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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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Prohlášení

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V Praze dne 1. dubna 2013 Marika Polechová

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.

Contents

8.1 Publications

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 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, Publicationes del Instituto geologico y minero de Espaňa*, 575–580. Instituto Geológico y Minero de Espaňa. 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.

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

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 Phanerozic, 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.

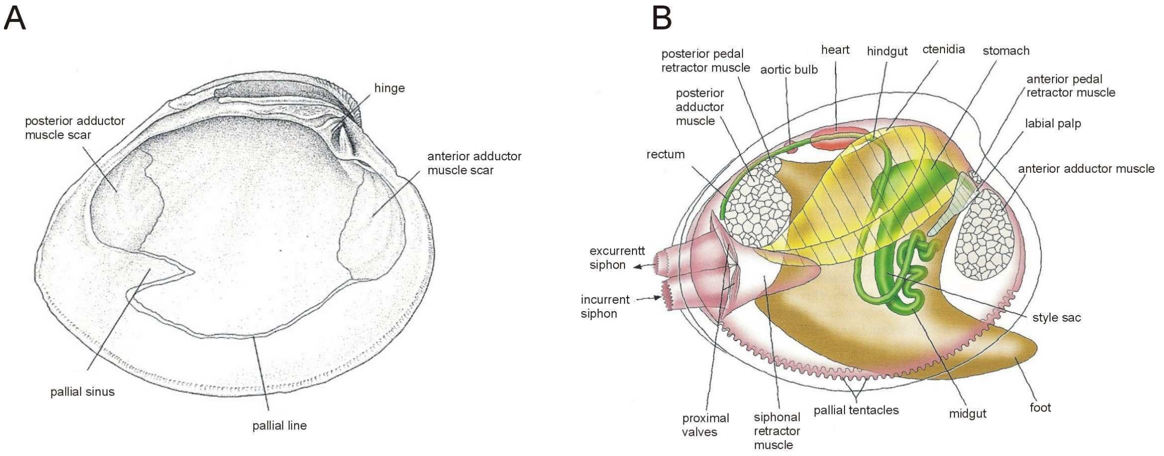

Figure 1. Overall bivalve morphology on the exemple of bivalve *Mercenaria mercenaria* (Linné, 1758), according to Mikkelsen & Bieler (2008) ● A – the features of the interior of the left valve ● B – the features of the soft body.

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 Pelseneer, 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 easy 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 modioliphorm 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 exemple, 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 Cardiollaridae, 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 Pelseneer, 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 extremeties 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).

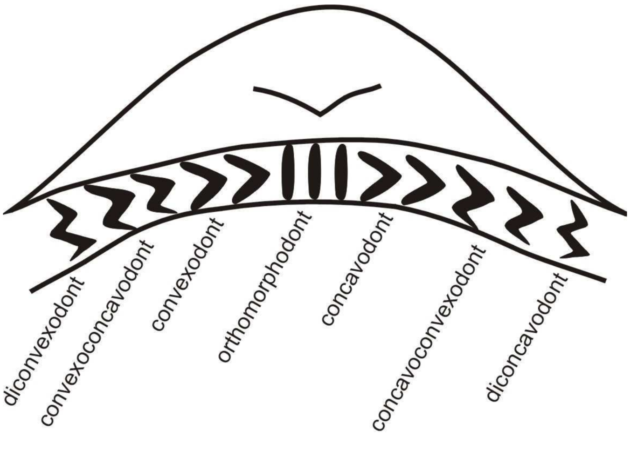

Figure 2. Types of teeth in taxodont hinge according to Carter *et al*. (2012).

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 succesful 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.

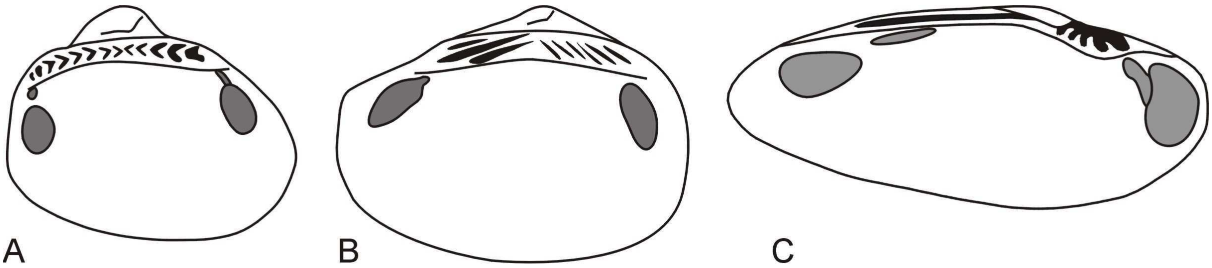

Figure 3. • A – taxodont hinge and muscle scars in *Praenucula dispar* (Barrande, 1881) • B – actinodont hinge and muscle scars in *Tatula petula* Polechová, 2013 • C – actinodont hinge and muscle scars in *Pseudocyrtodonta incola* (Barrande, 1881).

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 occured 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 *Arhouriella* 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 intrisic 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 shelfs 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 contolled 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 lecitotrophic 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 occurrs 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).

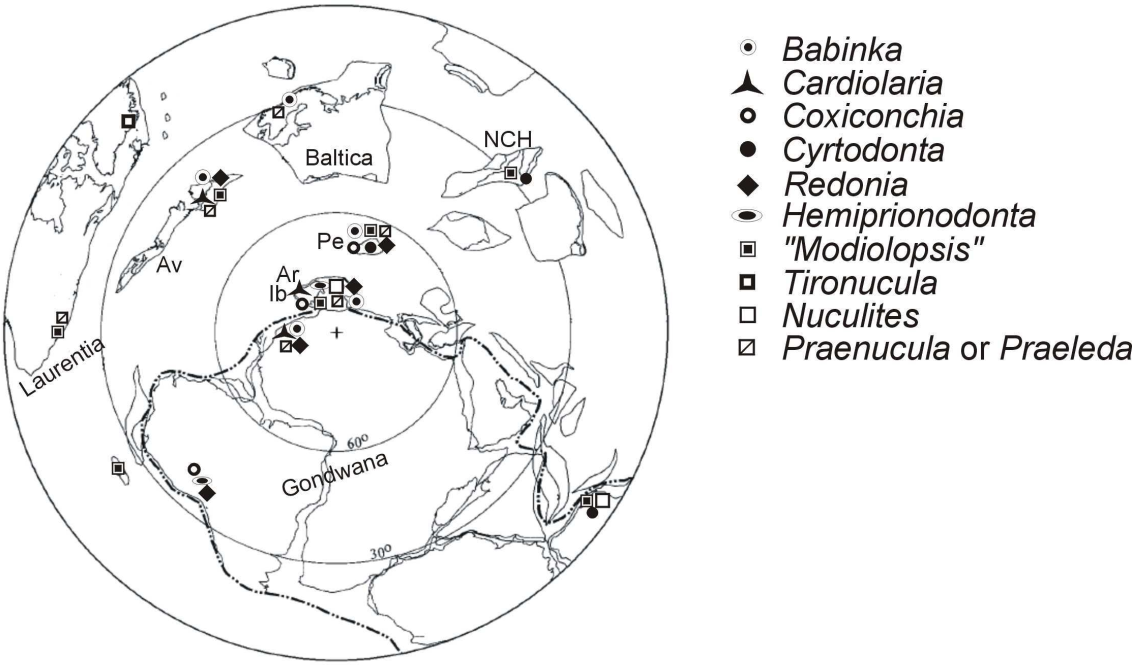

Figure 4. Palaeogeographic distribution of the bivalves during the Middle Ordovician, palaeogeographic map according to Cocks & Torsvik (2002). Abbreviations: Ar. – Armorica, Av. – Avalonia, Ib. – Iberia, NCH. – North China, Pe. – Perunica.

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, Guttiérez-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 Ordovican 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 bohemica* (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 occurred 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).

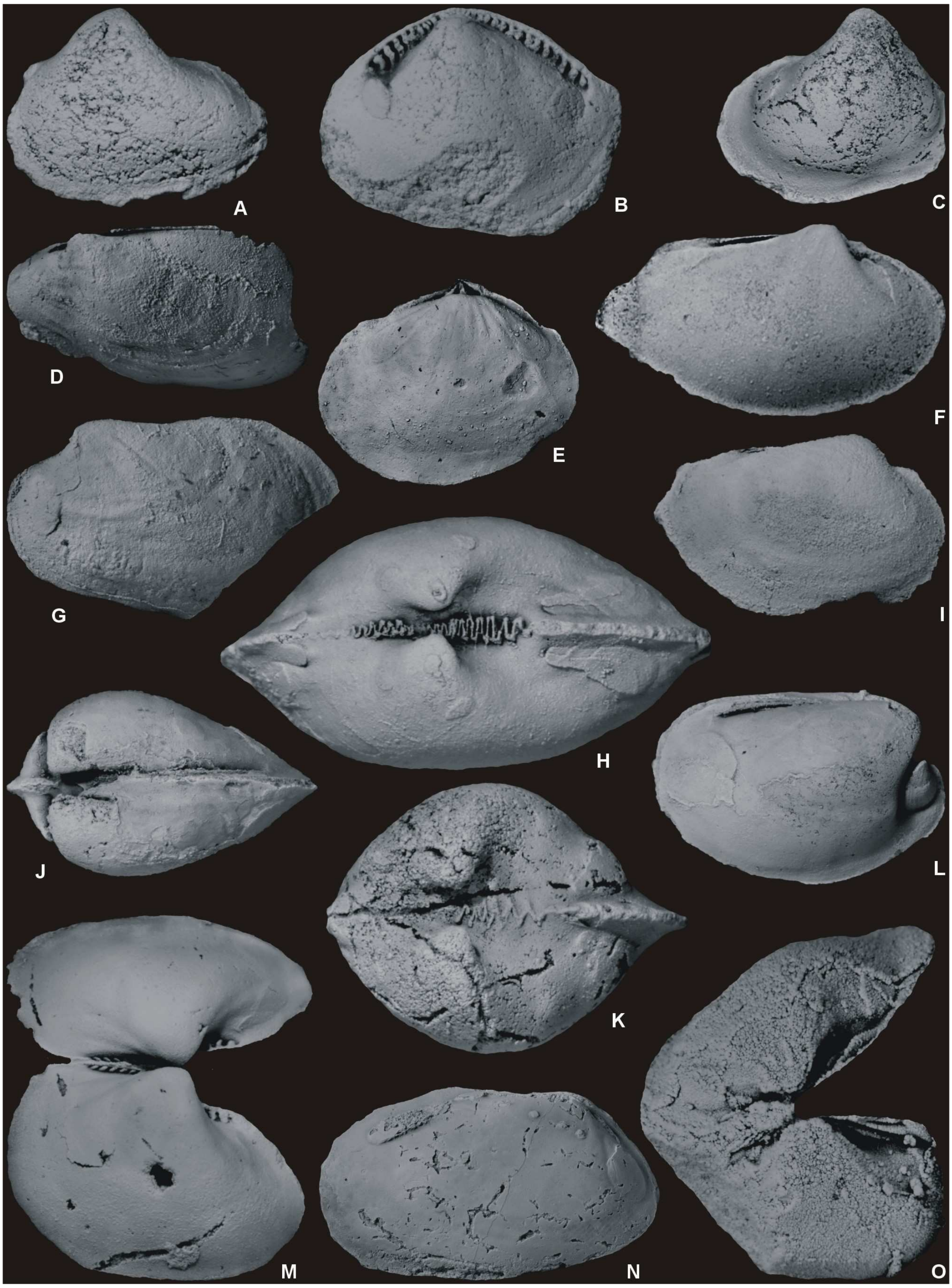

Figure 5. ● A – *Praenucula bohemica* (Barrande, 1881) – MBHR 14448, right valve, lateral view, x 6.6 ● B – *Concavodonta ponderata* (Barrande, 1881), NM L 42215, left valve, dorso- lateral view, x 10 ● C, K – *Praenucula dispar* (Barrande, 1881) MBHR 7982, articulated specimen; C – left lateral view, 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-oxygeneted 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.

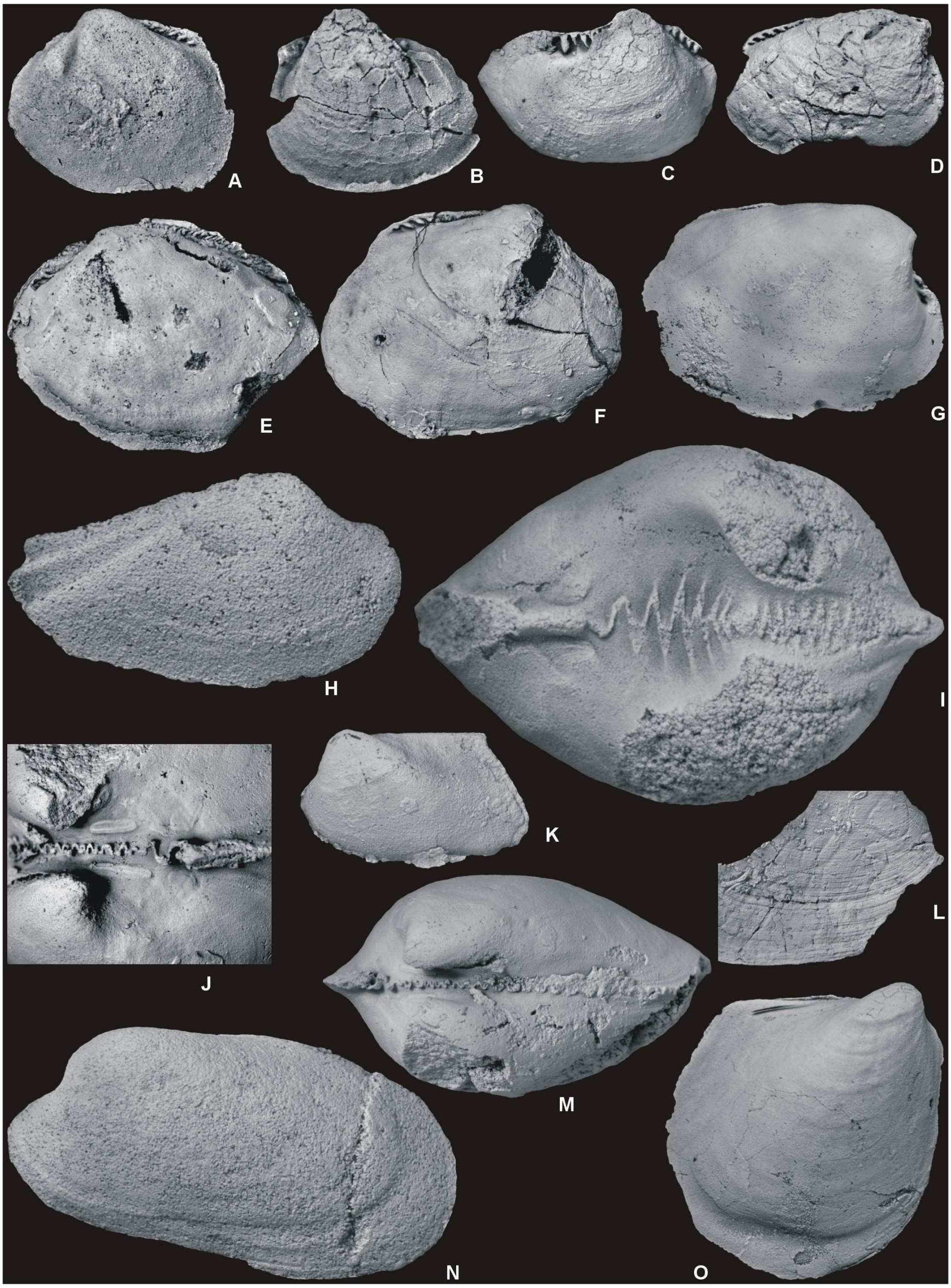

Figure 6. ● A – *Nuculites* aff. *planulatus.* – JK 14941, left valve, lateral view, x 4.5 ● B – *Praenucula dispar* (Barrande, 1881), JK 14931, right valve, lateral view, x 4 ● C – *Praenucula abrupta* (Kříž a Steinová, 2009), JK 14939, left valve, dorso-lateral view, x 4 ● D, F, L – *Sluha kosoviensis* (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 – *Modiolopsis 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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