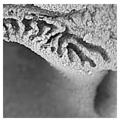
The Early Ordovician bivalve assemblages of the Montagne Noire (France): palaeobiogeography, palaeoecology, and early diversification

Marika Polechová



Early Ordovician bivalves from the Montagne Noire of France include eight taxa: *Babinka prima* Barrande, 1881, 1982, *Coxiconchia guiraudi* (Thoral, 1935), *Ekaterodonta courtessolei* (Babin, 1982), *Noradonta redoniaeformis* (Thoral, 1935), *Redonia michelae* (Babin, 1982), *Modiolodon* sp. (Thoral, 1935), *Synek thorali* (Babin, 1982) and *Thoralia languedociana* (Thoral, 1935). They are recorded from the late Tremadocian Saint Chinian Formation, the early Floian La Maurerie Formation, the middle Floian Cluse de l'Orb and Foulon formations, and the late Floian Llandeyran Formation. They represent a high palaeolatitude bivalve assemblage dominated by heteroconchs and protobranchs and exhibit strong similarities to contemporaneous Moroccan fauna, with dominance of *Redonia* and *Babinka*. However, Tremadocian bivalves are generally scarce, with only twenty-one known genera. They display diverse ecological strategies, including infaunal deposit and filter feeders, semi-infaunal and epifaunal filter feeders, and byssate semi-infaunal filter feeders. Tremadocian bivalves exhibited highly restricted global dispersion, with the majority of genera being endemic. Although *Babinka*, *Coxiconchia*, and *Pharcidoconcha* achieved a somewhat broader distribution during the Tremadocian, they still remained confined to Gondwana and its peri-Gondwana margin. Nevertheless, the western Gondwana corridor played a role in facilitating some faunal exchange, despite the general limitations on bivalve migration during this period. Key words: Bivalves, Early Ordovician, Montagne Noire, France.

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Global occurrences of Early Ordovician bivalves are rare, and mainly Tremadocian records of bivalves are limited to only a few regions, including NW Argentina (early and late Tremadocian; Sánchez 2008), Australia (late Tremadocian, Pojeta & Gilbert-Tomlinson 1977), Montagne Noire in France (late Tremadocian, Babin 1982), Iran (late Tremadocian, Cope & Ghobadi Pour 2020), and southern China (late Tremadocian, Fang 2006). Although rare, Early Ordovician bivalves show considerable diversity with almost all major clades represented. A recent revision of the Early Ordovician bivalves from Morocco has yielded new data regarding a Floian bivalve assemblage from high palaeolatitudes. Moroccan bivalves show close affinities to the assemblage of comparable age from the Montagne Noire of France (Polechová 2016). Lower Ordovician strata in the Montagne Noire have provided the bivalve association previously partly described by Thoral (1935) and Babin (1982), containing the earliest representatives of bivalves from the late Tremadocian. The new material described herein from the Montagne Noire, collected by Daniel Vizcaïno and supported by refined stratigraphic data, has facilitated a complete revision of the area's bivalves, thereby offering further insights into their early diversification. The bivalve faunas from Montagne Noire and Morocco significantly has implications for the early distribution of bivalves to other regions of European Gondwana and peri-Gondwana (Polechová 2016). In the present paper, all the bivalves from the Montagne Noire are systematically revised, and their occurrence, stratigraphical range, and palaeoecology are evaluated. Moreover, this study places these bivalves within the broader context of Tremadocian bivalves, a fauna that has been underestimated compared to Floian bivalves. This assemblage, unrevised since Babin (1982), is important for a comprehensive understanding of Early Ordovician bivalve faunas' composition, distribution, and palaeobiogeographical relationships on the high-latitude Gondwanan margins.

Geological setting

The Montagne Noire is situated in the southern prolongation of the French Massif Central (Fig. 1A). The

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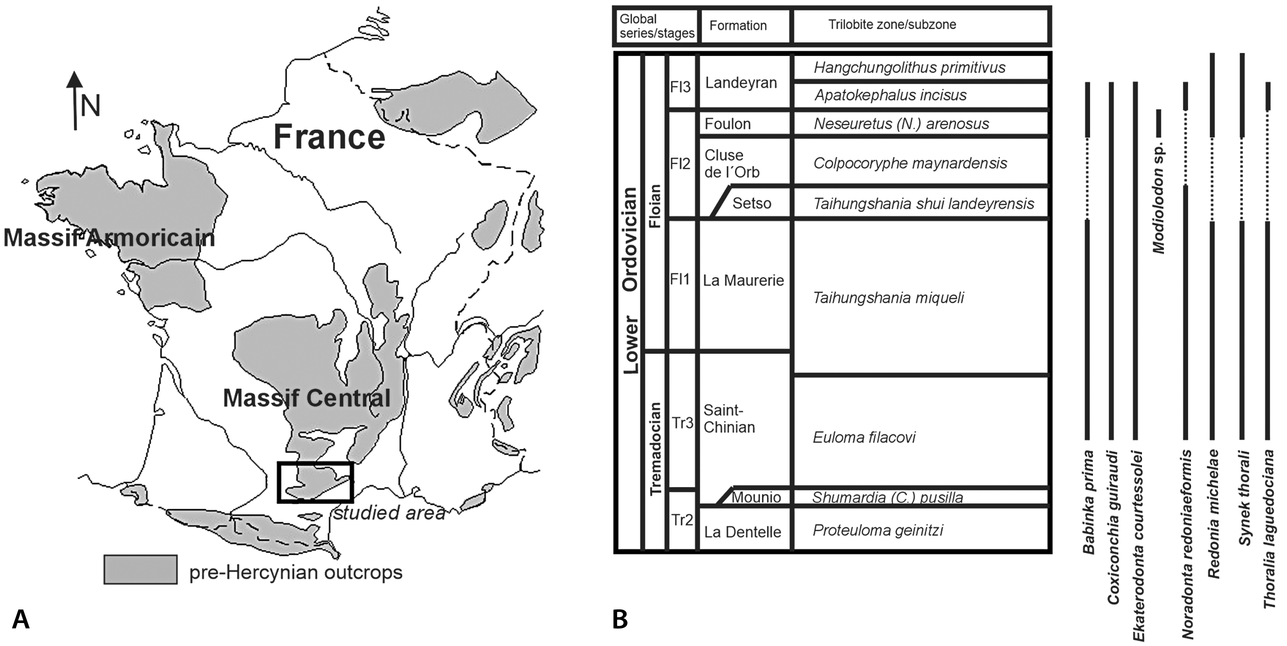


Figure 1. A – generalized map of position of the Montagne Noire (black rectangle) in France. • B – stratigraphic range of bivalves in the Lower Ordovician of the southern Montagne Noire. Stratigraphic column redrawn and modified from Courtessole *et al.* (1983). Stratigraphy based on Vizcaïno *et al.* (2001), Álvaro & Vizcaïno (2001), Tortello *et al.* (2006), and Serpagli *et al.* (2007).

stratigraphy and paleontology of Montagne Noire have been the subject of numerous publications (*e.g.* Miquel 1912; Thoral 1935; Courtessole *et al.* 1981, 1983, 1985; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003; Tortello *et al.* 2006; Serpagli *et al.* 2007). The earliest bivalves were found in the Saint-Chinian Formation of Tremadocian age (Fig. 1B). The Saint-Chinian Formation is mainly formed of claystone and siltstone with thin beds of sandstone. This unit provides numerous fossil remains, dominated by trilobites but also containing brachiopods, echinoderms, graptolites, hyolithids, machaeridians, and molluscs (Thoral 1935, Capéra *et al.* 1978, Babin 1982, Courtessole *et al.* 1983, Vidal 1996, Vizcaïno & Lefebvre 1999, Vizcaïno *et al.* 2001, Vizcaïno & Álvaro 2003, Kröger & Evans 2011). The environmental conditions of the Saint-Chinian Formation are interpreted as a relatively deep shelf with deposits that were formed at or slightly below storm-wave base (Vidal 1996, Vizcaïno & Lefebvre 1999, Vizcaïno *et al.* 2001, Lefebvre 2007). The overlying La Maurerie Formation of Floian age consists of numerous thick sandstones intercalated within shales with fossiliferous concretions. The assemblage of this unit is less diverse than those in Saint-Chinian with dominant trilobites and molluscs associated with brachiopods, echinoderms and graptolites (Thoral 1935, Capéra *et al.* 1978, Babin *et al.* 1982, Courtessole *et al.* 1983, Vizcaïno *et al.* 2001, Vizcaïno & Álvaro 2003, Kröger & Evans 2011), the sediments of La Maurerie Formation having been deposited at or slightly above storm-wave base, and considered as a slightly shallower than those in Saint-Chinian Formation (Noffke & Nitsch 1994, Vizcaïno & Lefebvre 1999, Vizcaïno *et al.* 2001, Vizcaïno & Álvaro 2003). The Cluse de l'Orb Formation of the Floian age with thin-bedded sandstones and shales alternating with thick successions of micaceous quartzites represented deposition on a storm-dominated platform. The Foulon Formation of Floian age is also composed of shallower storm-dominated deposits of sandy shales and decimetre-thick sandstones (Courtessole *et al.* 1985). Both formations show lower diversity than La Maurerie and Saint Chinian formations. The Landeyran Formation of the Floian age consists of homogeneous shales bearing siliceous nodules. The Landeyran Formation has yielded particularly abundant and diverse faunas dominated by trilobites but also comprising annelids, brachiopods, echinoderms, graptolites, hyolithids, molluscs, and ostracods (Dean 1966, Capéra *et al.* 1978, Babin *et al.* 1982, Courtessole *et al.* 1983, Vizcaïno & Lefebvre 1999, Vizcaïno *et al.* 2001, Vizcaïno & Álvaro 2003). This formation provides an exceptionally preserved fauna with vermiform organisms, sponge, algae, chelicerates *etc.*, namely the Cabrière Biota (Saleh *et al.* 2024). The assemblages of the Llandeyran Formation are characterized by the re-occurrence of various taxa (*e.g.* raphiophorid trilobites, stylophoran echinoderms, conulariids) which are absent in the underlying Cluse de l'Orb and Foulon formations but are present in the Saint-Chinian and La Maurerie formations (Courtessole *et al.* 1991, Henry & Vizcaïno 1996, Vizcaïno & Lefebvre 1999, Van Iten & Lefebvre 2020). This pattern agrees well with the interpretation of the Landeyran Formation as a transgressive unit consisting of relatively distal facies deposited at or below storm-wave base and thus comparable in origin to the Saint-Chinian and La Maurerie formations (Vizcaïno *et al.* 2001, Vizcaïno & Álvaro 2003, Bonin *et al.* 2007). While Babin (1982, tab. 1) showed a similar pattern with no bivalves recorded from the Cluse d'Orb Formation, Vizcaïno & Álvaro (2003) noted some specimens from the Cluse d'Orb Formation, which is confirmed by the new material of Daniel Vizcaïno establishing bivalves from this formation as well.

Material and methods

The material described and discussed herein comes from the palaeontological collection of the University Lyon (FSL, CAB), type material from the University of Brest (LPB). All bivalve specimens were measured, systematically determined, and statistically analysed to find their numerical and ranked abundance following the methodology of Stanley (1970) and Kříž (1999). The specimens were coated with ammonium chloride before being photographed.

Preservation and Taphonomy

Specimens presented here are preserved as internal or external moulds, indicating that their original shell has dissolved. However, some specimens bear a thin shell with fine ornamentation. Shell material replaced during diagenesis is often silicified, meaning the original carbonate has been dissolved and replaced by silica, or recrystallized, where the original carbonate material (like aragonite) transforms into a more stable form (like calcite). Moulds are preserved in siliciclastic sediments and generally exhibit average preservation; notably, specimens from nodules retain preserved hinge and muscle scars. The presence of articulated specimens and those in butterfly position (however rare) suggests limited post-mortem transport. Evidence of the trace fossil *Arachnostega* (Fig. 2E, F) is also present. While *Arachnostega* is often found associated with Ordovician skeletal faunas (Fatka *et al.* 2011; Vinn *et al.* 2014, 2024), it is absent in Early Ordovician bivalves from Morocco. Lefebvre (2007) documented *Arachnostega* in the Middle Ordovician of Bohemia in both deep-water, soft-bottom settings unaffected by currents, and in well-oxygenated middle shelf environments with quiet conditions at or below the average storm wave base. These ichnofossils serve as valuable paleoenvironmental indicators of firm, muddy, and coherent substrates (Gil Cid & Lebrón Moreno 2010).

Systematic palaeontology

The classification used by Carter *et al.* (2011) is used here. Synonymy list follows the recommendations by Matthews (1973).

Class Bivalvia Linné, 1758
Subclass Protobranchia Pelseneer, 1889
Superorder Nuculaniformii Carter, Campbell & Campbell, 2000

Order Cardiolariida Cope, 2000

Remarks. – Validity of the orders Cardiolariida and *Afghanodesmatida*. Zhang *et al.* (2024) discovered that the type material of the genus *Afghanodesma* consists only of wax impressions made in the field. These casts are invalid as type material according to ICZN rule 72.5.3. The genus *Afghanodesma* is therefore invalid and higher-level taxa named after it thus automatically become invalid. The appropriate replacement Order name for this is the order Cardiolariida (*ex* Cardiolariodea Cope, 2000, p. 88) Zhang *et al.* (2024, p. 2) had incorrectly constructed the ordinal name; correctly it is Cardiolariida.

Superfamily Tironuculoidea Babin, 1982
Family Tironuculidae Babin, 1982

Genus *Ekaterodonta* Babin, 1982

Type species. – *Ekaterodonta courtessolei* Babin, 1982 from the La Maurerie Formation, Floian, Montagne Noire, France.

***Ekaterodonta courtessolei* Babin, 1982**
Figure 2

1935 *Nucula*(?) *bussacensis* Sharpe. – Thoral, 1935, p. 167, pl. 13, fig. 7.
1981 *Ekaterodonta* n. sp. – Babin, pl. 1, fig. 10.
1982 *Ekaterodonta courtessolei* Babin; Babin, pl. 8, figs 1–16.
1991 *Ekaterodonta courtessolei* Babin. – Johnston, fig. 11b, c.
2016 *Ekaterodonta courtessolei* Babin. – Polechová, fig. 2l–p.

Holotype. – internal mould of the left valve, LPB 8872, figured *in* Babin (1982) in pl. 8, figs 1, 2; herein Fig. 2H, K, L.

Type horizon and locality. – Floian, La Maurerie Formation, zone *Taihungshania miqueli*. Canto Cigalos near the Prades/Vernazobre, Montagne Noire, France.

Material. – Seventy-five new specimens (measured specimens FSL 713386, 713392, 713394, 713406, 713412, 713413, 713423, 713433, 713444a–e, 713448, 713449a, 713450, 713451, 713460, 713461, 713466, 713526, 713543, the rest of the material is ill-preserved).

Diagnosis. – Tironuculid with pronounced myophoric buttress in anterior adductor. Anterior part of the hinge with two or three lateral teeth and one or two small cardinal teeth, posterior part of the hinge with 10 to 15 teeth, the part of the first tooth in posterior is prolonged at the end of the hinge.

Description. – Shell small (maximum length 12.5 mm), rounded or slightly oval, equivalve and inequilateral. Posterior part larger than anterior, both parts rounded. Umbo pronounced, blunt, prosogyre. Hinge heterotaxodont, anterior part of the hinge with two or three umburrid-like teeth, posterior part of the hinge with 10 to 15 teeth, with the dorsal part of first tooth extending to the end of the hinge. Ligament simply planar and opisthodetic. Anterior and posterior adductor muscle scars rounded, often deeply impressed. Myophoric buttress borders anterior adductor. Anterior pedal muscle scar joined dorsal-posteriorly to the adductor. Posterior pedal muscle scar antero-dorsal to the posterior adductor muscle scar, separated from it. Two or three small, rounded muscle scars in umbonal region, could be the pedal elevators. Outer surface sculpture consists of growth lines and bands.

Remarks. – *Ekaterodonta courtessolei* belongs to the Tironuculidae, which have a heterotaxodont hinge imitating an actinodont hinge (the dorsal part of the proximal chevron tooth seems to be prolonged). Stratigraphically younger *Ekaterodonta hesperica* Babin & Gutiérrez-Marco (1991) from the Middle Ordovician of Spain is very similar to *E. courtessolei*; however, it differs in less prominent anterior adductor. Babin (1982) also described possible juvenile stages of *E. courtessolei* and suggested that it is very problematic to distinguish juvenile stages of *E. courtessolei* and *N. redoniaeformis*. The juvenile hinge of *E. courtessolei* is characterised by one or two anterior teeth (probably taxodont, however not well preserved) and six to nine posterior taxodont teeth. Upper parts of the posterior teeth are close together and seems to be as one long tooth near the cardinal line. The juvenile hinge of *Noradonta* has two or three small teeth in anterior part and under the umbo, and one or two long teeth in the posterior part. Babin (1982, Fig. 16) figured these juvenile hinges, however, there are mistakes in the letters; the juvenile hinges of *Ekaterodonta* is figured in fig. 16a, c and *Noradonta* in fig. 16b.

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): Caunes Minervois, Ruisseau des Lavandiers, Canto Cigalos près de Prades/Vernazobre, Felines-Minervois, Vallée du Merlaux; (ii) La Maurerie Formation (Floian): Assignan, le bois de la Cabosse, Cessenon – Serre Malle, Cessenon – Col de la Maurerie, Cessenon Martelle, Prades sur Vernazobre, Saint Chinian – Saint Cels; (iii) Cluse de l'Orb Formation (Floian): Cessenon Coulobres, Trausses Minervois, Brama; (iv) Foulon Formation (Floian): Roquebrun, Vallée du Rieuberlou; (v) Landeyran Formation (Floian): Causses et Veyran, Vallée du Llandeyran.

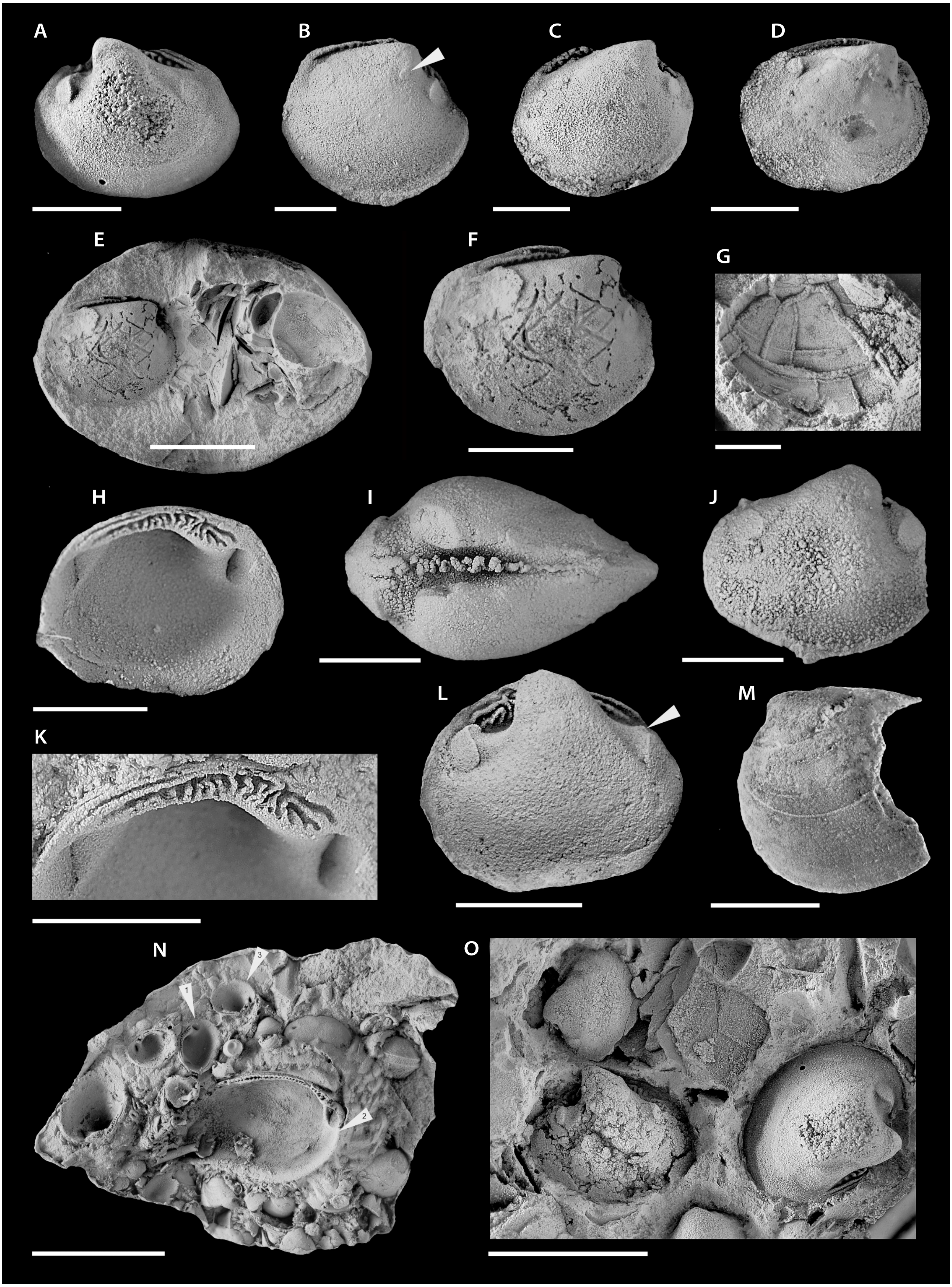
Superorder Nuculiformii Gray, 1824
Order Nuculoida Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Praenuculidae McAlester, 1969

Genus *Synek* Barrande, 1881

Type species. – *Synek antiquus* Barrande, 1881 (pl. 275, fig. 1.3–1.28, *partim*) from the Upper Ordovician, Katian, Králův Dvůr Formation, Lejškov, Barrandian area, Czech Republic.

Remarks. – Polechová (2022) proposed that the genus *Synek* likely represents several different genera. The oldest specimen attributed to *Synek*, described by Barrande (1881, pl. 275, fig. 1.1, 1.2) from the late Darriwilian Šárka Formation in Bohemia, was later reassigned to *Pseudocyrtodonta ala* by Steinová (2012). The extensive stratigraphic range of *Synek antiquus* (from the late

Figure 2. A–O – *Ekaterodonta courtessolei* Babin, 1982, Early Ordovician, Montagne Noire, France. A, O – internal mould of the left valve with preserved muscle scars and hinge (A), three specimens in concretion (O), lateral view, FSL 713460a. B – internal mould of the right valve with preserved muscle scars and hinge, arrow showing accessory muscle scar, lateral view, FSL 713394. C – internal mould of the right valve with preserved muscle scars and part of the hinge, lateral view (C), FSL 713413. D, G – internal mould of the right valve (D), external mould of the right? valve (G), lateral views, FSL 713412. E, F, M – concretion with two specimens (E), internal mould of the right valve showing *Arachnostega* traces (F), external mould of the right valve with *Arachnostega* traces (M), lateral views, FSL 713386 a, b. H, K, L, M, N – holotype, internal mould of the left valve, latex cast dorsal view (H), latex cast detail of the hinge (K), lateral view on internal mould of the left valve, arrow showing pedal retractor joined with posterior adductor muscle scar (L), latex cast of the concretion with holotype of *Ekaterodonta* (arrow 1), specimen of *Noradonta redoniaeformis* (arrow 2) and specimen of *Redonia michelae* (arrow 3) (N), LPB 8872. I, J – articulated specimen, dorsal view (I), right valve of the articulated specimen, lateral view (J), FSL740816. Scale bars: A, B, C, H, I, J, K, L = 2 mm. C, D, F, G, M, N, O = 5 mm, E = 10 mm.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Sandbian Letná Formation to the late Katian Králův Dvůr Formation) raises doubts about it being a single species. The frequent absence of hinge features in *Synek* specimens is particularly problematic. While the type species *Synek antiquus* possesses a taxodont hinge (Kříž 1995, fig. 1a, a specimen from the Bohdalec Formation, Katian in age), this feature is often poorly preserved, making specimens appear edentulous. Despite the frequent occurrence of *Synek antiquus* in the Bohdalec, Zahořany and Králův Dvůr formations of the Barrandian area, the taxodont hinge has been observed in only two specimens. In the Montagne Noire, this genus is difficult to distinguish from *Coxiconchia*, the only noted difference is a rounded anterior margin in *Synek*, which could merely represent variability in the shell shape.

Synek thorali **Babin, 1982**

Figure 3A, B

1935 *Synek antiquus*. – Thoral, p. 172.
1982 *Synek thorali*. – Babin, p. 43, pl. 10, figs 7–13.
1982 *Cymatonota*? – Babin, p. 45, pl. 11, fig. 17.

Holotype. – Internal mould of the left valve, LPB10760, figured *in* Babin (1982) in pl. 10, figs 8, 9; herein Fig. 3B.

Paratypes. – Internal mould of the left valve, LPB10769, figured *in* Babin (1982) in pl. 10, fig. 7.

Type horizon and locality. – Floian, La Maurerie Formation. Prades/Vernazobre, Montagne Noire, France.

Material. – Nine new specimens (measured specimens FSL 713517, 713435, 713492, 713518 and other ill-preserved specimens).

Diagnosis. – Small *Synek* with regular oval outline, narrower at the posterior.

Description. – Shell small (maximum length 11.1 mm), equivalve, inequilateral, posteriorly elongated. Anterior part of the shell smaller than the posterior part. Anterior part rounded. Posterior part also rounded, not truncate. Umbo in the anterior part. Hinge line straight, and hinge seemingly edentulous. Outer surface sculpture with fine comarginal lines.

Remarks. – *Synek antiquus* from the Late Ordovician of Bohemia is typically larger with a broader posterior. The taxonomic placement of *Synek thorali* is problematic, as only its shell shape is known. Although assigned to *Synek*, differentiating it from *Coxiconchia* is difficult. Nonetheless, herein it is accepted its taxonomic validity.

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): Caunes Minervois – Ourduvielle, Felines Minervois – Vallée du Merlaux; (ii) La Maurerie Formation (Floian): La Maurerie, Cessenon – Serre Mal; (iii) Landeyran Formation (Floian): Vallée du Llandeyran, pont Supérieur.

Subclass Autobranchia Grobben, 1894
Infraclass Heteroconchia Carter, Campbell & Campbell, 2000
Superfamily Lyrodesmatoidea Ulrich, 1894 *in* Ulrich & Scofield (1894)
Family Lyrodesmatidae Ulrich, 1894 *in* Ulrich & Scofield (1894)

Genus *Noradonta* Pojeta & Gilbert-Tomlinson, 1977

Type species. – *Noradonta shergoldi* Pojeta & Gilbert-Tomlinson, 1977 from the Nora Formation, Floian–Dapingian, Southern and Eastern Georgina Basin, Australia.

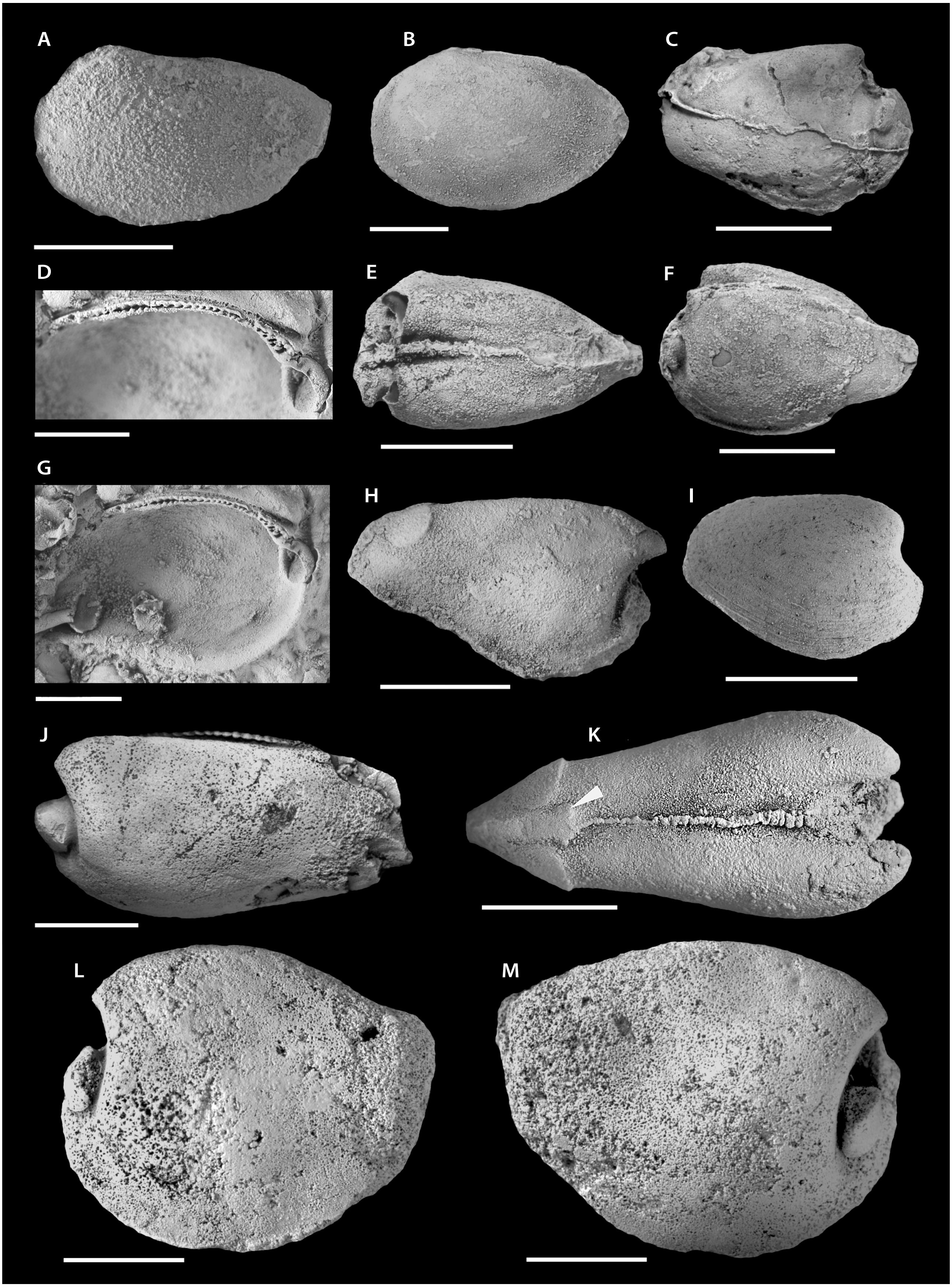
Noradonta redoniaeformis **(Thoral, 1935)**

Figure 3C–M

1935 *Nucula*(?) *redoniaeformis*; Thoral, 1935, p. 169, pl. 13, fig. 8a, b.
1935 *Redonia prisca*. – Thoral, p. 171, pl. 13, fig. 9.
1981 *Pradesiana* nov. sp. – Babin, p. 42, fig. 1c.
1982 *Redonia prisca* Thoral. – Babin & Le Pennec, fig. 2e.
1991 *Noradonta redoniaformis* (Thoral). – Johnston, 1991, fig. 11a.

Lectotype. – Articulated specimen, LPB 10730a, figured *in* Babin (1982) in pl. 9, figs 3, 4; herein Fig. 3C–F.

Figure 3. A, B – *Synek thorali* Babin, 1982, Early Ordovician, Montagne Noire, France. A – internal mould of the left valve, lateral view, FSL 713517. B – holotype, internal mould of the left valve, lateral view, LPB 10770. • C–M – *Noradonta redoniaeformis* (Thoral, 1935), Early Ordovician, Montagne Noire, France. C, E, F – holotype, articulated specimen with preserved adductor muscle scars and hinge, right valve, lateral view (C), hinge, dorsal view (E), left valve, lateral view (F), LPB 10730, lectotype. D, G, J – internal mould of the left valve, latex cast, lateral view (D), left valve, dorsolateral view (J), LPB 8872. H, K – articulated specimen, internal mould of the right valve, lateral view (H), hinge, arrow shows pedal muscle scar near the posterior adductor muscle scar, dorsal view (K), FSL 740810. I – external mould of the left valve, lateral view, FSL 713423. L, M – articulated specimen, left valve, lateral view (L), right valve, lateral view (M), FSL 740816. F, G – negative and positive of the left valve, lateral view, FSL 713423. H, K – articulated specimen, internal mould of the right valve, lateral view (H), hinge, dorsal view (K), FSL 740810. Scale bar = 5 mm.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Paralectotype. – Articulated specimen, LPB 10730b, figured *in* Babin (1982) in pl. 9, fig. 10.

Type horizon and locality. – Floian, La Maurerie Formation, zone *Taihungshania miqueli*. La Maurerie, Montagne Noire, France.

Material. – Thirty-eight new specimens (measured specimens FSL 713416, 713423, 713425, 713431, 713442, 713449b, 713452, 713460b, 713504, 713541, 713545 and other ill-preserved specimens).

Diagnosis. – Longitudinally elongated lyrodesmatid with pronounced myophoric buttress anteriorly. Anterior part of the hinge line possesses four to six taxodont teeth; in posterior part of the hinge one or two long crenulated teeth.

Description. – Shell small (maximum length 17.3 mm), posteriorly elongated, equivalve and strongly inequilateral. Posterior part larger than anterior; anterior outline rounded, posterior margin slightly truncate (Fig. 3H). Umbo pronounced, sharp, prosogyre and often terminal. Anterior part of the hinge with two to four cardinal teeth, posterior part of the hinge with one or two elongate microcrenulated teeth. The juvenile hinge has two or three small teeth in anterior part and under the umbo and one or two long teeth in posterior part. Ligament probably opisthodetic. Anterior adductor muscle scar often very deeply impressed, with myophoric buttress. Posterior adductor muscle scar slightly ovate. Posterior pedal muscle scars developed anteriorly from the posterior adductor muscle scar, close to the hinge line. Outer surface sculpture consists of fine growth lines (Fig. 3I).

Remarks. – The type species *N. shergoldi* from the Lower Ordovician of Australia is very similar to *N. redoniaeformis* in the shape of the shell and hinge structure. *N. redoniaeformis* seems to be only more elongated.

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): Felines-Minervois, Vallée du Merlaux; (ii) La Maurerie Formation (Floian): Cessenon – Serre Malle Cessenon – Est du Col de la Maurerie, Prades sur Vernazobre – Roquebrun, Métairie du Notaire; (iii) Cluse de l'Orb Formation (Floian): Cessenon – Coulobres; (iv) Foulon Formation (Floian): Cessenon – NE de Lugne; (v) Landeyran Formation (Floian): Cessenon, Vallée de l'Orb, Sources de Foulon.

Cohort Uniomorphi Gray, 1854
Family Thoraliidae Morris, 1980

Genus *Thoralia* Morris, 1980

Type species. – *Thoralia languedociana* (Thoral, 1935) from the Tremadocian, Saint Chinian Formation, France.

Thoralia languedociana **(Thoral, 1935)**
Figure 4I, J, L, M

1935 *Leda languedociana*; Thoral, 1935, p. 164, pl. 13, figs 2, 3.
1979 *Leda languedociana* Thoral. – Morris, p. 403, fig. 15.
1980 *Thoralia languedociana* Thoral. – Morris, p. 270, figs 1–7.
1982 *Miquelana languedociana* Thoral. – Babin, pp. 43, 44, pl. 11, figs 1–7.

Holotype. – External mould of right valve, LPB 10721, figured *in* Babin (1982) in pl. 11, fig. 1; herein fig. 4L.

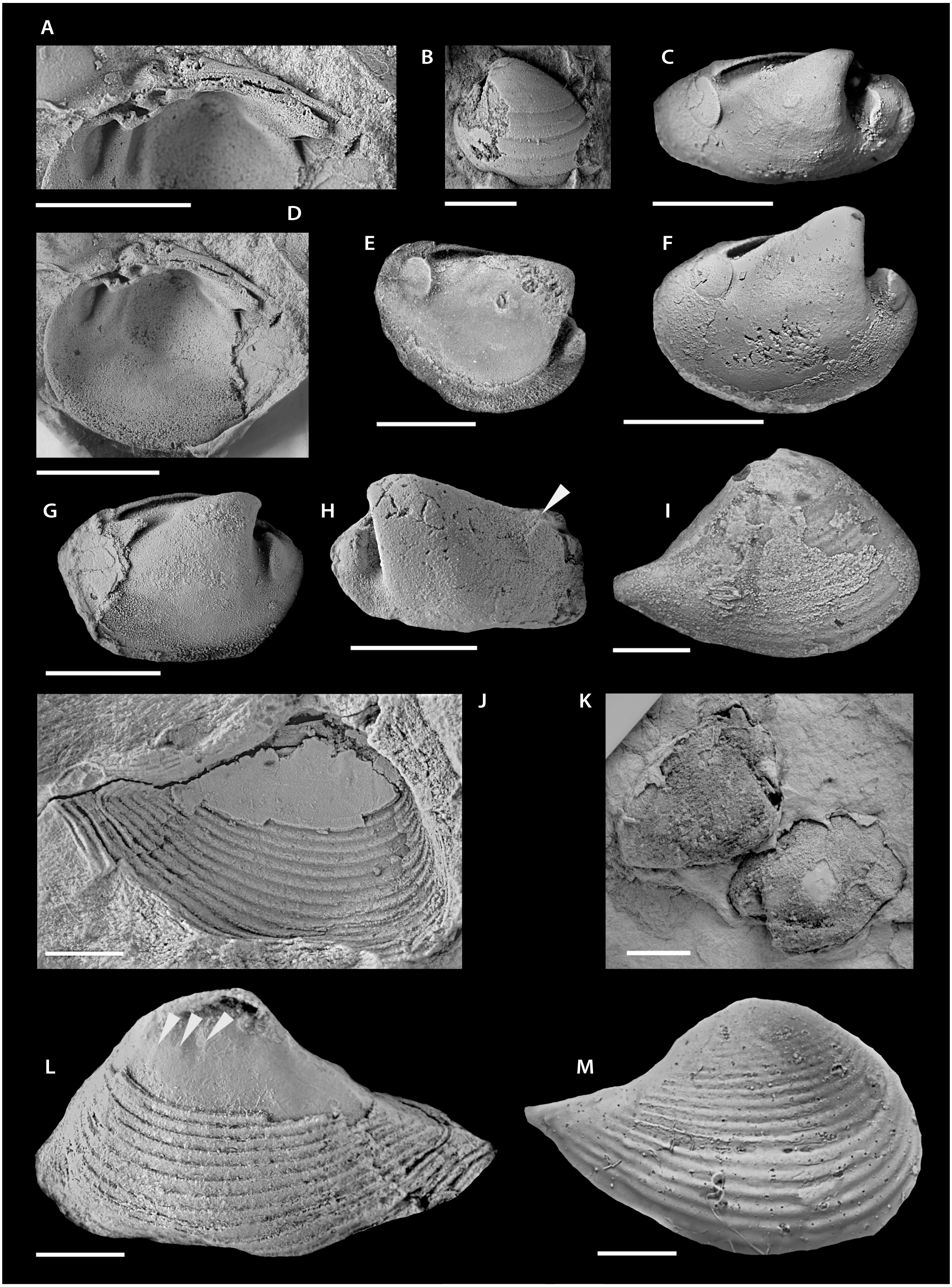
Paratype. – External mould of right valve, LPB 10720, figured *in* Babin (1982) in pl. 11, fig. 2.

Type horizon and locality. – Tremadocian, St. Chinian Formation. Bois da la Cabosse, north of Assignan, Montagne Noire, France.

Material. – Twenty-eight new specimens, measured specimens (FSL 713390, 713395, 713463, 713464, 713481, 713494, 713531, 713535 and other ill-preserved specimens).

Diagnosis. – Thoraliid with short and sharp rostrum, pronounced ornamentation of commarginal lines, and with four small teeth under the umbo.

Figure 4. A–H, K – *Redonia michelae* Babin, 1982, Early Ordovician, Montagne Noire, France. A, D, G – internal mould of a right valve, latex cast, detail of the hinge (A), latex cast lateral view (D), internal mould, lateral view, FSL 713380. B – external mould of the left valve, lateral view, FSL 740806. C, F – holotype, internal mould of the right valve with preserved adductor muscle scars and hinge, dorsolateral (C) and lateral views (F), LPB 9091a. E – internal mould of the right valve with preserved adductor muscle scars and posterior part of the hinge, lateral view, FSL 713511. H – internal mould of a left valve with preserved adductor muscle scars, arrow showing pedal muscle scar near the posterior adductor muscle scar, lateral view, FSL 713457. K – left and right valves of one individual, lateral view, CAB 34271. • I, J, L, M – *Thoralia languedociana* (Thoral, 1935), Early Ordovician, Montagne Noire, France. I – external mould of the right valve, lateral view, LPB 10720. J, L – negative and positive of one specimen, FSL 713395, external mould, lateral view (J), composite mould with accessory muscle scars marked by arrows and ornamentation (L). M – latex cast of the right valve, lateral view, LPB 10721. Scale bars A, B, C, D, E, F, G, H, J = 5 mm, I, J, L M = 2 mm.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Description. – Shell small (maximum length 13.2 mm), equivalve and slightly inequilateral with prominent rostrate posterior part. Posterior part slightly larger than anterior. Anterior part rounded. Ventral margin rounded anteriorly, becoming nearly straight posteriorly. Umbo almost central, blunt, opisthogyre. The carina is presented on both valves; corselet developed from the umbo to the posterior part of the shell. Hinge plate short; left valve probably with three small radiating teeth in the left valve and three sockets right valve with four small teeth (seen *in* Morris 1980, fig. 6). Anterior adductor muscle scar oval, posterior pedal muscle scar situated very close to dorsal margin. Accessory muscle scars well-developed, deeply impressed. Rounded anterior pedal protractor close to the anterior dorsal margin on the umbonal side of the anterior adductor (Morris 1980, fig. 7). The other five small rounded accessory muscle scars are situated between anterior and posterior adductor muscle scars. Posterior pedal retractor lies close to the dorsal margin on the umbonal side of the posterior adductor muscle scar. Outer surface sculpture consists of strong growth ribs (Fig. 4J, L, M).

Remarks. – Independently, Morris (1980) and Babin (1982) established new genera *Thoralia* and *Miquelana* for the same species previously identified as *Leda languedociana* (Thoral, 1935). Morris (1980) accommodates *Thoralia* in a new family Thoraliidae, characterised by small bivalves of nuculoid shape possessing four radiating subumbonal cardinal teeth. Typically, *Thoralia* specimens are preserved as external moulds, often exhibiting pronounced ornamentation (Babin 1982, pl. 11. figs 1, 3, 6; herein Fig. 4L, M). Nevertheless, internal features were previously known only from a single incomplete specimen (Morris 1980, figs 2, 6, 7). The specimen FSL 713395 (herein Fig. 4L) reveals both external and certain internal characters, including accessory muscle scars, part of the posterior adductor muscle scar and part of the hinge. These features align with those observed in the specimen described by Morris (1980).

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): Caunes Minervois – Villerembert, Caunes Minervois – Vallée de l'Ourdivieille, Felines-Minervois – Brama; (ii) La Maurerie Formation (Floian): Cessenon – Serre Malle; (iii) Landeyran Formation (Floian): Cabrière, Vallée du Llandeyran, pont Supérieur.

Cohort Cardiomorphi Férussac, 1822 *in* Férussac & Audebard (1822) (= Heterodonta)
Order Actinodontida Dechaseaux, 1952
Superfamily Anodontopsoidea Miller, 1889
Family Cycloconchidae Ulrich, 1894 *in* Ulrich & Scofield (1894)
Subfamily Cycloconchinae Ulrich, 1894 *in* Ulrich & Scofield (1894)

Genus *Redonia* Rouault, 1851

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

Redonia michelae Babin, 1982

Figure 4A–H, K

1981 *Redonia* sp. – Babin, p. 42, Fig. 1d–e.
1982 *Redonia michelae* Babin; Babin, p. 41, pl. 10, figs 1–6.
2016 *Redonia michelae* Thoral. – Polechová, fig. 2a–k.

Holotype. – Internal mould of the right valve, LPB 9091a, figured *in* Babin (1982) in pl. 10, fig. 1; herein Fig. 4C, F.

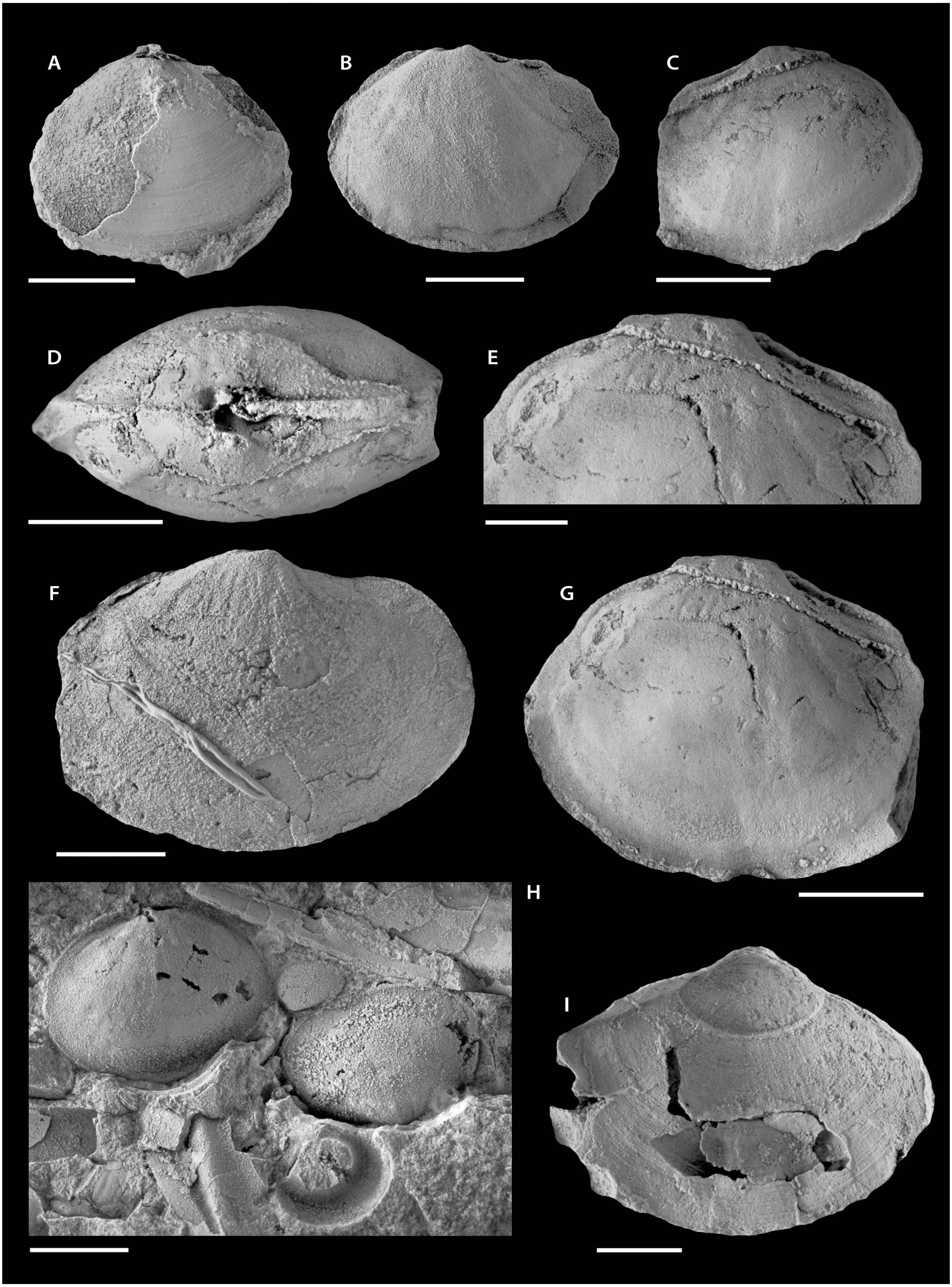
Paratypes. – Articulated specimen, LPB 10749, figured *in* Babin (1982) in pl. 10, fig. 6; internal mould of the left valve, LPB 9091c, figured *in* Babin (1982) in pl. 10, fig. 2; two internal moulds of left valves, LPB 10747, figured *in* Babin (1982) in pl. 10, figs 3, 4.

Type horizon and locality. – Tremadocian, St. Chinian Formation. St. Chinian, Montagne Noire, France.

Material. – Eighty-seven new specimens, (measured specimens FSL 713380, 713386, 713396, 713400, 713407, 713410, 713422, 713439, 713450, 713456, 713457, 713458a–c, 713460, 713461, 713486, 713488, 713499, 713501, 713502, 713505, 713506, 713508, 713510–13, 713532–34, 713551, 713561 and other ill-preserved specimens).

Diagnosis. – Small, rounded *Redonia* with a large myophoric septum in the anterior.

Figure 5. A–I – *Babinka prima* Barrande, 1881, Early Ordovician, Montagne Noire, France. A – internal mould of the right valve with the rest of the shell ornamentation, lateral view, FSL 713484. B – internal mould of the right valve, lateral view, FSL 713478. C, D, E, G – articulated specimen, right valve, lateral view (C), dorsal view (D), detail of the umbo region with accessory muscle scars and adductor muscle scars (E), left lateral view (G), FSL 740808. F – left lateral view on internal mould, FSL 713483a. H – internal moulds of the right and left valves, lateral views, FSL 713411. I – left lateral view on external mould, FSL 713483b. Scale bars = 5 mm, E = 2 mm.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Description. – Shell small (maximum length 13.2 mm), equivalve, inequilateral, the outline rather rounded, sometimes slightly elongated. Posterior part of the shell larger than the anterior part. Anterior and posterior margins rounded. Ventral margin convex. Umbos strongly developed, prosogyrate. Hinge actinodont, strong pseudocardinal chevron shaped tooth in the anterior part, two posterior pseudolateral teeth. Anterior adductor muscle scar narrow, but very deeply inserted with a myophoric buttress, posterior adductor muscle scar rounded. One posterior pedal muscle scar is developed antero-ventrally from the posterior adductor muscle scar. Inner surface sculpture is smooth, outer surface sculpture fine with commarginal lines.

Remarks. – *Redonia deshayesi* from the Middle Ordovician of Gondwana and peri-Gondwana margins has a smaller myophoric buttress; shell is more inequilateral, the umbo is more anterior placed, and ornamentation is more pronounced.

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): Assignan, Felines-Minervois, Les rocs de Sayrols; Saint Chinian; (ii) La Maurerie Formation (Floian): Roquebrun, l'Arboussié, Cessenon Martelle; (iii) Foulon Formation (Floian): localities Roquebrun, Vallée du Rieuberlou; (iv) Landeyran Formation (Floian): Cabrière, Vallée du Llandeyran, Saint Nazaire de Ladarez, Mas de Cayrol, pont Supérieur, Causses et Veyran, Cessenon, les Sources de Foulon.

Infrasubcohort Lucinidia Gray, 1854
Family Babinkidae Horný, 1960

Genus *Babinka* Barrande, 1881

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

Babinka prima Barrande, 1881
Figure 5

Synonymy *in* Polechová (2013).
2016 *Babinka prima* Barrande. – Polechová, fig. 5a–d, m.

Lectotype. – (SD by Růžička & Prantl in 1960, p. 48.) articulated specimen, figured *in* Barrande (1881) in pl. 266, as fig. 6.7–6.9.

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

Type horizon and locality. – Middle Ordovician, early and mid-Darriwilian, Šárka Formation. Osek, Prague Basin, Bohemia.

Material. – Sixty-two new specimens (measured specimens FSL 713382, 713384, 713387–89, 713411, 713438, 713473, 713475, 713478, 713479, 713482, 713483a, b, 713484, 713485, 713503, 713514, 713515, 713522, 713552 and other ill preserved specimens).

Description. – This species is well described and figured in many papers, *e.g.* McAlester (1965), Babin (1977) or Polechová (2013).

Remarks. – The species *Babinka prima* is widespread, having been described from numerous Gondwana and peri-Gondwana regions of the Early and Middle Ordovician age. *Babinka prima* is an easily recognizable species characteristic of this time interval. Sánchez (2008) described *B. notia* from the Early Ordovician of Argentina, distinguishing it from *B. prima* by its elongated posterior, more dorsal accessory muscle scars and ill-defined posterior adductor muscle scar. *Babinka oelandensis* Soot-Ryen, 1969 from the Darriwilian of Sweden differs slightly from *B. prima* in its overall shape and the more dorsal positioning of pedal muscle scars.

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): SSW de Cassagnoles, Trausses Minervois, Brama, Caunes Minervois, Plos de Sicard, Felines-Minervois – Vallée du Merlaux; (ii) La Maurerie Formation (Floian): Prades sur Vernazobre; Foulon Formation (Floian): Roquebrun – Vallée du Rieuberlou, Vallée du Llandeyran, l'Embouriel; (iii) Landeyran Formation (Floian): Vallée du Llandeyran, pont Supérieur, Cessenon, Vallée de l'Orb, Sources de Foulon. France – Armorican Massif (Dapingian–Darriwilian).

Figure 6. A – *Modiolodon* sp., Early Ordovician, Montagne Noire, France. A – internal mould of the left valve, (1) anterior teeth, (2) pedal muscle scar, lateral view, LPB 10758. • C–M – *Coxiconchia guiraudi* Babin, 1982, Early Ordovician, Montagne Noire, France. B – internal mould of a left valve, lateral view, FSL 713430. C, L – external mould with ornamentation (C) and internal mould of a right valve with preserved muscle scars (L), lateral views, FSL 713498. D – internal mould of a left valve, lateral view, accessory muscle scars marked by arrows, FSL 713382. E, F, G – articulated specimen, hinge, dorsal view (E), internal mould of a right valve (F), internal mould of a left valve, lateral view (G), FSL 740814. H, I, K, M – detail of the hinge on the right valve, accessory muscle scars marked by arrows (H), right lateral view (I), detail of the hinge on the latex cast of the right valve, cardinal teeth is marked by arrow (K), latex cast of the right valve (M), FSL 740813. J – holotype, internal mould of a right valve, lateral view, LPB 9092. Scale bar = 5 mm.


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Bohemia – Prague Basin (Floian, early and mid-Darriwilian). Spain – Cantabrian Zone, West Asturian-Leonense Zone, Iberian Cordillera, Central Iberian Zone, Ossa Morena Zone (Darriwilian). Wales – Carmarthenshire (Darriwilian). England – Shelve Inlier (Darriwilian). Morocco – Anti-Atlas (Floian, Dapingian, Darriwilian).

Family Coxiconchiidae Babin, 1977

Genus *Coxiconchia* Babin, 1966

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

Coxiconchia guiraudi (Thoral, 1935)
Figure 6B–M

1935 *Sanguinolites*? *guiraudi* Thoral; Thoral, p. 174, pl. 13, fig. 6.
1977 *Coxiconcha guiraudi* (Thoral). – Babin, p. 60, pl. 3, fig. 5.
1977 *Coxiconcha guiraudi* (Rouault). – Babin, pl. 3, figs 3, 4.
2016 *Coxiconchia guiraudi* (Thoral). – Polechová, fig. 5e–i, n.

Neotype. – Internal mould of the right valve, LPB 9092, figured *in* Babin (1982) in pl. 11, fig. 10; herein Fig. 6J.

Paratype. – Internal mould of the right valve, LPB10760, figured *in* Babin (1982) in pl. 11, fig. 11.

Type horizon and locality. – Floian, La Maurerie Formation. Southwest de la Croix de Roquebrun (vallée de Landeyran), Montagne Noire, France.

Material. – Fifty-five new specimens, (measured specimens FSL 713382, 713383, 713397, 713415, 713421, 713430, 713440, 713451, 713495–98, 713500, 713548–50, 713556 and other ill-preserved specimens).

Diagnosis. – *Coxiconchia* with a small shell and with accessory muscle scars under the umbo in a more dorsal position.

Description. – Shell small (maximum length 25 mm), equivalve, inequilateral, slightly ovate and posteriorly elongated, with cardinal line straight, sometimes slightly inclined to the posterior. Anterior margin convex to rather straight. Posterior part more variable, rounded or narrowed, sometimes shortened. Umbones not pronounced, in anterior position, prosogyrate. Hinge line straight, in some specimens forming small posterior wing (Fig. 6K). The hinge is heterodont; right valve with a distinct tooth (Fig. 6K). Muscle system very complex (see Babin 1977, fig. 3a, b). Anterior adductor muscle scar rounded, posterior muscle scar elongated along the cardinal line. Anterior pedal retractor and protractor are deeply impressed (usually joined together) and situated closed to the hinge line, postero-dorsally from the anterior adductor. Antero-dorsally from the posterior adductor are two pedal retractors, closer to the posterior adductor is the smaller one. The larger one is near the cardinal line and elongated. Between adductors in umbo region are developed four small, broadly elliptic to subcircular accessory muscle scars, which are more deeply impressed in posterior part of the valve. Ligament opisthodetic (Kříž 1999). Inner surface sculpture smooth. Outer surface sculpture with fine comarginal lines.

Remarks. – *Coxiconchia britannica* from the Middle Ordovician of Bohemia and France differs from *C. guiraudi* (Thoral, 1935) primarily in its larger size. Other features present some ambiguity, and Babin (1982) admitted considerable difficulty in differentiating these two species. *Coxiconchia sellaensis* Sánchez & Babin, 2005 found in the Floian of Bolivia and Argentina possesses a well-developed subumbonal carina and posteroventral slope. Furthermore, specimens of *C. sellaensis* from Argentina exhibit radial sculpture. *Coxiconchia babini* Sánchez, 2005 from the Tremadocian of Argentina, is characterized by a smaller shell and fewer accessory subumbonal muscles as well as an ill-defined posterior adductor muscle scar.

Occurrence. – France, Montagne Noire – (i) St. Chinian Formation (late Tremadocian): Felines-Minervois, Vallée du Merlaux; (ii) La Maurerie Formation (Floian): Cessenon Serre Mal, Prades sur Vernazobre; (iii) Cluse de l'Orb Formation (Floian): Cessenon Est de Lugné; (iv) Foulon Formation (Floian): Roquebrun – l'Escougoussou, Roquebrun – Vallée du Rieuberlou, Cessenon – versant-est du Pech de Lugne; (v) Landeyran Formation (Floian): Cabrière, Vallée du Llandeyran, pont Supérieur.

Infraclass Pteriomorphia Beurlen, 1944
Cohort Mytilomorphi Férussac, 1822 *in* Férussac & d'Audebard (1822)
Order Mytilida Férussac, 1822 *in* Férussac & d'Audebard (1822)
Superfamily Modiolopsoidea Fischer, 1886
Family Modiolopsidae Fischer, 1886

Genus *Modiolodon* Ulrich, 1894

Type species. – *Modiolodon oviformis* (Ulrich, 1890) by original designation, from the Middle Ordovician of U.S., Trenton of Kentucky.

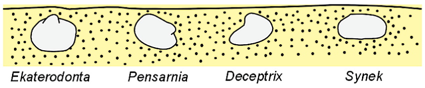
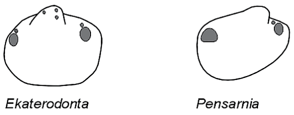
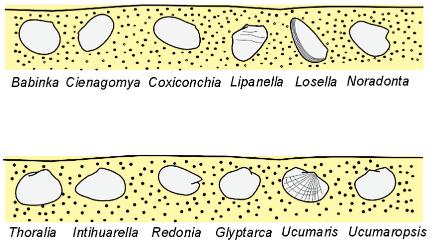
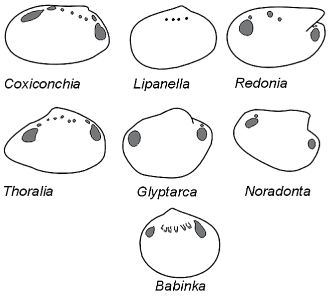
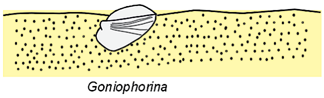
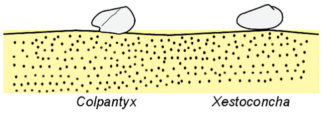
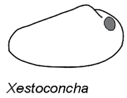
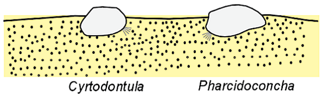
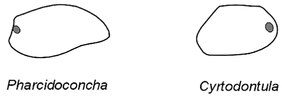
Mode of life	Genera and Hinge		Life position	Muscle system
Infaunal deposit feeders	*Ekaterodonta* *Deceptrix*? *Synek* *Pensarnia*	heterotaxodont taxodont taxodont taxodont		
Infaunal filter feeders	*Babinka* *Cienagomya* *Coxiconchia* *Glyptarca* *Intihuarella* *Lipanella* *Losella* *Noradonta* *Redonia* *Thoralia* *Ucumaris* *Ucumaropsis*	heterodont actinodont heterodont actinodont lateral tooth edentulous edentulous heterodont actinodont actinodont edentulous edentulous		
Semi-infaunal filter feeders	*Goniophorina*	edentulous		
Epifaunal filter feeders	*Colpantyx* *Xestoconcha*	one blunt tooth one blunt tooth		
Byssate semi-infaunal filter feeders	*Cyrtodontula* *Pharcidoconcha*	one long tooth in posterior one long tooth in posterior		

Figure 7. Mode of life, muscle scars and hinge in the Tremadocian bivalves.

***Modiolodon* sp.**
Figure 6A

1982 *Modiolopsis* sp. – Babin, p. 42, pl. 10, figs 14, 15.

Material. – One specimen (from old collection, LPB 10758).

Description. – Shell small in size (maximal length 18.5 mm), elongated, equivalve, strongly inequilateral. Shell inflated with umbo slightly projected above hinge line. Posterior part larger than anterior part. Anterior part is slightly lobate, rounded. Antero-dorsal margin slightly convex and ventral margin straight or slightly convex. Postero-dorsal margin straight. In anterior part of the shell probably two teeth. Ligament probably opisthodetic. Anterior adductor muscle scar deeply impressed, closed to the anterior margin and joined with elongated pedal muscle scar. Inner surface sculpture smooth.

Remarks. – According to Cope (1999), in all attributes except dentition, *Modiolodon* is very close to *Modiolopsis* Hall, 1847. *Modiolodon* shows one or two cardinal teeth in anterior part of the hinge, while *Modiolopsis* is edentulous. *Modiolopsis* is extensively documented globally from Middle to Late Ordovician strata, with numerous references supporting its widespread occurrence (*e.g.* Babin 1966, Pojeta 1971, Babin & Gutiérrez-Marco 1991 and Cope 1996). From North America alone more than 150 species of *Modiolopsis* are known (Pojeta 1971), showing clearly that this genus is overused and requires revision. In contrast, *Modiolodon* has been so far reported from North America and Wales, encompassing approximately ten species (Pojeta 1971, Cope 1999). The single specimen from Montagne Noire was described *in* Babin (1982), however, new collection revealed no new specimens. The dental characteristic supports a more appropriate assignment of the specimen to the genus *Modiolodon*.

Occurrence. – France, Montagne Noire – Foulon Formation (Floian): SW de la Croix de Roquebrun.

Global comparison of contemporary bivalve associations

Early Ordovician bivalve associations providing sufficient information for deeper analysis are known from Argentina (overview *in* Sánchez 2008), Australia (Pojeta & Gilbert Tomlinson 1977), France (Babin 1982), Morocco (Babin & Destombes 1990, Polechová 2016), and Wales (Cope 1996). The bivalve association from the Montagne Noire exhibits a composition very similar to those of comparable age and latitude in Morocco (Polechová 2016). The Moroccan bivalve association of Floian age, includes similar taxa such as *Babinka prima*, *Coxiconchia guiraudi*, *Ekaterodonta courtessolei*, and *Redonia michelae*. Numerical and ranked abundance reveals that both Morrocan and French bivalve associations are dominated by *Redonia michelae* and *Babinka prima* (herein Tab. 1; *in* Polechová 2016, tab.1). Heteroconchs prevail in both associations, but protobranchs are also well-represented, although more abundant in Montagne Noire (Polechová 2016, Fig. 4). Pteriomorphs are rare, with one doubtful *Modiolodon* specimen in the revised Montagne Noire assemblage and only one *Glyptarca* specimen in Morocco. The bivalve fauna of similar age and mid-palaeolatitudes in Argentina from Northwestern Basin (Tremadocian, Floian) and Famatina Basin (Floian) also shows some similar elements such as *Babinka*, *Coxixonchia*, and *Redonia*. In contrast, the Floian bivalve fauna of lower latitude from Wales is different, with a prevalence of pteriomorphs and no taxa in common with the Montagne Noire fauna. The dominance of heteroconchs is a characteristic compositional pattern for Ordovician high-latitude bivalve faunas. Cope (2002) demonstrated a latitudinal control on bivalve fauna composition, noting that high-latitude faunas are characterized by a dominance of heteroconchs and a lack of pteriomorphs, while low-latitude faunas typically exhibit abundant pteriomorphs. However, Sánchez (2008) comparison of Early Ordovician bivalve faunas from Argentina (Famatina Basin and NW Argentina), despite their similar latitude, revealed compositional differences likely due to contrasting tectono-sedimentary settings. Similarly, Cope & Kříž (2013) suggested that the differing bivalve faunas of the Montagne Noire and Wales could be attributed not only to latitudinal variations but also to differences in water depth.

Palaeoecology of the Cambrian and Tremadocian bivalves

Cambrian bivalves

Currently, only five genera from the Cambrian are generally accepted as bivalves, specifically *Fordilla* Barrande, 1881, *Pojetaia* Jell, 1980, *Tuarangia* MacKinnon, 1982, *Camya* Hinz-Schallreuter, 1995, and *Arhouriella* Geyer & Streng, 1998. However, only *Fordilla* and *Pojetaia* are described in detail, and their bivalve affinities are undisputed. All Cambrian bivalves are of very small size, measuring one or two milimetres. Many authors (*e.g.* Runnegar & Bentley 1983; Jermak 1986, 1988; Pojeta *et al.* 1976) suggest the infaunal way of life based primarily on the laterally compressed shell, articulated preservation, well developed anterior region with pronounced adductor muscle scar. Runnegar & Bentley (1983) remarked that *Pojetaia* from Australia is not bored by endolithic algae, however the monoplacophorans and other groups are affected in that way and these authors see that also as a support for infaunal

Table 1. Numerical and ranked abundance of bivalves, based on the collections of bivalves from the Montagne Noire, Lower Ordovician (Tremadocian, Floian). Legend: RV and LV – right and left valves (disarticulated specimens); A – shells with conjoined valves (articulated specimens); RA – percentage relative abundance; AA – percentage relative abundance of shells with conjoined valves; R – ranked abundance.

Species	Life habits	RV + LV	A	RA	AA	R
Redonia michelae	infaunal	87	8	21.0	15.5	1
Babinka prima	infaunal	57	21	20.2	42.4	2
Ekaterodonta courtessolei	infaunal	62	15	18.8	32.6	3
Coxiconchia guiraudi	infaunal	33	22	15.7	57.1	4
Noradonta redoniaeformis	infaunal	29	17	12.9	53.9	5
Thoralia languedociana	infaunal	17	8	6.7	48.5	6
Synek thorali	infaunal	7	7	4.3	66.7	7
Modiolodon sp.	semi-infaunal	2	0	0.4	0	8
Totals		294	98	100%	40%	

way of life. Conversely, other authors (Tevesz & McCall 1976, 1985; Vogel & Gutman 1980; Fang 2006; Elicki & Gürsu 2009; Fang & Sánchez 2012) proposed a suspension-feeding, epifaunal crawling mode of life, primarily on carbonate ramps. They interpreted these animals as surface-dwellers, epifaunal and/or interstitial crawlers, moving and feeding within the top few millimetres of microbial mats, utilizing ciliary currents on a ventrally emergent foot to gather food while crawling on firm substrates. The epifaunal way of life is supported by ontogenetic studies, when the early settled spat typically possesses flattened foot and exhibit a predominantly anterior feeding and respiratory current. This current system is arguably the most efficient for epibenthic creeping habits on firm substrates, and has therefore been considered plesiomorphic for both protobranchs and autobranchs (Yonge 1939; Allen 1978, 1985). Such a current is observed in all bivalves for at least during brief period of early post-metamorphic development (Stasek 1963, Allen 1985, Reid *et al.* 1992, Waller 1998), and likely also existed in Cambrian archetype bivalves (Fang 2006). Moreover, burrowing demands significant shell and foot movement. The foot must be a highly extensible, muscular, hydraulic organ. Modern bivalves tend to burrow in a standard, well-programmed manner described precisely by Trueman (1966). Burrowing into soft substrates involves repeated adduction and opening of the valves, combined with forward and backward rotational movements, and integrated with protraction and retraction of the foot. This complex process requires sophisticated coordination of the muscular system (Trueman 1966; Stanley 1970, 1975; Pojeta 1987). It is highly probable that the adaptive threshold for infaunal life was not crossed until the Ordovician (Fang 2006).

Tremadocian bivalves

Tremadocian bivalves differ markedly from the Cambrian ones, notably in size (increasing from 1–2 mm to 3 cm). However, preservation remains a limiting factor for Tremadocian bivalves, an actualistic aproach allow us to evaluate their modes of life. Burrowing was essential to the evolution of Tremadocian bivalves (see above). Another adaptive breakthrough is evolutionary transitions from burrowing to epifaunal byssal attachment, which have been important in early adaptive diversification of Bivalvia (Yonge 1957, 1962; Stanley 1972). Among living molluscs, the byssus is unique to Bivalvia, present in larvae and, through neoteny, persisting in adults. Stanley (1972) proposed that endobyssate forms were more primitive than epibyssate forms, suggesting that early endobyssate types evolved from free-burrowing Ordovician taxa. However, the Ordovician fossil record of bivalves presents challenges, as it seems that burrowing and epifaunal bivalves appear contemporaneously. This is likely due to a fossil gap in the late Cambrian and early Ordovician. A bivalve fossil gap exists in the upper Cambrian with *Pojetaia* from the Miaolingian of Siberia being the sole record (Gubanov *et al.* 2004), and no bivalves recorded from the Furongian. This gap extends into the early Tremadocian, with only *Goniophorina*, *Losella*, and *Palaeoneilo*? reported from Argentina (Harrington 1938, Sánchez 2008). *Goniophorina* is considered as a semi-infaunal filter feeder, *Losella* as an infaunal filter feeder, and *Palaeoneilo* as an infaunal deposit feeder. The fossil record from the Late Tremadocian is more diverse, with a wider range of ecological strategies recognized across different genera (Fig.7). The type of hinge, muscular systems and life habits are described in Figs 7, 8. In general, hinge types have been a conservative feature in bivalve evolution, and therefore it is more useful in taxonomy than in functional morphology. The taxodont hinge is found across groups with diverse life habits. Conversely, the heterodont hinge is largely restricted to burrowing species, particularly shallow burrowers, where it may facilitate rapid valve movements because of its low friction mechanism. The muscular system in Ordovician early bivalves is very complex. The presence of accessory muscle scars, such as those for protractors, retractors, dorsomedian, ventromedian, and visceral muscles, indirectly suggests a highly efficient foot. Polechová (2016) described two notable complex muscular systems, also observed in Tremadocian bivalves. The presence of myophoric buttress appears significant for effective burrowing, aiding in the support of visceral sac. This buttress is quite prominent in *Redonia*, a common genus among Early and Middle Ordovician bivalves, often dominating assemblages in regions of France, Morocco, and Bohemia. Life habits of Tremadocian bivalves include:

1) Infaunal deposit feeders representing by *Ekaterodonta*, *Synek*, and tentatively *Deceptrix*? (from Australia). *Deceptrix* was wrongly used by Pojeta and is essentially a Silurian–Devonian genus. Many of the Ordovician forms is better assigned to *Homilodonta* or *Praenucula* (Cope, 1997). Tremadocian *Synek* and *Deceptrix*? are known from a few poorly preserved specimens, mainly preserving only the shape of the shell. Their palaeoecology is interpreted from stratigraphically younger Middle and Upper Ordovician specimens. Tremadocian *Synek* and *Deceptrix*? (rather *Praenucula*) does not show any muscle scars, however Middle Ordovician *Praenucula* shows muscle scars in the umbonal region with similar pattern as *Ekaterodonta*. *Synek* from the Middle and Late Ordovician shows only badly preserved rounded and almost equal-sized adductor muscle scars. In contrast, *Ekaterodonta* (Protobranchs) is only known from the Early Ordovician. It shows very complex muscular system (adductor muscle

scars, protractor, retractor and muscle scars in umbo region), which had to manage an efficient foot. This genus displays a series of muscle scars in the umbonal region, which have triangular pattern. They can be interpreted as median and visceral muscle scars (*e.g.* Polechová 2016). The heterotaxodont hinge of *Ekaterodonta* resembles the actinodont hinge with one long branch of a chevron-shaped tooth. According to Stanley (1970) and his studies about functional morphology, all these genera show perfect adaptation for burrowing. The beaks of most burrowing clams are directed forward, so they are prosogyrous. According to Stanley (1975), the typical prosogyre shape of the clams is an adaptation to increase the burrowing efficiency.

2) Infaunal filter feeders include *Cienagomya*, *Intihuarella*, *Lipanella*, *Losella*, *Ucumaris*, *Ucumaropsis*, *Eoredonia* (Argentina), *Babinka* (Argentina, Montagne Noire), *Coxiconchia* (Argentina, Montagne Noire), *Noradonta* (Montagne Noire), *Redonia* (Montagne Noire), and *Thoralia* (Montagne Noire). These genera show variability in the muscle system, surface sculpture, and hinge. The robust muscle system is well known in *Babinka*, *Coxiconchia*, *Lipanella*, *Redonia*, and *Noradonta*. The muscle scars close to the adductors are probably retractors and protractors. *Babinka*, *Coxicochia*, *Lipanella*, *Redonia*, and *Thoralia* also show the line of small rounded muscle scars between adductors, probably serving to hold the visceral sac and also help to control the movement of the foot (McAlester 1965, Babin 1977, Polechová 2016). This muscle pattern differs from *Ekaterodonta* and *Praenucula*, and it is possible that it reflects a different arrangement inside the shell because of the different type of gills (Polechová 2016). *Thoralia* was considered an infaunal deposit feeder by Morris (1980), primarily based on the anterior shape of the shell. In modern bivalves, deposit feeding is rare and mainly found in protobranchs. The muscular pattern of *Thoralia* is more similar to infaunal filter feeders. The presence of numerous visceral muscles often preserved between adductors for holding the visceral sac and moving the foot seems to be characteristic for the Early Ordovician heteroconchs, considered as filter feeders (Polechová 2016). *Thoralia* is also specific in outer surface sculpture, consisting of very pronounced comarginal lines and in rostrate posterior end. A rostrate posterior is common in burrowing bivalves and seems generally to have evolved to reduce scour (Stanley 1975). However, recognizing filter feeders or deposit feeders in the Ordovician bivalves is difficult, herein is *Thoralia* considered rather an infaunal filter feeder. *Babinka*, *Coxiconchia*, *Noradonta*, *Redonia* and *Thoralia* possess a heterodont hinge, on the other hand *Lipanella*, *Losella*, *Ucumaropsis*, and *Ucumaris* are edentulous.

3) Semi-infaunal filter feeders are represented only by *Goniophorina* (Argentina, China). Its interpreted mode of life relies on the shell outline, specifically its anterior and posterior slopes. This morphology also suggests a lack of byssal attachment. Notably, the muscle system of *Goniophorina* remains unknown, and it possesses an edentulous hinge.

4) Epifaunal suspension feeders include *Colpantyx* and *Xestoconcha* (Australia). Our understanding of their muscle systems is limited; only *Xestoconcha* shows an anterior adductor muscle scar. They share a hinge characterized by a single blunt tooth. As Pteriomorphia, they are inferred to have been epifaunal, but whether they employed a byssus for attachment or rested freely on the seafloor is difficult to determine.

5) Semi-infaunal byssate filter feeders include *Cyrtodontula* (Australia) and *Pharcidoconcha* (China). This interpretation is supported by their shell outlines, which are very similar to those of extant byssate bivalves. Both genera show a small anterior adductor muscle scar and a long posterior tooth.

Palaeogeography of Cambrian and Tremadocian bivalves

The Tremadocian is a key interval in geological history, marking the transition between the Cambrian and the Palaeozoic evolutionary faunas (*e.g.* Saleh *et al.* 2022). Identification of Cambrian bivalves, typically only a few millimetres in size, is often challenging due to preservation limitations. Nevertheless, Cambrian bivalves, comprising 17 genera and nearly 30 species, have been recorded globally. However, many of these genera have been subsequently reassigned to other fossil groups such as brachiopods, bivalved arthropods, or stenotocoids (*e.g.* Havlíček & Kříž 1978, Pojeta 2000). Elicki & Gürsu (2009) suggest that only five genera *Fordilla*, *Pojetaia*, *Arhouriella*, *Camya* and *Tuarangia* are likely valid, but with some remaining uncertainty regarding *Arhouriella* and *Camya*. Furthermore, Peel (2021) classified *Tuarangia* close to Rostroconchia. In conclusion, *Fordilla* and *Pojetaia* are well-documented with preserved internal features and are considered as truly bivalves. During the Cambrian, these two genera were cosmopolitan, occurring across Laurentia, Baltica, and Gondwana (Fig. 9). *Fordilla* is known from New York, Quebec, Newfounland, Greenland, Labrador (Laurentia), Bornholm (Baltica), Germany (western Gondwana), Siberia, and Turkey. *Pojetaia* is known from Australia, Turkey (East Gondwana), Germany, Morocco (West Gondwana), Bornholm (Baltica), Greenland, Mongolia, North China, and Siberia. However, the systematic position of *Tuarangia*, *Camya* and *Arhouriella* is still uncertain, we preferred to show their distribution as well (Fig. 9). *Tuarangia* is known from New Zealand (East Gondwana),

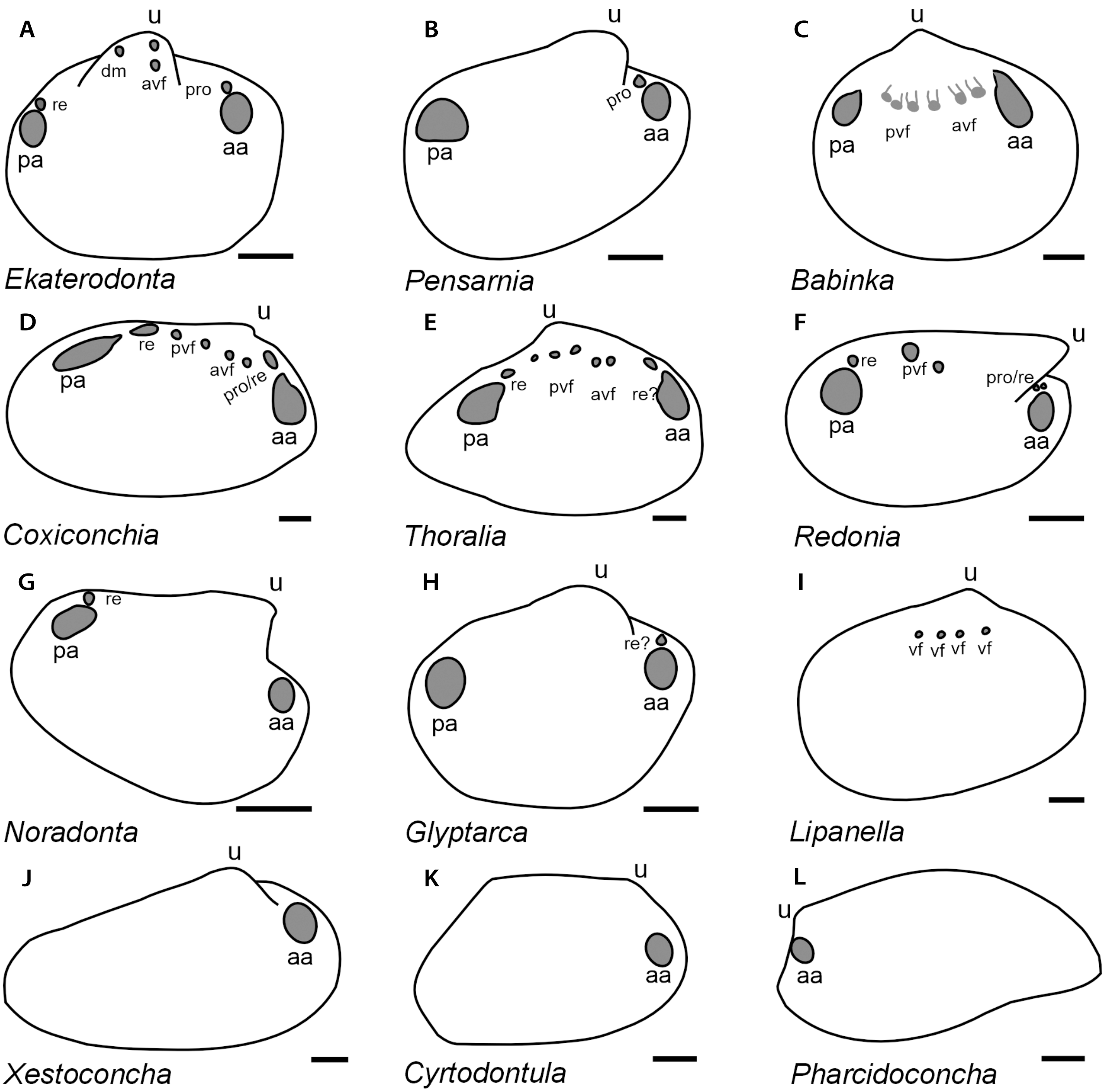


Figure 8. Tremadocian bivalves with preserved muscle scars. Partly published in Polechová (2016; Fig. 3, infaunal deposit feeders and infaunal filter feeders). A–B – infaunal deposit feeders. C–I – infaunal filter feeders. J – epifaunal filter feeders. K–L – byssate semi-infaunal filter feeders. Abbreviations: aa – anterior adductor muscle scar, avf – anterior visceral floor muscle scar, dm – dorsomedian muscle scar, pa – posterior adductor muscle scar, pro – protractor muscle scar, pvf – posterior visceral floor muscle scar, re – retractor muscle scar, vf – visceral floor muscle scar, vm – ventromedian muscle scar, u – umbo. Scale bar = 2mm.

Bornholm (Baltica), and Poland. *Camya* is known only from Bornholm (Baltica) and *Arhouriella* from Morocco (West Gondwana). All these occurrences are of early and middle Cambrian, Furongian bivalves are missing. Cambrian bivalves are mostly found in shallow carbonate platforms with a low rate of sedimentation, supporting the theory about epifaunal mode of life. Notably, they are no known Ordovician survivors of Cambrian bivalve genera, suggesting that bivalves were affected by the Cambrian extinction event with a new set of genera appearing in the Ordovician (Fang 2006). In contrast to the cosmopolitan distribution of Cambrian bivalves, Tremadocian bivalves, with twenty-one genera, were largely restricted to Gondwana and peri-Gondwanan margins (Argentina, Morocco, France, Australia, North China, Fig. 9), suggesting survival of a biotic crisis in one or more Gondwanan refugia. Most Tremadocian genera were endemic, with only *Pharcidoconcha*, *Coxiconchia*, and *Babinka* having a wider distribution. These bivalves are typically preserved in siliciclastic

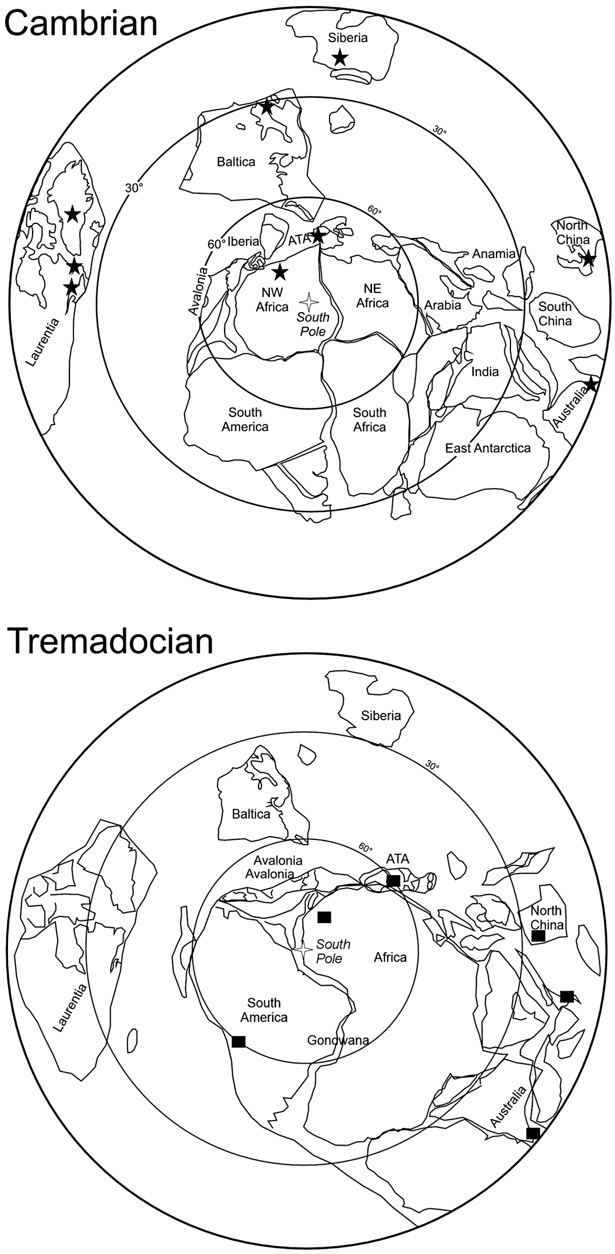


Figure 9. The palaeogeographic maps showing the distribution of bivalves during the Cambrian and Tremadocian.

sediments and are considered as burrowing taxa. The limited geographic dispersal of Tremadocian bivalves likely reflects a prevalence of stenotopic forms lacking planktotrophic larvae (Sánchez & Babin 2003). Specifically, *Pharcidoconcha* is found in Australia and North China, while *Babinka* and *Coxiconchia* occur in Argentina and Montagne Noire. *Pharcidoconcha* is limited to Tremadocian, whereas *Babinka* and *Coxiconchia* dispersed more widely during the Floian (Armorica, Perunica, Iberia, Morocco), and Darriwilian (Baltica and Laurentia). The earliest representatives of *Babinka* and *Coxiconchia* are known from Montagne Noire, Saint Chinian Formation (late Tremadocian, trilobite zone *Euloma filacovi*, graptolite zone?) and from the Northwestern Basin of Argentina (late Tremadocian, *Notopeltis orthometopa* trilobite zone, *Paltodus proetus* and *Acodus deltatus* conodont zones). Three radiation centres (Montagne Noire in France, Australia and Argentina) were recognized during the Tremadocian (Fang 2006, Polechová 2016). Faunal exchange occurred at least between France and Argentina during the Tremadocian, although significant bivalve fauna migration was limited until the definite establishment of the western Gondwana corridor in the Floian (Sánchez & Astini 2011, Polechová 2016).

Conclusions

(1) The Early Ordovician bivalve assemblage from the Montagne Noire is diverse, encompassing eight genera: *Babinka prima* Barrande, 1881; *Coxiconchia guiraudi* Babin, 1982; *Ekaterodonta courtessolei* Babin, 1982; *Noradonta redoniaeformis* (Thoral, 1935); *Redonia michelae* Babin, 1982; *Modiolodon* sp.; *Synek thorali* Babin, 1982 and *Thoralia languedociana* (Thoral, 1935). *Redonia* and *Babinka* are dominant elements of this association.

(2) The Early Ordovician bivalve fauna in the Montagne Noire is dominated by heteroconchs and protobranchs, a composition typical of higher latitudes. This pattern is similar to bivalve faunas found in Morocco, suggesting significant faunal exchange between the two regions.

(3) Although bivalve faunal exchange was restricted during the Tremadocian and bivalves were limited to Gondwana or peri-Gondwana margins, some taxa could migrate over long distances, such as *Babinka*, *Coxiconchia* and *Redonia*, which are found in Argentina and France or *Pharcidoconcha*, present in Australia and North China.

(4) The Tremadocian was a time of varied ecological strategies in bivalves. These included infaunal deposit and filter feeding, semi-infaunal filter feeding, epifanul filter feeding and byssate semi-infaunal filter feeding. Notably, the development of burrowing representing a major adaptive advance that necessitated a complex muscular system for foot control.

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