Lingulate brachiopods from the Vinařice Limestone (Devonian, Pragian) of the Barrandian area, Czechia

Michal Mergl & Nikola Šmídtová

The Vinařice Limestone (Praha Formation; Central Bohemia) of Pragian age contains a moderate diverse lingulate brachiopod fauna including a new species of discinid, *Acrosaccus robustus* sp. nov., associated with several other poorly preserved discinids including the trematid *Schizocrania*, one species of the biernatid *Havlicekion* and fragments of an obolid. Lingulate brachiopods are associated with diverse rhynchonelliformean brachiopods mainly strophomenoids and rhynchonelloids. Brachiopods, trilobites and other fauna confirm the presence of a shallow, rough-water environment that existed before the origin of the coral-stromatoporoid-algal Koněprusy reef in the area. The lingulate brachiopod assemblage described herein differs from the local Emsian (Suchomasty Limestone) and Eifelian (Acanthopyge Limestones) lingulate brachiopod assemblages by absence of the discinid *Chynithele.* Presence of *Schizocrania* sp. indicates derivation of the fauna from the Lochkovian brachiopod assemblage. An *Oichnus*-type drilling trace in the brephic shell is documented in the discinid *Praeohlertella*? sp. • Key words: Lingulata, Discinoidea, Pragian, Koněprusy, Barrandian.

Mergl, M. & Šmídtová, N. 2023. Lingulate brachiopods from the Vinařice Limestone (Devonian, Pragian) of the Barrandian area, Czechia. *Bulletin of Geosciences 98*(*3*), 199–214 (5 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received May 22, 2023; accepted in revised form August 1, 2023; published online August 27, 2023; issued October 31, 2023.

Michal Mergl & Nikola Šmídtová, Centre of Biology, Geosciences and Environmental Sciences, Faculty of Education, University of West Bohemia in Plzeň, Klatovská 51, Plzeň, 30619, Czech Republic; mmergl@cbg.zcu.cz

The Koněprusy area in SW part of the Silurian–Devonian sequence of the Barrandian area has been a famous and rich source of diverse and well-preserved Lochkovian, Pragian, Emsian and Eifelian fossils for more than one-and-half centuries. This richly fossiliferous area is restricted to the vicinity of the WNW–ESE trending submarine ridge, which appeared along the early Devonian tectonic uplift. The ridge formed extensive shallow water banks that provided an exceptional environment in basin in the Pragian. The Kotýs Limestone deposited on the rising zone was in the Lochkovian. These limestones formed the basement for the Koněprusy reef complex. The Vinařice Limestone is the transitional lower Pragian unit that upward continues to the white massive Koněprusy Limestone.

The initial studies of the reef complex have been accomplished by Svoboda & Prantl (1948, 1949) and elaborated by Chlupáč (1955, 1956, 1957, 1959). More supplementary contributions devoted to various aspects of the reef were provided by the same author (Chlupáč 1996, 1998a, 2003). Geology, the commonest fossils and benthic associations of the Koněprusy (Pragian), Suchomasty (upper Emsian), Acanthopyge (Eifelian) limestones and other lithological units have been described in tens of modern monographs, short reports, field guides and popular publications (for reference see Chlupáč 1984, 1996, 2003; Chlupáč *et al.* 1986, 1979; Havlíček & Vaněk 1998; Hladil 2000; Mergl 2022). All workers stressed the uniqueness of the Koněprusy reef complex in the Lower and Middle Devonian (Chlupáč 1984, 1994, 1998b).

Unlike the astonishing abundance and diversity of rhynchonelliformean brachiopods in the limestones of the reef complex, lingulate brachiopods are comparatively rare among fossil assemblages. To date, attention has been given to lingulate brachiopods of late Emsian and Eifelian age (Mergl 2008, 2019; Mergl & Jiménez-Sánchez 2015). Their occurrence in rocks of Pragian age is very rare (Barrande 1879, Mergl 2001). The currently observed faunule from the Vinařice Limestone partially fills the gap in lingulate brachiopod distribution.

Geological and palaeontological setting

The Vinařice Limestone is the laterally transitional unit between the Koněprusy reef Limestone and the Dvorce-Prokop and allied limestones of Pragian age (Chlupáč 1998b). The unit is restricted to a small area in the vicinity of Koněprusy, with a few fossiliferous localities between Suchomasty and Měňany (Havlíček & Vaněk 1998). The thickness ranges between 2–10 m in the NW (Kotýs and Čertovy Schody localities) to 70–80 m in the SE (Homolák and Oujezdce localities) (Svoboda & Prantl 1949). Pink

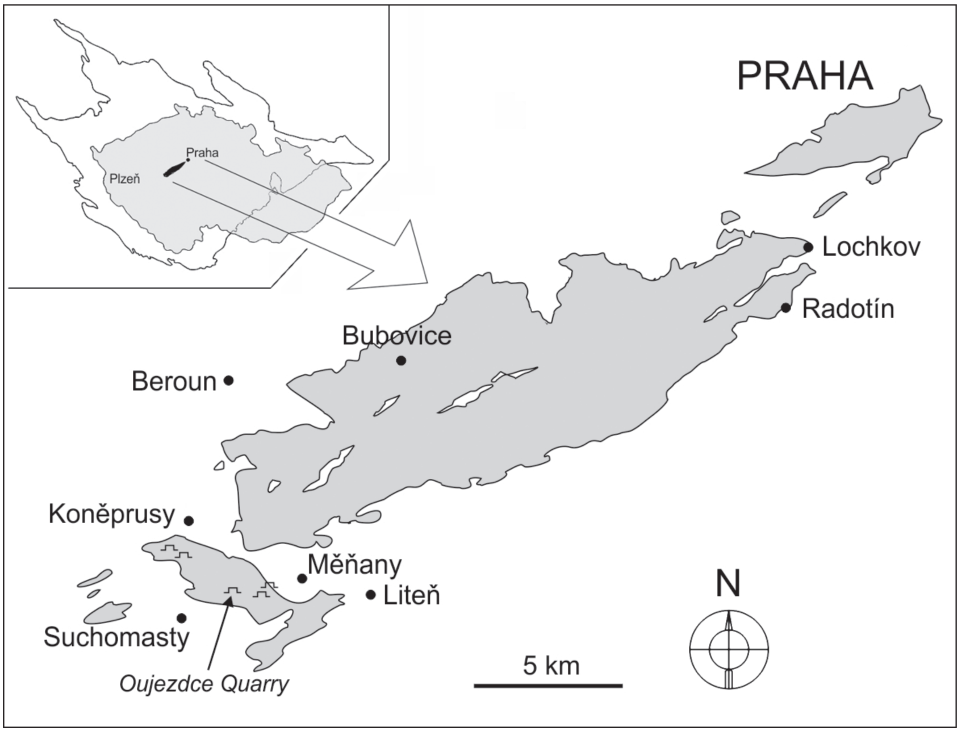


Figure 1. Schematic map showing location of the Prague Basin in Barrandian area in the Czech Republic (A) and distribution of the Devonian in Prague Basin with marked Koněprusy area and Oujezdce locality (B).

to red coloured limestone is composed of angular to subrounded crinoidal fragments and a variable amount of micritic component. The amout of micritic component increases eastwards into an almost exclusively micritic sequence near Měňany (Svoboda & Prantl 1949, Chlupáč 1955, Havlíček & Vaněk 1998, Vaněk 1999). Hummocky-cross stratification, stream laminar bedding, and broad ripple marks confirm a shallow-water environment during deposition of the Vinařice Limestone.

The fauna of the Vinařice Limestone exhibits a clear influence of the Koněprusy reef. There are many common brachiopods but uncommon and greatly different trilobite species (Havlíček & Vaněk 1998). The trilobite fauna becomes more richer and taxonomically unique toward the SE, with more than fifty described species. Therefore, Chlupáč (1983) distinguished the special *Platypeltis-Kolihapeltis* trilobite assemblage in the Vinařice Limestone near Měňany.

The most comprehensive review of the Vinařice Limestone brachiopods and trilobites was published by Havlíček & Vaněk (1998). Vaněk (1999) updated taxonomy on trilobites that was scattered in the publications of preceding authors (Barrande 1852, 1872; Přibyl 1949, 1964, 1965; Šnajdr 1960, 1980; Pillet 1968; Chlupáč 1972, 1983; Přibyl & Vaněk 1981a, b, 1986; Přibyl *et al.* 1986; Chlupáč & Šnajdr 1989; Vaněk *et al*. 1992).

Havlíček & Vaněk (1998) compiled a list of brachiopod and trilobite taxa known to date from the Vinařice Limestone. A single minute lingulate brachiopod, the obolid *Wadiglossa lingua* (Barrande, 1879), was noted in their list of fossils. During collecting of diverse rhynchonelliformean brachiopods in the locality Oujezdce (Fig. 1) two specimens of discinids were observed in pink and grey micritic limestone. These shells initiated the search for organophosphatic shells by chemical extraction from fossiliferous limestone beds in this locality.

Material and methods

All specimens here described were collected in the old abandoned quarry near Oujezdce (locality 5 by Havlíček & Vaněk 1998; Fig. 1). Dissolution of about 30 kg of limestone yielded a small collection of largely fragmented shells of lingulate brachiopods. They are often corroded or desquamated but some fine details may be observed in some fragments. Including smallest fragments, about a hundred specimens have been picked from the residuum that left after dissolution of limestone pieces by 15% solution of acetic acid. Associated fossils in the residuum show moderate diversity. Small, largely fragmented byronid tubes, phosphatic sclerites of *Eurytholia*, conodont elements, fragments of phyllocarid cuticles, silicified or phosphatised shells of bivalves, gastropods, hyoliths and ostracods, and phosphatic moulds of shell microborings have been observed.

Only two valves have been recovered during a field sampling. These shells have been released by a chemical removal of covering rock. The underside of the external part of a valve was covered by a mat of artificial acrylate resin Dentacryl and the carbonate rock covering the shell exterior was slowly removed by etching with a 15% solution of acetic acid.

Extracted shells were mounted on SEM stubs, covered by gold and examined by SEM JSM-6300. Two ammonium chloride coated specimens were photographed under a binocular lens OLYMPUS SZX 7 with use of the Deep Focus 3.1 software. Terminology of juvenile shells is that of Williams (2003).

Up to now all known lingulates from the Koněprusy Limestone and adjacent lithofacies of the Vinařice and Slivenec limestones (Barrande 1879, Havlíček & Vaněk 1998, Mergl 2001) have been obtained by mechanical splitting of hard rock. This method leaves fine external details of shell invisible because the shell has been broken up inside its wall. The shells extracted from the rocks by chemical methods, *e.g.* dissolution of carbonate rock by weak acids, often exhibit a peeled surface and shells are commonly shaded by clay lumps. Moreover, in the shells from the Vinařice Limestone, the organic substance of the organophosphatic shell was totally removed leaving very fragile blanched shells. On that account fragments instead of complete valves have been examined. Thus, the taxonomic conclusions are based on rare and often unimpresive specimens. Despite these issues, the description of lingulate brachiopods from Vinařice Limestone provides an important insight into the diversity and evolution of perireefal biota in tropical Devonian seas.

Abbreviations. – L – length, W – width.

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

Systematic part

Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Obolidae King, 1846
Subfamily Obolinae King, 1846

Obolidae gen. et sp. indet.
Figure 2A, B

Material. – One valve fragment (PCZCU 2594) and an incomplete dorsal valve (PCZCU 2601).

Description. – Two fragments likely belong to the same species, but material is very poor. Larger fragment belongs to 2 to 3 mm long dorsal valve. It is moderately convex, with a moderately thick shell, semielliptical posterior margin and weakly defined visceral area. The dorsal pseudointerarea consists of a broadly triangular, fairly long median groove bordered by narrow weakly defined propareas that rest on steep lateral slopes of valve floor. Transverse anterior border of the median groove is weakly elevated above the valve floor. Exterior of the second fragment (Fig. 2A) exhibits the acute edge of posterolateral commissure and shell exterior with uneven and weakly defined growth lines. The microornament of the postlarval shell is uknown.

Remarks. – Although rare and poorly preserved, these valves confirm the presence of an obolid among lingulate brachiopods of the Vinařice Limestone. Havlíček & Vaněk (1998) noted presence of *Kosagittella*? *lingua* (Barrande, 1879) from the quarry east from gamekeeper's lodge near Měňany (Havlíček & Vaněk 1998: tab. 1). This specimen was illustrated by Mergl (2001: pl. 3, fig. 15). However, confirmation of the identity of this valve and two new fragments is debatable because the interior of Havlíček's specimen cannot be examined due to the different mode of preservation. Mergl (2001) referred to *K.*? *lingua* more specimens from limestones of Pragian to Emsian age in the Barrandian area. Subsequent studies (Mergl 2008, Mergl & Ferrová 2009, Mergl & Jiménez-Sánchez 2015) proved the separation of specimens from the Chýnice, Suchomasty, and Acanthopyge limestones into particular species. The type specimen of *K.*? *lingua* likely came from the limestone of the Pragian Age. This specimen was refigured by Mergl (2001: pl. 3, fig. 13). It is very small and essentially featureless for a critical revision. Therefore, although by the size, outline and shape of the dorsal interarea, two of our fragments are similar to stratigraphically younger species of *Kosagittella*, they are left in open taxonomic nomenclature. The characteristic microornament of *Kosagittella* (Mergl & Ferrová 2009) was not observed in our fragments.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Superfamily Discinoidea Gray, 1840
Family Trematidae Schuchert, 1893

Genus *Opatrilkiella* Mergl, 2001

Type species. – *Opatrilkiella minuta* Mergl, 2001; Požáry Formation, Přídolí, Silurian; Prague Basin, Czech Republic.

***Opatrilkiella* sp.**
Figure 2H–J

Material. – One ventral (PCZCU 2575) and one dorsal valve (PZCZU 2582).

Remarks. – Poorly preserved shells differ from other discinid shells in the Oujezdce locality by ornament of fine uneven concentric fila which are largely interrupted sets of parallel-sided drapes (Fig. 2J, H). The ventral valve has a short steep posteriorly opened pedicle track (Fig. 2J). The shell is similar in its exterior and high posterior slope of the dorsal valve to the Emsin-Eifelian species *O. kobyla* Mergl, 2008. The type species *O. minuta* has a shorter posterior slope and more regular concentric fila. An open taxonomical position of the specimens is preferred due poor preservation of shells.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Genus *Schizocrania* Hall & Whitfield, 1875

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

***Schizocrania* sp.**
Figure 2C–G, K, L

Material. – Five fragments of (one?) dorsal valve (PCZCU 2581) and one small fragment with characteristic ornament (PCZCU 2593).

Description. – Shape of the entire shell is poorly known but available fragments indicate that the shell was at least 10 mm wide, having a weak convexity. The dorsal valve was apparently very thin relative to its size. Growth fila indicate a subcircular shell outline (Fig. 2F). The dorsal apex is located at the posterior margin. The brephic valve is 1.3 mm wide and 1.0 mm long, weakly convex in transverse and axial profiles, with apparently a very thin wall. It is covered by numerous weak concentric growth rings (Fig. 2D). The earliest concentric ring appears at 100 μm wide shell indicating that the larval shell was small relative to the size of brephic shell. The boundary with the early mature shell is sharp, marked by onset of the radial ornament (Fig. 2D). Fine rounded radial costellae are separated by somewhat broader interspaces. Arcuate costellae at flanks change to straight ones in the median sector of valve (Fig. 2C, E). Costellae are entire, never divided, with uninterrupted course along their whole length. Their width slowly increases toward the commissure. New costellae originate solely by intercalation between the older costellae in places where the interspaces exceed its width limit (Fig. 2L). Therefore, new costellae appear randomly over entire shell surface. The concentric ornament of the early mature shell is weak, formed by poor concentric bands accentuated by a ripple-like band (Fig. 2F). However, minute fragments of apparently larger shells indicate that rather wide (100 μm) low rounded costellae are separated by approximately double-sized interpaces (Fig. 2G). Interspaces are crossed by thin concentric lines. Radial and concentric lines form a reticulate ornament that is characteristic for the trematid clade (Fig. 2G).

Remarks. – Despite their poor preservation the fragments give evidence of the presence of *Schizocrania* in the Pragian of the Barrandian area. This extends data given by Mergl & Nolčová (2016) that described two valves of *Schizocrania* sp. from limestone of Lochkovian age. One shell of Lochkovian age is represented by an isolated ventral valve (Mergl & Nolčová 2016: pl. 3, figs 17, 18, 20, 21) which differs wholly from our material. The dorsal valve attached to a strophomenid brachiopod (Mergl & Nolčová 2016: pl. 3, figs 19, 22) exhibits macroornament nearly identical with that observed in fragments from the Vinařice Limestone.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Family Discinidae Gray, 1840
Subfamily Orbiculoideinae Schuchert & Le Vene, 1929

Genus *Acrosaccus* Willard, 1928

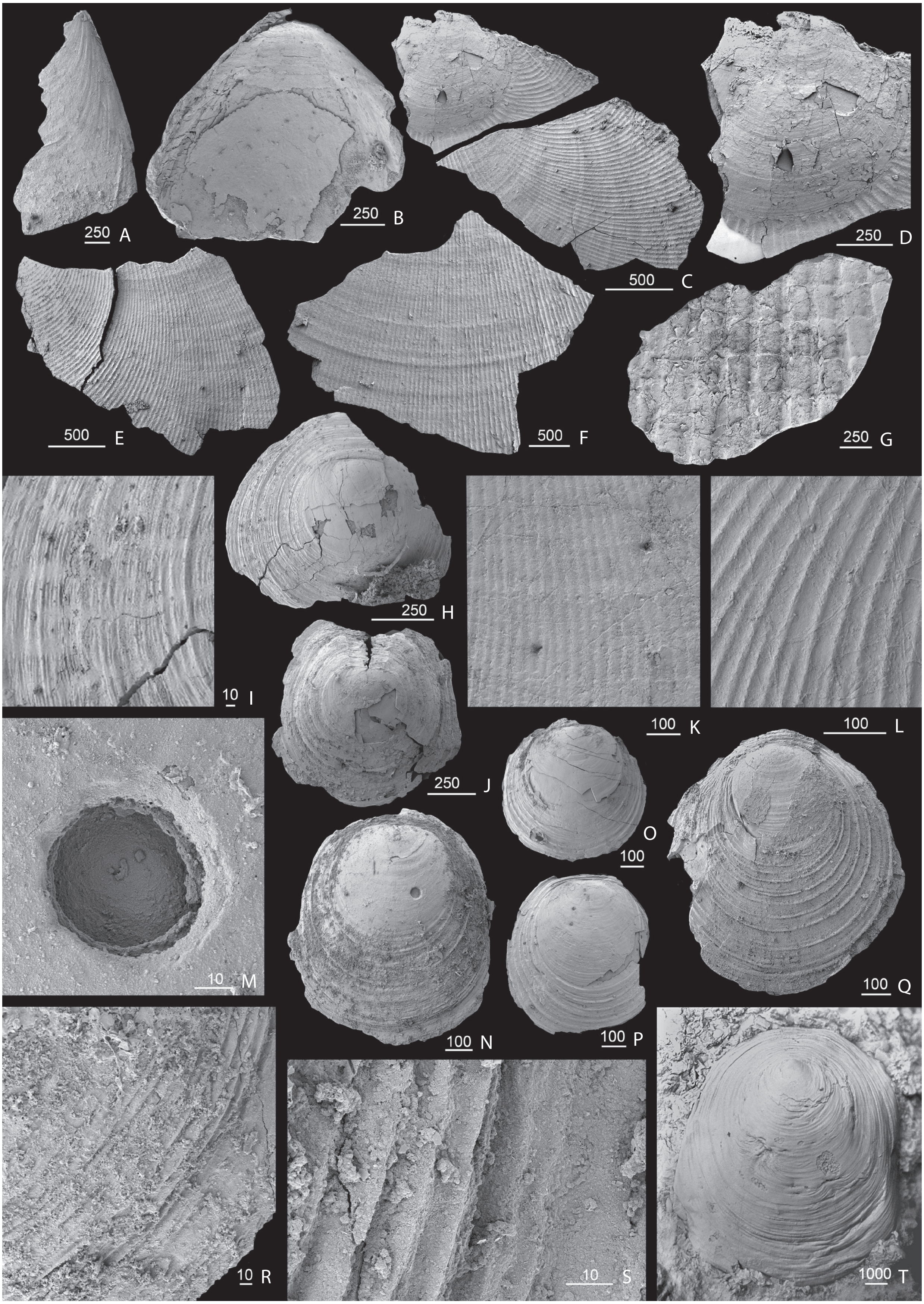
Type species. – *Acrosaccus schuleri* Willard, 1928; Rich Valley Formation, Sandbian, Ordovician; Virginia, USA.

***Acrosaccus robustus* sp. nov.**
Figures 3, 4

Holotype. – Dorsal valve in limestone (PCZCU 2566) and its counterpart attached to resin mat.

Material. – Apart of the holotype, five dorsal valves (PCZCU 2572, 2574, 2583, 2590, 2599), five incomplete

Figure 2. Lingulate brachiopods from the Vinařice Limestone (Pragian), Oujezdce locality. • A, B – Obolidae gen. et sp. indet.; A – fragment of (?) ventral valve, PCZCU 2594; B – interior of dorsal valve, PCZCU 2601. • C–G, K, L – *Schizocrania* sp., C–F, K, L – broken dorsal valve, apical part (C), detail of brephic valve (D), left flank (E), and central portion of shell (F), detail of E, and detail of L, PCZCU 2581; G – fragment of large shell, PCZCU 2593. • H–J – *Opatrilkiella* sp.; H, I – incomplete dorsal valve, and detail of microornament, PCZCU 2582; J – small ventral valve, PCZCU 2575. • M–P, R, S – *Praeoehlertella*? sp.; M, N, R, S – dorsal valve with drilled brephic shell, detail of drilling, and two details of ornament, PCZCU 2577; O – small dorsal valve, PCZCU 2603; P – small dorsal valve, PCZCU 2576. • Q – Orbiculoideinae gen. et sp. indet. A, dorsal valve, PCZCU 2595. • T – Orbiculoideinae gen. et sp. indet. B, large dorsal valve, partly exfoliated, PCZCU 2602. Bar length in micrometres.


250 A
250 B
500 C
250 D
500 E
500 F
250 G
250 H
10 I
250 J
100 K
100 L
10 M
100 N
100 O
100 P
100 Q
10 R
10 S
1000 T

ventral valves (PCZCU 2568, 2569, 2571, 2573, 2584) and several fragments having a characteristic ornament (PCZCU 2570, 2592).

Diagnosis. – *Acrosaccus* having a subcircular, thick-walled shell, an ornament of conspicuos tilted rugellae of uneven size and comparatively narrower deep interspaces in dorsal valve, a short and broad pedicle track having reversely tear-drop outline, and a small pedicle opening internally continuing into a long pedicle tube.

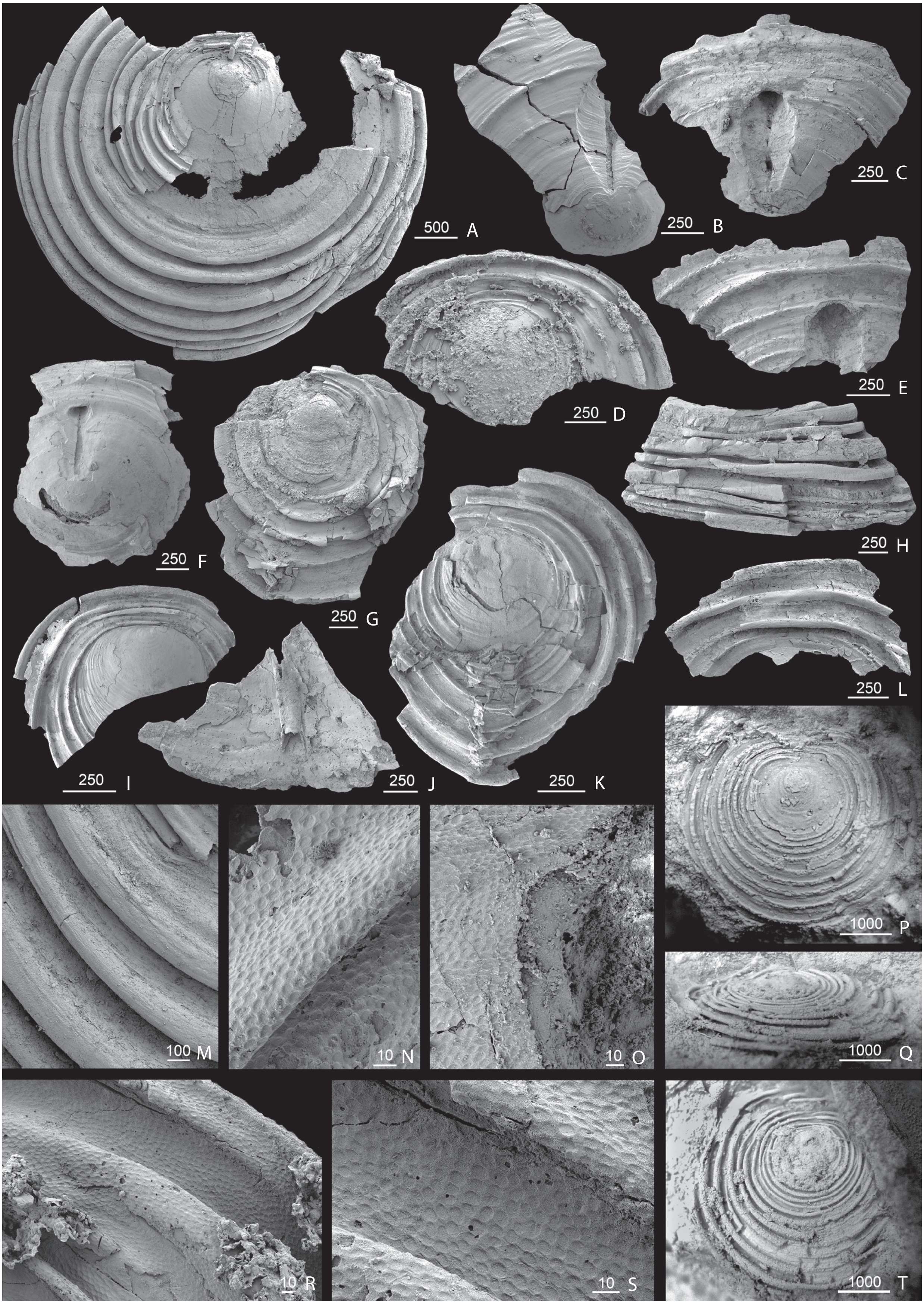
Description. – The shell is of medium size for the genus, with the largest complete shell 4.9 mm wide. The shell is thick-walled relative to its size, with a thickness increasing by development of gradually thicker rugellae. The shell has a nearly circular outline, with W/L = 1.07 (n = 2), the maximum width lies slightly posterior to the mid-length.

The dorsal valve is lid-like, low, 0.4 to1 mm high having the posterior margin of brephic shell situated at the posterior one-fourth of valve. Transverse diameter of almost circular brephic shell is 550 μm (Fig. 3I). The brephic shell forms a moderately convex dome-shaped elevation above the nearly flat surface of adjacent early mature shell. The posterior slope, flanks, and anterior portion of the valve outside the early mature shell, slightly slope down to the commissure (Fig. 3A). The earliest concentric ripple specifies the first formed shell having a diameter of 100 μm (Fig. 3I). The brephic shell has clearly elevated posterior and posterolateral edges which sharply delineate the contact with the mature shell (Fig. 3I). Its anterior and anterolateral boundaries are demarcated by the first arcuate incomplete rugella and by a sudden appearrance of vesicular pitting (Fig. 3G). The surface of the brephic shell is smooth except for numerous anteriorolaterally more conspicuous growth ripples (Fig. 3I). The macroornament of the mature dorsal valve consists of conspicuous rugellae that get bigger towards the commissure. The earliest entire rugella appears when the shell is approximately 700 μm wide. The early rugellae are fine, oriented almost vertically to the surface of the valve. Subsequent rugellae get coarser and higher with growing shell size, but their amplitudes and intervals are uneven (Fig. 3A, G, K). The rugellae are moderately to strongly inclined towards shell margins. Their crests are not undercut. Slender and lower rugellae are commonly intercalated between preceding and subsequent rugellae. The regular outline of rugellae occasionally fades and a new arcuate rugella intercalates on the floor of an interspace (Fig. 3A). Rugellae are generally less conspicuous on the posterior region of the shell, but high and almost lamellose closely packed rugellae are developed on the fragment from the steep posterior face of a large dorsal valve (Fig. 3H).

The ventral valve is low-conical having a steeper evenly sloping posterior face and a moderate concave anterior slope. The apex is situated near the centre of the valve but its exact location remains tentative because no complete large valve was examined. The pedicle track has a reversed tear-drop like outline (Fig. 3C). It is 750 μm long, 350 μm wide, with steep striated sides of the listrium which is inclined toward a narrow deep smooth pedicle groove (Fig. 3B). The lateral borders of track moderately diverge posteriorly at about 30° to three-quarters of its length (Fig. 3B, C) whilst its borders in the posterior quarter rapidly converge and encompas a small circular opening (Fig. 3C, E). The external pedicle opening is 100 to 120 μm wide and continues internally into a long pedicle tube with 100–120 μm diameter (Fig. 3J). The tube is weakly fixed along its length and highly elevated above the valve floor. Internal opening of the tube lies near the posterior commissure. The shape of a visceral field and muscle scars is unknown due to a scarcity of material. The macroornament of the ventral valve is less conspicuous that of the dorsal valve. It consists of prominent short ridge-like remote rugellae separated by much wider interspaces bearing low and broad concentric ripples (Fig. 3B, E). The size of rugellae evenly increase with shell size.

The microornament on the primary shell layer is the same in dorsal and ventral valves. Uniformly sized vesicular pits cover the entire surface apart from the brephic shell and the listrium (Fig. 3M, O, R). Pits have transversely oval to subcircular outline (Fig. 3N, S), with longer axis oriented parallel with growth lines. They are arranged in more or less discrete and tightly packed radial or oblique rows, without regular honey-comb arrangement. Their size is largely uniform, 6–7 μm length and 5 μm width, but these sizes and spacing may weakly vary. They are shallow, no more than 2 μm deep. Elevated

Figure 3. A–T – *Acrosaccus robustus* sp. nov., Pragian, Vinařice Limestone, Oujezdce locality; A, M – almost complete dorsal valve, and detail of ornament, PCZCU 2590; B – incomplete ventral valve, PCZCU 2584; C – incomplete ventral valve showing pedicle track, PCZCU 2568; D, R, S – incomplete dorsal valve, and two details of its microornament, PCZCU 2583; E, O – incomplete ventral valve showing microornament near the pedicle track, PCZCU 2569; F – partly exfoliated incomplete ventral valve, PCZCU 2573; G – incomplete dorsal valve, PCZCU 2591; H – fragment of large valve, PCZCU 2592; I, N – incomplete dorsal valve, and detail of its microornament, PCZCU 2572; J – fragment of ventral valve, interior showing internal pedicle tube, PCZCU 2571; K – partly collapsed dorsal valve, PCZCU 2574; L – fragment of dorsal valve showing ornament on posterior slope, PCZCU 2570; P, Q, T – complete dorsal valve, holotype, internal mould and exterior in oblique and apical views, PCZCU 2566. Bar length in micrometres.


500 A
250 B
250 C
250 D
250 E
250 F
250 G
250 H
250 I
250 J
250 K
250 L
100 M
10 N
10 O
1000 P
1000 Q
10 R
10 S
1000 T

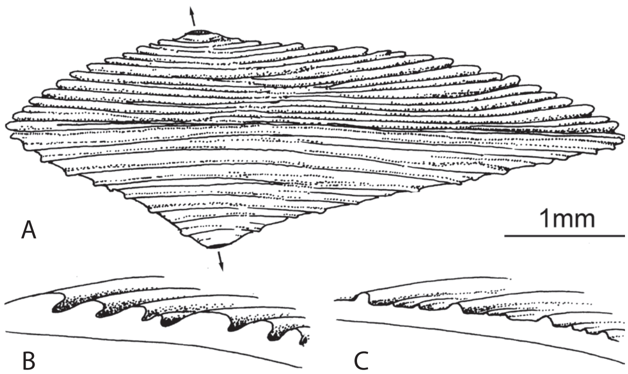


Figure. 4. *Acrococcus robustus* sp. nov. A – side view of reconstructed shell with arrows indicating directions of larval valves; B – macroornament of dorsal valve; C – macroornament of the ventral valve.

surface of primary layer between pits often exhibits very weak grooves (Fig. 3S) which likely represent casts of weak folds of periostracal sheet originating between much tougher vesicular bodies.

Remarks. – The new species belongs to a group of moderately sized discinids characterized by a subplanar, lid-, dish- or cap-like like dorsal valve with a subcentral apex and a conspicuous rugellate macroornament. All members have prominent narrowly to broadly spindle- or reversely tear-drop outline of the pedicle track and apparently have an internal pedicle tube. The early members of this group have been generally referred to *Orbiculoidea* d'Orbigny, 1847 or *Acrosaccus* Willard, 1928. Their occurrence can be traced back to the Ordovician (Willard 1928; Cooper 1956; Wright 1963; Harper 1984; Holmer 1987; Havlíček 1994; Sutton *et al.* 2000; Mergl 2002; Percival *et al.* 2011, 2016). More species having this morphology have been described from the Silurian and the Devonian (*e.g.* Mergl 1996, 2001, 2006, 2008, 2010; Valentine 2006; Valentine *et al.* 2006; Mergl & Ferrová 2009; Mergl & Vodrážková 2012; Mergl & Jiménez-Sánchez 2015; Mergl *et al.* 2018; Mergl & Valenzuela-Ríos 2020).

The type species *Acrosaccus shuleri* Willard, 1928, from the Upper Ordovician of Virginia, U.S.A., differs in having a more elongate shell outline, posteriorly tapering narrowly spindle-shaped pedicle track, and a much finer rugellate macroornament (Willard 1928; see also Holmer & Popov 2000). The new species is by its shell size, thickness and the conspicous macroornament similar to *A. cocksi* Mergl, 2010 from the Sheinwoodian and Homerian of England (Mergl 2010). The Bohemian species differs in having a shorter pedicle track, a more posteriorly located dorsal apex, and coarser macroornament. *Acrosaccus bubovicensis* (Mergl, 2001) from the Homerian of the Barrandian area differs by a more elongate shell, a centrally located dorsal apex, and less conspicuous rugellate ornament on the dorsal valve. The microornaments of *A. cocksi* and *A. bubovicensis* are unknown. The Emsian and Eifelian species referred to *Acrosaccus* from the Barrandian area [*A. vertex* Mergl & Ferrová, 2009; *A*. ssp. (Mergl 2008, Mergl & Jiménez-Sánchez 2015)] exhibit more remotely-spaced and finer rugellae. Remote and very high lamellose dorsal rugellae also distinguish *A*. sp. recorded in the Lochkovian and early Pragian in the Spanish Central Pyrenees (Mergl & Valenzuela-Ríos 2020).

Occurrence. – Vinařice Limestone; locality Oujezdce (abundant).

Genus *Praeoehlertella* Mergl, 2001

Type species. – *Praeoehlertella umbrosa* Mergl, 2001; Praha Formation, Pragian, Devonian; Prague Basin, Czech Republic.

***Praeoehlertella*? sp**.
Figure 2M–P, R, S

Material. – Three dorsal valves (PCZCU 2576, 2577, 2603).

Description. – The dorsal valve is elongate oval with regularly rounded posterior margin, short posterior slope and weak convexity. The brephic valve is circular, 500 µm wide, with very weak concentric ripples. The macroornament of the mature shell is formed by uneven, densely crowded raised concentric fila (Fig. 2N, R). The microornament is not preserved.

Remarks. – Poor preservation and small number of specimens make determination tentative. The shells are similar to *P*. sp. from the Chýnice Limestone (Emsian) and other, largely poorly preserved shells referred to the same genus from the Pragian and the Eifelian (Mergl & Vodrážková 2012, Mergl & Valenzuela-Ríos 2020).

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Genus *Rugadiscina* Mergl, 2010

Type species. – *Orbicula rugata* J. de C. Sowerby, 1839 *in* Murchison (1839); Ludfordian, Ludlow, Silurian; England.

***Rugadiscina* sp.**
Figure 5C–G

Material. – One incomplete ventral valve (PCZCU 2579).

Description. – The ventral valve is flat, gently depressed near the pedicle track, thin-walled, with width estimated at 3 mm. The valve has a subcircular to slightly elongate suboval outline (Fig. 5C). The apex is subcentral, with surface of the brephic shell slightly inclined posteriorly. The pedicle track is large, narrowly triangular in proximal part, becoming subparallel distally, with large external listrial plates gently sloping to a narrow pedicle groove. It is not clear whether the pedicle opening was posteriorly open or closed by mineralized shell due to breakage of the valve near the posterior margin. The macroornament consists of widely and equally spaced concentric rugellae evenly increasing in size towards the commissure (Fig. 5C). Crests of rugellae are rounded. Interspaces are wide and flat. The microornament consists of deep circular vesicular pits. They are uniformly sized, 3 μm in diameter, having a flat bottom and steep slopes (Fig. 5G), imprinting vesicles of discoidal or cylindrical shape. Pits are equidistantly distributed in a more or less regular honeycomb pattern (Fig. 5D, E) apart from the area adjacent to the pedicle track where they convert to discrete radial rows (Fig. 5F).

Remarks. – This species, although represented by a single incomplete shell, is distinguished by a flat ventral valve and large pedicle track surrounded by a depressed area. This is consistent with its attribution to *Rugadiscina* Mergl, 2006. The type species shows a similar microornament (Mergl 2006). The "orbiculoidean" morphology with subplanar ventral valve and depressed area adjoined to the pedicle track is rare among the discinoids of the Barrandian area (Mergl 2001). However, a small valve coming from the white limestone of Lochkovian or Pragian age from Hýskov (Mergl 2001: pl. 16, fig. 3) may belong to the same species (Barrande 1879: pl. 100, case II, fig. 3).

Genus *Sterbinella* Mergl, 2001

Type species. – Sterbinella daphne Mergl, 2001; Požáry Formation, Přídolí, Silurian; Prague Basin, Czech Republic.

***Sterbinella*? sp.**
Figure 5A, B

Material. – One small ventral valve (PCZCU 2578).

Description. – A single valve is small, only 1.2 mm wide, nearly circular in outline, showing a distinct, weakly diverging and likely posteriorly opened pedicle track, which becomes rather wide (150 μm) just beneath the posterior margin of the brephic shell (Fig. 5A). Listrial plates are well developed. Slightly transverse brephic shell, 550 μm in diameter, is not strongly distinguished from the mature shell. The macroornament of the early mature shell consists of weak and low, largely interrupted concentric rugellae (Fig. 5B). Feebly defined radial rays are visible on a median sector of the anterior slope (Fig. 5A). The microornament consists of very shallow imprints of elliptical vesicular pits, arranged in more or less distinct honeycomb pattern. The primary layer of the mature shell is very thin (Fig. 5B).

Remarks. – The sides of the pedicle track in the examined valve are less divergent compared to that of associated ventral valves of *Acrosaccus robustus* sp. nov. The latter is also distinguished by more conspicuous vesicular pitting. The size, convexity, outline, presence of rays on anterior slope, and the shape of pedicle track are similar to those of the type species *S. daphne* Mergl, 2001 from the Požáry Formation (Přídolí) of the Barrandian area. However, the different elliptical shape of vesicular pits examined in our specimen (*cf*. Mergl 2001: pl. 12, fig. 12) leaves the generic status of our shell uncertain.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Orbiculoideinae gen. et sp. indet. A
Figure 2Q

Material. – One dorsal valve (PCZCU 2595).

Remarks. – The moderate convex dorsal valve differs from *Praeohlertella*? sp. by the macroornament of the mature shell which is formed by regularly spaced raised fila separated by wide interspaces.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Orbiculoideinae gen. et sp. indet. B
Figure 2T

Material. – One dorsal valve (PCZCU 2602).

Remarks. – The asymmetrically low conical gently elongate dorsal valve was obtained by mechanical splitting of limestone. Therefore, the figured specimen (Fig. 2T) shows a seemingly nearly smooth surface which was generated by exfoliation of the outermost shell layers. Common irregularities in growth lines are visible on the shell. The actual macroornament of the mature shell consists of raised, densely crowded rope-like concentric fila, but because the exterior is largely covered by clayey clusters, it is not illustrated herein. Relationship of the valve to other material from the Oujezdce locality is unclear. The valve may belong to the genus *Rugadiscina*, which is characterised by similarly shaped cap-like dorsal valves (Mergl 2010). One fragment of a ventral valve of *Rugadiscina* was examined in our material from the Oujedce locality.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

Orbiculoideinae gen. et sp. indet. C
Figure 5H

Material. – One incomplete valve (PCZCU 2585).

Remarks. – The fragment comes from a moderately sized (3 mm or more wide) thin-walled and weakly convex dorsal valve having the apex located approximately at the posterior third of the valve. Growth lines indicate a subcircular shell outline. The shell differs from those of other discinids at the locality by numerous fine low growth fila of uniform size. The microornament was not examined.

Occurrence. – Vinařice Limestone; locality Oujezdce (rare).

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

Genus *Havlicekion* Mergl, 2001

Type species. – *Havlicekion splendidus* Mergl, 2001; Praha Formation, Pragian, Devonian; Prague Basin, Czech Republic.

***Havlicekion* cf. *holynensis* Mergl, 2001**
Figure 5I–T

cf. 2001 *Havlicekion holynensis* sp. n.; Mergl, p. 37, pl. 34, figs 1–14.

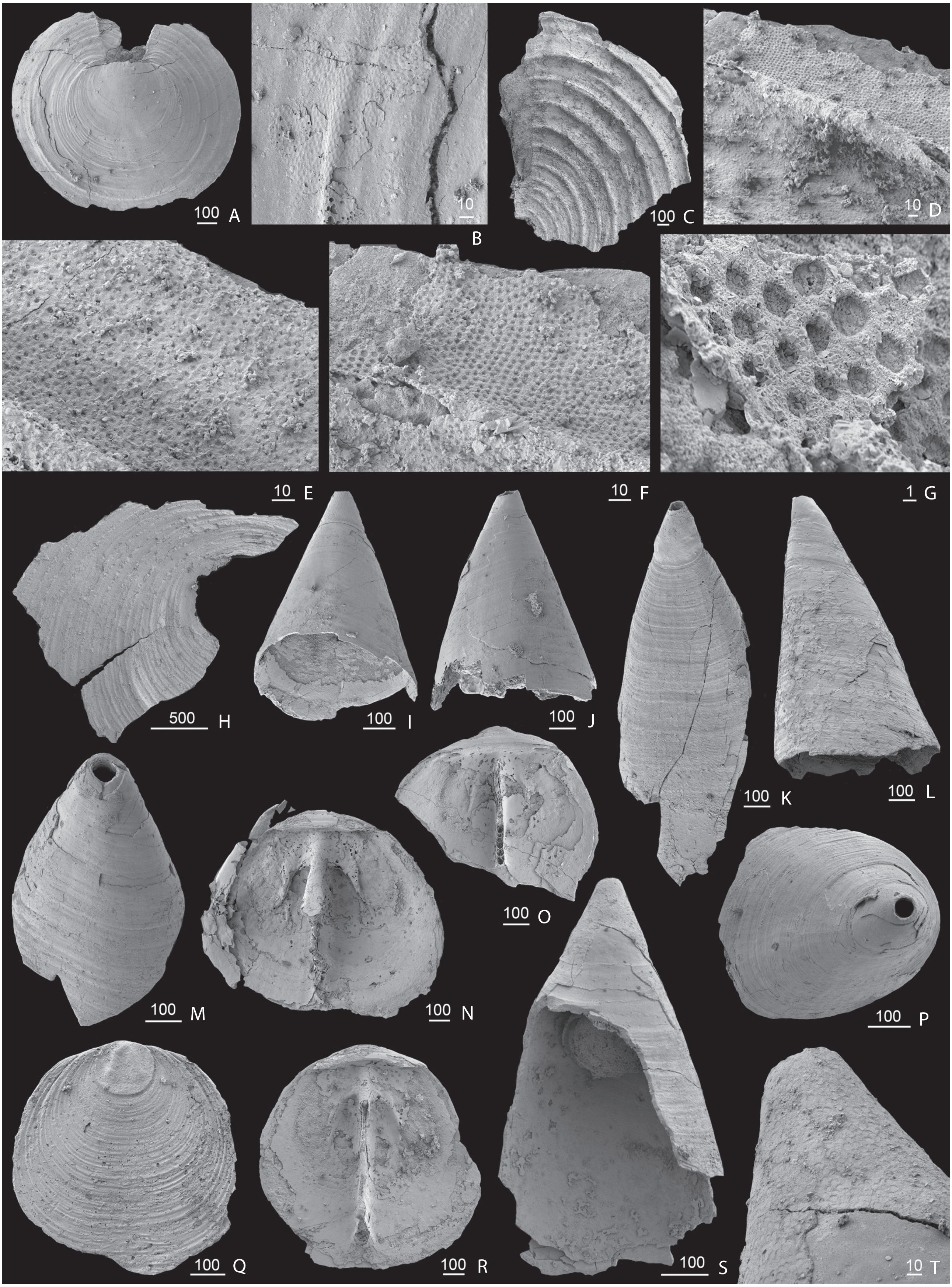
Material. – Four dorsal (PCZCU 2580, 2587, 2588, 2596) and seven ventral valves (PCZCU 2567, 2586, 2589, 2597, 2598, 2599, 2600).

Description. – The shell is thick-walled relative to its size (Fig. 5S), 1.2 mm wide in the largest specimen examined. The dorsal valve is subtrapezoidal, with rounded sides, having the maximum width anterior to the midlength (Fig. 5Q). Evenly rounded anterolateral sides continue into straight front margin. A weak and broad dorsal sulcus generates a gently unisulcate commissure. The brephic shell is 170 μm wide, almost circular, with a pair of distinct lobes and elevated periphery (Fig. 5Q). Concentric regular rounded fila of uneven size, gradually grow anteriorly to cover the surface of mature shell. Irregular growing folds and drapes are present in the depressed surface of the dorsal sulcus but disappear on flanks (Fig. 5Q). The dorsal pseudointerarea is apsacline, broadly triangular, forming a massive shelf along the posterior margin of valve (Fig. 5O, R). A broadly triangular and very shallow median groove has gently encavated anterior edge. The dorsal median septum extends nearly to the front margin. The thin and high septum exhibits two rods. The lower rod is thin, cylindrical, having a rounded end, and extends to almost 80% of valve length. The upper rod is three-times wider with a flattened crest, but its actual length is unknown because its distal part is always broken off (Fig. 5N). Cardinal muscle scars are large, of kidney-shaped outline, well impressed, extending to 40% of shell length (Fig. 5N). Weakly impressed central muscle scars are located between the median septum and the raised anteriomedian border of the cardinal scars (Fig. 5N).

The ventral valve is highly conical, with a narrow and weakly depressed catacline pseudointerarea. The pedicle foramen is comparatively large, 50 μm in diameter, directed ventrally (Fig. 5L, P). The brephic shell is regularly conical, with straight slopes and anterior border distinctly elevated above the earliest mature shell. The brephic shell is covered by circular shallow pits of subequal diameter, largely overlapping one another, forming a patchwork of crescentic imprints (Fig. 5T). The mature shell is covered by concentric fila of uneven size. Some fila continue without modification to weakly flattened depressed surface of the ventral pseudointerarea (Fig. 5M, P). Flanks and anterior slope exhibit fine growing drapes and folds intercalated between coarser growth fila. Gently inflated anterior slope exhibits a few weak radial rays (Fig. 5K).

Remarks. – Material from the Oujezdce locality is largely fragmented. The lack of information about the shape of

Figure 5. Lingulate brachiopods from the Vinařice Limestone (Pragian), Oujezdce locality. • A, B –*Sterbinella*? sp., small ventral valve, and detail of its microornament, PCZCU 2578. • C–G – *Rugadiscina* sp., fragment of ventral valve, and details of its microornament in posterolateral part, PCZCU 2579. • H – Orbiculoideinae gen. et sp. indet. C, fragment of dorsal valve, PCZCU 2585. • I–T – *Havlicekion* cf. *holynensis* Mergl, 2001; I – ventral valve, posterior view, PCZCU 2598; J – ventral valve, anterior view, PCZCU 2597; K – large ventral valve, anterior view, PCZCU 2586; L – ventral valve, side view, PCZCU 2600; M – ventral valve apex with exfoliated larval shell, PCZCU 2567; N – dorsal valve interior, PCZCU 2580; O – dorsal valve interior with broken median septum, PCZCU 2587; P – ventral valve apex with exfoliated larval shell, PCZCU 2589; Q – dorsal valve exterior, PCZCU 2596; R – dorsal valve interior, PCZCU 2588; S, T – broken ventral valve and detail of its larval shell, PCZCU 2599. Bar length in micrometres.


100 A
10
B
100 C
10 D
10 E
10 F
1 G
500 H
100 I
100 J
100 K
100 L
100 M
100 N
100 O
100 P
100 Q
100 R
100 S
10 T

rods in the dorsal median septum presents a problem for serious comparison with previsouly described Devonian species. Presence of comparatively thick shell wall and the conspicuous growth fila on the dorsal valve (Fig. 5Q) affirm its assignment to the genus *Havlicekion* Mergl, 2001. Our specimens, in displaying a sturdy dorsal pseudointerarea and prominent ridge bordering the cardinal muscle scars, are similar to *Havlicekion splendidus* Mergl, 2001 of the Pragian Age. However, the latter possesses a narrowly cylindrical and reduced upper rod in the dorsal septum while the single valve from Oujezdce locality (Fig. 5N) exhibits a broad upper rod having a flattened crest. Although this feature is seemingly weak, the shape of the upper rod is much closer to *H. holynensis* Mergl, 2001 of Lochkovian age. Another difference is the direction of a pedicle foramen. Whereas that of *H. splendidus* is directed posteroventrally, in shells from the Oujezdce locality it is just ventrally directed. Both differences indicate that our specimens more closely resemble *H. holynensis* than *H. splendidus*. Regrettably, damage to the dorsal septum in all examined individuals from the Oujezdce locality (Fig. 5N, O, R) leaves their taxonomic position uncertain.

Occurrence. – Vinařice Limestone; Oujezdce locality.

Discussion

Habitat of lingulates from the Vinařice Limestone

Low diversity, rarity of biernatids, miniaturization and paucity of obolids, absence of siphonotretids, and habitat diversification of discinids are apparent in the Vinařice Limestone. The trematid *Schizocrania* sp. was fixosessile on hard substrates. In recorded occurrences of this genus it has been observed attached on diverse hard substrates, with preference for large reclining strophomenates, conulariids and cephalopods (Hall & Clarke 1892, Cooper 1956, Lockley & Antia 1980, Harland & Pickerill 1987, Mergl 2010, Mergl & Nolčová 2016). Its planar and weakly mineralized ventral valves are generally rare (Mergl & Nolčová 2016). The evenly convex and thin-walled dorsal valve are the perfect hydrodynamically suitable adaptation to multidirectional currents, which one could expect in the proximity of the reef. The same or allied species is known in the subjacent Lochkov Formation (Mergl & Nolčová 2016). Shells of *Schizocrania* sp. in the Vinařice Limestone represent the stratigraphically youngest occurrence of the genus in the Prague Basin.

Rare occurrence of the small obolid similar to *Kosagittella* together with absence of tabulate and rugose corals in the Oujezdce locality are in striking contrast with abundance of this genus in rocks with abundant corals in the youger Devonian units in the area (Acanthopyge and Chýnice limestones; Emsian and EIfelian; Mergl 2008, Mergl & Ferrová 2009). This recalls interpretation about a possible endosymbiontic life mode with corals described by Newall (1970) and resembles that described for the micromorphic obolid *Rowellella*? *anticostiensis* by Tapanila & Holmer (2006).

Absence of the discinid *Chynithele* among brachiopods from the Oujezdce locality is likely for the same reason. Elsewhere its occurrence as well as that of the allied Silurian genus *Ivanothele* Mergl, 1996 are always associated by corals. Individuals of these genera were likely attached to firm coral substrates or occupied sheltered crevices between large clumps of corals and other bioclasts. Their dorsal valve forms a concave cap closing a deeply conical ventral valve.

Discinids are considered epibenthic dwellers (Bassett 1984, Emig 1997). Large- to moderate-sized Recent discinids live attached to firm substrate by a sucker-like pedicle and similar fixation is probable in their fossil relatives. Observations of Recent discinids indicate a cryptic mode of life on the underside of cobbles (Paine 1962) or even an infaunal mode of life on the underside of large boulders deeply embedded in coarse sand (Kato 1996). Unlike the cryptic habitat of some of the Recent relatives, the Pragian *Acrosaccus robustus* sp. nov. is considered an epibenthic dweller. It has a lid-like thick-walled dorsal valve with robust rugellae. Interspaces between rugellae likely collected fine sedimentary particles. That sedimentary infill together with robust rugellae and relatively hard phosphatic shell formed part of a visual camouflage and also was an effective barrier against boring of small predators. This adaptation supports an epibenthic instead of cryptic habitat for this species.

Life habits of observed micromorphic discinids (*Opatrilkiella*, *Praeohlertella*?, *Sterbinella*? etc.) is much more hypothetical. Their minute sizes and weak concentric ornament correspond to surviving in algal tufts and similar protected sites. Only several millimetres sized *Rugadiscina* sp. was adapted for close attachment to large skeletal debris. That habitat was corroborated in some Silurian species of the genus (Mergl 2010: fig. 9n).

A biernatid *Havlicekion* was likely a dweller of interstices between clumped bioskeletal clasts although an epiphytic mode of life, *e.g.* in algal tufts, is not excluded (see discussion on diverse hypothesis of its life by Mergl & Vodrážková 2012: p. 329).

A predation on lingulate brachiopods of the Vinařice Limestone is evident from the circular hole observed on a discinid *Praeoehlertella*? sp. (Fig. 2M, N). The hole is flat bottomed, perfectly circular with a countersunk edge. Similar boring traces are known as early as the Cambrian (Miller & Sundberg 1984, Robson & Pratt 2007) but their producers are ambiguous (Robson & Pratt 2007). The observed hole resembles in its size and shape the boreholes observed in *Artiotreta* from the Silurian Clarita Formation of Oklahoma. The identity of the boring organism on *Artiotreta* could not be determined (Chatterton & Whitehead 1987), but the predator was capable of dissolve its calcium phosphate shell.

Evolutionary significance of lingulates from the Vinařice Limestone

Outside the Barrandian area there are few studies on the Silurian and Devonian micromorphic lingulate brachiopods preserved in reefal and peri-reef limestones. Comparable quantitative data are usually lacking. Mergl & Valenzuela-Ríos (2020) described a lingulate faunule, including also basic quantitative data, from the Lochkovian and the Pragian limestones of the Spanish Pyrenees. The general aspect of the faunule, e.g. ratio of taxonomic groups, morphological groups *etc*., is similar to those in the Barrandian area. Pilot studies on Silurian and Devonian microbrachiopods recovered by acid dissolution (Ireland 1961; Ludvigsen 1974; Cocks 1979; von Bitter & Ludvigsen 1979; Mergl 1982, 1999, 2001; Biernat 1984) and subsequent studies in the Barrandian area (Mergl 2008, 2019; Mergl & Ferrová 2009; Mergl & Vodrážková 2012; Mergl & Jiménez-Sánchez 2015; Mergl *et al.* 2018), in New South Wales (Brock *et al.* 1995; Valentine & Brock 2003; Valentine *et al.* 2003, 2006; Valentine 2006) and other areas (*e.g.* Baliński & Holmer 1999; Mergl 2006, 2010) indicate a considerable diversity of these linguliformeans. However, the outstanding diversity of micromorphic acrotretids in Cambrian and Ordovician carbonate rocks (*e.g.* Holmer 1989, Popov & Holmer 1994) disappeared with the end-Ordovician extinction event (Wright & McClean 1991, Basset *et al.* 1999). During the Silurian the abandoned "micromorphic" niches were occuppied by micromorphic discinids, a few acrotretids (*Acrotretella*, *Artiotreta, Opsiconidion*), and micromorphic siphonotretids (*Orbaspina*). A conservative deep-water dweller *Paterula* also persisted to the Middle Devonian (Mergl 2001). The last records of these end-Ordovician crisis survivors appeared in the Middle Devonian. The environmental changes starting in the Emsian and Eifelian and likely also decreasing accesibility of phosphate caused by synchronous radiation of vertebrates (Kraft & Mergl 2022) led to stepped retreat of micromorphic lingulates in the Late Devonian tropical seas. The convexo-planar discinids and the lingulides have been the only survivors of the Devonian crises.

Conclusion

The Vinařice Limestone (Praha Formation, Pragian) yielded a small but important lingulate brachiopod assemblage within the taxonomically very rich rhynchonelliform brachiopod association. The lingulate assemblage is characterised by medium diversity. It is dominated by discinids including the medium-sized and thick-walled *Acrosaccus robustus* sp. nov. that has the closer relatives more in the Silurian than in the youger Devonian strata. The assemblage contains, based on tentative identifications, the common Silurian and Devonian genera *Opatrilkiella*, *Praeohlertella*, *Rugadiscina*, *Sterbinella*, and *Havlicekion* which are known in the older as well as the younger stratigraphic levels. The proved presence of the trematid *Schizocrania* sp. represents the stratigraphically youngest occurrence of the genus in the Barrandian area. The assemblage strikingly differs from the younger lingulate brachiopod associations in the Koněprusy area, namely those of Emsian (Suchomasty Limestone) and Eifelian (Acanthopyge Limestone) by absence of the discinid *Chynithele* and rarity of micromorphic obolids. The assemblage well illustrates the assumed taxonomic uniformity of lingulate brachiopods in carbonates of Lower Devonian age.

Acknowledgements

Comments and corrections provided by both reviewers, Ian G. Percival (Sydney, Australia) and Leonid E. Popov (Cardiff, Wales) greatly helped to improve the quality of the manuscript; authors are greatly indebted to both. The author appreciates J. Nebesářová and J. Vaněček (Academy of Science of the Czech Republic, České Budějovice) for help with the SEM study. The study was supported by a grant SGS-2022-011 at West Bohemia University at Plzeň.

References

Baliński, A. & Holmer, L.E. 1999. The Late Devonian trematid lingulate brachiopod *Schizobolus* from Poland. *Acta Palaeontologica Polonica 44(3)*, 335–346.

Barrande, J. 1852. *Systême silurien du centre de la Bohême. I. Trilobites*. 1100 pp. Prague & Paris. DOI 10.5962/bhl.title.14776

Barrande, J. 1872. *Systême silurien du centre de la Bohême. I^ére^ partie: recherches paléontologiques. Supplément au Vol. I. Trilobites, crustaces divers et poissons*. 647 pp. Prague & Paris.

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

Bassett, M.G. 1984. Life strategies of Silurian brachiopods. *Special Papers in Palaeontology 32*, 237–263.

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

Biernat, G. 1984. Silurian inarticulate brachiopods from Poland. *Acta Palaeontologica Polonica 29(1–2)*, 91–103.

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

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

Chatterton, B.D.E. & Whitehead, H.L. 1987. Predatory borings in the inarticulate brachiopod *Artiotreta* from the Silurian of Oklahoma. *Lethaia 20*, 67–74. DOI 10.1111/j.1502-3931.1987.tb00762.x

Chlupáč, I. 1955. Stratigraphical study of the oldest Devonian beds of the Barrandian. *Sborník Ústředního ústavu geologického, oddíl geologický 21(2)*, 91–224.

Chlupáč, I. 1956. Nové poznatky o stratigrafii středočeského devonu. *Věstník Ústředního ústavu geologického 31*, 233–243.

Chlupáč, I. 1957. Facial development and biostratigraphy of the Lower Devonian of Central Bohemia. *Sborník Ústředního ústavu geologického, oddíl geologický 23*, 369–485.

Chlupáč, I. 1959. Facial development and biostratigraphy of Daleje Shales and Hlubočepy Limestones (Eifelian) in the Devonian of Central Bohemia. *Sborník Ústředního ústavu geologického, oddíl geologický 24*, 446–511.

Chlupáč, I. 1972. New Silurian and Lower Devonian phacopid trilobites from the Barrandian area (Czechoslovakia). *Časopis pro mineralogii a geologii 17(4)*, 395–401.

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

Chlupáč, I. 1984. Devon Zlatého koně. *Český Kras 9*, 17–27.

Chlupáč, I. 1994. Devonský útes u Koněprus. *Vesmír 73*, 618–623.

Chlupáč, I. 1996. Neptunian dykes in the Koněprusy Devonian: Geological and palaeontological observations. *Věstník Českého geologického ústavu 71(3)*, 193–208.

Chlupáč, I. 1998a. K faciím a stratigrafii spodnodevonského útesového komplexu u Koněprus. *Věstník Českého geologického ústavu 73(1)*, 1–13.

Chlupáč, I. 1998b. Devonian, 101–133. *In* Chlupáč, I., Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian)*. Czech Geological Survey, Prague.

Chlupáč, I. 2003. Comments on facies development and stratigraphy of the Devonian, Barrandian area, Czech Republic. *Bulletin of Geosciences 78(4)*, 299–312.

Chlupáč, I. & Šnajdr, M. 1989. A remarkable Pragian trilobite assemblage from the Barrandian. *Věstník Českého geologického ústavu 64(3)*, 129–142.

Chlupáč, I., Lukeš, P. & Zikmundová, J. 1979. The Lower/Middle Devonian boundary beds in the Barrandian area. *Geologica et Palaentologica 13*, 125–156.

Chlupáč, I., Hladil, J. & Lukeš, P. 1986. *Barrandian – Moravian Karst 1986. Excursion – Guidebook.* Subcomission on Devonian Stratigraphy of the International Commission on Stratigraphy. 62 pp. Ústřední ústav geologický, Praha.

Cocks, L.R.M. 1979. New acrotretacean brachiopods from the Palaeozoic of Britain and Austria. *Palaeontology 22(1)*, 93–100.

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

Emig, C.C. 1997. Ecology of inarticulated brachiopods, 473–495. *In* Williams, A., Brunton, C.H.C., Carlson, S.J. et al. (eds) *Treatise on Invertebrate Paleontology, part H, Brachiopoda, Revised*. Geological Society of America Inc. & The University of Kansas, Boulder & Lawrence.

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

Hall, J. 1847. *Palaeontology of New York, vol. 1. Containing descriptions of organic remains of the lower division of the New-York System*. 338 pp. Charles van Benthuysen, New York. DOI 10.5962/bhl.title.32878

Hall, J. & Clarke, J.M. 1892. *An Introduction to the Study of the Genera of Palaeozoic Brachiopoda, Natural History of New York, Palaeontology, vol. 8, part 1.* 367 pp. New York Geological Survey, Charles van Benthuysen and Sons, Albany.

Hall, J. & Whitfield, R.P. 1875. Descriptions of invertebrate fossils mainly from the Silurian System: fossils of the Hudson River Group. *Ohio Geological Survey, Report (Geology and Palaeontology) 2(2)*, 67–347.

Harland, T.L. & Pickerill, R.K. 1987. Epizoic *Schizocrania* sp. from the Ordovician Trenton Group of Quebec, with comments on mode of life of conulariids. *Journal of Paleontology 61(4)*, 484–489. DOI 10.1017/S0022336000029176

Harper, D.A.T. 1984. Brachiopods from the Upper Ardmillan succession (Ordovician) of the Girvan District, Scotland. Part 1. *Monograph of the Palaeontological Society London 564*, 1–78. DOI 10.1080/25761900.2022.12131749

Havlíček, V. 1994. Kosovian inarticulate brachiopods and their ancestors (Late Ordovician, Prague Basin). *Věstník Českého geologického ústavu 69*, 59–68.

Havlíček, V. & Vaněk, J. 1998. Pragian brachiopods, trilobites, and principal biofacies in the Prague Basin (Lower Devonian, Bohemia). *Sborník geologických věd, Paleontologie 34*, 27–109.

Hladil, J. 2000. Paleontologická a geologická bibliografie koněpruského devonu. *Knihovna České speleologické společnosti 36*, 141–147.

Holmer, L.E. 1987. Discinacean brachiopods from the Ordovician Kullsberg and Boda limestones of Dalarna, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar 109(4)*, 317–326. DOI 10.1080/11035898709453096

Holmer, L.E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata 26*, 1–172.

Holmer, L.E. & Popov L.E. 2000. Lingulata, 30–146. *In* Williams, A., Brunton, C.H.C. & Carlson, S.J. et al. (eds)

Treatise on Invertebrate Paleontology, part H, Brachiopoda, Revised, Volume 2. Geological Society of America Inc. & The University of Kansas, Boulder & Lawrence.

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

Kato, M. 1996. The unique intertidal subterranean habitat and filtering system of a limpet-like brachiopod, *Discinisca sparselineata*. *Canadian Journal of Zoology 74(11)*, 1983–1988. DOI 10.1139/z96-225

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

Kraft, P. & Mergl, M. 2022. Struggle for phosphorus and the Devonian overturn. *Trends in Ecology and Evolution 37(8)*, 645–654. DOI 10.1016/j.tree.2022.03.009

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

Lockley, M.G. & Antia, D.D.J. 1980. Anomalous occurrences of the Lower Palaeozoic brachiopod *Schizocrania*. *Palaeontology 23(3)*, 707–713.

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

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

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

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

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

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

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

Mergl, M. 2006. A review of Silurian discinoid brachiopods from historical British localities. *Bulletin of Geosciences 81(4)*, 215–236. DOI 10.3140/bull.geosci.2006.04.215

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

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

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

Mergl, M. 2022. Devonský koněpruský útes jako cíl geologické exkurze. *Arnica 12(1–2)*, 16–42.

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

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

Mergl, M. & Nolčová, L. 2016. *Schizocrania* (Brachiopoda, Discinoidea): Taxonomy, occurrence, ecology and history of the earliest epizoan lingulate brachiopod. *Fossil Imprint 72(3–4)*, 225–238. DOI 10.14446/FI.2016.225

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

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

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

Miller, R.H. & Sundberg, F.A. 1984. Boring late Cambrian organisms. *Lethaia 17*, 185–190. DOI 10.1111/j.1502-3931.1984.tb01615.x

Murchison, R.I. 1839. *The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford; with descriptions of the coalfields and overlying formations*. 768 pp. John Murray, London. DOI 10.5962/bhl.title.88029

Newall, H. 1970. A symbiotic relationship between *Lingula* and the coral *Heliolites* in the Silurian, 335–344. *In* Crimes, T.P. & Harper, J.C. (eds) *Trace Fossils*. Seel House Press, Liverpool.

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

Paine, R.T. 1962. Filter-feeding pattern and local distribution of the brachiopod *Discinisca strigata*. *Biological Bulletin 123(3*), 597–604. DOI 10.2307/1539581

Percival, I.G., Simes, J.E., Cooper, R.A. & Zhen, Y.Y. 2011. Middle Ordovician linguliformean brachiopods from the Maruia-Springs Junction area, New Zealand. *Memoirs of the Association of Australasian Palaeontologists 42*, 459–492.

Percival, I.G., Engelbretsen, M.J., Brock, G.A. & Farrell, J.R. 2016. Ordovician (Darriwilian–Katian) lingulate brachiopods from central New South Wales, Australia. *Australasian Palaeontological Memoirs 49*, 447–484.

Pillet, J. 1968. Les *Calymene* Dévoniens d'Europe et d'Amerique du Nord. *Annales Paléntologie, série Invertebres 54(1)*, 67–89.

Popov, L.E. & Holmer, L.E. 1994. Cambrian–Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata 35*, 1–156. DOI 10.1111/j.1502-3931.1994.tb01571.x

Přibyl, A. 1949. O několika nových nebo málo známých trilobitech z českého devonu. *Věstník Státního geologického ústavu 24*, 293–330.

Přibyl, A. 1964. Neue Trilobiten (Proetidae) aus dem böhmischen Devon. *Spisanie na Bălgarskoto Geologičesko Družestvo 25(1)*, 23–51.

Přibyl, A. 1965. Proetidní trilobiti z nových sběrů v českém siluru a devonu – I. část. *Časopis Národního Muzea, oddíl přírodovědný 134(2)*, 91–98.

Přibyl, A. & Vaněk, J. 1981a. Studie zur Morphologie und Phylogenie der Familie Otarionidae R. et. E. Richter, 1926 (Trilobita). *Palaeontographica, Abteilung A 173*, 160–208.

Přibyl, A. & Vaněk, J. 1981b. A study of the morphology and phylogeny of the family Harpetidae Hawle et Corda, 1847 (Trilobita). *Sborník Národního Muzea v Praze, řada B 42(1–2)*, 1–72.

Přibyl, A., Vaněk, J. & Hörbinger, F. 1986. New trilobites of the families Odontopleuridae, Lichidae and Raphiophoridae from the Silurian and Devonian of Central Bohemia. *Časopis pro mineralogii a geologii 31(3)*, 267–278.

Robson, S.P. & Pratt, B.R. 2007. Predation of late Marjuman (Cambrian) linguliformean brachiopods from the Deadwood Formation of South Dakota, USA. *Lethaia 40*, 19–32. DOI 10.1111/j.1502-3931.2006.00003.x

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

Schuchert, C. & Le Vene, C.M. 1929. Brachiopoda (Generum et Genotyporum Index et Bibliographia), 1–140. *In* Pompeckj, J.F. (ed.) *Fossilium Catalogus, I: Animalia*, *part 42*. W. Junk. Berlin.

Šnajdr, M. 1960. A study of the family Scutelluidae (Trilobitae). *Rozpravy Ústředního ústavu geologického 26*, 1–263.

Šnajdr, M. 1980. Bohemian Silurian and Devonian Proetidae (Trilobita). *Rozpravy Ústředního ústavu geologického 45*, 1–324.

Sutton, M.D., Bassett, M.G. & Cherns, L. 2000. Lingulate brachiopods from the lower Ordovician of the Anglo-Welsh Basin. Part. 2. *Monograph of the Palaeontographical Society 154*, 61–114. DOI 10.1080/25761900.2022.12131793

Svoboda, J. & Prantl, F. 1948. Stratigraficko-paleontologický a tektonický výzkum devonské oblasti koněpruské. *Věstník Státního geologického ústavu 23*, 162–164.

Svoboda, J. & Prantl, F. 1949. Stratigraficko-tektonická studie o devonské oblasti koněpruské. *Sborník Státního geologického ústavu Československé republiky 16*, 5–92.

Tapanila, L. & Holmer, L.E. 2006. Endosymbiosis in Ordovician-Silurian corals and stromatoporoids: A new lingulid and its trace from Eastern Canada. *Journal of Paleontology 88(4)*, 750–759. DOI 10.1666/0022-3360(2006)80[750:EIOCAS]2.0.CO;2

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

Valentine, J. & Brock, G.A. 2003. A new siphonotretid brachiopod from the Silurian of Central-Western New South Wales, Australia. *Records of the Australian Museum 55(2)*, 231–244. DOI 10.3853/j.0067-1975.55.2003.1378

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

Valentine, J.L., Cole, D.J. & Simpson, A.J. 2006. Silurian linguliformean brachiopods and conodonts from the Cobra Formation, southeastern New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales 111*, 199–234.

Vaněk, J. 1999. Pražský stupeň (spodní devon) v Pražské pánvi a relativní stáří jeho facií, (Česká republika). *Palaeontologia Bohemiae 5(7)*, 39–67.

Vaněk, J., Vokáč, V. & Hörbinger, F. 1992. New trilobites from the Silurian and Devonian in the Prague Basin (Central Bohemia). *Věstník Ústředního ústavu geologického 67*, 97–108.

Waagen, W. 1885. Salt Range fossils, I. *Productus*-Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologica Indica (series 13) 4(5)*, 729–770.

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

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

Wright, A.D. 1963. The fauna of the Portrane limestone, 1: The inarticulate brachiopods. *Bulletin of the British Museum (Natural History), Geology 8*, 223–254. DOI 10.5962/p.313877

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