

An endemic community of Polish Late Ordovician gastropods

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The Mójca Limestone Formation exposed in the Holy Cross Mountains in southern Poland, being a part of the Małopolska microcontinent in the Ordovician, abounds in phosphate-coated originally calcareous fossils of microscopic size. Their geological age covers most of the Mid and Late Ordovician. The late Katian topmost bed of the Formation is especially rich in phosphatized larval and early postlarval gastropod conchs and yielded 8703 specimens taxonomically determinable at least at the genus rank. High-spined trochonetid conchs ornamented with delicate spiral striation between low ribs dominate the assemblage. Unlike other gastropod communities of similar age, this one was poor in bellerophonitids and openly coiled platyceratids and despite the geographic proximity, the typically Baltic planispiral leserillids are extremely rare. Comparable gastropod assemblages are unknown from the Perunica and Avalonia microcontinents or the continental Gondwana. Instead, specimens representing a few species of probable holopeids with smooth shell surface are abundant. Their conch geometry ranges from that already known among holopeids to the virtually planispiral, superficially resembling both, the coeval Baltic leserillids and geologically younger euomphalids. Presumably, this taxonomic composition of the Mójca gastropod community was a result of local speciation with a significant contribution from homoplasy to its taxonomic diversity. • Key words: palaeobiogeography, Palaeozoic, phosphatization, molluscs, Bellerophonitida, *Jinonicella*.

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Estimation of faunal or floral affinity is an important tool of testing palaeogeographic plate tectonic hypotheses inferred from palaeomagnetic and palaeoclimatic data. This requires that one deals with true phylogenetic connections between compared regions and not just a homoplastic similarity resulting from a selective pressure imposed by local ecological conditions. Such reliable phylogenetic signals may be provided by juvenile or larval ontogenetic stages of molluscs that are conservative in evolution. This refers especially to the morphology of embryonic and larval conchs of gastropods that are of special diagnostic value in their high taxonomic rank systematics (Frýda 2011). Unfortunately, it is usually difficult to match the larval conchs of early Palaeozoic gastropods, known mostly from acid-resistant microfossils, with their mature stages represented by macroscopic fossils. The Katian age topmost bed of the Mójca Limestone in southern Poland yielded a rich fossil assemblage of phosphatized fossils that may appear helpful in this task. A significant fraction of them are juvenile teleoconchs matching data on larval gastropods known from the early Palaeozoic ‘small shelly fossils’ (Dzik 1994d, 2020a) with those of macroscopic teleoconchs.

The Mójca Limestone Formation is a lithostratigraphic unit covering most of the Early Palaeozoic Małopolska Massif in southern Poland (Fig. 1B). The Massif presumably corresponds to a microcontinent that was located, together with Perunica and Avalonia, between Baltica and Gondwana in the Late Ordovician (e.g. Ebbestad *et al.* 2008, fig. 13; Trela 2023). The exact location of the Małopolska microcontinent is a matter of controversy. Usually it is considered to be a part of the Ordovician Baltic realm but geochemical data suggest its proximity to Gondwana in the Cambrian and migration towards Baltica in the Ordovician (Walczak & Belka 2017, Lindner *et al.* 2020). Gondwanan influences have been identified among the Darriwillian conodonts (Dzik 2020b) but palaeobiogeographic interpretations of other faunal elements remain equivocal.

The abundant gastropod fossil assemblage from the uppermost Mójca Limestone offers an opportunity to confront palaeontological evidence with independently achieved geotectonic interpretations. Somewhat surprisingly, the preliminary review of the Mójca gastropod fossil assemblages (Dzik 1994b) already showed that they significantly differ from both, those of Baltica, Laurentia,

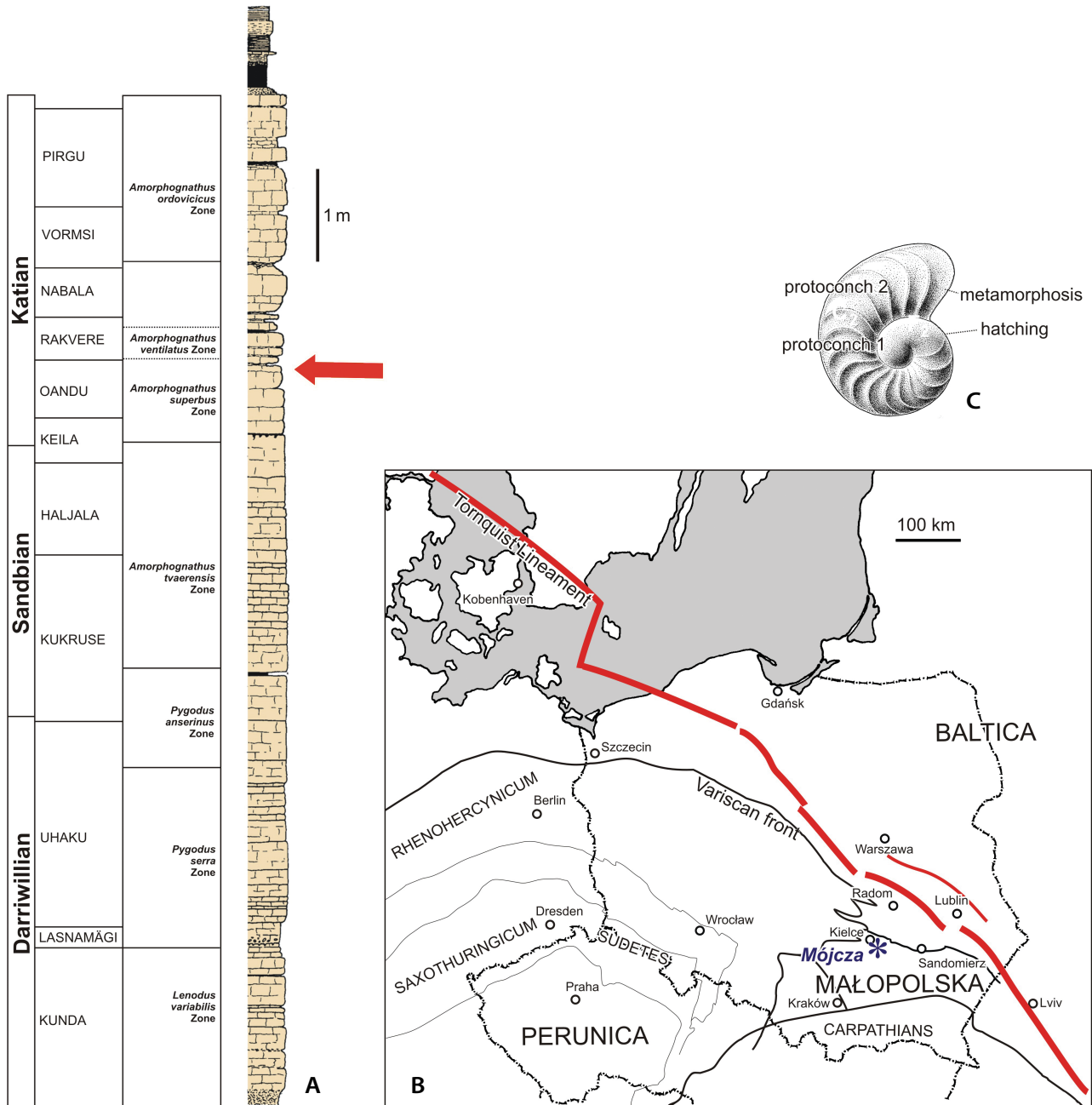


Figure 1. A – stratigraphic subdivision of the Ordovician strata exposed at Mójca, Holy Cross Mts., Poland, their correlation with Baltic stages, conodont zonation, and the rock column with position of the studied sample arrowed. • B – location of the Mójca exposure (asterisk) in respect to the Central European geotectonic units. • C – restoration of the larval conch of *Peelerophon?* sp. with sinuous aperture (that of the teleoconch was prosocline).

and Gondwana. Regrettably, the present lack of knowledge of mature teleoconchs in most Mójca gastropod species prevents their comparison with other Late Ordovician faunas analysed by Ebbestad *et al.* (2013a). It is further hindered by the limited evidence on Katian gastropods from Avalonia and Perunica. Hopefully, the recently obtained more complete fossil material may help in elucidating palaeobiogeographic relationships between those tectonic units located between Baltica and Gondwana.

Material and methods

The Mójca Limestone Formation is an extremely stratigraphically condensed rock unit. At its type locality at the village Mójca within the administrative boundaries of the city Kielce in southern Poland the Formation is about 8 m thick (Fig. 1A). According to the conodont biostratigraphy it covers the time span (together with the topmost calcareous part of the underlying Bukówka

Sandstone Formation and the overlying marly Zalesie Formation) from the early Darriwilian to the top of Katian. There is only one recognisable gap in sedimentation, ranging from the *Eoplacognathus pseudoplanus* conodont Zone (late Kunda Baltic age) to the *E. reclinatus* Zone (Dzik 1994a). This provides probably the most extensive and complete palaeontological record of metazoan evolution traced in a single section and in relatively stable ecological conditions (Dzik 1999). Phosphatized microfossils occur throughout the Mójca Limestone section but the richest fossil assemblage with gastropod shells has been collected from the topmost bed.

A rock sample of about 10 kilograms weight (Ma-192) was taken from near the top of the Formation at its type section. Fossils were extracted with application of the standard technique for conodonts by dissolving in dilute acetic acid. The decanted residue was composed almost exclusively of phosphoritic ooids and phosphate-coated skeletal debris, which made enrichment with the Frantz electromagnetic separator rather inefficient. Only taxonomically determinable gastropod conchs, that is those with well-preserved apex, were picked out. The sample has yielded 8703 specimens of gastropods and related molluscs. The specimens selected for SEM were coated with platinum.

Conodonts from the topmost Mójca Limestone layer determine its age as the Katian *Amorphognathus superbus* Zone (Dzik 1994a, 1999). The taxonomically identifiable skeletal components represent broken pieces of trilobite carapaces, echinoderm sclerites (Pisera 1994), receptaculitid meroms (Dzik 2024b), polyplacophoran plates (Dzik 2024a), mollusk conchs (Dzik 1994b), hyoliths (Dzik 1994b), bryozoans (Dzik 1992, 1994c), and ostracods (Olempska 1994). The abundance of juvenile bryozoan colonies, a phenomenon unknown in any other bryozoan fossil assemblages, is taphonomically instructive (Dzik 1992). They apparently were killed by some environmental factor soon after settlement of larvae and budding a few generations of zooids. This helps to understand why, unlike most environments promoting preservation of 'small shelly fossils', also the gastropod larvae survived metamorphosis to die soon after.

Remarkably, most of the bivalves and the ostracod *Longiscula* found at Mójca have closed valves. This means that they were covered with the sediment when still alive. They were able to survive for some time in an anoxic environment presumably owing to glycolysis. Fossils and detrital fragments are frequently joined together by a calcium phosphate matrix, which means that phosphatization was postdepositional. There is a mix of phosphatic debris fragmented in place with those transported from elsewhere. The originally aragonitic conchs frequently bear a thin phosphate coating with fidelity of replication enabling identification of fine

growth increments. Rarely, owing to similarity between aragonite and apatite molecules (e.g. Kasiopas *et al.* 2010), the shell matrix is replaced with phosphate.

The reasoning applied here to interpret the Mójca gastropod material is based on the assumption that the sub-spherical smooth protoconch lacking growth increments (Fig. 1C; Dzik 1978) represented an embryonic stage, in which the initial conch was secreted within the egg covers, as it is the case with e.g. the Recent halitoid or trochid gastropods (e.g. Moran 1997, Wong *et al.* 2010). Some of the Mójca material, owing to the accurate phosphatization of the shell, provides direct evidence on the larval mode of life. Growth increments emerged in the veliger larva after hatching (Fig. 1C) suggestive of being secreted outside the eggs. Such inference is precluded whenever only internal moulds of larval conchs are available. To overcome such limitation, while studying internal moulds, Nützel *et al.* (2006) arbitrarily used the conch diameter at 100 µm from its tip to determine whether the larva was planktotrophic or not. The metamorphosis from a free-swimming veliger into the benthic stage is rarely expressed by a significant change of the conch morphology (e.g. Frýda 2001, Frýda & Ferrová 2011) but it may result in increase of mortality (Dzik 1978, Nützel *et al.* 2006). In bivalves of similar preservation such peak of mortality strictly corresponds to the change in morphology demarcating metamorphosis (Dzik 1994b, fig. 33). Unfortunately, the fragmentation of the Mójca gastropod shells in result of winnowing and a short-distance transport (Dzik & Pisera 1994) prevents determination of their population dynamics.

The material is housed at the Institute of Paleobiology, Polish Academy of Sciences, in Warsaw, Poland (collection ZPAL V12).

Bilaterally symmetrical and sinistrally coiled molluscs

Taxonomic affiliation of bilaterally symmetrical early Palaeozoic molluscs with a tubular larval conch remains a matter of controversy (Peel 2001, 2004, 2006). They have been considered related to the monoplacophorans, untorted or torted gastropods, and scaphopods. Possibly, they were close to the root of the gastropod-cephalopod clade.

Putative ancestral scaphopod. – The extremely long-ranging and widespread *Jinonicella* lineage is among the most enigmatic molluscs of the Palaeozoic. It occurred from the Darriwilian of Ukraine and Belarus (Hynda 1986, Gubanov *et al.* 2022), Sandbian of Baltic erratics (Dzik 1994d), Katian of Poland (Dzik 1994b), Llandovery of Utah and Siberia (Gubanov *et al.* 2020), Wenlock to Ludlow of Czechia (Pokorný 1978a), Gotland (Peel &

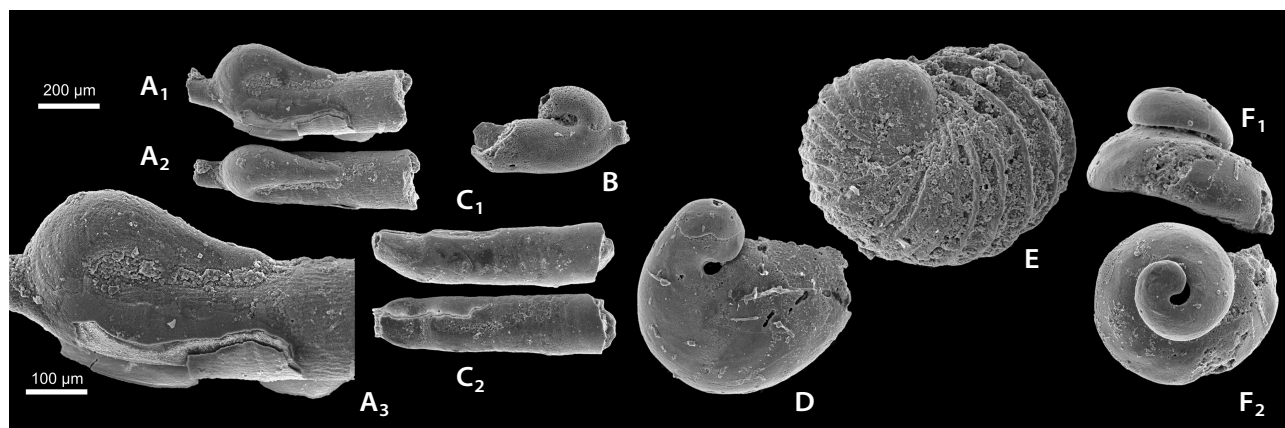


Figure 2. Phosphatized larval conchs of gastropod relatives from the Katian sample Ma-192 of the Mójca Limestone. • A–C – possible early scaphopod *Jinonicella* sp.; specimens ZPAL Ga1/185, 184 (phosphatized conchs), and 186 (internal mould), respectively. • D, E – *Laeogyra* cf. *volhynica* Hynda, 1983; specimens ZPAL Ga1/181 (internal mould) and 180 (phosphatized conch). • F – *Mimospira* cf. *alta* (Hynda, 1983); specimen ZPAL Ga1/182 (internal mould).

Jeppsson 2006) and the Carnic Alps (Gubanov *et al.* 2017, 2018, 2022), up to the Famennian of Germany (Piecha 2004). The bulbous apex of the conch of about 60 µm diameter, apparently represents the embryonic stage. The larval conch was mostly straight at the beginning and then formed a half coil that terminated its growth with developing a snorkel at the tip of a cylindrical teleoconch. The Mójca specimens with phosphatized shell wall show incremental irregularities (Fig. 2A₃) that provide a proof of planktotrophy of the larva. Even more prominent change and growth increments of the teleoconch have been identified on internal moulds in the Belorussian material by Gubanov *et al.* (2022). The cylindrical teleoconch and ‘snorkel’ developed after a prominent change in development that can be interpreted as a metamorphosis of pelagic larva into a benthic adult. This was marked by the development of a diaphragm separating the post-larval tubular conch from its half-coil predecessor. In result, the internal mould shows a dorsal depression in the place originally occupied by the larval conch (Fig. 2C). The Ordovician specimens differ from the Silurian and Devonian ones in a more open coil of the distal part of the larval shell (Fig. 2A, B).

The near-circular distal part of the *Jinonicella* larval conch (the coil diameter of about 270 µm) strengthens the suspicion that its closest relative was *Janospira* from the Floian of Australia (Paterson 2001, Peel 2006) and Darriwilian of Spitsbergen (Fortey & Whittaker 1976), having a coiled bellerophonitid-like larval conch but a tubular teleoconch undistinguishable from that of *Jinonicella*. The bellerophonitid-like larval conch of *Janospira* convinced Pokorný (1978a, b) that it was a gastropod. However, a coiled protoconch has been later identified also in the ribeiriid *Pinnocaris lapworthi* Etheridge, 1878, from the Ordovician Scottish Ardmillan Group at Balclatchie, Girvan (Peel 2004, 2006).

Runnegar (1977) proposed that the ‘snorkel’ of the Cambrian helcionellid *Yochelcionella* is homologous to that of *Janospira*. However, it developed in continuity with the low conical embryonic conch and there is a dramatic change in the shell ornamentation immediately below the ‘snorkel’ (Runnegar & Jell 1976). This was apparently a pre-metamorphosis structure, not homologous with that in *Jinonicella*. Anyway, the ribeiriid or bellerophonitid ties of *Jinonicella* seem more likely than its affinity to true gastropods (Peel 2006) or scaphopods (Engeser *et al.* 1993; see also Frýda 1999c).

Mimospirids. – The smooth embryonic conch of mimospirids is of asymmetric cap-like shape and relatively large size (Fig. 2E); the embryo was apparently rich in yolk. Coils of the larval conch developed underneath, with a bulbous initial chamber (Fig. 2D).

Mimospirids were diverse and widely distributed in the Ordovician (Frýda & Rohr 1999, Ebbestad *et al.* 2021). Shells of the roughly coeval Baltic species of *Mimospira* (Wängberg-Eriksson 1979, Frisk & Ebbestad 2007) differ from the Mójca specimens with preserved conch in their ornamentation. ‘*Laeogyra alta*’ Hynda, 1983 from the Darriwilian (Aseri Baltic age) of Ukraine is known only from internal moulds and its relationship with the Katian *Mimospira barrandei* Frýda, 1989 from Bohemia and *M. puhmuense* Isakar & Peel (1997) from Estonia (Rakvere) remains unclear. This refers also to the material from sample Ma-192, in which all the *Mimospira* specimens are internal moulds of the embryonic conch of about 130 µm diameter. Among specimens possibly conspecific with *Laeogyra*? cf. *volhynica* Hynda, 1983 one shows the external ornamentation and distinct cup-shaped smooth embryonic conch of about 230 µm width (Fig. 2E). It remains unclear whether the mimospirids had a free-living veliger larva (Dzik 1983).

Bellerophontids with a large embryonic conch. – The mid Cambrian *Protowenella*, the oldest planispirally coiled mollusk with an operculum that was interpreted by Peel (2021) as diagnostic for the orthothecid hyoliths, had a bulbous apex of about 300 µm diameter (Peel 2021) that suggests that this was the plesiomorphic trait for the bellerophontids. This finds support in relatively large embryonic conch of *Peelerophon* from the Floian Thung Song Formation of Tasmania. It shows also a rather sudden transition from a sinuous larval aperture to the prosocline one (Jell *et al.* 1984, fig. 1n). In *Modestospira* the change seems to be gradual (Yochelson 1964, pl. 145, fig. 2). This apparently corresponds to the metamorphosis from pelagic to benthic mode of life. A large protoconch 1 characterises at least two bellerophontid species from sample Ma-192: *Peelerophon*? sp. and *Cyrtodiscus*? sp. (*Temnodiscus disciformis* Hynda, 1983’).

The specimens attributed here tentatively to *Peelerophon* are internal moulds (Fig. 3A) with the apex of about 140 µm diameter. Their identification is based on similarity to specimens with preserved shell from

samples of late Darriwilian age from the same locality (Fig. 1; Dzik 1994b, fig. 5a). These larval shells show prominent costae that differ from those in teleoconchs of *Modestospira* from the underlying early Darriwilian strata (Yochelson 1964) in being convex on lateral sides of the conch and in forming a distinct selenizone. In this respect they are similar to those in juveniles of the Tremadocian to Sandbian species of *Peelerophon* (Jell *et al.* 1984, Ebbestad *et al.* 2013b).

The conch apex of *Cyrtodiscus*? sp. (*Temnodiscus disciformis* Hynda, 1983’) of about 120 µm diameter is smaller than that of *Peelerophon*? sp. but the first whorl of the juvenile larva has a similar cross section. The external keel developed gradually in the Mójcza specimens (Fig. 3B–D) and became ornamented with strongly inclined riblets. Fragmentary well-preserved specimens show a narrow selenizone, similar to that in the Darriwilian species of *Cyrtodiscus* (Horný 1997, pl. 2.2) and the Early Devonian (Pragian) *Kolihadiscus* (Frýda 1999b). Most specimens attributed to *Temnodiscus disciformis* Hynda, 1983 by Hynda (1986) may represent the Mójcza



Figure 3. Phosphatized larval conchs of bellerophontids from the Katian sample Ma-192 of the Mójcza Limestone. • A – *Peelerophon*? sp.; specimen ZPAL Ga1/198 (internal mould). • B, C – *Cyrtodiscus*? sp. (*Temnodiscus disciformis* Hynda, 1983’); specimens ZPAL Ga1/191 (phosphatized conch) and 192 (internal mould). • D – *Sinuities*? sp.; specimen ZPAL Ga1/200 (phosphatized conch). • E–H – *Tropidodiscus*? aff. *minus* Hynda, 1983; specimen ZPAL Ga1/193 (phosphatized conch), 199 (partially phosphatized conch, 194 and 195 (internal moulds). • I–K – *Kokenospira* sp. [cf. *K. esthona* (Koken, 1889)] or *Tetranota* sp.; specimens ZPAL Ga1/203 (phosphatized conch), 202 (internal moulds), and 201 (phosphatized conch).

species but the holotype, which comes from the Darriwilian (Aseri) stratum at the borehole Vysokoye in Volhynia, Ukraine (Hynda 1983, pl. 1.4) exhibits a minute embryonic conch and relatively wide larval conch, which seems to make it conspecific with *Tropidodiscus minimus* Hynda, 1983, the holotype of which comes from coeval stratum at the borehole Novoselki 29 (Hynda 1983, pl. 1.1). The larval conch of the latter species has an initially flat dorsal surface that changes into acute with age (Fig. 3E–H).

Bellerophontids with a minute embryonic conch. – Juvenile bellerophontids may dramatically differ from adult ones (e.g. Ebbestad 1999) and this may be the case with the species from sample Ma-192 tentatively classified as *Tropidodiscus*? aff. *minimus* Hynda, 1983 (Fig. 3E–H). Its conch apex is very small, of about 30 µm diameter (as in the Silurian *Bellerophon*; Frýda 1999b, fig. 1). It developed a relatively wide selenizone (Fig. 3E), in this respect resembling the co-occurring *Kokenospira* [cf. *K. esthona* (Koken, 1889)] or *Tetranota* sp.; Fig. 3I–K) that has a similar size embryonic conch apex of about 35 µm diameter but a wider larval conch. An acute venter and narrow umbilicus characterize *Sinuities*? sp. (Fig. 3D).

Dextrally coiled gastropods

The trochiform sinistrally and dextrally coiled gastropod conchs apparently represent lineages that independently emerged from bilaterally symmetrical ancestors in result of evolution towards genetically controlled chirality in opposite directions. Such conchs traditionally attributed to gastropods are known beginning from the early Cambrian (e.g. Dzik & Mazurek 2013). There are some problems with those supposed earliest gastropods: their mucronate embryonic conchs resemble rather those of hyoliths and the pattern of mortality suggests that they did not metamorphose, continuing planktonic life (Dzik & Mazurek 2013). Moreover, they bear bundles of chaetae unknown in extant gastropods, further supporting their pelagic larva-like adaptation (Thomas *et al.* 2020). Undoubted gastropods appeared in the fossil record not before the Late Cambrian and early evolution of their larvae remains to be clarified, especially in respect to open coiling of juvenile veliger conchs.

Gastropods with openly-coiled larval conch. – Extant gastropods have tightly coiled larval shells (Nützel 2014), but some Paleozoic forms had a bulbous minute embryonic protoconch 1 and almost straight part of the shell corresponding to the larval protoconch 2 (Frýda 1999a, Frýda *et al.* 2008, Dzik 2020a, Nützel *et al.* 2023). Such larvae are extremely rare at Mójca (Fig. 4J).

They were identified as a part of an *Eccyliomphalus* or *Pararaphistoma* teleoconchs (Dzik 1994d, fig. 22g) but probably characterized also other related Ordovician gastropods (Peel 2019).

Not so bizarre was the larval conch of *Platyostoma*? *obscura* (Hynda, 1986) (Fig. 4A, B), which resembles the mid Devonian (Givetian) *Eifelcyrtus blodgetti* of Frýda & Heidelberger (2003). It is virtually identical with that of the early Devonian *Praenatica* (Frýda *et al.* 2009) but differs in a much lower whorl expansion rate of the teleoconch that is similar to the holotype of Laurentian *H. brucei* Rohr, 1980 from the Mid Ordovician of California (Rohr 1980). In this respect it resembles also the co-occurring *H. pusilla* Hynda, 1986 (*Umbonellina*? sp. in Dzik 1994b) that had the embryonic conch of about 80 µm diameter (Fig. 4C, D). The openly coiled (but not almost straight) larval conch of the latter species (and presumably its teleoconch) is similar rather to that of the Carboniferous *Naticopsis* (Nützel *et al.* 2007), although the lower whorl expansion rate and open umbilicus make it closer to the associated ‘*Holopea*’ sp. 2 (Fig. 5I–O). This may mean that these Mójca Limestone species were near the ancestry of the major gastropod clade well established in the Silurian and Devonian (Frýda 2011).

Ebbestad *et al.* (2022) commented on the relatively low whorl expansion rate of the Katian platyceratids and their widespread Gondwanan localities. Possibly, the Mójca species belongs there, too. The lack of teleoconchs in the Polish (as well as Ukrainian) material and the larval conch unknown in the Gondwanan fossils prevent reliable taxonomic identifications.

Although the typically Baltic leseurillids are extremely rare at Mójca, they have their counterparts in virtually planispiral conchs lacking any spiral ribs.

Low-spined gastropods. – Perhaps the Mójca gastropods with low-spined smooth surface conchs are a result of local diversification of the holopeids (Frýda *et al.* 2001). There seems to be no alternative to their relationships to *Holopea* despite the different conch geometry. ‘*Holopea*’ sp. 1 (Fig. 5A–C) differs from ‘*H.*’ *norvegica* (Koken, 1925) in Koken & Perner (1925) only in height of the spire (Fig. 5D–H). Its embryonic conch of about 110 µm diameter is rather large. ‘*H.*’ sp. 2 has the spire a little higher and the embryonic conch of up to 120 µm diameter comparable to that of ‘*Holopea*’ sp. 1 (Fig. 5I–O). Another Mójca species of a similar general appearance has an almost two times smaller embryonic conch of about 70 µm diameter (Fig. 5D–H). It resembles the Carboniferous (Visean) ‘vetigastropods with unknown affinities’ of Nützel & Mapes (2001) as well as *Straparollina*? *norvegica* sensu Ebbestad *et al.* (2013b). The latter differs from other species of *Straparollina*, including the high-spined type species, *S. pelagica* Billings, 1865 (Rohr *et al.* 2004).



Figure 4. Phosphatized larval conchs of gastropods from the Katian sample Ma-192 of the Mójca Limestone. • A, B – *Platystoma?* *obscura* (Hynda, 1986); specimens ZPAL Ga1/207 (internal mould) and 208 (phosphatized conch). • C–E – *Holopea pusilla* Hynda, 1986; specimens ZPAL Ga1/210, 174 (phosphatized conchs), and 209 (internal mould). • F, G – *Loxonema?* sp.; specimens ZPAL Ga1/188 (phosphatized conch) and 187 (internal mould). • H, I – *Siluriphorus* sp.; specimens ZPAL Ga1/189 (phosphatized conch) and 190 (internal mould). • J – *Eccyliomphalus?* sp.; specimen ZPAL Ga1/227 (internal mould).

and *Palaeomphalus* sp. (Yochelson 1963, Ebbestad *et al.* 2013b), in the lack of any umbonal ridge (Rohr *et al.* 2015). I suggest that this was a holopeid with a very low spire conspecific with the Mójca one. Although teleoconchs of the Baltic species of *Pachystrophia* have a similarly smooth shell surface, its whorl expansion rate is much higher than in the proposed Mójca holopeids.

According to Horný (1997 p. 60) ‘the Mediterranean “holopeids”, widely distributed in the cold-water Caradocian sea, were probably not closely related to the otherwise similar species from Laurentia and Baltica’.

High-spined gastropods. – *Loxonema?* sp. (Fig. 4E, F) with the embryonic conch of about 110 µm diameter super-

ficially resembles the Katian *Eopagodea sevilana* from Spain (Frýda *et al.* 2001) but its whorls gradually decreased in diameter instead of continuing an isometric growth.

The conch of *Siluriphorus* sp. resembles associated sinistrally coiled mimospirids in the flat base. A specimen with well-preserved conch wall (Dzik 1994b, fig. 15c) shows a button-like callus near the inner lip. The embryonic conch is about 90 µm in diameter.

At least two species of high-spined gastropods are represented in the Mójca assemblage having probable close relatives in the Volhynian part of Baltica. The embryonic conch tip of *Trochonema?* *parva* Hynda, 1983 (Fig. 6A–E) was relatively large, of about 140 µm



Figure 5. Phosphatized larval conchs of gastropods from the Katian sample Ma-192 of the Mójca Limestone. • A–C – ‘*Holopea*’ sp. 1; specimens ZPAL Ga1/171 (internal mould), 172 and 173 (phosphatized conchs). • D–H – ‘*Holopea*’ *norvegica* (Koken, 1925) in Koken & Perner (1925); specimens ZPAL Ga1/170, 212, 176, 175 (internal moulds), and 213 (phosphatized conch). • I–O – ‘*Holopea*’ sp. 2; specimens ZPAL Ga1/215 (internal mould), 212 (phosphatized conch), 176, 175 (internal moulds), 177, 205 (phosphatized conchs), 215, 178 (internal moulds), 214, and 179 (phosphatized conchs).

diameter. The axis of the embryonic whorl axis is at an angle in respect to that of the larval conch. The larval conch of associated *Gyronema* sp. bears additional prominent ribs (Fig. 6F–J). It differs from species of *Lopho-*

spira (Ebbestad *et al.* 2013b) in a different disposition of spiral ribs. Its embryo apex of about 110 μm diameter was smaller than that of *T. parva* and the embryonic conch coil inclination continued in the larval conch. Most

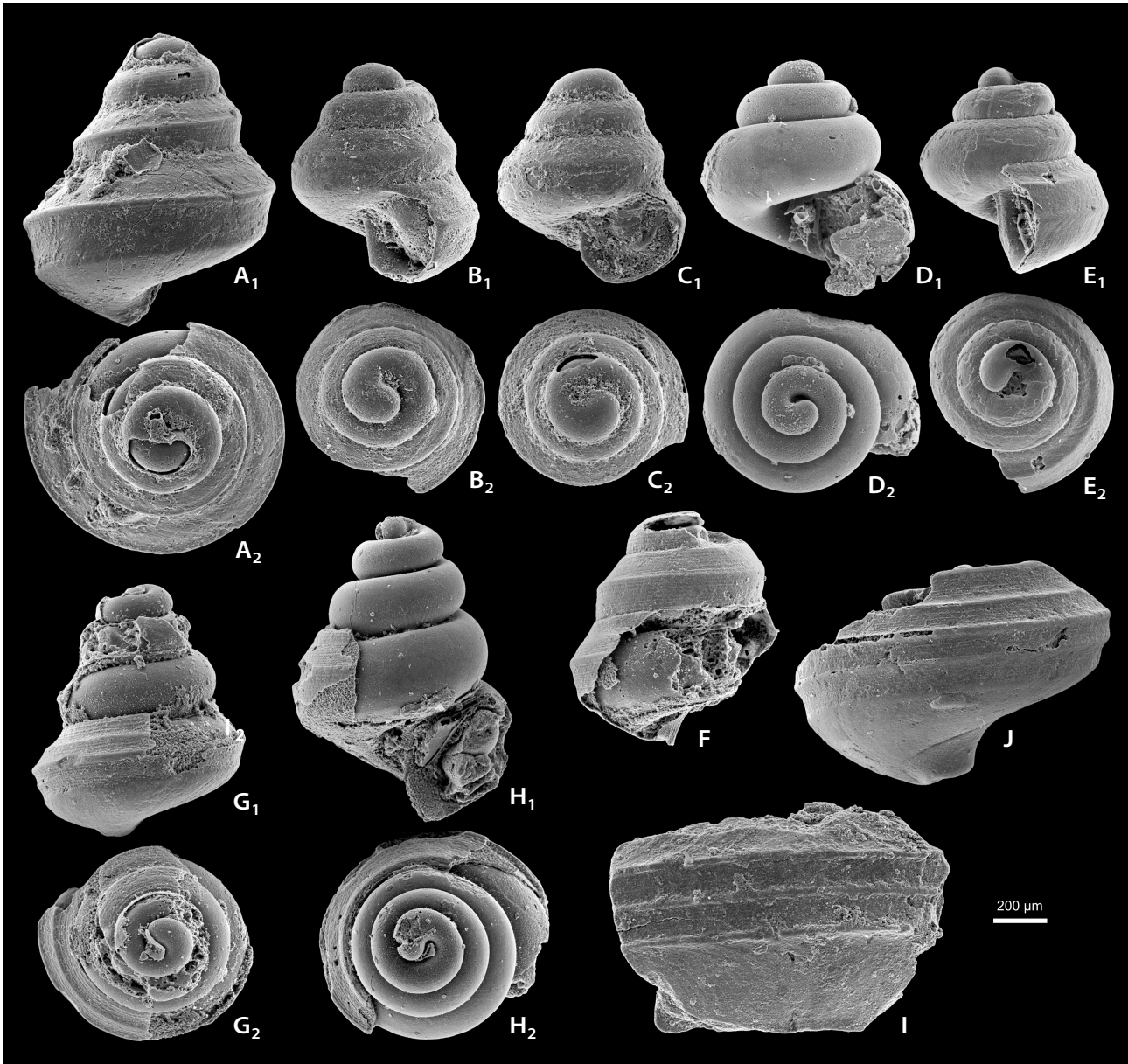


Figure 6. Phosphatized larval conchs of gastropods from the Katian sample Ma-192 of the Mójca Limestone. • A–E – *Trochonema?* *parva* Hynda 1983; specimens ZPAL Ga1/218, 219, 217, 216 (phosphatized conch), and 217 (internal mould). • F–J – *Gyronema* sp.; specimens ZPAL Ga1/221, 223, 225, 226, and 220 (phosphatized conchs).

specimens of *Gyronema* sp. are taller than those of *T.?* *parva* but their variability overlaps and especially internal moulds of juvenile larvae have been attributed to either species arbitrarily.

I failed to find any other report of Ordovician gastropods exhibiting fine spiral striation associated with stronger ribs. The type species of *Eunema strigillatum* Salter, 1859 lacks striae. *Cyclonema bilix* Conrad, 1842 is a platyceratid with calcitic shell ornamented with numerous spiral riblets but no stronger ribs. *Gyronema pulchellum* Ulrich & Scofield, 1897 is a little more similar to the Mójca species.

The Mójca gastropod community

At least eighteen species of gastropod-like molluscs and undoubted gastropods are represented in the Katian sample Ma-192 of the Mójca Limestone. Their numerical contribution to the assemblage of 8703 taxonomically identifiable specimens is as follows (Fig. 7): *Jinonicella* sp. – 125 specimens; *Peelerophon?* sp. – 9; *Tropidodiscus* aff. *minimus* Hynda, 1983 – 31; *Cyrtodiscus?* sp. (*Temnodiscus disciformis* Hynda, 1983) – 40; *Kokenospira* sp. – 414; *Sinuities* sp. – 1; *Mimospira* cf. *alta* (Hynda, 1983) – 43; *Laeogyra* cf. *volhynica* Hynda, 1983 – 22;

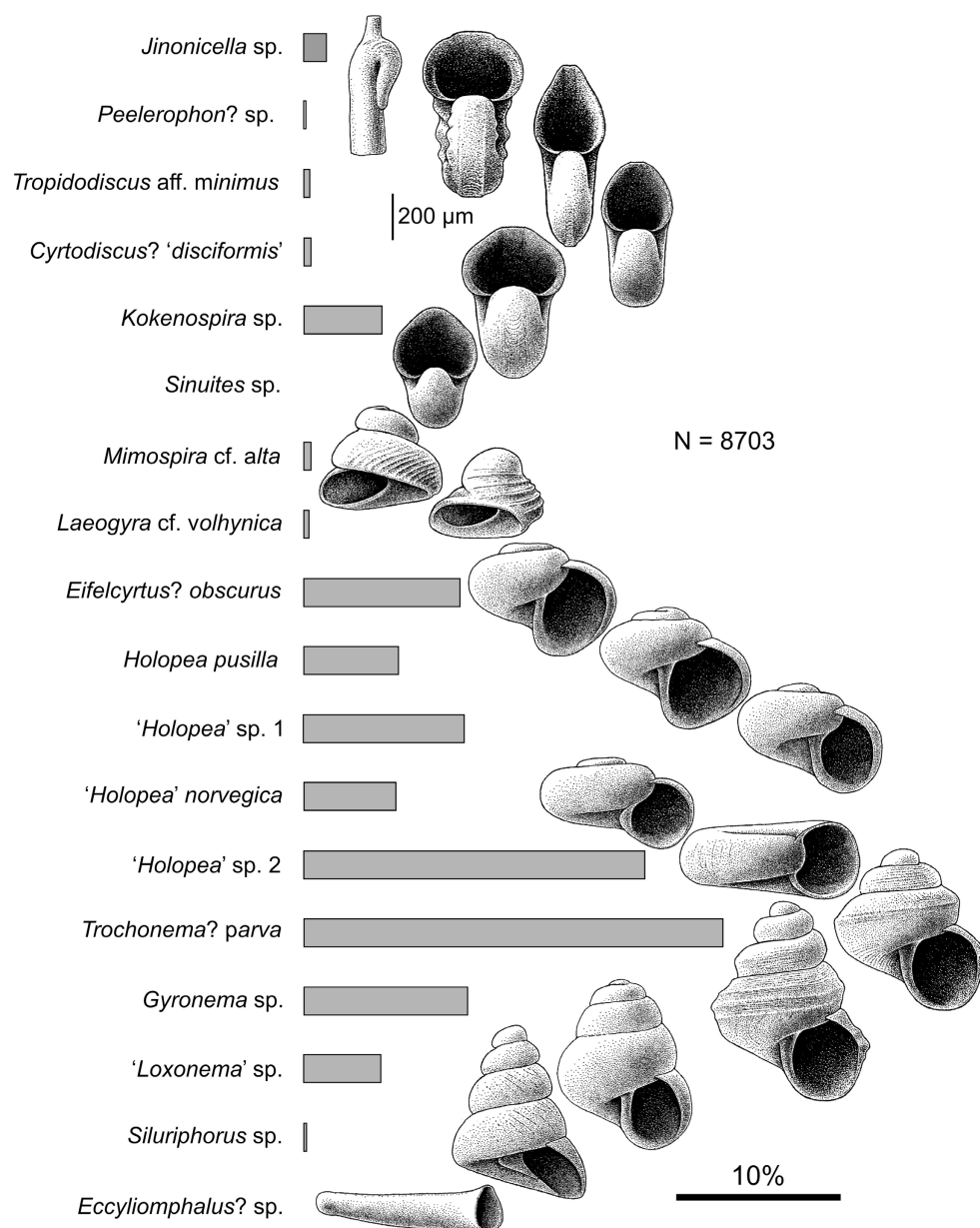


Figure 7. Percent contribution of phosphatized shells of particular conchiferan molluscs species to the Katian age sample Ma-192 of the Mójca Limestone.

Platystoma? *obscura* (Hynda, 1986) – 827; *Holopea* *pusilla* Hynda, 1986 – 508; '*Holopea*' sp. 1 – 851; '*Holopea*' *norvegica* (Koken, 1925) in Koken & Perner (1925) – 485; '*Holopea*' sp. 2 – 1817; *Trochonema?* *parva* Hynda, 1983 – 2231; *Gyronema* sp. – 873; '*Loxonema*' sp. – 407; *Siluriphorus* sp. – 17; *Eccyliomphalus?* sp. – 2.

This does not mean that proportions of teleoconchs in the biomass or biological productivity of the living Katian community was similar. Presumably, the mortality rate of lecithotrophic larvae equipped with yolk from embryos was lower than that of the planktotrophic species. Thus, one may expect more individuals of *Tropidodiscus* or trochonematids and holopeids with relatively large embryonic conchs were among survivors of the meta-

morphosis than, say, *Kokenospira* or *Eifelcyrtus*. This factor enhanced their dominant position in the sample.

The proportion of lecithotrophic vs. planktotrophic larvae increased also the difference between the Małopolska and Baltic gastropod faunas. Unlike the Darriwilian gastropod assemblages (with about 1500 specimens identified by Hynda 1986 in boreholes drilled near the western margin of Baltica), the high-spined trochonematids dominated numerically in the Katian of Mójca (about 36% against about 3% in the Baltic material, in which bellerophonitids with minute embryonic conchs contributed almost 60%, against about 5% at Mójca).

Rather unexpectedly, this refers also to the Darriwilian fossil assemblage from the San Juan Formation of Argen-

tina (Dzik 2020a, fig. 4). Bellerophontids with minute embryonic conch dominated there even more than in the Baltic samples and the most diverse were gastropods with openly coiled initial parts of their larval conchs. The Mójcza assemblage appears thus unique in the diversity of low-spired holopeids.

Conclusions

High-spired trochonematid conchs ornamented with delicate spiral striation between low ribs dominate the assemblage of larval and juvenile gastropod specimens from the Katian part of the Mójcza Limestone. Instead of the typically Baltic planispiral leseurillids the low-spired or planispiral probable holopeids with smooth shell surface are abundant. Presumably, this is a result of local homoplastic speciation, although at least the trochonematids and underived holopeids may have had their relatives in the Ukrainian part of Baltica, located near the opposite shore of the Ordovician Tornquist Sea to the Małopolska microcontinent.

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