Central Paratethyan Middle Miocene brachiopods from Poland, Hungary and Romania in the Naturalis Biodiversity Center (Leiden, the Netherlands)

A. Dulai

Dulai, A. Central Paratethyan Middle Miocene brachiopods from Poland, Hungary and Romania in the Naturalis Biodiversity Center (Leiden, the Netherlands). *Scripta Geologica*, **149**: 185-211, 1 fig., 4 pls., Leiden, August 2015.
Alfréd Dulai, Department of Palaeontology and Geology, Hungarian Natural History Museum, H-1431, Budapest, P.O.B. 137, Hungary (dulai@nhmus.hu)

Key words – Badenian, *Lingula*, *Disciniscа*, *Discradisca*, *Cryptopora*, *Gryphus*, *Argyrotheca*, *Joania*, *Megerlia*.
The world-famous collection of Naturalis Biodiversity Center in Leiden contains abundant fossil material, including brachiopods from the Central Paratethys (nine collecting sites from Poland, and one locality each from Hungary and Romania). More than 1400 (partly fragmentary) brachiopod specimens represent nine species of eight genera: *Lingula* cf. *dregeri* Andreae, *Discinisca leopolitana* (Friedberg), *Discradisca polonica* (Radwańska & Radwański), *Cryptopora nysti* (Davidson), *Gryphus* cf. *miocaenicus* (Michelotti), *Argyrotheca cuneata* (Risso), *A. bitnerae* Dulai, *Joania cordata* (Risso) and *Megerlia* sp. Most of the identified species are already known from the Central Paratethys, but the Leiden collection contains a new *Argyrotheca* species (*A. bitnerae*), which was described recently in a separate paper (on the basis of more material, but including also Naturalis specimens). Most of the studied brachiopods confirm earlier records known from the literature, but in some cases important new information is available on the distribution of the identified taxa within the Central Paratethys. These are, respectively, the first record of *Discinisca leopolitana* from Rybnica and Monastyrz, the genus *Gryphus* from Rybnica and from the Miocene of Poland, *Argyrotheca bitnerae* from Karsy, and *Joania cordata* from Várpalota. This is the first identification of *Argyrotheca cuneata* from Korytnica and Lăpugiu de Sus (earlier this form was mentioned under different names from these localities). One of the studied *Discradisca polonica* specimens was attacked by a predatory gastropod; this is the first record of predatory drill holes on phosphatic-shelled brachiopods in the Central Paratethys.

Contents

Introduction

The studied brachiopods are part of the Cainozoic Mollusca Collection of the Naturalis Biodiversity Center (Naturalis) in Leiden, the Netherlands. Arie W. Janssen, former curator of this famous Paleogene and Neogene collection has undertaken extensive fieldwork not only in the Netherlands, but also in numerous foreign countries in Europe. He spent some weeks in Central Europe in September-October 1979 and collected Middle Miocene (Badenian) samples mainly in Poland, but also in Hungary. The main goal was the enhancement of the mollusc collection, but all the other fossil groups were also separated from the washed residues. Molluscs are generally identified in the collection according to different species, while other groups, including brachiopods, can be found in separate boxes, organised according to the different localities. A smaller sample from Lăpugiu de Sus (Romania) was collected by Marc Grigis in August 2002.

The author spent two weeks in Leiden within the framework of a European Union Synthesys project studying the Neogene brachiopods in Naturalis (NL-TAF-3270). Besides checking the Fossil Brachiopoda Collection, most time was spent in the Cainozoic Mollusca Collection searching for brachiopods within the mollusc faunas. With the help of the present curator, Frank Wesselingh, this project was successful and thousands of unpublished brachiopods were found from different ages and palaeogeographic realms. These are mainly small-sized, so-called micromorphic forms, for example, from Kattendijkian of Belgium, Redonian of France, Oligo-Miocene of Malta and Middle Miocene of the Central Paratethys. These smaller and larger brachiopod faunas have or will be published as separate papers. A small fauna from the Upper Miocene of Borelli (Piemonte, northern Italy) is already published (Dulai, 2010). Another paper on the description of a new *Argyrotheca* species from the Central Paratethys was partly based also on material of Naturalis (Dulai & Stachacz, 2011). A paper on the Miocene brachiopods of Naturalis is recently published (Dulai, 2013), while some other papers are in preparation (Oligo-Miocene brachiopods from Malta; Redonian brachiopods from France; Pliocene brachiopods from Belgium; other Pliocene brachiopods). The present part of this series deals with the Badenian (Middle Miocene) brachiopods from the Central Paratethys.

Geological setting and previous research on Central Paratethyan brachiopods

The Paratethys was an epicontinental sea that appeared in the Early Oligocene, and was intermittently connected to the Mediterranean and the Indo-Pacific (Rögl, 1998). The area from present-day Austria to Poland, Ukraine, Romania, Bulgaria, Serbia and Slovenia is called the Central Paratethys. The Badenian (16.4 to 13.0 Ma) is a regional stage used in the Central Paratethys for part of the Middle Miocene (Langhian to Middle Serravallian) (Papp *et al*., 1978). The marine fauna of the Central Paratethys refers to a stable connection with the Mediterranean during the entire Badenian, most probably in the present-day Slovenia (Kókay, 1985; Rögl, 1998).

The Badenian has a three-fold subdivision (Moravian, Wieliczian, Kosovian) that is defined by stratotypes and boundary stratotypes (Papp *et al*., 1978). This subdivision correlates with global climatic and eustatic changes. The Early Badenian witnessed a climatic peak with the widest distribution of coral reefs in the Neogene (up to southern Poland; Pisera, 1996). The Middle Badenian corresponds to a global eustatic lowstand, with the formation of some evaporates in Poland and Romania (Cendón *et al*., 2004). The Late Badenian demonstrates again a climatic optimum with coral patch reefs in Hungary (Saint Martin *et al*., 2000). However, in contrast to the very diverse Early Badenian assemblages, the Late Badenian patch reefs are impoverished due to the less optimal climate and/or a slight change in salinity (e.g., bryozoans in Moissette *et al*., 2007). The Central Paratethyan shallow-water deposits are generally devoid of planktonic fossils hence their precise age is difficult to determine. Therefore, it is generally easier to use a twofold subdivision (Early and Late Badenian; see, e.g., Pisera, 1996; Moissette *et al*., 2006, 2007). Thick marine deposits accumulated in the Central Paratethys during the Badenian, and the sedimentation was of mixed siliciclastics and carbonates (Kováč *et al*., 2007).

Coralline algae and various invertebrates (e.g., molluscs, echinoids, corals, foraminiferans, ostracods and bryozoans) are abundant and diverse in Central Paratethyan Badenian sedimentary rocks, but brachiopods are generally rarer. With the exception of the large-sized terebratulides and some rhynchonellides, their representatives are mainly small-sized, so-called micromorphic species. Previous brachiopod research will be summarized only for the three countries, which are represented in the studied Naturalis collection. Within the Central Paratethys, Middle Miocene brachiopods are best known and most extensively studied in Poland. Barczyk & Popiel-Barczyk (1977) published a relatively diverse brachiopod fauna from the Korytnica Basin (several localities near Korytnica and Karsy). Later, a new *Discinisca* species was described by Radwańska & Radwański (1984) from the same area. A diverse Middle Miocene assemblage is known from the southern slopes of the Holy Cross Mountains (Popiel-Barczyk & Barczyk, 1990). Several localities in the Roztocze Hills (including Węglin) were studied by Bitner (1990), while Popiel-Barczyk (1977, 1980) described the genus *Cryptopora* from the southeastern part of the region (including Monastyrz). The Miocene brachiopod fauna of Poland was summarised by Popiel-Barczyk (1996). Later, some smaller faunas were described by Bitner & Pisera (2000) from southeastern Poland (Niechobrz) and by Bitner & Kaim (2004) from the intra-Carpathian Nowy Sącz Basin. The Central Paratethyan *Lingula* was revised on the basis of Polish material by Emig & Bitner (2005). A new *Argyrotheca* species was recently described from several Polish localities by Dulai *in* Dulai & Stachacz (2011).

In the Hungarian part of the Central Paratethys, Matyasovszky (1880) and Majer (1915) described some new brachiopod species. Later, Meznerics (1944) summarised the Tertiary brachiopod fauna of the Carpathian Basin in a small monograph. Bitner & Dulai (2004) revised the Miocene brachiopods of the Hungarian Natural History Museum, with special reference to the Meznerics collection. Dulai (2007) described a low diversity Badenian fauna from the Bakony Mountains (Bánd and Devecser, near to Várpalota). Middle Miocene brachiopods have been mentioned by several authors from Romanian localities, including Lăpugiu de Sus (e.g., Boettger, 1901; Zilch, 1934; Meznerics, 1944; Bitner & Dulai, 2004). Miocene brachiopods from several localities from Romania were summarised by Bărbulescu & Rado (1984).

Material

Most of the studied localities are situated at the northern margin of the Central Paratethys, in the Polish part of the fore-Carpathian Basin (Korytnica, Karsy, Rybnica, Węglin, Monastyrz; Poland). Very limited brachiopod material is available from the central part of the Central Paratethys (Pannonian Basin, Várpalota; Hungary) and from the eastern part of the Central Paratethys (Banat Basin, Lăpugiu de Sus; Romania) (Fig. 1).

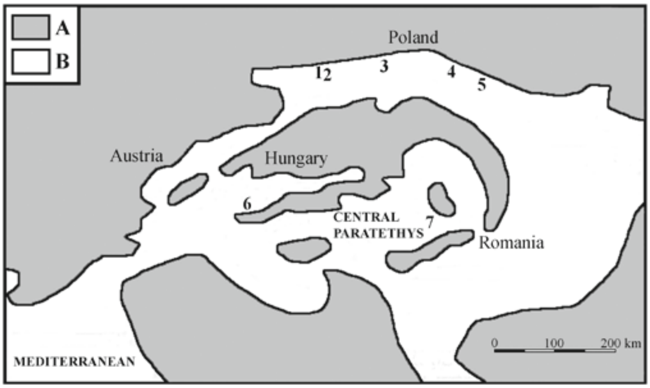


Fig. 1. Location of the studied samples and brachiopod faunas. Key: 1 = Korytnica; 2 = Karsy; 3 = Rybnica; 4 = Węglin; 5 = Monastyrz; 6 = Várpalota; 7 = Lăpugiu de Sus; A = land; B = sea. Although some of the localities are Late Badenian in age (Rybnica, Węglin, Monastyrz), all localities are illustrated on a single (Early Badenian) map. Map modified after Moissette *et al*. (2007).

The identified Middle Miocene brachiopod fauna is as follows (locality information according to the Naturalis labels of specimens and personal comments by Ronald Pouwer, collection manager of Naturalis). Abbreviations: fr – fragment; C – complete specimen; V – ventral valve; D – dorsal valve.

Korytnica (Poland, Kielce), surface material in fields NE and E of village (coordinates: *c*. 50.6620° N, 20.5170-20.5290° E). Miocene, Early Badenian, *Heterostegina* Sands; collected by A.W. Janssen, 2-3 October 1979.

Lingula cf. *dregeri* Andreae, 1893 (RGM 793.699) (13 fr).

Korytnica 1 (Poland, Kielce), exposure on the northern slope of Lysa Góra Hill, (coordinates: *c*. 50.6620° N, 20.5290° E). Miocene, Early Badenian, Korytnica Clay, Oyster Bed; collected by A.W. Janssen, 2-3 October 1979.

Discradisca polonica (Radwańska & Radwański, 1984) (RGM 793.695-696) (104 fr).
Argyrotheca cf. *cuneata* (Risso, 1826) (RGM 793.698) (7 fr).
Joania cf. *cordata* (Risso, 1826) (RGM 793.697) (25 fr).
Megerlia sp. (RGM 793.694) (1 fr).

Korytnica 3 (Poland, Kielce), exposure on the northern slope of Lysa Góra Hill, (coordinates: *c*. 50.6620° N, 20.5290° E). Miocene, Early Badenian, Korytnica Clay, *c*. 8 m below uppermost *Lithophaga*-zone; collected by A.W. Janssen, 2-3 October, 1979.

Lingula cf. *dregeri* Andreae, 1893 (RGM 793.693) (1 fr).
Discradisca polonica (Radwańska & Radwański, 1984) (RGM 793.686) (18 fr).
Argyrotheca bitnerae Dulai *in* Dulai & Stachacz, 2011 (RGM 793.690-692) (2 C, 5 V, 12 D).
Joania cordata (Risso, 1826) (RGM 793.685, RGM 793.687-689) (16 C, 25 V, 60 D).

Korytnica 5 (Poland, Kielce), exposure on the northern slope of Lysa Góra Hill, (coordinates: *c*. 50.6620° N, 20.5290° E). Miocene, Early Badenian, Korytnica Clay, *c*. 6 m below uppermost *Lithophaga*-zone; collected by A.W. Janssen, 2-3 October, 1979.

Lingula cf. *dregeri* Andreae, 1893 (RGM 793.671) (1 fr).
Discradisca polonica (Radwańska & Radwański, 1984) (RGM 793.668-670) (72 fr).

Argyrotheca bitnerae Dulai *in* Dulai & Stachacz, 2011 (RGM 607.738-741, RGM 793.675-680) (12 C, 32 V, 50 D).

Joania cordata (Risso, 1826) (RGM 793.667, RGM 793.672-674, RGM 793.682-684) (21 C, 63 V, 119 D).

Brachiopoda indet. (RGM 793.681) (8 fr).

Karsy (Poland, Kielce), top of hill south of village (coordinates: *c*. 50.646° N, 20.555° E). Miocene, Early Badenian, sandy upper part of Korytnica Clay, *Solecurtus* level, above level with Lucinidae; collected by A.W. Janssen, 4-5 October 1979.

Argyrotheca bitnerae Dulai *in* Dulai & Stachacz, 2011 (RGM 793.718) (1 D).

Rybnica (Poland, Lublin), exposure in forest. Miocene, Late Badenian, level 4 (*c*. 4.5-6 m from top of section); collected by A.W. Janssen, 30 September and 6 October 1979.

Discinisca leopolitana (Friedberg, 1921) (RGM 793.715-716) (24 fr).

Gryphus cf. *miocaenicus* (Michelotti, 1847) (RGM 793.717) (1 V).

Węglin (Poland, Lublin), small exposure on the road Węglin-Łychów (villages situated between Zaklikov and Krasnik). Miocene, Late Badenian, grey to yellowish grey fine-grained sands; collected by A.W. Janssen, 28 September 1979.

Joania cordata (Risso, 1826) (RGM 793.700-704) (56 C, 574 V, 79 D).

Monastyrz (Poland, Podkarpackie), exposure in hollow road near former monastry. Miocene, Late Badenian, from levels 18, 19 and 28 (see Jakubowski & Musiał, 1977); collected by A.W. Janssen, 24 September 1979.

Lingula cf. *dregeri* Andreae, 1893 (RGM 793.713-714) (10 fr).

Discinisca leopolitana (Friedberg, 1921) (RGM 793.711-712) (14 fr).

Cryptopora nysti (Davidson, 1874) (RGM 793.705-710) (11 C, 30 V, 23 D).

Várpalota (Hungary, Veszprém county), abandoned Szabó sand pit. Miocene, Early Badenian, greyish-brown fossiliferous sands; collected by A.W. Janssen, 15 October 1979.

Joania cordata (Risso, 1826) (RGM 793.719-720) (2 D).

Lăpugiu de Sus (Romania, Hunedoara), Valea Cosului (coordinates: 45.84595° N; 22.471583° E). Miocene, Early Badenian, unnamed beds; collected by M. Grigis, August 2002.

Argyrotheca cuneata (Risso, 1826) (RGM 793.721-722) (5 D, 1 V).

Korytnica and Karsy are typical Korytnica Clay localities in the Korytnica Basin and represent shallow marine environments (Bałuk & Radwański, 1977). The oyster bed sample from Korytnica is also derived from a very shallow and well-agitated littoral sea. Badenian sandy deposits with diverse fossil assemblages are exposed at Rybnica, along the southern slopes of the Holy Cross Mts (Studencka, 1986). In the vicinity of Węglin, the most diverse brachiopod fauna was recorded from calcareous marls rich in red algal and bryozoan fragments (Bitner, 1990). Sandy deposits and their brachiopods at Monastyrz and Huta Lubycka were described by Jakubowski & Musiał (1979) and Popiel-Barczyk (1980). Várpalota is famous for its mollusc-rich sand (e.g., Strausz, 1954), but brachiopods have never been mentioned from here. On the basis of its bryozoan fauna, Moissette *et al*. (2007) reconstructed a beach environment on a terrigenous platform, where skeletal remains from various depth intervals accumulated. The main sediment types of Lăpugiu de Sus are grey clay and yellow sand. The extremely diverse fossil assemblage of this locality is derived from littoral to sublittoral environments with palaeodepths from 5 to 90 m (Petrescu *et al*., 1990).

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806
Subphylum Linguliformea Williams, Carlson, Brunton, Holmer & Popov, 1996
Class Lingulata Gorjansky & Popov, 1985
Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Lingulidae Menke, 1828
Genus *Lingula* Bruguière, 1791

Type species – *Lingula anatina* Lamarck, 1801 (subsequent designation by Rowell, 1964).

***Lingula* cf. *dregeri* Andreae, 1893**
Pl. 1, figs. 1-4.

Material – Korytnica (13 fr), Korytnica 3 (1 fr), Korytnica 5 (1 fr), Monastyrz (10 fr).

Remarks – In spite of their low taphonomic potential (Emig, 1990), lingulides have been recorded several times from the Middle Miocene deposits of the Central Paratethys. These records were the following: Dreger (1889): *Lingula Suessi* n. sp. (= *L. dregeri*) from Loretto; Friedberg (1921): *L.* aff. *dumortieri* from Obertasów; Meznerics (1944) and Schmid *et al*. (2001): *L. dregeri* from St. Margarethen; Barczyk & Popiel-Barczyk (1977): *L. dumortieri* from Korytnica; Bărbulescu & Rado (1984): *Lingula* sp. from Lăpugiu de Sus; Popiel-Barczyk & Barczyk (1990): *L. dregeri* from Pinczów and Kików; and Bitner *et al*. (2012): *L. dregeri* from Budapest. As can be seen in the above list, two lingulide species were distinguished in the Badenian of the Central Paratethys: *Lingula dregeri* Andreae, 1893, and *"Lingula" dumortieri* Nyst, 1843, respectively.

However, Emig & Bitner (2005) assigned all studied Polish lingulide specimens to *L. dregeri*, but none to *Glottidia dumortieri*. Septa of the ventral valve, which are characteristic for *G. dumortieri* (Chuang, 1964; Dulai, 2013), could not be seen on any available Polish specimens. According to Emig & Bitner (2005), all lingulide specimens from the Miocene of Poland belong to *L. dregeri*. Therefore, although the studied lingulide specimens from Korytnica and Monastyrz are very fragmentary in the Naturalis collection, they belong to *Lingula* and most probably to *L. dregeri*. In earlier papers *Lingula* was reported from both the Korytnica and Monastyrz localities (e.g., Barczyk & Popiel-Barczyk, 1977; Popiel-Barczyk, 1977, 1980; Emig & Bitner, 2005).

Superfamily Discinoidea Gray, 1840
Family Discinidae Gray, 1840
Genus *Discinisca* Dall, 1871

Type species – *Orbicula lamellosa* Broderip, 1833 (by original designation).

***Discinisca leopolitana* (Friedberg, 1921)**
Pl. 2, figs. 1-4.

Material – Monastyrz (14 fr), Rybnica (24 fr).

Remarks – Although the organo-phosphatic shells of discinide brachiopods are rare in the Miocene, two species were recorded from the northern margin of the Central Paratethys, namely from Ukraine and Poland. *Discinisca leopolitana* was first noted by Łomnicki (1897) as *Discina* sp. (*leopolitana*), but without any illustrations or descriptions. Therefore, as discussed by Radwańska & Radwański (1984, p. 260), this name was a *nomen nudum* until adequate description by Friedberg (1921). Later this species passed into oblivion, that is, it was not mentioned in key summary papers, such as the *Atlas of Polish Neogene Fossils* (Popiel-Barczyk, 1996) or in the catalogue of brachiopods stored in Muzeum Ziemi, Warsawa (Popiel-Barczyk, 1992). Popiel-Barczyk (1977, 1980) alluded to *Discina* sp. from Monastyrz and Huta Lubycka, but without specific identification. Beyond the original description from Lwow, western Ukraine (Friedberg, 1921), this species was only recently recorded from other parts of the Central Paratethys: from St. Margarethen (Vienna Basin, Austria) by Schmid *et al*. (2001) and from Świniary (Holy Cross Mountains, Poland) by Radwański & Wysocka (2004). Some undeterminable *Discinisca* fragments were reported from Szydłów (Holy Cross Mountains, Poland) by Dulai & Stachacz (2011).

Most of the *D. leopolitana* specimens in Naturalis collection are small-sized (3-4 mm) and only one of them attains 5.5 × 6.6 mm (Pl. 2, fig. 1). However, even this specimen is significantly smaller than Friedberg's (1921) material from Western Ukraine (7 × 9 mm). The outline of the dorsal valves is generally circular, but sometimes slightly rectangular (Pl. 2, fig. 4), while the shape of the shell is low conical. The 0.6 mm wide larval shell is smooth; later, the shell surface is ornamented by numerous, dense, more or less concentric, growth lines.

Radwańska & Radwański (1984) described a new discinide species, *Discinisca polonica*, from the Middle Miocene sediments of the Korytnica Basin, Poland. These two discinide species are easily distinguishable from each other, as only dense growth lines occur on the dorsal valve of *D. leopolitana*, whereas *D. polonica* is distinctly ribbed.

Genus *Discradisca* Stenzel, 1964

Type species – *Orbicula antillarum* d'Orbigny, 1853 (by original designation).

Discradisca polonica (Radwańska & Radwański, 1984)
Pl. 1, figs. 5-10.

Material – Korytnica 1 (104 fr), Korytnica 3 (18 fr), Korytnica 5 (72 fr).

Remarks – This species was described from the littoral deposits of the Korytnica Basin, central Poland (Radwańska & Radwański, 1984) and only a few dozen small-sized, low conical dorsal valves were available for study. There are nearly 200 fragments of discinide dorsal valves from Korytnica samples in the Naturalis collection and most of them can be easily identified as *D. polonica* on the basis of the ribbed ornamentation of the outer shell surface. Several fragments are too small to identify confidently, but they most probably also belong to this species because all the larger sized fragments are ribbed and, until now, smooth discinides have never been reported from the Korytnica localities.

The studied specimens are too fragmentary to infer the shell outline or the exact position of apex. The 0.4 mm wide, circular larval shell is smooth, while the post-larval shell surface is densely ornamented by fine growth lines (Pl. 1, fig. 6). According to Radwańska & Radwański (1984), the radial ribs appear abruptly at a definite growth line (the margin of the post-larval shell), but in the Leiden material this is not always the case (e.g., Pl. 1, fig. 7). The cross-section of ribs is rounded and ribs are stronger towards the valve margin. The ribs generally intersect with growth lines giving a beaded character to the outer surface. The ribs do not bifurcate, but sometimes new ribs appear as intercalations (Pl. 1, fig. 7). The interspaces are generally much wider than ribs. The interior of the dorsal valves and the arrangement of muscle scars are not clear on the very fragmentary specimens. Similarly, only the holotype has completely preserved muscle scars in Radwańska & Radwański's (1984) material.

Discradisca was introduced by Stenzel (1964) as a subgenus of *Disciniscа*. When Stenzel described Danian (Paleocene) *Discinisca* (*Discradisca*) *littigensis*, he wished to distinguish those species having radial costae on the dorsal valve from those lacking costae. Later, Cooper (1977) elevated *Discradisca* to generic rank. The new, revised *Treatise* (Holmer & Popov, 2000, p. 86) distinguished *Discinisca* and *Discradisca* on the basis of the ventral valve: "similar to *Discinisca*, but with wide, transversely suboval pedicle track". Although the name *Discradisca* was introduced for a fossil species it is now widely used for Recent brachiopods and several living species were transferred to this genus (*D. antillarum*, *D. cumingi*, *D. indica*, *D. sparselineata*, *D. stella*, *D. strigata*; see, e.g., Emig, 1997; Bitner & Cahuzac, 2013); this genus name has not gained traction in palaeontological literature. One of the main reasons is the fact that the recently used definition of *Discradisca* concentrates on the characters of the ventral valve and fossil material generally only contains dorsal valves. However, if we return to Stenzel's original aim (to distinguish discinides with radial costae on the dorsal valve), several fossil discinide species should on this basis be transferred to *Discradisca*. One of these species is *D. polonica*, discussed herein. Similar systematic results were established recently regarding *Discradisca multiradiata* (de Morgan, 1915) by Bitner & Cahuzac (2013) and Dulai (2013) on the basis of Early and Middle Miocene material from France. Bitner & Cahuzac (2013) also listed several fossil species, including *D. polonica*, which should be transferred to *Discradisca*.

Discradisca polonica is similar to *D. scutellum*, described by Dreger (1889) from the contemporaneous Badenian sedimentary rocks of the Vienna Basin, Austria. However, this species is based on a single fragmentary dorsal valve without detectable muscle scars (see also in Kroh, 2003) and, therefore, it is not easy to compare with any other materials. Another finely ribbed Central Paratethyan discinide is *D. carpathica*, described by Čtyroký & Fejfar (1963), but this species is much larger and its muscle scar pattern is slightly different. The Central Paratethyan discinide brachiopods were discussed in detail by Radwańska & Radwański (1989), including *D. steiningeri* from the Upper Oligocene (Egerian) of Austria.

One of the Leiden specimens shows a very small (0.175 mm) drill hole indicating attack by a predatory gastropod (Pl. 1, fig. 10). Drilling predation has a long fossil record (Kowalewski *et al*., 1998), and has been intensely studied mainly in molluscs and partly in rhynchonelliform ("articulate") brachiopods. Predatory drill holes of nonarticulate brachiopods are rarely examined, and such studies focused mainly on fossil and Recent lingulides (e.g. Paine, 1963; Wiedman *et al*., 1988; Kowalewski & Flessa, 1994; Bitner, 1996; Kowalewski *et al*., 1997). Among other nonarticulate brachiopods, drill holes have been identified in fossil acrotretides (Miller & Sundberg, 1984; Chatterton & Whitehead, 1987). Lee (1987) noted that dead shells of craniids are sometimes drilled by gastropods. This is the first definite record of predatory drill holes on phosphatic shelled brachiopods in the Central Paratethys. One of the *D. steiningeri* paratypes (Radwańska & Radwański, 1989; Pl. 2, fig. 1a) bears a hole, but it seems to be irregular in outline and the authors did not mention any signs of predation in the text. Predation on discinide brachiopods elsewhere is also only sporadically mentioned. Lesport & Cahuzac (2005) illustrated a drilled discinide specimen without specific identification from the Lower Burdigalian of France. Recently, intense drilling predation was reported from the same area on the basis of a larger sample by Bitner & Cahuzac (2013); 12% of the *Discradisca multiradiata* specimens were attacked in the Early Miocene assemblage of Martillac (Aquitaine Basin, France). An even higher rate of drilling predation was indicated on the same species by Dulai (2013), where eight out of 34 specimens (23.5%) bear predatory drill holes in the Middle Miocene (Langhian) material from Amberre (Loire Basin, France). These two papers indicate that the Atlantic *D. multiradiata* was a common prey of drilling predatory gastropods, contrary to the contemporaneous Central Paratethyan discinides.

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer & Popov, 1996
Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order Rhynchonellida Kuhn, 1949
Superfamily Dimerelloidea Buckman, 1918
Family Cryptoporidae Muir-Wood, 1955
Genus *Cryptopora* Jeffreys, 1869

Type species – *Atretia gnomon* Jeffreys, 1876 (by original designation).

***Cryptopora nysti* (Davidson, 1874)**
Pl. 3, figs. 1-10.

Material – Monastyrz (11 C, 30 V, 23 D).

Remarks – *Cryptopora* is rare in Central Paratethyan Miocene rhynchonellide faunas. The small and translucent shells are thin and fragile, and therefore easily overlooked in sedimentary rocks. The outline is very variable (subtriangular to oval). The beak is high and acute (Pl. 3, fig. 1) or low and obtuse (Pl. 3, fig. 8). Foramen large, triangular and hypothyrid. Ventral valve interior shows distinct divergent dental plates. Deltidial plates are simple, triangular, without wing-like auriculation, characteristic of *Cryptopora lovisati*. Dorsal valve interior has moderately long, but high median septum (anterior end beyond the mid-length of the valve). Diverging (Pl. 3, fig. 4) or crescent-shaped (Pl. 3, fig. 9) adductor muscle scars at both sides of the median septum. Crura are partly broken in all available specimens. Mosaic pattern of secondary layer fibres is clearly visible on the internal surface of the shell (Pl. 3, fig. 10).

Popiel-Barczyk (1980) described three different *Cryptopora* species (*C. lovisati*, *C. nysti* and *C. discites*, respectively) from the sandy deposits of the studied region (Monastyrz and Długi Goraj, Lublin Upland, eastern Poland). However, after detailed investigation of the original material in the Muzeum Ziemi (Museum of the Earth, Warsaw), Bitner & Cahuzac (2004) concluded that all these specimens represent only one species, namely *C. nysti* (Davidson, 1874). Their observation is confirmed here on the basis of the much smaller sample in Naturalis, which represents also the wide variability of this species.

Some other records of *Cryptopora* are also known from the Miocene of the Central Paratethys: *C. discites* by Dreger (1889) from the Vienna Basin; *C. lovisati* by Popiel-Barczyk & Barczyk (1990) from Pinczów area, central Poland; *Cryptopora* sp. from Roztocze Hills by Bitner (1990); and *C. lovisati* from the Moravian Foredeep by Bitner *et al*. (2013a). *Hemithyris parvillima* Sacco, 1902, was reported from the Miocene deposits of Hungary by Meznerics (1944); this species later was referred questionably to *Cryptopora* by Cooper (1959). However, on the basis of their shell microstructure the Hungarian specimens belong not to *Cryptopora*, but the terebratulide genus *Gryphus* (Bitner & Dulai, 2004). Elsewhere, *C. nysti* is known from the Messinian of Spain (Llompart & Calzada, 1982). Toscano-Grande *et al*. (2010) illustrated *Cryptopora* sp. from the Miocene of the Guadalquivir Basin (SW Spain) and this specimen also appears identical with *C. nysti*. Recently, Dulai (2013) identified two fragmentary *C. nysti* specimens from the Miocene of Groß Pampau (Germany, North Sea Basin). Although not so common in the fossil record, *C. nysti* also seems to be widespread in the European Miocene.

Davidson (1874), Thomson (1927) and later Cooper (1959) assigned this species to the genus *Mannia*; however, in the revised *Treatise Mannia* was regarded as junior synonym of *Cryptopora* (Manceñido *et al*., 2002). Thomson (1927) identified it as a terebratulide, but its rhynchonellide affinity was demonstrated by Cooper (1959).

The small, pedunculate cryptoporides, living in sandy facies, attach to the sediment by a long, thin pedicle (Curry, 1983). Extant representatives of the family Cryptoporidae live in shallow to very deep water (60-4000 m; Curry, 1983; Richardson, 1997; Bitner & Cahuzac, 2004). The Miocene basin of the Lublin Upland was estimated as 100-200 m deep by Jakubowski & Musiał (1977).

Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Terebratuloidea Gray, 1840
Family Terebratulidae Gray, 1840
Subfamily Gryphinae Sahni, 1929
Genus *Gryphus* Megerle von Mühlfeld, 1811

Type species – *Anomia vitrea* Born, 1778 (by original designation).

***Gryphus* cf. *miocaenicus* (Michelotti, 1847)**
Pl. 2, figs. 5-6.

Material – Rybnica (1 V).

Remarks – Although only one ventral valve is available in the Naturalis collection, its external characters are consistent with those described for genus *Gryphus*. The relatively small-sized shell is smooth, moderately convex and the anterior commissure is rectimarginate. The beak is curved and the pedicle foramen is very small. It can be easily distinguished from the more widespread Central Paratethyan large terebratulides ("*Terebratula*" spp.), which have a much larger pedicle foramen and sulciplicate anterior commissure. *Gryphus* is known from the Eocene (Bitner *et al*., 2011) and is especially common in the Pliocene of the Mediterranean (*Gryphus minor*; Gaetani & Saccà, 1985; Saccà, 1985), as well as in the present-day Mediterranean and Atlantic Ocean (*Gryphus vitreus*; Emig, 1989). *Gryphus* was also mentioned from the Caribbean by Cooper (1977, 1979). This genus is not so common in the Miocene of the Central Paratethys, but *Gryphus miocaenicus* was recorded in the Badenian of Hungary (Meznerics, 1944; Bitner & Dulai, 2004). This species was also recently identified in the Lower Sarmatian of the Central Paratethys in Slovakia (Bitner *et al*., 2014). However, this is the first record of *Gryphus* from the Miocene of Poland; Popel-Barczyk (1992) noted *Gryphus* only from the Eocene deposits of Poland. This specimen maybe also the first reliable record of *Gryphus* from the northern margin of the Central Paratethys; however, Friedberg's (1921) material from Ukraine should be revised, as his *Liothyrina punctatissima* (Pl. 2, fig. 2) appears identical with *Gryphus*. On the basis of the previous records from the Central Paratethys, this ventral valve in the Naturalis collection can be identified as *G.* cf. *miocaenicus*.

Suborder Terebratellidina Muir-Wood, 1955
Superfamily Megathiridoidea Dall, 1870
Family Megathirididae Dall, 1870
Genus *Argyrotheca* Dall, 1900

Type species – *Terebratula cuneata* Risso, 1826 (by original designation).

***Argyrotheca cuneata* (Risso, 1826)**
Pl. 4, figs. 10-11.

Material – Korytnica 1 (7 fr), Lăpugiu de Sus (5 D, 1V).

Remarks – *Argyrotheca* is reported as one of the most common micromorphic brachiopod genera in the Middle Miocene sedimentary rocks of the Central Paratethys. Although it was widely distributed throughout the whole Central Paratethys, *A. cuneata* is less common in the fossil record than "*A*". *cordata*. The recently described *A. bitnerae* is even less common and until now was recorded only from the northern margin of this sea. However, "*Argyrotheca*" *cordata* was recently assigned type species of a new genus, *Joania*, by Álvarez *et al*. (2008). *Argyrotheca*, thus, can no longer be considered the most common brachiopod in the Miocene of the Central Paratethys. It is widespread, but generally not a dominant element of the brachiopod fauna, although some exceptions are known, such as at Węglin and Łychów in Poland (Bitner, 1990) or at Bivolare in Bulgaria (Bitner, 1993). However, the family Megathirididae (including genera *Megathiris*, *Argyrotheca* and *Joania*) is, without doubt, the most common constituent of Miocene shallow-water brachiopod assemblages in the Central Paratethys.

Argyrotheca cuneata is reported from several Badenian localities in Austria (Kroh, 2003), Hungary (Matyasovszky, 1880, under the name *Argiope hofmanni*; Bitner & Dulai, 2004; Dulai, 2007), Czech Republic (Bitner *et al*., 2013a; Pavézková *et al*., 2013), Poland (Bitner, 1990; Popiel-Barczyk & Barczyk, 1990; Bitner & Pisera, 2000; Bitner & Kaim, 2004) and Bulgaria (Bitner, 1993). This species was recently also recorded from the Lower Sarmatian of the Central Paratethys (Bitner *et al*., 2014). It can be easily distinguished from *Joania cordata* by its ribbed outer shell surface, position of maximum width and mainly by the internal morphological characters.

This species was described earlier from Korytnica by Popiel-Barczyk & Barczyk (1990) under the name *A. costulata*. Bărbulescu & Rado (1984) have illustrated *A. squamata* from Lăpugiu de Sus, which appears identical with *A. cuneata*. The former species requires detailed revision, as discussed by Bitner (1990).

Argyrotheca bitnerae Dulai *in* Dulai & Stachacz, 2011

Pl. 4, figs. 6-9.

Material – Korytnica 3 (2 C, 5 V, 12 D), Korytnica 5 (12 C, 32 V, 50 D), Karsy (1 D).

Remarks – Some small-sized megathiridid specimens in the Naturalis collection represent a recently described new *Argyrotheca* species, superficially similar to *Joania cordata*. However, it differs from the latter species by its subtriangular outline, the very high beak, the absence of a median sulcus on the brachial valve and the lack of tubercles on the internal margin of the valves. This form had already been illustrated by Popiel-Barczyk & Barczyk (1990) and Popiel-Barczyk (1996) from the Polish Badenian deposits. However, it was erroneously confused with the Recent Mediterranean *Argyrotheca cistellula* (see Dulai & Stachacz, 2011). *Argyrotheca cistellula* also lacks any tubercles on the internal margins; however, it is transversely subrectangular in outline with a short beak and straight hinge line (Logan, 1979). Although the limited Naturalis material clearly indicated a new species, it was more practical to describe *A. bitnerae* on the basis of a more numerous and more representative assemblage collected from the Badenian sedimentary rocks of Szydłów (Poland) and supplemented by the revision of some collections in the Muzeum Ziemi (Warsaw), but including also Naturalis specimens (Dulai & Stachacz, 2011). According to this original description, the palaeogeographic distribution of *A.*

bitnerae was limited to the northern part of the Central Paratethys (Poland); however, recently it was also recorded from four Upper Oligocene localities in the Aquitaine Basin, France (Bitner *et al*., 2013b).

Genus *Joania* Álvarez, Brunton & Long, 2008

Type species – *Terebratula cordata* Risso, 1826 (by original designation).

***Joania cordata* (Risso, 1826)**
Pl. 4, figs. 1-5.

Material – Korytnica 1 (25 fr), Korytnica 3 (16 C, 25 V, 60 D), Korytnica 5 (21 C, 63 V, 119 D), Węglin (56 C, 574 V, 79 D), Várpalota (2 D).

Remarks – *Joania cordata* is one of the most common brachiopod species in the Miocene of the Central Paratethys. Among others it was recorded (sometimes under different names) in Badenian deposits from Austria (Dreger, 1889), Hungary (Matyasovszky, 1880; Meznerics, 1944; Bitner & Dulai, 2004; Dulai, 2007), Romania (Boettger, 1901; Zilch, 1934; Meznerics, 1944; Bărbulescu & Rado, 1984; Bitner & Dulai, 2004), Bulgaria (Bitner, 1993), Ukraine (Friedberg, 1921), Poland (Barczyk & Popiel-Barczyk, 1977; Popiel-Barczyk & Barczyk, 1990; Bitner, 1990; Bitner & Pisera, 2000; Bitner & Kaim, 2004) and the Czech Republic (Bitner *et al*., 2013a). This species was recently also recorded from the Lower Sarmatian of the Central Paratethys in Slovakia (Bitner *et al*., 2014). It is easily distinguishable from other Central Paratethyan Megathirididae species by the row of tubercles on the internal margins of both valves (Pl. 4, figs. 2, 3, 5). In some earlier papers it was reported under various names, but Bitner (1990) published a full synonymy list and defined its characteristics in detail. With reference to the localities in the Naturalis collections, this species was already recorded from Korytnica (e.g., Barczyk & Popiel-Barczyk, 1977) and Węglin (e.g., Bitner, 1990). The Hungarian locality Várpalota is famous for its diverse and well-preserved mollusc fauna (e.g., Strausz, 1954), but this is the first record of any brachiopod from these Lower Badenian sandy deposits.

Superfamily Kraussinoidea Dall, 1870
Family Kraussinidae Dall, 1870
Genus *Megerlia* King, 1850

Type species – *Anomia truncata* Linnaeus, 1767 (by original designation).

***Megerlia* sp.**
Pl. 4, figs. 12-13.

Material – Korytnica 1 (1 fr).

Remarks – *Megerlia* is a well-documented genus in the Central Paratethyan Middle Miocene deposits, as well as in the Recent Mediterranean fauna. Its common species is *Megerlia truncata* which was recorded from the Central Paratethys by Dreger (1889), Friedberg (1921), Meznerics (1944), Bărbulescu & Rado (1984), Bitner (1990), Popiel-Barczyk & Barczyk (1990) and Bitner & Dulai (2004). Jakubowski & Musiał (1979) noted *Megerlia* sp. from Huta Różaniecka, but on the basis of their figure this identification is very uncertain. The only available specimen in the Naturalis collection is too fragmentary to identify at species level, but the characteristic ornamentation of the internal surface of the shell support this generic identification. To date the only recorded *Megerlia* species was *M. truncata* in the Central Paratethys; most probably this fragment also represents this species.

Discussion

Naturalis has a surprisingly diverse Middle Miocene (Badenian) brachiopod collection from the Central Paratethys (1403 partly fragmentary specimens, representing nine species of eight genera). These brachiopods have been collected from Poland, Hungary and Romania. Most of the identified species are already known from the Central Paratethys, but the Leiden material contains a new *Argyrotheca* species. This was described recently on the basis of a more representative assemblage from the Polish Miocene, but included also the Naturalis specimens (Dulai & Stachacz, 2011).

In accordance with the recent taxonomic study by Bitner & Cahuzac (2013) and Dulai (2013), this report suggests that the discinide species *D. polonica* should be transferred to the genus *Discradisca*. The limited Naturalis material confirms Bitner & Cahuzac's (2004) earlier opinion that the available Polish *Cryptopora* specimens belong to only one species (*C. nysti*). Although not so common in the fossil record as *C. lovisati*, *C. nysti* is also widespread in the European Miocene.

In most cases the Leiden specimens confirm earlier records. However, in some cases the collections have yielded new information on the distribution of these brachiopod species within the Central Paratethys. These new results are the following:

- First record of *Discinisca leopolitana* from Monastyrz and Rybnica. Until now, it was recorded from the Central Paratethys only from Lwow (western Ukraine), St Margarethen (Vienna Basin, Austria) and Świniary (Holy Cross Mountains, Poland).
- First record of *Gryphus* from Rybnica, as well as from the Miocene of Poland and maybe the northern margin of the Central Paratethys. Friedberg's (1921) *Liothyrina punctatissima* specimens require revision and they may belong to this genus.
- First record of *Argyrotheca bitnerae* from Karsy.
- First record of *Joania cordata* (and in fact, any brachiopod) from Várpalota.
- First identification of *Argyrotheca cuneata* from Korytnica (earlier it was reported as *A. costulata*) and from Lăpugiu de Sus (earlier it was reported as *A. squamata*).

One of the *Discradisca polonica* specimens shows a drill hole of a predatory gastropod. Drilling predation has a very long history (see Kowalewski *et al*., 1998) and there are substantial data on brachiopod predation. However, this is the first definite record of predatory drill holes on phosphatic shelled brachiopods in the Central Paratethys. Bitner & Cahuzac (2013) and Dulai (2013) recently indicated that the Atlantic *D. multiradiata* was the common prey of drilling predatory gastropods (12% and 23.5%, respectively). The contemporaneous Central Paratethyan discinides were apparently 'luckier' in this respect.

Acknowledgements

This study was supported by European Commission's Research Infrastructure Action (Synthesys project NL-TAF-3270) and the Hungarian Scientific Research Fund (OTKA T 49224 and K77451). Dr. Frank Wesselingh's help in the Cainozoic Mollusc Collection of Naturalis is greatly acknowledged. I thank Ronald Pouwer (collection manager) for discussion of the Naturalis samples. The useful comments by reviewers Professor David A.T. Harper (Durham University) and Dr Cor F. Winkler-Prins (Naturalis, Leiden) are deeply acknowledged. The SEM photos were taken in the SEM Laboratory of Hungarian Natural History Museum, Budapest. The *Gryphus* specimen was photographed by Eszter Hankó.

References

Álvarez, F., Brunton, C.H.C. & Long, S.L. 2008. Loop ultrastructure and development in Recent Megathiridoidea, with description of a new genus, *Joania* (type species *Terebratula cordata* Risso, 1826). *Earth and Environmental Science: Transactions of the Royal Society of Edinburgh*, **98**: 391-403.

Andreae, A. 1893. Die Brachiopoden des Rhät von Malsch. *Mitteilungen der Großherzoglichen Badischen Geologischen Landesanstalt*, **3**: 11-17.

Bałuk, W. & Radwański, A. 1977. Organic communities and facies development of the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **27**: 85-123.

Bărbulescu, A. & Rado, G. 1984. Contributions à la connaissance des brachiopodes badéniens de Roumanie. *75 years of the Laboratory of Paleontology*, **Special Volume**: 173-184.

Barczyk, W. & Popiel-Barczyk, E. 1977. Brachiopods from the Korytnica basin (Middle Miocene; Holy Cross Mountains, Poland). *Acta Geologica Polonica*, **27**: 157-167.

Bitner, M.A. 1990. Middle Miocene (Badenian) brachiopods from the Roztocze Hills, south-eastern Poland. *Acta Geologica Polonica*, **40**: 129-157.

Bitner, M.A. 1993. Middle Miocene (Badenian) brachiopods from coral reefs of north-western Bulgaria. *Acta Geologica Polonica*, **43**: 147-155.

Bitner, M.A. 1996. Brachiopods from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. *In*: Gazdicki, A. (ed.), Palaeontological Results of the Polish Antarctic Expeditions. *Palaeontologica Polonica*, **55**: 65-100.

Bitner, M.A. & Cahuzac, B. 2004. The genus *Cryptopora* (Brachiopoda) from the Miocene of France and its history and biogeography. *Geobios*, **37**: 1-12.

Bitner, M.A. & Cahuzac, B. 2013. New record of *Discradisca* (Brachiopoda: Discinidae) from the Early Miocene of the Aquitaine Basin, south-western France. *Comptes Rendus Palevol*, **12**: 23-29.

Bitner, M.A. & Dulai, A. 2004. Revision of Miocene brachiopods of the Hungarian Natural History Museum, with special regard to the Meznerics collection. *Fragmenta Palaeontologica Hungarica*, **22**: 69-82.

Bitner, M.A., Dulai, A. & Galácz, A. 2011. Middle Eocene brachiopods from the Szőc Limestone Formation (Bakony Mountains, Hungary), with a description of a new genus. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **259**: 113-128.

Bitner, M.A., Dulai, A., Kocsis, L. & Müller, P.M. 2012. *Lingula dregeri* (Brachiopoda) from the Middle Miocene of Hungary. *Annales Societatis Geologorum Poloniae*, **82**: 39-43.

Bitner, M.A. & Kaim, A. 2004. The Miocene brachiopods from the silty facies of the intra-Carpathian Nowy Sącz Basin (Poland). *Geological Quarterly*, **48**: 193-198.

Bitner, M.A., Lozouet, P. & Cahuzac, B. 2013b. Upper Oligocene (Chattian) brachiopod fauna from the Aquitaine Basin, southwestern France and its paleoenvironmental implications. *Geodiversitas*, **35**: 579-606.

Bitner, M.A. & Pisera, A. 2000. Brachiopod fauna from the Middle Miocene deposits of Niechobrz, south-eastern Poland. *Tertiary Research*, **20**: 7-15.

Bitner, M.A., Zágoršek, K., Halásová, E., Hudáčková, N. & Jamrich, M. 2014. Brachiopods and bryozoans from the Sandberg section (Vienna Basin, Central Paratethys) and their significance for environmental interpretation of the Early Sarmatian (= Middle Miocene) Sea. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **273**: 207-219.

Bitner, M.A., Zágoršek, K. & Hladilová, Š. 2013a. Deep-water brachiopod assemblage from the Middle Miocene of Kralice nad Oslavou, Moravia, southeastern Czech Republic. *Comptes Rendus Palevol*, **12**: 81-89.

Boettger, O. 1901. Zur Kenntniss der Fauna der mittelmiozänen Schichten von Kostej im Krassó-Szörényer Komitat. *Verhandlungen und Mitteilungen des siebenbürgischen Vereines für Naturwissenschaften zu Hermannstadt*, **51**: 1-200.

Born, I.E. 1778. Index rerum naturalium Musei Caesarei Vindobonensis, 1: Testacea. *Verzeichnis der natürlichen Seltenheiten des K. K. Naturalien Cabinets zu Wien*, **1**, Schaltiere: 458 pp.

Broderip, W.J. 1833. Description of some new species of Cuvier's family of Brachiopoda. *Proceedings Zoological Society, London*, **1833**: 124-125.

Bruguière, J.G. 1791. *Tableau Encyclopédique et Méthodique des trois Règnes de la Nature: vers, coquilles, mollusques et polypes divers*. Panckoucke, Paris: 172-344.

Buckman, S. 1918. The Brachiopoda of the Namyau Beds, northern Shan States, Burma. *Palaeontologica Indica*, **3**: 1-299.

Cendón, D.I., Peryt, T.M., Ayorac, C., Pueyo, J.J. & Taberner, C. 2004. The importance of recycling processes in the Middle Miocene Badenian evaporite basin (Carpathian foredeep): palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **212**: 141-158.

Chatterton, B.D.E. & Whitehead, H.L. 1987. Predatory borings in inarticulate brachiopod *Artiotreta* from the Silurian of Oklahoma. *Lethaia*, **20**: 67-74.

Chuang, S.H. 1964. The affinity of *Lingula dumortieri* Nyst with *Glottidia*. *Journal of Paleontology*, **38**: 155-157.

Cooper, G.A. 1959. Genera of Tertiary and Recent rhynchonelloid brachiopods. *Smithsonian Miscellaneous Collections*, **139**: 1-90.

Cooper, G.A. 1977. Brachiopods from the Caribbean Sea and Adjacent Waters. *Studies in Tropical Oceanography*, **14**: 1-211.

Cooper, G.A. 1979. Tertiary and Cretaceous brachiopods from Cuba and the Caribbean. *Smithsonian Contributions to Paleobiology*, **37**: 1-45.

Čtyroký, P. & Fejfar, O. 1963. Fauna der Sande und Sandsteine der karpatischen Formation (Mittelmiozän) bei Dolni Netcice in der Karpatenvortiefe. *Geologické Práce*, **27**: 143-168.

Curry, G.B. 1983. Ecology of the Recent deep-water rhynchonellid brachiopod *Cryptopora* from the Rockall Trough. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **44**: 93-102.

Dall, W.H. 1870. A Revision of the Terebratulidae and Lingulidae with Remarks on and Description of Some Recent Forms. *American Journal of Conchology*, **6**: 88-168.

Dall, W.H. 1871. Report on the Brachiopoda of the Straits of Florida, in Charge of L.F. de Pourtales, with a Revision of the Craniidae and Discinidae Obtained by the U. S. Coast Survey Expedition. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **3**: 1-45.

Dall, W.H. 1900. Some names which must be discarded. *Nautilus*, **14**: 44-45.

Davidson, T. 1874. On Tertiary Brachiopoda of Belgium. *Geological Magazine*, **118**: 150-189.

Dreger, J. 1889. Die tertiären Brachiopoden des Wiener Beckens. *Beiträge zur Paläontologie Österreich-Ungarns*, **7**: 179-192.

Dulai, A. 2007. Badenian (Middle Miocene) micromorphic brachiopods from Bánd and Devecser (Bakony Mountains, Hungary). *Fragmenta Palaeontologica Hungarica*, **24-25**: 1-13.

Dulai, A. 2010. Early Messinian (Late Miocene) micromorphic brachiopods from Borelli (Italy, Piemonte). *Fragmenta Palaeontologica Hungarica*, **28**: 21-31.

Dulai. A. 2013: Sporadic Miocene brachiopods in the Naturalis Biodiversity Center (Leiden, the Netherlands): Records from the Mediterranean, the North Sea, and the Atlantic Ocean. *Fragmenta Palaeontologica Hungarica*, **30**: 15-51.

Dulai, A. & Stachacz, M. 2011. New Middle Miocene *Argyrotheca* (Brachiopoda; Megathyrididae) species from the Central Paratethys. *Földtani Közlöny*, **141**: 445-468.

Duméril, A.M.C. 1806. *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Allais, Paris: 344 pp.

Emig, C.C. 1989. Distributional patterns along the Mediterranean continental margin (Upper Bathyal) using *Gryphus vitreus* (Brachiopoda) densities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **71**: 253-256.

Emig, C.C. 1990. Examples of post-mortality alternation in Recent brachiopod shells and (paleo)ecological consequences. *Marine Biology*, **104**: 233-238.

Emig, C.C. 1997. Ecology of inarticulated brachiopods. *In*: Kaesler, R.L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised 1*, Geological Society of America and University of Kansas Press, Boulder Colorado, and Lawrance Kansas: 471-495.

Emig, C.C. & Bitner, M.A. 2005. The brachiopod *Lingula* in the Middle Miocene of the Central Paratethys. *Acta Palaeontologica Polonica*, **50**: 181-184.

Friedberg, W. 1921. Les brachiopodes miocènes de la Podolie Occidentale. *Prace Naukowe Uniwersytetu Poznańskiego, Sekcja Matematyczno-Przyrodnicza*, **2**: 1-20.

Gaetani, M. & Saccà, D. 1985. Brachiopodi neogenici e pleistocenici della provincia di Messina e della Calabria meridionale. *Geologica Romana*, **22**: 1-43.

Gorjansky, W. & Popov, L. 1985. The morphology, systematic position, and origin of inarticulate brachiopods with carbonate shells. *Paleontological Journal*, **3**: 1-11.

Gray, J.E. 1840. *Synopsis of the Contents of the British Museum*. 42nd edition, G. Woodfall and Son, London: 370 pp.

Holmer, L.E. & Popov, L.E. 2000. Lingulata. *In*: Kaesler, R.L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised 2*, Geological Society of America and University of Kansas, Boulder Colorado, and Lawrance Kansas: 30-146.

Jakubowski, G. & Musiał, T. 1977. Lithology and fauna from the Upper Tortonian sands of Monastyrz and Długi Goraj (Southern Roztocze, Poland). *Prace Muzeum Ziemi*, **26**: 63-126.

Jakubowski, G. & Musiał, T. 1979. Middle Miocene sandy and carbonate deposits of Huta Lubycka and Huta Różaniecka (Roztocze Rawskie Region, South-eastern Poland) and their fauna. *Prace Muzeum Ziemi*, **32**: 71-100.

Jeffreys, J.G. 1869. The deep-sea dredging expedition in H.M.S. *Porcupine*, 1: natural history. *Nature*, **1**: 136.

Jeffreys, J.G. 1876. On Some New and Remarkable North-Atlantic Brachiopoda. *Annals and Magazine of Natural History* (series 4), **18**: 250-253.

King, W. 1850. A monograph of the Permian Fossils of England. *Palaeontographical Society Monograph*, **3**: 1-258.

Kókay, J. 1985. Central and Eastern Paratethyan interrelations in the light of Late Badenian salinity conditions. *Geologica Hungarica, Series Palaeontologica*, **48**: 9-95.

Kováč, M., Andreeva-Grigorovich, A., Bayraktarević, Z., Brzobohatý, R., Filipescu, S., Fodor, L., Harzhauser, M., Nagymarosy, A., Oszczypko, N., Pavelić, D., Rögl, F., Saftić, B., Sliva, L. & Studencka, B. 2007. Badenian evolution of the Central Paratethys Sea: paleogeography, climate and eustatic sea level changes. *Geologica Carpathica*, **58**: 579-606.

Kowalewski, M., Dulai, A. & Fürsich, F.T. 1998. A fossil record full of holes: The Phanerozoic history of drilling predation. *Geology*, **26**: 1091-1094.

Kowalewski, M. & Flessa, K. 1994. A predatory drillhole in *Glottidia palmeri* Dall (Brachiopoda; Lingulidae) from Recent tidal flats of northeastern Baja California, Mexico. *Journal of Paleontology*, **86**: 1403-1405.

Kowalewski, M., Flessa, K.W. & Marcot, J.D. 1997. Predatory scars in the shells of a Recent lingulid brachiopod: Paleontological and ecological implications. *Acta Palaeontologica Polonica*, **42**: 497-532.

Kroh, A. 2003. The Brachiopoda of the Langhian (Lower Badenian) of the Molasse Zone and the northern Vienna Basin (Austria). *Annalen des Naturhistorischen Museum in Wien*, **104A**: 145-153.

Kuhn, O. 1949. *Lehrbuch der Paläozoologie*. E. Schweizerbart, Stuttgart: 325 pp.

Lamarck, J.B. 1801. *Systéme des animaux sans vertèbres, ou tableau général des classes, des ordres, et des genres de ces animaux dans le Muséum National d'Historie Naturelle*. Paris: 432 pp.

Lee, D.E. 1987. Cenozoic and Recent inarticulate brachiopods of New Zealand: *Discina*, *Pelagodiscus* and *Neocrania*. *Journal of the Royal Society of New Zealand*, **17**: 49-72.

Lesport, J.-F. & Cahuzac, B. 2005. Découverte des sables à Mactres de la base du Burdigalien à Martillac (Nord Aquitaine; SW France); données paléontologiques. *Annales de Paléontologie*, **91**: 73-116.

Linnaeus, C. von 1767. *Systema Naturae*. 12th edition, Stockholm: 1154 pp.

Llompart, C. & Calzada, S. 1982. Braquiópodos messinienses de la isla de Menorca. *Boletin de la Real Sociedad Española de Historia Natural*, **80**: 185-206.

Logan, A. 1979. The Recent Brachiopoda of the Mediterranean Sea. *Bulletin de l'Institut océanographique de Monaco*, **72**: 1-112.

Łomnicki, M. 1897. Materiały do mioceńskiej fauny Lwowa I najbliższej okolicy. *Kosmos*, **22**: 18-37.

Majer, I. 1915. A Börzsönyi hegység északi részének üledékes képződményei. (Die sedimentären Bildungen des nördlichen Teiles vom Börzsönyer Gebirge). *Földtani Közlöny*, **45**: 18-40 (69-94).

Manceñido, M.O., Owen, E.F., Savage, N.F. & Dagys, A.S. 2002. Dimerelloidea. *In*: Kaesler, R.L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda revised 4, Rhynchonelliformea (part)*. Geological Society of America and University of Kansas Press, Boulder Colorado, and Lawrance Kansas: 1236-1245.

Matyasovszky, J. 1880. Paläontologische beiträge zur Kenntnis der jüngeren Mediterranen Schichten des Baranyaer Comitates. *Természetrajzi Füzetek*, **4**: 243-248.

Megerle von Mühlfeldt, J.C.M. 1811. Entwurf eines neuen Systems der Schaltiergehäuse. *Magazin der Gesellschaft Naturforschenden Freunde zu Berlin*, **5**: 38-72.

Menke, C.T. 1828. *Synopsis methodica molluscorum generum omnium et specierum earum, quae in Museo Menkeano adservantur; cum synonymia critica et novarum specierum diagnosibus*. G. Pyrmonti, Uslar: 91 pp.

Meznerics, I. 1944. Die Brachiopoden des ungarischen Tertiärs. *Annales historico-naturales Musei Nationalis Hungarici*, **36**: 10-60.

Michelotti, G. 1847. Description des fossils des terrains miocènes de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen*, Ser. 2, **3**: 1-408.

Miller, R.H. & Sundberg, F.A. 1984. Boring Late Cambrian organisms. *Lethaia*, **17**: 185-190.

Moissette, P., Dulai, A. & Müller, P. 2006. Bryozoan faunas in the Middle Miocene of Hungary: biodiversity and biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **233**: 300-314.

Moissette, P., Dulai, A., Escarguel, G., Kázmér, M., Müller, P. & Saint Martin, J.-P. 2007. Mosaic of environments recorded by bryozoan faunas from the Middle Miocene of Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**: 530-556.

Morgan, J. de 1915. Notes sur les Mollusques Brachiopodes des faluns de la Tourraine. *Bulletin de la Société Geologique de France* (t. 4), **15**: 260-273.

Muir-Wood, H.M. 1955. *A History of the Classification of the Phylum Brachiopoda*. British Museum (Natural History), London: 124 pp.

Nyst, P.-H. 1843. Description des coquilles et des polypiers fossiles des terrains tertiaires de la Belgique. *Mémoires Couronnés et Mémoires des savants étrangers de l'Académie royale de Bruxelles*, **17**: 1-676.

Orbigny, A. d'. 1853. *Histoire physique, politique et naturelle de l'ile de Cuba; Mollusques, Vol. 2*. A. d'Orbigny, Paris: 380 pp.

Paine, R.T. 1963. Ecology of the brachiopod *Glottidia pyramidata*. *Ecological Monographs*, **33**: 187-213.

Papp, A., Cicha, I., Seneš, J. & Steininger, F.F. (eds.) 1978. *M4 Badenien (Moravien, Wielicien, Kosovien). Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys*. Verlag der Slowakischen Akademie des Wissenschaften, Bratislava: 594 pp.

Pavézková, J., Hladilová, Š. & Bitner, M.A. 2013. Miocene brachiopods from the Židlochovice locality, Czech Republic. *Geologické výzkumy na Moravě a ve Slezsku*, **20**: 56-59.

Petrescu, I., Mészáros, N., Chira, C. & Filipescu, S. 1990. Lower Badenian paleoclimate at Lăpugiu de Sus (Hunedoara County), on account of paleontological investigations. *Studia Universitate Babes-Bolyai, Geologia*, **35**: 13-22.

Pisera, A. 1996. Miocene reefs of the Paratethys: a review. *In*: Franseen, E.K., Esteban, M., Ward, W.C. & Rouchy, J.-M. (eds.), *Models for Carbonate Stratigraphy from Miocene Reef Complexes of Mediterranean Regions. Concepts in Sedimentology and Paleontology*. SEPM: 97-104.

Popiel-Barczyk, E. 1977. A new locality of Miocene fauna in Roztocze region. *Przegląd Geologiczny*, **5**: 246-248.

Popiel-Barczyk, E. 1980. Brachiopod genus *Cryptopora* Jeffreys from the Miocene deposits of the Lublin Upland. *Acta Geologica Polonica*, **30**: 111-120.

Popiel-Barczyk, E. 1992. *Mesozoic and Cenozoic Brachiopods. Catalogue of the Collection*. Polish Academy of Sciences, Museum of the Earth, Warszawa: 55 pp.

Popiel-Barczyk, E. 1996. Typ Brachiopoda. *In*: Malinowska, L. & Piwocki, M. (eds.), *Atlas skamieniałości przewodnich i charakterystycznych. Budowa geologiczna Polski*, **3a**: 653-663.

Popiel-Barczyk, E. & Barczyk, W. 1990. Middle Miocene (Badenian) brachiopods from the southern slopes of the Holy Cross Mountains, Central Poland. *Acta Geologica Polonica*, **40**: 159-181.

Radwańska, U. & Radwański, A. 1984. A new species of inarticulate brachiopod, *Discinisca polonica* sp. n., from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **34**: 253-269.

Radwańska, U. & Radwański, A. 1989. A new species of inarticulate brachiopods, *Discinisca steiningeri* sp. nov., from the Late Oligocene (Egerian) of Plesching near Linz, Austria. *Annalen des Naturhistorischen Museums in Wien*, **90A**: 67-82.

Radwański, A. & Wysocka, A. 2004. A farewell to Świniary sequence of mass-aggregated, spine-coated echinoids *Psammechinus* and their associates (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **54**: 381-399.

Richardson, J.R. 1997. Ecology of articulated brachiopods. *In*: Kaesler, R.L. (ed.), *Treatise on Invertebrate Paleontology, part H, Brachiopoda, revised 1*, Geological Society of America and University of Kansas Press, Boulder, Colorado, and Lawrence, Kansas: 441-472.

Risso, A. 1826. *Histoire naturelle des principales Productions de l'Europe Méridionale, et particuliérement de celles des environs de Nice et des Alpes Maritimes, 4: Aperçu sur l'Histoire Naturelles des mollusques et des coquilles de l'Europe Méridionale*. Paris: 439 pp.

Rowell, A.J. 1964. *Lingula* Bruguière (1797) (Brachiopoda: Inarticulata): proposed designation of a type-species under the plenary powers. Z.N. (S.) 1598. *Bulletin of Zoological Nomenclature*, **21**: 222-224.

Rögl, F. 1998. Palaeogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien*, **99**: 279-310.

Saccà, D. 1985. Variabilità del Brachidio de *Gryphus minor* (Philippi) Terebratulida, Brachiopoda. *Rivista Italiana di Paleontologia e Stratigrafia*, **91**: 409-424.

Sacco, F. 1902. *I Brachiopodi dei terreni terziarii del Piemonte e della Liguria*. Carlo Clausen, Torino: 50 pp.

Sahni, M.R. 1929. A monograph of the Terebratulidae of the British Chalk. *Palaeontographical Society Monograph* (for 1927): 1-62.

Saint Martin, J.-P., Müller, P., Moissette, P. & Dulai, A. 2000. Coral microbialite environment in a Middle Miocene reef of Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **160**: 179-191.

Schmid, P.H., Harzhauser, M. & Kroh, A. 2001. Hypoxic events on a Middle Miocene carbonate platform of the Central Paratethys (Austria, Badenian, 14 Ma). *Annalen des Naturhistorischen Museums in Wien*, **102A**: 1-50.

Stenzel, H.B. 1964. Stratigraphic and paleoecologic significance of a new Danian brachiopod species from Texas. *Geologische Rundschau*, **54**: 619-631.

Strausz, L. 1954. Várpalotai felső-mediterrán csigák. (Les gastropodes du Méditerranéen supérieur (Tortonien) de Várpalota). *Geologica Hungarica, Series Palaeontologica*, **25**: 1-84 (87-129).

Studencka, B. 1986. Bivalves from the Badenian (Middle Miocene) marine sandy facies of Southern Poland. *Palaeontologica Polonica*, **47**: 1-128.

Thomson, J.A. 1927. Brachiopod morphology and genera (Recent and Tertiary). *New Zealand Board of Science and Art, Manual*, **7**: 1-338.

Toscano-Grande, A., García Ramos, D., Ruiz-Muñoz, F., González-Regalado, M.L., Abad, M., Civis-Llovera, J., González-Delgado, J.A., Rico-García, A., Martínez-Chacón, M.L., García, E.X. & Pendón-Martín, J.G. 2010. Braquiópodos neógenos del suroeste de la depresión del Guadalquivir (sur de España). *Revista Mexicana de Ciencias Geológicas*, **27**: 254-263.

Waagen, W. 1883. Salt Range Fossils. Vol. I, part 4. Productus-Limestone Fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologica Indica*, Series 13, **2**: 391-546.

Waagen, W. 1885. Salt Range Fossils. Vol. I, part 4. Productus-Limestone Fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologica Indica*, Series 13, **5**: 729-770.

Wiedman, L.A., Feldmann, R.L., Lee, D.E. & Zinsmeister, W.J. 1988. Brachiopoda from the La Meseta Formation (Eocene), Seymour Island, Antarctica. *In*: Feldmann, R.M. & Woodburn, M.O. (eds.), Geology and Paleontology of the Seymour Island, Antarctic Peninsula. *Geological Society of America Memoir*, **169**: 531-539.

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E. & Popov, L. 1996. A supraordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London*, **B351**: 1171-1193.

Zilch, A. 1934. Zur Fauna des Mittel-Miocäns von Kostej (Banat); Typus Bestimmung und Tafeln zu O. Boettger's Bearbeitungen. *Senckenbergiana*, **16**: 193-302.

Plate 1

Figs. 1-4. *Lingula* cf. *dregeri* Andreae, 1893, Monastyrz, Poland.
Fig. 1. RGM 793.713a, external view, × 20.
Fig. 2. RGM 793.713b, internal view, × 20.
Fig. 3. RGM 793.713c, external view, × 20.
Fig. 4. RGM 793.713d, internal view, × 20.

Figs. 5-10. *Discradisca polonica* (Radwańska & Radwański, 1984).
Fig. 5. RGM 793.668a, external view of dorsal valve, Korytnica 5, Poland, × 20.
Fig. 6. Detail of Fig. 5, showing the smooth embryonal part of the shell, × 33.
Fig. 7. RGM 793.695, external view of dorsal valve, Korytnica 1, Poland, × 20.
Fig. 8. Detail of Fig. 7, showing the fine ornamentation of the ribbed part of the shell, × 112.
Fig. 9. RGM 793.668b, external view of dorsal valve, Korytnica 5, Poland, × 20.
Fig. 10. RGM 793.668c, external view of a drilled dorsal valve, Korytnica 5, Poland, × 20.

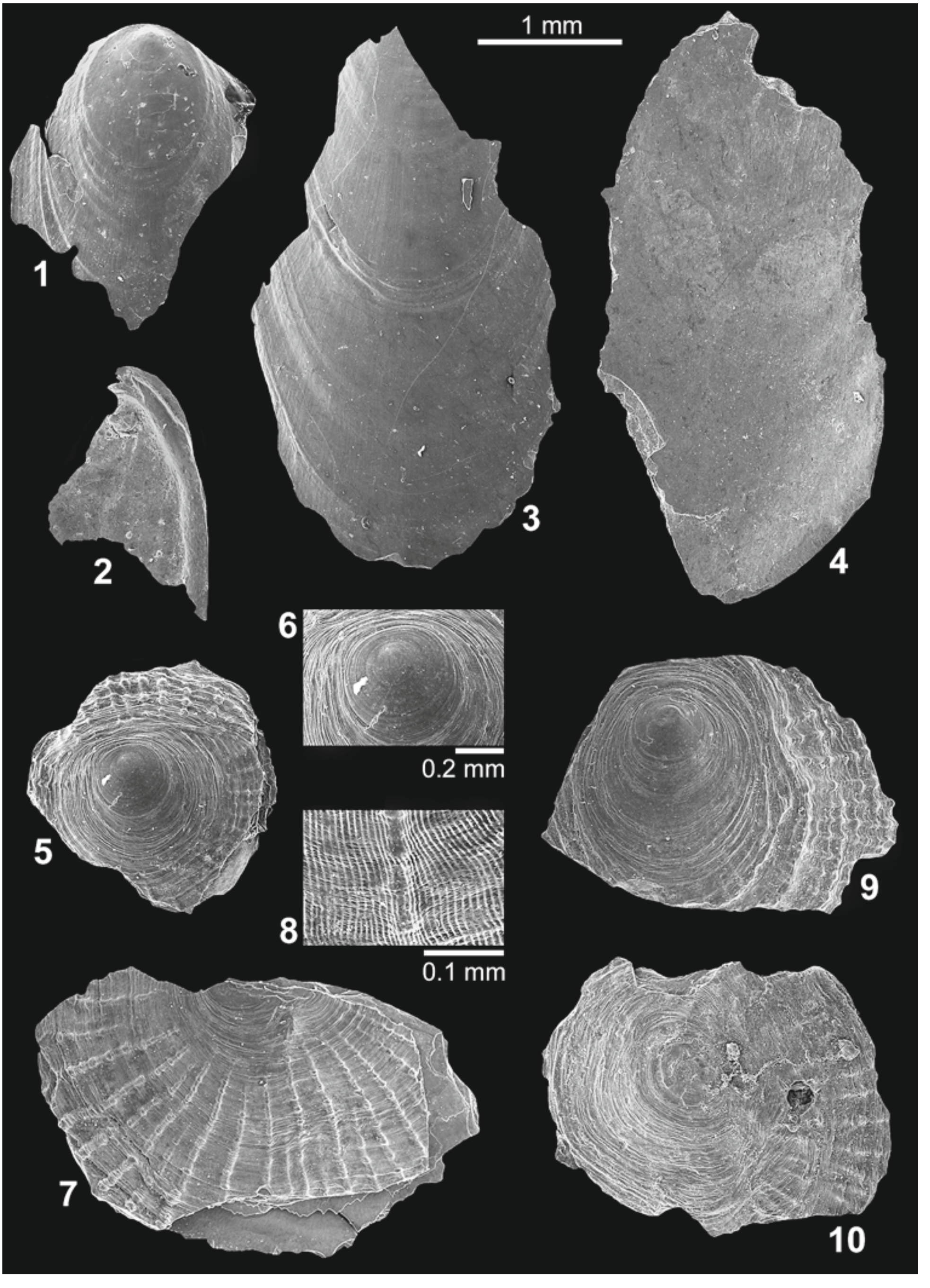

1 mm
1
2
3
4
6
0.2 mm
5
8
0.1 mm
9
7
10

Plate 2

Figs. 1-4. *Discinisca leopolitana* (Friedberg, 1921).
Fig. 1. RGM 793.715a, external view of dorsal valve, Rybnica, Poland, × 15.
Fig. 2. RGM 793.711, external view of dorsal valve, Monastyrz, Poland, × 15.
Fig. 3. RGM 793.715b, external view of dorsal valve, Rybnica,Poland, × 15.
Fig. 4. RGM 793.715c, internal view of dorsal valve, Rybnica, Poland, × 15.

Figs. 5-6. *Gryphus* cf. *miocaenicus* (Michelotti, 1847), Rybnica, Poland.
Fig. 5. RGM 793.717, external view of ventral valve, × 5.
Fig. 6. RGM 793.717, internal view of ventral valve, × 5.

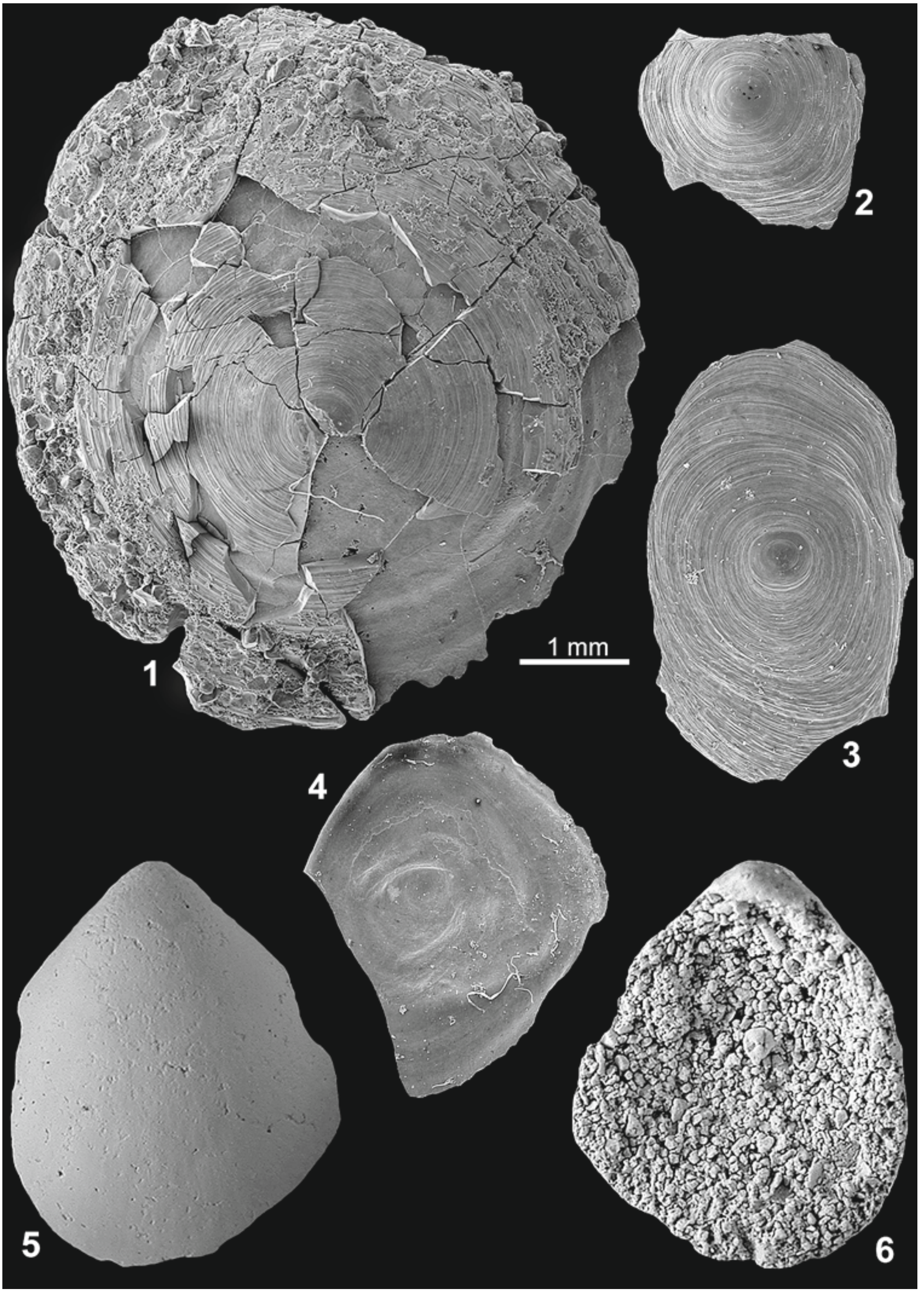

1
2
3
4
5
6
1 mm

Plate 3

Figs. 1-10. *Cryptopora nysti* (Davidson, 1874), Monastyrz, Poland.
Fig. 1. RGM 793.705a, dorsal view of fragmentary complete specimen, × 15.
Fig. 2. RGM 793.707a, internal view of ventral valve, × 15.
Fig. 3. detail of Fig. 2, showing the dental plate, × 65.
Fig. 4. RGM 793.706a, internal view of dorsal valve, × 15.
Fig. 5. RGM 793.705b, dorsal view of fragmentary complete specimen, × 15.
Fig. 6. RGM 793.705c, dorsal view of fragmentary complete specimen, × 15.
Fig. 7. RGM 793.707b, internal view of ventral valve, × 15.
Fig. 8. RGM 793.705d, dorsal view of fragmentary complete specimen, × 15.
Fig. 9. RGM 793.706b, internal view of dorsal valve, × 15.
Fig. 10. detail of Fig. 9, showing the shell structure and mosaic of secondary layer fibres, × 260.

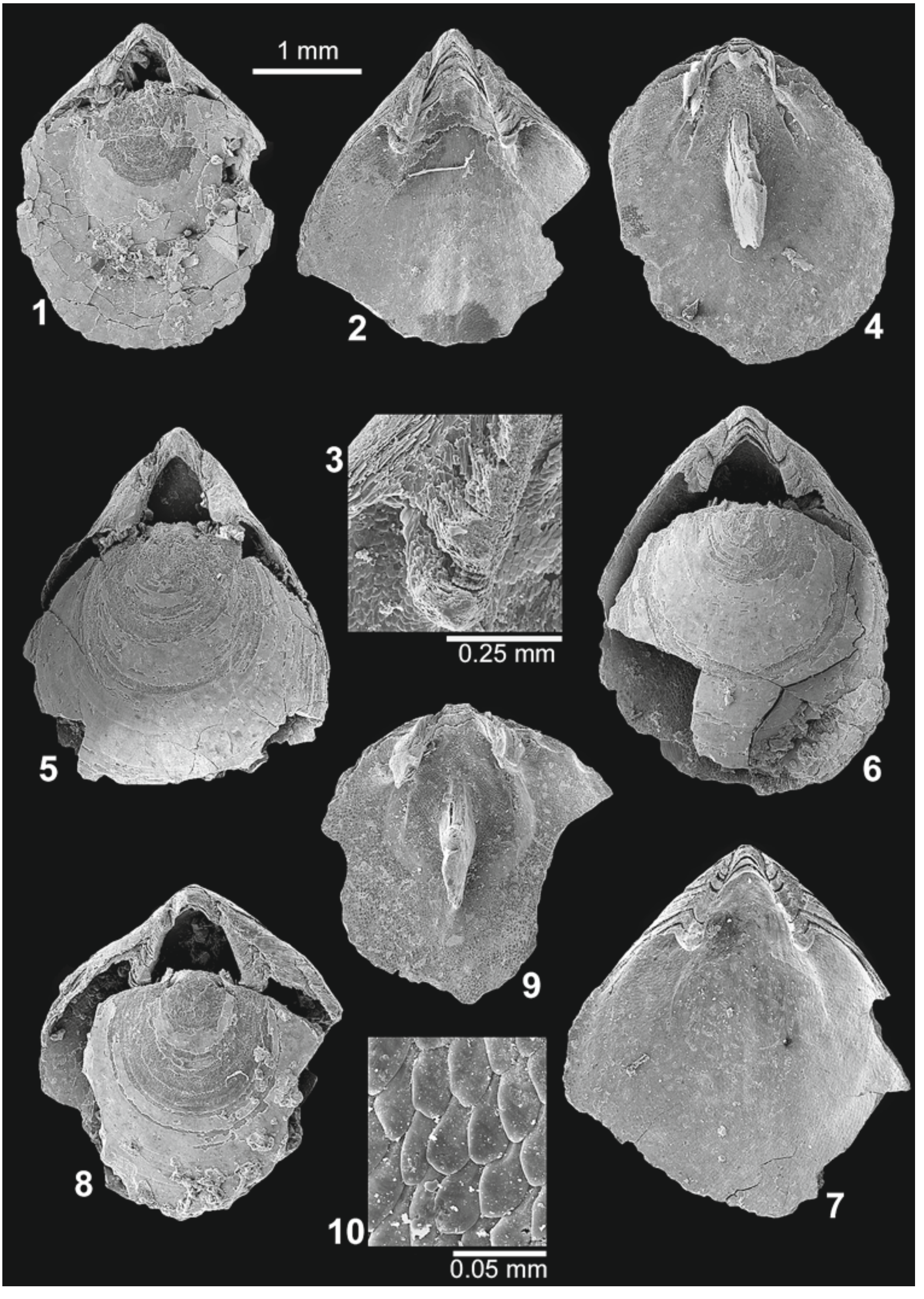

1 mm
1
2
4
3
0.25 mm
5
6
9
8
10
0.05 mm
7

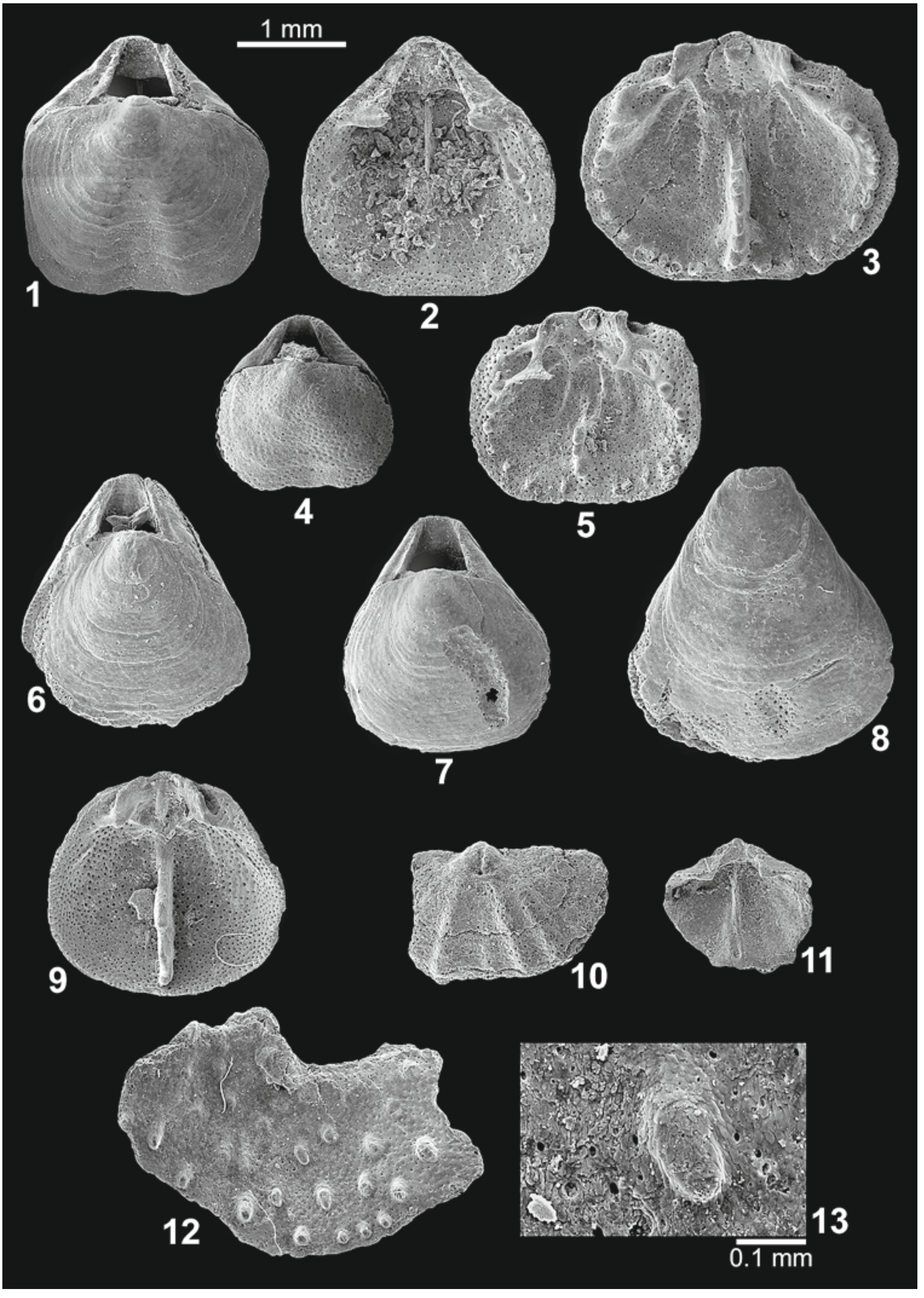
Plate 4

Figs. 1-5. *Joania cordata* (Risso, 1826).
Fig. 1. RGM 793.700a, dorsal view of complete specimen, Węglin, Poland, × 15.
Fig. 2. RGM 793.700b, internal view of ventral valve, Węglin, Poland, × 15.
Fig. 3. RGM 793.700c, internal view of dorsal valve, Węglin, Poland, × 15.
Fig. 4. RGM 793.685, dorsal view of juvenile complete specimen, Korytnica 3, Poland, × 15.
Fig. 5. RGM 793.667, internal view of juvenile dorsal valve, Korytnica 5, Poland, × 15.

Figs. 6-9. *Argyrotheca bitnerae* Dulai in Dulai & Stachacz, 2011, Korytnica 5, Poland.
Fig. 6. RGM 607.739, dorsal view of complete specimen, × 15.
Fig. 7. RGM 607.738, dorsal view of complete specimen, × 15.
Fig. 8. RGM 607.740, ventral view of complete specimen, × 15.
Fig. 9. RGM 607.741, internal view of dorsal valve, × 15.

Figs. 10-11. *Argyrotheca cuneata* (Risso, 1826), Lăpugiu de Sus, Romania.
Fig. 10. RGM 793.721, external view of dorsal valve, × 15.
Fig. 11. RGM 793.722, internal view of ventral valve, × 15.

Figs. 12-13. *Megerlia* sp., Korytnica 1, Poland.
Fig. 12. internal view of a fragmentary valve, × 15.
Fig. 13. detail of Fig. 12, × 100.


1 mm
1
2
3
4
5
6
7
8
9
10
11
12
13
0.1 mm