

EARLY OLIGOCENE BRACHIOPODS FROM THE ROCKY-SHORE DEPOSITS AT MAMMENDORF, CENTRAL GERMANY

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Abstract: Thirteen species, belonging to eleven genera, i.e., *Discinisca* Dall, *Novocrania* Lee and Brunton, *Lacazella* Munier-Chalmas, *Pliothyryna* van Roy, *Terebratulina* d'Orbigny, *Megathiris* d'Orbigny, *Argyrotheca* Dall, *Bronnothyris* Popiel-Barczyk and Smirnova, *Joania* Álvarez, Brunton and Long, *Platidia* Costa and *Megerlia* King, have been identified in the lower Oligocene rocky-shore deposits at Mammendorf, central Germany. The occurrence of the species *Discinisca fallens* (Wood), *Argyrotheca bitnerae* Dulai and *Megerlia truncata* (Linnaeus) extends their stratigraphic range back to the early Oligocene. The affinity to the early Oligocene brachiopod fauna of the Mainz Basin is noted.

Key words: Brachiopoda, early Oligocene, Rupelian, predation, North Sea Basin.

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INTRODUCTION

Cenozoic brachiopods, although of low diversity, are commonly found in the fossil benthic communities of Europe and have long been the subject of investigations. Among them, Eocene and Miocene brachiopods are especially well known. In contrast, Oligocene brachiopods were often neglected and only recently have begun to attract the attention of palaeontologists, being described systematically in several papers (e.g., Bitner and Kroh, 2011; Bitner *et al.*, 2013a, 2020; Bitner and Müller, 2015; Dulai and von der Hocht, 2020).

The present paper deals with the material that was first reported by Müller (2011a). The latter author provisionally attributed the early Oligocene brachiopods from the Mammendorf Quarry to eight species: *Discinisca* sp., *Lacazella* aff. *mediterranea* (Risso, 1826), "*Terebratula*" *grandis* (Blumenbach, 1903), *Terebratulina* sp., *Megathiris* cf. *detruncata* (Gmelin, 1791), *Argyrotheca* cf. *cuneata* (Risso, 1826), *A.* cf. *cordata* (Risso, 1826), and *Megerlia* sp. Here the authors present the revision and redescription of this interesting and rich material.

It is noteworthy that Oligocene brachiopods were described previously from nearby Magdeburg by Schreiber (1871). The latter recognized there three species and

described them under the names *Terebratula grandis* (= *Pliothyryna grandis*), *Terebratulina striatula* (= *T. tenuistriata*) and *Argiope rugosa* (= *Bronnothyris rugosa*). All these species also have been identified in the material from Mammendorf.

GEOLOGICAL SETTING

The lower Oligocene deposits, cropping out in the Mammendorf Quarry lie unconformably on Permian andesite. This is a large quarry (Cronenberger Steinindustrie, Franz Triches GmbH & Co KG), situated about 20 km NW of Magdeburg, central Germany (Fig. 1). Geologically, the quarry is located near the eastern slope of the Flechtingen Ridge. In the Palaeogene, the Flechtingen Ridge, being the northernmost rise of the Hercynian basement, played an important palaeogeographical role, separating the deeper North German Basin from the shallower marine area to the south. Until the Priabonian, the Flechtingen Ridge was an island and then became flooded and constituted a submarine barrier in the lower Oligocene (Müller, 2008, 2011a,b).

Rocky-shore environments with boulder beds developed on the andesite in two Palaeogene transgressive cycles.

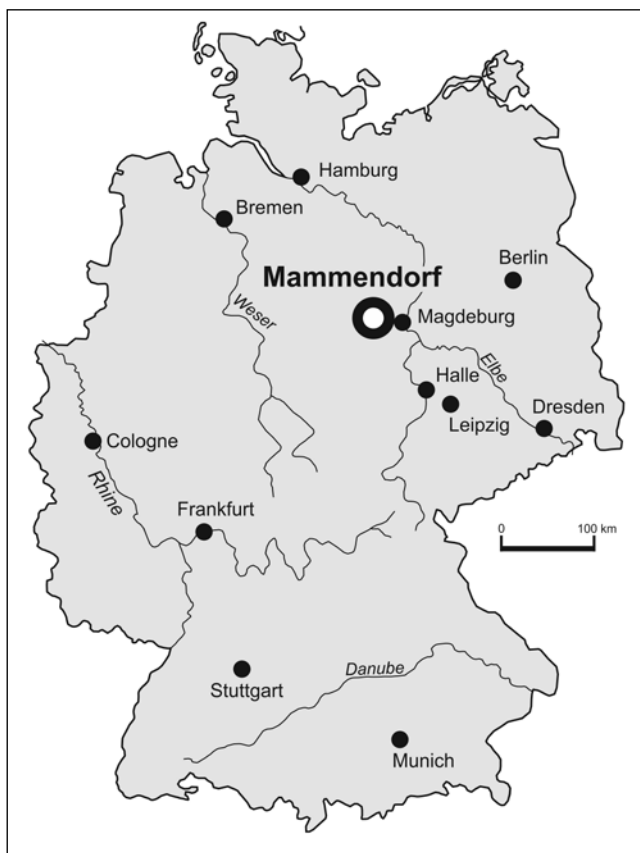


Fig. 1. Sketch map of Germany, showing the Mammendorf locality, at which the brachiopods were collected.

However, during the first cycle, the Flechtingen Ridge was not flooded completely. Extraordinarily fossil-rich sedimentary infillings were encountered in the block interstices and occasionally also in fissure fillings and larger sedimentary pockets. The lower cycle (horizons M1–M3) consists of boulder beds with glauconitic, green sands in the interstices. It contains a warm-water fauna with numerous corals, bryozoans, brachiopods and about 175 species of molluscs, with a mass occurrence of the oyster *Isognomon* and very common *Spondylus*, both characteristic for intertidal or shallow-subtidal, hard substrates (Müller, 2011a,b). This interval can be compared with the warm-water fauna of the Silberberg Formation near Latdorf (calcareous nannoplankton zone NP21). At the top of the deposits of the lower cycle, there is a brown horizon that is interpreted as palaeosol, indicating emersion. The upper cycle (horizons M4 to M7) is also characterized by boulder beds, but it contains larger sediment pockets as well. Here a transition from glauconitic sand (horizons M4/M6) to the Septaria Clay (horizon M5) and to green, hard clay (horizon M7) was observed. The faunal assemblage is also very rich but displays a structure differing from that of the first cycle. *Isognomon* and *Spondylus* are absent, but large *Angistoma* species and other molluscs are characteristic, which also typify the Magdeburg Greensand in the urban area of Magdeburg. A great number of fish otoliths, with the predominance of Gadidae, show a typical Rupelian spectrum. This stratigraphical level belongs to the nannoplankton zone NP 22 and corresponds

to Rupel 1 *sensu* Spiegler (1965). The Septaria Clay in the M5 horizon represents probably the NP23 zone. The whole upper cycle indicates rapid flooding and submerging of the Flechtingen Ridge and an abrupt transition from rocky-shore environments with boulder beds to a deeply submerged, rocky swell. For details of the geology, stratigraphy, and faunal content, see Müller (2011a).

MATERIAL AND METHODS

The material investigated was collected in the Mammendorf Quarry, central Germany (Fig. 1) during the fieldwork carried out from 2007 to 2010. Brachiopods were obtained from sediment bulk samples (about 800 kg), washed, if necessary, treated with hydrogen peroxide (horizon M7), and wet-sieved at mesh 0.4 mm. For details of the sampling, see Müller (2011a). The total number of specimens examined is 1,373 (see Tab. 1). The material is very variably preserved, from poorly to very well. There are also many fragmented shells, frequently undeterminable.

Specimens selected for scanning electron microscopy were mounted on stubs, coated with platinum and examined using a Philips XL-20 microscope at the Institute of Paleobiology, Warszawa. The collection is stored in the “Geological-Paleontological Collection” (GPSL) of the Institute for Geophysics and Geology of the Leipzig University, special collection Mammendorf (abbreviation MM_ and collection number).

SYSTEMATIC PALAEOLOGY

- Phylum Brachiopoda Duméril, 1805
 Subphylum Linguliformea Williams, Carlson, Brunton,
 Holmer and Popov, 1996
 Class Lingulata Gorjansky and Popov, 1985
 Order Lingulida Waagen, 1885
 Superfamily Discinoidea Gray, 1840
 Family Discinidae Gray, 1840
 Genus *Discinisca* Dall, 1871

Type species: *Orbicula lamellosa* Broderip, 1833, by original designation of Dall (1871).

Discinisca fallens (Wood, 1874)
 Fig. 2A–I

- 1874 *Discina fallens* – Wood, p. 172, pl. 11, fig. 6.
 2011a *Discinisca* sp. – Müller, p. 20, pl. 2, fig. 28.
 2013 *Discinisca fallens* (Wood) – Dulai, pp. 27–28, figs 15–24.
 2020 *Discinisca fallens* (Wood) – Dulai and von der Hocht, pp. 227–230, pl. 1, figs 1–12.

Material: 221 dorsal valves found in horizons M2, M3, M5, M6, M7 (Tab. 1); many specimens are fragmented.

Description: Dorsal valve thin, dark brown in colour, small (maximum observed length 7.2 mm), very variable in outline from subcircular to ovoidly elongate, often asymmetrical

Table 1

Brachiopod species recorded from the Mammendorf Quarry with the number of individuals per sampling horizons

Species	M1	M2	M3	M4	M5	M6	M7	Number of individuals
<i>Discinisca fallens</i>		6	8		9	85	113	221
<i>Novocrania</i> sp.							1	1
<i>Lacazella mediterranea</i>		1	35			1		37
<i>Pliothyryna grandis</i>	4	20	88	2	2	132	43	291
<i>Terebratulina tenuistriata</i>			10	2		43	68	123
<i>Megathiris detruncata</i>			5			38	14	57
<i>Argyrotheca bitnerae</i>		62	103		6	3	17	191
<i>Argyrotheca lunula</i>			8				6	14
<i>Argyrotheca megalcephala</i>		28	196		3	1	14	242
<i>Joania crenata</i>		20	95			2	12	129
<i>Bronnothyris rugosa</i>		12	24			4	6	46
<i>Platidia</i> sp.		3	4				2	9
<i>Megerlia truncata</i>			7			3	2	12
Number of individuals per horizon	4	152	583	4	20	312	298	1373

(see Fig. 2). Larval shell smooth, reaching about 0.4 mm (Fig. 2C, F). Shell surface smooth, marked by numerous, distinct, lamellose growth lines. Dorsal valve moderate conical in profile with the apex situated subcentrally. Muscle scars are weakly marked, often invisible; anterior adductor scars narrow, elongated, anteriorly curved in a horse-shoe-like shape (Fig. 2G).

Remarks: The specimens studied were initially assigned by Müller (2011a) to the genus level only. Dulai and von der Hocht (2020), who summarized existing knowledge about the Palaeogene and Neogene discinids of Europe, found the Mammendorf material consistent with the species *Discinisca fallens*. Originally described from the Pliocene Coralline Crag of Great Britain (Wood, 1874), this species also has been recognized in the upper Oligocene and Miocene deposits of Germany and the Netherlands (Dulai, 2013; Dulai and von der Hocht, 2020).

Externally, the specimens investigated are most similar to another species from the North Sea Basin, the Eocene *Discinisca insularis* Muir-Wood, 1939 from Great Britain. However, the shell of the latter species is larger and massive (Muir-Wood, 1939), differing strongly from the thin-shelled *D. fallens*. *Discinisca fallens* is also distinguished from *D. elslooensis* Radwańska & Radwański, 2003 from the Miocene Elsloo Conglomerate of the Netherlands; in *D. elslooensis* the shell is thick-walled, low conical to nearly flat with the apex situated subposteriorly to posteriorly (Radwańska and Radwański, 2003).

Occurrence: *Discinisca fallens* is reported from the Oligocene (Dulai and von der Hocht, 2020; this study), Miocene (Dulai, 2013) and Pliocene (Wood, 1874) of the North Sea Basin.

Subphylum Craniiformea Popov, Bassett, Holmer and Laurie, 1993

Class Craniata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Craniida Waagen, 1885

Superfamily Craniioidea Menke, 1828

Family Craniidae Menke, 1828

Genus *Novocrania* Lee and Brunton, 2001

Type species: *Patella anomala* Müller, 1776, by original designation of Lee and Brunton (1986).

Novocrania sp.

Material: One broken dorsal valve, horizon M7.

Remarks: The material is very limited and poorly preserved; the posterior part of the valve is broken. All this prevents any detailed taxonomic assessment. The valve is small, 6.3 mm in width, and thick. The anterior adductor muscle scars are ovate. Below the scars shallow, horizontally elongate depressions are visible. The support structure scars are attached to the adductor scars. The marginal rim is wide, with tubercles.

Occurrence: Early Oligocene of Mammendorf, central Germany. The genus *Novocrania* is widespread, having a stratigraphic range from Paleocene to Recent (e.g., Bitner *et al.*, 2013a; Bitner and Motchurova-Dekova, 2016; Bitner and Müller, 2017; Robinson, 2017).

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996

Class Rhynchonellata Williams, Carlson, Brunton, Holmer and Popov, 1996

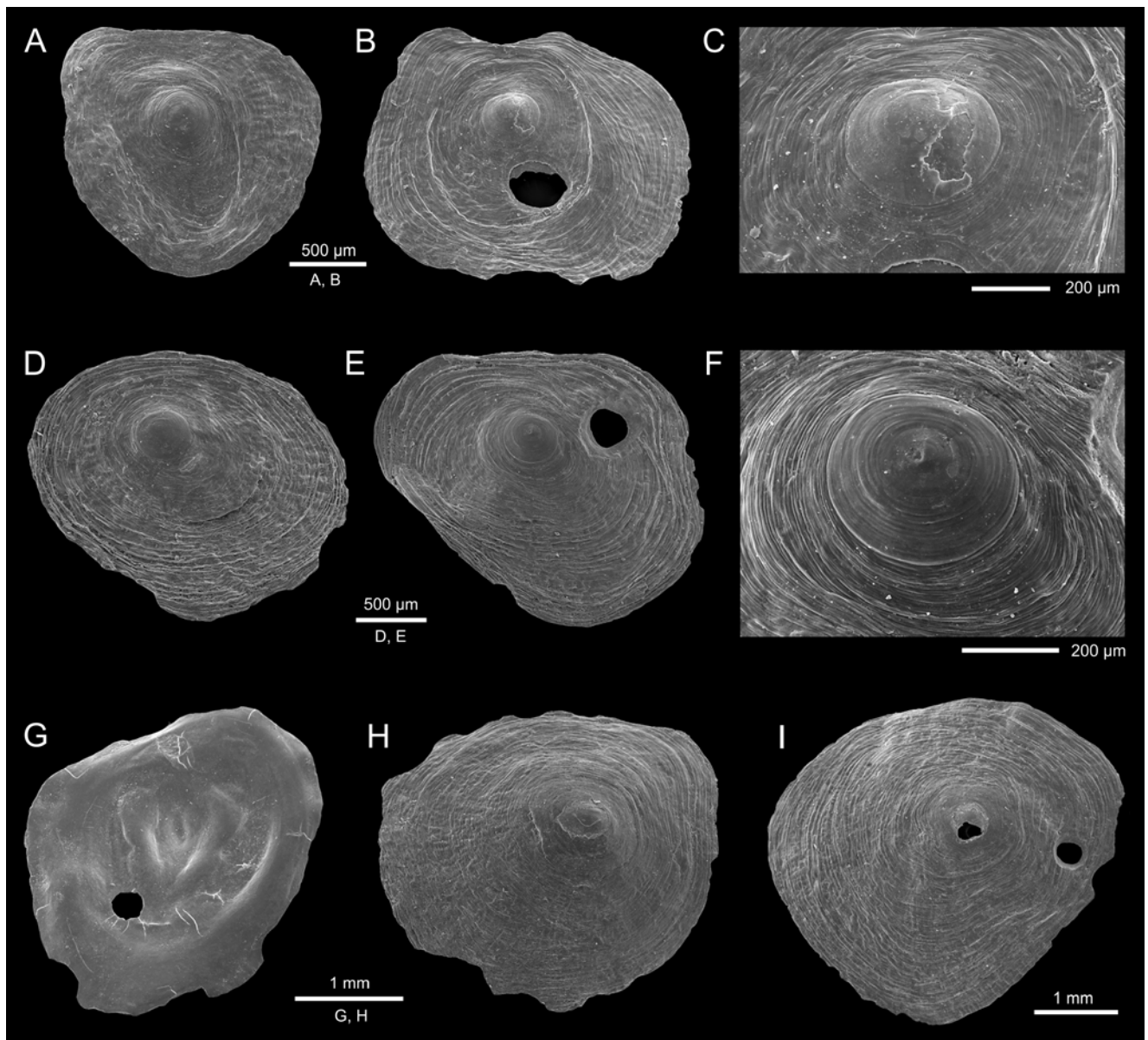


Fig. 2. *Discinisca fallens* (Wood, 1874), dorsal valves, Mammendorf, M6. **A.** Outer view of young individual, GPSL MM_869. **B, C.** Outer view and enlargement (C), showing the protegulum, GPSL MM_870. **D.** Outer view, MM_871. **E, F.** Outer view and enlargement (F), showing the apex, visible gastropod drillings, GPSL MM_872. **G.** Inner view, visible horseshoe-like anterior adductor muscle scars and well-developed limbus, GPSL MM_873. **H, I.** Outer views of adult specimens, GPSL MM_874–875. All are SEM images.

Order Thecideidea Elliott, 1958
 Superfamily Thecideoidea Gray, 1840
 Family Thecideidae Gray, 1840
 Subfamily Lacazellinae Backhaus, 1959
 Genus *Lacazella* Munier-Chalmas, 1880

Type species: *Thecidea mediterranea* Risso, 1826, by original designation of Munier-Chalmas (1880).

Lacazella mediterranea (Risso, 1826)
 Fig. 3A–J

- 1894 *Thecidium mediterraneum* L. var. *Lattorfense* Davidson – von Koenen, p. 1364, pl. 97, figs 11–16.
 1970 *Lacazella mediterranea* (Risso) – Pajaud, pp. 128–138, text-figs 50, 52, pl. 1, fig. 4; pl. 5, fig. 4; pl. 7,

fig. 3; pl. 10, figs 1–6; pl. 11, fig. 3; pl. 12, fig. 2; pl. 16 (*cum syn.*).

- 1979 *Lacazella mediterranea* (Risso) – Logan, pp. 73–76, text-fig. 22, pl. 10, figs 1–8.
 1987 *Lacazella mediterranea* (Risso) – Popiel-Barczyk and Barczyk, p. 101, pl. 3, figs 3–11.
 2005 *Lacazella mediterranea* (Risso) – Bitner and Dieni, pp. 109–110, fig. 4I–K.
 2008 *Lacazella mediterranea* (Risso) – Bitner and Dulai, p. 40, fig. 5.7–8.
 2011a *Lacazella* aff. *mediterranea* (Risso) – Müller, p. 20, pl. 3, fig. 14.
 2013a *Lacazella mediterranea* (Risso) – Bitner *et al.*, p. 595, fig. 9A–L

- 2016 *Lacazella mediterranea* (Risso) – Álvarez, pp. 37–39, pl. 4F–BB, 5A–CC, 6A–DD, 7A–JJ (*cum syn.*).
- 2017 *Lacazella mediterranea* (Risso) – Bitner and Müller, pp. 223–224, fig. 10A–M (*cum syn.*).
- 2019 *Lacazella mediterranea* (Risso) – Dulai, pp. 139–140, pl. 3, figs 21–24.
- 2019 *Lacazella mediterranea* (Risso) – Pedramara *et al.*, pp. 244–245, fig. 7A–K.
- 2020 *Lacazella mediterranea* (Risso) – Hoffmann *et al.*, p. 14, fig. 10D.

Material: One articulated specimen, three ventral and 33 dorsal valves, from the horizons M2, M3, M6 (Tab. 1).

Remarks: *Lacazella mediterranea* was already recognized in material from Mammendorf (Müller, 2011a). Its shell is small (maximum observed length 5.4 mm), with a smooth,

rough surface, strongly ventribiconvex. The ventral valve has a well-developed inter area with a convex rugideltidium, and internally with hemispondylium in forms of two small plates, supported by a short median septum (Fig. 3G, H). The dorsal valve is nearly circular with a prominent, subrectangular cardinal process and a trifurcating median septum. The inner valve margins are papillose.

Occurrence: *Lacazella mediterranea* has a very long, stratigraphic range with its oldest fossil record from the late Paleocene of Spain (Pajaud and Plaziat, 1972). In the Eocene and Oligocene of Europe, this species is widespread from France to Ukraine (von Koenen, 1894; Bitner and Dieni, 2005; Bitner and Dulai, 2008; Nebelsick *et al.*, 2011; Bitner *et al.*, 2013a; Bitner and Müller, 2017), while in the Neogene its occurrence is restricted to the Mediterranean Province (Logan *et al.*, 2004; Dulai, 2010, 2019; Hoffmann *et al.*, 2020). Recently, *L. mediterranea* was identified in

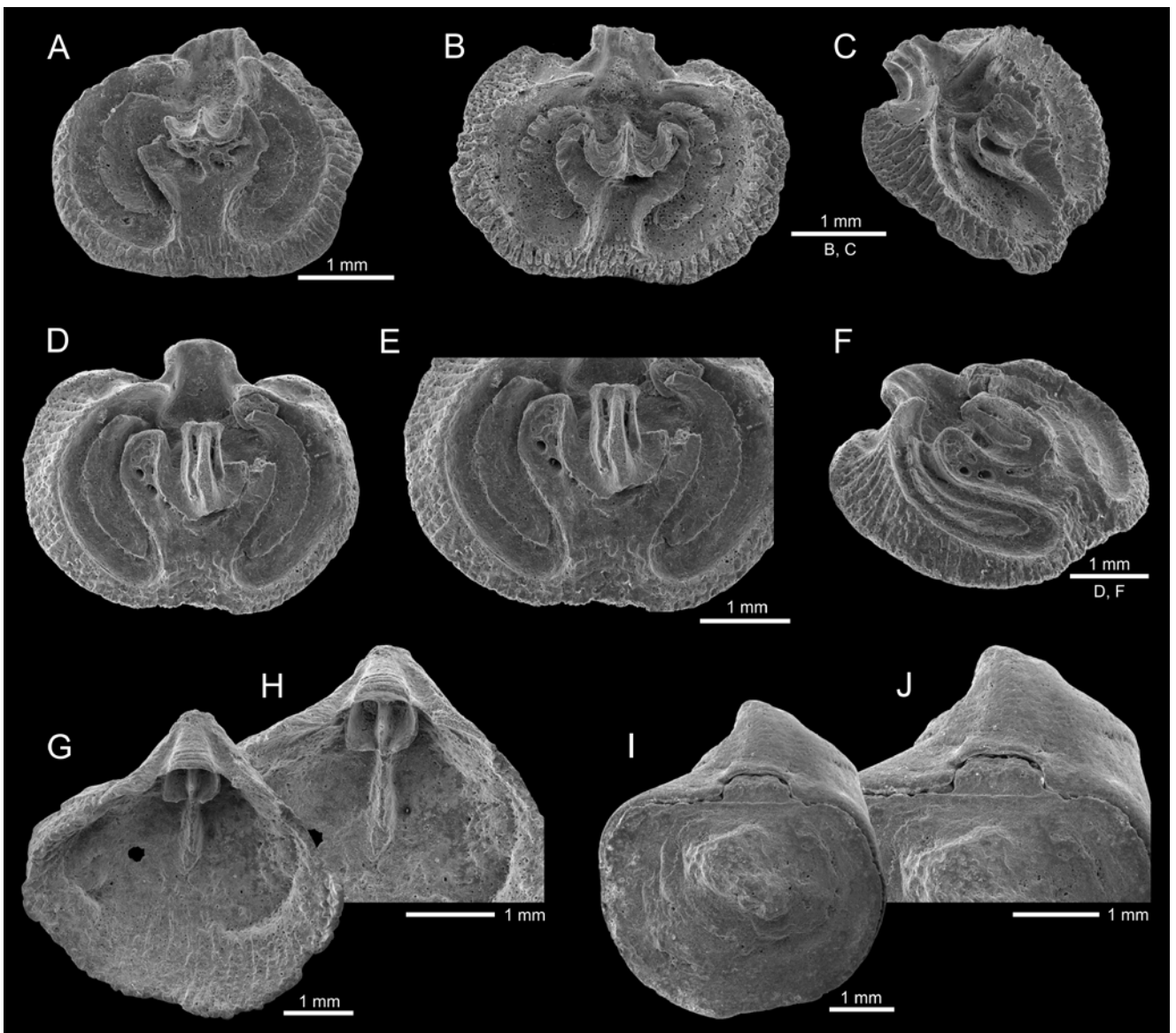


Fig. 3. *Lacazella mediterranea* (Risso, 1826), Mammendorf, M3. A–F. Inner and oblique (C, F) views of dorsal valves, and enlargement (E), showing details of brachidium, GPSL MM_877–879. G, H. Inner view of ventral valve and tilted enlargement (H), showing hemispondylium, GPSL MM_880. I, J. Dorsal view of articulated specimen and enlargement (J) of posterior part, GPSL MM_881. All are SEM images.

the early Miocene of Iran (Pedramara *et al.*, 2019). Today, it lives in the western part of the Mediterranean Sea at depth of 1–110 m (Logan, 1979, 2007; Álvarez, 2016; Emig, 2016), being considered as neoendemic to this region (Logan *et al.*, 2004).

Order Terebratulida Waagen, 1883
 Superfamily Terebratuloidea Gray, 1840
 Family Terebratulidae Gray, 1840
 Genus *Pliothyryna* van Roy, 1980

Type species: *Terebratula sowerbyana* Nyst, 1843, by original designation of van Roy (1980).

Pliothyryna grandis (Blumenbach, 1803)
 Fig. 4A–G

- 1803 *Terebratulites grandis* – Blumenbach, p. 18, pl. 1, fig. 4.
 1862 *Terebratula opercularis* – Sandberger, pl. 34, fig. 2.
 1863 *Terebratula opercularis* Sandb. – Sandberger, p. 384.
 1871 *Terebratula grandis* Blumb. – Schreiber, pp. 60–61, pl. 3, fig. 1a–c.
 1874 *Terebratula grandis* Blumenbach – Wood, p. 168, pl. 11, fig. 5a–g
 1894 *Terebratula grandis* Blumenbach – von Koenen, p. 1339, pl. 96, figs 1–3.
 1983 *Pliothyryna grandis* (Blumenbach) – Cooper, p. 237, pl. 5, figs 5, 6.
 2011a “*Terebratula*” *grandis* (Blumenbach, 1803) – Müller, p. 20, pl. 2, figs 29–31, pl. 3, figs 1, 2.
 2012 *Pliothyryna grandis* (Blumenbach) – Diedrich, p. 177, fig. 12.10.
 2015 *Pliothyryna* sp. cf. *P. grandis* (Blumenbach) – Bitner and Müller, pp. 676–677, fig. 3e–h.
 2020 *Pliothyryna grandis* (Blumenbach) – Dulai and von der Hocht, pp. 231–234, pl. 2, figs 2–25 (*cum syn.*).

Material: 38 articulated specimens, 100 ventral and 153 dorsal valves found in all horizons; there are also many fragments.

Remarks: *Pliothyryna grandis* is the most common species in the material studied, but it is poorly preserved; the majority of specimens are damaged and/or crushed. Müller (2011a) reported this species under the name “*Terebratula*” *grandis*. The smooth, short-looped Palaeogene and Neogene terebratulides, possessing inner hinge plates, are now placed in *Pliothyryna* (see van Roy, 1980; Cooper, 1983). The shell is elongate oval in outline, smooth with numerous fine growth lines. The foramen is large, subcircular, of mesothyrid type. The deltidial plates, disjunct in juvenile specimens, are conjunct in adults, forming a symphytium. The outer hinge plates are concave (Fig. 4G). The inner hinge plates form narrow, horizontal, flat plates. The loop is not preserved.

Occurrence: This species is restricted to the Oligocene of North Sea Basin (Sandberger, 1862–1863; von Koenen, 1894; Cooper, 1983; Diedrich, 2012; Bitner and Müller, 2015; Dulai and von der Hocht, 2020; this paper).

Superfamily Cancellothyridoidea Thomson, 1926
 Family Cancellothyrididae Thomson, 1926
 Subfamily Cancellothyridinae Thomson, 1926
 Genus *Terebratulina* d’Orbigny, 1847

Type species: *Anomia retusa* Linnaeus, 1758 by subsequent designation of Brunton *et al.* (1967).

Terebratulina tenuistriata (Leymerie, 1846)
 Fig. 4H–I

- 1862 *Terebratulina fasciculata* – Sandberger, pl. 34, fig. 3.
 1863 *Terebratulina fasciculata* Sandberger – Sandberger, p. 385.
 1871 *Terebratulina striatula* Sowbery – Schreiber, pp. 61–62, pl. 4, fig. 2a–c.
 2000 *Terebratulina tenuistriata* (Leymerie) – Bitner, pp. 118–120, figs 2, 3, 4A–F, 5A–G (*cum syn.*).
 2005 *Terebratulina* sp. cf. *T. tenuistriata* (Leymerie) – Bitner and Dieni, p. 108, fig. 6A.
 2008 *Terebratulina tenuistriata* (Leymerie) – Bitner and Dulai, pp. 33–35, fig. 4.1–8.
 2009 *Terebratulina tenuistriata* (Leymerie) – Bitner and Boukhary, pp. 396–397, fig. 3A–F.
 2010 *Terebratulina tenuistriata* (Leymerie) – Dulai *et al.*, p. 185, pl. 3, figs 1–11.
 2011 *Terebratulina tenuistriata* (Leymerie) – Bitner *et al.*, pp. 122–124, fig. 3A–C.
 2011 *Terebratulina tenuistriata* (Leymerie) – Dulai, pp. 299–300, fig. 4.
 2011a *Terebratulina* div. sp. – Müller, p. 20.
 2012 *Terebratulina tenuistriata* (Leymerie) – Bitner and Boukhary, fig. 2C, D.
 2015 *Terebratulina tenuistriata* (Leymerie) – Bitner and Müller, pp. 677–678, fig. 4A–F.
 2017 *Terebratulina tenuistriata* (Leymerie) – Bitner and Müller, pp. 214–216, fig. 3A–H (*cum syn.*).
 2020 *Terebratulina tenuistriata* (Leymerie) – Bitner *et al.*, p. 171, fig. 4B–G.

Material: 54 complete specimens, 28 ventral valves, 41 dorsal valves found in the horizons M3, M4, M6, M7 (see Tab. 1).

Remarks: The species *Terebratulina tenuistriata* is relatively common in the material studied and is represented mostly by juvenile individuals. All larger specimens are crushed and/or damaged. Müller (2011a) noted the presence of *Terebratulina* at Mammendorf, however, without assignment to any particular species. The specimens investigated are small, with the lengths rarely exceeding 10 mm. Their shell is elongate oval in outline, ornamented by numerous, fine ribs.

Occurrence: *Terebratulina tenuistriata* is common and widely distributed in the Eocene of Europe, from Great Britain and Spain to Ukraine (e.g., Bitner, 2000; Bitner and Dulai, 2008; Dulai, 2011; Bitner and Müller, 2017), also reported from the Eocene of Egypt and the United Arab Emirates (Bitner and Boukhary, 2009, 2012). Recently, this species was also identified in the lower Oligocene deposits of Germany and Italy (Bitner and Müller, 2015; Bitner *et al.*, 2020).

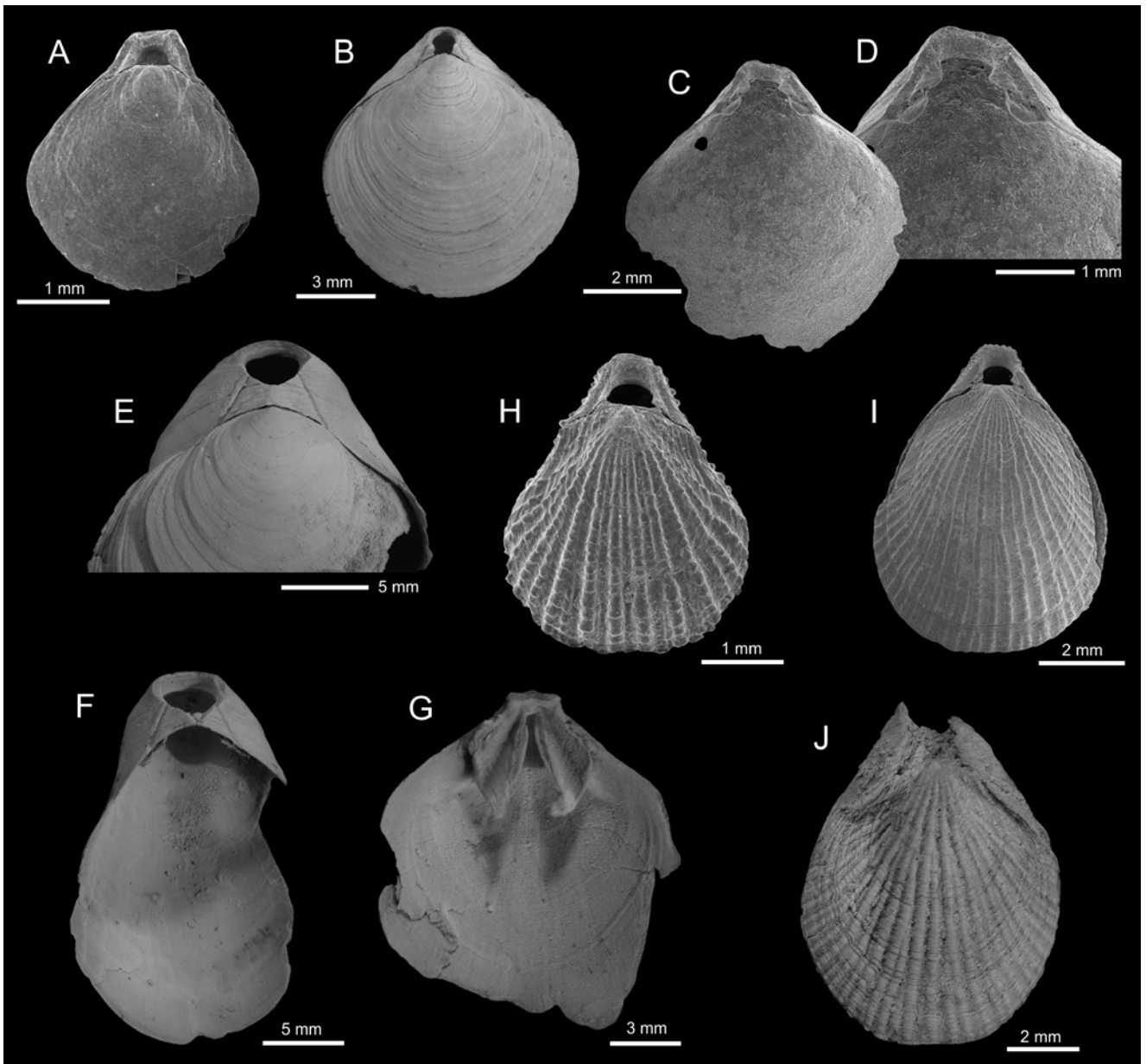


Fig. 4. *Pliothyris grandis* (Blumenbach, 1803) and *Terebratulina tenuistriata* (Leymerie, 1846), Mammendorf. **A–G.** *Pliothyris grandis* (Blumenbach, 1803); A, B – dorsal views of articulated juvenile specimens, A – M3, GPSL MM_882, B – M2, MM_883; C, D – interior view of ventral valve of juvenile specimen, and enlargement (D) of the umbonal part, M3, GPSL MM_884; E – dorsal view of articulated specimen, posterior part, showing details of the beak, M1, GPSL MM_885; F – interior of ventral valve, M6, GPSL MM_886; G – interior view of dorsal valve, visible cardinalia with outer and inner hinge plates, M1, GPSL MM_887. **H–J.** *Terebratulina tenuistriata* (Leymerie, 1846), dorsal views of articulated specimens, M6, GPSL MM_890–892. A, D, G–H are SEM images.

Superfamily Megathyridoidea Dall, 1870
 Family Megathyrididae Dall, 1870
 Genus *Megathiris* d'Orbigny, 1847

Type species: *Anomia detruncata* Gmelin, 1791, by subsequent designation of Dall (1920).

Megathiris detruncata (Gmelin, 1791)
 Fig. 5A–H

1864 *Argiope multicostata* – Bosquet, p. 3, figs 1–5.

1894 *Argiope multicostata* Bosquet – von Koenen, p. 1357, pl. 98, figs 16, 17.

1990 *Megathiris detruncata* (Gmelin) – Bitner, pp. 135–138, text-figs 3, 4; pl. 3, figs 1–8; pl. 6, figs 1–7 (*cum syn.*).

2003 *Megathiris detruncata* (Gmelin) – Bitner and Moissette, pp. 473–474, fig. 6G, H.

2004 *Megathiris detruncata* (Gmelin) – Bitner and Dulai, pp. 74–75, pl. 3, figs 11–15.

2007 *Megathiris detruncata* (Gmelin) – Dulai, pp. 2–3, fig. 2.1, 2.2.

2008 *Megathiris detruncata* (Gmelin) – Bitner and Dulai, pp. 35–36, fig. 5.1–5.4.

2009 *Megathiris detruncata* (Gmelin) – Bitner and Schneider, p. 127, fig. 6A–C.

- 2010 *Megathiris detruncata* (Gmelin) – Dulai, p. 26, pl. 3, fig. 1a, b.
 2011 *Megathiris detruncata* (Gmelin) – Dulai, p. 305, fig. 8A, B.
 2011a *Megathiris* cf. *detruncata* (Gmelin) – Müller, p. 20, pl. 3, figs 11–13.
 2012 *Megathiris detruncata* (Gmelin) – Zágoršek *et al.*, p. 27, fig. 6D, E.
 2013a *Megathiris detruncata* (Gmelin) – Bitner *et al.*, pp. 586–588, fig. 3A–M
 2013b *Megathiris detruncata* (Gmelin) – Bitner *et al.*, pp. 83–84, fig. 3J–L
 2016 *Megathiris detruncata* (Gmelin) – Bitner and Motchurova-Dekova, pp. 10–12, fig. 3A–L.
 2017 *Megathiris detruncata* (Gmelin) – Bitner and Müller, p. 216, fig. 4A–L.
 2019 *Megathiris detruncata* (Gmelin) – Pedramara *et al.*, pp. 241–242, fig. 5A
 2020 *Megathiris detruncata* (Gmelin) – Hoffmann *et al.*, p. 14, fig. 11C–I.
 2020 *Megathiris detruncata* (Gmelin) – Bitner *et al.*, pp. 172–173, fig. 4A.

Material: One articulated specimen, 25 ventral and 31 dorsal valves found in the horizons M3, M6, M7 (Tab. 1).

Remarks: Although relatively rare in the assemblage investigated, this species was already noted from Mammendorf (Müller, 2011a). Its shell is small, not exceeding 4 mm in length, transversely elongate with a long, straight hinge margin. The surface is covered with broad, rounded ribs. The presence of three septa on the interior of the dorsal valve makes *Megathiris detruncata* easily distinguishable and unique among megathyrinids.

In shell outline and ornamentation of broad, rounded ribs *M. detruncata* resembles *Bronnothyris rugosa* (Schreiber, 1871), however, clearly differing internally. The latter species has one dorsal septum and very wide, fused hinge plates.

Occurrence: *Megathiris detruncata* is a long ranging species, known since the Eocene (e.g., Bitner and Dulai, 2008; Dulai *et al.*, 2010; Dulai, 2011; Bitner and Müller, 2017). In the Oligocene being known only from few records (Bosquet, 1864; Bitner *et al.*, 2013a, 2020; this study), this species is very common and widespread in the Neogene of Europe (see Gaetani and Saccà, 1985; Bitner, 1990; Bitner and Dulai, 2004; Dulai, 2007; Bitner and Schneider, 2009;

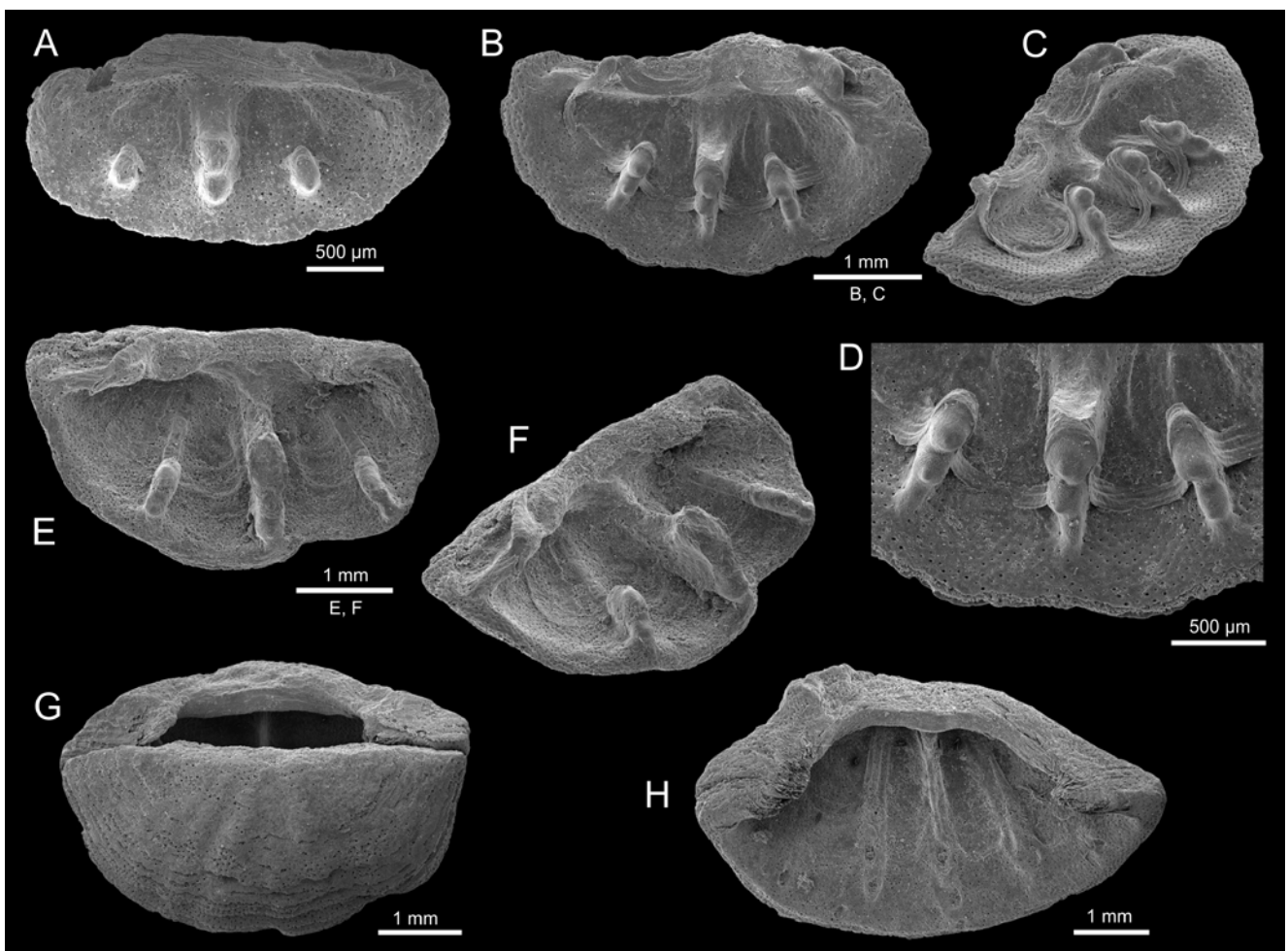


Fig. 5. *Megathiris detruncata* (Gmelin, 1791), Mammendorf; **A.** Inner view of dorsal valve of young individual, M7, GPSL MM_894. **B–D.** Inner and oblique views of dorsal valve, and enlargement (D) of the anterior part, showing descending lamellae fused to the septa, M6, GPSL MM_895; **E, F.** Inner and oblique views of dorsal valve, M6, GPSL MM_896. **G.** Dorsal view of articulated specimen, M6, GPSL MM_897. **H.** Inner view of ventral valve, M6, GPSL MM_898. All are SEM images.

Zágoršek *et al.*, 2012; Bitner *et al.*, 2013b; Bitner and Motchurova-Dekova, 2016; Hoffman *et al.*, 2020). Recently *M. detruncata* was also recognized in the lower Miocene of Iran (Pedramara *et al.*, 2019). Its Recent representatives live in the Mediterranean Sea and the north-eastern Atlantic at depths from 5 to 896 m (Logan, 2007).

Genus *Argyrotheca* Dall, 1900

Type species: *Terebratulula cuneata* Risso, 1826, by original designation of Dall (1900).

Argyrotheca bitnerae Dulai in Dulai and Stachacz, 2011
Fig. 6A–I

- 2011a *Argyrotheca* cf. *cordata* (Risso) – Müller, p. 20, pl. 3, figs 3, 4 (non figs 5, 6).
2011 *Argyrotheca bitnerae* n. sp. – Dulai in Dulai and Stachacz, pp. 285–289, figs 3: 1–11, 4: 1–6 (*cum syn.*).
2013a *Argyrotheca bitnerae* Dulai – Bitner *et al.*, pp. 588–590, fig. 5A–M, table 5.
2014 *Argyrotheca bitnerae* Dulai – Hladilová *et al.*, p. 268, fig. 4E–J.
2015 *Argyrotheca bitnerae* Dulai – Dulai, pp. 196–197, pl. 4, figs 6–9.
2018 *Argyrotheca bitnerae* Dulai – Kopecká *et al.*, p. 27, fig. 9F–I.
2019 *Argyrotheca bitnerae* Dulai – Pedramara *et al.*, p. 243, fig. 5B–F.
2020 *Argyrotheca bitnerae* Dulai – Dulai and von der Hocht, pp. 234–235, pl. 3, figs 1–8.

Material: 53 articulated specimens, 78 ventral and 60 dorsal valves, horizons M2, M3, M5, M6, M7 (Tab. 1).

Remarks: *Argyrotheca bitnerae* is one of the commonest species in the material investigated. Some specimens, attributed by Müller (2011a) to *Argyrotheca* cf. *cordata*, clearly represent *A. bitnerae* (see also Dulai and von der Hocht, 2020, p. 235). Its shell is very small (hardly exceeding 2 mm), triangular in outline, smooth except for concentric growth lines, weakly biconvex. The beak is high, with a large, triangular, hypothyril foramen, bordered by two narrow, elevated deltidial plates. The dorsal median septum is high, triangular in profile, without serrations. On the elevated part of the septum, there is a small swollen boss (Fig. 6G–I).

Externally, this species is similar to *Argyrotheca megalcephala* (Sandberger, 1862), differing in the character of the dorsal median septum; in *A. megalcephala* the septum has numerous serrations. From any smooth *Joania* species *A. bitnerae* can be distinguished by lacking marginal tubercles.

Occurrence: Originally described from the middle Miocene of the Central Paratethys (Dulai and Stachacz, 2011; Hladilová *et al.*, 2014; Dulai, 2015; Kopecká *et al.*, 2018), this species was also identified in the lower Miocene of Iran (Pedramara *et al.*, 2019) and upper Oligocene of France and Germany (Bitner *et al.*, 2013a; Dulai and von der Hocht, 2020). The present discovery at

Mammendorf in the early Oligocene is its oldest known fossil record.

Argyrotheca lunula (von Koenen, 1894)
Fig. 6J–N

- 1894 *Argiope lunula* – von Koenen, p. 1360, pl. 98, figs 6–10.
1894 *Argiope lunula* var. *percostata* – von Koenen, p. 1361, pl. 98, figs 11–13.
1975 *Megathyris lunula percostata* (von Koenen) – Zelinskaya, pp. 124–125, pl. 16, figs 6–12.
1987 *Argyrotheca lunula* (Koenen) – Popiel-Barczyk and Barczyk, pp. 98–99, text-fig. 5, pl. 2, figs 1–3.
2017 *Argyrotheca lunula* (von Koenen) – Bitner and Müller, pp. 216–219, fig. 5A–M.

Material: One juvenile articulated specimen, five ventral and eight dorsal valves, horizons M3, M7 (Tab. 1).

Remarks: This species, originally described from the late Eocene/early Oligocene of west Germany (von Koenen, 1894), is very rare in the Mammendorf material. It is characterized by ornamentation of broad, rounded ribs, a long, straight hinge margin and a wide interarea, truncated by a large, triangular, hypothyril foramen. The pedicle collar is well-developed, supported by a septum. In the dorsal valve, the hinge plates are attached to the septum, forming a broad, shallow trough (Fig. 6M). In size, shape, and ornamentation of broad, rounded ribs, *Argyrotheca lunula* resembles *Megathyris detruncata* and *Bronnothyris rugosa*, two other megathyridid species recognized in the material under study. It differs, however, internally from those species; from *M. detruncata* in having a single dorsal septum, whereas from *B. rugosa* in having narrow hinge plates and lacking septal flanges, extending from the dorsal septum.

Occurrence: Apart from the upper Eocene/lower Oligocene deposits of Germany (von Koenen, 1894; this study), *Argyrotheca lunula* is also recorded from the upper Eocene of southern Poland and eastern Ukraine (Popiel-Barczyk and Barczyk, 1987; Bitner and Müller, 2017).

Argyrotheca megalcephala (Sandberger, 1862)
Fig. 7A–L

- 1862 *Argiope megalcephala* – Sandberger, pl. 34, fig. 7.
1863 *Argiope megalcephala* Sandberger – Sandberger, pp. 387–388.

Material: 83 articulated specimens, 61 ventral and 98 dorsal valves, found in the horizons M2, M3, M5, M6, M7 (see Tab. 1).

Description: Shell small, not exceeding 3 mm in length, subtriangular to subpentagonal in outline, with shallow anterior sulcus. Shell surface smooth, except for growth lines. Beak high with sharp beak ridges. Foramen large, triangular, hypothyril, bordered by narrow, raised deltidial plates. Shell coarsely punctuate.

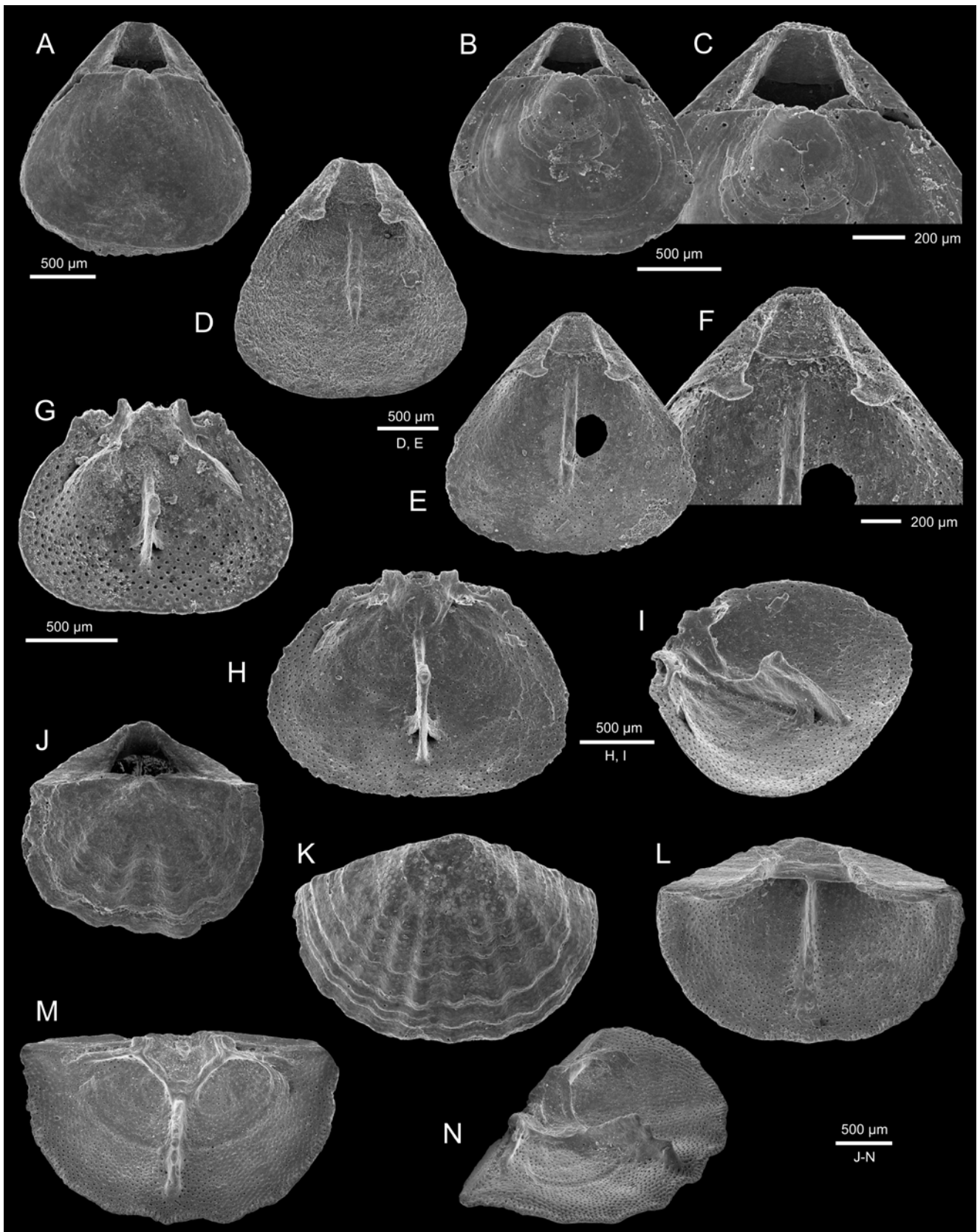


Fig. 6. *Argyrotheca bitnerae* Dulai in Dulai and Stachacz, 2011, and *Argyrotheca lunula* (von Koenen, 1894), Mammendorf. A–I. *Argyrotheca bitnerae* Dulai in Dulai and Stachacz, 2011; A–C – dorsal views of articulated specimens and enlargement (C) of the umbonal part, showing details of the beak, M2, GPSL MM_899, 900; D–F – inner views of ventral valves, and enlargement (F) of posterior part, M2, GPSL MM_901-902; G – inner view of juvenile dorsal valve, M7, GPSL MM_903; H, I – inner and oblique views of dorsal valve, M2, GPSL MM_904. J–N. *Argyrotheca lunula* (von Koenen, 1894), M3; J – dorsal view of articulated juvenile specimen, GPSL MM_905; K, L – outer and inner views of ventral valve, GPSL MM_906; M, N – inner and oblique views of dorsal valve, GPSL MM_907. All are SEM images.

Ventral valve interior with wide pedicle collar, supported by a median septum and hooked teeth. Dorsal valve interior with well-developed inner socket ridges and distinct cardinal process. Crural processes short, directed medially (Fig. 7J). Descending branches of loop extend only shortly, before uniting with valve floor, and emerge anteriorly to join the median septum. Median septum high, thin, triangular in profile, with up to seven serrations (Fig. 7L).

Remarks: *Argyrotheca megalocéphala* is the second most common species in the material under study. Originally, this species was described from the lower Oligocene of the Mainz Basin by Sandberger (1862–1863). Although Sandberger (1862) did not mention the internal structure, it is the only lower Oligocene species from central Germany with a smooth surface and shallow sulcus, thus the present authors decided to attribute the specimens to his species

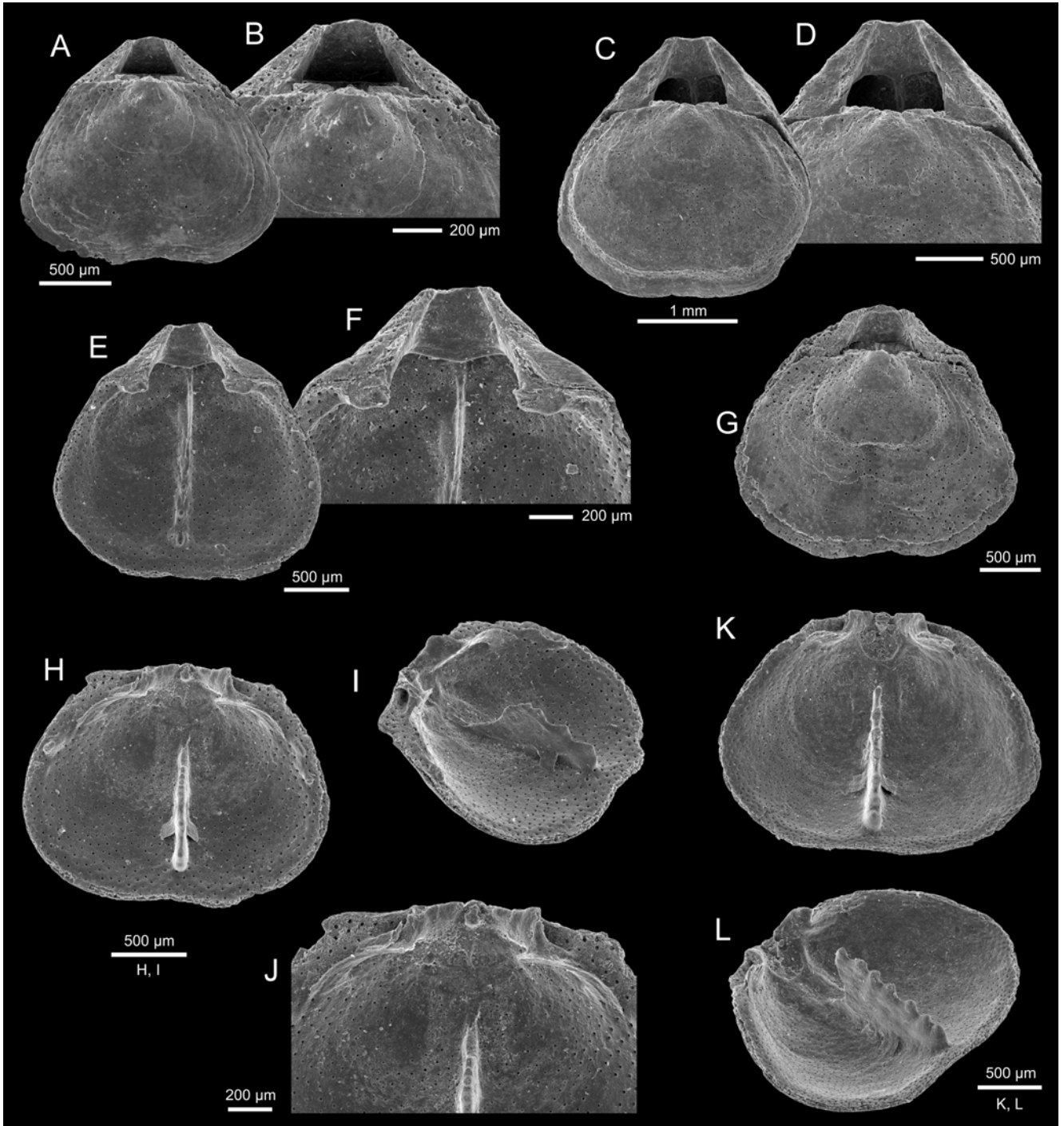


Fig. 7. *Argyrotheca megalocéphala* (Sandberger, 1862), Mammendorf. **A, B.** Dorsal view of juvenile articulated specimen and enlargement (B) of umbonal part, M3, GPSL MM_908. **C, D.** Dorsal view of articulated specimen and enlargement (D) of umbonal part, showing details of the beak, M2, GPSL MM_909. **E, F.** Inner view of ventral valve and enlargement of umbonal part, showing details of pedicle collar and teeth, M3, GPSL MM_910; **G.** Dorsal view of articulated specimen, M3, GPSL MM_911. **H–J.** Inner and oblique views of dorsal valve, and enlargement (J) of cardinalia, M3, GPSL MM_912. **K, L.** Inner and oblique views of dorsal valve, M3, GPSL MM_913. All are SEM images.

rather than create a new one. The smooth surface is observed as well in *Argyrotheca bitnerae*, but it lacks a sulcus. Those two species are easily distinguishable internally; the median dorsal septum in *A. bitnerae* is without serrations.

Externally, *A. megalcephala* is similar to *Joania cordata* (Risso, 1826), already noted by Sandberger (1863), who indicated the similarity to *Argiope neapolitana*, now *Joania cordata*. However, the absence of marginal tubercles in *A. megalcephala* makes the latter species clearly different internally from *J. cordata* that has distinct tubercles on the inner margins (Álvarez *et al.*, 2008).

Occurrence: This species is known so far only from the early Oligocene of the Mainz Basin and Mammendorf (Sandberger, 1862–1863; this study).

Genus *Bronnothyris* Popiel-Barczyk and Smirnova, 1978

Type species: *Terebratula brononii* Roemer, 1841, by original designation of Popiel-Barczyk and Smirnova (1978).

Bronnothyris rugosa (Schreiber, 1871)
Fig. 8A–L

- 1871 *Argiope rugosa* – Schreiber, p. 62, pl. 4, fig. 3a–d.
2011a *Argyrotheca* cf. *cuneata* (Risso) – Müller, p. 20, pl. 3, figs 7–10.
2011a *Argyrotheca* sp. – Müller, p. 20, pl. 3, figs 9, 10.

Material: Five articulated specimens, 15 ventral and 26 dorsal valves found in the horizons M2, M3, M6, M7 (Tab. 1).

Description: Shell small with length not exceeding 4.0 mm, thick, subrectangular in outline, wider than long, ventribiconvex. Shell surface ornamented by up to 10 broad, rounded ribs, forming scalloped anterior and lateral margins; growth lines numerous and distinct. Beak low, suberect with sharp beak ridges. Foramen large, subtriangular, hypothyril, bordered by narrow deltidial plates. Hinge line long, straight.

Ventral valve interior with short, wide teeth and wide pedicle collar, supported by a median septum; anterior to the septum there are small, shallow depressions to accommodate serrations of dorsal septum. Dorsal valve interior with widely divergent short inner socket ridges. Outer and inner hinge plates broad, fused, forming a single, coherent platform. Dorsal septum high, triangular in profile, with 3 serrations. Short septal flanges extend ventrally from the septum (Fig. 8K, L).

Remarks: This species, originally described as *Argiope rugosa* from the Oligocene deposits of the Magdeburg area (Schreiber, 1871), has been transferred here to the genus *Bronnothyris* on the basis of the presence of the septal flanges, which extend ventrally from the dorsal septum, the characteristic feature of this genus (Popiel-Barczyk and Smirnova, 1978). In his preliminary description of the Mammendorf fauna, Müller (2011a) assigned the specimens investigated to *Argyrotheca* cf. *cuneata* (Risso, 1826).

The broad, fused hinge plates in form of a single plate are also observed in two other *Bronnothyris* species, the late Eocene *B. danaparensis* Bitner and Müller, 2017 from Ukraine and the early Oligocene *B. subradiata* (Sandberger, 1862) from the Mainz Basin. However, those species differ

strongly from *B. rugosa* externally. In *B. danaparensis* the shell surface is smooth, marked only by distinct growth lines (Bitner and Müller, 2017), while *B. subradiata* has a high beak and is ornamented by weakly defined ribs (Sandberger, 1862–1863; Bitner and Kroh, 2011). In coarsely ribbed ornamentation the specimens investigated are close to *Bronnothyris rugicosta* (Zelinskaya, 1975) from the early Paleocene of Ukraine, however, differing internally in the character of the hinge plates, which are very narrow in the species from Ukraine (Zelinskaya, 1975; Smirnova *et al.*, 1983).

Occurrence: Oligocene of the Magdeburg region (Schreiber, 1871; this paper).

Genus *Joania* Álvarez, Brunton and Long, 2008

Type species: *Terebratula cordata* Risso, 1826, by original designation of Álvarez *et al.* (2008).

Joania crenata (Sandberger, 1862)
Figs 9A–J, 10A–I

- 1862 *Argiope crenata* – Sandberger, pl. 34, fig. 5.
1863 *Argiope crenata* Sandberger – Sandberger, p. 387.
2011a *Argyrotheca* cf. *cordata* (Risso) – Müller, p. 20, pl. 3, figs 5, 6.

Material: 27 articulated specimens, 40 ventral and 62 dorsal valves found in the horizons M2, M3, M6, M7 (Tab. 1).

Description: Shell small (rarely exceeding 3 mm), coarsely punctate, variable in outline from rounded subrectangular, subpentagonal to elongate oval, biconvex with dorsal valve more convex. Shell surface covered with 10–12 low, broad ribs. Beak high with sharp beak ridges and a large, triangular, hypothyril foramen bordered by two narrow deltidial plates. Anterior commissure rectimarginate.

Ventral valve interior with hook-like teeth and pedicle collar supported by a low median septum. Dorsal valve interior with well-developed inner socket ridges, extending beyond the margin. Cardinal process distinct, shafted (Fig. 10C, D, I). Crura not developed or extremely short, crural processes medially directed. Descending branches rapidly absorbed into valve floor, emerging to attach to the dorsal septum. Median septum high, triangular in profile, not connected to cardinal process, sloping by 5 to 7 serrations (Fig. 10B, F, H). Tubercles on inner margin of both valves, being more distinct on dorsal valve.

Remarks: This species was originally described from the lower Oligocene of the Mainz Basin, Germany under the name *Argiope crenata* by Sandberger (1862–63). The presence of marginal tubercles that are considered as a diagnostic character of the genus *Joania* (see Álvarez *et al.*, 2008) indicates the assignment to this genus.

In the character of the shallow, rounded ribs, the specimens from Mammendorf are similar to the species *Joania ageriana* (Taddei Ruggiero, 1993) from the lower Pleistocene of southern Italy. However, the number of ribs in *J. ageriana* is much higher, up to 18. Additionally, the latter species is larger, reaching 7 mm in length (Taddei Ruggiero, 1993). Another ribbed *Joania* species, *J. ukrainica* Bitner

and Müller, 2017 from the late Eocene of Ukraine has more distinct ribs with deeper grooves between them, differing clearly from *J. crenata*. The median dorsal septum in *J. ukrainica* is lower and thicker (Bitner and Müller, 2017). *Joania crenata* is also distinguished from the late Oligocene species from the Aquitaine Basin, SW France, *Joania peyrerensis* Bitner, Lozouet and Cahuzac, 2013.

In the latter species, the ribs are fewer and extended with large spaces between them, and its median dorsal septum is lower, with four serrations (Bitner *et al.*, 2013a).

Occurrence: This species is known exclusively from the lower Oligocene of Germany (Sandberger, 1862–1863; this study).

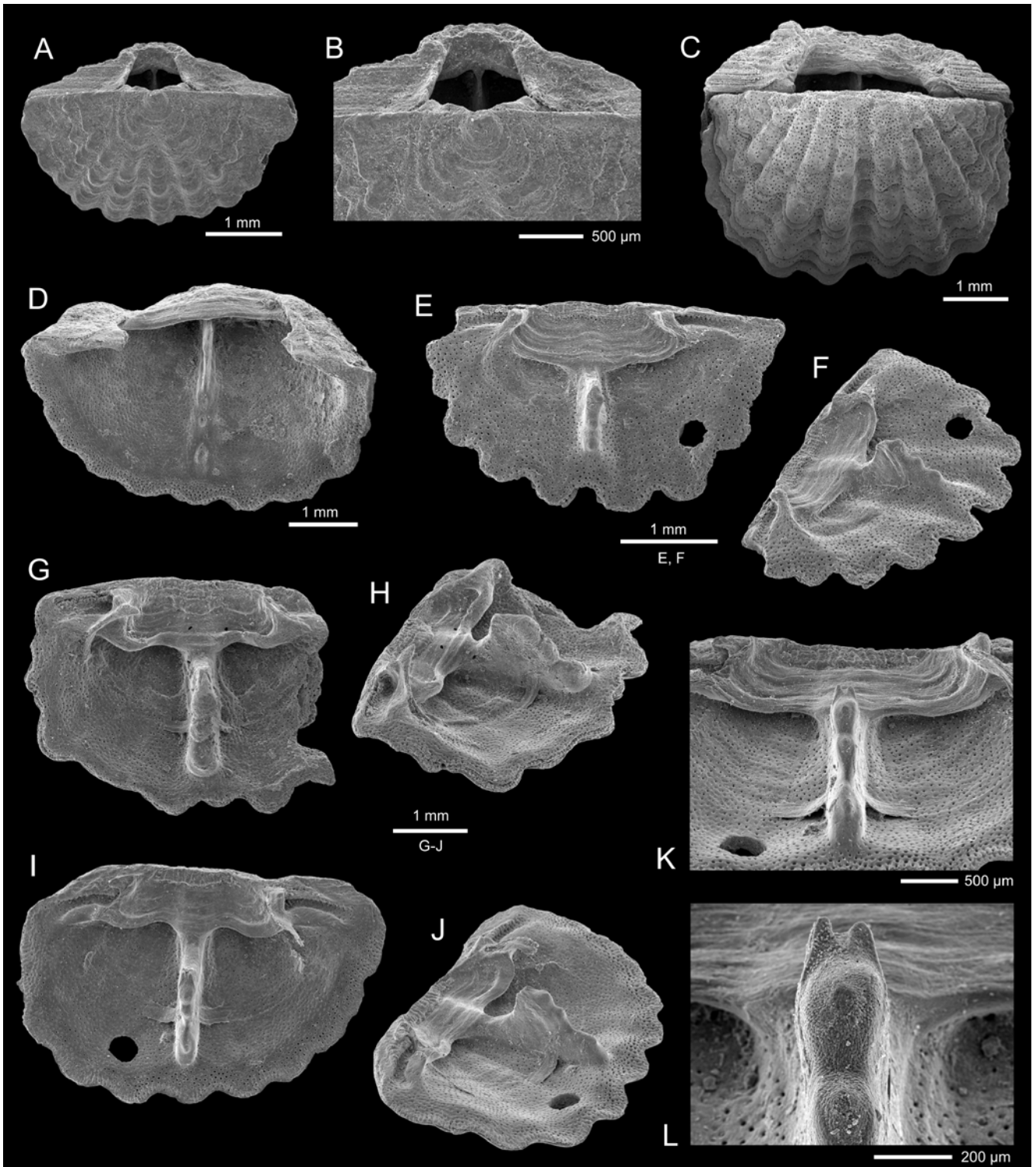


Fig. 8. *Bronnothyris rugosa* (Schreiber, 1871), Mammendorf, M2. **A–C.** Dorsal views of articulated specimens and enlargement (**B**) of the umbonal part, GPSL MM_915, 916. **D.** Inner view of ventral valve, GPSL MM_917. **E–H.** Inner and oblique views of dorsal valves, GPSL MM_918, 919. **I–L.** Inner and oblique views of dorsal valve, and enlargement tilted (**K**, **L**) of median septum, showing extended septal flanges, GPSL MM_920. All are SEM images.

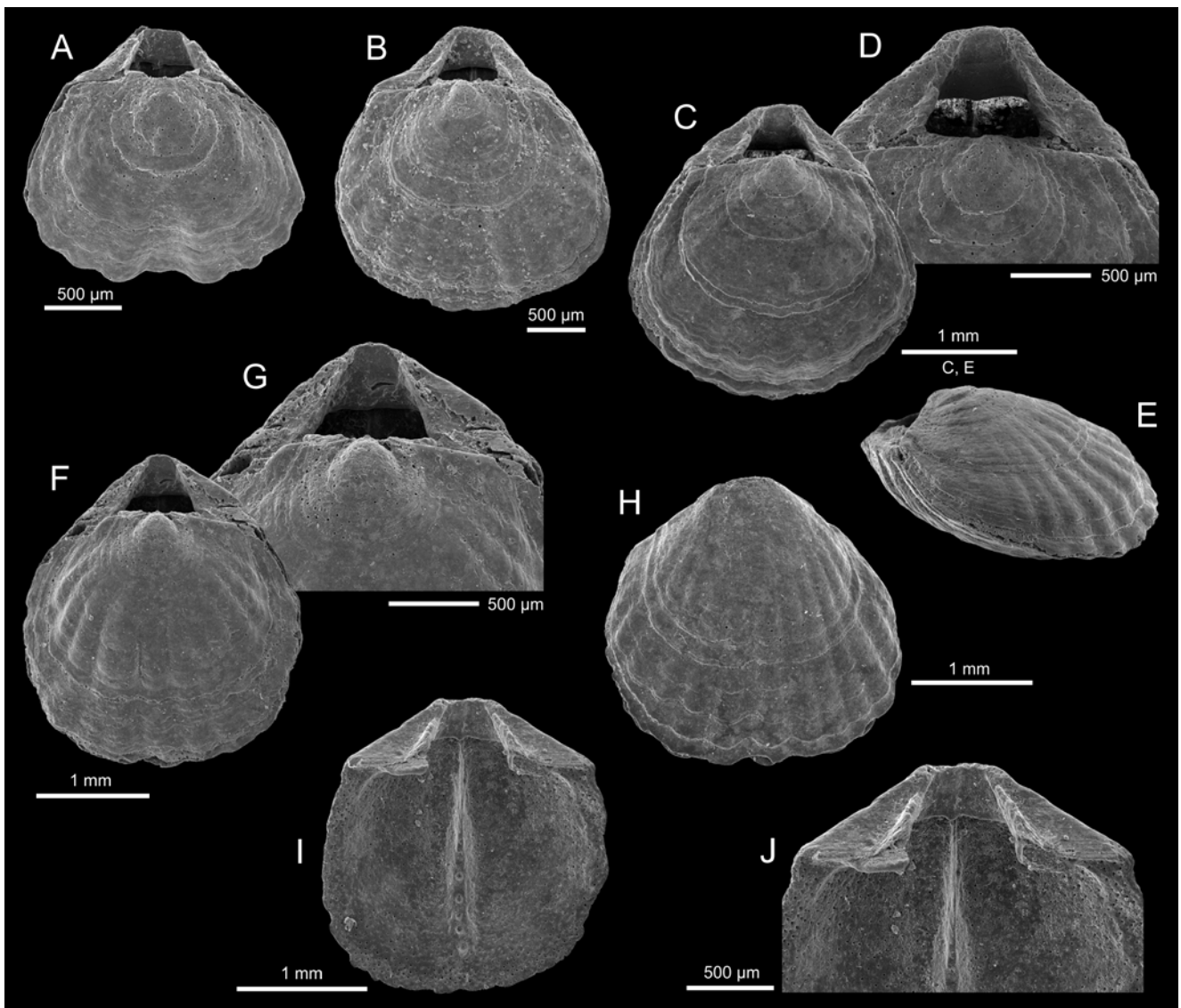


Fig. 9. *Joania crenata* (Sandberger, 1862), Mammendorf. **A, B.** Dorsal views of articulated specimens, M2, GPSL MM_921, 922; **C–E.** Dorsal view of articulated specimen, and enlargement (**D**) of umbonal part and oblique view (**E**), showing ornamentation, M3, GPSL MM_923. **F, G.** Dorsal view of articulated specimen and enlargement (**G**) of umbonal part, M2, GPSL MM_924. **H.** Ventral view of articulated specimen, M3, GPSL MM_925. **I, J.** Inner view of ventral valve and enlargement (**J**) of posterior part, showing details of pedicle collar and teeth, M3, GPSL MM_926. All are SEM images.

Superfamily Platidioidea Thomson, 1927
 Family Platidiidae Thomson, 1927
 Subfamily Platidiinae Thomson, 1927
 Genus *Platidia* Costa, 1852

Type species: *Orthis anomioides* Scacchi and Philippi in Philippi, 1844, by original designation of Costa (1852).

Platidia sp.
 Fig. 11A, B

Material: Five articulated specimens, 4 ventral valves, horizons M2, M3, M7 (Tab. 1).

Remarks: *Platidia* is very rare in the material studied. Its state of preservation precludes any possibility of examining internal structures and assignment to the species level. However, the specimens display typical features of

this genus, such as small size, smooth surface and large, rounded, amphithyrid foramen. The hinge line is short and straight.

Occurrence: The oldest record of the genus *Platidia* is from the Paleocene of Denmark (Johansen, 1987). Although usually not very common, *Platidia* is known from many localities of Palaeogene and Neogene deposits (e.g., Bitner, 1990; Bitner and Dulai, 2004; Dulai, 2011; Bitner *et al.*, 2013b; Hladilová *et al.*, 2014; Bitner and Motchurova-Dekova, 2016; Bitner and Müller, 2017; Pedramara *et al.*, 2019). Today, this genus, represented by five species, is living in all oceans, having a very wide depth range from 8 to 2,190 m (Logan, 2007).

Superfamily Kraussinoidea Dall, 1870
 Family Kraussinidae Dall, 1870
 Subfamily Megerliinae Hiller,

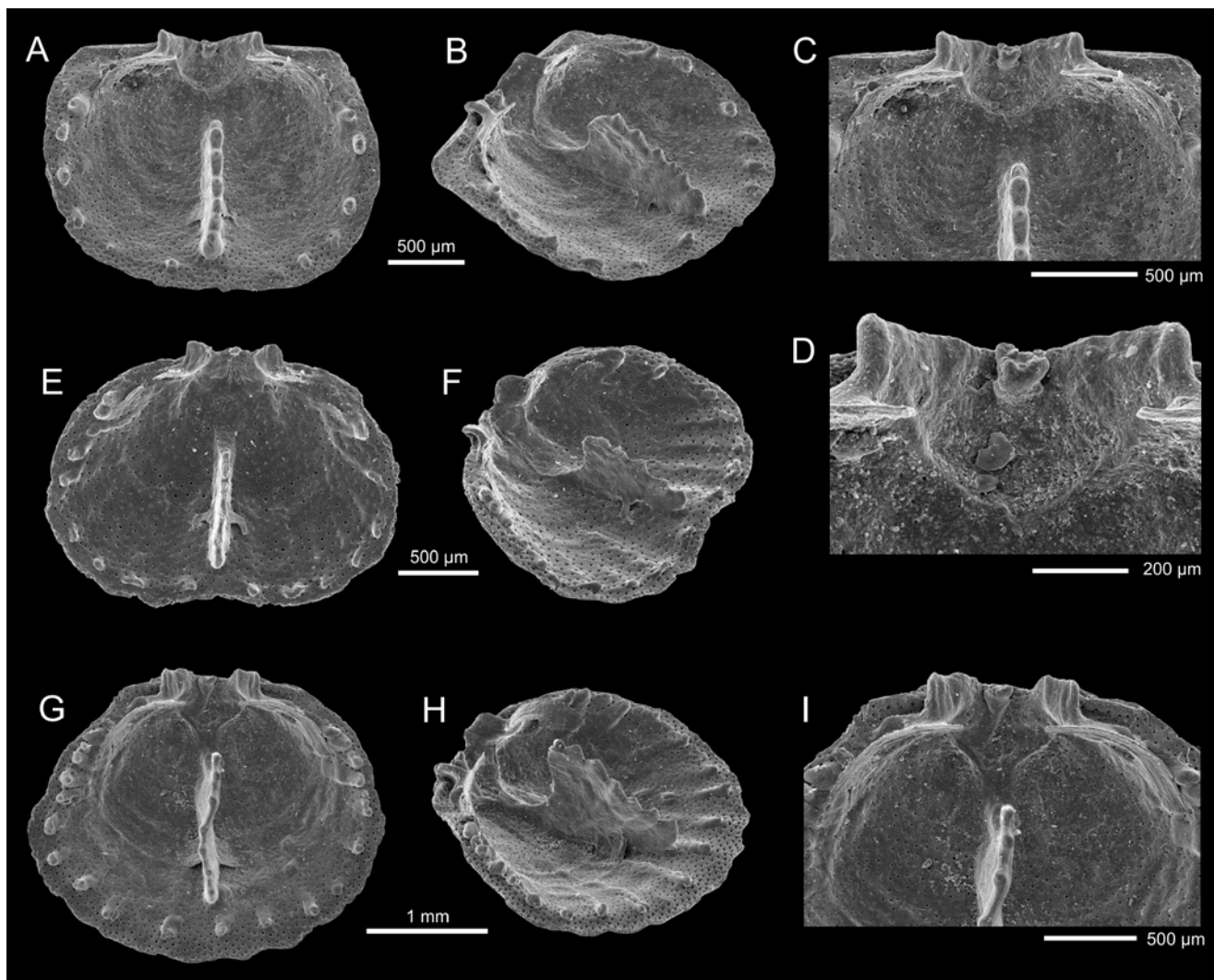


Fig. 10 *Joania crenata* (Sandberger, 1862), dorsal valves, Mammendorf, M3. **A–D.** Inner and oblique views, and enlargements (C, D) of posterior part, showing details of cardinalia and shafted cardinal process, GPSL MM_927. **E, F.** Inner and oblique views, GPSL MM_928. **G–I.** Inner and oblique views, and enlargement (I) of posterior part, GPSL MM_929. All SEM.

MacKinnon and Nielsen, 2008
Genus *Megerlia* King, 1850

Type species: *Anomia truncata* Linnaeus, 1767, by the original designation of King (1850).

Megerlia truncata (Linnaeus, 1767)
Fig. 11C–E

- 1990 *Megerlia truncata* (Linnaeus) – Bitner, pp. 145–147, pl. 2, figs 6–9, pl. 7, figs 3–6, pl. 8, figs 1–7 (*cum syn.*).
- 2010 *Megerlia truncata* (Linnaeus) – Dulai, p. 28, pl. 3, figs 4, 5.
- 2011a *Megerlia* sp. – Müller, p. 20.
- 2013a *Megerlia truncata* (Linnaeus) – Bitner *et al.*, p. 594, fig. 8.
- 2013b *Megerlia truncata* (Linnaeus) – Bitner *et al.*, p. 86, fig. 4H, I.
- 2016 *Megerlia truncata* (Linnaeus) – Álvarez, pp. 99–106, pls 59A–Z, 60A–AA, 61A–DD, 62A–AA, 63A–KK, 64A–V, 65A–Q, 66A–EE, 67A–BB, 68A–AA (*cum syn.*).

- 2016 *Megerlia truncata* (Linnaeus) – Bitner and Motchurova-Dekova, p. 16, fig. 6F–H.
- 2016 *Megerlia truncata* (Linnaeus) – Simon *et al.*, pp. 7–8, pls 1–5.
- 2019 *Megerlia truncata* (Linnaeus) – Dulai, p. 139, pl. 3, figs 13–20.
- 2020 *Megerlia truncata* (Linnaeus) – Hoffmann *et al.*, pp. 15–17, fig. 11J–M.

Material: Eleven ventral valves (two fragmented) and one dorsal valve from horizons M3, M6, M7 (Tab. 1).

Remarks: This species is very rare in the material studied, represented mostly by juvenile, ventral valves. However, the presence of *Megerlia* was recognized already in the Mammendorf Quarry by Müller (2011a). The shell is transversely oval, wider than long, with dorsal valve reaching 10.8 mm in length and 15.7 mm in width. The shell surface is ornamented by very fine, nodulose ribs. A thin, short median septum beneath the pedicle collar is present in the ventral valve. Interior of both valves is radially tuberculate.

Occurrence: The oldest occurrence of this species to date was from the late Oligocene of France (Bitner *et al.*,

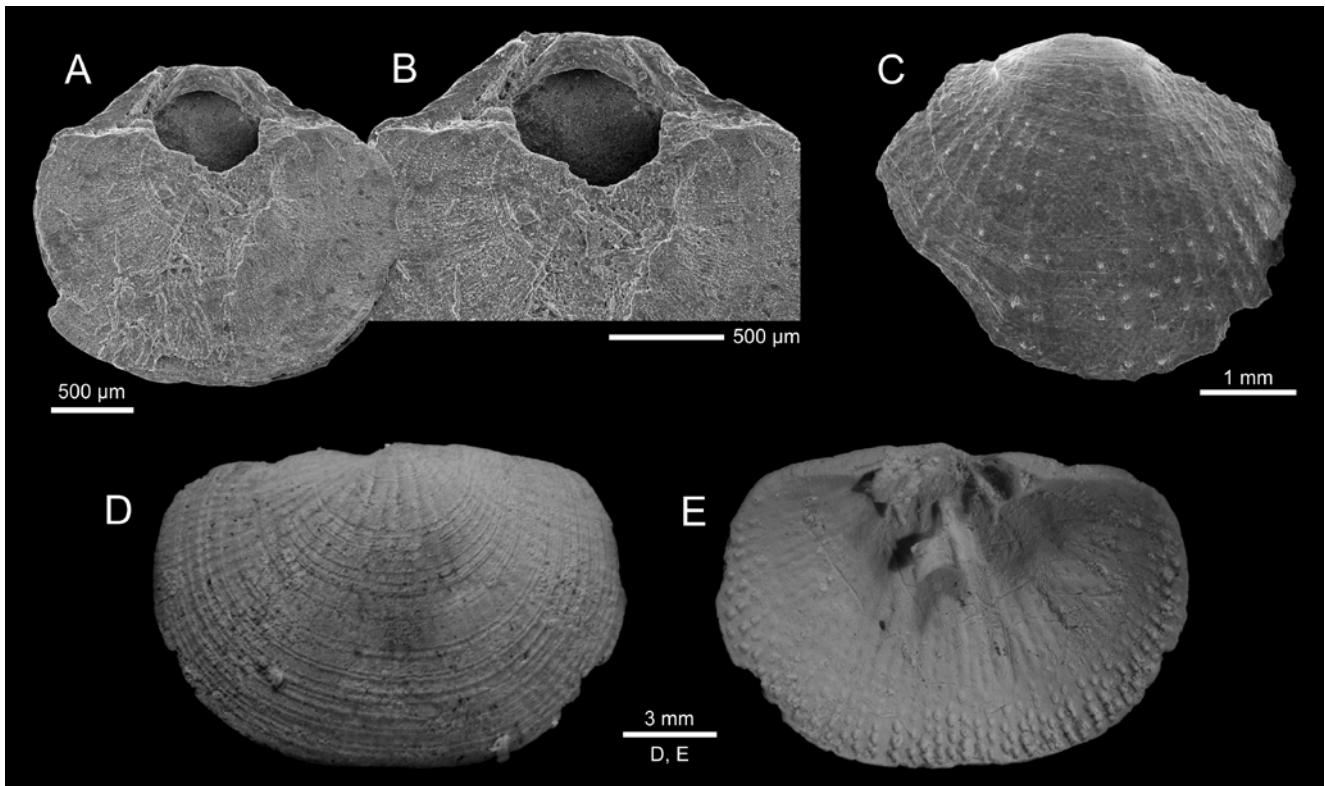


Fig. 11. *Platidia* sp. and *Megerlia truncata* (Linnaeus, 1767), Mammendorf. **A, B.** *Platidia* sp., dorsal view of articulated specimen and enlargement (B) of the umbonal part, M3, GPSL MM_930. **C–E.** *Megerlia truncata* (Linnaeus, 1767); **C** – outer view of ventral valve, M3, GPSL MM_931; **D, E** – outer and inner views of dorsal valve, Mammendorf, M6, GPSL MM_932. A–C are SEM images.

2013a). The present discovery extends its stratigraphic range. In the Neogene, *M. truncata* is very common and widely distributed, both in the Central Paratethys and the Mediterranean province (e.g., Gaetani and Saccà, 1985; Bitner, 1990; Bitner and Dulai, 2004; Dulai, 2010, 2019; Bitner *et al.*, 2013b; Bitner and Motchurova-Dekova, 2016; Hoffmann *et al.*, 2020). Its Recent representatives live in the Mediterranean Sea and eastern North Atlantic (Logan, 1979, 2007; Álvarez, 2016; Simon *et al.*, 2016; Emig, 2016, 2018) as well as in the western Indian Ocean (Bitner and Logan, 2016), having a very wide depth range from 8 to 1,086 m (Logan, 2007).

DISCUSSION

The early Oligocene brachiopod fauna from the rocky-shore deposits at Mammendorf, central Germany (Fig. 1), comprises 13 species, belonging to 11 genera. The inarticulate brachiopods are represented by two species, discinid *Discinisca fallens* and craniid *Novocrania* sp. The articulate brachiopods are represented by thecideides, with only one representative *Lacazella mediterranea*, and terebratulides that are a dominant group, including the representatives of five families. The short-looped *Pliothyryna grandis* is the most common species (21.2% of specimens), whereas the family Megathyrididae is the most diverse and abundant group, constituting nearly 50% of the material. Six megathyridid species have been recognized: *Megathiris detruncata*, three species of *Argyrothecca*, *A. bitnerae*, *A. lunula* and *A. megalocaphala*, *Bronnothyris rugosa*, and *Joania crenata*. Other terebratulide families each have one representative,

Terebratulina tenuistriata, *Platidia* sp. and *Megerlia truncata*. Three species each are represented by more than 200 specimens, while four species are represented by fewer than 20 specimens, and of these one species (*Novocrania* sp.) is only represented by one specimen (Tab. 1). The reported occurrence of the species *Discinisca fallens*, *Argyrothecca bitnerae* and *Megerlia truncata* extends their stratigraphic range back to the early Oligocene.

Spatial variability in abundance and diversity is observed along the section (Tab. 1). In the horizons M1, M4 and M5, brachiopods are very rare, both in species and specimens. The most individual-rich horizon is M3, with more than 40% of the material studied. The brachiopods are also numerous in horizons M6 and M7, constituting 22.7% and 21.7% of the material, respectively. The brachiopods from those three horizons are also the most diverse, with 10 to 12 species each. The species *Lacazella mediterranea* and megathyridids, apart from *M. detruncata*, are predominant elements in horizons M2 and M3, i.e., in the lower cycle with its warm-water fauna. In turn, *Discinisca fallens*, found in five horizons, is numerous only in the horizons M6 and M7. Similarly, *Pliothyryna grandis*, being the only species found in all horizons, reaches its maximum in the upper cycle that is interpreted as having cooler conditions. The very low frequency of *D. fallens* in the lower cycle might be a taphonomic effect and not an original feature. In a high-energy, rocky-shore environment, thin-shelled specimens of *D. fallens* can be damaged easily and their preservation potential is very low. The upper cycle is interpreted as a deeper and calmer environment, thus more favourable for the preservation of such shells. In contrast, the micromorphic

megathyridids that predominate in the lower-cycle assemblage could have found shelter under and between boulders and thus were less prone to damage.

Gastropod drilling predation is observed on some brachiopods from Mammendorf (Fig. 12). Drill holes were identified on 93 specimens, giving a drilling frequency of 6.8%. Similar low drilling frequency is characteristic for most Recent and fossil Cenozoic brachiopod populations (e.g., Delance and Emig, 2004; Simões *et al.*, 2007; Taddei Ruggiero and Bitner, 2008; Bitner *et al.*, 2013a; Bitner and Müller, 2015; Bitner and Motchurova-Dekova, 2016), although high frequencies were occasionally observed (see Baumiller and Bitner, 2004; Baumiller *et al.*, 2006). Drill holes were found on both valves, but the ventral valve was drilled at higher frequency. There are two morphological types of holes, conical (Figs 2B, E, I, 12A, B) and straight-sided (Fig. 12C–J), corresponding to naticid and

murricid attacks, respectively (Hoffman *et al.*, 1974). Both gastropod families have been recognized in the Oligocene deposits of Mammendorf (Müller, 2011a).

With thirteen species, the Mammendorf assemblage is surprisingly rich, when compared to other Oligocene assemblages from Germany (Sandberger, 1862–1863; Schreiber, 1871; von Koenen, 1894; Müller, 1983; Diedrich, 2012; Bitner and Müller, 2015; Dulai and von der Hocht, 2020). All species described here were previously recorded from the Cenozoic deposits and some of them are widely spread throughout the whole of Europe, including also the Latdorf Basin of central and northern Germany (von Koenen, 1894). In species composition, however, the Mammendorf fauna differs significantly from brachiopods from the late Eocene/early Oligocene Silberberg Formation of Atzendorf (Bitner and Müller, 2015). The main difference is a total absence of megathyridids in the Atzendorf assemblage, dominant

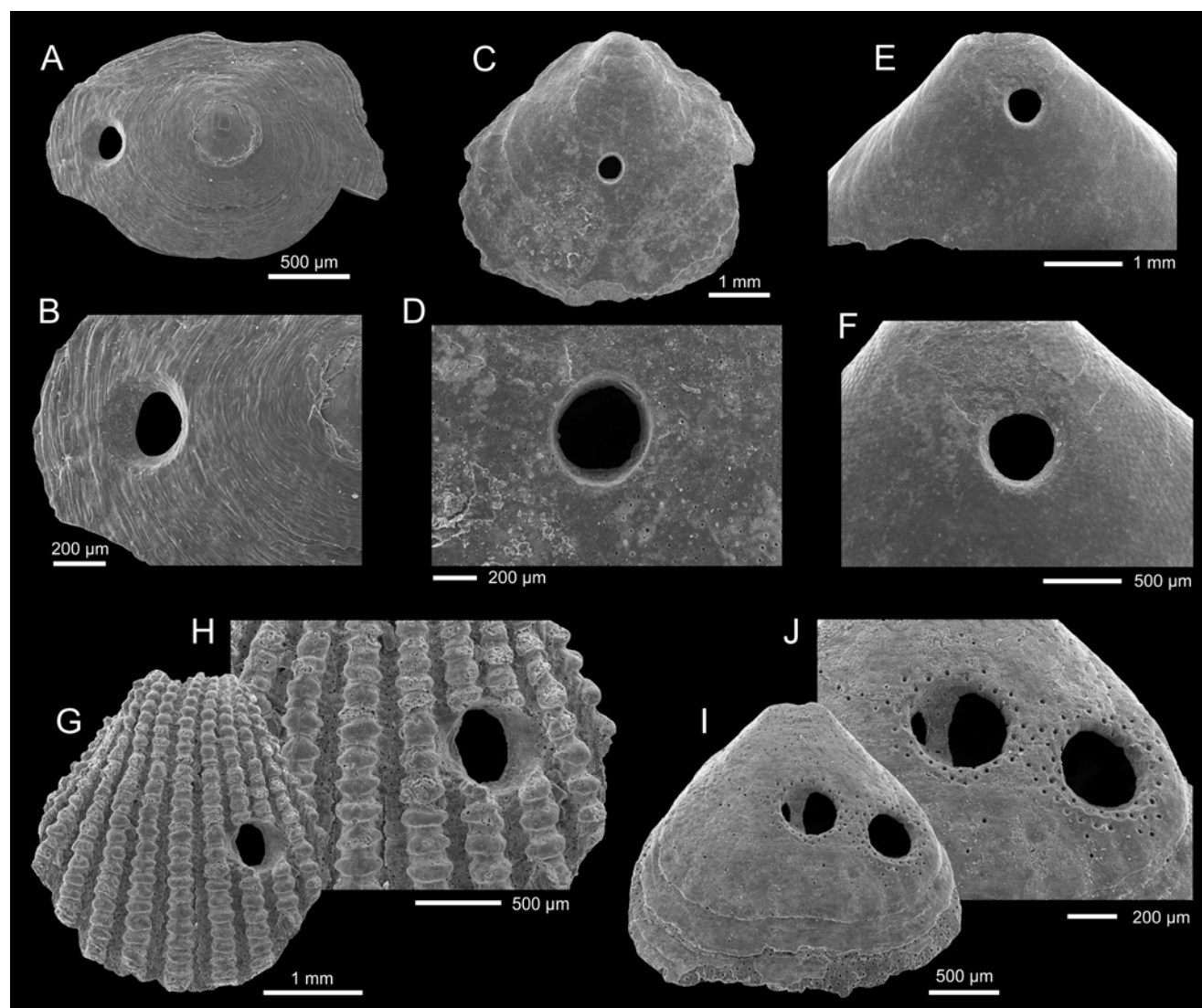


Fig. 12. Drilled brachiopods, lower Oligocene, Mammendorf. **A, B.** *Discinisca fallens* (Wood, 1874), exterior of dorsal valve and a close-up image of drill hole, horizon M6, GPSL MM_876. **C–F.** *Pliothyrina grandis* (Blumenbach, 1803), M6; **C, D** – exterior of dorsal valve and a close-up image of drill hole, GPSL MM_888; **E, F** – exterior of ventral valve and a close-up image of drill hole, GPSL MM_889. **G, H.** *Terebratulina tenuistriata* (Leymerie, 1846), exterior of dorsal valve and a close-up image of drill hole, M7, GPSL MM_893. **I, J.** *Argyrotheca megalcephala* (Sandberger, 1862), exterior of ventral valve and a close-up image of two drill holes, M3, GPSL MM_914. All are SEM images.

brachiopods in Mammendorf, and the presence of two chlidonophorid brachiopods, *Rhynchonellopsis nysti* (Bosquet, 1862) and *Orthothyris pectinoides* (von Koenen, 1894), not recognized in the Mammendorf material. The Mammendorf brachiopods display a great affinity to the early Oligocene fauna of the Mainz Basin, sharing five genera and four species (Sandberger, 1862–1863). Two species, *Argyrotheca megalcephala* and *Joania crenata*, considered so far as endemic to the Mainz Basin, have been recognized in the material from the Mammendorf Quarry. Also, the Mammendorf molluscan fauna shows similarity to that from the Mainz Basin and numerous molluscan species previously known only from the Mainz Basin were identified in the material from Mammendorf (Müller, 2011a). Thus, it is demonstrated that a connection and exchange of faunas existed between the Mainz Basin and southern North Sea Basin.

CONCLUSIONS

The lower Oligocene rocky-shore deposits at Mammendorf, central Germany yielded a surprisingly rich brachiopod fauna, containing 13 species, belonging to 11 genera. The short-looped *Pliothyris grandis*, species restricted to the Oligocene of North Sea Basin, is most common but the predominant and most diverse group, constituting nearly 50% of the material, is the family Megathyrididae, represented by six species in the Mammendorf assemblage. The internal structures allowed to resolve the taxonomical position of some poorly known species; the species *Argiope megalcephala* was assigned to the genus *Argyrotheca*, *Argiope rugosa* to *Bronnothyris*, and *Argiope crenata* to *Joania*. The discovery of the species *Discinisca fallens*, *Argyrotheca bitnerae* and *Megerlia truncata* at Mammendorf extends their stratigraphic range back to the early Oligocene. The Mammendorf brachiopod fauna displays a great affinity to the early Oligocene fauna of the Mainz Basin, having five genera and four species in common, among them two, *A. megalcephala* and *J. crenata*, previously considered as endemic to the Mainz Basin.

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