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# ORGANISMS ATTACHED TO CONULARIID THECAE FROM THE UPPER ORDOVICIAN OF THE BARRANDIAN AREA (CZECH REPUBLIC)

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**Abstract:** *In the middle Sandbian and lower Katian (Upper Ordovician) rocks of the Barrandian area, the fossil remains of conulariids are relatively abundant. Their thecae were sometimes used as solid surfaces for the attachment of epizoans, mostly craniid brachiopods of the genus* Petrocrania, *more rarely also echinoderms* Hemicystites *and* Agelacrinites, *and bryozoans* Ceramopora *and* Spatiopora. *The orientation of shells of* Petrocrania *suggests that conulariids (mostly belonging to the genus* Archaeconularia*) were dead at the time of the brachiopod attachment, their thecae were partly fragmentary and secondarily replaced. A find of* Pseudoconularia grandissima *attached to the theca of the cystoid* Codiacystis *is also reported.*

**Key words:** Epizoa, brachiopods, bryozoans, cystoids, Sandbian, Katian, Zahořany Formation, Letná Formation

## INTRODUCTION

During field palaeontological researches primarily focused on fossil cephalopods (Marek et al. 2023), that took place between 2004 and 2013 at three localities in the area around the city of Beroun (1. Foot of the Děd Hill – Letná Formation; 2. Počaply section and 3. Excavation at the building site of a multifunctional playground under a road by the school in Zahořany near the Zahořany stratotype section – both Zahořany Formation), conulariid thecae with attached organisms were found. Conulariids belonged to the widespread scyphozoan cnidarians (e.g. Van Iten *et al.* 2014a, 2014b) with steeply pyramidal, organic or organophosphatic periderm (Ford *et al.* 2016). The attached organisms include craniid brachiopods (*Petrocrania*; Plate I, figs 1–3, 6, 7), cystoporate bryozoans (*Ceramopora*; Plate I, figs 2, 3) and edrioasteroid echinoderms (*Hemicystites*; e.g. Prokop 1989, p. 213). Such finds are relatively rare despite the fact that systematic palaeontological research of the Lower Palaeozoic in Central Bohemia has been underway for more than 150 years. Conulariid thecae with epizoans were described from the Ordovician rocks of Bohemia already by Barrande (1867). They are also mentioned in the monograph on conulariids by Bouček (1928) and reported briefly also by Prantl (1952), Havlíček (1994), Havlíček & Vaněk (1990) and Prokop (1989). The specimens studied in the above mentioned papers and other material is deposited in the collections of the National Museum, Prague and the Czech Geological Survey, Prague. The material studied herein is deposited in the Czech Geological Survey in the collection of R. Šarič (prefix RŠ) unless otherwise stated.

## LETNÁ FORMATION

### Geological setting

In the vicinity of Beroun, the Letná Formation (middle Sandbian) is formed by irregularly alternating greywackes and quartzose sandstones with siltstones and sandy or claye shales. Their thickness may be up to 600 m. Body fossils occur mostly in upper parts of the formation (Havlíček 1982).

## Material

*Foot of the Děd Hill*

Seven conulariid thecae were found during our field researches (Marek et al. 2023, fig. 2). None of them showed attached epizoans. Conulariids with epizoans are rather sporadic to rare in the Letná Formation (conulariids themselves are very common) as observed by the present authors in the collections of the National Museum, Prague; Czech Geological Survey, Prague and the Faculty of Science of the Charles University, Prague.

In general, the occurrences of conulariid thecae with epizoans are sporadic in the Bohemian Ordovician. The data in the most extensive study of Bouček (1928, pp. 12, 19, 24, 25, 27, 28, 43; note that Letná Formation is presented as Drabov layers dδ) show that such occurrences never exceeds 1 % of studied thecae. This is despite the fact that Bouček (1928) had at his disposal hundreds to over a thousand specimens. Bouček (1928) mentioned only several conulariid specimens with epizoans from the Letná Formation. The epizoans include an edrioasteroid echinoderm of the species *Hemicystites bohemicus* (Barrande, 1887) (Bouček 1928; classified as *Agelacrinites bohemicus*, pp. 24, 27, 76, 78) and an "unknown fistuliporid bryozoan" (Bouček 1928, pp. 24, 25, 27, 28, 77–79) classified herein as the genus *Spatiopora*.

# ZAHOŘANY FORMATION

## Geological setting

The Zahořany Formation (lower Katian) is formed by alternating siltstones and fine-grained sandstones in the studied area. Its total thickness reaches 200 m. Body fossils are relatively abundant throughout the whole thickness of the formation (Havlíček 1982). A detailed description is provided by Marek *et al.* (2023) in this volume.

## Material

The Zahořany Formation is slightly richer in conulariid thecae with epizoans compared to the Letná Formation. The most common epizoans in the Zahořany Formation are craniid brachiopods *Petrocrania obsoleta* (Barrande, 1848), found sitting only on conulariid thecae until now (Havlíček 1994). Bouček (1928) reported not only *P. obsoleta* attached to conulariids (Bouček 1928, pp. 19, 21, 26, 43, 71, 77, 93) but also the bryozoan *Ceramopora vadosa* Počta, 1894 (Bouček 1928, pp. 19, 26, 71, 77) and the edrioasteroid echinoderm *Hemicystites bohemicus* (Barrande, 1887) (Bouček 1928; classified as *Agelacrinites bohemicus*, pp. 19, 21, 71).

*Počaply section*

Fifty-three conulariid thecae were found during excavations at the Počaply section. Thirty-one of them (i.e. 58.49 %) were overgrown by epizoans. The unusually high percentage of conulariid thecae covered by epizoans has probably a primary cause in the accumulation of allochtonous conulariid thecae. Only three best preserved specimens were studied in detail.

It was observed during the collecting that conulariids evenly decrease in abundance towards the west in the studied 150 m long and 1.8 m thick secion (Marek et al. 2023, fig. 8). Conulariids decrease in their abundance from the 36 specimens found in the east to zero after only 80 metres.

**Specimen RŠ 587** (Plate I, figs 2, 3). It is a fragment of the external mould of *Archaeconularia exquisita* (Barrande, 1867) with indistinct midline and delicate sculpture. Length and width of the fragment are 43 mm and 31 mm respecively. Five specimens of *Petrocrania obsoleta* are attached to the external surface near the margin of the fragment. They are grouped into two clusters with respective two and three specimens. Between these clusters are visible deformations of the thecal wall reflecting attachment of five another *Petrocrania* specimens. The diameter of slightly oval valves varies between 4 and 6 mm. The valves are of a low conical shape with assymetrically placed apex. They are smooth, only with sparse growth lines. All specimens are oriented with their umba facing the conulariid midline, i.e. with their axes perpendicular to the thecal axis. Along with brachiopods, three small colonies of bryozoan *Ceramopora vadosa* Počta, 1894 are attached to the external surface of conulariid. Zoaria are 3, 6 and 15 mm in diameter.

**Specimen RŠ 593** (Plate I, fig. 1). A deformed fragment of the external mould of *Archaeconularia* cf. *exquisita* (Barrande, 1867) with prominent midline and indistinct sculpture is 37 mm long and 21 mm wide. Two specimens of *Petrocrania obsoleta* are sitting close to each other on the external surface in the adapical part. One of them is well preserved while other is damaged. The apex of the first specimen faces obliquely apex of the conulariid theca, the second brachiopod is oriented with its apex more to the midline. Numerous burrows occur along the nearly entire fragment of the theca. They are represented by slender, 0.1 mm wide furrows of an undulated and bent shape, and of unknown origin. Adorally, on the right side of the fragment, there is visible a low, bent ridge delimiting a broken and subsequently healed wall of the theca.

Conulariid thecae with attached *Petrocania* and *Cerampora* are mentioned also by Bouček (1928, pp. 19, 43).

**Specimen RŠ 602** (Plate I, fig. 6). It is a poorly preserved small fragment (21 x 21 mm) of the external mould of *Conularia* sp. with prominent midline and indistinct sculpture. Two brachiopod specimens *Petrocrania* are attached close to each other in the adapical part of the conlariid theca. The diameters of the brachiopod valves are 4.5 mm and 5.5 mm.

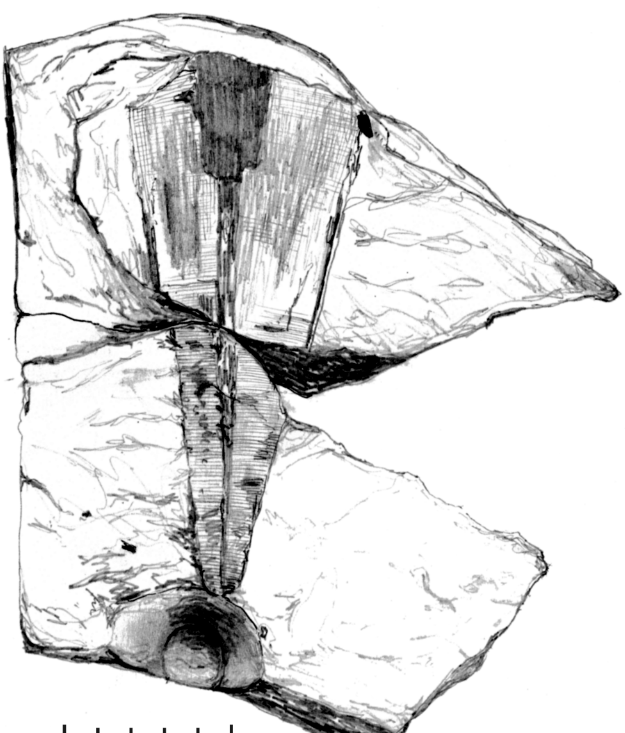


Figure 1. *Drawing of* Pseudoconularia grandissima *attached to theca of the cystoid* Codiacystis bohemica, *Počaply section, Zahořany Formation, RŠ 600. Scale bar equals 5 cm.*

In one case, the epizoan is a conulariid itself. **Specimen RŠ 600** (Figure 1; Plate I, figs 4, 5) represents a rare case of almost complete theca of *Pseudoconularia grandissima* (Barrande, 1867) attached to a large theca (45 mm in diameter) of the echinoderm *Codiacystis bohemica* (Barrande, 1887). The conulariid theca is 155 mm long and 75 mm wide near the aperture displaying the apical angle 23°. Midline and corner groove are distinct. Number of rib nodes is 16 in 10 mm. The conulariid theca is attached to the echinoderm by the circular holdfast having 6 mm in diameter.

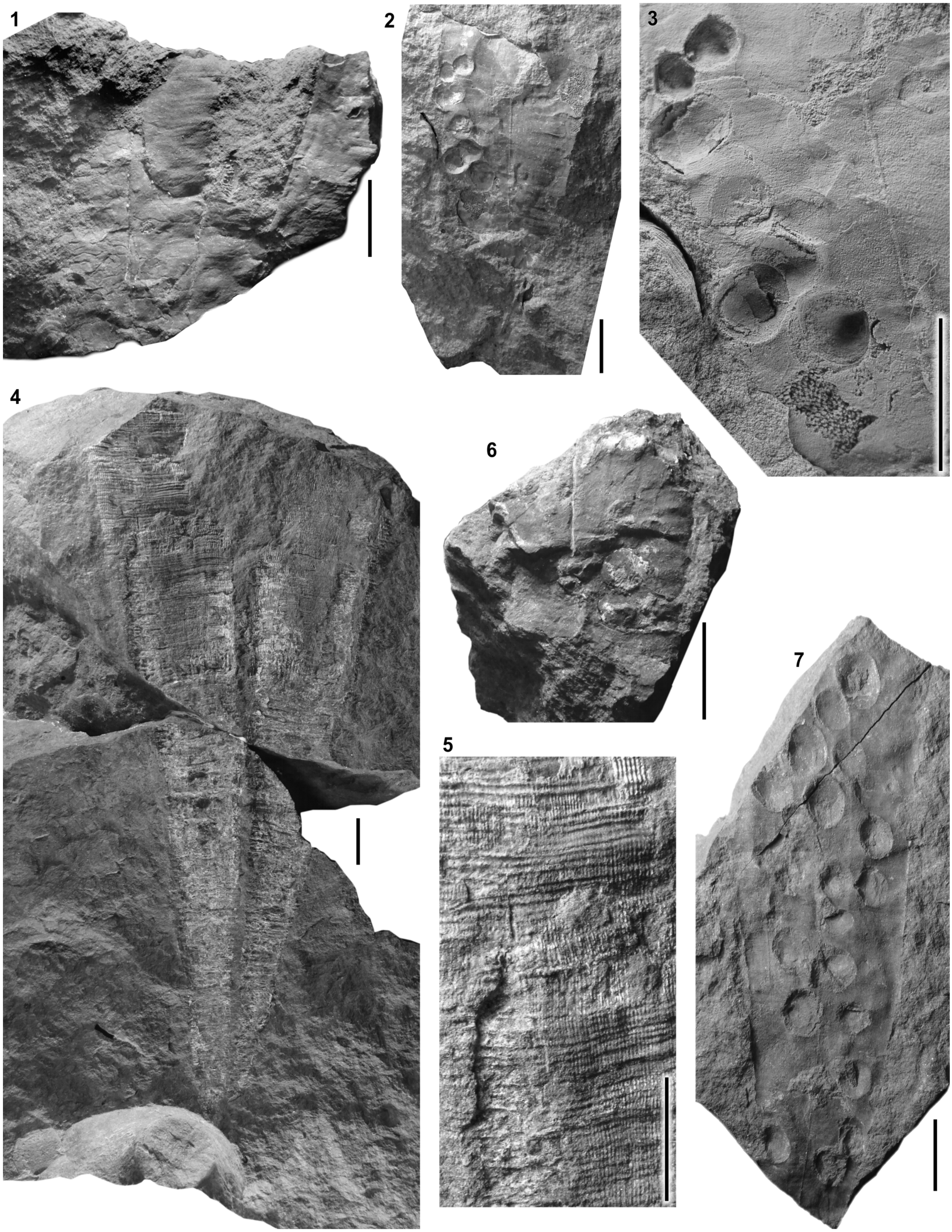
*Excavation at the building site of a multifunctional playground*

At the other studied section that was exposed during the construction of multifunctional playground near the Zahořany stratotype section (Marek et al. 2023, fig. X), only two conulariids were found in 2015; none with epibionts. However, **Specimen p 3654** (Plate I, fig. 7) can be closely related to this locality. It is deposited in the collections of the Czech Geological Survey and was found by I. Chlupáč at Zahořany – Hájek situated 20–40 m northward (note that it is not identical with the near locality Háj in the Letná Formation). It is a thecal fragment of *Archaeconularia exquisita*, 90 mm long, and 32 and 13 mm wide in its opposite ends. Twenty specimens of brachiopod *Petrocrania obsoleta* (Barrande, 1848) are attached to this fragment. The size of their valves ranges from 4 to 8 mm. They are irregularly distributed along the entire surface of the conulariid fragment with their umba more or less facing the midline.

## DISCUSSION

Solid substrates are appropriate for colonisation by planktonic larvae, which require hard surfaces to develop successfully into larger and heavier later growth stages. In cases where continuous solid substrates are lacking, hard parts of the bottom, rock fragments and boulders, and shells of living or dead organisms are used for attachment by such organisms. If the object chosen by a larva is too small to carry the adult individual, at a critical moment it is overturned from a stable position and falls into the surrounding substrate. This can lead to the decreasing the growth speed, damage or death of the attached organism as illustrated by

Plate I



rugose corals from the Silurian of Gotland (Kettnerová 1932). Only in some cases, such affected organism is able to survive without consequences. There are also organisms that have come to terms with a similar situation during their evolution and quite regularly react to a given event by changing the direction of growth from the more or less horizontal position to the vertical one. It can be exemplified by hook-shaped forms of rugose corals of the species *Acanthophyllum moravicum* from the Middle Devonian (Givetian) of Čelechovice na Hané, Czech Republic (Kettnerová 1932, pl. 2, fig. 6; pl. 3, fig. 3). In this case, the hard substrate is the shell itself, larger than the original base.

Shells of other organisms have also been used as solid substrates. Further development of colonising epizoans depends on whether they attach to the shells of dead organisms, abandoned shells or shells of living animals. Internal spaces of shells may be colonised by specialised epizoans as cryptic environments. Under more dynamic environmental conditions, relatively light shells may be overturned, rotated or buried by waves or currents. If the attached animals survive such action, they usually respond by growing to the side or upwards to reach a more convenient position (e.g. Marek *et al.* 2023, figs 12, 13). Special cases are represented by floating shells of dead cephalopods buoyed for some time by gases in the phragmocone chambers or large pieces of wood with crinoids of the genus *Seirocrinus* known from the Lower Jurassic of Germany (Müller 1960, p. 380).

Epibionts occur not only on contemporary shells but could attach also to those that had been already fossilised and partially weathered. Horizontally deposited orthocone cephalopod shells that were half-diameter weathered or eroded out and subsequently overgrown with encrusting colonies of the tabulate coral *Tiverina vermiculata* are an example from the Lower Devonian (Lochkovian, Czortkow Fm.) of Podolia, Ukraine (collection by J. Marek). It was not possible to determine the time span between deposition of cephalopods and their colonisation by corals. However, it is apparent that cephalopod shells were fossilised before their exposure as a substrate for colonisation.

If shells of living organisms are colonised, the epizoan strategy depends on whether they are attached to the sessile or vagrant benthos, or even nektonic or planktonic animals. Epibionts concentrate on free surfaces of host shells (e.g. dorsal sides of moving benthos; in sessile host filtrators, usually on the side against the direction of waves or currents, from which food particles are carried; Boucot 1981). This is generally related to the preferred orientation of attached epizoans on the host shell even in actively swimming organisms (e.g. anomyide bivalves on ammonites; Meischner 1968). For the same reason, epizoans commonly prefer to attach near apertures of host shells, close to entrances of inhalant water currents and also near the anuses such as the gastropod *Platyceras* on crinoid calixes (Müller 1960).

Also the properties of the substrate are important for the attached organism. The physical characteristics, such as the quality of the surface, its smoothness, structure or texture, may influence the possibility of attachment (Brenchley & Harper 1998). A colour representing camouflage can have a similar effect. Other physical factors include the intensity of light, water depth, dynamics of the aquatic environment, speed of currents and other (e.g. Ager 1963). The most important chemical properties are the composition (mineralogy) of the substrate, water acidity (pH), oxygen content and others (Brenchley & Harper 1998). The amount and quality of available nutrients are among the main biofactors (Ager 1963, Boucot 1981).

The orientation of attached brachiopods of the genus *Petrocrania* was studied on the herein

**Plate I.** 1 – *Archaeconularia* cf. *exquisita* with two attached brachiopods *Petrocrania obsoleta*, Počaply section, Zahořany Formation, RŠ 593. 2, 3 – *Archaeconularia exquisita* with attached craniid brachiopods *Petrocrania obsoleta* and colonies of the bryozoan *Ceramopora vadosa*; overall view (2) and detail (3); Počaply section, Zahořany Formation, RŠ 587. 4 – *Pseudoconularia grandissima* attached to the cystoid *Codiacystis bohemica*; overall view (2) and detail of conulariid theca sculpture; Počaply section, Zahořany Formation, RŠ 600. 6 – *Conularia* sp. with two attached brachiopods *Petrocrania obsoleta*, Počaply section, Zahořany Formation, RŠ 602. 7 – *Archaeoconularia exquisita* with attached brachiopods *Petrocrania obsoleta*, Zahořany – Hájek, Zahořany Formation, p 3654. Scale bars equal 1 cm.

reported conulariid specimens. In all cases, the brachiopods are attached with their longitudinal axes more or less perpendicularly to the axis of the conulariid theca and the apices irregularly oriented outwards or towards the midline. It is worth noting that brachiopods described and figured in previous studies are often attached with their longitudinal axis parallel with the longitudinal axis of the conulariid theca. Brachiopods attached near the aperture of conulariid theca usually point their apices towards the apex of the theca (e.g. Havlíček 1972, Havlíček & Vaněk 1996, Mergl & Nolčová 2016). In the apical region of the theca, the brachiopods are oriented with their apices towards the aperture of the theca (Harland & Pickerill 1987) or vice versa (Babcock & Feldmann 1986). The orientation of small and smooth valves of *Petrocrania* cannot be determined in cases of poorly preserved material or if published on figures of insufficient quality (Topper *et al.* 2018).

The interpretation of these different orientations is not unequivocal. However, it seems that brachiopods with longitudinal axis of the shell oriented parallel with the longitudinal axis (midline) of the conulariid theca attached to the living conulariid. They were probably able to capture food particles not consumed by the conulariid in position near the thecal aperture. When attached near the apex, the brachiopods could capture food particles raised from the bottom by water currents or by the currents created by the host animal. The orientation of brachiopods perpendicular to the longer axis of fragments of conulariid theca described herein probably indicates that epizoans attached to the empty allochtonous theca and used it simply as a solid substrate. The fact that the orientation of the brachiopod shells is also not random in this case can be explained by the hydrodynamic properties of the fragments of empty conulariid shells deposited in an oriented manner by weak currents or waves, which then determined the orientation of the epizoans.

The "unknown fistuliporid bryozoans"attached to conulariid thecae, that was found in the Letná Formation of mid Sandbian age and described by Bouček (1928, pp. 25, 27, 28, 77–79), were assigned to the genus *Spatiopora* herein. This determination is based on superficial resemblance to specimens attached to cephalopod shells discovered in the younger Zahořany Formation (lower Katian; Marek *et al.* 2023, see specimens RŠ 516, RŠ 570, and RŠ 576). Material studied by Bouček (1928) is unusual because all other specimens of bryozoan *Spatiopora* were described to be attached exclusively to cephalopod shells (e.g. Ulrich 1883, Bassler 1911, Ruedemann 1926, Frey 1988). This remarkable anomaly may be caused by lack of cephalopod shell substrate in quartzose sandstones of the Letná Formation and by similar shapes of cephalopod shells and conulariid thecae. Colonies of *Spatiopora* are usually attached along the entire circumference of apertural region of the host conical or pyramidal shells. It allowed to bryozoan zooids to catch and consume the missed food particles just near aperture of living animal.

## CONCLUSIONS

Among the studied excavations (Foot of the Děd Hill: Letná Formation, 6 x 2 x 1 m; Počaply section: Zahořany Formation, 150 x 2 x 1.8 m and Excavation at the building site of a multifunctional playground in Zahořany: Zahořany Formation, 24 x 2 m), conulariids with epibionts were found only in those excavated in the Zahořany Formation. Conulariids occur also in the Letná Formation but none of the specimens was found with attached epibionts although they were proved in this unit in past (e.g. Bouček 1928).

The Zahořany Formation was formed (e.g. Mikuláš 1998) under shallow-water conditions at a depth of approximately 30–60 m. The water dynamics through waves and/or currents was a source of well-oxygenated water and a sufficiency of food. This caused favourable living conditions for epizoans. Because the bottom surface was soft, the epizoans attached to allochtonous conulariid thecae which got caught and accumulated along low and flat elevations on the sea bottom. The presence of currents also corresponds to the fragmentation of transported conulariid thecae with missing apices and apertures. Complete thecae occur only exceptionally. Conulariids are relatively abundant in the Bohemian Ordovician (e.g. Bouček 1928 described hundreds of specimens) but they usually occur as single specimens. However, clusters of two to four individuals have been reported from elsewhere (e.g. Babcock & Feldmann 1986, Van Iten *et al.* 2013). Larger groups of individuals accumulated in one place do not seem to reflect their original living strategy. These cases thus point to mechanical accumulation of originally distant individuals rather than to remains of drifted more numerous colonies. Deposited thecae, slightly elevated above the surrounding soft substrate, were appropriate for attachment and therefore used by epizoans as local solid substrates. Considerations about this life strategy are also supported by high number of attached individuals in a situation of limited possibilities for sedentary behaviour.

The character of the surface of conulariid thecae probably influenced the taxonomic composition of attaching epizoans. They mostly include brachiopods *Petrocrania obsoleta*, less common echinoderms *Hemicystites bohemicus*, and rare bryozoans *Ceramopora vadosa* and *Spatiopora* sp. This is in contrast with associated, mostly allochthonous shells of orthocerid cephalopods that are heavily colonised by *Ceramopora vadosa*, moderately by *Sphenothallus* sp. and *Conchicolites meskai*, rarely by *Spatiopora* cf. *nodulosa* and *Codiacystis bohemica*, and by a cornulitid in a single case (Marek *et al*. 2023).

The presented study of conulariid thecae with attached epizoans confirms the results of similar studies of Ordovician rocks from elsewhere around the world (Babcock & Feldmann 1986, Harland & Pickerill 1987) and supplement data from the Upper Ordovician of the Barrandian area (Bouček 1928, Havlíček 1972, 1994, Mergl & Nolčová 2016).

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