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***Rhagasostoma* (Bryozoa) from the Late Cretaceous of Eurasia:
taxonomic revision, stratigraphy and palaeobiogeography**

Anna V. KOROMYSLOVA^{1*}, Paul D. TAYLOR², Silviu O. MARTHA³ & Matthew RILEY⁴

¹Borissiak Paleontological Institute of the Russian Academy of Science, Profsoyuznaya st. 123,
Moscow, 117997, Russian Federation.

²Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

³Senckenberg Forschungsinstitute und Naturmuseum, Sektion Marine Evertebraten III (Bryozoologie),
Senckenberganlage 25, 60325 Frankfurt am Main, Germany.

⁴The Sedgwick Museum of Earth Sciences, Department of Earth Sciences,
University of Cambridge, UK.

*Corresponding author: koromyslova.anna@mail.ru

²Email: p.taylor@nhm.ac.uk

³Email: silviu.martha@senckenberg.de

⁴Email: mlr44@cam.ac.uk

¹[urn:lsid:zoobank.org:author:852422E7-8592-4209-AE5F-AD0554D11E7D](https://zoobank.org/author/852422E7-8592-4209-AE5F-AD0554D11E7D)

²[urn:lsid:zoobank.org:author:7AFF2929-DF5B-46B2-94E6-B26B396CC2C8](https://zoobank.org/author/7AFF2929-DF5B-46B2-94E6-B26B396CC2C8)

³[urn:lsid:zoobank.org:author:C926B3E7-2C56-450E-9C81-B00793465CE0](https://zoobank.org/author/C926B3E7-2C56-450E-9C81-B00793465CE0)

⁴[urn:lsid:zoobank.org:author:8E9D3DB4-6D14-4895-AD34-77C51022DA05](https://zoobank.org/author/8E9D3DB4-6D14-4895-AD34-77C51022DA05)

Abstract. Species commonly assigned to the cheilostome bryozoan genus *Onychocella* Jullien, 1882 are numerous in deposits of Late Cretaceous age. Among these are 15 species with wide stratigraphical and geographical distributions that are better placed in the genus *Rhagasostoma* Koschinsky, 1885. These are used here to show similarities between Late Cretaceous bryozoan associations from Western Europe and Central Asia. Type and additional material was examined of several species from the Turonian to the Maastrichtian of Western Europe, including material studied by R.M. Brydone, E. Voigt and T.A. Favorskaya and undescribed material from the Campanian and Maastrichtian of several localities in Eastern Europe and Central Asia. The new species *Rhagasostoma brydonei* sp. nov., *R. aralense* sp. nov. and *R. operculatum* sp. nov. are introduced. New and published data on the morphology and the stratigraphical and geographical distributions of *R. inelegans* (Lonsdale, 1850), *R. gibbosum* (Marsson, 1887), *R. gibbosulum* Brydone, 1936, *R. rowei* (Brydone, 1906) and *R. mimosa* (Brydone, 1930) is presented.

Keywords. Cheilostomata, taxonomy, stratigraphy, palaeogeography, Late Cretaceous.

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Introduction

The cheilostome family Onychocellidae Jullien, 1882 includes well over 500 species, as well as numerous post-Cretaceous to Recent species. The huge number (over 200) of species assigned to the type genus *Onychocella* Jullien, 1882 is in part because the genus has been interpreted broadly and lacks a clear diagnosis (Favorskaya 1985; Gordon & Taylor 1999; Schmidt & Bone 2004; Taylor & McKinney 2006; Taylor & Gordon 2007; Taylor 2008; Koromyslova 2014a; Koromyslova & Shcherbinina 2015; Martha *et al.* 2015, 2017; Martha & Taylor 2016). A recent revision of Onychocellidae (Taylor *et al.* 2018b) suggests that most, possibly all, of the supposed species of *Onychocella* recorded from the Late Cretaceous belong to other onychocellid genera. Prominent among these genera is *Rhagasostoma* Koschinsky, 1885. Whereas *Onychocella* has bell-shaped opesia, immersed ovicells (i.e., with a brooding cavity sunken in the distal part of the maternal zooid, and vestigial oecium formed by the distal zooid and level with the colony surface or slightly above it) (Ostrovsky *et al.* 2009; Ostrovsky 2013) and may be exclusively encrusting, *Rhagasostoma* has opesia with indentations at the proximolateral corners, endozooidal ovicells (i.e., with brood cavity sunken in the proximal part of the distal zooid, and usually a well-recognizable oecium formed by the distal zooid and level with the colony surface) or, sometimes, immersed, and colonies are frequently erect. Late Cretaceous species of *Rhagasostoma* which were often assigned to *Onychocella* in the past are very common in Late Cretaceous bryozoan faunas, many having extensive stratigraphical and geographical distributions.

Voigt (1967), Favorskaya (1980, 1985, 1992, 1996) and Titova & Favorskaya (1994) pointed to similarities in Late Cretaceous bryozoan associations from Europe and Central Asia, with about 15 species seemingly shared between these two regions. The aim of the current paper is to describe some key species of *Rhagasostoma* from various localities in Europe and Central Asia. Type material has been studied – using SEM for the first time – of species described by Lonsdale (1850), Brydone (1906, 1913, 1930, 1936), Voigt (1949, 1967) and Favorskaya (1992, 1996). This taxonomic revision has allowed clarification of the stratigraphical and geographical distributions of Late Cretaceous species of *Rhagasostoma*, and evaluation of morphological variability.

Geological setting

The bryozoan fauna of the Eurasian Shelf Sea has been studied by many authors, but very few works have compared material between the western and eastern Eurasian Shelf Sea fauna, even though it has long been appreciated that the faunas show many similarities (e.g., Voigt 1967). The studied material in this work comes from localities spanning Western Europe (Belgium, France, United Kingdom), Central Europe (Belarus, Denmark, Germany), Eastern Europe and Central Asia (Kazakhstan, Turkmenistan, Uzbekistan) (Figs 1–2).

Material from the United Kingdom is from the Upper Chalk (Coniacian to Maastrichtian) of southeastern England. The Late Cretaceous of England was subdivided into several assemblage zones during the late 19th to early 20th century by A.W. Rowe. The specimens described here are from the collections of R.M. Brydone, W. Lonsdale and E. Voigt. The lithostratigraphical classification is based on the works of Brydone. An overview of the assemblage zones as used in Brydone's works and correlation with actual stages has been provided in Gale & Kennedy (2002: text-fig. 1.5), and a review of Brydone's bryozoan research by Taylor *et al.* (2018a). Thus, material from the Chalk of Norfolk can be assigned to the middle Campanian (Hartford/Norwich and Weybourne) or early Maastrichtian (Trimingham). Material from the Chalk of Hampshire and the Isle of Wight is of latest Turonian (Kings Lane, Froxfield, Alton), late Santonian (coast of Sussex between Brighton and Roedean, and an unknown locality along the coast of Sussex), early Campanian (Harnham, SW Salisbury, and Hensting Farm, Owslebury) and middle Campanian (High Down) age. The bryozoan fauna of Chatham in Kent is mainly of Coniacian age according to Voigt (1981).

From Belgium and France, material studied comes from six localities. Whether the chalk at Vigny in the Paris Basin is of Campanian, Maastrichtian or even Danian age has long been under discussion (e.g., Voigt 1964). According to Montenat *et al.* (2002), the chalk in the quarries in the vicinity of Vigny is of Danian age surrounded by Campanian chalk. It is not clear where exactly Voigt collected material at Vigny, and whether he collected from only one or several places. In his publications, however, he mentioned material from Vigny both of late Campanian (e.g., Voigt 1985) and Danian (e.g., Voigt 1987) age. The Cretaceous deposits cropping out at Hanches have been correlated with the earliest Campanian of the northern German standard section at Krons Moor-Lägerdorf-Hemmoor (Voigt & Gordon 1995). From Normandy, material of the examined species has been reported from Vasterival (late Santonian) and Chef-du-Pont (base of the late Maastrichtian). The fauna of Harmignies near Cibly, Belgium in the



Fig. 1. Map of Europe showing localities of bryozoan material studied (bold) or mentioned (italics) in this study. Abbreviations: Bbg = Blaue Berge near Dessau-Roßlau, Saxony-Anhalt, Germany; CdP = Chef-du-Pont, Normandy, France; Chm = Chatham, Kent, England, UK; Ffd = Froxfield south of Alton, Hampshire, England, UK; Hcs = Hanches, Centre-Val de Loire, France; HDn = High Down, Isle of Wight, England, UK; Hgs = Harmignies near Mons, Wallonia, Belgium; Hhm = Harnham SW of Salisbury, Wiltshire, England, UK; Hmr = Hemmoor, Lower Saxony, Germany; Höv = Alemannia quarry, Sehnde-Höver, Lower Saxony, Germany; Hro = quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region, Belarus; Hsg = Hensting Farm, Owslebury, near Winchester, Hampshire, England, UK; Kmr = Saturn quarry near Krons Moor, Schleswig-Holstein, Germany; Ksd = Kongsted Sogn in the Faxe Kommune, Sjælland, Denmark; Lbg = Lüneburg, Lower Saxony, Germany; Ldf = Lägerdorf, Schleswig-Holstein, Germany; Møn, Island of Møn, Denmark; Nhv = Newhaven, East Sussex, England, UK; Nwh = Norwich, Norfolk, England, UK; Obg = Lahstedt-Oberg, Lower Saxony, Germany; Rdn = between Brighton and Roedean, East Sussex, England, UK; Roy = Royan, Nouvelle-Aquitaine, France; Rüg = Rügen, Mecklenburg-Vorpommern, Germany; Thm = Trimingham, Norfolk, England, UK; Vgy = Vigny, Île-de-France, France; Vrl = Vasterival, Sainte-Marguerite-sur-Mer, Normandy, France; Wbe = Weybourne, Norfolk, Norfolk, England, UK.



Fig. 2. Map of the Caspian and Aral seas region showing localities of bryozoan material examined or mentioned in this study. Abbreviations: Emb = Emba River, Aqtöbe Region, Kazakhstan; Kop = western Kopetdag, Balkan Region, Turkmenistan; Man = Mangyshlak Peninsula, Mangystau Region, Kazakhstan; NAS = northern Aral Sea region, Kyzylorda Region, Kazakhstan; SAS = southern Aral Sea region north of Chimboy/Shimbay, Republic of Karakalpakstan, Uzbekistan; Tua = Tuarkyr, Balkan Region, Turkmenistan.

Mons Basin has been assigned to the late Campanian (Robaszynski & Christensen 1989), thus clearly pre-dating the bryozoan fauna previously described by Voigt (1957, 1987).

The northern German Late Cretaceous is one of the world's best studied fossil bryozoan faunas thanks to the works of Ehrhard Voigt (1905–2004). In this paper, we describe and mention material from eight localities. At Hemmoor, Krons Moor and Lägerdorf, white Chalk sediments from the Late Cretaceous have been lifted by salt diapirs and lie on a salt ridge (Mutterlose *et al.* 1998). Two quarries expose chalk from the middle Coniacian to early Campanian (Schinkel quarry; Ernst 1963), and early to late Campanian (Alsen quarry; e.g., Ernst 1963). Bryozoans can be found throughout the profile but are especially abundant in the late Campanian (Voigt 1979). Between Lägerdorf and Krons Moor, the Saturn quarry exposes white Chalk ranging from the late Campanian to the early Maastrichtian, and at Hemmoor early to late Maastrichtian deposits are exposed in an abandoned chalk quarry of a former brick factory (Voigt 1979). The successions at Lägerdorf, Krons Moor and Hemmoor have been combined into a standard section for the northwestern European white chalk (e.g., Ernst 1984). Although this is one of the best studied sections from the Late Cretaceous in the world, little has been published on the bryozoans. Near Lüneburg, almost the entire Late Cretaceous succession from early Cenomanian to early Maastrichtian was formerly exposed (Heinz 1928). Bryozoans occur in the abandoned quarry on the Zeltberg and have a stratigraphical range from Coniacian to early Maastrichtian age (Voigt 1979). The late Campanian to early Maastrichtian profile of Lüneburg has been correlated with the northern German standard section (Ehrmann 1986). The nearby localities Oberg (abandoned marl pit) and Höver (Alemannia quarry) reveal a similar fauna that has been dated into the early Campanian (e.g., Beck 1920; Voigt 1949). Along the northeastern coast of the Island of Rügen, the famous chalk cliffs of early Maastrichtian age exhibit a large fossil flora and fauna of over 1400 species among which there are at least 275 bryozoan species (Reich & Frenzel 2002). The early Maastrichtian sediments of Rügen have been correlated with deposits on the Island of Møn in Denmark (Herrig 1995).

The quarry near Hrodno/Grodno (chalk pit of the Integrated Building Material Plant) in Belarus lies approximately at the centre of studied localities from Western and Central Eurasia and can thus be regarded as a connecting link between the two faunas. Bryozoans occur in an erratic block in the quarry, the age of which was determined to be late Campanian based on findings of *Belemnitella mucronata* (Barskov & Weiss 1987; Ogg *et al.* 2004).

Part of the material from Kazakhstan was found in the bryozoan collections that T.A. Favorskaya transferred to the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, at the end of the 20th century. This material has not been previously described and is derived from an unknown outcrop of late Campanian (*Belemnitella lanceolata* Zone) age along the Emba River in western Kazakhstan and from another unknown outcrop of Maastrichtian age in the northern Aral Sea Region. Other material was collected in the 1980s by V.S. Sokurov from Maastrichtian deposits on the Mangyshlak Peninsula in the Mangystau Region.

Previously described material from Turkmenistan came from the following localities: Kara-Kala [boundary of early Campanian (*Cibicidoides temirensis/Bolivinooides decoratus decoratus* Zone; LS13) and middle Campanian (*Brotzenella monterelensis* Zone; LS14); Favorskaya 1992; zonal division according to Beniamovski 2008]; 'Kredin' gorge (late Campanian), Koimat and 'Kamyschli' gorges (late Maastrichtian) in the Kopet Dag Mountains, NW of Ashgabat; and late Maastrichtian of Tuarkyr (see Voigt 1967 for further information).

Material from Uzbekistan (southern Aral Sea Region, Republic of Karakalpakstan) that was described by Favorskaya (1992) came from the early Campanian (*Cibicidoides temirensis/Bolivinooides decoratus decoratus* Zone; LS13), the middle Campanian (*Brotzenella monterelensis* Zone; LS14) and the late

Campanian (*Cibicidoides voltzianus* Zone; LS15) (zonal division according to Beniamovski 2008). The exact locations of the outcrops in the southern Aral Sea region are unknown.

Material and methods

Collections

The material described in this study comes from several collections and, except for material from Belarus, has already been examined by previous researchers. It includes specimens collected or otherwise obtained by: W. Lonsdale during the early 19th century (Natural History Museum, London, United Kingdom); R.M. Brydone during the first quarter of the 20th century (Sedgwick Museum, Cambridge, United Kingdom); Ehrhard Voigt and his collaborators during the 1950s to 1980s (Voigt Collection at the Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, Germany); T.A. Favorskaya during the 1980s (Favorskaya Collection at the Central Scientific Research Geological Survey named after Academician F.N. Chernyshev, Saint Petersburg, Russian Federation); and T.A. Favorskaya, V.S. Sokurov and F.A. Weiss during the 1980s (collections from Kazakhstan and the Grodno quarry at the Borissiak Paleontological Institute of the Russian Academy of Science, Moscow, Russian Federation).

Repository abbreviations

NHMUK	=	Natural History Museum, London, UK
PIN	=	Borissiak Paleontological Institute of the Russian Academy of Science, Moscow, Russian Federation
PSM PSU	=	Palaeontological and Stratigraphical Museum at the Faculty of Geology, St. Petersburg State University, Russian Federation
SGN	=	Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, Germany
SM	=	Sedgwick Museum, Cambridge, UK
SMF	=	Senckenberg Gesellschaft für Naturforschung (for collections), Frankfurt am Main, Germany
TsNIGR Museum	=	Central Scientific Research Geological Survey, Saint Petersburg, Russian Federation

Study methods

The specimens from the NHMUK and SM were studied uncoated using a LEO 1455-VP scanning electron microscope (SEM) operating at low vacuum and imaged using backscattered electrons. Specimens from the PIN and TsNIGR Museum were imaged without coating using the backscattered electron detector (BSE) of a Tescan Vega XMU SEM operated at low vacuum (10 Pa) with an accelerating voltage of 30 kV. Specimens from the SMF were coated in gold/palladium (20:80) and imaged with a Camscan CS 24 SEM using secondary electron images.

Measurements were taken from SEM images and are given in microns (μm) as range and number of measurements, in brackets; arithmetic mean \pm standard deviation.

Measured character abbreviations

ARL	=	apex of avicularian rostrum, overlapping the proximal part of the distal autozoid, length
AvL	=	avicularian length (for <i>R. minuens</i> from the base of avicularium to curve of the rostrum)
AzL	=	autozoid length
AzW	=	autozoid width (near base of opesia)
CrOOL	=	avicularian cryptocyst, occupied by opesia and opesiules, length
CrOOW	=	avicularium cryptocyst, occupied by opesia and opesiules, width

CvL	=	peripheral cavern length in proximal part of cryptocyst (peripheral cavern is cavity developed in proximal or proximolateral part of a cryptocyst or a depression surrounding a cryptocyst, covered during lifetime by a thin cryptocystal lid (see Koromyslova <i>et al.</i> 2018b)
GL	=	gymnocyst length
KzL	=	kenozooid length
KzW	=	kenozooid width
OoL	=	ooecium length
OoW	=	ooecium width
OperL	=	operculum length
OperW	=	operculum width
OpL	=	opesia length (for <i>R. rowei</i> and <i>R. mimosa</i> from the base of the tongue)
OpsD	=	opesiules diameter
OpW	=	opesia width (at the base of the autozooidal opesia or the widest part of the avicularian and kenozooidal opesiae)
PrL	=	proximal part of avicularium, length
PrW	=	proximal part of avicularium, width
RCL	=	curve of rostrum, length
RL	=	avicularian rostrum, length
RW	=	avicularian rostrum, width (at the rostral base)
TL	=	tongue length
TW	=	tongue width
W-ISL	=	wedge-like structure, length

Results

Systematic palaeontology

Order Cheilostomata Busk, 1852

Suborder Flustrina Smitt, 1868

Superfamily Microporoidea Gray, 1848

Family Onychocellidae Jullien, 1882

Genus *Rhagasostoma* Koschinsky, 1885

Type species

Rhagasostoma hexagonum Koschinsky, 1885, by subsequent designation (Canu & Bassler 1917: 31). Eocene, Lutetian, Gosauemergel von Götzreuth (= Gerhartsreiter Schichten), graben near Siegsdorf-Gerhartsreit, Traunstein, Bavaria, Germany. A neotype was chosen and figured by Taylor *et al.* (2018b).

Amended diagnosis

Colony encrusting or erect, vincularian and dichotomously branching. Autozooids subhexagonal; zooidal boundaries raised. Cryptocyst extensive, granular, sometimes peripheral caverns present. Gymnocyst lacking or minutely present. Opesia terminal or subterminal, occupying about one-third of the frontal surface, longitudinally elliptical, with deep opesiular indentations at the proximolateral corners, sometimes with occlusor lamina. Ovicells endozooidal or immersed. Avicularia vicarious and about the same size as autozooids, or interzooidal; opesia roundish or longitudinally elliptical, located centrally, usually with thin articular ridges bearing two short teeth proximally and a short or long, slit-like opesiular indentation between the teeth; sometimes wedge-like structures present. Kenozooids rounded or oval bifoliated and located at edges of colonies with opesia roundish, small.

Rhagasostoma inelegans (Lonsdale, 1850)

Figs 3–4, Table 1

Flustra? inelegans Lonsdale, 1850: 319, pl. 18.B, figs 9, ?10, 11.

Rhagasostoma inelegans var. *angliæ* Brydone, 1936 pars: 74, pl. 35, fig. 8. **Syn. nov.**

Rhagasostoma inelegans – Brydone 1930 pars: 47, pl. 26, figs ?1, 2–3.

Onychocella inelegans – Voigt 1975: 245, pl. 5, figs 1–4. — Taylor 1991: 33, pl. 7, fig. 9. — Taylor 2002: 70, pl. 9, fig. 9.

non *Rhagasostoma inelegans* – Brydone 1930 pars: 47, pl. 25, figs 11–12.

non *Rhagasostoma inelegans* var. *angliæ* – Brydone 1936 pars: 74, pl. 35, figs 4–7.

Material studied

Lectotype (here designated)

UNITED KINGDOM • England; Chalk (?Santonian) of Sussex; NHMUK D2967 (Fig. 3A–C; figured by Lonsdale 1850: pl. 18.B, fig. 9).

Paralectotype (here designated)

UNITED KINGDOM • same data as for lectotype; NHMUK D2959 (Fig. 3D; figured by Lonsdale 1850: pl. 18.B, fig. 11).

Additional figured material

UNITED KINGDOM • England, Sussex coast; late Santonian (*Marsupites testudinarius* Zone); SM B36881 (Fig. 3E–G; figured by Brydone 1936: pl. 35, fig. 8) • England, Hampshire, near Winchester, Owslebury, Hensting Farm; early Campanian (*Goniotheutis quadrata* Zone); SM B36669 (Fig. 3H–J; figured by Brydone 1930: pl. 26, figs 2–3).

GERMANY • Lower Saxony, Sehnde-Höver, Alemannia quarry; early Campanian; SMF 24564 (Fig. 4A–B; figured by Voigt 1975: pl. 5, figs 1, 3–4 as coll. Voigt no. 7381) • Same data as for preceding; SMF 29915 (Fig. 4C).

BELARUS • 2 specs; Grodno Region, quarry near Hrodna/Grodno (Гродна/Гродно); erratic block of ?late Campanian age; PIN 2922/219 (Fig. 4D), 2922/273 (Fig. 4E–F).

Other material

GERMANY • Lower Saxony, Sehnde-Höver, Alemannia quarry; early Campanian; SMF 29916.

BELARUS • 2 specs; Grodno Region, quarry near Hrodna/Grodno (Гродна/Гродно); erratic block of ?late Campanian age; PIN 2922/217, 2922/250.

Fig. 3 (opposite page). *Rhagasostoma inelegans* (Lonsdale, 1850). **A–D**. Late Senonian, Sussex, England, UK. **A–C**. Lectotype, NHMUK D2967. **A**. Overview of erect bifoliate colony. **B**. Autozooids, avicularia, and endozooidal ovicells with ooecia having proximolateral processes. **C**. Avicularium. **D**. Paralectotype NHMUK D2959, overview of sheet-like colony; peripheral caverns arrowed. **E–G**. SM B36881, late Santonian (*Marsupites testudinarius* Zone) along the coast of Sussex, England, UK. **E**. Non-ovicellate autozooids and avicularia; peripheral caverns arrowed. **F**. Overview of encrusting sheet-like colony; peripheral caverns arrowed. **G**. Growing edge. **H–J**. SM B36669, early Campanian (*Goniotheutis quadrata* Zone), Hensting Farm, Owslebury, Hampshire, England, UK. **H**. Overview of erect bifoliate colony. **I**. Autozooids with endozooidal ovicells, avicularia and kenozooids. **J**. Opesia of non-ovicellate autozooid. Scale bars: A, H = 1 mm; B–C, I = 100 µm; D–G = 200 µm; J = 30 µm.

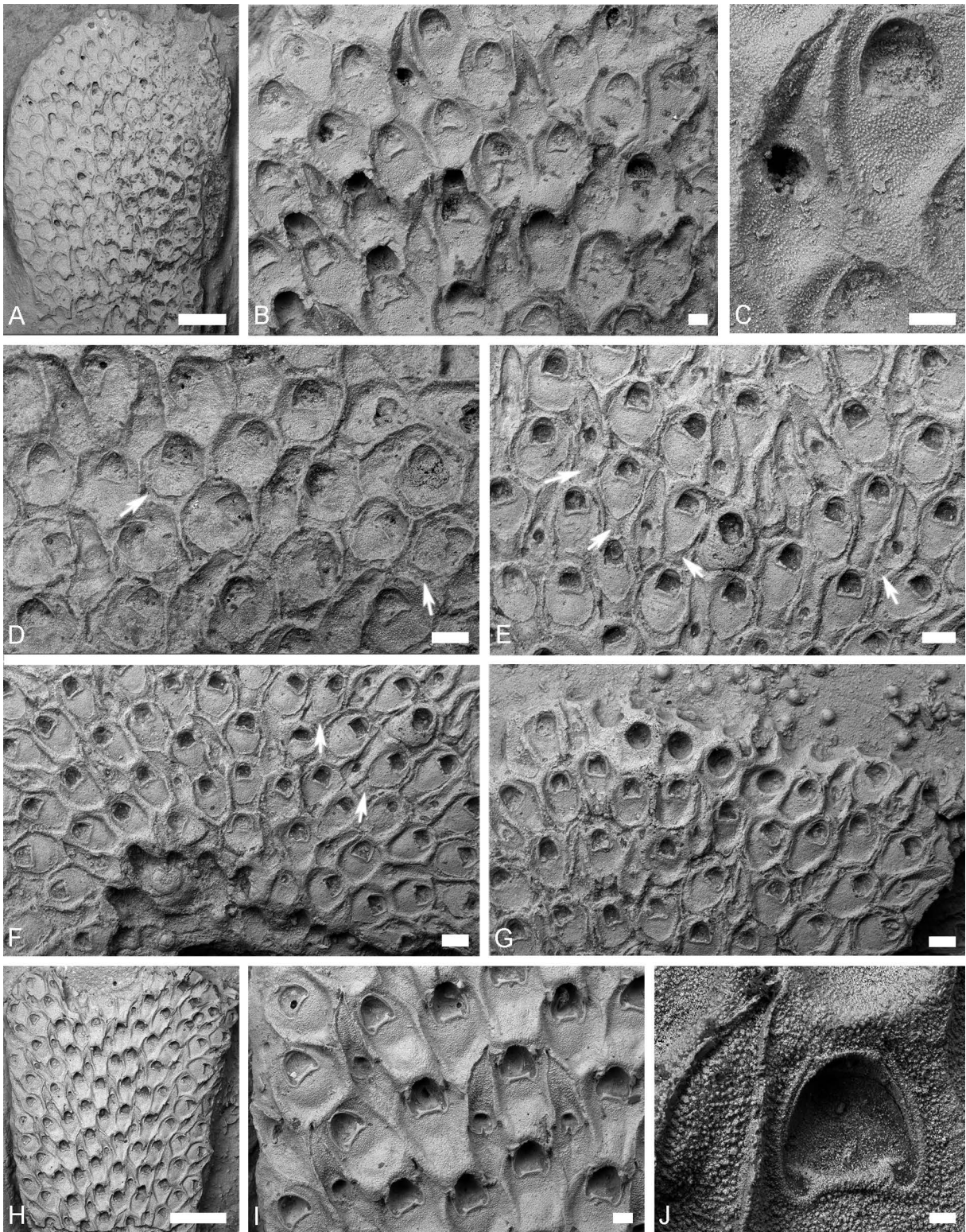


Table 1. Summary of measurements of *Rhagasostoma inelegans* (Lonsdale, 1850). For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Southern North Sea Basin	North German Basin	Polish Basin	
	Stratigraphy	Late Santonian to early Campanian	Early Campanian	?Late Campanian	Total
	Locality	Sussex, Hampshire	L. Saxony	Grodno Region	
Autozooids	AzL	300–600 (24) 475.42 \pm 59.71	510–830 (12) 630.83 \pm 97.56	470–580 (17) 520.59 \pm 35.44	300–830 (53) 525.09 \pm 87.76
	AzW	270–480 (24) 356.67 \pm 54.75	410–620 (12) 510.00 \pm 73.61	340–470 (16) 390.63 \pm 37.50	270–620 (52) 402.50 \pm 81.77
	CvL	40–170 (12) 94.17 \pm 37.77	Not observed		40–170 (12) 94.17 \pm 37.77
	OpL	140–190 (24) 157.92 \pm 12.15	160–250 (12) 199.17 \pm 25.03	150–220 (14) 187.14 \pm 18.16	140–250 (50) 176.00 \pm 24.99
	OpW	150–220 (24) 174.58 \pm 20.21	190–290 (12) 222.50 \pm 27.01	160–210 (14) 190.71 \pm 12.69	150–290 (50) 190.60 \pm 27.80
	OoL	170–240 (11) 195.45 \pm 24.23	240–290 (5) 268.00 \pm 21.68	280–330 (3) 306.67 \pm 25.17	170–330 (19) 232.11 \pm 51.05
	OoW	200–240 (12) 219.17 \pm 14.43	230–280 (5) 260.00 \pm 24.60	200–260 (3) 226.67 \pm 30.55	200–280 (20) 230.50 \pm 24.60
	Avicularia	AvL	520–740 (23) 659.57 \pm 54.89	660–1190 (12) 884.17 \pm 169.46	720–860 (9) 768.89 \pm 50.36
RL		320–430 (23) 390.43 \pm 31.11	340–680 (12) 527.50 \pm 105.75	440–580 (9) 480.00 \pm 43.87	320–680 (44) 446.14 \pm 86.38
RW		110–190 (23) 143.04 \pm 18.45	140–290 (12) 195.00 \pm 44.21	130–180 (9) 151.11 \pm 19.00	110–290 (44) 158.86 \pm 35.39
PrL		180–320 (24) 253.33 \pm 31.30	270–550 (12) 361.25 \pm 105.79	230–320 (10) 261.00 \pm 26.01	180–550 (46) 283.15 \pm 74.71
PrW		170–250 (23) 212.17 \pm 22.55	220–360 (12) 267.50 \pm 42.88	210–280 (9) 232.22 \pm 24.38	170–360 (44) 231.36 \pm 37.45
OpL		60–140 (14) 101.43 \pm 29.58	90–220 (10) 140.00 \pm 40.00	80–130 (8) 108.75 \pm 15.53	60–220 (32) 115.31 \pm 34.36
OpW		70–130 (14) 91.43 \pm 19.16	60–195 (10) 115.50 \pm 48.79	90–120 (8) 102.50 \pm 10.35	70–195 (32) 101.72 \pm 31.28
Kenozooids	KzL		290–740 (6) 500.00 \pm 159.00	340–400 (4) 372.50 \pm 27.54	290–740 (10) 449.00 \pm 136.50
	KzW	Not observed	160–370 (6) 296.33 \pm 83.80	360–400 (4) 377.50 \pm 20.62	160–400 (10) 328.80 \pm 76.16
	OpD		60–120 (6) 85.00 \pm 25.10	140–180 (4) 157.50 \pm 17.08	60–180 (10) 114.00 \pm 43.00

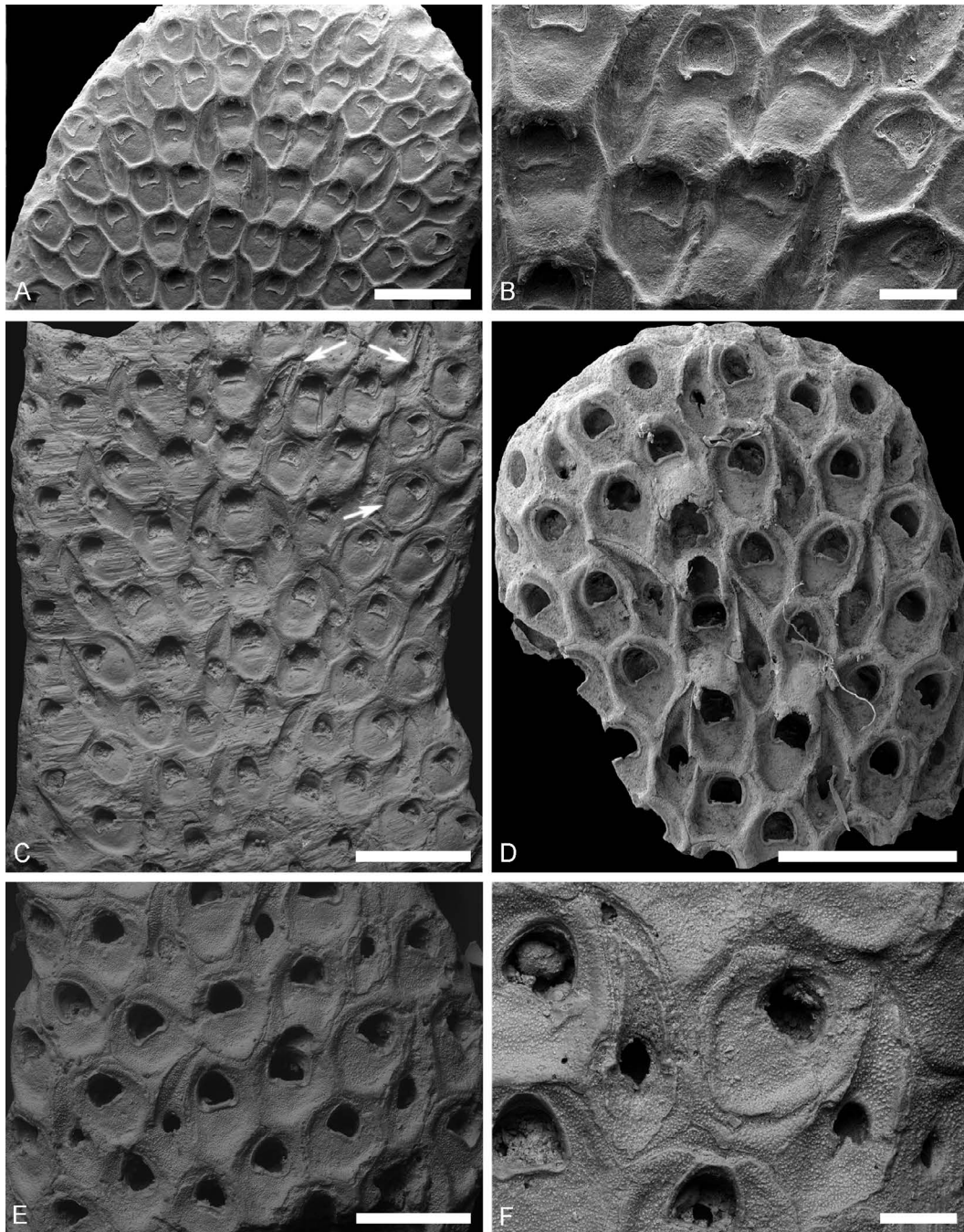


Fig. 4. *Rhagasostoma inelegans* (Lonsdale, 1850). **A–C.** Early Campanian, Alemannia quarry, Sehnde-Höver, Lower Saxony, Germany. **A–B.** SMF 24564. **A.** Distal part of erect bifoliate colony. **B.** Autozooids and avicularia (oecia of endozooidal ovicells are clearly visible). **C.** SMF 29915, fragment of erect bifoliate colony with rare ovicellate autozooids, intramural non-ovicellate autozooid within autozooid and intramural avicularia within avicularia (arrowed). **D–F.** Erratic block of Campanian age, quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region, Belarus. **D.** PIN 2922/219, overview of erect bifoliate colony with row of three ovicellate autozooids, one with a broken oecium, and avicularia. **E–F.** PIN 2922/273. **E.** Autozooid with broken oecium, avicularia and non-ovicellate autozooids. **F.** Intramural non-ovicellate autozooid within autozooid and intramural avicularium within avicularium, and normal avicularium. Scale bars: A, C–D = 1 mm; B = 300 μ m; E = 500 μ m; F = 200 μ m.

Description

Colony usually erect, with flattened bifoliate branches, fragments 2.0–7.0 mm long by 2.5–5.5 mm wide; encrusting sheet-like colonies, measuring up to 5.0–7.0 mm long by 3.5–7.0 mm wide. Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad, 6-sided and rhomboidal with rounded distal ends, zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose, depressed or slightly convex centrally, sometimes with proximal or proximolateral peripheral caverns, up to 0.17 mm long (Fig. 3D–G; and Taylor 1991, 2002). Opesiae terminal, rarely subterminal, semielliptical with narrow shelf in the distal part, formed by two walls, a thin inner wall delimiting the distolateral part and a salient, thickened outer wall delimiting the proximolateral part (Fig. 3J). Proximal edge of opesia straight, smooth, thickened, with outgrowths near the two proximolateral corners delimiting, small round opesiules (outgrowths are often broken, thus giving the opesiules the appearance of opesiular indentations or they may be obscured by sediment infills of the opesia). Septula not observed. Ovicells endozooidal, brooding cavity located within the proximal part of the distal zooid (Figs 3C, I, 4A–D); oecium is formed by the distal zooid, well-recognizable, with cryptocyst-like surface and arch-like proximal edge with elongated proximolateral processes extending along the cryptocyst of the maternal zooid. Avicularia interzooidal, longer than autozooids, elongate (Figs 3C, I–J, 4F). Rostrum channelled, with elevated wing-like walls and pointed apex, conical in outline, asymmetrical, dextral or sinistral. Proximal part rounded, shorter and wider than rostrum. Cryptocyst pustulose, concave, sometimes with proximal peripheral caverns (Fig. 3E). Opesia large, usually roundish, rarely oval, with thickened distolateral edge and with thin articular ridges bearing two short teeth in the proximal margin and a slit-like opesiular indentation between the teeth; opesiules lacking. Kenozooids round, located at edges of colonies (Fig. 4A, C–D). Cryptocyst finely pustulose, peripheral caverns not observed. Opesia roundish, small. Intramural reparative budding of autozooids and avicularia sometimes observed (Fig. 4C, F), all with the same polarity as the host zooid. Closure plates and reparative budding kenozooids not observed.

Remarks

We have restudied Lonsdale's syntypes in the NHMUK collection, choosing a lectotype (the bifoliate specimen figured by Lonsdale 1850: pl. 18.B, fig. 9), as well as material from the collections of R.M. Brydone, E. Voigt, and T.A. Favorskaya. One specimen identified by Brydone as *O. inelegans* (Brydone 1930: pl. 26, figs 2, 3) does indeed belong to this species, while another (Brydone 1930: pl. 25, figs 11, 12) is regarded as a new species, *Rhagasostoma brydonei* sp. nov. The specimen figured by Brydone (1930: pl. 26, fig. 1) was not restudied. The specimen described by Brydone (1936: pl. 35, fig. 8) as belonging to the subspecies *O. inelegans angliae* (Brydone, 1936) is conspecific with Lonsdale's encrusting sheet-like colony of *R. inelegans*. Favorskaya (1992, 1996) mentioned three specimens of this species from Campanian deposits in Uzbekistan and Turkmenistan, which according to our studies comprise two species: *R. aralense* sp. nov. (Favorskaya 1992: 125, pl. 64, fig. 6, pl. 65, fig. 1) and *R. operculatum* sp. nov. (Favorskaya 1992: pl. 64, fig. 7; 1996: pl. 3, fig. 4).

Rhagasostoma inelegans can be easily distinguished from *R. brydonei* sp. nov., *R. minuens* Brydone, 1936 and *R. operculatum* sp. nov. in having an avicularian rostrum conical in outline rather than spade-shaped or falciform. It further differs from *R. brydonei* sp. nov. by having endozooidal ovicells instead of immersed ovicells. *Rhagasostoma inelegans* differs from *R. angliae* in that the avicularian cryptocyst has a large roundish or oval opesia lacking opesiules, instead of a small subcircular opesia with two opesiules. It differs from *R. aralense* sp. nov., which also has an avicularian rostrum conical in outline, by the rostrum being asymmetrical instead of symmetrical, and the avicularian opesia roundish rather than egg-shaped.

Distribution

Late Santonian United Kingdom: Coast of Sussex, England. Early Campanian Germany: Alemannia quarry, Sehnde-Höver, Lower Saxony; Lahstedt-Oberg, Lower Saxony (according to Voigt 1949, 1975).

United Kingdom: Hensting Farm, Owslebury, Hampshire, England. Late Campanian Belarus: Quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region.

Rhagasostoma brydonei sp. nov.

[urn:lsid:zoobank.org:act:B229DB57-799E-494C-95EF-7F117080B3E9](https://zoobank.org/urn:lsid:zoobank.org:act:B229DB57-799E-494C-95EF-7F117080B3E9)

Fig. 5, Table 2

Rhagasostoma inelegans (Lonsdale, 1850) – Brydone 1930 pars: 47, pl. 25, figs 11–12.

non *Rhagasostoma inelegans* – Brydone 1930 pars: 47, pl. 26, figs 1–3.

Diagnosis

Colony erect, bifoliate. Autozooids rectangular, zooidal boundaries raised; gymnocyst lacking; cryptocyst extensive with peripheral caverns; opesia terminal, rarely subterminal, semielliptical with shelf in the distal part, proximal edge with small roundish opesiules; ovicells immersed, ooecia vestigial. Avicularia interzooidal, longer than autozooids; rostrum channeled with pointed tip, spade-shaped, symmetrical or asymmetrical; proximal part rounded, shorter and wider than rostrum; opesia oval or roundish with thickened articular ridges bearing two very short teeth proximally and a long, slit-like opesiular indentation between the teeth; opesiules lacking. Kenozooids rare, rounded or oval.

Etymology

In honour of Reginald Marr Brydone (1873–1943), a prolific author of bryozoan species from the English Chalk and collector of the type material of the new species.

Material studied

Holotype

UNITED KINGDOM • England, Hampshire, south of Alton, Froxfield, Kings Lane; latest Turonian (*Sternotaxis plana* Zone); SM B36666 (Fig. 5A–B; figured by Brydone 1930: pl. 25, figs 11–12).

Paratypes

UNITED KINGDOM • Same data as for holotype; SM B36667 (Fig. 5C–D) • 3 specs; England, Kent; Coniacian of Chatham; SMF 29939 (Fig. 5F), 29940 (Fig. 5E), 29941 (Fig. 5G–H).

Type locality and horizon

United Kingdom, England, Hampshire, south of Alton, Froxfield, Kings Lane; *Sternotaxis plana* Zone, late Turonian.

Description

Colony usually erect, with flattened bifoliate branches, fragments 3.5–6.0 mm long by 2.0–6.5 mm wide. Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad and roughly rectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose, depressed or slightly convex centrally, with peripheral caverns surrounding the cryptocyst (Fig. 5B, D, F–H) or rarely developed in proximal or proximolateral part of cryptocyst (Fig. 5E). Opesia terminal, rarely subterminal, semielliptical, with shelf in the distal part, formed by two walls, a thin inner wall delimiting the distolateral part and a salient, thickened outer wall delimiting the proximolateral part (Fig. 5H). Proximal edge of opesia straight, smooth, thickened, with outgrowths near the two proximolateral corners delimiting small, roundish opesiules (outgrowths are often broken thus giving the opesiules the appearance of opesiular indentations or they may be obscured by sediment infills of the opesia). Septula not observed. Ovicells immersed, ooecium formed by the distal zooid, vestigial, vizer-like, brooding

Table 2. Summary of measurements of *Rhagasostoma brydonei* sp. nov. For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Southern North Sea Basin
	Stratigraphy	Late Turonian to Coniacian
	Locality	Hampshire, Kent
Autozooids	AzL	440–620 (18) 541.67 \pm 55.65
	AzW	280–470 (18) 368.33 \pm 46.94
	CvL	80–180 (16) 120.00 \pm 31.83
	OpL	80–180 (18) 150.56 \pm 25.32
	OpW	140–190 (18) 168.89 \pm 12.78
	OoL	10–30 (5) 20.00 \pm 7.07
	OoW	50–110 (5) 76.00 \pm 21.91
Avicularia	AvL	610–880 (16) 705.00 \pm 73.48
	RL	350–460 (16) 406.25 \pm 34.03
	RW	140–200 (16) 173.13 \pm 15.80
	PrL	220–440 (16) 298.75 \pm 53.77
	PrW	180–300 (16) 226.88 \pm 31.77
	OpL	70–150 (15) 112.67 \pm 25.20
	OpW	70–130 (15) 90.00 \pm 14.64

cavity located in the distal part of the maternal zooid and below the colony surface (Fig. 5H). Avicularia interzooidal, elongate, longer than autozooids. Rostrum channelled, with elevated wing-like walls and pointed tip, spade-shaped, symmetrical or asymmetrical, dextral or sinistral. Proximal part rounded, shorter and wider than rostrum. Cryptocyst pustulose, concave, peripheral caverns rare. Opesia large, usually oval, rarely roundish, with thickened articular ridges bearing two very short teeth proximally and a long, slit-like opesiular indentation between teeth; opesiules lacking. Kenozooids rounded or oval, located usually at edges of colony (Fig. 5B). Cryptocyst finely pustulose with proximal peripheral caverns. Opesia roundish, small. Closure plates, intramural reparative budding of zooids not observed.

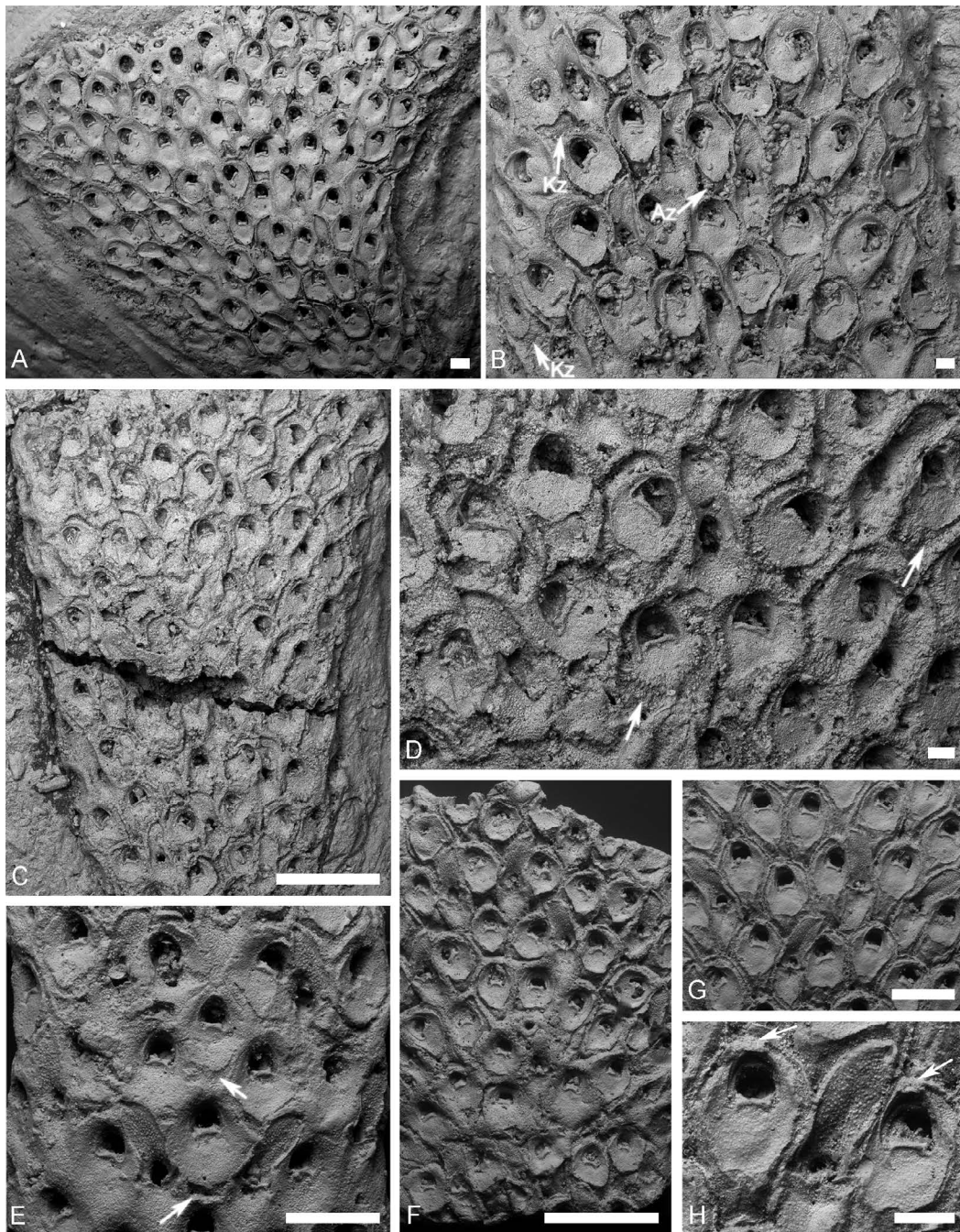


Fig. 5. *Rhagasostoma brydonei* sp. nov. **A–D.** Latest Turonian (*Sternotaxis plana* Zone), Kings Lane, Froxfield, south of Alton, Hampshire, England, UK. **A–B.** Holotype, SM B36666. **A.** Overview of erect bifoliate colony. **B.** Autozooids (Az) and kenozooids (Kz) with peripheral caverns (arrowed) and avicularia. **C–D.** Paratype SM B36667. **C.** Overview of erect bifoliate colony. **D.** Autozooids with peripheral cavern surrounding the cryptocyst (arrowed) and avicularia. **E–H.** Coniacian, Chatham, Kent, England, UK. **E.** Paratype, SMF 29940, autozooids with proximal peripheral caverns (arrowed) and avicularia. **F.** Paratype, SMF 29939, autozooids with peripheral cavern surrounding the cryptocyst and avicularia. **G–H.** Paratype, SMF 29941. **G.** Autozooids with peripheral cavern surrounding the cryptocyst and avicularia. **H.** Autozooids with peripheral cavern surrounding the cryptocyst and oecia of immersed ovicells (arrowed) and avicularia. Scale bars: A, D, H = 200 μ m; B = 100 μ m; C, F = 1 mm; E, G = 500 μ m.

Remarks

We have restudied Brydone's examples of *Rhagasostoma inelegans* in the SM collection. The specimen identified by Brydone as this species (Brydone 1930: pl. 25, figs 11, 12) does not belong to Lonsdale's species and is here regarded as a new species, *R. brydonei* sp. nov.

The new species differs from the closely related species *Rhagasostoma inelegans*, *R. minuens*, *R. angliae* and *R. aralense* sp. nov. in the avicularian rostrum being spade-shaped rather than having a conical outline shape or falciform. Moreover, the ovicells of *R. brydonei* sp. nov. are immersed. *Rhagasostoma brydonei* sp. nov. differs from *R. angliae* in having an avicularian cryptocyst with large oval or roundish opesia lacking opesiules, instead of a small subcircular opesia and two opesiules. The new species differs from *R. operculatum* sp. nov., which has a similar spade-shaped avicularian rostrum, by the rostrum being narrowed at the base, enlarged centrally and with a pointed tip, instead of being the same width along almost its entire length and having a pointed or rounded tip.

Distribution

Late Turonian United Kingdom: Kings Lane, Froxfield, south of Alton, Hampshire, England. Coniacian United Kingdom: Chatham, Kent, England.

Rhagasostoma minuens Brydone, 1936 Figs 6–7, Table 3

Rhagasostoma inelegans var. *minuens* Brydone, 1936: 74, pl. 35, figs 9–10.

Onychocella cf. *inelegans* (Lonsdale, 1850) – Voigt 1949: 26, pl. 8, figs 1–2.

Material studied

Lectotype (here designated)

UNITED KINGDOM • England, East Sussex, between Brighton and Roedean; late Santonian (*Uintacrinus socialis* Zone / lower *Marsupites testudinarius* Zone); SM B36883 (Fig. 6A–D; figured by Brydone 1936: pl. 35, fig. 10).

Paralectotype (here designated)

UNITED KINGDOM • England, Norfolk, Trimingham; early Maastrichtian (*Ostrea lunata* Zone, *Porosphaera* Beds); SM B36882 (Fig. 6E–F; figured by Brydone 1936: pl. 35, fig. 9).

Additional figured material

UNITED KINGDOM • 2 specs; England, Kent; Coniacian of Chatham; SMF 29921 (Fig. 7A–B), 29922 (Fig. 7C) • England, Wiltshire, SW of Salisbury, Harnham; early Campanian; SMF 29920 (Fig. 7D) • England, Norfolk, Trimingham; early Maastrichtian (*Ostrea lunata* Zone) [middle Campanian (*Belemnitella mucronata* Zone), Weybourne, Norfolk, in SM database]; SM B36678, specimen (a) (Fig. 7H) • 2 specs; England, East Sussex, Newhaven, Meeching Quarry; early Campanian; SMF 29943 (Fig. 7E), 29944 (Fig. 7F).

FRANCE • Hanches; Campanian; SMF 29918 (Fig. 7G).

Other material

UNITED KINGDOM • 3 specs; England, East Sussex, Newhaven, Meeching Quarry; early Campanian; SMF 29919, 29942, 29945.

GERMANY • Schleswig-Holstein, Lägerdorf; early Campanian; SMF 29917.

Description

Colony encrusting sheet-like, fragments about 10 mm in diameter, or erect with flattened bifoliate branches, fragments up to 2.0–10.0 mm long by 2.0–5.0 mm wide. Ancestrula (Fig. 6C) about 0.27 mm in diameter, rounded rhombic. Autozooids variable in shape, often broad and subrectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose,

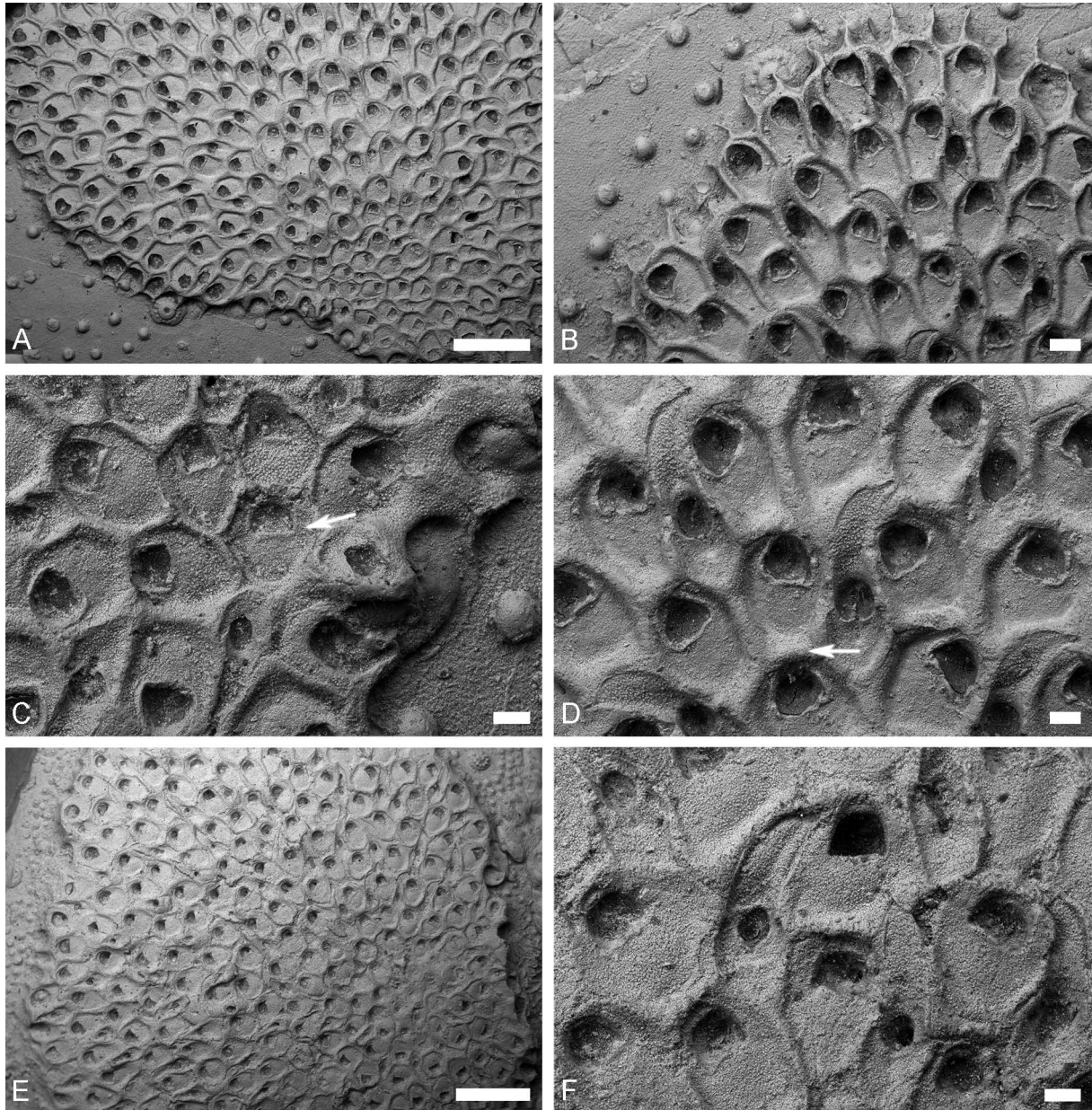


Fig. 6. *Rhagasostoma minuens* Brydone, 1936. **A–D.** Lectotype, SM B36883, late Santonian (*Uintacrinus socialis* Zone/lower *Marsupites testudinarius* Zone), between Brighton and Roedean, East Sussex, England, UK. **A.** Overview of encrusting colony. **B.** Growing edge. **C.** Early astogeny, ancestrula (arrowed), autozooids and avicularia. **D.** Autozooids with endozooidal ovicells (arrows) and avicularia. **E–F.** Paralectotype, SM B36882, early Maastrichtian (*Ostrea lunata* Zone, *Porosphaera* Beds), Trimingham, Norfolk, England, UK. **E.** Overview of encrusting colony. **F.** Autozooids and avicularia. Scale bars: A, E = 1 mm; B = 200 μ m; C–D, F = 100 μ m.

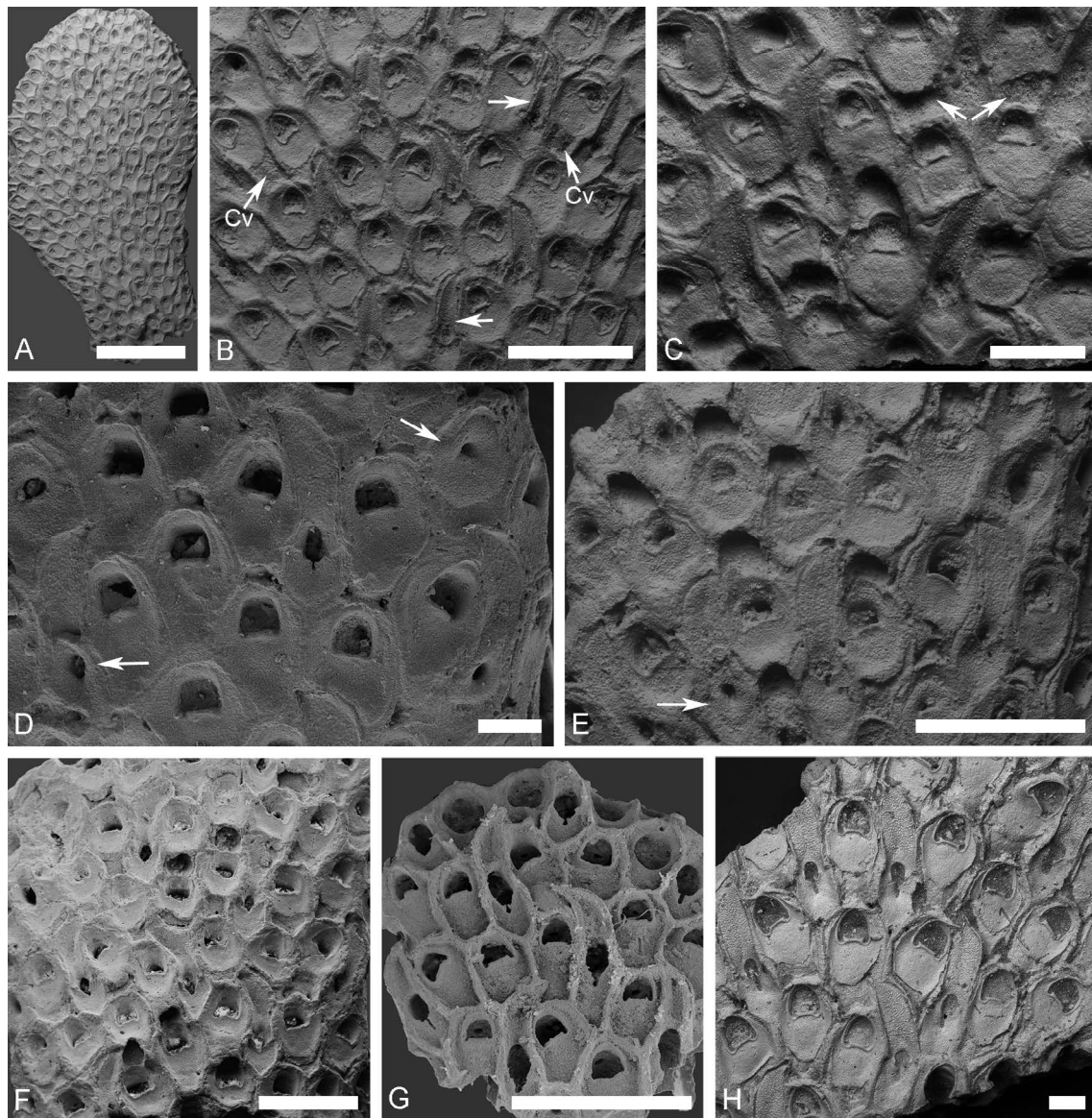


Fig. 7. *Rhagasostoma minuens* Brydone, 1936. **A–C.** Coniacian, Chatham, Kent, England, UK. **A–B.** SMF 29921. **A.** Overview of erect bifoliate colony. **B.** Autozooids with proximal lateral peripheral caverns (Cv) and broken oecia, avicularia, and intramural avicularia within host avicularia (arrowed). **C.** SMF 29922, autozooids with proximal lateral peripheral caverns (arrowed) and broken oecia (some with reparative sutures). **D.** SMF 29920, early Campanian, Harnham, SW of Salisbury, Wiltshire, England, UK; non-ovicellate autozooids, some with proximal peripheral caverns, and avicularia; intramural kenozooids observed within host autozoooid and avicularia (arrowed). **E–F.** Early Campanian, Meeching Quarry, Newhaven, East Sussex, England, UK. **E.** SMF 29943, ovicellate (with broken oecia) and non-ovicellate autozooids, some with proximal peripheral caverns, avicularia, and intramural kenozooid within a host avicularium (arrowed). **F.** SMF 29944, ovicellate (with broken oecia) and non-ovicellate autozooids with proximal peripheral caverns and avicularia. **G.** SMF 29918, Campanian, Hanches, France, overview of bifoliate colony showing autozooids and avicularia. **H.** SM B36678, specimen (a), late Campanian to early Maastrichtian (*Ostrea lunata* Zone) [middle Campanian (*Belemnitella mucronata* Zone), Weybourne, Norfolk, in SM database], Trimingham, Norfolk, England, UK; autozooids with peripheral caverns surrounding the cryptocyst and avicularia. Scale bars: A = 2 mm; B, E–G = 1 mm; C = 500 μ m; D = 300 μ m; H = 200 μ m.

Table 3. Summary of measurements of *Rhagasostoma minuens* Brydone, 1936. For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Southern North Sea Basin	North German Basin	
	Stratigraphy	Coniacian – Early Maastrichtian	Early Campanian	Total
	Locality	Sussex, Trimmingham, Kent, Wiltshire, Hanches	Lägerdorf	
Autozooids	AzL	360–830 (53) 575.09 \pm 115.42	550–780 (6) 705.00 \pm 83.61	360–830 (59) 588.31 \pm 118.80
	AzW	260–560 (53) 393.40 \pm 71.12	480–670 (6) 521.67 \pm 74.14	260–670 (59) 406.44 \pm 80.85
	CvL	30–220 (29) 122.41 \pm 48.82	60–180 (3) 133.33 \pm 64.29	30–220 (32) 123.44 \pm 49.29
	OpL	120–300 (53) 191.51 \pm 48.77	200–260 (5) 232.00 \pm 22.80	120–300 (58) 195.00 \pm 48.35
	OpW	140–280 (53) 201.13 \pm 32.62	230–260 (5) 242.00 \pm 13.04	140–280 (58) 204.66 \pm 33.41
	OoL	350–360 (2) 355.00 \pm 7.07	170–380 (4) 277.50 \pm 91.79	170–380 (6) 303.33 \pm 81.65
	OoW	250–260 (2) 255.00 \pm 7.07	250–320 (4) 285.00 \pm 28.87	250–320 (6) 275.00 \pm 27.39
Avicularia	AvL	520–1080 (46) 760.87 \pm 172.51	840–1030 (5) 916.00 \pm 76.35	520–1080 (51) 776.08 \pm 171.52
	RL	270–740 (46) 481.96 \pm 112.81	500–590 (5) 546.00 \pm 32.09	270–740 (51) 488.24 \pm 109.12
	RCL	0–330 (47) 152.77 \pm 73.74	200–270 (5) 236.00 \pm 25.10	0–330 (52) 160.77 \pm 74.62
	RW	100–330 (47) 180.21 \pm 48.12	160–210 (5) 190.00 \pm 20.00	100–330 (52) 181.15 \pm 46.13
	PrL	150–470 (45) 278.44 \pm 74.16	300–440 (5) 370.00 \pm 52.92	150–470 (50) 287.60 \pm 77.05
	PrW	160–400 (46) 260.00 \pm 59.10	260–340 (5) 300.00 \pm 30.82	160–400 (51) 263.92 \pm 58.00
	OpL	80–220 (42) 141.90 \pm 37.24	160–230 (5) 200.00 \pm 27.39	80–230 (47) 148.09 \pm 40.36
	OpW	60–200 (42) 104.29 \pm 30.21	120–170 (5) 138.00 \pm 20.49	60–200 (47) 107.87 \pm 30.99
Kenozooids	KzL	340–430 (4) 372.50 \pm 40.31	550 (1)	340–550 (5) 408.00 \pm 86.72
	KzW	190–260 (4) 245.00 \pm 51.96	350 (1)	190–350 (5) 266.00 \pm 65.04
	OpD	60–100 (4) 80.00 \pm 16.33	150 (1)	60–150 (5) 94.00 \pm 34.35

depressed or slightly convex centrally, sometimes with proximolateral peripheral caverns, up to 0.22 mm long (Fig. 7B–F), rarely peripheral caverns surrounding the cryptocyst (Fig. 7H). Opesia terminal, rarely subterminal, semielliptical with slight shelf in the distal part (Fig. 6D, F), formed by two walls, a thin inner wall delimiting the distolateral part and a salient, thickened outer wall delimiting the proximolateral part. Proximal edge of opesia straight, smooth, thickened, with outgrowths near the two proximolateral corners delimiting, small roundish opesiules (outgrowths are often broken thus giving the opesiules the appearance of opesiular indentations, or they may be obscured by sediment infills of the opesia). Septula not observed. Ovicells endozooidal, oecium is formed by the distal zooid, recognizable as a small swelling of its proximal cryptocyst (Figs 6D, 7C, E–F). Avicularia interzooidal, elongate, longer than autozooids. Rostrum channeled with elevated wing-like walls and pointed tip, falciform (almost the same width along the whole length of the rostrum or slightly expanding near apex, and pointed tip curved, sickle-shaped), asymmetrical, dextral or sinistral. Proximal part rounded, shorter and wider than the rostrum. Cryptocyst pustulose, concave, without peripheral caverns. Opesia large, roundish or oval, with thickened articular ridges bearing two short teeth proximally and a long, slit-like opesiular indentation between the teeth; opesiules lacking. Kenozooids rounded, rare, located at the margins of a colony. Cryptocyst finely pustulose. Opesia round. Intramural reparative budding of avicularia within host avicularia sometimes observed (Fig. 7B), all with the same polarity as the host zooid. Intramural reparative kenozooidal buds sometimes observed within host autozooids and avicularia (Fig. 7D–E). Closure plates not observed.

Remarks

Brydone (1936) introduced the subspecies *Rhagasostoma inelegans minuens* for unilaminar colonies lacking ovicells. We have restudied Brydone's syntypes in the SM collection, choosing a lectotype (the specimen figured by Brydone 1936: pl. 35, fig. 10); endozooidal ovicells are present in this colony. Voigt (1949) mentioned one specimen of "*Onychocella* cf. *inelegans*" from the early Campanian of Lägerdorf, Schleswig-Holstein of Germany but this belongs to *Rhagasostoma minuens*.

Rhagasostoma minuens can easily be distinguished from *R. inelegans*, *R. brydonei* sp. nov., *R. aralense* sp. nov. and *R. operculatum* sp. nov. in having a falciform avicularian rostrum. The species differs from *R. angliæ*, specimens of which may have similar falciform avicularian rostra, in the avicularian cryptocyst having large roundish or oval opesia without opesiules instead of small subcircular opesia and two opesiules.

Distribution

Coniacian United Kingdom: Chatham, Kent, England. Late Santonian United Kingdom: between Brighton and Roedean, East Sussex, England. Early Campanian United Kingdom, England: Harnham, SW of Salisbury, Wiltshire; Meeching Quarry, Newhaven, East Sussex. Germany: Lägerdorf, Schleswig-Holstein. Campanian France: Hanches. Early Maastrichtian United Kingdom: Trimmingham, Norfolk, England.

Rhagasostoma angliæ Brydone, 1936

Figs 8–9, Table 4

Rhagasostoma inelegans var. *angliæ* Brydone, 1936 pars: 74, pl. 35, figs 4, ?5, 6–7.

Onychocella dichotoma (Goldfuss, 1826) – Voigt 1949: pl. 8, fig. 3.

non *Rhagasostoma inelegans* var. *angliæ* – Brydone 1936 pars: 74, pl. 35, fig. 8.

Material studied

Lectotype (here designated)

UNITED KINGDOM • England, Norfolk, Norwich; Middle Campanian (*Belemnitella mucronata* Zone) of Hartford; SM B36877 (Fig. 8A–E; figured by Brydone 1936: pl. 35, fig. 4).

Paralectotype (here designated)

UNITED KINGDOM • England, Norfolk; early Maastrichtian (*Ostrea lunata* Zone) of Trimingham; SM B36879 (Fig. 8F–H; figured by Brydone 1936: pl. 35, figs 6–7).

Additional figured material

UNITED KINGDOM • England, Norfolk; middle Campanian (*Belemnitella mucronata* Zone) of Weybourne; SM B36671 (Fig. 9A–C).

FRANCE • Île-de-France; late Campanian of Vigny; SMF 29914 (Fig. 9D–E).

GERMANY • Early Maastrichtian of Hemmoor; SMF 26288 (Fig. 9F–G; figured by Voigt 1949: pl. 8, fig. 3).

Description

Colony encrusting, sheet-like, fragments up to 10 mm in diameter, or erect with flattened, bifoliate branches, fragments up to 6.0–7.0 mm long by 3.0–5.0 mm wide. Ancestrula (Fig. 8B) about 0.33 mm in diameter, rounded rhombic, surrounded by six periancestrular zooids, five zooids possibly budded directly from the ancestrula. Autozooids variable in shape, often broad and roughly rectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose, depressed or slightly convex centrally, sometimes with peripheral cavern surrounding the cryptocyst (Fig. 8C). Opesia terminal or subterminal, semielliptical with shelf distally, formed by two walls, a thin inner wall delimiting the distolateral part and a salient, thickened outer wall delimiting the proximolateral part (Figs 8E, H, 9C). Proximal edge of opesiae straight, smooth, thickened, with outgrowths near the two proximolateral corners delimiting small, roundish opesiules (outgrowths are often broken, giving the opesiules the appearance of opesiular indentations, or they may be obscured by sediment fillings inside the opesia). Septula not observed. Ovicells endozooidal, oocidium is formed by the distal zooid, ill-recognizable, with cryptocyst-like surface (Fig. 9E). Avicularia interzooidal, longer than autozooids, elongate. Rostrum channeled with elevated wing-like walls and pointed tip, conical in outline or sometimes falciform, asymmetrical, dextral or sinistral. Proximal part rounded, shorter and slightly wider than the rostrum. Cryptocyst pustulose, concave with depression centrally, sometimes with peripheral cavern surrounding the cryptocyst (Fig. 8C, E, H), having three openings: a distal small subcircular opesia; two lateral and parallel slit-like opesiules formed by long teeth of articular ridges, which grow together with proximal edge of opesia; a long and slit-like opesiular indentation proximally between the teeth (Figs 8E, H, 9C, E, G). Cryptocyst between openings frequently destroyed, causing the openings to coalesce into a single opening of variable outline that is sometimes tulip-shaped. Kenozooids rounded, very rare, located at the margins of a colony or between zooids (Fig. 9D). Cryptocyst finely pustulose. Opesia roundish, small. Closure plates, intramural reparative budding in autozooids and avicularia not observed.

Remarks

Brydone (1936) introduced the subspecies *Rhagasostoma inelegans angliae* for unilaminar colonies lacking ovicells. We have restudied Brydone's syntypes in the SM collection, choosing a lectotype (the specimen figured by Brydone 1936: pl. 35, fig. 4). The specimen figured by Brydone (1930: pl. 26, fig. 5) was not restudied.

Brydone (1936) compared his specimens of *Rhagasostoma inelegans angliae* from the Trimingham Chalk with the bilaminar, ovicellate *Onychocella dichotoma* sensu Levinsen (1925) from the early Maastrichtian white Chalk of southeastern Denmark and northern Jylland. However, Levinsen's drawing shows that his species has an avicularian opesiae similar to *Rhagasostoma inelegans incarcerata* sensu Brydone (1930). The avicularia of this subspecies apparently contain two pairs of lateral, parallel, slit-

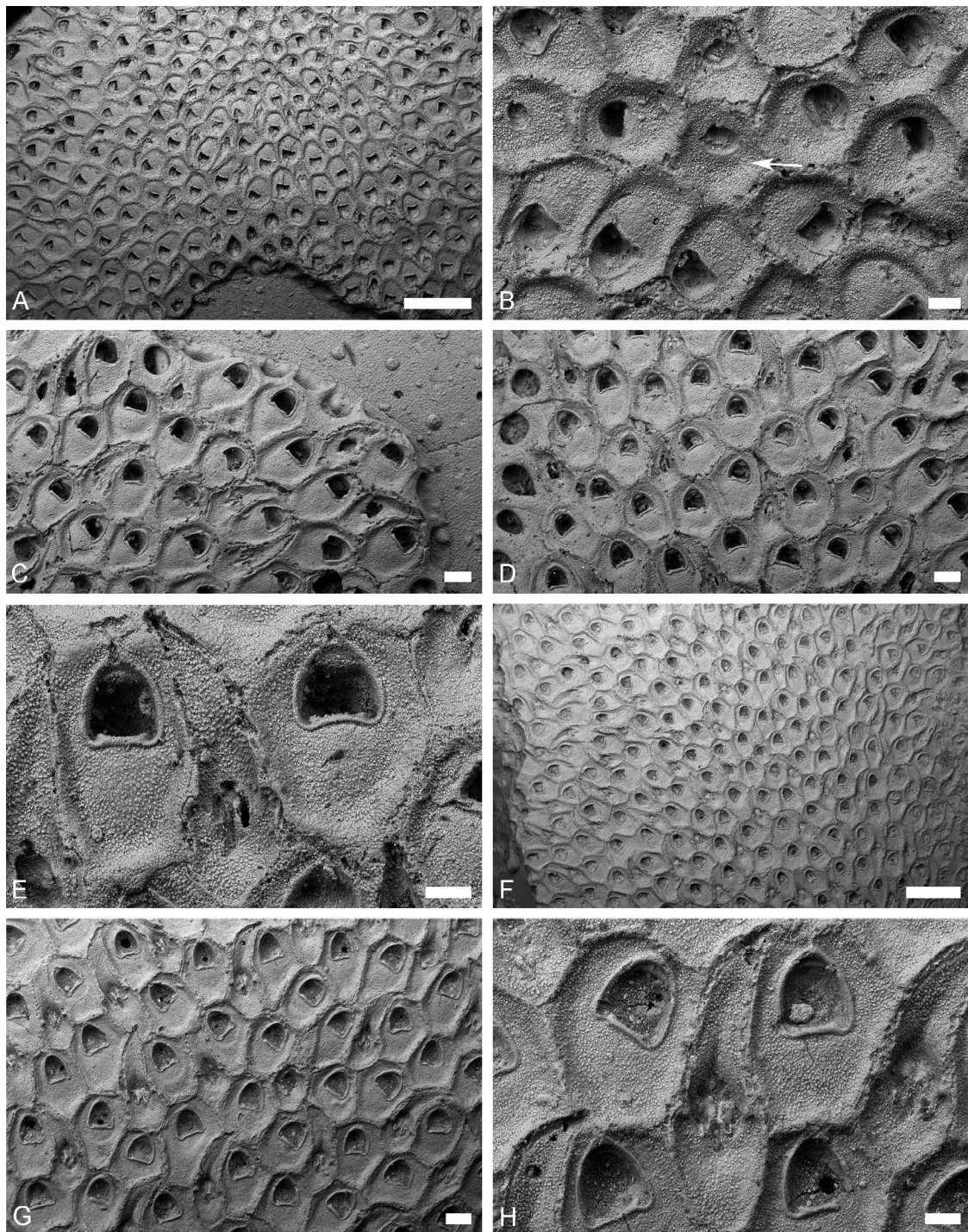


Fig. 8. *Rhagasostoma angliae* (Brydone, 1936). **A–E.** Lectotype, SM B36877, Middle Campanian (*Belemnitella mucronata* Zone) of Hartford, Norwich, Norfolk, England, UK. **A.** Overview of encrusting colony. **B.** Early astogeny, ancestrula arrowed. **C.** Growing edge, avicularia and some autozooids with peripheral caverns surrounding the cryptocyst. **D.** Autozooids and avicularia. **E.** Avicularium with peripheral caverns surrounding the cryptocyst and non-ovicellate autozooids. **F–H.** Paralectotype, SM B36879, early Maastrichtian (*Ostrea lunata* Zone) of Trimingham, Norfolk, England, UK. **F.** Erect bifoliate colony. **G.** Non-ovicellate autozooids and avicularia. **H.** Avicularia and non-ovicellate autozooids. Scale bars: A, F = 1 mm; B, E, H = 100 μ m; C–D, G = 200 μ m.

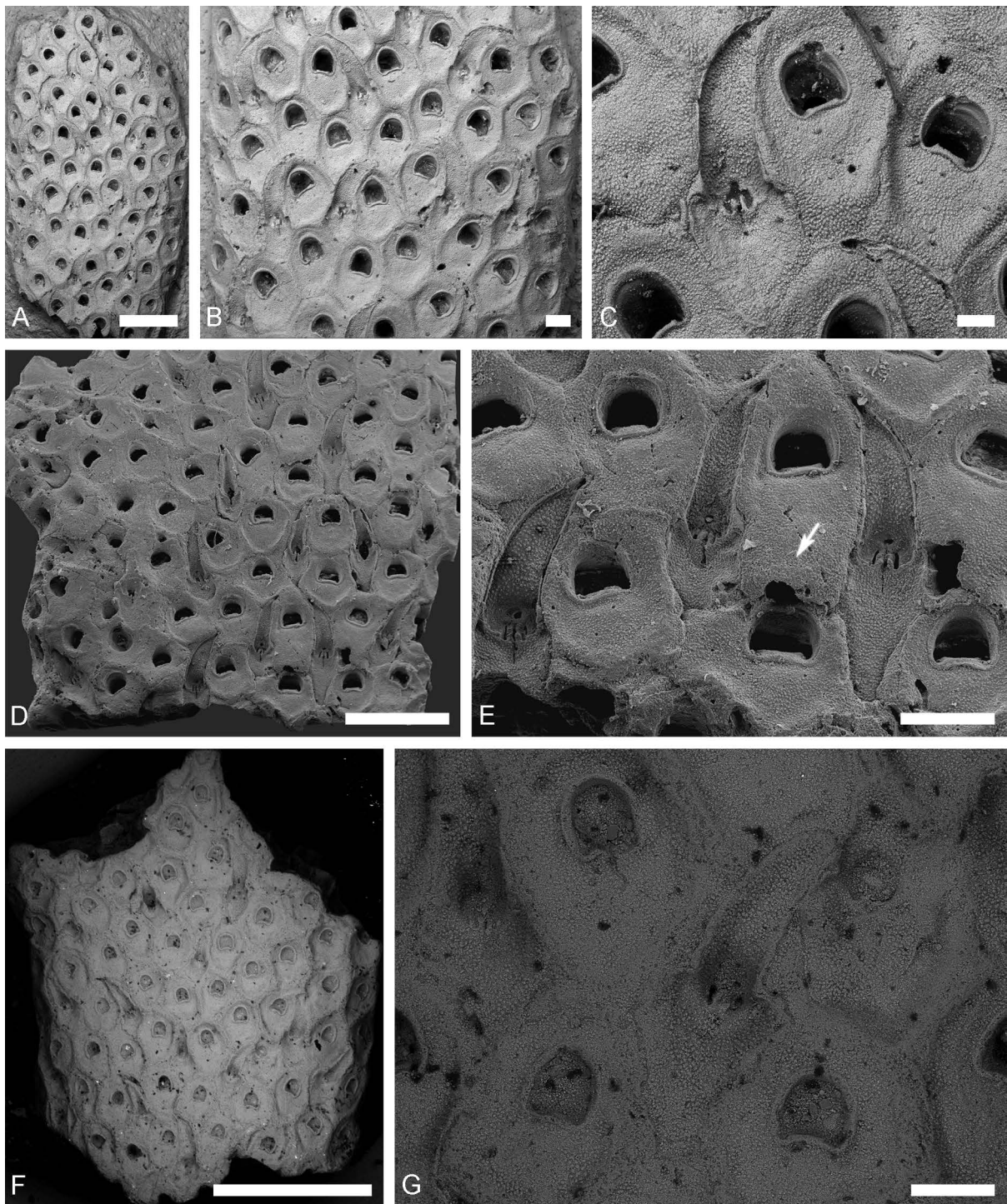


Fig. 9. *Rhagasostoma angliae* Brydone, 1936. A–C. SM B36671, Middle Campanian (*Belemnitella mucronata* Zone), Weybourne, Norfolk, England, UK. A. Overview of erect bifoliate colony. B. Non-ovicellate autozooids and avicularia. C. Opesiae of non-ovicellate autozooids with distal shelf and avicularium. D–E. SMF 29914, Late Campanian of Vigny, Île-de-France, France. D. Overview of erect bifoliate colony. E. Non-ovicellate and one ovicellate (with partially broken oecium, arrowed) autozooids and avicularia. F–G. SMF 26288, early Maastrichtian of Hemmor, Germany. F. Overview of erect bifoliate colony. G. Non-ovicellate autozooids and avicularia. Scale bars: A, D = 1 mm; B, G = 200 µm; C = 100 µm; E = 300 µm; F = 2 mm.

Table 4. Summary of measurements of *Rhagasostoma angliae* Brydone, 1936. For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Southern North Sea Basin	North German Basin	
	Stratigraphy	Middle Campanian to early Maastrichtian	Early Maastrichtian	Total
	Locality	Norwich, Weybourne, Trimingham, Vigny	Hemmor	
Autozooids	AzL	460–700 (24) 568.33 \pm 64.92	600–700 (6) 656.67 \pm 39.33	460–700 (30) 586.00 \pm 70.00
	AzW	340–530 (24) 418.33 \pm 53.46	400–540 (6) 465.00 \pm 52.44	340–540 (30) 427.67 \pm 55.69
	CvL		Not observed	
	OpL	140–220 (24) 185.42 \pm 19.11	160–190 (6) 170.00 \pm 10.95	140–220 (30) 182.33 \pm 18.70
	OpW	160–230 (24) 195.42 \pm 21.26	150–210 (6) 166.67 \pm 24.22	150–230 (30) 189.67 \pm 24.42
	OoL	270 (1)		270 (1)
	OoW	350 (1)	Not observed	350 (1)
Avicularia	AvL	690–1050 (23) 801.74 \pm 96.18	800–1060 (5) 936.00 \pm 143.63	690–1060 (28) 825.71 \pm 115.48
	RL	430–580 (23) 503.48 \pm 46.08	460–710 (5) 568.00 \pm 97.83	430–710 (28) 515.00 \pm 61.49
	RCL	170–300 (11) 218.18 \pm 36.01	150–260 (4) 177.50 \pm 60.21	150–300 (15) 207.33 \pm 45.27
	RW	120–170 (23) 146.52 \pm 14.34	150–250 (5) 200.00 \pm 43.01	120–250 (28) 156.07 \pm 29.61
	PrL	210–470 (23) 286.09 \pm 70.82	290–450 (5) 354.00 \pm 75.03	210–470 (28) 298.21 \pm 74.98
	PrW	200–320 (23) 246.96 \pm 25.12	270–340 (5) 300.00 \pm 29.15	200–340 (28) 256.43 \pm 32.68
	OpD	20–40 (16) 29.69 \pm 5.31	?	20–40 (16) 29.69 \pm 5.31
Kenozooids	KzL	260–620 (4) 360.00 \pm 173.59		260–620 (4) 360.00 \pm 173.59
	KzW	220–350 (4) 267.50 \pm 57.37	Not observed	220–350 (4) 267.50 \pm 57.37
	OpD	70 (4) 70.00 \pm 0.00		70 (4) 70.00

like opesiules in the central part of the cryptocyst, whereas *angliae* has only one pair of lateral, parallel, slit-like opesiules. Voigt (1949: 26) mentioned one specimen from the late Campanian (*Belemnitella lanceolata* Zone) of Hemmoor. Our study shows that the avicularian opesia in this specimen are similar to *angliae*, while Voigt (1949) described it as *Onychocella dichotoma* Goldfuss, 1826 and classified *O. inelegans incarcerata* as a junior synonym of *O. dichotoma*.

Rhagasostoma angliae can easily be distinguished from *R. inelegans*, *R. brydonei* sp. nov., *R. minuens*, *R. aralense* sp. nov. and *R. operculatum* sp. nov. as the avicularian cryptocysts have small, subcircular opesia and two opesiules instead of large, roundish or oval opesia without opesiules. *Rhagasostoma rowei* (Brydone, 1906) and *R. mimosa* (Brydone, 1930) also have avicularian cryptocysts with small subcircular opesia and opesiules, but *R. angliae* differs from these species in having articular ridges bearing teeth with proximal opesiular indentation between the teeth and interzooidal, and elongate avicularia with asymmetrical rostra instead of vicarious, rhomboidal avicularia with symmetrical rostra.

Distribution

Middle Campanian United Kingdom: Norwich and Weybourne, Norfolk, England (Brydone 1936). Late Campanian France: Vigny, Île-de-France. Early Maastrichtian Germany: Hemmoor (Voigt 1949). United Kingdom: Trimingham, Norfolk, England.

Rhagasostoma aralense sp. nov.

[urn:lsid:zoobank.org:act:BA58BA06-3D7D-4C8C-8125-3490AE0A37E7](https://zoobank.org/act:BA58BA06-3D7D-4C8C-8125-3490AE0A37E7)

Fig. 10, Table 5

Onychocella inelegans (Lonsdale, 1850) – Favorskaya 1992: 125, pl. 64, fig. 6, pl. 65, fig. 1.

non *Onychocella inelegans* – Favorskaya 1992: 125, pl. 64, fig. 7.

Diagnosis

Colonies erect, bifoliate. Autozooids subrectangular; gymnocyst lacking; cryptocyst extensive with proximolateral peripheral caverns; opesiae terminal, semielliptical without shelf in the distal part, proximal edge crenulated with small, roundish opesiules; ovicells endozooidal. Avicularia interzooidal, larger than autozooids; rostrum channeled with pointed top, conical in outline, almost symmetrical; proximal part rounded, shorter and wider than rostrum; opesia egg-shaped with thin articular ridges bearing two short teeth proximally and an opesiular indentation between the teeth; opesiules lacking. Kenozooids at the margins of a colony, roundish, with small opesia.

Etymology

The species is named after its type locality, the region south of the former Aral Sea in the Republic of Karakalpakstan, Uzbekistan.

Material studied

Holotype

UZBEKISTAN • Republic of Karakalpakstan; early Campanian (*Cibicidoides temirensis/Bolivinooides decoratus decoratus* Zone; LS13) of the southern Aral Sea Region; TsNIGR Museum 26/12582 (Fig. 10A–F; figured by Favorskaya 1992: pl. 64, fig. 6).

Paratypes

UZBEKISTAN • Same data as for holotype; middle Campanian (*Brotzenella monterelensis* Zone; LS14) of the southern Aral Sea Region; TsNIGR Museum 28/12582 (Fig. 10G; figured by Favorskaya 1992: pl. 65, fig. 1).

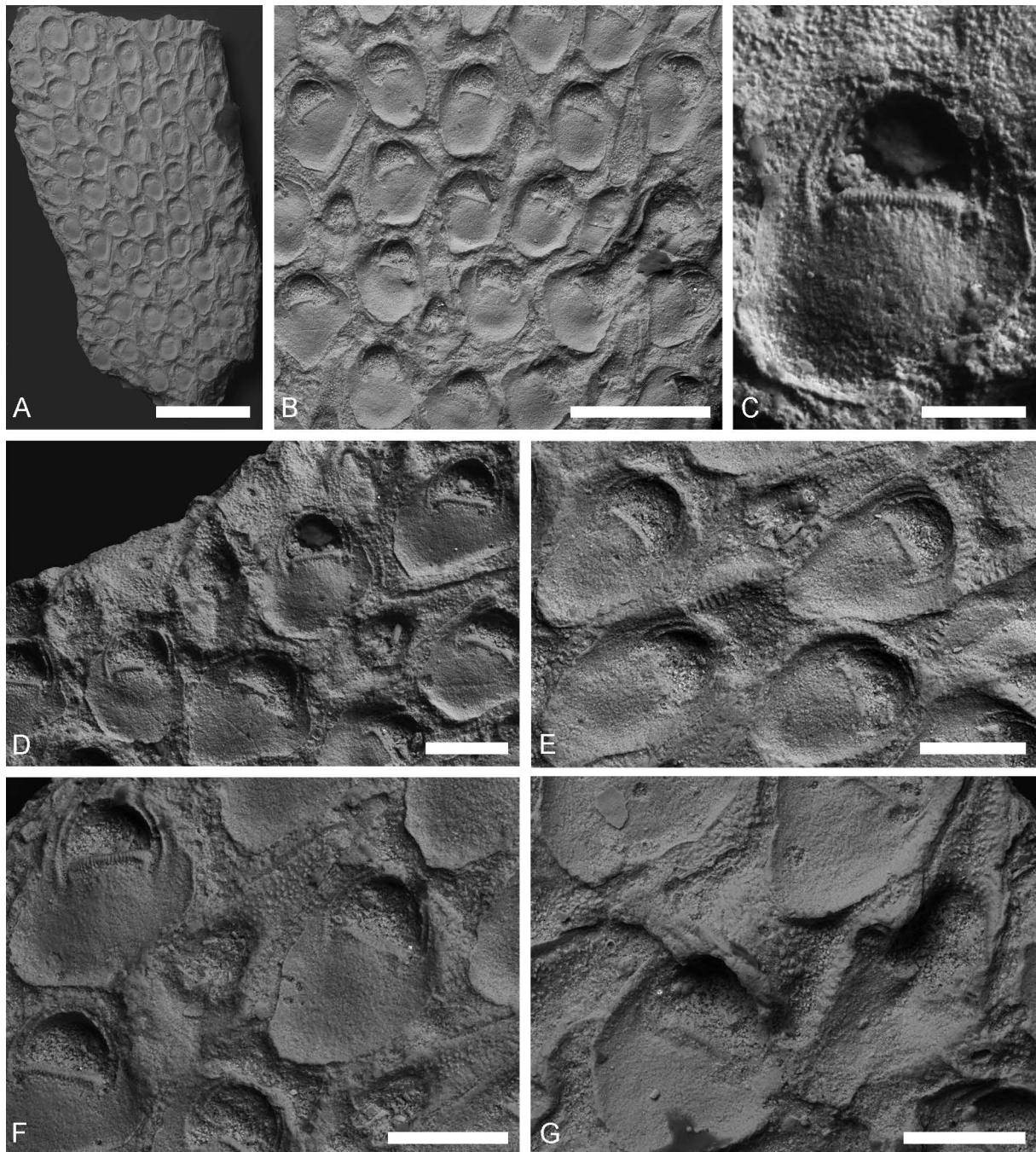


Fig. 10. *Rhagasostoma aralense* sp. nov., southern Aral Sea Region, Uzbekistan. **A–F.** Holotype, TsNIGR Museum 26/12582, early Campanian, *Cibicidoides temirensis*/*Bolivinooides decoratus decoratus* Zone. **A.** Overview of erect bifoliolate colony. **B.** Autozooids with proximal lateral peripheral caverns and avicularia. **C.** Opesia of non-ovicellate autozooid with crenulated proximal edge. **D.** Edge of the colony with autozooids, avicularia, and kenozooids. **E.** Non-ovicellate autozooids with proximal peripheral caverns and avicularium. **F.** Non-ovicellate autozooids and avicularia. **G.** Paratype, TsNIGR Museum 28/12582, middle Campanian, *Brotzenella monterelensis* Zone, ovicellate autozooid and avicularium. Scale bars: A = 1 mm; B = 500 μ m; C = 100 μ m; D–G = 200 μ m.

Table 5. Summary of measurements of *Rhagasostoma aralense* sp. nov. For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	North Ust-Yurt–Aral Basin
	Stratigraphy	Early to middle Campanian
	Locality	Southern Aral Sea Region
Autozooids	AzL	330–650 (12) 430.00 \pm 90.45
	AzW	230–300 (12) 259.17 \pm 23.53
	CvL	30–220 (12) 67.50 \pm 52.25
	OpL	90–160 (12) 117.50 \pm 19.60
	OpW	130–200 (12) 165.83 \pm 22.75
	OoL	110–140 (2) 125.00 \pm 21.21
	OoW	210 (2) 210.00
Avicularia	AvL	470–880 (10) 674.00 \pm 133.93
	RL	370–590 (10) 463.00 \pm 73.34
	RW	70–140 (10) 107.00 \pm 25.84
	PrL	100–300 (10) 211.00 \pm 72.95
	PrW	140–230 (10) 189.00 \pm 26.44
	OpL	110–180 (9) 137.78 \pm 26.35
	OpW	90–140 (9) 117.78 \pm 17.16
Kenozooids	KzL	180–250 (2) 215.00 \pm 49.50
	KzW	130–150 (2) 140.00 \pm 14.14
	OpD	20–30 (2) 25.00 \pm 7.07

Type locality and horizon

Uzbekistan, Republic of Karakalpakstan; southern Aral Sea Region; *Cibicidoides temirensis*/*Bolivinoidea decoratus decoratus* Zone (LS13), early Campanian.

Description

Colony erect, flattened, bifoliate, fragments 3.0–5.0 mm long by 2.0–3.0 mm wide. Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad and subrectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose, convex centrally, slightly depressed around edges, with proximolateral peripheral caverns; lateral wall of some caverns ribbed (Fig. 10B, E–G). Opesia terminal, semielliptical without shelf in the distal part, formed by two walls, a thin inner wall delimiting the distolateral part and a salient, thickened outer wall delimiting the proximolateral part (Fig. 10C, F). Proximal edge of opesia straight, crenulated, thickened, with outgrowths near the two proximolateral corners delimiting small, roundish opesiules (outgrowths are often broken thus giving the opesiules the appearance of opesiular indentations, or they may be obscured by sediment infilling the opesiae). Septula not observed. Ovicells endozooidal, oecium is formed by the distal zooid, seen as a low swelling of its proximal cryptocyst (Fig. 10G). Avicularia interzooidal, larger than autozooids, elongate. Rostrum channeled with elevated wing-like walls and a pointed tip, conical in outline, almost symmetrical. Proximal part rounded, shorter and wider than rostrum. Cryptocyst pustulose, concave, without peripheral caverns. Opesia egg-shaped with the narrow end pointing upwards and with thin articular ridges bearing two short teeth proximally and a short or long, slit-like opesiular indentation between the teeth; opesiules lacking. Kenozooids rounded, located at the margins of a colony. Cryptocyst finely pustulose. Opesia roundish, very small. Closure plates, intramural reparative budding of autozooids, avicularia and kenozooids not observed.

Remarks

Rhagasostoma aralense sp. nov. differs from *R. brydonei* sp. nov., *R. minuens* and *R. operculatum* sp. nov. in having avicularian rostra that are a conical in outline rather than spade-shaped or falciform. The new species differs from *R. inelegans* and *R. angliae*, which also have avicularian rostra conical in outline, in the rostrum being almost symmetrical and the avicularian opesia egg-shaped. The crenulated proximal edge of the autozooidal opesia is clearly another important character distinguishing this species from others. However, it is possible that the ribs are sediment particles or diagenetic crystals.

Distribution

Early to middle Campanian Uzbekistan: between Chimboy/Shimbay (Чимбой/Шымбай) and the Aral Sea in the Republic of Karakalpakstan.

Rhagasostoma operculatum sp. nov.

[urn:lsid:zoobank.org:act:23F08F8D-29DB-4470-B8FA-B176256858F8](https://zoobank.org/act:23F08F8D-29DB-4470-B8FA-B176256858F8)

Fig. 11, Table 6

Onychocella inelegans (Lonsdale, 1850) – Favorskaya 1992: 125, pl. 64, fig. 7. — Favorskaya 1996: pl. 3, fig. 4. — Koromyslova 2014b: pl. 3, fig. 1.

non *Onychocella inelegans* – Favorskaya 1992: 125, pl. 64, fig. 6, pl. 65, fig. 1.

Diagnosis

Colony erect, bifoliate. Autozooids subrectangular, zooidal boundaries raised; gymnocyst lacking; cryptocyst extensive; opesia terminal, semielliptical; putative calcified opercula rounded trapezoidal. Avicularia interzooidal; rostrum channeled with rounded tip, between conical in outline and spade-

Table 6. Summary of measurements of *Rhagasostoma operculatum* sp. nov. For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Tethys
	Stratigraphy	Boundary early to middle Campanian
	Locality	Western Kopetdag
Autozooids	AzL	550–690 (8) 602.50 \pm 49.50
	AzW	300–410 (8) 331.25 \pm 39.44
	OperL	130–180 (8) 155.00 \pm 17.73
	OperW	150–200 (8) 180.00 \pm 20.00
Avicularia	AvL	680–870 (8) 771.25 \pm 59.63
	RL	400–520 (8) 461.25 \pm 42.91
	RW	100–130 (8) 115.00 \pm 11.95
	PrL	270–380 (8) 318.75 \pm 35.23
	OpL	120–150 (6) 140.00 \pm 12.65
	OpW	100–140 (6) 118.33 \pm 11.69

shaped, asymmetrical; proximal part rounded, shorter and wider than rostrum; opesia egg-shaped with thin articular ridges bearing two short teeth proximally and a short opesiular indentation between the teeth; opesiules lacking.

Etymology

The species is named from the Latin ‘*operculum*’ because the opesiae of autozooids are presumably closed by calcified opercula.

Material studied

Holotype

TURKMENISTAN • Western Kopetdag, Kara-Kala; boundary layers of the early Campanian (*Cibicidoides temirensis*/*Bolivinoidea decoratus decoratus* Zone; LS13) to middle Campanian (*Brotzenella monterelensis* Zone; LS14) of the western Kopetdag; TsNIGR Museum 27/12582 (Fig. 11A–C; figured by Favorskaya 1992: pl. 64, fig. 7).

Type locality and horizon

Turkmenistan, Western Kopetdag; boundary layers of the early to middle Campanian.

Description

Colony erect, flattened, bifoliate; fragments 6.0 mm long by 2 mm wide. Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad and subrectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose, slightly depressed centrally, without peripheral caverns. Opesia terminal, semielliptical, presumably closed by calcified opercula. Putative opercula rounded trapezoidal and slightly concave, tubercular externally (Fig. 11C), proximal edge slightly arched and with ‘ears’ at the ends, which are 0.03–0.05 mm wide, ‘ears’ projecting 0.01–0.02 mm below the proximal edge. Septula not observed. Ovicells not observed. Avicularia interzooidal, longer than autozooids, elongate. Rostrum channeled with elevated walls and often rounded top, between conical in outline and spade-shaped, asymmetrical, dextral or sinistral. Proximal part rounded, shorter and wider than rostrum, cryptocyst pustulose, concave. Opesia egg-shaped with the narrow end pointing upwards and with thin articular ridges bearing two short teeth

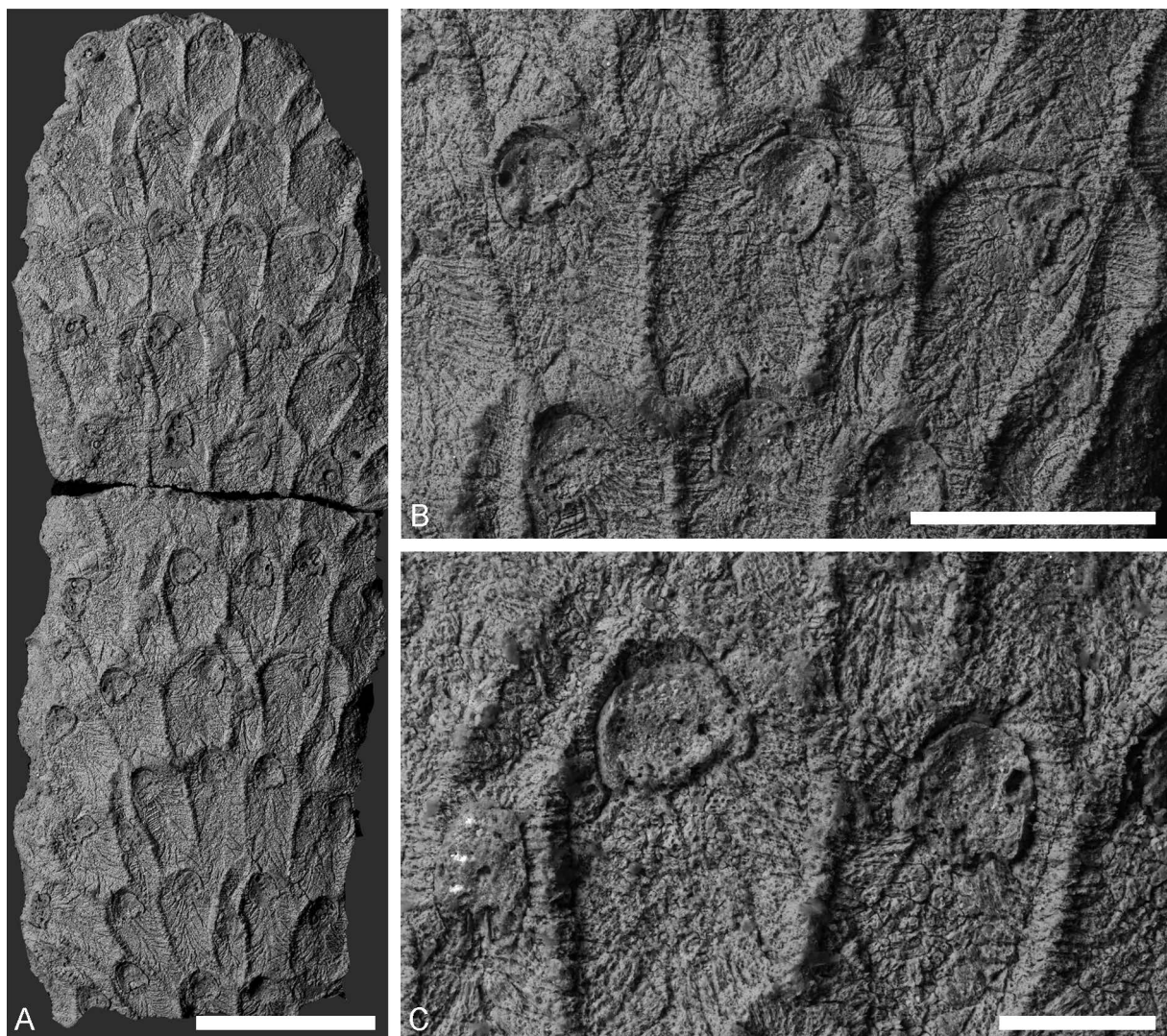


Fig. 11. *Rhagasostoma operculatum* sp. nov. A–C. Holotype, TsNIGR Museum 27/12582, western Kopetdag, Turkmenistan, boundary between the early and late Campanian (*Cibicidoides temirensis*/*Bolivinooides decoratus decoratus* Zone, LS13). A. Overview of erect bifoliate colony. B. Autozooids with putative opercula and avicularia. C. Autozooids with putative opercula and avicularium. Scale bars: A = 1 mm; B = 500 µm; C = 200 µm.

proximally and short opesiular indentation between the teeth; opesiules lacking. Kenozooids, closure plates, intramural reparative budding autozooids, kenozooids, and avicularia not observed.

Remarks

Rhagasostoma operculatum sp. nov. differs from *R. brydonei* sp. nov., another species with a spade-shaped avicularian rostrum, in the rostrum having almost the same width along the whole of their length and having a pointed or rounded rostral tip instead of the rostrum being narrowed at the base, enlarged centrally and with a pointed tip. The new species differs from the other species described herein in having a spade-shaped avicularian rostrum instead of one that is conical in outline or falciform. Moreover, opesia of autozooids of *R. operculatum* sp. nov. are presumably closed by calcified opercula.

Rhagasostoma operculatum sp. nov. is the earliest known species in cryptocystidean anascan cheilostomes that has putative calcified opercula. Late Cretaceous cheilostomes with calcified opercula from the family Onychocellidae include *Inversaria flabellula* (von Hagenow, 1846) from the late Campanian of Scania, Sweden, ?*Inversaria* sp. from the late Campanian to Maastrichtian of United Arab Emirates, and *Inversaria tubiporacea* (Goldfuss, 1826) and *Onychocella exilis* Koromyslova & Shcherbinina, 2015 from the Maastrichtian of NW Europe and Uzbekistan, respectively (Voigt & Williams 1973; Voigt 1974; Di Martino & Taylor 2013; Koromyslova 2014b; Koromyslova & Shcherbinina 2015). Calcified opercula have also been observed in several species belonging to the family Cribrilinidae Hincks, 1879 including *Castanopora lambi* Turner, 1975 from the Maastrichtian of USA (Turner 1975; McKinney *et al.* 2003; Taylor & McKinney 2006).

Distribution

Early to middle Campanian Turkmenistan: western Kopetdag, Kara-Kala.

Rhagasostoma gibbosum (Marsson, 1887)

Figs 12–13, Table 7

Eschara gibbosa Marsson, 1887: 71, pl. 7, fig. 2.

Rhagasostoma subgibbosum Brydone, 1930: 48, pl. 26, fig. 11. **Syn. nov.**

Rhagasostoma gibbosum var. *weyournensis* Brydone, 1930 pars: 48, pl. 26, figs 13–14. **Syn. nov.**

Rhagasostoma gibbosum – ?Levinsen 1925: 369. — Brydone 1930: pl. 26, fig. 15.

Onychocella gibbosa – ?Voigt 1930: 460, pl. 18, fig. 15. — ?Veenstra 1963: 107, pl. fig. 5.

non *Rhagasostoma gibbosum* var. *weyournensis* – Brydone 1930 pars: 48, pl. 26, fig. 12.

Material studied

Figured material

GERMANY • 2 specs; Schleswig-Holstein, Saturn quarry near Kronsmoor; early Maastrichtian; SMF 29906 (Fig. 12A–E), 29907 (Fig. 12F).

UNITED KINGDOM • England, Norfolk; early Maastrichtian (*Ostrea lunata* Zone) of Trimmingham; SM B36679 (Fig. 12G; figured by Brydone 1930: pl. 26, fig. 15).

BELARUS • 3 specs; Grodno Region; erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно); PIN 2922/216 (Fig. 13B), 2922/218 (Fig. 13A), 2922/275 (Fig. 13C).

KAZAKHSTAN • 2 specs; Emba River; late Campanian (*Belemnitella lanceolata* Zone); PIN 5502/3058 (Fig. 13D), 5502/3059 (Fig. 13E).

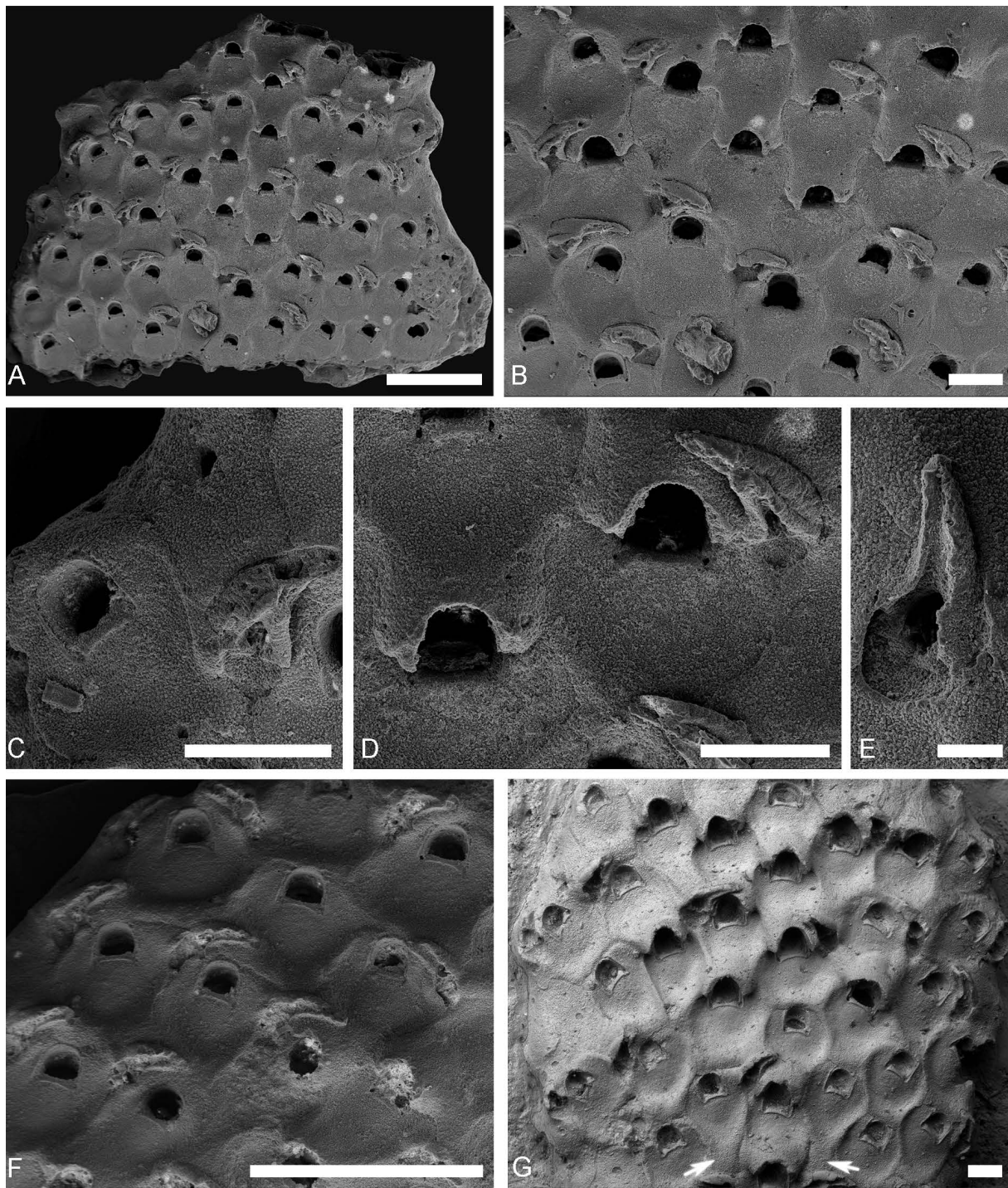


Fig. 12. *Rhagasostoma gibbosum* (Marsson, 1887). **A–F.** Early Maastrichtian, Saturn quarry near Krons Moor, Schleswig-Holstein, Germany. **A–E.** SMF 29906. **A.** Overview of erect bifoliate colony. **B.** Ovicellate and non-ovicellate autozooids and avicularia. **C.** Autozooid, avicularium with wedge-like structure and kenozooid. **D.** Ovicellate autozooids and avicularia with wedge-like structure. **E.** Avicularium with broken wedge-like structure. **F.** SMF 29907, autozooids and avicularia. **G.** SM B36679, Upper Chalk, early Maastrichtian, *Ostrea lunata* Zone, Trimingham, Norfolk, England, UK. Ovicellate and non-ovicellate autozooids, some with gymnocyst (arrowed), avicularia and kenozooids. Scale bars: A, F = 1 mm; B–D = 300 μ m; E = 100 μ m; G = 200 μ m.

Table 7. Summary of measurements of *Rhagasostoma gibbosum* (Marsson, 1887). For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	British–Belgian– Dutch	North German	Polish–South Baltic	North Ust–Yurt– Aral	
	Stratigraphy	Early Maastrichtian	Early Maastrichtian	?Late Campanian	Late Campanian	Total
	Locality	Norfolk	Kronsmoor	Grodno Region	Emba River	
Autozooids	AzL	420–690 (6) 523.33 \pm 113.25	450–810 (12) 598.33 \pm 99.89	410–640 (18) 511.67 \pm 55.44	500–740 (12) 574.17 \pm 70.12	410–810 (48) 550.42 \pm 85.80
	AzW	350–420 (6) 391.67 \pm 29.27	410–650 (12) 505.00 \pm 67.62	340–430 (18) 379.44 \pm 34.04	390–520 (12) 450.83 \pm 36.55	340–650 (48) 430.21 \pm 67.87
	OpL	140–160 (6) 151.67 \pm 7.53	150–200 (12) 173.33 \pm 18.26	120–160 (17) 142.35 \pm 12.00	170–210 (12) 185.83 \pm 13.79	120–210 (47) 162.55 \pm 22.79
	OpW	160–210 (6) 180.00 \pm 20.00	160–230 (12) 198.33 \pm 20.82	140–180 (17) 161.18 \pm 15.36	170–210 (12) 182.50 \pm 12.88	140–230 (47) 178.51 \pm 22.06
	CvL	Not observed		70–280 (15) 150.67 \pm 59.10	Not observed	70–280 (15) 150.67 \pm 59.10
	GL	180–220 (2) 200.00 \pm 28.28	Not observed	200 (1)	120–250 (4) 185.00 \pm 56.86	120–250 (7) 191.43 \pm 42.59
	OoL	140–180 (6) 141.67 \pm 33.12	190–300 (8) 246.25 \pm 35.43	110–180 (6) 143.33 \pm 27.33	190–270 (5) 242.00 \pm 30.33	110–300 (25) 195.60 \pm 60.14
	OoW	270–380 (6) 305.00 \pm 38.86	360–450 (8) 410.00 \pm 26.19	180–240 (6) 221.67 \pm 22.29	200–480 (6) 343.33 \pm 89.14	180–480 (26) 326.92 \pm 85.03
Avicularia	AvL	300–390 (5) 336.00 \pm 35.78	310–460 (10) 365.00 \pm 42.75	300–460 (16) 358.13 \pm 45.49	330–490 (10) 413.00 \pm 50.34	300–490 (41) 370.49 \pm 50.54
	RL	190–310 (5) 244.00 \pm 46.69	220–300 (11) 269.09 \pm 28.09	190–300 (16) 240.00 \pm 30.98	200–360 (10) 274.00 \pm 53.17	190–360 (42) 256.19 \pm 40.24
	W–ISL	Not observed	160–240 (6) 188.33 \pm 29.94	Not observed		160–240 (6) 188.33 \pm 29.94
	RW	100–180 (5) 130.20 \pm 30.15	90–160 (11) 122.73 \pm 24.94	80–180 (17) 134.71 \pm 29.82	90–170 (10) 137.00 \pm 26.69	80–180 (43) 131.65 \pm 27.52
	PrL	50–140 (5) 92.00 \pm 32.71	60–140 (11) 88.09 \pm 23.54	80–160 (17) 110.59 \pm 21.64	100–150 (10) 120.00 \pm 18.86	50–160 (43) 104.86 \pm 25.49
	PrW	100–180 (5) 126.00 \pm 32.86	70–150 (11) 107.27 \pm 23.28	70–180 (17) 138.82 \pm 32.76	90–170 (10) 132.00 \pm 33.60	70–180 (43) 127.67 \pm 32.35
	OpL	70 (1)	50–80 (2) 65.00 \pm 21.21	40–100 (14) 83.57 \pm 14.99	100 (1)	40–100 (18) 81.67 \pm 16.18
	OpW	80 (1)	30–50 (2) 40.00 \pm 14.14	40–100 (14) 78.57 \pm 14.06	80 (1)	30–100 (18) 74.44 \pm 17.90
Kenozooids	KzL	170–480 (4) 285.00 \pm 135.28	120–380 (8) 272.50 \pm 106.34	220–390 (7) 302.86 \pm 86.93	340–580 (6) 471.67 \pm 87.27	120–580 (25) 330.80 \pm 125.43
	KzW	170–300 (4) 222.25 \pm 92.16	120–370 (8) 258.75 \pm 97.31	130–370 (7) 244.29 \pm 77.00	230–400 (6) 336.67 \pm 61.86	120–200 (25) 267.56 \pm 88.45
	OpD	40–60 (4) 45.00 \pm 10.00	20–50 (8) 31.25 \pm 11.26	30–80 (7) 50.00 \pm 22.04	20–60 (6) 40.00 \pm 17.89	20–80 (26) 41.15 \pm 17.51

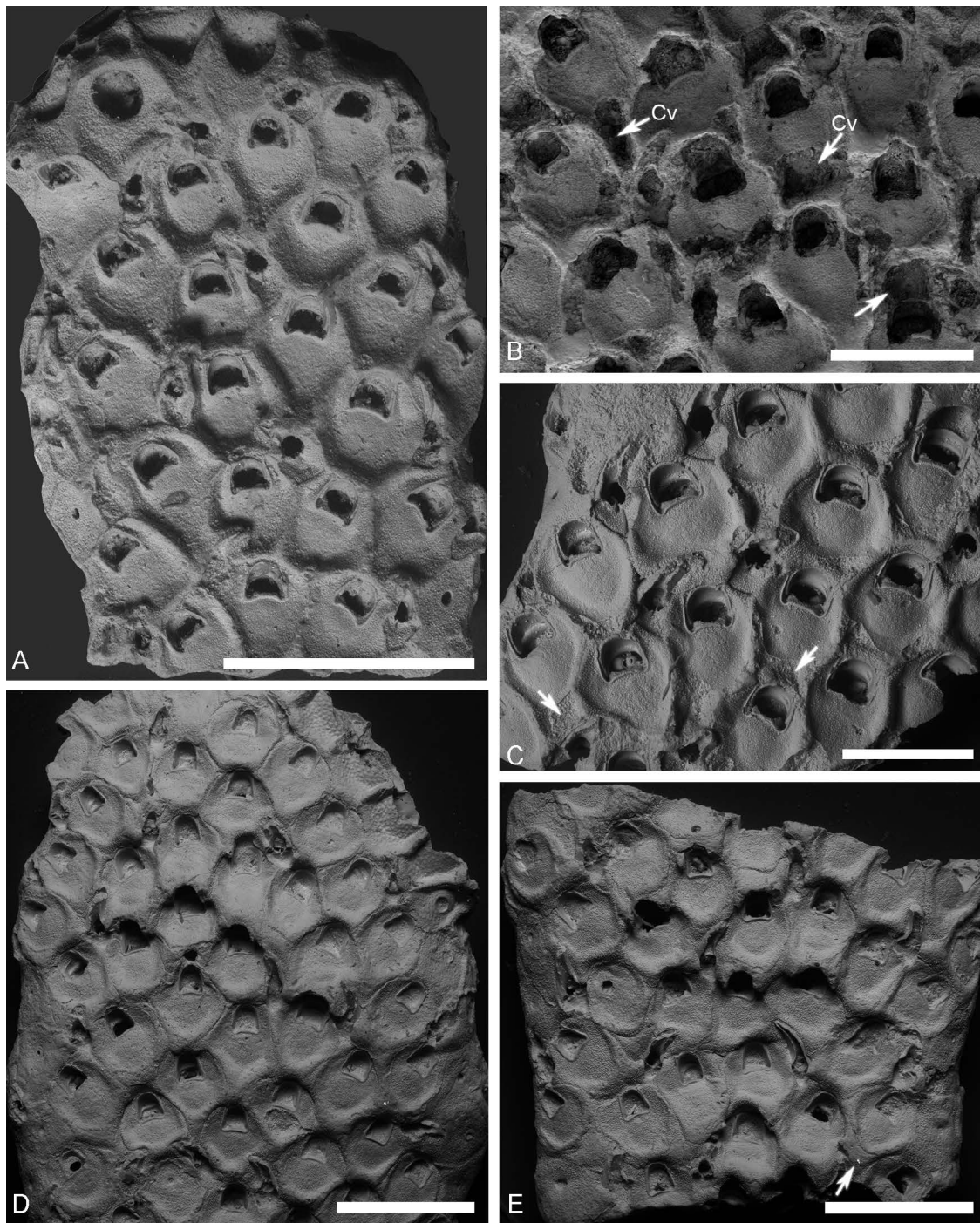


Fig. 13. *Rhagasostoma gibbosum* (Marsson, 1887). **A–C.** Erratic block of ?late Campanian age, quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region, Belarus. **A.** PIN 2922/218, overview of erect bifoliate colony showing autozooids, avicularia and kenozooids. **B.** PIN 2922/216, autozooids with proximal peripheral caverns (Cv) and broken oecium (arrowed), avicularia. **C.** PIN 2922/275, non-ovicellate autozooids with proximal caverns and avicularia. **D–E.** Late Campanian (*Belemnitella lanceolata* Zone), Emba River, Kazakhstan. **D.** PIN 5502/3058, overview of erect bifoliate colony showing autozooids (some ovicellate), avicularia and kenozooids. **E.** PIN 5502/3059, non-ovicellate and ovicellate autozooids, some with gymnocyst (arrowed), and avicularia. Scale bars: A, D–E = 1 mm; B–C = 500 μ m.

Other material

BELARUS • Grodno Region; erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно); PIN 2922/274.

Description

Colony erect, with flattened bifoliate branches (3–4 mm wide). Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad and subrectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst sometimes observed (Figs 12G, 13E). Cryptocyst extensive, finely pustulose, slightly depressed or slightly convex centrally, sometimes with proximal peripheral caverns (Fig. 13B, C). Opesia terminal, rarely subterminal, semielliptical with distal shelf, a thin inner wall delimiting the distolateral part of the opesia and a thickened, projecting outer wall delimiting the proximolateral part (Figs 12C, 13C). Proximal edge of opesia straight, smooth, thickened, with proximolateral outgrowths defining small opesiules at the corners; outgrowths often destroyed, giving opesiules the appearance of opesiular indentations. Septula not observed. Ovicells endozooidal, ooecium is formed by the distal zooid, well-recognizable, with cryptocyst-like surface and arch-like proximal edge with elongated proximolateral processes extending along the cryptocyst of the maternal zooid (Figs 12B, D, G, 13B, D–E). Avicularia interzooidal, smaller than autozooids, elongate. Rostrum channeled, symmetrical, with elevated wing-like walls and a pointed tip, rising above the surface of the colony and tilted to the right or left, rostral tip not reaching the opesia of the distal autozooid. Rostrum tilted over the proximal part of the distal autozooid or the ooecium of a maternal autozooid. Wedge-like structures present (Fig. 12B–D), extending from the base to the middle of the rostrum and partially covering the opesia, but often these structures are broken (Fig. 12E). Proximal part rounded, shorter and wider than rostrum, cryptocyst pustulose, concave, without peripheral caverns. Opesia roundish, with two short teeth proximally, opesiules lacking (Fig. 12E). Kenozooids subcircular, located along the branch margins (Fig. 12A). Cryptocyst finely pustulose, opesia roundish (Figs 12C, 13A, D–E). Intramural reparative kenozooidal buds sometimes observed within host autozooids and avicularia (Fig. 13D–E), all with the same polarity as the host zooid. Closure plates, intramural reparative budding autozooids and avicularia not observed.

Remarks

The type material of *Rhagasostoma gibbosum* (Marsson, 1887) could not be found, although part of the Marsson Collection has recently been recovered (Martha 2014). From the similar species *R. tchvanovi* (Favorskaya, 1992), *R. gibbosum* differs in having a rostrum that is short and tilted to the right or left instead of being long and almost straight. *Rhagasostoma gibbosum* can be distinguished from *R. gibbosulum* by the slightly convex border of the cryptocyst and the very rare presence of a gymnocystal portion.

Distribution

Late Campanian Belarus: Quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region. Kazakhstan: Emba River. Early Maastrichtian United Kingdom: Trimmingham, Norfolk, England. Germany: Saturn quarry near Krons Moor, Schleswig-Holstein, Island of Rügen, Mecklenburg-Vorpommern. Maastrichtian: unspecified localities in Denmark.

Rhagasostoma gibbosulum Brydone, 1936

Fig. 14, Table 8

Rhagasostoma gibbosulum Brydone, 1936: 74, pl. 36, fig. 1.

Material studied**Holotype**

UNITED KINGDOM • England, High Down; middle Campanian (*Belemnitella mucronata* Zone) of Isle of Wight; SM B36887 (Fig. 14A–D; figured by Brydone 1936: pl. 36, fig. 1).

Table 8. Summary of measurements of *Rhagasostoma gibbosulum* Brydone, 1936. For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Southern North Sea Basin	North German Basin	Polish Basin	Total
	Stratigraphy	Early Maastrichtian	Early Maastrichtian	?Late Campanian	
	Locality	Norfolk	Kronsmoor	Grodno Region	
Autozooids	AzL	330–510 (6) 420.00 \pm 75.37	410–880 (18) 558.33 \pm 108.97	390–480 (6) 435.00 \pm 32.09	330–880 (30) 506.00 \pm 111.31
	AzW	240–320 (6) 283.33 \pm 27.33	320–520 (18) 416.11 \pm 45.26	260–360 (6) 316.67 \pm 35.02	240–520 (30) 369.67 \pm 70.73
	OpL	80–110 (6) 100.00 \pm 12.65	80–140 (18) 108.89 \pm 16.05	90–130 (6) 106.67 \pm 13.66	80–140 (30) 106.67 \pm 14.93
	OpW	110–140 (6) 126.67 \pm 13.66	110–150 (18) 131.67 \pm 14.65	120–130 (6) 126.67 \pm 5.16	110–150 (30) 129.67 \pm 12.99
	GL	60–130 (6) 100.00 \pm 29.66	50–370 (18) 152.78 \pm 79.40	50–120 (3) 80.00 \pm 36.06	50–370 (27) 132.96 \pm 72.37
	OoL		260–270 (3) 263.33 \pm 5.77		260–270 (3) 263.33 \pm 5.77
	OoW	Not observed	230–360 (3) 293.33 \pm 65.06	Not observed	230–360 (3) 293.33 \pm 65.06
Avicularia	AvL	160–270 (6) 226.67 \pm 37.24	250–470 (14) 367.86 \pm 76.98	320–390 (6) 320.00 \pm 47.33	160–470 (26) 324.23 \pm 84.62
	RL	90–180 (6) 141.67 \pm 32.51	170–390 (14) 267.14 \pm 69.22	140–240 (6) 193.33 \pm 39.83	90–390 (26) 221.15 \pm 76.85
	W–ISL	Not observed	140–190 (6) 160.00 \pm 16.73	Not observed	140–190 (6) 160.00 \pm 16.73
	RW	70–140 (6) 93.33 \pm 25.03	70–140 (14) 105.71 \pm 20.65	80–120 (6) 98.33 \pm 14.72	70–140 (26) 101.15 \pm 20.46
	PrL	70–140 (6) 95.00 \pm 25.88	70–190 (14) 114.29 \pm 33.22	70–140 (6) 105.00 \pm 26.65	70–190 (26) 107.69 \pm 30.24
	PrW	60–130 (6) 91.67 \pm 29.27	70–150 (14) 104.29 \pm 23.11	90–130 (6) 101.67 \pm 16.02	60–150 (26) 100.77 \pm 22.96
	OpL		40–80 (8) 61.25 \pm 12.46	40–80 (4) 55.00 \pm 19.15	40–80 (12) 59.17 \pm 14.43
OpW	Not observed	30–70 (8) 52.50 \pm 16.69	40–70 (4) 47.50 \pm 15.00	30–70 (12) 50.83 \pm 15.64	
Kenozooids	KzL	380–400 (2) 390 \pm 14.14	180–370 (14) 261.43 \pm 67.24	130–270 (4) 207.50 \pm 64.49	130–400 (20) 263.50 \pm 78.15
	KzW	270–300 (2) 285.00 \pm 21.21	180–390 (14) 272.86 \pm 69.99	130–200 (4) 172.50 \pm 29.86	130–390 (20) 254.00 \pm 72.65
	OpD	20–30 (2) 25.00 \pm 7.07	20–40 (15) 24.67 \pm 6.40	20–60 (4) 30.00 \pm 20.00	20–60 (21) 25.71 \pm 9.78

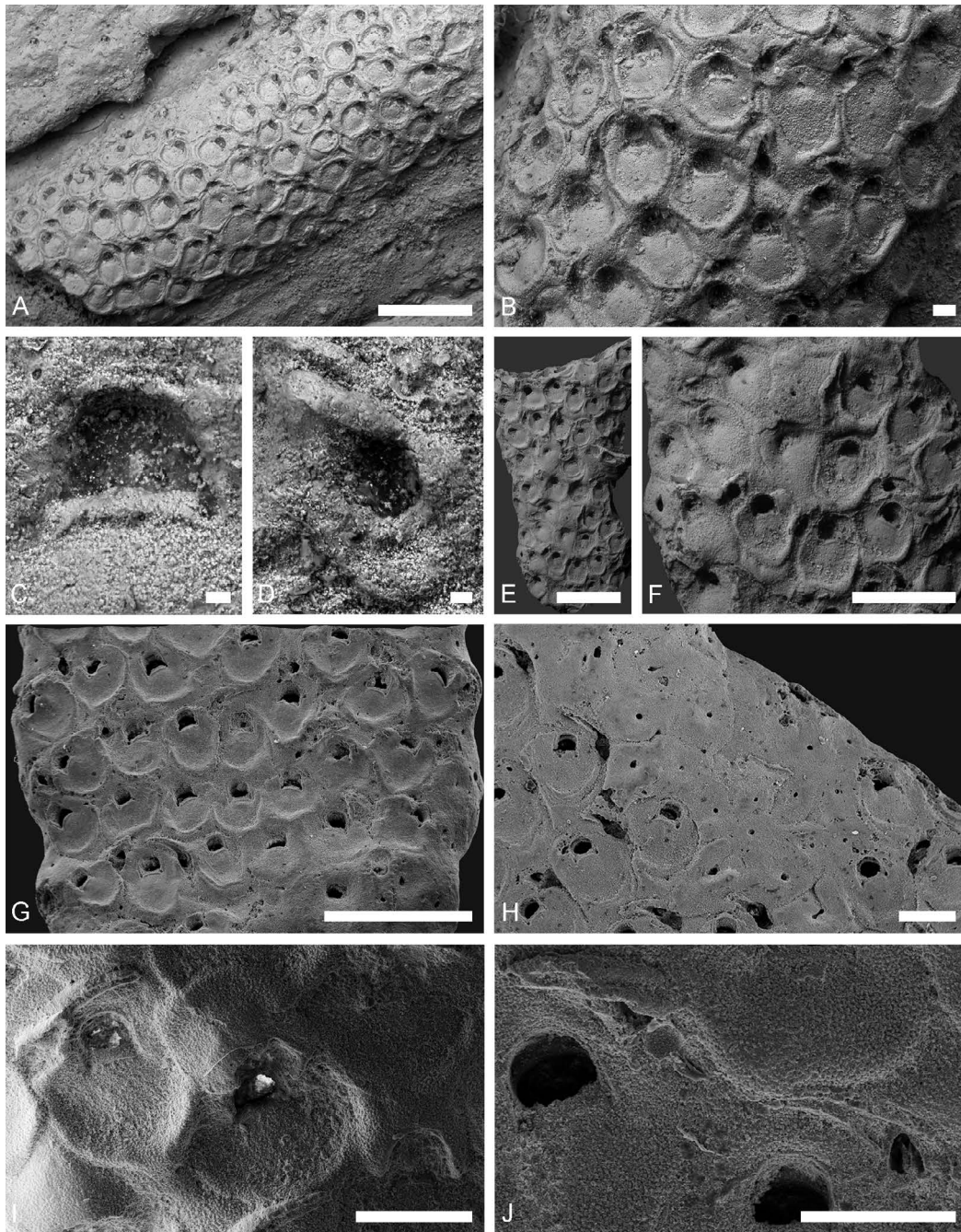


Fig. 14. *Rhagasostoma gibbosulum* Brydone, 1936. **A–D.** Holotype, SM B36887, middle Campanian (*Belemnitella mucronata* Zone) of Isle of Wight, High Down, England, UK. **A.** Overview of erect bifoliate colony. **B.** Non-ovicellate autozooids and avicularia. **C.** Opesia of autozooid. **D.** Avicularium. **E–F.** PIN 2922/242, erratic block of ?late Campanian age, quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region, Belarus. **E.** Overview of erect bifoliate colony. **F.** Non-ovicellate autozooids and avicularia. **G–J.** Early Maastrichtian, Saturn quarry near Krons Moor, Schleswig-Holstein, Germany. **G.** SMF 29908, overview of part of erect bifoliate colony. **H.** SMF 29909, autozooids, avicularia and kenozooids. **I.** SMF 29911, non-ovicellate autozooid with long gymnocyst(?), two ovicellate autozooids (with non-damaged ooecium to the right), and avicularium with wedge-like growth. **J.** SMF 29912, non-ovicellate autozooids and avicularia, one from which with wedge-like growth. Scale bars: A, E, G = 1 mm; B = 100 μ m; C–D = 20 μ m; F = 500 μ m, H–J = 300 μ m.

Additional figured material

BELARUS • Grodno Region; erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно); PIN 2922/242 (Fig. 14E–F).

GERMANY • 4 specs; Schleswig-Holstein, Saturn quarry near Kronsmoor; early Maastrichtian; SMF 29908 (Fig. 14G), 29909 (Fig. 14H), 29911 (Fig. 14I), 29912 (Fig. 14J).

Other material

GERMANY • 2 specs; same data as for preceding; SMF 29910, 29913.

Description

Colony erect, with flattened bifoliate branches (1–6 mm wide). Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad and roundish; zooidal boundaries raised. Gymnocyst? present proximolaterally, smooth (Fig. 14B, G, I), but usually not visible. Cryptocyst extensive, finely pustulose, usually slightly convex centrally. Opesia terminal or subterminal, semielliptical, delineated by two walls, a thin inner wall forming the distolateral rim and a projecting and thickened outer wall forming the proximolateral rim. Proximal edge of opesia straight, smooth, with outgrowths at the two proximolateral corners delineating small opesiules; outgrowths often destroyed, giving the opesiules the appearance of opesiular indentations (Fig. 14C, I–J). Septula not observed. Ovicells endozooidal, oecium is formed by the distal zooid, well-recognizable, with cryptocyst-like surface and arch-like proximal edge with elongated proximolateral processes extending along the cryptocyst of the maternal zooid (Fig. 14I). Avicularia interzooidal, smaller than autozooids, elongate. Rostrum channeled, asymmetrical, rarely symmetrical, with elevated wing-like walls and a pointed tip, rising above the surface of the colony and tilted to the right or left, rostral tip not reaching the opesia of distal autozooid. Rostrum tilted over gymnocyst of the distal autozooid or oecium. Wedge-like structures present (Fig. 14I–J), extending from the base to the middle of the rostrum and partially covering the opesia, but often these structures are broken (Fig. 14D). Proximal part of avicularium rounded, shorter and wider than rostrum, cryptocyst pustulose, concave, but often not visible. Opesia round with two short teeth proximally, opesiules lacking (Fig. 14J). Kenozooids sometimes numerous, located along edges of branches, roundish (Fig. 14H). Cryptocyst finely pustulose. Opesia round. Intramural reparative kenozooidal buds in host autozooids sometimes observed (Fig. 14B), all with the same polarity as the host zooid. Closure plates and intramural reparative budding of autozooids and avicularia not observed.

Remarks

Rhagasostoma gibbosulum can be distinguished from *R. gibbosum* by the convex border of the cryptocyst and the inferred, well-developed gymnocyst.

Distribution

Middle Campanian United Kingdom: High Down, Isle of Wight, England. Late Campanian Belarus: Quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region. Early Maastrichtian Germany: Saturn quarry, near Kronsmoor, Schleswig-Holstein.

Rhagasostoma tchvanovi (Favorskaya, 1992)

Fig. 15, Table 9

Onychocella tchvanovi Favorskaja, 1992: 126, pl. 68, figs 6–8.

?*Rhagasostoma gibbosum* var. *weyournensis* Brydone, 1930: 48, pl. 26, fig. 12.

non *Rhagasostoma gibbosum* var. *weyournensis* – Brydone 1930: 48, pl. 26, figs 13–14.

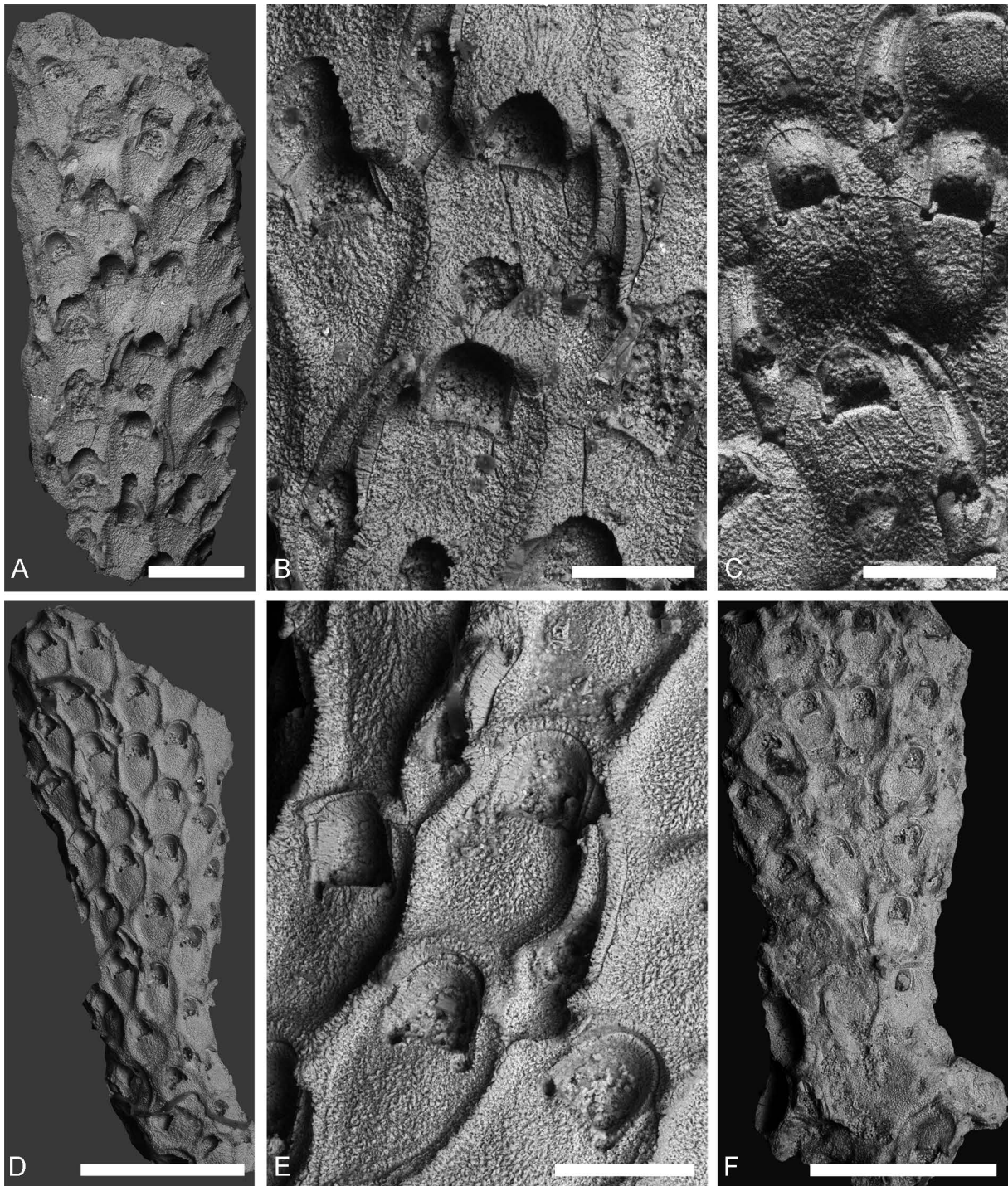


Fig. 15. *Rhagasostoma tchvanovi* (Favorskaya, 1992). **A–E.** Late Campanian (*Cibicidoides voltzianus* Zone; LS15), southern Aral Sea Region, Republic of Karakalpakstan, Uzbekistan. **A–C.** Holotype, TsNIGR Museum 33/12582. **A.** Overview of erect bifoliate colony. **B.** Ovicellate autozooids and avicularia. **C.** Non-ovicellate autozooids and avicularia. **D–E.** TsNIGR Museum 34/12582. **D.** Overview erect bifoliate of colony. **E.** Non-ovicellate autozooids and avicularia. **F.** TsNIGR Museum 32/12582, middle Campanian (*Brotzenella monterelensis* Zone; LS14), southern Aral Sea Region, Republic of Karakalpakstan, Uzbekistan; overview of erect bifoliate colony, cryptocyst of autozooids with proximolateral caverns. Scale bars: A = 500 µm; B, E = 200 µm; C = 250 µm; D, F = 1 mm.

Table 9. Summary of measurements of *Rhagasostoma tchvanovi* (Favorskaya, 1992). For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

Basin	North Ust-Yurt–Aral Basin
Stratigraphy	Early to middle late Campanian
Locality	Southern Aral Sea Region
Autozooids	AzL 340–550 (18) 418.89 \pm 50.98
	AzW 230–360 (18) 264.44 \pm 22.29
	CvL 70–100 (4) 80 \pm 14.14
	OpL 110–140 (14) 127.86 \pm 9.75
	OpW 110–140 (14) 120.00 \pm 2.96
	OoL 140–230 (5) 198.00 \pm 35.64
	OoW 180–230 (5) 210.00 \pm 18.71
	AvL 290–530 (11) 381.82 \pm 71.25
Avicularia	RL 160–350 (11) 254.55 \pm 58.20
	RW 80–120 (11) 93.64 \pm 13.62
	PrL 110–190 (10) 137.00 \pm 25.84
	PrW 70–120 (11) 94.55 \pm 17.53
	OpL 70–100 (8) 77.50 \pm 10.35
	OpW 30–70 (8) 53.75 \pm 11.88

Material studied

Holotype

UZBEKISTAN • Republic of Karakalpakstan; late Campanian (*Cibicidoides voltzianus* Zone; LS15) of the southern Aral Sea Region; TsNIGR Museum 33/12582 (Fig. 15A–C; figured by Favorskaya 1992: pl. 68, fig. 6).

Additional figured material

UZBEKISTAN • Same data as for holotype; TsNIGR Museum 34/12582 (Fig. 15D–E; figured by Favorskaya 1992: pl. 68, fig. 7) • Republic of Karakalpakstan; middle Campanian (*Brotzenella monterelensis* Zone; LS14) of the southern Aral Sea Region; TsNIGR Museum 32/12582 (Fig. 15F).

Description

Colony erect with flattened bifoliate branches (3–4 mm wide). Ancestrula and early astogeny not observed. Autozooids variable in shape, often broad and subrectangular with rounded distal ends; zooidal boundaries raised. Gymnocyst lacking. Cryptocyst extensive, finely pustulose, slightly depressed centrally, sometimes with proximolateral peripheral caverns (Fig. 15F). Opesia terminal, semielliptical, formed by two walls, a thin inner wall forms the distolateral part of the opesia, and a projecting thickened outer wall forms the proximolateral part (Fig. 15C, E). Proximal edge of opesia straight, smooth, with outgrowths at the two proximolateral corners which delineate small opesiules; outgrowths often destroyed giving the opesiules the appearance of opesiular indentations. Septula not observed. Ovicells endozooidal, oecium is formed by the distal zoid, well-recognizable, with cryptocyst-like surface and arch-like proximal edge with elongated proximolateral processes extending along the cryptocyst of the maternal zoid (Fig. 15A–B). Avicularia interzooidal, smaller than autozooids, elongate. Rostrum channeled with elevated wing-like walls and pointed tip, narrow, almost straight, asymmetrical, dextral or sinistral. Top of rostrum reaches opesia of distal autozoid. Wedge-like structures not observed. Proximal part rounded, shorter and wider than rostrum, cryptocyst pustulose, concave. Opesia round with short slit proximally, opesiules lacking (Fig. 15C). Closure plates, kenozooids, intramural reparative budding of autozooids and avicularia not observed.

Remarks

Rhagasostoma tchvanovi differs from the closely related species *R. gibbosum* in the avicularian rostrum being long and almost straight instead of short and tilted to the right or left. The specimen described by Brydone (1930: pl. 26, fig. 12) as *Onychocella gibbosum weybournensis* differs from *R. gibbosum* (Marsson, 1887) in having a long and straight avicularian rostrum and is conspecific with *R. tchvanovi*. Specimen 32/12582 in the collections of the TsNIGR Museum and labelled as “*O. subgibbosum* Brydone, 1930” is not the one that was depicted by Favorskaya (1992: pl. 67, fig. 3) and belongs to *R. tchvanovi*.

Distribution

Middle to late Campanian Republic of Karakalpakstan, Uzbekistan: six localities between Chimboy/Shimbay (Чимбой/Шымбай) and the Aral Sea.

Rhagasostoma rowei (Brydone, 1906)

Figs 16–18, Table 10

?*Eschara ampullacea* von Hagenow, 1839: 264.

?*Eschara volgensis* Eichwald, 1865: 193. **Syn. nov.**

Eschara rowei Brydone, 1906: 296, fig. 6.

Eschara delarueana – ?Marsson 1887: 69.

Eschara rowei – Brydone 1906: 296, fig. 6. — Brydone 1913: 249, pl. 8, fig. 12.

Onychocella (*Eschara*) cf. *delarueana* – Voigt 1925: pl. 1, fig. 15.

Onychocella rowei – Brydone 1930: pl. 28, fig. 3. — Voigt 1930: 455, pl. 15, fig. 11. — Voigt 1959: 9. — Voigt 1967: 41, pl. 18, figs 2–3. — Favorskaya 1996: pl. 4, fig. 1. — Koromyslova 2014a: pl. 9, figs 1–7, text-figs 1–4.

Woodipora mimosa (Brydone, 1930) – Voigt 1967: 50, pl. 18, fig. 4.

Woodipora rowei – Schubert 1986 pars: 39, pl. 3, figs 5–6, 8, pl. 5, figs 1–3, 6–8, pl. 8, fig. 1.

non *Eschara delarueana* d'Orbigny, 1851: 105, pl. 602, fig. 6–8, pl. 673, fig. 8

non *Woodipora rowei* – Schubert 1986 pars: 39, pl. 3, fig. 7, pl. 5, figs 4–5, pl. 8, figs 2–3.

Material studied

Holotype

UNITED KINGDOM • England, Norfolk, Trimmingham; early Maastrichtian (*Ostrea lunata* Zone); SM B36113 (Fig. 16C; not figured by Brydone 1906).

Additional figured material

RUSSIAN FEDERATION • 2 specs; Ulyanovsk Region; Late Cretaceous; PSM PSU 2/187 (Fig. 16A; figured by Eichwald 1868: pl. 8, fig. 9), MMI 15/49 (Fig. 16B; figured by Lahusen 1873: pl. 4, fig. 4).

UNITED KINGDOM • 2 specs; same data as for holotype; SM B36260 (Fig. 16D–E; figured by Brydone 1913: pl. 8, fig. 12), B36697 (Fig. 16F–G; labeled as *O. mimosa* in the Brydone Collection).

BELARUS • Grodno Region; erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно); PIN 2922/204 (Fig. 16H; figured by Koromyslova 2014a: pl. 9, fig. 6).

BELGIUM • Harmignies near Mons; late Campanian; SMF 29924 (Fig. 17A–B).

UZBEKISTAN • Southern Aral Sea Region; late Campanian, *Cibicidoides voltzianus* Zone; TsNIGR Museum 26/12939 (Fig. 17C; figured by Favorskaya 1996: pl. 4, fig. 1).

TURKMENISTAN • Western Kopetdag; late Campanian; TsNIGR Museum 35/9757 (Fig. 17D–E; figured by Voigt 1967: pl. 18, fig. 3) • Tuarkyr; late Maastrichtian; TsNIGR Museum 36/9757 (Fig. 18E; figured by Voigt 1967: pl. 18, fig. 2) • Western Kopetdag; late Maastrichtian; TsNIGR Museum 32/9757 (Fig. 18I; figured by Voigt 1967: pl. 18, fig. 4).

KAZAKHSTAN • Emba River; late Campanian (*Belemnitella lanceolata* Zone); PIN 5502/3051 (Fig. 17F–G) • 2 specs; Mangyshlak Peninsula; Maastrichtian; PIN 3421/1009 (Fig. 18F–G), 3421/1008 (Fig. 18H) • Northern Aral Sea Region; Maastrichtian; PIN 5502/3050 (Fig. 18J).

GERMANY • 2 specs; Rügen; early Maastrichtian; SMF 29931 (Fig. 17H–I), 29932 (Fig. 18A) • Hamburg-Hummelsbüttel; former brick factory; late Maastrichtian; SMF 29933 (Fig. 18D).

DENMARK • Island of Møn; early Maastrichtian; SMF 29925 (Fig. 18B–C).

Other material

BELARUS • 15 specs; Grodno Region; erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно); PIN 2922/200 (figured by Koromyslova 2014a: pl. 9, fig. 1), 2922/201 (figured by Koromyslova 2014a: text-fig. 1c), 2922/208 (figured by Koromyslova 2014a: pl. 9, fig. 7), 2922/210 (figured by Koromyslova 2014a: pl. 9, fig. 3, text-figs 1a, b, 2), 2922/223 (figured by Koromyslova 2014a: pl. 9, fig. 5, text-figs 1g, 3a), 2922/224 (figured by Koromyslova 2014a: pl. 9, fig. 4, text-fig. 4e),

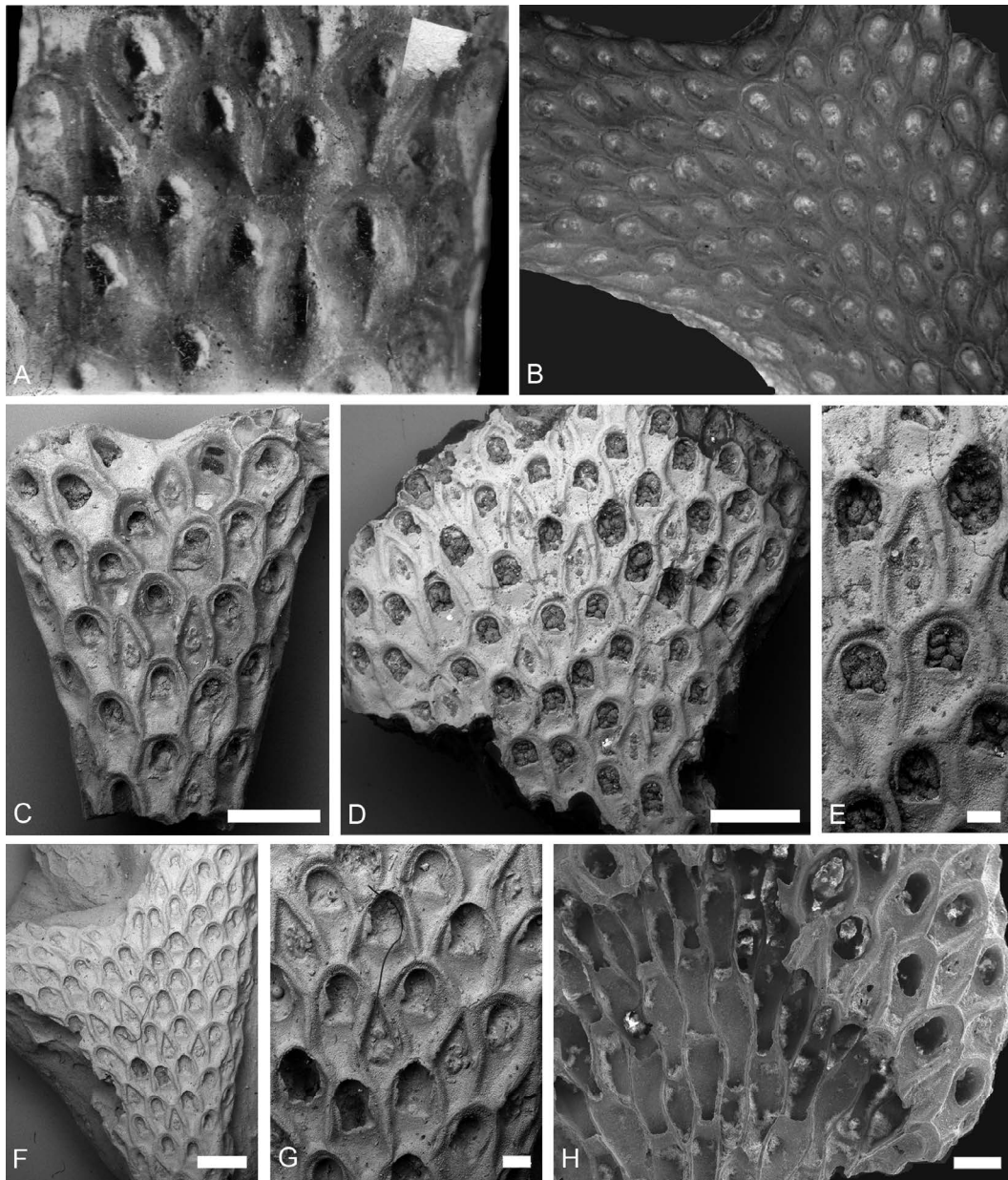


Fig. 16. *Rhagasostoma rowei* (Brydone, 1906). **A–B.** Late Cretaceous, Ulyanovsk Region, Russian Federation. **A.** PSM PSU 2/187, this specimen, which is the original figured by E. Eichwald (1868: pl. 8, fig. 9) as *Eschara volgensis* Eichwald, 1865, could not be traced but is represented by this photograph taken by E. Voigt in 1963; overview of part of erect bifoliate colony showing autozooids and avicularia. **B.** MMI 15/49, the specimen from Yazykov, which is the original figured by I.I. Lahusen (1873: pl. 4, fig. 4) as *Eschara volgensis* Eichwald, 1865; overview of erect bifoliate stem-like then dichotomously branching colony. **C–G.** Early Maastrichtian (*Ostrea lunata* Zone), Trimmingham, Norfolk, England, UK. **C.** Holotype, SM B36113, overview of erect bifoliate stem-like then dichotomously branching colony. **D–E.** Paratype, SM B36260. **D.** Overview of fan-like part of bifoliate colony. **E.** Autozooids and avicularia. **F–G.** SM B36697, specimen labelled as *O. mimosa* from the Brydone Collection. **F.** Overview of erect bifoliate stem-like then dichotomously branching colony. **G.** Non-ovicellate and two ovicellate (in the left lower corner) autozooids and avicularia. **H.** 2922/204, from an erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region, Belarus, view of undersides of zooidal frontal walls. Scale bars: A–B without scale bars; C–D, F = 1 mm; E, G = 200 μ m; H = 300 μ m.

2922/226 (figured by Koromyslova 2014a: text-fig. 4d), 2922/227, 2922/234 (figured by Koromyslova 2014a: text-fig. 1d), 2922/231, 2922/255 (figured by Koromyslova 2014a: text-fig. 4ac), 2922/256 (figured by Koromyslova 2014a: text-fig. 4h), 2922/257 (figured by Koromyslova 2014a: text-fig. 4f), 2922/268, 2922/279 (figured by Koromyslova 2014a: pl. 9, fig. 2).

KAZAHKSTAN • 4 specs; Emba River; late Campanian (*Belemnitella lanceolata* Zone); PIN 5502/3052 to 3055 • Mangyshlak Peninsula; Maastrichtian; PIN 3421/1006.

GERMANY • 5 specs; Rügen; early Maastrichtian; SMF 29926 to 29930 • 4 specs; Tornesch; late Maastrichtian; SMF 29935 to 29938 • Hamburg-Hummelsbüttel; former brick factory; late Maastrichtian; SMF 29934.

Description

Colony rigidly erect, bifoliate, multiseriate, branches 2.0–10.0 mm wide. Ancestrula and early astogeny not observed. Colony formed by pyriform and ovate autozooids and vicarious avicularia. Autozooids subrectangular with rounded distal ends; zooidal boundaries raised. Pyriform autozooids with a narrow proximal end, widening distally, the widening usually starting from the proximal margin of the opesia. In ovate autozooids, the proximal end is partly overlapped by the avicularian rostrum and the autozoid begins to widen considerably below the proximal margin of the opesia, usually at the boundary with an avicularium. Gymnocyst lacking. Cryptocyst slightly granulated, slightly depressed centrally and occupying half or more of the frontal surface of the autozoid, peripheral caverns lacking. Opesia terminal or subterminal. Opesial rim elevated, formed by projecting cryptocyst, bell-shaped due to small lateral projections (occlusor lamina) and opesicular indentations, between which there is a short or long, tongue-like projection of cryptocyst (Figs 16A, C, E, 17G, 18H–I), often broken, in which case the opesicular indentations are poorly defined and the proximal edge of the opesia is almost straight. In the complete absence of lateral projections and tongue the opesiae are subcircular (Figs 17C–E, H, 18A–B, D–G). Distal walls with two septula (Fig. 16H); septula in lateral walls not observed. Ovicells immersed, ooecia vestigial formed by the distal zooid, vizor-like, with slightly granulated surface, not protruding above colony surface (Figs 16G, 17C, E, G, 18G, I). Avicularia vicarious, rhomboidal. Rostrum conical in outline and symmetrical, usually with straight lateral walls; indentations or projections present at the rostral base. Three types of avicularia differing mainly in the length of the rostrum and rostral apex which partly overlaps the proximal end of the distal autozoid: avicularia with long rostra and long trough-like apices (130–210 µm); avicularia with short rostra and short trough-like apices (0–130 µm); and avicularia with rostra without projecting apices. Proximal part short, narrowing downwards, with convex lateral sides. Entire frontal surface of avicularium occupied by a fragile, slightly granulated cryptocyst containing five openings: two small, subcircular openings, distally and proximally, in between three slit-like, parallel openings (Figs 17I, 18G). Cryptocyst between openings frequently destroyed causing them to coalesce into a single opening of variable outline. Intramural reparative budding of autozooids and closure plates not observed. Intramural reparative budding of avicularia may be present in some or all avicularia depending on the colony (see Koromyslova 2014a), they are observed within host avicularia, numbering as many as three intramural buds, all apparently having the same polarity as the host avicularium.

Kenozooids not observed. Both the inner and outer sides of branches of colonies show concentrations of autozooids in which the opesiae are subcircular and the proximal part is shortened or completely absent, and deformed avicularia that are irregularly ovate to rhomboidal in shape and possess an elongated opening at the centre.

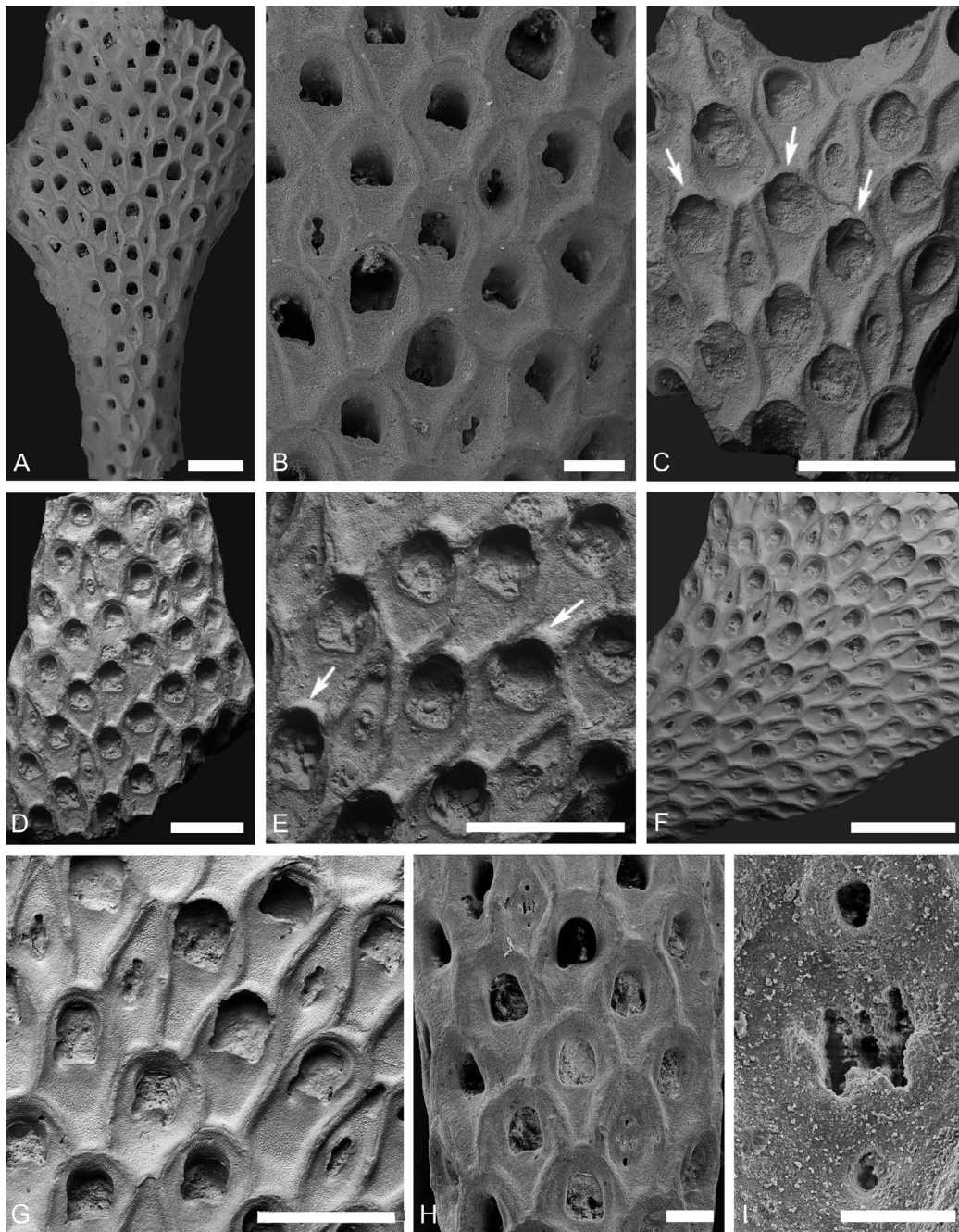


Fig. 17. *Rhagasostoma rowei* (Brydone, 1906). **A–B.** SMF 29924, late Campanian, Harmignies near Mons, Belgium. **A.** Overview of erect bifoliolate colony. **B.** Autozooids and avicularia. **C.** TsNIGR Museum 26/12939, late Campanian, *Cibicidoides voltzianus* Zone, Uzbekistan, southern Aral Sea Region, erect bifoliolate colony showing ovicellate (oecia arrowed) and non-ovicellate autozooids and avicularia. **D–E.** TsNIGR Museum 35/9757, late Campanian, western Kopetdag, Turkmenistan. **D.** Erect bifoliolate colony. **E.** Ovicellate autozooids (some oecia arrowed) and avicularia. **F–G.** PIN 5502/3051, late Campanian (*Belemnitella lanceolata* Zone), Kazakhstan, Emba River. **F.** Overview of erect bifoliolate stem-like then dichotomously branching colony. **G.** Ovicellate and non-ovicellate autozooids and avicularia. **H–I.** SMF 29931, early Maastrichtian, Rügen, Germany. **H.** Overview of erect bifoliolate stem-like colony. **I.** Opesia and opesiules of avicularium. Scale bars: A, C–E, G = 1 mm; F = 2 mm; B, H = 300 µm; I = 100 µm.

Table 10 (continued on next page). Summary of measurements of *Rhagasostoma rowei* (Brydone, 1906). For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

Basin	Southern North Sea Basin	North German Basin	Swedish–Danian Basin	Polish Basin	North Ust–Yurt–Aral Basin	Mangyshlak–East Caspian Basin	Tethys		
Stratigraphy	Late Campanian to early Maastrichtian	Maastrichtian	Early Maastrichtian	?Late Campanian	Late Campanian to Maastrichtian	Maastrichtian	Late Campanian to Maastrichtian	Total	
Locality	Norfolk, Harmignies near Mons	Rugen, Tornesch, Hummels–büttel	Island of Møn	Grodno Region	Emba River, Aral Sea Region	Mangyshlak Peninsula	Tuarkyr, West Kopetdag		
pyriform	AzL	700–1040 (20) 840.00 \pm 88.62	730–1300 (36) 943.06 \pm 140.42	820–1150 (6) 966.67 \pm 113.61	550–990 (36) 740.28 \pm 119.77	700–1130 (22) 907.27 \pm 127.29	710–1070 (18) 915.78 \pm 94.77	840–1200 (18) 1027.22 \pm 151.92	550–1300 (156) 885.47 \pm 153.23
	AzW	370–550 (20) 454.00 \pm 52.36	370–580 (36) 481.94 \pm 59.61	450–490 (6) 465.00 \pm 13.78	270–580 (36) 364.17 \pm 59.49	380–740 (22) 530.91 \pm 103.32	390–700 (18) 544.44 \pm 91.99	420–750 (18) 551.67 \pm 85.08	270–750 (156) 472.69 \pm 98.58
	OpL	220–410 (20) 311.00 \pm 61.46	190–460 (36) 318.61 \pm 56.78	280–360 (6) 300.00 \pm 56.21	240–400 (33) 304.24 \pm 43.88	290–410 (16) 355.00 \pm 30.77	210–390 (18) 312.22 \pm 51.05	250–450 (17) 359.41 \pm 56.84	190–460 (146) 321.51 \pm 54.54
	OpW	160–280 (20) 224.50 \pm 34.10	140–310 (36) 231.11 \pm 34.87	210–240 (6) 228.33 \pm 9.83	180–250 (33) 216.67 \pm 22.59	210–390 (16) 303.13 \pm 48.82	210–350 (18) 273.89 \pm 43.40	230–390 (17) 295.88 \pm 47.18	140–390 (146) 247.53 \pm 48.46
ovate	AzL	620–960 (19) 821.05 \pm 104.93	740–1230 (21) 840.48 \pm 109.52	680–880 (4) 782.50 \pm 81.80	490910 (34) 695.59 \pm 91.09	690–1080 (16) 911.88 \pm 104.32	760–950 (15) 854.00 \pm 48.52	700–1200 (12) 952.50 \pm 164.82	490–1230 (121) 817.02 \pm 133.22
	AzW	400–550 (19) 478.42 \pm 38.48	390–610 (19) 506.32 \pm 66.01	540–610 (4) 575.00 \pm 35.12	310–530 (34) 392.06 \pm 44.09	450–660 (16) 570.63 \pm 66.48	400–640 (15) 542.67 \pm 76.01	530–630 (12) 576.67 \pm 36.76	310–660 (119) 491.85 \pm 88.92
	OpL	160–400 (14) 295.00 \pm 64.30	180–390 (18) 305.00 \pm 47.68	270–350 (4) 310.00 \pm 33.67	240–430 (21) 293.81 \pm 47.38	280–420 (14) 342.14 \pm 42.28	240–380 (12) 321.67 \pm 39.50	240–430 (9) 343.33 \pm 60.62	160–430 (92) 312.72 \pm 51.89
	OpW	160–290 (14) 230.00 \pm 32.82	200–300 (18) 237.22 \pm 24.45	230–260 (4) 247.50 \pm 12.58	180–280 (21) 214.29 \pm 25.99	230–360 (14) 285.00 \pm 38.78	210–330 (12) 276.67 \pm 37.25	230–370 (9) 281.11 \pm 50.61	160–370 (92) 248.04 \pm 42.30
OoL	30–80 (8) 52.50 \pm 15.81	Not observed	60–90 (2) 75.00 \pm 21.21	30–80 (21) 52.86 \pm 12.31	40–80 (10) 64.00 \pm 15.78	50–90 (10) 70.00 \pm 17.00	60–100 (7) 81.43 \pm 14.64	30–100 (58) 61.90 \pm 17.52	
OoW	150–300 (8) 225.00 \pm 47.21		220–250 (4) 235.00 \pm 21.21	130–280 (21) 194.76 \pm 46.43	170–350 (10) 294.00 \pm 57.58	200–320 (10) 266.00 \pm 40.88	180–270 (7) 238.57 \pm 31.32	130–350 (58) 235.00 \pm 57.62	
TL	30–80 (16) 59.38 \pm 16.92	0–50 (36) 2.50 \pm 10.52	Not observed	0–70 (29) 12.07 \pm 20.59	0–130 (24) 47.50 \pm 45.61	0–170 (18) 66.11 \pm 55.85	0–190 (18) 43.33 \pm 65.53	0–190 (147) 30.95 \pm 44.03	
TW	100–150 (16) 123.13 \pm 17.02	100–180 (2) 140 \pm 56.57	Not observed	80–170 (9) 123.33 \pm 25.98	150–240 (14) 185.71 \pm 27.93	120–230 (12) 162.50 \pm 29.58	90–180 (6) 145.00 \pm 33.91	80240 (59) 148.90 \pm 36.16	

Table 10 (continued).

Basin	Southern North Sea Basin	North German Basin	Swedish–Danian Basin	Polish Basin	North Ust-Yurt–Aral Basin	Mangyshlak–East Caspian Basin	Tethys	Total	
Stratigraphy	Late Campanian to early Maastrichtian	Maastrichtian	Early Maastrichtian	?Late Campanian	Late Campanian to Maastrichtian	Maastrichtian	Late Campanian to Maastrichtian	Total	
Locality	Norfolk, Harmignies near Mons	Rugen, Tornesch, Hummels-büttel	Island of Møn	Grodno Region	Emba River, Aral Sea Region	Mangyshlak Peninsula	Tuarkyr, West Kopetdag	Total	
Avicularia	AvL	670–940 (17) 833.53 ± 91.65	710–1030 (26) 885.77 ± 84.15	830–960 (5) 906.00 ± 47.75	640–1050 (45) 841.56 ± 117.43	690–1130 (17) 944.12 ± 126.69	940–1120 (18) 970.00 ± 73.48	900–1110 (15) 1087.33 ± 151.87	640–1130 (143) 905.03 ± 132.08
	RL	420–580 (17) 504.71 ± 42.30	410–630 (26) 532.31 ± 54.50	520–590 (5) 554.00 ± 28.81	340–730 (46) 532.61 ± 91.64	360–690 (17) 565.29 ± 100.57	490–700 (18) 566.11 ± 64.73	460–700 (15) 618.67 ± 71.70	340–730 (144) 547.01 ± 80.39
	ARL	0–100 (17) 28.24 ± 41.11	0–110 (26) 15.00 ± 32.28	0 (5)	0–210 (44) 74.09 ± 73.62	0–110 (18) 29.44 ± 38.42	0–110 (18) 54.44 ± 46.17	0–160 (14) 42.86 ± 62.19	0–210 (142) 43.94 ± 58.30
	RW	270–410 (17) 331.18 ± 38.87	300–450 (24) 367.92 ± 34.13	310–380 (5) 352.00 ± 25.88	220–350 (36) 283.61 ± 29.19	260–430 (18) 372.78 ± 59.19	300–470 (18) 394.44 ± 51.25	330–450 (14) 395.71 ± 46.03	220–470 (132) 346.82 ± 59.29
	PrL	260–420 (17) 324.71 ± 63.75	280–530 (25) 365.60 ± 57.81	330–380 (5) 354.00 ± 24.08	240–430 (43) 308.60 ± 45.18	260–440 (17) 366.47 ± 49.99	300–490 (17) 384.12 ± 52.45	320–550 (13) 433.85 ± 76.00	240–550 (137) 351.09 ± 66.03
	CrOOL	210–280 (16) 231.88 ± 23.16	160–320 (23) 261.30 ± 51.28	250–280 (5) 262.00 ± 13.04	140–290 (35) 216.57 ± 31.62	150–320 (16) 237.50 ± 59.94	180–350 (16) 271.25 ± 56.32	170–300 (14) 246.43 ± 44.13	140–350 (125) 241.60 ± 47.22
	CrOOW	40–140 (16) 97.50 ± 36.24	60–110 (22) 79.55 ± 14.95	40–80 (5) 62.00 ± 16.43	70–130 (35) 87.71 ± 14.57	80–160 (17) 120.00 ± 25.50	80–170 (16) 116.88 ± 24.42	70–140 (14) 95.71 ± 23.11	40–170 (125) 95.52 ± 26.92

Remarks

Eschara volgensis Eichwald, 1865 from the Late Cretaceous of Simbirsk (now Ulyanovsk, Russian Federation) was regarded as possibly conspecific with *Rhagasostoma rowei* by Voigt (1967). Voigt, who examined the Eichwald Collection housed at the Palaeontological and Stratigraphical Museum at the Faculty of Geology, St Petersburg State University, found that the original material of this species from Simbirsk, Ulyanovsk Oblast, Russia differs from *R. rowei* only in the opesia being smaller and having a slightly visible tongue-like projection of the cryptocyst. Unfortunately, the specimen of *E. volgensis* (PSM PSU 2/187 and PSM PSU 2/188) could not be found during our visit to the collections. However, a photograph of the specimen made by Prof. E. Voigt in 1963 is reproduced here (Fig. 16A). This species was redescribed by I.I. Lahusen (1873) whose collection is stored in the Museum of the Mining Institute, St Petersburg. The specimen of *E. volgensis* (MMI 15/49) could not be examined using SEM, but a microphotograph is shown instead (Fig. 16B). The Lahusen material of *E. volgensis* is from the vicinity of Yazykov village in Simbirsk Province, Ulyanovsk Oblast. He stated that the sample described by Eichwald (1865) was not completely identical with his samples. Our findings show that the sample described by Lahusen is conspecific with *Rhagasostoma rowei*.

In a monograph on the development of different species of *Woodipora* Jullien, 1888 from the Coniacian to the Maastrichtian, Schubert (1986) transferred Brydone's species *rowei* to the genus *Woodipora*. He did not regard the presence of opesiules or opesiular indentations as being diagnostic for species and concluded that *rowei* and *mimosa* were synonymous, differing simply in the preservation of the opesiules (for a more detailed summary regarding a possible synonymy of *rowei* and *mimosa*, see the remarks for *R. mimosa*).

Rhagasostoma rowei has bell-shaped autozooidal opesia because of the small lateral projections and opesiular indentations separated by a short projecting tongue of cryptocyst. Opesia with a straight or rounded proximal edges are formed when the lateral projections and cryptocystal tongue become broken-off. When the cryptocyst located between the opesiules in autozooids of *R. mimosa* is destroyed, the opesia takes a shape similar to that of *R. rowei*. Thus, this similarity is related to the state of preservation and it is evident that pristine colonies of *R. rowei* have opesiular indentations whereas those of *R. mimosa* have opesiules.

We have restudied the type material from the collections of R.M. Brydone and also material from the collections of I.I. Lahusen, E. Voigt and T.A. Favorskaya. The specimens labelled as *O. mimosa* (SM B36697) from the Brydone Collection and (TsNIGR Museum 32/9757) from the Voigt Collection belong to *R. rowei* because the autozooids lack opesiules. Usually *R. rowei* is characterized by colonies that widen distally with numerous avicularia. The large number of avicularia is due to the fact that avicularia occur at the start of the new zooidal rows needed to widen the branches. From these avicularia, ovate autozooids are budded distally, from which in turn pyriform autozooids are budded (Koromyslova 2014a). However, there is one specimen of *R. rowei* from the Maastrichtian of Turkmenistan (Fig. 18E; figured by Voigt 1967: pl. 18, fig. 2) that differs from the holotype and many other specimens in having almost parallel-sided branches and rare avicularia. Additionally, some large colonies are almost parallel-sided at the base with rare avicularia but widen distally where numerous avicularia are present (Figs 17A–B, 18F–G). It can be assumed that the samples described by Voigt (1967) and other similar specimens (Fig. 18D) were broken-off from the bases of such colonies and hence have few avicularia. Ovate autozooids, which are budded from avicularia, are also rare and often poorly expressed. Obviously, *R. rowei* was usually characterized by stem-like colonies, which are almost parallel-sided at the base and have few avicularia, but become fan-like distally where numerous avicularia are present. Furthermore, colonies of this species can occasionally have bifurcating branches (Figs 16B–C, F, 18A–B, F). Entire colonies are rare and usually we can see only a small part of colonies, which were broken-off.

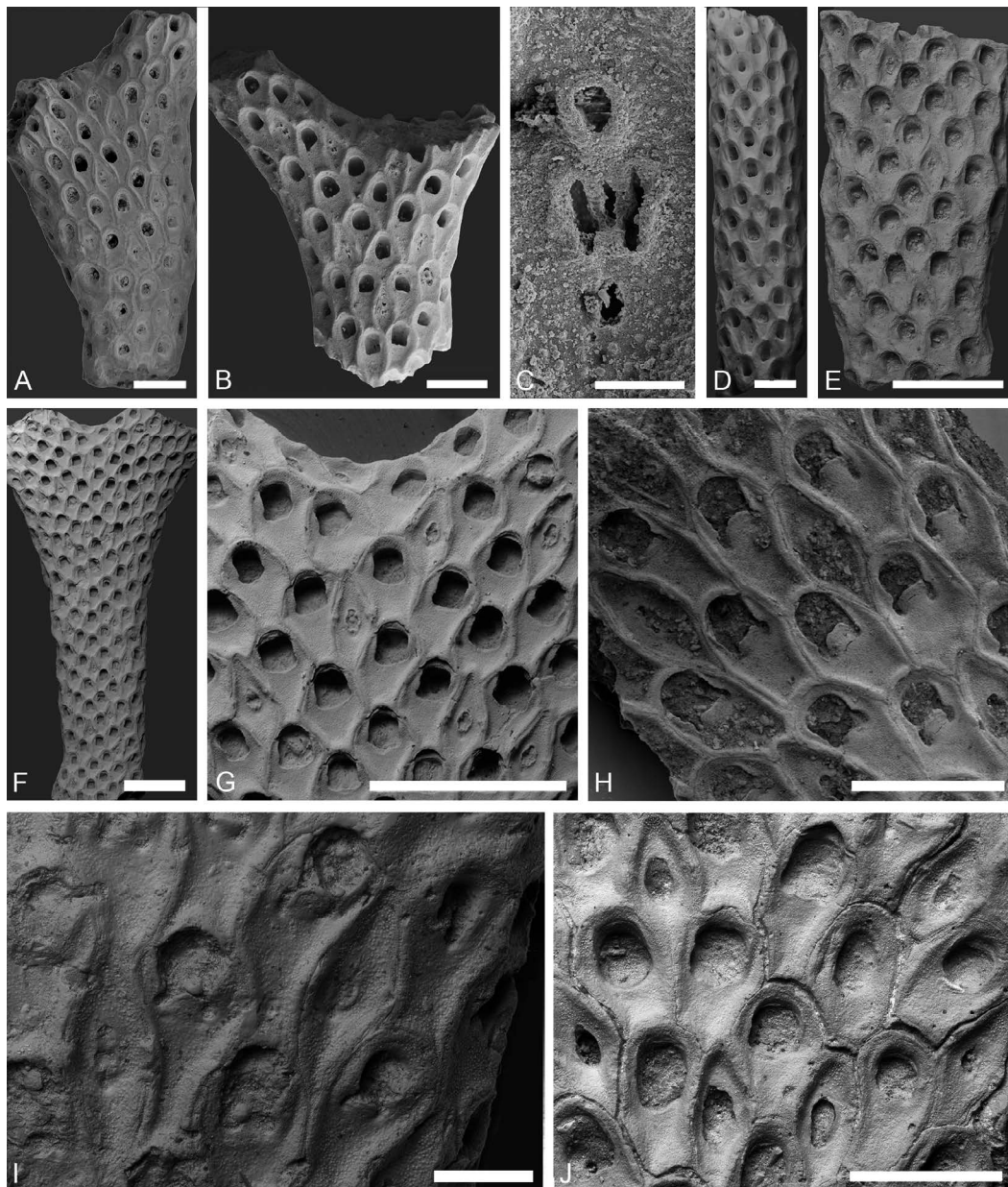


Fig. 18. *Rhagasostoma rowei* (Brydone, 1906). **A.** SMF 29932, early Maastrichtian, Rügen, Germany, overview of erect bifoliate stem-like then dichotomously branching colony. **B–C.** SMF 29925, early Maastrichtian, Island of Møn, Denmark. **B.** Overview of erect bifoliate stem-like then dichotomously branching colony. **C.** Opesia and opesiules of avicularium. **D.** SMF 29933, late Maastrichtian, former brick factory, Hamburg-Hummelsbüttel, Germany, showing the parallel-sided base of erect bifoliate colony with rare avicularia. **E.** TsNIGR Museum 36/9757, late Maastrichtian, Turkmenistan, Tuarkyr, showing the parallel-sided base of erect bifoliate colony with rare avicularia. **F–H.** Maastrichtian, Kazakhstan, Mangyshlak Peninsula. **F–G.** PIN 3421/1009. **F.** Erect bifoliate colony, almost parallel-sided but widening distally. **G.** The widest part of the colony showing autozooids and numerous avicularia. **H.** PIN 3421/1008, showing autozooids with long cryptocystal tongues, and avicularia. **I.** TsNIGR Museum 32/9757, late Maastrichtian, Turkmenistan, western Kopetdag, showing ovicellate (arrows) and non-ovicellate autozooids with long cryptocystal tongues, and avicularia. **J.** PIN 5502/3050, Maastrichtian, Kazakhstan, northern Aral Sea Region, showing autozooids and avicularia. Scale bars: A–B, D, H, J = 1 mm; C = 100 μ m; E–G = 2 mm; I = 500 μ m.

Schubert (1986) mentioned the presence of *R. rowei* in his distribution list from Royan in southwest France. However, it would be rather surprising to find this species in the Aquitaine Basin, as the bryofauna described so far from the Aquitaine Basin differs considerably from the northern Chalk Sea bryofauna. In his synonymy list and in his remarks, Schubert (1986) placed, following Voigt (1930), Marsson's (1887) *Eschara Delarueana* (non d'Orbigny, 1851) and Voigt's (1925) *Onychocella* cf. *delarueana* in synonymy with *R. rowei*. However, this material is derived from the early Maastrichtian of Rügen (Marsson 1887) and the late Maastrichtian of the 'Blue Hills' (Blaue Berge) in eastern Germany (Voigt 1925). The true *Rhagasostoma delarueana* (d'Orbigny, 1851) from Royan, however, is not conspecific with *R. rowei*. Since no samples of *R. rowei* were found among the material studied by Schubert (1986) labelled "Royan", this locality has to be deleted from the distribution list of *R. rowei*.

Schubert (1986) erroneously considered all material from Møns Klint in eastern Denmark as late Maastrichtian. However, no sediments from the late Maastrichtian crop out at Møns Klint (cf. Mutterlose *et al.* 1998) and the samples studied by Schubert (1986) are in fact labelled as early Maastrichtian.

A specimen comparable to *R. rowei* has recently been described as '*Onychocella*' sp. in Koromyslova *et al.* (2018a) from the early Maastrichtian of the Aktolagay Plateau, western Kazakhstan. The Aktoalagay species, however, is encrusting and only very poorly preserved.

Distribution

Late Santonian France: Vasterival near Sainte-Marguerite-sur-Mer, Normandy (Schubert 1986). Late Campanian Belgium: Harmignies near Mons. Belarus: Quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region (Koromyslova 2014a). Turkmenistan: "Kredin" gorge in the Kopet Dag Mountains NW of Aşgabat (Voigt 1967). Uzbekistan: southern Aral Sea Region, Republic of Karakalpakstan (Favorskaya 1996). Kazakhstan: Emba River. Early Maastrichtian Denmark: Møns Klint, Sjælland (Schubert 1986). Germany: Hemmoor and Lüneburg, Lower Saxony (Voigt 1967); Saturn quarry near Krons Moor, Schleswig-Holstein (Schubert 1986); Island of Rügen, Mecklenburg-Vorpommern (von Hagenow 1839; Voigt 1930). Kazakhstan: Along the Chobda river, and Kenderlyshor, Mangystau Region (Voigt 1967). United Kingdom: Trimingham, Norfolk, England (Brydone 1906). Late Maastrichtian Denmark: Kongsted (Faxe Kommune; Schubert 1986). France: Chef-du-Pont, Normandy (Schubert 1986). Germany: Blaue Berge near Dessau-Roßlau, Saxony-Anhalt (Voigt 1925), Tornesch, Hamburg-Hummelsbüttel. Turkmenistan: Koimat gorge and a gorge W of the "Kamyschli" gorge in the Kopet Dag Mountains NW of Aşgabat, Tuarkyr (Voigt 1967). Maastrichtian Kazakhstan: northern Aral Sea Region, Mangyshlak Peninsula.

Rhagasostoma mimosa (Brydone, 1930)

Fig. 19, Table 11

Onychocella mimosa Brydone, 1930: 49, pl. 28, figs 1–2.

Woodipora mimosa – Voigt 1967: 50, pl. 18, fig. 4. — Schubert 1986: 40.

Woodipora rowei (Brydone, 1906) – Schubert 1986 pars: 39, pl. 3, fig. 7, pl. 5, figs 4–5, pl. 8, figs 2–3.

Onychocella mimosa – Favorskaya 1992: 120 (mention). — Koromyslova 2014a: pl. 10, figs 1–2.

non *Woodipora rowei* – Schubert 1986 pars: 39, non pl. 3, figs 5–6, 8, pl. 5, figs 1–3, 6–8, pl. 8, fig. 1.

Material studied

Lectotype (here designated)

UNITED KINGDOM • England, Norfolk; *Porosphaera* Beds of Trimingham; early Maastrichtian (*Ostrea lunata* Zone); SM B36696 (Fig. 19AB; figured by Brydone 1930: pl. 28, figs 1–2).

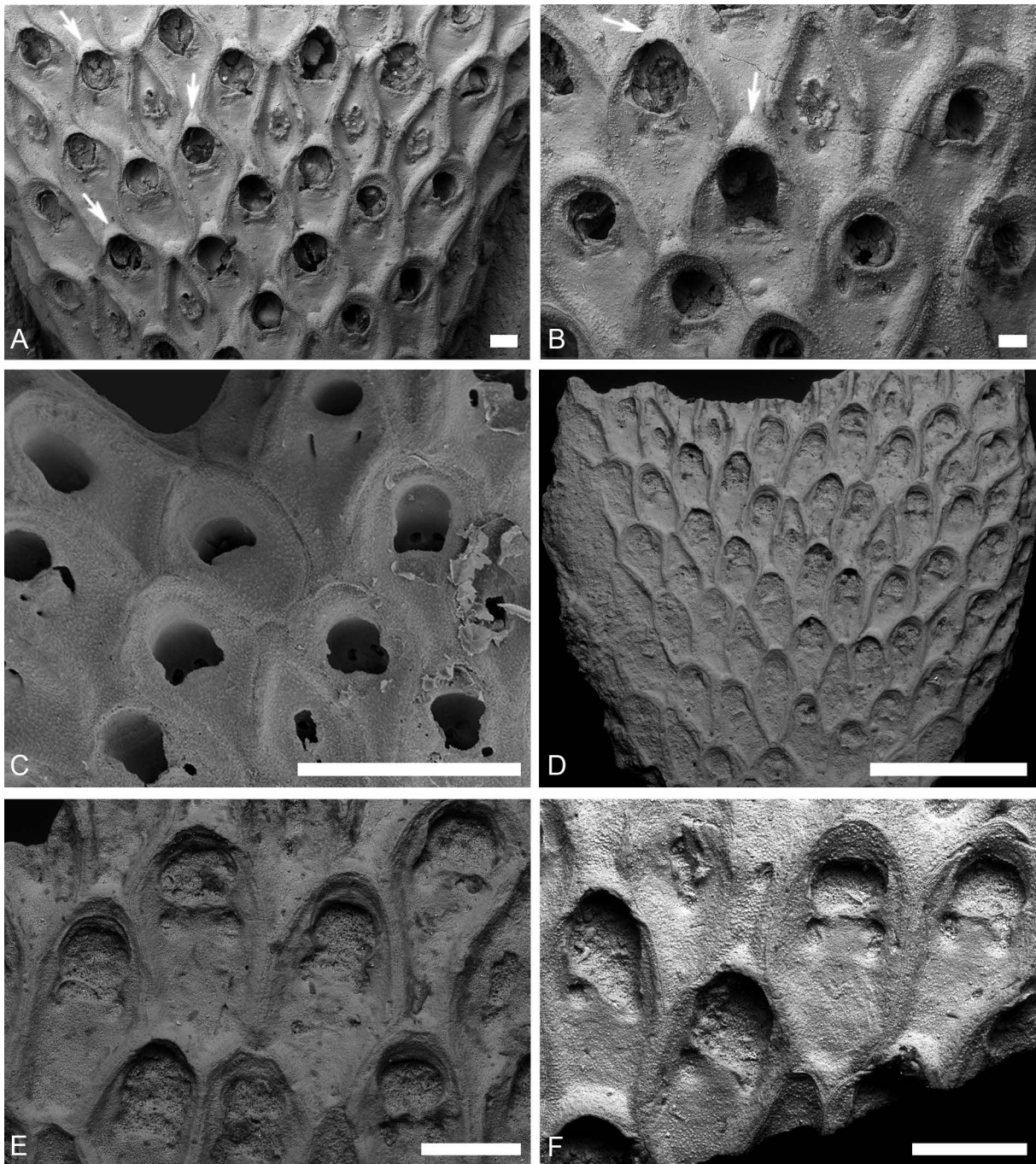


Fig. 19. *Rhagasostoma mimosa* (Brydone, 1930). **A–B.** Lectotype, SM B36696, early Maastrichtian (*Ostrea lunata* Zone), *Porosphaera* Beds of Trimingham, Norfolk, England, UK. **A.** Part of erect bifoliate colony showing ovicellate (some oecia arrowed) and non-ovicellate autozooids and avicularia. **B.** Detail of autozooids with opesiules and some with vestigial oecia (arrowed), and avicularia. **C.** SMF 29923, early Maastrichtian, Island of Møn, Denmark, bifurcating colony showing autozooids some opesiules and avicularia. **D–F.** Early Maastrichtian of an unknown locality on the Mangyshlak Peninsula, Mangystau Region, Kazakhstan. **D–E.** PIN 5502/3057. **D.** Part of erect bifoliate colony showing autozooids and avicularia. **E.** Detail of autozooids with opesiules and avicularia. **F.** PIN 5502/3056, autozooids with opesiules and avicularia. Scale bars: A = 200 μ m; B = 100 μ m; C = 1 mm; D = 2 mm; E–F = 500 μ m.

Table 11 (continued on next page). Summary of measurements of *Rhagasostoma mimosa* (Brydone, 1930). For each parameter the range is given with the number of measurements in brackets. The arithmetic mean is given \pm standard deviation. All measurements in μm .

	Basin	Southern North Sea Basin	Swedish–Danian Basin	Polish Basin	Mangyshlak–East Caspian	Total	
	Stratigraphy	Early Maastrichtian	Early Maastrichtian	?Late Campanian	Early Maastrichtian		
	Locality	Norfolk	Island of Møn	Grodno Region	Mangyshlak Peninsula		
Autozooids	pyriform	AzL	750–1060 (6) 871.67 \pm 117.03	900–1120 (6) 1006 \pm 100.33	640–780 (8) 710.00 \pm 46.90	850–1300 (8) 1047.50 \pm 145.58	640–1300 (28) 904.64 \pm 174.05
		AzW	460–490 (6) 475.00 \pm 12.25	460–570 (6) 511.67 \pm 41.67	320–360 (8) 347.50 \pm 14.88	520–630 (8) 565.00 \pm 35.86	320–570 (28) 472.14 \pm 90.81
		OpL	230–250 (4) 242.50 \pm 9.57	290–340 (6) 310.00 \pm 18.97	170–230 (8) 192.50 \pm 19.09	190–320 (8) 280.00 \pm 44.35	170–340 (25) 253.20 \pm 54.29
		OpW	230–250 (4) 237.50 \pm 9.57	190–290 (6) 231.67 \pm 38.17	180–220 (8) 197.50 \pm 15.81	280–340 (8) 308.57 \pm 21.16	180–340 (25) 243.20 \pm 49.81
	ovate	AzL	820–980 (6) 898.33 \pm 63.38	730–900 (4) 827.50 \pm 75.00	630–760 (8) 693.75 \pm 43.40	940–1260 (6) 1078.33 \pm 134.23	630–1260 (24) 863.33 \pm 169.42
		AzW	380–500 (5) 448.00 \pm 50.70	540–630 (4) 580.00 \pm 39.16	320–380 (8) 355.00 \pm 20.70	510–610 (6) 543.33 \pm 41.31	320–630 (23) 463.48 \pm 98.70
		OpL	230–240 (3) 233.33 \pm 5.77	150–320 (3) 243.33 \pm 86.22	190–210 (5) 196.00 \pm 8.94	260–280 (3) 266.67 \pm 11.55	150–320 (14) 229.29 \pm 44.63
		OpW	150–280 (3) 210.00 \pm 65.57	200–260 (3) 236.67 \pm 32.15	160–230 (5) 198.00 \pm 27.75	230–320 (3) 280.00 \pm 45.83	150–320 (14) 226.43 \pm 49.40
	OoL	50–130 (6) 70.00 \pm 31.62	60–90 (2) 75.00 \pm 21.21	50–70 (8) 58.75 \pm 6.41	70–120 (8) 92.50 \pm 15.81	50–130 (24) 74.17 \pm 23.02	
	OoW	180–310 (6) 238.33 \pm 54.19	160–190 (2) 175.00 \pm 21.21	140–240 (8) 191.25 \pm 33.57	240–410 (8) 298.75 \pm 49.70	140–410 (24) 237.50 \pm 64.35	
	TL	40–110 (6) 71.67 \pm 27.87	80–190 (5) 136.00 \pm 55.05	40–110 (8) 73.75 \pm 25.60	80–120 (8) 100.00 \pm 14.14	40–190 (27) 92.59 \pm 37.89	
	TW	100–160 (6) 140.00 \pm 22.80	150–180 (5) 164.00 \pm 11.40	90–140 (8) 116.25 \pm 17.68	160–230 (8) 185.00 \pm 22.04	90–230 (27) 150.74 \pm 33.50	
	OpsD	30–50 (6) 41.67 \pm 7.53	40–70 (4) 52.50 \pm 12.58	30–50 (8) 38.75 \pm 9.91	50–100 (8) 71.25 \pm 16.42	30–100 (26) 51.54 \pm 18.26	

Table 11 (continued).

	Basin	Southern North Sea Basin	Swedish–Danian Basin	Polish Basin	Mangyshlak–East Caspian	Total
	Stratigraphy	Early Maastrichtian	Early Maastrichtian	?Late Campanian	Early Maastrichtian	
	Locality	Norfolk	Island of Møn	Grodno Region	Mangyshlak Peninsula	
Avicularia	AvL	850–1030 (6) 941.67 ± 59.13	960–1060 (6) 1002.00 ± 38.99	620–960 (8) 797.50 ± 121.74	1060–1320 (5) 1160.00 ± 111.36	620–1320 (24) 951.67 ± 161.16
	RL	500–610 (6) 548.33 ± 47.92	580–630 (6) 596 ± 20.74	390–610 (8) 487.50 ± 87.63	630–730 (5) 676.00 ± 40.99	390–730 (24) 564.58 ± 90.84
	ARL	0–110 (6) 43.33 ± 50.07	0–160 (6) 76.67 ± 67.43	0–130 (8) 46.25 ± 64.13	0 (5)	0–160 (25) 43.60 ± 57.80
	RW	290–610 (6) 453.33 ± 148.68	420–430 (6) 426.00 ± 5.48	250–340 (8) 288.75 ± 30.44	400–510 (5) 452.00 ± 43.24	250–610 (24) 392.50 ± 105.55
	PrL	300 ± 440 (6) 393.33 ± 53.54	350–460 (6) 402.00 ± 44.38	290–380 (8) 310.00 ± 49.86	420 ± 590 (5) 484.00 ± 73.35	290–590 (24) 386.25 ± 82.61
	CrOOL	230–320 (6) 290.00 ± 32.86	220–290 (3) 256.67 ± 35.12	170–260 (8) 195.00 ± 30.71	260–340 (4) 305.00 ± 34.16	170–340 (21) 251.90 ± 56.53
	CrOOW	110–150 (6) 130.00 ± 14.14	70–130 (3) 96.67 ± 30.55	60–110 (8) 82.50 ± 14.88	110–150 (4) 132.50 ± 17.08	60–150 (21) 107.62 ± 28.44

Additional figured material

DENMARK • Island of Møn; early Maastrichtian; SMF 29923 (Fig. 19C).

KAZAKHSTAN • 2 specs; Mangystau Region; ?early Maastrichtian of Hanga-Baba (урочище Ханга-баба) on the Mangyshlak Peninsula; PIN 5502/3056 (Fig. 19F), 5502/3057 (Fig. 19D–E).

Other material

BELARUS • 2 specs; Grodno Region; erratic block of ?late Campanian age in a quarry near Hrodna/Grodno (Гродна/Гродно); PIN 2922/203, 2922/207 (imaged in Koromyslova 2014a: pl. 10, figs 1–2).

Description

Colony rigidly erect, bifoliate, multiserial, branches 2.0–10.0 mm wide. Ancestrula and early astogeny not observed. Colony formed by pyriform and ovate autozooids and vicarious avicularia. Autozooids subrectangular with rounded distal ends; zooidal boundaries raised. Pyriform autozooids with a narrow proximal end but widening distally, the widening usually starting from the proximal margin of the opesia. In ovate autozooids, the proximal end is partly overlapped by the avicularian rostra and the autozoid begins to widen considerably below the proximal margin of the opesia, usually at the boundary with an avicularium. Gymnocyst lacking. Cryptocyst slightly granulated, slightly depressed centrally and occupying half or more of the autozooidal frontal surface, peripheral caverns lacking. Opesia terminal or subterminal. Opesial rim elevated, formed by a projecting, thickened cryptocyst, subcircular, a pair of opesiules located 70–90 μm proximallateral of opesia and divided from the latter by a cryptocystal tongue. Fusion of cryptocyst distal of opesiules and tongue of cryptocyst incomplete. Septula in walls not observed. Ovicells immersed, oecium is formed by the distal zooid, triangular, vestigial, with slightly granulated surface, not protruding above the colony surface (Fig. 19A–B, D–F). Avicularia vicarious, rhomboidal. Rostrum conical in outline and symmetrical, usually with straight lateral walls; indentations or projections present at base of rostrum. Usually two types of avicularia differing mainly in the length of the rostrum and rostral apex, which partly overlaps the proximal end of the distal autozooids: avicularia with short rostra and short, trough-like apices (0–130 μm), and avicularia with long rostra without projecting apices. Proximal part short, narrowing downwards, with convex lateral sides. Entire frontal surface of avicularium occupied by a fragile, slightly granulated cryptocyst containing five openings: two small, subcircular openings, distally and proximally, in between three slit-like, parallel openings. Cryptocyst between openings frequently destroyed causing them to coalesce into a single opening of variable outline. Closure plates, kenozooids and intramural reparative budding in autozooids and avicularia not observed.

Remarks

Rhagasostoma mimosa was introduced by Brydone (1930) for species from the *Porosphaera* beds of Trimmingham very much resembling *R. rowei* (Brydone, 1906) but differing from the latter in having two opesiules. He considered the possibility that colonies of *R. rowei* were badly preserved samples of *R. mimosa* but concluded that the two must be different species because colonies of *R. rowei* are more slender and fragile, avicularia of *R. mimosa* have a central cavity enclosed by a marked wall, and *R. rowei* and *R. mimosa* never co-occur in the Chalk of England.

Voigt (1967) re-examined *R. rowei* and *R. mimosa* from Central Asia and rejected the morphological arguments used by Brydone (1930) to separate the two species. He concluded that except for *R. mimosa* having opesiules, the two species are completely identical, but as no intermediate stages occur, he regarded a separation of *R. rowei* and *R. mimosa* as justified. He argued that calcification of the frontal wall of *R. rowei* during the Late Cretaceous resulted over time in the formation of two opesiules completely separated from the opesia as passages for the bundles of parietal muscles. A similar development has

also been observed in *Rhagasostoma disparile* (d'Orbigny, 1851) and *Rhagasostoma strumulosum* Marsson, 1887 (cf. Schubert 1986: fig. 12), which are indeed closely related to *R. rowei* and *R. mimosa*. Furthermore, Voigt (1967) assigned *mimosa* to the genus *Woodipora* Jullien, 1888 because of the opesiules, but kept *rowei* in *Onychocella*.

In his *Woodipora* monograph, Schubert (1986) regarded *rowei* and *mimosa* as two different phenotypes of the same species, which he assigned to *Woodipora*. The length and width measurements that he conducted on autozooids and avicularia and their opesiades revealed no significant distinction between *rowei* and *mimosa*. Furthermore, he argued that colonies in the *mimosa* stage often have autozooids with and also without opesiules (cf. Schubert 1986: pl. 8, fig. 3). As the zooids without opesiules are of primary origin and cannot have been destroyed during preparation or other processes, he concluded that the occurrence of opesiules is not species-specific and cannot be considered an argument for the existence of *mimosa* as an independent species. He regarded the *mimosa* stage as an 'end-member' of a parallel development by progressive calcification of the cryptocyst from the Coniacian to the Maastrichtian resulting in the formation of two opesiules. Zooids with advanced calcification of the cryptocyst, however, did not completely replace the *rowei* stage, the two stages thus co-occurring in single colonies.

Voigt (1991) again regarded *mimosa* and *rowei* (and also *R. disparile* and *R. strumulosum*) as separate species. He saw the four species as an example of an intermediate status between onychocellid pseudomalacostegans and microporid or thalamoporellid coilostegans, placing *disparile* and *rowei* in *Onychocella* and *strumulosum* and *mimosa* in *Woodipora*. Thus, the microporid or thalamoporellid genus *Woodipora* would have originated several times by convergent evolution.

Without description or figures, Favorskaya (1992) mentioned *Onychocella mimosa* from the Maastrichtian of the southern Aral Sea Region in Uzbekistan and from Hanga-Baba (урочище Ханга-баба), 30 km east of Fort Shevchenko (Форт-Шевченко) in the Mangystau Region, Kazakhstan.

A comprehensive description of morphological differences between *R. rowei* and *R. mimosa* from the Grodno quarry in Belarus was undertaken by Koromyslova (2014a). As she showed, the two species are not conspecific and differ in the shape of the autozooidal opesia and in the cryptocyst that develops opesiular indentations in *R. rowei* and opesiules in *R. mimosa*. Furthermore, specimens of *R. rowei* show intramural reparative budding in avicularia, which has not been observed in colonies of *R. mimosa*. Based on the length of the rostrum and the apex, three different types of avicularia have been observed in *R. rowei*, while *R. mimosa* shows only avicularia with short rostra and short trough-like apices (Koromyslova 2014a). Avicularia of *R. rowei* and *R. mimosa* are indeed very distinct from most other species within the genus *Rhagasostoma*. Centrally located, there is an opesia and three opesiules in the avicularian cryptocyst.

We have restudied Brydone's syntypes in the SM collection, choosing a lectotype (figured by Brydone 1930: pl. 28, figs 1–2), as well as the material from the collection of E. Voigt (Fig. 18I, 19C) and T.A. Favorskaya (Fig. 19D–F). The specimens labelled as *Onychocella mimosa* (SM B36697) from the Brydone Collection and (TsNIGR Museum 32/9757) from the Voigt Collection belong to *R. rowei* because the autozooids lack opesiules. As already discussed by Brydone (1930) and Voigt (1967), *R. mimosa* and *R. rowei* are very similar, differing only in *R. mimosa* having opesiades that are round instead of bell-shaped and opesiules instead of opesiular indentations. The presence of autozooids with opesiular indentations in colonies of *R. mimosa* in most cases can be explained by post-mortem destruction of the cryptocystal tongue that separated the opesiules from the opesia, or by the fact that the opesiades and opesiules of these autozooids were not formed fully and they were in the *rowei* stage (cf. Schubert 1986: pl. 8, fig. 3).

Distribution

Late Campanian Belarus: Quarry near Hrodna/Grodno (Гродна/Гродно), Grodno Region (Koromyslova 2014a). Early Maastrichtian Germany: Saturn quarry near Kronsmoor, Schleswig-Holstein (Schubert 1986); glacial drift deposits in northern Germany (Voigt 1967). Kazakhstan: unknown locality on the Mangyshlak Peninsula, Mangystau Region (Favorskaya 1992). United Kingdom: Trimingham, Norfolk, England (Brydone 1930). Uzbekistan: southern Aral Sea Region, Republic of Karakalpakstan (Favorskaya 1992). Late Maastrichtian Denmark: Møns Klint, Sjælland (Schubert 1986). Turkmenistan: Gorge W of the “Kamyschli” gorge in the Kopet Dag Mountains NW of Aşgabat (Voigt 1967).

Key to species of *Rhagasostoma* described in this paper

1. Avicularia interzooidal, peripheral caverns usually present 2
– Avicularia vicarious, ovicells immersed, peripheral caverns lacking 3
2. Avicularia longer than autozooids, ovicells endozooidal or immersed 4
– Avicularia about ½ the autozoooid size or less, ovicells endozooidal 5
3. Opesia of autozooids with opesiular indentations *R. rowei* (Brydone, 1906)
– Opesia of autozooids with opesiules *R. mimosa* (Brydone, 1930)
4. Avicularian rostrum conical in outline, ovicells endozooidal 6
– Avicularian rostrum spade-shaped, ovicells immersed or not observed 7
– Avicularian rostrum falciform, ovicells endozooidal 8
5. Avicularian rostrum short and tilted to the right or left, gymnocyst present 9
– Avicularian rostrum long and straight, gymnocyst lacking *R. tchvanovi* (Favorskaya, 1992)
6. Avicularian rostrum asymmetrical 10
– Avicularian rostrum symmetrical 11
7. Avicularian rostrum narrowed at the base, enlarged centrally and ended with top, ovicells immersed *R. brydonei* sp. nov.
– Avicularian rostrum almost the same width along the whole of its length and with pointed or rounded top, ovicells not observed *R. operculatum* sp. nov.
8. Avicularian rostrum with one side of rostrum almost straight and other side curved near top
..... *R. minuens* Brydone, 1936
9. Autozooidal cryptocyst with slightly convex border; gymnocyst very rarely observed
..... *R. gibbosum* (Marsson, 1887)
– Autozooidal cryptocyst with convex border; gymnocyst well developed
..... *R. gibbosulum* Brydone, 1936
10. Avicularian opesia large, roundish or oval with thickened distolateral edge and with thin articular ridges bearing two short teeth proximally and a short or long, slit-like opesiular indentation between the teeth; opesiules lacking *R. inelegans* (Lonsdale, 1850)
– Avicularian opesia distal, small, subcircular; two lateral parallel slit-like opesiules formed by long teeth of articular ridges and a long, slit-like opesiular indentation between the teeth proximally below opesia *R. angliae* Brydone, 1936

11. Avicularian opesia egg-shaped, with thin articular ridges bearing two short teeth proximally and a short or long slit-like opesiular indentation between the teeth; opesiules lacking
 *R. aralense* sp. nov.

Discussion

Distribution of *Rhagasostoma* in the Late Cretaceous of Eurasia

Voigt (1967), Favorskaya (1980, 1985, 1992, 1996) and Titova & Favorskaya (1994) pointed to similarities in bryozoan associations from the Late Cretaceous of Europe and Central Asia. These authors gave the following data on species of *Rhagasostoma* (assigned by them to *Onychocella*) from the Campanian and Maastrichtian of Europe and Central Asia, namely the southern Aral Sea Region [SASR] and central Kyzylkum [CK], Uzbekistan; Mangyshlak Peninsula [MP], Kazakhstan; Tuarkyr, Pitnyak (lower reaches of Amu Darya) and western Kopetdag [WK], Turkmenistan:

- Early Campanian – four species shared between Europe and the SASR (*R. disparile*, *R. inelegans*, *R. palpigerum* (Brydone, 1912), *R. subgibbosum*); common species between Europe and CK, MP, Tuarkyr, Pitnyak and WK were not found.
- Late Campanian – nine species shared between Europe and the SASR [*R. disparile*, *R. inelegans*, *R. disparile hellotis* (Brydone, 1930), *R. nysti* (von Hagenow, 1851), *R. palpigerum*, *R. rowei*, *R. scheringense* (Brydone, 1936), *R. subgibbosum*, *R. trimense* (Brydone, 1936)]; four species in common between Europe and WK (*R. disparile*, *R. anglicum* (Brydone, 1930), *R. inelegans*, *R. rowei*); two species in common between Europe and MP [according to Titova & Favorskaya (1994) bryozoans were not found in the Campanian of the Mangyshlak Peninsula, but they are known from the *Belemnitella lanceolata* Zone, which is now placed in the late Campanian (Ogg *et al.* 2004; Remin 2012)]; common species for Europe, CK and PAD were not established.
- Early Maastrichtian – four species shared between Europe and the SASR (*R. mimosa*, *R. nysti*, *R. trimense*, *R. strumulosum*); five species in common for Europe and WK (*R. anglicum*, *R. calceolum* Brydone, 1936, *R. rowei*, *R. hercynum* (Brydone, 1930), *R. strumulosum*); three between Europe and MP (*R. disparile*, *R. rowei*, *R. strumulosum*); and one species in common between Europe and Pitnyak (*R. nysti*).
- Late Maastrichtian – one species shared between Europe and the SASR (*R. strumulosum*); four species in common between Europe and WK (*R. hercynum*, *R. rowei*, *R. mimosa*, *R. strumulosum*); two species in common between Europe and MP (*R. rowei*, *R. strumulosum*); one species in common between Europe and Pitnyak (*R. nysti*); and one species in common between Europe and Tuarkyr (*R. rowei*).
- Maastrichtian undifferentiated – one species shared between Europe and CK (*R. nysti*).

Of the species listed above, the following are redescribed in the present paper: *Rhagasostoma inelegans* (Lonsdale, 1850), *R. gibbosum* (Marsson, 1887), *R. gibbosulum* Brydone, 1936, *R. tchvanovi* (Favorskaya, 1992), *R. rowei* (Brydone, 1906), and *R. mimosa* (Brydone, 1930). Prior to this study, *R. inelegans* had been described from the late Turonian to early Campanian of England (Brydone 1930; Taylor 2002), the early Campanian of Germany (Voigt 1975), and the early to middle Campanian of Uzbekistan and Turkmenistan (Favorskaya 1992, 1996). Moreover, R.M. Brydone introduced several new subspecies of *O. inelegans* in his monograph on bryozoans from the Chalk of southeast England (Brydone 1929, 1930, 1936). We have restudied Lonsdale's syntypes in the NHMUK collection and material from the collections of R.M. Brydone, E. Voigt and T.A. Favorskaya. As result of this revision the new species *R. brydonei* sp. nov., *R. aralense* sp. nov. and *R. operculatum* sp. nov. are erected. The distribution of *R. inelegans* is restricted to the late Santonian to early Campanian of England, the early Campanian of Germany and the late Campanian of Belarus (Fig. 20). The former subspecies of *R. inelegans* and the new species have the following distributions: *R. brydonei* sp. nov. – late Turonian to

Coniacian of England; *R. minuens* – Coniacian, late Santonian, early Campanian and early Maastrichtian of England, early Campanian of Germany, and Campanian of France; *R. angliae* – middle Campanian and early Maastrichtian of England, late Campanian of France, early Maastrichtian of Germany; *R. aralense* sp. nov. – early to middle Campanian of Uzbekistan; and *R. operculatum* sp. nov. – early to middle Campanian of Turkmenistan. *Rhagasostoma inelegans* is excluded from the list of common onychocellids in the Late Cretaceous of Europe and Central Asia. This species and *R. brydonei* sp. nov., *R. minuens*, *R. angliae*, *R. aralense* sp. nov. and *R. operculatum* sp. nov. have narrow stratigraphical and geographical distributions.

As a result of studying new material of *Rhagasostoma gibbosum* and *R. gibbosulum*, their distributions have been extended (Fig. 20); *R. gibbosum* is now known from the late Campanian of Belarus and Kazakhstan, the early Maastrichtian of England and Germany, and the Maastrichtian of Denmark;

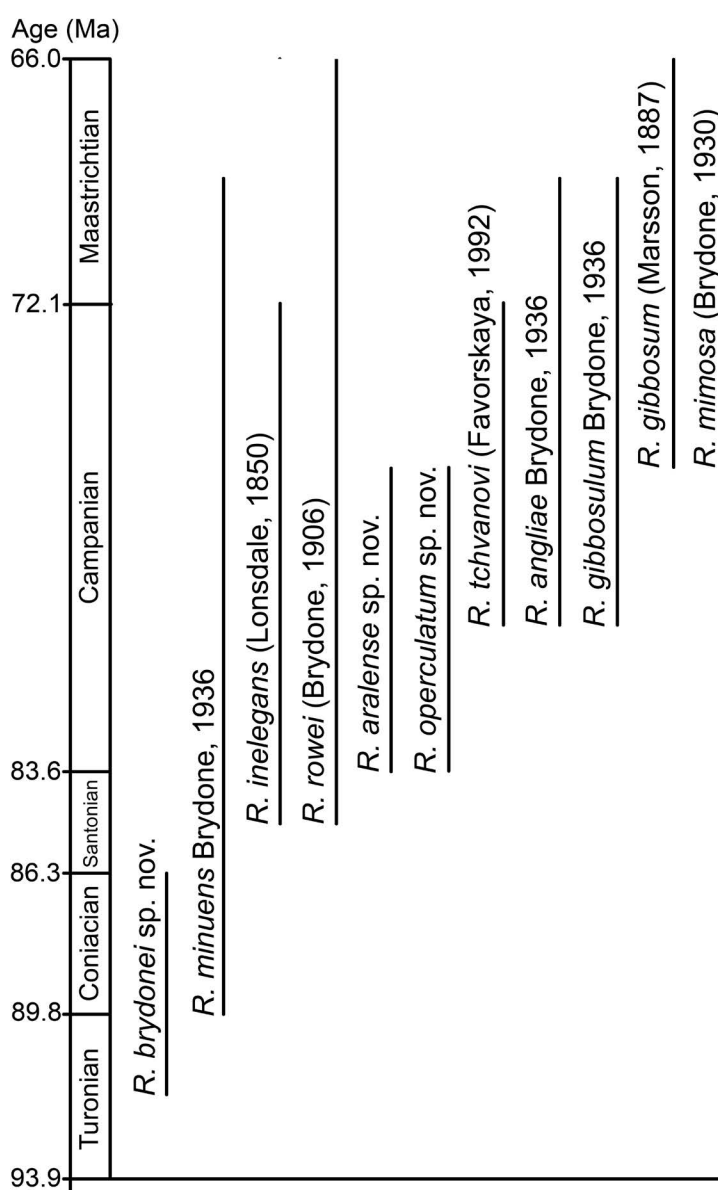


Fig. 20. Distribution of the studied species of the genus *Rhagasostoma* Koschinsky, 1885 in the Late Cretaceous of Eurasia.

R. gibbosulum is now known from the middle Campanian of England, the late Campanian of Belarus, and the early Maastrichtian of Germany. *Rhagasostoma tchvanovi* occurs in the middle to late Campanian of Uzbekistan.

We have restudied the type material of *Rhagasostoma rowei* (Brydone, 1906) and also material from the collections of I.I. Lahusen, E. Voigt and T.A. Favorskaya. This confirms that *R. rowei* has extensive stratigraphical and geographical distributions (Fig. 20). This species is recorded in the late Santonian of France, late Campanian of Belgium, Belarus, Turkmenistan, Uzbekistan and Kazakhstan; early Maastrichtian of England, Denmark, Germany and Kazakhstan; and late Maastrichtian of Denmark, France, Germany and Turkmenistan.

The study of new material of *Rhagasostoma mimosa* allows extension of its distribution, which now consists of: the late Campanian of Belarus; early Maastrichtian of Germany, Kazakhstan, England and Uzbekistan; and late Maastrichtian of Denmark and Turkmenistan.

Palaeobiogeography and size variability of *Rhagasostoma* species

Rhagasostoma brydonei sp. nov. is the oldest of the studied species of *Rhagasostoma* (Fig. 20), and is recorded only in the late Turonian and Coniacian of the southern North Sea Basin. Intra- and intercolonial variability are minor in colonies of the same geological age. In contrast to late Turonian specimens from Hampshire, the Coniacian specimens from Kent show the longest autozooids and avicularia (rostra and proximal part), and avicularia that are widest proximally.

During the Coniacian to the late Santonian, *Rhagasostoma minuens* was restricted to the southern North Sea Basin, where it existed until the early Maastrichtian. The species reached the North German Basin in the early Campanian. In contrast to bryozoans from the North German Basin with large autozooids and avicularia, bryozoans from the southern North Sea Basin show the greatest variability in all characters.

Rhagasostoma inelegans first appeared in the late Santonian of the southern North Sea Basin and existed there until the early Campanian. This species reached the North German Basin in the early Campanian and the Polish Basin in the late Campanian. The early and ?late Campanian bryozoans *R. inelegans* from the North German Basin and Polish Basin, respectively, in contrast to the southern North Sea Basin, have the largest autozooids, avicularia and oocia. In addition, the early Campanian examples from the North German Basin show the longest and widest autozooids, and longest avicularia with longest and widest rostra and proximal parts. On the whole, intra- and intercolonial variability is evident in the type of colonies (encrusting and bifoliate), and degree of asymmetry and concavity of the avicularian rostra. The shape of the rostrum may also vary, but it is usually approximately conical and narrower than the proximal part of the avicularium. In contrast to bifoliate colonies, the encrusting sheet-like colonies are characterized by the presence of cavities in the proximolateral parts of autozooids. All specimens are characterized by large variability in the length and width of autozooids and the length of avicularia, but early Campanian colonies from the North German Basin show the greatest variability of these structures.

Rhagasostoma rowei (Brydone, 1906) first appeared during the late Santonian in the southern North Sea Basin, reached the Polish and North Ust-Yurt–Aral basins and the Tethys in the late Campanian, and the North German, Swedish–Danian and Mangyshlak–East Caspian basins in the early Maastrichtian where it existed until the late Maastrichtian. Colonies from the Tethys and the North German Basin show the largest autozooids and opesia and the greatest variability, whereas colonies from the Polish Basin have the smallest autozooids and avicularia. Colonies from the southern North Sea Basin have the shortest avicularia. In this species there are three types of avicularia differing mainly in the length of the rostrum and rostral apex, which partly overlaps the proximal end of the distal autozooid: (1) avicularia with long rostra and long trough-like apices (130–210 µm); (2) avicularia with short rostra and short trough-

like apices (0–130 μm); and (3) avicularia with rostra lacking projecting apices. Colonies from the Polish–South Baltic Basin have all three types of avicularia; colonies from the southern North Sea, the North German, North Ust-Yurt–Aral and Mangyshlak–East Caspian basins have only the second type of avicularia; colonies from the Swedish–Danian Basin have the third type of avicularia; and colonies from the Tethys have the first and second types of avicularia.

Rhagasostoma aralense sp. nov. and *R. operculatum* sp. nov. are known from the early to middle Campanian of the North Ust-Yurt–Aral Basin and the Tethys, respectively, and *R. tchvanovi* from the middle to late Campanian of the North Ust-Yurt–Aral Basin.

Rhagasostoma angliae occurred in the southern North Sea Basin in the middle Campanian to early Maastrichtian, and reached the North German Basin in the early Maastrichtian. In contrast to specimens from the North German Basin with large autozooids and avicularia, specimens from the southern North Sea Basin show the greatest variability of all characters.

Rhagasostoma gibbosulum appeared in the southern North Sea Basin during the middle Campanian and reached the Polish Basin during the late Campanian and the North German Basin in the early Maastrichtian. Colonies from the North German Basin show the greatest sizes of all autozooidal and avicularian characters.

Rhagasostoma gibbosum occurred in the late Campanian in the Polish and the North Ust-Yurt–Aral basins and appeared in the southern North Sea and the North German basins in the early Maastrichtian. Bryozoans from the North German Basin show the longest and widest autozooids, and the largest oecia. Autozooids of specimens from the North Ust-Yurt–Aral Basin were smaller than those from the North German Basin, but larger than those from the southern North Sea and the Polish basins; in addition, they had the largest opesiae. The smallest oecia are observed in colonies from the Polish Basin. The smallest avicularia are observed in colonies from the southern North Sea Basin, but the largest avicularia with the longest rostra and proximal parts occur in colonies from the North Ust-Yurt–Aral Basin. On the whole, colonies from the North German Basin and the North Ust-Yurt–Aral Basin show the largest autozooids and avicularia.

Rhagasostoma mimosa first appeared the late Campanian in the Polish–South Baltic Basin and reached the southern North Sea, the Swedish–Danian, and the Mangyshlak–East Caspian basins in the early Maastrichtian. Colonies from the Swedish–Danian and the Mangyshlak–East Caspian basins show the largest autozooids, opesiae and avicularia, whereas colonies from the Polish Basin have the smallest autozooids and avicularia.

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