

Bivalves from the Middle Ordovician Šárka Formation (Prague Basin, Czech Republic)

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A rich bivalve fauna from the Middle Ordovician (Šárka Formation, early and mid Darriwilian) of Bohemia shows close affinities to Middle Ordovician bivalves from Spain (Iberian Peninsula) and France (Armorican Massif). Twelve species and nine genera (one new) are described: *Praenucula applanans* (Barrande, 1881), *Praenucula bohémica* (Barrande, 1881), *Praenucula dispar* (Barrande, 1881), *Concavodonta ponderata* (Barrande, 1881), *Pseudocyrtodonta ala* (Barrande, 1881), *Pseudocyrtodonta incola* (Barrande, 1881), *Tatula petula* gen. et sp. nov., *Redonia deshayesi* Rouault, 1851, *Babinka prima* Barrande, 1881, *Coxiconchia britannica* (Rouault, 1851), and the oldest pteriomorphids in the Prague Basin *Modiolopsis* sp. and *Cyrtodonta* sp. *Ctenodonta*, widely used as cumulative name for all praenuculids, was not recorded in the Middle Ordovician of Bohemia. Remarks on the characters of the Protobranchia shell are discussed, the value of the orientation of the teeth to the umbo or out from the umbo for higher systematic has been overestimated in the past. Accessory muscle scars in the Protobranchia help to move with foot, not only by retraction and protraction but also by elevation; some of them hold a visceral sac. The Recent Protobranchia mostly show simpler type of taxodont teeth in comparison with the Ordovician Protobranchia. Palaeoecological aspects of all the species are shown, infaunal burrowers dominate in the lithofacies of the black shales of the Šárka Formation. The bivalve association is dominated numerically by heterodonts, subdominant are several species of protobranchs and two pteriomorphids. The palaeogeographic distribution of the Middle Ordovician bivalves is discussed. Some of the Middle Ordovician bivalves are widely distributed, they reach Baltica and also the Laurentian margins and probably had to have planktotrophic larvae. Clear preference of the heterodonts for high latitude is confirmed by the dominant heterodonts (six species) in the bivalve association of the Middle Ordovician Šárka Formation. • Key words: bivalves, Middle Ordovician, Perunica, Bohemia, systematics, palaeoecology, palaeobiogeography.

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Since Barrande (1881) and Pfab (1934) works Ordovician bivalves from Bohemia were for a long time overlooked group except a few systematic studies, which were published by Horný (1960), McAlester (1965), Kříž (1995), Kříž & Steinová (= Polechová) (2009), and Steinová (= Polechová) (2012). Middle Ordovician bivalve faunas from Bohemia are very similar to Middle Ordovician bivalve faunas from Spain and France, where the Ordovician bivalves have been systematically studied for a long time (e.g. Babin 1966, 1977, 1985, 1982 in Babin *et al.* 1982; Babin & Gutiérrez-Marco 1985, 1991; Babin & Beaulieu 2003). All the authors pointed out the lack of modern information about the Ordovician bivalves from Bohemia. The preparation of the new *Treatise on Invertebrate Paleontology* for bivalves is in progress now and therefore it is an appropriate time for undertaking revision of the Ordovician bivalves from Bohemia.

Bivalves described here come from the Šárka Formation (Kettner & Kodým 1919) (Fig. 1). Havlíček & Vaněk (1966) correlated the Šárka Formation with the Llanvirn, Kraft *et al.* (2001) supposed that the Šárka Formation is isochronous with the late Arenig–early Llanvirn. Recently Budil *et al.* (2011) correlated the Šárka Formation with the early and middle Darriwilian and Fatka *et al.* (2013) correlates the Šárka Formation with the Oretanian Regional Stage, which is almost equal to the middle Darriwilian (Bergström *et al.* 2008).

The Šárka Formation has been studied for almost two hundred years (Barrande 1846; Lipold & Krejčí 1860; Krejčí 1877; Klouček 1909, 1916; Kettner & Kodým 1919; Hanuš 1923; Bouček 1927; Kettner & Prantl 1948; Kukal 1962, 1963; Havlíček 1961, 1967, 1980, 1981, 1982, 1998; Havlíček & Vaněk 1966; Bouček 1973; Kraft 1974; Kraft & Kraft 1992, 1993, 2003; Havlíček & Fatka 1992; Vaněk

1999; Budil *et al.* 2003a, 2003b, 2007; Drost *et al.* 2003; Fatka 2003; Chlupáč 2003; Kraft *et al.* 2003; Mikuláš 2003, Manda 2008 and Fatka & Mergl 2009).

Sedimentation of the Šárka Formation in the Prague Basin began by a significant transgression, which was contemporary for peri-Gondwanan regions. The largest part of the Šárka Formation is developed in black shale facies. The formation corresponds to two graptolite biozones, the earlier with *Corymbograptus retroflexus* and a later zone with *Didymograptus clavulus* (Bouček 1973; Kraft 1974; Kraft & Kraft 1992, 1993). Within the shales occur horizons with siliceous nodules containing a well-preserved and diverse fauna. According to Kukal (1962) these nodules were primarily of carbonate and then they were subsequently silicified. These nodules are restricted to several localities in Prague, around Rokycany and near Úvaly and Brandýs nad Labem. Black shales prevail in the central parts of the Prague Basin, while sedimentary iron ores are presented in onshore settings (Havlíček 1998) with best exposures in Ejpvovice area near Pilsen.

Accumulations of volcanic and volcanoclastic rocks are connected with submarine volcanism of the Komárov Volcanic Complex (Kukal 1962). The Ordovician volcanism reached maximum activity just within the Šárka Formation.

History of research of the Ordovician bivalves from Bohemia

Barrande (1881) figured and described these species from the Šárka Formation: *Babinka prima* Barrande, 1881, *Leda ala* Barrande, 1881 (= *Pseudocyrtodonta ala*), *Leda bohémica* Barrande, 1881 (= *Praenucula bohémica*), *Leda incola* Barrande, 1881 (= *Pseudocyrtodonta incola*), *Nucula applanans* Barrande, 1881 (= *Praenucula applanans*), *Nucula dispar* Barrande, 1881 (= *Praenucula dispar*), *Nucula faba* Barrande, 1881 (= *Redonia deshayesi*), *Redonia bohémica* Barrande, 1881 (= *Redonia deshayesi*) and *Synek antiquus* (= *Pseudocyrtodonta ala*, partim) Barrande, 1881. He allocated them to the genera *Nucula*, *Leda* and *Redonia* and defined the new genera *Babinka* and *Synek*.

Pfab (1934) systematically revised the species belonging to the Protobranchia Pelseneer, 1889 and reassigned some of the Barrande's species to: *Praeleda* Pfab, 1934, *Praenucula* Pfab, 1934, *Pseudocyrtodonta* Pfab, 1934 and mainly to *Ctenodonta* Salter, 1852, and some of them he left in open nomenclature. Pfab (1934) described these species from the Šárka Formation: *Ctenodonta applanans* (Barrande, 1881) (= *Praenucula applanans*), *Ctenodonta bohémica* (Barrande, 1881) (= *Praenucula bohémica*), *Ctenodonta ponderata* (Barrande, 1881) (= *Concavodonta ponderata*), *Praeleda compar* (Barrande, 1881) (= *Praenucula bohémica*), *Praeleda pulchra* Pfab, 1934

(= *Praenucula bohémica*), *Praenucula dispar dispar* (Barrande, 1881) (= *Praenucula dispar*), *Praenucula dispar expansa* Pfab, 1934 (= *Praenucula dispar*) and *Pseudocyrtodonta ala* (Barrande, 1881) (= *Pseudocyrtodonta ala* and *Pseudocyrtodonta incola*). Pfab (1934) was first who paid attention to the characters of the shell, like muscle scars and hinge. He recognized six hinge types according to the shape of their teeth and if the apex of the chevron-shaped teeth points towards or away from the umbo. He discussed also phylogenetic relations between *Ctenodonta*, *Praenucula* and *Nucula*.

After Pfab (1934) only a few authors have studied the Middle Ordovician bivalves. Růžička & Prantl (1960) designated the lectotype for *Babinka prima*. Horný (1960) revised *Babinka prima*, created the new family Babinkidae and interpreted the phylogeny of earliest bivalves from univalved molluscs through the new order Diplacophora Horný, 1960. The systematics, affinities and life habits of *Babinka* as an ancestral lucinid bivalve were reinterpreted by McAlester (1965). *Redonia bohémica* has been discussed and redescribed by Pojeta (1971), Babin (1977) and Babin & Gutiérrez-Marco (1991). Kříž (1995) described a representative of the genus *Coxiconchia* Babin, 1966 from the Šárka Formation and contributed to the knowledge of accessory muscle scars and their function in the Protobranchia. In 1997 Kříž briefly presented some remarks about palaeoecology of the Ordovician bivalves. Steinová (= Polechová) in 2012 revised actinodontid *Pseudocyrtodonta* (Pfab, 1934) from the Middle and Late Ordovician of the Prague Basin.

The large collections of the Middle Ordovician bivalves are deposited in the National Museum, including Barrande's and Pfab's type material. Fossiliferous nodules attracted the attention of many collectors, but particularly Klouček (1916) and Hanuš (1923) contributed markedly to the general knowledge of the Middle Ordovician fauna. In the collection of F. Hanuš (1860–1937) were found new specimens (*Tatula petula* gen. nov. et sp. nov., *Modiolopsis* sp. and *Cyrtodonta* sp.) from the important localities of Šárka villa and Šárka brickyard in Prague. No less important collection of the Middle Ordovician bivalves is stored in the Museum of Dr. Bohuslav Horák in Rokycany. Some of the specimens studied in this paper come from the older collection of Karel Holub and the new material were collected mainly by Jaroslav and Petr Kraft.

Middle Ordovician bivalves from the World often went through the modern revision and therefore their data are the most complex and allows us to study their relationships, distribution and biodiversification. Middle Ordovician bivalves are known from Argentina (Sánchez 1990), Australia (Pojeta & Gilbert-Tomlinson 1977), Belgium (Maillieux 1939), China (Fang & Cope 2004, Fang 2006, Fang & Cope 2008), France (De Verneuil & Barrande 1856, Barrois 1891, Babin 1966, Bradshaw 1970, Babin in

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Figure 1. Global and regional stratigraphic chart for the Middle and Upper Ordovician and stratigraphic occurrence of the Middle Ordovician bivalves from Bohemia.

Babin *et al.* 1982, Babin & Beaulieu 2003), Morocco (Babin & Destombes 1990), North America (Pojeta 1971), Portugal (Delgado 1908, Sharpe 1853, Sá 2008), Spain (Sharpe 1853; De Verneuil & Barrande 1856; Babin & Gutiérrez-Marco 1985, 1991; Gutiérrez-Marco & Babin 1999), Sweden (Soot-Ryen 1969) and Wales and the Welsh Borderland of England (Cope 1996, 1999).

Systematic palaeontology

Abbreviations. – V – valve; L – length of the shell; H – height of the shell; W – width of the shell; W/2 – width of one valve (Kříž 1969). JK, CW, PO – specimens deposited in the Czech Geological Survey, Prague; MBHR – specimens deposited in the Museum of Dr. Bohuslav Horák, Rokycany; NM – specimens deposited in the National Museum, Prague; LPB – specimens deposited in the University of Western Brittany, Brest; VPA – specimens deposited in the Complutense University, Madrid; MGM – specimens deposited in Museo Geominero, Madrid; USNM – specimens deposited in the Smithsonian Institution, Washington D.C., latex cast deposited in Czech Geological Survey, Prague. All measurements are in millimetres. The new classification used by Carter *et al.* (2011) is adopted here.

Class Bivalvia Linné, 1758
Subclass Protobranchia Pelseneer, 1889
Superorder Nuculiformii Gray, 1824
Order Nuculoida Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Praenuculidae McAlester, 1969

Genus *Praenucula* Pfab, 1934

Type species. – *Praenucula dispar* (Barrande, 1881), Bohemia, Prague Basin, Osek, Middle Ordovician, early and mid Darriwilian, Šárka Formation.

Discussion. – A lot of discussion was published about *Praenucula* and its similarity with *Praeleda* Pfab, 1934 and *Deceptrix* Fuchs, 1919 (Bradshaw 1970; Pojeta 1978; Tunnicliff 1982; Babin & Gutiérrez-Marco 1991; Cope 1997, 1999; Babin & Beaulieu 2003; Kříž & Steinová 2009). McAlester (1968) decided that *Deceptrix* is senior synonym of *Praeleda*. Cope (1997) considered genus *Deceptrix* as valid, but probably does not occur in the Ordovician at all, but it is a genus characteristic for the Devonian. Tunnicliff (1982) described the main features of *Deceptrix* (in his concept synonymous with *Praeleda*) and *Praenucula*: 1) the posterior teeth in *Deceptrix* are smaller and more numerous than anterior teeth while in *Praenucula* the posterior and anterior teeth are similar in the size and number; 2) umbos in *Praenucula* lie in the posterior half while in *Deceptrix* generally lie in anterior half; 3) in *Deceptrix* the adductor muscle scars are larger and in more ventral position, in *Praenucula* they are close to dorsal margin. Another important but also a somewhat problematic feature was added by Cope (1999), in *Praeleda* between anterior and posterior hinge ranges is commonly (although not always) discordance, which is observed under the umbo. Because of this feature Cope (1997, 1999) grouped *Praeleda* into the family Cardiolariidae. But because of this problematic character, the determination of *Praeleda* to the family Cardiolariidae is uncertain. Cope (1997) proposed also other genus *Homilodonta* with crowded row of gradidentate teeth

on the whole hinge plate. *Arca subtruncata* Portlock, 1843 was designated as type species. Tunnicliff (1982, pl. 9, figs 1–7, 9–11) had earlier revised this species under the name *Deceptrix subtruncata*. Kříž & Steinová (2009) preferred assignation of *Praeleda* to the Praenuculidae and this opinion is followed here. Bradshaw (1970) was also of the opinion that hinge of *Praeleda* is very often similar to hinge of *Praenucula* and it is difficult to distinguish between these genera. Furthermore *Praeleda compar*, the type species of *Praeleda* (Zahořany Formation, Sandbian, Late Ordovician), shows the same hinge as *Praenucula* (there is no discordance under the umbo) and the same size of the teeth in the anterior and posterior part. Also Pfab (1934, in schema on p. 27) described the shape of the shell and shape of adductors muscle scars of both genera and showed their similarity in these features. Therefore it seems that these two genera could be congeneric. The preservation mainly in the Late Ordovician is not ideal and for the type specimens a mixture of internal, external and composite moulds was used. On the other hand *Praeleda pulchra* Pfab, 1934 from the Zahořany Formation shows obvious discordance between hinge ranges exactly according the definition of Cope (1999). I conclude that the revision of all Ordovician species from Bohemia, which belong to *Praeleda* or to *Praenucula* is necessary. The species from the Šárka Formation are assigned to *Praenucula*, but some specimens show an indication of disruption between the hinge ranges.

Praenucula dispar (Barrande, 1881)

Figures 2A–M, 5A

- 1881 *Nucula dispar* Barr.; Barrande, pl. 273, figs VII/1–8, 13–16.
- 1934 *Praenucula dispar dispar* (n. var.); Pfab, pp. 235, 236, pl. 1, fig. 3c.
- 1934 *Praenucula dispar expansa* (n. var.); Pfab, p. 235, pl. 1, fig. 3d, pl. 3, figs 10, 11, 15 a, b.
- 1968 *Praenucula expansa* Pfab. – McAlester, pp. 46, 47, pl. 8, figs 3–9.
- 2009 *Praenucula dispar* Barr. – Kříž & Steinová, pp. 412–414, fig. 3C, D, I, J.

Lectotype. – (SD, Pfab 1934) Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 273, as figs VII/1–4, NM L 27176.

Paralectotypes. – Internal moulds of the shells with conjoined valves, figured by Barrande (1881) on pl. 273, as figs VII/ 5–7 and VII/8, NM L 27177 and NM L 27178.

Type locality. – Bohemia, Prague Basin, Osek near Rokycany.

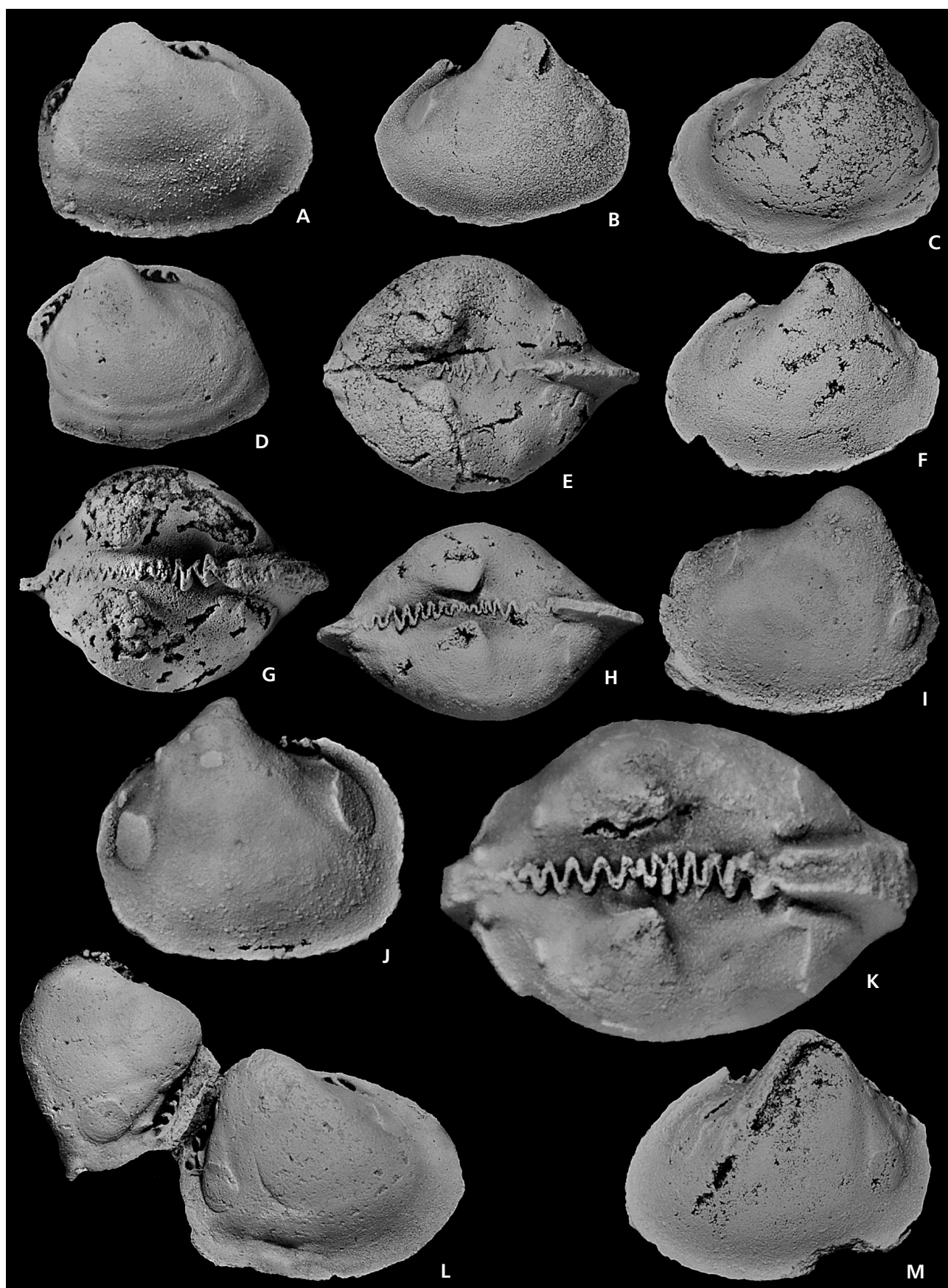
Type horizon. – Middle Ordovician, early and mid Darriwilian, Šárka Formation.

Material. – 162 specimens.

Diagnosis. – *Praenucula* with slightly elongated anterior part of the shell, with convexodont teeth in the posterior part, posterior adductor muscle scar placed more ventrally than anterior adductor muscle scar, three pairs of rounded accessory muscle scars in the posterior part of the umbo region.

Description. – Shell small, equivalve, inequilateral, and broadly ovate. Anterior part of the shell is larger than the posterior part. Anterior and posterior margins evenly rounded, ventral margin convex. Umbos located in the posterior half of the shell, prosogyrate. Hinge taxodont, teeth row continuous in the umbonal region (Figs 2G, H, K, 5A). Posterior part of the hinge with the convexodont teeth (the dentition comprises a varying number of teeth according to the size of the shell). In umbonal part the teeth are becoming smaller and toward the anterior slightly larger and convexodont (Fig. 11E). Anterior and posterior adductor muscle scars rounded (Fig. 2A, B, J), postero-dorsally from the anterior adductor muscle scar is a rounded pedal muscle scar (protractor) that joins the anterior adductor muscle scar (Fig. 2E, K). Dorsally from the posterior adductor muscle scar are one pair of rounded pedal muscle scars (retractor), separated from adductor muscle scar (Fig. 2J, K). Posterior adductor muscle scar placed more ventrally than anterior adductor muscle scar. Posteriorly from the umbo (but still in the umbonal region) three pairs of rounded

Figure 2. A–M – *Praenucula dispar* (Barrande, 1881). • A – right valve, MBHR 12944, right lateral view, anterior and posterior adductor muscle scars, × 6.1; B – articulated specimen, MBHR 14196, left lateral view, anterior and posterior adductor muscle scars, × 6.4. • C, E – articulated specimen, MBHR 7982; C – left lateral view, × 6.1; E – dorsal view, × 7.1. • D – right valve, MBHR 13559, right dorsolateral view, × 5.3. • F, H – articulated specimen, MBHR 14646; F – left lateral view, × 6.0; H – dorsal view, × 8.2. • G – articulated specimen, NM L 27178, dorsal view, × 6.9. • I – left valve, MBHR 12735, left lateral view, × 7.9. • J, K – articulated specimen, NM L 27176, lectotype; J – right lateral view with adductor and accessory muscle scars in the umbo region, × 10.5; K – dorsal view with pedal muscle scars, × 16.4. • L – two valves, MBHR 21027, lateral view, × 7.3. • M – articulated specimen, MBHR 13148, left lateral view, × 7.9. A – Prague Basin, Bohemia, Rokycany locality, early and middle Darriwilian; B – Prague Basin, Bohemia, Rokycany 17 locality, early and middle Darriwilian; C, D – Prague Basin, Bohemia, Osek 1 locality, early and middle Darriwilian; E – Prague Basin, Bohemia, Mýto 1 locality, early and middle Darriwilian; F, G, H – Prague Basin, Bohemia, Osek locality, early and middle Darriwilian; I – Prague Basin, Bohemia, Díly 4 locality, early and middle Darriwilian; L – Prague Basin, Bohemia, Rokycany 2 locality, early and middle Darriwilian; M – Prague Basin, Bohemia, Díly 1 locality, early and middle Darriwilian.



accessory muscle scars are impressed (Fig. 2J). Inner surface sculpture is smooth. The shell thickness is 0.5 mm.

Dimensions. –

Specimen	V	L	H	W/2
NM L 27176	A	5.1	4.4	1.7
NM L 27177	A	8.5	3.2	2.5
MBHR 2384a	A	9.6	7.9	2.6
MBHR 14586	A	8.8	5.9	2.9
MBHR 18914	L	8.2	7.0	3.1
NM L 27178	A	8.1	–	3.1
MBHR 13559	R	8.0	5.6	–
MBHR 7982	A	7.8	6.8	2.8
MBHR 12944	R	7.8	5.2	–
MBHR 2384b	A	7.3	5.5	2.5
MBHR 21027	R	7.1	6.1	–
MBHR 2384c	A	7.1	5.6	2.5
MBHR 14196	A	7.0	5.3	2.2
MBHR 14646	A	7.0	5.2	2.0
MBHR 13148	A	6.9	5.5	2.0
MBHR 12735	A	6.9	5.2	2.1
MBHR 17763	L	6.9	5.0	–
MBHR 20564	R	6.8	5.1	–
MBHR 2384 d	A	6.6	5.1	1.9
MBHR 13579	R	6.5	5.1	–
MBHR 13447	A	6.5	5.0	–
MBHR 15294b	A	6.1	5.1	2.2
MBHR 9041	A	6.1	5.1	2.0
MBHR 13121	L	6.1	5.1	–
MBHR 2384d	A	6.1	5.0	1.8
MBHR 20348	A	6.1	4.9	1.9
MBHR 20385	A	6.1	4.8	1.5
MBHR 20365	A	6.1	4.1	1.7
MBHR 20349	A	6.0	5.1	2.0
MBHR 14664	R	6.0	4.7	–
MBHR 20364	A	6.0	4.5	1.7
MBHR 20366	A	5.9	5.0	1.9
MBHR 2384f	A	5.8	4.9	1.5
MBHR 20386	A	5.5	4.8	1.7
MBHR 17776a	R	5.5	3.9	–
MBHR 2384g	A	5.5	4.1	1.7
MBHR 15294a	A	5.2	4.0	1.5
MBHR 20341	A	5.1	4.0	1.0
MBHR 13143	R	5.0	4.0	–
MBHR 2384h	A	5.0	3.8	1.5
MBHR 20387	A	4.9	3.9	1.5
MBHR 14694	R	4.9	–	0.9
MBHR 19154	R	4.8	3.9	–
MBHR 17798	A	4.8	3.8	1.5
MBHR 14204	R	4.7	3.9	–
MBHR 4624	L	4.5	3.8	–
MBHR 24050	A	4.5	3.1	0.8
MBHR 14360	R	4.1	3.5	1.9
MBHR 18846	R	4.1	2.9	–

MBHR 2384i	A	4.0	3.1	1.0
MBHR 20347	A	4.0	3.0	1.2
MBHR 15277	L	4.0	3.0	–
MBHR 13145	R	4.0	2.9	–
MBHR 14847	R	3.8	2.9	–
MBHR 55903	L	3.8	–	–
MBHR 20391	A	3.6	2.9	1.0
MBHR 19481	R	3.6	2.5	–
MBHR 14298	L	3.5	2.9	–
MBHR 14297	R	3.5	2.9	–
MBHR 14842	R	3.5	2.5	–
MBHR 20364	A	3.4	2.0	0.7
MBHR 18784b	R	3.3	2.9	–
MBHR 20388	A	3.2	2.0	0.7
MBHR 18784a	L	3.1	2.8	–
MBHR 1776	L	3.1	2.0	–
MBHR 2420	R	2.9	2.8	–
MBHR 14368	A	2.9	2.0	–
MBHR 20351	A	2.8	2.0	0.9
MBHR 19495	A	2.6	2.0	–
MBHR 20389	A	2.0	1.3	0.6

Discussion. – *P. dispar* differs from *P. bohemica* in convexodont teeth in the posterior part and in position of posterior adductor muscle scar, which is in *P. bohemica* close to the dorsal margin of the shell. *P. dispar* differs from *P. applanans* in the shape of the shell, in the more posterior position of the umbo, in convexodont teeth in the posterior part and in the position of the posterior adductor muscle scar, which is in *P. applanans* close to the dorsal margin. The comparison with the other species of *Praenucula* is in Kříž & Steinová (2009).

Occurrence. – Bohemia, Prague Basin, early and mid Darriwilian: Díly, Drahouš, Malé Přílepy, Mýto, Osek, Rokycany, Šárka brickyard, Šárka field, Těškov.

***Praenucula bohemica* (Barrande, 1881)**

Figures 3A–S, 5B

1881 *Leda bohemica* Barr.; Barrande, pl. 269, figs I/1–4, VII/1, 2.

1934 *Ctenodonta bohemica* Barr. – Pfab, p. 223, pl. 2 (3), figs 4–6.

Lectotype. – (SD, Pfab 1934) Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 269, as figs I/1–4, NM L 27114.

Type locality. – Bohemia, Prague Basin, Osek near Rokycany.

Type horizon. – Middle Ordovician, early and mid Darriwilian, Šárka Formation.

Material. – 182 specimens.

Diagnosis. – *Praenucula* with almost orthomorphodont or slightly concavodont teeth in posterior part, with ovate anterior adductor muscle scar placed more ventrally than posterior adductor muscle scar and with straight posterior margin.

Description. – Shell small, equivalve, inequilateral, and broadly ovate. Anterior margin is longitudinally elongated and posterior margin is straight, ventral margin slightly convex. Posterior part of the shell is shorter than anterior part. Umbos located in the posterior half of the shell, close to the middle of the shell, prosogyrate. Hinge taxodont, teeth row continuous in the umbonal region (Figs 3B, C, M, 5B). Posterior part of the hinge with almost orthomorphodont teeth, or slightly concavodont (Fig. 3E, F). Anterior part of the hinge with convexodont teeth (Fig. 3S). Posterior adductor muscle scar slightly elliptic, smaller than anterior adductor muscle scar (Fig. 3L). Anterior adductor muscle scar is ovate, posterior part of the anterior muscle scar is prominently narrower (Fig. 3L, M). Anterior adductor muscle scar placed more ventrally than posterior adductor muscle scar. Antero-dorsally from the posterior adductor muscle scars is separated pedal muscle scar (retractor) (Fig. 3M). Anterior pedal muscle scar joined with anterior adductor muscle scar (Fig. 3M). Inner surface sculpture is smooth.

Dimensions. –

Specimen	V	L	H	W/2
MBHR 2377	L	11.8	9.0	2.5
MBHR 2443	A	11.1	6.9	–
MBHR 2380	A	10.1	7.9	3.0
LPB 562 (France)	L	10.0	8.1	–
MBHR 14765	L	9.8	7.1	–
CW 1	R	9.7	8.7	2.5
MBHR 12584	L	9.5	7.2	–
MBHR 7911	L	9.0	6.6	2.2
MBHR 20457	A	8.9	7.0	2.8
MBHR 14694	L	8.5	7.0	–
MBHR 14768	A	8.2	6.0	2.2
MBHR 14841	L	8.0	5.9	–
MBHR 4724	R	8.0	5.5	1.5
MBHR 14692	R	7.5	5.5	–
NM L 27114	A	7.2	6.2	2.3
MBHR 20346	A	7.1	6.0	2.0
MBHR 14467	A	7.1	5.1	2.0
MBHR 7580a	A	6.8	5.0	1.7
MBHR 12417	A	6.6	–	2.0
MBHR 7580b	A	6.0	5.0	1.8
MBHR 14448	A	5.9	4.5	1.7
MBHR 20458	A	5.8	4.0	1.7
MBHR 20390	A	5.8	3.5	1.7
MBHR 7580c	A	5.2	3.8	1.8

MBHR 7580d	A	4.1	3.4	1.1
MBHR 2384j	A	3.3	3.0	0.9

Discussion. – Pfab (1934) mentioned that *Praealeda compar* (originally described from the Zahořany Formation, Sandbian) occurs also in the Šárka Formation. Because *Praealeda compar* and *Praenucula bohemica* are very similar, it is very difficult to recognise them well, but in my opinion *Praealeda compar* does not occur in the Šárka Formation. *P. bohemica* is very similar, if not conspecific with *P. costae* (Fig. 3O–Q) from the Middle Ordovician of France, Portugal and Spain. Nevertheless for now it is preferred to keep these two species, because *P. costae* always shows the pedal muscle scar half way along the posterior hinge plate, which is not preserved in *P. bohemica*. *P. costae* possesses convexo-concave and concave teeth in the posterior part of the hinge, in *P. bohemica* they are rather orthomorphodont. This *Praenucula*-like morphology was really frequent in the Middle and Late Ordovician bivalves. *P. bohemica* differs from *P. dispar* in the hinge (*P. bohemica* has in the posterior part almost orthomorphodont or slightly concavodont teeth) and in the position of adductor muscle scars (in *P. dispar* the posterior adductor muscle scar is placed more ventrally than the anterior adductor muscle scar). *P. applanans* differs from *P. bohemica* in the more centrally placed umbo and in larger posterior part of the shell. The shell of *P. applanans* is generally larger. The shorter form of *P. mayennense* Babin & Beau-lieu, 2003 from the Middle Ordovician of the Armorican Massif, France seems to be very similar with *P. bohemica*, it differs mainly in the more rounded anterior part of the shell and stronger anterior teeth. *P. dispersa* Tunnicliff, 1982 from the Bardahessiagh Formation, Late Ordovician of Ireland has convexodont teeth in the posterior part and smaller rounded adductor muscle scars. *P. infirma* Tunnicliff, 1982 from the Killey Bridge Formation, Late Ordovician of Ireland shows rounded anterior part of the shell, convexodont teeth in the posterior part and the smaller rounded adductor muscle scars. *P. praetermissa* Tunnicliff, 1982 from the Killey Bridge Formation, Late Ordovician of Ireland has convexodont teeth in posterior part and umbo in more central position.

Occurrence. – Bohemia, Prague Basin, Darriwilian: Čtyřdomky, Díly, Drahouš, Mýto, Osek, Rokycany, Šárka field, Úvaly, Malé Přílepy, Kařízek, Sandbian: Drabov, Trubín, Trubsko, Katian: Prague-Strašnice, Prague-Michle, Loděnice.

***Praenucula applanans* (Barrande, 1881)**

Figures 4A–R, 5C

1881 *Nucula applanans* Barr. – Barrande, pl. 272, figs III/1–12.

1934 *Ctenodonta applanans* Barr. – Pfab, p. 222, pl. 2 (3),
figs 1–3.

1991 *Praenucula sharpei* Babin & Gutiérrez-Marco; Babin
& Gutiérrez-Marco, pp. 115, 116, pl. 2, figs 1–6.

Lectotype. – (SD, Pfab 1934.) Internal mould of the shell
with conjoined valves, figured by Barrande (1881) on
pl. 272, as figs III/5–8, NM L 27163.

Paralectotypes. – Internal moulds of the shells with con-
joined valves, figured by Barrande (1881) on pl. 272, as
figs III/ 1–4 and III/9–12, NM L 27161 and NM L 27162.

Type locality. – Bohemia, Prague Basin, Osek near Roky-
cany.

Type horizon. – Middle Ordovician, early and mid Darriwil-
ian, Šárka Formation.

Material. – 172 specimens.

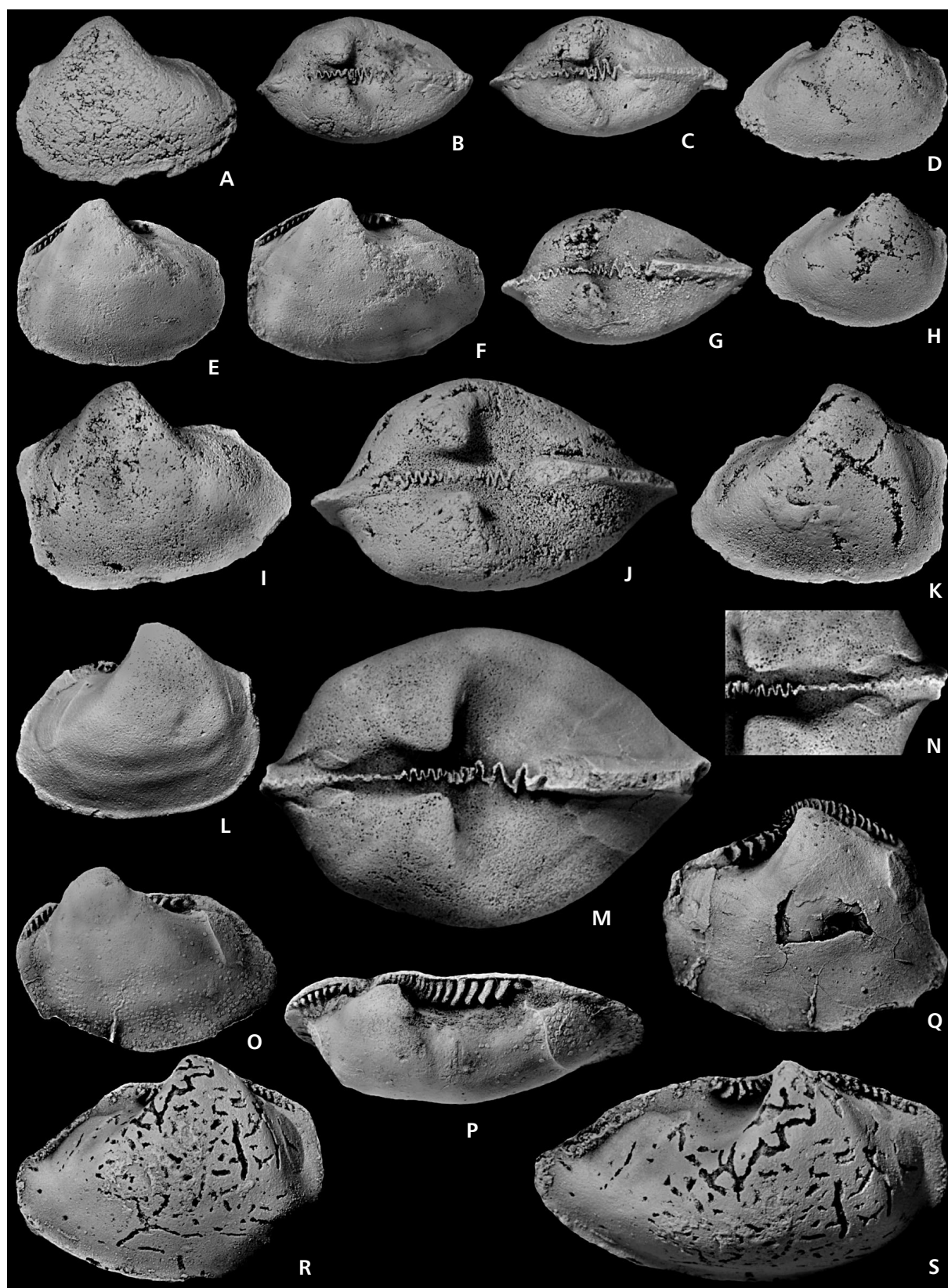
Diagnosis. – *Praenucula* with slightly larger posterior part
of the shell, umbo almost in the middle of the shell, slightly
prosogyrate, orthomorphodont teeth in the posterior part.

Description. – Shell small, equivalve, slightly inequilate-
ral, and broadly ovate. Posterior part of the shell is slightly
larger than the anterior part. Anterior part is elongated, po-
sterior part rounded. Ventral margin convex. The umbos
located slightly in the posterior part, more often in the mid-
dle of the shell, slightly prosogyrate. Hinge taxodont, con-
tinuous in the umbonal region (Figs 4B, K, 5C). Convexo-
dont teeth in the anterior part slightly larger, posterior teeth
orthomorphodont or slightly concavodont (Fig. 4B, K, P).
Anterior adductor muscle scar is elliptic, posterior part of
the anterior adductor muscle scar narrower. Anterior pedal
muscle scar is joined with adductor muscle scar (Fig. 4B, K).
Posterior adductor muscle scar slightly elongated, one po-
sterior pedal muscle scar is developed antero-dorsally from
the posterior adductor muscle scar (Fig. 4K). Three pairs of
rounded accessory muscle scars in the umbo region
(Fig. 3K). Inner surface sculpture is smooth.

Dimensions. –

Specimen	V	L	H	W/2
VPA 2144/OR (Spain)	A	14.8	11.0	–
MBHR 2350	R	13.9	8.0	–
MBHR 4624	R	12.2	7.9	2.5
MBHR 14852	A	11.5	7.6	2.5
NM L27163	A	11.0	6.9	2.1
MBHR 2384k	A	7.1	10.7	2.5
MBHR 15529	R	10.5	7.1	–
MBHR 14233	L	10.1	7.5	1.9
MBHR 2381	A	10.1	7.5	1.5
MBHR 2395	A	10.0	8.0	3.0
MBHR 2373	L	10.0	7.5	2.0
MBHR 2384l	A	10.0	6.8	2.4
MBHR 14663	L	10.0	6.8	–
MBHR 18858	A	10.0	–	2.0
MBHR 12570	L	9.8	6.5	–
MBHR 7585	A	9.5	7.0	4.9
MBHR 14619	A	9.4	6.6	2.5
MBHR 20406	A	9.3	5.5	3.8
MBHR 2395b	L	9.2	6.5	3.2
MBHR 4591	R	9.2	6.5	2.5
NM L27161	L	9.1	6.5	–
MBHR 50268	R	9.0	7.1	–
MBHR 21066	R	9.0	6.8	–
MBHR 15289	L	8.9	–	–
MBHR 24030	A	8.8	6.0	2.1
NM L27162	A	8.6	6.0	1.8
MBHR 14843	A	8.1	5.5	–
MBHR 20383	A	8.0	5.8	1.8
MBHR 2384m	A	8.0	5.4	1.5
MBHR 14607	A	7.9	6.0	2.0
MBHR 21040	A	7.9	5.1	1.7
MBHR 19027	A	7.2	4.3	1.0
MBHR 2384n	A	7.2	4.5	1.9
MBHR 13453	L	7.1	5.5	–
MBHR 4600	R	7.0	6.0	2.3
MBHR 13370	R	6.9	4.9	–
MBHR 2384o	A	6.5	5.0	1.4
MBHR 21191	R	6.5	5.0	–
MBHR 55831	R	6.2	4.9	–
MBHR 20451	A	6.1	4.5	1.2

Figure 3. A–N, R, S – *Praenucula bohémica* (Barrande, 1881). • A, B – articulated specimen, MBHR 14448; A – right lateral view, × 6.6; B – dorsal view, × 6.4. • C, D – articulated specimen, MBHR 20390; C – dorsal view, × 7.2; D – left lateral view with adductor muscle scars, × 6.5. • E, F – articulated specimen, CW 1; E – right lateral view, × 3.8; F – right dorsolateral view with orthomorphodont dentition in the posterior part, × 4.3. • G, H – articulated specimen, MBHR 7580c; G – dorsal view, × 8.6; H – left lateral view, × 6.3. • I–K – articulated specimen, NM L 27114, lectotype; I – right lateral view, × 6.5; J – dorsal view, × 9.0; K – left lateral view, × 6.1. • L–N – articulated specimen, MBHR 20457; L – left lateral view with adductor muscle scars, × 4.8; M – dorsal view with pedal muscle scars, × 8.8; N – detail of pedal muscle scars in the posterior part (retractors), × 9.2. • R, S – left valve, MBHR 2377; R – left lateral view, × 4.5; S – left dorsolateral view, × 6.1. • O–Q – *Praenucula costae* (Sharpe, 1853); O, P – right valve, MGM642–O; O – right lateral view, × 2.4; P – dorsal view, × 3.3; Q – left valve, LPB 562, left dorsolateral view, × 4.9. A, B – Prague Basin, Bohemia, Dřívý 1 locality, early and middle Darriwilian; C, D – Prague Basin, Bohemia, Dřívý 3 locality, early and middle Darriwilian; E–H – Prague Basin, Bohemia, Osek 1 locality, early and middle Darriwilian; I–K – Prague Basin, Bohemia, Osek locality, early and middle Darriwilian; L, N, R, S – Prague Basin, Bohemia, Rokycany locality, early and middle Darriwilian; O, P – Spain, Calzada-Viso del Marques locality, Darriwilian; Q – France, Morgat locality, late Darriwilian.



MBHR 17771	A	6.0	4.5	2.6
MBHR 17996	R	5.9	4.5	–
MBHR 20372	A	5.1	4.0	1.0

Discussion. – *P. applanans* differs from *P. dispar* in the larger posterior part of the shell, its umbo in the central position, concavodont teeth in the anterior part of the shell and in the elliptical adductor muscle scar. *P. applanans* differs from *P. bohémica* in the larger posterior part of the shell and in the umbo in central position. The shorter form of *Praenucula mayennense* Babin & Beaulieu, 2003 from the Middle Ordovician of the Armorican Massif, France differs in its more posteriorly placed umbo and stronger and larger anterior teeth. *P. dispersa* Tunnicliff, 1982 from the Bardahessiagh Formation, Late Ordovician of Ireland shows convexodont teeth in the posterior part and smaller, rounded adductor muscle scars. *P. infirma* Tunnicliff, 1982 from the Killey Bridge Formation, Late Ordovician of Ireland differs in the rounded anterior part of the shell, convexodont teeth in the posterior part and smaller, rounded adductor muscle scars. *P. praetermissa* Tunnicliff, 1982 from the Killey Bridge Formation, Late Ordovician of Ireland has convexodont teeth in the posterior part.

Occurrence. – Bohemia, Prague Basin, Darriwilian: Díly, Drahouš, Cheznovice, Osek, Malé Přílepy, Pětidomky, Rokycany, Šárka field; Spain, Hesperian Massif, Darriwilian: Alia Navalpino, Navas de Estena-Retuerta, Ventas.

Genus *Concavodonta* Babin & Melou, 1972

Type species. – *Concavodonta ponderata* (Barrande, 1881), Bohemia, Prague Basin, Middle and Late Ordovician, Darriwilian, Sandbian, Katian, Šárka, Dobrotivá, Libeň, Letná, Vinice, Zahořany and Bohdalec formations.

Concavodonta ponderata (Barrande, 1881)

Figure 7A–F

1881 *Nucula ponderata* Barr.; Barrande, pl. 271, figs IV/1–4.

- 1934 *Ctenodonta ponderata* Barr. – Pfab, p. 224, pl. 2, fig. 7.
 1972 *Concavodonta ponderata* Barr. – Babin & Melou, pl. 7, figs 5–7.
 1973 *Ctenodonta? ponderata* Barr. – Babin & Robardet, pl. 1, figs 1–6.

Holotype. – Internal mould of the shell with conjoined valves, figured by Barrande on pl. 271 as figs IV/1–4, NM L 22682.

Type locality. – Bohemia, Prague Basin, Loděnice.

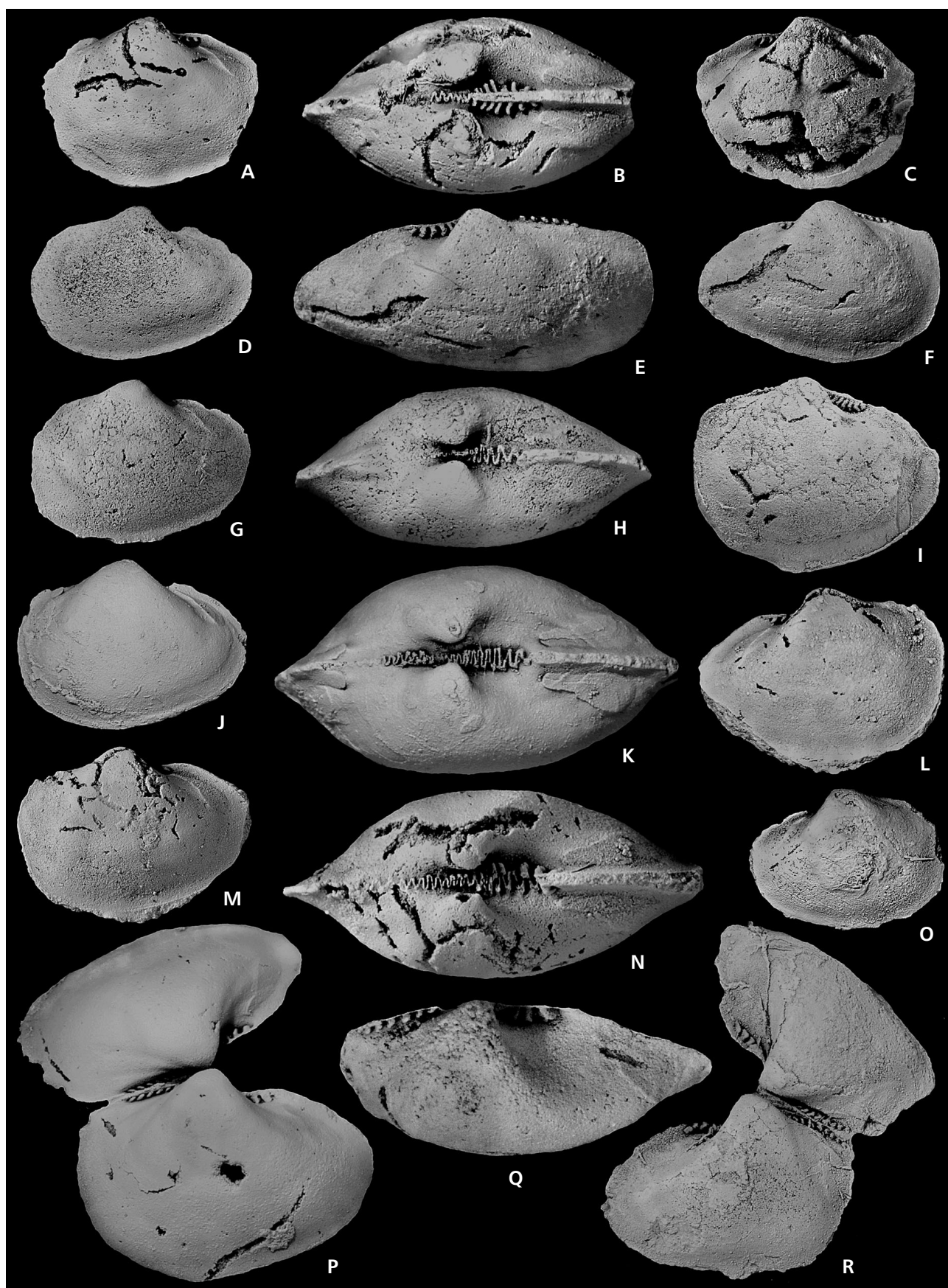
Type horizon. – Late Ordovician, early Katian, Zahořany Formation.

Material. – Two left valves, two right valves, one articulated specimen.

Diagnosis. – *Concavodonta* characterized by rounded outline, with rounded adductor muscle scars; anterior and posterior dorsal borders meet at an angle of 100°.

Description. – Shell small, equivalve, slightly inequilateral, and rounded. Anterior part of the shell is slightly smaller than the posterior part. Anterior and posterior dorsal borders meet at an angle of 100°. Ventral margin convex. The umbos located in the middle of the shell or very slightly in the anterior part, slightly prosogyrate. Hinge taxodont, continuous in the umbonal region. Concavodont teeth in the posterior, the most posterior teeth orthomorphodont, diconvexodont teeth in the anterior part slightly larger; under the umbo small orthomorphodont teeth (Fig. 7D, E). Anterior and posterior teeth increasing in size gradually from umbo towards distal hinge margins, but the most anterior and the most posterior teeth are again smaller. Anterior adductor muscle scar rounded, more deeply impressed than rounded posterior adductor muscle scar (Fig. 7D). Inner surface sculpture is smooth. Outer surface sculpture with commarginal rough lines (preserved in Late Ordovician *Concavodonta ponderata* from France, Babin & Melou 1972, pl. VI, fig. 7).

Figure 4. A–R – *Praenucula applanans* (Barrande, 1881). • A–C – articulated specimen, NM L 27161, paralectotype; A – right lateral view with anterior adductor muscle scar, $\times 4.0$; B – dorsal view, $\times 6.4$; C – left lateral view, $\times 4.1$. • D – articulated specimen, MBHR 14852, right lateral view, $\times 3.3$. • E, F – left valve, MBHR 12570, E – left dorsolateral view, $\times 6.5$; F – left lateral view, $\times 4.2$. • G, H, O – articulated specimen, NM L 27162, paralectotype; G – right lateral view, $\times 4.4$; H – dorsal view, $\times 7.3$; O – left lateral view, $\times 4.0$. • I – articulated specimen, VPA 2144/OR, right dorsolateral view, $\times 2.9$. • J, K – articulated specimen, MBHR 14619; J – right lateral view, $\times 3.5$; K – dorsal view with hinge and adductor and accessory muscle scars, $\times 6.1$. • L–N – articulated specimen, NM L 27163, lectotype; L – left lateral view, $\times 3.9$; M – right lateral view, $\times 3.7$; N – dorsal view, $\times 3$. • P – articulated specimen, opened shell, MBHR 2395, right lateral view with orthomorphodont teeth in the posterior part, $\times 5.3$. • Q – right valve, MBHR 4600, dorsal view, $\times 9.5$. • R – articulated specimen, opened shell, MBHR 2443, left lateral view, $\times 3.8$. A–C, G, H, O, L, M, Q – Prague Basin, Bohemia, Osek locality, early and middle Darriwilian; D, J, K, N – Prague Basin, Bohemia, Osek 1 locality, early and middle Darriwilian; E, F – Prague Basin, Bohemia, Rokycany 2 locality, early and middle Darriwilian; I – Spain, Ventas, early Darriwilian; P – Prague Basin, Bohemia, Rokycany locality, early and middle Darriwilian; R – Prague Basin, Bohemia, Drahouš 1 locality, early and middle Darriwilian.



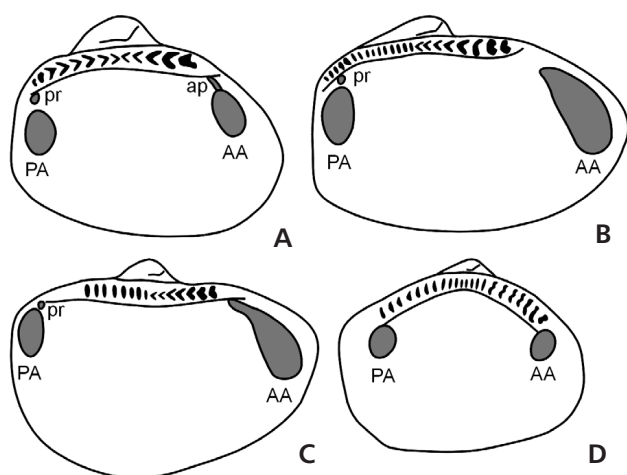


Figure 5. A – *Praenucula dispar* (Barrande, 1881), left lateral view showing hinge and muscle scars. • B – *Praenucula bohémica* (Barrande, 1881), left lateral view showing hinge and muscle scars. • C – *Praenucula applanans* (Barrande, 1881), left lateral view showing hinge and muscle scars. • D – *Concavodonta ponderata* (Barrande, 1881), left lateral view showing hinge and muscle scars. Key to letter symbols: AA – anterior adductor muscle scar; PA – posterior adductor muscle scar; ap – anterior protractor muscle scar; pr – posterior retractor muscle scar.

Dimensions. –

Specimen	V	L	H	W/2
NM L 42215	L	7.1	5.5	1.5
NM L 42216	L	7.9	6.8	1.2
NM L 42217	A	5.7	5.6	1.3

Discussion. – Barrande (1881) described *Concavodonta ponderata* from the Zahorany Formation (Katian, Late Ordovician) and Pfab (1934) found this species also in the Šárka Formation and assigned it to *Ctenodonta*. He noticed that the hinge is somewhat different. Babin & Melou (1972) designated *Ctenodonta ponderata* as the type species of their new genus *Concavodonta*. Sánchez (1999) included *C. ponderata* to the new subfamily Concavodontinae with the diagnosis: posterior teeth in chevron with concavities towards umbo (concavodont dentition); in anterior hinge, dentition is concavodont or convexodont. *C. ponderata* from Bohemia shows in the anterior part

diconvexodont teeth, which is different from the diagnosis of Concavodontinae (see below functional morphology in the Ordovician Protobranchia). *C. ovalis* Sánchez, 1999 from the Don Braulio Formation, Late Ordovician of Argentina differs from *C. ponderata* in its ovate outline and the ovate anterior adductor muscle scar. The shell borders meet with angle of 150° in *C. ovalis* and 100° in *C. ponderata*. *C. imbricata* (Portlock, 1843) from the Killy Bridge Formation, Late Ordovician of Ireland shows more ovate shell outline.

Occurrence. – Bohemia, Prague Basin, early and mid Darriwilian: Osek, Šárka field, Prague-Vokovice, Sandbian: Trubsko, Trubín, Vinice, Katian: Loděnice, Prague-Strašnice.

Infraclass Heteroconchia Hertwig, 1895

Cohort Cardiomorphi Férussac, 1822 (*in* Férussac & Audebard 1822) (= Heterodonta)

Order Actinodontida Dechaseaux, 1952

Superfamily Anodontopsoidea Miller, 1889

Family Cycloconchidae Ulrich, 1894 (*in* Ulrich & Scofield 1894)

Subfamily Cycloconchinae Ulrich, 1894 (*in* Ulrich & Scofield 1894)

Genus *Pseudocyrtodonta* Pfab, 1934

Type species. – *Pseudocyrtodonta ala* (Barrande, 1881), Bohemia, Prague Basin, Osek, Middle Ordovician, early and middle Darriwilian, Šárka Formation.

Pseudocyrtodonta ala (Barrande, 1881)

Figure 6A–C

1881 *Leda ala* Barr.; Barrande, pl. 273, figs II/1–3.

1881 *Syneke antiquus* Barr.; Barrande, pl. 275, figs I/1–2.

1968 *Pseudocyrtodonta ala* Barr. – McAlester, p. 48, pl. 29, figs 6–8.

2012 *Pseudocyrtodonta ala* Barr. – Steinová, p. 336, fig. 3.

Figure 6. A–C – *Pseudocyrtodonta ala* (Barrande, 1881). • A, B – articulated specimen, MBHR 2384a; A – left lateral view, $\times 4.8$; B – dorsal view, $\times 7.2$. • C – articulated specimen, MBHR 12701, right lateral view with part of the pseudolateral tooth, $\times 5.3$. • D–F – *Pseudocyrtodonta incola* (Barrande, 1881); D – left valve, MBHR 14442, left dorsolateral view with pseudolateral tooth in posterior part and pseudocardinal teeth in anterior, anterior adductor muscle scar with pedal muscle scar, $\times 10.4$; E – articulated specimen, MBHR 20353, dorsal view, $\times 10.1$; F – articulated specimen, MBHR 13415, right dorsolateral view, $\times 3.3$. • G–N – *Redonia deshayesi* (Rouault, 1851); G – left valve, NM L 22659, left lateral view, $\times 4.4$; H, N – articulated specimen, NM L 22656; H – dorsal view, $\times 5.8$; N – right lateral view, $\times 6.0$; I – right valve, LPB 796, neotype, right lateral view with posterior and anterior adductor muscle scars, $\times 3.2$; J – left valve, MGM643–O, left lateral view, part of the umbo was removed, $\times 5.0$; K – right valve, LPB 775, left lateral view without umbo with actinodont hinge, $\times 3.5$; L – right valve, L22660, right dorsolateral view, $\times 4.6$; M – right valve, NM L 22658, right dorsolateral view, $\times 6.0$. A, B – Prague Basin, Bohemia, Rokycany locality, early Darriwilian; C – Prague Basin, Bohemia, Osek 1 locality, early Darriwilian; D, E – Prague Basin, Bohemia, Díly 1 locality, early Darriwilian; F – Prague Basin, Bohemia, Díly 2 locality, early Darriwilian; G, H, L, M, N – Prague Basin, Bohemia, Osek locality, early Darriwilian; I – France, Armorican Massif, Morgat-môle locality, late Darriwilian; J – Spain, Alia Navalpino locality, Darriwilian; K – France, Morgat locality, early Darriwilian.



Remarks. – This species has been recently revised and described by Steinová (= Polechová) (2012).

***Pseudocyrtodonta incola* (Barrande, 1881)**

Figure 6D–F

1881 *Leda incola* Barr.; Barrande, pl. 270, figs III/1–4.

1934 *Pseudocyrtodonta ala* Barr. – Pfab, p. 237, pl. 3 (4), fig. 13.

2012 *Pseudocyrtodonta incola* Barr. – Steinová, p. 338, fig. 4.

Remarks. – This species has been recently revised and described by Steinová (= Polechová) (2012).

Genus *Tatula* gen. nov.

Type species. – *Tatula petula* gen. et sp. nov., Bohemia, Prague Basin, locality Šárka, Middle Ordovician, early and mid Darriwilian, Šárka Formation, by monotypy.

Derivation of name. – Derived from Latin *tatula*, masculine diminutive from *tata* = daddy (my daddy = tatínek in Czech).

Diagnosis. – Small cycloconchid with numerous pseudolateral and pseudocardinal teeth, the most dorsally placed pseudolateral tooth is short, the other pseudolateral teeth are longer, pseudocardinal teeth in the anterior part are elongated with almost the same size.

Discussion. – Steinová (2012) discussed actinodonts from the Šárka Formation (*Pseudocyrtodonta* and *Redonia*). The specimens of *Tatula petula* gen. et sp. nov. were found recently by the author in the collection of František Hanuš deposited in the National Museum, Prague and therefore this genus could not be mentioned by Steinová (2012). *Tatula* gen. nov. has very similar hinge to *Actinodonta* Phillips, 1848 from the Silurian, the difference is in pseudocardinal teeth, which are in *Tatula* almost the same size, in *Actinodonta* anteriorly placed pseudocardinals are longer. In *Tatula* the most dorsally placed pseudolateral tooth is

short. *Tatula* gen. nov. also shows some affinities to *Carminodonta* Cope, 1996 from the Floian (early Arenig) of Wales and to *Ananterodonta* Babin & Gutiérrez-Marco, 1985 from the Darriwilian (Llanvirn) of Spain. *Carminodonta* could be an ancestor for *Tatula* and *Ananterodonta*. All these genera have actinodont hinge with numerous pseudocardinal and pseudolateral teeth (Fig. 8A–C), which differs markedly from the other cycloconchids with simple type of actinodont hinge (Fig. 8D, E) like *Pseudocyrtodonta* (Fig. 8D) from the Middle and Late Ordovician of Bohemia and *Fasciculodonta* (Fig. 8E) from the Middle Ordovician (Dapingian–Darriwilian) of China.

Species included. – *Tatula petula* gen. et sp. nov., early and mid Darriwilian, Prague Basin, Šárka.

***Tatula petula* sp. nov.**

Figures 7G–L, 8A, 9

Holotype. – Internal mould of opened shell figured on Fig. 7G–I, K, L, NM L 41038.

Paratype. – Internal mould of opened shell figured on Fig. 7J, NM L 42218.

Derivation of name. – In honour of my father, Petr = Peřula (family nick-name), who brought me up and who supported me in my hobby and occupation – palaeontology.

Type locality. – Bohemia, Prague Basin, Šárka.

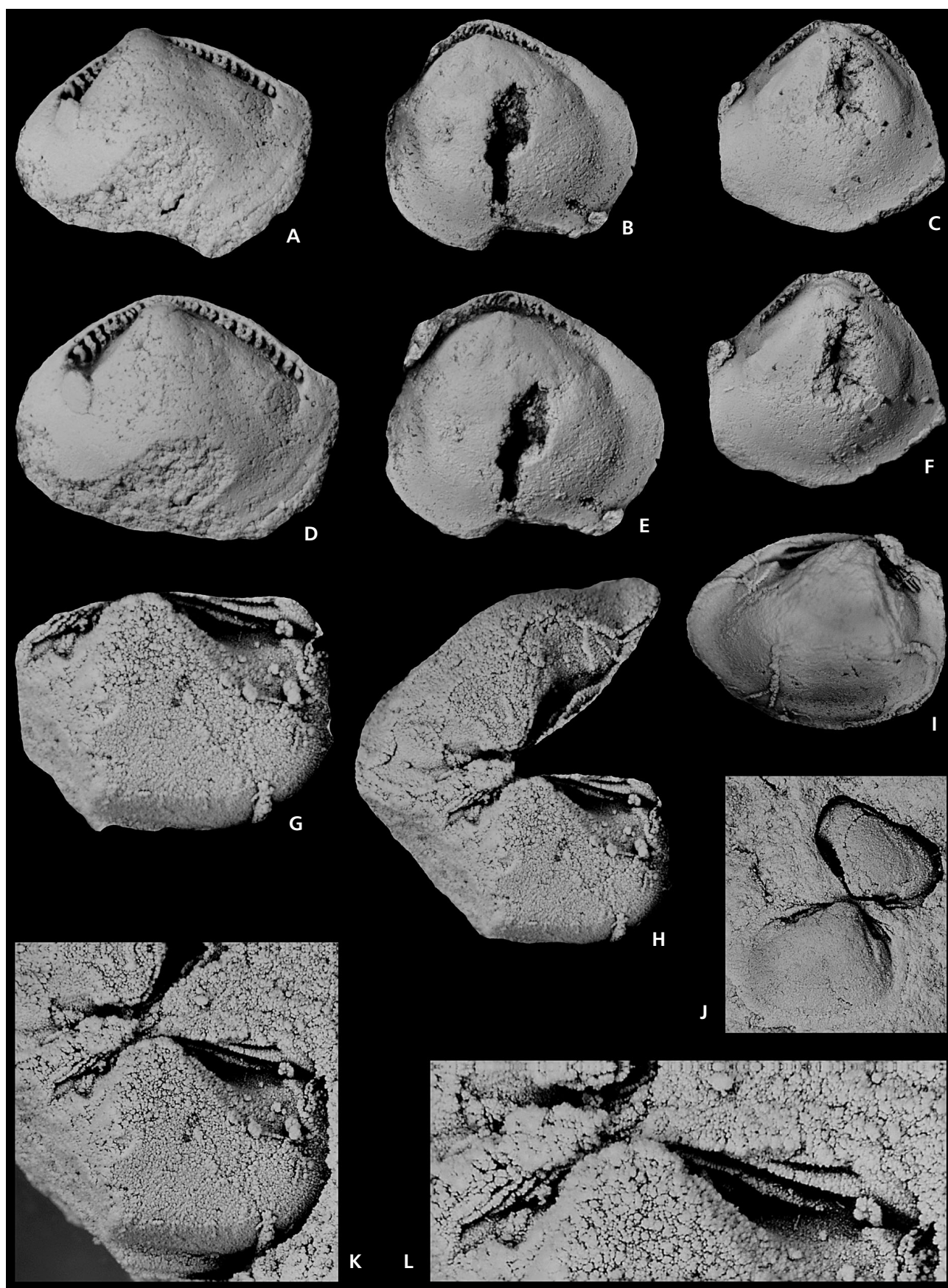
Type horizon. – Middle Ordovician, early and mid Darriwilian, Šárka Formation.

Material. – Two opened shells.

Diagnosis. – As for the genus.

Description. – Shell small, equivalve, slightly inequilateral, and broadly ovate. Posterior part is elongated, anterior part rounded. Ventral margin convex. Anterior part of the shell smaller than the posterior part. The umbos located in the anterior part, prosogyrate. Hinge actinodont, in the posterior part

Figure 7. A–F – *Concavodonta ponderata* (Barrande, 1881). • A, D – left valve, NM L 42215; A – left lateral view, $\times 10.2$; D – left dorsolateral view, $\times 11.2$. • B, E – left valve, NM L 42216; B – left lateral view, $\times 5.9$; E – left dorsolateral view, $\times 6.5$. • C, F – right valve, NM L 42217; C – right lateral view, $\times 9.4$; F – right dorsolateral view, $\times 8.1$. • G–L – *Tatula petula* gen. et sp. nov. G, H, I, K, L – holotype, two valves, opened shell, NM L 41038; G – left valve, left dorsolateral view with actinodont hinge, $\times 13.5$; H – two valves, dorsal view with actinodont hinge, $\times 11$; I – right valve with actinodont hinge and adductor muscle scars, $\times 11.2$; K – left lateral view with actinodont hinge, $\times 12.8$; L – detail of the actinodont hinge, pseudolateral teeth in the anterior part and pseudocardinal teeth in the posterior part, $\times 24$. • J – paratype, two valves, opened shell, NM L 42218, lateral view on the two valves, $\times 14.5$. A, D – Prague Basin, Bohemia, Osek locality, early and middle Darriwilian; B, C, E, F – Prague Basin, Bohemia, Šárka field locality, early and middle Darriwilian; G–L – Prague Basin, Bohemia, Šárka locality, early and middle Darriwilian.



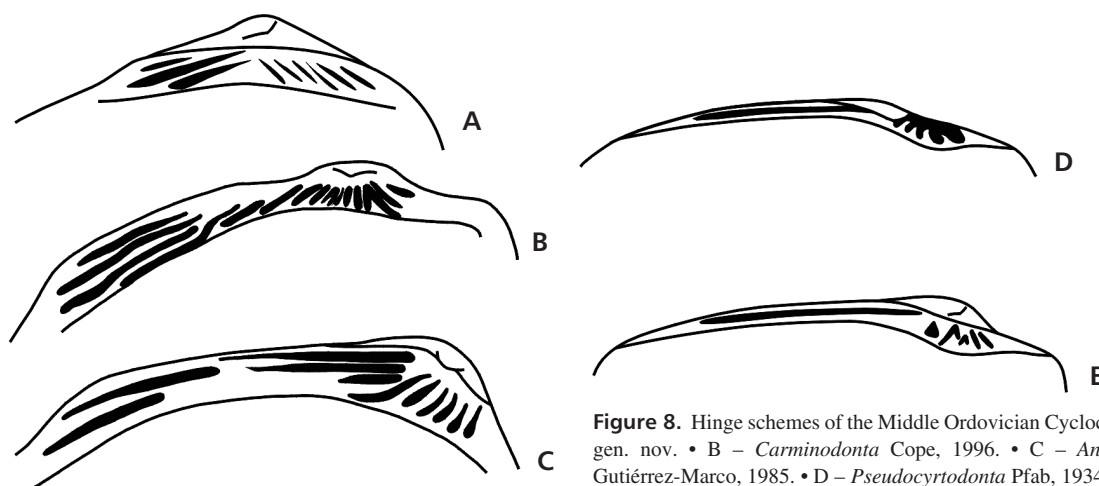


Figure 8. Hinge schemes of the Middle Ordovician Cycloconchidae. • A – *Tatula* gen. nov. • B – *Carminodonta* Cope, 1996. • C – *Ananterodonta* Babin & Gutiérrez-Marco, 1985. • D – *Pseudocyrtodonta* Pfab, 1934. • E – *Fasciculodonta* Fang & Cope, 2004.

three straight, slender pseudolateral teeth (Fig. 7L). In the anterior part of the hinge six straight, slender pseudocardinal teeth (Fig. 7G, K). Anterior and posterior adductor muscle scars ovate. Inner surface sculpture is smooth, thickness of the shell 0.01 mm. Outer surface sculpture unknown.

Dimensions. –

Specimen	V	L	H	W/2
L41038	A	4.3	3.6	1.0
L42218	A	2.8	2.1	0.9

Superfamily Anodontopsoidea Miller, 1889

Family Redoniidae Babin, 1966

Genus *Redonia* Rouault, 1851

Type species. – *Redonia deshayesiana* Rouault, 1851, France, Armorican Massif, Middle Ordovician, Darriwilian, Postolonnec Formation.

***Redonia deshayesi* Rouault, 1851**

Figure 6G–N

- 1851 *Redonia deshayesiana* Rouault; Rouault, p. 364, figs 1, 2.
- 1881 *Redonia bohémica* Barr.; Barrande, pl. 268, figs 1–26.
- 1881 *Nucula faba* Barr.; Barrande, pl. 273, figs IV/1–4.
- 1918 *Redonia deshayesiana* Rouault. – Born, p. 239, pl. 25, figs 1a–f.
- 1918 *Redonia deshayesiana* var. *duvaliana* Rouault. – Born, p. 341, pl. 25, figs 2a–f.
- 1934 *Redonia deshayesi* Roualt. – Gouzien, p. 179.
- 1950 *Redonia bohémica* Barrande. – Termier & Termier, p. 87, pl. 165, figs 1–3, 6–9.
- 1950 *Redonia megalodontoides* Termier & Termier; Termier & Termier, p. 87, pl. 165, figs 4, 5.

- 1951 *Redonia deshayesiana* Rouault. – Gigout, p. 296, pl. 2, fig. 14.
- 1966 *Redonia deshayesi* Rouault. – Babin, p. 246, pl. 10, figs 13–16.
- 1970 *Redonia deshayesi* Rouault. – Bradshaw, p. 638, pl. 25, figs 16–21.
- 1978 *Redonia bohémica* Barrande. – Pojeta, p. 233, pl. 4, figs 1–4.
- 1990 *Redonia deshayesi* Rouault. – Babin & Destombes, p. 246, pl. 1, fig. 12.
- 1991 *Redonia deshayesi* Rouault. – Babin & Gutiérrez-Marco, p. 129, pl. 9, figs a–e.
- 2003 *Redonia deshayesi* Rouault. – Babin & Beaulieu, p. 197, pl. 3, fig. 1.

Neotype. – Internal mould of the right valve, figured by Babin & Gutiérrez-Marco (1991) on text-fig. 9d and herein on Fig. 6I, LPB 796.

Type locality. – France, Armorican Massif, Morgat-môle near Crozon.

Type horizon. – Middle Ordovician, late Darriwilian, Postolonnec Formation.

Material. – 621 specimens.

Description. – Comprehensive description of this species was given by Babin & Gutiérrez-Marco (1991). Shell small, medium sized, equivalve, strongly inequilateral, more or less posteriorly elongated. Posterior part of the shell is much larger than the anterior part. Anterior part and posterior part rounded. Ventral margin convex. The umbos strongly in the anterior part, prosogyrate. Hinge actinodont, on the left valve a strong pseudocardinal chevron shaped tooth, two posterior pseudolateral teeth. On the right valve a socket and two posterior pseudolateral teeth

(Fig. 6K). Anterior adductor muscle scar very deeply inserted with a myophoric plate, posterior adductor muscle scar more or less rounded (Fig. 6I, L, M). One posterior pedal muscle scar is developed antero-ventrally from the posterior adductor muscle scar (Fig. 6M). Inner surface sculpture is smooth, outer surface sculpture with some grooves of growth more marked than other.

Dimensions. –

Specimen	V	L	H	W/2
L22657	L	20.5	10.5	3.1
LPB 796 (France)	R	19.2	10.2	3.0
L22663	R	15.2	11.0	1.6
JK14668	L	14.6	9.5	2.5
L22659	L	12.6	9.0	1.9
L22658	R	12.5	7.0	2.0
L22656	A	12.0	8.1	3.5
L22660	R	11.8	7.2	1.8
MGM643–O (Spain)	L	11.1	–	1.9
L22662	R	10.5	9.5	2.2
L22655	A	10.2	6.2	2.5
L22661	R	10.1	6.5	2.1
JK 14674b	R	2.9	1.2	0.7
JK14674c	A	5.6	2.1	0.8
JK14674d	R	4.3	1.9	0.7
JK14674e	L	5.9	4.5	–
JK 14595	L	7.5	4.2	0.7
JK 14670a	R	5.0	3.0	–
JK 14670b	R	12.1	7.2	1.6
JK 14670c	R	11.8	6.7	0.7
JK 14668a	L	12.6	8.3	1.9
JK 14675	A	9.1	4.9	1.6
JK 14668b	A	13.7	7.6	1.9
JK 14668c	R	13.8	6.9	2.5
LPB 775 (France)	R	–	–	2.0

Discussion. – Barrande (1881) described the species *R. bohémica*, which Babin & Gutiérrez-Marco (1991) consider conspecific with *R. deshayesi*. Material of both species was studied in Bohemia, France and Spain and the opinion of Babin & Gutiérrez-Marco (1991) is followed in this paper. Very probably *R. anglica* (Salter in Murchison 1859) is also conspecific with *R. deshayesi*. Barrande (1881) already mentioned that *R. deshayesi* is a good example of the species with the high variability mainly in the shape of the shell (short form and long form). *Redonia deshayesi* was described by Rouault (1851), but the original material was apparently lost and therefore Babin & Gutiérrez-Marco (1991) designated a neotype from the Postolonnec Formation of Morgat-môle near Crozon, France. *Redonia michaelae* Babin, 1982 from the lower Arenig (Floian) of France is generally smaller and myophoric septum is larger. *Redonia suriensis* Sánchez & Babin, 1994 from the Arenig (Floian–Dapingian) of Argentina differs in having a strong

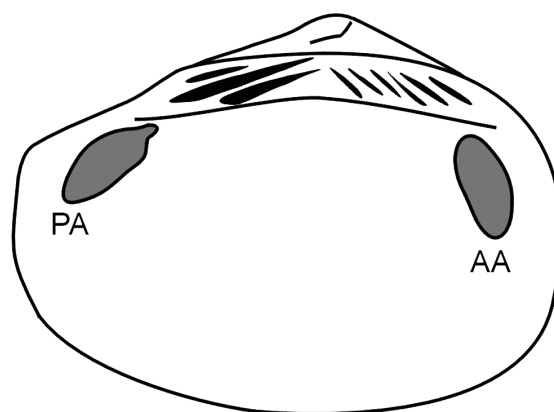


Figure 9. *Tatula petula* gen. nov. et sp. nov. – left lateral view showing hinge and muscle scars. Key to letter symbols: AA – anterior adductor muscle scar; PA – posterior adductor muscle scar.

umbo, less distinctive myophoric buttress and its pseudo-cardinal teeth are smaller. *Redonia riojana* Sánchez, 1997 from the middle Arenig (Dapingian) of Argentina has a less curved umbo and terminal protuberance of the beak.

Occurrence. – Bohemia, Prague Basin, Darriwilian: Kamenný Újezd, Osek, Rokycany, Šárka brickyard, Šárka field, Těškov, Volduchy, Malé Přílepy, Kařízek, Spain, Hesperian Massif, Darriwilian: Cantabrian Zone, West Asturian-leonense Zone, Iberian Cordillera, Central Iberian Zone, Ossa Morena Zone; France, Montagne Noire, early Tremadoc–Floian (early Arenig); France, Armorican Massif, Dapingian–Darriwilian; Morocco, Anti-Atlas, Darriwilian; Bolivia, Tarija area, early Darriwilian.

Subcohort Cardioni Férussac, 1822 (*in* Férussac & Audebard 1822) (= Euheterodonta Giribet & Distel, 2003)
Infrasubcohort Lucinidia Gray, 1854
Superfamily Babinkoidea Horný, 1960
Family Babinkidae Horný, 1960

Genus *Babinka* Barrande, 1881

Type species. – *Babinka prima* Barrande, 1881, Bohemia, Prague Basin, Osek, Middle Ordovician, early and middle Darriwilian, Šárka Formation.

***Babinka prima* Barrande, 1881**

Figure 10A–F, H

- 1881 *Babinka prima* Barr.; Barrande, pl. 266, figs VI/1–16.
- 1935 *Babinka prima* Barr. – Thoräl, p. 162, pl. 13, figs 4, 5.
- 1954 *Babinka prima* Barr. – Vokes, p. 235, fig. 1.
- 1960 *Babinka prima* Barr. – Růžicka & Prantl, p. 48.
- 1960 *Babinka prima* Barr. – Horný, p. 480, pl. 1.
- 1962 *Babinka prima* Barr. – Vogel, p. 235, pl. 5, figs 5, 6.

- 1965 *Babinka prima* Barr. – McAlester, p. 242, pl. 26, figs 3–12; pl. 27, figs 2–5; pl. 28, figs 1–4, 9–14.
 1969 *Babinka prima* Barr. – McAlester, p. 491, fig. E1.
 1969 *Babinka prima* Barr. – Soot-Ryen, p. 175, pl. 34, figs 6–8.
 1971 *Babinka prima* Barr. – Pojeta, p. 12, pl. 1, figs 12–14.
 1977 *Babinka prima* Barr. – Babin, p. 52, pl. 4, figs 1–14; pl. 5, figs 1–3, 6, 9, 10.
 1978 *Babinka prima* Barr. – Pojeta, p. 242, pl. 14, figs 10, 11.
 1982 *Babinka prima* Barr. – Babin, p. 40, pl. 11, figs 8, 9.
 1990 *Babinka prima* Barr. – Babin & Destombes, p. 244, pl. 2, fig. 2.
 1991 *Babinka prima* Barr. – Babin & Gutiérrez-Marco, p. 128, pl. 5, fig. 5.
 1997 *Babinka prima* Barr. – Cope, p. 738, pl. 3, figs 3, 6.
 1999 *Babinka prima* Barr. – Cope, p. 484, pl. 2, fig. 2.
 2008 *Babinka prima* Barr. – Giribet, p. 119, fig. 6B, C.

Lectotype. – (SD by Růžička & Prantl in 1960, p. 48.) Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 266, as figs VI/7–9, NM L 27086.

Paralectotypes. – Internal moulds of the shell, figured by Barrande (1881) on pl. 266, as figs VI/1 – NM L 27087, VI/2–3 – NM L 27088, VI/4–6 – NM L 41033, VI/10–12 – NM L 41034 and VI/13–15 – NM L 41035.

Type locality. – Bohemia, Prague Basin, Osek.

Type horizon. – Middle Ordovician, early and mid Darriwilian, Šárka Formation.

Material. – 115 specimens.

Description. – *Babinka prima* was figured and described by many authors, especially by Barrande (1881), McAlester (1965) and Babin (1977). Shell broadly elliptical, medium-sized, equivalve, more or less inequilateral. Anterior part of the shell is slightly larger than posterior part. Anterior part and posterior part rounded. Ventral margin convex. The umbos located almost in the middle of the shell or slightly in the posterior part. Hinge with one large, triangular, cardinal tooth on the right valve and two small cardinal teeth on the left valve (Fig. 10E, D). Anterior and posterior adductor muscle scars elongated (Fig. 10A, D) and connected ventrally by integripalliate line. Between adductor muscle scars is a range of small vertically elongated pedal muscle scars, the ventral part of these small muscle scars is rounded and more deeply impressed (Fig. 10A, D, E). Ventrally of the small muscle scars are impressed numerous very small dot like muscle scars interpreted by McAlester (1965) as

gill attachment muscle scars. Outer surface sculpture of commarginal ridges.

Dimensions. –

Specimen	V	L	H	W/2
NM L 41035	R	24.5	18.0	2.5
JK 14667	R	23.1	–	2.2
NM L 41033	R	21.1	13.6	2.2
NM L 27086	L	21.0	15.8	2.1
NM L 41034	L	20.5	14.1	1.9
NM L 27089	L	19.2	13.2	–
NM L 27087	L	11.6	9.1	2.0
NM L 27088	L	9.0	7.9	–

Discussion. – McAlester (1965) considered the larger part of the shell as anterior part. Starobogatov (1971) claimed that *Babinka* has the opposite orientation (the larger part is posterior). This opinion was dismissed by Pojeta (1978) who followed McAlester (1965). Also Cope (1999) followed the opinion of McAlester. Sánchez (2008) described *Babinka notia* with diagnosis posteriorly elongated *Babinka*, and therefore it seems that Sánchez followed the opinion of Starobogatov, but the orientation is not further discussed. *Babinka prima* was considered by several authors as the genus directly linked to the monoplacophorans (*e.g.* Horný 1960, McAlester 1965), mainly because of multiple pedal musculature. But this feature is not unique for *Babinka*, it was shown that multiple pedal musculature is known in more bivalves. McAlester (1965) and Carter *et al.* (2000) assigned *Babinka* close to *Ilionia* Billings, 1874, which they considered as the oldest known deep burrowing suspension feeding bivalve. Taylor & Glover (2000) concluded that lucinid character of *Babinka* is doubtful, because they described the anterior respiratory pouch in the lucinoids which in *Babinka* is apparently absent. Recent lucinoids also show enlarged and elongated anterior adductor muscle scar, in *Babinka* the anterior adductor muscle scar is only slightly larger than posterior adductor muscle scar. Babin (1982) in Babin *et al.* 1982 and Cope (1997) placed *Babinka* within the order Actinodontoida. *B. oelandensis* Soot-Ryen, 1969 from the late Arenig (Darriwilian) of Sweden differs from *B. prima* slightly in the shape and more dorsally placed pedal muscle scars.

Occurrence. – Bohemia, Prague Basin, early and mid Darriwilian: Díly, Drahouš, Kamenný Újezd, Mýto, Osek, Rokycany, Šárka brickyard, Šárka field; Spain, Hesperian Massif, Darriwilian: Cantabrian Zone, West Asturian-leonense Zone, Iberian Cordillera, Central Iberian Zone, Ossa Morena Zone; France, Montagne Noire, early Tremadoc–Floian (early Arenig); France, Armorican Massif, Dapingian–Darriwilian; Wales, Carmarthenshire, Darriwilian; England, Shelve Inlier, Darriwilian; Morocco, Anti-Atlas, Darriwilian.

Family Coxiconchiidae Babin, 1977

Genus *Coxiconchia* Babin, 1966

Type species. – *Lyonsia britannica* Rouault, 1851, France, Armorican Massif, Middle Ordovician, Darriwilian, Postolonnec Formation.

Coxiconchia britannica (Rouault, 1851)

Figure 10G, I–O

- 1851 *Lyonsia britannica* Rouault; Rouault, p. 362.
 1856 *Sanguinolites pellicoi* de Verneuil & Barrande; p. 992, pl. 27, figs 4, 4a.
 1889 *Orthonota? britannica* (Rouault). – Bigot, p. 80.
 1912 *Sanguinolites pellicoi* de Verneuil & Barrande. – Douvillé, p. 465, figs 65, 66.
 1918 *Sanguinolites pellicoi* de Verneuil & Barrande. – Born, p. 341, pl. 24, figs 3a, b.
 1935 *Sanguinolites pellicoi* de Verneuil & Barrande. – Thoral, p. 173.
 1966 *Coxiconchia britannica* (Rouault). – Babin, p. 282, pl. 11, fig. 13.
 1966 *Coxiconchia pellicoi* (de Verneuil & Barrande). – Babin, p. 282, pl. 11, fig. 6, text-fig. 73.
 1977 *Coxiconchia britannica* (Rouault). – Babin, p. 57, pl. 1–3, 5 (figs 4, 5, 7, 8, 11, 12).
 1995 *Coxiconchia britannica holubi* Kříž; p. 46, pl. 1, figs 1–11.

Neotype. – (SD, Babin 1966.) Internal mould of articulated shell figured by Babin (1966) on pl. 11 as fig. 13.

Type locality. – France, Armorican Massif, Ille et Vilaine, Guichen, Traveusot.

Type horizon. – Middle Ordovician, late Darriwilian, Postolonnec Formation.

Material. – Two right valves and two left valves, twelve specimens with conjoined valves.

Description. – Comprehensive description was given by Kříž (1995).

Dimensions. –

Specimen	V	L	H	W/2
JK 2998 (France)	R	37.1	21.8	5.7
JK18012 (France)	R	35.1	20.1	5.9
MBHR 5498	A	32.6	18.0	6.0
MBHR 5499	A	30.9	17.6	5.3
MGM644–O (Spain)	A	30.8	16.8	5.4
MBHR 5501	A	28.3	18.2	5.7
MBHR 12689	R	–	16.8	4.7

MBHR 5500	A	26.5	16.2	5.0
JK 2999	A	–	16.0	5.0
MBHR 10992	A	25.4	15.7	4.0
CW 2	A	25.5	15.2	5.0
CW 3a	A	28.6	13.9	6.1

Discussion. – Kříž (1995) considered *C. britannica holubi* different from *C. britannica britannica* in its larger shells, deeper and relatively larger anterior adductor muscle scars and visceral muscle scars and in the shape of posterior part, which is transversely elliptic. All these features are considered here as intra-specific variability. *C. britannica* is abundant in Spain, and among the specimens the variability is really high and therefore herein *Coxiconchia britannica* is regarded as being without subspecies. *C. britannica* differs from *C. guiraudi* (Thoral, 1935) from the Arenig (Floian) of France mainly in the larger size, other features are somewhat problematic and Babin *et al.* (1982) admitted that to distinguish these two species is very difficult. *C. sellaensis* Sánchez & Babin, 2005 from the Arenig (Floian) of Bolivia and Argentina has a well-developed subumbonal carina and posteroventral slope. *C. sellaensis* from Argentina also shows radial sculpture. *C. babini* Sánchez, 2005 from the Tremadoc of Argentina has a smaller size of the shell and shows fewer accessory subumbonal muscles and an ill-defined posterior adductor muscle scar.

Occurrence. – Bohemia, Prague Basin, early and mid Darriwilian: Rokycany, Osek, Sedlec, Drahouš; Spain, Hesperian Massif, Darriwilian: Central Iberian Zone, West Asturian-leonense Zone; France, Armorican Massif, Darriwilian; Wales, Camnant section, Darriwilian; Morocco, Anti-Atlas, Darriwilian; Bolivia, Tarija area, early Darriwilian.

Infraclass Pteriomorpha Beurlen, 1944

Cohort Mytilomorphi Férussac, 1822 (*in* Férussac & Audebard 1822)

Order Mytilida Férussac, 1822 (*in* Férussac & Audebard 1822)

Superfamily Modioloidea Fischer, 1886

Family Modioloidea Fischer, 1886

Genus *Modioloopsis* Hall, 1847

Type species. – *Pterinea modiolaris* Conrad, 1838, U.S.A., New York, Ordovician, Pulaski Formation.

Modioloopsis sp.

Figure 11A–H, J

Material. – Seven left valves, eight right valves and six articulated specimens.

Description. – Shell small in size (maximum L = 9.2), elongated, equivalve, inequilateral. Shells are inflated with no distinct umbonal ridge. Anterior part evenly rounded, posterior part of the shell larger than anterior part. Maximum height is reached approximately in the third quarter of the shell length from anterior. Umbos prominent and prosogyrate. Dorsal margin is long, more than one half of the shell length, straight. Ventral margin is convex. Posterior margin evenly rounded. Hinge plate edentulous, anterior muscle scar rounded (Fig. 11D). Outer surface sculpture composed of irregularly spaced growth (Fig. 11G).

Dimensions. –

Specimen	V	L	H	W/2
NM L 41028	L	9.2	5.8	1.9
NM L 41030	R	7.0	4.0	0.7
NM L 41031	R	6.5	4.2	1.2
NM L 41036a	L	9.4	6.3	2.1
NM L 41036c	R	9.9	6.2	2.6
NM L 41037a	R	14.6	8.8	2.1
NM L 41029	A	–	8.6	2.2

Discussion. – More than 163 species were classified from the Ordovician of North America under *Modiolopsis* Hall, 1847 by Pojeta (1971). In general, edentulous hinge and modiolophorm shape of the shell are only significant characters for this genus and therefore specific classification is very difficult (Kříž & Steinová 2009). This evolutionary important genus is well known from the Ordovician of Argentina (Sánchez 1990), France (Babin 1966, Babin & Beaulieu 2003), Morocco (Babin & Destombes 1990), North America (Pojeta 1971), Spain (Babin & Gutiérrez-Marco 1991) and Wales (Cope 1996). Barrande (1881) figured some species of *Modiolopsis* only from the Late Ordovician of Bohemia. *Modiolopsis* sp. described here from the Middle Ordovician differs from the type species *Modiolopsis modiolaris* (Conrad, 1838) from the Late Ordovician of North America in more elongated and larger shells, deeply impressed anterior and posterior adductor muscle scars and the pallial line. *M. draboviensis* Barrande, 1881 from the Late Ordovician, Sandbian, Letná Formation seems to be very similar to *Modiolopsis* sp. *Modiolopsis drabovi-*

ensis is only more posteriorly elongated. “*Modiolopsis*” *primula* Barrande, 1881 from the Late Ordovician, Sandbian, the Letná Formation has a higher and shorter shell. *M. veterana* Barrande, 1881 from the Late Ordovician, Sandbian, Zahořany Formation has the prominent umbonal ridge. This species probably does not belong to the genus *Modiolopsis*. *M. faba* Barrande, 1881 from the Late Ordovician, late Katian, Králův Dvůr Formation has the same width of the anterior and posterior part. *M. lenticularis* Barrande, 1881 from the Late Ordovician, late Katian, Králův Dvůr Formation shows more rounded shell and very probably this species does not belong to *Modiolopsis*. *M. minuta* Barrande, 1881 from the Late Ordovician, Katian, Králův Dvůr Formation has well developed posterior wing, separated by the radial sulcus and probably it should not be assigned to *Modiolopsis*. *M. tumescens* Barrande, 1881 also from the Králův Dvůr Formation differs from *Modiolopsis* sp. in the shape of the shell. *M. pragensis* Kříž & Steinová, 2009 from the Late Ordovician, Hirnantian, Kosov Formation has a less pronounced umbo. *M. cuyana* Sánchez, 1990 from the Hirnantian of Argentina seems to be very similar, but it lacks a prominent anterior lobe. *M. elegantulus* Sharpe, 1853 from the Middle Ordovician of Portugal and Armorican Massif has a concavo-convex ventral margin of the shell.

Occurrence. – Bohemia, Prague Basin, early and mid Darriwilian: Šárka villa.

Cohort Ostreomorphi Férussac, 1822 (*in* Férussac & Audebard 1822)

Subcohort Arcioni Gray, 1854

Order Cyrtodontida Scarlato & Starobogatov, 1971 (*in* Nevesskaya 1971)

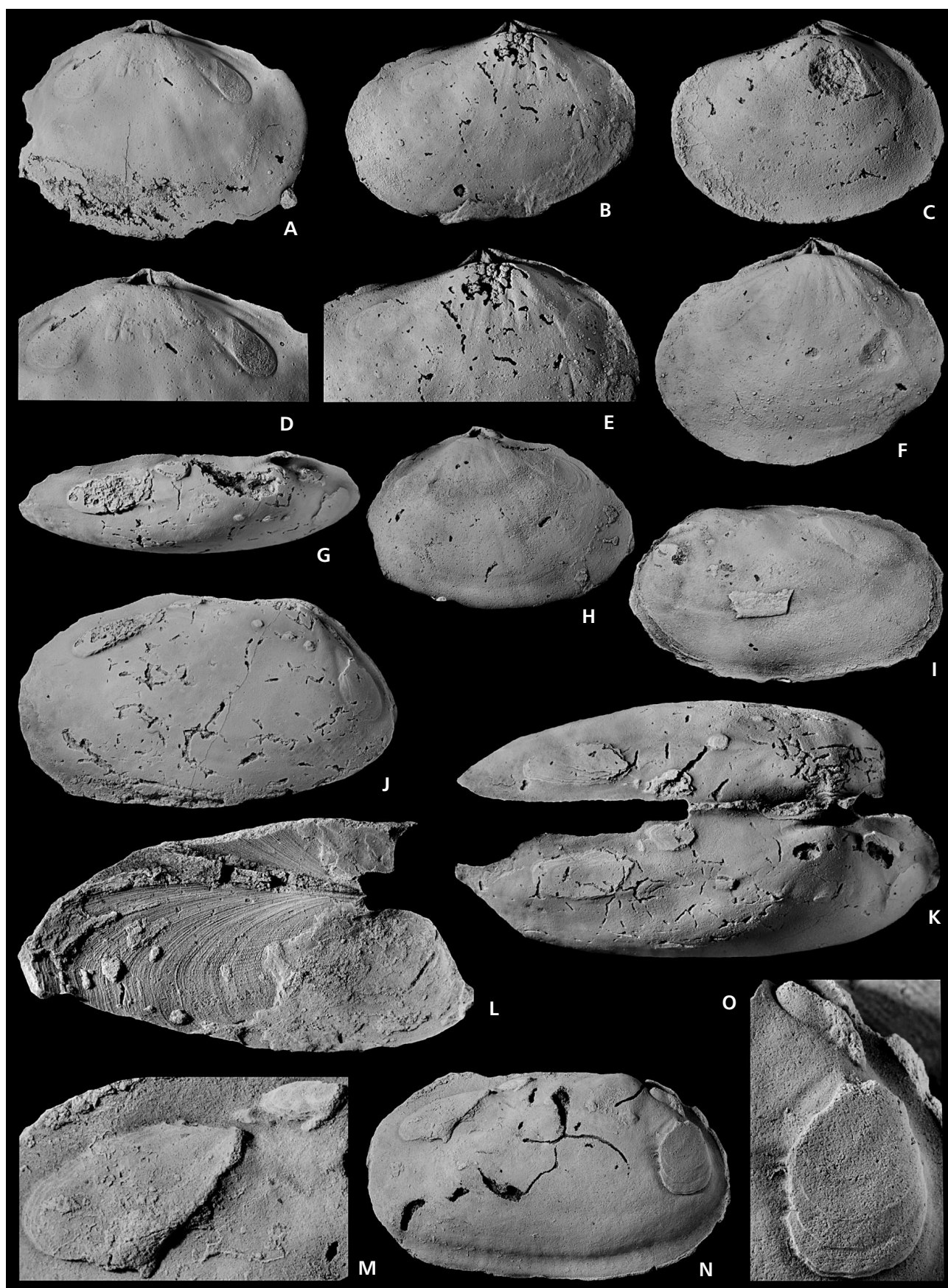
Suborder Cyrtodontidina Scarlato & Starobogatov, 1971 (*in* Nevesskaya 1971)

Superfamily Cyrtodontoidea Ulrich, 1894 (*in* Ulrich & Scofield 1894)

Family Cyrtodontidae Ulrich, 1894 (*in* Ulrich & Scofield 1894)

Subfamily Cyrtodontinae Ulrich, 1894 (*in* Ulrich & Scofield 1894)

Figure 10. A–F, H – *Babinka prima* Barrande, 1881. • A, D – right valve, NM L 41035; A – right lateral view with impressions of adductor muscle scars and row of accessory muscle scars between adductor muscle scars, $\times 2.0$; D – detail of the hinge and adductor and accessory muscle scars, $\times 3.1$. • B, E – left valve, NM L 41034; B – left lateral view, $\times 2.4$; E – detail of the hinge, $\times 3.2$. • C – left valve, NM L 27089, left lateral view, $\times 2.5$. • F – left valve, NM L 27086, lectotype, left lateral view, $\times 2.4$. • H – right valve, NM L 41033, right lateral view, $\times 2.2$. • G–J – *Coxiconchia britannica* (Rouault, 1851). G, J – left valve, CW 2; G – dorsal view, $\times 2.4$; J – right lateral view with adductor and accessory muscle scars, $\times 2.6$; I – left valve, MGM644–O, left lateral view, $\times 1.8$. • K – articulated specimen, CW 3a, dorsal view, $\times 3$. • L – part of the right valve, CW 3b, outer surface sculpture, $\times 2.4$. • M–O – right valve, JK 18012; M – posterior adductor muscle scar with posterior retractor, $\times 2.2$; N – right lateral view, $\times 1.7$; O – anterior adductor muscle scar with protractor, $\times 2.8$. A–H, J, K, L – Prague Basin, Bohemia, Osek locality, early and mid Darriwilian; I – Spain, Alia Navalpino locality, Darriwilian; M–O – France, Morgat locality, late Darriwilian.



Genus *Cyrtodonta* Billings, 1858

Type species. – *Cyrtodonta rugosa* Billings, 1858, Canada, Ordovician.

Cyrtodonta sp.

Figure 11I–L

Material. – One left valve.

Description. – Shell small, rectangle, equivalve, inequilateral. Anterior part evenly rounded, smaller, posterior part straight and elongated. Ventral margin slightly concave in the middle of the shell. Umbos not prominent, prosogyrate. Dorsal margin is straight and long, more than one half of the shell length. Posterior margin badly preserved. Hinge plate with one long tooth in the posterior part, and one long and smaller tooth in the anterior part (Fig. 11K, L). Muscle scars and pallial line not developed. Inner surface sculpture composed of irregularly spaced growth. Outer surface sculpture unknown.

Dimensions. –

Specimen	V	L	H	W/2
NM L 41036	L	10.5	6.3	2.4

Discussion. – *Cyrtodonta* is known from the Ordovician of Canada, Wales, Ireland, Australia, Sweden, China and United States. *Cyrtodonta* sp. from Bohemia is similar in the shape to *C. staffordae* Pojeta & Gilbert-Tomlinson, 1971 from the Ordovician of Australia and to *C. cf. staffordae* from the Lower Ordovician of Wales. One ill-preserved specimen from Bohemia does not allow precise determination and therefore it is left in open nomenclature.

Occurrence. – Bohemia, Prague Basin, early and mid Darriwilian: Šárka villa.

Functional morphology of the Ordovician Protobranchia

Orientation of the shell

A very problematic feature in the Ordovician Protobranchia is the orientation of the shell. Recent Protobranchia

show both orientations (larger part as anterior – Nuculidae or larger part as posterior – Nuculanidae). To determine anterior and posterior ends of the shell is easy in the Recent bivalves (pallial sinus is in the posterior part of the shell, foot is in anterior part). The situation is totally different in the Ordovician Protobranchia because of poorly studied or specialized groups, especially where the internal morphology of the shell is ambiguous, weakly impressed or limited by preservation of material. Driscoll (1964) was interested in the accessory muscle scars of bivalves and tried to use them as the indicator of the shell orientation. He pointed out that it is necessary to recognise precisely all the accessory muscle scars (anterior protractor, anterior retractor, posterior retractor, dorso-median muscle scar, ventro-median muscle scar and others). The success of this method is mostly limited by insufficient preservation. In the Ordovician bivalves from Bohemia, the muscle scars close to the adductor scars (probably retractor and protractor pedal muscle scars) are preserved relatively often, but other accessory muscle scars (mainly in umbo region) are preserved very rarely. Bradshaw & Bradshaw (1971) used the palaeotaxodont hinge as a guide to orientation with conclusion that larger teeth on one side indicate the anterior part. Some Protobranchia have often teeth of the same size (*e.g. P. dispar*) and it is impossible to use this method for them. Bailey (2009) proposed a new alternative, in the case that it is difficult to recognize the orientation of the shell, to avoid subjective terms like anterior or posterior. We can use terms, which describe bivalves with reference to the shell axes, shell extremities and shell dorsum and ligamental placement.

Hinge

Pfab's classification (1934) of the Protobranchia from the Prague Basin was based mainly on characters of the hinge. He recognized six hinge types according to their teeth's shape and if the apex of chevron-shaped teeth points toward the umbo or away from the umbo. According to Babin (1966) and Carter *et al.* (2012) the Protobranchia possess different types of taxodont teeth, including convexodont, concavodont, orthomorphodont, diconcavodont, diconvexodont, convexoconcavodont, and concavoconvexodont (Fig. 12). Babin (1966) considered the inclination to the umbo as systematically important character and Sánchez

Figure 11. A–H, J – *Modiolopsis* sp. • A – left valve, NM L 41028, left lateral view, × 5.3; B – articulated specimen, NM L 41029, left lateral view, × 3.4; C – right valve, NM L 41030, right lateral view, × 6.7; D – left valve, NM L 41036a, left lateral view with anterior adductor muscle scar, × 6.5; E, G – left valve, NM L 41037a; E – left lateral view, × 6.4; G – outer surface sculpture, × 6.1; F – right valve, NM L 41031, right lateral view; H, J – right valve, NM L 41036c; H – right lateral view, × 8.8; J – right dorsolateral view, × 6.5. • I, K, L – *Cyrtodonta* sp., left valve, NM L 41036b; I – dorsal view, × 8.1; K – left lateral view, × 6.2; L – left dorsolateral view with hinge, × 7.1. A–L – Prague Basin, Bohemia, Šárka brickyard locality, early and mid Darriwilian.



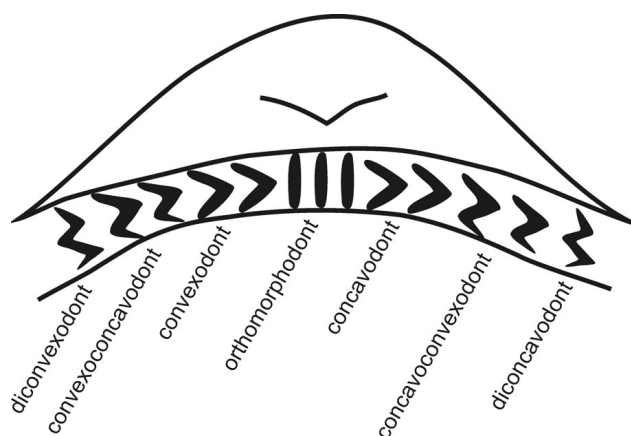


Figure 12. Teeth in taxodont hinge according to Carter *et al.* (2012).

(1999) established two subfamilies (Praenuculinae and Concaodontinae) mainly according to how their teeth incline to the umbo. On the contrary Pojeta (2007) is of the opinion that the direction to which the apex end of chevron-shaped teeth points is not a significant taxobasis. Also according to Cope (1999) a more important character is the discordance between anterior and posterior part of the shell and for Carter *et al.* (2000) the size of the teeth. The Protobranchia from the Middle Ordovician of Bohemia show three types of the taxodont hinge (Fig. 5A–D). *P. bohemia* and *P. applanans* have the same type of the hinge, but it is not possible to determine them in Praenuculinae or Concaodontinae, the hinge in anterior part is clearly convexodont, but the hinge in the posterior is not convexodont or concavodont, it is rather orthomorphodont. In *C. ponderata* the anterior teeth are diconvexodont, which is different from the diagnosis for Concaodontinae. On the other side *P. dispar* can be determined to Praenuculinae according to Sánchez (1999) without doubt. This character of the orientation of teeth to umbo or out from the umbo is mostly important for distinguishing species, but its value for higher systematic levels is probably overestimated.

The types of taxodont teeth in Ordovician bivalves show high variability. On the contrary, when I studied recently the Recent genera of the Protobranchia in the Natural History Museum in Paris and in the Smithsonian Institution in Washington D.C., they predominantly show convexodont teeth; the most anterior and posterior teeth and the teeth under the umbo are often orthomorphodont. Only some species of the genera *Tindaria* Bellardi, 1875 and *Malletia* Des Moulins, 1832 show concavodont and diconcaodont teeth. Generally, the taxodont teeth in the Recent Protobranchia are simpler.

Carter *et al.* (2000) used new term heterotaxodont hinge, which mean the hinge with the anterior teeth, which are abruptly much larger than the posterior teeth. He used *Praeclada subtilis* Cope, 1999 as an example. Carter *et al.* (2000) redefined the term gradidentate hinge in which the

teeth gradually change in size along the tooth row, typically becoming larger away from the beak. The more distal teeth may then gradually decrease in size, like example it can be shown the Late Ordovician *Similodonta similis* Ulrich, 1892. The other term, which could be a little confusing in comparing with two previous, is cardiolariid hinge. This is a hinge with posterior gradidentate teeth overlapping larger, subumbonal, radiating hinge teeth. *Cardiolaria beirensis* (Sharpe, 1853) is a good example. The Bohemian Middle Ordovician Protobranchia shows both gradidentate hinge and heterotaxodont hinge. *P. dispar* shows slightly gradidentate teeth (under the umbo the teeth are the smallest), in *P. bohemia* and *P. applanans* is the situation more complicated, in most specimens the hinge is gradidentate, but some specimens (Figs 3M, 4B) show rather heterotaxodont hinge.

Muscle scars

Heath (1937) and Yonge (1939) precisely described the system of muscles and the muscle scars in the Recent Protobranchia. Driscoll (1964) compared pedal and other accessory muscle scars on the recent genera *Acila* and *Nucula* and on the extinct genera *Ctenodonta* and *Nuculopsis*. He tried to use the muscle scars as an indicator of the orientation for bivalves. According to Driscoll (1964) the Ordovician Protobranchia shows more numerous accessory muscle scars than the recent Protobranchia and this opinion was based mainly on species *Myoplusia bilunata* (Barrande, 1881). According to my observation the preservation of pedal muscle scars and other accessory muscle scars on the shell in Recent bivalves is very rare. Kříž (1974 MS) and Kříž (1995, fig. 3) described and figured numerous accessory muscles in *Leionucula mirifica* (Dall, 1907) on before unknown wet syntype material dredged in 1906 Japan Hokkaido Island offshore and deposited in the U.S. National Museum, Smithsonian Institution. Accessory muscle scars in *Leionucula* are more numerous than in specimens of *Myoplusia bilunata* (Barrande, 1881) (Fig. 13). But it seems that accessory muscle scars in the Ordovician bivalves are generally larger.

Bradshaw (1970) studied and figured muscle scars in *Cardiolaria* and *Praenucula*, the species *Praenucula ciae* and *Praenucula costae* show almost the same muscle scars pattern like all the species of *Praenucula* from Bohemia (the anterior adductor muscle scar mostly larger with joined anterior pedal muscle scar, the posterior muscle scar mostly smaller with separated posterior pedal muscle scar and the accessory muscle scar very often placed in the umbo region in triangle pattern). According to Heath (1937) the ventro-median and dorso-median accessory muscle scars in the Recent protobranchs represent the attachment of visceral retractors, which reinforced the action of pedal

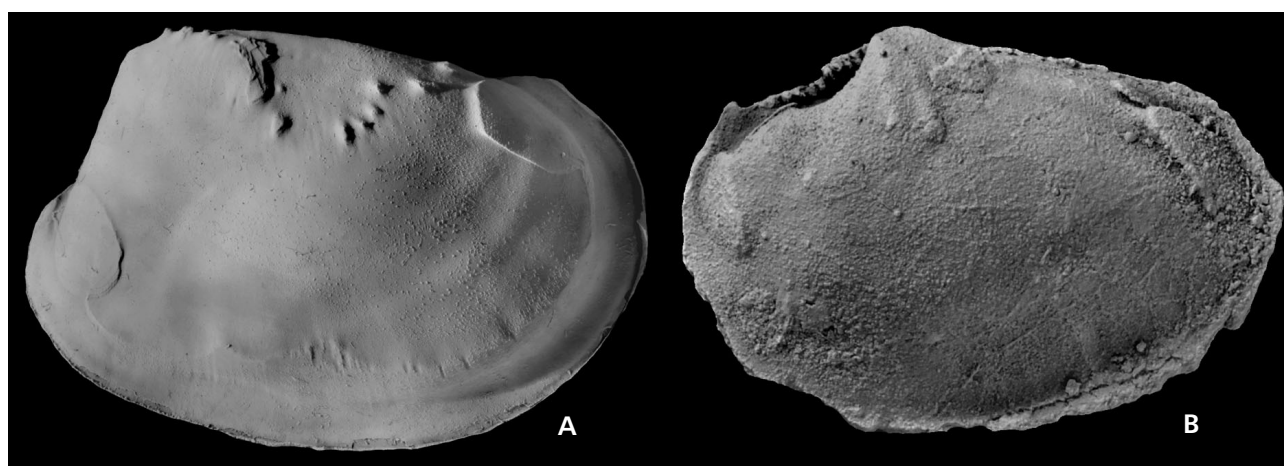


Figure 13. Muscle scars in *Leonucula mirifica* and *Myoplusia bilunata*. • A – *Leonucula mirifica* (Dall, 1907), JK 18425, latex cast after USNM 363746, left valve, left lateral view with numerous accessory muscle scars, $\times 2.2$. • B – *Myoplusia bilunata* (Barrande, 1881), NM L 27130, right valve, right lateral view with accessory muscle scars, $\times 9.6$.

retractors or provided a firm attachment of the pericardial region to the shell during vigorous movement of the foot. Another, sometimes rather deep muscle scars correspond in protobranchs to the visceral attachment muscles holding the muscular floor of visceral sac.

Palaeoecology

Using the known functional morphology of the shell in the Recent bivalves makes possible to interpret modes of life in the majority of fossil bivalves, and thus their palaeoenvironment. Bivalve living habit is divided into broad categories, each containing adaptive groups with certain unique morphologic features. Fang (2006) concluded that Cambrian bivalves were benthic crawlers and that infaunal mode of life in the bivalves is known from the Ordovician. Most part of the Ordovician bivalves is infaunal deposit feeders and filter feeders. Semi-infaunal and epifaunal elements are more abundant in the Late Ordovician. It corresponds also with studies of the Ordovician bivalves from Bohemia where in the Middle Ordovician Šárka Formation dominate heterodonts (infaunal filter feeders) and protobranchs (infaunal deposit feeders), possibly semi-infaunal bivalves like *Modiolopsis* and *Cyrtodonta* are very rare.

The palaeoecology of *Pseudocyrtodonta* was described in detail in Steinová (2012), *Pseudocyrtodonta* was most probably an active infaunal burrower.

Redonia, *Coxiconchia* and *Babinka* were considered by Babin & Gutiérrez-Marco (1991) as infaunal filter feeders. Typical character for *Redonia* is myophoric buttress on the anterior adductor muscle scar, which is developed in burrowers. The shell of *Redonia* is also often preserved with conjoined valves, which also supports the opinion that *Redonia* was infaunal burrower. *Coxiconchia* and *Babinka*

belong with uncertainty to the Lucinidia (see discussion in *Babinka prima*). Recent Lucinidia are filter feeders and they live in symbiosis with chemosymbiotic bacteria (Reid 1990). Many lucinids burrow deeply, most of them live vertically in the sediment with hinge uppermost and they can survive in anaerobic zone. Distinctly elongated anterior adductor muscle scar in recent lucinids is an adaption for chemosymbiosis. *Coxiconchia* and *Babinka* show very similar hinge to recent lucinids, but the anterior and posterior adductor muscle scars have almost the same size. Both *Coxiconchia* and *Babinka* have the accessory muscle scars under the umbo; they are interpreted as impressions of visceral attachment and pedal muscle scars (Heath 1937, Bradshaw 1978, Liljedahl 1994 and Babin & Farjat 1994, Kříž 1995). According to the degree of obesity (height/width ratio) *Babinka* and *Coxiconchia* were rapid burrowers. From the shape of *Babinka*, which is nearly circular in the lateral view, it is possible to conclude that they penetrated vertically downwards.

Modiolopsis and *Cyrtodonta* are considered as endobysate filter feeders even when the internal morphology of *Modiolopsis* and *Cyrtodonta* is not well known and other research is necessary.

Praenucula and *Concavodonta* are very probably infaunal deposit feeders, often preserved with conjoined valves or sometimes as the opened shell (Figs 2L, 4P, R).

Tatula was probably an infaunal filter feeder, like others actinodonts.

Fossil associations of the Šárka Formation

Diversified fauna from the Šárka Formation was studied by many authors almost two hundred years, but mainly Havlíček & Vaněk (1966, 1990), Havlíček (1982), Havlíček

(1998), Mikuláš (1991), Mergl (2002), Mergl *et al.* (2008), Budil *et al.* (2007), Lefebvre (2007), Fatka & Mergl (2009) determined its invertebrate communities. Havlíček (1982) established *Placoparia* Community, which was redefined as the *Euorthisina-Placoparia* Community by Havlíček & Vaněk (1990). Vavrdová (1982) studied phytoplankton communities. Mikuláš (1991) recognized ichnofossil assemblages, which he assigned to the *Cruziana* and *Zoophycos* ichnofacies and Mergl (2002) described *Rafanoglossa* Community within his *Paterula* Community Group. Budil *et al.* (2003a, b), Fatka (2003), Chlupáč (2003), Kraft *et al.* (2003), Kraft & Kraft (2003) and Mikuláš (2003) described faunal association from Prague – Červený vrch Hill, where the phyllocarids and graptolites dominated. Lefebvre (2007) distinguished two biofacies based on echinoderms; mitrocystitid biofacies in the shallower western part of the Prague Basin and lagynocystid biofacies in the deeper eastern part of the Prague Basin. Budil *et al.* (2007) discussed mainly trilobite associations and briefly described merostomes, phyllocarids, brachiopods, echinoderms, arcitarchs, chitinozoans and graptoloids.

Generally molluscs have been a neglected group and the complex data from the Middle Ordovician bivalves of Bohemia have not been published. During this revision of the Middle Ordovician bivalves I counted and determined all specimens and then statistically analysed the data using the methodology of Kříž (1999). This analysis is based on the specimens deposited in the collections of the National Museum, Prague, Museum of Dr. Bohuslav Horák, Rokycany, which were built especially by J. Barrande, F. Hanuš, K. Holub and J. and P. Kraft, in the private collection of Vladislav Kozák, and in my own collection deposited in the Czech Geological Survey.

***Euorthisina-Placoparia* Association**

Name. – Used for the first time by Havlíček & Vaněk (1990).

Age. – Šárka Formation, early and middle Darriwilian.

Type locality. – Osek near Rokycany, Bohemia.

Geographic distribution. – Prague Basin, Bohemia.

Composition. – The abundant brachiopods show relatively low diversity, dominated by genera *Eodalmannella* Havlíček, 1950 and *Euorthisina* Havlíček, 1950. The trilobites are significant group with various ecological types (particle feeders, filter feeders, scavengers, predators possible large predators, pelagic and nektonic elements, possible epiplankton and plankton, Budil *et al.* 2007). Very abundant are gastropods, univalved molluscs (*Tropidodiscus* Meek

& Worthen, 1866, *Gamadiscus* Horný, 1962, *Sinuities* Koken, 1896, *Mourlonia* de Koninck, 1883, *Lesuerella* Koken, 1896) and bivalves, where actinodonts and protobranchs dominate (*Redonia*, *Pseudocyrtodonta*, *Praenucula*, *Concavodonta*). The other frequent groups are hyolithids (*Gompholites* Marek, 1966, *Elengatilites* Marek, 1966, *Pauxillites* Marek, 1966, *Bactrotheca* Novák, 1891) and benthic ostracods (*Dilobella* Ulrich, 1894, *Cerninella* Přibyl, 1966, *Conchoprimites* Hessland, 1949). Highly diversified echinoderm fauna includes fourteen species, of which stylophoran taxa are dominant. Cephalopods represent mainly demersal predators (ellesmerocerids, endocerids, pseudoortocerids) and planktic orthocerids (Manda 2008a). Phyllocarids are widespread, but monotonous *Caryocaris*. Merostomes are represented by one rare species.

Environment. – The richly diversified fauna, which is assigned to *Euorthisina-Placoparia* Association was mostly gathered from the loose siliceous nodules. This fauna is preserved also in the shales, but the preservation is worse than in the siliceous nodules. According to Kukal (1962) these nodules were primarily carbonate and then they were subsequently silicified. Havlíček *et al.* (1994) considered bivalves in *Euorthisina-Placoparia* Association as vagile benthos. Kříž (1997) briefly described composition, general diversity, and modes of life in the Ordovician bivalve associations. He pointed out that the environment of unconsolidated dark clay to silty muds rich in organic matrix of the Šárka Formation was most favourable for infaunal deposit-feeders, especially protobranchs. Havlíček (1998) mentioned that infaunal elements are rare, but the bivalve association described here (Table 1, Fig. 14, 15) is quite diversified (12 species of bivalves) and abundant (1524 specimens collected during almost two hundred years). The bivalves are well preserved, mostly as the shells with conjoined valves (61.1%). In the subtidal, soft bottom environment the abundant infaunal deposit-feeding bivalves (*Praenucula*) occur (35.5%). The dominance of actinodonts (infaunal filter feeders 56.4%) could be partially artificial, because of *Redonia*. Fossiliferous nodules attracted attention of a lot of private collectors, who were focused mainly on trilobites and small bivalves were very often overlooked. *Redonia* is one of the large bivalves in the Šárka Formation and therefore it is more probable that it was more readily noticed and preferentially collected. In most of the bivalve species of the Šárka Formation the number of the articulated specimens is about 50% or more, but *Babinka* is represented by only 13% of the articulated specimens. It seems that *Babinka* was very shallow infaunal filter feeder.

Most of the bivalves are common to both parts of the Prague Basin (the eastern part – Prague area, and the western part – Rokycany area). The exceptions are *Coxiconchia* occurring only in the Rokycany area and *Cyrtodonta*, *Modiolopsis* and *Tatula* occurring only in the Prague area.

Table 1. Numerical and ranked abundance of bivalves from the old collections of bivalves in the *Euorthisina-Placoparia* Association, Šárka Formation, early and middle Darriwilian, Middle Ordovician of Bohemia. RV and LV – right and left valves (disarticulated); A – shells with conjoined valves; RA – percentage relative abundance; AA – percentage relative abundance of shells with conjoined valves; R – ranked abundance.

Species	Life habits	RV	LV	A	RA	AA	R
<i>Redonia deshayesi</i>	infaunal	154	181	286	41.3	63.1	1
<i>Praenucula bohémica</i>	infaunal	31	45	106	13.10	73.6	2
<i>Praenucula applanans</i>	infaunal	39	46	87	11.80	67.28	3
<i>Praenucula dispar</i>	infaunal	48	49	65	10.30	57.2	4
<i>Pseudocyrtodonta incola</i>	infaunal	40	28	65	9.00	65.7	5
<i>Pseudocyrtodonta ala</i>	infaunal	38	23	33	5.80	52	6
<i>Babinka prima</i>	infaunal	45	62	8	5.60	13	7
<i>Coxiconchia britannica</i>	infaunal	2	2	12	1.30	85.7	8
<i>Modiolopsis</i> sp.	infaunal	8	7	6	1.20	44.4	9
<i>Concavodonta ponderata</i>	infaunal	2	2	1	0.30	33.3	10
<i>Tatula petula</i>	infaunal	–	1	2	0.20	80	11
<i>Cyrtodonta</i> sp.	infaunal	–	1	–	0.05	–	12
Totals		407	446	671	99.95%	61.10%	

This bivalve fauna has some elements in common (*Babinka*, *Coxiconchia*, *Redonia*, *Modiolopsis*, *Cyrtodonta*) with the older faunas of the Montagne Noire, France and Wales (Babin 1982 in Babin *et al.* 1982, Cope 1996). According to Havlíček *et al.* (1994) Havlíček (1998) and Fatka & Mergl (2009) this similarity could indicate easy migration of mobile benthic larvae along deep shelves and between separate terranes (Avalonia, Armorica, Perunica and cratonic West Gondwana). According to Cope (2002) the Early and Middle Ordovician bivalves were already highly diversified and abundant group in many regions (collections from Montagne Noire – 249 specimens and nine species, South Wales – 1271 specimens and twenty species, mid-Wales – 490 specimens and thirteen species, Spain – 2419 specimens and fifteen species, Australia – 523 specimens and thirty species). In South Wales the bivalves even dominated the early Ordovician fauna from the Llangynog Inlier (Cope 1996). From France are described Middle Ordovician bivalve shell beds with dominant *Redonia* and *Praenucula* (Babin 1966, Dabard *et al.* 2007). The other bivalve shell beds are known from North America, the dominant element is *Modiolopsis* (Li & Droser 1999).

Diversification and paleobiogeography of bivalves during the Middle Ordovician

Ordovician diversification and palaeobiogeography of the bivalves was intensively studied by Babin (1993a, b, 1995, 2000), Cope (2002, 2004), Cope & Babin (1999), Sánchez

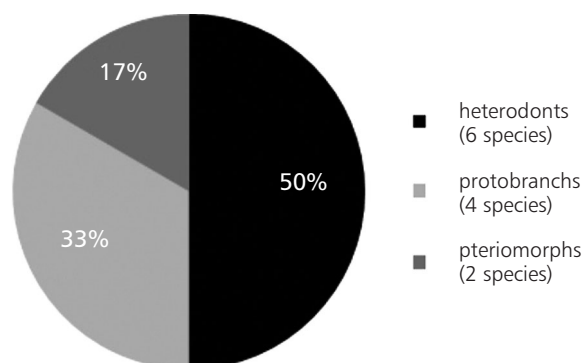


Figure 14. The species composition and diversity of the bivalve fauna from the Middle Ordovician Šárka Formation.

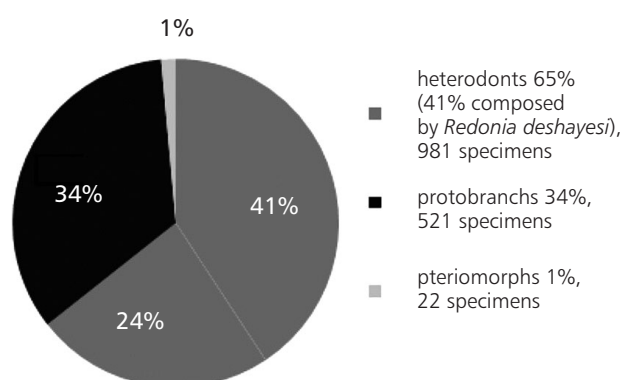


Figure 15. Abundance of bivalve individuals composing collections of the bivalve fauna from the Middle Ordovician Šárka Formation, according to Table 1.

(2008), Sánchez & Babin (2003) and Fang (2006). The Ordovician was the most significant period in bivalve diversification. Early Ordovician bivalves were restricted to peri-Gondwanan shelves and favoured inshore clastic sedimentary environments. During the Middle Ordovician the bivalves were able to migrate to other continents, but initially remained largely confined to nearshore clastic facies (Cope & Babin 1999). In the Late Ordovician the widespread occurrence of low-latitude carbonate platforms provided an ideal habitat for epifaunal bivalves and they became a very diverse class, adapted to many modes of life (Cope & Babin 1999).

Cope (2002) compared the Ordovician bivalves from high, median and low latitudes and revealed difference in both, bivalve diversity and faunal composition. The number of species at equatorial latitudes is twice that of the highest latitude. There was clear preference of the pteriomorphs for low latitudes and heterodonts for high latitudes. The conclusion of Cope (2002) is also confirmed by the composition of the Middle Ordovician Šárka Formation bivalve fauna from Bohemia where heterodonts prevail with six species (Fig. 14) and 981 specimens (Fig. 15, Table 1).

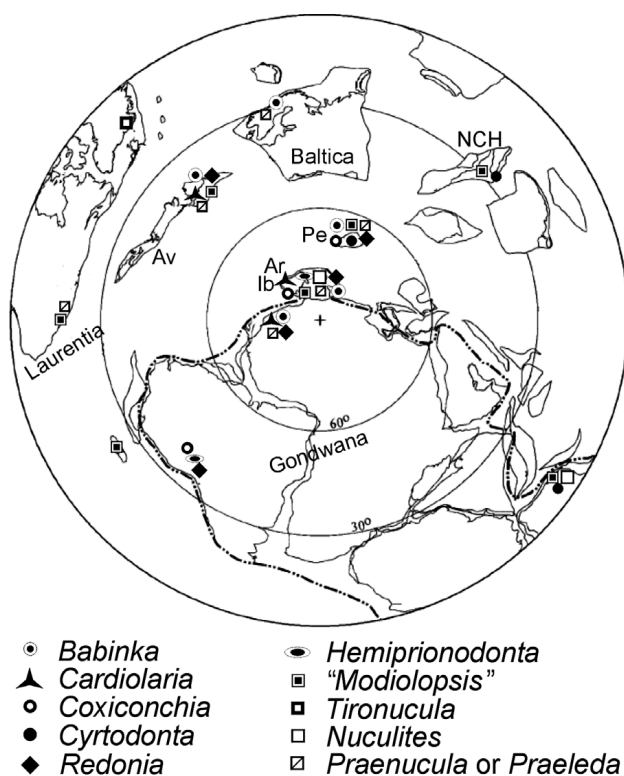


Figure 16. Palaeogeographic distribution of the bivalves during the Middle Ordovician, palaeogeographic map according to Cocks & Torsvik (2002). Abbreviations: Ar – Armorica, Av – Avalonia, Ib – Iberia, NCH – North China, Pe – Perunica.

Sánchez & Babin (2003) studied the palaeogeographical distribution of bivalves during the Ordovician and their suitability for palaeogeographical reconstruction. They concluded that bivalves are not relevant palaeobiogeographic indicators, because of the low percentage of shared genera among different localities (80% from 144 known genera are locally endemic). According to Cope & Kříž (2013) the number of the Ordovician genera increased during research history and today almost 170 genera of Ordovician bivalves are known. The possibility of colonising different areas depends on different factors: abiotic and biotic. The abiotic factors include the distance between the regions, the position of the geographic barriers, the directions and speed of the sea currents and the living conditions in the surroundings, which could be colonised. The biotic factors mainly include available ecospace, the competition between species and the characters of the species. Sánchez & Babin (2003) suggest that Ordovician bivalves were very probably stenotopic and their occurrence was controlled by the living conditions characteristic for each basin. Probably the taphonomic conditions are not the limiting factor for the record of the Ordovician bivalves, because other molluscs with aragonitic shells are abundant in strata where the bivalves are very rare or absent.

The other aspect, which is very important for the distribution of the Ordovician molluscs, is the larval type. According to Thorson (1961) or Jablonski & Lutz (1980) about 65–70% the Recent species of bivalves have planktotrophic larvae and this type of larva permits the dispersion over the large distances. Babin (1995) and Sánchez & Babin (2003) presumed that all the Ordovician bivalves had the lecithotrophic larvae and this could explain the spatial restriction for the Ordovician bivalve genera (for early ontogenetic strategies in other molluscs, see Nützel & Frýda 2003, Manda 2008b, Klug *et al.* 2010, Manda & Frýda 2010, Laptikhovsky *et al.* 2013). Thorson (1961) studied the length of pelagic larval life in Recent marine invertebrates (including bivalves) and the larval transport by ocean currents. Recent surface currents of average velocity can transport bivalves, with a pelagic larval life span of about 6 weeks, in one generation for a distance of 900–1,500 km.

The palaeogeographic distribution of the Middle Ordovician bivalves is shown on Fig. 16, for better clarity was chosen the genera, which are recorded in the three or more regions. *Tironucula* Morris & Fortey, 1976 is the exception, because Middle Ordovician bivalves from the North America are rare and it is important to mention all the bivalves, which occur there. The genus *Ctenodonta* was excluded from this analysis, because under this generic name was assigned many bivalves with different shape and hinge. After the revision of bivalve fauna in the peri-Gondwana and Gondwana region, many species, which belonged to *Ctenodonta*, were reassigned to *Praenucula* or *Praeleda*. *Praenucula* and *Modiolopsis* are also somewhat problematic (see discussion above about these genera) and therefore I prefer the designation *Praenucula* or *Praeleda* and “*Modiolopsis*”. Despite this problem with taxonomy, Middle Ordovician bivalves often went through modern revision and therefore their data are the most complex. Sánchez & Babin (2003, table 2) mentioned that no endemic genera are in Bohemia, but after the revision it is obvious that two genera (*Pseudocyrtodonta* and *Tatula*) are recorded only from Bohemia. The Middle Ordovician bivalves remain confined to the Gondwana and peri-Gondwana regions (including Avalonia and North China). But some of the Middle Ordovician genera could overcome long distances. *Modiolopsis* is recorded from Australia, Bohemia (Perunica), Spain (Iberia), Wales (Avalonia), Argentina (Argentine Precordillera), North China, and North America. *Babinka* is known from Morocco, Spain, France, Bohemia, Sweden (Baltica) and Wales. *Coxiconchia* is recorded from Bohemia, Spain, France and Bolivia. *Praenucula* or *Praeleda* are known from Bohemia, England, France, Iberia, Morocco, Sweden, Wales and probably North America. It seems that some of the Middle Ordovician genera had to have planktotrophic larvae and therefore they could be widely dispersed not only around the Gondwana but they could reach the margins of

Laurentia and Baltica. But it is only in the Late Ordovician that oceanic barriers had narrowed sufficiently for bivalves to become cosmopolitan again, for the first time since the Mid Cambrian (Cope & Kříž 2013). For the distribution of the Silurian bivalves the temperature, salinity, substrate, food, oxygen content, light, and depth were more limiting factors than geographical barriers, as was the distance between favourable environments. Silurian protobranchs are widely distributed, known from the regions close to equator (Baltica, Laurentia and Gondwana) but also from the regions distant from Silurian equatorial latitudes as South American Gondwana (Cope & Kříž 2013).

Middle Ordovician bivalve fauna from Bohemia (Perunica) shows close affinities to the Middle Ordovician fauna known from Spain (Iberia) and France (Armorica) (Fig. 16). Four species (*C. britannica*, *R. deshayesi*, *P. applanans*, *B. prima*) are in common with Spain and three species (*C. britannica*, *R. deshayesi* and *B. prima*) with France. The occurrence of *C. britannica*, *R. deshayesi* and *B. prima* in Bohemia is related to better sea communication between Perunica (Prague Basin) and other peri-Gondwana regions where they occurred earlier.

Conclusions

(i) *Ctenodonta* was widely used in the past as a cumulative name for all praenuculids. The genus *Ctenodonta* Salter, 1852 does not occur in the Middle Ordovician of Bohemia and very probably does not occur in whole Ordovician in the Prague Basin. All the species from the Middle Ordovician of Bohemia assigned in the past to *Ctenodonta* belong to *Praenucula*.

(ii) Actinodonts are dominant group of bivalves in the Middle Ordovician. A new genus *Tatula* gen. nov. with the new type of actinodont hinge is described herein.

(iii) The oldest representatives of pteriomorphans (*Modiolopsis* sp. and *Cyrtodonta* sp.) in the Prague Basin are described here.

(iv) The value of the orientation of teeth to umbo or out from the umbo for higher systematic of the Protobranchia is probably overestimated. The Recent Protobranchia mostly shows simpler types of taxodont teeth compared with the Ordovician Protobranchia. The accessory muscle scars serve in the Protobranchia to hold visceral sac and also support retraction, protraction and elevation of foot together with the protractor and retractor pedal muscle scars.

(v) The bivalve fauna from the Šárka Formation is diversified (12 species) and abundant (1524 specimens known in the Bohemian collections) and it forms part of the *Euorthisina-Placoparia* Association. Bivalves represent infaunal deposit and filter feeders, endobysate filter feeders are rare and they are firstly recorded from the Middle Ordovician of Bohemia.

(vi) Clear preference of the heterodonts for high latitudes (Cope 2002) is confirmed by the dominant heterodonts (six species) in the Middle Ordovician Šárka Formation.

(vii) The palaeogeographic distribution of the Middle Ordovician bivalves is presented. During the Ordovician about 80% known genera of bivalves were locally endemic. On the other hand it was observed that some of the Middle Ordovician bivalves (*Babinka*, *Modiolopsis*, *Praenucula*) could migrate over long distances, when they reach Baltica and Laurentian margins and thus had to have planktotrophic larvae. Bivalve fauna of Bohemia shows the most elements in common with France (Armorican Massif) and Spain (Iberian Peninsula).

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