

The youngest representatives of the genus *Ribeiria* Sharpe, 1853 from the late Katian of the Prague Basin (Bohemia)

Marika Polechová

Czech Geological Survey, Klárov 3, 11821 Prague 1, Czech Republic; marika.polechova@geology.cz

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Abstract. *Ribeiria apusoides* and *Ribeiria johni* sp. nov. are described from the late Katian of the Prague Basin (Bohemia) as the youngest representatives of the genus *Ribeiria*. The Ordovician ribeirioids from Bohemia (Perunica) show close affinities to the ribeirioids from Armorica and Iberia. The functional morphology of ribeirioids, mainly the pedal muscle system, is discussed, based on very well-preserved specimens of *R. apusoides*. The ribeirioids attained their diversity in the Lower Ordovician, since the Middle Ordovician their diversity declines, and during the late Katian only three genera are known worldwide. They are unknown from the Hirnantian but the last ribeirioids are recorded from the lower Silurian in South China.

Key words: Ribeirioida, systematics, functional morphology, Ordovician, Prague Basin.

INTRODUCTION

The study of rostroconchs was started by Martin (1809) and Sowerby (1815), but the systematic position of the group was for a long time unclear. Rostroconchs were allied mainly to bivalves (Branson et al. 1969) or even to arthropods (Schubert & Waagen 1904; Kobayashi 1933). Pojeta et al. (1972) established them as a separate group of molluscs and Pojeta & Runnegar (1976) presented three orders of rostroconchs, Ribeirioida, Ischyrioida and Conocardioida. Subsequently Pojeta (1987) included Ischyrioida within the Ribeirioida. The main reasons for the assignment of rostroconchs to the molluscs are the presence of a protoconch, calcareous shell with the growth lines and the prominent muscle scars, which also show growth increments (Pojeta & Runnegar 1976). In a large monograph (Pojeta et al. 1977) on the Cambrian and Ordovician rostroconchs from Australia their potential usefulness as biostratigraphic tools was presented. The research of rostroconchs continues with modern systematic studies focused mainly on the order Conocardioida (e.g. Hoare 1989, 1990, 2000; Amler 1996; Hoare et al. 2002; Amler & Rogalla 2004; Rogalla & Amler 2006a, 2006b, 2006c). On the other hand, the Ordovician ribeirioids have been an overlooked group and outside comprehensive palaeobiological and systematic studies.

The ribeirioids from Bohemia are not an exception: Schubert & Waagen (1904) described the genera *Ribeiria* Sharpe, 1853 and *Ribeirella* Schubert & Waagen, 1904 (now *Technophorus* Miller, 1889) from the Ordovician of the Prague Basin and assigned them to arthropods. These two genera were also figured in Perner (1903).

Pojeta & Runnegar (1976) briefly described and figured all known species of rostroconchs, including also species of ribeirioids from the Ordovician of the Prague Basin (Czech Republic). The rich material of rostroconchs from the Czech Republic is one of the best-preserved materials. It includes ribeirioids from the late Katian (Králov Dvůr Formation), among them the worldwide youngest representatives (*R. apusoides* Schubert & Waagen, 1903 and *Ribeiria johni* sp. nov.) of the genus *Ribeiria*.

SYSTEMATIC PALAEOLOGY

Abbreviation. NM – specimens deposited in the National Museum, Prague.

MOLLUSCA

Class ROSTROCONCHIA Pojeta, Runnegar, Morris & Newell, 1972

Order RIBEIRIOIDA Kobayashi, 1933

Family RIBEIRIIDAE Kobayashi, 1933

Genus *Ribeiria* Sharpe, 1853

Type species. *Ribeiria pholadiformis* Sharpe, 1853, Portugal, Sierra de Buçaco, Darriwilian.

Ribeiria johni sp. nov.
Figure 1A, C

1903 *Ribeiria apusoides* Schubert & Waagen; Perner, pl. 49, figs 14–17.

1976 *Ribeiria apusoides* Schubert & Waagen; Pojeta & Runnegar, p. 53, pl. 6, fig. 13.

Holotype. NM L 7859, internal mould of the shell, figured by Schubert & Waagen in Perner 1903, pl. 49, figs 14, 16, 17.

Paratype. NM L 7858, internal mould of the shell figured by Schubert & Waagen in Perner 1903, pl. 49, fig. 15.

Derivation of name. In honour of John Pojeta, Jr., who devotes his research to the Palaeozoic rostroconchs and bivalves.

Type locality. Bohemia, Prague Basin, Lejškov near Suchomasty.

Type horizon. Upper Ordovician, late Katian, Králův Dvůr Formation.

Diagnosis. Elongated and slender *Ribeiria* with straight dorsal margin, with terminal umbo and with narrow pegma.

Description. Shell elongated and slender with prosogyral umbo, which is terminal and not projecting above dorsal margin. Ventral margin arcuate, dorsal margin straight without posterior dorsal notch. Posterior margin rounded. Shell slightly attenuated posteriorly, pegma in the anterior part of the shell is long and thin, placed high in the anterior part of the shell. Muscle scars and ornamentation not preserved.

Discussion. *Ribeiria johni* differs from *R. apusoides* from the Middle and Late Ordovician of Bohemia in a slender shell, thin pegma, terminal umbo and straight dorsal margin.

Material. Six internal moulds of the shell.

Distribution. Bohemia, Prague Basin, Katian: Lejškov near Suchomasty, Levín.

Ribeiria apusoides Schubert & Waagen in Perner 1903
Figure 1B, D, F

1903 *Ribeiria apusoides* Schubert & Waagen; Perner, pl. 49, figs 5, 6, 18–26.

1904 *Ribeiria apusoides* Schubert & Waagen; Schubert & Waagen, p. 44, pl. I, figs 6–11.

1976 *Ribeiria apusoides* Schubert & Waagen; Pojeta & Runnegar, p. 50, pl. 5, figs 1–14; pl. 6, figs 1–12, 14, 15.

Lectotype. (SD Pojeta & Runnegar 1976) NM L 7860, internal mould of the shell, figured by Schubert & Waagen in Perner 1903, pl. 49, figs 18–20.

Paralectotypes. NM L 7861, internal mould of the shell, figured by Schubert & Waagen in Perner 1903,

pl. 49, fig. 21; NM L 7863, external mould of the left valve figured by Schubert & Waagen in Perner 1903, pl. 49, figs 24–25.

Type locality. Bohemia, Prague Basin, Loděnice.

Type horizon. Upper Ordovician, early Katian, Zahofany Formation.

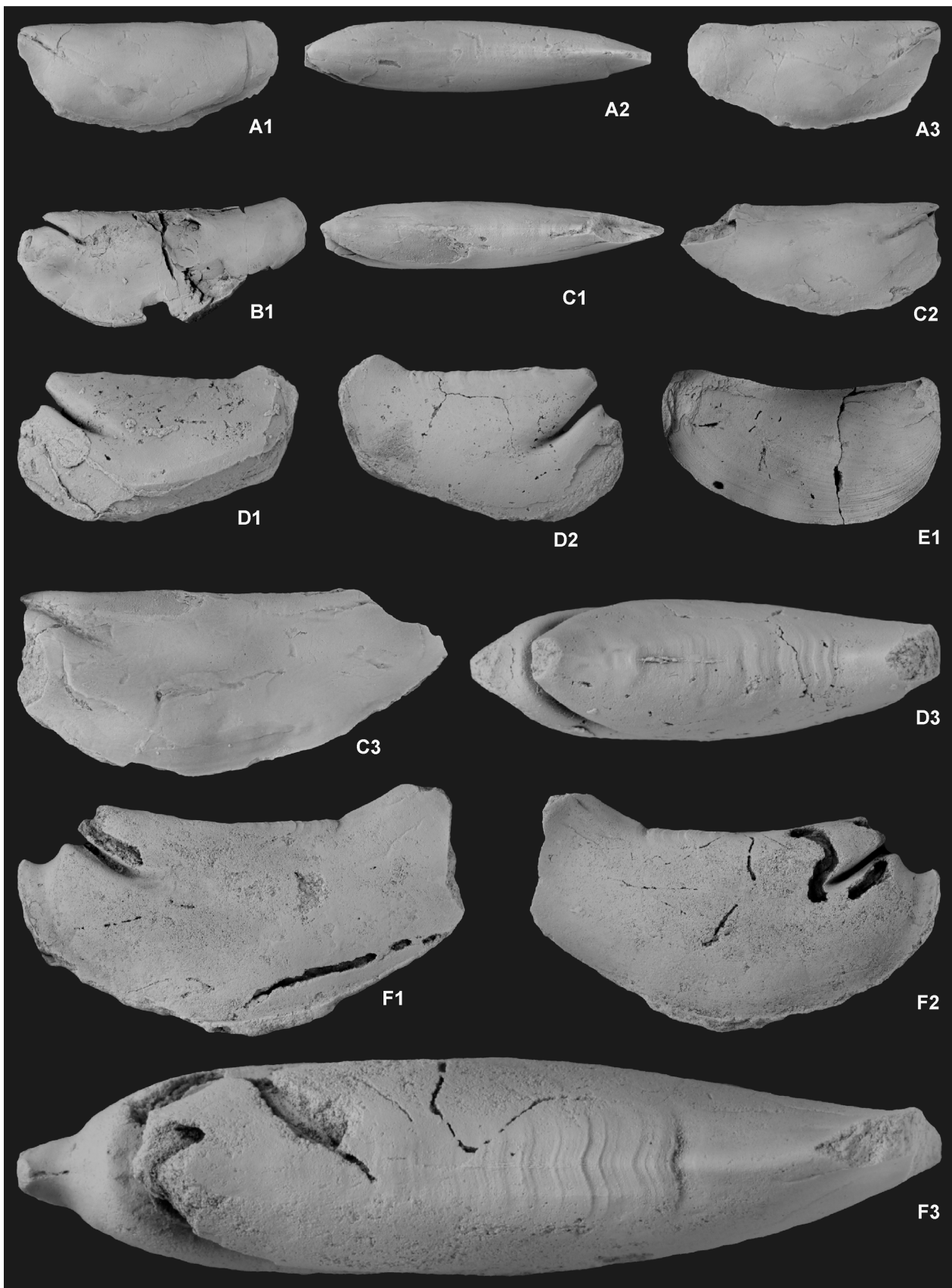
Diagnosis. Elongated and large *Ribeiria* with gently concave dorsal margin with posterior dorsal notch and well-marked cleft anterior from pegma.

Description. Shell large and ovate with prosogyral umbo, which is not terminal. Ventral margin arcuate, dorsal margin concave with posterior dorsal notch. Posterior margin straight. Shell slightly attenuated posteriorly, long and thick pegma placed high in the anterior part of the shell. Well-marked cleft anteriorly relating to pegma. Ornamentation comprising fine commarginal lines, in the posterior part these lines are rippling. Anteriorly from the posterior dorsal notch posterior median muscle scar is preserved, extended almost to the umbo. Anterior median muscle scar lying on the posterior part of the pegma. In one specimen (NM L 7852) slightly inserted side muscle scars between anterior and posterior median muscle scars are present.

Discussion. *Ribeiria apusoides* is the most similar to *R. pholadiformis* from the Darriwilian of Portugal, France, Morocco and Spain. The main difference in the diagnosis of the species, mentioned by Pojeta & Runnegar (1976) is lack of the prominent posterior dorsal notch in *R. apusoides*. This character is vague because in some specimens (NM L 7860) of *R. apusoides* the prominent notch is also visible. Also the outline of the shell, presence of the anterior cleft and posterior median muscle scars are very similar. The late Ordovician *R. apusoides* seems differ from *R. pholadiformis* in a concave dorsal margin. *Ribeiria spinosa* Babin & Branisa, 1987 from the middle Darriwilian (Llanvirn) of Bolivia and from the Floian (Arenig) of Northwestern Argentina differs in spinelike projection, placed ahead of the pegma. Sánchez (1997) described *R. spinosa* from the late Floian (middle Arenig) of western Argentina, but these specimens lack the characteristic spinelike projection and they are very similar to *R. pholadiformis* and *R. apusoides*. *Ribeiria johni* sp. nov. from the late Katian of Bohemia possesses a slender shell, thin pegma, terminal umbo and straight dorsal margin.

Material. About one hundred specimens (internal and external moulds).

Distribution. Bohemia, Prague Basin, Darriwilian: Osek, Rokycany, Díly, Pětídomky, Malé Přílepy; lower and upper Katian: Bohdalec, Loděnice, Prague-Lhotka,



Prague-Libeň, Prague-Radošín, Prague-Strašnice, Prague-Vysočany, Prague-Spořilov, Prague-Štěrboholy, Vinice, Zahofány.

FUNCTIONAL MORPHOLOGY IN RIBEIRIOIDA

Pojeta & Runnegar (1976) show the main aspects of functional morphology in rostroconchs. The determination of the morphological orientations in extinct groups is always difficult and therefore the orientations of the shells in bivalves were used as a certain example for describing the morphological orientations in rostroconchs. The system of muscles in bivalves also served as an example for the interpretation of the musculature in rostroconchs, which seems to work fairly well in the Ordovician Conocardiida like *Eopteria*. On the other hand, the system of muscle scars in Ribeirioida is more different from the system of muscle scars in bivalves. All three main representatives of ribeirioids (*Ribeiria*, *Technophorus*, *Tolmachovia*) show a similar pattern of muscle scars (Pojeta & Runnegar, 1976, fig. 3) with anterior and posterior median muscle scars and side muscle scars. Pojeta & Runnegar (1976) also interpreted the functions of these muscles.

Ribeiria apusoides from the Ordovician of Bohemia possesses a very well-preserved posterior median muscle scar (Fig. 1D3, F3) lying across the midline of the shell and serves to retract the foot. In *R. apusoides* the posterior median retractor is very large, extending almost from the umbo to the posterior notch, where it is more deeply inserted. The posterior median retractor is formed by two lobes (Fig. 1D3, F3) and differs markedly from the bivalve pedal musculature.

Side muscle scars are rarely preserved and their function is unclear. According to Pojeta & Runnegar (1976), they can help with moving the foot or support gills. Side muscle scars connect median muscle scars and they are in a similar position as accessory muscle scars in some Ordovician bivalves considered as infaunal burrowers (*Babinka*, *Coxiconchia* or *Praenucula*) (Fig. 2).

In bivalves these muscles serve as a support of retractors or can provide a firm attachment of the pericardial region to the shell during vigorous movement of the foot. They can also hold the muscular floor of the visceral sac (Heath 1937; Polechová 2013). The function of side muscles in Ribeirioida, also considered as infaunal burrowers, could be similar.

The anterior median muscle scar lies on the posterior part of the pegma (Pojeta & Runnegar 1976, pl. 5, fig. 4). Very rarely (seen in two specimens) this muscle scar is preserved also in *R. apusoides*. Similar to the posterior median muscle scar, it serves probably to retract the foot and therefore the function of the pegma could be in supporting this muscle. The bivalves *Redonia* or *Nuculites* as well show a myophoric plate, which supports the anterior adductor muscle.

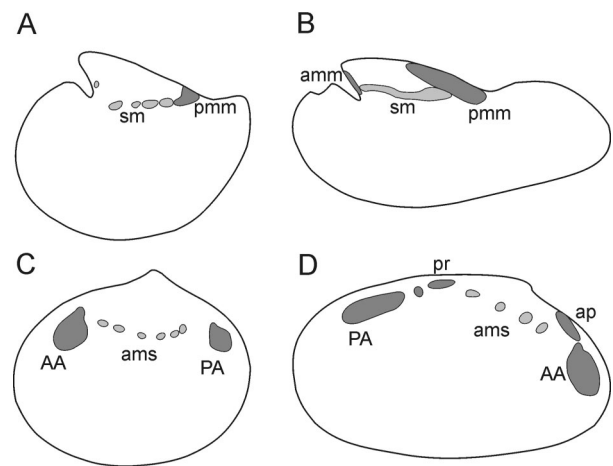


Fig. 2. Muscle system in selected ribeirioids (A, B) and bivalves (C, D). **A**, *Ribeiria lucan* (Walcott, 1924), left lateral view. **B**, *Ribeiria apusoides* Schubert & Waagen, 1903, left lateral view. **C**, *Babinka prima* Barrande, 1881, left lateral view. **D**, *Coxiconchia britannica* (Rouault, 1851), right lateral view. Key to letter symbols: AA, anterior adductor muscle scar; amm, anterior median retractor muscle scar; ams, accessory muscle scars; ap, anterior protractor muscle scar; PA, posterior adductor muscle scar; pmm, posterior median retractor muscle scar; pr, posterior retractor muscle scar; sm, side muscle scars.

Fig. 1. *Ribeiria apusoides* Schubert & Waagen, 1903 and *Ribeiria johni* sp. nov. from the Zahofány and Králův Dvůr formations (lower and upper Katian). **A, C**, *Ribeiria johni* sp. nov. **A1–A3**, internal mould of conjoined valves, holotype, NM L 7859, left lateral view $\times 1.5$, dorsal view $\times 2$, right lateral view $\times 1.6$, Prague Basin, Lejškov, Králův Dvůr Formation. **C1–C3**, internal mould of conjoined valves, paratype, NM L 7858, dorsal view $\times 2$, right lateral view $\times 1.5$, left lateral view $\times 2.5$, Prague Basin, Lejškov, Králův Dvůr Formation. **B, D, E, F**, *Ribeiria apusoides* Schubert & Waagen, 1903. **B1**, internal mould of conjoined valves, NM L 42443, left lateral view $\times 1.5$, Prague Basin, Lejškov, Králův Dvůr Formation. **D1–D3**, internal mould of conjoined valves, NM L 7852, left lateral view $\times 2.1$, right lateral view $\times 2.2$, dorsal view $\times 4$, Prague Basin, Prague, Zahofány Formation. **E1**, external mould of left valve, paralectotype, NM L 7863, left lateral view $\times 1.6$, Prague Basin, Loděnice, Zahofány Formation. **F1–F3**, internal mould of conjoined valves, lectotype, NM L 7860, left lateral view $\times 2.2$, right lateral view $\times 2$, dorsal view $\times 4.2$, Prague Basin, Loděnice, Zahofány Formation.

The pedal muscles are deeply inserted in the shell and have more chance to be preserved than pallial muscles, which are very rarely preserved also in bivalves.

DIVERSITY OF RIBEIRIOIDA DURING THE CAMBRIAN AND ORDOVICIAN

The Ribeirioida are well known from the late Cambrian to early Silurian. During the Cambrian ribeirioids occurred in eastern Gondwana – Australia (Pojeta et al. 1977; *Oepikila*, *Pinnocaris*, *Pleuropegma*, *Cymatopogma*, *Kimopogma*, *Ribeiria*), Laurentia (Grabau 1900; Pojeta & Runnegar 1976; *Watsonella*), western Gondwana – Argentina (Sánchez 2005; *Ribeiria*) and North China – Manchuria (Kobayashi 1933, 1934; *Wanwania*).

In the Early Ordovician they rapidly diversified in eastern Gondwana – Australia (Pojeta et al. 1977; *Pinnocaris*, *Pleuropegma*, *Ribeiria*, *Cymatopogma*, *Apoptopogma*, *Pauropogma*, *Ptychopogma*, *Technophorus*), northern and southern Laurentia (Billings 1865; Pojeta & Runnegar 1976; *Ribeiria*, *Ribeirina*), western Gondwana – Argentina (Harrington 1938; Sánchez 2005; *Ribeiria*, *Tolmachovia*), North China – Manchuria (Kobayashi 1933; *Ribeiria*, *Technophorus*, *Wanwanella*, *Wanwania*, *Wanwanoidea*), and appeared in eastern Gondwana – Bolivia (Babin & Branisa 1987; *Ribeiria*), Armorica – France (Thoral 1935; Babin et al. 1982; *Ribeiria*, *Tolmachovia*) and Avalonia – Wales (Cope 1996; *Ribeiria*).

From the Middle Ordovician their diversity decreased and they occurred in southern Laurentia (Pojeta & Runnegar 1976; *Ribeiria*, *Technophorus*), northern Gondwana – Australia (Pojeta et al. 1977; *Pinnocaris*, *Ribeiria*) and western Gondwana – Argentina (Sánchez 1986; Babin & Branisa 1987; *Talacastella*, *Tolmachovia*), newly appeared in Perunica – Bohemia (Schubert & Waagen in Perner 1903; *Ribeiria*, *Technophorus*), Iberia – Spain, Portugal (Thoral 1935; Babin et al. 1982; *Ribeiria*, *Technophorus*, *Tolmachovia*), Avalonia – Wales (Salter 1864, 1866; *Ribeiria*, *Myocaris*) and western Gondwana – Morocco (Babin & Destombes 1990; *Ribeiria*).

From the Late Ordovician only three genera are known (*Ribeiria*, *Technophorus*, *Pinnocaris*), but they are still widely dispersed in Laurentia (Etheridge 1878; Reed 1907; Pojeta & Runnegar 1976; *Pinnocaris*, *Technophorus*), Siberia (Pojeta & Runnegar 1976; *Technophorus*), Baltica – Norway (Soot-Ryen 1960; *Technophorus*) and Perunica – Bohemia (Schubert & Waagen in Perner 1903; *Technophorus*, *Ribeiria*). *Pinnocaris* and *Technophorus* survived until the lower Silurian in South China (Xu 1990).

The decrease in the diversity not only in Ribeirioida, but also in the whole group of rostroconchs was explained as a competition of this group with the Ordovician bivalves (Pojeta 1979), which are mostly considered similarly to rostroconchs like infaunal burrowers. According to Pojeta (1979), the main competitive advantage for bivalves could be their adaptation to burrowing because they could better establish and keep their position in the sediment. Thus they could burrow into a wider variety of substrates. This idea was disproved by Cope (2004), who showed that (1) initial early Ordovician bivalve radiations took place in Gondwana where there were few rostroconchs, (2) the early Middle Ordovician rostroconch decline was principally extra-Gondwanan (where there were few bivalves) and (3) the late Ordovician increase in rostroconch diversity, particularly in the Laurentian carbonate shelves, coincided with the arrival of bivalves on these shelves, where the latter rapidly diversified.

Furthermore, in conocardiids no apparent decrease in diversity is observable during the Ordovician, because the number of genera is almost the same (Early Ordovician – four genera, Middle Ordovician – four genera, Late Ordovician – five genera). The situation is different in ribeirioids; they reached the peak of their diversity in the Early Ordovician. Unlike the rostroconchs, the bivalves diversified significantly during the Middle Ordovician and Late Ordovician (e.g. Babin 1993; Polechová 2013) and the diversity during the Ordovician increased and reached almost 200 genera (Cope & Kříž 2013) in comparison with rostroconchs and their 26 genera. Ribeirioids never exceeded the diversity of bivalves even in the Early Ordovician, when the bivalves were rare and restricted to the Gondwana and peri-Gondwana terranes.

CONCLUSION

The genus *Ribeiria* is known from the late Cambrian (Australia, northwestern Argentina) to the late Katian (Bohemia). *Ribeiria johni* sp. nov. is restricted to the upper Katian of the Prague Basin only, whereas *R. apusoides* is known from the Darriwilian to the late Katian of the Prague Basin. In the Middle Ordovician the ribeirioids of Bohemia show close affinities to similar associations from Armorica and Iberia; in the Late Ordovician they share some taxa with Baltica.

The ribeirioids from Bohemia provide specimens with well-preserved muscle scars, such as anterior and posterior median retractors, and very rarely preserved side muscle scars. The function of the side muscle scars in ribeirioids seems to be very similar to that of the

accessory muscle scars in bivalves, which are preserved in the umbo region or between adductor muscle scars. The function of the pegma in ribeirioids could be in supporting the anterior median retractor.

The diversity of conocardiids is almost the same during the Ordovician. The ribeirioids reached their acme of diversity during the Lower Ordovician. Rostroconchs never exceeded the diversity of bivalves even in the Lower Ordovician, when the bivalves were rare and restricted to the Gondwana and peri-Gondwana terranes.

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