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ARTICLE

Affinities of the alleged earliest Cambrian gastropod *Aldanella*

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Abstract: Unlike true Palaeozoic gastropods, but similar to some coeval hyoliths, the cup-like hemispherical embryonic shell of *Aldanella attleborensis* (Shaler and Foerste, 1888) from the earliest Cambrian (early Tommotian) Erkeket Formation of northern Siberia bears a mucro. Also, the pattern of mortality, with right-skewed distribution and a peak at about 1.0 mm diameter, is not similar to that of early Palaeozoic gastropods; there is no evidence of metamorphosis that would end the pelagic larval stage of ontogeny. Specimens of larger size are rare in samples of phosphatized "small shelly fossils" but are known in related species of the genus, of up to 3–5 mm diameter. A phosphatized soft body is preserved in a few specimens of *A. attleborensis*, one bearing possible chaetae of about 5 μm diameter. Such bunches of chaetae arming locomotory organs were earlier identified in the genus *Pelagiella* Matthew, 1895, a more derived member of the same lineage. It shares with the genus *Aldanella* Vostokova, 1962 also the mucronate embryonic shell and acicular aragonitic shell wall microstructure. The presence of chaetae-bearing organs suggests pelagic mode of life of pelagiellids at maturity. Middle Cambrian *Pelagiella* shells reached 7 mm in diameter, suggesting evolutionary increase in mature size. Embryonic shell morphology, wall microstructure, and the presence of locomotory organs with a fan of chaetae contradicts gastropod, and even conchiferan affinity of the pelagiellids, but together with the pattern of ontogeny conforms to the enigmatic Palaeozoic hyoliths. They differ in having opercula closing the shell apertures and in lacking evidence of chaetae. The helens, paired apertural appendages of possible locomotory function occurring in apertures of some of them, do not reveal any similarity to chaetae in their development. We propose classifying the order Pelagiellida in the class Hyolitha rather than in the class Gastropoda, until its phylogenetic position is clarified. Such understood hyoliths may represent the earliest stage in evolution of molluscs, immediately following initial diversification of the spiralians (lophotrochozoans) into phyla.

Key words: Aldanella, Pelagiellida, Hyolitha, Cambrian, biometry, chaetae.

Résumé : Contrairement aux vrais gastéropodes paléozoïques, mais à l'instar de certains hyolithes contemporains, la coquille embryonnaire hémisphérique en forme de gobelet d'*Aldanella attleborensis* (Shaler et Foerste, 1888), de la Formation d'Erkeket du tout début du Cambrien (Tommotien précoce) de la Sibérie septentrionale, est dotée d'un mucron. En outre, la mortalité, qui présente une distribution asymétrique positive et un maximum à un diamètre d'environ 1,0 mm, n'est pas similaire à celle des gastéropodes du Paléozoïque précoce; rien n'indique la présence d'une métamorphose qui marquerait la fin du stade larvaire pélagique de l'ontogénie. Les spécimens de plus grande taille sont rares dans les échantillons de « petits fossiles à coquilles » phosphatisés, mais ils ont été trouvés dans des espèces apparentées du genre, atteignant de 3 à 5 mm de diamètre. Un corps mou phosphatisé est préservé dans quelques spécimens d'*A. attleborensis*, dont un comporte de possibles soies d'environ 5 μm de diamètre. De tels amas de soies sur les organes locomoteurs ont déjà été identifiés chez le genre *Pelagiella* Matthew, 1895, un membre plus dérivé de la même lignée. Il a également en commun avec le genre *Aldanella* Vostokova, 1962 une coquille embryonnaire à mucron et une microstructure d'aragonite aciculaire des parois de la coquille. La présence d'organes comportant des soies semble indiquer un mode de vie pélagique des pélagiéllidés à la maturité. Des coquilles de *Pelagiella* du Cambrien moyen atteignent un diamètre de 7 mm, indiquant une augmentation évolutive de la taille à la maturité. La morphologie de la coquille embryonnaire, la microstructure des parois et la présence d'organes locomoteurs dotés d'un éventail de soies contredisent une affinité des pélagiéllidés avec les gastéropodes et même avec les conchifères, mais ces observations, combinées à l'ontogénie, sont conformes aux hyolithes paléozoïques énigmatiques. Ils s'en distinguent par la présence d'opercules qui ferment l'ouverture de la coquille et par l'absence apparente de soies. Les hélènes, des appendices en paire ayant possiblement une fonction locomotrice présents dans les apertures de certains d'entre eux, ne présentent aucune similitude avec les soies dans leur développement. Nous sommes proposé de classer les Pélagiellidés dans la classe des hyolithes plutôt que dans celles des gastéropodes jusqu'à ce que leur position phylogénétique soit précisée. De tels hyolithes pourraient représenter le stade le plus précoce de l'évolution des mollusques, immédiatement après la diversification initiale des spiraliens (lophotrochozoaires) en des phylums distincts. [Traduit par la Rédaction]

Mots-clés : Aldanella, Pélagiellidés, hyolithes, Cambrien, biométrie, soies.

Introduction

It is widely believed that *Aldanella attleborensis* (Shaler and Foerste, 1888) occurring in the basal Tommotian strata in Newfoundland and northern Siberia and having close relatives of similar and slightly younger ages in many other places of the world is one of the oldest gastropods. It has a low trochospiral, dextrally coiled shell of millimetre size. Its successors, with equally vast occurrences in younger Cambrian strata, are species of the genus *Pelagiella* Matthew, 1895. They have strongly asymmetric shell, too, but with an almost flat spire. Although these shells are gastropod-like, many

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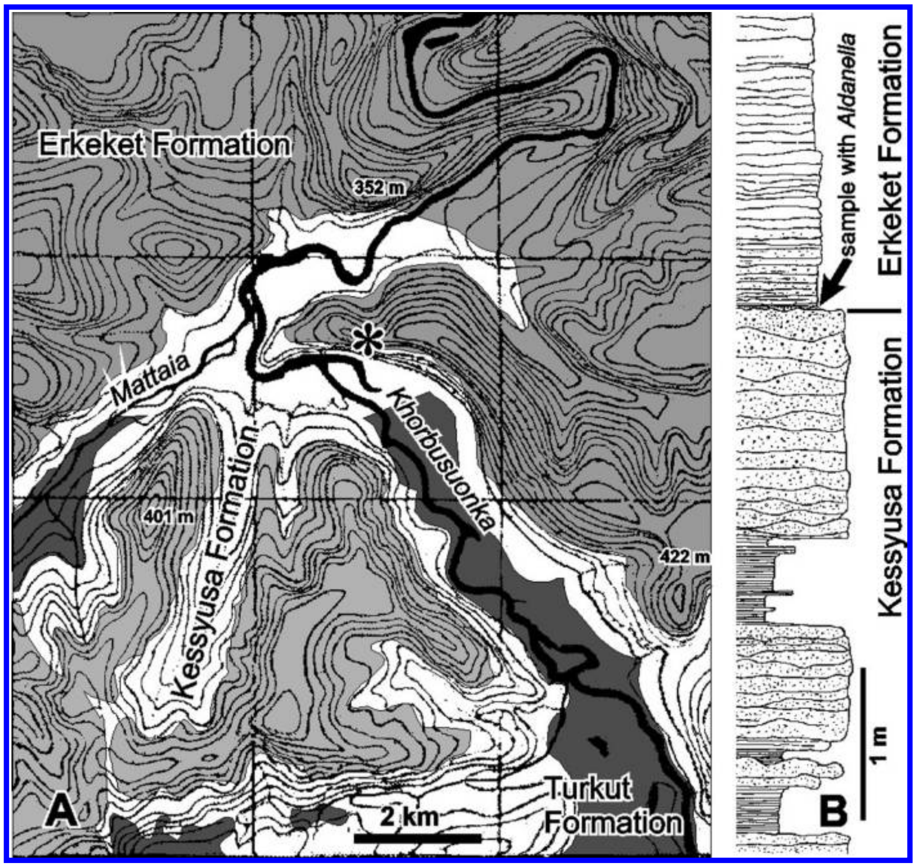
Fig. 1. (A) Geological map showing the location of the sampled bed of the Erkeket Formation with an asterisk (modified from Dzik 2005) and (B) the rock column with the sampled level marked.



of their aspects, as well as the muscle scars (Runnegar 1981), are difficult to reconcile with the assumed basal position within the class Gastropoda.

The first reason of concern is the small size of these fossil shells. Minute gastropod (and other molluscs) conchs are common in samples of post-Cambrian phosphatized "small shelly fossils", but these are mostly larval conchs that usually can be matched with adults of centimetre size (Dzik 1991); they are not true microgastropods. At present, the Ordovician free-living pelagic larvae metamorphosed into benthic molluscs and this event was expressed in increased mortality. As a result, countless minute conchs were supplied to the sediment, where they could phosphatize if the environment was favourable. In many cases, the metamorphosis has its expression also in the concentration of shell increments, and more commonly, in a change in surface ornamentation. It is possible to match these aspects of shell morphology with the peak of mortality in gastropods and bivalves. One may thus expect that this could be shown also for the genus *Aldanella* Vostokova, 1962.

The second puzzling aspect of the Cambrian pelagiellids is their shell microstructure. In the three major classes of molluscs (i.e., bivalves, cephalopods, and gastropods), the most anatomically primitive members have nacre as the inner layer of the shell. Somewhat still enigmatic phylogenetically, bellerophontoids had aragonitic crossed lamella. Still, it is reasonable to consider this trait to be plesiomorphic and expect its occurrence also in the geologically oldest gastropods. Yet, neither *Aldanella* nor *Pelagiella* had nacre in their shells. They were built either solely of a prismatic layer or with an inner layer of most probably originally aragonitic (preserved as a phospatic replacement) fibers fused into lamellar units (Bengtson et al. 1990). To resolve this inconsistency, Kouchinsky (2000*b*; also Vendrasco et al. 2010) proposed that "nacreous and crossed-lamellar aragonitic microstructures evolved in the Cambrian from such lamellar aragonitic microstructures independently in different groups of molluscs". This is hardly a parsimonious solution (but for possible explanations see, e.g., Jackson et al. 2010).

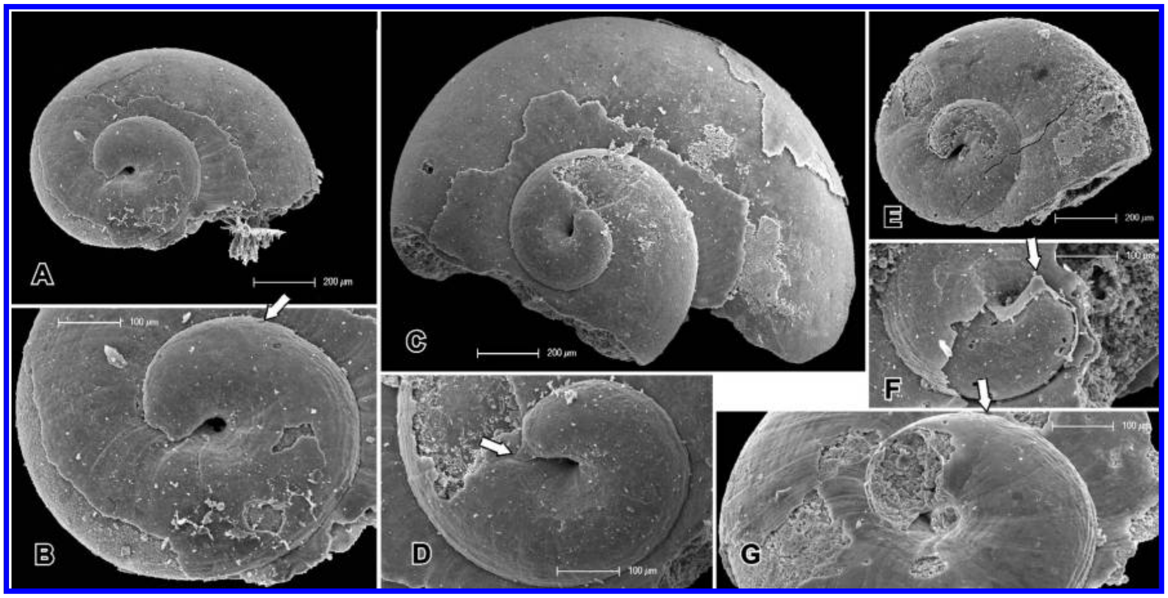
The third problem with the genera *Aldanella* and *Pelagiella* is the most serious. Several dozen specimens of *Pelagiella* were found in the Early Cambrian Kinzers Formation with chaetae protruding from within their apertures (Thomas et al. 2010*a*, 2010*b*; Thomas and Vinther 2012). Although chaetae are considered a plesiomorphic trait of the Lophotrochozoa (Zakrzewski 2011), they do not occur in such spatial position in Recent gastropods or any other molluscs. They are characteristic rather of annelids and brachiopods. The distribution of this trait recalls the situation with nacre: to solve the problem, we should accept independent loss of chaetae in each of the lineages leading to the main molluscan classes, both regarding Conchifera and Aculifera.

The shell morphology of *Aldanella* was described in detail, including also specimens from the same bed our material was extracted, and its taxonomy discussed in the recent monograph by Parkhaev and Karlova (2011). In the present paper, we consider details of the shell morphology and population dynamics, which were neglected by earlier authors but are of crucial importance in understanding the phylogenetic position of the pelagiellids. We also present data on a probable phosphatized soft body of *Aldanella*, with purported chaetae preserved inside.

Materials and methods

The material of *Aldanella* comes from the lowermost bed of the Erkeket Formation exposed near the mouth of the Mattaia Creek entering the Khorbusuonka River (a tributary of the Olenek River,

Fig. 2. Embryonic shell of the earliest Cambrian *Aldanella attleborensis* from the base of Erkeket Formation at the mouth of Mattaia Creek, northern Siberia. Specimens ZPAL Mo.XX/4/10 (A, B), ZPAL Mo.XX/4/9 (C, D), ZPAL Mo.XX/4/8 (E), ZPAL Mo.XX/6/8 (F), and ZPAL Mo.XX/2/7 (G). Arrows point to the end of the embryonic stage and mucrones.



northern Siberia), site 17 of Karlova and Vodanjuk (1985; Parkhaev and Karlova 2011, Fig. 5). Erkeket Formation overlies the sandstone of the Kessyusa Formation, which represents the Manykai–Daldynian stage with the oldest skeletal fossils in Siberia (Fig. 1). The first occurrence of *Manykodes* ("*Treptichnus*") *pedum* (Seilacher, 1955), which is the commonly used guide fossil for the base of the Cambrian, is about 6 m below in the section (Dzik 2005).

According to Knoll et al. (1995), the lower Erkeket Formation is represented by sediments of an open, shallow-marine carbonate platform, with the carbonates of the whole formation accumulated during a highstand in relative sea level and representing regional onlap on the Olenek platform, which followed subaerial exposure of the upper Kessyusa Formation sediments. The sample of a red variegated limestone was taken from immediately above the sedimentary discontinuity surface. The basalmost limestone layer fills their depressions in the underlying bed and is full of phosphatized skeletal debris, mostly of hyoliths, chancelloriids, halkieriids, hyolithelminths, and hexactinellid sponges.

The acetic-acid-resistant residue yielded numerous phosphatized steinkerns and phosphate-coated shells of various taxonomic affinities, *A. attleborensis* being the most numerous species. Altogether 508 specimens of it were collected. All of them are dextrally coiled. Specimens were photographed under binocular microscope and measured from photographs under ImageJ software. Some specimens were drawn under camera lucida and some chosen for scanning electron microscopy (SEM).

Principal components analysis (PCA) was conducted using PAST software.

The specimens of *Aldanella polonica* Lendzion, 1977 examined come from a dark grey mudstone of the earliest Cambrian Mazowsze Formation of the Łopiennik borehole in northeastern Poland at depths 5297.8–5306.8 m, associated with the helcionellid *Anabarella* sp., probable agglutinating foraminifer *Platysolenites antiquissimus* Eichwald, 1860, and tubes of *Onuphionella aglutinata* Kirjanov, 1968 built of mica flakes by an unknown worm. Only two specimens (including the holotype) were deposited at the collection of the State Geological Institute in Warsaw. The others were probably not deposited in any collection and are presumably lost.

Material of phosphatized gastropod larval and juvenile shells from the Ordovician (early Caradoc) was extracted by dissolving in acetic acid bulk samples from the borehole core drilled at Lesieniec 1 in northeastern Poland (Modliński 1973). Acid-resistant residue with similarly preserved mollusc conchs from the Mississippian (Meramecian) Barnett Formation of Texas (e.g., Loucks and Ruppel 2007) was transferred to the collection of the Institute of Paleobiology by R.H. Mapes to be used for comparatives purposes.

Shell ontogeny

Embryonic shell

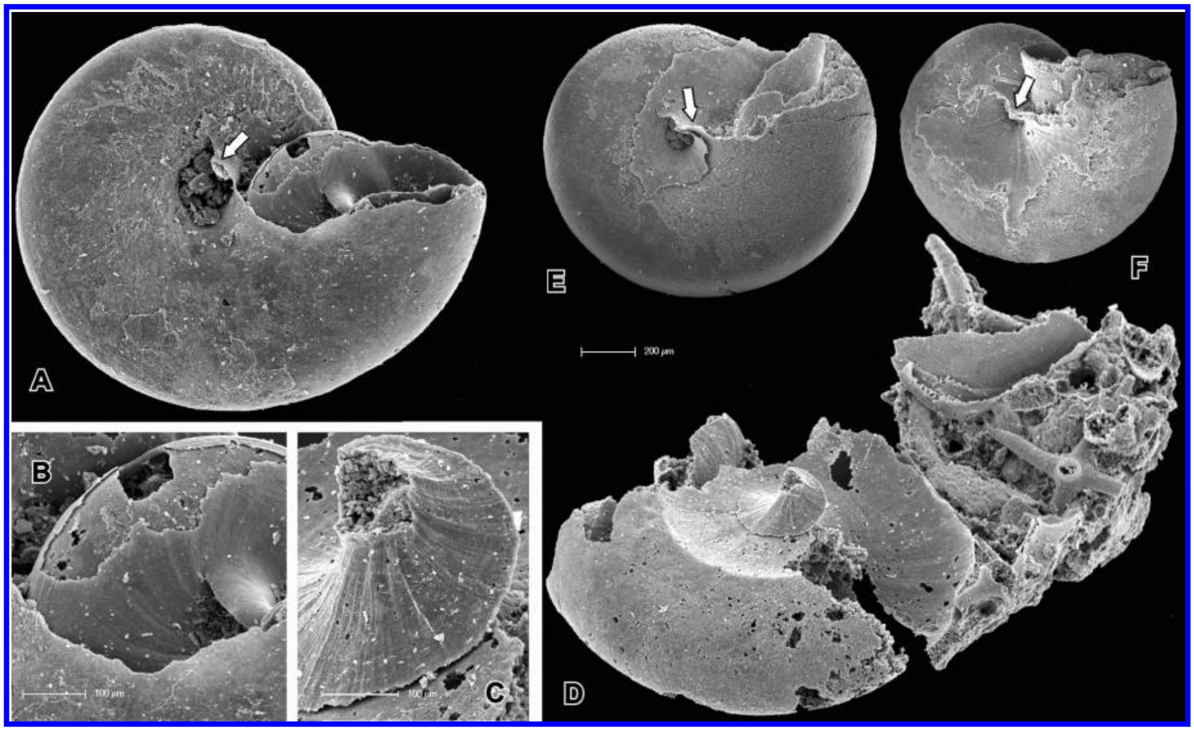
It remains unclear at what stage of its embryonic (or larval) development the *Aldanella* shell started incremental growth. Its apex is rounded, but in all specimens that have external phosphatic coating of the shell preserved, it bears a distinct mucro (Figs. 2A–2G). The growth increments are unrecognizable in the initial cap-like portion of the shell that is ca. 175 μm wide at its inferred aperture and ca. 250 μm high. Although smooth, it probably grew incrementally, as suggested by irregularities on the shell surface. The mucro is oriented parallel to the aperture on a side of the shell. The embryonic shell boundary is clearly demarcated, presumably marking hatching.

Teleoconch

Unquestionable growth increments develop at about half of the first coil, and they are discordant with respect to the embryonic shell margin (Fig. 2G). Parkhaev (2006; Parkhaev and Karlova 2011) believed that septa developing in the shell apex can be used to determine the boundary between the protoconchs I and II. This is a result of a misunderstanding of the nature of septa in the molluscan shell. Development of septa of this kind is connected with retreat of the soft body from the apex because of fast growth of the shell at its aperture. The soft body surface loses then contact with the internal shell surface and secretes a thin wall of the inner shell layer at distance from the preceding layers. There is no correspondence between septa and surface morphology above them, as their formation takes place long after the larval stage is completed. In this regard, *Aldanella* is not different from any animal with a high-conical shell, including cephalopods or tentaculites.

The shell aperture was near transverse to the coiling (radial) but gradually, within the next half of the whorl, it became oblique. It is expressed in an arched course of growth increments on the

Fig. 3. Phosphate-coated shells (A, B, E, F) and phosphatic negative replica of earliest Cambrian *Aldanella attleborensis* from the base of the Erkeket Formation at the mouth of Mattaia Creek, northern Siberia. Specimens ZPAL Mo.XX/6/11 (A, B; note the sheltered juvenile within the aperture; in both specimens, the shell lip is completely preserved; spiral ornament developed only locally), ZPAL Mo.XX/6/2 (C, D; note poorly developed spiral ornamentation and associated hexactinellid sponge spicules), ZPAL Mo.XX/4/5 (E), and ZPAL Mo.XX/4/1 (F). Arrows point to complete lips.



upper surface of the dorsal shell side visible in specimens with preserved external phosphatic coating (Figs. 2B, 2G), but also as growth irregularities on steinkerns. The thin phosphatic coating covering the originally aragonitic shell wall in its umbonal part shows that the apertural lip merged the preceding coil under a high angle and that there was virtually no secretion over the preceding whorl (Figs. 3A–3F). The umbilicus was open and a small perforation was present also in the shell apex, surrounded by the first coil.

The shell wall was thin for the shell size. In the space between the surface of the steinkern and the external coating, an acicular microstructure is visible in a form of remnants of phosphate separating original locus of now dissolved aragonite crystals (Fig. 3A). Apparently, the shell was composed of only single mineral layer of acicular crystals showing a fan-like pattern of distribution. This is not consistent with the presence of the prismatic layer, inferred by Kouchinsky (2000*b*; Vendrasco et al. 2010) from the presence of irregularly polygonal imprints on the embryonic part of the shell steinkerns (interpreted as attachments of muscles by Parkhaev 2006). We have not found any such imprints on our specimens. It is possible that these polygons are rather imprints of epithelial cells left by the visceral sac within the shell apex at later stages of ontogeny.

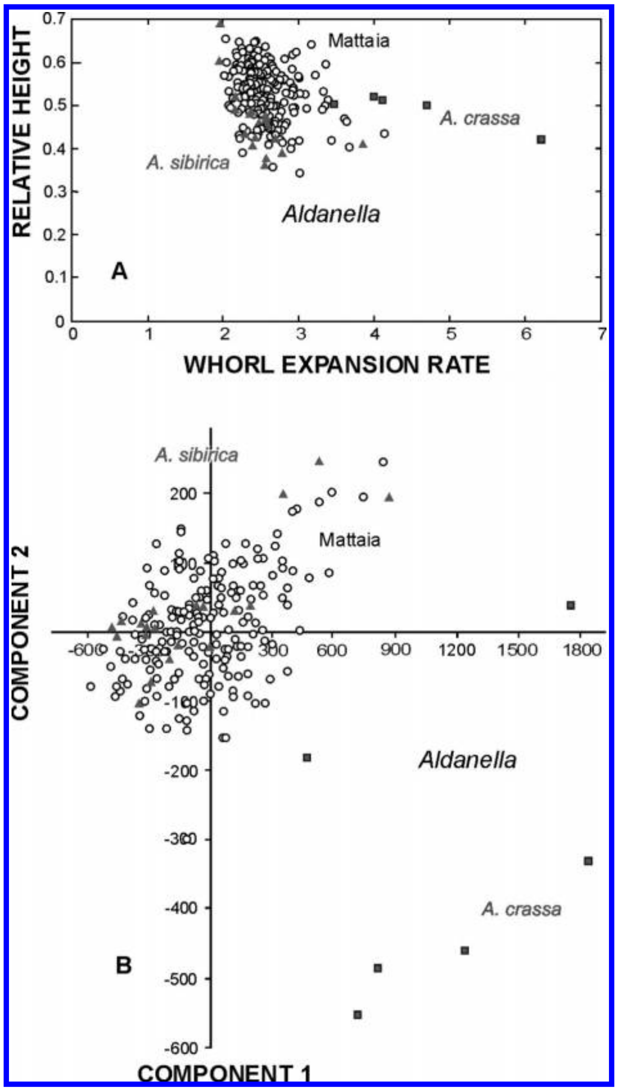
The shell surface was ornamented mostly with transverse growth increments, as shown on negative phosphatic shell moulds, replicating the shell surface in a great detail (Fig. 3C). The thin external coating is not so precise, but in many specimens spiral (longitudinal) riblets are visible. They are best developed in the areas close to the suture between whorls and gradually disappeared during ontogeny (Figs. 2A–2G).

Species identity

Based on stratigraphic succession in Siberia, Parkhaev and Karlova (2011, Fig. 6) proposed a lineage evolving towards smaller conch expansion rate and a higher spire. *Aldanella attleborensis* occupies in this succession a transitional position between *Aldanella sibirica* Parkhaev and Karlova, 2011 and *Aldanella crassa* Missarzhevsky in Rozanov et al., 1969 (including *A. polonica*). The type locality of *A. attleborensis* is the Hoppin Reservoir North in Massachusetts, where it occurs in the lowermost limestone bed with skeletal fossils of presumably Tommotian age (Landing 1988). The type locality of *A. sibirica* is Boroulakh section on the Olenek River in northern Siberia, the type horizon being *Dokidocyathus regularis* Zone of the Tommotian (Parkhaev and Karlova 2011). *Aldanella crassa* has its type locality on the north Siberian Kotui River and it is the oldest of these species, coming from the *Nochoroicyathus sunnaginicus* Zone (Parkhaev and Karlova 2011).

We measured specimens from our sample to determine as precisely as possible its relationship to the type populations of *A. crassa* and *A. sibirica* (Figs. 4A, 4B). If coefficients proposed by Parkhaev and Karlova (2011) to characterize shells of *Aldanella* conchs are used to produce PCA plot, the resulting cluster shows homogeneity of the Mattaia sample. *Aldanella sibirica* specimens from the type population are within the range of variability of the population, whereas those of *A. crassa* depart well outside it (Fig. 4B). A different picture emerges when plotting more specific aspects of the shell geometry, namely the translation of the helix and whorl expansion rate (Fig. 4A). The type population sample of *A. sibirica* shows then morphology distribution clearly different from that of our Mattaia sample. The former conchs are generally more trochospiral, whereas consistently narrow umbilicus results in the conchs with higher expansion rate being proportionally less trochospiral. In this regard, the Mattaia population is less derived and resembles the type population of *A. attleborensis*, although the difference in shell geometry alone does not substantiate species-rank distinction between the Mattaia sample and the type specimens of *A. sibirica*. If we are dealing with a phylogenetic lineage(s) composed of populations of chronospecies, boundaries

Fig. 4. Population variability of *Aldanella attleborensis* in the sample from the base of the Erkeket Formation at the mouth of Mattaia Creek (*N* = 200) compared with biometrics of related species. (A) Distribution of the relative shell height in the sample from Mattaia and topotype material of related species described by Parkhaev and Karlova (2011). (B) Principal components analysis based on measurements that follow those used to determine spirality of the shell by Parkhaev and Karlova (2011, Figs. 7*a*, 7*b*). Measurement of topotype specimens of *Aldanella crassa* (squares) and *Aldanella sibirica* (triangles) are also included.



between species (defined on samples of different geological age) must be seen as arbitrary and provisional.

Ornamentation of the shell surface may appear helpful in species identification of the studied sample of *Aldanella*. A specimen of *A. sibirica* from the *Dokidocyathus regularis* Zone in the lower part of the Erkeket Formation at the Suordakh section on the Olenek River, that is within the type horizon of the species and in proximity to its type locality, shows well preserved external phosphatic coating (Parkhaev and Karlova 2011, pl. 11: 9). Like the Mattaia specimens, it has a smooth cap-shaped embryonic shell of about 50 μm high and poorly preserved mucro, followed by the ornamented shell stage with spiral (longitudinal) riblets. The major difference is in prominence of the spiral ornament. In this regard, *A. sibirica* is unlike the Mattaia specimens, which have only a weak striation in the initial parts of the postembryonic shell, restricted in their distribution to marginal regions of the coil (Fig. 2G). The remaining shell surface is ornamented only with growth increments. Spiral riblets, if occur in places, are indistinct.

Parkhaev and Karlova (2011) collected two samples from the base of the Erkeket Formation at the mouth of the Mattaia Creek at Khorbusuonka, the same locality where our material came from. They illustrated several steinkerns from there (Parkhaev and Karlova 2011, pl. 7: 1–9), classified by them in *A. sibirica*. Perhaps their specimens are from a sample somewhat younger than ours. Because of differences in shell ornamentation, we prefer to consider our specimens as distinct from *A. sibirica* and representing rather a late population of the *A. attleborensis* chronospecies, occurring also in the *Nochoroicyathus sunnaginicus* Zone, as understood by Parkhaev and Karlova (2011). That the Siberian samples are parts of a single phylogenetic lineage can be supported by close proximity on the PCA plot (Fig. 4B).

Aldanella crassa is the oldest member of the lineage occurring in the *Nochoroicyathus sunnaginicus* Zone of the Kotui River in northern Siberia and ranging back to the latest Vendian (Parkhaev and Karlova 2011). It has a high expansion rate, the ratio between subsequent whorls being usually four or greater, whereas it is mostly between two and three for the Mattaia *Aldanella*. Conchs of another early species (*Aldanella utchurica* Missarzhevsky in Rozanov et al., 1969) are, on average, bigger, have more whorls, and have lower expansion rate.

Possible chaetal organ

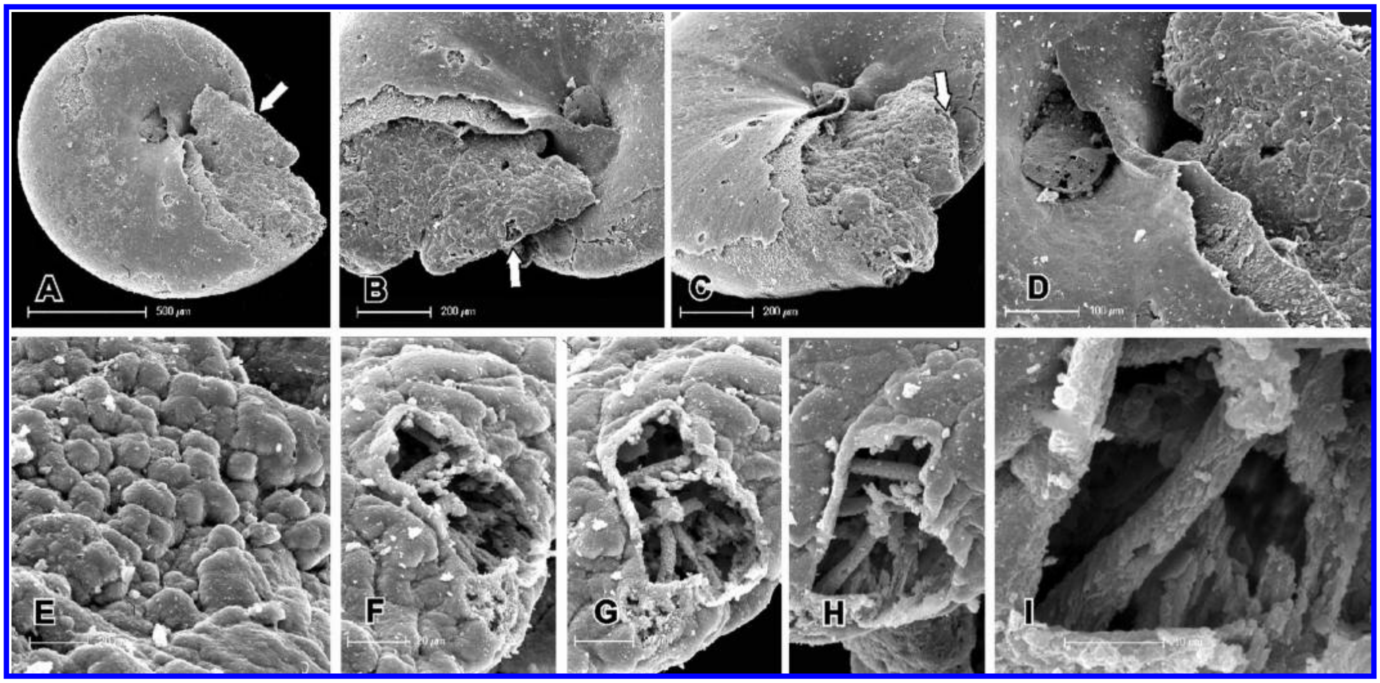
In some of our specimens of *A. attleborensis*, probable phosphatized soft tissue is preserved. The distal surface of the phosphatic shell infill is rugose with protuberances resembling spherulitic growth but in places with more or less flattened surface of rather regularly distributed units, mostly about 12 μm diameter, separated by shallow furrows (Fig. 5E). Possibly, these are phosphatic replicas of decaying epithelial cells. In the most informative specimen ZPAL Mo.XX/6/6 (Figs. 5A–5I), the shape of the body is rather indifferent, although a lobe-like structure can be discerned in the part of the tissue mass closer to the umbilicus. Its distal margin extends transversely. On the surface of the lobe is a rectangular elevation, the tip of which is crushed exposing the interior. Inside are tubular structures of approximately 5 μm diameter. Some of them emerged outside from the structure (Fig. 5F). Apatite crystals tend to be arranged parallel to their longitudinal axes and in places form parallel subunits of 3 μm diameter (Fig. 5I). This roughly corresponds to the diameter of microvilli and capillaries within the annelid chaetae (Hausam and Bartolomaeus 2001).

We suggest that the broken structure on the surface of the *Aldanella* body is the base of a locomotory organ armed with a bunch of chaetae. Such chaetae were earlier identified in the advanced member of the same group, *Pelagiella* (Thomas et al. 2010*a*, 2010*b*; Thomas and Vinther 2012).

Little more is known about the soft-body anatomy of the pelagiellids. The structure interpreted by Bischoff (1990) as a digestive gland in a species of the genus *Costipelagiella* Horný, 1964 is a phosphatic fill of void spaces within a calcareous object resembling that of echinoderm stereom. Runnegar (1981) relied mostly on purported muscle scars in a single specimen of *Pelagiella atlantoides* Matthew, 1894 while discussing phylogenetic position of pelagiellids. If such their nature is accepted, there were at least two insertion sites on either side of the shell (a third, smaller located posteriorly), do not oppose one another, the left being situated more anteriorly with respect to the apex. This may correspond to muscles operating the paired chaetal organ. Ridges on the shell nucleus surface similar to those described by Runnegar (1981) were identified also in *Costipelagiella* sp. cf. *Costipelagiella zazvorkai* Horný, 1964 from the Middle Cambrian of New Zealand by Mackinnon (1985).

Other finds of Cambrian capillary chaetae are restricted to annelids from the Burgess Shale type deposits (Conway Morris 1979;

Fig. 5. Phosphatized soft tissues preserved inside the shell of *Aldanella attleborensis* from the base of the Erkeket Formation at the mouth of Mattaia Creek. Specimen ZPAL Mo.XX/6/6: basal view of the phosphate-coated lip showing that the shell is complete (A, D), various views of its phosphatized soft body (B, C), remnants of phosphatic coatings of aragonitic aciculae (D), magnification of cells on the surface of the body (E), and magnification of the chaetal organ (F–I; arrows point to chaetal organ in A–C).



Conway Morris and Peel 2008; Butterfield 1990). Recently, Kouchinsky et al. (2013), based on microstructure of specimens from the Tommotian–Atabanian Emyaksin Formation of Siberia, reinterpreted sclerites of the genus *Rhombocorniculum* Walliser, 1958 as annelid-type chaetae (for a different view see Caron et al. 2013).

The apertural location of the chaetal organ strongly suggests its locomotory function. Obviously, such locomotion makes sense only in a free-living, pelagic organism. The *Aldanella* phosphatized specimens would then be at least analogous, if not homologous, to the veliger larvae of modern gastropods. The specimens of *Pelagiella* with well-preserved chaetal organ from the Kinzers Formation are approximately 2.0 mm in size (Thomas et al. 2010*a*, 2010*b*; Thomas and Vinther 2012). An emerging question is whether they ever settled down to become benthic animals? Their pattern of mortality may help in finding the answer.

Pattern of mortality

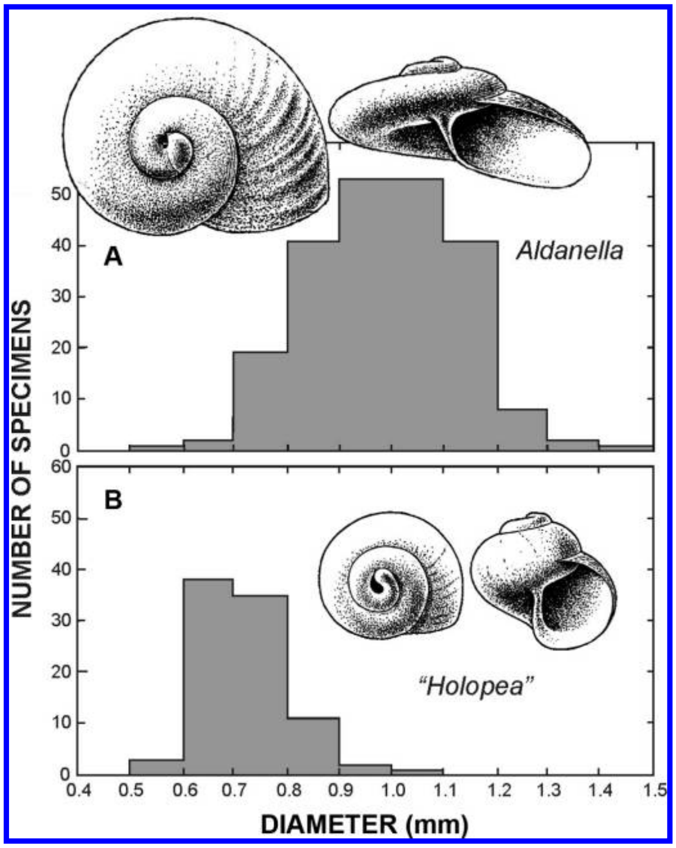
Most of the material of *A. attleborensis* at our disposal are phosphatic steinkerns with broken apertures. One may consider them to represent either complete coiled shell or just its phosphate-filled apex (cf. Martí Mus et al. 2008). Which of these interpretations is correct may be decided only on the basis of specimens completely covered with phosphate from outside of the shell. Such phosphate coating is preserved only in some specimens, while in other cases the phosphate coating is probably removed from exposed parts of the fossils during dissolution and by mechanical abrasion during handling of the residue. The region best protected against abrasion is the interior of the umbilicus, which is funnel-shaped. The inner lip of the aperture, well preserved in such shells (Figs. 3A–3F), proves that they were intact at the time of deposition. One of these specimens is preserved within the aperture of the other one (Figs. 3A, 3B), which is a case of the "sheltered preservation" phenomenon. Preservation of intact apertures in all specimens with preserved phosphatic membrane coatings makes likely that the steinkerns also represent complete specimens, not just broken off pieces of larger shells.

Phosphatized fossils in the residuum from the sample are of various sizes and there is no reason to suggest size selection during deposition of *Aldanella* shells. If the phosphatization were blamed for the selective preservation of the youngest individuals of *Aldanella*, small fragments of large adults should also be preserved, which was not the case. This enables determination of population dynamics based on size frequency distribution in the sample, which is assumed to express the distribution of mortality during growth of these animals. While measuring specimens with broken external portions of aperture but with the aperture preserved in the umbilicus, we extrapolated the size of the broken portion of the aperture by inferring how much of the aperture was missing.

In case of post-Cambrian gastropods, most of the phosphatized specimens found in "small shelly fossils" assemblages are veliger larvae that settled down on an anoxic sediment. They failed to metamorphose and survive in conditions unsuitable for life (Dzik 1978, 1983, 1994; Nützel and Mapes 2001). In many cases adult specimens of the same species from coeval strata representing more suitable conditions can be matched with larvae, but most species remain known only after their larval shells. This may be exemplified by the sample of an unidentified gastropod from the Ordovician (early Caradoc) pelagic limestone from the borehole Lesieniec 1 in northeastern Poland (Fig. 6B). Like other such occurrences, the size frequency distribution is unimodal. In the case of early Palaeozoic bivalves that dramatically change their shell ornamentation at metamorphosis, matching the peak of mortality with metamorphosis is possible based on material from the same sample (Dzik 1994, Fig. 33). It seems reasonable to propose a working hypothesis that *A. attleborensis* adults can be found in strata representing environments different from what is typical of where "small shelly fossils" occur. To test this, we determined size frequency distribution in the sample from the Erkeket Formation to compare it with specimens of related species found as not phosphatized skeletal fossils collected on the rock bedding plane.

The sample studied shows unimodal distribution of shell sizes. The inferred peak of mortality corresponds to about 1.0 mm di-

Fig. 6. Pattern of mortality as expressed by the sample of (A) *Aldanella attleborensis* from the base of the Erkeket Formation at the mouth of Mattaia Creek (*N* = 209) and (B) *Holopea*? sp. aff. *Holopea*? *pusilla* Hynda, 1986 (*N* = 90) from the early Caradoc at the Lesieniec borehole, northeastern Poland. Note the unimodal distribution with a peak at about 1.0 mm in the Cambrian sample and at about 0.7 mm in the Ordovician sample.



ameter of the shell, that is ca. 1.75 whorls (Fig. 6A). This may imply either a benthic settlement of veliger larvae at this period of life, connected with mass mortality, or these are adults dying on their way to developing their maximum body size. The distribution is right skewed, which suggests that not too many larger size adult specimens are represented in the sample. This is opposite to the pattern of size frequency distribution in the Ordovician sample (Fig. 6B). Moreover, the Ordovician gastropod larvae are significantly smaller than those of *Aldanella* (Nützel et al. 2006, Fig. 2). The peak of mortality in the pleurotomariid genus *Clathrospira* Ulrich and Scofield, 1897 is at about 0.7 mm diameter, whereas the peak of mortality in the bellerophontid genus *Kokenospira* Bassler, 1915 is even less at about 0.6 mm (Dzik 1978, Fig. 5). These gastropod shells are similar in size with the associated probable larvae of hyoliths, taking into account different geometry of their straight shells. The hyolithid genus *Recilites* Marek, 1967, with embryonic shell mucronate and having its surface covered with growth increments suggestive of free life outside of egg covers, had a very prominent peak of mortality (Dzik 1978, Fig. 2). From some reason the species of the genus *Carinolithes* Sysoyev, 1958, with subspherical smooth embryonic shells suggesting early development within egg covers, shows much less pronounced peak of mortality at inferred metamorphosis. Also, the Silurian bivalve genus *Butovicella* Kríž, 1965 had larvae of smaller size than *Aldanella* specimens, metamorphosis being completed, as expressed both in morphology and in a peak in mortality at 0.55 mm in size (Dzik 1994, Fig. 33).

To be sure that the analogy with the Ordovician "small shelly fossils" is valid, one should identify larger *Aldanella* specimens preserved without help from phosphatization. But even in the "small shelly fossils" assemblages, specimens of size significantly exceeding the peak of mortality in the Erkeket Formation sample are known. *Aldanella rozanovi* Missarzhevsky in Rozanov and Missarzhevsky, 1966, synonymized with *A. attleborensis* by Parkhaev and Karlova (2011), reaches 1.8 mm in diameter. Another Tommotian species (*A. utchurica*), different in having a larger apex, has the largest observed diameter at 3.6 mm. In this case, it is possible that the final size is correlated with the embryonic shell size, which is larger than in other species of the genus. Also, phosphatic specimens of the more advanced *Pelagiella subangulata* Tate, 1982 from the Parara and Ajax limestones reach 2 mm.

Aldanella polonica is known from 21 specimens preserved as crushed shells within a mudstone without phosphatization (Lendzion 1977; Lendzion and Posti 1983). The largest specimen has a diameter of 3.0 mm, while others are within the range of 2.5–2.7 mm. Parkhaev and Karlova (2011) considered this species synonymous with *A. crassa*, specimens of which are known to have a diameter of 5.0 mm. The latter species is characterized by a high whorl expansion rate, which makes it not quite comparable with *A. attleborensis*. Specimens of *Pelagiella* found in coarse sandstone of the Middle Cambrian *Paradoxides pinus* Zone at Jugoszów in the Holy Cross Mountains reach 7 mm in diameter (Orłowski 1964, p. 62). This may mean that the final body size increased during the course of evolution of the pelagiellids.

On the other hand, the only known specimen of *C. zazvorkai* from the Middle Cambrian Skryje Beds of Bohemia was nearly an adult, according to Horný (1964), but only 1.6 mm in diameter. It is also possible that conspecific forms preserved as phosphatic steinkerns from New South Wales (Mackinnon 1985) and New Zealand (Bischoff and Pendergast 1987) are of small size. Similarly preserved *Costipelagiella nevadense* Skovsted, 2006 from the latest Early Cambrian Emigrant Formation of Nevada, the oldest representative of the genus, is based on specimens less than 1.5 mm (Skovsted 2006). *Cambretina mareki* Horný, 1964 from the same beds as *C. zazvorkai* measures 1.3–2.7 mm.

All these forms could theoretically represent shells of veliger larvae, which are known to rarely reach the size of ca. 2 mm (Mapes and Nützel 2009); however, this would not explain why no adults of so many taxa have ever been found. This means that the adults of *Aldanella* were most probably of small size and the studied sample did not represent veligers at the stage of metamorphosis, contrary to expectations expressed in the working hypothesis.

Relationships

The cup-like hemispherical embryonic shell with mucro appears to be typical for most, if not all, the pelagiellids. Phosphate-coated specimens of *P. subangulata* from the Parara and Ajax limestones show smooth initial part of the protoconch, of morphology that is closely similar to the Siberian *Aldanella* (Bengtson et al. 1990, Fig. 167H) with gradual emergence of growth increments. Unfortunately, the tip of the shell is not visible, but the similarly smooth protoconch with gradually emerging growth increments of the latest Early Cambrian *C. nevadense* from the basal Emigrant Formation of Nevada has a mucro at its tip. Also, the shell microstructure is shared by *Aldanella* with *Pelagiella*. *Pelagiella deltoides* Runnegar and Jell, 1976 from the Parara Formation shows the same kind of acicular shell microstructure that is recognizable in the Siberian specimens.

Embryonic shell with mucro, acicular shell wall microstructure, and the presence of locomotory organs with a fan of chaetae contradict gastropod, as well as conchiferan, affinity of the pelagiellids. The pelagiellid pattern of ontogeny, however, characterizes the enigmatic Palaeozoic hyoliths. The pointed apex is similar to that described for the hyolithid *Recilites* (Dzik 1978) and many other Cambrian forms (e.g., Bengtson et al. 1990).

Mucrones similar to those present in the pelagiellids and hyoliths are known among true molluscs only in the embryonic conchs of orthoceratid cephalopods (e.g., Ristedt 1968, pl. 4: 11a; Dzik 1994, Fig. 34a) and derived pteropod gastropods (Bandel and Hemleben 1995). The latter is a quite recent evolutionary achievement. Palaeozoic ancestors of the opisthobranch molluscs, to which the Pteropoda belongs, had a heterostrophic larval shell with smooth rounded apex (Hua-Zhang et al. 2003). The function of mucro remains unknown.

It is possible, and even likely, that the mucro-bearing embryonic shells of the pelagiellids and hyoliths are homologous. Except for being uncoiled, the hyolith shell is in many respects similar to that of the pelagiellids not only in morphology and microstructure (Kouchinsky 2000*a*), but also during the course of their ontogenetic development. The main difference between these ancient shelled animals is that hyoliths had a thick calcareous operculum protecting the shell aperture. There are no pelagiellid opercula known, which is understandable given the purported planktonic locomotion by means of two bunches of chaetae.

At least three different body plans are recognizable among the early Palaeozoic hyoliths. Morphologically closest to pelagiellids and their probable bilaterally symmetrical coiled ancestors are relatives of the genus *Turcutheca* Rozanov et al., 1969 (cf. Dzik, 2010), with a laterally compressed and anteriorly curved conch. They were minute in size and could have been pelagic (Dzik 2010). The opposite life style was represented by orthothecids, apparently benthic mud eaters, as shown by their complex folded intestine filled with sediment (e.g., Horný 1998). Their conch is at least slightly flattened, if not concave, on the presumably anterior side. In the third group of hyolithids, it is also flattened but remains convex and bears a projecting apertural lip. Their gut is simple, loop-shaped, may be preserved as phosphatized, which is an indication of organic-rich food (Butterfield and Nicholas 1996). It seems possible that pelagiellids are trochospirally coiled derivatives of the turcuthecid hyoliths that lost the operculum in connection with pelagic life.

Some hyolithids had paired organs, helens, extending from sides of the conch aperture (Marek 1967), which is in a location similar to that of the chaetal organ of the pelagiellids. These are solid calcareous structures and their growth was accretionary (Yochelson 1974). The surface of helens bears an ornament of transverse growth increments except at their basal portions, which apparently embedded in a soft tissue. Microstructurally, the elements were composed of concentric lamellae around a flat core, rich in organics (Martí Mus and Bergström 2007). Although tempting, homology of the organic core of helens with the pelagiellid chaeta is difficult to substantiate. At present, calcareous chaetae are known only in the amphinomid polychaetes. In the amphinomid genus *Cryptonome* Borda, Kudenov, Bienhold and Rouse, 2012, each chaeta consists of a calcareous outer cortex and gelatinous to solid medulla (Borda et al. 2012).

Phylogenetic meaning of the chaetal organ

The presence of chaeta alone does not exclude molluscan affinities of the pelagiellids, but makes the phylogenetic scheme more complex. In its location, the chaetal organ of the pelagiellids corresponds with the ciliated lobes (velum) of the gastropod veliger larva, used for propulsion and the collection of food particles from the water. This is connected with the significantly smaller size of the larva with respect to pelagiellids. It is possible that the chaetal organ disappeared during the course of evolution, being suppressed by the ciliary bands with diminution of the larva stage. The most basal of gastropods, the vetigastropods, had a prolonged planktotrophic larval stage in the Palaeozoic, unlike their modern successors (Nützel and Mapes 2001). According to Nützel et al. (2006, 2007), gastropod larva planktotrophy arose somewhere at the Cambrian–Ordovician boundary. When, in later stages of the gastropod phylogeny, larger veligers developed, armed with complex lobate velum, it was too late to restore the chaetal locomotion. Typical chaetae are unknown in the present-day molluscs, but there are suggestions that the sensory hairs of chitons (Leise and Cloney 1982) and the Kölliker's tufts in pelagic octopod paralarvae are homologous to the annelid chaetae (Brocco et al. 1974). The possible presence of true chaetae in the earliest molluscs may fill the gap in diversity of body plans of the lophophorate (spiralian) phyla.

Not only in molluscs do chaetae occur without connection to parapodia. The brachiopod setae are secreted by the mantle, which makes them different from those of polychaetes, despite their close structural similarity (Gustus and Cloney 1972; Orrhage 1973; Lüter 2000). They were present in larvae of Palaeozoic linguloids (Baliński 1997), as well as in postlarval stages (Jin et al. 2007).

A fan-like arrangement of chaetae, similar to that in *Pelagiella*, characterizes parapodia of the Middle Cambrian polychaete *Canadia* Walcott, 1911 and its Early Cambrian relatives *Phragmochaeta* Conway Morris and Peel, 2008 and *Pygocirrus* Vinther, Eibye-Jacobsen and Harper, 2011 (Conway Morris 1979, Conway Morris and Peel 2008, Vinther et al. 2011). The Cambrian polychaetes were presumably closer anatomically to the common ancestor of annelids and molluscs than any recent representative of these phyla because of the much smaller geological time distance (Dzik 2011). This may mean that the common ancestor of polychaetes and molluscs was already equipped with such organs. Their presence would be a highly plesiomorphic trait and may not be so phylogenetically informative as it is frequently assumed (Vinther et al. 2008).

Conclusions

Why are large molluscan shells virtually missing in the Cambrian remains a mystery (Dzik 1991; Martí Mus et al. 2008). It is paralleled by the scarcity of molluscan trace fossils in the Early Cambrian deposits that are contemporaries with the "small shelly fossils" assemblages (Mazurek 2013). Earliest molluscs might have truly been of microscopic size at maturity, with macroscopic representatives being a novel component. A scenario of evolutionary bottleneck may be envisioned for the origin of the phylum Mollusca and its classes. The new evidence on the embryonic shell morphology and ontogeny of *Aldanella* concurs with the recent discovery of chaetal organs in *Pelagiella* by Thomas et al. (2010*a*). The minute adult pelagiellids using their paired chaetal organ for propulsion may represent transitional forms between the ancient polychaete annelids and the true molluscs. The mode of development, with mucronate embryonic shell and planktotrophic later developmental stage, as well as non-nacreous shell wall microstructure, suggest hyolith affinities of the pelagiellids. The Pelagiellida may be provisionally classified in the class Hyolitha, instead of Gastropoda, until the phylogenetic meaning of their chaetal organ (Thomas et al. 2010*a*) is better understood.

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