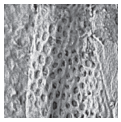
Lingulate brachiopods from the Kotýs Limestone (Lochkov Formation, Lochkovian) from Branžovy ridge near Bubovice (Barrandian area, Czech Republic)

Michal Mergl



Lingulate brachiopods are described from an outcrop of the Kotýs Limestone (Lochkovian) at Branžovy ridge near Bubovice in Central Bohemia (Czech Republic). Twelve species are systematically described. Two new genera and species, *Rarepora tumulamen* gen. et sp. nov. (Family Obolidae) and *Branzodiscus porosus* gen. et sp. nov. (Family Discinidae) are erected, and one new species *Paterula postsilurica* sp. nov. is described. Four formerly described species (*Barrandeoglossa perneri*, *Lochkothele intermedia*, *Opsiconidion holynensis* and *Orbiculoidea magnifica*) are recognised and six other species are left in the open nomenclature being more or less tentatively affiliated with the genera *Kosoidea*, *Praethele* and *Schizotreta*. The lingulate brachiopods come from beds that yield abundant, diverse and well silicified rhynchonelliform brachiopods, rugose and tabulate corals, and diverse epibiontic invertebrates (craniids, bryozoans, graptolites, microcrinoids, byroniids). • Key words: Lochkovian, Devonian, Kotýs Limestone, organophosphatic brachiopods, Barrandian.

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Lingulate brachiopods were an important component of benthic invertebrate associations throughout the Cambrian and Ordovician Periods. They have been monographed by many authors (*e.g*. Walcott 1912; Cooper 1956; Goryansky 1969; Biernat 1973; Holmer 1989, Holmer *et al*. 2001; Popov *et al.* 1989; Popov & Holmer 1994; Sutton *et al.* 1999, 2000; Mergl 2002; Robson & Pratt 2007). Their diversity declined dramatically during the end-Ordovician glaciation event (Wright & McClean 1991; Holmer & Popov 1996; Bassett *et al*. 1999, 2002; Curry & Bruton 2007), so it is not surprising that modern taxonomic studies on their Silurian and Devonian descendants are scarce (Biernat 1983; Bassett 1986; Cocks & Popov 2009; Valentine 2006a, b; Valentine *et al.* 2003, 2006).

Over the last two decades, several taxonomic works focused on lingulate brachiopods from Silurian and Devonian strata in the Prague Basin, Czech Republic have been published (Wenlock: Mergl 2024; Ludlow: Mergl *et al*. 2018; Pragian: Mergl & Šmídtová 2023; Emsian: Mergl & Ferrová 2009; Mergl & Jiménez-Sánchez 2015; Eifelian: Mergl 2008, 2019; Mergl & Vodrážková 2012). These studies have greatly expanded upon a pioneer survey (Mergl 2001) and a few earlier short studies (Mergl 1982, 1996, 1999a, b, 2003a; Havlíček & Mergl 1988). All these studies follow in the footsteps of the monograph published by Joachim Barrande (1879) who named and illustrated many lingulate brachiopod species but without the formal systematic descriptions or adequate stratigraphic and locality data. The current study contributes to elucidation of the evolutionary history of lingulates during the late Lochkovian.

Geological setting

The Lochkov Formation is the oldest unit of the Devonian succession in the Prague Basin in Central Bohemia (Fig. 1A, B). The Lochkovian to Eifelian succession of the basin is characterised by shallow water biodetrital mostly crinoidal limestones substituted basinwards by neritic tentaculitic limestone (Chlupáč *in* Chlupáč *et al.* 1998). The reef and mud-mound bioskeletal accumulations of Pragian, Emsian and Eifelian ages are predominantly located along the north-western limb of the basin. Deeper pelagic lithofacies of the same age are situated more south-eastward (Chlupáč *in* Chlupáč *et al.* 1998). These are represented mostly by dark coloured calcisiltites (Daleje Shale), occasionally with radiolarite

beds (Kačák Beds). The overlying siliciclastic Givetian succession (Srbsko Formation) indicates the beginning of the Variscan Orogeny (Chlupáč *in* Chlupáč *et al.* 1998, Vacek & Žák 2019).

Shallow-water biodetrital and peri-reefal accumulations of Lochkovian age, with abundant crinoid limestones of the Kotýs Limestone are exposed along the north-western limb of the Prague Basin (Chlupáč *in* Chlupáč *et al.* 1998). This unit is characterised by grey bioclastic well-bedded limestones with common chert nodules in the middle part of the sequence. The limestone is rich in brachiopods and crinoidal detritus, with the fauna referred to the *Coniproetus–Decoroscutellum* Trilobite Assemblage (Chlupáč 1983). This SW–NE strip of the shallow-water Kotýs Limestone subsides towards the south-east, where the Radotín Limestone represents the Lochkovian Stage. The Radotín Limestone is distinguished by dark-grey to black bituminous platy limestone beds rhythmically alternating with black calcareous shales. Its fauna contains many planktonic and nektonic organisms including graptolites and dacryoconarids. The comprehensive survey of the Lochkov Formation has been given by Chlupáč *in* Chlupáč *et al.* (1998). Slavík & Hladil (2020) presented a detail survey of bioevents and conodont zonation of the Lochkov Formation, that synthetised and updated former conodont data (Slavík 2011, Slavík *et al.* 2012). Unlike the previously published data on the age of the fossiliferous beds at the Branžovy locality (Mergl 2003b, 2021, 2022; Mergl & Kraft 2023), the current conodont data (L. Slavík, pers. comm.) confirm the Late Lochkovian age of the beds hosting the lingulate brachiopods described herein.

All organophosphatic brachiopods described come from the Branžovy locality situated at the northern limb of the Devonian infill of the basin, between the villages Bubovice and Loděnice (Fig. 1A, B). The studied short survey trench is located at the northern side of a small abandoned quarry in the Kotýs Limestone (Fig. 1C). Grey platy limestone beds exposed in the trench are steeply dipping toward the south (Fig. 1D). Limestone beds

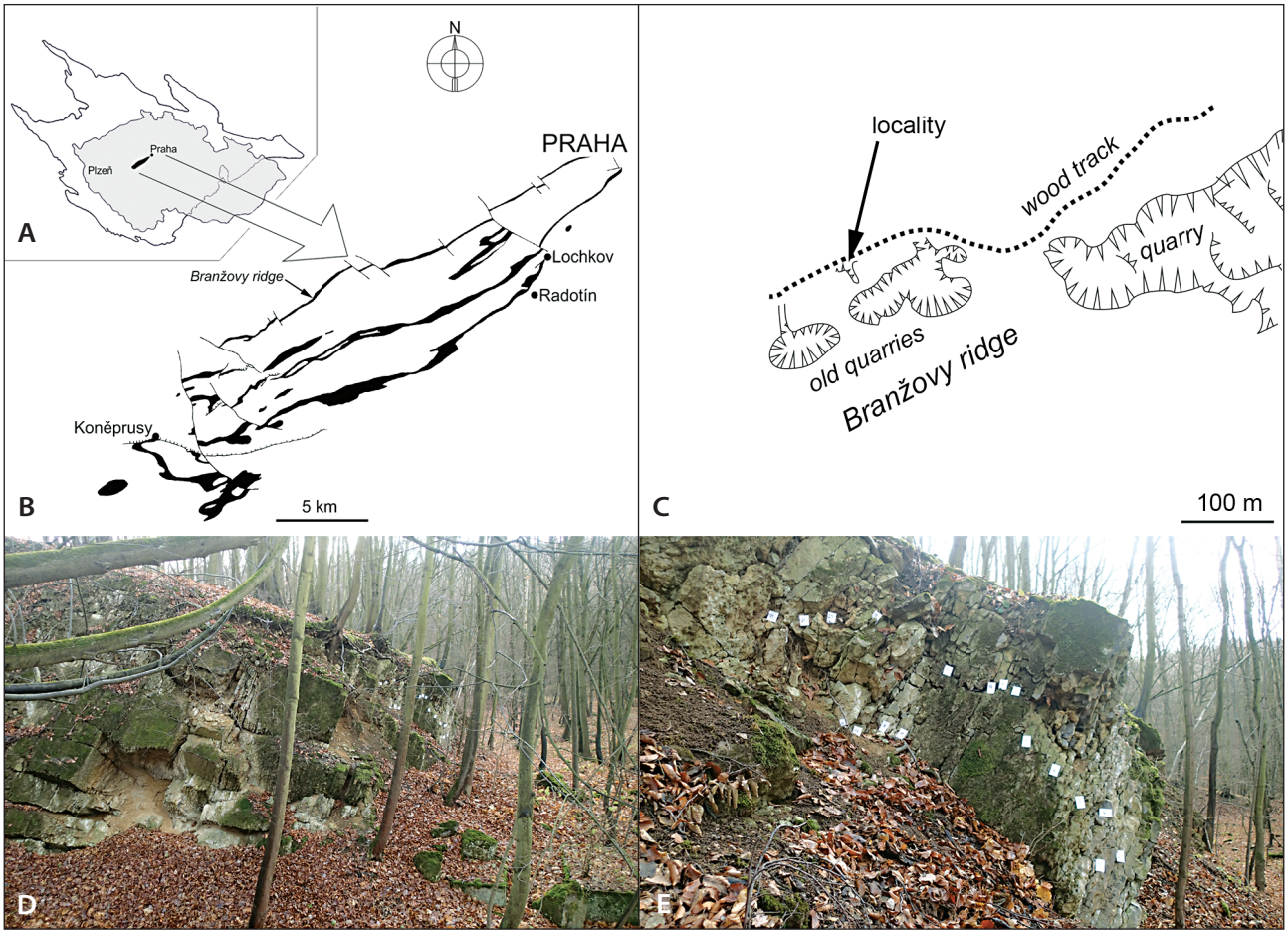


Figure 1. Geographical setting of the Barrandian area (A) and distribution of the Lochkov Formation in the Prague Basin with marked locality (B), location of quarries at Branžovy and the sampled section in old trench (indicated by arrow) (C), the richly fossiliferous part of the trench (D) and the lowest exposed limestone beds (E) from which lingulate brachiopods are derived.

contain chert nodules and locally dense accumulations of fossils, mainly brachiopod shells. The lowest exposed beds (~5 metres) yielded the most diverse association with more than forty rhynchonelliform brachiopod species, rugose corals, favositids, pisocrinids, platyceratid gastropods and sclerobionts (see Mergl 2003b, 2021, 2022). In a decreasing abundance, the brachiopods belonging to genera *Navispira*, *Skenidioides*, *Plectodonta*, *Atrypina*, *Dalejina*, *Parmorthina*, *Isorthis*, *Resserella*, *Iridistrophia*, *Lissatrypa*, *Gypidula* and strophomenid brachiopods are distinctive. The middle part of the section (~8 metres) contains abundant *Spinatrypa* and *Spinatrypina*, associated mostly with *Dalejina* and *Skenidioides*. The highest limestone beds (~3 metres) are poor in brachiopods carrying mainly smooth-shelled shells of *Lissatrypa*. Conodonts indicate the Late Lochkovian (*pandora*–beta–*gilberi* Zone; L. Slavík, pers. comm. in January 2024).

Material and methods

All specimens have been retrieved exclusively by the dissolution of ~20 kg of limestone in 15% acetic acid for 5 to 7 days. All samples were cleaned but unsieved under the weak water flow. The residuum was dried and stored in the Petri dishes for subsequent hand-picking of the fossils. About three hundred complete shells or larger shell pieces were hand-picked from dried residuum with use of the binocular lens. The shells are sometimes weakly corroded or covered by a thin limonitic coating. In general, finest details may be observed in the majority of fragments. The well-preserved byronid tubes and their attachment discs, conodont elements, fragments of phyllocarid cuticles, and phosphatised internal moulds of bivalves, gastropods and minute brachiopods occur together with the phosphatic shells of lingulate brachiopods and the silicified shells of rhynchonelliformean brachiopods. The association of phosphatic microfossils is rather similar to other Silurian and Devonian acid-treated microfossil associations from the Prague Basin (Mergl 2008, 2019; Mergl & Ferrová 2009; Mergl & Jiménez-Sánchez 2015; Mergl & Šmídtová 2023). In decreasing abundance, from 255 determined valves or shell fragments, 147 valves (= 57.6%) belong to *Opsiconidion holynensis* (Mergl, 2001), 25 valves (= 9.8%) belong to *Branzodiscus porosus* gen. et sp. nov. and 22 valves (= 8.5%) belong to *Praethele* sp. All other species are represented by 3 to 18 specimens, and about 50 fragments have been undetermined.

Selected phosphatic shells were mounted on SEM stubs, covered by gold and examined using a SEM JSM-6300. One dorsal valve with weak coating of ammonium chloride was photographed under a binocular lens OLYMPUS SZX 7 with use of the Deep Focus 3.1 software.

Terminology. – The terminology used to describe the growth stages of brachiopod shells generally follows Williams (2003). In an acrotretid shell morphology, the author follows Holmer *et al.* (2020) with the use of the terms metamorphic and post-metamorphic shells.

Abbreviations. – DvL – length of the dorsal valve; DvW – width of the dorsal valve.

Repository. – All specimens including the types are housed in the palaeontological collections of the Centre of Biology, Earth and Environmental Sciences in the Faculty of Education of the University of West Bohemia in Plzeň (PCZCU).

Systematic palaeontology

Subphylum Linguliformea Williams *et al.*, 1996
Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Obolidae King, 1846
Subfamily Glossellinae Cooper, 1956

Genus *Barrandeoglossa* Mergl, 2001

Type species. – *Lingula fissurata* Barrande, 1879, designated by Mergl (2001) from the Motol Formation (Wenlock, Silurian) of the Prague Basin, Czech Republic.

***Barrandeoglossa perneri* Mergl, 2001**
Figure 2A, B, F, H

2001 *Barrandeoglossa perneri* sp. n.; Mergl, p. 16, pl. 8, figs 1–7.

Material. – Four incomplete valves (illustrated specimens PCZCU 2795 to PCZCU 2797).

Description. – See Mergl (2001).

Remarks. – The shells are similarly incomplete as the type material of Mergl (2001) but the characteristic external macroornament of regularly spaced concentric fila separated by smooth bands is present in the newly sampled specimens (Fig. 2B, F).

Occurrence. – Lochkov Formation, lower part of the Kotýs Limestone; locality Praha-Řeporyje, Černý Quarry (Mergl 2001) (abundant); the same formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (rare).

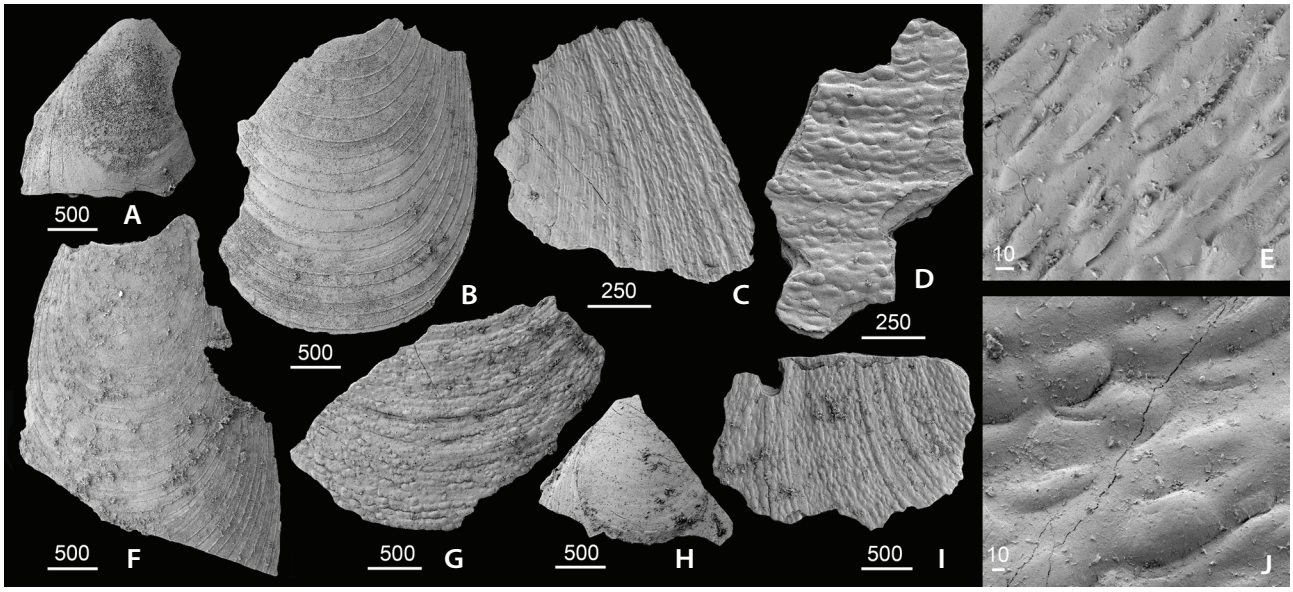


Figure 2. A, B, F, H – *Barrandeoglossa perneri* Mergl, 2001, Kotýs Limestone, Lochkov Formation; Branžovy locality. A – incomplete ventral valve, exterior, PCZCU 2795. B – incomplete valve, exterior showing characteristic macroornament, PCZCU 2796. F – incomplete ventral valve, exterior, PCZCU 2797. H – fragment of ventral valve, exterior, PCZCU 2829. • C–E, G, I, J – Gen. et sp. indet., Kotýs Limestone, Lochkov Formation; Branžovy locality. C, E – fragment of posterolateral part of shell showing a fine macroornament and its detail, PCZCU 2798. D, J – shell fragment showing coarse macroornament, and its detail, PCZCU 2799. G – shell fragment of an axial part of valve, PCZCU 2801. H – shell fragment showing coarse macroornament, PZZCU 2800. Bars in μm.

***Rarepora* gen. nov.**

Type species. – Here designated, *Rarepora tumulamen* sp. nov. from the Lochkov Formation (Lower Devonian) of the Prague Basin, Czech Republic.

Etymology. – *Rārus* (Latin) – small; *porus* (Latin) – pores.

Diagnosis. – Small-sized glosselline with biconvex, thin-walled shell of elongately elliptical outline; both valves weakly convex; dorsal interior without pseudointerarea, with high raised thickened but undifferentiated posterior shell wall; ventral interior with short, deep, broad pedicle groove and very small undifferentiated propareas; visceral area and muscle scars weakly defined, pallial markings lacking; very small endopores present in shell wall; first-formed shell mound-shaped, smooth, distinctly elevated above adjacent surface of brephic shell; macroornament of mature shell of shortly lamellose concentric fila; fila densely packed in early mature shell becoming larger and more spaced in later growth stages.

Remarks. – The new genus is assigned to the Glossellinae due to the absence of the dorsal pseudointerarea, the small ventral pseudointerarea and the weakly defined visceral field. Some genera of the subfamily have a radial papillose ornament (*Glossella* Cooper, 1956; *Fezzanoglossa* Havlíček, 1973 *in* Havlíček & Massa 1973) or exhibit a distinct median ridge (*Glyptoglossella* Cooper, 1956; *Leptobolus* Hall, 1871, *Rafanoglossa* Havlíček, 1982, *Rafanoglossella* Havlíček, 1998). *Casquella* Percival, 1978 differs by strongly thickened visceral area. *Ectenoglossa* Sinclair, 1945 is distinct by a strongly parallel-sided large shell. *Plectoglossa* Cooper, 1956 has concentric rugae. *Pachyglossella* Cooper, 1960 differs by a thicker shell and a pitted post-larval shell. The macroornament of *Rarepora* is somewhat similar to the scalloped concentric lamellae of *Glyptoglossella* but differs by median ridge in dorsal valve interior. The overall shell shape of *Rarepora* is similar to *Lingulipora* Girty, 1898. This genus has similar outline and similarly elevated the first-formed shell (Baliński 1997, 2001). The mature shell of *Lingulipora* exhibits the similar macroornament to *Rarepora*. However, the new genus is distinct by possessing fewer pores and an absence of radiating ridges at the first-formed shell (Baliński 1997, 2001; Mergl 2019). There is stratigraphical continuity in the ranges of *Rarepora* and *Lingulipora*; *Rarepora* occurs in the Lochkovian to the Emsian (Holmer *et al*. 2020) whilst the FAD (First Appearance Datum) of *Lingulipora* occurs in the late Eifelian (Mergl 2019), having its commonest occurrence in the Frasnian and the Famennian (Girty 1898; Biernat 1970; Baliński 1979, 1988, 1997). The last records of *Lingulipora* are from the Pennsylvanian of Oklahoma (Morse 1931) and Russia (Kuznetsov 1960, Kalashnikov 1970).

Species included. – *Rarepora tumulamen* gen. et sp. nov; Lochkov Formation, Lochkovian; Prague Basin, Bohemia; *Lingulipora*? sp.; Ogilvie Formation, Middle Emsian; mid-east Alaska (Holmer *et al.* 2020).

***Rarepora tumulamen* sp. nov.**
Figures 3–5

Holotype. – Almost complete dorsal valve, illustrated in Fig. 3, stored in the collections of the West Bohemia University, Plzeň (PCZCU 2794).

Type horizon and locality. – Devonian, Lochkovian, Lochkov Formation, Kotýs Limestone; Central Bohemia.

Etymology. – *Tumulamen* (Latin) – mound, small hill: referring shape of juvenile shell.

Material. – Apart of the holotype, eleven incomplete dorsal valves (PCZCU 2861 to PCZCU 2871), one ventral valve (PCZCU 2873) and several shell fragments (one illustrated: PCZCU 2872).

Diagnosis. – As for genus.

Description. – Shell elongately oval, thin-walled, 6 mm long in the largest examined specimen, lacking sulcus or flattening along along axial part of the shell. DvL/DvW is 1.66 to 1.89 (n = 2). The shell size calculated from small fragments indicate a larger size, with extrapolated length 10 mm or even more.

The dorsal valve has an elongately oval outline, with maximum width at the midlength. Weakly rounded posterolateral sides enclose an apical angle of some 130° (Fig. 5A, C). The lateral sides are weakly rounded to subparallel, while anterolateral and anterior margins are evenly

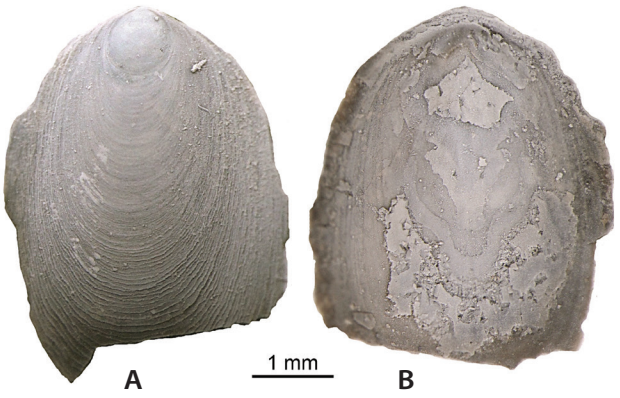


Figure 3. *Rarepora tumulamen* gen. et sp. nov., Kotýs Limestone, Lochkov Formation; Branžovy locality. Almost complete dorsal valve, holotype, PCZCU 2794, exterior (A) and interior (B); light photo. Scale in mm.

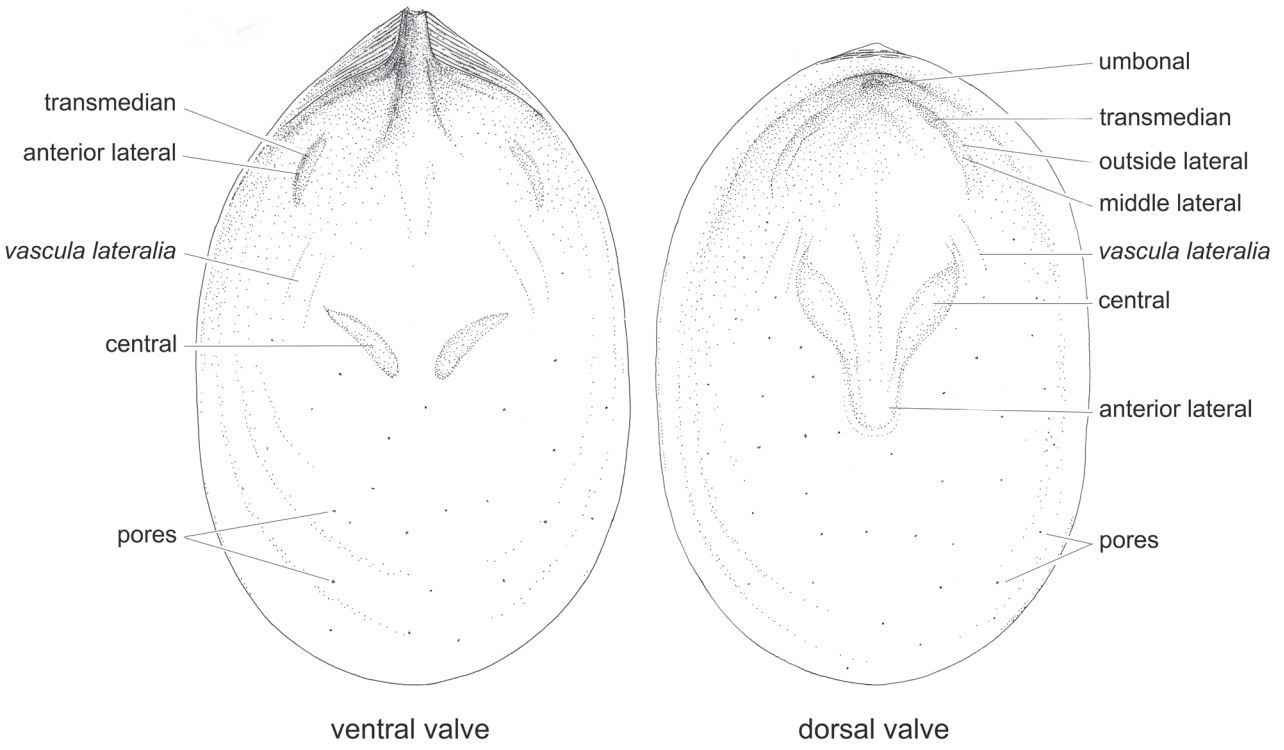


Figure 4. *Rarepora tumulamen* gen. et sp. nov. Schematic illustration of shell interiors.

rounded. The valve is weakly convex in a longitudinal profile, but moderately convex in a transverse profile. The dorsal pseudointerarea is not developed (Fig. 5J, K, M). The wall of the valve forms the broad elevated arcuate shelf along the posterior margin of the valve. This elevated shelf fades anterolaterally and disappears in the valve floor.

The ventral valve is similarly weakly convex, with a much more posteriorly protruding beak. The apical angle is between 90° to 100°. The ventral pseudointerarea is well developed, divided by a short, deep and anteriorly expanding pedicle groove (Fig. 5L). Small highly elevated triangular propareas are present. Their surface has prominent but uneven oblique growth striations.

The dorsal valve floor displays weakly defined muscle scars and pallial markings (Fig. 3). Paired small scars likely corresponding to umbonal, transmedian, outside and middle lateral muscles are poorly defined near the base of the steeply sloping posterolateral shell floor. Large, oblique oval central muscles scars occupy a roughly triangular area that is one-third as wide as the valve (Figs 3, 4). The scars are located just posterior to the shell midlength. The wide anterior projection extends anteriorly from the visceral area, but lacks distinct imprints of the anterior lateral muscles. A median ridge is absent. *Vascula lateralia* are feebly impressed having moderately diverging proximal parts (Fig. 4). *Vascula media* are not discernible. Shallow pits cover the posterior part of the visceral platform of large specimens (Fig. 5M). Very small, widely spaced endopores (diameter ~5 μm) are poorly visible on the shell floor (Fig. 5J, K).

The ventral valve floor has similarly poorly preserved muscle scars. Only the narrow, oblique central muscle scars are discernible, located approximately in the posterior one-third of the floor (Fig. 5L). The whole visceral area is poorly defined, indistinctly bordered on the posterolateral slopes by divergent strips of undifferentiated muscle scars.

Macroornament consists of densely crowded, short lamellar growth lines, which are almost equally distributed anteromedially and anterolaterally in large shells (Figs 3A, 5O). The early mature shell bears uneven fine growth fila separated by deep incisions (Fig. 5I, U). There are some 15 concentric growth lines per 1 mm anteromedially separated by wider interspaces (Fig. 5O), but 40 or even more densely crowded thin lines at the posterolateral flanks of the valve (Fig. 5I, U, V). The brephic shell is clearly defined, having a gently elongate outline, 550 to 700 μm wide. The prominent mound-like protuberance at the first-formed shell is present (Fig. 5P, Q, T). The surface of the brephic shell is smooth (Fig. 5P).

Remarks. – Apart of the type species, the shells of *Linguli-pora*? sp. from the Ogilvie Formation (Emsian) of Alaska (Holmer *et al.* 2020) can be referred to the new genus. It has the similar morphology of the ventral pseudointerarea, lacks the dorsal pseudointerarea, show fewer pores and exhibits the similarly elevated first-formed shell but differs from *Rarepora tumulamen* gen. et sp. nov. by a much uniformly-sized lamellose macroornament of mature shell, less rounded posterior margin of the dorsal valve, and by a much distinct openings of endopunctae on the shell floor.

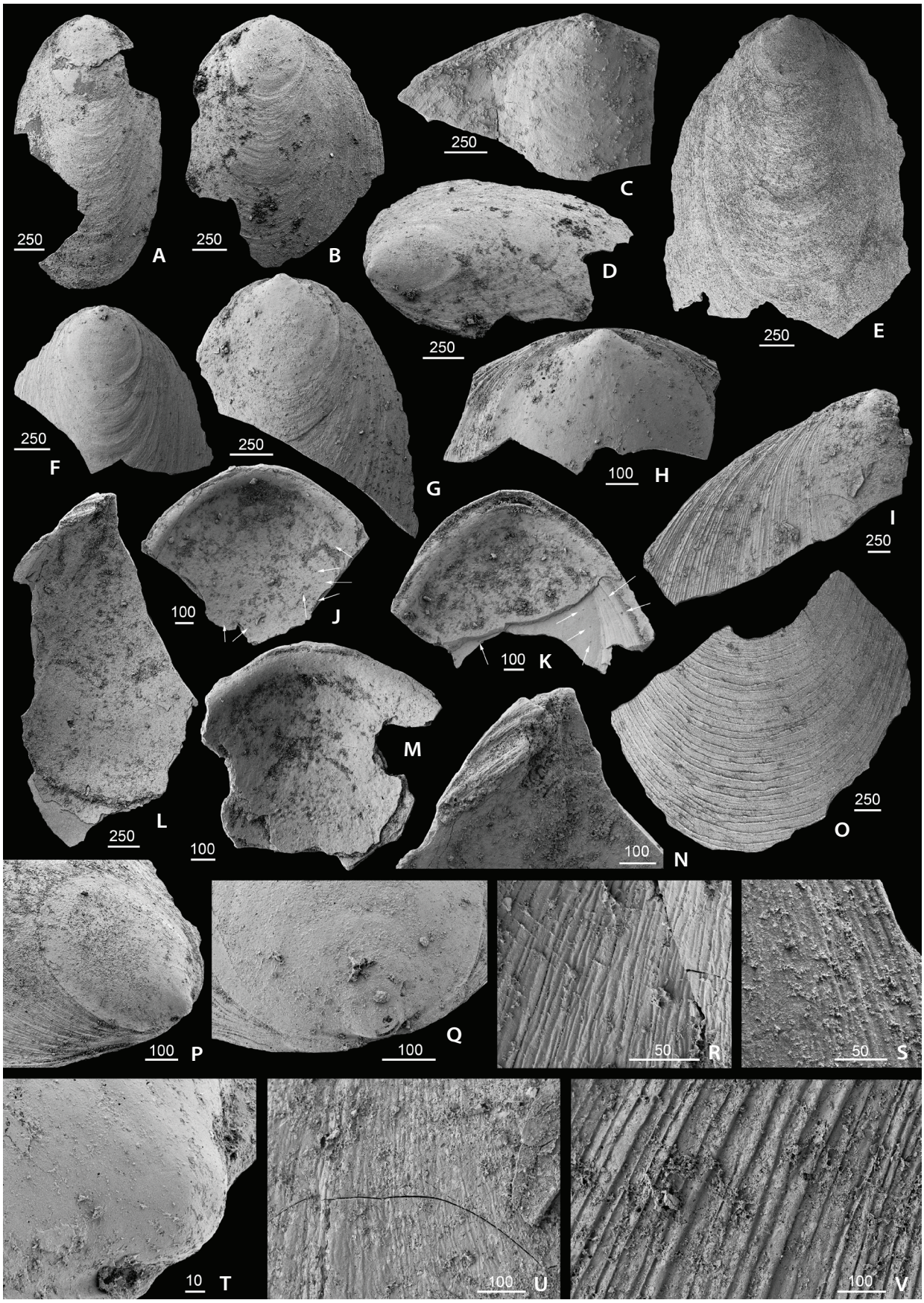
Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (abundant).

Gen. et sp. indet.
Figure 2C–E, G, I, J

Material. – Four figured fragments (PCZCU 2798 to PCZCU 2801) and numerous small fragments.

Description. – The fragments come from shells of moderately large (estimated length is 5 mm or more) and moderate thick-walled, gently elongate lingulate. The shell has evenly rounded anterior margin lacking any sign of a flattening or a sulcus (Fig. 2G). The macroornament consist of rows of low tubercles arranged in concentric growth strips (Fig. 2I). Some of rows are accentuated by low concentric elevated bands or incised concentric grooves. Shapes of tubercles differ with location on the shell. Tubercles are narrow and elongately drop-like in the posterolateral parts of the shell (Fig. 2C, E) while those located anteromedially are transversally oval (Fig. 2D, E, I). The size and definition of tubercles are similarly uneven. They are about 10 to 20 μm wide, some 40 to

Figure 5. A–V – *Rarepora tumulamen* gen. et sp. nov., Kotýs Limestone, Lochkov Formation; Branžovy locality. A – small almost complete dorsal valve, exterior, PCZCU 2861. B, D, P, S, T – dorsal valve, exterior, oblique view, detail of a larval shell (P) and its posterior mound (T), and detail of the macroornament of left posterolateral margin (S), PCZCU 2862. C, R – fragment of large dorsal valve, exterior, and detail of its macroornament, PCZCU 2867. E – medium-sized dorsal valve, exterior, PCZCU 2863. F, Q – incomplete dorsal valve, exterior, and a detail of its larval shell, PCZCU 2864. G – medium-sized dorsal valve, exterior, PCZCU 2865. H – fragment of large dorsal valve, exterior, PCZCU 2869. I, U, V – fragment of large valve, exterior, and details of its macroornament at posterior and posterolateral parts, PCZCU 2868. J – dorsal valve, interior, PCZCU 2870. K – dorsal valve, interior, PCZCU 2877. L, N – ventral valve, interior, and detail of the pseudointerarea, PCZCU 2873. M – dorsal valve, interior showing muscle scars, PCZCU 2866. O – fragment of large shell showing the macroornament, PCZCU 2872. Bars in μm. Arrows mark the pores on the shell floor or inside the shell wall.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70 µm long posterolaterally but 20 to 50 µm long and 60 to 90 µm thinly to widely oval much anteriorly.

Remarks. – This form of a tuberculate macroornament has not been described in any linguloid brachiopods from the Prague Basin. The most similar is the macroornament of *Barrandeoglossa* sp. from the Kopanina Formation (Gorstian) of the Prague Basin (Mergl 2001, pl. 8, fig. 11) but its mounds are much more elongate. None of the Silurian linguloids reviewed by Cocks & Popov (2009) has the similar ornament.

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (abundant but extremely fragmental).

Family Paterulidae Cooper, 1956

Genus *Paterula* Barrande, 1879

Type species. – By original designation, *Paterula bohemica* Barrande, 1879 from the Vinice Formation (Sandbian, Ordovician) of the Prague Basin, Czech Republic.

***Paterula postsilurica* sp. nov.**
Figure 6

Holotype. – The dorsal valve, illustrated in Fig. 6A, G, stored in the collections of the West Bohemia University, Plzeň (PCZCU 2802).

Paratype. – The ventral valve, illustrated in Fig. 6B, C, F, H stored in the collections of the West Bohemia University, Plzeň (PCZCU 2803).

Type horizon and locality. – Devonian, Lochkovian, Lochkov Formation, Kotýs Limestone; Central Bohemia.

Etymology. – Post (Latin) – after: referring the stratigraphic position of the species.

Material. – Apart of the types, one incomplete dorsal valve (PCZCU 2825).

Diagnosis. – Species of *Paterula* with posteriorly protruding posterior margin, slightly elongate shell outline, maximum width slightly posterior to shell midlength.

Description. – Shell weakly biconvex, thin-walled, small, 1.5 mm long, with broadly elongate outline, with DvL/DvW is 1.15 (one valve). The dorsal valve is weakly convex, with rounded sides and anterior margin. The posterior margin slightly protrudes posteriorly (Fig. 6A), defining nearly straight posterolateral sides united by a markedly rounded posterior margin. The dorsal apex is situated slightly posterior to one-fourth of the valve. The posterior shell is weakly sloping. Sides and anterior slope are weakly and evenly convex.

The ventral valve has the same outline, with a shortly protruding posterior margin which is cleft by a short, broadly V-shaped pedicle notch (Fig. 6F). The ventral apex is submarginal, with the posterior slope forming less than 10% of the valve length. Sides are weakly convex. The broad triangular anteromedian part of the valve is feebly flattened.

The dorsal valve interior has a distinct limbus which is marked by a subperipheral groove accommodating the setal embayments (Fig. 6E). The visceral field is poorly defined, lacking discernible muscle scars.

The ventral brephic shell is poorly separated from the mature shell. The surface of the first-formed shell exhibits packed irregular pits, substituted by rhombic pits just behind a periphery of the first-formed shell (Fig. 6C). The elongate rhombic pits cover the entire surface of the mature shell (Fig. 6B, G). They are uniformly sized, interlocking and regularly spaced, 13 µm wide and 3 µm long at the anteromedian part of the valve (Fig. 6H).

Remarks. – The protruding posterior slope in the dorsal valve of *Paterula postsilurica* sp. nov. is known in very few species of the genus. It is present in *Paterula linguata* Mergl, 1999b from the Bohdalec Formation (upper Sandbian to lower Katian) of the Prague Basin, and in *P. fissura* Lockley & Williams, 1981 from the Llan Mill Formation (upper Llandeilo) of Wales (Lockley & Williams 1981, Sutton *et al*. 2000, pl. 10, figs 14, 15). The Silurian *Paterula argus* Mergl, 1999b (Aeronian, Želkovice Formation) possesses a similar evenly rounded posterior margin. *Paterula holynensis* Mergl, 2001 (Eifelian to the Eifelian–Givetian boundary; Choteč Limestone and the Upper dark horizon of the Acantopyge Limestone in the Koněprusy area of the Prague Basin: Mergl 2019) possesses a rounded posterior margin but lacks the pedicle notch developed in *P. postsilurica*. The pedicle notch is present in all Ordovician representatives of the genus and also appears in *P. argus* but in *P. holynensis* the pedicle notch is substituted by a posteriorly directed ridge. Details of morphology of *Paterula* sp. from the lower Emsian (Chýnice Limestone: Mergl & Ferrová 2009) are not known due to a poor preservation, nevertheless the dorsal valve has well rounded posterior margin.

The protruding dorsal valve posterior margin of *P. postsilurica* may be an apomorphy shared with some Ordovician species. Indeed, the species *Paterula linguata*, *P. fissura* and *P. postsilurica* potentially represent a particular clade within the paterulids. However, this

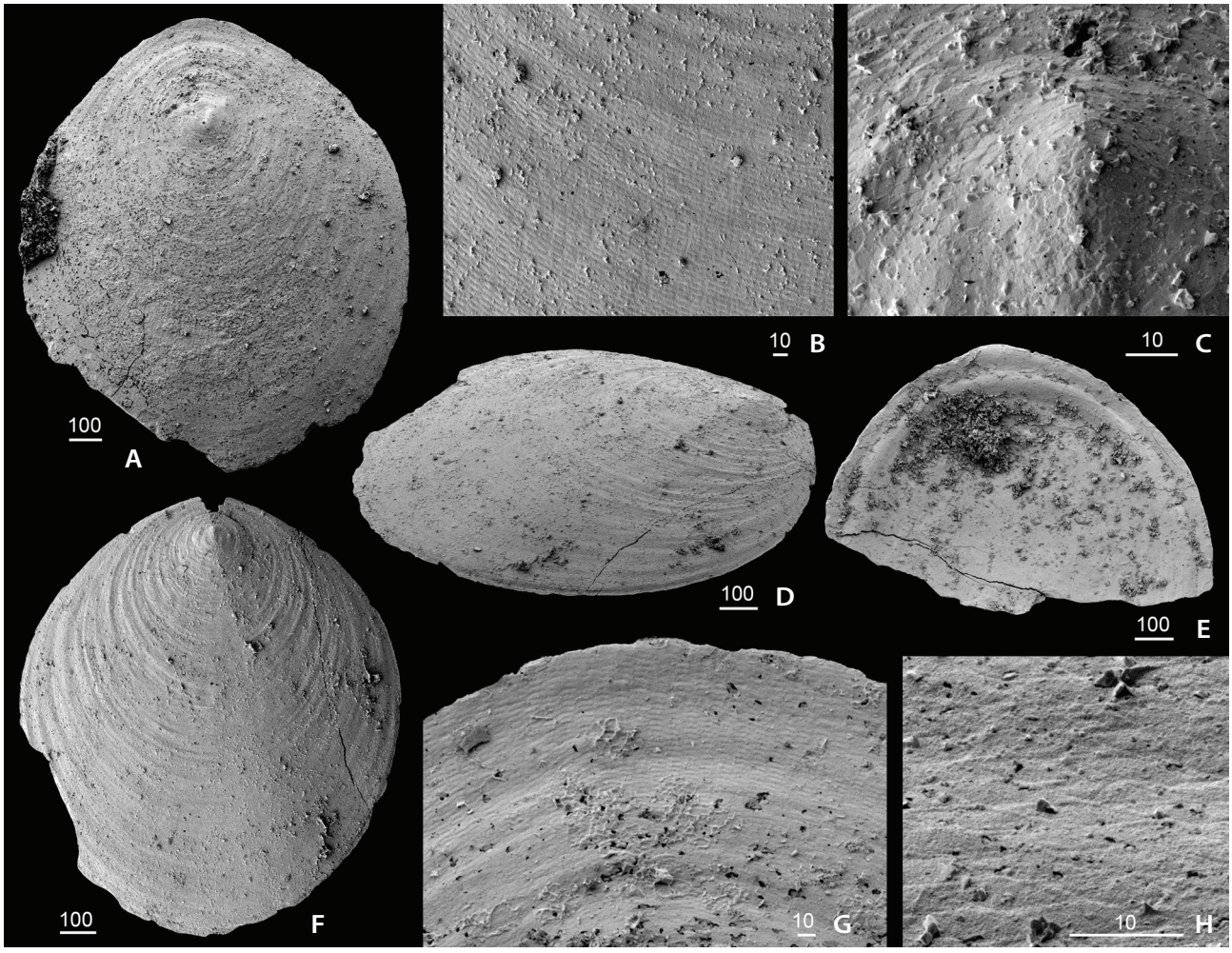


Figure 6. A–H – *Paterula postsilurica* sp. nov., Kotýs Limestone, Lochkov Formation; Branžovy locality. A, G – dorsal valve, holotype, exterior, and detail of posterior margin, PCZCU 2802. B–D, F, H – ventral valve, exterior (F) and its oblique view (D), and details of anteromedian microornament (B), microornament of a larval shell (C), and rhombic pits on a postlarval shell (H), PCZCU 2803. E – dorsal valve, interior, PCZCU 2825. Bars in μm.

suggestion cannot be tested and is beyond the scope of this study.

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (rare).

Superfamily Discinoidea Gray, 1840
Family Discinidae Gray, 1840

Genus *Acrosaccus* Willard, 1928

Type species. – By original designation, *Acrosaccus shuleri* Willard, 1928 from the Rich Valley Formation (Sandbian, Ordovician) of Virginia, USA.

***Acrosaccus*? sp.**
Figure 9M, P

Material. – One fragment of ventral valve (PCZCU 2877).

Remarks. – The small fragment of a posterior part of the ventral valve possesses a distinct subparallel shallow pedicle track covered by concave listrial plates (Fig. 9M). The track occupies about 50% of the posterior slope. The listrium is halved by narrow and depressed inner listrial plates and the axial callus. The track is almost 300 μm wide and terminates by a transversally elliptical foramen of the same size. Fine oblique growth striation covers the surface of the outer listrial plates. The macroornament of the mature shell consists of low, unevenly developed, densely crowded fine growth lines (Fig. 9M). The coarse rugellae are absent. The microornament consists of fine vesicular pitting that entirely cover a surface of the fragment (Fig. 9P). The diameters of pits are 3 to 4 μm.

The fragment is tentatively referred to *Acrosaccus* due to characteristic microornament and morphology of the pedicle track. Despite the very fragmentary material, the fine macroornament excludes this specimen from affiliation to other discinids at the locality. It is also

dissimilar to any of discinids described from the Silurian and the Devonian of the Prague Basin (Mergl 2001, Mergl & Ferrová 2009, Mergl & Jiménez-Sánchez 2015, Mergl & Šmídtová 2023).

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (very rare).

Genus *Kosoidea* Havlíček & Mergl, 1988

Type species. – By original designation, *Kosoidea fissurella* Havlíček & Mergl, 1988 from the Kopanina Formation (Ludfordian, Ludlow, Silurian) of the Prague Basin, Czech Republic.

***Kosoidea*? sp.**
Figure 8A–F, H

Material. – One incomplete dorsal valve (PCZCU 2833) and two fragments (PCZCU 2834, 2860).

Remarks. – The posterior half of the thick-walled dorsal valve has origin in 4 mm or even larger shell (Fig. 8A). The dorsal apex shows a distinctive smooth brephic shell of 300 µm diameter. The posterior slope is short and steep, indicating that the apex is situated at about 20% of the valve length. The posterior margin is evenly rounded. The lateral slopes are weakly convex.

The macroornament consists of unevenly sized concentric growth fila. The fila are medium coarse on the posterior slope, shrinking anteriorly. Some fila transfer into fine rugellae separated by much wider interspace in the anterior part of the valve (Fig. 8E, F). The microornament is formed by the radial strips of several radial rows of circular vesicular pits (Fig. 8B, C). Pit diameters vary around 5 µm. Adjacent surface inside each pitted strip exhibits a radially rheomorphic microornament (Fig. 8H). The strips with vesicle pits are intercalated by smooth radial bands of a comparable size (Fig. 8H).

The poor material makes a taxonomic affiliation to the particular discinid genus somewhat problematic. The microornament is similar to *Kosoidea fissurella* Havlíček & Mergl, 1988 which is abundant in the Kopanina Formation (Ludfordian) of the Prague Basin. However, *Kosoidea fissurella* differs by having a more prominent macroornament of higher and more densely spaced rugellae. The microornament of *K. fissurella* is also formed by radial rows of vesicular pits separated by smooth bands (see Mergl *et al*. 2018, fig. 6b3, b4, d2, d3), but the strips consist of one or double row of aligned pits and do not exhibit the multiple rows of pits (Fig. 8B, C, E) that occur in *Kosoidea*? sp.

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (very rare and fragmentary).

Genus *Lochkothele* Havlíček & Mergl, 1988

Type species. – *Discina intermedia* Barrande, 1879; designated by Havlíček & Mergl (1988) from the Lochkov Formation (Lochkovian, Devonian) of the Prague Basin, Czech Republic.

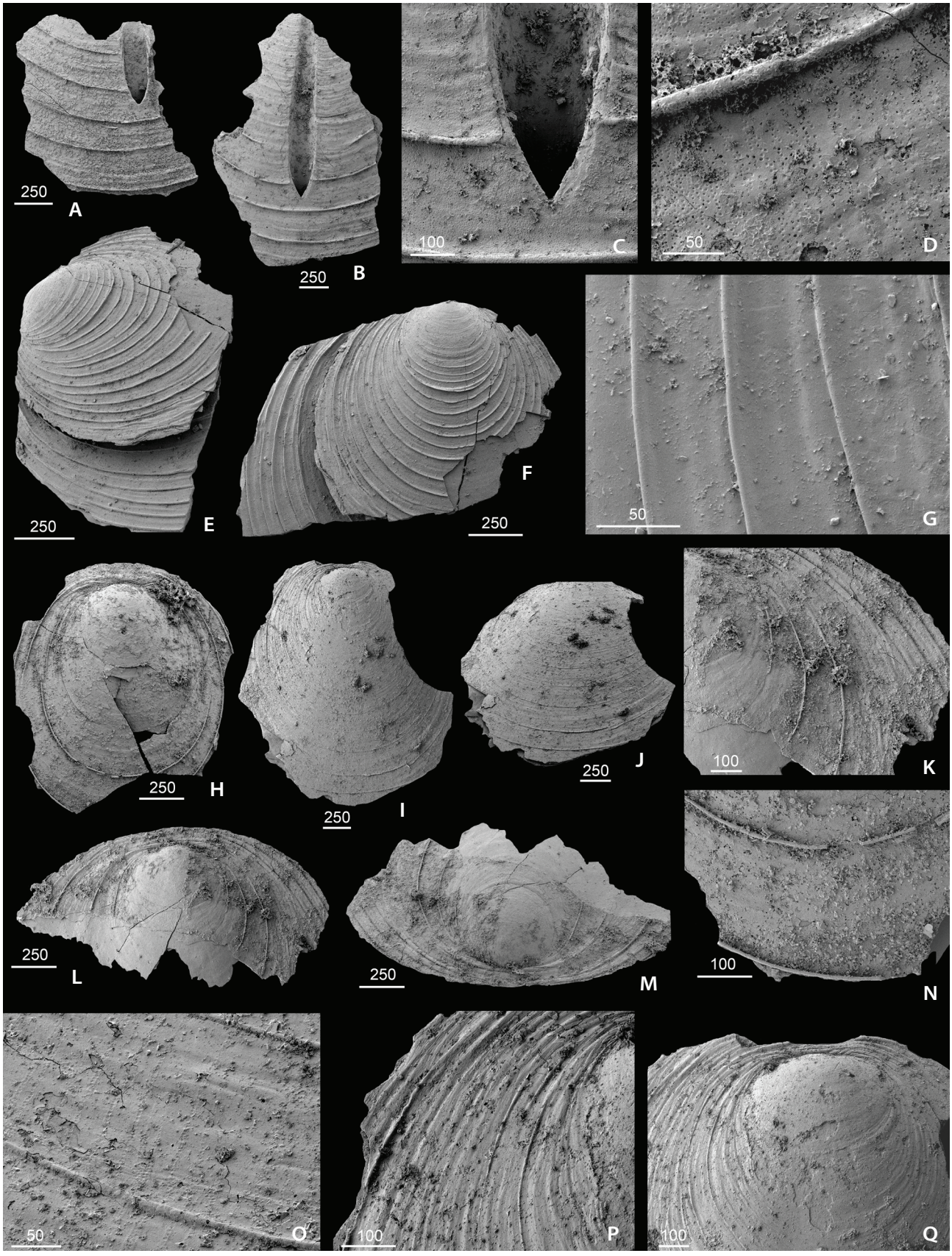
***Lochkothele intermedia* (Barrande, 1879)**
Figure 7A–D

1879 *Discina intermedia* Barr.; Barrande, pl. 99, cases 5, 6.
1879 *Discina signata* Barr.; Barrande, pl. 99, case 2.
1879 *Discina triangularis* Barr.; Barrande, pl. 101, case 1.
1988 *Lochkothele intermedia* (Barrande, 1879). – Havlíček & Mergl, p. 170, pl. 1, figs 1, 2, pl. 2, figs 1–3, text-fig. 1.
1999 *Lochkothele intermedia* (Barrande). – Havlíček, pl. 2, figs 1–4, 18.
2001 *Lochkothele intermedia* (Barrande, 1879). – Mergl, pl. 18, figs 1–12.

Material. – Two fragments of ventral valves (PCZCU 2816, 2817).

Remarks. – The species was described and illustrated in fine detail, including the pallial markings and musculature. However, apart from a poorly preserved fragment showing the nature of the pedicle track, fine details of the track have been unknown. The new material exhibits the narrow, weakly posteriorly expanding pedicle track closed by an acute angle in 3 mm sized shells (Fig. 7A–C). The floor of the pedicle track is undivided, lacking the striated listrial plates which are present in many discinid genera. The

Figure 7. A–D – *Lochkothele intermedia* (Barrande, 1879), Kotýs Limestone, Lochkov Formation; Branžovy locality. A – fragment of ventral valve, exterior, PCZCU 2816. B–D – fragment of ventral valve, exterior, showing a pedicle track, its detail, and postlarval microornament, PCZCU 2817. E–G – *Schizotreta*? sp. B, Kotýs Limestone, Lochkov Formation; Branžovy locality, dorsal valve, exterior (E, F), and detail of macroornament (G), PCZCU 2818. H–Q – *Schizotreta*? sp. A, Kotýs Limestone, Lochkov Formation; Branžovy locality. H, N – dorsal valve, exterior (H), and detail of its macroornament (N), PCZCU 2821. I, J, O–Q – dorsal valve, exterior, (I), its anterodorsal view (J), in details of its microornament (O), macroornament (P), and larval shell (Q), PCZCU 2819. K–M – incomplete dorsal valve, exterior (K), its posterodorsal view (M), and detail of its macroornament (L), PZCZU 2820. Bars in µm.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macroornament of the ventral valve is formed by regularly spaced fine concentric rugellae separated by much wider subplanar interspaces (Fig. 7B). The microornament consists of shallow vesicular pits of 3 μm diameter. The pits are arranged, at least at the posterior slope, into radial rows (Fig. 7D). The rows constitute a simple chain of pits but may consists of two or more, unevenly spaced pits at the same growth band. Spaces between radial rays are smooth or with weakly rheomorphic folds. Indeed, the microornament of the type species of *Lochkothele* has the same microornament and the morphology of the pedicle track as these observed in the stratigraphically subsequent species *Lochkothele rugellata* Mergl & Jiménez-Sánchez, 2015 (lower Emsian to Eifelian: Mergl 2001, Mergl & Ferrová 2009, Mergl & Vodrážková 2012, Mergl & Jiménez-Sánchez 2015).

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (rare).

Genus *Orbiculoidea* d'Orbigny, 1847

Type species. – *Orbicula forbesii* Davidson, 1848, designated by d'Orbigny (1847), from the Much Wenlock Limestone (Homerian, Wenlock, Silurian) of West Midlands, England.

***Orbiculoidea magnifica* Mergl, 2001**
Figure 8G, I–N

1879 *Discina maeotis* Eich.; Barrande, pl. 100, case 2, fig. 3.
1999 *Orbiculoidea* sp. n.; Havlíček, p. 305, pl. 4, fig. 19.
2001 *Orbiculoidea magnifica* sp. n.; Mergl, p. 23, pl. 16, figs 1–9, 12.

Material. – One incomplete ventral valve (PCZCU 2838) and two fragments of ventral valves (PCZCU 2836, 2837).

Remarks. – The fragments come from rather thin-shelled, at least 6 mm wide shells. The ventral valve is planar, with centrally to slightly anteriorly located apex (Fig. 8I). The anterior margin is evenly rounded. The posterior half of the valve is posteriorly extended, with less rounded posterolateral margin (Fig. 8J). The pedicle track is expanding posteriorly, but its posterior termination is poorly known. The track is likely closed somewhere at the midway of the posterior slope, because a narrow constriction is observable on one fragment (Fig. 8G). There are gently concave listrial plates that are medially connected by a distinct callus. The macroornament is formed by distinct concentric, rather fine rugellae that form nearly complete circles (Fig. 8I). These may be entire, evenly sized along whole course but gently fade near the pedicle track. The rugellae continues in a form of coarses growth striations on a surface of the listrial plates. The interspaces are much wide, subplanar. The microornament is formed by densely packed vesicular pits covering entire shell surface except of listrial plates (Fig. 8K–M). The pits are uniformly sized, regularly circular, about 3 μm in diameter (Fig. 8N).

All fragments show features observed in the much larger specimens of *O. magnifica* Mergl, 2001, which occur in the Radotín Limestone of the Lochkov Formation of the Prague Basin and are of the same age. Fine morphological details of *O. magnifica* are unknown, but shape and spacing of rugellae and the form of the pedicle track are the same. The similarly fragmental material with a fine vesicular microornament has been recently described from the Vinařice Limestone (Pragian, Devonian) of the Prague Basin (Mergl & Šmídtová 2023). This poor material was affiliated to *Rugadiscina* Mergl, 2010 due round and not trapezoidal outline of the posterior slope of the ventral valve. All these shells share the dense vesicular pitting that has been observed also in the type species *O. forbesii* (Davidson, 1848) (see Mergl 2010, fig. 6o).

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; localities Bubovice, Branžovy ridge (rare); the same formation, the Radotín Limestone; localities Kosoř, Praha-Podolí, Lejškov, Železná (Vápenice) (rare).

Genus *Praethele* Mergl, 2024

Type species. – *Discina vexata* Barrande, 1879, designated by Mergl (2024) from the Motol Formation (Sheinwoodian, Wenlock, Silurian) of the Prague Basin, Czech Republic.

***Praethele* sp.**
Figure 9A–L, N, O, Q, R

Material. – Four incomplete dorsal valves (PCZCU 2822 to PCZCU 2824, PCZCU 2832), one ventral valve (PCZCU 2826), numerous fragments, some illustrated (PCZCU 2828, 2830, 2831).

Description. – The shell is ventri-biconvex, thick-shelled relative to its size, subcircular in outline, 4 to 5 mm wide. The dorsal valve is poorly convex with a gently concave posterior slope and a weakly convex anterior slope (Fig. 9A, B, G). The apex is located in the posterior 20% of the shell length. The brephic shell is 300 μm wide, circular, gently convex. It is encircled by numerous fine growth fila that rapidly increase in a size with shell growth (Fig. 9H). The coarser rugellae appear in shells larger than 500 μm in size (Fig. 9F). The rugellae progressively and evenly increase in size with shell growth (Fig. 9B, H).

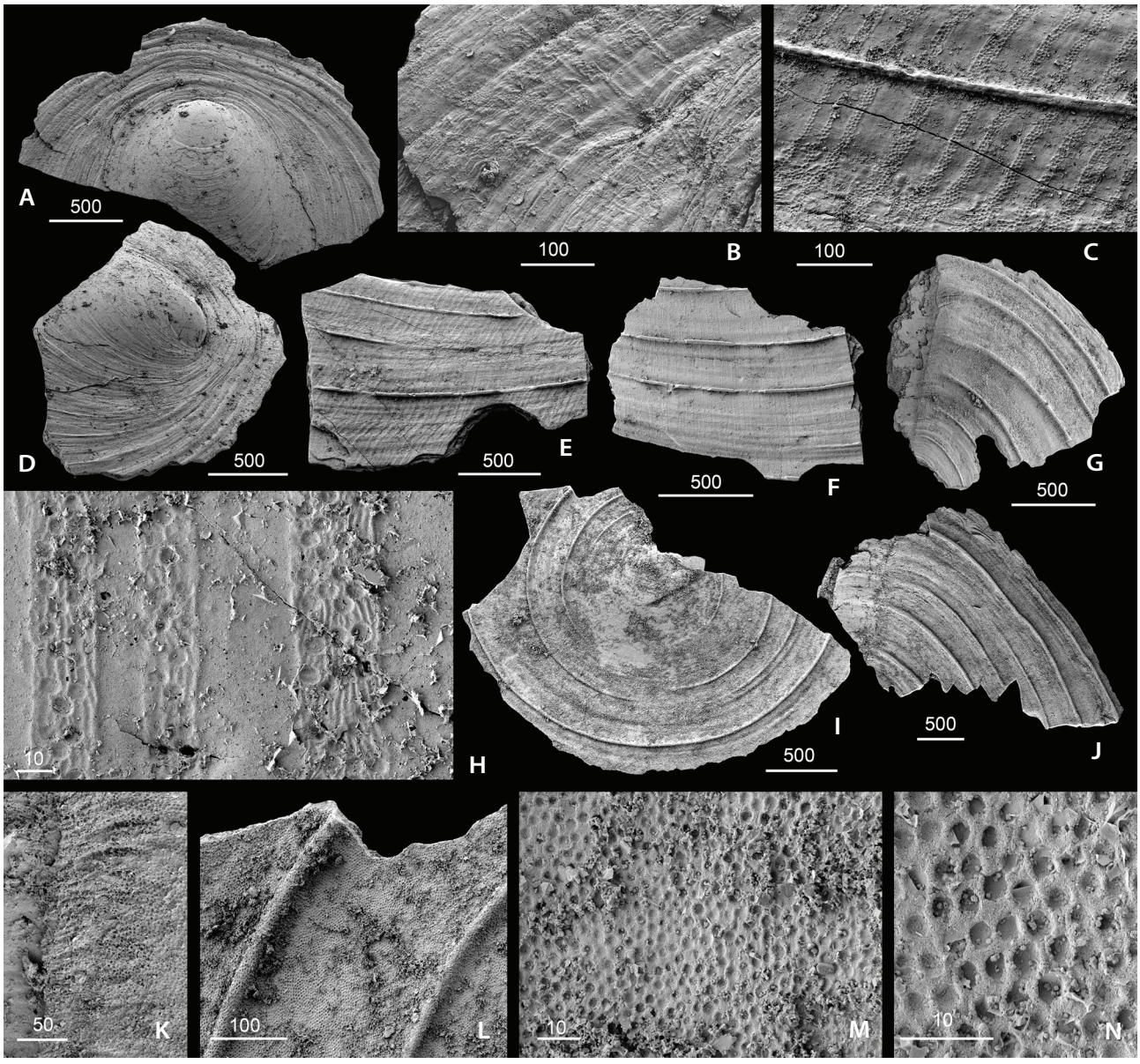


Figure 8. A–F, H – *Kosoidea*? sp., Kotýs Limestone, Lochkov Formation; Branžovy locality. A, B, D – incomplete dorsal valve, exterior (A), oblique view (D), and detail of macroornament (B), PCZCU 2833. C, E – shell fragment, exterior (E), and its microornament (C), PCZCU 2834. F, H – shell fragment, exterior (F), and its microornament (H), PCZCU 2860. G, I–N – *Orbiculoidea magnifica* Mergl, 2001, Kotýs Limestone, Lochkov Formation; Branžovy locality. G, K – shell fragment, exterior (G) and its microornament (K), PCZCU 2836. I, L–N – fragment of ventral valve with a pedicle track, exterior (I), and details of its microornament (L–N), PCZCU 2838. J – fragment of ventral valve, exterior, PCZCU 2837. Bars in μm.

Rugellae are high, having thinner shaft and swollen crests, resting subvertically onto shell surface. Their crests are gently inclined toward the shell periphery (Fig. 9K). Some rugellae form the full circle. The crescentic rugellae originating on flanks rapidly reach the same size (Fig. 9B). The interpaces are deep, narrower or wide as the nearby rugellae (Fig. 9J–L).

The ventral valve has a low conical form with a subcentral apex (Fig. 9N). The pedicle track is narrow, parallel-sided, but otherwise poorly known. The macroornament consists of regular rugellae, likely somewhat finer than those on the dorsal valve. Interiors of both valves are unknown.

The microornament consists of elliptical vesicular pits that entirely cover the surface of the mature shell (Fig. 9L, O). The pits are 4 to 5 μm wide and 3 to 4 μm long on the mature shell. The size of pits changes rapidly in the contact zone between the brephic and the mature shells (Fig. 9F, Q, R). Very fine pits smaller than one micrometre cover a periphery of the brephic shell (Fig. 9R). Than follows 20 μm wide zone with 2 to 3 μm sized pits immediately converted to larger pits on the mature shell.

Remarks. – The gross morphology of the shells is very near to that of *Praethele vexata* (Barrande, 1879) and *P. postvexata* Mergl, 2024. The main difference in the Kotýs Limestone specimens is the profile of the rugellae, which lack the acute rim present on *P. vexata*. The very subtle differences between *P. postvexata* and these shells include a more transverse outline and a less excavated posterior slope of rugellae in *P. postvexata*.

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (abundant but very fragmental).

Genus *Schizotreta* Kutorga, 1848

Type species. – By original designation, *Orbicula elliptica* Kutorga, 1846 from the Volkhov or Kundan regional stages (Ordovician) of northwestern Russia.

***Schizotreta*? sp. A**
Figure 7H–Q

Material. – Three dorsal valves (PCZCU 2819 to PCZCU 2821).

Remarks. – The shell is thin-walled, elongate–oval on outline, with estimated 3 mm length (Fig. 7H, L). The dorsal valve is weakly convex, with evenly rounded posterior, lateral and anterior margins. The dorsal apex is sited near the posterior margin. The posterior slope is very short, weakly sloping, with the brephic shell distinctly elevated above its surface (Fig. 7Q). The macroornament consists of fine, narrow and high rope-like rugellae of uniform size, separated by much wider nearly smooth interspaces (Fig. 7H, K, P). The surface of interspaces bears very low ripple-like concentric growth bands (Fig. 7O). The size of rugellae increases towards the posterior margin, where they are densely packed one to another (Fig. 7M). The microornament consists of weakly imprinted radial rows of vesicular pits separated by much wider smooth interspaces (Fig. 7O).

The species has fine, regularly spaced rugellae similar to these present at shells referred to *Schizotreta* sp. A from the Lochkovian of the Spanish Central Pyrenees (Mergl & Valenzuella-Ríos 2020), but the latter likely have a much more posteriorly located dorsal beak. Similarly spaced rugellae and a submarginal beak exhibit the dorsal valve *Praeoehlertella umbrosa* Mergl, 2001 from black shales of the Pragian age from the Prague Basin. However, as the ventral valve of *Schizotreta*? sp. A is unknown, its affiliation to *Praeoehlertella* Mergl, 2001 or *Schizotreta* is tentative.

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (rare).

***Schizotreta*? sp. B**
Figure 7E, F

Material. – One dorsal valve (PCZCU 2818).

Remarks. – This valve differs from all other observed shells by regularly arranged finely lamellose, anteriorly inclined rugellae separated by wider interspaces and by a smooth surface without signs of a pitted microornament (Fig. 7E, F). The valve likely represents a particular species, but its affinity is unclear.

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (very rare).

Genus *Branzodiscus* gen. nov.

Type species. – Here designated, *Branzodiscus porosus* sp. nov. from the Lochkov Formation (Lower Devonian) of the Prague Basin, Czech Republic.

Diagnosis. – Small-sized discinid with dorsi-biconvex, thick-walled shell of subtrapezoidal outline; dorsal valve moderately convex, with submarginal beak; ventral valve depressed conical, with subcentral apex; pedicle track short, broadly triangular, posteriorly opened by a broad transverse slit and a short longitudinal slot between large planar listrial plates; dorsal macroornament of regularly spaced, low, almost entire rounded rugellae gently inclined anteriorly; the size of rugellae gradually swells anteriorly; rugellae on ventral valve finer than those on dorsal valve; external microornament of vesicular pits absent; interior with poorly defined visceral areas and muscle scars; shell floor with small, uniformly sized an regularly spaced circular 6 to 8 μm sized pores.

Remarks. – The new genus is characterized, apart from the small size, by the relatively large pedicle track (Fig. 10O, P) and by moderate and regular concentric rugellate macroornament. It is unique by (1) absence of superficial vesicular pitting and by (2) presence of the uniformly-sized pores on the shell floor. All so far described Silurian and Devonian discinid genera studied for the microornament of the mature shell (Holmer 1987, 1989; Mergl 2001, 2006, 2008, 2010, 2019; Williams 2003; Mergl & Ferrová 2009; Mergl & Vodrážková 2012; Mergl & Jiménez-Sánchez 2015; Mergl *et al*. 2018) display the vesicular pitting. Some of them (e.g. *Acrosaccus*, *Chynithele*) have the entire surface covered by pits (Mergl & Ferrová 2009, Mergl & Jiménez-Sánchez 2015, Mergl & Šmídtová

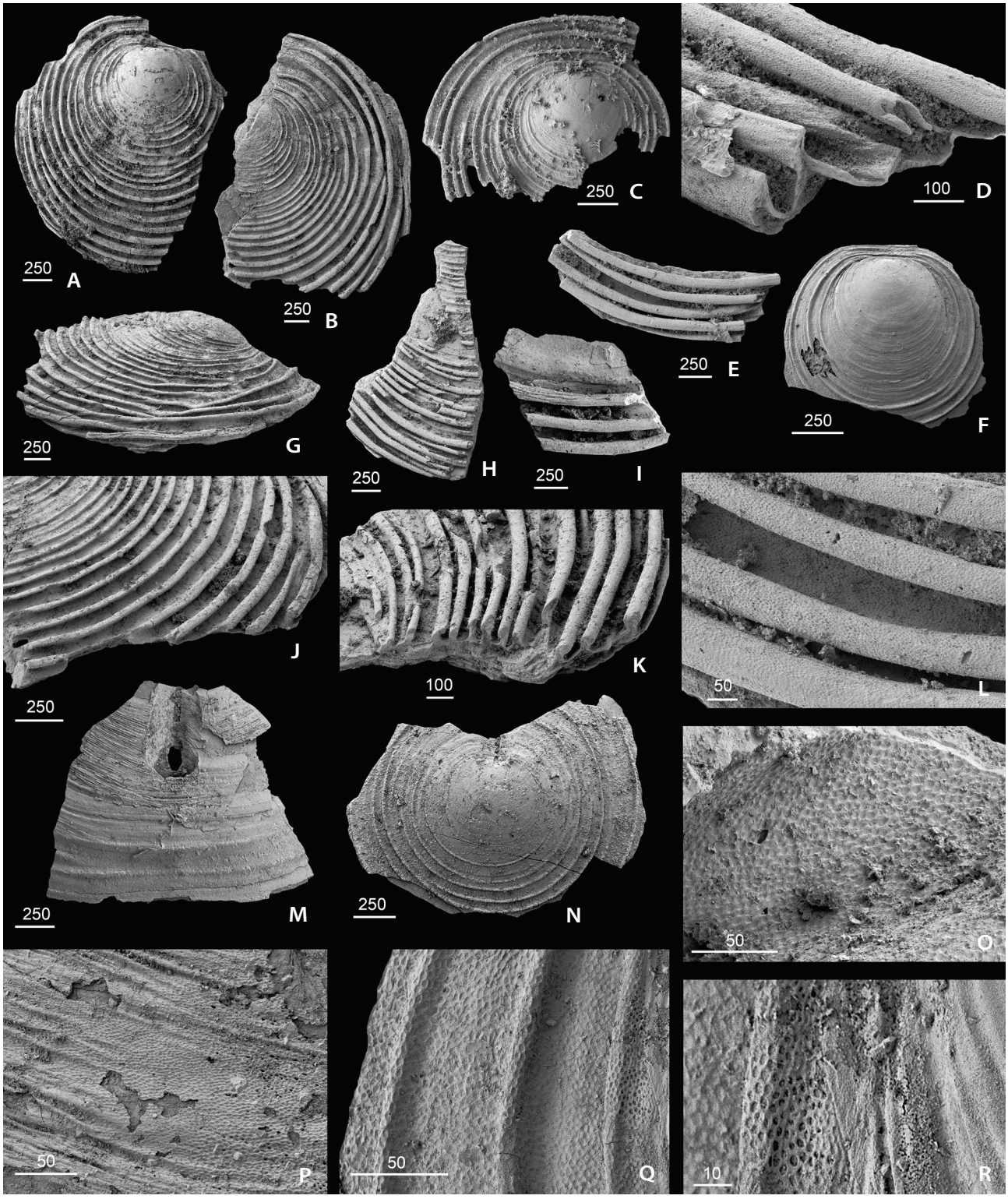


Figure 9. A–L, O, R – *Praethele* sp., Kotýs Limestone, Lochkov Formation; Branžovy locality. A – dorsal valve, exterior, PCZCU 2822. B, G, J – incomplete dorsal valve, exterior (B), oblique view (G, and detail of its macroornament (J), PCZCU 2823. C – incomplete dorsal valve, exterior, PCZCU 2824. D, E, L – fragment of dorsal valve, exterior (E), and details of macroornament (D, L), PCZCU 2830. F, Q, R – small dorsal valve, exterior (F), details of its postlarval microornament (Q), and contact of a larval shell with a postlarval shell (R), PCZCU 2832. I, O – shell fragment (I), and its microornament (O), PCZCU 2831. N – fragment of ventral valve, exterior PCZCU 2826. M, P – *Acrosaccus*(?) sp., Kotýs Limestone, Lochkov Formation; Branžovy locality, fragment of ventral valve, exterior (M), and microornament (P), PCZCU 2830. Bars in μm.

2023) while others (e.g. *Kosoidea*, *Schizotreta*) have pits arranged in the radial rows separated by rheomorphic or smooth surfaces (Mergl & Jiménez-Sánchez 2015, Mergl *et al*. 2018, Mergl 2024). Absence of the vesicular pitting in *Branzodiscus* is not an artefact of preservation, because other discinid shells from the same beds have the well-developed pitting (see Figs 7C, D; 8M, N; 9O, Q, R).

The endopores present on the shell floor of *Branzodiscus* are unknown in other discinid genera. Somewhat similar but larger and less regular pitting has been observed in fragmentary shells of *Opatrilkiella* from the Suchomasty Limestone of upper Emsian age (Mergl & Jiménez-Sánchez 2015). The pores observed in *Branzodiscus* likely are not homologous to pits commonly present in obolids (Sutton *et al.* 2000). The pits in obolids are generally crowded in the visceral area. They also enlarge with shell growth and often follow a course of growth bands. The uniform size of pores observed in *Branzodiscus* and their spacing greatly outside the visceral area are much alike the internal pores of *Lingulipora*, but in the latter the pores are opened on the shell exterior. In *Branzodiscus*, the pores are blind-ended, restricted to only most internal lamina of the secondary shell layer.

The size, gross morphology and submarginal dorsal beak in *Branzodiscus* is most similar to *Sterbinella* Mergl, 2001. However, this genus differs by a having narrower pedicle track with and open pedicle notch, and by weaker external macroornament and microornament of distinct vesicular pitting.

Species included. – *Branzodiscus porosus* sp. nov., Devonian, Lochkovian; Bohemia.

***Branzodiscus porosus* sp. nov.**
Figures 10, 11

Holotype. – Complete shell, illustrated in Fig. 10K, L, stored in the collections of the West Bohemia University, Plzeň (PCZCU 2812).

Type horizon and locality. – Devonian, Lochkovian, Lochkov Formation, Kotýs Limestone, Central Bohemia,

Etymology. – *Porósus*, *-í*, due to presence of pores in a shell wall.

Material. – Apart of the holotype, two complete shells (PCZCU 2811, PCZCU 2813), six dorsal valves (PCZCU 2804 to PCZCU 2808, PCZCU 2815), two ventral valves (PCZCU 2809, PCZCU 2810) and several unfigured fragments.

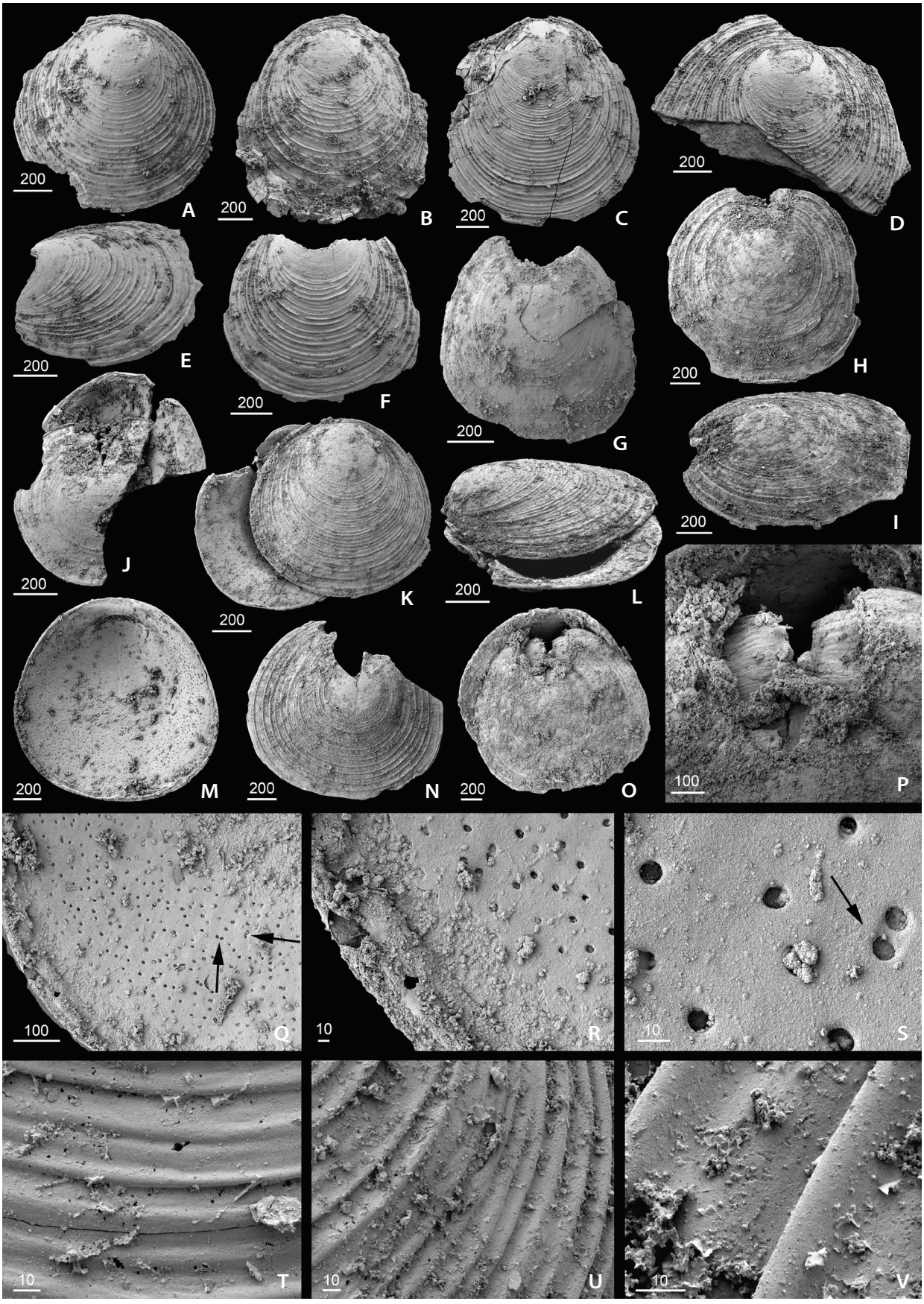
Description. – The shell is dorsi-biconvex, small (only 2 mm long), thick-walled in relation to its size. Shell outline is subcircular in small and medium sized specimens (Fig. 10A) to weakly elongate, with maximum width anterior to the midlength. Shells have a subtrapezoidal outline in large individuals (Fig. 10B, C).

The dorsal apex is submarginal, directed posterodorsally. The posterior slope is very short and steep. Lateral, posterior and anterior margins are evenly rounded. Maximum shell height is located posterior to midlength. Shell convexity decreases on flanks and anterior slope.

The ventral apex is placed at the posterior one-third of the shell, directed slightly posteroventrally (Fig. 10H, N, O). Sides and posterior slope are feebly convex, the anterior slope is flattened. The pedicle track is large relative to shell size. It has a broadly triangular ouline, showing a rapid initial expansion achieving subparallel borders in later growth stages (Fig. 10O, P). The track occupies about 25% of shell width. The pedicle foramen is T-shaped, formed by broad and short transverse slit posteriorly and narrow slot between the posterior edges of listrial plates (Fig. 10P). The listrial plates are large, planar, bearing a distinct transverse, weakly sinusoid growth striation. The slot between listrial plates is anteriorly closed by a featureless callus except for the posterior part which is open and linked to transverse slit of the foramen.

The dorsal valve interior has weakly defined visceral area, which is 40% as wide and 40% as long as the valve (Fig. 10M). It is featureless apart from a very weak median ridge. The posterior oblique muscle scars are paired, small-sized, almost linear and deeply impressed. These paired scars and oblique set of undifferentiated muscle impressions border (likely sites of posterior adductor and oblique internal muscles) the posterior and posterolateral sides of the visceral area. Large but feebly impressed anterior adductor scars lay at the shell midlength anterior to the visceral area. The very narrow limbus is developed

Figure 10. A–V – *Branzodiscus porosus* gen. et sp. nov., Kotýs Limestone, Lochkov Formation; Branžovy locality. A, V – dorsal valve, exterior (A) and its postlarval macroornament (V), PCZCU 2804. B – dorsal valve, exterior, PCZCU 2805. C, T – dorsal valve, exterior (C), and its macroornament (T), PCZCU 2806. D – large dorsal valve, exterior, PCZCU 2807. E, F – dorsal valve, exterior (F) and its oblique view (F), PCZCU 2808. G – ventral valve, exterior, PCZCU 2809. H, I – ventral valve, exterior (H), and its side view (I), PCZCU 2810. J – complete shell displaying exterior of ventral valve and part of dorsal valve interior, PCZCU 2811. K, L, U – holotype, complete shell displaying exterior of dorsal valve (K), its side view (L) and detail of macroornament (U), PCZCU 2812. M, Q–S – dorsal valve, interior (M), its anteromedian floor (Q), details of its periphery (R), and punctation of shell floor (S), arrows indicate couples of pores, PCZCU 2815. N – ventral valve, exterior, PCZCU 2814. O, P – complete shell displauing exterior of ventral valve (O), and detail of its pedicle track, PCZCU 2813. Bars in μm.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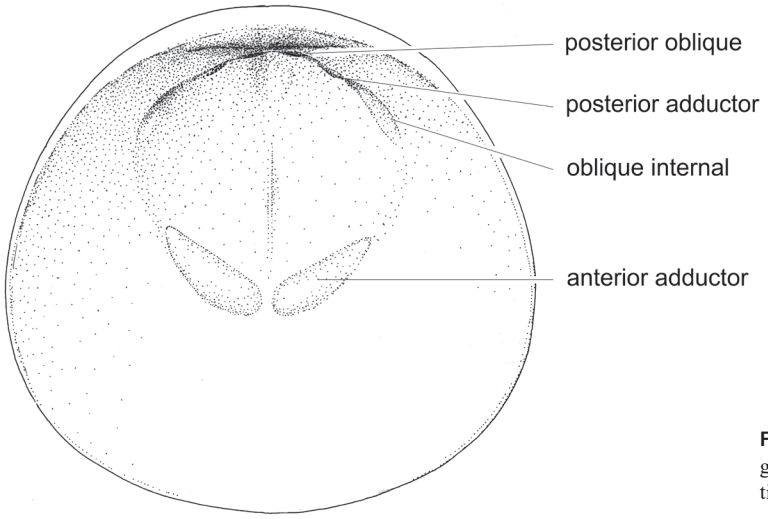


Figure 11. *Branzodiscus porosus* gen. et sp. nov. Schematic illustration of the dorsal valve interior.

along whole shell periphery (Fig. 10M). There are no traces of pallial markings.

The shell floor inward to the limbus and outside the visceral area and muscle scars bears uniformly sized, circular, 6 to 8 µm sized pores (Fig. 10M, O). They are equidistributed, lacking any correlation with growing bands. Weaker and much scattered pores are also present in the visceral area. The floor of individual pores is flat (Fig. 10S). The shell surface closely adjoining to pores are slightly depressed, more clearly accentuated in pore couplets (see arrows in Fig. 10Q, S).

The ventral valve interior is poorly known. Internal surface of the pedicle track does not significantly differ from the adjacent shell floor. The pores of the same size and distributional pattern are present in the ventral valve floor (Fig. 10K).

The brephic shell, defined by the first growth band, is subcircular, 200 µm wide, having weakly convex surface (Fig. 10B). The mature macroornament of the dorsal valve is formed by full regular concentric rugellae which begin to be more distinct in 400 to 500 µm long shell (Fig. 10A–C, F). Rugellae are low to moderate high, ripple-shaped, some slightly overhanging anteriorly, about 10 µm wide (Fig. 10T, U). Rugellae are separated by flat interspaces of the same size (Fig. 10T). The macroornament of the ventral valve is similarly shaped but weaker, with more accentuated interspaces and suppressed rugellae. Rugellae in the anteromedian part are weaker than rugellae in the posterolateral part (Fig. 10N). The pitted microornament has not been observed on the shell exterior (Fig. 10V).

Occurrence. – Lochkov Formation, upper part of the Kotýs Limestone: Bubovice, Branžovy ridge (moderate common).

Order Acrotretida Kuhn, 1949
Superfamily Acrotretoidea Schuchert, 1893
Family Biernatidae Holmer, 1989

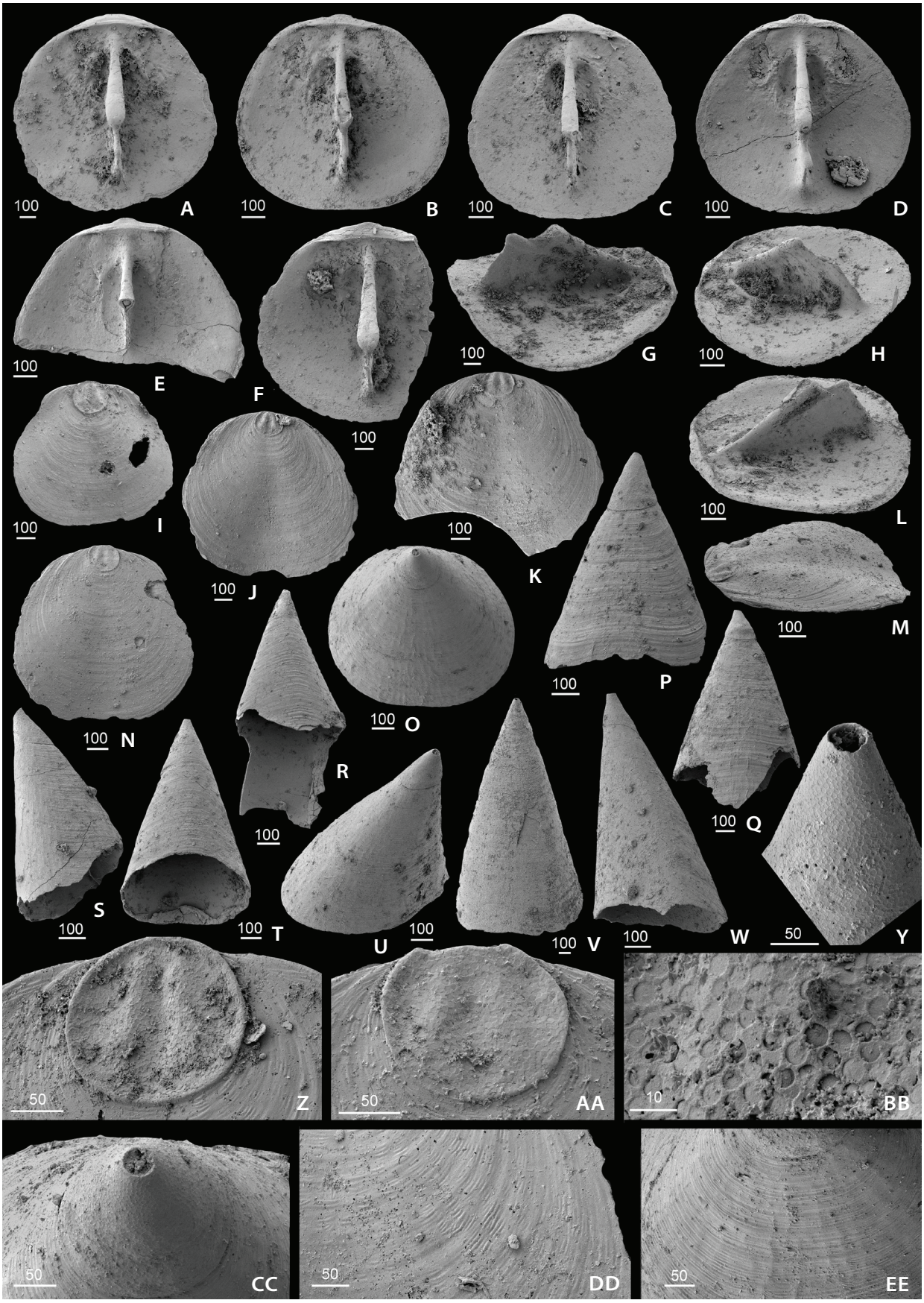
Genus *Opsiconidion* Ludvigsen, 1974

Type species. – By original designation, *Opsiconidion arcticon* Ludvigsen, 1974 from the Emsian (Devonian) of Yukon, Canada.

***Opsiconidion holynensis* (Mergl, 2001)**
Figure 12

2001 *Havlicekion holynensis* sp. n.; Mergl, p. 37, pl. 34, figs 1–13.

Figure 12. A–EE – *Opsiconidion holynensis* (Mergl, 2001), Kotýs Limestone, Lochkov Formation; Branžovy locality. A – dorsal valve, interior, PCZCU 2839. B, L – dorsal valve, interior (B) and its oblique view (L), PCZCU 2840. C – dorsal valve, interior, PCZCU 2841. D – dorsal valve, interior, PCZCU 2842. E – dorsal valve, interior, PCZCU 2843. F – dorsal valve, interior, PCZCU 2844. G – dorsal valve, interior in side view, PCZCU 2845. H – dorsal valve, interior in side view, PCZCU 2846. I – dorsal valve, exterior, PCZCU 2847. J – dorsal valve, exterior, PCZCU 2848. K – dorsal valve, exterior, PCZCU 2873. M, N, AA – dorsal valve, exterior (N), its side view (M) and detail of its metamorphic shell (AA), PCZCU 2849. O, U, CC, EE – ventral valve, exterior in apical (O) and oblique (U) views, and details of its metamorphic shell (CC) and post-metamorphic macroornament (EE), PCZCU 2850. P – ventral valve, exterior, anterior view, PCZCU 2855. Q – ventral valve, exterior, anterior view, PCZCU 2856. R – ventral valve, exterior of pseudointerarea, and partly showing interior of an anterior slope, PCZCU 2853. S – ventral valve, exterior, side view, PCZCU 2851. T – ventral valve, exterior, posterior view, PCZCU 2852. V – ventral valve, exterior, anterior view, PCZCU 2857. W – ventral valve, exterior, side view, PCZCU 2858. Y – ventral valve, exterior of metamorphic shell, PCZCU 2854. Z, BB, DD – dorsal valve, larval shell (Z), detail of pitting on its metamorphic shell (BB) and post-metamorphic macroornament (DD), PCZCU 2859. Bars in µm.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Material. – Thirteen dorsal valves (PCZCU 2839 to PCZCU 2850, PCZCU 2859, PCZCU 2873), eight ventral valves (PCZCU 2850 to PCZCU2858) and numerous shell fragments.

Diagnosis (emended). – Dorsal valve roundly trapezoidal to subpentagonal; metamorphic shell protruding posteriorly, prominent median septum with rounded rod-like surmounting plate; lower rod half-sized to upper rod; cardinal scars large, moderately diverging; anterocentral scars well-impressed on anteriorly elevated pad; dorsal larval shell with periphery distinctly elevated above surface of post-metamorphic shell; mature macroornament of very low concentric growth lines crossed by rays of fine wavy folds; ventral valve tall, conical, with catacline pseudointerarea; foramen directed just ventrally; metamorphic pitting of almost uniformly sized flatt-bottomed pits.

Description of new material. – The shell is thin-shelled, shallow unisulcate, with roundly trapezoidal to subpentagonal outline, having the maximum width anterior to the midlength. The maximum shell width is 850 μm.

The dorsal valve is weakly convex, with a narrow and shallow sulcus. The anterior and anterolateral margins are evenly rounded. The posterolateral margins are less rounded, creating a distinctly trapezoidal to subpentagonal shell outline (Fig. 12A–E). The dorsal pseudointerarea is anacline, 50% as wide as the valve, with broadly triangular shallow median groove. The metamophic shell clearly protrudes backwards.

The posterior platform in the dorsal valve floor is well-developed. The median ridge is prominent, blade-like, narrowly triangular in a side view, with the base projecting to proximity of the anterior margin (Fig. 12G, H, L). The surmounting plate is rod-like, gently concave in side view, unflattened, having a rounded end (Fig. 12C, D). Its end lies anterior to the shell midlength. The lower rod is smaller, thinner, having a rounded end which attains nearly the same height as the surmounting plate (Fig. 12G). Cardinal muscle scars are large, oblique oval. Anterocentral scars are smaller, oblique elliptical, located on an elevated pad posterior to the midlength of the valve (Fig. 12C–E). The visceral area between the cardinal and anterocentral scars is deeply excavated posteriorly. Pallial markings are not discernible.

The ventral valve is high conical, about 180% as high as long, with a catacline pseudointerarea (Fig. 12S, W). The circular foramen is directed straight ventrally (Fig. 12V, W, Y). The anterior slope is very weakly but distinctly convex (Fig. 12W).

The macroornament of the post-metamorphic shell consists of fine growth lines crossed by few rays composed of fine ripple-like folds (Fig. 12DD, EE). The dorsal metamorphic shell is circular, having the periphery distinctly elevated above the surface of the post-metamorphic shell (Fig. 12Z, AA). A pair of elongate diverging ridges are present on the dorsal metamorphic shells (Fig. 12Z). Each ridge exhibits distinct posterior and anterior nodes. The ventral metamorphic shell is high conical, having a distinct border (Fig. 12W, CC). The metamorphic shell is covered by circular flatt-bottomed pits, partly but occasionally overlapping, leaving lunate imprints (Fig. 12BB). The diameter of the pits is almost uniform, about 5 μm.

Remarks. – The species has been referred to *Havlicekion* Mergl, 2001 by Mergl (2001) but the new examination confirms its closer relationship to *Opsiconidion* Ludvigsen, 1974 because of the lack of prominent rugellate macroornament. The genus *Opsiconidion* is represented by a dozen species and many of its other occurrences have been left in an open nomenclature. The differences between particular species are quite subtle and concern mainly the incline of the ventral pseudointerarea, the shape of the dorsal median septum and the outline of the dorsal valve (Brock *et al.* 1995). The organization of the metamorphic shell microornament seems to be taxonomically significant (see Mergl *et al.* 2018). The differences between species have been discussed by more authors (Cocks 1979; Brock *et al.* 1995; Mergl 2001, 2019; Holmer *et al.* 2020). The family Biernatidae awaits modern revision including some aberrant Silurian and Devonian relatives (*Eschatelasma* Popov, 1981: Holmer *et al.* 2020; *Concaviseptum* Brock, Engelbretsen & Dean-Jones, 1995: Brock *et al*. 1995; gen. et sp. indet: Mergl 2019).

No doubt the species *Opsiconidion holynensis* (Mergl, 2001) and *O. arcticon* Ludvigsen, 1974 are close relatives. The holotype of the latter is the dorsal valve coming from the uppermost Michelle Formation of the Yukon Territory which is confidently dated as the early Emsian (Ludvigsen 1974). The topotypic dorsal valve subsequently figured by von Bitter & Ludvigsen (1979, pl. 91, figs 8, 9) shows the frequent overlap of flatt-bottomed pits on the metamorphic shell. Such extensive overlaps of pits have not been observed in *O. holynensis* (Fig. 12Y, BB). However, other shells referred to *O. arcticon* from the Onondaga Formation (Middle Devonian) by von Bitter & Ludvigsen (1979, pl. 90) likely belong to separate species as they display clearly different pitting organization. The North American occurrences (Ludvigsen 1974, von Bitter & Ludvigsen 1979), post-dated the known occurrence of *O. holynensis*.

Brock *et al.* (1995) referred to *O. arcticon* specimens coming from the late Lochkovian and the early Pragian of the Victoria, Australia. The gross morphology of Bohemian *O. holynensis* and Australian *O. arcticon* is

almost identical. The differences may be seen in the much subpentagonal outline having less curved posterolateral margins, and somewhat much elongate dorsal valve of *O. holynensis*. The figured Australian ventral valves (Brock *et al*. 1995, fig. 4d, e) seems much acutely conical. In addition, the pitting on the metamorphic shell and details of macroornament of the post-larval shell surface are not illustrated by Brock *et al.* (1995) making these features incomparable. At present state of knowledge seems eligible to consider *O. arcticon* and *O. holynensis* separate but closely related species. *Opsiconidion holynensis* with its FAD in the early Lochkovian may be ancestral to *O. arcticon*.

Occurrence. – Lochkov Formation, lower part of the Kotýs Limestone; locality Praha-Řeporyje, Černý Quarry (Mergl 2001) (abundant); the same formation, upper part of the Kotýs Limestone; locality Bubovice, Branžovy ridge (abundant).

Affinity of the lingulates from the Branžovy locality

The lingulate brachiopods from the Branžovy locality share only three species previously described in the Kotýs Limestone in other localities. However, the known distribution of the lingulates in the Prague Basin and their environmental demands are affected by rarity of the serious field data on micromorphic brachiopods: apart of the Branžovy locality only the Černý Quarry near Praha-Řeporyje provided data on microbrachiopod distribution of the Kotýs Limestone. The limestone beds at Řeporyje yielded two species that appear in the Branžovy locality: *Barrandeoglossa perneri* Mergl, 2001 and *Opsiconidion holynensis* Mergl, 2001. The abundant small obolid *Kosagittella pinguis* Mergl, 2001 and rare *Acrotretella triseptata* Mergl, 2001 sampled at Řeporyje have not been observed at Branžovy. Interestingly, the two most abundant discinids at Branžovy, *Branzodiscus porosus* gen. et sp. nov. and *Praethele* sp. are not known from Řeporyje. This and the other differences, *e.g.* common presence of *Rarepora tumulamen* gen. et sp. nov. at Branžovy, may reflect not only differences in environmental factors but may indicate slightly different stratigraphic ranges of some taxa. The beds at Řeporyje sampled by Mergl (2001) lie near the base of the Lochkov Formation (early Lochkovian), while beds in the Branžovy represent the very high part of the Lochkov Formation (late Lochkovian). Noteworthy, the occurrence of *Acrotretella triseptata* at Řeporyje represents the youngest known stratigraphic occurrence of the genus, which is common in the Silurian of the Prague Basin (Mergl 2001) and which is widespread from the Middle Ordovician and to the Silurian (Ireland 1961; Holmer 1986, 1989; Biernat & Harper 1999; Valentine *et al*. 2006; Mergl 2001; Mergl *et al*. 2018).

Furthemore, the differences between Řeporyje and Branžovy localities are likely related with a different palaeoenvironment. This may be deduced from presence of *Kosagittella* at Řeporyje. This genus is represented by several subsequent abundant species from the Pragian to the Eifelian, all from limestone of a suggested very shallow environment, often with diverse coral fauna (Chýnice and Acanthopyge limestones: Mergl 2008, Mergl & Ferrová 2009). Presence of *Paterula postsilurica, Lochkothele intermedia* and *Orbiculoidea magnifica* also refer to a deeper environment at Branžovy. The majority of known *Paterula* occurrences (see *e.g*. Mergl 1999b, 2001) are related with deeper and probably also hypoxic environment (Mergl 2002). *Lochkothele intermedia* is the abundant discinid in the dark-grey Radotín Limestone (Havlíček & Mergl 1988) which represents a deeper lithofacies of the Lochkov Formation (Chlupáč & Kukal 1988). *Orbiculoidea magnifica* has also been known from the Radotín Limestone (Mergl 2001). Assumption on the different bathymetry of localities is supported by sea-level changes in the Early Devonian (see Slavík & Hladil 2020). The fauna from Řeporyje immediately followed the sea-level drop of the S–D boundary event, while the fauna from Branžovy thrived during a high-stand of the late Lochkovian (Slavík & Hladil 2020).

The roughly coeval fauna (= Lochkovian to lower Pragian) of lingulates from the Spanish Pyrenees (Mergl & Valenzuela-Ríos 2020) include some related taxa (*e.g. Lochkothele* cf. *intermedia*, *Schizotreta* sp., *Opsiconidion* cf. *holynensis*, probably also *Praethele* [? = *Chynithele* aff. *fritschi* (Barrande, 1879)], but also species so far unknown from the Prague Basin (*Acrosaccus* sp. A). Nonetheless, basic knowledge of the distribution of Early Devonian lingulates is very poor and serious stratigraphical, environmental, and palaeogeographical analyses are required to better correlate faunas and environments.

Conclusions

The fauna of lingulate brachiopods from the Kotýs Limestone (late Lochkovian) on the Branžovy locality comprises 13 species of lingulate brachiopods, mostly members of the family Discinidae Gray, 1840. The taxonomic composition of the fauna differs considerably from the fauna known from the lower part of the Kotýs Limestone near Řeporyje (Mergl 2001) as well as from the fauna of the Radotín Limestone. The new fauna partially fills the information gap on the Early Devonian lingulate distribution in the Prague Basin. Two new genera and three new species were established. Some specimens are only tentatively identified:

1) The punctate linguloid *Rarepora tumulamen* gen. et sp. nov. is established. This species may be the ancestor of the genus *Lingulipora*, which is widespread in Late Devonian and Carboniferous strata.

2) The discinid *Branzodiscus porosus* gen. et sp. nov. is described. This genus is unique for the presence of evenly spaced endopunctae in the shell floor and for the absence of vesicular pitting on the outer surface of the primary shell.

3) A new collection of well-preserved shells of the biernatid *Opsiconidion holynensis* (Mergl, 2001) clarifies the validity, systematic position and stratigraphic range of this species originally described (Mergl 2001) on much poorer material. The species is closely related and may be ancestral *O. arcticon* Ludvigsen, 1974.

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References

Baliński, A. 1979. Brachiopods and conodonts from the Frasnian of the Debnik Anticline, Southern Poland. *Palaeontologia Polonica 39*, 3–93.

Baliński, A. 1988. Shell morphology and structure of *Lingulipora* Girty. *Acta Palaeontologica Polonica 33*, 123–133.

Baliński, A. 1997. Evolution of embryonic development in lingulid brachiopods. *Acta Palaeontologica Polonica 42*, 45–56.

Baliński, A. 2001. Embryonic shell of Devonian linguloid brachiopods, 91–101. *In* Brunton, C.H.C., Cocks, L.R. & Long, S. (eds) *Brachiopods past and present. The Systematic Association Special Volume 63*. Taylor & Francis. London, New York. DOI 10.1201/9780203210437.ch10

Barrande, J. 1879. *Systême silurien du centre de la Bohême. Iére partie. Recherches paléontologiques. Vol. 5. Classe des Mollusques. Ordre des Brachiopodes*. 226 pp. Prague & Paris.

Bassett, M.G. 1986. Brachiopod Inarticules, 85–97. *In* Racheboeuf, P.R. (ed.) *Le Groupe de Liévin. Pridoli – Lochkovien de l'Artois (N. France). Biostratigraphiedu Paléozoique 3*.

Bassett, M.G., Popov, L.E. & Holmer, L.E. 1999. Organophosphatic brachiopods: patterns of biodiversification. *Geobios 32(1)*, 145–163. DOI 10.1016/S0016-6995(99)80026-6

Bassett, M.G., Popov, L.E. & Holmer, L.E. 2002. Brachiopods: Cambrian-Tremadoc precursors to Ordovician radiation events, 13–23. *In* Crame J.A. & Owen, A.W. (eds) *Palaeobiogeography and biodiversity change: the Ordovician and Mesozoic-Cenozoic Radiations*. *Geological Society London, Special Publication 194.* DOI 10.1144/GSL.SP.2002.194.01.02

Biernat, G. 1970. Lower Famennian Brachiopods from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica 15(1)*, 33–56.

Biernat, G. 1973. Ordovician inarticulate brachiopods from Poland and Estonia. *Palaeontologia Polonica 28*, 1–116.

Biernat, G. 1983. Silurian inarticulate brachiopods from Poland. *Acta Palaeontologica Polonica 29(1–2)*, 91–103.

Biernat, G. & Harper, D.A.T. 1999. A lingulate brachiopod *Acrotretella*: New data from Ordovician of Poland. *Acta Palaeontologica Polonica 44*, 83–92.

Bitter, P.H. von & Ludvigsen, R. 1979. Formation and function of protegular pitting in some North American acrotretoiid brachiopods. *Palaeontology 22(3)*, 705–720.

Brock, G.A., Engelbretsen, M.J. & Dean–Jones, G. 1995. Acrotretoid brachiopods from the Devonian of Victoria and New South Wales. *Memoirs of the Association of Australasian Palaeontologists 18*, 105–120.

Chlupáč, I. 1983. Trilobite assemblages in the Devonian of the Barrandian area and their relations to palaeoenvironments. *Geologica et Palaentologica 17*, 43–73.

Chlupáč, I. 1998. Devonian, 101–133. *In* Chlupáč, I. et al. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian)*. Czech Geological Survey, Prague.

Chlupáč, I. & Kukal, Z. 1988. Possible global events and the stratigraphy of the Palaeozoic of the Barrandian (Cambrian – Middle Devonian, Czechoslovakia). *Sborník geologických věd, Geologie* 43, 83–146.

Cocks, L.R.M. 1979. New acrotretacean brachiopods from the Palaeozoic of Britain and Austria. *Palaeontology 22*, 93–100.

Cocks, L.R.M. & Popov, L.E. 2009. Generic homes for British Silurian linguloid brachiopods. *Palaeontology 52(2)*, 349–367. DOI 10.1111/j.1475-4983.2009.00847.x

Cooper, G.A. 1956. Chazyan and related brachiopods. *Smithsonian Miscellaneous Collection 127*, 1–1245.

Cooper, G.A. 1960. Correction of brachiopod names. *Journal of Paleontology 34*, 601.

Curry, G.B. & Brunton, C.H.C. 2007. Stratigraphic distribution of brachiopods, 2901–3081. *In* Williams, A., Brunton, C.H.C. & Carlson, S.J. et al. *Treatise on Invertebrate Paleontology, part H, Brachiopoda, Revised, Volume 6: Supplement.* Geological Society of America Inc. Boulder, The University of Kansas, Lawrence.

Davidson, T. 1848. Mémoire sur les brachiopodes du Système silurien supérieur de l'Angleterre. *Bulletin de la Société géologique de France, série 2, 5*, 309–338, 370–374.

Girty, G.H. 1898. Description of a fauna found in the Devonian black shale of eastern Kentucky. *American Journal of Science (series 4) 6*, 384–395. DOI 10.2475/ajs.s4-6.35.384

Goryansky, V.J. 1969. Bezzamkovyje brachiopody kembrijskich i ordovikskich otlozhenij severo-zapada Russkoj platformy [Inarticulate Brachiopods of Cambrian and Ordovician deposits of northwest of Russian platform]. *Ministerstvo geologii RSFSR, Severo-zapadnoje territorialnyje geologitcheskoje upravlenie 6*, 3–76. [in Russian]

Gray, J.E. 1840. *Synopsis of the contents of the British Museum, 42nd edition*. 370 pp. British Museum, London.

Hall, J. 1871. *Descriptions of some new species of fossils, from the shales of the Hudson River Group, in the vicinity of Cincinnati, Ohio*. 8 pp. State Cabinet of Natural History, 24th Report, Advance Copy, Albany.

Havlíček, V. 1982. Lingulacea, Paterinacea, and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sborník geologických věd, Paleontologie 25*, 9–82.

Havlíček, V. 1998. *Rafanoglossella* n. gen. and *Plectoglossa* Cooper (Glossellinae, Brachiopoda) in the Upper Ordovician of the Prague Basin. *Journal of the Czech Geological Society 43(3)*, 161–168.

Havlíček, V. 1999. Lochkovian brachiopods of the Prague Basin (Lower Devonian, Czech Republic). *Věstník Českého geologického ústavu 74(3)*, 299–322.

Havlíček, V. & Massa, D. 1973. Brachiopodes de l'Ordovicien Supérieur de Libye Occidentale. Implication stratigraphiques Régionales. *Geobios 6(4)*, 267–290.
DOI 10.1016/S0016-6995(73)80020-8

Havlíček, V. & Mergl, M. 1988. Two new discinid genera (Brachiopoda) from the Silurian and Devonian of the Prague Basin, Czechoslovakia. *Věstník Českého geologického ústavu 63(3)*, 169–172.

Holmer, L.E. 1986. Inarticulate brachiopods around the Middle–Upper Ordovician boundary in Västergötland. *Geologiska Föreningens i Stockholm Förhandlingar 108*, 97–126.
DOI 10.1080/11035898609452633

Holmer, L.E. 1987. Discinacean brachiopods from the Ordovician Kullsberg and Boda limestones of Dalarna, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar 109*, 317–326. DOI 10.1080/11035898709453096

Holmer, L.E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata 26*, 1–172.
DOI 10.18261/8200374254-1989-01

Holmer, L.E. & Popov, L.E. 1996. Early Paleozoic radiation and classification of organophosphatic brachiopods, 117–121. *In* Copper, P. & Jin, J. (eds) *Brachiopods. Proceedings of the Third International Brachiopod Congress.* Sudbury, Ontario.
DOI 10.1201/9781315138602-22

Holmer, L.E., Popov, L.E., Koneva, S.P. & Bassett M.G. 2001. Cambrian – early Ordovician brachiopods from Malyi Karatau, the western Balkhash region, and Tien Shan, Central Asia. *Special Paper in Palaeontology 65*, 1–180.

Holmer, L.E., Blodgett, R.B., Liang, Y. & Zhang, Z. 2020. The Early Devonian (Emsian) acrotretid microbrachiopod *Opsiconidion minor* Popov, 1981, from the Alaska/Yukon Territory border and Novaya Zemlya. *Estonian Journal of Earth Sciences 69(3)*, 143–153.
DOI 10.3176/earth.2020.10

Ireland, H.A. 1961. New phosphatic brachiopods from the Silurian of Oklahoma. *Journal of Paleontology 35*, 1137–1142.

Kalashnikov, N.V. 1970. O bezzamkovykh brakhiopodakh karbona severnogo Urala i ikh ekologii, 5–15. *In* Plotnikov, M.A. (ed.) *Fauna i Flora Paleozoia Severo-Vostoka Evropeiskoi chasti SSSR*. Akademiia Nauk SSSR, Komi Filial, Institut Geologii, Nauka, Leningrad.

King, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History (series 1) 18*, 26–42.
DOI 10.1080/037454809494387

Kuhn, O. 1949. *Lehrbuch der Paläozoologie*. 326 pp. Schweizerbart, Stuttgart.

Kutorga, S.S. 1846. Ueber das Silurische und Devonische Schichten-System von Gatschina. *Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersbourg, Verhandlungen 1845–1846*, 85–139.

Kutorga, S.S. 1848. Ueber die Brachiopoden–familie der Siphonotretaceae. *Russisch–Kaiserliche Mineralogische Gesellschaft zu St. Petersbourg, Verhandlungen 1847*, 250–286.

Kuznetsov, Y.I. 1960. Linguly srednego karbona Tatarii. *Paleontologicheskii Sbornik (L'vov) 3(16)*, 125–132.

Lockley, M.G. & Williams, A. 1981. Lower Ordovician Brachiopoda from mid and southwest Wales. *British Museum (Natural History), Bulletin (Geology) 35(1)*, 1–78.

Ludvigsen, R. 1974. A new Devonian acrotretid (Brachiopoda, Inarticulata) with unique protegular ultrastructure. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 3*, 133–148.

Menke, C.T. 1828. *Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur*. 91 pp. G. Uslar, Pyrmonti.
DOI 10.5962/bhl.title.13182

Mergl, M. 1982. *Caenotreta* (Inarticulata, Brachiopoda) in the Upper Silurian of Bohemia. *Věstník ústředního ústavu geologického 57(2)*, 115–116.

Mergl, M. 1996. Discinid brachiopods from the Kopanina Formation (Silurian) of Amerika Quarries near Mořina, Barrandian, Central Bohemia. *Časopis Národního muzea, Řada přírodovědná 165(1–4)*, 121–126.

Mergl, M. 1999a. Genus *Lingulops* (Lingulata, Brachiopoda) in Silurian of the Barrandian. *Journal of the Czech Geological Society 44(1–2)*, 155–158.

Mergl, M. 1999b. Genus *Paterula* (Brachiopoda) in Ordovician-Silurian sequence of Central Bohemia. *Věstník Ústředního ústavu geologického 74(3)*, 347–361.

Mergl, M. 2001. Lingulate brachiopods of the Silurian and Devonian of the Barrandian. *Acta Musei nationalis Pragae, Series B – Historia naturalis 57(1–2)*, 1–49.

Mergl, M. 2002. Linguliformean and craniiformean brachiopods of the Ordovician (Třenice to Dobrotivá Formations) of the Barrandian, Bohemia. *Acta Musei nationalis Pragae, Series B – Historia naturalis 58(1–2)*, 1–82.

Mergl, M. 2003a. *Orbaspina chlupaci* sp. nov., a new siphonotretid brachiopod from the Silurian of the Barrandian area, Bohemia. *Bulletin of Geosciences 78(4)*, 419–421.

Mergl, M. 2003b. Silicified brachiopods of the Kotýs Limestone (Lochkovian) in the Bubovice area (Barrandian, Bohemia). *Acta Musei nationalis Pragae, Series B – Historia naturalis 59(3–4)*, 99–150.

Mergl, M. 2006. A review of Silurian discinoid brachiopods

from historical British localities. *Bulletin of Geosciences 81(4)*, 215–236. DOI 10.3140/bull.geosci.2006.04.215

Mergl, M. 2008. Lingulate brachiopods from the *Acanthopyge* Limestone (Eifelian) of the Barrandian, Czech Republic. *Bulletin of Geosciences 83(3)*, 281–298. DOI 10.3140/bull.geosci.2008.03.281

Mergl, M. 2010. A review of Silurian discinoid brachiopods from Gotland, Sweden. *Bulletin of Geosciences 85(3)*, 367–384. DOI 10.3140/bull.geosci.1176

Mergl, M. 2019. Lingulate brachiopods across the Kačák Event and Eifelian–Givetian boundary in the Barrandian area, Czech Republic. *Bulletin of Geosciences 94(2)*, 169–186. DOI 10.3140/bull.geosci.1740

Mergl, M. 2021. Dead or alive? Brachiopods and other shells as substrates for endo- and sclerobiont activity in the early Devonian (Lochkovian) of the Barrandian, Czechia. *Bulletin of Geosciences 96(4)*, 401–429. DOI 10.3140/bull.geosci.1838

Mergl, M. 2022. The earliest *Cyrtina* (Brachiopoda, Cyrtinidina) in the Devonian of the Barrandian (Czech Republic). *Folia Musei Rerum Naturalium Bohemiae Occidentalis, Geologica et Palaeobiologica 56*, 1–10. DOI 10.2478/fbgp-2022-0001

Mergl, M. 2024. Lingulates of the *Monograptus belophorus* Biozone (Motol Formation, Sheinwoodian, Wenlock) of the Barrandian area, Czech Republic: insight into remarkable lingulate brachiopod diversity in the Silurian. *Bulletin of Geosciences 99(1)*, 1–42. DOI 10.3140/bull.geosci.1897

Mergl, M. & Ferrová, L. 2009. Lingulate brachiopods from the Chýnice Limestone (upper Emsian, Barrandian; Czech Republic). *Bulletin of Geosciences 84(3)*, 525–546. DOI 10.3140/bull.geosci.1143

Mergl, M. & Jiménez–Sánchez, A. 2015. Lingulate brachiopods from the Suchomasty Limestone (upper Emsian) of the Barrandian, Czech Republic. *Bulletin of Geosciences 90(1)*, 173–193. DOI 10.3140/bull.geosci.1533

Mergl, M. & Kraft, P. 2023. Byronids and similar tubular fossils from the Devonian of the Barrandian area (Czech Republic). *Earth and Environmental Transactions of the Royal Society of Edinburgh 113*(*4*), 373–390. DOI 10.1017/S1755691023000099

Mergl, M. & Šmídtová, N. 2023. Lingulate brachiopods from the Vinařice Limestone (Devonian, Pragian) of the Barrandian area, Czechia. *Bulletin of Geosciences 98(3)*, 199–214. DOI 10.3140/bull.geosci.1880

Mergl, M. & Valenzuela-Ríos, J.I. 2020. Uniformity of tropical micromorphic brachiopods from the Lower Devonian: lingulates from the section Compte-I of Spanish Central Pyrenees. *Bulletin of Geosciences 95(2)*, 215–230. DOI 10.3140/bull.geosci.1783

Mergl, M. & Vodrážková, S. 2012. Emsian–Eifelian lingulate brachiopods from the Daleje–Třebotov Formation (Třebotov and Suchomasty limestones) and the Choteč Formation (Choteč and Acanthopyge limestones) from the Prague Basin; the Czech Republic. *Bulletin of Geosciences 87(2)*, 315–332. DOI 10.3140/bull.geosci.1298

Mergl, M., Frýda, J. & Kubajko, M. 2018. Response of organophosphatic brachiopods to the mid–Ludfordian (late Silurian) carbon isotope excursion and associated extinction events in the Prague Basin (Czech Republic). *Bulletin of Geosciences 93(3)*, 369–400. DOI 10.3140/bull.geosci.1710

Morse, W.C. 1931. The Pennsylvanian invertebrate fauna of Kentucky. *Geological Survey of Kentucky (series 6) 36*, 295–348.

Orbigny, A. d' 1847. Considérations zoologiques et géologiques sur les Brachiopodes ou Palliobranches. *Comptes Rendus Hebdomodaires des Séances de l'Académie des Sciences 25*, 193–195, 266–269.

Percival, I.G. 1978. Inarticulate brachiopods from the Late Ordovician of New South Wales, and their palaeoecological significance. *Alcheringa 2(2)*, 117–141. DOI 10.1080/03115517808619083

Popov, L.E. 1981. Pervaia nakhodka mikroskopicheskikh bezzamkovykh brakhiopod semeistva Acrotretidae v Silure Estonii [The first record of microscopic inarticulate brachiopods of the family Acrotretidae from the Silurian of Estonia]. *Eesti NSV Teaduste Akadeemia Toimetised (Keemia, Geoloogia) 30*, 34–41.

Popov, L.E. & Holmer, L.E. 1994. Cambrian–Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils & Strata 35*, 1–156. DOI 10.18261/8200376516-1994-01

Popov, L.E., Khazanovitch, K.K., Borovko, N.G., Sergeeva, S.P. & Sobolevskaya, R.F. 1989. The key sections and stratigraphy of the Cambrian Ordovician phosphate-bearing obolus beds on the north-eastern Russian platform. *Akademia nauk SSSR, Ministerstvo Geologii SSSR, Mezhvedomstvennym stratigraficheskij komitet SSSR, Trudy 18*, 1–222. [in Russian]

Robson, S.P. & Pratt, B.R. 2007. Late Marjuman (Cambrian) linguliformean brachiopods from the Deadwood Formation of South Dakota, USA. *Palaeontographica Canadiana 27*, 1–95. DOI 10.1111/j.1502-3931.2006.00003.x

Schuchert, C. 1893. Classification of the Brachiopoda. *American Geologist 11*, 141–167.

Sinclair, G.W. 1945. Some Ordovician lingulid brachiopods. *Royal Society of Canada, Transactions (series 3, section 4) 39*, 55–82.

Slavík, L. 2011. *Lanea carlsi* conodont apparatus reconstruction and its significance for subdivision of the Lochkovian. *Acta Palaeontologica Polonica 56(2)*, 313–327. DOI 10.4202/app.2009.0046

Slavík, L. & Hladil, J. 2020 Early Devonian (Lochkovian – early Emsian) bioevents and conodont response in the Prague Synform (Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology 549*, art. 109148. DOI 10.1016/j.palaeo.2019.04.004

Slavík, L., Carls, P., Hladil, J. & Koptíková, L. 2012. Subdivision of the Lochkovian Stage 2 based on conodont faunas from the stratotype area (Prague Synform, Czech Republic). *Geological Journal 47*, 616–631. DOI 10.1002/gj.2420

Sutton, M.D., Bassett, M.G. & Cherns, L. 1999. Lingulate brachiopods from the Lower Ordovician of the Anglo–Welsh Basin. Part 1. *Monograph of the Palaeontographical Society London 610*, 1–60. DOI 10.1080/25761900.2022.12131790

Sutton, M.D., Bassett, M.G. & Cherns, L. 2000. Lingulate brachiopods from the Lower Ordovician of the Anglo–Welsh Basin. Part 2. *Monograph of the Palaeontographical Society London 613*, 61–114.
DOI 10.1080/25761900.2022.12131793

Vacek, F. & Žák, J. 2019. A lifetime of the Variscan orogenetic plateau from uplift to collapse as recorded by the Prague Basin, Bohemian Massif. *Geological Magazine 156(3)*, 485–509. DOI 10.1017/S0016756817000875

Valentine, J.L. 2006a. Early Devonian brachiopods from the Cobar Supergroup, western New South Wales, 192–259. *In* Valentine J.L. *Taxonomic assessment, biostratigraphy and faunal turnover of Silurian–early Devonian linguliformean brachiopods from New South Wales, Australia*. MS, Ph.D. thesis. Macquarie University, Sydney.

Valentine, J.L. 2006b. A thorny problem revisited: a cladistic analysis of the Siphonotretida (Linguliformea, Brachiopoda), 261–342. *In* Valentine J.L. *Taxonomic assessment, biostratigraphy and faunal turnover of Silurian–early Devonian linguliformean brachiopods from New South Wales, Australia*. MS, Ph.D. thesis. Macquarie University, Sydney.

Valentine, J.L., Brock, G.A. & Molloy, P.D. 2003. Linguliformean brachiopod faunal turnover across the Ireviken Event (Silurian) at Boree Creek, central–western New South Wales, Australia, 301–327. *In* Königshof, P. & Schindler, E. (eds) *Mid–Palaeozoic bio– and geodynamics: the north Gondwana–Laurasian interaction. Courier Forschungsinstitut Senckenberg 242.*

Valentine, J.L., Cole, D. & Simpson, A.J. 2006. Silurian linguliformean brachiopods and conodonts from the Cobra Formation, Southeastern New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales 127*, 199–234.

Waagen, W. 1885. Salt Range fossils, I. *Productus*–Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologica Indica (series 13) 4*, 729–770.

Walcott, C.D. 1912. Cambrian Brachiopoda. *United States Geological Survey Monograph 51. Parts 1 & 2*, 1–872, 1–363.

Willard, B. 1928. The brachiopods of the Ottosee and Holston formations of Tennessee and Virginia. *Bulletin of the Harvard Museum of Comparative Zoology 68*, 255–292.

Williams, A. 2003. Microscopic imprints on the juvenile shells of Palaeozoic linguliform brachiopods. *Palaeontology 46(1)*, 67–92. DOI 10.1111/1475-4983.00288

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L. & Popov, L.E. 1996. A supra–ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society, Biological Sciences 355*, 1171–1193.
DOI 10.1098/rstb.1996.0101

Wright, A.D. & McClean, A.E. 1991. Microbrachiopods and the End Ordovician Event. *Historical Biology 5*, 123–129. DOI 10.1080/10292389109380395