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The serpulid tube worm *Laqueoserpula reussi* (Weinzettl, 1910) from the Upper Cretaceous of the Bohemian Cretaceous Basin – an alleged gastropod which has turned out to be a characteristic faunal element of marine nearshore high-energy environments

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ABSTRACT:

Jäger, M., Kočí, T., Sklenář, J. and Zágoršek, K. 2024. The serpulid tube worm *Laqueoserpula reussi* (Weinzettl, 1910) from the Upper Cretaceous of the Bohemian Cretaceous Basin – an alleged gastropod which has turned out to be a characteristic faunal element of marine nearshore high-energy environments. *Acta Geologica Polonica*, **74** (2), e12.

The serpulid tube worm *Laqueoserpula reussi* (Weinzettl, 1910), originally introduced as a gastropod named *Burtinella*(?) *reussi*, is described from the Upper Cenomanian and Lower Turonian of the Bohemian Cretaceous Basin. It had usually been confused with other species and genera before 2008. Comparison with specimens from the type locality of the type species of the genus *Laqueoserpula* Lommerzheim, 1979 confirms the affiliation of the Bohemian species to this genus. The simple prismatic (SP) ultrastructure of the tube wall of *L. reussi* agrees with an assignment to the tribe Serpulini Rafinesque, 1815. In the Upper Cretaceous, representatives of *Laqueoserpula* are exclusively found in nearshore deposits, where they are accompanied by a high diverse marine invertebrate fauna. By its compact, large and robust tube forming a spiral and extremely thick tube wall, *L. reussi* was well-adapted to live in nearshore high energy environments, where its tube could be encrusted by bryozoans, brachiopods and oysters, and infested by hydroids and borers.

Key words: Polychaeta; Serpulidae; *Laqueoserpula reussi*; Taxonomy; Cretaceous; Bohemia; Czech Republic.

INTRODUCTION

By building a tube consisting of calcium carbonate around their soft body, serpulid tube worms, together with other marine organisms which precipicate calcium carbonate and/or encrust solid submarine surfaces, play an important role in removing carbon from seawater and consolidation of sediment on the seafloor. Studies on fossil serpulids are hampered by the limited set of morphological features available from their tubes, which in most cases are the only remains to be found. In addition, in only a part of the many serpulid genera does the operculum consist of calcareous material and may be preserved, but mostly it is found separated from the tube and often overlooked due to its small size. Moreover, research on the systematics and phylogeny of fossil and recent serpulid tubes is hindered partly by their high intraspecific and intragenetic variability and also by the considerable number of homeomorphies between tubes of different serpulid taxa. In contrast, morphological details of the body and the operculum, together with research on genetics, yield the vast majority of features suitable for research on the systematics of recent serpulids and phylogeny. Recognizing which kind of fossil tubes belongs to either the same or to a different species or genus, and how to phylogenetically and taxonomically connect fossil tubes to the already well-established systematics of recent serpulids (Kupriyanova and Flaxman 2023; Kupriyanova *et al.* 2023) is an important prerequisite for reconstruction and palaeoecological interpretation, and for determination of fossil habitats. This, of course, should be done in connection with similar research on other components of the taphocenoses and their presumed ecology, sedimentology, regional geology and palaeogeography. During our studies on *Laqueoserpula reussi* (Weinzettl, 1910), we had temporarily considered assigning the species *reussi* to a different genus, *Placostegus* Philippi, 1844. Such an assignment would have led to a slightly different palaeoecological interpretation. Only after direct morphological comparison with a number of specimens from the type locality of the type species of *Laqueoserpula* we are convinced that this genus is the correct name for the species *reussi*.

Serpulid worm tubes are a common component of the mesofauna of Upper Cretaceous nearshore marine sediments. In the Bohemian Cretaceous Basin (BCB), Velim near Kolín, Chrtníky near Pardubice, Kamajka near Chotusice, and Kaňk near Kutná Hora belong to the most important localities of the fossil-rich and highly diverse nearshore facies around the Cenomanian/Turonian boundary. Apart from the classic 19th century monographs by Reuss (1845–1846) and Geinitz (1875), the most detailed information about serpulid tubes from the BCB was given in a monograph by Ziegler (1984). This monograph and several additions and revisions (e.g., Jäger and Kočí 2007; Jäger 2014; Kočí and Jäger 2015) include descriptions of several species of serpulid tube worms from that area.

The aim of the present article is a deep revision of *L. reussi*, mainly to discriminate between the three species mixed by Weinzettl (1910), to select, describe and refigure the lectotype and syntypes of *L. reussi*, to clear the many misidentifications of this species in a synonymy list, to describe and figure the morphology of *L. reussi* in detail, and to describe and discuss its palaeoecology, especially the symbiont *Protulophila gestroi* Rovereto, 1901, which had infested many of the tubes, and the bryozoans which often had settled upon the tubes.

HISTORY OF RESEARCH – HOW AN ALLEGED GASTROPOD TURNED OUT TO BE A CHARACTERISTIC FAUNAL ELEMENT OF MARINE NEARSHORE HIGH-ENERGY ENVIRONMENTS

The species name *reussi* was introduced by Weinzettl (1910). However, he misinterpreted this species as a gastropod and named it *Burtinella*(?) *reussi*. Moreover, his type series is a mixture of three different species. Only three of his six figured specimens belong to *L. reussi*, as we discuss below in the present study.

Before, as well as after Weinzettl's (1910) publication, tubes which we assign to *L. reussi* had repeatedly been described by several authors (see below and synonymy list), who correctly identified these fossils as serpulids, not gastropods. However, all these authors before Kočí (2008) misidentified these tubes at the species level by describing them under several well-established species names, which represent other serpulid species clearly different from *L. reussi*. In 2008, one of us (JS) re-discovered Weinzettl's original specimens in the museum's collection. Subsequently, JS and TK recognized that these specimens represent serpulids rather than gastropods and thereby triggered the correction of Weinzettl's error concerning the systematic position of '*Burtinella*' *reussi*. As a result, MJ proposed a new combination of genus and species names as '*Laqueoserpula reussi*', and TK mentioned this new combination in Kočí (2008) and several later papers. However, before this study, we have never discussed nor described *L. reussi* in detail. Presumably unaware of Kočí's (2008) publication, Bieler and Petit (2011), in their important *Catalogue of Recent and fossil 'worm-snail' taxa* among gastropods, correctly listed the species *reussi* as a polychaete, but these authors also did not provide any further details.

Concerning historical designations of *L. reussi* and the localities where it has been collected, one of the first was Reuss (1845–1846), who referred to specimens from the Lower Turonian of Želenice

('Schillinge') and Novosedlice ('Weisskirchlitz') near Bílina and Teplice, respectively, and classified them as '*Serpula ampullacea* Sowerby'.

Geinitz (1875) described and figured the present species as '*Serpula depressa* Goldfuss' from the Upper Cenomanian of the Gamighübel at Dresden-Kauscha in Saxony. This locality has several serpulid species in common with Velim, for example *Placostegus velimensis* Jäger and Kočí, 2007 and *Dorsoserpula bipartita* (Reuss, 1845), syn. *gamigensis* (Geinitz, 1875) (see Kočí 2007 and Jäger 2014).

Lommerzheim (1979) listed '*Laqueoserpula* cf. *plana*' from Velim, which very probably represents *L. reussi*.

Ziegler (1984) described and figured several specimens of *L. reussi* under at least six different established species names (see synonymy list). When describing '*Eoplacostegus sulcatus*', Ziegler (1984) figured one specimen from the Lower Turonian of Velim, which in our opinion belongs to *L. reussi*. On p. 236, he mentioned Lower Turonian occurrences at additional localities of '*Eoplacostegus sulcatus*': Nová Ves near Kolín, Radim, and Vítězov. However, he did not figure specimens of '*Eoplacostegus sulcatus'* from these sites, and TK did not find tubes of *L. reussi* at any of these localities, neither in Ziegler's collection nor in other material from the three localities. Therefore it remains uncertain if *L. reussi* occurs there at all. These uncertain localities are not shown in Text-fig. 1.

Laqueoserpula reussi had also been figured from Chrtníky by Žítt *et al.* (2006), who determined it as '*Serpula* cf. *rauca* Ziegler' from 'unit 7' belonging to the Lower Turonian *Helvetoglobotruncana helvetica* Zone.

All the localities where *L. reussi* has been proven to occur are shown in Text-fig. 1.

Text-fig. 1. Map of localities with representatives of *Laqueoserpula* Lommerzheim, 1979: A – in Europe: 1 – Bielawy Quarry, Poland (*L. intumescens*); 2–3 – Rauen Quarry at Mülheim-Broich, Germany (*L. litoralis* and *L. plana*), and former quarries in the city of Essen, Germany (*L. litoralis*); 4 – Bohemian Cretaceous Basin (*L. reussi*; see B for details); 5a –Lengede, Germany; 5b – Gehrden, Germany (*Laqueoserpula*? sp. at both localities); 6a – ENCI-Heidelberg Cement Group Quarry, Maastricht, The Netherlands; 6b – Albert Canal near Neerkanne, Belgium (*L. schmidwallisi* at both localities); and B – in the Bohemian Cretaceous Basin (green).

MATERIAL AND METHODS

Several thousand serpulid tubes including several hundred specimens of *L. reussi* were collected between 2001–2016 in the localities (mainly old, abandoned quarries) at Velim near Kolín, Kaňk and Turkaňk near Kutná Hora, and Kamajka near Chotusice; and the Chrtníky working quarry, mainly by TK, and some by MJ and Radek Vodrážka (for details see below).

The material from Velim was gained by the washing and sieving of more than 50 kg of loose rubble, which had accumulated below sublocality VII (also known as'pocket Václav'; for a detailed description of the old Velim quarry, also known as 'Skalka u Velimi' or 'Skalka near Velim', see Žítt *et al.* 1997). The material from Chrtníky was collected using the same method (for a detailed description of the Chrtníky working quarry, see Žítt *et al.* 2006). However, the fossil-rich section at Chrtníky is now destroyed by quarrying (Radek Vodrážka, personal communication 2009). At the other localities, the specimens were mainly hand-picked from the surface of loose rubble. After washing, the adhering sediment was removed, when necessary, by a needle, and the specimens were studied under a binocular microscope.

Moreover, we have studied under a binocular microscope the original specimens of Weinzettl (1910) and Ziegler (1984), and the material from old collections (collection of Antonín Culek, Starkoč locality, and those collected by Olga Nekvasilová during 1960–1967), all kept in the National Museum (Národní Muzeum), Prague, Department of Palaeontology. MJ studied some specimens from the Saxon part of the BCB kept in the Senckenberg Naturhistorische Sammlungen in Dresden, including the original specimen of Geinitz (1875).

For ultrastructure studies, selected tubes from Velim and Chrtníky were ground longitudinally and transversely, polished and etched with 1% acetic acid for ten minutes before SEM examination by JS.

All specimens of *L. reussi* are which are figured in the present paper and/or mentioned in the text are recorded by their NM-O numbers, and several more such specimens are deposited in the National Museum (Národní Muzeum), Prague, Department of Palaeontology. Their numbers are: NM-O3537 (2nd syntype), NM-O3538 (lectotype), NM-O3539 (1st syntype), NM-O5167, 5377, 5379–5381, 5397, 5398, 6661–6668, 7681–7693, 9493, 9500, 9501, and NM-Os392. Serial sections of the tube ultrastructure are labelled NM-d17a/2016 and NM-d17b/2016. Moreover, several specimens belonging to other species but mentioned also herein, are numbered NM-O3536 and 3540. Old museum bulk material without a given collector is stored under NM akc. 36675/1957 (ČL 3637), bulk material from Antonín Culek's collection under NM akc. 228/1968.

SYSTEMATIC PALAEONTOLOGY

Class Polychaeta Grube, 1850
Subclass Sedentaria Lamarck, 1818
Infraclass Canalipalpata Rouse and Fauchald, 1997
Order Sabellida Levinsen, 1883
Family Serpulidae Rafinesque, 1815
Subfamily Serpulinae Rafinesque, 1815
Tribe Serpulini Rafinesque, 1815
Genus *Laqueoserpula* Lommerzheim, 1979

TYPE SPECIES: *Laqueoserpula litoralis* Lommerzheim, 1979.

Laqueoserpula reussi (Weinzettl, 1910)
(Text-figs 2A–I, 3A–D, 4A–D)

non 1829. *Serpula ampullacea*; Sowerby, p. 199, pl. 597, figs 1–5.
non 1831. *Serpula depressa*; Goldfuss, pp. 236, 237, pl. 70, fig. 6.
?1844. *Serpula gordialis* Schloth. var. *spirata* m.; Reuss, p. 216.
non 1845. *Serpula depressa* v. Münst.?; Reuss, part 1, p.18, pl. 5, fig. 28a, b.
part 1845. *Serpula ampullacea* Sow.; Reuss, part 1, p. 20, pl. 5, fig. 22a–c.
1846. *Serpula ampullacea* Sow.; Reuss, part 2, p. 106, pl. 24, figs 6, 7.
?1846. *Serpula depressa* Goldfuss; Geinitz, p. 250.
1875. *Serpula depressa* Goldf.; Geinitz, p. 286, pl. 63, fig. 22.
non 1889. *Serpula depressa*, v. Münst.; Frič, pp. 22, 57, 96.
*part 1910. *Burtinella*(?) *Reussi*; Weinzettl, pp. 23, 24, 54, pl. 3, figs 46, 47, 51, non 48, 49, 50.
1911. *Burtinella*(?) *Reussi*, Weinz.; Frič, p. 18, fig. 75.
1911. *Serpula depressa*, Goldf.; Frič, p. 101.
1979. *Laqueoserpula* cf. *plana*; Lommerzheim, p. 150.
part v 1984. *Spiraserpula spirographis* (Goldfuss, 1831) – *Mucroserpula arcuata* (Münster, 1831); Ziegler, pp. 225, 228, 229, pl. 3, fig. 7 [NM-O5377], non fig. 6.
v 1984. *Mucroserpula arcuata* (Münster, 1831); Ziegler, pp. 228, 229, pl. 4, figs 3, 4. [NM-O5379, NM-O 5380]
v 1984. *Mucroserpula mucroserpula* H. Regenhardt, 1961; Ziegler, p. 229, pl. 4, fig. 5. [NM-O5381]
v 1984. *Eoplacostegus sulcatus* (Sowerby, 1829); Ziegler, pp. 235, 236, pl. 5, fig. 8. [NM-O5167, not NM-O5389, as erroneously stated by Ziegler (1984, p. 253)]
v 1984. *Hepteris septemsulcata* (Roemer, 1841); Ziegler, pp. 240, 241, pl. 7, figs 3, 4. [NM-O5397]
v 1984. *Hamulus sexsulcatus* (Münster, 1831); Ziegler, p. 240, pl. 7, fig. 5. [NM-O5398]
2006. *Serpula* cf. *rauca* Ziegler; Žítt *et al.*, p. 66, fig. 12M.
v 2008. *Laqueoserpula reussi*; Kočí, p. 45.
v 2009. *Laqueoserpula reussi* (Weinzettl); Kočí, pp. 209, 211–214.
2011. *Burtinella reussi* Weinzettl, 1910 [polychaete]; Bieler and Petit, p. 55.
2012. *Laqueoserpula* sp.; Kočí, p. 122, fig. 1G.
2014. *Laqueoserpula reussi* (Weinzettl, 1910); Jäger, p. 67, fig. 2d1–3.
2015. *Laqueoserpula reussi* (Weinzettl, 1910); Kočí and Jäger, pp. 35, 36, pl. 1, fig.7.

ORIGINAL DIAGNOSIS BY WEINZETTL (1910) [translation]: *A very variable, and apparently largely imitating form. The shell is attached to foreign objects and is coiled in the juvenile stage. The coils are either dextral or sinistral, usually not visible externally, forming a single mass, which shows its compo-*

sition of regular coils only in cross-section. Coils are circular in cross-section, the shell is apparently composed of three different layers (fig. 48.) and thick.

Later, the last coil starts to straighten out. The aperture is round with either sharpened or thickened edges; in the latter case, the former apertures remain recognizable as bulges (fig. 46.). The aperture is armed with an either straight or curved inwards denticle, recognizable only in well-preserved specimens. On the outer surface, four grooves run along the last coil. The deepest one, recognizable even in cross-section (fig. 48.), ends with a denticle at the base. Often its edges are raised, forming a common keel. The second groove runs along the side opposite to the denticle, and the other two run along both sides. The surfaces between the grooves are variously developed. They are either simply rounded or widely protruding or wing-like extended. In the last case, edges are usually studded with spiny tubercles, which increase towards the aperture, so that they resemble a fragment of a limb of a decapod (fig. 49.).

EMENDED DIAGNOSIS: A relatively large species of *Laqueoserpula* forming a rather regular, conical or cylindrical spiral composed of 1½ to 6 whorls. Usually, umbilicus narrow, less often closed or moderately wide. Tube somewhat depressed and possessing one thin and low but distinct median keel, which transforms into a wide and low bulge with a narrow median furrow in the anterior tube portion. Incremental lines distinct and strongly curved forward toward the keel, causing a spine protruding at the aperture, and toward the base. When more strongly developed, incremental lines forming weak 'alae'-shaped peristomes. Rarely, peristomes very strongly developed and possessing additional 'ears'. Tube wall extremely thick.

Free tube portion rising steeply, curved like a corkscrew. Cross-section of free tube portion circular to very much rounded triangular or quadrangular. Three or five spines protruding at the aperture.

RESTRICTION OF THE EXTENT OF THE SPECIES 'REUSSI': Weinzettl (1910) figured six specimens which he determined as '*Burtinella*(?) *reussi*'. In our opinion, these six specimens represent a mixture of three different species belonging to three different genera. Weinzettl did not state which of his specimens should be the holotype. Therefore firstly it is crucial to decide which of these three species should represent the real *reussi*. In Weinzettl's (1910) pl. 3, one species is represented by three figured specimens, the second species is represented by two figured specimens, and the third species is represented by a single figured specimen. We decide herein that the three specimens figured by Weinzettl (1910) in his pl. 3, figs 46, 47 and 51 should represent the real *reussi*.

Before we select the lectotype and syntypes from Weinzettl's (1910) type series (see below) in accordance with ICZN Recommendation 73F, the other three specimens figured by him should be addressed: Figs 48 (specimen from Korycany, not found otherwise in the NM collections) and 50 (NM-O3536) belong to a species similar to *Pyrgopolon tricostatum* (Goldfuss, 1841). Weinzettl's fig. 49 (NM-O3540) belongs to *Placostegus velimensis* Jäger and Kočí, 2007 and should be added to the synonymy list of that species.

TYPE SPECIMENS: The lectotype is specimen NM-O3538, original of Weinzettl (1910, pl. 3, fig. 51, figured upside down), here refigured in Text-fig. 2A1–A2, from the Lower Turonian of Kamajka near Chotusice. It is a dextrally coiled spiral; the spiral diameter at the base is 9.2 mm, tube diameter of aperture is 6.8 mm, height of specimen is 17.2 mm. The thickness of the tube wall at the aperture is 2.4 mm.

The 1st syntype is specimen NM-O3539, original of Weinzettl (1910, pl. 3, fig. 46), refigured herein in Text-fig. 2C1–C2, from the Lower Turonian of Kamajka near Chotusice. It is the free tube portion of a dextrally coiled specimen bearing two peristomes and protruding spines at the aperture. The peristomes and the fine transverse striae are V-shaped.

The 2nd syntype is specimen NM-O3537, original of Weinzettl (1910, pl. 3, fig. 47, figured upside down), refigured herein in Text-fig. 2B1–B2, from the Lower Turonian of Kamajka near Chotusice. It is a part of the free tube portion showing the aperture with protruding spines. The thickness of tube wall at the aperture is 2.6 mm. Bryozoa encrust the specimen. See Table 1 for size data and registration numbers of types and other figured specimens.

STRATUM TYPICUM: Upper Cretaceous, Lower Turonian.

LOCUS TYPICUS: Old quarry at Kamajka near Chotusice (Čáslav district, Czech Republic).

MATERIAL: Often the number of tubes is higher than the number of physical specimens, because occasionally two or more tubes are attached to each other or to a common substrate, forming a single cluster.

– 220 tubes (174 specimens) from Velim near Kolín,

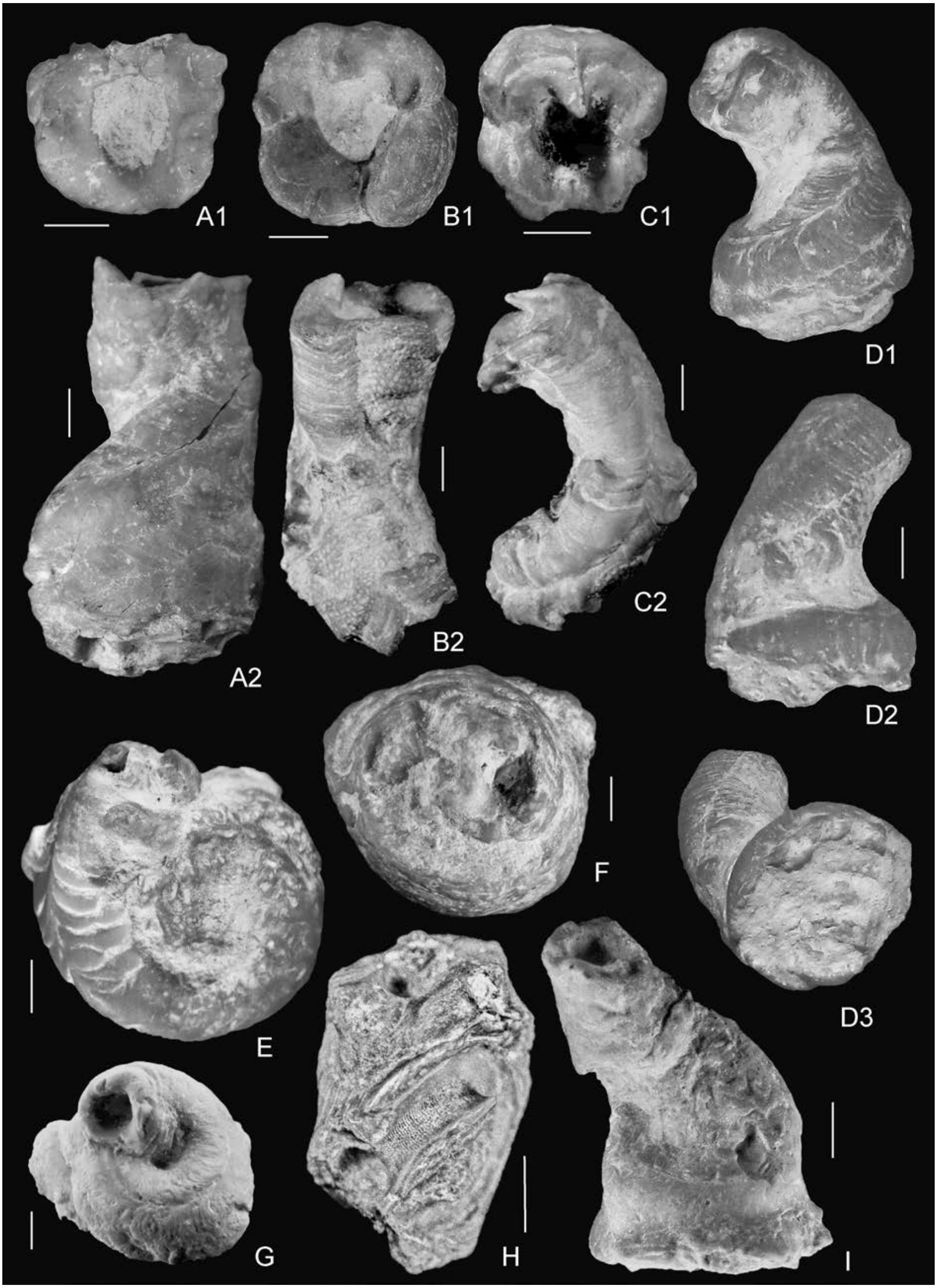
Inventory number	Type / Original	Text-figure	Diameter of base	Tube diameter at aperture or anterior end	Height of specimen	Notes
NM-O3538	lectotype	2A1–2	9.2 mm	6.8 mm	17.2 mm	
NM-O3537	2nd syntype	2B1–2	not preserved	7.0 mm	15.7 mm	
NM-O3539	1st syntype	2C1–2	not preserved	6.4 mm	14.8 mm	
NM-O5167	original of Ziegler (1984 pl. 5, fig. 8)	2D1–3	7.9 mm	4.6 mm	11.8 mm	
NM-O7681	–	2E	10.9 mm	5.1 mm	6.7 mm	infested by *Protulophila gestroi* Rovereto, 1901
NM-O7682	–	2F	12.7 mm	6.4 mm	9.4 mm	infested by *Protulophila gestroi* Rovereto, 1901
NM-O7683	–	2G	10.1 mm	4.9 mm	7.4 mm	
NM-O7684	–	2H, 3D	8.8 mm (incomplete)	5.1 mm	8.5 mm	
NM-O7685	–	2I	9.9 mm	4.0 mm	12.6 mm	
NM-O7686	–	3A1–4	upper tube 8.1 mm, lower tube 8.0 mm	upper tube 5.3 mm, lower tube 4.2 mm	A1 = 14.0 mm, A2 = 15 mm, total 14.5 mm	
NM-O7687	–	3B1–3	larger tube 14.6 mm, smaller tube 8.6 mm	larger tube 5.2 mm, smaller tube damaged anteriorly	not measured	infested by *Protulophila gestroi* Rovereto, 1901
NM-O7688	–	3C1–3	left 8.0 mm, right 7.5 mm	5.0 mm	view C1 = 7.5 mm, tube C2, C3 = 14.2 mm	
NM-O7689	–	4A	upper tube 8.1 mm, middle tube 9.4 mm, lower tube 7.0 mm	only upper aperture preserved, 5.5 mm	21.9 mm	infested by *Protulophila gestroi* Rovereto, 1901
NM-O7690	–	4B	base of one tube 8.5 mm	aperture of smaller tube preserved only, 4.5 mm	total height 11.4 mm	
NM-O7692	–	4C	not preserved	4.0 mm	preseved height 7.3 mm	
NM-O7693	–	4D	not preserved	4.5 mm	18.7 mm	

Table 1. Dimensions of the analysed specimens of *Laqueoserpula reussi* (Weinzettl, 1910).

sublocality VII ('pocket Václav'), including: 3 tubes figured by Ziegler (1984), see synonymy list; 185 tubes collected by TK during 2001–2007; 32 tubes collected by MJ in 2006. 217 tubes or 171 specimens out of this material from Velim were examined in detail by MJ, forming the core of the database for the morphologic description;

– 126 tubes (112 specimens) from Chrtníky, layer 8f (see Žítt *et al.* 2006): 106 tubes collected by MJ in 2006; several tubes collected by Radek Vodrážka in 2006;
– 7 tubes from Chrtníky, layer 5 with *Cyathidium depressum* Sieverts, 1932 (see Žítt *et al.* 2006);
– 23 tubes (22 specimens) from Kaňk near Kutná Hora: 10 tubes or 9 specimens collected by MJ and TK during 2005–2007; 13 tubes collected by TK during 2014–2016;
– 7 specimens from Turkaňk near Kutná Hora: 1 tube collected by TK in 2016 and 6 specimens collected by TK in 2017;
– c. 89 tubes (c. 86 specimens) from Kamajka near Chotusice: 3 tubes (lectotype and two syntypes)

Text-fig. 2. *Laqueoserpula reussi* (Weinzettl, 1910), Lower Turonian. A – NM-O3538, lectotype, original of Weinzettl (1910, pl. 3, fig. 51, figure has been reversed), Kamajka near Chotusice; dextrally coiled spiral; A1 – aperture; A2 – lateral view of attached and free tube portions. B – NM-O3537, 2nd syntype, original of Weinzettl (1910, pl. 3, fig. 47, figure has been reversed), Kamajka near Chotusice; part of free tube showing aperture with protruding spines; note encrusting bryozoans; B1 – aperture; B2 – lateral view of free tube. C – NM-O3539, 1st syntype, original of Weinzettl (1910, pl. 3, fig. 46), Kamajka near Chotusice; free tube portion of a dextrally coiled specimen bearing two peristomes and spines protruding from the aperture; note V-shaped peristomes and fine transverse striae; C1 –aperture with spines; C2 – lateral view of free tube. D – NM-O5167, original of Ziegler's (1984, pl. 5, fig. 8) *Eoplacostegus sulcatus* (Sowerby, 1829), Velim; D1, D2 – lateral views of attached and free tube portions; D3 –oblique view from below of attached and free tube portions. E – NM-O7681, Velim; spiral attached tube portion with extremely well-visible incremental lines; tube infested by the symbiont *Protulophila gestroi* Rovereto, 1901. F – NM-O7682, Velim; planar spiral attached tube portion with well-preserved aperture; tube infested by the symbiont *P. gestroi*. G – NM-O7683, Velim, pocket Václav; low spiral attached tube portion showing incremental lines and a low median keel turning into a median furrow. H – NM-O7684, Chrtníky; broken attached tube portion showing transverse ornamentation of tube inner surface, same specimen as in Text-fig. 3D. I – NM-O7685, Velim; high spiral attached tube portion with long free tube portion. Scalebars equal 2 mm. →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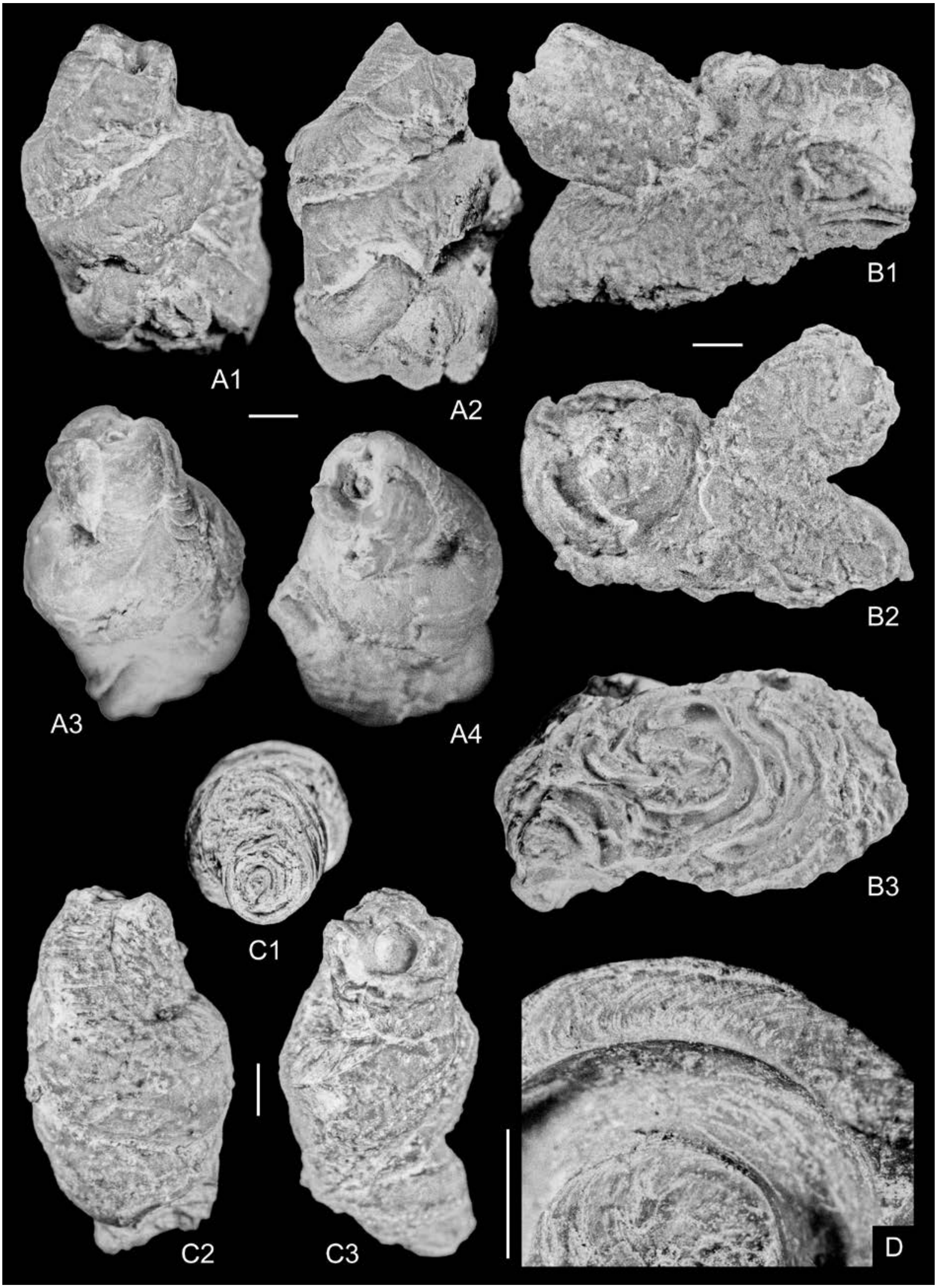
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D

figured by Weinzettl (1910); 8 additional tubes (formerly labelled *Serpula ampullacea* Sowerby) deposited in the collection of the National Museum at Prague (NM-O9500–9501, NM-Os392), 1 unusually ornamented specimen consisting of 4 tubes collected by Radek Vodrážka in 2006 labelled NM-O7693, 74 tubes of additional material from an unknown collector labelled NM akc. 36675/1957 (ČL 3637);

– 5 tubes from Zbyslav No. 51 near Čáslav, figured by Ziegler (1984), see synonymy list;
– 40 tubes from Starkoč: 33 tubes collected by Antonín Culek, NM akc. 228/1968; 7 tubes collected by Vlastimil Zázvorka, NM akc. 29173/1946;
– 6 specimens from Předboj near Prague (Předboj u Prahy), collected by Olga Nekvasilová during 1960–1967;
– 3 tubes from Gamighübel at Dresden-Kauscha in Saxony, including the original specimen of Geinitz (1875) in the collection of the Senckenberg Naturhistorische Sammlungen Dresden (Jäger 2014).

We have had no opportunity to study the specimens from Želenice ('Schillinge') near Bílina and Novosedlice ('Weisskirchlitz') near Teplice, but from literature data and figures (Reuss 1845–1846) it is obvious that *L. reussi* occurs also there.

OCCURRENCE: Upper Cenomanian, Předboj near Prague, Gamighübel at Dresden-Kauscha in Saxony; Lower Turonian, Velim, Chrtníky, Kaňk near Kutná Hora, Turkaňk near Kutná Hora, Kamajka near Chotusice, Zbyslav No. 51 near Čáslav, Starkoč, Želenice ('Schillinge') near Bílina, Novosedlice ('Weisskirchlitz') near Teplice.

DESCRIPTION

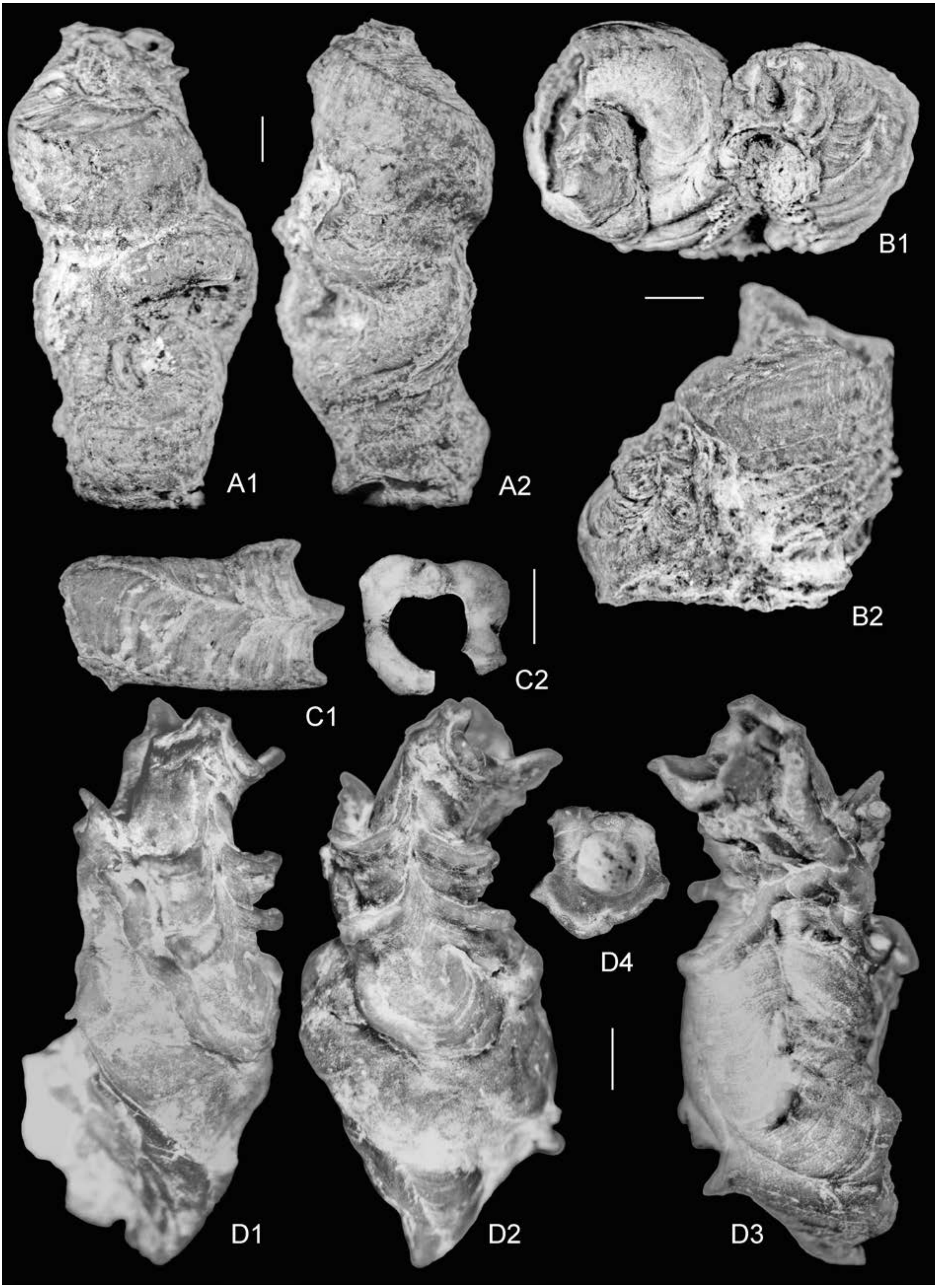
Course of the attached tube portion: Most tubes occur as single individuals, and some form small clusters (Text-figs 3A1–A4, 3B1–B3, 4A1–A2, 4B1–B2) consisting of usually only 2 or 3, in a few cases of up to 6 specimens cemented to each other. The largest cluster was found at Chrtníky, it measures 22×10 mm (Text-fig. 4A1–A2). Within the clusters, the tubes may be equal or different in age and sense of coiling.

The attached tube portion consists of the non-spiral initial tube portion and the main tube portion forming a spiral.

The non-spiral initial tube portion is clearly visible only in juvenile tubes. It may be straight or slightly curved, either regularly or irregularly. In adult tubes it is only partly visible either on the underside of the spiral main tube portion which is usually detached from the substrate (Text-fig. 3B3, C1) or as a cross-section on the base of the lateral view of the spiral main portion. The longest preserved initial tube portion is 9 mm long, its width is 0.7–2.3 mm and increases only slowly.

The main tube portion forms a low conical or cylindrical spiral usually composed of 1½ to 4 whorls, but a specimen from Chrtníky possesses 4 1/3 whorls, another specimen from the same locality 6 whorls. The average number of whorls per tube is c. 2.84 (n = 39 tubes from Velim). The first whorls are attached directly to the substrate. In adult tubes, they are visible only from the underside, after the tube is detached from its former substrate, because they were overgrown more or less completely by the last whorl (Text-figs 3B3, C1, 5B). Only the last whorl (or slightly more) is seen in lateral view and from above. Moreover, the tube's basal seam may become rather wide in some tubes and smoothes the boundary between whorls, sometimes making differentiation between whorls difficult. The diameter of the spiral grows larger in the first whorls. Later it stays more or less constant or diminishes within the last whorl, thereby forming a low cylinder or low conus. This spiral is up to 10.5 mm high and up to 13 mm in diameter. Usually, the diameter is somewhat larger than the height, less often the height is larger than the diameter. In most specimens the spiral is more or less regular, but in some the diameter of the spiral is distinctly larger in one axis than in another axis perpendicular to the first one, depending on the substrate, which may either be more or less plain (though uneven) or somewhat undulating. The spirals may be somewhat irregular especially when situated closely to one another in the clusters.

← Text-fig. 3. *Laqueoserpula reussi* (Weinzettl, 1910), Lower Turonian. A – NM-O7686, Velim; irregular high spiral composed of at least three tubes attached to each other, the uppermost tube possessing a short free tube portion with well-preserved aperture; A1–A2 – lateral views; A3–A4 – oblique lateral and top views. B – NM-O7687, Velim; spiral attached tube portions of two specimens laterally attached to each other, one infested by the symbiont *Protulophila gestroi* Rovereto, 1901, one possessing a free tube portion, the other broken anteriorly; B1–B2 – two opposite lateral views; B3 –broken tube portions on the underside. C – NM-O7688, Chrtníky, lithounit 8f; high and slender spiral attached tube portion; C1 – broken tube portions from the underside, note non-spiral initial tube portion; C2 – oblique lateral and top view; C3 – lateral view. D – NM-O7684, Chrtníky; detail of longitudinally broken spiral attached tube portion showing (in the top of the image) parabolic incremental lines, same specimen as in Text-fig. 2H. Scalebars equal 2 mm.


A1
A2
B1
B2
C1
C2
D1
D2
D3
D4

There is no preference in the sense of coiling. Out of 182 tubes from Velim, 95 (52.2%) are sinistrally coiled, and 87 (47.8%) are dextrally coiled. Out of 58 tubes from Chrtníky, 28 (48.3%) are sinistral and 30 (51.7%) are dextral (we use the terms 'sinistral' and 'dextral' in the same sense as zoologists when describing spirorbin serpulids).

Out of 107 tubes from Velim, about 69 (64.5%) show a narrow or very narrow umbilicus, in 21 tubes the umbilicus is totally closed, and 17 tubes show a moderately wide umbilicus. In 22 tubes from Chrtníky, the respective numbers are 15, 3, and 4.

Within the spiral, the diameter of the tube increases moderately and reaches usually 3.5–5 mm, in a few tubes up to 6 mm.

Although the 3 tubes available from Gamighübel in Saxony represent a set too small to enable reliable statistics, it is remarkable that they all are considerably small (Jäger 2014): $1^{3}/_{4}$–$2^{1}/_{3}$ spiral whorls, spiral diameter up to 7.5 mm, spiral height up to 5 mm, tube width up to 2.5 mm when measured excluding basal seam and 3.2 mm when including basal seam, no free tube portion was detected.

Course of the free tube portion: In about one-third of the specimens, a free tube portion is developed or is preserved at least as a loose fragment. At the end of the spiral, the whorl base loses contact to the prior whorl, and the tube rises steeply while still continuing the sense of coiling of the spiral (Text-figs 2A2, B2, C2, D1–D3, I, 3B1–B2). The free tube portion consists of ¼–¾ whorls only. It resembles a short portion of a corkscrew. Except for a regular torsion related to the corkscrew shape, the free tube portion is not twisted irregularly around its longitudinal axis, with only one specimen showing slight torsion. Thus, the orientation of the animal inside its tube remained fairly constant for all of its life. Usually, the free tube portion is 4–11.8 mm high, rarely reaches over 14 mm or even 17.5 mm in an extraordinary specimen from Kaňk. One of the fragments from Starkoč is at least 18.5 mm high but incomplete.

In the free tube portion, the tube diameter increases slowly and reaches usually 5–6 mm, but rarely it may stay as small as only 2.6 mm, or reach up to 7 mm.

Longitudinal ornamentation: In the attached tube portion there is a single thin and low but distinct line-like median keel. Only very rarely the keel may be slightly higher and somewhat undulating for a short part of its length. In the anterior part of the spiral, the keel usually transforms into a wide and low bulge with a narrow median furrow. Bulge and furrow continue in the free tube portion.

In the anterior part of the spiral, there is a narrow lateral furrow on each side. These furrows also continue in the free tube portion, so that the free tube portion possesses at least three more or less distinct longitudinal furrows. Moreover, in few specimens a fourth furrow may be seen on the underside of the free tube portion.

Transverse ornamentation: Incremental lines situated close to each other are distinctly developed. Along the tube, the incremental lines are strongly curved forward toward the keel, resulting in a protruding spine at the aperture (for example, Text-figs 2B1, C1–C2, 4C1, 5A1). However, only in a few specimens the spine points forward. Usually, it points obliquely forward/downward over the aperture at c. 45º. At the base of the attached tube portion, the incremental lines are also curved forward, but less strongly. This curvature continues in the free tube portion, resulting in a second and third blunt spine or 'ears' at the aperture. The incremental lines are somewhat curved backward in the upper left and right of the tube.

A few incremental lines may be stronger or joined by an incision resulting in somewhat bulging alae-shaped weak peristomes. In an unusual specimen from Velim (Text-fig. 2E), the incremental lines are very strongly developed and situated at wider distances than usual, giving the tube's surface a leafy aspect.

No distinct discrimination between strong incremental lines and weak peristomes can be drawn. Such weak peristomes resemble the 'alae' of *Cementula* Regenhardt, 1961 and *Spiraserpula* Regenhardt, 1961. Moreover, irregular slight bulging may occur.

In a few tubes, the peristomes are so strongly developed that at first sight, these tubes look very different from the usual aspect. However, in all other

← Text-fig. 4. *Laqueoserpula reussi* (Weinzettl, 1910), Lower Turonian. A – NM-O7689, Chrtníky; extremely high spiral composed of at least three individuals attached to each other, infested by the symbiont *Protulophila gestroi* Rovereto, 1901; A1–A2 – lateral views. B – NM-O7690, Chrtníky, lithounit 8f; spiral portions of two tubes laterally attached to each other, both broken anteriorly, showing keel and incremental lines; B1 – top view; B2 – lateral view. C – NM-O7692, Chrtníky; fragment of free tube portion showing keel, incremental lines, and a well-developed spine at the aperture; C1 – top view; C2 – aperture (tube damaged in lower right). D – NM-O7693, Kamajka near Chotusice; attached and free tube portions showing extremely strong peristomes; D1–D3 – different top lateral views; note oyster shell attached to D1–D2; D4 – aperture. Scalebars equal 2 mm.

characters except the shape of the peristomes, these tubes do not differ from the others. For this reason, no taxonomic discrimination is made. This is the case for three tubes unique for Kamajka, Velim, and Chrtníky (layer 5), respectively, all described below. Moreover, this feature is seen in one tube fragment from Chrtníky (layer 8f). In these unusual peristomes, not only the alae are strongly developed, especially in the region of the upper spine and the two lower spines, but additionally there is one sharp angular 'ear' developed each in the upper left and upper right position where the incremental lines are curved backward. This is in contrast to the aspect of the normal weak peristomes, where no trace of such 'ears' is detectable in that position. These 'ears' can be up to 1.3 mm high. The three spines and two 'ears' give the unusual peristomes an aspect consisting of five parts altogether.

The specimen from Kamajka (Text-fig. 4D1–D4) possesses four strong peristomes. The first is situated in the spiral one-half whorl behind the transition to the free tube portion. The second peristome follows at a longitudinal distance of approximately 10 mm and is situated directly in front of the transition from the attached to the free tube portion. The second, third and fourth peristomes follow closely one after the other so that the (somewhat damaged) fourth peristome (which had been the final aperture) is situated only 6 mm in front of the second peristome. Three juvenile tubes of the same species grow in different directions on the adult tube, thereby disturbing the clear picture of the four peristomes. The specimen from Velim possesses four strong peristomes as well. Here all four are situated in the free tube portion. The longitudinal distance from the first to the fourth peristome is 5–6 mm. The tube is attached to an oyster, and several small oysters are attached to the tube as epibionts, thereby likewise disturbing the clear picture of the four peristomes. In the specimen from Chrtníky (layer 5), there are three strong peristomes, the first two situated in a distance of 4 mm and the third in less than 1 mm from the second.

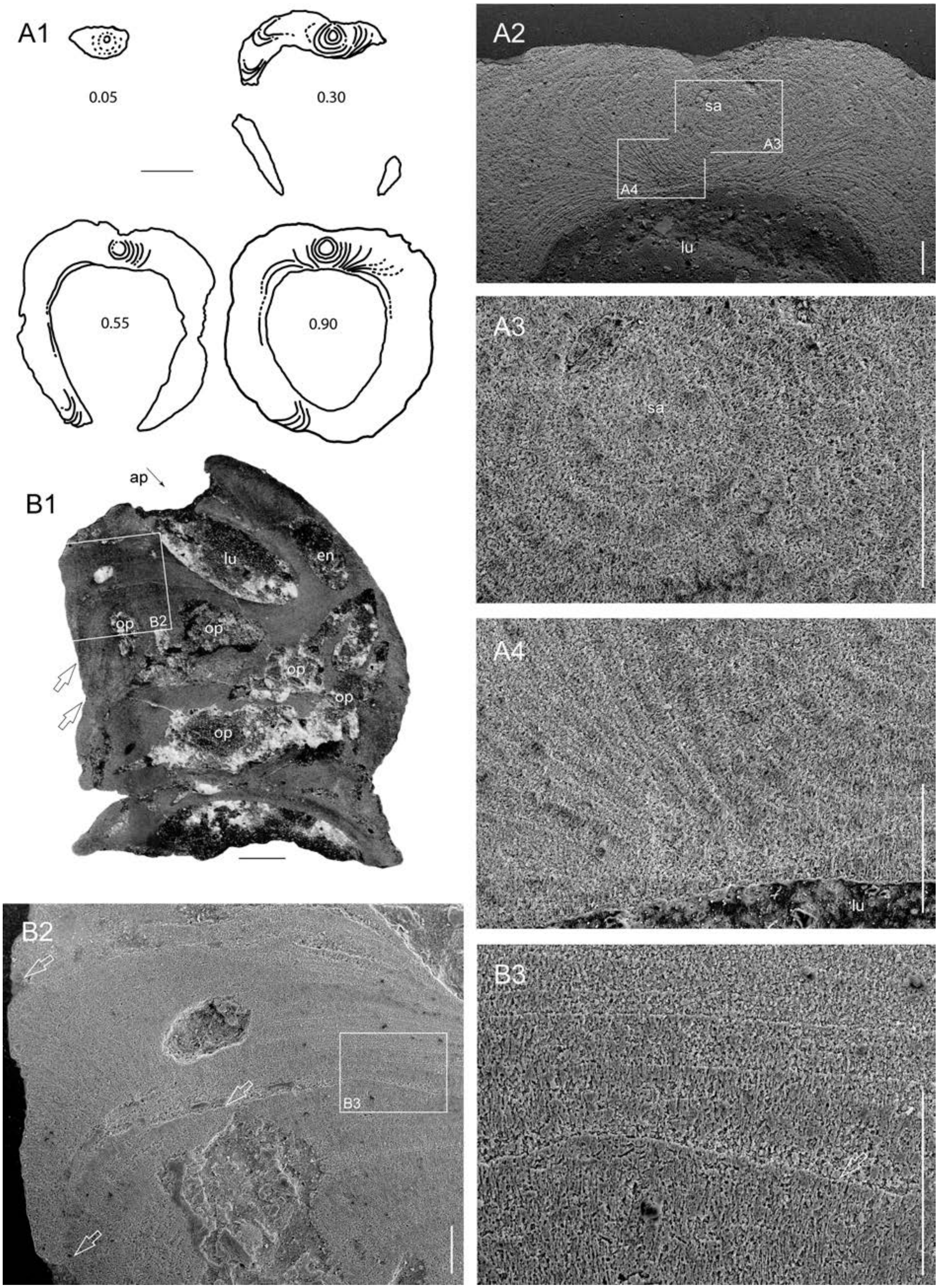
Cross-section: In the attached tube portion, the small longitudinal keel does not affect the shape of the cross-section, which is more or less circular or rounded trapezoid. However, often the upper side is somewhat flattened so that the tube appears somewhat depressed. Moreover, the tube base may or may not be somewhat broadened by a seam.

In the free tube portion, the cross-section is roughly circular to very much rounded triangular or rounded quadrangular (Text-fig. 5A). Here the longitudinal furrows slightly modify the shape of the cross-section.

The tube wall is extremely thick (Text-fig. 5A–B). In most specimens the diameter of the lumen measures between one-half and one-third of the diameter of the tube, in a few specimens even only between one-third and one-fourth. Usually, the lumen measures 1.5–2.0 mm in the anterior part of the attached tube portion and in the free tube portion. In two specimens the lumen in the anterior part of the attached tube portion measures only 1.2 mm and 1.4 mm, respectively. Usually the lumen is circular, but it may be rounded subquadrangular if the aperture is subquadrangular.

Tube structure: No tabulae were found. The surface of the tube is light brownish. Nearly the entire tube wall consists of the parabolic layer, whereas the cylindrical layer is very thin. In many longitudinal sections the parabolic lamellae are visible at once, without any chemical treatment. Although the pattern is variable depending in part on the location and direction of the section, the inner and outer rami of the parabolic lamellae are often more or less symmetrical to each other. However, in the section shown in Text-fig. 3D the outer rami appear to be longer than the inner rami. The shape of the parabolic lamellae is also visible in the longitudinal section treated chemically for ultrastructure investigation (see below) in Text-fig. 5B2. The characteristic parabolic arrangement of the lamellae visible in the longitudinal sections

Text-fig. 5. Tube structure and ultrastructure of *Laqueoserpula reussi* (Weinzettl, 1910), Velim, 'pocket Václav' (for details see Žítt *et al.* 1997), Lower Turonian. Tubes partially opalised. A – NM-d17a/2016; serial transverse sections through tube aperture; A1 – schematised serial transverse sections from the apertural spine tip to the fully enclosed lumen showing a characteristic morphology of the aperture and its laminar structure; numbers indicate distance from the tip of the spine in mm, scale-bar equals 1 mm; A2–A4 – detail of the 0.90 transverse section, SEM images showing concentric incremental lamellae of the simple prismatic (SP) structure. The lamellae, circular when close to apertural spine axis (sa, A3 detail), laterally pass into lobes giving the whole structure a cross-section resembling a rounded anvil (A2). A4 shows a detail of the lamellae at transition to lobes (to the left) and close to the lumen (lu); scale-bars equal 200 µm. B – NM-d17b/2016, longitudinal section of tube, single section oriented almost identically to the plane of symmetry of the adapertural portion of tube (lu = lumen); B1 – peel of a longitudinal section of the tube; arrows point to inter-whorl seams shown also in B2–B3 (ap = aperture, en = endoskeletozoan or incorporated polychaete tube of a different specimen, op = heavy opalisation obscuring the structures); scale-bar equals 1 mm; B2 – detail of a polished etched section of the same specimen showing tube structure with whorl seam arrowed; SEM image, scale-bar equals 200 µm; B3 – detail of increments showing diagenetically affected simple prismatic ultrastructure and discordance at one of the marked whorl seams; SEM image, scale-bar equals 200 µm.


A1
0.05
0.30
0.55
0.90
A2
sa
A3
A4
lu
A3
sa
A4
lu
B1
ap
lu
en
op
B2
op
op
op
op
B2
B3
B3

is a feature by which even fragments of *L. reussi* may well be discriminated from tube fragments of the co-occurring other serpulid species which either possess non-symmetric lamellae or do not have distinct lamellae. As the parabolic lamellae are increments representing earlier ontogenetic stages, they even allow the reconstruction of the tube shape of a younger stage, at least in longitudinal section.

The inner surface of the tube wall is either smooth or (presumably when somewhat worn) bears delicate striae more or less parallel to each other (Text-fig. 2H). There are c. 15 striae per millimetre of tube length. The striae run perpendicular to the tube's longitudinal axis but are curved backward at the roof of the lumen.

Ultrastructure: Selected specimens from Velim and Chrtníky were ground longitudinally and transversely, polished and etched with 1% acetic acid for ten minutes before SEM examination (Text-fig. 5). The tube wall consists of 10–15 µm long, slender, irregular crystallites that are arranged approximately parallel in layers (Text-fig. 5A4, B3). The crystallites are arranged approximately perpendicular to the surface of the tube wall and follow its curvature at the aperture (Text-fig. 5A3). This structure is 'simple prismatic (SP)' following Vinn *et al.* (2008) and is present in the entire tube including its basal part.

COMPARISON AND DISCUSSION

Weinzettl (1910, p. 24) stated as follows (translated): *In very various sizes from Korycany's sediments* [i.e., Korycany Member], *especially at Kamajka and Zbislav* [Zbyslav]. *The fact that even elsewhere, namely in the Cretaceous of Saxony, similar if not identical forms are found, is proven by depiction in Geinitz's Elbthalgeb. I. 2. plate 63, labeled as* Serpula. *Also in Roemer (Nordd. Kreideg. plate 16) and Goldfuss (Petref. Germ. III. plates 70, 71), similar forms determined as* Serpula *are figured, some of which already Stoličzka (Cret. gastr. of South India page 238) claimed as members of the Vermetid family.* – However, according to morphology and ultrastructure, it is obvious that *L. reussi* belongs to the family Serpulidae.

In all likelihood, the earliest description of *L. reussi* from the BCB was given by Reuss as early as in 1844. He described it very briefly as "*Serpula gordialis* Schloth. Var. *spirata* m." from the "Conglomeratschichten von Teplitz" and "Gehänge von Liebschitzer Thales bei Bilin" (Reuss 1844, p. 216; i.e., Novosedlice near Teplice and Želenice near Bílina), but provided no figure. In 1845–1846 his taxonomical attitude shifted, and he left the original variety '*spirata*' for '*Serpula ampullacea* Sow.', this time indicating particular localities as 'Weisskirchlitz' (i.e., Novosedlice) and 'Schillinge' (i.e., Želenice). Recent fieldwork by JS and Radek Vodrážka in 2006 detected only the overlying hemipelagic marlstones of the Teplice Formation (Upper Turonian) within the Želenice area. Even Reuss himself knew no outcrops, but had to rely on scattered rock fragments lying around (Reuss 1844, p. 63). The original material studied by Reuss was destroyed in 1956, while micropalaeontological data are missing, but the material from Schillinge either stored in other collections or published by Reuss shows a *Tylocidaris* (*T.*) *sorigneti*–'*Cidaris vesiculosa*'–*Amphidonte* (*A.*) *reticulatum* taphocenosis typical for the basal layers of the Lower Turonian in analogous 'rocky-coast' localities of the BCB.

Lommerzheim (1979) introduced the new genus *Laqueoserpula* and three new species: *L. litoralis* (type species), *L. dolioformis* and *L. plana*; the type locality and type stratum of all these three species is Rauen quarry at Mülheim-Broich, Westphalia, north-west Germany, lowermost Cenomanian, *Hypoturrilites carcitanensis* Zone. At the end of the section about *L. plana*, Lommerzheim (1979) also briefly mentioned a '*Laqueoserpula* cf. *plana*' from Le Mans (France) and Velim near Kolín. Although we were not able to detect any specimen of the genus *Laqueoserpula* in the Cenomanian of Le Mans region (Kočí *et al.* 2017), it seems very probable that '*Laqueoserpula* cf. *plana*' *sensu* Lommerzheim from Velim may well belong to *L. reussi*.

One of us (MJ) is studying (work in progress) sabellid and serpulid tubes from the type locality of Lommerzheim's three *Laqueoserpula* species. The preliminary results are: (1) the *Laqueoserpula* tubes from Mülheim-Broich closely resemble *L. reussi* from the BCB. However, *Laqueoserpula* tubes from both regions still remain easily distinguishable. (2) Despite Lommerzheim's descriptions and figures, in practise his three *Laqueoserpula* species from Mülheim-Broich are hardly distinguishable from each other; this is due to several factors: overall similarity of the three species, the wide individual morphological variability within each species, the fragmentary and worn preservation of most specimens, and the predominance of specimens which are not fully grown and lack a free anterior tube portion. While *L. plana* may stay a separate species morphologically marked by its generally low-lying growth which, however, may have resulted from local ecological conditions, the two upward-rising species are so similar to each other that *L. dolioformis* may be considered a subjective synonym of the type species *L. litoralis*. (3) At Mülheim-Broich, small spiral tubes of *Laqueoserpula* closely resemble those of *Cementula* and *Spiraserpula*, both of Regenhardt, 1961, especially *C. spirographis* (Goldfuss, 1831), but when comparing small specimens of about an equal diameter of the spirals from Mülheim-Broich, *Laqueoserpula* may be distinguished from *C. spirographis* by its slightly larger tube diameter and somewhat lower number of whorls visible when viewed from above (partly caused by a narrower umbilicus in *Laqueoserpula*). Moreover, smoothing of the boundaries between the whorls is more advanced in *Laqueoserpula*. When growing larger, the course of the tube may become considerably more irregular in *Laqueoserpula* than in *Cementula* or *Spiraserpula*.

Generally, small clusters consisting of more than only a single tube occur more commonly in *Laqueoserpula* than in the usually solitary *Cementula* or *Spiraserpula*. When comparing *L. reussi* with *Laqueoserpula* tubes from Mülheim-Broich, *L. reussi* slightly more often forms clusters consisting of 2–3, rarely up to 6 tubes, whereas clusters consisting of only 2 tubes are rather rare at Mülheim-Broich. *Laqueoserpula reussi* may reach a considerably larger tube diameter already in the posteriormost initial tube portion as well as in the free anterior tube portion. Its tube is robust and its tube wall is extremely thick. Moreover, spirals of *L. reussi* often grow somewhat higher than at Mülheim-Broich where the low-lying *L. plana* dominates in abundance over the two upward rising species. In contrast, the difference in spiral diameter is smaller, and due to the low-lying but widely-spreading morphology of *L. plana* whose whorls often irregularly cover the earlier built ones incompletely and obliquely. The maximum spiral diameter is even slightly larger in species from Mülheim-Broich than in *L. reussi*. While the usual number of whorls per spiral is equal in either region, only *L. reussi* may exceptionally have up to 6 whorls. The width of the umbilicus is rather variable, but at Mülheim-Broich, specimens with a closed umbilicus are the most common, whereas in *L. reussi* specimens with a narrow or very narrow umbilicus dominate. While in most *Laqueoserpula* specimens from either region a free anterior tube portion is short or lacking (not built or broken off), in a few specimens it may grow to a considerable length: up to 18.5 mm in *L. reussi*, up to 25 mm in *L. litoralis* according to Lommerzheim (1979), and if this free portion forms a steeply rising corkscrew, it has ¼–¾ whorls in *L. reussi* and up to 1½ whorls in specimens from Mülheim-Broich. Lommerzheim (1979) mentioned a curved and horizontal free portion in *L. plana*, a corkscrew in *L. litoralis*, and a straight and vertical tube in *L. dolioformis*. Well-developed five-spined peristomes occur only rarely in a few exceptional specimens of *L. reussi*, but well-developed incremental lines or weakly developed peristomes are rather common. In contrast, at Mülheim-Broich a single well-developed peristome is common at the final aperture, and in some specimens, peristomes also occur in positions slightly posterior to the final aperture. But only rarely one or two weakly developed peristomes occur in the attached spiral tube portion, and incremental lines, if developed at all, are considerably less conspicuous than in *L. reussi*.

Already Lommerzheim (1979) assigned *Laqueoserpula* to his informal 'I. Formenkreis' including the genera *Serpula* Linnæus, 1758, *Hydroides* Gunnerus, 1768, *Crucigera* Benedict, 1887, and others *sensu* Zibrowius (1972), and later Pillai (1993) and Pillai and ten Hove (1994) recognised the close relationships of *Cementula* Regenhardt, 1961, *Spiraserpula* Regenhardt, 1961 and *Serpula sensu stricto*. These genera belong to the 'Clade AI *Serpula*-group' *sensu* Lehrke *et al.* (2007), Kupriyanova *et al.* (2009) and Ippolitov *et al.* (2014), respectively, to the tribe Serpulini Rafinesque, 1815 of the subfamily Serpulinae Rafinesque, 1815 according to the most recent scheme of Kupriyanova *et al.* (2023). The general shape of *Laqueoserpula* tubes is definitely much closer to that of *Cementula* and *Spiraserpula* (Clade AI, Serpulini Rafinesque, 1815) than to *Placostegus* Philippi, 1844 or *Vitreotubus* Zibrowius, 1979 (Clade AII, Ficopomatini Pillai, 1960) or to *Filogranula* Langerhans, 1884 and *Metavermilia* Bush, 1905 (Clade BI, Filograninae Rioja, 1923) as presumed by Ippolitov *et al.* (2014, p. 133) who wrote about *Laqueoserpula*: "doubtful status, may be related to *Filogranula, Metavermilia* or other genera".

However, in *L. reussi* a discrepancy in assignment occurs between tube morphology pointing to Clade AI, Serpulini, and the simple prismatic (SP) ultrastructure which rather points to Clade AII, Ficopomatini, according to the scheme of structures of Vinn *et al.* (2008). Among serpulid tubes, the simple prismatic ultrastructure is not very common but none the less it is wide-spread, occurring in all four clades, although in different frequencies: It occurs, e.g., in the Oxfordian *Placostegus planorbiformis* (Münster in Goldfuss, 1831) (see Vinn and Furrer 2008, fig. 1.6, as '*Tetraserpula planorbiformis* Münster'), the

Miocene *Placostegus polymorphus* Rovereto, 1895 (see Vinn 2007, fig. 1.5, 1.6), the extant *Placostegus tridentatus* (Fabricius, 1779) (see Vinn 2007, fig. 5.3, 5.4, and Vinn *et al.* 2008, table 2), and the extant *Vitreotubus digeronimoi* Zibrowius, 1979 (see Vinn *et al.* 2008, table 2, fig. 5A, B). The simple prismatic ultrastructure in tubes of the closely related genera *Placostegus* and *Vitreotubus* (Clade AII, Ficopomatini) results in the translucent, sometimes even transparent glass-like aspect of their tubes, at least in recent specimens, whereas most fossil tubes are not translucent or even shiny anymore. Also most of the Jurassic species of the genus *Nogrobs* de Montfort, 1808 whose clade is questionable but it may also belong to Clade AII (Ippolitov *et al.* 2014), have a simple prismatic ultrastructure (Vinn 2005; Kupriyanova and Ippolitov 2015). Even some extant species of Clade BII, Spirorbinae, have a simple prismatic ultrastructure and vitreous tubes (Ippolitov and Rzhavsky 2008; Kupriyanova and Ippolitov 2015). Moreover, a simple prismatic ultrastructure is present in a few Callovian and Oxfordian serpulid tubes whose determinations according to their old labels cannot be proven anymore, because they have been ground for SEM examination (Vinn and Furrer 2008).

Multi-layered tubes are common among Clade AI serpulids, Serpulini. The simple prismatic ultrastructure does occur, but only in some of the many species of *Serpula* and *Spiraserpula* and only in some of their tube layers or respectively tube parts. The simple prismatic ultrastructure is present in the outer tube layer of *Serpula crenata* (Ehlers, 1908) (see Vinn *et al.* 2008, table 2) and in the internal 'keel' (= internal tubestructure, ITS) in the extant *Spiraserpula caribensis* Pillai and ten Hove, 1994 (see Vinn 2007, fig. 6.6) and in the Miocene *Spiraserpula* sp. (see Vinn 2007, fig. 4.6). According to ten Hove and Kupriyanova (2009, p. 95), "a hyaline granular overlay is present in tubes of *Spiraserpula* species (see Pillai and ten Hove 1994), as well as in *Serpula oshimae* and *S. hartmanae*, in *Hydroides mongeslopezi* and also in an undescribed species of *Apomatus* (ten Hove unpubl.). It may have been overlooked in other taxa." *Apomatus* Philippi, 1844 belongs to Clade B1, Filograninae.

We have also considered the possibility that *reussi* may alternatively belong to the genus *Placostegus* Philippi, 1844 whose simple prismatic ultrastructure would fit better. Already Lommerzheim (1979) discussed some similarities of *Laqueoserpula* and *Placostegus*. Moreover, when describing *Placostegus velimensis* Jäger and Kočí, 2007, we also suggested expanding the genus *Placostegus* to encompass some fossil species which are somewhat different from the small transparent tubes of the extant *Placostegus* species. Compared to the case in *P. velimensis*, the overall shape of *L. reussi* agrees even better with the extant *Placostegus* species by the formation of a spiral in the attached tube portion and by its steeply rising free tube portion possessing usually three protruding spines at the aperture (instead of four in *P. velimensis*). However, some other arguments favour the assignment of *reussi* to the genus *Laqueoserpula*: There is a very close morphological similarity of *Laqueoserpula* to *Cementula* and *Spiraserpula* by size, by the formation of spirals whose boundaries between whorls are smoothed, and by the possession of alae-shaped peristomes. *Laqueoserpula reussi* is much larger than the extant *Placostegus* species, and its tube wall is much thicker. Like other fossil *Laqueoserpula* species, *L. reussi* tends to form small clusters composed of several specimens, in which the single spiral may be somewhat deformed. The fact that the spiral curvature is also kept in the corkscrew-shaped free tube portion agrees better with some of the Lower Cenomanian *Laqueoserpula* species than with *Placostegus* species, whose free tube portion is usually more or less straight. Moreover, like in other fossil *Laqueoserpula* species, a remarkably high percentage of the specimens of *L. reussi* is infested by the symbiont *Protulophila gestroi* Rovereto, 1901. Therefore, when searching for a genus for the species *reussi*, *Laqueoserpula* seems to be the best candidate.

Spiral tubes representing *Protectoconorca* Jäger, 1983 may have a shape similar to *L. reussi*, but they possess a very characteristic ornamentation around the umbilicus that is not present in *Laqueoserpula*. Moreover, the spiral of *Protectoconorca* is almost always sinistral and normally does not possess a free anterior tube portion.

Specimens of *Conorca* Regenhardt, 1961 and *Orthoconorca* Jäger, 1983 are usually more gracile, higher than wide, and often their spiral consists of a higher number of whorls.

Many different species names are mentioned in our synonymy list, for example, '*Serpula* cf. *rauca* Ziegler' of Žítt *et al.* (2006, fig. 12M and p. 66) and '*Eoplacostegus sulcatus* (Sowerby, 1829)' of Ziegler (1984, p. 235, pl. 5, fig. 8); these are misdeterminations of tubes belonging to *L. reussi*. The original name of the last mentioned Jurassic (Callovian to Kimmeridgian) species is *Serpula* (*Vermilia*?) *sulcata* J. de C. Sowerby, 1829 (combination preoccupied), and its subjective synonym is *Serpula tricarinata* J. de C. Sowerby, 1829. The actual valid name is *Mucroserpula tricarinata* (J. de C. Sowerby, 1829) (see Ippolitov

2007). '*Serpula*' *rauca* V. Ziegler, 1984 is a species of *Placostegus* similar to *P. aduncus* (Regenhardt, 1961) and is clearly different from *L. reussi*.

The holotype of *Martina martina* Ziegler, 1984 from the Lower Turonian of Velim is not included in our synonymy list. It was restudied by TK and MJ in 2006. It is a cluster composed of two serpulid tubes which cannot be determined and may even belong to two different species. The upper of the two tubes may or may not be a juvenile specimen of *L. reussi*. As the holotype, and by this also the type species *M. martina* and the genus *Martina* Ziegler, 1984 are doubtful, these names should be considered as *nomina dubia* and avoided in zoological taxonomy. The other species mentioned under the genus *Martina* by Jäger (2005) should be reassigned to the genus *Orthoconorca* Jäger, 1983.

PALAEOECOLOGY

Substrate. Taylor and Wilson (2003) and Taylor (2016) studied the competition between encrusters on marine hard substrates. Although presumably all tubes of *L. reussi* were originally attached to a hard substrate, the only well-preserved substrates are the tubes of the same species as can often be seen in the clusters. In a few specimens a larger tube of a different but undetermined serpulid species may have been used as a substrate.

The only preserved substrates except serpulid tubes are two oyster valves and a bryozoan colony. However, in the case of the two oyster valves, it is uncertain if they were really used as substrates or if they were only transported by chance to their position underneath the dead tubes. Otherwise, no other substrate could be identified from the shape of the impression at the tube underside, as no distinct ornamental pattern was found. This means that distinctly ornamented substrates such as mollusc shells (except oysters) were probably not used as substrates. Usually, the tube underside is more or less plain but uneven, whereas in a few specimens the tube underside is somewhat curved; not in a single specimen is the underside strongly concave. That means that marine plants possessing a cylindrical stem of small diameter did not serve as a substrate for *L. reussi*.

Not only *Laqueoserpula*, but also *Protectoconorca* and some other serpulid genera were smaller in the lowermost Cenomanian at Mülheim-Broich compared to other, geologically younger Upper Cretaceous localities. Therefore it may be questioned if increase in size soon after the start of new phylogenetic lineages is a phylogenetic phenomenon or rather an ecological phenomenon caused by specific ecological conditions at Mülheim-Broich.

The small size is certainly due to the cryptic environment between boulders and/or in erosional depressions of the sea-floor: approximately circular or irregular crater-like potholes or pockets, or longitudinal grooves. Some of the small organisms lived inside these potholes, whereas others are washed into them from the nearby slightly deeper sea. At Mülheim-Broich, these erosional depressions were eroded into the surface of the tilted Carboniferous sandstone by the abrasive action of pebbles and sand grains which were moved by the agitated transgressive sea. Kahrs (1927) provided some impressive photographs of the outcrops at Mülheim-Broich and a schematic drawing of a vertical section through a pothole. Formerly, all these geological details had been well exposed by quarrying and, at a smaller scale, also by the activities of geologists and fossil collectors. Lommerzheim (1979) interpreted the site at Mülheim-Broich as a coral reef on a sandy seafloor with many boulders in c. 5–30 m deep, moderately agitated, eutrophic waters. In the hollow spaces between the boulders plenty of small shelly remains accumulated, especially near the somewhat sheltered margins inside the potholes where they were locally preserved from later erosion. Although most of these small fossils were found loose, most probably many of these organisms had originally been attached to the boulders or the sea-floor or the potholes.

Likewise, many of the localities where *L. reussi* is found in the BCB are fossil-rich sediment fillings of hollow depressions ('pockets') in the seafloor, described in detail by Žítt *et al.* (1997, 2006). In the nearshore shallow water localities of the BCB, *L. reussi* was also well adapted for living in a high energy environment as evidenced by its thick tube wall and a compact spiral tube. Presumably also this species lived attached to hard rocks, boulders and cobbles.

It is striking that the geological setting and the palaeoenvironment were very similar in the two regions where fossil tubes of *Laqueoserpula* are most commonly found: in the lowermost Cenomanian at Mülheim-Broich and in the Upper Cenomanian and Lower Turonian of the BCB. Other, geologically younger Upper Cretaceous species of *Laqueoserpula* were found, although in a lower abundance, in other nearshore shallow water environments which, however, are not small-sized depressions – potholes or 'pockets' – on the seafloor, but somewhat wider, more horizontal strata that were formed a little further from the ancient coastlines. These additional occurrences are: (1) *Laqueoserpula*? sp. of Jäger (1983) in the Middle Santonian iron-ore deposit (‘Trümmererz’, consisting of iron-rich concretions originally deposited in Lower Cretaceous claystones, but later eroded, partly broken, partly strongly rounded, and accumulated in a matrix of fossil-rich Middle Santonian marlstones by the agitated transgressive sea) at Lengede in Lower Saxony in Germany, plus a single tube of the same species from coarse-grained Upper Santonian marlstones/limestones at Gehrden in Lower Saxony; and (2) *Laqueoserpula schmidwallisi* Jäger, 2005 in the uppermost Maastrichtian Meerssen Member in the city of Maastricht in The Netherlands and at the nearby Albert Canal in Neercanne in Belgium.

It is uncertain if *Laqueoserpula intumescens* Radwańska, 2004 from the Lower Kimmeridgian sponge/microbe bioherm facies (previously assigned to the Upper Oxfordian, before the downward shift of the Oxfordian/Kimmeridgian boundary) of Wapienno/Bielawy, Kuiavia region, north-central Poland, is a true *Laqueoserpula* or rather a spiral *Placostegus* similar to but not identical with the widespread *Placostegus*? *planorbiformis* (Münster in Goldfuss, 1831).

Remarkably, all the above mentioned localities where *Laqueoserpula* was found (Text-fig. 1), without any exception, yielded plenty of small to medium-sized fossils, representing a high diversity of organisms. Among these, at least all the Upper Cretaceous localities represent nearshore or even extremely nearshore shallow water localities. Only the single Upper Jurassic locality, where the occurrence of true *Laqueoserpula* is slightly uncertain, may have been deposited in somewhat more offshore and deeper waters in the lower part of the photic zone.

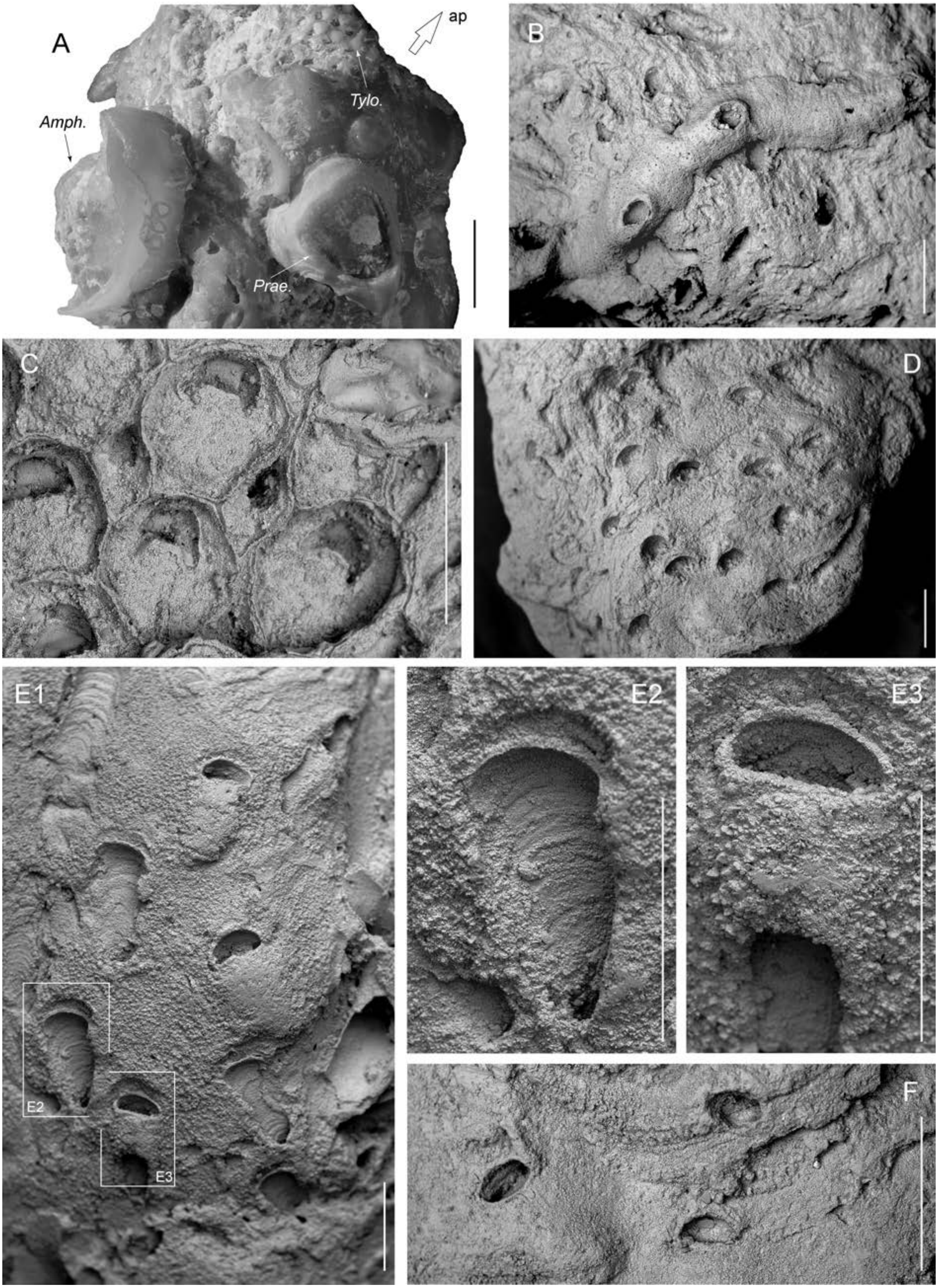
Encrusters, symbionts and microborers. The total number of sclerobionts *sensu* Taylor and Wilson (2002) including epibionts and macro- and microborers is statistically unimportant, reaching up to c. 5%. The main reason for this low number is the fact that the majority of tubes is abraded; therefore it is impossible to determine the full number and diversity of sclerobionts which had originally settled on and in the tubes of *L. reussi*. The most common relics of epibionts are other tubes of the same species in the clusters. Tubes of presumably different serpulid species also occur as encrusters, e.g., possibly *Dorsoserpula bipartita* (Reuss, 1845), syn. *gamigensis* (Geinitz, 1875).

The most common non-serpulid organisms encrusting *L. reussi* are foraminifers, e.g., *Axicolumella cylindrica* (Perner, 1892), juvenile oysters, e.g., *Amphidonte* sp., other bivalves, e.g., juvenile *Atreta* sp., brachiopods, e.g., *Praelacazella lacazelliformis* (Elliott, 1953), and bryozoan colonies (see below). A single specimen is encrusted by a questionable sponge (cf. *Neuropora* sp.). The largest observed epibionts are an oyster and a bryozoan colony each reaching 9 mm in size.

A considerable number of the tubes of *L. reussi* is infested by the symbiont hydroid *Protulophila gestroi* Rovereto, 1901 (see Scrutton 1975; Zágoršek *et al.* 2009; Słowiński *et al.* 2020). However, in many cases, it is difficult to decide if the holes in the tube were actively built around the *Protulophila* symbiont by the serpulid or if they are ordinary small boreholes caused by unknown borers perforating the formerly intact tube. This is especially true for some worn tubes. However, detailed observations indicate that the zooidal orifices are smaller and they occur in regular positions, which point to *P. gestroi*, if compared to different microboreholes which are irregularly located, e.g., ichnospecies of *Trypanites* Mägdefrau, 1932, *Caulostrepsis* Clarke, 1908, and *Maeandropolydora* Voigt, 1965, and the latter being bored by acrothoracican cirripedes *Rogerella* Saint-Seine, 1951. At Velim, approximately half of the specimens are infested by *Protulophila*, whereas at Chrtníky only about 10–20% of the specimens are infested. Within the clusters composed of several tubes of *L. reussi*, all possible combinations may occur: either all tubes or none of the tubes are infested, or only some are infested.

Sclerobionts on nine specimens of *L. reussi* (NM-O6661–6668, NM-O9493) were examined in detail. Seven of them show only one type of en-

Text-fig. 6. Encrusting fauna and the symbiont *Protulophila gestroi* Rovereto, 1901 on/in *Laqueoserpula reussi* (Weinzettl, 1910) tubes, Lower Turonian. A – NM-O9493, Kamajka; anterior portion of loosely coiled tube of *L. reussi* colonized by dense community of cemented fauna: juvenile oysters [Amph. = *Amphidonte* cf. *reticulatum* (Reuss, 1846)], encrusting bryozoans (Tylo. = cf. *Tyloporella reussi* Voigt, 1989), thecideid brachiopods [Prae. = *Praelacazella lacazelliformis* (Elliot, 1953)]. Serpulid epizoans (*Dorsoserpula bipartita* Reuss, 1845) are also present on the surface of the specimen (not visible in the figure). Arrow points to adapertural direction (ap); scale-bar equals 2 mm. B – NM-O6662, Chrtníky, lithounit 8f; bryozoan *Stomatopora* cf. *simplicissima* Novák, 1877 encrusting a tube of *L. reussi*; scale-bar equals 500 µm. C – NM-O6661, Chrtníky, lithounit 8f; bryozoan *Onychocella reussi* Prantl, 1938 occupying almost the entire surface of a *L. reussi* tube (specimen described in detail in the text); scale-bar equals 500 µm. D – NM-O6663, Chrtníky, lithounit 8f, *P. gestroi* infesting a tube of *L. reussi*; scale-bar equals 500 µm. E – NM-O6665, Chrtníky, lithounit 5; *P. gestroi* infesting a tube of *L. reussi*; E1 – general view; scale-bar equals 1 mm; E2 – detail; scalebar equals 500 µm; E3 – detail; scale-bar equals 200 µm. F – NM-O6664, Chrtníky, lithounit 8f; *P. gestroi* infesting a tube of *L. reussi*; scale-bar equals 500 µm. →


A
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cruster. Specimens NM-O6663-NM-O6668 were infested by *Protulophila*. NM-O6662 is both encrusted and infested by a stomatoporid bryozoan and by *Protulophila*. Several bryozoan taxa encrust the *Laqueoserpula* tubes, for example *Tyloporella reussi* Voigt, 1989 (Text-fig. 6A), *Stomatopora* cf. *simplicissima* Novák, 1877 (Text-fig. 6B), and *Onychocella reussi* Prantl, 1938 (Text-fig. 6C). *Tyloporella reussi* covers the surface of the anterior tube part of *Laqueoserpula* (NM-O9493); this could either be interpreted as mutual overgrowth *sensu* Rosso and Sanfilippo (2005), or as an encrusting bryozoan colony on the dead serpulid tube. Moreover, this tube was a hard substrate for the juvenile oyster *Amphidonte* cf. *reticulatum* (Reuss, 1846) and the brachiopod *Praelacazella lacazelliformis* (Elliott, 1953), which fed on suspended food particles just like *L. reussi*. Although preservation of this specimen is insufficient due to natural abrasion, the orientation of the bryozoa and the brachiopod directed toward the aperture (Text-fig. 6A) points to a possible mutual relationship.

NM-O6661 (Text-fig. 6C) was encrusted by the largest colony of the bryozoan *Onychocella* Jullien, 1882. *Stomatopora simplicissima* Novák, 1877 and/or *Voigtopora* Bassler, 1952, as well as two juvenile oysters are also present. *Onychocella* indicates water depths ranging from shallow coast (Zágoršek and Kroh 2003) down to deeper shelf around 200 m (Zágoršek and Vodrážka 2006). *Onychocella reussi* Prantl, 1938 (Text-fig. 6C) was already described from Chrtníky by Zágoršek and Vodrážka (2006). On NM-O 6661 the *Onychocella* colony occupies almost the entire surface (the specimen is incomplete), but several zooidal orifices of *P. gestroi* are also present; this hydroid supports evidence that it infested the serpulid tube before the bryozoan settled and shows a *post mortem* preservation of this hydroid due to being overgrown by the increasing bryozoan colony. This specimen indicates several phases of encrustation: first by the bryozoans *Onychocella reussi* and *Stomatopora simplicissima* and then by three juvenile oysters *Amphidonte* sp. It is disputable if this specimen is an example of space competition *sensu* Taylor (2016, fig. 4), when the juvenile *Amphidonte* sp. overgrew the bryozoan *Onychocella reussi*, which locally may have shown some response.

The *Protulophila* specimens (Text-fig. 6D, E1–E3, F) show features similar to those described by Zágoršek *et al.* (2009), especially the positive elevations of individuals and visibility of growth line inside the individual chambers (Text-fig. 6E2). This feature was not described in other specimens of *Protulophila* worldwide but is very common in the BCB material. The revision of *Protulophila* by Słowiński (work in progress) is badly needed to solve the questions if and how *Protulophila gestroi*, which actually is the only nominal species of this genus ranging from the Early Jurassic till present, may be assigned to several different species and if the above mentioned features of the BCB specimens may be useful for separating the species.

Organisms causing bioerosion of the tubes of *L. reussi* comprise the ichnogenera *Trypanites* Mägdefrau, 1932, *Caulostrepsis* Clarke, 1908, *Maeandropolydora* Voigt, 1965, *Orthogonum* Radtke, 1991, *Entobia* Bronn, 1837, and *Rogerella* Saint-Seine, 1951; they indicate the typical sclerobiont community of nearshore shallow water palaeoenvironment in the BCB (see Heřmanová *et al.* 2023).

PALAEOGEOGRAPHY

Palaeogeographical occurrence

Species assigned to *Laqueoserpula* have been recorded from the following localities (Text-fig. 1):

1. *Laqueoserpula*? *intumescens* Radwańska, 2004; affiliation uncertain – Bielawy Quarry, Kuiavia region, north-central Poland, Lower Kimmeridgian (*bimammatum* to *planula* zones).

2. *Laqueoserpula litoralis* Lommerzheim, 1979 and its subjective synonym *Laqueoserpula dolioformis* Lommerzheim, 1979 – Rauen Quarry at Mülheim-Broich, Northrhine-Westphalia, north-west Germany, lowermost Cenomanian, *Hypoturrilites carcitanensis* Zone, and former exposures in the city of Essen, Lower to Middle Cenomanian.

3. *Laqueoserpula plana* Lommerzheim, 1979 – Rauen Quarry at Mülheim-Broich, Northrhine-Westphalia, north-west Germany, lowermost Cenomanian, *Hypoturrilites carcitanensis* Zone.

4. *Laqueoserpula reussi* (Weinzettl, 1910) – (a) Želenice (‘Schillinge’) near Bílina and Novosedlice (‘Weisskirchlitz’) near Teplice, Reuss (1845–1846), but not re-discovered later, presumably Lower Turonian; (b) Gamighübel at Dresden-Kauscha in Saxony, Geinitz (1875), Jäger (2014), Upper Cenomanian; (c) Předboj near Prague (Předboj u Prahy), leg. Olga Nekvasilová 1960–1967, Kočí and Jäger (2015), Upper Cenomanian; (d) Zbyslav No. 51 near Čáslav, Ziegler (1984), Lower Turonian; (e) Chrtníky quarry, Žítt *et al.* (2006), Lower Turonian, layer 5 with *Cyathidium depressum* and layer 8f; (f) Kamajka near Chotusice, Čáslav district, this work, Lower Turonian; (g) Kaňk

near Kutná Hora, this work, Lower Turonian; (h) Turkaňk near Kutná Hora, this work, Lower Turonian; (i) Velim near Kolín, sublocality VII ('pocket Václav'), Žítt *et al.* (1997), this work, Lower Turonian; (j) Starkoč, this work, Lower Turonian.

5. *Laqueoserpula*? sp. of Jäger (1983) – (a) Lengede, between Braunschweig and Hildesheim, north Germany, Middle Santonian; (b) Gehrden, southwest of Hannover, north Germany, Middle or Upper Santonian.

6. *Laqueoserpula schmidwallisi* Jäger, 2005 – (a) ENCI-Heidelberg Cement Group quarry, city of Maastricht, The Netherlands, latest Maastrichtian, Meerssen Member; (b) Albert Canal near Neerkanne, Belgium, latest Maastrichtian, Meerssen Member.

While in the case of the only *Laqueoserpula* mentioned from the Jurassic of Poland the affiliation to this genus is uncertain, true members of *Laqueoserpula* occurred in the entire Late Cretaceous from the earliest Cenomanian to the latest Maastrichtian, and at many localities in the Czech Republic, but only at few localities in north and southeast Germany, the Netherlands and Belgium. All these Upper Cretaceous occurrences of *Laqueoserpula* represent nearshore localities in normal marine shallow water inhabited by a high diverse invertebrate fauna.

CONCLUSIONS

Laqueoserpula reussi is a serpulid species occurring in the Upper Cenomanian and Lower Turonian nearshore shallow water facies of the Bohemian Cretaceous Basin. Although it is common in some localities, previous authors either did not recognize it as a separate species or erroneously interpreted it as a gastropod. Nevertheless, comparison of Bohemian specimens with tubes from the type locality of two or three species of the genus *Laqueoserpula* confirm that they belong to that genus, and the ultrastructure supports evidence for a serpulid tubeworm close to the tribe Serpulini (Clade AI).

The tube of *L. reussi* can be distinguished from other species of the same genus by its large size, its relatively regular spiral, distinct incremental lines, and extremely thick tube wall, which together with the accompanying highly diverse fauna and palaeogeography, indicates life in high energy shallow water environments. The tube of *L. reussi* is often infested by the symbiont hydroid *Protulophila gestroi* and sometimes encrusted, e.g., by bryozoans of several species, small oysters and brachiopods and bored by several organisms.

Perhaps the genus *Laqueoserpula* existed already in the Kimmeridgian (Late Jurassic), and assuredly in the entire Late Cretaceous in Central and Eastern Europe. Although the tubes of other *Laqueoserpula* species are usually smaller than those of *L. reussi* and have a thinner tube wall, all hitherto known Late Cretaceous *Laqueoserpula* tubes were found in high diverse, fully marine, nearshore environments and therefore may be considered indicators for such an environment also when studying hitherto less well-known Upper Cretaceous deposits.

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REFERENCES

Bassler, R.S. 1952. Taxonomic notes on genera of fossil and Recent Bryozoa. *Journal of the Washington Academy of Sciences*, **42** (12), 381–385.

Benedict, J.E. 1887. Descriptions of ten species and one new genus of annelids from the dredging of the U.S. Fish Comm. Steamer Albatross. *Proceedings of the United States National Museum*, **9**, 547–553.

Bieler, R. and Petit, R.E. 2011. Catalogue of Recent and fossil 'worm-snail' taxa of the families Vermetidae, Siliquariidae, and Turritellidae (Mollusca: Caenogastropoda). *Zootaxa*, **2948**, 1–103.

Bronn, H.G. 1837. Lethaea Geognostica, Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen, 1, I–VI + 1–544. Schweizerbart; Stuttgart.

Bush, K.J. 1905. Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. Harriman Alaska Expedition, 12 (for 1904), 169–346.

Clarke, J.M. 1908. The beginnings of dependent life. *New York State Museum Bulletin*, **121**, 146–196.

Ehlers, E. 1908. Die bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition. In: Chun, C. (Ed), Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898–1899, 16 (1), 168 pp. Gustav Fischer; Jena.

Elliott, G.F. 1953. The classification of thecidean brachiopods. *The Annals and Magazine of Natural History*, **6**, 693–701.

Fabricius, J.C. 1779. Reise nach Norwegen mit Bemerkungen aus der Naturhistorie und Oekonomie, 388 pp. Carl Ernst Bohn; Hamburg.

Frič, A. 1889. Studien im Gebiete der Böhmischen Kreideformation. Palaeontologische Untersuchungen der einzelnen Schichten. IV. Die Teplitzer Schichten. *Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen*, **7** (2), 119 + 1 pp.

Frič, A. 1911. Studien im Gebiete der Böhmischen Kreideformation. Palaeontologische Untersuchungen der einzelnen Schichten. Ergänzung zu Band 1. Illustriertes Verzeichniss der Petrefacten der cenomanen Korycaner Schichten. *Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen*, **15 (**1), 1–101.

Geinitz, H.B. 1846. Grundriss der Versteinerungskunde, 813 pp. Arnold; Dresden und Leipzig.

Geinitz, H.B. 1875. Vermes. Würmer. In: Geinitz, H.B. (1871–1875), Das Elbthalgebirge in Sachsen. Erster Theil. Der untere Quader. *Palaeontographica*, **20** (1), 282–287.

Goldfuss, A. 1826–1844. Petrefacta Germaniae, 252 + 312 + 128 pp. Arnz and Co; Düsseldorf.

Grube, A.E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte*, **16**, 249–364.

Gunnerus, J.E. 1768. Om Nogle Norske Coraller. *Det Kongelige Norske Videnskabers Selskabs Skrifter*, **4**, 38–73.

Heřmanová, Z., Kočová Veselská, M., Kočí, T., Jäger, M., Bruthansová, J. and Mikuláš, R. 2023. Comparison of methods: micro-CT visualization method and epoxy cast-embedding reveal hidden details of bioerosion in the tube walls of Cretaceous polychaete worms. *Palaeontologia Electronica*, **26** (2), a18.

Hove, H.A. ten and Kupriyanova, E.K. 2009. Taxonomy of Serpulidae (Annelida, Polychaeta): The state of affairs. *Zootaxa*, **2036**, 1–126.

Ippolitov A.P. 2007. Contribution to the revision of some Late Callovian serpulids (Annelida, Polychaeta) of central Russia: Part 2. *Paleontological Journal*, **41** (4), 429–436.

Ippolitov, A.P. and Rzhavsky, A.V. 2008. On the tube microstructure of Recent spirorbids (Annelida, Polychaeta). *Doklady Biological Sciences*, **418**, 20–22.

Ippolitov, A.P., Vinn, O., Kupriyanova, E.K. and Jäger, M. 2014. Written in stone: history of serpulid polychaetes through time. *Memoirs of Museum Victoria*, **71**, 123–159.

Jäger, M. 1983. Serpulidae (Polychaeta sedentaria) aus der norddeutschen höheren Oberkreide – Systematik, Stratigraphie, Ökologie. *Geologisches Jahrbuch*, *Reihe A*, **68**, 3–219.

Jäger, M. 2005. Serpulidae und Spirorbidae (Polychaeta sedentaria) aus Campan und Maastricht von Norddeutschland, den Niederlanden, Belgien und angrenzenden Gebieten. *Geologisches Jahrbuch*, *Reihe A*, **157** (for 2004), 121–249.

Jäger, M. 2014. 4. Serpuliden und Sabelliden. In: Niebuhr, B. and Wilmsen, M. (Eds), Kreide-Fossilien in Sachsen, Teil 1. *Geologica Saxonica*, **60** (1), 57–81.

Jäger, M. and Kočí, T. 2007. A new serpulid, *Placostegus velimensis* sp. nov., from the Lower Turonian of the Bohemian Cretaceous Basin. *Acta Geologica Polonica*, **57** (1), 89–96.

Jullien, J. 1882. Note sur une nouvelle division des Bryozoaires Cheilostomiens. *Bulletin de la Société zoologique de France*, **6**, 271–285.

Kahrs, E. 1927. Zur Paläogeographie der Oberkreide in Rheinland-Westfalen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band, Abteilung B*, **58**, 627–687.

Kočí, T. 2007. New occurrence of serpulid worms from locality at Velim-Skalka in Bohemian Cretaceous Basin. *Geoscience Research Reports*, **2006**, 109–111.

Kočí, T. 2008. Sabellid and serpulid worms from the Lower Turonian of Kaňk – Na Vrších (Bohemian Cretaceous Basin, Czech Republic). In: Pisera, A., Bitner, M.A. and Halamski, A.T. (Eds), 9th Paleontological Conference, Warszawa, 10–11 October 2008, Abstracts, p. 45. Polish Academy of Sciences, Institute of Paleobiology; Warszawa.

Kočí, T. 2009. New finds and preliminary reports of the revision of serpulid worms (Polychaeta, Canalipalpata) from localities Velim and Kaňk – Na Vrších, Czech Republic (nearshore facies of the Bohemian Cretaceous Basin). *Vlastivědný zpravodaj Polabí*, **39** (2007–2008), 207–238. [In Czech with English summary]

Kočí, T. 2012. Serpulid worms from nearshore/shallow water locality Předboj near Prague from the collection of Dr. Olga Nekvasilová – part I. *Geoscience Research Reports*, **2011**, 120–123.

Kočí, T. and Jäger, M. 2015. Sabellid and serpulid worms (Polychaeta, Canalipalpata, Sabellida, Sabellidae, Serpulidae) from the rocky coast facies (Late Cenomanian) at Předboj near Prague. *Acta Musei Nationalis Pragae, Series B – Historia Naturalis*, **71** (1–2), 31–50.

Kočí, T., Jäger, M. and Morel, N. 2017. Sabellid and serpulid worm tubes (Polychaeta, Canalipalpata, Sabellida) from the historical stratotype of the Cenomanian (Late Cretaceous; Le Mans region, Sarthe, France. *Annales de Paléontologie*, **103** (1), 45–80.

Kupriyanova, E.K., Hove, H.A. ten, Sket, B., Zakšek, V., Trontelj, P. and Rouse, G.W. 2009. Evolution of the unique freshwater cave-dwelling tube worm *Marifugia cavatica* (Annelida: Serpulidae). *Systematics and Biodiversity*, **7**, 389–401.

Kupriyanova, E.K. and Ippolitov, A.P. 2015. Deep-sea serpulids (Annelida: Polychaeta) in tetragonal tubes: on a tube convergence path from the Mesozoic to Recent. *Zootaxa*, **4044** (2), 151–200.

Kupriyanova, E.K. and Flaxman, B. 2023. A new species of the mysterious genus *Spirodiscus* (Annelida: Serpulidae) of the Eastern Australian Abyss. *Records of the Australian Museum*, **75** (3), 155–166.

Kupriyanova, E., Hove, H.A. ten and Rouse, G.W. 2023. Phylogeny of Serpulidae (Annelida, Polychaeta) inferred from morphology and DNA sequences, with a new classification. *Diversity*, **15**, 398.

Lamarck, J.-B. de 1818. Histoire naturelle des animaux sans vertèbres, préséntant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; precedes d'une Introduction offrant la determination des caracteres essentiels de l'animal, sa distinction du vegetal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie, 5, 612 pp. Deterville and Verdière; Paris.

Langerhans, P. 1884. Die Wurmfauna von Madeira, IV. *Zeitschrift für Wissenschaftliche Zoologie*, **40**, 247–285.

Lehrke, J., Hove, H.A. ten, Macdonald, T.A., Bartolomaeus, T. and Bleidorn, C. 2007. Phylogenetic relationships of Serpulidae (Annelida: Polychaeta) based on 18S rDNA sequence data, and implications for opercular evolution. *Organisms, Diversity and Evolution*, **7**, 195–206.

Levinsen, G.M.R. 1883. Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn*, **1882**, 160–350.

Linnæus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata, 1, 824 pp. Laurentius Salvius; Holmiae.

Lommerzheim, A. 1979. Monographische Bearbeitung der Serpulidae (Polychaeta sedentaria) aus dem Cenoman (Oberkreide) am Südwestrand des Münsterländer Beckens. *Decheniana*, **132**, 110–195.

Mägdefrau, K. 1932. Über einige Bohrgänge aus dem unteren Muschelkalk von Jena. *Paläontologische Zeitschrift*, **14**, 150–160.

Montfort, D. de 1808. Conchyliologie systématique et classification méthodique des coquilles, 1. Coquilles univalves, cloisonées. lxxxvii + 409 pp., 100 figs. F. Schoell; Paris.

Novák, O. 1877. Beitrag zur Kenntniss der Bryozoen der böhmischen Kreideformation. *Denkschriften der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe*, **37** (2), 79–126.

Perner, J. 1892. Foraminifery českého cenomanu. Über die Foraminiferen des böhmischen Cenomans. *Česká Akademie Císaře Frantiska Josefa, Pro Vědy, Slovesnost a Umění v Praze 2 (Palaeontographica Bohemiae)*, **1**, 1–65.

Philippi, A. 1844. Einige Bemerkungen über die Gattung *Serpula*, nebst Aufzählung der von mir im Mittelmeer mit dem Thier beobachteten Arten. *Archiv für Naturgeschichte*, **10** (1), 186–198.

Pillai, T.G. 1960. Some marine and brackish-water serpulid Polychaeta from Ceylon, including new genera and species. *Ceylon Journal of Science (Biological Sciences)*, **3** (1), 1–40.

Pillai, T.G. 1993. A review of some Cretaceous and Tertiary serpulid polychaetes of the genera *Cementula* and *Spiraserpula* Regenhardt 1961, *Laqueoserpula* Lommerzheim 1979 and *Protectoconorca* Jäger 1983. *Paläontologische Zeitschrift*, **67** (1–2), 69–88.

Pillai, T.G. and Hove, H.A. ten 1994. On Recent species of *Spiraserpula* Regenhardt, 1961, a serpulid polychaete genus hitherto known only from Cretaceous and Tertiary fossils. *Bulletin of the Natural History Museum London, Zoology series*, **60** (1), 39–104.

Prantl, F. 1938. Lower Turonian Bryozoa from Předboj (Bohemia). *Rozpravy Státniho geologického Ústavu Československé Republiky*, **8**, 1–71.

Radtke, G. 1991. Die mikroendolithischen Spurenfossilien im Alt-Tertiär West-Europas und ihre palökologische Bedeutung. *Courier Forschungsinstitut Senckenberg*, **138**, 1–185.

Radwańska, U. 2004. Tube-dwelling polychaetes from the Upper Oxfordian of Wapienno/Bielawy, Couiavia region, north-central Poland. *Acta Geologica Polonica*, **54**, 35–52.

Rafinesque, C.S. 1815. Analyse de la nature ou tableau de l'universe et des corps organisés. 224 pp. L'Auteur, Jean Barravecchia; Palerme.

Regenhardt, H. 1961. Serpulidae (Polychaeta sedentaria) aus der Kreide Mitteleuropas, ihre ökologische, taxionomische und stratigraphische Bewertung. *Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg*, **30**, 5–115.

Reuss, A.E. 1844. Geognostische Skizzen aus Böhmen. 2. Die Kreidegebilde des westlichen Böhmens, ein monographischer Versuch. Nebst: Bemerkungen über die Braunkohlenlager jenseits der Elbe und eine Uebersicht der fossilen Fischreste Böhmens. vi + 304 pp. C.W. Medau and Comp.; Prag.

Reuss, A.E. 1845–1846. Die Versteinerungen der Böhmischen Kreide-Formation. 58+148 pp. Schweizerbart; Stuttgart.

Rioja, E. 1923. Estudio sistemático de las Especies Ibéricas del suborden Sabelliformia. *Trabajos del Museo nacional de ciencias naturales*, **48**, 5–144.

Rosso, A. and Sanfilippo, R. 2005. Bryozoans and serpuloideans in skeletobiont communities from the Pleistocene of Sicily: spatial utilisation and competitive interactions. *Annali dell'Università degli Studi di Ferrara, Sezione di Museologia Scientifica e Naturalistica, volume speciale*, **2005**, 109–124.

Rouse, G.W. and Fauchald, K. 1997. Cladistics and polychaetes. *Zoologica Scripta*, **26**, 139–204.

Rovereto, G. 1895. Di alcuni anellidi del terziario in Austria. *Atti del Società ligustica di Scienze naturali e geografiche*, **6** (2), 152–158.

Rovereto, G. 1901. Briozoi, anellidi e spugne perforanti del Neogene Ligure. *Palaeontographia Italica*, **7**, 219–234.

Saint-Seine, R. de 1951. Un cirripède acrothoracique du Crétacé; *Rogerella lecointrei*, nov. gen., nov. sp. *Compte Rendu de l'Academie des Sciences*, **223**, 1051–1053.

Scrutton, C.T. 1975. Hydroid-Serpulid symbiosis in the Mesozoic and Tertiary. *Palaeontology*, **18** (2), 255–274.

Sieverts, H. 1932. *Cyathidium depressum* n. sp. aus dem Oberen Cenoman Rheinland-Westfalens. *Jahrbuch der Preussischen Geologischen Landesanstalt*, **52** (1931), 159–176.

Słowiński, J., Surmik, D., Duda, P. and Zatoń, M. 2020. Assessment of serpulid-hydroid association through the Jurassic: A case study from the Polish Basin. *PloSONE*, **15** (12), e0242924.

Sowerby, J. de C. 1829. The mineral conchology of Great Britain, 6, 230 pp. The Author; London.

Taylor, P.D. 2016. Competition between encrusters on marine hard substrates and its fossil record. *Palaeontology*, **59** (4), 481–497.

Taylor, P.D. and Wilson, M.A. 2002. A new terminology for marine organisms inhabiting hard substrates. *Palaios*, **17**, 522–525.

Taylor, P.D. and Wilson, M.A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, **62**, 1–103.

Vinn, O. 2005. The tube ultrastructure of serpulids (Annelida, Polychaeta) *Pentaditrupa subtorquata*, Cretaceous, and Nogrobs cf. vertebralis, Jurassic, from Germany. *Proceedings of the Estonian Academy of Sciences, Geology*, **54** (4), 260–265.

Vinn, O. 2007. Taxonomic implications and fossilisation of tube ultrastructure of some Cenozoic serpulids (Annelida, Polychaeta) from Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **244**, 115–128.

Vinn, O. and Furrer, H. 2008. Tube structure and ultrastructure of serpulids from the Juarassic of France and Switzerland, its evolutionary implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **250**, 129–135.

Vinn, O., Hove, H.A. ten, Mutvei, H. and Kirsimäe, K. 2008. Ultrastructure and mineral composition of serpulid tubes (Polychaeta, Annelida). *Zoological Journal of the Linnean Society*, **154**, 633–650.

Voigt, E. 1965. Über parasitische Polychaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. P*aläontologische Zeitschrift*, **39** (3/4), 193–211.

Voigt, E. 1989. Beitrag zur Bryozoen-Fauna des sachsischen Cenomaniums. Revision von A.E. Reuss' "Die Bryozoen des unteren Quaders" in H.B. Geinitz' "Das Elbthalgebirge in Sachsen" (1872). Teil I: Cheilostomata. *Abhandlungen des staatlichen Museums für Mineralogie und Geologie zu Dresden*, **36**, 8–87.

Weinzettl, V. 1910. Gastropoda českého křídového útvaru. *Palaeontographica Bohemiae*, **8**, 1–56.

Zágoršek, K. and Kroh, A. 2003. Cretaceous Bryozoa from Scharrergraben (Santonian, Austria). *Geologica Carpathica*, **54**, 395–407.

Zágoršek, K. and Vodrážka, R. 2006. Cretaceous Bryozoa from Chrtníky (Bohemian Massif). *Courier Forschungsinstitut Senckenberg (CFS)*, **257**, 161–177.

Zágoršek, K., Taylor, P.D. and Vodrážka, R. 2009. Coexistence of symbiotic hydroids (*Protulophila*) on serpulids and bryozoans in a cryptic habitat at Chrtníky (lower Turonian, Czech Republic). *Bulletin of Geosciences*, **84**, 631–636.

Zibrowius, H. 1972. Mise au point sur les espèces méditerranéennes de Serpulidae (Annelida Polychaeta) décrites par Stafano delle Chiaje (1822–1829, 1841–1844) et Oronzio Gabriele Costa (1861). *Tethys*, **4**, 113–126.

Zibrowius, H. 1979. *Vitreotubus digeronimoi* n. g., n. sp. (Polychaeta Serpulidae) du Pléistocène inférieur de la Sicile et de l'étage bathyal des Açores et de l'Océan Indien. *Tethys*, **9**, 183–190.

Ziegler, V. 1984. Family Serpulidae (Polychaeta, Sedentaria) from the Bohemian Cretaceous Basin. *Sborník Národního Muzea v Praze*, **39 B** (4), 213–254.

Žítt, J., Nekvasilová, O., Bosák, P., Svobodová, M., Štemproková-Jírová, D. and Štastný, M. 1997. Rocky coast facies of the Cenomanian–Turonian boundary interval at Velim (Bohemian Cretaceous Basin, Czech Republic), first part. *Věstník Českého geologického Ústavu*, **72**, 83–102.

Žítt, J., Vodrážka, R., Hradecká, L., Svobodová, M. and Zágoršek, K. 2006. Late Cretaceous environments and communities as recorded at Chrtníky (Bohemian Cretaceous Basin, Czech Republic). *Bulletin of Geosciences*, **81**, 43–79.

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