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# CRETACEOUS BRYOZOA FROM SCHARRERGRABEN (SANTONIAN, GOSAU GROUP, EASTERN ALPS)

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**Abstract:** The bryozoan fauna of the famous coral-locality Scharrergraben near Piesting, Lower Austria consists of 18 taxa, 13 of which encrust corals or more rarely rudists. This fauna is one of the richest bryozoan faunas described from the Late Santonian of Europe, a time slice in which few bryozoan faunas have been studied. Thus the fauna of Scharrergraben is an important piece in the puzzle of Santonian bryozoan biogeography. The faunal composition indicates a shallow marine, relatively strongly agitated habitat with a moderate sedimentation rate in a tropical setting.

**Key words:** Santonian, Austria, Northern Calcareous Alps, Gosau Group, Bryozoa, taxonomy, paleoecology.

## Introduction

Scharrergraben near Piesting, Lower Austria is a famous and important locality within the Gosau Group. Fossils from this outcrop have been studied for more than 150 years and various taxonomic groups have been reported. The coral fauna of Scharrergraben is especially abundant and diverse. First noted by Reuss (1854), the fauna includes 60 coral taxa (Beauvais 1982), placing it among the richest in the Eastern Alps. Apart from corals, bivalves (Zittel 1865–66; Stur 1877; Bittner 1882), gastropods (Stur 1877; Bittner 1882), cephalopods (Brinkmann 1935; Summesberger 1997) and a single bryozoan species (Stur 1877) have been reported from this outcrop.

Bryozoans are very rare and usually poorly preserved in the Upper Cretaceous sediments of Austria. Only two papers dealing with bryozoans from these strata have been published up to now: one (Reuss 1854) concerns the Santonian bryozoan fauna from the locality Neffgraben near Gosau, Upper Austria; the other considers a small fauna from the Santonian strata of Kössen, Tyrol (Voigt 1928). Nearly all taxa known from these two outcrops are encrusting species attached to corals or rudists. Since bryozoans are generally rather rare in the Santonian strata of southern Europe, where very few localities with biogeographically important bryozoan faunas exist (Voigt 1979, 1983), the bryozoan fauna recovered from the locality Scharrergraben adds an important piece to the puzzle of Tethyan bryozoans.

## Study area and geological setting

The Gosau Group, which comprises Upper Cretaceous to Paleogene sediments, lies unconformably on folded and faulted rocks of Permian to Early Cretaceous age (Wagreich & Faupl 1994; Sanders et al. 1997; Faupl & Wagreich 2000). Whereas the Late Cretaceous transgression started during the Late Turonian in the western part of the Northern Calcareous Alps (NCA) (e.g. in the type area of the Gosau Group; Summesberger & Kennedy 1996), it began earlier in the south-east of the NCA (Wagreich & Marschalko 1995).

In the Grünbach–Neue Welt–Piesting area, the sediments of the Gosau Group form a continuous outcrop belt in the Grünbach Syncline (Plöchinger 1961, 1967). These sediments were the subject of geological and paleontological studies in the first part of the 19th century and are well known for their Upper Cretaceous fossils (Zekeli 1852; Zittel 1865–66). These studies profited from exploitation of coal seams within the Grünbach Formation (Čžjžek 1851; Summesberger 1997), during which also the only Austrian reptile fauna of Late Cretaceous age was discovered (Bunzel 1871; Seeley 1881). Al-

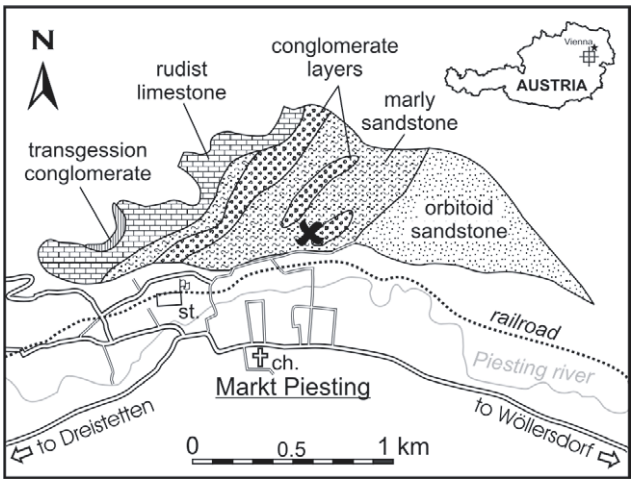


**Fig. 1.** Distribution of the Cretaceous sediments north of Piesting. The position of the studied section is indicated by an **X** (based on the geological map of Austria, Sheet 76, Brix & Plöchinger 1982). Small inset in upper right corner shows the position of Piesting in Austria (indicated by a star).

though the existence of an overturned syncline had already been recognized by Cžjžek (1851), and several studies on litho- and biostratigraphy of this area have been published recently (Summesberger 1997; Hradecká et al. 1999; Summesberger et al. 2000 and in print), the structural relationship to the Upper Cretaceous sediments in the north-eastern part of this area, around Piesting, is still poorly known. This is caused partly by the lack of outcrops in this area and by Tertiary strike-slip faulting along the E-W trending Piesting valley (Decker & Peresson 1996), which complicates the already complex situation.

The locality Scharrergraben is situated northeast of Piesting in a small valley between the two hills Steinkogel and Kranzkogel. Outcrop conditions are very poor and no section could be taken. However, a schematic cross-section and short profile of the locality can be found in Karrer (1877: 87), Stur (1877: 172), Bittner (1882: 239) and Summesberger (1997: 86–87). Exposed are fossiliferous sandy marls with a rich coral fauna, interbedded between marls and sandstones with conglomerate intercalations. The age of the section is Late Santonian according to Summesberger (1997: 86), who reported *Placenticeras polyopsis* (Dujardin) from beds just below the coral layer. The occurrence of "*Hemitissotia*" *randoi* Gerth in a neighbouring valley indicates Early Santonian for the basal part of the succession of Piesting (Summesberger 1997: 86).

## Material and methods

The specimens were obtained by collecting fragments of corals from weathered material in the outcrop. The corals were cleaned using $H_2O_2$ and ultrasonically. After drying all specimens were carefully scanned for encrusting bryozoans. Additionally, two bulk samples of approximately 5 kg each were taken and washed using $H_2O_2$ to macerate the samples. From the washed material bryozoans (erect and encrusting) were picked using a binocular microscope. Specimens for microphotography were further cleaned using treatments of $H_2O_2$, ultrasonic and Quaternary "O" (see Zingula 1968). To obtain further material unweathered sediment was dissolved in concentrated acetic acid (for a detailed description of the method see Zágoršek & Vávra 2000). However, the residue did not yield any recognizable bryozoans.

All photos were taken with a Jeol type JSM-6400 SEM at the Institute of Palaeontology, University of Vienna. All material used in this study is deposited in the collection of the Natural History Museum, Vienna (Department of Geology & Palaeontology). Specimens which could not be determined due to their poor preservation have been deposited under the inventory number NHMW 2002z0119/0067.

## Systematics

The systematics of Cyclostomata have been modified on the basis of Bassler (1953) and Taylor (pers. com. 2001, 2003). The systematics of Cheilostomata are modified according to Gordon (1989, pers. com. 2002) and Zágoršek (in print). All measurements are given in μm in Table 1.

Class **Stenolaemata** Borg, 1926
Order **Cyclostomata** Busk, 1852
Suborder **Tubuliporina** Milne Edwards, 1838
Family **Diastoporidae** Gregory, 1899
Genus *Berenicea* Lamouroux, 1821

*"Berenicea"* sp.
Fig. 2a

?v*1877 *Berenicea radians* nov. sp.; Novák p. 22, Pl. 4, Figs. 15–18

**Material:** 3 specimens from the locality Scharrergraben (NHMW 2002z0119/0007, 0008a, 0009).

**Description:** The colony is encrusting, very thin, uniserial and fan-shaped. The autozooecia are tubular and grow radially from the centre of the colony. They develop a long peristome which protrudes from the colonial margin. The distal fringe of the basal lamina is very narrow. Brood chambers were not observed.

**Remarks and notes:** External features are identical with the specimens described by Novák (1877) as *Berenicea radians*, stored in the National Museum in Prague (Inv. No. ČL 2429), but none of the colonies developed brood-chambers and identification to species level is impossible. As gonozooecia are necessary even for generic identification of bryozoans of this type, the studied specimens can only be referred to the form-genus "*Berenicea*" following the protocol suggested by Taylor & Sequeiros (1982).

**Distribution in time and space:** Early Turonian (?) to Late Santonian. (?) Kamajka (Czech) — Early Turonian. Scharrergraben (Austria) — Late Santonian.

Family **Oncousoeciidae** Canu, 1918
Genus *Proboscina* Audouin, 1826

*"Proboscina" bohemica* Novák, 1877
Fig. 2b

v*1877 *Proboscina bohemica* nov. sp.; Novák p. 25, Pl. 5, Figs. 24, 25

**Material:** 7 specimens from the locality Scharrergraben (NHMW 2002z0119/0055a, 0055b, 0056, 0057a, 0058, 0059a, 0060).

**Description:** The colonies are multiserial encrusting, corresponding to the "runner type". Usually 4–7 parallel longitudinal zooecial rows are developed. The outer shape of the colonies is irregular, with one, rarely two, branches situated on opposite sides of the ancestrula. Young colonies show the so-called "*Stomatopora*" stadium (Hillmer 1971), when the colony is uniserial encrusting. The autozooecia are tubular, relatively short (in comparison with other species of *Proboscina*), with large, circular, terminal apertures. Gonozooecia were not observed.

**Remarks and notes:** In most of the studied specimens only one branch leading away from the ancestrula is developed. However, the type material stored in the National Museum in Prague (Inv. No. ČL 6297) usually developed two branches. Apart from this, all other features are identical. Characteristic features of this species are short autozooecial tubes,

**Table 1**

| Taxa | measured individual | | | Aperture | | Ovicell | | Inv. No. |
|---|---|---|---|---|---|---|---|---|
| | | length | width | length | width | length | width | |
| *Akatopora subwintonensis* (Voigt, 1967) | Autozooecium+ovicell | 383 | 163 | 141 | 99 | 99 | 95 | NHMW 2002z0119/0012b |
| | Autozooecium | 331 | 215 | 183 | 131 | | | NHMW 2002z0119/0012b |
| | Avicularium (adventitious) | 174 | 119 | 87 | 62 | | | NHMW 2002z0119/0012b |
| | Avicularium (vicarious) | 136 | 128 | 59 | 50 | | | NHMW 2002z0119/0012a |
| *Alderina dilatata* (Reuss, 1872) | Autozooecium+ovicell | 527 | 301 | 353 | 217 | 149 | 165 | NHMW 2002z0119/0003 |
| | Autozooecium | 438 | 303 | 357 | 220 | | | NHMW 2002z0119/0003 |
| | Avicularium | 603 | 343 | 452 | 196 | | | NHMW 2002z0119/0003 |
| "*Berenicea*" sp. | Autozooecium | 502 | 306 | 98 | 86 | | | NHMW 2002z0119/0008a |
| | Autozooecium | 437 | 257 | 106 | 78 | | | NHMW 2002z0119/0008a |
| *Biflustra* cf. *teres* (Novák, 1877) | Autozooecium | 580 | 341 | 230 | 157 | | | NHMW 2002z0119/0010 |
| *Disporella* cf. *confluens* (Roemer, 1841) | Autozooecium | 155 | 111 | 53 | 49 | | | NHMW 2002z0119/0022 |
| *Marginaria ostiolata* Reuss, 1846 | Autozooecium+ovicell | 537 | 236 | 203 | 136 | 160 | 140 | NHMW 2002z0119/0024 |
| with vicariuos avicularia | Autozooecium | 455 | 247 | 275 | 159 | | | NHMW 2002z0119/0024 |
| | Avicularium (vicarious) | 301 | 201 | 119 | 49 | | | NHMW 2002z0119/0024 |
| | Avicularium (adventitious) | 173 | 82 | 96 | 36 | | | NHMW 2002z0119/0024 |
| *Marginaria ostiolata* Reuss, 1846 | Autozooecium+ovicell | 392 | 283 | 169 | 124 | 155 | 129 | NHMW 2002z0119/0025 |
| | Autozooecium | 321 | 271 | 177 | 148 | | | NHMW 2002z0119/0025 |
| | Avicularium (adventitious) | 186 | 118 | 97 | 36 | | | NHMW 2002z0119/0025 |
| *Membraniporidra bohemica* (Prantl, 1938) | Autozooecium | 323 | 243 | 211 | 150 | | | NHMW 2002z0119/0035 |
| | Autozooecium | 292 | 238 | 177 | 137 | | | NHMW 2002z0119/0035 |
| *Onychocella cyclostoma* (Goldfuss, 1826) | Autozooecium | 624 | 453 | 293 | 251 | | | NHMW 2002z0119/0036 |
| | Autozooecium | 563 | 448 | 262 | 240 | | | NHMW 2002z0119/0036 |
| | Avicularium | 902 | 425 | 600 | 188 | | | NHMW 2002z0119/0036 |
| *Onychocella depressa* (v. Hagenow, 1851) | Autozooecium | 543 | 441 | 117 | 219 | | | NHMW 2002z0119/0038 |
| | Autozooecium | 494 | 426 | 158 | 185 | | | NHMW 2002z0119/0038 |
| | Avicularium | 707 | 340 | 264 | 211 | | | NHMW 2002z0119/0038 |
| *Onychocella michaudiana* (d'Orbigny,1850) | Autozooecium+ovicell | 337 | 223 | 59 | 109 | 93 | 147 | NHMW 2002z0119/0041a |
| | Autozooecium | 292 | 265 | 76 | 111 | | | NHMW 2002z0119/0041a |
| | Avicularium | 299 | 160 | 39 | 54 | | | NHMW 2002z0119/0041a |
| *Onychocella pseudoirregularis* Voigt,1924 | Autozooecium+ovicell | 381 | 292 | 69 | 121 | 119 | 150 | NHMW 2002z0119/0039b |
| | Autozooecium | 342 | 206 | 60 | 99 | | | NHMW 2002z0119/0039b |
| | Avicularium | 428 | 111 | 75 | 42 | | | NHMW 2002z0119/0039b |
| *Onychocella reussi* Prantl,1938 | Autozooecium+ovicell | 512 | 194 | 100 | 115 | 98 | 134 | NHMW 2002z0119/0041b |
| | Autozooecium | 388 | 233 | 101 | 105 | | | NHMW 2002z0119/0041b |
| | Avicularium | 370 | 122 | 98 | 49 | | | NHMW 2002z0119/0041b |
| *Osculipora truncata* Goldfuss,1826 | Autozooecium | 437 | 108 | 42 | 40 | | | NHMW 2002z0119/0046 |
| | Autozooecium | 661 | 122 | 71 | 62 | | | NHMW 2002z0119/0048 |
| "*Proboscina*" *bohemica* Novák, 1877 | Autozooecium | 235 | 163 | 71 | 66 | | | NHMW 2002z0119/0060 |
| *Reptomultelea* sp. aff. *Elea lamellosa* | Autozooecium | 337 | 285 | 119 | 102 | | | NHMW 2002z0119/0031 |
| (d'Orbigny,1850) | Autozooecium | 341 | 252 | 129 | 106 | | | NHMW 2002z0119/0031 |

the obscured shape of the autozooecia and the irregular shape of the colonial branches.

Pitt & Taylor (1990) argued that *Proboscina* could be used only informally as "*Proboscina*" because of doubt over the identity of the type species (the type material of the type species is unknown).

**Distribution in time and space:** Coniacian to Late Santonian. Velký Újezd by Kolín (Czech) — Coniacian. Scharrergraben (Austria) — Late Santonian.

Family **Eleidae** d'Orbigny, 1852
Genus *Reptomultelea* d'Orbigny, 1853

*Reptomultelea* sp. aff. *Elea lamellosa* (d'Orbigny, 1850)
Fig. 2i–j

? 1850 *Bidiastopora lamellosa* d'Orb., 1847; d'Orbigny p. 266
?v1922 *Meliceritites lamellosa* d'Orbigny; Canu & Bassler p. 85, Pl. 14, Fig. 13
? 1994 *Elea lamellosa* (d'Orbigny 1852), Taylor p. 14, Figs 17–28 (cum. syn)

**Material:** 7 specimens from the locality Scharrergraben (NHMW 2002z0119/0026–0032).

**Description:** The colony is encrusting or unilamellar. The autozooecia have a slightly porous frontal wall and a semilunar to oval aperture usually with a straight proximal margin. The distal fringe of the basal lamina is very narrow, sometimes not preserved. Gonozooecia and avicularia (eleozooecia) were not observed.

**Remarks and notes:** The studied specimens very much resemble *Elea lamellosa* (d'Orbigny) in shape and size of autozooecia and pattern of distribution of pseudopores. *Elea* has, however, erect colonies, the large, globular gonozooecia and *E. lamellosa* has a terminal oeciopore (Canu & Bassler 1922; Taylor 1994). The encrusting grown form of the studied specimens suggests placement in *Reptomultelea* d'Orbigny, 1853 as revised in Taylor (1994). Although we have seven specimens in our collection, none of them show gonozooecia or "avicularia" (eleozooecia) and therefore species determination remains uncertain. The studied specimens represent, with large probability, a new species, but more and better-preserved specimens are needed to establish this.

**Distribution in time and space:** Late Santonian. Scharrergraben (Austria) — Santonian.

Suborder **Cancellata** Gregory, 1899
Family **Cytididae** d'Orbigny, 1854
Genus *Osculipora* d'Orbigny, 1849

*Osculipora truncata* Goldfuss, 1826
Fig. 2d–e

*1826 *Retepora truncata* nobis.; Goldfuss p. 29, Pl. 9, Fig. 14a–d
1922 *Osculipora truncata* Goldfuss; Canu & Bassler p. 57, Pl. 23, Figs. 1–6

**Material:** 9 specimens from the locality Scharrergraben (NHMW 2002z0119/0043–0051).

**Description:** The colony is erect, sometimes dichotomously branching with autozooecial apertures opening on one side only. The autozooecia are tubular with apertures opening in cluster (fascicles). Each cluster comprises 6–10 autozooecial apertures. The clusters are circular to oval, slightly elevated from the frontal surface of the colony. The dorsal side of the colony is slightly ribbed and porous due to the presence of short kenozooecia (so-called nematopores of Canu & Bassler 1922). Gonozooecia have not been observed.

**Remarks and notes:** According to Canu & Bassler (1922), the gonozooecia are globular and developed on the dorsal or the frontal side of the colony, with a non-porous, slightly granular frontal wall. The studied specimens do not have gonozooecia, but in all other features are identical with the type material of *O. truncata.* Therefore we believe that the studied specimens and the type material are conspecific. This species is very common in the Campanian strata of France.

**Distribution in time and space:** Late Santonian to Maastrichtian. Scharrergraben (Austria) — Late Santonian. Many localities in France — Campanian. Maastricht (Netherlands) — Maastrichtian.

Family **Petaloporidae** Gregory, 1899
Genus *Petalopora* Lonsdale, 1850

*Petalopora*? sp.
Fig. 2f

? 1953 *Petalopora* Lonsdale; Bassler p. 63, Fig. 30/1

**Material:** 3 specimens from the locality Scharrergraben (NHMW 2002z0119/0052–0054).

**Description:** The colony is erect, sometimes dichotomously branching with cylindrical branches. The autozooecia are long, tubular and arranged around the colonial stems. Kenozooecia (mesopores) are abundant and arranged in 2–5 longitudinal rows proximally from the autozooecial apertures. Gonozooecia were not observed.

**Remarks and notes:** Species of *Petalopora* typically have a fixed number of rows of kenozooids (Taylor 2002). The studied specimens have, however, different numbers of rows of kenozooecia, and probably represent more than one species. Due to the poor preservation of the studied specimens and the lack of gonozooecia, more precise generic and species determination is not possible.

**Distribution in time and space:** Late Santonian. Scharrergraben (Austria) — Late Santonian.

Genus *Reteporidea* d'Orbigny, 1849

*Reteporidea*? sp.
Fig. 2h

? 1953 *Reteporidea* d'Orbigny; Bassler p. 63, Fig. 30/1

**Material:** 2 specimens from the locality Scharrergraben (NHMW 2002z0119/0061–0062).

**Description:** The colony is erect and branching. Autozooecia are arranged in uniserial fascicles on one side of the colony only. Kenozooecia (mesopores) are very abundant, situated around the entire branch circumference. Gonozooecia were not observed.

**Remarks and notes:** On the basis of the presence of numerous mesopores and the arrangement of the autozooecia in fascicles, these specimens are tentatively referred to *Reteporidea*. Precise determination is impossible due to the very poor preservation.

**Distribution in time and space:** Late Santonian. Scharrergraben (Austria) — Late Santonian.

Suborder **Rectangulata** Waters, 1887
Family **Lichenoporidae** Smitt, 1866
Genus *Disporella* Gray,1848

*Disporella* cf. *confluens* (Roemer, 1841)
Fig. 2g

*1841 *Rosacilla confluens* N; Roemer p. 19
v?1877 *Berenicea confluens* Roemer; Novák p. 22, Pl. 4, Figs. 19–22

**Material:** 2 specimens from the locality Scharrergraben (NHMW 2002z0119/0021, 0022).

**Description:** The colony is encrusting, discoidal with central maculae. The maculae are surrounded by a relatively steeply sloping margin and have non-porous and slightly granular surface, possibly the remnants of gonozooecia. The autozooecia are short with oval to circular apertures without peristomes. The apertures are arranged in uniserial, slightly visible radial ribs. Rarely, an autozooecial aperture may occur also in the central macula. Kenozooecia are slightly smaller than autozooecia. The distal fringe of the basal lamina is very narrow and usually not preserved. Gonozooecia are possibly developed at maculae centres, but no frontal walls are preserved.

**Remarks and notes:** The studied specimens are almost identical with Novák's (1877) specimens stored in the National Museum in Prague except for the less steeply sloping margin of the macular centre. The main characteristic feature of this species is the occurrence of autozooecial apertures inside the maculae centre.

*Disporella* Gray, 1848 has non-stalked colonies, with a non-porous basal part, and autozooecia arranged on the frontal surface in radial fascicles with kenozooecia situated between them (Brood 1972). Due to the presence of gonozooecia in the maculae centre and arrangement of autozooecia in

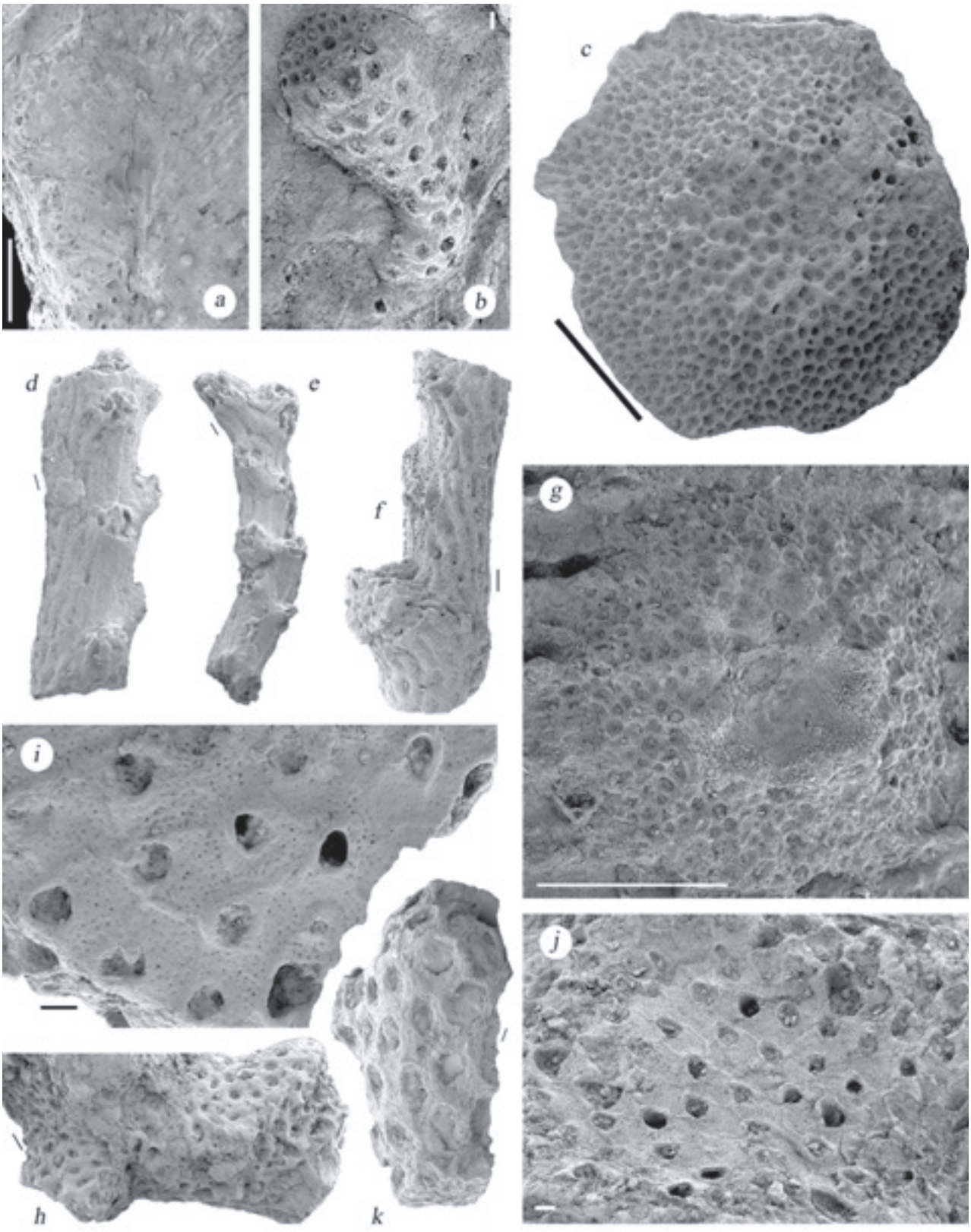


**Fig. 2. a** — "*Berenicea*" sp. (cf. *Berenicea radians* Novák, 1877) (NHMW 2002z0119/0008a). **b** — "*Proboscina" bohemica* Novák, 1877 (NHMW 2002z0119/0055a). **c** — *Disporella* sp. (note porous maculae center) (NHMW 2002z0119/0023). **d** — *Osculipora truncata* Goldfuss, 1826, lateral view (NHMW 2002z0119/0046). **e** — *Osculipora truncata* Goldfuss, 1826, frontal view (NHMW 2002z0119/0048). **f** — *Petalopora* sp. (NHMW 2002z0119/0053). **g** — *Disporella* cf. *confluens* (Roemer, 1841) (note non-porous maculum centre) (NHMW 2002z0119/0021). **h** — *Reteporidea* sp. (NHMW 2002z0119/0062). **i** — *Reptomultelea* sp. aff. *Elea lamellosa* (d'Orbigny, 1850), detail (NHMW 2002z0119/0031). **j** — *Reptomultelea* sp. aff. *Elea lamellosa* (d'Orbigny, 1850), general view (NHMW 2002z0119/0028). **k** — *Biflustra* cf. *teres* (Novák, 1877) (NHMW 2002z0119/0010). All specimens from Scharrergraben, Austria; scale bar equals 100 μm.

radial ribs with development of smaller kenozooecia between them, this species is listed under *Disporella.*

Roemer (1841) described *Berenicea confluens* with gonozooecia, but unfortunately, he did not illustrate them. According to Voigt (pers. com., 1980) the type material is lost. Because Novák's (1877) specimens developed no gonozooecia and the studied specimens have only remnants of the gonozooecia, the correct species determination of the present specimens remains uncertain.

**Distribution in time and space:** Cenomanian to Late Santonian. Kamajka and Zbislav (Czech) — Cenomanian. Scharrergraben (Austria) — Late Santonian.

*Disporella* sp.
Fig. 2c

*1929 *Lichenopora perneri* sp.n.; Prantl p. 250, Pl. 1, Figs. 1–2
?v1938 *Lichenopora perneri* Prantl 1929; Prantl p. 29, (64), Pl. 1, Fig. 20

**Material:** 1 specimen from the locality Scharrergraben (NHMW 2002z0119/0023).

**Description:** The colony is encrusting, discoidal with central, circular, porous maculae. Autozooecia are slightly raised, oval to circular in shape without a peristome. Autozooecia are arranged chaotically and not in radial ribs and have almost the same size as kenozooecia. The kenozooecia are slightly larger in the maculae centre. The distal fringe of the basal lamina is narrow, but always developed. Gonozooecia are unknown.

**Remarks and notes:** The studied specimen is very similar to *Lichenopora perneri* Prantl, 1929 in general shape and development of the colony. We have only one specimen of this species, which developed no gonozooecia. Therefore specific determination is impossible.

According to Gordon & Taylor (1997), *Lichenopora* should be restricted to species characterized by conical/stalked (pedunculate) colonies, with apertures only on the top of the cone. The side of the cone is formed by exterior wall and the surface shows a smooth texture. *Disporella* Gray, 1848, in contrast, has non-stalked colonies, with autozooecia arranged in radial fascicles on the frontal part and kenozooecia situated between the autozooecia (Brood 1972). The specimen from Scharrergraben shows these features and is therefore placed in the genus *Disporella.*

**Distribution in time and space:** Early Turonian to Late Santonian. (?) Předboj (Czech) — Early Turonian. Scharrergraben (Austria) — Late Santonian.

Class **Gymnolaemata** Allman, 1896
Order **Cheilostomata** Busk, 1852
Suborder **Malacostegina** Levinsen, 1902
Superfamily **Membraniporoidea** Busk, 1852
Family **Membraniporidae** Busk, 1852
Genus *Biflustra* d'Orbigny, 1852

*Biflustra* cf. *teres* (Novák, 1877)
Fig. 2k

?v*1877 *Semieschara teres* nov. sp.; Novák p. Pl. 3, Figs. 8–11

**Material:** 1 specimen from the locality Scharrergraben (NHMW 2002z0119/0010).

**Description:** The colony is erect, developing cylindrical branches of almost circular cross-section. Autozooecia are arranged in parallel, longitudinal rows. They are rhomboidal with an elongated opesia and a slightly depressed cryptocyst. Ovicells, avicularia and kenozooecia were not observed.

**Remarks and notes:** The shape and size of autozooecia of the studied specimen are very similar to *Semieschara teres* (Novák, 1877) stored in the National Museum in Prague (Inv. No. ČL 444). The size of the colonies of the type material is, however, much larger and differs, furthermore, in the presence of ovicells distally of the autozooecia. On the basis of the presence of features characteristic for *Biflustra*, (i.e. large opesia with flat cryptocyst and erect growth form of the colony) this species is placed into this genus.

**Distribution in time and space:** (?) Turonian to Late Santonian. (?) Kamajka (Czech) — Early Turonian. Scharrergraben (Austria) — Late Santonian.

Suborder **Flustrina** Smitt, 1868
Superfamily **Calloporoidea** Norman, 1903
Family **Calloporidae** Norman, 1903
Genus *Akatopora* Davis, 1934

*Akatopora subwintonensis* (Voigt, 1967)
Fig. 3a–c

*1967 "*Membranipora*" *subwintonensis* sp.n.; Voigt p. 28, Pl. 4, Figs. 4–6

**Material:** 6 specimens from the locality Scharrergraben (NHMW 2002z0119/0011, 0012a, 0012b, 0013, 0020, 0066).

**Description:** The colony is encrusting. Autozooecia are oval to triangular with distal margin slightly narrower than proximal margin. The opesium is large, almost triangular (narrower distally); the mural rim is narrow, granular or slightly radially ribbed. Two pairs of oral spines are situated on the distalmost margin of mural rim. The distal pair of the oral spines is always smaller than the proximal one. Two types of avicularia occur: large, vicarious rhomboidal avicularia, which are rare and have a narrow, oval opesium; and smaller oval to polygonal avicularia. This second type of the avicularium is interzooecial, situated between 2 or 3 autozooecia and often shows a long process (peristome-like structure). The ovicells are hyperstomial, globular and are deeply immersed inside the secondary calcification of the colony.

**Remarks and notes:** The studied specimens have smaller vicarious avicularia than the specimens described by Voigt (1967). In our material the vicarious avicularia are about half the size of the autozooecia and the opesium is subcircular. Other features, especially type and position of ovicells, are identical with the type material as described by Voigt (1967). The differences observed are therefore considered to represent intraspecific variation.

Based on the presence of interzooecial avicularia and deeply immersed hyperstomial ovicells, this species is listed under the genus *Akatopora* (as revised in Gordon 1986).

**Distribution in time and space:** Late Santonian to Campanian. Scharrergraben (Austria) — Late Santonian. Locality unknown (west Kazakhstan) — Campanian.

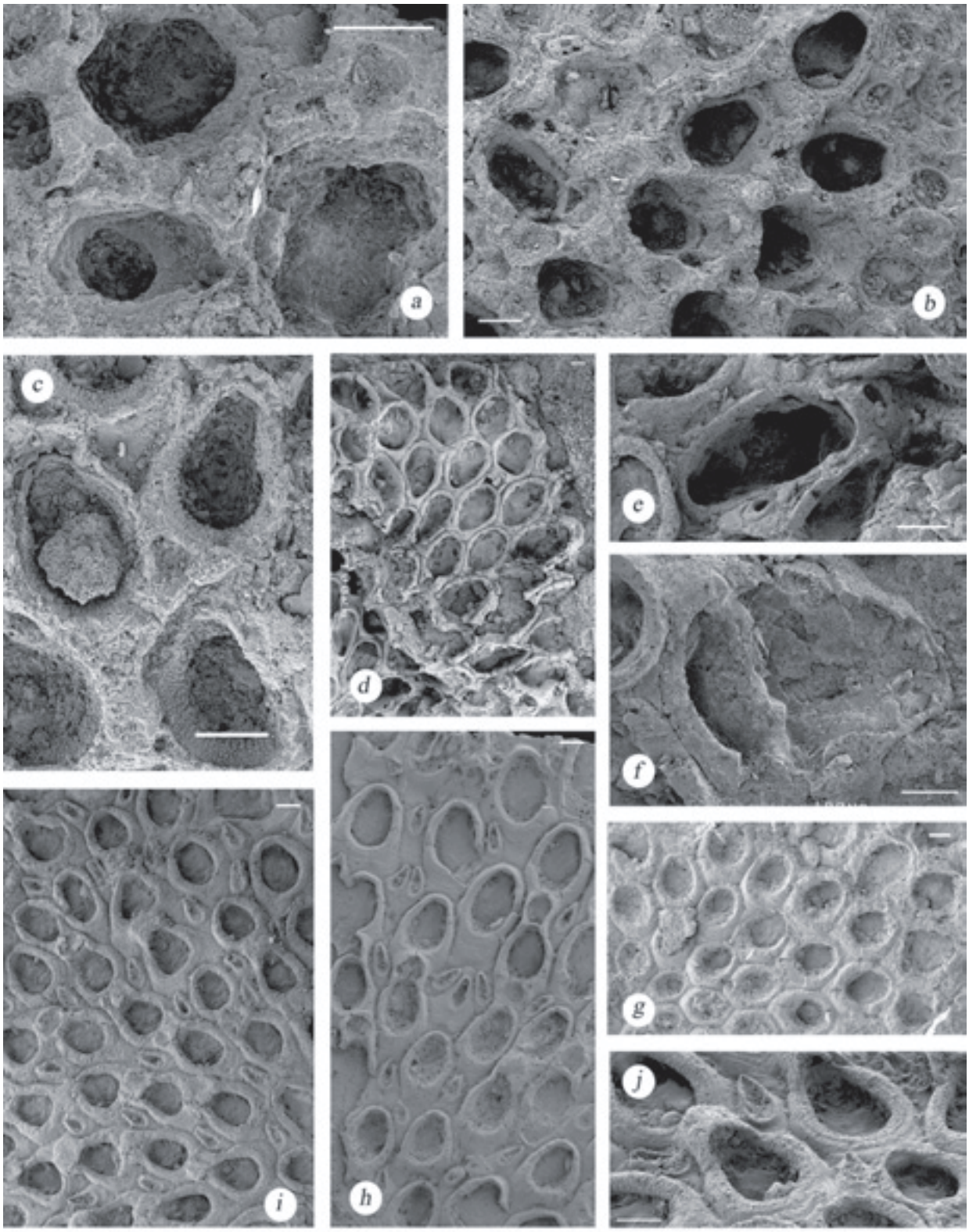


**Fig. 3.** **a** — *Akatopora subwintonensis* (Voigt, 1967), detail of avicularium (NHMW 2002z0119/0013). **b** — *Akatopora subwintonensis* (Voigt, 1967), detail of marginal spines and deeply immersed ovicells (NHMW 2002z0119/0013). **c** — *Akatopora subwintonensis* (Voigt, 1967), detail of autozooecia with two pairs of marginal spines (NHMW 2002z0119/0013). **d** — *Alderina dilatata* (Reuss, 1872), general view (NHMW 2002z0119/0003). **e** — *Alderina dilatata* (Reuss, 1872), detail of kenozooecia and globular, small ovicell (NHMW 2002z0119/0003). **f** — *Alderina dilatata* (Reuss, 1872), detail of avicularium (NHMW 2002z0119/0003). **g** — *Membraniporidra bohemica* (Prantl, 1938) (NHMW 2002z0119/0034). **h** — *Marginaria ostiolata* (note large vicarious avicularium in the center) (NHMW 2002z0119/0024). **i** — *Marginaria ostiolata* Reuss, 1846, general view (NHMW 2002z0119/0025). **j** — *Marginaria ostiolata* Reuss, 1846, detail of avicularia and ovicells (NHMW 2002z0119/0025). All specimens from Scharrergraben, Austria; scale bar equals 100 μm.

Genus *Alderina* Norman, 1903

*Alderina dilatata* (Reuss, 1872)
Fig. 3d–f

*1872 *Membranipora dilatata* n. sp.; Reuss p. 100; Pl. 24, Fig. 2
v1877 *Membranipora perisparsa* nov. spec.; Novák p. 15, Pl. 2, Figs. 6–8
1989 *Alderina dilatata* (Reuss), Voigt p. 19, Pl. 1, Fig. 1-4, Pl. 2, Figs. 3–5

**Material:** 6 specimens from the locality Scharrergraben (NHMW 2002z0119/0001a, 0002–0006).

**Description:** The colony is encrusting. The zooecia are oval with large oval to irregular opesia and without gymnocyst. The mural rim is narrow, rarely with intramural buds, and without any traces of spines. A small tubular kenozooecium is sometimes developed inside the narrow interzooecial space. Avicularia are vicarious, as large as the autozooecia and have a well developed pivotal bar. Ovicell globular, hyperstomial, slightly immersed with a smooth, non-porous frontal wall.

**Remarks and notes:** The ovicells of the studied specimens are identical with those described by Voigt (1989). The avicularia, however, are slightly larger in the present material, probably demonstrating intraspecific variability in this feature. According to Voigt (1989), *Membranipora perisparsa* Novák, 1877 is a junior synonym of *Alderina dilatata* (Reuss, 1872).

**Distribution in time and space:** Early Cenomanian to Late Santonian. Mülheim-Broich (Germany) — Early Cenomanian. St. Calais (France) — Late Cenomanian. Kamajka (Czech) — Early Turonian. Scharrergraben (Austria) — Late Santonian.

Genus *Membraniporidra* Canu & Bassler, 1917

*Membraniporidra bohemica* (Prantl, 1938)
Fig. 3g

v1877 *Membranipora elliptica* Reuss; Novák p. 84, Pl. 2, Figs. 11–14
non1877 *Membranipora elliptica* Reuss; Novák p. 84, Pl. 2, Figs. 15–16
v*1938 *Membranipora bohemica* nov. sp.; Prantl p. 5 (41)
1989 *Membraniporidra bohemica* (Prantl); Voigt p. 25, Pl. 2, Figs. 1–2, Pl. 7, Fig. 7

**Material:** 4 specimens from the locality Scharrergraben (NHMW 2002z0119/0033–0035, 0008b).

**Description:** The colony is encrusting. The autozooecia are oval with very large opesia and short, but well developed, gymnocyst. No cryptocyst is developed. The mural rim is narrow, usually smooth and only rarely with traces of oral spines. Avicularia absent, ovicells not observed.

**Remarks and notes:** Prantl (1938) established the species *M. bohemica* on the basis of the material of Novák (1877) described as *Membranipora elliptica* Reuss (Novák 1877, p. 84, Pl. 2, Figs. 11–12). According to Voigt (1989) specimens of *Membranipora elliptica* Reuss as illustrated by Novák (1877, Pl. 2, Figs. 15–16) do not belong to this species.

The studied specimens are almost identical with the type material stored in the National Museum in Prague (Inv. No. ČL 457). A minor difference is the narrower mural rim.

**Distribution in time and space:** Turonian to Late Santonian. Many localities in Czech — Turonian. Scharrergraben (Austria) — Late Santonian.

Genus *Marginaria* Roemer, 1841

*Marginaria ostiolata* Reuss, 1846
Fig. 3h–j

*1846 *Marginaria ostiolata* Reuss; Reuss p. 69, Pl. 15, Fig. 14
1989 *Marginaria ostiolata* (Reuss); Voigt p. 33, Pl. 5, Figs. 1–5, Pl. 13, Fig. 2

**Material:** 2 specimens from the locality Scharrergraben (NHMW 2002z0119/0025 and (NHMW 2002z0119/0024).

**Description:** The colony is encrusting and multilamellar. The autozooecia are oval to triangular with a large opesium. The gymnocyst is short or well developed, smooth and slightly granular. Mural rim wide, sometimes with an intramural bud, without any traces of mural spines. Two types of avicularia are present: interzooecial and vicarious. The interzooecial avicularia are drop-like with an oval opesium, sometimes with pivotal bar and tapering distally. Usually, among four autozooecia, there are one or two avicularia. The vicarious avicularia are as large as an autozooecium, rare and rhomboidal with a small oval opesium. The ovicells are hyperstomial, globular with smooth frontal wall.

**Remarks and notes:** The studied specimen developed fewer avicularia than the specimens described and illustrated by Voigt (1989), which show up to 5 avicularia around each autozooecium. On the basis of the development of the ovicells and the general features of the colony, the specimen is determined as *Marginaria ostiolata* Reuss, 1846. Although vicarious avicularia are previously unknown in *Marginaria ostiolata*, according to Taylor (pers. comm. 2003) it is not unusual, for calloporid species to develop occasional larger avicularia. On the other hand, the size of the autozooecia and avicularia shows differences between specimens with or without large vicarious avicularia (see Table 1). More and better preserved specimens are needed to solve the question whether one or two species are represented.

**Distribution in time and space:** Early Cenomanian to Late Santonian. Mülheim-Broich (Germany) — Early Cenomanian. St. Calais (France), Bílina (Czech) — Late Cenomanian. Kamajka (Czech) — Early Turonian. Scharrergraben (Austria) — Late Santonian.

Superfamily **Microporoidea** Gray, 1848
Family **Onychocellidae** Jullien, 1881
Genus *Onychocella* Jullien, 1882 (=*Semieschara* d'Orbigny, 1852)

*Onychocella cyclostoma* (Goldfuss, 1826)
Fig. 4a

*1826 *Eschara cyclostomata* nobis: Goldfuss p. 23, Pl. 8, Fig. 9a–c
1985 *Onychocella cyclostoma* (Goldfuss): Voigt p. 63, Figs. 3–4

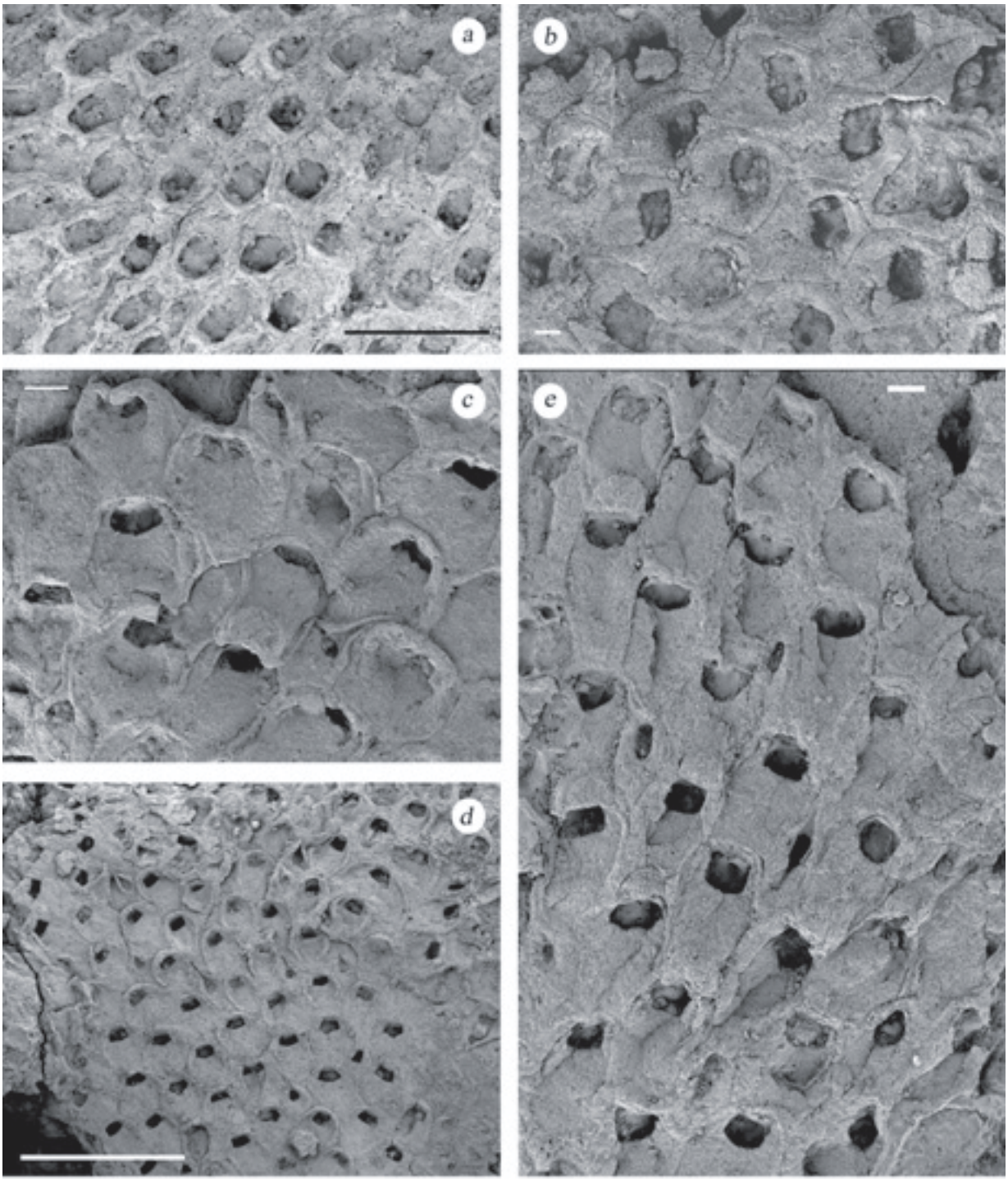


**Fig. 4. a** — *Onychocella cyclostoma* (Goldfuss, 1826) (NHMW 2002z0119/0036). **b** — *Onychocella depressa* (v. Hagenow, 1851) note large avicularium on the upper left corner (NHMW 2002z0119/0038). **c** — *Onychocella michaudiana* (d'Orbigny, 1850), detail shown ovicells and avicularium with curved narrow palate (NHMW 2002z0119/0041a). **d** — *Onychocella pseudoirregularis* Voigt, 1924 (note avicularia with straight palate) (NHMW 2002z0119/0040b). **e** — *Onychocella reussi* Prantl, 1938 (note ovicells and narrow straight avicularia) (NHMW 2002z0119/0041). All specimens from Scharrergraben, Austria; scale bar equals 100 μm.

**Material:** 2 specimens from the locality Scharrergraben (NHMW 2002z0119/0036, 0037).

**Description:** The colony is erect, bilamellar. Autozooecia are oval to circular with very large opesia and a poorly developed or no cryptocyst. The mural rim is slightly elevated, but not very wide. Adventitious avicularia (onychocellaria) are rare, slightly narrower than autozooecia and taper slightly distally; a palate is usually not developed.

**Remarks and notes:** The studied specimens possess only two avicularia which are almost identical with the mate-

rial described by Voigt (1985). In some cases, our material shows a slightly larger cryptocyst than that of Voigt (1985). Apart from this feature the specimens are very similar.

The characteristic feature of *Onychocella cyclostoma* (Goldfuss, 1826) is a very short cryptocyst, which may be absent altogether.

**Distribution in time and space:** Late Santonian to Maastrichtian. Scharrergraben (Austria) — Late Santonian. Maastricht (Netherlands) — Maastrichtian.

*Onychocella depressa* (v. Hagenow, 1851)
Fig. 4b

*1851 *Cellepora* (*Discop.*) *depressa*, Hag.: von Hagenow p. 93; Pl. 11, Fig. 13a–b
1989 *Onychocella depressa* (v. Hagenow); Voigt p. 57, Pl.13, Figs. 3–6

**Material:** 1 specimen from the locality Scharrergraben (NHMW 2002z0119/0038).

**Description:** The colony is encrusting or unilamellar. The autozooecia are rhomboidal to oval and are arranged in regular longitudinal rows. The opesia occupy almost the entire distal halves of the autozooecia and have enlarged proximo-lateral corners for parietal muscles. The cryptocyst is well developed, almost flat to concave, and slightly granular. Adventitious avicularia (onychocellaria) are large, longitudinally narrow about half of the width of the autozooecia and tapering on both sides. The opesia of avicularia are small and oval.

**Remarks and notes:** The studied specimen is encrusting and shows wider avicularia than specimens described by Voigt (1989). All other features are identical, suggesting that these specimens are conspecific.

*Onychocella depressa* (v. Hagenow, 1851) differs from other similar species of *Onychocella* in developing a large concave cryptocyst.

**Distribution in time and space:** Late Santonian to Maastrichtian. Scharrergraben (Austria) — Late Santonian. St. Pietersberg by Maastricht — Maastrichtian.

*Onychocella michaudiana* (d'Orbigny, 1850)
Fig. 4c

*1850 *Escharina michaudiana*, d'Orb. 1847; d'Orbigny p. 175
v1938 *Aechmella michaudiana* (d'Orbigny); Prantl p. 8, Pl. 1, Fig. 1
1989 *Onychocella michaudiana* (d'Orbigny); Voigt p. 63, Pl. 10, Figs. 1–10

**Material:** 3 specimens from the locality Scharrergraben (NHMW 2002z0119/0039a, 0040a, 0041a).

**Description:** The colony is encrusting and small. The autozooecia are rhomboidal to hexagonal with a distally developed mural rim. The cryptocyst is well developed, concave and slightly granular. The opesia are small, oval, sometimes with enlarged proximo-lateral corners, or with a straight proximal margin. The avicularia (onychocellaria) are usually as long as the autozooecia, but are only half as wide and are sharply tapering distally. The distalmost end of the avicularium (palate) is sometimes very narrow and slightly curved laterally. The avicularian opesia are oval to semicircular and narrow. Ovicells are very rare, globular, probably endozooidal, deeply immersed, thereby slightly deforming the distal neighbour autozooecia.

**Remarks and notes:** The avicularia are distinctly tapering distally in the studied specimens, whereas in the material described by Voigt (1989) the avicularia do not taper. The specimens described by Prantl (1938), however, have identical avicularia to the specimens from Scharrergraben. Other features visible on the studied specimens are identical with those described by Voigt (1989) and Prantl (1938).

The characteristic features of *Onychocella michaudiana* (d'Orbigny, 1850) are a distal mural rim around the autozooecia and the presence of small, immersed ovicells.

**Distribution in time and space:** Cenomanian to Late Santonian. Le Mans (France) — middle Cenomanian. St. Calais (France) — Late Cenomanian. Předboj and Velim by Kolín (Czech) — Turonian. Scharrergraben (Austria) — Late Santonian.

*Onychocella pseudoirregularis* Voigt, 1924
Fig. 4d

1851 *Cellepora irregularis*; v. Hagenow p. 92; Pl. 11, Fig. 14
*1924 *Onychocella pseudoirregularis* nom. nov.; Voigt p. 203–205; Pl. 7, Figs. 13–14
1989 *Onychocella pseudoirregularis* Voigt; Voigt p. 53, Pl. 11, Figs. 2–6

**Material:** 3 specimens from the locality Scharrergraben (NHMW 2002z0119/0040b, 0042, 0039b).

**Description:** The colony is encrusting with autozooecia arranged in chaotic rows. The autozooecia are oval with a well-developed distal part of the mural rim and a flat or slightly convex, granular cryptocyst. The autozooecial opesia are oval to elongated oval, very small. Adventitious avicularia (onychocellaria) are abundant and have a long, straight and very narrow distal part (palate). The ovicells are globular, hardly visible because they are deeply immersed in the direction of the distal neighbouring autozooecium.

**Remarks and notes:** The studied specimens are identical with those described by Voigt (1989), except that the distal part of the avicularia is narrower. This slight difference in the development of the avicularia may be considered as within species variability.

The main differences between *Onychocella pseudoirregularis* Voigt, 1924 and *Onychocella michaudiana* (d'Orbigny, 1850) are in the size of the autozooecial opesia and the fact that *O. michaudiana* has avicularia with curved palates.

**Distribution in time and space:** Late Santonian to Maastrichtian. Scharrergraben (Austria) — Late Santonian. Many localities around Maastricht (Netherlands) — Maastrichtian.

*Onychocella reussi* Prantl, 1938
Fig. 4e

v*1938 *Onychocella reussi* sp.n.; Prantl, p. 7 and 43
1989 *Onychocella reussi* Prantl; Voigt p. 54, Pl. 6, Figs. 6–9

**Material:** 1 specimen from the locality Scharrergraben (NHMW 2002z0119/0041b).

**Description:** The colony is encrusting. The autozooecia are elongated with comparatively small oval opesia which usually have straight distal margins. Sometimes enlarged proximo-lateral corners for parietal muscles are developed. The cryptocyst is flat, non-porous and smooth (not granular). Adventitious avicularia (onychocellaria) are abundant and have a short distal part (palate), which is sometimes slightly curved. The avicularian opesia are oval, sometimes slightly tapering proximally. The ovicells are small, hyperstomial deeply immersed to the distal autozooecium. The frontal wall of the ovicell is smooth, non-porous and slightly granular.

**Remarks and notes:** Apart from the less prominent enlarged proximo-lateral corners of opesia in the type material, all other features, including the elongated shape of the autozooecia and the shape and size of the avicularian palate, are identical.

This species differs from other species of *Onychocella* mainly in its elongated autozooecia, and the small opesia with straight distal margin.

**Distribution in time and space:** Late Cenomanian to Late Santonian. St. Calais (France) — Late Cenomanian. Many localities in Czech — Turonian. Scharrergraben (Austria) — Late Santonian.

## Conclusions

The studied bryozoan assemblage represents one of the most diverse bryozoan faunas reported from the Late Santonian of Europe. A total of 18 species were identified, 8 of which are Cyclostomata and 10 Cheilostomata.

Nearly all of the species found developed encrusting colonies (13 of 18 species); other growth forms occur only rarely. Four species developed delicate branching colonies and one species robust branching colonies.

The encrusting bryozoans are nearly exclusively found on the thecae of branched corals, only very few specimens are located on the underside of massive coral colonies and on mollusc shells (rudists). The dominance of encrusting bryozoans with additional erect delicate branching forms in areas with suitable substrates indicates an inter- to subtidal position with moderate sedimentation rate and relatively strong wave action according to McKinney & Jackson (1989) and Smith (1995).

The highly diverse coral fauna (more than 60 taxa; Beauvais 1982) of the locality Scharrergraben indicates optimal living conditions for hermatypic corals, as found today in the tropical climate zone. The dominance of encrusting growth forms of Bryozoa indicates shallow water and warm temperate conditions (McKinney & Jackson 1989) and therefore, does not contradict the data of the corals. According to Smith (1995), diverse bryozoan faunas are characteristic of nontropical settings. However, the importance of Bryozoa might be underestimated in extant tropical settings, as were, for example, brachiopods (Kowalewski et al. 2002).

Recent studies on the Campanian Grünbach flora (Herman & Kvaček 2002), from nearby localities suggested a humid subtropical to marine mesothermal climate for the plant bearing strata. However, the lithostratigraphic correlation and tectonic relation of the Neue Welt Basin (including the Campanian sediments bearing the Grünbach flora) with the strata north of Piesting (Scharrergraben) is unclear (Summesberger 1997; Summesberger et al. in print). Paleomagnetic data for the Gosau Basin (Preisinger et al. 1986), which indicate a paleolatitude of 32°N for the Late Maastrichtian/Early Paleogene of the Elendgraben-Section (Salzburg) are controversial according to Herman & Kvaček (2002). Paleomagnetic data for the Neue Welt Basin (including the locality Scharrergraben) indicate a paleolatitude of 20.6°±5.8° in the Late Santonian to Early Maastrichtian (calculated by R. Scholger from the Neue Welt area mean data presented in Haubold et al. 1999; pers. com. March 2003). Thus, the question on the paleoclimate of the marine strata exposed at Scharrergraben has to remain open, but evidence suggests that it was tropical.

Although bryozoans are often abundant and well preserved in Santonian chalk deposits of north-western Europe (e.g. Taylor 2002) few faunas have been systematically studied. Contrary to these faunas, which belong to the Kalaian paleorealm (new name for Boreal Province, see Kollmann 2002), the Gosau Group belongs to the Theian paleorealm (new name for Tethyan Province, see Kollmann 2002). Santonian Bryozoa from the Gosau Group, however, are rather rare and have been reported only in four other localities. Detailed investigations on their taxonomy have been done for just two of these outcrops (Voigt 1979). Reuss (1854) was the first to describe the bryozoans from Neffgraben (Austria) in a monograph on the fauna of Cretaceous sediments of the Eastern Alps. Later, Voigt (1928) described another Santonian bryozoan fauna from Kössen, Tyrol, Austria (originally described as the locality Dichtleralm).

The bryozoan fauna from Neffgraben (Austria) is similar to the fauna from Scharrergraben; in both localities mainly encrusting bryozoans attached to corals are found. Reuss (1854) described seven genera, from which five also occur in the studied section. A revision of the Neffgraben fauna is, however, needed for more detailed comparison.

Voigt (1928) reported six species in six different genera from the locality Dichtleralm (Kössen in Tyrol). This bryozoan fauna is different from that of Scharrergraben; only one genus is present in both localities. Moreover, at Dichtleralm the bryozoans are associated with molluscs and serpulids and represent, therefore, a different paleoecological setting.

Beside these two known bryozoan associations, Voigt (1979) reported two more localities where bryozoans occur in the Santonian of the Gosau Group: Edelbachgraben bei Gosau (Austria) and Baumgarten near Rosenheim (Germany). These faunas are similar to that of Scharrergraben in the respect that here the bryozoans also encrusted corals and rudists. However, since no systematic investigations on these faunas have been published, a comparison is not possible.

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