Badenian (Middle Miocene) micromorphic brachiopods from Bánd and Devecser (Bakony Mountains, Hungary)

by
Alfréd DULAI

Abstract — The described brachiopod assemblage (427 specimens from the Lower Badenian shallow water deposits of the Bakony Mts) comprises 3 micromorphic species belonging to two genera of Megathyrididae. *Argyrotheca cordata* and *A. cuneata* are relatively common members of the coral-bearing, diverse fauna at Bánd. The very limited Devecser material yielded isolated but well-preserved *A. cordata* and *Megathiris detruncata* valves. All the three species are widespread in the Miocene of the Central Paratethys, as well as in the Recent seas. The Bánd assemblage is more or less autochthonous while the Devecser brachiopods suggest only short transportation. The two *Argyrotheca* species show bell-shaped size-frequency distribution indicating low juvenile mortality. Protected, cryptic environments among coral branches and under boulders resulted in the unimodal, bell-shaped size distribution, indicating a stable community. Epifaunal encrusters (Bryozoa, serpulid Polychaetes) are recorded for the first time on micromorphic brachiopods in the Central Paratethys. The situation of epibionts suggests that they encrusted the ventral valves during the life of brachiopods. The serpulid probably benefits from the feeding currents of the brachiopod. Few brachiopod specimens (3.5%) show drill holes of predatory gastropods. No taxon selectivity can be observed, but *A. cuneata* shows valve and site selectivity.

Keywords — Brachiopoda, *Argyrotheca*, *Megathiris*, Middle Miocene, Badenian, Hungary, Central Paratethys, size-frequency distribution, drilling predation, encrustation.

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Introduction

Brachiopods were important in the Palaeozoic and partly in the Mesozoic marine assemblages, but they are generally rare in the Cenozoic deposits. The Badenian (Middle Miocene) marine fauna is very abundant and diverse in Hungary, but brachiopods are scarce elements of these fossil assemblages. Hungarian Miocene brachiopods were mainly mentioned in faunal lists. Some new species were described by MATYASOVSZKY (1880) and MAJER (1915). MEZNERICS (1943) summarized the Hungarian Tertiary brachiopod fauna in a small monograph and described 42 species (6 new) from 11 Eocene, 3 Oligocene and 31 Miocene localities. Recently BITNER & DULAI (2004) revised the Miocene brachiopods in the palaeontological collections of the Hungarian Natural History Museum, Budapest. Altogether 16 species were recognized in this material from which *Argyrotheca cuneata* was reported for the first time from the Miocene of Hungary.

Some earlier authors over-splitted the Paratethyan and Mediterranean Miocene brachiopod faunas and mentioned many species, subspecies and varietas (e. g. SACCO 1902; FRIEDBERG 1921; MEZNERICS 1943). The Badenian (Middle Miocene) fauna of the Central Paratethys recently was critically evaluated on the basis of the very rich material of the Roztocze Hills in Poland (nearly 14000 specimens) by BITNER (1990). She resolved several taxonomical problems and identified some of the Paratethyan species with the Recent Mediterranean fauna. The rich Polish material permitted to establish the range of variability for several species, including also the three species discussed here.

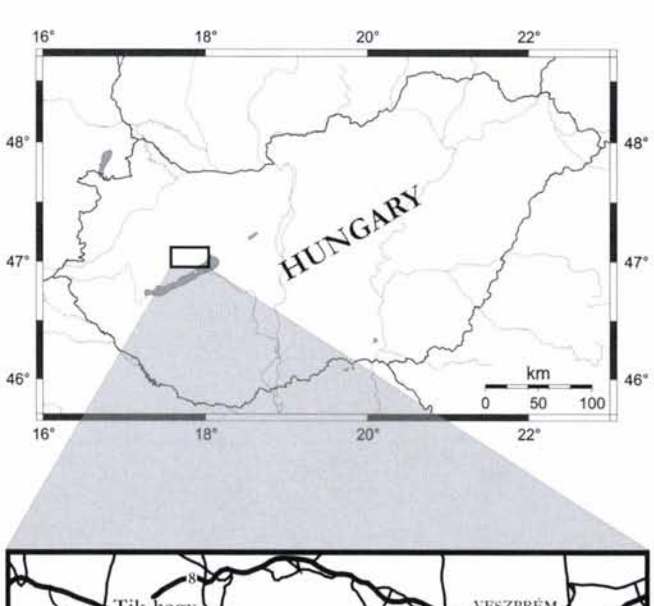

Figure 1 — **Sketch map showing the location of Bánd and Devecser outcrops.**

The aim of this paper is to describe a local, Early Badenian (Middle Miocene) brachiopod fauna from the Bakony Mountains (Transdanubian Central Range). Since all of the three species are well-known from other parts of the Central Paratethys, as well as from the Recent waters, the systematic part is confined to short synonymy lists of the most recent records, some remarks, distribution and paleoecological data. The two *Argyrotheca* species are sufficiently numerous at Bánd locality to study size-frequency distributions. Finally, some comments on the observed epifaunal encrusters and predatory drill holes will be discussed.

Localities and material

The studied micromorphic brachiopods derive from two localities of the Bakony Mountains. The majority of the specimens were collected from Bánd, while Devecser yielded only poor material of isolated valves (Figure 1). Bánd is a well-known Miocene locality, from where bivalves and gastropods (KÓKAY 1966), corals (HEGEDŰS 1970; OOSTERBAAN 1990) and polyplacophorans (DULAI 2005) were described. Recently, two amateur collectors (Tibor BERTA, Tamás NÉMETH) have performed intensive collecting in 2003 and 2004 (BERTA & NÉMETH 2004). With several gastropod, bivalve, scaphopod, polyplacophoran, scleractinian, cirripedian, echinoid, fish, calcareous algae, bryozoan and decapod species, they have collected 422 micromorphic brachiopods, which belong to two species of *Argyrotheca*:

Argyrotheca cuneata (RISSO, 1826) (147),
Argyrotheca cordata (RISSO, 1826) (275).

The second locality is situated east of village Devecser, at Tik-hegy (Figure 1). CSEPREGHY–MEZNERICS (1958) listed several mollusc species from this locality and recently DULAI (2005) described 2 polyplacophoran species. The same amateur collectors have collected very diverse fauna from several artificial trenches in 2004 and 2005 (NÉMETH 2005). The yellow, calcareous sand yielded very few isolated brachiopod valves (5 specimens):

Megathiris detruncata (GMELIN, 1790) (3),
Argyrotheca cordata (RISSO, 1826) (2).

Though the studied brachiopods originate from T. NÉMETH's and T. BERTA's private collections, a significant part of their material has been deposited in the regional Bakony Natural History Museum, Zirc. Some specimens were also donated to the Hungarian Natural History Museum, Budapest.

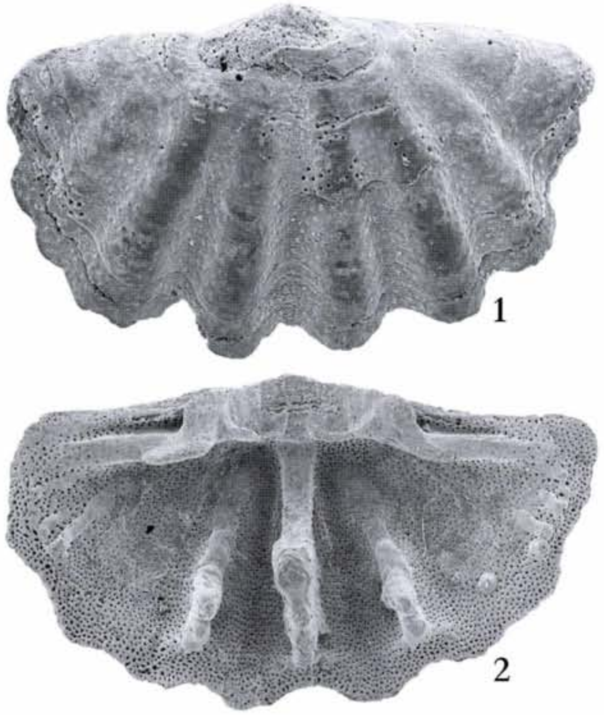

Figure 2 — *Megathiris detruncata* (GMELIN, 1790), Devecser. — 1: Outer view of a dorsal valve (L: 1.9 mm; W: 3.2 mm), ×24; **2:** Inner view of a dorsal valve (L: 3.4 mm; W: 5.9 mm), ×13.

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
Suborder Terebratellidina MUIR–WOOD, 1955
Superfamily Megathyridoidea DALL, 1870
Family Megathyrididae DALL, 1870
Genus *Megathiris* D'ORBIGNY, 1847

Megathiris detruncata (GMELIN, 1790)

(Figure 2: 1–2)

1990: *Megathiris detruncata* (GMELIN, 1790) — BITNER, pp. 135–138, text-figs 3–4, pl. 3, figs 1–8, pl. 6, figs 1–7. (cum. syn.)
2003: *Megathiris detruncata* (GMELIN, 1790) — KROH, pp. 147–148, pl. 1, figs 4–6.
2003: *Megathiris detruncata* (GMELIN, 1790) — BITNER & MOISSETTE, pp. 473–474, figs 6G, H.
2004: *Megathiris detruncata* (GMELIN, 1790) — BITNER & DULAI, pp. 74–75, pl. III, figs 11–15.

Material — 3 specimens (1 ventral and 2 dorsal valves) from Devecser.

Dimensions (mm)	**Length**	**Width**
	1.9	3.2
	3.4	5.9
	6.3	6.1 (broken)

Remarks — This species is rare in the investigated material, but very common at other localities of the Central Paratethys (e. g. more than 4000 specimens in the Roztocze Hills; BITNER 1990). The variability in shape and ornamentation was mentioned by many authors and recently was discussed by BITNER (1990, text-fig. 4). She has mentioned some asymmetrical specimens that are not seen in the Devecser material. The internal characters of the brachial valve make this species easily distinguishable from *Argyrotheca*: two rudimentary lateral septa appearing in the specimens about 2 mm wide (Figure 2: 2).

Palaeoecology — Attached by a short pedicle to firm substrates in cryptic habitats (cave walls and roofs, under boulders, coralligéne). It has a wide depth range from 5 to 896 m, but being most common in shallow waters (infralittoral-circalittoral) (BRUNTON & CURRY 1979; LOGAN & NOBLE 1983; LOGAN 2003; LOGAN et al. 2004).

Distribution — Well-known species from the Eocene to Recent. Eocene: Italy (DAVIDSON 1870; SACCO 1902; FABIANI 1913), Hungary (BITNER & DULAI in press); Miocene: Poland (JAKUBOWSKI & MUSIAŁ, 1979 a–b; KRACH 1950; BARCZYK & POPIEL–BARCZYK 1977; STUDENCKI 1988; BITNER 1990; POPIEL–BARCZYK & BARCZYK 1990); Ukraine (FRIEDBERG 1921); Austria (DREGER 1889; MEZNERICS 1943; KROH 2003; BITNER & DULAI 2004); Hungary (MATYASOVSZKY 1880; MEZNERICS 1943); Romania (MEZNERICS 1943, BĂRBULESCU & RADO 1984; BITNER & DULAI 2004); Italy (DAVIDSON 1870; SACCO 1902); France (JULIEN 1940); Spain (CALZADA 1978; LLOMPART & CALZADA 1982); Pliocene: Italy (DAVIDSON 1870); Spain (PAJAUD 1977; ENCINAS & MARTINELL 1992); Algeria (BITNER & MOISSETTE 2003); Pleistocene: Italy (GAETANI & SACCA 1983); Recent: Mediterranean Sea (LOGAN 1979, 2003; LLOMPART 1988; LOGAN et al. 2004); Atlantic Ocean (BRUNTON & CURRY 1979; LOGAN 1983, 1988, 1993); Caribbean Sea (COOPER 1977).

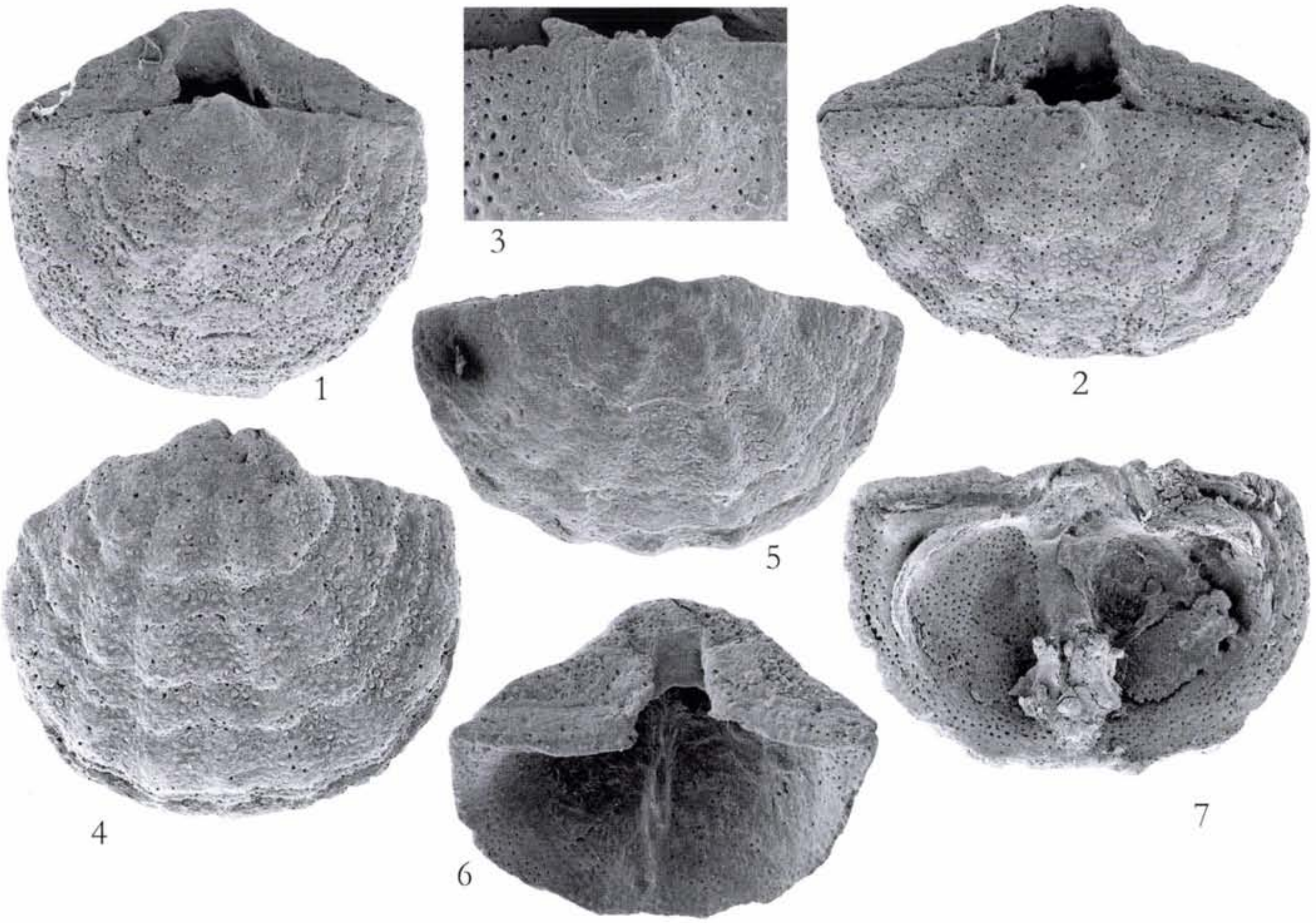

Figure 3 — ***Argyrotheca cuneata*** **(RISSO, 1826), Bánd.** — **1**: Dorsal view of a complete specimen (L: 2.3 mm; W: 2.5 mm), ×22; **2**: Dorsal view of a complete specimen (L: 2.2 mm; W: 3.1 mm), ×21; **3**: Dorsal view of brachial valve of a complete specimen showing the embryonal part, ×40; **4**: Ventral view of a complete specimen (L: 2.3 mm; W: 2.7 mm), ×22; **5**: Ventral view of a complete specimen (L: 1.7 mm; W: 3.0 mm), ×22; **6**: Inner view of a ventral valve (L: 2.2 mm; W: 2.8 mm), ×20; **7**: Inner view of a dorsal valve (L: 2.0 mm; W: 2.9 mm), ×21.

Genus *Argyrotheca* DALL, 1900

Argyrotheca cuneata (RISSO, 1826)

(Figure 3: 1–7)

1990: *Argyrotheca cuneata* (RISSO, 1826) — BITNER, pp. 138–140, text-figs 5–6, pl. 4, figs 1–9. (cum. syn.)
1993: *Argyrotheca cuneata* (RISSO, 1826) — BITNER, pp. 149–150, pl. 2, figs 1–6, pl. 3, figs 1–6.
2000: *Argyrotheca cuneata* (RISSO, 1826) — BITNER & PISERA, p. 9, pl. 1, figs 1–7.
2002: *Argyrotheca cuneata* (RISSO, 1826) — TOSCANO & SORGENTE, pl. 20, figs 2(?)–3.
2002: *Argyrotheca* cf. *cuneata* (RISSO, 1826) — KOWALEWSKI et al., fig. 2A.
2003: *Argyrotheca cuneata* (RISSO, 1826) — KROH, p. 148, pl. 1, figs 1–3.
2004: *Argyrotheca* cf. *cuneata* (RISSO, 1826) — SIMÕES et al., pp. 523–524, text–figs 3A–B, text–figs 5F–N.
2004: *Argyrotheca cuneata* (RISSO, 1826) — BITNER & KAIM, p. 196, figs 2A–C.
2004: *Argyrotheca cuneata* (RISSO, 1826) — BITNER & DULAI, p. 78, pl. III, figs 9–10.

Material — 147 specimens (94 complete shells, 25 dorsal valves, 28 ventral valves) from Bánd.

Remarks — Although the genus *Argyrotheca* was widely distributed within the Central Paratethys, *A. cuneata* was less frequent than *A. cordata.* The ornamentation and the shell outline of *A. cuneata* may be similar to *Megathiris detruncata.* However, it is much smaller, having fewer and not so strong ribs, and it has only one septum on the dorsal valve. The specimen figured by TOSCANO & SORGENTE (2002, fig. 2) shows very strong ribs, but without informations on the internal characters it is impossible to decide between *A. cuneata* and *M. detruncata*. *A. cuneata* can also be distinguished from *A. cordata* by having broad ribs on the external surface of both valves, and by the internal characters (no tubercles at the internal anterior margin of the valves). Some earlier authors distinguished the Tertiary specimens under the name *costulata*, and suggested that *costulata* could be the Miocene ancestor of the Recent *cuneata.* BITNER (1990) synonymized these two species and she also discussed the similarity with species *A. squamata* (EICHWALD) and *A. jacksoni* COOPER.

Palaeoecology — Attached by a short pedicle to firm substrates in cryptic habitats (under boulders, undersides of overhangings, coralligène, cave walls and roofs). Its depth range is similar to that of *A. cordata*, from few metres to more than 600m, but more frequent in shallow waters (infralittoral-circalittoral) (LOGAN 1979, 1983, 2003; LOGAN & NOBLE 1983; LOGAN et al. 2004).

Distribution — Well-known species from the Miocene to Recent. Miocene: Poland (BITNER 1990; POPIEL–BARCZYK & BARCZYK 1990; BITNER & PISERA 2000; BITNER & KAIM 2004); Austria (KROH 2003); Hungary (MATYASOVSZKY 1880; BITNER & DULAI 2004); Bulgaria (BITNER 1993); Italy (DAVIDSON 1870; SACCO 1902); Recent: Mediterranean Sea (LOGAN 1979, 2003; LOGAN & NOBLE 1983; BRUNTON 1988; LOGAN et al. 2002, 2004); Atlantic Ocean (BRUNTON & CURRY 1979; LOGAN 1983, 1988, 1993; KOWALEWSKI et al. 2002; SIMÕES et al. 2004).

Argyrotheca cordata (RISSO, 1826)

(Figure 4: 1–9)

1990 *Argyrotheca cordata* (RISSO, 1826) — BITNER, pp. 140–143, text-figs 7–8, pl. 5, figs 1–14, pl. 7, fig. 1. (cum. syn.)
1993 *Argyrotheca cordata* (RISSO, 1826) — BITNER, p. 150, pl. 4, figs 1–5, pl. 5, figs 1–8.
2000 *Argyrotheca cordata* (RISSO, 1826) — BITNER & PISERA, pp. 9–10, pl. 2, figs 1–9.
2002 *Argyrotheca cordata* (RISSO, 1826) — TOSCANO & SORGENTE, pl. 20, fig. 1.
2004 *Argyrotheca cordata* (RISSO, 1826) — BITNER & KAIM, pp. 196–197, figs 2D–K, 3A–E.
2004 *Argyrotheca cordata* (RISSO, 1826) — BITNER & DULAI, p. 74, pl. III, figs 2–8.

Material — 275 specimens (191 complete shells, 39 dorsal valves, 45 ventral valves) from Bánd, 2 specimens (2 dorsal valves) from Devecser.

Remarks — This is the most frequent species within the studied material. In some earlier papers it was reported under the name *A. neapolitana* (SCACCHI) but the name *cordata* has priority over the name *neapolitana* (LOGAN, 1977). The two BOETTGER's (1901) species, *A. subcordata* and *A. subcuneata* are also conspecific with *A. cordata*, because they are within the intraspecific variability ranges of this species (BITNER 1990). BITNER (1990) has also synonymized DEMORGAN's (1915) species (*Cistella laevigata*, *C. Marie*), as well as FRIEDBERG's (1921) species (*Cistella dertomutiensis*, *C. zboroviensis*) with *A. cordata*. MEZNERICS (1943) used three different names for *A. cordata* specimens: *neapolitana*, *subcordata*, *subcuneata*. This species is easily distinguishable from *A. cuneata* by the internal features: the internal anterior margin of both valves is covered with tubercles (4–20, from small to large specimens). The triangular median septum shows 3–4 (BITNER 1990) or 5–6 (LOGAN 1979) serrations. The Hungarian specimens have 4 serrations (Figure 4: 5, 7–9).

Palaeoecology — The species is attached by a short pedicle to firm substrates in cryptic habitats (under boulders, undersides of overhangings, coralligène, cave walls and roofs). Its depth range is from few metres down to more than 600m, but it is more common in shallow waters (infralittoral–circalittoral). Densities of up to 100 specimens/m^2 were recorded (LOGAN & NOBLE 1983; LOGAN 2003; LOGAN et al. 2004).

Distribution — Well-known species from the Miocene to Recent. Miocene: Poland (BARCZYK & POPIEL–BARCZYK 1977; STUDENCKI 1988; BITNER 1990, 2002; POPIEL–BARCZYK & BARCZYK 1990; BITNER & PISERA 2000; BITNER & KAIM 2004); Ukraine (FRIEDBERG 1921); Austria (DREGER 1889); Hungary (MATYASOVSZKY 1880;

MEZNERICS 1943; BITNER & DULAI 2004); Romania (BOETTGER 1901; ZILCH 1934; MEZNERICS 1943; BĂRBULESCU & RADO 1984; BITNER & DULAI 2004); Bulgaria (BITNER 1993); France (DEMORGAN 1915; JULIEN 1940); Pliocene: Italy (DAVIDSON 1870); Spain (ENCINAS & MARTINELL 1992); Recent: Mediterranean Sea (DAVIDSON 1870; LOGAN 1979, 2003; LOGAN & NOBLE 1983; BRUNTON 1988); Atlantic Ocean (LOGAN 1983, 1988, 1993).

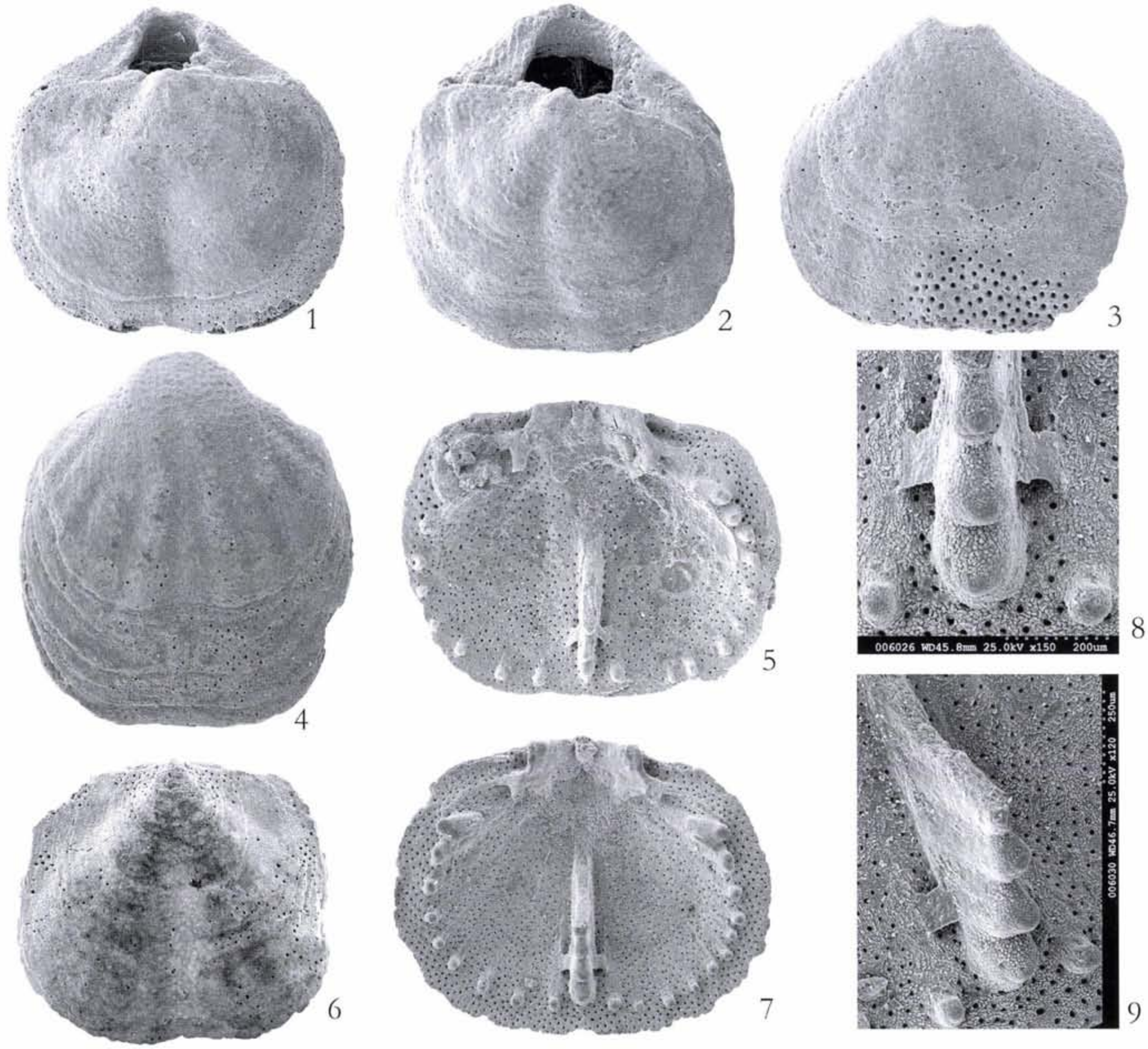

Figure 4 — ***Argyrotheca cordata*** **(RISSO, 1826), Bánd and Devecser.** — **1**: Dorsal view of a complete specimen (L: 2.2 mm; W: 2.3 mm), ×22, Bánd; **2**: Dorsal view of a complete specimen (L: 2.8 mm; W: 2.7 mm), ×18.5, Bánd; **3**: Ventral view of a complete specimen (L: 2.3 mm; W: 2.6 mm), ×20, Bánd; **4**: Ventral view of a complete specimen (L: 3.1 mm; W: 2.8 mm), ×17.5, Bánd; **5**: Inner view of a dorsal valve (L: 1.9 mm; W: 2.5 mm), ×22.5, Bánd; **6**: Outer view of a dorsal valve (L: 2.1 mm; W: 2.3 mm), ×20, Devecser; **7**: Inner view of a dorsal valve (L: 2.0 mm; W: 2.5 mm), ×22.5, Devecser; **8**: Detail of Figure 4: 7; showing the median septum; ×75, Devecser; **9**: Detail of Figure 4: 7; showing oblique-lateral view of the median septum; ×56, Devecser.

Taxonomic composition of the fauna

The brachiopod assemblage of Bánd locality is of low diversity and contains only two species of *Argyrotheca*, *A. cordata* (65%) and *A. cuneata* (35%). As the specimen number of this sample is relatively high (422), these data probably represent more or less the real composition of the original assemblage. The Devecser sample is slightly different, it contains *Megathiris detruncata* (60%) and *Argyrotheca cordata* (40%), but the low number of specimens (5) may give false percentages.

The taxonomic composition of the Bánd fauna is not exceptional in the Middle Miocene. *Argyrotheca* is often the dominant element of the brachiopod assemblages in the Central Paratethys. Two *Argyrotheca* species are present with a strong dominance of *A. cordata* at Łychów, Roztocze

Hills (BITNER 1990). This locality was interpreted as shallow water kelp assemblage (HOFFMAN et al. 1978). The brachiopod fauna also consists of these two species in the oyster bioherm at Zdziechowice, but *A. cuneata* is dominant (BITNER 1990). Very similar brachiopod assemblages were found at Radwanówka (BITNER 1990), Ohrid, Bulgaria (BITNER 1993) and Niechobrz (BITNER & PISERA 2000), with the dominance of *A. cordata*. However, there are two additional species in negligible amounts at the last three localities. All of these localities were interpreted as shallow water environments. BITNER & KAIM (2004) reported the same two *Argyrotheca* species, with the dominance of *A. cordata* (89%), from an atypical facies: dark grey sandy–silty deposits of the intra-Carpathian Nowy Sącz Basin. They suggested that this assemblage might be transported basinward from a shallower setting. These three species (*M. detruncata*, *A. cuneata*, *A. cordata*) commonly occur together in the Recent Adriatic Sea (LOGAN 2003), as well as in the whole Mediterranean Sea (LOGAN 1979), mainly in the shallow water environments.

Palaeoecological review of megathyridids

Previously, the paedomorphic family Megathyrididae have been generally considered primitive, but nowadays most authors consider them advanced, rapidly evolved neotenous forms (ASGAARD 1986). *Megathiris* and *Argyrotheca* are known from the Late Cretaceous and are widely distributed in modern seas, and most species are continental shelf dwellers. *Megathiris* and *Argyrotheca* are common in coralligenous biocoenoses (LOGAN 1979). They also inhabit small crevices and interstices, or the walls of submarine cliffs and caves. *M. detruncata* has been observed attached to rocks and stalagmites in the deepest recesses of a submarine cave, under conditions of virtually no water movement and light (LOGAN 1979). Elsewhere within the shallow part of the coralligenous biocoenosis small brachiopods may be found attached to almost any hard substrate, including shells, rocks and man-made objects. Both *Argyrotheca* species are very small and have simple, bilobed schizolophe lophophores, regarded less effective for food extraction (RUDWICK 1970). *Megathiris* is only slightly larger and ptycholophous, the lophophore never developing beyond a four-lobed stage (LOGAN 1979). The small forms with simple, less efficient lophophore prefer shallow-water regions, where particulate organic matter is more plentiful (LOGAN 1979).

Recent brachiopods generally have wide depth ranges, therefore we can use fossil brachiopods as depth indicators with great uncertainty. LOGAN (1979) divided the Recent Mediterranean brachiopods into two depth groups: shallow water (typical of the infralittoral and circalittoral zone) and eurybathic species. Both *Argyrotheca* and *Megathiris* belong to the shallow water group (shelf species ranging down to 200m), but sometimes occur at deeper environments on coralline algae bottoms and gravels, too. The maximum occurrence is from 20 to 60m for *A. cuneata* and *A. cordata*, and 20–120m for *M. detruncata*. All shallow water species show patchy distributions, with isolated high densities of several hundreds specimens per square meter being occasionally recorded (LOGAN 1979). Members of the shallow water group are all small in size, inhabiting protected, light-poor environments, such as caves. Extant representatives of *Megathiris* and *Argyrotheca* exhibit mainly cryptic mode of life in shallow depth in light-poor environments (crevices, caves, undersides of boulders). *Argyrotheca* is known from cryptic habitats in Recent reef environments (e.g. LOGAN 1975). TOSCANO & SORGENTE (2002) reported these two *Argyrotheca* species from maerl deposits and molluscan–bryozoan assemblage of the rhodalgal-bryomol temperate carbonates of the Apulian Shelf. According to TADDEI RUGGIERO (1987, 1990) *A. cordata* often lives in association with living thalli of *Peyssonelia rosa-marina*.

LOGAN (1975) gave a detailed ecological study on *A. bermudana* from the Bermuda platform. The specimens usually attached by the pedicle to the underside of foliaceous and encrusting corals or underside of boulders. The shell is normally oriented in an almost vertical position. The distribution of individuals is patchy, probably resulting from late release of brooded larvae, rapid settlement and post-settlement competition with other organisms (LOGAN 1975). JACKSON et al. (1971) mentioned that *A. johnsoni* from Jamaican fore-reef slopes increased in density with depth, and suggested that density can be correlated with low light intensity. The competition for living space may also be an important limiting factor. Colonization of cryptic habitats enables brachiopods to avoid the intense competition for space, which occurs on more exposed surfaces. The presence of firm substrate for attachment is regarded as the main limiting factor. Water energy and light operate mainly in the larval stages prior to settlement (LOGAN 1979).

According to SIMÕES et al. (2004) *A.* cf. *cuneata* is more common in the shelf than in the coastal samples of Brazilia. They recognized three distinct brachiopod associations; one of them is the *Terebratulina–Argyrotheca* fauna, which is common at depths ranging between 100–200 m.

Experiments on the settlement patterns of *Argyrotheca cordata* and *Argyrotheca cuneata* in the eastern Mediterranean confirm their preference for cryptic habitats within crevices and fractures of blocks of rocks (ASGAARD & BROMLEY 1991). The larvae settle late in the autumn and their lifespan does not exceed two years. A major limiting factor in brachiopod colonization in shallow water may be the grazing pressure from chitons and echinoids. VALENTINE & JABLONSKI (1983) showed that nonplanktotrophic groups, such as the articulate brachiopods, have relatively few offsprings and some species of *Argyrotheca* protect the larvae in brood pouches. Cryptic habitats aid the reproductive and developmental strategy of these low-energy species with a low fecundity. *Argyrotheca* probably pursued r-selected life-strategies, small, short-lived organisms generated by slow growth (HARPER et al. 1995).

Size-frequency distributions of brachiopods

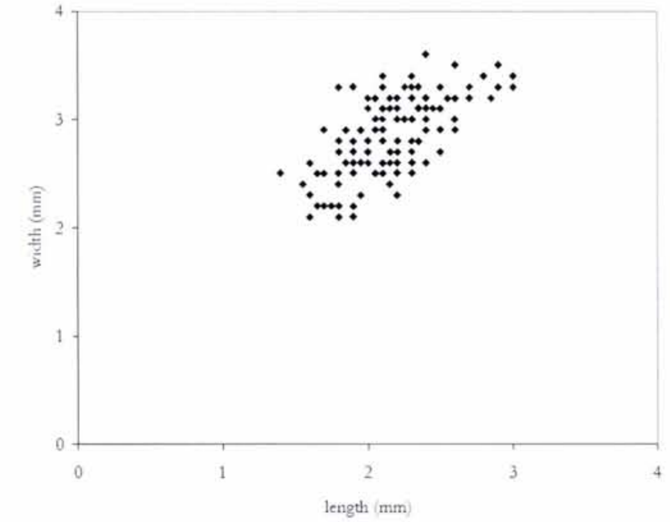

Figure 5 — Scatter diagram of length-width relationships for specimens of *Argyrotheca cuneata* (RISSO, 1826), Bánd.

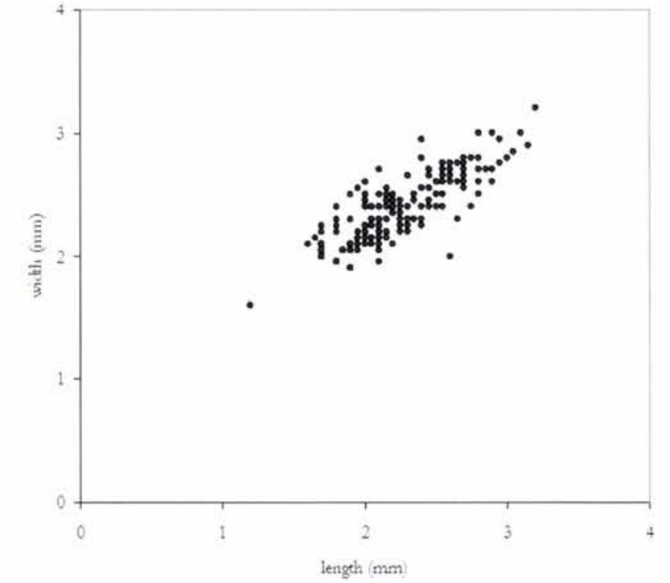

Figure 6 — Scatter diagram of length-width relationships for specimens of *Argyrotheca cordata* (RISSO, 1826), Bánd.

Size-frequency distributions of brachiopods are frequently used to study population dynamics. High juvenile mortality is characteristic for most marine invertebrates in Recent assemblages (e.g. NOBLE & LOGAN 1981), but TADDEI RUGGIERO (1996) demonstrated that *Neocrania anomala* has stable population structure and much more adult specimens in protected cave environment than elsewhere. LOGAN (1975) published width-frequency histograms of reef-dweller *Argyrotheca bermudana*, which generally showed normal distribution. THAYER (1975) suggested that unimodal size-frequency distributions may indicate patchy larval dispersion. STEWART (1981) correlated differences in population structure with environmental conditions. BITNER (2002) have studied the size-frequency distributions for 28 assemblages of four species from different Middle Miocene environments. These assemblages showed variation even within a single species, but different species from the same environment gave similar size-frequency distributions. The assemblages collected from reef cavities produced bell-shaped distributions both in *A. cuneata* and *A. cordata* (BITNER 2002). It suggests that the protected and stable cryptic habitats are characterised by lower juvenile mortality and enable the brachiopods to reach larger size (BITNER 2002).

Size-frequency histograms are very useful but several factors can influence the results (inadequate sampling, taphonomic processes, diagenetic solution, mechanical destruction, predation) (see detailed discussion in BITNER 2002). The studied Hungarian Middle Miocene brachiopods contain three species from which *Megathiris detruncata* is present in small number (3 specimens). However, the other two species are sufficiently numerous at Bánd locality (*A. cuneata*: 147 specimens; *A. cordata*: 275 specimens) for size-frequency studies. The specimens are derived from bulk samples, washed on 0.5 mm sieve, therefore the sampling method is adequate. A very significant part of the material contains complete shells (64% at *A. cuneata* and 69% at *A. cordata*) and the numbers of isolated dorsal and ventral valves are nearly the same (25 vs. 28 at *A. cuneata* and 39 vs. 45 at *A. cordata*). It suggests that the studied assemblage is more or less autochthonous, without significant transportation, selective removal of smaller specimens or mechanical destruction. The associated mollusc fauna yielded well-preserved calcitic and aragonitic shells, so diagenetic dissolution did not influence the composition of the fauna. The predation was also a limited affecting factor, only 3.4% of *A. cuneata* and 3.6% of *A. cordata* specimens were drilled by predatory gastropods (see below). All the above mentioned circumstances justify that the size-frequency distributions of these two *Argyrotheca* species give reasonable results.

All *Argyrotheca* specimens are rather small and their sizes are concentrated in very narrow interval, mainly between 1.5 and 3.0 mm (Figures 5–6). Generally, *A. cuneata* has slightly smaller average size than *A. cordata*. Both *Argyrotheca* species show bell-shaped size-frequency histograms in the Bánd material (Figures 7–8). The lack of juvenile peak indicates low juvenile mortality. These results correspond well with the above referred literature data. The geological context and the associated fauna suggest that a small patch reef existed at Bánd in the Early Badenian (HEGEDŰS 1970, OOSTERBAAN 1990). The micromorphic *Argyrotheca* specimens lived in sheltered, hidden places of the reef; they attached to the lower surfaces of colonial corals, mollusc shells or other hard substrates. Patchy larval distribution is common in these microenvironments, and unimodal, bell-shaped size distribution suggests a stable community without high juvenile mortality.

ASGAARD & BROMLEY (1991) have found three peaks for Recent *A. cordata*: at 0.5 mm for newly settled larvae, 1.2 mm for juveniles and 2.4–2.8 mm for mature specimens (they used width instead of length measurements). Assuming the same growth rate in Middle Miocene, there are no newly settled larvae in the Bánd sample and the number of juveniles is also very low. Most of the specimens probably belong to young adult and mature brachiopods.

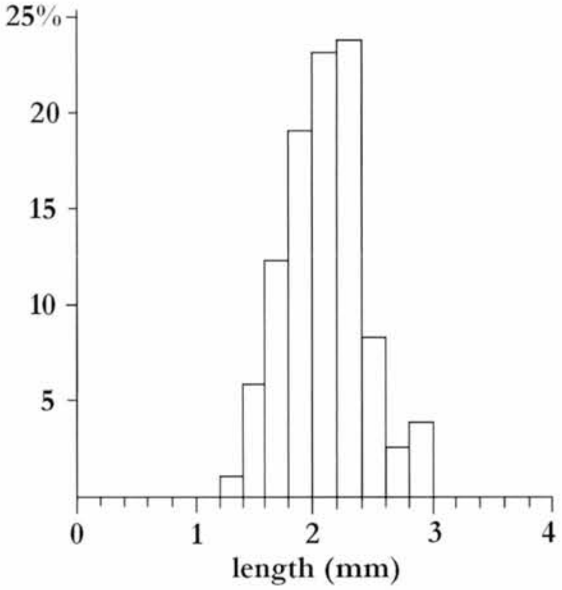

Figure 7 — **Size-frequency histograms of *Argyrotheca cuneata* (RISSO, 1826), Bánd.**

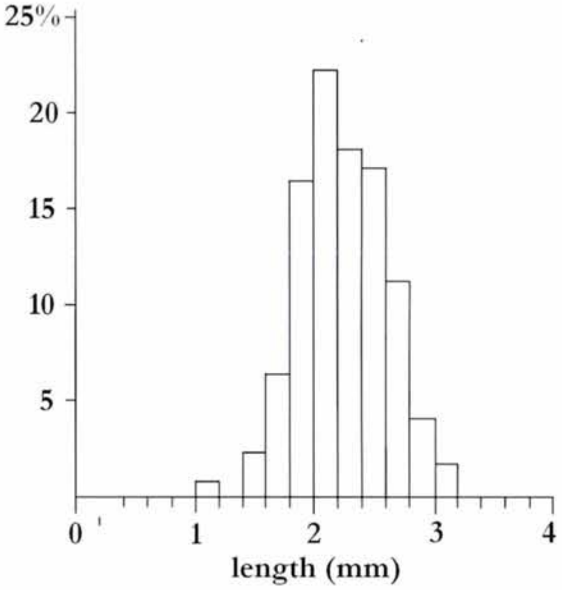

Figure 8 — **Size-frequency histograms of *Argyrotheca cordata* (RISSO, 1826), Bánd.**

Epizoans on micromorphic brachiopods

Encrusters may provide information about life orientation of the host and may have also some sedimentological implications (CUFFEY et al. 1995). Brachiopods can offer hard substrate for epizoans, but the amount of encrusters is very variable on fossil and Recent forms. About 10% of the Eocene brachiopods from Antarctica were encrusted by epifaunal organisms (bryozoans, foraminifers, serpulid polychaetes, cirripeds, octocorals; BITNER 1996). However, 80% of Recent *Neocrania huttoni* carried epibionts in New Zealand (LEE 1987).

Only a very small part of the studied Hungarian specimens (427) were encrusted (Figure 9). None of the brachiopods carried more than one specimen of encrusters. No encrustation is observed on the three *M. detruncata* specimens. Only one out of 147 specimens (0.7%) of *A. cuneata* shows the possible remain of a serpulid. The serpulid tube already disappeared, but the meandering attachment place can be seen at the middle part of the dorsal valve (Figure 9: 6). Two out of 275 specimens (0.7%) of *A. cordata* carry encrustation (one bryozoan and one serpulid). The bryozoan larva settled on the ventral valve near to the anterior margin (Figure 9: 1–3). Unfortunately, the studied bryozoan is very badly-preserved, but shows some similarities to *Annectocyma?* (MOISSETTE pers. com.). *Annectocyma major* is generally common in Hungarian Badenian Bryozoa fauna (MOISSETTE et al. 2006). The serpulid polychaete tube is also situated on the ventral valve, at the most terminal part of the anterior margin (Figure 9: 4–5). Taking into consideration the life position of megathyridids, the ventral valve and mainly the terminal part of the ventral valve is situated at the highest point. These brachiopods are sometimes very densely packed, and in these cases only the above mentioned parts of the shells are available as solid substrate for the settlement of different larvae. It suggests that both the Bryozoa and the serpulid Polychaeta probably encrusted the ventral valves of *A. cordata* during the life of these brachiopods. As the serpulid attached very near to the anterior commissure, it may benefit from the feeding currents of the brachiopod. Similar situations were reported on the Palaeozoic *Mucrospirifer* (SCHUMANN 1967), on the Eocene *Paraplicirhynchia* (BITNER 1996), and on Cenozoic and Recent *Tegulorhynchia* (LEE 1980). The possible serpulid on the middle part of dorsal valve of *A. cuneata* probably settled after the death of the brachiopod.

Generally the larger sized brachiopods show traces of epibionts. The encrustation of micromorphic brachiopods is not well-represented in palaeontological literature. RUDWICK (1962) observed epifauna associated usually with larger brachiopod shells. LEE (1987) found that most of the epibiont-free valves were juveniles, i. e. less than 8 mm at Recent *Neocrania huttoni*. BITNER (1996) noted that in the case of Eocene *Terebratulina buckmanni*, absence of epibionts might be the result of its small size. She also mentioned another possible explanation: some Recent *Terebratulina* are very often covered by encrusting sponges leaving no traces in the fossil record (SURLYK 1972). Using of micromorphic brachiopods as solid substrate for attachment is also interesting because there are lots of molluscs and colonial corals in the associated fauna, which probably offer more suitable attachment surfaces. Epifaunal encrusters are recorded for the first time on the micromorphic brachiopods in the Miocene Central Paratethys.

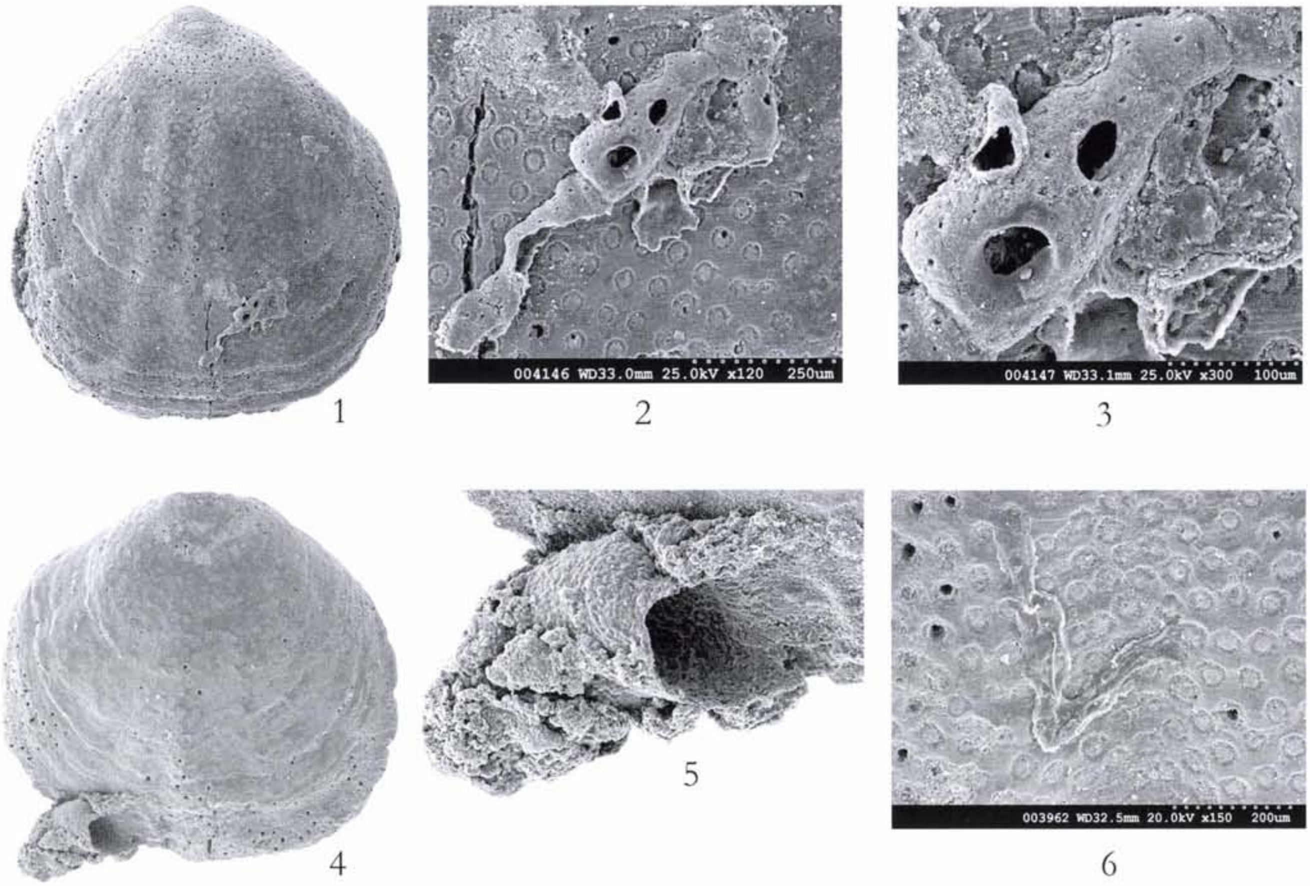

Figure 9 — Bryozoan and serpulid encrusters on micromorphic brachiopods, Bánd — 1: Bryozoan encrustation on the ventral valve of *Argyrotheca cordata* (RISSO, 1826) (L: 3.0 mm; W: 2.8 mm), ×18; **2**: Detail of Figure 9:1, showing the encrusting Bryozoa, ×75; **3**: Detail of Figure 9: 2, showing the encrusting Bryozoa, ×170; **4**: Serpulid encrustation at the anterior end of ventral valve of *Argyrotheca cordata* (RISSO, 1826) (L: 2.0 mm, W: 2.1 mm), ×24; **5**: Detail of Figure 9: 4, showing the serpulid tube, ×75; **6**: Remain of serpulid (?) encrustation at the middle part of the dorsal valve of *Argyrotheca cuneata* (RISSO, 1826), ×80.

Drilling predation

Drilling predation has long evolutionary history with rich fossil record (KOWALEWSKI et al. 1998). Gastropod drillings are especially frequent from Late Cretaceous to Holocene, but up to now, relatively few drilled brachiopods have been reported from the Cenozoic (LEIGHTON 2003; BAUMILLER & BITNER 2004). The drilling frequencies can be rather variable even in localities near to each other: 39% at Węglin, 2% at Szczaworyż and 3.7% at Węglinek (BAUMILLER & BITNER 2004).

Table 1 — Drill hole data for Badenian brachiopods of the Bakony Mts.

Species	not drilled	drilled	drilled ventral valve	drilled dorsal valve	drilled on margin
Megathiris detruncata	3	-	-	-	-
Argyrotheca cordata	267	10	5	3	2
Argyrotheca cuneata	142	5	4	1	-

No drill holes were observed at the 5 Devecser specimens. Drill hole frequency is low at Bánd locality, too. Altogether 15 out of 422 specimens show traces of predatory gastropod activities (3.5%) (Figure 10). If the two *Argyrotheca* species are counted separately, the result is very similar, although *A. cordata* has a slightly higher drilling frequency (*A. cordata*: 10 drilled specimens out of 275 (3.6%); *A. cuneata*: 5 drilled specimens out of 147 (3.4%)). It suggests that no taxon selectivity can be observed at the Hungarian material, in contrast with the Polish Węglin locality, where *Megathiris detruncata* was preferentially drilled (BAUMILLER & BITNER 2004). Drill holes can be found on either the ventral or the dorsal valve but in some cases the drill hole occurs on the margin, penetrating both valves (Table 1). Altogether 9 drill holes were found on the ventral valve, 4 drill holes on the dorsal valve and 2 drill holes at the margin of the valves. It suggests valve selectivity to ventral valve's advantage, which does not correspond with BAUMILLER & BITNER's (2004) results where the dorsal valve was more frequently drilled. (However, it has to be mentioned that the Hungarian results are based only on 15 drilled specimens, while the Polish data are based on 514 drilled brachiopods). At the same time, similarly to the Polish results, some differences can be seen in valve selectivity at the two separated *Argyrotheca* species. Valve selectivity is lower at *A. cordata* because 5 drill holes were found on ventral and 3 holes on dorsal valves (50% and 30%) (two holes are at the margins). More significant valve selectivity seems to be at *A. cuneata* where 4 drill holes were found on the ventral valve and only one on the dorsal valve (80%–20%, but based only on five specimens). Ventral valve selectivity can be explained assuming that predatory gastropods attack the living brachiopod specimens, because the ventral valve is more accessible for predators in life position. *A. cordata* shows random drill hole distribution on both valves (Figure 12), but the drill holes are concentrated on a small area on the ventral valve of *A. cuneata* (Figure 11). It may suggest site selectivity in the predators of the latter species. As all of the studied *Argyrotheca* specimens are very small, and their size-interval is rather narrow (most of the specimens are between 1.5 and 3 mm in length), it is not worth comparing the size of drilled and undrilled brachiopods. Anyway, no statistically significant size differences were found between drilled and undrilled specimens by BAUMILLER & BITNER (2004) on a much larger database.

Two of the drill holes are unfinished (e.g. Figure 10: 5), therefore the predation was unsuccessful. No multiple holes occurred on the studied brachiopods. Axes of the holes are perpendicular to the shell surface. These features, as well as the outline and size of the drill holes refer to predator activity, not substrate penetration (KELLEY & HANSEN 2003). The drill holes are both cylindrical and conical in cross section, but conical holes are much more common. The former ones refer to muricid gastropods, while the latter ones can be attributed to naticid gastropods. Both muricids and naticids were diverse and abundant at the studied Bánd locality (e.g. *Murex* cf. *aquitanicus*, *Murex subtorularius*, *Muricopsis cristatus*, *Polinices redempta dertoconvexa*, *Polynices olla*, *Natica tigrina hörnesi*; KÓKAY 1966), therefore it is impossible to identify the predator species.

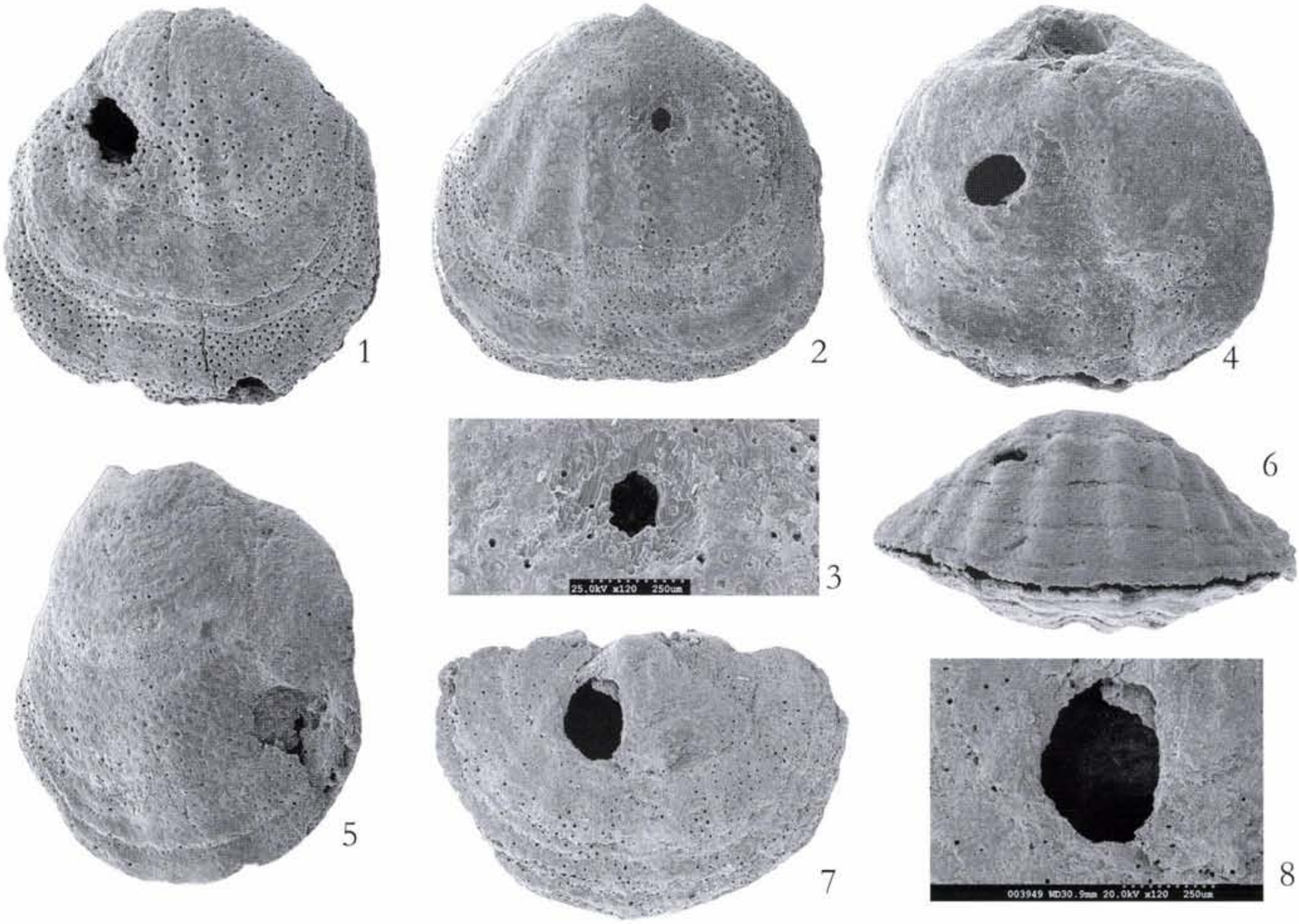

Figure 10 — Traces of drilling predation on micromorphic brachiopod valves by predatory gastropods, Bánd. — **1**: Ventral view of a drilled *Argyrotheca cordata* (L: 2,7 mm; W: 2.6 mm), ×19; **2**: Ventral view of a drilled *Argyrotheca cordata* (L: 2.4 mm; W: 2.5 mm), ×20; **3**: Detail of Figure 10: 2, showing the drillhole, ×48; **4**: Dorsal view of a drilled *Argyrotheca cordata* (L: 2.6 mm; W: 2.7 mm), ×20; **5**: Ventral view of a drilled *Argyrotheca cordata*, showing an unsuccessful drilling (L: 2.4 mm; W: 2.2 mm), ×23; **6**: Anterior view of a drilled *Argyrotheca cuneata* (L: 2.3; W: 2.5 mm), ×22; **7**: Ventral view of a drilled *Argyrotheca cuneata* (L: 2.2 mm; W: 3.1 mm), ×18; **8**: Detail of Figure 10: 7, showing the drillhole, ×48.

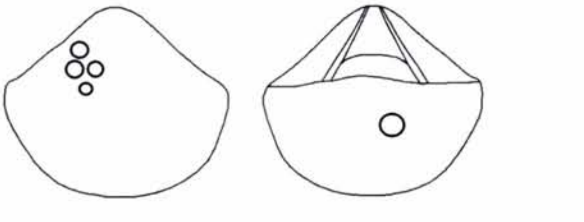

Figure 11 — Distribution of drill holes on *Argyrotheca cuneata* (Risso, 1826) specimens. Circle diameters are proportional with the observed drill hole sizes.

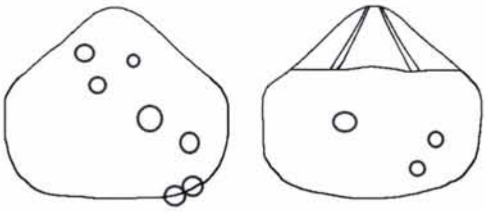

Figure 12 — Distribution of drill holes on *Argyrotheca cordata* (Risso, 1826) specimens. Circle diameters are proportional with the observed drill hole sizes.

Conclusion

More than 400 specimens of Middle Miocene micromorphic brachiopods yielded three species of Megathyrididae (*Megathiris detruncata*, *Argyrotheca cuneata*, *A. cordata*) from two localities of the Bakony Mts. These three species are common in the shallow water environments both in fossil and Recent assemblages. Until now, all the three species were represented by only few specimens in the Hungarian Miocene fossil record (Bitner & Dulai 2004).

The high percentage of complete, well-preserved shells at Bánd suggests that the studied assemblage is more or less autochtonous, without significant transportation, selective removal of smaller specimens or mechanical destruction. All of the Devecser brachiopods are isolated valves, but the good preservation refers only to short transport.

The two *Argyrotheca* species are sufficiently numerous in the examined material for size-frequency distribution studies. Both *A. cuneata* and *A. cordata* show bell-shaped size-frequency histograms, indicating low juvenile mortality. It corresponds well with other data from Miocene and Recent reef-associated micromorphic brachiopod assemblages. *Argyrotheca* specimens lived in protected, cryptic environments of the reef. Patchy larval distribution resulted in unimodal, bell-shaped size distribution, suggesting stable community. Recent data indicate that nearly all of the Bánd specimens belong to young adult and mature brachiopods.

Epifaunal encrusters are recorded for the first time on the micromorphic brachiopods in the Central Paratethys. Three brachiopods (0.7 %) carry epibionts on their valves (1 Bryozoa and 1 serpulid on *A. cordata* and 1 serpulid? on *A. cuneata*). Both the Bryozoa (*Annectocyma*?) and the serpulid situated on the ventral valves near to the anterior margin, which is the highest point of the *Argyrotheca* valves in life position. It suggests that these epizoans encrusted the ventral valves during the life of these brachiopods. The serpulid probably benefitted from the feeding currents of the brachiopod.

Fifteen out of 422 *Argyrotheca* specimens show drill holes of predatory gastropods (3.5%). No taxon selectivity can be observed (*A. cordata*: 3.6%; *A. cuneata*: 3.4%). Valve selectivity to ventral valve's advantage is more significant in the case of *A. cuneata* (80%–20%). Ventral valve selectivity suggests that predatory gastropods attacked the living brachiopods, because the ventral valve was more accessible in life position. Site selection is also present at *A. cuneata*. As both muricid and naticid gastropods were diverse and abundant at Bánd locality, it is impossible to identify the predator species.

* * *

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