

New Data on the Morphology of Ancient Gastropods of the Genus *Aldanella* Vostokova, 1962 (Archaeobranchia, Pelagielliformes)

P. Yu. Parkhaev

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: pparkh@paleo.ru

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Abstract—The position of attachment of the shell muscle is discovered in the columellar area of the shell of the Early Cambrian univalved genus *Aldanella* (family Aldanellidae, order Pelagielliformes, subclass Archaeobranchia), the structure of its protoconch is described, and the presence of series of septa in the embryonic part of their shell is confirmed. These new features confidently support the position of the family Aldanellidae within the gastropod class and allow them to be considered ancestral to younger gastropod lineages with a turbospiral shell.

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INTRODUCTION

The restudy of old collections and handling of a new material on Cambrian mollusks originating from the Siberian Platform were recently started in the Paleontological Institute of the Russian Academy of Sciences with the main focus on the taxonomic revision of the group. However, besides the amendment of taxonomic status of various genera and species, this work resulted in the discovery of completely new morphological features in some representatives of ancient mollusks. In particular, scars of shell muscles were found among members of several mollusks families (Parkhaev, 2002b, 2004; Ushatinskaya and Parkhaev, 2005), casts of the cells of outer mantle epithelium were described (Ushatinskaya and Parkhaev, 2005), pores in shells of Cambrian mollusks were described and typified, and proposals for their possible function were made (Parkhaev, 2006).

All these new observations are evidently restricted to the ultrastructural morphology of Cambrian mollusks (shell microstructure, microornamentation of internal mold surface). It is possible that these details were missed by previous researchers because of some objective (the level of scientific equipment) or subjective reasons (different goals and objectives of studies). Nowadays it has become obvious that ultrastructural data have a primary importance in determination of biology and systematic position of Cambrian mollusks, in understanding of the earliest stages of evolution of the phylum Mollusca. As it was emphasized on the last XV World Malacological Congress (Perth, 2004), the greatest progress in the study of ancient mollusks should be expected from microstructural studies and from the study of their embryonic shells.

The present paper describes casts of the shell muscles of the species *Aldanella rozanovi* and the morphology of the initial shell of *A. operosa* and *A. rozanovi*. Both aldanellid species come from the Lower Cambrian of the Siberian Platform, thus showing once again the greatest importance of this particular region not only for the stratigraphic investigation, but also for the morphological and paleobiological studies.

MATERIAL

The collection studied (no. 5083) is housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

SCARS OF SHELL MUSCLES

Aldanella rozanovi. The species *Aldanella rozanovi* Missarzhevsky, 1966 was originally described by V.V. Missarzhevsky from the Sunnagin Horizon (Tommotian Stage, *N. sunnaginicus* Zone) in the lower reaches of the Lena River, near the village of Chekurovka (Rozanov and Missarzhevsky, 1966, p. 104). Later the species was repeatedly reported from the lower part of the Tommotian Stage (*N. sunnaginicus*–*D. regularis* zones) of different regions of the Siberian Platform (Zhegallo, 1983; Khomentovskii et al., 1990; Vassiljeva, 1998). Any ultrastructural data are absent from published papers, except for the article by Zhegallo (1980), in which he used microstructural studies in order to make the assumption that the shell was originally composed of prismatic crystals of calcium carbonate.

The present investigation is based on the collection of aldanellids from the Siberian Platform housed in the

Laboratory of Ancient Organisms of the Paleontological Institute, Russian Academy of Sciences. In total, several hundred variously preserved specimens of *A. rozanovi* were inspected. The most plentiful and best preserved material comes from the sections of the western Anabar Region. Most of the collection was collected in 1985 by M.I. Barskova and T.A. Sayutina from the lower part of the Medvezh'ya Formation (*D. regularis* Zone, *L. tortuosa* Subzone) on the Kotui River, 0.5 km upstream of the mouth of Ary-Mas-Yuryakh Creek.

SEM studies of internal molds have revealed a zone of polygonal microrelief in the columellar area of many specimens (Pl. 3, figs. 2, 3). The relief is composed of elevated polygons of irregular shape, 6–8 μm in diameter, and dividing furrows, 1–2 μm wide (Pl. 3, figs. 2c–2f, 3c, 3d). The microrelief is most prominent near the apertural margin, while on areas of internal molds that correspond to earlier parts of the shell, and hence more distant from the aperture, it is less pronounced.

Other species of the genus *Aldanella*. After the polygonal microrelief had been revealed in the columella region of internal molds of *A. rozanovi*, other species of the genus *Aldanella* were inspected to reveal the same pattern. Unfortunately, such prominent microrelief was not found in other representatives of the genus. However, a few internal molds of the species *A. operosa* and *A. costata* Missarzhevsky, 1989 have a poorly defined netlike pattern in the columellar region, while the rest of the mold surface is smoother in respect of microornamentation. It is quite possible that this smoothed netlike pattern is analogous to the polygonal microrelief of *A. rozanovi*, but in *A. operosa* and *A. costata* it has been found in specimens with a poor state of preservation.

Discussion. A polygonal microrelief identical to that of *A. rozanovi* was recently described in different species of Cambrian mollusks, i.e., *Bemella incomparabilis* Parkhaev, 2001 from the Botomian Stage of the Fleurieu Peninsula, South Australia (Parkhaev, 2002b, pl. 3, fig. 3), *Bemella* sp. from the Tommotian Stage of Plakhino Island, Siberian Platform (Parkhaev, 2002b, pl. 4, fig. 5), *Latouchella korobkovi* (Vostokova, 1962) from the Tommotian Stage of the Kotui River, Siberian Platform (Parkhaev, 2004, pl. 2, fig. 1), *Tuoraconus acutatus* Missarzhevsky, 1989 from the Tommotian Stage of the Khara-Ulakh Range, Siberian Platform (Ushatinskaya and Parkhaev, 2005, text-fig. 1), and *Securiconus* sp. from the Tommotian Stage of the Rasokha River, Siberian Platform (Ushatinskaya and Parkhaev, 2005, text-fig. 5). In all these cases the polygonal microrelief was interpreted as a cast from the surface of the prismatic shell layer. Judging from the shape and position of the zone with polygonal microrelief, it was concluded that this zone was most probably the area of attachment of shell muscles, and the polygonal microrelief replicated the surface of pallial myostracum. This is supported by the shell microornamenta-

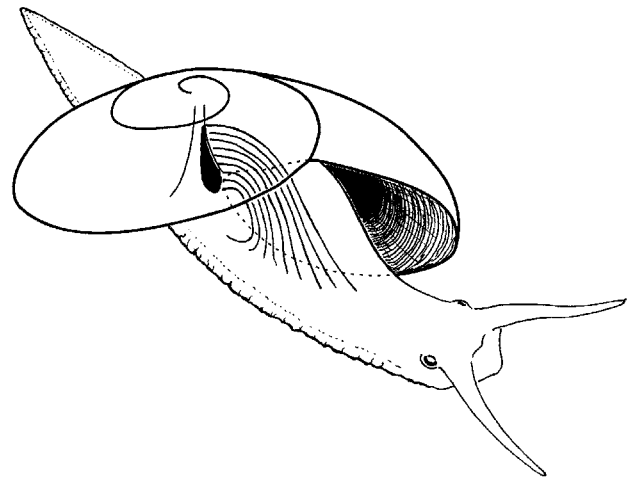


Fig. 1. Reconstruction of aldanellid gastropod (zone of columellar muscle attachment is black).

tion of recent gastropods and bivalves (Taylor and Kennedy, 1969; Popov, 1977; Parkhaev, 2002b) and even brachiopods (Williams and Wright, 1970).

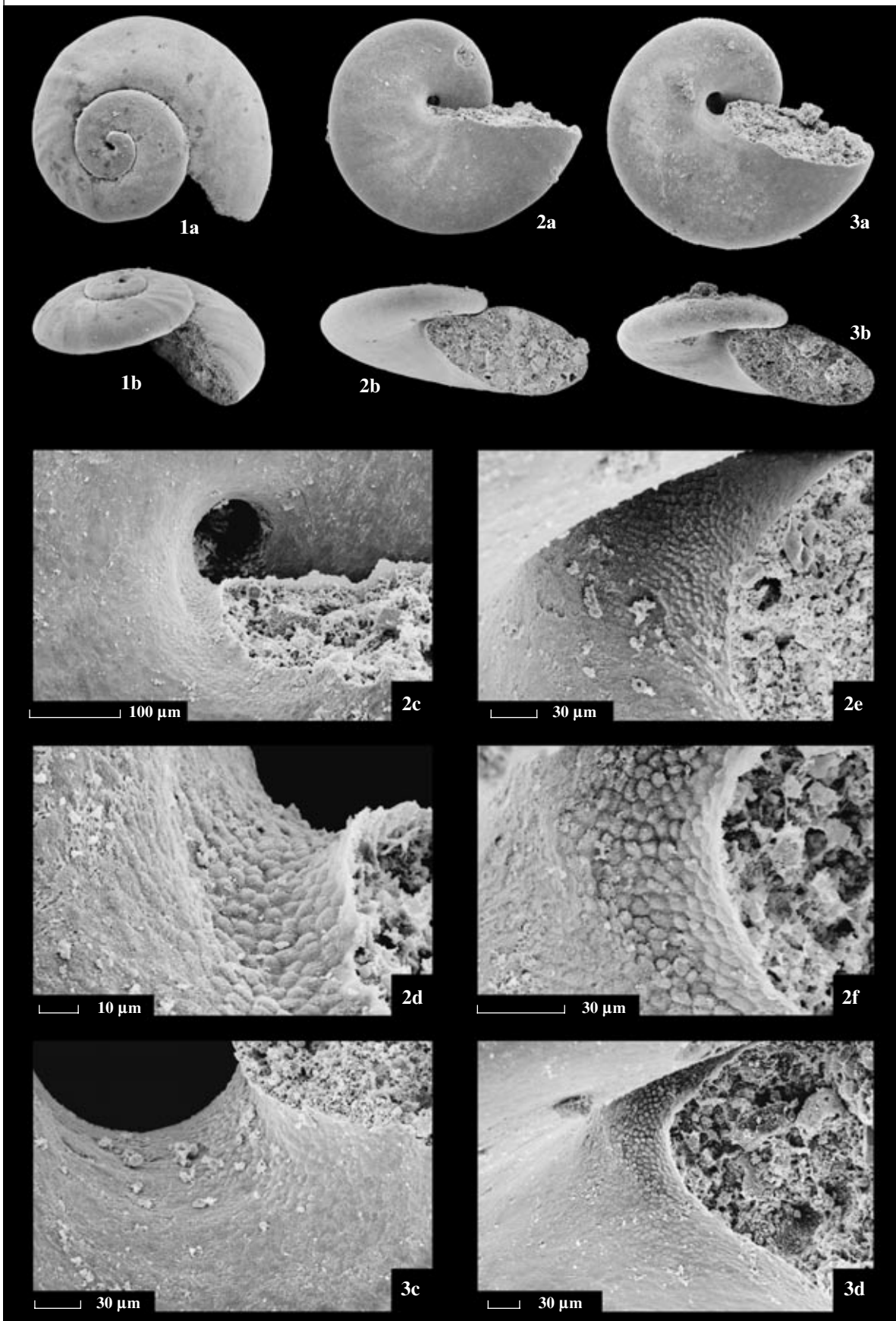
Considering the aldanellids, we also have every reason to believe that the discovered polygonal microrelief is a cast of the surface of the pallial myostracum, which occurred in the columellar area of the aldanellid shell. Thus, aldanellids, like most typical gastropods with a turrsoidal shell, bear a single main shell muscle, i.e., columellar one, the base of which was attached to the columella. This position of shell muscle is consistent with the functional morphology of *Aldanella* shell, and Runnegar (1981, text-fig. 5A) suggested a hypothetical reconstruction of aldanellids in which these have a columellar muscle.

In addition to the microrelief of the scar and its position, its muscular nature is also supported by the general shape of the scar (Pl. 3, figs. 2c, 3c; Fig. 1). It is this elongated form of the columellar muscle scar that the recent gastropods with a turrsoidal shell have due to the ribbonlike shape of the columellar muscle.

It is very significant that the muscle scars of *Aldanella* and *Latouchella* are very similar in localization and microrelief pattern (Parkhaev, 2004, pl. 4, fig. 1). It is most likely that the columellar muscles of these mollusks are homologous, supporting the relationship between aldanellids and coreospirids, which, in turn, are considered (Parkhaev, 2002a) to be ancestral to the order Pelagielliformes, comprising two families, Aldanellidae and Pelagiellidae.

THE MORPHOLOGY OF INITIAL PART OF THE SHELL

***Aldanella operosa*.** The species *Aldanella operosa* Missarzhevsky, 1966 was originally described by V.V. Missarzhevsky from the Kenyadin Horizon (Tom-



motian Stage, *D. regularis* Zone) in the lower reaches of the Lena River, near the village of Chekurovka. The original description runs that the “initial chamber is drop-shaped and is separated from the rest of the shell by a septum” (Rozanov and Missarzhevsky, 1966, p. 105). However, the holotype illustration (Missarzhevsky, 1966, pl. 10, fig. 7) does not show any septum, while the illustration of the paratype (Missarzhevsky, 1966, pl. 10, figs. 8, 9) shows the broken apical part of the mold. Only a later publication by Missarzhevsky (1989, pl. 8, fig. 12) contains the photograph of *A. operosa* with a possible septum separating the initial part of the shell. The description of the species is absent from this publication, the explanation of pl. 8, fig. 12 was omitted by the editor, and only the morphology of the specimen suggests that this is an illustration of *A. operosa*. In addition, Missarzhevsky did not mention the presence of a septum at all in the diagnosis of the genus *Aldanella*, but he only noted that “the protoconch is prominent, divided from the rest of the shell by a constriction” (Missarzhevsky, 1989, p. 182).

As a result of these circumstances, such an important morphological feature as the presence of septa in the initial part of the shell of *A. operosa* passed unnoticed by specialists.

The studied collection of the Cambrian mollusks from the Siberian Platform includes several thousand specimens representing several species of the genus *Aldanella*. In this material I found 14 specimens of *A. operosa*, originating from the Tommotian Stage (*D. regularis* Zone) of the lower reaches of the Lena River (village of Chekurovka) and from the Atdabanian Stage (*P. pinus/P. anabarus* Zone) of the middle reaches of the Lena River (Achchagyi-Kyyry-Taas Creek). All specimens are characterized by the presence of one or two septa in the initial part of the shell (Pl. 4, figs. 1–6).

The largest specimens (Pl. 4, figs. 1, 4, 6), ranging from 740 to 900 μm in diameter, bear two septa: the first is approximately 100 μm long, and the second is approximately 150 μm long. The angle between these septa is about 90° or slightly larger. The smaller specimens, ranging from 600 to 700 μm , show only the first septum, which is 100 μm long (Pl. 4, figs. 2, 3). One more specimen, represented by an internal mold (Pl. 4, fig. 5), has a flattening in the apical part of the spire that is as large as the second septum. This also accords with the total size of the mold, which is 770 μm in diameter.

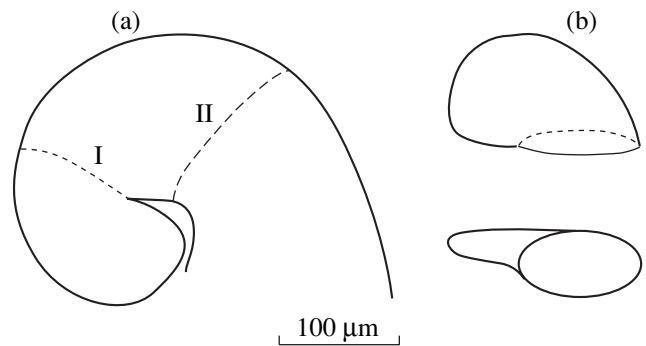


Fig. 2. Structure of the initial part of shell and reconstruction of the protoconch of *Aldanella operosa* Missarzhevsky, 1966: (a) initial part of the shell; (b) protoconch reconstruction. Designations: (I) first septum; (II) second septum.

The material studied suggests that the second septum started to form in ontogeny when the shell reached 700–740 μm in diameter.

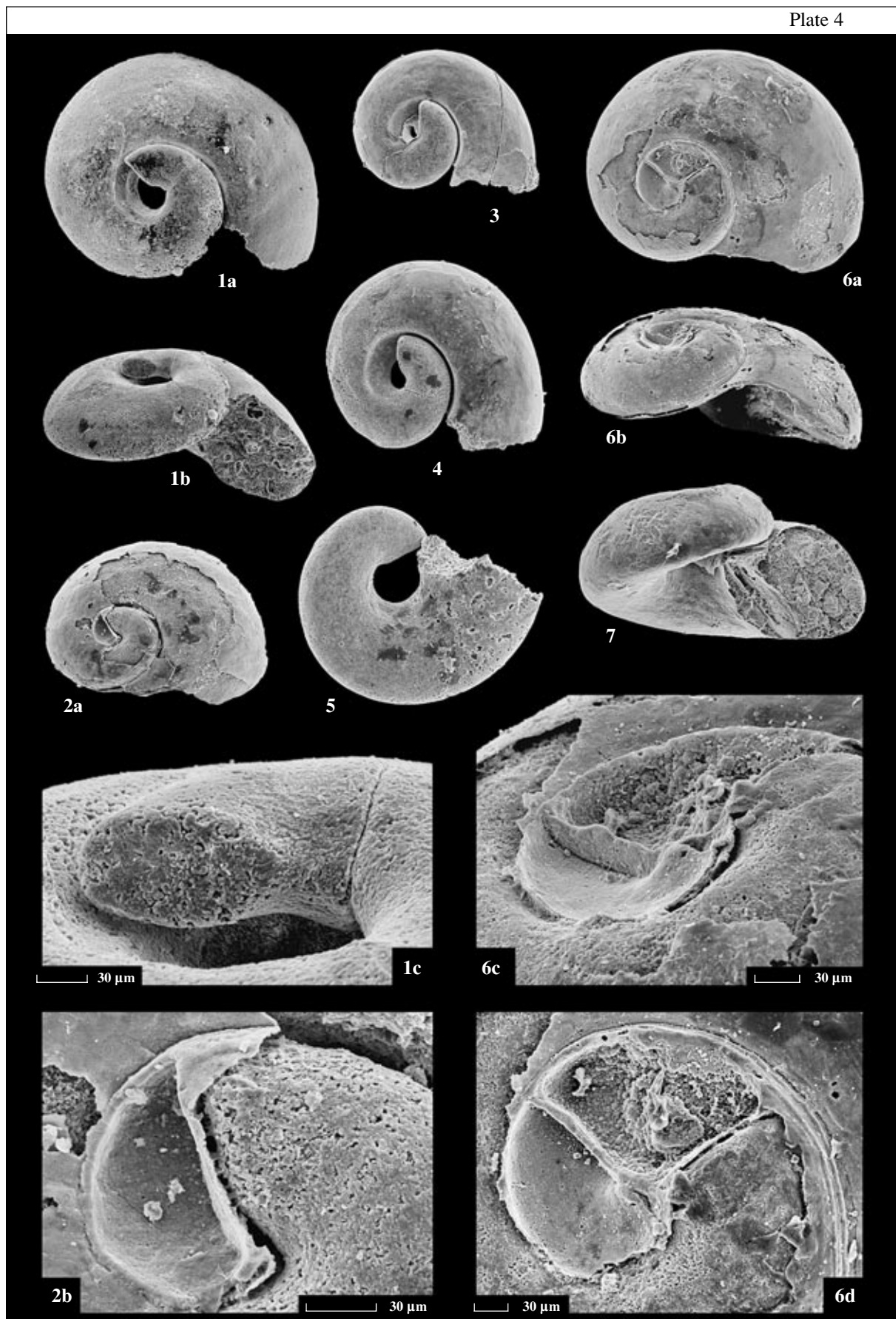
The character of the preservation of the material also leads to interesting conclusions. The specimens with preserved shell matter (Pl. 4, figs. 2, 3, 6) demonstrate that the initial part of the shell separated by the first septum is not filled with phosphatic matrix and is always empty. This part is always absent from the specimens represented by internal molds (Pl. 4, figs. 1, 3, 5). It can be supposed that this part of the shell probably corresponds to the protoconch (Fig. 2) and that in the above-mentioned specimens it was completely isolated from the shell by the first septum. Thus, the phosphatic matrix could not get into the protoconch during the fossilization.

One of the internal molds shows a slit left by the dissolution of shell matter during chemical treatment of the material (Pl. 4, fig. 1c). From the size and position of the slit it is obvious that it corresponds to the second septum. At the same time, the space between the first and second septa is completely filled with phosphatic matrix and remains in a state of presentation typical of internal molds. Possibly, the formation of the second septum was just started in this particular specimen, and, thus, no considerable barriers existed to prevent the space between the first and second septa from filling by phosphatic matrix during the fossilization.

In another specimen (Pl. 4, fig. 6) this space is only partly filled with phosphatic granules (Pl. 4, figs. 6c, 6d). Probably, the fossilization occurred during the develop-

Explanation of Plate 3

Figs. 1–3. *Aldanella rozanovi* Missarzhevsky, 1966; Lower Cambrian, Tommotian Stage, *D. regularis* Zone, *L. tortuosa* Subzone; Medvezh'ya Formation; Siberian Platform, western Anabar Region, Kotui River, 0.5 km upstream of the mouth of Ary-Mas-Yuryakh Creek (see Rozanov et al., 1969, text-fig. 9, locality M412); collected by M.I. Barskova and T.A. Sayutina, 1985, sample BiS-85-III/5-IV (=member 14 in the locality M412); (1) specimen PIN, no. 5083/1443, internal mold, $\times 23$: (1a) apical view, (1b) oblique apertural view; (2) specimen PIN, no. 5083/1447, internal mold: (2a) basal view, $\times 23$, (2b) apertural view, $\times 23$; (2c–2f) microornamentation of columellar area: (2c) basal view, (2d) same view, magnified, (2e) apertural view, (2f) same view, magnified; (3) specimen PIN, no. 5083/1446, internal mold: (3a) basal view, $\times 23$, (3b) apertural view, $\times 23$, (3c–3d) microornamentation of columellar area: (3c) basal view, (3d) apertural view.



mental stage corresponding to the completion of the second septum, when the space between the first and second septa was communicating with the rest of the shell interior through a narrow foramen or a series of small holes in the second septum. It is noteworthy that the second septum is still rather thin, i.e., 4 μm thick, whereas the completely formed septum is 8-10 μm thick.

And finally, we can see the stage with a completely formed second septum in the specimen represented by an internal mold in which its initial part bears only a flattened area adjoining the second septum and the earlier shell parts are absent (Pl. 4, fig. 5).

***Aldanella rozanovi*.** In addition to the peculiarities of microornamentation of the surface of internal molds of *A. rozanovi*, which have allowed establishment of the presence of columellar muscles in this species, new data were obtained regarding the structure of the initial part of the shell. A single specimen from the collection has almost completely preserved the shell wall (Fig. 3a). The apical part of the shell is of the greatest interest (Fig. 3b), since there the appearance of fine growth lines, preserved in the sutural zone, clearly mark the beginning of the teleoconch. It is supposed that the apical part of the shell lacking growth lines corresponds to the protoconch (Fig. 3c). The protoconch of *A. rozanovi* (Fig. 3d) reconstructed based on these specimens had a cap-shaped form with the apex shifted slightly posteriorly; the protoconch height is approximately 100 μm , the length of the aperture is approximately 90 μm .

Discussion. The presence of septation in the initial part of the shell is a common phenomenon among recent and fossil gastropods. Among the fossil representatives, the forms with septa are found in the Paleozoic from the Early Ordovician and occur among members of euomphalids, pleurotomariids, and loxonematids (Yochelson, 1971). In recent lower gastropods (e.g., orders Trochiformes and Turbiniformes), the initial shell part is filled with calcium carbonate (Golikov and Starobogatov, 1988). Other groups (e.g., Turritelli-

formes and Ranelliformes) form a series of septa. All these accessories have an evident function, i.e., to maintain the watertightness of the apical part of the shell, which is the oldest part, during the lifetime of a mollusk and, hence, is subject to the most prolonged corrosive action of sea water. In addition, in most gastropods the apex is the most prominent part of the shell and, thus, suffers from mechanical impacts (shocks, abrasion, etc.).

Possibly, the septation in *A. operosa* performed the same function, i.e., maintenance of watertightness of the shell in the case of damage of its initial parts. It is noteworthy that this morphology originated within the youngest species of the genus with the most projected spire of the shell (Pl. 4, fig. 7). Possibly, such an extent of spire projection became critical, and the necessity to form septa had evolved.

The presence of a series of septa in the initial parts of shells or a single septum dividing protoconch from teleoconch has already been supposed for some species of Cambrian mollusks. In particular, the septum separating the initial part of the shell is described in *Hampilina goniospira* Kobayashi, 1958 from the Middle Cambrian of South Korea (Eiko Formation, Bunkei District) (Kobayashi, 1958), while series of septa in the initial parts of shells are known in *Tannuella elata* Missarzhevsky, 1969 from the Botomian Stage of the Tannu-Ola Range, Tuva (Rozanov et al., 1969) and *T. elinorae* Brock et Paterson, 2004 from the Botomian Stage (Mernmerna Formation, Flinders Range) of South Australia (Brock and Paterson, 2004). The surface adjoining the septum with a distinct trace of the foramen is illustrated for the species *Davidella tommotica* Zhegallo, 1996 from the Tommotian Stage of Mongolia (Esakova and Zhegallo, 1996, pl. 23, fig. 7). All these cases suggest that the formation of septa in the initial part of cap-shaped Cambrian mollusks is not infrequent. The presence of septation in aldanellids expand this phenomenon to turbospiral forms as well.

Explanation of Plate 4

All figured specimens originate from the Lower Cambrian of the Siberian Platform: (1) Tommotian Stage, *D. regularis* Zone, *L. bella* Subzone; Tyuser Formation, middle subformation, member 5; lower reaches of the Lena River, village of Chekurovka, mouth of the Biskeebit River; collected by V.V. Missarzhevsky, sample M-30/19 (see Rozanov et al., 1969, text-fig. 7); (2-7) Atdebabanian Stage, *P. pinus/P. anabarus* Zone; Pestrotsvet Formation; middle reaches of the Lena River, Achchagyi-Kyryyy-Taas Stream; collected by N.P. Meshkova, 1965, sample 46 (29 m above the shoreline; see *Subdivision...*, 1984, text-fig. 19).

Figs. 1-7. *Aldanella operosa* Missarzhevsky, 1966; (1) specimen PIN, no. 5083/0003, internal mold: (1a) apical view, $\times 65$; (1b) oblique apertural view, $\times 65$; (1c) fragment of the initial part of the internal mold showing the flattened surface adjoining the first septum and a slit left by the dissolution of the second septum, $\times 75$; (2) specimen PIN, no. 5083/0268, internal mold with fragments of the shell wall: (2a) apical view, $\times 65$; (2b) fragment of initial part of the shell showing the first septum, separating the initial part of the shell (unfilled with rock) from the internal mold, the second septum has not been formed; (3) specimen PIN, no. 5083/0269, internal mold with fragments of the shell wall viewed from the spire showing the flattened surface adjoining the first septum, the second septum has not been formed, $\times 65$; (4) specimen PIN, no. 5083/0266, internal mold viewed from the spire showing the flattened surface adjoining the first septum and a slit left by the dissolution of the second septum, $\times 65$; (5) specimen PIN, no. 5083/0265, internal mold, basal view showing the flattened surface adjoining the second septum, $\times 65$; (6) specimen PIN, no. 5083/0264, shell with a partially broken wall: (6a) apical view, $\times 65$; (6b) oblique apertural view, $\times 65$; (6c) oblique view of the initial part of the shell showing the first septum, separating the initial part of the shell (unfilled with rock) from the next chamber, closed by the second septum; (6d) fragment of the initial part of the shell showing the unfilled initial part of the shell, first septum, second chamber partially filled with phosphate, second septum, and internal mold; (7) specimen PIN, no. 5083/0262, internal mold, apertural view.

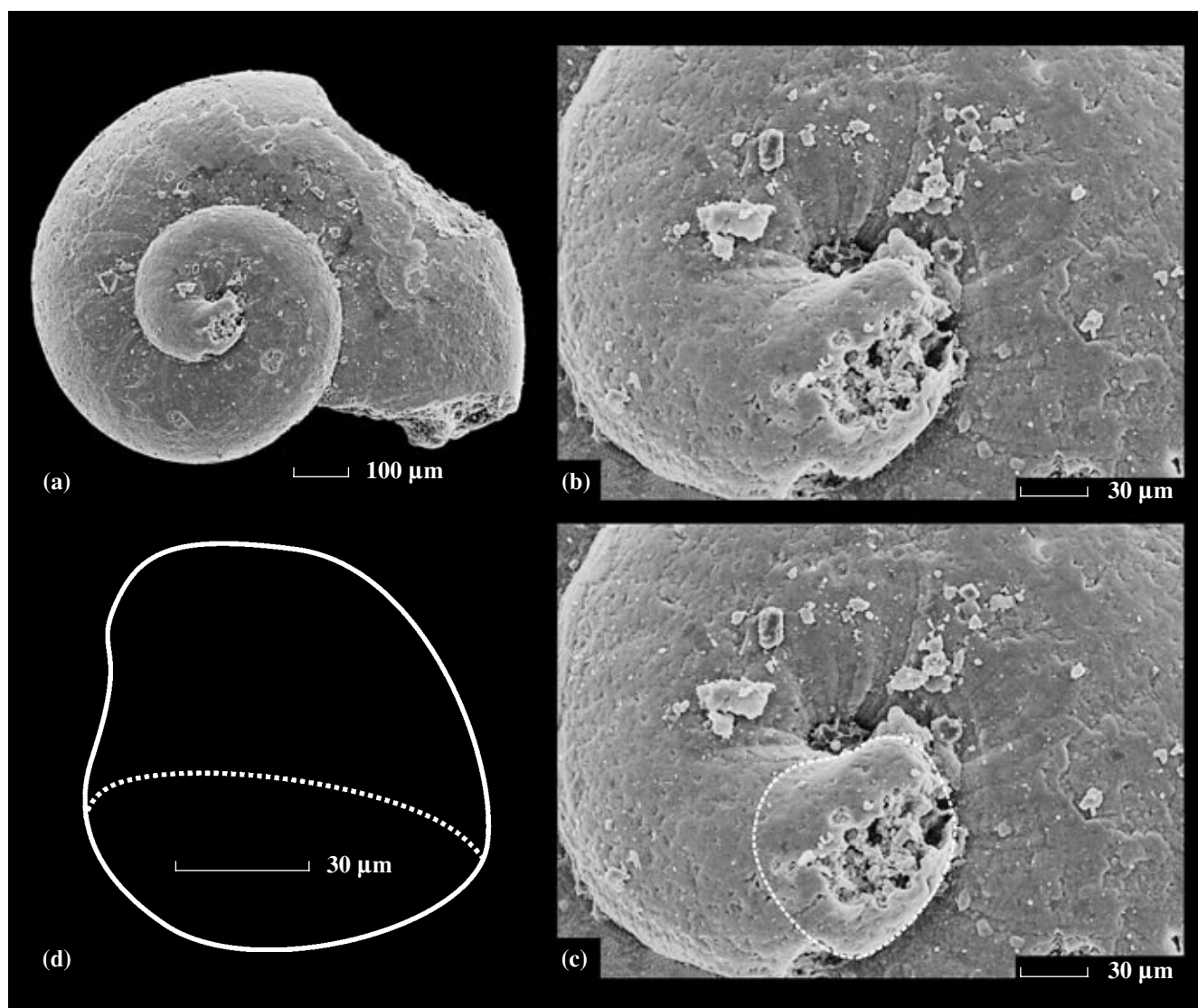


Fig. 3. Structure of the initial part of the shell of *Aldanella rozanovi* Missarzhevsky, 1966; specimen PIN, no. ?5083/0127; Lower Cambrian, Tommotian Stage, *N. sunnaginicus* Zone; Siberian Platform, western Anabar Region, Rassokha River (collected by N.P. Meshkova, 1972): (a) shell, apical view; (b) initial part of shell; (c) the same, protoconch is outlined by a dotted line; (d) protoconch reconstruction.

Comparison between the reconstructed protoconchs of *A. operosa* (Fig. 2b) and *A. rozanovi* (Fig. 3d) reveals that both of these aldanellid species have a rather small embryonic shell: less than 100 µm in *A. rozanovi* and slightly larger than 100 µm in *A. operosa*. A protoconch of a such size suggests (Jablonski and Lutz, 1983; Nützel and Frýda, 2003) a possible planktonic larval development of aldanellids, which is consistent with general assumptions about the development of ancient mollusks (Haszprunar, 1988; but compare Chaffee and Lindberg, 1986 for an opposite view). However, according to other studies, the size and morphology of protoconch is not strictly connected with the type of larval development, and in some recent gastropods with a similar type of protoconchs even species of closely related genera or, sometimes, of a single genus may dif-

fer in larval development (Hadfield and Strathmann, 1990; Hickman, 1992; Sasaki, 1998).

Analysis of protoconch shapes in recent primitive gastropods (Sasaki, 1998, text-fig. 107) shows that morphologically the aldanellid protoconch occupies an intermediate position between the elongated, bell-shaped protoconch of patellid gastropods and the turbospiral paucispiral protoconch of the lower pectini-branchians (e.g., Trochoidea). But the presence of septa shows that aldanellids are closer to the patellids, in which the protoconch becomes separated from the teleoconch by a septum when the general size of the shell is less than 1–2 mm (Sasaki, 1998). A small scar may be left after the closure of the foramen at the center of the septum surface. The apical part of the visceral mass

was removed from the protoconch through the foramen during the final stage of septum formation (Warén, 1988, text-fig. 14; Sasaki, 1998). As previously mentioned, possibly this ontogenetic stage is observed in the *A. operosa* specimen figured in Pl. 4, fig. 6.

A slight asymmetry of the protoconch of *A. rozanovi* (Fig. 2b; Pl. 4, fig. 6c), which is typical for many gastropod groups, is noteworthy. It was supposed that asymmetry in paucispiral protoconchs of gastropods could be caused by a mechanic deformation of still unmineralized (hence, pre-torsional) shell by the activity of the larval retractor (Bandel, 1982). Possibly, this activity is directly connected with the torsion process (Crofts, 1935, 1955); however, there are more recent opinions that torsion is only a result of differential growth of visceral mass and does not involve any muscular activity (Bandel, 1982; Haszprunar, 1988).

CONCLUSIONS

The new morphological features discovered by the present study make significant addition to our knowledge on the structure of the most ancient members of the phylum Mollusca and led to the following important conclusions: (1) the presence of protoconch and septa in the initial part of the aldanellid shell and the regular character of the septation (Burchette and Riding, 1977) exclude Yochelson's assignment of aldanellids to sedentary polychaetes (Yochelson, 1975, 1978; Bockelie and Yochelson, 1979), and prove their molluscan nature; (2) the presence of columellar muscles in aldanellids and the morphological similarity of their protoconch with larval shells in primitive gastropods supports the position of the family within one of the stem gastropod groups, possibly at the base of the subclass Pectinibranchia; (3) the great morphological similarity between muscle scars in *Aldanella* and *Latouchella* supports the close relationship between the families Aldanellidae and Coreospiridae, thus phylogenetically linking symmetrical helcionelloid mollusks (order Helcionelliformes) with turbospiral members of archaeobranchians (order Pelagielliformes).

New data are not inconsistent with the model considering the helcionelloid mollusks as primitive gastropods (Parkhaev, 2000, 2001). All things considered, we should admit that gastropods had already appeared within the Early Cambrian, when they were represented by morphologically diverse, cap-shaped, symmetrically coiled and turbospiral forms (Parkhaev, 2005).

In addition, the present study expands the stratigraphic range of the species *Aldanella operosa*, the most recent record of which was previously known only from the base of the Atdabanian, *R. zegebarti* Zone, in the middle reaches of the Lena River (Missarzhovsky, 1989, p. 95). The material collected by N.P. Meshkova proves the presence of *A. operosa* in the *P. pinus/P. anabarus* Zone in the section of Achchagy-Kyyry-Taas Creek 29 m above the shoreline. This level

corresponds to the middle part of the Atdabanian Stage in the stratotype region (*Subdivision...*, 1984, text-fig. 19).

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