

Ordovician to Devonian diversification of the Bivalvia

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Abstract: Studies of the Paleozoic Bivalvia have accelerated in the last three decades and we have numerous new data dealing with the diversification of this Class of mollusks. After the extreme scarcity of the Cambrian data, the abruptness of the diversity of the bivalve faunas in the fossil record during the Early Ordovician is an outstanding event. It is also noteworthy that both this first explosion and the succeeding diversification during the Middle Ordovician were located primarily on the Gondwanan and Avalonian shelves in shallow clastic facies. By contrast, from the late Ordovician, Baltica and Laurentia were more propitious for the further diversifications of bivalves, notably epibenthic ones. Thus before the close of the Period, all the subclasses of bivalves were established and the Class was dispersed throughout the world oceans. After the uppermost Ordovician extinctions, an important replacement at familial and generic levels occurred during the Silurian. The Pteriomorpha, many of them adapted to an epibyssate mode of life, underwent an explosive evolution, particularly during the Ludlow, while many free-burrowing suspension-feeding genera were adapted to the broad expanses of soft muds. During the Devonian, bivalves continued their diversification at both familial and generic levels, and for the first time, some of them colonized fresh-water. The continuing paleogeographic changes favored faunal exchanges, for example between Appalachian and western European areas, and led to the establishment of cosmopolitan faunas.

Key Words: bivalves, diversification, Paleozoic, Ordovician, Silurian, Devonian

"The evolutionary radiation of the bivalves is one of the success stories of invertebrate evolution; few other marine taxa have shown such a steady and consistent increase in diversity" (Gould, 1977:273). At present, the Class Bivalvia constitutes a major part of modern marine benthic faunas even without consideration of the freshwater representatives. This diversity of the bivalves (about 9000 living species according to Nicol, 1989) is the successful conclusion of a long history (Fig. 1), and it is interesting to attempt to track the key stages marking the beginning of this odyssey, especially the initial diversifications of the Class. The difficulties for such a process are numerous and any reconstruction is largely provisional. However in the three last decades, numerous new investigations have brought important data dealing with the Lower Paleozoic faunas of bivalves. Nevertheless, to estimate the value of the study of early diversifications we have to enumerate the main sources of difficulty.

MAIN DIFFICULTIES OF THE STUDY

- Systematics. Identifying the times of diversification requires expressing the succession of taxonomic diversities. For that, it is fitting to choose adequate taxonomic levels, obviously a subjective process. In previous papers

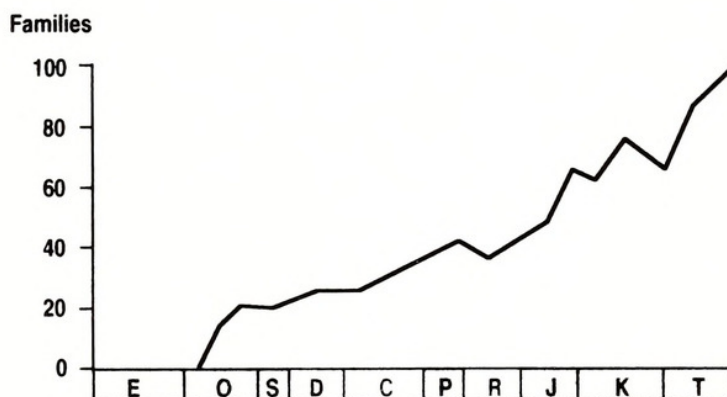


Fig. 1. The continuous increase of the diversity of the bivalves during the Phanerozoic. (after Paul, 1989).

(Babin, 1993a, 1995) I used genera and regrouped them at subclass level. I think that the results were conclusive enough but undoubtedly that procedure is not without problems.

In the literature, the genus concept of authors is probably only a little less insecure than the species one. The latter is the result of diverse splittings and regroupings. For instance, comparing Devonian faunas from Europe and North America, Bailey (1983) proposed a regrouping of 99 fossil species into only 16 species. Nevertheless, the notion of the genus is also sometimes the subject of dramatic

changes. For instance, two classical genera in the old literature, the "praecardioids" *Cardiola* from the Silurian and *Buchiola* from the middle and upper Devonian have been split, the former into twelve genera (Kříž, 1979a), and the latter into six genera (Grimm, 1998).

Regarding the subclasses, there are also some differences of opinion amongst authors. The neontologists generally recognize two subclasses of Bivalvia, Protobranchia and Autobranchia, while paleontologists, basing their classification on the dentition, make use of more subclasses, considering them as evolutionary units. The latter are regarded rather as superorders in the former classification. Pojeta (1987) uses five subclasses: Palaeotaxodonta, Isofilibranchia, Heteroconchia, Pteriomorphia and Anomalodesmata. Cope (1995) defines seven subclasses: Palaeotaxodonta, Lipodonta (for the single solemyoids included in the Cryptodonta by Newell, 1969 and in the Palaeotaxodonta by Pojeta, 1988), Palaeoheterodonta (including the mytiloids which are Isofilibranchia for Pojeta), Heterodonta (these two units are included in Heteroconchia by Pojeta), Neotaxodonta, Pteriomorphia and Anomalodesmata. We retained Cope's classification in a recent paper about the Ordovician diversification (Cope and Babin, 1999); nevertheless, Cope (1998) recently proposed that "some long-accepted palaeoheterodonta are in fact heterodonta, and that even in the early Ordovician heterodonta were already present." In these works all extant bivalve subclasses were represented from the early Ordovician. However, another subclass, never mentioned in all these papers, is the Cryptodonta, which included (Newell, 1969) two orders, solemyoids and praecardioids. The former are possibly paleotaxodonta or lipodonta (see above) but the latter raise a true problem. They were abundant during the Paleozoic, particularly during the Silurian; Kříž (1965, 1979) has put a large part of them into the isofilibranchs and the pteriomorph arcoids (which would be neotaxodonta for Cope) but he has lately kept Cryptodonta for the praecardiids and antipleurids (Kříž, 1996). More recently, Johnston and Collom (1998) have used afresh the subclass Cryptodonta for numerous bivalves. It is not an unimportant choice regarding the evolution of the bivalves because Cryptodonta, if they include only the praecardioids, would be the single subclass of Bivalvia without modern representatives.

Last but not the least, it is evident that these problems of classification also reflect different conceptions about the phylogeny of the bivalves (see for instance, Cope, 1995; Waller, 1998). Notwithstanding their importance, these points are beyond the present enquiry and they are not really constraining for my purpose. So, despite these undeniable divergences and difficulties, it remains possible to appraise the properties of the initial bivalve diversifications.

- Fossil determinations correspond to another problem of taxonomy. Paleontological material is often of poor preservation. Paleozoic bivalve fossils are often poor molds showing few characters without the dentition for instance. So many determinations have been based solely on shell shape explaining many "wastebasket" taxa; in the older literature genera such as *Ctenodonta* or *Modiomorpha* can appear to have had a very large spatio-temporal distribution. It is another cause of weakness for the inventory in addition to the splitting or regrouping cited above.

- Field investigations and study of the new material are of course among the most important factors initiating change in diversity estimates. The comparison of recent graphs of the Ordovician bivalve diversification, for example, shows an important amplification of the generic numbers for South Gondwana and Avalonia (Fig. 2). It is the result of new data from Argentina on the one hand (Sánchez, 1999), and from Wales on the other (Cope, 1996).

Another example may be given. There is no paleotaxodont in my database for the middle Ordovician from Baltica. However, in a recent paper Dzik (1994, Fig. 24, A-C) figured a minute specimen of a juvenile paleotaxodont bivalve (*Praenucula?*) from the lower Llanvirn of Baltica.

- Chronology. Identifying the times of diversification requires having a sufficient resolution of the geologic time scale and precise chronologic correlations between the different parts of the Earth. The stratigraphic information concerning the lower Paleozoic is indeed various and of irregular quality according to the regions. In addition there are several regional scales and they often remain without clear correlation. In this way, I have underlined (Babin, 1995), for example, the equivocal use of middle Ordovician in the North American literature compared with the standard scale of Great Britain. The American Blackriverian stage, containing bivalves, considered as middle Ordovician corresponds really to the lower part of the Caradoc Series from the upper Ordovician in the standard scale. On that basis, we have not known until now bivalves from the middle Ordovician in North America.

Elsewhere, in regions where stratigraphical investigations are incomplete, we can sometimes read Ordovician, Silurian or Devonian without more precision and we are hazy about the times. In the *Treatise on Invertebrate Paleontology* (1969), such vagueness is common enough too, even though it has been the reference for several published compilations.

To establish the database one must evidently consult the old fundamental publications of the last century. Unfortunately, the stratigraphical location of the fossils, which are described and figured, is usually imprecise. Barrande (1881) published the volume VI of his monumental "Système silurien du centre de la Bohême." Devoted to

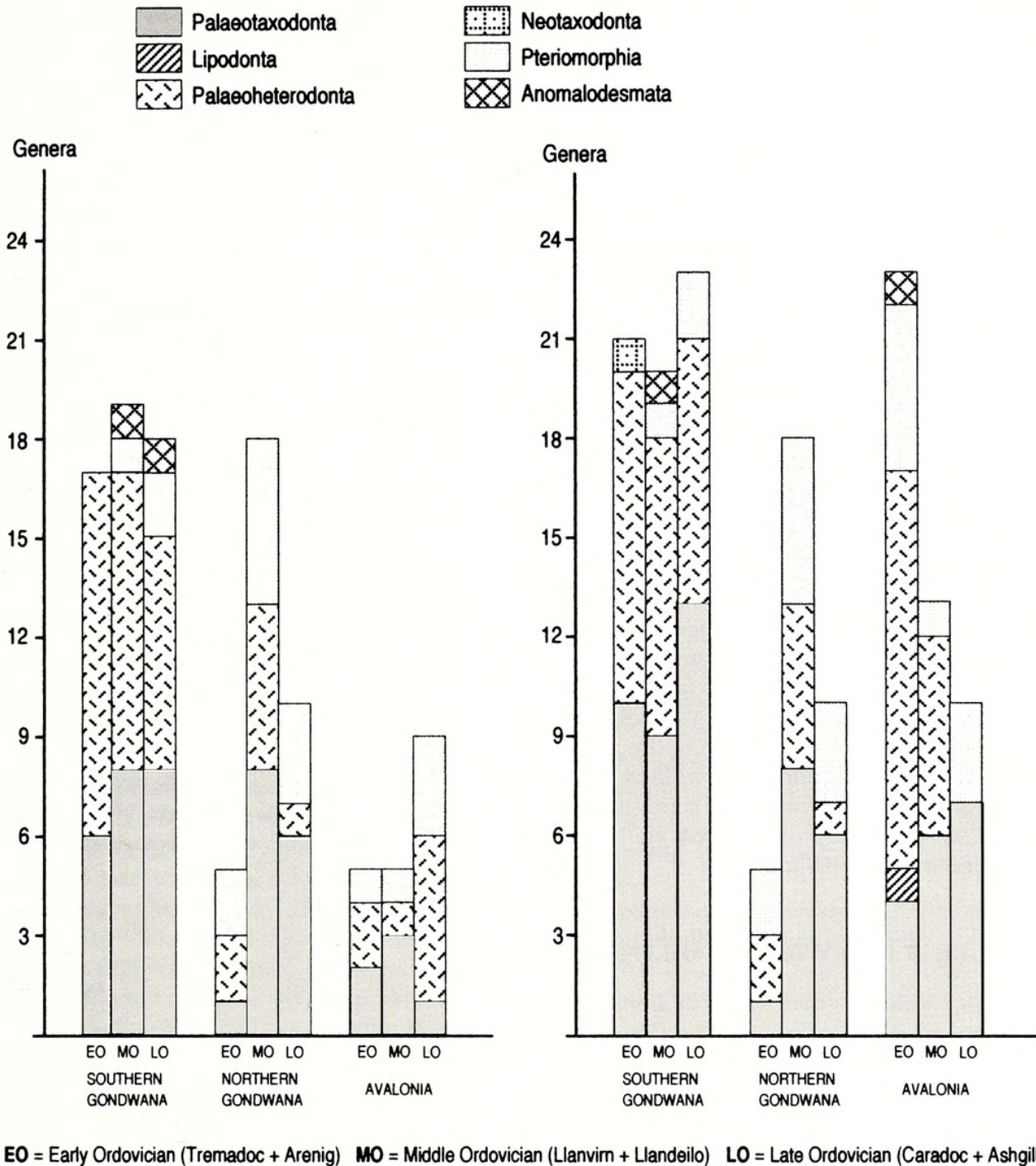


Fig. 2. Comparison of two successive compilations of data concerning the Ordovician bivalves. It shows the effect of the recent investigations in the field. Left: data from 1993 (after Babin). Right: data from 1999.

the "Acéphalés" (*i.e.* to the bivalves), it comprises 342 pages and 361 plates to describe 1269 species distributed among 58 genera, of which 20 are new. However, they are not all from the Silurian, as the title mentions, but they are distributed from the lower Ordovician (Llanvirn) to the middle Devonian (Givetian) because Barrande always used Murchison's original definition (1835) of the Silurian Period. Thus, to utilize Barrande's data, one needs to refer to more recent documents of Czech geologists for the tem-

poral correlations. Concerning the Devonian, the important books of Hall (1884, 1885) with the description of 69 genera, of which 49 were established in North America, and of Beushausen (1895) with the description of 46 genera from the Rhineland, excluding the pteriomorphs studied by Frech (1891), are easier to consult regarding the stratigraphical assignment. Nevertheless, the utilization of the data for the database requires the establishing of synonymies between all these works.

These non-exhaustive remarks go to show that every database is imperfect, provisional and could be continually improved.

- **Paleogeography.** To locate the paleodiversifications in space we have at our disposal numerous and more or less different paleogeographic reconstructions. Despite great strides over three decades in this field following the plate tectonics model, we know that these reconstructions remain difficult for the Paleozoic. However, a general enough agreement exists today about the broad outlines of the relative position of the large paleocontinents and it is sufficient for the present matter.

Taking all these restrictions into consideration, I will consider the available data to draw the main events regarding bivalve paleodiversifications from the Ordovician to the Devonian. Nevertheless, before examining the rough data, diversifications need some consideration. Actually, when the radiations are put in evidence, the question remains of their explanation. Two categories of causes need consideration. Are the diversifications the result of intrinsic factors or of inductive extrinsic conditions? The former may particularly correspond to key innovations and it is understandable that many new structures, innovative ones, are not preserved in the fossil record. The interpretation of the material, more often than not hypothetical, will be an inescapable way to reconstruct the soft parts. As for the extrinsic factors, some of them are given by the sediments like the grain-size or some information regarding the bathymetry, the oxygenation, etc., but many other factors will remain hypothetical too.

THE GREAT ORDOVICIAN RADIATION

The need to look at the Ordovician diversification has been renewed for some years because this Period encompasses one of the most important evolutionary radiations. This is particularly clear regarding the bivalves, which offer in the fossil record a true explosion during the Arenig (late Lower Ordovician). In reality, there is a very poor record and important gaps in the story of Bivalvia before the Arenig and one may consider that this apparent explosive diversification is an artefact. The extremely scarce representatives of Cambrian bivalves, small shells of perhaps meiofauna and "the abysmally poor record of bivalves from the Tremadoc Series (early Lower Ordovician) of the Ordovician" (Cope, 1995) suggest such an artefact. Diverse reasons can be offered to explain this lack of fossil bivalves, such as their particular fragility, unfavorable environmental conditions for their preservation, or geodynamical causes such as the rifting of the near-shore shelves that they inhabited, or even deficiency of the investigations, among others. No one consideration is really

convincing. There are fossils of other marine benthic groups during the upper Cambrian and Tremadoc. Finally, as the Ordovician was a period of important radiation for many groups, it is not surprising to observe the same for bivalves. However, its explosive aspect with the simultaneous appearance of representatives of each subclass is very peculiar. Unfortunately, the paucity of information before the Arenig remains a serious handicap to understanding the temporal relations between the subclasses.

Considering the known fossil record, it is noticeable that these Arenig bivalve faunas were located on the peri-Gondwanan shelves (Babin, 1993b), Avalonia being considered as a neighboring area (Fig. 3). Possible reasons to explain this spatial restriction have been considered (Babin, 1995, Cope and Babin, 1999). Clearly the temperature of the sea water was not a deciding factor since the faunas were settled from very high latitudes (Morocco, Montagne Noire) to very low latitudes (Argentina, Australia), in spite of some obvious preferences such as the deposit-feeding paleotaxodonts, for instance, which are more numerous and varied in the high latitudes. On the other hand, a condition shared by the whole peri-Gondwanan shelves is siliciclastic sedimentation, and it is clear that all these first bivalves inhabited clastic sea-beds wherein they had infaunal or semi-infaunal modes of life. This relationship was probably linked with food supply because terrigenous sediments are considered more favorable from this point of view. Moreover, another distinctive feature of the Early Ordovician bivalve settings is their shallowness. The deep-

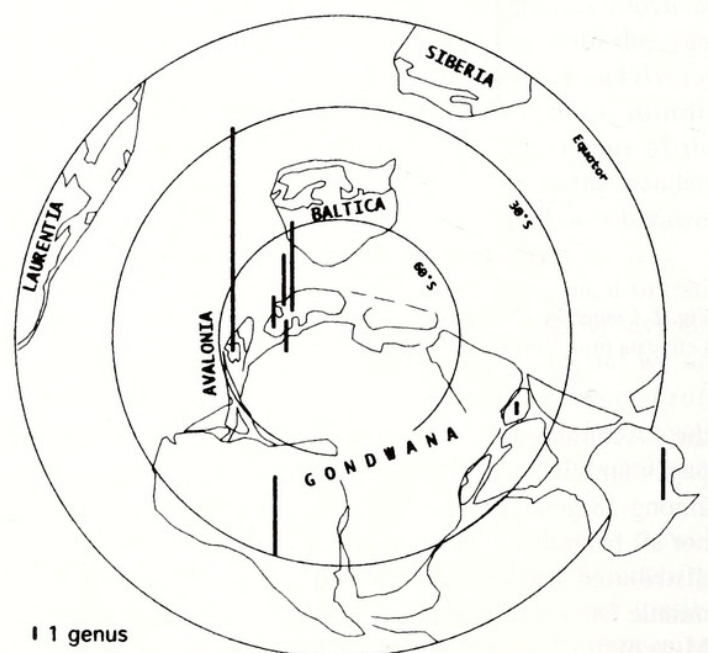


Fig. 3. Peri-Gondwanan location of the bivalves during the late Tremadoc-Arenig, south polar view.

est environments were perhaps those of the Montagne Noire (France), but it was certainly less than fifty meters in depth. So, it is clear that the early bivalve diversification was globally located in relatively shallow waters and is in accordance with Jablonski and Bottjer's model (1990) regarding the role of the onshore settings for the appearance of the major groups. In these environments, the empty ecospace hypothesis (Erwin, 1994) may help explain the burst of the endobenthic and semi-infaunal bivalves, which were the first representatives of shelly burrowers.

Finally, it seems that this preference for siliciclastic sedimentation may have been the restrictive factor against a geographic expansion towards other plate margins like Baltica or Laurentia [the recent assertion of Droser *et al.* (1995) and of Droser *et al.* (1996) that "bivalves occur in Ibexian strata" in shell beds is probably erroneous. The oldest North American described bivalves are from the uppermost Whiterockian or very lowest Blackriveran (pers. comm. of R. Ross, 4 Oct. 1999)]. It is also plausible that sheer ocean width was a barrier to the migration of the planktic larvae. Bivalve larvae live about six weeks before settlement; however Baltica, for instance, was not so far from Gondwana-Avalonia (Fig. 3). Prevailing surface currents could have been unfavorable but other benthic Arenig mollusks like rostroconchs were nevertheless cosmopolitan.

The other aspect to consider about the initial diversification concerns the possible impact of some intrinsic factor. I have said that it is difficult with the fossil material, that is with the hard parts (shells) only, to discern one or several key characters that induced the adaptive radiation. Stanley (1975, 1977) suggested that "the delayed radiation (since the first Cambrian bivalves) was triggered by the origin of the byssus" and that "retention of the byssus into the adult stage was an important aspect of the initial adaptive radiation of the class." However, this consideration seems based on North American bivalves with emphasis on the upper Ordovician faunas with pteriomorphs. Tevesz and McCall (1976, 1985) who proposed an epifaunal mode of life for Cambrian bivalves, suggested "that the Ordovician expansion of pelecypods is due to their invasion of the infauna habitat" and "that the delayed radiation of pelecypods was due to the Ordovician evolution of some other non-preserved structure that promoted survival of the group, such as, for example, some essential pedal musculature or a more efficient circulatory system."

One fundamental anatomical change could have been realized with the development of gills involved in the feeding process, that is with the appearance of the filibranch gill (Yonge 1947). Waller (1988) suggested that the *Tironucula* group, small paleotaxodonts from the Llanvirn (Middle Ordovician; see below), "probably had already evolved filibranchiate gills", and since 1995 Cope has cor-



Fig. 4. *Cardiolaria beirensis* (Sharpe, 1853) from the mid Ordovician of Spain. This paleotaxodont shows two separate series of teeth anterior and posterior; Cope (1995) assumed that this arrangement could be functionally related with filibranch gills. x6.

related this change of the gills with the early diversification of the bivalves. Cope also looked for paleotaxodonts that could have acquired this important novelty. By analysis of the dentition allowing rapid fluttering of the valves to void the pseudofaeces, Cope (1995) proposed that it could have been the *Cardiolaria* group (Fig. 4). The advantages and changes of the mode of life resulting from this key innovation have been discussed elsewhere (Cope and Babin, 1999).

However that may be, it appears that the Arenig bivalve faunas, located in Gondwana and Avalonia, contained representatives of all subclasses except Cryptodonta, if that is restricted to the praecardioids. The causes of this explosive radiation remain unclear, probably an interference of intrinsic and extrinsic factors, but the first unknown divergences took place probably before the Arenig (five or six genera are known from the latest Tremadoc of Gondwana).

During the Middle Ordovician, that is the Llanvirn of the standard stratigraphical scale, bivalve faunas remain located in essentially the same areas, often with a great abundance and variety such as in the Ibero-Armorican massif (Babin and Gutiérrez-Marco, 1991). Seven genera are also known in Avalonia (Cope, 1999). The Llanvirn was a period of transgression, and the flooding of the Gondwana craton also stimulated the burst of other groups like the trilobites. However, the geodynamic activity simultaneously modified the relations between the continental plates; thus, the progressive reduction of the Iapetus Ocean allows some communication between both its sides (Fortey and Cocks, 1988). For the first time we find some scarce bivalves in Baltica with *Babinka* and in Laurentia (Svalbard) with *Tironucula*.

A large dispersal of the bivalves over an extensive area (Baltica, Laurentia, Siberia) took place during the Upper Ordovician (Fig. 3) probably favored by the mid-Caradoc transgression, perhaps the most extensive in Phanerozoic history. The Chinese Ordovician bivalves probably proceed too from the upper Ordovician. It is no doubt the case for some of the genera in Yunnan cited by

Guo (1985) and assigned possibly to the Arenig-Llanvirn. Then, the dispersal in the earliest Late Ordovician provides bivalves firstly in the inshore siliciclastic environments such as the St. Peter Sandstone (Minnesota) but it corresponds rapidly to a second important diversification exploring particularly the epibenthic mode of life on the favorable carbonate platforms of these low latitudes. The pteriomorphs, for instance, at the time rapidly radiate while some modiomorphoids (*Modiolopsis*, *Corallidomus*, and *Whiteavesia*) are the first gregarious genera. Are Cryptodonta also present in the Late Ordovician of Laurentia? A species of *Vlasta* (*V. americana*) was cited by Fritz (1951) in the Richmondian of Canada but Kříž (1998) considers it is not a *Vlasta*. Elsewhere, other genera of the Upper Ordovician, such as *Shanina* from China and *Shaninopsis* from Sweden are not Vlastidae after Kříž (1998). We do not know precisely whether there were Cryptodonta in the Upper Ordovician. The origin of this subclass is obscure.

Simultaneously, in the high latitudes of south Gondwana (Ibero-Armorican area, Bohemia) bivalves became scarce and we do not know the reason. It is long before the cooling of the latest Ordovician and in any case some bivalves continue during the Ashgill in Morocco near the Gondwanan cap-ice.

Thus, the major paleodiversification of bivalves took place on the Gondwanan and neighboring Avalonian shelves as early as Late Tremadoc-Early Arenig. The dispersal and migration during the Late Ordovician favored particularly the radiation of epifaunal bivalves. The first peak of the diversity of the suspension feeding bivalves took place throughout the Upper Ordovician (Bretsky, 1973).

It is noticeable also that the sizes of the first bivalve representatives were small or moderate, the largest known form is a *Modiolopsis* from the Arenig of Wales of almost 50 mm length (Cope, 1996). The increase of size in the Middle and Upper Ordovician affected especially the pteriomorphs and paleoheterodonts but the largest bivalve known from the Ordovician is the problematic "*Vlasta*" *americana* quoted above with a length of about 120 mm (Fritz, 1951).

THE SILURIAN - DOWNTURN FOR THE BIVALVES

The mass extinction of the latest Ordovician, probably one of the most drastic crises, evidently affected the bivalves; nevertheless all the subclasses crossed the threshold of the Silurian. Moreover it is noteworthy that the Bivalvia have stood up to all the mass extinctions (Fig. 1), and their better success than other benthic groups (bra-

chiopods for instance) is often explained by this remarkable adaptive resistance to major crises.

In a fundamental paper Kříž (1984) gave a quantitative overview of changes in bivalve faunas between the Ordovician and Silurian and of the new Silurian radiation of the Class. He worked with data taken from the *Treatise on Invertebrate Paleontology* (1969) modified by his own taxonomic concepts classifying, for instance, a large part of the Cryptodonta of the *Treatise* in the pteriomorphs. In spite of the new data gathered since 1984, this analysis is still probably conclusive enough. It shows that about 30% of the Ordovician genera survived into the Silurian; 35% of them were free-burrowers and 58% were endobyssate infaunal and semi-infaunal. Obviously, the epifaunal bivalves were less resistant against this crisis from which the causes (climatic deterioration, regression then transgression with anoxic conditions) are probably many and are poorly established. The widespread anoxic conditions persisted during the Early Silurian (Llandovery) and it was only a period of survival for the bivalves without clear recovery (Fig. 5). Among the fauna, the paleotaxodonts included several surviving Ordovician genera (about eleven after Liljedahl, 1994), but their diversity had distinctly decreased; they were widely distributed but with a possible preference for the equatorial areas (Laurentia, Baltica, South China, Australia). However, they were sometimes present at higher latitudes (South America; Sánchez *et al.*, 1995). Locally, as in Gotland (Baltica) some endemic genera appeared (Liljedahl, 1984). However, the subclass did not experience Silurian expansion. The paleoheterodonts, anomalodesmatans, some pteriomorphs, endobyssate infaunal and semi-infaunal suspension feeders, were the major participants of a very weak diversity increase while the epifaunal pteriomorphs remained inconspicuous after an almost total extinction at the end of the Ordovician (Fig. 5).

The environmental changes of the Middle Silurian (Wenlock) induced a new bivalve diversification which continued during the Ludlow (early Late Silurian). In several basins (Bohemia, Montagne Noire, Morocco, etc.), the development of alternating soft muds and biodetritral deposits favored the abrupt diversification of shallow free-burrowing suspension-feeders. Following Kříž (1979), the new specialized genera, such as *Cardiola* (Fig. 9) and others that he considers as pteriomorphs (see above), proceeded from epi- or endobyssate ancestors by a reversion neoteny. In these environments endobyssate infaunal and endobyssate semi-infaunal suspension-feeders also showed a rapid development with, for instance, Modiomorphidae and some (?) Pterineidae [Stanley (1972) and Bailey (1983) admitted that some Paleozoic pterineids were endobyssate; for Johnston (1993), these views are poorly supported, and all the pterineids were epibyssate]. Lastly, the epibyssate

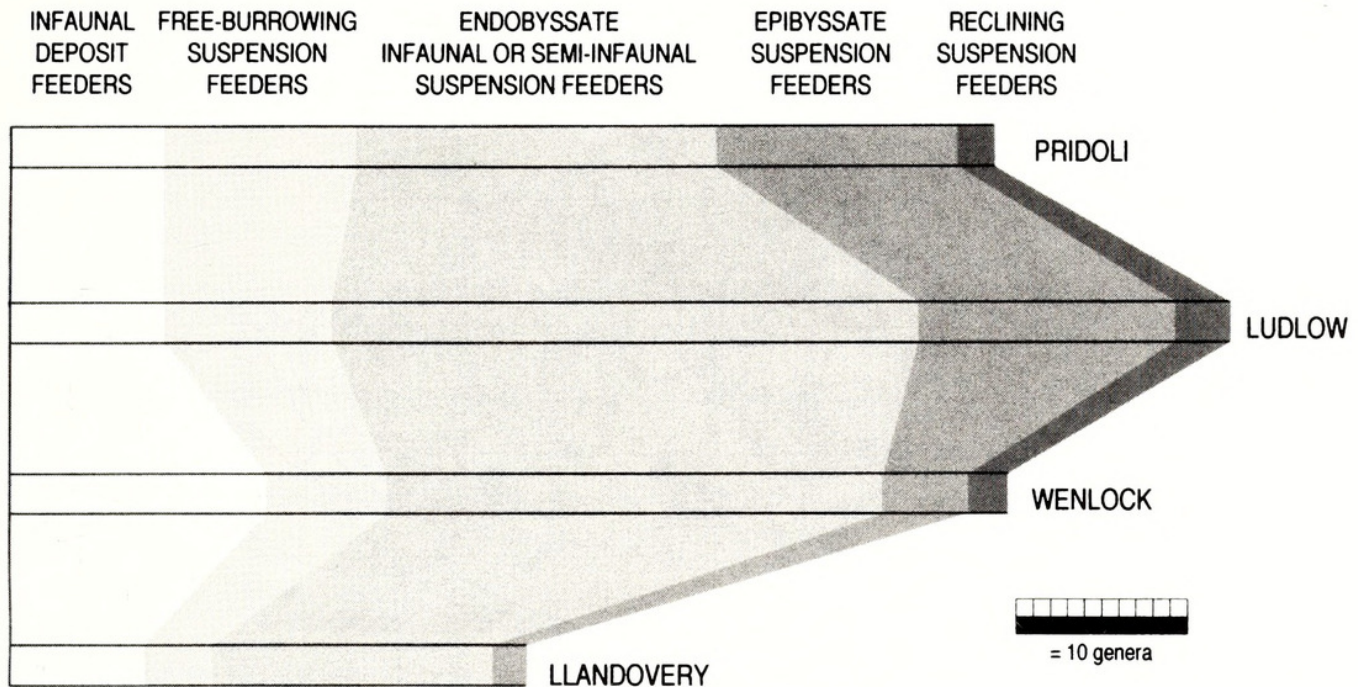


Fig. 5. Silurian diversification of the bivalves with their life habits (after Kříž, 1984, modified).

bivalves increased rapidly after the Wenlock and during the Late Silurian, and Kříž (1984) considers that this extensive adaptation is "one of the most important characteristics of the evolution of the Bivalvia in the Period." The distribution of the Bohemian-like fauna, linked with low oxygen conditions on the sea-bed is explained by the surface current circulation (Bogolepova and Kříž, 1995). Johnston and Collom's new ideas on cryptodonts as chemoautotrophs (1998) are supported by the existence of these low oxygen conditions. It is interesting to note that in their paper, Bogolepova and Kříž (1995) indicate the presence of such fossils as early as the lower Llandovery (basal Silurian) in Siberia, considering them as ancestral forms of the Bohemian-type bivalves. Can we regard the Siberian area as the cradle of these forms? It is not possible to reply with certainty to such a question. To locate precisely the cradles of the groups remains another problem generally insoluble for the paleodiversifications. During the Wenlock and Ludlow, some rare elements of the Bohemian-type fauna could have reached other areas, *Slava* is known in Laurentia (Pojeta and Norford, 1987), *Dualina* is cited in South America (Sánchez, 1991) and Florida (Pojeta *et al.*, 1976).

The fauna considered in these above-mentioned basins is different from that of the other areas dominated by paleotaxodonts, paleoheterodonts, and anomalodesmatans (Fig. 6). In these associations occurring in both clastic and carbonate platform muds, deposit-feeding species (paleotaxodonts) generally formed a large majority of the bivalves. Lastly, in the reef communities developed in sev-

eral areas the bivalves constituted a minor group (Watkins, 1997). They were represented especially by epibyssate suspension-feeders like ambonychiids, pterineids, with genera known in other level-bottom associations with a lower species diversity and with larger specimen sizes. Apart from the megalodont *Megalomoidea* known in some reefs, there were no bivalves specialized for reef environments.

Finally, succeeding the Late Ordovician mass extinction, the Silurian was a Period of progressive recovery for the bivalves. Two major kinds of environments induced different adaptive responses. On the platforms, with normally oxygenated waters and at all latitudes, representatives of the main subclasses are found. In the Bohemian-type basins, environmental conditions with a low oxygenation induced an explosive evolution of the Pteriomorpha and Cryptodonta giving an odd cachet to the faunas. A slight decrease in bivalve diversity occurred during the Pridoli (Late Silurian); however, there was not a crisis like that of the Upper Ordovician.

THE DEVONIAN - DIVERSIFICATION AND DISPERSAL OF BIVALVE FAUNAS

The Devonian was another period of important diversification for the bivalves. According to Kříž (1979b), basing his argument on the *Treatise on Invertebrate Paleontology* (1969), the Devonian diversity in comparison with that of the Silurian increased 59% for genera and 36% for families. Amongst the latter it is noticeable that a dozen

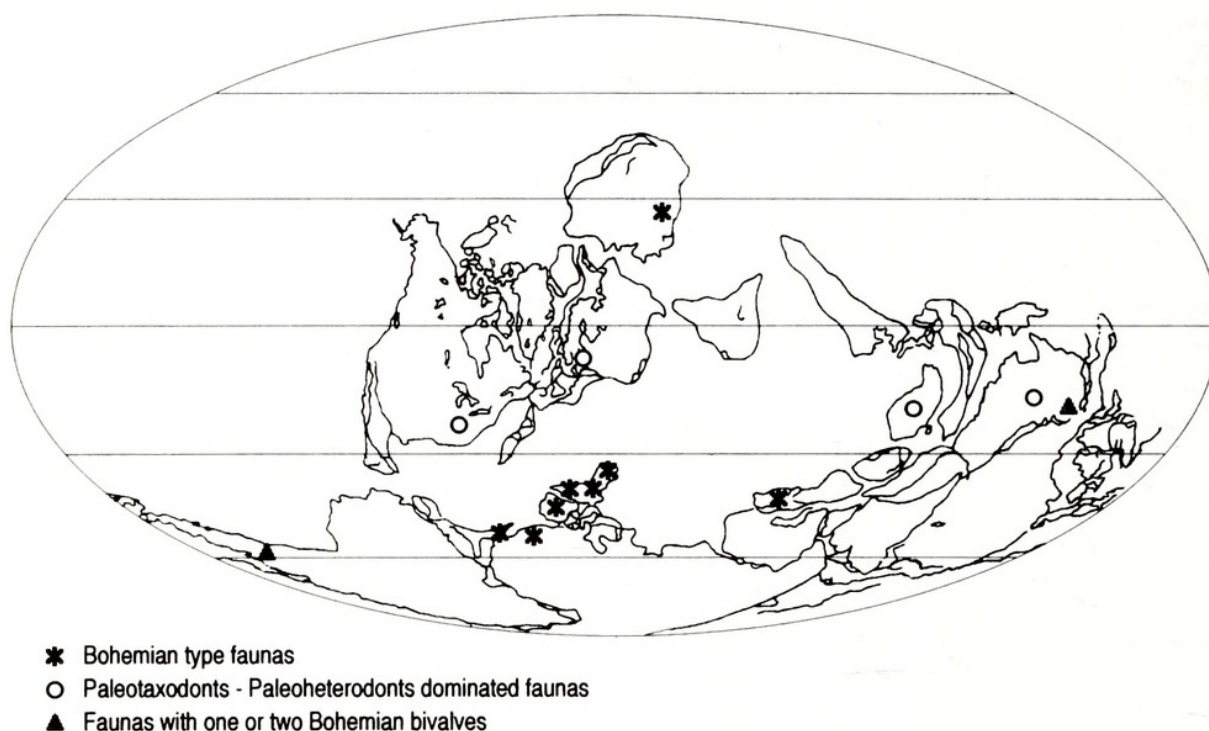


Fig. 6. Distribution of Wenlockian bivalve faunas (after Babin, 1993a, updated).

of them are extant families, four of which are new families of Heterodonta. Thus the Devonian bivalve fauna acquired a more modern aspect.

The increase in diversity was progressive during the Early Devonian and attained a peak in the Emsian. A first decrease took place during the Middle Devonian (Fig. 7) with different aspects according to the regions. After the Givetian, the global decrease became more pronounced until the end of the Devonian. It may be the result of "plate-tectonic regulation" (Kříž, 1979b) but it was also probably related to the development of regional environmental deterioration, especially in regard to benthic oxygen.

The Early Devonian bivalve faunas were particularly numerous on the terrigenous shallow sea-floors. The paleotaxodonts remained abundant in such environments and sometimes associations of *Palaeoneilo* or *Nuculites* were almost monospecific. Nevertheless, the pteriomorphs and the anomalodesmatans were particularly varied. Some of the former were possibly attached to flexible algae (Johnston, 1993) though the largest of them were fixed on elements on the sea-bed. In Europe, the Lower Devonian bivalves have been described and listed since the nineteenth century in the siliciclastic sediments of the Rhenish area (Frech, 1891; Beushausen, 1895; Maillieux, 1937, etc.) where they were especially numerous, a proportion of them being endemic genera. Similarly, in the carbonate facies of Bohemia a large part of the bivalve genera were endemic such as the cryptodonts *Antipleura* or *Kralovna*. In North America the generic variety is lesser but recent investiga-

tions (Johnston and Goodbody, 1988; Desbiens, 1994a, b) show, in siliciclastic sediments of Canada, the presence of several Rhenish genera. In South America in cool water the genera cited (Sánchez *et al.*, 1995) were cosmopolitan. In North China, 28 genera are cited, all of which were cosmopolitan, whereas 13 of the 56 Lower Devonian genera cited in South China were endemic, especially during the

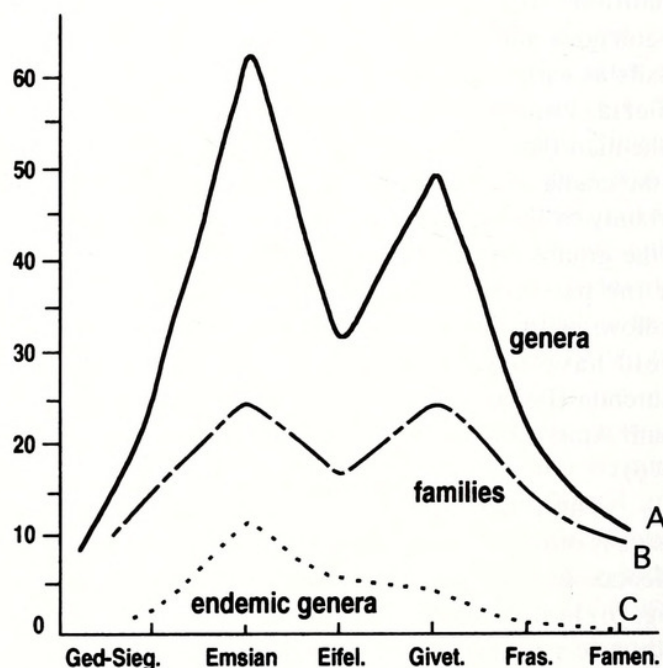
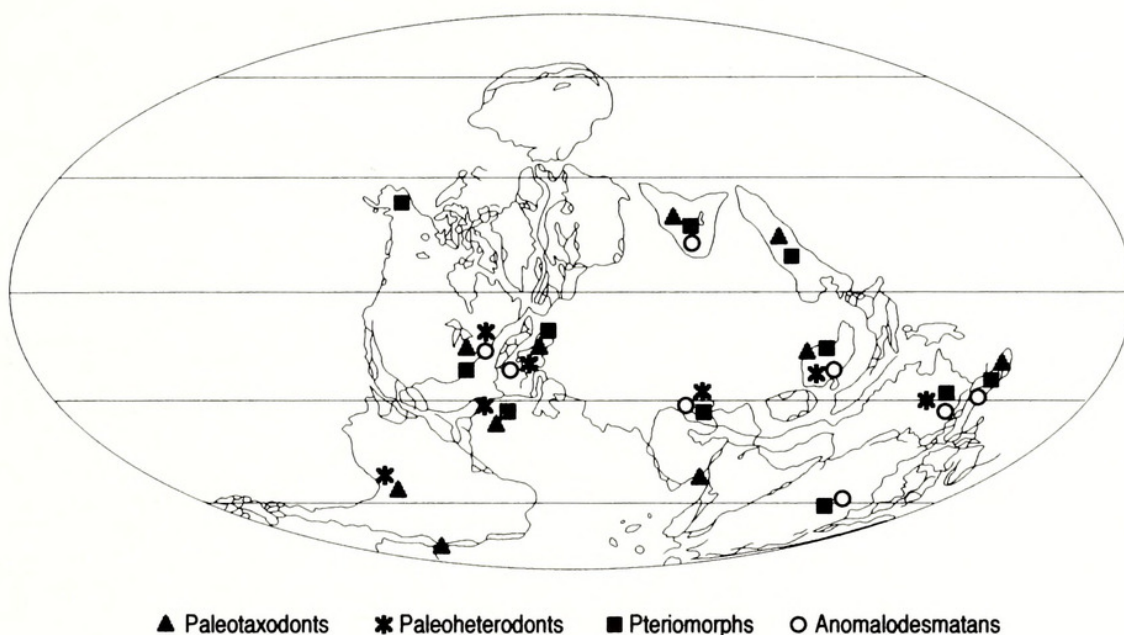


Fig. 7. Curves showing variations of Devonian bivalves in China. The Y-axis is Number (after Zhang, 1988).



▲ Paleotaxodonts * Paleoheterodonts ■ Pteriomorphs ○ Anomalodesmatans

Fig. 8. Characteristics of Emsian bivalve faunas. West-European faunas have been taken as reference, and for each region those groups are shown that have at least three genera in common with them (after Babin, 1993a, updated).

Emsian (Zhang, 1988). Like the Rhenish area, the latter region was apparently an important center of diversification (Fig. 8). In southeastern Australia, Chapman (1908) described 27 genera and noted that they were known in North America or Europe. More recently, from a shallow marine carbonate shelf environment Johnston (1993) described a remarkably preserved silicified fauna of bivalves. Amongst 24 genera cited, two or three are endem-

ic; the others show close affinities with the bivalves of central Europe. From the lower Devonian (probably Emsian) of New Zealand, Bradshaw (1999) lists 27 genera and she acknowledges only "a distant link with Europe" for her fauna, however at the generic level, at least 16 of these taxa are known also in Europe. Finally, bivalves experienced a noteworthy diversification during Emsian times but they evolved only at family, genus and species levels. This radiation is probably related to the Emsian transgressions, and the most favorable environments seem have been shallow terrigenous shelves located at low latitudes such as central Europe or south China.

After the Emsian acme a slight decline occurred during the Middle Devonian. However bivalve faunas were still flourishing in many regions but with little new radiation. For instance, the megalodontids show some adaptive diversification with new genera such as *Megalodon* and *Eomegalodus*, these having a thick shell related to coral environments. The most significant for Middle Devonian times is the continued dispersal of the bivalve faunas, resulting in increased cosmopolitanism. It is the result of the progressive restriction of some oceanic areas such as the Rheic between Europe and North America. Bailey (1983) has finely illustrated the similarities between the Rhenish and Appalachian communities; however, there was some diachronism, since the Middle Devonian faunas of North America include Lower Devonian forms from Western Europe. Therefore, the fauna migrated westwards giving a large expansion to the genera initiated primarily in the Rhineland.

The decline of the bivalve faunas continued through

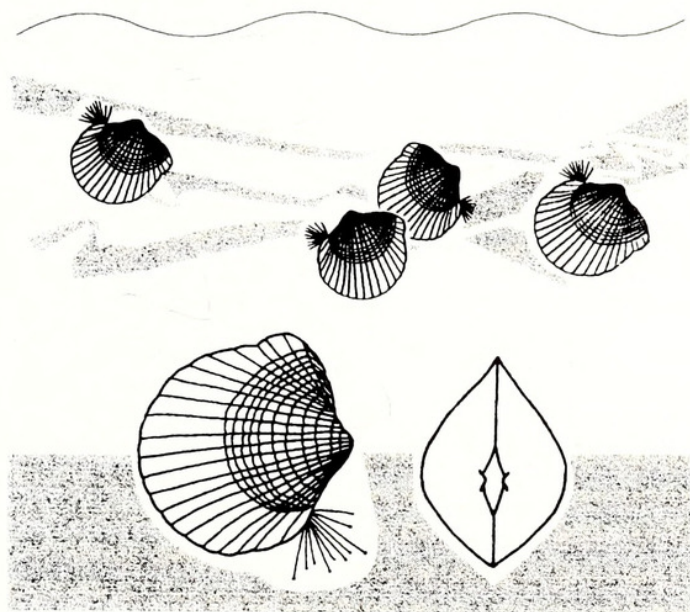


Fig. 9. Possible life habits of small praecardioids. *Cardiola* (below; Silurian) as semi-endobysate according to Kříž (1979a). *Buchiola* (above; upper Devonian) as epibyssate pseudoplankton according to Babin (1966) (after Vannier *et al.*, 1995; modified).

the Late Devonian, but the paleogeographic changes induced some new limited diversifications. For instance, the development of large continental areas such as the Red Sandstone continent was favorable to the first appearance of fresh-water bivalves with *Archanodon*. In the marine environments a new extension of dysaerobic facies induced the development of small praecardioids (*Buchiola*) and pterioids (*Guerichia* = *Posidonia* in previous papers like Babin 1966) which were probably attached to floating algae or wood fragments (Fig. 9) although Grimm (1998) argues that *Buchiola* was infaunal. After the drastic decrease by the end of the Frasnian some bivalve faunas of the latest Famennian (Strunian) dominated by pteriomorphs and located at the southern margin of Laurussia initiated a new diversification (Amler 1996). Nevertheless, a clear decline in bivalve diversity is related to the global crisis near the end of the Devonian.

CONCLUSION

After a very discrete appearance during the Lower Cambrian and an obscure history during the Cambrian and the earlier Ordovician (Tremadoc), bivalves showed during the Arenig a dramatic phase of radiation corresponding to the famous Ordovician diversification. It seems that in a few millions years all or nearly all, the subclasses appeared. This drastic paleodiversification coincided with key innovations like the filibranchiate gills and the retention of the postlarval byssus in the adult. It was located on shallow clastic sea-beds, apparently on the peri-Gondwanan and Avalonian shelves. After a major dispersal during the Upper Ordovician corresponding notably to the diversification of the semi-endobyssate and epibyssate forms, the bivalves underwent a first decline with the latest Ordovician mass extinction. New radiations occurred during the Middle and Upper Silurian especially with the development of the cryptodonts related to particular dysaerobic environments, and with an explosive evolution of the pteriomorphs. The Devonian opened another period of paleodiversification at family, genus and species levels but with a progressive acquisition of a more modern cachet. The acme of this diversification took place during the late Early Devonian (Emsian), and the paleogeographic changes led to the establishment of cosmopolitan faunas. During this Period the bivalves dispersed into various marine environments and for the first time into fresh-water. A second decline coincided with the Late Devonian mass extinction.

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