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Vybraní mlži z ordoviku pražské pánve

Selected bivalves from the Ordovician of the Prague Basin

DISERTAČNÍ PRÁCE

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V Praze dne 1. dubna 2013

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Abstrakt

Cílem této disertační práce je revize vybraných ordovických mlžů z pražské pánve. Ordovičtí mlži patřili dlouhodobě k opomíjené skupině paleozoických bezobratlých. Úvodní část disertační práce se skládá z pěti kapitol, ve kterých jsou popsány hlavní charakteristiky mlžů, dále jsou podrobně popsáni ordovičtí mlži s důrazem na jejich systematiku, diverzifikaci, paleobiogeografii a paleoekologii. Těžištěm práce je revize mlžů ze šáreckého a kosovského souvrství pražské pánve. Zvláštní pozornost je věnována evolučně důležitým skupinám *Protobranchia* Pelseneer, 1889 a *Actinodontida* Dechaseaux, 1952. Všechny kapitoly jsou doplněny o nejnovější poznatky, které byly publikovány v šesti článcích zaměřených zejména na systematiku, paleobiogeografii, paleoekologii, diverzifikaci a ranou evoluci vybraných ordovických mlžů.

Abstract

The submitted PhD. thesis deals with selected Ordovician bivalves from the Prague Basin. They were neglected group for a long time in comparison with many other palaeozoic invertebrates. The first chapter is devoted to the major characteristics of bivalves, next chapters are focused on taxonomy, diversification, palaeobiogeography and palaeoecology of the Ordovician bivalves in general. The last chapter is focused on the bivalves from the Šárka and Kosov formations in the Prague Basin, which were completely revised during my PhD. studies. Special attention is given to the evolutionary important groups Protobranchia Pelseneer, 1889 and Actinodontida Dechaseaux, 1952. Up-to-date information, which was published in the six attached papers, are included in all chapters.

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1 Introduction

This doctoral thesis is focused on the selected Ordovician bivalves from Bohemia (Czech Republic). Initially, the thesis was oriented to the Middle Ordovician bivalves with taxodont teeth from the Šárka Formation (early and middle Darriwilian), which was the most problematic group needing urgently revision. However, it was revealed since beginning of my work, that the bivalves have to be studied in wider context and that it is not possible to study bivalves with different hinges separately. Therefore, the main aim of my thesis was the revision of selected bivalves from the Ordovician of the Prague Basin. These neglected fossils have much to offer in biodiversity, palaeoecology, and palaeobiogeography. The preparation of the new *Treatise on Invertebrate Palaeontology* for bivalves is in progress now and therefore it is an appropriate time for undertaking revision of the Ordovician bivalves from Bohemia. The main supplements of this thesis are papers, which were published during my doctoral studies:

- RÖHLICH, P., BUDIL, P., & **STEINOVÁ (= POLECHOVÁ), M.** 2008. Fauna bohdaleckého souvrství z dočasného odkryvu v Praze 4. *Zprávy o geologických výzkumech v roce 2007*. 132–133.
- KŘÍŽ, J. & **STEINOVÁ (= POLECHOVÁ), M.** 2009. Uppermost Ordovician bivalves from the Prague Basin (Hirnantian, Perunica, Bohemia). *Bulletin of Geosciences* 84(3), 409–436.
- STEINOVÁ (= POLECHOVÁ), M.** 2011a. Middle Ordovician bivalves from Bohemia, Spain and France. In GUTTIÉREZ-MARCO, J., C., RABÁNO I. & BELLIDO, D. G. *Ordovician of the World, Publicaciones del Instituto geológico y minero de España*, 575–580. Instituto Geológico y Minero de España. Madrid.
- STEINOVÁ (= POLECHOVÁ), M.** 2011b. *Praeleda* Pfab, 1934 a *Praenucula* Pfab, 1934 (Bivalvia) z ordoviku pražské pánve. *Zprávy o geologických výzkumech v roce 2010*, 117–119.

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POLECHOVÁ, M. 2013. Bivalves from the Middle Ordovician Šárka Formation (Prague Basin, Czech Republic). *Bulletin of Geoscience* 88(3).

All these articles are cited in the appropriate chapters of my doctoral thesis.

2 The major characteristics of the bivalves

Bivalves (Fig. 1A, B) are bilateral molluscs lacking a distinct head (also jaws, radular teeth, and cephalic sense organs known from other groups of molluscs). They are usually protected by two shelly valves, which are covered by a thin outer organic layer, the periostracum. Typically they are bilaterally symmetrical, a plane of symmetry runs between the valves. But in some forms bilaterally symmetry has been lost, usually as the result of cementation of the one valve to the substrate. At the umbos the valves are connected by calcified elastic structure (ligament) and by interior hinge teeth and sockets. The shell surface has various sculptures, like growth lines, wrinkles or furrows and radial ribs etc. The interior of the shell is commonly nacreous or porcelaneous. Soft parts include the foot, mantle that secretes the shell, gills, visceral sac containing digestive and other organs. The adductor muscles between valves close the shell. Pedal muscles control the movement of the muscular foot, serving as the main tool for burrowing into soft sediment (Cox 1969).

Bivalves occupy marine, brackish and fresh water environments. They are microphagous animals, i.e. feeding on microscopic particles, they can be deposit, suspension or filter feeders. Suspension and filter feeding bivalves need to be well fixed or anchored in the sediment where they can use the water current for filtering organic particles and microorganisms at minimal energy cost. Bivalves burrow in the sediment, or bore into the wood or rocks, or may cement or attach to firm substrates with byssal threads (Kauffman 1969).

The shell grows by accretion at the valve margins, and represents the ontogenetic development of the individual from the earliest stages of the shell to the adult. Evolutionarily the bivalves represent one of the most successful groups of benthic organisms. They first appeared in the "lower" Cambrian (Terreneuvian), survived all periods of mass extinction through the Phanerozoic, and gradually occupied the majority of niches in and on the bottom sediment. In the Recent they represent one of the most diversified classes of molluscs (Cox 1969).

In Bohemia, fossil bivalves are represented in the Ordovician, Silurian and Devonian of the Prague Basin, in the Moravian and Silesian Carboniferous, in the Bohemian Cretaceous Basin and in the Moravian marine Tertiary.

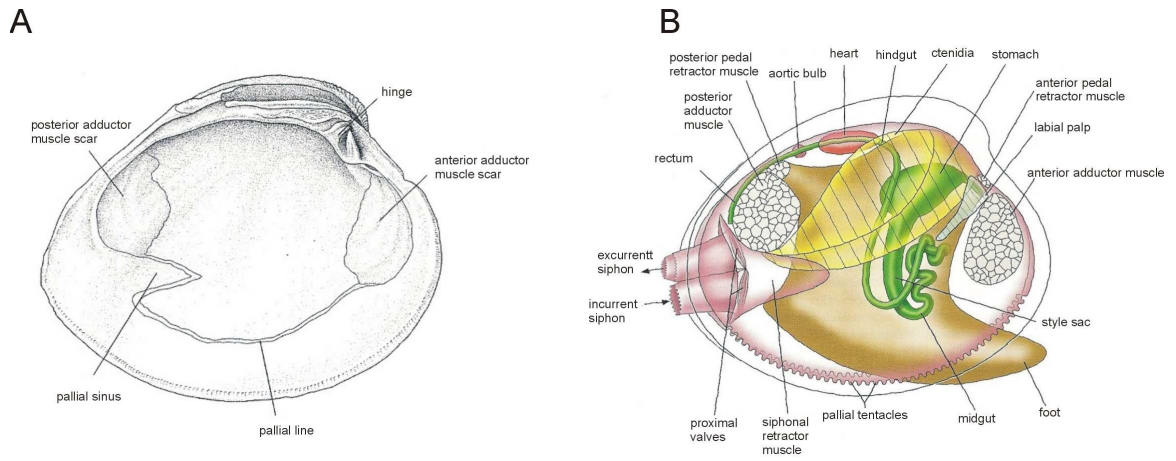


Figure 1. Overall bivalve morphology on the example of bivalve *Mercenaria mercenaria* (Linné, 1758), according to Mikkelsen & Bieler (2008) • A – the features of the interior of the left valve • B – the features of the soft body.

3 Ordovician bivalves

Ordovician was one of the most important periods for the bivalves. Despite this fact the Ordovician bivalves were neglected group comparing with other taxa of molluscs. Only a few species of bivalves are known from the Cambrian, but in the Ordovician there are already known almost 170 genera and all main groups of bivalves have been identified from the Ordovician (Cope 1997, Cope & Kříž 2013).

Ordovician bivalves were studied since 19th century. Conrad (1838), Hall (1847), Bigsby (1868) and Miller (1874, 1877, 1889) published important papers about Ordovician bivalves from North America. Ulrich (1893, 1894) began with the systematic study of the Ordovician bivalves and his two monographs became essential papers for classification of North American species. Series of very important papers and monographs were published in Europe: Sharpe (1853), De Verneuil & Barrande (1856) on Portuguese, Eichwald (1860) on Estonian, Barrande (1881) on Bohemian, and Barrois (1891) French material. The 20th century is crucial for the systematics of the Ordovician bivalves (Soot-Ryen & Soot-Ryen 1960; Babin 1966; Babin & Beaulieu 2003; McAlester 1968; Pojeta 1971; Pojeta & Gilbert-Tomlinson 1977; Tunnicliff 1982; Babin & Gutiérrez-Marco 1991 and Cope 1996, 1999, etc). The fundamental publication was the *Treatise on Invertebrate Palaeontology* for bivalves (1969). Several papers were published on diversification (Babin 1993, 2000; Cope & Babin 1999; Cope 2002; Fang & Cope 2008; Sánchez 2008; Sánchez & Babin 2003, etc.), and the evolution and the phylogeny of the Ordovician bivalves (Pojeta 1978, 1988; Runnegar & Pojeta 1992; Carter *et al.* 2000; Cope 1997, 2000; Fang 2006 and Giribet 2008, etc.).

3.1 Taxonomy of the Ordovician bivalves

The classification of modern bivalves is complex and is based on the gills, hinge, ligament, muscles and muscle scars, labial palps, siphons, stomach, number of loops of the guts and other features. It is obvious that soft parts are very exceptionally preserved and they cannot be used for the taxonomy of extinct

bivalves. Thus, the characters of the shell are highly important for the systematics of the fossils: e.g. shape, type of the hinge, position, type and size of the muscle scars, position of ligament and pallial line (when preserved).

Very problematic feature in the Ordovician bivalves, particularly in the Protobranchia Pelsener, 1889, is the orientation of the shell. The modern bivalves show both orientations (larger part as anterior, or larger part as posterior) and it is not difficult to determine anterior and posterior ends of the shell (siphons and pallial sinus in the posterior part of the shell, foot in the anterior part can easily help). The situation is different in the Ordovician bivalves 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. The significant problem, mentioned by McAlester (1968) and Pojeta (1971), is genus *Ctenodonta* Salter, 1852, which was used as a “waste basket” name mainly for bivalves with taxodont hinge. The other problematic genus in the similar way is *Modiolopsis* Hall, 1847. Pojeta (1971) showed that more than 163 of North American species are assigned under the name *Modiolopsis*. In general, edentulous hinge and modioliform shape of the shell are only significant characters for this genus and the classification on the species level is very difficult (Kříž & Steinová 2009, Polechová 2013). In spite of the fact that a lot of Ordovician bivalves (especially those from the Early and Middle Ordovician) have been recently revised, the problems still remain. As an example, it is very difficult to determine *Praenucula* vs. *Praeleda* described firstly by Pfab (1934) from Bohemia (Steinová 2011b, Polechová 2013). Cope (1997, 1999) includes *Praeleda* to Cardiolaridae, Kříž & Steinová (2009) and Polechová (2013) group *Praeleda* together with *Praenucula* to Praenuculidae McAlester, 1969. It also seems that these two genera could be congeneric, but a revision of all Ordovician species belonging to *Praeleda* or *Praenucula* is necessary. In my thesis I was focused in detail on evolutionary important Protobranchia Pelsener, 1889 and Actinodontida Dechaseaux, 1952, which are abundant in the Ordovician of Bohemia.

3.1.1 Protobranchia

Protobranchia (syn. Palaeotaxonta Korobkov, 1954) is a very successful group of bivalves, its stratigraphical range is from the Cambrian to the Recent. They possess taxodont hinge (Fig. 3A), simple shape of the shell and protobranch gills. This group is very abundant in the Ordovician but its systematics is very complicated (e. g. Pojeta 1971, McAlester 1968). It is a group, which urgently need a revision. As mentioned above the main problem is the genus *Ctenodonta* originally described from the Ordovician of North America. According to Pojeta (1971), 183 of North American species were assigned to this genus. Pfab (1934), who revised Bohemian protobranchs described by Barrande (1881), also overused the name *Ctenodonta* but, on the other hand, he correctly recognized and described new important genera *Praenucula*, *Praeleda* and *Pseudocyrtodonta*. A lot of species, classified as *Ctenodonta*, were reassigned to *Praenucula* or *Praeleda* (Babin & Gutiérrez-Marco 1991, Cope 1999, Sá 2008 and Polechová 2013) after the revision of the bivalve fauna in the peri-Gondwanan regions.

Praenucula is widespread in peri-Gondwanan and Gondwana regions (Bohemia, France, Morocco, Spain) in the Early and Middle Ordovician. It is also known from Baltica and North America during the Middle Ordovician. *Ctenodonta* has not been recorded from the Middle Ordovician of Bohemia and does not very probably occur in the Ordovician of Bohemia. All the species from the Middle Ordovician of Bohemia assigned to *Ctenodonta* in the past belong to *Praenucula* (Polechová 2013).

The main characters important for the taxonomy of Protobranchia such as the orientation of the shell, the type of the taxodont hinge and the position of muscle scars are discussed in detail in Polechová (2013).

Orientation of the shell: The modern protobranchs are the bivalves with both possible morphologies of the shell with larger part as anterior or posterior. It is very difficult to determine the orientation of the shell in the Ordovician Protobranchia. Pallial line is preserved very rarely and foot as a soft part with

almost no chance of preservation is not effectively traced in the inner morphology of the shell.

Driscoll (1964) tried to use the pattern of accessory muscle scars as a guide to the animal orientation. It works in some genera but it is necessary properly to recognize all type of the muscle scars and a comparison with modern bivalves is essential. The modern protobranchs are also in many aspects difficult to be studied because their systematics at the genera and species level is confusing: some modern genera are established on the hard parts (the characters of the shell), some on the soft parts (e.g. the number of loops in the gut, e.g. Allen & Hannah 1989). During my research I studied the modern protobranchs in the Natural History museum in Paris and in the Smithsonian Institution in Washington, D.C. A usage of Driscoll's methodology for determination of anterior and posterior margins of the shell is problematic because the preservation of the accessory muscle scars in the interior of the valve is very rare and it was possible to study this pattern only in some modern genera of Nuculidae (e.g. *Acila* Adams & Adams, 1858 and *Leionucula* Quenstedt, 1934). Contrary to Driscoll (1964), I concluded that modern Protobranchia could have very similar number of the accessory muscle scars like the Ordovician protobranchs (Polechová 2013), being a conservative feature.

Bradshaw & Bradshaw (1971) used the taxodont hinge in combination with the pattern of muscle scars for determination of the shell orientation. They concluded that larger teeth on one side indicate anterior part. It can be applied for the orientation of the shell but some protobranchs have teeth of the same size (e.g. *P. dispar* from the Ordovician of Bohemia) and it is not allowed to use this method for them.

Bailey (2009) published a new alternative. He proposed to avoid subjective terms such as anterior or posterior when it is difficult to recognize orientation of the shell. Terms, which describe bivalves with reference to the shell axes, shell extremities and shell dorsum and ligamental placement, are considered to be used. But it is very difficult to apply this terminology in practice.

Hinge: All protobranchs have taxodont hinge, which can be divided into three types (heterotaxodont, gradidentate and cardiolariid, Carter *et al.* 2012). Taxodont hinge is variable and several types of taxodont teeth have been established

depending on its inclination to the umbo: convexodont, concavodont, orthomorphodont, diconcavodont, diconvexodont, convexoconcavodont and concavoconvexodont, (Fig. 2) (Babin 1966, Carter *et al.* 2012 and Polechová 2013). It is an important question if the types of taxodont teeth are significant character for the systematics. It should be mentioned that main recently publishing specialists for the Ordovician bivalves have different opinions. John Cope (oral communication) and Pojeta (2007) suggested that the type of the teeth is not significant taxobasis character. On the other hand, Babin (1966) and Sánchez (1999) used this character for higher systematics. According to my own studies the teeth inclination to or out the umbo is mostly important for distinguishing species, but its value for higher systematics is overestimated. The types of taxodont teeth in the Ordovician bivalves are highly variable. Contrary to the Ordovician bivalves, the modern bivalves predominantly possess convexodont teeth, terminal anterior and posterior teeth and the teeth under the umbo are often orthomorphodont. Only some species of *Tindaria* Bellardi, 1875 and *Malletia* Des Moulins, 1832 show concavodont and diconcavodont teeth. The taxodont teeth in recent protobranchs are simpler in general (Polechová 2013).

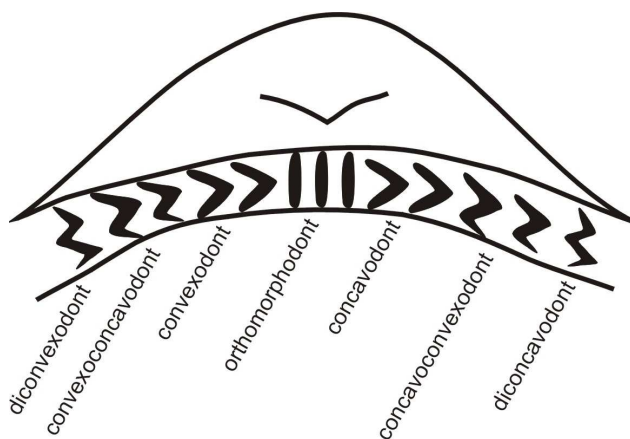


Figure 2. Types of teeth in taxodont hinge according to Carter *et al.* (2012).

Muscle scars: Like other bivalves, protobranchs have adductor muscles and accessory muscles (Fig. 3A). Accessory muscles include also pedal muscles. Muscle scars are often preserved in the internal mould of the shell and they are an important character for the taxonomy and for the functional morphology of the bivalves. The adductor muscles (anterior and posterior) close the shell and pedal

muscles control the movement of the foot. They are divided into retractors, which retract the foot, protractors which eject the foot, and in some cases to elevators, which elevate foot. Other accessory muscle scars, which are preserved in the Ordovician bivalves in the umbo region (*Praenucula*) or between adductor muscle scars (*Babinka* Barrande, 1881, *Coxiconchia* Babin, 1966), reflect the attachments of visceral retractors, which reinforced the action of pedal retractors or provided a firm attachment of the pericardial region to the shell during vigorous movements of the foot. Another, sometimes rather deep muscle scars correspond in protobranchs to the visceral attachment muscles holding the muscular floor of visceral sac (Heath 1937, Kříž 1995 and Polechová 2013).

3.1.2 Actinodontida

This group was very successful during the Early and Middle Ordovician. They extincted in the Silurian but some modern bivalves (e.g. *Prelametila* Allen & Sanders, 1973) possess the hinge very similar to actinodont one (Allen & Sanders, 1973 and Steinová, 2012). Cope (1997) supposed that it is only a convergence. The actinodont hinge (Fig. 3B, C) displays high variability, the hinge patterns present in the important genera are figured and discussed in Steinová (2012). Actinodont hinge is composed of the smaller pseudocardinal (pseudotaxodont) and elongated pseudolateral teeth. *Pseudocyrtodonta* Pfab, 1934 occurring in the the Middle and Upper Ordovician of Bohemia shows very interesting hinge with one elongated pseudolateral tooth in the posterior and more pseudocardinal teeth in the anterior. Pseudocardinal teeth in *Pseudocyrtodonta* are very similar to taxodont teeth. Thus *Pseudocyrtodonta* seems to be a phylogenetically important genus with ancestral type of the actindodont hinge (fig. 3C, see chapter 3. 1. 3). On the other hand *Tatula* Polechová, 2013 from the Middle Ordovician of the Prague Basin possesses a modern type of the actinodont hinge (fig. 3B) closely related to the hinge of *Actinodonta* Phillips, 1848 from the Silurian of Great Britain (Cox *et al.* 1969). *Tatula* also shows some affinities to *Carminodonta* Cope, 1996 from the Floian (early Arenigian) of Wales and to *Ananterodonta* Babin & Gutiérrez-Marco, 1985 from the Darriwilian (Llanvirnian) of Spain. *Carminodonta* could be an ancestor for *Tatula* and

Ananterodonta. All these genera have actinodont hinge with numerous pseudocardinal and pseudolateral teeth (Fig. 3B), which differs markedly from the other cycloconchids with simple type of actinodont hinge like *Pseudocyrtodonta* (Fig. 3C) from the Middle and Late Ordovician of Bohemia and *Fasciculodonta* Fang & Cope, 2004 from the Middle Ordovician (Dapingian–Darriwilian) of China.

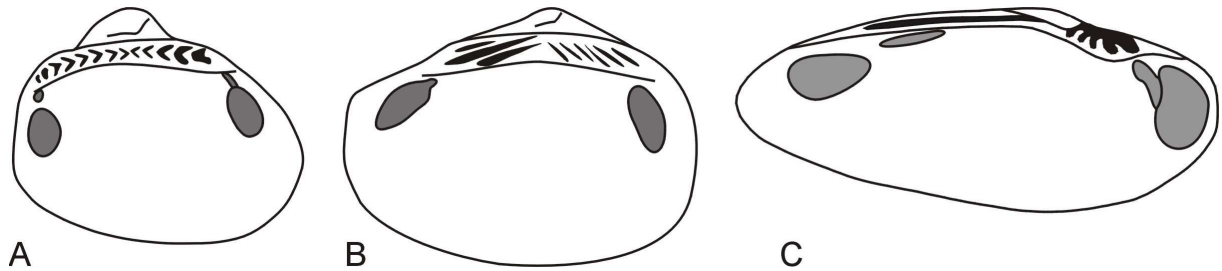


Figure 3. • A – taxodont hinge and muscle scars in *Praenucula dispar* (Barrande, 1881) • B – actinodont hinge and muscle scars in *Tatula petula* Polechová, 2013 • C – actinodont hinge and muscle scars in *Pseudocyrtodonta incola* (Barrande, 1881).

3.1.3 The phylogenetic considerations about protobranchs and actinodonts

Protobranchs and actinodonts are important for understanding the early phylogeny of the bivalves. There are three hypotheses explaining the early evolution of protobranchs and actinodonts, which are generally accepted: **1)** some authors accept an idea that the actinodont teeth are derived from the taxodont ones (Babin 1966; Newell 1969; Pojeta 1971, 1978; Jell 1980; Babin & Le Pennec 1982; Runnegar & Bentley 1983; Pojeta & Runnegar 1985; Waller 1990; Sánchez 1995, Cope 1996, 1997 and Ratter & Cope 1998) **2)** others prefer an opposite view, the taxodont teeth derived from the actinodont ones (Morris & Fortey 1976, Morris 1980) **3)** Sánchez & Babin (1998) published another alternative that protobranchs and actinodonts originated independently. Carter *et al.* (2000) agreed with their opinion and advocated that the Actinodontida has apparently evolved convergently among the Protobranchia. However, a lack of the data from the Cambrian (Furongian) and the Lower Ordovician leaves the question about the early divergence of bivalves lineages open. *Pseudocyrtodonta* from the Middle

Ordovician of Bohemia shows very simple hinge (Fig. 3C) like *Fasciculodonta*. This hinge could be considered close to the ancestral type of the actinodonts if the group was derived from the protobranchs (Fang & Cope 2004, Steinová 2012).

3.2 Diversification of the Cambrian and Ordovician bivalves

Ordovician was one of the most significant periods in the bivalve diversification. From a small stock of the Cambrian protobranchs, a fundamental radiation occurred in the early Ordovician.

The earliest bivalves appeared within the “early and mid” Cambrian (Terreneuvian and unnamed “epoch 2” and “epoch 3”). *Fordilla* Barrande, 1881 and *Pojetaia* Jell, 1980 are two known early Cambrian bivalve genera. *Fordilla* is more widespread and occurs in Gondwana (including still attached Avalonia), Laurentia, Baltica and Siberia, while *Pojetaia* is restricted to Gondwana and Siberia. *Pojetaia* survived to the “mid” Cambrian and new three genera *Tuarangia* MacKinnon, 1982, *Camya* Hinz-Schallreuter, 1995 and *Arhouria* Geyer & Streng, 1998 (even if Carter *et al.* 2000 supposed, that the holotype is an ostracod in fact) are recorded from the “mid” Cambrian. The “late” Cambrian (Furongian) bivalves are represented only by one specimen of *Tuarangia* recorded from the lower part of the “upper” Cambrian of Baltica (Berg-Madsen 1987). *Fordilla* and *Pojetaia* are classified in the Protobranchia family Fordillidae, *Tuarangia* is assigned to the Protobranchia with reserve and *Camya* remains of uncertain position. There is a gap of bivalve record between the early part of the “late” Cambrian (Furongian) and the Early Ordovician. The questions about the origin of the bivalves still remain, according to Sánchez & Babin (1998) and Carter *et al.* (2000) the bivalves could be paraphyletic group (see also chapter 3.1.3).

The oldest Ordovician bivalve fauna is described from the lower Tremadocian of Argentina (Harrington 1938, Sánchez 2005). Other nine species of Tremadocian bivalves were recorded from France (Babin *et al.* 1982), and Australia (Pojeta & Gilbert Tomlinson 1977). Thirty-five species are known from the Floain, Dapingian and early Darriwilian (Arenigian). Six of seven currently recognised bivalve subclasses are known from the upper part of the Lower

Ordovician (Cope 1997). The initial stage of this explosive radiation occurred in the very earliest Ordovician (early Tremadocian). Despite of the poor knowledge it is clear that during a short time interval bivalves became according to Cope & Babin (1999):

- a) more abundant (one locality from the lower Tremadocian, dozen localities at the top of the Lower Ordovician, and more than one hundred localities in the Middle Ordovician).
- b) more diverse (one family at the end of the Cambrian, seventeen families belonging to six subclasses by the end of the Early Ordovician)
- c) larger (1-2mm length of Cambrian bivalves, 15 mm in the Early Ordovician bivalves, more than 30 mm in the Middle Ordovician bivalves).

Cope & Babin (1999) claimed that an intrinsic factor was the most significant for the rapid bivalve diversification in the Early Ordovician. It was a development of the feeding gill, which allowed more effective feeding strategies, permitting bivalves to take advantage of the increased Ordovician nutrient supply. This allowed rapid size increase, diversification, and colonization of a variety of habitats from entirely infaunal into semi-infaunal and epifaunal. The peri-Gondwanan shelves played a key role in the initial diversification during the Early and Middle Ordovician (Babin 1993, Cope 2002, Sánchez & Babin 2003). Bivalves are known worldwide from the Cambrian, but have not been recorded in the Ordovician of Laurentia up to the Darriwilian (Babin 1993, Babin 2000, Cope 2004, Stewart 2011 and Polechová 2013). In the Early Ordovician they were confined to Gondwana. Some important groups (redoniids and coxiconchiids) have very probably originated in Northwestern Argentina Basin (Sánchez 2008). According to Cope (2002), the Early and Middle Ordovician bivalves became highly diversified and abundant group in many regions. They even dominated in the Lower Ordovician fauna from the Llangynog Inlier in South Wales (Cope 1996). Middle Ordovician bivalve shell beds with dominant *Redonia* Rouault, 1851 and *Praenucula* are described from France (Babin 1966, Dabard *et al.* 2007). The other Middle Ordovician bivalve shell beds are known from North America, the dominant element is *Modiolopsis* (Li & Droser 1999).

The Late Ordovician radiation was largely controlled by extrinsic factors, as the development of low latitude carbonate platforms promoted the evolution of many epifaunal groups, particularly the modiomorphids and the pteriomorphids (Cope &

Babin, 1999). The development of extensive low latitude carbonate platforms was a significant factor in this evolution, but shallow water sands and silts provided further opportunities for these forms. Away from the shallow waters, protobranchs evolved many new species in the muds and silts of deeper water areas and here were frequently the dominant forms (Tunnicliff 1987, Cope & Kříž 2013).

3.3 Palaeobiogeography of the Ordovician bivalves

The palaeogeographic distribution of the bivalve faunas has been studied by Babin (1993a, b, 1995, 2000), Cope (2002, 2004), Cope & Babin (1999), Sánchez (2008), Sánchez & Babin (2003) and Fang (2006).

The Lower Ordovician bivalves are known from the higher paleolatitudes (Montagne Noire in France and Wales) as well as from the low paleolatitudes (Argentine Precordillera and Australia).

The rapid expansion of the bivalves is characteristic for the Darriwilian (Middle Ordovician). Genus *Praenucula*, the dominant element of praenuculids, is common in Bohemia, France, Morocco, Spain and Wales. *Babinka*, belonging to lucinids, appears in the upper Tremadocian in Northwestern Argentina Basin and in Montagne Noire. During the Darriwilian, *Babinka* occurred in Armorica and Avalonia, Baltica, Iberia and Perunica. *Coxiconchia* is also known from the Floian of Montagne Noire and Northwestern Argentina Basin. During the Darriwilian *Coxiconchia* became more abundant in France and Spain. Kříž (1995) recorded this genus also in Bohemia. *Redonia* is known from the Floian of Montagne Noire and it is widespread during the Darriwilian (Bohemia, France, Morocco, Portugal, Spain and Wales).

Sánchez & Babin (2003) concluded that bivalves are not relevant palaeobiogeographic indicators, because of the low number of common genera among different localities (80% from 144 known genera are locally endemic; according to Cope & Kříž, 2013, the total number of Ordovician genera valid in present day is almost 170). Babin (1995) and Sánchez & Babin (2003) presumed that Ordovician bivalves had the lecithotrophic larvae explaining the restricted extent along Gondwana in the Ordovician. According to Cope & Kříž (2013) and Polechová (2013), it seems that some of the Middle Ordovician genera could

overcome long distances. *Modiolopsis* is recorded from Australia, Bohemia, Spain, Wales, Argentina (Argentine Precordillera) and North America. Similarly, *Cyrtodonta* Billings, 1858 occurs in Australia, North China and probably in Bohemia. *Babinka* is known from Bohemia, France, Morocco, Spain, Sweden (Baltica) and Wales. *Coxiconchia* is recorded from Bohemia, Bolivia, France and Spain. *Praenucula* or *Praeleda* are known from Bohemia, France, Morocco, Spain, Sweden, Wales, and probably from North America. Some of these genera very probably had the planktotrophic larvae to be widely dispersed (Polechová, 2013) (Fig. 4).

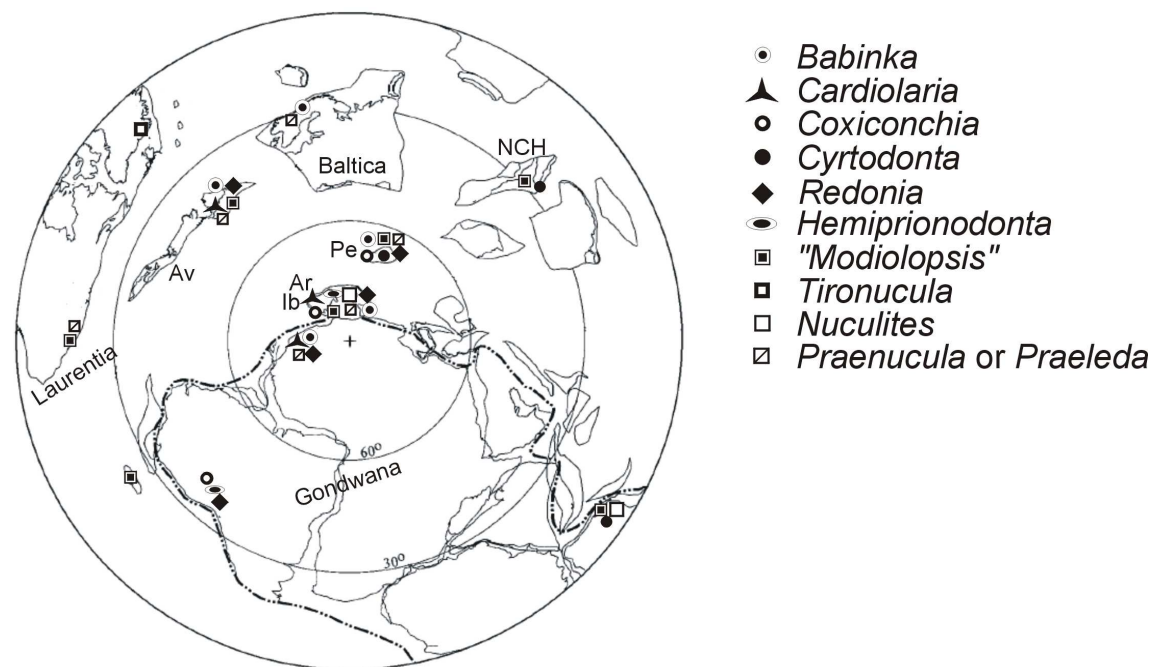


Figure 4. Palaeogeographic distribution of the bivalves during the Middle Ordovician, palaeogeographic map according to Cocks & Torsvik (2002). Abbreviations: Ar. – Armorica, Av. – Avalonia, Ib. – Iberia, NCH. – North China, Pe. – Perunica.

Cope & Kříž (2013) discussed Early Palaeozoic palaeobiogeography of the bivalves and they analysed composition of faunas in terms of major groups. Major groups of bivalves for the Ordovician are Afghanodesmatids, Glyptarcoids, Redoniids, Cyrtodontids and Ambonychiids. These groups show a considerable degree of positive correlation with latitude, especially in the Early and Middle Ordovician and therefore they can be used as a tool for palaeogeographical

reconstruction. In the Upper Ordovician the principal control of composition of the bivalve assemblages depend more on the facies.

Cope (2002) compared the Ordovician bivalves from high, middle and low latitudes and revealed difference in both bivalve diversity and assemblage composition. The number of species at equatorial latitude is twice compared to the highest latitude. There is a clear preference of the pteriomorphids proved in the low latitudes and heterodonts in the high latitudes. The problem is a lack of complex data from many regions. Sufficient data for exemple for the Middle Ordovician bivalves are available only from Australia, North China, Spain, Wales, and recently from Bohemia.

Early Ordovician bivalves are completely different from the Cambrian ones (Fang 2006). Ordovician bivalves are much larger as mentioned above, they are deposit and suspension feeders and probably the feeding gill had been evolved among them. Their foot became to be used for burrowing (Cope & Babin 1999, Fang 2006). Bivalves ranged from very shallow silts and sands to the deeper shelf muds and they had migrated into estuarine waters within the Early Ordovician for the first time (Sánchez & Benedetto 2007). During the Early Ordovician, bivalve larvae were unable to cross the oceans to other continental shelf seas and they most probably remained confined to the shelves around the Gondwanan continent (where they ranged from equatorial to south polar latitudes).

Middle Ordovician faunas still remained to be confined essentially around the Gondwana but they occur also in Baltica and North America. How it was mentioned above, heterodonts prevail in high latitude, while pteriomorphids are most abundant at middle and high latitudes. The conclusions of Cope (2002) are also confirmed by the composition of the bivalve fauna from the Šárka Formation of Bohemia where heterodonts prevail, being represented by six species (Polechová 2013).

Late Ordovician bivalves were cosmopolitan (Cope & Kříž 2013), they occur also in shallow water carbonate platforms that existed in low latitudes such as Baltica, Laurentia and Siberia. The Hirnantian glaciation at the end of the Ordovician caused sea-level changes. It was accompanied by a major extinction event in the bivalves (Kříž & Steinová 2009) particularly in those forms adapted to life on carbonate platforms and two thirds of all genera became extinct in a very short time span (Cope & Kříž 2013).

3.4 Palaeoecology of the Ordovician bivalves

Using the functional morphology of the shell in living bivalves it makes possible to interpret modes of life in the majority of fossil bivalves, and thus model their palaeoenvironment. Bivalve living habit is divided into broad categories, each containing adaptive groups with certain unique morphologic features. Fang (2006) concluded that the Cambrian bivalves were benthic crawlers and that infaunal mode of life in the bivalves appeared in the Ordovician.

In general, there are three main categories of bivalve living habit 1) infaunal 2) semi-infaunal and 3) epifaunal.

Most of the Ordovician bivalves are infaunal deposit feeders and filter feeders. Semi-infaunal and epifaunal elements are more abundant in the Late Ordovician. It corresponds also to studies on the Ordovician bivalves from Bohemia: in the Middle Ordovician, heterodonts (infaunal filter feeders) and protobranchs (infaunal deposit feeders) dominate, semi-infaunal bivalves such as *Modiolopsis* and *Cyrtodonta* are very rare (Polechová 2013); semi-infaunal bivalves are more abundant in the Upper Ordovician Letná Formation and in the uppermost Ordovician they dominate (Kříž 1997, Kříž & Steinová 2009).

Ordovician protobranchs are considered as infaunal deposit feeders with similar mode of life to recent protobranchs. They are often preserved with conjoined valves, sometimes in living position. Their pedal muscle scars are large, often well preserved. They controlled the movement of the large foot, which was used for burrowing. They inhabited the sediments, which are rich in organic matter and the sea bottom interface had to be well oxygenated. The most abundant protobranch in the Ordovician of Bohemia is *Praenucula*, which ranges from the Šárka Formation (Middle Ordovician) to the Kosov Formation (uppermost Ordovician).

Pteriomorphids are infaunal, semi-infaunal and byssate filter feeders. The most abundant pteriomorphid in the Bohemian Ordovician is *Modiolopsis*, which is known from the Šárka to the Kosov formations, often found in the sandy facies. It is difficult to determine mode of life of *Modiolopsis*, because it does not provide enough features, only shape of the shell and edentulous hinge line are available. According to Stanley (1970) it could be semi-infaunal or infaunal.

Heterodonts are probably infaunal filter feeders (McAlester 1965, Pojeta 1971, Babin & Gutiérrez-Marco 1991). *Redonia* is dominant element in the Middle Ordovician of Bohemia (Šárka and Dobrotivá formations). Typical character for *Redonia* is myophoric buttress on the anterior adductor muscle scar, which is developed in burrowers. Heterodonts in the Late Ordovician are rare.

4 Ordovician bivalves from Bohemia

Ordovician bivalves from Bohemia have been almost overlooked for a long time since studies of Barrande (1881) and Pfab (1934). The Middle Ordovician bivalves from Bohemia are very similar to bivalves from Spain and France where the Ordovician bivalves were studied in detail for a long time (e. g. Babin 1966, 1977, 1985; Babin *et al.* 1982; Babin & Beaulieu 2003, and Babin & Gutiérrez-Marco 1991). All the authors pointed out the lack of modern information about Ordovician bivalves from Bohemia. Barrande (1881) figured and described nineteen bivalve genera from the Ordovician of the Prague Basin. Pfab (1934) was the only one, who did a subsequent systematic revision but it deals only with bivalves possessing taxodont hinge. He reassigned some of the Barrande's (1881) species to the genera: *Praeleda* Pfab, 1934, *Praenucula* Pfab, 1934, *Pseudocyrtodonta* Pfab, 1934 and mainly to *Ctenodonta* and some of them he left in open nomenclature. Polechová (2013) concluded that *Ctenodonta* (for detailed comment see above) is not recorded from the Middle Ordovician and very probably does not occur in the whole Ordovician of the Prague Basin.

After Pfab (1934) only a few authors have studied the Ordovician bivalves. Růžička & Prantl (1960) designated the lectotype for *Babinka prima* Barrande, 1881. Horný (1960) revised *Babinka prima*, established new family Babinkidae and interpreted the phylogeny of the earliest bivalves from monoplacophorids through the new order Diplacophora Horný, 1960. The systematics, affinities and life habits of *Babinka* as ancestral lucinid bivalve were reinterpreted by McAlester (1965). Kříž (1995) described a representative of the genus *Coxiconchia* from the Šárka Formation and contributed to the knowledge of accessory muscle scars and their function in the Protobranchia. Kříž (1997) briefly commented palaeoecology of the Ordovician bivalves in Bohemia.

The main topics of my research were the Middle and uppermost Ordovician bivalves from the Prague Basin (Kříž & Steinová 2009, Steinová 2011a, Steinová 2012 and Polechová 2013). Two contributions concerning to the Upper Ordovician bivalves were published in Röhlich *et al.* (2009) and Steinová (2011b).

4.1 Middle Ordovician bivalves from Bohemia

Bivalves, which were chosen for this doctoral thesis, come from the Šárka Formation (Middle Ordovician, Darriwilian). Bivalves from the Middle Ordovician of the Prague Basin are better preserved than those from the Upper Ordovician and therefore preferentially revised.

The Šárka Formation was deposited during the early and middle Darriwilian. The largest part of this unit is developed in the grey shale facies. Horizons with siliceous nodules containing well-preserved and diverse fauna occur within the successions. These nodules are restricted to several localities in Prague, Rokycany vicinity and near Úvaly and Brandýs nad Labem.

The other reason for study of the Middle Ordovician bivalves from the Prague Basin was recent revisions and thus complex data from several regions. Thus, it was possible to make a comparison with the bivalve faunas from Argentina (Sánchez 1990), Australia (Pojeta & Gilbert-Tomlinson 1977), Belgium (Maillieux 1939), China (Fang & Cope 2004, Fang 2006), France (De Verneuil & Barrande 1856, Barrois 1891, Babin 1966, Bradshaw 1970, 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, Babin & Gutiérrez-Marco 1991, Gutiérrez-Marco & Babin 1999), Sweden (Soot-Ryen 1969) and Wales (Cope 1996, Cope 1999).

The large collections of the Middle Ordovician bivalves, including Barrande's types, are deposited in the National Museum. The collection of František Hanuš was especially important because undescribed bivalves from the Šárka Formation was discovered (*Tatula petula* gen. et sp. nov. Polechová, 2013, *Modiolopsis* sp., and *Cyrtodonta* sp.). Other large collections from the Middle Ordovician bivalves are housed in the Museum of Dr. Bohuslav Horák, Rokycany. The specimens deposited here were mainly collected by Karel Holub and by Petr and Jaroslav Kraft.

Reviewed rich bivalve fauna from the Middle Ordovician of Bohemia proved close affinities to the coeval bivalves from Spain (Iberian Peninsula) and France (Armorican Massif, Montagne Noire). According to Havlíček *et al.* (1994), this similarity could indicate easy migration of mobile pelagic larvae of benthos along

deep shelves and between separate terranes (Avalonia, Armorica, Perunica and cratonic Western Gondwana). The following twelve species and eight genera (one new) were described from the Šárka Formation (Fig. 5): *Praenucula applanans* (Barrande, 1881), *Praenucula dispar* (Barrande, 1881), *Praenucula bohémica* (Barrande, 1881), *Concavodonta ponderata* (Barrande, 1881), *Pseudocyrtodonta ala* (Barrande, 1881), *Pseudocyrtodonta incola* (Barrande, 1881), *Tatula petula* Polechová, 2013, *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.

B. prima and *C. britannica* are in common with Spain and France, furthermore *Praenucula applanans* is in common with Spain. *Ctenodonta* does not occur in the Middle Ordovician of Bohemia. After the revision of all praenuculids from the Šárka Formation, all species, which were in the past recognized as *Ctenodonta*, were reassigned to *Praenucula*.

The bivalve association from the Šárka Formation is dominated by actinodonts, subdominant are several species of protobranchs and two pteriomorphids. The bivalves are well preserved, mostly with conjoined valves (61.1%). In the subtidal, soft bottom environment the abundant infaunal deposit-feeding bivalves (*Praenucula*) occur. The dominance of actinodonts could be partially artificial. Fossiliferous nodules attracted attention of a lot of private collectors, who were focused mainly on trilobites and small bivalves were very often overlooked. On the other hand *Redonia* is one of the large bivalves in the Šárka Formation and therefore it was more often collected. Paleoecological aspects of all species are shown, infaunal burrowers dominate in the bivalve fauna from the Šárka Formation (Polechová 2013).

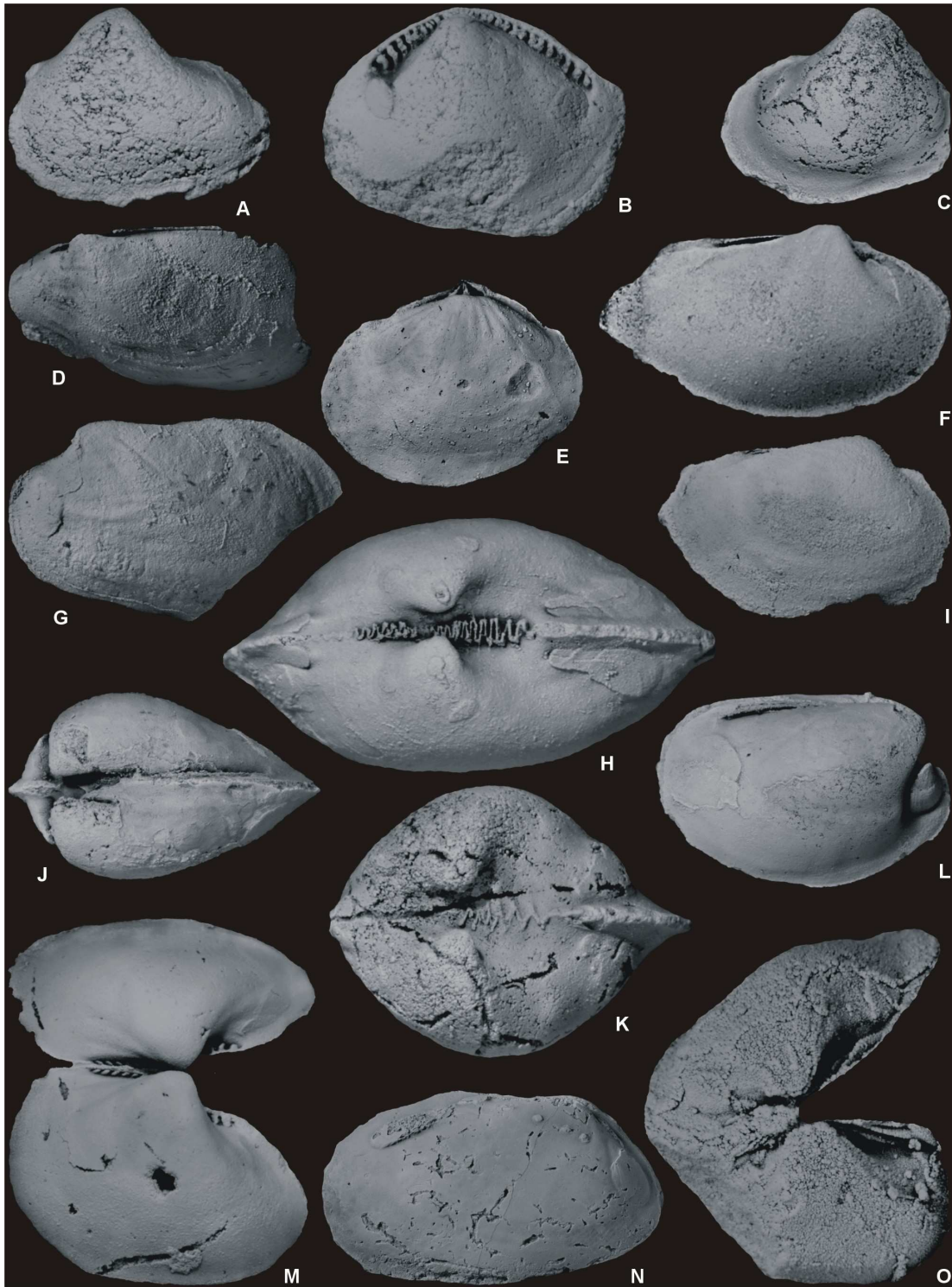


Figure 5. • A – *Praenucula bohémica* (Barrande, 1881) – MBHR 14448, right valve, lateral view, x 6.6 • B – *Concavodonta ponderata* (Barrande, 1881), NM L 42215, left valve, dorso-lateral view, x 10 • C, K – *Praenucula dispar* (Barrande, 1881) MBHR 7982, articulated specimen; C – left lateral view, x 6.1; K – dorsal view, x 7.1 • D – *Cyrtodonta* sp., NM L 41036b, left valve, dorso-lateral view, x 7 • E – *Babinka prima* Barrande, 1881, NM L 27086, left valve, lateral view, x 2.4 • F – *Pseudocyrtodonta incola* (Barrande, 1881), MBHR 13415, right valve, lateral view, x 3.3 • G – *Modiolopsis* sp., NM L 41036a, left valve, lateral view, x 5.5 • H, M – *Praenucula applanans* (Barrande, 1881); H – MBHR 14619, articulated specimen, dorsal view, x 5.8; M – MBHR 2395, articulated specimen, dorsal view, x 5.3 • I – *Pseudocyrtodonta ala* (Barrande, 1881), MBHR 12701, right valve, lateral view, x 5.3 • J, L – *Redonia deshayesi* Rouault, 1891, NM L 22656, articulated specimen; J – dorsal view, x 5.5; L – right lateral view, x 5.6 • N – *Coxiconchia britannica* (Rouault, 1851), CW 2, right valve, lateral view, x 1.7 • O – *Tatula petula* Polechová, 2013, NM L 41038, articulated specimen, dorsal view, x 11.

4.2 Uppermost Ordovician Bivalves from Bohemia

During my studies, it was given to me an opportunity to study the bivalves from the uppermost Ordovician in the Prague Basin. This material was collected by L. Marek, who systematically searched for the fossiliferous uppermost Ordovician rocks in the Prague Basin. He discovered and exposed important localities in the Kosov Formation (Nová Ves Gorge near Praha-Butovice and Praha-Běchovice) and systematically collected the fossils. This material and some new collections were studied and described by Kříž & Steinová (2009).

Twelve species (four new) and nine genera of bivalves (Fig. 6) were described from the uppermost Hirnantian, Upper Ordovician of the Prague Basin, Bohemia: *Praenucula dispar* (Barrande, 1881), *Praenucula abrupta* sp. nov., *Sluha kosoviensis* (Barrande, 1881), *Nuculites* aff. *planulatus* Conrad, 1841, *Myoplusia contrastans* (Barrande, 1881), *Myoplusia incisa* (Barrande, 1881), *Myoplusia* sp., *Metapalaeoneilo dromon* sp. nov. Kříž & Steinová, 2009, *Praeleda compar* (Barrande, 1881), *Mytilarca mareki* sp. nov. Kříž & Steinová, 2009, *Modiolopsis pragensis* sp. nov. Kříž & Steinová, 2009, and ?*Sphenolium* cf. *parallelum* Ulrich, 1894.

Almost monospecific *Modiolopsis pragensis* Community of the *Modiolopsis* Community Group was described from the coarse, storm generated sandstones. It indicates restricted living conditions.

The redefined *Hirnantia sagittifera*–*Sluha kosoviensis* Community represents the most diversified community of the *Hirnantia* Community Group known the world-wide. It was supposed that the *Hirnantia sagittifera*–*Sluha kosoviensis* Community occupied the well-oxygenated environment of the soft bottom carbonate silts with high organic content. The community was most probably autochthonous, with minimum transport as indicated by the common preservation with conjoined valves (articulated brachiopods, semi-infaunal bivalve *Mytilarca mareki*, and infaunal bivalves).

For the analogous and homologous communities was described the *Hirnantia* Community Group as a substitute for the term “*Hirnantia* fauna”. The *Hirnantia* Community Group was most probably extending from the circumpolar into the temperate to tropical zones in proximity to the carbonate platforms. In Bohemia and elsewhere it occurs just a few metres below the Ordovician-Silurian boundary

and represents the evidence of the environmental recovery during the latest Ordovician transgression following the Late Ordovician global glaciation.

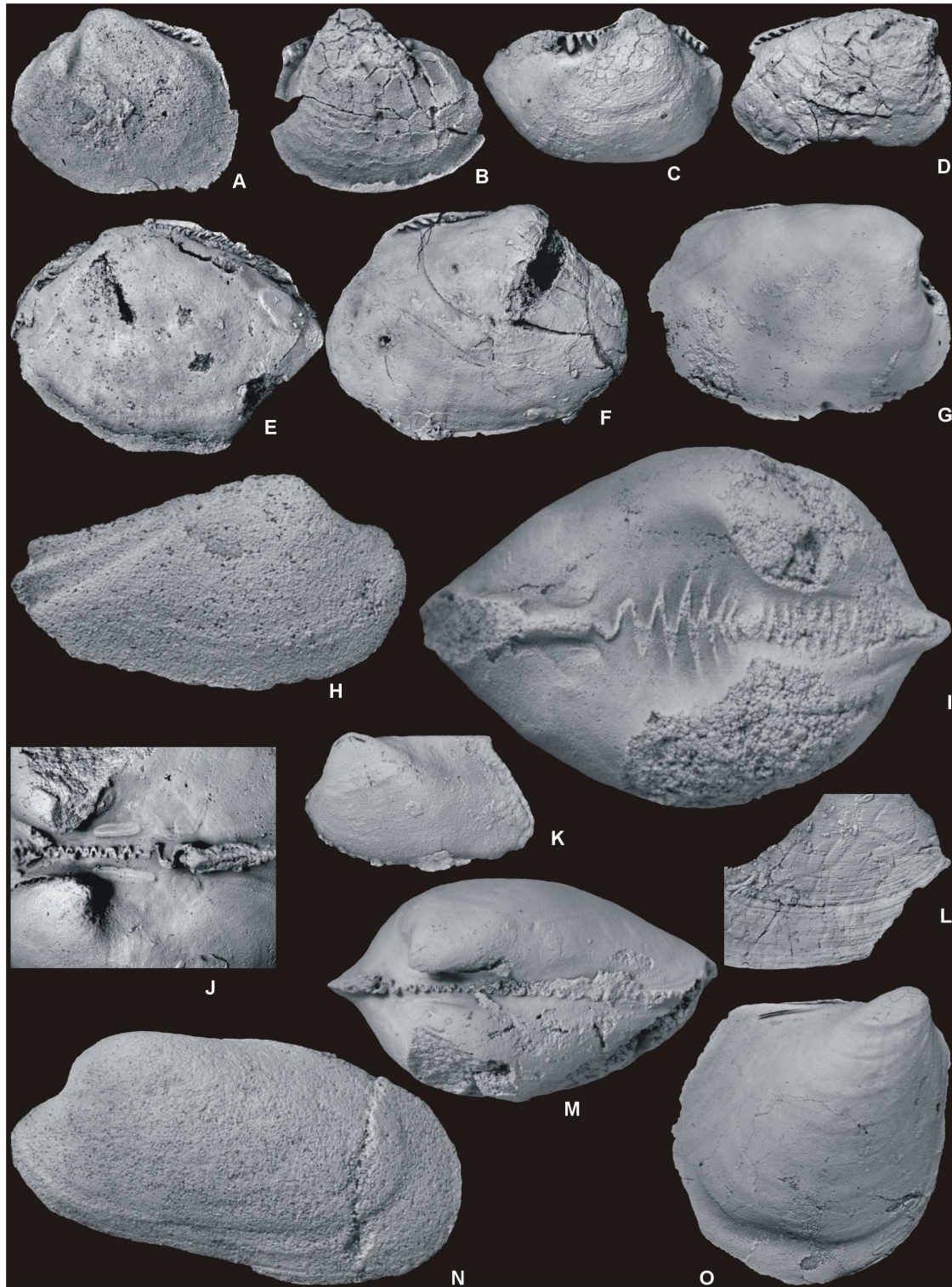


Figure 6. ● A – *Nuculites* aff. *planulatus*. – JK 14941, left valve, lateral view, x 4.5 ● B – *Praenucula dispar* (Barrande, 1881), JK 14931, right valve, lateral view, x 4 ● C – *Praenucula abrupta* (Kříž a Steinová, 2009), JK 14939, left valve, dorso-lateral view, x 4 ● D, F, L – *Sluha kosoviensis* (Barrande, 1881); D – JK 14966, right valve, dorso-lateral view, x 3; F – JK 14961, right valve, lateral view, x 2.1; L – JK 14985 – detail of outer surface sculpture, x 2 ● G – *Myoplusia contrastans* (Barrande, 1881), JK 14980, left valve, dorso-lateral view, x 2.5 ● H – *Metapalaeoneilo dromon* (Kříž a Steinová, 2009), JK14958, right valve, lateral view, x 5.8 ● I – *Praeleda compar* (Barrande, 1881), articulated specimen, dorsal view, x 7.2 ● J, M – *Myoplusia incisa* (Barrande, 1881), articulated specimen, JK 14942; J – detail of pedal muscle scars, x 6.9; M – dorsal view on the hinge, x 3.1 ● K – ? *Sphenolium* cf. *parallelum* – JK 14953, articulated specimen, lateral view, x 3.6 ● N – *Modioloopsis pragensis* (Kříž a Steinová, 2009), JK 15097, articulated specimen, dorsal view, x 3.1 ● O – *Mytilarca mareki* (Kříž a Steinová, 2009), JK 15020, right valve, lateral view, x 4.0.

5 Conclusions

The main aim of this thesis was a revision of selected Ordovician bivalves. This aim was accomplished by my research and by published papers, which are focused mainly on the systematics, palaeoecology, palaeobiodiversification of the Middle and uppermost Ordovician bivalves.

The Middle Ordovician bivalves from the Šárka Formation were studied by Steinová (2011a, 2012) and Polechová (2013). One new genus and one new species were described. It was shown importance of genus *Pseudocyrtodonta* for understanding of early evolution of bivalves (Steinová 2012). The features important for systematics of protobranchs are presented. It was revealed that *Ctenodonta*, widely overused name for a lot of Ordovician bivalves, does not occur in the Middle Ordovician of Bohemia and very probably does not occur in the Ordovician of the Prague Basin at all. The palaeogeographic distribution of the Middle Ordovician bivalves was discussed in detail and it was shown that they were widely paleogeographically dispersed and therefore interpreted to have planctotrophic larvae. Middle Ordovician bivalves of Bohemia show close affinities to Middle Ordovician bivalves from Spain and France (Steinová 2011a, Polechová 2013).

The other research was focused on the uppermost Ordovician bivalves and their evolution after the following Upper Ordovician glaciation (Kříž & Steinová 2009). Four new species and two new communities (*Modiolopsis pragensis* Community and *Hirnantia sagittifera*–*Sluha kosoviensis* Community) were described from the Hirnantian. *Hirnantia sagittifera*–*Sluha kosoviensis* Community represents the most diversified community of the *Hirnantia* Community Group known world-wide.

During my research some other bivalves from the Upper Ordovician were briefly described in short papers (Röhlich *et al.* 2009, Steinová 2011b).

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8 Appendages

8.1 Publications

- 8.1.1 RÖHLICH, P., BUDIL, P. & STEINOVÁ (= POLECHOVÁ), M. 2008. Fauna bohdaleckého souvrství z dočasného odkryvu v Praze 4. *Zprávy o geologických výzkumech v roce 2007*, 132–133.

FAUNA BOHDALECKÉHO SOUVRSTVÍ Z DOČASNÉHO ODKRYVU V PRAZE 4

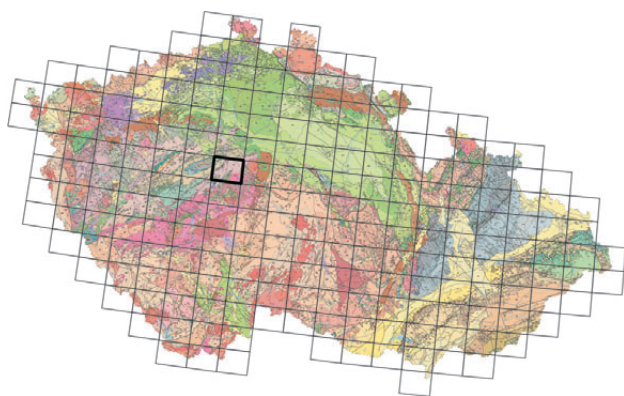
Fauna of the Bohdalec Formation from a temporary outcrop in the southern part of Prague

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Key words: Barrandian area, Prague Basin, Upper Ordovician, Bohdalec Formation, facies development

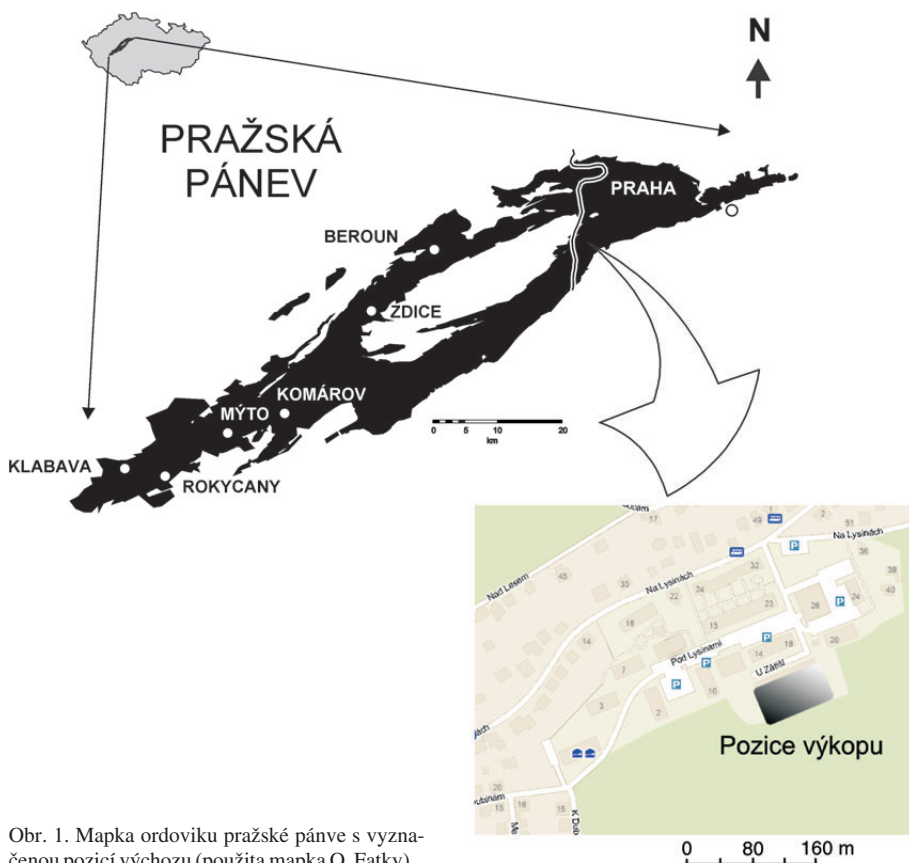
Abstract: New temporary outcrop of the Bohdalec Formation is described. Although the site belongs to the area with outcrops of

the “Polyteichus facies”, no siltstones and limestone intercalations have been observed. Also the fauna shows slightly different character, with dominating bivalves and trilobites, but with almost absent brachiopods and bryozoans.

V létě roku 2005 probíhaly výkopové práce pro stavbu rezidence „Lesní brána“ jižně od ulice U Zátíší v Praze 4 – Hodkovičkách. Staveniště sousedilo s blokem K (č. p. 479–481) tamějšího sídliště. V základové jámě byly odkryty až do hloubky 5 m silně zvětralé tektonicky porušené jílové břidlice bohdaleckého souvrství, převážně strmě ukloněné k VJV ($115^\circ/75^\circ$ v jv. rohu staveniště). Vrtání děr pro velkopřůměrové piloty vyneslo na povrch čerstvý materiál vhodný ke sběru fosilií, které byly místy velmi hojné.

Břidlice bohdaleckého souvrství, zastižené dočasným výchozem, byly tmavošedé, v některých polohách výrazně slídnaté, s jemnou prachovou příměsí. Lokalita patří do oblasti tzv. polyteichové facie, litologicky se vyznačující výskytem prachovcových až pískovcových vložek, vzácněji i nečistých vápenců. Žádná z těchto vložek však nebyla na staveništi zastižena, ačkoliv jsou známy z blízkého okolí v geografické vzdálenosti několika stovek metrů. Břidlice obsahovaly velmi hojné pelokarbonátové konkrce od průměru několika milimetrů do cca 10 cm, zčásti pyritické, místy nahloučené a často spojené s výskytem fosilií. Tektonické porušení břidlic z vývrtů se projevuje hojností tektonických zrcadel, většinou v rovině vrstevnatosti, a ohlasy na povrchu konkrce. Stratigraficky patří lokalita do svrchní nebo střední části bohdaleckého souvrství. Lze vyloučit jeho spodní část, pro kterou je charakteristický výskyt trilobita *Declivolithus alfredi* (viz RÖHLICH 2006); ten nebyl zjištěn ani v jediném úlomku. Spodní část bohdaleckého souvrství se ostatně liší i litologicky, je čistě pelitická.

Ve fauně dominují zbytky mlžů s určitelnými *Ctenodonta* cf. *disputabilis*, *Palaeoneilo* cf. *magna* a množstvím blíže neurčitelných, protože špatně zachovalých drobných nuculidů a trilobitů *Onnia* cf. *superba* (velmi hojně), *Marroli-*



Obr. 1. Mapa ordoviku pražské pánve s vyznačenou pozicí výchozu (použita mapa O. Fatky).

thus sp., *Sokhretia solitaria* (velmi hojně), *Chattiaspis?* sp., *Eudolites cf. angelini*, *Calymenella media*, *Nobiliasaphus?* sp. aj. Z další fauny byly zjištěny zbytky drobných gastropodů a hyolitů, *Metaconularia* sp., *Plumulites* sp., *Glyptograptus* sp., „*Orthoceras*“ sp. a jedna miska neurčitelného orthidního brachiopoda. Navzdory hojnému výskytu není zachování fauny příliš příznivé (většinou nejsou zachovány skulptury a nalézt lze pouze vnitřní jádra, zatímco negativy často bývají pokryty jílovitou mázdrou). Tanatocenóza na lokalitě je pro bohdalecké souvrství neobvyklá. Rozhodně ji nelze zařadit do tzv. polyteichové facie, a to pro téměř úplnou nepřítomnost sesilního bentosu, který v této facii nikdy nechybí (ve zjištěné asociaci zcela chybějí mechovky a z brachiopodů, tak hojných na jiných lokalitách polyteichové facie, je zachován jediný fragment; naopak infauní mlži jsou ale velmi hojní). Společenstvo se poměrně výrazně liší i od bohatších nalezišť mimo „polyteichovou facii“ (např. Velká Chuchle – Na hvězdárně). Téměř úplná absence sesilního bentosu svědčí o trvale nevhodných podmínkách pro tento typ organismů. To může znamenat anoxické prostředí nebo nestabilní substrát, případně kombinaci obojího. Naproti tomu hojnost trilobitů a mlžů svědčí o relativně příznivých podmínkách pro vagilní bentos, přinejmenším občas. Tento rozpor lze vysvětlit redepozicí alespoň části zbytků fauny krátce po odumření orga-

nismů z nestabilního svahu pánevního dna do anoxického prostředí. Fauna je totiž rozlámaná a často tvoří akumulace (např. drobných nuculidů a trilobitů), což ukazuje na stopy hrnutí a gravitačního sesouvání bahnatého sedimentu na mořském dně. Ačkoli většina elementů patří k infauním, kvaziinfauním či vagilně bentickým prvkům, nebyly zjištěny žádné ichnofosilie. Některé konkrece ovšem svým tvarem upomínají na ichnorod *Thalassinoides* isp. a není vyloučeno, že původně mohlo jít o částečně zpevněné výplně chodeb, hrnuté spolu s organickým detritem.

Prostředí sedimentace lze považovat za přechodné mezi typickou „polyteichovou facii“ a hlubokovodnějším vývojem pánve. Blízkost odkrytů typické „polyteichové facie“ lze vysvětlit tektonickým zkrácením i pravděpodobnou synsedimentární tektonikou, vyzdvihující a relativně poklesávající některé dílčí bloky i v rámci pankráckého segmentu ve studované oblasti (viz RÖHLICH 2006).

Práce byla podporována projektem VaV DE08P04OMG002.

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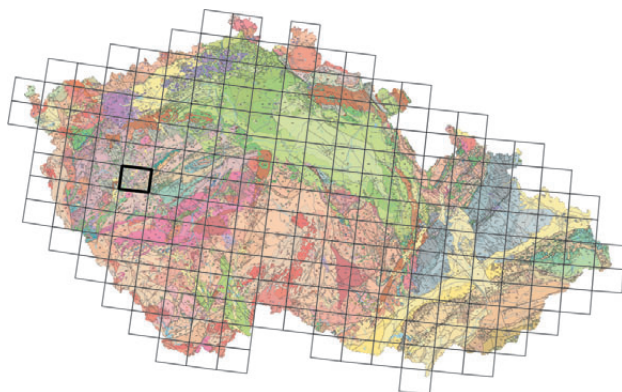
REVIZE DRUHU *CTENODONTA BOHEMICA* (BARRANDE, 1881) (BIVALVIA) Z ČESKÉHO DARRIWILU (ORDOVIK)

Revision of species *Ctenodonta bohemica* (Barrande, 1881) (bivalves) from Darriwilian (Ordovician, Prague Basin)

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Key words: Middle Ordovician, Prague Basin, taxonomy, Bivalvia, Nuculids, *Ctenodonta bohemica*

Abstract: The generic name *Ctenodonta* is very largely used. Most of nuculoid bivalvia from the Middle Ordovician of Prague

Basin were classified as *Ctenodonta bohemica*. But it was found out, that this species is relatively rare.

Nuculidi jsou velmi důležitou skupinou, od níž se odvozuje vznik všech ostatních skupin mlžů (Bivalvia). Přesto je tato skupina velmi zanedbávána. Jde o mlže se zdánlivě jednoduchými znaky, ale jejich systematika je velmi složitá. Jedinci jsou často špatně zachováni, některé znaky jsou nedoceněny (zámek), jiné naopak přeceňovány (tvar schránky). Časté nedostatky také vznikají špatnou orientací schránky (přední část schránky se zaměňuje za zadní a obráceně).

BARRANDE (1881) popsal ze šáreckého souvrství zejména druhy *Leda bohemica*, *Leda ala*, *Leda incolata*, *Nucula applanans*, *Nucula dispar* a *Nucula faba*. Revizí těchto druhů mlžů se zabýval PFAB (1934). Analyzoval u nich význam hlavních znaků pro systematiku jako jsou taxodontní zámek, svalové vtisky, plášťová čára a zabýval se i jejich systematikou. Popsal nové rody *Praeleda*, *Praenucula*, *Pseudocyrtoodonta* a některé Barrandovy druhy přeřadil do jiných rodů. MCALLESTER (1968) zrevidoval všech 64 rodů,

- 8.1.2 KŘÍŽ, J. & STEINOVÁ (= POLECHOVÁ), M. 2009. Uppermost Ordovician bivalves from the Prague Basin (Hirnantian, Perunica, Bohemia). *Bulletin of Geosciences* 84(3), 409–436.

Uppermost Ordovician bivalves from the Prague Basin (Hirnantian, Perunica, Bohemia)

JIRÍ KRÍŽ & MARIKA STEINOVÁ



Twelve species (four new) and 9 genera of bivalves are described from the uppermost Hirnantian, Upper Ordovician of the Prague Basin, Bohemia: *Praenucula dispar* (Barrande, 1881), *Praenucula abrupta* sp. nov., *Sluha kosoviensis* (Barrande, 1881), *Nuculites* aff. *planulatus* Conrad, 1841, *Myoplusia contrastans* (Barrande, 1881), *Myoplusia obtusa* (Barrande, 1881), *Myoplusia* sp., *Metapalaeoneilo dromon* sp. nov., *Praeleda compar* (Barrande, 1881), *Mytilarca mareki* sp. nov., *Modiolopsis pragensis* sp. nov., and *?Sphenolium* cf. *parallelum* Ulrich, 1894. From the coarse, storm generated sandstones representing the additional regressive event, when the shelf was channelled, and coarse material transported from the shore in the late Hirnantian, the low diversified, almost monospecific *Modiolopsis pragensis* Community, of the *Modiolopsis* Community Group, was described. It indicates restricted living conditions. 11 bivalve species form, together with 25 species of brachiopods, 5 species of gastropods, and undescribed conulariids, hexactinellids, trepostomate bryozoans, annelids, hyolithids, orthocone nautiloids, rare ostracods, phyllocarids, blastoids, cystoids, crinoids, dendroids, graptolites, and chlorophytes (receptaculitids) the redefined *Hirnantia sagittifera*–*Sluha kosoviensis* Community. It represents the most diversified community of the *Hirnantia* Community Group known in the World. We suppose that the *Hirnantia sagittifera*–*Sluha kosoviensis* Community occupied the well-ventilated environment of the soft bottom carbonate silts with high organic content. The community was most probably autochthonous, with minimal transport as is indicated by the common preservation of shells with conjoined valves (articulate brachiopods, semi-infaunal bivalve *Mytilarca mareki*, and infaunal bivalves). The bivalves *Mytilarca mareki* and *Metapalaeoneilo dromon* sp. nov., *Nuculites* aff. *planulatus*, and *?Sphenolium* cf. *parallelum* may have originated in the Baltica carbonate platforms and the equatorial regions of Avalonia and Laurentia and support the ideas about the position of the Kosov Province in the temperate-to-subtropical zone (between 30° to 45° S). For the analogous and homologous communities we described the *Hirnantia* Community Group as a substitute for the term “*Hirnantia* fauna”. The *Hirnantia* Community Group was most probably extending from the circumpolar sphere into the temperate to tropical zones in proximity to the carbonate platforms. In Bohemia and elsewhere it occurs just a few metres below the Ordovician–Silurian boundary and represents the evidence of the environmental recovery during the uppermost Ordovician transgression following the Upper Ordovician global glaciation. • Key words: Bivalvia, uppermost Ordovician, late Hirnantian, systematics, palaeoecology, Perunica, Prague Basin, Bohemia.

KRÍŽ, J. & STEINOVÁ, M. 2009. Uppermost Ordovician bivalves from the Prague Basin (Hirnantian, Perunica, Bohemia). *Bulletin of Geosciences* 84(3), 409–436 (9 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received April 27, 2009; accepted in revised form June 5, 2009; published online August 14, 2009; issued September 11, 2009.

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The Kosov Formation (Hirnantian, Ordovician) reflects in the Prague Basin, Bohemia a remote global large-scale Gondwanan glaciation, glacial regressions, post-glacial transgressions and related biodiversity changes in the mid-to outer-shelf settings (Brenchley & Štorch 1989; Štorch 1986a, 2006). From alternating shale and sandstone beds in the middle parts of the Kosov Formation Mikuláš (1992) described numerous ichnogenera and assigned them to the shallow-water *Cruziana* Ichnofacies or *Nereites* Facies. The rhythmically bedded unit is terminated by the clayey shale and siltstones with inferior sandy intercalations.

The upper part of the Kosov Formation is developed as the banks of glacial regressive (Štorch 1986a) ill-sorted, coarse-grained pebbly sandstone and fine-grained conglomerate (Havlíček 1950, 1998) with rare ichnofauna (Mikuláš 1992). In the eastern parts of the Prague Basin (Tachlovice, Praha-Nová Ves, Praha-Hodkovičky, Praha-Běchovice a.o.) the almost monospecific *Modiolopsis pragensis* Community known already to Barrande (1881), accompanied by rare brachiopods, rostroconchids, gastropods, *Cornulites* sp. and trilobites (Marek & Havlíček 1967, Havlíček 1987) is characteristic.

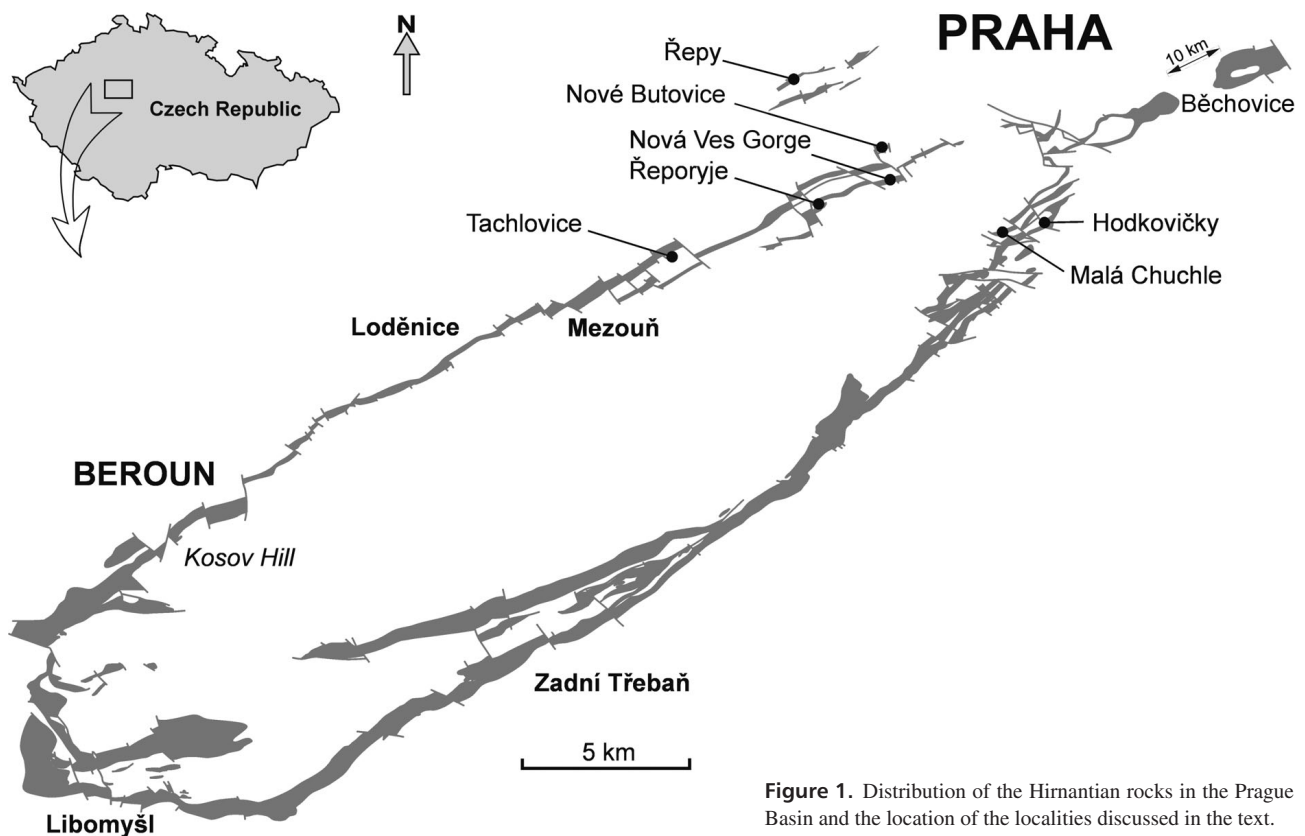


Figure 1. Distribution of the Hirnantian rocks in the Prague Basin and the location of the localities discussed in the text.

The uppermost part of the Kosov Formation in the eastern part of the Prague Basin (Praha-Běchovice locality, Marek 1963b; Praha-Řeporyje, Kříž in Štorch 1986b; Tachlovice, Prantl & Příbyl 1944 a.o.) is developed as a post-glacial transgressive grey micaceous shale with flat nodules of decalcified light grey siltstone. In the highest part of this unit at the locality Praha-Nové Butovice were recorded by Mikuláš (1992) very strong bioturbation (*Planolites* and *Arenicolites*). The siltstone nodules contain the *Hirnantia sagittifera*–*Sluha kosoviensis* Community dominated by the brachiopods *Kinnella kielanae proclinis* Havlíček, 1977 and *Dalmanella testudinaria* (Dalman, 1828) and composed of 23 other species of brachiopods (Marek & Havlíček 1967; Havlíček 1977, 1987, 1994, 1998) accompanied by conulariids, hexactinellids, annelids, bryozoans, hyolithids, bivalves, gastropods, orthocone nautiloids, trilobites, bryozoans, ostracods, phyllocarids, blastoids, cystoids and crinoids, graptolites, dendroids, and chlorophytes (Marek 1963a, b; Havlíček 1987).

The research of the Hirnantian in the Prague Basin has a long tradition started already by Barrande (1881) who first described from the upper Hirnantian sandstones in the vicinity of Prague (Tachlovice and Praha-Hodkovičky localities) bivalve *Modiolopsis draboviensis* (= *Modiolopsis pragensis* sp. nov.). In 1943 Prantl (Prantl & Příbyl 1944) discovered in the Tachlovice borehole the uppermost

Hirnantian shales with limestone nodules and layers with a graptolite fauna (*Normalograptus* sp.) and the trilobite *Brongniartella* sp. In the vicinity of Úvaly (east of Prague), north of Běchovice village, Havlíček mapped at the end of first half of the last century poorly exposed shallow syncline comprising the Kosov Formation (Hirnantian) and the lowermost Silurian Želkovice Formation (Havlíček 1950). He described here the high Kosov Formation coarse sandstone beds (up to 30 cm thick) and levels of clayey shale with the trilobite *Brongniartella platynota* (Dalman, 1828).

Very important are the studies of late Ladislav Marek (1928–1995) from the Academy of Sciences, Czechoslovakia, who systematically searched for the fossiliferous latest Ordovician rocks in the Prague Basin. In 1950 he discovered and exposed in Nová Ves Gorge near Praha-Butovice (Marek 1951) upper parts of the Kosov Formation (uppermost Hirnantian). In 140 cm thick bank of the coarse grained sandstone he found internal moulds of *Modiolopsis* sp. (= *Modiolopsis pragensis* sp. nov.) and *Brongniartella* sp. The bank is overlain by a few metres of grey green thin-bedded clayey and micaceous shale with *Normalograptus* sp., brachiopods of the *Hirnantia* Community (Marek & Havlíček 1967), trilobites, bivalves, bryozoans, crinoids and sponge spicules.

The most important locality with the uppermost Ordovician fauna occurrence north of Praha-Běchovice was dis-

covered by Marek at the end of 1961 (Marek 1963b). He collected here, in the level with flat lenses and nodules of decalcified clayey siltstone, a well-preserved fauna representing 16 classes of organisms. The most common are the brachiopods of the *Hirnantia* Community (Marek & Havlíček 1967), bivalves, gastropods, trilobites, graptolites, crinoids and bryozoans. Marek (1963a) systematically described bellerophonid gastropods, and Havlíček (1994) inarticulate brachiopods from this locality.

Marek & Havlíček in 1967 described detailed section of the Praha-Běchovice locality. The upper Kosov Formation (Hirnantian) consists of predominant pelites with the intercalations and beds of light-coloured quartz sandstone and quartzite. In the higher Kosov Formation the light-coloured mostly coarse-grained sandstone of unknown thickness is developed. It splits readily into thin laminae. By far the most prevalent fossil is *Modiolopsis pragensis* and different ontogenetic stages are represented, but adult single valves are the most common and frequently cover the bedding planes.

The sandstone is overlain by ash-grey clayey micaceous shale representing the uppermost Ordovician sediments just below the Silurian (Llandovery). Their thickness was estimated at 5–10 m. In the shale were found deformed trilobite *Mucronaspis mucronata* (Brongniart, 1822), brachiopods *Dalmanella testudinaria* (Dalman, 1828), *Rafinesquina* sp. and *Elegantilites* sp. The shale contains the level of a large flat lenses and nodules of light-grey decalcified, slightly clayey compact siltstone. The largest nodule found was 60 cm in diameter and about 10 cm thick. The nodules are crowded with the perfectly preserved specimens of the highly diversified *Hirnantia sagittifera* Community (several tens of species), especially brachiopods and molluscs (Havlíček 1982).

Štorch (Štorch 1980, 1982, 1986a, b, 1988, 1990, 2006; Štorch & Loydell 1996; Brenchley & Štorch 1989; Brenchley *et al.* 1991) paid during the last three decades extensive attention to the Ordovician and Silurian boundary rocks and fossils in the Prague Basin. He discovered several new uppermost Ordovician fossiliferous localities (temporary outcrops in Praha-Řepy area, Praha-Řeporyje, Praha-Velká Ohrada and Praha-Nové Butovice area, and Loděnice-Mezouň area). In 1980 Štorch mentioned and figured bivalves from the Řepy area temporary outcrops [*Cyrtodonta* sp. 1 and *Cyrtodonta* sp. 2 (= *Mytilarca mareki* sp. nov.)].

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 14 931–JK 15 114 (181 specimens) deposited in the collection of Jiří Kříž in the Czech

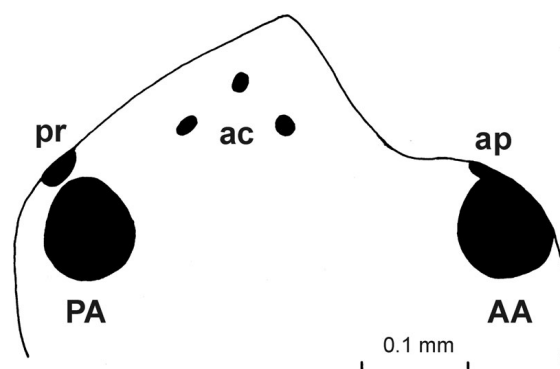


Figure 2. Diagrammatic side view showing the position of principal and accessory musculature of *Praenucula dispar* (Barrande, 1881). Key to letter symbols: PA – posterior adductor muscle scar; AA – anterior adductor muscle scar; pr – posterior retractor muscle scar; ap – anterior protractor muscle scar; ac – accessory muscle scars.

Geological Survey, Prague; NM bivalves deposited in the National Museum, Prague. All measurements are in millimetres.

Class Bivalvia Linné, 1758
 Subclass Protobranchia Korobkov, 1954
 Order Nuculoida Dall, 1889
 Superfamily Nuculoidea Gray, 1824
 Family Praenuculidae McAlester, 1969

Genus *Praenucula* Pfab, 1934

Type species. – *Praenucula dispar expansa* Pfab, 1934, *Praenucula dispar* (Barrande, 1881) = senior synonym. Bohemia, Prague Basin, Osek, Middle Ordovician, Darrwilian, Šárka Formation.

Remarks. – Pfab (1934) described two genera *Praenucula* and *Praeleda*, very similar in general shape. McAlester (1968, 1969) revised the type material of these two genera and included *Praeleda* into the synonymy of *Deceptrix* Fuchs, 1919. McAlester (1969) showed that *Praenucula* differs from *Deceptrix* by the anterior and posterior teeth similar in the size and number. Bradshaw (1971) was of the opinion, that *Praeleda* is valid and that it could be an ancestor of *Deceptrix*. Tunnicliff (1982) supposed that *Praeleda* is the synonym of *Deceptrix*. Tunnicliff (1982) also described the main features of *Deceptrix* (in his concept) 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) umbones in *Praenucula* lie in the posterior half while in *Deceptrix* they generally lie in anterior half; 3) in *Deceptrix* the adductor muscle scars are larger and in more ventral position, in *Praenucula* close to dorsal margin. Babin & Gutiérrez-Marco (1991) were of the same opinion.

To the contrary Cope (1997, 1999) proposed that genus *Praealeda* is valid and described the main features of *Praealeda* and *Praenucula*: 1) the umbones in *Praenucula* lie in the posterior half of the shell, in *Praealeda* the umbones are or in the posterior half of the shell, or in the central position; 2) in *Praenucula* the hinge plate has an approximately equal number of teeth in the anterior and posterior part of the hinge or, in some species, the number of the teeth in the anterior is higher than in the posterior. The anterior teeth may differ little in size from the posterior teeth, or may be markedly larger. The hinge axis is parallel to the dorsal margin and formed by both, the anterior and posterior dentition.

***Praenucula dispar* (Barrande, 1881)**

Figures 2, 3C, D, I, J

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

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

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 L27177 and L27 178.

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

Type horizon. – Middle Ordovician, Darriwilian, Šárka Formation.

Material. – One right valve, one left valve from Praha-Běchovice.

Diagnosis. – *Praenucula* with slightly elongated anterior

part of the shell, with convex anterior part of the dorsal margin and with three pairs of rounded accessory muscle scars in the posterior part of the shell.

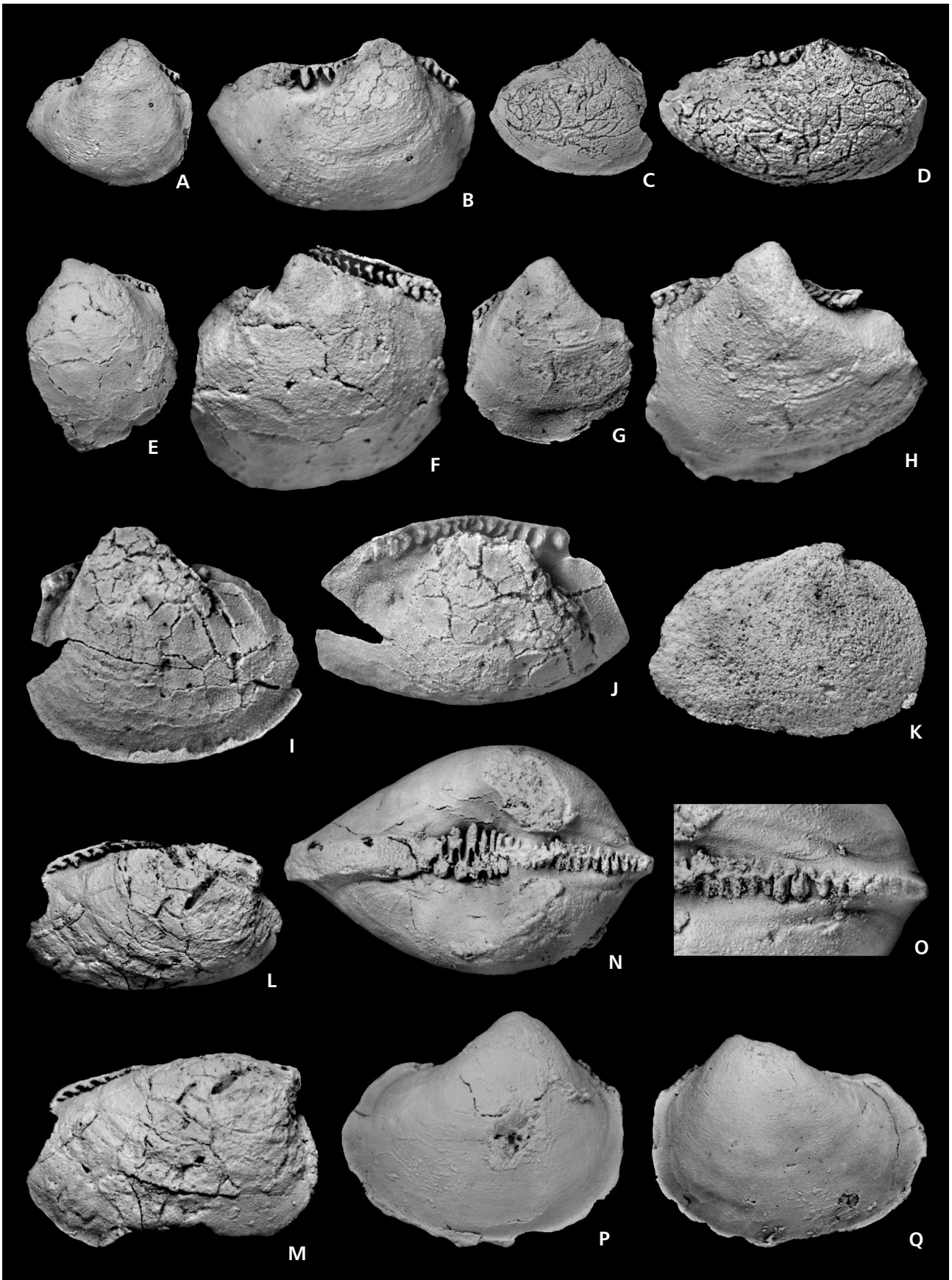
Description. – Shell small, equivalve, inequilateral, and broadly ovate. Anterior part of the shell is larger than the posterior part. Anterior and posterior margins evenly rounded, ventral margin convex. Umbones located in the posterior half of the shell, prosogyrate. Inner surface sculpture is smooth. Hinge taxodont, teeth row continuous in the umbonal region. Posterior part of the hinge is with the convex teeth (6–8 in number). In umbonal part the teeth are becoming smaller and toward the anterior slightly larger and of the orthomorph shape (according to Babin 1966, p. 39). In anterior part of the hinge are 5–6 teeth. Anterior and posterior adductor muscle scars rounded, posteriorly from the anterior adductor muscle scars one pair of the pedal muscle scars (protractors) and anteriorly from the posterior adductor muscle scars one pair of the rounded pedal muscle scars (retractors) are developed. Posteriorly from the umbo (but still in the umbonal region) three pairs of rounded accessory muscle scars are impressed (Fig. 2). Outer surface sculpture and the shell thickness are unknown.

Dimensions. –

specimen	V	L	H	W/2
NM L27176	A	4.6	3.8	1.6
JK 14931	R	5.9	5.8	3.1
NM L27177	A	6.25	5.3	1.9
NM L27178	A	8.1	–	3.1
JK 14943	L	8.4	8.6	3.2

Discussion. – Pfab (1934) described *Praenucula dispar expansa*, which he designated as the type species of *Praenucula* Pfab, 1934. It differs from the nominotypical subspecies only by reduced one orthomorph tooth under the umbo. We do not consider this to be so important feature to distinguish a new subspecies occurring at the same locality as the nominotypical subspecies. *Praenucula dispar* differs from *Praenucula abrupta* sp. nov., in more broadly ovate than triangular shape and by convex anterior dorsal margin. *Praenucula sharpei* Babin & Gutiérrez-Marco, 1991 from the Middle Ordovician of Spain has a more elongated anterior part of the shell. *Praenucula mayennense* Babin &

Figure 3. A, B, E–H – *Praenucula abrupta* sp. nov. (Barrande, 1881). • A, B – left valve, JK 14939, holotype; A – lateral view, × 2.9; B – dorso-lateral view, × 4.6. • E, F – left valve, JK 14937, paratype; E – lateral view, × 4.3; F – dorso-lateral view, × 6.5. • G, H – right valve, JK 14944, paratype; G – lateral view, × 4.2; H – dorso-lateral view, × 7.4. • C, D, I, J – *Praenucula dispar* (Barrande, 1881). • C, D – left valve, JK 14943; C – lateral view, × 2.9; D – dorso-lateral view, × 5.3. • I, J – right valve, JK 14931; I – lateral view, × 7.6; J – dorso-lateral view, × 10. • K – *Myoplusia* sp., right valve, lateral view, JK 14968, × 3.5. • L, M – *Sluha kosoviensis* (Barrande, 1881), right valve, JK 14966; L – dorso-lateral view, × 3.5; M – lateral view, × 4. • N–Q – *Praealeda compar* (Barrande, 1881), articulated specimen, JK 14935; N – dorsal view, × 5.7; O – detail of the posterior part of hinge with pedal muscle scars, × 8; P – left lateral view, × 4.2; Q – right lateral view, × 4.3. • A–J, L–Q – decalcified siltstone nodules, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek 1963b). • K – coarse sandstones, Kosov Formation, Hirnantian, uppermost Ordovician, shallow syncline north of Praha-Běchovice.



Beaulieu, 2003 from the Middle Ordovician of the Armorican Massif has more elongated and also concave anterior part of the dorsal margin. *Praenucula dispersa* Tunnicliff, 1982 from the Bardahessiagh Formation, Upper Ordovician of Pomeroy, Ireland, has more numerous teeth in the posterior (12 and more in number) and anterior (13 and more in number) parts of the hinge. *Praenucula infirma* Tunnicliff, 1982 from the Killee Bridge Formation, Upper Ordovician of Pomeroy, Ireland, differs from *Praenucula dispar* by larger teeth in the anterior part of the shell and also by elongated anterior part of the shell. *Praenucula praetermissa* Tunnicliff, 1982 from the Killee Bridge Formation, Upper Ordovician of Pomeroy has umbones more in central position and more numerous teeth than *Praenucula dispar*. *P. infirma* and *P. praetermissa* also differ from *Praenucula dispar* in concave anterior part of the shell.

***Praenucula abrupta* sp. nov.**

Figure 3A, B, E–H

Holotype. – Internal mould of the left valve, JK 14939, figured on Fig. 3A, B.

Paratypes. – Internal moulds of the left valve JK 14937 and the right valve JK 14944, figured on Fig. 3E–H.

Derivation of name. – From Latin *abruptus*, precipitous, steep.

Type locality. – Bohemia, Prague Basin, temporary outcrop in the research institutions area, north of Praha-Běchovice (Marek 1963b).

Type horizon. – Upper Ordovician, late Hirnantian, Kosov Formation.

Material. – Two left valves and three right valves.

Diagnosis. – *Praenucula* with triangular shell, prominent prosogyrate umbones, and with concave anterior part of the dorsal margin.

Description. – Shell small, equivalve, inequilateral, triangular. Anterior part of the shell is larger. Anterior part of

the dorsal margin is concave, posterior part straight. Anterior and posterior margins rounded, ventral margin convex. Prominent umbones are in the posterior half of the shell length or in central position, prosogyrate. Hinge taxodont. Posteriorly of umbo the teeth are small (7–10 in number), anteriorly slightly larger (7–8 in number). In posterior part of the shell the hinge line is straight. In anterior part of the shell the hinge line is concave. Inner surface with narrow growth bands and furrows developed. Anterior adductor muscle scar rounded. Other muscle scars unknown. Outer surface sculpture and the shell thickness are unknown.

Dimensions. –

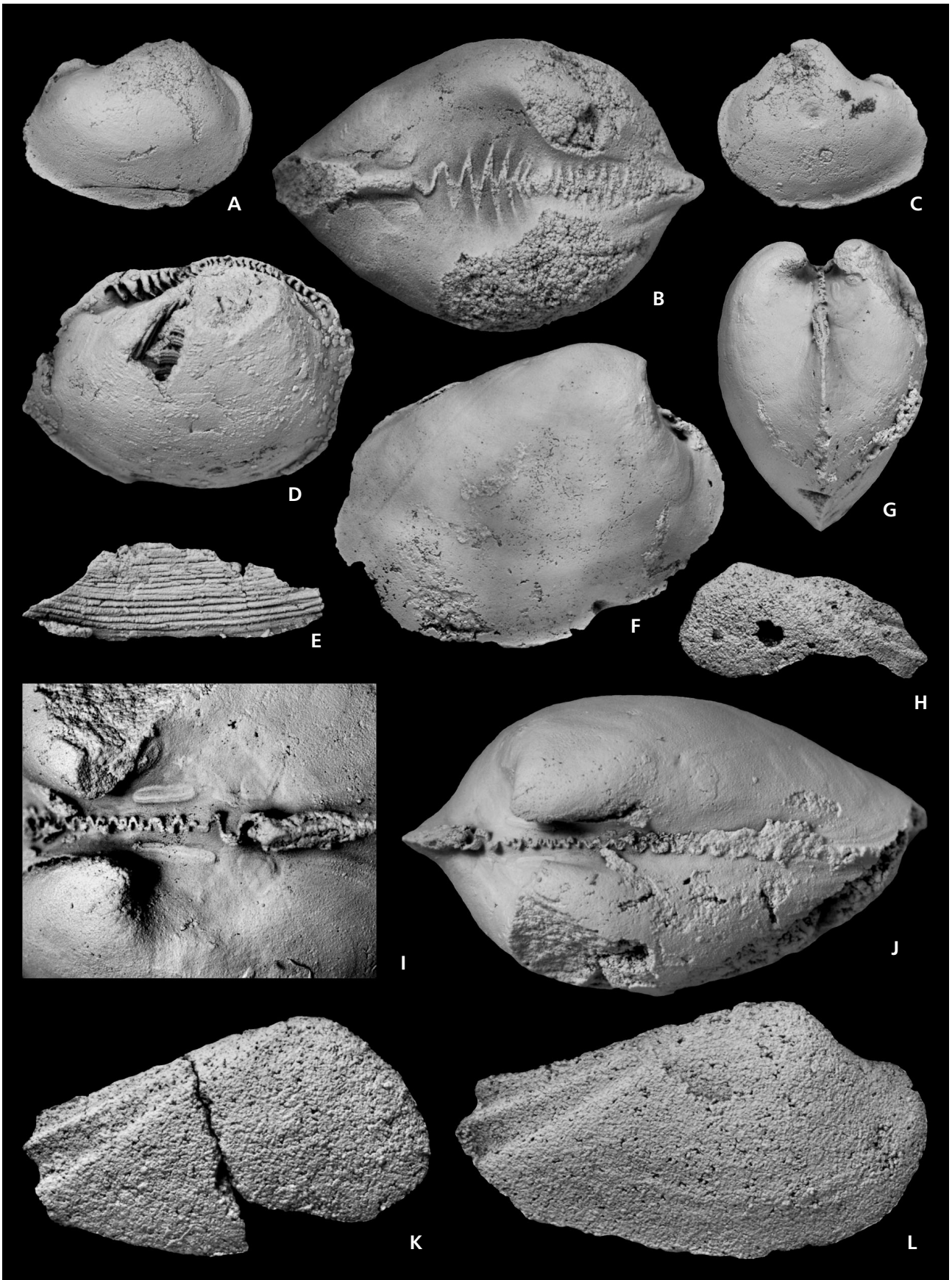
specimen	V	L	H	W/2
JK 14950	R	5.6	4.9	2.2
JK 14937	L	–	8.4	2.9
JK 14944	R	8.2	8.7	2.8
JK 14939	L	11.1	10.2	4.0

Discussions. – *Praenucula sharpei* Babin & Gutiérrez Marco, 1991 is more longitudinally elongated than *Praenucula abrupta* sp. nov. *Praenucula mayennense* Babin & Beaulieu, 2003 has more elongated anterior part and less prominent umbo, but very similar concave anterior part of the dorsal margin. *Praenucula dispar* has more numerous teeth in the posterior (12 and more in number) and in the anterior (13 and more in number) parts of the hinge and more elongated anterior part of the shell. *Praenucula infirma* Tunnicliff, 1982 differs from *Praenucula abrupta* sp. nov. by larger teeth in the anterior part of the shell and also by elongated anterior part of the shell. *Praenucula praetermissa* Tunnicliff, 1982 has very similar shape with *Praenucula abrupta* sp. nov., but has more teeth in the anterior part of the hinge (more than 9 in number). *P. infirma* and *P. praetermissa* show concave anterior part of the dorsal margin as in *Praenucula abrupta* sp. nov.

Genus *Praeleda* Pfab, 1934

Type species. – *Praeleda compar* (Barrande, 1881), Bohemia, Prague Basin, Loděnice, Ordovician, late Sandbian, Zahořany Formation.

Figure 4. A–E – *Praeleda compar* (Barrande, 1881). • A–C – articulated specimen, JK 14930; A – left lateral view, × 3.8; B – dorsal view, × 7.1; C – right lateral view, × 3.4. • D, E – left valve, JK 14936; D – dorso-lateral view, × 4.8; E – detail of the outer surface sculpture, × 5.7. • F, G, I, J – *Myoplusia obtusa* (Barrande, 1881), articulated specimen, JK 14942; F – right lateral view, × 3.8; G – anterior view, × 3.5; I – detail of pedal muscle scars, × 8.3; • J – dorsal view, × 5. • H, K, L – *Metapaleoneilo dromon* sp. nov., H – left valve, lateral view, JK 14958, paratype, × 3.4; K – right valve, lateral view, JK 14956, paratype, × 5.8; L – right valve, lateral view, JK 14959, holotype, × 6.2. • A–G, I, J – decalcified siltstone nodules, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek 1963b). • H, K, L – coarse sandstones, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek 1963b).



Remarks. – In *Praeleda* the posterior part of the hinge plate is much longer than the anterior and bears variable number of equal-sized teeth. The few of the anterior teeth increase in size anteriorly and there is commonly (but not always) angular discordance between anterior and posterior dentitions. The hinge axis lies along the line of more numerous posterior teeth, and anterior commonly larger teeth lie ventrally of it. Because of these features Cope (1997, 1999) grouped into the family Cardiolaridae Cope, 1997 (Cardiolarioidea Cope, 2000) also *Praeleda* having the posterior dentitions in which the hinge axis lies parallel with the line of posterior teeth. The anterior line of teeth, which may be enlarged, lie below the hinge axis but the teeth row between the umbones is continuous contrary to Ordovician *Cardiolaria* Munier-Chalmas, 1876.

Carter (2001, p. 220) is of the opinion that the most important for diagnosis of Cardiolaridae is the presence of anterior palaeotaxodont or pseudotaxodont teeth abruptly enlarged relative to the posterior palaeotaxodont teeth. According to Cope (2005) the cardiolaroids are a small group of taxodont bivalves with hinge designed for wider valve opening facilitating more effective disposal of pseudo-faeces and directly linked to the development of the filibranch gill. According to Cope (1999) they represent the earliest autolamellibranch bivalves. We are of the opinion that *Praeleda* should be classified in Praenuculidae where it was placed by Babin & Beaulieu (2003), and summarised by Pojeta & Stott (2007).

***Praeleda compar* (Barrande, 1881)**

Figures 3N–Q, 4A–E

- 1881 *Nucula compar* Barr.; Barrande, pl. 271, figs III/1–14.
- 1881 *Nucula amica* Barr.; Barrande, pl. 271, figs I/1–16.
- 1934 *Praeleda compar* (Barr.). – Pfab, pl. III, figs 1–3.
- 1968 *Praeleda compar* (Barrande). – McAlester, p. 46, pl. 7, figs 1–9, pl. 8, figs 1, 2.

Lectotype. – Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 271, as figs III/9–11, NM L 27 176. Designed by McAlester (1968).

Paralectotypes. – Internal moulds of the shells with conjoined valves, figured by Barrande (1881) on pl. 271, as

figs III/ 1–4, 5–8, 12–14, 15–16, NM L27144, L27148, L27146, L27147.

Type locality. – Bohemia, Prague Basin, Loděnice.

Type horizon. – Upper Ordovician, late Sandbian, Zahořany Formation.

Material. – Three shells with conjoined valves, one left valve from Praha-Běchovice.

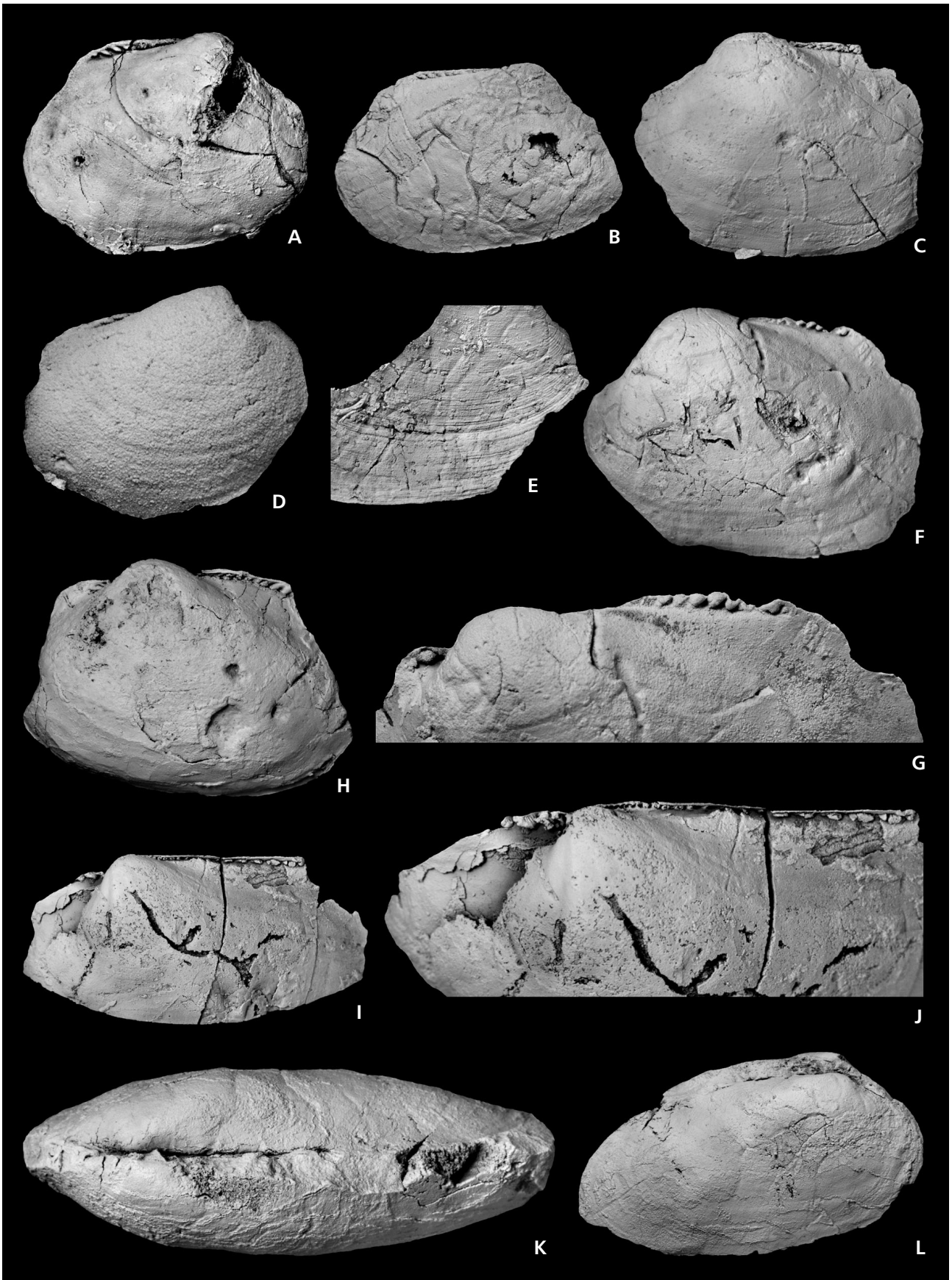
Diagnosis. – *Praeleda* with broadly subelliptic to ovate shells, with 7 to 8 teeth in the anterior part of the hinge and with 15–20 teeth in the posterior part of the hinge.

Description. – Small, equivalve, inequilateral, and broadly subelliptic to ovate shell. Anterior and posterior margins evenly rounded, ventral margin convex. Anterior part is larger part of the shell. Umbones are in the posterior half of the shell length. Dorsal margin in the anterior part of the shell is slightly concave, in the posterior part of the shell it is convex. Outer surface sculpture consists of numerous, regularly spaced growth bands and furrows. Inner surface sculpture is smooth. The hinge taxodont, the posterior part with small numerous teeth (15–20 in number), and the anterior part of the shell with abruptly much larger teeth (7–8 in number). Teeth row between the umbones is not interrupted. Anterior adductor muscle scar elliptic and larger than rounded posterior adductor muscle scar. One pair of rounded pedal muscle scars (protractors) is developed posteriorly from the anterior adductor muscle scars, one pair of transverse elliptic pedal muscle scars (retractors) is developed anteriorly from the posterior adductor muscle scar, and two pairs of the narrowly elliptical accessory muscle scars are developed in the umbonal region.

Dimensions. –

specimen	V	L	H	W/2
JK 14934	A	10.1	8.5	2.5
JK 14930	A	11.5	8.9	2.8
NM L27144	A	11.5	9.1	3.2
NM L27146	A	11.9	9.3	3.6
JK 14936	L	12.0	–	4.2
JK 14935	A	12.1	9.7	3.5
NM L27145	A	12.5	9.3	3.75
NM L27143	A	13.2	11.3	3.7

Figure 5. A–C, E–L – *Sluha kosoviensis* (Barrande, 1881). • A – right valve, JK 14961, lateral view, × 2.2. • B – right valve, JK 14979, lateral view, × 2.3. • C – left valve, JK 14972, lateral view, × 2.4. • E – left valve, JK 14985, detail of outer surface sculpture, × 2.4. • F, G – left valve, JK 14984; F – lateral view, × 2.5; G – dorso-lateral view, × 4.4. • H – left valve, JK 14962, lateral view, × 1.9. • I, J – left valve, JK 14976; I – lateral view, × 2.1; J – dorso-lateral view, × 4.0. • K, L – articulated specimen, JK 14978; K – dorsal view, × 3; L – right lateral view, × 2.0. • D – *Myoplusia* sp., right valve, lateral view, JK 14955, × 12. All specimens come from the decalcified siltstone nodules, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek 1963b).



Discussion. – Pfab (1934) determined four species of the genus *Praealeda*: *Praealeda compar* (Barrande, 1881), *Praealeda amica* (Barrande, 1881), *Praealeda pulchra* Pfab, 1934 and *Praealeda contrastans* (Barrande, 1881). Babin & Melou (1972) recognized the species *Praealeda contrastans* as *Myoplusia contrastans*. We suppose that *Praealeda compar* and *Praealeda amica* are synonymous. *Praealeda pulchra* is more elongated than other two species of *Praealeda* recognized by Pfab (1934) and also the anterior dorsal margin is more concave. Our specimens are also closely related to *Praealeda costae* (Sharpe, 1853) from the Middle Ordovician, Finistère, France (Bradshaw 1971, 1978), but they differ by less longitudinally elongated shells and by generally more numerous teeth. *Praealeda multidentata* Cope, 1999 from the Middle Ordovician of Mid-Wales and the Welsh Borderland has more numerous and smaller teeth in the anterior part of the shell than *Praealeda compar*. *Praealeda subtilis* Cope, 1999 from the Middle Ordovician of Mid-Wales and the Welsh Borderland differs from *Praealeda compar* by slight posterior alation, and by smaller teeth.

Family Nuculitidae Bradshaw, 1999

Genus Nuculites Conrad, 1841

Type species. – *Nuculites oblongatus* Conrad, 1841, USA, New York, Chenango County, near Smyrna, Middle Devonian.

***Nuculites* aff. *planulatus* Conrad, 1841**

Figure 6A–I

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

Description. – Shell equivalved, inequilateral, ovate or longitudinally elongated. Umbones are prominent, in the anterior part of shell, beaks prosogyrate. The septum is relatively short and extends from anterior part of the hinge line towards the anterior margin of the shell. Posterior hinge line straight, the anterior hinge line curved ventrally. Orthomorph teeth are larger in the posterior part of the hinge. Inner surface sculpture is smooth. The anterior adductor muscle scar is mostly distinct, occupying much of

the portion of the shell anteriorly to the septum. A transversely narrowly elliptic pedal muscle scar is developed anteriorly of the umbo close to the dorsal margin. Posterior adductor muscle scar, outer surface sculpture and thickness of the shell are unknown.

Dimensions. –

specimen	V	L	H	W/2
JK 14957	R	7.2	4.8	2.3
JK 14941	L	9.0	7.1	3.0
JK 14983	R	10.0	6.1	1.9
JK 14945	L	13.2	6.5	2.1
JK 14974	A	–	8.9	4.2
JK 14932	A	–	10.6	4.1

Discussion. – Variation in the shell form is characteristic for *Nuculites*. Bretsky & Bretsky (1977) demonstrated high variability in *Nuculites planulatus* Conrad, 1841 from the Nicolet River Formation type section, Upper Ordovician of Quebec, Canada. They revised four previously described species: *Nuculites postvolutus* (Foerste, 1914) with well developed radial sinus extending to the postero-ventral edge of the shell, *Nuculites praevolutus* (Foerste, 1914) with radial sinus extending to the antero-ventral edge of the shell, *Nuculites planulatus* Conrad, 1841 s.s. with smooth shell and no sinus, and *Nuculites brevis* (Foerste, 1914), which is relatively short and high. They refer all these species, on the base of systematic detailed study of morphological variability, to *Nuculites planulatus*, which differs from the Bohemian specimens by the development of the radial sinus, except the specimens of *Nuculites planulatus* s.s.

The high variability in *Nuculites cylindricus* (Portlock, 1843) from the Killey Bridge Formation, Upper Ordovician of Pomeroy, Ireland, which is very similar to *Nuculites planulatus*, was described by Tunnicliff (1982). In *Nuculites cylindricus* is also developed the posterior shallow radial sinus close to the ventral margin, which is not developed in our specimens. Both species *Nuculites planulatus* and *Nuculites cylindricus* from the Upper Ordovician are very closely related and because of their similar variability and general shell form they may be synonymous. In that case, *Nuculites cylindricus* (Portlock, 1843) is the junior synonym of *Nuculites planulatus* Conrad, 1841. Barrande (1881) figured *Nuculites fissa* (pl. 267, figs VI/1–3) from the Upper Ordovician, Prague Basin,

Figure 6. A–I – *Nuculites* aff. *planulatus* Conrad, 1841. • A, D, E – left valve, JK 14941; A – dorsal view, detail of pedal muscle scar, × 7.5; D – lateral view, × 6; E – dorso-lateral view, × 7. • B – left valve, lateral view, JK 14945, × 3.9. • C, G – articulated specimen, JK 14974; C – dorsal view, × 2.2; G – dorsal view, × 4.9. • F, H, I – articulated specimen, JK 14932; F – right lateral view, × 2.7; H – dorsal view, × 4.2; I – dorso-lateral view, detail of the septum, × 5.7. • J, K – *Myoplusia contrastans* (Barrande, 1881), left valve, JK 14980; J – dorso-lateral view, × 9.4; K – dorsal view, × 7.9. All specimens come from the decalcified siltstone nodules, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek 1963b).



Praha-Krč, Bohemia, which differs by the short septum oriented slightly posteriorly.

Superfamily Nuculanoidea Adams & Adams, 1858

Family Mallettiidae Adams & Adams, 1858

Genus *Sluha* Barrande, 1881

Type species. – *Sluha expansus* Barrande, 1881, Bohemia, Prague Basin, Lejškov Hill, Upper Ordovician, middle and upper Katian, Králův Dvůr Formation.

Sluha kosoviensis (Barrande, 1881)

Figures 3L–M, 5A–C, E–L

- 1881 *Arca? kosoviensis* Barr.; Barrande, pl. 265, figs III/1–12.
- 1881 *Arca? disputabilis* Barr.; Barrande, pl. 265, figs I/13–15.
- 1881 *Arca? innotata* Barr.; Barrande, pl. 265, figs II/1–20.
- 1891 *Praearca kosoviensis* (Barr.). – Neumayr, p. 755.
- 1934 *Praearca kosoviensis* (Barr.). – Pfab, p. 220, pl. 3, fig. 21.
- 1934 *Ctenodonta praecox* (Barr.). – Pfab, p. 228, pl. 2, fig. 14.
- 1934 *Ctenodonta disputabilis* (Barr.). – Pfab, p. 228, pl. 2, fig. 15.
- 1934 *Ctenodonta (Palaeoneilo) flectens* (Barr.). – Pfab, p. 230, pl. 2, fig. 18.
- 1934 *Ctenodonta (Palaeoneilo) magna* (Barr.). – Pfab, p. 231, pl. 2, fig. 19.
- 1968 *Praearca kosoviensis* (Barrande). – McAlester, pp. 44, 45, pl. 30, figs 1–8.
- 1969 *Sluha kosoviensis* (Barrande). – McAlester, p. N235.

Lectotype. – Internal mould of a right valve figured by Barrande (1881) on pl. 265, as figs III/9–10, NM L27070. Designed by Pfab (1934).

Paralectotypes. – Internal mould of the shell with articulated and opened valves figured by Barrande (1881), on pl. 265 as fig. III/1, NM L27072; internal mould of the shell with articulated and opened valves figured by Barrande (1881), on pl. 265, as fig. III/2, NM L27071; internal mould of the left valve figured by Barrande (1881) on pl. 265 as figs III/3–5, NM L27073; internal mould of the right valve figured by Barrande (1881), pl. 265, as figs III/6–8, NM L27069; internal mould of a left valve figured by Barrande (1881), pl. 265, as figs III/11–12, NM L27068.

Type locality. – Bohemia, Prague Basin, Kosov Hill near Beroun.

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

Material. – Eight right valves, five left valves, and one shell with conjoined valves from Praha-Běchovice.

Diagnosis. – Upper Ordovician longitudinally elongated *Sluha* with the anterior smaller and the posterior larger part; taxodont dentition developed anteriorly and posteriorly of umbo.

Description. – Shell medium size, equivalved, inequilateral, broadly ovate, and longitudinally elongated (H/L = 0.5–0.8). Anterior part of the shell is smaller. Anterior and posterior margins evenly rounded, ventral margin long and convex, postero-dorsal angle rounded, and dorsal margin slightly convex. Umbones prominent, in anterior half of the shell, beaks are prosogyrate. Umbonal ridge well defined, becoming obsolete before reaching post-inferior extremity. Outer surface sculpture consists of fine growth wrinkles. Inner surface is smooth. Ligament is probably external. Hinge line in anterior part of the shell slightly curved ventrally, in posterior part straight or slightly convex. Taxodont teeth are small, in the posterior part of the hinge line slightly larger, and with obliquely orthomorph shape (according to Babin 1966, p. 39). Muscle scars unknown.

Dimensions. –

specimen	V	L	H	W/2
JK 14966	R	16.2	10.1	–
JK 14971	R	–	14.4	4.2
JK 14960	R	21.1	–	3.5
JK 14973	R	21.4	15.2	4.2
JK 14979	R	22.4	17.0	5.6
JK 14961	R	24.1	19.0	6.5
NM L27072	A	25.9	12.0	5.6
NM L27071	A	26.2	15.2	5.6
JK 14972	L	–	17.2	6.2
JK 14984	L	27.3	21.1	7.1
NM L27070	R	29.0	17.2	3.1
NM L27069	R	31.1	21.8	3.5
JK 14978	A	31.3	15.7	5.1
NM L27068	L	31.8	21.2	2.5
JK 14964	L	–	23.7	6.5
JK 14962	L	34.1	24.5	6.3

Discussions. – Pfab (1934) included *Arca? kosoviensis* Barrande, 1881 and *Arca? innotata* Barrande, 1881 in the genus *Praearca* established by Neumayr (1891) for *Arca? kosoviensis* Barrande, 1881 and *Arca? disputabilis* Barrande, 1881. McAlester (1969) concluded that *Praearca* represents a junior synonym of *Sluha* Barrande, 1881. *Sluha kosoviensis* (Barrande, 1881) is probably a direct descendant of *Sluha expansus* Barrande, 1881, and differs from it by the longitudinally more elongated shells and by a fine taxodont dentition along the posterior and anterior hinge margins.

Genus *Myoplusia* Neumayr, 1884

Type species. – *Myoplusia bilunata* (Barrande, 1881), Bohemia, Prague Basin, Štěrboholy, Upper Ordovician, late Sandbian, Zahořany Formation.

***Myoplusia contrastans* (Barrande, 1881)**

Figure 6J, K

- 1881 *Nucula contrastans* Barr.; Barrande, pl. 271, figs II/1–16.
- 1934 *Praeleda contrastans* (Barr.). – Pfab, p. 233, pl. III, figs 4, 7–9.
- 1972 *Myoplusia contrastans* (Barrande). – Babin & Melou, pp. 83–85, pl. 7, figs 8–10, pl. 8, figs 1–3.

Lectotype. – Internal mould of the shell with conjoined valves figured by Barrande (1881), pl. 271, as figs II/1–4, NM L22680. Designated by Pfab (1934).

Paralectotypes. – Internal mould of the shell with conjoined valves figured by Barrande (1881), pl. 271, as figs II/5–8, NM L22681; other specimens figured by Barrande (1881) on pl. 271 as figs 9–16, could not be located.

Type locality. – Bohemia, Prague Basin, Praha-Libeň.

Type horizon. – Upper Ordovician, late Sandbian, Zahořany Formation.

Material. – One left valve from Praha-Běchovice.

Diagnosis. – *Myoplusia* with the hinge teeth of similar size in anterior and posterior parts, and with the straight anterior part of the dorsal margin.

Description. – Shell small, equivalve, inequilateral, ovate, and longitudinally elongated. Umbones are in the anterior half of the shell length, beaks prosogyrate. Anterior part of the shell is smaller than the posterior part of the shell. Hinge taxodont, teeth in the anterior part of the hinge are ill-preserved, posterior part of the hinge consists of convex and orthomorph teeth (according to Babin 1966, p. 39). Convex teeth are close to the umbo, orthomorph teeth are far from the umbo, close to the posterior end of the dorsal margin. Inner surface sculpture is smooth. Anterior adductor muscle scar is less distinct, elliptical, posterior adductor muscle scar prominent, elliptical. One pair of narrowly transversely elliptical pedal muscle scars is developed posteriorly from the anterior adductor muscle scar. Three accessory narrowly elliptical muscle scars preserved in the umbonal region. Integripallial line well preserved, composed of the radially elongated pallial muscle scars. Outer surface sculpture and shell thickness are unknown.

Dimensions. –

specimen	V	L	H	W/2
JK 14980	L	11.3	10.1	4.1
NM L22680	A	11.9	9.0	3.5

Discussion. – Pfab (1934) included erroneously *Nucula contrastans* Barrande, 1881 (pl. 271, figs II/1–16) and *Nucula applanans* Barrande, 1881 (pl. 272, figs III/13–16) in *Praeleda* Pfab, 1934 which has the larger anterior part of the shell (Bradshaw 1971), and prosogyrate umbo in the posterior position. *Myoplusia* has the larger posterior part of the shells, umbo in anterior position and is prosogyrate. *Myoplusia contrastans* differs from *Myoplusia bilunata* (Barrande, 1881) in straight anterior part of the dorsal margin, the less prominent umbo and by the anterior and posterior teeth of same size. *Myoplusia obtusa* (Barrande, 1881) differs from *Myoplusia contrastans* in more obese shell and by shorter anterior part of the hinge.

***Myoplusia obtusa* (Barrande, 1881)**

Figure 4F, G, I, J

- 1881 *Nucula obtusa* Barr.; Barrande, pl. 272, figs I/1–17.
- 1934 *Pseudocyrtodonta obtusa* (Barr.). – Pfab, pl. III, fig. 12.

Lectotype. – Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/12–14, NM L22683. Designated by Pfab (1934).

Paralectotypes. – Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/1–4, NM L27150; internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/5–8, NM L22684; internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/9–11, NM L22685; internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/15–17, NM L22686.

Type locality. – Bohemia, Prague Basin, Praha-Štěrboholy.

Type horizon. – Upper Ordovician, late Sandbian, Zahořany Formation.

Material. – One shell with conjoined valves from Praha-Běchovice.

Diagnosis. – *Myoplusia* with obese shell, very short anterior part of hinge and with the teeth increasing in size anteriorly and posteriorly from umbo.

Description. – Shell is small, equivalve, inequilateral, inflated, posteriorly elongated; anterior part of the shell is

shorter. Umbones are prominent, in anterior position, and beaks prosogyrate. Posterior dorsal margin of the shell is slightly convex. Anterior, ventral and posterior margins are evenly rounded. Hinge is taxodont, teeth row continues below the umbo without interruption. Teeth below the umbo are smaller and their size slightly increases anteriorly and posteriorly. Internal surface is smooth. Anterior adductor muscle scar is relatively large, broadly elliptical. Posterior adductor muscle scar is larger than anterior muscle scar, broadly elliptical. Two pairs of pedal muscle scars are developed posteriorly of the anterior adductor muscle scar. First pair of elliptical pedal protractor muscle scars is close to the anterior adductor and close to hinge line. Second pair of transversely narrowly elliptical anterior pedal retractor muscle scars is developed posteriorly from the protractors, which are close and subparallel to the hinge line. Other deeply impressed elliptical accessory muscle scar is developed on the left valve close to the umbo and ventrally from the second pair of the pedal muscle scars. We suppose that it was probably the third pair of the pedal muscle scars or a median muscle scar.

Dimensions. –

specimen	V	L	H	W/2
NM L22686	R	6.5	5.6	2.6
NM L27150	A	6.6	5.5	2.1
NM L22684	A	8.5	6.3	2.3
NM L22683	A	8.6	5.8	2.0
JK 14942	A	19.2	14.2	4.6

Discussion. – Pfab (1934) classified Barrande's two (1881) species "*Leda*" *ala* and "*Nucula*" *obtusa* as the genus *Pseudocyrtodonta* Pfab, 1934 with the type species *Pseudocyrtodonta ala* (Barrande, 1881). In the type material of this species the hinge is mostly not preserved, and this was probably the main reason why Pfab distinguished the new genus. In other two specimens of "*Leda*" *ala* Barrande, 1881 (pl. 273, figs II/4–5, 6–8) the hinge shows taxodont teeth in the smaller anterior part of the shell and in the larger posterior part of the shell. McAllester (1969) classified *Pseudocyrtodonta* as synonym of *Myoplusia*. The other species classified by Pfab (1934) as *Pseudocyrtodonta* was "*Nucula*" *obtusa* Barrande, 1881. The lectotype of this species exhibits a different shape of shell, not so much longitudinally elongated and with less narrowed posterior part. The taxodont hinge is preserved only in the anterior part of the shell. Lectotype shows preserved three elongated umbonal accessory muscle scars in the umbonal region. The general shape is very similar to the genus *Myoplusia*.

"*Leda*" *incola* Barrande, 1881 (pl. 270, III/1–4), classified by Pfab (1934) as *Pseudocyrtodonta ala* (Barrande, 1881) has prominent prosogyrate beaks, very elongated shell, narrowed posteriorly. The taxodont hinge is well preserved in the anterior part of the shell. Posterior and ante-

rior rounded adductor muscle scars and elongate accessory muscle scars in the umbonal region are well developed. Most of these features are characteristic for *Myoplusia*, only the elongated shape with narrowed posterior of the shell differs. This shape is very similar to the Recent genus *Propeleda* Iredale, 1924.

Myoplusia bilunata (Barrande, 1881) differs from *Myoplusia obtusa* by less obese, more longitudinally elongated shell, and by larger anterior part of the shell.

***Myoplusia* sp.**

Figures 3K, 5D

Material. – Two right valves, one left valve.

Discussions. – Poorly preserved specimens with only general shape of the shell preserved. Umbones are prominent, almost in central position, beaks prosogyrate. The anterior part of the shell is smaller than the posterior part of the shell. Anterior, ventral, and posterior margins are evenly rounded. Part of taxodont hinge (Fig. 5D) is preserved in posterior part of the dorsal margin. Inner surface with regularly spaced narrow growth bands and furrows (Fig. 5D).

Occurrence. – One (Fig. 3K) specimen was found in the sandstone beds with the *Modiolopsis pragensis* Community exposed by temporary pipeline outcrop along the western margin of the research institution's area north of Praha-Běchovice. The point is marked on the geological map as the geologically significant locality No. 6 in Straka (1987, p. 66). The other specimen (Fig. 5D) was found in the temporary outcrop in the territory of the research institution's area north of Praha-Běchovice (Marek 1963b).

Genus *Metapalaeoneilo* Lamcke, 1934

Type species. – *Palaeoneilo (Metapalaeoneilo) baltica* Lamcke, 1934, Germany, Schilksee near Kiel, Beyrichienkalk, upper Přídolí, late Silurian.

***Metapalaeoneilo dromon* sp. nov.**

Figure 4H, K, L

Holotype. – Internal mould of the left valve, JK 14959, figured on Fig. 4L.

Paratypes. – Internal moulds of the left valve and the right valve, JK 14958 and JK 14956 figured on Fig. 4H, K.

Derivation of name. – From Greek *dromon* – light, fast vessel.

Type locality. – Bohemia, Prague Basin, temporary outcrop in the research institutions area, north of Praha-Běchovice (Marek 1963b).

Type horizon. – The Upper Ordovician, late Hirnantian, upper Kosov Formation, coarse sandstone with the *Modiolopsis pragensis* Community.

Material. – Two right valves and one left valve.

Diagnosis. – Posteriorly elongated *Metapalaeoneilo* with two radial umbonal ridges and two wide radial sinuses or folds developed closely to dorsal margin and extending radially from the umbo to the posterior extremity.

Description. – Shell small, equivalve, inequilateral, posteriorly elongated. The umbones are relatively large, prosogyrate, anteriorly of central part of the shell. Dorsal margin is straight. Ventral margin long, convex. Anterior margin evenly rounded. Between the umbo and the posterior extremity two radial umbonal ridges and two deep sinuses are developed. Inner surface with the growth bands and furrows developed. Muscle scars and hinge unknown.

Dimensions. –

specimen	V	L	H	W/2
JK 14956	R	13.1	8.1	1.6
JK 14959	R	14.2	8.3	1.4
JK 14958	L	15.0	6.6	1.6

Discussion. – *Metapalaeoneilo dromon* sp. nov. differs from the type species *Metapalaeoneilo baltica* by the longitudinally elongated shell and by the two umbonal ridges and two deep sinuses developed closely to dorsal margin and extending radially to the posterior extremity.

Occurrence. – Type locality only.

Subclass Autolamellibranchiata Grobben, 1894
 Superorder Pteriomorpha Beurlen, 1944
 Superfamily Ambonychioidea Miller, 1877
 Family Ambonychiidae Miller, 1877

Genus *Mytilarca* Hall & Whitfield, 1869

Type species. – *Inoceramus chemungensis* Conrad, 1842, U.S.A., New York, Upper Devonian, Chemung Stage.

Remarks. – The genus *Mytilarca* is known from the Upper Ordovician, Silurian and Devonian. In general, the specific classification is very difficult when only general mytiliform shape, outer and inner surface sculpture is known

(Růžička & Prantl 1961, Pojeta 1966, Kříž 2008). Since it is out of the scope of this paper to revise all the representatives of *Mytilarca* described in the past we compare our specimens found in upper Hirnantian only with the Upper Ordovician species described in the past from Sweden (Isberg 1934).

Mytilarca mareki sp. nov.

Figure 7A–T

1982 *Cyrtodonta* sp. – Štorch, p. 231, pl. 2, fig. 9.

Holotype. – Internal mould of the right valve with posterior laterals preserved, JK 15020, figured on Fig. 7N–P.

Paratypes. – JK 14986–JK 15015, JK 15018–JK 15019, JK 15021–JK 15046, JK 15054–JK 15062 measured for dimensions, included into assemblage analysis and figured on Fig. 7A–M, Q–T.

Derivation of name. – In honour of Ladislav Marek, palaeontologist from the Czech Academy of Sciences, expert in the Lower Paleozoic Hyolitha.

Type locality. – Bohemia, Praha-Běchovice, temporary outcrop in the research institution's area, north of the village (Marek 1963b).

Type horizon. – Upper Ordovician, latest Hirnantian, uppermost Kosov Formation, decalcified nodules in the bioturbated claystones.

Material. – 21 left, 41 right valves, and eight shells with conjoined valves.

Diagnosis. – *Mytilarca* with postero-ventrally elongated broadly ovate shells.

Description. – Shells are small (L = 11.5–29.8; H = 11.8–24.6), broadly ovate, equivalved, inequilateral, and obese (W = 6.2–14.6), lacking the anterior lobe. Umbones are prominent, in extreme terminal position, beaks prosogyrate. Outer surface sculpture consists of growth wrinkles and of irregular flat growth bands and furrows. Byssal sinus weak, no byssal gape developed. Ligament external, low ligament area with numerous duplivincular grooves and ridges. Hinge in the left valve composed of two elongated cardinal teeth just behind umbo, posterior one longer. In the posterior part of the shell, close to the hinge line one to three narrow lateral teeth are developed. A relatively large, subcircular posterior adductor muscle scar is developed in postero-dorsal part of the shell. Shell very thin (>0.05 mm).

Dimensions. –

specimen	V	L	H	W/2
JK 15 018	R	4.1	3.6	1.3
JK 15 021	L (A)	5.5	5.4	1.5
JK 14 992	R	8.7	9.2	2.6
JK 15 004	R	9.8	9.2	2.4
JK 14 993	R	11.5	11.8	3.1
JK 15 020	R	>12.5	13.4	4.1
JK 15 042	L (A)	16.7	16.8	4.8
JK 15 036	L	–	19.8	7.1
JK 14 987	R	23.5	21.1	7.3
JK 15 012	R	29.8	>24.6	7.1

Discussion. – *Mytilarca mareki* sp. nov. differs from all the species described by Isberg (1934) by broadly ovate, posteroventrally elongated shells. *Mytilarca semicircularis* Isberg, 1934 from the late Ordovician of Dalarna, Sweden differs by very broadly ovate to broadly elliptic shells and hinge composed of three small cardinals of which the middle one is longest. Some species of toothless *Cleionychia* Ulrich, 1892 from the Middle and late Ordovician of North America, Korea, Ireland, Norway, Sweden and Kazakhstan, Russia (Pojeta 1966) have similar general shape.

Mode of life. – Semi-infaunal, byssate.

Occurrence. – Type locality and Praha-Řepy, temporary outcrop, uppermost Kosov Formation, late Hirnantian, Upper Ordovician (Štorch 1982).

Superfamily Modiolopsoidea Fischer, 1887
Family Modiolopsidae Fischer, 1887

Genus *Modiolopsis* Hall, 1847

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

***Modiolopsis pragensis* sp. nov.**

Figures 8H–U, 9

Holotype. – Internal mould of the left valve, JK 15097, figured on Fig. 8M.

Paratypes. – JK 15047–15053, 15065–15096, 15098–15114, measured for dimensions, included into assemblage analysis and figured on Fig. 8H–L, N–U.

Derivation of name. – After the capital of the Czech Republic, Praha (Lat. Praga).

Type locality. – Bohemia, Praha-Běchovice, temporary outcrop in the research institution's area, north of village (Marek 1963b).

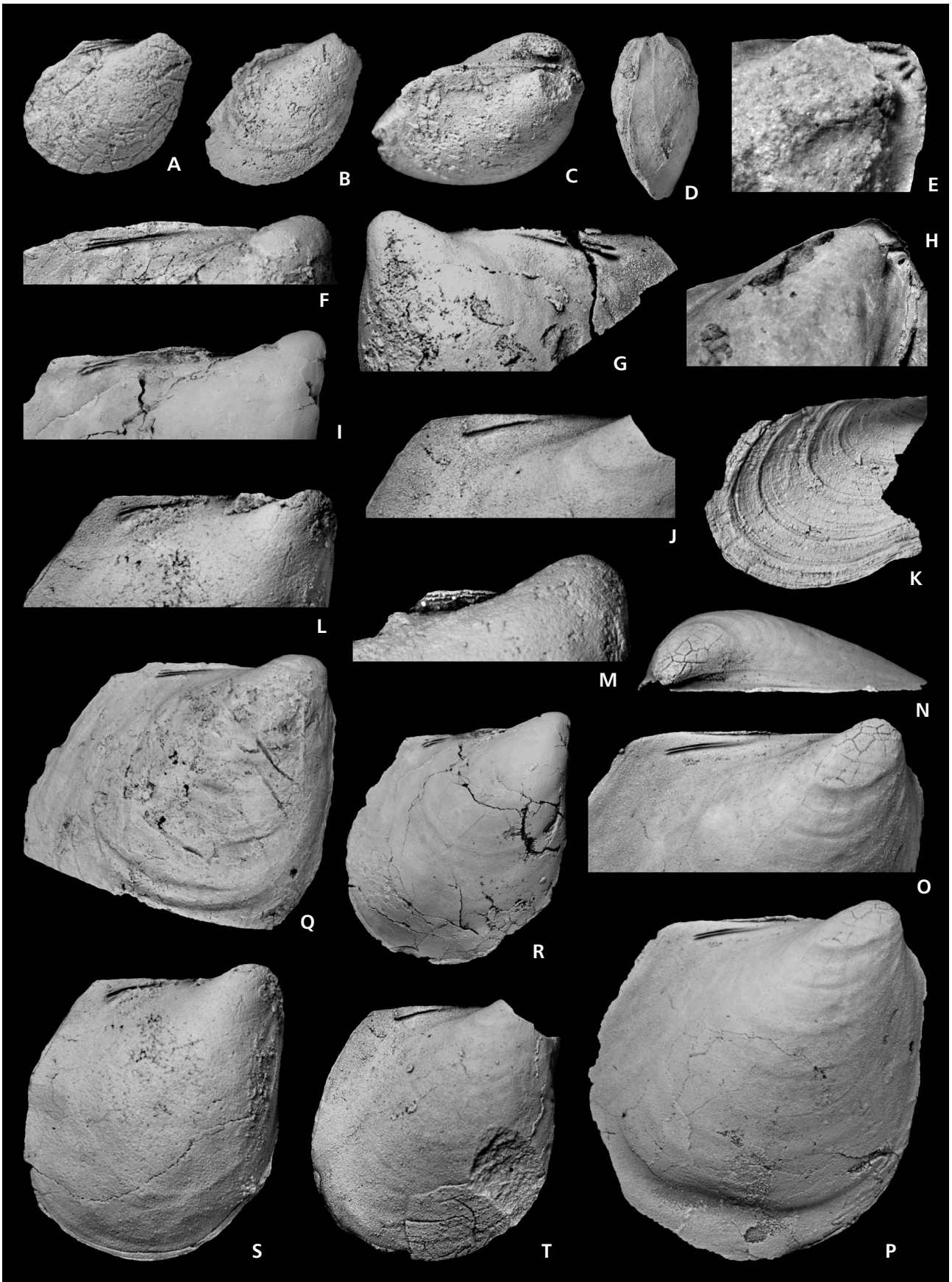
Type horizon. – Upper Ordovician, latest Hirnantian, uppermost Kosov Formation, decalcified nodules from the bioturbated claystones.

Material. – One shell with conjoined valves, 45 left and 54 right valves.

Diagnosis. – The elongated late Ordovician *Modiolopsis* with the lobate anterior part and with the posterior part a little larger than the anterior part of the shell, the outer surface sculpture formed by irregular growth wrinkles; hinge edentulous.

Description. – Shell medium in size (maximum L = 38.0), elongated, slightly diagonally modioliform, equi-valve, inequilateral (L/H = 1.33–2.10). Shells are inflated with no distinct umbonal ridge; maximum width at about one third of the shell length from anterior (H/W = 1.05–2.13, high variability is probably caused by vertical diagenetic deformations). Anterior part lobate, evenly rounded, posterior part of the shell is a little larger than anterior part. Maximum height is reached approximately in the last quarter of the shell length from anterior. Umbones not prominent, beaks small, close together, slightly above the hinge line, in one quarter of the shell length from anterior, and prosogyrate. Dorsal margin is long, more than one half of the shell length, straight. Ventral margin is long, slightly convex. Posterior margin evenly rounded. Outer surface sculpture composed of irregularly spaced growth wrinkles. Ligament opisthodontic. Hinge plate edentulous, muscle scars and pallial line not developed.

Figure 7. *Mytilarca mareki* sp. nov. • A – right lateral view, JK 15018, paratype, × 7. • B, C – articulated specimen, JK 15021, paratype; B – right lateral view, × 4.8; C – dorso-lateral view, × 7.2. • D – antero-lateral left view, JK 15042, paratype, × 1.7. • E – right lateral view, detail of hinge, JK 15005, paratype, × 10.5. • F, Q – right valve, JK 15061, paratype; F – dorso-lateral view, detail of the lateral teeth, × 4.6; Q – lateral view, × 3.3. • G – dorso-lateral view of the left valve, detail of the lateral teeth, JK 14989, paratype, × 4.3. • H – right lateral view, detail of hinge, JK 15000, paratype, × 4.4. • I, R – right valve, JK 14987, paratype; I – lateral view, detail of the lateral teeth, × 3.4; R – lateral view, × 2.1. • J, T – right valve, JK 14993, paratype; J – dorso-lateral view, detail of the lateral teeth, × 6.3; T – lateral view, × 4.1. • K – left valve, outer surface sculpture, JK 15029, paratype, × 3.6. • L, S – right valve, JK 14992, paratype; L – dorso-lateral view of the left valve, detail of the lateral teeth, × 7.4; S – lateral view, × 6. • M – dorso-lateral right view, detail of duplivincular ligament area, JK 14997, paratype, × 8.0. • N–P – right valve, JK 15020, holotype; N – dorsal view, × 4; O – dorso-lateral view, detail of the lateral teeth, × 5.2; P – lateral view, × 4.8. • All specimens come from the decalcified siltstone nodules, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek 1963b).



Dimensions. – Longer forms (L/H = 1.62–2.10)

specimen	V	L	H	W/2	L/H
JK 15073	L	8.9	4.8	1.9	1.85
JK 15111	R	15.1	8.6	2.9	1.76
JK 15112	R	16.8	9.6	3.6	1.75
JK 15047	L	20.1	10.2	4.5	1.97
NM L40574	R	22.5	11.2	–	2.00
JK 15075	L	23.1	13.6	4.5	1.70
JK 15049	L	23.3	14.1	4.1	1.65
JK 15092	R	23.5	13.3	5.6	1.77
JK 15050	R	24.0	12.0	4.6	2.00
JK 15077	R	24.2	13.6	5.4	1.78
JK 15079	R	24.3	11.6	5.5	2.09
JK 15085	R	26.3	15.7	5.4	1.68
JK 15114	L	26.4	13.5	6.0	1.96
JK 15088	R	27.0	14.9	7.1	1.81
JK 15097	L	27.7	13.9	6.0	1.99
JK 15086	R	28.2	16.6	5.4	1.70
JK 15051	R	29.3	18.1	6.3	1.62
JK 15091	R	29.5	16.3	7.1	1.81
NM L40576	R	31.5	17.4	5.6	1.81
NM L40575	L	34.0	17.8	–	1.91
JK 15099	L (A)	34.4	16.4	6.9	2.10
JK 15090	R	34.7	18.5	7.0	1.88
NM L40577	L	38.0	20.1	6.9	1.89

Shorter forms (L/H = 1.33–1.67)

specimen	V	L	H	W/2	L/H
JK 15069	L	10.6	7.5	2.9	1.41
JK 15102	R	15.0	11.0	4.0	1.36
JK 15084	R	15.0	11.3	4.6	1.33
JK 15093	L	19.1	12.7	4.9	1.50
JK 15082	L	19.5	12.7	4.5	1.54
JK 15094a	L	22.0	13.2	5.8	1.67
JK 15103	L	>22.0	14.4	4.5	1.53
JK 15067	L	22.1	13.5	4.9	1.64
JK 15094b	R	23.1	16.1	7.0	1.43
JK 15087	L	23.4	16.3	6.0	1.44
NM L40573	L	25.8	17.1	4.5	1.51
JK 15098a	R	25.9	16.4	6.0	1.58
JK 15104	R	26.0	18.0	7.0	1.44
JK 15089	R	26.1	17.3	6.0	1.51
JK 15096	L	26.9	16.6	5.5	1.62
JK 15098b	R	27.6	18.7	6.1	1.48
JK 15106	L	28.1	17.0	5.9	1.65
JK 15095	L	28.3	17.2	5.9	1.65
JK 15052	L	29.1	20.8	8.9	1.40
JK 15108	R	31.6	20.9	4.9	1.51

Discussion. – In the past, more than 163 Ordovician species were classified under *Modiolopsis* Hall, 1847 (Pojeta 1971). In general, the specific classification is very difficult when only general modioliform shape and outer surface sculpture formed by growth wrinkles, are known.

Since it is out of the scope of this paper to revise all the representatives of the Ordovician *Modiolopsis* described in the past, we compare *Modiolopsis pragensis* with the Ordovician type species *Modiolopsis modiolaris* (Conrad, 1838) which differs generally by more elongated and larger shells, elongated prominent anterior lobe, slightly concave ventral margin and deeply impressed anterior adductor muscle scar and pallial line. On the specimen figured by Pojeta 1971 (pl. 15, figs 1–3) the posterior myophoric buttress described by Liljedahl (1994) in *Modiolopsis alvae* Liljedahl, 1994 from the late Wenlock of Gotland is clearly visible.

Most closely is related *Modiolopsis draboviensis* Barrande, 1881 from the Upper Ordovician, Sandbian, Letná Formation sandstones, Děd Hill near Beroun, the Prague Basin. It is similar to *Modiolopsis pragensis* in early juvenile stages with almost parallel dorsal and ventral margins but late in ontogeny the posterior part becomes distinctly larger and higher than anterior part of the shell (see lectotype of *Modiolopsis draboviensis*, Fig. 8V). Adult specimens of *Modiolopsis veterana* Barrande, 1881 from the late Sandbian, Zahořany Formation, Zahořany near Beroun, the Prague Basin, differ from *Modiolopsis pragensis* in postero-ventrally extended shells, relatively short dorsal margin, in prominent umbonal ridge, slightly concave ventral margin, regularly spaced growth bands and furrows, and in deeply impressed anterior adductor muscle scar. “*Modiolopsis*” *primula* Barrande, 1881, from the Upper Ordovician, Sandbian, Letná Formation, sandstones, Děd Hill near Beroun, the Prague Basin, differs from *Modiolopsis pragensis* in very high and short shells (L = 17.6, H = 16.8, L/H = 1.05) and in prominent impression of the anterior adductor muscle scar. “*Modiolopsis*” *lenticularis* Barrande, 1881 and “*Modiolopsis*” *faba* Barrande, 1881 from the Upper Ordovician, late Katian, upper Králův Dvůr Formation, Prague Basin, Bohemia have very high shells (L/H = 1.16 and 1.11) and most probably do not represent the genus *Modiolopsis*. “*Modiolopsis*” *minuta* Barrande, 1881 from the Králův Dvůr Formation (late Katian), differs from the genus *Modiolopsis* in its well-developed posterior wing, separated from the rest of shell by a radial sulcus. *Modiolopsis tumescens* Barrande, 1881 described from the same stratigraphic level differs in a less developed anterior lobe. *Modiolopsis cuyana* Sánchez, 1990 from the Hirnantian of Argentina differs from *Modiolopsis pragensis* in distinctly shorter shells with relatively very high posterior part. *Modiolopsis elegantulus* Sharpe, 1853 from the Middle Ordovician of Portugal and the Massif Armoricain, France, and from the Upper Ordovician of Finistère (Babin & Beaulieu 2003) differs from *Modiolopsis pragensis* in concave ventral margin.

Occurrence. – *Modiolopsis pragensis* occurs in the Prague area, Prague Basin, Bohemia and is known from the Home-

rian, the upper Kosov Formation coarse-grained sandstones and quartzites of Tachlovice, Praha-Nová Ves, Praha-Hodkovičky, and Praha-Běchovice.

Mode of life. – Most probably infaunal. The valves of *Modiolopsis pragensis* are mostly found disarticulated and washed out on the bedding planes of the sandstone. Shells with conjoined valves also occur but they are rare. On some bedding planes very abundant, disarticulated and relatively very small juveniles are found. Two overlapping forms (shorter – $L/H = 1.33–1.67$ and longer – $L/H = 1.62–2.10$) co-occur in the coarse grained sandstones to quartzites of the high Hirnantian, Kosov Formation at the Praha-Běchovice, Praha-Hodkovičky and Tachlovice localities.

Superorder Anomalodesmata Dall, 1889
Superfamily Pholadomyoidea Gray, 1847

?Genus *Sphenolium* Miller, 1889

Type species. – *Orthodesma cuneiforme* Miller, 1881, Upper Ordovician, upper part of the Hudson River Group, near Versailles, Indiana, U.S.A.

Remarks. – *Sphenolium* Miller, 1889 was first related by Newell (1969, p. N818) and by Pojeta 1971 (*?Sphenolium striatum* Ulrich, 1894) to anomalodesmatans. Later Pojeta (1978, pl. 7, figs 7–9, pl. 8, fig. 6) figured *Sphenolium* sp. nov., under investigation, with the anterior tooth above the anterior adductor muscle scar, the posterior tooth above the posterior adductor muscle scar, and with the ligament area crossed by horizontal grooves as the typical Ordovician cyrtodontid. In agreement with Pojeta (1971) we consider *?Sphenolium parallelum* Ulrich, 1894 and *?Sphenolium striatum* Ulrich, 1894 to be closely related to anomalodesmatans. The Bohemian specimens determined here as *?Sphenolium* cf. *parallelum* Ulrich, 1894 are closely related to *?Sphenolium parallelum* by general shape of the shell. *?Sphenolium striatum* from the Upper Ordovician, Goodhue County, Minnesota differs in development of radial striae on the inner surface of dorsal slopes and on the umbonal ridge. More precise comparison and generic determination is impossible due to lack of material.

?*Sphenolium* cf. *parallelum* Ulrich, 1894

Figure 8A–G

Material. – One incomplete left valve and one open articulated shell.

Description. – Small lanceolate shell ($L = 10.4$, $H = 5.1$, $W/2 = 2.4$) is strongly inequilateral, longitudinally elon-

gated, inflated ($H/W = 1.06$). Umbo is prominent, in almost terminal anterior position, closely incurved, prosogyrate. Valve is subdivided by sinuous, prominent rounded diagonal umbonal ridge between umbo and postero-ventral extremity. Dorsal margin is straight, more than half of the shell length. Posterior end of dorsal margin is blunt. Dorsal and ventral margins are subparallel. Posterior margin is obliquely rounded. Ventral margin is long, convex. Short anterior margin is evenly rounded. In front of the umbo small lunule is developed. Inner surface sculpture is formed of irregularly spaced narrow growth bands and furrows. Other features not preserved.

Discussion. – *?Sphenolium parallelum* Ulrich, 1894 from the Upper Ordovician, Trenton Formation, Mineral Point, Wisconsin (Bassler, 1915, p. 1170 listed this species as being from the Platteville of Blackriver age and from Richmond age rocks) is not congeneric with *Sphenolium* and differs from the type species *Sphenolium cuneiforme* (Miller, 1881), *Sphenolium richmondense* Miller, 1889 from the Upper Ordovician of Indiana, and from *Sphenolium faberi* Miller, 1889 from the Upper Ordovician of Ohio especially by the longitudinally elongated shells with almost parallel dorsal and ventral margins.

Occurrence. – Uppermost Ordovician, late Hirnantian, upper Kosov Formation, siltstone nodules, Bohemia, Prague Basin, Praha-Běchovice, temporary outcrop in the research institution's area, north of village (Marek 1963b).

Mode of life. – Burrowing, infaunal.

Community analysis

Two communities were already distinguished in the upper Hirnantian of the Prague Basin by Havlíček (1982). The community dominated by *Modiolopsis* aff. *draboviensis* Barrande, 1881 (= *Modiolopsis pragensis* sp. nov.) inhabited the shallow-water plains with a substrate of light-coloured, coarse grained quartzose sandstones. In the moderately deepened eastern part of the Prague Basin in the uppermost Hirnantian at the top of the Kosov Formation Havlíček distinguished (1982) the *Hirnantia sagittifera* Community. It is formed by a rich suite of articulate brachiopods described in detail by Marek & Havlíček (1967), inarticulate brachiopods, gastropods, bivalves, orthocone nautiloids, sedentary cystoids, crinoids, trilobites, ostracods, chlorophytes, and graptolites, which were not revised in 1982. For the classification and analysis of the Bivalvia dominated communities we followed the methodology used by Kříž (1999).

Modiolopsis Community Group

Barrande (1881) described *Modiolopsis draboviensis* as the only common bivalve in the Upper Ordovician, Sandbian, Letná Formation sandstones, Děd Hill near Beroun, the Prague Basin. Here it occurs in the community together with dominant *Dalmanitina socialis* (Barrande, 1852) and *Deanaspis goldfussi* (Barrande, 1846). Barrande (1881) also figured *Modiolopsis draboviensis* (= *Modiolopsis pragensis* sp. nov.) from the late Hirnantian sandstones, the upper Kosov Formation, localities Tachlovice and Praha-Hodkovičky where it is dominant and forms the characteristic community. The species of the genus *Modiolopsis* are dominant in many communities since the Lower Ordovician (Babin 1966, Babin & Hamman 2001). Walker & Bambach (1974) described and analyzed as example the low diversity *Modiolopsis* Community with dominant *Modiolopsis* sp. from the unstable, high stress shallow environment of the lower Silurian Ross Brook Formation, Arisaig, Nova Scotia, Canada. From the less rigidly controlled facies of the lower Silurian Ross Brook Formation, Arisaig, Nova Scotia they described and analyzed the *Pteronitella*–*Nuculites* Community, where *Modiolopsis* sp. is also dominant but the community is more diversified and contains less dominant pterineid and grammysoid bivalves, nuculoids, gastropods, cephalopods and trilobites. The *Modiolopsis* Community Group is characteristic for the shallow, high energy, and sandy inner shelf environment.

Modiolopsis pragensis Community

Name. – Used here for the first time.

Community group assignment. – *Modiolopsis* Community Group.

Composition. – Almost absolutely dominant *Modiolopsis pragensis* occurs together with rare gastropods *Bucanella bohémica* (Perner, 1903), *Bucanellidae* gen. indet., bivalves *Myoplusia* sp., *Metapalaeoneilo dromon* sp. nov., ros-

troconch *Ribeiria* sp., trilobites *Brongniartella* sp., phyllocarid *Ceratiocaris* sp., brachiopods *Aegiromena* sp., *Plectothyrella* sp., common *Cornulites* sp., and sponge spicules. *Modiolopsis pragensis* is represented mostly by the disarticulated adult stages but on some bedding planes the juvenile stages are abundant.

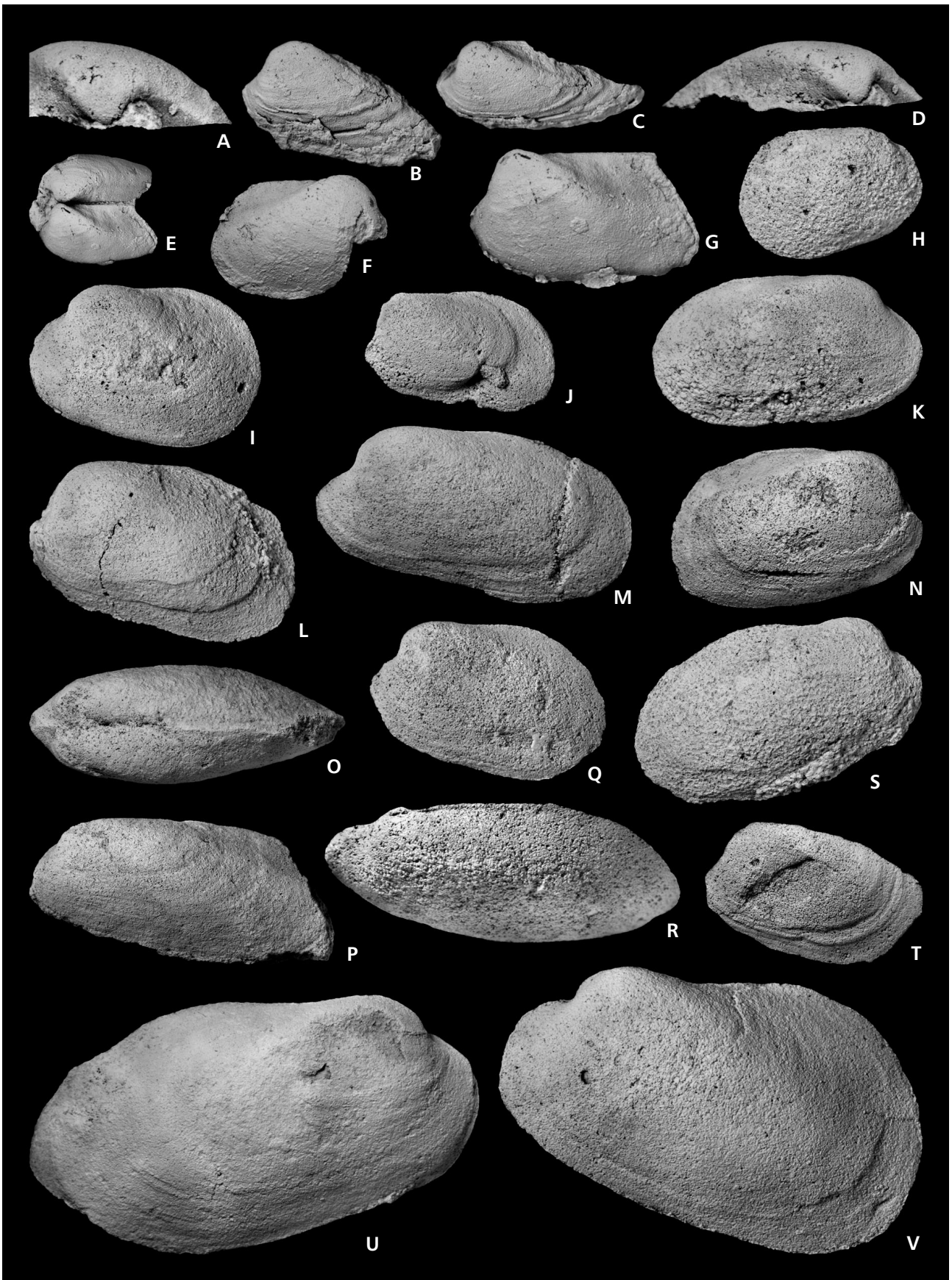
Age. – Upper Kosov Formation, late Homeric, uppermost Ordovician. In the shales immediately above the sandstone with *Modiolopsis pragensis* occurs *Normalograptus persculptus* (Elles & Wood, 1907).

Type locality. – Bohemia, Praha-Běchovice, shallow syncline north of the village. The best material was found in the pipeline outcrop along the western margin of the research institution's area. The point is marked as the geologically significant locality No. 6 in Straka (1987, p. 66).

Geographic distribution. – The *Modiolopsis pragensis* Community is known only from the Prague Basin, Bohemia. It is analogous and homologous (Boucot & Kříž 1999) with the similar *Modiolopsis draboviensis* Community from the sandstones and quartzites, Upper Ordovician, Sandbian, Letná Formation, Děd Hill near Beroun, the Prague Basin. Here it occurs on the locally tectonically uplifted bottom of the basin. The *Modiolopsis cuyana* Community described by Sanchez (1990) from the Don Braulio Formation, Hirnantian, Argentina is also analogous and homologous to the *Modiolopsis pragensis* Community.

Environment interpretation. – The bivalves occur in the light-coloured mostly coarse-grained sandstone splitting readily into thin laminae. They are mostly disarticulated but rarely found as shells with conjoined valves. Other fossils are quite rare and frequently fragmentary. According to Štorch (1990) the coarse, storm generated sandstones represent the maximum regression in the upper part of the Hirnantian. According to Brenchley & Štorch (1989) their sedimentation was result of an additional regressive event when the shelf was channelled, and coarse material trans-

Figure 8. A–G – ?*Sphenolium* cf. *parallelum* Ulrich, 1894. • A–D – left valve, JK 15016; A – dorsal view, detail of lunule, × 8.0; B – lateral view, × 3.2; C – dorso-lateral view, × 3.6; D – dorsal view, × 6.2. • E–G – open articulated shell, JK 14953; E – dorsal view, × 2.0; F – right lateral view, × 2.9; G – left lateral view, × 3.7. • H–U – *Modiolopsis pragensis* sp. nov.; H – right valve, JK 15084, paratype, lateral view, × 2.3; I – left valve, JK 15087, paratype, lateral view, × 1.8; J – left pathological valve, JK 15081, paratype, lateral view, × 1.8; K – right valve, JK 15088, paratype, lateral view, × 1.8; L – left valve, JK 15052, paratype, lateral view, × 1.7; M – left valve, JK 15097, holotype, lateral view, × 2.1; N – right valve, JK 15104, paratype, lateral view, × 1.6; O, P – shell with conjoined valves, JK 15099, paratype; O – dorsal view, × 1.7; P – left lateral view, × 1.7; R – left valve, JK 15082, paratype, dorso-lateral view, detail of the dorsal margin, × 3.4; S – right valve, JK 15051, lateral view, × 1.8; T – pathological left valve, JK 15101, paratype, lateral view, × 1.5; U – right valve, JK 15090, lateral view, × 2.4. • V – *Modiolopsis draboviensis* Barrande, 1881, left valve, NM L 27042, holotype, lateral view, × 2.9. • A–G – decalcified siltstone nodules, Kosov Formation, Hirnantian, uppermost Ordovician, Praha-Běchovice (Marek, 1963b). • H–U – coarse sandstones, Kosov Formation, Hirnantian, uppermost Ordovician, shallow syncline north of Praha-Běchovice. • V – sandstones, Letná Formation, Sandbian, Upper Ordovician, Děd Hill near Beroun.



ported from the shore. The *Modiolopsis pragensis* Community is of low diversity (four species of bivalves) and has high population densities. It indicates restricted living conditions. Shells of the dominant semi-infaunal or infaunal *Modiolopsis pragensis* are mostly disarticulated, quite well preserved, almost none fragmented. Rarely also conjoined valves occur. Quite common adult pathological shells of *Modiolopsis pragensis* exhibit repairs of the shell border or fractures when mantle tissue was not permanently injured (Fig. 8J, T), and indicate high-energy environment during episodic events (storms *etc.*). On the bedding planes are concentrated mostly adult valves and on some bedding planes juveniles, most probably sorted by storm events. Other bivalves, gastropods, rostroconchs, brachiopods and trilobites occur rarely, disarticulated and fragmented. The *Modiolopsis pragensis* Community may be compared with the lower and middle Llandovery Orbiculoid-Linguloid and Pelecypod communities Benthic Assemblage 1–2 life zone of Boucot (1975), Havlíček & Vaněk (1990).

Hirnantia Community Group

Temple (1965) described for the first time and analysed the Upper Ordovician *Hirnantia* fauna from the Holy Cross Mountains of Poland, Bardo syncline, Stawy Section (10 species of brachiopods), and from the Aber Hirnant, South-east of Bala, North Wales, Hirnant Quarry locality (11 species of brachiopods). Marek & Havlíček (1967) described a diverse *Hirnantia* fauna (25 species of brachiopods) from the Prague Basin, Praha-Běchovice locality. Since that times the *Hirnantia* fauna has been described from many other parts of the World, *e.g.*, Ireland, Sweden, central East Baltic, Carnic Alps, Morocco, Libya, North America, Kazakhstan, Norway, Yangtze and Western Yunnan-Tibet Regions, China (Havlíček 1989). Endemism is significant in the Hirnantian faunas (Lespérance 1974). According to Rong & Harper (1988), and Sheehan (2001) the *Hirnantia* fauna extended from the circumpolar sphere into the temperate to tropical zones from the cold water environment of the Tindouf Basin (Morocco) to the South Sweden, Oslo-Asker District in Norway, and Ireland in proximity to the carbonate platforms (Havlíček 1989). The absence of the Hirnantian fauna over cratonic North America is explained as the result of the well-known unconformity at the base of the Silurian in the Mid-Continent (Lespérance 1974).

Lespérance & Sheehan (1976) proposed the *Hirnantia* Community be used exclusively instead the *Hirnantia* fauna. We describe for the analogous and homologous communities the *Hirnantia* Community Group to substitute the term “*Hirnantia* fauna”.

Hirnantia sagittifera – *Sluha kosoviensis* Community

Name. – The *Hirnantia sagittifera* Community was introduced by Havlíček (1982). The community is also characterized by the common nuculoid *Sluha kosoviensis*, by the diversified community of other nuculoids and by the dominant ambonychiid *Mytilarca mareki*. We propose to change the community name to the *Hirnantia sagittifera* – *Sluha kosoviensis* Community to characterize better the brachiopod – bivalve dominance.

Community group assignment. – *Hirnantia* Community Group.

Composition. – Havlíček (1976) lists from the Bohemian localities in the eastern Prague Basin more than 25 species of benthic brachiopods (draboviids, aegiromenids, heterorthis and orthostrophiiids and inarticulates), described by Marek & Havlíček (1967), and by Havlíček (1977, 1994). The articulate brachiopods are commonly preserved as shells with conjoined valves (*Cryptothyrella* sp., *Plectothyrella platystrophoides* Temple, 1965, *Drabovia agnata* Havlíček, 1967, *a.o.*). Inarticulate brachiopods are represented by the infaunal lingulid *Rafanoglossa siliqua* Havlíček, 1994, the epibenthic attached discinid *Schizotretinia euxina* Havlíček, 1994 and the trematid *Tethyrete frigerum* Havlíček, 1994, free-lying craniid *Philhedra* sp., and attached craniopsid *Sanxiaella* sp. (Mergl 1986). *Rafanoglossa siliqua* and *Tethyrete frigerum* occur mostly as the shells with conjoined valves. The gastropods *Sinuitopsis hornyi* Marek, 1963a, *Grandostoma taconicum* Marek, 1963a, *Bucanella bohémica* (Perner, 1903), *Bucanellidae* gen. indet., and *Temnodiscus evolvens* (Perner, 1903) were described by Marek (1963a). Important are bivalves *Mytilarca mareki* sp. nov., *Modiolopsis* cf. *pragensis* sp. nov., *?Sphenolium* cf. *parallelum* Ulrich, 1894, *Sluha kosoviensis* (Barrande, 1881), *Nuculites* aff. *planulatus* Conrad, 1841, *Praealeda compar* (Barrande, 1881), *Praenucula abrupta* sp. nov., *Myoplusia* sp., *Praenucula dispar* (Barrande, 1881), *Myoplusia obtusa* (Barrande, 1881), and *Myoplusia contrastans* (Barrande, 1881), trilobites *Mucronaspis mucronata* (Brongniart, 1822), *Brongniartella platynota* (Dalman, 1828), *Eoleonaspis vondraceki* (Šnajdr, 1987) and graptolite *Normalograptus persculptus* (Elles & Wood, 1907). The conulariids, hexactinellids, trepostomate bryozoans, annelids, hyolitids, orthocone nautiloids, rare ostracods, phyllocarids, blastoids, cystoids, crinoids (preserved as individual columnals), dendroids and chlorophytes (receptaculitids) have not yet been systematically revised.

Age. – The *Hirnantia sagittifera*–*Sluha kosoviensis* Community occurs a few metres below the base of the Silurian in the Uppermost Kosov Formation, late Homeric, upper

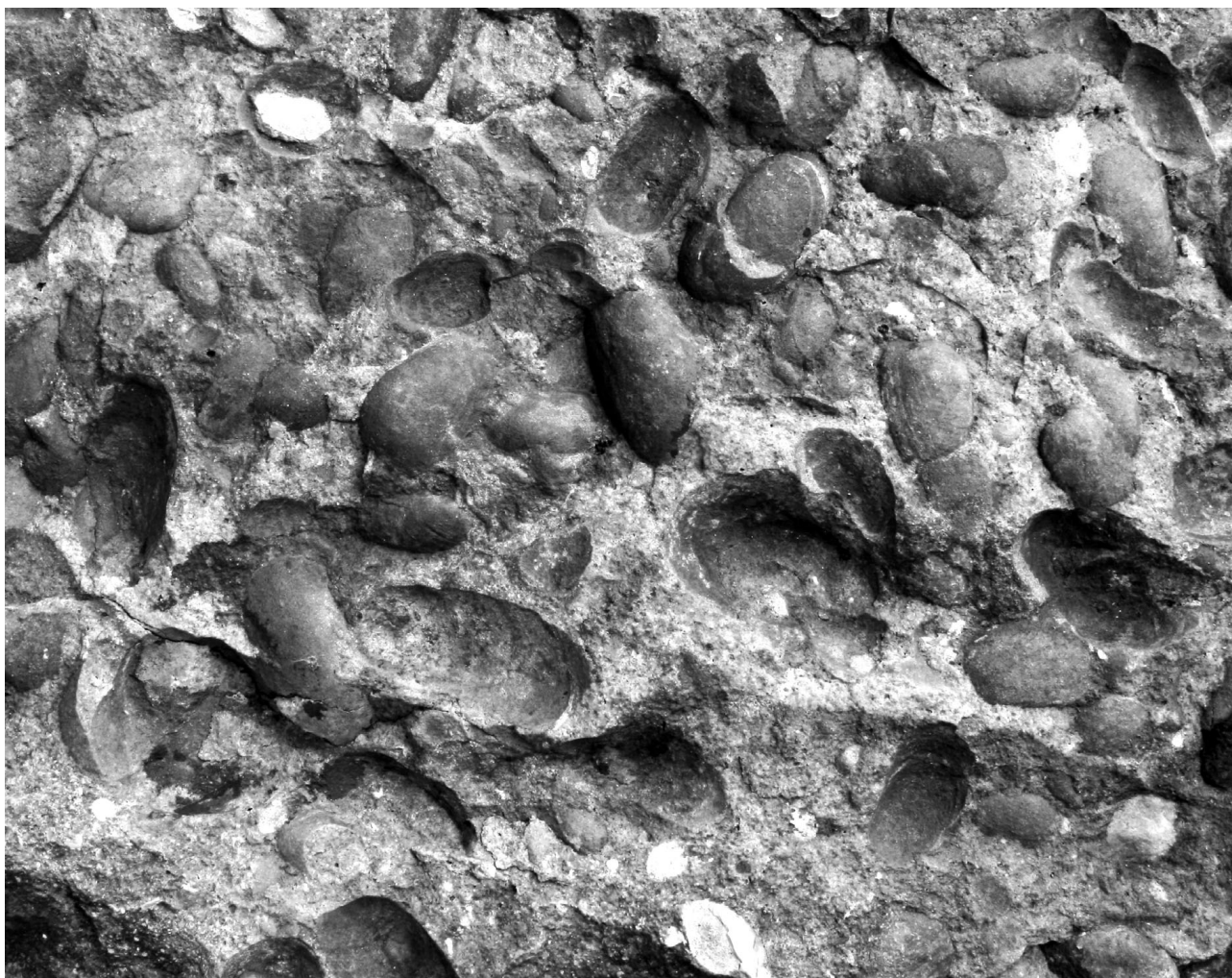


Figure 9. Bedding plane with *Modiolopsis pragensis* sp. nov., paratypes, coarse sandstones, Kosov Formation, Hirnantian, uppermost Ordovician, shallow syncline north of Praha-Běchovice, $\times 1.05$.

most Ordovician, together with *Normalograptus persculptus* (Elles & Wood, 1907).

Type locality. – Bohemia, Praha-Běchovice, shallow syncline north of the village, temporary outcrops in the research institution's area (Marek 1963b).

Geographic distribution. – The *Hirnantia sagittifera*–*Sluha kosoviensis* Community is known only from the Prague Basin, Bohemia. It is analogous and homologous with the similar communities of the *Hirnantia* Community Group. It differs namely by its high diversity. In Bohemia it replaced the shallow water *Modiolopsis pragensis* Community dominated by infaunal elements after a moderate transgressive deepening of the sea (Havlíček 1982). Havlíček (1989) pointed out that the *Hirnantia* fauna of Bohemia and China, in spite of enormous distance, is closely similar and contains not only genera but also many species com-

mon to both the regions. Abundant nuculoids, together with *Pterinea?* sp. were mentioned, and *Praenucula* sp. and *Palaeoneilo* sp. were figured from the Hirnantian of the Anti-Atlas, Morocco by Babin & Destombes (1990). Indeterminable Hirnantian bivalves were mentioned in the lower Hirnantian as the part of the *Hirnantia* Association, in the higher *Trematis*-bivalve assemblages, and in the *Holorhynchus* Association of the Oslo-Asker area, Norway (Brenchley & Cocks 1982).

Environment interpretation. – The *Hirnantia sagittifera*–*Sluha kosoviensis* Community occurs in the flat lenses and nodules of light-grey decalcified slightly clayey compact siltstone, which forms the level in the ash-grey clayey micaceous shale. The bivalve community described herein (Table 1) is quite diversified (11 species of bivalves). The bivalves are mostly well preserved, not fragmented, mostly disarticulated (71.4%) but also quite commonly preserved

Table 1. Numerical and ranked abundance of bivalves in the *Hirnantia sagittifer–Sluha kosoviensis* Community, Uppermost Kosov Formation, late Hirnantian, uppermost Ordovician, Praha-Běchovice, shallow syncline north of the village, outcrops in the research institutions area, Bohemia (Marek 1963b). 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 = rank abundance.

Species	Life habits	RV	LV	A	RA	AA	R
<i>Mytilarca mareki</i>	semi-infaunal	41	19	11	64.1	26.8	1
<i>Sluha kosoviensis</i>	infaunal	8	5	1	11.7	13.3	2
<i>Nuculites</i> aff. <i>planulatus</i>	infaunal	2	2	2	6.3	50.0	3
<i>Praeleda compar</i>	infaunal	–	1	3	5.5	85.7	4
<i>Praenucula abrupta</i>	infaunal	3	2	–	3.9	–	5
? <i>Sphenolium</i> cf. <i>parallellum</i>	infaunal	–	1	1	2.3	66.7	6
<i>Myoplusia</i> sp.	infaunal	1	1	–	1.6	–	7
<i>Praenucula dispar</i>	infaunal	1	1	–	1.6	–	8
<i>Myoplusia obtusa</i>	infaunal	–	–	1	1.6	100.0	9
<i>Myoplusia contrastans</i>	infaunal	–	1	–	0.8	–	10
<i>Modiolopsis</i> cf. <i>pragensis</i>	infaunal	1	–	–	0.8	–	11
Totals		57	33	19	100.2%	28.8%	

as shells with conjoined and articulated open valves (28.8%). In the soft-bottom environment the abundant infaunal deposit-feeding nuculoid bivalves (33%) occur; diversified group is represented by 67.5% disarticulated shells and by 32.5% shells with conjoined valves. The dominant ambonychiid *Mytilarca mareki* (64.1%) was most probably semi-infaunal, byssate (percentage relative abundance of conjoined shells with conjoined valves is relatively high – 26.8%).

The Recent nuculoids (Nuculacea and Nuculanacea) inhabit all types of soft substrates from the fine muddy sand or silt, muddy sands to clay, sandy gravel to clayey gravel rich in organic material and well ventilated (e.g., Yonge 1939, Davitašvili & Merklin 1966). We suppose that the *Hirnantia sagittifera–Sluha kosoviensis* Community occupied the well-ventilated environment of the soft bottom silts with high organic content. The community was most probably autochthonous and with minimal transport. The idea is supported by the common preservation of the articulate brachiopods, semi-infaunal *Mytilarca mareki* and infaunal bivalves as shells with conjoined valves.

Hirnantia sagittifera–Sluha kosoviensis Community may be compared with the lower and middle Llandovery level bottom, non-reef *Linoporella* and *Dicoelosia-Skenidioides* communities, Benthic Assemblage 3–4 life zone of Boucot (1975, cf. Havlíček & Vaněk 1990). Ordovician silts in the Prague Basin were favoured by nuculoids. The most diversified community (27 nuculoid species) is known from the siltstones of the Zahořany Formation (late Sandbian). In general the nuculoids occur quite commonly in the Prague Basin Ordovician also in the well-ventilated claystone and sandy facies bottoms (Kříž 1997).

Conclusions

1. The Bivalvia dominated low diversity *Modiolopsis pragensis* Community occurs in the uppermost few metres of the high Hirnantian in the eastern part of the Prague Basin, Bohemia. It originated just at the end of the glaciation period when the sea level was still low due to locally tectonically uplifted bottom. The regressive Kosov Formation (Hirnantian) sequence culminated here by a shallow water, storm generated petromictic conglomerates and heavy-bedded shallow water sandstones.

2. The *Hirnantia sagittifera–Sluha kosoviensis* Community from the uppermost Hirnantian occurs in eastern part of the Prague Basin, Bohemia where it occupied a well-ventilated quiet environment of the soft carbonate siltstone bottom during the uppermost Hirnantian transgression following the end of glaciation. It represents the most diversified known community of the *Hirnantia* Community Group in the World yet known.

3. In the uppermost Ordovician (Hirnantian) a total disappearance of barriers made possible faunal migrations between Perunica, Baltica and Avalonia (Havlíček *et al.* 1994) after global sea level rise at the end of the glaciation before the oceanic circulation stagnated at the base of the Silurian. The bivalves *Mytilarca mareki* and *Metapalaeoneilo dromon* sp. nov., support the possibility of migrations from the equatorial region of Baltica carbonate platforms to Perunica and the bivalves *Nuculites* aff. *planulatus* and ?*Sphenolium* cf. *parallellum* migrated probably from the equatorial regions of Avalonia and Laurentia. The *Hirnantia sagittifera–Sluha kosoviensis* Community fauna extended eastwards from Perunica to Central China (Rong & Harper 1988, Sheehan

2001). The same authors assign this fauna to the temperate-to-subtropical zone of the Kosov Province (between 30° to 45° S). Perunica (Bohemia) placed on the continental reconstructions for the late Ordovician in circumpolar region at higher latitudes than 60°S (Torsvik 1998, Cope 2002) was according to our opinion probably at a lower latitude position.

4. Previous conclusions support the data of Havlíček *et al.* (1994), who situated the microcontinent Perunica close to Baltica in the lowermost Ordovician, drifted during the Ordovician and Silurian from high latitudes (Lower Ordovician – around 28° S) in the southern hemisphere towards the palaeoequator (Lower Devonian – between 5–9° S).

5. In the Hirnantian two pulses of the extinction occurred. During the beginning of the glaciation the sea level declined and the climatic gradient intensified. A second, short pulse of extinction came when the glaciation ended, sea level rose, and the climatic gradient lessened. Endemic faunas in epicontinental seas were especially hard hit in contrast to the biota in open marine settings (Droser & Sheehan 1995, Sheehan 2001). Before end of the Hirnantian the evolution of the *Hirnantia* Community Group represents the evidence of the environment recovery during transgression following the glaciation. Further rapid rise of the sea level, together with the sedimentation of the euxinic facies of dark graptolitic shale at the base of the Silurian, represented drastic reduction in sedimentation rate with a lack of the sea bottom ventilation in open marine systems on a global scale, and caused extinction of the *Hirnantia* Community Group fauna.

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- 8.1.3 STEINOVÁ (= POLECHOVÁ), M. 2011a. Middle Ordovician bivalves from Bohemia, Spain and France. *In* GUTIÉRREZ-MARCO, J., C., RABÁNO I. & BELLIDO, D. G. *Ordovician of the World, Publicaciones del Instituto geológico y minero de España*, 575–580. Instituto Geológico y Minero de España. Madrid.

MIDDLE ORDOVICIAN BIVALVES FROM BOHEMIA, SPAIN AND FRANCE

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INTRODUCTION

Middle Ordovician bivalves from Bohemia have been an overlooked group for a long time. In France Babin (1966, 1977, 1981), Bradshaw (1970), Babin and Robardet (1972), Babin and Mélou (1972) and Babin and Beaulieu (2003), and in Spain Babin and Gutiérrez-Marco (1985, 1991), and Gutiérrez-Marco et al. (1999) systematically revised the bivalves from the Ordovician. A modern revision of Middle Ordovician bivalves was also realized by Soot-Ryen and Soot-Ryen (1960) in Norway, Pojeta (1971) in North America, Babin and Destombes (1990) in Morocco, Sánchez (1990, 2003) in Argentina, Cope (1999) in Wales, Fang and Cope (2004), and Fang (2006) in China, and Sá (2008) in Portugal. In Bohemia they were described by Barrande (1881) and revised by Pfab (1934). Middle Ordovician bivalves from the Šárka Formation of Bohemia (lower and middle Darriwilian), are being revised by the author.

GEOLOGICAL SETTING

The Šárka Formation was deposited during the early and mid Darriwilian. The largest part of the Šárka Formation is developed in shale facies. Within the shales occur horizons with siliceous nodules containing a well-preserved and diverse fauna. Black shales prevail in the central parts of the Prague Basin, while sedimentary iron ores are present in onshore settings (Havlíček, 1998). Accumulations of volcanic and volcanoclastic rocks are also very common in the Šárka Formation.

MIDDLE ORDOVICIAN BIVALVES OF BOHEMIA

Barrande (1881) described nine species from the Šárka Formation (early to mid Darriwilian) of Bohemia. He allocated them to the genera *Nucula* and *Leda*, and defined the new genera *Babinka*,

Redonia and *Synek*. Pfab (1934) revised them and reassigned some of Barrande's species to other genera: *Praeleda* Pfab, 1934, *Praenucula* Pfab, 1934, *Pseudocyrtodonta* Pfab, 1934 and mainly to *Ctenodonta* Salter, 1852, and some of them were left in open nomenclature. Kříž (1995) described a representative of the genus *Coxiconchia* Babin, 1966 from the Šárka Formation.

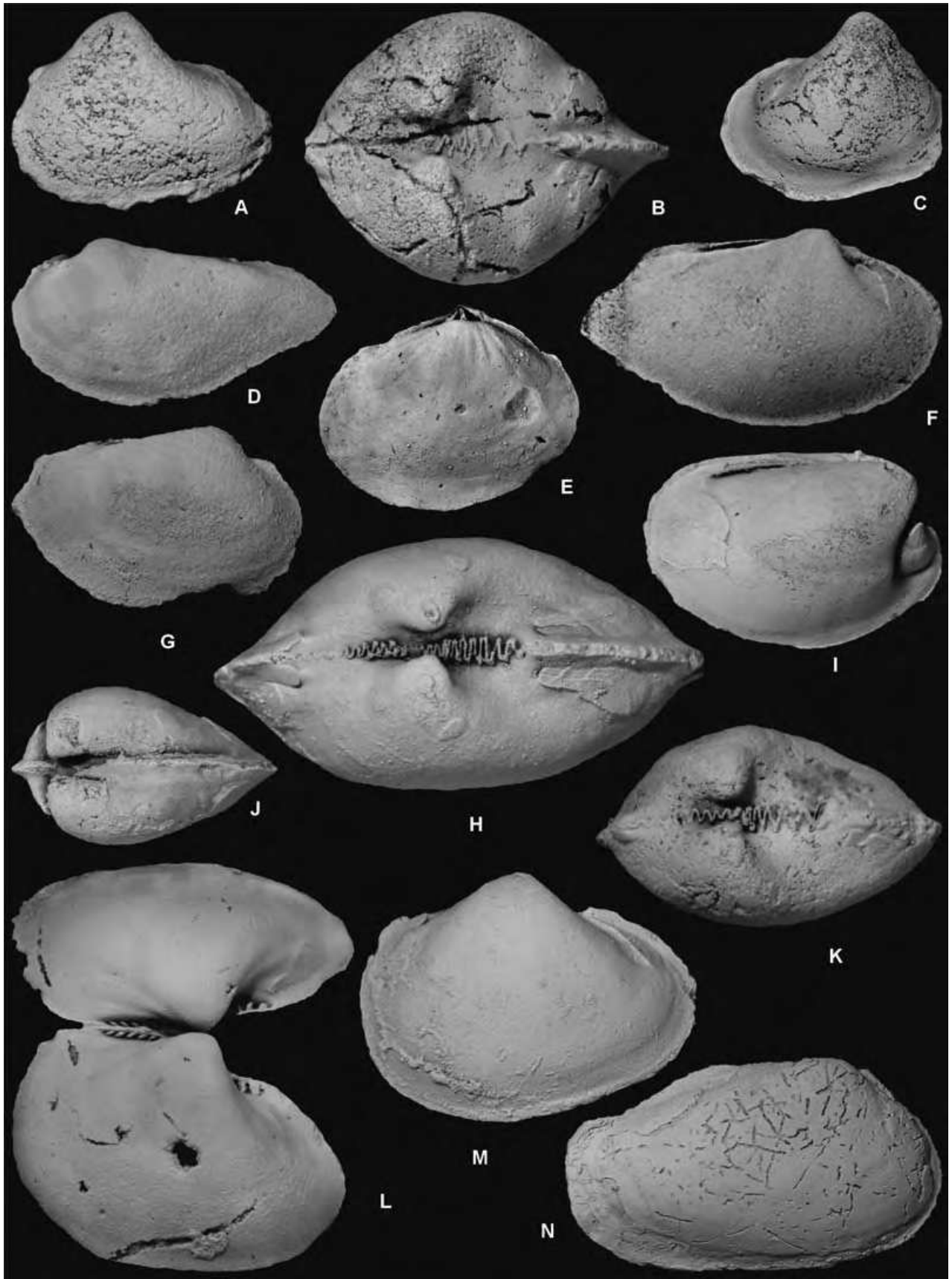
Modern revision is in progress now and shows that in the Šárka Formation of Bohemia occur the following bivalve taxa (Plate 1): *Pseudocyrtodonta ala*, *Pseudocyrtodonta incola*, *Praenucula dispar*, *Praenucula bohémica*, *Praenucula applanans*, *Praeleda pulchra*?, *Babinka prima*, *Redonia deshayesi*, *Coxiconchia britannica holubi*. Occurrence of *Praeleda pulchra* in the Šárka Formation is uncertain, because this species is very similar to *Praenucula bohémica*, and *Praeleda* and *Praenucula* are not well defined yet. I consider that *Ctenodonta* does not occur in the Middle Ordovician of Bohemia. *Ps. ala*, *Ps. incola* and *Redonia deshayesi* belong to the Actinodontida; *Praenucula dispar*, *Pr. bohémica*, *Pr. applanans* and *Praeleda pulchra* belong to the Palaeotaxodonta; *Babinka prima* belongs to the Lucinida and *Coxiconchia britannica holubi* is presently classified as Lucinida (Bieler et al., 2010).

RELATIONSHIPS OF THE MIDDLE ORDOVICIAN BIVALVES OF BOHEMIA, SPAIN AND FRANCE

Babin and Gutiérrez-Marco (1991) described from the Middle Ordovician bivalves of Spain the species ?*Ctenodonta escosurae*, *Praenucula costae*, *Praenucula sharpei*, *Cardiolaria beirensis*, *Ekaterodonta hesperica*, *Myoplusia bilunata perdentata*, *Cadomia britannica*, *Goniophora (Cosmogoniophora) sp.*, *Modiolopsis elegantulus*, *Cyrtodontula sp.*, *Glyptarca? lusitanica* [now *Hemiprionodonta lusitanica*: see Cope (1996)], *Ananterodonta oretanica*, *Babinka prima*, *Coxiconchia britannica*, *Redonia deshayesi*, *Dulcinea manchegana*.

Hemiprionodonta lusitanica has its older record in the Lower Ordovician of Bolivia (Sánchez and Babin, 2005), and *B. prima* in the Lower Ordovician of France (Babin, 1977, 1982). *Praenucula costae* from Spain and *Praenucula bohémica* from Bohemia seem to be conspecific: they have similar hinges with concavodont teeth in posterior part of the shell, convexodont teeth in anterior part of the shell, rounded posterior adductor muscle scar and elongated anterior adductor muscle scar. *Praenucula costae* has more anteriorly elongated shell than *Praenucula bohémica*. *Praenucula costae* is also abundant in the Middle Ordovician of France. *Praenucula sharpei* (Spain) is probably a younger synonym of *Praenucula applanans* (Bohemia), which has a characteristic shape and hinge (concavodont teeth in the posterior part of the shell, convexodont teeth in the anterior part of the shell). *Coxiconchia britannica britannica* has larger shells, and deeper, relatively larger anterior adductor muscle scars than *Coxiconchia britannica holubi*. *Coxiconchia britannica holubi* differs from *Coxiconchia britannica guiraudi* in having smaller shell, reduced cardinal teeth, and smaller accessory muscle scars in a more dorsal position (Kříž, 1995). I agree with Babin and Gutiérrez-Marco (1991) that *Redonia bohémica* from Bohemia is conspecific with *Redonia deshayesi* from

Plate 1. Bivalves from the Šárka Formation, Bohemia. A, K, *Praenucula bohémica* (Barrande, 1881), articulated specimen, MBHR 14448; A, right lateral view (x 7.1); K, dorsal view (x 10.5). B, C, *Praenucula dispar* (Barrande, 1881), articulated specimen, MBHR 7982; B, dorsal view (x 7.6); C, left lateral view (x 4.6). D, F, *Pseudocyrtodonta incola* (Barrande, 1881); D, left valve, MBHR 12569, left lateral view (x 8.3); F, right valve, MBHR 12701, dorso-lateral view (x 11). E, *Babinka prima* Barrande, 1881, right valve, L 27086, right lateral view (x 2.3). F, *Pseudocyrtodonta incola* (Barrande, 1881), right valve, MBHR 13415, right lateral view (x 11). G, *Pseudocyrtodonta ala* (Barrande, 1881), right valve, MBHR 12701, dorso-lateral view (x 6.7). H, L, M, *Praenucula applanans* (Barrande, 1881); H, M, articulated specimen, MBHR 14619 in dorsal view (H, x 9.1) and right lateral view (M, x 6.9); L, two valves, MBHR 2395, lateral view (x 6.1). J, I, *Redonia deshayesi* Rouault, 1851, articulated specimen, L22656; J, dorsal view (x 4); I, right lateral view (x 4.5). N, *Coxiconchia britannica holubi* Kříž, 1995, right valve, MBHR 5498, lateral view (x 1.9).



Spain and France. I would like to mention here that also *Redonia anglica* (Salter in Murchison, 1859) from Wales, is most probably conspecific with *Redonia deshayesi*.

PALAEOECOLOGY

Middle Ordovician bivalves from Bohemia are relatively small (with *C. britannica holubi* as the only exception), and are regarded as infaunal deposit feeders or shallow infaunal filter feeders (Table 1). No isofilibranchs and pteriomorphs are known from Bohemia, similarly to the Ibero-Armorican area, where the isofilibranchs and pteriomorphs are scarce (Babin and Gutiérrez-Marco, 1991), being these forms frequent in Baltica (Soot-Ryen and Soot-Ryen, 1960).

Genera	Mode of life
<i>Praenucula</i>	infaunal deposit feeder
<i>Concavodonta</i>	infaunal deposit feeder
<i>Praeleda</i>	infaunal deposit feeder
<i>Pseudocyrtodonta</i>	shallow infaunal filter feeder
<i>Redonia</i>	shallow infaunal filter feeder
<i>Babinka</i>	shallow infaunal filter feeder
<i>Coxiconchia</i>	shallow infaunal filter feeder

Table 1. Mode of life.

Stratigraphical occurrence of the same species in Bohemia, Spain and France

Myoplusia bilunata perdentata is known from the Middle Ordovician (Darriwilian) of Spain, from the Upper Ordovician (Sandbian) of Bohemia, and from the Upper Ordovician (Katian) of France. *Babinka prima* is known from the Middle Ordovician (Darriwilian) of Spain, from the Middle Ordovician (Dapingian and Darriwilian) of Bohemia and from the Lower Ordovician (Floian) and Middle Ordovician (Dapingian) of France. *Praenucula applanans* is known from the Middle Ordovician (Darriwilian) of Bohemia and Spain. *Redonia deshayesi* is known from the Middle Ordovician (Darriwilian) of Bohemia, Spain and France. *Redonia anglica* occurs in the Lower Ordovician (Floian) and in the Middle Ordovician (Darriwilian) of Wales.

CONCLUSIONS

The study of the Bohemian Darriwillian bivalves from the Šárka Formation contributes to our knowledge of the Middle Ordovician fauna of the world. The Middle Ordovician Bohemian bivalves are closely related to those of Spain and France.

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- 8.1.4 STEINOVÁ (= POLECHOVÁ), M. 2011b. *Praeleda* Pfab, 1934 a *Praenucula* Pfab, 1934 (Bivalvia) z ordoviku pražské pánve. *Zprávy o geologických výzkumech v roce 2010*, 117–119.

Praeleda Pfab, 1934 a *Praenucula* Pfab, 1934 (Bivalvia) z ordoviku pražské pánve

Praeleda Pfab, 1934 and *Praenucula* Pfab, 1934 (Bivalvia) from the Ordovician of the Prague Basin

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Key words: Palaeotaxodonta, *Praeleda*, *Praenucula*, taxonomy, Ordovician, Prague Basin

Abstract: Palaeotaxodonta is an important group of bivalves. The



genera *Praeleda* and *Praenucula* belonging to this taxon were established on Bohemian material. *Praeleda* is considered to be evolutionary important genus, however *Praeleda* is very similar to *Praenucula* and the modern revision of both genera is necessary. The type species of *Praeleda* and *Praenucula* are discussed in this paper.

Palaeotaxodonti jsou důležitou skupinou mlžů, známou již od spodního kambria. Někteří autoři (Pojeta 1978, Jell 1980, Runnegar – Bentley 1983, Waller 1990) od ní odvozují vznik ostatních skupin mlžů. Sánchez a Babin (1998) a Carter et al. (2000) se naopak domnívají, že je to skupina zcela samostatná, která se významně liší od ostatních mlžů protobranchiátními žábry a není předkem ostatních skupin mlžů.

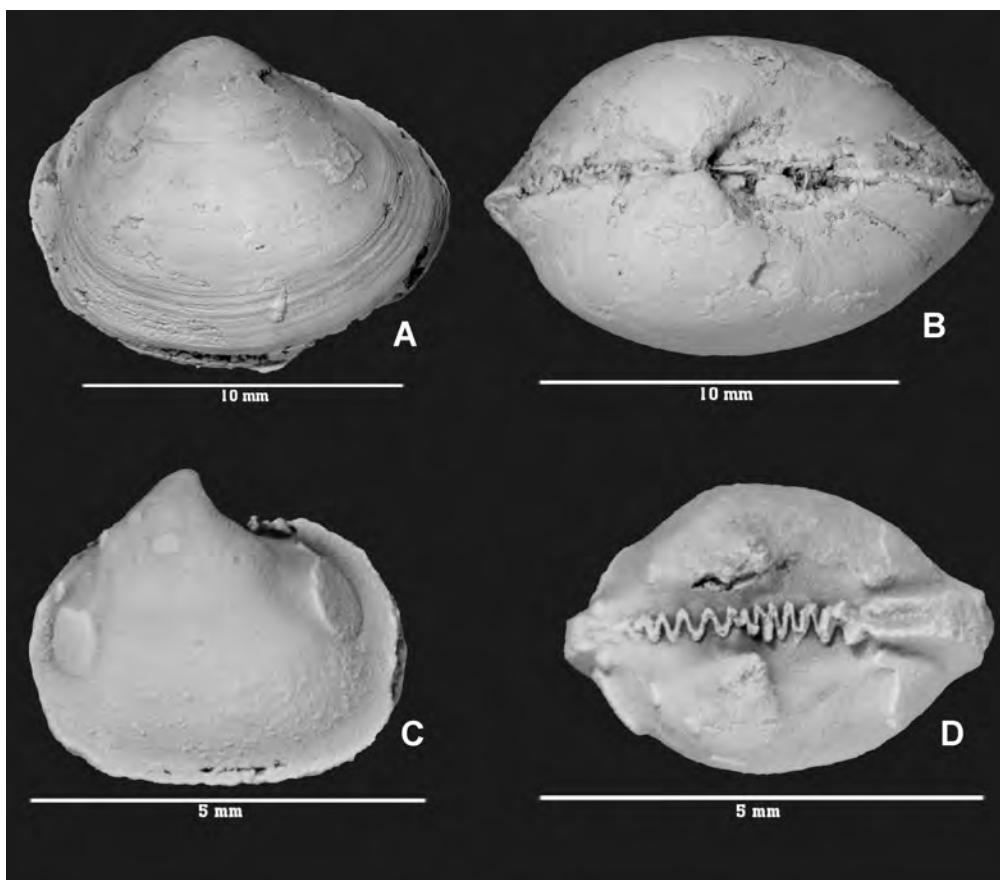
Palaeotaxodonti v pražské pánvi

V pražské pánvi se palaeotaxodonti vyskytují v ordoviku. Barrande (1881) palaeotaxodonta vyobrazil a zařadil je k recentním rodům *Leda* (neplatný, synonymizován s rodem *Nuculana*) a *Nucula*. Většinu Barrandových druhů Pfab (1934) přeřadil k rodu *Ctenodonta*, popsal i nové rody *Praeleda*, *Praenucula* a *Pseudocyrtodonta*. Nejasnosti se tím nevyřešily, protože k rodu *Ctenodonta* byla v té době zahrnuta většina fosilních nuculidů, *Praeleda* a *Praenucula* nebyly Pfabem (1934) dobře definovány a *Pseudocyrtodonta* byla chybně zařazena k palaeotaxodontům. Rod *Ctenodonta* se podle mého názoru se v ordoviku pražské pánve zřejmě vůbec nevyskytuje. Druhy, které byly k rodu *Ctenodonta* řazeny, patří k rodům *Concavodonta* Babin, 1972, *Myoplusia* Neumayr, 1884, *Praeleda* a *Praenucula*. *Praeleda* a *Praenucula* jsou si velmi podobné a je těžké je od sebe odlišit, zároveň jsou hojné v mnoha oblastech (Španělsko, Francie, Wales, Čína, Austrálie, Argentina, USA a Skandinávie) a mohou být i evolučně významné (Cope 1997). *Praeleda* a *Praenucula* se v pražské pánvi vyskytují od středního ordoviku (darriwil) do svrchního ordoviku (hirnant). K rodu *Praeleda* jsou řazeny dva druhy – *P. compar* (Barrande, 1881) a *P. pulchra* (Barrande, 1881). K rodu *Praenucula* jsou řazeny dva druhy *Pr. dispar* (Barrande, 1881) a *Pr. abrupta* Kříž a Steinová, 2009. Rod *Pseudocyrtodonta* patří k mlžům s aktinodontním zámekem. K palaeotaxodontním mlžům ordoviku pražské pánve patří ještě rody *Sluha* Barrande, 1881 a *Synek* Barrande, 1881.

Historie výzkumu a přehled názorů k rodům *Praeleda* a *Praenucula*

Rody *Praeleda* a *Praenucula* byly stanoveny na materiálu z ordoviku pražské pánve (Pfab 1934). Typovými druhy jsou *Praeleda compar* (Barrande, 1881) a *Praenucula dispar* (Barrande, 1881). Pfab (1934) sice velmi pečlivě popsal jejich jednotlivé druhy, rozdíl mezi těmito dvěma rody však nezmiňuje. McAlester (1968, 1969) revidoval typový materiál rodů *Praeleda* a *Praenucula* a domníval se, že *Praeleda* je neplatná a je synonymická k rodu *Deceptrix*. Bradshaw a Bradshaw (1971) se naopak domnívali, že *Praeleda* je platná a mohla by být předkem rodu *Deceptrix*. Tunnicliff (1982) souhlasil s McAlesterem (1969) a popsal hlavní rozdíly mezi rody *Deceptrix* a *Praenucula*: 1. *Praeleda* má větší zuby v přední části schránky, 2. vrchol u rodu *Praenucula* leží v zadní části schránky, u rodu *Praeleda* v přední části schránky, 3. vtisky po adduktorech u rodu *Praeleda* jsou větší a více ventrálně položené.

Cope (1999) potvrdil rozdíl ve velikosti zubů, s pozicí vrcholu však nesouhlasil, domníval se, že *Praenucula* i *Praeleda* ho mají v zadní části schránky (přední část schránky je tak větší částí schránky), maximálně u některých druhů rodu *Praeleda* ve střední části schránky. Zároveň se snažil dokázat, že právě zámek je nejdůležitější znak pro jejich odlišení a zdůraznil, že u rodu *Praenucula* zámková linie vykazuje přibližně stejný počet zubů v přední i zadní části schránky, u některých jedinců může být více zubů v přední části schránky. Zuby v přední části schránky mohou být buď stejně velké, nebo větší než zuby v zadní části schránky. U rodu *Praeleda* jsou posteriorní zuby vždy početnější a mohou být menší než anteriorní zuby. Zároveň zde je (ale také nemusí být) angulární diskordance mezi anteriorní a posteriorní řadou zubů a zámková osa leží v linii posteriorních zubů a anteriorní zuby leží ventrálně od ní. Kvůli tomuto znaku ji Cope (1997) zařadil k čeledi Cardiolariidae Cope, 1997. Od této čeledi Cope (1997, 1999) odvozuje vznik mlžů s autolamelibranchiálními žábry. Carter et al.



Obr. 1. *Praeleda compar* (Barrande, 1881), jádro, L27145, lektotyp: A – laterální pohled na pravou misku, B – dorzální pohled na zámek; *Praenucula dispar* (Barrande, 1881), jádro, L27176, lektotyp: C – laterální pohled na pravou misku, D – dorzální pohled na zámek.

(2000) jsou naopak názoru, že důležitějším znakem pro rod *Praeleda* i pro samotnou čeleď *Cardiolaria*idae je náhlé zvětšení anteriorních zubů.

Diskuse k typovým druhům rodů *Praeleda* a *Praenucula*

Názory na studované rody jsou rozmanité (viz předchozí kapitulu) a diskuse okolo nich velmi široká. Málokterý z uvedených autorů diskutuje typový materiál z Čech, přestože jej dobře vyobrazili Barrande (1881), Pfab (1934) i McAlester (1968).

Typovým druhem rodu *Praeleda* je *P. compar* (popsaný a vyobrazený Barrandem 1881, Vol. VI, Pl. 271, III/9–11) ze zahořanského souvrství (svrchní ordovik, sandb; obr. 1A, B). Lektotyp a paralektotypy byly vybrány Pfabem (1934). Lektotyp není příliš dobře zachován, přesto lze poznat, že zámek neukazuje angulární diskordanci a ani anteriorní zuby nejsou větší. Svalové vtisky nejsou zachovány. Dobře zachované jsou přírůstkové linie, velmi výrazné zejména ve ventrální části schránky.

Typovým druhem rodu *Praenucula* je *Pr. dispar* (popsaný a vyobrazený Barrandem 1881, Vol. VI, Pl. 273, VII/1–4) ze šáreckého souvrství (střední ordovik, darriwil, obr. 1C, D). Lektotyp a paralektotypy byly vybrány Pfabem (1934). Lektotyp je malý jedinec (délka 4,2 mm, výška 4,0 mm, vnitřní jádro) s dobře zachovanými svalovými vtisky i zámkem.

Vtisky svěračů jsou kruhové, zachovány jsou též pedální svalové vtisky a čtyři akcesorické svalové vtisky pod vrcholem. Vtisky zadních svěračů leží více ventrálně než vtisky předních svěračů, což je pro tento druh charakteristický znak. Zuby jsou v přední i zadní části schránky stejně velké. Žádná angulární diskordance nebyla na zámku pozorována.

Závěr

Detailní revize těchto rodů je nezbytná, protože mohou reprezentovat evolučně důležité taxony. Pro čeleď *Cardiolaria*idae je typická angulární diskordance v zámkové linii. Copeova diagnóza rodu *Praeleda* je však nepřesná: může mít angulární diskordanci, ale také nemusí, zuby mohou být větší, ale nemusí (Cope 1999). *Praeleda* a *Praenucula* jsou si velmi podobné, mají mnoho podobných i totožných znaků. Po důkladné revizi rodů *Praeleda* a *Praenucula* je možno uvažovat o jejich sloučení do jednoho rodu.

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- 8.1.5 STEINOVÁ (= POLECHOVÁ), M. 2012. Probable ancestral type of actinodont hinge in the Ordovician bivalve *Pseudocyrtodonta* Pfab, 1934. *Bulletin of Geosciences* 87(2), 333–346.

Probable ancestral type of actinodont hinge in the Ordovician bivalve *Pseudocyrtodonta* Pfab, 1934

MARIKA STEINOVÁ



The type species of *Pseudocyrtodonta*, *P. ala* and other two species *P. incola*, *P. obtusa* are known from the Middle and Upper Ordovician of the Prague Basin, Bohemia. Because of the actinodont type of the hinge, *Pseudocyrtodonta* is excluded from the subclass Protobranchia and is transferred to the Autobranchia, family Cycloconchidae. The family Pseudocyrtodontidae is considered invalid. Early and Middle Ordovician Cycloconchidae were highly diversified, containing 24 genera. Their diversity suddenly decreased during the Upper Ordovician to three genera only. The hinge of *Pseudocyrtodonta* could be considered morphologically close to the ancestral type of the hinge of the actinodonts. A complete species list of Ordovician actinodonts, including schematic figures of their hinge for the most important genera is presented. *Pseudocyrtodonta* was most probably an active burrower. • Key words: Bivalvia, Actinodontida, Cycloconchidae, *Pseudocyrtodonta*, Ordovician, Bohemia, systematics, palaeoecology.

STEINOVÁ, M. 2012. Probable ancestral type of actinodont hinge in the Ordovician bivalve *Pseudocyrtodonta* Pfab, 1934. *Bulletin of Geosciences* 87(2), 333–346 (5 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received December 12, 2011; accepted in revised form January 26, 2012; published online March 23, 2012; issued xxxxx xx, 2012.

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The Ordovician bivalves from Bohemia have been overlooked since Barrande (1881) and Pfab (1934) described them and their systematics should be revised. The preparation of the new *Treatise on Invertebrate Paleontology* for bivalves is in progress now and therefore it is an appropriate time for doing a revision of the Ordovician bivalves from Bohemia. Kříž & Steinová (2009) began a revision with Hirnantian bivalves from Bohemia; this continues on well-preserved bivalves from the Middle Ordovician (early Darriwilian, Šárka Formation). First results reveal that the order Actinodontida Dechaseaux, 1952 in Bohemia is not confined only to the genus *Redonia* Rouault, 1851 but also to *Pseudocyrtodonta* Pfab, 1934.

Barrande (1881) figured Darriwilian *Redonia bohémica*, which clearly belongs to the Actinodontida. Barrande also figured two species, *Leda ala* and *Leda incola*, which Pfab (1934) considered as conspecific and assigned them to the new genus *Pseudocyrtodonta*. The other species that Pfab (1934) placed into *Pseudocyrtodonta* was *P. obtusa* (Barrande, 1881) from the Zahořany Formation (early Katian). Pfab (1934) defined *Pseudocyrtodonta* in his work about bivalves with taxodont hinge but he noticed that the hinge differs from the “normal” taxodont hinge. Maillieux (1939) described *P. obtusa* from Belgium and defined the new family Pseudocyrtodontidae. McAllester (1969) considered *Pseudocyrtodonta* as conspecific with *Myoplusia* Neumayr, 1884.

Bieler *et al.* (2010) and Carter *et al.* (2011) in their works, which are the basis for the new classification of bivalves, placed the Pseudocyrtodontidae into the Protobranchia Pelseneer, 1889 (Palaeotaxodonta Korobkov, 1954).

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). 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. PO specimens deposited in the collection of Marika Steinová in the Czech Geological Survey, Prague. All measurements are in millimetres.

Class Bivalvia Linné, 1758
Subclass Heterodonta Neumayr, 1884
Order Actinodontida Dechaseaux, 1952

Remarks. – In the *Treatise on Invertebrate Paleontology* (Newell 1969) Actinodontida was considered as synonym of Modiomorphoidea Newell, 1969. Actinodontida differs

from Modiomorphoidea and they are important for early phylogeny of bivalves. There are three hypothesis about the early phylogeny of bivalves 1) some workers accept theory that actinodont teeth are derived from taxodont teeth (Babin 1966; Newell 1969; Pojeta 1971, 1978; Jell 1980; Babin & Le Pennec 1982; Runnegar & Bentley 1983; Pojeta & Runnegar 1985; Waller 1990; Sánchez 1995, Cope 1996, 1997 and Ratter & Cope 1998) 2) but some workers prefer an opposite view, namely that taxodont teeth are derived from actinodont teeth (Morris & Fortey 1976, Morris 1980) 3) Sánchez & Babin (1998) offered another alternative that palaeotaxodonts and palaeoheterodonts originated independently. Carter *et al.* (2000) confirm their hypothesis and showed that Actinodontida has apparently evolved convergently among Palaeotaxodonta. The oldest known species, which belongs to the Actinodontida is *Intihuaella simplicidentata* Sánchez in Sánchez & Vaccari (2003) from Tremadocian of Argentina. Allen & Sanders (1973) consider *Prelametila* Allen & Sanders, 1973 as a possible living actinodont, but this has been dismissed by later authors (*e.g.* Cope 1997).

Actinodontida from the Ordovician (Table 1) were described from Argentina (Sánchez 1986, 1997, 2001, 2005; Sánchez & Babin 1994, Sánchez & Vaccari 2003, and Sánchez & Benedetto 2007), Australia (Pojeta & Gilbert Tomlinson 1977), China (Guo 1985, 1988; Fang & Cope 2004, 2008), Bohemia (Barrande 1881, Pfab 1934), France (Rouault 1851, Barrois 1891, Babin 1966, Babin *et al.* 1982), North America (Meek 1871; Miller 1874; Foerste 1914; Ulrich 1893; Pojeta 1971, 1978), Spain (Babin & Gutiérrez-Marco 1985, 1991) and Wales (Salter 1859, Cope 1996).

Babin (1966) described some specimens from the Middle Ordovician of France, which he determined with uncertainty to *Actinodonta* Phillips, 1848. The type species of *Actinodonta* is *A. cuneata* Phillips, 1848 from the Silurian. Cope (2002) mentioned that this genus is problematic because Pojeta (1978) incorrectly recorded the type species as from the Ordovician. Furthermore, stratigraphical occurrence of the genus *Actinodonta* is incorrectly recorded in the *Treatise on Invertebrate Paleontology* (Newell 1969) as the Middle Ordovician in spite of fact that, the type species *Actinodonta cuneata* occurs correctly in the Silurian. It seems that *Actinodonta* is confined to the Silurian and therefore Ordovician specimens from France need revision (Cope 2002). Babin (1966, fig. 59) figured schemes of the hinge in some species of Actinodontida. According to these schemes, hinge of "*Actinodonta cuneata*" from France differs from the type species, hinge of the "*Actinodonta carinata*" is very similar to *Cycloconcha ovata* but they differ in shape, and "*Actinodonta obliqua*" differs from other actinodonts in shape, which is more similar to lyrodesmatids.

Schemes of the Ordovician actinodont hinges are shown on the Fig. 1. The hinge of the family Pucamyidae is

not figured, because the anterior part of the hinge is unknown.

Superfamily Anodontopsoidea Miller, 1889

Family Cycloconchidae Ulrich in Ulrich & Scofield, 1894

Subfamily Cycloconchinae Ulrich in Ulrich & Scofield, 1894

Genus *Pseudocyrtodonta* Pfab, 1934

Figures 2, 3, 4, 5

Type species. – *P. ala* (Barrande, 1881), Bohemia, Osek, Middle Ordovician, Darriwilian, Šárka Formation.

Diagnosis. – Equivalved, inequilateral, prosogyrate and posteriorly elongated cycloconchid. The dentition consists of numerous pseudocardinal teeth (looking like taxodont teeth) in anterior and one pseudolateral tooth in posterior part.

Description. – Shell equivalved, posteriorly elongated, inequilateral, with or without rostrate posterior. Umbos prosogyrate, projecting above the hinge margin, situated in the anterior half of the shell length. Anterior part of the shell is smaller than the posterior. Anterior margin is rounded, posterior margin elongated and also rounded, ventral margin convex.

Dentition (Fig. 2) with pseudocardinal teeth (pseudotaxodont) in anterior part, lying slightly below hinge line, one pseudolateral tooth in posterior part, long and slender, parallel to the hinge margin. Hinge continues below the umbos, without any gap. Anterior adductor muscle scar rounded or ovate, more pronounced than ovate posterior adductor muscle scar. Rounded pedal muscle scar in anterior part, joins with adductor muscle scar. Elongated pedal muscle scar in posterior part, separated from adductor muscle scar. Accessory muscle scars in the umbo region.

Discussion. – Pfab (1934) placed *Pseudocyrtodonta* in the Palaeotaxodonta, with a note that the hinge is different from "normal" taxodont hinge. Maillieux (1939) made *Pseudocyrtodonta* the type genus for the new family Pseudocyrtodontidae. McAlester (1969) included *Pseudocyrtodonta* in the synonymy of *Myoplusia* Neumayr, 1884. I was also of the opinion (Kříž & Steinová 2009) that *Pseudocyrtodonta obtusa* belongs to *Myoplusia*, but in rediscovered type material of Barrande (1881) and also in the collection of J. Kříž (Czech Geological Survey) there are specimens from the Zahořany Formation (early Katian), which show actinodont hinges and the shape of the shell is very similar to Barrande's specimens of *P. obtusa*. *Myoplusia* and *Pseudocyrtodonta* from the Zahořany Formation are very similar in their general shape, but they differ in the type of the hinge, which is very often not well preserved. *Myoplusia* shows taxodont whereas *Pseudocyrtodonta* has an

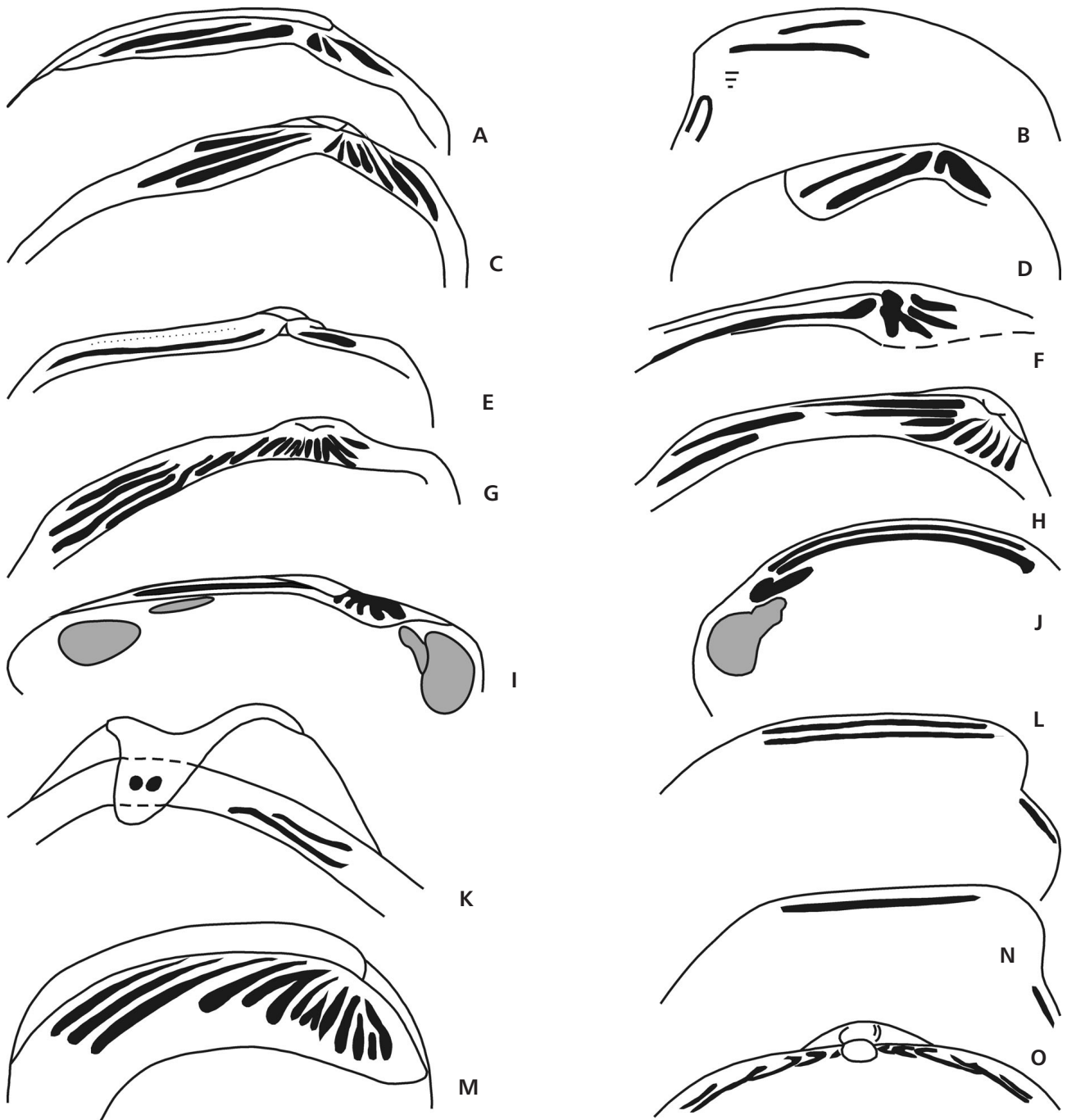


Figure 1. Hinge schemes of the important genera of the Ordovician Actinodontida. • A–I – Cycloconchidae Ulrich, 1884; A – *Cycloconcha*, according to fig. 3 in Babin & Gutiérrez-Marco (1985), left valve; B – *Zhenxiongella*, according to fig. 4 in Fang & Cope (2008), right valve; C – *Actinodonta*, according to Treatise on Invertebrate Paleontology (1969), left valve; D – *Famatinodonta*, according to fig. 3 in Sánchez (2001), left valve; E – *Fortowensia* according to fig. 6D in Cope (1996), left valve; F – *Poladonta*, according to fig. 5 in Sánchez *et al.* (2003), left valve; G – *Carminodonta*, according to fig. 6A in Cope (1996), left valve; H – *Ananterodonta*, according to fig. 3C in Babin & Gutiérrez-Marco (1985), left valve; I – *Pseudocyrtodonta*, according to specimen BHMR 14442, left valve. • J – Redoniidae Babin, 1966; *Redonia* according to specimen LPB 775, right valve. • K – Baidiostracidae Fang & Cope, 2008; *Baidiostraca*, according to fig. 4 in Fang & Cope (2008), right valve. • L, N – Intihuerallidae Sánchez, 2003; L – *Cienagomya*, according to fig. 3 in Sánchez (2005), left valve; N – *Intihuaella*, according to fig. 3 in Sánchez (2005), left valve. • M – Nyassidae Miller, 1877; *Copidens* according to fig. 3E in Babin & Gutiérrez-Marco (1985), left valve. • O – Lametilidae Allen & Sanders, 1973, *Prelametila*, according to fig. 36 in Allen & Sanders, 1973, left valve.

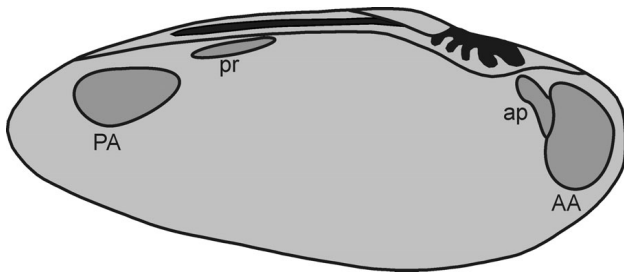


Figure 2. *Pseudocyrtodonta incola*, dorsolateral view showing hinge and muscle scars. Key to letter symbols: AA – anterior adductor muscle scar; PA – posterior adductor muscle scar; ap – anterior protractor muscle scar; pr – posterior retractor muscle scar.

actinodont type of hinge. So here the correction is made, *Myoplusia obtusa* described from the Kosov Formation (Kříž & Steinová 2009, pp. 421, 422, fig. 4F, G, I, J) should be classified as *Myoplusia incisa* (Barrande, 1881).

Bieler *et al.* (2010) and Carter *et al.* (2011) placed the Pseudocyrtodontidae in the Protobranchia Pelsener, 1889 (Palaeotoxodonta). As mentioned above, the Pseudocyrtodontidae cannot be placed in the Palaeotoxodonta, because *Pseudocyrtodonta* has an actinodont hinge. Furthermore, there is no reason to keep family Pseudocyrtodontidae, which is not well defined. Its diagnosis from Mailieux (1939): “bivalves with dentition half taxodont and half heterodont” is common for the most part of the bivalves, which belong to Actinodontida. The genera with different types of the actinodont hinge are grouped in the family Cycloconchidae (Fig. 1A–I) and *Pseudocyrtodonta* does not show any unique characters for describing a new family. Therefore *Pseudocyrtodonta* is placed within the Cycloconchidae.

Relationships. – *Ananterodonta* Babin & Gutiérrez-Marco, 1985 differs from *Pseudocyrtodonta* mainly in its hinge, which shows more numerous teeth in the posterior part and its anterior adductor muscle scar is more deeply impressed in the shell.

Mangbuina Guo, 1988 differs from *Pseudocyrtodonta* in the rounded shape of the shell, in the carina developed in the posterior part of the shell and in having three posterior teeth.

Zhenxiongella Fang & Cope, 2008 differs from *Pseudocyrtodonta* in having two posterior teeth, small subumbonal teeth and only one anterior tooth. Anterior and posterior myophoric buttresses are characteristic.

Fasciculodonta Fang & Cope, 2004 differs from *Pseudocyrtodonta* in its more deeply inserted adductor muscle scars and in its prominent shoulder in the posterior part of the shell.

Taselasmodum Guo, 1985 differs from *Pseudocyrtodonta* in having a more rounded shell, two elongated posterior teeth and more deeply impressed adductor scars.

Carminodonta Cope, 1996 differs from *Pseudocyrtodonta* in having a pronounced shoulder in the posterior part and in having more numerous teeth. Its hinge plate is wider than in *Pseudocyrtodonta*.

Fortowensia Cope, 1996 differs from *Pseudocyrtodonta* in having only one tooth in the anterior part.

Famatinodonta Sánchez, 2001 differs from *Pseudocyrtodonta* in having two strong pseudocardinals (one of them is in posterior part of the shell) and more pronounced adductor muscle scars.

Poladonta Sánchez in Sánchez *et al.* (2003) differs from *Pseudocyrtodonta* in having three pseudolateral teeth in the posterior part of the hinge.

Cycloconcha Miller, 1874 differs from *Pseudocyrtodonta* in having two pseudolateral teeth in posterior part and a more rounded shape.

Actinodonta Phillips, 1848 differs from *Pseudocyrtodonta* in having three pseudolateral teeth in the posterior part, more elongated anterior teeth, and more inserted anterior adductor muscle scars.

***Pseudocyrtodonta ala* (Barrande, 1881)**

Figure 3

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

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

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

Lectotype (SD, Pfab 1934). – Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 273 as figs II/1–3, NM L 27173. Other specimens on pl. 273, fig. II do not belong to *Pseudocyrtodonta ala*.

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

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

Material. – 18 shells with conjoined valves, 10 right valves, and 8 left valves.

Diagnosis. – *Pseudocyrtodonta* with longitudinally elongated shell without prominent rostrum, and with less pronounced umbos.

Description. – Shell small (length maximally 9.6 mm, height maximally 5.6 mm and width maximally 4 mm), equivalve, inequilateral and longitudinally elongated, without prominent rostrum. Anterior part of the shell is smaller than the posterior part. Anterior margin is rounded, posterior margin elongated and also rounded, ventral

Table 1. List of the Ordovician and early Silurian species belonging to order Actinodontida.

Country	Species	Family	Stratigraphy
Argentina (North Western Argentina Basin)	<i>Cienagomya bidentata</i> Sánchez, 2005	Intihuerallidae	Tremadocian, Floian
	<i>Intihuaella simplicidentata</i> Sánchez & Vaccari, 2003	Intihuerallidae	Tremadocian (Floresta Formation)
	<i>Redonia condorensis</i> Sánchez & Benedetto, 2007	Redoniidae	Darriwilian
	<i>Pseudoredonia radialis</i> Sánchez & Benedetto, 2007	Redoniidae?	Darriwilian
	<i>Pucamyra wira</i> Sánchez & Benedetto, 2007	Pucamyidae	Darriwilian
Argentina (Sierra de Famatina)	<i>Famatiodonta gonzaloi</i> Sánchez, 2001	Cycloconchidae	Floian/Dapingian (middle Arenigian)
Argentina (Western Argentina)	<i>Redonia riojana</i> Sánchez, 1997	Redoniidae	Floian/Dapingian (middle Arenigian)
	<i>Poladonta sanjuanina</i> Sánchez <i>et al.</i> , 2003	Cycloconchidae	Sandbian
	<i>Redonia suriensis</i> Sánchez & Babin, 1994	Redoniidae	Lower Ordovician
Argentina (Provincia de Salta)	<i>Cycloconcha cf. oblonga</i> Foerste, 1914	Cycloconchidae	Middle Ordovician
Australia	<i>Copidens browni</i> Pojeta & Gilbert-Tomlinson, 1977	Nyassidae	Darriwilian (Nora Formation)
Bohemia	<i>Pseudocyrtodonta incola</i> (Barrande, 1881)	Cycloconchidae	Darriwilian
	<i>Pseudocyrtodonta ala</i> (Barrande, 1881)	Cycloconchidae	Darriwilian
	<i>Pseudocyrtodonta obtusa</i> (Barrande, 1881)	Cycloconchidae	lower/middle Katian
	<i>Redonia deshayesi</i> Rouault, 1851	Redoniidae	Darriwilian
China (East Yunnan)	<i>Manguina prima</i> Guo, 1988	Cycloconchidae	Floian (Hongshiyai Formation)
	<i>Zhenxiongella septata</i> Guo, 1988	Cycloconchidae	Floian (Hongshiyai Formation)
	<i>Zadimerodia fastigiata</i> Guo, 1988	Nyassidae	Floian (Hongshiyai Formation)
	<i>Baidiostraca aberrans</i> Guo, 1988	Baidiostracidae	Floian (Hongshiyai Formation)
China (West Yunnan)	<i>Fasciculodonta impressa</i> Fang & Cope, 2004	Cycloconchidae	Dapingian–Darriwilian (Upper Arenigian)
	<i>Fasciculodonta fengyiensis</i> (Guo, 1985)	Cycloconchidae	Dapingian–Darriwilian (Upper Arenigian)
	<i>Taselasmodum decussatum</i> Guo, 1985	Cycloconchidae	Dapingian–Darriwilian (Upper Arenigian)
	<i>Yunnanoredonia laevis</i> Fang & Cope, 2004	Redoniidae	Dapingian–Darriwilian (Upper Arenigian)
France (Armorican massive)	<i>Redonia deshayesi</i> Rouault, 1851	Redoniidae	Darriwilian (Shiste à Calymenes)
	<i>“Actinodonta cuneata”</i> Phillips, 1848	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	<i>“Actinodonta carinata”</i> Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	<i>“Actinodonta obliqua”</i> Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	<i>“Actinodonta secunda”</i> Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	<i>“Actinodonta acuta”</i> Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	<i>“Actinodonta lata”</i> Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	<i>“Actinodonta obtusa”</i> Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
France (Montagne Noire)	<i>Redonia michelae</i> Babin <i>et al.</i> , 1982	Redoniidae	Floian and Dapingian
North America	<i>Cycloconcha ovata</i> Ulrich, 1893	Cycloconchidae	Upper Ordovician
	<i>Cycloconcha milleri</i> (Meek, 1871)	Cycloconchidae	Upper Ordovician
	<i>Cycloconcha mediocardinalis</i> Miller, 1874	Cycloconchidae	Upper Ordovician
	<i>Cycloconcha oblonga</i> Foerste, 1914	Cycloconchidae	Upper Ordovician
Spain	<i>Ananterodonta oretanica</i> Babin & Gutiérrez-Marco, 1985	Cycloconchidae	Darriwilian (Schiste à Neseuretus)
	<i>Redonia deshayesi</i> Rouault, 1851	Redoniidae	Darriwilian
	<i>Dulcineaia manchegana</i> Babin & Gutiérrez-Marco, 1991	Redoniidae	Darriwilian
Wales (Llangyng Inlier)	<i>Actinodonta cuneata</i> Phillips, 1848	Cycloconchidae	Silurian (Llandoverly)
	<i>Carminodonta crossi</i> Cope, 1996	Cycloconchidae	Floian
	<i>Fortowensia grandis</i> Cope, 1996	Cycloconchidae	Floian
	<i>Celtoconcha foveata</i> Cope, 1996	Cycloconchidae	Floian
	<i>Moridunia simplicidens</i> Cope, 1996	Redoniidae	Floian
	<i>Redonia anglica</i> Salter, 1859	Redoniidae	Floian/Dapingian (Arenigian)

margin convex. Less pronounced, strongly prosogyrate umbos are in the anterior half of the shell length. Hinge plate narrow with actinodont hinge, 2–4 pseudocardinal (pseudotaxodont) teeth in the anterior part (Fig. 3E, H), lying slightly below the hinge line. Single straight and slender pseudolateral tooth in the posterior part of hinge (Fig. 3E, H, L), and parallel to the hinge margin. Inner surface sculpture is smooth. Adductor muscle scars very badly preserved. Pedal and accessory muscle scars unknown. Outer surface sculpture and shell thickness is unknown.

Dimensions. –

Specimens	V	L	H	W/2
MBHR 2384a	A	9.6	5.6	2.0
MBHR 8902	A	9.6	5.1	1.4
MBHR 13159	R	7.9	4.9	–
MBHR 21039	A	7.8	4.9	1.5
MBHR 20368	A	7.8	4.8	1.5
MBHR 12701	R	7.6	4.1	–
MBHR 6334	R	7.5	4.5	–
MBHR 20567	L	7.3	3.0	–
MBHR 2420b	L	7.5	5.0	1.4
MBHR 14763	R	7.1	5.0	–
MBHR 4645	L	7.1	4.9	1.4
MBHR 18833	L	6.9	4.8	–
MBHR 20400	A	6.9	4.5	1.3
MBHR 20369	A	6.8	4.5	1.5
MBHR 21175	A	6.6	3.9	1.2
MBHR 18802	L	6.1	5.0	–
MBHR 7580	A	–	4.0	1.0
MBHR 20378	A	6.1	4.0	1.0
MBHR 20376	A	6.0	4.0	1.1
MBHR 18803	L	6.0	3.9	–
MBHR 20377	A	5.9	3.9	1.0
NM L 27173	A	5.9	3.8	–
MBHR 14293	L	5.9	2.8	–
MBHR 5067	R	5.9	4.0	–
MBHR 12908	A	5.8	3.5	1.0
MBHR 12826	A	5.6	3.2	0.9
MBHR 12647	R	5.2	3.5	–
MBHR 14294	A	5.1	3.5	1.0
MBHR 24036	L	5.0	3.5	–
MBHR 14236	R	5.0	2.9	1.3
MBHR 14421	R	4.5	2.5	–
MBHR 20410	A	4.2	3.0	1.2
MBHR 18840	R	4.1	2.9	–
MBHR 9774	R	3.8	2.1	0.2
MBHR 20411	A	3.1	2.1	0.4
MBHR 20345	A	2.8	1.4	0.4

Discussion. – Barrande (1881) figured two species from the Šárka Formation *Leda ala* and *Leda incola*. Pfab (1934) regarded them as conspecific. Here the view is taken, following the opinion of Barrande (1881), that they are different. They differ in shape, *P. incola* is more longitudinally elongated and has a rostrate posterior part. The umbos in *P. incola* are more pronounced than in *P. ala*. The hinge seems to be very similar, with one pseudolateral tooth in posterior part and several small pseudocardinal (pseudotaxodont) teeth in anterior part. However, the hinge in *P. ala* is ill-preserved. McAlester (1968) figured as the lectotype of *Pseudocyrtodonta ala* (pl. 29, figs 6–8), the specimen from the collection of National Museum, Prague but it differs from Barrande’s figures in having a damaged hinge, contrary to the specimen figured by Barrande (1881) and designated by Pfab (1934) as the lectotype. *Fasciculodonta impressa* Fang & Cope, 2004 from West Yunnan of China (Dapingian/Darriwilian) seems to be similar to *P. ala* in its longitudinally elongated shell, prosogyrate umbos and mainly in its hinge with one pseudolateral tooth in the posterior part and numerous pseudocardinal teeth in the anterior part. But *F. impressa* differs from *P. ala* in having more deeply impressed adductor muscle scars and in having a prominent shoulder in the posterior part of the shell.

Occurrence. – Bohemia, Prague Basin, early Darriwilian: Dily, Dily 1, Osek near Rokycany, Osek 1, Rokycany, Rokycany 2 – near cemetery, Rokycany 17.

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

Figure 4

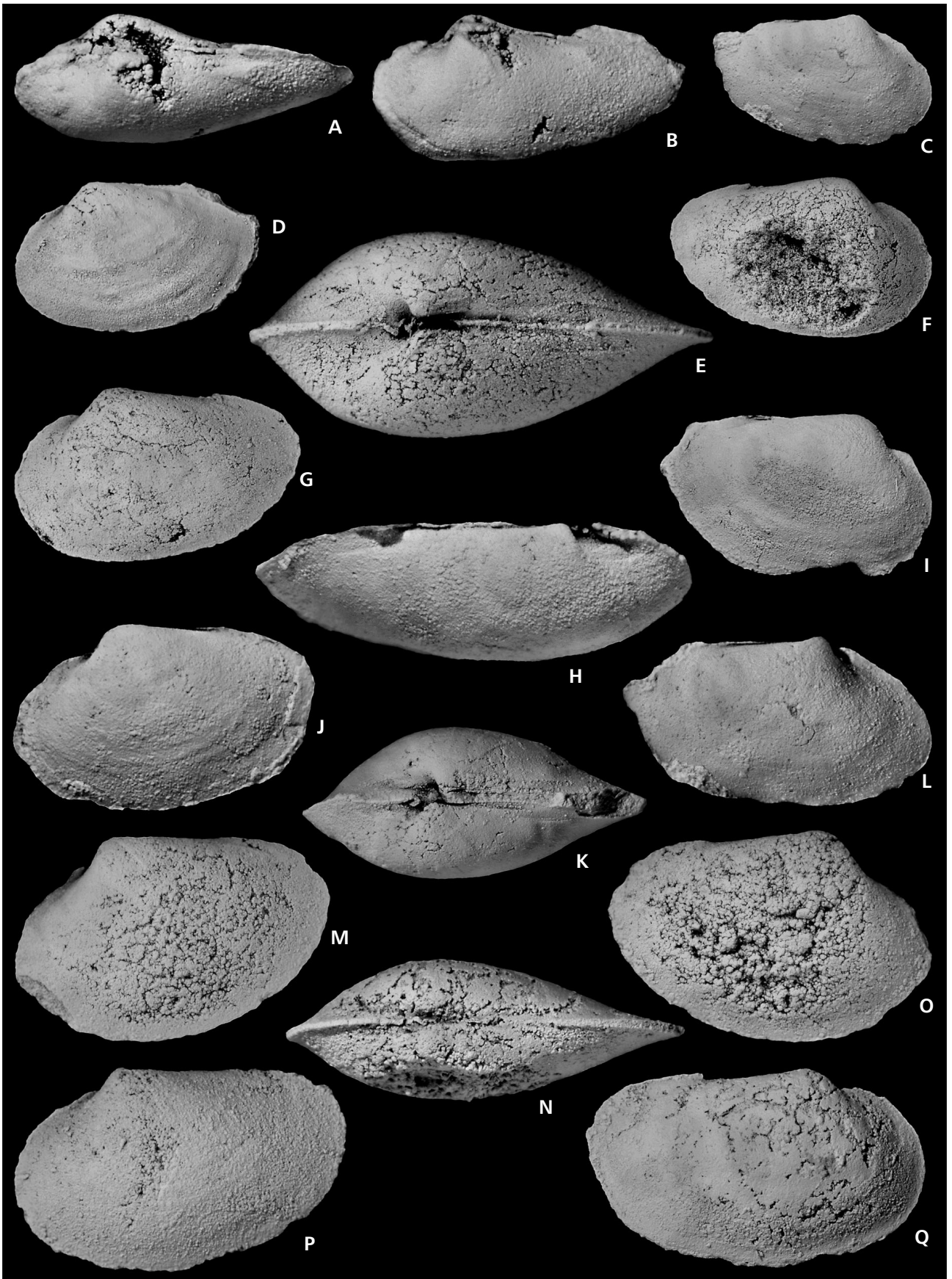
1881 *Leda incola* Barr.; Barrande, pl. 270, figs III/1–4.

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

Lectotype (SD, herein). – Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 270, as figs III/1–4, NM L 27117. Other specimens figured on the pl. 270, fig. III do not belong to *P. incola*.

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

Figure 3. A–Q – *Pseudocyrtodonta ala* (Barrande, 1881). • A, B – articulated specimen, NM L27173, lectotype; A – dorso-lateral view, × 9.7; B – left lateral view, × 6.4. • C, L – right valve, MBHR 6334; C – lateral view, × 4.1; L – dorsolateral view, pseudolateral tooth in the posterior part, × 8.1. • D – articulated specimen, MBHR 21039, left lateral view, × 9.1. • E–G – articulated specimen, MBHR 2384a; E – dorsal view, pseudocardinal teeth in anterior part and pseudolateral tooth in posterior part, × 18.2; F – right lateral view, × 5.9; G – left lateral view, × 4.6. • H, I – right valve, MBHR 12701; H – dorsal view, long tooth in posterior part, two pseudocardinals in anterior part, × 4.6; I – right lateral view, × 8.2. • J – left valve, MBHR 18803, left lateral view with part of the pseudolateral tooth in the posterior, × 6.4. • K, P – articulated specimen, MBHR 12826; K – dorsal view, × 10.5; P – right lateral view, × 7.2. • M, O – articulated specimen, MBHR 20373; M – left lateral view, × 4.3; O – right lateral view, × 6.6. • N, Q – articulated specimen, MBHR 8902; N – dorsal view, × 5; Q – right lateral view, × 6. • A–B, D – Prague Basin, Bohemia, Osek locality, early Darriwilian. • C, L – Prague Basin, Bohemia, Dily locality, early Darriwilian. • E–G, N, Q – Prague Basin, Bohemia, Rokycany locality, early Darriwilian. • H, I – Prague Basin, Bohemia, Osek 1 locality, early Darriwilian. • J – Prague Basin, Bohemia, Dily 1 locality, early Darriwilian. • K, P – Prague Basin, Bohemia, Dily 3 locality, early Darriwilian.



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

Material. – 44 shells with conjoined valves, 20 right valves, and 11 left valves.

Diagnosis. – *Pseudocyrtodonta* with longitudinally elongated shell, with rostrate posterior part and with more pronounced umbos.

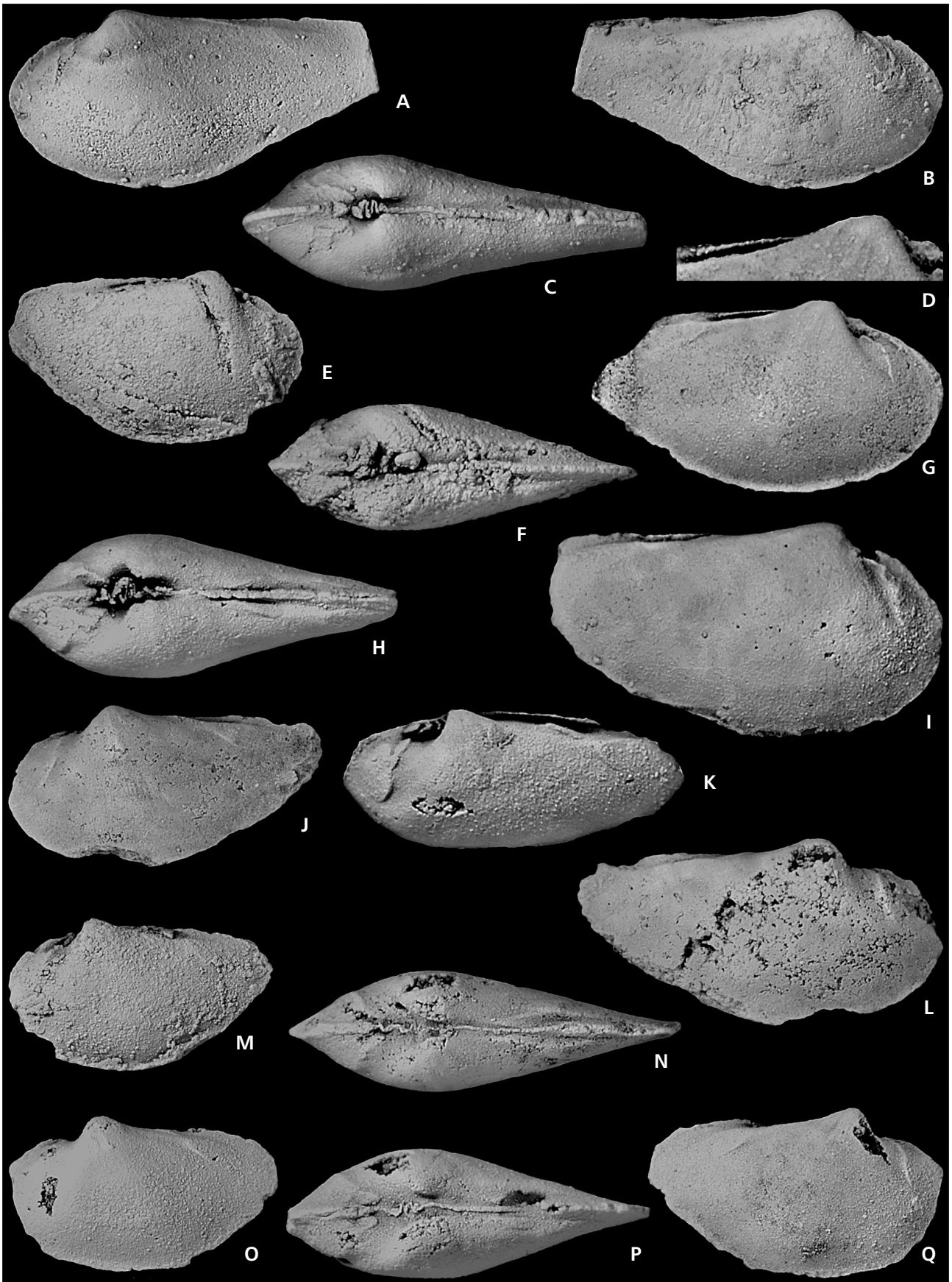
Description. – Shell small (length maximally 9 mm, height maximally 5 mm and width maximally 3.2 mm), equi-valve, inequilateral and longitudinally elongated, with rostrate posterior part. More pronounced, strongly prosogyrate umbos situated in the anterior part of the shell. Anterior margin of the shell rounded, posterior margin rostrate, ventral margin convex. Hinge actinodont, in the anterior part 3–6 pseudocardinal (pseudotaxodont) teeth (Fig. 4C, H, K), lying under hinge line. After Babin (1966) anterior teeth can be classified as convexodont. In the posterior part of the shell one straight, slender pseudolateral tooth (Fig. 4G). Anterior adductor muscle scar is almost elliptic, more deeply impressed than elliptic posterior adductor muscle scar. Rounded pedal muscle scar in anterior part, joins with adductor muscle scar (Fig. 4K, P). Elongated pedal muscle scar in posterior part, separated from adductor muscle scar (Fig. 4K). In the umbo region of the lectotype two accessory narrow elliptic muscle scars (Fig. 4A) are developed. Inner surface sculpture is smooth. Shell thickness and outer surface sculpture unknown.

Dimensions. –

Specimens	V	L	H	W/2
MBHR 13340	A	9.0	4.1	1.5
MBHR 20341	A	8.1	3.9	1.1
NM L 40913	L	8.0	4.1	–
MBHR 21193	R	7.8	3.0	1.2
MBHR 4166	A	7.5	–	–
NM L 40914	L	7.1	3.6	–
MBHR 14763	R	7.1	5.0	–
MBHR 12569	A	7.0	3.5	1.0
NM L 27117	A	6.9	3.5	1.2
MBHR 20393	A	6.8	3.1	0.9

MBHR 13527	R	6.5	4.5	–
MBHR 4727a	R	6.5	3.9	1.0
MBHR 4726	R	6.5	–	–
MBHR 12423	A	6.2	2.9	1.6
MBHR 20354	A	6.2	3.1	1.0
MBHR 12723	A	6.1	3.0	0.9
MBHR 20353	A	6.0	3.5	1.0
MBHR 20459	A	6.0	3.1	0.9
MBHR 13452	R	6.0	3.0	–
MBHR 55902	A	6.0	3.0	0.6
NM L 40915	R	5.9	3.4	–
MBHR 20350	A	5.9	3.1	1.0
MBHR 2384b	A	5.9	3.0	0.8
MBHR 20370	A	5.9	2.9	0.9
MBHR 8980	R	5.9	2.7	–
MBHR 12432	A	5.8	3.1	1.0
MBHR 13140	L	5.8	3.0	–
MBHR 20355	A	5.8	3.0	0.9
NM L 40916	A	5.7	3.4	0.8
MBHR 20344	A	5.7	3.1	0.8
MBHR 20356	A	5.6	2.8	0.9
MBHR 13415	R	5.5	3.5	1.2
MBHR 13538	A	5.5	3.1	0.9
NM L 40917	A	5.5	2.9	0.9
MBHR 14840	R	5.5	3.1	–
MBHR 20357	A	5.5	2.9	1.0
MBHR 20460	A	5.5	2.9	0.6
MBHR 5820	R	5.5	2.8	–
MBHR 19516	A	5.4	2.9	0.7
MBHR 17795	L	5.4	2.5	–
MBHR 20358	A	5.3	3.2	1.0
MBHR 20374	A	5.2	3.0	0.9
NM L 40918	A	5.2	2.9	1.0
MBHR 14696	A	5.2	2.9	–
MBHR 14580	R	5.1	3.5	–
MBHR 55918	L	5.1	3.1	–
MBHR 20395	A	5.1	2.9	0.7
MBHR 14442	L	5.1	2.9	–
MBHR 20375	A	5.1	2.8	0.7
MBHR 14299	A	5.1	2.1	–
MBHR 14352a	L	5.0	3.0	–
MBHR 19207	R	5.0	2.9	–
MBHR 20373	A	5.0	2.9	0.7
MBHR 18813	A	5.0	2.9	0.5
MBHR 20398	A	5.0	2.6	0.7
MBHR 20494	A	5.0	2.6	0.7
MBHR 14273	R	5.0	2.5	–
MBHR 20359	A	4.9	2.9	0.8
MBHR 13368	A	4.8	3.0	0.7

Figure 4. A–Q – *Pseudocyrtodonta incola* (Barrande, 1881). • A–C – articulated specimen, NM L27117, lectotype; A – left lateral view with two accessory muscle scars in the umbo region, × 5.4; B – right lateral view, × 5.2; C – dorsal view with actinodont hinge, adductor muscle scars with pedal muscle scars, × 10.3. • D, G – right valve, MBHR 13415; D – detail of the pseudolateral tooth in posterior part, × 8.2; G – right lateral view with lateral tooth in the posterior part, × 6.3. • E, F, M – articulated specimen, MBHR 20355; E – right lateral view with pseudolateral tooth in posterior and pseudocardinal teeth in anterior, × 3.4; F – dorsal view with actinodont hinge, × 9.4; M – left lateral view, × 3.5. • H, I – articulated specimen, MBHR 12432; H – dorsal view with actinodont hinge, × 10.3; I – right lateral view with anterior adductor muscle scar, × 5.2. • J, L, N – articulated specimen, MBHR 2384b; J – left lateral view, × 7.1; L – right lateral view, × 7.3; N – dorsal view with actinodont hinge, × 7.6. • K – left valve, MBHR 14442, dorsolateral view with pseudolateral tooth in posterior and pseudocardinal teeth in anterior, anterior adductor muscle scar with pedal muscle scar. × 7.2. • O–Q – articulated specimen, MBHR 20353; O – left lateral view, × 7.2; P – dorsal view with actinodont hinge, adductor muscle scars with pedal muscle scars, × 11.4; Q – right lateral view, × 6.6. • A–C – Prague Basin, Bohemia, Osek locality, early Darriwilian. • D, G – Prague Basin, Bohemia, Dily 2 locality, early Darriwilian. • E, F, K, M, O–Q – Prague Basin, Bohemia, Dily 1 locality, early Darriwilian. • H, I – Prague Basin, Bohemia, Osek 1 locality, early Darriwilian. • J, L, N – Prague Basin, Bohemia, Rokycany locality, early Darriwilian.



MBHR 20399	A	4.5	2.9	0.6
MBHR 4727b	A	4.5	2.3	–
MBHR 55096	L	4.3	2.5	–
MBHR 20461	A	4.2	2.2	0.6
MBHR 14838	L	4.0	2.9	–
MBHR 14295	L	4.0	2.1	0.6
MBHR 14450	R	4.0	2.1	–
MBHR 14429a	L	3.9	1.9	–
MBHR 14429b	R	3.9	2.0	0.5
MBHR 14297	R	3.8	2.5	–
MBHR 14352b	R	3.8	1.3	–
MBHR 20462	A	3.5	1.9	0.5
MBHR 20371	A	3.0	1.5	0.4
MBHR 19129	A	2.0	1.4	–
MBHR 14764	R	1.8	1.0	–

Occurrence. – Bohemia, Prague Basin, early Darriwilian: Díly, Díly 1, Díly 2, Díly 3, Díly 4 – south slope of Hůrka, Díly 6, Drahouš 3, Drahouš 4, Mýto 1, Osek near Rokycany, Osek 1, Pětídomky, Rokycany, Rokycany 2, Rokycany 17, Šárka cihelna, Těškov 1.

***Pseudocyrtodonta obtusa* (Barrande, 1881)**

Figure 5

- 1881 *Nucula obtusa* Barr.; Barrande, pl. 272, figs I/1–17.
- 1934 *Pseudocyrtodonta obtusa* Barr. – Pfab, p. 238, pl. III (IV), fig. 12.

Lectotype (SD, herein). – Internal mould of the shell with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/12–14, NM L22683.

Paralectotypes. – Other four internal moulds of shells with conjoined valves, figured by Barrande (1881) on pl. 272, as figs I/1–4, 5–8, 9–11, 15–17, NM L 27150, NM L 22684, NM L 22685, NM L 22686.

Type locality. – Bohemia, Prague Basin, Štěrboholy.

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

Material. – 4 shells with conjoined valves, 1 right valve, and 2 left valves.

Diagnosis. – *Pseudocyrtodonta* with obese shells having pronounced projection in anterior part, large and strong pseudotaxodont teeth in anterior part increasing anteriorly.

Description. – Shell small (length maximally 11.1 mm, height maximally 7.8 mm and width maximally 5.8 mm), equivalve, inequilateral, obese and slightly longitudinally elongated. Anterior and posterior margin of the shell rounded. Anterior part is much smaller than posterior part. A strong projection is developed in the anterior part. Strongly prosogyrate umbos are situated in the anterior part of the shell. Hinge actinodont, in the anterior part with 3–5 pseudocardinal (pseudotaxodont) teeth, lying under hinge line. The most anterior teeth are larger (Fig. 5D, J, M). In the posterior part of the shell one straight pseudolateral tooth (Fig. 5J, M) is developed parallel to the hinge margin. Anterior adductor muscle scar rounded (Fig. 5F, I). Posterior adductor muscle scar not well preserved. In the umbo region of lectotype three accessory rounded muscle scars (Fig. 5J) are developed. Inner surface sculpture is smooth. Shell thickness and outer surface sculpture unknown.

Dimensions. –

Specimens	V	L	H	W/2
PO 1	L	11.1	7.8	2.9
PO 2	L	10.5	6.8	–
NM L 22684	A	9.3	6.4	2.6
NM L 22686	R	8.4	6.6	2.5
NM L 22683	A	8.2	6.0	2.1
NM L 27150	A	7.5	5.5	2.1
NM L 22685	A	–	6.5	2.5

Discussion. – Maillieux (1939) described and figured *P. obtusa* from the Middle Ordovician (Darriwilian). It is not possible to observe actinodont hinge on the figured specimen. Also in his description of *P. obtusa* it is mentioned that hinge in the Belgian specimens is not preserved. It is here considered that the shape of the shell is also completely different and therefore it is not possible to determine this specimen as *P. obtusa*. *P. obtusa* is similar to *Myoplusia incisa* (from the Zahořany Formation, early Katian), but they differ in hinge, which is taxodont in *M. incisa*. When the hinge is not preserved it is possible to distinguish them from the pronounced projection in the anterior part, which is developed in *P. obtusa*. *P. obtusa* differs from *P. ala* and *P. incola* in having

Figure 5. A–N – *Pseudocyrtodonta obtusa* (Barrande, 1881). • A, H, C – articulated specimen, NM L 27150, paralectotype; A – left lateral view, × 6.2; H – right lateral view, × 7.7; C – dorsal view, × 11. • B, E, F, I – articulated specimen, NM L 22684, paralectotype; B – left lateral view, × 8.4; E – dorsal view with pseudocardinal teeth in anterior and pseudolateral tooth in posterior, × 12.1; F – detail of the anterior adductor muscle scar, × 9.3; I – right lateral view with anterior adductor muscle scar. • D – articulated specimen, NM L 22686, paralectotype, dorsal view with pseudocardinal teeth, the most anterior tooth is the largest, × 8.8. • G, J, K – articulated specimen, NM L 22683, lectotype; G – left lateral view, × 7.7; J – dorsal view with actinodont hinge × 16; K – right lateral view with anterior adductor muscle scar, × 8.1. • L–N – articulated specimen, NM L 22685, paralectotype; L – left lateral view with adductor muscle scar, × 5.2; M – dorsal view with actinodont hinge, × 10.5; N – right lateral view, × 8.8. • A, H, C – Prague Basin, Bohemia, Loděnice locality, early Katian. • B, E–G, I–N – Prague Basin, Bohemia, Štěrboholy locality, early Katian. • D – Prague Basin, Bohemia, Butovice locality, early Katian.



more obese and rounded shells, the anterior teeth are larger and stronger, the adductor muscle scars are rounded, and the shell has an anterior projection.

Occurrence. – Bohemia, Prague Basin, early Katian: Butovice, Loděnice, Štěrboholy.

Palaeoecology

Babin & Gutiérrez-Marco (1991) considered actinodonts from Spain (*Redonia* and *Ananterodonta*) as shallow infaunal filter feeders (mentioning one specimen of *Redonia* with bryozoan incrustation supporting the idea that it was probably partly projected above the sediment-water interface). Allen & Sanders (1973) described two interesting recent families Lametilidae and Siliculidae. They consider Lametilidae and mainly genus *Prelametila* closely related to the bivalves with actinodont hinge consider *Prelametila* as possible living actinodont. Cope (1997) showed that this pseudo-actinodont dentition developed by fusing of teeth of nuculoids in one case and development of teeth is solemoids-like forms in another case. These forms are not related to the actinodonts, but their hinge are somewhat similar. After Allen & Sanders (1973) taxodont teeth lock the valves together, distal elongate teeth are able to roll against one another. Therefore the tendency of the valves to shear is thus reduced. Because of the relatively equilateral shell, the more inflated form and small foot they consider *Prelametila* as not an active burrower. They are relatively sedentary forms, possibly lying in horizontal or near horizontal position close to the sediment surface. All the actinodonts known from the Ordovician have the umbo moved to the anterior part of the shell. *Pseudocyrtodonta* is not an exception. *Pseudocyrtodonta* is more similar to *Silicula* Jeffreys, 1879 in the shape of the shell. *Silicula* is considered to be active burrower. It has less inflated shell with the umbo in the anterior part, and large foot. It is also supposed that *Pseudocyrtodonta* was active infaunal burrower. This opinion is also supported by the common preservation of the shells with conjoined valves.

Diversification

Pseudocyrtodonta is the other genus newly determined as belonging to the Cycloconchidae and confirms that cycloconchoids were highly diversified during the Early and Middle Ordovician. Actinodonts in the Upper Ordovician are less diversified but it could be caused also by the lack of knowledge about bivalves from this series. Only *Poladonta*, *Cycloconcha* and *Pseudocyrtodonta* are known from the Upper Ordovician. Cope (2002) showed that heteroconchian bivalves are particularly characteristic of high

latitudes and few Upper Ordovician high latitude faunas have been described.

Phylogenetic considerations – probable ancestral type of actinodont hinge?

This question is very important for the early evolution of bivalves – did the actinodont teeth evolve from the palaeotaxodont teeth and/or vice versa, or are these groups independent. The oldest known actinodont *Intihuarella* has got very simple hinge (Fig. 1N) and differs from other actinodonts in not having pseudocardinals. Therefore it is uncertain if this genus is correctly determined to Actinodontida.

Pseudocardinal teeth are similar to taxodont teeth (sometimes they are called also pseudotaxodont teeth), mainly in some genera (*Fasciculodonta* and *Pseudocyrtodonta*) and could show close relationships between actinodonts and palaeotaxodonts. Fang & Cope (2004) consider the hinge of *Fasciculodonta* (numerous pseudocardinals in anterior part and one pseudolateral in posterior part of the shell) as close to the ancestral type for the actinodonts, if the group was derived from the cardiolaroids. *Pseudocyrtodonta* from Bohemia possesses a very similar type of hinge to *Fasciculodonta*. *Pseudocyrtodonta obtusa* from the Upper Ordovician has almost the same hinge as *P. ala* and *P. incola* from the Middle Ordovician, and therefore it seems that the type of hinge is a very conservative feature. However, Carter *et al.* (2001) in their cladistic analysis support the theory about independent groups, they still place Cardiolaria (Cardiolaridae Cope, 1997, Protobranchia) close to actinodonts. Also the lack of information about bivalves from the Furongian and Lower Ordovician leaves the question about early evolution of bivalves still open. Fang & Cope (2008) discussed some phylogenetic considerations between cycloconchoids. Also they conclude that in general, determination of the relationships between taxa is hampered by the lack of material from many localities. *Pseudocyrtodonta* from Bohemia with the simple hinge and shell shape is closely related to *Fasciculodonta* from West Yunnan, China.

Conclusions

(i) Family Pseudocyrtodontidae Maillieux, 1939, which is assigned in the new Classification System for Bivalvia (Carter *et al.* 2011) as a member of the Protobranchia, is not correct. *Pseudocyrtodonta* is herein shown to belong to the Cycloconchidae and contains three species: *P. ala*, and *P. incola* from the early Darriwilian and *P. obtusa* from the early Katian.

(ii) In the Early and Middle Ordovician the family Cycloconchidae is highly diversified (24 genera), but is

much less diversified in the Upper Ordovician (3 genera). The decrease in diversity could be artificial and may be caused by the lack of the information about bivalves in the Upper Ordovician (see above).

(iii) *Pseudocyrtodonta* was probably an active infaunal burrower.

(iv) *Pseudocyrtodonta* shows a very simple hinge like *Fasciculodonta*. This hinge could be considered close to the ancestral type for the actinodonts, if the group was derived from the cardiolaroids.

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- 8.1.6 POLECHOVÁ, M. 2013. Bivalves from the Middle Ordovician Šárka Formation (Prague Basin, Czech Republic). *Bulletin of Geoscience* 88(3).

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

MARIKA POLECHOVÁ



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; Kukul 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 bohemica* Barrande, 1881 (= *Praenucula bohemica*), *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 bohemica* 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 bohemica* (Barrande, 1881) (= *Praenucula bohemica*), *Ctenodonta ponderata* (Barrande, 1881) (= *Concavodonta ponderata*), *Praeleda compar* (Barrande, 1881) (= *Praenucula bohemica*), *Praeleda pulchra* Pfab, 1934

(= *Praenucula bohemica*), *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 bohemica* 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*

GLOBAL							REGIONAL											
SYSTEM	SERIES	STAGES	STAGE SLICES	TS	TU	STAGES	FORMATIONS	STRATIGRAPHIC RANGE										
ORDOVICIAN	UPPER	KATIAN	Ka2	5d	18	BEROUNIAN	BOHDALEC ZAHOŘANY VINICE LETNÁ LIBEŇ											
			Ka1	5c	16													
			Sa2	5b	15													
		SANDBIAN	Sa1	5a	14													
			Dw3	4c	13													
		DARRIWILIAN	Dw2	4b	12		DOBROTVIVIAN					DOBROTVIVÁ						
	Dw1		4a	11	ORETANIAN	ŠÁRKA												
			Dp3	3b			ARENIGIAN					KLABAVA						
	Dp2	9	<i>P. applanans</i>		<i>P. bohémica</i>	<i>P. dispar</i>							<i>C. ponderata</i>	<i>Ps. ala</i>	<i>Ps. incola</i>	<i>T. petula</i>	<i>R. deshayesi</i>	<i>B. prima</i>

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 *Praealeda* 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 *Praealeda*. 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 *Praealeda*) 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 *Praealeda* 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 *Praealeda* into the family Cardiolariidae. But because of this problematic character, the determination of *Praealeda* 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 *Praealeda* to the Praenuculidae and this opinion is followed here. Bradshaw (1970) was also of the opinion that hinge of *Praealeda* is very often similar to hinge of *Praenucula* and it is difficult to distinguish between these genera. Furthermore *Praealeda compar*, the type species of *Praealeda* (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 *Praealeda 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 *Praealeda* 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.

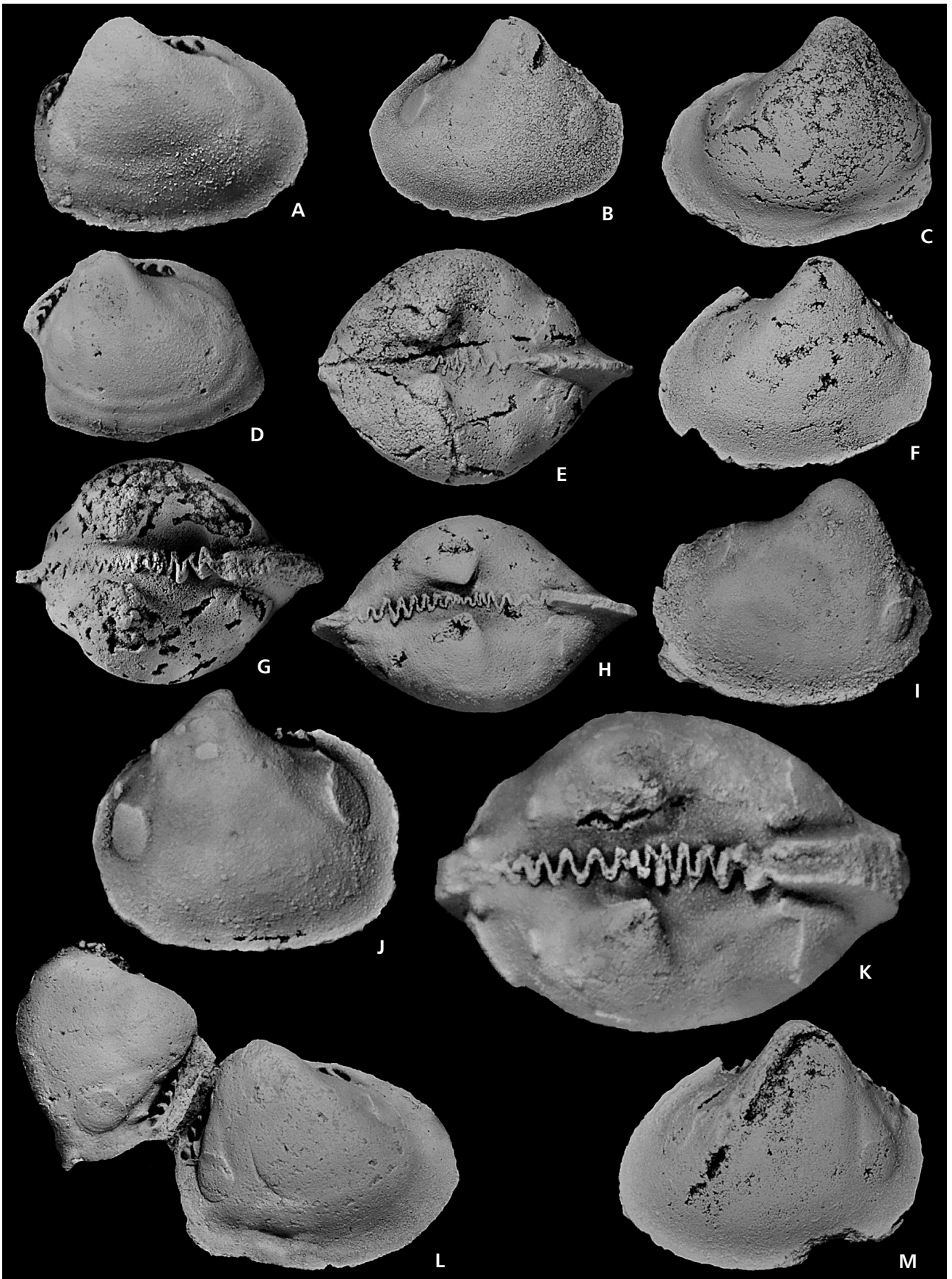
Type horizon. – Middle Ordovician, early and mid Darriwilian, Šárka Formation.

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; F–H – Prague Basin, Bohemia, Mýto 1 locality, early and middle Darriwilian; G, J, K – 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.

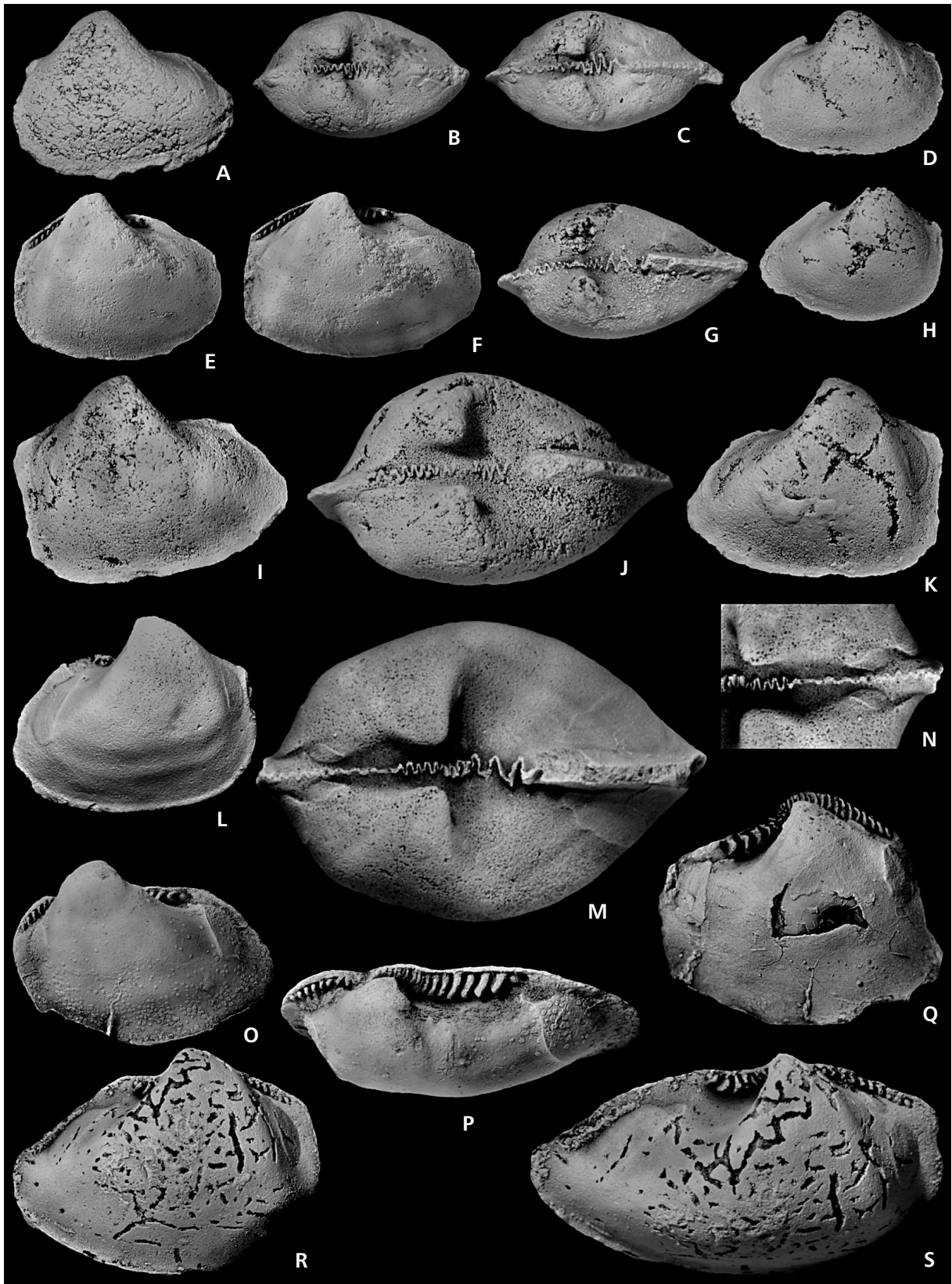
Praenucula applanans (Barrande, 1881)

Figures 4A–R, 5C

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

1934 <i>Ctenodonta applanans</i> Barr. – Pfab, p. 222, pl. 2 (3), figs 1–3.	<i>Dimensions.</i> –				
1991 <i>Praenucula sharpei</i> Babin & Gutiérrez-Marco; Babin & Gutiérrez-Marco, pp. 115, 116, pl. 2, figs 1–6.	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
<i>Lectotype.</i> – (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.	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	–
<i>Paralectotypes.</i> – 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.	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
<i>Type locality.</i> – Bohemia, Prague Basin, Osek near Roky- cany.	MBHR 2384l	A	10.0	6.8	2.4
	MBHR 14663	L	10.0	6.8	–
	MBHR 18858	A	10.0	–	2.0
<i>Type horizon.</i> – Middle Ordovician, early and mid Darriwil- ian, Šárka Formation.	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
<i>Material.</i> – 172 specimens.	MBHR 20406	A	9.3	5.5	3.8
	MBHR 2395b	L	9.2	6.5	3.2
<i>Diagnosis.</i> – <i>Praenucula</i> with slightly larger posterior part of the shell, umbo almost in the middle of the shell, slightly prosogyrate, orthomorphodont teeth in the posterior part.	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	–
<i>Description.</i> – 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.	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, NML 22682.

Type locality. – Bohemia, Prague Basin, Loděnice.

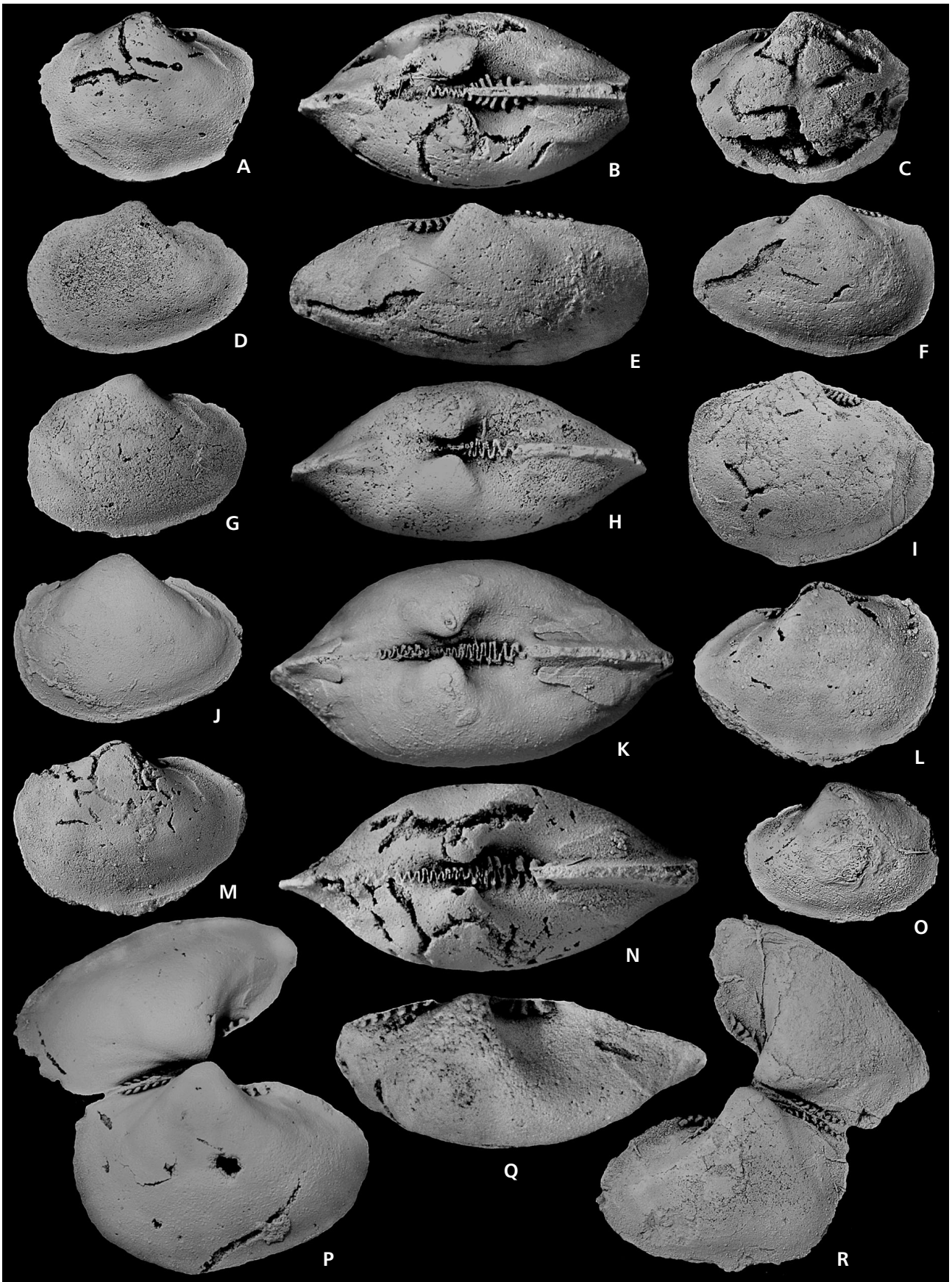
Type horizon. – Late Ordovician, early Katian, Zahořany Formation.

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 comarginal 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, NML 27161, paralectotype; A – right lateral view with anterior adductor muscle scar, × 4.0; B – dorsal view, × 6.4; C – left lateral view, × 4.1. • D – articulated specimen, MBHR 14852, right lateral view, × 3.3. • E, F – left valve, MBHR 12570, E – left dorsolateral view, × 6.5; F – left lateral view, × 4.2. • G, H, O – articulated specimen, NML 27162, paralectotype; G – right lateral view, × 4.4; H – dorsal view, × 7.3; O – left lateral view, × 4.0. • I – articulated specimen, VPA 2144/OR, right dorsolateral view, × 2.9. • J, K – articulated specimen, MBHR 14619; J – right lateral view, × 3.5; K – dorsal view with hinge and adductor and accessory muscle scars, × 6.1. • L–N – articulated specimen, NML 27163, lectotype; L – left lateral view, × 3.9; M – right lateral view, × 3.7; N – dorsal view, × 3. • P – articulated specimen, opened shell, MBHR 2395, right lateral view with orthomorphodont teeth in the posterior part, × 5.3. • Q – right valve, MBHR 4600, dorsal view, × 9.5. • R – articulated specimen, opened shell, MBHR 2443, left lateral view, × 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.



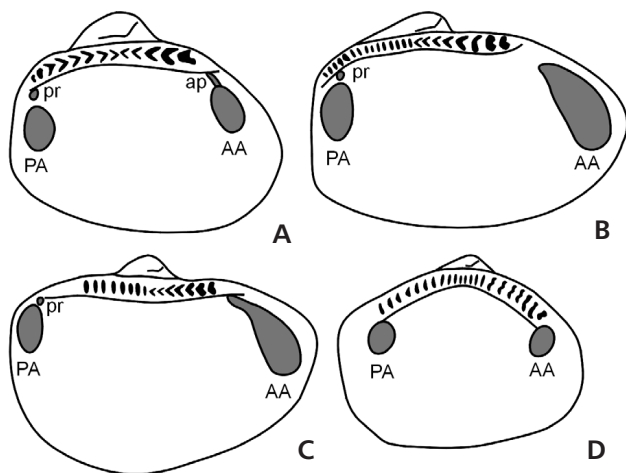


Figure 5. A – *Praenucula dispar* (Barrande, 1881), left lateral view showing hinge and muscle scars. • B – *Praenucula bohémica* (Barrande, 1881), left lateral view showing hinge and muscle scars. • C – *Praenucula applanans* (Barrande, 1881), left lateral view showing hinge and muscle scars. • D – *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 Zahořany 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 *Synek 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, × 4.8; B – dorsal view, × 7.2. • C – articulated specimen, MBHR 12701, right lateral view with part of the pseudolateral tooth, × 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, × 10.4; E – articulated specimen, MBHR 20353, dorsal view, × 10.1; F – articulated specimen, MBHR 13415, right dorsolateral view, × 3.3. • G–N – *Redonia deshayesi* (Rouault, 1851); G – left valve, NM L 22659, left lateral view, × 4.4; H, N – articulated specimen, NM L 22656; H – dorsal view, × 5.8; N – right lateral view, × 6.0; I – right valve, LPB 796, neotype, right lateral view with posterior and anterior adductor muscle scars, × 3.2; J – left valve, MGM643–O, left lateral view, part of the umbo was removed, × 5.0; K – right valve, LPB 775, left lateral view without umbo with actinodont hinge, × 3.5; L – right valve, L22660, right dorsolateral view, × 4.6; M – right valve, NM L 22658, right dorsolateral view, × 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.

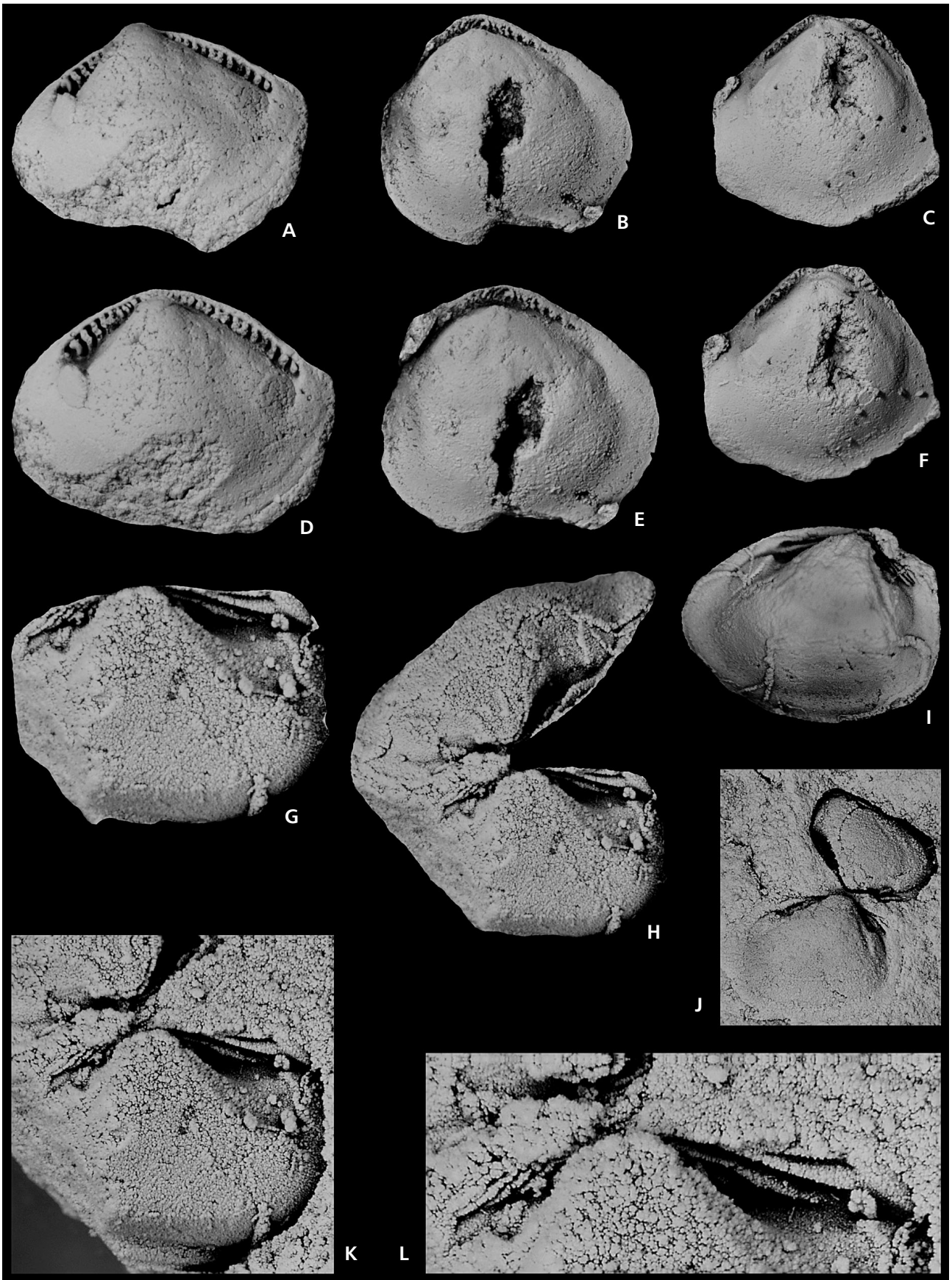
Type horizon. – Middle Ordovician, early and mid Darriwilian, Šárka Formation.

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, × 10.2; D – left dorsolateral view, × 11.2. • B, E – left valve, NM L 42216; B – left lateral view, × 5.9; E – left dorsolateral view, × 6.5. • C, F – right valve, NM L 42217; C – right lateral view, × 9.4; F – right dorsolateral view, × 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, × 13.5; H – two valves, dorsal view with actinodont hinge, × 11; I – right valve with actinodont hinge and adductor muscle scars, × 11.2; K – left lateral view with actinodont hinge, × 12.8; L – detail of the actinodont hinge, pseudolateral teeth in the anterior part and pseudocardinal teeth in the posterior part, × 24. • J – paratype, two valves, opened shell, NM L 42218, lateral view on the two valves, × 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.



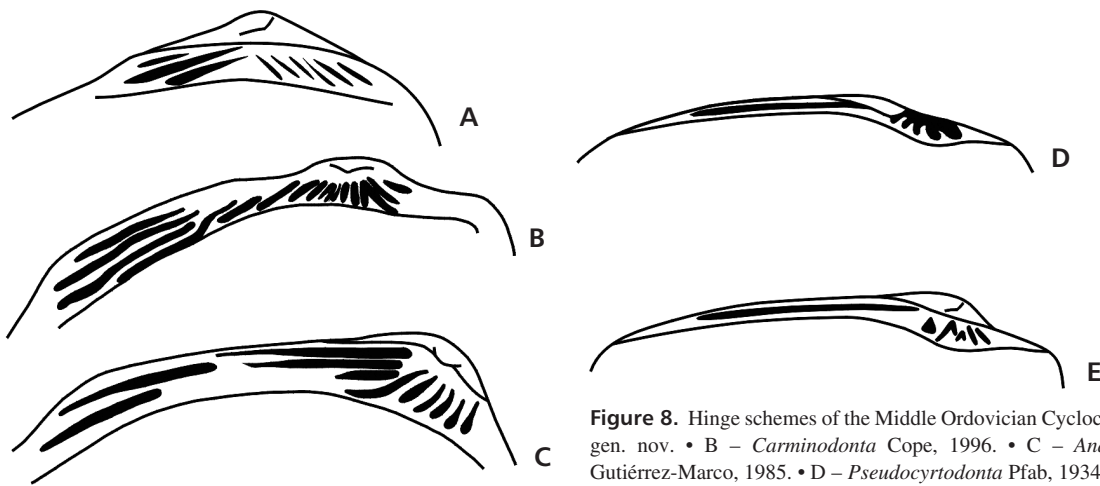


Figure 8. Hinge schemes of the Middle Ordovician Cycloconchidae. • A – *Tatula* gen. nov. • B – *Carminodonta* Cope, 1996. • C – *Ananterodonta* Babin & Gutiérrez-Marco, 1985. • D – *Pseudocyrtodonta* Pfab, 1934. • E – *Fasciculodonta* Fang & Cope, 2004.

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

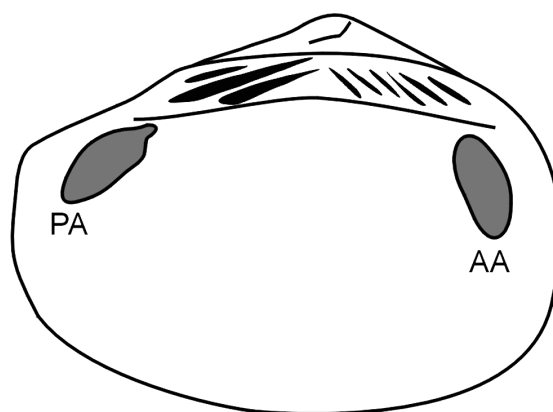


Figure 9. *Tatula petula* gen. nov. et sp. nov. – left lateral view showing hinge and muscle scars. Key to letter symbols: AA – anterior adductor muscle scar; PA – posterior adductor muscle scar.

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. – Thoral, p. 162, pl. 13, figs 4, 5.
- 1954 *Babinka prima* Barr. – Vokes, p. 235, fig. 1.
- 1960 *Babinka prima* Barr. – Růžička & 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 Modiolopsoidea Fischer, 1886

Family Modiolopsidae Fischer, 1886

Genus *Modiopsis* Hall, 1847

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

***Modiopsis* 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

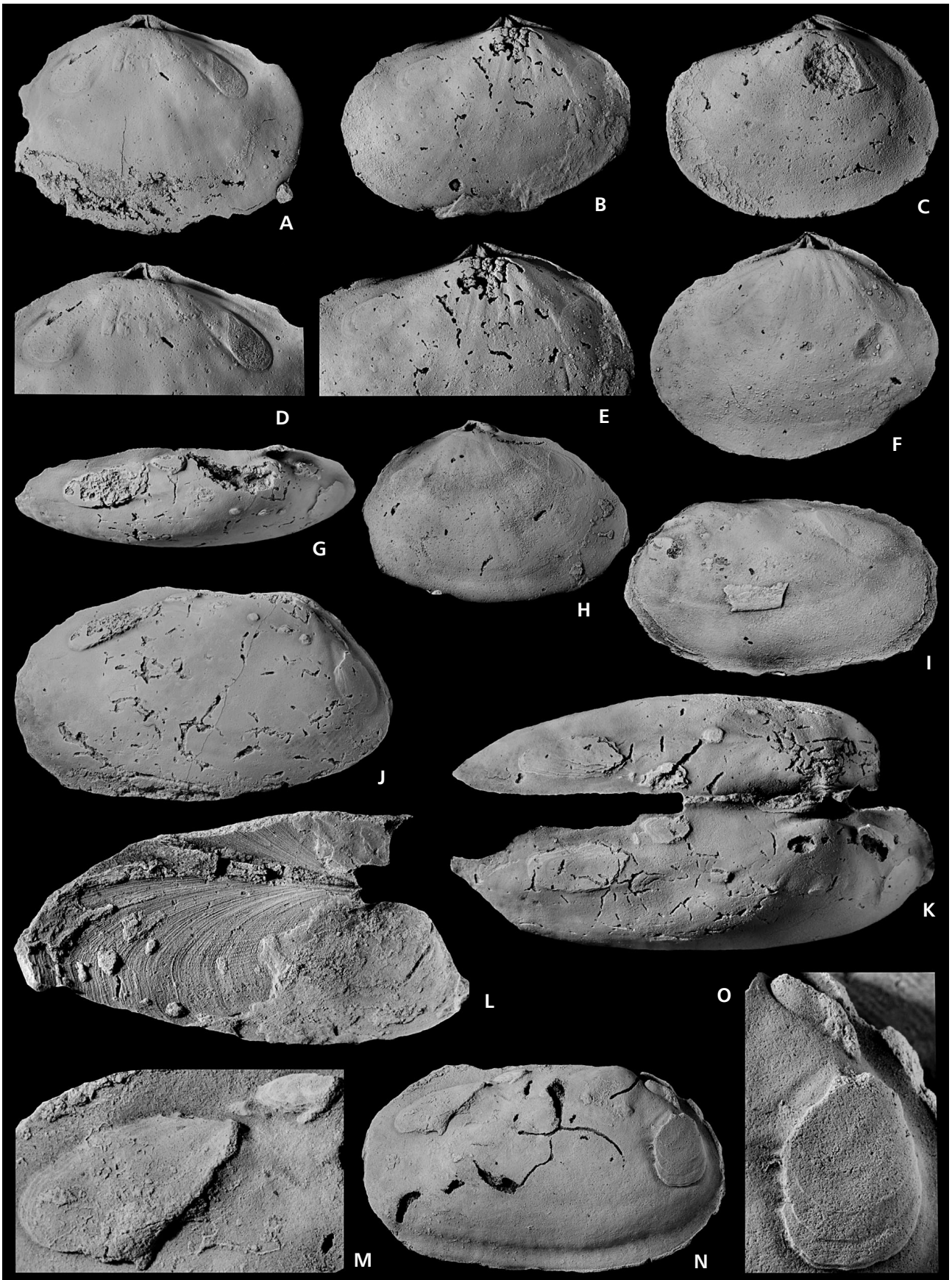
Discussion. – More than 163 species were classified from the Ordovician of North America under *Modiolopsis* Hall, 1847 by Pojeta (1971). In general, edentulous hinge and modiolophorm shape of the shell are only significant characters for this genus and therefore specific classification is very difficult (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* Neveškaya 1971)
 Suborder Cyrtodontidina Scarlato & Starobogatov, 1971 (*in* Neveškaya 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, × 2.0; D – detail of the hinge and adductor and accessory muscle scars, × 3.1. • B, E – left valve, NML 41034; B – left lateral view, × 2.4; E – detail of the hinge, × 3.2. • C – left valve, NM L 27089, left lateral view, × 2.5. • F – left valve, NM L 27086, lectotype, left lateral view, × 2.4. • H – right valve, NM L 41033, right lateral view, × 2.2. • G–J – *Coxiconchia britannica* (Rouault, 1851). G, J – left valve, CW 2; G – dorsal view, × 2.4; J – right lateral view with adductor and accessory muscle scars, × 2.6; I – left valve, MGM 644–O, left lateral view, × 1.8. • K – articulated specimen, CW 3a, dorsal view, × 3. • L – part of the right valve, CW 3b, outer surface sculpture, × 2.4. • M–O – right valve, JK 18012; M – posterior adductor muscle scar with posterior retractor, × 2.2; N – right lateral view, × 1.7; O – anterior adductor muscle scar with protractor, × 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.



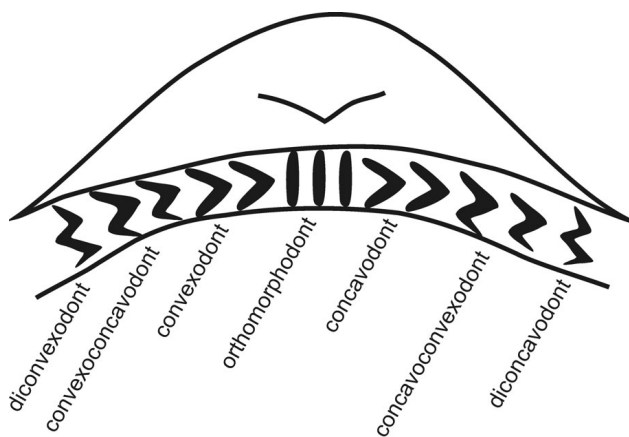


Figure 12. Teeth in taxodont hinge according to Carter *et al.* (2012).

(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 dicaconcaodont 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 *Praealeda 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

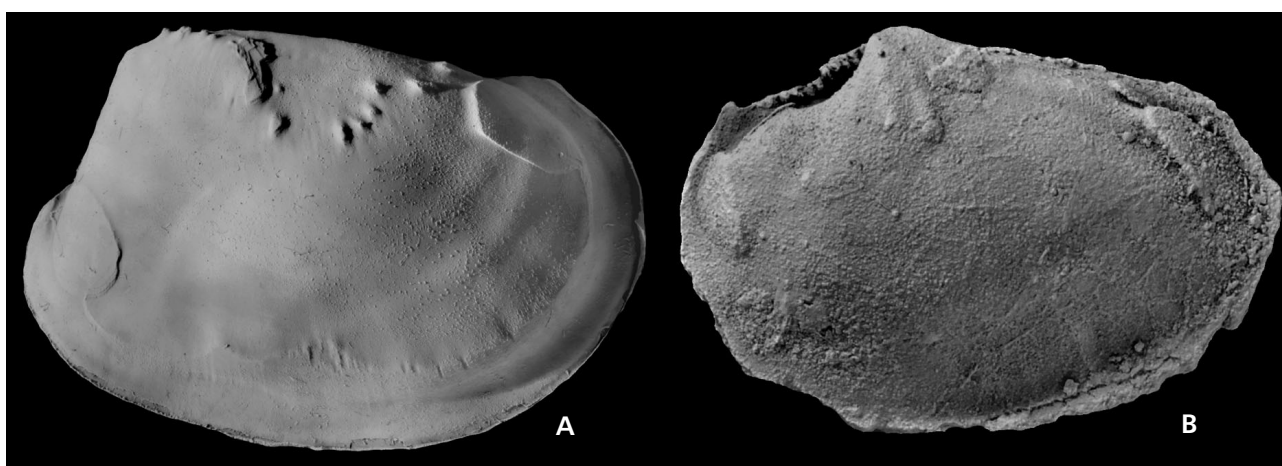


Figure 13. Muscle scars in *Leionucula mirifica* and *Myoplusia bilunata*. • A – *Leionucula mirifica* (Dall, 1907), JK 18425, latex cast after USNM 363746, left valve, left lateral view with numerous accessory muscle scars, $\times 2.2$. • B – *Myoplusia bilunata* (Barrande, 1881), NM L 27130, right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

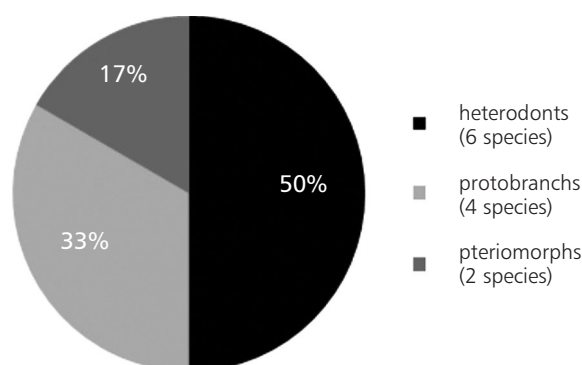


Figure 14. The species composition and diversity of the bivalve fauna from the Middle Ordovician Šárka Formation.

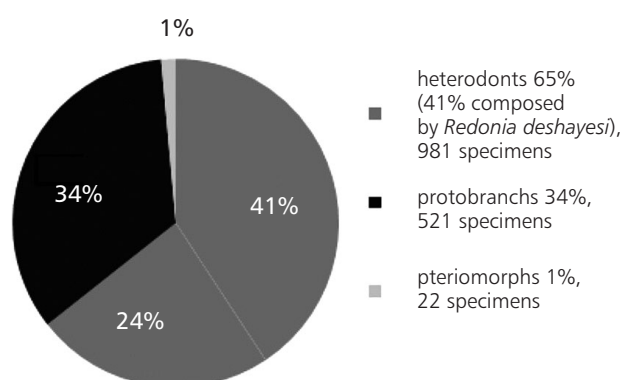


Figure 15. Abundance of bivalve individuals composing collections of the bivalve fauna from the Middle Ordovician Šárka Formation, according to Table 1.

(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).

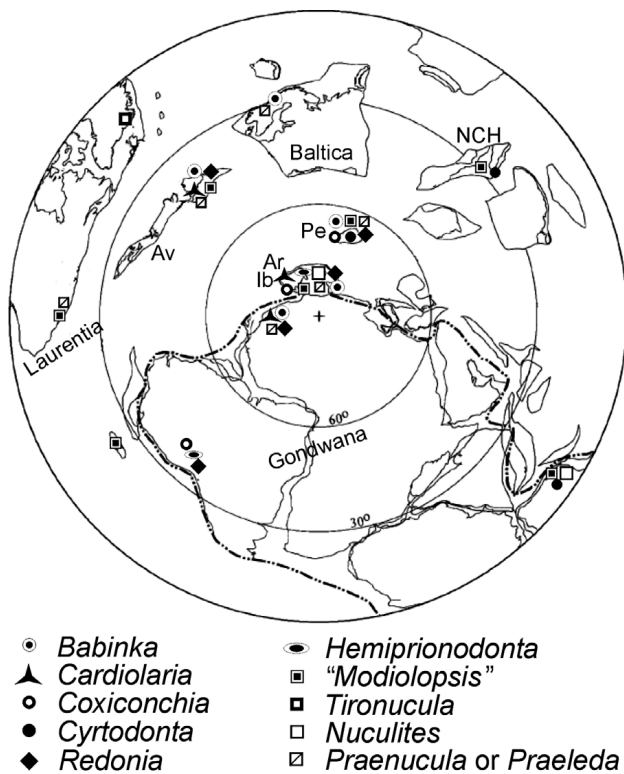


Figure 16. Palaeogeographic distribution of the bivalves during the Middle Ordovician, palaeogeographic map according to Cocks & Torsvik (2002). Abbreviations: Ar – Armorica, Av – Avalonia, Ib – Iberia, NCH – North China, Pe – Perunica.

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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