

Trace-fossil assemblages with a new ichnogenus in “spotted” (Fleckenmergel–Fleckenkalk) deposits: a signature of oxygen-limited benthic communities

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Abstract: Highly-bioturbated “spotted” limestones and marls (Fleckenmergel–Fleckenkalk facies) of the Early Jurassic, which were deposited in broad and recurrent deep-shelf habitats of the Northern Tethys, are characterized by rare benthic carbonate-producing macroinvertebrates. To address this paradox, we analyse trace-fossil assemblages in a ~85 m-thick succession of Pliensbachian spotted deposits (Zliechov Basin, Western Carpathians). They are dominated by infaunal and semi-infaunal deposit-feeders, with 9 ichnogenera and pyritized tubes of the semi-infaunal foraminifer *Bathysiphon*, being dominated by *Chondrites*, *Lamellaechinus* (new ichnogenus), and *Teichichnus*. *Lamellaechinus*, represented by a horizontal basal cylindrical burrow and an upper row of stacked convex-up gutters, was produced by a mobile deposit-feeder inhabiting shallow tiers because it is crossed by most other trace fossils. We show that the spotty appearance of the deposits is generated by a mixture of (1) dark, organic-rich shallow- and deep-tier traces (TOC = 0.16–0.36), and (2) light grey, organic-poor mottled or structureless sediment (TOC = 0.09–0.22). The higher TOC in shallow-tier burrows of *Lamellaechinus* demonstrates that uppermost sediment layers were affected by poor redox cycling. Such conditions imply a limited mixed-layer depth and inefficient nutrient recycling conditioned by hypoxic bottom-waters, allowed by poor circulation and high sedimentation rates in depocenters of the Zliechov Basin. Hypoxic conditions are further supported by (1) dominance of trace-fossils produced by infaunal deposit feeders, (2) high abundance of hypoxia-tolerant agglutinated foraminifer *Bathysiphon*, and (3) high abundance of *Chondrites* with ~0.5 mm-sized branches. Oxygen-deficient bottom-conditions can thus simultaneously explain the rarity of benthic carbonate-producing macroinvertebrates and high standing abundance of tolerant soft-shell and agglutinated organisms in spotted deposits.

Key words: Jurassic, Western Carpathians, community paleoecology, dysoxia, bioturbation, ichnofacies, trace-fossil assemblage.

Introduction

Distinctly bioturbated mudstones (the so-called Fleckenmergel or Fleckenkalk facies or “spotted” marls and limestones) that originated in deep-shelf environments (below the storm wave base) were widely distributed during the Early and Middle Jurassic in the Northern Tethys, occurring in the Betic Cordillera, Eastern Alps, Central Western Carpathians, Pieniny Klippen Belt, Dinaric Alps, Mecsek, Apuseni and Timor (Mišík 1959, 1964; Jacobshagen 1965; Tyszka 1994a, 2001; Wieczorek 1995; Raucsik & Varga 2008). They were deposited in intrashelf basins generated by synsedimentary tectonic collapse of the Triassic carbonate platforms and ramps. This collapse enhanced topographic complexity and differentiated the Northern Tethys into tectonic blocks with footwall and hangingwall successions, forming pelagic carbonate platforms and plateaus, barriers, and restricted basins (Bernoulli & Jenkyns 1974; Eberli 1988; Häusler et al. 1993; Böhm et al. 1995; Koša 1998; Jach 2002, 2005; Plašenka 2003; Santantonio & Carminati 2011). The Lower Jurassic spotted deposits of the Northern Tethys can alternate with crinoidal calcarenites and spiculitic limestones, but the spotted deposits themselves are relatively uniform in sedimentological and taphonomic attributes, forming meters to hundreds of meters

thick, well-bedded successions, with abundant trace fossils and sponge spicules (Mišík 1964; Mišík & Rakús 1964; Jach 2002).

The spotted deposits are marked by conspicuous and dense mottling, ranging from relatively mixed fabric with indistinct dark grey spots up to well-demarcated dark grey trace fossils that are embedded in a light grey micritic matrix, implying high standing density of burrowers. Remarkably, such a high abundance of soft-bodied trace-fossil producers contrasts with a low abundance of benthic carbonate macroinvertebrates in the spotted deposits. Skeletal packing density of infaunal and epifaunal macrobenthic skeletal invertebrates (e.g. bivalves, echinoderms, or brachiopods) is mostly very low (operationally, no or very few skeletal remains encountered along 5 m-long bed transects), implying the presence of conditions that were limiting calcimass production by macroinvertebrates. Beds with relatively frequent bivalves, echinoderms, or brachiopods occur but are rather scarce at outcrop and formation scales (Gaździcki et al. 1979; Sulser & Furrer 2008) and skeletal-rich deposits are absent in the spotted deposits. However, this paradox and the causes of the paleocommunity structure that characterizes spotted deposits are poorly explored (Wieczorek 1995; Uchman & Myczyński 2006), even when this type of habitat was highly widespread

and recurrent in environments of the Tethys during the Early Jurassic. Benthic communities preserved in the Middle Jurassic spotted facies imply significant oxygen-limitation (Tyszka 1994a,b), and we assess whether oxygen-limiting conditions also account for the structure of macrobenthic communities in the Lower Jurassic spotted deposits in the Western Carpathians. Although multiple environmental factors such as salinity, sedimentation or food supply can limit abundance and productivity of macrobenthic carbonate producers, hypoxia can be one of the most important controls determining the functioning of benthic ecosystems (e.g. Barras & Twitchett 2007; Pruss et al. 2010; van de Schootbrugge et al. 2013) and influencing whether sediments are in fact fossiliferous or barren (Peters 2007).

Analyses of trace fossil assemblages can add much detail to paleoenvironmental analyses and can capture gradients in bottom oxygenation that are not detected by traditional paleobiological, taphonomic, or sedimentologic criteria (Savrda & Bottjer 1986, 1991; Monaco 1995; Bromley 1996; Taylor et al. 2003; Rajchel & Uchman 2012). Although diverse geochemical approaches can detect redox conditions in the sediment (Zaton et al. 2009), ichnofacies analyses allow us to identify the location of redox changes in the sediment column because infaunal organisms differ in their depth penetration. Here, to test whether environmental variation during the deposition of the spotted facies can be unmasked by trace fossil assemblages, we (1) describe a new and highly diagnostic ichnospecies and interpret the behaviour of its producer, (2) analyse temporal changes in the composition of trace-fossil assemblages from the Western Carpathians (Zliechov Basin), and (3) evaluate whether the trace fossil assemblages can be segregated into distinct assemblage groups and whether they can shed light on the structure of Early Jurassic communities preserved in the spotted deposits. We focus on the Pliensbachian spotted deposits exposed in the Skladaná Skala section in northern parts of the Veľká Fatra Mountains (Zliechov Basin, Central Western Carpathians).

Paleogeography and stratigraphy of Lower Jurassic bioturbated limestones and marls in the Western Carpathians

The Central Western Carpathians were located on the northern passive margin of the Tethys during the Early Jurassic, approximately at 25–30° N in the tropical climatic belt (Thierry 2000; Jach 2005) (Fig. 1). Spotted limestones and marls of the Sinemurian-Aalenian age in the Western Carpathians were previously assigned to the “Fleckenmergel” and “Fleckenkalk” facies or to the Allgäu Formation (Rakús 1963, 1964; Aubrecht et al. 2002; Gradzínski et al. 2004; Schlögl et al. 2004). Gaždzicki et al. (1979) introduced the Janovky Formation as a lithostratigraphic unit that encompasses the Sinemurian-Aalenian spotted limestones and marls in the Western Carpathians, on the basis of the Janovky section at Mt Havran (Mišk 1959) in the Belanské Tatry Mountains. Lefeld et al. (1985) assigned the bioturbated marlstones and limestones with layers of spiculitic and crinoidal limestones of the same age and in the same region to the Sołtysia

Marlstone Formation. However, even when spatial and temporal variation in the proportion of calcium carbonate, in the contribution of spiculitic and crinoidal facies, and in the thickness and age of the spotted facies is relatively high (Mišk & Rakús 1964; Lefeld et al. 1985), these two formation names seem to capture the same lithostratigraphic unit. We thus refer to the Janovky Formation as the formation with the spotted limestone and marly deposits in the Western Carpathians. This formation is underlain by the mixed carbonate-siliciclastic Kopienec Formation (Hettangian-Lower Sinemurian) or sandstone-dominated Medodoly Formation (Lower Sinemurian) at locations with the maximum stratigraphic range that spans the Upper Sinemurian and Aalenian. However, the actual stratigraphic range of this formation is frequently smaller owing to complex horizontal and stratigraphic relations with other formations. It can be horizontally replaced by crinoidal limestones, spiculitic limestones, or nodular limestones of the Adnet Formation (Mišk & Rakús 1964; Jach 2002, 2005). In the upper part, it can be replaced by spiculitic limestones (Świńska Turnia Member of the Huciska Formation, Western Tatras Mountains), nodular limestones (Adnet Formation, Veľká Fatra Mountains), crinoidal limestones (Lefeld et al. 1985), or by radiolarian limestones of the Sokolica or Ždiar Formations (Lefeld et al. 1985; Polák & Ondrejčíková 1993; Polák et al. 1998). Similar stratigraphic replacements characterize the Allgäu Formation in the Eastern Alps (Böhm 2003).

Geographic and geological setting

Trace fossils of the Janovky Formation were primarily studied in the Skladaná Skala section in the northernmost parts of the Veľká Fatra Mountains (Fatric Unit, Krížna Nappe, Central Western Carpathians). A new ichnogenus found in this section was also sampled at three other sections, including Furkaska, Kamenná Poruba (both belong to the Fatric Unit), and Trlenská Valley (Tatric Unit) (Fig. 1).

(1) The Skladaná Skala quarry is situated in the northernmost part of the Veľká Fatra Mountains (49°7' 15.66" N; 19°13' 27.98" E, Fig. 2). Rakús (1963, 1984) showed that this section exposes about 400 meters of the Janovky Formation and consists of a succession of moderately- to highly-bioturbated marls, marlstones, and mudstones, with intercalations of infrequent crinoidal calcarenites and spongiolitic limestones. The lower, about 70 m-thick interval is represented by marly limestones with thin marly interlayers and contains the Upper Sinemurian ammonites *Echioceras raricostatum* and *Oxynoticeras oxynotum*. The middle, about 225 m-thick interval is formed by alternation of equally-thick marly limestones and marls, with some spiculitic and sandy limestones, and ammonites of Pliensbachian age (*Amaltheus stokesi* and *Pleuroceras spinatum*). The uppermost, about 105 m-thick interval (Lower-Middle Toarcian) is dominated by marls. This interval contains the ammonites *Dactylioceras cf. semicellatum*, *D. atheticum*, *Harpoceras ex gr. falciferum*, and *Hildoceras ex gr. bifrons*. Rare remains of rhynchonelliformean brachiopods are represented by calcitic shells, bivalves and ammonites are preserved as moulds. Here, we

analyse an ~85 m-thick portion of the succession that predominantly captures the Upper Pliensbachian, with a few samples also capturing the lowermost Toarcian.

(2) Furkaska is located in the Western Tatra Mts in a creek ravine on the western side of the Furkaska peak ($49^{\circ}15' 33.54''$ N; $19^{\circ}47' 6.02''$ E). The Janovky Formation

in this section is represented by the basal, 20 m-thick spotted marls, and the upper, about 60 m-thick spotted marly limestones that alternate with marls (Gaździcki et al. 1979).

(3) Trlenská Valley ($49^{\circ}2' 26.37''$ N; $19^{\circ}15' 1.37''$ E) is located in the northern parts of the Veľká Fatra Mts. Poorly exposed natural outcrops consist of marly limestones of the

Janovky Formation in the strata overlying the crinoidal limestones of the Trlenská Formation (Mišík & Rakús 1964).

(4) Kamenná Poruba is situated in Malá Fatra Mts. Samples with marly limestones of the Janovky Formation were collected in a poorly exposed ravine at Porubský potok Creek ($49^{\circ}4' 2.35''$ N; $18^{\circ}41' 29.99''$ E).

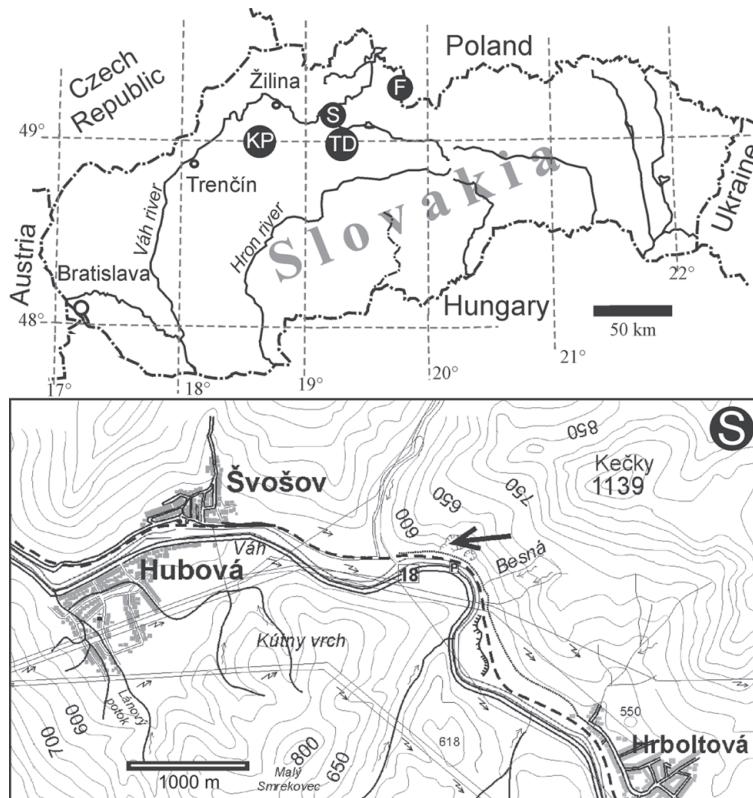


Fig. 1. Locality map. F — Furkaska, S — Skladaná Skala Quarry, TD — Trlenská Valley, KP — Kamenná Poruba. The lower plot S displays the location of Skladaná Skala section (black arrow). The dashed line refers to a railway line, bolts of lightning represent electricity networks.

Methods

Trace fossils were documented on photographs of cross-sections of ~200 polished slabs and in bed-by-bed observations in the field (Fig. 3). The new ichnogenus and ichnospecies *Lamellaeichnus imbricatus* described in the systematic part is represented by 363 specimens from Skladaná Skala, two specimens from the Trlenská Valley, 24 specimens from Kamenná Poruba, and 13 specimens from Furkaska. The morphology of trace fossils was studied in cross- and in longitudinal sections. Longitudinal sections were cut either vertically or horizontally (relative to burrow orientation). Two slabs were serially cross-sectioned for three-dimensional morphological study of *Lamellaeichnus* (Fig. 5). Distances between sections ranged between 0.2 to 1 mm. The trace fossil fill and the composition of the surrounding matrix were detected in thin-sections.

Morphological study and statistical analyses of six morphological parameters (Fig. 4) were

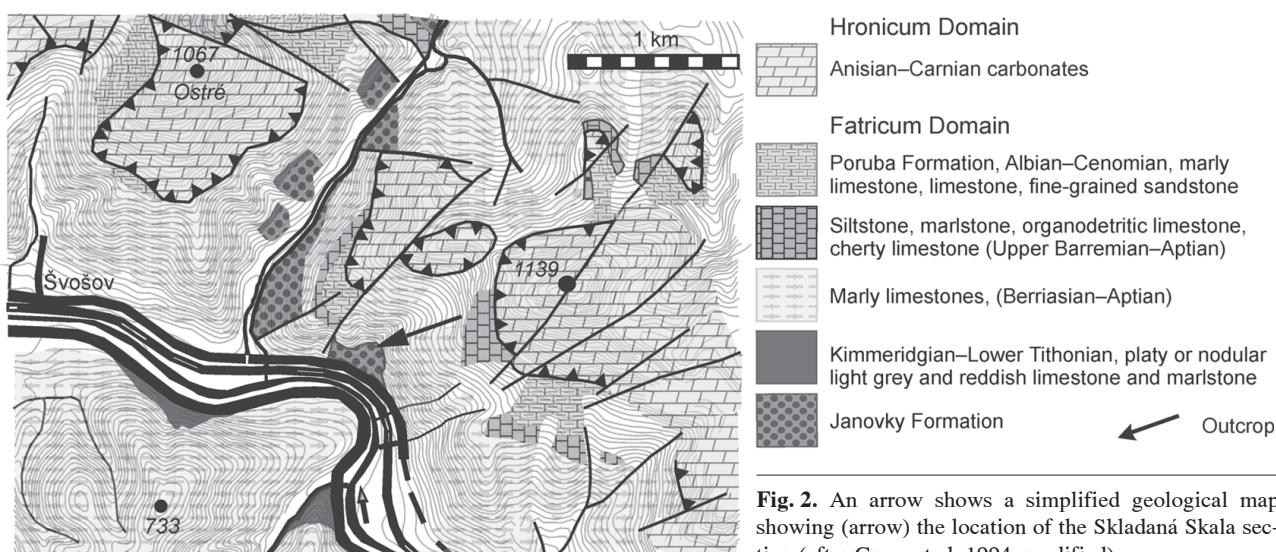


Fig. 2. An arrow shows a simplified geological map showing (arrow) the location of the Skladaná Skala section (after Gross et al. 1994, modified).

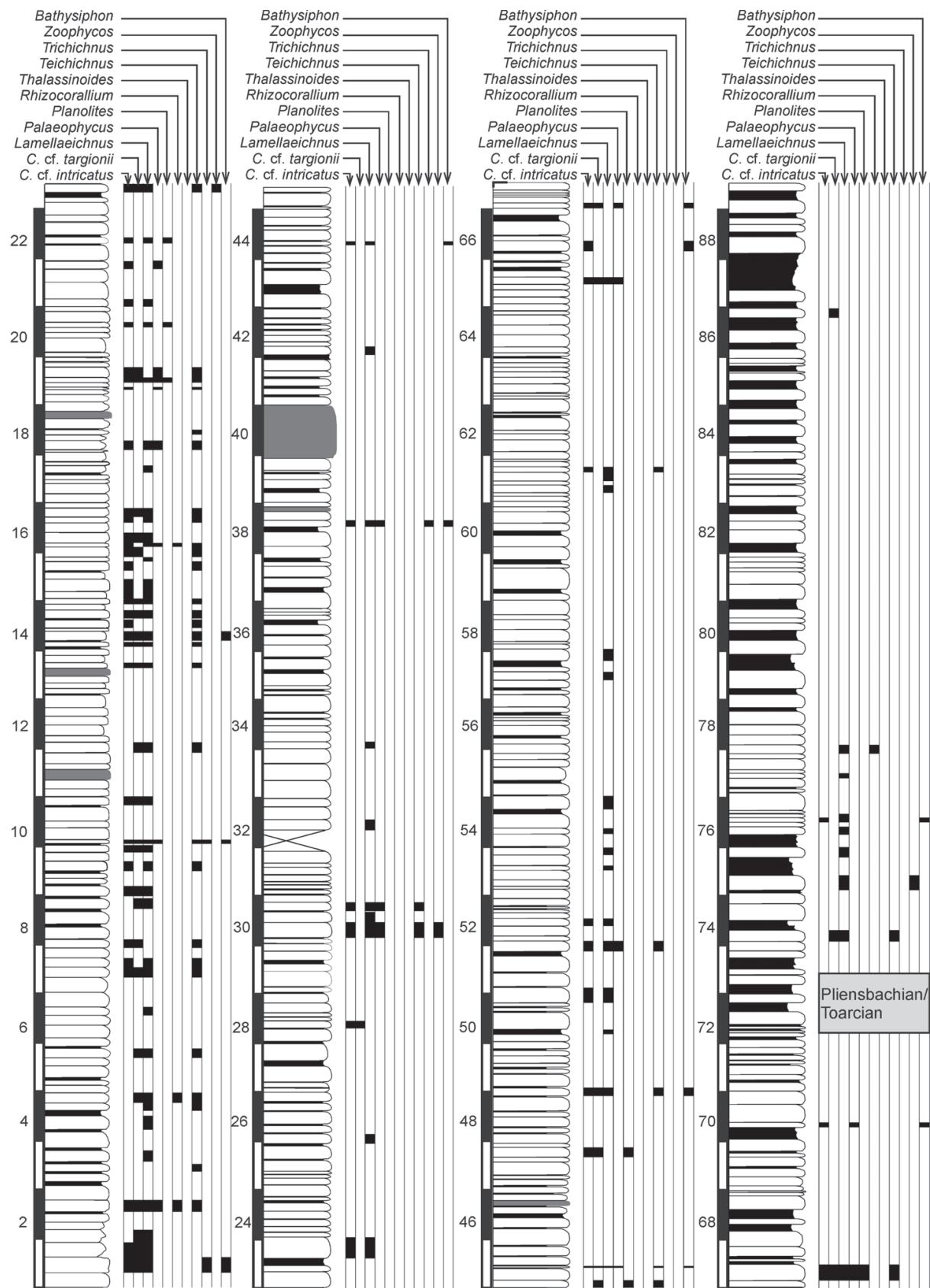


Fig. 3. The stratigraphic distribution of trace fossils and *Bathysiphon* in the Skladaná Skala section. White beds represent marly limestones, grey beds represent cherty spiculites, and black beds represent marls. The location of the Pliensbachian/Toarcian boundary is approximate and is placed at the boundary between the carbonate-rich and the marl-rich interval on the basis of ammonites (Rakús 1984). C — Chondrites.

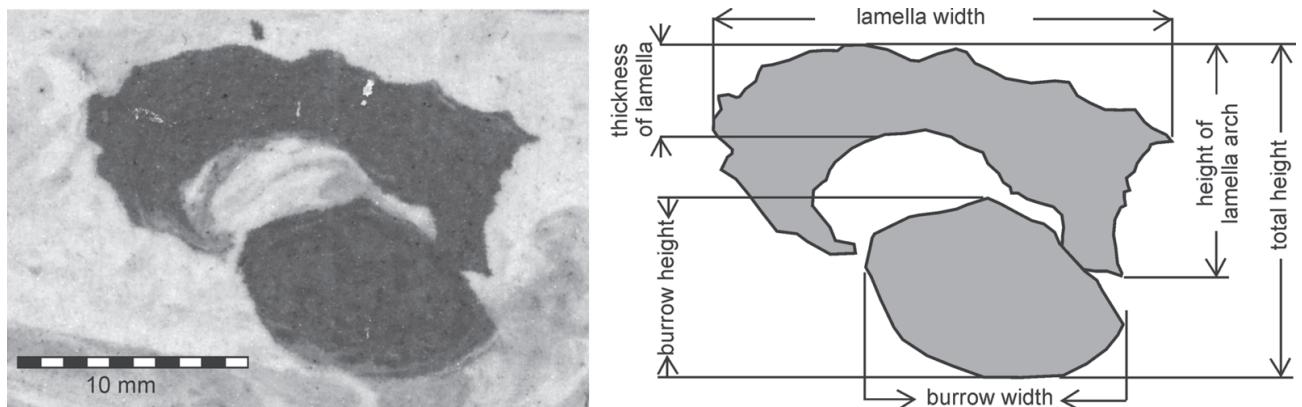


Fig. 4. Six morphometric parameters of *Lamellaechinus* measured in a cross-sectional view. Cross-sections are perpendicular to the bedding plane (the trace fossil has predominantly horizontal orientation). The asymmetry of the cross-section can be generated either by compaction or by inaccurate orientation of the sample during the sectioning. The cross-section shown in this figure comes from the Furkaska section.

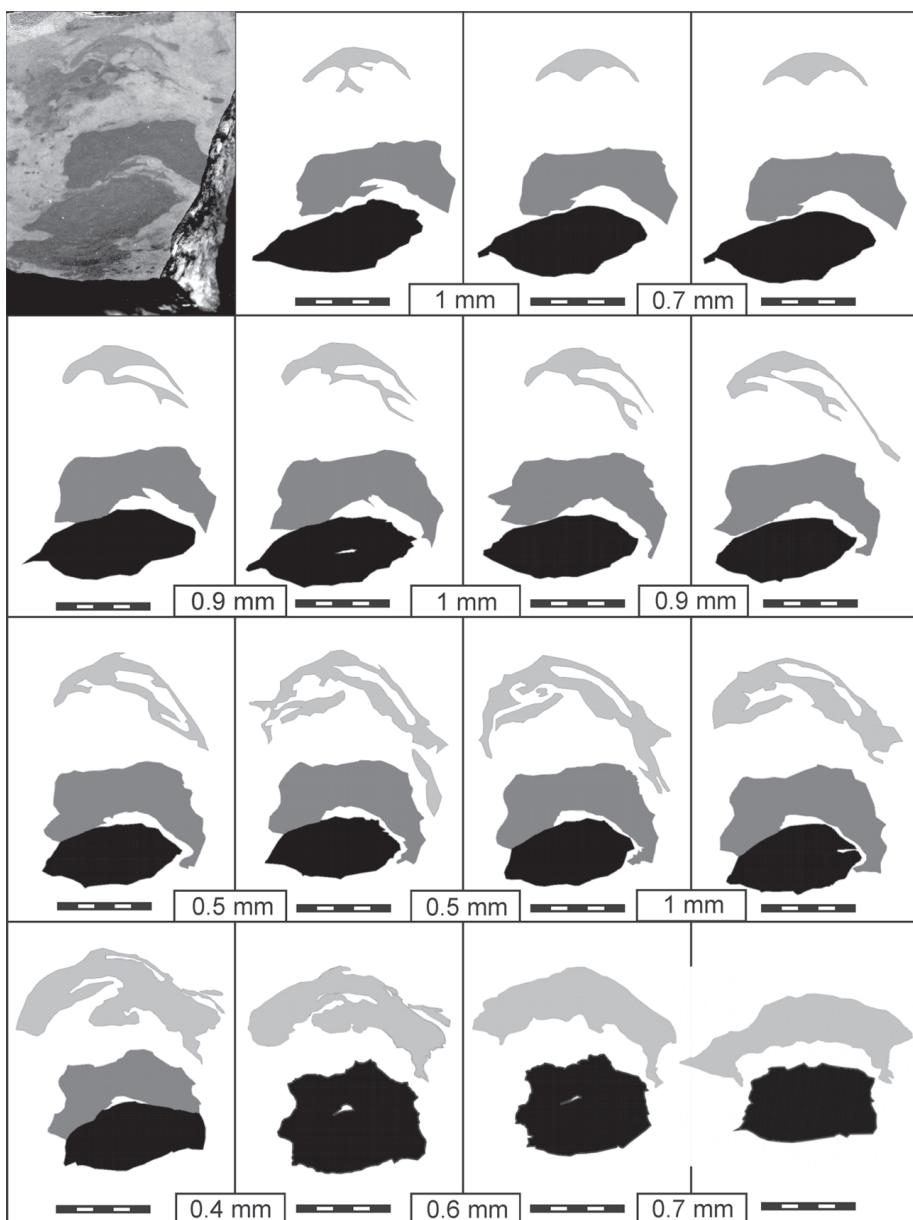


Fig. 5. Serial sections show how the lamella merges with the basal burrow. The lamellae and basal burrows have the same colour, but they are coloured differently here for a better visualization. Each identical part is coloured by the same tone: **light grey** — uppermost lamella, **dark grey tone** — lower lamella, and **black** — basal burrow. Lamellae are widening downward. The lamella situated closest to the basal burrow (dark grey) is successively merging with the burrow. Burrow fill has mostly uniform dark colour and merged lamellae are not distinguishable within the basal burrow. Distances between cross-sections are placed at the bottom. Scale bar: 5 mm. The specimen is from the Skladaná Skala section.

performed on 103 cross-sectioned specimens of *Lamellaeichnus* from Skladaná Skala (1 — lamella width, 2 — total height, 3 — burrow width, 4 — burrow height, 5 — thickness of lamella, 6 — height of lamella arch). Although the morphology of lamellae and basal burrow are affected to some degree by compaction, the parameters were measured on cross-sections that were constructed perpendicularly relative to the burrow orientation. We analysed size-frequency distributions of these parameters, and tested whether the cross-sectional shape of the new trace fossil changes isometrically or allometrically with increasing size, using reduced major axis (RMA) regressions.

The cluster analysis and non-metric multidimensional scaling (NMDS) based on presence-absence data of 9 ichnogenera and the agglutinated foraminifer *Bathysiphon* in 55

beds were performed to detect variation in trace-fossil assemblage composition. We used Sorenson dissimilarity as a basis for quantifying between-bed relationships, and weighted average linkage method to generate clusters. We used Mantel test to evaluate whether there are any temporal changes in the composition of trace-fossil assemblages.

The holotype (numbered Z36999a) and several tens of additional specimens of *Lamellaeichnus imbricatus* from Skladaná Skala (numbered samples Z36999b,c; Z36995, Z36996, Z36997, Z36998, Z37000), Trlenská Valley (Z37750, Z37751), Kamenná Poruba (Z37748), and Furkaska (Z37749) are deposited in the Slovak National Museum in Bratislava. Whole polished slabs (196 samples) were also scanned, numbered (No. Z37752) and deposited in the Slovak National Museum.

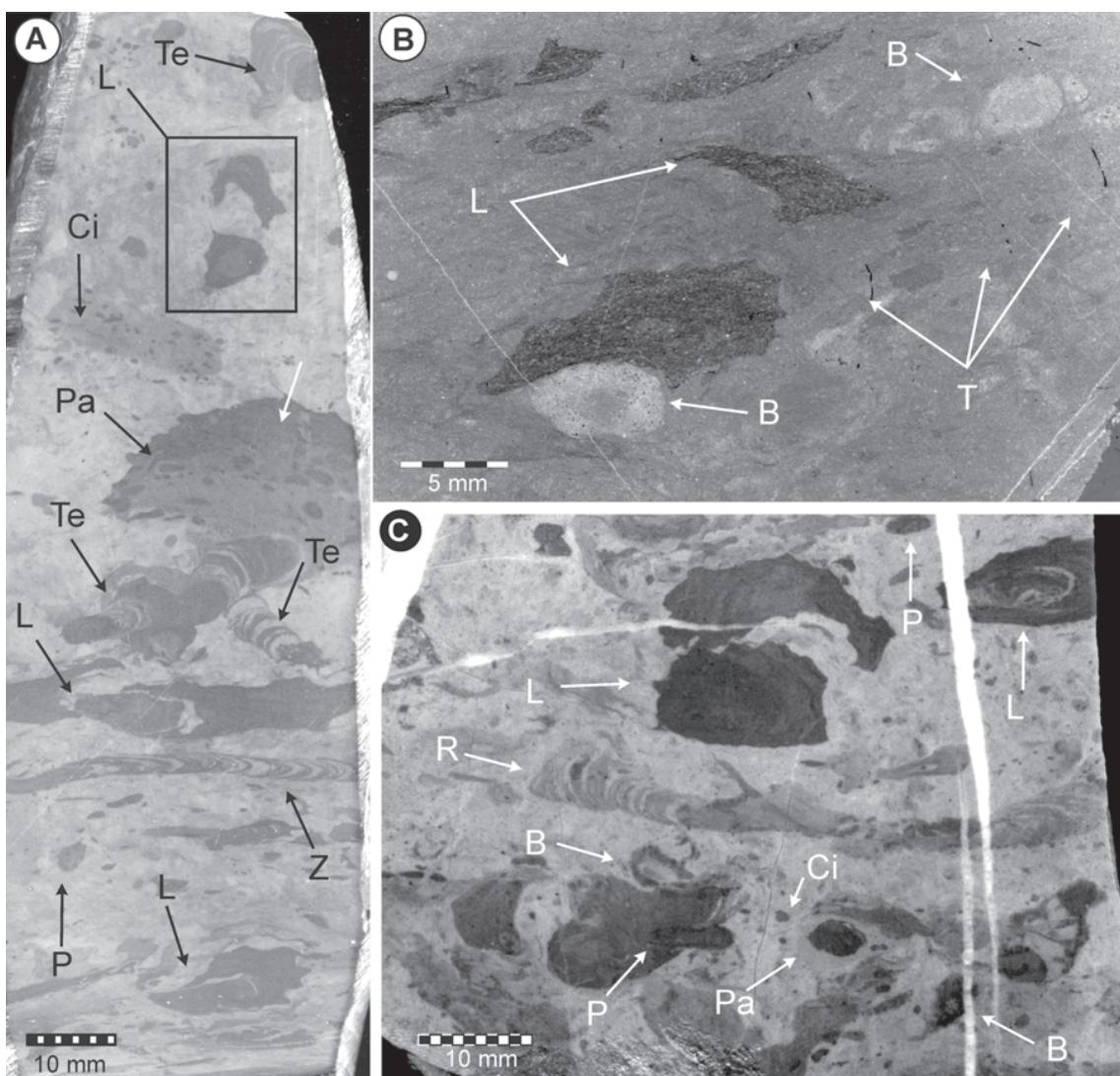


Fig. 6. A — *Lamellaeichnus* (L) vertical sections, a specimen in the inset was designated as holotype (numbered Z36999a). *Chondrites* cf. *intricatus* (Ci) and *Palaeophycus* (Pa) occupied burrows of older generation (probably *Thalassinoides* — white arrow). *Teichichnus* (Te), *Zoophycos* (Z) are formed by crescent-shaped spreite structure. *Planolites* (P) is represented by unwalled, simple, dark burrows. B — Thin-section (cut perpendicularly to bedding) view shows a dark bioclastic infill of *Lamellaeichnus* (L), light-coloured walls of *Bathysiphon* tests are silicified, hair-like *Trichichnus* (T) is filled with pyrite. Scale bar is 5 mm. C — Vertical section shows *Lamellaeichnus* (L), *Rhizocorallium* (R), *Bathysiphon* (B), *Chondrites* cf. *intricatus* (Ci) and *Planolites* (P). Skladaná Skala.

Total organic carbon (TOC) was measured in 4 samples of dark grey sediment fills of *Lamellaechinus*, 4 samples of mottled, brownish sediments with relicts of *Lamellaechinus*, and 4 samples of structureless, light grey sediments with a Ströhlein C-MAT 5500 automatic infrared detector. Approximately 0.05 g of sample (pulverized and dried at 110 °C) was burned down in the oxygen atmosphere at the temperature range 50–1000 °C. The CO₂ produced during combustion was detected by the C-MAT 5500 infrared detector and converted to total carbon content. Another split of sample was treated with hot HCl in order to dissolve carbonates. The insoluble residue was analysed to obtain the percentage of TOC.

Systematic ichnology

Lamellaechinus new ichnogenus

Derivation of name: Derived from "lamellae" that correspond to crescent-shaped packets of backfilled sediment and from Greek *ichnos* — trace.

Type ichnospecies: *Lamellaechinus imbricatus*.

Diagnosis: Structure composed of inclined lamellae that protrude at an acute angle from horizontal basal cylinder.

Lamellaechinus imbricatus new ichnospecies
(Figs. 4, 5, 6, 7, 8, 9, 11, 12)

Diagnosis: As for the ichnogenus.

Derivation of name: Derived from "imbrication" — imbricately-arranged lamellae.

Holotype: The holotype (Z36999a) is preserved with two other specimens (Fig. 6A) that were assigned to paratypes (Z36999b,c). They are deposited at the Slovak National Museum in Bratislava.

Comparative material: *Skladaná Skala*: Specimen Z36996 preserved on the bedding plane is also assigned to the paratype material. The polished slab Z36997 with 18 *Lamellaechinus* cross-sections is supplemented by illustrations of 14 sections (Z37752). Sample Z37000 contains seven *Lamellaechinus* cross-sections. The sample with longitudinal horizontal *Lamellaechinus* section corresponds to Z36998 (Fig. 7).

Kamenná Poruba: Three specimens from one sample (Z37748a,b,c).

Furkaska: One sample cut perpendicularly relative to the bedding plane with four specimens of *Lamellaechinus* (Z37749a,b,c).

Trlenská Valley: Two samples with two specimens (Z37750, Z37751).

Additionally, 194 polished slabs with *Lamellaechinus imbricatus* and other trace fossils were photographed and saved in JPG format on the compact disk with a number (Z37752). All material is housed at the Slovak National Museum in Bratislava.

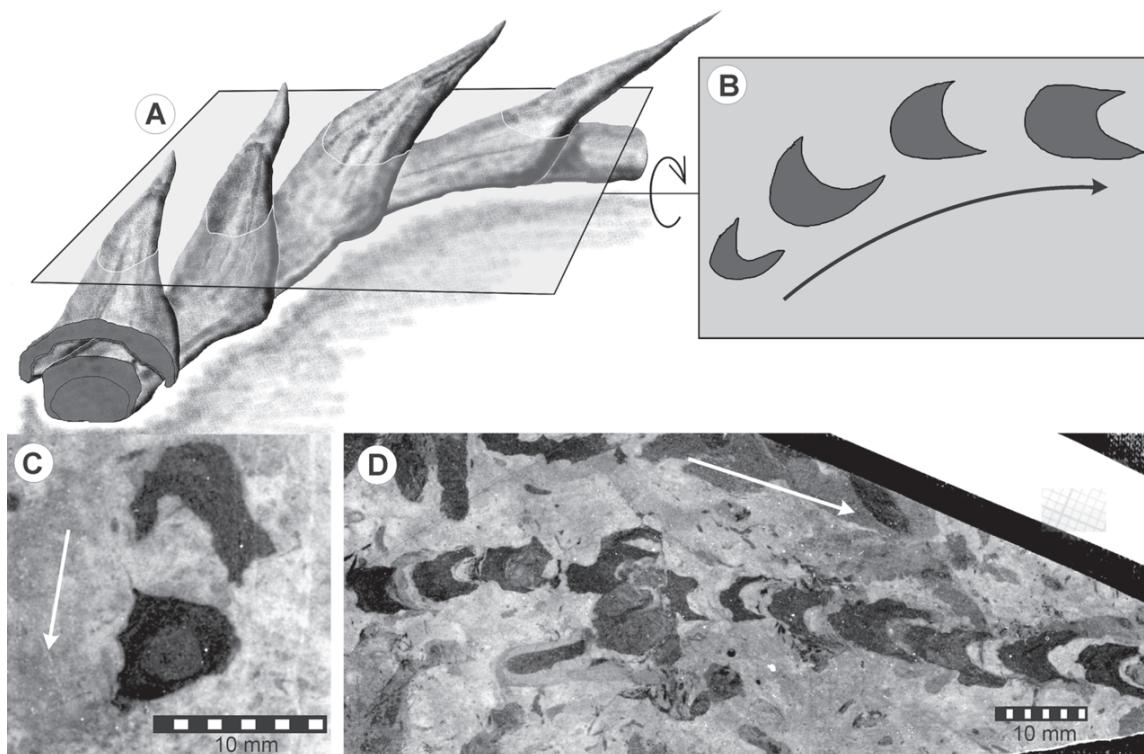


Fig. 7. Three-dimensional reconstruction of *Lamellaechinus* with a cross-section and a horizontal longitudinal section. **A** — Reconstruction of *Lamellaechinus* with a cross-section. **B** — Idealized longitudinal horizontal section above the basal burrow oriented according to Fig. 7A. **C** — The cross-section of the holotype (No. Z36999a), detail of Fig. 6A. A central part of the basal burrow is lighter and differs from peripheral, darker part of fill. **D** — horizontal-section (No. Z36998). Scale bar: 10 mm. The arrows are pointing to expected directions of producer movement. Skladaná Skala.

Type horizon and type locality: Janovky Formation, Skladaná Skala Quarry.

Description: Guttered, wedge-shaped lamellae have convex-up orientation and merge with the basal cylindrical burrow at an acute angle. They are separated from each other by surrounding sediment and gradually taper upward so that they produce sharp, thin-bladed or leaf-like structures. In cross-sections, typically one lamella, or sporadically two or three lamellae, appear as distinct convex-up crescents located above the basal tunnel-shaped burrow. These crescents are typically wider at their base relative to the diameter of the basal burrow. Circular or lenticular cross-sections of the basal burrow locally consist of asymmetric concentric layers, with their centroid being asymmetrically located at the bottom of the burrow. These layers represent basal extensions of lamellae that are stacked in the basal burrow. In the longitudinal horizontal sections located above the basal burrow, lamellae form a row of discrete, crescent-shaped structures. In the longitudinal vertical sections, these lamellae are arranged in a row at an acute angle, and they merge with the basal cylinder

gradually. Secondary successive branching occurs, but true branching is absent.

Cross-sectional shapes

The most frequent and the most diagnostic attribute of this trace fossil is visible in cross-sections: dark-coloured, convex-up crescent sections of lamellae are located above an elliptical or rounded section of the basal burrow with the same sediment colour. In sporadic cases, one cross-section captures two or three crescent-shaped lamellae (Fig. 5). Such cross-sections of *L. imbricatus* are partly similar to *Heimdallia chatwini* of Fillion & Pickerill (1990: plate 8, fig. 8, p. 99). In the longitudinal horizontal sections located just above the main cylindrical burrow, lamellae form discrete crescent-shaped structures (Figs. 7, 8). In the longitudinal vertical sections, lamellae extend upward from a horizontal tunnel at an acute angle and gradually taper upward towards a pointed and thin, blade-like protrusion. The basal burrow is represented by a horizontal, elongated tunnel with rounded or elliptic

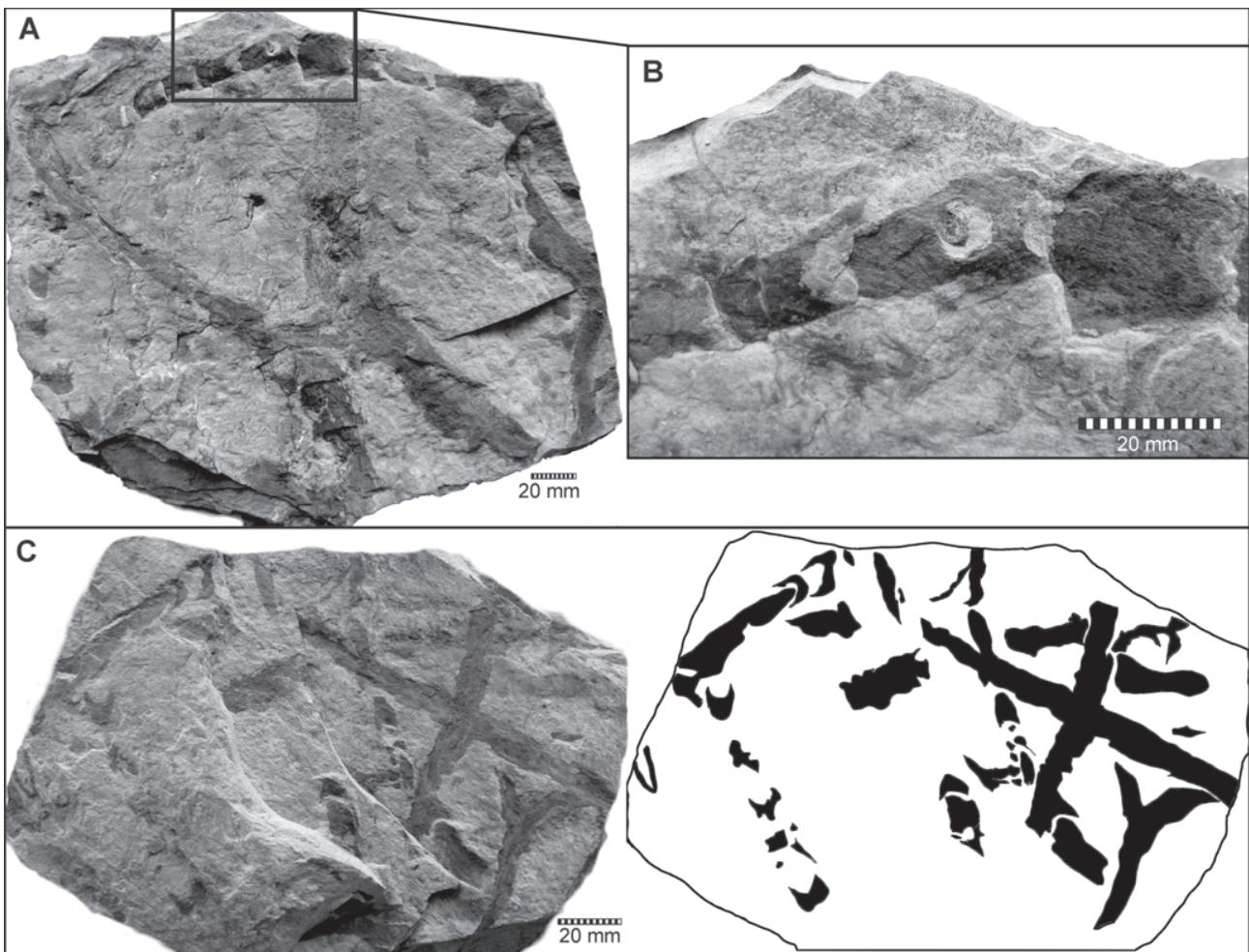


Fig. 8. Horizontal sections of *Lamellaechinus*. **A** — *Lamellaechinus* with well-preserved lamellae in a longitudinal section on a weathered bedding plane. **B** — The detail of the best preserved lamellae. Preservation is considerably marked by compaction. **C** — Crescent shapes arranged in rows are similar to *Taenidium* and horizontal sections that cross basal burrows of *Lamellaechinus* are similar to *Planolites* or *Thalassinoides*. Skladaná Skala.

cross-section, 2–19 mm in horizontal diameter, and 1–19 mm in vertical diameter. The width of lamellae attains 4–28 mm in cross-sections. The lamellae close to the point of merging with the basal cylindrical tunnel attain the largest width and thickness. The height of lamellae in cross-sections is between 2–30 mm. The length of the whole burrow likely exceeds several tens of centimeters.

Burrow orientation

The trace fossil is predominantly horizontal, slightly waved horizontally and vertically.

Branching

Secondary successive branching (Bromley 1996) was observed in horizontally-sectioned specimens (Fig. 8B).

The trace fossil filling

The fill of the lower cylindrical burrow and the wedge-shaped lamellae is formed by identical, fine-grained sedimentary material, which is much darker relative to the light grey colour of the surrounding matrix, although the sediment grain size is identical. Sponge spicules in the filling are evidently rearranged by bioturbation. The boundary between matrix and the fill is sharp, although the trace fossil is without a wall. The

fill of the basal burrow can locally display very thin, vertically-stacked basal parts of lamellae (Fig. 9). Boundaries between distinct, convex-up crescent-shaped sections are sporadically visible within the upper part of cylindrical burrows (Fig. 7), and become less visible in their central parts.

Shape and its dependency on size

The height and width of *Lamellaechinus* change isometrically with respect to each other because the allometric coefficients are not significantly different from one (Fig. 10). In other words, the burrow width and burrow height increase at the same rate as lamella width, and total height also increases at the same rate as lamella width. This isometry can imply that the producer also grew isometrically during the ontogeny. Size-frequency distributions are right-skewed (Fig. 10), showing that most burrows have a small diameter of the basal burrow (<6 mm). The total height of some burrows attains 30 mm.

Preservation: Endogenic full reliefs within bioturbated sediments, observed in vertical longitudinal and horizontal cross-sections, are most frequent. Specimens with secondary successive branching are sporadically visible on bedding planes.

Remarks: The lamellae of *Lamellaechinus imbricatus* extend upward and form wedge-shaped structures and coalesce with a tube-shaped burrow at the base. The lower cylindrical burrow can be branched (secondary successive

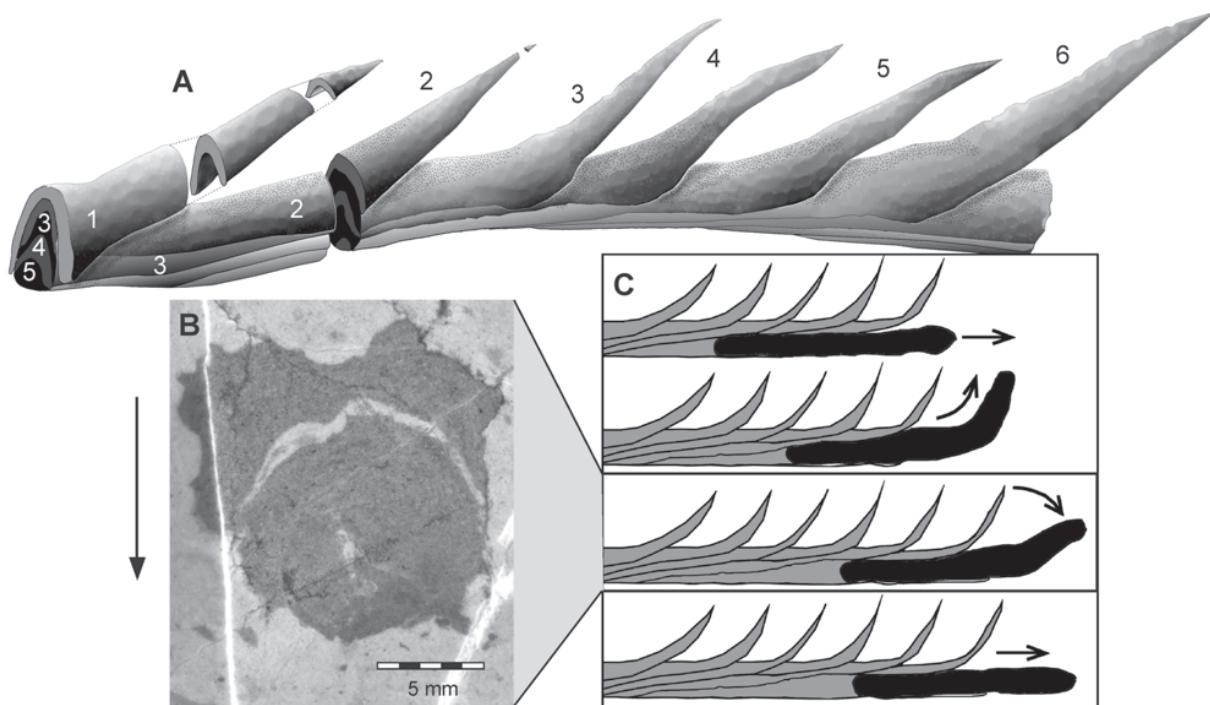


Fig. 9. The sketches illustrate the arrangement of lamellae and their coalescence within the basal burrow of *Lamellaechinus*. A — Lamellae (on the cross-sectional view) are colour-differentiated. Each lamella has one number. B — The most typical *Lamellaechinus* cross-section (Kamenná Poruba locality). An arrow shows downward direction of the trace maker's movement. C — A hypothesized construction of *Lamellaechinus*. Black part represents a hypothetical producer. The grey field shows fodinichnial substrate reworked into the inclined lamellae. Arrows show direction of the producer's movement. The third figure from above illustrates downward movement of anterior part of the producer. The third figure is captured by the cross-section in Fig. 9B.

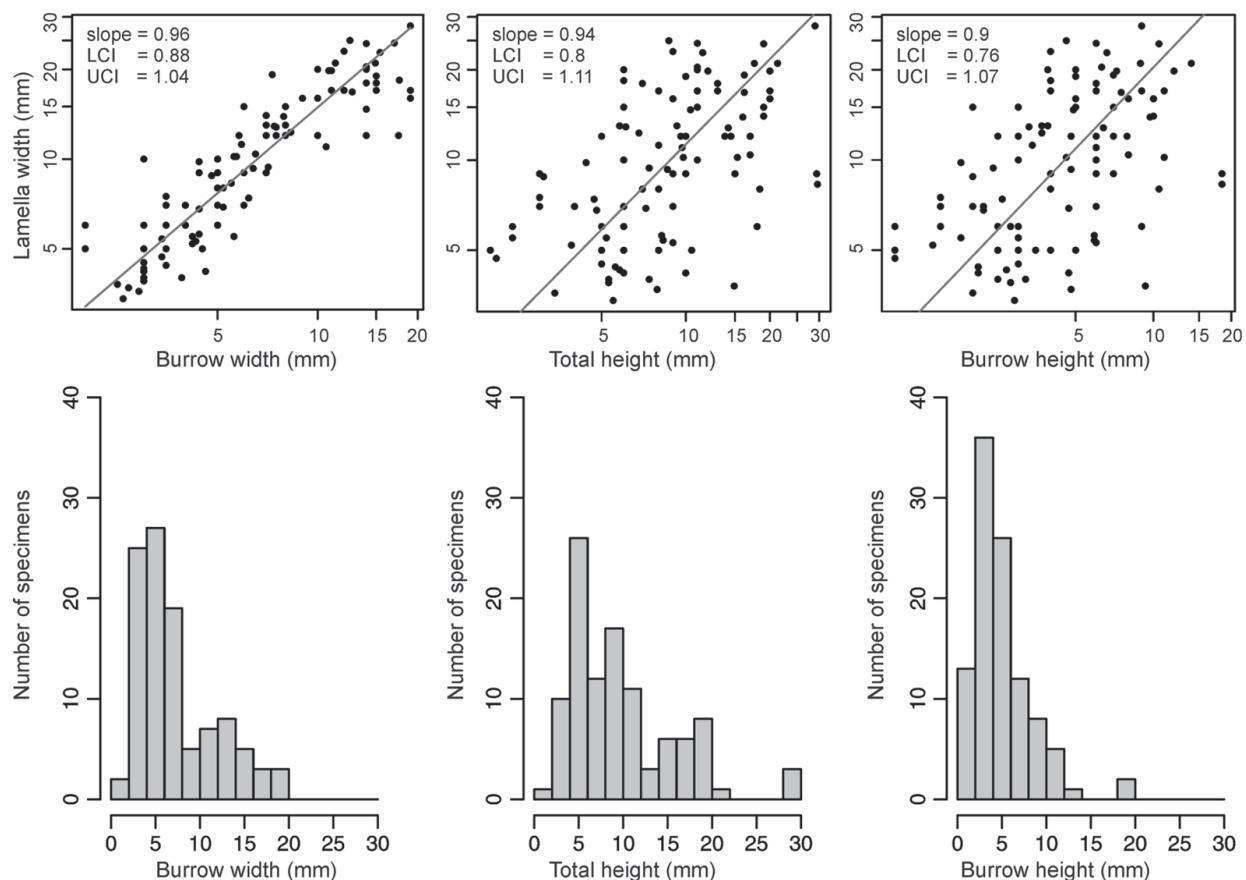


Fig. 10. Bivariate relationships with allometric coefficients for three pairs of morphological dimensions imply that the trace grew isometrically with increasing size (top row). The relations among other dimensions also show isometric growth (not shown). Frequency distributions of three morphological dimensions are right-skewed and show that the total burrow height, including the basal burrow and lamellae, ranges up to 30 mm (bottom row). LCI and UCI correspond to lower and upper 95% confidence intervals.

branching only) and thus can be confused with *Planolites* or *Thalassinoides*. In addition, the parallel crescent sections located above the basal burrow running through the wedge-shaped lamellae can resemble a row of menisci without wall, and these can be confused with *Taenidium*. Two or three concave crescent-shaped lamellae that are sporadically present in cross-sections of *L. imbricatus* (Figs. 5, 11A,B) are similar to a protrusive teichichnid trace fossil (Seilacher 1990, 2007). Although the cross-sections of *Teichichnus* are generally retrusive (Buckman 1996; Seilacher 2007), some minor proportion of teichichnid structures is protrusive. Indeed, *Teichichnus* from Skladaná Skala is predominantly characterized by protrusive cross-sections. Cross-sections of *Teichichnus* from Skladaná Skala display a chain of protrusive meniscate structures terminated by oval basal burrow. Protrusive *Teichichnus* cross-sections thus strongly differ from protrusive *L. imbricatus*, consisting of one to maximally three crescent-shaped sections situated above the basal burrow and separated from each other by the surrounding matrix.

The lamellar structure of *L. imbricatus* can be compared with trace fossils that have a heterogeneous type of backfill such as *Taenidium* and do not possess any wall. The striking feature of *L. imbricatus* is represented by long and asymmetrically prolonged lamellae (menisci in sections) of reworked

sediment. Irregular, deeply asymmetric menisci in the backfill are typical of *Taenidium crassum* (Bromley et al. 1999) and deeply arcuate menisci are typical of *Taenidium cameronensis* (Brady 1947). *Taenidium* Heer, 1877 is defined as an unlined or very thinly lined, unbranched, straight or sinuous cylindrical trace fossil containing a segmented fill articulated by meniscus-shaped partings (D'Alessandro & Bromley 1987). However, all menisci in *Taenidium* are present within the cylindrical burrow, whereas menisci in *L. imbricatus* protrude above the basal burrow.

The morphology of *L. imbricatus* is also comparable to trace fossils that possess vertical or inclined spreite structures, abruptly passing into a horizontal basal burrow. This description complies with the description of trace fossils *Heimdallia* Bradshaw, 1981 and *Dictyodora* Weiss, 1884. Cross-sections of *Heimdallia* (illustrated in Buckman 1996) and *Dictyodora* (illustrated in Benton & Trewin 1980) are characterized by basal burrows with reworked sediment of spreite structure located above them. Spreite structures of these trace fossils differ from the fill of *Lamellaechnus* basal burrows, and spreite concave lamellae are densely packed (Buckman 1996: fig. 2). In contrast, lamellae of *L. imbricatus* are separated by the surrounding matrix and are arranged in sparser rows than those of *Heimdallia*.

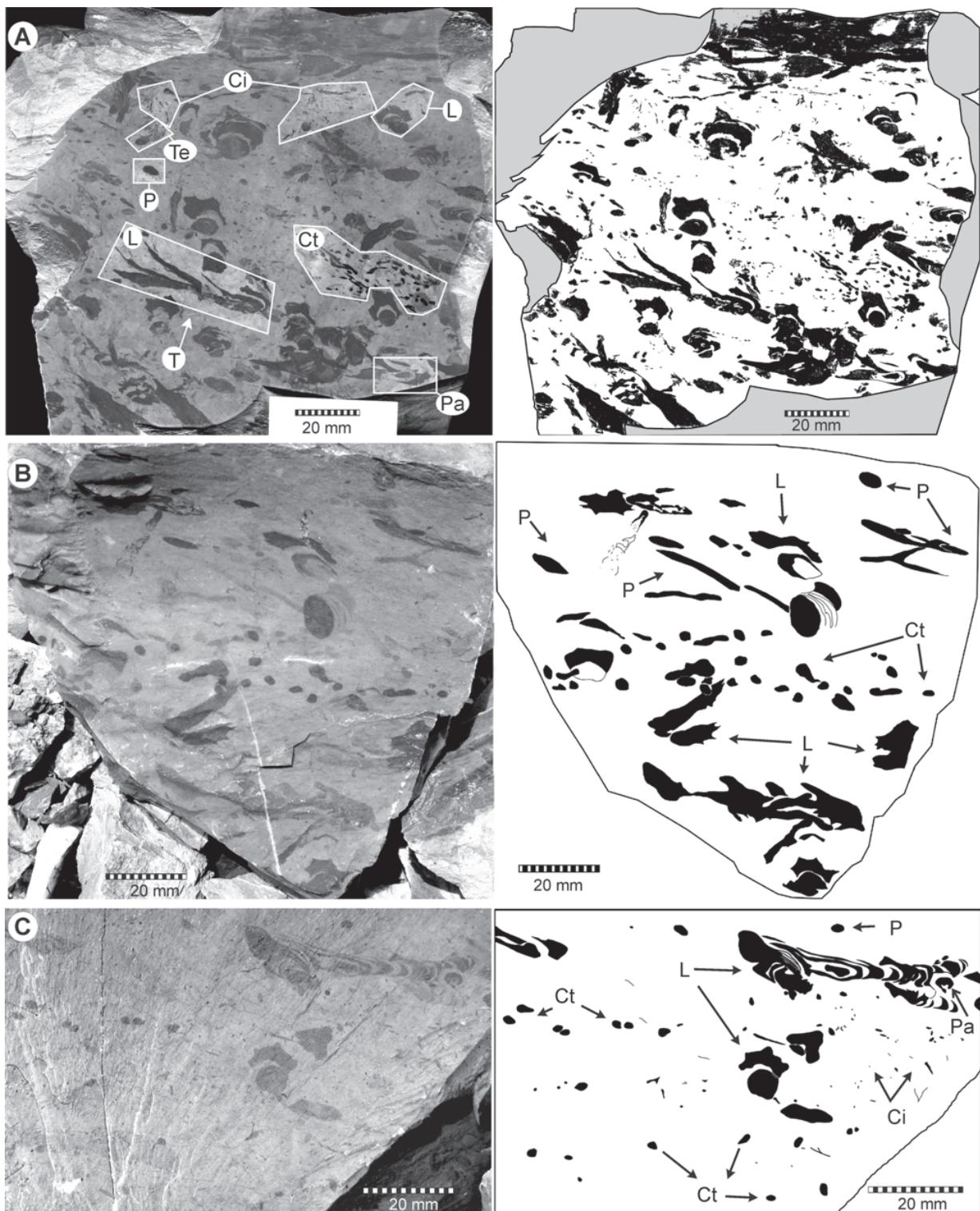


Fig. 11. Sections perpendicular to bedding planes. A — Polished slab (No. Z 36997) with high abundance of *Lamellaeichnus*. The specimen in the top right part of the section (L) has two lamellae. The specimen close to the centre of the section is longitudinally cross-sectioned. *Chondrites cf. intricatus* (Ci), *Chondrites cf. targionii* (Ct), *Teichichnus* (Te), *Palaeophycus* (Pa), *Planolites* (P) and *Trichichnus* (T) were also found. The right sketch highlights the whole trace fossil assemblage. Scale bar: 20 mm. B — Unpolished slab, cut perpendicularly to bedding plane with *Chondrites cf. targionii* (Ct), *Lamellaeichnus* (L) and *Planolites* (P). The lowermost specimen of *Lamellaeichnus* has two lamellae. Skladaná Skala. Scale bar: 20 mm. C — Unpolished slab, cut perpendicularly to the bedding plane with *Chondrites cf. intricatus*, *Chondrites cf. targionii*, *Lamellaeichnus* (L), *Palaeophycus* (Pa), and *Planolites* (P). *Lamellaeichnus* in the upper right corner passes into a structure similar to *Taenidium* (this *Lamellaeichnus* is probably represented by an oblique longitudinal section) which is cut by *Palaeophycus* (Pa). Skladaná Skala.

Ethological and burrow construction model

Meniscate, crescent-shaped spreite structures are generally considered as backfill structures in trace fossils (e.g. Bromley & Asgaard 1979; D'Alessandro & Bromley 1987; Bromley 1996; Seilacher 2007). *Lamellaeichnus* is also clearly formed by backfills because crescent-shaped meniscate structures are stacked in the main basal burrow and the lamellae represent their extensions. The oblique orientation of these crescent-shaped structures (in longitudinal sections, Figs. 7B, 8, 9) implies that the producer was moving in two directions. First, it pushed the processed sediment backwards and upwards, with the anterior part moving slantwise-up and the posterior part remaining in the main burrow. Second, the producer returned back to the original horizontal orientation and progressed forward. *Lamellaeichnus* thus represents a horizontal structure left by a deposit-feeder (fodinichnion), which consists of relatively large extended backfilled packets of reworked sediment. The *Lamellaeichnus* tracemaker was thus imbricating its backfill under an acute angle relative to the direction of its movement. This direction and the mode of burrow construction is comparable to *H. mullaghmori* (Buckman 1996: fig. 8).

Parataenidium consists of similarly inclined and extended packets of reworked sediment arranged within horizontal burrows (*Margaritichnus reptilis* was synonymized to *Parataenidium moniliformis* by Buckman in 2001). These packets of sediment were placed downward close to the abdominal part of the trace maker (Seilacher 2007: plate 17, *Margaritichnus* picture; Buckman 2001: figs. 2A,B, 9B). The tracemaker of *Parataenidium* imbricated backfill under an obtuse angle relative to the direction of its movement. The same mode of the burrow construction also applies to *Parataenidium seymourensis* Uchman & Gaždzicki, 2006. The diagnostic key for detecting the direction of locomotion in *Parataenidium* and *Lamellaeichnus* is thus represented by orientation of crescent-shaped structures formed by reworked sediment.

Chondrites Sternberg, 1833

Diagnosis: Regularly branching tunnel systems consisting of a small number of mastershafts that are connected with the surface and ramify at depth into a dendritic network (Uchman 1999).

Remarks: *Chondrites* is interpreted as a feeding system produced by a deposit-feeder or by a chemosymbiotic organism (Fu 1991; Uchman 1999; Hertweck et al. 2007).

Larger form of *Chondrites* cf. *C. targionii* (Brogniart, 1828) (Figs. 11, 12A)

Diagnosis: Dendritic network with well expressed primary successive branching. The angle of branching is usually acute (Uchman 1998).

Material: Several tens of specimens.

Description: The large form of *Chondrites* with successive branching. Diameter of the shaft varies from 1.5 to 3 mm. Branching was only observed on sections parallel

with bedding planes. Angles of branching range from 40° to 48°. Sections perpendicular to bedding planes display clusters of spots that belong to *Chondrites*.

Larger form of *Chondrites* cf. *recurvus* (Brogniart, 1823) (Fig. 12B)

Diagnosis: Lateral branches arising on one side of a masterbranch only. All lateral branches on each masterbranch are bent in the same direction, or lateral branches on one masterbranch can be bilaterally opposed relative to lateral branches on an opposite masterbranch. One or two orders of branching, rarely a third (Fu 1991).

Material: Two specimens.

Description: Specimens were preserved on a bedding plane. Tunnels are filled with dark grey micritic sediment. Diameter of the shafts varies from 2 to 4 mm. Second-order branches arise from the convex side of bowed first-order branch. Third-order branches are poorly visible. Length of first-order branch is 55 mm. Second-order branches are 16 to 30 mm long. Angles of branching are 31° to 38°.

Smaller form of *Chondrites* cf. *intricatus* (Brogniart, 1823) (Figs. 6A,C, 11)

Diagnosis: Small *Chondrites* consisting of numerous, downward-radiating, mostly straight branches. The angle of branching is usually less than 45°. The branches are less than 1.0 mm wide (mostly about 0.5 mm). The burrow system is more than 20 mm wide (Fu 1991; Uchman 1999).

Material: Several tens of specimens.

Description: Small form of *Chondrites* with downward- to sideward-branching tunnels. Clusters of tiny spots on the vertical sections are situated mostly inside larger burrows (*Thalassinoides*, *Planolites*). Diameters of shafts are smaller than 1 mm (Figs. 6A, 11A, 12C). Angles of branching vary from 24° to 35°. The sediment fill is darker than the surrounding sediment. Aberrant forms situated within *Planolites* and *Thalassinoides* (referred to Bandchondriten — Fu 1991) are relatively frequent.

Palaeophycus Hall, 1847

Palaeophycus heberti (Saporta, 1872) (Figs. 6A,C, 11A,C)

Diagnosis: Branched, unbranched, smooth or ornamented, typically lined, essentially cylindrical, predominantly horizontal, oblique burrows of variable diameter, burrow fill without any structure (Pemberton & Frey 1982).

Material: 25 samples with several tens of specimens.

Description: *Palaeophycus* with a light-coloured wall-lining and a darker internal burrow fill. Burrow diameter varies from 3.5 to 7.8 mm. Pale wall lining is 0.4 to 1.8 mm-thick.

Remarks: *Palaeophycus* is interpreted as an open burrow of vagile, omnivorous or carnivorous polychaetes (Pemberton & Frey 1982).

Planolites Nicholson, 1873

Planolites isp. (Figs. 6A, 8B, 11A,B,C)

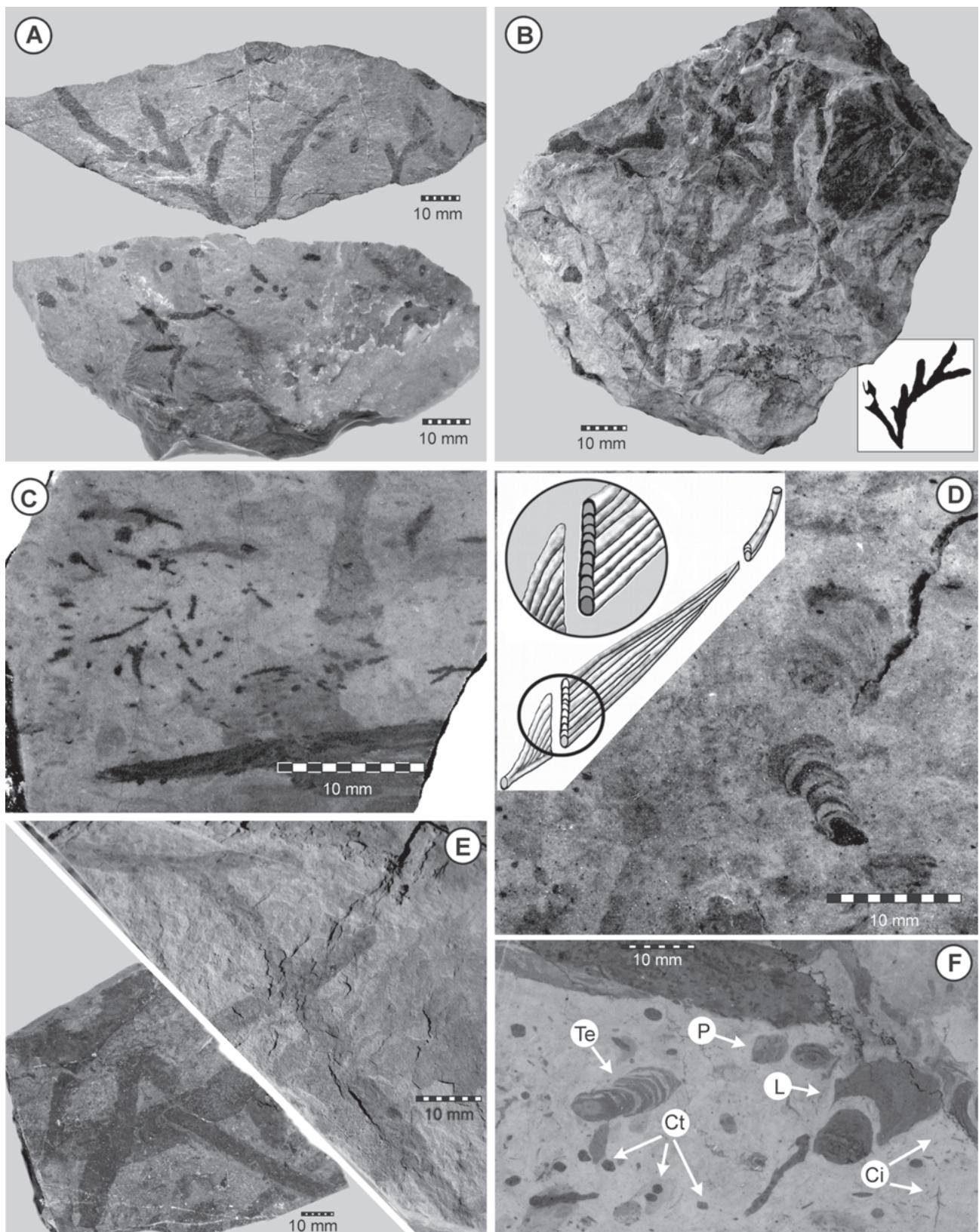


Fig. 12. Trace fossils from the Skladaná Skala section. **A** — *Chondrites* cf. *targonii*. **B** — *Chondrites* cf. *recurvus*. **C** — *Chondrites* cf. *intricatus*. **D** — *Teichichnus* cf. *sigmoidalis*. **E** — *Thalassinoides* isp. **F** — *Chondrites* cf. *targonii* (Ct), *Lamellaeichnus* (L), *Teichichnus* (Te). Scale bar: 10 mm.

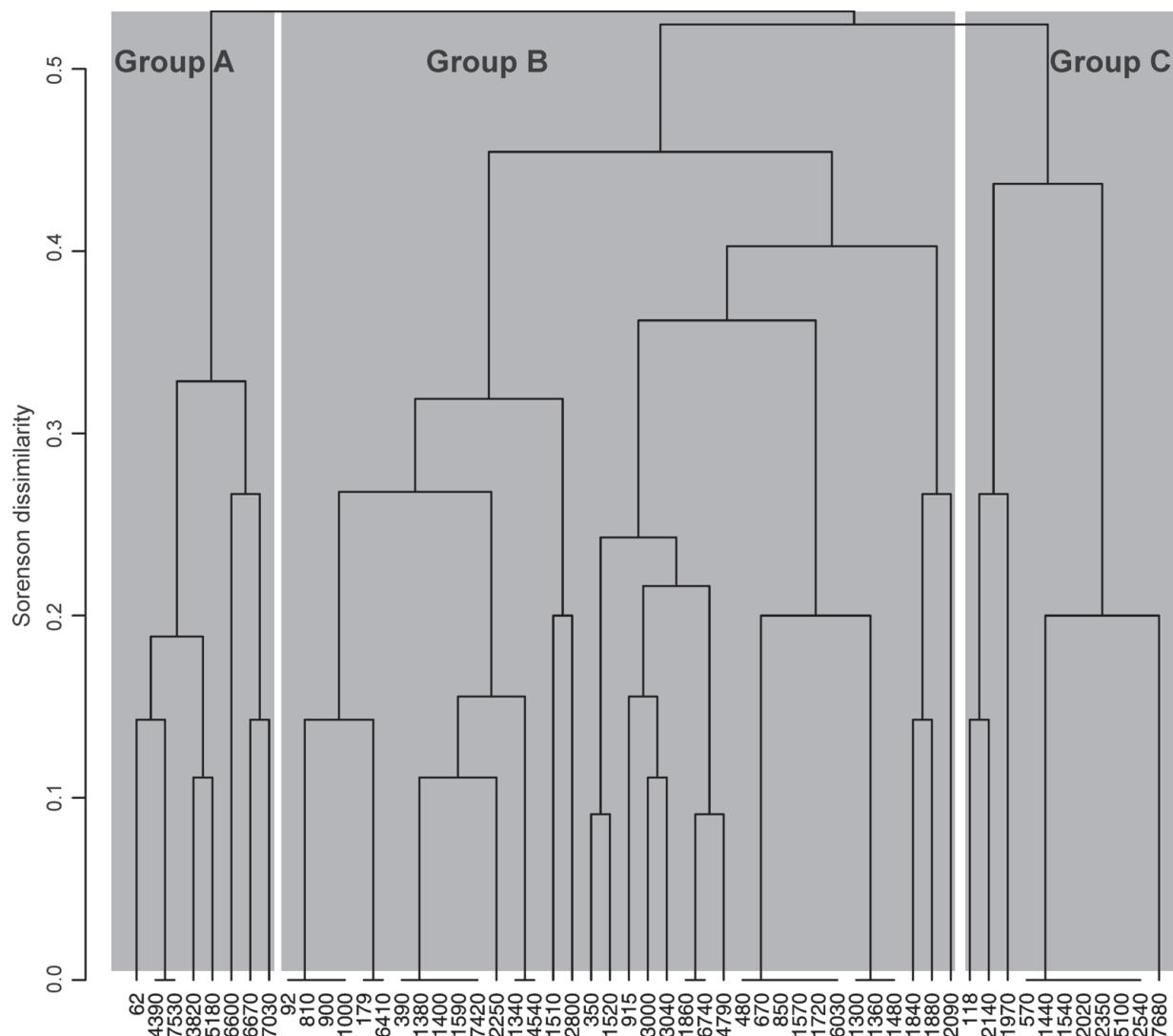


Fig. 13. Cluster analysis of 55 samples on the basis of Sorenson dissimilarity (presence-absence data) and weighted average linkage method. We separated the dendrogram into three assemblage groups.

Diagnosis: Straight or irregularly waved, horizontal, cylindrical trace fossil without bioglyphes and wall (Fillion & Pickerill 1990).

Material: Several tens of specimens.

Description: Cross-sections are elliptical, flattened by compaction. Diameters of these burrows vary from 2 to 6 mm. They can be misclassified with sections of large *Chondrites*.

Remarks: *Planolites* is an eurybathic trace fossil interpreted as the work of a deposit feeder. Ichnotaxonomy of *Planolites* and *Palaeophycus* was discussed by Pemberton & Frey (1982).

Rhizocorallium Zenker, 1836
Rhizocorallium isp. (Fig. 6C)

Diagnosis: U-shaped spreite burrows, parallel or oblique to bedding plane; limbs more or less parallel and distinct; ratio of tube diameter to spreite width usually 1:5 (Fürsich 1974; Uchman 1998; Schlirf 2011).

Material: Two specimens.

Description: *Rhizocorallium* was distinguished on the basis of cross-sections that show concordant spreite (crescent-shaped) structures and do not possess any wall. The width of *Rhizocorallium* cross-sections is 53 mm.

Remarks: *Rhizocorallium* is produced by deposit- and suspension-feeders, and typically occurs in shallow-water environment of the upper offshore zone (Jaglarz & Uchman 2010). However, deep-water *Rhizocorallium* with *Zoophycos* occurs in the Paleogene flysch of the Outer Western Carpathians (Uchman 1992).

Teichichnus Seilacher, 1955
Teichichnus cf. *T. sigmoidalis* Seilacher, 1955
 (Figs. 6A, 11A, 12D,F)

Diagnosis: Long, wall-shaped septate structures that consist of a pile of gutter-shaped laminae (Fillion & Pickerill 1990; Seilacher 2007).

Material: Several tens of specimens.

Description: Backfill of *Teichichnus* shows a downward movement of its producer. This protrusive structure indicates that it belongs to *T. sigmoidalis* (according to Seilacher 2007: plate 41). Diameters of basal burrows range from 2.5 to 5 mm. The width of the spreite chain slightly widens towards the top and attains diameters from 3.5 to 6 mm. The height of the spreite chain in vertical cross-sections varies between 5.5 to 19 mm.

Remarks: Teichichnid forms have similar cross-sections as other trace fossils (e.g. *Rhizocorallium*, *Diplocraterion*, or *Syringomorpha*).

Thalassinoides Ehrenberg, 1944

Thalassinoides isp. (Figs. 6A, 12E)

Diagnosis: Three-dimensional system of smooth-walled burrows with variable shaft diameter. Shafts branch into Y- or T-shaped burrows that are broader at bifurcation points (Uchman 1998, 1999). The sediment fill of *Thalassinoides* is not structured but the fill can be meniscate (Fürsich 1973; Seilacher 2007).

Material: Two samples.

Description: Truly branching burrows were assigned to *Thalassinoides*. Several undetermined branching structures, observed on bedding planes, can also belong to *Thalassinoides*. The burrow diameter varies between 3 and 15 mm.

Remarks: *Thalassinoides* occurs in a broad range of environments (e.g. Archer & Maples 1984; Ekdale & Bromley 2003; Miller III. et al. 2004). *Thalassinoides* producers are assigned mostly to crustaceans (e.g. Carvalho et al. 2007).

Trichichnus Frey, 1970

Diagnosis: Branched or unbranched, hair-like, cylindrical, straight to sinuous trace fossils, oriented at various angles (mostly vertical) with respect to the bedding. Burrow wall distinct or indistinct, lined or unlined (Frey 1970; Fillion & Pickerill 1990; Uchman 1999).

Remarks: Uchman (1999) noted that the preservation of *Trichichnus* lining was affected by diagenetic processes. Three ichnospecies of *Trichichnus* were distinguished, including *T. linearis*, *T. simplex* (Fillion & Pickerill, 1990) and *T. appendiculatus* (Uchman, 1999). *Trichichnus* occurs in shallow-water (Fillion & Pickerill 1990) and deep-sea deposits (Wetzel 1981). The location of *Trichichnus* in deeper tiers together with *Chondrites* can imply that its producers — meiofaunal deposit-feeders or chemosymbionts — tolerated oxygen-deficient conditions (Uchman 1995).

Trichichnus simplex Fillion & Pickerill, 1990
(Figs. 6B, 11A)

Diagnosis: Unlined *Trichichnus* (Fillion & Pickerill, 1990).

Material: Several tens of specimens.

Description: *Trichichnus* is one of the common trace fossils in the Skladaná Skala section. The diameter of predominantly pyritic, inclined and vertical burrow attains

0.1–0.2 mm. *Trichichnus* with sporadic branching was observed on polished slabs and in thin sections, and was also detected by X-ray microtomography (Šimo 2012).

Zoophycos Massalongo, 1855

Zoophycos isp. (Fig. 6A)

Diagnosis: Spreiten structures consisting of numerous small, more or less U- or J-shaped protrusive burrows of variable length and orientation. Causative U- or J-shaped burrows widen downward or upward to a helicoidal spiral. Spreiten are arranged in helicoid spirals with an overall circular, elliptical or lobate outline, a central vertical tunnel or marginal tube may be present. The whole helicoidal structure is composed of protrusive lamellae that can extend to the lobe, marginal helicoidal parts could be lined by marginal tube (modified according to Olivero 2003).

Remarks: This structure was interpreted as a "streep miner" (Seilacher 1967), later it was explained as a refuse dump or garden (Bromley 1991). The producer of this structure can be attributed to sipunculoids (Wetzel & Werner 1981), polychaete annelids, arthropods (Uchman 1998 and references therein) and echiuran "worms" (Kotake 1989).

Material: Three samples.

Description: Rare trace fossil, spreite lamellae of *Zoophycos* occur sporadically on bedding planes. Parallel meniscate lines are visible in cross-sections. The width of the spreite spiral attains 1.5–2.5 mm.

Variation in composition of trace-fossil assemblages

The diversity of trace-fossil assemblages with nine ichnogenera in the Skladaná Skala section is generally larger than previously reported from other Lower Jurassic spotted deposits. They are comparable to the assemblage with *Chondrites*, *Paleophycus*, *Phycosiphon*, *Planolites*, *Taenidium*, *Teichichnus*, *Thalassinoides*, *Trichichnus*, and *Zoophycos* from the Lejowa Valley in the High Tatra Mountains (Uchman & Myczyński 2006). For example, Jacobshagen (1965) reported *Phymatoderma* and *Zoophycos* from the Allgäu Formation (Eastern Alps) and Wieczorek (1995) reported *Zoophycos*, *Chondrites*, *Helminthoida*, *?Taenidium*, *?Teichichnus* and U-shaped trace fossils from the Janovky Formation (High Tatra Mountains). On the basis of presence-absence data of 9 ichnogenera and the agglutinated foraminifer *Bathysiphon*, 55 samples from the Skladaná Skala section do not markedly differentiate in an ordination space (NMDS) into distinct assemblage groups. The median number of ichnogenera per bed is 3. All samples contain small-sized *Chondrites* and primarily differ in the presence of three ichnotaxa produced by deposit-feeders and one deposit-feeding foraminifer (*Lamellaeichnus*, *Chondrites* cf. *targonii*, *Teichichnus* and *Bathysiphon*).

The cluster analysis delimited three assemblage groups (Fig. 13). However, these groups overlap in NMDS (Fig. 14) and the different linkage methods produce different clusters, demonstrating that the grouping of beds into the three assemblage groups does not correspond to distinct community

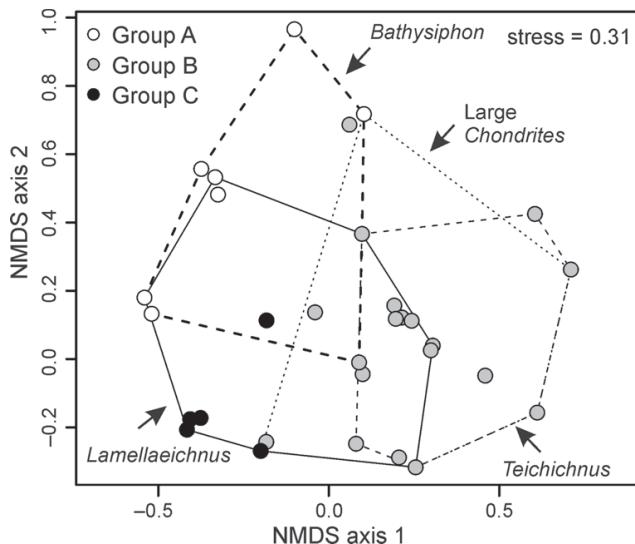


Fig. 14. Non-metric multidimensional scaling of 55 beds, based on Sorenson dissimilarity. The convex hulls delimit the presence of four common genera (small-sized *Chondrites* occurs in all samples). The three circle symbols of different colour correspond to three groups delimited by the cluster analysis.

groups. The average Jaccard dissimilarity among all samples is 0.52, implying that the probability of drawing the same ichnotaxon from two randomly-selected beds is about 50 %. The relationship between Sorenson dissimilarity and the stratigraphic distance among samples is very low (Mantel-test Pearson correlation = 0.11, $p = 0.054$), showing no clear temporal change in trace-fossil composition up-section. Therefore, trace-fossil assemblages in the Pliensbachian part of the succession correspond to one basic community type with omnipresent *Chondrites* cf. *intricatus*, which is associated with taxa with moderate occupancy (i.e. proportion of beds with at least one occurrence), including *Lamellaechinus* (0.78 %), *Teichichnus* (0.51 %), *Chondrites* cf. *targonii* (0.4 %), *Palaeophycus* (0.31 %), and *Bathysiphon* (0.2 %). However, fine-scale stratigraphic analyses of changes in size and numerical abundance of trace fossils will be needed to reveal whether high-frequency fluctuations can be detected up-section.

Ichnofabric and tiering patterns

Trichichnus crosses *Chondrites* and all other trace fossils, *Chondrites* crosses *Lamellaechinus*, and *Palaeophycus* frequently penetrates through *Lamellaechinus*. These relations imply separation of the transitional layer into two or three tiers, although the ichnofabric clearly shows an unbroken overprinting of successive colonization events under continuous sediment aggradation, generating complex tiering patterns (Taylor et al. 2003). The deepest tier is thus represented by *Trichichnus simplex*, the deep to intermediate tier by *Chondrites*, and the shallow tier by mobile deposit-feeders represented by *Lamellaechinus imbricatus* and *Palaeophycus* (and less frequent *Planolites*). This tiering pattern and cross-cutting relations are similar to those in the spotted facies in

the Lower Toarcian Fuente de la Vidriera section in the Betic Cordillera (Rodríguez-Tovar & Uchman 2010) and in Cenomanian-Turonian hemipelagic sediments in the Polish Carpathians (Uchman et al. 2013). The presence of wall-lined *Palaeophycus* points to softground conditions, but the boundaries between shallow-tier burrows of *Lamellaechinus* and sediment are sharp, implying a relatively stiff sediment consistency in the upper tiers (Wetzel & Uchman 1998).

The lithological difference between burrows and the surrounding sediment is primarily caused by differences in the organic matter content. This difference generates the diagnostic spotted appearance of “Fleckenmergel” and “Fleckenkalk” deposits. The dark organic-rich infill of *Lamellaechinus* (mean TOC = 0.23 %, maximum TOC = 0.36 %) contrasts with the light grey, structureless surrounding sediment (mean TOC = 0.15 %, maximum TOC = 0.21 %). Organic matter enrichment in burrow fills of shallow-tier trace fossils such as *Lamellaechinus* and *Palaeophycus* cannot be simply explained by the lack of oxygen in deeper portions of transitional layers where organic matter reactivity is reduced (Aller 2004). Such enrichment rather shows that the organic matter (e.g. generated by decay, mucus secretion, buildup of metabolites, or by chemoautotrophic bacterial production) even in the shallow tiers of the transitional layer was not completely decomposed, oxidized, or consumed by subsurface deposit-feeders (Aller 1982). However, the relictual, less well-defined mottled traces of *Lamellaechinus* of yellowish or light grey colour (mean = 0.16 %, maximum = 0.22 % — Fig. 15) have similar TOC levels as in structureless and homogenized sediment without any mottled structure. The preservation of these relictual, organic-poor traces thus shows that *Lamellaechinus* was temporarily subjected to higher redox cycling above the redox potential discontinuity (RPD) layer. In summary, the

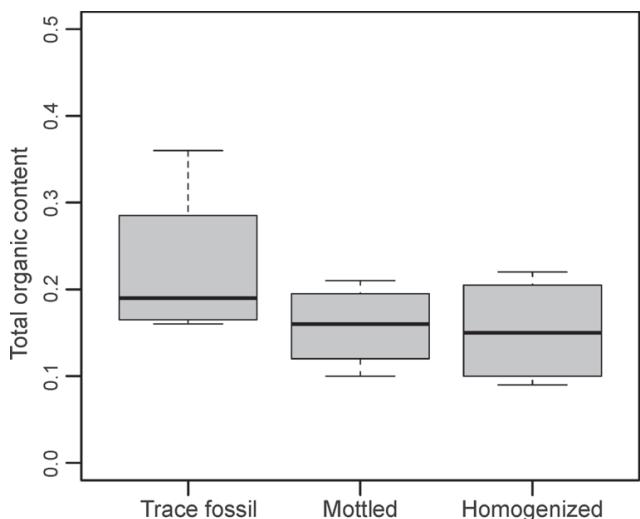


Fig. 15. Dark grey, well-delimited burrows of *Lamellaechinus* have higher percentage of TOC (mean TOC = 0.23 %, maximum TOC = 0.36 %) than yellowish or light grey, relictual, mottled traces of *Lamellaechinus* (mean = 0.16 %, maximum = 0.22 %) and than light grey, structureless surrounding sediment (mean TOC = 0.15 %, maximum TOC = 0.21 %). Boxplots show median values, 25th and 75th quantiles and extreme values.

ichnofabric pattern represented by abundant organic-rich *shallow-tier burrows* persisting for several tens of meters of deposits at Skladaná Skala implies that the *uppermost layers* of the sediment column close to the sediment–water interface were frequently subjected to poor redox cycling. This persistence seems to primarily reflect long-term recurrence of oxygen-deficient bottom-water conditions that did not allow stronger redox cycling and inhibited long-term development of a thicker mixed-layer. The agglutinated foraminifer *Bathysiphon* was probably an inhabitant of the uppermost parts of the mixed-layer because (1) its tubes do not cross trace fossils, (2) tube sediment infill does not differ from the light grey surrounding sediment, and (3) recent species of *Bathysiphon* are semi-infaunal deposit-feeders protruding above the surface or located closely below the sediment–water interface (Gooday et al. 1992, 2002).

Oxygen-limited benthic communities

A poor redox cycling in the uppermost parts of the sediment column, associated with the reduced thickness of the mixed-layer in present-day soft-bottom environments, is typically associated with reduced bottom-water oxygen concentrations (Savrda & Bottjer 1991; Smith et al. 2000). The role of oxygen-limitation in determining the structure of benthic communities of the Janovky Formation is further supported by (1) dominance of trace-fossils produced by infaunal deposit-feeders rather than by infaunal suspension-feeders (Ekdale & Mason 1988; Lavaleye et al. 2002), (2) high abundance of tubes of the hypoxia-tolerant agglutinated foraminifer *Bathysiphon* (Gooday et al. 2000, 2002), and (3) high abundance and occupancy of *Chondrites* with ~0.5 mm-sized branches (Bromley & Ekdale 1984; Savrda & Bottjer 1986; Wetzel 1991; Parisi et al. 1996; Martin 2004), all pointing to low oxygen concentrations in bottom and interstitial waters. We suggest that the spotted character of deposits, with dark organic-rich fills in burrows of shallow-tier organisms separated from a lighter surrounding matrix, generally imply a shallow location of RPD in the sediment because organic matter recycling and decomposition in the transitional layer were not effective enough during their deposition. With some exceptions (Thompson et al. 1985), oxygen-deficient conditions (<0.3–0.5 ml/l O₂) not only increase mortality rates (Riedel et al. 2012) but also significantly reduce energetically-costly calcification rates and can shift the community structure towards the dominance of soft-bodied fauna (Rhoads & Morse 1971; Rhoads et al. 1991; Levin et al. 2000). Hypoxia can thus explain the rarity of carbonate-producing benthic macroinvertebrates in the Lower Jurassic spotted deposits, rather than limitation by soupy substrate or low food supply that can also reduce productivity of heterotrophic benthic macroinvertebrates. We note that the presence of belemnites and ammonites — i.e. taphonomic control groups for calcitic and aragonitic macroinvertebrates — implies that the rarity of benthic carbonate-producing macroinvertebrates in the Janovky Formation is not related to their low preservation potential.

The host rock at Skladaná Skala contains minute sponge spicules that are either dispersed in sediment or densely-

packed in tube-walls of *Bathysiphon*, documenting the presence of epifaunal components in the community structure. These spicules either represent relicts of poorly-developed sponge communities or they were transported from sponge communities in the northern parts of the Zliechov Basin where spiculite-rich packstones are more widespread and recurrent than at the Skladaná Skala section. Such packstones, locally with *in situ* sponges (Jach 2002), signify the presence of sponge-dominated meadows on the foot and slopes of topographic elevations (Jach 2002, 2005) that were rimming the depocenters with spotted deposits. Therefore, the deposition of Pliensbachian bioturbated deposits at Skladaná Skala partly coincides with the deposition of spiculites in shallower, more proximal, northern parts of the Zliechov Basin, now preserved in the northern parts of the Malá Fatra and High Tatra Mountains. For example, spiculite-rich packstones (1) underlie the spotted deposits of the Toarcian age in the Malá Fatra Mountains, (2) alternate with "spotted" marlstones and limestones of the Janovky Formation in the Western Tatra Mountains, and (3) overlie the spotted deposits of the Sinemurian–Early Pliensbachian age in the Polish part of the High Tatra Mountains (Lefeld et al. 1985). In the Skladaná Skala section, several isolated spiculitic limestone beds thus probably represent temporary and relatively short-term sponge colonization events of deeper habitats.

Restricted circulation and high sedimentation rates

The development of oxygen-deficient bottom-water conditions is probably related to a combined effect of restricted circulation (promoting stratified water columns) and high sedimentation rates that characterized Early Jurassic depocenters of the Zliechov Basin. First, spotted deposits are consistently reduced in the thickness across less than 20 km from several hundreds of meters (Skladaná Skala section) up to a few meters (e.g. at Borišov and Horná Turecká sections in the Veľká Fatra Mountains — Mišik & Rakús 1964) in southern locations of the Zliechov Basin (central and southern parts of the Veľká Fatra Mountains). Second, spotted deposits in the northern parts of the Veľká Fatra Mountains are horizontally and stratigraphically replaced by nodular limestones of the Adnet Formation in the southward direction (Mišik & Rakús 1964). Third, frequent spiculitic and crinoidal beds imply proximity of slope, and thus more northward limit of the depocenter of the Zliechov Basin, in the eastern part of the High Tatra Mountains (Lefeld et al. 1985; Jach 2005). Therefore, the thickness reduction by two orders of magnitude and the spatial replacement of deep-water "spotted" facies by sponge meadows, by shallower sediments exposed to stronger current action (crinoidal facies), and by highly condensed and bioturbated sediments (nodular facies) imply topographic differentiation of the Zliechov Basin into plateaus and semi-enclosed, sediment-catching and high-subsidence depocenters. Topographic barriers can significantly restrict circulation, while high sedimentation rates can be expected to reduce organic-matter decomposition and redox cycling, favouring oxygen-deficient bottom-water conditions. Such spatial variation in the thickness of different sediment types thus indi-

cates both (1) higher sedimentation rates in areas with the deposition of spotted facies, and (2) the presence of a deeper trough in the Zliechov Basin, now preserved in the northernmost parts of the Veľká Fatra Mountains.

This scenario is analogous to the scenario developed for the Middle Jurassic spotted deposits in the Pieniny Klippen by Tyszka (1994a). We suggest that recurrent hypoxic conditions seem to be the main cause of the rarity of macrobenthic carbonate skeletal invertebrates in spotted deposits, effectively prevailing over significant temporal durations almost during the whole Early Jurassic in depocenters of the Zliechov Basin. This interpretation does not imply that all spotted deposits of the Janovky (or Soltyisia Marlstone) Formation in more marginal parts of the Zliechov Basin reflect hypoxic conditions. The oxygen concentrations were probably less limiting towards the southern and northern parts of the Zliechov Basin, as implied by increasing abundance of spiculite-rich deposits and carbonate producers in both northward and southward directions.

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