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

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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.

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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 bohemica*, 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 Modiomorphoida Newell, 1969. Actinodontida differs

from Modiomorphoida 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 *Intihuarella 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 & Guttiérez-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 occurence 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

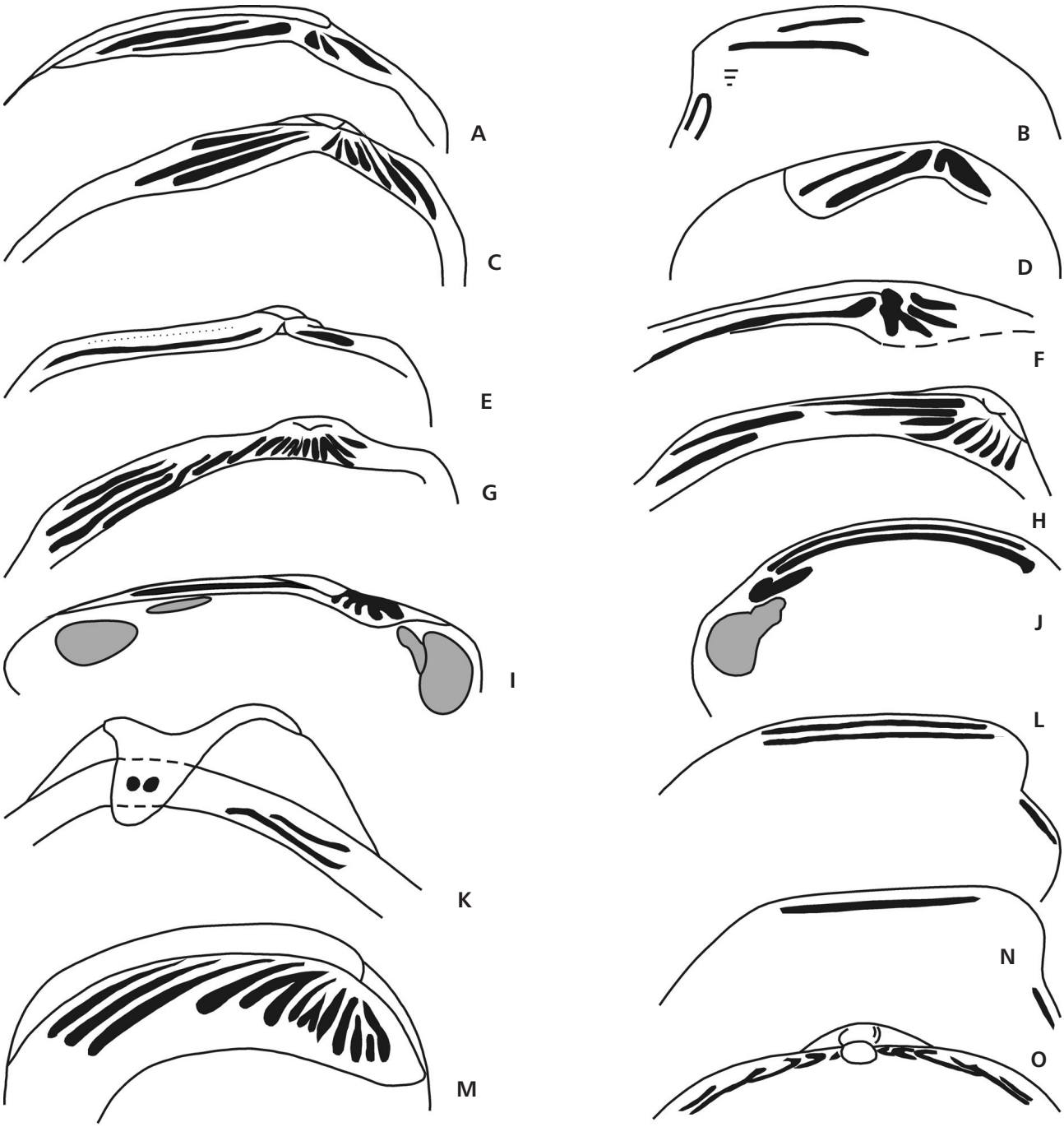


Figure 1. Hinge schemes of the important genera of the Ordovician Actinodontida. • A–I – Cycloconchidae Ulrich, 1884; A – *Cycloconcha*, according to fig. 3 in Babin & Gutiérrez-Marco (1985), left valve; B – *Zhenxiongella*, according to fig. 4 in Fang & Cope (2008), right valve; C – *Actinodonta*, according 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 – *Intihuarella*, 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.

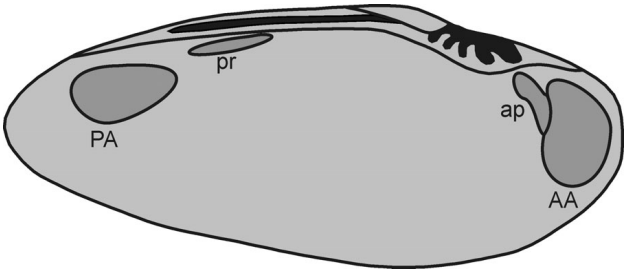


Figure 2. *Pseudocyrtodonta incola*, dorsolateral view showing hinge and muscle scars. Key to letter symbols: AA – anterior adductor muscle scar; PA – posterior adductor muscle scar; ap – anterior protractor muscle scar; pr – posterior retractor muscle scar.

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 Pelseneer, 1889 (Palaeotaxodonta). 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 & Guttiérrez-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)	*Cienagomya bidentata* Sánchez, 2005	Intihuerallidae	Tremadocian, Floian
	Intihuarella simplicidentata Sánchez & Vaccari, 2003	Intihuerallidae	Tremadocian (Floresta Formation)
	Redonia condorensis Sánchez & Benedetto, 2007	Redoniidae	Darriwilian
	Pseudoredonia radialis Sánchez & Benedetto, 2007	Redoniidae?	Darriwilian
	Pucamya wira Sánchez & Benedetto, 2007	Pucamyidae	Darriwilian
Argentina (Sierra de Famatina)	*Famatinodonta gonzaloi* Sánchez, 2001	Cycloconchidae	Floian/Dapingian (middle Arenigian)
Argentina (Western Argentina)	*Redonia riojana* Sánchez, 1997	Redoniidae	Floian/Dapingian (middle Arenigian)
	Poladonta sanjuanina Sánchez *et al*., 2003	Cycloconchidae	Sandbian
	Redonia suriensis Sánchez & Babin, 1994	Redoniidae	Lower Ordovician
Argentina (Provincia de Salta)	*Cycloconcha* cf. *oblonga* Foerste, 1914	Cycloconchidae	Middle Ordovician
Australia	*Copidens browni* Pojeta & Gilbert-Tomlinson, 1977	Nyassidae	Darriwilian (Nora Formation)
Bohemia	*Pseudocyrtodonta incola* (Barrande, 1881)	Cycloconchidae	Darriwilian
	Pseudocyrtodonta ala (Barrande, 1881)	Cycloconchidae	Darriwilian
	Pseudocyrtodonta obtusa (Barrande, 1881)	Cycloconchidae	lower/middle Katian
	Redonia deshayesi Rouault, 1851	Redoniidae	Darriwilian
China (East Yunnan)	*Mangbuina prima* Guo, 1988	Cycloconchidae	Floian (Hongshiay Formation)
	Zhenxiongella septata Guo, 1988	Cycloconchidae	Floian (Hongshiay Formation)
	Zadimerodia fastigiata Guo, 1988	Nyassidae	Floian (Hongshiay Formation)
	Baidiostraca aberrans Guo, 1988	Baidiostracidae	Floian (Hongshiay Formation)
China (West Yunnan)	*Fasciculodonta impressa* Fang & Cope, 2004	Cycloconchidae	Dapingian–Darriwilian (Upper Arenigian)
	Fasciculodonta fengyiensis (Guo, 1985)	Cycloconchidae	Dapingian–Darriwilian (Upper Arenigian)
	Taselasmodum decussatum Guo, 1985	Cycloconchidae	Dapingian–Darriwilian (Upper Arenigian)
	Yunnanoredonia laevis Fang & Cope, 2004	Redoniidae	Dapingian–Darriwilian (Upper Arenigian)
France (Armorican massive)	*Redonia deshayesi* Rouault, 1851	Redoniidae	Darriwilian (Shiste à Calymenes)
	"Actinodonta cuneata" Phillips, 1848	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	"Actinodonta carinata" Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	"Actinodonta obliqua" Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	"Actinodonta secunda" Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	"Actinodonta acuta" Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	"Actinodonta lata" Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
	"Actinodonta obtusa" Barrois, 1891	Cycloconchidae	Floian/Dapingian (Grès armoricain)
France (Montagne Noire)	*Redonia michelae* Babin *et al.,* 1982	Redoniidae	Floian and Dapingian
North America	*Cycloconcha ovata* Ulrich, 1893	Cycloconchidae	Upper Ordovician
	Cycloconcha milleri (Meek, 1871)	Cycloconchidae	Upper Ordovician
	Cycloconcha mediocardinalis Miller, 1874	Cycloconchidae	Upper Ordovician
	Cycloconcha oblonga Foerste, 1914	Cycloconchidae	Upper Ordovician
Spain	*Ananterodonta oretanica* Babin & Gutiérrez-Marco, 1985	Cycloconchidae	Darriwilian (Schiste à Neseuretus)
	Redonia deshayesi Rouault, 1851	Redoniidae	Darriwilian
	Dulcineaia manchegana Babin & Gutiérrez-Marco, 1991	Redoniidae	Darriwilian
Wales (Llangyong Inlier)	*Actinodonta cuneata* Phillips, 1848	Cycloconchidae	Silurian (Llandovery)
	Carminodonta crossi Cope, 1996	Cycloconchidae	Floian
	Fortowensia grandis Cope, 1996	Cycloconchidae	Floian
	Celtoconcha foveata Cope, 1996	Cycloconchidae	Floian
	Moridunia simplicidens Cope, 1996	Redoniidae	Floian
	Redonia anglica 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 numerus 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: Díly, Díly 1, Osek near Rokycany, Osek 1, Rokycany, Rokycany 2 – near cemetery, Rokycany 17.

Pseudocyrtodonta incola (Barrande, 1881)

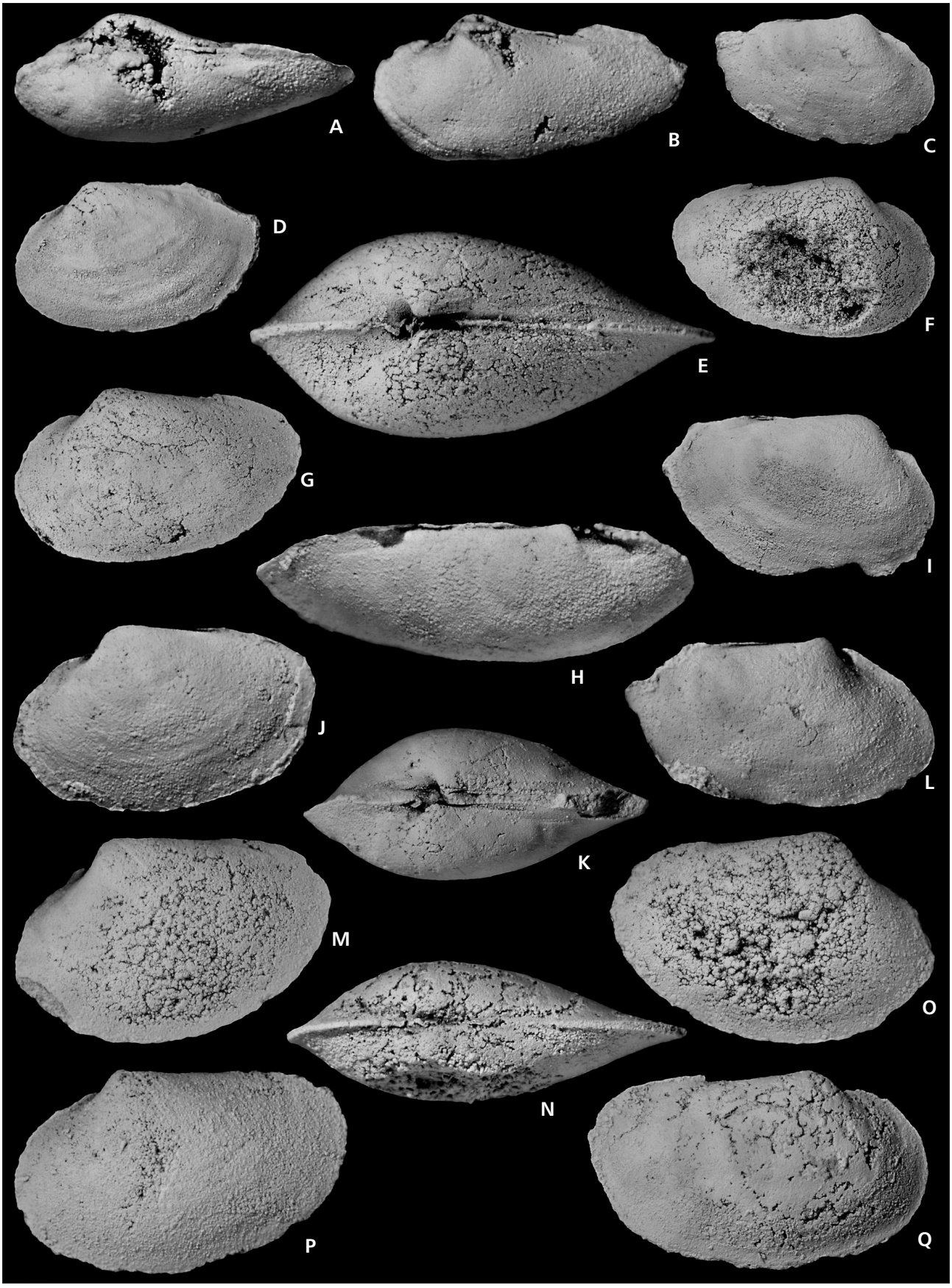
Figure 4

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, Díly 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, Díly 1 locality, early Darriwilian. • K, P – Prague Basin, Bohemia, Díly 3 locality, early Darriwilian.


A
B
C
D
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Q

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

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

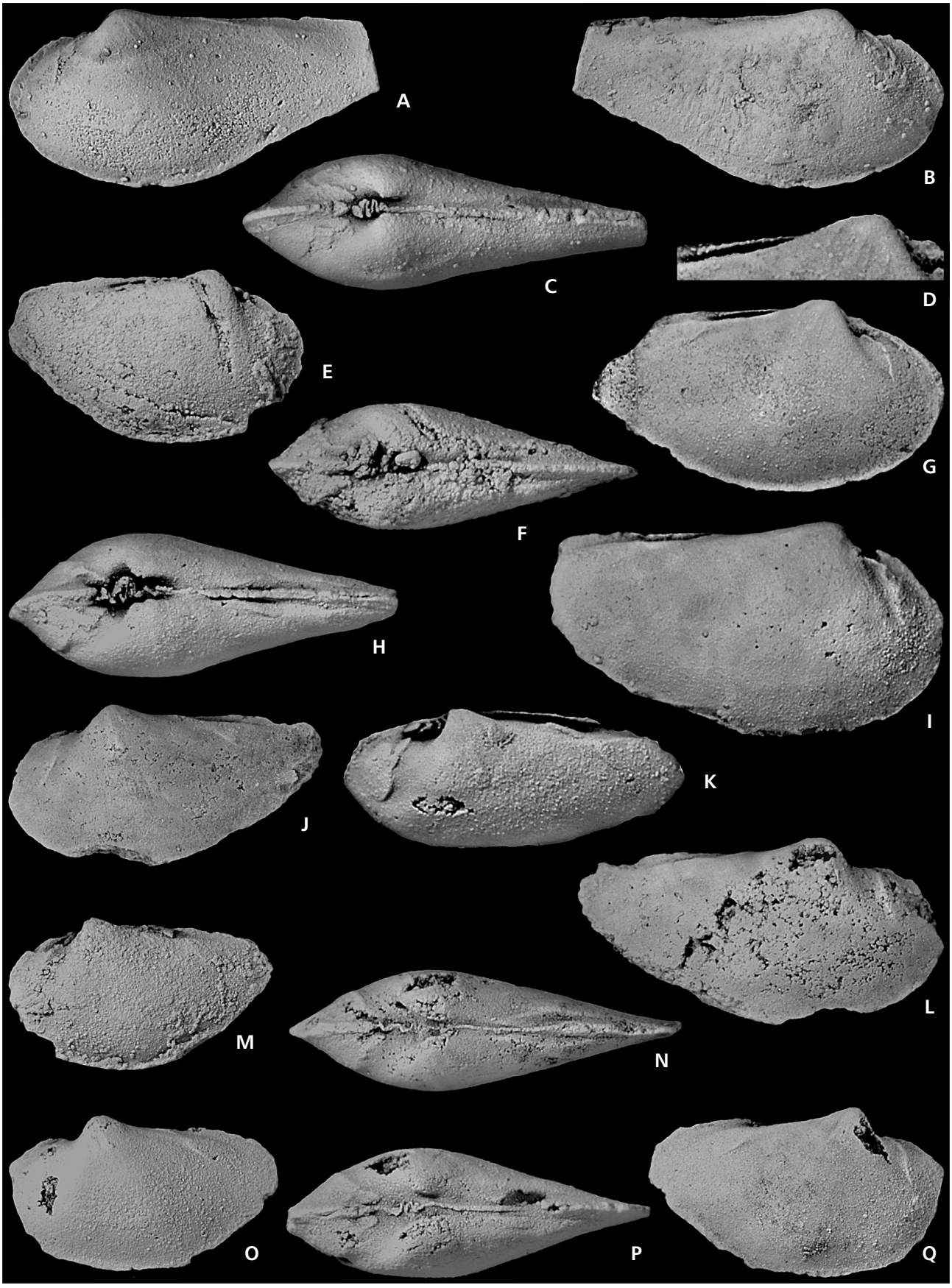
Diagnosis. – *Pseudocyrtodonta* with longitudinally elongated shell, with rostrate posterior part and with more pronounced umbos.

Description. – Shell small (length maximally 9 mm, height maximally 5 mm and width maximally 3.2 mm), equivalve, 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, Díly 2 locality, early Darriwilian. • E, F, K, M, O–Q – Prague Basin, Bohemia, Díly 1 locality, early Darriwilian. • H, I – Prague Basin, Bohemia, Osek 1 locality, early Darriwilian. • J, L, N – Prague Basin, Bohemia, Rokycany locality, early Darriwilian.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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, Pětidomky, 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 viewwith anterior adductor muscle scar. • D – articulated specimen, NM L22686, 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.


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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 & Guttiérrez-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 solemyoids-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 an 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 cardiolarioids. *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 cladisitic 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 cardiolarioids.

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