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, Lamellaeichnus (new ichnogenus), and Teichichnus. Lamellaeichnus, 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 structurless sediment (TOC=0.09–0.22). The higher TOC in shallow-tier burrows of Lamellaeichnus 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; Raucík & 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; Plišienka 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 (Gadzicki et al. 1979; Sulser & Furrer 2008) and skeletal-rich deposits are absent in the spotted deposits. However, this paradox and the causes of the paleo-community 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 productivility 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 & Twitchett 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 & Twitchett 2013) and influencing whether sediments are in fact fossiliferous or barren (Peters 2007).

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

The Central Western Carpathians were located on the northern part 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 “Fleckenkalk” and “Fleckenkalk” facies or to the Allgäu Formation (Hettangian–Lower Sinemurian) or sandstone-dominated Medofoly 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 (Mišík & Rakús 1964; Jach 2002, 2005). In the upper part, it can be replaced by spiculitic limestones (Świńska Turnia Member of the Hučiska Formation, Western Tatra Mountains), nodular limestones (Adnet Formation, Velká Fatra Mountains), crinoidal limestones (Lefeld et al. 1985), or by radiolarian limestones of the Sokolica or Ždiar Formations (Lefeld et al. 1985; Polák & Ondrejičková 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 Sklandá Skala section in the northernmost parts of the Velká 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 Sklandá Skala quarry is situated in the northernmost part of the Velká 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 spongiolithic limestones. The lower, about 70 m-thick interval is represented by marly limestones with thin marly interlayers and contains the Upper Sinemurian ammonites Echioceras rariocostatum 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. semielatum, D. atheticum, Harpoceras ex gr. falceiferum, and Hildoceras ex gr. bifrons. Rare remains of rhynchonelliform craniopods 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°15′ 33.54″ N; 19°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 lime-
stones that alternate with marls (Gaździcki et al. 1979).

(3) Trlenská Valley (49°2′ 26.37″ N; 19°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 (Mišik & 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°4′ 2.35″ N; 18°41′ 29.99″ E).

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. Longitudi-
nal sections were cut either vertically or hori-
zontally (relative to burrow orientation). Two
slabs were serially cross-sectioned for three-di-
mensional morphological study of *Lamellae-
ichnus* (Fig. 5). Distances between sections
ranged between 0.2 to 1 mm. The trace fossil
fill and the composition of the surrounding ma-
trix were detected in thin-sections.

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

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<td>Marly limestones, (Berriasian–Aptian)</td>
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<td>Kimmeridgian–Lower Tithonian, platy or nodular light grey and reddish limestone and marlstone</td>
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<td>Janovky Formation</td>
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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.

Fig. 2. An arrow shows a simplified geological map showing (arrow) the location of the Skladaná Skala sec-
tion (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 *Lamellaeichnus* 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 ichno-genera 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.

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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 *Lamellaeichnus*, 4 samples of mottled, brownish sediments with relicts of *Lamellaeichnus*, 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**

*Lamellaeichnus* new ichnogenus

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

**Type ichnospecies:** *Lamellaeichnus imbricatus*.

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

*Lamellaeichnus 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 *Lamellaeichnus* cross-sections is supplemented by illustrations of 14 sections (Z37752). Sample Z37000 contains seven *Lamellaeichnus* cross-sections. The sample with longitudinal horizontal *Lamellaeichnus* 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 *Lamellaeichnus* (Z37749a,b,c).

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

Additionally, 194 polished slabs with *Lamellaeichnus 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.

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**Fig. 7.** Three-dimensional reconstruction of *Lamellaeichnus* with a cross-section and a horizontal longitudinal section.  
**A** — Reconstruction of *Lamellaeichnus* 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...
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 *Lamellaichnus* 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 *Lamellaichnus 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

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**Fig. 9.** The sketches illustrate the arrangement of lamellae and their coalescence within the basal burrow of *Lamellaichnus*. A — Lamellae (on the cross-sectional view) are colour-differentiated. Each lamella has one number. B — The most typical *Lamellaichnus* cross-section (Kamenná Poruba locality). An arrow shows downward direction of the trace maker’s movement. C — A hypothesized construction of *Lamellaichnus*. 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.
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 1997). 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 Lamellaeichnus 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. 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.
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* tracer 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 (*Margariticnhus 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, *Margariticnhus* picture; Buckman 2001: figs. 2A,B, 9B). The trace-maker 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 seymoureensis* Uchman & Gądzicki, 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*.

**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* (Spaorta, 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 vague, omnivorous or carnivorous polychaetes (Pemberton & Frey 1982).

*Planolites* Nicholson, 1873

*Planolites* isp. (Figs. 6A, 8B, 11A,B,C)
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. sigmoidealisis (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 sinuose 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. appendicisus (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 Trichichus (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 Quarry (Simo 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 helicoidal 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, Phycisphion, 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 agglomerated 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 (Lamellaechnus, Chondrites cf. garganii, 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
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 one occurrence, including Lamellaechinus (0.78%), Teichichnus (0.51%), Chondrites cf. targioni (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 Vidrieria section in the Betic Cordillera (Rodriguez-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. 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.

**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 TOC=0.16%, maximum TOC=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 relics 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 Boríšov and Horná Turecká sections in the Veľká Fatra Mountains — Mišík & Rakúš 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 (Mišík & Rakúš 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 de-
position of spotted facies, and (2) the presence of a deeper
trough in the Zliechov Basin, now preserved in the northern-
most 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 car-
bonate skeletal invertebrates in spotted deposits, effectively
prevailing over significant temporal durations almost during
the whole Early Jurassic in depocenters of the Zliechov Ba-
sin. This interpretation does not imply that all spotted de-
posits of the Janovky (or Soltysia Marlstone) Formation in more
marginal parts of the Zliechov Basin reflect hypoxic condi-
tions. The oxygen concentrations were probably less limiting
towards the southern and northern parts of the Zliechov Ba-
sin, as implied by increasing abundance of spiculite-rich de-
posits and carbonate producers in both northward and southward
directions.

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