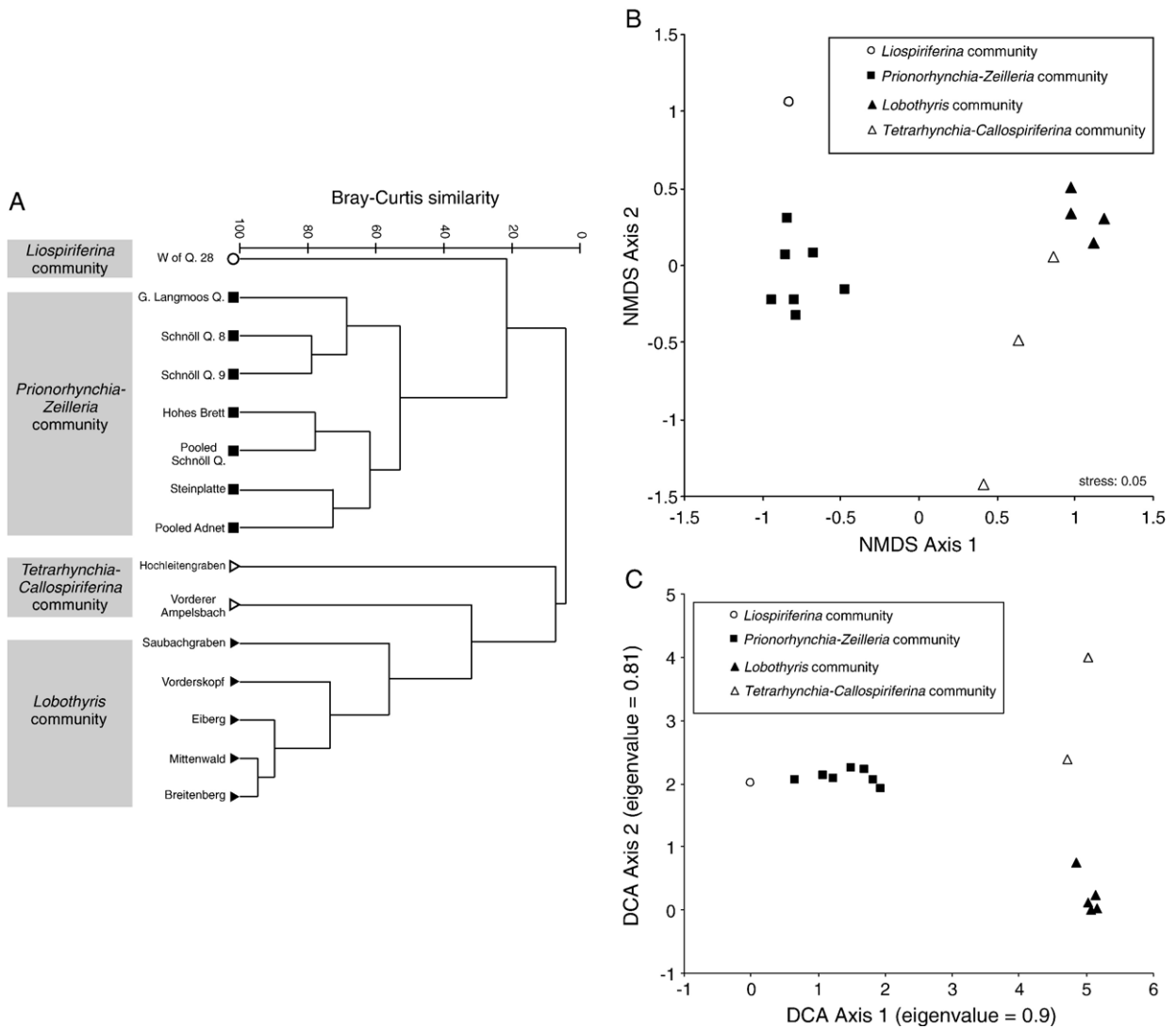


Fig. 10. Hettangian communities. (A) Q-mode cluster analysis. (B) Q-mode non-metric multidimensional scaling (NMDS). The configuration is rotated to have the greatest variation along the first axis for visual convenience. (C) Detrended correspondence analysis of samples (genera are shown in Fig. 12).

Tomašových, 2004). In contrast, *R. pyriformis* occurred in the West Carpathian habitats that were more distal to the shoreline (Hronic Unit, Michalík, 1973). Based on growth line patterns, Tomašových and Farkaš (2005) demonstrated that *R. gregaria* lived in habitats with relatively higher environmental instability (e.g., higher seasonality leading to variations in temperature, nutrient supply or turbidity) in contrast to *R. pyriformis*. The lower environmental variation caused by reduced proximity to shoreline and better connection with open sea can thus

explain the replacement of *R. gregaria* by *R. pyriformis* in the higher part of the Hochalm Member.

The appearance of the *Zugmayerella* community and the *Zeilleria*–*R. pyriformis* subcommunity in the Kössen Basin correlated with the onset of widespread colonization of the Kössen Basin by corals. Both communities were consistently associated with coral habitats above MSWB. This increase in compositional variation (i.e., several communities in Unit 4 in contrast to *R. pyriformis* in Unit 3) could reflect an increase in

Fig. 9. Compositional variation of Rhaetian communities along depth gradients. Note that habitats were occupied by different communities at each stratigraphic level. (A) Hochalm Member — units 3 and 4. (B) Eiberg Member — units 5–7. (C) Eiberg Member — Unit 8.

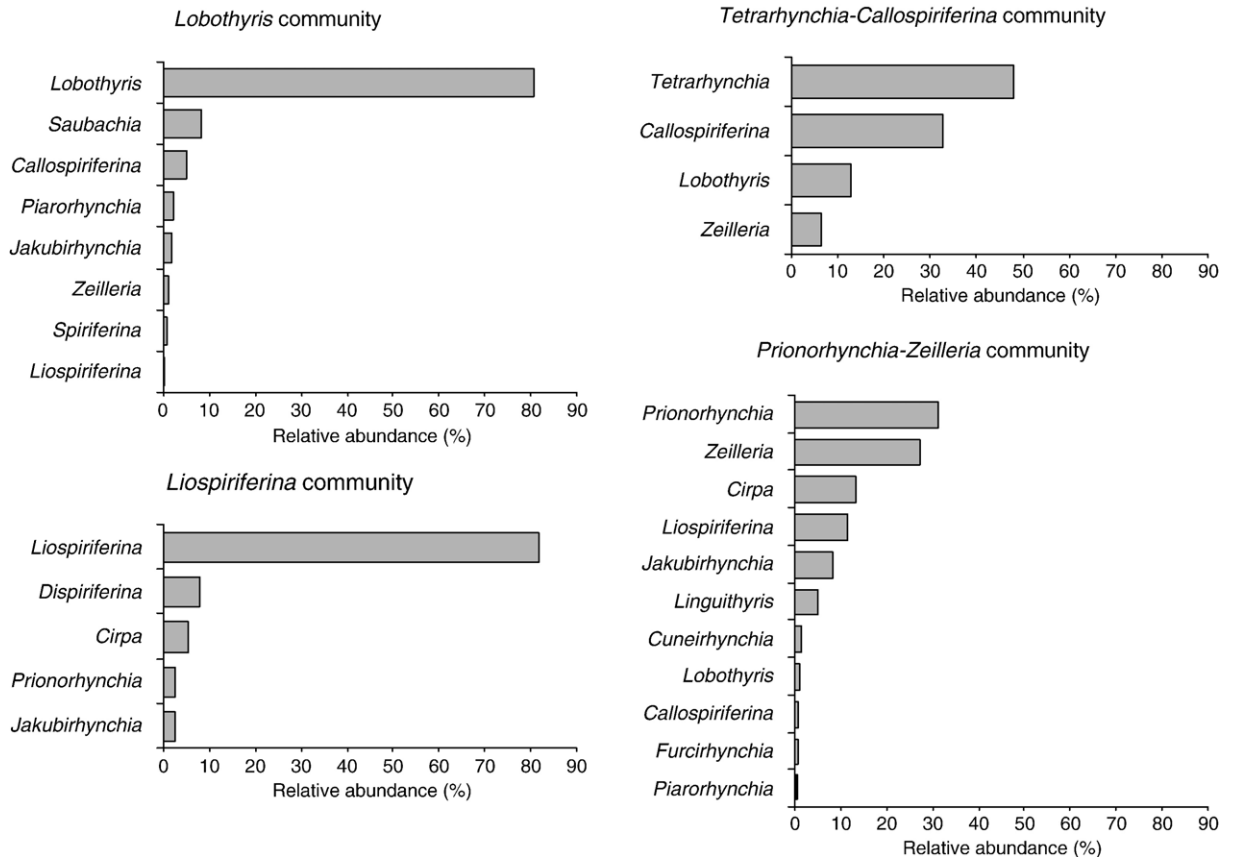


Fig. 11. Relative abundances of brachiopods in four Hettangian communities.

heterogeneity in coral reefs habitats and a decrease in siliciclastic supply and turbidity (as compared to thin coral carpets between siliciclastic beds in Unit 3).

With the onset of basinal deposition of the Eiberg Member, the Rhynchonellid and *Oxycolpella* communities inhabited soft-bottom habitats below MSWB. The compositional change between the Hochalm and Eiberg Member might be related to a change in sediment supply and substrate stability. In the siliciclastic intervals, palynofacies and trace elements indicate nutrient-rich conditions coupled with low oxygen levels (Holstein, 2004). Increase in sea level might also have led to new immigration episodes (e.g., *Oxycolpella* appears in Unit 5 for the first time). Finally, deposits of Unit 8 indicate new shallowing and perhaps restriction of the Kössen Basin (e.g., progradation of the 'Oberrhät' Limestone over the Eiberg Member at Steinplatte, Stanton and Flügel, 1989, 1995; Bernecker et al., 1999). The community replacement in the Kössen Basin thus reflects combined effects of habitat tracking and immigration/local extinction events, possibly related to climatic and sea level changes (e.g., Aberhan, 1993; Brett, 1998; Buzas and Culver, 1998).

5. Hettangian

5.1. Hettangian brachiopod communities

Although the samples from the Kendlbach Formation form one cluster (Fig. 10A), two samples dominated by *Tetrarhynchia* and *Callospiriferina* have a distinct composition in contrast to other five samples dominated by *Lobothis*. The *Lobothis* sample group forms one cluster at Bray–Curtis similarity of 50 (Fig. 10A) and its separation from the samples dominated by *Tetrarhynchia* and *Callospiriferina* is also visible in Q-mode NMDS (Figs. 10B–C). Therefore, the samples from Hochleitengraben and Vorderer Ampelsbach are assigned to the *Tetrarhynchia*–*Callospiriferina* sample group, although each sample is dominated by different genera. The third sample group is typical of the Schnöll Formation and the Enzesfeld Limestone. One sample from the Schnöll Formation is dominated by *Liospiriferina* (Fig. 11). NMDS and DCA show a strong compositional segregation of the first two sample groups from the Kendlbach Formation in comparison

to the samples from the Schnöll Formation and Enzesfeld Limestone (Fig. 10B–C). The gradient length along the first DCA axis is five SD units long, indicating a complete turnover and relatively high beta diversity.

The *Lobothyris* community is represented by five samples with 368 specimens. *Lobothyris* dominates (81%), rhynchonellid *Saubachia* (8%) and spiriferinid *Callospiriferina* (5%) are less common. Other rhynchonellids (*Piarorhynchia* and *Jakubirhynchia*, 2%) and *Zeilleria* (1%) are rare. Bivalve *Plagiostoma* can be very common. This community consistently occurs in micro-intraclastic–crinoidal packstones/grainstones in the upper part of the Breitenberg Member (*P. calliphyllum* Zone). Rhynchonellid *Saubachia* is abundant at Saubachgraben where packstones alternate with marlstones (Fig. 4).

The *Tetrarhynchia*–*Callospiriferina* community is represented by two samples with 216 specimens. Rhynchonellid *Tetrarhynchia* (48%) and spiriferinid *Callospiriferina* (33%) are dominant. *Lobothyris* (13%) and *Zeilleria* (6%) are less common. They occur in marly limestones and marlstones of the Breitenberg Member (*P. calliphyllum* Zone).

The *Prionorhynchia*–*Zeilleria* community is represented by seven samples with 353 specimens. *Prionorhynchia* (31%) and *Zeilleria* (27%) dominate. *Cirpa* (13%), *Liospiriferina* (11%), *Jakubirhynchia* (8%) and *Linguithyris* (5%) are less common. One sample comes from a dyke infill (*P. calliphyllum* Zone) in the Late Triassic Dachstein Limestone (Hohes Brett). Four samples are from bioclastic–oncoloidal wackestones of the Langmoos Member (*K. megastoma* Zone) and two

samples from crinoidal biomicrites of the Enzesfeld Limestone (*A. marmoreum* Zone).

One sample from the Langmoos Member (*K. megastoma* Zone) with 38 specimens is dominated by *Liospiriferina* (82%). *Dispiriferina* (8%) and *Cirpa* (5%) are less common. *Prionorhynchia* (3%) and *Jakubirhynchia* (3%) are rare.

5.2. Co-existence patterns of Hettangian brachiopod genera

R-mode NMDS and DCA (Fig. 12) show that the genera typical of the Kendlbach and Schnöll formations have distinct abundance patterns. A group typical of the Kendlbach Formation is represented by *Lobothyris*, *Callospiriferina*, *Tetrarhynchia*, *Saubachia* and *Piarorhynchia*. A group typical mainly of the Schnöll Formation and Enzesfeld Limestone is represented by *Prionorhynchia*, *Cirpa*, *Zeilleria* and *Liospiriferina*. The Bray–Curtis similarities among the genera of the Schnöll Formation and Enzesfeld Formation are higher than similarities among the genera of the Kendlbach Formation.

5.3. Linking Hettangian brachiopods to stratigraphy

There is a significant difference in community composition between the Early Hettangian *P. calliphyllum* Zone and the Middle Hettangian *K. megastoma* Zone ($R=0.53$, $p=0.007$; Table 1). Although the *Prionorhynchia*–*Zeilleria* community occurs already in the *P. calliphyllum* Zone, the

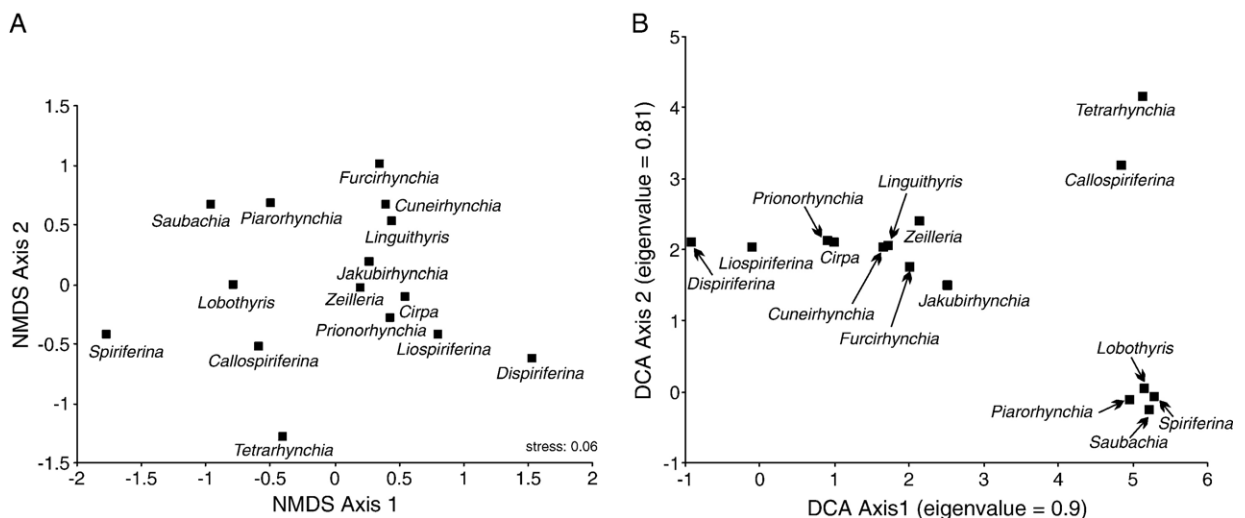


Fig. 12. Abundance patterns of Hettangian brachiopods. (A) R-mode non-metric multidimensional scaling (NMDS). The configuration is rotated to have the greatest variation along the first axis for visual convenience. (B) Detrended correspondence analysis of genera.

Early Hettangian deposits are characterized mainly by the *Lobothyris* and *Tetrarhynchia*–*Callospiriferina* communities typical of the Breitenberg Member. Although *Lobothyris* rarely occurs in the Middle Hettangian deposits of the Breitenberg Member, this stratigraphic difference indicates that the Early Hettangian communities were rather unique in composition. The Middle and Late Hettangian habitats were occupied mainly by the *Prionorhynchia*–*Zeilleria* community.

5.4. Linking Hettangian brachiopods to environment

The samples from three habitats are significantly different in composition ($R=0.89$, $p<0.0001$; Table 2). Packstones/grainstones and marlstones of the Kendlbach Formation, representing the habitats above and below NSWB, are significantly different in composition from wackestones of the Schnöll Formation, which represent the habitats below MSWB (Table 2). The habitats below NSWB with common marlstone interbeds with abundant rhynchonellids (*Tetrarhynchia* or *Saubachia*) differ in composition from the habitats above NSWB dominated by *Lobothyris* (Fig. 13, $R=0.53$; Table 2).

5.5. Discussion

Differences in the sediment supply within the Breitenberg Member can be related to the compositional segregation of siliciclastic habitats with abundant rhynchonellids (*Tetrarhynchia* and *Saubachia*), in contrast to carbonate-rich habitats with high input of

microintraclastic and crinoidal debris with abundant *Lobothyris* (Fig. 13). The difference between the communities of the Kendlbach and Schnöll formations correlates with the environmental history of the NCA. Böhm et al. (1999) suggested that carbonate-rich intervals in the upper part of the Kendlbach Formation and approximately coeval sponge layer of the Schnöll Formation were deposited during a sea level rise, leading to reduced siliciclastic supply due to sediment trapping in shallow habitats and sediment starvation in deep habitats. Environmental separation between communities from the Breitenberg Member on one hand and the Schnöll Formation and Enzesfeld Limestone on the other probably reflects this environmental change (i.e., a change in substrate stability, rate of sedimentation, possibly also in trophic and oceanographic regime). The deposition of the upper part of the Schnöll Formation and Enzesfeld Limestone thus reflects a phase with stable substrate, low turbidity and reduced sedimentation rate. Such conditions favoured the recruitment and colonization by brachiopods of the *Prionorhynchia*–*Zeilleria* community during the Middle and Late Hettangian.

5.6. Recovery of Hettangian brachiopods

5.6.1. Definition

The recovery pattern may be defined in several ways, but in general a boundary between a phase characterized by prolonged stress (i.e., extinction/survival phase) and recovery phase is characterized by an increase in origination rates and/or decrease in extinction rates, and

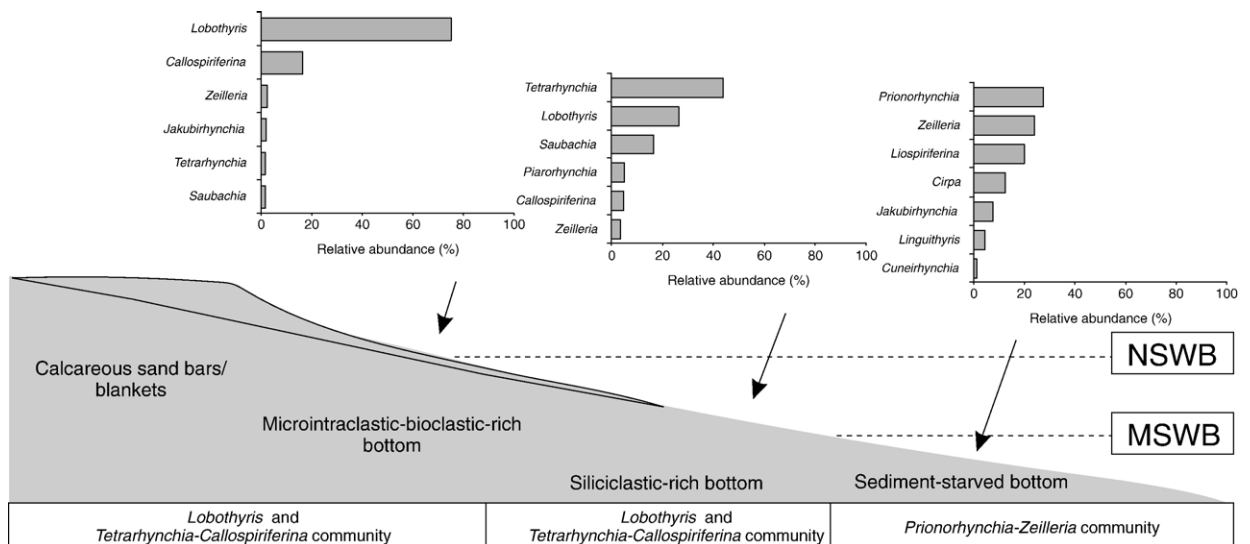


Fig. 13. Compositional variation of Early Hettangian communities along a depth gradient. Carbonate-rich habitats above NSWB were dominated by *Lobothyris*. Rhynchonellids were common in siliciclastic-rich habitats below NSWB. *Prionorhynchia* and *Zeilleria* dominated in deep, sediment-starved habitats.

a return of community-level properties to pre-extinction levels (Erwin, 1998). As taxonomic inconsistencies do not allow evaluation of variations in diversity and extinction rates at this stage, compositional variation of brachiopod communities and their environmental distribution are used to evaluate recovery patterns. Communities in the survival interval are generally supposed to be dominated by ecologic opportunists which occupy physically unstable, disrupted habitats (Schubert and Bottjer, 1995; Kauffman and Harries, 1996; Harries et al., 1996). During the survival interval, the communities should be dominated by a few taxa with broad environmental ranges, and between-habitat differentiation of communities should be poor. In contrast, the recovery should be characterized by an increase in the number of community types, and their between-habitat segregation. Numerically abundant taxa should belong to those habitats that are typical of stable, normal marine conditions after mass extinction, in contrast to opportunists which are typical of high-stress habitats during “background” times (Harries et al., 1996).

5.6.2. Extinction/survival interval

Rhynchonelliformean brachiopods are very rare in the basal parts of the Kendlbach Formation in the NCA. The only known rhynchonelliformean brachiopods are rhynchonellids from the Karwendelmunde section, which occur in red marls about 1.3 m above the top of the Kössen Formation (Axel von Hillebrandt, pers. comm., 2005). The multicostate rhynchonellids without planareas are 8–11 mm long, possess slightly developed sulcus and fold with 3 or 4 costae. They differ from the rhynchonellids known from the Rhaetian of the western Tethys. They are rather similar to representatives of the family Wellerellidae and Basiliolidae. It is unclear whether they represent surviving opportunists, new immigrants from other regions, or progenitor taxa (i.e., taxa that evolved during the highly stressed intervals during mass extinctions; Kaufman and Harries, 1996). The rarity of brachiopods in the boundary marl is probably a large-scale regional phenomenon because comparable siliciclastic deposits devoid of brachiopods are present also in other areas of the western Tethys (Gaździcki et al., 1979; Michalík et al., 1991). Highly abundant bivalves in the lower parts of the boundary marl indicate that the taphonomic bias alone does not account for the observed rarity of brachiopods. This implies that the rarity of brachiopods in the lower parts of the boundary marl is a real ecologic signal.

The lower parts of the boundary marl contain abundant shallow infaunal and epifaunal bivalves (Golebiowski and Braunstein, 1988; Rakús and Lobitzer,

1993; McRoberts et al., 1997). *Cardinia* locally forms monospecific, densely-packed concentrations, and is a candidate taxon with high population turnover and opportunistic behaviour typical of habitats with high environmental stress (Rodland and Bottjer, 2001). Local signs of lamination, rare bioturbation and bedding planes covered with concordant and complete, disarticulated pteriid and pectinid bivalves imply high environmental stress. The upper clay-rich parts of the boundary marl are mostly completely devoid of shelly benthos.

The lower part of the boundary marl is marked by a negative carbon isotope anomaly, followed by a shift to background levels and a second negative anomaly that characterizes the middle part of the Tiefengraben Member (Krystyn et al., 2005). The return to ‘background’ values approximately correlates with an increasing proportion of bioclastic limestones. This return corresponds with the onset of the Breitenberg Member and the appearance of abundant brachiopods. In addition, palynologic data indicate that an abrupt warming coincides with the initial carbon isotope anomaly. Palynomorph assemblages are characterized by a disappearance of Rhaetian dinoflagellate cysts and a high abundance of prasinophytes (Krystyn et al., 2005). This excursion hints at an increase in release of methane through dissociation of gas hydrates, an increase in volcanic CO₂ outgassing and/or a decrease in primary productivity (Ward et al., 2001; Pálffy et al., 2001; Hesselbo et al., 2002; Pálffy, 2003; Guex et al., 2004). The second negative carbon-isotope anomaly coincides with a marked turnover in terrestrial palynomorphs (Krystyn et al., 2005). Hautmann (2004) and Galli et al. (2005) suggested that the increased levels of carbon dioxide could lead to a temporary undersaturation of sea water with respect to calcium carbonate and thus to a biocalcification crisis. The combined sedimentologic, geochemical and palaeobiologic evidence thus indicates that high-stress conditions were initiated at the base of the boundary marl and continued up to the upper parts of the Tiefengraben Member.

5.6.3. Recovery interval

Three arguments suggest that late Early and Middle Hettangian deposits in the NCA correspond to the recovery interval (Fig. 14). First, between-habitat (beta) diversity was even higher during the Middle Hettangian than during the Rhaetian. The Hettangian is represented by lower sample numbers compared to the Rhaetian so sampling effects do not account for this difference. In any case, beta diversity of the Middle Hettangian communities was comparable to pre-extinction levels.

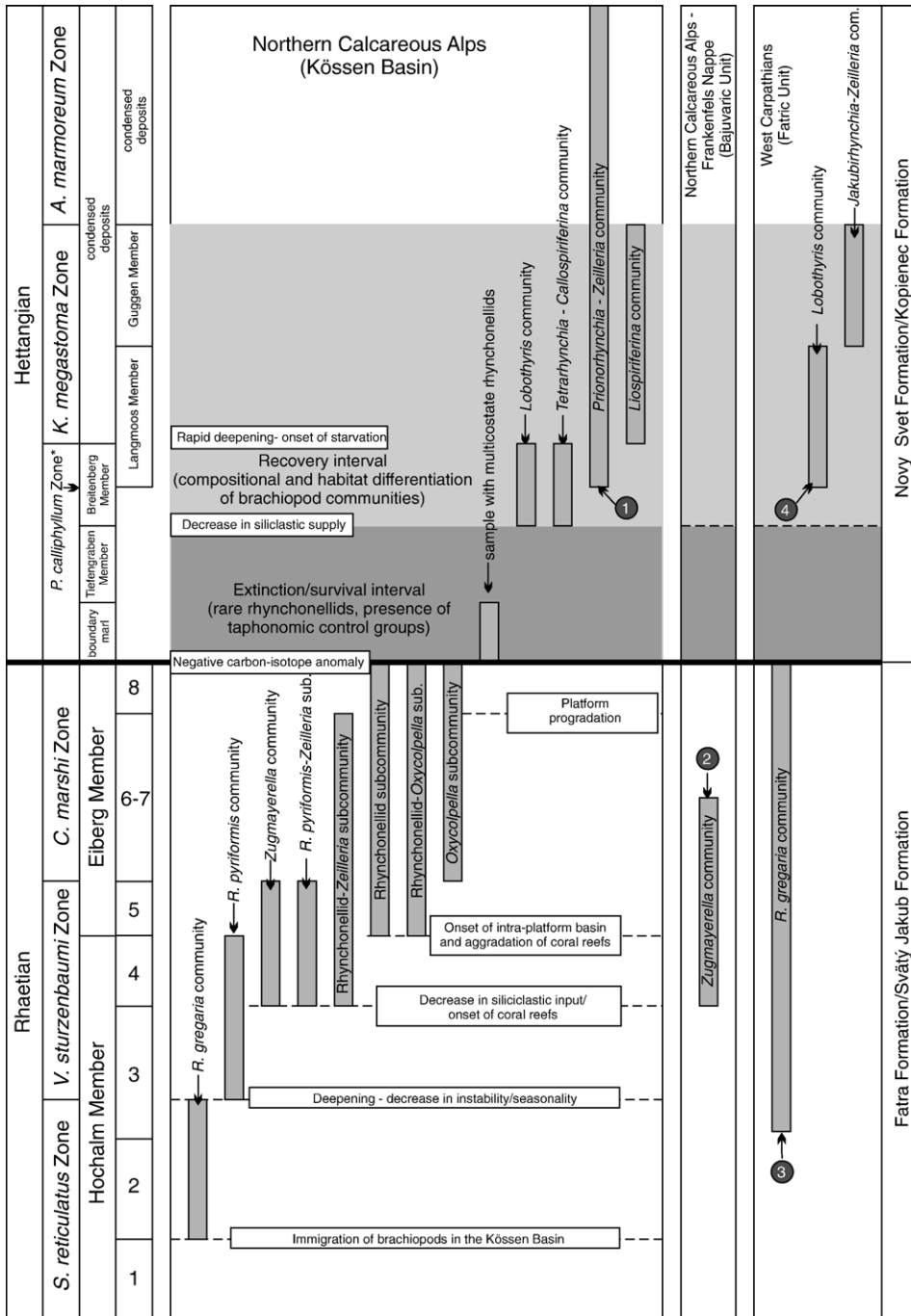


Fig. 14. Stratigraphic distribution of brachiopod communities at the T/J boundary in the Kössen Basin. Note that the *R. gregaria* and *Zugmayerella* communities persisted to the *C. marshi* Zone in the Frankenfels Nappe (Bajuvaric Unit) and in the West Carpathians. Each zone has the equal column height which does not correspond to the stratigraphic thickness or age span. Lithostratigraphic and biostratigraphic units are not to scale. * — The *P. calliphyllum* Zone is restricted to the Breitenberg Member. 1 — The first appearance of this community is represented by the dyke infill (*P. calliphyllum* Zone). The dyke is tentatively correlated with the Langmoos Member. 2 — The age is determined by conodonts as the *C. marshi* Zone (Golebiowski, 1990). 3 — The age of its appearance is not precisely known. The community ranges to the top of the Fatra Formation. 4 — The age of the first appearance is the Early or Middle Hettangian. The *Jakubirhynchia-Zeilleria* community is dated by an ammonite to the Middle Hettangian (Tomašových and Michalik, 2000).

Second, the between-habitat differentiation of Hettangian brachiopod communities with respect to depth and substrate was comparable to between-habitat differentiation of Rhaetian brachiopod communities. Calcareous sand habitats above NSWB, siliciclastic habitats below NSWB, and carbonate-starved habitats below MSWB were dominated by different brachiopods, implying their distinct environmental preferences. Compositionally, comparable communities occurred also in other regions of the western Tethys during the Hettangian, indicating that the recovery pattern is not restricted to the NCA only. Third, the brachiopods dominating the Hettangian communities were also typical of normal marine habitats during the Sinemurian and Pliensbachian.

Similarly as in the NCA, *Lobothyris* dominated in calcareous sand deposits originating in shallow habitats above NSWB in the Southern Alps and Transdanubian Central Range (TCR) (Gaetani, 1970; Dulai, 1993a,b, 2003). *Lobothyris* also dominated in offshore habitats below MSWB in the Early and Middle Hettangian deposits of the West Carpathians (Tomašových and Michalík, 2000). *Lobothyris* belongs to the first brachiopod colonizers in the Hettangian deposits. Some features may indicate that *Lobothyris* belongs to taxa with opportunistic tendencies. This possibility might be indicated by its high community-level abundance and the occurrence in parautochthonous, loosely or densely packed shell beds, which can indicate rapid population turnover. Its abundance in habitats above NSWB might indicate that it tolerated some fluctuations in rate of sedimentation, nutrient supply or substrate stability. However, *Lobothyris* was well established in normal marine habitats in the later Early Jurassic (Hallam, 1961; Tchoumatchenco, 1972, Aberhan, 1992; Tchoumatchenco, 1993; Gahr, 2002) and does not occur in the high-stress habitats in the aftermath of mass extinction or in marginal unstable habitats during ‘background’ times.

The communities dominated by rhynchonellids and *Zeilleria* also have compositional counterparts in the Hettangian of the West Carpathians (Tomašových and Michalík, 2000) and Southern Alps (Gaetani, 1970), and in the Sinemurian of the NCA and TCR. Similarly as in the Hettangian of the NCA, these typically occur in carbonate habitats with minimum siliciclastic input and reduced sedimentation rate. Dulai (1990) and Vörös et al. (2003) described assemblages of Sinemurian age dominated by *Zeilleria*, *Liospiriferina* and rhynchonellids such as *Prionorhynchia* and *Cirpa*. Communities dominated by *Tetrarhynchia* and *Saubachia* may be comparable to those with common rhynchonellids typical of siliciclastic habitats below MSWB, which

are typical of the Early Jurassic habitats of NW Europe (e.g., *Calcirhynchia* dominates in siliciclastic offshore deposits, Hallam, 1960; Alméras and Hanzo, 1991).

6. Rhaetian vs. Hettangian brachiopod communities

6.1. Hypothesis 1 — composition of Rhaetian vs. Hettangian brachiopod communities

6.1.1. Analytical approach

To evaluate community turnover during mass extinctions, it is important to distinguish between local turnovers caused by habitat tracking, basin-scale immigration/local extinction, and within-lineage replacement, and turnovers due to a real extinction of dominant taxa that leads to a change in phylogenetic structure of communities (Webb et al., 2002). Habitat tracking can lead to apparent turnover if a temporal change is associated with an environmental change and the compared time intervals record different habitats. This problem can be accommodated by comparing equivalent parts of onshore–offshore gradients (Smith et al., 2001). The opportunities for comparison of onshore–offshore gradients in the Kössen Basin between the Rhaetian and the Hettangian are limited. In contrast to the Rhaetian, coral patch-reefs were completely missing in the Hettangian of the NCA. During the Hettangian, carbonate deposition with much reduced sedimentation rate due to starvation is typical of some habitats below MSWB. Such habitats do not have comparable counterparts in the Rhaetian. However, the Rhaetian and Hettangian deposits record mixed carbonate–siliciclastic habitats with equivalent depths and can be generally comparable. Effects of local extinction can be understood using data from adjacent geographic areas. For the Kössen Basin, the significant differences in generic composition between Rhaetian zones and between Hettangian zones are mainly caused by local extinctions and immigrations. The communities which lived in the Kössen Basin during the Early Rhaetian tracked their habitats beyond the Kössen Basin during the Late Rhaetian. Effects of within-lineage replacement can be partly accommodated by evaluating turnover on several taxonomic levels. Although explicit phylogenetic analyses of Triassic and Jurassic brachiopods are not available, this approach assumes that taxonomic categories above the generic level reflect biologically meaningful units (Carlson, 1991; Sepkoski and Kendrick, 1993).

We use one-factorial ANOSIM as the method for estimating the compositional turnover at the T/J boundary (e.g., Pandolfi, 1996; Bonuso et al., 2002). Theoretically, there can be a substantial compositional change in benthic communities without invoking any

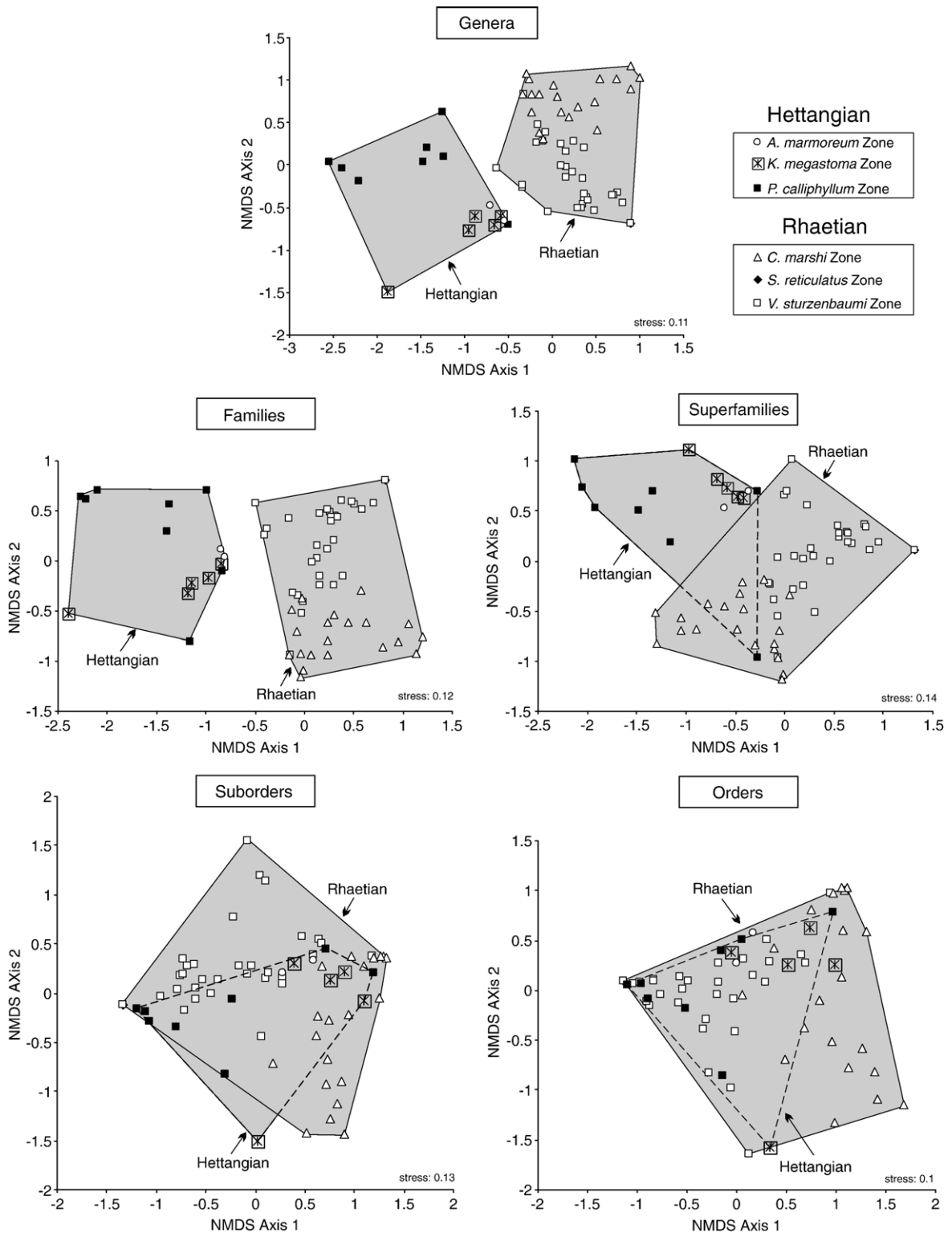


Fig. 15. Q-mode non-metric multidimensional scaling (NMDS) comparing Rhaetian and Hettangian samples at five taxonomic levels. The configurations are rotated to have the greatest variation along the first axis for visual convenience. Note that the segregation persists up to the superfamily level. Rhaetian “rhynchonellids” were assigned to the family Cyclothyridae and superfamily Hemithiridoidea.

Table 3
ANOSIM results showing differences in composition between Rhaetian and Hettangian samples at five taxonomic levels

	<i>R</i> -genera	<i>p</i> -value	<i>R</i> -families	<i>p</i> -value	<i>R</i> -superfamilies	<i>p</i> -value	<i>R</i> -suborders	<i>p</i> -value	<i>R</i> -orders	<i>p</i> -value
Comparison of stages										
Rhaetian vs. Hettangian	0.49	<0.0001	0.61	<0.0001	0.5	<0.0001	0.02	0.36	−0.06	0.81
Comparison of zones										
<i>K. megastoma</i> Zone vs. <i>A. marmoreum</i> Zone	0.28	(0.24)	0.3	(0.24)	0.31	(0.24)	−0.16	(0.57)	−0.15	(0.57)
<i>P. calliphylum</i> Zone vs. <i>K. megastoma</i> Zone	0.53	0.007	0.46	0.01	0.38	0.02	0.26	0.05	0.23	0.06
<i>C. marshi</i> Zone vs. <i>P. calliphylum</i> Zone (T/J)	0.94	<0.0001	0.95	<0.0001	0.79	<0.0001	0.56	<0.0001	0.47	<0.0001
<i>V. sturzenbaumi</i> Zone vs. <i>C. marshi</i> Zone	0.57	<0.0001	0.57	<0.0001	0.57	<0.0001	0.55	<0.0001	0.56	<0.0001
<i>S. reticulatus</i> Zone vs. <i>V. sturzenbaumi</i> Zone	0.28	0.005	0.29	0.01	0.29	0.005	0.34	0.001	0.08	0.17
Comparison of Rhaetian units										
Rhaetian Unit 8 vs. <i>P. calliphylum</i> Zone (T/J)	0.83	0.0003	0.89	0.0003	0.72	0.0005	0.51	0.003	0.58	0.001
Rhaetian Unit 6–7 vs. Rhaetian Unit 8	0.01	0.38	0.01	0.38	0.01	0.38	0.02	0.31	0.01	0.34
Rhaetian Unit 5 vs. Rhaetian Unit 6–7	0.15	0.05	0.15	0.05	0.15	0.05	0.15	0.06	0.1	0.13
Rhaetian Unit 4 vs. Rhaetian Unit 5	0.29	0.01	0.29	0.01	0.29	0.01	0.3	0.01	0.35	0
Rhaetian Unit 3 vs. Rhaetian Unit 4	0.16	0.11	0.16	0.1	0.16	0.1	0.15	0.11	−0.1	0.8
Rhaetian Unit 2 vs. Rhaetian Unit 3	0.64	0.002	0.64	0.002	0.64	0.002	0.64	0.002	0.61	0.002

Note that the highest turnovers on genus, family and superfamily levels occurred at the T/J boundary (in bold). The *p*-values in parentheses are inconclusive due to low number of permutations.

mass extinction event (e.g., coordinated turnover, Boucot, 1983; Brett and Baird, 1995; Sheehan, 1996; Ivany, 1996; Patzkowsky and Holland, 1997; Olszewski and Patzkowsky, 2001; DiMichele et al., 2004). However, a mass extinction event can be supposed to be an end-member along a turnover continuum because an environmental disturbance is supposed to be an important agent causing the coordinated turnover. In order to estimate the compositional turnover at the T/J boundary, we extend the method used in testing of “coordinated stasis” by two inter-related approaches. First, in order to evaluate intensity of turnover, ANOSIM compares the Rhaetian and Hettangian communities on several taxonomic levels. Second, *R* values that reflect compositional turnover between stratigraphic zones are compared within the Rhaetian and within the Hettangian with an *R* value at the T/J boundary. This approach thus enables us to estimate if the intensity of turnover between the Rhaetian and Hettangian is indeed higher than during “background” times.

Evaluation of compositional turnover in community-level abundance of taxa on several taxonomic levels can be a robust measure of ecological impact of mass extinc-

tion. Any survivors passing through the mass extinction will depress the extinction rate which is supposed to be a main measure of evolutionary impact. However, that these survivors never re-attain their previous community-level abundance is obviously of ecological importance. This information is missed by taxonomic rate metrics or taxonomic diversity measures (Foote, 2000). This measure should be only weakly affected by sampling and preservation biases that influence diversity comparisons because it is based on relative abundances.

6.1.2. Results

ANOSIM demonstrates that the Rhaetian and Hettangian brachiopod communities are significantly different in composition on the generic level ($R=0.49$, $p<0.0001$; Fig. 15, Table 3). One genus (*Zeillera*) crossed the T/J boundary in this area. If the generic assignment of *?Calcirhynchia subrimosa* is supported, this genus will also belong to survivors because it is reported from the Hettangian of the western Tethys. However, it was mainly abundant during the Hettangian in the NW European province. In addition, there are significant differences between the Rhaetian and

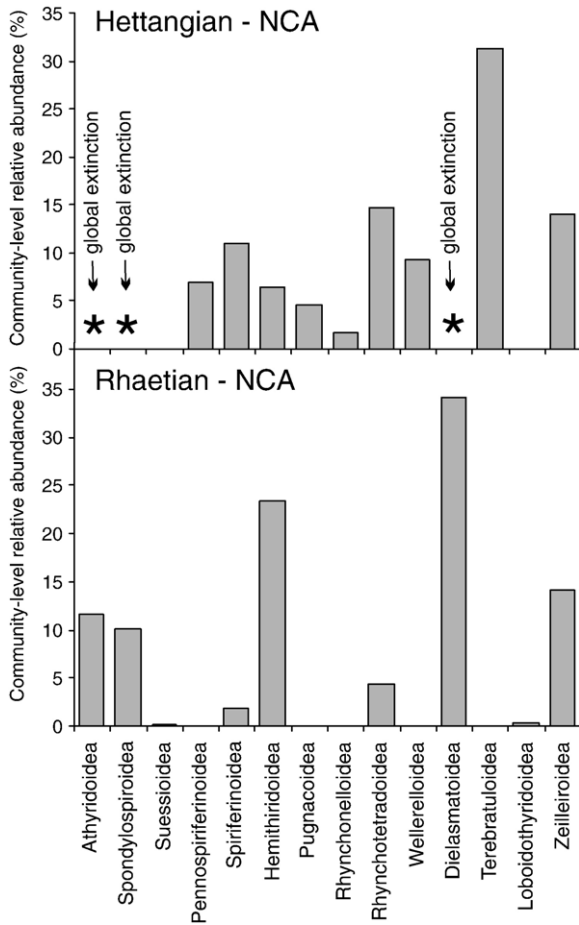


Fig. 16. The change in community-level abundances of superfamilies after the T/J boundary in the NCA. It demonstrates the effect of the end-Triassic mass extinction on the composition of the post-extinction brachiopod communities. The relative abundances are based on pooled relative abundances of all samples. Note that the superfamilies Athyrdoidea, Spondylospiroidea and Dielasmatoidea went globally extinct at the T/J boundary.

Hettangian communities on the family and superfamily level (Fig. 15, Table 3). The superfamily Zeillerioidea and rhynchonellids belonging to the superfamilies Hemithiridoidea and Rhynchotetradoidea persisted into the Hettangian. One Hettangian sample dominated by *Tetarhynchia* (superfamily Hemithiridoidea) groups together with the Rhaetian samples in NMDS based on superfamily-level abundances. The differences between Hettangian and Rhaetian communities disappear on suborder and order levels (Fig. 15). Therefore, the compositional turnover at the T/J boundary took place on the superfamily level.

ANOSIM also shows that the compositional turnover of brachiopod communities on generic level at the T/J

boundary ($R=0.94$) is substantially higher than turnovers between the Rhaetian zones ($R=0.27-0.57$) and between the Hettangian zones ($R=0.28-0.53$). Note that the difference is even more pronounced when compositional differences are estimated among the Rhaetian units (Table 3). Although this test is conservative because it does not take into account the samples from other regions where some communities may have migrated during the Late Rhaetian, it shows that turnover at the end of the Rhaetian was of higher magnitude than within-Rhaetian turnovers. The same pattern is visible on the family and superfamily level (Table 3). On the suborder and order level, the difference between the *V. sturzenbaumi* and *C. marshi* zones is comparable to the difference at the T/J boundary. This pattern is mainly caused by differential proportions of athyrids and spiriferinids between the *V. sturzenbaumi* and *C. marshi* zones. With the exception of a strong difference between units 2 and 3 (*R. gregaria* is the only brachiopod in Unit 2), the differences between the Rhaetian units ($R=0.008-0.28$) contrast with the turnover at the T/J boundary ($R=0.83$).

6.1.3. Discussion

The significant compositional turnover on superfamily level implies that the T/J boundary event had substantial consequences on community ecology of Jurassic brachiopods. This event changed the phylogenetic structure of brachiopod communities (Fig. 16). Although there are as yet no consistent data on long-term compositional changes of Jurassic brachiopod communities, it seems that this changeover in the dominance at the superfamily level had long-standing effects on the composition of brachiopod communities. Brachiopod communities comparable in composition to those in the Hettangian are typical of the Early Jurassic (e.g., Manceñido and Owen, 2001).

The Rhaetian brachiopods that were numerically abundant in local communities belong to extinct athyrdoidea, spondylospiroidea and dielasmatoidea (Fig. 16). Zeillerioidea were abundant in both Rhaetian and Hettangian communities. In contrast, the Hettangian dominants belong to spiriferinoidea, pennospiriferinoidea and terebratuloidea, which were rare in the Rhaetian (Fig. 16). Evaluation of rhynchonellid turnover is obscured by taxonomic inconsistencies and a lack of explicit phylogenetic framework, but rhynchonelloidea, wellerelloidea and rhynchotetradoidea are known to be abundant in the Jurassic communities, in spite of their rarity in the Late Triassic. Note that this pattern does not follow from stratigraphic ranges of brachiopod superfamilies. Spiriferinoidea, zeillerioidea and rhynchotetradoidea occur both in Rhaetian and

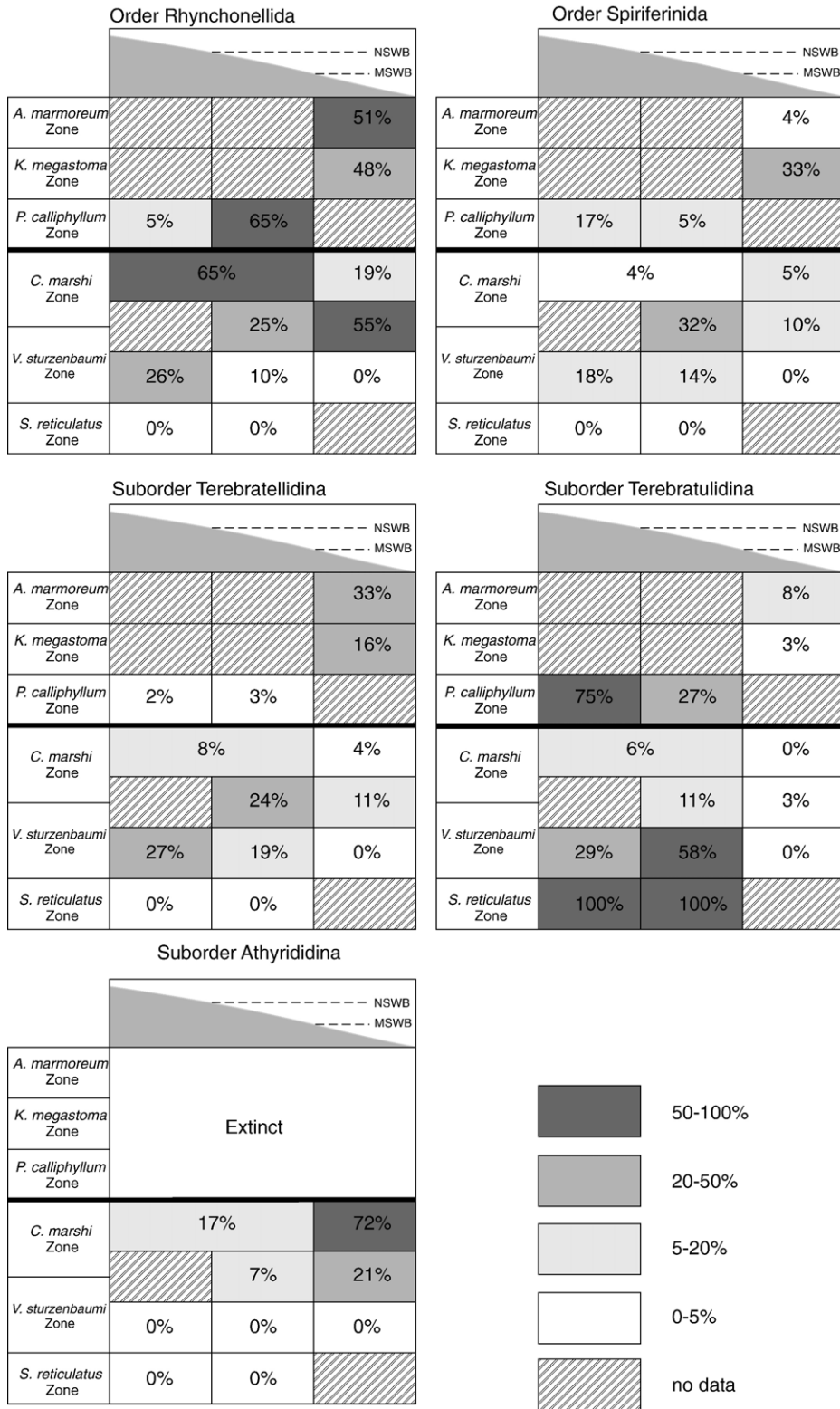


Fig. 17. Time-environment diagrams of five suborders/orders. Note that short-looped terebratulids occupied shallow habitats both in the Rhaetian and Hettangian and rhynchonellids were generalistic in distribution. Long-looped terebratulids and spiriferinids may indicate shift to deeper habitats after the end-Triassic mass extinction event.

Hettangian, but their community-level abundance and co-existence with other superfamilies differ.

Most of the short-looped terebratulids which have dominated in Triassic communities belong to dielasmatooids (e.g. *Coenothyris* in the Middle Triassic, *Crurata* and *Rhaetina* in Late Triassic). One exception is represented by endemic plectoconchid terebratuloids *Plectoconcha* and *Pseudorhaetina*. They were locally abundant in Late Triassic shallow habitats of the Eastern Pacific region (Sandy and Stanley, 1993; Stanley et al., 1994). Although Late Triassic terebratuloids are not represented in our dataset, they are rare in the Norian and Rhaetian deposits of the NCA. For example, *Lobothyris* occurs in the Carnian limestones of the Brock Mountain in California (Sandy, 2001) and is a subordinate component of brachiopod communities from Norian deposits of the NCA and Rhaetian deposits of the West Carpathians (Siblík, 1967). Therefore, the dominance of dielasmatooids was typical of the Triassic communities. In contrast, terebratuloids with *Lobothyris* were numerically abundant in the Early Jurassic communities.

Spiriferinids at the level of order or suborder decreased in the diversity during the Early Jurassic and finally went extinct in the Early Toarcian (Ager, 1987). Jablonski (2001) supposed that they are an example of a dead clade walking (i.e., survival without recovery, leading to decline in the aftermath of mass extinction) after the T/J boundary. However, spiriferinoids and pennospiriferinoids were abundant in some Early Jurassic brachiopod communities (Aberhan, 1992; Gahr, 2002), in contrast to their rarity in Triassic communities. On superfamily level, spiriferinoids and pennospiriferinoids were probably less affected by extinction than spondylospiroids because their community-level abundance increased after the T/J boundary.

The lower levels of the turnover between the Rhaetian zones and between the Hettangian zones demonstrate that the turnover at the T/J boundary was rather abrupt (i.e., restricted to the interval between the uppermost parts of the Kössen Formation and the *P. calliphyllosum* Zone) and not due to prolonged extinctions throughout the Late Triassic (Hallam, 2002; Lucas and Tanner, 2004). In addition to the measure of the compositional turnover, from 21 brachiopod species known from more than one occurrence in the NCA, at least 14 species range to the latest Rhaetian deposits in this area (Unit 8 of the Eiberg Member, see Mostler et al., 1978; Golebiowski, 1990; Siblík, 1998). Although some rhynchonellid superfamilies and zeillerioids may show pseudo-extinction, none of these 14 species crosses the T/J boundary.

6.2. Hypothesis 2 — environmental preferences of Rhaetian vs. Hettangian brachiopods

The second hypothesis concerns whether environmental distribution of brachiopods did substantially change after the T/J boundary. Sandy (1995) hypothesized that brachiopod suborders and orders show different environmental preferences before and after the end-Triassic mass extinction, partly as a consequence of vacated deep habitats after the extinction of athyridoids. He hypothesized that rhynchonellids became more abundant in shallow, high-energy habitats, in contrast to their deep water preference in the Rhaetian. In contrast, short-looped terebratulids were typical of shallow water habitats in the Rhaetian, but changed their preference to deeper waters in the Early Jurassic. Spiriferinids and long-looped terebratulids (suborder Terebratellidina) shifted to the deepest parts of the transect during the Early Jurassic.

We evaluate the hypothesis with help of time-environment diagrams using relative abundances of orders/suborders in three depth habitats (Fig. 17). The predictions of Sandy with respect to the expected change in environmental distribution are not met by Hettangian rhynchonellids and short-looped terebratulids (suborder Terebratulidina). Several rhynchonellids dominated in relatively deep habitats below MSWB during the Hettangian. In addition, some rhynchonellids were common in shallow habitats during the Rhaetian. Short-looped terebratulids were abundant in shallow habitats above NSWB both in the Rhaetian and Hettangian. This distribution is in accord with the observations from the TCR where *Lobothyris* dominated in shallow habitats during the Hettangian (Dulai, 2003). Dulai (2003) suggested that the change in depth distribution of short-looped terebratulids predicted by Sandy took place after the Hettangian in the western Tethys. Alternatively, the shift of short-looped terebratulids towards deeper habitats might be related to their differential environmental preference at family level (Sandy, 1995). Smooth and sulcate terebratulids belonging to the family Nucleatidae (e.g., *Linguithyris*, *Securithyris* and *Phymatothyris*, Manceñido, 1993) were typical of carbonate-starved Tethyan habitats and commonly occurred in deep habitats below MSWB in the Early Jurassic (Vörös, 1986, 2005).

Although the depth distribution of short-looped terebratulids and rhynchonellids did not change after the end-Triassic mass extinction in the NCA, long-looped terebratulids and spiriferinids seem to show the predicted shift towards deeper habitats after the end-Triassic mass extinction (Fig. 17). After the extinction of Athyrididina,

both suborders were relatively common in habitats below MSWB during the Hettangian, in contrast to their higher abundance in shallower habitats during the Rhaetian. However, the missing data about the Middle and Late Hettangian shallow habitats are needed for confirmation of their distributional shift.

7. Conclusions

The T/J boundary extinction–survival interval in the Northern Calcareous Alps (NCA) is marked by a boundary marl at the base of the Kendlbach Formation that is several metres thick and shows distinct geochemical, sedimentologic and palynofacies features. The interval contains rare rhynchonellid brachiopods. A relatively rapid recovery during late Early and Middle Hettangian is indicated by the presence of several brachiopod communities that differ in their depth and substrate preferences and by relatively high between-habitat (beta) diversity.

The significant differences in composition of Rhaetian and Hettangian communities on superfamily level demonstrate that the end-Triassic mass extinction had substantial ecologic effects on brachiopods. With the exception of zeillerioids and some rhynchonellid superfamilies, dominant brachiopods of the Rhaetian communities belonged to superfamilies that went extinct on the T/J boundary. In contrast, the dominants of the Hettangian communities belonged to spiriferinoids, pennospiriferinoids, terebratuloids and rhynchotetradoids that were subordinate in Rhaetian communities. The end-Triassic extinction thus re-directed and constrained the composition of Jurassic brachiopod communities. This study thus highlights the role of large-scale physical perturbations in mediating biotic replacements. Measuring turnover in terms of community-level abundance of taxa during mass extinctions should be highly relevant because taxonomic extinction rate metrics miss the information about their community-level abundance.

Although some brachiopod communities occur in the lower part of the Kössen Formation only, they are present in other regions adjacent to the Kössen Basin up to the Late Rhaetian. This implies relatively high persistence of brachiopod communities during the Rhaetian. Analyses of similarities demonstrate that the compositional turnover of brachiopod communities on the genus level at the T/J boundary ($R=0.94$) is substantially higher than the turnovers within the Rhaetian ($R=0.28–0.57$) and within the Hettangian ($R=0.28–0.53$). This pattern indicates that a rather abrupt turnover took place between the uppermost parts of the Kössen Formation and the lower parts of the Kendlbach Formation.

Time-environment diagrams indicate that the environmental distribution of brachiopods on suborder/order level did not substantially change after the T/J boundary in the NCA. Although long-looped terebratulids and spiriferinids showed the increase in their depth range, short-looped terebratulids were still common in shallow habitats and rhynchonellids were generalists both during the Rhaetian and the Hettangian.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2006.06.028](https://doi.org/10.1016/j.palaeo.2006.06.028).

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