PalZ (2020) 94:697–714
https://doi.org/10.1007/s12542-019-00509-3

RESEARCH PAPER

Early Maastrichtian cheilostome bryozoans from the middle Volga River region

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Received: 16 August 2019 / Accepted: 28 December 2019 / Published online: 29 January 2020

Abstract
Eight species in six genera of cheilostome bryozoans are described from an early Maastrichtian outcrop located in the Saratov Region, middle Volga River region, southern Russia. The studied bryozoan assemblage includes a new species, *Cheethamia volgaensis* sp. nov., as well as *Dionella* sp., *Cheethamia aktolagayensis* Koromyslova et al., *Rhagasostoma* cf. *saltans* (Brydone), and *Luganella goldfussi* (von Hagenow). A few poorly preserved specimens are tentatively assigned to the genera *Hoplitaechmella* and *Acoscinopleura*. Some of the recorded species encrusted a *Cataceramus* shell and internal moulds of *Baculites* ammonoid shell fragments; whereas others produced erect, flattened, bifoliate colonies. A single species, *L. goldfussi*, had free-living, discoidal colonies. The palaeobiogeography of early Maastrichtian bryozoans is discussed. The recorded bryozoans belong to genera ubiquitous in the early Maastrichtian of Europe and, to a lesser degree, other regions.

Keywords Bryozoa · Cheilostomata · Taxonomy · Maastrichtian · Paleoecology · Paleobiogeography

Introduction

During the Late Cretaceous, the part of Eurasia extending from the British Isles as far as the Fergana Valley in Central Asia was occupied by multiple shallow epicontinental seas no deeper than a few hundred meters (Naidin et al. 1986; Mosquin 1987; Beniamovski 2008). The bryozoan fauna of such western and eastern basins has been studied by several authors (Levinsen 1925; Brydone 1929, 1930, 1936; Voigt 1930, 1949, 1967; Berthelsen 1962; Favorskaya 1980, 1981, 1987, 1988, 1992, 1996; Titova and Favorskaya 1994) and some of them have pointed to similarities between Late Cretaceous bryozoan associations from Europe and Central Asia. However, the Late Cretaceous bryozoan fauna from the central basins remains poorly known. One of them covered the territory of the present-day Saratov Region in the middle Volga Region of the Russian Federation. Despite the fact that bryozoans are widespread in Late Cretaceous deposits of the Saratov Region, only a few species have been described to date (Voigt 1962; Kvachko 1995a; Viskova 1965, 1972, 2004, 2005).

Here, we describe eight species of cheilostome bryozoans, including one new species, from the Lower Maastrichtian of the 'Krasnyj Oktyabr' quarry located in the southern environs of the town of Volsk on the right bank of Volga in the Saratov Region. The aim of this paper is to increase our knowledge of the taxonomic diversity of bryozoans in the Volga region and their paleobiogeography and paleoecology in Eurasian epicontinental seas during the early Maastrichtian.

Geological setting

The Maastrichtian deposits in the study area are exposed in quarries in the immediate vicinity of the Volga River bank near Volsk (Saratov Region) (Fig. 1). The outcrops with the Upper Cretaceous beds are confined to the Volsk Depression on the southern slope of the Ulyanovsk–Saratov Trough. The Maastrichtian deposits in the region belong to the Karsun

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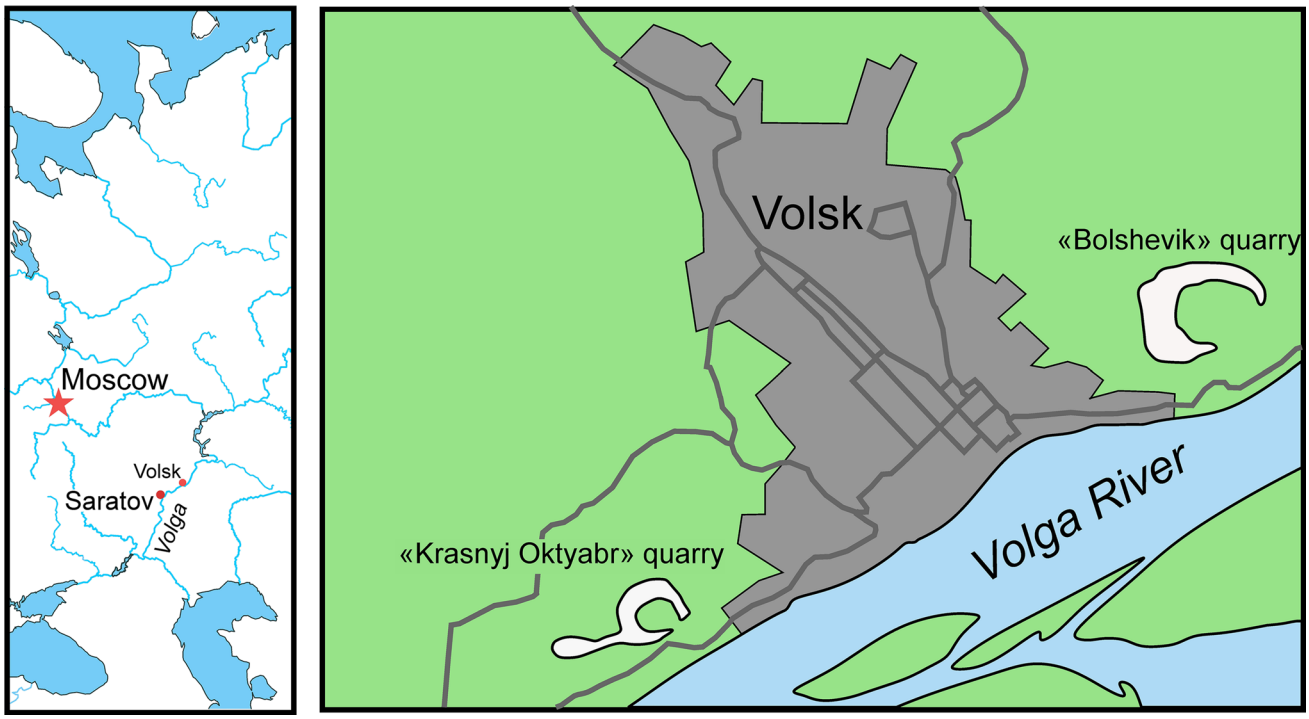

Fig. 1 Location of the 'Krasnyj Oktyabr' quarry, southern environs of the town of Volsk, Saratov Region, Russia

(Lower Maastrichtian) and the Radishchevo (Upper Maastrichtian) formations (Olferiev and Alekseyev 2005); they lie horizontally and are exposed as debris on hill slopes and as broken blocks on quarry benches. In the 'Krasnyj Oktyabr' quarry, the Maastrichtian comprises the main part of the section; it overlies the older (Turonian–Campanian) sediments that are incomplete. The total thickness of the Maastrichtian is 66–70 m, including both the lower and the upper substages. This age has been substantiated by the faunas of ammonoids, belemnites, benthic foraminifers and calcareous nannoplankton (Olferiev et al. 2009a, b, 2014). The beds are represented by white chalk with darker interlayers of marl (Fig. 2).

Materials and methods

The bryozoan specimens studied here are preserved at the Earth Science Museum at Moscow State University (ESM MSU), Moscow, Russian Federation. The encrusting cheilostome species, some with frontal surfaces visible but others seen from the underside, were found on a *Cataceramus* sp. shell and internal moulds of *Baculites* ammonoid shell fragments (Fig. 3); whereas the erect colonies, with flattened bifoliate branches, and discoidal colonies were extracted from samples selected for microfaunal determinations.

All specimens were imaged at the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN) in Moscow, Russian Federation, without coating, using the backscattered electron (BSE) detector of a Tescan Vega 2 scanning electron microscope (SEM) operated at low vacuum (10 Pa) and an accelerating voltage of 20 kV. Zooidal measurements were taken from SEM images. The measurements are given in µm as the arithmetic mean ± standard deviation, observed range, and (in parentheses) the number of specimens (N) and the total number of measurements (n).

Abbreviations for measurements are as follows. AL, avicularian length; AW, avicularian width; AOpL, avicularian opesia length; AOpW, avicularian opesia width; ARL, avicularian rostrum length; ARW, avicularian rostrum width (measured at the rostral base); AzL, autozooidal length; AzW, autozooidal width; AzLL, autozooidal length (for long autozooids); AzLW, autozooidal width (for long autozooids); AzSL, autozooidal length (for short autozooids); AzSW, autozooidal width (for short autozooids); KL, kenozooidal length; KW, kenozooidal width; OvL, ovicell length; OvW, ovicell width; OpL, autozooidal opesia length; OpW, autozooidal opesia width; OpLL, autozooidal opesia length (for long autozooids); OpLW, autozooidal opesia width (for long autozooids); OpSL, autozooidal opesia length (for short autozooids); OpSW, autozooidal opesia width (for short autozooids).

Systematic paleontology

Phylum **Bryozoa** von Ehrenberg, 1831
Class **Gymnolaemata** Allman, 1856

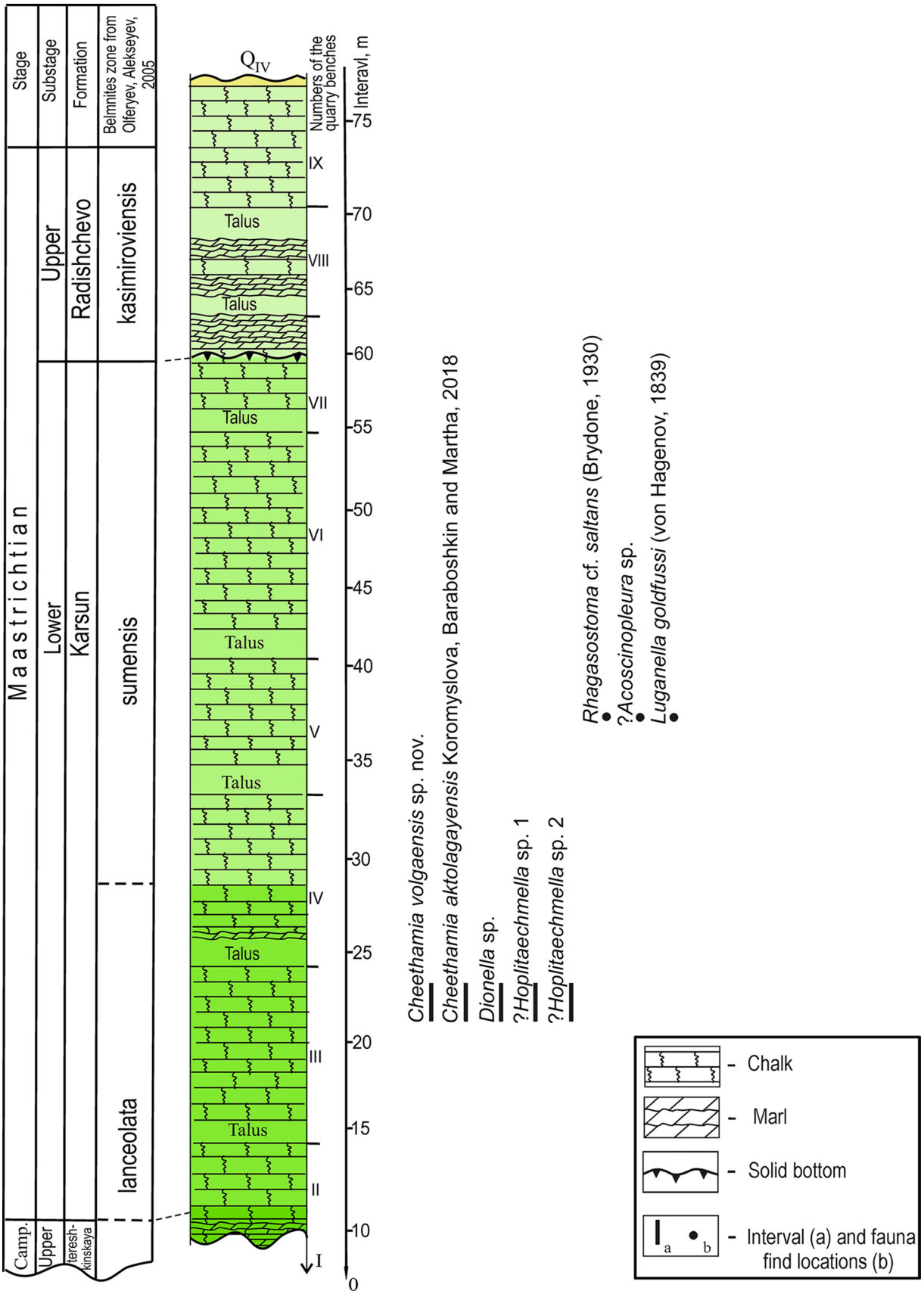

Fig. 2 Maastrichtian stratigraphy in the 'Krasnyj Oktyabr' quarry from Volsk

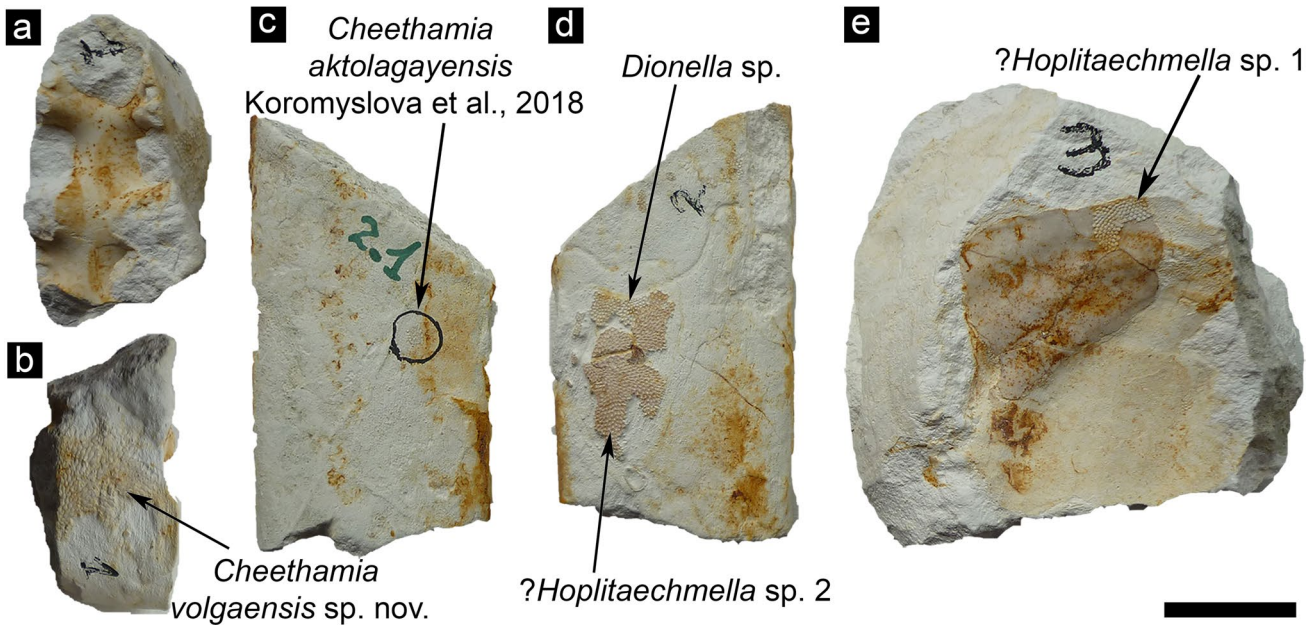

Fig. 3 Some bryozoan-bearing *Baculites* ammonoid shells from the lower Maastrichtian of 'Krasnyj Oktyabr' quarry, Volsk. **a**, **b** Fragment of *Baculites* cf. *vertebralis* Lamarck, phragmocone. **a** Transverse split. **b** Lateral surface. **c**, **d** Fragment of *Baculites* sp., phragmocone. **c** Lateral surface. **d** Opposite lateral surface. **e** Colony on the inner surface of a *Cataceramus* sp. shell. *Scale bar* 2 cm

Order **Cheilostomata** Busk, 1852
Suborder **Neocheilostomina** d'Hondt, 1985
Infraorder **Flustrina** Smitt, 1867
Superfamily **Calloporoidea** Norman, 1903
Family **Calloporidae** Norman, 1903

Genus ***Dionella*** Medd, 1965

Type species. Cellepora trifaria von Hagenow, 1846, Maastrichtian, Germany.

Dionella sp.
Figures 3d, 4a–c

Studied material. ESM MSU 133/1, a colony visible from the underside on the lateral surface of a *Baculites* sp. phragmocone.

Measurements. AzL 530 ± 78 µm, 380–640 µm (N 1, n 12); AzW 454 ± 51 µm, 370–540 µm (N 1, n 12); OpL 371 ± 43 µm, 280–430 µm (N 1, n 12); OpW 275 ± 35 µm, 210–340 µm (N 1, n 12); OvL 146 ± 18 µm, 120–180 µm (N 1, n 12); OvW 203 ± 28 µm, 150–250 µm (N 1, n 12); AL 100 ± 14 µm, 90–110 µm (N 1, n 2); AW 110 ± 14 µm, 100–120 µm (N 1, n 2).

Description. Colony encrusting, multiserial, sheet-like, visible from underside (Fig. 4a, b). Putative pore chambers visible along lateral zooidal walls (Fig. 4b, c). Ancestrula and early astogeny poorly preserved. Putative ancestrula small, about 220 µm long by 240 µm wide, apparently budding one distal and two distolateral zooids (Fig. 4b). Basal walls of zooids not preserved. Autozooids quincuncially arranged, rounded-rhomboidal. Inner surfaces of gymnocyst (?) and cryptocyst observed proximal to opesia, extensive, concave; inner surface of cryptocyst concave, narrow laterally and negligible distally. Opesia extensive, occupying most of the frontal surface, rounded or oval. Putative inner surfaces of ovicells trapezoidal; avicularia rounded distally to some autozooids (Fig. 4b, c). Closure plates, kenozooids, and intramural reparative zooids not observed.

Remarks. This specimen is referred to the genus *Dionella* because it possesses pore chambers and small interzooidal avicularia, which are located distal to the autozooids. This species has a zooidal morphology and size ranges comparable to that of *Dionella trifaria* (von Hagenow, 1846), described and figured by Voigt (1962: 20, pl. 12, fig. 3) from the early Maastrichtian of Khvalynsk, Saratov Region (here Fig. 4d, e): AzL 380–640 µm v. 500–580 µm in *D. trifaria*; AzW 370–540 µm v. 400–440 µm in *D. trifaria*; OpL 280–430 µm v. 330–410 µm in *D. trifaria*; OpW 210–340 µm v. 270–310 µm in *D. trifaria*;

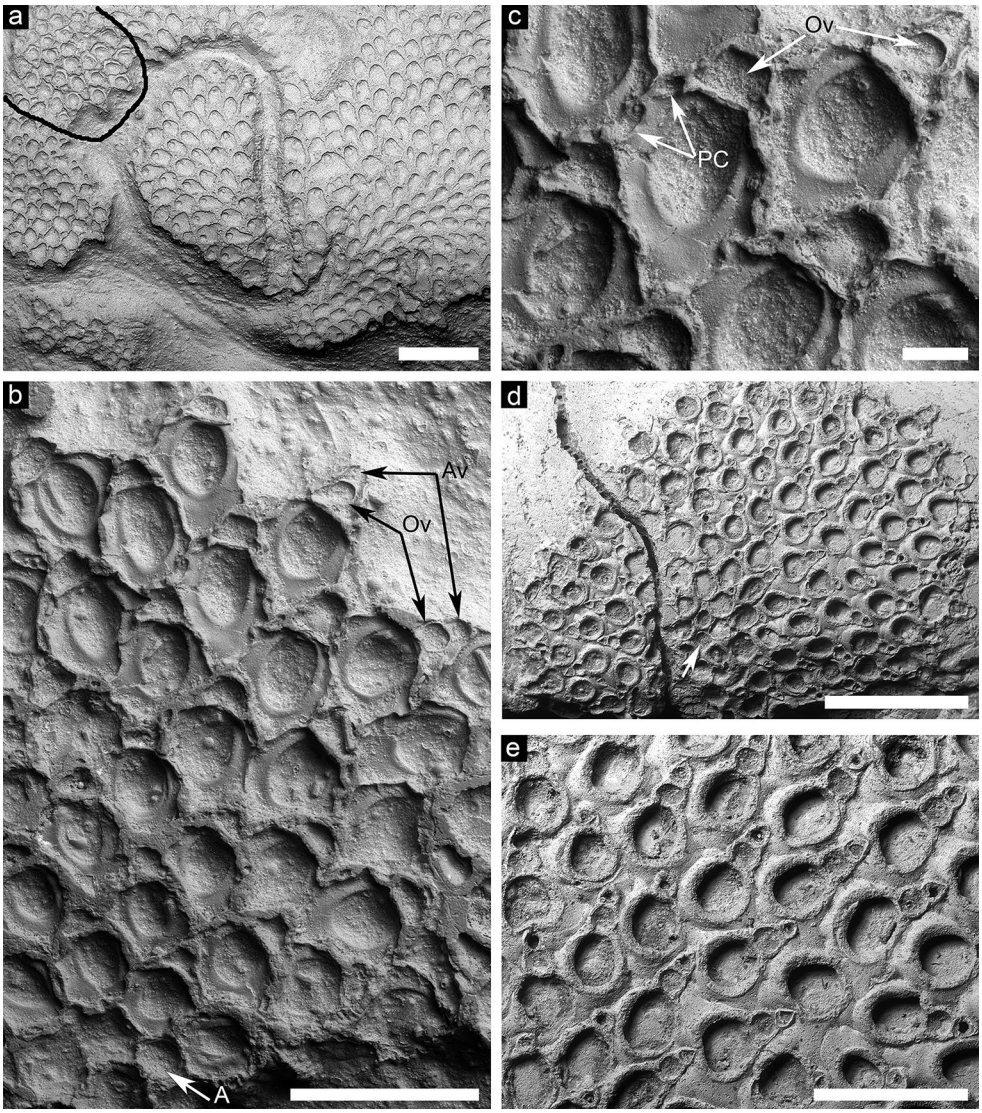

Fig. 4 *Dionella* sp., ESM MSU 133/1. **a** Adjoining colonies of *Dionella* sp. (outline marked) and ?*Hoplitaechmella* sp. 2. *Scale bar* 2 mm. **b** Inner view of the sheet-like colony; putative ancestrula (A), ovicells (Ov) and avicularia (Av) arrowed. *Scale bar* 1 mm. **c** Close-up of the inside of autozooids; putative pore chambers (PC) and ovicells (Ov) arrowed. *Scale bar* 200 µm. **d**, **e** *Dionella trifaria* (von Hagenow, 1846), early Maastrichtian of Khvalynsk, Saratov Region. **d** Sheet-like colony; putative ancestrula arrowed. *Scale bar* 2 mm. **e** Autozooids, ovicells and avicularia. *Scale bar* 1 mm

OvL 120–180 µm v. 130–180 µm in *D. trifaria*; OvW 150–250 µm v. 150–180 µm in *D. trifaria*. However, poor preservation of the studied material prevents species-level identification.

Superfamily **Microporoidea** Gray, 1848
Family **Onychocellidae** Jullien, 1882

Genus ***Cheethamia*** Shaw, 1967

Type species. Cheethamia howei Shaw, 1967, Maastrichtian, Saratoga Chalk, Arkansas, USA.

Cheethamia aktolagayensis Koromyslova, Baraboshkin and Martha, 2018
Figures 3c, 5

2018 *Cheethamia aktolagayensis* n. sp.—Koromyslova et al.: p. 324, fig. 14.

Studied material. ESM MSU 133/2, encrusting the lateral surface of a *Baculites* sp. phragmocone.

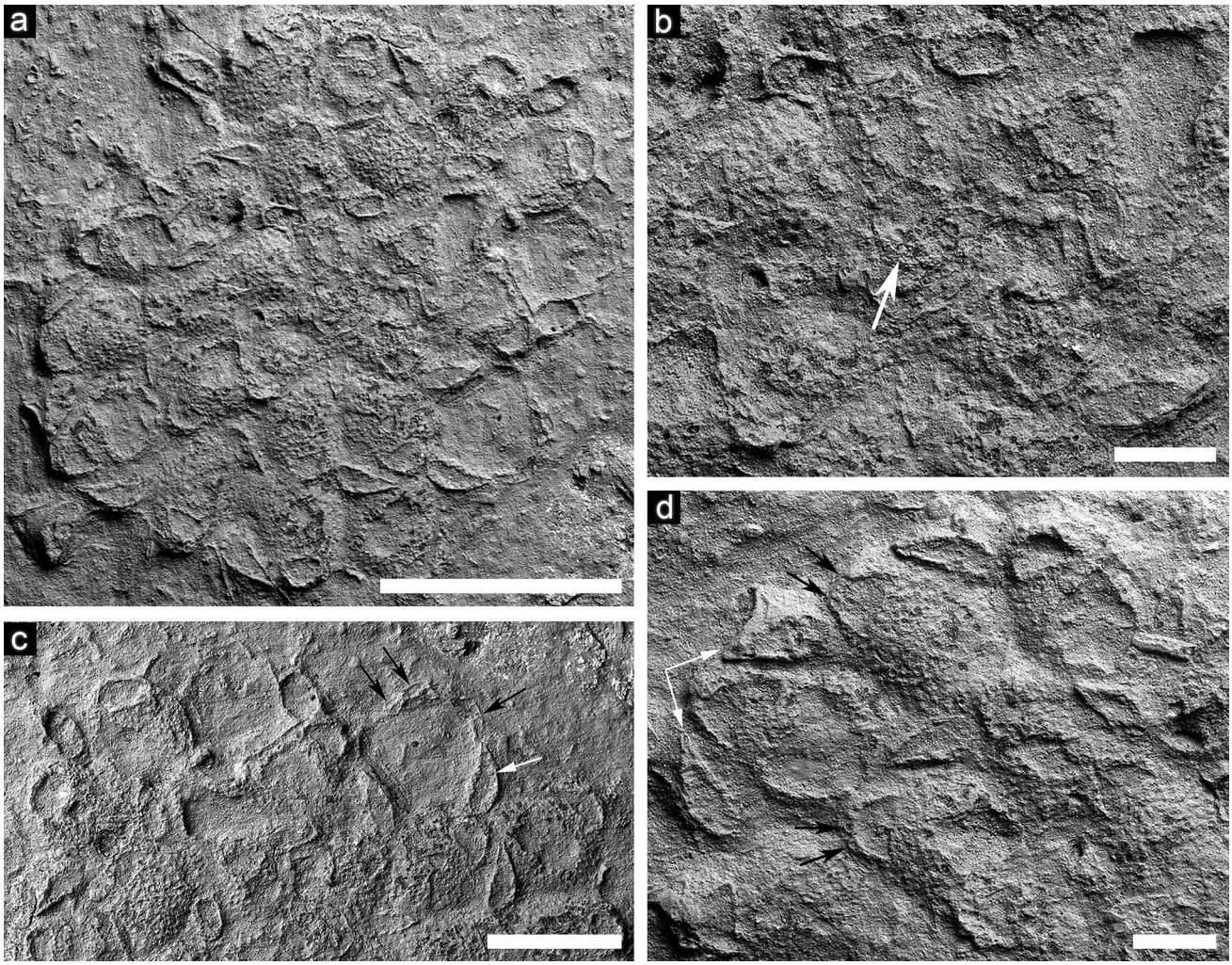

Fig. 5 *Cheethamia aktolagayensis* Koromyslova, Baraboshkin and Martha, 2018, ESM MSU 133/2. **a** General view of the colony. *Scale bar* 1 mm. **b** Zone of early astogeny; putative ancestrula arrowed. *Scale bar* 200 µm. **c** Growing edge of the colony; pore chambers (black) and avicularium (white) arrowed. *Scale bar* 500 µm. **d** Autozooids and avicularia; distal oral spine bases (black) and avicularia (white) arrowed. *Scale bar* 200 µm

Measurements. AzL 411 ± 41 µm, 360–500 µm (N 1, n 9); AzW 334 ± 41 µm, 290–410 µm (N 1, n 9); OpL 96 ± 11 µm, 80–110 µm (N 1, n 9); OpW 147 ± 16 µm, 130–180 µm (N 1, n 9); AL 263 ± 20 µm, 220–290 µm (N 1, n 9); AW 100 ± 14 µm, 70–120 µm (N 1, n 9).

Description. Colony encrusting, multiserial, unilaminar, spot-like, 2.6 mm in diameter (Fig. 5a). Ancestrula and early astogeny poorly preserved. Ancestrula pear-shaped, about 300 µm long by 210 µm wide, apparently budding one distal and two distolateral zooids (Fig. 5b, arrowed). Pore chambers poorly visible on zooids at colony's growing edge, small, oval, laterally placed (Fig. 5c). Autozooids ovoidal, separated by distinct furrows. Gymnocyst lacking. Cryptocyst occupying most of the frontal surface, convex, with apparent faint reticulate pattern of polygonal ridges. Mural rim not raised. Opesia subterminal on cryptocyst, semielliptical, without shelf in distal part and, presumably, with small opesiular indentations at proximolateral corners; proximal edge straight; distal edge curved, bearing an uncertain number of distal oral spine bases, two or three (Fig. 5d, arrowed), maybe more. Avicularian morphology uncertain, avicularia interzooidal, elongate, seemingly drop-shaped (Fig. 5c, d); rostrum symmetrical or weakly asymmetrical. Ovicells, closure plates, kenozooids, and intramural reparative zooids not observed.

Remarks. A single very small, poorly preserved colony can be identified as *Cheethamia aktolagayensis* described by Koromyslova et al. (2018a) from the Maastrichtian of the Aktolagay Plateau, in western Kazakhstan, based on similarities in the morphology of the autozooids and avicularia.

However, the number of distal oral spine bases in the autozooids of the Volga River specimen is uncertain; while in *C. aktolagayensis* from the Aktolagay Plateau, it varies from seven (in the zone of early astogeny) to two (in the zone of astogenetic repetition).

Stratigraphic and geographic distribution. Early Maastrichtian of the middle Volga River region, Saratov Region, Russia, and the Aktolagay Plateau, western Kazakhstan.

Cheethamia volgaensis sp. nov.
Figures 3b and 6

Etymology. Named after the type locality, the Volga River.

Holotype. ESM MSU 133/3, encrusting the lateral surface of a *Baculites* cf. *vertebralis* Lamarck phragmocone.

Locality and Horizon. Middle Volga River region, Saratov Region, Russia; early Maastrichtian.

Measurements. AzL 932 ± 101 µm, 790–1140 µm (N 1, n 12); AzW 631 ± 72 µm, 490–740 µm (N 1, n 12); OpL 140 ± 4 µm, 130–150 µm (N 1, n 12); OpW 179 ± 9 µm, 160–190 µm (N 1, n 12); AL 832 ± 54 µm, 760–900 µm (N 1, n 5); AW 412 ± 63 µm, 300–450 µm (N 1, n 5); ARL 450 ± 25 µm, 420–490 µm (N 1, n 5); ARW 126 ± 15 µm, 110–140 µm (N 1, n 5).

Diagnosis. Colony encrusting, multiserial, unilaminar. Autozooids rounded-hexagonal; gymnocyst lacking. Cryptocyst extensive, convex, pustulose. Opesia subterminal, semielliptical; distal edge raised, with pair of oral spine bases; proximal edge smooth with small, lateral opesiular indentations.

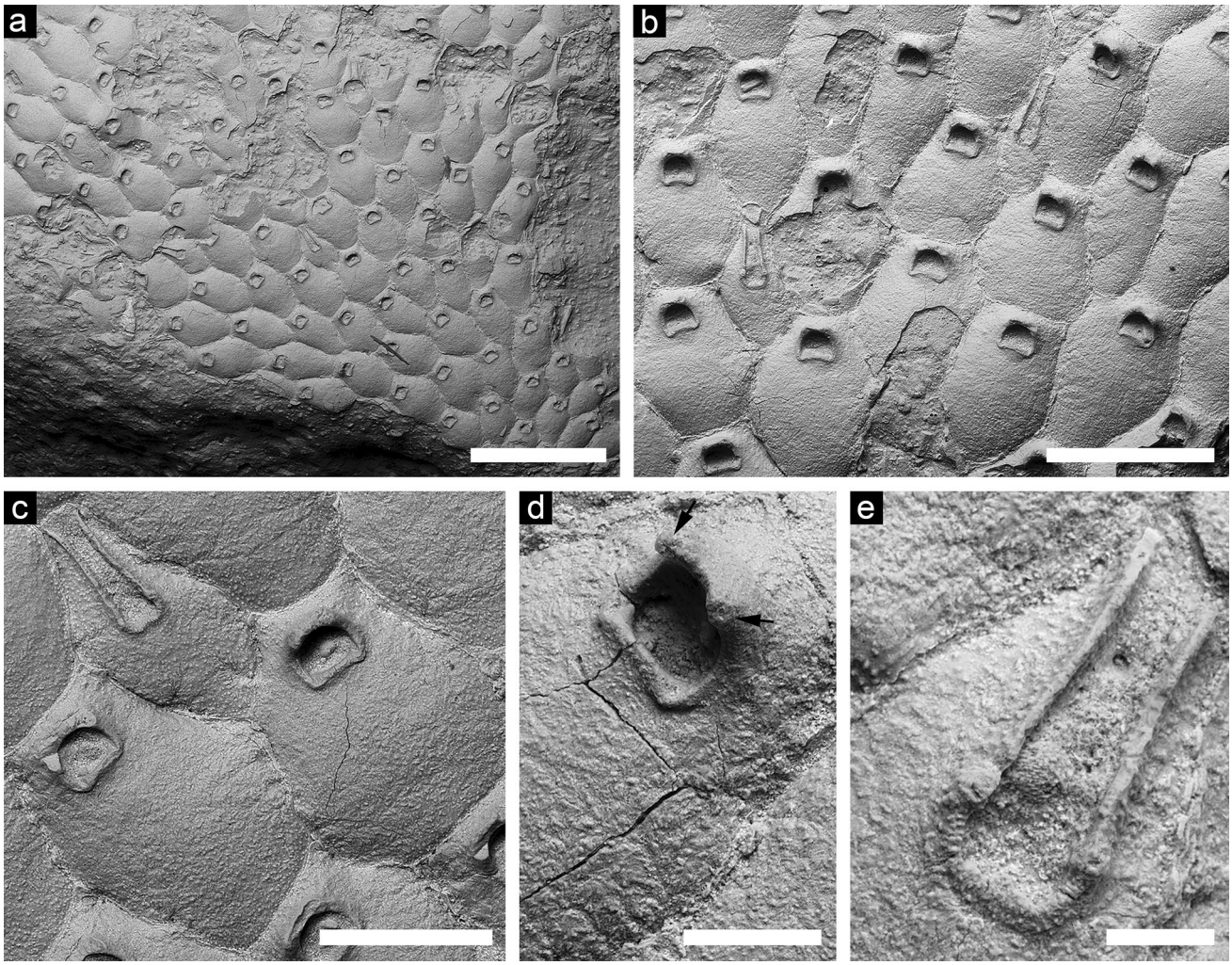

Fig. 6 *Cheethamia volgaensis* sp. nov., ESM MSU 133/3. **a** Part of the encrusting colony. *Scale bar* 2 mm. **b** Autozooids and avicularia. *Scale bar* 1 mm. **c** Autozooids and avicularium. *Scale bar* 500 µm. **d** Autozooidal opesia and a pair of oral spine bases (arrowed). *Scale bar* 200 µm. **e** Avicularium. *Scale bar* 200 µm

Avicularia vicarious, sparse, rhomboidal; rostrum channeled, symmetrical, with opesia having crenulated concave proximal edge. Kenozooids absent.

Description. Colony encrusting, multiserial, sheet-like, unilaminar (Fig. 6a). Ancestrula, early astogeny and pore chambers not observed. Autozooids distinct, separated by shallow furrows, quincuncially arranged, rounded-hexagonal. Gymnocyst lacking. Mural rim not raised. Cryptocyst extensive, convex, pustulose. Opesia subterminal on cryptocyst, semielliptical, partially closed by raised distal edge with pair of oral spine bases (Fig. 6d); proximal edge straight, smooth, thickened, with small lateral opesiular indentations (Fig. 6b–d). Vicarious avicularia sparse, rhomboidal, symmetrical; gymnocyst lacking, cryptocyst pustulose; rostrum channeled; opesia having crenulated, slightly concave proximal edge, obscured by sediment grains (Fig. 6a–c, e). Ovicells, kenozooids, closure plates, and intramural buds not observed.

Remarks. This new species, represented by a well-preserved colony, is referred to the genus *Cheethamia* because the vicarious avicularia are symmetrical and very similar in shape to those of the type species of the genus, *Cheethamia howei* Shaw, 1967 from the Campanian and Maastrichtian of the United States (Taylor and McKinney 2006; Taylor et al. 2018). *Cheethamia volgaensis* sp. nov. is similar to *Cheethamia incrustans* (Canu, 1922), redescribed by Di Martino et al. (2018), in the structure of avicularia, but differs in having a pair of oral spine bases, the avicularian rostrum channeled rather than raised and acuminate, and also much larger zooids and vicarious avicularia (AzL 790–1140 µm v. 433–598 µm in *C. incrustans*; AzW 490–740 µm v. 311–477 µm in *C. incrustans*; AL 760–900 µm v. 464–551 µm in *C. incrustans*; AW300–450 µm v. 223–321 µm in *C. incrustans*). The presence of ovicells in *Cheethamia volgaensis* sp. nov. is unclear because the distal edge of all observed autozooids is raised.

Genus ***Hoplitaechmella*** Voigt, 1949

Type species. Cellepora vespertilio von Hagenow, 1839, early Maastrichtian, Rügen, Germany.

?***Hoplitaechmella*** sp. 1
Figures 3e, 7

Studied material. ESM MSU 133/4, encrusting the inner surface of a *Cataceramus* sp. shell.

Measurements. AzL 563 ± 65 µm, 440–680 µm (N 1, n 12); AzW 531 ± 67 µm, 440–590 µm (N 1, n 12); OpL 103 ± 5 µm, 100–110 µm (N 1, n 12); OpW 141 ± 9 µm, 130–160 µm (N 1, n 12); AL 95 ± 17 µm, 80–120 µm (N 1, n 4); AW 75 ± 13 µm, 60–90 µm (N 1, n 4).

Description. Colony encrusting, multiserial, sheet-like, unilaminar (Fig. 7a). Ancestrula and early astogeny poorly preserved. Putative ancestrula small, about 320 µm long by 460 µm wide (Fig. 7b). Pore chambers small, oval, laterally placed, visible on zooids at the colony growing edge (Fig. 7d). Autozooids globular, separated by distinct furrows; enlarged zooids rare, usually equal to the width of two ordinary zooids (Fig. 7e). Gymnocyst lacking. Cryptocyst occupying most of frontal surface, convex, covered by tubercles. Mural rim not raised. Opesia subterminal on cryptocyst, semielliptical, without shelf in the distal part; opesiular indentations at proximolateral corners lacking; proximal edge straight; distal edge semielliptical, bearing an uncertain number of oral spine bases (Fig. 7c, f). Avicularia rare, interzooidal, very small, drop-shaped, symmetrical; opesia obscured by sediment grains (Fig. 7f). Ovicells, vicarious avicularia, closure plates, kenozooids, and intramural reparative zooids not observed.

Remarks. This species is tentatively referred to the genus *Hoplitaechmella*, because of the presence of small interzooidal avicularia distally of some autozooids and the occurrence of oral spine bases and pore chambers as in the type and other species of the genus (Voigt 1949, 1962, 1967, 1979; Berthelsen 1962; Gordon and Taylor 1999; Taylor et al. 2018). However, vicarious avicularia were not observed. The species ?*Hoplitaechmella* sp. 1 differs from the ?*Hoplitaechmella* sp. described by Koromyslova et al. (2018a) from the early Maastrichtian of the Aktolagay Plateau, western Kazakhstan, in having larger, globular autozooids with semielliptical opesia instead of elliptical autozooids with trapezoidal opesia (AzL 440–680 µm v. 400–590 µm in Kazakh species; AzW 440–590 µm v. 290–430 µm in Kazakh species).

?***Hoplitaechmella*** sp. 2
Figures 3d, 4a, 8a–c

Studied material. ESM MSU 133/5, a colony visible from the underside on the lateral surface of a *Baculites* sp. phragmocone.

Measurements. AzL 665 ± 84 µm, 480–780 µm (N 1, n 12); AzW 435 ± 77 µm, 340–610 µm (N 1, n 12); OpL 154 ± 19 µm, 130–190 µm (N 1, n 12); OpW 155 ± 9 µm, 140–170 µm (N 1, n 6); AL 204 ± 26 µm, 150–250 µm (N 1, n 12); AW 166 ± 21 µm, 110–190 µm (N 1, n 12).

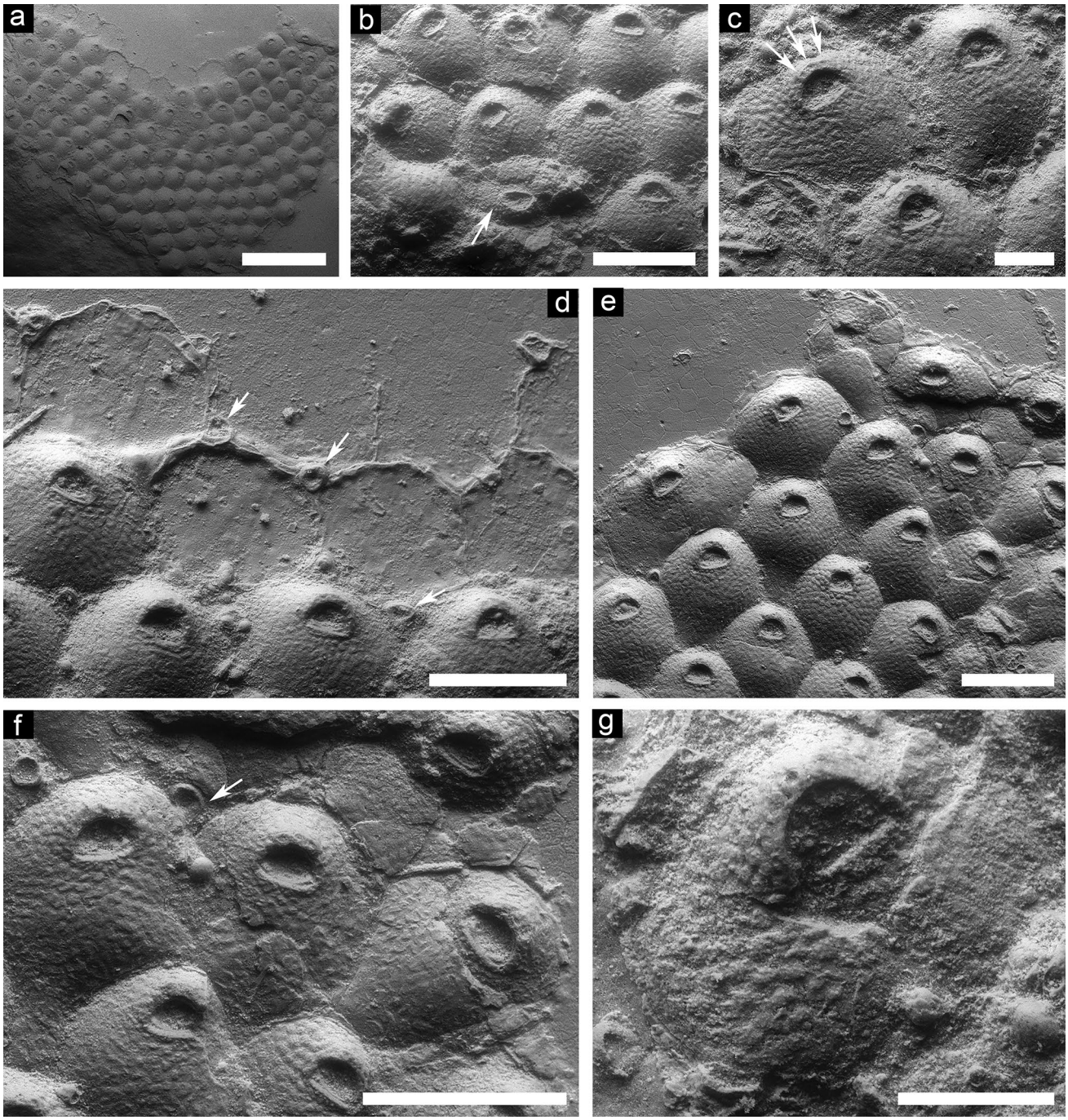

Fig. 7 ?*Hoplitaechmella* sp. 1, ESM MSU 133/4. **a** Part of the encrusting colony. *Scale bar* 2 mm. **b** Zone of early astogeny; putative ancestrula arrowed. *Scale bar* 500 µm. **c** Non-ovicellate autozooids; distal oral spine bases arrowed. **d** Growing edge of colony; putative avicularia arrowed. *Scale bar* 500 µm. **e** Normal and enlarged autozooids. *Scale bar* 500 µm. **f** Autozooids and avicularium (arrowed). *Scale bar* 500 µm. **g** Autozooid. *Scale bar* 200 µm

Description. Colony encrusting, multiserial, unilaminar, sheet-like, fan-shaped with lobes, showing the underside, 15 mm long by 25 mm wide (Figs. 3d, 4a, 8a). Ancestrula and early astogeny not observed. Putative pore chambers along distal and lateral autozooidal and avicularian margins present (Fig. 8b, c). Basal walls of zooids not preserved. Autozooids rounded-rhomboidal in outline, longer than wide. Gymnocyst not observed. Inner cryptocyst occupying most of frontal surface, concave, pustulose (Fig. 8b, c). Opesia terminal or subterminal, rectangular–trapezoidal, likely with opesiular indentations at proximolateral corners; distal edge semielliptical; proximal edge slightly

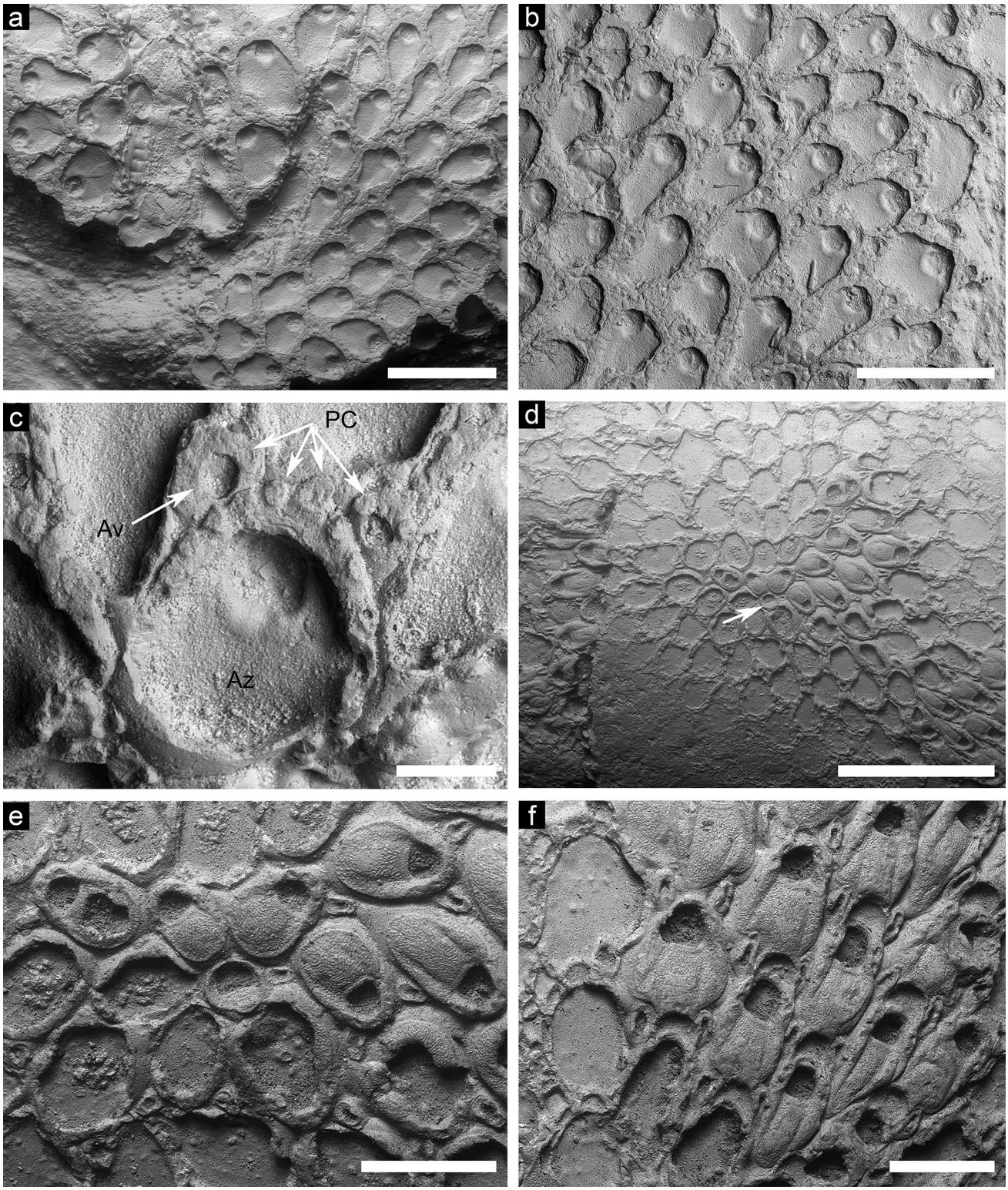

Fig. 8 ?*Hoplitaechmella* sp. 2, ESM MSU 133/5. **a** Proximal part of the fan-shaped colony. *Scale bar* 1 mm. **b** The inside of the colony showing autozooids and avicularia. *Scale bar* 1 mm. **c** Close-up of inside of an autozooid; autozooid (Az), avicularium (Av) and putative pore chambers (PC) marked. *Scale bar* 200 µm. **d**–**f** *Hoplitaechmella nitescens* (Brydone, 1914), early Maastrichtian of Khvalynsk, Saratov Region. **d** The sheet-like colony; ancestrula arrowed. *Scale bar* 2 mm. **e** Ancestrula and early astogeny. *Scale bar* 500 µm. **f** Abraded zooids showing pore chambers, autozooids, ovicells, and avicularia. *Scale bar* 500 µm

concave; oral spine bases not observed. Avicularia interzooidal, small, oval, located distolaterally of each autozooid (Fig. 8b, c). Ovicells, vicarious avicularia, closure plates, kenozooids, and intramural reparative zooids not observed.

Remarks. This specimen, visible from the underside, is tentatively referred to the genus *Hoplitaechmella* because of the presence of pore chambers and small interzooidal avicularia distolaterally of each autozooid. However, oral spine bases and vicarious avicularia were not observed. The species ?*Hoplitaechmella* sp. 2 has a rectangular–trapezoidal opesia similar to that of *Hoplitaechmella nitescens* (Brydone, 1914) described and figured by Brydone (1914: 98, pl. 4, figs. 10–12) from the Middle Campanian (*Belemnitella mucronata* Zone) of Hartford, Norwich, Norfolk, UK, and by Voigt (1962: 41, pl. 19, figs. 2, 3; in this paper Fig. 8d–f) from the early Maastrichtian of Khvalynsk, Saratov Oblast': OpL 130–190 µm v. 130–190 µm in *H. nitescens*; OpW 140–170 µm v. 120–160 µm in *H. nitescens*. Also, both of these species lack vicarious avicularia. However, poor preservation of the studied material, the larger autozooidal size [AzL 480–780 µm v. 510–640 µm in *H. nitescens*; AzW 340–610 µm v. 280–480 µm in *H. nitescens*], and the lack of ovicells in ?*Hoplitaechmella* sp. 2 prevent a definitive assignment. In addition, the zooidal morphology in ?*Hoplitaechmella* sp. 2 is similar to that of ?*Hoplitaechmella* sp. described by Koromyslova et al. (2018a) from the early Maastrichtian of the Aktolagay Plateau, in western Kazakhstan, but differs in having much larger autozooids and a rectangular–trapezoidal instead of trapezoidal opesia.

Genus ***Rhagasostoma*** Koschinsky, 1885

Type species. Rhagasostoma hexagonum Koschinsky, 1885; a neotype was chosen and figured by Taylor et al. (2018); Eocene, Lutetian, Gosaumergel von Götzreuth (= Gerhartsreiter Schichten), Gerhartsreiter Graben near Siegsdorf-Gerhartsreit, Traunstein, Bavaria, Germany.

Remarks. The species *Rhagasostoma* cf. *saltans* (Brydone, 1930) described below can be attributed to the genus *Latereschara* d'Orbigny, 1852 following Brydone (1930, 1936) and Voigt (1967). However, according to Gordon and Taylor (2005) and Taylor et al. (2018), the type species of *Latereschara*, sic. *Eschara achates* d'Orbigny, 1851, has marginal avicularia, absent in other species attributed to *Latereschara*, and is the only one recognized as belonging to this genus. The species described here is instead more closely related to some other species in the genus *Rhagasostoma*, such as *R. gibbosum* (Marsson, 1887), *R. gibbosulum* Brydone, 1936 and *R. tchvanovi* (Favorskaya, 1992), redescribed by Koromyslova et al. (2018c) and having interzooidal avicularia, smaller than the autozooids and located distolaterally of autozooids.

Rhagasostoma cf. ***saltans*** (Brydone, 1930)
Figure 9

Studied material. ESM MSU 133/6–133/14.

Measurements. AzLL 783 ± 98 µm, 650–1020 µm (N 9, n 26); AzLW 430 ± 59 µm, 320–540 µm (N 9, n 20); AzSL 625 ± 42 µm, 560–700 µm (N 9, n 22); AzSW 407 ± 59 µm, 280–520 µm (N 9, n 18); OpLL 175 ± 25 µm, 150–230 µm (N 9, n 13); OpLW 160 ± 16 µm, 130–180 µm (N9, n 13); OpSL 163 ± 23 µm, 120–210 µm (N 9, n 13); OpSW 155 ± 25 µm, 120–190 µm (N 9, n 13); AL 472 ± 62 µm, 380–590 µm (N 8, n 13); AW 189 ± 27 µm, 140–240 µm (N 8, n 13); KL 395 ± 92 µm, 330–460 µm (N 1, n 2); KW 260 ± 14 µm, 250–270 µm (N 1, n 2).

Description. Colony erect with flattened bifoliate branches; fragments 2–3 mm long by 1–3 mm wide (Fig. 9a, c–f, h, i). Ancestrula and early astogeny not observed. Autozooids of two sizes, both subrectangular with rounded distal ends and raised zooidal boundaries, arranged in alternating horizontal rows. Gymnocyst not observed. Cryptocyst extensive, finely pustulose, depressed centrally; peripheral caverns sometimes present (Fig. 9f, g). Opesia subterminal, semielliptical with opesiular indentations at proximolateral corners, presence of distal shelf unclear, proximal edge straight. Ovicells endozooidal, ooecium formed by distal zooid, well-recognizable, with cryptocyst-like surface and crescent-shaped proximal edge with elongated proximolateral processes extending along cryptocyst of maternal zooid (Fig. 9a–c, i, j). Avicularia interzooidal, smaller than autozooids, lozenge-shaped, starting at level of proximal edge of opesia of long autozooid, rostral tip not reaching opesia of next distal short autozooid (Fig. 9a–d, i, j); rostrum channeled, symmetrical, with elevated wing-like lateral walls and rounded tip; proximal part rounded, shorter and wider than rostrum (Fig. 9j). Kenozooids subcircular, located along branch margins (Fig. 9h). Cryptocyst finely pustulose, opesia rounded, about 60 µm in diameter. Closure plates and intramural reparative zooids not observed.

Remarks. This species is similar to the early Maastrichtian (*Ostrea lunata* Zone) species '*Latereschara*' *saltans* Brydone, 1930 from Trimingham, Norfolk, UK, described and figured by Brydone (1930: 51, pl. 29, figs. 9–12; 1936: 61), in having zooids of two sizes, long and short, arranged in alternating horizontal rows. '*Latereschara*' *saltans* Brydone, 1930 was also described and figured by Favorskaya (1992: 128, pl. 74, fig. 1) from the early Maastrichtian of

Fig. 9 *Rhagasostoma* cf. *saltans* (Brydone, 1930). **a**, **b** ESM MSU 133/11. **a** The erect, flattened bifoliate colony. *Scale bar* 1 mm. **b** Ovicellate autozooids and avicularium. *Scale bar* 500 µm. **c** ESM MSU 133/7. Autozooids and avicularia. *Scale bar* 500 µm. **d** ESM MSU 133/8. Long autozooids and avicularium. *Scale bar* 500 µm. **e** ESM MSU 133/9. Long autozooids and avicularia. *Scale bar* 500 µm. **f**, **g** ESM MSU 133/10. **f** The erect, flattened bifoliate colony (peripheral caverns arrowed). *Scale bar* 500 µm. **g** Autozooids and avicularia, some with peripheral caverns (arrowed). *Scale bar* 500 µm. **h** ESM MSU 133/12. Autozooids, avicularia, and kenozooids (arrowed). *Scale bar* 500 µm. **i**, **j** ESM MSU 133/6. **i** The erect, flattened bifoliate colony. *Scale bar* 500 µm. **j** Ovicellate autozooids and avicularia. *Scale bar* 200 µm. **k**, **l** ESM MSU 133/14. **k** The rod-shaped colony. *Scale bar* 1 mm. **l** Autozooids and an avicularium. *Scale bar* 500 µm

the southern Aral Sea Region, Republic of Karakalpakstan, Uzbekistan. Unfortunately, poor preservation of the studied material and poor quality of the figures in Brydone (1930) and Favorskaya (1992) prevent a definitive assignment.

Rhagasostoma saltans and the species described here are similar to *R. gibbosum*, *R. gibbosulum*, and *R. tchvanovi* in having interzooidal avicularia, smaller than the autozooids and located distolaterally of autozooids, but differ from them, and also from the type species of the genus *Rhagasostoma* and other species attributed to this genus (Taylor et al. 2018; Koromyslova et al. 2018c), in having autozooids of two sizes, long and short, arranged in alternating horizontal rows. The latter character is also absent in other onychocellid genera, based on a recent revision by Taylor et al. (2018), but was found in the genus *Tobolocella* Koromyslova et al. 2019, where short autozooids, named as T-zooids, based on their position in the colony, form, size, number of septula, and also the absence of ovicells, can be interpreted as autozooidal polymorphs or heterozooids. However, ovicells are present in both short and long autozooids of *Rhagasostoma* cf. *saltans*, and obviously all of them may be ordinary zooids. Nevertheless, the presence of long and short autozooids in *Rhagasostoma* cf. *saltans*, and supposedly also of the T-zooids in *Tobolocella* species, probably can increase the distance between autozooidal polypides to improve their feeding efficiency.

Family **Coscinopleuridae** Canu, 1913

Genus ***Acoscinopleura*** Voigt, 1956

Type species. Coscinopleura foliacea Voigt, 1930, early Maastrichtian, Rügen, Germany.

?***Acoscinopleura*** sp.
Figure 10

Studied material. ESM MSU 133/19.

Measurements. AzL 433 ± 51 µm, 340–490 µm (N 1, n 8); AzW 344 ± 43 µm, 250–390 µm (N 1, n 8); OpL 105 ± 11 µm, 90–110 µm (N 1, n 8); OpW 129 ± 10 µm, 110–140 µm (N 1, n 8); VL 310 µm (N 1, n 1); VW 100 µm (N 1, n 1).

Description. Colony rigidly erect, bifoliate, adeoniform (Fig. 10a–b). Zooids arranged quincuncially, separated by furrows. Pore chambers, ancestrula, and early astogenetic stages not observed. Autozooids pyriform or hexagonal, with straight proximal ends and weakly convex distal ends (Fig. 10c). Gymnocyst lacking. Cryptocyst extensive, finely pustulose, depressed, sloping towards opesia from all sides. Peripheral caverns not observed. Opesia small, semielliptical, not terminal, surrounded laterally and distally by prominent and probably ribbed margin, with two symmetrical and short opesiular indentations, proximolaterally enclosing broad and short tongue with unribbed margin (Fig. 10c). Putative vibracula present at lateral margin of colony (Fig. 10a). Cryptocyst finely pustulose, weakly convex. Peripheral caverns, craticula, and opesia in vibracula not observed. Ovicells and kenozooids not observed.

Remarks. One very poorly preserved specimen is tentatively assigned to the genus *Acoscinopleura* because of the

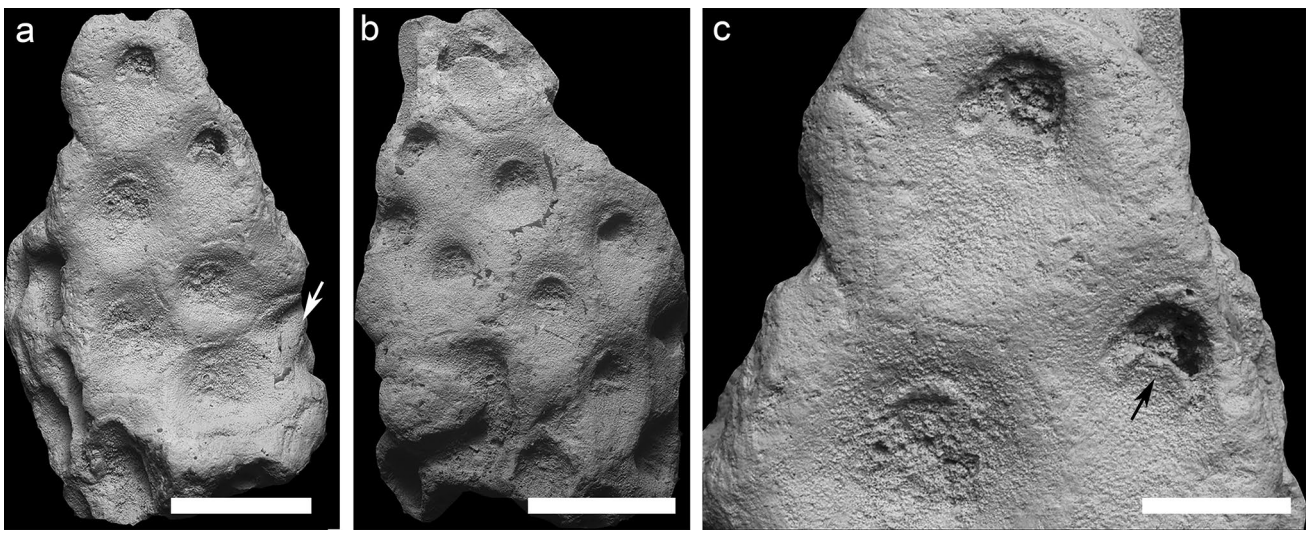

Fig. 10 ?*Acoscinopleura* sp., ESM MSU 133/19. **a** Autozooids and a putative vibraculum (arrowed). *Scale bar* 500 µm. **b** Other side of the colony showing autozooids. *Scale bar* 500 µm. **c** Close-up of autozooids; tongue arrowed. *Scale bar* 200 µm

morphology of autozooids and the presence of what is very likely to be a vibracula. This species resembles *A. rugica* Voigt, 1956 and *A. crassa* Koromyslova et al., 2018b from the Maastrichtian of Germany in the morphology of the autozooidal opesia. However, scarcity of the available material, its poor preservation, and impossibility to study the internal morphology prevent us from any specific assignment.

Family **Lunulitidae** Lagaaij, 1952

Genus ***Luganella*** Kvachko, 1995b

Type species. Luganella pulchra Kvachko, 1995b, early Maastrichtian of the Ukraine.

Luganella goldfussi (von Hagenow, 1839)
Figure 11

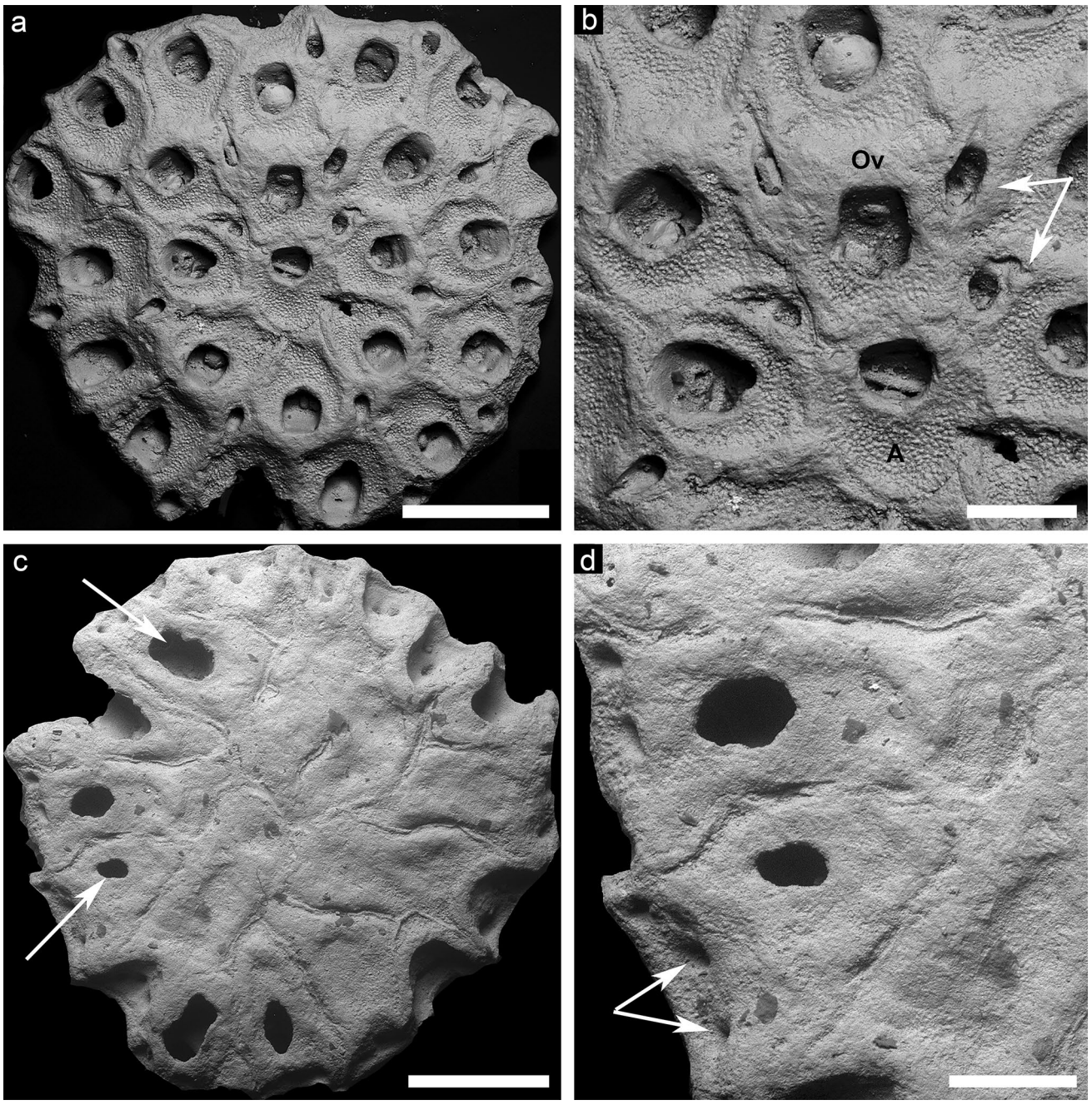

Fig. 11 *Luganella goldfussi* (von Hagenov, 1839), ESM MSU 133/20. **a** General view of a colony. *Scale bar* 500 µm. **b** Ancestrula (A), ovicells (Ov) and avicularia (arrowed). *Scale bar* 200 µm. **c** Basal surface of the colony, showing sectors and windows (arrowed). *Scale bar* 500 µm. **d** Close-up of three sectors; septula arrowed. *Scale bar* 200 µm

1839 *Lunulites goldfussi* n. sp.—von Hagenow: p. 287, pl. 5, fig. 10a–c.
1887 *Lunulites goldfussi* von Hagenow, 1839—Marsson: p. 80, pl. 7, fig. 13.
1930 *Lunulites goldfussi* von Hagenow, 1839—Voigt: p. 484, pl. 19, fig. 16.
1959 *Lunulites goldfussi* von Hagenow, 1839—Voigt: p. 39.
1967 *Lunulites goldfussi* von Hagenow, 1839—Voigt: p. 53, pl. 16, figs. 2-3.
1986 *Lunulites goldfussi* von Hagenow, 1839—Cook and Chimonides: fig. 3.
2002 *Lunularia goldfussi* (v. Hagenow, 1839)—Reich and Frenzel: p. 175.
2002 *goldfussi* (v. Hagenow, 1839); *Lunularia*—Reich and Frenzel: p. 263.

Studied material ESM MSU 133/20.

Measurements AzL 352 ± 36 µm, 310–410 µm (N 1, n 12); AzW 303 ± 34 µm, 240–340 µm (N 1, n 12); OpL 172 ± 22 µm, 140–220 µm (N 1, n 12); OpW 140 ± 12 µm, 120–160 µm (N 1, n 12); OvL 100 µm (N 1, n 1); OvW 270 µm (N 1, n 1); AL 201 ± 30 µm, 160–250 µm (N 1, n 9); AW 105 ± 17 µm, 90–140 µm (N 1, n 8); AOpL 87 ± 6 µm, 80–90 µm (N 1, n 3); AOpW 57 ± 6 µm, 50–60 µm (N 1, n 3).

Description Colony free-living, multiserial, unilamellar, subcircular in shape, 1.5 mm in diameter (Fig. 11a). Ancestrula oval, 320 µm long by 280 µm wide, surrounded by six periancestrular autozooids and two avicularia (Fig. 11a, b). Pore chambers not observed. Basal surface of colony divided into sectors (Fig. 11c). Basal wall incompletely calcified, with elliptical uncalcified window present in some sectors (Fig. 11c, d). Distal wall with two septula (Fig. 11d). Autozooids radially arranged around ancestrula, rounded-rhomboidal to hexagonal, with mural rim thickened and raised; zooidal size continuously increasing from ancestrula for two to three generations. Gymnocyst and spines lacking. Cryptocyst occupying most of frontal surface, pustulose, depressed. Opesia terminal or subterminal on cryptocyst, rounded-rectangular, longer than wide, without opesiular indentations at proximolateral corners; proximal edge straight or gently convex, smooth, thickened. Ovicells endozooidal, rounded-quadrate, covering most of proximal cryptocyst of distal autozooid (Fig. 11b). Avicularia located at beginning of each row of autozooids, longitudinally elliptical, considerably smaller than autozooids (Fig. 11a, b). Avicularian opesia occupying most of frontal surface, longitudinally elliptical. Rostrum symmetrical or sometimes slightly curved, pointed, lapping onto cryptocyst of next distal autozooid. Closure plates, kenozooids, and intramural reparative zooids not observed.

Remarks. Represented by one well-preserved specimen, this species is assigned to the genus *Luganella* proposed by Kvachko (1995b) for lunulitiform species with an avicularium located at the beginning of each row of autozooids.

Stratigraphic and geographic distribution. Early Maastrichtian of Rügen, Germany (von Hagenow 1839; Marsson 1887; Voigt 1930; Cook and Chimonides 1986; Reich and Frenzel 2002), of Chobda River and Mangyshlak Peninsula, Kazakhstan, of western Kopetdag, Turkmenistan (Voigt 1967; Titova and Favorskaya 1994), and of the middle Volga River region, Saratov Region, Russia. Late Maastrichtian of western Kopetdag, Turkmenistan (Voigt 1967; Titova and Favorskaya 1994).

Discussion

The bryozoan species previously described from the early Maastrictian of the middle Volga River region included (Voigt 1962; Viskova 1965, 1972, 1992, 2004, 2005; Kvachko 1995a): seventeen species of cyclostome bryozoans, i.e., *Phormopora irregularis* Marsson, 1887, *P. langethalii* (Marsson, 1887), *Sulcocava cristata* Orbigny, 1854, *S. klimovkensis* Viskova, 1972, *S. torulosa* Viskova, 1972, *Meliceritites radioporatus* Viskova, 1965, *M. volskensis* Viskova, 1965, *M. dentiferus* Viskova, 1965, *M. matesovae* Viskova, 1972, *M. spinosus* Viskova, 1972, *Stomatoporopsis multigemmans* (Illies, 1974), *S. arguta* Viskova, 2004, *S. illiesae* Viskova, 2004, *S. mirabilis* Viskova, 2004, *Proboscina khvalynskensis* Viskova, 2005, *Diplosolen pavonius* Voigt, 1929, and *D. verus* Viskova, 2005 (among these, the seven latter species encrusted echinoid tests, mollusc shells, and belemnite rostra); five species of encrusting cheilostome bryozoans, i.e. *Dionella trifaria* (von Hagenow, 1846), *Hoplitaechmella nitescens* (Brydone, 1914), *H. vespertilio* (von Hagenow, 1839), *Stichomicropora biconstricta* (von Hagenow, 1839), and *Aechmella anglica* (Brydone, 1909), which colonized belemnite rostra, and two free-living cheilostome species, *Lunulites distinctus* Kvachko, 1995a and *L. sengilejsis* Kvachko, 1995a; and a ctenostome, *Spathipora prima* Voigt, 1962, boring into belemnite rostra.

Sampling in the vicinity of the Volga River bank near Volsk has revealed eight additional species of cheilostome bryozoans. These included the erect colonies, with flattened bifoliate branches, of *Rhagasostoma* cf. *saltans* and ?*Acoscinopleura* sp., and the free-living discoidal colonies of *Luganella goldfussi*. Other cheilostomes were encrusting and were found on the surfaces of nautiloid and inoceramid shells and echinoid tests (the latter were not studied

in this paper). Bryozoan colonies, some with frontal surfaces visible but others seen from the underside, were most abundant on *Baculites* ammonoid shells. In some such shells, the body chambers and phragmocones were well preserved; whereas in others, the outer shell walls had been destroyed and only the interior chambers were observed (Seltser 2012). The studied bryozoans occurred on the lateral surface of internal moulds of *Baculites* sp. and *Baculites* cf. *vertebralis* Lamarck phragmocones. *Cheethamia aktolagayensis* and *C. volgaensis* sp. nov., with frontal surfaces visible, directly overgrew aragonite outer lateral walls of *Baculites* sp. and *Baculites* cf. *vertebralis* phragmocones, respectively, which had possibly been replaced by carbonates. The colonies of *Dionella* sp. and ?*Hoplitaechmella* sp. 2, seen from the underside, overgrew a wall of *Baculites* sp. phragmocone from its inner surface, which had been completely dissolved. It is suggested that bryozoans grew on both the outer and inner lateral surfaces of empty intact or broken shells of baculitids lying on the sea floor.

To date, a total of thirty-three bryozoan taxa are known from the early Maastrichtian of the middle Volga River region, including seventeen (52%) cyclostomes, fifteen (45%) cheilostomes, and one (3%) ctenostome. The proportion of cheilostomes in the middle Volga River region is lower than in coeval deposits from the Aktolagay Plateau (56%) (Koromyslova et al. 2018a) and Luhansk Oblast, Ukraine (75%) (Voigt 1962). The low proportion of cheilostomes known from the early Maastrichtian of the middle Volga River region is probably due to the limited sampling, which focused mainly on the cyclostome bryozoans (Viskova 1965, 1972, 2004, 2005), while descriptions of cheilostomes remained scarce (Voigt 1962; Kvachko 1995a).

The species *Rhagasostoma* cf. *saltans* and *Luganella goldfussi* have extensive geographical distribution, as the former species is known from the early Maastrichtian of England (UK) and the southern Aral Sea Region (Uzbekistan) (Brydone 1930; Favorskaya 1992, 1996), while the latter species, from the Maastrichtian of Rügen (Germany), Chobda River and Mangyshlak Peninsula (Kazakhstan), the western Kopetdag (Turkmenistan), and the middle Volga River region (von Hagenow 1839; Marsson 1887; Voigt 1930, 1967; Cook and Chimonides 1986; Titova and Favorskaya 1994; Reich and Frenzel 2002). *Cheethamia aktolagayensis* is known from the early Maastrichtian of the Aktolagay Plateau (Kazakhstan) and the middle Volga River region; while *Cheethamia volgaensis* sp. nov. may have been endemic to the middle Volga River region.

All the recorded bryozoan species belong to genera and species ubiquitous in the early Maastrichtian of Europe (von Hagenow, 1839, 1846; Marsson 1887; Brydone 1909, 1914, 1930, 1936; Voigt 1929, 1930, 1949, 1956; Medd 1965; Illies 1974), and, to a lesser degree, North America (Taylor and McKinney 2006), the United Arab Emirates–Oman border region (Di Martino and Taylor 2013), Madagascar (Di Martino et al. 2018), Luhansk Oblast, Ukraine (Voigt 1962), the Mangyshlak Peninsula of Kazakhstan, the western Kopetdag in Turkmenistan (Voigt 1967; Titova and Favorskaya 1994), and the southern Aral Sea region in Uzbekistan (Favorskaya 1992, 1996).

Acknowledgements The authors thank N.I. Krupina (Earth Science Museum of the Moscow State University, Moscow, Russian Federation) for providing access to originals of some species described by E. Voigt (1962). Roman A. Rakitov (Borissiak Paleontological Institute of the Russian Academy of Science, Moscow, Russian Federation) is thanked for providing technical assistance with SEM work and for linguistic assistance. Emanuela Di Martino (University of Oslo, Norway), Paul D. Taylor (Natural History Museum, London, United Kingdom), and the editor-in-chief Mike Reich (Bayerische Staatssammlung für Paläontologie und Geologie, München) are thanked for their helpful reviews and comments on the manuscript. The reported study was funded by RFBR according to the research Project № 18-05-00245-A.

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