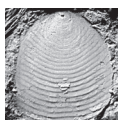


Lingulates of the *Monograptus belophorus* Biozone (Motol Formation, Sheinwoodian, Wenlock) of the Barrandian area, Czech Republic: insight into remarkable lingulate brachiopod diversity in the Silurian

MICHAL MERGL



Lingulate brachiopods are described from the mid-Sheinwoodian “*Miraspis*” Limestone in the famous Loděnice-Špičatý vrch locality near Loděnice in the Barrandian area. Twenty-three species have been determined, some only identified to generic or family rank due to rarity or poor preservation. Two new genera *Platylops* (Subfamily Elliptoglossinae) and *Praethele* (Family Orbiculoideidae) and three new species are described: *Schizotreta elegantia* sp. nov., *Praethele postvexata* sp. nov., and *Orbaspina involuta* sp. nov. Several poorly known species erected by Joachim Barrande in 1879 are redescribed and their taxonomic rank and stratigraphic occurrences are elucidated. Species assigned to genera *Pseudolingula*, *Barrandeoglossa*, *Kacakiella*, *Wadiglossella*, *Lingulops*, *Schizocrania*, *Schizobolus*, *Acrosaccus*, *Sterbinella*, *Artiotreta*, *Acrotretella*, *Havlicekion* and *Opsiconidion* are described. The brachiopods come from sediments where *Cooksonia barrandei* and other earliest land plants have been observed. The unexpectedly high taxonomic diversity indicates a favourable marine environment in the surroundings of a volcanic island(s). The common presence of the widespread acrotretid brachiopods and small but remarkably diverse discinid brachiopods corroborate the dominance of the epibenthic or epiphytic life habit of lingulates over the burrowing style of the pedunculate forms. • Key words: Sheinwoodian, Silurian, organophosphatic brachiopods, Barrandian.

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The first report on lingulate brachiopods of the Silurian from the Barrandian area came from Joachim Barrande (Barrande 1879). He illustrated tens of species but all lacked formal descriptions. His type specimens often lack exact locality details and stratigraphical data of the present standard. He gave reference to locality only by mentioning nearby villages in the figure captions. Such inadequately documented types are problematic for comparative use without a modern revision. With some exceptions when locality and stratigraphical data are without doubt (Kříž 1970, 1992, 1999; Chlupáč 1983), other species are waiting for clarification of their stratigraphical and geographical setting.

Mergl (2001a) provided the first attempt to enhance their taxonomy and stratigraphy. However, the overall rarity of organophosphatic brachiopods in limestones and technical possibilities left many questions unresolved. Generally, poor knowledge of Silurian lingulate brachiopods at the

beginning of 21st century has little improved over the last two decades. Apart from the contributions of J.L. Valentine, published or compiled in his thesis (Valentine *et al.* 2003, 2006; Valentine 2006a, b), few other papers on Silurian lingulates have appeared (Mergl 2003, 2006, 2010; Cocks & Popov 2009; Mergl *et al.* 2018). The current interest on lingulate brachiopods focuses on their stem groups (*e.g.* Holmer *et al.* 2002, 2008; Holmer & Caron 2006), faunas of exceptional preservation (*e.g.* Topper *et al.* 2015, Zhang *et al.* 2020) or their Cambrian and Ordovician history and palaeogeography (Popov *et al.* 2013, Lavié & Benedetto 2016, Claybourn *et al.* 2020 and many others). The history of lingulates in the Silurian seemingly represents an unattractive research direction. However, the climatic changes in the Silurian (Frýda *et al.* 2021) and their impact on biota are topical (Kaljo *et al.* 1996; Lehnert *et al.* 2003, 2007a, b; Manda & Kříž 2006; Loydell 2007; Calner 2008; Eriksson *et al.*

2009; Loydell & Frýda 2011; Gocke *et al.* 2012; Jeppsson *et al.* 2012; Manda *et al.* 2012; Frýda & Manda 2013). The pilot study (Mergl *et al.* 2018) indicates that the Silurian history of lingulates may be similarly significant as their Cambrian and Ordovician history.

The discovery of terrestrial vegetation in marine sediments of Sheinwoodian age (Silurian, Wenlock) at the famous locality Loděnice-Špičatý vrch in Central Bohemia (Libertín *et al.* 2018a, b; Bek *et al.* 2022) has inspired the current study. The area between Loděnice and Bubovice was a source of many of Barrande's brachiopod types. This study helps to elucidate the taxonomical position and stratigraphical range of his newly erected species. It also reveals the up to now hidden taxonomic diversity of organophosphatic brachiopods contemporaneous with the invasion of land by plants.

Geological setting and previous studies

All lingulate brachiopods described in the present article come from the road cut south of Loděnice, on the western slope of the small hill named Špičatý vrch in the Central Bohemia (Fig. 1A, B). This locality has been known since the 1940s, but the nearby localities were exploited by Joachim Barrande since the middle 19th century. The geology and palaeontology of the road section have been described by Bouček (1941a, b; 1951) who noted the presence of richly fossiliferous tuffaceous shales ("Miraspis Shale") and thinly bedded limestones ("Miraspis Limestone") overlying a submarine alkaline basalt lava flow followed by a 4.6 m thick sequence of bedded tuffs and tuffites (Fig. 1C–E).

The studied section is exposed in a sharp left curve of the local road from Loděnice to Bubovice but the outcrops are greatly covered by scree now (Fig. 1E). The details of the locality have been published by Horný (1955, 1962, 1965) and Kříž (1984, 1992). Fossils belong to the trilobite *Miraspis* Community (Chlupáč 1987) and brachiopod *Miraspis*–*Mezounia* Community (Havlíček & Štorch 1990, 1999), respectively. The fossils indicate a quiet-water, well-oxygenated, subtidal moderately deep environment of benthic assemblage 4–5 (Bek *et al.* 2022; *sensu* Boucot 1975). However, the lamination of grey platy limestones and the absence of trace fossils are interpreted as indicating hypoxic to dysaerobic conditions near or just below the water/sediment interface. The fossils of the "Miraspis Limestone" are often disarticulated, heavily fragmented, and deformed by compaction of sediment. Bioclasts show no traces of bioerosion. These features indicate that the bioclasts were mechanically transported and sorted. Lists and descriptions of benthic fossils (mainly brachiopods and trilobites) are accessible in more papers (Bouček 1941a; Šnajdr 1980; Kříž 1984,

1992; Havlíček & Štorch 1990; Havlíček 1995; Mergl 2001a). The locality's significance has increased in recent years, because the outcropping section yielded the oldest terrestrial plant remains in the Barrandian area (Libertín *et al.* 2018a). Spores, prasinophytes and scolecodonts from the "Miraspis Shales" have been described in detail by Bek *et al.* (2022).

The Špičatý vrch locality is a highly significant geological site of the Silurian of the Barrandian area. The episode of sea level fall in the late Aeronian (Loydell 1998, Frýda & Štorch 2014) first brought the diverse benthic biota into the basin, but only outside the Svätý Jan volcanic area where the Špičatý vrch locality is located. The rich fauna in volcanic-carbonate facies in the Hýskov area north of the Beroun is unique in the Llandovery in northern peri-Gondwanan regions (Havlíček & Kříž 1973, Šnajdr 1978, Kraft 1982, Havlíček & Štorch 1990, Štorch 2001, Tonarová *et al.* 2019).

The next acme of lingulate brachiopods in the preserved part of the basin began in the mid-Sheinwoodian, during the *Monograptus belophorus* Biozone. The active volcanism of the Svätý Jan Volcanic Centre formed shoals and likely emergent islands in the mid-Sheinwoodian. A shallow sea in a temperate climate and a supply of nutrients from volcanic rocks boosted the expansion of a diverse marine biota. The Špičatý vrch locality is one of the sites with rich marine fauna of this age. Nearby restricted but sufficiently stable emergent areas at island(s) formed an ecospace for the growth of the early terrestrial plants (Bek *et al.* 2022). Their remains washed into the sea associated with the marine fossils. The age of the rich fauna and associated flora at the Špičatý vrch is proven by an eponymous graptolite (Bek *et al.* 2022, Štorch 2023). It was correctly defined firstly by Bouček (1941a) and confirmed by Kříž (1984, 1992). According to Havlíček (1995) the fossiliferous section including also a higher (herein unstudied) part of the section covers the *Monograptus belophorus* to *Cyrtograptus ramosus*–*C. perneri* biozones. The current study of the fauna at the Špičatý vrch near Loděnice offers an insight into real lingulate brachiopod diversity in mid-Silurian time (431.5 Ma).

Sampling method

Apart from a few specimens coming from old collections, all described organophosphatic brachiopods come from a bulk sample, represented by about one hundred kilograms of the "Miraspis Limestone" sampled from scree in the Špičatý vrch locality. Limestone blocks, on average 5 to 10 cm thick, were mechanically split to pieces less than 2–3 cm length and width and less than 1 cm thick. All fossils, mainly brachiopods, trilobites,

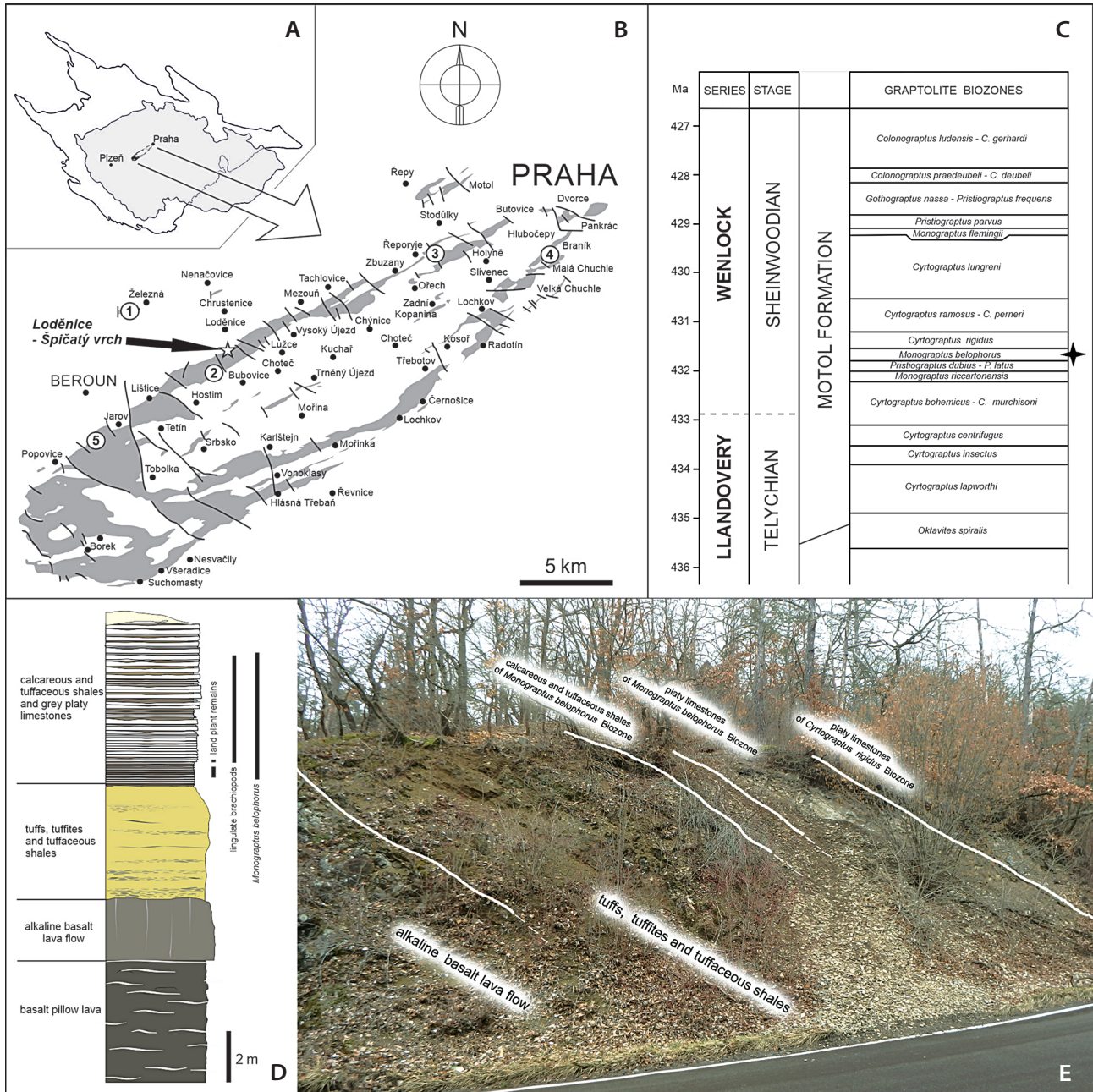


Figure 1. A – schematic map of the Bohemian Massif, the Czech Republic and the Silurian of the Barrandian area. • B – map of the Silurian outcrop area with position of the Loděnice-Špičatý vrch locality (arrow) and other localities mentioned in the text: 1 – Hýskov, 2 – Elektrárna, Svätý Jan, 3 – Praha-Řeporyje, Daleje Valley, 4 – Praha-Malá Chuchle, 5 – Kosov Quarry. • C – stratigraphical position of lingulate fauna within graptolite zones of the Motol Formation (after Štorch 2023, modified). • D – schematic section of the Loděnice-Špičatý vrch locality, with the marked position of examined lingulate brachiopod fauna, occurrences of the earliest records of *Cooksonia*, and the index graptolite *Monograptus belophorus*. • E – road-cut section Špičatý vrch – Barrandovy Jámy near Loděnice (2023).

gastropods, conulariids, graptolites and others have been sampled and counted. In total, some 3000 brachiopod specimens have been determined on species or genus ranks. Organophosphatic brachiopods represent less than 3% of all brachiopod specimens, with 73 determined specimens. Rhynchonelliformean brachiopods are represented, in descending abundance, by *Strophochonetes*

soror (Barrande, 1879), *Streptis grayii* (Davidson, 1848), *Mezounia bicuspis* (Barrande, 1879) and *Cyrtia maior* Bouček, 1941c; other species are less common. The diversity of lingulate brachiopod fauna is rather high, with at least 23 species, but the majority of specimens belong to small-sized species. Subsequently, 20 kg of these limestone pieces were etched with a 15% solution

of acetic acid for four to five days. The residue was sieved and cleaned under water, air-dried, and the fraction larger than 0.25 mm was hand-picked under a binocular lens. All fossils were extracted. These are represented, in a descending abundance, by phosphatic byronid tubes (*Byronia* sp.) and their attachment discs (*Phosphannulus* sp.), diverse and heavily fragmented organophosphatic brachiopods, small conulariid fragments, conodonts, small phosphatic coprolites and other phosphatic or phosphatised organic, likely algal and fungal remains. Associated scolecodonts are moderately abundant; their presence and taxonomy have been evaluated by Bek *et al.* (2022). Two types of sponge spicules, (1) gracile tetraxons and pectactines and (2) robust tetraxons, all interpreted as derived from hyalosponges, have been observed. It is worthy of note that, unlike the acid-treated limestone residues of Ludlow and Přídolí age in the Barrandian area, phyllocarid remains, phosphatic “pearls”, and fish scales have not been observed in the Špičatý vrch locality.

Shell preservation

The preservation of organophosphatic brachiopods in the “*Miraspis* Limestone” is excellent in minute details, but shells are extremely broken to pieces (Fig. 18J) due to diagenetic compression. Therefore, the shells extracted from the rock by acid solution are only rarely complete, and even micromorphic dorsal valves of acrotretides are often fragmented. Only two juvenile specimens of *Acrotretella* have been observed with both valves conjoined (Fig. 16G, H). In general, the laboratory dissolution of limestone pieces resulted in the disintegration of valves broken in pieces. Therefore, the loose shell fragments in the residuum represent a real puzzle: a mixture of different parts of valves of a more than twenty species. These minute fragments often exhibit the finest details of the shell exterior and interior. The microornament has been used as the key for grouping of fragments into the main taxonomic groups and, in some cases, into the particular species.

Valves directly observed on bedding planes of limestone were generally fractured inside the shell wall. Thus, their “internal” moulds do not show the real shell interior, and similarly, the “external” moulds do not exhibit the actual shell exterior. For examination of the entire shell morphology of discinoidean species, selected “external” moulds were poured by an artificial resin (Dentacryl) and after hardening the samples were macerated with 15% acetic acid for three or four days to remove the limestone below the shell. The phosphatic shells remained fixed to the resin pads. As seen in Fig. 11C, D, the complete valves demonstrate excellent morphologic details, although compression by compaction, network of fractures and

delamination of shell layers partially obscure the original morphology. The diagenetic minerals often penetrate the shell. These mineral grains are firmly affixed to the shell surface and cannot be removed without shell damage. Ultrasonic cleaning was avoided because of the brittleness of the shells.

Important data on the internal shell morphology have been observed in two valves split within their phosphatic walls. The higher content of organic matrix inside the shell wall below the muscle scars caused the accumulation of iron sulphides during the diagenetic process. The subsequent weak weathering of sulphides distinctly marks the attachment sites of the muscles (Fig. 12G).

Illustration. – The loosed specimens were photographed using a Scanning Electron Microscope (JSM-7401F JEOL) at the Biology Centre of the Academy of Sciences of the Czech Republic at České Budějovice, South Bohemia. The specimens preserved in rocks and those attached to the resin pads were whitened by ammonium chloride and photographed under a binocular lens (OLYMPUS SZX 7) with the use of the Deep Focus 3.1 software.

Repository. – The majority of 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, Czechia (prefix PCZCU). Some studied specimens come from the palaeontological collections of the National Museum, Prague, Czechia (prefix NML), the palaeontological collections of the Museum of Dr. Bohuslav Horák, Rokycany, Czechia (prefix MBHR) and the Natural History Museum, London, Great Britain (prefix B).

Terminology and abbreviations. – Terminology of shell morphology is that of Williams (2003). Taxonomy follows Holmer & Popov (2000). Abbreviations: L – length, W – width, dv – dorsal valve, vv – ventral valve, tr – pedicle track.

Systematic palaeontology

Subphylum Linguliformea Williams *et al.*, 1996
Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Pseudolingulidae Holmer, 1991

Remarks. – Rare, poorly preserved remains of medium to large-sized lingulates of linguloid outline have been observed. Fragments present a reduced dorsal pseudo-interarea restricted to a narrow-raised band along the

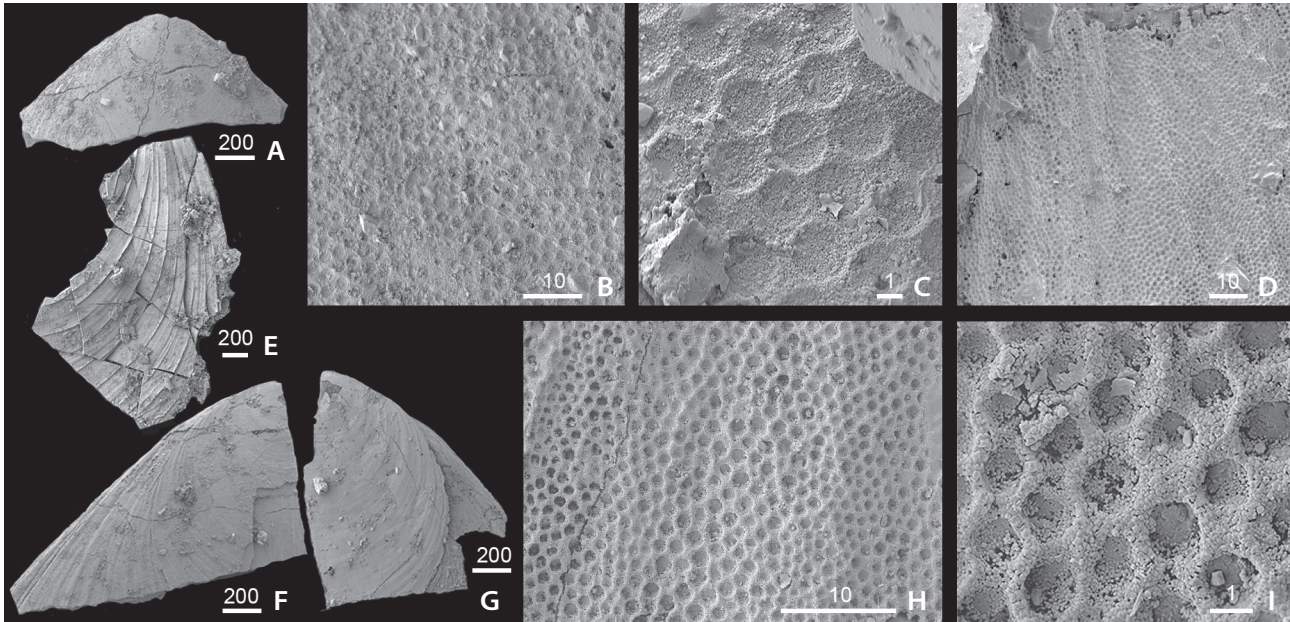


Figure 2. A–C, E – *Pseudolingula?* sp. A; A–C – incomplete ventral valve and details of its microornamentation, PCZCU 2622; E – fragment of valve, PCZCU 2625. • D, F–I – *Pseudolingula?* sp. B; D, G–I – incomplete ventral valve and details of its microornamentation, PCZCU 2623; F – fragment of ventral valve, PCZCU 2624. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in μm .

posterior margin. Shells are referred as two separate species due to the differences in the microornament. Elucidation of their affinity needs much better material.

Genus *Pseudolingula* Mickwitz, 1909

Type species. – *Crania quadrata* Eichwald, 1829. Vormsi Regional Stage (Ordovician); Estonia.

Pseudolingula? sp. A

Figure 2A–C, E

Material. – Two fragments (PCZCU 2622, 2625).

Description. – Data about the shape of shell are very restricted, but the species is likely of medium size, thin-walled, and having an elongated outline. The posterior of the dorsal valve is weakly acuminate, with a beak angle of 110° . The dorsal valve interior lacks a distinct pseudointerarea. Thin and imperfect concentric fila are separated by broad flat bands. The larval shell is $600\ \mu\text{m}$ wide, smooth, gently convex. The mature shells bear a microornament of very shallow, circular pits with a flat bottom (Fig. 2B, C). Pits display a honeycomb distributional pattern and never intersect each other although they are in a close contact. The observed diameter of the pits is about $2\ \mu\text{m}$.

Remarks. – The shell cannot be referred to any of the species so far known from the Motol Formation. Although there is a similarity in shell size with *Barrandeoglossa fissurata* (Barrande, 1879), the postlarval macroornamen-

tation is wholly different. Knowledge of microornament of similarly shaped Silurian species *Pseudolingula lewisii* (J. de C. Sowerby, 1839) from the Ludlow of Britain is poor (Cocks & Popov 2009). The raised concentric fila in the Bohemian specimens differ from the almost uniformly sized and more closely spaced growth fila of the British species (see Cocks & Popov 2009, pl. 1, figs 5, 11).

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone, locality Loděnice (Špičatý vrch) (rare).

Pseudolingula? sp. B

Figure 2D, F–I

Material. – Two fragments of dorsal valves (PCZCU 2623, 2624).

Description. – The knowledge of this species is poor. The dorsal valve had a large juvenile shell, which is more than $1\ \text{mm}$ wide and is nearly smooth, covered by weak concentric bands. The mature shell exterior is covered by deep pits about $1\ \mu\text{m}$ in diameter, slightly varying in size (Fig. 2D, H, I). The macroornamentation of the mature shell is formed by raised unevenly sized growth fila and bands.

Remarks. – The suggested larger size of this species greatly exceeds the calculated shell size of the preceding species. The specimen is distinguished by its unusually large juvenile shell that indicates a large adult shell.

The observed macroornamentation of mature shells (Fig. 2F) and suggested beak angle are similar to that of *Pseudolingula lewisii* (J. de C. Sowerby, 1839) from the Ludlow of Britain (Cocks & Popov 2009). However, the British species (whose microornamentation is unknown) is stratigraphically younger with its first occurrence in the Gorstian. Another comparable species from the Wenlock of Britain is *Tunisiglossa? symondsii* (Davidson, 1866) but the knowledge of its microornamentation is similarly insufficient (Cocks & Popov 2009).

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (rare).

Family Obolidae King, 1846
Subfamily Obolinae King, 1846

Genus *Kacakiella* Mergl, 2001a

Type species. – By original designation, *Kacakiella bouceki* Mergl, 2001a. Motol Formation (Sheinwoodian, Wenlock, Silurian); Prague Basin, Czech Republic.

Kacakiella bouceki Mergl, 2001a

Figures 3, 4

2001a *Kacakiella bouceki* sp. n.; Mergl, p. 13, pl. 5, figs 1–12.

Material. – Two complete dorsal valves (PCZCU 2608, 2607), one entire ventral valve (PCZCU 2609), and numerous incomplete valves and their fragments, some illustrated (PCZCU 2610–2621).

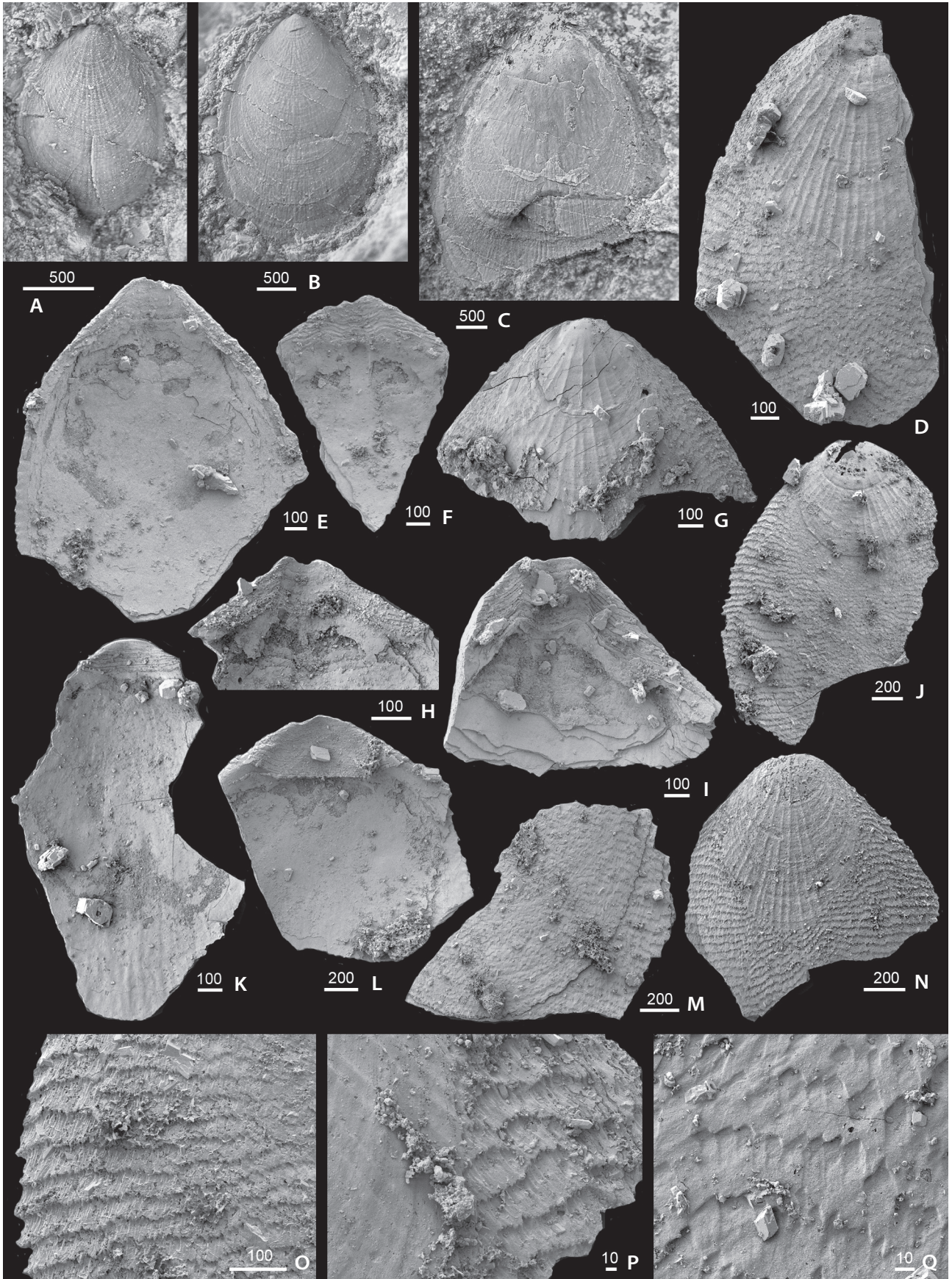
Description (emended). – The shell is thick-walled relative to its size, medium-sized, with 10 mm maximum width anterior to shell midlength. A distinct limbus is absent. The margins of the shell are finely serrated (Fig. 3O). The dorsal valve is elongated oval in small specimens (Fig. 3A) becoming more subtriangular to drop-like in outline in larger individuals (Fig. 3C), rectimarginate. The Wdv/Ldv ratio is 0.75 to 0.86 (calculated on one small and one large complete valve). The axial profile is evenly convex with maximum convexity at midlength. The axial sector is not depressed. The transverse shell convexity is

moderate, with evenly sloping constantly convex flanks. The posterior margin is gently pointed, with a beak angle of 120°. The lateral sides and anterior margin are evenly rounded. The dorsal pseudointerarea has narrow propareas and a broadly and deeply concave median groove (Fig. 3K, L) that is about 50% as long as wide. The anterior edge of the median groove is strictly transverse and weakly but distinctly elevated above the valve floor (Fig. 3L). Transverse growth lines that are obviously deflexed posteriorly near the propareas cover the surface of the median groove. An evenly rounded posterior margin of the larval shell protrudes over the median groove (Fig. 3K).

The visceral area is poorly defined, large, as long as wide, with a nearly smooth surface lacking any moulds of epithelial cells (Fig. 3K). The muscle scars are weakly impressed but their locations are well manifested by a different structure of the shell floor. The paired scars of umbonal muscles are large, located just anterior to the median groove (Fig. 3L). The scars lie near each other, with the triangular outline expanding laterally. The narrowly crescentic undivided paired scars after the transmedian, outside lateral and middle lateral muscles are located lateral to umbonal muscles on a steep posterolateral slope of the shell floor. The paired central muscle scars are small, elongate oval, located in the posterior one-third of the valve, separated from by each other by a broad flat visceral area. The anterior lateral muscle scars lie at about midvalve on an indistinctive anterior projection. These scars have a distinctly elongated outline having the same size as the central scars (Fig. 3C, K). The median ridge is absent. The *vascula lateralia* are not impressed, but radial ridges 50 µm wide separated by equally wide interspaces cover the entire shell floor outside the visceral area. They likely correspond to distal canals of the vascular system. The ventral valve is elongate oval, with a pointed beak, having its maximum width in the anterior two-fifths of the shell.

The Wvv/Lvv ratio is 0.70 to 0.78 (calculated on five entire valves). The axial profile is evenly convex with maximum convexity at the posterior one-third. The transverse shell convexity is moderate to prominent posteriorly, with evenly sloping undepressed flanks. The posterior margin is distinctly acuminate, with a beak angle of 80 to 90°. Lateral sides are gently rounded, becoming progressively rounded anteriorly. The anterior

Figure 3. *Kacakiella bouceki* Mergl, 2001a; A – exfoliated small dorsal valve, PCZCU 2608; B – exfoliated small dorsal valve, PCZCU 2609; C – internal mould of dorsal valve, PCZCU 2607; D – exterior of dorsal valve, PCZCU 2610; E – interior of ventral valve, PCZCU 2614; F – interior of ventral valve, PCZCU 2615; G – exterior of dorsal valve, PCZCU 2613; H – ventral pseudointerarea, PCZCU 2616; I – ventral pseudointerarea, PCZCU 2617; J, O – exterior of dorsal valve, and detail of its terrace lines, PCZCU 2611; K – interior of ventral valve, PCZCU 2618; L – dorsal pseudointerarea, PCZCU 2619; M, Q – shell fragment and detail of divaricate lines, PCZCU 2620; N – exterior of ventral valve, PCZCU 2612; P – contact of larval shell (left) with mature shell, PCZCU 2621. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A–C), all others SEM photos. Bars in µm.



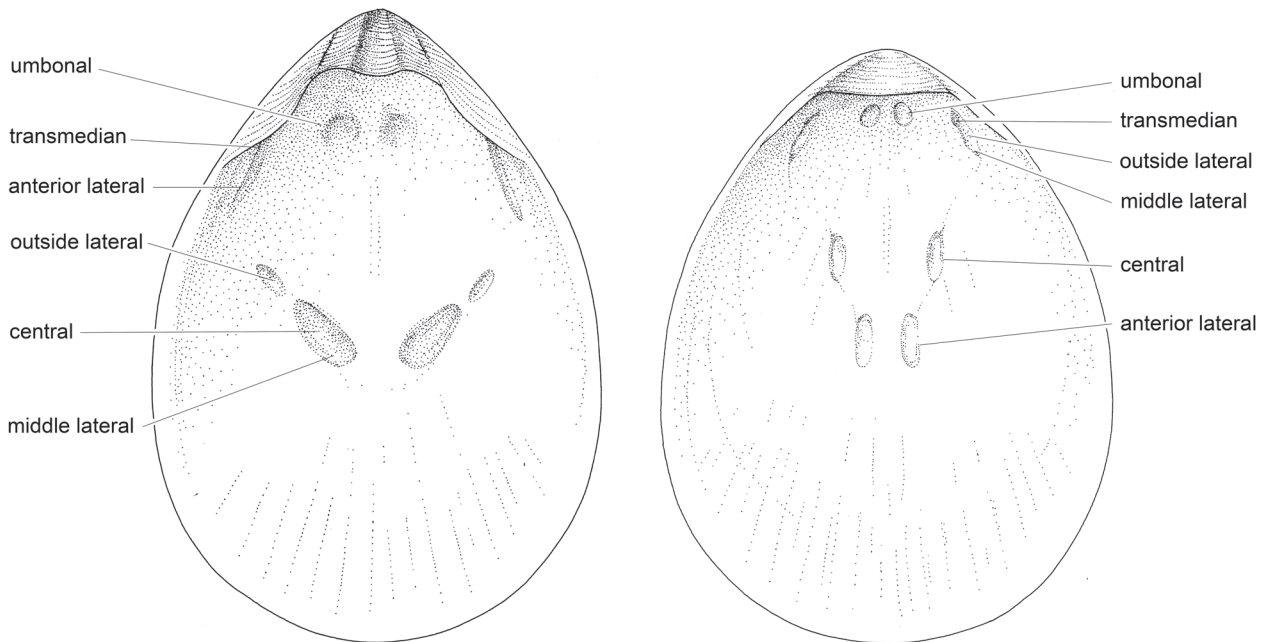


Figure 4. *Kacakiella bouceki* Mergl, 2001a; schematic illustration of musculature.

margin is evenly rounded. The ventral pseudointerarea has broad propareas showing the flexure lines (Fig. 3E). The pedicle groove is short, deep and wide, expanding anteriorly, about half-length of the propareas (Fig. 3E, F, H, I). The floor of the groove is arched anteriorly. Propareas are narrowly triangular. The outer propareas are longer and narrower than the inner propareas. The surface of propareas and the floor of the pedicle groove bear distinct growth bands (Fig. 3I). The inner edges of propareas are shortly excavated in their anterior portion (Fig. 3E). The paired scars of umbonal muscles are rather large, subtriangular, located anterolaterally to the pedicle groove (Fig. 3E, Fig. 4). A pair of narrow scars after the transmedian and anterior lateral muscles borders the visceral area on its posterolateral slope. The outside lateral muscles left a pair of subcircular scars. These scars, slightly larger than the umbonal scars, lie near the lateral sides of the visceral area. The middle lateral and central muscle scars are united and form a pair of large narrowly elongate oblique scars posterior to the midvalve (Fig. 3E). A broad undivided area separates these muscle scars. Imprint of the pedicle nerve has not been ascertained. Vascular canals have not been observed but radiating ridges of the same type as in the dorsal valve are present on the shell floor outside the visceral field.

Shell ornamentation progressively changed during ontogenesis. The juvenile shell to 800 μm length is principally smooth, bearing only prominent radial ribs (Fig. 3D, G, J, N). The larval shell is subcircular, 150 to 180 μm in diameter, defined by a weak halo from the

postlarval shell. Fine concentric growth lines cover the early postlarval shell. Some shells show a prominent growth ring at 300 μm shell size (Fig. 3G, J), but other shells indicate an interrupted growth (Fig. 3D, N). Up to seven radial ribs extend from the larval shell. The new ribs appear exclusively by intercalation between older ribs to separate equal sized interspaces. There may be some 30 ribs discernible along the periphery of juvenile shell. The ornament of the mature shell appears abruptly (Fig. 3P). As the growth lines diminish, the ornament of serrated oblique lines superimposed on growth fila becomes dominant (Fig. 3D, J, N). These subparallel oblique lines run towards the lateral sides. Along the axial sector of the shell, these lines intersect each other to form a divaricate but rather irregular pattern. The size of divaricate lines varies and depends on the place on a shell, with an average width of 30 to 40 μm . Observable length and width of particular teeth at the serrated edge of lines vary between 5 and 15 μm (Fig. 3Q).

Remarks. – The occurrence and taxonomic relation of *Kacakiella* have been discussed by Mergl (2001a). The serrated edge of terrace lines is unusual and differs from the simple acute edges of many lingulates having the terrace lines (Mergl *et al.* 2017). However, detailed investigation of terrace lines of *Westonia mardini* Mergl *et al.*, 2017 confirmed the presence of weakly serrate edges of terraces bearing the triangular outgrowths and similarly sized triangular pits anteriorly to them. The size and triangular outline of outgrowths and pits are likely related

to the grain size of sedimentary particles, to enable the terrace edges to work efficiently in particle removal during a burrowing. Adopting this suggestion, the living individual of *Kacakiella bouceki* buried into sediment with particles generally smaller than 40 µm, because terrace lines were likely ineffective in removing larger particles. Interestingly, a volcanic fly ash commonly ranges between 1 to 150 microns, with very fine ash < 30 µm (Hornby *et al.* 2023). A tempting but hypothetical interpretation of the life habit of *Kacakiella* seems to suggest that it burrowed on a sea floor occasionally affected by fine ash fallout.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; localities Loděnice (Špičatý vrch) (abundant), and Sv. Jan (Elektrárna) (abundant).

Genus *Wadiglosella* Havlíček, 1995

Type species. – *Lingula carens* Barrande, 1879. Motol Formation (Sheinwoodian, Wenlock, Silurian); Prague Basin, Czech Republic.

Wadiglosella carens (Barrande, 1879)

Figure 5

- 1879 *Lingula carens* Barr.; Barrande, pl. 103, case 5, figs 1, 2.
- partim* 1879 *Lingula carens* Barr.; Barrande, pl. 103, case 6, fig. 1.
- partim* ? 1879 *Lingula carens* Barr.; Barrande, pl. 104, case 7, fig. 1.
- 1879 *Lingula carens* Barr.; Barrande, pl. 105, case 2.
- ? 1879 *Lingula carens* Barr.; Barrande, pl. 105, case 3, figs 1, 2.
- 1995 *Wadiglosella odiosa* sp. n.; Havlíček, p. 55, pl. 1, figs 1–4.
- 2001a *Careniellus carens* (Barrande, 1879). – Mergl, p. 9, pl. 5, figs 1–12.

Material. – Lectotype, entire ventral valve (NM L 24458), paralectotype, entire dorsal valve (NM L 24457), two entire dorsal valves (NM L 34243, NM L 34245) and two entire ventral valves (MBHR 73388, PCZCU 500), all preserved on bedding planes of limestone, and loose greatly fragmented shells (PCZCU 2626–2631).

Description (extended). – See Mergl (2001a) for the first formal description of the species but without any data about the microornament and only restricted information on the pseudointerareas. The dorsal pseudointerarea is small relative to the shell size, forming a thin crescentic plate weakly raised above the floor of the valve, with undifferentiated propareas and the median groove (Fig. 5G).

Its surface is covered by fine posteriorly converging wrinkles while the growth lines are not perceptible (Fig. 5H). The ventral pseudointerarea is small, apsacline, short, with very small undivided propareas and a short and deep anteriorly expanding pedicle groove (Fig. 5I). The propareas are highly raised above the valve floor. The anterior edge of the propareas is not excavated. In side view, the floor of the pedicle groove is arcuate, and dorsally convex. The posterior of the ventral apex shows a distinct incision produced by the pedicle groove (Fig. 5I).

The shell exterior is covered by fine but conspicuous growth fila widely spaced over the mature shell (Fig. 5C–E). The microornament is remarkably variable, but always consists of elongate oval pits, with length 2 to 5 µm (Fig. 5F, J, K). Their W/L ratio is 0.60 to 0.70. The floor of the pits is evenly concave (Fig. 5O). The spatial arrangement of pits depends on their location on the shell. The first pits appear just after the last growth halo of the juvenile shell, which is 500 µm wide (Fig. 5F). Longer axes of the earliest pits are more or less parallel with a course of concentric growth lines. The pits are densely crowded with each other, often wedged between other pits (Fig. 5M). In the more anterior sites of the shell surface, the pits form single to double chains (Fig. 5J, K). In the double chains, the axes of pits usually converge anteriorly. The sizes of pits differ in particular stripes, but within the particular stripe they are more or less uniformly sized (Fig. 5L, N). This reflects the real size differences of vesicles, not only differences in the depth of imprints left inside a primary shell. There likely was not enough space for larger vesicles in the observed package of pits in the double chains (Fig. 5N). The chains are separated by a smooth shell surface bearing only small ripples, which represent weak deformations of the lower surface of the periostracal layer wedged between the particular vesicles. Observable irregularities of pit orientation (Fig. 5L) likely originated from a rotation of the free vesicle below the periostracum layer before its fixation by the primary shell layer formation.

Remarks. – *Wadiglosella carens* is the earliest member of the *Wadiglosella*–*Kosagittella* evolutionary lineage. The earliest occurrence of *Wadiglosella* comes from the Aeronian (Mergl 2001a), the latest known species is of Pragian age (Mergl 2001a). The earliest occurrence of *Kosagittella* Mergl, 2001a is known from the Ludfordian (Mergl 2001a, Mergl *et al.* 2018), and the latest species of the genus occurs in the Eifelian (Mergl 2008). Both genera share a characteristic shape of pseudointerareas which distinguish this group from the other Silurian and Devonian obolids. The ventral pseudointerarea is small in relation to the shell size. It is highly raised above the shell floor and significantly strengthens the beak region. Propareas are vestigial. Fine posteriorly converging

wrinkles cover the floor of the pedicle groove which is arcuate in side view; a trace of the pedicle is imprinted on the steep valve floor as a shallow canal (see Mergl, 2001a, pl. 3, figs 11, 12). The dorsal pseudointerarea of both genera is deeply concave, with a broad median groove covered by posteriorly converging wrinkles (Fig. 5G, H; Mergl 2008, fig. 3i; Mergl *et al.* 2018, fig. 4a).

New data confirm conspicuous differences in the microornament between both genera. In *Wadiglosella carens* this consists of elongate pits, but the microornament in other species of this genus needs further study. The microornament in *Kosagittella* consists of circular pits (Mergl 2001a, pl. 4, fig. 15; Mergl 2008, fig. 3c; Mergl & Ferrová 2009, fig. 2; Mergl & Jiménez-Sánchez 2015, fig. 4k, m).

Species of *Wadiglosella* living in a deeper and likely more hypoxic environment (*Wadiglosella carens*, *W. nigricula* Havlíček, 1995, *W. aff. nigricula* Havlíček, 1995; Mergl 2001a) are larger, with small pseudointerareas relative to the shell size and having their shells ornamented by raised concentric fila. The species assigned to *Kosagittella* occupied shallower and better-oxygenated waters. These are smaller, the concentric fila are reduced and their ventral valves are more acuminate. The diminutive size of *Kosagittella* is likely related to oligotrophic conditions in a perireefal environment.

Occurrence. – Aeronian, Želkovice Formation *Litui-graptus convolutus* Biozone, locality Hýskov (V Jakubínkách); Telychian, Motol Formation, *Oktavites spiralis* Biozone, locality Praha-Malá Chuchle (nearby the entrance to the railway tunnel); Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone, localities Loděnice (Špičatý vrch) (common), Sv. Jan (Elektrárna) (common), Praha-Řeporyje (Daleje Valley) (rare).

Subfamily Glossellinae Cooper, 1956

Genus *Barrandeoglossa* Mergl, 2001a

Type species. – *Lingula fissurata* Barrande, 1879. Motol Formation (Sheinwoodian, Wenlock, Silurian); Prague Basin, Czech Republic.

Barrandeoglossa? sp.

Figure 6D, E

Material. – One shell fragment (PCZCU 2744).

Remarks. – One fragment (Fig. 6D, E) with macroornamentation of regular ca 40 to 50 µm wide concentric fila likely comes from a shell of a large obolid. The concentric fila lack any traces of dimpled microornament which is characteristic for similarly shaped fragments

of discinoidean brachiopods. The identical ornament of concentric fila was observed in *Barrandeoglossa fissurata* (Barrande, 1879), which is known from beds of the nearly same age in Svatý Jan pod Skalou, at the Elektrárna locality (Mergl 2001a, pl. 7, figs 12, 13). Although it seems highly probable that the fragment originated from this species, an open taxonomy is preferred.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (rare).

Genus *Striatilingula* Cocks & Popov, 2009

Type species. – *Lingula? striata* J. de C. Sowerby, 1839. Elton Formation (Gorstian, Ludlow, Silurian); Welsh Borderland, Great Britain.

Striatilingula zebra (Barrande, 1879)

Figure 7

1879 *Lingula zebra* Barr.; Barrande, pl. 105, case 5.

2001a *Pseudolingula (?) dilatata* (Barrande, 1879). – Mergl, p. 16, pl. 8, fig. 10 (*partim*).

Material. – Holotype (by monotypy), complete, likely dorsal valve figured by Barrande (1879) in pl. 105, case 5, stored in the collections of the National Museum, Prague (NM L 24464). New material comprises several shell fragments; two of them are illustrated (PCZCU 2678, 2679).

Description (emended). – The only known complete valve (Fig. 7A) is elongate oval, with rounded posterior, subparallel lateral sides and a rounded frontal margin with a less curved axial part. The convexity is very low both axially and transversally. The interior of the valve is unknown. The shell exterior is distinguished by evenly wide low transverse terrace lines, limited by the low and steep slope at the anterior edge of each terrace. Terraces are distinct along the shell axis but may disappear just near lateral sides. Their width ranges from 120 to 200 µm. Terraces are distinctly bent along the larval shell in the posterior which encompasses almost right angle with the posterolateral sides. With growth, the terraces become less bent toward the anterior margin. Judging from the only complete shell, the bands are nearly parallel with the anterior margin of the mature shell. The terraces are straight to gently deflected posteriorly along the shell axis (Fig. 7B, C). One fragment indicates an interruption of the terrace edge near shell axis (Fig. 7B, D). This interruption may reflect the disappearance of the terrace lines along the axis during shell growth but this assumption needs further confirmation.



Figure 5. *Wadiglosella carens* (Barrande, 1879); A – partly exfoliated ventral valve, PCZCU 500; B – fragment of ventral valve, PCZCU 2626; C, F, K, M, N – fragment of ventral valve, and details of its microornamentation, PCZCU 2627; D, J, L, O – fragment of ventral valve, and details of its microornamentation, PCZCU 2628; E – fragment of valve, PCZCU 2629; G, H – dorsal valve interior and detail of its pseudointerarea, PCZCU 2630; I – ventral pseudointerarea, PCZCU 2631. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A), all others SEM photos. Bars in µm.

The microornament consists of crowded radial rows of shallow pits (Fig. 7E). Pits are circular, of uniform size, approximately 1 µm in diameter. Pits densely cover the exposed surface of terraces as well as the slopes between adjacent terraces.

Remarks. – The holotype comes from the Motol Formation in the vicinity of Bubovice (Barrande 1879), but the exact sampling site and the horizon are unclear. The holotype is very similar to *Striatilingula striata* (J. de C. Sowerby, 1839) which is reported from the Homerian, Gorstian,

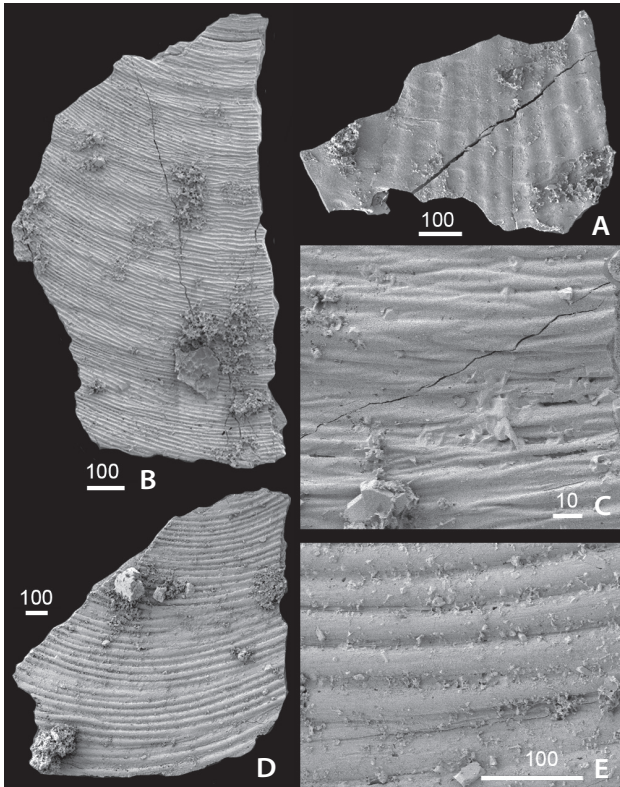


Figure 6. A – *Schizocrania* sp., fragment of the valve, PCZCU 2701. • B, C – Glossellinae gen. et sp. indet., fragment of valve and details of its microornamentation, PCZCU 2700. • D, E – *Barrandeoglossa?* sp., fragment of valve and details of its microornamentation, PCZCU 2744. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in µm.

Ludfordian and Přidolí of Brittany (Cocks & Popov 2009). The British and Bohemian specimens share the unique shape of terrace lines, and strongly flattened slightly elongate thin shell. Figured dorsal valves of *S. striata* show the development of a fine median septum (Cocks & Popov 2009, pl. 2, figs 11, 16). However, the interior of the Bohemian specimens is unknown. In contrast, there are no data about the microornament in the British specimens. Indeed, it is problematic to evaluate the relationships of *S. zebra* to *S. striata*. Although rare, the new material from the Špičatý vrch locality is of Sheinwoodian age and indicates that *S. zebra* stratigraphically preceded the British species.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone, localities Loděnice (Špičatý vrch) (rare) and Bubovice (old material).

Glossellinae gen. et sp. indet.

Figure 6B, C

Material. – One shell fragment (PCZCU 2700).

Remarks. – One shell fragment (Fig. 6B, C) with macroornamentation of imperfect concentric ripples likely originates from a shell of large glosselline. The fila lack any traces of pitted microornament but are crossed by oblique grooves (Fig. 6C). Mergl (2001a, pl. 8, figs 9, 11, 12) described a very similarly ornamented shell coming from the lower part of the Kopanina Formation (Gorstian) as *Barrandeoglossa* sp. It likely represents a so far undescribed new species of an unnamed genus, and its assignment to *Barrandeoglossa* must be considered erroneous.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (rare).

Subfamily Elliptoglossinae Popov & Holmer, 1994

Genus *Lingulops* Hall, 1872

Type species. – By original designation, *Lingulops whitfieldi* Hall, 1872. Upper Ordovician; USA.

***Lingulops fragilis* Mergl, 2001a**

Figures 8, 9A

2001a *Lingulops fragilis* Mergl sp. n.; p. 18, pl. 9, figs 9–15.

Material. – Four complete valves in rock (PCZCU 2604, 2605, 2719, 2720) and ten loose greatly incomplete dorsal and ventral valves (PCZCU 2636–2646).

Description (emended). – The external features were described by Mergl (2001a), but the presence of marginal beaks and a thin shell wall must be stressed (Fig. 8A–D). Both valves have a distinct internal limbus bordering lateral sides and posterolateral margins, interrupted by an incipient depression near the posterior margin. These shallow depressions correspond to the pedicle groove (Fig. 8K), and the median groove (Fig. 8G), respectively.

The interior of the dorsal valve shows a large visceral area near the centre of the valve. It occupies 50 to 60% of the valve width and some 30% of the valve length (estimated) (Fig. 8J). The area is bordered by shallow but clearly impressed muscle scars and weakly impressed interconnecting lines that limit a visceral space. The unpaired umbonal scar is horizontally crescentic in outline. The similarly sized crescentic scars of transmedian muscles are located anterolaterally to the umbonal scar. Outside lateral muscles left crescentic imprints anterolaterally to the transmedian scars. Middle lateral muscles are weakly impressed anterior to outside lateral muscle scars. The central muscle scars are the largest of all muscle scars. These paired scars are located anteromedially, converging

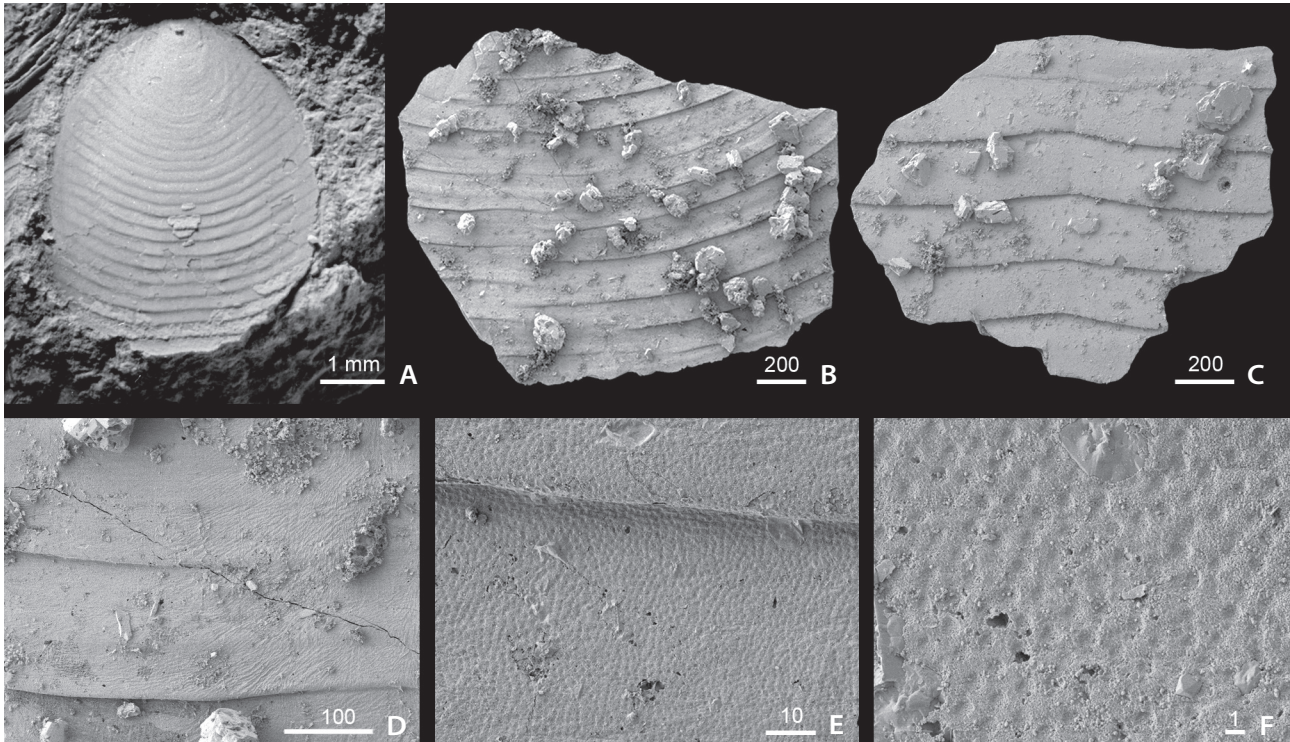


Figure 7. *Striatilingula zebra* (Barrande, 1879); A – holotype, complete (?) dorsal valve, NM L 24464; B, D–F – fragment of shell, and details of its microornamentation, PCZCU 2678; C – fragment from the axial portion of shell, PCZCU 2679. Bubovice, exact locality unknown (A), and Špičatý vrch locality (B–F); Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A), all others SEM photos. Bars in µm.

toward the shell axis, with anterior borders resting on an elevated pad. The anterior lateral muscles left their small ovate imprints on the anterior end of a shortly extended elevated anterior projection of the visceral field (Fig. 9).

The interior of the ventral valve shows a large triangular platform, having a raised anterior margin on an elevated pad (Fig. 8I). The central muscle scars are large, leaving oblique lines after their anterior migration on the valve floor. Other paired muscle scars are weakly defined. The scars limit the visceral area having an elongated triangular outline (Fig. 9). A weak median ridge that defines the axis of the visceral area is bordered by weak impressions, likely after the pedicle nerve. Traces of the vascular system are obscure, with only the proximal part of *vascula lateralia* observable lateral to the central muscle scars.

The shell macroornamentation is formed by weak concentric elevated bands of uneven size. These bands (Fig. 8L, M) are paralleled or weakly crossed by fine uniformly sized lines (approximately 5 µm wide) separated by much finer (1 to 2 µm) but clearly incised slits (Fig. 8N–P).

Remarks. – The species was erected on specimens coming from the Elektrárna locality near Svätý Jan. This locality has the same age and consequently any differences between the type specimens and new specimens have not been observed. The species is similar to younger

Lingulops barrandei Mergl, 1999 from the Kopanina Formation but that differs in its much thicker shell.

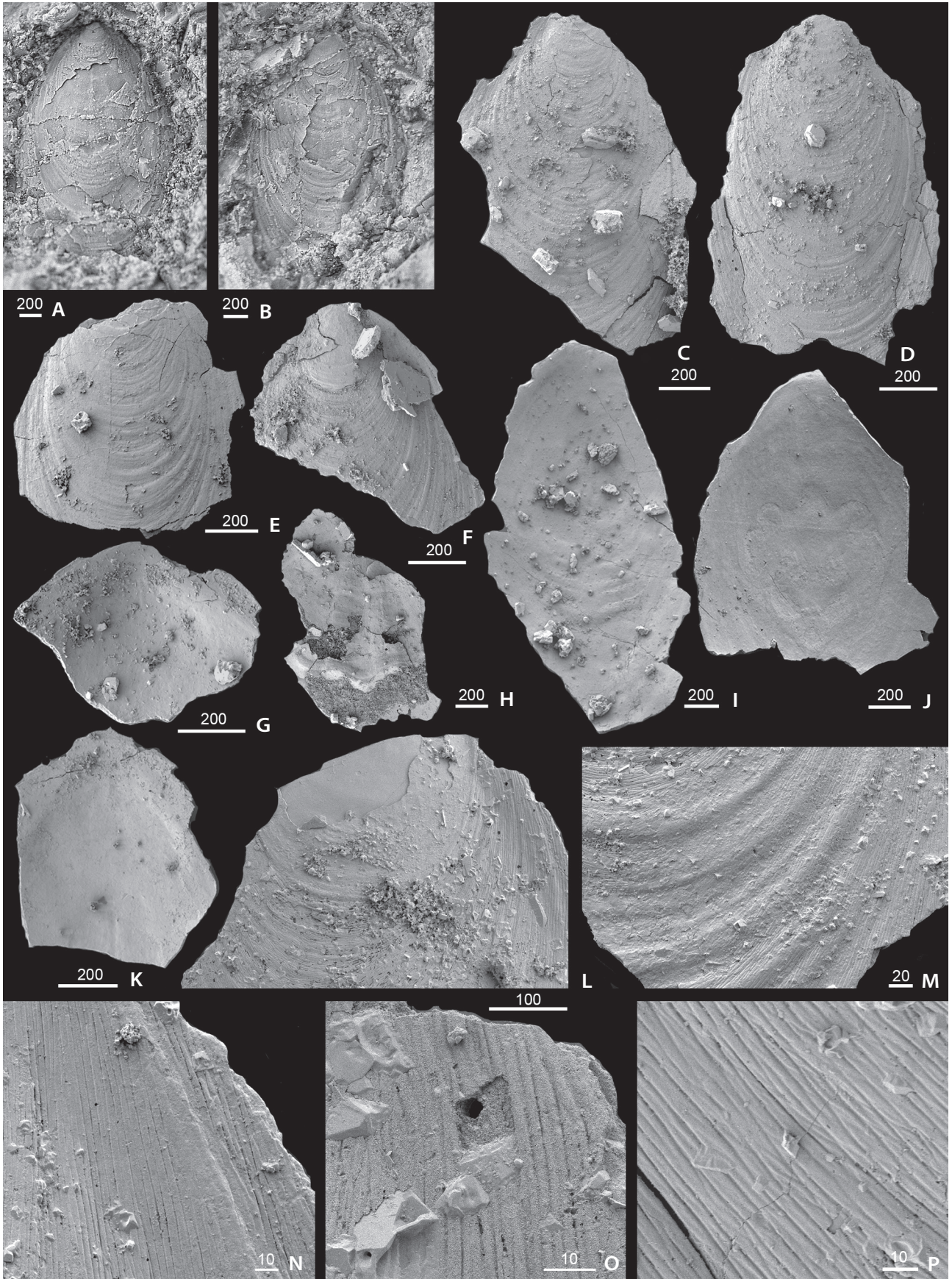
Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; localities Loděnice (Špičatý vrch) (common), Sv. Jan (Elektrárna) (rare).

Genus *Platylops* gen. nov.

Type species. – *Discina varissima* Barrande, 1879. Motol Formation (Sheinwoodian, Wenlock, Silurian); Prague Basin, Czech Republic.

Diagnosis. – Shell minute, thin-walled, aequivalved, with elongately elliptical outline; both valves are very weakly convex; pseudointerareas and pedicle groove vestigial; both valves internally having distinct limbus; growth holoperipheral, with dorsal and ventral beaks separated from the posterior margin by a broad subplanar area; interior of both valves with weakly defined visceral area situated near the centre of the valve; the dorsal valve with scars of anterior lateral muscles anteriorly projecting between low platforms with central muscle scars; exterior with very fine concentric fila.

Remarks. – The new genus is distinguished by a flat shell and a holoperipheral growth that leaves the ventral and



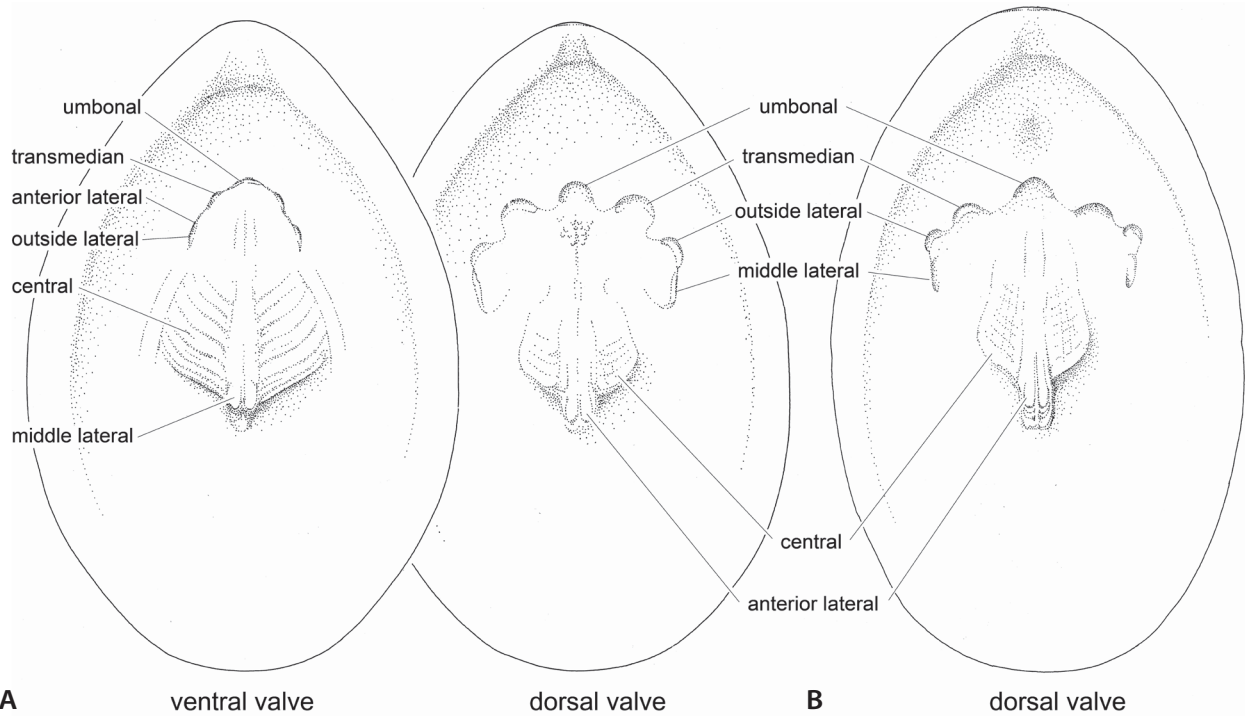


Figure 9. Schematic illustrations of musculature of (A) *Lingulops fragilis* (Mergl, 1982) and (B) *Platyllops rarissimus* (Barrande, 1879).

dorsal beaks conspicuously separated from the posterior margin. Other genera of the Subfamily Elliptoglossinae (*Elliptoglossa* Cooper, 1956; *Lingulops* Hall, 1872; *Litoperata* Sutton *et al.*, 1999) have marginal beaks and more convex shells. *Litoperata* differs by much prominent concentric macroornamentation.

There is distinct conservatism in the arrangement of visceral areas, with a triangular elevated platform in the ventral valve already developed in the Ordovician representatives (*cf.* the ventral valve of *Litoperata agolensis* Sutton *et al.* 1999, pl. 9, fig. 2). The same arrangement has been observed in *Platyllops rarissimus* and the Bohemian representatives of *Lingulops* (Mergl 1999, 2001a and herein). The new genus represents an evolutionary offshoot of the extremely thin-walled and flat elliptoglossines.

The species *Schizotreta? cf. rarissima* (Barrande, 1879) represented by three specimens (B3629, B34887, B47846) from the Much Wenlock Formation limestone (Wenlock, Homerian) from Dudley, England has the typical “lingulopsid” microornamentation of fine fila crossing the concentric bands (Mergl 2006, fig. 8g). Beaks of all known specimens (Mergl 2006, fig. 8b, c, d)

are widely separated from the posterior margin and their valves are thin and very weakly convex. The British specimens are similarly thin-walled without a distinctly limited visceral area. The relationship of the British specimens to the Bohemian *P. rarissimus* is not clear. The type specimen of Barrande (1879) is a deformed valve with unclear location of the beak (Mergl 2001a, pl. 17, fig. 13). The new shells from Bohemia (Fig. 10A) exhibit an elongate outline much similar to the outline of the holotype, while the British specimens are wider, having an elongate elliptical outline and more anteriorly located beak. The British specimens are of Homerian age and likely represent a separate species derived from ancestral *P. rarissimus*. *Lingulops austrinus* Valentine *et al.*, 2003 from the late Llandovery and early Wenlock of N.S.W., Australia, exhibits holoperipheral growth, with a strikingly extended posterior part of both valves and a long anterior projection of the dorsal visceral area. These features qualify to assign that species to the new genus.

Species included. – *Discina rarissima* Barrande, 1879; Silurian, Wenlock, Sheinwoodian, Motol Formation;

Figure 8. *Lingulops fragilis* (Mergl, 2001a); A – exterior of ventral valve, PCZCU 2604; B – exterior of ventral valve, PCZCU 2605; C – exterior of (?) dorsal valve, PCZCU 2636; D, P – exterior of (?) dorsal valve and detail of microornamentation, PCZCU 2637; E – exterior of (?) dorsal valve, PCZCU 2638; F – exterior of ventral valve, PCZCU 2639; G – dorsal pseudointerarea, PCZCU 2642; H – interior of ventral valve, PCZCU 2643; I – interior of ventral valve, PCZCU 2640; J – interior of dorsal valve, PCZCU 2641; K – ventral pseudointerarea, PCZCU 2644; L, O – exterior of (?) dorsal valve and detail of its microornamentation, PCZCU 2645; M, N – exterior of ventral valve and detail of its microornamentation near beak, PCZCU 2646. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A, B), all others SEM photos. Bars in μm .

Bohemia. *Lingulops austrinus* Valentine, Brock & Molloy, 2003; Silurian, Llandovery-Wenlock, Boree Creek Formation; New South Wales, Australia. *Schizotreta?* cf. *rarissima* (Barrande, 1879); Silurian, Wenlock, Homerian, Much Wenlock Limestone Formation; England.

***Platylops rarissimus* (Barrande, 1879)**

Figure 10

- 1879 *Discina rarissima* Barr.; Barrande, pl. 102, case 5.
2001a *Schizotreta rarissima* (Barrande, 1879). – Mergl, p. 24, pl. 17, fig. 13.

Material. – Holotype (NM L 24448), one valve preserved in rock (PCZCU 2606), and four incomplete loose valves (PCZCU 2632–2635).

Description (emended). – See Mergl (2001a). The dorsal valve interior has a weakly defined visceral area. Umbonal, transmedian, and outside lateral muscle scars are weakly impressed, restricted to the posterior half of the visceral area (Fig. 10C). The central muscle scars rest on an elongate triangular platform which is weakly elevated anteriorly. The anterior lateral muscles rest on an elevated projection extending anteriorly between the central scars (Fig. 10D). Ventral interior is unknown.

The exterior bears fine concentric fila separated by narrow slits. The fila are 3 to 5 µm wide and uniformly sized over the entire shell surface. Broad concentric bands have been observed in an entire shell (Fig. 10A). The larval shell is circular, flat, 250 µm wide, with a plain surface (Fig. 10F, G).

Remarks. – New material can be reliably referred to *Discina rarissima* Barrande, 1879, which Mergl (2001a) assigned to *Schizotreta* Kutorga, 1848. The shell morphology and the microornamentation of the new shells and the holotype are the same. This differs significantly from the pitted microornamentation known in *Schizotreta* and related discinoideans. *Platylops austrinus* differs from *P. rarissimus* by more posteriorly placed beaks and also somewhat coarser concentric macroornamentation.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (rare).

Superfamily Discinoidea Gray, 1840
Family Trematidae Schuchert, 1893

Genus *Schizocrania* Hall & Whitfield, 1875

Type species. – *Orbicula? filosa* Hall, 1847. Trenton Group (Ordovician); New York State, USA.

***Schizocrania* sp.**

Figure 6A

Material. – One fragment of the valve (PCZCU 2701).

Description. – A tiny fragment of the phosphatic shell shows radial fila 50 µm wide separated by equally wide interspaces. Radial fila are interconnected by concentric fila, thus forming irregular latticed ornament.

Remarks. – The genus *Schizocrania* is the only lingulate genus of Silurian age with this type of ornament. Two species, *S. verneuillii* (Davidson, 1848) and *S. striata* (J. de C. Sowerby, 1839) are known in the Silurian of Gotland (Mergl 2010), and Britain (Mergl 2006, Cocks 2008). In the Barrandian area this genus is represented by several species in the Ordovician and the early Devonian (Lochkovian and Pragian) (Mergl & Nolčová 2016, Mergl & Šmídová 2023), but with no record from the Silurian. Thus, the described fragment is the first proven evidence of the genus in the Silurian in the Barrandian region.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (very rare).

Family Discinidae Gray, 1840

Genus *Acrosaccus* Willard, 1928

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

***Acrosaccus* sp. A**

Figures 11C, D; 15D

Material. – One ventral valve (PCZCU 2721).

Description. – The ventral valve is thin-walled, having a circular outline. It is 5.7 mm in length and width, with the maximum width at the midlength. The beak is placed slightly posterior to the midlength. The valve is depressed conical, with evenly sloping sides, a weakly convex posterior slope, and a gently concave anterior slope. The pedicle track is small, 1.2 mm long and 0.5 mm wide, gently expanding posteriorly where it is terminated by a circular foramen.

The macroornament consists of concentric rugellae of uneven size. The rugellae are generally thin, low, with rounded crests and steep anterior slopes, and weaker posterior slopes. The interspaces of 0.2–0.3 mm width are much wider than the rugellae. Fine concentric fila, often imperfect and occupying only a short part of the shell

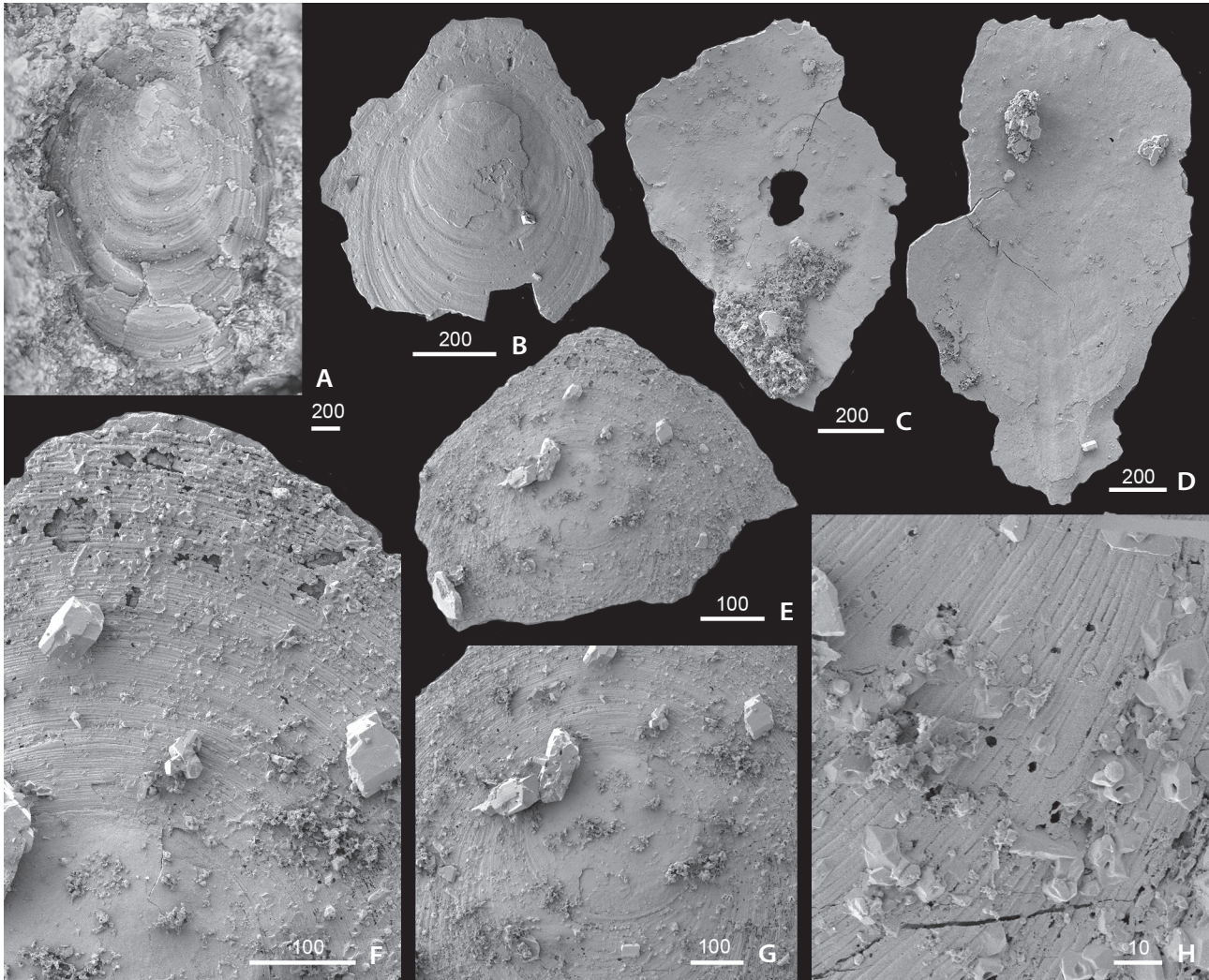


Figure 10. *Platyllops rarissimus* (Barrande, 1879); A – exterior of dorsal valve, PCZCU 2606; B – exterior of dorsal valve, PCZCU 2632; C – interior of dorsal valve, PCZCU 2633; D – interior of dorsal valve, PCZCU 2634; E–H – exterior of dorsal valve, and details of its posterior region, larval shell and microornamentation, PCZCU 2635. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A), all others SEM photos. Bars in μm .

circumference, are present. The microornamentation is unknown.

Remarks. – The shell differs from other discinoideans observed at the locality by uneven concentric macroornamentation. The most similar is *Orbiculoidea patelliformis* (Barrande, 1879) which rarely occurs in the beds of the same age in the Elektrárna locality near Sv. Jan. However, *O. patelliformis* is only known in specimens preserved on bedding planes of limestone. It is also much larger and fine details of its ventral apex are unknown (Mergl 2001a).

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (very rare), Bohemia.

Acrosaccus? sp. B

Figures 11E, 15E

Material. – One ventral valve (PCZCU 2725).

Description. – The ventral valve is thin-walled, with a circular outline, 3.1 mm wide, 95% as long as wide, with the maximum width at the midlength (Fig. 11E). The beak is at the centre of the valve. The valve is almost flat or with an incipiently elevated beak, but there is apparent diagenetic squeezing of the ventral beak into the shell. The pedicle track is large relative to shell size, having acute sides and deeply concave listrial plates. The track is opened posteriorly or was closed by a non-mineralized sheet. The concentric macroornamentation consists of rugellae which are distinct on the posterior slope and flanks

but become inconspicuous anteriorly, forming imperfect concentric fila. The concentric fila are only 30 µm apart anteromedianly. The posterolateral slopes bear weak radial rays with 200 to 300 µm spacing. The larval shell is 320 µm wide, and weakly convex with a plain surface. Interior and microornamentation are unknown.

Remarks. – The valve is tentatively assigned to *Acrosaccus*. It differs from other discinoideans observed at the locality by an inconspicuous macroornamentation on the anterior slope, a large pedicle track, almost planar valve, and the beak placed at the centre of the valve.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (very rare).

Acrosaccus? sp. C

Figures 11P, Q

Material. – One fragment (PCZCU 2754).

Remarks. – The small fragment (Fig. 11P) differs from other remains of discinoideans by an uneven concentric macroornamentation, rather thick shell wall, and a conspicuously large, more than 400 µm wide, larval shell. The microornamentation consisting of densely packed vesicular pitting (Fig. 11Q) differs from other examined shell fragments. The fragment could originate from the dorsal valve of the species described herein as *Acrosaccus* sp. A, but also may be derived from another large discinoidean.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (very rare).

Genus *Schizobolus* Ulrich, 1886

Type species. – *Lingula concentrica* (Vanuxem, 1842), designated by Ulrich (1886). Middle Devonian; Tennessee, USA.

Schizobolus sp.

Figures 11F–J, 15A

Material. – One dorsal valve (PCZCU 2722) and few shell fragments, one figured (PCZCU 2757).

Description. – The dorsal valve is planar, thin-shelled, subcircular in outline, 3 mm wide, with a marginal beak. The maximum width is slightly anterior to the midlength. The macroornamentation consists of thin, elevated rugellae, separated by much wider (100 to 200 µm) flat interspaces (Fig. 11F, G). Fine low ripples cover the floor of interspaces. Rugellae regularly increase in size with shell growth and occupy a great part of the valve circumference but rugellae on the left flank may be disconnected from those on the right flank. The microornamentation consists of sparse radial chains of 2 to 3 µm sized circular vesicular pits (Fig. 11H, I). These chains of pits are present only on shell flanks. The median sector of the valve lacks this microornamentation but fine radially arranged wrinkles (Fig. 11J) are superimposed on the mineralized shell surface there.

Remarks. – The valve is assigned to *Schizobolus* with some doubts, but the marginal dorsal beak, concentric macroornamentation, and the smooth surface with few radial chains of vesicular pits are similar to those observed in shells on *Schizobolus* sp. from the Kopanina Formation (Ludfordian, Ludlow) (Mergl *et al.* 2018). However, no ventral valve showing the nature of ventral pseudointerarea is known from the Špičatý vrch locality.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (very rare).

Genus *Schizotreta* Kutorga, 1848

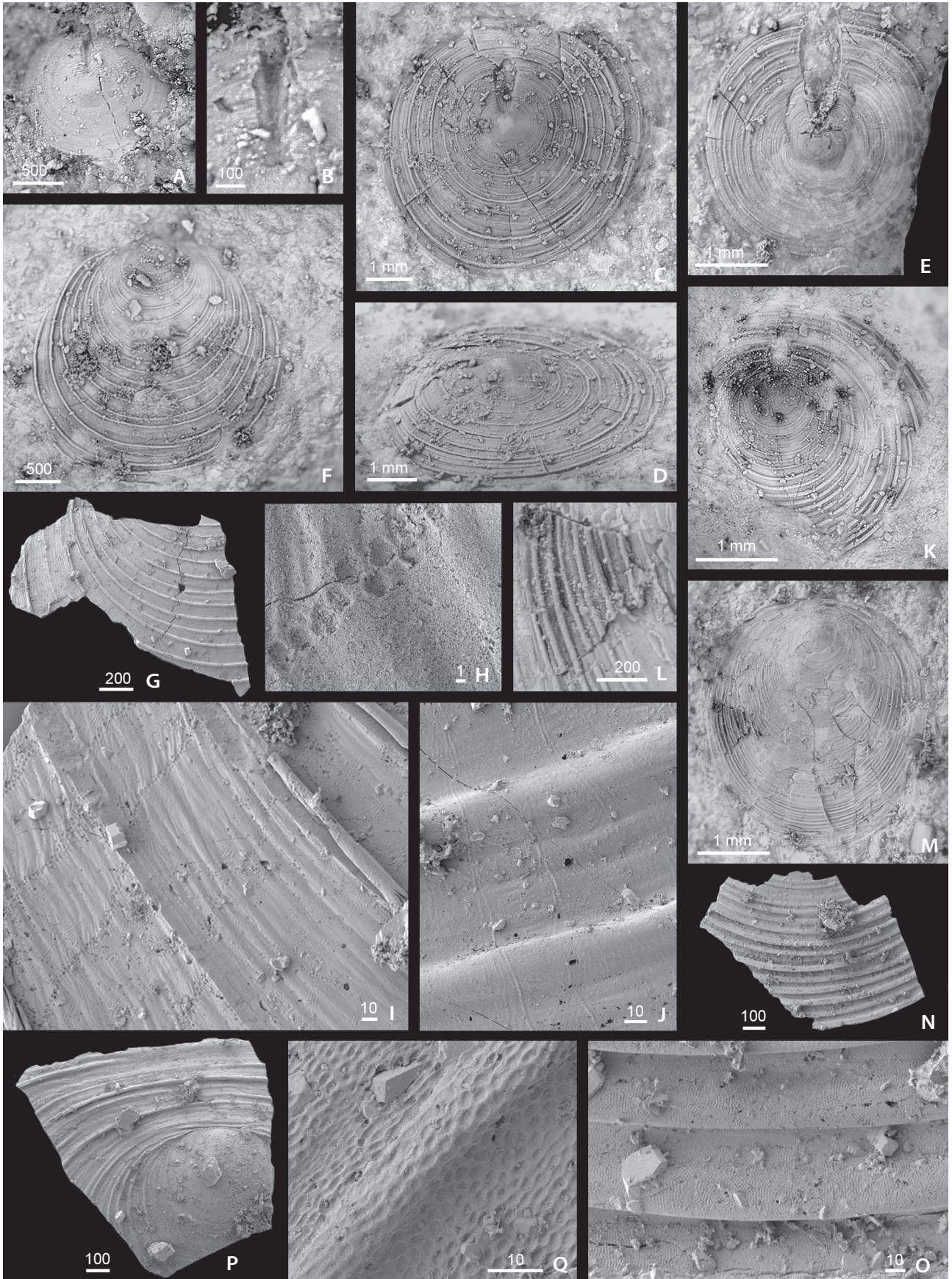
Type species. – By original designation, *Orbicula elliptica* Kutorga, 1846. Volkhov or Kundan regional stages (Ordovician); northwestern Russia.

Schizotreta elegantia sp. nov.

Figures 12, 15B

Holotype. – The dorsal valve, PCZCU 2715, figured in Fig. 12B, C, E.

Figure 11. A, B – *Sterbinella* sp., exterior of the small ventral valve, PCZCU 2714. • C, D – *Acrosaccus* sp. A, exterior of ventral valve in ventral and oblique views, PCZCU 2721. • E – *Acrosaccus?* sp. B, exterior of ventral valve, PCZCU 2725. • F–J – *Schizobolus* sp.; F – exterior of dorsal valve, PCZCU 2722; G–J – fragment of dorsal valve with details of rugellae and microornament, PCZCU 2757. • K–O – *Schizotreta* sp.; Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. K – exterior of ventral valve, PCZCU 2713; L, M – detail of ornament, and exterior of dorsal valve, PCZCU 2707; N, O – fragment of (?) dorsal valve and detail of microornament, PCZCU 2758. • P, Q – *Acrosaccus?* sp. C, fragment of dorsal valve and details of its microornament, PCZCU 2754. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A–F, K–M) and SEM photos (G–J, N–Q). Bars in µm if not stated otherwise.



Etymology. – *Elegantier* (Latin), nice.

Type horizon and locality. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone, “*Miraspis Limestone*”; Bohemia, Barrandian area, Loděnice (Špičatý vrch) locality.

Material. – Fifteen complete or almost complete valves (dorsal valves PCZCU 2703–2706, 2708, 2710, 2015, 2018, 2024; ventral valves 2702, 2709, 2711, 2712, 2017, 2024) and numerous fragments (figured specimens PCZCU 2752, 2753, 2755, 2756).

Diagnosis. – Shell with holoperipheral growth, small, thin-walled, elongate oval in outline; ventral apex in the posterior one-third of valve; ventral valve depressed conical, with weakly concave slopes; posterior slope of dorsal valve with ornament of sparse fine moderate high rugellae which anteriorly continue into densely crowded low concentric fila; pedicle track small, parallel-sided, with circular pedicle foramen; pedicle tube narrow.

Description. – The shell is small, very thin-walled relative to its size, with a 3 mm maximum width anterior to the midvalve.

The dorsal valve is broadly elongate-oval to subcircular with an evenly rounded posterior margin, lateral sides and anterior margin (Fig. 12A–D). The Wdv/Ldv ratio is 0.80 to 0.90. The dorsal apex is located at 15% of the valve length. The maximum height is at the apex. The posterior slope is gently concave. The anterior and lateral slopes are weakly convex. The dorsal visceral area is weakly defined, posteriorly with very fine median septum (Fig. 12F, G). The visceral area shows a complete set of muscle scars (Fig. 12F, G). Minute undivided transverse scars of the posterior oblique muscles are weakly defined on the posterior slope. Scars of posterior adductors are large, oblique, having triangular outlines. Scars of oblique internal muscles are oval, anterolaterally placed to the posterior adductor scars. Scars of anterior adductors are narrowly triangular, anteriorly converging to the midline. Scars of oblique internal muscles are subcircular, located anteromedially to the anterior adductor scars. Vascular canals are not perceptible.

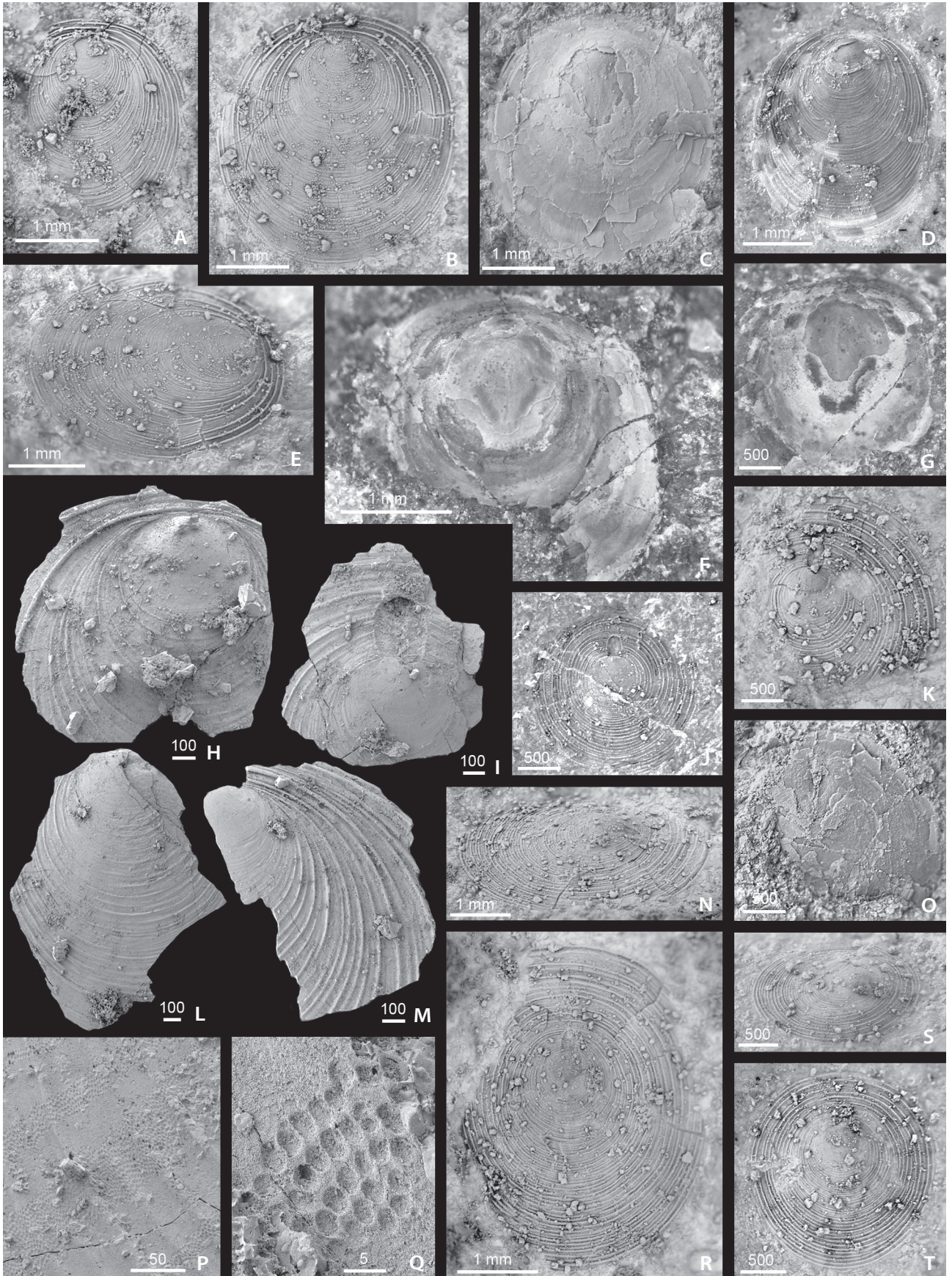
The ventral valve is depressed conical, thin-walled, with the beak at 32 to 40% of the valve length, with

evenly rounded sides. The posterior and anterior slopes and the lateral slopes are weakly concave. The pedicle track is small, parallel-sided, only 150 µm wide and 350 µm long, with small steeply sloping side listrial plates (Fig. 12I). The foramen is circular, and continues with a 50 to 70 µm wide internal pedicle tube which opens near the posterior margin (Fig. 12O). The ventral valve interior presents only weakly impressed muscle scars (Fig. 12O). Scars of oblique internal muscle are small, circular, located anterior to the apical pit. Scars of anterior adductors are narrow, markedly diverging posteriorly, lying lateral to the external pedicle track. Scars of posterior adductors and oblique muscles are small and weakly defined.

The macroornamentation of the dorsal valve is formed by sparse raised, moderate high, thin rugellae on a posterior slope and low rugellae which anteriorly continue into closely spaced low concentric fila separated by narrower interspaces. Rugellae and fila rest at right angles to the shell surface (Fig. 12B, E, H, M). These rugellae are 50 to 70 µm apart, while fila on anterior slope are only 25 to 40 µm apart. The ventral valve bears concentric fine rugellae regularly growing toward a valve periphery, separated by interspaces of the same size (Fig. 12J, N, R, T). The ornament of the ventral valve is more prominent than that of the dorsal valve. The larval shell is smooth, almost circular in outline, ca 350 µm wide, gently arched, having the apex directed posterodorsally (Fig. 12H, M). The microornamentation consists of fine pits covering the entire surface of the mature shell (Fig. 12P). Apart from this fine pitting, radial rays of larger pits, arranged into several adjacent strips in each ray, are located on posterior and posterolateral slopes (Fig. 12P, Q).

Remarks. – The species represents the commonest discinoidean at the Špičatý vrch locality, both among specimens yielded by splitting of limestone and acid etching. The shells are very thin and fragile and their fragmentation began before fossilization as seen on some examined shells. There are no other species of Silurian and Devonian ages in the Barrandian area which are similar to *S. elegantia*. The most similar is *Orbiculoidea karlstejnensis* Mergl, 1996 from the Kopanina Formation (Ludlow) which differs by its greater size and much coarser concentric macroornamentation. *Schizotreta walkeri* Mergl, 2006, a common species of the Sheinwoodian in England (Mergl 2006, fig. 8h–q),

Figure 12. *Schizotreta elegantia* sp. nov.; A – exterior of dorsal valve and its internal mould, PCZCU 2710; B, C, E – holotype, exterior of dorsal valve in dorsal and oblique views and its internal mould, PCZCU 2715; D – exterior of dorsal valve, PCZCU 2703; F, G – external and internal mould of dorsal valve, with muscle scars, PCZCU 2704; H – fragment of dorsal valve, PCZCU 2752; I – fragment of ventral valve, PCZCU 2753; J – exterior of incomplete ventral valve, PCZCU 2723; K, O – exterior and internal mould of incomplete ventral valve, PCZCU 2709; L, P, Q – fragment of dorsal valve and details of its microornament, PCZCU 2755; M – fragment of dorsal valve, PCZCU 2756; N, R – holotype, ventral valve in oblique and ventral views, PCZCU 2702; S, T – small ventral valve in oblique and ventral views, PCZCU 2717. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illuminations (A–G, J, K, N, O, R–T), and SEM photos (H, I, L, M, P, Q). Bars in µm if not stated otherwise.



also has coarser macroornamentation and differs by a much more posteriorly placed ventral beak. Valentine *et al.* (2003) described two species from the late Llandovery–early Wenlock of N.S.W., Australia. Of them, *Schizotreta cristatus* Valentine *et al.*, 2003 has a similarly fine macroornamentation, but its rugellae are much more widely spaced than those in *S. elegantia*. North American Ordovician species of this genus reviewed by Cooper (1956) differ in their coarser macroornamentation (*S. corrugata* Cooper, 1956), or else their macroornamentation is poorly known (*S. subconica* Cooper, 1956). The Ordovician and Silurian representatives of the genus are often inadequately known (Krause & Rowell 1975; Nazarov & Popov 1980; Harper 1984; Holmer 1989; Popov *et al.* 1994, 2002; Popov 2000; Mergl 2002; Percival *et al.* 2016).

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (abundant).

***Schizotreta* sp.**
Figures 11K–O, 15C

Material. – Three valves (PCZCU 2707, 2713, 2716) and several fragments, one of them illustrated (PCZCU 2758).

Description. – The shell is thin-walled, and has holoperipheral growth, elongate oval outline with the maximum width (3 mm) at midlength. The dorsal beak is placed in the posterior 15% of shell length (Fig. 11M). The dorsal valve is weakly convex in transverse and axial profiles. The macroornamentation consists of elevated closely spaced rugellae of uniform size, gently growing in size toward the shell periphery. Interspaces are of similar width to the rugellae (Fig. 11L, N). The microornamentation consists of densely packed vesicular pits covering the entire shell surface.

The ventral valve has a posteriorly located moderately elevated beak. The pedicle track is short and narrow, parallel-sided, opened into an internal pedicle tube by circular pedicle foramen. The macroornamentation consists of fine elevated concentric rugellae separated by interspaces of the same size (Fig. 11K).

Remarks. – The examined valves differ from *Schizotreta elegantia* sp. nov. by more conspicuous rugellate macroornamentation. The rugellae of *S. elegantia* are finer and separated by wider interspaces. There is a distinct difference in size and height of rugellae on posterior and anterior slopes of the dorsal valve in *S. elegantia* (Fig. 12B), whereas in *S. sp.* the rugellae are coarser, separated by narrower interspaces and their size is uniform on the entire shell (Fig. 11M). These differences may have

a taxonomic value and *S. sp.* thus represents a separate species, but it cannot be excluded that the shells having a coarser macroornamentation only represent the extreme phenotype of *S. elegantia*.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (rare).

Genus *Sterbinella* Mergl, 2001a

Type species. – By original designation, *Sterbinella daphne* Mergl, 2001a. Požáry Formation (Přidolí, Silurian); Prague Basin, Czech Republic.

***Sterbinella* sp.**
Figure 11A, B; 15F

Material. – Two ventral valves, one illustrated (PCZCU 2714).

Description. – The ventral valve is very small, only 1.5 mm wide, circular, low conical, with the beak slightly posterior to the centre of the valve. The anterior slope is gently concave. The posterior slope is bisected by a narrow deep pedicle track having distinct evenly wide listrial plates and a deep intertrough. The track is opened posteriorly. The shell lacks distinct growth lines. A few radial rays are perceptible on the anterior slope.

Remarks. – By its minute shell size and shape of the pedicle track these shells are very similar to ventral valves of the minute discinoidean *Sterbinella daphne* Mergl, 2001a. This species is restricted to the Požáry Formation (Přidolí) in the Kosov locality in the Barrandian area. *Sterbinella* sp. represents the stratigraphically oldest record of the genus which likely continued to the Eifelian (Mergl 2001a). Poorly known *Sterbinella* sp. is recorded by Valentine (2006a) from the early Devonian of N.S.W., Australia.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (rare).

Genus *Praethele* gen. nov.

Type species. – By original designation, *Discina vexata* Barrande, 1879. Motol Formation (Sheinwoodian, Wenlock, Silurian); Prague Basin, Czech Republic.

Diagnosis. – Medium sized discinid with plano-convex thick-walled shell; dorsal valve subplanar, subcircular, with posterior dorsal beak; ventral valve depressed conical,

with subcentral apex; pedicle track short, almost parallel-sided, with long internal pedicle tube opened in valve floor near the posterior margin; dorsal macroornamentation of high, lamellose rugellae having a swollen crest, towards shell periphery with extended rim; anterior side of rugellae excavated; rugellae of uniform shape, slowly and evenly increasing in size towards shell margins; rugellae on ventral valve finer than those in the dorsal valve, with similarly shaped crests, anteriorly excavated; external microornamentation of closely spaced circular pits.

Remarks. – In its subplanar dorsal valve of subcircular outline, long internal pedicle tube and dense rugellate macroornamentation, the new genus is similar to *Ivanothele* Mergl, 1996 and *Chynithele* Havlíček, 1996 in Havlíček & Vaněk (1996). *Praethele* is distinguished by a low conical ventral valve which is ornamented by prominent concentric rugellae similar to those on the dorsal valve. It is also distinguished by its smaller size from *Ivanothele* and *Chynithele*, the ventral valves of which are much higher, often showing asymmetry. Their ventral beaks are deflexed anteriorly (Mergl & Jiménez-Sánchez 2015, fig. 6a, e) and their pedicle tracks are very short. All three genera have prominent rugellae in dorsal valves and crests of rugellae are formed into rims extended over the anterior slope of rugellae. Moreover, the swollen crests are gently undercut also along the posterior slope of rugellae in *Chynithele*.

These three genera likely represent an evolutionary offshoot of the discinids. The swollen crests and thinner bases of rugellae are a suggested synapomorphy of the Ivanothelinae Mergl, 1996. This feature developed from the common ancestor of *Ivanothele* and *Praethele* in the Early Silurian. The further thinning of the rugellae bases and their posterior excavation is a probable apomorphy of *Chynithele*. The earliest member of the Ivanothelinae is *Praethele* of the Sheinwoodian age. This genus continued at least to the Ludfordian (Mergl *et al.* 2018) and likely to the Přídolí (unpublished). The first proven *Ivanothele* appeared in the Gorstian (*I. mordor* Mergl, 1996) with the next record in the Ludfordian (*I. pilidium* Lindström, 1861); however, it is possible that this genus may appear already in the Telychian (Mergl 2010a). The earliest report of *Chynithele* comes from the Lower Emsian [*C. fritschi* (Barrande, 1879) and *C. ventricona* Havlíček, 1996 in Havlíček & Vaněk (1996)] followed by the upper Emsian *C. intermedia* Mergl & Jiménez-Sánchez, 2015 and *C. amoena* Mergl, 2008 in the Eifelian.

The genus *Acrosaccus* Willard, 1928 differs from *Praethele* by the moderate convexity of the dorsal valve. The morphology of *Acrosaccus* has been discussed by Percival *et al.* (2016). The common feature of the type species *A. schuleri* Willard, 1928 and some other

species referred to *Acrosaccus* is the long spindle-shaped pedicle track and reduced pedicle tube (Holmer & Popov 2000).

***Praethele vexata* (Barrande, 1879)**

Figures 13, 14, 15G

1879 *Discina vexata* Barr.; Barrande, pl. 100, case 3, figs 1, 3, 4.

1879 *Discina reversa* Barr.; Barrande, pl. 96, case 1, fig. 6.

1879 *Discina planula* Barr.; Barrande, pl. 102, case 3.

2001a *Acrosaccus vexatus*. – Mergl, p. 26, pl. 19, figs 15, 16, pl. 20, figs 1–10.

non 2018 *Chynithele vexata*. – Mergl *et al.*, p. 382, fig. 5a–k.

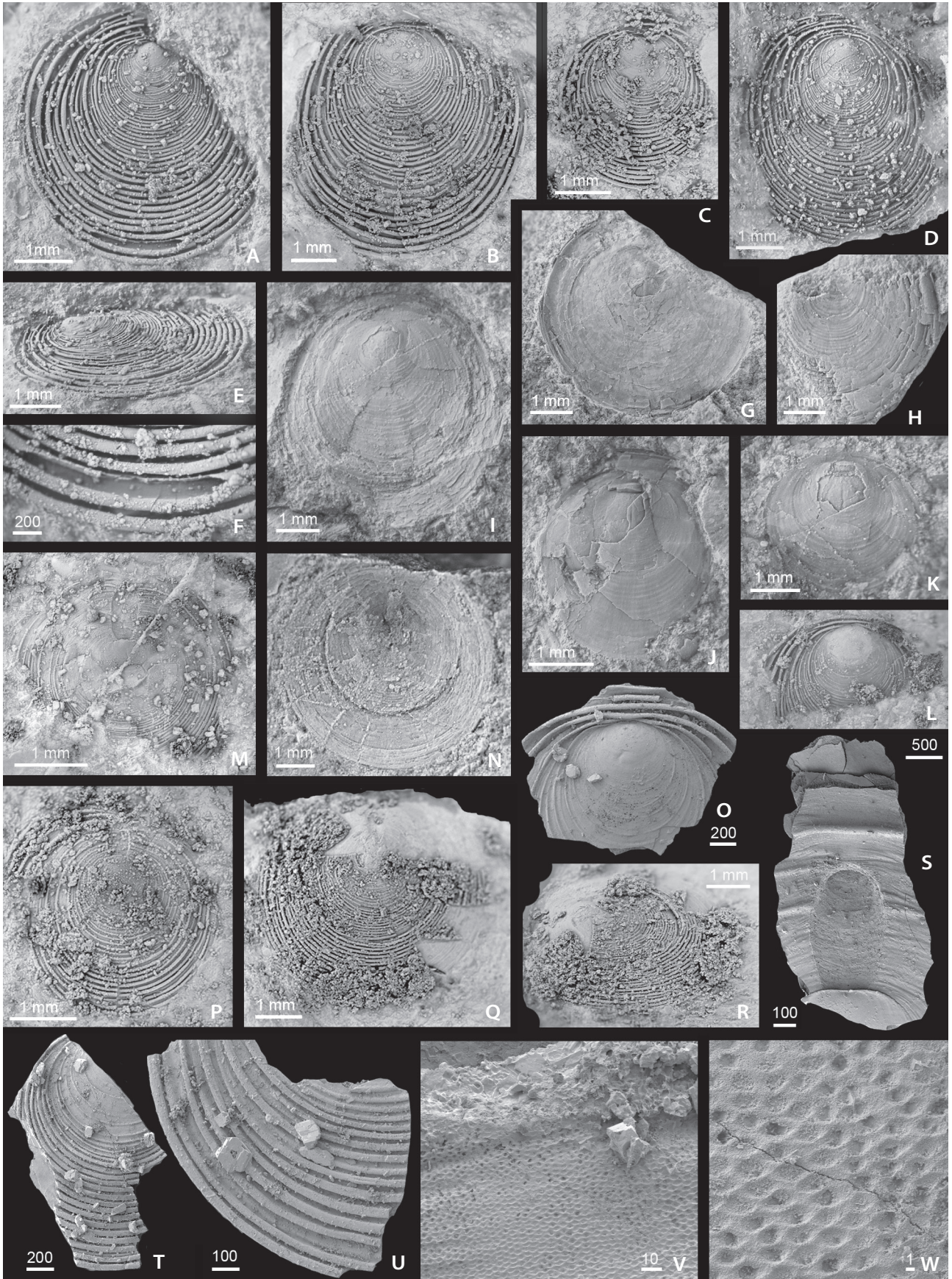
Material. – Lectotype, entire dorsal valve (NM L 16065), 14 entire dorsal valves (PCZCU 514, 2727–2729, 2731, 2732, 2734–2739, 2741, 2743), four entire ventral valves (PCZCU 2726, 2730, 2733, 2742) and more fragments, some illustrated (PCZCU 2745–2751).

Description. – The shell width reaches 3.5 to 4 mm with a rather thick wall relative to shell size. The structure of the wall consists of several lamellose layers, with the compact primary layer about 5 to 6 µm thick (Fig. 14G). The macroornamentation of the ventral valve is slightly finer than that of the dorsal valve.

The dorsal valve is circular to gently elongate-oval (Fig. 13A–D), with maximum width at midvalve, with Wdv/Ldv 0.95 to 1.05. The beak is placed in the posterior 17 to 40% of shell length. Anterior and lateral sides are regularly rounded, the posterior margin is evenly rounded. The shell in early growth stages is weakly arched, with the larval shell forming the highest point of the valve, but with growth, the valve becomes almost planar (Fig. 13E, O). The dorsal valve interior has a fine median septum in the posterior of the visceral area (Fig. 13J, K). Muscle impressions are unknown.

The ventral valve is low conical, with a beak at the posterior one-third of the valve (Fig. 13N, Q). Posterior, lateral, and anterior slopes evenly decline towards rounded margin. The pedicle track on the ventral valve is short, only weakly expanding posteriorly, terminated by a circular pedicle foramen (Fig. 13P, S). The posterior end of the pedicle track is rounded. The length of the track is less than 1 mm, with Wtr/Ltr 0.50. The listrium is indistinctly divided into a lateral pair of wider sloping listrial plates and a weakly defined narrower median interthrough. The surface of the listrium bears anteriorly bent fine growth lines (Fig. 13S). The internal pedicle tube is long and evenly wide with an internal opening near the posterior margin (Fig. 13N).

The larval shell of the dorsal valve is transversely oval, about 300 µm wide, separated by a weak halo from



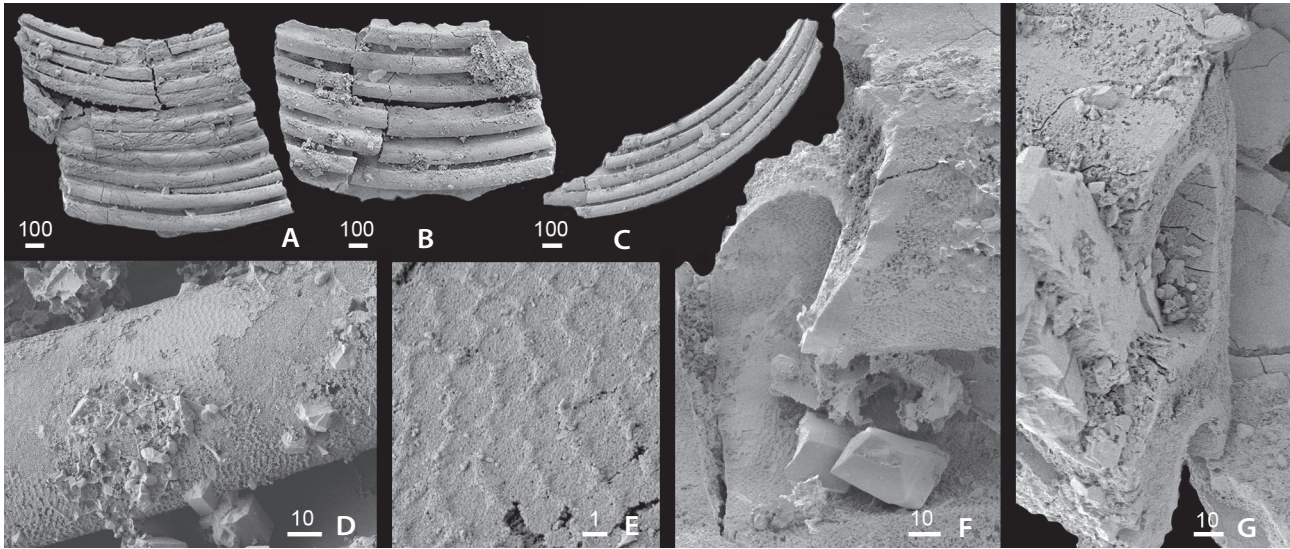


Figure 14. *Praethele vexata* (Barrande, 1879); A, G – fragment of dorsal valve, and two naturally sectioned rugellae, PCZCU 2749; B, F – fragment of dorsal valve, and detail of rugella, PCZCU 2750; C, D, E – fragment of dorsal valve, and detail of rugellae, PCZCU 2751. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in μm .

the early postlarval shell. This early postlarval shell is surrounded by weak concentric growth lines becoming coarser with subsequent growth (Fig. 13O). The first concentric rugellae appears at a 1 mm shell width and each subsequent rugellae become gently higher and wider. The adult (4 mm wide) shell has some 40 rugellae (Fig. 13A, B). Only several rugellae form complete rings. Intercalated semicircular rugellae appear on the posterolateral shell sides and rapidly attain the same size as the entire rugellae (Fig. 13A, B). The crest of each large rugellae is convex and extends to the broad rim over the vertical basal shaft of the rugella. The anteriorly facing edge of the rim is acute (Fig. 14F, G). The interspaces between bases of adjacent rugellae are only slightly wider than the width of nearby crests. Thus, only a narrow slit between crests of adjacent rugellae is developed (Figs 13F, 14A–C). The interspaces between the rugellae on the posterolateral slope of the dorsal valve are wider than those on the anterior axial sector. This difference is caused by the development of thinner crests in higher rugellae on the posterior slope (Fig. 13O). The width of rugellae near the anterior margin of large dorsal valves is about three times greater than the width of the rugellae on the early mature valves. The microornamentation consists of broadly lenticular dimples with 2 μm sized circular

vesicular pits at their centres. The pits are arranged in a honeycomb pattern on the posterior slope and on the early postlarval shell (Fig. 13V, W) but become arranged in more regular radial rows on the anterior part of the large mature shells (Fig. 14D, E).

Remarks. – *Praethele vexata* (Barrande, 1879) was referred by Mergl (2001a) to *Chynithele* Havlíček, 1996 in Havlíček & Vaněk (1996) due to the macroornamentation with overhanging dorsal rugellae which rapidly enlarge during shell growth. However, in *Praethele* this overhanging has a different development, with an acute anterior edge that differs from the rounded and swollen edge of *Chynithele*. In addition, in *Chynithele* the rim is excavated also along the posterior slope of rugellae. This posterior excavation is not developed in *Praethele*. The difference in the macroornamentation between the ventral and dorsal valve, a flat lid-like dorsal valve, and the shape of the pedicle track, are further features that justified the re-assignment of Barrande's (1879) species *Discina vexata* to the new genus.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; locality Loděnice (Špičatý vrch) (abundant), Bohemia.

Figure 13. *Praethele vexata* (Barrande, 1879). A, E, F – exterior of dorsal valve, side view and detail of rugellae, PCZCU 514; B, I – exterior of dorsal valve and its internal mould, PCZCU 2734; C, J – exterior of dorsal valve and its internal mould, PCZCU 2737; D – exterior of dorsal valve, PCZCU 2738; G, H – internal mould of dorsal valve and its counterpart showing lamellose shell wall, PCZCU 2729; K – internal mould of dorsal valve showing median ridge, PCZCU 2743; L – exterior of incomplete dorsal valve, PCZCU 2735; M – exterior of small ventral valve, PCZCU 2730; N, Q, R – interior, and exterior of ventral valve in ventral and oblique views, PCZCU 2742; O – fragment of dorsal valve, PCZCU 2745; S, V, W – fragment of ventral valve with pedicle track, and detail of its microornament, PCZCU 2746; T – fragment of small dorsal valve, PCZCU 2747; U – fragment of large dorsal valve, PCZCU 2748. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. Standard illumination (A–N, P–R), and SEM photos (O, S–U). Bars in μm if not stated otherwise.

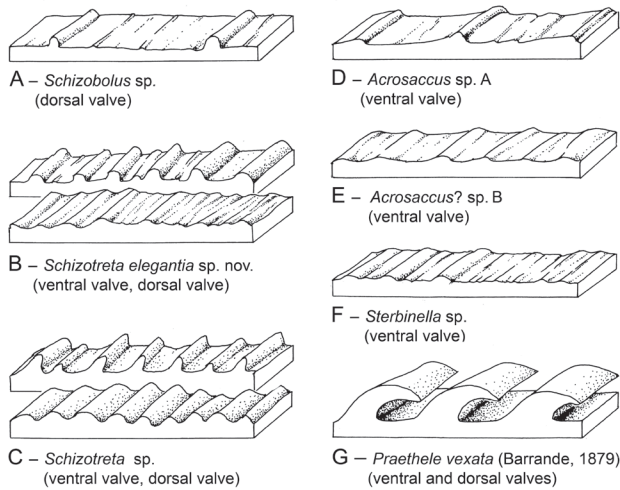


Figure 15. Schematic illustration of macroornamentation of discinoid species; pad length is approximately 250 µm.

***Praethele postvexata* sp. nov.**

2018 *Chynithele vexata*. – Mergl *et al.*, p. 382, fig. 5a–k.

Holotype. – The dorsal valve figured by Mergl *et al.* (2018) on figure 5G1–G2, stored in the collections of the Geological Survey, Prague (JF195_79).

Type horizon and locality. – Ludfordian, Kopanina Formation, upper part; Kosov Quarry, Bohemia.

Diagnosis. – *Praethele* with circular to weakly transverse outline of the dorsal valve; the dorsal valve macroornamentation of high densely crowded, entire and evenly growing rugellae having deeply excavated anterior slope; rugellae have rounded swollen crest distinctly protruding over the adjacent external interspace; the anterior rim of the protruded crest is rounded; rugellae rest at almost right angle at shell surface; interspaces of approximately the same width as the crests of adjacent rugellae.

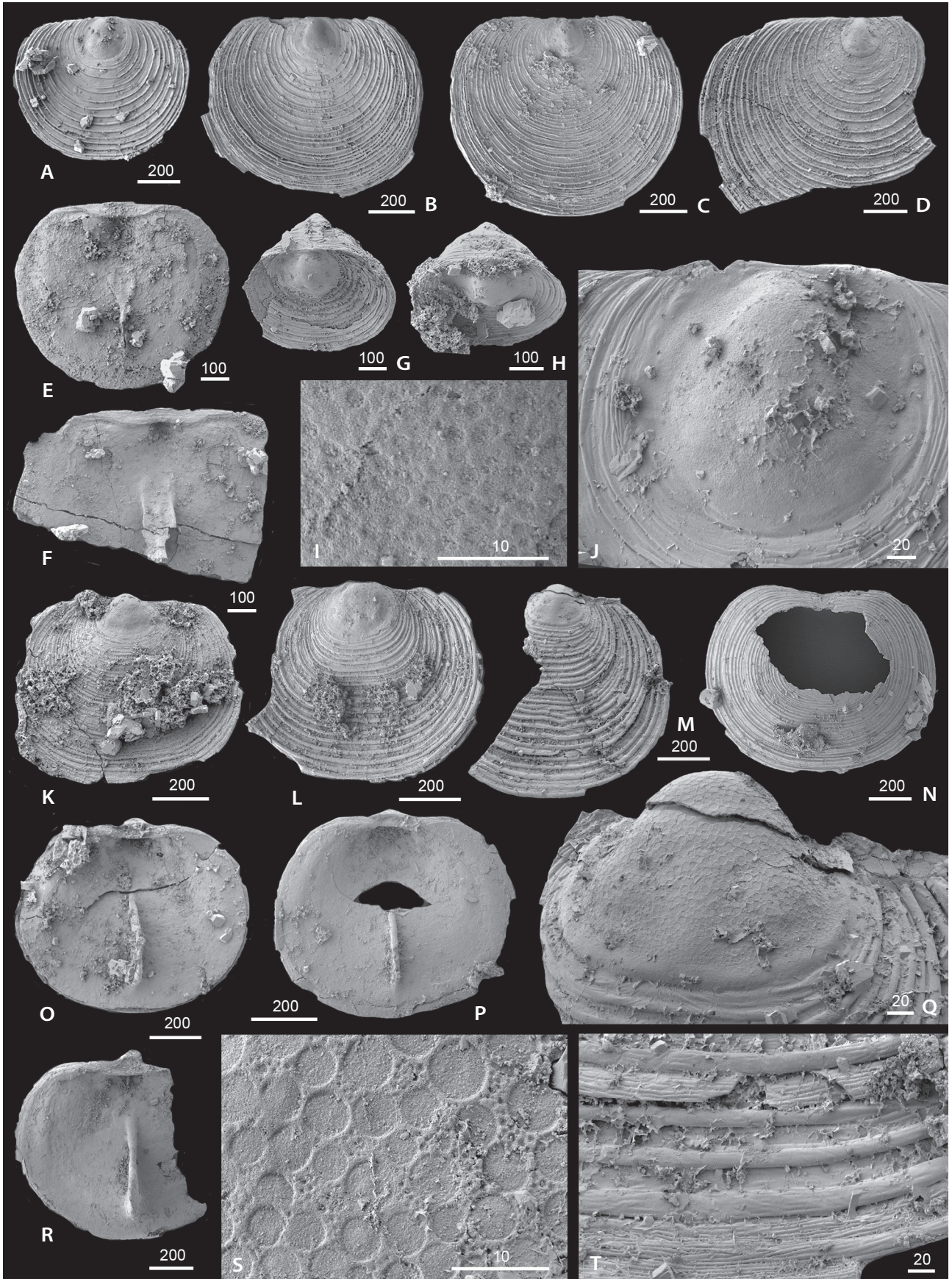
Description. – For detailed illustrations and comments see Mergl *et al.* (2018). The shell width reaches 4 to 5 mm with a thick wall relative to shell size. The macroornamentation of the ventral valve markedly differs from that of the dorsal valve.

The dorsal valve is circular to gently transverse posterior to the midlength, with the beak located in the posterior 20 to 25% of shell length. Anterior and lateral sides are regularly rounded. The posterior margin is almost evenly rounded but may be less rounded in the axial part in particular shells (Mergl *et al.* 2018, fig. 5b). The shell of the early growth stage is weakly arched but during subsequent growth becomes almost planar. The interiors of both valves are unknown.

The ventral valve is low conical, with a subcentral beak. The pedicle track is short, weakly expanding posteriorly, with the listrium clearly divided into a pair of wider sloping lateral plates and a narrower intertrough. The external pedicle foramen is almost circular and continues internally into a long pedicle tube. The macroornamentation of the dorsal valve consists of prominent densely spaced concentric rugellae. Each rugella has a moderately swollen crest which is extended over the adjacent interspace and excavated wall of the rugella. The thinner basal shaft of rugella crest rests almost vertically to the shell surface. The size of rugellae weakly but steadily increases with the size of the individual shell, with the earliest rugellae developed just at the early post-larval shell. The most peripheral rugellae in large fragments are about two- to three times higher than wide. Interspaces are deeply and narrowly U-shaped. The macroornamentation of the ventral valve is much finer than this on dorsal valve. It consists of fine unexcavated rugellae steadily increasing in size. Ventral rugellae are separated by much wider interspaces having weak growth bands. The microornamentation consists of subcircular concave vesicular pits of ca 5 µm diameter arranged in a regular pattern. Radial rows of pits are distinct in some parts of the shell, but generally, a more honeycomb arrangement prevails. Pits cover the entire external shell surface including interspaces and crests of rugellae but pitting is missing on the larval shell.

Remarks. – The new species was originally assigned to *Chynithele vexata* (Barrande, 1879). However, the new material from the Motol Formation is much like the lectotype of *Discina vexata*. This similarity is accentuated by a suggested provenance of Barrande’s types. Unfortunately, the dorsal valve (lectotype) is preserved as the partly exfoliated shell with the exterior entirely embedded in rock and only the almost smooth and weakly

Figure 16. A–J – *Acrotretella siluriana* Ireland, 1961; A, J – exterior of small dorsal valve and detail of its larval shell, PCZCU 2685; B – exterior of medium dorsal valve, PCZCU 2686; C – exterior of large dorsal valve, PCZCU 2687; D – exterior of large dorsal valve, PCZCU 2688; E – interior of medium dorsal valve, PCZCU 2689; F – interior of large dorsal valve, PCZCU 2692; G, I – complete young shell and details of microornament of its larval shell, PCZCU 2690; H – complete young shell, PCZCU 2691. • K–T – *Artiotreta parva* Ireland, 1961; K – exterior of dorsal valve, PCZCU 2693; L – exterior of small dorsal valve, PCZCU 2694; M, Q, S, T – exterior of dorsal valve, and details of its larval shell, microornament of larval shell and microornament of mature shell, PCZCU 2695; N – exterior of incomplete ventral valve, PCZCU 2696; O – interior of dorsal valve, PCZCU 2697; P – interior of dorsal valve, PCZCU 2698; R – interior of dorsal valve showing pseudointerarea, PCZCU 2699. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in µm.



exfoliated interior visible (Mergl 2001a, pl. 20, fig. 5). Therefore, to stabilize the taxonomy, the specimens sampled in the Kopanina Formation (Ludfordian) and preserved with fine details of external macroornamentation are described as the new species. There is an apparent morphological progression of the external macroornamentation, evidenced by the transformation of the acute rim of dorsal rugellae in the ancestral *P. vexata* into the rounded rim in *P. postvexata*.

Occurrence. – Ludfordian, upper part of the Kopanina Formation; locality Kosov (quarry) (abundant), Bohemia.

Order Acrotretida Kuhn, 1949
Superfamily Acrotretoidea Schuchert, 1893
Family Acrotretidae Schuchert, 1893

Genus *Acrotretella* Ireland, 1961

Type species. – By original designation, *Acrotretella siluriana* Ireland, 1961. Clarita Formation (Wenlock, Silurian); Oklahoma, USA.

Acrotretella siluriana Ireland, 1961

Figure 16A–J

- 1961 *Acrotretella siluriana* sp. n.; Ireland, p. 1140, pl. 137, figs 13–18.
2001a *Acrotretella siluriana*. – Mergl, p. 31, pl. 25, figs 1–17.
2018 *Acrotretella siluriana*. – Mergl *et al.*, p. 385, figs 7, 8h–p.

Material. – Two complete juvenile shells (PCZCU 2690, 2691), six dorsal valves (PCZCU 2685–2689, 2692) and numerous fragments of dorsal shells.-

Description. – See Mergl (2001a).

Remarks. – The first occurrence of *A. siluriana* in Bohemia is of Aeronian age (Mergl 2001a) and its last occurrence comes from the Ludfordian (Mergl *et al.* 2018), where it co-occurs with *A. triseptata* Mergl, 2001a. The relationship and distribution of Bohemian specimens of the genus are extensively discussed by Mergl *et al.* (2018). The specimens from the *Monograptus belophorus* Biozone cannot be differentiated from those illustrated by Ireland (1961) except for the larger shell size of the Bohemian specimens. This difference is considered inadequate for the erection of a new species.

All so far illustrated specimens come from the Elektrárna locality near Svätý Jan pod Skalou, although its presence in the Špičatý vrch (= Černidla) has been mentioned in the text (Mergl 2001a). The newly examined specimens from the Špičatý vrch locality are identical in

size, ornamentation, and outline with to those from Svätý Jan pod Skalou.

Occurrence. – Aeronian, Želkovice Formation *Lituigraptus convolutus* Biozone, locality Hýskov (V Jakubinkách) (rare); Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone, localities Loděnice (Špičatý vrch) (common), and Sv. Jan (Elektrárna) (common); Ludfordian, Kopanina Formation, *Neocucullograptus inexpectans* to *Pristiograptus fragmentalis* biozones, Kosov quarry (rare); Bohemia. Wenlock; Oklahoma, Illinois, Missouri, USA (Ireland 1961, Satterfield & Thompson 1969, Chatterton & Whitehead 1987); Wenlock; Woolhope Anticline, Scutterdin Quarry; Britain (Ireland 1961).

Family Scaphelasmataceae Rowell, 1965

Genus *Artiotreta* Ireland, 1961

Type species. – By original designation, *Artiotreta parva* Ireland, 1961. Clarita Formation (Wenlock, Silurian); Oklahoma, USA.

Artiotreta parva Ireland, 1961

Figure 16K–T

- 1961 *Artiotreta parva* sp. n.; Ireland, p. 1138, pl. 137, figs 1–12.
partim 2001a *Artiotreta krizi*. – Mergl, p. 32, pl. 28, figs 8–11 (non pl. 28, figs 1–7).

Material. – Seven dorsal valves (PCZCU 459, 2693–2695, 2697–2699) and two ventral valves (PCZCU 244, 2696).

Description. – The shell is minute, ventribiconvex, recti-marginate, transversely broadly oval, 1.2 mm wide in the largest known specimen, in relation to shell size rather thick-walled. The anterior margin and lateral sides are evenly rounded, the posterior margin is nearly straight with a dome-shaped larval shell posteriorly extended behind the dorsal pseudointerarea (Fig. 16K, M, O).

The dorsal valve is weakly convex near the beak becoming subplanar anteriorly. The dorsal pseudointerarea is small, formed by a small concave median groove laterally extended into linear weakly defined propareas (Fig. 16O, P, R). The valve interior is the deepest just below the pseudointerarea and lacks signs of muscle scars. The median septum is thin, moderately high, blade-like, starting at one-third length of the valve. The septum is anteriorly terminated by a weakly defined marginal rim (Fig. 16O, P, R). The marginal rim is more apparent along posterolateral sides than anteriorly.

The macroornamentation of the dorsal valve is formed by concentric rugellae interrupted by a few concentric

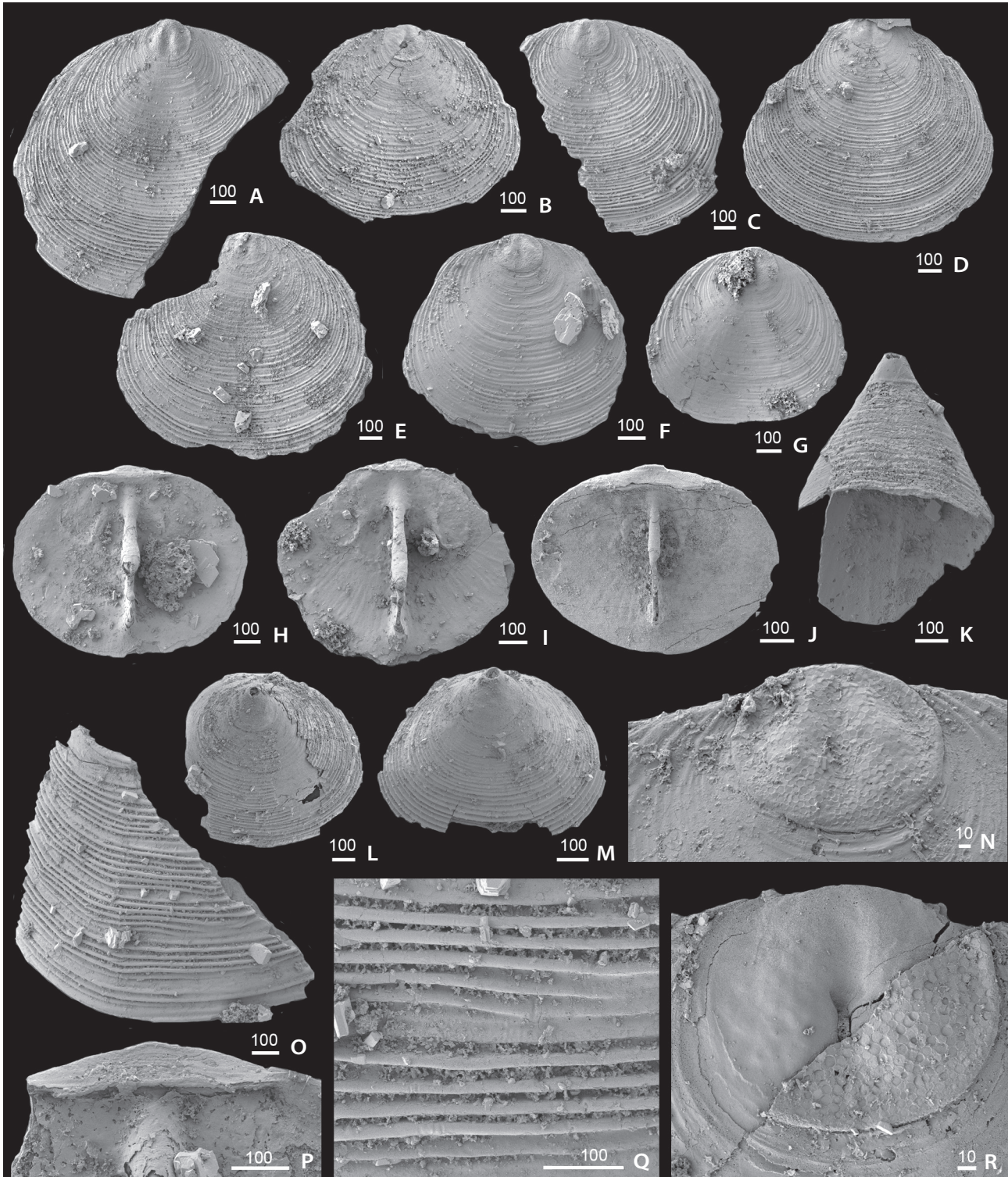


Figure 17. *Havlicekion ivanensis* Mergl, 2001a; A – exterior of large dorsal valve, PCZCU 2647; B, R – exterior of medium sized dorsal valve, and detail of its larval partly exfoliated shell showing cell moulds, PCZCU 2648; C – exterior of medium sized dorsal valve, PCZCU 2649; D – exterior of large dorsal valve, PCZCU 2650; E – exterior of large dorsal valve, PCZCU 2651; F – exterior of dorsal valve with weaker concentric fila, PCZCU 2652; G – exterior of dorsal valve with weaker concentric fila, PCZCU 2653; H – interior of dorsal valve, PCZCU 2654; I – interior of dorsal valve, PCZCU 2655; J – interior of dorsal valve in slightly posteroventral view, PCZCU 2656; K – pseudointerarea of ventral valve, PCZCU 2657; L – exterior of ventral valve in top view, PCZCU 2658; M – exterior of ventral valve, PCZCU 2659; N – larval shell of dorsal valve, PCZCU 2660; O, Q – fragment of ventral valve and detail of its ornamentation, PCZCU 2661; P – pseudointerarea of dorsal valve, PCZCU 2662. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in µm.

lamellae (Fig. 16K–M). The size of rugellae enlarges with shell growth. There are about 25 rugellae in the adult shells. The rugellae and the interspaces of similar size are covered by fine, concentric growth fila having a gently irregular course (Fig. 16T). The larval shell (Fig. 16Q) is prominent, 200 to 220 µm wide, with a slightly transverse outline, having a highly arched central mound anterolaterally associated with two smaller lobes (Fig. 16Q). The border of the larval shell forms a raised rim elevated above the surface of the early postlarval shell. The surface of the larval shell is covered by flat-bottomed circular pits of subequal, 4 to 5 µm size (Fig. 16S). These pits are often in contact but never intersect, and are almost regularly spaced. The interspaces are gently elevated and densely covered by minute semiglobular pits of about 1 µm size (Fig. 16S).

The ventral valve has a distinctly depressed nearly procline pseudointerarea. The macroornamentation is similar to that of the dorsal valve.

Remarks. – The shells are referred to *A. parva* Ireland, 1961 based on shell size and thickness, rounded outline and macroornamentation. Mergl (2001a) referred this species to *Artiotreta krizi* Mergl, 2001a, the species erected on specimens of Aeronian (Llandovery) age coming from the Hýskov (V Jakubinkách) locality near Beroun, Bohemia. The specimens from the Špičatý vrch locality have a more circular outline of the shell and the dorsal median septum is finer and lower than the conspicuously robust septum observed in specimens from Hýskov. *Artiotreta krizi*, which is likely ancestral to *A. parva*, is restricted to the Llandovery. In Bohemia, *A. parva* occurs in two localities of the Sheinwoodian age. The type material (Ireland 1961) and subsequent records of *A. parva* from Oklahoma, Illinois and Missouri (Satterfield & Thompson 1969, Chatterton & Whitehead 1987) indicate the comparable age of Bohemian and American specimens. *Artiotreta longisepta* Valentine *et al.*, 2003 which is abundant near the level of the Ireviken Event in the Borenore Limestone, N.S.W., Australia is distinct by its very high dorsal median septum and clearly impressed cardinal muscle scars.

Occurrence. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone; localities Loděnice (Špičatý vrch) (rare) and Sv. Jan (Elektrárna) (rare), Bohemia; Wenlock; Oklahoma, Illinois, Missouri, USA (Ireland

1961, Satterfield & Thompson 1969, Chatterton & Whitehead 1987).

Family Biernatidae Holmer, 1989

Genus *Havlicekion* Mergl, 2001a

Type species. – By original designation, *Havlicekion splendidus* Mergl, 2001a. Praha Formation (Pragian, Devonian); Prague Basin, Czech Republic.

Havlicekion ivanensis Mergl, 2001a

Figure 17A–R

2001a *Havlicekion ivanensis* sp. nov.; Mergl, p. 36, pl. 33, figs 1–13.

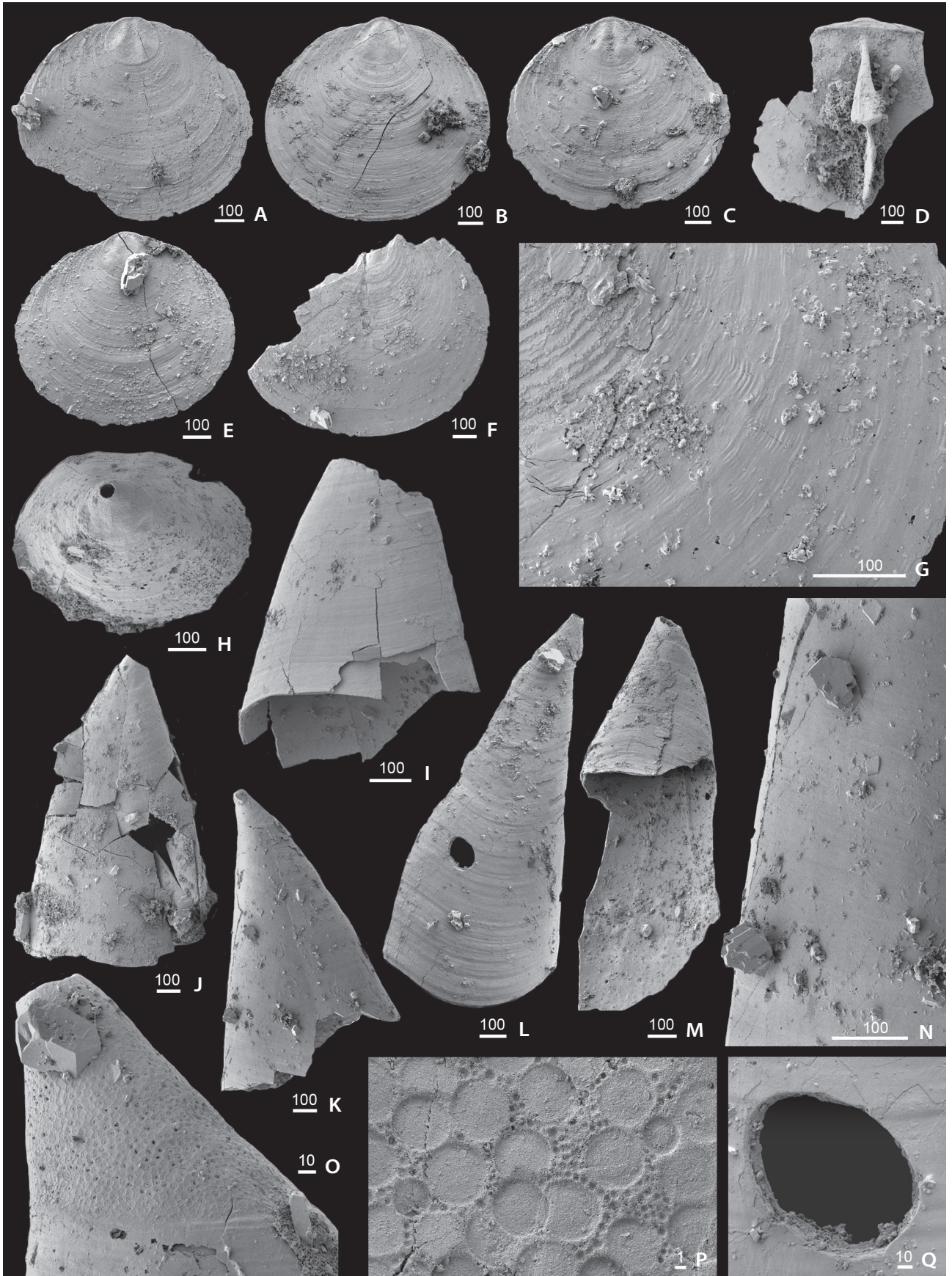
Material. – Eleven illustrated dorsal valves (PCZCU 2647–2656, 2662) and four illustrated ventral valves (PCZCU 2657–2659, 2661) and numerous other shells, often fragmentary.

Description. – See Mergl (2001a).

Remarks. – *Havlicekion ivanensis* is the earliest member of this evolutionary clade which likely disappeared at the end of the Eifelian. All members are characterized by prominent concentric growth fila, thick shell and moderately conical ventral valve compared to species of *Opsiconidion* Ludvigsen, 1974 (Mergl 2001a, Mergl & Ferrová 2009, Mergl & Vodrážková 2012, Mergl & Jiménez-Sánchez 2015).

This species is the largest of the Family Biernatiidae (Fig. 17A), with about 1.5 mm wide shell. Similar to other species from the Devonian of the Barrandian area, the ventral valve is more widely conical (Fig. 17K) than ventral valves of commonly associated species of *Opsiconidion*. *Havlicekion ivanensis* Mergl, 2001a is distinguished by a rather thick shell that displays prominent imprints of the large posterior adductors on the dorsal valve interior (Fig. 17H, I). Radially arranged canals of the vascular system are perceptible anterior to the shell midlength in the dorsal valves (Fig. 17I, J) and imprints of the *vascula media* are apparent on the interior of the ventral valve (Fig. 17K). The dorsal pseudointerarea is broadly triangular with a distinct median groove (Fig. 17P). The dorsal sulcus is well developed and produces a distinctly unisulcate

Figure 18. *Opsiconidion ephemerus* (Mergl, 1982); A – exterior of dorsal valve, PCZCU 2664; B, P – exterior of dorsal valve, and detail of its larval shell pitting, PCZCU 2665; C – exterior of dorsal valve, PCZCU 2666; D – interior of dorsal valve, PCZCU 2667; E – exterior of dorsal valve, PCZCU 2668; F, G – exterior of dorsal valve and detail of its ornament, PCZCU 2669; H – exterior of ventral valve in top view, PCZCU 2670; I – incomplete smooth ventral valve, PCZCU 2671; J – collapsed ventral valve, PCZCU 2672; K, N – ventral valve in side view and detail of its surface, PCZCU 2673; L, Q – exterior of ventral valve and detail of predatory boring, PCZCU 2674; M – interior of ventral valve, PCZCU 2675; O – larval shell of ventral valve, PCZCU 2676. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in µm.



commissure. The external macroornamentation consists of regular raised concentric fila about 20 µm wide (Fig. 17O, Q). The fila may be conspicuous over the whole surface (Fig. 17A, E) but some become less distinct on the flanks and sides of the dorsal sulcus in the examined dorsal valves (Fig. 17F, G). One exfoliated dorsal larval shell (Fig. 17R) shows the base of the dorsal median septum and moulds of shallow poorly defined pits (about 20 in number on an exposed part) on the internal surface of the larval shell. These pits are likely imprints of mantle or gonadal cells of a larval stage.

Occurrence. – Sheinwoodian, Motol Formation, *Mono-graptus belophorus* Biozone; localities Loděnice (Špičatý vrch) (abundant) and Sv. Jan (Elektrárna) (abundant).

Genus *Opsiconidion* Ludvigsen, 1974

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

Opsiconidion ephemerus (Mergl, 1982)

Figure 18A–Q

- 1982 *Caenotreta ephemera* sp. n.; Mergl, p. 115, pls 1, 2.
2001a *Opsiconidion ephemerus*. – Mergl, p. 33, pl. 29, figs 1–9.
2018 *Opsiconidion ephemerus*. – Mergl *et al.*, p. 388, fig. 9a–l.

Material. – Six illustrated dorsal valves (PCZCU 2664–2669), six illustrated ventral valves (PCZCU 2670–2675) and numerous shell fragments.

Description. – See Mergl (1982, 2001a). The fine details of microornamentation have been subsequently described by Mergl *et al.* (2018).

Remarks. – The shells from the Špičatý vrch locality are externally almost indistinguishable from the specimens coming from the Kopanina Formation, for the first time described and figured by Mergl (1982). The similarity is apparent especially in the shape of the upper rod on the dorsal median septum (Fig. 18D) and in a suppressed concentric fila in the dorsal (Fig. 18A–C, E–G) and ventral (Fig. 18I, K, L, N) valves. However, two minor differences are evident. The first is the more rounded outline of dorsal valves sampled in the Kopanina Formation. The dorsal valves from the Špičatý vrch locality have anterior and posterior margins less rounded than the sides (Fig. 18A–C, E). The second difference refers to the arrangement of flat-based pits on the larval shell. While pits in the specimens coming from the Kopanina Formation

are often intersected and leave only small interspaces (Mergl *et al.* 2018, fig. 9K6), the pits observed on the larval shells in actual specimens are complete, having a much regular honeycomb arrangement (Fig. 18P). The interspaces between flat-based pits are larger and bear numerous distinct closely-packed, *ca* 1 µm sized semiglobular pits (Fig. 18P). The variability of protetular pitting on biernatines has been discussed by several authors (Ludvigsen 1974, Bitter & Ludvigsen 1979, Williams 2003) but the taxonomical significance of different patterns is not wholly understood. Therefore, the specimens from the Motol Formation are with some caution assigned to *O. ephemerus*.

The imprints of gently divergent *vascula lateralia* have been observed on one shell (Fig. 18M). Another ventral valve (Fig. 18L) bears on the anterior slope a subcircular 100 µm sized hole. The outline of the hole is remarkably regular and differs from other similar predatory borings (*e.g.* Chatterton & Whitehead 1987) by its vertical walls and by the absence of abrasion or traces of bites around the hole. Predatory borings of similar form have been known in organophosphatic brachiopods from the Cambrian to Recent (Chatterton & Whitehead 1987, Kowalewski & Flessa 1994, Kowalewski *et al.* 1997, Robson & Pratt 2007, Vinn *et al.* 2021, Mergl & Šmídtová 2023).

Occurrence. – Sheinwoodian, Motol Formation, *Mono-graptus belophorus* Biozone; localities Loděnice (Špičatý vrch) (abundant).

Superfamily Siphonotretoidea Kutorga, 1848
Family Siphonotretidae Kutorga, 1848

Genus *Orbaspina* Valentine & Brock, 2003

Type species. – By original designation, *Orbaspina gelasinus* Valentine & Brock, 2003. Boree Creek Formation (Llandovery to Wenlock, Silurian); New South Wales, Australia.

Orbaspina involuta sp. nov.

Figure 19A–G

- 2001a *Acanthambonine* sp. – Mergl, p. 38, figs 1–7.
2001b *Siphonotretid* sp. – Mergl, p. 348, figs 35.3a–c.

Holotype. – Incomplete dorsal valve, PCZCU 2680, figured in Fig. 19A.

Paratype. – Incomplete ventral valve, PCZCU 2682, figured in Fig. 19D.

Etymology. – *Involutus* (Latin), curled.

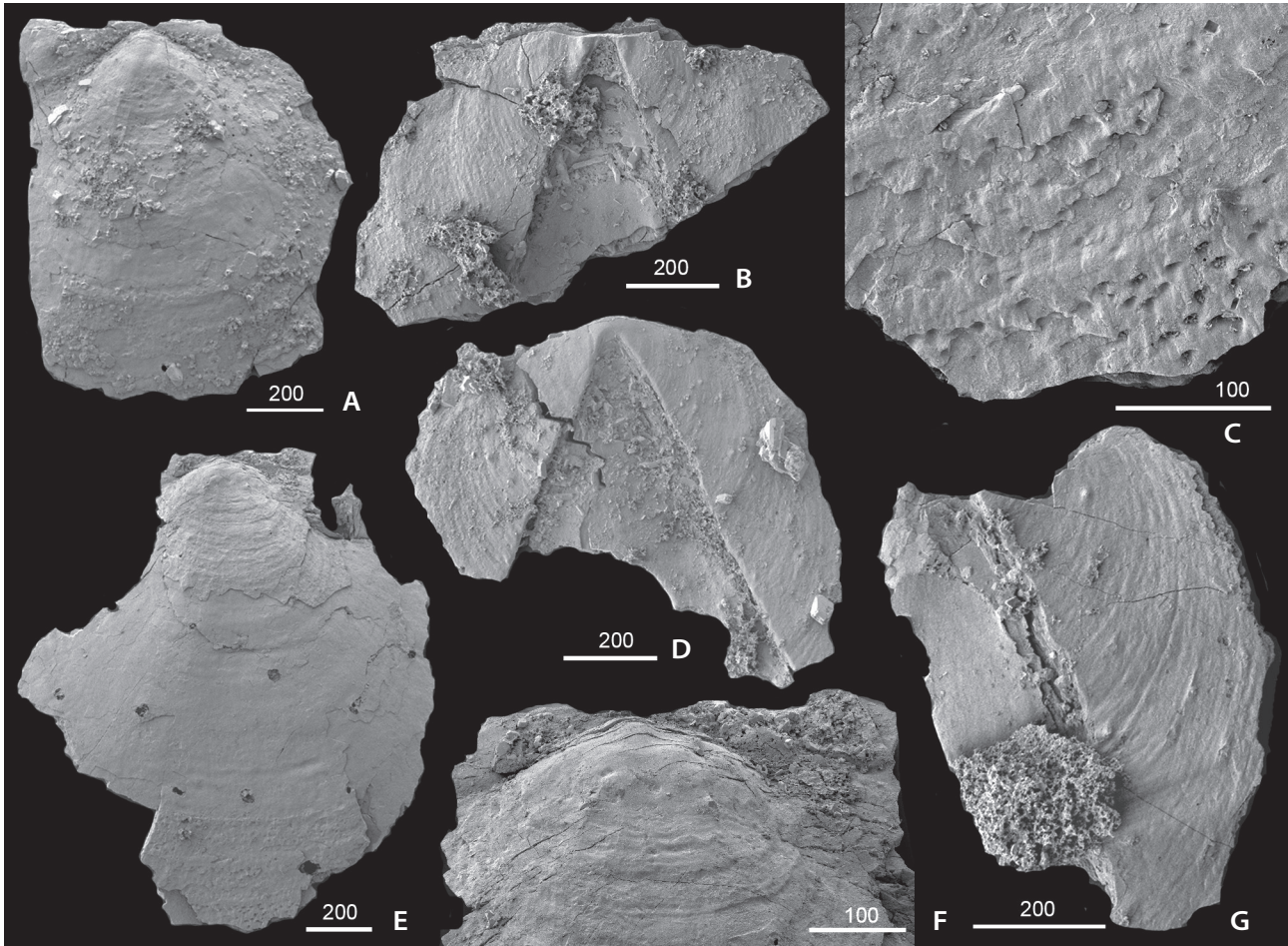


Figure 19. *Orbspina involuta* sp. nov.; A – holotype, exterior of dorsal valve, PCZCU 2680; B – exterior of incomplete ventral valve, PCZCU 2681; C, E, F – exterior of dorsal valve, detail of its ornament and larval shell, PCZCU 2683; D – paratype, exterior of incomplete ventral valve, PCZCU 2682; G – fragment of ventral valve showing spine bases, PCZCU 2684. Špičatý vrch locality; Motol Formation, *Monograptus belophorus* Biozone. All SEM photos. Bars in µm.

Type horizon and locality. – Sheinwoodian, Motol Formation, *Monograptus belophorus* Biozone, “*Miraspis* Limestone”; Bohemia, Barrandian area, Loděnice (Špičatý vrch) locality.

Material. – Four dorsal valves (PCZCU 108, 202, 2680, 2683) and three ventral valves (PCZCU 2681, 2682, 2684), all incomplete.

Diagnosis. – Dorsal valve with thickened posterior margin, with the pseudointerarea forming a subplanar shelf; the dorsal beak sinks into this shelf; the pedicle track is broadly triangular, with a weakly concave plate; spinose ornament suppressed; ornamentation of both valves consisting of a few broadly scattered fine hollow spines and minute dimples of lenticular outline; posterolateral margins spineless.

Description. – The shell is small, with estimated 2 mm minimum width, subcircular in outline, rectimarginate.

The dorsal valve is moderately convex in transverse profile, moderately convex in axial profile with evenly convex flanks. The valve is very weakly depressed in the axial anterior part. The dorsal beak is prominent, posterolaterally bordered by a flat extended surface of the dorsal pseudointerarea that forms a subplanar shelf along the posterior margin. The larval shell at the beak is curled and partially sunk into the posterior shelf (Fig. 19A, E) (see also Mergl 2001a, pl. 36, figs 1, 4, 5). The dorsal valve interior shows a deep umbonal chamber separated from the dorsal pseudointerarea by an elevated border. The dorsal pseudointerarea is orthocline, extended posteriorly.

The ventral valve is subplanar in the axial profile and gently convex in the transverse profile. The ventral pseudointerarea is apsacline, low triangular. The ventral beak is prominent, elevated, and gently posteriorly protruding (Fig. 19D). The beak angle is 150° or slightly more. The pedicle foramen is large but never well preserved in the available material. Its posterior part is

closed by a large gently concave plate (Fig. 19B, D). The sides of the pedicle track subtend 50° angle.

The macroornamentation consists of uneven concentric fila and low concentric ridges. The spinose ornament is strongly suppressed (Fig. 19A, C, G). The preserved bases of shallow spines are sparsely and randomly scattered on the surface of both valves. Small, shallow, about 10 µm long dimples of lenticular outline regularly cover the entire surface of the mature shell (Fig. 19C). The larval shell is subcircular, 300 µm wide, with prominent lateral nodes separated by a shallow axial depression (Fig. 19F).

Remarks. – The new species is distinguished by a posteriorly extended dorsal pseudointerarea and the dorsal beak sunk into the shell wall. *Orbaspina chlupaci* Mergl, 2003 from the Ludfordian (Kopanina Formation) of the Barrandian area (Mergl 2003, Mergl *et al.* 2018) resembles the new species in the scarcity of hollow spines on the shell. However, it differs by a free marginal dorsal beak, by a denser and deeper dimpling of mature shell, by a narrower pedicle track and by a row of posteriorly extended hollow spines aligned along the posterolateral margins.

The type species *O. gelasinus* from the early Wenlock of N.S.W., Australia (Valentine & Brock 2003) differs from the new species by a free dorsal beak, rows of spines along the posterior margin, a distinctly depressed axial sector in the dorsal valve and by a narrower pedicle track. The hollow spines of *O. gelasinus* are similarly fewer and fine as observed in the new species. The Australian species, although comparable in age with the new species, more closely resembles the Ludfordian species *O. chlupaci* than the Sheinwoodian *O. involuta*.

Occurrence. – Sheinwoodian, Motol Formation, *Mono-graptus belophorus* Biozone; localities Loděnice (Špičatý vrch) (rare) and Sv. Jan (Elektrárna) (rare), Bohemia.

The Silurian decline of acrotretids and siphonotretids

The lingulate brachiopod fauna from the Špičatý vrch locality exhibits a remarkably high diversity. Although the preservation is less favourable, the sample yielded more than 20 species. Such a high diversity at one locality is comparable with the proliferation of lingulates in the late Cambrian and the early Ordovician (Krause & Rowell 1975, Holmer & Popov 1996, Bassett *et al.* 1999, Curry & Brunton 2007). However, there is a significant changeover in the representation of different orders. Lingulids together with acrotretids and siphonotretids dominated in the early Ordovician (Holmer 1989; Wright & McClean 1991; Bassett *et al.* 1999, 2002; Popov & Holmer 1994; Holmer

et al. 2001; Mergl 2002 and others). In the Silurian, the importance of acrotretids rapidly decreased, the siphonotretids almost vanished while the significance of discinoideans increased. This changeover is also evident in the Silurian of the Barrandian area. It is reasonable to envisage that this is not only due to changes in lithology, although a change from siliciclastic sedimentation in the Ordovician to carbonatic sedimentation in the Silurian likely affected some marine biota. It is worth mentioning that the lingulid and acrotretid rich brachiopod associations were well adapted to carbonatic and marly sedimentation already in the Cambrian and Ordovician outside the Barrandian area (Holmer 1989, Bassett *et al.* 1999).

The end-Ordovician glaciation negatively affected diverse groups of micromorphic brachiopods, including acrotretids, siphonotretids, and paterinates (Wright & McClean 1991, Bassett *et al.* 1999). Few acrotretids (*e.g.* *Acrotretella*, *Artiotreta*, *Opsiconidion*) were able to overcome this climatic change, but their decline continued in the Silurian. Newly emerged genera, *e.g.* *Eschatelasma* Popov, 1981 in the Silurian and *Concaviseptum* Brock *et al.*, 1995 in the Devonian, disappeared rapidly. Having its ancestors among the Early Ordovician scaphalasmatides, *Artiotreta* disappeared before the Ludlow. Similarly, having the earliest species in the Middle Ordovician (Holmer 1989, Biernat & Harper 1999), *Acrotretella* weakly diversified in the Wenlock, but became extinct in the Lochkovian. The first report of *Opsiconidion* came from the Middle Ordovician (Sutton *et al.* 2000). A weak radiation of biernatids took place in the Wenlock and their moderate diversification continued to the Eifelian but this clade disappeared before the end of the Devonian, with the latest report in the Eifelian or Givetian (Langer 1971, Arno 2010, Mergl 2019, Holmer *et al.* 2020).

There is direct evidence of the epiphytic habitat of the earliest acrotretids from the Cambrian (Wang *et al.* 2012). The shell micromorphism was a great advantage because the host algal thallus was not robust enough to support the larger shells. A direct analogy exists with Recent molluscs, *e.g.* small mytilids and acmaeids. However, current studies indicate that specific chemical, structural and morphological characteristics of the algal species determine selection of epibionts rather than the amount of habitable area (Schmidt & Scheibling 2006). The same mechanism of algal-epibiont interaction can be assumed for algal-brachiopod associations. Epibiont brachiopod habitat on algal hosts seems to be a plausible explanation for diverse shell concentrations of acrotretides described in the Cambrian and Ordovician (Holmer 1989). Life on floating algal seaweeds was first suggested by Schuchert (1911) but direct evidence is missing. The same assumption supported by logical arguments has appeared repetitively (*e.g.* Havlíček 1972, Rowell & Krause 1973, Bednarczyk & Biernat 1978, Percival 1978,

Williams & Lockley 1983, Havlíček *et al.* 1993, Mergl & Vodrážková 2012). Habitat above the substrate on host benthic seaweeds is suggested for some Ordovician acrotretids (Rowell & Krause 1973, Holmer 1989). Ordovician acrotretids and other micromorphic lingulates likely adopted an epizoan-like strategy being attached to different, non-algal elevated substrates. Possible sponge-brachiopod and conulariid-brachiopod commensal relationships have also been suggested (Wright & Nölvak 1997, Percival 1978, Harland & Pickerill 1987, Lenz 1993, Popov *et al.* 1994, Mergl 2002, Holmer *et al.* 2005). The evolutionary success of linguliformen brachiopods in the Cambrian to the Darriwilian may have also been related to their low energy requirements and tolerance to high daily fluctuations of oxygen (Bassett *et al.* 1999). However, the suggested better oxygen fluctuations in shallow marginal environments of the Palaeozoic oceans and their impact on marine biota are topics of active debate (Krause *et al.* 2018, Brandt *et al.* 2021).

It is reasonable to suggest that the epibiont acrotretids on the algal hosts were negatively affected by a relative paucity of suitable elevated macromorphic algae within the euphotic zone in Silurian and Devonian reefs. There is evidence that at least some tabulate corals were photosymbiotic (Coates & Jackson 1987, Copper & Scotese 2003, Zapalski 2014, Zapalski *et al.* 2017). Except for coralline algae, the spatial competition for light avoided the growth of macromorphic algae in the Recent reefs. The same competition may be suggested in the Palaeozoic reefs. The corals, stromatoporoids, crinoids, and other pelmatozoans in a reef environment did not provide the alternative substrates because these have developed diverse repellent strategies against epibionts. Toxic nematocytes in coral polyps, an overgrowing reaction of the echinoderm stereome and other suggested defensive mechanisms prevented successful settling of brachiopod larva and its subsequent growth. This was certainly not the only problem faced by Silurian acrotretids but it may have contributed to their decline. Just as nutrient enrichment negatively affects Recent coral reefs (*e.g.* D'Angelo & Wiedenmann 2014), the same mechanism may be suggested for fossil reefs. The collapse of the Devonian reefs is linked to a breakdown of photosymbiosis and the extinction of photosymbiotic coral taxa (Bridge *et al.* 2022). *Vice versa*, the expansion of reefs in the Silurian and the Devonian with the growing importance of photosymbiotic coral taxa may have increase the limitation of some elements, namely phosphorus. Indeed, this limitation affected not only the linguliformen brachiopods but also their macroalgal substrates. Shell micromorphism and shell thinning (*e.g.* in *Opsiconidion*) were strategies to combat a low phosphorus supply.

New life strategies emerged with this micromorphism, such as an interstitial habit (Bassett 1984) or the ability to

push a micromorphic shell upward in fine carbonatic mud (Cocks 1979). The concurrent micromorphism of other linguliformeans in Silurian and Devonian reefs is apparent. Some unequivocal reef dwelling obolids are diminutive (*e.g.* *Microbolus* Mergl, 2008). The miniaturization of shell size can be traced in some evolutionary lineages that turn from the level-bottom sea floor to the reef environments (*e.g.* obolids *Wadiglossella* to *Kosagittella*). The coral-stromatoporoid lingulate endosymbiotic relationships emerged in small obolids (*e.g.* *Rowellella* Wright, 1963) in the late Ordovician and Silurian (Newall 1970, Richards & Dyson-Cobb 1976, Tapanila & Holmer 2006). Altogether, the change in availability of algae and accessibility of phosphorus brought the acrotretids to extinction at the end of the Middle Devonian.

The siphonotretids achieved their acme in the Lower Ordovician. Their decline began already in the Floian and continued to the Katian, with three genera known in this age (*Acanthambonia* Cooper, 1956; *Multispinula* Rowell, 1962; *Nushbiella* Popov, 1986 in Kolobova & Popov 1986). The last Ordovician siphonotretids come from the late Katian (Wright & McClean 1991, Mergl 2012). Silurian and Devonian siphonotretids are very rare, always micromorphic, and only *Orbaspina* persisted from the Llandovery (Valentine & Brock 2003) to the end of the Eifelian (Mergl 2019). This micromorphic genus has a very large pedicle foramen relative to the shell size. It is reasonable to assume that it was likely attached by a wholly functional pedicle, but its host substrate is unclear. *Orbaspina* is by size and spinose ornament like *Acanthambonia* and likely shared the same life habit. As in the Ordovician *Acanthambonia* (Wright & Nölvak 1997), fixation to small cylindrical objects, likely algal strands above the sea floor, is assured in *Orbaspina*. But unlike the densely spinose Ordovician siphonotretids, which utilised their marginal spines to block coarse particles entering the mantle cavity (Wright & Nölvak 1997, Mergl *et al.* 2007), the short and sparse spines of *Orbaspina* had another, likely anchoring, function.

The Silurian success of discinoideans

Mid- and Upper Ordovician discinoideans (Cooper 1956, Holmer 1987) were likely epibenthic, some attached by a discoidal ventral valve to substrate of corresponding size, *e.g.* brachiopod, gastropod and cephalopod shells and conulariid tests (see Richards 1972, Havlíček 1972, Gabbott 1999, see also Mergl & Nölváková 2016). The discinoideans occasionally used the elevated firm substrate for a higher tier (Mergl 2001a, pl. 14, fig. 1; Bassett *et al.* 2009, fig 4.1; Mergl 2010, fig. 9n) or occupied cryptic spaces as do their Recent relatives (Paine 1962, LaBarbera 1985, Kato 1996, Mergl 2010). The mode

of life can be plausibly inferred from their shell shape (Mergl 2010), known life habits of their Recent relatives (Paine 1962, LaBarbera 1985) and also uncommon direct fossil evidence of their sometimes gregarious life habit (Richards 1972, 1974; Basset *et al.* 2009; Mergl 2010).

In the Silurian and Early and Mid- Devonian, discinoidean morphological diversity reached its peak. Their shells were micromorphic to gigantic, thin- to thick-shelled, having concave to conical dorsal or ventral valves, with a subcentral to marginal pedicle foramen. The morphological disparity indicates widely varying modes of life. Some discinoideans followed an acrotretoid strategy having a highly conical ventral valve and lid-like dorsal valve (*Chynithela*) or forming a micromorphic box-like shell (*Opatrikiella*, *Schizobolus*) with marginal pedicle foramen. Others, generally medium-sized genera, were epibenthic, firmly and closely attached by the pedicle to hard or firm substrates, some likely sunken or wedged between or buried beneath bioclasts on the sea floor. Their mode of life was similar to some Recent byssate bivalves, e.g. pectinids and anomids.

The Špičatý vrch locality records discinoid history at the time of their peak. Although they are not frequent, at least seven different species of discinoideans confirm the maximum of their morphological disparity. Comparable disparity is seen in other Silurian discinoidean faunas (Mergl 2006, 2010). This disparity continued with a few new modifications of the shell shape and ornament to the Eifelian or even later (Mergl 2008, 2010). The disparity disappeared during the late Devonian environmental crises. Recent discinoideans strictly follow the morphology of their Carboniferous ancestors, characterized by a subplanar, sometimes very thin, ventral valve and low-conical dorsal valve with subcentral beak. Indeed, during discinoidean evolution, the initial Ordovician morphologic diversification was followed by narrowing of the morphospace in the Late Devonian. Since the end-Devonian extinction, stabilization with only a single viable morphological design of planar ventral and conical dorsal valve continues up to the Recent.

Conclusions

The brachiopod sample from the Špičatý vrch locality plausibly illustrates the turnover in the composition of linguliformean brachiopod assemblages following the Ordovician glaciation and after the Ireviken Event but before the Mulde Event. It should be stressed that the sample comes from a site near a volcanic island in the age when the earliest land plants diversified and the plant detritus washed down to the sea began to affect the marine ecosystems. In the Wenlock, the linguliformean brachiopods already were a subordinate component of the

benthic fauna. They represent only 3% of all brachiopods in the sample dominated by the remarkably rich rhychonelliformean brachiopod fauna. However, their alpha-diversity with 21 species is outstanding. The data also confirm that the gradual withdrawal of acrotretids and siphonotretids continued while discinoideans expanded and occupied new vacant ecospace in the benthic ecosystems. This rare sample represents the earliest stratigraphical record of a taxonomically diverse lingulate brachiopod assemblage in the Silurian.

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