

Sibling echinoderm taxa on isolated Ordovician continents: Problem of center of origin

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Morphologically similar echinoderm genera are mostly known from the Ordovician of two isolated continents, Baltica and Laurentia, although these landmasses were strictly isolated biogeographically by the Iapetus Ocean and had different climates during the Early and Middle Ordovician. The morphological characters of most of these echinoderm genera exclude the possibility that Baltic genera evolved from Laurentian forms or vice versa and suggest that their common ancestral group was from a different region. I proposed to name such genera 'sibling genera', or twin genera by analogy with sibling species. Eocrinoid sibling genera are representatives of the cryptocrinid-rhipidocystid clade. Baltic *Paracryptocrinites* and *Cryptocrinites* are sibling genera of Laurentian *Columbocystis*, *Springerocystis* and *Foerstecystis*, Baltic *Rhipidocystis* is a sibling genus of Laurentian *Mandalacystis* and Baltic *Neorhipidocystis* is sibling genus of Laurentian *Batherocystis*. It is assumed that North American platycystid paracrinooids, cryptocrinid and rhipidocystid eocrinoids evolved from a common ancestral eocrinoid, similar to *Paracryptocrinites*. Sibling genera are also known among other Ordovician echinoderms, for example, crinoids (hybocrinids), edriasteroids (edrioblastoids) and rhombiferans. Some genera migrated from Baltica to Laurentia and vice versa. The temperate warm water seas of eastern Gondwana in the northern China-Australian region were a possible biogeographical center of origin, diversification or distribution of Laurentian and Baltic sibling genera. Biogeographical analysis of Baltic echinoderms shows that the Baltic Region could be viewed as a 'museum' or 'storehouse' for many of them, they immigrated and survived there for some considerable time, rather than a 'cradle', where they arose and from where they migrated to other continents.

- Key words: Ordovician, echinoderms, sibling taxa, biogeography, Baltica, Laurentia, Gondwana.

ROZHNOV, S.V. 2010. Sibling echinoderm taxa on isolated Ordovician continents: Problem of center of origin. *Bulletin of Geosciences* 85(4), 671–678 (4 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received February 1, 2010; accepted in revised form September 6, 2010; published online November 30, 2010; issued December 20, 2010.

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Biogeographical analysis of the distribution of taxa is particularly important at the point of significant evolutionary radiation as it provides a more reliable foundation for one or another phylogenetic reconstruction based on morphological data. The Ordovician evolutionary radiation during which many metazoan classes, including Recent taxa, appeared, is of particular interest in this respect (review in Webby 2004). Echinoderms compose one of the most important benthic groups of Ordovician invertebrates (Rozhnov 2002, 2007a; Sprinkle & Guensburg 2004). In the Ordovician, ten echinoderm classes originated, including all the present day retained forms, *i.e.*, crinoids, sea urchins, starfishes, ophiuroids and, probably, holothurians (Rozhnov 2002). The relationships between these classes and the higher taxa containing them, centers on their origin, features of geographical distribution and development in the epeiric seas of separated continents. They are important problems in the study of echinoderms which display gene-

rally valid patterns of macroevolution. The present paper develops an approach which takes into account probable biogeographical links between the epeiric seas of separated continents.

Geographical, climatic and sedimentological features of Ordovician continents

In the Ordovician, there were four large isolated continents (Fig. 1) positioned relatively far from each other: Baltica, Laurentia, Siberia and Gondwana (Cocks & Torsvik 2002). Siberia was close to the equator in the tropical climatic zone (Cocks & Torsvik 2007). The echinoderm fauna of the Ordovician seas of this continent has not been studied in detail; however, it was probably relatively poor. Otherwise, they would be well represented in collections of

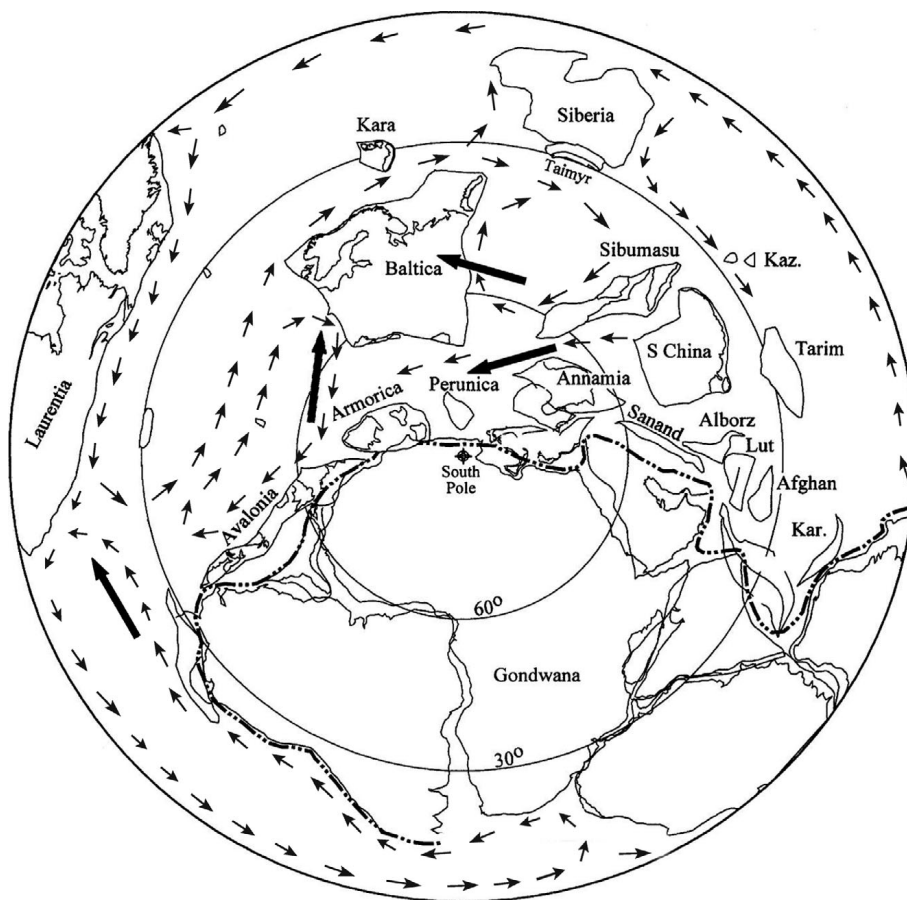


Figure 1. Early Ordovician geography (after Cocks & Torsvik 2002). Large arrows show possible migration routes of sibling echinoderm genera from East Gondwana to West Gondwana and Laurentia. Small arrows show possible oceanic currents based on the data from Christiansen & Stouge (1999) with additions.

marine invertebrates from hard-to-reach areas of Ordovician deposits of this continent, collected by the many stratigraphers and paleontologists by the middle of the 20th century. Gondwana was the largest continent, extending from the South Pole to tropical latitudes. Cold climatic conditions were characteristic for most of its area in the Ordovician, although eastern Gondwana extended to the equator, with a much warmer climate (Cocks & Torsvik 2002). The most thoroughly investigated echinoderm fauna comes from the cold marginal areas of West Gondwana (Gondwanan Africa and peri-Gondwanan Europe), with mostly terrigenous sedimentation (Lefebvre & Fatka 2003). Laurentia was near the equator during the entire Ordovician. A tropical climate prevailed, with mostly carbonate type sedimentation. This continent has yielded the richest echinoderm fauna (Sprinkle & Guensburg 2004). During the Ordovician, Baltica moved from high latitudes towards the equator (Cocks & Torsvik 2005). Consequently, at the beginning of the Middle Ordovician, cold epeiric seas were replaced by temperate seas; they became warm from the end of the Middle Ordovician and tropical by the middle of the Upper Ordovician (Dronov & Rozhnov 2007). Carbonate sedimentation was established and prevailed from the very end of the Early Ordovician, even under cold-water conditions. Echinoderms appeared in Baltica

simultaneously with the beginning of carbonate sedimentation and rapidly became a dominant group in many benthic communities (Rozhnov 2007a). Echinoderm faunas of these continents differ considerably in composition and include many endemic genera. Nevertheless, they show certain similar features, in particular, morphologically similar taxa, which are undoubtedly closely related. The center of origin and distribution of these taxa and their migration routes are an interesting biogeographical problem, and are important for the resolution of phylogenetic problems of various taxa, that were prominently manifest during the Ordovician evolutionary radiation.

Opportunity of dispersal of Ordovician echinoderms

The majority of Ordovician echinoderms were sessile animals, and migrated only during the larval stage. Free-living Ordovician echinoderms migrated mostly by means of planktonic larvae since the adults were slow moving. Expansion usually occurred along continental coasts due to transportation of larvae by coastal currents, and was rather rapid, covering all shelves. In some cases, migrations may have occurred in directions opposite to the prevailing

currents due to the displacement of larvae during storms and unusual changes in the prevailing winds. Only considerable changes in water temperature and salinity prevented expansion along a coast. Larvae could be transported from one continent to another only by oceanic currents, as all Ordovician echinoderms were shallow-water animals and it was impossible for them to cross oceans in the manner of a step-by-step migration. Migration of echinoderms from one continent to another required either the opportunity for larvae to remain in currents for some considerable time or successive migration via a series of islands and microcontinents. All modern crinoid larvae are lecithotrophic, that is unable to eat independently (Holland 1991, Smith 1997). Therefore, they are unable to endure long-term travel in oceanic currents. Paleozoic crinoids, like other pelmatozoan echinoderms, were probably considerably restricted with reference to migration using oceanic currents. Lecithotrophic larvae live only a number of days whereas planktotrophic larvae usually live for several weeks before setting (Ivanova-Kasas 1978). An average speed for large-scale oceanic currents is 10–20 cm/sec. (360–720 m/h), that is, approximately 50–100 km per week. Thus, with a current of normal speed, even typical planktotrophic larvae can travel at the most 400 km. Accordingly, the tropical benthic fauna of the eastern Atlantic is much poorer than the west Atlantic fauna (Briggs 2007). These data explain the considerable endemism at generic level in echinoderm faunas of different continents in the Ordovician. In some cases, the effect of great distances between these continents was intensified by considerable climatic differences. It is more difficult to explain certain similarity between the echinoderm faunas of these continents than the differences between them.

Probable causes of similarity between Ordovician echinoderm faunas from separated continents

As continents are strictly isolated from each other, the similarity of their faunas may be explained by several factors. First, the similarity could be residual, *i.e.*, accounted for by the absence of strict isolation between these continents in a previous time. Another probable cause is migration of some taxa from one continent to another due to the unique conditions and (or) unique characters of a particular taxon. An example is provided by the global distribution of *Scyphocrinites* (Crinoidea) at the Silurian-Devonian boundary interval, which became possible due to the transformation of their attachment structure into a float (lobolith) (Haude 1972). Finally, the third possible cause of similarity is penetration of the two continents by similar taxa from a third region, which was the center of dispersal. To designate morphologically almost indiscernible species,

having a common ancestor but isolated reproductively, Mayr (1942) introduced the term twin (or sibling) species. These similar species often inhabit different isolated regions or biotopes. In paleontology the majority of benthic species with wide geographical and stratigraphical ranges may in fact be mixed sibling species in the biological sense, since they were established based on a limited number of characters, as compared with living taxa, and they could have been isolated reproductively both geographically and chronologically. By analogy with sibling species, morphologically similar genera and higher rank taxa, for example, families having a common ancestor at the same taxonomic level can be termed *sibling taxa*. In other words, morphologically similar genera, with a common ancestral genus, are designated *sibling genera*. The families having a common ancestral family are *sibling families*. The presence of sibling taxa on separated continents suggests that they migrated from a specific third region where their common ancestor dwelt (Rozhnov 2007b). At the same time, the ancestral taxon and its immediate descendant could be taken as sibling taxa because of the considerable changes in morphology connected with migration from one region to another. Travel in oceanic currents may have resulted in considerable morphological changes due to heterochronies, primarily pedomorphosis, which was provoked by an unusual duration of the larval stage (Rozhnov 2007c, 2009b). It is possible to distinguish sibling taxa from others by the analysis of individual and age variation, and also aberrant forms which may bring to light both important ontogenetic features and the morphogenetic potential of the taxa compared. As the forms compared are an ancestor and its descendant, morphogenetic potential of the first must be greater than that of the second; this may be manifested in the morphology of aberrant forms and in ontogenetic features. In sibling taxa, these features are not necessarily manifested. Many sibling taxa occurred in the echinoderm faunas of Ordovician epeiric seas of separated continents.

Sibling genera of northern marginal areas of Gondwana and Baltica

Many echinoderms, which were widespread in Baltica came there from the northern marginal areas of West Gondwana, probably using Avalonia as a biogeographical bridge. They include first of all the rhombiferans *Echinospaerites* and *Hemicosmites* and the diploporites *Sphaerorites* and *Haplosphaeronis*. This follows in that these genera first appeared in Gondwanan Africa and peri-Gondwanan Europe (Lefebvre & Fatka 2003), and penetrated into Baltica from the west. They entered Baltica Darriwilian: both genera of Diploporita entered at the end of the Volkhovian time, *Hemicosmites* at the end of the Kunda, and *Echinospaerites* at the beginning of the Aseri.

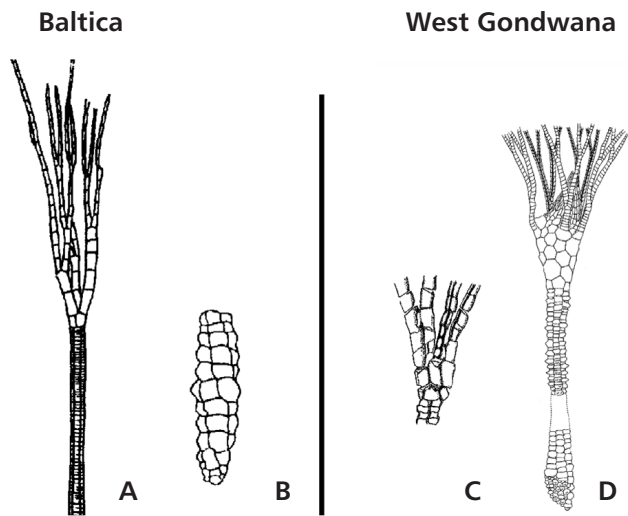


Figure 2. Possible sibling crinoid genera from Baltica and West Gondwana. • A, B – Baltic genera: A – *Tetragonocrinus pygmaeus* (adapted from Rozhnov 1988), B – *Hemistreptocrinus babinensis* (adapted from Arendt & Rozhnov 1995). • C, D – Gondwanan genera: C – *Ramseyocrinus cambriensis* (adapted from Cope 1988), D – *Aethocrinus moorei* (adapted from Ubaghs 1969).

In Baltica, these genera flourished, and for *Echinosphaerites* this continent was probably a secondary center of dispersal. Crinoids were poorly represented in the northern marginal areas of Gondwana, probably because of the prevalence of terrigenous sedimentation (Lefebvre & Fatka 2003). Two genera however were recorded in this area, Early Ordovician (Tremadocian) *Ramseyocrinus* and *Aethocrinus* (Lefebvre & Fatka 2003). These are unusual crinoids with a simplified structure (Fig. 2), which undoubtedly evolved from more complex ancestors as a result of paedomorphic changes. In particular, *Ramseyocrinus* has a quadriradial calyx (Fig. 2C), quadriradial column, and five simple arms deviating directly from the basal plates (the calyx lacks a radial circlet). In addition to the unusual structure of the calyx, *Aethocrinus* has a short pentapartite column (Fig. 2D) with prominent pentameres (Ubaghs 1969). Both genera probably migrated here from another region since suitable ancestors have not yet been recorded here. Baltica was inhabited by similar north Gondwanan genera.

Ramseyocrinus is similar to the Baltic *Tetragonocrinus* (Fig. 2A), which also has a quadriradial calyx and quadriradial column and lacks a radial circlet in the calyx, and with only three simple arms (Arendt 1985, Rozhnov 1988). Both genera probably evolved by paedomorphosis from the usual pentaradial forms with a radial circlet in the calyx. Apparently, *Tetragonocrinus* had undergone more profound paedomorphic changes, which resulted in the preservation of only three arms. *Tetragonocrinus*, along with some other crinoid genera, migrated into Baltica from the east at the end of the Latorpian. It is certainly probable

that *Ramseyocrinus* and *Tetragonocrinus* had a direct common ancestor which inhabited eastern Gondwana. Thus, they are also possible sibling genera.

Aethocrinus is similar to several genera known in Baltica only from columnal fragments (Fig. 2B). Arendt (1976) assigned them to a separate class, Hemistreptocrinoidea, as he took these fragments to be an unusual theca. However, the similarity to the column of *Aethocrinus* strongly suggests that all hemistreptocrinoids genera represent columnal fragments of the same single genus closely related to *Aethocrinus* (Arendt & Rozhnov 1995). If these Baltic columnal fragments actually belong to one genus, only the generic name *Hemistreptocrinus* should be retained for Baltic forms. *Hemistreptocrinus* appeared in Baltica at the beginning of the Volkhovian (Dapingian) and also penetrated there from the east. It is quite probable that it should be regarded as a sibling genus of the north Gondwanan *Aethocrinus*. These are probably the only two examples of sibling genera of Baltica and the northern marginal areas of Gondwana. Sibling genera of Baltica and Laurentia are more numerous and diverse.

Sibling crinoid genera of Baltica and Laurentia

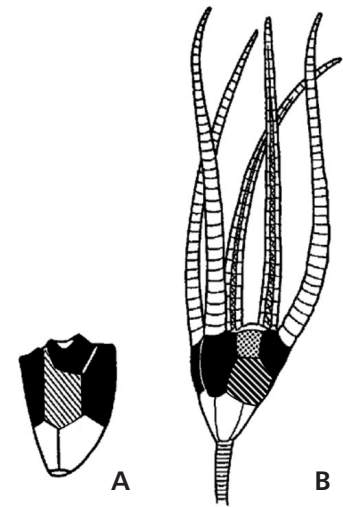
Among the crinoids of the two separated continents, the most prominent example of sibling genera is provided by the hybocrinids, Baltic *Hoplocrinus* and North American *Hybocrinus* (Fig. 3). These genera are similar in morphology and differ mostly in the presence of a special plate in the anal interradius of the calyx of *Hybocrinus* (Fig. 3B). This plate is similar in shape and position to the radial plate of cladid inadunates, although it is not homologous to the latter since it lacks an additional series of plates at the beginning of the anal sac (Rozhnov 1985). Above this plate, there are plates of the tegmen, which are connected to the anal cone. The anal interradius of *Hoplocrinus* lacks a special ossicle, instead it has a continuation of the lower radial plate of the radius C (Fig. 3A). I decline to comment on an interesting and ambiguously solved problem of plate homology in hybocrinids and other crinoids. However, it is possible to conclude that the two genera are rather similar and had a common ancestor outside both Baltica and Laurentia rather than having evolved from one another. This is supported, among several factors by the stratigraphic distribution of these genera: *Hoplocrinus* appeared in Baltica simultaneously with the first crinoids at the end of the Latorpian (Floian), when the biogeographic connection between Baltica and Laurentia was extremely weak due to the great width of the Iapetus Ocean, which separated them, and a sharp difference in water temperature (it was cold in Baltica and tropical in Laurentia). *Hoplocrinus* survived in Baltica up to the Oandu and never displayed features of

Hybocrinus even as rare aberrations (Rozhnov 1985, 2007d). This suggests that *Hybocrinus* and *Hoplocrinus* should be regarded as sibling genera, which developed independently on separated continents but had a common ancestor on a different continent, probably, in a specific eastern region of Gondwana. The location of the ancestral region of the sibling genera of Baltica and Laurentia will be discussed in a separate section after consideration of sibling genera in the rhipidocystid-cryptocrinitid lineage of Ordovician eocrinoids.

Sibling eocrinoid genera of Baltica and Laurentia

The most widespread and abundant Ordovician eocrinoids are rhipidocystids, which have a flat theca, and cryptocrinitids, with a spherical theca, as well as the similar North American genera, which however have not been combined with them as one family (Fig. 4). Despite considerable differences in appearance between rhipidocystid and cryptocrinitid eocrinoids, analysis of the plate arrangement has distinctly shown that the two families had a common ancestor closely related to cryptocrinitids (Rozhnov 1994). Representatives of these families (*Rhipidocystis* and *Paracryptocrinites*) entered Baltica almost simultaneously at the very end of the Latorpian (Floian) (Rozhnov 1989, Rozhnov & Fedorov 2001). Their common ancestor probably dwelt outside Baltica. Cryptocrinitid and rhipidocystid eocrinoids are an example of sibling families, which simultaneously migrated to the united continent and, then developed independently. Since one genus of each family immigrated into Baltica (the two genera probably evolved from a common ancestral genus), *Paracryptocrinites* and *Rhipidocystis* are sibling genera, which developed in the same area but were formed outside it. However, when compared with North American rhipidocystids and forms similar to cryptocrinitid eocrinoids, the picture seems much more complex. Two rhipidocystid genera, *Mandalacystis* and *Batherocystis*, in Laurentia are similar in morphology to the Baltic *Rhipidocystis* and *Neorhipidocystis* (Fig. 4A, B, E, F). *Mandalacystis* is similar to *Rhipidocystis*, but the composition and arrangement of plates of its theca are more similar to the original cryptocrinitid ancestor, while its specialized peristomal region significantly deviates from the ancestral type (Lewis *et al.* 1987, Rozhnov 1994). This may be viewed as an example of mosaic development, which complicates the reconstruction of phylogenetic relationships. Nevertheless, it is probable that *Mandalacystis* and *Rhipidocystis* had a common ancestor, which occurred in a region other than Baltica or Laurentia. In contrast to *Mandalacystis* and *Rhipidocystis*, which attached to solid objects on the sea bottom and extended the theca upwards into the water column, *Batherocystis* (Fig. 4F)

Figure 3. Sibling hybocrinid genera (Crinoidea) from Baltica and Laurentia. • A – Baltic *Hoplocrinus* (adapted from Rozhnov 1985). • B – Laurentian *Hybocrinus* (adapted from Sprinkle *in* Sprinkle & Moore 1978). The radials are black, infraradial is hatched, and anal is dotted.



lacked an attachment structure and laid on the sea bottom, flat side downwards. Instead of an attachment structure and true column, it had only a short thickened bulbous columnal outgrowth (Ubaghs 1967). This genus is similar to the Baltic *Neorhipidocystis* (Fig. 4B) in shape and mode of life but differs from it in some morphological characters (Rozhnov 1989), such as the bulbous outgrowth in place of a short pointed column characteristic of *Neorhipidocystis*. The ancestor of *Batherocystis* is unknown in Laurentia, but it was probably similar to *Mandalacystis* and dwelt outside Laurentia. *Neorhipidocystis* could have descended from *Rhipidocystis* within Baltica. This conclusion follows from their successive stratigraphic ranges in Baltica and a certain similarity in morphology. If this is the case, *Neorhipidocystis* and *Batherocystis* are an example of parallel development of similar morphological characters in taxa having a remote common ancestor. Otherwise, *Neorhipidocystis* and *Batherocystis* emerged outside Baltica and Laurentia from a common ancestor similar to *Mandalacystis* or *Rhipidocystis* and, then migrated to these continents. In this case, they are sibling genera. Use of data on morphology and variation between the two genera, particularly, *Batherocystis*, is insufficient to resolve this problem.

In the Ordovician of Baltica, there were two cryptocrinitid genera, which successively replaced one another in sections (Fig. 4C, D). *Paracryptocrinites* (Fig. 4C) is known from the beginning of the Volkhovian (Dapingian) (Rozhnov & Fedorov 2001). In Kunda (Darriwilian), it gave rise to *Cryptocrinites* with fewer circlets in the theca and a shortened ambulacra. In the terminal Kunda, the genus *Bockia* appeared; it differs considerably from cryptocrinitid eocrinoids in the number of plates and its thecal size. In addition, this genus is characterized by an extended peristomal part of the theca and branching brachiolas (Rozhnov 2009a). In Laurentia, there were four genera similar to the Baltic cryptocrinitids in both thecal

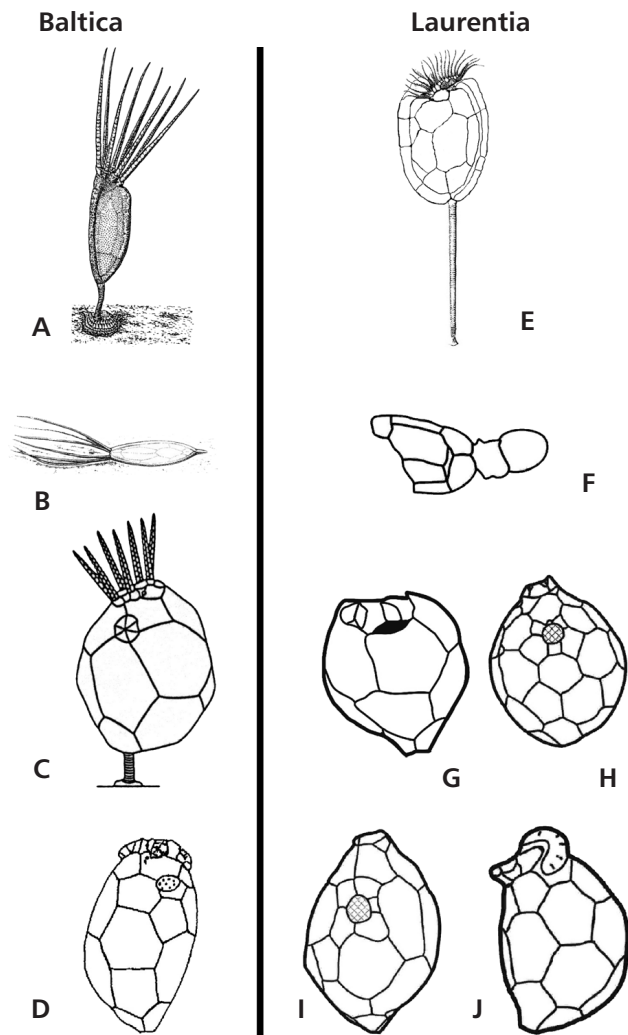


Figure 4. Sibling eocrinoid genera from Baltica and Laurentia: A – *Rhipidocystis*, reconstruction (from Rozhnov 1989), B – *Neorhipidocystis*, reconstruction (from Rozhnov 1989), C – *Cryptocrinites*, reconstruction (from Rozhnov 2002), D – *Paracryptocrinites bockelie* (adapted from Rozhnov & Fedorov 2001). • E–J – Laurentian genera: E – *Mandalacystis dockeryi* (adapted from Lewis *et al.* 1987), F – *Batherocystis* (adapted from Parsley in Ubaghs 1967), G – *Foerstecystis oblique*, USNM93400, H – *Columbocystis ovata*, USNM25935b, I – *Springerocystis longicollis*, USNM93397, J – paracrinoid (?) *Canadocystis tennesseensis*, USNM241264.

shape and plating pattern (Fig. 4G–J): *Columbocystis*, *Foerstecystis*, *Springerocystis* and *Canadocystis*. Sprinkle (1973) assigned all four genera to the paracrinoids, taking *Springerocystis* as a synonym for *Columbocystis*. Parsley (1975) believed that *Columbocystis* was closer to the eocrinoids, while considering *Springerocystis* to be a separate genus. Parsley & Mintz (1975) included *Canadocystis* in the Paracrinoidea. According to my study of these genera, the thecal plating of *Foerstecystis* is similar to that of young *Columbocystis* but, it also has much in common with the Baltic *Paracryptocrinites* and *Cryptocrinites*. Thus, *Foerstecystis* is a morphological link between Baltic

cryptocrinitid eocrinoids and the North American *Columbocystis*. The great number of plates in the theca of *Columbocystis* resulted from the development of extra plates between primary plates during ontogeny, these being arranged in circlets. Extra plates, which go against the standard arrangement of plates in a circlet, were recorded in the aberrant *Cryptocrinites*. The curved theca observed in the majority of eocrinoid genera under study is connected with the underdevelopment or overdevelopment of elevation in the larvae (Rozhnov 1998), that is, displacement of the vestibule which marks the position of the future mouth, from the lateral side onto the upper end of the attached larva. In living crinoids, elevation results in straightening of the column and crown along a uniform axis. If this process is delayed or overdeveloped, the aberrant animal becomes curved. Therefore, this curvature, which results in the position of the anus on the side opposite to the columnal facet of the theca, may be formed in parallel as a result of heterochronies in both phylogenetically close and phylogenetically remote taxa (Rozhnov 1998, 2002). This character has a distinct adaptive significance, as it forms a typical feeding posture, which is characteristic of down stream filter-feeders. This feature should not be used as a reliable taxonomic character, as has sometimes been assumed. *Springerocystis* and *Canadocystis* show certain features of both cryptocrinitid eocrinoids and typical platicystid paracrinoids. We assume that the formation of platicystid paracrinoids is closely connected to the cryptocrinitid lineage of eocrinoids. Although there is reasonable evidence to support this statement, it requires further consideration, which is beyond the scope of the present paper. Here we only note that the North American *Foerstecystis* (or *Columbocystis*) and the Baltic *Paracryptocrinites* are sibling genera, whose common ancestor inhabited another continent. In Baltica, the cryptocrinitid lineage did not exhibit extensive diversification, whereas in Laurentia this lineage produced great taxonomic diversity, and probably gave rise to platicystid paracrinoids, which are characteristic of Laurentia.

Sibling genera are also known in other classes, which inhabited Baltica and Laurentia. In the glyptocystitid rhombiferans, they are probably represented by the Baltic *Cheirocrinus* and the initial representative, the Laurentian cheirocrinid *Cheirocystella*.

Baltic edrioblastoids include a genus which has not yet been described, but which is probably a sibling genus of the North American *Lampteroblastus* (Guensburg & Sprinkle 1994).

The list of sibling genera from Baltica and Laurentia will probably be extended as a result of further detailed studies of various echinoderm groups. For this research it is important to determine a region or regions which were inhabited by the ancestors of sibling genera, rather than to expand this list.

Probable regions inhabited by ancestors of Baltic and Laurentian sibling genera

In each separated continent, sibling taxa show definite directions of immigration into the continent, a certain conditional azimuth. The intersection of these directions traced back from the separate continents indicates the region which was probably inhabited by the ancestral taxon and, hence, the center of origin of sibling taxa or, at least, the center of their dispersal. In Baltica, the sibling genera under study migrated from the east, bypassing the northern marginal areas of the Gondwanan Africa and peri-Gondwanan Europe with its well-known echinoderm fauna (Fig. 1). These genera probably migrated to Baltica from temperate waters or, if they came from warm or tropical seas, they were relatively eurythermal, as Baltica had cold-water conditions at that time. A large proportion of the genera (*Paracryptocrinites*, *Rhipidocystis*, and most of crinoids) were probably from temperate-water and relatively stenothermal since they disappeared as a result of conditions warming; a small proportion were eurythermal because they penetrated into Baltica at a the time of cold water conditions and survived up to the onset of tropical conditions (*Hoplocrinus*). In no circumstances do the tropical seas of Siberia correspond to these conditions, especially as the echinoderm fauna of this region was relatively poor. The region inhabited by the ancestors of sibling echinoderm genera should be looked for in the extensive region of temperate, warm seas of eastern Gondwana. An abundant and diverse fauna of Early Ordovician echinoderms has not yet been recorded in this region. However, its traces probably remained in the Middle-Upper Ordovician deposits of South China, and Myanmar (Reed 1917, Sun 1948). The finds of Upper Ordovician echinoderms in southern Mongolia and Kazakhstan probably indicate migration routes of Early and Middle Ordovician echinoderms from eastern Gondwana to Baltica (Rozhnov *et al.* 2009). The route from eastern Gondwana to Laurentia was probably different. It possibly passed along the opposite margin of Gondwana (Fig. 1) and ran in the opposite direction (following the earth's rotation and counterclockwise).

Conclusions – Baltica was a storehouse rather than the cradle of echinoderms

Our biogeographic study of sibling genera indicates that the center of their origin and primary center of dispersal was in eastern Gondwana. Many taxa migrated to Baltica from the cold northern seas of Gondwana and small closely located terrains in the area of modern North Africa, France and Spain. It is possible to regard Gondwana, as a whole, as the 'cradle' of Ordovician echinoderms, many of which migrated from there to Baltica and Laurentia, while others

developed exclusively in Gondwana. It is possible to regard Laurentia as a 'nursery' for echinoderms, where they developed directly from their Cambrian ancestors or, migrated there from Gondwana, and gave rise to a great diversity of morphological forms and taxa. The Ordovician Baltic basin was first inhabited by echinoderms only at the end of the Early Ordovician and an increase in generic diversity was caused mostly by immigration of various echinoderms from Gondwana and, in the Upper Ordovician, also from Laurentia. Only a few genera migrated from Baltica to other continents. Evolutionary radiation at generic and higher taxonomic levels did not play a dominant role in the increase in diversity of echinoderms. Therefore, it is possible to regard the Baltic as a 'museum', or 'storehouse' of echinoderms, where many immigrants from other continents were preserved.

Acknowledgments

I am grateful to G. Mirantsev for help with figure preparation. The valuable comments of O. Fatka and an anonymous reviewer helped to improve the manuscript significantly. Ronald Parsley (Tulane University, New Orleans) improved the English. This study was supported by the Russian Foundation for Basic Research (project No. 08-04-01347), Presidium of the Russian Academy of Sciences, programs No. 15 (1) "Evolution of Geobiological Systems" and No. 23 "Biological Diversity", and IGCP project 503. The Smithsonian Institution grant (1999) made possible my study of North American eocrinoids and paracrinoids in the National Museum of Natural History (NMNH).

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