RESEARCH PAPER

The internal morphology of *Acoscinopleura* Voigt, 1956 (Cheilostomata, Bryozoa) from the Campanian–Maastrichtian of Central and Eastern Europe

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Abstract

Coscinopleurid cheilostome bryozoans are widespread in Latest Cretaceous sediments throughout the whole Boreal Chalk Sea. Despite having many polymorphs that can readily be distinguished, intraspecific plasticity is high and polymorph morphology shows only little variation over time. This significantly hampers taxon differentiation in coscinopleurids. In this study, we revise type material of three coscinopleurid species, *Acoscinopleura foliacea* (Voigt, 1930), *A. fallax* Voigt, 1956 and *A. rugica* Voigt, 1956, from the Maastrichtian of northern Germany using combined scanning electron microscopy and X-ray microtomography. The three species are morphologically very similar and were distinguished by the original author only in the shape and position of peripheral caverns inside their cryptocyst and in the position of vibracular polymorphs. X-ray microtomography allowed study of the internal morphology of the species and provided additional parameters that can be used for species differentiation. Septula, arch-like and channel-like cavities and microcavities could be identified inside the calcified walls. While the original identity of the type material of *A. foliacea* and *A. rugica* remains unchanged, the type material of *A. fallax* is shown to belong to three different species: *A. fallax*, *A. occulta* sp. nov. and *A. dualis* sp. nov. Additionally, hitherto-unstudied material from the late Campanian and Maastrichtian of northern Germany and Belarus is described as *A. crassa* sp. nov. and *A. albaruthenica* sp. nov.

Keywords Bryozoa · Cheilostomata · Micro-CT · Taxonomy · Morphology · White Chalk

Kurzfassung

Coscinopleuride cheilostome Bryozoen haben eine große Verbreitung in oberkretazischen Sedimenten des gesamten borealen Schreibkreide-Meeres. Obwohl sie zahlreiche Polymorphe haben, die sich leicht unterscheiden lassen, ist die intraspezifische Plastizität groß und die morphologische Variation der Polymorphe im Laufe der Zeit nur gering. Dies beeinträchtigt die Artunterscheidung innerhalb der Coscinopleuriden deutlich. In unserer Studie wird das Typusmaterial dreier coscinopleuriden Arten aus dem Maastrichtium Norddeutschlands—*Acoscinopleura foliacea* (Voigt, 1930), *A. fallax* Voigt, 1956 und *A. rugica* Voigt, 1956—anhand von Rasterelektronenmikroskopie und Mikro-Computertomographie untersucht. Diese drei Arten sind morphologisch sehr ähnlich und wurden vom Erstbeschreiber nur anhand der Form und Lage peripherer Kavernen innerhalb der Kryptozyste und der Lage von vibrakularen Polymorphen unterschieden. Mikro-Computertomographische Untersuchungen geben Einblicke in die innere Morphologie der Arten und ermöglichen außerdem die Bestimmung weiterer Parameter, die für die Artunterscheidung verwendet werden können. Septula, schlitzförmige Höhlen, kanalartige Hohlräume und Mikrokavitäten konnten in den kalzifizierten Wänden identifiziert werden. Während die ursprüngliche Identität von *A. foliacea* und *A. rugica* unangetastet bleibt, wird das Typusmaterial von *A. fallax* in drei verschiedene Arten aufgeteilt;

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A. fallax, *A. occulta* sp. nov. und *A. dualis* sp. nov. Zusätzliches, bisher unbeschriebenes, Material aus dem Obercampanium und Maastrichtium von Norddeutschland und Weißrussland wird als *A. crassa* sp. nov. und *A. albaruthenica* sp. nov. beschrieben.

Schlüsselwörter Bryozoa · Cheilostomata · Micro-CT · Taxonomie · Morphologie · Oberkreide

Introduction

Coscinopleuridae Canu, 1913 is a family of cheilostome bryozoans that were locally abundant in sediments from the Santonian to Thanetian. Coscinopleurid cheilostomes have erect, bifoliate colonies, and autozooids strongly resemble those of Onychocellidae Jullien, 1882. However, the opesia is never terminal in coscinopleurid species and always shows short opesiular indentations. Furthermore, the vibracular polymorphs found in Coscinopleuridae are unique in morphology among cheilostomes. Another distinctive feature is that many coscinopleurid species have hollows or grooves in their cryptocysts. These 'peripheral caverns' sensu Voigt (1956), the occurrence of which is usually very irregular, are found outside Coscinopleuridae in only a few onychocellid species from the Late Cretaceous and have no analogy in Recent cheilostomes. The function and causes of formation of peripheral caverns have not yet been understood (Voigt 1956; Voigt 1985; Taylor and McKinney 2006).

For our study, we investigated the type material of three species of *Acoscinopleura* Voigt, 1956 from Western and Central Europe first described in Voigt (1956): *A. foliacea* (Voigt, 1930), *A. fallax* Voigt, 1956 and *A. rugica* Voigt, 1956, and compared it with new material from Eastern Europe. The three species are morphologically very similar and were discriminated by Voigt (1956) mainly because of the presence or absence of peripheral caverns and their shape. *Acoscinopleura* is found in the Latest Cretaceous of the Boreal Chalk Sea (e.g. Voigt 1956; Maryańska 1969; Georgala and Brood 1974; Favorskaya 1992) that extended in Late Cretaceous times from Western Europe to Central Asia. Our examinations included traditional scanning electron microscopy (SEM) and X-ray microtomography (micro-CT), which is a well-established non-destructive method to study internal structures. For fossil bryozoan material, Viskova and Pakhnevich (2010) first applied micro-CT on a ctenostome bryozoan from the Middle Jurassic of western Russia, while Fedorov et al. (2017) used micro-CT to visualise the internal structures of esthonioporate bryozoans from the earliest Floian (Early Ordovician) of northwestern Russia. Micro-CT on fossil bryozoans from the Late Cretaceous was first applied by Koromyslova and Pakhnevich (2016) on cheilostome bryozoans from the late Campanian of Belarus and by Martha et al. (in press) on a cyclostome species from the middle Santonian of the Subhercynian Cretaceous Basin in Germany. The material of *Acoscinopleura* studied herein proved suitable for micro-CT

analyses since the preservation of the colonies was very good with hardly any sediment infillings in the bryozoan chambers. Internal structures could be visualised, and thus information on the internal morphology of the acoscinopleurid species was obtained. In addition to the zooid chambers and septula, some new characters were visualised that have not previously been described from any other bryozoan species. This includes cavities inside the lateral and transverse walls, described here as lateral and transverse channel-like cavities, respectively, and cavities encircling the distal septula, described here as arch-like cavities.

The aims of this study are (1) to revise the family Coscinopleuridae Canu, 1913 and the genus *Acoscinopleura* Voigt, 1956; (2) to redescribe the species *A. foliacea*, *A. fallax* and *A. rugica* and four new species of *Acoscinopleura* using combined micro-CT and SEM results; and (3) to discuss the internal morphology of examined species.

Geological setting

Acoscinopleura is one of the commonest cheilostome genera found in Campanian to Maastrichtian deposits of the Boreal Chalk Sea from Western Europe and Central Asia. The material examined in this study is from several outcrops in northern Germany, Poland and western Belarus (Fig. 1). A comprehensive overview of the bryozoan-rich fossil sites in Western and Northern Europe, including most of the outcrops with material for this study, has been provided by Voigt (1979a).

The White Chalk cliffs on the northeastern coast of the Island of Rügen are one of the world's best studied exposures of White Chalk and the type locality for many different species (Reich and Frenzel 2002 and references therein). The chalk cliffs expose a section from the early Maastrichtian (*Belemnella obtusa* to *B. fastigata* belemnite zones). Bryozoan research on Rügen includes the famous works of von Hagenow (1839) and Marsson (1887). At least 275 species of early Maastrichtian Rügen bryozoans have been described (see fauna list in Reich and Frenzel 2002).

At Hemmoor, bryozoans were found in the White Chalk deposits of an abandoned chalk pit of a former brick factory (e.g. Christensen et al. 2004; Niebuhr et al. 2007) and in a smaller chalk pit near Hemmoor-Basbeck (Voigt 1979a). The White Chalk section at Hemmoor ranges from the upper parts of the early Maastrichtian to the late Maastrichtian (*Belemnella sumensis* to *Belemnitella baltica/danica*

Fig. 1 Location of material used for this study (bold) and of other localities mentioned in the text (italics) in Central and Eastern Europe

belemnite zones) and comprises the upper part of the northern German standard section of Lägerdorf–Kronsmoor–Hemmoor (e.g. Niebuhr et al. 2007). Although it is one of the best studied sites from the Late Cretaceous of Germany and bryozoans are numerous, no overview of the bryozoan fauna from Hemmoor has been given.

The material examined from Eastern Europe is from Stara Kornica in eastern Poland, where there is an outcrop section of the latest Campanian to early Maastrichtian (Alexandrowicz 1965) and from material of an erratic block in a chalk pit of the Integrated Building Material Plant near Hrodna/Grodno (гродна/гродно), Belarus. The age of the erratic block was determined to be late Campanian based on findings of *Belemnitella mucronata* (Barskov and Weiss 1987).

Materials and methods

For this study, we investigated material of *Acoscinopleura* from two collections. Material from the Maastrichtian of northern Germany is part of the Voigt Collection housed at the Senckenberg Gesellschaft für Naturforschung (SGN), Frankfurt am Main, Germany and was collected by Ehrhard Voigt in the middle of the 20th century, while material from western Belarus is stored at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN), Moscow, Russian Federation and was collected in the 1980s by A.F. Weiss. Material from the Voigt Collection includes

type material of three species that were first imaged and described in Voigt (1956).

Scanning electron microscopy (SEM) images of material stored at the PIN and in part of material stored at the SGN were produced on uncoated samples using the backscattered electron detector of a Tescan Vega XMU equipped with a low-vacuum chamber (10 Pa), while most specimens from the Voigt Collection were coated in gold/palladium (20/80) and imaged at the SGN using a Camscan CS 24 SEM producing secondary-electron images.

X-ray micro-computed tomography (micro-CT) was carried out at the PIN on selected samples showing excellent preservation of internal features using an X-ray SkyScan 1172. An Al filter (1 mm) was used. The voltage was at 100 kV, while the current was at 100 mA. For each sample, 520 virtual sections in three directions (transverse: parallel to the transverse walls of the zooids; coronal: parallel to the frontal and basal walls of the zooids; and sagittal: parallel to the lateral walls of the zooids) were produced at a rotation of 180°. The resolution was 4–5 μm for each sample, and the rotation angle was 0.7°.

Biometrical measurements were performed on micro-CT and SEM images. Measurements are given as range and arithmetic mean ± standard error and coefficient of variation. The total number of measurements is indicated.

Abbreviations used in the figures: Alc: arch-like cavities; Az: autozooid; ClcLt: lateral channel-like cavities; ClcTr: transverse channel-like cavities; Cr: cryptocyst; Cv: peripheral cavern; Ct: craticula; ICh: internal chamber of ovicell;

Ins: insula; Mc: microcavity; Ov: ovicell; SpB: basal septulum; SpD: distal septulum; SpL: lateral septulum; Tb: tube for passage of lophophore; Vb: vibraculum; WB: basal wall; WV: vertical wall.

Systematic palaeontology

Phylum **Bryozoa** Ehrenberg, 1831
Class **Gymnolaemata** Allman, 1856
Order **Cheilostomata** Busk, 1852
Infraorder **Flustrina** Smitt, 1867
Superfamily **Microporoidea** Gray, 1848
Family **Coscinopleuridae** Canu, 1913

Emended diagnosis. Colony erect, bifoliate. Cryptocyst surrounding the opesia from all sides. Opesia semicircular, never terminal, with two proximolateral opesiular indentations. Occlusor laminae maybe developed in the distal part of opesia. Ovicell endozooidal, ooecia cryptocystal, well-developed. Vibracula vicarious, always asymmetrical. Kenozooids present.

Remarks. This family of cheilostome bryozoans ranges from the middle Santonian of Vendôme, France [*Acoscinopleura*? *vindocinensis* (Filliozat, 1908)] to the Thanetian of Vincentown, USA [*Coscinopleura digitata* (Morton, 1834)]. Recently, *Eschara lineolata* Reuss, 1874 from the Strehlen Formation (mid-late Turonian) of Dresden-Strehlen or Weinböhla was identified to be a badly preserved coscinopleurid species (Martha et al. 2017). However, there is no indication of the provenance or the stratigraphy on the label, and the Turonian identity is therefore dubious. Furthermore, the presence of vibracula is not ascertained for this specimen.

The position of Coscinopleuridae within the Cheilostomata is uncertain. There are several reasons that make it reasonable to place the Coscinopleuridae within the suborder Flustrina Smitt, 1867 and within the superfamily Microporoidea Gray, 1848. Coscinopleurid bryozoans show clear morphological similarities with Onychocellidae Jullien, 1882, suggesting a close relationship between these two families (Voigt 1956) and even a possible origin of the Coscinopleuridae from the Onychocellidae. This is in particular visible in the presence of peripheral caverns in the cryptocyst of several species belonging to *Acoscinopleura*, *Coscinopleura* and *Tremocoscinopleura*, a feature known only from few non-coscinopleurid species of the Latest Cretaceous, all of which belong to the Onychocellidae Jullien, 1882.

In the emended diagnosis of this family, we consider the presence of vibracular polymorphs as a key character for Coscinopleuridae. This is justified by vibracula being an apomorphy in Coscinopleuridae, distinguishing this family from its probable ancestor Onychocellidae Jullien, 1882. Species of the genus *Escharifora* d'Orbigny, 1852, previously included in Coscinopleuridae, have avicularia that resemble those in onychocellid genera. Huge pores piercing through the autozooidal cryptocyst and resembling the peripheral caverns in several coscinopleurids are not considered justification enough to include this genus in Coscinopleuridae, as they also occur in some onychocellid species. *Escharifora* is therefore excluded herein from Coscinopleuridae. Excluding *Escharifora*, three genera are currently assigned to the Coscinopleuridae, mainly distinguished by the arrangement and morphology of the vibracula (Table 1). Species of *Coscinopleura* Marsson, 1887 have asymmetric vibracula (termed 'coscinozooids' in Voigt 1956) arranged in uniserial rows at the lateral margins of each colony and with a cryptocyst pierced by several small pores (termed 'coscinopores' in Voigt 1956). Species of *Acoscinopleura* Voigt, 1956 have vibracula irregularly arranged between the autozooids, and the vibracular cryptocyst lacks pores, whereas species of *Tremocoscinopleura* Voigt, 1956 have vibracula irregularly arranged between the autozooids and with a huge pore (termed 'frontal pore' in Voigt 1956).

Stratigraphic range. Middle Santonian (or late Turonian?) to Thanetian.

Genus *Acoscinopleura* Voigt, 1956
Type species. Coscinopleura foliacea (Voigt, 1930), early Maastrichtian, Rügen, Germany.

Table 1 Comparison of key morphological characters of the coscinopleurid genera *Acoscinopleura* Voigt, 1956, *Coscinopleura* Marsson, 1887 and *Tremocoscinopleura* Voigt, 1956

	Acoscinopleura	*Coscinopleura*	*Tremocoscinopleura*
Type species	*A. foliacea* (Voigt, 1930)	*C. elegans* (von Hagenow, 1839)	*T. monops* Voigt, 1956
Type species range	Early Maastrichtian	Maastrichtian to Danian (?)	Late Maastrichtian
Vibracularian position	Irregular	Marginal rows	Irregular
Vibracularian cryptocyst	Unporous	Porous	Large median pore
Genus range	?Santonian to Maastrichtian	Campanian to ?Danian	Campanian to Maastrichtian

Emended diagnosis. Colony erect, bifoliate, eschariform or adeoniform and then dichotomously branching. Zooids arranged quincuncially. No gymnocyst. Cryptocyst pustulose, surrounding the opesia from all sides. Peripheral caverns sometimes present inside the cryptocyst, distally, laterally or proximally. Opesia not terminal, but a little more proximal, small, with two proximolateral opesiular indentations. Occlusor laminae maybe developed in the distal part of opesia. No spine bases. Ovicells endozooidal, ooecia cryptocystal, well-developed. Vibracula vicarious, irregularly placed among autozooids or forming rows at the lateral margins of a colony. Kenozooids present at margins of a colony.

Remarks. The genus *Acoscinopleura* was established in Voigt ([1956](#)) in a comprehensive revision of coscinopleurid cheilostomes. It includes coscinopleurid species with vicarious vibracula that are irregularly placed among the autozooids and a cryptocyst that is not pierced by pores. Vibracula can form, however, sometimes also short uniserial rows at the margins of a colony, similar to those usually found in *Coscinopleura* Marsson, [1887](#). *Acoscinopleura* was considered by Voigt ([1956](#)) to be the most primitive of the coscinopleurid genera.

Stratigraphic and geographic distribution. Middle Santonian (?) to late Maastrichtian of Western and Eastern Europe; late Maastrichtian of Central Asia.

Acoscinopleura foliacea (Voigt, [1930](#))

Figures [2](#)a–m, [3](#)a, b

1925 *Rhagasostoma elegans* (von Hagenow, [1839](#)) Varietet b—Levinsen: p. 369.

* 1930 *Coscinopleura foliacea* n. sp.—Voigt: p. 491; pl. 25, fig. 19; pl. 39, fig. 8.

? 1933 *Coscinopleura foliacea* Voigt, [1930](#)—Schönfelder: p. 93; pl. 14, figs. 23a, b.

1956 *Acoscinopleura foliacea* (Voigt, [1930](#))—Voigt: p. 52; pl. 8, figs. 6–7; pl. 9, figs. 3–5.

2015 *Acoscinopleura foliacea* (Voigt, [1930](#))—Koromyslova et al.: p. 55; fig. 1A–г.

Studied material. Neotype: SMF 26421 [former Voigt photocard number 933], White Chalk from the early Maastrichtian, Rügen, Vorpommern, Germany (Figs. [2](#)a–f, [3](#)a, b). Other material: SMF 29949 (Fig. [2](#)g–j), SMF 24105 [former Voigt photocard number 2427] (Fig. [2](#)k–m), same locality and stratigraphy as the neotype.

Description. Colony rigidly erect, bifoliate, adeoniform. Zooids arranged quincuncially (Fig. [2](#)a–c, g, k–m) and perfectly back-to-back (Fig. [2](#)e–f, h–j), separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids pyriform, long (L 543–850 µm; W 543–850 µm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, thick, distal to opesia 1.5–6 times thicker than proximal to opesia, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of almost all autozooids, proximolaterally, large, irregular in shape, sometimes with ribbed lateral and proximal walls and granular bottom, gradually deepening towards the proximal end of an autozooid, occupying less than half or half of the thickness of the cryptocyst (Fig. [2](#)a, d–m), cryptocystal lid covering the peripheral caverns rarely preserved (Fig. [2](#)e). Opesia small (L 60–107 µm; W 128–218 µm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent and ribbed margin, with two symmetrical and short opesiular indentations proximolaterally enclosing a broad tongue with prominent but always unribbed margin (Fig. [2](#)a, g, k–m). Autozooidal chamber long (L 580–690 µm; W 260–360 µm), wide near basal walls, deep, tight, boot-shaped with tapering proximal end and well-rounded corners, with short, transversely elliptical and tight tube for the passage of the lophophore distofrontally (Figs. [2](#)b–f, h–j, [3](#)a, b). Ovicells rare, endozooidal, immersed in the proximal cryptocyst of the distal zooid. Ooecia cryptocystal, well-developed, large, with two protruding proximolateral wings (Fig. [2](#)m). Ovicellate autozooids with enlarged opesiae, cryptocyst is more steeply sloping towards the opesia.

Vibracula vicarious, shorter and narrower than autozooids (L 353–873 µm, W 227–417 µm), irregularly placed among autozooids (Fig. [2](#)a, b, k, m). Cryptocyst finely pustulose, weakly convex, thickening proximally, always thinner than autozooidal cryptocyst, sometimes with peripheral caverns proximally. Craticula not observed. Opesia terminal, round, small, usually hidden by short, protruding tooth (Fig. [2](#)m). Vibracular chamber shorter and deeper than autozooidal chambers, but of the same width (L 480–670 µm, W 260–330 µm), egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. [2](#)b, d).

Calcification of vertical and basal walls thick. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally (Fig. [2](#)b, c). In vibracular walls centrolateral septulum sometimes lacking. Vertical walls gradually thickening from the centrolateral septula to the distal septula (Fig. [2](#)b, c), with lateral channel-like cavities (Dm: 20–30 µm) beginning on the level of the proximo- and centrolateral septula and connected with them (Fig. [2](#)b–d,
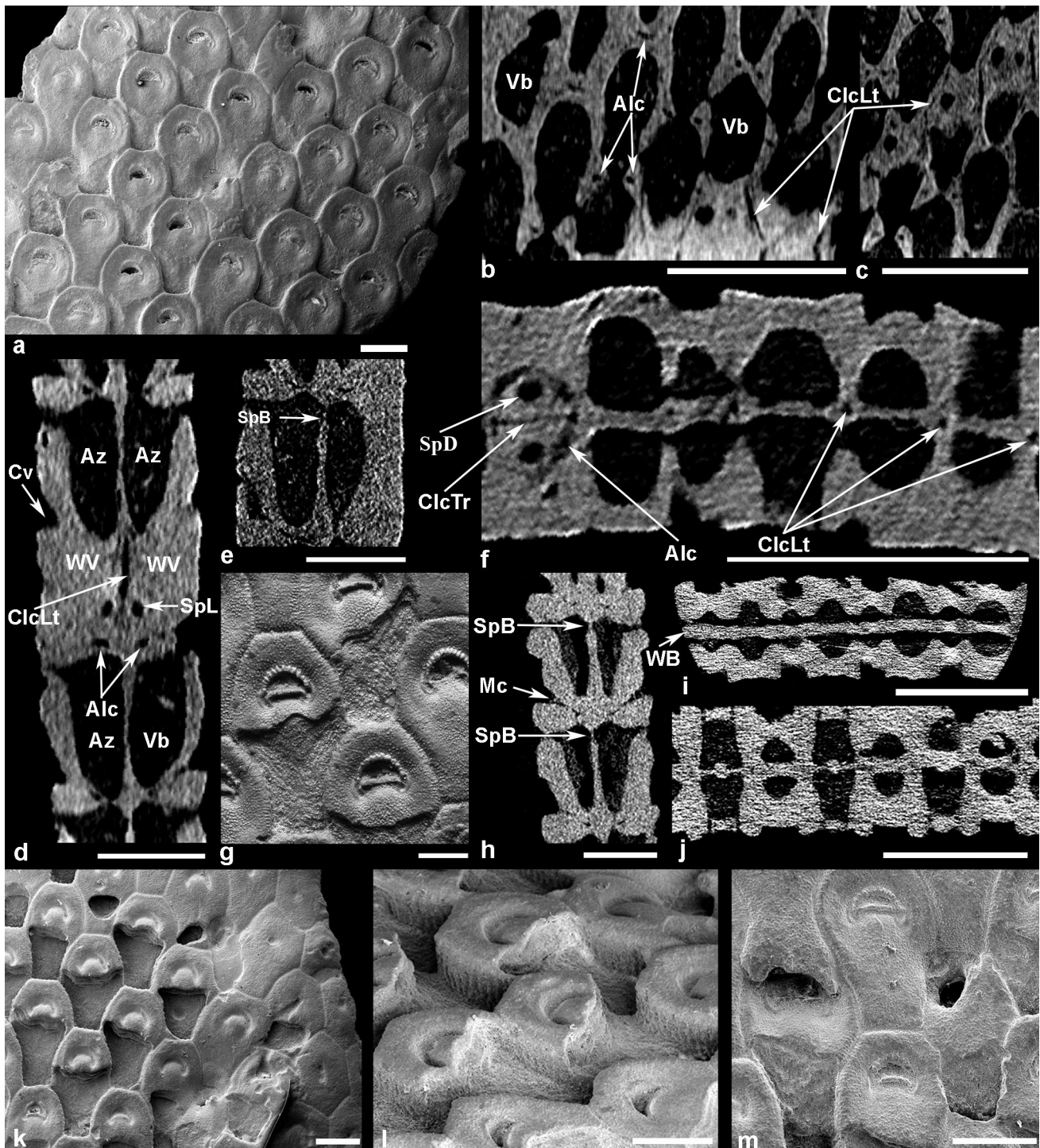
Fig. 2 *Acoscinopleura foliacea* (Voigt, 1930), White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany. **a–f** Neotype SMF 26421. **a** Autozooids and vibracula. *Scale bar* 300 μm. **b** Coronal section showing vibracular chambers on different levels, autozooids and septula. *Scale bar* 1000 μm. **c** Coronal section showing pair-wise basal septula in the basal walls. *Scale bar* 1000 μm. **d** Sagittal section showing back-to-back arrangement of zooids. *Scale bar* 500 μm. **e** Sagittal section showing two autozooidal chambers and peripheral cavern covered by a thin cryptocystal lid. *Scale bar* 500 μm. **f** Transverse section. *Scale bar* 1000 μm. **g–j** SMF 29949.

g Autozooids with granular bottom of peripheral caverns. *Scale bar* 200 μm. **h** Sagittal section showing peripheral caverns and arch-like cavities connected with microcavities. *Scale bar* 500 μm. **i** Transverse section showing lateral septula. *Scale bar* 1000 μm. **j** Transverse sections showing pair-wise basal septula. *Scale bar* 1000 μm. **k–m** SMF 24105. **k** Autozooids with peripheral caverns and kenozooids at the colony's margin. *Scale bar* 300 μm. **l** Autozooids with ribbed lateral walls of the peripheral caverns. *Scale bar* 300 μm. **m** Autozooids (one with ovicell) and vibraculum. *Scale bar* 300 μm
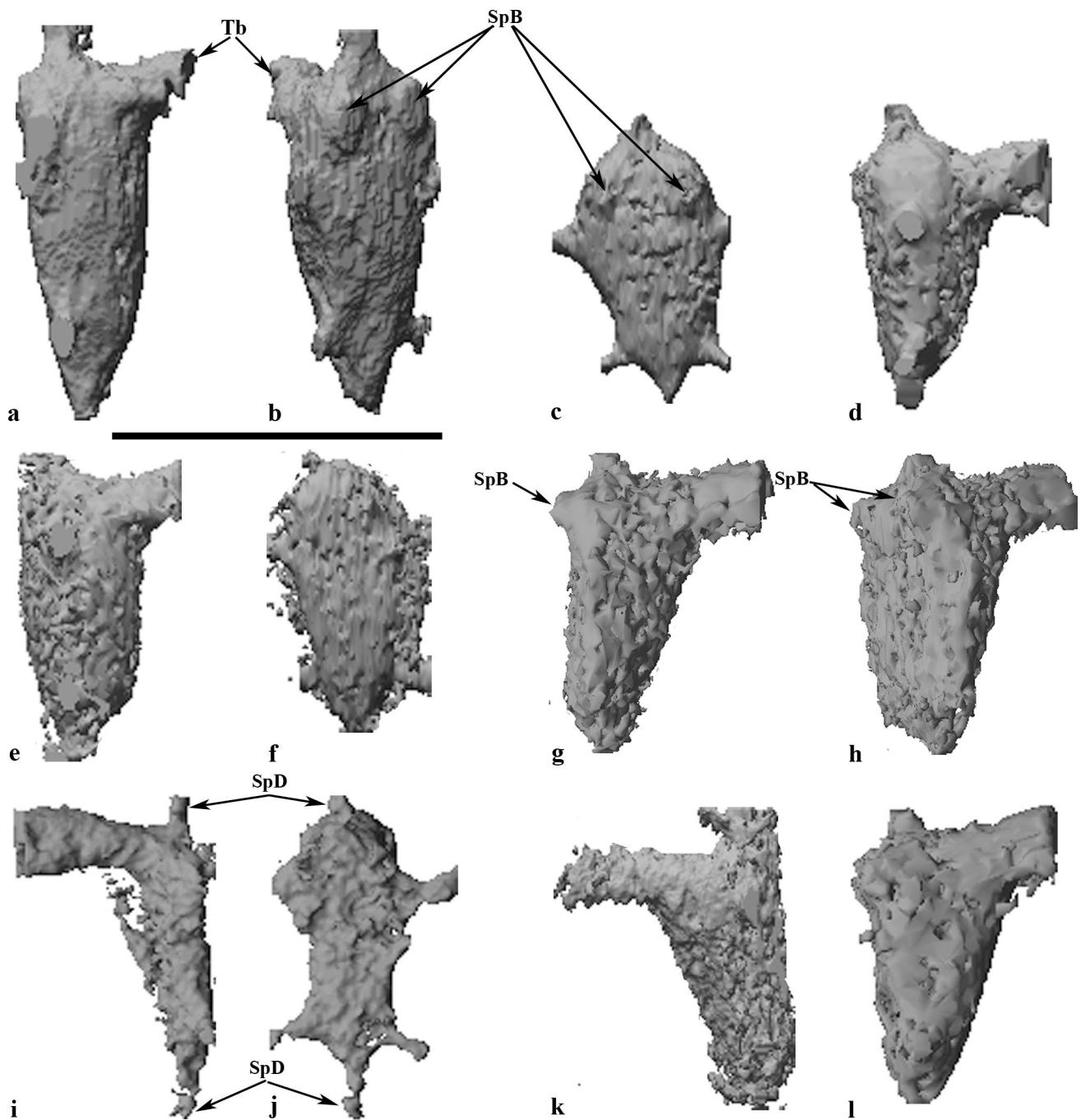
Fig. 3 Virtual models of autozooidal chambers. **a**, **b** *A. foliacea* (Voigt, 1930), SMF 26421 (neotype), White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany. **a** Lateral view showing two lateral septula and tube. **b** Basal view showing lateral and basal septula. **c**, **d** *A. albaruthenica* sp. nov., PIN 2922/244 (holotype), erratic block from the late Campanian of a quarry near Grodno, Grodno Region, Belarus. **c** Basal view showing lateral and basal septula. **d** Lateral view showing lateral septula and tube. **e**, **f** *A. rugica* Voigt, 1956, SMF 24091 (holotype), White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany. **e** Lateral view showing two lateral septula and tube. **f** View on the basal side showing septula. **g**,

h *A. dualis* sp. nov., SMF 24098 (holotype), White Chalk from the early Maastrichtian, Rügen, Vorpommern, Germany. **g** Lateral view. **h** Basal view showing tube and basal septula. **i**, **j** *A. crassa* sp. nov., SMF 29950 (holotype), late Maastrichtian, Hemmoor, Lower Saxony, Germany. **i** Lateral view showing distal septula and tube. **j** Basal view showing six septula. **k** *A. fallax* Voigt, 1956, SMF 24097 (holotype), late Maastrichtian, Hemmoor, Lower Saxony, Germany, lateral view showing tube. **l** *A. occulta* sp. nov., SMF 24086 (holotype), late Maastrichtian, Hemmoor, Lower Saxony, Germany, lateral view showing tube. *Scale bar* 500 μm

f), with transverse channel-like cavities (Dm: 10–20 μm) beginning near the basal walls and not connected with the distal septula (Fig. 2f), with centrodistal arch-like cavities (Dm: 20–30 μm) encircling the distal septula and sometimes connected with them (Fig. 2b–f, h). Channel-like cavities connected with each other and forming a network that has the same shape as the zooid (Fig. 2b, c). Basal autozooidal and vibracular wall thin centrally, about 2–4 times thicker proximally and laterally (Fig. 2d–f, h–j), in autozooids with one pair of basal septula encircled by depressions opposite to the opesia (Fig. 2b, c, h, j). Microcavities connecting the peripheral caverns and slit-like cavities sometimes present (Fig. 2h).

Kenozooids present (Fig. 2k), variable in shape and size (*L* 242–676 μm; *W* 200–584 μm), sometimes similar in shape to autozooids, usually polygonal and smaller than autozooids, forming the lateral margins in some colonies. Cryptocyst flat, finely pustulose. Aperture very small (Dm: 43–84 μm), almost central, circular.

Biometrical details are summarised in Table S1 in the Electronic Supplementary Material.

Remarks. Acoscinopleura foliacea is the only species with proximolateral peripheral caverns. It differs from all other species examined, except for *A. rugica*, in having longer autozooids and the largest zooidal chambers. Also, the depressions encircling the basal septula are larger than in all other species. Peripheral caverns in *A. foliacea* are usually connected via microchannels with the slit-like cavities. A more detailed comparison of key morphological characters of species of *Acoscinopleura* studied herein is summarised in Table 2.

Stratigraphic and geographic distribution. Early Maastrichtian of Denmark: Island of Møn, Sjælland Region; Aalborg, North Denmark Region. Belgium: Phosphatic Chalk near Ciply in the Municipality of Mons, Wallonia.

Acoscinopleura albaruthenica sp. nov.
Figures 3c, d, 4a–j

2015 *Acoscinopleura fallax* Voigt, 1956—Koromyslova et al.: p. 55; fig. 1д–ж.

Etymology. From Latin albaruthenica, '*Belarussian*', referring to the type locality (Grodno) of the species Belarus.

Holotype. PIN 2922/244 (Figs. 3c, d, 4e–j).

Paratypes. PIN 2922/243 (Fig. 4a–d), PIN 2922/245.

Locality and Horizon. Quarry near Hrodna/Grodno (гродна/гродно), Grodno Region, Belarus, erratic block from the late Campanian.

Description. Colony rigidly erect, bifoliate, adeoniform. Zooids arranged quincuncially (Fig. 4a, b, d, e, i, j) and perfectly back-to-back (Fig. 4c, g, h), separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids hexagonal, short (*L* 370–533 μm; *W* 194–385 μm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, very thick, thickening proximally, distal to opesia 2–3 times thicker than proximal to opesia, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of almost all autozooids, proximally, short and shallow, occupying less than half or half of the thickness of the cryptocyst, transversely rectangular, with walls steeply sloping inwards (Fig. 4a–c, e–i), cryptocystal lid covering the peripheral caverns rarely preserved (Fig. 4c). Opesia small (*L* 67–121 μm; *W* 113–143 μm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent and ribbed margin, with two symmetrical and short opesiular indentations proximolaterally enclosing a broad but short tongue with prominent and ribbed margin (Fig. 4a, b, e). Autozooidal chamber short (*L* 400–500 μm; *W* 120–270 μm), narrow near basal walls, shallow, tight, boot-shaped with tapering proximal end and well-rounded corners, with long, transversely elliptical and tight tube for the passage of the lophophore distofrontally (Figs. 3d, 4g, h). Ovicells endozooidal, immersed in the proximal cryptocyst of the distal zooid. Ooecia cryptocystal, well-developed, sometimes placed underneath a peripheral cavern. Ovicellate autozooids with enlarged opesiae and the cryptocyst more steeply sloping towards the opesia.

Vibracula vicarious, shorter and narrower than autozooids (*L* 338–457 μm; *W* 139–203 μm), irregularly placed among autozooids. Cryptocyst finely pustulose, weakly convex, thickening proximally, thinner than autozooidal cryptocyst, sometimes with peripheral caverns. Craticula not observed. Opesia terminal, round, small, usually hidden by a protruding small tooth. Vibracular chamber shorter, shallower and usually narrower than autozooidal chamber (*L* 310–430 μm; *W* 160–210 μm), egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. 4g, i, j).

Calcification of vertical and basal walls thick. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally. In vibracular walls centrolateral septulum sometimes lacking (Fig. 4j). Vertical walls gradually thickening from the centrolateral septula to the distal septula, with poorly observable lateral and transverse channel-like cavities (Dm: ~10 μm) (Fig. 4d), with centrodistal arch-like

Table 2 Comparison of key morphological characters of seven species of the genus *Acoscinopleura* Voigt, 1956 studied herein (all values in μm)

	A. foliacea (Voigt, 1930)	A. albaruthenica sp. nov.	A. rugica Voigt, 1956	A. dualis sp. nov.	A. crassa sp. nov.	A. fallax Voigt, 1956	A. occulta sp. nov.
Range	Early Maastrichtian	Late Campanian	Early Maastrichtian	Early–late Maastrichtian	Early–late Maastrichtian	Late Maastrichtian	Late Maastrichtian
Shape of colony	Adeoniform	Adeoniform	Eschariform or adeoniform	Adeoniform	Adeoniform	Adeoniform	Adeoniform
Position of vibracula	Irregular	Irregular and in rows at the lateral margins	Irregular	In rows at the lateral margins	In rows at the lateral margins	In rows at the lateral margins	In rows at the lateral margins
Length of autozooidal chamber	580–690	400–500	480–710	450–560	380–580	480–540	430–500
Depth of autozooidal chamber	200–280	150–230	200–290	130–250	140–250	180–270	190–250
Width of autozooidal chamber	260–360	120–270	200–360	160–360	150–230	190–250	210–270
Length of tube	80–200	120–190	90–180	90–200	90–260	150–230	60–130
Height of tube	40–100	70–150	70–130	60–120	30–100	70–90	70–90
Length of vibracular chamber	480–670	310–430	440–630	340–470	270–500	350–540	310–420
Depth of vibracular chamber	220–310	120–210	150–320	130–280	130–270	150–240	160–210
Width of vibracular chamber	260–330	160–210	170–300	170–260	130–180	160–220	190–230
Thickness of cryptocyst distal to opesia	220–370	210–330	190–310	190–310	140–350	210–360	240–330
Thickness of cryptocyst proximal to opesia	60–160	60–120	40–170	60–180	60–220	60–210	70–110
Peripheral caverns	Proximolateral, large	Proximal, small	Proximal, small	Proximal, small	Proximal, small	Proximal, large	Usually interconnected
Length of peripheral caverns	201–522	48–141	63–213	90–140	57–128	96–191	–
Depth of peripheral caverns	110–170	70–180	80–170	50–210	50–170	170–290	80–120
Thickness of vertical walls	20–180	50–130	30–170	50–200	60–200	50–140	50–180
Thickness of basal wall centrally	20–70	20–30	20–80	20–90	60–120	30–50	30–60
Diameter of lateral septulum	50–80	20–50	40–70	20–50	20–60	30–50	30–70
Diameter of distal septulum	30–70	30–60	50–100	30–60	30–40	40–50	40–60
Diameter of basal septulum	70–130	50–70	40–90	40–80	50–70	40–50	60–90
Diameter of arch-like cavities	20–30	10–20	10–20	10–20	10–20	30–40	10–30
Diameter of channel-like cavities	10–30	~10	10–20	10–20	10–20	20–30	10–30
Microcavities connecting peripheral caverns and arch-like cavities	Present	Absent	Present	Absent	Present	Present	Absent

cavities (Dm: 10–20 μm) encircling the distal septula and sometimes connected with them and with the ovicell, if present (Fig. 4c, d, f–h, j). Basal autozooidal and vibracular wall thin centrally, about 1.5–2 times thicker proximally and laterally, in autozooids with one pair of basal septula encircled by depressions opposite to the opesia (Fig. 4d). Microcavities not observed.

Kenozooids present, variable in shape and size (*L* 383–562 μm; *W* 158–214 μm), usually polygonal and smaller than autozooids, forming the lateral margins of each colony (Fig. 4b). Cryptocyst flat, finely pustulose. Aperture very small (Dm: 46–51 μm), almost central, circular to elliptical.

Biometrical details are summarised in Table S2 in the Electronic Supplementary Material.

Remarks. Acoscinopleura albaruthenica sp. nov. is from a morphological point of view most closely related to *A. fallax*, *A. foliacea* and *A. dualis* sp. nov. It can be distinguished from these in the lack of microcavities and the channel-like cavities being very narrow. Furthermore, it differs from *A. foliacea* in having peripheral caverns only in the most proximal position, short hexagonal autozooids and smaller autozooidal chambers, from *A. fallax* in having shorter and shallower peripheral caverns and autozooidal chambers and from *A. dualis* sp. nov. in having smaller autozooidal and vibracular chambers and thinner vertical and basal walls.

Stratigraphic and geographic distribution. Late Campanian of Grodno Region, Belarus.

Acoscinopleura rugica Voigt, 1956
Figures 3e, f, 5a–k

* 1956 *Acoscinopleura rugica* gen. et sp. nov.—Voigt: p. 53; pl. 9, figs. 1–2; pl. 12, figs. 1–3.
? 1969 *Acoscinopleura rugica* Voigt, 1956—Maryańska: p. 116; pl. X, fig. 2; pl. XI, fig. 4.
2015 *Acoscinopleura rugica* Voigt, 1956—Koromyslova et al.: p. 55; fig. 13-M.

Studied material. Holotype: SMF 24091 [former Voigt photocard number 2381], White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany (Figs. 3e, f, 5a–d). Other material: SMF 24095 [former Voigt photocard number 2379] (Fig. 5i–k), SMF 24102 [former Voigt photocard number 2380] (Fig. 5e–h), SMF 29946, SMF 29947, SMF 29948, same locality and stratigraphy as the holotype.

Description. Colony rigidly erect, bifoliate, eschariform or adeoniform. Zooids arranged quincuncially (Fig. 5a, c, e–f, i, j) and perfectly back-to-back (Fig. 5d, h), separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids pyriform, short (*L* 483–550 μm; *W* 340–445 μm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, very thick, thickening proximally, distal to opesia 1.5–3 times thicker than proximal to opesia, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of only few autozooids, proximally, short and shallow, occupying less than half or half of the thickness of the cryptocyst, transversely rectangular, with walls steeply sloping inwards (Fig. 5a). Opesia small (*L* 70–95 μm; *W* 123–140 μm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent and ribbed margin, with two symmetrical and short opesiular indentations proximolaterally enclosing a broad but short tongue with prominent and unribbed margin. Occlusor laminae in the distal part of opesia probably present (Fig. 5a). Autozooidal chamber long (*L* 480–710 μm; *W* 200–360 μm), wide near basal walls, deep, tight, shaped like a wedge, with well-rounded corners, with short, transversely elliptical and tight tube for the passage of the lophophore distofrontally (Figs. 3e, f, 5d). Ovicells endozooidal, immersed in the proximal cryptocyst of the distal zooid. Ooecia cryptocystal, well-developed, with two protruding proximolateral wings (Fig. 5e, h–k). Ovicellate autozooids with enlarged opesiae and the cryptocyst more steeply sloping towards the opesia.

Vibracula vicarious, same length as or longer but much narrower than autozooids (*L* 488–635 μm; *W* 148–258 μm), irregularly placed among autozooids, never forming rows at the lateral margins (Fig. 5a, e, i). Cryptocyst finely pustulose, weakly convex, thickening proximally, thinner than autozooidal cryptocyst, lacking peripheral caverns. Craticula small. Opesia terminal, circular, small, hidden by a short protruding tooth. Vibracular chamber about the same length as, but narrower and deeper than autozooidal chambers (*L* 440–630 μm; *W* 170–300 μm), egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. 5d).

Calcification of vertical walls thick, of basal walls thin. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally (Fig. 5c). In vibracular walls centrolateral septulum sometimes lacking. Vertical walls gradually thickening from the centrolateral septula to the distal septula, with lateral channel-like cavities (Dm: 10–20 μm) beginning on the level of the proximo- and centrolateral septula and connected with them (Fig. 5c, f–h, j, k), with transverse channel-like cavities (Dm: 10–20 μm) beginning near the distal margin of the basal walls and not connected with the distal septula (Fig. 5c, f, g, k), with centrodistal arch-like cavities (Dm: 10–20 μm) encircling the distal septula and sometimes connected with them and with the ovicell, if
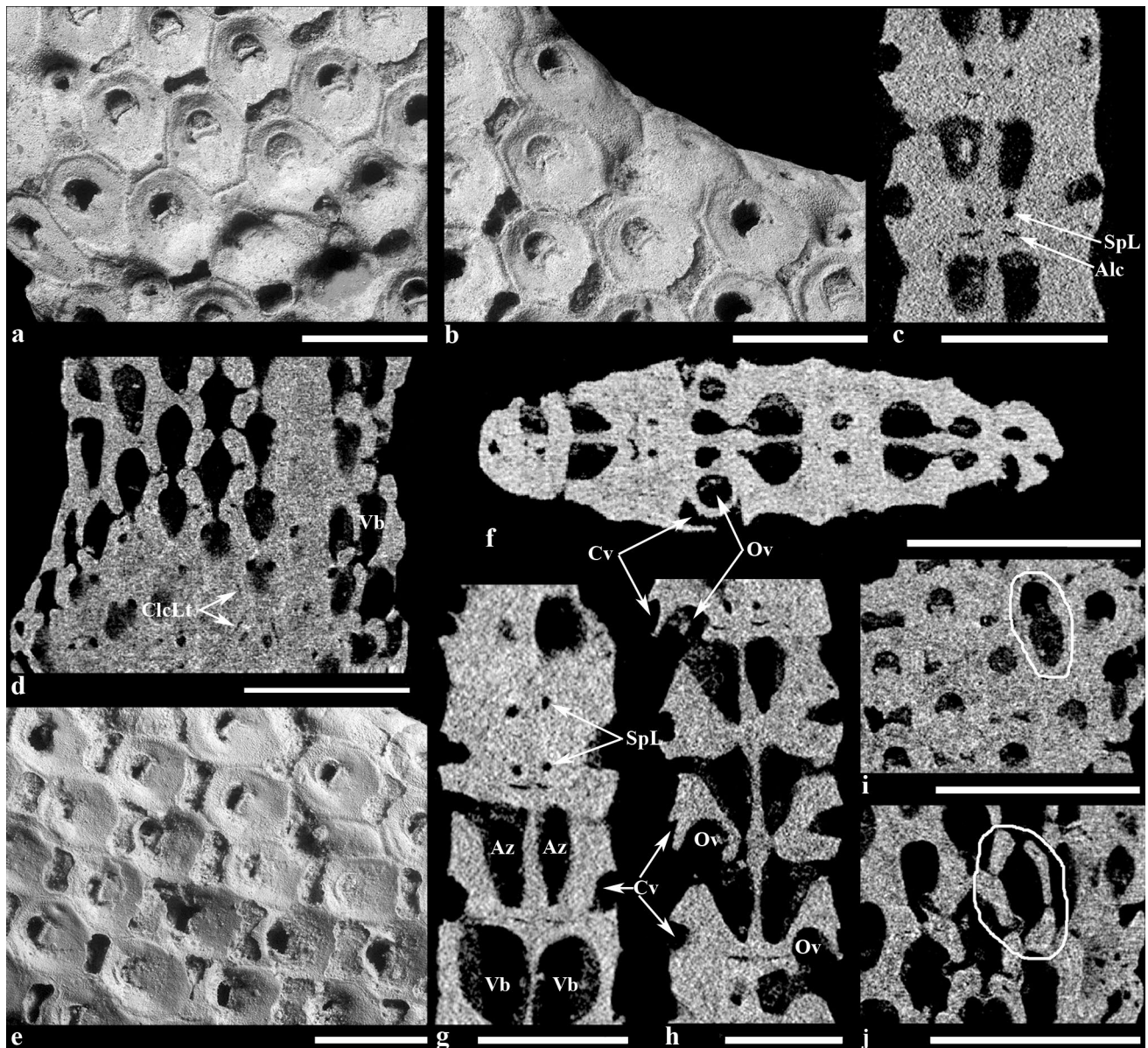
Fig. 4 *Acoscinopleura albaruthenica* sp. nov.; erratic block from the late Campanian of a quarry near Grodno, Grodno Region, Belarus. **a–d** Paratype PIN 2922/243. **a** Part of colony showing autozooids, some of which ovicellate, with peripheral caverns and vibracula. *Scale bar* 500 μm. **b** Autozooids with peripheral caverns, vibracula and kenozooids. *Scale bar* 500 μm. **c** Sagittal section showing autozooids with peripheral cavern. *Scale bar* 500 μm. **d** Coronal section showing lateral channel-like cavities and several septula. *Scale bar* 1000 μm. **e–j** Holotype PIN 2922/244. **e** Autozooids, some of which ovicellate, with peripheral caverns, and vibracula. *Scale bar* 500 μm. **f** Transverse section showing an ovicell underneath a peripheral cavern. *Scale bar* 1000 μm. **g** Sagittal section showing back-to-back arrangement of zooids. *Scale bar* 500 μm. **h** Sagittal section showing autozooids with peripheral caverns and one ovicell located underneath a peripheral cavern. *Scale bar* 500 μm. **i** Coronal section with vibracular chamber outlined. *Scale bar* 1000 μm. **j** Coronal section on the level of the vertical septula with a vibracular chamber outlined and autozooidal chamber with pore plates. *Scale bar* 1000 μm

present (Fig. 5c, g, h, j, k). Channel-like cavities connected with each other and forming a network that has the same shape as the zooid (Fig. 5f). Basal autozooidal and vibracular wall thin centrally, about 1.5–3 times thicker proximally and laterally (Fig. 5d), in autozooids with one pair of basal septula encircled by depressions opposite to the opesia

(Fig. 5f, h, j, k). Microcavities connecting the peripheral caverns and arch-like cavities sometimes present.

Kenozooids present (Fig. 5e), variable in shape and size (*L* 203–233 μm; *W* 203–210 μm), usually polygonal and smaller than autozooids, forming the lateral margins of each colony. Cryptocyst flat, finely pustulose. Aperture very small (Dm: 25 μm), almost central, circular to elliptical. Intramural
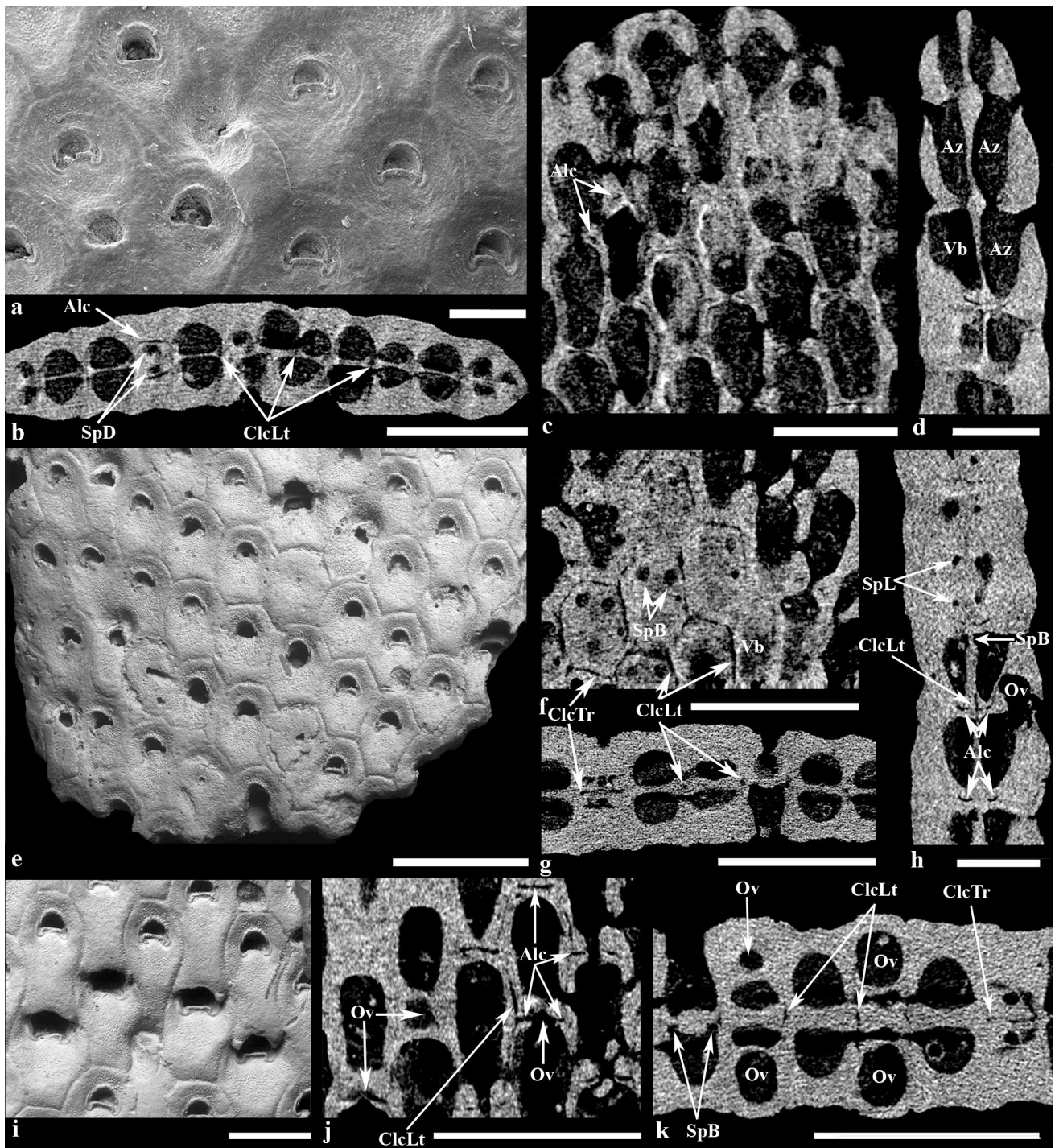
Fig. 5 *Acoscinopleura rugica* Voigt, 1956; White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany. **a–d** Holotype SMF 24091. **a** Autozooids and vibracula. *Scale bar* 300 µm. **b** Transverse section. *Scale bar* 1000 µm. **c** Coronal section in the distal part of the colony showing channel-like cavities and septula. *Scale bar* 1000 µm. **d** Sagittal section in the distal part of the colony. *Scale bar* 500 µm. **e–h** SMF 24102. **e** Autozooids, some of which ovicellate, vibracula, kenozooids at the lateral margin and intramural reparative budding kenozooids. *Scale bar* 1000 µm. **f** Coronal section showing basal walls of zooids. *Scale bar* 1000 µm. **g** Transverse section. *Scale bar* 1000 µm. **h** Sagittal section. *Scale bar* 500 µm. **i–k** SMF 24095. **i** Autozooids, some of which ovicellate, and vibraculum (bottom centre). *Scale bar* 500 µm. **j** Coronal section. *Scale bar* 1000 µm. **k** Transverse section. *Scale bar* 1000 µm

reparative budding kenozooids within host autozooids sometimes present (Fig. 5e).

Biometrical details are summarised in Table S3 in the Electronic Supplementary Material.

Remarks. The holotype of *Acoscinopleura rugica* is an eschariform colony, while the other two samples imaged in Voigt (1956) are adeoniform. Still, the morphological differences, also of the internal structures, are within the error margins and do not allow any species discrimination between eschariform and adeoniform colonies. *A. rugica* seems most closely related with *A. crassa* sp. nov. and *A. dualis* sp. nov. All three species have only rare and small peripheral caverns that are found scattered over the colony in only few autozooids. However, no correlation with the occurrence of peripheral caverns and the position of autozooids inside the colony could be found. *A. rugica* differs from *A. crassa* sp. nov. and *A. dualis* sp. nov. in having rare vibracula that are never aligned in rows at the lateral margins, in the calcification of the cryptocyst and the vertical and basal walls being thinner and in having the largest autozooidal and vibracular chambers.

Maryańska (1969) described 12 fragments from glauconitic sandstones of Nasiłów, Poland that she assigned to *A. rugica*. The colonies are eschariform, and vibracula are found irregularly placed among the autozooids and not in rows at the lateral margins. However, the autozooids are significantly smaller than in species of *A. rugica* from Rügen, conspecificity with the latter being therefore questionable but still within the realm of possibility.

Stratigraphic and geographic distribution. Early Maastrichtian of Rügen, Germany. ?Late Maastrichtian of Poland.

Acoscinopleura dualis sp. nov.
Figures 3g, h, 6a–j

p 1956 *Acoscinopleura fallax* n. g. n. sp.—Voigt: p. 54; pl. 10, figs. 3, 6–7 (non pl. 10, figs. 1, 2, 4–5).

Etymology. From Latin dual ('*dual*'), in reference to the new species having morphological features of both *A. albaruthenica* sp. nov. and *A. rugica*.

Holotype. SMF 24098 [former Voigt photocard number 2384] (Figs. 3g, h, 6a–h).

Locality and Horizon. Jasmund Peninsula, Isle of Rügen, Vorpommern, Germany, early Maastrichtian.

Paratypes. SMF 24092 [former Voigt photocard number 2388] (Fig. 6i), late Maastrichtian, Hemmoor-Basbeck, Lower Saxony, Germany; SMF 24093 [former Voigt

photocard number 2386] (Fig. 6j), same locality and stratigraphy as the holotype.

Description. Colony rigidly erect, bifoliate, adeoniform. Zooids arranged quincuncially (Fig. 6a–c, f, g) and perfectly back-to-back (Fig. 6d, e, i, j), separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids pyriform or hexagonal, long (*L* 467–684 μm; *W* 317–452 μm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, very thick, thickening proximally, distal to opesia 2–3 times thicker than proximal to opesia, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of few autozooids, irregularly occurring, proximally, short and shallow, occupying less than half or half of the thickness of the cryptocyst, transversely rectangular, with walls steeply sloping inwards (Fig. 6a, c, e). Opesia small (*L* 48–84 μm; *W* 119–151 μm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent and unribbed margin, with two symmetrical and short opesiular indentations, proximolaterally enclosing a broad but short tongue with prominent and unribbed margin (Fig. 6b, c). Autozooidal chamber short (*L* 450–560 μm; *W* 160–360 μm), wide near basal walls, shallow, tight, boot-shaped with tapering proximal end and well-rounded corners, with long, transversely elliptical and tight tube for the passage of the lophophore distofrontally (Figs. 3g, h, 6d, e, i, j). Ovicells endozooidal, immersed in the proximal cryptocystal portion of the distal zooid. Ooecia cryptocystal, well-developed (Fig. 6c, e). Ovicellate autozooids with enlarged opesiae and the cryptocyst more steeply sloping towards the opesia.

Vibracula vicarious, shorter and narrower than autozooids (*L* 504–676 μm; *W* 147–222 μm), irregularly placed among autozooids in central part of the colonies and forming a row of few at the lateral margins of a colony (Fig. 6a–c). Cryptocyst finely pustulose, weakly convex, thickening proximally, thinner than autozooidal cryptocyst, sometimes with peripheral caverns. Craticula small (Fig. 6b). Opesia terminal, round, small, hidden by a protruding small tooth. Vibracular chamber shorter, deeper and usually narrower than autozooidal chambers (*L* 340–470 μm; *W* 170–260 μm), egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. 6j).

Calcification of vertical walls thick, of basal walls thin. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally. In vibracular walls centrolateral septulum usually lacking (Fig. 6g). Vertical walls gradually thickening
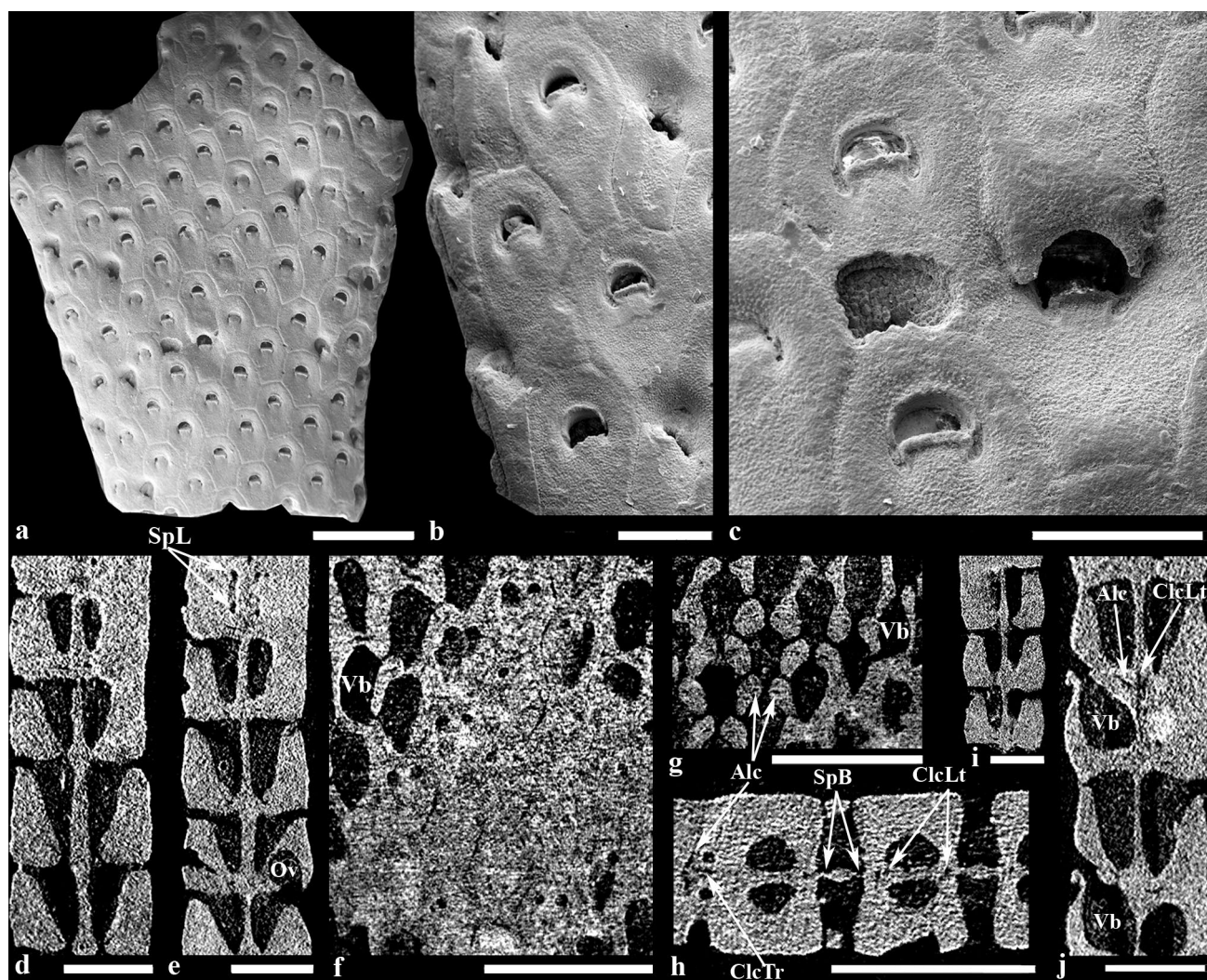
Fig. 6 *Acoscinopleura dualis* sp. nov. **a**–**h** Holotype SMF 24098; White Chalk from the early Maastrichtian, Rügen, Vorpommern, Germany. **a** Colony fragment. *Scale bar* 1000 μm. **b** Autozooids, rows of vibracula and kenozooids at the lateral margin. *Scale bar* 300 μm. **c** Ovicellate autozooid and autozooid with peripheral cavern. *Scale bar* 300 μm. **d** Sagittal section showing autozooidal chambers without peripheral caverns. *Scale bar* 500 μm. **e** Sagittal section showing autozooidal chambers, two of which with peripheral cavern. *Scale bar* 500 μm. **f** Coronal section showing channel-like cavities and pair-wise basal septula. *Scale bar* 1000 μm. **g** Coronal section showing the vertical walls. *Scale bar* 1000 μm. **h** Transverse section. *Scale bar* 1000 μm. **i** Paratype SMF 24092; late Maastrichtian, Hemmoor-Basbeck, Lower Saxony, Germany. Sagittal section showing autozooidal chambers without peripheral caverns. *Scale bar* 500 μm. **j** Paratype SMF 24093; same locality and stratigraphy as the holotype. Sagittal section showing back-to-back arrangement of zooids. *Scale bar* 500 μm

from the centrolateral septula to the distal septula, with lateral channel-like cavities (Dm: 10–20 μm) beginning on the level of the proximo- and centrolateral septula and connected with them (Fig. 6f, h), with transverse channel-like cavities (Dm: 10–20 μm) beginning near the distal margin of the basal walls and not connected with the distal septula (Fig. 6f, h), with centrodistal arch-like cavities (Dm: 10–20 μm) encircling the distal septula and sometimes connected with them (Fig. 6g, h). Channel-like cavities connected with each other and forming a network that has the same shape as the zooids (Fig. 6f). Basal autozooidal and vibracular wall thin centrally, about 1.5–3 times thicker proximally and laterally, in autozooids with one pair of basal septula encircled by depressions opposite to the opesia (Fig. 6f, h). Microcavities not observed.

Kenozooids present, variable in shape and size, usually polygonal and smaller than autozooids (*L* 259–325 μm; *W* 162–400 μm), forming the lateral margins of each colony (Fig. 6b). Cryptocyst flat, finely pustulose. Aperture very small (Dm: 29–37 μm), almost central, roundish to elliptical.

Biometrical details are summarised in Table S4 in the Electronic Supplementary Material.
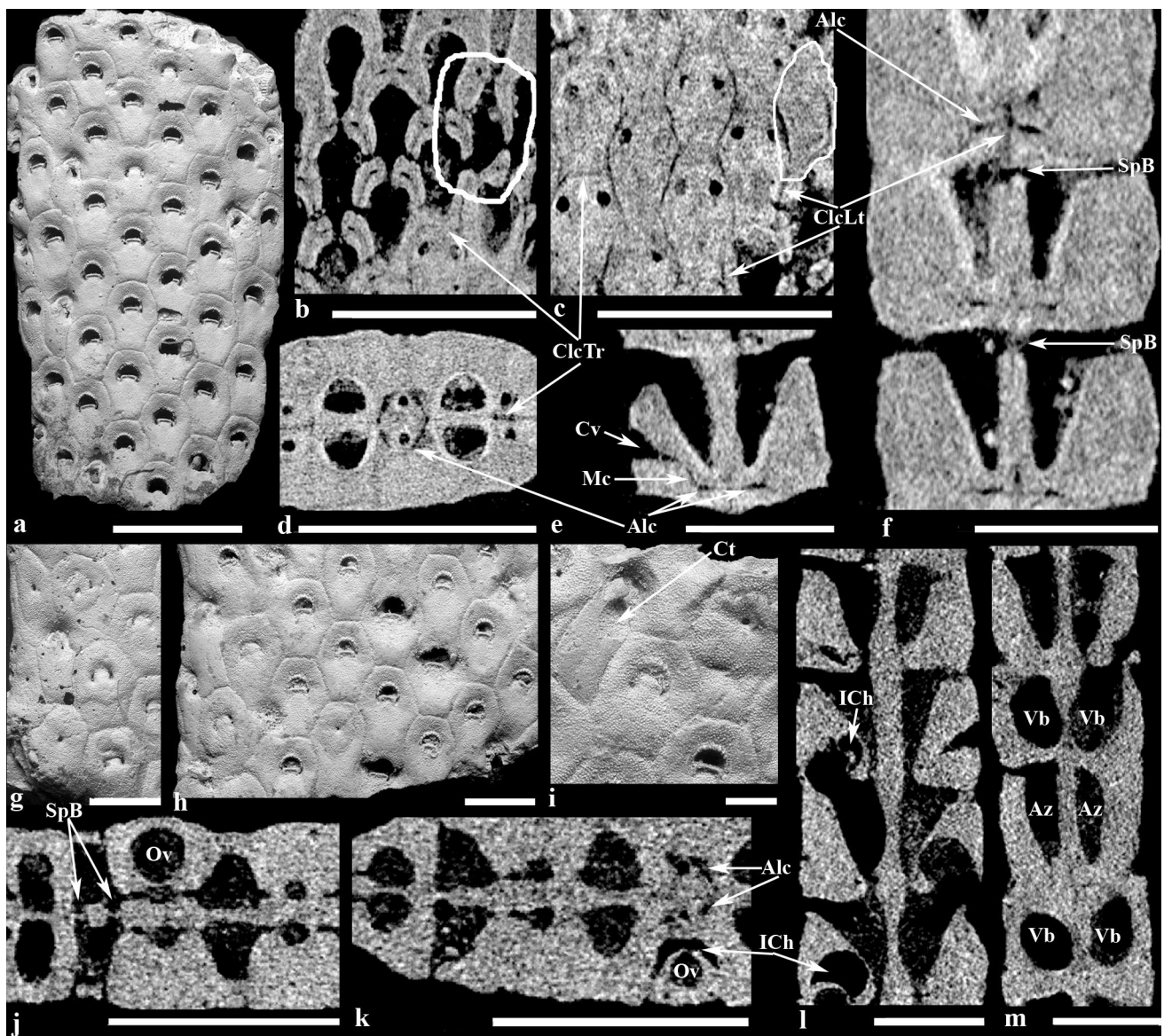
Fig. 7 *Acoscinopleura crassa* sp. nov. **a–f** Holotype SMF 29950; late Maastrichtian, Hemmoor, Lower Saxony, Germany. **a** Adeoniform colony. *Scale bar* 1000 μm. **b** Coronal section with one vibracular chamber outlined and showing arch-like cavities, channel-like cavities as well as various septula. *Scale bar* 1000 μm. **c** Coronal section with one vibracular basal wall outlined and showing a network of channel-like cavities and pair-wise basal septula. *Scale bar* 1000 μm. **d** Transverse section. *Scale bar* 1000 μm. **e** Sagittal section showing two autozooidal chambers. *Scale bar* 500 μm. **f** Sagittal section showing autozooidal chambers with very thick calcification of the cryptocyst and the basal walls. *Scale bar* 500 μm. **g–m** Paratypes SMF 29951 and SMF 29952; White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany. **g** Paratype SMF 29951. Auto-

zooids, vibraculum, kenozooids and intramural reparative budding kenozooid within host autozooid. *Scale bar* 500 μm. **h–m** Paratype SMF 29952. **h** Autozooids, some of which ovicellate, vibracula and intramural reparative budding kenozooid within host autozooid. *Scale bar* 500 μm. **i** Intramural reparative budding kenozooid within host autozooid and vibraculum with craticula. *Scale bar* 200 μm. **j** Transverse section. *Scale bar* 1000 μm. **k** Transverse section showing an ovicell with internal chamber. *Scale bar* 1000 μm. **l** Sagittal section showing autozooidal chambers, some of which with peripheral caverns and three ovicells, two of which with internal chambers. *Scale bar* 500 μm. **m** Sagittal section showing autozooidal and vibracular chambers. *Scale bar* 500 μm

Remarks. Re-examination of the material formerly described in Voigt ([1956](#)) as *Acoscinopleura fallax* showed that the samples imaged on pl. 10, Figs. [3](#), [6](#), [7](#) significantly differ from the holotype. Specimens assigned to

A. dualis sp. nov. have only few peripheral caverns, which are small and compare well with those of *A. albaruthenica* sp. nov. The new species compares well with *A. rugica* and *A. crassa* sp. nov., but differs from them in microcavities

connecting the peripheral caverns with the arch-like cavities lacking. Furthermore, *A. dualis* sp. nov. differs from *A. rugica* in having a row of vibracula at the lateral margins and from *A. crassa* sp. nov. in having a thinner calcification of the basal walls.

Stratigraphic and geographic distribution. Early to late Maastrichtian of Germany.

Acoscinopleura crassa sp. nov.
Figures 3i, j, 7a–m

Etymology. From Latin crassus ('*fat*'), in reference to the thick calcification of the cryptocyst and autozooidal walls.

Holotype. SMF 29950 (Figs. 3i, j, 7a–f).

Locality and Horizon. Hemmoor, Lower Saxony, Germany, late Maastrichtian.

Paratypes. SMF 29951 (Fig. 7g), SMF 29952 (Fig. 7h–m), White Chalk of the early Maastrichtian, Rügen, Vorpommern, Germany.

Description. Colony rigidly erect, bifoliate, adeoniform (Fig. 7a). Zooids arranged quincuncially (Fig. 7a–c, h, i) and perfectly back-to-back (Fig. 7e–f, l, m). Zooids separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids hexagonal or pyriform (*L* 450–675 μm; *W* 360–451 μm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, very thick, thickening proximally, distal to opesia 2 times thicker than proximal to opesia, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of very few autozooids, proximally, short and shallow, occupying half or more of the thickness of the cryptocyst, transversely rectangular, with walls steeply sloping inwards (Fig. 7e, l). Opesia small (*L* 73–94 μm; *W* 110–167 μm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent and ribbed margin, with two symmetrical and short opesiular indentations proximolaterally enclosing a broad tongue with prominent and unribbed margin (Fig. 7a, g–i). Autozooidal chamber short (*L* 380–580 μm; *W* 150–230 μm), narrow near basal walls, shallow, tight, shaped like a wedge, with well-rounded corners, with long, transversely elliptical and tight tube for the passage of the lophophore distofrontally (Figs. 3i, j, 7b, e, f, l, m). Ovicells rare, endozooidal, immersed in the proximal cryptocystal portion of the distal zooid, sometimes with internal chamber, ooecia cryptocystal well-developed, with two protruding proximolateral wings (Fig. 7h, j–l). Ovicellate autozooids show enlarged opesiae, and the cryptocyst is more steeply sloping into the opesia (Fig. 7h).

Vibracula vicarious, same length as or shorter and much narrower than autozooids (*L* 373–639 μm; *W* 139–245 μm), irregularly placed among autozooids and usually forming a row of few at the lateral margins of the colony. Cryptocyst finely pustulose, weakly convex, thickening proximally, thinner than autozooidal cryptocyst. Peripheral caverns lacking. Craticula small (Fig. 7i). Opesia terminal, circular, small, hidden by a short protruding tooth. Vibracular chamber shorter and narrower than autozooidal chamber (*L* 270–500 μm; *W* 130–180 μm), egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. 7m).

Calcification of vertical and basal walls thick. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally. In vibracular walls centrolateral septulum usually lacking (Fig. 7b). Vertical walls gradually thickening from the centrolateral septula to the distal septula, with lateral channel-like cavities (Dm: 10–20 μm) beginning on the level of the proximo- and centrolateral septula and connected with them (Fig. 7b, c, f), with transverse channel-like cavities (Dm: 10–20 μm) beginning near the distal margin of the basal walls and not connected with the distal septula (Fig. 7b–d), with centrodistal arch-like cavities (Dm: 10–20 μm) encircling the distal septula and sometimes connected with them and with the ovicell, if present (Fig. 7d–f, k). Channel-like cavities connected with each other and forming a network that has the same shape as the zooids (Fig. 7c). Basal autozooidal and vibracular wall only slightly thickening from the centre towards the proximal and lateral margins (Fig. 7d, f, j, m), in autozooids with one pair of basal septula encircled by depressions opposite to the opesia (Fig. 7c). Microcavities connecting the peripheral caverns and arch-like cavities sometimes present (Fig. 7e).

Kenozooids present, variable in shape and size (*L* 253–655 μm; *W* 123–363 μm), usually polygonal and smaller than autozooids, forming the lateral margins of each colony (Fig. 7g). Cryptocyst flat, finely pustulose. Aperture very small (Dm: 21–43 μm), almost central, circular to elliptical. Intramural reparative budding kenozooids within host autozooids sometimes present (Fig. 7h, i).

Biometrical details are summarised in Table S5 in the Electronic Supplementary Material.

Remarks. *A. crassa* sp. nov. differs from *A. foliacea*, *A. albaruthenica* sp. nov. and *A. fallax* in having only few autozooids with peripheral caverns. Furthermore, it shows the thickest calcification of the cryptocyst and of
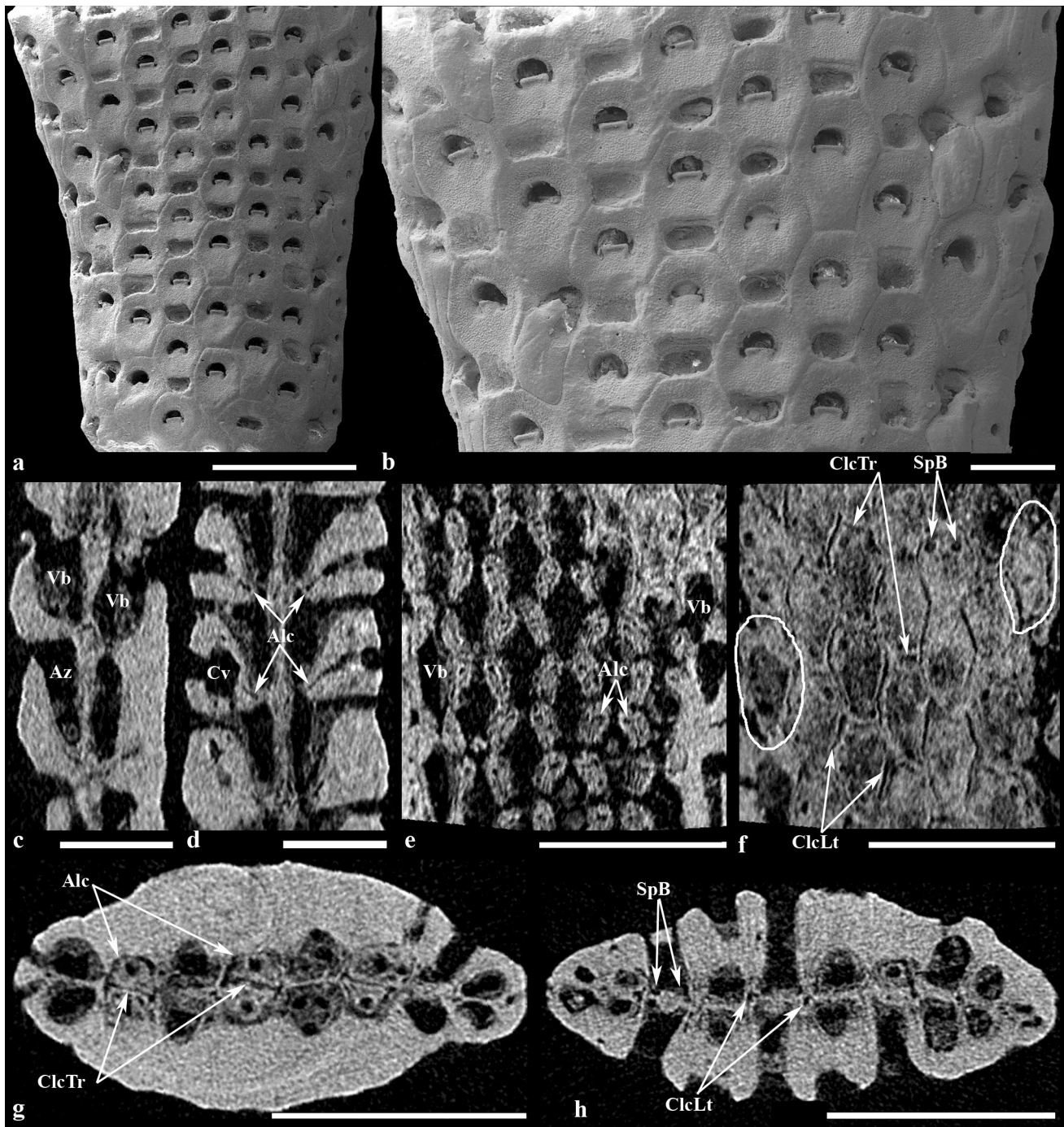
Fig. 8 *Acoscinopleura fallax* Voigt, 1956. **a–h** Holotype SMF 24097, late Maastrichtian, Hemmoor, Lower Saxony, Germany. **a** Adeoniform colony. *Scale bar* 1000 μm. **b** Close-up view showing autozooids with peripheral caverns, vibracula and kenozooids. Occlusor laminae are visible in the distal part of the opesia. *Scale bar* 300 μm. **c** Sagittal section showing autozooidal and vibracular chambers. *Scale bar* 500 μm. **d** Sagittal section showing autozooidal chambers, most of which with peripheral caverns and arch-like cavities that are sometimes connected with the peripheral caverns. *Scale bar* 500 μm. **e** Coronal section showing autozooidal and vibracular chambers, septula and arch-like cavities. *Scale bar* 1000 μm. **f** Coronal section on the level of the basal septula with the vibracular walls outlined. *Scale bar* 1000 μm. **g** Transverse section showing arch-like cavities encircling the distal septula and transverse channel-like cavities. *Scale bar* 1000 μm. **h** Transverse section showing pair-wise basal septula, lateral channel-like cavities and arch-like cavity encircling the distal septulum. *Scale bar* 1000 μm

the vertical and basal walls. Thus, it can readily be distinguished in CT sections.

Stratigraphic and geographic distribution. Early to late Maastrichtian of Germany.

Acoscinopleura fallax Voigt, 1956
Figures 3k, 8a–h

? 1840 *Eschara gladiiformis* n. sp.—von Hagenow: p. 645.

? 1930 *Coscinopleura lamourouxi* (von Hagenow, 1851)—Voigt: p. 491; pl. 25, fig. 18.

*p 1956 *Acoscinopleura fallax* n. g. n. sp.—Voigt: p. 54; pl. 10, fig. 1 (non pl. 10, figs. 2–7).

? 1959a *Eschara gladiiformis* von Hagenow, 1840 = *Acoscinopleura fallax* Voigt, 1956—Voigt: p. 47.

? 1969 *Acoscinopleura fallax* Voigt, 1956—Maryańska: p. 115; pl. XI, fig. 1.

? 1992 *Acoscinopleura fallax* Voigt, 1956—Favorskaya: p. 130; pl. 69, fig. 6–8.

non 2015 *Acoscinopleura fallax* Voigt, 1956—Koromyslova et al.: p. 55; fig. 1д–ж.

Studied material. Holotype: SMF 24097 [former Voigt photocard number 2389], late Maastrichtian, Hemmoor, Lower Saxony, Germany (Figs. 3k, 8a–h).

Description. Colony rigidly erect, bifoliate, adeoniform. Zooids arranged quincuncially (Fig. 8a, b, e, f) and perfectly back-to-back (Fig. 8c, d). Zooids separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids hexagonal, moderately large (*L* 405–598 µm; *W* 302–359 µm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, very thick, distal to opesia 2–3 times thicker than proximal to opesia, thickening proximally, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of almost all autozooids, proximally, short and deep, transversely rectangular, with walls steeply sloping inwards (Fig. 8a, b, d), cryptocystal lid covering the peripheral caverns not observed. Opesia small (*L* 84–105 µm; *W* 115–169 µm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent and ribbed margin, with two symmetrical and short opesiular indentations proximolaterally enclosing a broad but short tongue with prominent but unribbed margin. Occlusor laminae in the distal part of opesia present (Fig. 8b). Autozooidal chamber short (*L* 480–540 µm; *W* 190–250 µm), narrow near basal walls, deep, tight, boot-shaped with tapering proximal end and well-rounded corners, with long, transversely elliptical and

tight tube for the passage of the lophophore distofrontally (Figs. 3k, 8d). Ooecia not observed.

Vibracula vicarious, longer than or about the same length as autozooids but usually narrower (*L* 390–681 µm; *W* 91–182 µm), irregularly placed among autozooids or forming a row of few at the lateral margins of the colony (Fig. 8a, b). Cryptocyst finely pustulose, weakly convex, thickening proximally, thinner than autozooidal cryptocyst, sometimes with peripheral caverns. Craticula small. Opesia terminal, round, small, usually hidden by a protruding small tooth. Vibracular chamber almost the same length as autozooidal chambers (*L* 350–540 µm; *W* 160–220 µm), but shallower, egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. 8c).

Calcification of vertical and basal walls thick. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally. In vibracular walls proximolateral septulum usually lacking (Fig. 8e). Vertical walls gradually thickening from the centrolateral septula to the distal septula, with lateral channel-like cavities (Dm: 20–30 µm) beginning on the level of the proximo- and centrolateral septula and connected with them (Fig. 8e–h), with transverse channel-like cavities (Dm: 20–30 µm) beginning near the distal margin of the basal walls and not connected with the distal septula (Fig. 8f, g), with centrodistal arch-like cavities (Dm: 30–40 µm) encircling the distal septula and sometimes connected with them and with the peripheral caverns (Fig. 8d, e, g, h). Channel-like cavities connected with each other and forming a network that has the same shape as the zooids (Fig. 8f). Basal autozooidal and vibracular wall only slightly thickening from the centre towards the proximal and lateral margins (Fig. 8d, g, h), in autozooids with one pair of basal septula encircled by depressions opposite to the opesia (Fig. 8f, h). Microcavities connecting the peripheral caverns and arch-like cavities sometimes present (Fig. 8d).

Kenozooids present, variable in shape and size (*L* 212–533 µm; *W* 89–154 µm), usually polygonal and smaller than autozooids, forming the lateral margins of each colony. Cryptocyst flat, finely pustulose. Aperture small (Dm: 24–44 µm), almost central, circular to elliptical (Fig. 8a, b).

Biometrical details are summarised in Table S6 in the Electronic Supplementary Material.

Remarks. Voigt (1956) already noted that the samples imaged by him and assigned to *Acoscinopleura fallax* show many variations and may represent several species. Re-examination of the type material showed that the holotype of *A. fallax* has numerous autozooids with large peripheral caverns, while peripheral caverns are very rare in other samples assigned to *A. fallax* in Voigt (1956). Moreover,

peripheral caverns are smaller and compare with those of *A. albaruthenica* sp. nov. from the late Campanian of Belarus. We therefore restrict *A. fallax* to the holotype only and the other material described in Voigt (1956) as *A. fallax* is here described as two new species. The specimens imaged as *A. fallax* in Voigt (1956, pl. 10, figs.3, 6–7) are redescribed as *A. dualis* sp. nov., while the samples imaged as *A. fallax* in Voigt (1956, pl. 10, figs. 2, 4–5) are redescribed as *A. occulta* sp. nov.

Voigt (1959) suggested that *Acoscinopleura fallax* Voigt, 1956 might be a subjective junior synonym of *Eschara gladiiformis* von Hagenow, 1840. He invalidated the name *gladiiformis* declaring it as a nomen nudum since von Hagenow (1840) had no image of the species and his description was too inadequate to allow subsequent recognition of the species without re-examination of von Hagenow's material. Voigt (1959, p. 47) noted: "*Nach der nichtssagenden Beschreibung v. Hagenows kann die Art unmöglich erkannt werden, zumal die charakteristischen Vibracularien nicht erwähnt werden*" ("It is impossible to recognize this species because of the inadequate description of v. Hagenow, especially as the characteristic vibracula are not mentioned"). Taking into account the strong variability of *A. fallax* sensu Voigt (1956) and since there is no redescription and no image of the von Hagenow material in Voigt (1959), it cannot be decided if *A. gladiiformis* and *A. fallax* are conspecific or not.

The material (40 fragments) assigned to *A. fallax* from late Maastrichtian glauconitic sandstones of Nasiłów, Poland in Maryańska (1969) are adeoniform colonies with proximal peripheral caverns. Without re-examination of the material, it cannot be decided to which species it belongs. Favorskaya (1992) described material found in late Campanian to Maastrichtian strata of the southern Aral Sea region that she assigned to *A. fallax*. As with the material from Poland, re-examination is necessary to clarify its identity. Bryozoans from the late Campanian of Belarus described as *A. fallax* in Koromyslova et al. (2015) belong to *A. albaruthenica* sp. nov. Peripheral caverns in *A. fallax* are found proximally and are similar in shape and position to those observed in *A. albaruthenica* sp. nov., but usually significantly larger.

Stratigraphic and geographic distribution. Late Maastrichtian of Lower Saxony, Germany.

Acoscinopleura occulta sp. nov.
Figures 3l, 9a–o

p 1956 *Acoscinopleura fallax* n. g. n. sp.—Voigt: p. 54; pl. 10, figs. 2, 4–5 (non pl. 10, figs. 1, 3, 6–7).

Etymology. From Latin occulta ('*hidden*'), in reference to the interconnected internal peripheral caverns that are evident only when studying the interior morphology.

Holotype. SMF 24086 [former Voigt photocard number 2385] (Figs. 3l, 9a–i).

Paratypes. SMF 24099 [former Voigt photocard number 748] (Fig. 9n, o), SMF 24104 [former Voigt photocard number 2387] (Fig. 9j–m).

Locality and Horizon. Hemmoor, Lower Saxony, Germany, late Maastrichtian.

Description. Colony rigidly erect, bifoliate, adeoniform. Zooids arranged quincuncially (Fig. 9a, b, d–f, l) and perfectly back-to-back (Fig. 9h–k, n, o). Zooids separated by broad and distinct furrows. Pore chambers lacking. Ancestrula and early astogenetic stages not observed.

Autozooids hexagonal, moderately large (*L* 462–545 µm; *W* 320–357 µm), with straight proximal ends and straight to weakly convex distal ends. Gymnocyst lacking. Cryptocyst extensive, very thick, distal to opesia 2–3 times thicker than proximal to opesia, finely pustulose, slightly depressed, weakly sloping towards the opesia from all sides. Peripheral caverns developed inside the cryptocyst of almost all autozooids, usually fully covered by a thick cryptocystal portion and not visible on the surface, interconnected with each other, comprising most of the cryptocyst except the portion around the tube for the passage of the lophophore (Fig. 9d, e, g, i, k). Some few peripheral caverns that are visible on the colony surface occur proximally, short and shallow, transversely rectangular, with walls steeply sloping inwards (Fig. 9n). Opesia small (*L* 79–100 µm; *W* 103–122 µm), semi-elliptical, not terminal, surrounded laterally and distally by a prominent margin, with two symmetrical opesiular indentations advancing deep into the cryptocyst proximolaterally and enclosing a broad and long tongue with prominent margin (Fig. 9a, b). Occlusor laminae in the distal part of opesia present (Fig. 9b). Autozooidal chamber short (*L* 430–500 µm; *W* 210–270 µm), narrow near basal walls, shallow, tight, boot-shaped with tapering proximal end and well-rounded corners, with short, transversely elliptical and tight tube for the passage of the lophophore distofrontally (Figs. 3l, 9i, j, n, o). Ovicells endozooidal, immersed in the proximal cryptocystal portion of the distal zooid. Ooecia cryptocystal well-developed, sometimes placed beneath a peripheral cavern (Fig. 9j, l, m).

Vibracula vicarious, about the same length as or longer but usually narrower than autozooids (*L* 512–614 µm; *W* 136–184 µm), forming a row of few at the lateral margins of the colony (Fig. 9a). Cryptocyst finely pustulose, weakly convex, thickening proximally, thinner than cryptocyst of autozooids, sometimes with internal caverns. Craticula small. Opesia terminal, round, small, usually hidden by a protruding small tooth. Vibracular chamber shorter,
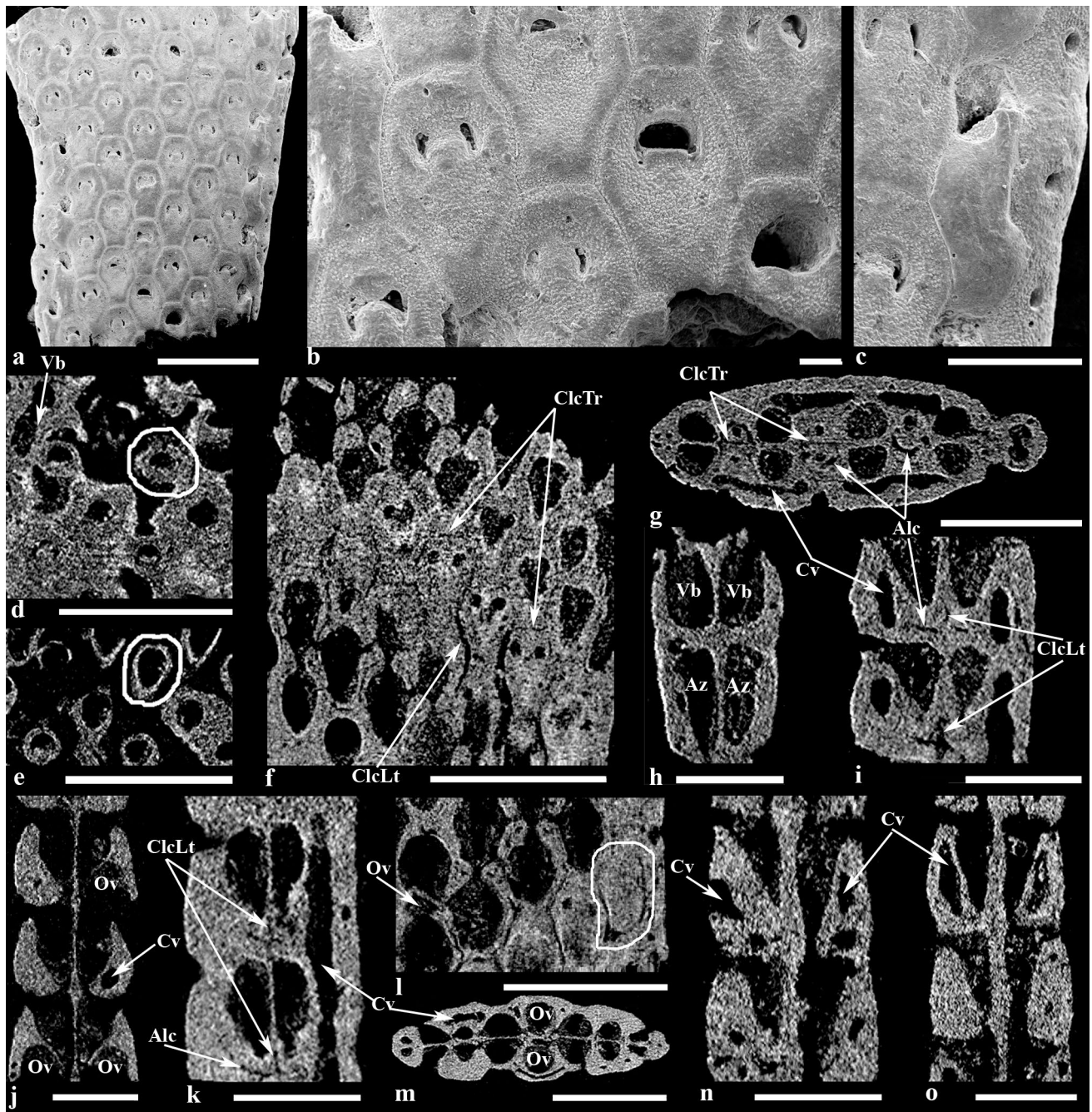
Fig. 9 *Acoscinopleura occulta* sp. nov., late Maastrichtian, Hemmoor, Lower Saxony, Germany. **a–i** Holotype SMF 24086. **a** Adeoniform colony. *Scale bar* 1000 μm. **b** Autozooids with opesiae partly closed. *Scale bar* 100 μm. **c** Vibraculum and kenozooids at the lateral margin. *Scale bar* 300 μm. **d** Coronal section showing a vibracular chamber and a tube for passage of the lophophore (outlined). *Scale bar* 1000 μm. **e** Coronal section showing several tubes and autozooidal chambers. *Scale bar* 1000 μm. **f** Coronal section showing various septula and channel-like cavities. *Scale bar* 1000 μm. **g** Transverse section showing interconnected internal peripheral caverns. *Scale bar* 1000 μm. **h** Sagittal section showing autozooidal and vibracular chambers. *Scale bar* 500 μm. **i** Sagittal section showing internal peripheral caverns. *Scale bar* 500 μm. **j–m** Paratype SMF 24104. **j** Sagittal section showing ovicells and internal peripheral cavern. *Scale bar* 500 μm. **k** Sagittal section showing interconnected internal peripheral caverns. *Scale bar* 500 μm. **l** Coronal section showing the basal wall of a vibraculum (outlined), pair-wise basal septula and a network of channel-like cavities. *Scale bar* 1000 μm. **m** Transverse section showing ovicells and one internal peripheral cavern. *Scale bar* 1000 μm. **n, o** Paratype SMF 24099. **n** Sagittal section showing peripheral caverns. *Scale bar* 500 μm. **o** Sagittal section showing internal peripheral caverns and autozooids lacking peripheral caverns. *Scale bar* 500 μm

shallower and usually narrower than autozooidal chamber (*L* 310–420 μm; *W* 190–230 μm), egg-shaped, with well-rounded corners, with very short, transversely rounded tube for the passage of the setae distofrontally (Fig. 9d, h).

Calcification of vertical walls thick, of basal walls thin. Vertical autozooidal and vibracular walls with six tube-like septula connecting each zooid with all neighbouring zooids, two proximolaterally, two centrolaterally, one proximally and one distally. In vibracular walls centrolateral septulum usually lacking. Vertical walls gradually thickening from the centrolateral septula to the distal septula, with lateral channel-like cavities (Dm: 10–30 μm) beginning on the level of the proximo- and centrolateral septula and connected with them (Fig. 9f, i, k, l), with transverse channel-like cavities (Dm: 10–20 μm) beginning near the distal margin of the basal walls and not connected with the distal septula (Fig. 9f, g), with centrodistal arch-like cavities (Dm: 10–30 μm) encircling the distal septula and sometimes connected with them and with the ovicell, if present (Fig. 9f, g, i, k, l). Channel-like cavities connected with each other and forming a network that has the same shape as the zooids (Fig. 9f, l). Basal autozooidal and vibracular wall thin centrally, about 2–3 times thicker proximally and laterally, in autozooids with one pair of basal septula encircled by depressions opposite to the opesia (Fig. 9f, l). Microcavities not observed.

Kenozooids present, variable in shape and size (*L* 290–347 μm; *W* 191–228 μm), usually polygonal and smaller than autozooids, forming the lateral margins of colony. Cryptocyst flat, finely pustulose. Aperture small (Dm: 34–41 μm), almost central, circular to elliptical (Fig. 9a, c).

Biometrical details are summarised in Table S7 in the Electronic Supplementary Material.

Remarks. Superficial differences of the new species *Acoscinopleura occulta* sp. nov. with *A. fallax* include the vibracula being larger and the opesiular indentations being longer (Fig. 9a). Micro-CT analyses revealed further significant internal morphological differences between *A. fallax* and *A. occulta* sp. nov. *A. occulta* sp. nov. developed internal peripheral caverns inside the cryptocyst of each autozooid, which completely surround the opesial tube. The internal peripheral caverns usually show no connection with the autozooidal chamber, but they are interconnected with each other, both laterally and vertically, a feature not observed in any other species of *Acoscinopleura* studied. Internal caverns which surround the opesia may result in cryptocystal insulae surrounding the opesia when the cryptocyst breaks away post mortem, as found in some other coscinopleurid species, for example *Coscinopleura lamourouxi* (von Hagenow, 1851). The specimens SMF 24099 and SMF 24104 are assigned to the new species, although they differ from the holotype in interconnected the internal peripheral caverns

being rarer and not well developed (Fig. 9j, k, n, o). Furthermore, these specimens show rare peripheral caverns on the colony's surface, which are small and morphologically compare well with those in *A. albaruthenica* sp. nov. (Fig. 9n).

Stratigraphic and geographic distribution. Late Maastrichtian of Lower Saxony, Germany.

Discussion

Distinguishing the species of *Acoscinopleura* Voigt, 1956

The late Turonian or middle Santonian to Thanetian Coscinopleuridae Canu, 1913 is a family of locally very abundant species that have not been comprehensively studied. A problem in the study of Coscinopleuridae is the distinction of species, which is severely hampered by the colonies showing very strong variability in appearance. For example, the size of autozooids strongly varies depending on how far they are positioned from the base of the colony. Furthermore, zooidal morphology in Coscinopleuridae shows only little variation over time (Håkansson and Thomsen 2001). Therefore, only few characters have proven suitable for taxon differentiation. Voigt (1956) considered especially the size of the opesia in fertile autozooids, the position of the vibracula and the peripheral caverns important to discriminate species. Voigt (1956) also gave the most comprehensive revision of this problematic bryozoan family to date. He distinguished 18 species and subspecies that were divided into three genera, two of which, *Acoscinopleura* and *Tremocoscinopleura*, were newly proposed. One additional species assigned to *Acoscinopleura* was first described in Georgala and Brood (1974) from the late Campanian of Scania, Sweden. Moreover, only a few authors have included coscinopleurid species in faunistic studies (e.g. Berthelsen 1962; Veenstra 1963; Maryańska 1969; Voigt 1979b).

We re-examined the type material of three closely related species of *Acoscinopleura*, *A. fallax* Voigt, 1956, *A. foliacea* (Voigt, 1930) and *A. rugica* Voigt, 1956, from the Maastrichtian of northern Germany and additional material from the Voigt Collection and from the late Campanian of Belarus. Our study included not only traditional SEM but also the use of micro-CT, which allowed non-destructive examination of the interior morphology of the bryozoan colonies. Therefore, the examination of zooidal chambers and internal features such as septula, pore chambers, endozooidal ovicells etc. was possible and additional characters could be identified that proved useful for species differentiation. These include the size of autozooidal and vibracular chambers, the occurrence and position of arch-like and channel-like

cavities and microcavities and the thickness of calcification of the cryptocyst and the basal and vertical walls.

Our studies confirm the identification of the material of *A. foliacea* and *A. rugica* as provided in Voigt (1956) and also confirm the concerns Voigt (1956) expressed regarding the conspecifity of the material included by him in *A. fallax*. Type material of the latter is shown to belong to three different species, two of which, *A. dualis* sp. nov. and *A. occulta* sp. nov., are newly described herein, and the specific name *fallax* is restricted to the holotype only. The holotype of *A. fallax* differs significantly from other colonies assigned to *A. fallax* by Voigt (1956) as it has larger autozooidal chambers and the largest peripheral caverns. Two new species, *A. dualis* sp. nov. and *A. occulta* sp. nov., are created for the material excluded from *A. fallax*. *A. dualis* sp. nov. has few proximal peripheral caverns, which are smaller than those in *A. fallax* and compare with those of *A. albaruthenica* sp. nov. *A. occulta* sp. nov. has large caverns inside the cryptocyst of each autozooid, which completely surround the opesial tube. The internal caverns are interconnected with each other, and if the cryptocystal cover would break, an insula surrounding the opesia would be observable. However, in the studied material, the cryptocyst was largely intact and only few peripheral caverns were observed in the proximal portion of the cryptocyst, which are comparable to the peripheral caverns observed in *A. albaruthenica* sp. nov.

Two further new species were created for material not studied in Voigt (1956). *A. crassa* sp. nov. is based on material from the Voigt Collection from the early Maastrichtian of Rügen and the late Maastrichtian of Hemmoor. It has thick calcification of the cryptocyst and the vertical and basal walls. Peripheral caverns are rare and only very small. The other species, *A. albaruthenica* sp. nov., is created for material from the late Campanian of Belarus. It has small autozooidal chambers and vibracula occur irregularly among autozooids but never as rows at the lateral margins.

On the vertical and basal walls

Each autozooid in a colony of a species of *Acoscinopleura* is surrounded by seven zooids; six autozooids hexagonally encircle the autozooid in the same lamina, while one autozooid is placed perfectly back-to-back. Interzooidal communication is achieved via septula that are located in the vertical and basal walls. Septula in the vertical walls allow communication with all six neighbouring zooids via one septulum, while communication with the autozooid on the back side is achieved via two septula. Despite this, septula in the basal walls are usually, but not invariably, larger than septula in the vertical walls. Vibracula are usually surrounded by only six zooids, five of which are located in the same lamina, plus one vibraculum placed perfectly back-to-back. This results in the number of septula in the vertical walls being reduced by one. There are no septula in the basal wall, and therefore communication with the vibraculum on the back side is not possible.

Calcification of the vertical walls is thick in all species examined, and the walls usually gradually thicken in each autozooid from the centrolateral septula to the distal septulum. Deep inside the vertical walls, small channel-like cavities with diameter <30 µm are visible in CT sections of all specimens examined (Fig. 10). Channel-like cavities
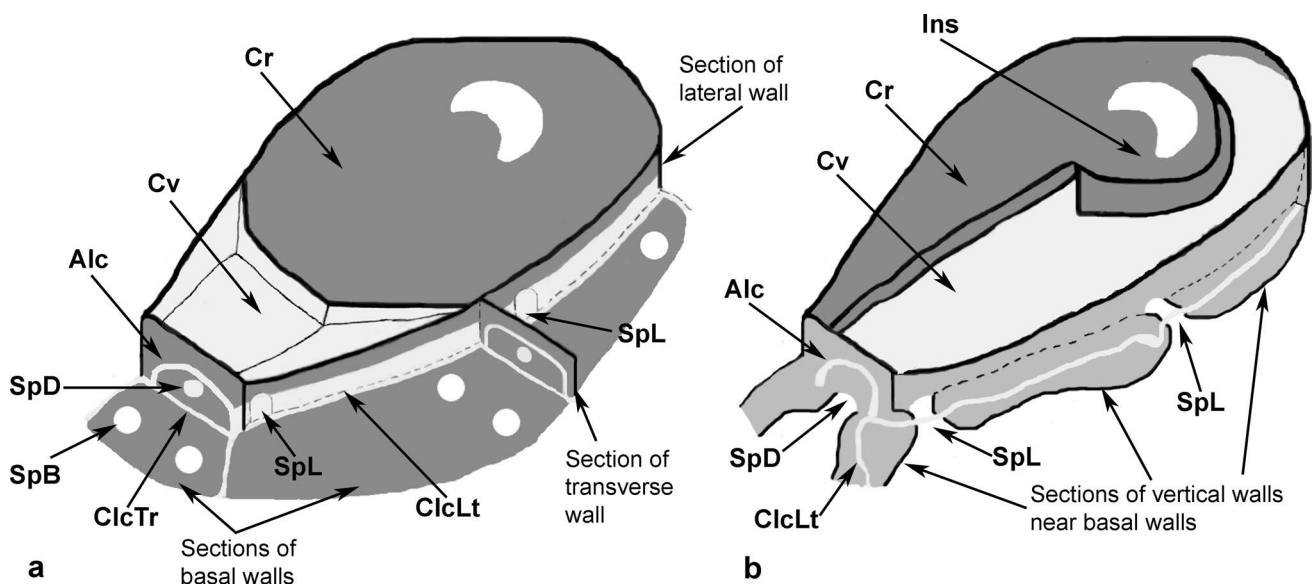
Fig. 10 Scheme showing (**a**) type 1 peripheral caverns and (**b**) type 2 peripheral caverns, and location of septula, channel-like cavities and arch-like cavities inside walls

in the lateral walls begin at the level of the proximo- and centrolateral septula and are connected with them, while in the transverse walls, they begin near the distal margin of the basal wall but are not connected with the distal septula. Channel-like cavities in the lateral and transverse walls are interconnected and completely surround each autozooid. The majority of Recent cheilostomes are believed to have double lateral vertical walls but only single transverse vertical walls (Levinsen 1891; Banta 1968a, b). Calcareous parts of the lateral walls therefore, consist of two calcareous laminae separated by an unpaired intercalary cuticle. The lateral and transverse channel-like cavities of *Acoscinopleura* might be gaps in the skeleton, which were occupied in life by the intercalary cuticle. However, in this case, the transverse walls in the studied specimens must also have been double, since channel-like cavities are interconnected. A comparable network of cavities between the primary basal zooid walls and the visible calcified basal surface was also reported from lunulitiform bryozoans (Chimonides and Cook 1994). A second type of cavity was found in the centrodistal part of the vertical walls. These cavities encircle the distal septula and are termed 'arch-like cavities' herein. The arch-like cavities are connected with the channel-like cavities and usually, but not invariably, with the distal septula and the ovicells.

The function and formation of the arch-like cavities remain unclear.

Calcification of the basal wall in *Acoscinopleura* is usually much thinner than calcification of the vertical walls, but in two species (*A. crassa* sp. nov. and *A. fallax*), calcification of the basal walls is thick, thus comparing with the calcification of the vertical walls. The basal wall in some Recent cheilostome bryozoans with erect bifoliate colonies is double, indicating that the colony grew as two independent layers, back to back (Carson 1978; Silén 1981). Double basal walls have also been observed in late Campanian tessaradomid cheilostomes using micro-CT (Koromyslova and Pakhnevich 2016). However, in the studied material of *Acoscinopleura*, there are no indicators found in the basal walls that would suggest that they are double.

Peripheral caverns

Peripheral caverns in the cryptocyst of autozooids are a morphological feature found only in few cheilostome bryozoans belonging exclusively to the families Onychocellidae Jullien, 1882 and Coscinopleuridae Canu, 1913. Furthermore, only species from the Late Cretaceous developed such structures (Table 3). The peripheral caverns can develop in different parts of the cryptocyst and usually the cryptocystal portion

Table 3 List of cheilostome bryozoans from the Latest Cretaceous with type 1 peripheral caverns

Species	Locus (neo)typicus	Stratigraphic range
Acoscinopleura adenticulata Georgala and Brood, 1974	Båstad, Sweden	Late Campanian
Acoscinopleura albaruthenica sp. nov.	Grodno, Belarus	Late Campanian
Acoscinopleura clio (d'Orbigny, 1851)	Meudon, France	Campanian
Acoscinopleura crassa sp. nov.	Rügen, Germany	Early Maastrichtian
Acoscinopleura fallax Voigt, 1956	Hemmoor, Germany	Late Maastrichtian
Acoscinopleura foliacea (Voigt, 1930)	Rügen, Germany	Early Maastrichtian
Acoscinopleura occulta sp. nov.	Hemmoor, Germany	Late Maastrichtian
Acoscinopleura rimosa Voigt, 1956	Ciply, Belgium	Late Maastrichtian
'*Biflustra*' *limbata* (d'Orbigny, 1852)	Sainte-Colombe, Manche, France	Late Maastrichtian
Collura athulia (d'Orbigny, 1851)	Néhou, Manche, France	Late Maastrichtian
Coscinopleura lamourouxi (von Hagenow, 1851)	Curfs quarry, The Netherlands	Early to late Maastrichtian
Inversaria aff. *flabellula* (von Hagenow, 1846)	Hemmingslycke, Sweden	Late Campanian
Latereschara galeata (von Hagenow, 1839) sensu Voigt (1967)	Kredin Gorge, Kopet Dag, Turkmenistan	Late Campanian
Onychocella alveolata Taylor and McKinney, 2006	Neuse River, North Carolina, USA	Maastrichtian
Onychocella cavernosa Voigt and Schneemilch, 1986	Alemannia quarry near Sehnde-Höver, Germany	Early Campanian
Onychocella formosa (Giebel, 1848)	Quedlinburg, Germany	Santonian
Onychocella nysti (von Hagenow, 1851)	Maastricht, The Netherlands	Early Campanian to late Maastrichtian
Onychocella sexangularis (Goldfuß, 1826)	Maastricht, The Netherlands	Late Maastrichtian
Solenonychocella hennigi Voigt and Williams, 1973	Maltesholms slot near Kristianstad, Sweden	Coniacian/Santonian to late Campanian
Tremocoscinopleura holsatica Voigt, 1956	Lägerdorf, Germany	Late Campanian
Tremocoscinopleura monops Voigt, 1956	Voerendaal-Kunrade, The Netherlands	Late Maastrichtian

surrounding the opesia is not affected. Two types of peripheral caverns can be distinguished. In type 1, small, single hollows are developed inside the cryptocyst (Fig. 10a). Type 1 peripheral caverns usually affect only some autozooids of a colony and occur very irregularly. However, they affect always the same parts of the cryptocyst and are always identical in shape and size. Type 1 peripheral caverns are therefore considered taxon dependent on a species level and can thus be used for discriminating species. In type 2 peripheral caverns, a depression surrounds a 'raised' cryptocystal portion, the 'insula' in the sense of Voigt (1956), around the opesia (Fig. 10b). The occurrence of type 2 peripheral caverns seems to be the more primitive state and is much more regular than the occurrence of peripheral caverns, as it usually affects all autozooids of a colony. It is noteworthy that both species with type 1 and type 2 peripheral caverns have mostly bifoliate colonies. While material of *A. foliacea*, *A. albaruthenica* sp. nov., *A. rugica*, *A. dualis* sp. nov., *A. crassa* sp. nov. and *A. fallax* developed type 1 peripheral caverns, *A. occulta* sp. nov. has type 2 peripheral caverns. However, since the cryptocystal lid covering the peripheral caverns did not break away, type 2 peripheral caverns are not visible on the surface but could be visualised only using micro-CT.

Canu (1900) and Voigt (1989) interpreted the evolution of type 2 peripheral caverns as a sign of ageing of the bryozoan colony, as younger autozooids often lack such structures [e.g. *Onychocella latilabris* (Reuss, 1872) in Voigt 1989; pl. 14, fig. 7]. Voigt (1956) suggested that peripheral caverns in Coscinopleuridae could have developed in older zooids as a result of recess of calcite for the relief of the skeleton, as all *Acoscinopleura* species show unusually thick calcification of the cryptocyst. However, in the material that we examined, autozooids closer to the base of the colony, i.e. older autozooids, are not more likely to develop peripheral caverns than autozooids located more distally, i.e. younger autozooids. This puts into question the interpretation of peripheral caverns as a result of ageing. Voigt (1985) and Taylor and McKinney (2006) argued that peripheral caverns may develop during overgrowth of the primary cryptocyst by a secondary cryptocyst, the peripheral caverns then having been occupied with diagenetically unstable aragonite or high-Mg calcite. If this was the case, our study suggests that the layer of aragonite/high-Mg calcite must have been covered by a small layer of low-Mg calcite. This would mean that peripheral caverns developed post mortem after dissolution of aragonite/high-Mg calcite and breakage of the thin low-Mg cover.

Another possible explanation for the evolution of peripheral caverns is a correlation with the hydrostatic system (Voigt 1956). Peripheral caverns may have been filled with coelomic fluid, as suggested in an alternative model for the evolution of peripheral caverns presented in Voigt (1985). In the material studied, we found microcavities connecting the peripheral caverns with the arch-like cavities in specimens of *A. foliacea*, *A. rugica*, *A. crassa* sp. nov. and *A. fallax*. However, evidence for such connections of the peripheral caverns with other parts of the zooids is insufficient. A problem in the explanation of the evolution of peripheral caverns is why only certain autozooids of a colony developed such structures. We observed no correlation with the position of the autozooids in a colony having or lacking peripheral caverns. Despite the irregular occurrence of peripheral caverns, there is no indication that they were produced by boring predators, so predation can be excluded as a reason for the evolution of peripheral caverns. It remains therefore unclear what triggered certain autozooids to develop peripheral caverns. A convincing model for the evolution of peripheral caverns can therefore not be suggested.

Conclusions

The following conclusions can be made based on the results presented in this paper:

- The internal morphology of species of *Acoscinopleura* is complex. The material examined shows cavities inside the lateral and transverse walls (=lateral and transverse channel-like cavities, respectively) and encircling the distal septula (=arch-like cavities).
- Interzooidal communication in *Acoscinopleura* is done via septula. Each zooid is connected via one septulum with each of the encircling zooids in the same lamina. Furthermore, autozooids are connected via two septula in the back wall with the autozooid on the back side, while vibracula arranged back-to-back are not interconnected.
- Examination of the internal morphology may add a sufficient amount of characters useful for taxon differentiation in complicated taxa such as coscinopleurid cheilostomes. For the material examined, these include the size of autozooidal and vibracular chambers, the occurrence and position of arch-like and channel-like cavities and microcavities and the thickness of calcification of the cryptocyst and the basal and vertical walls.
- Peripheral caverns can be subdivided into two types: type 1, small, single hollows developed inside the cryptocyst, and type 2, a depression surrounding an insular cryptocystal portion around the opesia. Both types were covered during lifetime by a thin cryptocystal lid.

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