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EARLY COMPLEX TIERING PATTERN: UPPER ORDOVICIAN, BARRANDIAN AREA, THE CZECH REPUBLIC

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Abstract: Upper Ordovician shallow marine fine-grained sandstones and siltstones exposed in the Loděnice – vinice locality yielded a distinct and well-preserved tiering pattern of trace fossils. The two uppermost tiers are composed mainly of *Bifungites* and *Nereites*. Deeper in the sediment, tiers dominated by *Thalassinoides*, *Zoophycos* and *Teichichnus* occur. Most of the succession is completely bioturbated; however, several storm layers enabled study of a well-preserved frozen tiering pattern. Large portions of the bedding planes (ichnologic snapshots) showed a considerable patchiness of intensive surface bioturbation and a preferred orientation of *Bifungites*. The identified tiering pattern is one of the earliest examples of a well-documented complex tiering of burrows documented in detail.

Key words: ichnofossils, tiering, Ordovician, Barrandian area, peri-Gondwana

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Introduction

In ichnology tiering denotes vertical zonation of trace fossils below the substrate surface (e.g., Bromley 1996). Although this phenomenon has been informally used since the 1960s (Griggs et al. 1969), it was defined and thoroughly discussed only much later (Ekdale et al. 1984, Ekdale and Bromley 1991, a.o.) despite its obvious significance. So far, Mesozoic and Cenozoic tiering patterns have been studied more intensively than Palaeozoic ones for two reasons: 1. the concept was elaborated primarily in Mesozoic and Cenozoic rocks (e.g., chalk – Ekdale and Bromley 1991); 2. as tiering patterns developed through time, complex Mesozoic and Cenozoic patterns are much more frequent. Any ichnofabric that originated prior to the Cambrian Substrate Revolution (Bottjer et al. 2000) had a simple tiering pattern because it was limited to the surface and shallow subsurface. Increasing depth and intensity of bioturbation during the Ordovician (Droser and Bottjer 1989) allowed for the appearance of early complex tiering patterns.

The study of tiering is often based on observations in drill cores or restricted outcrops providing only limited information on the extent of lateral structures. Thus, larger burrow systems cannot be reliably interpreted.

This contribution presents a case study focused on a complex 3D analysis of tiering in a large lateral extent. We consider the methods applied, including GIS, as useful for proper assessment of both the horizontal aspects (bedding planes and horizontal cross-cuts of the rock) and vertical aspects (vertical cross-sections of the beds). Even if applied at a single site such 3D analysis is crucial for understanding the origin and temporal stability of tiering patterns.

Geological setting

The studied locality Loděnice – vinice (vinice = vineyard) is situated 22 km WSW of Prague near Loděnice on a low cuesta at the SW edge of the village. The main exposure area is situated on the dip slope in the topmost part of the vineyard below a narrow wooded ridge (Text-fig. 1).

The measured section is exposed along the eastern (exactly ENE) side of that area (GPS coordinates 49° 59′ 34.1″ N; 14° 09′ 1.5″ E) and represents a thin stratigraphic interval

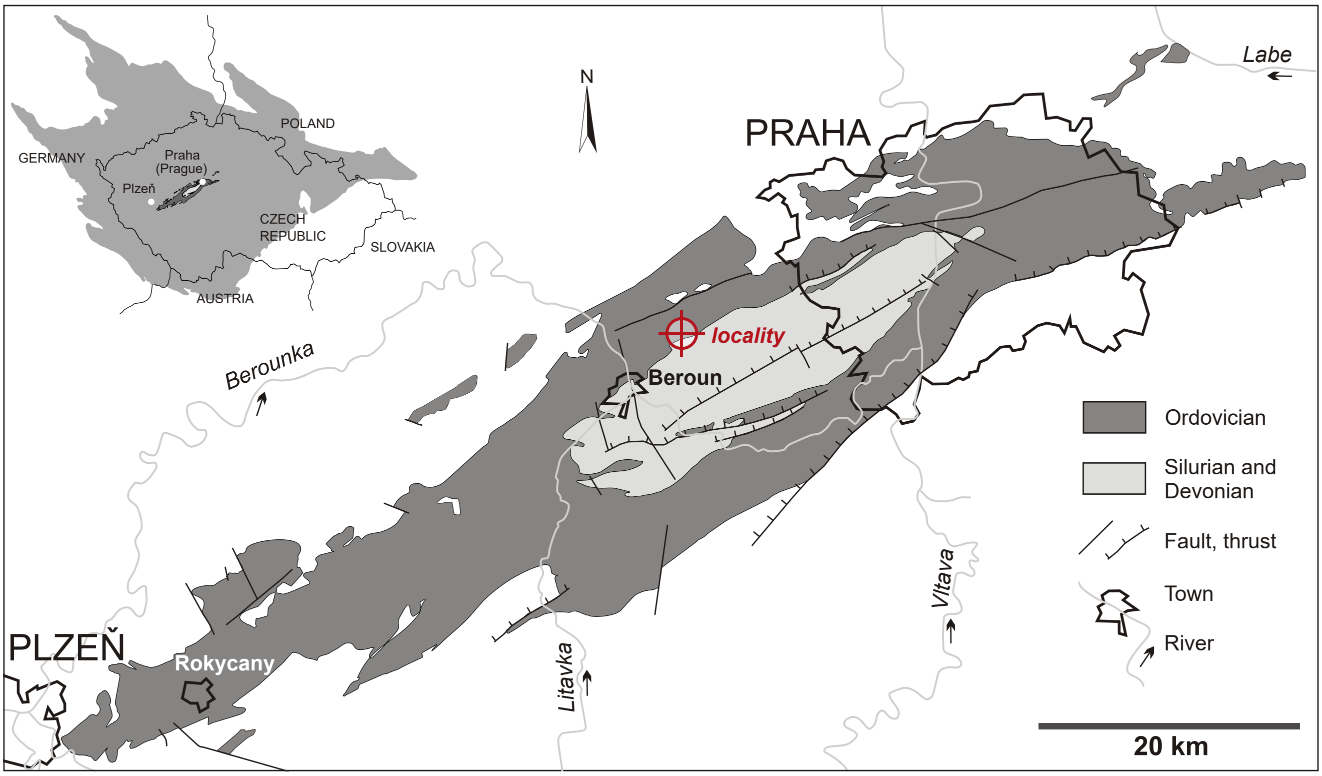
Text-fig. 1. Photograph of the studied outcrop with wide bedding planes on the Loděnice – vinice above the topmost step of the vineyard.

within a succession of the Zahořany Formation. This lithostratigraphic unit belongs to the Berounian Stage on a regional scale and it is inferred as an equivalent of the lowermost Katian (Gutiérrez-Marco et al. 2017) but a late Sandbian age cannot be excluded. The Zahořany Formation forms a distinct portion of a very thick Upper Ordovician infill of the Prague Basin in the Barrandian area, the eastern portion of the Teplá-Barrandian Unit (central Bohemian Massif; see Text-figs 2, 3; for more information see Havlíček 1981, 1998); it is slightly more than 200 m thick in the locality area.

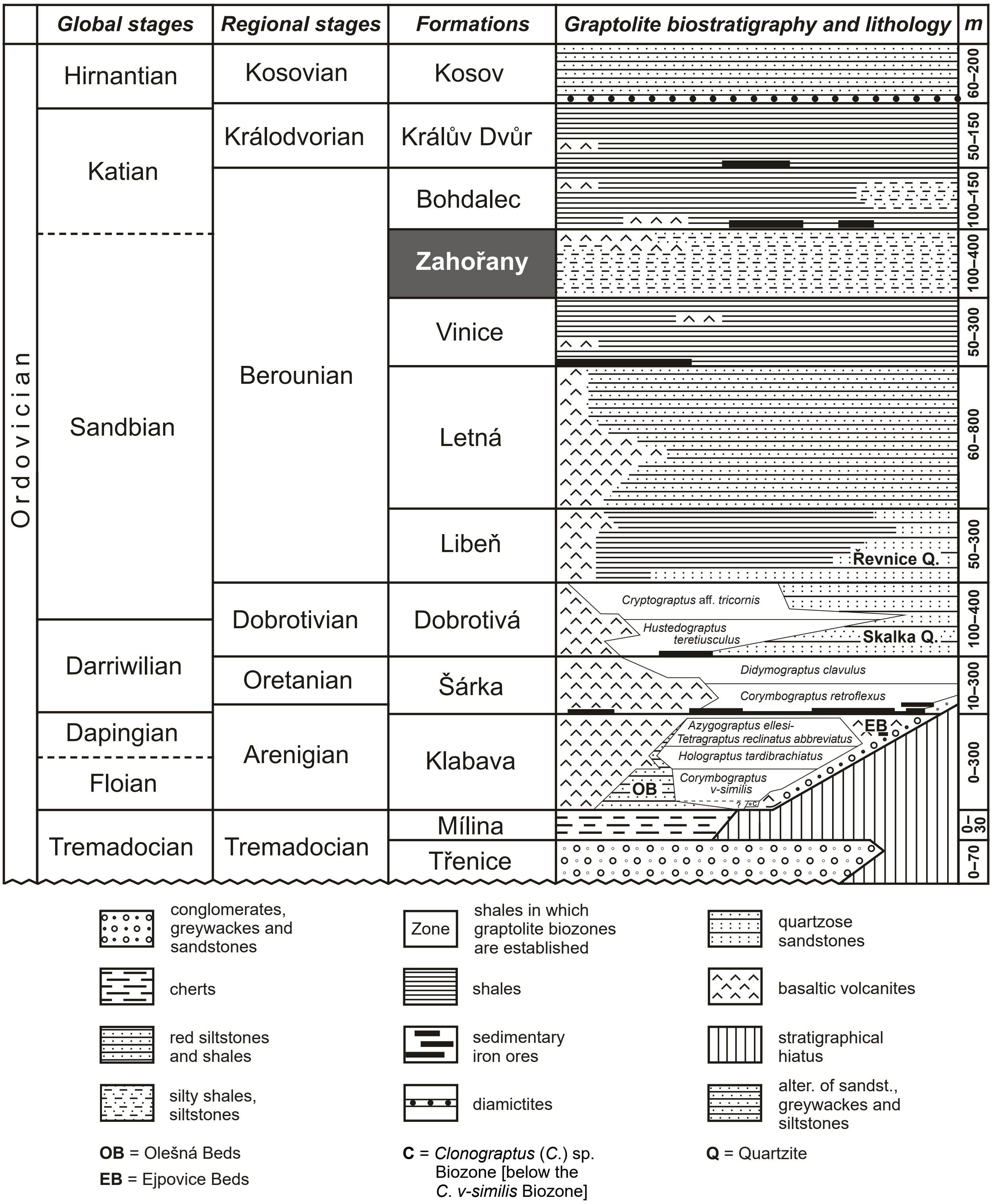
The formation is dominated by siltstones with rare intercalations of sandstones and silty shales; the sandstones often contain a carbonate matrix (Havlíček 1998). Lithology of the studied locality was characterised by Kukal (1960; under a confusing locality name Vráž) as an irregular alternation of siltstones, sandy siltstones and silty sandstones with variable amount of carbonate admixture in the matrix.

In comparison with the underlying Vinice and overlying Bohdalec formations, the Zahořany Formation is represented by coarser grained, well-oxygenated sediments. The fossil assemblages follow this trend and conform with the predominately slightly shallower conditions. The diversified Drabovia-Aegiromena fauna (Havlíček in Chupáč et al. 1998), of Benthic Assemblages 3 to 4 (sensu Boucot 1975, see Havlíček and Vaněk 1990), inhabited the main parts of the preserved sedimentary infill of the basin. These areas include the shallowest known parts on the supposed elevations of tectonically rising zones occurring mainly in Prague (Havlíček and Štorch 1990). They are typified by the Drabovia latior Community (Havlíček 1982, Havlíček and Fatka 1992, Havlíček in Chupáč et al. 1998) with rich trilobites, brachiopods, echinoderms, molluscs and other fauna. This association was also recorded in the study area near Loděnice (Havlíček in Chupáč et al. 1998). Deeper in the basin, it passes into the Aegiromena aquila-Marrolithus ornatus Community (Havlíček and Vaněk 1990, Havlíček and Fatka 1992, Havlíček 1998), characterised by lower diversity and the predominance of molluscs, brachiopods and rare trilobites (Havlíček 1998).

Body fossils are generally common in the locality but are mostly concentrated in small lenses and clusters. They belong to the Drabovia latior Community assigned by Havlíček (1982) to Benthic Assemblages 3 to 4. Common are brachiopods *Drabovia latior* Havlíček, *Aegiromena aquila aquila* (Barrande), *Heterorthina notata* (Barrande), *Rafinesquina pseudoloricata* (Barrande), and mainly disarticulated trilobites *Dalmanitina proaeva* (Barrande) and *Marrolithus ornatus* (Sternberg). Large, bunch-like



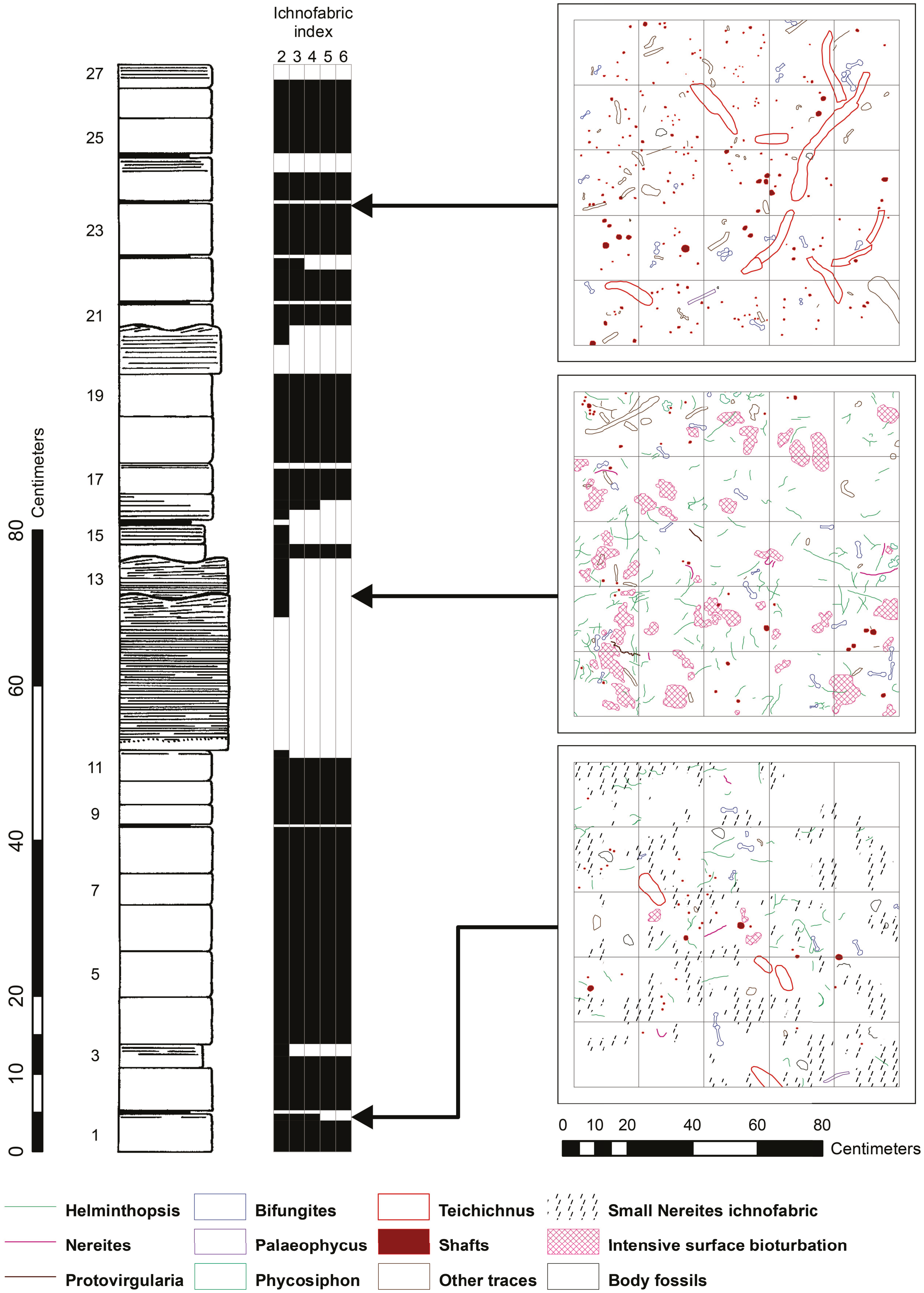
Text-fig. 2. Schematic map of the Prague Basin with position of the Loděnice – vinice locality.



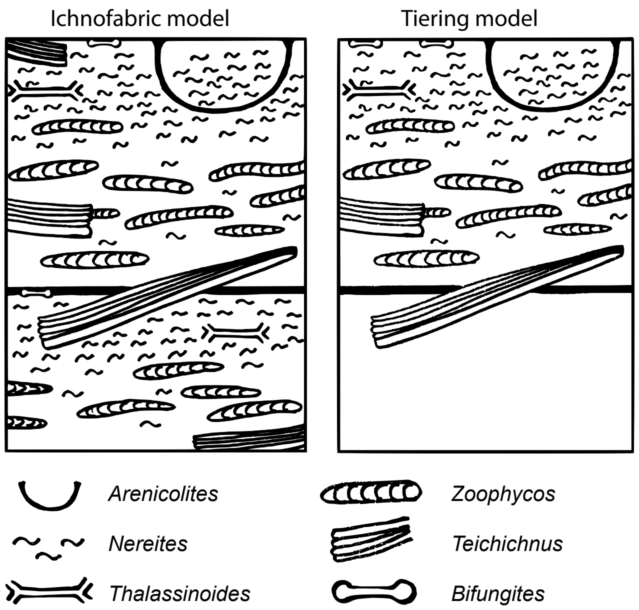
Text-fig. 3. Schematic stratigraphic chart of the Ordovician of the Prague Basin modified after Chlupáč (1993), Kraft et al. (2001), Kraft and Kraft (2003).

bryozoans showing no indication of transport are frequent in a large lens rich in carbonate (Ernst et al. 2014), which is a possible equivalent of layers No. 17 to 19 described herein (Text-fig. 4). Fragmented cystoids, small bivalves and conulariids are less common (Mikuláš 1998a).

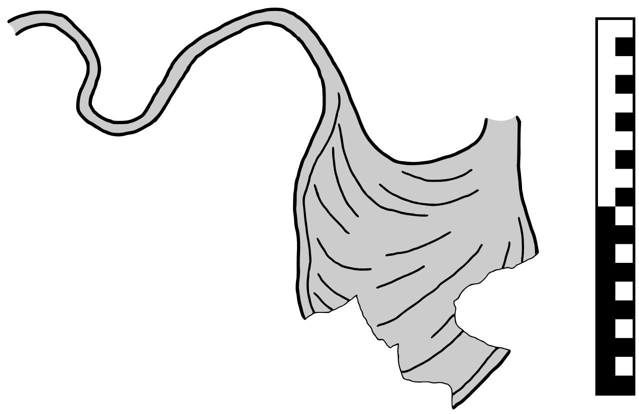
Sediments of the Zahořany Formation are usually bioturbated (Havlíček 1982, 1998). The principal ichnologic investigations of this unit were carried out by Mikuláš (1990); further remarks on the ichnofossils of the Zahořany Formation were published by Mikuláš (1998b). In the first-mentioned paper, a survey of ichnotaxa from the Loděnice – vinice locality is also mentioned. The same author also concluded that the assemblage belongs to the Zoophycos ichnofacies although some elements typical for the Cruziana ichnofacies also occur (Text-figs 5 and 6). Comments on the ichnological content of the locality within a wider palaeoenvironmental



Text-fig. 4. The studied section showing ichnofabric index and ichnological snapshots on the upper bedding planes of layers No. 1, 12 and 23.



Text-fig. 5. Ichnofabric and tiering models for the Loděnice – vinice locality.



Text-fig. 6. *Zoophycos* showing spreiten structure with a continuously meandering tunnel. Schematic drawing of the specimen from unidentified layer from a block out of the measured profile. Scale in centimetres.

and palaeontologic framework were published by Mikuláš (1998a) and Mikuláš in Kraft et al. (1999), respectively. The site was interpreted as situated in the vicinity of an elevated zone, under the influence of heavy storms. This is in accordance with the interpretations of Havlíček (1982), Havlíček and Vaněk (1990), Havlíček and Štorch (1990), Havlíček and Fatka (1992), Havlíček (1998), and also Fatka and Mergl (2009). Thus, the original environment recorded in the locality may be interpreted as situated at moderate depths on the slope of an elevation along a supposed zone in the basin which was continuously emerging during sedimentation.

Methods

The presented analysis refers to a part of the section situated in the eastern part of the outcrop with maximum continual exposure and large areas of bedding planes. The available continuous, 1.5 m thick section was divided into 27 beds with bedding planes exposed ranging from several square meters to tens of square meters in size. The thickness of the individual beds varied from several to tens of centimetres.

The section was described bed by bed. It was facilitated because the lithology of each bed appears to control the bioturbation distribution and rhythmicity. A special attention was paid to biogenic structures, their cross-cutting relationships and whether they penetrated several beds.

First of all, about 1 m^2 areas usually at full thickness of the beds were studied in detail by subsequent breaking to cm pieces. The intensity of bioturbation was characterised. For all ichnofossils, which could be taxonomically classified, their characters, abundance, cross-cutting relationships and tiering (depth ranges) were logged. Their relative abundance was studied using a semi-quantitative approach. The following frequency scale was used: very frequent (one or more specimens per 1 dm^2 of whole bed thickness), common (4 or more specimens recorded in an area of 1 m^2 of whole bed thickness), rare (2–3 specimens per 1 m^2 or an equivalent number from the whole exposed area) and solitary (a sole specimen in a 1 m^2 area or several individuals in the whole exposed area). The data gained were compared with observations from the entire exposure.

In addition, some beds exposed in large areas allowed synoptic studies focused especially on documentation of ichnofabric on the upper or basal bedding planes. Such very detailed studies were made on the three upper bedding planes of layers No. 1, 12 and 23. A square of 1 m^2 was selected on the bedding plane, marked and measured (ichnologic relevés). Subsequently, the studied area was divided into 25 smaller squares of 20 × 20 cm. All ichnofabric elements on the bedding plane were marked using a washable colour marker and all the squares were photographed. The obtained images were processed with SW ESRI ArcMap. First, a polynomial rectification of the overall relevé into its own coordinate system was made. Next, components of smaller squares were also rectified into the same coordinate system. After composing, all ichnofabric features in the relevé were vectorised.

As a high number of specimens belonging to the ichnogenus *Bifungites* were recorded on the upper bedding plane of layer No. 24, this presented the opportunity to analyse its orientations and size range. A Chi-squared test for uniform distribution was utilised to test for any statistical significance within the results.

Abbreviations

BK collection of the Czech Geological Survey, Prague, the Czech Republic

Ichnological features

As mentioned above, 27 beds were distinguished in the studied section. Thin laminae (up to 2 cm) of dark shales that intercalated some of the sandstone beds were not studied as separate beds and are described together with the overlying bed. The description of the whole section is summarized in Table 1.

Table 1. Description of the individual layers of the studied section. Abbreviations of abundance: vf – very frequent, c – common, r – rare, s – solitary.

Layer No.	Thickness (cm)	Ichnofabric index	Lithology	Ichnofossils and ichnofabric
1	5	6/2–6/3	Fine-grained sandstone	**Full relief:** *Thalassinoides* (c), *Planolites* (c), *Palaeophycus* (c), *Teichichnus* (c), *Nereites* (vf), *Zoophycos* (vf), undeterminable spots (vf). **Epirelief:** *Nereites* (vf), *Bifungites* (c), *Helminthopsis* (c), *Palaeophycus* (r), *Spirocircus* (s), *Didymaulichnus* (s), *Megagrapton* (s). **Penetrating from overlying strata:** *Teichichnus* (r).
2	5–6	6/3	Fine-grained micaceous sandstone	**Full relief:** *Nereites* (vf), *Zoophycos* (c), *Thalassinoides* (s), undeterminable spots (vf). **Hyporelief:** *Bifungites* (c), *Teichichnus* (r).
3	2.5–3	lower part: 6/3; upper part: 2	Fine-grained micaceous sandstone to siltstone	**Full relief:** *Zoophycos* (vf), undeterminable spots (vf).
4	5–6	6/2–3	Fine-grained micaceous sandstone; claystone shreds	**Full relief:** *Nereites* (vf), *Teichichnus* (c), *Zoophycos* (c), *Planolites* (c), *Thalassinoides* (s), undeterminable spots (vf). **Penetrating from overlying strata:** *Teichichnus* (r).
5	6	6/2–3	Fine-grained micaceous sandstone; claystone shreds	**Full relief:** *Nereites* (vf), *Zoophycos* (c), *Arenicolites* (s), undeterminable spots (vf).
6	6	6/2–3	Fine-grained micaceous sandstone	**Full relief:** *Nereites* (vf), *Zoophycos* (vf), *Teichichnus* (c), *Planolites* (c), *Helminthopsis* (c), *Arenicolites* (s), *Palaeophycus tubularis* (r), *Palaeophycus sulcatus* (s), *Scolicia* (s), *Spirophycus* cf. *bicornis* (s), undeterminable spots (vf).
7	4–5	6/2–3	Fine-grained micaceous sandstone	**Full relief:** *Nereites* (vf), *Zoophycos* (vf), *Teichichnus* (c), *Palaeophycus tubularis* (r), undeterminable spots (vf).
8	5–6	6/2–3	Fine-grained micaceous sandstone; carbonate nodules	**Full relief:** *Nereites* (vf), *Zoophycos* (vf), *Teichichnus* (c), *Palaeophycus tubularis* (s), undeterminable spots (vf).
9	2.5–3	6/2–3	Fine-grained micaceous sandstone; clay lamina at the base	**Full relief:** *Nereites* (vf), undeterminable spots (vf). **Hyporelief to full relief at the base:** *Bifungites* (c), *Palaeophycus tubularis* (c), *Teichichnus* (r).
10	3–4	6/2–3	Fine-grained micaceous sandstone	**Full relief:** *Nereites* (vf), *Zoophycos* (vf), undeterminable spots (vf). **Epirelief:** *Teichichnus* (c), *Helminthopsis* (c), *Palaeophycus tubularis* (c), undeterminable crosscuttings of shafts (vf). **Hyporelief to full relief at the base:** *Jamesonichnites* (s).
11	3–4	lower part: 6/2; upper part: 2	Fine-grained micaceous sandstone; clay lamina at the base	**Full relief:** undeterminable spots (vf).
12	20	1–2	Laminated, finegrained, micaceous, carbonaceous sandstone; ripples at the top	**Full relief:** undeterminable spots (r). **Epirelief:** *Helminthopsis* (vf), *Bifungites* (c), *Nereites* (c), *Phycosiphon* (c), *Palaeophycus tubularis* (c), *Protovirgularia* (r), *Gordia* (s).
13	0–?	1–2	Lens of fine-grained, carbonaceous sandstone	**Full relief:** *Polykladichnus* (c).
14	1,5	6/2	Siltstone	**Full relief:** undeterminable spots (r).
15	3	2	Laminated siltstone	**Full relief:** undeterminable crosscuttings of shafts (vf).
16	2–4	1–3; uppermost part: 6	Laminated, fine-grained, micaceous, carbonaceous sandstone; clay lamina at the base	**Hyporelief to full relief at the base:** *Bifungites* (c), *Palaeophycus tubularis* (c), *Palaeophycus sulcatus* (r), *Megagrapton* (r). **Full relief:** *Zoophycos* (c), *Palaeophycus tubularis* (r), *Teichichnus* (r).
17	4–6	6/2–3; uppermost part: 1–2	Laminated, fine-grained, micaceous, carbonaceous sandstone	**Full relief:** *Nereites* (vf), *Zoophycos* (vf), *Planolites* (c), *Palaeophycus tubularis* (c), undeterminable spots (vf).
18	5–6	6/2–3	Fine-grained, micaceous, carbonaceous sandstone	**Full relief:** *Zoophycos* (vf), *Teichichnus* (c), *Nereites* (c), *Planolites* (c), *Palaeophycus tubularis* (c), *Arenicolites* (s), *Jamesonichnites* (s), *Polykladichnus* (s), undeterminable spots (vf).
19	6	6/2–3	Fine-grained, micaceous, carbonaceous sandstone	**Full relief:** *Zoophycos* (vf) *Nereites* (c), *Planolites* (r), *Jamesonichnites* (r), undeterminable spots (vf).
20	6–7	1; uppermost part: 2	Micaceous clayey limestone, partly laminated	**Full relief:** undeterminable spots (r). **Penetrating from overlying strata:** *Zoophycos* (r), *Teichichnus* (r).
21	2.5–3.5	6/2–3	Fine-grained, micaceous sandstone; clay lamina at the base	**Full relief:** *Zoophycos* (c), *Teichichnus* (c), undeterminable spots (vf).
22	6	4–5	Laminated, finegrained, micaceous sandstone; clay lamina at the base	**Full relief:** *Zoophycos* (vf), *Teichichnus* (c), *Palaeophycus tubularis* (r), *Palaeophycus sulcatus* (s), undeterminable spots (vf).
23	6–8	6/2–3	Fine-grained, micaceous sandstone; clay lamina at the base	**Full relief:** *Zoophycos* (vf) *Nereites* (vf), *Teichichnus* (c). **Epirelief:** *Nereites* (vf), *Bifungites* (c), *Palaeophycus tubularis* (c), *Planolites* (r), *Helminthopsis* (r), *Jamesonichnites* (r), *Spirophycus* (s). **Penetrating from overlying strata:** *Teichichnus* (c).

Table 1. continued

Layer No.	Thickness (cm)	Ichnofabric index	Lithology	Ichnofossils and ichnofabric
24	5–7	6/2–3; uppermost part: 1–2	Fine-grained micaceous sandstone, laminated in the uppermost part	**Hyporelief to full relief at the base:** *Bifungites* (c), *Palaeophycus tubularis* (c), *Teichichnus* (c). **Full relief:** *Zoophycos* (vf) *Nereites* (vf), *Teichichnus* (c) *Palaeophycus tubularis* (r), undeterminable spots (vf).
25	5	6/2–3	Fine-grained micaceous sandstone; clay lamina at the base	**Hyporelief to full relief at the base:** *Bifungites* (c), *Palaeophycus tubularis* (c), *Teichichnus* (c). **Full relief:** *Zoophycos* (vf) *Nereites* (vf), *Teichichnus* (c), *Palaeophycus tubularis* (c), undeterminable spots (vf). **Epirelief:** *Nereites* (vf), *Bifungites* (c), *Palaeophycus tubularis* (c), *Planolites* (r), *Jamesonichnites* (r).
26	3–4	6/2–3	Fine-grained micaceous sandstone	**Hyporelief to full relief at the base:** *Bifungites* (c), *Palaeophycus tubularis* (c), *Teichichnus* (c). **Full relief:** *Zoophycos* (vf) *Nereites* (vf), *Teichichnus* (c), *Palaeophycus tubularis* (c), *Planolites* (r), *Jamesonichnites* (r), *Arenicolites* (s), undeterminable spots (vf).
27	3–4	6; uppermost part 1–2	Fine-grained micaceous sandstone, ripples on top	**Full relief:** *Zoophycos* (vf) *Nereites* (vf), undeterminable spots (vf). **Epirelief:** *Palaeophycus tubularis* (c).

Intensity of bioturbation. It was specified using the ichnofabric index scale (abbreviated to ii) as presented by Droser and Bottjer (1986). The ii was determined for separate beds in their entirety; lower, middle and upper parts of a bed were specified where possible. Particular values of ii are listed in Table 1 and on Text-fig. 4. Most of the studied beds are entirely bioturbated and homogenized (i.e., ii = 6) and the ii of subsequent bioturbation structures in the same substrate mostly attains values between 2 and 3 (Text-fig. 7). Because of this intense bioturbation, primary sedimentary structures are not preserved. It is a limiting factor for sedimentological interpretations. Sandstones occurring approximately in the middle portion of the section (layers No. 12, 13, 15, 16 and 20) are an exception as they show well-preserved parallel lamination and/or ripple bedding.

Backfill. An active backfill of burrows can be clearly distinguished from passive infill in the studied material. Most of the passively filled traces were preserved with a muddy dark-coloured infilling; the same material forms thin dark intercalations in the sandstone layers. On the contrary, actively filled burrows are filled with material similar to the host rock. In the case of *Zoophycos*, oblique entrance tunnels and marginal tunnels are filled with dark mudstone; the spreite itself, however, is filled with material derived from the host rock. *Arenicolites* and *Polykladichnus* represent the best examples of passive infill.

Cross-cutting relationships and the succession of ichnotaxa. All crosscuttings of determinable ichnofossils were recorded during fieldwork to document the succession of burrows in the substrate. Only 20 undoubted cases were recorded. Therefore, an accurate succession could not be modelled. Despite this, variable cross-cutting relationships were discovered. Namely, *Nereites* tunnels preserved in full relief are cross-cut by *Zoophycos* and both these ichnogenera are cross-cut even by *Teichichnus*. *Thalassinoides* and *Bifungites* are also cross-cut by *Teichichnus*. Thus, *Teichichnus* represents the youngest component of the preserved ichnofabric. This ichnogenus together with *Zoophycos* constitute the late phase of the ichnotaxa succession. Thus, certain life strategies represented by body fossils clearly appeared at the same time, as indicated by the mutual cross-cutting.

Depth of individual burrows. Several of the studied layers at the section (particularly layer No. 1) preserve a frozen ichnofabric/tiering profile (Savrda and Bottjer 1986), in which the depth intervals for individual ichnotaxa were ascertained. They were transformed into the ichnofabric and tiering models (Text-fig. 5).

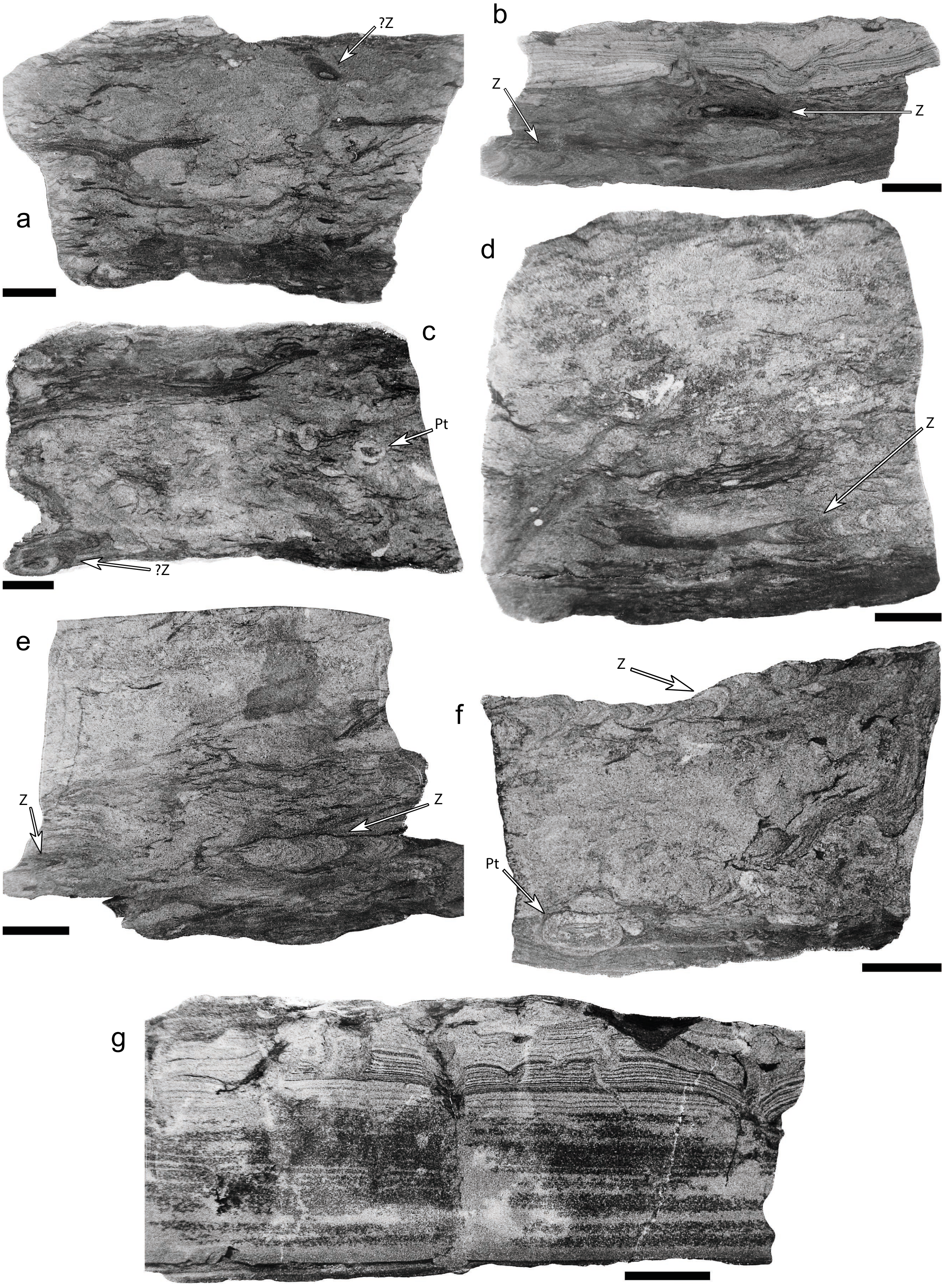
The ichnofabric model represents a generalised view of the ichnofabric as visible in the section. In fact, it is a rather “cumulative” temporal record. The tiering model, on the other hand, presents the distribution of trace fossils at a particular point in time. In the studied sequence, both models are similar to each other in the above-mentioned “frozen” beds. Only *Teichichnus* can be interpreted as the burrow of a multi-layered colonizer. All other recorded ichnotaxa resulted from the activity of single-layer colonizers.

Systematic synopsis

The finds of ichnofossils were determined mostly on the ichnogeneric level, to avoid unnecessary speculations regarding the absence or presence of sometimes speculative ichnospecific ichnotaxobases. The ichnogeneric level corresponds better with the way of preservation of most of the studied trace fossils. All the ichnotaxa are arranged in alphabetical order.

Arenicolites isp. (Text-fig. 9a) occurs as simple vertical U-shaped burrows, unlined, with the shafts perpendicular to the bedding. The openings are 3–4 cm apart and ca. 2–3 cm deep. Systematic classification follows the papers of Crimes et al. (1977) and Bjerstedt (1988).

Bifungites isp. (Text-fig. 9b–f) is a horizontal trace, dumb-bell-like, with two chambers/lobes joined by a tunnel.



Text-fig. 7. Vertical polished sections of samples from selected layers. a: Layer No. 2, completely bioturbated, collection of the Czech Geological Survey (abbr. BK), BK 7; b: Layer No. 3, low: nearly completely bioturbated, upper: cross- to ripple bedding, weakly bioturbated, BK 6; c: Layer No. 7, incompletely bioturbated siltstone/mudstone, BK 5; d: Layer No. 8, low: totally bioturbated background with *Zoophycos* ichnofabric, upper: spotted, completely bioturbated siltstone, BK 4; e: Layer No. 8, low:

From each of the chambers, a short shaft, up to 3 mm long, protrudes upwards; it is usually not preserved. The centres of the lobes are 2 to 4.5 cm (exceptionally 6 cm) apart. The width of the horizontal tunnel varies from 3 to 8 mm. One specimen yielded a longitudinally doubled horizontal tunnel. Determination follows Gutschick and Lamborn (1975).

Didymaulichus isp. (Text-figs 9g, 11a) is a horizontal, epichnial, bilobated ridge, slightly curved, smooth, 6 cm long and 0.5 cm wide. The systematics follows the work of Young (1972).

Gordia isp. (Text-fig. 10a) is represented by a shallow, 3 cm long and 1 mm wide epichnial furrow, twice looping, once falsely branching. Systematic classification is based on Davies et al. (2006), Lin et al. (2010).

Helminthopsis isp. (Text-fig. 10b–c) is present as horizontal, smooth grooves, moderately winding to irregularly meandering; branching, if present, appears to be false. The preserved length varies from a few centimetres up to 15 cm, the width ranges from 2 to 5 mm. The grooves occur as concave epireliefs or endichnial full reliefs. *Helminthopsis* isp. can pass gradually to the structure described below as *Nereites* isp.; hence, it can be presumed that at least some specimens of both traces were produced by the same trace makers. The systematic classification of *Helminthopsis* follows the papers by Fillion and Pickerill (1990) and Wetzel and Bromley (1996).

Jamesonichnites isp. (Text-fig. 10d) was observed in the form of cross-cuttings of vertical, very thick-bedded shafts. These are often in clusters or rows (2–5 shafts altogether). The overall diameter of a shaft hole is 4 to 8 mm, the thickness of the lining is 2 to 4 mm. Cross-cuttings of the shaft were found mostly on the upper bedding planes. Analogous structures were described by Mikuláš (1990) as a new ichnogenus and ichnospecies *Liholites vinolentus*. According to the original description, it is characterised by U-shaped, shallow tubular traces with extremely thick lining. Structures of the same character were described by Dam (1990) and assigned to a new ichnogenus *Jamesonichnites*. As the latter name was published several months prior to the former, *Liholites* is a junior synonym of *Jamesonichnites* (Mikuláš 1998a).

? *Megagrapton* isp. occurs as smooth, shallow, 1–2 mm wide, irregularly branched grooves (concave hyporeliefs or convex epireliefs) that presumably represent remains of irregular networks. Overall size of the preserved fragments ranges from 3 to 7 cm. The systematic classification is based on the criteria given by Uchman (1998).

Nereites isp. (Text-fig. 10e–i) is represented by horizontal, loosely meandering traces usually 2–7 cm long and 4–10 mm wide, preserved as concave epireliefs or full reliefs. The traces are trough-like, with elevated, irregularly lobated lateral ridges in the former case. If a full relief, they are flat tunnels, filled with dark clayey material, often with poorly visible meniscate backfill. The systematics is based on Uchman (1995).

Palaeophycus sulcatus Miller et Dyer, 1878 is represented by simple, horizontally lined tunnels (one specimen is falsely branched; Text-fig. 8d), 4–15 cm long and 5–12 mm wide, preserved in full reliefs or as convex hyporeliefs. Their surface possesses shallow irregular longitudinal striation/sulcation. The systematics follows Pemberton and Frey (1982).

Palaeophycus tubularis Hall, 1847 (Text-fig. 11b–d) consists of smooth, horizontal to subhorizontal, lined burrows. These are few cm long (up to 20 cm), and 2 to 10 mm wide. They occur either as full reliefs or semireliefs. Some specimens are secondarily flattened by compaction, which may lead (especially on upper bedding planes) to a brittle deformation of the lining; the collapsed tunnels thus have a bilobate surface. The trace is placed in *P. tubularis* in accordance with Pemberton and Frey (1982).

Phycosiphon isp. (Text-fig. 11e) is represented by minute horizontal to subhorizontal lobes preserved as concave epireliefs. A spreiten-structure can be observed inside the lobes in part of the samples. Maximum length of an individual lobe is 5 cm. These traces occur in clusters. Their classification follows Wetzel and Bromley (1994).

Planolites isp. consists of straight to moderately curved, smooth, unlined, simple horizontal tunnels, 2–10 cm long and 4–10 mm in diameter. The tunnels are filled either with material analogous to the surrounding rock, or with a contrasting, fine-grained dark clay/silt. *Planolites* isp. is classified in accordance with Pemberton and Frey (1982).

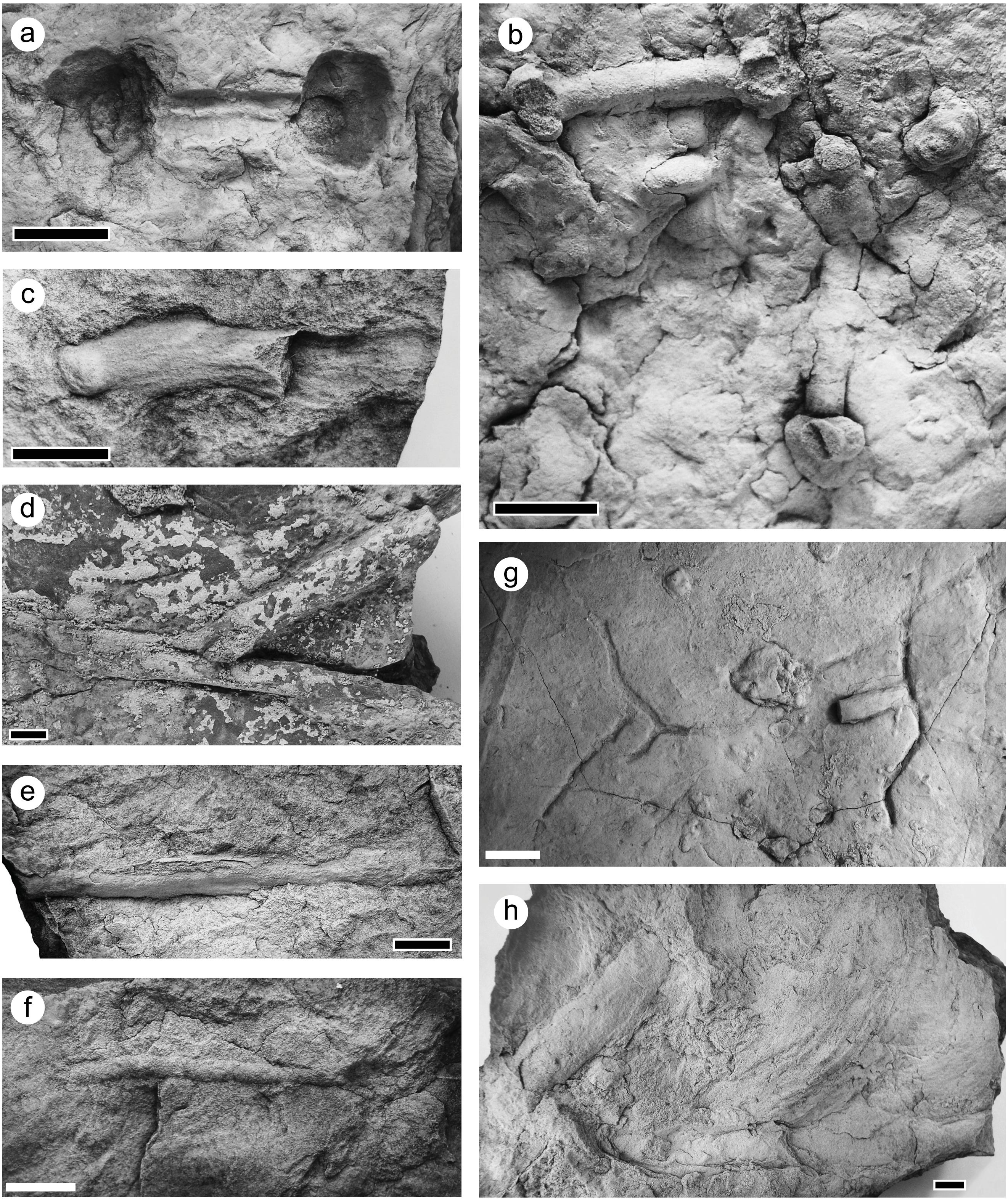
Polykladichnus isp. (Text-fig. 11f) is composed of vertical and oblique shafts, circular in cross-section, 2–6 mm in diameter that branch upwards at acute angles. They are preserved as full reliefs; filled with contrasting dark clay/silt. The structure is assigned to *Polykladichnus* in accordance with Fürsich (1981).

?*Protovirgularia* isp. (Text-fig. 11g) is a minute chainlike concave epirelief composed of a row of meniscate to broad V-shaped or U-shaped pits. The width of these traces ranges between 1 and 1.5 mm, the length of the cope of specimens is 5 and 13 cm. One specimen is straight, another meandering. Assignment to *Protovirgularia* is suggested based on Uchman (1998), although the specimens also resemble some taphonomy-influenced types of *Nereites* (Uchman 1995).

"*Scolicia*" isp. (Text-fig. 11h) is a horizontal, tightly meandering epichnial form composed of a median tunnel and broad margins. The tunnel fill is composed of fine-grained sandstone; the margins consist of finer/silty material. The trace is 19 cm long. Medial tunnel size is 5–8 mm in diameter, the margins are 6–12 cm wide; therefore, the overall width of the trace reaches 29–30 mm. In basic morphology, the discovered specimen resembles *Scolicia* sensu Uchman (1998); however, a reliable determination as *Scolicia* is not possible due to the lack of significant morphological features.

Spirocircus isp. is a flat tape in full relief forming several circular loops that mostly overlap each other. The diameter of the loops is ~18 cm, the width of the tape varies between 1.2 and 1.6 mm. Systematics of the trace is based on Mikuláš

totally bioturbated background with *Zoophycos* ichnofabric, upper: spotted, completely bioturbated siltstone, BK 3; f: Lower part of layer No. 24, completely bioturbated siltstone with *Zoophycos* and *Palaeophycus*, BK 1; g: Layer No. 16, planar-laminated fine grained sandstone with mechanical structures and bioturbation of its topmost part, BK 2. Scale bar = 1 cm; Z = *Zoophycos*; ?Z = cf. *Zoophycos*; Pt = *Palaeophycus tubularis*.

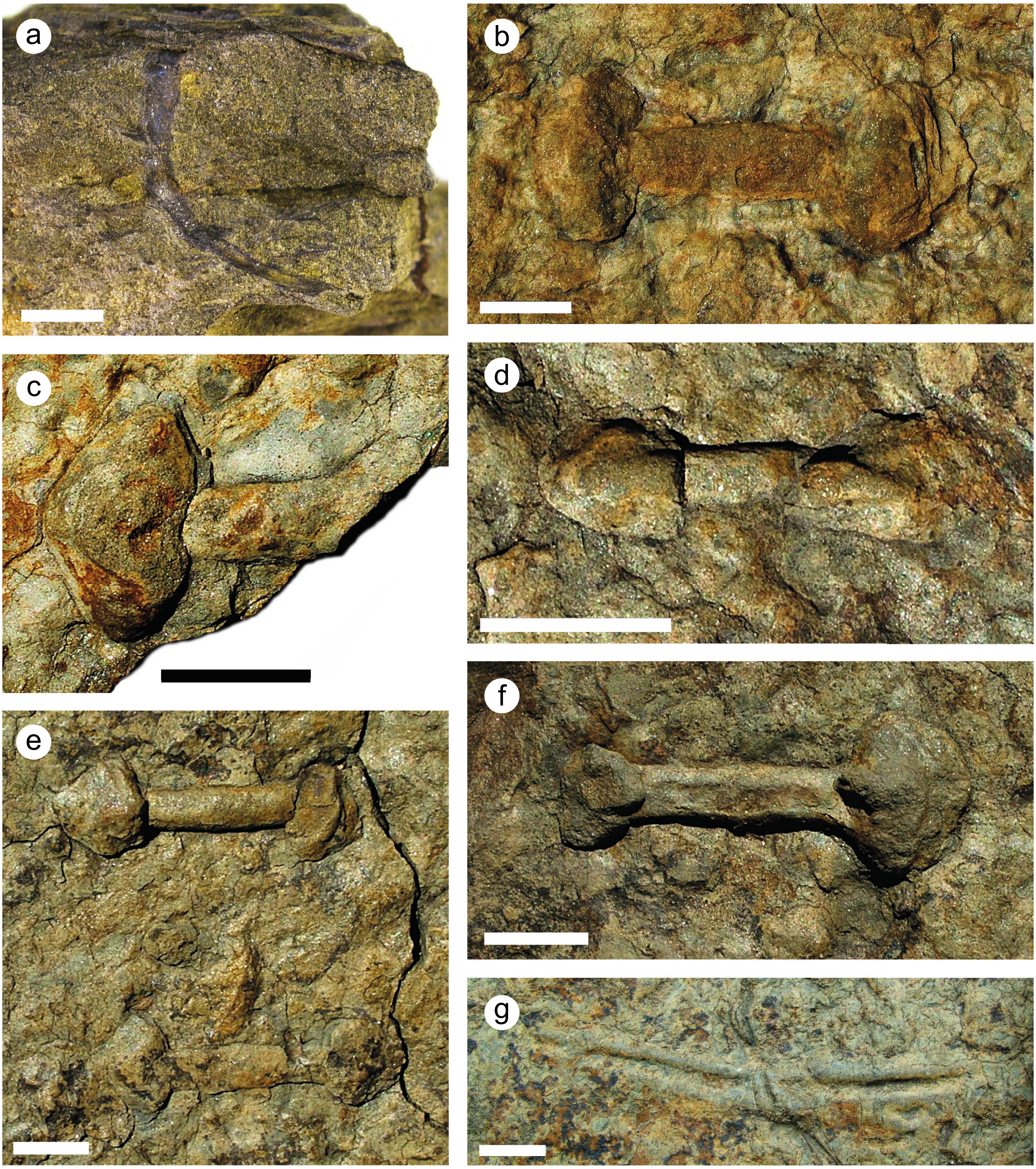


Text-fig. 8. a, b: *Bifungites* isp. with fragments of vertical shafts, a – concave hyporelief BK 20, Layer No. 26, b – full relief BK 33, Layer No. 23; c–e: *Palaeophycus sulcatus* (Miller et Dyer, 1878), c – BK 29, Layer No. 22, d – BK 18, Layer No. 16, e – BK 31, Layer No. 6; f: *Palaeophycus* cf. *tubularis* Hall, 1847, BK 25, Layer No. 22; g: *Megagrapton* isp., concave hyporelief, BK 32, Layer No. 16; h: *Teichichnus* isp. (bottom) crossing *Zoophycos* isp. (centre to right bottom), BK 16, Layer No. 22. Scale bar = 1 cm.

(1998c). The ichnogenus requires revision as the type ichnospecies of *Spirocircus* was assigned to *Gyrochorte* by Uchman and Hanken (2013).

Spirophycus cf. *bicornis* (Heer, 1877) (Text-fig. 12a) is a cylindrical, almost horizontal, 0.6 to 1.0 cm wide, approx. 20 cm long, meandering tunnel preserved in full relief. At one end, the tunnel is coiled into a spiral. The trace is classified in accordance with Książkiewicz (1977).

Spirophycus isp. (Text-fig. 12b) is a horizontal tunnel, 4 mm wide, becoming spirally coiled towards one end, the

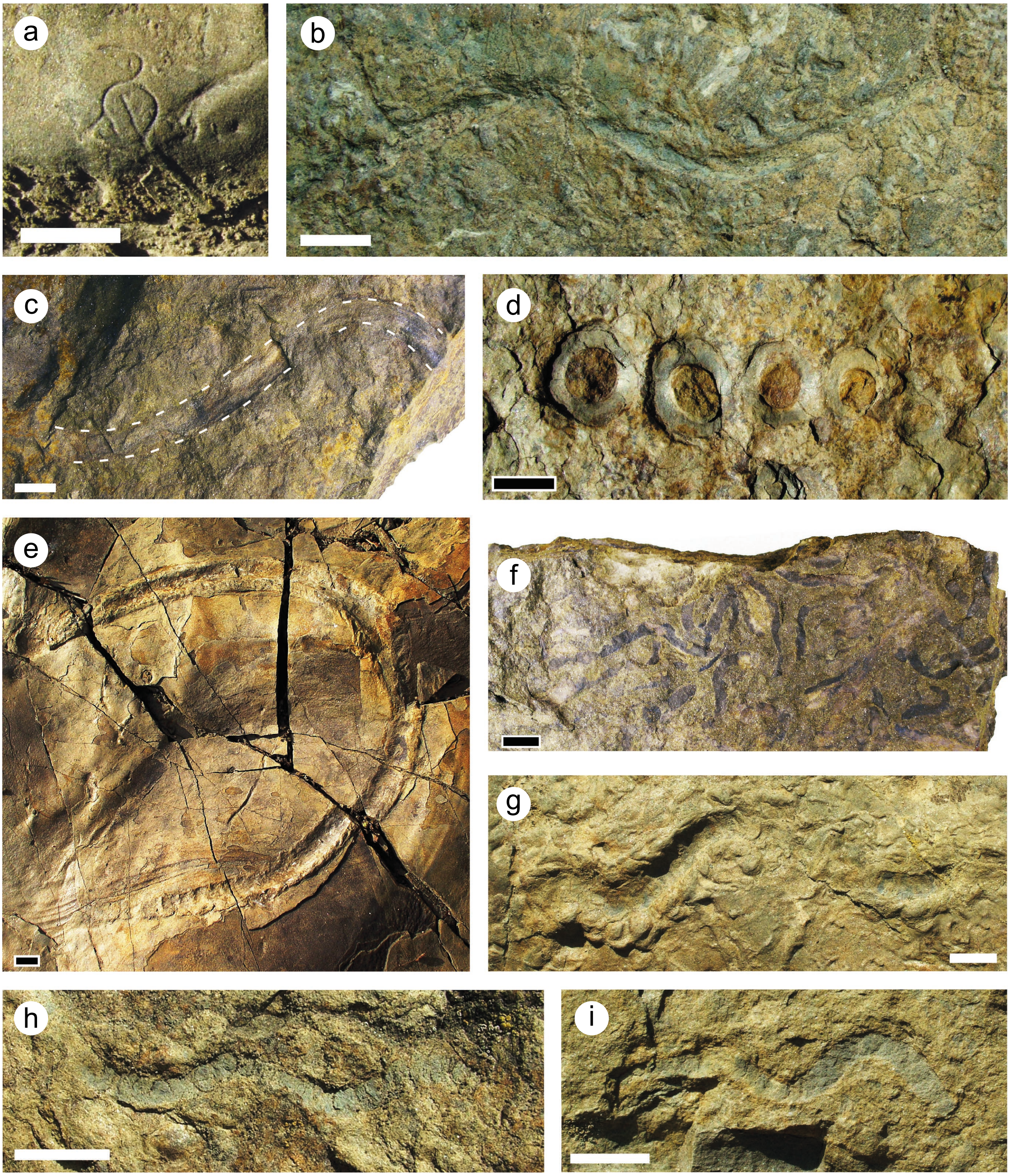


Text-fig. 9. a: *Arenicolites* isp., BK 13, Layer No. 6; b–f: *Bifungites* isp., a set of specimens showing variability in chamber shape, b – field photograph, Layer No. 23, c – field photograph, Layer No. 23, d – field photograph, Layer No. 23, e – parallel-orientated specimens, field photograph, Layer No. 23, f – field photograph, Layer No. 23; g: *Didymaulichnus* isp., convex epirelief, field photograph, Layer No. 1. Scale bar = 1 cm.

spiral is 10 mm in diameter. Another tunnel emerges at an angle of 80° from the spiral region; it is straight, 20 mm long.

Teichichnus isp. (Text-fig. 12c–e) is a vertical spreiten-structure consisting of a set of smooth, flattened, horizontal to subhorizontal troughs and a marginal tunnel. The spreite in some cases branches at acute angles. Most of the spreiten-structures are retrusive (i.e., the spreite was produced from downwards to upwards). Each spreite consists of 3–10 troughs 10–30 mm wide and up to several decimetres in length, occasionally more than 50 cm. *Teichichnus* occurs as full relief regardless of its position within beds; it often penetrates bed boundaries. The systematic assignment follows Seilacher (1955) and Baldwin (1977).

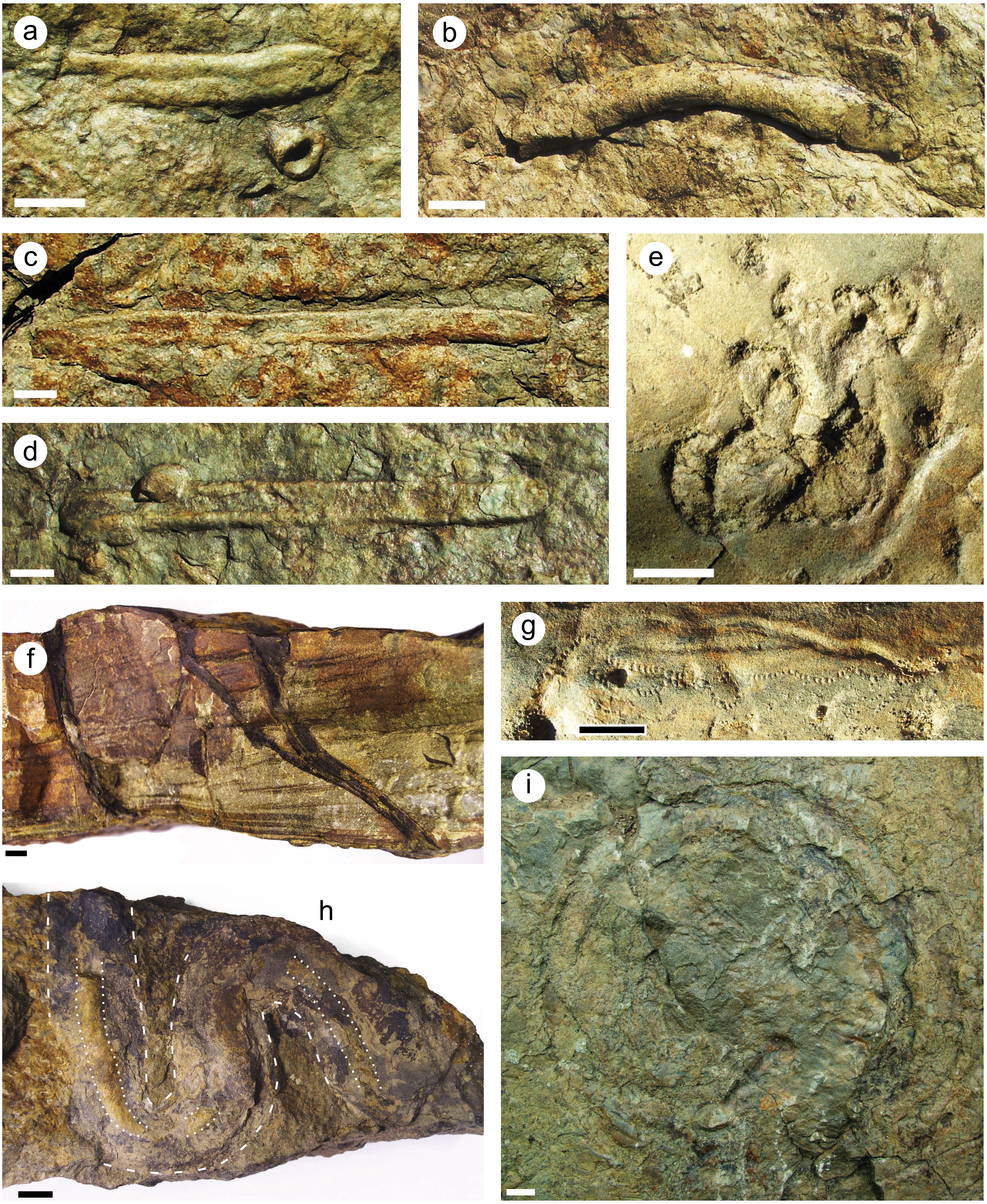
Thalassinoides isp. (Text-fig. 12f–g) consists of horizontal, compacted tunnels organised as a more-or-less regular pentagonal to hexagonal networks developed in



Text-fig. 10. a: *Gordia* isp., concave epirelief, field photo, Layer No. 12; b, c: *Helminthopsis* isp., b – field photo, Layer No. 1, c – BK 34, Layer No. 6; d: *Jamesonichnites* isp., horizontal cross-section of broad lined shafts, field photo, Layer No. 23; e–i: *Nereites* isp., e – concavo-convex epirelief, field photo, Layer No. 12, f – full relief of the Nereites ichnofabric, BK 14, Layer No. 2, g – concave epirelief, field photo, Layer No. 12, h, i – full relief solitary specimens, field photo, Layer No. 8. Scale bar = 1 cm.

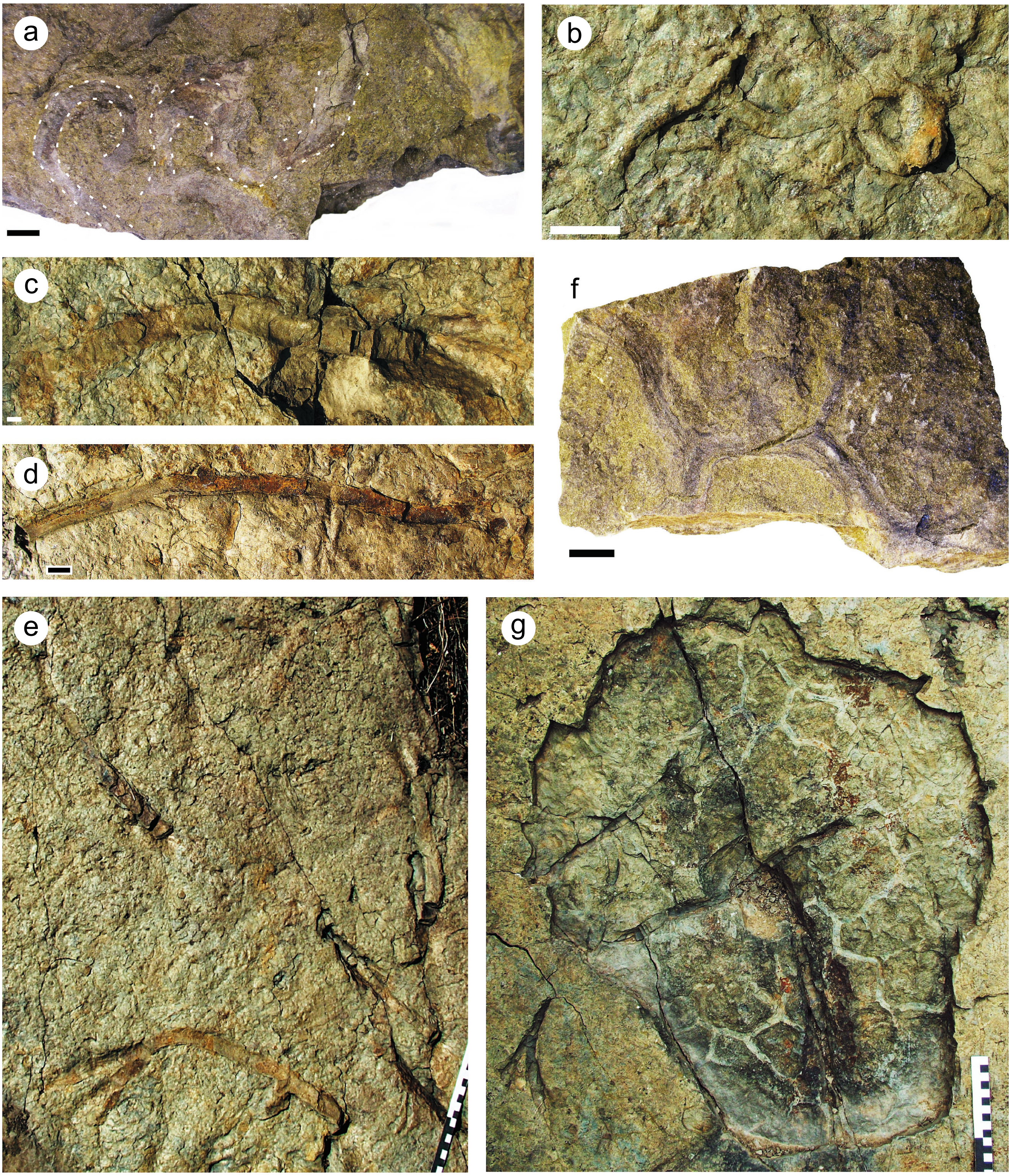
full relief, usually 1–2 cm below the upper bedding plane of "frozen" beds. The tunnels are 7–10 cm in length, wide, smooth to irregularly, sparsely sulcated. Individual meshes of the network are usually 4–6 cm wide; branchings are typically Y-shaped. The maximum measured size of the whole structure is 60 × 40 cm. The systematic assignment is in accordance with Mikuláš (1990).

Zoophycos isp. (Text-fig. 13a–i) is represented by large, horizontal to (more often) subhorizontal spreiten structures of variable shape and size. Most of them are basically lobate, helicoid- or propeller-shaped, or they represent combinations of these shapes. Neighbouring spreiten-structures are in some cases interconnected by straight, curved or meandering tunnels. A spreite is usually formed mostly of the same



Text-fig. 11. a–d: *Palaeophycus tubularis* Hall, 1847, full relief, mostly flattened, a – field photo, Layer No. 23, b – field photo, Layer No. 10, c – field photo, Layer No. 23, d – field photo, Layer No. 23; e: *Phycosiphon* isp., concave epirelief of spreite, field photo, Layer No. 12; f: *Polykladichnus* isp., full relief on a vertical rock section, BK 11, Layer No. 13; g: *Protovirgularia* isp., epirelief, field photo, Layer No. 12; h: *Scolicia* isp., BK 30, Layer No. 6; i: *Spirocircus* isp., field photo, Layer No. 1. Scale bar = 1 cm.

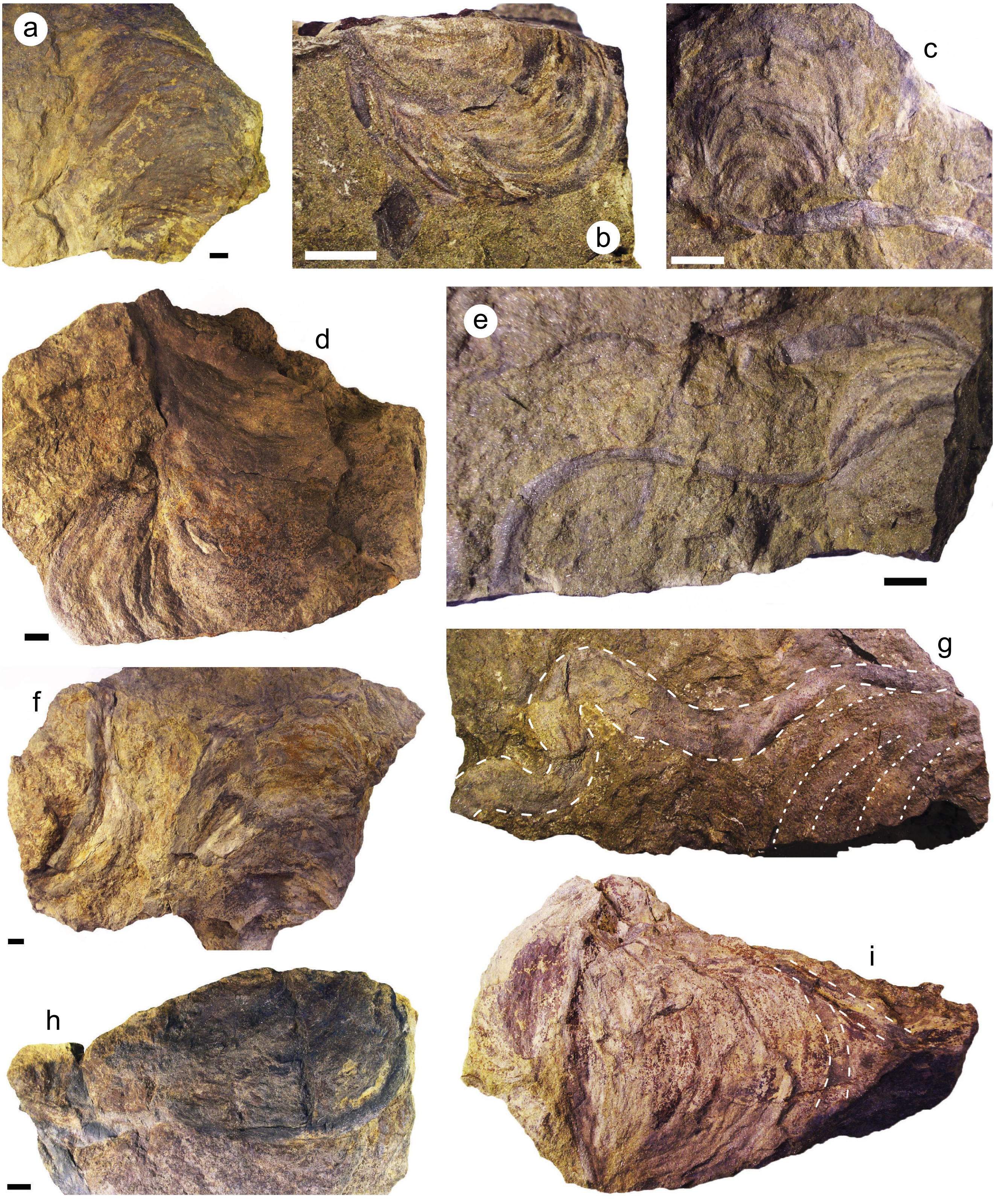
material as the host rock. Connecting and peripheral tunnels may either be filled with the host rock, or they may contain clayey material. The size of the spreiten-structures is between 3 to 30 cm; the tunnel diameter reaches from 4 to 20 mm. The tunnels themselves, if found aside the spreiten-structures, would probably be classified as *Planolites* or *Helminthopsis* (see above); otherwise, assignment of the complex traces to *Zoophycos* follows Uchman (1995).



Text-fig. 12. a: *Spirophycus* cf. *bicornis* (Heer, 1877), BK 19, Layer No. 6; b: *Spirophycus* isp., field photo, Layer No. 23; c–e: *Teichichnus* isp., full relief, partly weathered, from the upper side, field photos, Layers No. 23, 10 and 23; f, g: *Thalassinoides* isp., f – BK 12, Layer No. 4, g – field photo, Layer No. 1. Scale bar = 1 cm; field scale in centimetres.

Discussion

The existing studies of the Ordovician of the Prague Basin, on the Zahořany Formation, and particularly at the Loděnice – vinice site (Havlíček 1982, Mikuláš 1990, 1998a, Bokr 2007) interpret the layers of fine-grained sandstone in the described section as possible tempestites (storm layers), in most cases manifold reworked by bioturbation. The origin of tempestites was probably connected to a tectonically based elevation of the sea floor; deeper parts of the basin contained almost exclusively siltstone sedimentation without any indication of storm deposits (Mikuláš 1998a). Because of the sedimentation regime, the ichnoassemblage at Loděnice – vinice is considerably different when compared with many other sites, where only *Zoophycos* and a completely bioturbated background is typically observed (Mikuláš 1990).



Text-fig. 13. ***Zoophycos*** **isp. a: BK 17, Layer No. 6; b: BK 27, Layer No. 8; c: lateral tunnel continuing from spreite side to the surrounding rock, BK 28, Layer No. 23; d: BK 22, Layer No. 1; e: "juvenile" stage of the structure on a horizontal winding tunnel, BK 21, Layer No. 26; f: BK 24, Layer No. 17; g: broad winding tunnel adjacent to spreite, BK 26, Layer No. 6; h: BK 15, Layer No. 18; i: BK 23, Layer No. 2. Scale bar = 1 cm.**

The diversity of ichnofossils is augmented by the fact that not all the higher physical energy events were also sedimentation events. In several cases, the local material was only reworked, which left ripples and ripple bedding. The rippled surfaces bear minute surface ichnofossils preserved as epireliefs, and ripple-bedded layers may provide otherwise poorly preserved traces of shallow tiers. Good preservation of these traces was enabled by the low bioturbation of the ripple-bedded portions (ii = 1–2).

Yet another random circumstance contributed to the good preservation of ichnofossils: the usual thickness of layers (i.e., 5–8 cm) corresponds well to the maximum depth of bioturbation at the locality. Therefore, most colonizers are single-layered, and bed boundaries are clearly visible despite the high intensity of bioturbation. It is likely that the preservation of trace fossils was not even affected by any substantial erosion (and truncation of structures). There is no evidence of such erosion (except the rather thin ripple bedding), neither truncated beds, filled channels nor sorted bioclasts.

The above-mentioned circumstances contributed to the good preservation of both shallow and deeper tiers; moreover, the tiers can be convincingly distinguished. They are as follows, from the shallowest to the deepest: 1. *Bifungites*, 2. *Nereites* (+ *Arenicolites*), 3. *Thalassinoides*, 4. *Zoophycos*, 5. *Teichichnus*.

Compared to the Mesozoic and Cenozoic ichnoassemblages, knowledge of tiering in lower Palaeozoic assemblages is limited. Some evidence was presented in the summary paper by Mángano et al. (2016). These authors highlighted that during the GOBE (i.e., Great Ordovician Biodiversification Event), the complexity of tiering increased; however, they quoted only a few specific examples; most of those are mentioned in the following:

Seilacher (2000) and Mángano and Buatois (2011) recorded gradual moving of the ichnogenera *Arthrophycus* and *Phycodes* to deeper tiers during the Ordovician. Several authors concentrated on the ichnogenus *Trichophycus*, which already appeared as a deep-tier trace fossil during the lower Cambrian in the palaeocontinent Laurentia; in peri-Gondwana, the same ichnofossil would be expected in an analogous position, as late as the base of the Ordovician (e.g., Jensen 1997, Mángano and Buatios 2011). However, Mikuláš (2001) described the trace fossil *Rejkovicichnus* Mikuláš et al., 1996 (probably synonymous with *Trichophycus*) from a middle Cambrian deep tier in the peri-Gondwana Bohemian Massif.

Knowledge of the Ordovician occurrences of the deeper-tier ichnogenus *Thalassinoides* is relatively extensive (e.g., Sheehan and Schieffelbein 1984, Droser and Bottjer 1989, Dronov et al. 2002). However, Ordovician *Thalassinoides* are mostly reported from limestones. Furthermore, the hypothesis presented by Knaust and Dronov (2013) suggests that a certain (possibly substantial) proportion of the Ordovician *Thalassinoides* may be more accurately accommodated in the ichnogenus *Balanoglossites* Mägdefrau, 1932.

A rather complex tiering system can be found as early as middle Cambrian; the locality Buchava (the Czech Republic; Mikuláš 2000) provided clues for identification of the succession/tiering *Planolites* – *Thalassinoides* – *Teichichnus*. However, density of occurrence of these trace fossils at Buchava is low and thus the interpretation is rather uncertain.

In the above-mentioned sequences in the Upper Ordovician of the east Baltic region, the following tiering succession was recorded: shallow thin shafts – *Thalassinoides*/*Megagrapton* – *Teichichnus* – (*Chondrites*) were found in the sediments affiliated to the regional stratigraphic stage Kunda. The underlying Volkhov sedimentary sequence contains numerous hardgrounds; tiering patterns (and distribution of trace fossils in general) follow the substrate consistency (surface crusts covering softer deeper levels; patchy hardgrounds) rather than depth in the substrate (Dronov et al. 2002).

There is still no report of the ichnogenus *Zoophycos* among the representatives of lower Palaeozoic deeper tiers; from this point of view, the occurrence, density and tiering pattern of *Zoophycos* at the Loděnice – vinice locality is crucial.

Mángano et al. (2016) did not mention the ichnogenus *Zoophycos* in their chapter on the ichnology of GOBE; neither is it quoted among the typical shallow-marine trace fossils nor among the deep-marine ones; furthermore, *Zoophycos* is not named among trace fossils typical in the Ordovician carbonates. The work of Mángano et al. (2016) emphasizes the dissimilarity (i.e., the simplicity) of the Cambrian to Ordovician tiering patterns in comparison to the Mesozoic and Cenozoic in-faunal tiering patterns. The ichnoassemblage, described in detail herein, nevertheless shows several common features with Mesozioc and Cenozoic trace fossil assemblages, in particular the deep-sea ones (Mángano and Buatois 2016: Chapter 9). Generally, the downward succession *Nereites* – *Thalassinoides* – *Zoophycos* is typically “Mesozioc and Cenozoic” (Mángano and Buatois 2016: Chapter 9, and references therein).

Conclusions

1) Siliciclastic tempestites of the Upper Ordovician of the Prague Basin (Bohemian Massif, peri-Gondwana area) yielded an ichnoassemblage that exhibits a clearly demonstrable tiering pattern in the order from the shallowest to the deepest: 1. *Bifungites*, 2. *Nereites* (+ *Arenicolites*), 3. *Thalassinoides*, 4. *Zoophycos*, 5. large *Teichichnus*. The above mentioned ichnofossils occur in the studied locality Loděnice – vinice in large amounts, altogether producing an Ichnofabric Index usually of a value of 4–5. Other collected ichnogenera were found in limited numbers; therefore, they could not be assumed to be connected to the tiers where they were found.
2) The ichnogenus *Zoophycos* Massalongo, 1855, i.e., the key ichnofossils in the ichnoassemblage studied herein, was found in the suite corresponding to lower Palaeozoic shallow-marine trace fossils, in a relatively deep tier.
3) In comparison with the so far described tiering patterns of the GOBE (Great Ordovician Biodiversification Event), the here described ichnoassemblage shows close relationships to the Mesozoic and Cenozoic assemblages of siliciclastic deep-marine sediments, namely proximal turbidites. The studied locality shows unique taphonomic circumstances for the preservation of the ichnoassemblage; therefore, we surmise that the uniqueness of the documented assemblage is more likely caused by these taphonomic circumstances than the actual “pre-maturity” of the seemingly advanced tiering pattern.

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