

MIDDLE MIOCENE (BADENIAN) BRACHIOPODS FROM THE BORAČ AREA (CARPATHIAN FOREDEEP, MORAVIA, CZECH REPUBLIC)

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Bitner, M. A., Hladilová, Š., Šamánek, J. & Turek, T., 2024. Middle Miocene (Badenian) brachiopods from the Borač area (Carpathian Foredeep, Moravia, Czech Republic). *Annales Societatis Geologorum Poloniae*, 94: 00–00.

Abstract: Four brachiopod species, i.e., *Terebratula* cf. *styriaca* Dreger, *Terebratulina retusa* (Linnaeus), *Megathiris detruncata* (Gmelin) and *Megerlia truncata* (Linnaeus), have been recognised in the Middle Miocene (lower Badenian) deposits at the localities Borač and Borač-Podolí, Carpathian Foredeep, Moravia, Czech Republic. The species *M. truncata* predominates in the assemblage studied, while *M. detruncata* is very rare, found only at the locality Borač. *Terebratula* cf. *styriaca* and *Terebratulina retusa* are reported for the first time from the Moravian part of the Carpathian Foredeep. Two types of trace fossils have been observed on the brachiopod shells: drill holes penetrating the shell (ichnogenus *Oichnus* Bromley) and etching scars, produced by a brachiopod pedicle (ichnogenus *Podichnus* Bromley and Surlyk).

Key words: Brachiopoda, Middle Miocene, Langhian, Carpathian Foredeep, Central Paratethys, trace fossils.

Manuscript received 11 March 2024, accepted 7 May 2024

INTRODUCTION

Brachiopods are common fossils in the Middle Miocene deposits of the Central Paratethys. However, their abundance and diversity are very variable in different areas and localities. In the Moravian part of the Carpathian Foredeep (Czech Republic), they are rare, both in species and specimens. So far, brachiopods have been reported and taxonomically described from 11 Moravian localities (Reuss, 1860; Zágorský *et al.*, 2012; Bitner *et al.*, 2013b, c, 2023; Pavézková *et al.*, 2013; Hladilová *et al.*, 2014; Kopecká *et al.*, 2018) but only the assemblage from the locality Kralice nad Oslavou is rich and diverse, with eight species recognised (Bitner *et al.*, 2013b).

The aim of this study is to describe a newly collected brachiopod fauna from two localities, Borač and Borač-Podolí in the Moravian part of the Carpathian Foredeep (Fig. 1). Although the investigated assemblage contains only four species, it provides new data on the Miocene brachiopods of Moravia. Its taxonomic composition differs from other Moravian assemblages, with two species reported for the first time from the Miocene of the Czech Republic.

GEOLOGICAL SETTING

The Miocene sediments in the study area occur only as isolated, erosional relics with areal extents that are poorly known because of the thick Quaternary cover. They are of marine origin and belong to the sedimentary infill of the Carpathian Foredeep, a peripheral foreland basin, formed on the loaded eastern margin of the Bohemian Massif, owing to tectonic emplacement of the Carpathian thrust wedge. Sedimentation in this sector of the basin started in the Egerian/early Eggenburgian and continued into the early Badenian (Brzobohatý and Cicha, 1993). In the early Middle Miocene (Badenian), the basin geometry of the Carpathian Foredeep was reorganized and thus the Badenian deposits represent a distinct period of basin evolution (Oszczypko, 1998; Kováč, 2000; Nehyba and Šikula, 2007).

In the wider surroundings of Borač and Borač-Podolí, the Miocene sediments lie on the pre-Neogene basement. It is composed mostly of metamorphic rocks of the Svratka Unit in the Moravian Zone. These are Precambrian under a Devonian cover – mainly gneisses, mica schists, phyllites, metabasites, granitoids, crystalline limestones

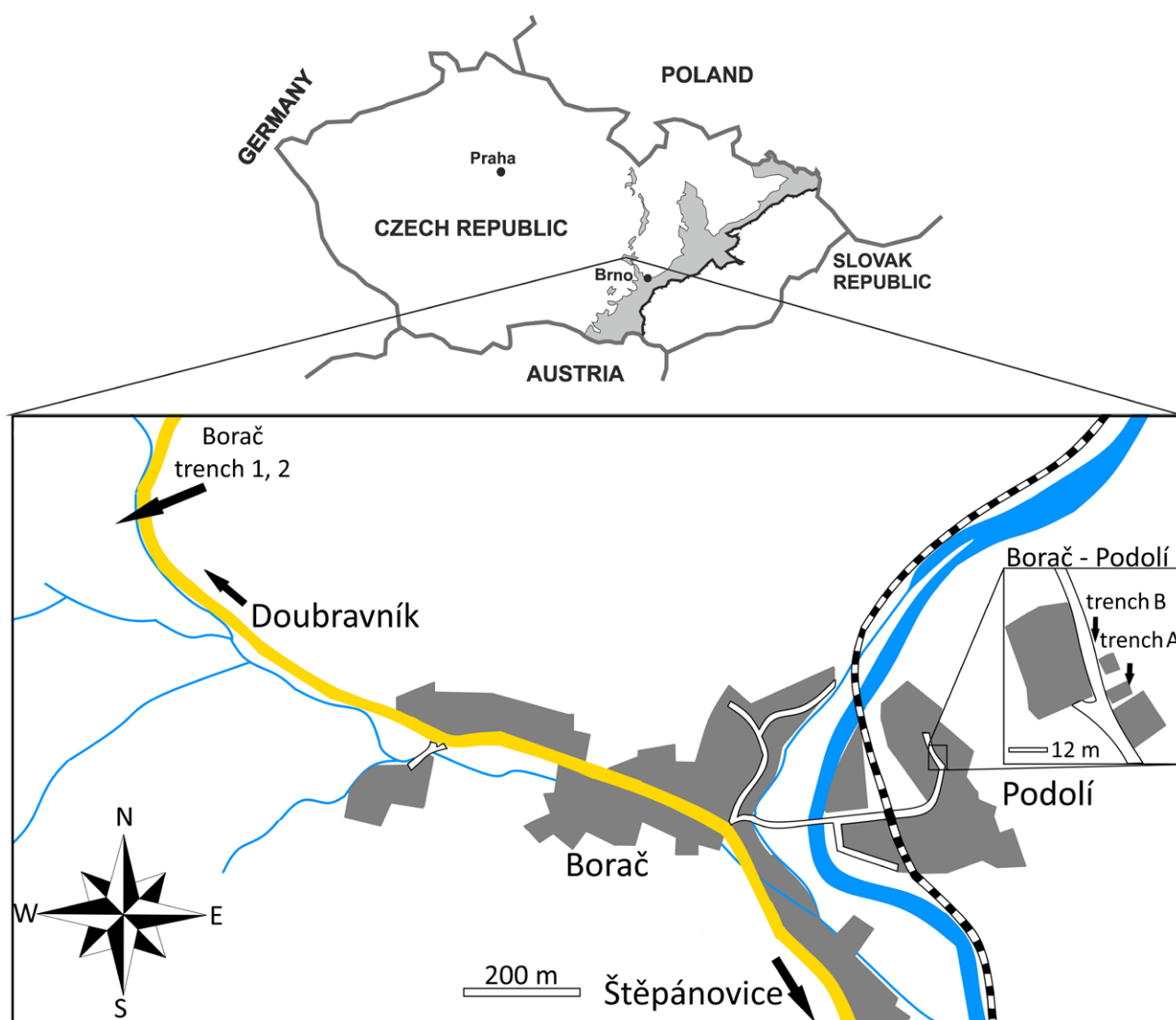


Fig. 1. Geographical location of the Neogene Carpathian Foredeep in the Czech Republic and a sketch of the studied localities in the Borač area.

and quartzites (Jaroš and Misař, 1976; Misař *et al.*, 1983). Locally, Permo–Carboniferous sediments of the Boskovice Trough are developed, comprising conglomerates, claystones, siltstones, and argillaceous carbonates (Jaroš, 1963; Buriánková *et al.*, 2001; Pešek *et al.*, 2001; Ivanov, 2003, among others). Sporadically, Cretaceous sediments occur (Cicha and Dornič, 1958; Kettner, 1959).

At present, two localities exist in the area of Borač (Fig. 1). The famous Borač palaeontological locality is situated in the fields, about 800 m NW from the village, to the left of the Borač–Doubravník road. It comprises marine (euhaline) green-grey, grey-yellow or grey-blue, strongly calcareous clays (so-called tegels) of early Badenian age, transgressing directly on the metamorphic rocks of the Moravian Zone, without basal clastics. These sediments are not exposed in natural outcrops and can be studied only in excavations. The last two trenches were made in 2016 and 2017 by one of the authors (TT). Since the second half of the 19th century, this locality has attracted the attention of a number of researchers, owing to its exceptional richness in

macro- and microfossils, mainly nannoplankton, foraminifers, radiolarians, sponge spicules, anthozoans, molluscs, ostracods, and fish otoliths (Procházka, 1892a, b, 1893, 1899; Rzehak, 1923; Cicha *et al.*, 1957; Cicha and Dornič, 1959; Krystek and Tejkal, 1968; Weyer, 1974; Brzobohatý and Cicha, 1978; Seitzl, 1981; Říha, 1983; Brzobohatý, 1997; Pekař and Lehotský, 2015, among others). The locality Borač was designated by Brzobohatý and Cicha in Papp *et al.* (1978) as a parastratotype of the lower Badenian (= the Moravian substage of the regional Badenian stage), corresponding to the lower part of the Langhian in the standard chronostratigraphy (Hohenegger *et al.*, 2014).

The second locality, named Borač–Podolí, was documented in 2015 by Jaroslav Šamánek and Lucie Kleprlíková, students from the Department of Geological Sciences, Faculty of Science, Masaryk University, Brno. Two test trenches, about 2 m deep, were open on the property of Mr. Uher (house number 33). Trench A was situated behind the garage wall (49°24'6.031"N, 16°22'2.864"E) and it revealed no macrofossils. Trench B was situated 1.55 m to the N from

the high-voltage pole, parallel to the road (49°24'6.509"N, 16°22'2.434"E). In this trench, Badenian sediments can be described as alternating layers of green-greyish, calcareous clays (up to 25 cm thick) and yellow-brownish, fine-grained, quartz-rich sands (up to 10 cm thick). Sandy layers were rich in fossils (molluscs, corals, otoliths, echinoids, etc.). Finally, both trenches were covered up. Some fossils from this locality were studied in three MSc. theses so far (Kleprlíková, 2016 – corals, Šamánek, 2017 – trace fossils, and Turek, 2018 – molluscs), and the results already have been published in part (Kleprlíková and Doláková, 2016; Kleprlíková, 2018; Šamánek *et al.*, 2018).

Although the Badenian clays near Borač are very rich in fossils, the brachiopods are only sporadically mentioned in the literature. Procházka (1892a) noted that brachiopods are very rare in the Borač clays. He reported one individual of *Cistella squamosa* (Eichwald, 1830) and three individuals of *Platidia anomioides* (Scacchi and Philippi in Philippi, 1844).

MATERIAL AND METHODS

The investigated material was collected by two of us (JŠ and TT) at two localities, Borač and Borač-Podolí (Fig. 1), during fieldwork, carried out between 2015 and 2018 (see above). At Borač, two test trenches (50 x 50 x 80 cm) were made by TT approximately 4 m NE from the high-voltage pole (N 49°24'19.271" E 16°20'47.577"). The majority of brachiopods (samples 1a, 1b, 2a, 2b) come from the sediment bulk samples, washed using sieves with 5 mm, 2 mm and 0.5 mm mesh. Some specimens were collected by hand, while digging and doing fieldwork (including samples 6a, 6b). The studied material from the locality Borač-Podolí comes from field work (trench B – 207 cm thickness of the profile, in total 5 samples from various depths), carried out by JŠ and Lucie Kleprlíková during autumn 2015 (Šamánek *et al.*, 2018). The total number of specimens is 141. For calculation also fragmented specimens were taken into consideration, if ventral or dorsal valves were recognisable. The brachiopods are poorly preserved and the majority of specimens are damaged, fragmented and/or crushed. The SEM micrographs were taken in the SEM laboratory of the Institute of Paleobiology using a Philips XL-20 scanning microscope. The material is housed at the Institute of Geological Sciences, Masaryk University, Brno, under the collection number UGV PAL Bp.03.

SYSTEMATIC PALAEONTOLOGY

Phylum Brachiopoda Duméril, 1805
 Subphylum Rhynchonelliformea Williams, Carlson,
 Brunton, Holmer and Popov, 1996
 Class Rhynchonellata Williams, Carlson, Brunton,
 Holmer and Popov, 1996
 Order Terebratulida Waagen, 1883
 Suborder Terebratulidina Waagen, 1883

Superfamily Terebratuloidea Gray, 1840
 Family Terebratulidae Gray, 1840
 Genus *Terebratula* Müller, 1776

Type species: *Anomia terebratula* Linnaeus, 1758, by subsequent designation of Lee and Brunton (1998).

Terebratula cf. *styriaca* Dreger, 1889

Fig. 2A–E

- cf. 1889 *Terebratula Styriaca* n. sp. – Dreger, p. 187 (9), pl. 3, figs 1–6.
- cf. 1977 *Terebratula styriaca* Dreger – Barczyk and Popiel-Barczyk, pp. 160–161, text-fig. 3, pl. 2, fig. 10.
- cf. 1990 *Terebratula styriaca* Dreger – Popiel-Barczyk and Barczyk, pp. 165–167, text-fig. 6, pl. 3, figs 1–10.
- cf. 2000 “*Terebratula*” *styriaca* Dreger – Bitner and Pisera, p. 9, pl. 1, figs 12–13.
- cf. 2004 *Terebratula styriaca* Dreger – Bitner and Dulai, p. 72, pl. 2, figs 1–6.

Material: Two articulated specimens, 13 ventral valves and 10 dorsal valves from the locality Borač, and 11 ventral valves and five dorsal valves from Borač-Podolí; their state of preservation is very poor; most specimens are strongly fragmented, broken and/or crushed.

Description: Shell medium- to large-sized (maximum observed length 28.6 mm), subpentagonal to widely oval in outline. Shell surface smooth with weakly marked, numerous growth lines. Beak short, with large, circular foramen of permesothyrid type. Deltidial plates conjunct forming partially visible symphytium.

Ventral valve interior with wide but very short teeth and narrow pedicle collar. Dorsal valve interior with high inner socket ridges, prominent cardinal process, and U-shaped hinge plates. In adult specimens, low median ridge present in dorsal valve. Loop not preserved.

Remarks: With 41 specimens, *Terebratula* cf. *styriaca* is the second most common species in the material studied. However, it is very poorly preserved. Although all available characters point to the species *Terebratula styriaca*, known from the Middle Miocene of the Central Paratethys (Dreger, 1889; Barczyk and Popiel-Barczyk, 1977; Popiel-Barczyk and Barczyk, 1990; Bitner and Pisera, 2000; Bitner and Dulai, 2004), the lack of a preserved loop does not allow a precise identification.

Occurrence: Middle Miocene – lower Badenian, Borač and Borač-Podolí, Moravia, Czech Republic. It is worth mentioning that the genus *Terebratula*, represented by single valves of young individuals, was already mentioned from Moravia (Zágoršek *et al.*, 2012; Bitner *et al.*, 2013b, 2023). The species *Terebratula styriaca* is restricted to the northern part of the Central Paratethys (Dreger, 1889; Popiel-Barczyk and Barczyk, 1990; Bitner and Pisera, 2000; Bitner and Dulai, 2004).

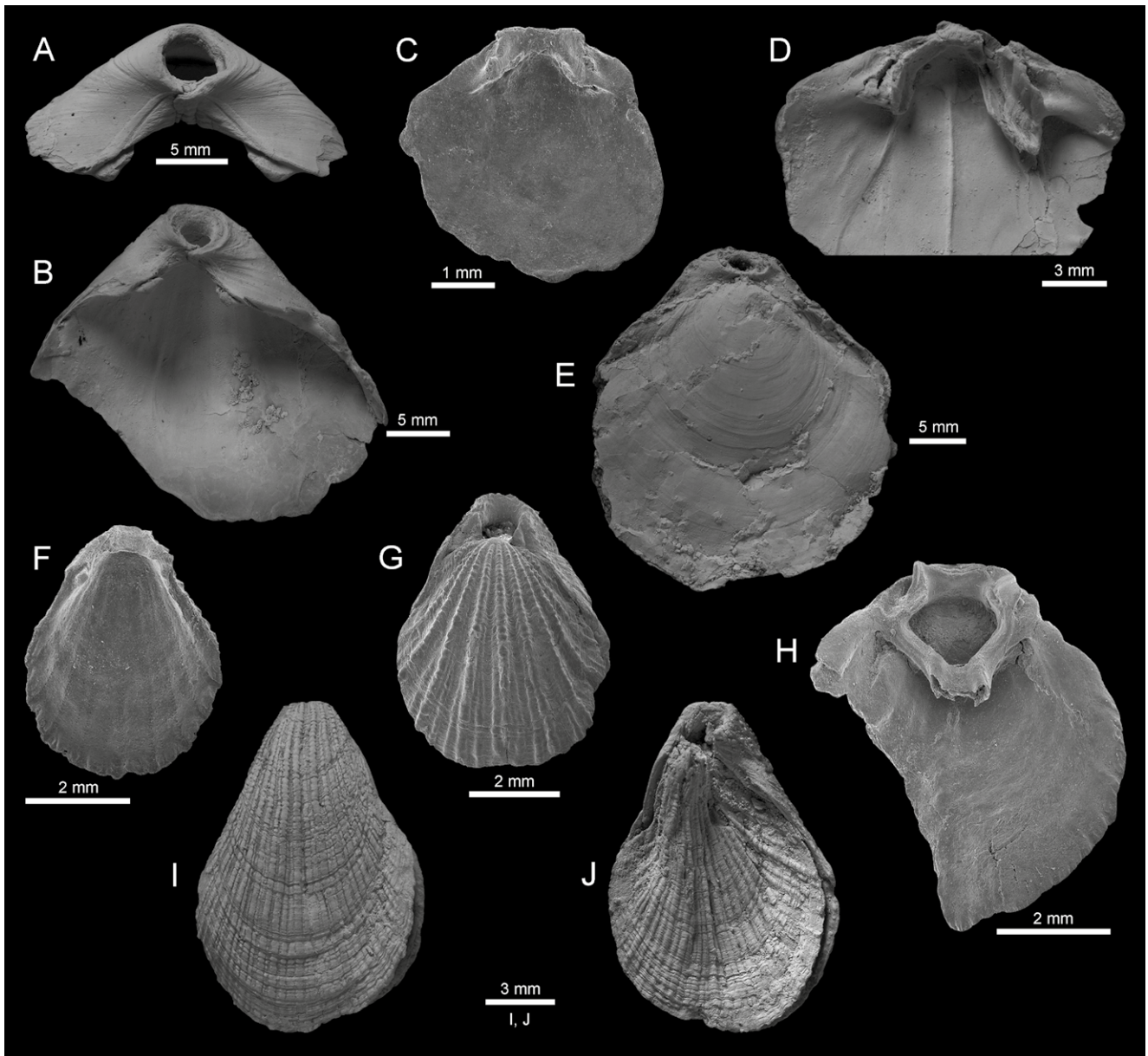


Fig. 2. Brachiopods from the Middle Miocene (Badenian), Carpathian Foredeep, Moravia, Czech Republic. **A–E.** *Terebratulula* cf. *styriaca* Dreger, 1889; A – posterior part of ventral valve, Borač, trench 2, sample 2b (UGV PAL Bp.03/B/01); B – inner view of ventral valve, Borač-Podolí, trench B, sample 4 (UGV PAL Bp.03/BP/01); C, D – inner views of dorsal valves, visible high inner socket ridges, prominent cardinal process and low median ridge, Borač, sample 6a (UGV PAL Bp.03/B/02–03); E – dorsal view of articulated specimen, Borač-Podolí, trench B, sample 4 (UGV PAL Bp.03/BP/02). **F–J.** *Terebratulina retusa* (Linnaeus, 1758), Borač; F – inner view of ventral valve, trench 2, sample 2a (UGV PAL Bp.03/B/04); G – dorsal view of young articulated specimen, sample 6a (UGV PAL Bp.03/B/05); H – inner view of dorsal valve, visible the loop forming a ring-like structure typical of the genus, trench 1, sample 1b (UGV PAL Bp.03/B/06); I, J – ventral and dorsal views of articulated specimen, trench 1, sample 1a (UGV PAL Bp.03/B/07). C and F–H SEM images.

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

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

Terebratulina retusa (Linnaeus, 1758)
 Fig. 2F–J

- 2013a *Terebratulina retusa* (Linnaeus) – Bitner *et al.*, pp. 584–586, fig. 2e–h (*cum syn.*).
- 2016 *Terebratulina retusa* (Linnaeus) – Álvarez, pp. 47–50, pls. 12E–DD, 13A–II, 14A–II, 15A–C (*cum syn.*).
- 2016 *Terebratulina retusa* (Linnaeus) – Dulai, pp. 87–89, figs 49–54 (*cum syn.*).
- 2018 *Terebratulina retusa* (Linné) – Emig, pp. 28–29, figs 5–6.

- 2019 *Terebratulina retusa* (Linnaeus) – Dulai, p. 129, pl. 1, figs 10–15.
- 2020 *Terebratulina retusa* (Linnaeus) – Hoffmann *et al.*, p. 14, fig. 10H–K.

Material: Seven articulated specimens, nine ventral valves and 20 dorsal valves from Borač, and one articulated specimen from Borač-Podolí. There are also many fragments not attributable to any valves; most specimens are damaged and/or crushed.

Remarks: This is the first record of *Terebratulina retusa* from the Miocene of Moravia. The shell is small to medium-sized (maximum observed length 14.1 mm), elongate oval to subpentagonal in outline, longer than wide. Externally the shell is covered with numerous, fine ribs. The cardinalia are with prominent inner socket ridges. The crural processes are united, forming a short ring-like loop, peculiar to the genus (Fig. 2H).

Occurrence: The oldest fossil record of *Terebratulina retusa* is from the Upper Oligocene of the Aquitaine Basin (Bitner *et al.*, 2013a). This species is well-known and common in the Neogene deposits of the Mediterranean province (Gaetani and Saccà, 1985; Taddei Ruggiero, 1985, 1994; Bitner and Moissette, 2003; Koskeridou, 2007; Dulai, 2016, 2019; Hoffmann *et al.*, 2020) but very rare in the Miocene of the Central Paratethys. So far, it has been recorded from Austria (Dreger, 1889), Hungary (Bitner and Dulai, 2004) and the Czech Republic (this study). The genus *Terebratulina* also was mentioned from the Miocene of Poland (Popiel-Barczyk and Barczyk, 1990). In modern

waters, *T. retusa* lives in the north-eastern North Atlantic and the Mediterranean Sea with a wide depth range from 9 to 3,614 m (Logan, 2007; Emig, 2018). However, its highest density is between 100 and 500 m (Curry, 1982).

Suborder Terebratellidina Muir-Wood, 1955

Superfamily Megathyridoidea Dall, 1870

Family Megathyrididae Dall, 1870

Genus *Megathiris* d'Orbigny, 1847

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

Megathiris detruncata (Gmelin, 1791)

Fig. 3A–F

- 1860 *Argiope decollata* Chemn. – Reuss, pp. 227–228.
- 1990 *Megathiris detruncata* (Gmelin) – Bitner, pp. 135–138, text-figs 3, 4; pl. 3, figs 1–8; pl. 6, figs 1–7 (*cum syn.*).
- 2016 *Megathiris detruncata* (Gmelin) – Álvarez, pp. 69–72, pls. 29A, C–AA, 30A–X, 31A–S, 32A–V, 33A–MM, 34B–I, K–U (*cum syn.*).
- 2018 *Megathiris detruncata* (Gmelin) – Emig, p. 30, figs 5–7.
- 2022 *Megathiris detruncata* (Gmelin) – Bitner and Müller, pp. 93–95, fig. 5A–H (*cum syn.*).
- 2023 *Megathiris detruncata* (Gmelin) – Bitner *et al.*, p. 40, fig. 2B–F.

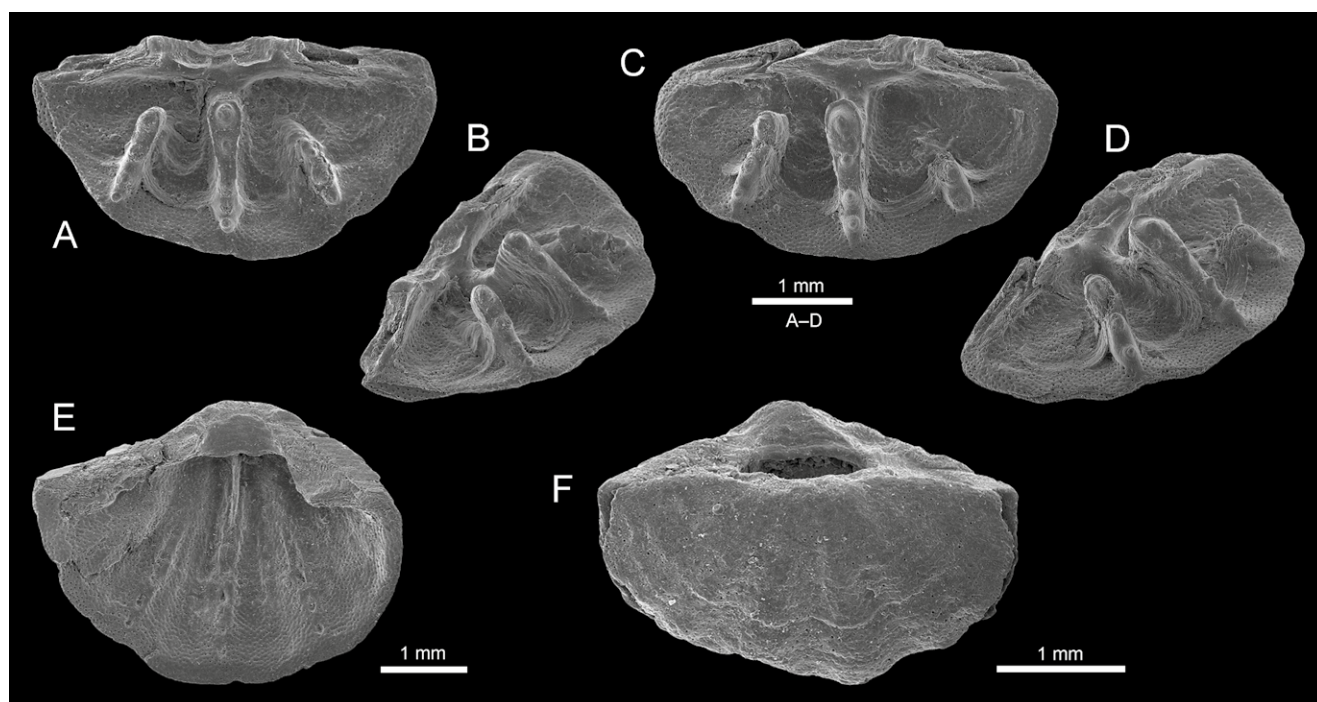


Fig. 3. *Megathiris detruncata* (Gmelin, 1791), Middle Miocene (Badenian), Borač, Moravia, Czech Republic. A–D. Inner and oblique (B, D) views of dorsal valves; A, B sample 6a (UGV PAL Bp.03/B/08); C, D trench 2, sample 2a (UGV PAL Bp.03/B/09). E. Inner view of ventral valve, trench 2, sample 2a (UGV PAL Bp.03/B/10). F. Dorsal view of articulated specimen, sample 6a (UGV PAL Bp.03/B/11). All SEM images.

Material: One articulated specimen, two ventral valves and four dorsal valves from Borač; two specimens are strongly damaged.

Remarks: *Megathiris detruncata* is very rare in the material studied, found only at the locality Borač. Its shell is very small (maximum observed length 3.4 mm), transversely elongate with a long, straight hinge line, ornamented by single, broad, rounded ribs. Internally, this species is characterised by the presence of three septa on the dorsal valve (Fig. 3A–D).

Occurrence: In the fossil record, this species is known since the Eocene (e.g., Bitner and Dieni, 2005; Bitner and Dulai, 2008, Dulai *et al.*, 2010; Dulai, 2011; Bitner and Müller, 2017). In the Miocene of the Central Paratethys, it belongs to one of the most common species (e.g., Bitner, 1990; Popiel-Barczyk and Barczyk, 1990; Bitner and Dulai, 2004; Dulai, 2007; Bitner and Schneider, 2009; Bitner and Motchurova-Dekova, 2016). In Moravia, although not common, it already was reported from five localities (Reuss, 1860; Zágoršek *et al.*, 2012; Bitner *et al.*, 2013b, 2023; Pavézková *et al.*, 2013). Extant *M. detruncata* lives in the Mediterranean Sea and the north-eastern Atlantic at the depth range 5–896 m (Logan, 2007; Emig, 2018).

Superfamily Kraussinoidea Dall, 1870

Family Kraussinidae Dall, 1870

Subfamily Megerliinae Hiller, MacKinnon and Nielsen, 2008

Genus *Megerlia* King, 1850

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

Megerlia truncata (Linnaeus, 1767)

Fig. 4A–F

- 1860 *Megerlea oblita* Micht. – Reuss, p. 227, pl. 6, fig. 2.
 1990 *Megerlia truncata* (Linnaeus) – Bitner, pp. 145–147, pl. 2, figs 6–9, pl. 7, figs 3–6, pl. 8, figs 1–7 (*cum syn.*).
 2016 *Megerlia truncata* (Linnaeus) – Álvarez, pp. 99–106, pls 59B–R, T–BB, 60A–E, G–O, R, T–AA, 61A, C–G, K–T, V–DD, 62A–AA, 63A–KK, 64A–V, 65A–Q, 66A–EE, 67A, C–BB, 68A–K (*cum syn.*).
 2018 *Megerlia truncata* (Linné) – Emig, pp. 32–33, fig. 5–9, pl. 2A–D.
 2022 *Megerlia truncata* (Linnaeus) – Bitner and Müller, pp. 101–102, fig. 11C–E (*cum syn.*).

Material: Seven ventral valves and 31 dorsal valves from Borač, and five articulated specimens, eight ventral valves and five dorsal valves from Borač-Podolí, and fragments; most specimens are damaged and fragmented.

Remarks: *Megerlia truncata* is the most common species in the material studied. The shell is small, hardly exceeding 10 mm, transversely oval to subcircular, ventribiconvex, with radial ornamentation of numerous, delicate ribs slightly nodulose. In larger specimens, the distinct growth lines can obscure the ribbed ornamentation (see Fig. 4F). The interior of both valves is radially tuberculate (Fig. 4A, C).

Occurrence: The oldest occurrence of *Megerlia truncata* is from the Lower Oligocene of Germany (Bitner and Müller, 2022). In the Neogene, this species is well known, both in the Mediterranean province and the Central Paratethys (e.g., Gaetani and Saccà, 1985; Taddei Ruggiero, 1985,

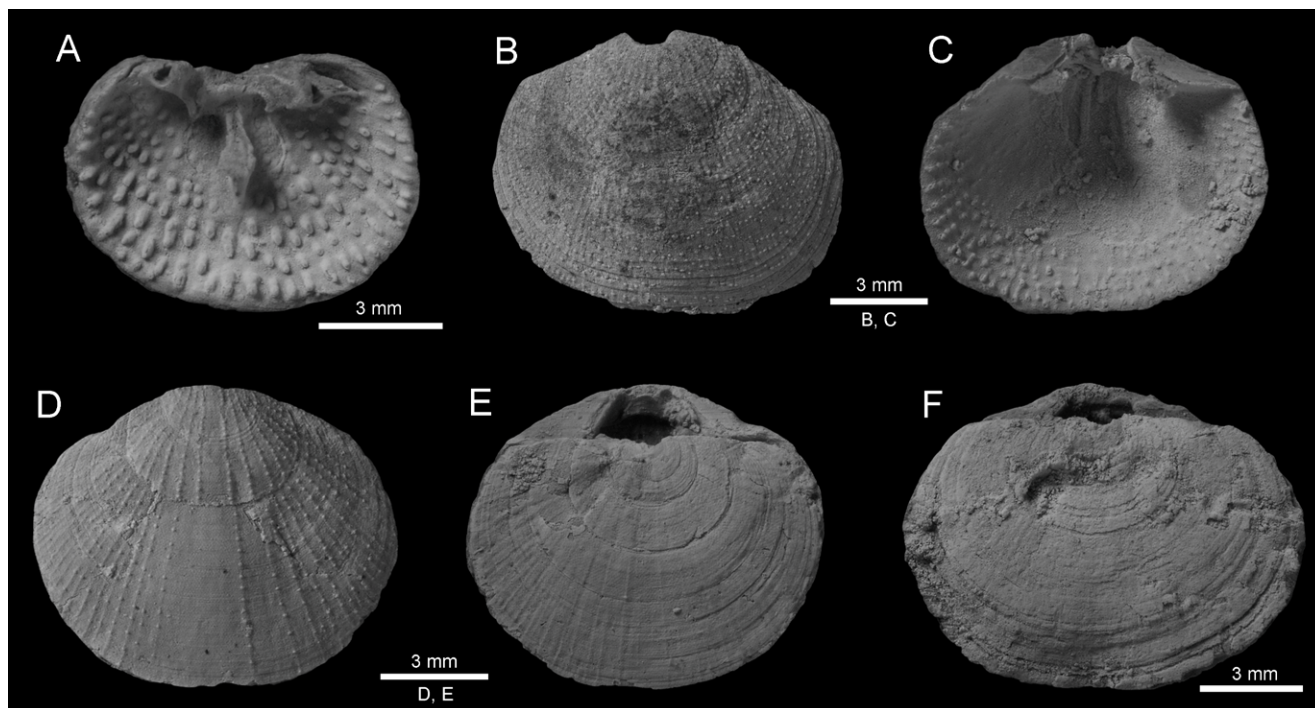


Fig. 4. *Megerlia truncata* (Linnaeus, 1767), Middle Miocene (Badenian), Moravia, Czech Republic. **A.** Inner view of dorsal valve, Borač, trench 2, sample 2a (UGV PAL Bp.03/B/12). **B.** **C.** Outer and inner views of ventral valve, Borač-Podolí, trench B, sample 4 (UGV PAL Bp.03/BP/03). **D.** **E.** Ventral and dorsal views of articulated specimen, Borač-Podolí, trench B, sample 4 (UGV PAL Bp.03/BP/04). **F.** Dorsal view of articulated specimen, Borač-Podolí, trench B, sample 2 (UGV PAL Bp.03/BP/05).

1994; Bitner, 1990; Bitner and Dulai, 2004; Dulai, 2010, 2019; Bitner and Motchurova-Dekova, 2016; Hoffmann *et al.*, 2020). However, in the Moravian Miocene it is very rare, so far recorded from only two localities, Rudoltice and Kralice (Reuss, 1860; Bitner *et al.*, 2013b). Today, *M. truncata* is widely distributed, with representatives in the Mediterranean Sea and eastern North Atlantic (Logan, 2007; Álvarez, 2016; Emig, 2018), as well as in the western Indian Ocean (Bitner and Logan, 2016). Its depth range is very wide from 8 to 1,970 m (Logan, 2007; Emig, 2018).

BORINGS ON BRACHIOPOD SHELLS

Some studied brachiopod shells bear the presence of boring traces. Four shells of *Megerlia truncata* from the locality Borač display small rounded, fully penetrating drillings, ranging from 0.2 to 1.0 mm in diameter (Fig. 5A–D). They are cylindrical and straight-sided, occurring on both dorsal (three) and ventral (one) valves. They can be assigned to the ichnospecies *Oichnus simplex* Bromley, 1981. The ichnogenus *Oichnus* Bromley, 1981 is regarded as a predichnion (trace of predation; Wisshak *et al.*, 2019). Although *Oichnus* is frequently associated with predatory gastropods of the families Muricidae and Naticidae, it may be also produced by other types of borers, such as nudibranchs or octopods

(Young, 1969; Bromley, 2004 and references therein). The oldest examples of the ichnogenus *Oichnus* come from the late Precambrian of China (Bengtson and Zhao, 1992; Hua *et al.*, 2003). Although it occurs throughout the Palaeozoic, *Oichnus* became more abundant during the Late Cretaceous with the appearance of two major boring families of gastropods, Muricidae and Naticidae (Bromley, 2004).

Three traces on fragments of *Terebratula* cf. *styriaca* shells from Borač are groups of circular pits ranging from 30 to 178 µm in diameter, covering roughly circular to oval-shaped areas, 2.2 to 3.5 mm in diameter (Fig. 5E, F). The diameter of the circular pits increases from the centre outwards and the orientation of the pits to the shell changes from a right angle to sharp angles of more peripheral penetrations. The inner side of the shell fragments bears signs of repair in the form of dome-shaped structures, ranging from 1.4 to 2.8 mm in diameter. The present authors attribute them to *Podichnus centrifugalis* Bromley and Surlyk, 1973. Ichnogenus *Podichnus* Bromley and Surlyk, 1973 is produced by pedunculate brachiopods of the orders Orthida, Rhynchonellida, and Terebratulida (Santos *et al.*, 2014). *Podichnus* is regarded as a fixichnion (attachment trace; Gibert *et al.*, 2004; Wisshak *et al.*, 2019), occurring in calcareous and phosphatic substrates (Bromley and Surlyk, 1973; Robinson and Lee, 2008; Mergl, 2021). The oldest *Podichnus* is known from the Lower Ordovician of

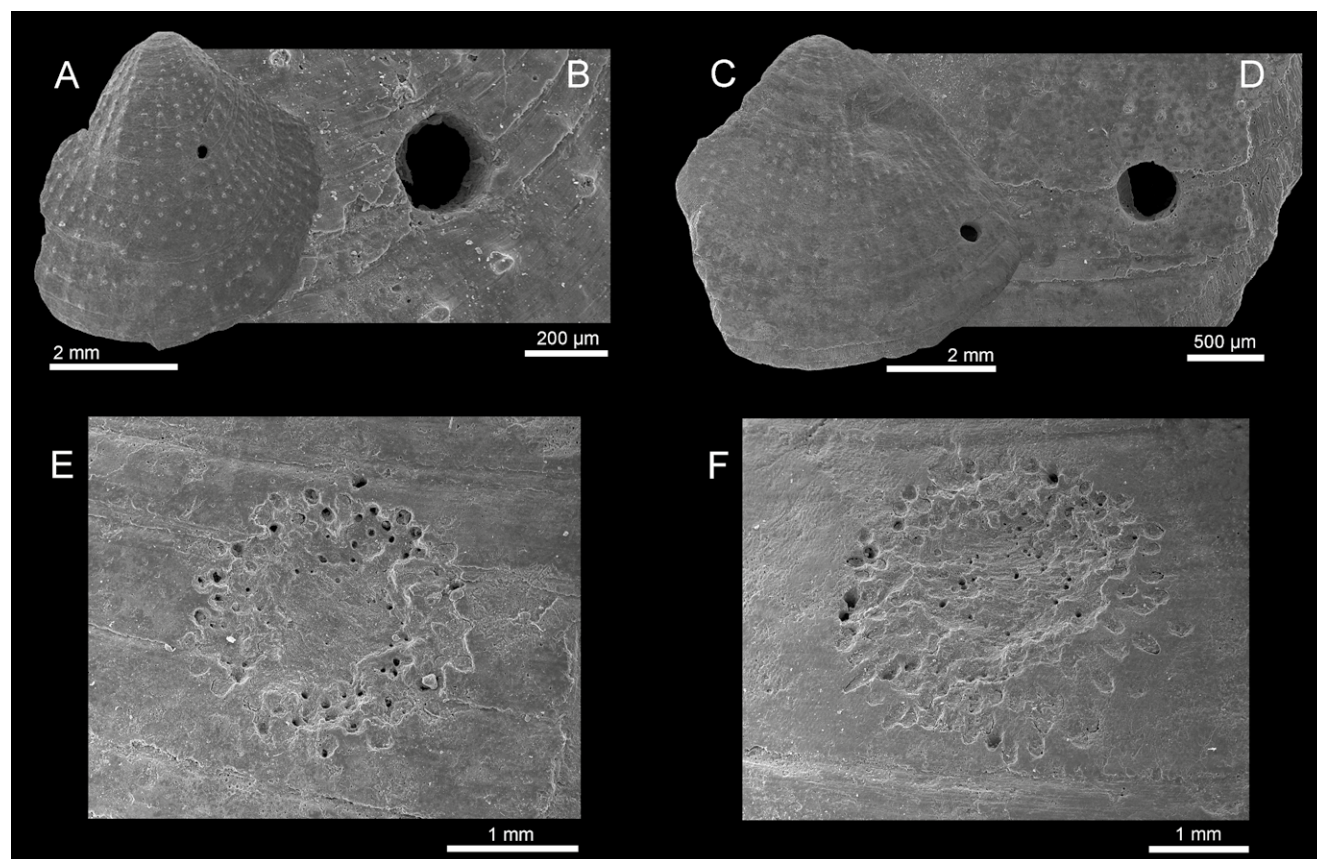


Fig. 5. Trace fossils, Middle Miocene (Badenian), Borač, Moravia, Czech Republic. **A–D.** Predatory boring *Oichnus simplex* Bromley, 1981 on *Megerlia truncata*, trench 1, sample 1b; **A, B** – outer view of ventral valve and enlargement (**B**), showing details of boring (UGV PAL Bp.03/B/13); **C, D** – outer view of dorsal valve and enlargement (**D**) of boring (UGV PAL Bp.03/B/14). **E, F.** Attachment scars *Podichnus centrifugalis* Bromley and Surlyk, 1973 on *Terebratula* cf. *styriaca* Dreger, 1889, sample 6b (UGV PAL Bp.03/B/15–16). All SEM images.

Argentina (Santos *et al.*, 2014) and it occurs throughout the rest of the Phanerozoic (see Bromley, 2004; Taddei Ruggiero and Bitner, 2008).

DISCUSSION

The Middle Miocene brachiopods, collected at the localities Borač and Borač-Podolí, Moravia, Czech Republic, are of low diversity, containing four species, belonging to four genera. In species composition, however, the assemblage studied shows a considerable difference in comparison with other Moravian assemblages. All species recognised herein belong to the order Terebratulida. The large-sized, short-looped terebratulides have one representative, *Terebratula* cf. *styriaca*. Although the genus *Terebratula* was already mentioned from three Moravian localities (Žágoršek *et al.*, 2012; Bitner *et al.*, 2013b, 2023), for the first time the material was sufficient enough, including adult individuals, for assignment, even tentatively, to the species level. The cancellothyridid species *Terebratulina retusa* is recorded for the first time from the Miocene of Moravia. This species is relatively common in the material from the Borač locality but very rare, represented by one specimen only, at Borač-Podolí. In the Central Paratethys, *T. retusa* is rare, reported so far from Austria and Hungary (Dreger, 1889; Bitner and Dulai, 2004). Interesting is the predominance of *Megerlia truncata* in the material under study. Although one of the most common species in the Central Paratethys, *M. truncata* is rare in the Moravian part; this is its third occurrence. So far, it has been recorded only from two localities, Rudoltice and Kralice nad Oslavou (Reuss, 1860; Bitner *et al.*, 2013b). The fourth species recognised in the investigated material is *Megathiris detruncata* (family Megathyrididae). This species is very rare in the material under study and was found only in the samples from the Borač locality. In Moravia, *M. detruncata* is relatively common, known from the localities Rudoltice, Přemyslovice, Kralice nad Oslavou, Židlochovice, and Oslavany (Reuss, 1860; Žágoršek *et al.*, 2012; Bitner *et al.*, 2013b, 2023; Pavězková *et al.*, 2013). Surprising is the absence of other members of the family Megathyrididae, such as *Argyrotheca cuneata* (Risso, 1826) or *Joania cordata* (Risso, 1826), the species most frequent in Moravia, found at eight and nine localities, respectively (Reuss, 1860; Žágoršek *et al.*, 2012; Bitner *et al.*, 2013b, c, 2023; Pavězková *et al.*, 2013; Hladilová *et al.*, 2014; Kopecká *et al.*, 2018). The rarity of megathyrid brachiopods might be caused by the absence of the shallow-water, cryptic habitats, preferred by this group.

Procházka (1892a) reported from Borač two brachiopod species, *Cistella squamosa* (Eichwald, 1830) and *Platidia anomioides* (Scacchi and Philippi in Philippi, 1844). The validity of the species *C. squamosa* is, however, uncertain. Its internal structures were neither described nor illustrated by Eichwald (1830, 1850, 1853). Nevertheless, he suggested a similarity to “*T. detruncata*”, implying the attribution of this species to the genus *Megathiris* (see also discussion in Popiel-Barczyk and Barczyk, 1990). Thus, one can assume that the brachiopod recorded by Procházka (1892a) belongs to *Megathiris detruncata*, the species recognised by the

authors in the material from Borač. The representatives of the species *P. anomioides* were not recognised in the material under study.

Although most living brachiopod species have very wide depth ranges (Logan, 2007) and are not considered to be good palaeobathymetric indicators, usually their optimum depth range is more restricted. Logan (1979) divided the Mediterranean brachiopods into two depth groups: shallow-water and eurybathic. Recent representatives of *Terebratulina retusa* and *Megerlia truncata* belong to a eurybathic group. In the Mediterranean Sea, *T. retusa* is most common between 200 to 300 m (Logan, 1979), while in the waters off Scotland this species is most commonly found at depths between 100 and 500 m (Curry, 1982). The species *M. truncata* is typical of bathyal zone. In turn, *Megathiris detruncata* belongs to a shallow-water group with its maximum occurrence from 60 to 160 m, preferring cryptic habitats (Logan, 1979). Little is known about palaeoecology of the extinct genus *Terebratula*. Recently, García-Ramos *et al.* (2020) investigated the palaeocommunity of *Terebratula* in the Águilas Basin, SE Spain, where this brachiopod forms shell beds in the Pliocene deposits. On the basis of the analysis of associated benthic and planktic foraminiferal and nanoplankton assemblages, they suggested that *Terebratula* thrived in relatively warm, well-oxygenated environments, at depths of 60–90 m on fine-grained sediments.

There are two types of borings observed on the studied brachiopod shells. The predichnion type is associated with muricid, naticid, and nudibranch gastropods as well as octopods (Young, 1969; Bromley, 1981, 2004). In the case under consideration, the most likely tracemakers are muricid and/or naticid gastropods, as they are common in the assemblage from Borač (Procházka, 1892a; Seitzl, 1981; Pekař and Lehotský, 2015; Turek, 2018). On the other hand, tracemakers such as nudibranchs and octopods cannot be totally ruled out, as their preservation potential is very low, owing to the lack of shells and their soft-body anatomy. The etching traces *Podichnus* are a fixichnion type of bioerosion, produced by the pedicles of brachiopods. These traces are restricted to the shells of *Terebratula* cf. *styriaca*, and most probably are of conspecific origin. This is further supported by the occurrence of signs of repair on the inner sides of the shells, which means that the brachiopod host was alive during the boring activity.

CONCLUSIONS

The Middle Miocene brachiopods, described herein from two Moravian localities, Borač and Borač-Podolí comprise four species, belonging to four genera within the order Terebratulida. Among them, three species, i.e., *Terebratula* cf. *styriaca*, *Terebratulina retusa* and *Megerlia truncata*, were found at both localities, while the fourth species, *Megathiris detruncata* is absent from the material, collected at Borač-Podolí. The species *T. cf. styriaca* and *T. retusa* are reported for the first time from the Moravian part of the Central Paratethys. The brachiopods bear two types of trace fossils, predatory borings (*Oichnus*) and etching scars, produced by a brachiopod pedicle (*Podichnus*).

Acknowledgements

We are grateful to Grażyna Dziewińska (Institute of Paleobiology, Warszawa) for taking the macrophotographs. The Uher family is acknowledged for the permission to dig on their private ground at Borač-Podolí as well as for their enthusiasm and supportive attitude towards our research. We thank the reviewers Miroslav Bubík (Czech Geological Survey, Czech Republic) and Alfréd Dulai (Hungarian Natural History Museum, Hungary) for providing helpful comments on the manuscript.

REFERENCES

- Álvarez, F., 2016. Recent brachiopods in the Ehlert Collection. In: Álvarez, F., Emig, C. C. & Tréguier, J. (eds), *Brachiopodes actuels: historique et révision de la collection D.-P. Ehlert (Laval); brachiopodes des côtes françaises métropolitaines. Bulletin de la Société des Sciences naturelles de l'Ouest de la France, hors-série*, 2016-1: 25–109.
- Barczyk, W. & Popiel-Barczyk, E., 1977. Brachiopods from the Korytnica basin (Middle Miocene; Holy Cross Mountains, Poland). *Acta Geologica Polonica*, 27: 157–167.
- Bengtson, S. & Zhao, Y., 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science*, 257(5068): 367–369.
- Bitner, M. A., 1990. Middle Miocene (Badenian) brachiopods from the Roztocze Hills, south-eastern Poland. *Acta Geologica Polonica*, 40: 129–157.
- Bitner, M. A. & Dieni, I., 2005. Late Eocene brachiopods from the Euganean Hills (NE Italy). *Eclogae Geologicae Helvetiae*, 98: 103–111.
- 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., 2008. Eocene micromorphic brachiopods from north-western Hungary. *Geologica Carpathica*, 59: 31–43.
- Bitner, M. A., Hladilová, Š. & Hrouzek, S., 2023. New record of Middle Miocene (Badenian) brachiopods from Moravia, Czech Republic. *Geological Research in Moravia and Silesia*, 30: 38–44.
- Bitner, M. A. & Logan, A., 2016. Recent Brachiopoda from the Mozambique-Madagascar area, western Indian Ocean. *Zoosystema*, 38: 5–41.
- Bitner, M. A., Lozouet, P. & Cahuzac, B., 2013a. Upper Oligocene (Chattian) brachiopod fauna from the Aquitaine Basin, south-western France and its paleoenvironmental implications. *Geodiversitas*, 35: 579–606.
- Bitner, M. A. & Moissette, P., 2003. Pliocene brachiopods from north-western Africa. *Geodiversitas*, 25: 463–479.
- Bitner, M. A. & Motchurova-Dekova, N., 2016. Middle Miocene (Badenian) brachiopods from Yasen, northwestern Bulgaria: taxonomic composition and biogeographical significance. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 279: 7–22.
- Bitner, M. A. & Müller, A., 2017. Late Eocene (Priabonian) brachiopod fauna from Dnipropetrovsk, eastern Ukraine. *Bulletin of Geosciences*, 92: 211–231.
- Bitner, M. A. & Müller, A., 2022. Early Oligocene brachiopods from the rocky shore deposits at Mammendorf, Central Germany. *Annales Societatis Geologorum Poloniae*, 92: 87–107.
- 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. & Schneider, S., 2009. The Upper Burdigalian (Ottangian) brachiopod fauna from the northern coast of the Upper Marine Molasse Sea in Bavaria, Southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 254: 117–133.
- Bitner, M. A., Zágorský, K. & Hladilová, Š., 2013b. Deep-water brachiopod assemblage from the Middle Miocene of Kralice nad Oslavou, Moravia, south-eastern Czech Republic. *Comptes Rendus Palevol*, 12: 81–89.
- Bitner, M. A., Zágorský, K. & Hladilová, Š., 2013c. Middle Miocene (Badenian) brachiopods from the Carpathian Foredeep in Moravia (Czech Republic) – rediscovered. In: Bąk, M., Kowal-Kasprzyk, J., Waśkowska, A. & Kaminiski, M. A. (eds), *14th Czech-Slovak-Polish Palaeontological Conference and 9th Micropaleontological Workshop, Abstracts Volume. Grzybowski Foundation Special Publication*, 19: 5–6.
- Bromley, R. G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispánica*, 16: 55–64.
- Bromley, R. G., 2004. A stratigraphy of marine bioerosion. In: McIlroy, D. (ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society, London, Special Publications*, 228: 455–479.
- Bromley, R. G. & Surlyk, F., 1973. Borings produced by brachiopod pedicles, fossil and Recent. *Lethaia*, 6: 349–365.
- Brunton, C. H. C., Cocks, L. R. M. & Dance, S. P., 1967. Brachiopods in the Linnaean collection. *Proceedings of the Linnean Society of London*, 178: 161–183.
- Brzobohatý, R., 1997. Paleobathymetry of the Lower Badenian (Middle Miocene, Carpathian Foredeep, South Moravia) based on otoliths. In: Hladilová, Š. (ed.), *Dynamika vztahů marinního a kontinentálního prostředí (projekt GA ČR 205/95/1211)*. Masarykova Univerzita, Brno, pp. 37–46. [In Czech, with English summary.]
- Brzobohatý, R. & Cicha, I., 1978. Faziostratotypus Borač, Karpatische Vortiefe in Mahren, Tschechoslowakei. In: Papp, A., Cicha, I., Seneš, J. & Steininger, F. (eds), *Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys, Bd. VI, M₄ Badenien (Moravien, Wielicien, Kosovien)*. VEDA, Bratislava, pp. 171–173.
- Brzobohatý, R. & Cicha, I., 1993. Carpathian Foredeep. In: Přichystal, A., Obstová, V. & Suk, M. (eds), *Geology of Moravia and Silesia*. Moravské Zemské Muzeum a Sekce geologických věd Přírodovědecké fakulty Masarykovy University, Brno, pp. 123–128 [In Czech, with English summary.]
- Buriánková, K., Čtyroká, J., Čurda, J., Gilíková, H., Gürtlerová, P., Hanžl, P., Kabátník, P., Kratochvílová, H., Manová, M., Maštera, L., Neudert, O., Otava, J., Petrová, P., Šalanský, K., Šrámek, J., Švecová, J. & Vít, J., 2001. *Výsvětlivky k základní geologické mapě ČR 1:25000, 24–321, Tišnov*. Česká geologická služba, Praha.
- Cicha, I. & Dornič, J., 1958. Neuer Fund der Kreideformation im westlichen Teil der Boskovicer Furche bei Lomnice, nördlich

- Tišnov. *Věstník Ústředního ústavu geologického*, 33: 443–444. [In Czech, with German summary.]
- Cicha, I. & Dornič, J., 1959. Die Entwicklung des Miozäns der Boskowitz Furche zwischen Tišnov und Ústí and Orlicí. *Sborník Ústředního ústavu geologického*, 26: 393–434. [In Czech, with German and Russian summaries.]
- Cicha, I., Paulík, J. & Tejkal, J., 1957. Bemerkungen zur Stratigraphie des Miozäns des Südwestlichen Teiles des ausserkarpatischen Beckens in Mähren. *Sborník Ústředního ústavu geologického*, 23: 307–364. [In Czech, with Russian and German summaries.]
- Curry, G. B., 1982. Ecology and population structure of the Recent brachiopod *Terebratulina* from Scotland. *Palaeontology*, 25: 227–246.
- Dall, W. H., 1870. A revision of the Terebratulidae and Lingulidae, with remarks on and descriptions of some recent forms. *American Journal of Conchology*, 6: 88–168.
- Dall, W. H., 1920. Annotated list of the Recent Brachiopoda in the collection of the United States National Museum, with description of thirty-three new forms. *Proceedings of the United States National Museum*, 57: 261–377.
- d'Orbigny, A., 1847. Considérations zoologiques et géologiques sur les Brachiopodes ou Palliobranches. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, 25: 266–269.
- 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., 2011. Late Eocene (Priabonian) micromorphic brachiopods from the Upper Austrian Molasse Zone. *Memoirs of the Association of Australasian Palaeontologists*, 41: 295–313.
- Dulai, A., 2016. Sporadic Pliocene brachiopods in Naturalis Biodiversity Center (Leiden, the Netherlands): Records from the Mediterranean, and the North Sea Basin. *Fragmenta Palaeontologica Hungarica*, 33: 65–98.
- Dulai, A., 2019. New data on the Late Miocene brachiopod fauna of Tetti Borelli (Piedmont, N Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 125: 125–145.
- Dulai, A., Hradecká, L., Konzalová, M., Less, G., Švábenická, L. & Lobitzer, H., 2010. An Early Eocene fauna and flora from “Rote Kirche” in Gschliefgraben near Gmunden, Upper Austria. *Abhandlungen der Geologischen Bundesanstalt*, 65: 181–201.
- Duméril, A.-M. C., 1805. *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Allais, Paris, 344 pp.
- Eichwald, E., 1830. *Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht*. Wilna, 256 pp.
- Eichwald, E., 1850. *Paleontologija Rossii*. Sankt Petersburg, 284 pp.
- Eichwald, E., 1853. *Lethaea Rossica ou Paléontologie de la Russie. Vol. 3, dernière période*. Stuttgart, 533 pp.
- Emig, C. C., 2018. Brachiopodes récoltés lors de campagnes (1976–2014) dans l'étage bathyal des côtes françaises méditerranéennes. Redéfinition des limites du système phytal dans le domaine marin benthique. *Carnets de Géologie*, CG2018_B01: 1–100.
- Gaetani, M. & Saccà, D., 1985. Brachiopodi neogenici e pleistocenici della provincia di Messina e della Calabria meridionale. *Geologica Romana*, 22: 1–43.
- García-Ramos, D. A., Čorić S., Joachimski, M. M. & Zuschin, M., 2020. The environmental factors limiting the distribution of shallow-water terebratulid brachiopods. *Paleobiology*, 46: 193–217.
- Gibert, J. M. de, Domènech, R. & Martinell, J., 2004. An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class, fixichnia. *Lethaia*, 37: 429–437.
- Gmelin, J. F., 1791. Vermes. In: Gmelin, J. F. (ed.), *Caroli a Linnaei Systema Naturae per Regna Tria Naturae, Ed. 13. Tome 1(6)*. G. E. Beer, Lipsiae [Leipzig], pp. 3021–3910.
- Gray, J. E., 1840. *Synopsis of the Contents of the British Museum. 42nd Edition*. G. Woodfall and Son, London, 370 pp.
- Hiller, N., MacKinnon, D. I. & Nielsen, S. N., 2008. A review of the systematic, biogeography and evolutionary relationships of Recent and fossil brachiopods of the Superfamily Kraussinoidea Dall, with descriptions of two new fossil species from New Zealand and Chile. In: Cusack, M. & Harper, D. A. T. (eds), *Brachiopod Research into the Third Millennium. Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 98: 379–390.
- Hladilová, S., Nehyba, S., Zágoršek, K., Tomanová Petrová, P., Bitner, M. A. & Demény, A., 2014. Early Badenian transgression on the outer flank of Western Carpathian Foredeep, Hlučov area, Czech Republic. *Annales Societatis Geologorum Poloniae*, 84: 259–279.
- Hoffmann, R., Bitner, M. A., Pisera, A., Jager, M. & Schneider, S., 2020. Late Miocene biota from the Abad Member of the Carboneras-Níjar Basin (Spain, Andalusia): A bathyal fossil assemblage pre-dating the Messinian salinity crisis. *Geobios*, 59: 1–28.
- Hohenegger, J., Čorić, S. & Wagreich, M., 2014. Timing of the regional Badenian Stage (Middle Miocene, Central Paratethys). *Geologica Carpathica*, 65: 55–66.
- Hua, H., Pratt, B. R. & Zhang, L. Y., 2003. Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *Palaos*, 18: 454–459.
- Ivanov, M., 2003. History of palaeontological investigations in Permo-Carboniferous deposits of the Boskovice Graben (Moravia). *Acta Musei Moraviae, Scientiae Geologicae*, 88: 3–112. [In Czech, with English summary.]
- Jaroš, J., 1963. Lithostratigraphie des Permokarbons von Boskovická brázda. *Věstník Ústředního ústavu geologického*, 38: 115–118. [In Czech, with German summary.]
- Jaroš, J. & Misař, Z., 1976. Nomenclature of the tectonic lithostratigraphic units in the Moravian Svratka Dome (Czechoslovakia). *Věstník Ústředního ústavu geologického*, 51: 113–122.
- Kettner, R., 1959. Bemerkung zum angeblichen Fund der Kreide bei Lomnice nördlich Tišnov. *Věstník Ústředního ústavu geologického*, 34: 382–383. [In Czech, with German summary.]

- King, W., 1850. A monograph of the Permian Fossils of England. *Palaeontographical Society Monograph*, 3: 1–258.
- Klepříková, L., 2016. Anthozoa from Badenian of south Moravia. Unpublished MSc. Thesis, Masaryk University, Brno, 61 pp. [In Czech, with English summary.]
- Klepříková, L., 2018. Scleractinia from a new locality Borač-Podolí (southern part of the Carpathian Foredeep, Czech Republic). *Acta Musei Moraviae, Scientiae Geologicae*, 103: 59–66. [In Czech, with English summary.]
- Klepříková, L. & Doláková, N., 2016. Lower Badenian solitary corals suborder Caryophyllida (order Scleractinia) from locality Borač (southern part of the Carpathian Foredeep, Czech Republic). *Acta Musei Moraviae, Scientiae Geologicae*, 101: 75–86. [In Czech, with English summary.]
- Kopecká, J., Holcová, K., Nehyba, S., Hladilová, Š., Brzobohatý, R. & Bitner, M. A., 2018. The earliest Badenian *Planostegina* bloom deposit: reflection of an unusual environment in the westernmost Carpathian Foredeep (Czech Republic). *Geological Quarterly*, 62: 18–37.
- Koskeridou, E., 2007. Pliocene brachiopods from Rhodes Island (Cape Vagia section). *Bulletin of the Geological Society of Greece*, 40: 121–133.
- Kováč, M., 2000. *Geodynamický, paleogeografický a štruktúrny vývoj karpatsko-panónskeho regiónu v miocéne: nový pohľad na neogénne panvy Slovenska*. Veda, Bratislava, 176 pp. [In Slovak.]
- Krystek, I. & Tejkal, J., 1968. Zur Lithologie und Stratigraphie des Miozäns im SW Teile der Karpatischen Vortiefe in Mähren. *Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis, Geologia*, 9, 7: 1–31. [In Czech, with German summary.]
- Lee, D. E. & Brunton, C. H. C., 1998. *Terebratula* Müller, 1776 (Brachiopoda): proposed designation of *Anomia terebratula* Linnaeus, 1758 as the type-species. *Bulletin of Zoological Nomenclature*, 55: 220–223.
- Linnaeus, C., 1758. *Systema Naturæ per Regna tria Naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th edition. Holmiae, Stockholm, 823 pp.
- Linnaeus, C., 1767. *Systema Naturæ per Regna tria Naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 12th edition. Holmiae, Stockholm, pp. 533–1327.
- Logan, A., 1979. The Recent Brachiopoda of the Mediterranean Sea. *Bulletin de l'Institut Océanographique Monaco*, 72: 1–112.
- Logan, A., 2007. Geographic distribution of extant articulated brachiopods. In: Selden, P. A. (ed.), *Treatise on Invertebrate Paleontology. Part H. Brachiopoda Revised. Vol. 6*. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 3082–3115.
- Mergl, M., 2021. First record of *Podichnus* in byronid shell from the Lower Devonian (Pragian) of the Prague Basin, Czechia. *Folia Musei rerum naturalium Bohemiae occidentalis. Geologica et Paleobiologica*, 55: 39–44.
- Misař, Z., Dudek, A., Havlena, V. & Weiss, J., 1983. *Geologie ČSSR I, Český masív*. Státní pedagogické nakladatelství, Praha, 333 pp. [In Czech.]
- Muir-Wood, H., 1955. *A History of the Classification of the Phylum Brachiopoda*. British Museum (Natural History), London, 124 pp.
- Müller, O. F., 1776. *Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium*. Typis Hallagerii, Havniae, Copenhagen, 282 pp. [In Latin.]
- Nehyba, S. & Šíkula, J., 2007. Depositional architecture, sequence stratigraphy and geodynamic development of the Carpathian Foredeep (Czech Republic). *Geologica Carpathica*, 8: 53–69.
- Oszczypko, N., 1998. The Western Carpathian Foredeep – development of the foreland basin in front of the accretionary wedge and its burial history (Poland). *Geologica Carpathica*, 49: 415–431.
- Papp, A., Cicha, I., Seneš, J. & Steininger, F., 1978. *Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys, Bd. VI, M₄ Badenien (Moravien, Wielicien, Kosovien)*. VEDA, Bratislava, 600 pp.
- Pavězková, J., Hladilová, Š. & Bitner, M. A., 2013. Miocene brachiopods from the Židlochovice locality, Czech Republic. *Geological Research in Moravia and Silesia*, 20: 56–59.
- Pekař, P. & Lehotský, T., 2015. Fossil Gastropoda from the Borač-locality – systematic analysis of the collection from Museum of Natural History in Olomouc. *Přírodovědné studie Muzea Prostějovska*, 17: 23–62. [In Czech, with English summary.]
- Pešek, J., Holub, V., Jaroš, J., Malý, L., Martínek, K., Prouza, V., Spudil, J. & Tásler, R., 2001. *Geologie a ložiska svrchnopaleozoických limnických pánví České republiky*. Český geologický ústav, Praha, 243 pp. [In Czech.]
- Philippi, R. A., 1844. *Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit*. Vol. 2. E. Anton, Halle, 303 pp.
- 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.
- Procházka, V. J., 1892a. Vorläufiger Bericht über die stratigraphischen und faunistischen Verhältnisse des westlichen Miocaengebietes von Mähren. *Věstník Královské české společnosti nauk, třída mathematicko-přírodovědecká, Praha*, pp. 326–368. [In Czech, with German summary.]
- Procházka, V. J., 1892b. Das Miocæn von Mähren. I. Beitrag zur Kenntniss der Fauna der marinen Tegel und Mergel des nordwestlichen und mittleren Gebietes von Mähren. *Věstník Královské české společnosti nauk, třída mathematicko-přírodovědecká, Praha*, pp. 458–475. [In Czech, with German summary.]
- Procházka, V. J., 1893. Miocén kralický u Náměště na Moravě. *Věstník Královské české společnosti nauk, třída mathematicko-přírodovědná*, art. 16: 1–84. [In Czech.]
- Procházka, V. J., 1899. Miocén moravský. Druhý příspěvek ku poznání rázu zvířeny mořských jílů a slínů severozápado- a středomoravské oblasti. *Věstník Královské české společnosti nauk, třída mathematicko-přírodovědecká*, art. 29: 1–45. [In Czech.]
- Reuss, A. E., 1860. Die marinen Tertiärschichten Böhmens und ihre Versteinerungen. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 39: 207–285.
- Říha, J., 1983. Sponge spicules of the Karpatian and Lower Badenian of the Carpathian Foredeep in Moravia, Czechoslovakia. *Knihovnička Zemního plynu a nafty*, 4: 171–194.

- Risso, A., 1826. *Histoire naturelle des principales productions de l'Europe méridionale, et particulièrement de celles des environs de Nice et des Alpes maritimes. IV.* F.-G. Levrault, Paris, 439 pp.
- Robinson, J. H. & Lee, D. E., 2008. Brachiopod pedicle traces: recognition of three separate types of trace and redefinition of *Podichnus centrifugalis* Bromley & Surlyk, 1973. *Fossils and Strata*, 54: 219–225.
- Rzehak, A., 1923. *Moravské třetihory*. Knihovnička Státního geologického ústavu ČR, Praha, 39 pp. [In Czech.]
- Santos, A., Mayoral, E., Villas, E., Herrera, Z. & Ortega, G., 2014. First record of *Podichnus* in orthide brachiopods from the Lower Ordovician (Tremadocian) of NW Argentina and its relation to the early use of an ethological strategy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 399: 67–77.
- Seitl, L., 1981. Molluskenfauna der Lokalität Borač. *Acta Musei Moraviae, Scientiae Naturales*, 66: 33–50. [In Czech, with German summary.]
- Šamánek, J., 2017. Bioerosive processes of organisms from locality Borač-Podolí (Badenian, Carpathian Foredeep). Unpublished MSc. Thesis, Masaryk University, Brno, 77 pp. [In Czech, with English summary.]
- Šamánek, J., Mikuláš, R., Doláková, N. & Hladilová, Š., 2018. Borings of the ichnogenus *Gastrochaenolites* as a living space of bivalves from the locality Borač-Podolí (Carpathian Foredeep, Czech Republic). *Geological Research in Moravia and Silesia*, 25: 49–57. [In Czech, with English abstract.]
- Taddei Ruggiero, E., 1985. Paleoeccologia e biostratigrafia delle calcareniti a brachiopodi di Castro (Lecce). *Bollettino della Società dei Naturalisti in Napoli*, 92: 347–413.
- Taddei Ruggiero, E., 1994. Neogene Salento brachiopod palaeocommunities. *Bollettino della Società Paleontologica Italiana*, 33: 197–213.
- Taddei Ruggiero, E. & Bitner, M. A., 2008. Bioerosion on brachiopod shells – a Cenozoic perspective. In: Cusack, M. & Harper, D. A. T. (eds), *Brachiopod Research into the Third Millennium. Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 98: 369–378.
- Thomson, J. A., 1926. A revision of the subfamilies of the Terebratulidae (Brachiopoda). *Annals and Magazine of Natural History, Series 9*, 18: 523–530.
- Turek, T., 2018. *Molluscs from the Miocene locality Borač-Podolí*. Unpublished MSc. Thesis, Masaryk University, Brno, 176 pp. [In Czech, with English summary.]
- Waagen, W. H., 1883. Salt Range fossils. I. *Productus* Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 13*, 4: 391–546.
- Weyer, D., 1974. *Tortoflabellum* Squires 1958 (Scleractinia) im Miocän von Borač (Tertiär der Westkarpaten, ČSSR). *Zeitschrift für Geologische Wissenschaften*, 4: 507–513.
- Williams, A., Carlson, S. J., Brunton, C. H. C., Holmer, L. E. & Popov, L., 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London*, B 351: 1171–1193.
- Wisshak, M., Knaust, D. & Bertling, M., 2019. Bioerosion ichnotaxa: review and annotated list. *Facies*, 65(2): art. no. 24. <https://doi.org/10.1007/s10347-019-0561-8>
- Young, D. K., 1969. *Okadaia elegans*, a tube-boring nudibranch mollusc from the central and west Pacific. *American Zoologist*, 9: 903–907.
- Zágoršek, K., Nehyba, S., Tomanová-Petrová, P., Hladilová, Š., Bitner, M. A., Doláková, N., Hrabovský, J. & Jašková, V., 2012. Local catastrophe caused by tephra input near Přemyslovice (Moravia, Czech Republic) during the mid-Miocene. *Geological Quarterly*, 56: 269–284.