Seagrass-associated Middle Miocene brachiopods from the Central Paratethys, with description of a new species of *Bronnothyris*

ALFRÉD DULAI

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The Middle Miocene brachiopod fauna of the Mecsek Hills (Southern Hungary) is poorly known. In this paper the brachiopods of a new fossil site discovered by private collectors on the outskirts of Mecsekpölöske village is described. The studied assemblage from the lower Badenian clayey sand (Lajta Limestone Formation) is very abundant (5248 specimens), and represented partly by some species well-known from other shallow marine sites of the Central Paratethys (*Joania cordata*, *Megathiris detruncata*, *Gryphus miocenicus*, *Megerlia truncata*, and *Discradisca* sp.). However, the most abundant taxon is a new species of *Bronnothyris* (i.e., *B. attilavorosi* sp. nov.), characterised by subcircular outline; four to seven single, weak, rounded ribs; distinct cardinal process; strongly prominent triangular dorsal median septum, with septal flanges and four strong serrations on its anterior slope; short, slightly divergent inner socket ridges; narrow fused hinge plates. This is the first record of *Bronnothyris* from the Central Paratethys and from the Miocene. The Hungarian species extends the stratigraphic range of *Bronnothyris*: it is known from the Upper Cretaceous to the Middle Miocene. The taxonomic composition of the Mecsekpölöske brachiopod assemblage (with strong dominance of Megathyrididae), together with several elements of the associated fauna (e.g., gastropods, foraminifers, ostracods, otoliths, and fish teeth), suggests that the palaeoenvironment may have been a shallow marine seafloor covered with seagrass meadows. Both the recently published upper Pliocene brachiopod assemblage from Italy (Villalvernia, Piedmont) and this Middle Miocene assemblage presented here from Hungary confirm that micromorphic Megathyrididae brachiopods can be used as indirect palaeo-seagrass indicators (IPSIs). However, since they do not occur exclusively in this environment, other direct or indirect evidence of the former presence of seagrass meadows is also necessary.

Key words: Brachiopoda, Megathyrididae, seagrass meadows, indirect palaeo-seagrass indicator (IPSI), Badenian, Miocene, Mecsek Hills, Hungary.

Alfréd Dulai [dulai.alfred@nhmus.hu; ORCID: https://orcid.org/0000-0002-9366-5217], Department of Palaeontology and Geology, Hungarian National Museum Public Collection Centre – Hungarian Natural History Museum, Ludovika Square 2–6, H-1083 Budapest, Hungary.

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Introduction

Shallow marine fauna of the Middle Miocene Central Paratethys was extremely diverse, and the various sedimentary formations contain abundant fossil remains of many invertebrate and vertebrate groups (Moissette et al. 2006; Hyžný and Dulai 2021; Harzhauser et al. 2024). Although brachiopods generally play a subordinate role in the Cenozoic, they are regularly found in smaller to larger quantities in Neogene formations. This is particularly true for the small-sized, so-called micromorphic brachiopod species, which can sometimes be significantly enriched in screen-washed residues.

When discussing a large palaeogeographical unit, the knowledge and exploration of individual sub-areas can often vary greatly. This is the case for the Central Paratethys and the Mecsek Hills in southern Hungary. Compared to other Central Paratethyan areas, there are very few publications and limited data available on Miocene brachiopods from this region. Even the only major publication (Matyasovszky 1880) would need revision (Dulai 2025a).

The role of private collectors, who often discover previously unknown sites and valuable new fossils, is increasing. This was the case here, where the new fossil site at Mecsekpölöske was discovered by private collector Tamás Németh (Balatonkenese, Hungary), who drew attention to the extremely diverse fossil material found there.

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The aim of this paper is to discuss the Middle Miocene brachiopod assemblage from the Mecsekpölöske site, to describe a new species of *Bronnothyris* from there and to interpret the palaeoenvironment on the basis of the taxonomic composition of the identified brachiopods and some associated fossil groups. In addition to reconstructing the local palaeoenvironment, the possible use of micromorphic Megathyrididae brachiopods as indirect palaeo-seagrass indicators in a broader sense is also examined.

Institutional abbreviations.—HNHM, Hungarian National Museum Public Collection Centre – Hungarian Natural History Museum, Budapest, Hungary.

Other abbreviations.—A, articulated specimen; D, dorsal valve; fr, fragment; IPSI, indirect palaeo-seagrass indicator; MNI, minimal number of individuals; V, ventral valve.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in Zoobank: urn:lsid:zoobank.org:pub:6766FAF0-DC54-4E4A-AF63-07E18DF428C8.

Geological setting

The Paratethys was a large inland sea intermittently connected to the Mediterranean (Rögl 1998; Popov et al. 2004). Its diverse marine fauna refers to a stable connection with the Mediterranean in the present-day Slovenia (Kókay 1985) (Fig. 1). However, the biogeographic differentiation necessitated the establishment of a regional stratigraphic scheme (Harzhauser and Piller 2007). The Badenian (16.303–12.829 Ma) is a regional stage used in the Central Paratethys for part of the Middle Miocene (Langhian to middle Serravallian) (Papp et al. 1978; Hohenegger et al. 2014).

During the Miocene, islands of Permian and Mesozoic rocks of the Mecsek Hills were surrounded by the Central Paratethys, leaving a variety of lagoonal, coastal and nearshore sediments (Hámor 1970; Chikán 1991; Sebe et al. 2015). Three Lower and Middle Miocene sedimentary cycles are observed in the Mecsek Hills (Sebe et al. 2015). The upper part of the second cycle is represented by the lower Badenian Pécsszabolcs Limestone Member of the Lajta Limestone Formation (Selmeczi et al. 2024), it consists of varied shallow marine sediments (conglomerate, glauconitic sandstone, bioclastic limestone, calcareous sandstone and sandy clays). The rich macrofaunal content of the red algal “lower Leitha limestone” consists mainly of mollusc, echinoid and bryozoan remains, which are indicative of the *Chlamys elegans*/*Pecten revolutus* Subzone of the *Flabellipecten besseri* Assemblage Zone (Bohn-Havas et al. 1987). *Amphistegina*, *Miliolina*, and *Heterostegina* species are the most common in the benthic Foraminifera assemblages (Korecz-Laky 1968).

The geology of the area around Mecsekpölöske is described in Strausz (1928) and Chikán (1991). The studied new site is located 1 km east of the village, in a gully on the western side of the Nagy Hill (46.22311° N, 18.22904° E; Kovács and Vicián 2021) (Fig. 2). The outcropping layers, which are about 3 m thick, are composed of mollusc-bearing limestone layers alternating with yellowish sandy clays (Fig. 3). The latter contain a very well-preserved and diverse fossil fauna, including molluscs and brachiopods. Additional faunal elements in the screen-washed residues are foraminifers, ostra-

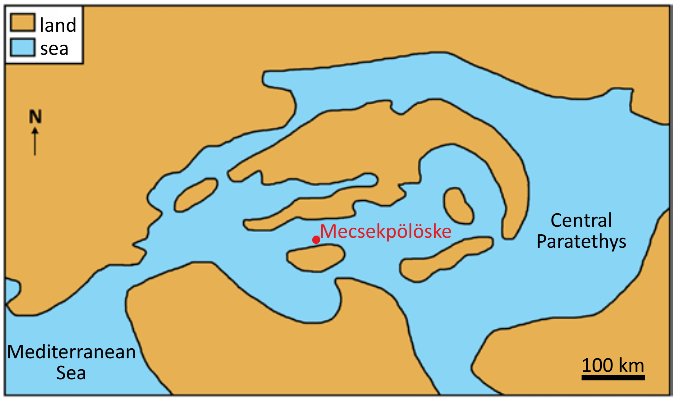

Fig. 1. Palaeogeographic sketch map of the the Middle Miocene Central Paratethys (modified from Rögl 1998), indicating the studied locality in the Mecsek Hills (Mecsekpölöske, Southern Hungary).

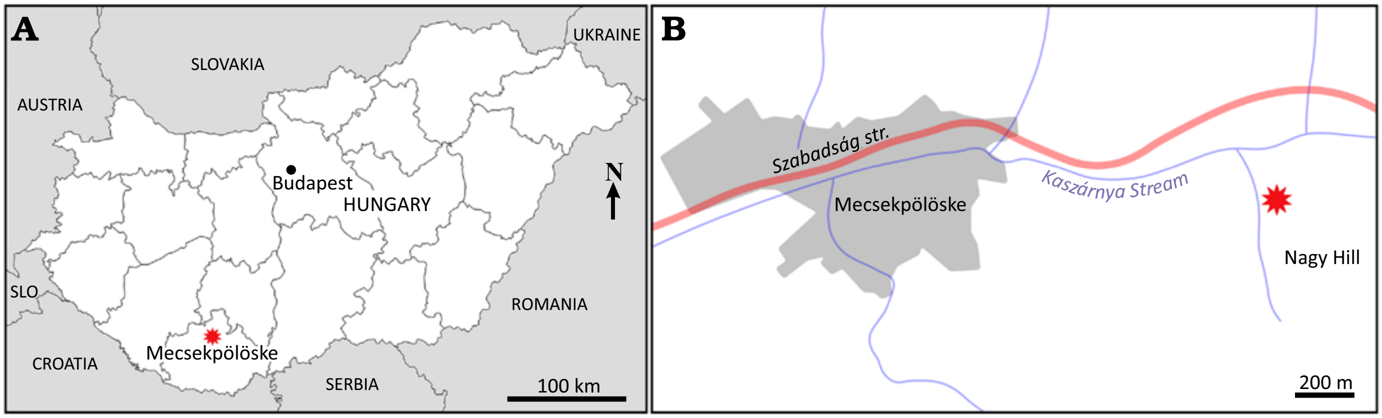

Fig. 2. Geographic location of Mecsekpölöske fossil site. **A**. Location of Mecsekpölöske in Southern Hungary. Abbreviation: Slo, Slovenia. **B**. Location of the fossil site on the western side of Nagy Hill.

Fig. 3. Mecsekpölöske fossil site. **A**. Outcropping Middle Miocene layers (lower Badenian Pécsszabolcs Limestone Member of the Lajta Limestone Formation) along the western side of the Nagy Hill, Mecsekpölöske. **B**. Soft yellowish sandy clays, containing abundant micromorphic brachiopod assemblage. Length of hammer 315 mm (photos by Márton Szabó).

cods, bryozoans, decapods, worms, echinoids, otholiths, and fish teeth. Among the molluscs, representatives of the family Muricidae (Kovács 2020: 12 species, e.g., *Purpurellus cyclopterus* [Millet, 1865], *Aspella subanceps* [d'Orbigny, 1852], *Murexsul sandbergeri* [Hörnes, 1856], and *Favartia suboblonga* [d'Orbigny, 1852]) and the family Cancellariidae (Kovács and Vicián 2021: *Bivetiella dertonensis* [Bellardi, 1841], *Scalptia hidasensis* [Hoernes & Auinger, 1890]) have been published so far. The fragmentary colonial corals from Mecsekpölöske are mentioned briefly by Strausz (1923, 1928), Soós-Kablár (2013), and Dulai et al. (2021), without more detailed investigations. The processing of the fish teeth (Márton Szabó, personal communication 2025), as well as polyplacophoran (AD and Márton Szabó, unpublished data) assemblages recovered from the site are ongoing.

Historical background

In the Neogene shallow marine environments, the screen-washed residues commonly yield an abundant but not very diverse micromorphic brachiopod fauna. These are dominated mainly by members of the families Megathyrididae and Thecideidae. The family Thecideidae is known from only two sites (Bivolare and Yasen) of the Central Paratethys in Bulgaria (Bitner 1993; Bitner and Motchurova-Dekova 2016). However, Megathyrididae taxa (*Megathiris*, *Argyrotheca*, *Joania*) are very common in the Central Paratethyan Miocene materials (e.g., Bitner 1990, 1993; Bitner and Pisera 2000; Bitner and Kaim 2004; Dulai 2007, 2015; and further references therein).

Although members of the family Megathyrididae belong to the most common shallow marine brachiopods, it contains few genera with rather uneven distribution. *Phragmothyris* Cooper, 1955, is limited to the Paleogene of Cuba (Cooper 1955), while *Borellithyris* was only recently described from the Upper Miocene of the Mediterranean by Dulai (2019). *Bronnothyris* Popiel-Barczyk & Smirnova, 1978, was restricted to the Upper Cretaceous and lower Paleocene of N-NW Europe (Denmark, England, Germany, and Poland) according to the revised Treatise (Lee et al. 2006), however, later it was also recorded from the upper Eocene of Ukraine (Bitner and Müller 2017) and from the Oligocene of Germany (Bitner and Kroh 2011; Dulai and von der Hocht 2020; Bitner and Müller 2022). Until now, it was not identified from the Miocene and from the Central Paratethys. The other three genera (*Megathiris* d'Orbigny, 1847; *Argyrotheca* Dall, 1900; and *Joania* Álvarez et al., 2008) are much more common and widely distributed in the Neogene brachiopod assemblages. *Megathiris detruncata* (Gmelin, 1791) is common almost everywhere in the European Neogene (Kocsis et al. 2020), and can therefore be found at numerous sites in the Central Paratethys (e.g., Bitner 1990; Dulai 2007; Bitner and Motchurova-Dekova 2016; and further references therein). Even more common were *Argyrotheca* (= *Cistella*, *Argiope*) records, for which numerous species names were used in the earlier literature. Without the need for completeness or details, only at the level of enumeration: *Argyrotheca cistellula* (Wood, 1841), *A. cordata* (Risso, 1826), *A. cuneata* (Risso, 1826), *A. dertomutinensis* (Sacco, 1902), *A. interponens* (Dreger, 1889), *A. neapolitana* (Scacchi, 1833), *A. squamata* (Eichwald, 1830), *A. subcordata* (Boettger, 1901), *A. subcuneata* (Boettger, 1901), and *A. zboroviensis* (Friedberg, 1921) were recorded from several Neogene sites. However, based on revisions of the last decades (e.g., Bitner 1990), only two valid *Argyrotheca* species remained in the Middle Miocene of the Central Paratethys: *A. cuneata* and *A. cordata*. The latter was reclassified in 2008 as the type species of the new genus *Joania* (Álvarez et al. 2008). These three Miocene Central Paratethyan megathyridid species (*M. detruncata*, *A. cuneata*, *J. cordata*) were later complemented by *A. bitnerae* Dulai in Dulai & Stachacz, 2011, described from some

Table 1. Detailed data of Middle Miocene (Badenian) brachiopods identified from the screen-washed residues of Mecsekpölöske site (Mecsek Hills, S Hungary). Abbreviations: A, articulated specimen; D, dorsal valve; V, ventral valve; fr, fragment; MNI, minimal number of individuals (A+D or V).

Species	Specimens (A, V, D, fr)	Total	MNI
Discradisca sp.	1 fr	1 (0.02%)	1 (0.03%)
Gryphus miocenicus	56 A, 31 V, 17 D	107 (2.04%)	90 (2.31%)
Bronnothyris attilavorosi sp. nov.	1046 A, 1271 V, 858 D	3204 (61.05%)	2325 (59.73%)
Joania cordata	728 A, 707 V, 447 D	1892 (36.05%)	1443 (37.08%)
Megathiris detruncata	22 A, 6 V, 4 D, 6 fr	42 (0.8%)	31 (0.8%)
Megerlia truncata	1A, 1 fr	2 (0.04%)	2 (0.05%)

Middle Miocene sites in Poland (Dulai and Stachacz 2011), and this species was later found within the Central Paratethys in the Czech Republic (Hladilová et al. 2014; Kopecká et al. 2018), in Hungary (Zebegény; Dulai 2021) and in Romania (Buituri; Dulai 2021).

Material and methods

The Mecsekpölöske fossil site was brought to my attention by private collector Tamás Németh (Balatonkenese, Hungary), and a smaller part of the studied material comes from his collection. In addition to my own collecting efforts, Márton Szabó (HNHM Department of Palaeontology and Geology) has also screen-washed and selected a considerable amount of material from Mecsekpölöske.

The studied micromorphic brachiopods are deposited in the Palaeontological Collection of the Hungarian Natural History Museum (type material: HNHM PAL 2025.11.1–23.1; additional material: HNHM INV 2025.261–277).

The minimal number of individuals (MNI) was calculated in every species: A + V or D, depending on the higher value.

Middle Miocene brachiopod assemblage of Mecsekpölöske.—More than five thousand micromorphic brachiopods collected from the screen-washed residues are well preserved and comprise several articulated specimens. The majority of isolated valves were separated during the screen-washing treatment and ultrasonic cleaning. The brachiopod assemblage is not diverse (6 species), and the two dominant species, as well as a third species belong to the typical shallow-water family Megathyrididae. Among the well-known megathyridid species, *Joania cordata* is common, while *Megathiris detruncata* is rare (Fig. 4). The most common species in this assemblage is another member of Megathyrididae, a new species of *Bronnothyris* (see Systematic palaeontology section). In addition to the dominant Megathyrididae specimens, several juvenile *Gryphus miocenicus*, a few *Megerlia truncata* and a single *Discradisca* sp. fragment were also present in the studied samples. Detailed data of the brachiopods identified from the washed residues (articulated specimens, ventral valves, dorsal valves, total number of specimens, minimum number of individuals) are presented in Table 1.

Independently of the screen-washed materials from the sandy clays, some larger brachiopod specimens were also found in the debris of the hillside, possibly derived from the more massive limestone layers and represent *Gryphus miocenicus* and *Megerlia truncata*.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1805

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 *Bronnothyris* Popiel-Barczyk & Smirnova, 1978

Type species: *Terebratula bronni* Roemer, 1841, by original designation of Popiel-Barczyk and Smirnova (1978: 41); Rügen, Germany, Maastrichtian.

Bronnothyris attilavorosi sp. nov.

Figs. 5, 6.

ZooBank LSID: urn:lsid:zoobank.org:act:F633147E-1D3E-472B-90C9-CA578CE19F00.

Etymology: In honour of Attila Vörös (Hungarian Natural History Museum, Budapest; member of the Hungarian Academy of Sciences), eminent researcher of Mesozoic (mainly Jurassic) brachiopods, on the occasion of his 80th birthday.

Type material: Holotype, HNHM PAL 2025.11.1 (Fig. 5A), articulated specimen. Paratypes: HNHM PAL 2025.12.1 (Fig. 5B), articulated specimen; HNHM PAL 2025.13.1 (Fig. 5C), articulated specimen; HNHM PAL 2025.14.1 (Fig. 5D), articulated specimen; HNHM PAL 2025.15.1 (Fig. 6A), ventral valve; HNHM PAL 2025.16.1 (Fig. 6B), ventral valve; HNHM PAL 2025.17.1 (Fig. 6C), ventral valve; HNHM PAL 2025.18.1 (Fig. 6D), dorsal valve; HNHM PAL 2025.19.1 (Fig. 6E), dorsal valve; HNHM PAL 2025.20.1 (Fig. 6F), dorsal valve; HNHM PAL 2025.21.1 (Fig. 6G), dorsal valve; HNHM PAL 2025.22.1 (Fig. 6H), dorsal valve; HNHM PAL 2025.23.1 (Fig. 6I), dorsal valve. All from the type locality and horizon.

Type locality: Nagy Hill, Mecsekpölöske, Mecsek Hills, Hungary (46.22311° N, 18.22904° E).

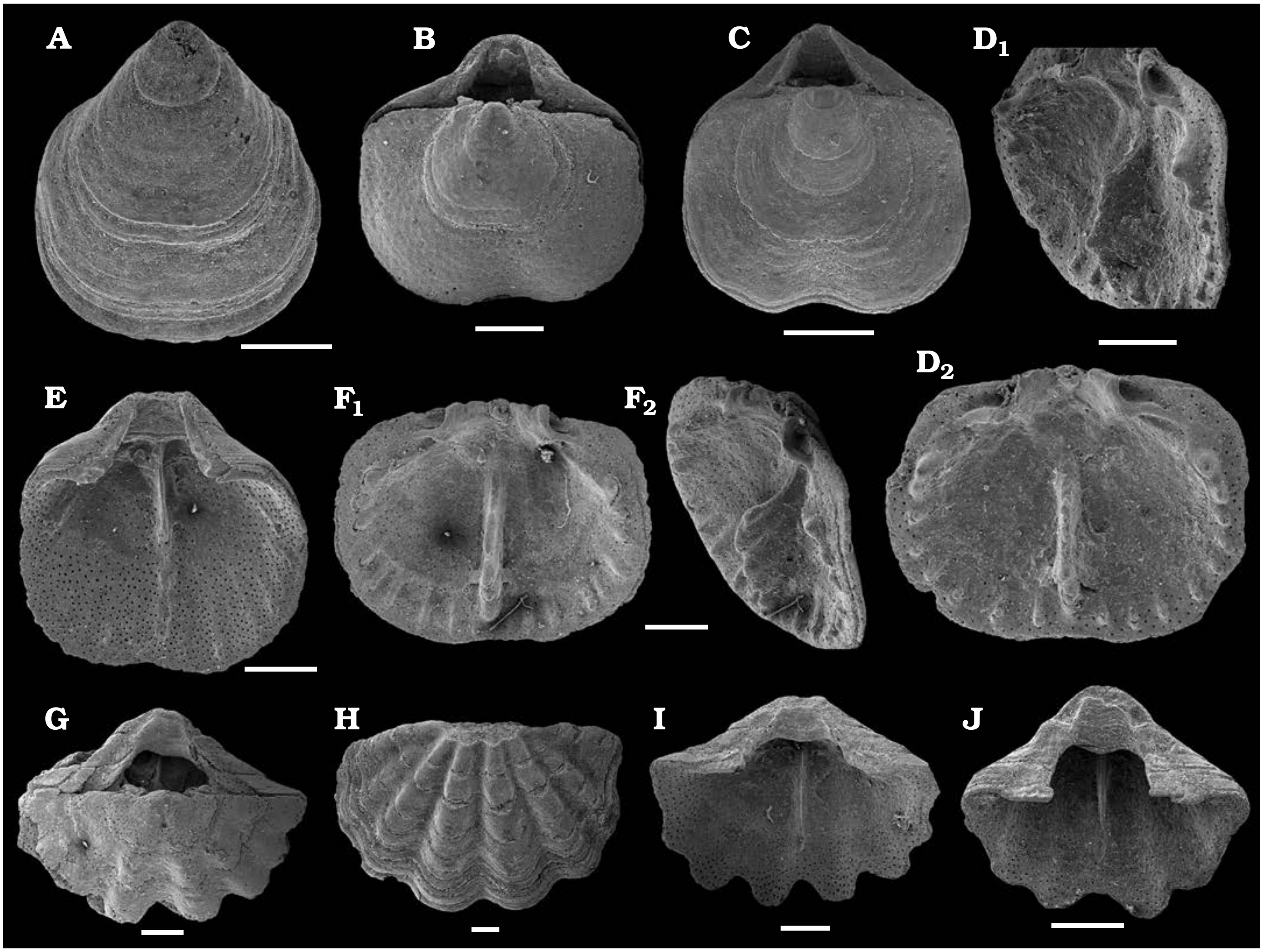

Fig. 4. Middle Miocene micromorphic megathyridid brachiopods from Mecsekpölöske, Mecsek Hills, Hungary, Middle Miocene (Badenian). **A**–**F**. *Joania cordata* (Risso, 1826). **A**. Articulated specimen, HNHM INV 2025.261., ventral view. **B**. Articulated specimen, HNHM INV 2025.262., dorsal view. **C**. Articulated specimen, HNHM INV 2025.263., dorsal view. **D**. Dorsal valve, HNHM INV 2025.264., oblique lateral (D_1) and internal (D_2) views. **E**. Ventral valve, HNHM INV 2025.265., internal view. **F**. Dorsal valve, HNHM INV 2025.266., internal (F_1) and oblique lateral (F_2) views. **G**–**J**. *Megathiris detruncata* (Gmelin, 1791). **G**. Articulated specimen, HNHM INV 2025.267., dorsal view. **H**. Dorsal valve, HNHM INV 2025.268., external view. **I**. Ventral valve, HNHM INV 2025.269., internal view. **J**. Ventral valve, HNHM INV 2025.270, internal view. Scale bars 500 µm.

Type horizon: Pécsszabolcs Limestone Member, Lajta Limestone Formation, Badenian, Middle Miocene.

Material.—Holotype, 12 paratypes, and additional rich material (1053 articulated specimens, 1272 ventral valves, 879 dorsal valves).

Diagnosis.—Small-sized *Bronnothyris* species with subcircular outline; shell surface with four to seven single, weak, rounded ribs; distinct cardinal process; strongly prominent triangular dorsal median septum, with short septal flanges and four strong serrations on its anterior slope; short, slightly divergent inner socket ridges; narrow, fused hinge plates.

Measurements.—See Table 2.

Description.—*External characters*: Shell small (maximum observed length 3.1 mm), thin, equibiconvex in lateral profile (Fig. $5A_2$, C_2). Slightly variable in outline, mostly subcircular (Fig. $5A_1$) or rounded subpentagonal (Fig. $5C_1$). Length and width more or less the same. Maximum width situated at mid-length or slightly moved forward the posterior third (Fig. $5A_1$, C_1). Maximum thickness at mid-length to posterior third (Fig. $5C_2$). The apical angle varies between 95° and 110°. Hinge line long and straight, its length near to maximum width (Fig. $5A_1$, C_1). Beak high, erect with sharp beak ridges (Fig. $5C_2$) and transversely striated, wide interarea (Figs. $5A_1$, C_1, 7A, B). Beak truncated by large and wide subtriangular hypothyrid foramen, bordered by narrow, disjunct deltidial plates (Fig. $5A_1$, C_1). Lateral commissures straight (Fig. $5C_2$), anterior commissure rectimarginate with shallow median sulcus on ventral valve (Fig. $5A_2$). Shell surface covered with four to seven single, weak, rounded ribs running through from umbo to anterior margin (Fig. $5A_1$, B, C_1, D), space between ribs wider than ribs. No bifurcation or intercalation. The seventh shorter median rib only sometimes visible (Fig. $5C_1$, D). Distinct growth lines on some

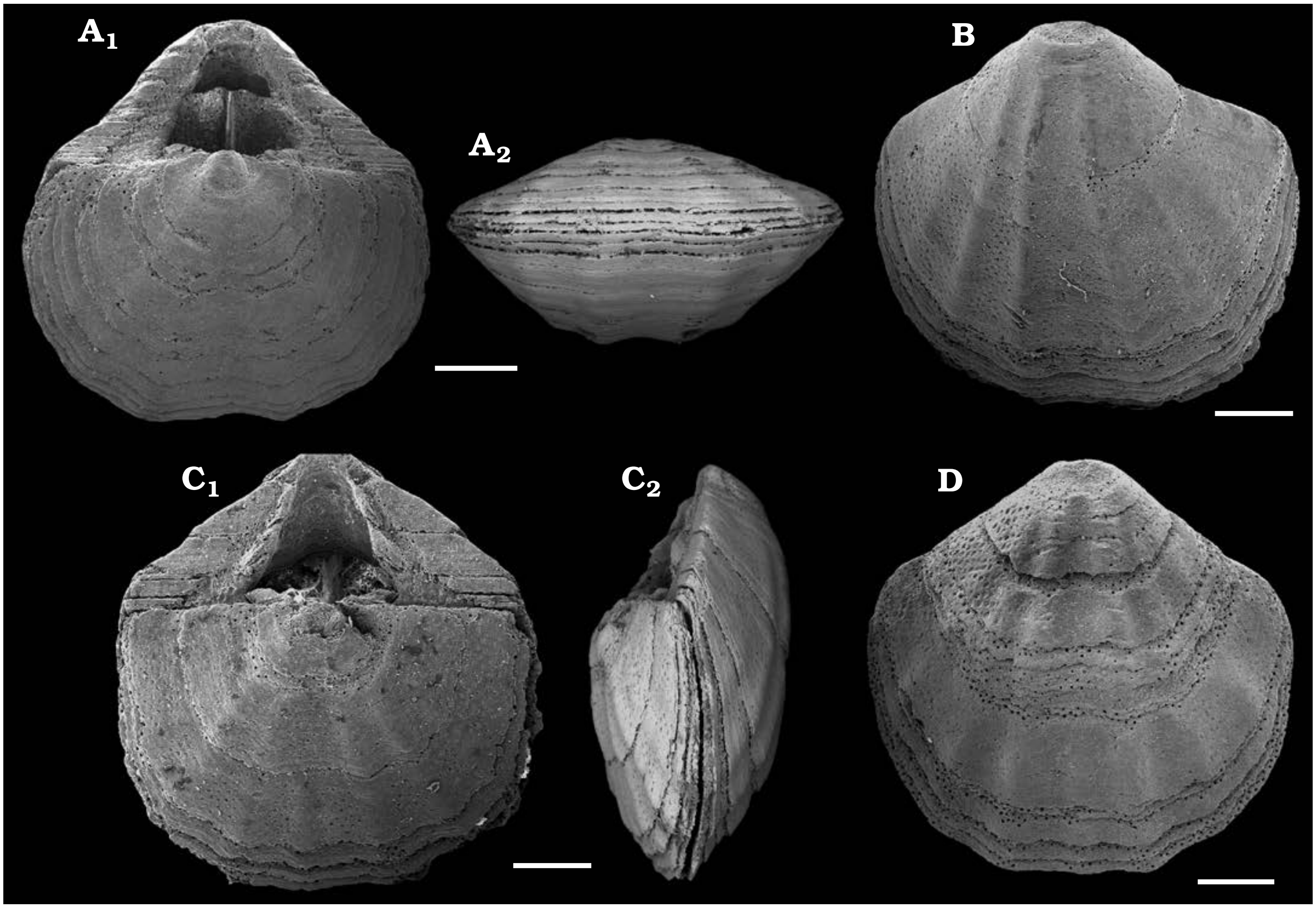

Fig. 5. Megathyridid brachiopod *Bronnothyris attilavorosi* sp. nov., Mecsekpölöske, Mecsek Hills, Hungary, Middle Miocene (Badenian); holotype (A) and paratypes (B–D); external morphological characters. **A**. Articulated specimen, HNHM PAL 2025.11.1, dorsal (A$_1$) and anterior (A$_2$) views. **B**. Articulated specimen, HNHM PAL 2025.12.1, ventral view. **C**. Articulated specimen, HNHM PAL 2025.13.1, dorsal (C$_1$) and lateral (C$_2$) views. **D**. Articulated specimen, HNHM PAL 2025.14.1, ventral view. Scale bars 500 μm.

specimens, denser near to the anterior and lateral margins (Fig. 5A$_1$, B, C$_1$, D).

Internal characters: Both valves coarsely endopunctate (Fig. 6A, D). Ventral valve interior with poorly developed short teeth lying parallel to hinge line (Fig 6A). Well-developed large, highly triangular pedicle collar, with dense transverse striation (Fig. 6A–C), supported by a low ventral median septum extending to mid-valve (Fig. 6A, B), sometimes longer (Fig. 6C). Anteriorly to ventral septum three ovoid depressions accommodate dorsal septum serrations (Fig. 6A, B). Dorsal valve interior with moderately deep subhorizontal sockets (Fig. 6D$_1$, F, H$_1$, I$_1$); short, slender socket ridges situated near to each other and extending beyond posterior margin (Fig. 6D$_1$, H$_1$, I). Distinct cardinal process breaks down into parallel lamellae (Fig. 6D$_1$, E, G$_1$) and continued anteriorly in a triangular (Figs. 6E, G$_1$, H$_1$, I) or in a longer ridge (Fig. 6D$_1$). Hinge plates fused mid-dorsally with valve floor to form a narrow platform (Fig. 6D$_1$, E, I). Dorsal median septum beginning from anterior margin of hinge plates (Fig. 6D$_1$, E), low posteriorly, becoming high at anterior third (Fig. 6G$_2$); triangular in profile (Fig. 6F, G$_2$, H$_2$), the posterior edge rise at 45°, the anteroventral edge sloping towards anterior margin with four strong, sharp or rounded serrations (Fig. 6F, G$_2$, H$_2$). Short septal flanges extend posteroventrally from top of dorsal median septum (Fig. 6D, I$_1$). Crura short, medially directed crural processes

Table 2. Measurements (in mm) of *Bronnothyris attilavorosi* sp. nov. type specimens. Abbreviations: A, articulated specimen; D, dorsal valve; V, ventral valve.

Specimen	Length	Width	Thickness
Holotype (A)	2.4	2.4	1.3
HNHM PAL 2025.12.1 (A)	2.8	2.7	1.4
HNHM PAL 2025.13.1 (A)	2.7	2.7	1.2
HNHM PAL 2025.14.1 (A)	2.8	2.7	1.4
HNHM PAL 2025.15.1 (V)	2.2	2.3	–
HNHM PAL 2025.16.1 (V)	2.5	2.5	–
HNHM PAL 2025.17.1 (V)	3.1	3.1	–
HNHM PAL 2025.18.1 (D)	1.8	2.4	–
HNHM PAL 2025.19.1 (D)	1.8	2.5	–
HNHM PAL 2025.20.1 (D)	1.7	2.3	–
HNHM PAL 2025.21.1 (D)	2.6	3.1	–
HNHM PAL 2025.22.1 (D)	1.4	1.8	–
HNHM PAL 2025.23.1 (D)	1.9	2.4	–

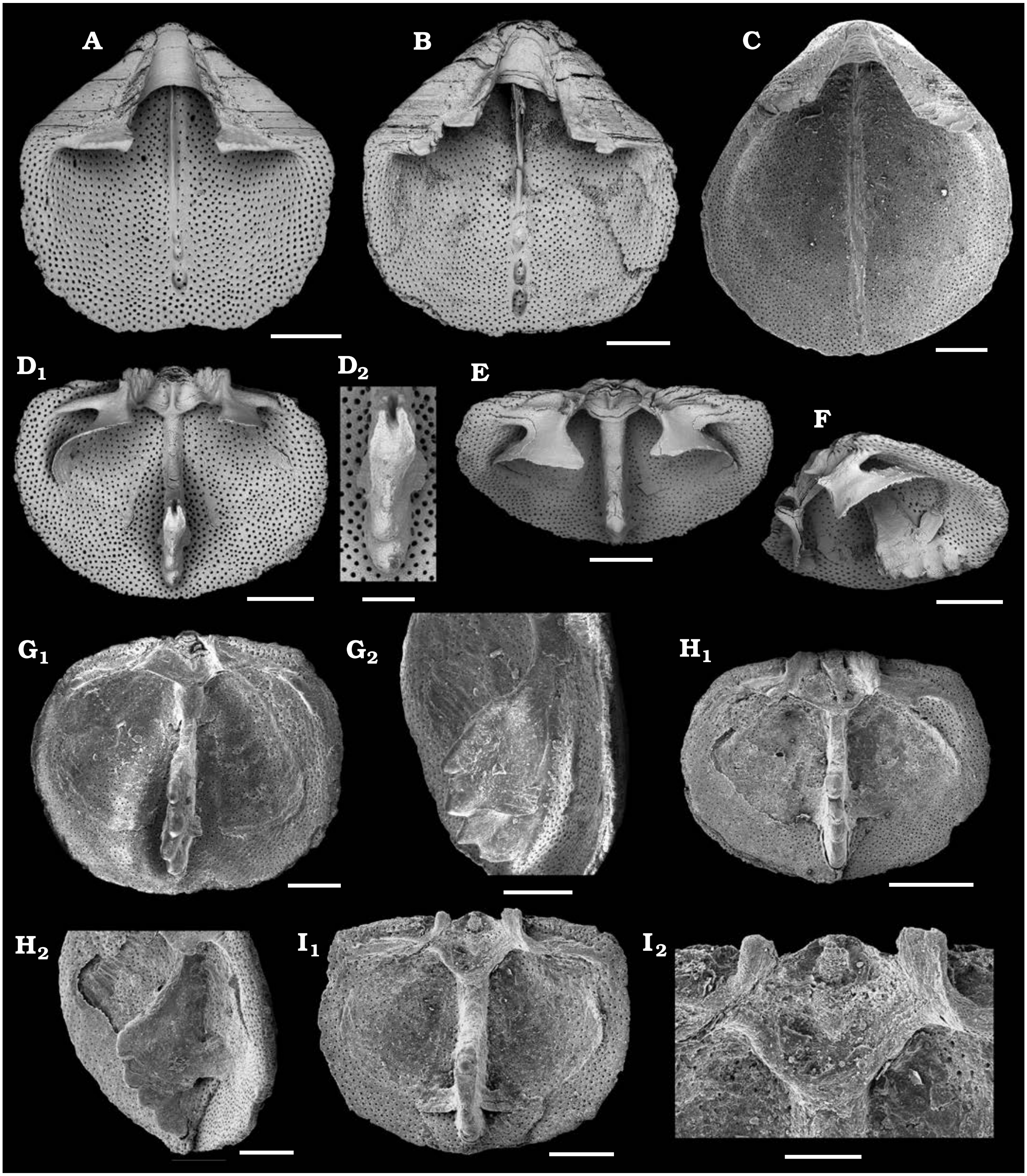

Fig. 6. Megathyridid brachiopod *Bronnothyris attilavorosi* sp. nov., Mecsekpölöske, Mecsek Hills, Hungary, Middle Miocene (Badenian); paratypes; internal morphological characters. **A**. Ventral valve, HNHM PAL 2025.15.1, internal view. **B**. Ventral valve, HNHM PAL 2025.16.1, internal view. **C**. Slightly eroded ventral valve, HNHM PAL 2025.17.1, internal view. **D**. Dorsal valve, HNHM PAL 2025.18.1, internal view (D_1) and enlarged part of dorsal median septum with septal flanges (D_2). **E**. Dorsal valve, HNHM PAL 2025.19.1, oblique posterior view. **F**. Dorsal valve, HNHM PAL 2025.20.1, oblique lateral view. **G**. Dorsal valve, HNHM PAL 2025.21.1, internal (G_1) and oblique lateral (G_2) views. **H**. Dorsal valve, HNHM PAL 2025.22.1, internal (H_1) and oblique lateral (H_2) views. **I**. Dorsal valve, HNHM PAL 2025.23.1, internal view (I_1) and enlarged part of the posterior part with sockets, oblique socket ridges, and cardinal process (I_2). Scale bars 500 µm, except D_2, and I_2, 250 µm.

wide and relatively long (Fig. 6D$_1$, E, F). Loop poorly calcified and poorly developed. Laterally curved descending branches united with valve floor (Fig. 6D$_1$, E, F) and their anterior ends join to median septum (Fig. 6F, H$_2$, I$_1$).

Remarks.—Within the megathyridid brachiopods found in Mecsekpölöske, the *Megathiris* and *Joania* specimens can be easily distinguished based on their internal morphological characters (*Megathiris*: three septa in the dorsal valve; *Joania*: series of tubercles on the inner margins of both valves). Two species of the genus *Argyrotheca* are known from the Central Paratethys. *Argyrotheca bitnerae* Dulai in Dulai & Stachacz, 2011, clearly differs from the Mecsekpölöske specimens by its subtrigonal outline and unornamented, smooth valves. *A. cuneata*, which is known from many sites since the end of the Paleogene to the present day, slightly resembles the new species described here, but can be clearly distinguished on the basis of short septal flanges on the high and triangular dorsal median septum and the fused hinge plates. Both characters refer to the genus *Bronnothyris*, previously unknown from both the Central Paratethys and the Miocene. In the case of strongly eroded Lower Miocene *Argyrotheca* cf. *subradiata* (Sandberger, 1862) specimens published by Bitner and Schneider (2009) from the Bavarian part of the Molasse Basin, their affiliation to the genus *Bronnothyris* cannot be confirmed due to the absence of septal flanges.

The Mecsekpölöske specimens can be clearly distinguished from all known *Bronnothyris* species, thus justifying the introduction of a new species for this material. The previously described taxa differ from the new species in the following characters:

- *Bronnothyris bronni* (Roemer, 1841) (Upper Cretaceous) in transversely slightly elongated bilobate outline; flat dorsal valve in adults, more numerous and stronger ribs extend slightly beyond the shell margin; not so high ventral beak, hinge plates form two separated and concave circular discs, indistinct, flat cardinal process (Steinich 1965; Surlyk 2025);
- *Bronnothyris coniuncta* (Steinich, 1965) (Upper Cretaceous) in transversely strongly elongated, “*Spirifer*-like” outline, more numerous and stronger ribs slightly extend beyond the shell margin, low ventral beak, fused hinge plates form a broad platform, wide and flat cardinal process, short dorsal median septum without anterior serrations (Steinich 1965; Surlyk 2025);
- *Bronnothyris lacunosa* (Steinich, 1965) (Upper Cretaceous) in rectangular outline, few rounded ribs, hinge plates form two concave discs, indistinct, flat cardinal process; anterior slope of dorsal median septum without strong serrations (Steinich 1965);
- *Bronnothyris obstinata* (Steinich, 1965) (Upper Cretaceous) in rectangular outline, few rounded ribs, indistinct, flat cardinal process, anterior slope of lower dorsal median septum without serrations (Steinich 1965);
- *Bronnothyris stevensis* (Nielsen, 1928) (Upper Cretaceous) in strongly inflated valves, much stronger ribs in two bundles, extend beyond the shell margin; hinge plates form two concave discs, higher septal flanges (Nielsen 1928; Simon 1998; Surlyk 2025);
- *Bronnothyris rugicosta* (Zelinskaya, 1975) (lower Paleocene) in more numerous, very strong and wide ribs, extend slightly beyond the shell margin, fused hinge plates form a broad platform, anterior slope of dorsal median septum without strong serrations (Zelinskaya 1975);
- *Bronnothyris wansinensis* (Vincent, 1923) (upper Paleocene) in transversely strongly elongated outline, fused hinge plates forming a broad platform; stronger ribs do not extend to the anterior margin (Vincent 1923; Dulai 2025b);
- *Bronnothyris danaperensis* Bitner & Müller, 2017 (upper Eocene) in transversely elongated outline, smooth surface, fused hinge plates forming a broad platform, eroded ventral beak area (Bitner and Müller 2017);
- *Bronnothyris subradiata* (Sandberger, 1862) (lower Oligocene) in transversely elongated, more irregular outline, more numerous and partly stronger ribs; strongly eroded ventral beak area, fused hinge plates forming a broad platform (Sandberger 1862; Bitner and Kroh 2011);
- *Bronnothyris rugosa* (Schreiber, 1871) (lower Oligocene) in much wider than long outline, lower and wider beak area, longer hinge line, more numerous, stronger and tuberculate ribs, broad and fused hinge plates forming a coherent platform (Bitner and Müller 2022).

The presence of septal flanges on the dorsal median septum and the fused hinge plates indicate a relationship between the Mecsekpölöske material and *Bronnothyris*. However, the narrowness of the fused hinge plates is striking when compared to previously known Cenozoic *Bronnothyris* species (*B. wansinensis*, Vincent 1923: fig. 3; *B. danaperensis*, Bitner and Müller 2017: fig. 7E–G, I, J; *B. subradiata*, Bitner and Kroh 2011: fig. 3C–I; *B. rugosa*, Bitner and Müller 2022: fig. 8E–K). After thorough examination of all the species classified in the genus *Bronnothyris* it might be concluded that the aspect of hinge plates is rather diverse. Three different morphotypes can be distinguished, what may result oversplitting into as many as three genera: (i) fused hinge plates forming a broad platform: *Bronnothyris coniuncta*, *B. rugicosta*, *B. wansinensis*, *B. danaperensis*, *B. subradiata*, *B. rugosa*; (ii) hinge plates form a narrow, single plate: *B. obstinata*, *B. attilavorosi* sp. nov.; (iii) hinge plates form two concave, separated circular discs: *B. bronni*, *B. lacunosa*, *B. stevensis*.

For the time being, I consider the new species *B. attilavorosi*, known from a single locality, to be a member of the genus *Bronnothyris*, reserving the possibility that the discovery of further similar materials or more detailed investigation of the available materials may justify the description of some new genera in the future within the family Megathyrididae.

Bitner and Kroh (2011) emphasised in the morphological description of *B. subradiata* that the ventral beak of most specimens is heavily eroded, which may indicate a very short pedicle and very tight attachment to the hard substrate. The situation was similar with *B. danaperensis* specimens from the Ukrainian upper Eocene (Bitner and Müller 2017).

In the case of *B. attilavorosi* sp. nov., the vast majority of the specimens is in very good preservation, with no signs of erosion around the ventral beak. This may indicate that this Miocene species had a longer pedicle than older Cenozoic relatives, but it is more likely that the different palaeoenvironment and nature of preferred substrate could have played a more significant role (see the assessment of palaeoenvironment of Mecsekpölöske site in the discussion).

Stratigraphic and geographic range.—Middle Miocene (Badenian), Mecsek Hills (Southern Hungary).

Discussion

Palaeoenvironmental consideration on the Mecsekpölöske site.—The brachiopod assemblage collected from the screen-washed residues is strongly dominated by species of Megathyrididae generally typical of shallow-water environments (*Bronnothyris* + *Joania* + *Megathiris* = 97.91%), with negligible amounts of species typical of deeper waters (*Gryphus* + *Megerlia* = 2.07%) and the representatives of the latter group are mostly small-sized, juvenile specimens (Fig. 7). The fragmentary *Discradisca* sp. also tends to be more typical of shallow-water environments. The preservation of brachiopods is excellent, most of the specimens were originally articulated, but in several individuals the valves became separated during screen-washing and ultrasonic cleaning (because of the small ventral teeth and loose connection of valves). The percentage ratio of the number of specimens of each species and the calculated minimum number of individuals is almost identical (Table 1), also confirming that this is an autochthonous assemblage unaffected by significant transport.

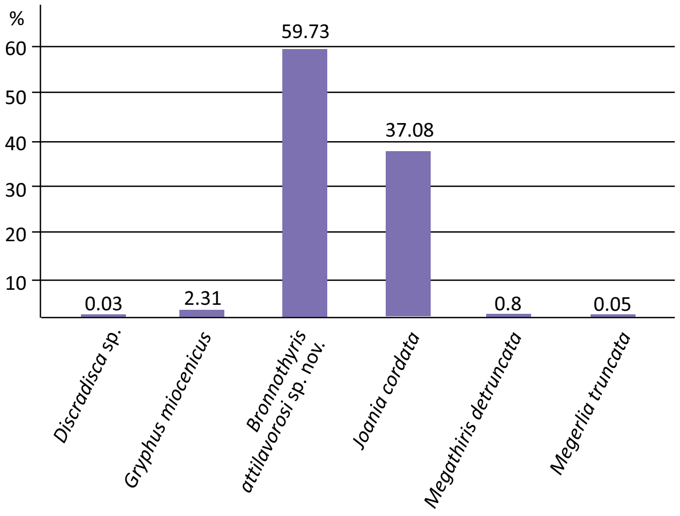

Fig. 7. Taxonomic composition of the Middle Miocene (Badenian) brachiopod assemblage from Mecsekpölöske, Mecsek Hills, Hungary.

Shallow-water micromorphic brachiopods are most commonly found in sheltered environments (caves, crevices, rocky bedrock) and on coralligenous substrates (Logan 1979). Following some rare previous records (e.g., Taddei Ruggiero 1985; Evangelisti et al. 2011), it has recently been confirmed that the rhizome level of *Posidonia* seagrass meadows provide excellent sheltered habitat for the attachment of micromorphic brachiopod assemblages with distinctive taxonomic composition. Albano and Stockinger (2019) described an abundant population of *Joania cordata*–*Argyrotheca cuneata* from the *Posidonia oceanica* meadows area in Plakias (SW Crete). Shortly afterwards, the first known fossil brachiopod assemblage associated with seagrass meadows from the Neogene of the Mediterranean was published from the Pliocene of Rio Vaccaruza, Italy by Pavia et al. (2022). In this latter assemblage, *Joania cordata* was dominant, while the few additional elements were *Argyrotheca cuneata* and *Terebratula* juv. sp. In that publication, Pavia et al. (2022) argued that some possible seagrass palaeoenvironments of the Central Paratethys could be interpreted based on their brachiopod assemblages dominated by Megathyrididae (e.g., Bitner 1990, 1993; Bitner and Pisera 2000; Bitner and Kaim 2004; Dulai 2007), but beside the taxonomic composition of the brachiopod fauna, these environmental assessments were supported by few additional evidences. For example, the presence of submarine flora was suggested by Pisera (1985) at Radwanówka (Roztocze Hills, Poland), some foraminifers indicated the presence of non-calcified submarine flora at Niechobrz, SE Poland (Gonera 1994) and several gastropod taxa referred to possible seagrass environment at Bánd, Hungary (Kókay 1966; Kovács and Vicián 2021).

The taxonomic composition of the brachiopod assemblage at Mecsekpölöske (dominanated by species of *Bronnothyris* and *Joania*, with some additional of *Gryphus* and *Megathiris*) and their excellent preservation may also be explained by a shallow marine bottom covered with seagrass meadows. This assessment of the palaeoenvironment is consistent with morphological observations showing that while in the Eocene *B. danaperensis* (Bitner and Müller 2017) and the Oligocene *B. subradiata* (Bitner and Kroh 2011) almost all specimens have heavily eroded ventral beak, whereas *B. attilavorosi* sp. nov. is almost without exception excellently preserved, very few specimens showing any signs of physical erosion. According to Bitner and Kroh (2011), the *B. subradiata* species had a very short pedicle, which allowed it to attach itself firmly to the solid surfaces, so that the beak in contact with the hard attachment surface was heavily eroded by the strong water movement prevailing in the shallow sea. On the other hand, *B. attilavorosi* sp. nov. was attached to the rhizomes of living seagrass or to smaller solid surfaces (e.g., fossil fragments) in the fine sandy sediment trapped in the rhizome level of seagrass meadows, so it did not erode significantly even if it did not have a longer pedicle than its older Cenozoic relatives.

Regardless of brachiopods, there are some other fossil groups in the Mecsekpölöske material that can also be considered indirect palaeo-seagrass indicators (Reich et al. 2015). The abundance of herbivorous gastropods recovered from the studied strata supports this interpretation. The seagrass environment is suggested by the presence of *Bittium tani* Harzhauser, Guzhov, & Landau, 2025 (very common), *Bittium praescabrum* Harzhauser, Guzhov, & Landau, 2025 (common), *Thecidium zeuschneri* (Pusch, 1836) (common), *Oligodia bicarinata* (Eichwald, 1830) (common), *Mitrella viennensis* Harzhauser & Landau, 2021 (very common), *Conolithes brezinae* (Hoernes & Auinger, 1879) (common), among many others. Some additional very common gastropod genera, such as *Alvania*, *Manzonia*, *Rissoina*, and *Zebinella* also occur in seagrass environments of the Recent seas (Zoltán Kovács, personal communication 2025). The almost monospecific *Amphistegina mammilla* (Fichtel & Moll, 1798) foraminifer assemblage, some epiphytic ostracod species (Emőke Mohr, personal communication 2025), otoliths of Gobiidae, Sparidae, and Gadidae fishes, which use seagrass meadows as a nursery habitat (Mariann Bosnakoff, personal communication 2025), as well as some sharks and other fishes: angel sharks (Squatinidae), reef sharks (Carcharhinidae), whiptail stingrays (Dasyatidae), wrasses (Labridae), porgies and seabreams (Sparidae) (Márton Szabó, personal communication 2025) also may indicate the presence of a palaeo-seagrass environment. A comprehensive palaeoenvironmental assessment of the Mecsekpölöske site is in preparation by AD and other colleagues.

Both the Italian Pliocene (Pavia et al. 2022) and the Hungarian Middle Miocene Megathyrididae assemblages confirm that these micromorphic brachiopods can be useful as indirect palaeo-seagrass indicators. Considering the criteria for the usefulness of IPSIs defined by Reich et al. (2015), Megathyrididae brachiopods: (i) have appropriate stratigraphic (Upper Cretaceous–Recent; Lee et al. 2006) and geographical (worldwide except for the polar regions; Logan 2007: fig. 1954) distribution; (ii) have excellent fossilization potential (Kocsis et al. 2020); (iii) based on known examples, they occur in sufficiently large numbers in palaeo-seagrass meadows (Pavia et al. 2022; this paper); however, (iv) they are not strictly limited to seagrass meadows and can also occur in many other shallow marine habitats (Logan 1979), therefore, additionally to well-preserved Megathyrididae brachiopods, further evidence from other groups is needed at the studied fossil sites.

Conclusions

An abundant but low-diversity micromorphic brachiopod fauna was found in the Badenian (Middle Miocene) sandy clays (Lajta Limestone Formation) of the Mecsekpölöske fossil site in southern Hungary. More than five thousand specimens were identified from the screen-washed residues, representing six brachiopod species. The taxonomic composition of the brachiopod assemblage was found to be fairly uniform, with almost 98% of the specimens representing the species of *Bronnothyris*, *Joania*, and *Megathiris* (Megathyrididae). The most common species was identified as a new species of *Bronnothyris* (*B. attilavorosi* sp. nov.). *Bronnothyris* was long thought to have disappeared after the end-Cretaceous mass extinction, but more and more *Bronnothyris* records are being found in the Cenozoic strata. This is the first known occurrence of *Bronnothyris* from the Central Paratethys and from the Miocene. The youngest known stratigraphic occurrence of the genus is *B. attilavorosi* sp. nov. from the Middle Miocene of Mecsekpölöske.

The dominance of the family Megathyrididae and the low abundance (2%) of deeper water forms (*Gryphus*, *Megerlia*; mainly juvenile specimens) clearly indicate a shallow water environment. The taxonomic composition of the brachiopod assemblage and the co-occurrence of some specific other fossils groups (e.g., gastropods, foraminifers, ostracods, otoliths, fish teeth) suggest that the shallow-marine substrate was covered by seagrass meadows. This is the first evidence that *Bronnothyris*, like other megathyridid genera (*Argyrotheca* and *Joania*), may have been associated with seagrass meadows. Reich et al. (2015) published an excellent summary of IPSI groups, but only mentioned brachiopods in passing, stating that although they occur in seagrass beds, no detailed studies have been published on them. Following their confirmed occurrence in Recent *Posidonia* meadows (Albano and Stockinger 2019), both the recently published similar Italian Pliocene *Joania–Argyrotheca* material (Pavia et al. 2022) and this Hungarian Miocene *Bronnothyris–Joania–Megathiris* assemblage confirmed that micromorphic Megathyrididae brachiopods can be used as indirect palaeo-seagrass indicator. However, since their distribution is not limited to this habitat, they can only be used for this purpose in conjunction with some further positive evidences from the studied site.

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