

A conocardiid rostroconch mollusk from the Ordovician of Siberia

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Abstract

Conocardiid rostroconchs were enigmatic Palaeozoic molluscs with their bodies closed in shells superficially similar to those of bivalves but lacking ligament and presumably increasing in size during growth by the shell resorption at its dorsum. They have not been known from the Ordovician of Siberia until a limestone concretion from the Krivaya Luka Formation, dissolved in formic acid for conodonts, revealed external moulds and silicified fragments of shells of the morphology characteristic for the genus *Eopteria*. Although they may represent the same species, an open taxonomic nomenclature is applied to their description to avoid creation of a chimera. Despite the late Darriwilian age (Kirensk-Kudrino local stage) of the source stratum, the rostroconch represents a rather underived morphotype, possibly having its relative in an unnamed species from the Baltic region. The fossil record of the conocardiids is sparse, presumably because very narrow environmental requirements and despite probably free-living planktonic larval stage. However, as long as Siberia was located that time in low latitudes, whereas Baltica was closer to the Ordovician southern pole, the distribution of early conocardiids was apparently not controlled by climate.



1. Introduction

Mollusc conchs are relatively rare fossils in the Ordovician strata, in comparison with brachiopod shells or trilobite carapaces (e.g., [Fortey and Cocks, 2003](#)). Preserved as calcitic pseudomorphoses or imprints of their aragonitic shells, they are difficult to prepare from the rock matrix and rarely expose traits of importance from taxonomic point of view. The most informative are nuclei in acid-resistant rocks remaining after natural or artificial dissolution of the shells (e.g., [Ebbestad et al., 2017](#)). The most numerous fossils of this kind are phosphatic nuclei of larval and juvenile conchs. In the Ordovician strata, they represent mostly gastropods and hyoliths with insignificant contribution from bivalves, unlike the Silurian assemblages dominated by bivalves or the Cambrian ones dominated by hyoliths ([Dzik, 1994](#), fig. 37; [Dzik 2020a, 2020b](#); [Dzik, 2025](#)). The rostroconchs are underrepresented among mollusks with such mode of preservation. Their hemispherical embryonic shell ([Dzik, 1994](#), fig. 24D and E) proves that their larvae were not lecithotrophic and fed while growing until their shell attained the typical rostroconch morphology. Further growth required resorption at the dorsal ligament-like zone, as in unrelated early Palaeozoic polyplacophorans ([Dzik, 2024](#)). This was probably a mechanism similar to remodelling of the hinge in articulate brachiopods ([Carlson, 1989](#)).

Presumably, highly specific environmental requirements are among the factors causing the endemic and generally sparse distribution of fossil rostroconchs. This is exemplified by the Ordovician of Siberia, that time a separate continent, where the only reported rostroconch is the ribeiriid *Tolmachovia concentrica* [Howell and Kobayashi, 1936](#) from the early Darriwilian (Moyero River Formation, Vikhorevo-Volgino local stage; [Ebbestad et al., 2017](#)). The presented here new record of a slightly younger, late Darriwilian (Kirensk-Kudrino local stage), anteriorly gaping conocardiid rostroconch *Eopteria* seems to support the claim by [Runnegar \(1978\)](#) that in the early Palaeozoic ‘rostroconchs were principally tropical and subtropical animals’.



2. Material and methods

The material under study comes from exposure VK-741 ([Fig. 1A](#)) of the Krivaya Luka Formation (Kirensk-Kudrino local stage of late Darriwilian age; [Dronov et al., 2009](#); [Percival, 2009](#); [Kanygin et al., 2010](#)) in the

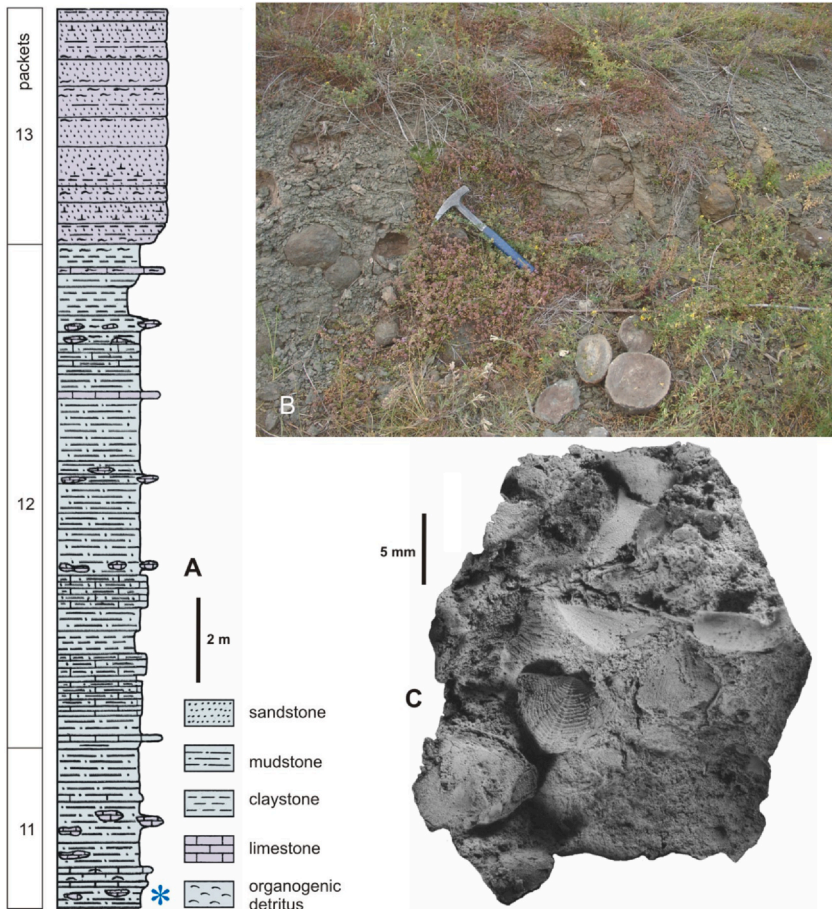


Fig. 1 (A) Rock column of the Krivaya Luka formation of the Kirensk-Kudrino local stage near the village Krivaya Luka, approximate position of the processed concretion is marked with asterisk. (B) Limestone concretions in the sandy mudstone packet 11 at exposure VK-741 in the slope at the Lena River shore. (C) Latex cast taken from the mudstone that remained after dissolution of the studied concretion in formic acid; note abundance of fossil shells. A modified from [Kanygin et al. \(1977\)](#).

slope at the Lena River shore near the village Krivaya Luka ([Kanygin et al., 1977, 1989](#)). A limestone concretion from sandy mudstone packet 11 ([Fig. 1B](#)) was dissolved in diluted formic acid for conodonts. In the residue a low diversity conodont assemblage typical for the lithostratigraphic unit, with *Microcoleodus* and *Erraticodon* was identified. Some portions of the concretion remained intact as a brittle porous mudstone with moulds of

numerous bivalve and rostroconch shells. A moistened piece of such decalcified mudstone remains was repeatedly covered with the latex milk to produce casts (Fig. 1C), which resulted in partial destruction of some of them. Additionally, fragments of silicified rostroconch shells were found loose in the residue.

Terminology of morphologic structures applied here follows that by Ebbestad et al. (2017). Material is housed at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, Poland, under collection number ZPAL V29.

3. External moulds

Although rostroconch shells superficially resemble those of bivalves, they did not disintegrate *post mortem* being firmly unified dorsally and ‘held rigidly together during day-to-day living’ (Pojeta and Runnegar, 1976, p. 12). In bivalves, when the adductor muscles contraction is released, the elastic ligament automatically opens the shell. In result, fossils of bivalves usually reveal their

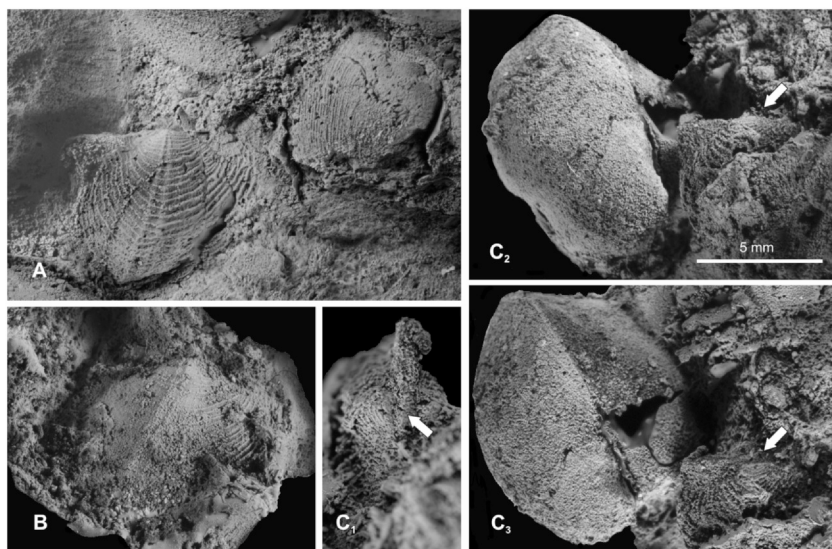


Fig. 2 Latex casts of external moulds of the *Eopteria* sp. shells in a mudstone piece left after dissolving the studied concretion. (A) Lateral view of shell ZPAL V29/125a associated with an undetermined densely striated bivalve. (B) Poorly preserved shell ZPAL V29/125b. (C) Shell ZPAL V29/125c with poorly preserved embryonic part (arrowed), associated with a bulbous smooth-shelled bivalve; apical, lateral and oblique views.

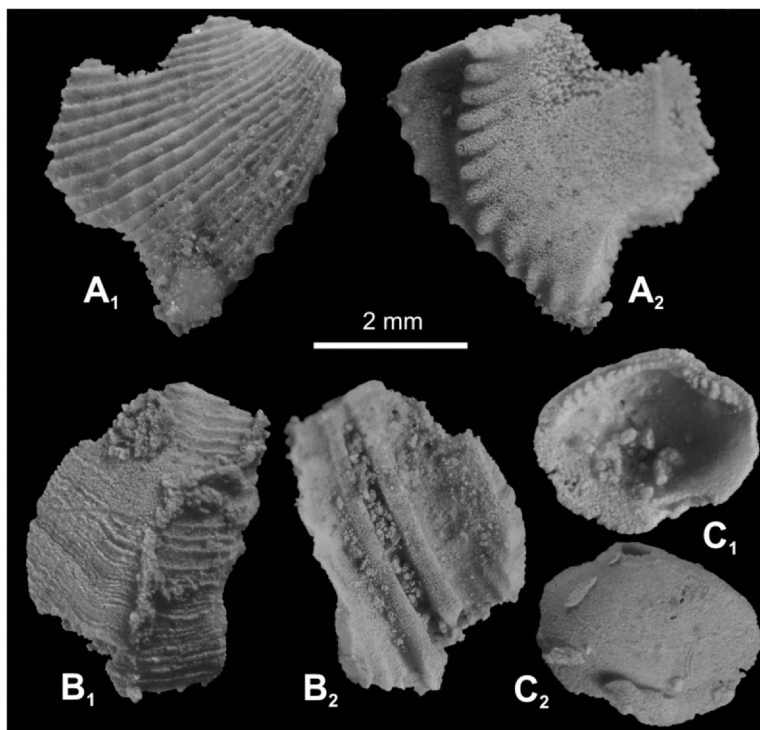


Fig. 3 Silicified mollusk shells from the studied concretion. (A) Anterior portion of presumably the Siberian *Eopteria* sp. shell ZPAL V29/126 in external and internal views. (B) Posterior portion of *Eopteria* sp. shell ZPAL V29/127 in external and internal views. (C) Associated smooth bivalve *Palaeoneilo* sp. shell ZPAL V29/128 in internal and external views.

valves inner morphology. Instead, the rostroconchs show their inner sides only when preserved as internal moulds or crushed skeletons. This is exemplified by the Siberian material described here. The latex casts reveal only the surface ornament of the shells, the size of mineral grains of the rock matrix imposing the limited resolution. However, because the growth increments of the Siberian conocardiids are prominent, it is rather easy to distinguish them from associated bivalves, having the shell surface either relatively smooth or covered with delicate increment lines (Figs. 1C, 2A and C, and 3).

The casts of external shell imprints of the Siberian conocardiid show that the prominent growth increments continue throughout the snout and rostrum without any recognizable change at the boundaries. A single prominent radial rib is developed in the middle of the shell, followed by a

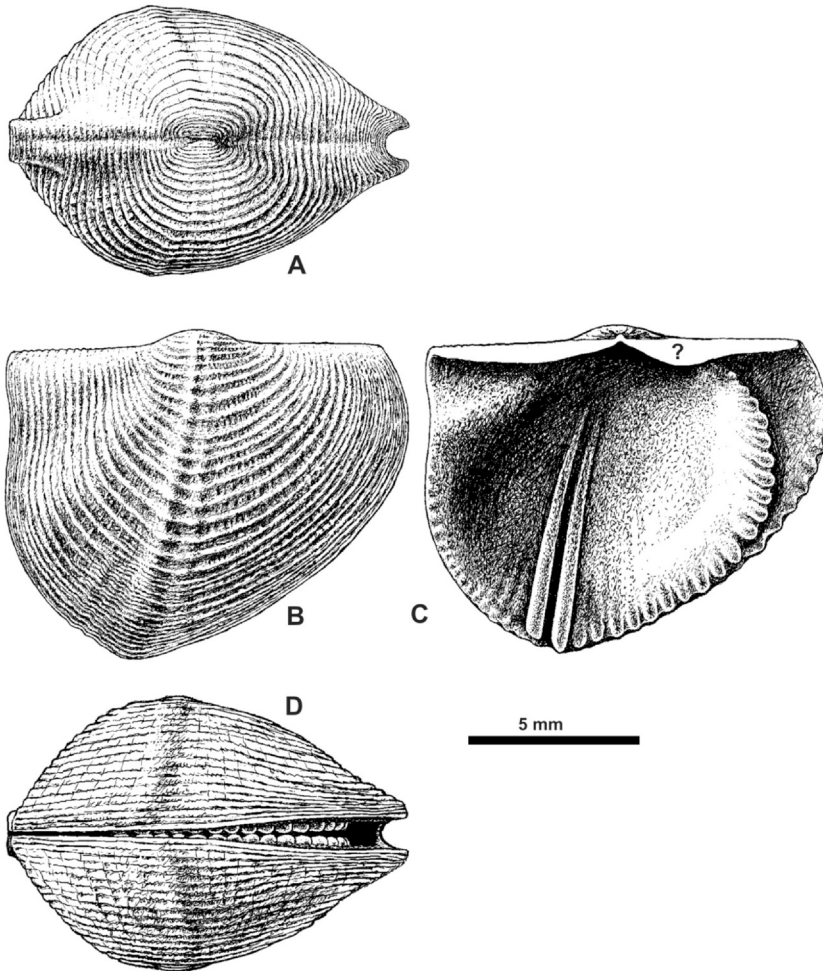


Fig. 4 Restoration of the Siberian *Eopteria* sp. shell based on assumption that external moulds and silicified fragments from the sample represent the same species; apical (A), lateral external (B), internal (C), and ventral (D) views.

depression in front of it. Minute radial riblets may be present, hidden between growth increments. They became weaker and weaker towards the snout and rostrum.

The 'hinge' disposition is virtually linear (Fig. 2C), presumably easing its rearrangement by resorption during the shell growth. The embryonic conch is poorly preserved, though there was enough space for it between umbones of the lateral lobes. Its fragmentary preservation seems to be a result of coarseness

of the mudstone matrix. The suggestion of [Pojeta and Runnegar \(1976, p. 4\)](#) that ‘the protoconch is normally destroyed in conocardiaceans by crushing caused by inrolling of the umbos’ and ([Ebbestad et al., 2017, p. 405](#)) that ‘during growth the conocardiid protoconch is enveloped by the incurving umbos of the growing shell and therefore often obscured’, does not necessarily apply to the Siberian specimens.

Two fragmentary impressions of the shells venter show a narrow, almost slit-like anterior opening ([Fig. 4D](#)).



4. Silicified shells

Two pieces of silicified shells have been found in the acid-resistant residue from the same sample. Their rather robust external ornamentation makes them similar to the conocardiid shells represented by mudstone moulds ([Fig. 3A and B](#)). It is thus likely (but regrettably not certain) that these are conspecific. I tentatively included them in restoration of the shell ([Fig. 4](#)). Both pieces show fine crenulation of the lobes’ margins. The piece from the snout ([Fig. 3A](#)) bears an arch of prominent anterior denticles. An unexpected aspect of the inner shell morphology of the piece from the middle of the shell are prominent radial ridges underlining the external radial rib ([Fig. 3B](#)).



5. Taxonomic identity

The type species of the genus *Eopteria*, *E. typica* [Billings, 1865](#), from the early Ordovician of Port aux Choix, Newfoundland, was not figured in the original description by [Billings \(1865, p. 221\)](#) and the holotype has been lost. The species was implicitly synonymized by [Pojeta and Runnegar \(1976\)](#) with *E. richardsoni* [Billings, 1865](#), the holotype of which comes from the early Ordovician (Beekmantown) age stratum at St. Antoine de Tilly, Quebec. *E. richardsoni* is similar to the Siberian species in general shape of the shell but differs in being covered with numerous minute radial ribs.

The genus *Eopteria* is probably ancestral to the remaining conocardiids. Its transitional position in respect to the ribeiriids is evidenced by the presence of a plate-like structure (pegma) joining the lobes in front of the umbo in *E. struszi* [Pojeta et al., 1977](#) from the early Tremadocian Ninmaroo Formation of Queensland, Australia. The pegma apparently made

difficult rearrangement of the shell valves and perhaps developed at maturity. An advanced aspect of *E. struszi* morphology is its rostrum 'marked off from the rest of the shell by posterior longitudinal clefts' (Pojeta et al., 1977, p. 5, pl. 25, figs. 11, 13).

Equally ancient member of the *Eopteria* lineage is probably *E. agustini* Sánchez, 2000 from the early Tremadocian Cardonal Formation, Sierra de Cajas, Argentina, ornamented with fine radial riblets and with wide, distinctly separated rostrum (Sánchez, 2000). Next in geological age is *E. crassa* (Thoral, 1935) from the Furongian of Montagne Noire, France (Morris, 1967; Babin, 1982).

There is no clear separation of the rostral part of the shell, considered diagnostic for *Eopteria* by Pojeta et al. (1977) in the Siberian species. There seems to be no such separation also in two shells illustrated as 'Lamelli-branchia' by Neben and Krueger (1971, pl. 19: 1, 2), although only the basal parts of rostra with no change in ornamentation are preserved in both of them. They come from glacial erratic boulders of the 'grauen Vaginatenkalk' of early Darriwilian age (Kunda Baltic stage). Such glauconitic sandy limestone is typical for the eastern Baltic region and in Estonia it yielded *Eopteria* specimens as well. The specimens from the German erratics share prominent radial ribs in the centre of their shells that grade posteriorly into less and less distinct radial riblets, whereas anteriorly the shells bore only concentric sharp growth marks. They differ in prominence and number (4 or 6) of the ribs, that likely expresses a within species variability.

A sample of a red cephalopod limestone of early Darriwilian age (coeval to the 'grauen Vaginatenkalk') collected in sample G-8 at the Gullhögen quarry in Billingen, Sweden yielded 18 internal moulds of juvenile (larval?) specimens of *Eopteria* that may belong to the same species (Dzik, 1994, fig. 24D, E; here Fig. 5). All show well-preserved hemispherical embryonic conch. Apparently, during subsequent early post-embryonic growth the shell developed lateral lobes, which eventually merged at the venter. Further growth required rearrangement of the valves by resorption and secretion at the shell 'hinge'. It is not quite clear, what happened after hatching and before lateral lobes of the shell met at the venter. All individuals found in Gullhögen were at such stage of their ontogeny. This would prevent further growth unless resorption and remodeling at the dorsum took place. The specimens are preserved as internal moulds do not showing whether the conch developed by accretion at the mantle margin or rather was secreted instantaneously at the body surface. Anyway, they co-occur with 316 gastropods (bellerophonitids, mimospirids, and others) of

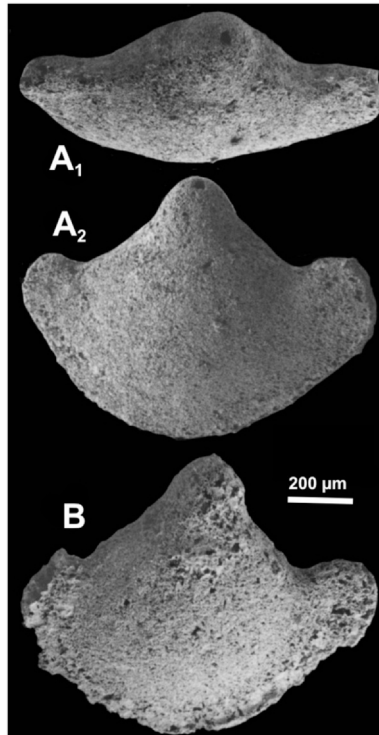


Fig. 5 Internal moulds of juvenile (larval?) conchs in dorsal (A_1) and lateral (A_2 , B) views of *Eopteria* specimens from sample G-8 of the red cephalopod limestone of early Darriwilian age (*Lenodus variabilis* Zone, Kundan Baltic stage) collected at the Gullhögen quarry in Billingen, Sweden. A modified after [Dzik, 1994](#), fig. 24D and E.

similar size that apparently died at the metamorphosis, that is while changing their mode of life from planktonic larva to a benthic juvenile ([Dzik, 1978, 2020a](#)). Possibly, such was also the fate of the *Eopteria* individuals. The moment of metamorphosis would then correspond to development of the mechanism of shell resorption. There is no other sign of change in geometry or retention of growth in the Swedish juveniles that could correspond to metamorphosis. However, the lack of any marginal denticles restricting the opening in the snout may be meaningful. It suggests that they developed after the metamorphosis, with modification of the ciliated (possibly velum-like) feeding organ. Just four associated specimens of bivalves at earlier, pre-metamorphosis stage of development found in sample G-8 suggest that their larval biology was different.

Unlike mature *E. struszi*, in most *Eopteria* species no pegma developed that would hamper their accommodation to the results of secretion at the mantle margin. Presumably, instead of ligament elasticity, hydraulic pressure secured expansion of the shell (Pojeta and Runnegar, 1976).

However, the alternative that *Eopteria* did not have pelagic veliger larva and led benthic life after hatching from the egg cannot be excluded with so limited evidence. This would explain why the fossil record of rostroconchs is so sparse. In fact, this has to be expected in case of benthic animals lacking any free-living planktonic propagules. Such forms rarely offer enough complete record to trace their evolution bed-by-bed (e.g., Olempska, 1989). The fossil record of the genus *Eopteria* is too incomplete and chaotic to reveal any chronomorphocline. Just opposite, the most ancient early Tremadocian *Eopteria* forms, *E. struszi* and *E. agustini* are the most advanced in respect to developing the rostrum, morphologically distinct from the rest of the shell.

The genus *Eopteria* is ‘a suitable ancestor’ for the conocardiids (Pojeta and Runnegar, 1976, p. 38). *Eopteria conocardiiformis* Pojeta and Runnegar, 1976, with an expanded snout suggesting affinity to advanced conocardiids is the only member of the genus of Sandbian age (Pojeta and Runnegar, 1976). The sharp ridges backing depression at the basis of the rostrum in *Eopteria aiteneria* Popov et al., 2003 from the Katian age Angrensor Formation of Kazakhstan may be an incipient hood, already well developed as a collar enclosing the ‘body tube’ at the venter in the approximately coeval *Bitrignonocardia lindstroemi* (Isberg, 1934) from the Öjlemyr chert (Baltic Pirgu stage; Ebbestad et al., 2017; the hood was omitted in the restoration on their fig. 21). Perhaps such morphology fulfils phylogenetic expectation connected with its late stratigraphic position. If correctly interpreted, this would make *E. aiteneria* an ancestral hippocardiid that require a separate generic name.

As it follows from the above review of the fossil *Eopteria* occurrences, the Siberian late Darriwilian form is an underived member of the lineage rooted in *E. richardsoni* and the unnamed early Darriwilian Baltic species.



6. Biogeographic context

There are too few finds of *Eopteria* to speculate on biogeographic aspects of its phylogeny. The suggestion that it diversified during the late early and mid Ordovician mainly in Laurentia, associated with low-latitude

carbonate facies (Popov et al., 2003, p. 175) seems to be contradicted not only by the presence of *E. crassa* (Thoral, 1935) in the Furongian of Montagne Noire (Babin, 1982), ‘Lamellibranchia’ of Neben and Krueger (1971) and its possible juveniles in early Darriwilian of Baltica, but also by the late Darriwilian Siberian finding described herein (Fig. 6).

However, it may be true that the *Eopteria* species distribution was ‘influenced by sediment type, a common occurrence in benthonic invertebrates’ (Pojeta et al., 1977, p. 11). Pojeta et al. (1977, p. 26) proposed that ‘*Eopteria* was a semi-infaunal to infaunal mobile deposit feeder’. Yet, the rows of anterior denticles partially closed the opening at the *Eopteria* snout, do not leaving enough space for a regular mud-eater’s proboscis. An alternative may be that hydrogen sulphide was inhaled through the snout,

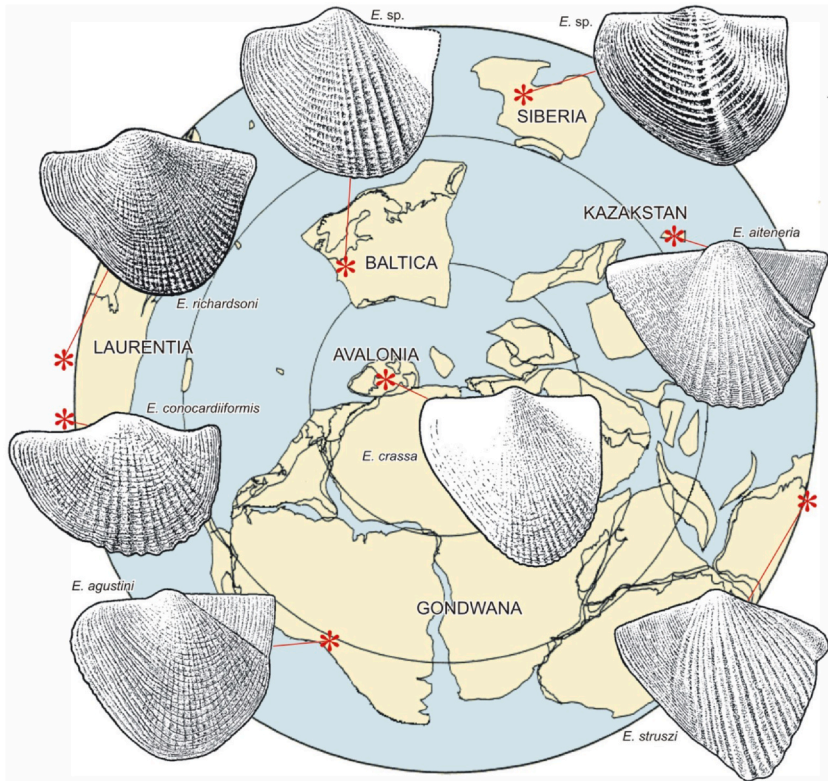


Fig. 6 Spatial distribution of *Eopteria* species with best known external ornamentation of their shells (palaeogeography of the Ordovician southern hemisphere after Cocks and Torsvik, 2002). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

the anterior denticles performing only a protective function. Remarkably, the ‘body tube’ of hippocardiid rostroconchs (Ebbestad et al., 2017) in its disposition corresponds to the foot of the lucinid bivalves probing for hydrogen sulphide to feed chemosymbiotic bacteria (Taylor and Glover, 2006). The rostrum would then house an exhalant canal. A dependence on microbial symbiosis was already suggested for hood-bearing rostroconchs (Rogalla and Amler, 2005).



7. Conclusions

The reports on the occurrences of *Eopteria* in the Ordovician Siberian tropics and Baltic high latitudes may be used in discussions on biogeography of early conocardiids. It supplements both the suggestion that in the early Palaeozoic ‘rostroconchs were principally tropical and subtropical animals’ (Runnegar, 1978, p. 327) and the more recent one that *Eopteria* ‘diversified during the late early and mid Ordovician mainly in Laurentia’ (Popov et al., 2003, p. 175). The data on *Eopteria* early ontogeny may also help to explain the sparse spatial distribution of the genus and the endemic occurrences of its species.

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