

# Ichnofabric and substrate consistency in Upper Turonian carbonates of the Bohemian Cretaceous Basin (Czech Republic)

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**Abstract:** The basal bed of the Upper Turonian sediments at the Úpohlavý Quarry, corresponding to clayey limestone in its character, bears obvious signs of rapid lithification from softground to firmground (*Ophiomorpha-Thalassinoides-Spongeliomorpha*). Immediately before reaching the firmground stage, the substrate was colonized by tracemakers of chemichnia (*Chondrites*). Biogenic reworking of the overlying, irregularly rhythmically bedded limestone/marlstone beds does not fit the idea that the differences between the limestone and marlstone ichnofabrics are due to primary fluctuations in oxygen content in water and in sediments. Documentation of a section of approximately 10–13 m above the base of the succession revealed that bioturbation down to the depth of ca. 20 cm is more intensive in beds with higher calcium carbonate content (*Thalassinoides* often passively filled with clay-richer substance and subsequently colonized by *Chondrites* tracemakers). Beds with lower calcium carbonate content are usually dominated by *Chondrites* but *Thalassinoides*, *Palaeophycus* and *Phycodes* are also present. These differences in ichnofabrics rather indicate a different succession of colonization (marls — *Chondrites* followed by *Thalassinoides*; calcareous beds — *Thalassinoides* followed by *Chondrites* filling the *Thalassinoides* burrows). Therefore, the consistency of the substrate and its increase through time after depositional events, and the content of primary organic matter widely used by the “homogenizers” of marly substrates were the decisive factors. After a partial compaction, the substrate was utilized by less demanding r-strategic substrate feeders (tracemakers of ichnogenus *Phycosiphon*) and lastly by chemosymbionts, which also made successful use of the trapping potential of abandoned domichnia. This situation (i.e. high concentration of fluids in abandoned tunnels) is also evidence of a considerable compaction and rapid diagenesis of limestones, allowing even surfaces of limestone beds to function as firmgrounds.

**Key words:** Cretaceous, Czech Republic, Ichnofossils, shallow-marine settings, firmground, softground.

## Introduction

The active quarry at Úpohlavý located 70 km NW of the centre of Prague is one of the most significant exposures of Upper Cretaceous sediments in the northwestern Bohemian Cretaceous Basin. The mining area includes extensive areal exposures suitable for collection of macrofauna as well as fresh and easily accessible vertical sections. This makes the quarry area a favourable excursion (Čech et al. 1996) and collection site, a subject of sequence-stratigraphic analysis (Svobodová et al. 2002; Laurin, pers. comm. 2003) and an important finding place of unique fauna (plesiosaurid teeth; Ekrt et al. 2001).

Bioturbation structures (effect of sediment mixing due to biogenic activity) and ichnofossils (individualized biogenic structures) are very common. All aspects of the fossil record formed by bioturbation and bioerosion in all scales (i.e. ichnofabric) are directly related to the ongoing sequence stratigraphic studies (Laurin, pers. comm. 2003) as well as to the paleontological and paleobiological research (e.g. Ekrt et al. 2001). The knowledge of this topic is fragmentary; however, lists of ichnotaxa in the Coprolite Beds and the overlying beds together with elementary spatial relations and descriptions of complex ichnofabrics in marlstone beds were provided by Laurin (1996). The study of ichnofabrics should respect the succession of substrate colonization, thus avoiding the principal pitfalls of the

“Seilacherian” ichnofacies analysis; the problem of ichnofabric interpretation lies, however, in the fact that most ichnotaxa can be hardly determined from vertical sections (cf. Uchman & Mikuláš 2002). The gap in the understanding of the locality thus lies in the absence of “classic” systematic ichnological studies, which would not only improve the interpretation of ichnofabrics but also serve as material for comprehensive paleobiological studies. The significance of the Úpohlavý locality is given by the number of specific situations observed, suitable for fabrication of general schemes. Moreover, these situations are framed by the completed or culminating sequence stratigraphic and paleozoological studies. The aim of the paper is to display the interaction between bottom colonization and substrate consistency, which can be considered a relevant contribution to the integration of the ichnofacies studies based primarily on substrate quality (cf. Buatois et al. 1998) and ichnofabric study based on the succession of the individual episodes of bioturbation and bioerosion (Bromley 1996).

## Description of the locality

The Úpohlavý Quarry displays Upper Turonian sediments (lower part of the Teplice Formation) in a thickness of ca. 25 m. The lowermost beds are exposed primarily in a system of drainage ditches and retention pools. They are

formed by dark grey marlstones with scarce fossils. The uppermost part of this member contains two highly fossiliferous beds with increased calcium carbonate contents. These beds can be petrologically characterized as limestones with a high admixture of clay and silt, and frequent primary and diagenetic inhomogeneities (phosphorite-rich coprolites; ichnofabric-controlled concretionary structures). They are traditionally termed the Lower and Upper Coprolite Beds. Higher above, clayey limestones close to classic "opukas" alternate with light grey to dark grey marlstones; both these lithotypes are exploited for cement production. The first 8 meters above the Upper Coprolite Bed are strongly dominated by limestones. In the following 8 m, the two lithotypes alternate rhythmically, with limestone beds from 0.4 to 2 m thick and marlstone beds from 0.2 to 0.8 m thick. The top part of the preserved sedimentary succession (approx. 5 m, see Fig. 6.1) is dominated by marlstones (4 beds, 0.5–1.3 m in thickness) prevailing over limestones (4 beds, 0.3, 0.2, 0.4 and 0.8 m thick, respectively) (Čech et al. 1996; Ekrt et al. 2001; Svobodová et al. 2002; Laurin pers. comm. 2003).

### A review of previous ichnological research

Laurin (1996) provided a survey of ichnological data from the section and summarized them in the paper of Čech et al. (1996). In the Lower Coprolite Bed, he recognized macroborings of clionid sponges within thick prismatic layers of inoceramid bivalve shells; phosphate particles are bored, for example by *Gastrochaenolites* isp. The lower contact of the bed is densely penetrated by a monotypic omission surface suite of burrows (*Thalassinoides ?suevicus*). Infills of the burrows are rich in skeletal as well as non-skeletal coarse-grained detritus. In the interval between the coprolite beds, relics of primary stratification are recognizable; *Chondrites*, *Planolites*, *Trichichnus* and *?Helminthopsis* constitute a low-abundance trace fossil assemblage. Laurin (1996) also noted complex ichnofabrics with generally moderate to high ichnodiversities in the succession of rhythmically bedded calcareous mudstones and limestones; the most common ichnotaxa include *Thalassinoides*, *Planolites*, *Chondrites*, *Palaephyucus*, *?Astrosoma* and *Taenidium*. A channel incised into slightly deformed units described above bears frequent skeletal particles at its base, some of them having traces of macro- and microbioerosion; at the base, an omission suite of burrows is well developed. The channel fill, formed mostly by calcareous mudstone to wackestone, revealed sparse ichnofabric dominated by *Anconichnus horizontalis*, *?Muensteria* isp., and *Bergaueria* isp. It should be noted that the "ichnogenus" *Muensteria* is not recommended for further use by Mikuláš & Uchman (1996) for the heterogeneity of the type material, and that Laurin (1996) designated as *?Muensteria* isp. most probably *Taenidium*-like traces.

### Systematic ichnology

The ichnotaxa described below are grouped into informal groups; the groups are ordered according to the fre-

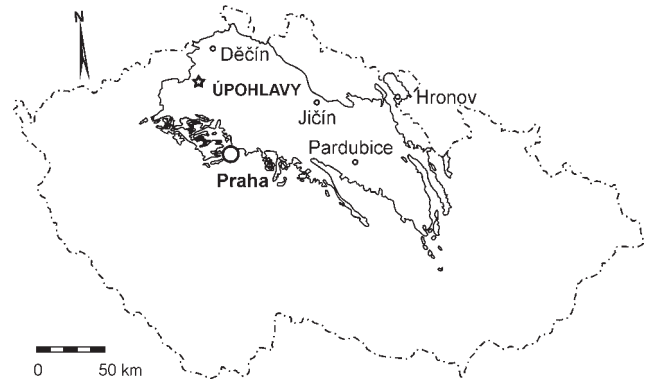


Fig. 1. A sketch map of the Czech Republic showing the extent of the Bohemian Cretaceous Basin (area bordered by the continuous line) and the location of the Úpohlavý Quarry (marked by an asterisk).

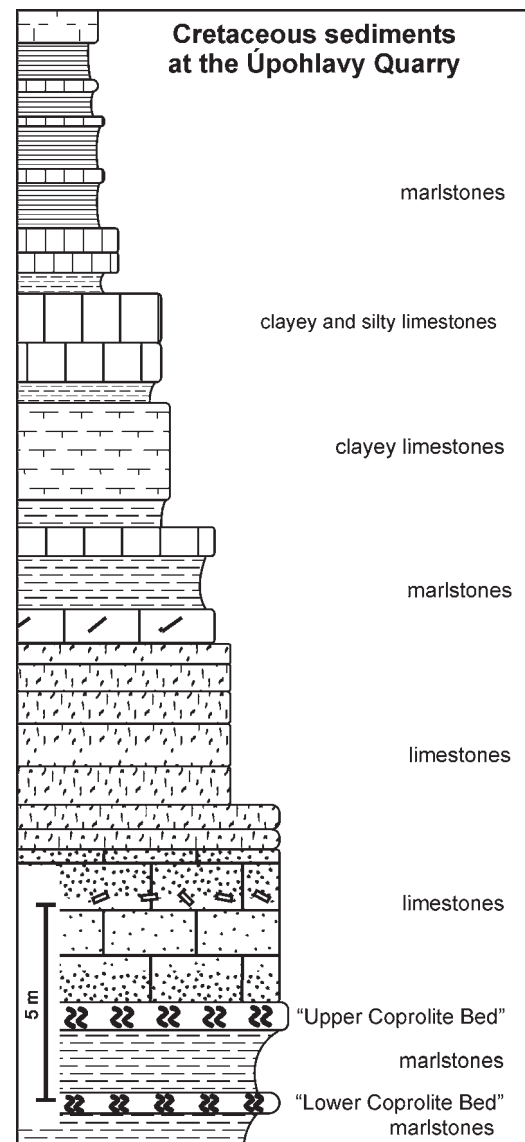
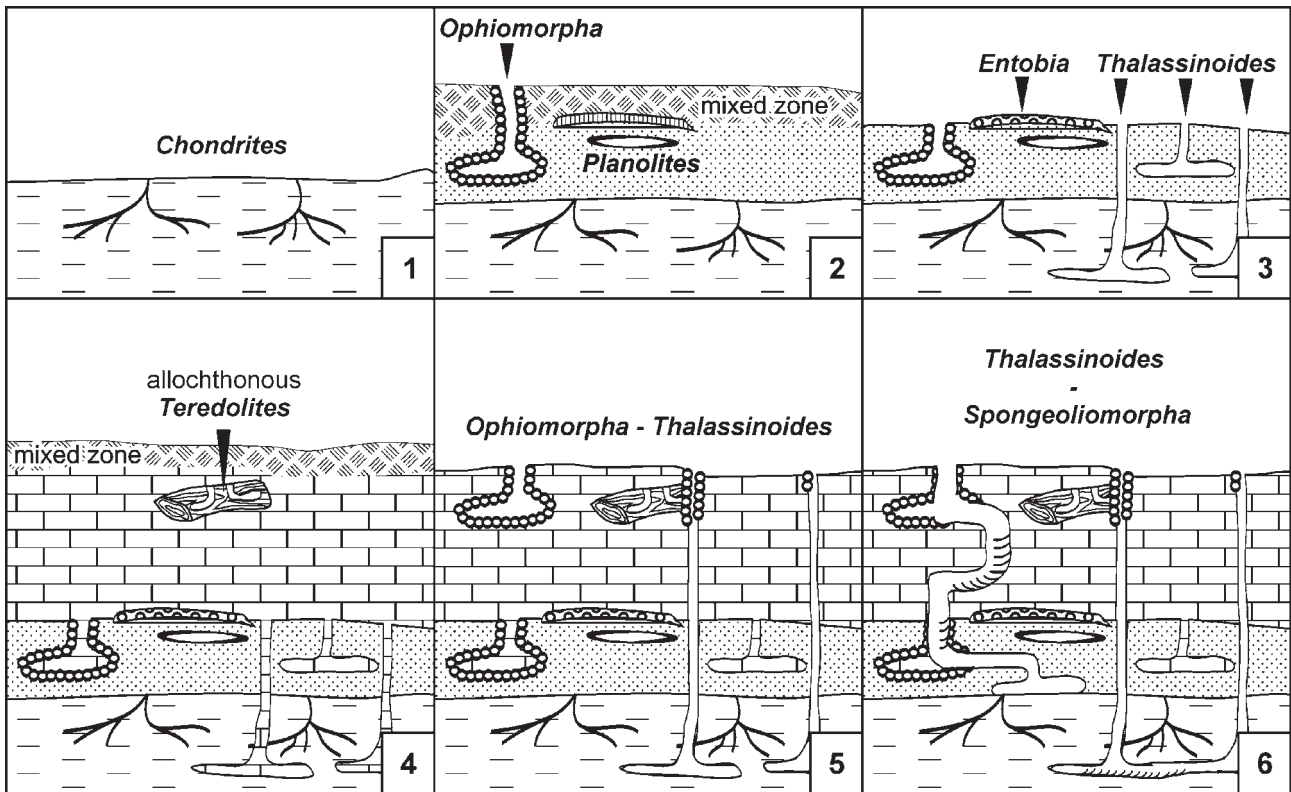


Fig. 2. Lithofacies of the Upper Turonian in the Úpohlavý Quarry (after Košťák et al. 2003).



**Fig. 3.** Ichnological, sedimentation/erosion and hardening story of the Upper Coprolite Bed reconstructed according to the exposure in the SW part of the Úpohlavy Quarry. Overall thickness of the figured sediment is approximately 50 cm; not to the scale. **1** — colonization of marlstones by the tracemaker of *Chondrites*; **2** — deposition of calcareous siltstone with bioclasts; mixing the upper layer; origin of lined burrows of the ichnogenus *Ophiomorpha*; **3** — erosion of the mixed layer and appearance of firmground; colonization window functioned for bioclasts (*Entobia*) as well as for the firmground (*Thalassinoides*); **4** — deposition of clayey limestone with bored pieces of wood; mixing its uppermost part; origin of lined burrows of the ichnogenus *Ophiomorpha*; **5** — erosion of the mixed layer; the substrate remains soft; origin of softground/shiftground burrows *Ophiomorpha*/*Thalassinoides*; **6** — compaction and early diagenesis of the substrate; re-elaborating the existing burrows in the firmground (appearance of *Spongiomorpha* isp.).

quency of their representatives and importance for the interpretation of the ichnofabrics.

The depicted material is, at present, housed in the Institute of Geology, AS CR Prague. It will be subsequently delivered to the National Museum in Prague. A few specimens are in private collections as indicated in the figure captions.

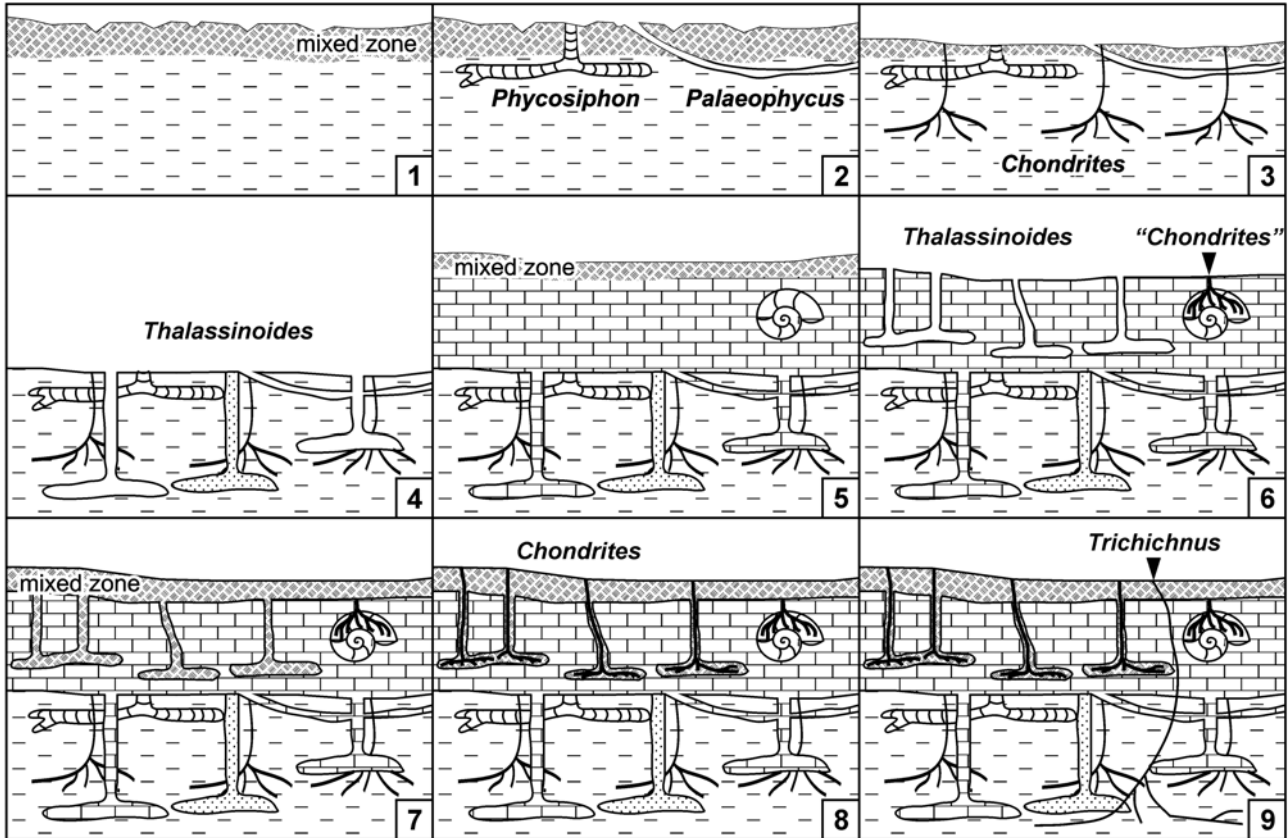
**Branched structures related to the *Ophiomorpha* group**

*Spongiomorpha* de Saporta, 1887  
*Spongiomorpha* isp.  
 Fig. 5.1,4,8

**Material:** Ten fillings of simple tunnels or segments of branched systems, either collected or documented *in situ* from the Upper Coprolite Bed.

**Description:** Horizontal to inclined, cylindrical tunnels 14 to 20 mm in diameter, locally branching, with no lining of walls and sharp, thin ridges and grooves on walls. These sculptures are usually subparallel and meet at very acute angles. They are roughly parallel (Fig. 5.1), diagonal to almost perpendicular (Fig. 5.8) to the tunnel axes.

**Remarks:** A factually and historically complicated discussion is being continued on the validity or, more exactly, synonymy of ichnogenera *Spongiomorpha* de Saporta, 1887, *Thalassinoides* Ehrenberg, 1944 and *Ophiomorpha* Lundgren, 1891. Schirf (2000) advocated the synonymy of all the above mentioned genera pointing out that transitional forms are often found, and morphological differences depend exclusively on the character of the tunnel wall (*Spongiomorpha*: ridges and grooves after exploitation of firmground mud; *Ophiomorpha*: knobby lining in loose substrates; *Thalassinoides*: lined or unlined tunnels in softgrounds). Most reactions to this proposal are, however, reserved, as in most cases the tracemaker (usually whole populations of decapods) created tunnels in sediments of more or less uniform consistency. Regardless of the ichnotaxonomic interpretation, however, the study of these traces gives a good chance to track down the changes in substrate consistency in time and space. For example, Fig. 5.8 shows a thin cylinder of *Spongiomorpha* isp. adjoining to a larger cylinder of *Thalassinoides* isp. The succession of trace fossils well documents the rapidly increasing hardness of the substrate.



**Fig. 4.** Ichnological, sedimentation/erosion and hardening history of the rhythmically alternating beds ca. 10–13 m above the Upper Coprolite Bed. Reconstructed on the basis of exposures in the SW part of the Úpohlavý Quarry. Overall thickness of the figured sediment is approximately 90 cm; not to the scale. **1–3** — colonization of marlstone; **4** — truncation; **5** — deposition of silty limestone; **6** — colonization of resulting firmground; **7** — deposition of clayey layer and passive filling of the open burrows; **8** — re-colonization of the filled burrows and inner space of nautiloid shells; **9** — origin of *Trichichnus* isp.

*Ophiomorpha* Lundgren, 1891

*Ophiomorpha* isp.

Fig. 5.2,3

**Material:** Six tunnel fillings or segments of branched systems, collected or documented *in situ* from the Upper Coprolite Bed.

**Description:** Fragments of fillings of simple vertical shafts or systems of vertical shafts and horizontal tunnels having circular cross-sections 18–20 mm in diameter. Walls lined by oval granules 1–2 mm in size, produced by agglutination of the ambient substrate.

**Remarks:** See remarks to ichnogenus *Spongiomorpha*.

*Thalassinoides* Ehrenberg, 1944

*Thalassinoides* isp.

Figs. 5.5,6,8,10; 6.2,4,5,7; 7.1,4,5,7–9.

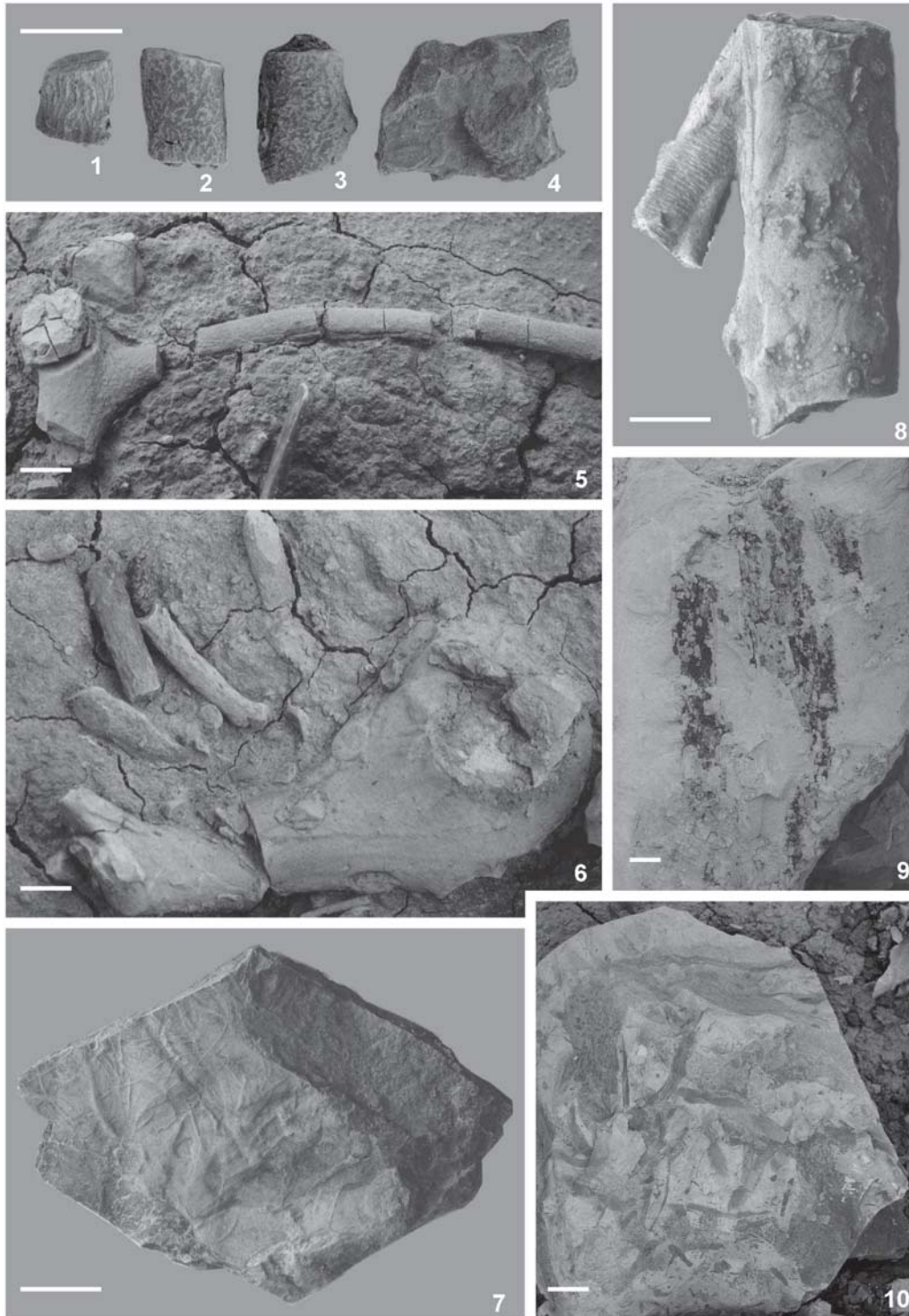
**Material:** Tens to hundreds of tunnels and tunnel systems, collected or documented *in situ* or in blocks of rock on spoil tips in all units and lithotypes of the Úpohlavý Quarry.

**Description:** Horizontal or vertical, more rarely inclined, filled tunnels and shafts forming commonly branched systems. Tunnel diameters are not constant within

the whole systems in the Upper Coprolite Bed; some tunnels have diameters several times larger than the others (Fig. 5.5–6; usually 1.5–4 cm in diameter) and often broaden in the proximity of branching. Tunnels are smooth and unlined. Their fill is homogeneous, structureless; the tunnels may differ from the ambient rock in their petrological composition (higher carbonate content, higher degree of lithification, diagenetic effects — formation of concretions). Transitions to ichnogenus *Ophiomorpha* (remnants after pelletal imprints in walls) or *Spongiomorpha* (scratches) are common. Vertical range of some systems exceeds 50 cm. The system was probably functioning for a number of generations of tracemakers and maybe even hosted different biotaxa at different times. It was rebuilt many times, as evidenced by the crossing of tunnels bearing typical features of all three participating ichnotaxa.

In the limestones and marlstones of the lower part of the Teplice Formation, traces classified as *Thalassinoides* are present with different frequencies as densely branched systems including horizontal tunnels (ca. 80 %) and inclined or vertical shafts (ca. 20 %). Tunnel diameters are usually constant in the whole system (roughly 1–1.5 cm), exceptionally larger near the branching.





**Fig. 5.** Trace fossils from the Upper Coprolite Bed and the overlying clayey limestones. **1, 4, 8** — *Spongliomorpha* isp.; **2, 3** — *Ophiomorpha* isp.; **5, 6, 8, 10** — *Thalassinoides* isp.; **7 (partim), 10 (partim)** — *Chondrites* isp.; **9** — *Teredolites clavatus* Leymerie, 1842. Scale bar = 2 cm.

Tunnels are unlined, smooth, and filled with homogeneous sediment, generally contrasting with the surrounding rock in its petrological composition. The tunnels are sometimes lined by trough-like forms (i.e. spreiten-structures), which were formed during the reconstruction of

damaged or unsatisfactory segments of the system, and which represent relicts of older tunnels. Fillings are repeatedly reworked by other tracemakers (see Description and Remarks to ichnogenus *Chondrites*).

**Remarks:** See remarks to ichnogenus *Spongliomorpha*.

*Phycodes* Richter, 1850  
cf. *Phycodes* isp.  
Fig. 6.6

**Material:** The only find from the bed of light grey marlstone some 10 m above the Upper Coprolite Bed.

**Description:** Horizontal system of smooth tunnel fillings having oval cross-sections, preserved in full relief. The specimen is composed of the main tunnel ("runway" sensu Uchman & Mikuláš 2002) and three tunnels branching in a fan-like manner. All tunnels are lined by trough-like structures (spreiten); different magnitudes of mutual displacement of the "troughs" and their different numbers in each tunnel result in different widths of the individual branches: 9 mm; 12 mm; 22 mm.

**Remarks:** In its general construction plan, the described trace fossil equals the ichnogenus *Phycodes* (see, e.g. Fillion & Pickerill 1990); it cannot be, however, excluded — due to the uniqueness of the find — that it is a morphologically abnormal segment of *Thalassinoides*.

### Borings

*Teredolites* Leymerie, 1842  
*Teredolites clavatus* Leymerie, 1842  
Fig. 5.9

**Material:** A singular find of coalified wood with borings, found in clayey limestones some 2 m above the Upper Coprolite Bed.

**Description:** Borings in wood, teardrop to spherical in shape, 3–6 mm in maximum diameter.

**Remarks:** Borings of bivalves which serve dwelling purposes (i.e. not traces after feeding on wood substrate). For ethological and ichnotaxonomic classification see Kelly & Bromley (1984).

*Teredolites longissimus* Kelly et Bromley, 1984

**Material:** A singular find of coalified wood with a boring in clayey limestones some 2 m above the Upper Coprolite Bed.

**Description:** Borings in wood, elongate, cylindrical in shape, ca. 5 mm in maximum diameter, with calcite linings.

**Remarks:** For classification see Kelly & Bromley (1984).

*Entobia* Bronn, 1837  
*Entobia* cf. *cretacea* (Portlock, 1843)

**Material:** Two finds of shell fragments of bivalve *Inoceramus* sp. with the described trace fossil from the Upper Coprolite Bed.

**Description:** Filled chambers of roughly oval, egg-shaped or irregular nodular shape, with smooth surface, interconnected with all neighbouring chambers by thin tunnels. The whole trace fossil thus forms a network developed several mm below the surface of the shell fragment. The chambers are 3–6 mm in diameter, the tunnels

ca. 0.3 mm in diameter; the removed material represents approx. 50 % of the original mass of the shell.

**Remarks:** Clionid sponges were mostly bored by tracemakers of the ichnogenus *Entobia*. *Entobia* isp. is very frequent approximately from the mid-Mesozoic at all places where hard carbonate substrates in marine settings (rocky coasts, lithoclasts or bioclasts) are exposed to high physical-energy conditions for at least the life cycle of the tracemakers (i.e. months and years on average); deep- and quiet-water representatives have also been recorded but they are not so diverse and frequent (cf. Bromley 1994).

### Spreiten-structures

*Phycosiphon* Fischer-Ooster, 1858  
*Phycosiphon incertum* Fischer-Ooster, 1858  
Fig. 7.6

**Material:** Several finds in a block of light grey marlstone from a broken bed several meters above the Upper Coprolite Bed.

**Description:** Flat lamellae of darker reworked material indistinctly laminated due to biogenic activity (spreite), bounded by meandering lines which may represent poorly preserved marginal tunnels. Width of lobes 5–10 mm.

**Remarks:** Traces of complex feeding strategy, comprising sediment feeding and maybe also its modification (loosening) permitting repeated effective feeding on the same portions (cf. Wetzel & Bromley 1994).

### Simple structures

*Palaeophycus* Hall, 1847  
*Palaeophycus tubularis* Hall, 1847  
Fig. 7.3

**Material:** Approximately 10 specimens collected or documented *in situ* in a limestone bed ca. 16 m above the Upper Coprolite Bed and in limestone clasts on spoil banks of the quarry.

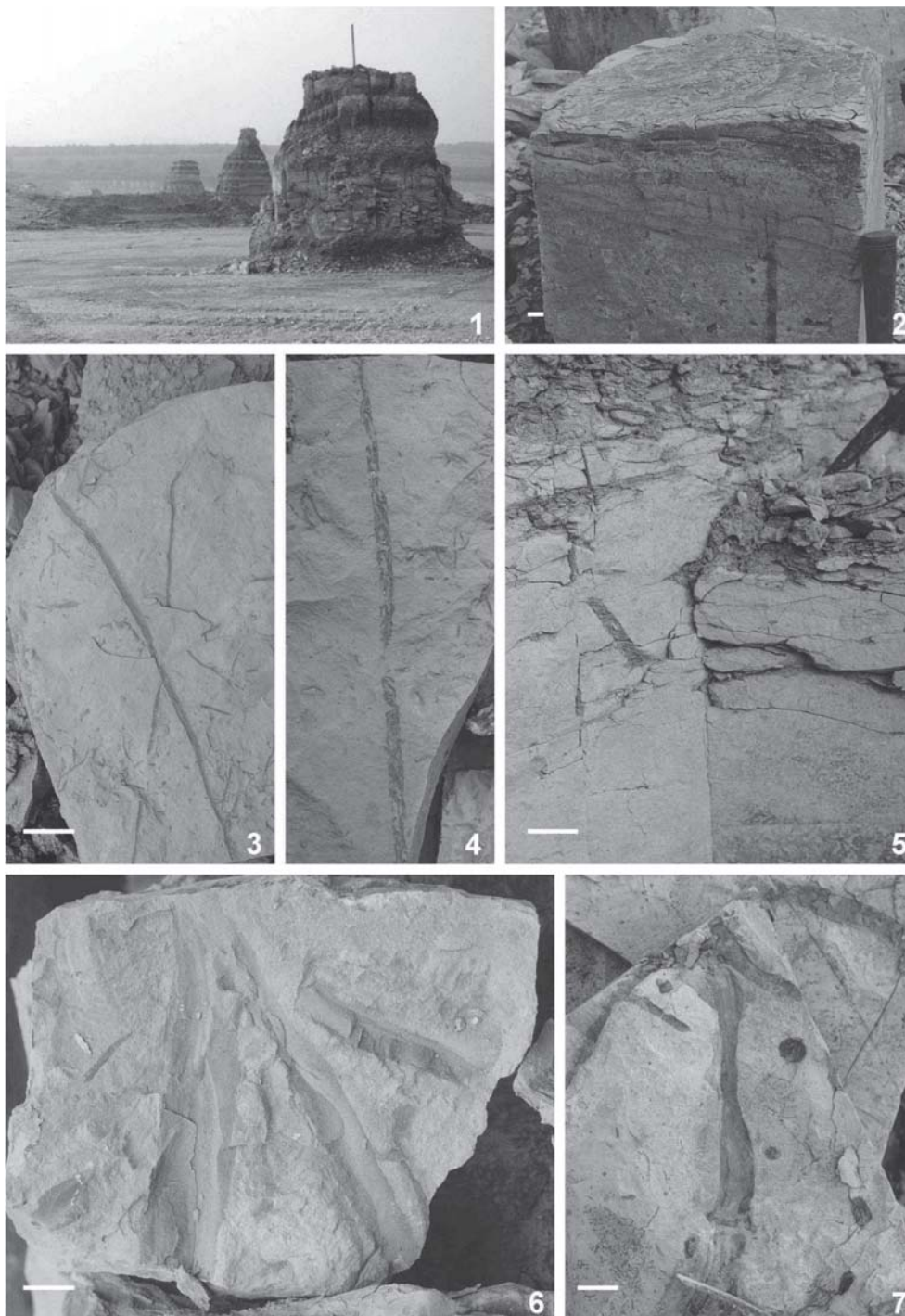
**Description:** Straight or slightly curved horizontal tunnels with a markedly smooth surface and a distinct lining. The tunnels are 3–4 mm in diameter, the traced segments are several cm to several tens of cm long.

**Remarks:** For taxonomy of *Palaeophycus* see Pemberton & Frey (1982). *Palaeophycus* is usually interpreted as dwelling burrows of predators.

*Planolites* Nicholson, 1873  
*Planolites beverleyensis* (Billings, 1862)  
Figs. 5.7 (*partim*), 7.2, 7.7 (*partim*)

**Material:** Several tens of observations *in situ* or on spoil banks, or collected specimens from the Upper Coprolite Bed and from different beds of light grey to dark grey marlstones of the Teplice Formation.

**Description:** Straight or curved, horizontal or inclined, mostly unbranched, smooth, filled tunnels, with no wall lining. The infill of the tunnels usually differs from



**Fig. 6.** Upper part of the Úpohlavy section: clayey limestones close to classic “opuka” lithotype alternating with light grey to dark grey marlstones. **1** — overall view of the outcrops; **2, 4, 5, 7 (partim)** — *Thalassinoides* isp.; **3 (partim)** — *Pilichnus dichotomus* Uchman, 1999; **4, 7 (partim)** — *Chondrites* isp.; **6** — *Phycodes* isp. from the bed of light grey marlstone some 10 m above the Upper Coprolite Bed. Scale bar = 2 cm.

the ambient rock in petrological character. The tunnels are about 10–20 mm in diameter, the traced segments are max. several tens of cm long.

**Remarks:** For discussion of *Planolites* see Pemberton & Frey (1982). *Planolites* is usually interpreted a sediment-feeding trace fossil or a locomotion trace fossil. Minute rock fragments of *Thalassinoides* cannot be dis-

tinguished from *Planolites* isp.; description of those ichnofossils on outcrops is therefore imperative. The identification of ichnospecies at the locality is possible by finds such as the one depicted on Fig. 7.2; here, two shells of *Inoceramus* sp. are interconnected by a broad curved tunnel, which is not connected with any two- to three-dimensional system of tunnels.



### *Branched structures of the Chondrites group*

*Pilichnus* Uchman, 1999

*Pilichnus dichotomus* Uchman, 1999

Fig. 6.3

**Material:** Several tens of observations *in situ* or on spoil banks, or collected specimens from different beds of light grey to dark grey marlstones of the Teplice Formation.

**Description:** A system of horizontal, straight or slightly curved, irregularly branching thin tunnels, usually ca. 1 mm wide, largely filled with material contrasting with the ambient substrate by its darkness. Branching takes place at angles close to 90° or at acute angles. Any indications of concentric structure are missing.

**Remarks:** Trace fossils of similar morphology from different (mostly pelitic formations) were described as *Chondrites* isp. by many authors. Uchman (1999) revealed the groundlessness of this interpretation and erected ichnogenus *Pilichnus*, which was also identified by Mikuláš (2003) in the Ordovician Šárka Formation of the Barrandian. The existing evidence suggests that these are “deep-tier” trace fossils, similarly like *Chondrites*, having a high potential for preservation.

*Chondrites* Sternberg, 1833

*Chondrites* isp.

Figs. 5.8 (*partim*), 5.10 (*partim*), 6.4 (*partim*),  
6.7 (*partim*), 7.4 (*partim*), 7.5 (*partim*), 7.7 (*partim*),  
7.8 (*partim*), 7.9 (*partim*)

**Material:** Hundreds observations in the field and dozens of collected specimens.

**Description:** Systems of narrow, inclined or subhorizontal, radially branching tunnels having circular cross-section, typically 1–2 mm in diameter, filling 1/5 to 1/20 of the substrate volume. More completely preserved systems have a fan-like appearance. The infill of the tunnels differs from the ambient rock in its composition — it is usually darker.

**Remarks:** *Chondrites* is one of the most common ichnofossils in fine-grained marine sediments. Its tracemaker was very abundant in conditions posing ecological stress for the rest of the infauna (lack of oxygen near the bottom and in the sediment, relatively deeply buried or already partly lithified substrates; see, e.g. Wetzel & Uchman 2001). From the ethological point of view, it represents probably most often “chemichnia”, structures developed to absorb methane and hydrogen sulphide from the sediment (see, e.g. Mikuláš 1997). As a result, the tracemaker of ichnogenus *Chondrites* was attracted by abandoned and passively filled tunnels of ichnotaxon *Thalassinoides* isp. In this case, once filled trace fossils were reworked repeatedly (see, e.g. Fig. 7.5). The limited space did not allow the *Chondrites* tracemakers to build classic radial structures, which generated a major problem for ichnotaxonomy (cf. Bertling et al. 2004). In such case, the analogy with borings is respected here (isomorphic and xenomorphic borings, cf. Bromley & D’Alessandro 1987): even highly bizarre forms (see Fig. 6.4) are attributed to ichno-

genus *Chondrites* because the tracemaker and the ethological purpose were probably identical with the “typical” *Chondrites*. More information on aberrant *Chondrites* can be found in the paper by Uchman & Wetzel (1999).

### *Trace fossils preserved on surfaces of internal moulds of nautiloids*

“*Chondrites*” isp.

Fig. 8.3,4

**Material:** Three finds of the fossil *Euthrepoceras* sp. with the described trace fossil from the limestones of the Teplice Formation (coll. J. Valíček and J. Filous).

**Description:** Filled tunnels resembling overlapping systems of the ichnogenus *Chondrites*, restricted exclusively to the surface of internal moulds of the nautiloid *Euthrepoceras* sp. They were probably formed in a soft fill of the shell of the dead nautiloid before its diagenetic dissolution.

**Remarks:** See remarks to the ichnotaxon “*Urohelminthoida*” isp.

“*Cochlichnus*” isp.

Fig. 8.6

**Material:** A singular find of the fossil *Euthrepoceras* sp. with the described trace fossil from limestones of the Teplice Formation (coll. Mr. Filous).

**Description:** Meandering, thin, shallow groove resembling the ichnogenus *Cochlichnus*, exclusively restricted to the surface of internal mould of the nautiloid *Euthrepoceras* sp. It probably originated in the soft fill of the shell of a dead nautiloid before its diagenetic dissolution.

**Remarks:** See remarks to the ichnotaxon “*Urohelminthoida*” isp.

“*Megagraption*” isp.

Fig. 8.1,2,5

**Material:** Three finds of the fossil *Euthrepoceras* sp. with the described trace fossil from limestones of the Teplice Formation (coll. J. Valíček and J. Filous).

**Description:** Systems of thin filled tunnels branching at angles close to 90° thus resembling the ichnogenus *Megagraption*, exclusively restricted to the surfaces of internal moulds of the nautiloid *Euthrepoceras* sp. They probably originated in the soft fill of the shell of a dead nautiloid before its diagenetic dissolution.

**Remarks:** See remarks to the ichnotaxon “*Urohelminthoida*” isp.

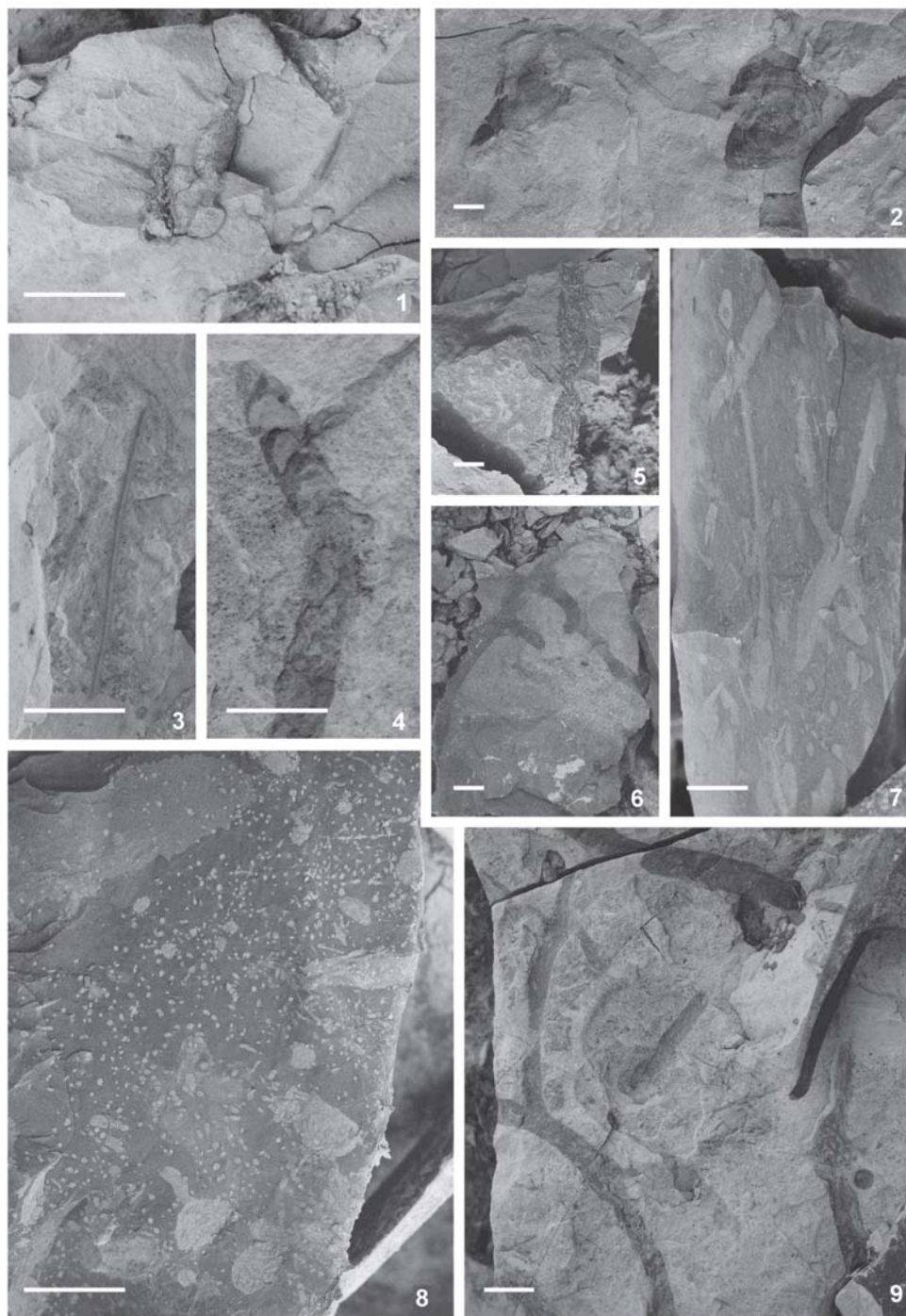
“*Urohelminthoida*” isp.

Fig. 8.5

**Material:** A singular find of the fossil *Euthrepoceras* sp. with the described trace fossil from limestones of the Teplice Formation (coll. J. Valíček).

**Description:** Systems of thin filled tunnels turning at acute angles, with short extensions behind the turns





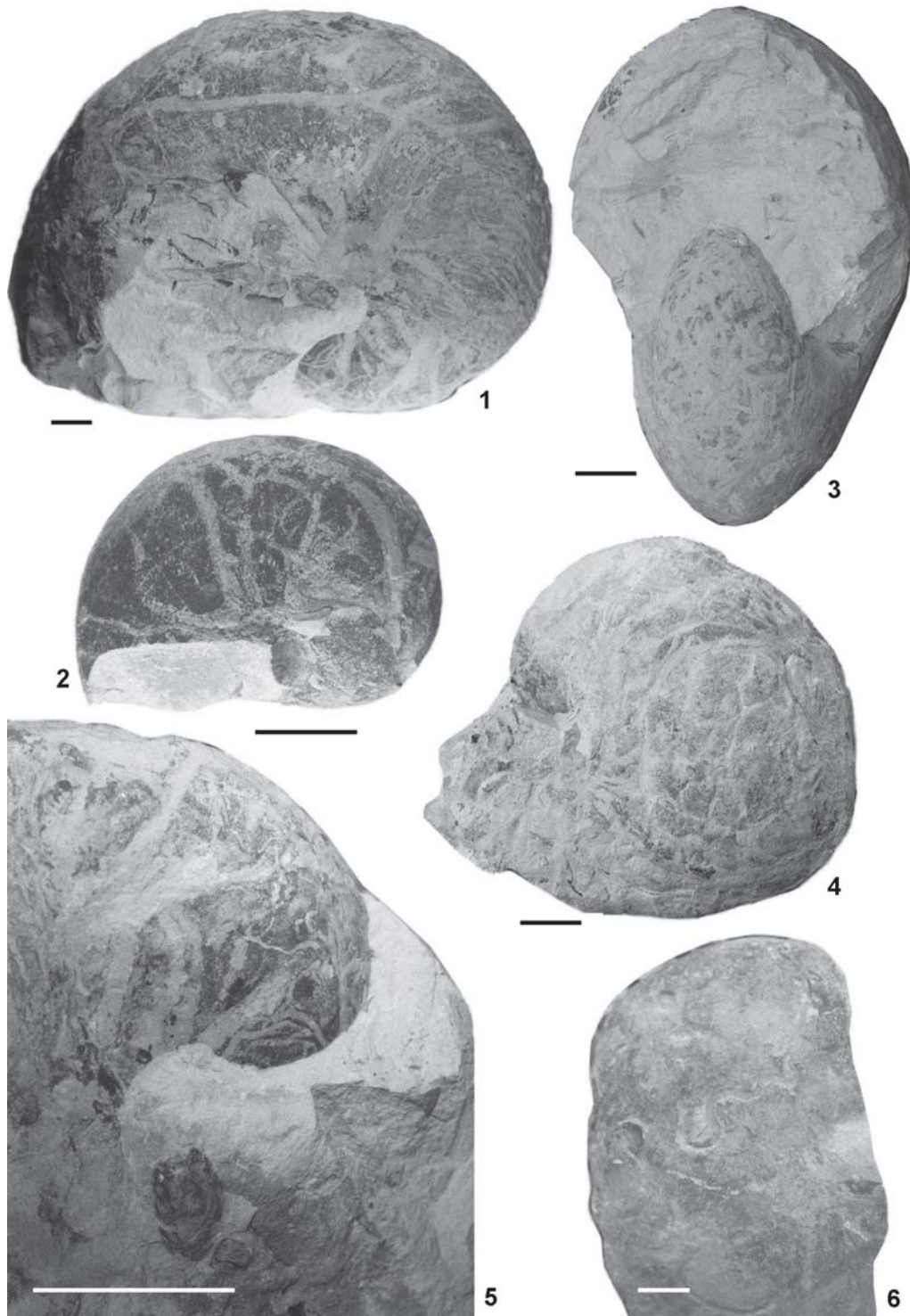
**Fig. 7.** Trace fossils from grey marlstones in the upper part of the Úpohlavý section. **1, 4, 5, 7, 8, 9** — ichnofabrics containing *Thalassinoides* isp.; **2, 7** — ichnofabrics containing *Planolites beverleyensis* (Billings, 1862); **3** — *Palaeophycus tubularis* Hall, 1847; **4, 5, 7, 8, 9** — ichnofabrics containing *Chondrites* isp.; **6** — *Phycosiphon incertum* Fischer-Ooster, 1858. Scale bar = 2 cm.

in their course. The trace fossil thus resembles the ichnospecies *Urohelminthoida*, exclusively restricted to the surface of an internal mould of the nautiloid *Euthrepoceras* sp. It probably originated in the soft fill of the shell of a dead nautiloid before its diagenetic dissolution.

**Remarks:** Classification of ichnofossils inside closed spaces of shells still poses an open problem of ichnologic taxonomy; it is questionable to what degree the morpho-

logical elements resulting from spatial restriction can be considered an ichnotaxobase (cf. Bertling et al. 2004).

It should be noted that Bertling (1992) erected the ichogenus *Arachnostega* for irregular ramifying or net-like burrows in the sediment fill of shells, visible on the surface of internal moulds. The size of the network may vary from micrometers to centimeters. The diagnosis of *Arachnostega* fits well the traces described herein preliminarily as “*Megagraption*” isp.



**Fig. 8.** Trace fossils restricted to surfaces of internal moulds of the nautiloid *Euthreoceras* sp.; upper “opuka” layers of the Úpohlavy section. **1, 2, 5** — “*Megagraptus*” isp.; **3, 4** — “*Chondrites*” isp.; **5** — “*Urohelminthoidea*” isp.; **6** — “*Cochlichnus*” isp. Scale bar = 2 cm.

However, burrows preserved in internal moulds, as evidenced also by the material from the Úpohlavy Quarry, are variable in morphology, and cannot be merely synonymized with *Arachnostega*. As this issue is currently studied by A. Uchman (pers. comm. 2002) and the present author, no relevant taxonomic proposals are presented here.

#### Paleobiological notes

The essential ethological types of ichnofossils present at the locality are domichnia (*Thalassinoides*–*Ophiomorpha*–*Spongeliomorpha*) — typical dwelling burrows of minor predators, scavengers or filtrators, and “chemichnia”

(Bromley 1996) represented by the ichnogenera *Chondrites* or possibly *Pilichnus*.

Less frequent are ichnotaxa participating in direct substrate-feeding (*Phycosiphon*, *Planolites*, *Phycodes*), which, moreover, concentrate to specific horizons. Domichnia are characteristic for both main lithotypes (limestones and marlstones), while chemichnia are restricted almost exclusively to marlstones with the exception of Coprolite Beds, but also to marl-dominated infills of trace fossils in limestones and to partly closed enclaves limited by nautiloid shells. The last mentioned occurrence indicates that the paucity of chemichnia in the limestones was not due to unfavourable substrate consistency but to the lack of fluids suitable for chemosymbiosis; these were, in contrast, present in sufficient amounts in the cephalopod shells. Transported fragments of wood substrates and lithoclasts (shells of *Inoceramus* sp.) contain borings. Whereas borings in wood were obviously transported from pelagic settings, borings of clionid sponges in bioclasts of the Upper Coprolite Bed are probably autochthonous, corresponding to the presumed shallowing and high physical energy of the environment (Ekrt et al. 2001).

### Intensity of bioturbation, character of ichnofabric and environmental parameters

The intensity of substrate mixing in upper tiers of sediment is difficult to assess because primary sedimentary structures in pelitic and carbonate rocks are generally poorly visible. However, weakly re-bioturbated syndimentary structures were found in the Upper Coprolite Bed: the hyporelief of *Planolites* cf. *beverleyensis* is such a structure; it can be, therefore, speculated, that substrate mixing was not absolutely pervasive, or that the homogenized layer (cf. Uchman 1999) did not reach too deep. The Coprolite Beds show obvious signs of rapid hardening from softground to firmground (*Ophiomorpha-Thalassinoides-Spongeliomorpha*), with substrate colonization by tracemakers of chemichnia immediately before reaching the firmground level (Fig. 5.8). A more complicated problem from the viewpoint of ichnofabrics is the alteration of limestone and marlstone beds. The idea that the differences between limestone and marlstone ichnofabrics were primarily controlled by fluctuations in the oxygen content of the water and sediment is questionable. As shown by the partial documentation of the interval of 10–13 m above the Upper Coprolite Bed, more intensive bioturbation in CaCO<sub>3</sub>-rich beds reaches to a depth of ca. 20 cm (*Thalassinoides* often passively filled with clay-richer substance and secondarily colonized by *Chondrites* tracemakers). CaCO<sub>3</sub>-poor beds are usually dominated by *Chondrites*, but *Thalassinoides*, *Palaeophycus* and *Phycodes* are also present. Differences in ichnofabrics thus rather point to a different colonization succession (marlstones — *Chondrites* followed by *Thalassinoides*; CaCO<sub>3</sub>-rich beds — *Thalassinoides* followed by *Chondrites* in the infills of the *Thalassinoides* burrows). The controlling factors therefore included substrate consistency and its increase through time following depositional events, as

well as the content of primary organic matter widely used by “homogenizers” of marly substrates, later — after a partial compaction — by less demanding r-strategic substrate-feeders (tracemakers of the ichnogenus *Phycosiphon*), and in the last stage by chemosymbionts also successfully using the trapping potential of abandoned domichnia. This situation of high fluid concentration in abandoned tunnels indicates, among other things, a significant compaction of limestones and early diagenesis; then, the surfaces of limestone beds could have also functioned as firmgrounds.

As an analogy, the Volkhov sequence, as old as the Early Ordovician, can be mentioned. Dronov et al. (2002) described rich *Thalassinoides-Chondrites* ichnofabrics with numerous varieties of cross-cutting relationships; borings and epibionts document that the carbonate substrate was capable of obtaining the hardground consistency.

On the other hand, *Chondrites* might even in this situation function as an indicator of oxygenation. It occurs preferentially in marly substrates, including the marly fillings of *Thalassinoides* tunnels in the limestone beds. Marlstones are less porous than limestones and clay minerals diminish fluid exchange. As a result, trapping of fluids for chemosymbiosis is easier in marly beds than in limestones (cf. Kedzierski & Uchman 2001).

Ichnoassemblages attributable to firmgrounds in the upper part of the quarry show occasional signs of bioclast concentration. This condensation was probably not induced by increased flow intensity but by the absence of sediment (starvation s.s.). In these cases, the trace fossils are filled with bioclasts (scales, plant material), probably biologically sorted — transported inside by the activity of the tracemaker, as opposed to the passive infill typical, for example, of the Upper Coprolite Bed (cf. J. Laurin, pers. comm. 2002).

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