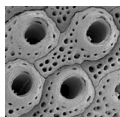


# Bryozoa from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland)

KAMIL ZÁGORŠEK, URSZULA RADWAŃSKA & ANDRZEJ RADWAŃSKI



New cyclostome and cheilostome bryozoan material from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland) has yielded 51 taxa (with some remaining in open nomenclature), among which *Stephanollona korytnicensis* sp. nov. is established as new to science. The occurrence of the previously known free-living cheilostomes (*Cupuladria*, *Reussirella*, *Lunulites*) and boring ctenostomes is reviewed with regard to the phenomenon of the Bryozoan Event which spread over the Paratethys basins in Europe. The extreme shallowness of this basin and its apparently peculiar environmental conditions are inferred to have prevented the contemporaneous Bryozoan Event from developing here within the world-famous organic communities of the Korytnica Basin. • Key words: Bryozoa, new species, Korytnica Basin, Bryozoan Event, Carpathian Foredeep, Middle Miocene, Holy Cross Mountains, Poland.

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The Middle Miocene climatic optimum (Langhian/Serravallian boundary, Badenian local stage) which correlated with the large transgression over the Central Paratethys in Europe, has recently been recognized in connection with the associated Bryozoan Event (Holcová & Zágoršek 2008; Zágoršek 2010a, b). Its origin and rise, well recorded in many parts of the Central Paratethys, has not previously been detected in the Fore-Carpathian realm in Poland, including the paramount fossil-bearing sequence of the Korytnica Basin. The aim of the present report, prepared by cooperation between the Faculty of Geology, University of Warsaw, and the National Museum in Prague, is to reduce this gap in knowledge.

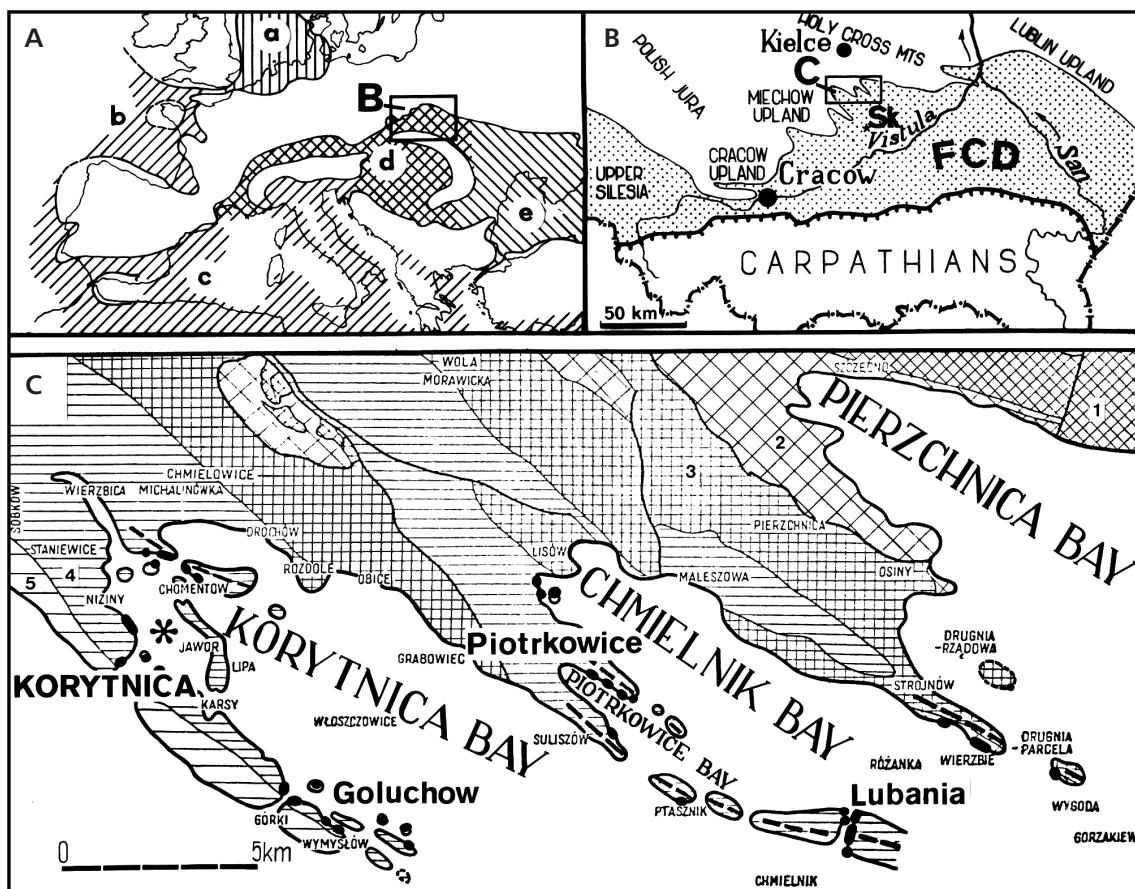
## The Korytnica Basin

The Korytnica Basin was formed as a terminal part of a large bay during the Middle Miocene (Badenian), when a transgression encroached upon the diversified pre-Miocene topography of the southern slopes of the Holy Cross Mountains in Central Poland (see Fig. 1A, B). This resulted in a Dalmatian-type coast sculptured by terrestrial valleys, dependent upon tectonic units of Early Alpine (Laramian) age, and by elevated ranges composed of limestones of

variable age (Devonian, Triassic, Jurassic; see Radwański 1969, 1970). These weathering-resistant belts formed the ancient rocky shores which bounded the flooding waters in several bays, the largest of which was the Korytnica Bay (see Fig. 1C). At its terminal, northwestern tip, distinguished as the Korytnica Basin (see Fig. 2), a relatively thick (max. 30–60 m) sequence was formed of soft, creamy-yellowish clays, the Korytnica Clays, which pass into marly, oyster shellbeds at the junction with the rocky shore. These two principal facies are the focus of bryozoan research in the present study, while the other facies (see Radwański 1969, Małeck 1985) are not included.

The environmental conditions of the Korytnica Basin, its development and demise, have been studied in detail (Radwański 1969, Bałuk & Radwański 1977a, Radwańska 1992), as has its ubiquitous organic communities which have been world-famous for over two centuries (Jaśkiewicz 1787, Zeuschner 1830, Murchison 1845, Hörnes 1856; see Bałuk & Radwański 1977a, 1979a; other references in Hoffman 1977, 1987, and Bałuk 1995).

The total number of taxa in the diverse biota, both invertebrates and fish, is remarkable, exceeding that of other classical localities in the Central Paratethys. For instance, the number of gastropods, still incompletely inventoried (see Bałuk 1995, 2006), is much higher than that of the



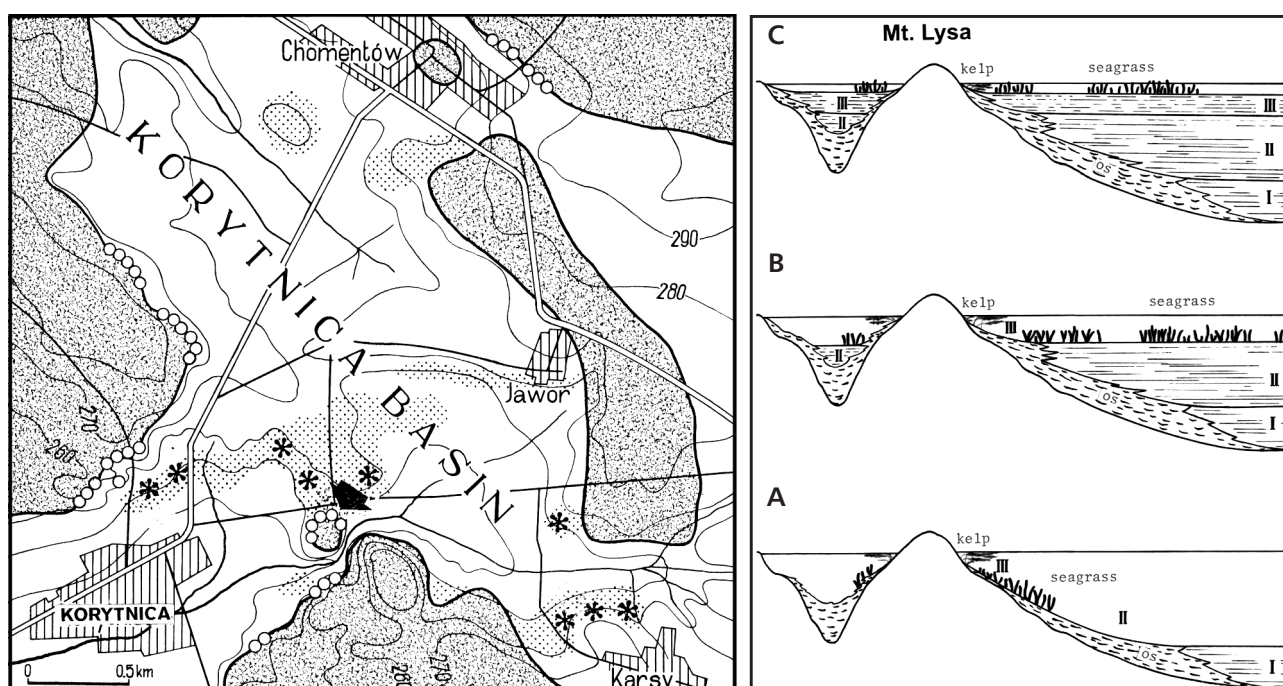
**Figure 1.** Palaeogeographic setting of the Middle Miocene (Badenian) shorezone of the Holy Cross Mountains, Central Poland. • A – marine basins in the Middle Miocene of Europe: a – North Sea Basin, b – Atlantic gulfs (Brittany, Touraine, and Anjou Basin, Aquitanian Basin, Lisbon Basin), c – Western Mediterranean Basin (= Tethys Basin), d – Paratethys basins, e – Euxinian Basin; the area enlarged in Fig. 1B is enclosed within a rectangle. • B – extent of the Middle Miocene (Badenian) sea in the Fore-Carpathian Depression (FCD, stippled); the area enlarged in Fig. 1C is enclosed within a rectangle. • C – Middle Miocene (Badenian) shoreline and extent of the bays on the southern slopes of the Holy Cross Mountains; preserved localities of littoral structures are marked with black spots along the shoreline; the Korytnica Basin (see Fig. 2), situated in the terminal part of the Korytnica Bay (cf. Radwański 1969, fig. 25; 1970, fig. 1), is marked by an asterisk. Within the inland areas the following occurrence zones are distinguished: 1 – Cambrian (including locally Ordovician and Silurian), 2 – Devonian, 3 – Triassic, 4 – Jurassic, 5 – Cretaceous; the heavy dashes indicate ridges which separate particular bays.

famous, gastropod-rich Badenian stratotype at Baden-Sooss in the Vienna Basin (see Rögl *et al.* 2008). The invertebrate macrofossils represent all mineralized phyla (see Bałuk & Radwański 1977a, pp. 97–99; Hoffman 1987; Radwańska 1992, pp. 311–315; Bałuk 1995, p. 161). The remains of teleost fish, represented by otoliths, are also diverse (105 species from 47 families: Radwańska 1992); while elasmobranchs are less abundant. Little research has as yet been focused upon the microfossils (see *e.g.* Szczechura 1985). In this context, the paucity of bryozoans of any kind in all the studied biotopes and their organic communities has long been intriguing.

The sessile, epibiotic cyclo- and cheilostome bryozoans from the Korytnica Clays were first studied by Vávra (1984), who analyzed three sampling sites along the rocky coastal slope of Mt. Lysa (Fig. 2). Among the twenty-two taxa recognized, Vávra (1984) noted the significance of

the cyclostome *Bobiesipora*, known then solely from the Vienna Basin, and the cheilostome *Steginoporella* indicative of tropical/subtropical climatic conditions. The depth evaluation proposed by Vávra (1984) is much greater than that indicated by other biota (see Bałuk & Radwański 1977a, Radwańska 1992, pp. 147–149). Additionally, several specimens of the still problematic microfossil *Bifissurinella*, recently classified as a cheilostome bryozoan, were reported from this location (see Szczechura 1985).

Bryozoans from the Korytnica Clays were also carefully collected by the late Professor Jerzy Małeckı (see Bałuk & Radwański 1977a, p. 97), whose preliminary account (Małeckı 1985) noted 28 species from the clays, the rest being from other facies of the Korytnica Basin. We are unable to find his original collections, either at the University of Warsaw or in Cracow. Therefore we have



**Figure 2.** Palaeoenvironmental sketch of the Korytnica Basin (see Fig. 1C), with locations of sampling sites (*asterisks*) of the studied bryozoans in the Korytnica Clays outcrops (*stippled*); littoral structures of the shorezone (*shaded*) are circled; bryozoan samples collected by Vávra (1984) on the slopes of Mt. Lysa (*arrowed*). The sections show gradual filling (stages A–C) of the basin by Korytnica Clays (oyster shellbed along the slope) which incorporate successive (I–III) organic communities yielding the studied bryozoans.

attempted to revise his material from the illustrations given in his paper; the proposed revision is presented in Table 1.

The Korytnica sequence can be correlated with the Vienna Basin sediments of the Lower Lagenidae Zone (see Harzhauser *et al.* 2003, p. 328). According to this recently undertaken study, the Korytnica sequence is older than the uppermost part of the Upper Lagenidae Zone and also the lower part of the Spiroplectammina Zone, as formerly determined by Vávra (1984, p. 225). Therefore, the absolute age of the Korytnica sequence may be roughly estimated as 14.8–14.6 Ma (see Rögl *et al.* 2008, fig. 3).

## Material and methods

The locality at Korytnica (GPS position: 50° 39' 50" to 50° 40' 50" N and 20° 31' 20" to 20° 33' 00" E) comprises many small outcrops located in agricultural land. The studied material comes from a trench excavated along the slope of Mt. Lysa (Fig. 2), to transect both the oyster shellbed and the interfingering clays (see Radwańska 1992, Fig. 2B). Some bryozoans come from various samples of the clays.

The studied material is deposited in the collections of the National Museum, Prague, abbreviated NM-PM2.

Specimens were cleaned ultrasonically before sorting with the aid of a binocular microscope. Well-preserved and/or fertile examples of each species were selected for study using a low-vacuum scanning electron microscope, LV Hitachi S-3700N, at the National Museum, Prague. This instrument allowed backscattered electron images to be obtained of uncoated specimens temporarily mounted onto stubs using adhesive carbon tabs, or affixed to stage mounts with carbon plastic.

## Results

The newly discovered bryozoan fauna from the Korytnica Clays is dominated volumetrically by small, nodular, celled-poriform cheilostomes. These bryozoans are usually very poorly preserved, so exact determination is impossible; in Table 1 they are therefore listed under the name Celleporids.

Bryozoans from the Korytnica Clays are rare, but are a very important part of the taphocoenoses, studied previously by Vávra (1984) and Małeckı (1985). Vávra (1984) mentioned altogether 24 species and gave short descriptions. Except for three species (*Amphiblestrum appendiculatum*, *Biflustra texturata* and *Pseudofrondipora davidi*), we found all the bryozoans species recorded by Vávra (1984). Almost simultaneously, Małeckı (1985)

**Table 1.** List of all formerly reported and newly found bryozoan species from the Korytnica Clays, with proposed revision of the lists of species given in Vávra (1984) and Małecki (1985).

TAXA (proposed correct name)	This study	Vávra (1984)	Malecki (1985) (proposed revised taxonomy)
<i>Acanthodesia savartii</i> (Audouin, 1826)	*	*	
<i>Adeonella polystomella</i> (Reuss, 1847)	*	*	*
<i>Adeonellopsis coscinophora</i> (Reuss, 1847)	*		
<i>Amphiblestrum appendiculatum</i> (Reuss, 1847)		*	
<i>Antropora?</i> sp.	*		
<i>Biflustra</i> sp.		<i>Biflustra savartii</i> <i>texturata</i>	
<i>Bobiesipora fasciculata</i> (Reuss, 1847)	*	*	
<i>Cellaria</i> cf. <i>fistulosa</i> (Linnaeus, 1758)	*	*	<i>C. crassa</i> , <i>C. salicornoides</i> , <i>C. johnsoni</i> and <i>C. farciminoidea</i>
Celleporids	*	*	<i>Costacia costazii</i> , <i>Cellepora globularis</i> , <i>Schizmopora</i> <i>scruposa</i> , <i>Osthimosa coronopus</i> , <i>Holoporella palmata</i> and <i>Holoporella cerioporoides</i>
<i>Coronopora</i> cf. <i>disticha</i> (von Hagenow, 1851)	*		
<i>Cosciniopsis</i> sp.	*	unidentified cheilostome	
<i>Crisia hoernesii</i> Reuss, 1848			*
<i>Cupuladria</i> sp.	*		<i>C. canariensis</i>
<i>Diplosolen obelium</i> (Johnston, 1838)			*
<i>Disporella</i> cf. <i>hispida</i> (Fleming, 1828)	*		<i>Lichenopora cumulata</i>
<i>Disporella</i> cf. <i>radiata</i> (Savigny & Audouin, 1826)	*	<i>Lichenopora</i> sp.	<i>Lichenopora echinulata</i>
<i>Disporella goldfussi</i> (Reuss, 1864)			*
<i>Escharella</i> cf. <i>tenera</i> (Reuss, 1874)	*		
<i>Escharoides coccinea</i> (Abildgaard, 1806)			*
<i>Exidmonea atlantica</i> David, Mongereau & Pouyet, 1972	*		as <i>Idmonea</i> and <i>E. delicatula</i>
<i>Exidmonea giebeli</i> (Stoliczka, 1862)			<i>E. concava</i>
<i>Fron dipora</i> cf. <i>verrucosa</i> (Lamouroux, 1821)	*		
<i>Hiantopora</i> sp.			<i>Tremopora radificifera</i>
<i>Hippopleurifera semicristata</i> (Reuss, 1847)	*		
<i>Hornera</i> cf. <i>frondiculata</i> Lamourox, 1821	*	<i>Hornera</i> sp. div.	*
<i>Hornera verrucosa</i> Reuss, 1866	*	*	<i>H. striata</i>
<i>Idmidronea coronopus</i> (Defrance, 1822)	*	*	
<i>Lumulites</i> cf. <i>androsaces</i> Manzoni, 1877	*		*
<i>Margaretta cereoides</i> (Ellis & Solander, 1786)	*	*	as <i>Tubucellaria</i>
<i>Mecynoecia pulchella</i> (Reuss, 1847)	*	*	as <i>Entalophora</i>
<i>Oncousoecia?</i> <i>biloba</i> (Reuss, 1847)	*		
<i>Onychocella angulosa</i> (Reuss, 1847)	*		*
<i>Phoceana?</i> <i>tubulifera</i> (Reuss, 1847)	*		

mentioned 28 taxa of which eight were given short descriptions. In the current investigation a total of 51 species are recognized. We also tried to revise both Vávra's (1984) and Małecki's (1985) material which is partly deposited at Vienna University (Austria) and the University of Warsaw (Poland). All previously known species, some with proposed revised names, together with recently discovered species are listed in Table 1. The total number of known bryozoan species from the Korytnica Clays is now 62.

Among these are one new species belonging to the genus *Stephanollona* and one indeterminate cheilostome.

### Systematic palaeontology

A full taxonomic description is presented for the single new species introduced in this paper. For well-known species that are newly reported here from the Korytnica Clays,

Table 1 – continued

TAXA (proposed correct name)	This study	Vávra 1984	Malecki 1985 (proposed revised taxonomy)
<i>Platonea pluma</i> (Reuss, 1847)	*		as <i>Tubulipora</i>
<i>Pleuronea pertusa</i> (Reuss, 1847)	*		and <i>P. fenestrata</i> and <i>P. reticulata</i>
<i>Polyascoecia cancellata</i> Canu, 1920	*	*	<i>Reteporidaea coronopus</i>
<i>Pseudofrondipora davidi</i> Mongereau, 1970		*	
<i>Puellina venusta</i> (Canu & Bassler, 1925)			<i>Cribrilaria radiata</i>
<i>Pyriporella</i> cf. <i>loxopora</i> (Reuss, 1847)	*		
<i>Reptadeonella</i> cf. <i>violacea</i> (Johnston, 1847)	*		
<i>Reteporella kralicensis</i> Zágóršek, Holcová & Třasoň, 2008	*		<i>Sertella beaniana</i>
<i>Reteporella</i> sp.	*	*	<i>Sertella cellulosa</i>
<i>Reussirella haidingeri</i> (Reuss, 1847)	*		*
<i>Rosseliana brevipora</i> Canu & Lecointre, 1927			*
<i>Saevitella inermis</i> Bobies, 1956	*		
<i>Scrupocellaria elliptica</i> (Reuss, 1848)			*
?? <i>Scrupocellaria scruposa</i> ??			?? [ <i>Scrupocellaria scruposa</i> (Linnaeus, 1758)]
<i>Schizomavella protuberans</i> (Reuss, 1847)	*		<i>Sch. aculifera</i> and <i>Sch. tenella</i>
<i>Schizoporella tetragona</i> (Reuss, 1847)	*		<i>Sch. unicornis</i>
“ <i>Schizoporella</i> ” <i>geminipora</i> (Reuss, 1847)	*	*	*
<i>Schizostomella grinzigenensis</i> (David & Pouyet, 1974)	*		<i>Adeonella tessulata</i>
<i>Smittina cervicornis</i> (Pallas, 1766)	*	*	as <i>Porella</i>
<i>Steginoporella cucullata</i> (Reuss, 1847)	*	<i>S. manzonii</i>	<i>S. elegans</i>
<i>Stephanollona korytnicensis</i> sp. nov.	*		
<i>Tervia irregularis</i> (Meneghini, 1844)	*	*	<i>Tervia disticha</i> and <i>Tubigerina alternata</i>
<i>Tetrocycloecia dichotoma</i> Canu, 1919	*	<i>Tetrocycloecia</i> sp.	
<i>Tholopora neufferi</i> Vávra 1983	*		
<i>Tubulipora dimidiata</i> (Reuss, 1847)	*		and <i>T. partschi</i>
<i>Tubulipora foliacea</i> (Reuss, 1847)	*		? <i>Diaperoecia flabellum</i>
<i>Umbonula granulata</i> Zágóršek, 2010	*	<i>U. cf. endlicheri</i>	
<i>Umbonula macrocheila</i> (Reuss, 1847)	*	<i>U. endlicheri</i>	
<i>Ybseleosecia typica</i> (Manzoni, 1878)	*	*	*

only brief synonymies and remarks, as well as figures, are provided.

Phylum Bryozoa Ehrenberg, 1831  
 Class Stenolaemata Borg, 1926  
 Order Cyclostomatida Busk, 1852  
 Suborder Tubuliporina Milne-Edwards, 1838  
 Family Oncousoeciidae Canu, 1918

### Genus *Oncousoecia* Canu, 1918

#### *Oncousoecia? biloba* (Reuss, 1847)

Figure 3A

v.\* 1847 *Hornera biloba* m.; Reuss, p. 43, pl. 6, fig. 21.

v. 2010a *Oncousoecia? biloba* (Reuss). – Zágóršek, p. 27, pl. 2, figs 1–4 (cum syn.).

*Material.* – Two well-preserved, small, fertile colonies (with gonozooecia), and many additional fragments.

*Description.* – The colonies are unilaminar with 5 to 10 autozooeical rows obliquely parallel to each other. Gonozooecia are large, both with partly damaged frontal wall spread among 5 to 8 autozooeical tubes. Ooeciopore not clearly recognizable, smaller than autozooeical apertures situated in the middle of the gonozooecium.

*Remarks.* – This species is not consistent with the type species of *Oncousoecia* selected by Taylor & Zatoń (2008). At present there is no suitable genus in which this species

could be accommodated, and to establish a new one is beyond the scope of this paper. For detailed discussion see Zágöršek (2010a).

Family Tubuliporidae Johnston, 1838

### Genus *Tubulipora* Lamarck, 1816

#### *Tubulipora foliacea* Reuss, 1847

Figure 3B

- v.\* 1847 *Tubulipora foliacea* m.; Reuss, p. 49, pl. 7, fig. 5.  
1977 *Tubulipora foliacea* Reuss, 1847. – Vávra, p. 23 (cum syn.).

**Material.** – Three fragments of colonies with well-developed gonozooecia.

**Description.** – The colony is encrusting, irregular, unilaminar with long autozooecial peristomes. Apertures not arranged in fascicles, but two or three peristomes may be merged. Gonozooecium (brood chamber) large, spread between 8 to 10 peristomes, with a small ooeciopore situated on the distal margin, close to one aperture.

**Remarks.** – The gonozooecium is very rare in this species and has not yet been described from the Korytnica sequence.

Suborder Fasciculina d'Orbigny, 1853  
Family Frondiporidae Busk, 1875

### Genus *Frondipora* Link, 1807

#### *Frondipora* cf. *verrucosa* (Lamourox, 1821)

Figure 3C

- v. cf. 1977 *Frondipora verrucosa* (Lamourox, 1821). – Vávra, p. 50 (cum syn.)  
v. 2010a *Frondipora* cf. *verrucosa* (Lamourox, 1821). – Zágöršek, p. 33, pl. 20, figs 1–5.

**Material.** – Two fragments, unfortunately without gonozooecia.

**Description.** – The colonies are small, branching. Apertures and polygonal kenozoecia almost the same size, open only on the frontal side of the colony branch. Autozooecial fascicles (bundles) consist of about 8 to 20 apertures. Transverse fascicles elongated. Dorsal side smooth, perforated only by pseudopores. No gonozooecium observed.

**Remarks.** – The colonies are much smaller than those described by Vávra (1977) and the transverse fascicles are more elongated. Only two specimens without gonozooecia have been recognized, this is insufficient to judge if these differences are significant at the species level or represent within-species variability.

The Recent specimens (*e.g.* Hayward & McKinney 2002) always have very large, extended fascicles. A detailed comparison between Recent and fossil material is therefore needed to confirm this attribution.

Suborder Cerioporina von Hagenow, 1851  
Family Cerioporidae Reuss, 1866

### Genus *Tholopora* Gregory, 1909

#### *Tholopora neufferi* Vávra, 1983

Figure 3D

- v.\* 1983 *Tholopora neufferi* n. sp.; Vávra, p. 83, pl. 3, fig. 8–11.  
2007 *Tholopora neufferi* Vávra. – Zágöršek *et al.*, p. 210, fig. 4A, B.

**Material.** – Five well preserved colonies but without any trace of gonozooecia.

**Description.** – The colonies are columnar, developing characteristic subcolonies. Subcolonies are short, with a well developed basal lamella but without basal kenozoecia. Autozooecial tubes are circular, arranged chaotically, sometimes in quincunx. Kenozoecia single, rare, usually arranged in central area. No gonozooecia observed.

### Genus *Coronopora* Gray, 1847

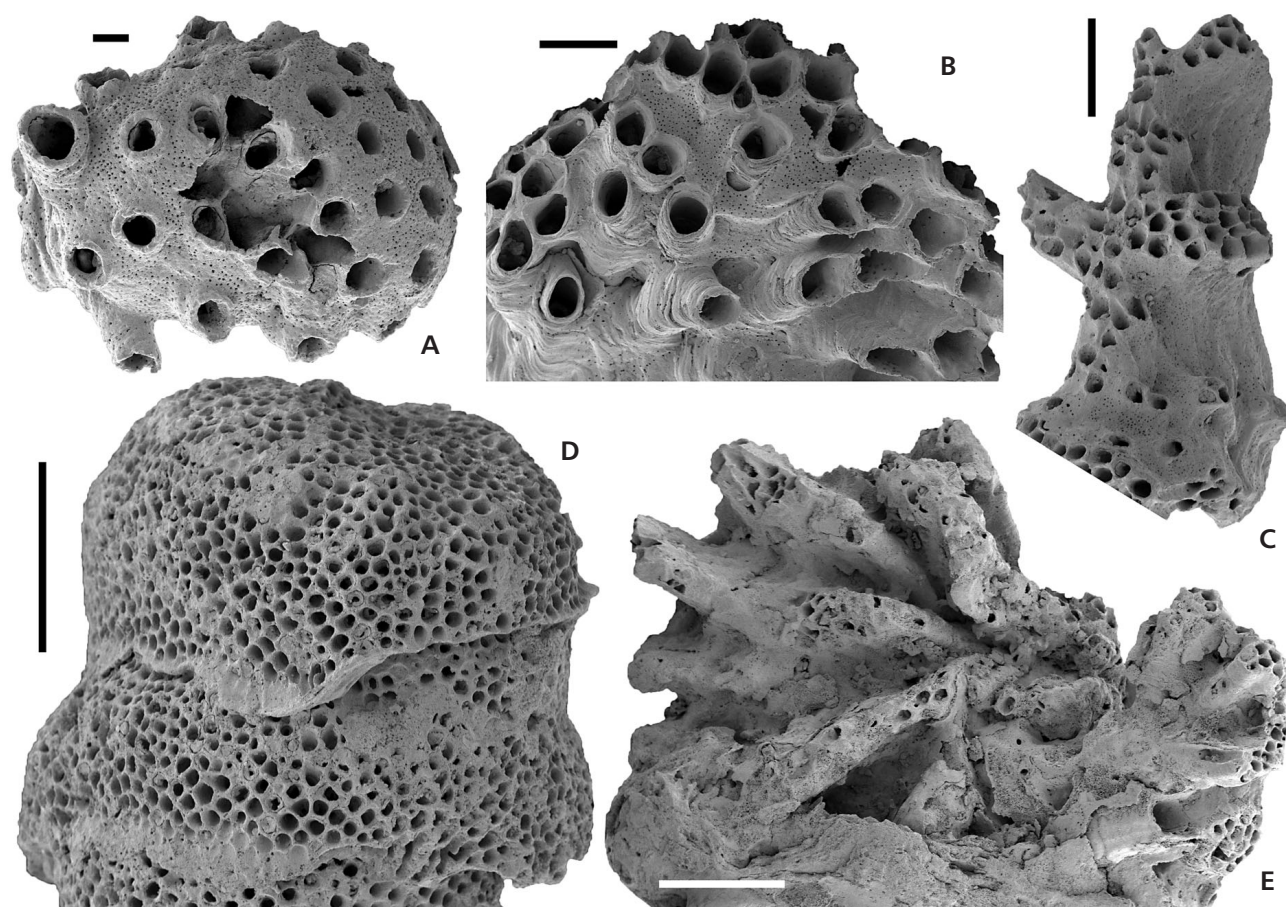
#### *Coronopora* cf. *disticha* (von Hagenow, 1851)

Figure 3E

- cf. \* 1851 *Defrancia disticha* sp. n.; von Hagenow, p. 142, pl. 4, fig. 1.

**Material.** – One colony but with preserved gonozooecium which allows a precise determination.

**Description.** – The colony is lobate, encrusting. Autozooecia arranged in biserial to multiserial radial rows with very long peristomes. Gonozooecium poorly preserved, situated on the margin of the colony, elongated transversely to the rows, spread over 4–5 autozooecial rows. Ooeciopore not visible.



**Figure 3.** A – *Oncousoecia? biloba* (Reuss, 1847), showing damaged frontal wall of the gonozoecium. Length of scale bar 100 µm. • B – *Tubulipora foliacea* Reuss, 1847, general view showing gonozoecium with small oeciopore. Length of scale bar 100 µm. • C – *Frondipora cf. verrucosa* (Lamouroux, 1821), general view showing arrangement of autozoecia on frontal side of the colony. Length of scale bar 1 mm. • D – *Tholopora neufferi* Vávra, 1983, general view of the colony showing subcolonies with basal lamella. Length of scale bar 1 mm. • E – *Coronopora cf. disticha* (von Hagenow, 1851), showing arrangements of autozoecia in biserial to multiserial radial rows with very long peristomes. Length of scale bar 1 mm.

**Remarks.** – *Coronopora* as described by Hayward & Ryland (1985) developed the same type of gonozoecium, and the fascicle characters are also identical with the studied specimens. Although *Coronopora* should grow in nodular colonies (Hayward & Ryland 1985), the studied specimen perhaps represents the encrusting base.

Class Gymnolaemata Allman, 1896  
 Order Cheilostomatida Busk, 1852  
 Suborder Flustrina Smitt, 1868  
 Superfamily Calloporoidea Norman, 1903  
 Family Calloporidae Norman, 1903

### Genus *Pyriporella* Canu, 1911

#### *Pyriporella cf. loxopora* (Reuss, 1847)

Figure 4A

cf. v.\* 1847 *Cellepora loxopora*.; Reuss, p. 97, pl. 11, fig. 24.

cf. 1977 *Hincksina loxopora* (Reuss, 1847). – Vávra, p. 79 (cum syn.).

v. 2010a *Pyriporella cf. loxopora* (Reuss, 1847). – Zągoršek, p. 44, pl. 47, fig. 1–4.

**Material.** – Only one small fragment of a colony encrusting an erect bryozoan.

**Description.** – A colony with chaotically arranged autozoecia. Gymnocyst short without any spines. Cryptocyst very narrow. Adventitious avicularia small, oval, without pivotal bar. About 3–5 avicularia situated around a single autozoecium. Ovicell unknown.

**Remarks.** – Only one specimen with poorly preserved features has been identified in the studied material, so exact determination is not possible.

The type material (Reuss' specimen number 1878.11.98 deposited in NHM Vienna) differs from the studied specimen in the growth pattern of the autozoecia.

Autozooezia in the type are arranged more or less in regular longitudinal rows, not as chaotically as in the studied specimens. This feature however may be the result of micro-environmental factors rather than species identity. Miocene material from Moravia (Zágoršek 2010a) is identical with the described specimen. As shown by Zágoršek (2010a), the characteristic arrangement of adventitious avicularia, lack of spines, together with autozooezial characters allow probable attribution of this species to the genus *Pyriporella*. Another possibility would be *Parantropora* especially *P. laguncula* (Canu & Bassler, 1929) as revised and described by Tilbrook (2006) which also has 5 avicularia surrounding each autozooezium, but it differs in having much wider opesia and an extended gymnocyst.

Family Antroporidae Vigneaux, 1949

### Genus *Antropora* Norman, 1903

#### *Antropora?* sp.

Figure 4B

**Material.** – Only one fragment with characteristically developed autozooezia and small avicularia, but without ovicells.

**Description.** – The colony is free or encrusting. Autozooezia are rhomboidal to oval separated by narrow furrows. Cryptocyst large, granular, opesia triangular. Pore chambers developed over a large area. Heterozooezia (avicularia or vibracula) are adventitious, small, short, drop-like to square shaped, without a pivotal bar, always single, one situated distally from each autozooezium. No ovicell observed.

**Remarks.** – The well developed cryptocyst, reduced gymnocyst and absence of spines resemble the genus *Antropora* as redescribed by Tilbrook (2006). The main difference is in the position of the avicularia: *Antropora* always has avicularia situated laterally from the autozooezia and often there are more than one around each autozooezium.

*Ellisina* Norman, 1903 is also similar to the described specimen in the development of the avicularia (always situated at the distal tip of the autozooezia), but differs in almost lacking a cryptocyst. Canu & Bassler (1925) described *Ellisina grandis* from the Vienna Basin but their illustrations do not allow a precise comparison. The species has been referred to by other authors (e.g. Moissette 1988), but synonymized with *Hincksina loxopora* (Reuss, 1847).

More specimens are needed for a correct determination of this material, particularly to ascertain whether ovicells are present or entirely absent.

Suborder Ascophora Levinsen, 1909  
Infraorder Umbonulomorpha Gordon, 1989  
Superfamily Adeonoidea Busk, 1884  
Family Adeonidae Busk, 1884

### Genus *Adeonellopsis* MacGillivray, 1886

#### *Adeonellopsis coscinophora* (Reuss, 1847)

- v.\* 1847 *Eschara coscinophora* m.; Reuss, p. 67, pl. 8, fig. 20.  
v. 2010b *Adeonellopsis coscinophora* (Reuss). – Zágoršek, p. 142, pl. 76, fig. 1–4 (cum syn.).

**Material.** – Seven well-preserved, erect colonies.

**Remarks.** – The studied specimens are identical with the Moravian material described by Zágoršek (2010b).

### Genus *Reptadeonella* Busk, 1884

#### *Reptadeonella* cf. *violacea* (Johnston, 1847)

Figures 4C, D

- v. 1977 *Reptadeonella violacea* (Johnston, 1847). – Vávra, p. 149 (cum syn.).  
?cf. 1999 *Reptadeonella violacea* (Johnston, 1847). – Hayward & Ryland, p. 186, figs 70A, B, 71 (cum syn.).  
v. 2010b *Reptadeonella* cf. *violacea* (Johnston, 1847). – Zágoršek, p. 143, pl. 78, figs 1–6 (cum syn.).

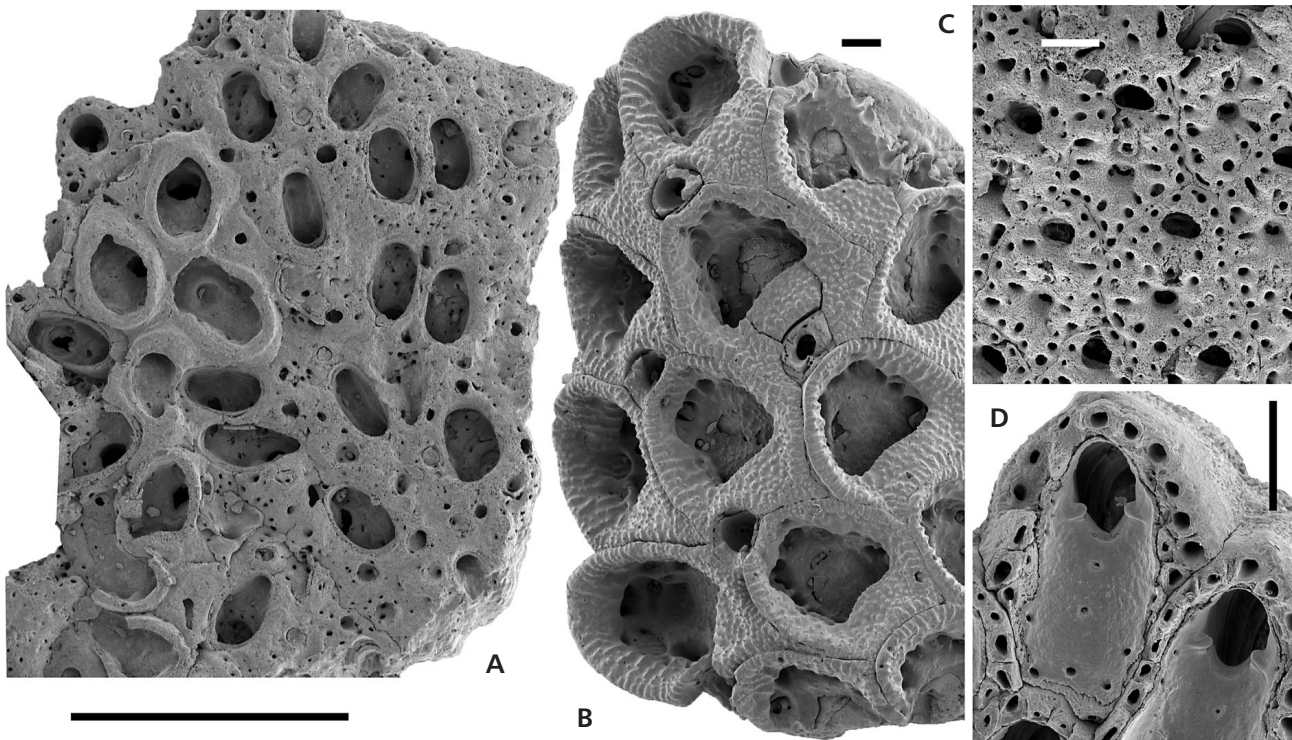
**Material.** – More than 10 fragments, with characteristically preserved autozooezia.

**Description.** – The colonies are encrusting. Autozooezia are regularly hexagonal with marginal areolar pores, semilunar spiramen and drop-like, small, median avicularia. Primary orifice has a broad sinus and well developed condyles on proximolateral corners. Ovicell not observed. Small pores perforate the frontal shield also from the interior side.

**Remarks.** – The studied fossil material is very similar to recent specimens as described by Hayward & Ryland (1999). The main difference is in the shape of the spiramen. The recent specimens have an almost circular spiramen, but the fossil ones studied here, as well as those described by Vávra (1977), often have a semilunar or even a slightly curved spiramen. Detailed study of intraspecific variability of this species is needed to decide if the fossil and recent material are conspecific.

Moravian material (Zágoršek 2010b) shows a smaller spiramen and more lateral communication pores than specimens from Korytnica. In addition, pores penetrating the frontal shield which are visible from interior side were not observed in the Moravian material.





**Figure 4.** A – *Pyriporella* cf. *loxopora* (Reuss, 1847), general view showing chaotically arranged autozoecia and small adventitious avicularia. Length of scale bar 1 mm. • B – *Antropora?* sp., general view showing rhomboidal autozoecia with triangular opesia and small, circular adventitious avicularia. Length of scale bar 100 µm. • C, D – *Reptadeonella* cf. *violacea* (Johnston, 1847); C – detail showing shape of autozoecia and drop-like avicularia; D – interior view of the autozoecia showing marginal areolar pores and large sinus on primary aperture. Length of scale bar 100 µm.

Superfamily Lepralielloidea Vigneaux, 1949  
Family Escharellidae Levinsen, 1909

**Genus *Escharella* Gray 1847**

***Escharella* cf. *tenera* (Reuss, 1874)**

Figure 5A

cf. v.\* 1874 *Lepralia tenera* m.; Reuss, p. 167, pl. 2, fig. 4.  
cf. v. 2010b *Escharella tenera* (Reuss, 1874). – Zągoršek, p. 147, pl. 89, figs 1–4 (cum syn.).

*Material.* – Two small encrusting colonies.

*Description.* – The colonies are encrusting, radiating from a point at or near the aperture of the ancestrula of the colony. Autozoecia are oval to hexagonal with a smooth, slightly convex, frontal wall and large marginal areole. Lateral walls slightly raised. The aperture is oval with a median denticle. Avicularia unknown. Ovicell not observed.

*Remarks.* – The studied specimens more closely resemble *Escharella tenera* (Reuss, 1874) than *Escharella serrulata* (Reuss, 1847) as described by Berning (2006). *E. serrulata* has less regularly shaped autozoecia and more pronoun-

ced lateral walls. Because no ovicells were observed in the studied material, the exact determination remains uncertain. *E. tenera* has globular ovicells separated by smaller areolar pores, while *E. serrulata* has more deeply immersed ovicells separated by areolar pores of the same size as the autozoecial areolae.

Family Umbonulidae Canu, 1904

**Genus *Umbonula* Hincks, 1847**

***Umbonula granulata* Zągoršek, 2010**

Figure 5B, C

v.\* 2010b *Umbonula granulata* sp. n.; Zągoršek, p. 148, pl. 95, figs 1–6.

*Material.* – Three fragments of encrusting colonies.

*Remarks.* – The studied material is identical with the species recently described from Moravia (Zągoršek 2010b). *Umbonula spinosa* (Procházka, 1893) is similar but has only one tubercle (referred to as a short spine by Procházka 1893).

Family Romancheinidae Jullien, 1888

### Genus *Hippopleurifera* Canu & Bassler, 1925

#### *Hippopleurifera semicristata* (Reuss, 1847)

Figure 5D

v.\* 1847 *Cellepora semicristata* m.; Reuss, p. 82, pl. 10, fig. 3.

2006 *Hippopleurifera semicristata* (Reuss, 1848). – Berning, p. 75, figs 84, 85 (cum syn.).

v. 2010b *Hippopleurifera semicristata* (Reuss, 1847). – Zágoršek, p. 149, pl. 97, figs 1–7 (cum syn.).

**Material.** – Only one fragment has been identified among the studied samples.

**Remarks.** – The fragment is identical with the Moravian material (Zágoršek 2010b) and also with the specimens described by Berning (2006), which include detailed descriptions. The pivotal bar in the avicularium seems to be incomplete considering the large number of specimens of this species observed to date.

### Genus *Phoceana* Jullien, 1903

#### *Phoceana? tubulifera* (Reuss, 1847)

Figure 5E, F

v.á 1847 *Eschara tubulifera* m.; Reuss, p. 67, pl. 8, fig. 19.

v. 2010b *Phoceana tubulifera* (Reuss, 1847). – Zágoršek, p. 155, pl. 114, figs 1–5 (cum syn.).

**Material.** – More than 10 colonies, none with ovicells.

**Description.** – The colonies are large, erect, columnar with circular to oval cross sections and a median lamella. Autozooecia arranged in 6 to 10 longitudinal rows with perforated frontal walls. Nonporous area of the frontal wall is very small, restricted to the proximal margin of the aperture. Peristome short, aperture circular with median ridges forming a halfpipe along the proximal edge of the aperture. No avicularia, no ovicells known. Numerous basal pore chambers present; the interior frontal wall evenly pierced by tiny pseudopores. Nonporous area below the aperture very restricted.

**Remarks.** – The species was placed in *Phoceana* because of its great similarity in autozooecial exterior features, mainly in the presence of a nonporous area proximal to the orifice and a median narrow ridge inside the aperture (the specimens illustrated by Hayward & McKinney 2002 especially show great similarity).

However, the type species of *Phoceana* Jullien, 1903 (*P. columnaris*) has an imperforate frontal shield as stated by Harmer in his personal notes. The type material should be restudied for proof of the status of the genus.

However, material from Korytnica also allows study of the interior features of the frontal wall which is not possible in the Moravian material. As shown in Fig. 5F, the frontal pores are very small, the nonporous area is very restricted and the primary orifices have a wide pseudolyrula (according to Canu & Bassler 1920).

A similar genus is *Dengordonia* Soule, Soule & Chaney, 1995, especially in its external features such as the narrow median channel inside the aperture, and the strongly perforated frontal wall. No interior features of the frontal wall are provided, so its similarity with *Phoceana? tubulifera* cannot be fully assessed.

The studied specimens are identical with the Moravian material (Zágoršek 2010b), as well as with the Reuss types. However, the interior features of the frontal walls cannot be proven in the type, and the preservation of Moravian material does not allow study of the interior of the frontal wall.

Infraorder Lepraliomorpha Gordon, 1989

Superfamily Smittinoidea Levinsen, 1909

Family Gigantoporidae Bassler, 1935

### Genus *Cosciniopsis* Canu & Bassler, 1927

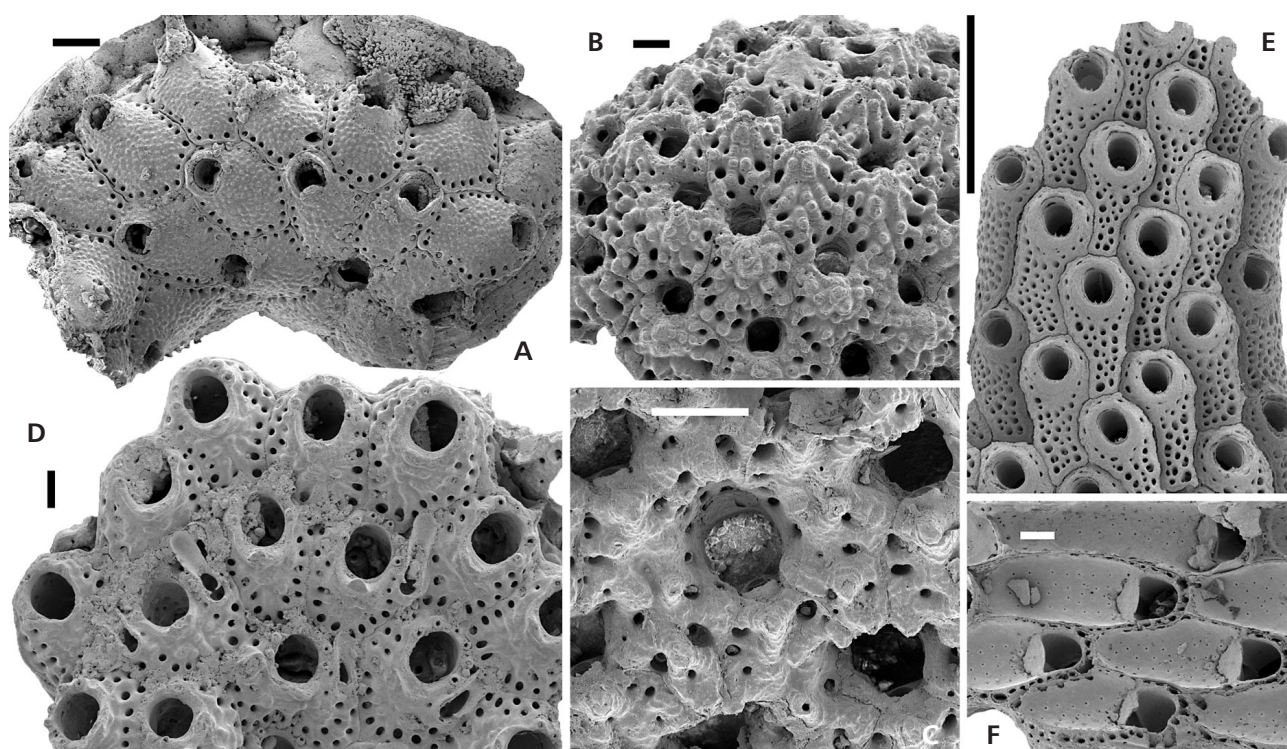
#### *Cosciniopsis* sp.

Figure 6A, B

**Material.** – Only one well preserved colony.

**Description.** – The colony is encrusting. Autozooecia oval, irregularly polygonal, with convex frontal wall, strongly perforated by many pores. Orifice with wide distal rim and characteristically broad proximal part. Lateral denticles are prominent. Peristomes short and wide. No oral spine. A single suboral avicularium at the proximolateral corner of the peristome, rostrum curved along the peristomial rim, directed proximomedially, with a complete pivotal bar. Ovicell recumbent on distal autozooecium, with a strongly porous frontal surface forming the autozooecial frontal shield.

**Remarks.** – The specimen somewhat resembles *Cosciniopsis lonchaea* (Busk, 1884) as described by Tilbrook (2006) in general habit, shape of the orifice and presence of avicularia. The main differences include the size of the pores (the studied specimen has much larger pores on the frontal wall) and the position of the avicularia (the studied specimen has avicularia more closely attached to the



**Figure 5.** A – *Escharella* cf. *tenera* (Reuss, 1874), general view showing chaotically arranged autozooezia with smooth frontal wall and marginal areole. Length of scale bar 100 µm. • B, C – *Umbonula granulata* Zągoršek, 2010b; B – detail showing chaotically arranged small tubercles on frontal wall and suboral avicularium deeply immersed in the aperture; C – detail of oral avicularia and granular frontal wall. Length of scale bar 100 µm. • D – *Hippopleurifera semicristata* (Reuss, 1847), general view showing regularly arranged autozooezia with two or more rows of areolar pores and large avicularia with long rostrum. Length of scale bar 100 µm. • E, F – *Phoceana? tubulifera* (Reuss, 1847); E – general view showing columnar colony and autozooezia arranged in longitudinal rows with perforated frontal wall. Length of scale bar 1 mm; F – detail of interior of autozooezia showing small marginal areolar pores, tiny central pseudopores and primary apertures with shallow median denticle. Length of scale bar 100 µm.

orifice). More specimens are needed for a detailed taxonomic study.

Superfamily Celleporoidea Johnston, 1838  
Family Hippopodinidae Levinsen, 1909

### Genus *Saevitella* Bobies, 1956

#### *Saevitella inermis* Bobies, 1956

Figure 6C, D

v.\* 1956 *Saevitella inermis*.; Bobies, p. 251, pl. 8, figs 21, 22.

v. 2010b *Saevitella inermis* Bobies, 1956. – Zągoršek, p. 162, pl. 129, figs 1, 2 (cum syn.).

**Material.** – Two colonies, both with well-developed ovicells.

**Remarks.** – These excellently preserved specimens slightly differ from the type in having a more regular growth form and more rectangular aperture. Other features are identical with the type as well as with Moravian material (Zągoršek 2010b).

Family Phidoloporidae Gabb & Horn, 1862

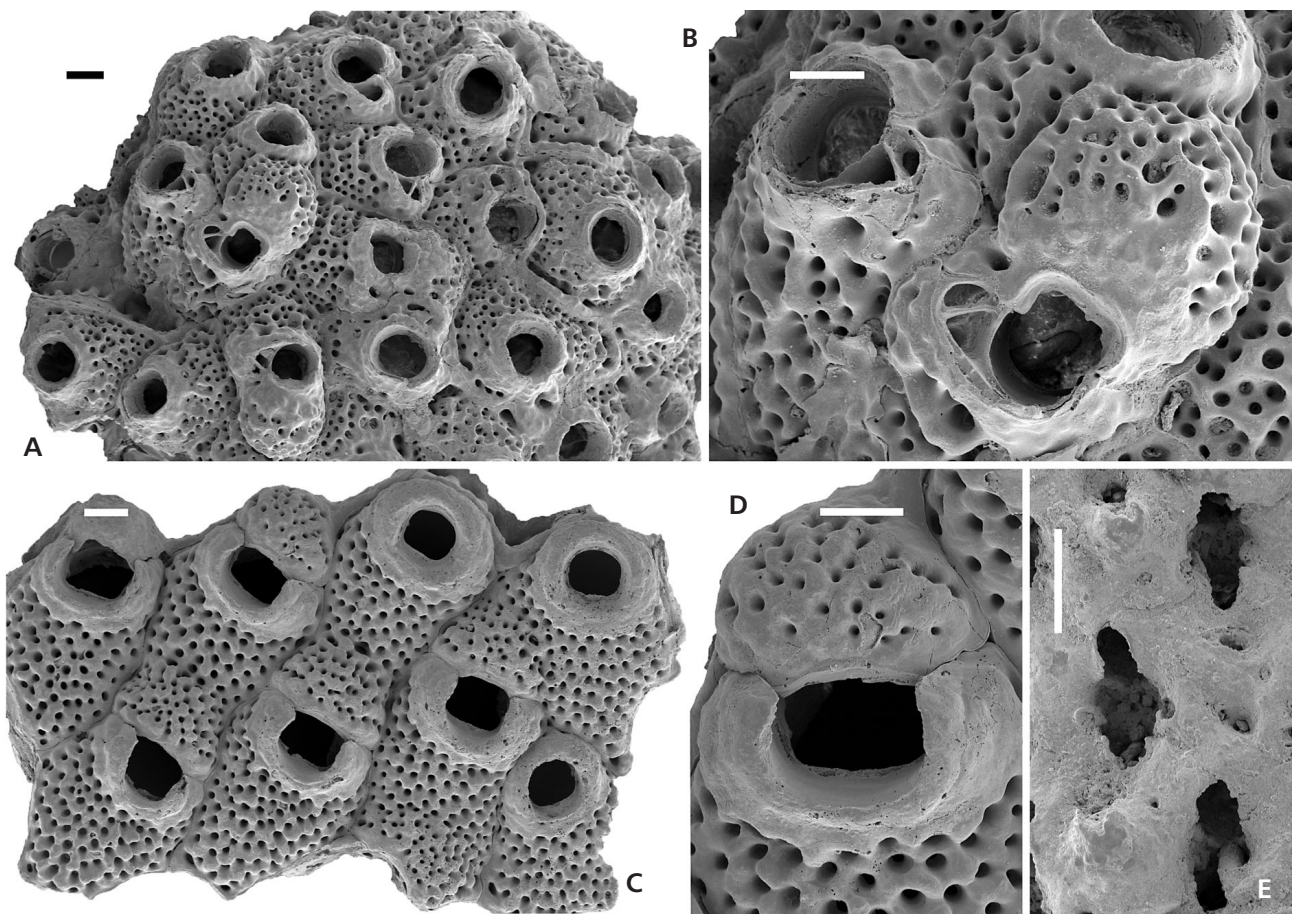
### Genus *Stephanollona* Duvergier, 1920

**Description.** – The colony is encrusting. Frontal wall with marginal areolar pores only. Primary orifice with sinus and a denticulate distal rim, oral spines may be present. Avicularia adventitious, dimorphic, situated laterally from the aperture with a large palate. Sometimes paired. Ovicell slightly immersed or recumbent, with imperforate frontal wall.

#### *Stephanollona korytnicensis* sp. nov.

Figure 7A–E

**Diagnosis.** – Colony encrusting, autozooezia with marginal pores only and large, cleithridiate aperture. Primary orifice with wide sinus, prominent condyles and serrated distal margin. Oral spines very large. Adventitious avicularia large, spatulate with pivotal bar and large rostrum, suboral avicularia small, rare. Ovicell globular with nonporous frontal wall.



**Figure 6.** A, B – *Cosciniopsis* sp.; A – general view showing chaotically arranged autozooecia in encrusting colony; B – detail showing ovicelled autozooecium with small suboral avicularium. Length of scale bar 100  $\mu$ m. • C, D – *Saevitella inermis* Bobies, 1956; C – general view showing autozooecia arranged in longitudinal rows, NM PM2 – P01934; D – detail of ovicelled autozooecium. Length of scale bar 100  $\mu$ m. • E – *Reteporella kralicensis* Zágorsšek, Holcová & Třasoň, 2008, detail of immersed autozooecia with ovicell showing wide frontal fissure. Length of scale bar 100  $\mu$ m.

*Holotype.* – The specimen depicted in Fig. 7A, from Korytnica, deposited in the National Museum, Prague, under number PM2 – P 01938.

*Paratypes.* – Five specimens from Korytnica, deposited in the National Museum, Prague, under numbers PM2 – P 01939 to PM2 – P 01943.

*Derivatio nominis.* – After its type location, Korytnica.

*Locus typicus.* – Korytnica, Korytnica Clays.

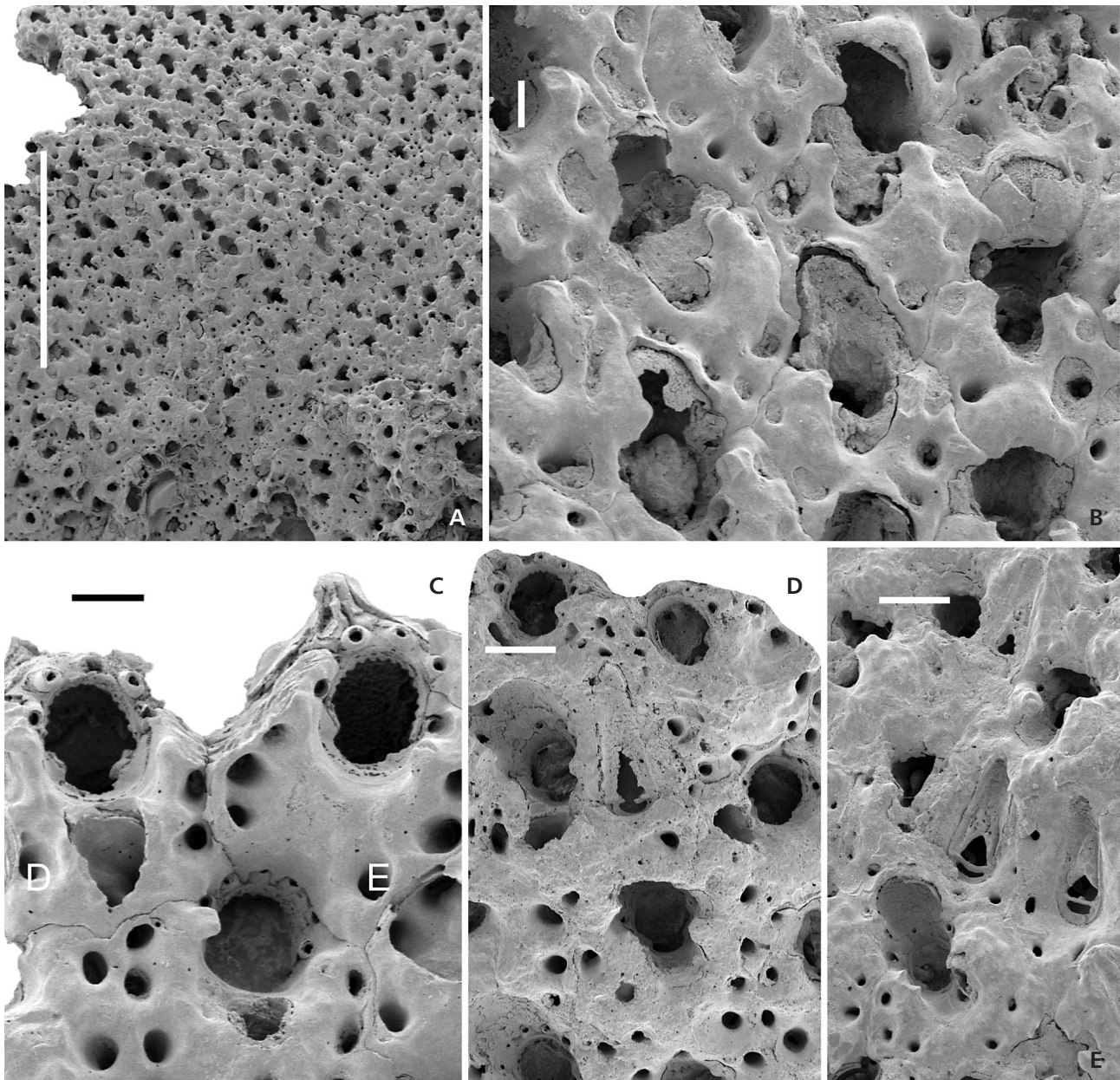
*Stratum typicum.* – Langhian–Lower Badenian.

*Dimensions.* – (in  $\mu$ m;  $x$  = average) – 20 measurements of each character

length of autozooecia: 385–490,  $x$  = 413;  
width of autozooecia: 236–335,  $x$  = 268;  
length of autozooecial orifice: 104–135,  $x$  = 128;

width of autozooecial orifice: 98–121,  $x$  = 105;  
length of ovicell: 125–185,  $x$  = 151;  
width of ovicell: 163–203,  $x$  = 178;  
length of oral avicularium: 56–78,  $x$  = 65;  
width of oral avicularium: 30–43,  $x$  = 36;  
length of adventitious avicularium: 312–345,  $x$  = 335;  
width of adventitious avicularium: 116–138,  $x$  = 127.

*Description.* – Colonies encrusting with autozooecia growing in more or less parallel rows. Autozooecia oval to irregular in shape with very pronounced, large marginal pores. The number of pores varies from 4 to 7. Frontal shield convex, slightly undulose, nonporous. Orifice cleithriate, with almost circular, serrated distal margin and oval proximal margin. Condyles prominent. Oral spines prominent, usually five around the distal margin of the aperture. Avicularia adventitious, spatulate with a large rostrum usually tapering distally. Pivotal bar complete, with a median columella. Suboral avicularia rarely observed,



**Figure 7.** *Stephanollona korytnicensis* sp. nov. • A – general view of the holotype, showing arrangement of autozoecia. Length of scale bar 1 mm. • B – detail of ovicelled autozoecia with highly developed secondary calcification showing partly damaged frontal wall of ovicell and deeply immersed apertures. Length of scale bar 100 µm. • C – detail of autozoecia with less developed secondary calcification showing wide sinus, serrated distal margin and spines around the aperture. Length of scale bar 100 µm. • D – detail showing more calcified colony with well-developed adventitious avicularium squeezed between autozoecia. Length of scale bar 100 µm. • E – detail of two large avicularia, close to each other with complete pivotal bar carrying median columella. Length of scale bar 100 µm.

small, drop-like with pivotal bar hidden in secondary calcification. Ovicell globular, with imperforate frontal wall deeply immersed by secondary calcification in distal autozoecium. Ectooecium partly calcified, endooecium partly exposed when secondary calcification is not entire or eroded, surface granular without ribs. Secondary calcification very commonly developed in fertile and ontogenetically older colony regions.

*Comparison.* – The most similar species is *Stephanollona contracta* (Waters, 1899) known from the Atlantic (Souto *et al.* 2010). The main differences are the size, shape and position of the avicularia (*S. contracta* has suboral avicularia with a rounded rostrum) and size of the ovicell (*S. contracta* has much smaller ovicells).

The species is also similar to *Lepralia pauper* Reuss, 1874, which was reassigned to *Hippoporella* by David

(1949) but also belongs to the genus *Stephanollona* (Zágoršek, 2010b). The main differences are the deeply immersed ovicells [in *S. pauper* the ovicells are prominent and globular, which may however be due to the loss (dissolution) of the aragonitic secondary calcification as in *Plesioleidochasma mediterraneum* (Pizzaferrri & Berning, 2007)], serrated distal margin of the primary orifice, and highly developed secondary calcification in *S. korytnicensis* sp. nov.

*Schedocleidochasma incisa* (Reuss, 1874) is similar to *Stephanollona korytnicensis* sp. nov. in having a cleithridiate aperture and small suboral avicularia, but differs in the absence of oral spines, serrated distal margin of the primary orifice, as well as in the presence of prominent globular ovicells with two short lateral fissures.

**Remarks.** – In the strongly calcified parts of colonies, avicularia may resemble vicarious types (see Fig. 7E) when situated close to each other, while in less calcified parts of colonies they resemble adventitious avicularia (Fig. 7D). No avicularia have been observed on parts of the colony without secondary calcification, so the true nature of the avicularia remains uncertain. Vicarious avicularia are however not known in any of the Recent species (Bock 2011), so it is unlikely, that they would be present in *Stephanollona korytnicensis* sp. nov.

We listed the proposed new species in the genus *Stephanollona* due to the presence of a cleithridiate orifice, slightly serrated distal margin of the primary orifice (Fig. 7C), large oral spines and spatulate adventitious avicularia (Fig. 7D, E). All these features characterize the genus *Stephanollona*, as revised by Gordon (1994).

***Reteporella kralicensis* Zágoršek,**

**Holcová & Třasoň, 2008**

Figure 6E

v.\* 2008 *Reteporella kralicensis* sp. n.; Zágoršek *et al.*, p. 843, fig. 7.

**Material.** – Five fragments, three with preserved anastomosing branches.

**Remarks.** – Even though the preservation of the material is not excellent, the characteristic separate polymorphs with large avicularium and an open, wide frontal fissure on the ovicell are present in the studied material. The material can therefore be considered identical with the Moravian specimens (Zágoršek 2010b).

**Discussion of the Korytnica bryozoans**

The bryozoans in the Korytnica Basin have always been recorded as being very uncommon, or extremely rare, compo-

nents of an otherwise very rich organic assemblage (see Bařuk & Radwański 1977a, p. 97; Vávra 1984, Mafecki 1985). The free-living cheilostome (‘lunulitiform’ or ‘cupuladriid’) bryozoans are exceptions, having been relatively common and recorded from here earlier than other forms (Cook 1965, p. 199). They have been subjected to comprehensive studies, both morphological and taphonomic, by Bařuk & Radwański (1977b, 1984a, b). The three species present (see Bařuk & Radwański 1984a, b; Reguent & Maluquer 1992; Reguant 1993; Dulai 1995; O’Dea *et al.* 2008) are, in diminishing order of frequency: *Cupuladria “vindobonensis”* (Bařuk & Radwański, 1984), *Reussirella haidingeri* (Reuss, 1847), *Lunulites androsaces* Manzoni, 1869.

All are represented both by large-sized (see Bařuk & Radwański 1977b, p. 147), sexually reproduced dome-shaped colonies, that are mostly preserved as fragments, and by small-sized, asexually grown regenerated colonies, always flat and unbroken. Of special interest are the latter which may be extremely rare in the geological record (see Boucot 1990, pp. 174–176; O’Dea *et al.* 2008). They were obtained exclusively by sifting the passive fillings of larger gastropod shells, such as *Clavatula* (see Bařuk & Radwański 1977a, p. 104; 1977b, p. 146), serving evidently either as preservation traps, or as nurseries for the specimens regenerated from fragments of damaged original colonies. The most impressive are clonal colonies of *Cupuladria “vindobonensis”* (see Cook & Chimonides 1994 concerning the taxonomic problem related to this taxon), which all attain a similar, stunted size (see Bařuk & Radwański 1984b, pl. 2, figs 1–12, and pl. 3, figs 1–12). Some grew from a fragment composed merely of one or two zooids which could have survived a predatory attack upon the parental colony (see Bařuk & Radwański 1984b, figs 1–3 in pls 2, 3; O’Dea *et al.* 2008, p. 852 and fig. 5/C). In all clonal specimens, a general rule is apparent: larger fragments regenerate a thinner rim of autozoecia to acquire their final size.

In the Korytnica Basin, all colonies that reproduced by asexual (clone) propagation are interpreted as being adults which grew to a similar, genetically controlled stunted size. Evidently, they are not juveniles, the term vaguely used by Mafecki (1985, pl. 3, figs 2a, 2b) for three equal-sized specimens which in reality represented *Reussirella haidingeri*.

The endolithic ctenostomes were also comprehensively studied previously. A special study was made (Bařuk & Radwański 1979b) of the three genera (*Spathipora*, *Terebripora* and *Penetrantia*) boring adapertural parts of thick-walled gastropod shells domiciled by the hermit crabs with which these bryozoans were probably commensal. Their unique preservation provides important information not only in respect to the taphonomic analysis of Korytnica fossils, but also in the recognition of their biological relationships (see Boucot 1990, pp. 355, 356 and figs 289, 290).

## Paleoecology

The remarkable rarity of bryozoans in the Middle Miocene (Badenian) of the Korytnica Basin is difficult to explain. As shown by previous research dealing with the Bryozoan Event (Zągoršek *et al.* 2008; Holcová & Zągoršek 2008; Zągoršek 2010a, b), bryozoans dominate in subtropical-to-temperate shallow waters of normal salinity, high oxygen content, and very good trophic conditions (Hoffman 1977); it was also stated that such conditions associated with the 'Bryozoan Event' were detrimental for the development of corals and red algae. However, environmental conditions in the Korytnica Basin were the same as those described above with regard to the temperature (may have been even higher), oxygen supply, and nutrition (Bałuk & Radwański 1977a, Hoffman 1977), yet bryozoans were very subordinate, and the not uncommon corals and red algae were prolific.

To recapitulate, the Korytnica Basin in which the studied bryozoans lived is filled by a shallowing-up sedimentary sequence composed primarily of clays, interfingering locally with oyster shellbeds. The Korytnica Clays accumulated over a terrestrial valley flooded by the Middle Miocene (Badenian) transgression, and thus constituted a coastal marine bay. The oyster shellbeds developed exclusively along the coast, as seen in an inundated hill which extends as Mt. Lysa in the present-day topography (see Fig. 2). The rocky shorezone, sculptured by diverse rock-borers (sponges, polychaetes, acrothoracican cirripedes, bivalves) and greatly exposed in the present-day topography (see Radwański 1969, 1970) clearly indicates that the depth of the Korytnica Basin was not greater than the depth of the flooded valley. The successive accumulation of clay involved a gradual decrease in depths (see Fig. 2, stages A–C), ranging from 40–60 meters to almost zero for the top parts of the Korytnica Clays (Radwański 1969, pp. 103 and 142; Bałuk & Radwański 1977a).

When the depth had decreased to the lower limit of the phytal/photoc zone, seagrass bloomed profusely and their peculiar inhabitants appeared. The seagrass beds spread more or less patchily all over the clay bottom, having been locally substituted for by kelp/seaweed *Caulerpa* on the elevated shore (Bałuk & Radwański 1977a, fig. 6; Radwańska 1992, p. 314; see also stages B, C in Fig. 2 herein).

Of the bryozoans studied, the seagrass vegetation is the best evidenced *Schizoporella geminipora*, the colonies of which adjusted themselves to the plant fronds, as first recognized by Vávra (1984, p. 230), and is also consistent with presence of a species of the genus *Reteporella*.

The *Buffonellaria-Rhynchozoon* assemblage has been identified as characteristic for a seagrass association in Moravia (Holcová & Zągoršek 2008). This cluster was not identified in the Korytnica Clays. On the other hand, *Stephanollona* produced colonies similar to *Buffonellaria*,

so may have occupied the same niches and may be representative of the same cluster.

It is less clear on which substrates the rest of the sessile bryozoans may have grown. It is intriguing that on skeletal invertebrates, which quite often bear diverse epibionts (see Bałuk & Radwański 1977a; mostly polychaetes – Radwańska 1994), no bryozoans have been found in the Korytnica Clays. This is in contrast to the rocky shore facies, where bryozoans densely encrust diverse objects, the cliff boulders for instance (locality Skotniki, outside the Korytnica Basin, see *Sk* in Fig. 1B). On the latter, there were 51 species noted by Malecki (1966), mostly cheilostomes, occupying cryptic habitats inside empty borings of rock-boring bivalves (see Radwański 1969, pp. 43, 44 and pl. 9).

In addition to the very specific conditions prevailing in the Korytnica Basin, as suggested above, a shift of bathymetric conditions since the Miocene should also be taken into account. This was postulated by Hoffman (1979), with respect to cupuladriid bryozoans and discussed by Radwańska (1992, p. 314) in connection with certain fish. The present-day free-living colonies (cupuladriids and *Lunulites*) prefer a stable sea floor and very low energy water (McKinney & Jackson 1989, Hageman *et al.* 1997). We therefore suggest a quieter environment, at shallow depths, with a firm bottom of yellow clay and very clear water (of low suspension and nutrient content).

The most probable scenario for the Korytnica Basin in mid-Miocene time is that it was a very shallow marine bay, protected by rocky thresholds from the open sea and its more vigorous dynamics, and where restricted conditions therefore applied. These are inferred to have been shallow, calm water, potentially over-warmed by the sun, inducing subtropical/tropical rather than subtropical-to-temperate conditions, as revealed by the sessile inhabitants (see Bałuk & Radwański 1977a), and some fish which migrated for spawning, or prowled for prey (see Radwańska 1992). These conditions are physically reminiscent of calm lagoons in modern coral-reef atolls (!), regardless that the Korytnica Basin was in the northernmost area within the whole Paratethys (see Fig. 1A).

It is noteworthy that under such extreme conditions in the topmost part of the Korytnica Clays, where fluctuations in salinity could potentially have been excessive (higher due to evaporation, lower due to rainfall or brackish runoff), both the free-living cheilostomes and the colonial corals *Tarbellastraea* were most successful. All clonal colonies of cupuladriid bryozoans, preserved in their gastropod shell traps, or nurseries, come from this interval (see Bałuk & Radwański 1977b, p. 145 in explanation to fig. 1). The same interval has also yielded the creusioid cirripede, *Creusia santacruzensis*, commensally inhabiting *Tarbellastraea*, and some other invertebrates, such as the bivalved gastropod *Berthelinia*, and the amphineuran *Cryptoplax*,

all making up a quite unique assemblage for the Paratethys (Bałuk & Radwański 1977a, pl. 9).

Cupuladriids also rarely occur in the sections Oslavany, Vranová Lhota, Drnovice, Vranovice, Rousínov-pumpa in the Moravian part of the Carpathian Foredeep and in the section Mikulov in the Moravian part of the Vienna Basin (Zágoršek 2010a). All of these sections are characterized by a low diversity of Bryozoa, but the presence of molluscs and other faunal elements indicative of very shallow and quiet water, so the palaeoenvironment appears to have been similar to that interpreted for the Korytnica Basin. The quantitative differences between the Moravian sections and Korytnica (Moravian cupuladriids are very rare) may be caused by the relatively higher water energy indicated by the presence of red algae in all Moravian sections.

Cupuladriids are very common in the Miocene sediments in the Başıyayla section (Mut Basin) in southern Turkey, which has been interpreted (Elsa Gliozzi, pers. comm.) to represent a deeper environment (about 100 m). A speculative interpretation is that the much higher water temperature than in the Korytnica Basin (Başıyayla was located in the tropical belt) allowed cupuladriids to live there in an environment deeper than the northern part of the Paratethys.

In summary, the Korytnica Basin had the shallowest conditions of all Central Paratethyan basins to be colonized by an extremely diverse biota. This *per se ipse*, plus other environmental conditions suggested above, are interpreted as unfavourable for most of the bryozoans, possibly excepting free-living cheilostomes and endolithic ctenostomes. The inferred unfavourable environmental conditions may have been responsible for suppressing the mid-Miocene Bryozoan Event in the Korytnica Basin.

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