

The Cambrian 'basement' of gastropod evolution

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Abstract: The oldest gastropods are known from the uppermost Nemakit-Daldynian to lowermost Tommotian deposits. However, to trace ancestry before this time, when most metazoans did not possess shells, is difficult. Study of the oldest gastropods, diagnosed and discussed here, sheds some light on the earliest stages of evolution of major gastropod branches. It appears that the subclass Archaeobranchia served as the base for this early radiation.

Gastropods represent the largest class of the phylum Mollusca: different estimates of diversity vary from 80 000 to 150 000 species. Besides such huge species diversity, gastropods are characterized by several, strikingly different body plans, reaching such variability and ecological success over a long evolutionary history, at least 540 million years of the Phanerozoic.

The earliest fossil gastropods are known from the uppermost Nemakit-Daldynian to the lowermost Tommotian deposits (Khomentovsky *et al.* 1990; Parkhaev 2002a; Fig. 1). But tracing the gastropod family tree back in time to and beyond the Precambrian–Cambrian boundary is difficult, especially in times before true skeletons developed. Little, if anything, is known about 'ancestors' or transitional forms linking other molluscs such as the non-torsioned monoplacophorans.

Nevertheless, the study of the oldest fossil gastropods preserved in Cambrian strata is of special interest as it could shed light on the origin of the class and outline the earliest stages of evolution of its major branches. Molluscs have been studied for more than 150 years. The resulting systematics of the Cambrian molluscs is complicated and contradictory with many opposing opinions (for reviews, see Runnegar 1996; Parkhaev 2002a). Fossil gastropods show few of the features used by modern zoologists in their morphological and systematic analyses. Analysis of the shells in palaeontology is the main approach. Such analyses have been carried out repeatedly (Pojeta & Runnegar 1976; Runnegar & Jell 1976; Runnegar 1981; Peel 1991).

In my own studies on early molluscs (Parkhaev 2000, 2001, 2002a, b, 2004) the emphasis was on morphological structures of shells especially from the Cambrian from a functional viewpoint. Features connected with water current circulation patterns inside the shell (grooves, siphons, sinuses, etc.) and the nature of shell musculature arrangement are of a special importance. As a result, details of

internal anatomy of the Cambrian molluscs have been reconstructed, their ecological peculiarities outlined and, finally, this data used for approaching systematics. This paper focuses on the morphological diversity among the Cambrian univalved molluscs (Fig. 1), and suggests that these are the earliest gastropods, giving a synopsis of the main groups of Cambrian gastropods, including diagnostic characters for each taxon and an estimate of the placement of each group on the gastropod evolutionary tree.

Major groups of Cambrian gastropods

Family Helcionellidae Wenz, 1938

Family includes numerous and diverse forms but with a simple morphology. Shell varies from a low conical to high conical structure with central, subcentral or posteriorly shifted apex. Aperture simple, always lacking grooves or deep sinuses. Posterior or anterior shallow notches occur in some advanced genera. The oldest known taxa occur in terminal Precambrian sediments (uppermost Nemakit-Daldynian). Forms with low shell and marginally-placed apex are very similar to monoplacophorans, which are thought to be helcionellid ancestors. Some monoplacophoran genera may be included in this family since their distinction from the most primitive gastropods is still quite obscure, based as it is on shell characters alone, without data on the internal anatomy. A thorough study of protoconch morphology and microstructure could provide useful input to sort out this current taxonomic enigma.

Exemplary genera. *Scenella* Billings, 1872; *Helcionella* Grabau & Shimer, 1909; *Bemella* Missarzhevsky in Rozanov *et al.*, 1969; *Tannuella* Missarzhevsky in Rozanov *et al.*, 1969; *Obtusiconus* Yu, 1979; *Emarginiconus* Yu, 1979; *Securiconus* Jiang, 1980; *Ilsanella* Missarzhevsky, 1981;

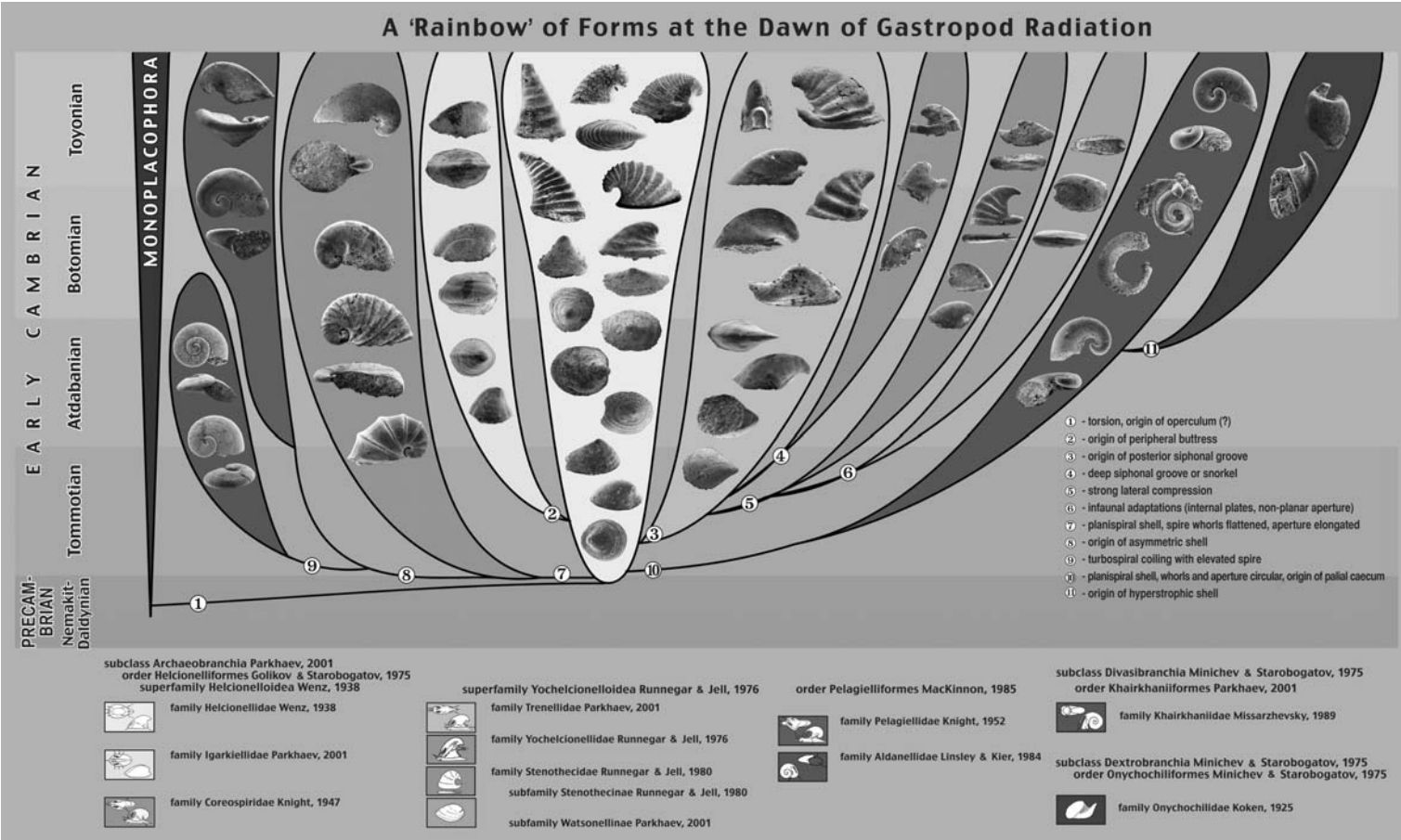


Fig. 1. A 'rainbow' of shell forms at the dawn of gastropod radiation. Numbers in circles indicate the main apomorphies of each group.

Pseudopatella Zhegallo in Esakova & Zhegallo, 1996; *Aequiconus* Parkhaev in Gravestock *et al.*, 2001; *Anuliconus* Parkhaev in Gravestock *et al.*, 2001.

Family Igarkiellidae Parkhaev, 2001

Members of this group have a shell very similar to that of the Helcionellidae in general form. One peculiar, apomorphic feature distinguishes igarkiellids from their helcionellid ancestors. The buttress, running along the anterior field of a cap-like shell from the apex towards the anterior margin of the aperture. The buttress corresponds to a groove on the internal shell surface, which is supposedly a standage, or a water drainage sump in the mantle cavity, which accumulates and expels exhaust water along with excrement from the shell. Earliest members of the family appear in the uppermost Nemakyt-Daldynian. The presence of the peripheral buttress, and hence a similar water circulation pattern, suggests that igarkiellids may be ancestral to Palaeozoic bellerophonitids, but this assumption is still not fully supported by fossils from the Middle–Upper Cambrian interval.

Exemplary genera. *Protoconus* Yu, 1979; *Gonamella* Valkov & Karlova, 1984; *Igarkiella* Vassiljeva, 1998.

Family Coreospiridae Knight, 1947

Family includes genera with planispirally coiled shells. Earliest members occur in sediments of the latest Nemakyt-Daldynian age. Family is likely to be derived from helcionellid ancestors, which include some forms with strongly hooked apices, and hence intermediate between typical cap-shaped helcionellids and coiled coreospirids. A slight deviation from the symmetrical planispiral coiling is noteworthy. Such an initial dextrality or sinistrality of shell, which can simultaneously occur within the same genus and even species (along with normal, bilaterally symmetric specimens) corresponds to the primitive state of coiling, when the advantage of the dextral or sinistral asymmetry of body is not genetically fixed by selection among the most ancient forms (Minichev & Starobogatov 1979).

Main genera included. *Coreospira* Saito, 1936; *Latouchella* Cobbold, 1921; *Oelandiella* Vostokova, 1962; *Cambrospira* Yu, 1979; *Tichkaella* Geyer, 1986; *Kutanjia* Kruse, 1991.

Family Trenellidae Parkhaev, 2001

Members of family characterized by a shell with a parietal train with a groove located on posterior margin of aperture. Groove is supposed to facilitate

water intake. This apomorphic character first appears in gastropods of Early Tommotian age suggesting an origin from helcionellids. Further development of this intake structure takes place in the family, Yochelcionellidae.

Exemplary genera. *Oelandia* Westergård, 1936; *Prosinuites* Poulsen, 1967; *Xianfengella* He & Yang, 1982; *Parailsanella* Zhegallo in Voronina *et al.*, 1987; *Mackinnonia* Runnegar in Bengtson *et al.*, 1990; *Trenella* Parkhaev, 2001.

Family Yochelcionellidae

Runnegar & Jell, 1976

Members of this family have the most striking shell morphology among Cambrian molluscs. Its diagnostic feature is a tubular projection on the posterior shell surface. This siphon (called 'snorkel' after the similarity with a breathing tube) is supposedly homologous with the parietal groove of the trenellids. The transitional condition from the groove to snorkel is present among species in the genus *Eotebena*, which have very deep grooves with merging lower edges but remain divided by a narrow slit. The oldest yochelcionellids appear during the Early Tommotian, but the acme of the family is Botomian to Middle Cambrian.

Genera included. *Yochelcionella* Runnegar & Pojeta, 1974; *Eotebenna* Runnegar & Jell, 1976; *?Enigmaconus* MacKinnon, 1985; *Runnegarella* Parkhaev, 2002.

Family Stenothecidae

Runnegar & Jell, 1980

The family representatives have trenellid-like shell, but are characterized by strong lateral compression. The oldest members of the family are known from the uppermost Nemakyt-Daldynian and Early Tommotian, but the family was most diverse beginning in the late Atdabanian–Botomian. Strong lateral compression of the shell is supposedly an adaptation to new types of habitats occupied by stenothecids, i.e. dense algal fields (subfamily Stenothecinae) or associated with soft-sediments (subfamily Watsonellinae). In addition to lateral compression, adaptation for infaunal living was accompanied by increasing of curvature of the aperture and the origin of internal plates for attachment of strong pedal musculature (in genera *Eurekapegma* and *Watsonella*).

Exemplary genera. *Stenotheca* Salter in Hicks, 1872; *Watsonella* Grabau, 1900; *Anabarella* Vostokova, 1962; *Mellopegma* Runnegar & Jell, 1976; *Eurekapegma* MacKinnon, 1985.

Family Pelagiellidae Knight, 1952

This family is characterized by turbospiral, dextrally coiled shells with a somewhat triangular aperture. The basal angulation of the aperture is thought to be a water intake area, and hence homologous with the posterior train of coreospirids, thought to be pelagiellid ancestors. The oldest members of the family appear in the earliest Atdabanian. The Late Atdabanian–Toyonian through to the Middle Cambrian is the acme of the family.

Genera included. *Pelagiella* Matthew, 1895; *Costipelagiella* Horny, 1964; *Tannuspira* Missarzhevsky, 1989.

Family Aldanellidae Linsley & Kier, 1984

Members of the family have turbospiral, most are dextrally coiled with a protruding spire and an elliptical aperture. Morphologically, members of this family can be derived from the pelagiellids, with further development of shell asymmetry resulting in spire protrusion. However, the oldest aldanellids appear in sediments of the basal Tommotian, an interval which still has undescribed pelagiellids. So, the independent origin of the aldanellids from the coreospirids is also possible.

Genera included. *Aldanella* Vostokova, 1962; *Nomgoliella* Missarzhevsky, 1981.

Family Khairkhaniidae Missarzhevsky, 1989

Family is characterized by spirally coiled shell. The planispiral shells, along with slightly dextral or sinistral forms, are included in the family. In contrast to the coreospirids which are characterized by an elongated cross-section of the whorls, khairkhaniids have almost circular cross-section. Thus, the family represents another offspring of the helcionellids, which first appeared in the uppermost Nemakyt–Daldynian, and evidently independently developed a spirally coiled shell. The coiling of a relatively narrow tube in a tight spiral was accompanied by deep transformations inside the palial cavity, resulted in origin of palial caecum (Parkhaev 2002a, fig. 4).

Exemplary genera. *Philoxenella* Vostokova, 1962; *Michniakia* Missarzhevsky, 1966; *Protowenella* Runnegar & Jell, 1976; *Barskovia* Golubev, 1976; *Khairkhania* Missarzhevsky, 1981; *Xinjispira* Yu & Rong, 1987; *Arrossania* Runnegar in Bengtson *et al.*, 1990.

Family Onychochilidae Koken, 1925

Most members of the family are Early Palaeozoic taxa with hyperstrophic shells, but a few forms

from the Earliest Cambrian also belong in this group. Onychochilids are Early Cambrian molluscs that do not belong to the subclass Archaeobranchia, but have been assigned to the Dextrobranchia. Members of the subclass are characterized by a hyperstrophic turbospiral shell, a palial cavity with a palial caecum, which retains only the right part of the palial complex (Starobogatov 1976). Perhaps the khairkhaniids gave rise to the onychochilids. The gradual transition from the nearly planispiral Khairkhaniidae to the hyperstrophic Onychochilidae is clearly visible within the *Protowenella*–*Xinjispira*–*Beshtashella* the lineage.

Exemplary Genera. Besides numerous Early Palaeozoic genera, a single genus occurs in the Early Cambrian, i.e. *Beshtashella* Missarzhevsky in Missarzhevsky & Mambetov, 1981 [= *Yuwenia* Runnegar, 1981].

Discussion

Gastropods appeared in the latest Precambrian (Nemakyt–Daldynian)–Earliest Cambrian (Tommotian). At that time the subclass Archaeobranchia had already formed. It seems to be a monophyletic group including eight families arranged in two orders (see Parkhaev 2001 for further references) (Fig. 1). This subclass was the most diverse in the Cambrian, surviving into the Ordovician (Gubanov & Peel 2001). The most primitive members had a simple, cap-shaped shell with a central or sub-central apex and an apertural margin lacking notches. Two major morphogenetic trends occurred in the archaeobranchian radiation. The first was development of structures which increased water circulation efficiency (special sinuses, grooves, buttresses, and tubes facilitating uptake and/or expulsion of water). A second trend was the development of a spirally coiled shell. Possibly, such developments were not unique, and originated in at least two separate lineages (coreospirids and khairkhaniids). The most advanced coiled archaeobranchians developed an asymmetrical, turbospiral shell (pelagiellids and aldanellids).

The high level systematics and phylogenetic interpretations of gastropod taxa are far from agreed upon (Golikov & Starobogatov 1988; Haszprunar 1988; Ponder & Lindberg 1997, etc.), because most major taxa represent crown-groups of different stems with rather advanced characters, which are difficult to trace through the lengthy record of gastropods and combine into some uniform phylogenetic sequence. It is possible to link at least some major stems by using the oldest and most primitive gastropod group, archaeobranchians, as a reference point. Certainly, it is a very difficult task, since our knowledge on the Cambrian molluscs is far from complete.

Moreover, there is a considerable gap in the fossil record between Cambrian and Ordovician molluscs, most of which already resemble typical modern gastropods and fit within commonly accepted groups more firmly, than the Cambrian univalves do. However, the first attempt to connect archaeobranchians with the recent high-level groups gives some hope for success.

Gastropod systematics for the Russian record was introduced in 1975 by A. N. Golikov and Y. I. Starobogatov, and later improved and amended in a series of subsequent publications (Starobogatov 1976; Minichev & Starobogatov 1979; Golikov & Starobogatov 1988) and their taxonomy works for fossil gastropods. Incorporating a variety of anatomical features, their systematic scheme is based on the general plan of palial complex organization. In contrast to radular type, ctenidian structure and peculiarities of the nervous and digestive systems (features which are extremely important for systematics of recent forms, but inapplicable for fossils), the general organization of the palial complex can be reconstructed using shell morphology. This approach generally allows the definition of eight extant subclasses, and it is possible to trace these groups from the Cambrian archaeobranchians to some modern groups (Fig. 2).

Possibly, the internally asymmetrical forms (Parkhaev 2000; Fig. 3) with turbospiral shell from the order Pelagielliformes gave rise to members of the subclass Scutibranchia, which, in turn, led to the earliest pectinibranchians with a reduced right side of the palial complex. The

position of bellerophonts is of especial interest with respect to the origin of Scutibranchia. Golikov & Starobogatov (1988) included them as a root of, and the most primitive order in, the subclass Scutibranchia, due to the presence of an exhalant anteromedian slit making them intermediate between the pectinibranchians and the Archaeobranchia (Fig. 3).

But the shell slit is present in many different taxa of recent gastropods, where it is considered as convergent and hence the 'shell slit, used alone, is of little phylogenetic importance' (Haszprunar 1988, p. 372). It is better to exclude the order Bellerophontiformes from Scutibranchia, and place it in the subclass Archaeobranchia due to planispiral shell coiling of the bellerophonts (Fig. 2). The bellerophonts can be derived from the family Igarikiellidae, which possesses peripheral buttresses.

Another extant subclass, Dextrobranchia, is supposed to have originated from the family Khairkhanidae. In Golikov's & Starobogatov's system (Starobogatov 1976), this subclass originates supposedly from the Divasibranchia, which is characterized by having two veins connected by a single auricle. The origin of this state is thought to be a result of the merging of two auricles in primitive ancestor into one (Golikov & Starobogatov 1988). That transformation from a wide conical shell to a shell shaped as a spirally coiled narrow tube likely facilitated the development of ctenida. Hence, it could have facilitated the merging of auricles. Such transformation of the shell also occurs in the lineage leading from the Helcionellidae to the

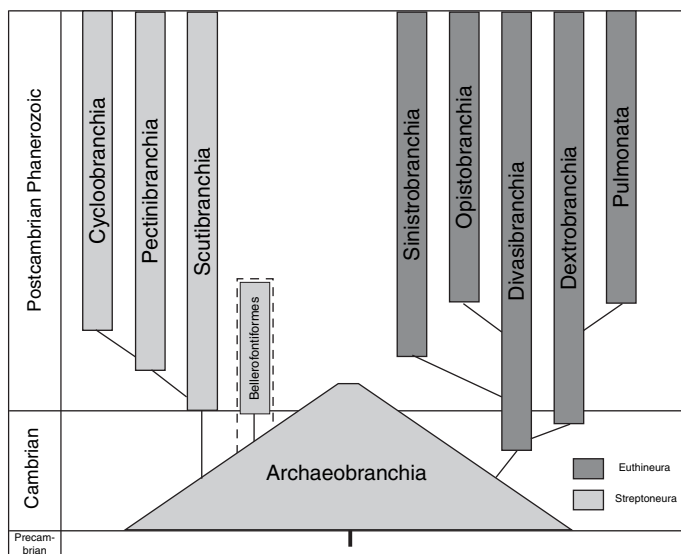


Fig. 2. Supposed phylogenetic relationships of gastropod subclasses.

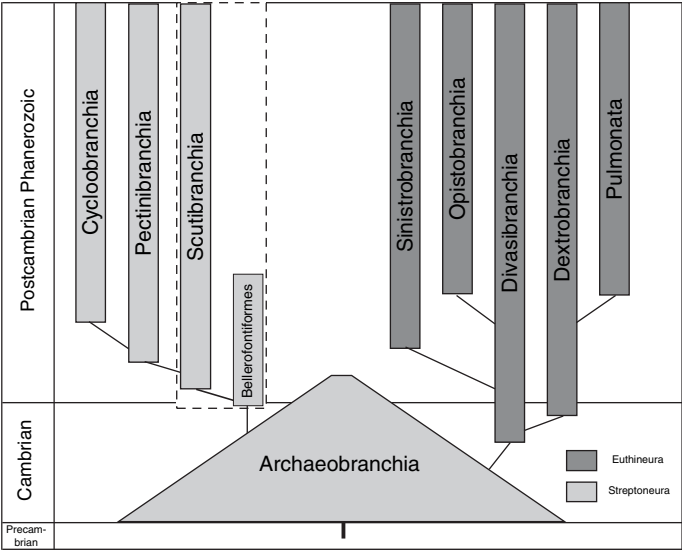


Fig. 3. Supposed phylogenetic relationships of gastropod subclasses. Note the position of bellerophonts between the Archaeobanchia and Scutibranchia, at the base of the latter subclass (compare with Fig. 2).

Khairkhaniidae (Parkhaev 2002a; Fig. 4), so the later family likely represents the state with a single auricle, and consequently falls within the diagnosis of the subclass Divasibranchia.

Archaeobanchians can be connected with representatives of four extant subclasses, the Scutibranchia, Pectinibranchia, Divasibranchia

and Dextrobranchia. Three other euthyneuran subclasses (Sinistrobranchia, Opisthobranchia and Pulmonata) are later offshoots of the Divasibranchia and the Dextrobranchia (see Golikov & Starobogatov 1988; Fig. 2). The sole recent subclass without certain relationships with Cambrian archaeobanchians is the Cyclobranchia

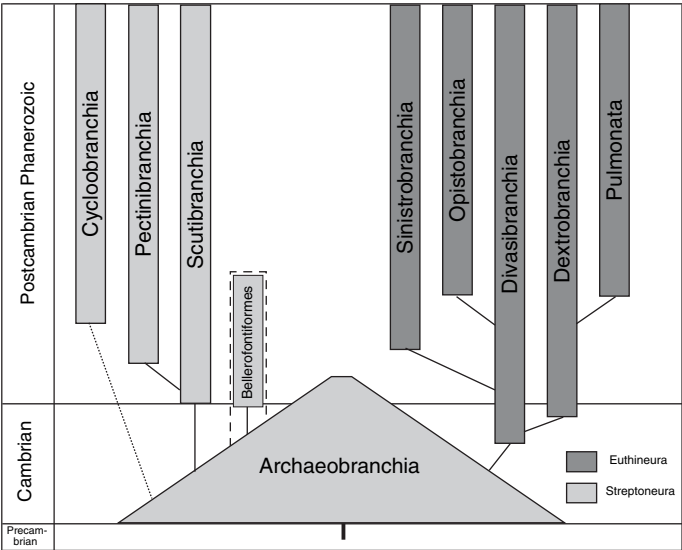


Fig. 4. Supposed phylogenetic relationships of gastropod subclasses. Note the branching of Cyclobranchia from archaeobanchian ancestors, but not pectinibranchians (compare with Fig. 2).

[=Patellogastropoda, Docoglossa]. It is paradoxical that in most studies this group is considered the most primitive, and usually serves as a base of radiation for all other taxa (Golikov & Starobogatov 1975, 1988; Lindberg 1988; Haszprunar 1988; Ponder & Lindberg 1997). There are two theories concerning the evolutionary position of the cyclobranchians. The first is that they are derived from primitive pectinibranchians with coiled shells and have since reduced the right side of palial complex (Fig. 2). If this is the case, the limpet shell is advanced or apomorphic with respect to the pectinibranchians. The second theory is that there is a direct link between cyclobranchians and archaeobranchians (Fig. 4). In this case, the limpet shell is a primitive or plesiomorphic character held over from the Cambrian cap-like ancestors. It is difficult to understand the reasons for the loss of the right part of the palial complex on the pectinibranchians. Probably, further fieldwork and study of Cambrian gastropods, especially concerning their protoconch morphology and shell microstructure will help clarify the taxonomic position of limpets within the gastropods.

Based on Golikov & Starobogatov's studies (1975, 1988) combined with data from Cambrian univalved molluscs, yields the phylogenetic tree shown in Figure 2. The subclass Archaeobranchia in this scheme is considered as basement for radiation of the entire gastropod class.

The study was supported by the Russian Foundation for Basic Researches (project 03-04-48367), The Grants of President of the Russian Federation for Support of Young Russian Scientists and Leading Scientific Schools (projects nos. NSh-974.2003.5 and MK-723.2004.4), and academician programme 'Evolution of the Biosphere'. Thanks to reviewers C. Tassell and A. Braun for comments on the manuscript.

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