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PORAMBONITES HAVLICEKI SP. NOV., A NEW BRACHIOPOD FROM THE ŠÁRKA FORMATION (DARRIWILIAN) FROM BOHEMIA AND ITS CONTRIBUTION TO EARLY HISTORY OF THE PORAMBONITIDAE

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Abstract. Unique find of a porambonitid brachiopod in the Šárka Formation (Darriwilian) in the Prague Basin, the Czech Republic, is described. *Porambonites havliceki* sp. nov. is characterized by thin shell with finely pitted radial multicostellate ornament, long parallel brachiophore plates and long dental plates. It is the earliest known representative of the family Porambonitidae in the West Gondwana. *Poramborthis*, an orthid-like syntrophiid genus abundant in the Tremadocian of the West Gondwana, is assumed the evolutionary ancestor of the *Porambonites*. Pitted multicostellate ornament is suggested synapomorphy of the porambonitid brachiopods.

■ Porambonitoidea, *Porambonites*, Brachiopoda, Ordovician, Prague Basin

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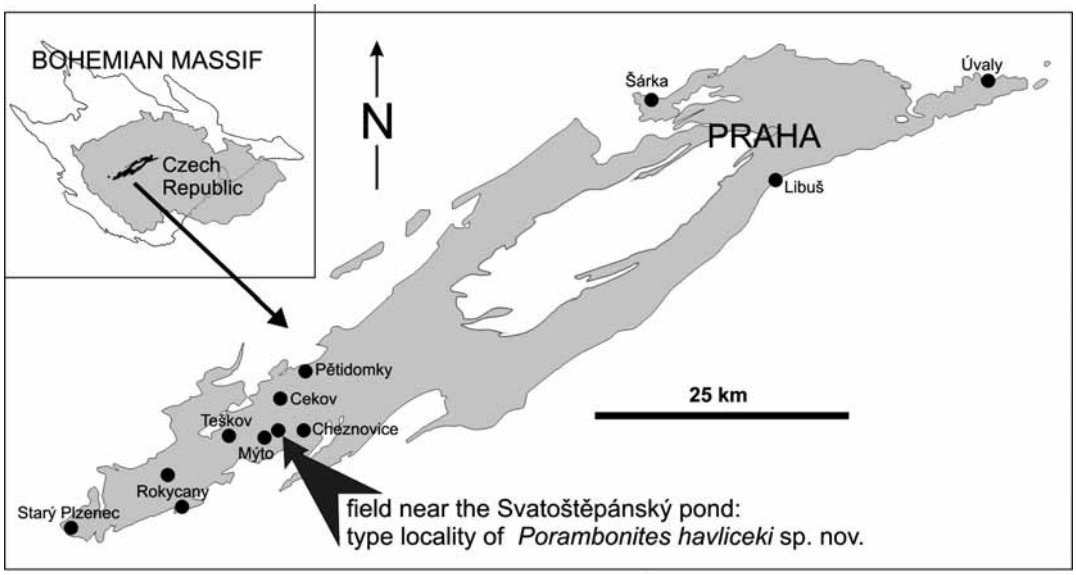
Introduction

Porambonites PANDER, 1830 and related genera constitute a taxonomically complicated group of rhynchonelliform brachiopods. Popov et al. (2005) stated that the Porambonitidae is not well understood family: more species are poorly known or their descriptions do not fit present taxonomic standards (Pander 1830, Teichert 1930, Spjeldnaes 1957, Lockley and Williams 1981, Hansen 2008). Furthermore, many details of a shell morphology and evolutionary history of the Porambonitidae still remains still unclear. New observations based on unique finds of *Porambonites* in the early Middle Ordovician of Bohemia, the Czech Republic, help to elucidate the early evolution of this unique brachiopods.

Geological setting

The new unique complete shell attributed to *Porambonites* PANDER, 1830 has been found in a small siliceous nodule of the Šárka Formation at a ploughed field near the northern margin of the Svatoštěpánský Pond near Mýto (text-fig. 1).



Text-fig. 1. Bohemian Massif with position of the Prague Basin (in black) and distribution of Ordovician rocks in the Prague Basin, with geographic position of main localities of the siliceous nodules.

These nodules are quite common in soil at patched places in several ploughed fields in a broad vicinity of Rokycany and Mýto towns in SW part of the Prague Basin. These nodules are known over 150 years as a source of remarkably rich, deeper-water atheloptic trilobite-dominated fauna (for details see Havlíček and Vaněk 1966).

The Šárka Formation represents the Darriwilian Stage in the Prague Basin. The unit is formed by clayey shale in the central part of the basin and by oolitic iron ore in flanks of the basin (Havlíček and Vaněk, 1966, Havlíček 1998). Occurrence of siliceous nodules is restricted to shale at several localities surrounding the central depression of the basin, mostly along its northern margin. In these parts, the thickness of the formation varies between 25 to 50 m, with the 75 m as the maximum. Although the nodule with the new species *Porambonites* itself does not contain any index fossils, from the sampling situation is evident, that nodule derives from the *Corymbograptus retroflexus* Zone.

Repository

Figured specimen is stored in the palaeontological collections of the University of West Bohemia at Plzeň, Plzeň (PCZCU).

Abbreviations: W = width, L = length, H = heigth, Dv = dorsal valve, Vv = ventral valve.

Systematic palaeontology

Order **Pentamerida Schuchert et Cooper, 1931**

Suborder **Syntrophiidina Ulrich et Cooper, 1936**

Superfamily **Porambonitoidea Davidson, 1853**

Family **Porambonitidae Davidson, 1853**

R e m a r k s . Radial rows of minute pits (fenestrate microornament) is not confined only the stratigraphically later species of *Porambonites* (Popov et al. 2005). Orthid-like genus *Poramborthis* HAVLÍČEK, 1949, recently referred to tetralobulids (Mergl 2011), also has a multicostellate ornament with rows of minute pits, long dental plates, sessile ventral muscle field, weakly impressed muscle scars and digitate mantle canal system. The main difference between *Porambonites* and *Poramborthis* is the strophic shell, short notothyrial platform with the cardinal process, and very short brachiophore plates of the latter genus. These features likely disappeared in the early evolution of *Porambonites*, which took place in the Late Tremadocian or Floian. The loss of the cardinal process, an anterior extension of brachial plates, a reduction of interareas up to astrophic shell, and the development of uniplicate commissure became an autapomorphy of *Porambonites*.

There are few reports of assumed porambonitids in West Gondwana. Small shell fragments with multicostellate ornaments are known from the Klabava Formation (Dapingian) of the Prague Basin (Mergl 1991), but their fragmental state of preservation and lack of any data about shell internal structures make these occurrences greatly useless for a porambonitid phylogeny. However, rows of circular pits (fenestrae) are discernible in shell fragments (Pl. 1, Fig. 11; see also Mergl 1991, pl. 4, fig. 1) and firmly assigned these fragments among the porambonitids.

Genus ***Porambonites* Pander, 1830**

T y p e s p e c i e s . *Porambonites intermedius* Pander, 1830; Upper Ordovician, Estonia.

***Porambonites havliceki* sp. nov.**

Pl. 1, figs 1-10

H o l o t y p e . Complete, partly broken shell preserved as internal and external moulds in siliceous nodule, illustrated on Pl. 1, figs 1-10 (PCZCU 1842).

T y p e h o r i z o n . Darriwilian, Šárka Formation, *Corymbograptus retroflexus* Zone.

T y p e l o c a l i t y . Mýto, a field NW of the Svatoštěpánský pond.

E t y m o l o g y . In honour of Vladimír Havlíček, a late outstanding Czech brachiopodist.

M a t e r i a l . Only the holotype.

D e s c r i p t i o n . Shell astrophic, equally biconvex, thin-shelled, with weakly uniplicate commissure, 22 mm wide.

Dorsal valve subsubcircular, with evenly curved anterior and lateral margins. Posterior margin almost evenly rounded with a poorly defined beak. Transverse profile evenly convex. Axial profile unevenly convex, with maximum height at posterior third. A very poorly developed median fold apparent from midvalve, becoming well defined only near the anterior margin.

Ventral valve subcircular, with well defined beak and palintrope. Anterior margin and sides evenly curved. Palintrope low, occupying some 40 % of the valve width, apsacline. Delthyrium unknown.

Dorsal valve interior with thin parallel brachiophore plates, which extend to 20–25 % of the valve length. Brachiophore plates gently converging toward the valve floor. Mantle canal system digitate, distinctly impressed. Vascula media are thin canals, evenly wide along whole length, gently divergent and almost straight. Their distal ends are not clearly divided and almost touch the anterior margin of the valve. Vascula myaria has the same width of canals as vascula media, and also almost touch the shell margins, but they are more strongly diverging anteriorly and are slightly curved laterally along whole length. Posteriorly, both canal systems extend near the anterior termination of the brachiophore plates. Vascula genitalia are formed by three pairs of short and weakly impressed canals in posterior flanks. Two pairs of elongate oval, small adductor scars weakly impressed posterior to mid valve. Posterior pair located between proximal parts of vascula myaria and vascula media, anterior scars impressed between proximal parts of vascula media. A broad periphery along anterior and lateral margins by radially arranged, evenly sized and spaced striae which correspond to external multicostellate ornamentation.

Ventral valve interior with thin, long parallel dental plates confining an elongate, undivided sessile ventral muscle field. A thin myophragm developed anteriorly. Adductor imprints extend anteriorly by two acute lobes

leaving a triangular valve floor in between. Teeth large. Mantle canal system digitate, distinctly impressed. Vascula media are thin canals, evenly wide along whole length, moderately divergent and slightly curved anterolaterally along the length. Their distal ends not clearly divided, nearly touching the shell margin (Pl. 1, Fig.7). Internal radial striation of the same size and density as on the dorsal valve.

External ornamentation is multicostellate, uniform over whole shell surface. Capillae almost evenly sized, flat-topped, numbering 5 per 1 mm anteriorly. Interspaces narrow and deep, with deep subrhomboidal pits aligned in distinct radial rows. Pits are evenly spaced numbering 6 per 1 mm. New costellae originate exclusively by bifurcation. New costellae narrower in their proximal parts than the mother costella, but rapidly attain nearly the same width. Flat crest of costellae surface bears radially arranged and wrinkled striation. Concentric ornament restricted to very low, short, but distinct concentric lamellae. The single examined shell bears only one lamella situated anteriorly, with a few obscure concentric bands in posterolateral sector.

S i z e . The dimensions are re-calculated from incomplete partly broken shell to entire unbroken shell: DvW = 22mm, DvL = 19mm, DvH = 4mm, VvL = 20mm, VvH = 5mm.

R e m a r k s . The new species is nearest to *Porambonites intermedius* PANDER, 1830 and *P. trigonus* PANDER, 1830 from the the East Baltic (Popov et al. 2005). The new species has similar shell shape, weakly uniplicate commissure, similar shapes and arrangements of brachiophore plates and dental plates, respectively. The main difference is a distinct multicostellate ornament with radial rows of pits (fenestrate structure: Popov et al. 2005) of the new species, whereas *P. intermedius* and *P. trigonus* shells are smooth (Popov et al. 2005). More regularly rounded anterior margin and lower convexity of the new species are further differences to East Baltic species. *Porambonites trigonus* is also smaller species having less than 20 mm long shell. *Porambonites intermedius* differs from the new species by longer dental plates and anteriorly divergent brachiophore plates.

Porambonites dubius WILLIAMS et CURRY, 1985 from the Tourmakeady Limestone (Ireland) is very similar to the new species by outline, size and ornamentation. A feature shared with the new species is presence of subparalell bosses between the inner flanks of the dental plates. The main difference is presence of broad, rectangular sulcus in the ventral valve of the Irish species. Williams and Curry (1985) noted a unusually fine pitted radial ornamentation, but they provide no detailed information about its shape.

O c c u r r e n c e . Only the type locality.

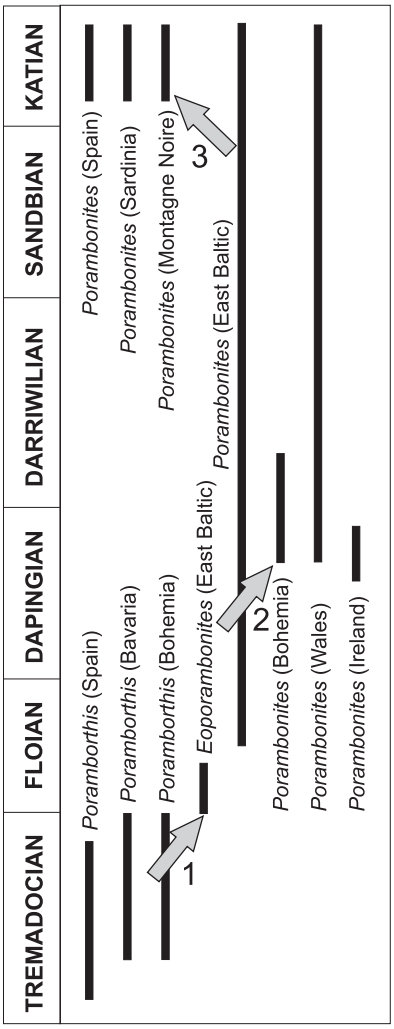
Discussion

Porambonites around Rheic and Tornquist Oceans

In the Early Ordovician, the syntrophiidine brachiopods were important constituent on the shallow shelves on a low latitude continents (Bassett et al. 2002). The porambonitid brachiopods were in the greater part confined to the periphery of the Baltica palaeocontinent, with the occurrence centred to East Baltic and Oslo regions since the Middle Ordovician. They are commonly assumed a typical Baltic element among the brachiopod faunas (Hints and Harper 2003). With the earliest report in the Floian (Popov et al. 2005), the porambonitids became common elements in the Baltica, attaining their maximum diversity in the Mid- and early Upper Ordovician (Teichert 1930, Spjeldnaes 1957, Hansen 2008). Comprehensive review of the Early Ordovician history of this brachiopod group of the East Baltic has been presented by Popov et al. (2005).

In Avalonia palaeocontinent, there came a few records of porambonitids from the British Ordovician [for the reviews see Cocks (2008)]. Their occurrence ranges from the Dapingian to Early Katian, but the Middle Ordovician occurrences are rare or tentative (Williams 1962, Lockley and Williams 1981). Their Sandbian occurrence coincides with the approach of Avalonia to Baltica and closure of the Tornquist Ocean. In Ireland, a porambonitid occurs in the earlier, Dapingian aged brachiopod association of the assumed Laurentian affinity (Williams and Curry 1985).

In West Gondwana, the porambonitid brachiopods became common in the Katian (Villas 1983) for the first time. This rapid spread of *Porambonites* to West Gondwanan shelves



Text-fig. 2. Stratigraphic ranges of selected porambonitid taxa in West Gondwana (Iberica), Baltica, Perunica and Avalonia. Arrows indicate derivation of early Baltic porambonitids from Gondwanan *Poramborthis* (1), derivation of *Porambonites* in Perunica and Avalonia from Baltica (2), and expansion of *Porambonites* from Baltica and/or Avalonia to West Gondwana (3).

(present-day Spain, Montagne Noire, Carnic Alps and Sardinia: Villas 1983, 1985, Havlíček 1981, Havlíčet et al. 1986) coincided with the global warming of the Boda event (sensu Fortey and Cocks 2005). Its dispersion follows the southward expansion of the *Nicolella* Fauna in the same time, probably incoming from Avalonia.

Presented short review of porambonitid distributions explains the exceptionality of *Porambonites* presence in the strata of the Darriwilian age in the Prague Basin. The Bohemia was a part of Perunica, a small terrain with the West Gondwanan affinity (Havlíček et al. 1994, Fatka and Mergl 2009). There is not any proved stratigraphically older occurrence of *Porambonites,* but small similar multicostellate and pitted shells of unclear affinity are known in the shallow-water sediments of the Dapingian age (top part of the Klabava Formation). *Porambonites* has not been recorded in the Prague Basin even in the Sandbian and Katian, when the genus greatly expanded into other parts of the high-latitude West Gondwana.

Porambonites in the Prague Basin

Porambonites havliceki sp. nov. occurs within a deeper-water faunal fossil association of the Šárka Formation (Darriwilian), by Havlíček and Vaněk (1990) named *Euorthisina – Placoparia* Community. This "community" is characterised by invertebrates adapted to soft muddy bottom: trilobites, hyolithids, nuculid bivalves, gastropods, ostracods, asteroids, ophiouroids, mitrates, cystoids, and machaeridians. Planktonic and nektonic biota are common in the fossil assemblage, represented by graptoloids, cephalopods and cyclopygid trilobites. Sessile brachiopods are less common, with orthids *Eodalmanella* and *Euorthisina* (often forming monospecific clusters), and minute, likely infaunal obolids. Composition and preservation indicate a deeper-water environment of the outer shelf type, with more taxa, especially among the trilobites, common with the contemporaneous deeper-water associations of Avalonia and Iberia (Fatka and Mergl 2009).

Rarity and deeper-water origin of *Porambonites havliceki* in this fossils association indicates, that several tens up to a few hundred metres deep sea was generally a hostile environment for the porambonitids. Enviroment was much deep, cold, with muddy sea floor and possible weak oxygen deficiecy. There may be also other explanations of the *Porambonites* rarity in the Šárka Formation. A small porambonitid population originated by a peripatric speciation from the distant Baltic source occupied for a short time the shallower shelves of the Perunica. The unique find simply represents a unique example of the specimen transported from presently unpreserved shallower shelf. Notwithstanding the rarity of *P. havliceki*, the presence of a porambonitid in the Prague Basin indicates, that barrier of the Rheic Ocean between Perunica and Baltica could be over-crossed in the Darriwilian.

Origin of *Porambonites*

Unique feature of the majority of porambonitid species is a pitted (=fenestrate) ornament. Similar ornament (subcircular pits of various shape and depth intercalated between capillae) are present also in punctolirinids, but this subfamily is strophic, with sessile spondylium and saccate ventral mantle canal system (Carlson 2002). Finely pitted ornament is a feature known in more porambonitid genera (*Noetlingia*, *Porambonites*), but this ornament has been assumed as missing in the early Ordovician representatives of *Porambonites* and the related *Eoporambonites* (Popov et al. 2005). A syntrophioiod genus *Tetralobula* and related genus *Poramborthis* display a similar fenestrate ornament (Havlíček 1977, Popov et al. 2005, Mergl 2011). The ornament of porambonitids, with fine costellae separated by narrow interspaces having a row of small pits (= fenestrae) indicates that the tetralobulids are the best evolutionary candidates for origin of the porambonitid clade. Carlson (2002) listed necessary changes for derivation of pentameridines from the orthide-like ancestor: commissure change from rectimarginate to uniplicate, decrease of hinge line width, reduction of interareas, dental plate change from divergent to convergent, lost of cardinal process, and weak impression of muscles.

All these advanced features are present in the *Porambonites* Pander, 1830, a genus likely derived from *Tetralobula* or a similar ancestor. Unlike *Tetralobula*, the genus *Poramborthis* lacks distinctly uniplicate commissure, has strophic shell with narrow hinge line and weakly impressed muscle fields, diplays distinct cardinal process, and possesses subparallel dental plates and same digital pallial canal mantle system as *Porambonites*. Multicostellate ornament of *Poramborthis* is likely a synapomorphy with *Porambonites*, although some of the earliest members of the Porambonitidae are described as possessing only multicostellate ornament without pits or have shell devoid of distinct costellation (Popov et al. 2005). *Poramborthis* was likely confined to the Tremadocian of Western Gondwana (Mergl 2011), with several stratigraphically subsequent or overlapping species in present-day Bavaria, Bohemia and Spain (Havlíček 1949, 1950, 1977, Sdzuy 1955, Havlíček and Josopait 1972, Sdzuy et al. 2001). The earlier presence of *Poramborthis* in West Gondwana shelves indicates, that the porambonitid fauna of Baltica, having the first occurrence in the Floian, may be derived from the West-Gondwanan Tremadocian-aged ancestors. *Poramborthis* is therefore assumed the missing link to the Late Cambrian tetralobulids, the earliest member of the family Porambonitidae, and also the evolutionary forerunner of *Porambonites.*

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Explanation of the plates

PLATE 1

***Porambonites havliceki* sp. nov.** Šárka Formation, field near Svatoštěpánský Pond, PCZCU1842,

1. siliceous nodule with external mould, length of bar: 5 mm.
2. internal mould of dorsal valve, length of bar: 5 mm.
3. internal mould of ventral valve, length of bar: 5 mm.
4. posterodorsal view to internal mould, length of bar: 5 mm.
5. latex cast of exterior of dorsal valve, length of bar: 5 mm.
6. detail of ornamentation, length of bar: 1 mm.
7. striation at internal periphery of shell, internal mould, length of bar: 1 mm.
8. detail of radial rows of pits, external mould, length of bar: 1 mm.
9. detail of ornament showing pits and wrinkles on costellae, latex cast, length of bar: 1 mm.
10. detail of ornament, latex část, length of bar: 1 mm.

***Porambonites* ? sp.** Klabava Formation, old mine near Osek, PCZCU 1897,

11. fragment of shell, external mould, length of bar: 1 mm.

PLATE 1