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Phylogenesis and the System of the Cambrian Univalved Mollusks

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Abstract—The history of the study and the development of ideas about the systematic position of the Cambrian univalved mollusks is reviewed. On the basis of the functional morphology of shells (Parkhaev, 2000a, 2001a), the phylogenetic scenario of the evolution of the group is reconstructed and its systematics is determined. Several new taxa are described, i.e., Archaeobranchia subclas. nov., Khairkhaniiformes ordo nov., Igarkiellidae fam. nov., Trenellidae fam. nov., Watsonellinae subfam. nov., and *Runnegarella* gen. nov.

HISTORY OF THE STUDY OF THE CAMBRIAN UNIVALVED MOLLUSKS

The first mollusks from the Cambrian deposits were described in the mid-19th century by Hall and d'Orbigny. In the second half of the 19th century, the number of taxa of the Cambrian mollusks significantly increased due to the numerous publications focused on the fauna of that geological period (Barrande, 1867; Billings, 1872; Shaler and Foerste, 1888; Tate, 1892; Matthew, 1895, 1899). The authors put the described species and genera within already existing families and orders of gastropods: the cap-shaped forms were grouped together with patelloids, and the spirally coiled ones were grouped together with trochids or other primitive gastropods. Such an approach to the systematic position of the Cambrian mollusks dominated even later, in the first half of the 20th century, in the works of Cobbold (Cobbold, 1921, 1935; Cobbold and Pocock, 1934), Kobayashi (1933, 1935, 1937, 1939), and other malacologists.

In the mid-20th century, Odhner (Odhner in Wenz, 1940) introduced the term Monoplacophora; later, Wenz (Wenz in Knight, 1952) used this name for the order of cap-shaped Paleozoic gastropods. At the beginning of the 1950s, deep-sea dredging in the Atlantic Ocean discovered live monoplacophorans. In 1957, Lemche (1957) used the term Monoplacophora as a class name. In the molluskan volume of "Treatise on Invertebrate Paleontology," Knight and Yochelson also raised the Monoplacophora to the rank of class and included all the known Cambrian mollusks with cap-shaped shells in this taxon (Knight and Yochelson, 1960).

Since the mid-1960s, a new period of the study of the Cambrian fauna has begun. At the Geological Institute (Moscow), a laboratory for the mass chemical extraction of organic remains from the Lower Cambrian rocks was organized. It was discovered that deposits of this age contain a rich assemblage of small shelly fossils (SSF), including numerous mollusks. This new method of fossil preparation resulted in an increased number of publications on the Cambrian fauna and, therefore, in an increased number of described taxa of small shelly fossils (including mollusks).

The number of specialists that studied the Cambrian mollusks also increased, and different, in some cases even contradictory, opinions on the systematics of this group appeared.

Missarzhevsky (Missarzhevsky and Rozanov, 1966; Rozanov *et al.*, 1969; Missarzhevsky and Mambetov, 1981; Missarzhevsky, 1981, 1989) supported this view, which had become classic since the works of Wenz and Knight. He placed all cap-shaped *Helcionella*-like forms into the class of monoplacophorans, while those spirally coiled, like *Pelagiella* or *Aldanella*, were assigned to gastropods. In one of his last monographs, Missarzhevsky (1989) suggested the establishment of a conventional group of the ordinal rank for the helcionelloideans and to name it Eomonoplacophora. He justified the separation of this group from typical monoplacophoran mollusks by the absence of multiple muscle scars on the interior surface of the shell.

In the early 1970s, Runnegar, Jell, and Pojeta described the rich molluskan assemblage from the lower Middle Cambrian of Australia (New South Wales, Coonigan Formation). The excellent preservation of the material from this locality (silicified shells) and its diversity gave the opportunity to study the functional morphology of mollusks and make assumptions on their ecology and systematic position. The authors proposed to place the cap-shaped helcionelloid mollusks among monoplacophorans. This proposal was based on the interpretation of the first finds of an astonishing mollusk, *Yochelcionella*, which possessed a tubular structure (snorkel) on the subapical part of the shell. The authors believed that the snorkel took the anterior position and was used for water input inside the palial cavity. Having such a position of the snorkel, the shell appears to be exogastrically coiled, and this corresponds with the monoplacophoran diagnosis. This reconstruction of the general morphology of helcionellids was used as a base for the phylogenetic scheme that was proposed by the authors (Runnegar and Pojeta, 1974, 1985; Runnegar and Jell, 1976, 1980; Pojeta and Runnegar, 1976, 1985; Runnegar, 1981, 1983, 1985).

Another opinion on the systematic position of the Cambrian mollusks was expressed by Yochelson. Several taxa were completely removed from the Mollusca; he considered spirally coiled *Aldanella* to be the tubes of worms (Yochelson, 1978; Bockelie and Yochelson, 1979) and cap-shaped wide shells, such as *Scenella* or *Palaeacmaea*, to be imprints of cnidarian medusoid organisms (Yochelson and Gil Cid, 1984; Webers and Yochelson, 1999). The morphology of *Yochelcionella* was also interpreted in a different way. Yochelson believed these mollusks to be endogastric and untorted with a posterior exhalant snorkel. In a similar way, i.e., with the posteriorly directed apex, all the other helcionelloid shells were reconstructed. Thus, Yochelson was the first to suggest a separate taxonomical position for the helcionelloids. In addition, he proposed a rather unconventional treatment of the *Pelagiella* systematic position. He regarded this form to be an asymmetric, endogastric but untorted mollusk and, therefore, to be removed from both Gastropoda and Monoplacophora and placed into a special group (Yochelson, 1978). A similar conclusion was later reached by Runnegar (1981), who proposed the consideration of *Pelagiella* as an intermediate form between Monoplacophora and Gastropoda that already evolved the asymmetric shell but failed to complete torsion.

Linsley and Kier (1984) studied the morphology of the Paleozoic hyperstrophic shells from the functional aspect and came to the conclusion that those forms experienced no torsion. Thus, they had to remove several Paleozoic taxa from the class Gastropoda, including the Cambrian Onychochilidae, Pelagiellidae, and Aldanellidae, and establish for them a new class, Paragastropoda.

Peel developed on Yochelson's view in his works on the functional morphology, evolution, and systematics of the Early Paleozoic univalved mollusks (Peel and Yochelson, 1987; Peel, 1991). He showed that the gross morphology of helcionelloid mollusks is that of the endogastric but untorted organisms and separated them into a new class, Helcionelloida.

Geyer also came to similar conclusions on the systematic position of the helcionelloids (Geyer, 1986, 1994). In addition, he reconstructed the pelagiellids to be exogastric, untorted mollusks and put them into the class Amphigastropoda Simroth in Wenz, 1940 (=Galeroconcha Salvini-Plaven, 1980, =Tergomya Peel, 1991) along with the bellerophontids and classic monoplacophorans, triblidiids.

Since the late 1960s to the early 1970s, Russian malacologists have started the taxonomic study of the higher gastropod taxa and the entire phylum Mollusca as well (Starobogatov, 1970, 1976, 1977; Golikov and Starobogatov, 1975; Minichev and Starobogatov, 1979; Starobogatov and Moskalev, 1987). This study resulted in a new and, to my mind, rather harmonious and tenable system of gastropods. The class Gastropoda was divided into eight subclasses in the framework of this system (Golikov and Starobogatov, 1988), and the systematic position of some taxa was revised, including several groups of Early Paleozoic mollusks. The major part of the Cambrian univalved mollusks was interpreted as gastropods. The helcionelloid mollusks were put into the most primitive gastropod subclass, Cyclobranchia, along with the patelloid gastropods. Based on the similarity in their shell forms, the pelagiellids were lumped together with the Early Paleozoic macluritids into the subclass Divasibranchia, which also contains the recent siphonariids. The family Onychochilidae was assigned to the subclass Dextrobranchia, which contains the recent pteropods.

PHYLOGENESIS AND SYSTEM OF THE CAMBRIAN UNIVALVED MOLLUSKS

In my recent papers (Parkhaev, 2000a, 2001a), I supported the opinion of Starobogatov and his coauthors (Golikov and Starobogatov, 1975, 1988; Minichev and Starobogatov, 1979), considering the helcionelloid mollusks to be gastropods.

Let us try to determine the system of this group. We should base this system on the commonly accepted hypothesis that monoplacophoran mollusks are ancestral to gastropods. A simple cap-shaped shell with a central or subcentral apex could be considered to be the most primitive shell type, like in *Helcionella*, *Bemella*, or *Ilsanella*. These genera form the backbone of the extensive family Helcionellidae Wenz, 1938. Its members had the shell of the above-mentioned type and were characterized by the symmetrical palial complex and postero-anterior water circulation: water entered the shell through the posterior edge of the aperture and was discharged over the mollusk head through the anterior edge. The possibility of this type of circulation pattern was claimed by Golikov and Starobogatov (1988). According to their assumption, the postero-anterior circulation type of the primitive gastropods was inherited from monoplacophoran ancestors. Monoplacophorans had a posterior palial cavity, which received water owing to the function of the ciliar epithelium of the foot and mantle and the muscular activity of the foot. Torsion had resulted in the anterior position of the palial cavity; however, the main water transport function was carried out by the foot.

No structures aimed at increasing the efficiency of water inhalation or exhalation are known among the representatives of Helcionellidae. Later, such structures appeared in several groups. The genera *Igarkiella*, *Gonamella*, and *Rozanoviella* evolved the buttress along the middle of the anterior field of the shell that formed a groove on the interior surface of the shells.

Probably, it functioned to collect waste water inside the palial cavity and to discharge it with excrement through the anterior edge of the aperture (Parkhaev, 2000a). Mollusks with this morphological peculiarity could be combined within a new family, Igarkiellidae fam. nov.

Another morphogenetic way was chosen by the mollusks that improved the inhalant structure, i.e., genera *Mackinnonia, Parailsanella, Trenella*, etc. They formed a siphonal groove (modified parietal train) on the posterior subapical part of the aperture. This adaptation allowed them to input water when the shells were attached to hard substrate or even in the case when the edges of the aperture were shallowly buried in softer sediment. Evidently, the siphonal groove significantly improved the adaptability to a variety of ecological niches and, thus, had great evolutionary success among the helcionelloids. The great diversity of the helcionelloids having a well-defined siphonal groove could be divided into three groups: (1) mollusks with a cap-shaped shell similar to that of typical Helcionellidae but are distinguished from the latter by the presence of the siphonal groove (genera *Mackinnonia, Parailsanella, Trenella*, and *Udzhella*), (2) mollusks having closely approaching lower parts of the groove up to their merging into a tube (genera *Eotebena* and *Yochelcionella*), and (3) mollusks with strongly laterally compressed cap-shaped shells (genera *Stenotheca* and *Anabarella*). I propose to establish a new family, Trenellidae fam. nov., for the first group under discussion, while the second and the third groups are traditionally accepted as separate families: Yochelcionellidae Runnegar et Jell, 1976 and Stenothecidae Runnegar et Jell, 1980.

Probably, the family Trenellidae separated from the Helcionellidae to become the ancestor of the other two families, Yochelcionellidae and Stenothecidae (Fig. 1). The latter family contains a specialized group of mollusks (genera *Watsonella* and *Eurekapegma*) characterized by a significant curvature of the arcuate aperture margin and the presence of an internal plate.[1] The curved form of the aperture indicates the infaunal mode of the life of these organisms, and the development of the plates may be apparently explained by the reinforcement of the pedal muscles providing the movement of the animal through the sediment. It is reasonable to separate *Watsonella* and its possible descendant *Eurekapegma* from the other stenothecids into a group of subfamily rank, Watsonellinae subfam. nov.

In addition to the modifications in the apertural edge of the shell that were caused by water movement, the morphogenesis of the helcionelloids showed a tendency to the transformation of the shell form. Originally, the shell of the Helcionellidae was cap-shaped, but the increase in the shell volume had resulted in the planispiral coiling. Probably, this transformation took place repeatedly (at least twice). All planispiral forms containing one or more coils can be divided into two distinct groups: (1) the spire coils are strongly compressed laterally, aperture elongated in a longitudinal direction (genera *Coreospira, Latouchella*, etc.); (2) the cross section of the spire coils and aperture are nearly circular in shape (genera *Khairkhania, Protowenella, Ardrossania*, etc.). It is supposed that these two groups originated independently from the Helcionellidae; thus, they should be separated into different families, Coreospiridae Knight, 1952 and Khairkhaniidae Missarzhevsky, 1989. Representatives of the Coreospiridae remained to fairly closely related to the ancestral Helcionellidae; thus, this family should be combined with the Igarkiellidae fam. nov. in the superfamily Helcionelloidea.

It is noteworthy that the Coreospiridae evolved an asymmetric shell as a result of the increase in the number of whorls. One possible developmental mechanism of this asymmetry was already discussed by the author (Parkhaev, 2001a). It should be noted that the asymmetry of the relatively primitive forms (*Latouchella* and *Archaeospira*) shows itself in the outlines of the posterior edge of the aperture rather than in the general shape of the last whorl; these genera constitute the family Coreospiridae. More evolutionary advanced forms, the representatives of the family Pelagiellidae Knight, 1952, had distinctly asymmetric shells. Apparently, this may be due to a further transformation of the palial cavity.

In the changes in the general shell form from the ancestral group, the Coreospiridae, to its descendant Pelagiellidae, and further to the Aldanellidae, one can easily trace a trend toward more pronounced turbospiral coiling. The feasibility of such an evolutionary line is proved by the analysis of the early coils in the shells of these groups. The shells of the immature pelagiellids are nearly indistinguishable from those in some members of the coreospirid family, since the juvenile pelagiellids are symmetrical. The increase in the asymmetry is observable not only in the ontogenetic development but also in the pelagiellids phylogenesis as well: the later forms (*Pelagiella madianensis* Zhou et Xiao, 1984 from the Botomian of China and *Tannuspira magnifica* Missarzhevsky, 1989 from the Botomian of Tuva) are characterized by more asymmetric shells as compared with the earlier species (*P. lorenzi* Kobayashi, 1939 and *P. adunca* Missarzhevsky, 1966 from the Atdabanian of Siberia).

The fact that the Pelagiellidae originated from the Coreospiridae is almost evident, but the phylogenetic line connecting the Pelagiellidae and the Aldanellidae does require discussion.

The close relation between the aldanellid and pelagiellid was already noted by Golubev (1976), who placed the family Aldanellidae into the superfamily Pelagiellacea. He studied the ontogenesis of *Aldanella* and *Pelagiella* and came to the conclusion that these

[1] This plate is called either pegma (in *Watsonella*) or zygion (in *Eurekapegma*). Despite the differences in the form and position in the shell, the plates of these mollusks apparently performed similar functions, i.e., to support the strongly developed foot muscles of these infaunal animals.

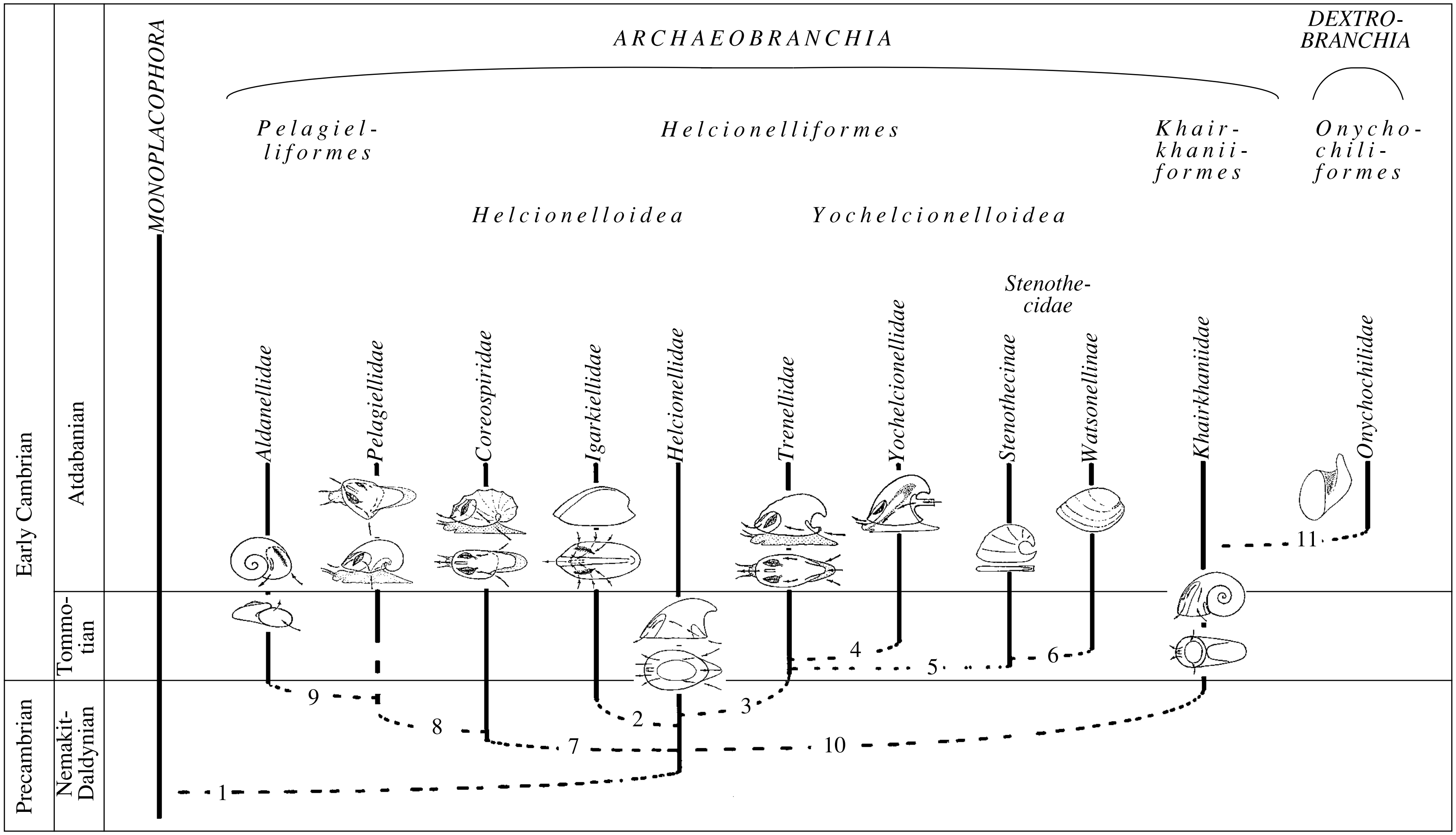

Fig. 1. Phylogenetic scheme of gastropod families at the Precambrian–Early Cambrian Boundary. Legend: (1) torsion; (2) peripheral buttress; (3) posterior siphonal groove; (4) deep siphonal groove or snorkel; (5) strong lateral compression; (6) infaunal (?) adaptations (internal plates, non-planar aperture); (7) planispiral shell, spire whorls compressed laterally, aperture elongated; (8) shell asymmetry; (9) asymmetry increase (turbospiral coiling with projected spire); (10) planispiral shell, spire whorls and aperture circular, palial caecum; (11) hyperstrophy.

genera may be related (Golubev, 1976, p. 37). In addition, he noted the following evolutionary tendency in *Aldanella*: the phylogenesis of this genus is characterized by an increase in the coil number and in the shell height and a decline in the whorl expansion rate, a more isometric sections of the whorls, etc. These changes are typical for the line *A. crassa* Missarzhevsky, 1969 ⟶ *A. utchurica* Missarzhevsky, 1969 ⟶ *A. rozanovi* Missarzhevsky, 1966 ⟶ *A. operosa* Missarzhevsky, 1966. The fossil remains of these species replace each other in the Tommotian part of certain sections on the Siberian Platform. More recently, almost the same conclusion was made by Missarzhevsky (1989, text-fig. 7). All these changes in *Aldanella's* shell indicate that the phylogenesis of the genus shows a strong tendency toward a more pronounced asymmetry and better expressed turbospiral coiling of the shell. Thus, it is reasonable to assume that the shell of the ancestor group was more symmetrical, possessing a slightly projecting spire and fewer coils. Such morphological features are characteristic of the pelagiellid family. In addition, the earliest aldanellids, *Aldanella crassa*, are similar to the pelagiellids (see Rozanov *et al.*, 1969, pl. 3, figs. 15–17; Golubev, 1976, pl. 3, figs. 1, 2). Thus, we can conclude that the aldanellids originated from the pelagiellids. The fact that *Aldanella* is restricted to the Tommotian, whereas the earliest pelagiellids appeared only in the Atdabanian, can be explained by the incomplete geological record or by the bad luck of paleontologists still missing Tommotian pelagiellids. However, the pelagiellid finds in the Tommotian of South Australia, Mount Terrible Formation, Fleurie Peninsula (Daily, 1976; Yarusnoe raschlenenie …, 1984), which unfortunately remain undescribed monographically, gave birth to hopes that the Tommotian Stage might be included in the stratigraphic range of the family Pelagiellidae.

In addition to *Aldanella* and the closely related genus *Paraaldanella*, the family Aldanellidae should include the genus *Nomgoliella* (Fig. 2), which is distinguished by the coiling direction: the shell of *Nomgoliella* is sinistral. The first member of the genus, the species *N. sinistrovolubilis* Missarzhevsky, 1981, is similar to *Aldanella crassa* (the specimen defined by Golubev (1976, pl. 3, fig. 13) as a pathological form of *Aldanella* sp. is probably *N. sinistrovolubilis*). This suggests that *Nomgoliella* originated from *Aldanella*. The evolutionary parallelism shown by these genera is noteworthy. The phylogenesis of *Nomgoliella* demonstrates the same tendency in the shell transformation as in the genus *Aldanella*: the shells of the late Atdabanian–Botomian representatives of *Nomgoliella* (i.e., *N. rotunda* and *N. australiensis*) gained a stronger asymmetry to become distinctly trochoid.

The second group with a planispiral shell, the family Khairkhaniidae (Fig. 3), shows a more remote relationship to the ancestral taxon Helcionellidae. This group is characterized by a shell with a relatively small member

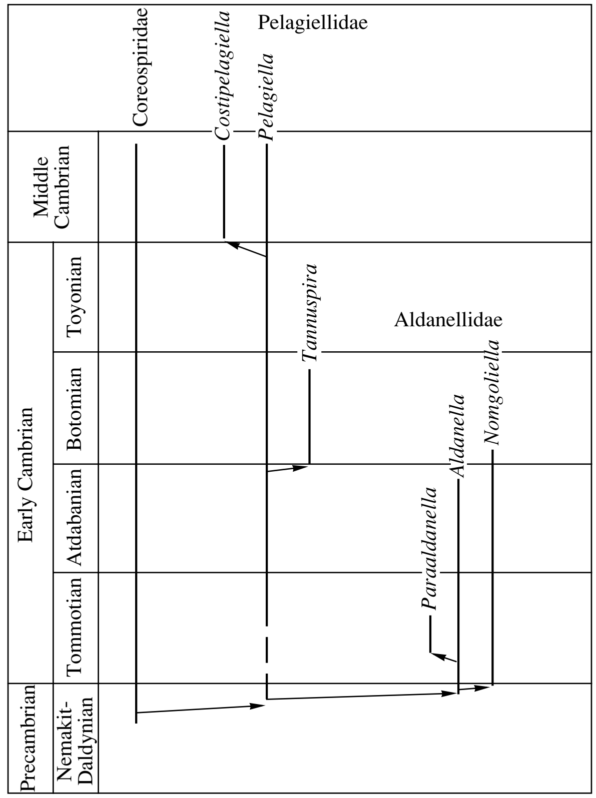

Fig. 2. Phylogenetic scheme of the families Pelagiellidae and Aldanellidae (order Pelagielliformes).

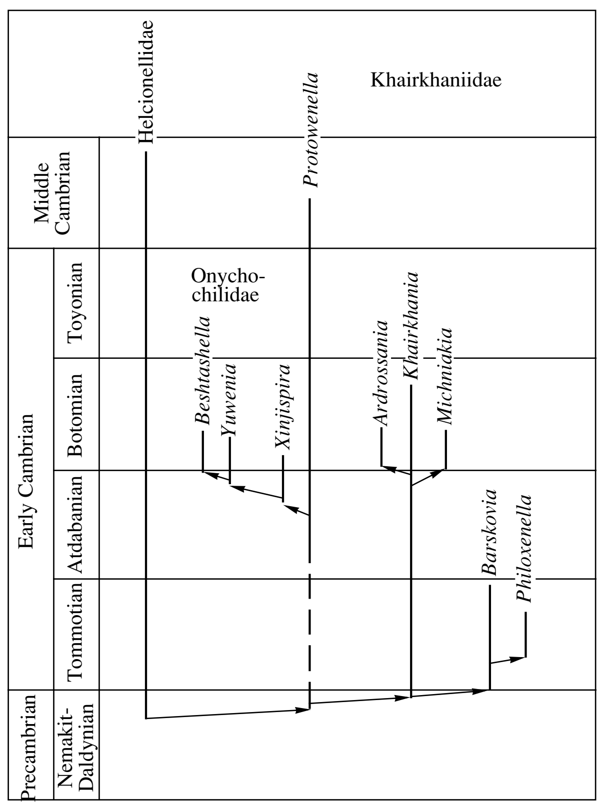

Fig. 3. Phylogenetic scheme of the families Khairkhaniidae and Onychochilidae.

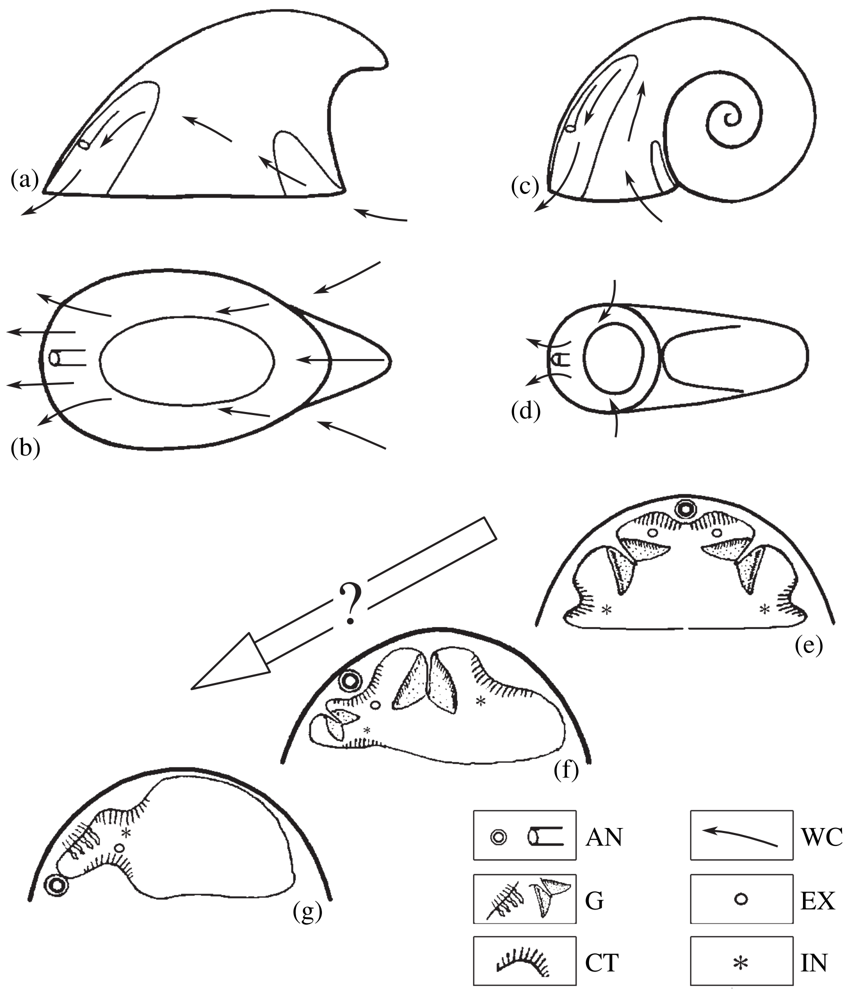

Fig. 4. Suggested origin of the palial caecum of gastropod mollusks: (a) and (b) water currents in a cap-shaped shell; (c) and (d) water currents in a planispiral shell (the transition from cap-shaped shell to the planispiral one caused a contraction of the palial cavity into a compact tube, approach of paired ctenidia and water currents; as a result, the ciliar tracks originated, which drive water inside the palial cavity and out of it); (e)–(g) cross section of the palial cavity of gastropods having a palial caecum: (e) reconstruction of the palial cavity of planispiral Khairkhaniidae; (f) palial cavity of recent turbospiral *Pyramidella* (simplified after Haszprunar, 1988); (g) palial cavity of hypothetical form explaining the inversion of the location of inhalant and exhalant ciliar tracts during the transformation from the planispiral shell to the turbospiral one (the projection of the spire results in the change of the palial cavity shape, rectum, and anus are shifting from the saggital plane and getting lateral position. One of the gills is partly or completely reducing, while another one getting the position on the roof of the palial cavity). Abbreviations: AN (anus), G (gills), CT (ciliar tracts), WC (water currents), IN (inhalant current), EX (exhalant current).

of whorls (three or four) and whorls circular in cross section.

The transformation of the shell form could not occur without changes in the anatomy of the palial complex. Compression of the palial cavity into a compact tube brought the paired ctenidia, as well as the inhalant and exhalant water currents, close together. Probably, it is under such conditions that the palial caecum of gastropods evolved (Fig. 4). The genus *Protowenella* can be regarded as the most primitive member of the Khairkhaniidae. Its shell has a form intermediate between those of the Helcionellidae and typical Khairkhaniidae. The assignment of the genus *Barskovia* to the family under discussion could seem rather unexpected, as it is usually placed in the family Aldanellidae. However, the suggested position of the genus is justified by the morphological difference between *Barskovia* and Aldanellidae members, in spite of the common trochoid shell shape. The whorls of *Barskovia* have nearly circular cross sections (as in *Khairkhania*), whereas in the Aldanellidae, they are oval;[2] the open coiling characteristic of *Barskovia*

[2] All representatives of the genus *Aldanella* and the earliest (Tommotian) *Nomgoliella* have whorls with cross sections elongated in the direction perpendicular to the axis of coiling. This primitive feature probably indicates a close affinity between the Aldanellidae and the ancestral group, Pelagiellidae. Only the latest *Nomgoliella* from the uppermost Atdabanian–lowermost Botomian had whorls with more rounded cross sections.

(common in *Khairkhania*) is not typical for the Aldanellidae. I suppose that it was the Khairkhaniidae that gave rise to the first Onychochilidae (Atdabanian–Botomian genera *Beshtashella* Missarzhevsky, 1981, and *Yuwenia* Runnegar, 1981) and, consequently, the subclass Dextrobranchia Minichev et Starobogatov, 1975, which is characterized by having a hyperstrophic turbospiral shell and the palial cavity with a palial caecum that retains only the right part of the palial complex (Starobogatov, 1976). The transition from the planispiral Khairkhaniidae to the hyperstrophic Onychochilidae is clearly visible in the lineage *Protowenella* ⟶ *Xinjispira* ⟶ *Yuwenia* ⟶ *Beshtashella*.

Thus, I suggest to divide all helcionelloid mollusks into three orders: Helcionelliformes, Pelagielliformes, and Khairkhaniiformes. Two superfamilies can be distinguished within the first order: Helcionelloidea (includes the families Helcionellidae, Igarkiellidae, and Coreospiridae) and Yochelcionelloidea (includes the families Trenellidae, Yochelcionellidae, and Stenothecidae). The order Pelagielliformes consists of two families, i.e., Aldanellidae and Pelagiellidae, while the order Khairkhaniiformes is monotypic. Possible phylogenetic relationships between these taxa are given in Fig. 1. All three orders consistute a monophyletic branch, which can be characterized by the following features: (1) the shell is originally symmetric, cap-shaped, or planispiral; the higher representatives possess a turbospiral shell with a slightly projecting spire; and (2) the palial complex is symmetric with primitive postero-anterior water circulation inside the palial cavity.

The analysis of the gastropod system suggested by Starobogatov and coauthors shows that the diagnostic features of the helcionelloid mollusks bring them together with the subclass Cyclobranchia, which contains recent Patelliformes. However, I believe that the Patelliformes should not be combined with the helcionelloid mollusks within the same subclass since their similarity is, possibly, secondary in nature. First, the shell of the Patelliformes is secondarily cap-shaped: this is proved by the larval turbospiral shell having an operculum. Second, the palial complex of the primitive Patelliformes in which the original gills were not reduced is asymmetric (only the left ctenidium is present), while the respiratory currents also have an asymmetric pattern. Third, the symmetric postero-anterior water current of the Patellidae is probably a secondary phenomenon (Haszprunar, 1988) caused by the reduction of the ctenidia in the palial cavity and the formation of the secondary adaptive gills within the circum-pedal furrow (even in this case, the typical current in the palial cavity is preserved: water enters the cavity from the left anterior side and goes out through the posterior right side). All these facts allow us to conclude that the Patelliformes derived from an ancestral group that had a turbospiral shell with an asymmetric palial complex. Thus, the helcionelloid gastropods should be separated from the Cyclobranchia and assigned to a new subclass, Archaeobranchia, distinguished from all other gastropods by the originally symmetric cap-shaped or planispiral shell with primitive original postero-anterior water current in the palial cavity. The scheme of the phylogenetic relationship of the other eight gastropod subclasses should be slightly modified as a result of the establishment of the new subclass, which probably gave rise to the radiation of the entire gastropod class. However, I will not discuss this problem here, because it requires a separate study. Below a monographic description of the taxa of the Cambrian univalved mollusks at the family level and higher is given. I realize that the suggested system and phylogeny (Figs. 1–3) are far from perfection and will arouse some objection from my colleagues, especially those who have the opposite opinion on the biology of this mollusk group. However, I hope that this system will serve as a stimulus or base for the development of more complete and thorough systematics.

SYSTEMATIC PALEONTOLOGY

CLASS GASTROPODA CUVIER, 1797

SUBCLASS ARCHAEOBRANCHIA PARKHAEV SUBCLASSIS NOV.

D i a g n o s i s. Gastropods with originally symmetrical cap-shaped or planispiral shell. Advanced representatives could have turbospiral shells with a slightly projected spire.

R e m a r k s. In addition to the diagnosis, which contains only conchological features observable in the paleontological material, the following anatomical characteristics are suggested based on the morphofunctional analysis of archaeobranchian shells. Archaeobranchians are supposed to have a symmetrical mantle complex with primitive postero-anterior water current inside the palial cavity.

C o m p a r i s o n. As was already mentioned in the diagnosis, Archaeobranchia possessed a primarily symmetric shell. This very important feature clearly distinguishes the group under discussion from all other representatives of the gastropod class, in which the shell is always asymmetrical and could attain the secondary symmetry (in some groups) only at mature stages. In addition, the Archaeobranchia apparently differs from other gastropods in having a primitive postero-anterior water current inside the palial cavity and in the absence (?) of operculum.

C o m p o s i t i o n. Three orders: Helcionelliformes Golikov et Starobogatov, 1975, Khairkhaniiformes Parkhaev, ordo nov., and Pelagielliformes MacKinnon, 1985.

Order Helcionelliformes Golikov et Starobogatov, 1975

D i a g n o s i s. Shell symmetrical, cap-shaped, planispiral or close to planispiral with few coils. Forms with planispiral shell have elongated aperture, with the length larger, equal or slightly smaller than the shell diameter. Palial caecum probably absent.

C o m p a r i s o n. The order differs from the orders Khairkhaniiformes and Pelagielliformes mainly in having a poorly coiled shell: the forms with planispiral shell always have an elongated aperture with a length larger, equal, or slightly smaller than the shell diameter.

C o m p o s i t i o n. Two superfamilies, i.e., Helcionelloidea Wenz, 1938 and Yochelcionelloidea Runnegar et Jell, 1976 (rank nov.).

S u p e r f a m i l y Helcionelloidea Wenz, 1938

D i a g n o s i s. Shell without siphonal groove on the posterior margin of aperture.

C o m p a r i s o n. The superfamily differs from Yochelcionelloidea in the absence of the siphonal groove on the posterior margin of the aperture.

C o m p o s i t i o n. Three families, i.e., Helcionellidae Wenz, 1938, Coreospiridae Knight, 1947 and Igarkiellidae Parkhaev, fam. nov.

Family Helcionellidae Wenz, 1938

Helcionellidae Wenz, 1938: Wenz, 1938, p. 88 (subfamily rank, partim, quoad *Helcionella*); Runnegar and Jell, 1976, p. 116 (partim, excl. *Coreospira, Latouchella, Oelandia, Oelandiella*); MacKinnon, 1985, p. 66 (partim, quoad *Helcionella*); Missarzhevsky, 1989, pp. 23–24 (partim, excl. *Purella*).

Palaeacmaeidae Grabau et Shimer, 1909: Knight, 1952, p. 46 (partim, quoad *Helcionella, Scenella*).

Scenellidae Wenz,1938: Wenz, 1938, p. 86 (subfamily rank, partim, quoad *Scenella*); Runnegar and Jell, 1976, p. 117 (partim, quoad *Scenella, Tannuella*); MacKinnon, 1985, p. 68 (partim, quoad *Obtusoconus*).

Yangtzeconidae Yu, 1979: Yu, 1979, pp. 241, 262 (partim), syn. nov.

Securiconidae Missarzhevsky, 1989: Missarzhevsky, 1989, pp. 23–24, 174 (partim, excl. *Mastakhella*).

D i a g n o s i s. Shell cap-shaped without peripheral buttress.

C o m p a r i s o n. The family differs from the Coreospiridae Knight, 1947 in having a cap-shaped rather than planispiral shell; from the family Igarkiellidae fam. nov., it can be distinguished by the absence of peripheral buttress.

C o m p o s i t i o n. The family includes the following genera: *Scenella* Billings, 1872; *Randomia* Matthew, 1899; *Helcionella* Grabau et Shimer, 1909; *Hampilina* Kobayashi, 1958; *Bemella* Missarzhevsky in Rozanov *et al.*, 1969 (=*Charaulachella* Vassiljeva, 1990); *Tannuella* Missarzhevsky in Rozanov *et al.*, 1969; *Igorella* Missarzhevsky in Rozanov *et al.*, 1969; *Obtusoconus* Yu, 1979; *Emarginoconus* Yu, 1979; *Securiconus* Jiang, 1980; *Ilsanella* Missarzhevsky, 1981; *Marocella* Geyer, 1986; *Igorellina* Missarzhevsky, 1989; *Pararaconus* Runnegar in Bengtson *et al.*, 1990; *Lenoconus* Vassiljeva, 1990; *Asperconella* Landing in Landing et Bartowski, 1996; *Pseudopatella* Zhegallo in Esakova et Zhegallo, 1996; possibly *Paucella* Vassiljeva, 1998, and others.[3]

Family Igarkiellidae Parkhaev, fam. nov.

Helcionellidae Wenz, 1938: Missarzhevsky, 1989, pp. 23–24 (partim, quoad *Rozanoviella*).

Securiconidae Missarzhevsky, 1989: Missarzhevsky, 1989, pp. 23–24, 174 (partim, quoad *Mastakhella*).

Purellidae Vassiljeva, 1990: Vassiljeva, 1990, p. 9 (partim excl. *Purella*); Parkhaev, 2000b, p. 177 (partim, excl. *Purella*); Parkhaev, 2000c, p. 23 (partim, excl. *Purella*).

T y p e g e n u s. *Igarkiella* Vassiljeva, 1998 (=*Trilobella* Vassiljeva, 1990, non *Trilobella* Woodward, 1924, non *Trilobella* Ivanova, 1955).

D i a g n o s i s. Shell cap-shaped with peripheral buttress.

C o m p a r i s o n. The new family differs from the Coreospiridae and Helcionellidae in having a prominent peripheral buttress.

C o m p o s i t i o n. The family includes six genera, i.e., *Protoconus* Yu, 1979 (=*Asperoconus* Yu, 1979), *Rozanoviella* Missarzhevsky, 1981, *Gonamella* Valkov et Karlova, 1984 (=*Patellella* Vassiljeva, 1990), *Mastakhella* Missarzhevsky, 1989, *Squamiconus* Vassiljeva, 1990, and *Igarkiella* Vassiljeva, 1998 (=*Trilobella* Vassiljeva, 1990).

R e m a r k s. The composition of this family is very similar to that of Purellidae Vassiljeva, 1990. However, all the species of the genus *Purella* and some species of the genus *Rozanoviella* have a very specific microstructure of the shell wall, which is untypical for gastropods (Kerber, 1988). This microstructure is similar to that of sclerite-like elements such as *Maikhanella* Zhegallo, 1982, which are not related to gastropods. According to recent studies (Kouchinsky, 2000), the type species of *Purella—P. cristata* Missarzhevsky, 1974 also has the same microstructure. Consequently, we keep the genus *Purella* within the family Purellidae, while all the other genera having a peripheral buttress but lacking the scleritic type of microstructure are placed here into a new family, Igarkiellidae.

Vassiljeva (1990) established the family Purellidae with four genera in its composition, i.e., *Purella* Missarzhevsky, 1974, *Rozanoviella* Missarzhevsky, 1981, *Patellella* gen. nov., and *Trilobella* gen. nov. Probably, she was unaware of the genus *Gonamella* Valkov et Karlova, 1984, the diagnosis of which is indistinguishable from that of her genus *Patellella*. I consider *Patellella* as a junior synonym of *Patellella.*

[3] It is very difficult to list all the genera assigned to the Helcionellidae without a detailed review of all Cambrian mollusks. I describe here only those genera that can be undoubtedly referred to the family and have more or less clear taxonomic boundaries.

Family Coreospiridae Knight, 1947

Coreospiridae Knight, 1947: Golikov and Starobogatov, 1988, p. 70; Missarzhevsky, 1989, pp. 23–24 (partim).

Archaeospiridae Yu, 1979: Yu, 1979, pp. 254 and 265.

Yangtzespiridae Yu, 1987: Yu, 1987, p. 208.

Latouchellidae Golikov et Starobogatov, 1988: Golikov and Starobogatov, 1988, p. 70 (syn. nov.).

Diagnosis. Shell planispiral or almost planispiral with few coils.

Comparison. The family differs from the Helcionellidae in having a planispiral rather than cap-shaped shell; from the family Igarkiellidae, it can be distinguished by the absence of the peripheral buttress.

Composition. The family includes the following genera: *Coreospira* Saito, 1936; *Latouchella* Cobbold, 1921; *Oelandiella* Vostokova, 1962 (?=*Archaeospira* Yu, 1979, *Yangtzespira* Yu, 1979, and *Pseudoyangtzespira* Bokova, 1990), *Cambrospira* Yu, 1979; *Hugiagouella* Chen et Zhang, 1980, *Cambroconus* Yu, 1981; *Hubeispira* Yu, 1981; *Chabaktiella* Missarzhevsky, 1981; *Uncinaspira* He, 1984; *Gibbaspira* He, 1984; *Anhuiconus* Zhou et Xiao, 1984; *Tichkaella* Geyer, 1986; *Kutanjia* Kruse, 1991.

Superfamily Yochelcionelloidea Runnegar et Jell, 1976 (rank nov.)

Diagnosis. Shell with parietal train modified into siphonal groove.

Comparison. The superfamily differs from the Helcionelloidea in the presence of the siphonal groove on the posterior apertural margin.

Composition. The superfamily includes three families, i.e., Trenellidae, Yochelcionellidae, and Stenothecidae.

Family Trenellidae Parkhaev, fam. nov.

Mellopegmidae Missarzhevsky, 1989: Missarzhevsky, 1989, pp. 23 and 24, and 179 (partim).

Trenellidae Parkhaev, 2000: Parkhaev, 2000c, p. 23 (invalid).

Type genus. *Trenella* Parkhaev, 2001.

Diagnosis. Shell relatively wide, cap-shaped, without siphonal tube (snorkel).

Comparison. The new family differs from the family Yochelcionellidae in having a siphonal groove, the margins of which do not merge to form the snorkel; from the family Stenothecidae, it differs in having a relatively wide shell.

Composition. The family includes the following genera: *Oelandia* Westergard, 1936; *Prosinuites* Poulsen, 1967; *Xianfengella* He et Yang, 1982 (=*Obscurella* Vassiljeva, 1990, *?Rugaeconus* Vassiljeva, 1990); *Parailsanella* Zhegallo in Voronina *et al.*, 1987 (?=*Bemellina* Vassiljeva, 1998); *Mackinnonia* Runnegar in Bengtson *et al.*, 1990; *Udzhella* Vassiljeva, 1990; and *Trenella* Parkhaev, 2001.

Remarks. The following species having the parietal train with a distinct siphonal groove should probably be assigned to the new genus and referred to the family Trenellidae: *"Helcionella" terraustralis* Runnegar et Jell, 1976; *"Latouchella" merino* Runnegar et Jell, 1976; *"L." accordionata* Runnegar et Jell, 1976 from the Middle Cambrian of Australia (New South Wales, Coonigan Formation); *"L." comma* Geyer, 1986 from the uppermost Lower–lowermost Middle Cambrian of Morocco; *"L." holmdalense* Peel, 1988; and *"L." pearylandica* Peel, 1988 from the Middle Cambrian of Greenland (Holm Dal Formation).

Family Yochelcionellidae Runnegar et Jell, 1976

Yochelcionellidae Runnegar et Jell, 1976: Runnegar and Jell, 1976, p. 129; Missarzhevsky, 1989, p. 178.

? Enigmaconidae MacKinnon, 1985: MacKinnon, 1985, p. 72 (syn. nov.).

Diagnosis. Shell relatively wide and cap-shaped, margins of siphonal groove approach each other sometimes forming a siphonal tube (snorkel).

Comparison. The family differs from the Trenellidae fam. nov. and Stenothecidae in having a siphonal groove with approached margins forming a siphonal tube (snorkel).

Composition. The family includes the following genera: *Yochelcionella* Runnegar et Pojeta, 1974; *Eotebenna* Runnegar et Jell, 1976; *Runnegarella* gen. nov.; and, probably, *Enigmaconus* MacKinnon, 1985.

Remarks. I assign the genus *Enigmaconus* MacKinnon, 1985 to the family Yochelcionellidae assuming that the septa that have been interpreted by MacKinnon as the structure dividing the internal shell cavity into two unequal parts actually represents the posterior wall of the shell. If this is true, the smaller part of the internal shell cavity (not including the apex) separated by this septa is a siphonal tube directed upward and along the whole length consolidated with the posterior wall of the shell.

Genus *Runnegarella* Parkhaev, gen. nov.

Etymology. In honor of the Australian paleomalacologist Bruce Runnegar.

Type species. *Yochelcionella americana* Runnegar et Pojeta, 1980, Lower Cambrian of the USA and Canada.

Diagnosis. Shell cap-shaped, strongly compressed laterally, with free siphonal tube directed posteriorly and curved apertural margin.

Comparison. The new genus differs from the similar *Yochelcionella* in having a strongly laterally compressed shell with a convex apertural margin; from *Enigmaconus*, it can be distinguished by the free siphonal tube directed posteriorly.

Composition. Type species.

Family Stenothecidae Runnegar et Jell, 1980

Procarinariidae Wenz, 1938: Runnegar and Jell, 1976, p. 117 (partim).

Coreospiridae Knight, 1947: Missarzhevsky, 1989, pp. 23–24 (partim).

Stenothecidae Runnegar et Jell, 1980: Runnegar and Jell, 1980, p. 111; MacKinnon, 1985, p. 69.

Mellopegmidae Missarzhevsky, 1989: Missarzhevsky, 1989, pp. 23–24, and 179 (partim).

D i a g n o s i s. Shell strongly compressed laterally.

C o m p a r i s o n. The family differs from Trenellidae fam. nov. and Yochelcionellidae in having a strong lateral compression of the shell.

C o m p o s i t i o n. The family includes two subfamilies, i.e., Stenothecinae and Watsonellinae subfam. nov.

Subfamily Stenothecinae Runnegar et Jell, 1980 rank nov.

D i a g n o s i s. Shell with straight or slightly curved apertural margin. Siphonal groove shallow. Internal platelike structures absent.

C o m p a r i s o n. The subfamily differs from the Watsonellinae subfam. nov. in having a straight or slightly curved apertural margin and shallow siphonal groove and in the absence of internal platelike structures.

C o m p o s i t i o n. The subfamily includes three genera, i.e., *Stenotheca* Salter in Hicks, 1872; *Anabarella* Vostokova, 1962; and *Mellopegma* Runnegar et Jell, 1976.

Subfamily Watsonellinae Parkhaev, subfam. nov.

T y p e g e n u s. *Watsonella* Grabau, 1900.

D i a g n o s i s. Shell with strongly curved apertural margin. Siphonal groove deep. Internal platelike structures could be present.

C o m p a r i s o n. The new subfamily differs from the Stenothecinae in having a strongly curved apertural margin and deep siphonal groove and in the presence of internal platelike structures.

C o m p o s i t i o n. The subfamily includes two genera, i.e., *Watsonella* Grabau, 1900 and *Eurekapegma* MacKinnon, 1985.

Order Khairkhaniiformes Parkhaev, ordo nov.

D i a g n o s i s. Shell planispiral or almost planispiral. Coils up to three or four in number. Aperture almost circular, with its diameter significantly less than diameter of shell. Presence of paired palial caecum supposed.

C o m p a r i s o n. The new order differs from the Pelagielliformes and Helcionelliformes in having a planispiral or almost planispiral shell and circular or almost circular aperture, the diameter of which is significantly smaller then that of the shell.

C o m p o s i t i o n. The single family, Khairkhaniidae Missarzhevsky, 1989.

Family Khairkhaniidae Missarzhevsky, 1989

Multifaritidae Byalyy, 1973: Runnegar and Jell, 1976, p. 121 (partim); Starobogatov and Moskalev,1987, p. 9 (partim).

Khairkhaniidae Missarzhevsky, 1989: Missarzhevsky, 1989, pp. 24 and 180.

D i a g n o s i s. The same as for the order.

C o m p o s i t i o n. The family includes the following seven genera: *Philoxenella* Vostokova, 1962; *Michniakia* Missarzhevsky, 1966; *Protowenella* Runnegar et Jell, 1976; *Barskovia* Golubev, 1976 (=*Nekolenia* Vassiljeva, 1998); *Khairkhania* Missarzhevsky, 1981; *Xinjispira* Yu et Rong, 1987; and *Ardrossania* Runnegar in Bengtson *et al.*, 1990.

Order Pelagielliformes MacKinnon, 1985

(trans. hic ex Pelagiellida MacKinnon, 1985)

D i a g n o s i s. Shell turbospiral. Aperture oval, elongated in direction perpendicular to axis of coiling. Palial caecum probably absent.

C o m p a r i s o n. The order differs from the Khairkhaniiformes ordo nov. and Helcionelliformes in having a turbospiral shell.

C o m p o s i t i o n. The order includes two families, i.e., Pelagiellidae Knight, 1952 and Aldanellidae Linsley et Kier, 1984.

Family Pelagiellidae Knight, 1952

Pelagiellidae Knight, 1952: Runnegar and Jell, 1976, pp. 133–134 (partim); Linsley and Kier, 1984, p. 250 (partim); MacKinnon, 1985, p. 75.

D i a g n o s i s. Shell turbospiral, its asymmetry due to the protrussion of the basal (left) part of penultimate whorl. Spire slightly projected.

C o m p a r i s o n. The family differs from the Aldanellidae in having a turbospiral shell, the asymmetry of which is due to the protrusion of the basal (left) part of the penultimate whorl and slightly projected spire.

C o m p o s i t i o n. The family includes the following genera: *Pelagiella* Matthew, 1895; *Costipelagiella* Horny, 1964; *Tannuspira* Missarzhevsky, 1989; and, possibly, *Tianzhushanospira* Yu, 1979.

Family Aldanellidae Linsley et Kier, 1984

Aldanellidae Linsley et Kier, 1984: Linsley and Kier, 1984, p. 250 (partim).

D i a g n o s i s. Shell turbospiral, assymmetry due to projected spire.

C o m p a r i s o n. The family differs from the Pelagiellidae in having a turbospiral shell the assymmetry of which is due to the projected spire.

C o m p o s i t i o n. The family includes three genera: *Aldanella* Vostokova, 1962; *Paraaldanella* Golubev, 1976; and *Nomgoliella* Missarzhevsky, 1981.

SUBCLASS DEXTROBRANCHIA MINICHEV ET STAROBOGATOV, 1975

(for diagnosis see Starobogatov, 1976; composition is cited in Golikov and Starobogatov, 1988)

Superorder Umbraculiformii Minichev et Starobogatov, 1975

(for diagnosis see Minichev and Starobogatov, 1975; composition is cited in Golikov and Starobogatov, 1988)

Order Onychochiliformes Minichev et Starobogatov, 1979

(for diagnosis see Minichev and Starobogatov, 1979; composition is cited in Golikov and Starobogatov, 1988)

Family Onychochilidae Koken, 1925

Onychochilidae Koken, 1925: Linsley and Kier, 1984, p. 250 (partim).

Diagnosis. Shell strongly hyperstrophic, sinistral.

Composition. The complete composition of this Early Paleozoic family is difficult to cite. In the Cambrian, it is represented by two genera, *Beshtashella* Missarzhevsky in Missarzhevsky et Mambetov, 1981, and *Yuwenia* Runnegar, 1981.

Remarks. I suppose that the genus *Kistassella* Missarzhevsky, 1989 should be considered as a junior synonym of the genus *Yuwenia* Runnegar, 1981, as its type species *K. sipralis* Missarzhevsky, 1989 is indistinguishable from *Y. bentleyi* Runnegar, 1981, the type species of the genus *Yuwenia*.

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