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

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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 rhyynochelliformean brachiopods mainly strophomenoids and rhyynochelloids. 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.


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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 Svooboda & 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 rhyynochelliformean 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 (Hmolůk and Oujezdce localities) (Svooboda & Prantl 1949). Pink
to red coloured limestone is composed of angular to subrounded crinoidal fragments and a variable amount of micritic component. The amount 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.


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 rhyononelliformean 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 unimpressive 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 Linguloida 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 unknown.

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; Pořáry Formation, Přídoli, Silurian; Prague Basin, Czech Republic.

Opatrilkiella sp.
Figure 2H–J

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

**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
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 conspicuous tilted rugellae of uneven size and comparatively narrower deep inter-spaces 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 to 1 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 appearance 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 center 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 encompass 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 than 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 honeycomb 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, Oujezdec 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.
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 *Orbiculioidea* d’Orbigny, 1847 or *Acrosaccus* Willard, 1928. Their occurrence can be traced back to the Ordovician (Willard 1928; Cooper 1956; Wright 1984; Holmer 1987; Hlavíček 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 conspicuous macroornament similar to *A. cocksi* Mergl, 2010 from the Silurian 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 2001). However, a small valve coming 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).

Orbiculoidae 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).

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

Material. – One dorsal valve (PCZCU 2602).

Remarks. – The asymmetrical 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 Oujezdce 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 excavated 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, cylindrically, 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 cataclinal 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

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**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.
rods in the dorsal median septum presents a problem for serious comparison with previously 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 younger Devonian units in the area (Acanthopyge and Chýnice limestones; Emsian and Elffelian; Mergl 2008, Mergl & Ferrová 2009). This recalls interpretation about a possible endosymbiotic life mode with corals described by Newall (1970) and resembles that described for the micromorphic obolid Rowellella? anticoestisensis 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 (Opatrulkiiella, Praeoehlertella?, 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 occupied 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 accessibility 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 rhyonchelliform 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 younger Devonian strata. The assemblage contains, based on tentative identifications, the common Silurian and Devonian genera Opatriilkella, Praeohlertella, Rugadiscina, Sterbinella, and Havlicekion which are known in the older as well as the younger stratigraphic levels. The proved presence of the trematid Schizocrinaria 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.

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