

First record of the genus *Bronnothyris* (Brachiopoda: Megathyrididae) from the Oligocene of the Mainz Basin (Germany)

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Abstract: The genus *Bronnothyris*, with the type species *Terebratula bronnii* Roemer, 1841, was erected for those *Argyrotheca* species that have septal flanges extended ventrally from the dorsal valve. Four other Late Cretaceous and one Early Paleocene species were attributed to this genus (i.e. *Argyrotheca coniuncta* Steinich, 1965, *A. lacunosa* Steinich, 1965, *A. obstinata* Steinich, 1965, *A. stevensis* Nielsen, 1928 and *A. rugicosta* Zelinskaya, 1975). After examination of Oligocene material from Waldböckelheim, Mainz Basin, Germany we transfer the species *Argiope subradiata* Sandberger, 1862 into the genus *Bronnothyris*. This new combination extends the stratigraphic range of *Bronnothyris* into the Oligocene.

Key words: Oligocene, Germany, Mainz Basin, Brachiopoda, Megathyrididae, *Bronnothyris*.

Introduction

The genus *Bronnothyris*, with the type species *Terebratula bronnii* Roemer, 1841, was erected by Popiel-Barczyk & Smirnova (1978) for Late Cretaceous megathyridid brachiopods resembling *Argyrotheca* but having short septal flanges that extend ventrally from the dorsal septum. Apart from *Argyrotheca bronnii*, Popiel-Barczyk & Smirnova (1978) attributed to this genus four other species from the Upper Cretaceous white chalk: *A. coniuncta* Steinich, 1965, *A. lacunosa* Steinich, 1965, *A. obstinata* Steinich, 1965 and *A. stevensis* Nielsen, 1928. Later one further species, *Argyrotheca rugicosta* Zelinskaya, 1975 from the Lower Paleocene of Ukraine was transferred to *Bronnothyris* by Smirnova et al. (1983).

In the present study we have placed another *Argyrotheca* species, *A. subradiata* (Sandberger, 1862) from the Oligocene of Germany in the genus *Bronnothyris*, thus considerably extending the stratigraphic range of the genus. The aim of this paper is to re-describe and re-illustrate this poorly known species.

Geological setting and material

The Mainz Basin lies along the Rhine Graben fault system in south-western Germany. It is subdivided into a northern part (Rüsselsheim Basin) and a southern part (Eisenberg Subbasin, Marnheim Bay). The material studied here comes from the Rüsselsheim Basin. There the sedimentary succession started in the Middle Eocene with the deposition of terrestrial and limnic basal clays. These unfossiliferous beds locally extend into the Late Eocene and are not exposed on the surface, being known only from wells. In the Priabonian to Lower Rupelian limnic and flu-

vio-marine beds of the Pechelbonn Group were deposited. Earlier interpreted as basal beds and/or marginal facies of the “Rupelton” (Bodenheim Formation), these deposits are now regarded as separate lithostratigraphic units. The Pechelbonn Group contains a rich fauna and flora deriving from a largely limnic to brackish shallow-water setting. Above the Pechelbonn Group, the Rupelian to Chattian Selztal Group is developed and it is these units that have delivered the marine fossils for which the Mainz Basin is famous. The Selztal Group is subdivided into several formations, starting with the laterally interfingering Bodenheim (former “Rupelton”) and Alzey Formation (former “Meeressand”), overlain by the Stackeden Formation (former “Schleichsand” and “Schleichsandmergel”), which in turn is overlain by the Sulzheim Formation (former “Cyrenenmergel”, “Cyrenenkalk”, and “Süßwasserschichten”). On top of these beds, the Mainz Group with a rich succession of carbonate platform deposits interfingering with siliciclastic deposits of the Rhine Graben is developed. These beds are of Late Oligocene (Chattian) to Early Miocene (Burdigalian) age. For more detailed data on the lithostratigraphic subdivision of the Mainz Basin and associated biostratigraphic data see Grimm (2002, 2005) and Grimm & Grimm (2003), which also contain an extensive description of the outcrops in the area, both historical and modern.

The material studied here derives from the Alzey Formation exposed in the area of Waldböckelheim, 10 km west of Bad Kreuznach, SW Mainz, Germany (Fig. 1). There, the Alzey Formation crops out on the southern and south-western slopes of the Welschberg, north of Waldböckelheim and on the north-western slope of the Heimberg, south-east of Waldböckelheim. Both areas are classical localities of the 19th century and have delivered a huge number of fossils (predomi-

nantly mollusks), both in number of species and specimens. Grimm & Grimm (2003) attribute the exceptional high diversity of the Waldböckelheim deposits to the fact that these faunas actually derive from a variety of small sandpits that exposed different levels in the succession and possibly stem from slightly different paleoenvironments. Like most Waldböckelheim material, the specimens studied here carry no specific sandpit or sub-locality information. It seems likely, though, that they derive from the outcrops at Heimberg which are characterized by their abundant occurrence of *Argyrotheca subradiata* (Grimm & Grimm 2003: p. 91). According to Grimm et al. (2000) the Alzey Formation was deposited during the Rupelian, based on calcareous nannoplankton data (Zones NP23 and lower NP24).

The material is housed in the Institute of Paleobiology, Warszawa under the number ZPAL Bp.67 and in the Natural History Museum Vienna under the numbers NHMW 1863/0017/0061, 1866/0058/0068, 1868/0001/0820, and 2010/0169/0001 to .../0007.

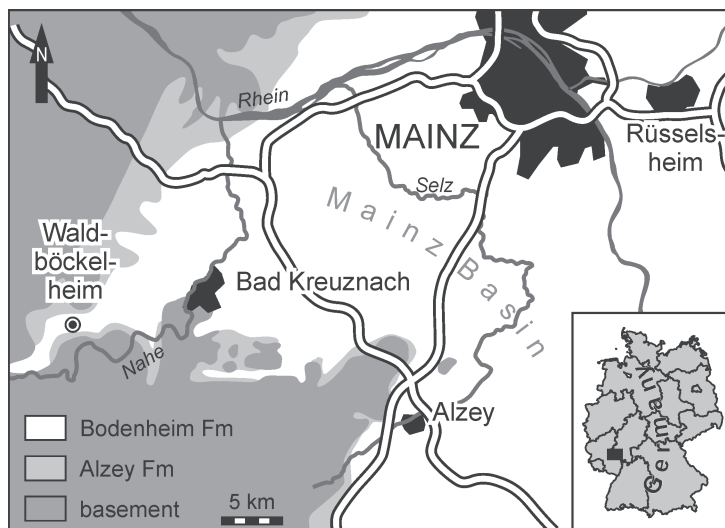


Fig. 1. Geographic position of Waldböckelheim in the Mainz Basin. Inset shows position of map in relation to Germany. Distribution of Lower Oligocene marine deposits (Alzey Formation, Bodenheim Formation) based on Grimm & Steurbaut (2001: fig. 1C).

Systematics

Phylum: **Brachiopoda** Duméril, 1806

Subphylum: **Rhynchonelliformea** Williams, Carlson,

Brunton, Holmer & Popov, 1996

Class: **Rhynchonellata** Williams, Carlson, Brunton, Holmer & Popov, 1996

Order: **Terebratulida** Waagen, 1883

Superfamily: **Megathyridoidea** Dall, 1870

Family: **Megathyrididae** Dall, 1870

Genus: *Bronnothyris* Popiel-Barczyk & Smirnova, 1978

Type species: *Terebratula bronnii* Roemer, 1841 by original designation of Popiel-Barczyk & Smirnova (1978: 41).

Bronnothyris subradiata (Sandberger, 1862)
Figs. 2–4

?p.p. 1853 *Terebratula* sp. — Sandberger, p. 8

*1862 *Argiope subradiata* Sandberger, pl. 34, fig. 4, 4a–d

1863 *Argiope subradiata* Sand. — Sandberger, p. 386–387

1883 *Argiope subradiata* Sandberger — Lepsius, p. 56

1986 *Argyrotheca subradiata* (Sandberger) — von der Hocht, p. 208

Type material: The syntypes studied by Sandberger (1863) came from the Weinkauff collection from a locality at Waldböckelheim-Heimberg. According to K. Grimm from the Natural History Museum Mainz (pers. comm. Dec. 2007), the Weinkauff collection was kept at the Bayerische Staatssammlung für Geologie und Paläontologie, Munich, where it was destroyed during the Second World War (Gürs 1995). Thus, we have selected a neotype for this species.

Neotype: The specimen figured in Fig. 2D–G, ZPAL Bp.67/3.

Material examined: Waldböckelheim, Rheinland-Pfalz, Germany (Alzey Formation, Rupelian, Early Oligo-

cene): 4 complete specimens, 2 ventral valves, 12 dorsal valves (ZPAL Bp.67/1–4, NHMW 2010/0169/0001 to .../0007); additionally numerous complete and disarticulated specimens are kept at the NHMW under the nos. NHMW 1863/0017/0061, 1866/0058/0068, and 1868/0001/0820.

Dimensions (in mm):

Specimen number	Length	Width	Thickness
ZPAL Bp.67/2	5.2	5.8	3.4
ZPAL Bp.67/3 (neotype)	6.0	5.7	3.4

Description: Shell small, subrectangular to subpentagonal in outline, usually wider than long, ventriconvex. Shell surface covered with up to 10 rounded ribs that become less distinct at the anterior margin; growth lines distinct. Both valves coarsely punctate. Beak high, suberect to erect, eroded to some degree in most specimens (Fig. 2E,H), suggesting a very short pedicle and close attachment to the substrate. Sometimes part of the dorsal valve is also corroded (Fig. 2H). Beak ridges sharp, subtending an angle of about 90–100° at umbo. Interarea relatively narrow, transversely striated. Foramen large, subtriangular, hypothyrid, flanked by two narrow, disjunct deltidial plates. Hinge line long, straight, often equal to maximum width. Lateral commissures straight, anterior commissure rectimarginate.

Ventral valve interior with short wide teeth lying parallel to hinge line; teeth bear weak diagonal ridges. Pedicle collar wide, supported by a slender median septum that extends to about mid-valve; anteriorly to septum there are two or three shallow ovoid depressions to accommodate serrations of the dorsal septum.

Dorsal valve nearly flat, its interior bears short, widely divergent inner socket ridges. Cardinal process in form of short, indistinct ridges, situated between socket ridges. Hinge plates broad, fused mid-dorsally to form a single co-

herent platform; the boundary between inner and outer plates are indistinct, indicated only by a shallow fold. Crura very short; crural processes medianly directed, massive and relatively long (Figs. 2I, 3H). Descending branches curved laterally and united with valve floor; they emerge from the valve floor and are attached to the median septum. Short septal flanges extend ventrally from dorsal septum (Figs. 2G, 4D-F). Septum high, triangular in profile, beginning from hinge plates and sloping towards the anterior margin with 3-4 serrations.

The secondary fibres of the shell observed on the inner surface are regularly packed forming a characteristic mosaic (Fig. 4C).

Remarks: The presence of the septal flanges which extend ventrally from the dorsal septum clearly indicates the attribution of the investigated specimens to the genus *Bronnothyris*. Externally, in shell outline and number of ribs, the specimens are most similar to the Late Cretaceous *B. bronnii* (Roemer, 1841), from which they differ internally, however; *B. bronnii* possesses hinge plates that are developed as two concave circular separated discs, situated anteriorly to the cardinal process (Steinich 1965; Popiel-Barczyk 1968; Surlyk 1972, 1982; Bitner & Pisera 1979; Johansen 1987; Johansen & Surlyk 1990).

In turn, *B. coniuncta* (Steinich, 1965) differs externally from *B. subradiata* in having strongly transversely elongate

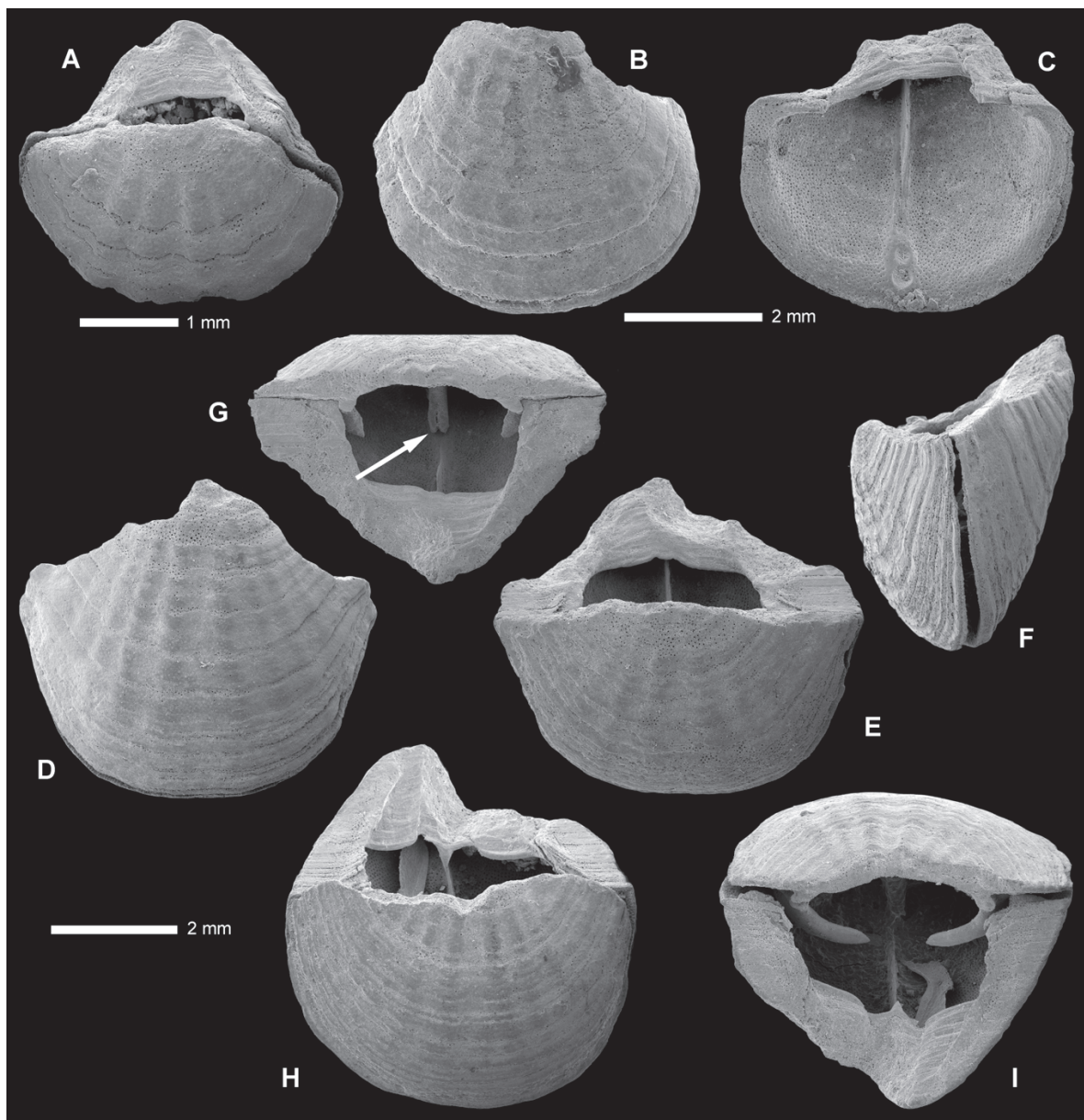


Fig. 2. A-I — *Bronnothyris subradiata* (Sandberger, 1862), Oligocene, Waldböckelheim, Mainz Basin, Germany. A — dorsal view of complete specimen, ZPAL Bp.67/1; B, C — outer and inner views of ventral valve, ZPAL Bp.67/2; D-G — ventral, dorsal, lateral and posterior views of complete specimen, septal flanges extending from a dorsal septum arrowed, neotype, ZPAL Bp.67/3; H, I — dorsal and posterior views of complete specimen, massive crural processes visible (I), ZPAL Bp.67/4. All SEM.

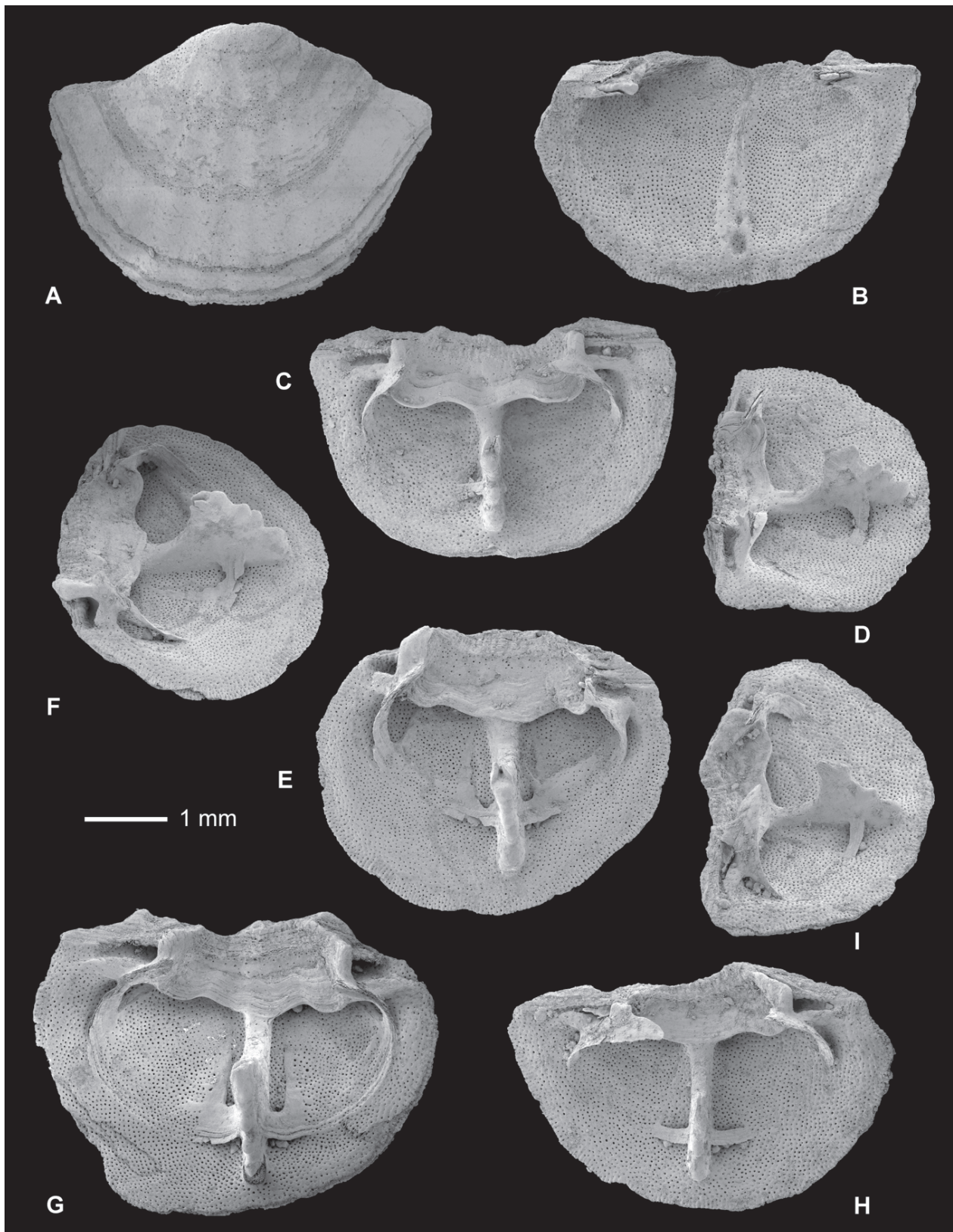


Fig. 3. A–I — *Bronnothyris subradiata* (Sandberger, 1862), Oligocene, Waldböckelheim, Mainz Basin, Germany. **A** — Ventral valve, exterior view, NHMW 2010/0169/0007; **B** — ventral valve, inner view, NHMW 2010/0169/0005; **C** — dorsal valve, inner view, NHMW 2010/0169/0006; **D** — dorsal valve, lateral view, NHMW 2010/0169/0002; **E**, **F** — dorsal valve, inner and lateral views, NHMW 2010/0169/0001; **G** — inner view of dorsal valve, NHMW 2010/0169/0004; **H**, **I** — dorsal valve, inner and lateral views, NHMW 2010/0169/0003. All SEM.

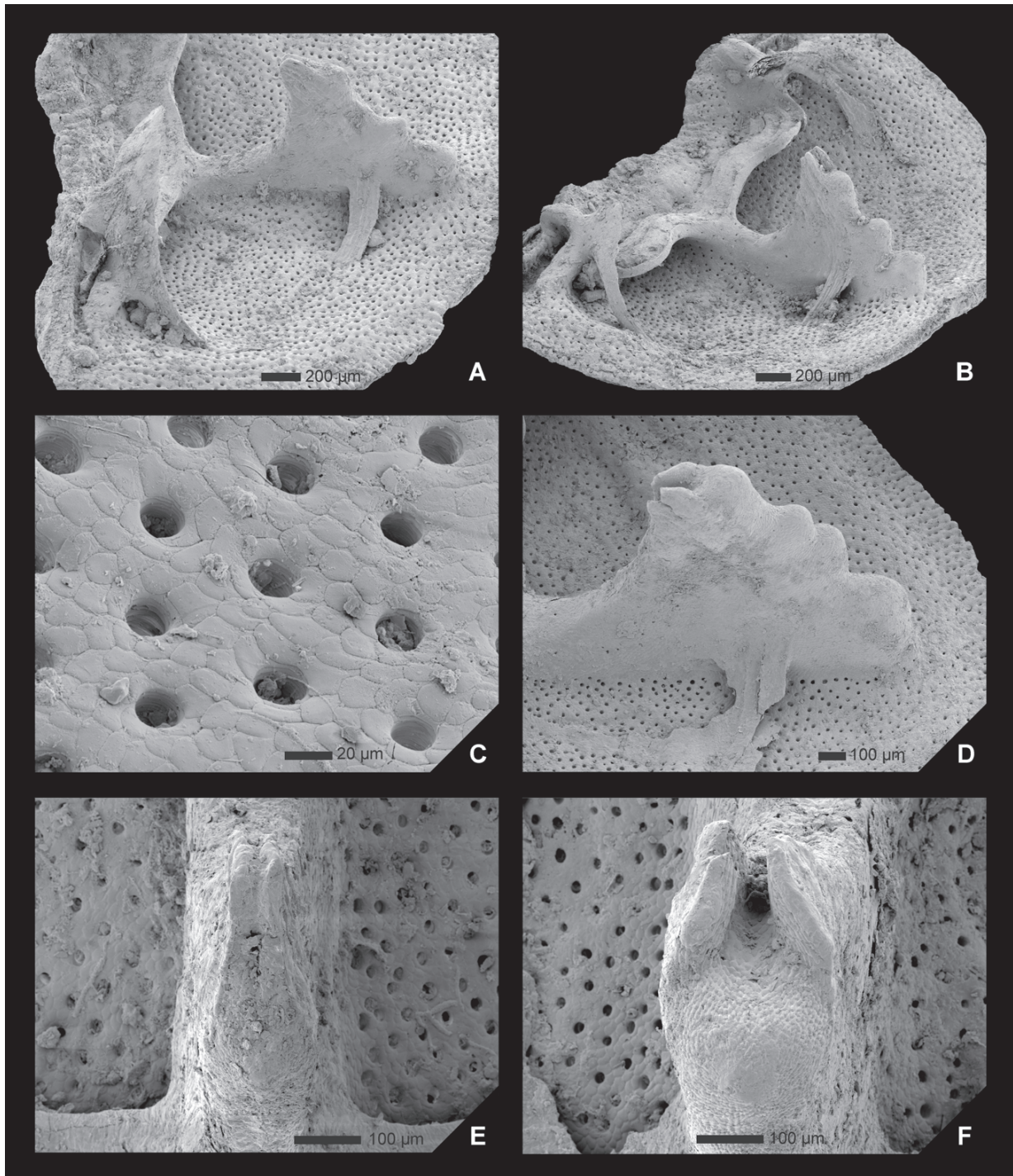


Fig. 4. A–F — *Bronnotheris subradiata* (Sandberger, 1862), Oligocene, Waldböckelheim, Mainz Basin, Germany. **A, B** — lateral views of dorsal valve interior to show median septum and cardinalia, NHMW 2010/0169/0003, NHMW 2010/0169/0006; **C** — inner surface of ventral valve, visible punctae and mosaic of secondary fibres, NHMW 2010/0169/0005; **D** — dorsal valve, side view of median septum, NHMW 2010/0169/0001; **E, F** — interior views of dorsal valves to show details of septal flanges extending from median septum, NHMW 2010/0169/0003, NHMW 2010/0169/0001. All SEM.

outline, although its hinge plates, as in *B. subradiata*, are fused and form a coherent, distinct platform (Steinich 1965; Bitner & Pisera 1979; Surlyk 1982; Johansen 1987; Johansen & Surlyk 1990).

The species *B. obstinata* (Steinich, 1965) and *B. lacunosa* (Steinich, 1965) are distinguished from the Oligocene *B. subra-*

diata by having a smaller shell size and fewer ribs (Steinich 1965). Additionally, hinge plates in *B. lacunosa* form two concave discs, whereas in *B. obstinata* hinge plates form a single plate which is much narrower than that in *B. subradiata*.

The Oligocene specimens can also be easily distinguished from the fifth Late Cretaceous species, *B. stevensis* (Nielsen,

1928) which has disc-shaped, concave hinge plates (Johansen 1987; Simon 1998). Additionally, two septal flanges are higher in *B. stevensis* than in *B. subradiata* (see Simon 1998: pl. 7, fig. 4).

From the Early Paleocene *B. rugicosta* (Zelinskaya, 1975), the investigated specimens differ strongly in ornamentation; in *B. rugicosta* the shell surface is coarsely ribbed (Zelinskaya 1975: pl. 16, figs. 3, 4a, 5, 6a).

Argyrotheca wansinensis Vincent, 1923 from Wansin, southern Belgium (now attributed to the early-middle Thanetian; compare De Geyter et al. 2006: p. 205; Jagt et al. 2007: p. 40) is quite similar to *A. subradiata*. Vincent's (1923) illustrations, however, are insufficient for proper comparison. We were unable to trace his type material, nor did we succeed in locating topotypic specimens. Thus for the time being, the relation between these two forms, albeit similar, must remain unresolved.

Bitner & Schneider (2009) have described Late Burdigalian (Early Miocene) *Argyrotheca* cf. *subradiata* (Sandberger, 1862) from the Bavarian part of the Molasse Basin (Paratethys). Externally that material is similar to that from the Mainz Basin, but differs in having much narrower hinge plates, which are very wide in typical *B. subradiata* and form a single plate. *A.* cf. *subradiata* also lacks the septal flanges extending from the septum (Bitner & Schneider 2009) which prevents the attribution of this species to *Bronnothyris*.

Externally the studied specimens also resemble *Megathiris detruncata* (Gmelin, 1791), however, they can be readily distinguished internally by the lack of the lateral septa (e.g. Logan 1979; Bitner 1990).

Occurrence: Early Oligocene (Rupelian) of Waldböckelheim, Mainz Basin, Germany. This species has also been reported (Sandberger 1863; Lepsius 1883; von der Hocht 1986) from numerous other sites in the Mainz Basin (e.g. Eckelsheim, Alzey-Weinheim, and Heimberg). Additionally, numerous "*Argyrotheca*" specimens from these and further localities are available at the Natural History Museum of Mainz (Grimm & Grimm 2005), which need to be studied in future to confirm their specific identity with *Bronnothyris subradiata*.

Discussion

Until recently, the family Megathiridae contained two extant (*Megathiris*, *Argyrotheca*) and two fossil (*Bronnothyris*, *Phragmothyris*) genera. Recently Álvarez et al. (2008b) erected a new genus *Joania* (with type species *Terebratula cordata* Risso, 1826) for those *Argyrotheca* species that have a narrow hinge line, prominent cardinal process and tubercles on the inner margin. Apart from *Phragmothyris*, all the genera are externally very similar; the genus *Phragmothyris* from the Eocene of Cuba, in contrast, differs strongly from other members of the family in having a multicostellate surface (up to 40 ribs) and conjunct deltidial plates forming a symphytium (Cooper 1955).

The placement of the Oligocene species *Argiope subradiata* in the genus *Bronnothyris* considerably extends the stratigraphic range of this genus. So far *Bronnothyris* has been re-

corded from the Upper Cretaceous to Lower Paleocene (Lee et al. 2006). Thus, the genus *Bronnothyris* presently contains 7 valid species: *B. bronni*, *B. coniuncta*, *B. lacunosa*, *B. obstinata*, *B. stevensis*, *B. rugicosta* and *B. subradiata*. Judging from the data available, the genus seems to have a distribution restricted to Europe.

In adult specimens of *A. cuneata* (Risso, 1826) two ventrolaterally directed prongs often diverge from the septum posterior to the crest (Logan 1979; Brunton 1988; Álvarez et al. 2008a,b); they are interpreted as possible rudimentary ascending branches. It is possible that the septal flanges extending from the septum in *Bronnothyris* could also be interpreted as rudimentary elements of ascending branches.

The extant species *Argyrotheca schrammi* (Crosse & Fischer, 1866), from Barbados illustrated by Álvarez et al. (2008b: fig. 7C,D) exhibits two short septal flanges as well. Although further data are needed to check the consistency of this feature in *A. schrammi*, this suggests that this species might also belong to *Bronnothyris*, further extending the range of the genus, both in terms of stratigraphic and spatial distribution. *A. schrammi* differs from *B. subradiata* by the presence of spines on the posterior slope of the median septum.

Argyrotheca is a very diverse genus, both today and in the Cenozoic, and even back to the Cretaceous (Cooper 1977). Further detailed examinations of other Cenozoic and extant *Argyrotheca* species may reveal that there are more, as yet unrecognized species of *Bronnothyris*. In the *Treatise* Lee et al. (2006) suggest, that "*Argyrotheca* may include species that should be assigned to several different genera". Thus, further investigations and a thorough revision are needed, and the diversity of *Bronnothyris* may increase significantly with future studies.

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