



Silurian Bivalvia – Evolution, Palaeoecology, Palaeogeography, Importance for Biostratigraphy and Correlation

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*Silurian
Bivalvia
Evolution
Palaeoecology
Palaeogeography
Biostratigraphy*

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Silurische Bivalven – Evolution, Paläoökologie, Palaeogeographie, Bedeutung für Biostratigraphie und Korrelation

Zusammenfassung

Die zur Kenntnis der Entwicklungsgeschichte, Paläoökologie und Paläogeographie silurischer Bivalvia im 20. Jahrhundert errungenen Fortschritte werden überblickt. Am Beispiel des Obersilurs des Europäischen Gondwana und Perunica wird die Bedeutung der Bivalvia zur Biostratigraphie und Korrelation hervorgehoben.

Abstract

20th century progress in knowledge of evolutionary history, palaeoecology and palaeogeography of the Silurian bivalves is reviewed. Importance of Bivalvia for biostratigraphy and correlation is demonstrated with examples of the upper Silurian of Gondwanan Europe and Perunica.

1. Introduction

Most of the knowledge on the systematics of the Silurian Bivalvia is still concentrated in classic monographs written in the 19th and during the first decades of the 20th century e. g. GOLDFUSS (1837), MURCHISON (1839), MÜNSTER (1840), BARRANDE (1881), HALL (1884,

1885), CLARKE (1899), CHAPMAN (1908), HEDE (1915), JANIŠEVSKIJ (1918), MCLEARN (1918, 1924), HELLER (1925), HERITSCH (1929) and CHAUBET (1937). Little new information has appeared since these publication. KŘÍŽ (1979a) wrote:

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"Bivalves are a somewhat neglected group when compared with other fossils such as trilobites, brachiopods and graptolites that are widely used for biostratigraphical, and palaeogeographical studies of Devonian rocks. It is surprising that so little attention is paid to the group, which is highly diversified and distributed in many various environments, and which retains the same various modes of life from Ordovician times onwards. Modern studies of relationships between shell form and life habits (e.g. STANLEY, 1970) make possible well-supported paleoecological interpretations of fossil bivalves to a degree that is hardly possible with extinct groups. Bivalves may also be used for biostratigraphical purposes in the same way as any other group when their phylogeny and stratigraphical ranges are sufficiently known."

However, it became apparent that revisions of the classic works were needed and new systematic studies of Bivalvia necessary. Since 1984 only 22 new genera of bivalves have been most probably described from the Silurian, and at the end of the 20th century only a limited number of modern studies are available for a review on the evolution, palaeogeography and palaeoecology of Silurian Bivalvia.

A number of systematic revisions and studies of Silurian bivalves are available from the Gondwanan region, Peru (as of HAVLÍČEK et al., 1994) and China, e.g. BABIN (1966), BABIN & ROBARDET 1974, BRANISA (1965), CASTELLARO (1966), FREITAS et al. (1993), IORDAN (1981), JOHNSTON (1991), KEGEL (1953), KŘÍZ (1966, 1967, 1969, 1979b, 1984, 1985, 1996a, 1996b, 1998a, in press), KŘÍZ & IORDAN (1975), KŘÍZ & PARIS (1982), KŘÍZ & SERPAGLI (1993), KŘÍZ & VESELINOVIČ (1975), POJETA, KŘÍZ & BERDAN (1976), SÁNCHEZ (1991, 1992), SÁNCHEZ et al. (1995), SHERRARD (1959), TALENT & PHILIP (1956), TERMIER & TERMIER (1950), and ZHANG (1984).

Silurian bivalves of the Baltica region were mainly studied by KOREJWO & TELLER (1964), LILJEDAHL (1984, 1985, 1989a, 1989b, 1989c, 1992a, 1992b, 1992c, 1994), SALADŽJUS (1966), SINICYNA (1964, 1968), SOOT-RYEN (1964), and TOMCZYKOVA (1958).

Laurentian bivalves of Silurian age have been studied during the last few decades especially by BOLTON (1972), FISCHER (1957), HARRISON and HARRISON (1975) and POJETA & NORFORD (1987).

English and Scottish Silurian bivalves have been studied by REED (1931), WATKINS (1978, 1979), and WATKINS & BERRY (1977).

The Silurian bivalves of Siberia and Kazakhstan were studied during the last half of the century especially by BOGOLEPOVA & KŘÍZ (1995), SINICYNA (1986, 1993), KULIKOVA (1973, 1983), KRASILOVA (1963), and KŘÍZ & BOGOLEPOVA (1995).

2. Evolution of Silurian Bivalves

During the Silurian the Bivalvia underwent their second major radiation following abrupt changes in the Earth's environment with accompanying extinctions in the uppermost Ordovician and lowermost Silurian (KŘÍZ, 1984). Only 26 genera of Bivalvia (35 % of which were free-burrowing and 65 % endobyssate infaunal and semi-infaunal) survived this mass extinction. At present 111 genera and 25 families of Silurian bivalves are known. Adaptation to unique Silurian environments led to the development of 86 new genera and 13 new families.

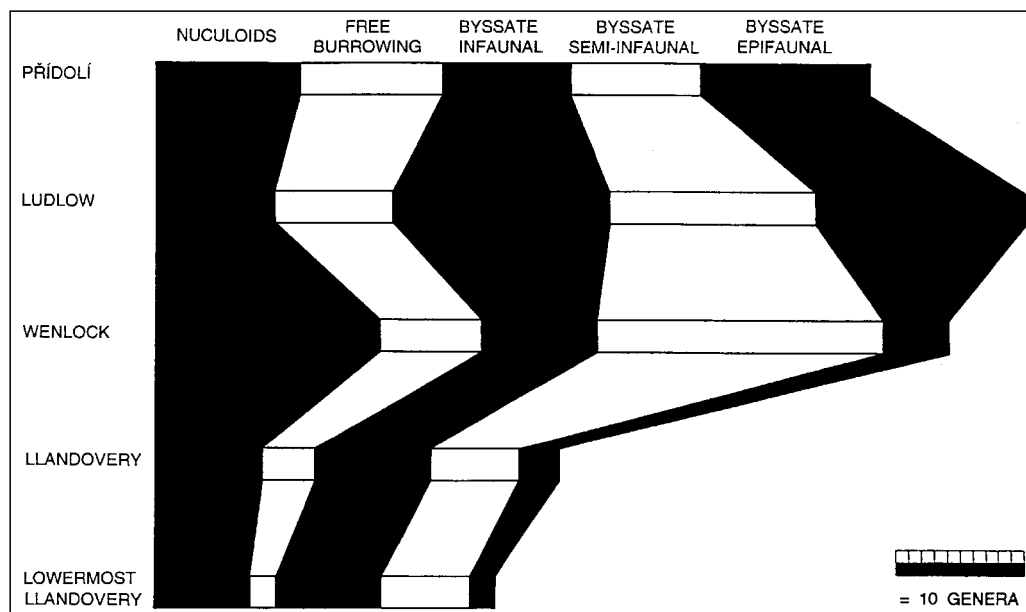
3. Palaeoecology of Silurian Bivalves

The Silurian is characterized by the development of suspension-feeding, free-burrowing, and epibyssate bivalves in particular, from endobyssate forms through rapid evolutionary transitions (KŘÍZ, 1984). During the Silurian, bivalves employed all major life styles, except for cementation of the shell to the substrate (KŘÍZ, 1984, 1996a, LILJEDAHL, 1992c).

The majority of Silurian nuculoids, most of which were shallow burrowers (WALKER & BAMBACH, 1974a, b) are included in infaunal deposit feeders. As in Recent nuculoids, Silurian nuculoids appear to have been adapted to living in soft muds (LILJEDAHL, 1984). They represent an ecologically conservative group without prominent radiation during the Period. The number of genera increases from the lowermost Llandovery up into the Přídolí. Seventeen genera are known from the Wenlock, most of them from Gotland (Text-Figs. 1 and 2).

Free burrowing genera also increased during the Silurian. Two are known in the lowermost Llandovery, four in the Llandovery, eight in the Wenlock, nine in the Ludlow, and 11 in the Přídolí (Text-Figs. 1 and 2).

A maximum of 17 infaunal byssate genera are recorded from the Ludlow and also show a continuous increase in



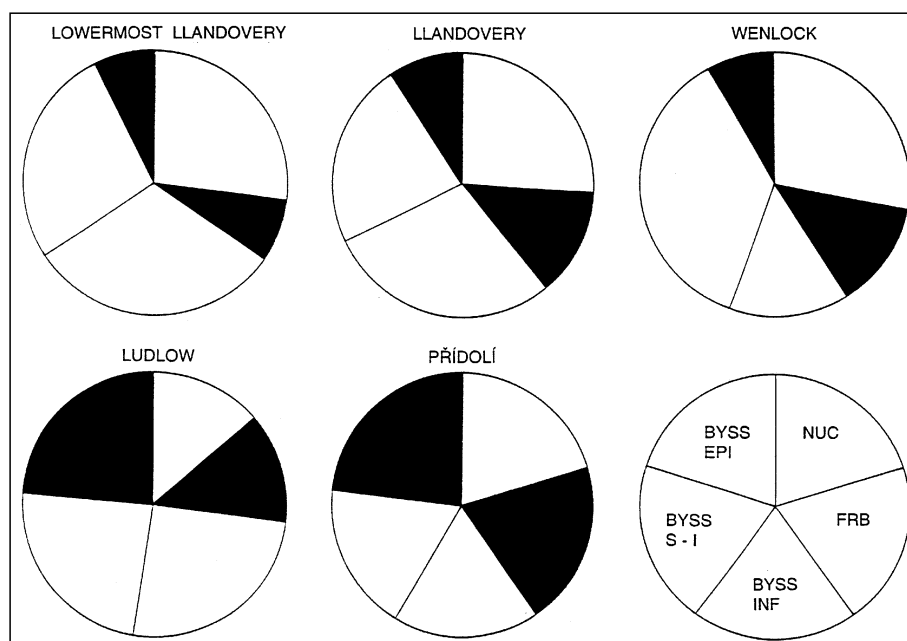
Text-Fig. 1.
Changes in life habit spectrum of the Bivalvia during the Silurian.
Figures based on the number of genera known per stratigraphic interval.
Modified after KŘÍZ (1984).

Text-Fig. 2.

Changes in percentages of bivalve life habits during the Silurian.

NUC = "nuculoids" – free-burrowing deposit feeders; FRB = free burrowing suspension feeders; BYSS INF = byssate infaunal suspension feeders; BYSS S-I = byssate semi-infaunal suspension feeders; BYSS EPI = byssate epifaunal suspension feeders.

Figures based on percentage of genera per stratigraphic interval (modified after KŘÍZ, 1984).



number. From the lowermost Llandovery eight genera are recorded, in the Llandovery nine, in the Wenlock nine and in the Přídolí 10 genera (Text-Figs. 1 and 2).

A maximum number of byssate semi-infaunal genera (22) is described from the Wenlock, but a small decrease is recorded later in the Silurian (16 in the Ludlow and 10 in the Přídolí).

Especially interesting is the distinct increase in the number of byssate epifaunal bivalves during the Silurian. From two genera in the lowermost Llandovery, to three in the Llandovery, five genera in the Wenlock, 16 in the Ludlow and 13 in the Přídolí (Text-Figs. 1 and 2).

The number of epibyssate bivalves in the lowermost Llandovery represents about 7 % of all Llandoveryan bivalves (Text-Fig. 2). During the Silurian this number increases and by the Přídolí represents about 23 % of all bivalves (nuculoids – 20 %, free burrowing bivalves – 20 %, byssate infaunal – 18.2, and byssate semi-infaunal – 18.2 %).

4. Palaeogeography of Silurian Bivalves

Three main climate regions may be distinguished in the Silurian on the basis of bivalve distribution. These are a tropical region in the equatorial zone, temperate zones north and south of the Silurian equator and a cold zone known only from the Gondwana region (South American Precordillera, northwestern Argentina basins and Bolivia).

A clearly tropical reef-associated habitat is known in the Silurian represented by "giant clams" megalodonts in the Canadian Arctic, west-central New York, Michigan Basin and Australia (FREITAS et al., 1993) and from Gotland (LINDSTRÖM, 1885). It agrees with the most recent reconstructions of the Silurian and Early Devonian palaeogeography published by COCKS & SCOTSE (1991) and with the reconstructions of the Silurian oceanic and atmospheric circulation by WILDE, BERRY & QUINBY-HUNT (1991).

LILJEDAHL (1984 and 1985) described mainly a deposit-feeder dominated community of bivalves (e.g. *Nuculoidea*, *Nuculodonta*, *Palaeostraba* and *Caesariella*) from the Silurian (Wenlock, Homerian) tropical region of Gotland. Rare representatives of the mainly epibyssate genera (*Maminka*, *Mytilarca*, *Kenzieana* and *Procarinaria*) were also described from the same region (LILJEDAHL, 1984, 1989c). These genera are also known from the temperate zone communities of the Bohemian type fauna of Gondwanan Europe (KŘÍZ & SERPAGLI, 1993 and KŘÍZ, 1996b) and from the Perunica - Prague Basin (BARRANDE, 1881).

A littoral zone tropical association of bivalves was described by FISCHER (1957) from the west-central New York Vernon Shales (late Silurian). This low diversity community is dominated by an epibyssate pterineid described as "*Pterinea*" (most probably congeneric with *Joachymia* RUŽIČKA, 1949) which is homologous and analogous with the upper Přídolí age *Joachymia falcata* Community of the temperate zones of Gondwana (Sardinia) and Perunica.

Another Silurian tropical bivalve community of the Silurian bivalves was described by WATKINS (1997) from the reefs of the Racine Formation (Wenlock) of the Michigan Basin. Bivalves form less than 1 % of skeletal material in the reef and are mostly represented by byssate epifaunal and semi-infaunal suspension-feeders. One species was a recliner on the surface and another was a shallow-burrower. It is interesting that rare representatives of some mainly epibyssate genera of the Bohemian type of fauna of Gondwanan Europe (*Cardiola*, *Mytilarca*, *Actinopteria*, *Cypricardina*, *Rhombopteria* and *Modiolopsis*) are also found in this community.

A nearshore, warm, carbonate mud bottom bivalve community was described from the lower Silurian of Ohio (Brassfield Formation) by HARRISON & HARRISON (1975). An interesting diminutive fauna is composed of the deposit-feeders *Palaeoneilo*, *Nuculites*, *Praenucula*, *Palaeoconcha* and *Deceptrix*, and by the infaunal suspension-feeder *Lyrodesma*.

The Silurian Malvinokaffric faunas are considered to represent the coldest water associations of Silurian Bivalvia. They were described and listed recently by SÁNCHEZ et al. (1995) from the Silurian South American Precordillera, northwestern Argentina basins and Bolivia. These associations are characterized by a rich occurrence of deposit-feeders (e.g. *Nuculites* and *Palaeoneilo*). Occurring more rarely are representatives of some genera known from the Bohemian type of fauna of Gondwanan Europe (*Actinopteria* and *Dualina*).

The highest diversity of the Silurian bivalves is known in the carbonate facies of the temperate zone in Gondwanan Europe. The facies is characterized by the development of the "Bohemian type" fauna (KŘÍZ, 1984, 1991, in press), best known from the Prague Basin of Bohemia described by KŘÍZ (1979, 1996b), KŘÍZ & PARIS (1982), KŘÍZ & SER-

PAGLI (1993), and also from other European basins (Sardinia, Montagne Noire, Massif Mouthoumet, Massif Armoricaire, and the Carnic Alps).

The Bohemian type of fauna is characterized especially by epibyssate representatives of the families Cardiolidae, Lunulacardiidae, Butovicellidae, Praeostreidae, Pterineidae, and Pterinopectinidae. Reclining, endobyssate and free burrowing forms are represented by the family Antipleuridae and Praecardiidae. About 22 Silurian and Devonian "Bohemian type" communities that are dominated by Bivalvia and described from Bohemia, North Africa, Sardinia, France, Italy, Austria, Turkey and related regions (eastern Serbia, Poland, Florida), are grouped into five community groups on the basis of homology and analogy (KŘÍZ, in press, BOUCOT & KŘÍZ, in press). The *Cardiola* Community group (Wenlock to lowermost Přídolí) is characterized by 10 recurring communities formed by mostly epibyssate forms living in the cephalopod limestone biofacies environment (FERRETI & KŘÍZ, 1993, KŘÍZ, in press). The *Snoopyia* Community Group (upper Přídolí) is characterized by mostly infaunal forms living in micritic limestone – cephalopod limestone biofacies. The *Patrocardia* Community Group (upper Přídolí to Upper Devonian) is dominated by epibyssate forms living in the facies represented by biotrital limestones – micritic limestones and shales. In the Lower Devonian the *Antipleura-Hercynella* Community Group is dominated by burrowing and reclining Antipleuridae and Praecardiidae. The *Cheiopteria* Community Group (Ludlow to Upper Devonian) is characterized by mass occurrences of semi-infaunal forms in the deeper facies of micritic limestones – claystones.

The Silurian non-carbonate facies, represented mainly by shales with graptolites, cephalopods and bivalves, is especially developed in England (Welsh Borderland – WATKINS, 1979), Sweden (Gotland and Skane – LAUFELD, BERGSTRÖM & WARREN, 1975), France (Normandie, Massif Armoricaire, Montagne Noire, and Massif Mouthoumet – BABIN & ROBARDET, 1974, KŘÍZ, 1996b), Czech Republic (Prague Basin and Brunovistulicum – KŘÍZ, 1991, BOUČEK, 1935), Poland (Góry Swietokrzyskie, eastern Poland – TOMCZYKOVA, 1958, KOREJWO & TELLER, 1964), Romania (Moesian Platform – IORDAN, 1981), Guinea, Africa (KŘÍZ, 1985), Nova Scotia (LEVINTON & BAMBACH, 1975) and Arctic Canada (POJETA & NORFORD, 1987). The facies was in general described by BERRY & BOUCOT (1967) as having a pelecypod – graptolite association from North Africa northward into Scandinavia and from the Atlantic Coast of Europe to the Caucasus.

WATKINS (1978, 1979) and WATKINS & BERRY (1977) studied in detail communities of bivalves from the muddy shelf Wenlockian and Ludlovian sediments of the Welsh Borderland and Wales. These are mostly composed of suspension feeders living together with deposit feeders at shallow depth. They consider the muddy substrate to be a high-stress environment where bivalves are the most numerous invertebrates.

Similar conclusions for soft muddy substrates were made by LEVINTON & BAMBACH (1975) based on three communities from the McAdam Brook Formation, Arisaig Group, Nova Scotia. These are dominated by deposit feeding bivalves which comprise 60–90 % of the total bivalve fauna of the formation. Suspension feeders are never dominant.

The expansion of bivalve dominated communities from shallow environments to deeper environments during the Silurian and Lower Devonian was well documented by KŘÍZ (in press). The trend which began in the Upper Ordovician,

when bivalve dominated communities were restricted to the inner-shelf shallow water environments (JABLONSKI et al., 1983), continued during the Silurian.

5. Importance of Silurian Bivalves for Biostratigraphy and Correlation

Detailed study of the Silurian family Cardiolidae from the Prague Basin, Bohemia and other world regions (KŘÍZ, 1979b), extensive collections and systematic study of the Silurian and Lower Devonian Bivalvia from the Prague Basin, Perunica (KŘÍZ, 1966, 1967, 1969, 1979b, 1985, 1996a, 1998, in press), and from Gondwana, e.g. Armoricaire Massif, Bolivia, Carnic Alps, Eastern Serbia, Florida and Georgia, Montagne Noire, Moesian Platform, Mouthoumet Massif, Sardinia and Turkey (KŘÍZ, 1979, 1996b, KŘÍZ & PARIS, 1982, KŘÍZ & SERPAGLI, 1993, KŘÍZ & VESELINOVIČ, 1975, KŘÍZ & IORDAN, 1975, POJETA, KŘÍZ & BERDAN, 1976), provided sufficient material to define bivalve dominated communities of the Bohemian type (KŘÍZ, in press).

In the upper Silurian (Ludlow and Přídolí) sequences of Gondwanan Europe, bivalve-rich horizons occur in the cephalopod limestones and represent stratigraphical markers. Each of these horizons contains a characteristic bivalve-dominated community of the *Cardiola* Community Group which consists of about 11 recurrent communities dominated by different species of the genus *Cardiola*. These levels correspond to one, or at the most, two graptolite zones in Gondwanan Europe. Their exact stratigraphic position is controlled by the occurrence of graptolites, conodonts and chitinozoans in the Prague Basin (KŘÍZ et al., 1986, KŘÍZ et al., 1993, KŘÍZ in KALJO et al., 1996, KŘÍZ, 1998), conodonts, graptolites and chitinozoa in Sardinia (DUFKA & GNOLI, 1996, KŘÍZ & SERPAGLI, 1993), the Armoricaire Massif (KŘÍZ & PARIS, 1982), and in the Carnic Alps (SCHÖNLAUB, 1980). Cardiolidae and the recurring communities dominated by *Cardiola* species may have stratigraphic significance in Gondwanan areas where graptolites are scarce and where the cephalopod limestones are developed. Species of *Cardiola* are easy to recognize because of their characteristic ontogeny, which concerns the swollen band in the umbonal part (KŘÍZ, 1979b). The proposed biostratigraphy of the Wenlock, Ludlow and Přídolí based on bivalve dominated communities characteristic of different levels of the cephalopod limestones (KŘÍZ, in press) is shown on Table 1.

KŘÍZ (1998) and KŘÍZ et al. (in press) demonstrated that Silurian bivalves are also valuable for interbasinal correlations (Prague Basin, Montagne Noire, the Armoricaire Massif, Spain, Guinea, Morocco, Carnic Alps, Sardinia, Eastern Serbia and Western Macedonia) within Gondwanan Europe and Africa. Bivalve dominated communities studied in the South Armoricaire Domain, Sardinia, Prague Basin, the Carnic Alps, Mouthoumet Massif and the Montagne Noire by KŘÍZ & PARIS (1982), KŘÍZ & SERPAGLI (1993), and KŘÍZ (1991, 1996b, 1998, in press) show closer relationships between the northern margin of the Gondwana regions than with the communities described from the Prague Basin on the Perunica microcontinent. Bivalve dominated communities on Perunica show higher diversity than the same communities known from the other Gondwana basins (KŘÍZ et al., in press).

Biostratigraphy of the subsurface Silurian rocks of Florida (POJETA, KŘÍZ & BERDAN, 1976) and their correlation with Gondwanan Europe is based mainly on the Bohemian type

Table 1.
Biostratigraphy of the Silurian and Lower Devonian based on the Bivalvia dominated communities.

CHRONO-STRATIGRAPHY			BIOSTRATIGRAPHY BASED ON GRAPTOLITES	BIOSTRATIGRAPHY BASED ON BIVALVE DOMINATED COMMUNITIES
DEVONIAN	LOWER DEVONIAN	PRAGIAN		<i>Panenka</i> Community
		LOCHKOVIAN		<i>Hercynella-Neklania</i> Community
			<i>M. uniformis</i> Zone	<i>Antipleura bohemica</i> Community
SILURIAN	PŘÍDOLÍ		<i>M. transgrediens</i> Zone	<i>Snoopyia insolita</i> Community <i>Joachymia</i> - <i>Cardiolinka</i> - <i>Pygolfia</i> Community <i>Pterinopecten</i> (P.) <i>cybele cybele</i> Community <i>Patrocadia</i> - <i>Dualina</i> Community
			<i>M. perneri</i> Zone	
			<i>M. bouceki</i> Zone	
			<i>M. lochkovenski</i> Zone	<i>Cardiolinka sardiniana</i> Community
			<i>M. ultimus</i> Zone	<i>Cardiolinka bohemica</i> Community
			<i>M. parultimus</i> Zone	<i>Cardiola conformis</i> Community
	LUDLOW	LUDFORDIAN	<i>M. fragmentalis</i> Zone	
			<i>M. latilobus</i> Zone	<i>Cardiola alata</i> Community
			<i>N. kozłowski</i> Zone	
			<i>N. inexpectatus</i> Zone	
			<i>B. bohemicus tenuis</i> Zone	<i>Cardiola docens</i> Community
			<i>S. linearis</i> Zone	
	GORSTIAN		<i>S. chimaera</i> Zone	<i>Cardiola signata</i> Community <i>Cardiola consaguus</i> Community <i>Cardiola donigala</i> Community
			<i>C. colonus</i> Zone	<i>Cardiola gibbosa</i> Community
			<i>P. ludensis</i> Zone	
			<i>P. praedeubeli</i> - <i>P. deubeli</i> z.	
			<i>G. nassa</i> Zone	
			<i>P. parvus</i> Zone	<i>Cardiola figusi</i> Community <i>Cardiola agna</i> Community
			<i>C. lundgreni</i> Z.	
			<i>T. testis</i> Subz.	
			<i>C. radians</i> Subz.	
	WENLOCK	HOMERIAN		
			<i>C. perneri</i> / <i>C. ramosus</i> z.	
			<i>C. rigidus</i> Zone	<i>Carnalpia nivosa</i> Community
			<i>M. belophorus</i> Zone	
			<i>P. dubius</i> Zone	
	SHEINWOODIAN		<i>M. riccartonensis</i> Zone	

The Wenlock and Ludlow are indicated by the characteristic Gondwanan bivalve *Butovicella migrans*, and the Přídolí by the *Cheiopteria bridgei* Community and the *Lunulacardium excellens* Community first described from the Prague Basin, Bohemia (Kříž, in press). The Silurian (Přídolí)/Devonian (Lochkovian) boundary community of bivalves is characterized by *Prothyris*, *Arisaiga*, *Pleurodapis* and *Nuculites* and shows close relationships to the bivalve community described by KOREJWO & TELLER (1964) from the East European Platform of Baltica and also to the community of bivalves known from Arisaig, Nova Scotia (MCLEARN, 1924).

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