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Decline in diversity of early Palaeozoic loosely coiled gastropod protoconchs

JERZY DZIK

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Quantitative data on molluscan larval conch fossil assemblages of ages ranging from the Ordovician (Argentina and the Baltic region), through Silurian (Austria), Devonian (Poland) to Carboniferous (Texas) supplement knowledge of early planktonic gastropods communities transformations. They show that larval shells of the bilaterally symmetrical bellerophontids and dextrally coiled gastropods with a hook-like straight apical portion of the first whorl initially dominated. Their relative frequency, as well as that of the sinistrally coiled 'paragastropods', diminished during the Ordovician and Silurian to virtually disappear in the Late Devonian and Early Carboniferous. Already during the Ordovician, diversity of larvae with gently loosely coiled first whorl increased, to be replaced then with more and more tightly coiled forms. Both the aperture constrictions and mortality peaks, probably connected with hatching and metamorphosis, indicate that the Ordovician protoconchs with hook-like first coil represent both the stage of an embryo developing within the egg envelope and a planktonic larva. The similarity of the straight apex to larval conchs of hyoliths and advanced thecosome pteropods is superficial, as these were not homologous stages in early development. ☐ *Conodonts, Ordovician, Gastropoda, Early Palaeozoic, larvae.*

Jerzy Dzik ✉ [dzik@twarda.pan], Institute of Paleobiology, Polish Academy of Sciences PAN, Twarda 51/55, 00-818 Warszawa, Poland and Faculty of Biology, University of Warsaw, Aleja Żwirki i Wigury 101, Warszawa 02-096, Poland; manuscript received on 2/01/2019; manuscript accepted on 15/03/2019.

The origin and early evolution of gastropods remain elusive, despite the relatively high fossilization potential of molluscan shells and hundreds of years of palaeontological research on them. The major obstacle with interpreting the gastropod fossil record is a relatively low phylogenetic signal that can be recovered from the morphology of their post-larval stages (teleoconchs). They are highly homoplastic, with closely similar morphologies repeatedly developing in unrelated lineages (Wagner & Erwin 2006). To solve this conundrum, data on both embryonic conchs and teleoconchs of the oldest unquestionable gastropods are needed. Unfortunately, present knowledge of early Palaeozoic gastropod larvae is highly limited. In this paper, I try to extend the already available scarce evidence by recovering a few new assemblages of fossil larvae and tracing how their composition in changes the geological time.

The mass occurrence of minute mollusc conch phosphoritic nuclei is a phenomenon typical for the early Palaeozoic strata. They are especially frequent in the early Cambrian deposits, and the concept of 'Cambrian explosion' was inferred to much degree from such fossil evidence, frequently referred to as 'small shelly fossils'. Secondarily phosphatized microscopic size shells are common also in sediments deposited in temperate climate zone of the Ordovician (Hynda 1983, 1986; Nützel *et al.* 2006; Nützel 2014; Lindskog *et al.* 2015) but they decrease in frequency through the Silurian and Devonian (Dzik 1994b; Nützel & Frýda 2003). The youngest truly rich 'small shelly fossils' assemblages known to date are those of Early Carboniferous age. They are supplemented in the Late Palaeozoic and Mesozoic strata by abundant occurrences of larval gastropod, bivalve and cephalopods conchs with their original aragonitic walls preserved in black shales, in which fossil mature specimens are virtually missing (Nützel & Mapes 2001; Seuss *et al.* 2012). Although it cannot be excluded that some of these minute mollusc conchs belonged to adult individuals of micromorphic species, at least the overwhelming majority of them represent planktonic larvae. They apparently failed to metamorphose after encountering an oxygen-deficient environment on the sea bottom (Nützel & Mapes 2001)

Taken together, the fossil record of such kind gives an insight into two important aspects of the gastropod early history. First, a quantitative research on the time-ordered series of planktonic larvae assemblages may be used to exploit the problem whether the planktotrophy or perhaps lecithotrophy dominated among early planktonic molluscan larvae and which of these life strategies is the plesiomorphic one (Frýda 1999, 2012; Frýda *et al.* 2008; Nützel 2014). It is also possible to trace the loosely coiled larvae,

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unique for the Palaeozoic, to assemblages with exclusively modern larval morphologies. Moreover, the second line of inference offers some insight into rarely accessible data on the evolution of ecosystems. The increased mortality of metamorphosing larvae followed by the process of phosphatization of larval shells requires a local coincidence of various factors controlling it (relatively low pH and Eh and high phosphate ions supply). This means that the recorded changes in composition of fossil assemblages reflect transformations of larval communities adapted to quite a narrow range of physical factors that apparently remained similar for hundreds of million years.

The main limitation of such attitude to the fossil record is that only rarely fossil larval shells of such ancient age can be convincingly matched with teleoconchs of the same species (Bandel *et al.* 2002). Similar larval conch may belong to Palaeozoic gastropods teleoconch of completely different shape (Cook *et al.* 2008). This makes phylogenetic studies based exclusively on the teleoconch morphology (Wagner 2002) not reliable. Rarely a settling larva survived metamorphosis to grow for some time before being phosphatized (Dzik 1984, 1994a), and then, juvenile teleoconchs may provide crucial information that can be used to determine generic or family level identity. This makes studies on earliest gastropod larval conchs of special interest.

In this paper, I will use the available data on gastropod larvae from ‘small shelly fossils’ assemblages to trace quantitatively changes in contribution of openly coiled protoconchs to them to supplement and specify already identified general patterns (Nützel & Frýda 2003). I hope that a backward extrapolation of the observed trend will also allow to determine, which shell morphology is the most primitive and, implicitly, ancestral to gastropods.

Material

As already mentioned above, the mass occurrence of secondarily phosphatized minute shells is generally interpreted as a result of increased mortality at attempted metamorphosis on the oxygen-deficient sea bottom, thus in an environment promoting secondary phosphatization (Dzik 1978, 1994a; Nützel & Mapes 2001; Mapes & Nützel 2009). This was a common phenomenon in shelf areas of the early Palaeozoic presumably owing to the generally shallower bioturbation of sediments that time. Shelly detritus was then exposed for long enough to enable extensive phosphatization, especially in temperate climate regions close to upwellings, characterized by a high biological productivity. The action of micro-organisms releasing phosphate ions resulted in the frequent development of phosphatic coatings around skeletal grains. The same discrepancy between mass occurrence of larval conchs and extreme rarity of their mature counterparts is known also from younger strata, although not being so common as in the Cambrian or Ordovician (Dzik 1994b). Here, both already published and newly obtained data on samples with gastropod larvae of ‘small shelly fossils’ type of preservation are used.

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

Darriwilian San Juan Formation

A sample about 2 kg weight from the top of the San Juan Formation was collected during excursion to the Don Braulio Creek in the Villicum Range near San Juan, Argentina, organized in 2013 by Guillermo Albanesi (Córdoba). The rock is a cephalopod limestone with aggregation of endoceratid nautiloids conchs. The top of this unit is represented by a red ochre grainstone and burrowed greenish dark grey bioclastic wackestone (Mestre *et al.* 2013). Its age was determined by Mestre *et al.* (2013) as the *Yangtzeplacog nathus crassus* Zone. Platform P_1 elements with elongated posterior process in my collection identify *Eoplacognathus zgierzensis* (Appendix S1 Fig. 3R), which indicates a slightly younger age than the strata with *Y. crassus*, but still below the *E. pseudoplanus* Zone. The whole conodont assemblage (Appendix S1 Figs 1–3) is different from that in coeval strata of the Baltic region but shares with it a set of cosmopolitan species. The rock matrix abounds in secondarily silicified (originally phosphatic) nuclei of gastropod larvae (Fig. 1) already reported and illustrated by Mestre *et al.* (2013) who identified a few

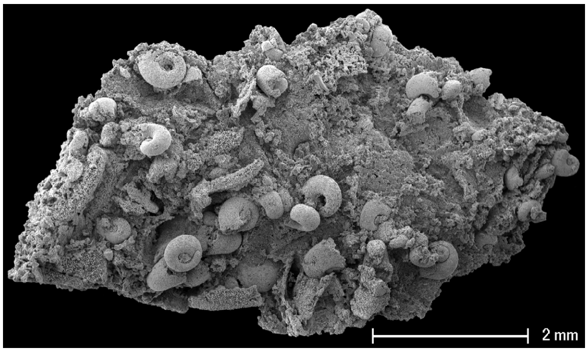

Fig. 1. A piece of silicified limestone rock matrix from the acid-resistant residue of the San Juan Formation sample from its top layer exposed at Don Braulio Creek, Villicum Range, Argentina.

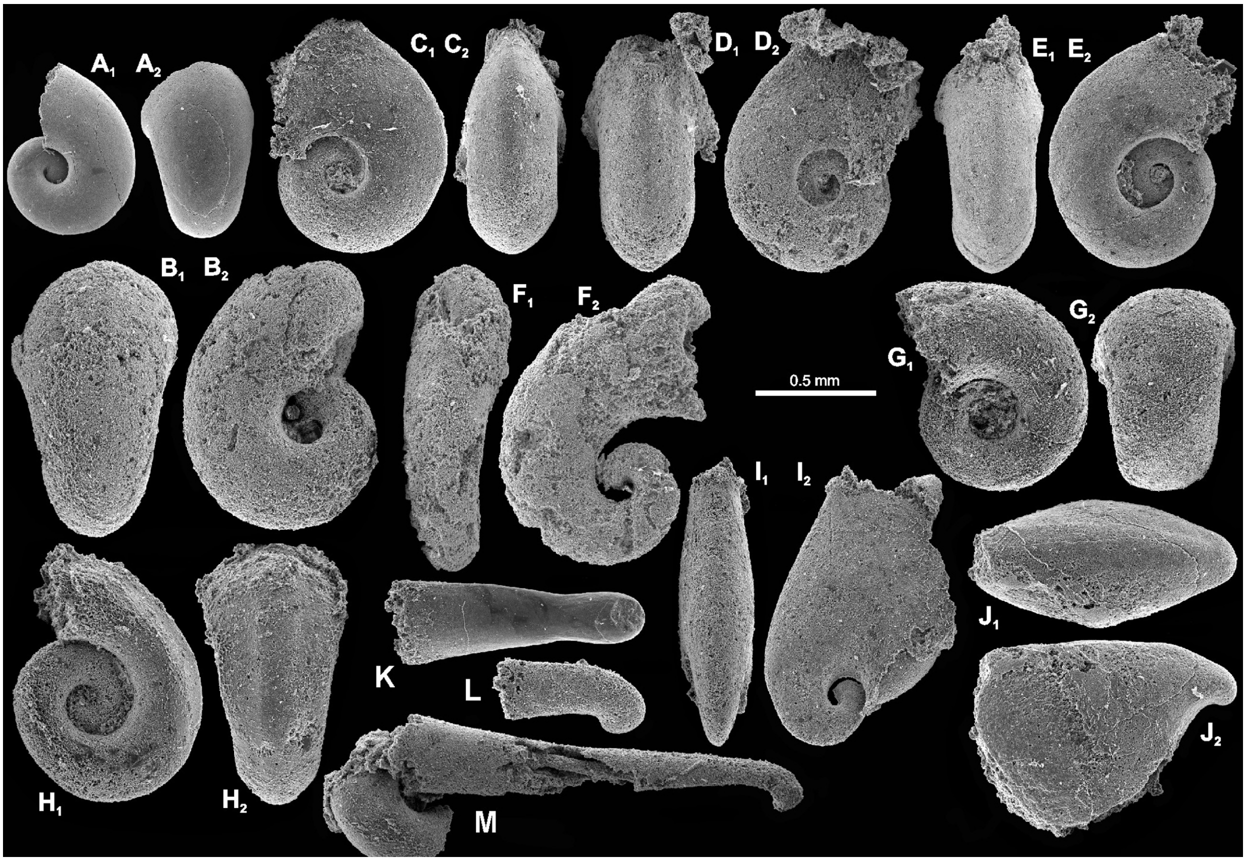

Fig. 2. Tentative taxonomic identifications of secondarily silicified juvenile and larval bellerophontid, hyolith and rostroconch conch nuclei from the top of the Darriwilian San Juan Formation at Don Braulio Creek, Villicum Range, Argentina in lateral and apertural or abapertural views. A, B, *Sinuites* sp. specimens ZPAL SJ 8 (with preserved original phosphatic matrix) and 20. C, D, *Tropidodiscus* sp. A, specimens ZPAL SJ 15 and 19. E, *Tropidodiscus* sp. B, specimen ZPAL SJ 14. F. ZPAL SJ 25. G, H, *Carcassonella* or *Modestospira* sp. specimens ZPAL SJ 16 and 9. I, *Lamaureriella*? sp., ZPAL SJ 24. J. Ribeirid rostroconch ZPAL SJ 21. K, larval hyolithid, ZPAL SJ 22. L, larval orthothecid ZPAL SJ 23. M, juvenile orthothecid ZPAL SJ 26.

morphologic types, including those with open initial coil. 1822 nuclei with preserved apex were picked out from the sample. Some specimens are tectonically deformed, which prevents biometric study on their morphological variability. Many of these gastropod protoconchs are smooth and openly coiled.

Like conodonts, the gastropod assemblage composition differs from those of the Baltic region. Possibly, the Argentinian larval shells belong to gastropod species known after mature specimens from coeval strata elsewhere in Gondwana (Horný 1997; Ebbestad 2008).

Darriwilian Baltic borehole core samples and erratics

The lowest Darriwilian (middle Kundan) limestone in the Baltic area abounds in phosphatized larval and juvenile conch nuclei (Lindskog *et al.* 2015) although fossil teleoconchs are virtually missing there. The early Darriwilian glacial erratic boulder E-355 collected from Weichselian till at Międzyzdroje on the Polish shore of the Baltic Sea is representative for strata of similar age in the Baltic region and the San Juan Formation in Argentina. It has yielded 176 nuclei of larval conchs.

The fossil assemblage of gastropod larvae closely similar in taxonomic composition, although of significantly younger Sandbian (early Caradoc) age, from the borehole Lesieniec in the East European craton part of Poland (thus representing the ancient continent of Baltica) was already reviewed and illustrated by myself (Dzik 1994b). Not so similar, both with respect to taxonomy and taphonomy, is the early Katian (sample Ma-99) fossil assemblage from the Mójcza Limestone in the Holy Cross Mountains, Poland. Although almost all identifiable molluscan conchs from the Mójcza Limestone represent early ontogenetic stages, there is not so prominent peak in frequency distribution at the stage of metamorphosis as in the San Juan Formation or Baltic fossil assemblages. Apparently, most molluscs at Mójcza successfully settled at the bottom and died somewhat later

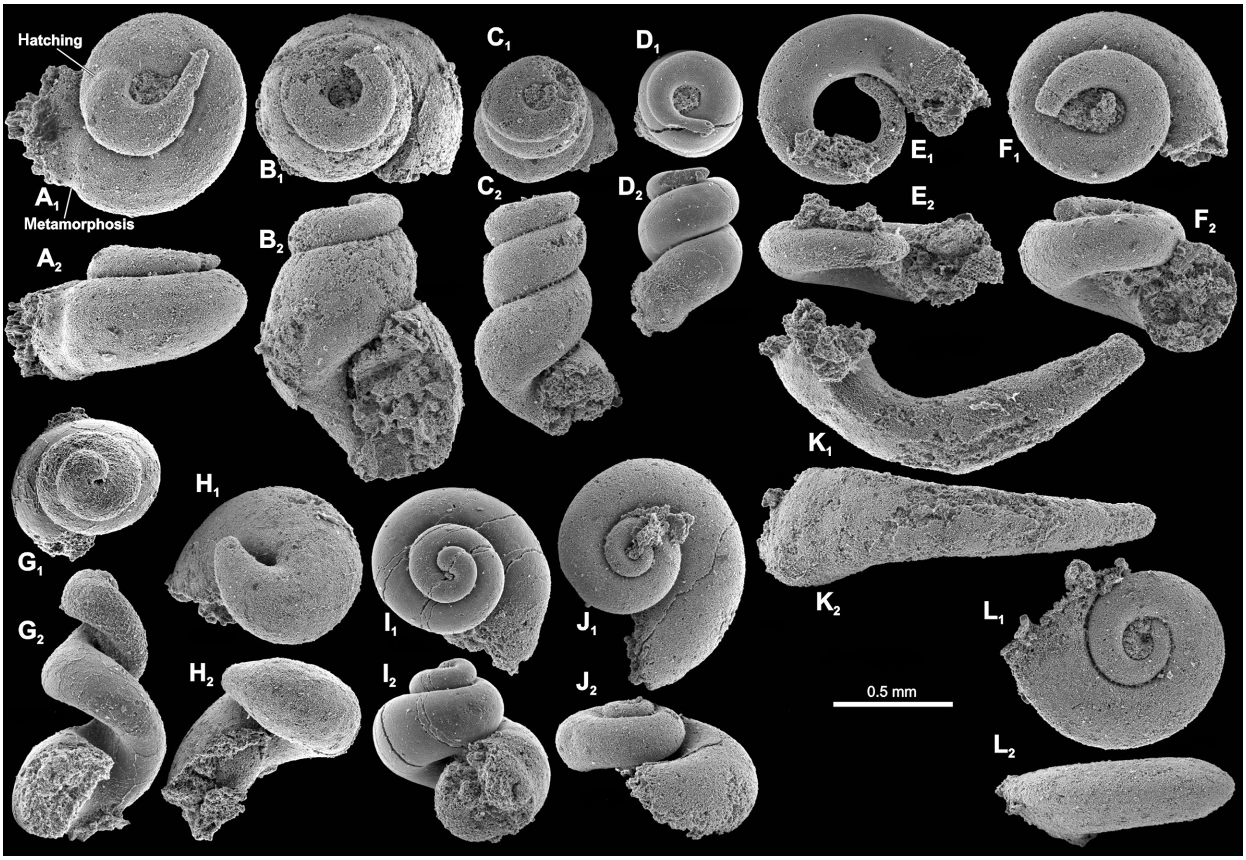

Fig. 3. Tentative taxonomic identifications of secondarily silicified juvenile and larval gastropod conchs nuclei from the top of the Darriwilian San Juan Formation at Don Braulio Creek, Villicum Range, Argentina in lateral and apertural or abapertural views. A, *Pararaphistoma*? sp. A, specimen ZPAL SJ 2, showing constrictions marking boundaries of both the embryonic and larval stages. B, *Subulites* sp. A, specimen ZPAL SJ 3. C, D, *Subulites*? sp. B, specimens ZPAL SJ 4 and 5. E, *Raphistoma*? sp., specimen ZPAL SJ 18. F. *Pararaphistoma*? sp. B, specimen ZPAL SJ 17. G. *Mimospira* sp., specimen ZPAL SJ 11. H. *Clisospira* sp. specimen ZPAL SJ 10. I, *Holopea* sp. A, specimen ZPAL SJ 6. J, *Holopea* sp. B, specimen ZPAL SJ 7. K, *Ecculiomphalus*? Sp, specimen ZPAL SJ 12. L. *Raphistoma*? sp. specimen ZPAL SJ 13.

in a non-hospitable environment. The fossil assemblage from Mójcza differs also from that of the San Juan Formation in that most specimens are preserved with a thin phosphatic coat usually well replicating external shell morphology. Specimens with the original aragonitic shell replaced with calcium phosphate are also common. Unfortunately, complete lack of macroscopic fossils in most of the section prevents reliable generic level taxonomic identification of early post-larval juveniles. This is especially disappointing because most gastropods represented by larvae and minute juveniles at Mójcza are not known from the Baltic region (Dzik 1994a). Because of somewhat different taphonomy, the Mójcza material is not used here for quantitative comparisons.

Ludlow part of the Kok Formation

The Silurian 'small shelly fossils' assemblage from a loose block of cephalopod limestone derived from the Ludlow part of the Kok Formation collected by myself at the Cellonetta Lavinerinne in the Carnic Alps, Austria, was illustrated and reviewed (Dzik 1994b). The only macrofossils recognizable in the block are orthoconic nautiloids. Like specimens from the Mójcza Limestone, those from the Kok Formation usually have a thin phosphatic coat. Many specimens show pyritized or phosphatized shell. Larvae of bivalves, instead of gastropods, dominate there (Dzik 1994b).

Famennian of the Holy Cross Mountains

Phosphatization of molluscan larval and juvenile conchs is a common phenomenon in Late Devonian black cephalopod limestones of the Holy Cross Mountains, Poland, especially in strata bordering the sedimentary discontinuity between the *Conditolepis marginifera* and *Palmatolepis trachytera* Zones of the Famennian in the classic Łagów-Dule locality (Dzik 1978, 1994b). Like the material from the Kok Formation, here also pyritization of shell wall is a common

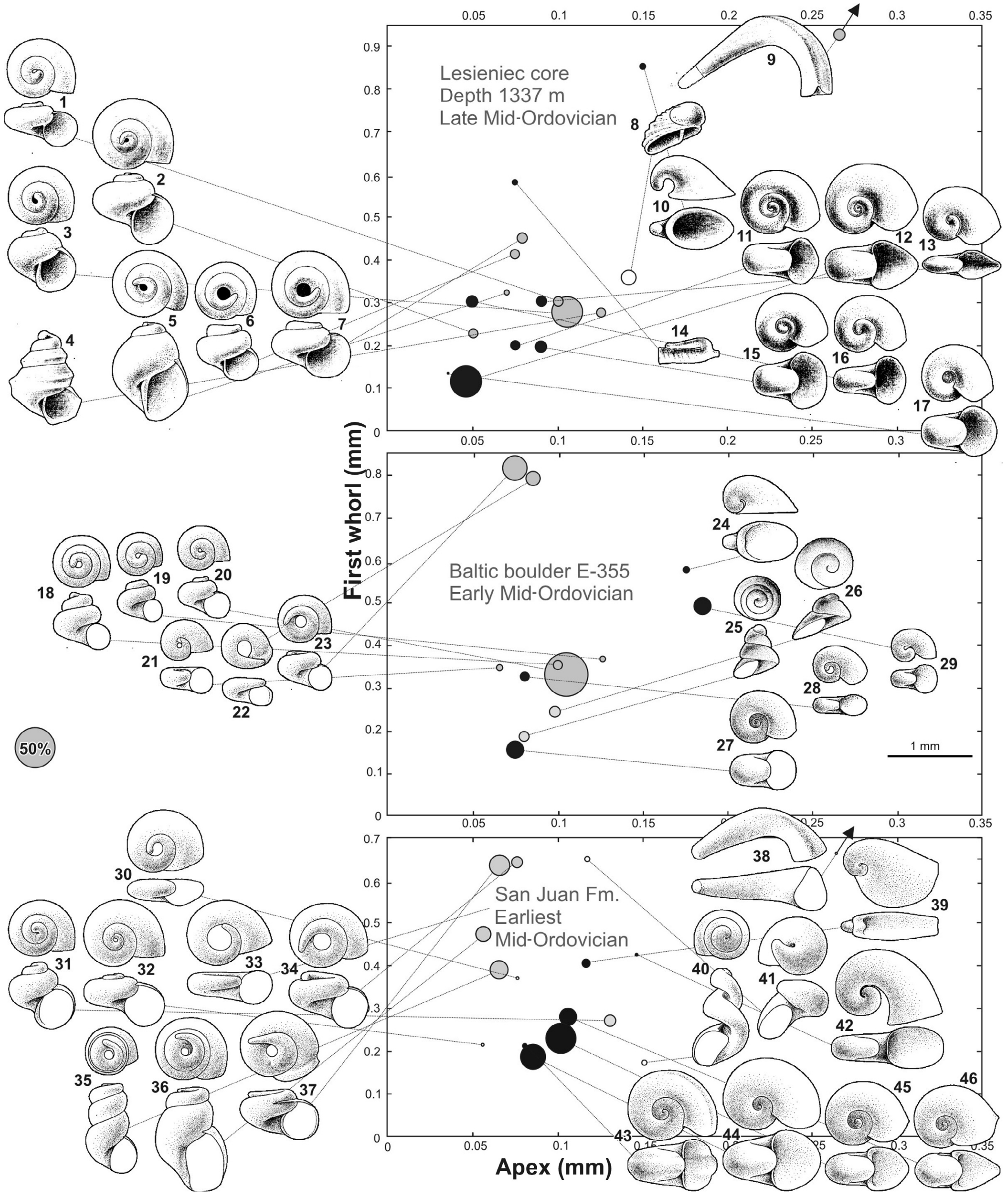

Fig. 4. Relative contribution of larval gastropod conch morphologies to Ordovician ‘small shelly fossils’ assemblages. Diameters of apex and the first coil are plotted to characterize the embryonic conch morphology, size of points is proportional to per cent contribution to the sample. The San Juan Formation and the erratic boulder E-355 are early Darriwilian, the sample from the Lesieniec borehole is Sandbian in age (illustrations from Dzik 1994b, fig. 23 are adapted). Size of circles reflects per cent contribution to the sample; black circles denote belerophontid, grey chiral gastropod conchs. Tentative taxonomic identifications: 1—‘*Straparollus*’ sp.; 2— ‘*Naticonema*’ sp.; 3—*Holopea*? aff. *pusilla* Hynda 1983; 4—*Trochonema* sp.; 5—*Subulites* cf. *revalensis* Koken, 1925; 6—subulitid indet.; 7— ‘*Clathrospira*’ *obscura* (Hynda 1983); 8—*Clisospira* sp.; 9—*Ecculiomphalus*? sp.; 10—*Archinacella*? sp. A; 11—cf. *Bucania christianiae* (Koken, 1925); 12—*Tropidodiscus* (*Peruniscus*) *minimus* Hynda 1983; 13—*Temnodiscus disciformis* Hynda 1983; 14—*Jinonicella* sp. n.; 15—*Kokenospira*? aff. *subglobosa* Hynda 1983; 16—*Severynella trochlearis* Hynda 1983; 17—*Sinuites* sp.; 18—*Holopea*? sp. a; 19—*Holopea*? sp. B; 20—*Holopea*? sp. C; 21—*Raphistoma*? sp.; 22—*Pararaphistoma*? sp. A; 23—*Subulites*? sp.; 24—*Archinacella*? sp. B; 25—*Mimospira* sp.; 26—*Clisospira* sp.; 27—*Sinuites*? sp.; 28—*Sinuitopsis*? sp. 29—*Cyclocyrtonella* sp.; 30—*Raphistoma*? sp.; 31—*Holopea* sp. A; 32—*Holopea* sp. B; 33— ‘*Vltaviella*’ sp.; 34—*Pararaphistoma*? sp. B; 35—*Subulites*? sp. B; 36—*Subulites* sp. A; 37—*Pararaphistoma*? sp. A; 38—*Eccyliomphalus*? sp.; 39 –; 40—*Mimospira* sp.; 41—*Clisospira* sp.; 42—*Cyclocyrtonella* sp.; 43—*Carcassonnella* or *Modestospira* sp.; 44—*Sinuites* sp.; 45—*Tropidodiscus* sp. B; and 46—*Tropidodiscus* sp. A.

phenomenon. Although preservation of the material is perfect, with details of ornamentation well visible (Dzik 1978, fig. 4A, B), they are not numerous enough to enable quantitative studies. This is possible to be done with the material from roughly coeval strata at the nearby locality Miedzianka (sample of 274 specimens). Nuclei of gastropod larval conchs are there secondarily silicified in a manner somewhat similar to that in the San Juan Formation. Amler (2004) reported similar abundant occurrences of pyritic internal moulds of gastropod, bellerophontid and ammonoid larval conchs in black shales of the Late Famennian (Clymenia Stufe) in the Rhenish Slate Mountains, Germany. No larger specimens co-occur with them.

Viséan Barnett Formation

The dark grey to black, laminated mudstone of the Barnett Shale of the Fort Worth Basin, Texas, contains limestone concretions. Samples from them, collected at Barnett, Texas and processed by Royal H. Mapes (Ohio University, Athens), has yielded extremely abundant assemblage of phosphatized molluscan larval conchs nuclei, looking like a phosphatic sand with a naked eye. The most common there are ammonoid and bactritid larvae. The frequency of gastropods is also high but bivalves are subordinate. Only rarely the shell wall is locally preserved showing the external conch morphology.

Co-occurrence of the conodonts *Gnathodus texanus*, *Cavusgnathus unicornis* and *Lochriea commutata* indicates late Viséan (lower Chesterian) age (Wardlaw 2007).

Methods

Early and mid-Palaeozoic gastropod protoconchs generally differ strongly from their corresponding adults in their general morphology (Seuss *et al.* 2012). This makes any taxonomic analysis difficult at the moment and only provisional attributions to genera known from teleoconchs are possible. Therefore, the main line of reasoning presented here follows changes in geometry of recovered larval conchs and their per cent contribution to fossil assemblages rather than mature conch morphology.

Identification of particular stages of early ontogeny in the fossil material was based on incremental marks and shell geometry. Growth increments visible on surface of the conical portion of the conch suggest that the embryonic and larval shell wall was at least weakly mineralized. The hemispherical tip of the hook-shaped portion of the *Platyceras*-like conch probably corresponds to the initiation of the activity of shell gland in the early development of embryo. A thickening of aperture (corresponding to a constriction on nuclei; Fig. 3A_1) seems to reflect hatching. This would mean that the size of the initial part of the embryonic conch does not correspond to the size of yolk sac, in which the larva of these ancient gastropods was equipped by the maternal animal. The hatching took place after growth of half of the whorl was completed. These two dimensions of an embryonic conch characterize important aspects of its biology and have been used by myself to construct plots. Also in other gastropods, the diameter of the hemispherical tip and the first coil expresses roughly the size of embryonic conch that is only rarely traceable in unornamented conchs. At least it shows only how tight is the coiling of the conch. Based on analogy with Recent gastropods (Bandel 1975), Nützel (1998, fig. 27) used this dimension to distinguish planktotrophic from lecithotrophic early caenogastropods. According to him, first whorl diameter larger than 0.25 mm indicates lecithotrophy and more than 0.4 mm indicates direct development. This is not necessarily applicable to early Palaeozoic gastropods with widely open first coil.

In order to include both biometrical data on embryonic conchs and frequency of particular larval conch morphologies, their per cent contribution to sample is shown as proportional to size of points on the graph. It has to be remembered that the pattern expressed in such way does not necessarily reflects the structure of ancient communities (standing crop) but rather contribution of particular species to the bulk biological productivity.

Darriwilian San Juan Formation fossil assemblage

The most striking aspect of the fossil assemblage from the top of San Juan Formation is the domination of bilaterally symmetrical conchs, mostly of bellerophontids (Figs 2, 4). Among them are forms with a relatively large apex that may have tergomyan affinity (Fig. 3F, I), one of them resembling the somewhat older Dapingian *Lamaureriella* from the Montagne Noire, France (Peel & Horný 2004). The size and form of apex make them similar to roughly coeval *Sinuitopsis* and *Modestospira* (Dzik 1981a, 1994a). The embryonic apex of unquestionable bellerophontids is small, and the conch is tightly coiled. Hyolith larvae, represented by both hyolithids (Fig. 2K; cf. Dzik 1978) and orthothecids (Fig. 2L, M; cf. Dzik 1980), as well as sinistrally coiled mimospirines

(Fig. 3G, H), are subordinate. The latter are represented by two distinct morphologies, probably different species of the genera *Mimospira* and *Clisospira*. All specimens within each group are of similar size, suggesting that they represent planktonic larvae experiencing increase in mortality at metamorphosis (Fig. 3G, H). Similar specimens from other sources with preserved external shell morphology show a distinct, cap-shaped embryonic part bearing distinct growth increments (Dzik 1984). This means that also in this case, the conch wall was mineralized at its growth.

There are also rare ribeirid rostroconch larvae in the sample (Fig. 2J), with a hemispherical embryonic part. It is not possible to determine the pattern of embryonic growth based only on conch nuclei.

Among dextrally coiled true gastropods dominate those with hook-like embryonic part of the larval conch. Those with straight embryonic part show not only the constriction corresponding to hatching but also at the end of the larval stage, an apparent expression of metamorphosis (Fig. 3A). Others have the embryonic part gently curved, although deviating from the post-embryonic conch coils. There is a gradation between these two morphologic classes. Also the geometry of the whole larval conchs with uncoiled embryonic parts form a morphologic series from those almost planispirally coiled (Fig. 3E) to almost cylindrical appearance of at least three post-embryonic coils (Fig. 3C, D). Some of these conchs may represent early post-larval stage of development (Fig. 3B) with the morphology similar to *Subulites*. A somewhat isolated position in the spectrum of morphologic diversity is occupied by rare relatively large conchs with truncated apex, straight conical embryonic part and curved terminal portion with a ridge (Fig. 3K) revealing affinity to *Leseurilla* or its uncoiled relative.

There are also gastropods with relatively tightly coiled embryonic part of the conch (although the first coil always shows perforated umbo). They also exhibit a wide range of geometries of the larval conch (Fig. 3I, J, L). Most specimens are of a similar size that indicates metamorphosis of the larva at three coils of its conch.

Darriwilian and Sandbian Baltic fossil assemblages

All the Baltic Ordovician 'small shelly fossils' assemblages known to me (Dzik 1978, 1983, 1984, 1994b; Nützel *et al.* 2006; Lindskog *et al.* 2015) are of similar composition. The gastropod planktonic larvae community was apparently rather stable and changed their composition gradually in geological time. The main difference between the Gondwanan San Juan Formation assemblage and those from coeval strata in the Baltic area is a somewhat lower contribution from bellerophontids and domination of relatively tightly coiled embryonic conchs among dextral true gastropods (Fig. 4). In the case of the *Subulites*-like conchs, those from the Sandbian show a much smaller diameter of the embryonic coil with respect to the Darriwilian forms. Small larvae with straight embryonic part are almost missing, except for the enigmatic *Jinonicella*. The Sandbian fossil assemblage shares the large leseurillid with the San Juan Formation. Along with isolated probable larval conchs, an imprint in a phosphorite from a Darriwilian glacial boulder is known (Dzik 1994b, fig. 22G), which shows that the protoconch had a hemispherical tip usually missing in isolated specimens (thus possibly weakly mineralized) and that growth increments emerge suddenly after the conch curves to develop the first coil. This may correspond to both hatching and metamorphosis. The teleoconch was tightly coiled at least in a few earliest whorls, which suggests that these extremely large Ordovician embryonic conchs belonged to the *Leseurilla-Eccyliomphalus* stock.

The conundrum most difficult to solve is the difference in earliest growth stages between the latest Dapingian *Janospira* and *Jinonicella*, the oldest occurrence of the latter being the Sandbian of the Lesieniec borehole in the Polish part of the East European craton. The *Janospira* protoconch is hardly different from that of bellerophontids, whereas the protoconch of *Jinonicella* is of the same morphology as those of the early Mid Ordovician leseurillid gastropods. Teleoconch is tubular, scaphopod-like, in both cases. According to Peel (2006), they both are derivatives of the ribeirioid rostroconchs. This would mean that the larval stage was more homoplastic than mature stages in this case, in contrast to other molluscs.

There is a gradation between all the larval conch sizes and morphologies among the sinistrally coiled mimospirines (Dzik 1984), unlike the San Juan Formation, but two distinct species may be represented in this sample, anyway.

Ludlowian Kok Formation fossil assemblage

The bellerophontids diversity is strongly reduced in this Silurian assemblage with respect to those from the Ordovician. Still, along with a typical advanced

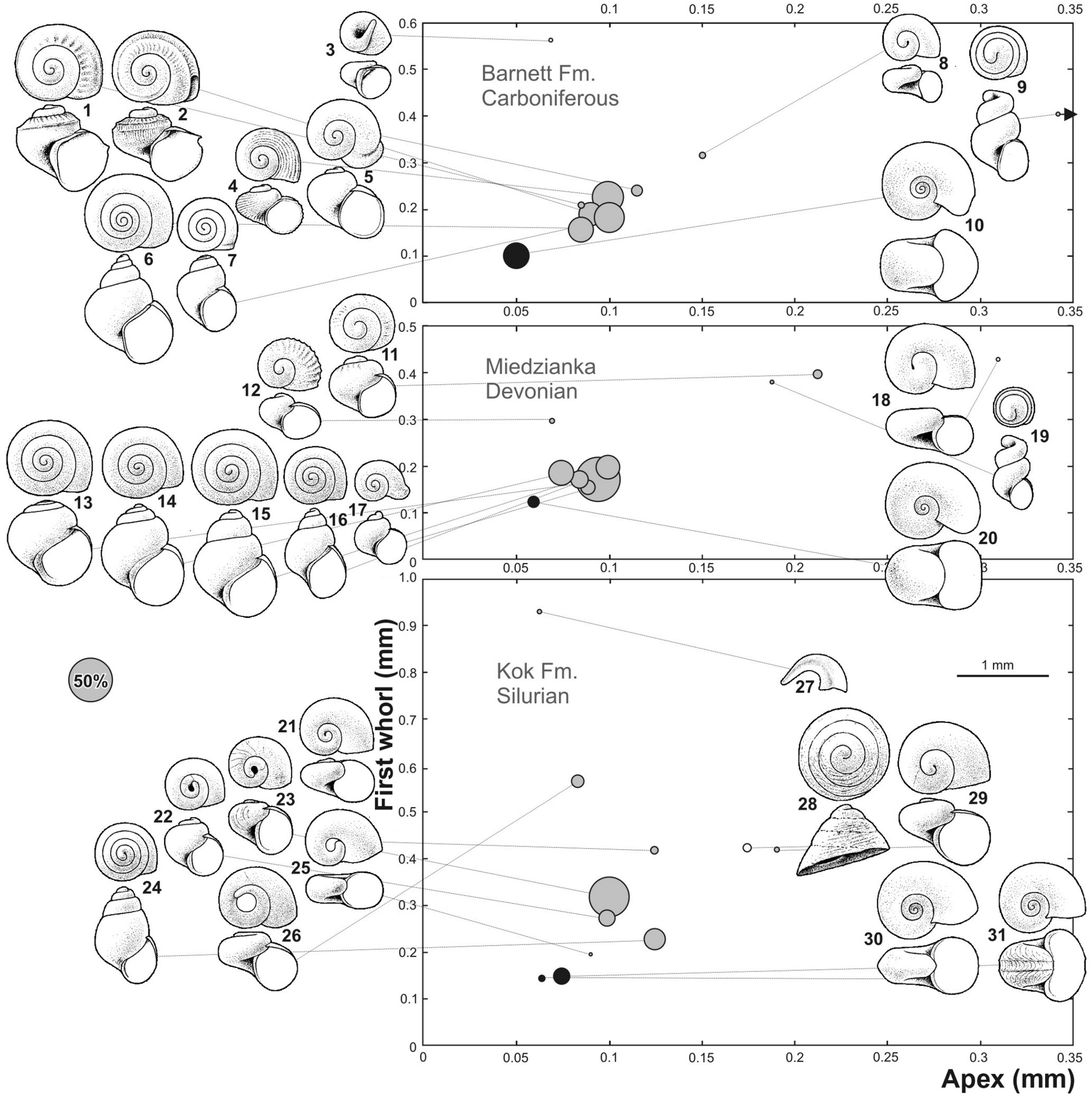

Fig. 5. Relative contribution of larval gastropod conch morphologies to post-Ordovician 'small shelly fossils' assemblages. The Kok Formation is of Ludlovian age; the strata exposed at Miedzianka are Famennian; and the Barnett Formation is Viséan in age. Tentative taxonomic identifications: 1—*Worthenia* sp. A; 2—*Worthenia* sp. B; 3—*Platyceras* sp.; 4—*Compsonema* sp.; 5—*Naticopsis*? sp.; 6—*Strobeus* sp. A; 7—*Girtyspira* sp.; 8—*Euomphalus* sp. A; 9—*Pseudozygopleura*? sp.; 10—*Bellerophon* sp. A; 11—*Naticopsis* sp. A; 12—*Naticopsis* sp. B; 13—*Strobeus* sp. B; 14—*Soleniscus* sp. A; 15—*Soleniscus* sp. B; 16—*Bulimorpha*? sp.; 17—*Globobulimorpha* sp.; 18—*Euomphalus* sp. B; 19—*Pseudozygopleura*? sp.; 20—*Bellerophon* sp. B; 21— '*Umbospira nigricans*' sensu Heritsch; 22—*Naticopsis plicatula*; 23— '*Platyceras*' *otiosum*; 24—*Imogloba*? sp.; 25—*Euomphalus* sp.; 26—*Vltaviella* sp.; 27— '*Lytospira*' *subuloidea*; 28—*Antigyra* sp.; 29—*Straparollus*? sp.; 30—*Tropidodiscus*? sp.; and 31—*Bellerophon* sp. C.

Bellerophon-like species, there is a discoidal form of *Tropidodiscus* type. Umbo of the embryonic shell is perforated in all species but some earlier unknown morphologies have appeared.

The almost planispirally coiled larval (or juvenile) conchs with a relatively large apex may represent a species of *Eomphalus*. The typical tightly coiled *Euomphalus* protoconch that comprises less than one almost planispiral whorl with a small umbonal opening, thus still openly coiled, was reported from the Early Carboniferous by Bandel & Frýda (1998) and Nützel (2002). There was no separate larval conch stage. Like most extant archaeogastropods, the euomphalids were not planktotrophic and the discontinuity in conch growth immediately after this protoconch stage corresponded to metamorphosis.

Nützel (2002), following Batten (1984), Bandel & Frýda (1998), Frýda *et al.* (2008) and Frýda (1998, 2012), suggested that this is a plesiomorphic patellid (docoglossan) trait. This peculiar protoconch morphology can be traced back to the Late Ordovician (early Katian) of the Mójcza Limestone (Dzik 1978, fig. 4C). However, no direct evidence is available to prove connection between the Palaeozoic euomphalids and the Mesozoic patellids (Frýda *et al.* 2008).

The taxonomic identity of Silurian *Platyceras*-like gastropods remains uncertain. According to Fryda *et al.* (2009), the alleged platyceratid from the Herefordshire Wenlock concretions (Sutton *et al.* 2006) may belong to the stem group of the patellids. Some information on the soft anatomy of this gastropod is available but it is of little evolutionary importance, perhaps except for a rather simple alimentary canal, with weakly expanded stomach part. No operculum is associated with the specimen, despite its extraordinary preservation, which may suggest a limpet-like adaptation.

Another Kok Formation gastropod lineage has a small embryonic conch similar to that of the Late Devonian (Famennian) *Naticopsis*, except for its larger size and the lack of any fingerprint-like ornament of subsequent whorls (Dzik 1978, fig. 4A). Although extant neritopsids teleoconch is closely similar to these Palaeozoic gastropods, the *Neritopsis* strongly convoluted larval shell is basically different (Bandel 1982; 2007). The origin of neritopsids, characterized also by operculum calcifying from its basal side (Kaim & Sztajner 2005), remains to be traced.

In the Kok Formation, there are gastropods with a relatively large tip of the embryonic conch and trochospiral morphology that may provide a connecting link to the true archaeogastropods (Fig. 5). It should be remembered, however, that the Late Devonian slit-bearing gastropods with possible affinities to pleurotomariids had multispiral smooth embryonic conch (Dzik 1978, fig. 4B), unlike their extant relatives.

The Kok Formation assemblage probably includes also one of the latest leseurillid, with its larval conch of morphology similar to that of Ordovician relatives but of a much smaller size (Fig. 5, 27). Although this is the only Kok Formation gastropod with a straight conical embryonic conch, Frýda & Heidelberger (2003) reported such protoconch associated with high turbiniform teleoconch of *Krameriella* from the coeval Kopanina Formation of the Prague Basin and with even more diverse morphologies in the Early Devonian.

The loosely coiled first whorl in all other Kok Formation gastropods is of spiral geometry, and thus, these gastropod may belong to the clade of *Perunela*, as interpreted by Frýda & Bandel (1997); Frýda 2012). However, the Ordovician and Silurian 'small shelly fossils' assemblages show a complete gradation between variously coiled embryonic conchs. This varied even among specimens of the same species of *Vltaviella* (Frýda & Manda 1997, pl. 9). The open embryonic umbilicus probably represents a grade in the evolution of gastropod larvae and may not be of much taxonomic value.

Probably, larval gastropod conchs from the Kok Formation assemblage with shapes similar to adult subulitoid conchs are more important. The one with relatively high spire and minute umbonal opening (Fig. 5, 24) resembles somewhat the late Viséan to Namurian *Imogloba* (Nützel *et al.* 2000; Nützel & Mapes 2001). It may represent the same clade, although lacks the surface ornamentation, which was used as evidence for the caenogastropod affinity of the Tournaisian *Chlorozyga* by Nützel & Cook (2002).

The late Palaeozoic alleged subulitoids Soleniscidae and Meekospiridae had rather tightly coiled protoconchs (Herholz 1992; Nützel *et al.* 2000) not similar to those of the Ordovician subulitids. Possibly, the subulitoid larval shell changed its morphology in evolution, which may be suggested by the apparent decrease in diameter of the first coil between the Sandbian Lesieniec species and that from the Ludlowian Kok Formation and those from the Czech Emsian (Frýda 2001). More likely, however, the similarity in teleoconchs is a result of ecological adaptation to infaunal scavenging (Stanley 1977) and the Ordovician true subulitids are not related to the 'subulitoids' from the late Palaeozoic. The type species of *Subulites* comes from the Trenton Limestone of New York (Sandbian to early Katian). This means that the use of the taxonomic names of all ranks derived from this genus should be restricted to the early Palaeozoic.

Famennian Miedzianka fossil assemblage

The most apparent distinction of this Late Devonian assemblage of gastropod larvae is the domination of globular conchs with a rather tight first embryonic coil. The diversity of bellerophontids, represented by just one morphology of the larval conch, is reduced, and high-spired conchs with relatively large tip. *Naticopsis*-like pyritized shells from Łagów (Dzik 1978, fig. 4A; Dzik 1994b, fig. 35H) show a smooth embryonic shell comprising of about half whorl and non-collabral vein-like ornament on the probable larval conch. Such ornamentation pattern was considered to be diagnostic for caenogastropods by some authorities (Nützel *et al.* 2000; Nützel & Cook 2002). The Tournaisian material from Australia clearly shows the boundary between the larval and post-larval stages in these gastropods. However, such ornament was presented also on the teleoconchs of slit-bearing Famennian 'pleurotomariids' with multispiral smooth embryonic conch (Dzik 1978, fig. 4B; Dzik 1994b, fig. 35F, G).

Some globular larval shells from the Famennian of Miedzianka resemble the Permian *Globobulimorpha* in their embryonic part showing an incipient heterostrophy (Yoo 1994). More globular larval conchs and probably also teleoconchs with a very low spire may be related to the Early Permian *Strobeus* as interpreted by Nützel *et al.* (2000, p. 583). A similar form from the late Viséan Ruddle Shale has been illustrated as '*Anomphalomorpha*' by Nützel & Mapes (2001).

Viséan Barnett Formation fossil assemblage

Unlike the Miedzianka assemblage, the Barnett Formation gastropods are mostly represented by slit-bearing 'pleurotomariids'. Probably, this is a matter of local ecological difference, because such gastropods are common in another Famennian locality at Łagów as well (Dzik 1978). Unfortunately, their statistically not significant sample prevents using them in quantitative comparisons. The second in number gastropod larval morphology is the globular one, probably being a continuation of the soleniscid clade represented at Miedzianka, to which it is similar. Also, the bellerophontids continue to be represented by just one larval morphology and known to occur until the Early Triassic (Foster *et al.* 2016) and several teleoconch-based species may correspond to it. High- and low-spired larvae continue to occur. Rare specimens with a straight conical embryonic conch probably represent *Platyceras* as a relic of once diverse clade. The youngest report on occurrences of such larval shells comes from the Late Carboniferous (Desmoinesian; Bandel & Frýda 1999) and the palaeobiological evidence suggests that the platyceratids continued to occur at least to the Permian (Baumiller & Gahn 2002). However, the post-Viséan fossil assemblages of larval gastropods reveal different structures of gastropod communities, with a high contribution from caenogastropods (Bandel 1997; Nützel 1998; Bandel *et al.* 2002).

The general picture emerging from the quantitative evidence assembled here shows more or less gradual changes in importance of main gastropod (or rather molluscan, if some of the tubular embryonic and larval conchs are interpreted as tergomyan) clades. Within the Ordovician, the bellerophontids dominated but their morphologic diversity decreased and this trend continued in subsequent periods of geological time.

Early evolution of gastropod embryonic conch

Two conclusions can be drawn rather safely from data presented above. First, in early gastropods (as well as in sinistrally coiled 'paragastropods' of the Mimospirina clade), the embryo developed the shell gland rather early and from this moment produced embryonic conch by marginal secretion of at least partially mineralized tissues. Second, in both these molluscan groups, the embryo was covered by an egg envelope until hatched to conduct planktonic life that ended in metamorphosis leading to benthic life. Although the boundary between the larval conch and teleoconch, easily identifiable in most caenogastropods, is usually difficult to trace in early gastropods, the dramatic increase in mortality (resulting in formation of 'small shelly fossils' assemblages) marks the moment of metamorphosis (Dzik 1978, 1994b). This refers also to the bellerophontids, in some cases clearly showing the change in the conch ornamentation corresponding to hatching (Dzik 1994a).

All the true, dextrally coiled Ordovician gastropods had a loosely coiled embryonic conch. Nützel & Frýda (2003, fig. 2) revealed the gradual decrease in per cent contribution of openly coiled protoconchs to the spectrum of known gastropod larvae species from the Ordovician to Permian (although the archaeogastropods with tightly coiled larval conch significantly contributed to the Ordovician faunas; Frýda & Rohr 2004; Frýda 2012). According to these authorities, the open-coiled larval conchs were weak and the tight coiling developed as a protection against predation (also Seuss *et al.* 2012; Nützel 2014). This is in conflict with the fact that the oldest probable gastropods with bilaterally symmetrical conchs (bellerophontids) show already a tight embryonic conch coiling. Moreover, the same tendency, but diachroneously (hundred million years later), can be observed in much larger, better equipped with yolk, ammonoid larvae (De Baets *et al.* 2012). Most probably, subspherical embryonic conch and planktonic larval stage were plesiomorphic trait of the cephalopods (Dzik 1981b, 2010; Mapes & Nützel 2009). It seems that rather open coiling is the ancestral state that gradually changed because of constructional improvements of the skeletal geometry.

It remains unclear whether the more and more tight coiling of the embryonic conch was a result of general tendency to more compact form of the shell or rather a replacement of ancient gastropod lineages with open coils with those showing a close conch coiling (Frýda 1998). One may guess that both were the case. The co-occurrence of very different larval conchs with closely similar embryonic parts suggests recurrent diversification events that resulted in formation of separate clades characterized by similar embryonic morphology. Such is the *Subulites*-like plexus in the Ordovician and the *Soleniscus*-like plexus in the Devonian (probably of caenogastropod affinity; Seuss *et al.* 2012). But even more general question has to be invoked in this context: is the presence of planktonic early stage of development, namely the trochophore that together with spiral cleveage characterizes the superphylum Lophotrochozoa, truly plesiomorphic? In other words: how looked like the ancestor of gastropods?

The main difficulty with determining the exact course of early evolution of gastropods is the lack of data on embryonic and larval morphology of their dextrally coiled late Cambrian relatives. The high morphologic diversity of latest Dapingian and early Darriwilian gastropods strongly contrasts with their Tremadocian (Gasconadian), and even more the late Cambrian paucity. Only sinistrally coiled sinuopeids co-occur with monoplacophorans in the classic late Cambrian (lower Franconian) Mill Street conglomerate in Minnesota (Yochelson & Webers 2006). Similarly, the late Cambrian molluscan fossil assemblage from Wanwankou Member of the Fengshan Formation, Benxi, Liaoning, China (that includes the oldest known occurrence of the typical monoplacophoran *Pilina*), has yielded only two species of sinistrally coiled 'paragastropods', and a loosely coiled member of the Leseurillidae (classified in *Lytospira*; Yu & Yochelson 1999). A similar loosely coiled *Macluritella* was found in the late Cambrian strata of Missouri and Nevada (Yochelson & Stinchcomb 1987). Larval whorls of an Ordovician *Macluritella* species are openly and dextrally coiled, in contrast to the sinistrally coiled teleoconch (Frýda & Rohr 2006).

The Tremadocian Fezouata Formation in Anti-Atlas, Morocco yielded the bellerophontids *Sinuites* and *Carcassonnella* associated with sinistrally coiled mimospirine *Pelecyogyra.* Its teleoconchs were up to 27 mm in diameter, with only three rapidly expanding whorls (Ebbestad & Lefebvre 2015). The true gastropod *Lesueurilla* occurs in the Moroccan section not before the early Floian (Ebbestad 2016).

In the Tremadocian of northern Vietnam (Dzik & Phong 2016, p. 84) and central Siberia (Dzik 2010, p. 100), late Cambrian of Argentina (Pinilla *et al.* 2008), as well as the Baltic region and Wales (Berg-Madsen & Peel 1994; Peel & Berg-Madsen 2007), only bellerophon tids with tight larval coils occur. Their presence can be traced backward to the mid-Cambrian. *Protowenella* of such age resembles bellerophontids in its rather tight coiling of the embryonic conch but its larval conch aperture is transversely expanded, without any sinuses except for some controversial circumumbilical structures (Berg-Madsen & Peel 1978; Brock 1998; Wotte 2006).

The first undisputable gastropods did not appear before the late Cambrian or perhaps even the Early Ordovician. This is the consequence of discovery that mature individuals of the alleged Cambrian gastropods, the pelagiellids, were equipped with bunches of cirri (Thomas *et al.* 2010; Thomas 2012; Dzik & Mazurek 2013). This is suggestive of a rather annelidan than molluscan affinity. The embryonic conch of the oldest known pelagiellid bears mucro, unknown in any other Palaeozoic gastropod but common among hyoliths (Dzik & Mazurek 2013). Such apical spur is known elsewhere only in orthoceratid cephalopods and in the most advanced pteropods. Its function remains unknown, but one may guess that it helped in freeing the embryo from the egg covers. Also, the shell microstructure makes *Pelagiella* different from basal gastropods (Li *et al.* 2016) although this may be a variant of the ancestral molluscan state (Moore & Porter 2018).

It appears that available data on early gastropods are not decisive in choosing the most plausible evolutionary hypothesis on their ancestry. In this state of knowledge, taking alone just the stratigraphic distribution of teleoconch morphologies, two alternative scenarios for the origin of gastropods may be considered. One derived from assumption that the bellerophontid tight coiling of the embryonic conch is ancestral to that of gastropods, the other based on assumption that rather the conical embryonic conch 'recapitulates phylogeny'.

Hypothetical ancestor with coiled embryonic conch

In extant gastropods, the embryonic conch tight coiling is usually associated with its subspherical tip. The embryo secretes such conch on its whole surface, and it remains unmineralized (Bandel 1982). The surface is smooth or ornamented, but without any linear growth increments. A similar (although larger) subspherical tip of ancient cephalopods embryonic conch shows distinct growth increments (Klofak *et al.* 2007), which means that this has little to do with the presence of yolk sac but rather expresses the shape of embryo.

Subspherical tips of the conch characterize all the bellerophontids. Those from the Ordovician are generally of relatively large size. This may or may not mean that originally they depended more on the yolk in their embryonic and larval life than in more advanced stages of the evolution. Advanced bellerophontids had small embryonic conch apex, which was interpreted by Frýda (1999) as evidence of planktotrophic life. Probable Ordovician tergomyans had tips of their embryonic conch even larger than those of the bellerophontids (Dzik 1981a). The present-day and Silurian monoplacophorans, as well as their possible Cambrian relatives, had a relatively flat, large embryonic shell (Dzik 1994b, fig. 30A).

Nützel *et al.* (2006; see also Freeman & Lundelius 2007; Runnegar 2007; Nützel *et al.* 2007, and Nützel 2014) compared the size of embryonic conch in bilaterally symmetrical Cambrian molluscs with that of oldest Ordovician gastropods to conclude that planktotrophy is a derived trait that originated at the Cambrian–Ordovician transition, mainly due to increased benthic predation. Such interpretation of available data implies that the common ancestor of gastropods and tergomyans had a large embryonic conch and lacked any planktonic stage in its development. To test reliably the Nützel *et al.* (2006; Nützel 2014) hypothesis, one has to identify the exact ancestry of gastropods but this is not possible at the moment, as discussed above.

Hypothetical ancestor with conical embryonic conch

The similarity of the straight portion of loosely coiled gastropod embryonic conch to hyolith or pteropod larval conch is superficial and misleading.

The shell of a young thecosome pteropod consists of the rounded or ovoid embryonic part, which is laid down before hatching, and the pyramidal shell, which forms during the free-swimming veliger stage (Lalli & Gilmer 1989, p. 116). In these respects, its body plan is not different from that of other gastropods planktonic larva. During metamorphosis, the larval velum is replaced with wings, which are of pedal origin and the animal remains planktonic. Despite superficial similarity to Ordovician gastropods embryonic conchs, such anatomy is a relatively recent achievement of the thecosome evolution. The teleoconch of the late Early Eocene pteropod *Camptoceratops* was already almost straight but preserved a loose sinistral coiling (Janssen *et al.* 2011) that indicates origin from a trochospiral ancestor. The process of despiralization of the teleoconch was initiated in the earliest Eocene *Altaspiratella* (Janssen & Peijnenburg 2017) although its larval conch remained tightly coiled (Janssen *et al.* 2016), which makes clear that the straight initial portion of its embryonic conch originated in a completely different way than in early gastropods.

The mentioned above similarities of the early Cambrian pelagiellid *Aldanella* to hyoliths, generally believed to be the oldest gastropod despite commented above annelidan traits, require a brief discussion. The pelagiellids were probably planktonic as adults, and there are no signs of hatching or metamorphosis on their conchs. It remains unknown whether this is their ancestral or rather derived trait. Whatever are true affinities of hyoliths (Li *et al.* in press), they were epibenthic filtrators passively laying on the sea bottom and evolved in a direction opposite to their possible pelagiellid relatives. The presence of tentacles in their most advanced group, the hyolithids, proves their filter-feeding abilities (Moysiuk *et al.* 2017).

The closest recent ecological analogue of hyolithids is probably the turritellid gastropods (Dzik 1980). These are mainly stationary semi-infaunal ciliary suspension feeders, but some may be deposit feeders. Food particles are caught by them on the elongate ctenidium. The turritellids may move but their feeding position is with the aperture exposed at the sediment surface and the apex pointed down at a low angle into the sediment (Allmon 1988, 2011; Waite & Allmon 2013). In some of related sedentary vermetids, their ctenidia are transformed into prominent tentacles (Morton 1955, fig. 1e). The tentacular apparatus of vermetida (as well as hyolithids) is an adaptation to filter feeding that does not necessarily prove a lophophorate relationship.

The second hyolith clades, the orthothecids, were probably deposit feeders as suggested by findings of their sediment-filled intestines. Hyolithids differ from orthothecid in having a simple U-shaped intestine and in the presence of a pair of peculiar appendages located near the shell aperture (helens, they were suggested to be homologous to chaetae of the pelagieliids by Dzik & Mazurek 2013). Both these hyolith clades are too derived to be directly related to gastropods or cephalopods. In fact, the embryonic portion of various hyolith conchs may show distinct growth increments or be smooth (Dzik 1978) but it is invariably swollen (Fig. 2K–M). This makes it comparable with the cephalopod larval shells (Dzik 1981b, 2010) rather than with advanced gastropods. Such relationship can be reasonably discussed only with respect to the most primitive hyoliths with their conch of circular section or laterally compressed and with opercula lacking any additional structures on their inner side (Dzik 2010; Kouchinsky *et al.* 2017).

The hypothesis that both trochoidal gastropods and bilaterally symmetrical bellerophontids independently developed from a hyolith-like ancestor is hard to support with the fossil evidence. The main difficulty is imposed by the peculiar shell microstructure of hyoliths (Kouchinsky 2000). It does not resemble nacre or any other shell microstructure that could be considered primitive for molluscs.

So more that it is still undetermined how ancient is the nacre. The oldest direct evidence of archaeogastropods with nacre was provided by the Late Carboniferous (Desmoinesian) Buckhorn Asphalt (Bandel *et al.* 2002). The columnar nacre is shared by them with the cephalopod *Nautilus*, as well as its Ordovician orthoconic relative *Isorthoceras* (Vendrasco *et al.* 2013). Nacre occurs also in some extant monoplacophorans, protobranch and trigonioid bivalves, which makes its plesiomorphic status the most parsimonious hypothesis. Nacre is fracture-resistant at expense of a relatively high protein contents and slow growth (Palmer 1992). Its replacement with less expensive and harder crossed-lamellar structure seems to be an improvement. However, Vendrasco *et al.* (2013, 2015) proposed the opposite that it originated independently in unrelated molluscs under selective pressure from shell-crushing predators. This may find indirect support from a complex crossed-lamellar microstructure of advanced bellerophontids (MacClintock 1968). Also the euomphalid gastropods lack the nacreous shell layer having the outer shell layer calcitic and the inner aragonitic. The latter includes a variety of crossed-lamellar microstructure (Batten 1984). It remains unknown what microstructure characterized the Ordovician gastropods with loosely coiled embryonic conchs.

Conclusions

Both the apertural constrictions and mortality peaks, probably connected with hatching and metamorphosis, indicate that the Ordovician protoconchs with hook-like first coil represented stages of an embryo developing within the egg envelope and the subsequent coiled stage corresponds to the planktonic larva. It is unlikely that uncoiled apices of embryonic shells of early gastropods had any adaptive value during pelagic life of the larva. No evidence of predation on this part of the conch has been reported yet. This peculiar shell geometry is rather a developmental epiphenomenon resulting from mechanisms of the shell gland growth. There is a general tendency towards more and more tight coiling of embryonic conchs not only in the evolution of Palaeozoic 'true' dextrally coiled gastropods. This refers as well to bilaterally symmetrical bellerophontids and sinistrally coiled mimospirine 'paragastropods'. With a few exceptions, only tightly coiled larval conchs are represented in the Late Devonian and Early Carboniferous assemblages. The similarity of the straight apex to larval conchs of hyoliths and advanced thecosome pteropods is superficial, as they do not represent homologous stages in early development.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Conodonts from the top of San Juan Formation at Don Braulio Creek