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Review

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Bryozoan assemblages of the Gulpen Formation (upper Campanian – upper Maastrichtian) in the Liège-Limburg area (Belgium, the Netherlands)

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Abstract

Renewed interest in bryozoan assemblages from the various members of the Gulpen Formation (upper Campanian–upper Maastrichtian) in the Liège-Limburg area (southeast Netherlands and northeast Belgium) during recent years has resulted in the discovery of a number of species previously unrecorded from the area. Nineteen species are here recorded from the Zeven Wegen, Vijlen, Lixhe and Lanaye members (Gulpen Formation) in the study area, occurring in three distinct assemblages. The vast majority of the bryozoan taxa belong to the order Cheilostomata; only two taxa are assigned to the order Cyclostomata. The species recorded here are *Clinopora* aff. *costulata, Disporella obvallata, 'Vincularia'* (*sensu lato*) *marssoniana, Herpetopora laxata, Heteroconopeum ovatum, Wilbertopora* aff. *oxyteichos, Biaviculigera sacerdotalis, Semiflustrella britannica, Aechmellina anglica, Escharifora papyracea, Onychocella cyclostoma, Onychocella cylindrica, Onychocella matrona, Rhebasia disparilis, Stichomicropora sicksi, Coscinopleura elegans, Coscinopleura lamourouxi, Pachydermopora pachyderma* and *Beisselina aviculifera.* While not previously recorded from the Liège-Limburg area, the bryozoan taxa identified from the Gulpen Formation are well known from coeval Cretaceous strata elsewhere in Europe, North America and Russia, highlighting their broad palaeobiogeographical distribution.

Introduction

The Upper Cretaceous (Campanian–Maastrichtian) deposits of the Liège-Limburg area, that is, the Maastrichtian type region, are famous for the rich, diverse and excellently preserved bryozoan faunas that have attracted the attention of many palaeontologists ever since the early 19th century. Scholars like August Goldfuß (1782–1848), Friedrich von Hagenow (1797–1865), Alcide d'Orbigny (1802–1857), Eduard Pergens (1862–1917) and Casimir Ubaghs (1829–1894) discovered and described hundreds of species from this region, predominantly recovered from the upper part of the Maastricht Formation (i.e., Nekum and Meerssen members). These levels yield vast numbers of well-preserved bryozoan species that can generally be easily collected and prepared for examination. As a result, many hundreds of species have so far been recognised, and numbers are continuously growing. At lower levels within the Maastricht Formation and within the underlying Gulpen Formation (upper Campanian to lower Maastrichtian), bryozoans are far less common and of limited diversity in comparison to assemblages from the higher levels of the Maastricht Formation.

In the present paper, 19 species, collected during recent years from the Gulpen Formation, are briefly discussed and illustrated, providing insights into the bryozoan assemblages from this formation. Many of these have previously been recorded from stratigraphically coeval strata in England, France, Germany and the Baltic region but are here documented for the first time from the Liège-Limburg area.

Stratigraphy and localities

The Gulpen Formation is a stratigraphical unit comprising Upper Cretaceous strata (Fig. 1). It is divided into five members, in ascending order: Zeven Wegen, Beutenaken, Vijlen (subunits 0–6), Lixhe 1–3 and Lanaye members (Jagt, 1999). At the top, the Gulpen Formation is separated from the overlying Maastricht Formation (upper Maastrichtian) by the Lichtenberg Horizon. At its base, the Zeven Wegen Horizon separates the Gulpen Formation from the underlying Vaals Formation (lower Campanian).

Zeven Wegen Member

This unit consists predominantly of white or light grey, very fine-grained, soft chalks that contain small quartz pebbles and a richly glauconitic basal layer, of about 0.50–1.50 m thick.

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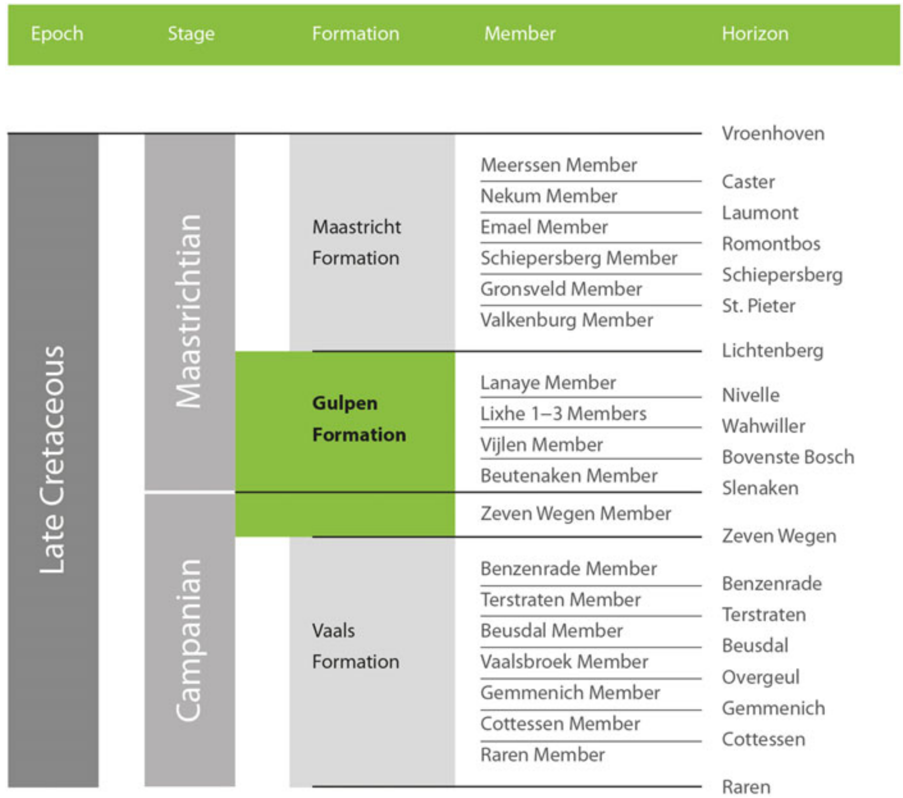

Figure 1. Lithostratigraphical subdivision and chronostratigraphy of Upper Cretaceous strata in the Liège-Limburg Basin (after W.M. Felder, 1975a, b; W.M. Felder & Bosch, 2000; Jagt & Jagt-Yazykova, 2012).

The overall thickness of the Zeven Wegen Member varies between 0 and 30 m. When complete, its upper limit is marked by the Slenaken Horizon, the contact with the overlying Beutenaken Member. Yet, since the Beutenaken Member is present only in a small area around the rivers Geul and Gulp, in most of the outcrops of the Liège-Limburg area the top of the Zeven Wegen is marked by the Bovenste Bosch Horizon, the transition to the Vijlen Member (Felder & Bosch, 2000).

Beutenaken Member

This member comprises soft, fine-grained, glauconitic clayey and calcareous marls that are light grey to whitish yellow in colour and contain sparsely dispersed quartz pebbles. The overall thickness ranges between 0 and 10 m. The Slenaken Horizon separates this unit from the underlying Zeven Wegen Member. The upper boundary is formed by the Bovenste Bosch Horizon (Jagt, 1999).

Vijlen Member

This unit predominantly consists of yellow to light grey, fine-grained, soft chalks with a richer glauconitic portion in its basal layers. The total thickness generally ranges between 15 and 25 m but locally reaches up to 100 m. This member was subdivided into seven intervals or subunits, numbered 0 to 6 (Felder & Bless, 1994). For a detailed description of these seven individual intervals, reference is made to Jagt (1999) and Jagt & Jagt-Yazykova (2012).

Lixhe 1–3 members

These units comprise white, fine-grained chalks with irregular dark, blue-grey to black flint nodules. The total thickness is about 25 m. Based on the type and abundance of flint nodules, three units have been recognised west of the River Meuse (Maas). These, combined with the overlying Lanaye Member, comprise about 75 continuous flint layers. Zijlstra (1994) linked this rhythmic sequence of horizontal continuous flint layers with the rhythmicity of the Milankovitch cycles (eccentricity, obliquity and precession).

Lanaye Member

This unit comprises white, fine-grained chalks with up to 23 flint layers. The colour of the irregular, tubular or platy nodules in these layers ranges from light to dark-blue grey. The total thickness of this member may reach up to 20 m. Planar-parallel flint nodule layers occur at 0.5–1.5 m interspaces (Jagt & Jagt-Yazykova, 2016) and reflect Milankovitch rhythmicity as described by Zijlstra (1994).

The strata assigned to the Gulpen Formation are easily accessible at several quarries between Maastricht and Haccourt/Lixhe. The simplified map (Fig. 2) shows the positions of the quarries (both still working and disused) from which the present bryozoan material has been collected, in addition to the type localities of members of the lithostratigraphical scheme for the Liège-Limburg area (Fig. 1).

Material and methods

Every species figured in the present paper is represented by specimens collected from strata assigned to the various members within the Gulpen Formation (Fig. 1). Whenever certain morphological features were lacking in material recovered from the Gulpen Formation, we decided to add images of more completely preserved specimens from the overlying Maastricht Formation, in an attempt to illustrate every species as completely as possible. Naturally, these 'filler specimens' are listed in the section 'Material' below.

Figure 2. Schematic map of southern Limburg (the Netherlands) and contiguous areas in Belgium and Germany, showing the quarries from which the bryozoan material described in the present paper has been recovered (red dots), as well as some lithostratigraphical type localities (grey dots; after W.M. Felder & Bosch, 2000).

Specimens that had to be dislodged from the matrix were levered out with a small needle after having scratched out a sufficiently deep furrow around them. All material was washed in tap water, sieved and/or put in an ultrasonic cleaner using tap water. All specimens illustrated are housed in the collections of the Natuurhistorisch Museum Maastricht (prefix NHMM). Images were taken using digital cameras and binocular microscopes; scanning electron micrographs (SEMs) were taken at the KU Leuven (Belgium). To generate SEM images presented here, a Jeol JSM 6360 was used, with the exception of that of *Heteroconopeum ovatum*, which was captured using a TESCAN MIRA 4FEG. In some instances, illustrations of material contained in the collections of the Natural History Museum, London (prefix NHMUK) are added, with proper links to the source.

Measurements and counts

All measurements were made either by using the calibrated SEM scale or by transferring the scale of a photographed ruler into digital scaling in Adobe Photoshop. Each measurement is given in the text as a mean plus or minus standard deviation, observed range and, between parentheses, the number of specimen and the total number of measurements or counts made.

For cheilostomes, measurements are in μm, identified by the following abbreviations:

AD = dimensions of equidimensional aperture.
AL = avicularium length.
ASW = distance between midpoints of adjacent apertures within a row or fascicle.
AW = avicularium width.
OL = orifice length.
OW = orifice width.
OpL = opesia length.
OpW = opesia width.
ZL = zooid length.
ZW = zooid width.
OvL = ovicell length.
OvW = ovicell width.

For cyclostomes, measurements are in μm, identified by the following abbreviations:

AD = dimensions of equidimensional aperture.
ASW = distance between midpoints of adjacent apertures within a row or fascicle.
FS = distance between centres of successive fascicles.
GAP = distance between edges of adjacent fascicles.

Systematic palaeontology

Class Stenolaemata Borg, 1926
Order Cyclostomata Busk, 1852
Family *incertae sedis*
Genus *Clinopora* Marsson, 1887

Clinopora* aff. *costulata Marsson, 1887
Figure 3

*1887 *Clinopora costulata* Marsson, p. 24, pl. 2, fig. 2a–c.
?1874 *Entalophora lineata* Beissel; Reuss, p. 133, pl. II. 25, figs 5, 6.
1899 *Clinopora costulata* Marsson; Gregory, p. 273.

Material

A single specimen, NHMM LG2144, CPL (Kreco) quarry, Haccourt (Belgium), Zeven Wegen Member.

Description

The single specimen forms a 0.65- to 1-mm-wide cylindrical stem. Colony surface formed of thin layer of anastomosing kenozooids oriented parallel to the direction of growth. Outlines of kenozooids ribbon-like and polygonal. Internal walls of kenozooids visible as darker coloured stripes on surface of stem. Autozooidal apertures (diameter *c.* 0.12–0.15 mm) rounded, slightly upwardly directed and arranged in slightly irregular quincuncial pattern. Gonozooids unknown.

Measurements

AD 141 ± 14, 127–163 (1,10), ASW 443 ± 22, 418–491 (1,8).

Remarks

Clinopora costulata and *Clinopora lineata* (Beissel, 1865) are closely related; however, the latter forms thinner stems (0.27–0.54 mm; *sensu* Beissel (1865), cited by Marsson (1887)), with

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Figure 3. *Clinopora* aff. *costulata,* (a) frontal view of stem with distinct kenozooidal boundaries.

more regularly and straightly arranged kenozooids (see Marsson, 1887). The number of vertical rows with autozooidal apertures is either 4 or 5 in both *C. lineata* and *C. costulata*, judging from the original descriptions. Marsson (1887) regarded *Entalophora lineata* Beissel, 1865 in Reuss (1874) as conspecific with his *Clinopora costulata*, although Reuss's specimens had more (5 to 7) autozooidal apertures encircling the stems. Furthermore, Reuss's specimens originated from upper Turonian to lower Coniacian deposits. The width of the kenozooids is smaller in *C. lineata*, measuring 0.02–0.03 mm, whereas it ranges between 0.04 and 0.05 mm in the present specimen of *C. costulata*.

The genus *Siphoniotyphlus* is closely related to *Clinopora*; on account of the paucity of available material, these have not been sufficiently compared. Voigt (1967) mentioned that the proximal/basal parts of *S. tenuis* (von Hagenow, 1840) were slender and cylindrical, which raises the question of whether or not at least some of the specimens that have been named *Clinopora* are basal fragments of *Siphoniotyphlus*. It is questionable if both species of *Clinopora* mentioned here may remain distinct, because the digitalised specimens of *Clinopora* in the Voigt Collection at the Senckenberg Museum, Frankfurt am Main (Germany), contain intermediate colony forms. Further research is needed. Pending additional studies and based on slight morphological differences, we consider it reasonable to retain *Clinopora lineata* and *C. costulata* as distinct species.

Stratigraphical range

Campanian to lower Maastrichtian.

Localities

Liège-Limburg area and Germany (Rügen, (?)Strehlen).

Family Lichenoporidae Smitt, 1867
Genus *Disporella* gray, 1848

Disporella obvallata (Marsson, 1887)
Figure 4

*1887 *Defrancia obvallata* Marsson, p. 38, pl. 3, fig. 12.
1951 *Lichenopora obvallata* (Marsson); Voigt, p. 45, text-pl. 7, fig. d–f.

Material

Two specimens, NHMM 47EYS, Marnebel quarry, Eben Emael (Belgium), Lanaye Member and NHMM 46EYS, Marnebel Quarry, Eben Emael (Belgium), Emael Member, above Lava Horizon.

Description

Discoidal colonies with radially arranged fascicles containing two or three alternating rows of polygonal autozooids. Colony fully attached to substrate. Space between fascicles and sunken central area formed of large alveoli, mostly wider than autozooidal apertures. Gonozooids covering entire colony, leaving out autozooidal apertures. Roofs of gonozooids porous surfaced by shallow vertical kenozooidal walls.

Measurements

NHMM 46EYS, AD 63 ± 8, 50–75 (1,10), ASW 80 ± 11, 58–100 (1,10), FS 329 ± 36, 291–383 (1,7), GAP 173 ± 28, 116–200 (1,7).

Remarks

Gonozooids were previously unknown in *Defrancia obvallata*; they are here illustrated for the first time. Given the inherent uncertainties in defining lichenoporid genera, we tentatively propose to transfer *Defrancia obvallata* to *Disporella*. Since *Lichenopora* is restricted to conical colony forms (Gordon & Taylor, 1997), the numerous Cenozoic adnate lichenoporids would be better placed in *Patinella* or *Disporella*, which are differentiated by brood chamber construction (Schäfer, 1991) and the presence of subdivided ('secondary') alveoli in the former genus. Additional similar Cretaceous genera (i.e., *Unicavea* or *Discocavea*) were considered junior synonyms of *Disporella* by Brood (1972), who transferred *Lichenopora irregularis* to *Disporella*, establishing the then earliest occurrence of this genus.

Stratigraphical range

Lower to upper Maastrichtian.

Localities

Liège-Limburg area and Germany (Rügen).

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852

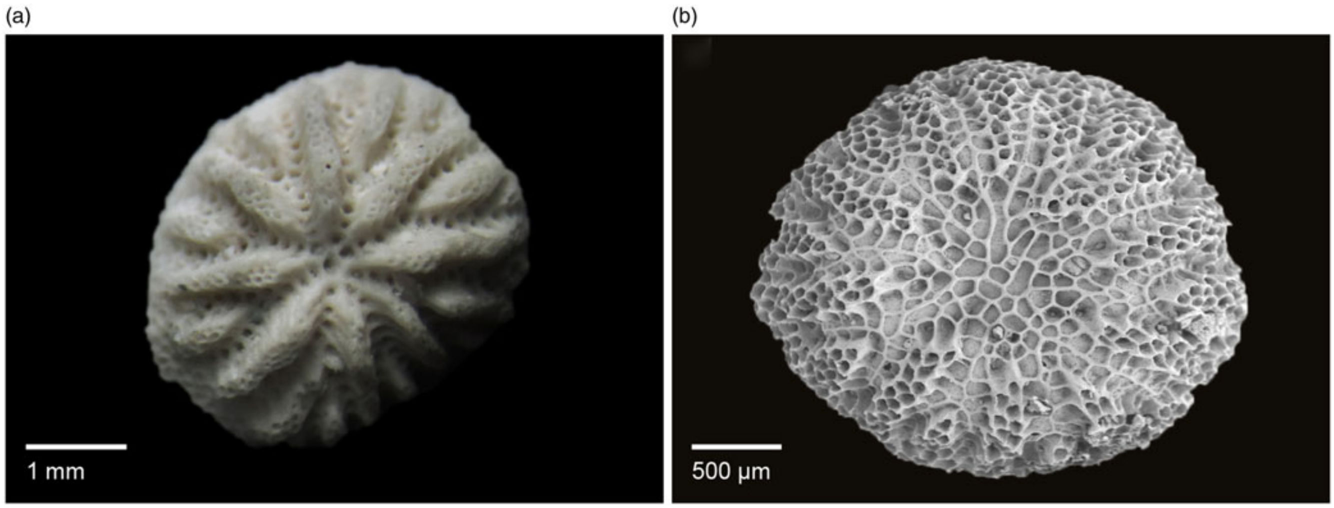

Figure 4. *Disporella obvallata*, (a) top view of colony (NHMM 47EYS), (b) top view of colony with brood chamber covering all interfascicular spaces (NHMM 46EYS).

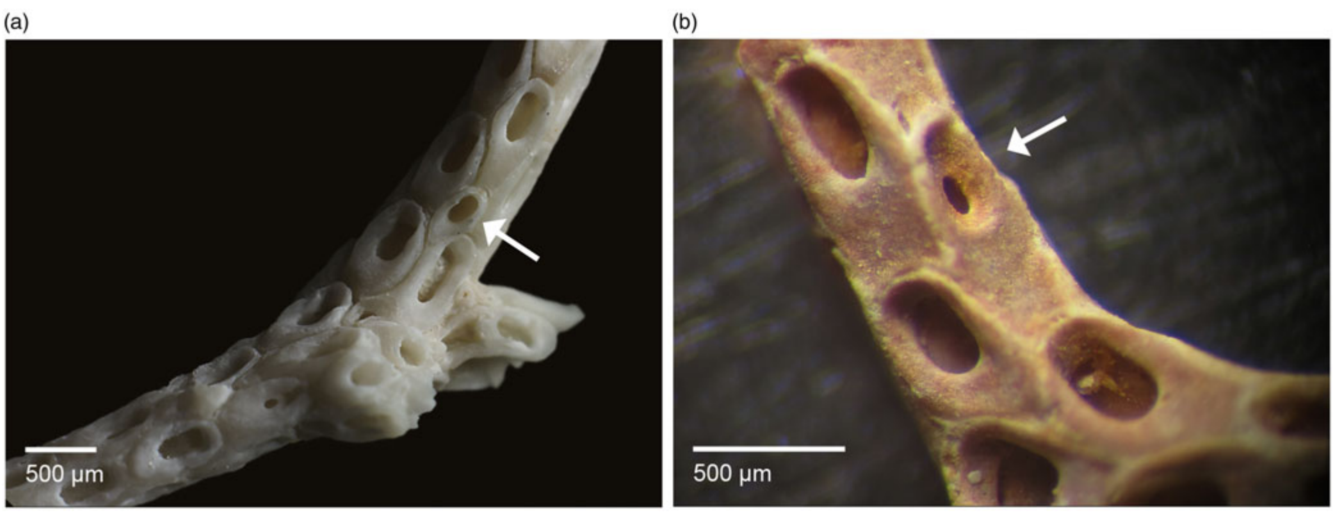

Figure 5. '*Vincularia*' (*sensu lato*) *marssoniana*, (a) branching stem with one avicularium (arrow; NHMM LG2124), (b) kenozooidal structure? (NHMM KSGV_37).

Family Vinculariidae Busk, 1852
Genus *'Vincularia'* Defrance, 1829 (*sensu lato*)

'Vincularia' (*sensu lato*) ***marssoniana*** (Voigt, 1924)
Figure 5

*1924 *Membranipora marssoniana* Voigt, p. 6, pl. 1, fig. 13.
1930 *Membranipora marssoniana* Voigt; Voigt, p. 422, pl. 12, figs 14, 15.
1979 '*Membranipora marssoniana*' Voigt; Voigt, p. 37, pl. 1, fig. 4.

Material

Two specimens, NHMM LG2124, CPL (Kreco) quarry, Haccourt (Belgium), Zeven Wegen Member and NHMM KSGV_37, Kunrader Steengroeve quarry, Voerendaal (Netherlands), Maastricht Formation, Kunrade facies.

Description

Slender (0.5–1.0 mm), four- to five-sided, dichotomously branched, erect branches with prismatic cross section. Longitudinally oval, distally rounded and clearly bulging autozooids becoming slightly smaller proximally. Surface of cryptocyst smooth, proximal area sloping down centrally. Long oval opesia situated in upper half of zooids. Avicularia smaller than autozooids, oval with rounded distal and pointed proximal end. Hyperstomial ovicells.

Remarks

The taxonomic position of this species is not certain; additional studies of this species and numerous other vinculariiform genera from the Upper Cretaceous of the Liège-Limburg area are called for.

Measurements

NHMM LG2124, ZL 772 ± 71, 650–880 (1,8), ZW 407 ± 95, 302–558 (1,6), OL 501 ± 52, 419–558 (1,6) OW 197 ± 13, 186–209 (1,6).

Stratigraphical range

Upper Campanian to Danian.

Localities

Liège-Limburg area and Germany (Rügen, Hamburg area).

Family Electridae Stach, 1937
Genus *Herpetopora* Lang, 1914

Herpetopora laxata (d'Orbigny, 1852)
Figure 6

*1852 *Hippothoa laxata* d'Orbigny, pl. 711, figs 12–15.
1854 *Hippothoa cruciata* Reuss, p. 134, pl. 28, fig. 1.
1914 *Herpetopora clavigera* Lang, p. 6, pl. 2, figs 4, 5.
1930 *Herpetopora dispersa* (von Hagenow); Voigt, pp. 409, 553, pl. 1, fig. 1.
1960 *Pyripora laxata* (d'Orbigny); Thomas & Larwood, p. 371, pl. 60, figs 1, 2; pl. 61, fig. 2.
1988 *Herpetopora laxata* (d'Orbigny); Taylor, pp. 519–547, text-figs. 1–11 and 13, tabs. 1–4.
2019 *Herpetopora laxata* (d'Orbigny); Taylor et al., p. 428, fig. 2e; p. 430, fig. 3b, c; p. 439, fig. 9a and p. 441, fig. 12d.

Material

A single specimen, NHMM LG2148, CPL (Kreco) quarry, Haccourt (Belgium), Vijlen Member (interval 6).

Description

Simple, encrusting, runner-like colonies, growing abundantly on hard substrates such as echinoid tests, brachiopods and belemnites. Zooids budding at distal end and both lateral sides of parent zooid. Distal buds continuing growth direction of parent zooid; lateral buds oriented at 85–90° to parent zooid. Autozooids oval with long and thin proximal cauda. Opesiae longitudinally oval or elliptical. Cryptocyst, avicularia, ovicells and apertural spines absent. Irregularly shaped or subtriangular kenozooids with small circular central opesia present, albeit rarely. Kenozooids smaller than autozooids. Intramural budding observed. Closure plates often present, occasionally with impression of operculi on distal end.

Measurements

NHMM LG2148 (non-caudate zooids), ZL 482 ± 49, 417–552 (1,5), ZW 350 ± 22, 325–375 (1,6), OpL 465 ± 223, 225–800 (1,6), OpW 204 ± 28, 175–250 (1,6)

NHMM LG2148 (caudate zooids), ZL 845 ± 132, 702–1050 (1,6)

Remarks

For a better visualisation of the kenozooids, a photomicrograph of NHM UK PI D 42361 ('*Herpetopora laxata*' (d'Orbigny, 1852)) is here added.

Stratigraphical range

Upper Campanian to upper Maastrichtian.

Localities

Widely distributed across northwest Europe.

Family Chiplonkarinidae Taylor & Gordon, 2007
Genus *Heteroconopeum* Voigt, 1983

Heteroconopeum ovatum (Canu & Bassler, 1926)
Figure 7

*1926 *Conopeum ovatum* Canu & Bassler, p. 32, pl. 4, figs 1–4.
1962a, b *Solenophragma ovatum* (Canu & Bassler); Voigt, p. 34, pl. 18, figs 1–3.
2006 *Heteroconopeum ovatum* (Canu & Bassler); Taylor & McKinney, p. 66, pls. 42, 43.

Material

A single specimen, NHMM Y53, Marnebel quarry, Eben Emael (Belgium), Lanaye Member, between flint levels 21 and 22.

Description

Colony starting as large encrusting base, subsequently developing number of erect, cylindrical and multilamellar branching stems. Autozooids longitudinally elliptical to inverted oval with elliptical or inverted oval opesiae occupying most of zooid surface; arranged in longitudinal rows. Cryptocyst narrowing distally, granulated and sloping inwards. Basal walls of autozooids visible in distal half, containing two latero-distal depressions (muscle scars?). Spaces between autozooids occupied by small polymorphs (avicularia?). One rounded teardrop-shaped avicularium-like polymorph detected (about three-quarters length of autozooid). Ovicells not detected.

Measurements

NHMM Y53, ZL 425 ± 20, 402–455 (1,8), ZW 254 ± 39, 198–301 (1,8), OpL 330 ± 11, 310–342 (1,8), OpW 167 ± 25, 149–204 (1,8), AL 217 ± 28, 190–245 (1,3), AW 125 ± 13, 110–135 (1,3).

Remarks

The present species is, along with *Semiflustrella britannica*, one of two forms here described that is also known from the Maastrichtian of the United States (see Taylor & McKinney, 2006); this is the first record for the study area.

Stratigraphical range

Lower to upper Maastrichtian.

Localities

Liège-Limburg area, United States (Tennessee, North Carolina, Georgia, Alabama) and Ukraine (Crimea).

Family Calloporidae Norman, 1903
Genus *Wilbertopora* Cheetham, 1954

Wilbertopora* aff. *oxyteichos (Voigt, 1930)
Figure 8

*1930 *Membranipora* (*Membraniporidra*) *oxyteichos* Voigt, p. 427, pl. 5, figs 5–8.
1949 *Membranipora oxyteichos* Voigt; Voigt, p. 12, pl. 2, fig. 1.
2019 *Wilbertopora oxyteichos* (Voigt); Martha et al., p. 309, fig. 46c, d.

Material

A single specimen, NHMM LI21, CBR quarry, Lixhe (Belgium), Zeven Wegen Member.

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(a) (b)

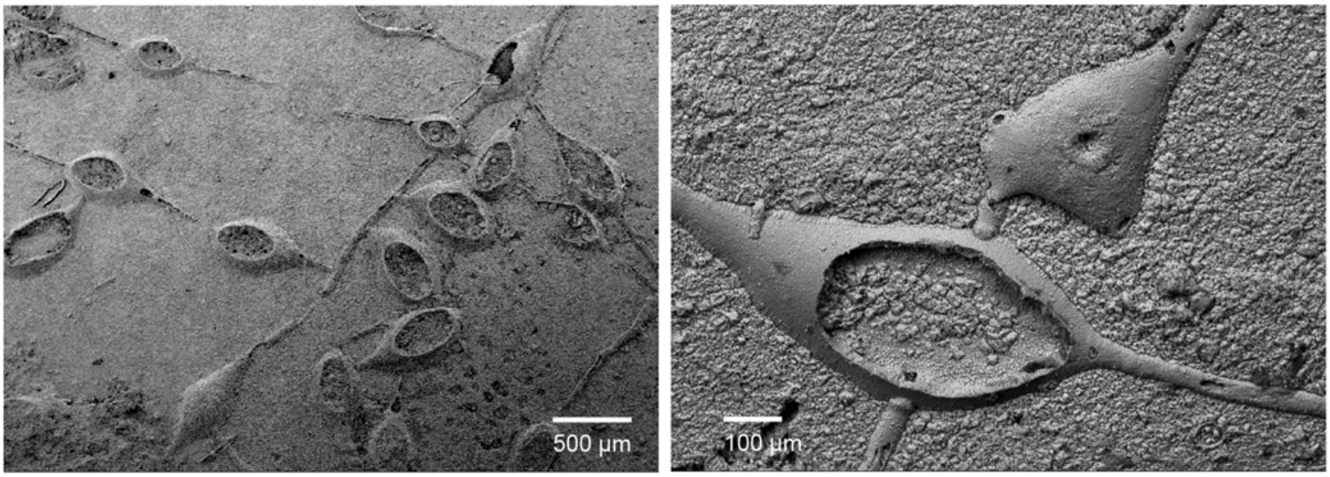

Figure 6. *Herpetopora laxata*, (a) several autozooids with lateral and distal budding (NHMM LG2148), (b) auto- and kenozooid (NHMUK PI D 42361) (https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/4128144 (licensed under http://creativecommons.org/licenses/by/4.0/).

(a) (b)

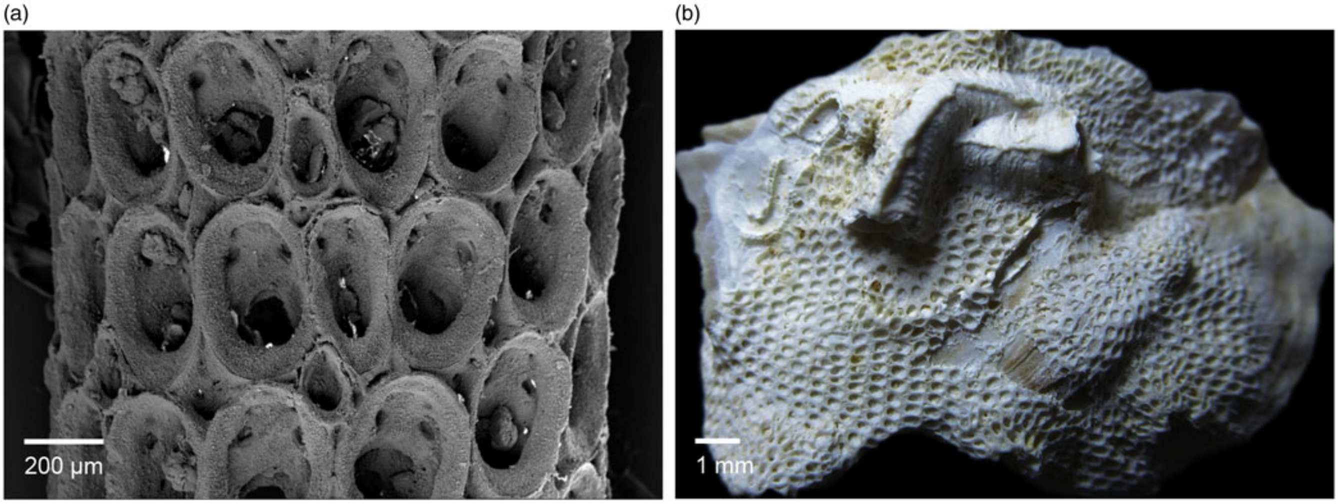

Figure 7. *Heteroconopeum ovatum*, (NHMM Y53), (a) frontal view of stem with autozooids and interzooidal avicularia-like polymorph, (b) encrusting base on oyster shell.

(a) (b)

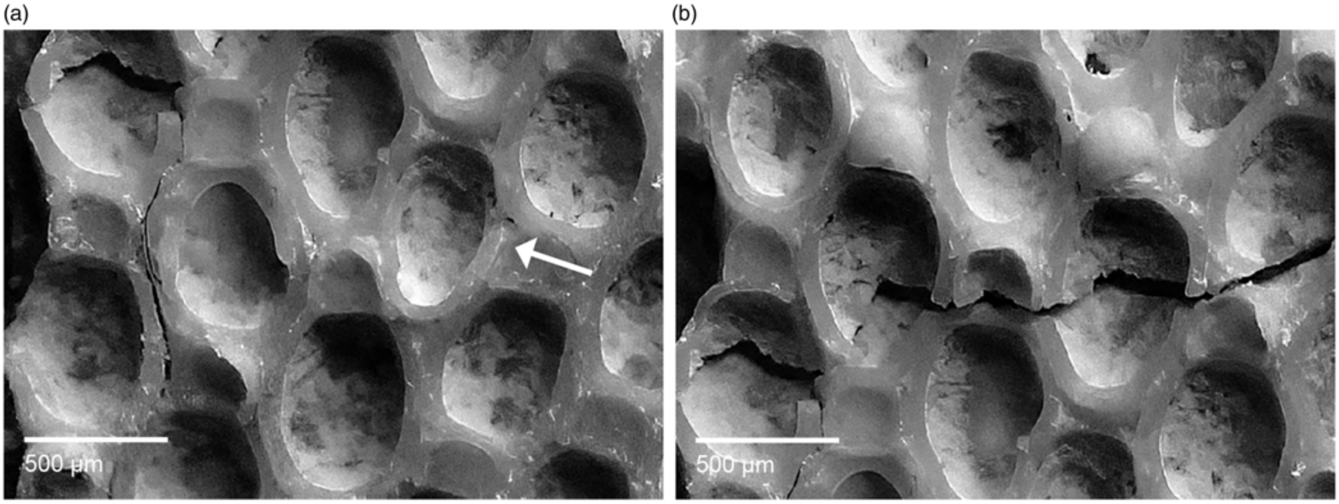

Figure 8. *Wilbertopora* aff. *oxyteichos*, (NHMM LI21), (a) closeup of autozooids and avicularium, (b) autozooids with broken and preserved ovicells.

Description

Colonies with rounded hexagonal or inverted pear-shaped, alternatingly arranged zooids, separated from each other by thin furrows. Opesiae elliptical to oval and occasionally slightly bent. Width of cryptocyst consistently small. Trapezoidal gymnocyst in proximal part of autozooids often covered by ovicell of proximal zooid. Size of vicarious avicularia similar to or smaller than that of autozooids, shaped like autozooids, except for proximal protruding horseshoe-shaped rim, distally turning inwards. Numerous hyperstomial ovicells pill-shaped.

Measurements

NHMM LI21, ZL 848 ± 51, 822–918 (1,5), ZW 532 ± 23, 496–555 (1,5), OpL 572 ± 58, 522–658 (1,5), OpW 408 ± 18, 380–422 (1,5), OvL 274 ± 18, 246–300 (1,5), OvW 262 ± 16, 242–272 (1,5).

Stratigraphical range

Lower to upper Campanian.

Localities

Germany (Misburg) and Liège-Limburg area (only Zeven Wegen Member).

Genus *Biaviculigera* Voigt, 1989

Biaviculigera sacerdotalis (Brydone, 1914)
Figure 9

*1914 *Membranipora sacerdotalis* Brydone, p. 482, pl. 35, figs 8–10.
1930 *Membranipora sacerdotalis* (Brydone); Voigt, p. 421, pl. 10, fig. 11.
1989 *Biaviculigera sacerdotalis* (Brydone); Voigt, pp. 22, 23.

Material

A single specimen, NHMM_LI74, CBR quarry, Lixhe (B), Vijlen Member (interval 6).

Description

Encrusting anascan species with inverted pear-shaped autozooids with large oval or elliptical opesiae. Very thin cryptocyst tilted inwards; gymnocyst broad proximally but gradually becoming narrower distally. Two types of vicarious avicularia: one inverted pear-shaped with highly convex frontal wall in distal part, descending towards proximal end; opesia inverted oval, tilted to face proximally and bearing a pivotal bar. Second type of avicularia smaller with long, narrowly elliptical opesia and small spoon-shaped rostrum. Lateral gymnocystal walls partly overlap opesia. No intact ovicells detected. Remains of apertural spines not observed.

Measurements

NHMM LI 74, ZL 785 ± 28, 754–828 (1,5), ZW 555 ± 14, 537–575 (1,5), OpL 570 ± 11, 550–575 (1,5), OpW 375 ± 18, 348–402 (1,5).

Remarks

Very rare in the Liège-Limburg area and recorded here for the first time.

Stratigraphical range

Lower to mid-Maastrichtian.

Localities

Liège-Limburg area, Germany (Rügen) and England (Norfolk).

Genus *Semiflustrella* d'Orbigny, 1853

Semiflustrella britannica (Brydone, 1906)
Figure 10

*1906 *Membranipora britannica* Brydone, p. 294, text-fig. 3.
1910 *Membranipora britannica* Brydone; Brydone, p. 76, pl. 8, fig. 3 (*non* 4).
1962 *Ellisina britannica* (Brydone); Berthelsen, p. 76, pl. 5, fig. 4.
1976 *Ellisina britannica* (Brydone); Thomsen, pp. 142–144, fig. 9B.
1979 *Ellisina britannica* (Brydone); Medd, p. 13, fig. 3, pls 1.7–1.10, 2.1, 2.2.
2006 *Semiflustrella brittanica* (Brydone); Taylor & McKinney, p. 99, pl. 67.

Material

A single specimen, NHMM LG2109, former ENCI quarry, Maastricht (Netherlands), Lanaye Member.

Description

Encrusting multiserial species, forming rhomboidal autozooids with well-defined mural rim and very reduced or absent cryptocyst. Autozooids closely packed, separated only by thin furrows. Avicularia droplet-shaped, interzooidal and positioned distally above every non-ovicellate autozooid. Hyperstomial ovicells are slightly sunken, covered by a convex roof and at least partially overlapping the gymnocyst of the distal autozooid.

Measurements

ZL 582 ± 41, 550–650 (1,10), ZW 397 ± 34, 325–450 (1,10), OpL 507 ± 61, 425–575 (1,10), OpW 297 ± 27, 275–350 (1,10).

Remarks

Medd (1979) described a pair of condyles or – very rarely – a transverse bar in the proximolateral part of the avicularia. We have only detected very small remains of condyles in a few avicularia. Taylor & McKinney (2006) revived the genus *Semiflustrella* in favour of 'ellisinids' which, unlike the type species of *Ellisina*, do not have the distal avicularia immersed in a kenozooid. As *Membranipora britannica* lacks morphological features seen in other 'ellisinid' genera (e.g., *Hincksina, Cranosina, Parellisina, Dionella, Kristerina* and *Periporosella*) or differs from these, it was transferred to *Semiflustrella*. *Semiflustrella britannica* is here recorded for the first time in the Liège-Limburg area. Cheetham (1971) misspelt the species name as '*brittanica*'; this was adopted by Taylor & McKinney (2006).

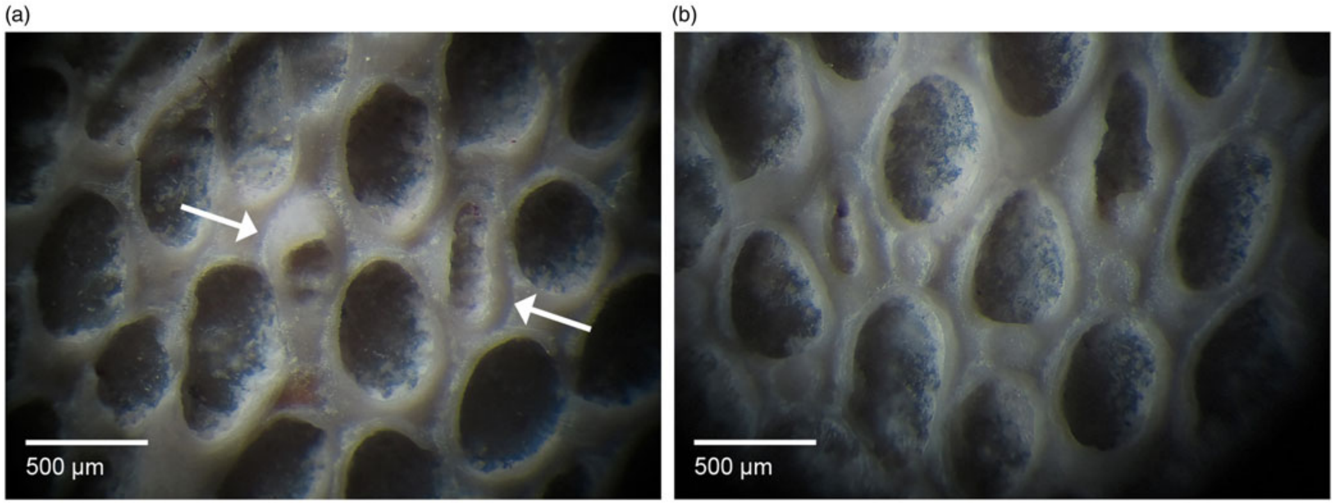

Figure 9. *Biaviculigera sacerdotalis*, (NHMM LI74), (a) autozooid and two types of avicularia, (b) several ovicellate autozooids in lower central area.

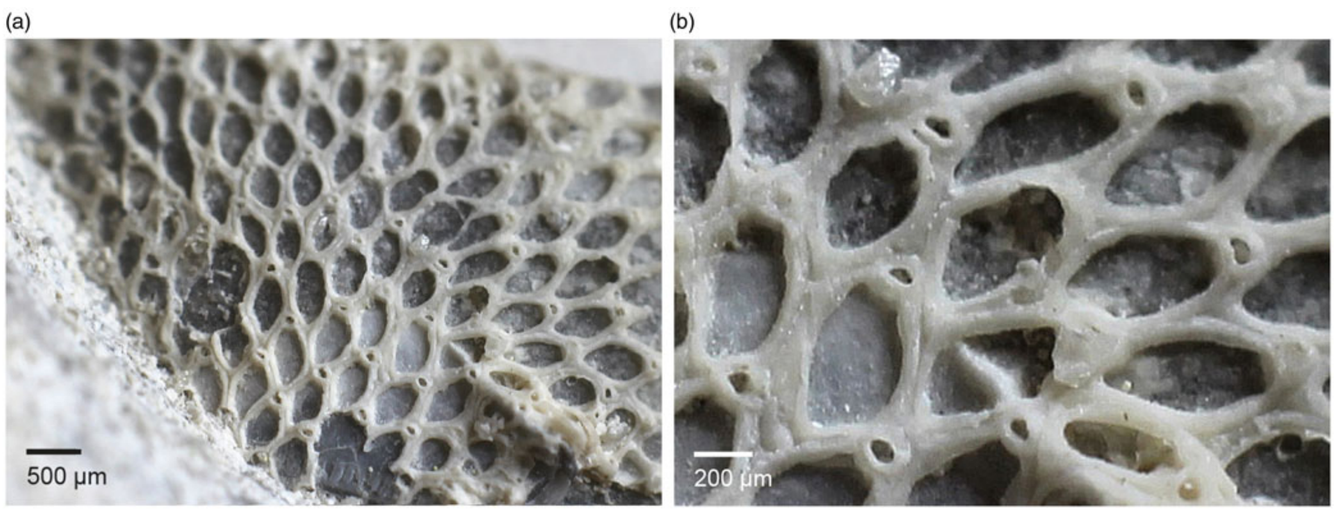

Figure 10. *Semiflustrella britannica*, (NHMM LG2109), (a) colony encrusting outer surface of flint nodule, (b) closeup of same colony.

Stratigraphical range

Lower to upper Maastrichtian.

Localities

Northwest Europe and United States (Alabama),

Family Onychocellidae Jullien, 1882
Genus *Aechmellina* Taylor et al., 2018

Aechmellina anglica (Brydone, 1909)
Figure 11

*1909 *Homalostega anglica* Brydone, p. 337, pl. 14, figs 1, 2.
1930 *Aechmella anglica* (Brydone); Voigt, p. 480, pl. 23, figs 7, 8.
1959 *Aechmella anglica* (Brydone); Voigt, p. 18, text-fig. 4c (*non* 4b).
2018 *Aechmellina anglica* (Brydone); Taylor et al., p. 1668.

Material

Two specimens, NHMM LG2311, former ENCI quarry, Maastricht (Netherlands), Lixhe 1 Member and NHMM JJ 2631, CPL (Kreco), Haccourt (Belgium), Vijlen Member (Interval 6), base + *c.* 4 m.

Description

Encrusting colonies with approximately 0.6-mm-long, distinctly convex autozooids, surrounded by thin vertical wall. Opesia semicircular to crescent-shaped and surrounded by rim, ascending towards distal side. On distal edge of rim, one or two microscopic bases of oral spines. Cryptocyst convex and slightly granulated. Avicularia interzooidal and oriented more or less perpendicularly to left or right of opesia, three to four times smaller than autozooids, rounded on proximal side and tapering distally into a point. Ovicells lacking in specimens examined. Commonly found on tests of the irregular echinoid genus *Echinocorys* in the Lixhe 1 Member.

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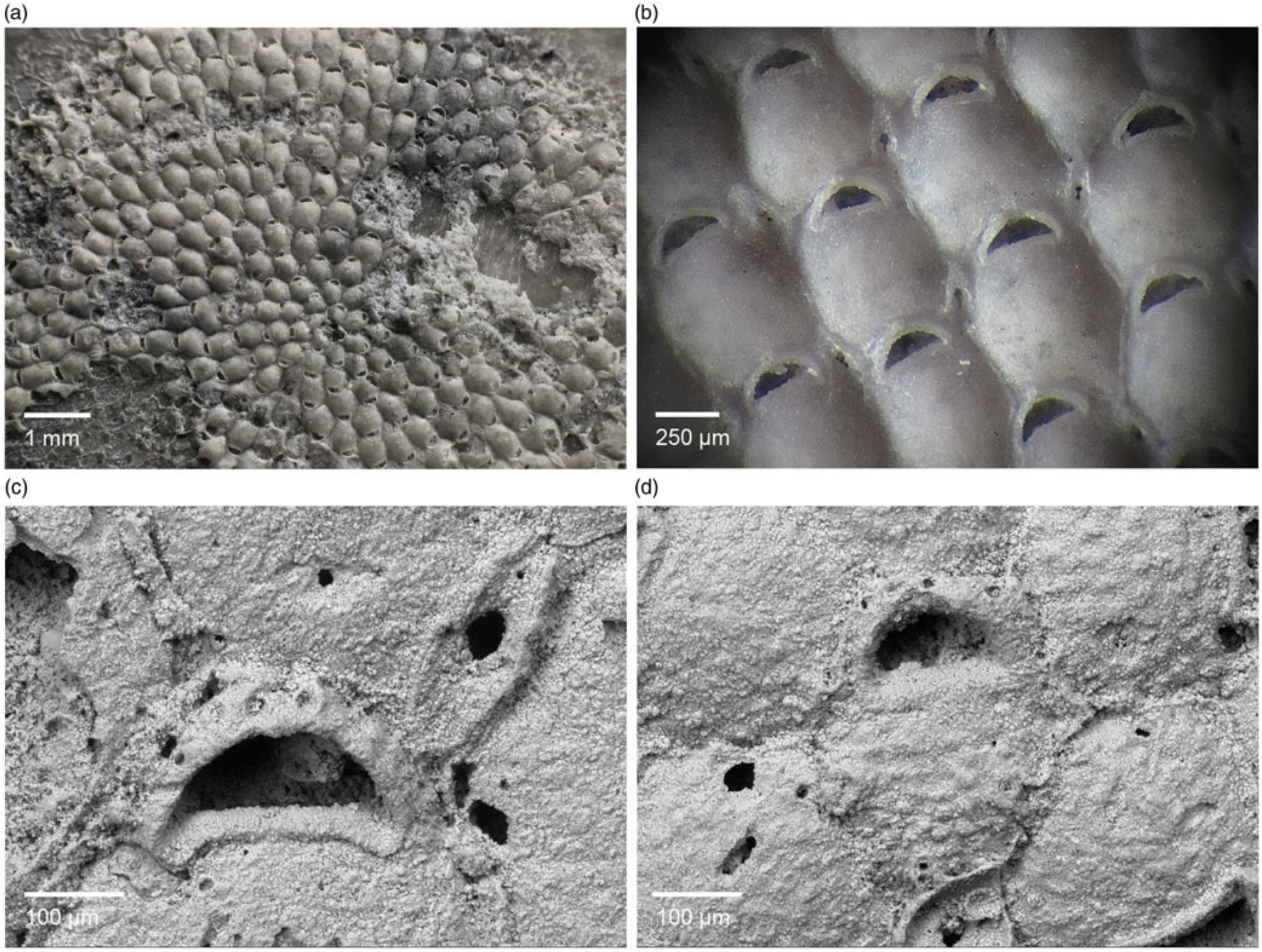

Figure 11. *Aechmellina anglica*, (a) radially arranged zooids with preserved ancestrular region (NHMM LG2311), (b) closeup of several autozooids with interzooidal avicularia (NHMM JJ 2613, identified by Professor E. Voigt), (c) closeup of opesial rim bearing two(?) mediodistal spine bases (NHMUK PI D 38923), (d) closeup of ancestrula (NHMUK PI D 38923), same provenance (https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/4124740 (licensed under http://creativecommons.org/licenses/by/4.0/).

Measurements

NHMM LG2311, ZL 690 ± 42, 633–750 (1,6), ZW 582 ± 35, 550–650 (1,6), OL 256 ± 12, 250–267 (1,9), OW 87 ± 10, 75–100 (1,9), AL 261 ± 15, 239–267 (1,6), AW 108 ± 9, 100–116 (1,6).

Remarks

The species is recorded here for the first time from the Liège-Limburg area. For a better understanding of this form, in particular of the oral spines, two photomicrographs are here added of specimen NHMUK PI D 38923.

Stratigraphical range

Lower and upper Maastrichtian, possibly extending into Danian.

Localities

Liège-Limburg area, Germany (Rügen), Denmark and England (Norfolk).

Genus *Escharifora* d'Orbigny, 1852

Escharifora papyracea (von Hagenow, 1851)
Figure 12

*1851 *Eschara papyracea* von Hagenow, p. 80, pl. 9, fig. 21.
?1930 *Escharifora papyracea* (v. Hagenow); Voigt, p. 492, pl. 25, fig. 27.
1930 *Escharifora quoyiana* (v. Hagenow); Voigt, pp. 492, 347 (*partim*), pl. 25, figs 24–26.
1975 *Escharifora papyracea* (v. Hagenow); Voigt, p. 82, pl. 3, figs 3, 4.
1979 *Escharifora papyracea* (v. Hagenow); Voigt, p. 50, pl. 11, figs 3–6.

Material

Three specimens, NHMM LG3012, former ENCI quarry, Maastricht (Netherlands), Meerssen Member, NHMM 519GRA, former ENCI quarry, Maastricht (Netherlands), Nekum Member and NHMM LANENC_003, former ENCI quarry, Maastricht (Netherlands), Lanaye Member.

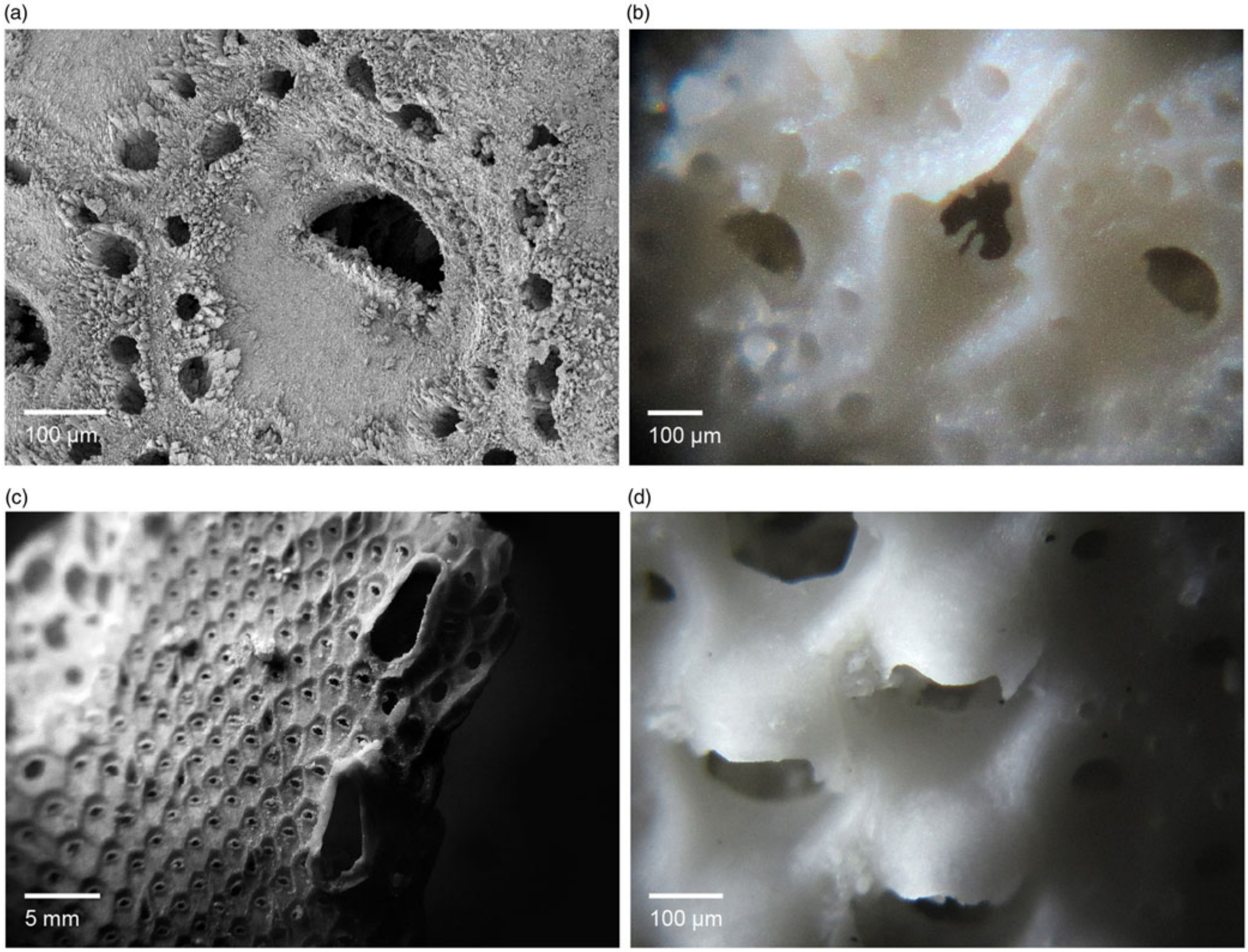

Figure 12. *Escharifora papyracea*, (a) autozooid with voids along outer margin of cryptocyst (NHMM LG3012), (b) avicularium (NHMM LANENC_003), (c) two abnormally large vicarious avicularia (NHMM 519GRA), (d) three ovicellate autozooids (NHMM LANENC_003).

Description

Fragile bilaminate branching leaves. Zooids more or less elongated, hexagonal to near-rhombic and surrounded by flat rim and row of voids along inside. Opesia at some distance from distal margin above centre of zooid; semicircular to crescent-shaped with arcuate distal margin and two small proximal teeth. Avicularia elongate rhombic to pyriform with oval opesia located in centre of zooid and, when well preserved, with median slit. Distally pointed rostrum slightly overlapping front of zooid along disto-lateral margins. Fertile autozooids generally enlarged, having distinctly enlarged transversely elliptical to circular opesia, almost completely covered by ovicell. Near fertile zooids, avicularia also enlarged. Third form of avicularium developing near edges of colony, 3 to 4 times larger than autozooids and with hooked rostrum.

Measurements

NHMM LANENC_003, ZL 567 ±140, 400–750 (1,6), ZW 470 ± 57, 400–550 (1,5), OL 164 ± 25, 140–200 (1,5), OW 268 ± 58, 200–350 (1,5), AL 700 ± 106, 650–800 (1,5), AW 224 ± 25, 200–250 (1,5).

Remarks

Species of *Escharifora* from the Liège-Limburg area are in need of revision using SEM imaging and the study of large numbers of specimens in order to assess the high morphological variation within this group.

Distribution

Mid- to upper Maastrichtian.

Localities

Liège-Limburg area.

Genus *Onychocella* Jullien, 1882

Onychocella cyclostoma (Goldfuss, 1826)
Figure 13

*1826 *Eschara cyclostoma* Goldfuss, p. 23, pl. 8, fig. 9.
1851 *Eschara cyclostoma* (Goldfuss); von Hagenow, p. 75, pl. 9, figs 7, 8; pl. 12, fig. 3.

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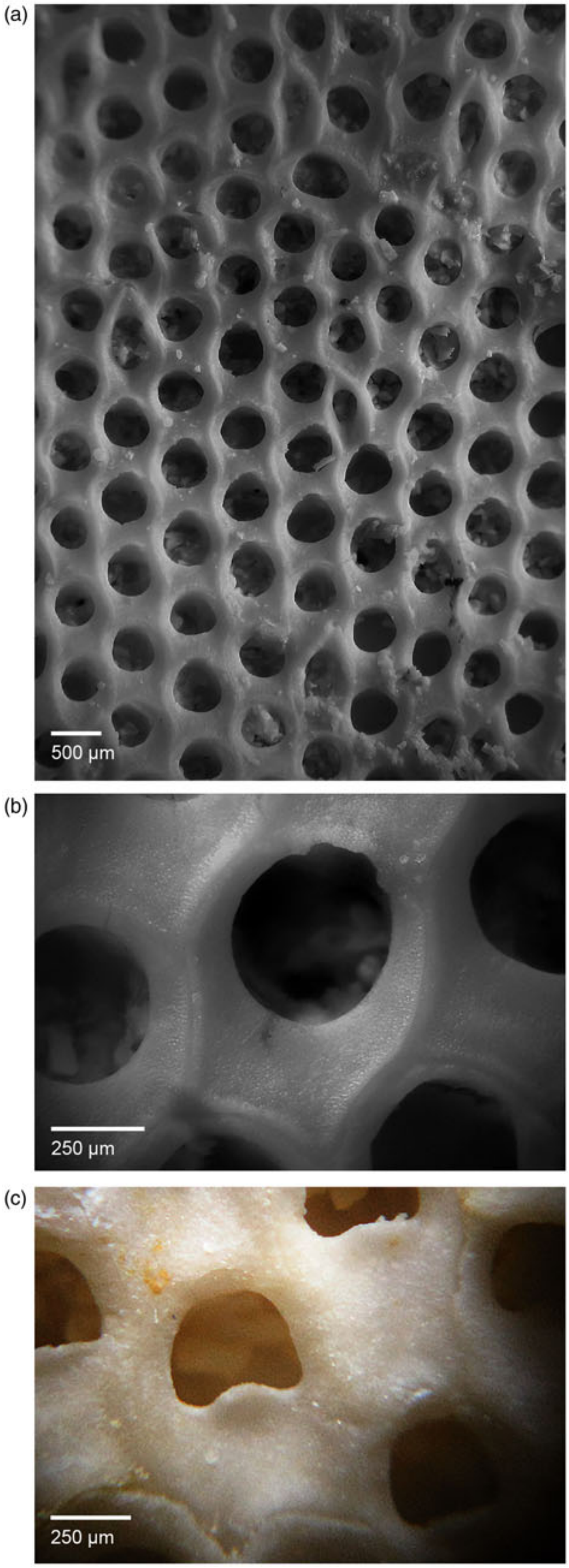

Figure 13. *Onychocella cyclostoma,* (a) colony fragment with ovicellate and non-ovicellate autozooids and avicularia (NHMM LANENC_002), (b) closeup of ovicellate autozooid (NHMM LANENC_002), (c) autozooid with distinct cryptocyst, distally extending into convex suboral lip (NHMM 34EYS).

1930 *Onychocella cyclostoma* (Goldfuss); Voigt, p. 456, pl. 16, fig. 6.

1977 *Onychocella cyclostoma* (Goldfuss); Jebram & Voigt, p. 165, pl. 1, figs 1, 2; pl. 2, figs 1–3.

1979 *Onychocella cyclostoma* (Goldfuss, 1826); Voigt, p. 40, pl. 4, fig. 1.

Material

Two specimens, NHMM LANENC_002, former ENCI quarry, Maastricht (Netherlands), Lanaye Member, NHMM 34EYS, former ENCI quarry, Maastricht (Netherlands), Meerssen Member.

Description

Bi- or unilamellar, erect or encrusting, massive, leaf-shaped colonies comprising large autozooids arranged in alternating vertical rows and surrounded by distinct margin. In early astogenetic stages opesiae semi-elliptical or semicircular due to presence of distinct cryptocyst. In later stages cryptocyst successively regressing (see Voigt & Ernst, 1985) and opesiae becoming larger and circular. Avicularia with blunt proximal and pointed distal sides, with rostrum tilted or bent to left or right. Avicularian opesia large, oval or elliptical. Ovicells endozooidal, forming small convex swellings above autozooidal opesia.

Measurements

NHMM LANENC_002, ZL 789 ± 31, 733–833 (1,10), ZW 703 ± 34, 667–760 (1,10), OpL 513 ± 47, 467–600 (1,10), OpW 464 ± 27, 433–500 (1,10), AL 1073 ± 103, 1060–1166 (1,5), AW 520 ± 77, 400–600 (1,5).

Stratigraphical range

Mid- to upper Maastrichtian.

Localities

Liège-Limburg area.

Onychocella cylindrica (von Hagenow, 1851)
Figure 14

*1851 *Siphonella cylindrica* von Hagenow, p. 84, pl. 6, fig. 5.

non 1930 Onychocella cylindrica d'Orbigny; Voigt, p. 454, pl. 15, fig. 7.

1951 *Siphonella cylindrica* von Hagenow, 1851; Voigt, p. 61, text-fig. 1; pl. 10, figs 1, 2.

1979 *Onychocella cylindrica* (von Hagenow, 1851); Voigt, p. 42, pl. 4, fig. 4.

Material

Three specimens, NHMM_14EYS, Marnebel quarry, Eben Emael (Belgium), Lanaye Member (level unspecified), NHMM 60EYS, Marnebel quarry, Eben Emael (Belgium), Lanaye Member, between flint levels 12 and 14, and NHMM 400EYS, Marnebel quarry, Eben Emael (Belgium), Lanaye Member, between flint levels 14 and 20.

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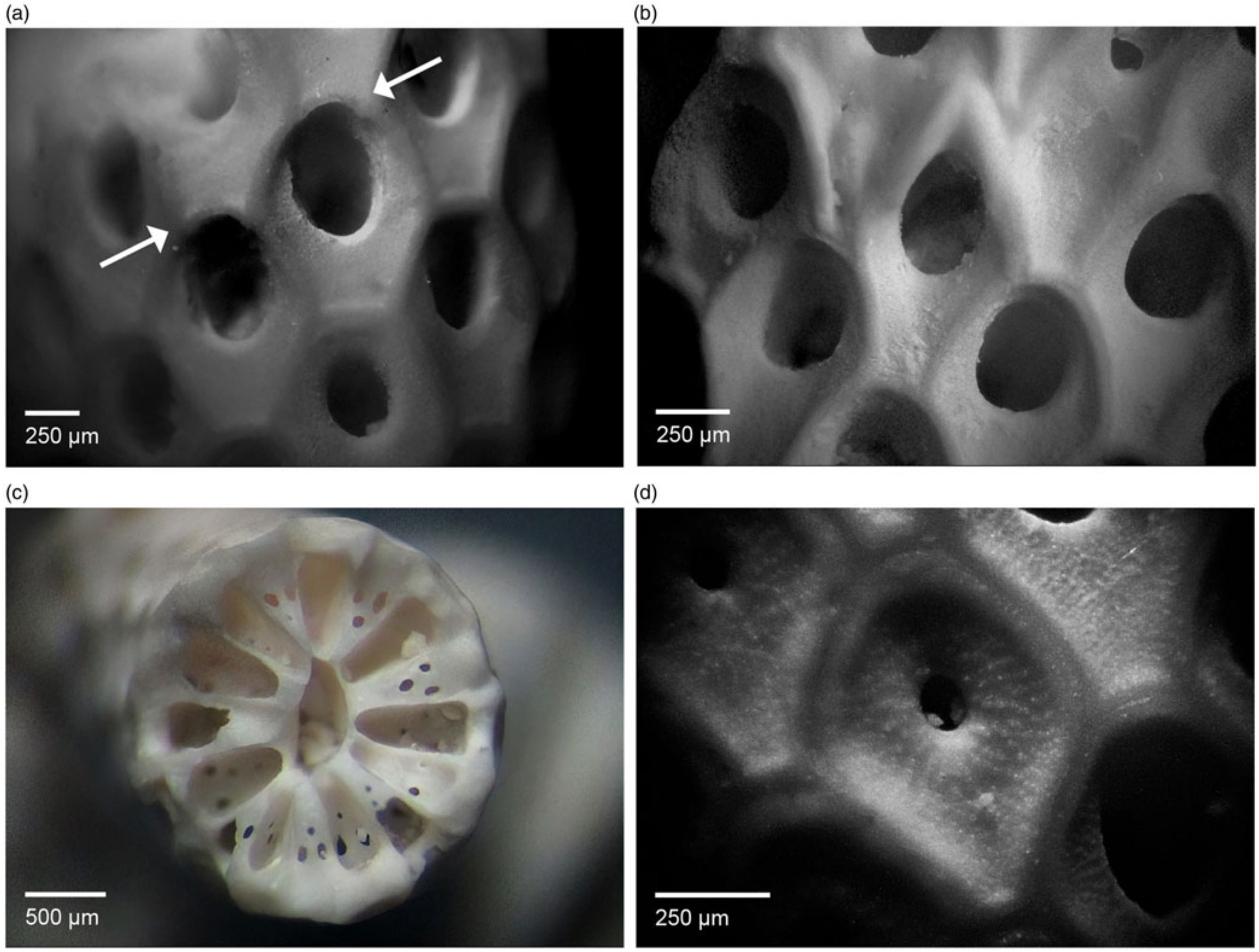

Figure 14. *Onychocella cylindrica*, (a) closeup of stem with ovicellate autozooids (arrows; NHMM 400EYS), (b) closeup of avicularium (NHMM 14EYS), (c) transverse section showing median channel ('sipho'; NHMM 400EYS), (d) closeup of kenozooid (NHMM 60EYS).

Description

Cylindrical, bifurcating stems with central canal, occasionally squashed and barely visible. Autozooids inverted pear-shaped or slightly hexagonal and surrounded by distinct blunt rim. Where rim meets rim of neighbouring zooids, thin groove formed. Opesiae oval, positioned terminally and covering about half of height of autozooids. Autozooidal cryptocyst granulated. Avicularia symmetrical, having about same size as autozooids; pentagonal with straight proximal side and short pointed rostrum. Avicularia also surrounded by distinct blunted rim. Avicularian opesiae elliptical or slightly oval and positioned terminally. Ovicells endozooidal(?), partly immersed in next distal zooid. Roof very slightly convex, forming small, indistinct cap. Ovicells previously unknown and described and figured here for the first time.

Measurements

NHMM_14EYS, ZL 825 ± 137, 650–1000 (1,6), ZW 570 ± 115, 450–750 (1,5), OL 414 ± 22, 400–450 (1,5), OW 324 ± 25, 300–350 (1,5), AL 890 ± 94, 820–1000 (1,3), AW 533 ± 29, 500–550 (1,3).

Remarks

The original generic name, *Siphonella*, referred to the central canal ('sipho') in this species. However, it was preoccupied by Macquart's (1835) genus of flies. Voigt (1979) assigned the present species to *Onychocella*, based in particular on the shape of the avicularia.

Stratigraphical range

Mid- to upper Maastrichtian.

Localities

Liège-Limburg area.

Onychocella matrona (von Hagenow, 1839)
Figure 15

*1839 *Glauconome matrona* von Hagenow, p. 292.
1851 *Eschara arcas* d'Orbigny, p. 127, pl. 666, figs 1–3.
1865 *Eschara arcas* d'Orbigny; Beissel, p. 17, pl. 1, fig. 9.
1930 *Onychocella matrona* (von Hagenow); Voigt, p. 458, pl. 16, fig. 12.

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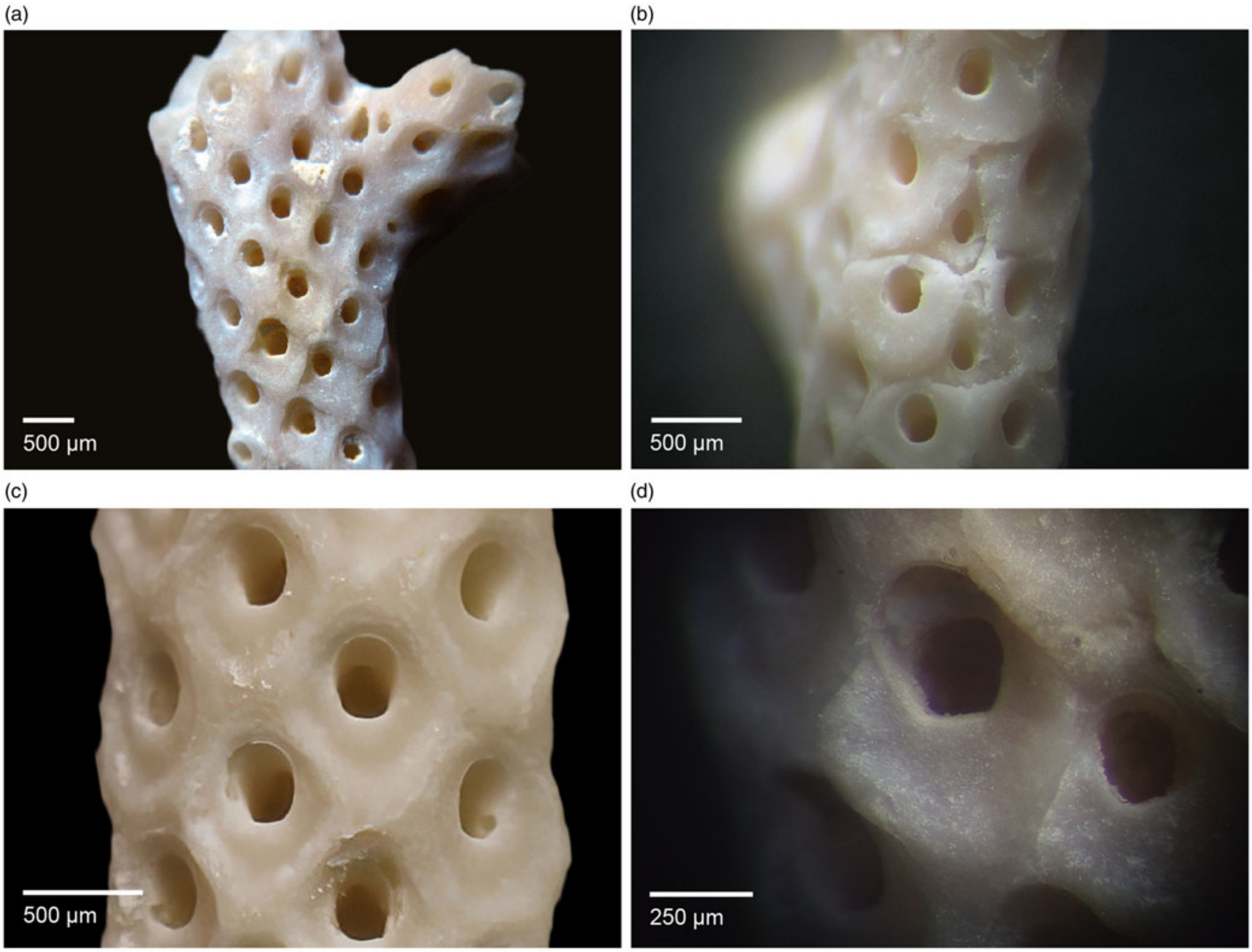

Figure 15. *Onychocella matrona*, (NHMM ZWHC05), (a) branching stem with autozooids, (b) two avicularia on lateral side of stem, (c) several autozooids, (d) closeup of ovicellate autozooid.

Material

Two specimens, NHMM ZWHC05, CPL (Kreco) quarry, Haccourt (Belgium), Zeven Wegen Member, NHMM LG2265, CPL (Kreco) Quarry, Haccourt (Belgium), Zeven Wegen Member.

Description

Ramose bifurcating stems with autozooids arranged in vertically alternating rows; width of branches ranging between 1.0 and 1.5 mm. Autozooids rhombic or subhexagonal, latero-distal part may be rounded or end in pointed or straight area. Elliptical/oval opesia with flattened proximal end, positioned terminally and surrounded by very thin rim. Autozooids separated from each other by fine groove and funnel-shaped cryptocysts slightly granulated. Ongoing extensive calcification of cryptocyst leading to change of outer appearance of autozooids in overlapping zooidal boundaries. Extensively calcified cryptocysts leading to rhombic, rectangular or irregularly rounded appearance of zooid. Avicularia varying in size and shape but mostly smaller than autozooids, drop-shaped with centrally placed oval or elliptical opesia. Avicularia common on lateral margins of colony, rare on frontal areas. Endozooidal ovicells causing some swelling of proximal part of distal autozooids. Opesia of fertile zooids tilted inwards towards median axis of colony.

Measurements

NHMM LG2265, ZL 781 ± 79, 698–884 (1,10), ZW 605 ± 45, 512–651(1,10), OL 302 ± 19, 279–326 (1,10), OW 205 ± 18, 186–233 (1,10).

Remarks

In the present paper, avicularia are described and illustrated for the first time.

Stratigraphical range

Upper Campanian to lower Maastrichtian.

Localities

Liège-Limburg area, Germany (Rügen, Hemmoor and Aachen) and Denmark (Møn).

Genus *Rhebasia* Jullien, 1882

Rhebasia disparilis (d'Orbigny, 1851)
Figure 16

1839 *Glauconome undulata* von Hagenow, p. 292, pl. 5, fig. 12.

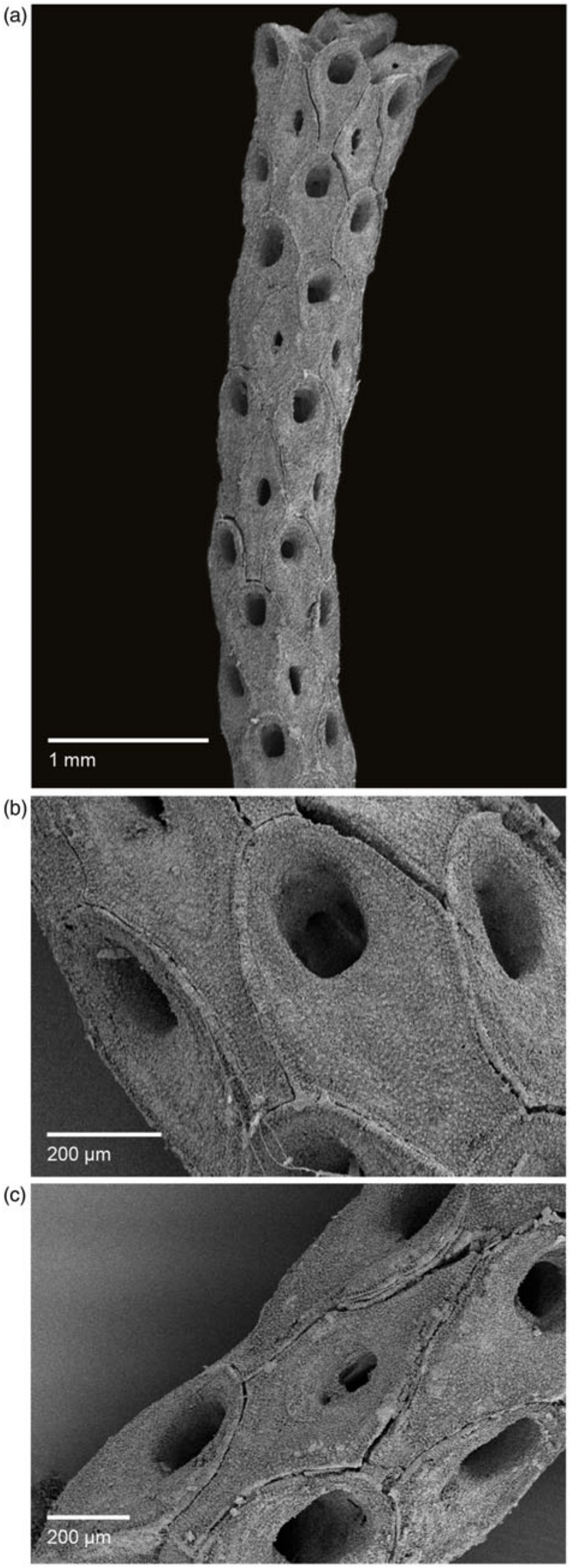

Figure 16. *Rhebasia disparilis*, (NHMM LG2129), (a) colony fragment with several autozooids and avicularia, (b) closeup of autozooid, (c) closeup of avicularium.

*1851 *Vincularia disparilis* d'Orbigny, p. 193, pl. 681, figs 16–18.

1930 *Woodipora disparilis* (d'Orbigny); Voigt, p. 486, pl. 25, fig. 2.

1986 *Woodipora disparilis* (d'Orbigny); Schubert, p. 18 (*partim*), pl. 1, figs 1–3; pl. 2; pl. 3, figs 1–4; pl. 4; pl. 6, figs 6–8; pl. 8, figs 4–9; pl. 9.

Material

A single specimen, NHMM LG2129, CPL (Kreco) quarry, Haccourt (Belgium), Zeven Wegen Member.

Description

Thin, dichotomously branching, vincularian stems with rather long and narrow, inverted pear-shaped autozooids. Suboval opesia situated in upper part of autozooid; cryptocyst slightly sunken and granulated. Autozooids and avicularia surrounded by rounded margin. Large avicularia (length >1 mm) lanceolate with straight, long, pointed rostrum. Proximal end of avicularia truncated and straight. Avicularian opesia elongate, elliptical, distinctly smaller than autozooidal opesia, and placed approximately in central part of zooid. Small constriction in form of 'tooth' on each disto-lateral side. Small bridge running from left to right in proximal part of opesia.

Measurements

ZL 712 ± 88, 662–850 (1,8), ZW 373 ± 9, 360–381 (1,7), OL 233 ± 29, 160 –283 (1,8), OW 156 ± 17, 119–182 (1,8).

Remarks

This species is described here for the first time for the study area. Schubert (1986) transferred *Vincularia disparilis* to *Woodipora*. However, the type species of that genus, *Flustra holostoma*, is an encrusting onychocellid from the Pliocene of England. Its cryptocyst is pierced by a pair of opesiules not found in any of the specimens from the Liège-Limburg area. Therefore, *Vincularia disparilis* cannot remain in *Woodipora* and we propose to transfer the species to *Rhebasia*, because its type species, *Eschara dorilas*, forms erect vincularian colonies with symmetrical onychocellid avicularia that are larger than the autozooids. Taylor et al. (2018) considered *Rhebasia* to be a subjective synonym of *Ogiva*. The two genera are similar, but the type species of the latter, *Eschara actaea*, forms bifoliate palmate colonies with avicularia that are not larger than the autozooids.

Stratigraphical range

Upper Campanian to Maastrichtian.

Localities

Liège-Limburg area, England (Norfolk), France (Paris Basin), Germany (Aachen area, Rügen); eastern Poland, Denmark.

Family Monoporellidae Hincks, 1882
Genus *Stichomicropora* Voigt, 1949

Stichomicropora sicksi Voigt, 1949
Figure 17

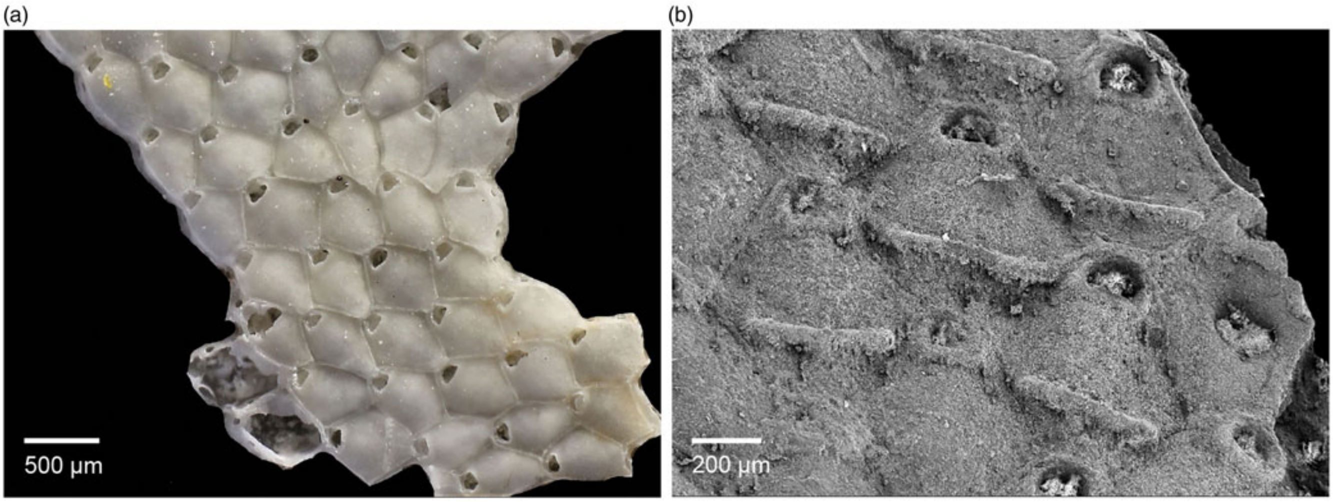

Figure 17. *Stichomicropora sicksi* (NHMM LG2309), (a) non-fertile autozooids, (b) ovicellate autozooids with transversely oriented spine bases; originally, downwardly bent spines formed walls of ovicells.

*1949 *Stichomicropora sicksi* Voigt, p. 34, pl. 7, figs 1–3.
2019b *Stichomicropora sicksi* Voigt; Martha et al., p. 325, fig. 55e, f.

Material

A single specimen, NHMM LG2309, CPL (Kreco) quarry, Haccourt (Belgium), Zeven Wegen Member.

Description

Encrusting zoarium with long hexagonal autozooids, arranged in regular quincunx pattern. Opesiae semicircular. Rather flat cryptocyst, slightly arched along central line. Every autozooid surrounded by distinct rim and clear furrow separating individual edges. Along lateral margins six or seven pairs of very small opesiulae present. Transverse bar present in proximal half of zooid, interpreted as remains of ovicells of proximal zooids.

Measurements

ZL 719 ± 57, 604–810 (1,8), ZW 675 ± 101, 554–875 (1,8), OL 115 ± 11, 98–133 (1,8), OW 145 ± 17, 117–166 (1,8).

Stratigraphical range

Lower to upper Campanian.

Localities

Liège-Limburg area and Germany (Lägerdorf).

Family Coscinopleuridae Canu, 1913
Genus *Coscinopleura* Marsson, 1887

Coscinopleura elegans (von Hagenow, 1839)
Figure 18

*1839 *Eschara elegans* von Hagenow, p. 265, pl. 4, fig. 3a–c.
1930 *Coscinopleura elegans* (v. Hagenow); Voigt, p. 490 (*partim*), pl. 25, fig. 16 (*non* 17).
1956 *Coscinopleura elegans elegans* (v. Hag.); Voigt, p. 41, pl. 2, figs 7, 8; pl. 3, figs 1–4; pl. 4, figs 6, 7.
1979 *Coscinopleura elegans* (v. Hagenow); Voigt, p. 49, pl. 10, fig. 3.
1991 *Coscinopleura elegans* (v. Hagenow); Voigt, pl. 3, fig. 9.
2001 *Coscinopleura elegans*; Håkansson & Thomsen, fig. 11.5.E.
2019 *Coscinopleura elegans*; Martha et al., p. 316, fig. 50e, f.

Material

Two specimens, NHMM LG2123a, former ENCI Quarry, Lanaye Member, and NHMM KSG_016_KIE, Kunrader Steengroeve quarry, Voerendaal, Maastricht Formation, Kunrade facies.

Description

Zooids inverted pear-shaped, arranged in very regular pattern and separated from each other by thin furrow. Barely recessed cryptocysts smooth; opesiae in upper half of zooecia at some distance from distal rim, their semi-lunar openings having straight lateral and proximal sides and arcuate distal side. Borders of opesiae are crenate in latero-distal part with broad proximal lip, directed inwards at sides. Occlusor laminae present. Zoarial margins bordered by vertical rows of vibracula (‘coscino-zooids’) with porous front (typically between 18 and 30 pores) and kenozooids. Small, oval opesiae with inwardly directed denticulum. Ovicells hyperstomial.

Measurements

NHMM LG2123a, ZL 589 ± 32, 550–625 (1,8), ZW 341 ± 17, 313–363 (1,8), OL 125 ± 7, 112–138 (1,8), OW 142 ± 13, 125–162 (1,8).

Remarks

Compared to *Coscinopleura lamourouxi* (see below), the present species has wider branches (3.0 to 3.5 mm), zooids are slightly longer, yet less wide, and the number of vertical rows of zooids is typically between 9 and 12.

Stratigraphical range

Lower to upper Maastrichtian.

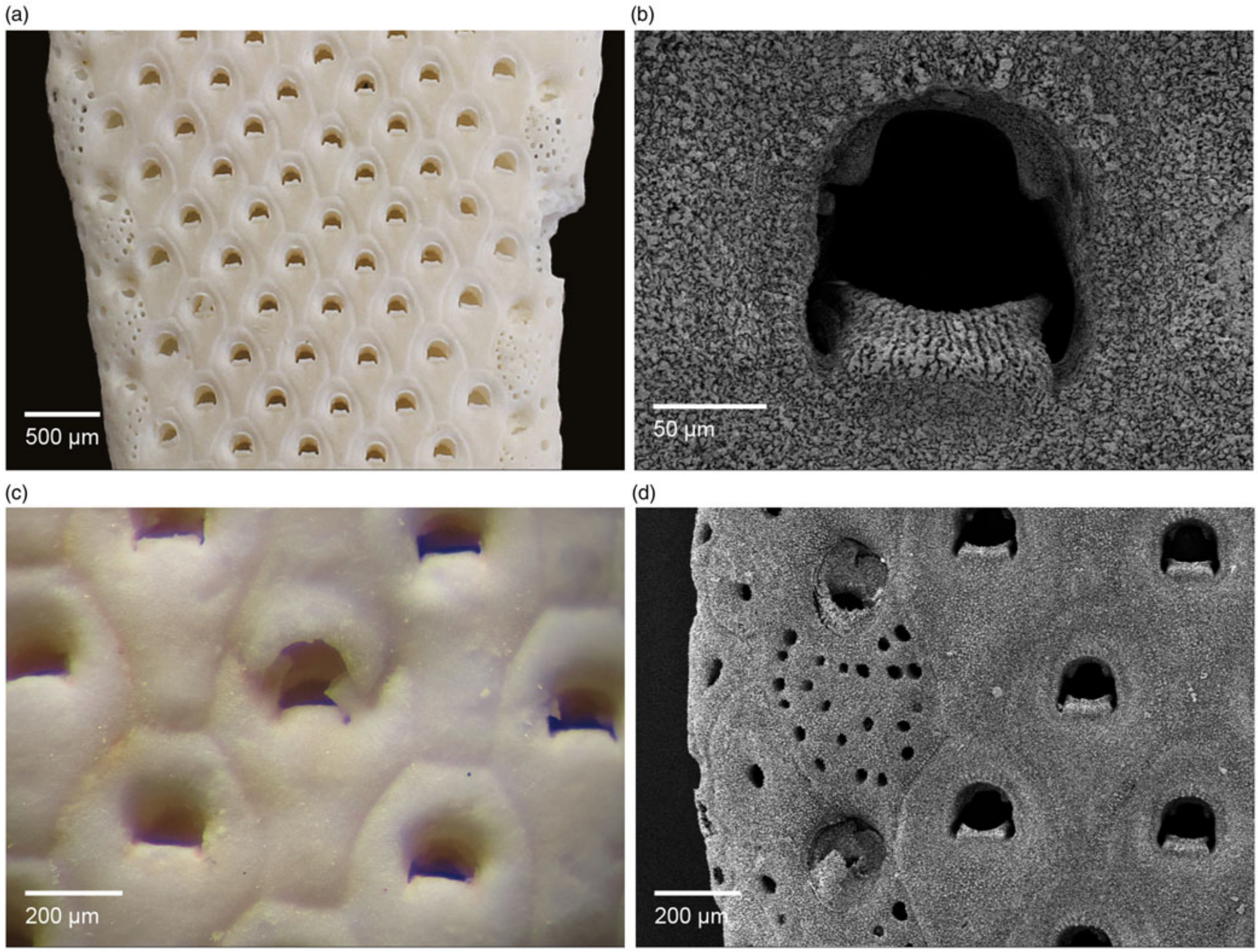

Figure 18. *Coscinopleura elegans*, (a) frontal surface with preserved coscino-zooids along lateral sides (NHMM LG2123a), (b) closeup of autozooidal opesia (NHMM LG2123a), (c) ovicellate zooid (NHMM KSG_016_KIE), (d) lateral side of colony with three types of zooids, from left to right: kenozooids, coscino-zooids and autozooids (NHMM LG2123a).

Localities

Liège-Limburg area, Germany (Rügen, Hemmoor, Lüneburg), Belgium (Ciply); England (Norfolk) and Denmark (Stevns Klint and numerous other localities).

Coscinopleura lamourouxi (von Hagenow, 1851)
Figure 19

*1851 *Eschara lamourouxi* von Hagenow, p. 73, pl. 8, fig. 20; pl. 12, fig. 11.
1851 *Eschara microstoma* von Hagenow, p. 73, pl. 8, fig. 19.
1956 *Coscinopleura lamourouxi* (von Hagenow); Voigt, p. 45, pl. 1, figs 1-6; pl. 2, figs 1–4.
1979 *Coscinopleura lamourouxi* (von Hagenow); Voigt, p. 49, pl. 10, fig. 4.
1988 *Coscinopleura lamourouxi* (von Hagenow); Favorskaya, pl. 2, figs 2–5.
1996 *Coscinopleura lamourouxi* (von Hagenow); Favorskaya, pl. 4, fig. 7.
2001 *Coscinopleura lamourouxi* (von Hagenow); Håkansson & Thomsen, figs 11.4.C, 11.5.D.
2019 *Coscinopleura elegans*; Martha et al., p. 318, fig. 52a, b.

Material

Two specimens, NHMM 14EYSa, Marnebel Quarry, Eben Emael (Belgium), Lanaye Member, between flint levels 10 and 11; NHMM 11_1_KUN, Kunrader Steengroeve Quarry, Voerendaal, Maastricht Formation, Kunrade facies.

Description

Flattened, bilamellar, dichotomously branched colonies, branch width 1.5 to 2.0 mm, with 5 to 8 rows of alternatingly arranged autozooids. Autozooids inverted pear-shaped or hexagonal with straight proximal and distal ends. Semi-elliptical or semicircular opesiae, not terminal, surrounded by serrated rim. At proximal end of opesiae rim showing left and right and upwardly directed saddle-shaped bracket, in distal area occlusor lamina visible. Autozooids separated from each other by tiny groove with central lamella. Cryptocyst centrally slightly recessed and granulated. Vibracula forming straight rows at margins of colony and granulated cryptocyst ('tremocyst' *sensu* Voigt, 1956) showing 20 to 25 pores. Opesiae with broad denticulum, tilted inwards. Rectangular peripheral caverns at proximal edge of autozooids. (?)Hyperstomial ovicells with crescent-shaped roof partially covering opesia.

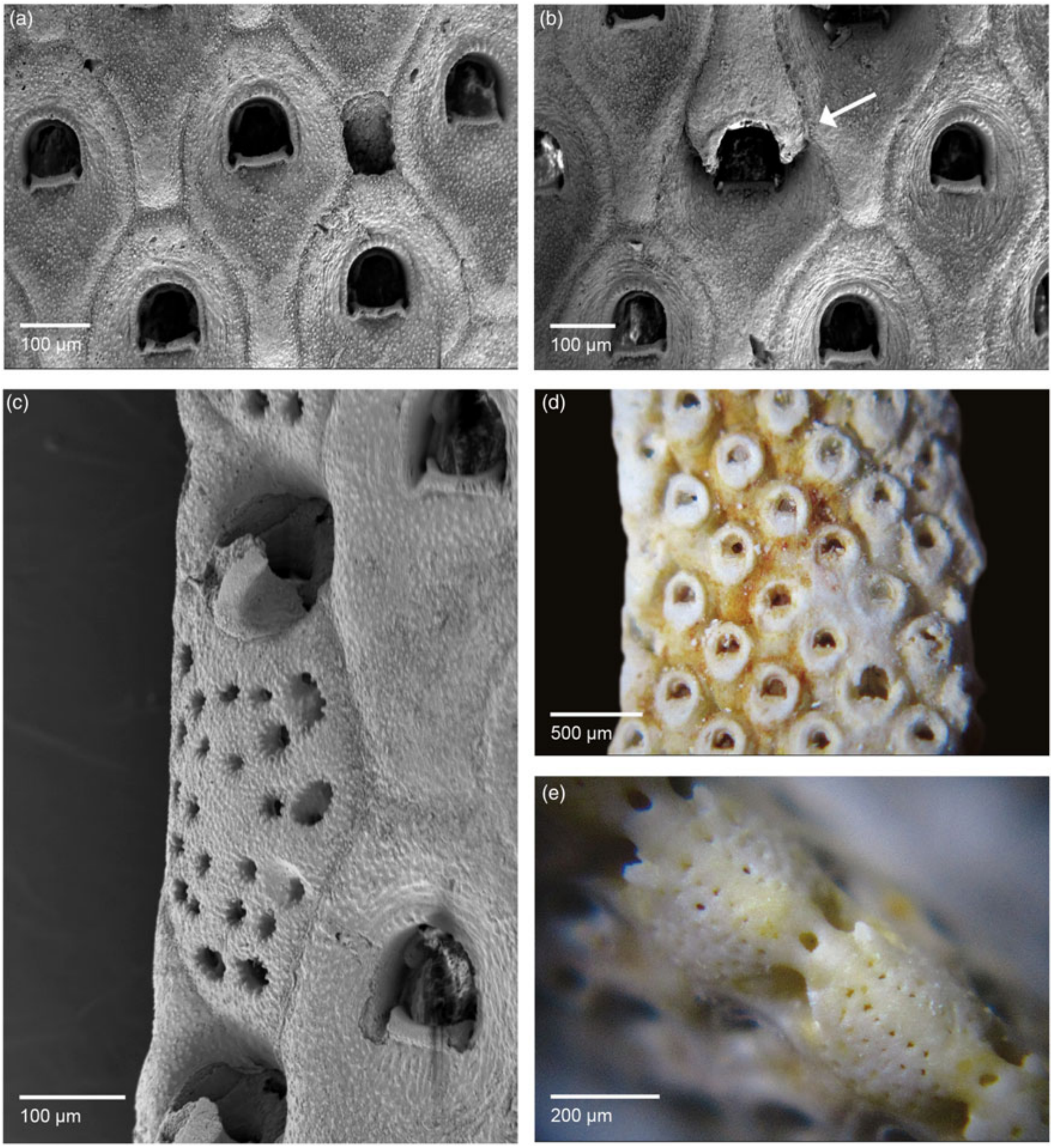

Figure 19. *Coscinopleura lamourouxi*, (a) several autozooids (NHMM 14EYSaa), (b) one ovicellate autozooid (NHMM 14EYSa), (c) closeup of coscino-zooid (NHMM 14EYSa), (d) worn specimen with 'type-2' peripheral caverns (NHMM 11_1_KUN), (e) lateral view of coscino-zooids (NHMM 14EYSa).

Measurements

NHMM 14EYSa, ZL 644 ± 34, 622–711 (1,8), ZW 383 ± 31, 333–701 (1,8), OL 122 ± 12, 111–133 (1,8), PW 122 ± 12, 111–133 (1,8).

Remarks

One of the specimens, NHMM 11_1_KUN, shows extensive peripheral caverns, only leaving out a circular cryptocystal area around the opesia ('insula', *sensu* Voigt, 1956). This corresponds with the 'type 2' peripheral caverns described by Koromyslova et al. (2018).

Stratigraphical range

Mid- to upper Maastrichtian.

Localities

Liège-Limburg area, Belgium (Mons Basin), France (Haute-Garonne, Midi-Pyrénées, Occitanie), Germany (Hemmoor, Ilten), Spain (Olazti/Olazagutía), Tadjikistan and Uzbekistan (Kydzylkum desert)

Family Tessaradomidae Jullien & Calvet, 1903
Genus *Pachydermopora* Gordon, 2002

Pachydermopora pachyderma (Marsson, 1887)
Figure 20

*1852 *Porina pachyderma* Marsson, p.87, pl. 8, fig. 13.
1925 *Monoporella pachyderma* (Marsson); Levinsen, p. 401, pl. 7, fig. 79.

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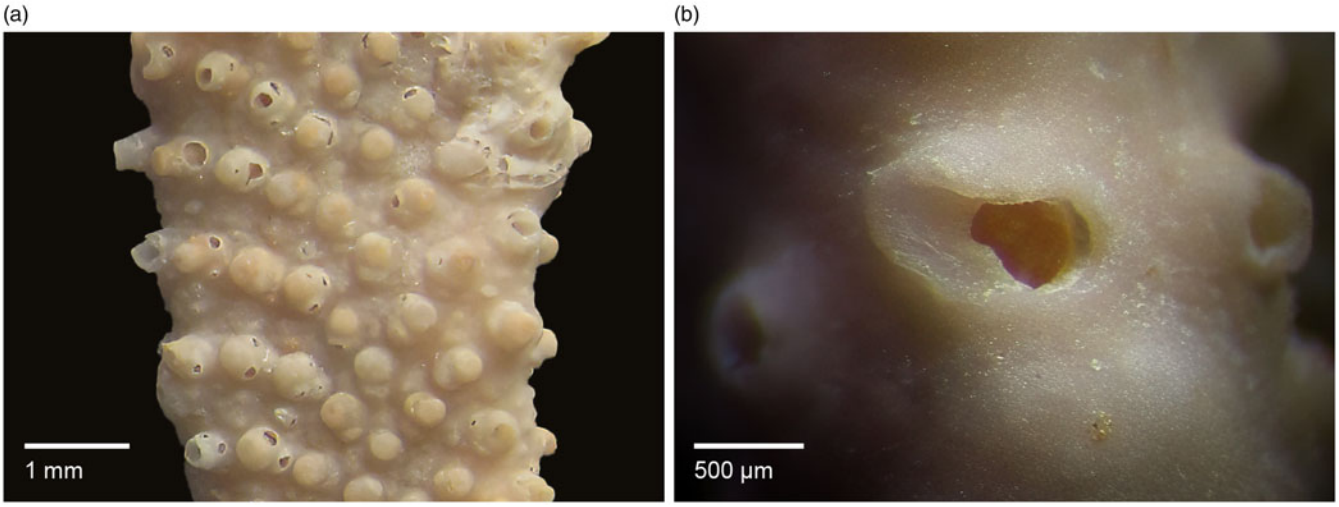

Figure 20. *Pachydermopora pachyderma* (NHMM ZWHC04), (a) frontal view of stem, (b) lateral avicularium.

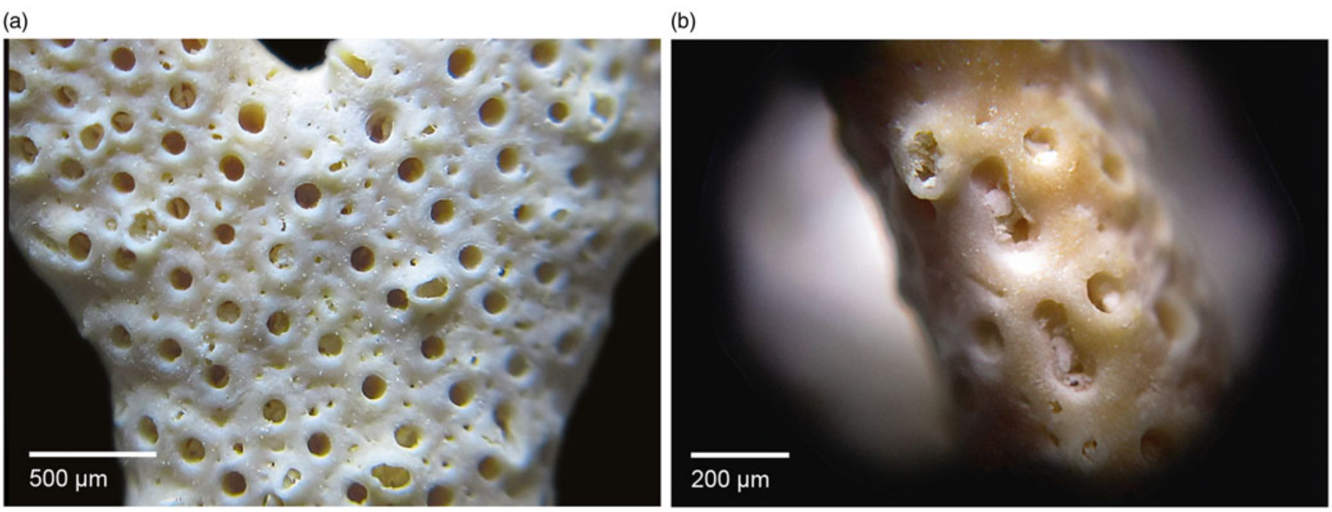

Figure 21. *Beisselina aviculifera* (NHMM 53_EYS), (a) frontal surface of bifurcating stem, (b) closeup of two lateral avicularia.

1967 *Porina pachyderma* Marsson; Voigt, p. 69, pl. 26, fig. 6; pl. 27, figs 1, 2.

2002 *Pachydermopora pachyderma* (Marsson); Gordon, p. 116, figs 18–21.

Material

A single specimen, NHMM ZWHC 04, CPL (Kreco) quarry, Haccourt (Belgium), Zeven Wegen Member.

Description

Sturdy, bilamellar, dichotomously branched colonies mostly thickened by secondary calcification; autozooids arranged in V-shaped, slightly bent rows. Secondary orifice ending in slightly elevated cylindrical peristomes, surrounded by one or more small, round or oval avicularia, giving surface knobbly appearance. Occasionally between rows, but more often on lateral margins of colony, bispatulate vicarious avicularia, varying in size, present. Surface of colonies granular. Spiramen present proximal to every orifice. Ovicells not detected.

Measurements

ASW 556 ± 44, 483–603 (1, 8).

Remarks

This common early Maastrichtian species has previously been recorded from northern Germany, England and Denmark; the present record is the first from the upper Campanian of the study area.

Stratigraphical range

Upper Campanian to lower Maastrichtian.

Localities

Liège-Limburg area, Germany (Rügen, Lüneburg), France (?Meudon, Chavot/Marne) and Denmark.

Genus *Beisselina* Canu, 1913

Beisselina aviculifera Wiesemann, 1963
Figure 21

Table 1. Bryozoan taxa recorded from the Gulpen Formation and their currently known stratigraphical distribution in the study area. Taxa described in the present paper are marked with an asterisk (*). Other species collected and identified by the authors Kesselhut and Goffings

	Gulpen Formation						
	Members					Maastricht Formation	
Taxa	Zeven Wegen	Beutenaken	Vijlen	Lixhe	Lanaye	Maastricht	Kunrade facies
Order Cyclostomata							
Clinopora aff. *costulata* Marsson, 1887*	x						
Disporella obvallata (Marsson, 1887)*				x	x	x	
'Lichenopora' reticulata (von Hagenow, 1851)				x		?	x
Patinella sp.				x			
Petalopora sp.					x		
Petalopora cf. *pulchella* (Roemer, 1840)					x		x
Plagioecia sp.				x			
Proboscina cf. *crassa* (Roemer, 1840)			x	x			
Order Cheilostomata							
Aechmellina anglica (Brydone, 1909)*			x	x			
Amphiblestrella ringens (von Hagenow, 1839)				x		x	
Beisselina aviculifera Wiesemann, 1963*					x	x	x
Biaviculigera sacerdotalis (Brydone, 1914)*			x				
Castanopora sp.					x		
Coscinopleura elegans elegans (von Hagenow, 1839)*					x	x	x
Coscinopleura lamourouxi (von Hagenow, 1851)*					x	x	x
Escharifora papyracea (von Hagenow, 1851)*					x	x	x
Escharipora elegans d'Orbigny, 1852					x		
Floridina cf. *impressipora* (Marsson, 1887)			x				x
Herpetopora laxata (d'Orbigny, 1852)*			x	x			
Heteroconopeum ovatum (Canu & Bassler, 1926)*					x		
Onychocella cyclostoma (Goldfuss, 1826)*					x	x	x
Onychocella cylindrica (von Hagenow, 1851)*					x	x	
Onychocella matrona (von Hagenow, 1839)*	x						
Pachydermopora pachyderma (Marsson, 1887)*	x						
Rhebasia disparilis (d'Orbigny, 1851)*	x						
Semiflustrella britannica (Brydone, 1906)*					x		
Setosinella aff. *prolifica* Canu & Bassler, 1933					x		
Stichomicropora sicksi Voigt, 1949*	x						
'Vincularia' (sensu lato) marssoniana (Voigt, 1924)*	x					?	x
Wilbertopora aff. *oxyteichos* (Voigt, 1930)*	x						

*1963 *Beisselina aviculifera* Wiesemann, p. 31, pl. 3, figs 1–6.

Material

A single specimen, NHMM 53_EYS, Marnebel quarry, Eben Emael (Belgium), Lanaye Member, between flint levels 21 and 22.

Description

Colonies bifurcating bilamellar stems, elliptical in cross section. Autozooids arranged in slightly bent V-shaped rows. Autozooidal peristomes flat and thick, occasionally protruding distally in well-preserved colonies (compare Wiesemann, 1963). Secondary orifice circular, slightly sunken and with a thin and sharp rim. Spiramen small, circular or transversely oriented and positioned proximally to secondary orifice. Avicularia of three kinds: 1 – small interzooidal avicularia often positioned centrally above peristomes of autozooids, oriented proximally, laterodistally with arched, slightly protruding rostrum, pivotal bar present; 2 – large interzooidal avicularia, outline oval to rounded trigonal, oriented proximally or transversely, rostrum elevated; pivotal bar present; 3 – lateral avicularia (positioned in vertical rows on lateral margins of colony, often in groups of two or more); outline elongate, lateral sides concave, rostrum sunken, spatulate. Ovicells internal.

Measurements

AD 90 ± 7, 80–100 (1,8) ASW 200 ± 21, 190–230 (1,8)

Remarks

This species belongs to the highly variable *Beisselina striata* group, extensively studied and described by Wiesemann (1963). Features that differentiate it from *B. striata*, *B. boryana* and *B. distaviculoecia* are (*sensu* Wiesemann, 1963) the large protruding frontal avicularia and the distally protruding autozooidal peristomes; the latter are observed in well-preserved colonies only. As these differences are often slight and many intermediate and variable forms occur, it is questionable if all of the newly introduced species by Wiesemann (1963) are valid. Further investigations of this complex group are called for.

Stratigraphical range

Mid- to upper Maastrichtian.

Localities

Liège-Limburg area and (?)southern Belgium (Ciply)

Discussion and conclusions

The nineteen bryozoan species from the Gulpen Formation described in the present paper contribute significantly to our understanding of their geographical and stratigraphical distribution. Together with another 11 species from the Gulpen Formation (see Table 1), which have been identified by the authors Kesselhut and Goffings, these allow comparisons to be made with localities across Europe, for instance, with northern Germany (Rügen, Hemmoor, Hannover area) and with European Russia.

Based on the species listed in Table 1, the Gulpen Formation appears to comprise three distinct bryozoan assemblages. The late Campanian Zeven Wegen Member contains a characteristic assemblage of Cheilostomata. The lower to mid-Maastrichtian Vijlen and Lixhe members comprise a mixed assemblage of Cheilostomata and Cyclostomata. Taxa represented in the Zeven Wegen and Vijlen-Lixhe assemblages generally have a wide distribution across northwest Europe. The late Maastrichtian Lanaye Member comprises a distinctly different assemblage, dominated by Cheilostomata. Several of the species from this assemblage also occur in the overlying Maastricht Formation. This is consistent with recent findings that suggest that the Lanaye Member represents a transition to a shallower depositional environment with higher nutrient availability, more closely similar to that of the Maastricht Formation (Vancoppenolle et al., 2022; Jagt et al., 2024). Two of the species in this assemblage, *Heteroconopeum ovatum* and *Semiflustrella britannica*, are added to the list of Late Cretaceous bryozoans known from both Europe and the southeast or east of the United States, highlighting palaeobiogeographical connections in the Late Cretaceous. The new findings, particularly in the morphology of some of the species described herein, underscore that it is essential to pursue further studies using current technologies. The focus here must be primarily on the countless species that were described, often inadequately, and with poor illustrations, by authors in the 19th and early 20th centuries.

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