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Shell Chirality in Cambrian Gastropods and Sinistral Members of the Genus *Aldanella* Vostokova, 1962

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Abstract—Shell chirality among Cambrian gastropods is discussed. It is demonstrated that the earliest members of the class include chiral aberrations with abnormal opposite coiling of the shell. It is assumed that, in Cambrian gastropods, speciation could have occurred by mutation in the locus determining the chirality, as is proposed for extant gastropods. In contrast to modern gastropods, the existence of chiral morphs within single species has not been recorded in Cambrian mollusks, whereas the presence of chiral twin species is possible. The systematic position of sinistral representatives of the genus *Aldanella* Vostokova, 1962 is considered. *Aldanella golubevi* sp. nov. with sinistral shell is described from the base of the Tommotian Stage of the Anabar Region. Aberrant sinistral specimens of the normally dextral species *Aldanella utchurica* Missarzhevsky in Rozanov et al., 1969 and *Pelagiella adunca* Missarzhevsky in Rozanov et al., 1969 are figured.

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INTRODUCTION

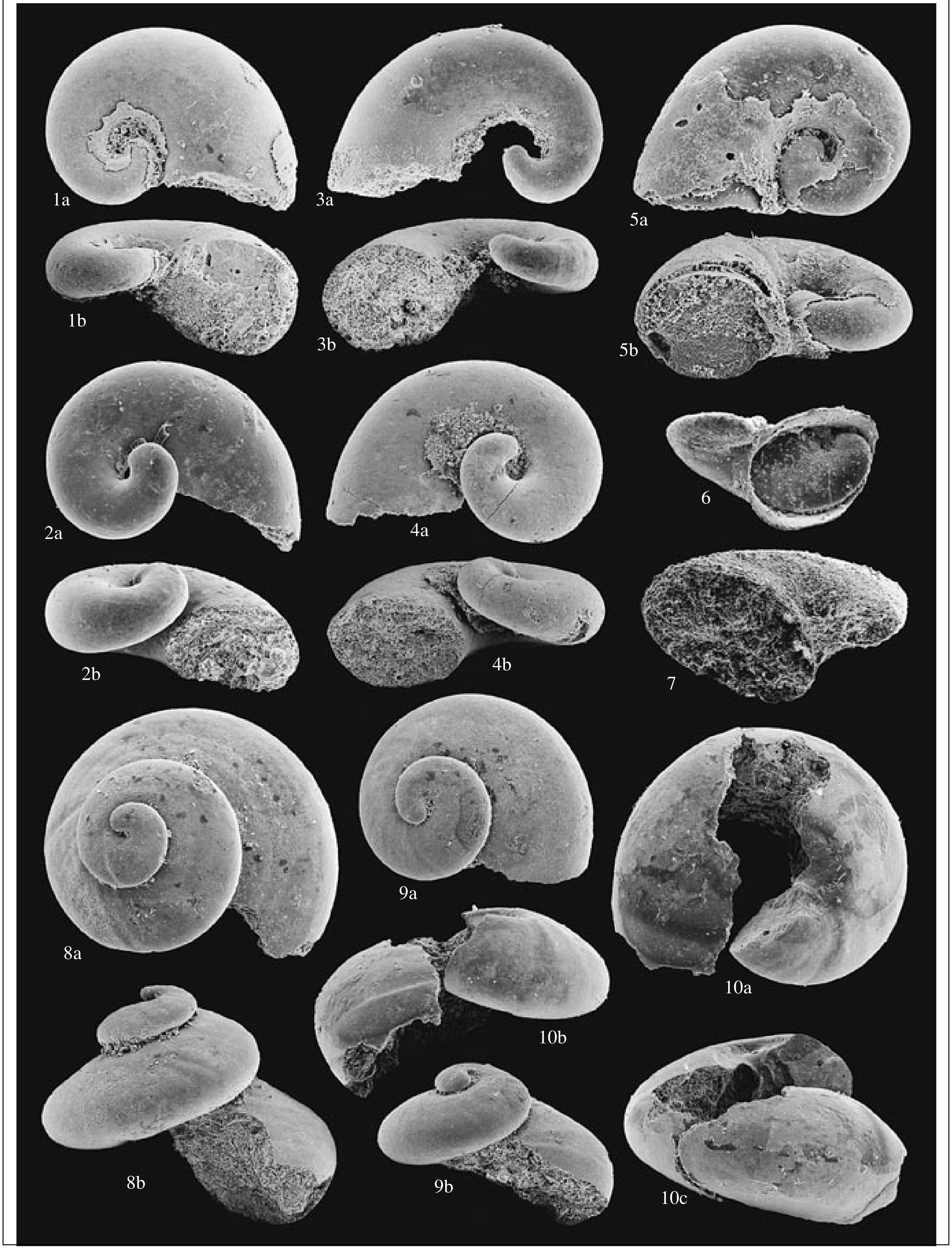
Gastropods are characterized by pronounced anatomical asymmetry (Palmer, 1996). In most cases, internal asymmetry of gastropods is accompanied by external asymmetry, since the overwhelming majority of members of the class have a turbospiral shell in which the coiling occurs in more than one plane with a transition along the axis. Due to the asymmetrical structure, gastropods display chirality, i.e., the existence of right and left morphotypes within a taxon. Chiral morphs have been known for a long time in extant and relatively recent extinct gastropods (Vermej, 1975; Hendricks, 2002); however, this phenomenon has remained almost unstudied in the oldest members of the class. However, recent finds in the Lower Cambrian deposits of various regions of the world have revealed chirality even among the earliest gastropods. Discovery of one more feature peculiar to modern gastropods among the Early Cambrian univalved mollusks supports the hypotheses of the Early Cambrian origin of the class Gastropoda (Parkhaev, 2004b, 2005).

SHELL CHIRALITY IN EXTANT GASTROPODS

No more than 10% of modern gastropod species are sinistral, whereas others are dextral forms (Vermej, 1975; Asami, 2001). The sinistrality as a normal, nonaberrant, condition can be typical of taxa of different hierarchical levels, i.e., from species to family. For instance, all members of some families, such as marine Triphoridae and Limacinidae, freshwater Physidae and Bulinidae, and terrestrial Clausiliidae, have a sinistral shell. Exceptionally, few species or, seldom, genera in these families are dextral (possibly, it is a secondary condition). At the generic level, the following members of typically dextral families have a sinistral shell: *Lanistes* (Pilidae), *Prosipho* (Buccinidae), *Sinistralia* (Fasciolariidae), *Sinistrella* (Turridae), *Thoanteus* (Buliminidae), *Vertilla* (Vertiginidae), *Dyakia* (Ariophantidae), etc. At the species level, a normal, nonaberrant sinistrality occurs even more widely, because some genera with prevailing dextral species include sinistral species. The majority of such genera are pulmonate gastropods. Among 46 families and 889 genera of pulmonate snails, 35 genera include species with both right-handed and left-handed shells (Asami et al., 1998).

It was revealed that chirality of gastropods is coded in a single locus (Boycott et al., 1930; Asami, 2001; Stone and Björklund, 2002); mutation in this locus reverses the direction of shell coiling. Possibly, the probability of fixation of such a mutation is higher among mollusks with internal fertilization, such as Pulmonata, than in marine taxa with external fertilization, as the former have pronounced sexual selection (Stone and Björklund, 2002) because successful copulation is possible within a chirally uniform pair, whereas copulation of oppositely coiling animals is difficult or even impossible (Asami, 2001; Davison et al., 2005). It has been proposed that, because of this, a chiral population and, later, a separate species could have appeared. However, the possibility of such sympatric speciation is rather questionable (Aleksandrov and Sergievsky, 1979; Gittenberger, 1988; Johnson et al., 1990; Stone and Björklund, 2002; Anistratenko, 2004; Davison et al., 2005).

Plate 1



In addition to sinistral species that normally have a left-handed shell, aberrant sinistral forms occur among normally dextral species.

Here is a far from complete list of modern gastropod families with reported chiral aberrant specimens: Turbinidae, Naticidae, Viviparidae, Pilidae, Diplomatinidae, Triviidae, Cypraeidae, Muricidae, Buccinidae, Nassariidae, Columbellidae, Melongenidae, Turbinellidae, Fasciolariidae, Olividae, Mitridae, Marginellidae, Volutidae, Conidae, Terebridae, Turridae, Architectonicidae, Lymnaeidae, Acavidae, Achatinidae, Clausiliidae, Ariophantidae, Bradybaenidae, Bulimulidae, Spiraxidae, Ceriidae, Camaenidae, Megalobulimidae, Discidae, Helicarionidae, Polygyridae, Zonitidae, and Helicidae. As is evident from the list, this anomaly occurs in terrestrial and freshwater pulmonates (16 of 38 families listed) and in marine gastropods (22 of 38 families). This possibly results from the fact that the probability of mutation in the locus determining the chirality does not depend on the mollusk's habits.

Chiral aberrants are rare in almost all species, with the exception of several pulmonate genera, which include species with almost equal proportions of dextral and sinistral populations (e.g., genus *Achatinella*, family Achatinellidae; genus *Partula*, family Partulidae; and genus *Amphidromus*, family Camaenidae).

It is noteworthy that a chirally aberrant shell is not a mirror image of a normal shell, but is distorted to some extent. The rate of whorl transition along the shell axis is usually higher in aberrant forms, giving the shell a more slender appearance. It was suggested that the distorted shell shape in chiral aberrants is cased by a conflict between the gene determining the direction of chirality and genes determining normal shell growth (Asami, 2001).

SHELL CHIRALITY IN CAMBRIAN GASTROPODS

The pronounced asymmetry of the shell is typical for the following families of Cambrian gastropods: Coreospiridae, Aldanellidae, Pelagiellidae, Khairkhaniidae, and Onychochilidae (Parkhaev, 2002, 2005). Members of the family Onychochilidae always have a sinistral (possibly hyperstrophic) shell (Parkhaev, 2001b, pl. 43, figs. 10–16; 2005, p. 77, pl. 9, figs. 9, 10). No taxa with a dextral shell, or dextral aberrant specimens, are known for Cambrian Onychochilidae. The other four families of Cambrian gastropods include members with both dextral and sinistral shells.

The family Coreospiridae, usually characterized by a planispiral shell, includes species with a left or right shift in the shell spire. For instance, in *Latouchella korobkovi* (Vostokova, 1962), the chirality is not yet fixed by natural selection (Parkhaev, 2001a), so we see planisipiral, slightly sinistral or slightly dextral specimens of this species. Such variability, accompanied by changeable ornamentation of the shell, results in the establishment of separate genera and species in cases when the fossil material is studied based on small samples of specimens. However, the analysis of representative samples reveals an extremely wide range of morphological variability in *L. korobkovi*, and suggests its synonymy with many taxa established later, e.g., *Archaeospira ornata* Yu, 1979, *Yangtzespira exima* Yu, 1979, *Hunaglingella polycostata* Chen, Chen et Zhang, 1981, *Gibbaspira acutumbonalis* He, 1984, *Uncinaspira pristina* He, 1984, etc. (Demidenko and Parkhaev, 2006). Possibly, the only valid taxon among the forms similar to *L. korobkovi* is *Pseudoyangtzespira selindeica* Bokova, 1990, because almost all specimens from the type locality (Bokova, 1990, p. 123, text-fig. 1) are characterized by faint but stable dextral asymmetry of the shell (Parkhaev, 2005, pl. 4, fig. 1).

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Explanation of Plate 1

Shell chirality in Cambrian gastropods: chiral twin species (Figs. 1, 2 and Figs. 3, 4), sinistral chiral aberrations (Fig. 7 and Fig. 10) of normally dextral species (Fig. 6 and Figs. 8, 9, respectively).

Figs. 1 and 2. *Philoxenella spirallis* Vostokova, 1962; Siberian Platform, Lower Cambrian, Tommotian Stage; internal molds: (1) specimen PIN, no. 5083/0639, ×28: (1a) spire view, (1b) oblique apertural view; Uchuro-Maiskii District, Selinde River; (2) specimen PIN, no. 5083/0018, ×48: (2a) spire view, (2b) oblique apertural view; western Anabar Region, Rassokha River.

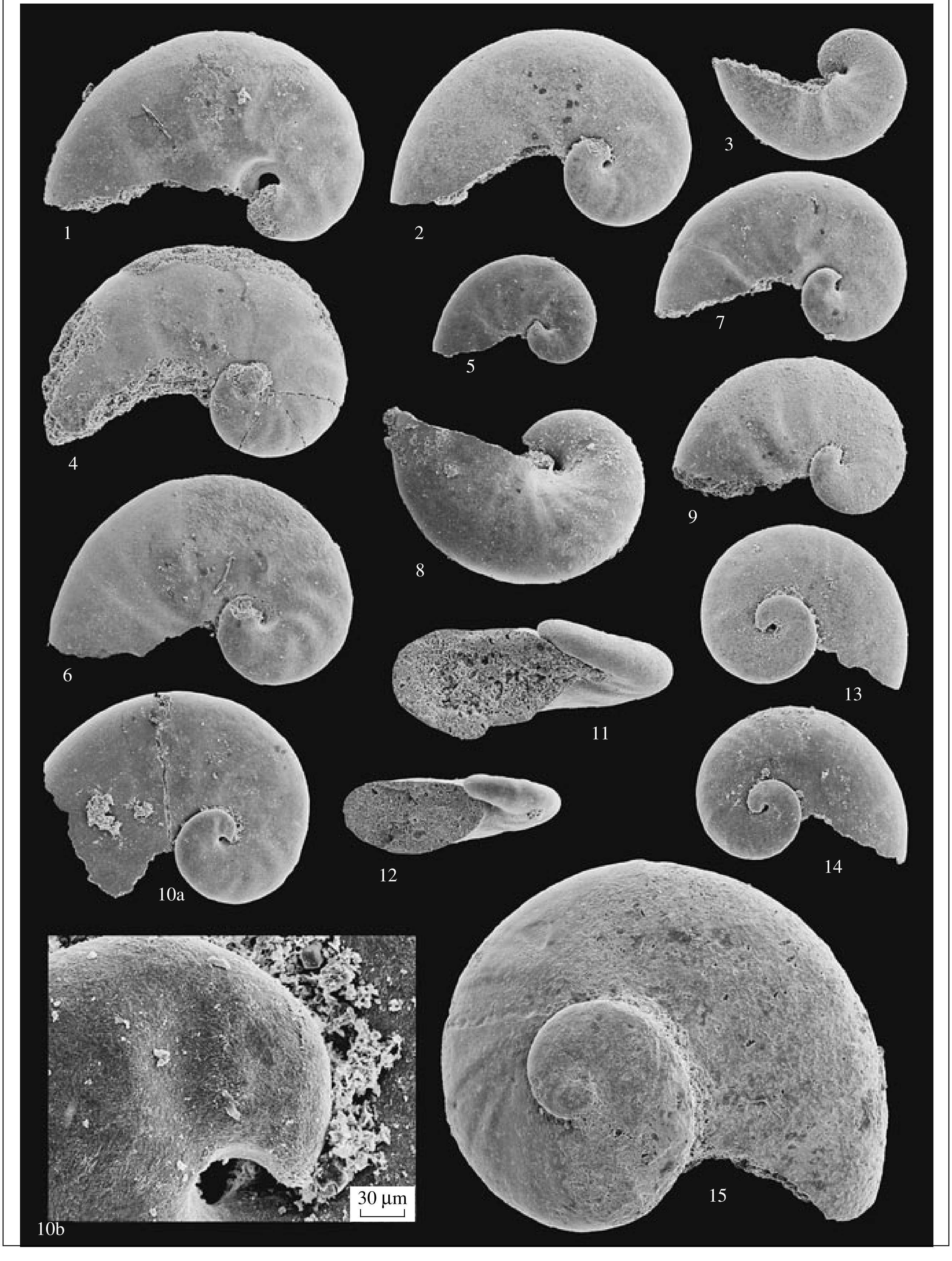
Figs. 3 and 4. *Barskovia hemisymmetrica* Golubev, 1976; Siberian Platform, Lower Cambrian, Tommotian Stage; internal molds, ×43: (3) specimen PIN, no. 5083/0132: (3a) spire view, (3b) oblique apertural view; western Anabar Region, Rassokha River; (4) specimen PIN, no. 5083/0475: (4a) spire view, (4b) oblique apertural view; Uchuro-Maiskii District, Selinde River.

Fig. 5. *Khairkhania rotata* Missarzhevsky, 1981; Siberian Platform, western Anabar Region, Rassokha River; Lower Cambrian, Tommotian Stage; specimen PIN, no. 5083/0153, internal mold with shell fragments, ×53: (5a) left view, (5b) oblique view from the aperture.

Figs. 6 and 7. *Pelagiella adunca* Missarzhevsky in Rozanov et Missarzhevsky, 1966; eastern Transbaikalia, village of Georgievka, Uslon Section; Lower Cambrian, upper part of the Atdabanian Stage, ×51: (6) specimen PIN, no. 2019/1018, shell viewed from the aperture; (7) specimen PIN, no. 2019/1116, internal mold.

Figs. 8–10. *Aldanella utchurica* Missarzhevsky in Rozanov et al., 1969; Siberian Platform, Uchuro-Maiskii District, Maimakan River, Khotu-Oldondo Creek; Lower Cambrian, Tommotian Stage; internal molds, ×30: (8) specimen PIN, no. 5083/0463: (8a) spire view, (8b) oblique apertural view; (9) specimen PIN, no. 5083/0464: (9a) spire view, (9b) oblique apertural view; (10) specimen PIN, no. 5083/0462: (10a) spire view, (10b) oblique apertural view; (10c) oblique view from the palatal wall of the last whorl.

Plate 2



Explanation of Plate 2

All figured specimens come from the lower part of the Medvezh'ya Formation, Lower Cambrian, Tommotian Stage, *N. sunnaginicus* Zone of the right bank of Kotui River (1 km above the mouth of the Ary-Mas-Yuryakh Creek), western Anabar Region, Siberian Platform (specimens in Figs. 1–14 are from rock sample no. BiS-85-IV/11-II-a, specimen in Fig. 15 is from rock sample no. BiS-85-IV/11-II-b; magnification is ×31, except Fig. 10b).

Figs. 1–12. *Aldanella golubevi* sp. nov.: (1) specimen PIN, no. 4386/1501, internal mold viewed from the spire; (2) specimen PIN, no. 4386/1504, internal mold viewed from the spire; (3) specimen PIN, no. 4386/1526, internal mold viewed from the base; (4) specimen PIN, no. 4386/1515, internal mold viewed from the spire; (5) specimen PIN, no. 4386/1524, internal mold of immature specimen viewed from the spire; (6) specimen PIN, no. 4386/1508, internal mold viewed from the spire; (7) holotype PIN, no. 4386/1523, internal mold viewed from the spire; (8) specimen PIN, no. 4386/1527, internal mold viewed from the base; (9) specimen PIN, no. 4386/1537, internal mold viewed from the spire; (10) specimen PIN, no. 4386/1513, internal mold viewed from the spire: (10a) general view, (10b) fragment of the apical part of the mold; (11) specimen PIN, no. 4386/1520, internal mold viewed from the aperture; (12) specimen PIN, no. 4386/1525, internal mold viewed from the aperture.

Figs. 13–15. *Aldanella crassa* Missarzhevsky, 1969; (13) specimen PIN, no. 4386/1516, internal mold viewed from the spire; (14) specimen PIN, no. 4386/1512, internal mold viewed from the spire; (15) specimen PIN, no. 5083/0446, internal mold of adult specimen viewed from the spire.

The shell of the family Pelagiellidae acquired a more asymmetrical appearance compared with the Coreospiridae (Parkhaev, 2001a, text-fig. 3). All pelagiellids genera and species are characterized by an exceptionally dextral shell. The find of sinistral *Pelagiella* (Parkhaev, 2004a, pl. 2, fig. 12) undoubtedly represents a chiral aberration of the normally dextral species *Pelagiella adunca* Missarzhevsky in Rozanov et Missarzhevsky, 1966, as it is a single sinistral specimen (Pl. 1, fig. 7) among hundreds of dextral shells known for this species (Pl. 1, fig. 6).

The genus *Khairkhania* Missarzhevsky, 1981, with a planispiral shell, is the type species of the family Khairkhaniidae. Along with other planispiral genera, the family includes (Parkhaev, 2002, 2005) the dextral genus *Philoxenella* Vostokova, 1962 and the sinistral genus *Barskovia* Golubev, 1976. The morphology of the type species of these genera, i.e., *Philoxenella spirallis* Vostokova, 1962 and *Barskovia hemisymmetrica* Golubev, 1976, are so similar that they can be considered as chiral twins, distinguished only by the direction of coiling (Pl. 1, figs. 1–4). It is noteworthy that both species have specimens with different extents of asymmetry, varying from slightly asymmetrical (Pl. 1, figs. 1, 3) to distinctly turbospiral shells (Pl. 1, figs. 2, 4). This suggests a close relationship between the two species, which is also supported by a similar microstructure of the shell with identical shell pores (Parkhaev, 2006). Possibly, *P. spirallis* and *B. hemisymmetrica* are extreme forms in the range of variability of a single species; in this case, the central position may be occupied by the planispiral *Khairkhania rotata* Missarzhevsky, 1981 (Pl. 1, fig. 5). To clarify the taxonomic status of these three species, their distribution pattern and possible co-occurrence should be analyzed.

The family Aldanellidae includes two genera (Parkhaev, 2005), i.e., *Aldanella* Vostokova, 1962 and *Nomgoliella* Missarzhevsky, 1981.[1] Until now, the first genus included only dextral species, while the second was characterized by a sinistral shell with loosely coiling whorls.

A sinistral specimen of *Aldanella* was found for the first time by S.N. Golubev in the *N. sunnaginicus* Zone, Tommotian Stage of the southeastern slope of the Anabar Massif. This specimen is a single internal mold of a sinistral shell (Golubev, 1976, pl. 3, fig. 13), which was found among many typical dextral *A. attleborensis* (Shaler et Foerste, 1888). Due to the unique character of the specimen, Golubev (1976, p. 37) determined it as a pathological example of one of the species of the genus *Aldanella*. No other similar specimens were found in any localities of the northern part of the Siberian Platform.

The study of extensive field material from the Lower Cambrian of the Siberian Platform revealed more than twenty specimens of sinistral *Aldanella* in the collection of T.A. Sayutina and M.I. Barskova (collected in 1985). The material comes from the Tommotian Stage (*N. sunnaginicus* Zone) of the Kotui River, western Anabar Region. Sinistral shells come from a single stratigraphic level (rock sample no. BiS-85-IV/11-II-a) from the lower part of the Medvezh'ya Formation of the Ary-Mas-Yuryakh Creek section (1 km above the mouth of the creek).

These aldanellas (Pl. 2, figs. 1–12) are morphologically identical to the sinistral specimen figured by Golubev (1976, pl. 3, fig. 13). The significant number of specimens and their stable morphology repudiate Golubev's assumption about the pathological nature of this form. In this case, we are possibly dealing with a new species of the genus *Aldanella*, or a stable chiral morph of some previously known species, rather than with a chiral aberration.

The rock sample that contained the sinistral shells yielded many specimens of *Aldanella crassa* Missarzhevsky in Rozanov et al., 1969 (Pl. 2, figs. 13, 14). One can assume that the sinistral form is a chiral morph of the dextrally coiled *A. crassa.* Figure 1 displays at the same scale a mirror image of the sinistral form (Fig. 1a) and normal image of *A. crassa* (Fig. 1b).

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[1] The genus *Paraaldanella* Golubev, 1976, previously included in the family as a valid taxon (Parkhaev, 2001b, 2002), should be regarded as a synonym of the genus *Aldanella*, since the morphology of its type species, *P. kotuica* Golubev, 1976, corresponds to the diagnosis of *Aldanella*.

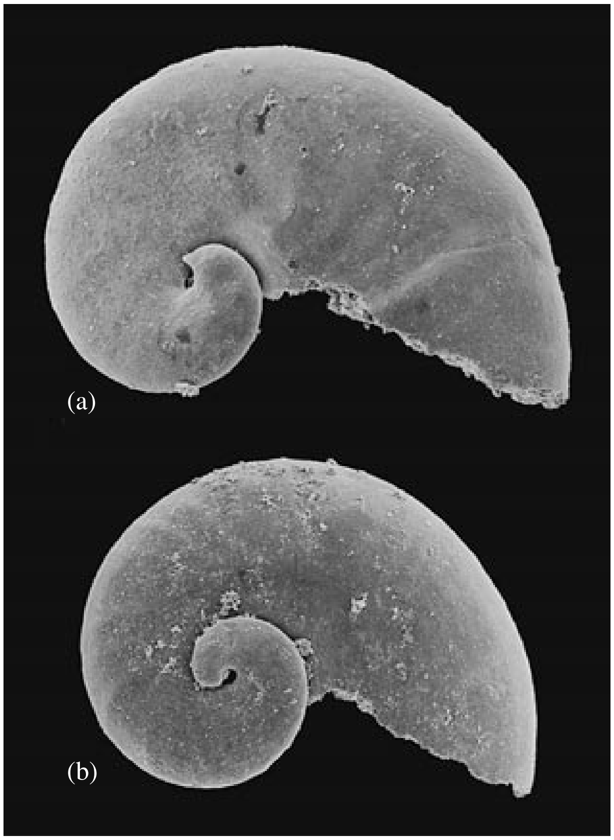

Fig. 1. Members of the genus *Aldanella* Vostokova, 1962 from the lower part of the Medvezh'ya Formation (Lower Cambrian, Tommotian Stage, *N. sunnaginicus* Zone) Ary-Mas-Yuryakh Creek, Kotui River basin, western Anabar Region, Siberian Platform; internal molds, ×48: (a) mirror image of the sinistral species *A. golubevi* sp. nov.; holotype PIN, no. 4386/1523; (b) normal image of dextral species *A. crassa* Missarzhevsky in Rozanov et al., 1969; specimen PIN, no. 4386/1512.

Indeed, both forms are very similar, only the rate of the whorl expansion in *A. crassa* is a little lower than in the sinistral form. Considering the observation that chiral morphs are not mirror images of normal specimens due to the conflicting interaction in the genome (see above), one can suggest that the sinistral *Aldanella* is a chiral variety of *A. crassa.* If this is the case, by analogy with modern gastropods, we expect to find sinistral specimens in all other populations of *A. crassa*, or at least in a large part of them.

However, in the Ary-Mas-Yuryakh Creek section only a single level with sinistral *Aldanella* is found, while *A. crassa* is present at several levels, both above and below the bed with sinistral specimens. Moreover, no sinistral specimens are known from any other numerous localities of *A. crassa* of the Siberian Platform (Rozanov et al., 1969; Missarzhevsky, 1989; Khomentovsky and Karlova, 1989; Vassiljeva, 1998). As was mentioned above, a similar sinistral form in the Golubev's material co-occurs with the other species, *A. attleborensis*, but not with *A. crassa.* Therefore, the sinistral *Aldanella* from the Ary-Mas-Yuryakh Creek section should be assigned to a separate species of this genus that existed during a rather short period in the West and East Anabar regions. This species is described below as *Aldanella golubevi* sp. nov.

The difference in the morphology of the apical part of internal molds of *A. golubevi* sp. nov. and *A. crassa* favors their independent taxonomic status, i.e., *A. golubevi* sp. nov. has a pointed apex (Pl. 2, figs. 7, 10), while the apex of *A. crassa* is evenly rounded (Pl. 2, figs. 13, 14). However, the obvious morphological similarity of the two species (Fig. 1) suggests that *A. golubevi* probably evolved from *A. crassa* by mutation in the locus that determines chirality.

Another sinistral *Aldanella* was found in the lower part of the Tommotian Stage (*N. sunnaginicus–D. regularis* zones) of the Khotu-Oldondo Creek section in the Maimakan River basin (Uchuro-Maiskii District, southern Siberian Platform; collected by M.I. Barskova in 1984). A single sinistral specimen (Pl. 1, fig. 10) was found among dozens of normally dextral internal molds of *A. utchurica* Missarzhevsky in Rozanov et al., 1969 (Pl. 1, figs. 8, 9). The uniqueness of this specimen and its morphology leaves no doubt that we are dealing with a chiral aberration similar to that previously recorded in another species of Cambrian mollusk, *Pelagiella adunca* (Pl. 1, figs. 6, 7).

CONCLUSIONS

Thus, chiral aberrations, i.e., abnormal specimens with an oppositely coiled shell, which occur among modern and fossil gastropods, were already present among the oldest members of the class. As in modern gastropods, the potential for speciation by means of mutation in the locus that determines chirality is also supposed for Cambrian mollusks. In contrast to modern gastropods, the presence of chiral morphs within a single species of Cambrian mollusks has not yet been reported, but it is assumed that chiral twin species may have existed among them.

The collections studied (nos. 2019, 4386, and 5083) are housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

SYSTEMATIC PALEONTOLOGY

CLASS GASTROPODA

SUBCLASS ARCHAEOBRANCHIA

Order Pelagielliformes

Family Aldanellidae Linsley et Kier, 1984

Genus *Aldanella* Vostokova, 1962

Aldanella golubevi Parkhaev, sp. nov.

Plate 2, figs. 1–12

Aldanella sp.: Golubev, 1976, p. 37, pl. 3, fig. 13; Parkhaev, 2005, pl. 8, figs. 12 and 13.

Etymology. In honor of S.N. Golubev, who reported the first sinistral specimen of *Aldanella*.

Holotype. PIN, no. 4386/1523, internal mold; Siberian Platform, western Anabar Region, right bank of the Kotui River, 1 km above the mouth of the Ary-Mas-Yuryakh Creek; Lower Cambrian, Tommotian Stage, *N. sunnaginicus* Zone (Medvezh'ya Formation, lower part).

Description. The shell is sinistral, up to 2 mm in diameter, rather low (height to greatest diameter ratio is about 0.35–0.45), composed of 1.5–1.8 rapidly expanding whorls (ratio of greatest diameter to width of the last whorl is about 1.6–1.7). The spire is flattened, slightly projecting. The aperture is wide and low (width to height ratio is about 1.8–2.0), irregularly egg-shaped, its upper margin is flattened, the basal margin is convex, the columellar margin is narrow, the palatal margin is wide. The umbilicus is very narrow. The external shell ornamentation is unknown. Internal mold is smooth, or often has, on the upper surface and at the base, wide smooth folds which are parallel to the apertural margin. The apical part of the mold is hemispherical, 170–180 μm in diameter, with a pointed initial part (Pl. 2, fig. 10b).

Measurements, in μm:

Specimen PIN, no.	Maximum shell diameter	Minimum shell diameter	Apertural width	Shell height
Holotype 4386/1523	1530	1060	905	–
4386/1501	1970	1345	1315	–
4386/1504	1875	1250	1095	–
4386/1526	1185	845	720	–
4386/1515	1875	1345	1030	–
4386/1524	1000	685	590	–
4386/1508	1845	1310	1030	–
4386/1527	1655	1220	1060	–
4386/1537	1440	970	875	–
4386/1520	1750	–	1250	750
4386/1525	1345	–	845	500

Comparison. The new species differs from all members of the genus in the sinistral shell and the pointed initial part of the apex.

Remarks. Excluding the coiling direction of the shell, *A. golubevi* sp. nov. is very similar in shell shape and form of the aperture to *A. crassa* (Pl. 2, figs. 13–15; Fig. 1b) from the Tommotian Stage of the Siberian Platform, which is possibly the ancestor of *A. golubevi* sp. nov. The new species has rather tightly coiled whorls, excluding assignment to the sinistral aldanellid genus *Nomgoliella* Missarzhevsky, 1981.

Material. Twenty-four internal molds from the type locality.

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