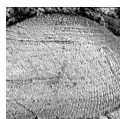


# On the early evolution of parallelodontid Arcoidea (Bivalvia)

MICHAEL R.W. AMLER & JULIA C. FRIEDEL



The Parallelodontidae is one of six families within the arcoid Bivalvia that are considered to have a temporal range extending from the Ordovician to the Recent. Nevertheless, its origin and early diversification remain poorly understood, despite over 150 years of research. We reviewed the Devonian and pre-Devonian taxa attributed to the Parallelodontidae with respect to parallelodontid morphology in the strict sense, particularly shell outline and hinge characteristics. Out of some fifty species, only a few match the typical parallelodontid morphology. Most of them can only vaguely be attributed to the Parallelodontidae, as poor preservation can obscure diagnostic features, causing potential confusion with coeval genera of the Heterodonta and Protobranchia with comparable external morphology. All Ordovician and Silurian taxa previously attributed to *Parallelodon* or presumed to possess parallelodontid characteristics turned out to be misclassified. *Parallelodon mandelensis* from the upper Emsian shallow marine Rhenotypic (Rhenish) Facies of Germany undoubtedly has a parallelodontid hinge and appears to be the earliest member of the family. In the Middle Devonian, primarily in the shelf region deposits of the Rheic Ocean in Central Europe and eastern North America, a first, minor radiation occurred. With the transition from the Devonian to the Carboniferous, a second, more pronounced radiation of parallelodontids led to significantly higher parallelodontid diversity. • Key words: Parallelodontidae, *Parallelodon*, evolution, radiation, Devonian, Rhenotypic Facies, Hercynotypic Facies.

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The Arcida Gray, 1854 are one of eight orders in the bivalve subclass Pteriomorpha (Carter *et al.* 2011), and an example of outstanding evolutionary adaptation. Originating in the Early Ordovician, the Arcida have a continuous and comprehensive fossil record and occur with a global diversity of approximately 600 species in eleven families today (MolluscaBase 2025). However, the fossil, particularly Palaeozoic Arcida, remain relatively unexplored by taxonomists (Oliver & Holmes 2006).

Currently, three or four superfamilies, respectively, are considered valid in the Arcida (Bieler *et al.* 2010, 2014; Carter *et al.* 2011; Combosch & Giribet 2016). Of these, the Glyptarcoidea Cope, 1996 (Cope 1996b) are confined to the Ordovician, while the Limopsoidea Dall, 1895 (and Philobryoidea Bernard, 1897, if separated) are restricted to the Mesozoic and Cenozoic (Amler 1999, Carter *et al.* 2011, also see Nevesskaja 2009 and Combosch & Giribet 2016 for alternative views). Only the Arcoidea Lamarck, 1809, which are composed of six families (Bieler *et al.* 2010, Carter *et al.* 2011), persisted from

the Ordovician to the Recent, but even in Mesozoic to Recent families, relationships are not yet resolved (Oliver & Holmes 2006). Hitherto, all Palaeozoic species are grouped within the families Catamarcaidae Cope, 2000, Frejidae Ratter & Cope, 1998, and Parallelodontidae Dall, 1898. However, the origin of the clades is still matter of debate due to differing opinions about hinge-ligament evolution (*e.g.* Sánchez 1995, Ratter & Cope 1998, Cope 2000, Combosch & Giribet 2016). The Parallelodontidae are believed to form the root of all younger arcoid families, and, therefore, a link between late Palaeozoic and Mesozoic taxa.

The terse diagnosis of the Parallelodontidae given in the Treatise on Invertebrate Paleontology (Newell 1969) was never adequately revised and expanded, save for the discussion of characters by Amler (1987, 1989) and a cursory treatment by Astafieva-Urbajtis (1994). Knight & Morris (2019), however, studied Lower Jurassic arcoids in some detail, but did not affect genus- and family-level taxonomy. As a result, Parallelodontidae, in its present

composition, and the name-giving genus *Parallelodon* Meek & Worthen, 1866 in particular, are thought to conceal a major part of the phylogeny of Palaeozoic and Mesozoic Arcoidea. Until the systematic revision of the species attributed to *Parallelodon* is completed, we retain the use of this generic name here.

Beyond the focus of the present contribution is the fact that, to date, the ‘dustbin taxon’ *Parallelodon* is still the preferred generic attribute for Devonian to Triassic ark shells. Originally and subsequently, a plethora of Palaeozoic and Mesozoic species was transferred to or newly described in *Parallelodon* (e.g. Meek & Worthen 1866, De Koninck 1885, Hind 1897), although several authors preferred to use older, preoccupied, misspelt, or invalid genera, such as *Arca*, *Bysoarca*, *Cucullaea*, *Macrodon*, *Macrodonus*, or *Grammatodon*, and even Spriestersbach (1942) used *Macrodonus*, although *Parallelodon* was the accepted and correct name at that time (Arkell 1930).

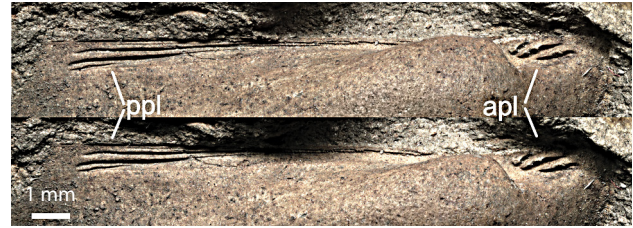
The scope of this contribution is to provide an overview of the current knowledge on the early occurrence and evolution of parallelodontid arcoids (Parallelodontidae: *Parallelodon*) in the Devonian and their possible ancestors. We would also like to honour Jiří Kříž, who very carefully studied and documented the revision of several bivalve groups of the Middle Palaeozoic, particularly of Perunica and the Bohemian (Hercynotypic) Facies.

## Parallelodontid morphology

Unlike modern arcids, Palaeozoic parallelodontids are equipped with a characteristic ‘parallelodontid’ hinge (Amler 1989, Friedel & Amler 2024; Fig. 1), which is combined with a plesiomorphic amphidetic, duplivincular (‘chevron-type’) ligament, common to most arcids (Thomas 1978a, Knight & Morris 2019). However, the terminology used till now is oversimplified since the hinge-ligament apparatus of parallelodontids is more complex, and several sub-types exist (Amler 1989, Amler *et al.* 2024). Thomas (1976, 1978a, b) assessed the functional morphology and evolution of the arcid ligament in Mesozoic and Cenozoic representatives, but its Palaeozoic (Devonian–Mississippian) origins and its early development are virtually unknown.

For any taxonomical and evolutionary conclusions, we like to emphasise that some morphological characters are essential for inclusion or exclusion from the parallelodontid taxonomic concept.

The primary feature is the hinge morphology, basically termed ‘taxodont’ (Knight & Morris 2019), although a taxodont dentition in the strict sense, as exemplified e.g. by members of the genera *Arca*, *Glycymeris*, *Nucula*, *Nuculites* or *Ctenodonta*, is not known in Palaeozoic



**Figure 1.** Characteristic parallelodontid/cosmetodontid hinge morphology exemplified by *Parallelodon michelini* (d’Archiac & de Verneuil, 1842) from Silesia (Poland). The steinkern preservation of a right valve shows three postero-pseudolateral teeth (ppl) parallel to the long, straight hinge margin and a set of four oblique to horizontal anterior pseudolateral teeth (apl). In addition, the pronounced anterodorsal corner is rectangular in outline. Close-up of specimen BGR-B-STGR-000346070 (Fig. 2C) in lateral view and slightly oblique view to show the central part of the hinge below umbo and beak.

parallelodontids. In *Parallelodon*, however, the hinge consists of 3–7 short, oblique teeth in different orientation in front of the umbo and 2–4 elongated teeth  $\pm$  subparallel to the centrodorsal and posterodorsal margin behind the umbo. Whereas early authors (e.g. Arkell 1930) preferred to use ‘anterior teeth’ and ‘posterior teeth’, Newell (1969, p. N256) termed them ‘anterior and medial cardinals’ and ‘posterior laterals’; Stiller (2006) used ‘cardinals’ and ‘posterior pseudolaterals’; Amler (1989) ‘anteromediale Kardinalzähne’ and ‘Lateralzähne’. Newton *et al.* (1987) and Gardner & Campbell (1997) applied the terms ‘anterior pseudolaterals’ and ‘posterior pseudolaterals’, which perfectly match the situation in parallelodontids, because the terms ‘cardinalia’ and ‘lateralia’ should only be used for the heterodont hinge (Carter *et al.* 2012). In consequence, we apply the term ‘parallelodont’ as a sub-type of the taxodont dentition, with modifications as ‘parallelodontid’, ‘grammatodontid’, ‘cucullopsid’, ‘cosmetodontid’ or ‘nemodontid’ according to Amler (1989) consisting of 3–7 anterior pseudolaterals (apl) in differing orientation and 2–4 elongated posterior pseudolaterals (ppl) almost parallel to the hinge margin (Fig. 1). In addition, the ligament area is external, narrow in most species, wide and chevron-like in few thick-shelled taxa.

Secondly, the outline (in detail) serves as a characterising feature. Parallelodontids possess a rounded rectangular to trapezoidal outline with a more or less pronounced elongation in the posterior or posteroventral region, usually, but not exclusively, almost twice as long as high. In detail, the shape can be distinguished as ‘parallelodontiform’, ‘scaphiform’, ‘grammatodontiform’, ‘anadariform’, or ‘catelliform’ (terms from Amler 1989). The valves are inequilateral with the umbo situated in the anterior third of the dorsal margin in most species. The anterodorsal corner is rectangular or narrowly rounded and defines a characteristic, anterodorsal auricle-like shell

area. The posterior wing is depressed, often separated from the central body of the valve by a distinct umbonal ridge (in the literature variably called posterodorsal ridge, posterior ridge, posterior carina, umbonal carina, or carina), and the central body of the shell is moderately inflated; a byssal sinus and sulcus can be developed (Friedel & Amler 2024).

The presumed evolution of hinge patterns was described by Thomas (1978a), but some of his implications (Thomas 1978a, p. 187) are apparently incorrect. The parallelodontid hinge, *e.g.* can be developed not only on massive, broad hinge plates, but also on elegant, delicate hinge margins, as exemplified in the early Mississippian *Parallelodon meridionalis* De Koninck, 1885. In addition, a continuous row of teeth contrasting with a gap (lacuna) below the umbo was thought to be systematically relevant. But our studies of parallelodontid hinge ontogeny have shown that a dental lacuna can be developed even in closely related species.

The hinge structure and the arrangement of the teeth are the most important and diagnostic features for identifying genera or families. However, in the Early Palaeozoic, these structures are often not preserved, obscured, or damaged due to poor fossil preservation. As a result, taxonomic assignment frequently relies on general morphological characteristics typical of the Parallelodontidae. But our studies have also shown that many specimens can be analysed in detail via non-destructive observations based on CT-scanning.

## Research history and previous ideas on early arcoid evolution

The origin of the Arcida is enigmatic, as their direct ancestor is not established (Cope 1997a, b, 2000, 2004; Ratter & Cope 1998; Waller 1998). Combosch & Giribet (2016) confirmed the monophyly of the Arcida, which had been supported previously (Waller 1998, Carter *et al.* 2000), in all their analyses, although relationships among families remained somehow unresolved.

In the Ordovician, the Arcida underwent their first radiation (*e.g.* Cope 1996a, 2004; Cope & Babin 1999; Cope & Kříž 2013), followed by a decline in the Early and Middle Devonian, a second radiation in the Early Mississippian, and a major decline at the Permian–Triassic boundary. Further radiations and declines of the group during the Mesozoic and Cenozoic are less pronounced or understudied (Reinhart 1935, Knight & Morris 2019).

Research over the last five decades has provided various ideas and arguments for the assumed early development of the Arcida and Arcoidea, particularly with respect to the genera *Glyptarca* Hicks, 1873, *Alytodonta* Cope, 1997, *Uskardita* Ratter & Cope, 1998, *Catamarcaia*

Sánchez & Babin, 1993, *Freja* Liljedahl, 1984, and their possible affinities to palaeoheterodonts and pteriomorphs (Newell 1954; Thomas 1978a, b; Liljedahl 1984a, b; Sánchez & Babin 1993; Sánchez 1995; Cope 1997a, b, 2000). These assumptions are primarily based on hinge and ligament morphology and evolution, probably also on shell microstructure, but suffer from the fact that the ontogeny of the hinge-ligament apparatus is rarely observed in the respective taxa due to a limited number of specimens and incomplete preservation (Thomas 1976, 1978a). Nonetheless, no unequivocal evolutionary picture has been established yet (*e.g.* Newell 1954; Cox 1959; Pojeta 1971; Thomas 1978a; Liljedahl 1984a, b; Amler 1989; Ratter & Cope 1998).

The origin of the family Parallelodontidae was placed in the Ordovician by Newell (1969, p. N256), based on the inclusion of *Glyptarca*, which is now assigned to the Glyptarcoidea (*e.g.* Bieler *et al.* 2010, Carter *et al.* 2011). However, all taxa from the Ordovician or Silurian that were either described as *Parallelodon* or assumed to have parallelodontid affinities have since been shown to be misclassified. This particularly concerns the oldest species yet described as belonging to the genus *Parallelodon*, *Parallelodon antiquus* Barrois, 1891, reported from the upper Arenig (upper Lower Ordovician) of Brittany, France (Barrois 1891, p. 200). The only known specimen, said to be lost, is very elongated with subparallel dorsal and ventral margins, truncated posteriorly, but incomplete and does not reveal the hinge characters as illustrated by Barrois (Babin 1966, p. 146). Douvillé (1912, p. 440) placed the species in the genus *Actinodonta* Phillips, 1848 in Phillips & Salter (1848), but in contrast, Babin retained the assignment to *Parallelodon*, based on Cox (1960, p. 74), who stated that it showed a morphology similar to other members of *Parallelodon*. Pojeta (1971, p. 18) suggested that ‘*P.* *antiquus*’ might belong to *Pseudarca* Tromelin & Lebesconte, 1875, but that genus has a taxodont-like dentition (McAlester 1968, pp. 47, 131; Liljedahl 1984a, p. 39). Following our own studies on parallelodontid hinge morphology, we like to emphasise that ‘*Parallelodon*’ *antiquus* Barrois, 1891 does not show the characteristic morphology of middle and late Palaeozoic parallelodontids, particularly with respect to the typical arrangement of anterior and posterior pseudolateral teeth (Amler *et al.* 2024).

Further species from the uppermost Ordovician of Bohemia introduced by Barrande (1881) in ‘*Arca?*’, *i.e.* *Arca? kosoviensis*, *A.? innotata*, and *A.? disputabilis*, were revised by Kříž & Steinová (2009) and placed in *Sluha* Barrande, 1881, a malletiid nuculanoid. Consequently, verified Ordovician representatives of parallelodontid arcoids are not known. Also, from Silurian strata no species have been recorded so far to be part of parallelodontid arcoids (*e.g.* Barrande 1881; Isberg 1934; Pojeta *et al.*

1976; Liljedahl 1984a, b; Kříž 1999, 2008, and references therein). Thus, Thomas (1978b, p. 336) and Nicol (1984) concluded that the earliest true parallelodontid arcoids were of (Middle) Devonian age. However, in his short overview of Devonian bivalves, Kříž (1979) did not even mention the genus *Parallelodon*.

### Latest Silurian, Devonian and earliest Carboniferous parallelodontid arcoids

Up to fifty species have been described from Devonian strata which match the parallelodontid morphology either by hinge details or in ‘general’ outline, shell characteristics, and ornamentation. Most of which can only vaguely be attributed to *Parallelodon*, as preservation in most cases leaves space for doubts, because several other coeval genera show comparable external morphology and outline. Consequently, we constricted morphological features and focused on characters such as straight hinge line, rectangular anterodorsal corner, posterior wing, and umbonal ridge (see above; Amler 1989, Friedel & Amler 2024). However, the parallelodontid hinge serves as most distinctive separating character. Keeping these circumstances in mind, in most cases relationships to *Parallelodon* or even to arcoids are mostly uncertain, unresolved, or rather vague, and many of the presumed parallelodontids belong to the Protobranchia or ‘anomalodesmatid’ Heterodonta. Several goniophorids, modiomorphids, and sanguinolitids mimic the overall shape of *Parallelodon*, but, of course, lack the distinguishing hinge morphology.

In the following chapters, we retain the original combination of genera and species names of the respective authors, even if we accept an assignment to parallelodontid arcoids or even the genus *Parallelodon*.

### Latest Silurian–Early Devonian

Lack of continuous shallow shelf sedimentary successions due to the sea level fall following the Caledonian Orogeny and sporadic bivalve sampling minimises the record of parallelodontids from the Silurian–Devonian transition, although sedimentary rocks of Lochkovian, Pragian and Emsian age occur widespread in Central Europe and North America. Faunal assemblages of the Rhenotypic (or Rhenish) Facies (Jansen 2016), *i.e.* the shallow marine, mostly arenaceous-calcareous facies, in western Germany and Luxembourg, *e.g.* the Siegen regional stage (Pragian and lowermost Emsian), the Klerf Beds (upper Lower Emsian) or the Berlé Quartzite (Upper Emsian), are almost void of parallelodontids (Franke 2006, 2016; Eichele 2014; see also references therein)

apart from a single questionable occurrence (*Macrodon* sp., without illustration, without posterior pseudolaterals; Kegel 1913, p. 70). The same applies to the Hercynotypic (or Hercynian, Jansen 2016), deeper marine pelitic-calcareous Facies of the late Silurian and Early Devonian of Baltica, Perunica, Morocco, and adjacent regions (Barrande 1881; Isberg 1934; Kříž 1999, 2000, 2008 and references therein). From upper Silurian–lower Devonian sedimentary rocks of SE Australia (Talent 1965, Johnston 1993, Bradshaw 1999) no unequivocal parallelodontids have been described so far, although the assemblages are highly diverse and habitats appear environmentally adequate. Three species introduced by Chapman (1908), *i.e.* *Parallelodon aequalis*, *P. kilmoriensis*, and *P. spryi*, were misclassified and most probably can be assigned to protobranchians. Some specimens, which superficially resemble the parallelodontid outline, may also be attributed to modiomorphids or sanguinolitids, which are common in the respective facies (Johnston 1993). In most cases, hinge characters have not been observed. The same applies to species described from coeval sedimentary rocks of NE North America, *e.g.* *Macrodon matthewi* Clarke, 1907 and *M.?* *baileyi* Clarke, 1907 from the Lower Devonian of New Brunswick (Canada) (Clarke 1907, see also Williams & Breger 1916). In fact, no convincing parallelodontid taxa have yet been reported from that region.

*Parallelodon insignis* Korejwo & Teller, 1964 and *Parallelodon* ‘a’ sp. nov. (Korejwo & Teller 1964) from the Upper *Monograptus angustidens* (= *Uncinograptus uniformis angustidens*) Zone of eastern Poland (Chelm Borehole), originally correlated with the Ludlowian (upper Silurian) and presently considered to represent the lowermost Devonian (Becker *et al.* 2012), appear to be the oldest Devonian parallelodontid taxa. Both, however, do not show any indications of a parallelodontid hinge line and, in addition, their anterodorsal corner is not pronounced. Thus, we consider both species as not belonging to the parallelodontid arcoids.

From Emsian strata, two species have been mentioned so far. *Parallelodon guangxiensis* Pojeta, Zhang & Yang, 1986, from the Sipai Formation (Emsian) of China does not show any hinge characters at all. The overall morphology is not typical for parallelodontids; thus, we doubt arcoid affinities. Quite the opposite is shown in *Macrodon (Parallelodon) mandelensis* Dahmer, 1915, described from the German ‘upper Koblenz-Schichten’, today upper Emsian strata (Mandeln Formation; Bender 2008). One of the figured specimens, a steinkern of a right valve, undoubtedly has a parallelodontid hinge and is here considered as the first reliable representative of the parallelodontid arcoids (Fig. 2A, B). Slightly older, from the Katzenelnbogen Formation (‘Taunus-Quarzit’; upper Siegenian or lower Emsian; Requadt 2008) Kegel (1913,

p. 70) described *Macrodon* sp. without illustration. We have not traced the single specimen and cannot assess this occurrence (see above).

## Middle Devonian

The Middle Devonian comprises most of the parallelodontid taxa described from this period. High sea level offered wide shelf areas with different habitats ideal for parallelodontid evolution. Nonetheless, the relatively few specimens indicate that parallelodontids were restricted to certain palaeoenvironments not developed everywhere. Single species were described by several authors, the only two compilations for Central European and eastern North American faunal assemblages, respectively, were presented by Beushausen (1895) and Hall (1883, 1885).

## Southern Laurussia (Central Europe)

Two species were described from the ‘Lenne-Schiefer’, today Ohle Formation (upper Eifelian). *Macrodon kochi* Priestersbach, 1919 is not a *Parallelodon*, but probably a protobranchiid, e.g. *Nuculites*; *Macrodon praecursor* Priestersbach, 1942 (p. 175), may belong to *Parallelodon*, but the hinge is not preserved.

*Arca michelini* d’Archiac & de Verneuil, 1842, in part *Arca inermis* Sandberger & Sandberger, 1856, (p. 274) from the ‘Übergangskalk von Villmar’ (Hesse, Germany), Sötenich (Eifel Hills, Germany), and Paffrath (near Cologne, Germany) (all most probably Givetian age), is typically elongate (arciform)-scaphiform (Amler 1989) with faint commarginal ornamentation. Several hypotypes display the characteristic hinge (Figs 1, 2C), thus, we accept this taxon as a member of *Parallelodon* (Figs 1; 2C, J).

*Macrodon delitescens* Beushausen, 1895 from Sötenich (Eifel Hills, Germany) was based on a single left valve, which is completely broken into small fragments. Nicely preserved hypotypes from the upper Givetian ‘Unterer Plattenkalk’ near Bergisch Gladbach (Bergisches Land, Germany) allow a revised description and show the entire parallelodontid hinge (Fig. 2G, H).

*Arca carinata* Goldfuss, 1841 from the ‘Übergangskalk der Eifel’ (probably Givetian age; Eifel Hills, Germany) lacks hinge characters and an anterodorsal corner; the outline and the distinct umbonal ridge or keel resembles sanguinolitids. We doubt affiliation with *Parallelodon*. Incidentally, *Arca carinata* Goldfuss, 1841 (p. 283) is a junior homonym of *Cucullaea carinata* Sowerby, 1813, renamed as *Arca carinata* by Goldfuss (1837, p. 150), type of *Grammatodon* (*Nanonavis*) Stewart, 1930.

*Pholadomya venusta* Steininger, 1853 (p. 49) and *Pterinea Brilonensis* Kayser, 1872 (p. 675), from the upper Givetian ‘Stringocephalen-Eisenstein’, were united by Beushausen (1895) and placed in *Macrodon*. The specimen of Kayser (1872) is typically (arciform)-parallelodontiform (Amler 1989) in outline and shows two or three long postero-pseudolateral teeth. We accept the classification as *Parallelodon venustus* (Steininger, 1853) (Fig. 2I).

The illustrated specimen of *Arca* (?) *Bodana* Roemer, 1860, from the Givetian or lower Frasnian of the Harz Mountains (Germany), shows a typical parallelodontid outline with an elongated hinge line, but characters of the hinge are unknown. Later authors were unable to locate the specimen.

## Southern Laurussia (North America)

*Macrodon hamiltoniae* Hall & Whitfield, 1869 (Hall 1885, p. 349), with typical parallelodontid outline and hinge morphology as well as commarginal lamellar ornamentation (Fig. 2D), appears to be the first reliable Devonian parallelodontid in North American southern Laurussia, from the Hamilton Group of Pennsylvania, and the Romney Formation (Middle Devonian) of Maryland (Prosser & Kindle 1913, p. 248). *Parallelodon hamiltoniae* was also recorded from the Givetian of western Europe (Brittany) by Babin *et al.* (2001, p. 36) and may act as connecting link along the southern margin of Laurussia. However, the North American and West European specimens differ in morphology, so we assume that the European specimens represent a separate taxon.

## Perunica (Bohemia)

*Sufia paradoxa* Prantl & Růžička, 1955 and *Mnataia pribyli* Prantl & Růžička, 1955, both from the Middle Devonian Choteč Limestone of Bohemia, are based on few small incomplete specimens; Prantl & Růžička assumed affinities with *Parallelodon* based on the anterior part of the hinge. Newell (1969, p. N256) included *Sufia* and *Mnataia* questionably in *Parallelodon*, whereas the authors themselves were uncertain about the systematic affiliation. Unless further material is reported, we cannot finally decide whether they possess cyrtodontid or parallelodontid affinities.

## Late Devonian

In the European part of the southern Laurussian shelf area, Frasnian and lower to middle Famennian deeper marine Hercynotypic Facies is almost void of parallelodontids,

and this also applies to the equivalent facies in North America (Clarke 1904). In contrast, from the Chemung Group of northeastern North America several species were described, most of which only superficially placed in parallelodontids. Some of the taxa not discussed here are based on incomplete type material, or their type material is lost. Modern revisions of hercynotypic bivalves did not mention any parallelodontid taxa at all (e.g. Kříž 2004; Nagel-Myers & Amler 2007; Nagel-Myers *et al.* 2008, 2009).

### Southern Laurussia (North America)

From the Upper Devonian of eastern North America several species were described as parallelodontid arcoids or show parallelodontid morphology. Revision and direct comparison of the material is pending, and, in most cases, the stratigraphic level is only roughly known. *Macrodon chemungensis* Hall & Whitfield, 1869 (Hall 1885, p. 350) is the best known parallelodontid from the lower Upper Devonian (see also Chadwick 1935). Hall's material was revised by McAlester (1962, p. 25) and classified in *Grammatodon* (*Cosmetodon*) (Fig. 2E). This taxon comes from the 'upper part of the Chemung Group', today Brallier Formation, Upper Devonian (Berg *et al.* 1983) of New York State, from Pennsylvania, and the Jennings Formation of Maryland (Clarke & Swartz 1913, p. 627), and links the Middle Devonian species with the latest Devonian taxa (see below). Noteworthy is the fact that McAlester did not mention any of the various other species described and figured by Hall from the Chemung Group, e.g. *Prorhynchus angulatum* Hall, 1885, *Prorhynchus nasutum* Hall, 1885, *Palaeonatina quadrata* Hall, 1883 (later placed in *Prorhynchus*; Hall 1885) or other earlier workers. Although Newell (1969, p. N256) synonymised *Prorhynchus* with *Parallelodon*, we question affinities with parallelodontid arcoids in these cases as no hinge characters are preserved. Other species listed as parallelodontids are *Macrodon parvus* White & Whitfield, 1862 and *Macrodon cochlearis* Winchell, 1863, both also from the Chemung Group or younger strata. *Macrodon parvus* (White & Whitfield 1862, p. 299)

was not figured but described as having parallelodontid hinge characters. Additionally, *Leptodesma parallelum* Simpson, 1890 and *Ptychopteria obsoleta* Simpson, 1890, both assigned to *Prorhynchus* by Chadwick (1935, p. 330) are assumed but not confirmed parallelodontids.

### Latest Devonian–earliest Mississippian

Although stratigraphy across the Devonian–Carboniferous boundary is well studied, bivalves did not raise particular interest. Thus, the precise age of old samples is not always certain as indicated below.

### Southern Laurussia (Central Europe)

*Parallelodon pauli* Friedel & Amler, 2024 from the Etroeung Formation, uppermost Famennian (equivalent to Wocklum regional stage), is one of the well-known species that evolved during the latest Devonian (Strunian) transgression and most probably gave rise to the early Tournaisian radiation of the parallelodontids in central and western Europe (Fig. 2F).

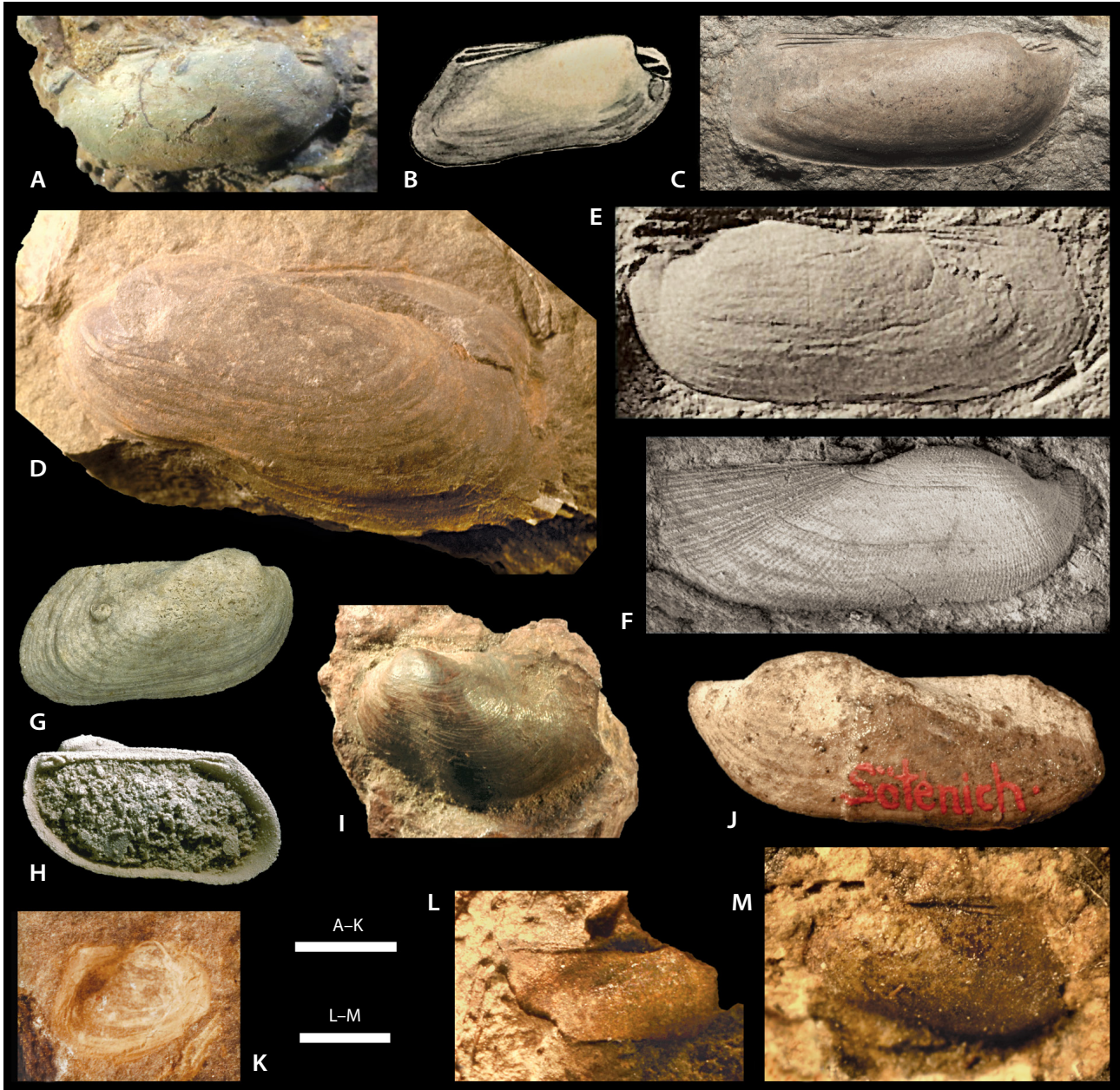
*Macrodon ratingensis* Paeckelmann, 1913, from the Etroeung Formation or Velbert beds, uppermost Famennian, does not possess parallelodontid hinge characters and shell outline, instead, this taxon was placed in *Guerichia* Rzehak, 1910 by Amler (2004a, p. 165; 2004b, p. 193; 2014).

*Macrodon pygmaeus infans* Whidborne, 1896 is based on three-minute specimens (Whidborne 1896, p. 112; Fig. 2L, M) not very similar to *Macrodon pygmaeus* (*pygmaeus*) Whiteaves, 1892 (p. 299). One of Whidborne's specimens is comparable with *Prorhynchus angulatum* Hall, 1885 (see above) from the Chemung Group, but comes from the significantly younger Pilton Formation (uppermost Famennian) and shows the postero-pseudolateral teeth (Fig. 2M), so this material may be a small or juvenile *Parallelodon*.

Whidborne (1896, p. 109) also described and discussed several species under *Cucullaea*, which he assumed to be an arcid taxon together with *Parallelodon*. All

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**Figure 2.** Selected Devonian parallelodontid arcoids. • A, B – *Parallelodon mandelensis* (Dahmer, 1915). A – steinkern of a right valve, parallelodontiform, SMF.67525 (coll. Forschungsinstitut und Naturmuseum Senckenberg Frankfurt, Germany); Hauberg hill near Mandeln (Dietzhölztal), Hesse, Germany; Mandeln Formation, upper Emsian. B – original drawing of specimen SMF.67525 in Dahmer (1915, pl. 8 fig. 15a). • C – *Parallelodon michelini* (d'Archiac & de Verneuil, 1842); steinkern of a right valve, scaphiform, BGR-B-STGR-000346070 (coll. Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany); precise locality unknown, Silesia, Poland; probably Givetian or lower Frasnian. • D – *Parallelodon hamiltoniae* (Hall & Whitfield, 1869); left valve, parallelodontiform, GZG.INV.2428 (coll. Hall, GeoZentrum Göttingen, Germany); Earlville, Madison County, New York, U.S.A.; 'Hamilton Group'. • E – *Parallelodon chemungensis* (Hall & Whitfield, 1869); photograph of McAlester (1962, pl. 4 fig. 1); holotype steinkern of a left valve, scaphiform, AMNH 6132/1:1 (coll. American Museum of Natural History, New York, NY, U.S.A.); near Elmira, New York; Chemung Stage. • F – *Parallelodon pauli* Friedel & Amler, 2024; paratype right valve, scaphiform, BGR-B X13470 (coll. Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany); Ratingen, North Rhine-Westphalia, Germany; Etroeung Formation,



Strunian, uppermost Famennian (copy of Friedel & Amler 2024, fig. 4b). • G, H – *Parallelodon delitescens* (Beushausen, 1895); external view (G) and internal view (H) of a right valve, parallelodontiform, MB.M.21250.1 (coll. Ebbighausen, Museum für Naturkunde Berlin, Germany); Bergisch Gladbach, Bergisches Land, North Rhine-Westphalia, Germany; ‘Unterer Plattenkalk’, upper Givetian. • I – *Parallelodon venustus* (Steininger, 1853); left valve, parallelodontiform, MB.M.400 (coll. Schülcke, Museum für Naturkunde Berlin, Germany), figured in Kayser (1872, pl. 27, fig. 2a, b as *Pterinea Brilonensis* Kayser, 1872) and Beushausen (1895, pl. 4, fig. 4); Brilon, North Rhine-Westphalia, Germany; ‘Stringocephalen-Eisenstein’, upper Givetian. • J – *Parallelodon michelini* d’Archiac & de Verneuil, 1842; left valve, scaphiform, MB.M.74 (coll. Museum für Naturkunde Berlin, Germany), figured in Beushausen (1895, pl. 4, fig. 1); Sötenich, Eifel Hills, Germany; Givetian. • K – *Parallelodon cooperi* Cox, 1946; holotype right valve, short parallelodontiform, NHMUK PI PL 485 (coll. Natural History Museum London, UK), figured in Cox (1946, pl. 13, fig. 4); coast of Ghana; Takoradi Sandstone or Takoradi Shales, Sekondi Series; probably Late Devonian. • L, M – *Parallelodon pygmaeus infans* Whidborne, 1896. L – paralectotype steinkern of a right valve, scaphiform, SM.H.325 (coll. Porter, Sedgwick Museum Cambridge, UK), figured in Whidborne (1896, pl. 12, fig. 4) and Amler (1995, pl. 1, fig. 10); Poleshill, Barnstaple, North Devon, UK; Pilton Formation, Strunian, upper Famennian. M – lectotype steinkern of a left valve, parallelodontiform, SM.H.324 (coll. Porter, Sedgwick Museum Cambridge, UK), figured in Whidborne (1896, pl. 12, fig. 5) and Amler (1995, pl. 1, fig. 11); Poleshill, Barnstaple, North Devon, UK; Pilton Formation, Strunian, upper Famennian. • Terminology of shell outline after Amler (1989). Abbreviations of repository: AMNH – American Museum of Natural History, New York, NY, U.S.A.; BGR – Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany; GZG – GeoZentrum Göttingen, Germany; MB – Museum für Naturkunde Berlin, Germany; NHMUK – Natural History Museum London, UK; SM – Sedgwick Museum Cambridge, UK; SMF – Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M., Germany. Scale bars: 5 mm (A–K) and 1 mm (L–M).

these species or morphotypes are far removed from parallelodontid morphology and may be related to the Trigoniida Dall, 1889 instead of the Arcoidea.

### Southern Laurussia (North America)

From the Devonian–Mississippian transition several assumed parallelodontids have been described. After revision and more precise definition of stratigraphic successions, some of the following taxa may be latest Famennian or early Tournaisian in age.

*Macrodon hamiltoniae irvinensis* Foerste, 1909, placed in *Parallelodon* and raised to species level by Hyde (1953, p. 300), as well as *Parallelodon modioliformis* Hyde, 1953 are doubtfully assigned to *Parallelodon*. Both are most probably early Mississippian in age.

*Macrodon striatocostatus* Herrick, 1888, from the lower part of the Waverly Group (Herrick 1888, p. 37) is probably of late Famennian age and matches parallelodontid morphology.

### Other regions and taxa

#### Eastern Laurussia (Russia)

Several unrevised species were described during the geological survey of Russia more than 150 years ago. Most of them need a revised stratigraphic and taxonomic classification: *Arca oreliana* de Verneuil, 1845 in de Verneuil & Keyserling (1845, p. 314) and *Megalodon suboblongus* de Verneuil, 1845 in de Verneuil & Keyserling (1845, p. 305) are most likely parallelodontids based on their overall morphology; *Arca elytra* Venyukov, 1886 is questionable.

#### Other regions

From other regions, Devonian parallelodontids are rarely recorded. *Parallelodon cooperi* Cox, 1946 from the Takoradi Sandstone or Takoradi Shales of the Sekondi Series in Ghana is probably Late Devonian in age and matches well the short parallelodontid morphology (Fig. 2K). *Macrodon Hohmanni* Knod, 1908 (p. 530) from the Devonian of Bolivia is taxonomically indeterminable. Even the original author noted that its morphology is atypical and several diagnostic features significantly deviate from comparable taxa. An alternative systematic placement appears plausible and was already considered by Knod himself.

Unequivocal occurrences of Devonian parallelodontids from China and Australia are unknown.

### Discussion of Devonian parallelodontid arcoids

Up to now, some fifty taxa at the species level are listed from Devonian strata with variable certainty on taxonomy or age. Most of which are vaguely described and studied, many of which incompletely preserved or prepared. Although originally attributed to genera such as *Arca*, *Byssosarca*, *Cucullaea*, *Macrodon*, *Grammatodon*, or *Parallelodon*, the assessed systematic position can rely on the hinge characters only. In some cases, we also considered details in shell morphology, *i.e.* the anterodorsal corner, the straight hinge line and the posterodorsal corner as stated above. But, if compared with better known Carboniferous taxa, the outline may vary and resemble pteriods, modiomorphids or sanguinolitids as well as protobranchiids.

Taking these considerations into account, the first convincing parallelodontid, *Parallelodon mandelensis* (Dahmer, 1915), appeared in the Emsian. Older records turned out to disagree with parallelodontid morphology in the strict sense. However, *P. mandelensis* already has a fully developed parallelodontid hinge, so that morphologically less advanced progenitors are to be expected in the early Lower Devonian. Cyrtodontids and pteriods occurred coevally and can be considered as ancestors (Thomas 1978a; Liljedahl 1984a, b; Amler 1989; Ratter & Cope 1998). In the Eifelian, *Parallelodon praecursor* (Priestersbach, 1942) followed with the first radiation acme in the Givetian with *P. hamiltoniae* (Hall & Whitfield, 1869), *P. delitescens* (Beushausen, 1895), *P. villmarensis* (Beushausen, 1895), *P. venustus* (Steininger, 1853), and *P. michelini* (d'Archiac & de Verneuil, 1842). Although in European Laurussia a relative decline may be apparent during Frasnian and early Famennian time, several taxa seem to persist in the western (North American) part of the Laurussian shelf, where shallow and middle shelf environments continued. Thus, *Parallelodon chemungensis* (Hall & Whitfield, 1869) and probably some other less known taxa connect the Frasnian parallelodontids with the latest Devonian radiation. *Parallelodon pauli* Friedel & Amler, 2024, *P. striatocostatus* (Herrick, 1888) and *P. infans* (Whidborne, 1896) represent the Strunian radiation and most probably gave rise to the early Tournaisian radiation of parallelodontids on the southern margin of Laurussia. The uppermost Frasnian Kellwasser Event may have had impact on parallelodontid evolution, but the meagre record of material does not show reliable evidence.

Unfortunately, many of the taxa mentioned in the previous chapter only show vague or incomplete parallelodontid morphology, but further material or CT-analyses could confirm their affiliation to the Arcoidea. Thus, we can only assume that parallelodontid diversity

was probably higher than the confirmed species suggest. Nonetheless, from the Middle Devonian onwards, parallelodontid arcoids became a minor but consistent part of the middle shelf bivalve communities.

From the palaeogeographical point of view, records of Devonian parallelodontids are rather confined to shelf environments of the Rheic Ocean and the Palaeotethys. Apparently, the equatorial oceans most probably were the centre of parallelodontid evolution, as most taxa hitherto known occur in open shelf neritic palaeoenvironments and inter-reefal facies (Rhenotypic Facies) of low latitudes bordering the adjacent continents. Consequently, the southern margin of Laurussia as well as the margins of the Armorican Terrane Assemblage comprise most of the type localities and occurrences. In contrast, palaeoenvironmental conditions around Perunica and adjacent terranes as well as deeper marine, Hercynotypic Facies appear to be almost void of parallelodontids and related taxa (e.g. Kříž 1999, 2000, 2004, 2008 and references therein; Nagel-Myers & Amler 2007; Nagel-Myers *et al.* 2008, 2009). Our evaluation of the numerous Devonian bivalve assemblages revealed that parallelodontids did not migrate into the deeper marine Hercynotypic Facies before the Middle Mississippian (Friedel & Amler 2024). Instead, they developed in the Rhenotypic Facies and began to differentiate morphology (outline, ornamentation) for adaptation to different habitats. This evolutionary trend peaked during the Mississippian (McCoy 1844, De Koninck 1885, Hind 1897, Paul 1941 and own observations).

At present, eastern Laurussian, northern Gondwanan, and Chinese shelf areas are rather understudied and need to complete the current database. Noteworthy is the fact that Zhang (1988) regarded China as one of the centres for bivalve evolution but parallelodontids are rarely recorded from that region. Nonetheless, it needs to be mentioned that lack of scientific interest has led to biased and incomplete knowledge on bivalve distribution in the Devonian. Furthermore, most if not almost all taxa with presumed parallelodontid affinities occur in very low abundance, in many cases restricted to the holotype or a very small number of syntypes.

## Conclusions

Our review of some fifty Devonian and pre-Devonian species attributed to the Parallelodontidae shows that most of them can only vaguely be attributed to the Parallelodontidae, as poor preservation can obscure diagnostic features, causing potential confusion with coeval genera of ‘anomalodesmatid’ Heteroconchia showing comparable characteristics. If parallelodontid morphology in the strict sense regarding hinge details and external shell

characteristics is considered, only few species remain as convincing early members of parallelodontid Arcoidea. All Ordovician and Silurian taxa previously attributed to *Parallelodon* or presumed to possess parallelodontid characteristics turned out to be misclassified. *Parallelodon mandelensis* (Dahmer, 1915) from the upper Emsian Rhenotypic (shallow marine) Facies of Germany undoubtedly has a parallelodontid hinge and seems to be the earliest member of the family. Following unequivocal parallelodontids have been noted in the Middle Devonian, primarily in the shelf region deposits of the Rheic Ocean in Central Europe and eastern North America, where up to ten species were identified. The relatively high sea level and, accordingly, wide shelf areas during this period provided ideal conditions for the diversification of parallelodontids. The Late Devonian evolution of the group is mainly documented in North America, as facies conditions in Europe seem to have been unfavourable. With the transition from the Devonian to the Carboniferous, a remarkable radiation of parallelodontids led to significantly higher parallelodontid diversity and gave rise to the extensive early Tournaisian radiation in the highly diverse shelf environments bordering Laurussia and Gondwana documented in the monographs on bivalves from the Carboniferous Limestone (e.g. McCoy 1844, De Koninck 1885, Hind 1897).

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