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LINGULATE AND CRANIATE BRACHIOPODS FROM THE TOP OF THE KRÁLŮV DVŮR FORMATION (LATEST KATIAN) AND THEIR CONTRIBUTION TO PALAEOGEOGRAPHY

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Abstract. Rare lingulate and craniate brachiopods from the topmost beds ('Perník bed') of the Králův Dvůr Formation (uppermost Katian) are described: *Acrosaccus squamosus*, *Acanthambonia* (?) sp., *Hisingerella* sp., *Pseudopholidops anteglacialis*, *Deliella* sp., and *Philhedra* (?) sp. Apart from *Acrosaccus*, the brachiopod taxa are unknown in the older stratigraphical succession of the Prague Basin. However, the genera *Pseudopholidops* and *Philhedra* are present in the overlying Kosov Formation (Hirnantian) as rare elements of the *Hirnantia* Fauna. The first occurrence of all these brachiopods in the 'Perník bed' in the Králův Dvůr Formation is evidence of the Boda Event. Lingulate and craniate brachiopods, similar to some trilobites and rhynchonelliform brachiopods, represent Avalonian and Baltic warm-water immigrants which arrived before the onset of the Hirnantian glaciation.

■ Craniida, Craniopsida, *Acrosaccus*, Boda Event, Katian, Hirnantian, Prague Basin, palaeogeography

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Introduction

The Králův Dvůr Formation (mid- to upper Katian) is famous for its diverse and well-preserved fossils, represented mainly by trilobites (see Shaw 2000) and moderately diverse but small-sized deep water brachiopods (see Havlíček 1967, 1977). Organophosphatic brachiopods are generally scarce (Mergl 1998) with the rare exception of a deep-water infaunal dweller *Rafanoglosella leiskowiensis* (Barrande 1879). A few other species of lingulate brachiopods have been reported in the Králův Dvůr Formation (Barrande 1879) which includes richly fossiliferous carbonatic claystone (so called 'Perník bed' by Štorch and Mergl 1989) situated at the top of the Králův Dvůr Formation (Havlíček 1989, Havlíček and Mergl 1982). During the last decades, rare but remarkable brachiopods were sampled from the 'Perník bed' including lingulate and also previously unknown craniate brachiopods. Despite their rarity and poor preservation, these brachiopods have great importance for the history of the Prague Basin. For this reason, these brachiopods are briefly described and their significance is discussed.

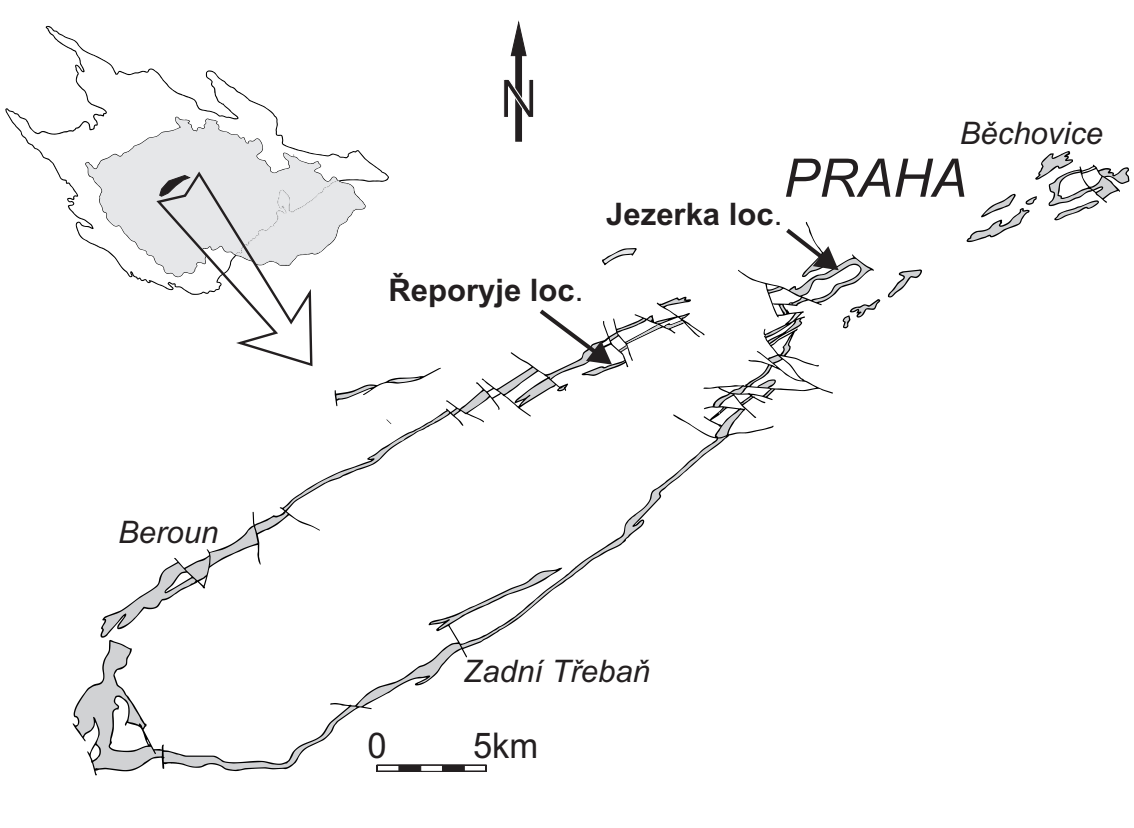
Geological and geographical setting

The 'Perník bed' is a richly fossiliferous carbonatic claystone forming the top part of the Králův Dvůr Formation (Štorch and Mergl 1989; see pl. 1, p. 128). The bed is currently interpreted as the results of climatic and glacioeustatic changes around the Katian/Hirnantian boundary, followed by Hirnantian glaciomarine deposits. After the pioneering work on this stratigraphical interval (Marek 1951, Havlíček and Vaněk 1966), the importance of this fauna were summarized by Štorch and Mergl (1989) and Havlíček (1982, 1989). Since these first publications, further publications concentrated on the taxonomical content of the 'Perník bed' have appeared (Frýda 1989, Shaw 2000). The earliest occurrence of the *Hirnantia* Fauna in the area just above the 'Perník bed' has been documented only recently (Mergl 2011a).

Newly described brachiopod fauna sampled from the 'Perník bed' have been observed at only two localities. The first one, the Jezerka locality within the territory of Prague-Nusle, has been observed by Havlíček and Mergl (1982) and described in detail by Štorch and Mergl (1989). The second locality, the temporary artificial outcrop in Praha-Řeporyje was discovered by Jiří Kříž, and its fauna has been partially described by Mergl (2011a). Other localities described by Štorch and Mergl (1989) did not yield any lingulate or craniate brachiopod.

Repository

Figured specimens are stored in the palaeontological collections of the Geological Survey, Prague (MM), the palaeontological collections of the District Museum of Dr. B. Horák at Rokycany (3RO), and the palaeontological collections of the University of West Bohemia in Plzeň (PCZCU).



Text-fig. 1. Distribution of the Králův Dvůr Formation (Upper Katian) in the Prague Basin of the Czech Republic, the location of the localities noted in text (modified, after Štorch and Mergl 1989).

Systematic part

Order Lingulida Waagen, 1885

Superfamily Discinoidea Gray, 1840

Family Discinidae Gray, 1840

Genus ***Acrosaccus*** **Willard, 1928**

Type species. – *Acrosaccus shuleri* Willard, 1928; Upper Ordovician, Virginia, USA.

Acrosaccus squamosus **(Barrande, 1879)**

Text-figs 2A-L

1879 *Discina squamosa* Barr.; Barrande, pl. 96, case 6.
1982 *Orbiculoidea squamosa* (Barrande, 1879); Havlíček and Mergl, pl. 1, figs 2, 3.

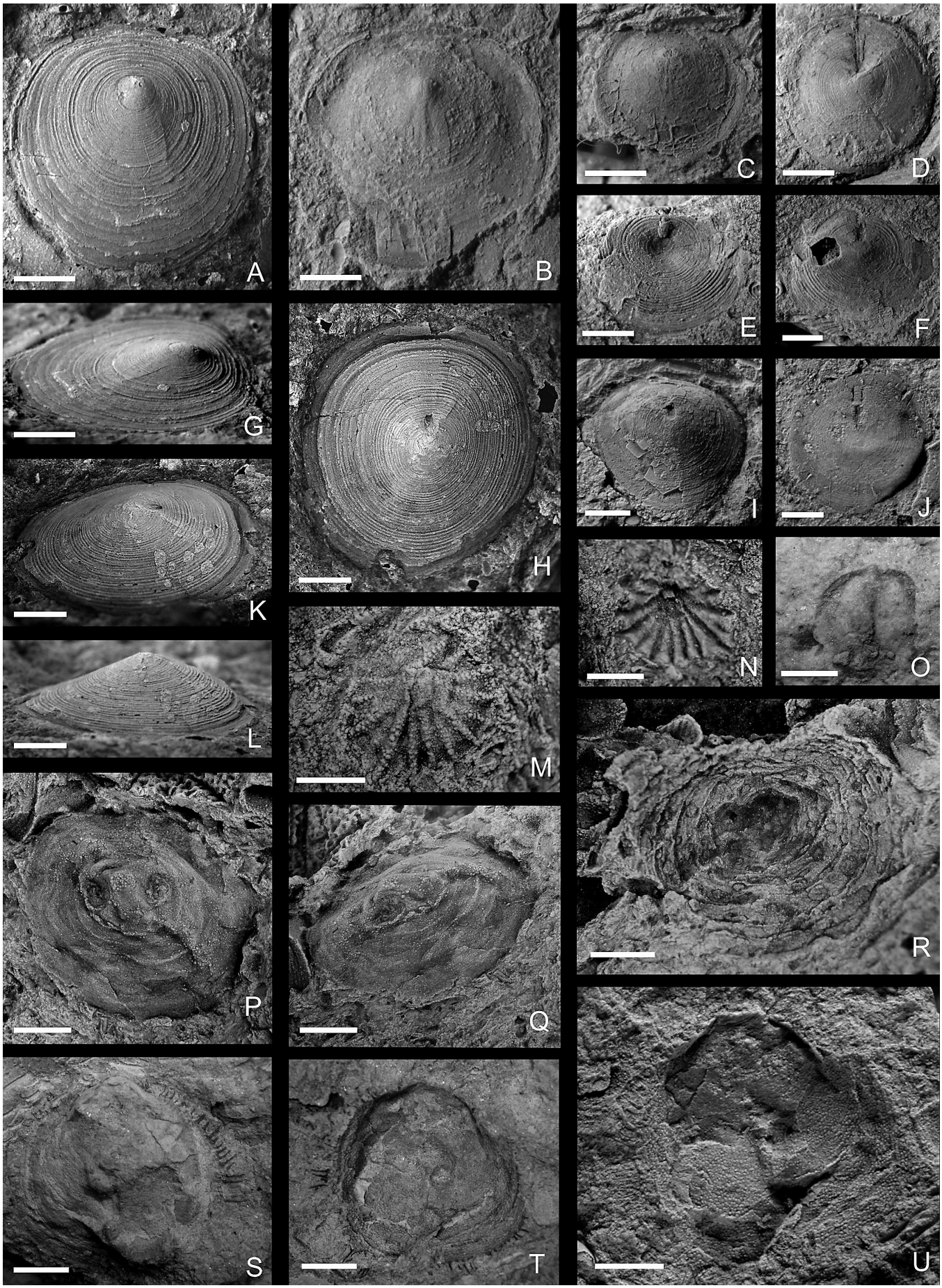
M a t e r i a l : Fifteen specimens from the collection of V. Havlíček (dorsal valves 3RO 64968-64971, 3RO 64973, 3RO 64975, 3RO 64977, ventral valves 3RO 64964, 3RO 64967, 3RO 64972, 3RO 64974, 3RO 64976, 3RO 64978-64980), one dorsal and one ventral valve (MM 047, MM 048), and three dorsal and three ventral valves from new material (PCZCU 1844 to 1849).

D e s c r i p t i o n : Shell is small, biconvex, thin-walled, 4.5 mm wide in the largest specimen, showing gentle deviation from the bilateral symmetry.

Dorsal valve is flat conical, subcircular, with the apex situated between 20 to 25% of the shell length. The maximum shell width is slightly posterior to midlength. Anterior margin and lateral margins are evenly rounded. The posterior margin is less curved. Anterior slope is straight with gently convex apical area. Lateral slopes are straight. Posterior slope is gently convex. Dorsal larval shell is circular, with less rounded posterior margin, about 500 μm long and 600 μm wide, slightly and evenly convex without distinct growth lines. Sides of the larval shell are distinguished by a weak halo and a periphery distinctly elevated above the postlarval shell surface.

Ventral valve is low conical, subcircular with the apex near the centre of the valve. Anterior slope is straight to gently concave. Lateral slopes are straight. Posterior slope is weakly to distinctly convex. Pedicle track is small, elongate oval, widest along its posterior third, occupying 15% of the length and c. 5% of the width of the shell. The listri-

▶ Text-fig. 2. A–L – ***Acrosaccus squamosus*** **(Barrande, 1879), Králův Dvůr Formation, 'Perník bed', Jezerka locality. Bar = 1 mm. A, B, G – Dorsal valve, latex cast of exterior, internal mould, and oblique view, 3RO 64971. C – Dorsal valve, internal mould, PCZCU 1845. D – Ventral valve, internal mould, 3RO 64972. E – Ventral valve, external mould, 3RO 64980. F – Ventral valve, internal mould with partly preserved shell, 3RO 64978. H, K, L – Ventral valve, latex cast of exterior in apical, posterolateral and lateral views, 3RO 64976. I – Ventral valve, internal mould, PCZCU 1844. J – Ventral valve, internal mould, 3RO 10043. M, N –** ***Deliella*** **sp., Králův Dvůr Formation, 'Perník bed', Praha–Řeporyje locality. Bar = 0.5 mm. Ventral valve, internal and external moulds, PCZCU 1823. O –** ***Hisingerella*** **sp.; Králův Dvůr Formation, 'Perník bed', Jezerka locality. Bar = 0.5 mm. Dorsal valve, internal mould,**



PCZCU 1824. P–R – *Philhedra* ? sp., Králův Dvůr Formation, 'Perník bed', Jezerka locality. Bar = 1 mm. Dorsal valve internal mould, oblique view and external mould, PCZCU 1850. S–U – *Acanthambonia* ? sp., Králův Dvůr Formation, 'Perník bed', Jezerka locality. Bar = 0.5 mm. Dorsal valve internal mould, external mould and detail of internal surface, MM 027.

um is divided into a narrow inner listrial plate and broader weakly concave outer listrial plates. External pedicle opening is at the deepest posterior end of the pedicle track.

Interior of dorsal valve has deep apical pit from which a thin weak median septum extends up to one-third of the anterior slope. Muscle imprints and vascular system are not clearly impressed. Ventral valve interior shows distinct internal pedicle tube which has a constant width along its whole length. The tube is opened posteriorly by an unrestricted internal foramen just anterior to weak internal brim.

Ornamentation consists of fine regular concentric rugellae. These are weaker and less distinct on the dorsal valve than on the ventral valve. Size of rugellae mildly but regularly increase toward shell periphery, peripheral rugellae being about double-sized that of early concentric fila near the apex. Rugellae are uninterrupted, undivided and almost uniformly sized along their courses except for rugellae on the posterior slope of the dorsal valve. Some of these rugellae are taller and thicker but some of the rugellae distinct on shell flanks and anterior slope are weaker or disappearing. Interspaces having broadly U-shaped profile are narrower than bases of rugellae. There are about 40 rugellae on large shells. Several early concentric fila have a posterior course hidden below the larval shell. These early fila are substituted by coarser and taller rugellae anteriorly. Microornamentation is unknown.

R e m a r k s : The species was erected by Barrande (1879) based on the ventral valve collected in Králův Dvůr (Koenigshof in original German spelling), but the species has never been formally described despite its illustration by subsequent authors (Havlíček and Mergl 1982). The variation in shell shape is likely to be original, but variation of shell convexity maybe accounted for by post-mortal deformation of the somewhat flexible organophosphatic shell in the sediment.

There are numerous but generally poorly known Late Ordovician discinoids similar to *Acrosaccus squamosus* (Barrande, 1879). Dorsal valves of *Acrosaccus shuleri* Willard, 1928 illustrated by Cooper (1956; pl. 18, fig. B7) and re-illustrated by Holmer and Popov (2000; p. 87, figs 2c and 2g) have clearly coarser ornamentation and a much more posteriorly located dorsal apex compared with *A. squamosus*. The ventral valve of *A. shuleri* displays a much longer and acutely closed pedicle track. The figured type specimen of *A. posteroconvexus* (Cooper, 1956; pl. 28B) has a taller ventral valve with a more concave anterior slope than *A. squamosus* and its pedicle track is narrower. Nikitin et al. (1996) described and illustrated *A.* aff. *posteroconvexus* (Cooper, 1956) from the Late Ordovician of Central Kazakhstan. This small discinoid shows some resemblance by its fine ornamentation, but differs from *A. squamosus* by its taller ventral valve. Another species, *Acrosaccus* sp., from the Late Ordovician of Kazakhstan (Popov 2000) differs by a narrower ventral pedicle track but the comparison is somewhat uncertain due to its fragmental preservation. Sutton et al. (2000) re-described and illustrated several species of *Schizotreta* Kutorga, 1848 from the Middle Ordovician (Llanvirn to Upper Llandeilo of the British regional subdivision, in Sutton et al. 1999). The species *S.*? *transversa* Williams, 1974 redescribed by these authors has a similar shell morphology but displays a coarser ornamentation than *A. squamosus*. Among the discinoids described by Holmer (1989) from the Middle Ordovician of Sweden the species *Orbiculoidea*? sp. resembles the Bohemian species in its finely rugellate ornamentation.

Orbiculoidea concentrica (Wahlenberg, 1818) described from the *Dalmanitina* Beds (Hirnantian) of Wästergötland, Sweden by Bergström (1968) differs from *A. squamosus* by a longer pedicle track, coarser rugellate ornamentation and a larger shell size. *Orbiculoidea radiata* Troedsson, 1918 described from the Hirnantian of Poland (Temple 1965) differs by its almost flat ventral valve and longer pedicle track.

There are several late Ordovician species from the British Isles which are similar to *A. squamosa*. The species *Orbiculoidea shallochensis* Reed, 1917 from the Ashgill Series, Pushgillian, *Dicellograptus complanatus* Zone of the Girvan District, Scotland (Harper 1984), also reported by Wright (1963) from the Portrane Limestone of Ireland, differs from *A. squamosus* by a larger shell size and having a larger and longer lanceolate-shaped pedicle track. *Orbiculoidea inopia* Harper, 1984 from the *Dicellograptus complatus* Zone of Girvan District resembles *A. squamosa* by its small shell size and ornamentation. Although the ornamentation of the Scottish species is similarly fine, the rugellae are more distantly spaced than in *A. squamosus*. The outline of *O. inopia* is apparently more regularly circular than of *A. squamosus*. *Orbiculoidea armstrongi* Reed, 1917 from the Ashgill Series, Rawtheyan, *Dicellograptus anceps* Zone of Girvan District, Scotland (Harper 1984) differs by a flatly conical pedicle valve, a more centrally situated dorsal apex and a more convexly conical dorsal valve.

O c c u r r e n c e : Except for the type specimen figured by Barrande (1879), which was sampled from the Králův Dvůr area (=Koeningshof), all other specimens were collected in Jezerka where the species belongs among the moderately common fossils.

Order Acrotretida Kuhn, 1949

Superfamily Acrotretoidea Schuchert, 1893

Family Acrotretidae Schuchert, 1893

Genus ***Hisingerella*** **Henningsmoen, 1948**

Type species. – ? *Atrypa nitens* von Hisinger, 1837; Upper Ordovician, Sweden.

Hisingerella **sp.**

Text-fig. 2O

1982 *Conotreta* sp.; Havlíček and Mergl, p. 39, pl. 1, fig. 1.
1989 *Conotreta* sp.; Štorch and Mergl, table 2.

M a t e r i a l : Three dorsal valves, poorly preserved in claystone (VH 3832, PCZCU 1824, 1825).

D e s c r i p t i o n : Dorsal valve is about 1 mm wide, thin-shelled, mildly convex, circular in outline having the

dorsal larval shell distinctly overhanging the posterior margin. Dorsal median septum is tall, thin and long, extending close to the anterior margin of the valve. Ventral valve and other shell details are unknown.

R e m a r k s : The species was reported by Havlíček and Mergl (1982) as *Conotreta* sp. *Conotreta* is a late Lower to Upper Ordovician genus (Holmer 2000). Numerous authors used the generic name *Conotreta* as a provisional standard of reference (Holmer 2000). This is also the case for the dorsal valves collected by Havlíček and Mergl (1982) from the 'Perník bed'. The morphology of shells from the 'Perník bed' correspond more with the morphology of *Hisingerella,* by the long, thin dorsal septum, almost circular shell outline and posteriorly extended dorsal larval shell.

O c c u r r e n c e : Rare at Jezerka and Praha-Řeporyje.

Order Siphonotretida Kuhn, 1949

Superfamily Siphonotretoidea Kutorga, 1848

Family Siphonotretidae Kutorga, 1848

Genus *Acanthambonia* Cooper, 1956

Type species. – *Acanthambonia minutissima* Cooper, 1956; Middle Ordovician, Alabama, USA.

Acanthambonia (?) sp.

Text-figs 2S-U

1982 *Acanthambonia* sp. Havlíček and Mergl, p. 39.
1989 *Acanthambonia* sp. Štorch and Mergl, table 2.

M a t e r i a l : One dorsal valve (MM 027).

D e s c r i p t i o n : Ventral valve unknown. Dorsal valve is 4 mm wide, subcircular, thin-shelled, and despite the deformation due to its collapse, it displays considerable convexity. The dorsal apex is marginal and gently extended posteriorly. Exterior lacks prominent growth lamellae. The valve shows prominent, short, tapering and radially arranged hollow spines of almost uniform size along anterior, lateral and posterolateral margins. Shorter spines directed posteriorly are tightly spaced just laterally to the dorsal apex. Valve interior is unknown, but the bases of spines are distinct as a fine internal pustulation. However, this feature may be of a taphonomic origin.

Ventral valve is unknown.

R e m a r k s : The record of Upper Ordovician siphonotretids is scarce. *Acanthambonia* Cooper, 1956 and *Multispinula* Rowell, 1962 are only known from the late Katian. The new shell is referred to *Acanthambonia* because *Multispinula* has strong concentric ornamentation. It is stratigraphically the youngest siphonotretid known from the Ordovician of Bohemia.

O c c u r r e n c e : Very rare at Jezerka.

Order Craniopsida Gorjansky et Popov, 1985

Superfamily Craniopsoidea Williams, 1963

Family Craniopsidae Williams, 1963

Genus *Pseudopholidops* Bekker, 1921

Type species. – *Pholidops scutellata* Bekker, 1921; Upper Ordovician, Estonia.

Pseudopholidops anteglacialis sp. nov.

Text-fig. 3

H o l o t y p e : Ventral valve, internal mould, illustrated in Fig. 3 I, J (PCZCU 1835).

T y p e h o r i z o n : Upper Katian, Králův Dvůr Formation, 'Perník bed'.

T y p e l o c a l i t y : Praha – Řeporyje, a temporary outcrop.

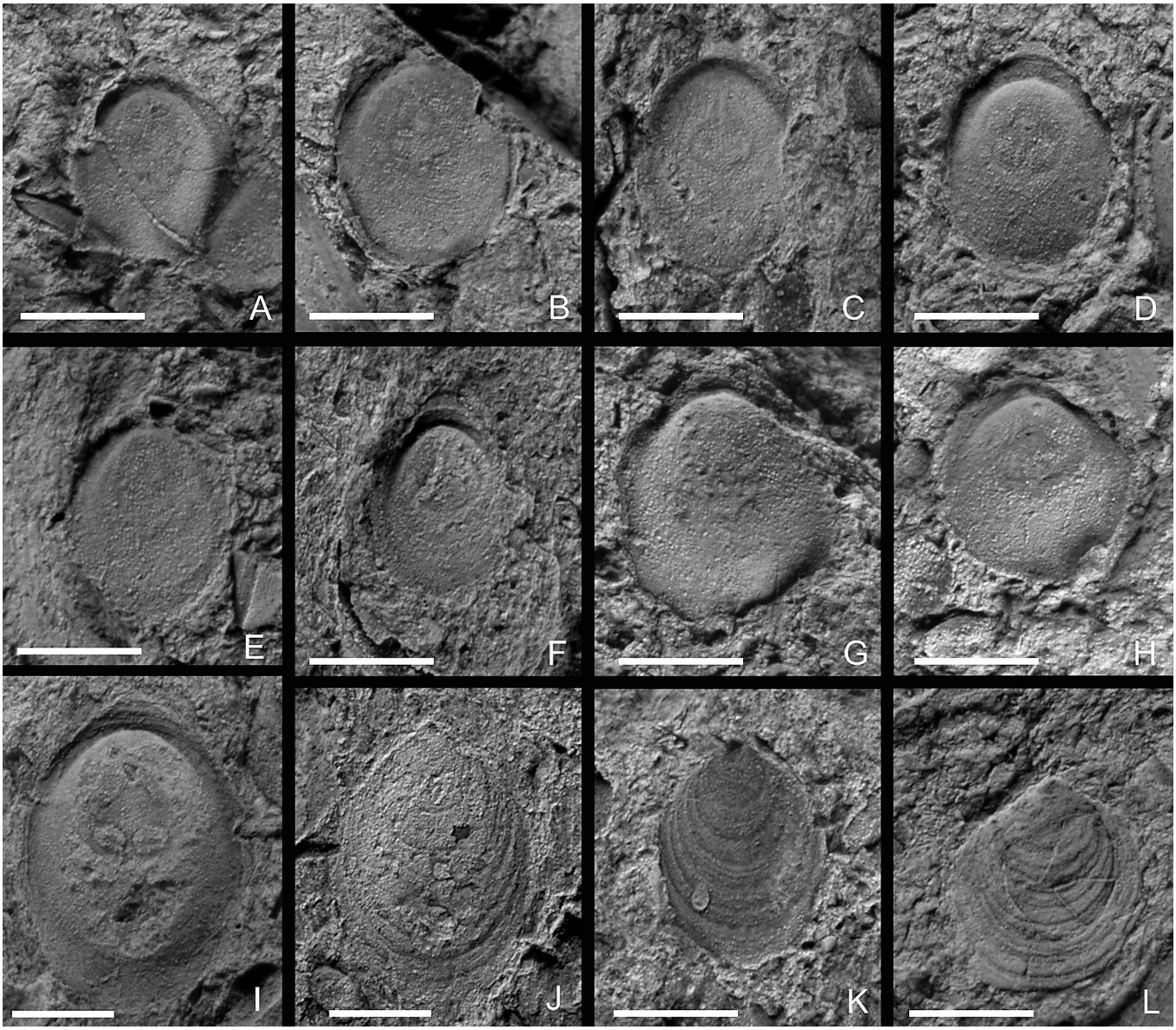
E t y m o l o g y : *Ante* (Latin) – before, and *glaciális* (Latin) – glacial.

M a t e r i a l : Eighteen valves preserved as internal and external moulds in claystone (PCZCU 1826 to 1843).

D e s c r i p t i o n : Shell is small, biconvex, 2.1 mm wide in the largest collected specimen, having maximum width anteriorly to shell midlength.

Dorsal valve is elongate oval, 133 % as long as wide in specimens measured (n = 2), thick-walled posteriorly, but anteriorly having a comparatively thin shell wall. Sides and anterior margin are evenly curved. Apex is marginal. Limbus is prominent posteriorly and posterolaterally and rapidly weakens anteriorly. Anterior margin is without the limbus. Shallow incision is present on anterior edge of posterior limbus. Valve is moderately and evenly convex transversally and axially. Dorsal pseudointerarea is low anacline, with transversally striated surface. Dorsal visceral area is weakly impressed in posterior part of the valve, being some 40 % as wide as the valve, and anteriorly limited by the shell midlength. Paired anterior adductor scars are large, subtriangular, divided from each other by elongate subrectangular scars of brachial protractors. Posterior unpaired median scars extend significantly posteriorly from the visceral field. Posterior adductor and oblique internal muscle scars are undivided and weakly impressed.

Ventral valve is elongate-oval, moderately convex in transverse and axial profiles, deepest posteriorly, having gently evenly rounded sides and more rounded anterior margin. Valve is 117 to 140 % as long as wide (n = 12), with outline range from narrowly to broadly oval but it is difficult to distinguish the original variability due to deformation in the clayey shale. Broadly triangular low apsacline ventral pseudointerarea bears fine transverse striation. Apex is marginal, extended posteriorly. Apical angle is approximately 100°. Ventral limbus is tall and broad posteriorly and posterolaterally but vanishing anteriorly. Ventral visceral area is trapezoidal in outline, weakly impressed, some 40 % as wide as valve and extended into the valve midlength. Paired large anterior adductor scars are divided by a short



Text-fig. 3. ***Pseudopholidops anteglacialis*** **sp. nov., Králův Dvůr Formation, 'Perník bed', Praha-Řeporyje locality. Bar = 1 mm. A – Dorsal valve, internal mould, PCZCU 1843. B – Dorsal valve, internal mould, PCZCU 1840. C, K – Ventral valve, internal and external moulds, PCZCU 1831. D – Ventral valve, internal mould, PCZCU 1827. E – Dorsal valve, internal mould, PCZCU 1826. F – Ventral valve, internal mould, PCZCU 1830. G – Ventral valve, internal mould, PCZCU 1832. H – Dorsal valve, internal mould, PCZCU 1841. I, J – Holotype, ventral valve, internal and external moulds, PCZCU 1835. L – Exterior, external mould, PCZCU 1836.**

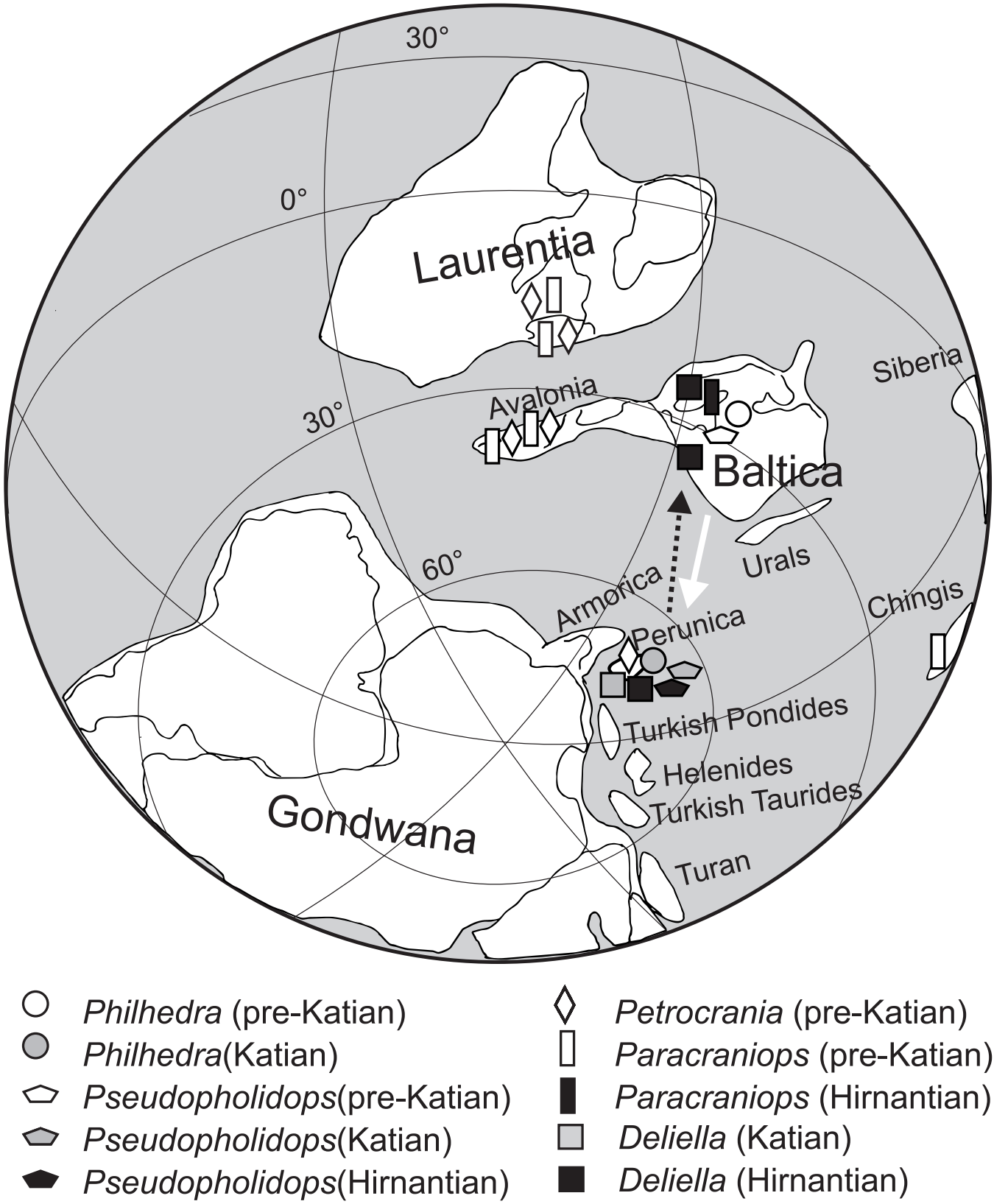
tongue, which is the site of oblique internal muscle attachments.

Exteriors of both valves bear fine growth lines, which are at regular intervals extended into coarser concentric lamellae. There are 8 to 10 lamellae in large shells.

R e m a r k s : Apart from the absence of a ventral median ridge, the outline is consistent with attribution of the new species to *Pseudopholidops* Bekker, 1921. The type species *P. scutellata* (Bekker, 1921) figured by Popov and Holmer (2000) differs by more numerous growth lamellae and narrower limbus. The new species is very similar to *Pseudopholidops stolleyana* (Huene, 1900) from the Baltic area (Huene 1900, Popov and Pushkin 1986). The only difference are weaker impressions of the muscle scars in *P. stolleyana*. The new material is described as a new species also due to a biological reason. Despite a distinct relationship between the Baltic and Bohemian shelly taxa in the late Katian, it is taxonomically related only at a generic or higher level. There are no species common to both areas.

Sanxiaella Rong et Chang, 1981 (in Chang 1981) is a suggested synonym for *Pseudopholidops* Bekker, 1921 after Popov and Holmer (2000). *Pseudopholidops partibilis* (Rong, 1979), the type species of the invalid genus *Sanxiaella*, is not a well known species. This Chinese species has a smaller and more distinct visceral platform and its shell is less elongate in comparison with *P. anteglacialis*.

Pseudopholidops is a characteristic genus for the *Hirnantia* Fauna of China (Rong and Chang 1981), and has been also reported from the *Hirnantia* Fauna of Bohemia (Mergl 1986). *Sanxiaella* sp. material from the Kosov Formation (Hirnantian) is poor (Mergl 1986, Havlíček 1994a), but it seems that the Hirnantian species differs from the new species by a weaker posterior limbus, higher visceral platforms and a less extended posterior margin lacking a dis-



Text-fig. 4. Palaeogeographical reconstruction of the Katian (after Popov et al. 2011, modified) showing geographical distribution of the Middle and Late Ordovician craniides and craniopsides. White arrow = Boda Event expansion of craniiates and craniopsides to Perunica; black arrow = Hirnantian low-latitude expansion of the *Hirnantia* Fauna.

tinct pseudointerarea. Based on the last feature, Mergl's (1986) *Sanxiaella* sp. is more related to the unnamed Hirnantian species of *Pseudopholidops* which was originally referred to *Paracraniops* by Bergström (1968).

O c c u r r e n c e : Only in the type locality where it is moderately frequent.

Family Craniidae Menke, 1828

Genus *Deliella* Halamski, 2004

Type species: *Deliella deliae* Halamski, 2004; Middle Devonian, Germany.

***Deliella* sp.**

Text-figs 2M, N

M a t e r i a l : One dorsal valve (PCZCU 1823).

D e s c r i p t i o n : The dorsal valve is tall, conical, 1.1 mm wide, thin-walled, circular, with scalloped outline. It bears 16 coarse radial ribs, a few of them originating by intercalation, remaining extended from the apex. Growth lines are not preserved.

R e m a r k s : The shell most likely represents a young individual. The coarse radial ribbing of the shell is unique among Bohemian Ordovician craniides, which are smooth or have a scalloped surface and therefore have been referred to *Petrocrania* (Havlíček 1994b). The Katian and Hirnantian costate craniides are generally rare and therefore they are often left in open taxonomic nomenclature. Ordovician craniides with distinct radial ornamentation were attributed by many authors (Cooper 1956, Bergström 1968, Popov and Pushkin 1986, Havlíček 1994a) to *Philhedra* Koken, 1889, but *Philhedra* is an endemic Baltic craniid genus characterised by radial rows of hollow spines (Basset 2000). True *Philhedra* is pre-Katian in age (Basset 2000).

Halamski (2004) erected the genus *Deliella* for radially costate craniides. *Deliella* is known from the Middle Devonian, but these Devonian species (Halamski 2004, Franke 2012) have unknown Silurian or Ordovician ancestors. However, the similarity in shape and ornamentation of Devonian *Deliella* species to radially costate Upper Ordovician shells is striking (e.g. *Philhedra metatypotheisa* Huene, 1900). Therefore the single described shell is referred to *Deliella*, and the Hirnantian craniides mentioned below may be referred to this genus.

Havlíček (1994a) described and illustrated *Philhedra* sp. from the top of the Hirnantian in the Prague Basin. Temple (1965) described *Philhedra*? *stawyensis* from the Hirnantion of Poland, but this species clearly shows a different mimic type of coarse ornamentation and should be reassigned to *Petrocrania*. Bergström (1968) described and illustrated the Hirnantian *Philhedra* sp. A. from Västergötland, Sweden as having distinct radial ornamentation.

O c c u r r e n c e : Rare at Praha–Řeporyje.

Genus *Philhedra* Koken, 1889

Type species: *Philhedra baltica* Koken, 1889; Middle Ordovician, Estonia.

***Philhedra* (?) sp.**

Text-figs 2P, R

M a t e r i a l : One dorsal valve (PCZCU 1850).

D e s c r i p t i o n : The dorsal valve is subconical, 4 mm wide, thin-walled, subcircular with less rounded posterior margin, having a scalloped commissure. It bears irregular and uneven growth lamellae developed from finer concentric lines. The bases or circular structures, probably bases of hollow spines, are arranged in several weakly marked radial rays. The diameter of these structures rapidly increases toward the shell margin, but their size is almost uniform within the same growth band. Interior is almost smooth, with a pair of small, moderately elevated oval scars of anterior adductor and deep apical pit.

R e m a r k s : The circular structures are most likely the bases of short hollow spines or some knob-like outgrowths on the shell surface. Such structure is uknown in any other Ordovician craniide from Bohemia. It is somewhat similar to the radially aligned spines of the type species *Philhedra baltica* Koken, 1889, but their diameter is larger than in the type species. The generic assignment is provisional.

O c c u r r e n c e : Rare at Praha–Řeporyje.

Discussion

Lingulate and craniate brachiopods are rare to very rare elements in the otherwise very rich and diverse trilobite, brachiopod, bryozoan and ostracod fauna of the 'Perník bed'. The origin of this fauna has been discussed by many authors (Havlíček and Mergl 1982, Havlíček 1982, 1989, Štorch and Mergl 1989, Mergl 2011b), but interpretations were based on trilobites or rhynchonelliform brachiopods. Ostracods still require evaluation, as well as bryozoan, gastropod and other invertebrate groups. The fauna preserved in the 'Perník bed' clearly differs by its diversity and composition from that in the older parts of the Králův Dvůr Formation succession as well as from the *Hirnantia* Fauna above the 'Perník bed'. The 'Perník bed' contains trilobite genera unknown in older units of the Prague Basin, such as proetids, cheirurids, *Staurocephalus*, *Diacanthaspis,* and *Trochurus*, and *vice versa*, cyclopygid and remopleurid trilobites are absent. The occurrence of the above mentioned trilobite genera together with first occurrence of rhynchonelliform brachiopods taxa, namely *Epitomyonia*, *Salopina*, *Cliftonia*, *Leptaena*, *Cryptothyrella*, and *Eoanastrophia* has been explained by the expansion of temperate climatic belt taxa into high-latitudes in the late Katian (Štorch and Mergl 1989).

Lingulate and craniiate brachiopods described herein are another manifestation of the Boda Event (Boucot et al. 2003, Fortey and Cocks 2005) in the Prague Basin.

Discinids *Acrosaccus* and *Schizotreta* are quite common in temperate and tropical belts (Cooper 1956, Wright 1963,

Harper 1984, Holmer 1987) in the Ordovician. Thus, discinides are represented by more taxa in Laurentia and Avalonia, while in the high-latitude Gondwana, these small to moderately-sized discinoids are absent or comparatively rare (Havlíček 1994a) and only large trematids are common (*Schizocrania*, *Trematis*, *Drabodiscina*).

Acrotretid *Hisingerella* is a characteristic genus in the Middle to Upper Ordovician of Baltica (Holmer 1986, 1989). Its Katian spread into Bohemia coincides with climatic warming.

Siphonotretids, after the acme in the upper Tremadocian, have their latest appearance in Bohemia in the Darriwilian (Šárka Formation; Mergl 2002). In Baltica, Kazakhstan and Laurentia, this clade continued as more genera (*Acanthambonia*, *Multispinula, Nushbiella, Siphonotreta,*) into the Middle and Upper Ordovician (Cooper 1956, Gorjansky 1969, Holmer 1989, Nazarov and Popov 1980, Popov 2000, Popov et al. 2002). *Acanthambonia* is reported from the Ashgill of Ireland and Estonia (Wright 1963, Popov and Nõlvak 1987), but siphonotretids are unknown from the periphery of high-latitude Gondwana from that time. Therefore, the presence of *Acanthambonia* in the late Katian 'Perník bed' is palaeogeographically highly indicative.

Craniides, with the exception of *Petrocrania*, are unknown in the Middle and Upper Ordovician of Bohemia and their distribution before the Boda Event is restricted to tropical and temperate climatic belts. In Baltica, the remarkable craniides evolved in the Middle and Upper Ordovician, with the endemic libero-sessile *Orthisocrania* and cementing *Acanthocrania* and *Philhedra* (Huene 1899, Gorjansky 1969, Popov and Pushkin 1986, Popov et al. 2011). The similar cementing craniides (e.g. *Acanthocrania*, *Petrocrania*, ?*Philhedra*) are known to occur in Middle and Upper Ordovician of Laurentia and Avalonia (Cooper 1956, Wright 1963, Hiller 1980, Lockley 1980, Harper 1984). Some of them with radial ribbing may belong to *Deliella* (Popov and Pushkin 1986). Data from other low latitude terraines are scarce (Popov et al. 1999), although *Orthisocrania* has been reported from the Katian of Kazakhstan (Gorjansky 1972) and Sandbian-Early Katian of Avalonia (Wright 1970, Lockley 1980). A few craniides became elements of the rich *Hirnantia* Fauna in Europe (Temple 1965, Bergström 1968, Havlíček 1994a) but they are significant in the *Hirnantia-Draborthis* Association in South China (Rong and Harper 1988).

Craniopsides have a similarly striking restriction to temperate and tropical belts. *Paracraniops* is known from more sites in the Upper Ordovician of Avalonia (Williams 1963, Hurst 1979, Hiller 1980, Harper 1984), Kazakhstan (Gorjansky 1972, Popov et al. 2000) and Laurentia (Cooper 1956). *Pseudopholidops* is confined to the Middle and Upper Ordovician in Baltica (Estonia, Lithuania, Belorussia) (Popov and Pushkin 1986) and Zagros Mountains, Iran (Popov et al. 2011), with subsequent spread in the Hirnantian into new regions (Sweden, Wales, Poland, South China, Bohemia). There is no record of craniopsids in the Middle and Upper Ordovician of European Gondwana prior to the Boda Event.

Summarizing the available data, the presence of *Acanthambonia, Acrosaccus, Hisingerella*, *Deliella*, *Philhedra* and *Pseudopholidops* in the uppermost Katian in Bohemia corresponds well with the model of the Boda Event. Those genera, or their ancestors, proliferated in shallow waters of tropical and temperate climatic belts in Middle and early Late Ordovician. They expanded into higher latitudes during the warming Boda Event and these immigrants formed new local species during the late Katian. Some of them survived the subsequent begining of the Hirnantian cooling, becoming regular members of the rich, temperate climatic belt-located *Hirnantia-Draborthis* Association in Bohemia, South China and probably also other mid-latitude sites with the *Hirnantia* Fauna. These taxa survived to the Silurian (Rong and Harper 1988, 1999).

In Bohemia, *Pseudopholidops* and *Deliella* became rare elements of the *Hirnatia* Fauna, well documented by Havlíček (1994a) from the top of the Kosov Formation. The rich *Hirnantia* Fauna from the upper Hirnantian in Bohemia with elements evolved from originally warm-water low latitude faunas indicates that the cooling could not have been so striking in Bohemia. A plausible explanation is the location of Bohemia (= Perunica), far enough from ice seas in the South and persistent contact between brachiopod populations of Perunica with those in warmer, low-latitude parts of Gondwana and Baltica.

Conclusions

Predominantly cool siliciclastic shelves in the European part of Gondwana were not suitable environments for settlement and successive expansion of small discinides, siphonotretides, cementing craniides and probably also liberosessile craniopsides in the Middle and early Late Ordovician. The global warming Boda Event made possible the expansion of some of these brachiopod stocks into higher latitudes. In the Late Katian, newly formed pelmatozoan and bryozoan biostromes were invaded by craniides, craniopsides, siphonotretides and small sized discinides. Acrotretid *Hisingerella* expanded into higher latitudes at the same time. It is remarkable that some of these stocks survived the begin of glaciation, became regular members of the *Hirnantia* Fauna and continued upto the early Silurian.

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