

ACCUMULATIONS OF FOSSIL CEPHALOPOD SHELLS AND ATTACHED EPIZOANS FROM SOME LATE ORDOVICIAN LOCALITIES (BARRANDIAN AREA, CZECH REPUBLIC)

Jaroslav Marek¹, Radko Šarič² & Petr Kácha³

¹ Institute of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic

² Czech Geological Survey, Klárov 3, 118 21 Prague 1, Czech Republic

³ Institute of Rock Structure and Mechanics, Czech Academy of Sciences, V Holešovičkách 41, 182 09 Prague 8, Czech Republic

Abstract: *As yet undescribed accumulations of shells of orthoconic cephalopods, which are in some aspects comparable to cephalopod limestones known from the Silurian and Lower Devonian of the Barrandian area and other regions of the world, occur in the Letná and Zahořany formations (middle Sandbian and lower Katian stages, Upper Ordovician, central Bohemia). These accumulated shells are often colonized by sessile organisms. Only a small proportion of these organisms could be attached to shells of alive cephalopods; the majority of them used empty shells as solid substrates. The most abundant epizoan is the cystosporate bryozoan of the genus Ceramopora that often overgrows the cephalopod shells extensively. Holdfasts of the genus Sphenothallus and problematic fossils assigned to the genus Conchicolites are common. Rarer epibionts include the bryozoan Spatiopora, the cystoid echinoderm Codiacystis and the brachiopod Ptychopeltis. Varying sizes of bryozoan colonies occurring on the same cephalopod shell point to several recurring attachment events, probably reflecting reproduction cycles.*

Key words: Sandbian, Katian, Letná Formation, Zahořany Formation, orthoconic cephalopods.

INTRODUCTION

Cephalopod shells colonized by sessile organisms were identified in large number between 2004 and 2013 in three excavations in Late Ordovician rocks in the close vicinity of Králův Dvůr near Beroun. It was studied the locality at the hill of Děd near Beroun (Figure 1) in the Letná Formation (middle Sandbian) and two localities in the Zahořany Formation (lower Katian): a linear excavation near the village of Počaply (Figure 2) and excavation at the construction site of a multifunctional playground below the road at the school in Zahořany (Figure 3). At the Děd and Počaply localities, the shells of orthoconic cephalopods form small accumulations (both in their number and extent) that have not been described from the Ordovician of the Barrandian area, yet. The locality near the school in Zahořany, which is situated in the proximity of the Zahořany Formation stratotype section, provided only individual shells of fossil cephalopods and has been included in the present study for the comparison with the locality of Počaply.

Epizoans are ecologically important in all environments – in seas, fresh waters and terrestrial environments. The relationship between epizoans and host organisms can be very specific for many reasons; it can be only mechanical, very close to directly dependent. Especially in the Early Paleozoic, epizoans commonly colonized cephalopod shells because the shells represented appropriate solid substrates for their attachment. Epizoans were able to grow on shells of living cephalopods as well as on empty shells after the death of the animal. Attachment after a long time period, even after a shell fossilisation and its subsequent partial weathering out revealing its sedimentary infill, also occurred (e.g. the colony of tabulate coral *Tiverina* on the rest of orthoconic cephalopod shell from the Lower Devonian of Podolia, Ukraine; coll. J. Marek; unpublished). The most common epizoans attached to the shells of cephalopods in the Ordovician of Bohemia are bryozoans, sphenothallids, conchicolites, brachiopods, crinoids and other echinoderms, and bivalves (e.g. Kácha & Šarič 2009).

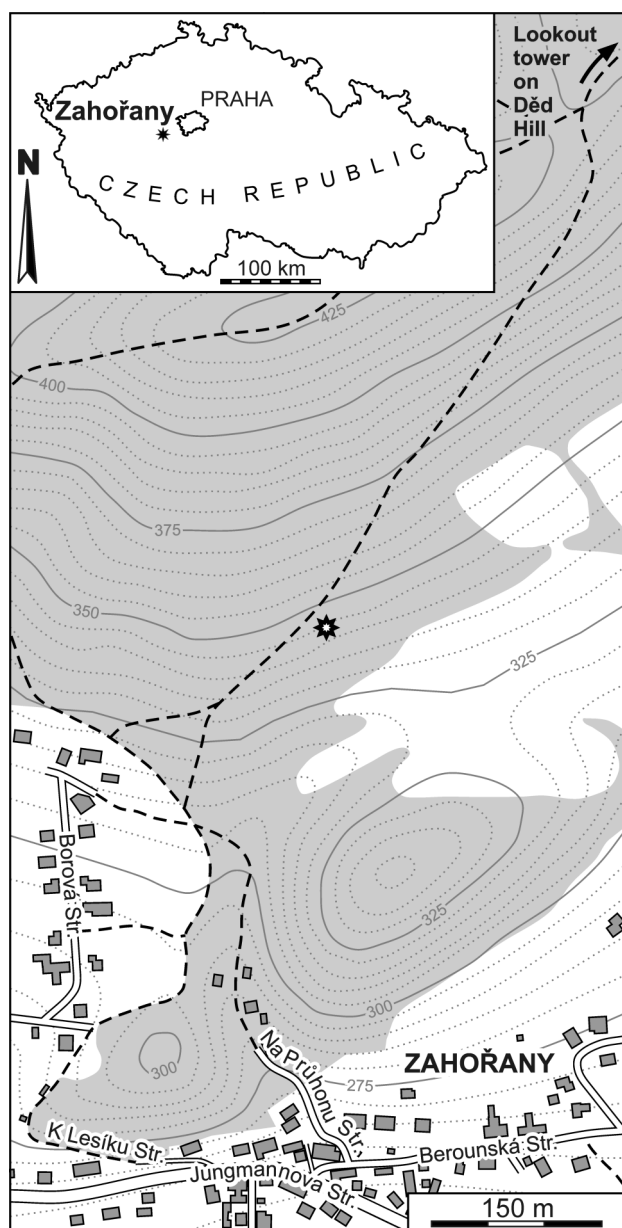


Figure 1. Sketch map of Děd near Beroun with location of the test pit (indicated by asterisk) in the Letná Formation (middle Sandbian Stage).

MATERIAL

The studied material is deposited in the collections of the Czech Geological Survey, Prague unless stated otherwise.

Preservation of the material

Due to the unfavourable preservation of cephalopod shells in sandstones and siltstones the genus

and species specific features, such as a character of the siphuncle, septal necks and cameral deposits cannot be often observed. Consequently, the determination at the genus and species level was possible only in some cases and was based on a set of characteristic features of the shells (Figure 4) selected through comparison with better preserved specimens described by Barrande (1874, 1877). However, an unequivocal generic determination of the cephalopods (or establishing new species) was not essential with regard to the main purpose of this study that is a description of cephalopod accumulations and associated epizoans.

Remarks to the taxonomic determination of the cephalopods

Fossil cephalopods of the Bohemian Sandbian and Katian have been originally described by Barrande (1874, 1877) who classified all of them under the cumulative genus *Orthoceras*. Their taxonomy has not so far been revised, and taking into account their general poor preservation, it is difficult to determine the genera more precisely. The issue has been partly resolved through the study of Kröger *et al.* (2011) who assigned the species *Orthoceras bisignatum* Barrande, 1870 to the genus *Isorthoceras* Flower, 1962. Additionally, the species *Orthoceras fractum* Barrande, 1877 and *Orthoceras sodale* Barrande, 1870 are assigned to the genus *?Transorthoceras* according to Kröger *et al.* (2011).

Besides the Letná and Zahořany formations, the species *Orthoceras sodale* was also described from the Šárka Formation (Darriwilian) and Králův Dvůr Formation (Katian) by Barrande (1870) in the same publication. As the Darriwilian *O. sodale* has a nomenclatorial priority (Barrande 1870, pl. 417, figs 9–14), and specimens from the Middle and Upper Ordovician of the Barrandian area slightly differ in morphology (Barrande 1870, pl. 417, figs 15–21), we left the specimens from the Katian in open nomenclature and assigned them to *?Transorthoceras* aff. *sodale*.

We assigned the yet undescribed cephalopod species from the Sandbian and Katian strata of Bohemia to the genera *Sactoceras* Hyatt, 1884 and *Geisonoceras* Hyatt, 1884. However, it was not possible to assign them to the species due to their poor preservation.

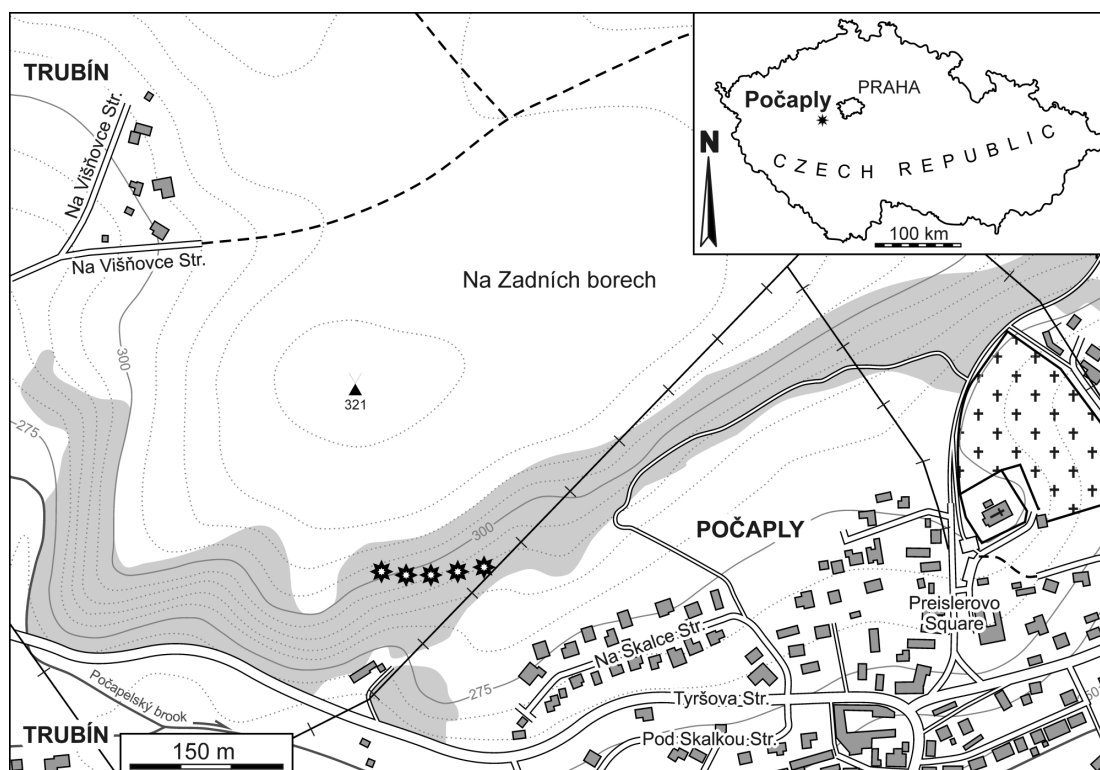


Figure 2. Sketch map of northern surroundings of Počaply near Beroun with locations of the test pits (indicated by asterisks) in the Zahořany Formation (lower Katian Stage).

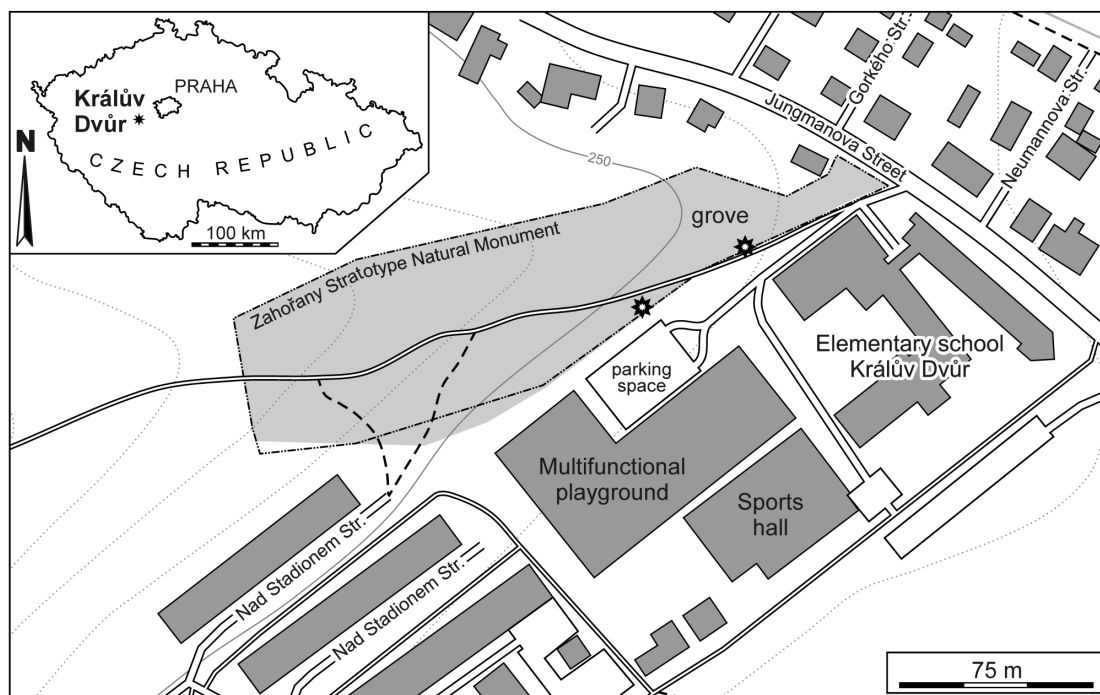


Figure 3. Sketch map of the surroundings of the Elementary school Králův Dvůr with location of the excavation in the Zahořany Formation (lower Katian Stage) at the construction site of a multifunctional playground (indicated by asterisks) in the proximity of the Zahořany Formation stratotype section.

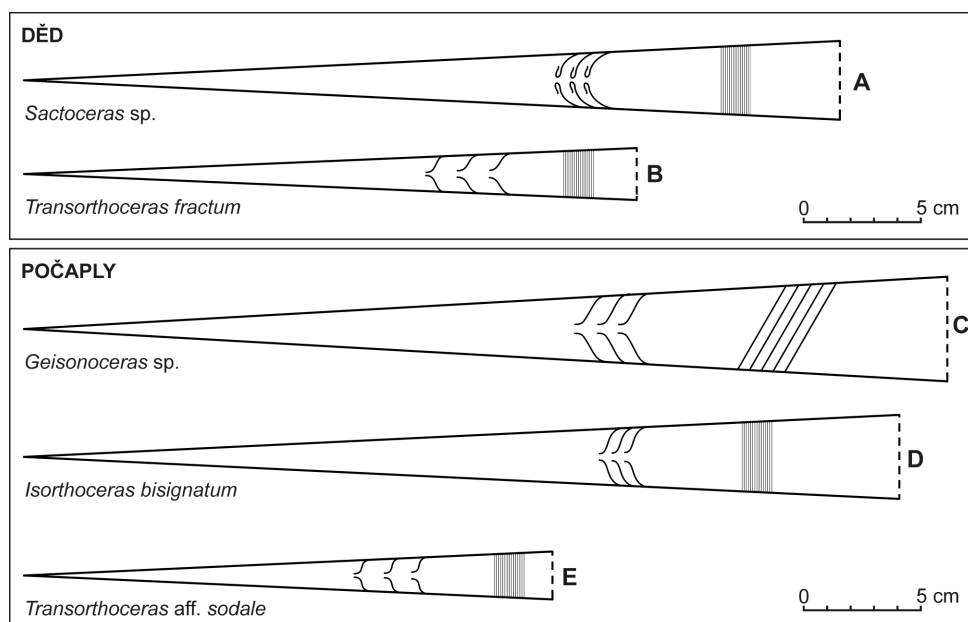


Figure 4. Division scheme of cephalopods at the localities DĚD and Počaply. DĚD, Letná Formation (middle Sandbian Stage): A. *Sactoceras* sp.; B. ?*Transorthoceras fractum* (Barrande, 1877). Počaply, Zahořany Formation (lower Katian Stage): C. *Geisonoceras* sp.; D. *Isorthoceras bisignatum* (Barrande, 1870); E. ?*Transorthoceras aff. sodale* (Barrande, 1870).

The list of studied cephalopod species from the Sandbian and Katian of Bohemia is therefore as follows (Figure 4):

Sactoceras sp. – Letná Formation, locality DĚD
 ?*Transorthoceras fractum* (Barrande, 1877) – Letná Formation, locality DĚD
Isorthoceras bisignatum (Barrande, 1870) – Zahořany Formation, locality Počaply
 ?*Transorthoceras aff. sodale* (Barrande, 1870) – Zahořany Formation, locality Počaply
Geisonoceras sp. – Zahořany Formation, locality Počaply

LETNÁ FORMATION

Geological settings and localities

In the vicinity of Beroun, the Letná Formation (middle Sandbian Stage) has a flysch-like character. It is formed by of greywackes, lithic or quartzose sandstones irregularly alternating with siltstones and shales, sometimes with sandy or silty admixture. The thicknesses of individual layers range from centimetres to decimetres. The total thickness of the formation near Beroun may reach up to 600 m (Havlíček 1982). Ichnofossils occur in varying abundance throughout the entire formation (Mikuláš 1998a). Body fossils are limited only to its upper part, otherwise, they are rare (Havlíček 1982).

The single locality studied in the Letná Formation was a trench excavated at the foot of the DĚD Hill to the north of Zahořany (49°57'29"N, 14°01'29"E; Figure 1). The section (Figure 5), that was excavated in the area of 6 x 2 m, consists of platy (thickness 5–10 cm), yellow, brown and gray quartzose sandstone in the overall thickness of 1.8 m. The direction of the layers is 33° and inclination is 35° to SE. The typical fossils of the Letná Formation such as echinoderms, cephalopods, brachiopods, bivalves, bryozoans, trilobites and conulariids are abundant in the entire exposed succession. They are preserved as internal and external molds, often coated with yellow, orange and brown limonite. There are diverse occurrence modes within the layers: complete single specimens, small coquinas, debris of fine shell fragments and tiny elements of disintegrated echinoderm skeletons.

At the base of the section, there is a relatively thin layer with abundant and poorly preserved ichnofossils. Their diversity is low; most of them can be assigned to two genera (dominant *Zoophycos* and less common *Bifungites*). Higher up in the section, echinoderms *Dendrocystites barrandei* Bather, 1913 are abundant in three layers and are preserved in clusters of complete individuals alternating with coquinas and shell debris. Brachioles of these cystoids are oriented to the southeast on the bedding planes and, at the same time, they incline at a low

Table 1. Dimensions of studied cephalopod specimens from the Letná Formation. Specimens from the lower and upper layer are separated and listed respectively in the lower and upper part of the table.

Species	Inventory number	Angle of expansion	Length (mm)	Adoral diameter (mm)	Adapical diameter (mm)	Estimated complete length (mm)	Epibionts
? <i>Transorthoceras fractum</i>	RŠ 587/1		45	9	8		
? <i>Transorthoceras fractum</i>	RŠ 587/2	4	90	15	8	310	
? <i>Transorthoceras fractum</i>	RŠ 587/3	5	70	20	14	150	
? <i>Transorthoceras fractum</i>	RŠ 587/4	5	90	18	8	220	
? <i>Transorthoceras fractum</i>	RŠ 587/5	6	75	14	7	150	
? <i>Transorthoceras fractum</i>	RŠ 587/6		35	10	9		
<i>Sactoceras</i> sp.	RŠ 596	5	37	11	9.5	270	
? <i>Transorthoceras fractum</i>	RŠ 567	5	75	14	4	130	
? <i>Transorthoceras fractum</i>	RŠ 568/1	5	150	20	9	250	<i>Ceramopora</i> (11 x 5 mm)
? <i>Transorthoceras fractum</i>	RŠ 568/2		30	15			<i>Ceramopora</i> (20 x 10 mm)
? <i>Transorthoceras fractum</i>	RŠ 568/3	5	48	8	3	90	<i>Ceramopora</i> (2 zoaria)
? <i>Transorthoceras fractum</i>	RŠ 569/1	5	100	21	9	180	
? <i>Transorthoceras fractum</i>	RŠ 569/2	6	93	18	8	170	
? <i>Transorthoceras fractum</i>	RŠ 603	5	118	21	18	220	<i>Ptychopeltis incola</i>
? <i>Transorthoceras fractum</i>	RŠ 604	6	250	21	4	360	
? <i>Transorthoceras fractum</i>	RŠ 605	5	78	26	18	240	
? <i>Transorthoceras fractum</i>	RŠ 606/1	5	123	21	10	220	
? <i>Transorthoceras fractum</i>	RŠ 606/2	5	92	21	11	130	

angle into the sediment. This direction is approximately perpendicular to the most common orientation of the shells of orthoconic cephalopods, which are oriented in the NE–SW direction, with apertures facing southwest. Besides cystoids, specimens of brachiopods, bivalve molluscs, trilobites and rare conulariids also occur irregularly here.

Between the layers with echinoderms and associated fauna, there are two 10 cm thick layers, situated approximately 10 cm apart, with numerous cephalopod shells (Figure 5). In the lower layer, in the proximity to the overlying layer with ichnofossils, there are abundant fragmentary cephalopod shells less noticeably orientated than in the the upper layer. However, they occur with attached epibionts, mainly bryozoans. In the upper layer

with cephalopods, the shells are less numerous and with the shell orientation mentioned above, i.e. NE–SW oriented with apertures facing SW. Epizoans were not found on cephalopod shells in this layer.

Description of fossils

Cephalopods

Cephalopod shells occur in small accumulations (tens of individuals at most) in the Letná Formation. In the studied section, the accumulations occur in two separate layers characterized above (Figure 5) and are of limited extents. The lower layer contains cephalopods in its whole thickness while in the upper layer, cephalopods occur only

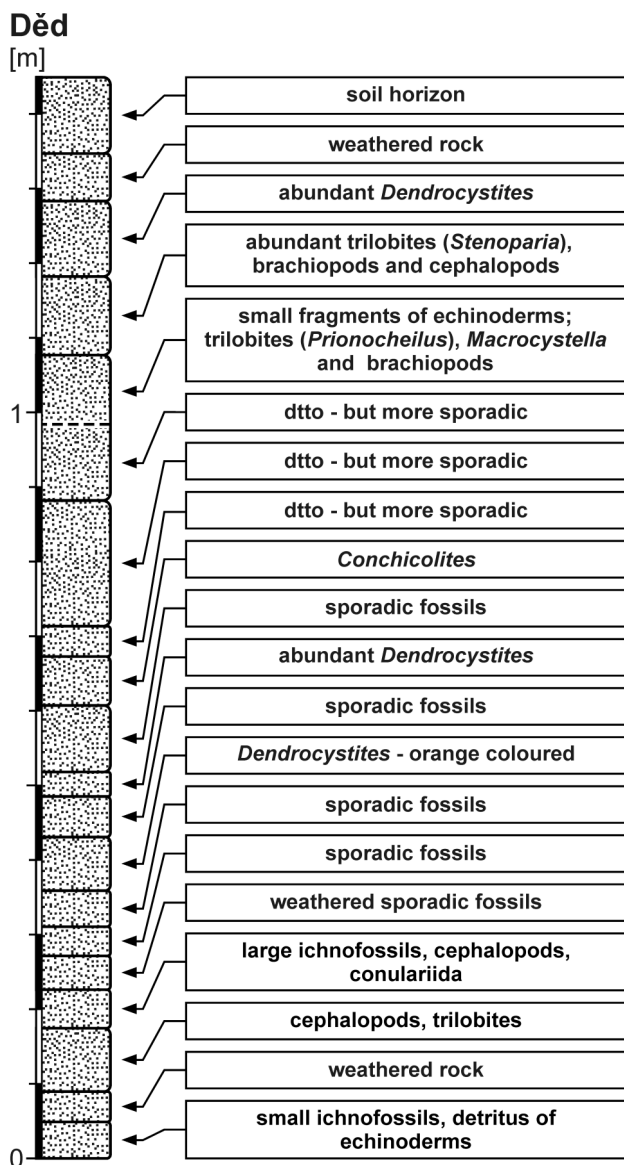


Figure 5. Paleontological characteristics and fossil associations of the investigated section at the locality Děd near Beroun.

in its lower part. The preservation of individual shells is generally poor and fragmentary. The apical parts are usually not preserved and large parts of body chambers are often missing.

The lower layer with cephalopod accumulations is formed by dark-colored rock. The accumulations consist of a mixture of large and small shells. All shells are incomplete; apical parts or parts of body chambers are missing or the shells are fragmented. Large shells (100–150 mm in length) are ar-

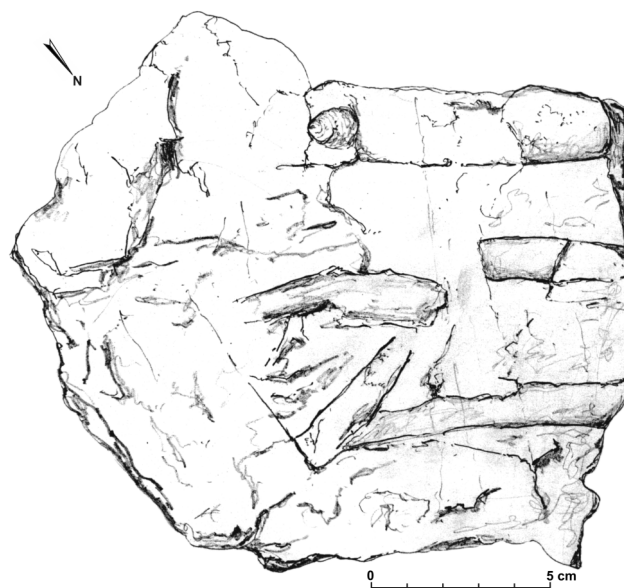


Figure 6. Accumulation of cephalopods ?*Transorthoceras frantum* (Barrande, 1877); RŠ 603, Letná Formation, lower layer, Děd Hill.

ranged more or less parallel to each other and usually with apertures and apices oriented in one direction (see specimens RŠ 603 on Figure 6). Fragments and small shells can sometimes indicate a prevailing orientation but they are usually distributed irregularly or chaotically (see specimens RŠ 568 on Figure 7). However, orientation of the small fragments is in different directions compared to the large shells.

The upper layer with cephalopod accumulations is formed by light-colored rock. The accumulations consist of slightly damaged, large orthoceraconic shells (ca. 100–300 mm in length). They are usually orientated parallel with small deviations ranging between 5° and 10° but sometimes, they form narrow fans of angle 15–20° (see specimens RŠ 587 on Figure 8). Shells with different orientation were recorded only sporadically but their apertures always pointed in the same direction. The large shells usually do not occur together with small fragments of shells. However, if single small shells occur they are orientated chaotically in various directions (Figure 9 reflecting the state of excavation in 2014). The orientation of shells was measured only in several specimens and it was found that the cephalopod apertures point to the southwest (similar to Ferretti & Kříž 1995; Kříž 1992,

1999 and Petránek & Komárková 1953 in some Silurian strata).

A total of 121 cephalopod shells were found at the locality Děd. Epibionts were attached to only four of them (i.e. 4.84 %).

The studied material was divided into three groups based on preservation. More complete specimens, usually with attached epibionts, are synoptically listed in Table 1. Fragmentary and unfavorably preserved specimens are briefly described in the following text. Small fragments or poorly preserved specimens are omitted.

Specimen RŠ 605; ?*Transorthoceras fractum* (Barrande, 1877). It consists of 64 mm long body chamber (infill consists of isolated echinoderm plates) and two phragmocone chambers, each 7 mm long.

Specimen RŠ 567; ?*Transorthoceras fractum*. Body chamber filled with calcite crystals.

Sample RŠ 606; ?*Transorthoceras fractum*. It includes four orientated shells of orthoconic cephalopods. All shells probably belong to the same species. Best preserved is a fragment labelled RŠ 606/1. It is the 55 mm long body chamber and 17 phragmocone chambers with the total length of 68 mm and individual lengths of 3.5–5.0 mm. RŠ 606/2 is a small part of a body chamber and phragmocone. The body chamber is 18 mm long. Phragmocone chambers are indistinct, thus, their number is unknown.

Sample RŠ 569; ?*Transorthoceras fractum*. It consists of four undirected orthoconic shells. Two larger are 107 and 120 mm, and two smaller 52 and 66 mm long.

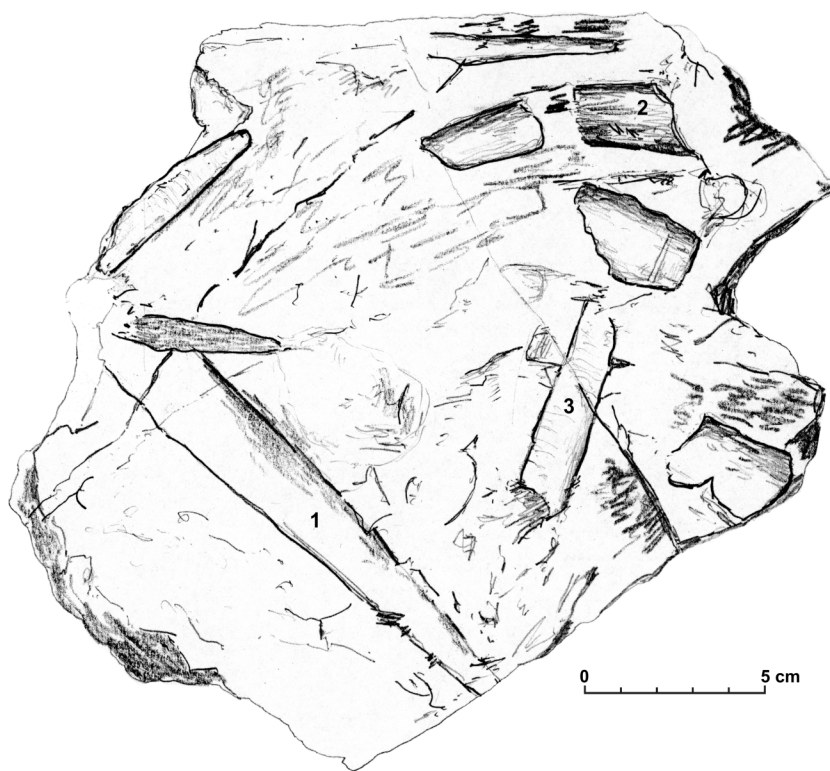


Figure 7. Accumulation of cephalopods ?*Transorthoceras fractum* (Barrande, 1877); RŠ 568, Letná Formation, lower layer, Děd Hill.

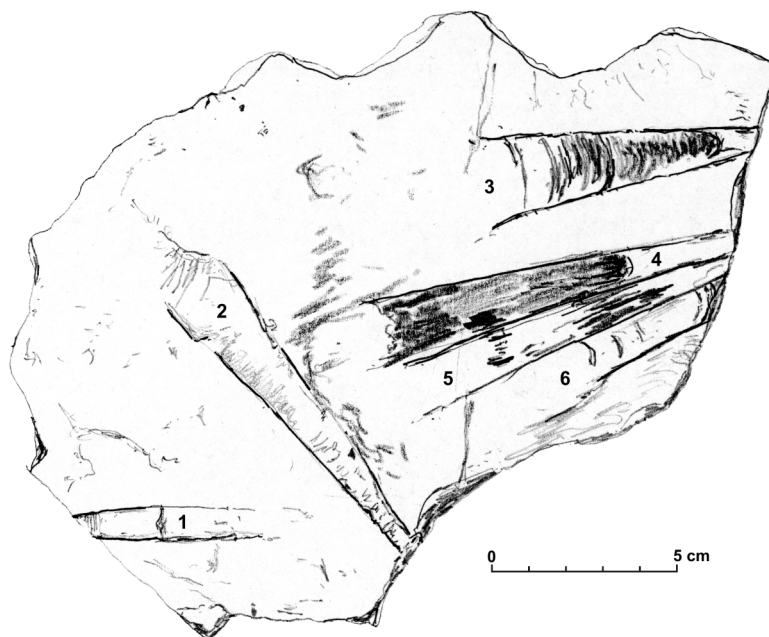


Figure 8. Accumulation of cephalopods ?*Transorthoceras fractum* (Barrande, 1877); RŠ 587, Letná Formation, upper layer, Děd Hill.

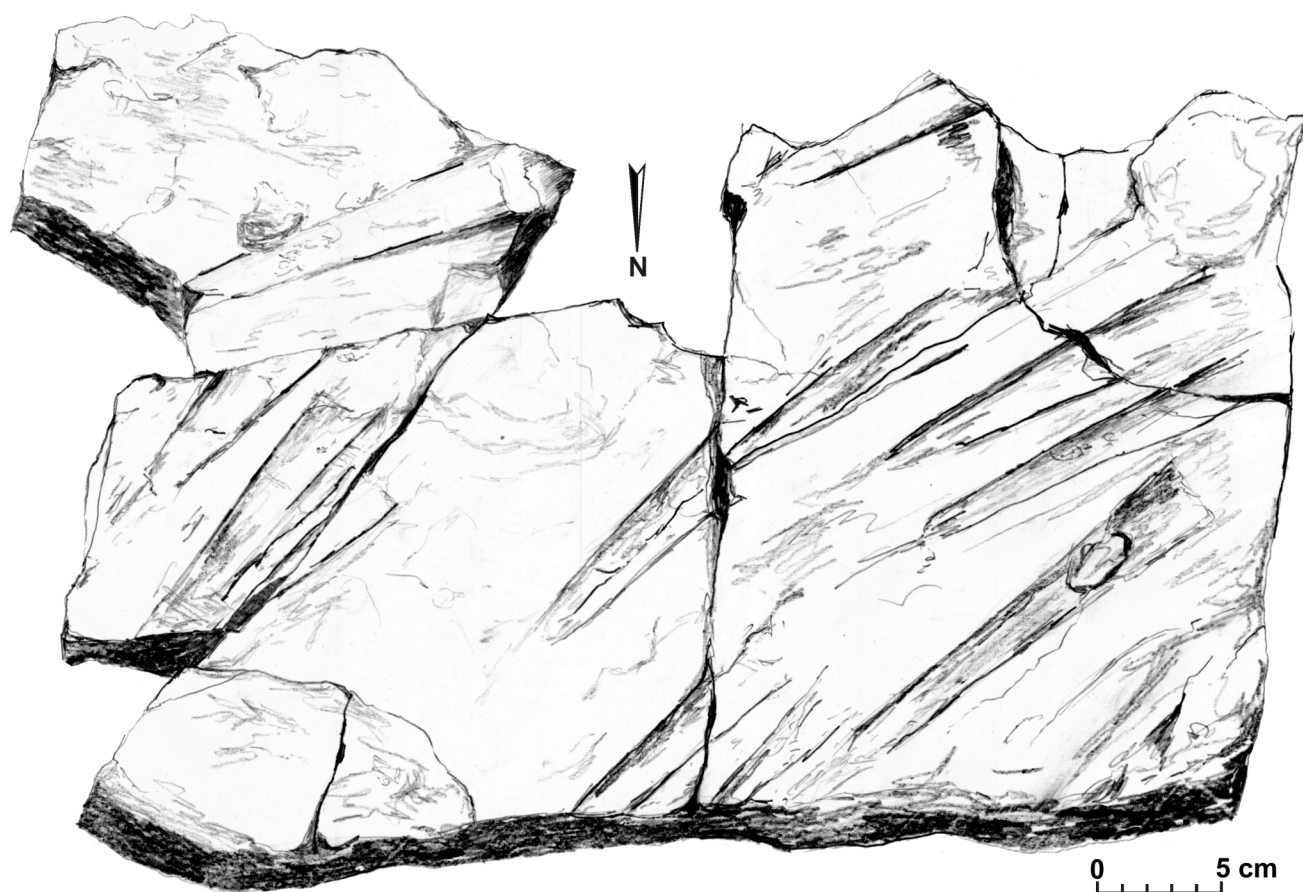


Figure 9. Accumulation of cephalopods ?*Transorthoceras fractum* (Barrande, 1877); Letná Formation, upper layer, Děd Hill; state of excavation on 29. 6. 2014.

Specimen RŠ 596; *Sactoceras* sp., Plate I, fig. 1. It is a body chamber and a part of phragmocone. The preserved part of the body chamber has a length of 7.5 mm. The preserved part of the phragmocone consists of 11 chambers with a total length of 29 mm. The length of the phragmocone chambers varies between 2.0 and 3.5 mm, i.e. 5–6 chamber per shell diameter. The siphuncle is not preserved but based on the gap between septa it is possible to infer its ventrocentral position and estimate its diameter of about 1.8 mm, i.e. 1/5–1/6 of the shell diameter. Well developed episepetal cameral deposits are present in the phragmocone chambers.

Epibionts

Brachiopod *Ptychopeltis incola* Perner, 1903

Sample RŠ 603; ?*Transorthoceras fractum* (Barrande, 1877) (Figure 6). It is a cluster of six fragments of orthoconic cephalopods. The largest four specimens are parallel oriented, all with aperture pointed to southeast (measured directly in the section). Two smaller fragments are oriented with apertures to the northeast. Craniid brachiopod *Ptychopeltis incola* is attached near aperture of the largest specimen, which is situated in the margin of the cluster. The brachiopod shell is 12 mm long and 15 mm wide. Delicate radial ribs, visible especially along the shell margin, are very dense, in number of 26–30 in 2 mm. The brachiopod apex is facing the cephalopod shell aperture. A similar specimen was figured by Havlíček (1972; pl. II, figs 2, 3; p. 230).

Conchicolites meskai Prantl, 1948

Conchicolites are relative common in the overlying Zahořany Formation (see below). They were also recorded in the Letná Formation at the locality Děd. However, they are rarer here and were not found sitting on the cephalopod shells compared to the Zahořany Formation. They are attached to isolated valves of disarticulated bivalves in small clusters that often compose of three specimens. Based on comparison of lithologies, composition of the fossil assemblages and also epibionts it seems that the environments were similar in the basin during deposition of both studied formations. The above described difference of the occurrences of conchicolites can be explained by different size and stability of the available substrate (large cephalopod shells versus small bivalves) influencing growth and length of the conchicolit tubes.

Bryozoan *Ceramopora vadosa* Počta, 1894

Sample RŠ 568; ?*Transorthoceras fractum* (Barande, 1877) (Figure 7; Plate I, fig. 2). It is a slab with irregularly oriented eight orthiconic cephalopod shells. Zoaria of the bryozoan *Ceramopora* are attached to the outer surface of three of them. Fragment 568/1 (Plate I, fig. 2) has a zoarium, 11 x 5 mm in size, attached to its surface approximately in one third of its length from the wider end. Fragment 568/2 is almost entirely covered with the colony of 20 x 10 mm in size. Fragment 568/3 displays two indistinct colonies sitting on its narrower half; maybe they are spread around the entire circumference of the shell.

ZAHOŘANY FORMATION

Geological settings and localities

In the vicinity of Beroun, the Zahořany Formation (lower Katian) consists of rhythmically alternating siltstones (locally sandy or calcareous) and fine-grained sandstones. The total thickness of the formation reaches here 200 m. The prevailing and abundant ichnofossil of the genus *Zoophycos* indicates sedimentary settings of the *Zoophycos* ichnofacies close to the storm wave base (Mikuláš 1990, 1998b, 1999). The body fossils are relatively abundant in the entire thickness of the formation (Havlíček 1982).

The first studied locality of the Zahořany Formation are excavations in its upper part in the woody slope situated west of the village Počaply (49°56'30"N, 14°00'42"E; Kácha & Šarič 2009; Figure 2). The section of the thickness of 2 m was exposed by excavation along the direction of layers in the area of 150 x 2 m (Figure 10). It consists of dark-gray micaceous siltstones with sandy admixture, the amount of which increases towards the overlying layers (Kácha & Šarič 1995, 2009).

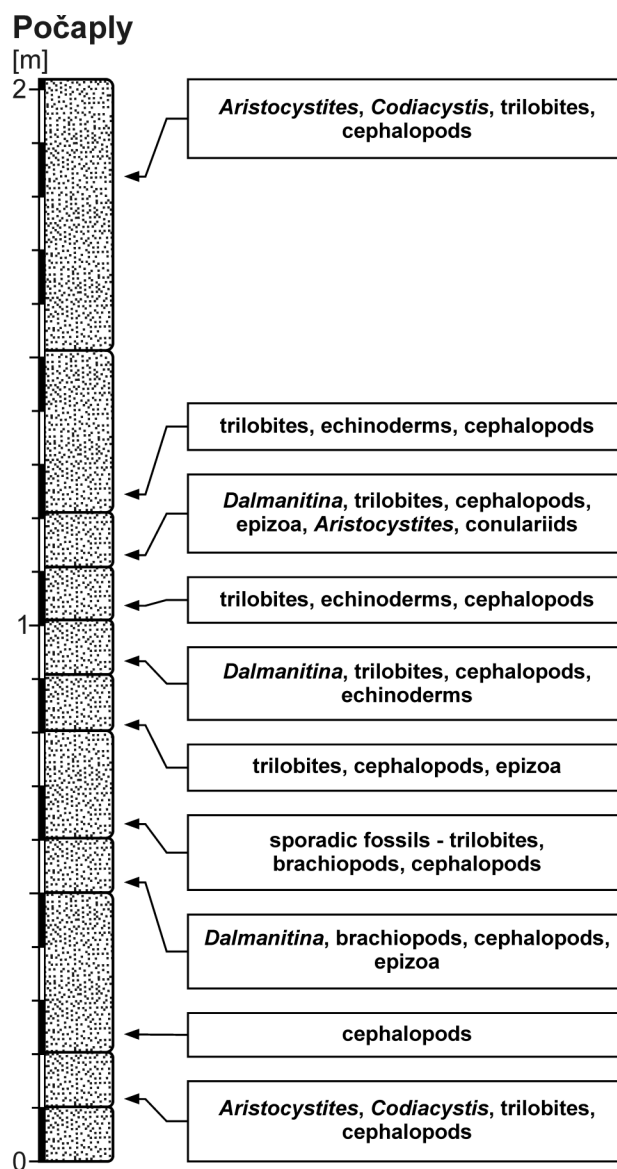
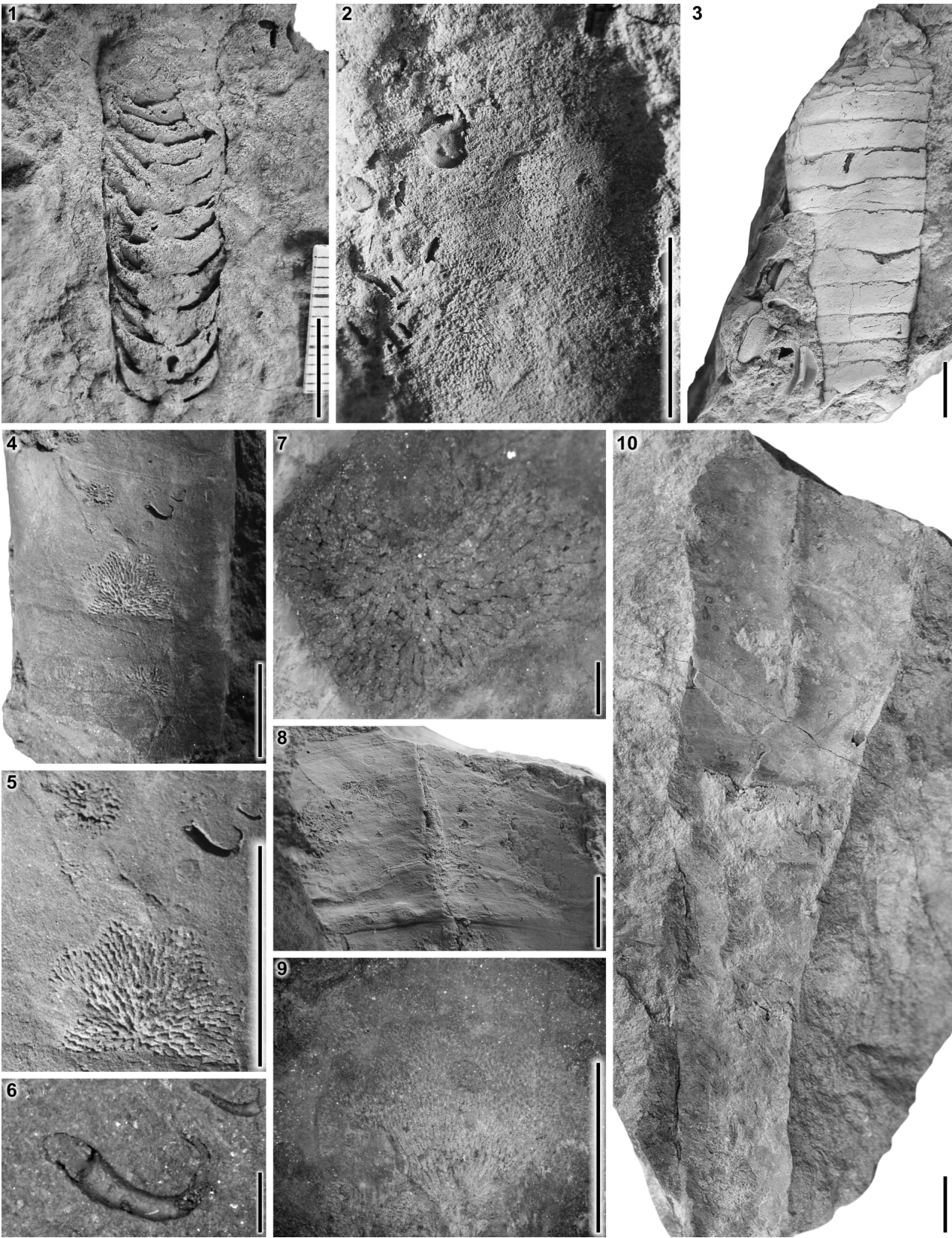


Figure 10. Paleontological characteristics and fossil associations of the investigated section at the locality Počaply near Beroun.

Plate I



The typical fossils of the Zahořany Formation such as echinoderms, trilobites, bryozoans, brachiopods, cephalopods, bivalves, conulariids and ichnofossils are abundant throughout the whole thickness of the formation. The fossils are preserved as internal and external molds coated with yellow and dark brown limonite.

At the locality of Počaply, cephalopods are abundant and distributed more or less evenly across the whole studied thickness of the section. Their shells are not markedly oriented but large shells display some indications of prevailing orientation. Smaller shells are even less clearly directed. However, they are usually at an acute angle to the large shells and with apical parts pointing in approximately the same direction. The compass directions of shells were not measured during excavation (2004–2013) because the original intention of the excavations was to collect trilobites. Tiny cephalopod shells are completely absent. The apices of the shells are broken off but body chambers are sometimes preserved with their apertures. The total of 321 cephalopod shells were found at the locality. It was observed that the cephalopod abundance decreases evenly towards the west in the investigated 150 m long profile. It can be illustrated by a decline from 107 cephalopod specimens in the east to zero in the west along the entire length of the profile.

Empty body chambers of the cephalopod shells are often covered inside or largely filled with bryozoans of the genus *Ceramopora*. The outer surface of the shells is also often covered with bryozoan colonies of different sizes (i.e. different growth stages; e.g. specimens RŠ 597, 598, 580, 612, 614 and 616). Multiple attached epibionts were recorded on each of 203 of the total 321 (i.e. 63.23 %) cephalopod shells combining different taxa, e.g. *Ceramopora*, *Spatiopora* or *Sphenothallus* and

Conchicolites. Bryozoans were found attached also to other fauna, especially on the cephalons of the trilobites *Dalmanitina proaeva* (Emmrich, 1839) (see Kácha & Šarič 2009). Among the cephalopod shells, there are irregularly scattered complete thecae and individual plates of echinoderms *Aristocystites bohemicus* Barrande, 1887 and *Codiacystis bohémica* (Barrande, 1887), the cephalons and pygidia of the trilobite *Dalmanitina proaeva* (Emmrich, 1839), rare trilobites *Stenopareia panderi* (Barrande, 1852), *Kloucekia phillipsi* (Barrande, 1846), brachiopods, bivalves, gastropods, ichnofossils and very rare conulariids.

The second studied locality in the Zahořany Formation was an excavation for the construction of a multifunctional playground under the road near the school in Zahořany, close to the stratotype section of the Zahořany Formation (figure 3). The construction was carried out between February and April 2015. The exposed section in the approximately west-east direction was 24 m long and 2 m thick. The lithological and paleontological characteristics of the exposed rocks are the same as at the nearby locality Počaply. The excavated section was examined and fossils were collected by the specialists from the Czech Geological Survey (P. Bokr, P. Budil, E. Kadlecová, M. Polechová, R. Šarič), and private collectors I. Vyhnánková and P. Kácha. Twenty-four individual cephalopod shells were found there. Only two shells (i.e. 8.3 %) had individual zoaria of *Ceramopora vadosa* attached to them.

The nearby classic stratotype section of the Zahořany Formation is now covered with vegetation (wooded and covered with grass and bushes) and at the same time strictly protected. Excavations may only be carried out with a special permission.

Plate I. Epibionts on cephalopod shells; middle Sandbian, Letná Formation, Děd Hill near Beroun. 1 – *Sactoceras* sp., RŠ 596. 2 – *Transorthoceras fractum* (Barrande, 1877) overgrown by bryozoan *Ceramopora vadosa* Počta, 1894 and two holdfasts of *Sphenothallus* sp., RŠ 568/1. Epibionts on cephalopods; lower Katian, Zahořany Formation, Počaply near Beroun. 3 – *Isorthoceras bisignatum* (Barrande, 1870), internal mold of phragmocone, RŠ 590. 4–6 – *Transorthoceras* aff. *sodale* (Barrande, 1870) with colonies of bryozoans of *Ceramopora vadosa* Počta, 1894, holdfasts of *Sphenothallus* sp. and two undetermined tubes of unknown organisms (polychaetans ?) in the different magnifications, RŠ 577. 7 – Detail of the colony of *Ceramopora vadosa* on *Isorthoceras bisignatum*, RŠ 572. 8, 10 – *Isorthoceras bisignatum*, RŠ 571; 8 – adoral part of external mold of the body chamber with minute colonies of *Ceramopora vadosa* and numerous holdfasts of *Sphenothallus* sp.; 10 – overall view on the internal mold of the shell. 9 – *Isorthoceras bisignatum*, detail of the bryozoan *Ceramopora vadosa*, on which the holdfast of *Sphenothallus* sp. is attached, RŠ 572. Scale bars 1–5 and 7–10 equal 10 mm, 6 equal 1 mm.

Description of fossils

Cephalopods

Like the material from the Letná Formation, the cephalopods from the Zahořany Formation were also divided into three groups based on their preservation. The more complete specimens (usually those with attached epibionts) are listed in the Table 2. Fragmentary and less completely preserved specimens are described in the following text.

Specimen RŠ 618; *Geisonoceras* sp. Fragment of a phragmocone of an orthoconic cephalopod. Sutures of 11 phragmocone chambers are discernible, each chamber is 6 mm long on average.

Specimen RŠ 590; *Isorthoceras bisignatum* (Barande, 1870). A fragment of a slightly flattened cephalopod shell with distinct sutures of 12 phragmocone chambers, the average length of which varies between 5 and 6 mm.

Specimen RŠ 622; *Geisonoceras* sp. A fragment of a cephalopod shell with a large portion of the body chamber and the phragmocone with four preserved chambers. The length of the chambers is 5 to 6 mm. No chambers are preserved on the remaining part of the phragmocone.

Specimen RŠ 589; *Isorthoceras bisignatum*. A slightly deformed fragment of a shell consisting of a small portion of the body chamber and nine phragmocone chambers. The fragment of the body chamber is 15 mm long and phragmocone chambers are 5 mm long on average.

Specimen RŠ 613; ?*Transorthoceras* aff. *sodale* (Barande, 1870). Strongly deformed fragment of a large part of the body chamber with three phragmocone chambers. The body chamber is 48 mm long, the length of the phragmocone chambers varies between 2 and 2.5 mm.

Besides the above described material, three other cephalopod shells with attached bryozoans of the genus *Ceramopora* are known from the Zahořany Formation (O. Zicha, private collector, pers. com.). The specimens are known from Králův Dvůr and Prague and geographically extend the area of occurrence of cephalopod shells with epibionts.

Individual species can be discerned using Figure 4.

Epibionts

Sphenothallus sp. (holdfast)

Only holdfasts, identified based on the features published by Neal & Hannibal (2000), were pre-

served and found attached mostly to body chambers of cephalopods (specimens RŠ 571+, 571– and RŠ 577). Holdfasts of *Sphenothallus* attached to a phragmocone fragment were only recorded in the specimen RŠ 572.

Specimen RŠ 571; *Isorthoceras bisignatum* (Barande, 1870) (Plate I, figs 8, 10). The entire body chamber of the cephalopod shell is covered by about 60 more or less regularly distributed holdfasts. It seems that holdfasts are grouped to small clusters comprising 3 to 6 specimens. (Plate I, fig. 8). They are circular in shape and their diameter varies between 0.5 and 2.2 mm, most often between 0.9 and 1.7 mm. They are mostly pello-morphously flattened. In better preserved specimens, they have form of overturn low bowl, with central circular elevation possessing small pit at its top. The central elevation is usually ca. 0.5 mm in diameter but its dimension depends on holdfast size. In addition to the described holdfasts, the body chamber is densely covered by small circular bodies, especially along its aperture. These bodies are 0.1–0.2 mm in diameter, usually of white color and resemble holdfasts. Thus, they can be considered as attachment discs of juvenile sphenothallids or may belong to other, unknown organisms. Although it is difficult to prove, some of them can be inorganic mineral aggregates. It is worth noting that the host cephalopod has preserved the body chamber along its entire length, which is indicated by the more densely arranged growth lines near its aperture as a result of slowing down growth in old age. The body chamber is 60 mm long, i.e. about 1/7 of the estimated length of the complete shell.

Sample RŠ 572; *Isorthoceras bisignatum*. It is a 46 mm long fragment of the phragmocone consisting of 9 short chambers. Sutures of the phragmocone are slightly oblique to the shell axis and are 4–6 mm apart, usually 5 mm. Nine holdfasts are irregularly distributed on the shell surface. They are 1.4–2.0 mm in diameter, circular, some of them oval. A small oval elevation, 0.6 mm in diameter, is preserved in the centre of the two largest holdfasts. It is worth mentioning that two holdfasts overgrew partly the edge of bryozoan zoaria and in one case the holdfast was attached by its entire basal plane to the bryozoan colony (Plate I, fig. 7). It clearly illustrates a sequence of epibiont attachments and shell colonization primary by bryozoans and subsequently by sphenothallids (see the section Bryozoans below).

Table 2. Dimensions of studied cephalopod specimens from the Zahořany Formation.

Species	Inventory number	Angle of expansion	Length (mm)	Adoral diameter (mm)	Adapical diameter (mm)	Estimated complete length (mm)	Epibionts
<i>Geisonoceras</i> sp.	RŠ 581	8	92	25	18	190	<i>Ceramopora</i> (4 zoaria)
<i>Geisonoceras</i> sp.	RŠ 591	6	125	38	33	500	<i>Ceramopora</i> (5 zoaria)
<i>Geisonoceras</i> sp.	RŠ 598	7	103	38	26	310	<i>Ceramopora</i> (4 zoaria)
<i>Geisonoceras</i> sp.	RŠ 617	11	61	33	17	165	<i>Ceramopora</i> (1 zoarium)
<i>Geisonoceras</i> sp.	RŠ 618	5	68	28	22	350	
<i>Geisonoceras</i> sp.	RŠ 619	8	114	41	33	370	
<i>Geisonoceras</i> sp.	RŠ 622	6	104	32	29	300	
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 570	8	74	13	4.5	110	<i>Spatiopora</i> (1 zoarium)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 573	4	48	12	10	220	<i>Ceramopora</i> ; <i>Conchicilotes</i>
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 575	4	98	19	7.5	210	<i>Ceramopora</i> (2 zoaria)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 577	4	55	23	19	310	<i>Sphenothallus</i> (13 holdfasts), <i>Ceramopora</i> (4 zoaria), ? <i>Polychaetes</i> (2 specimens)
? <i>Transorthoceras</i> aff. <i>sodale</i>	Rš 582	5	88	15.5	4.5	120	<i>Ceramopora</i> (7 zoaria), <i>Conchicolites</i> (2 tubes)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 583	3	105	17	10	350	<i>Codiacystis bohémica</i>
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 584	5	24	15	13	260	<i>Codiacystis bohémica</i>
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 586	5	45	6	2.5	65	<i>Ceramopora</i> (cover)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 594	6	35	16	12	150	<i>Ceramopora</i> (cover)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 599	5	120	19	11	270	<i>Ceramopora</i> (1 zoarium and cover)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 607	5	54	20	8	190	<i>Ceramopora</i> (fill)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 608	5	110	17	9	230	<i>Ceramopora</i> (2 zoaria and cover)
? <i>Transorthoceras</i> aff. <i>Sodale</i>	RŠ 611	8	45	6	2	55	
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 613	4	60	16	9	300	
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 615	4	30	9	8	150	<i>Ceramopora</i> (1 zoarium)
? <i>Transorthoceras</i> aff. <i>sodale</i>	RŠ 621	6	106	20	8	220	
<i>Isorthoceras bisignatum</i>	RŠ 571	6	145	39	22	440	<i>Sphenothallus</i> (60 holdfasts)
<i>Isorthoceras bisignatum</i>	RŠ 572	7	46	27	22	190	<i>Ceramopora</i> (7 zoaria), <i>Sphenothallus</i> (9 holdfasts)
<i>Isorthoceras bisignatum</i>	RŠ 574	5	80	37	31	400	<i>Ceramopora</i> (2 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 576	? 6	49	36	? 30	? 320	<i>Spatiopora</i>
<i>Isorthoceras bisignatum</i>	RŠ 578	9	114	34	11	195	<i>Ceramopora</i> (3 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 579		34	29			<i>Ceramopora</i> (6 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 580	9	35	22	17	190	<i>Ceramopora</i> (2 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 585	8	65	35	27	260	<i>Ceramopora</i> (4 zoaria), <i>Conchicolites</i> (2 tubes)

Table 2 (continued).

Species	Inventory number	Angle of expansion	Length (mm)	Adoral diameter (mm)	Adapical diameter (mm)	Estimated complete length (mm)	Epibionts
<i>Isorthoceras bisignatum</i>	RŠ 588	5	76	27	19	370	<i>Ceramopora</i>
<i>Isorthoceras bisignatum</i>	RŠ 589	8	52	23	18	180	
<i>Isorthoceras bisignatum</i>	RŠ 590	8	69	29	18	240	
<i>Isorthoceras bisignatum</i>	RŠ 592	5	36	32	27	470	<i>Conchicolites</i>
<i>Isorthoceras bisignatum</i>	RŠ 595	8	73	34	25	150	<i>Conchicolites</i> (7 tubes)
<i>Isorthoceras bisignatum</i>	RŠ 597	5	63	25	18	350	<i>Ceramopora</i> (3 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 610		33	36			<i>Ceramopora</i>
<i>Isorthoceras bisignatum</i>	RŠ 612		35	38			<i>Ceramopora</i> (2 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 614	5	80	38	33	420	<i>Ceramopora</i> (4 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 616		35	28			<i>Ceramopora</i> (3 zoaria)
<i>Isorthoceras bisignatum</i>	RŠ 620	7	87	33	29	280	
<i>Orthoceras</i> gen. et sp. indet	RŠ 516	8	70	37	30	330	<i>Spatiopora</i> (1 zoarium), <i>Conchicolites</i>
<i>Orthoceras</i> gen. et sp. indet	RŠ 609	9	84	30	17	150	<i>Ceramopora</i> (4 zoaria)

Specimen RŠ 577; ?*Transorthoceras* aff. *sodale* (Barrande, 1870) (Plate I, figs 4–6). It is a fragment of the body chamber with a smooth surface bearing only growth lines. Seven attached holdfasts are preserved in the central part of the fragment. They are of a circular, low and flat button-like shape, with a diameter of 0.7, 0.7, 0.7, 0.7, 0.8, 1.1 and 1.25 mm. Six small, circular, cupola-like objects are attached to the shell in its adoral portion. They differ from holdfasts of sphenothalids in smaller dimension and hemispherical shape. Thus, they can represent holdfasts belonging to unknown organisms. Bryozoans and tubes of the hook-like shape are also attached to the described specimen (see respective sections Bryozoans and *Conchicolites* below).

Conchicolites meskai Prantl, 1948

The tubes of *Conchicolites* occur on cephalopod shells usually associated in clusters in the lower Katian of the Barrandian area (Röhlich & Chlupáč

1952). Fan-shaped to almost circular clumps are composed of 3 to 15 specimens. Their orientation related to the apertures of the cephalopod shells is various. *Conchicolites* grew usually on the outer shell surface.

Four fragments of cephalopod shells, RŠ 573, RŠ 585, RŠ 592, RŠ 595+ and 595–, with internal and external molds of conchicolites without preserved shells were available for study. The conchicolite tubes are 7–10 mm long and about 2.5 mm in diameter by aperture. They are usually slightly laterally bent. They are attached to the host shell by the most (60–85 %) of the tube length. Ventral sides of the tubes are flattened at the contact with the cephalopod shell. Free apertural parts of the tube are slightly risen above the host shell; the apertures are circular. The tube wall is 0.2–0.3 mm thick, longitudinally undulated (i.e. transversally annular) on both inner and outer surfaces; no longitudinal striae are visible on the outer surface.

Plate II. Epibionts on cephalopod shells; lower Katian, Zahorany Formation, Počaply near Beroun. 1–2 – Internal mold of *Conchicolites meskai* Prantl, 1948 bent along missing shell infilled with bryozoan *Ceramopora vadosa* Pošta, 1894 in different views, RŠ 573. 3, 6–7 – Body chamber of *Isorthoceras bisignatum* (Barrande, 1870) with overgrowths of *Conchicolites meskai* around the aperture, RŠ 595; 3 – detail of one cluster of *C. meskai*; 6–7 – overall view, counterparts. 4 – Flattening of the tubes of *Conchicolites meskai* at the contact with the shell of *Isorthoceras bisignatum*, RŠ 585. 5 – ?*Transorthoceras* aff. *sodale* (Barrande, 1870), the pitted surface of episetal cameral deposits discernible in two broken parts of the septum and colony of *Ceramopora vadosa* developed inside the adapical part of the shell, RŠ 594. Scale bars 1; 5 and 7 equal 10 mm, 2–4 equal 1 mm.

Plate II



Specimen RŠ 573; ?*Transorthoceras* aff. *sodale* (Barrande, 1870) (Plate II, figs 1, 2). It is a fragment of the body chamber belonging to a slender orthoconic cephalopod. Its inner surface is completely covered with bryozoan zoaria of *Ceramopora*. In addition, an internal mold of *Conchicolites* (Plate II, figs 1, 2) is preserved sitting adorally on the outer surface of the fragment. Its axis is oriented obliquely to the cephalopod shell axis with aperture facing latero-adorally, probably in the direction to the dorsal side of the cephalopod shell. The conchicolit tube is bent, 7.5 mm long, 1 and 2 mm wide in the apical and apertural ends, respectively. The internal mold of the tube is 3-D preserved proving that its curvature followed the substrate, i.e. the outer surface of the cephalopod shell. It protrudes above the preserved surface of bryozoans, which covered inner surface of the cephalopod shell (Plate II, fig. 1 down). The position of the tube indicates that the conchicolit attached to the living cephalopod whereas bryozoans started to grow posthumously inside the empty shell.

Specimen RŠ 585; *Isorthoceras bisignatum* (Barrande, 1870) (Plate II, fig. 4, Plate V, fig. 5). It is a large fragment of the cephalopod shell comprising of the body chamber and large part of phragmocone; maybe, it was originally a complete shell damaged during the field collection. Growth lines are posteriorly bent on the ventral side inclining 60° to the shell axis. Two closely adjacent specimens of *Conchicolites meskai* (Plate II, fig. 4), and two large and two small bryozoan zoaria of *Ceramopora vadosa* (Plate V, fig. 5) are attached to the body chamber. Both conchicolits sit ventro-sinistrally near the aperture and their tubes point ventrally at an acute angle to the cephalopod shell axis. They are 7 and 9 mm long and respectively 2.5 and 3 mm wide in aperture. The flattening of the tubes and a reduction of the transversal rings are clearly developed along the attachment surface (Plate II, fig. 4). The position of the tubes indicates that the conchicolits attached to the cephalopod during his life. A considerable weight of large bryozoan zoaria concentrated on the lateral surface of the body chamber probably caused an

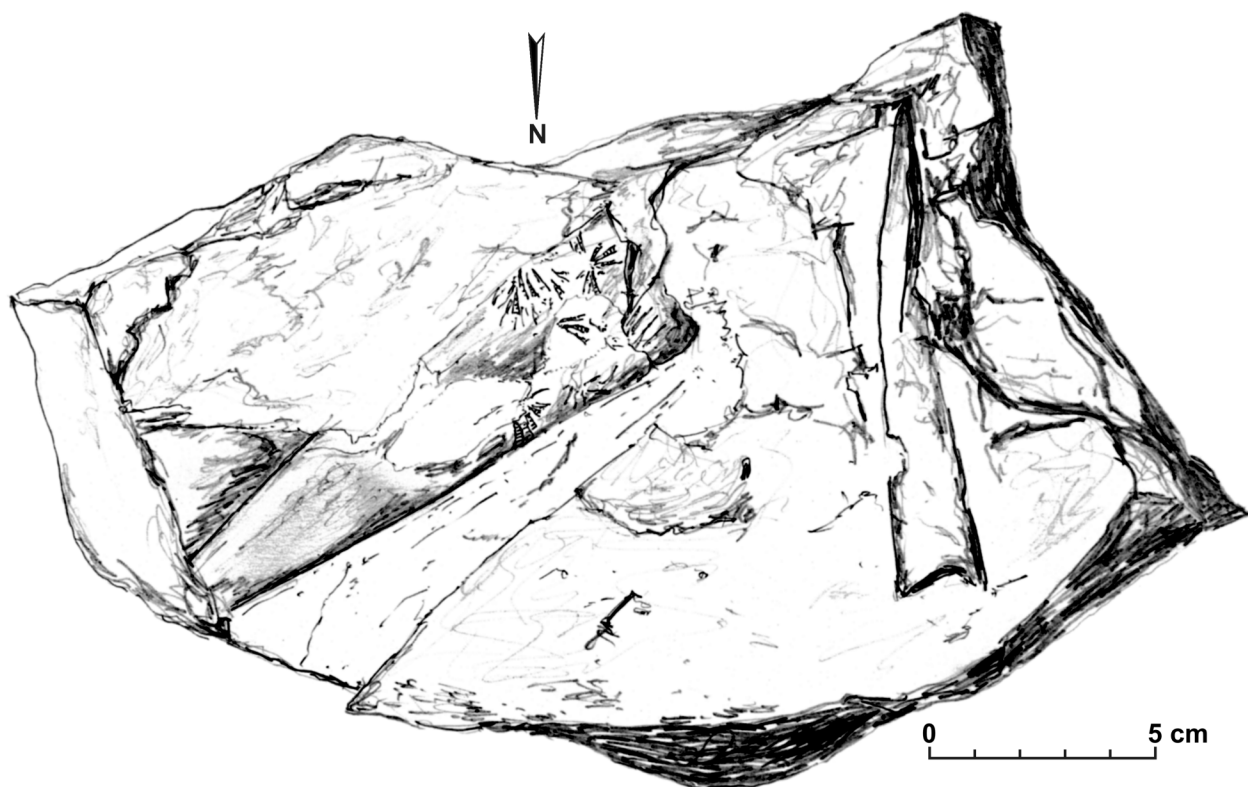


Figure 11. Clusters of *Conchicolites meskai* Prantl, 1948 overgrowing the outer surface around the shell aperture of *Isorthoceras bisignatum* (Barrande, 1870); RŠ 595, Zahořany Formation, Počápy near Beroun.

unusual post-mortem orientation of the shell in the sediment left side down.

Specimen RŠ 592; *Isorthoceras bisignatum*. It is a small fragment of the orthocerid body chamber with a single attached *Conchicolites*. Its tube sits on the outer surface with its axis almost perpendicularly to the cephalopod shell axis, i.e. parallel to the growth lines. The tube is slightly laterally bent, 9 mm long and 1.7 mm wide.

Specimen RŠ 595; *Isorthoceras bisignatum* (Figure 11; Plate II, figs 3, 6–7). It is a damaged complete cephalopod shell. All seven visible clusters of conchicolits are concentrated near the shell aperture. Clusters consist of 6 to 10 tubes and are star-like arranged. The straight or slightly laterally bent tubes are 7–8 mm long on average and 1.2–1.5 mm wide by aperture. Flattened region of the tubes corresponds to the area of attachment to the surface of the cephalopod shell. The arrangement of the visible conchicolit clusters suggests that they are located in a 35 mm wide ring around the entire circumference of the body chamber. It probably indicates their attachment to the host cephalopod during his life (Figure 11).

Tubes of the unknown vermiform organism

Specimen RŠ 577; ?*Transorthoceras* aff. *sodale* (Barrande, 1870) (Plate I, figs 4–6). Two imprints of the hook-like shells resembling those of polychaetes are preserved in the middle part of the shell fragment. Their surface is structured into low irregular transversal rings, i.e. it is of an undulated outline. The specimens are 1.2 and 2.5 mm

long. They differ from the above described *Conchicolites meskai* Prantl, 1948, that is common at the same locality in Počaply, by their shape, smaller size and the shell sculpture.

Echinoderms

Specimen č. RŠ 583; ?*Transorthoceras* aff. *sodale* (Barrande, 1870) (Figure 12; Plate III, figs 7–8). It is a fragment of a large part of the phragmocone and a small portion of the body chamber with its ventral side exposed on the slab. A septal perforation of 1 mm in diameter seems to be visible slightly ventro-centrally situated in the infill of one chamber of the phragmocone. A theca of the cystoid *Codiacystis bohémica* (Barrande, 1887) protrudes from the body chamber and absorbs the whole chamber aperture. A cystoid larva is interpreted to settle inside the empty body chamber in a protected environment. After the space of the chamber became limited for the growing and enlarging echinoderm it deflected out the chamber and continued growing outside vertically upwards. This interpretation is supported by flattened basal part of cystoid theca, which is completely hidden inside the chamber in contrast to remaining spherical parts of the theca overgrowing its aperture up and to the sides (Figure 12).

Specimen RŠ 584; ?*Transorthoceras* aff. *sodale* (Figure 13; Plate III, figs 5–6). It is a short, only 24 mm long, small fragment of cephalopod shell associated with attached theca *Codiacystis bohémica* (Barrande, 1887). It is apparent that the cystoid theca started to grow on that small shell frag-

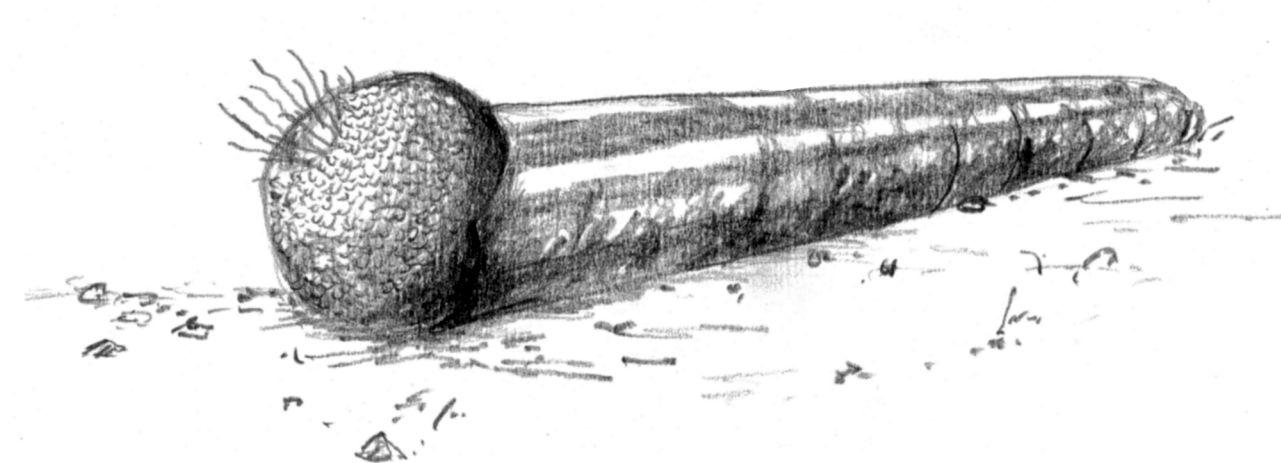


Figure 12. Reconstruction of *Codiacystis bohémica* (Barrande, 1887) growing out of the body chamber of *Transorthoceras* aff. *sodale* (Barrande, 1870); RŠ 583, Zahořany Formation, Počaply near Beroun.

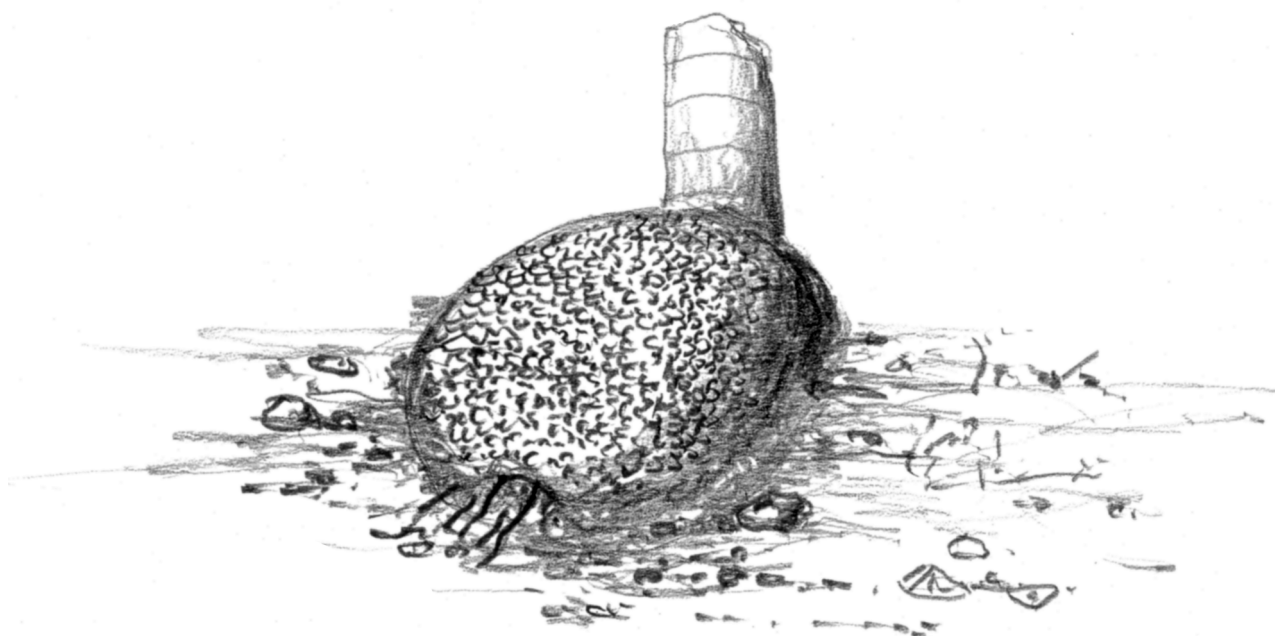


Figure 13. Reconstruction of the growth of *Codiacystis bohémica* (Barrande, 1887) after orientation of the cephalopod shell was changed from horizontal to vertical; RŠ 584, Zahořany Formation, Počaply near Beroun.

ment and overgrew it completely very soon. Subsequently, a flattened plane formed on the thecal base and stabilized the growing theca against overturning along the longitudinal axis of the cephalopod shell. However, the large cystoid theca overturned due to the next growth upwards and the fragment of the cephalopod shell, originally laying horizontally on the sea bottom, reoriented to the vertical position. It also seems that overturned cystoid sank with its peristomal region into the sediment and died (Figure 13).

Bivalve *Praenucula* sp.

Specimen RŠ 601; “*Orthoceras*” gen. et sp. indet (Plate III, fig. 1). Right valve of the bivalve *Praenucula* sp. is associated with a small fragment of the cephalopod shell, 25 x 18 mm in size. However,

this position of both specimens close together is rather random than a relationship of the epibiont and its substrate.

Bryozoans

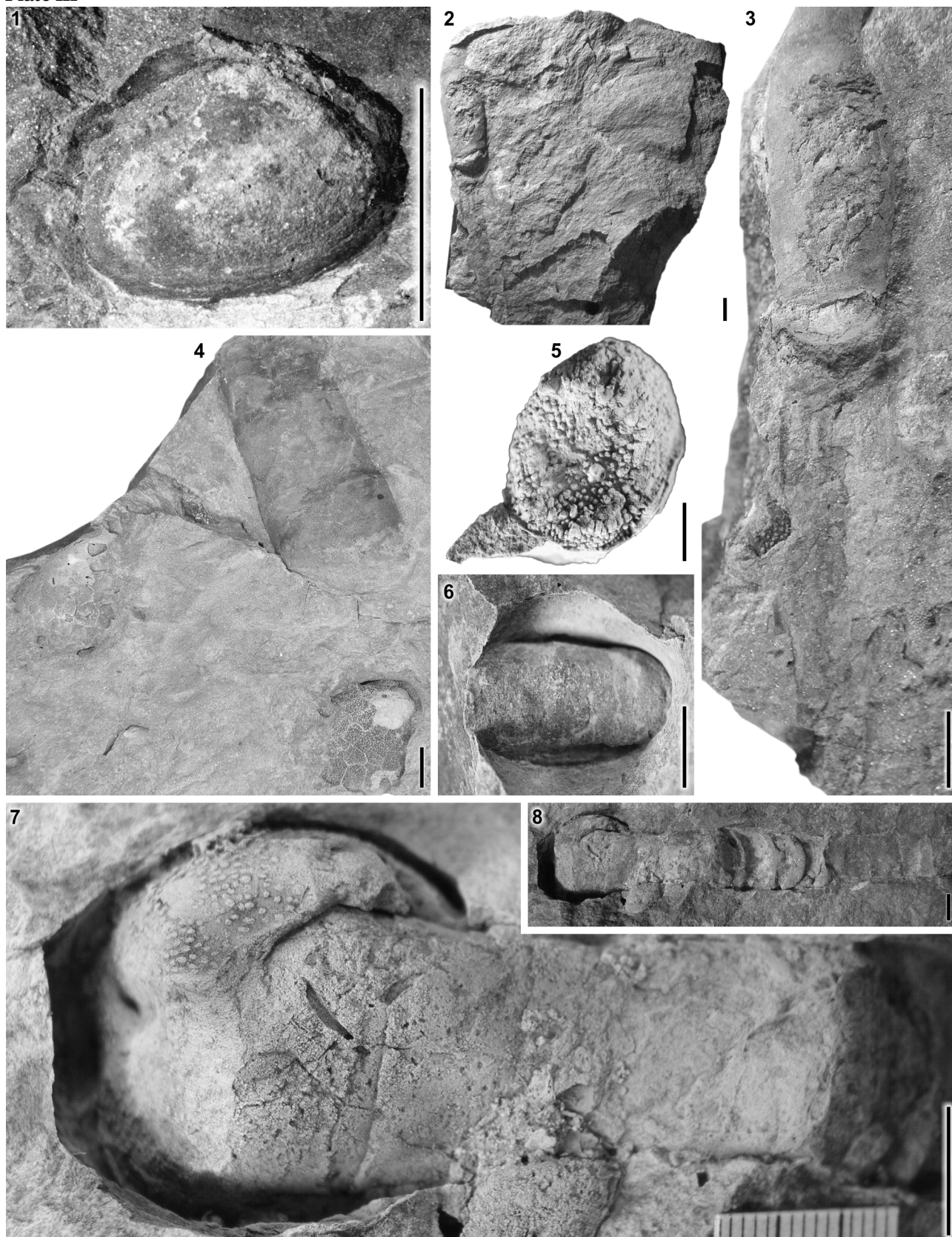
A high proportion of the discovered cephalopod shells is covered with colonies of cystoporate bryozoans *Ceramopora* Hall in Silliman *et al.*, 1851 and rarely also *Spatiopora* Ulrich, 1882 (see Kácha & Šarič 2009; Plate I).

Ceramopora vadosa Počta, 1894

Bryozoan colonies of *Ceramopora* most often occur on shells of cephalopods, conulariids and trilobites, rarely also brachiopods, gastropods and cystoids (Kácha & Šarič 2009).

Plate III. Epibionts associated with cephalopod shells; lower Katian, Zahořany Formation, Počaply near Beroun. 1 – Right valve of *Praenucula* sp. probably only randomly associated with cephalopod shell, RŠ 601. 2–3 – Shell of ?*Transorthoceras* aff. *sodale* (Barrande, 1870) with colonies of *Ceramopora vadosa* Počta, 1894 and with trace fossil *Zoophycos* sp. on the same bedding plane, RŠ 599; 2 – overall view; 3 – detail of the cephalopod fragment. 4 – Shell of *Isorthoceras bisignatum* (Barrande, 1870) with colonies of *Ceramopora vadosa*. Two thecae of *Aristocystites bohemicus* Barrande, 1887 nearby, RŠ 574. 5–6 – *Codiacystis bohémica* overgrowing the shell of ?*Transorthoceras* aff. *sodale*, RŠ 584; 5 – imprint of the inner basal part of this cystoid; 6 – view into cavity after the cystoid shell. 7–8 – *Codiacystis bohémica* Barrande, 1887 growing from the inside of the body chamber of ?*Transorthoceras* aff. *sodale*, RŠ 583; 7 – detail; 8 – overall view. All scale bars equal 10 mm.

Plate III



Specimen RŠ 572; *Isorthoceras bisignatum* (Barrande, 1870) (Plate I, figs 7, 9). See also the section *Sphenothallus*. Seven small and flat colonies of *C. vadosa* are attached to the fragment of the cephalopod shell. The zoaria are 4.8, 4.8, 5.3, 6.0, 6.4, 8.4 and 12.0 mm in diameter and more or less circular. Only the largest colony is fan-shaped with its shape axis perpendicular to the cephalopod shell axis (Plate I, fig. 7). As mentioned above, three bryozoan colonies are overgrown by sphenothallids holdfasts (Plate I, fig. 9).

Specimen RŠ 577; ?*Transorthoceras* aff. *sodale* (Barrande, 1870) (Plate I, figs 4–6). See also the section *Sphenothallus*. Colonies of *C. vadosa* attached to the cephalopod shell are irregularly distributed on its surfaces. Two modes of preservation can be clearly identified from their molds. Better preserved zoaria have zoecia with apertures pointing inward into the shell. It indicates that they covered the inner surface of the body chamber. Four colonies of this preservational type were identified; two are smaller and circular, 1.2 and 2.6 mm in diameter, and two are larger, semicircular and 4.0 and 7.7 mm in diameter (Plate I, figs 4, 5). The latter zoaria have partly straight margin limited by distinct wrinkles of growth lines on the cephalopod shell. Thus, the bryozoan colonies are semicircularly spread in adoral direction. The other mode of preservation includes three worse preserved zoaria, which are indicated only as abraded and indistinct remnants. It can be supposed that these colonies were distributed on the outer surface. They are also markedly larger than the previous type being 11.0, 11.0 and 12.0 mm in diameter. Their shape was probably circular. Below the colony situated latero-adorally on the shell fragment, there are visible indications of a small injury healed by cephalopod after breaking the shell edge.

Specimen RŠ 591; *Geisonoceras* sp. It is a fragment of the cephalopod body chamber. A large colony of *C. vadosa*, 27 x 38 mm in size, is attached to the outer surface in the posterior part of the chamber. Another zoarium is smaller, of the oval shape, 5.5 x 3 mm in size, and is situated in the central part of the chamber. Two circular colonies of the similar size, 5 and 6 mm in diameter, are sitting near the chamber aperture. Last, the smallest zoarium, having 1 mm in diameter is situated nearby.

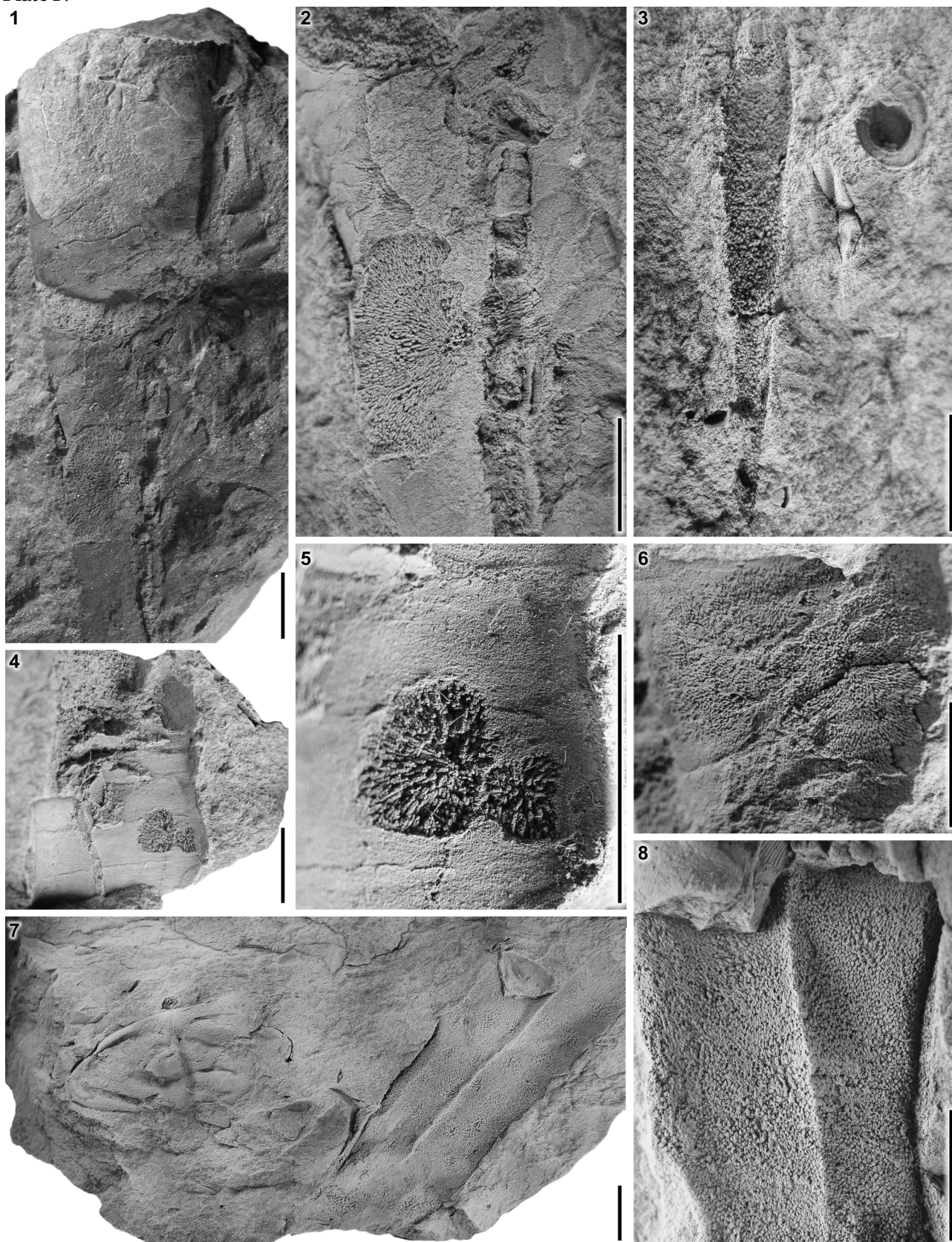
Specimen RŠ 578; *Isorthoceras bisignatum* (Plate IV, figs 1–2). It is a large fragment of cephalopod shell with a part of the body chamber. The overall length of the shell fragment is 114 mm, the uncomplete body chamber is 42 mm long. The first chamber behind the body chamber, preserved as an internal mold because of its filling with sediment, is 7 mm long. Deformed remains of the subcentral siphuncle are 3 mm in diameter. Two colonies *C. vadosa* are attached to the outer surface of the phragmocone; one is 9 x 7 mm in size and attached at the apical end of the phragmocone, dimension the other situated in its centre is 20 x 14 mm (Plate IV, fig. 2). Another zoarium, 18 x 13 mm in size, is situated on the inner surface of the body chamber near its aperture (Plate IV, fig. 1).

Specimen RŠ 607; ?*Transorthoceras* aff. *sodale*. Entire inner surface of the shell is covered with colonies *C. vadosa* Počta, 1894. The distribution pattern of the bryozoans indicates that they colonized the empty shell after septa was broken off.

Specimen RŠ 608; ?*Transorthoceras* aff. *sodale*. It is a 110 mm long fragment of cephalopod shell with part of the body chamber 42 mm long. Two zoaria of *C. vadosa*, 2.5 and 10.0 mm in diameter, are attached to the outer surface of the body chamber. The entire inner surface of the phragmocone with missing septa is covered by bryozoan

Plate IV. Epibionts on cephalopods; lower Katian, Zahořany Formation, Počaply near Beroun. 1–2 – *Isorthoceras bisignatum* (Barrande, 1870) with colonies of *Ceramopora vadosa* Počta, 1894, RŠ 578; 1 – overall view; 2 – detail. 3 – Shell of ?*Transorthoceras* aff. *sodale* (Barrande, 1870) filled with bryozoan *Ceramopora vadosa*, RŠ 586. 4–5 – Two differently sized colonies of *Ceramopora vadosa* on shell of *Isorthoceras bisignatum*, external mold, RŠ 580; 4 – overall view; 5 – detail. 6 – *Isorthoceras bisignatum* with colonies of *Ceramopora vadosa*, RŠ 597. 7 – Body chamber of *Isorthoceras bisignatum* infilled with *Ceramopora vadosa*, fragment of cephalon belonging to the trilobite *Dalmanitina proaeva* (Emmrich, 1839) nearby, RŠ 588. 8 – Shell of *Isorthoceras bisignatum* with body chamber infilled with bryozoan *Ceramopora vadosa*, RŠ 588. All scale bars equal 10 mm.

Plate IV



colonies. The distribution pattern of the zoaria indicates that after the empty cephalopod shell dropped to the bottom (it could also partly sank into sediment) the body chamber was filled with sediment and the inner surface of the phragmocone completely covered by bryozoans, probably after some part of the shell was broken off and its inner space became accessible for their larvae.

Specimen RŠ 599; *?Transorthoceras* aff. *sodale* (Plate III, figs 2–3). Fragment of a cephalopod shell is 120 mm long. It consists of the body chamber and poorly preserved phragmocone with two distinct chambers, 4 and 5 mm long. A single colony *C. vadosa*, 4.5 mm in diameter, is attached about half of the length of the phragmocone, probably to its outer surface. On the same bedding plane, there is an ichnofossil *Zoophycos* near the cephalopod (Plate III, fig. 2).

Specimen RŠ 586; *?Transorthoceras* aff. *sodale* (Plate IV, fig. 3). Shell is preserved without septa; its entire inner surface is covered by colonies of *C. vadosa*.

Specimen RŠ 574; *Isorthoceras bisignatum* (Plate III, fig. 4). Fragment of the cephalopod shell consists of the body chamber and four chambers of the phragmocone, the length of them is (ordered from the body chamber adapically) 8.2, 7.7, 5.0 and 7.5 mm. Two colonies of *C. vadosa*, both 20 mm in diameter, are attached to the outer surface of the body chambers. One zoarium is situated near aperture of the shell, other across the limit of the body and first phragmocone chamber. Two thecae of the cystoid *Aristocystites bohemicus* Barrande, 1887 are preserved near the cephalopod on the same bedding plane.

Sample RŠ 588; *Isorthoceras bisignatum* (Plate IV, figs 7–8). It is an association of orthoconic cephalopod shell, external mold of the bivalve *Ctenodonta* sp. near the cephalopod shell aperture, and cephalon and pygidium of the trilobite *Dalmanitina proaeva* (Emmrich, 1839) nearby

(Plate IV, fig. 7). Entire surfaces of the cephalopod and the bivalve are covered with *C. vadosa* Počta, 1894 (Plate IV, fig. 8).

Specimen RŠ 615; *?Transorthoceras* aff. *sodale*. A colony of *C. vadosa*, 3.5 mm in diameter, is attached near the narrower edge of the cephalopod shell fragment.

Specimen RŠ 616; *Isorthoceras bisignatum*. It is a fragment of the cephalopod shell, 35 mm long and 28 mm in diameter, with three colonies *C. vadosa* on its outer surface. The sizes of zoaria are 7 x 1.5 mm, 10 x 10 mm and 12 x 6 mm.

Specimen RŠ 580; *Isorthoceras bisignatum* (Plate IV, figs 4–5). It is a fragment of a 24 mm long part of the phragmocone consisting of four chambers, which are (ordered in the adapical direction) 4.0, 5.4, 4.8 and 4.4 mm long. A subcentral, dorso-ventrally flattened septal neck with a maximum diameter of 1.8 mm is visible on the single preserved septum. Two adjacent colonies of *C. vadosa*, 6.0 and 3.5 mm in diameter, are visible attached to the external mold near its wider edge.

Specimen RŠ 597; *Isorthoceras bisignatum* (Plate IV, fig. 6). Three almost touching colonies of *C. vadosa* are attached to the cephalopod shell near its wide end. They are 12, 12 and 16 mm in diameter.

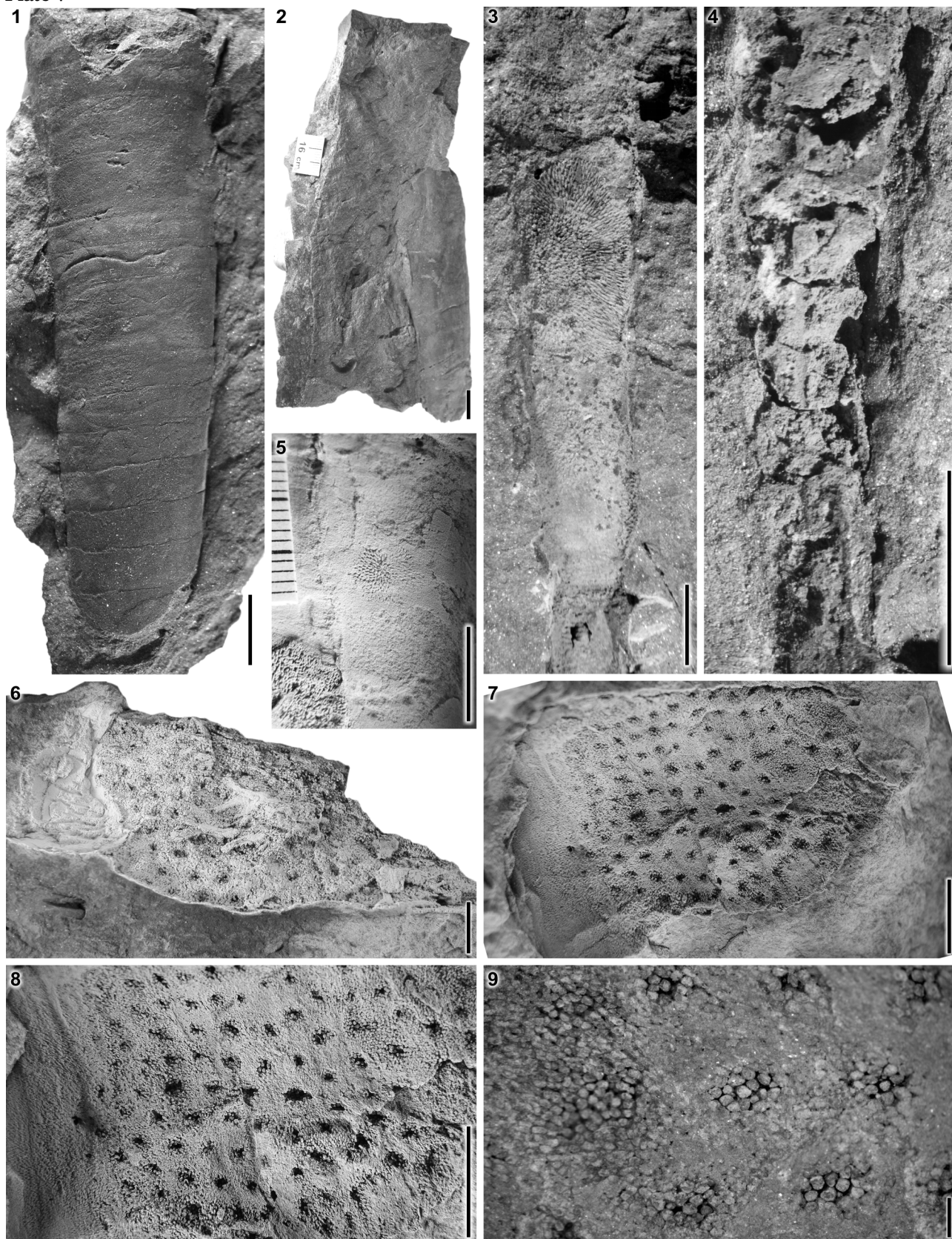
Specimen RŠ 614; *Isorthoceras bisignatum*. It represents an external mold of the cephalopod shell. Four colonies of *C. vadosa*, situated close to each other, cover the shell near its narrower end. The diameters of the colonies are 8, 11, 19, and 23 mm.

Specimen RŠ 612; *Isorthoceras bisignatum*. It is a small fragment of the cephalopod body chamber. Two adjacent zoaria of *C. vadosa*, 5 and 10 mm in diameter, cover the chamber near its supposed aperture.

Specimen RŠ 579; *Isorthoceras bisignatum*. It is represented by a fragment of the external mold of the cephalopod body chamber, 34 x 29 mm in size.

Plate V. Epibionts on cephalopods; lower Katian, Zahořany Formation, Počaply near Beroun. 1 – Internal mold of *Geisonoceras* sp. with characteristic oblique sutures, RŠ 581. 2 – Four colonies of *Ceramopora vadosa* Počta, 1894 on *Geisonoceras* sp., RŠ 598. 3 – *?Transorthoceras* aff. *sodale* (Barrande, 1870) with nine colonies of *Ceramopora vadosa*, RŠ 582. 4 – Corroded shell of *?Transorthoceras* aff. *sodale* with discernible siphuncle, RŠ 570. 5 – Colony of *Ceramopora vadosa* on the external surface of body chamber of *Isorthoceras bisignatum* (Barrande, 1870), RŠ 585. 6 – Bryozoan *Spatiopora* cf. *nodulosa* Frey, 1988 overgrowing the shell of a cephalopod, RŠ 516. 7–9 – Bryozoan *Spatiopora* cf. *nodulosa* overgrowing the aperture of shell of *Isorthoceras bisignatum*, RŠ 576; 7 – overall view; 8 – detail; 9 – Detail of monticules of *Spatiopora*. Scale bars 1–8 equal 10 mm, 9 equal 1 mm.

Plate V



Six colonies of *C. vadosa* are attached to the outer surface of the shell. They are distributed near edges of the fragment: three large zoaria, 8.5, 8.5 and 10 mm in diameter at one edge, three small ones 1.5, 1.5 and 2.0 mm in diameter at the other. It seems that these two associations reflect time-different stages of the shell colonization.

Specimen RŠ 581; *Geisonoceras* sp. (Plate V, fig. 1). It is a fragment of the phragmocone consisting of 15 chambers. The chambers are 4.6–8.0 mm long; the most frequent values are 4.7 and 5.3 mm. Four colonies of *C. vadosa* are attached to the outer surface of the shell. Their diameters are 7.5, 9.5, 11.5 and 14.0 mm.

Specimen RŠ 610; *Isorthoceras bisignatum*. Fragment of the cephalopod shell is 33 x 36 mm in size. The entire preserved outer surface of the shell is covered by *C. vadosa*.

Specimen RŠ 609; “*Orthoceras*” gen. et sp. indet. It is a very poorly preserved fragment of the cephalopod shell. Four colonies of *C. vadosa*, 6.4, 5.5, 6.6 and 7.1 mm in diameter, are attached to its outer surface.

Specimen RŠ 598; *Geisonoceras* sp. (Plate V, fig. 2). It is represented by a cephalopod shell consisting of the body chamber and a small part of the phragmocone. Four colonies of *C. vadosa*, sizing 10, 12, 13 and 20 mm in diameter, are attached near the shell aperture.

Specimen RŠ 582; ?*Transorthoceras* aff. *sodale* (Plate V, fig. 3). Seven colonies of *C. vadosa* are attached along the entire length of the cephalopod shell. Their diameters are 9.0, 8.0, 6.5, 15.0, 7.0, 4.7, and 5.0 mm (ordered from wider to narrower end of the shell). In addition, two tubes of *Conchicolites meskai* Prantl, 1948 are sitting on one bryozoan colony near the apex of the cephalopod shell.

Specimen RŠ 575; ?*Transorthoceras* aff. *sodale*. It is a poorly preserved cephalopod shell with two colonies of *C. vadosa* attached to its outer surface in its central part. Diameters of the zoaria are 3 and 4 mm.

Specimen RŠ 617; *Geisonoceras* sp. It is represented by a fragment of the cephalopod phragmocone consisting of 10 chambers, each about 6 mm long. Colony of *C. vadosa* with a diameter 11 mm is attached to its outer surface near the widest part of the phragmocone.

Specimen RŠ 594; ?*Transorthoceras* aff. *sodale* (Plate II, fig. 5). It is a short fragment represented

by the internal mold of an orthoconic cephalopod. Its unusual mode of preservation gives the impression of problematic fossil or structure when superficially observed. A pitted, uneven surface of episeptal cameral deposits (just looking like an individual problematic fossil) are visible through two oval, symmetrically placed holes in the broken shell, which seemingly look like impressions after attachments of epibionts. The entire inner surface in the apical end of the cephalopod fragment is covered by the bryozoan *Ceramopora*.

Spatiopora cf. *nodulosa* Frey, 1988

Bryozoans *Spatiopora* are less common than *Ceramopora* discussed above. According to published data, they occur attached exclusively to cephalopod shells (e.g. Bassler 1911, Ulrich 1883), most often to their body chambers where the colonies often grow adorally reaching to the aperture (RŠ 516, RŠ 576; Frey, 1988, Ruedemann, 1926).

It is worth noting that we found an interesting information about *Spatiopora* attached to conulariid thecae from the Letná Formation (middle Sandbian) during preparation of our study about epizoans attached to conulariids (Marek *et al.* 2023). The specimens were described by Bouček (1928, pp. 25, 27, 28, 77–79), however he classified *Spatiopora* as an unknown fistuliporid bryozoan.

Our assignment of bryozoans to the genus *Spatiopora* and species *S. nodulosa* is tentative and is based on regularly distributed, roughly circular monticules (Plate V, fig. 6–9) resembling *S. nodulosa* figured by Frey (1988, pl. 3, fig. 5). Other Upper Ordovician species of *Spatiopora* differ in having elongated monticules. However, *S. nodulosa* is probably a *nomen nudum* because Frey (1988, p. 89) indicated this taxon as a new species without any formal description. A precise determination is also limited by unfavourable preservation of our material (P.D. Taylor and K. Zagoršek, oral communication).

Specimen RŠ 516; “*Orthoceras*” gen. et sp. indet. (Plate V, fig. 6) It is a fragment of the body chamber of a large cephalopod shell. The entire outer surface of the chamber is covered with *Spatiopora* cf. *nodulosa* Frey, 1988 with typical circular monticules, each about 1.5 mm in diameter and 4 mm apart from each other on average. However, there is 5 mm wide zone along the chamber aperture where the zoarium lacks the monticules. One tube

of *Conchicolites* with its aperture pointing to the aperture of the cephalopod shell is overgrown by bryozoan in this zone. Based on the observation of the zone without monticules, the colony of *Spatiopora* is interpreted to grow on the shell of living cephalopod in an adoral direction up to its aperture (Frey 1988, p. 89).

Specimen RŠ 570; ?*Transorthoceras* aff. *sodale* (Barrande, 1870) (Plate V, fig. 4). It is represented by almost complete cephalopod shell with a large part of the phragmocone and a part of the body chamber. The shell is 74 mm long, of which the body chamber occupies 20 mm. Phragmocone consists of 17 chambers; their length varies between 2.7 and 4.3 mm. Siphuncle is subcentral, narrow, 0.8 mm in diameter, cylindrical with shortly orthochoanic septal necks. About half the length of the phragmocone, there is a bryozoan colony laterally attached. The zoarium is composed of minute zoecii and possesses distinct monticules. Other structures are masked by secondary limonite. The colony, visible part of which is 12.0 x 5.5 mm in size, probably belongs to *Spatiopora* cf. *nodulosa*.

Specimen RŠ 576; *Isorthoceras bisignatum* (Barrande, 1870) (Plate V, figs 7–9). It is a fragment of the body chamber belonging to a relatively large cephalopod shell. This fragment is completely covered by bryozoan *Spatiopora* cf. *nodulosa*. The zoarium is of a uniform appearance near the shell aperture but 10 mm abaperturally, distinct monticules begin to appear. They are 1.5 mm in diameter and regularly distributed in distances 4 mm from each other.

DISCUSSION

Accumulations of orthoceraconic cephalopod shells similar to those in the Silurian cephalopod or “*Orthoceras*” limestones have not yet been described from the Ordovician of Bohemia. Although much smaller in their extent and thickness compared to the Silurian occurrences they were noticed by private collectors and paleontologists (e.g. V. Turek, 2014, oral communication). The present authors identified three layers with abundant shells of orthoceraconic cephalopods during their field researches; two layers were recorded in the Letná Formation at the locality of Děd near Beroun and one layer was found in the Zahořany Formation at the locality Počaply near Beroun.

The studied cephalopod accumulations were not found in the same area in the section near the multifunctional playground in Zahořany.

Letná Formation

Both layers with cephalopods in the Letná Formation remotely resemble the Silurian cephalopod limestones of the Braník type known, e.g., from the Kosov Quarry near Beroun (Ferretti & Kříž 1995, collections of Czech Geological Survey, National Museum Prague, geopark in the Institute of Geophysics of the Czech Academy of Sciences), even though they are incomparable in much smaller thickness and geographical extent. The type of sedimentation is also different, which, unlike the Silurian cephalopod limestones, is silici-clastic (sandy to clayey). However, there are similarities in the appearance and arrangement of fossil remains within the accumulations and certain environmental conditions of their formation, e.g. a depth of approximately 30–60 m (Mikuláš 1998b, Töneböhn 1991). Also the paleoecologic conditions, under which the Letná Formation presumably deposited, correspond to shallow, open marginal sea during the time of the maximum subsidence of the Prague Basin during the Ordovician (Mikuláš 1998b, pp. 154, 155).

Similar to the Silurian limestones (Ferretti & Kříž 1995), the cephalopod shells of the Letná Formation are generally disordered in depressions, while on low elevations they are regularly aligned in the NE–SW direction, with body chambers pointing to the southwest (Ferretti & Kříž 1995). The shells were probably oriented by currents or waves, probably during storms (Petránek & Komárková 1953; Turek 1974, 1999; Ferretti & Kříž 1995). This is also in accordance with paleogeographic reconstructions (Mikuláš 1998b). This orientation of cephalopod shells in the Letná Formation is similar to the well-studied orientation of cephalopod shells in the Silurian limestones (e.g. Ferretti & Kříž 1995, Kříž 1992, 1999, Petránek & Komárková 1953). Such comparison with Silurian limestones is possible because the direction of the longitudinal axis of the Prague Basin has not changed from the Early Ordovician to the Middle Devonian (Havlíček 1981). Exceptionally, cephalopod shells from the Děd locality are oriented in a different direction, as seen for example in the specimen RŠ 603 (Figure 6).

It is worth noting the similar situation regarding the orientation of echinoderms *Dendrocystites barrandei* with brachioles oriented to the SE. Since the behavior of echinoderm shells in currents is unknown, the reason for this difference in orientation cannot yet be explained. However, the orientation of dendrocystids is interpreted by Chlupáč *et al.* (2002, p. 80) as a current direction.

The cephalopod shells in the Letná Formation represent a suitable solid substrate for the attachment of various organisms in the environment of the soft, claye to sandy bottom.

The brachiopod *Ptychopeltis incola* is attached to a cephalopod shell no. RŠ 603 and is oriented with its apex towards the aperture of the cephalopod shell (i.e. towards a possible source of food; Figure 6). This orientation implies that the brachiopod attachment occurred while the cephalopod was still alive. In contrast, undirected bryozoan colonies of *Ceramopora vadosa* (RŠ 568; Plate I, fig. 2) and the extensive overgrowth on the specimen 568/2 (Figure 7) rather indicate attachment to empty cephalopod shells, which were not covered with sediment for a relatively long time.

Zahořany Formation

Accumulations of cephalopod shells in the lower Katian Zahořany Formation at Počaply are more frequent and more or less evenly distributed in the section (i.e. they are not restricted to any particular layers), unevenly directed and consisted of fewer individuals than those in the underlying Letná Formation. However, the apices of the shells usually point in one direction (about to the NE; estimate based on conditions in the Letná Formation – see text above). This implies deposition in a flowing environment. The current or waves could not be very strong because the cephalopod shells are not excessively damaged, with body chambers often preserved. Also numerous extensive or massive overgrowths of epibionts (conchicolits, cornulitids, bryozoans), which most likely formed at the place where cephalopod shells were deposited, can indicate that food was brought by water movement (Figure 14). For the same reason, the deposited cephalopods were not quickly covered by sediment.

The breaking off of the thin, long and fragile shells of sphenothallids, after which only holdfasts remained, can most likely be explained by the

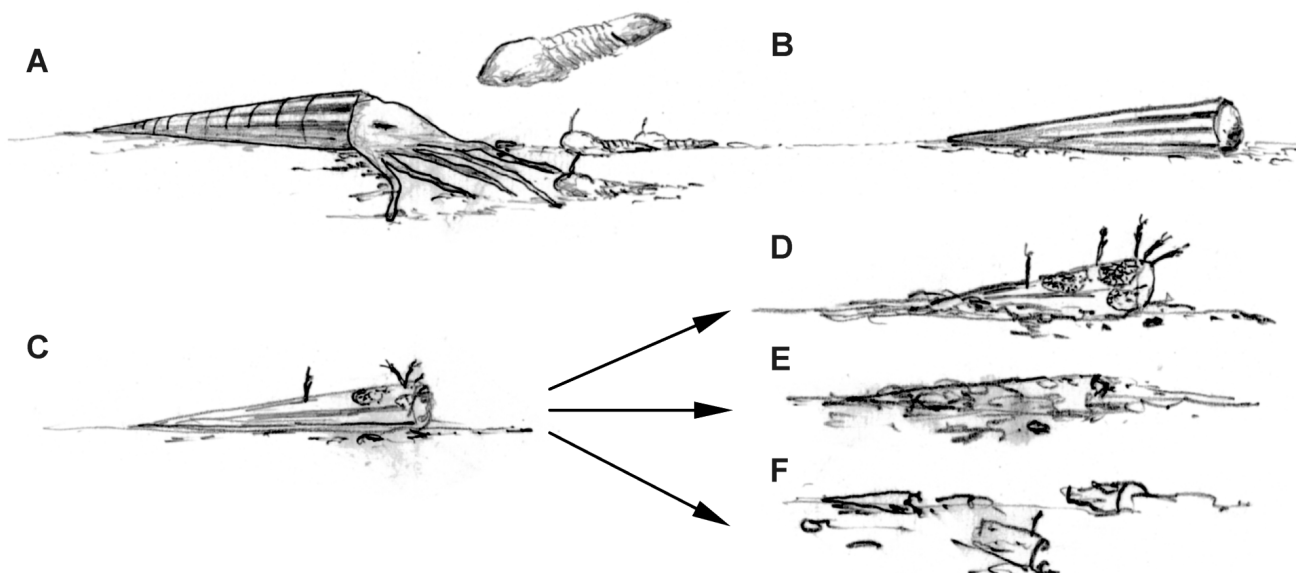


Figure 14. Model of preservation of cephalopod shells under different depositional settings. A – dead cephalopod; B – empty shell; C – epibionts begin to grow over the shell; D – number of epibionts colonizes the internal and external surfaces of the shell under slow sedimentation in a calm environment; E – epibionts are not able to grow over the shell under fast sedimentation; F – shell is fragmented in a high-energy environment.

(repeated) rolling of the cephalopod shells by deep storm waves. This would also explain that the growth of some epibionts (cornulitids, *Petrocrania*) seems to have stopped abruptly.

Estimated depth of 30–60 m is confirmed by the paleogeographic reconstructions published by Mikuláš (1998b) and the detailed research of Töneböhn (1991) in similar but stratigraphically younger (Devonian) sediments. Compared to the Letná Formation, the finer sediment deposited in a slightly deeper environment, but still well-oxygenated to allow the life of abundant epibionts.

The characteristics of most of the observed basal discs correspond to holdfasts of the genus *Sphenothallus* (Neal & Hannibal 2000). Holdfasts of dendroid graptolites, conulariids and those of some echinoderms with stems are similar. However, graptolites and echinoderms with stems can

be probably excluded, because their remains were not found at all during the extensive, several-year long research of the locality. The conulariid *Pseudoconularia grandissima* (Barrande, 1867), that probably had holdfast, is rarely found at the locality but its size reaching about 15 cm in length excludes holdfasts with a diameter of about 1.0 mm.

In all cases, holdfasts occur exclusively on the surface of body chambers of cephalopod shells, they have never been found on phragmocones. It appears that sphenothallids attached to the shell surface of living cephalopods (Figure 15). This assumption can be supported by their position near the cephalopod shell aperture, where food particles from the prey of cephalopod were more easily available. Additionally, not even a single attached shell of *Sphenothallus* has been found.

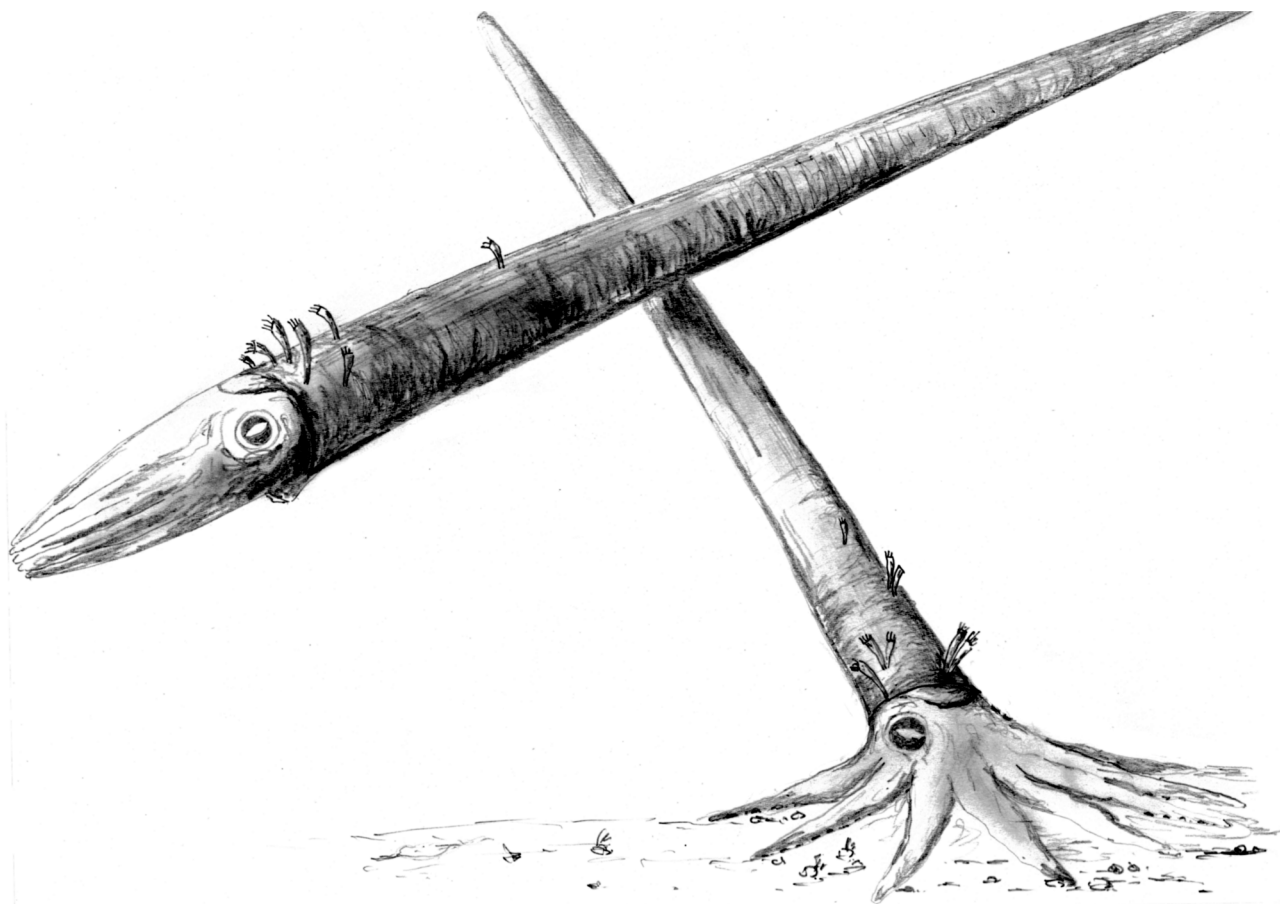


Figure 15. Reconstruction of sphenothallids attached to shells of living cephalopods in the proximity of the shell aperture. It is mainly based on the specimen RŠ 571.

All of them were probably broken off when empty cephalopod shells were rolled by waves. Sphenothallids also could not attach to the inner surface of the empty cephalopod shells after the animal death and decay of soft tissues because the space inside the body chamber was too small. If such a situation occurred, most likely at least some attached sphenothallid tubes would be preserved.

Conchicolits overgrow the shells of cephalopods in small, fan-shaped groups from the outside. A probable reason for such arrangement is the possibility of successful reproduction in environments with an insufficient offer of suitable hard substrates for attachment (Richards 1974). Conchicolits generally preferred shallow water marine conditions. They occur in two different sedimentary environments (Vinn & Gutiérrez-Marco 2016). In carbonate platform sediments (Scandinavia), they are usually found attached to the shells of large brachiopods. In siliciclastic sediments (e.g. Czech Republic, Peru), the individuals form clusters that appear to be typical for these facies. Our findings confirm this assumption.

The systematic classification of conchicolits has been discussed by many authors for more than 70 years. During this time, they were assigned to various animal groups ranging from stromatoporoids to radiates, fusulinides, bryozoans, annelids and molluscs (e.g. Barrande 1867, Vinn & Mutvei 2005, Zhan & Vin 2007). The assignment of the genus *Conchicolites* to a separate group of tentaculitids seems to be the most probable (Vinn *et al.* 2014).

An overview of epizoic bryozoans on cephalopod shells was provided by Wyse Jackson & Key (2014). It is interesting that several cephalopod shells were recorded in Počaply, on which bryozoan zoaria of various sizes were found together. For example, colonies with a diameter of 1 mm, 5–6 mm and 27 x 30 mm are attached to the specimen RŠ 591. These size groups occur regularly in all observed overgrowths of the bryozoan *Ceramopora*. Specifically, these are groups 1–4 mm (9 occurrences), 5–8 mm (18 occurrences), 9–14 mm (19 occurrences), 15–38 mm (10 occurrences). It could indicate that these are successive attachments separated in time by one reproductive cycle. This view can be supported by sporadic data on the growth rate of recent encrusting bryozoans of the

order Cheilostomatida (Haderlie, 1970; Stebbing 1971; Smith 2014), which also form circular overgrowths more or less incrustated with CaCO₃. Published data on growth rates vary depending on the type of bryozoan, climatic belt, season, average temperature, amount of food, etc. Smith (2014) studied material from New Zealand and recorded the growth rate of the bryozoan colony generally 1–10 mm/year with maximum 77 mm/y; Stebbing (1971, fig. 3) mentioned the growth rate approximately 15 mm/y for the bryozoans from Wales; Haderlie (1970) studied different species from California and measured respective values of 4 mm/month = 48 mm/y and 8–10 mm/month = 96–120 mm/y. The above data are roughly comparable with data from the Bohemian Upper Ordovician because the Barrandian area was located in a cold climate zone during the Ordovician (e.g. Scotese *et al.* 1979) and a slower growth rate may be expected (Smith 2014, p. 205; Stebbing 1971).

Since many recent invertebrates reproduce depending on the lunar cycles (e.g. Haderlie 1970 recorded newly attached bryozoans every month on experimental panels), a similar situation can be assumed in the Ordovician. However, a different length of year and a different number of days in a year will require correction (according to <http://spacemath.gsfc.nasa.gov>, the year in the Late Ordovician had 414 days and one day lasted 21.2 hours). In the case of bryozoans attached to specimen RŠ 591 with a colony diameters of 1 mm, 5–6 mm and 27 x 30 mm, the attachment intervals could really correspond to a lunar month.

Whether the bryozoans attached to cephalopod shells with periodicity of lunar or seasonal (once a year at a certain period) cycles, their observed overgrowth succession or massive fillings of body chambers are evidences of a relatively long time during which cephalopod shells were not covered by sediment. The concurrent occurrences of epibiontic bryozoan colonies of different sizes may also imply on whether the colonization of the shells happened during the cephalopod life or whether it started on necroplanktic or necrobenthic shells. During the cephalopod lifetime, bryozoans usually attached close to the aperture of the shell, where they have a better chance of gaining food particles from the cephalopod prey. As the cephalopod shell grows, the bryozoans are located further back from the aperture, while the younger

bryozoan generations attach again near the shell aperture. For this reason, the largest (i.e. oldest) bryozoan colonies tend to be closer to the shell apex and smaller colonies are located towards aperture (Gabbott 1999). When attached on a dead, empty cephalopod shell, colonies of varying size can be scattered irregularly with respect to the shell aperture. If the shell floats in water due to the gas-filled phragmocone chambers, its hydrostatic properties eliminate massive overgrowth with epibionts, which can interfere with the shell floating. For the same reason, the body chambers of floating shells cannot be completely filled with bryozoan zoaria. Colonization of a dead shells lying on or partially buried in the sediment (necrobenthic shell) is limited only to the part above the sediment, where epibionts often occur in large numbers on the outer surface and also fill open cavities, typically body chambers (cryptic environment). The different size groups (generations) of zoaria are spaced irregularly with no preference for the position near the aperture of the cephalopod shell.

The material studied herein shows that these are mostly necrobenthic shells of cephalopods inhabited by several types of epibionts (Figure 14), in some cases (bryozoans) in different developmental stages. The bryozoan overgrowths are very often large and massive, completely filling body chambers. Sometimes, the epibionts occur almost around the whole circumference of the cephalopod shell. This can be explained by their remaining on a relatively hard bottom (with a minimal layer of soft sediment or with shallow sink into sediment) or by a subsequent rotation of the cephalopod shell around its longitudinal axis, including the already discussed possibility of the shell floating. The growth of epibionts around circumference of the phragmocone was also possible when the cephalopod shell sank obliquely into the sediment with the living chamber usually filled with sediment. In such a position, cephalopod shells buried obliquely into the soft bottom occur sporadically in the lower Silurian (Homerian) graptolitic shales in the Kosov Quarry near Beroun, where graptolite rhabdosomes, caught by them and bent by the current around them form so-called “graptolite comets” (Bouček 1932, Turek, 1983, Ferretti & Kříž 1995).

CONCLUSIONS

The so far undescribed cephalopod accumulations from the Sandbian and Katian stages of the Barandian area (Czech Republic) are similar in their conditions of their formation to the much more extensive and thicker Silurian strata of the same area. In addition to a significantly smaller area and vertical extent, it differs mainly in the type of sedimentation, which is clastic. Carbonate sedimentation was very limited in the Prague Basin during the Ordovician due to the paleogeographic position in the cool climatic zone. There are also fewer layers with accumulations of cephalopod shells in the Ordovician compared to the Silurian (three vs. twelve).

Epibionts attached to the accumulated shells are mainly represented by colonies of bryozoans of genera *Ceramopora* and *Spatiopora*. The rarer *Spatiopora* (three specimens found) grew on cephalopod shells probably during the cephalopod life as indicated by its distribution along apertures of the shells and its growth stages following the growth of the shells. On the other hand, the very abundant *Ceramopora* often fills the empty body chambers on a mass scale. Regarding the abundant circular colonies on the outer surface of the shells, it cannot be unequivocally decided whether they attached to living cephalopods or only to their empty shells. In several cases, their different diameters (ages of the colonies) indicate several, up to three, phases of attachment events (breeding periods, generations).

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