MALACOLOGIA, 2010, 52(1): 97–113

BRACHIOPOD IDENTITY OF THE ALLEGED MONOPLACOPHORAN ANCESTORS OF CEPHALOPODS

Jerzy Dzik

Instytut Paleobiologii PAN, Twarda 51/55, 00-818 Warszawa and
Instytut Zoologii Uniwersytetu Warszawskiego, Banacha 2, 02-079 Warszawa, Poland;
dzik@twarda.pan.pl

ABSTRACT

Because of a serial arrangement of supposed pedal muscles and its high-conical shell, *Hypseloconus* from the Late Cambrian to Early Ordovician of North America is generally believed to be a monoplacophoran relative of cephalopods. The distinctive pattern of muscle attachments and shell form indicates its close relationship to roughly coeval Siberian *Kirengella* and several other genera classified in the order Kirengellida. Newly collected material from the Early Ordovician of Siberia shows that the bivalved *Angarella*, with its ventral valve cementing to a hard substratum, is closely similar to *Kirengella* and *Hypseloconus* in the arrangement of shell muscles. Permanently fixed to its substratum was also another probable member of the group, *Pygmaeoconus*. Musculature of *Angarella* in some aspects resembles that of the Early Cambrian mobergellans with phosphatic shells, but in the calcitic shell structure it is similar to the craniopsid brachiopods. Irrespective of whether the kirengellids are brachiopods or not, they should be removed from considerations on the ancestry of cephalopods. The alternative to *Hypseloconus* as a candidate for cephalopod ancestry is the Early Cambrian *Turcutheca*, an enigmatic mollusk with endogastrically curved and laterally compressed conch and relatively large subspherical embryonic conch, in both aspects resembling the earliest ellesmeroceratid nautiloids.

Key words: Monoplacophora, Ordovician, Cephalopoda, Siberia, evolution.

INTRODUCTION

Embryological and comparative anatomical evidence is widely used to interpret the origin of aspects of cephalopod soft anatomy distinctive for them, whereas palaeontological data show how their shell, of originally hydrostatic function, changed in the course of evolution. The most widely accepted palaeontological interpretation of the origin of cephalopods, advanced by Yochelson et al. (1973) and reaffirmed in Webers & Yochelson (1989) and Kröger (2007), proposes that they originated from a high-conical monoplacophoran with serially arranged pedal muscles. The only available evidence that such monoplacophorans occurred in the Cambrian, before the appearance of earliest cephalopods, are specimens of *Hypseloconus* cf. *H. stabilis* Berkey, 1898, from the Davis Formation of Missouri described by Stinchcomb (1980). Webers et al. (1991) and Stinchcomb & Angeli (2002) transferred this species to the roughly coeval Siberian genus *Kirengella*, which shows a similar disposition of muscle attachments on the shell interior. *Kirengella* differs from *Hypseloconus* in having a low-conical shell. As shown below, an even lower shell, but virtually the same pattern of muscle attachment scars, characterizes *Angarella*, fossil shells of which abundantly occur in the Ordovician strata of the region. But at this point of reasoning a great difficulty emerges: *Angarella* shells are bivalved and were basally cemented to a hard substratum! These extinct organisms appear to be more similar to the craniopsid brachiopods than to the monoplacophorans.

In the present paper I present data on the morphology of *Angarella* and discuss its evolutionary relationships with coeval brachiopods and possibly ancestral Cambrian problematica. An alternative direction of search for cephalopod ancestry will be proposed.

MATERIAL

Angarella shells are the most common fossils in the Badaranovo Formation of the Irkutsk

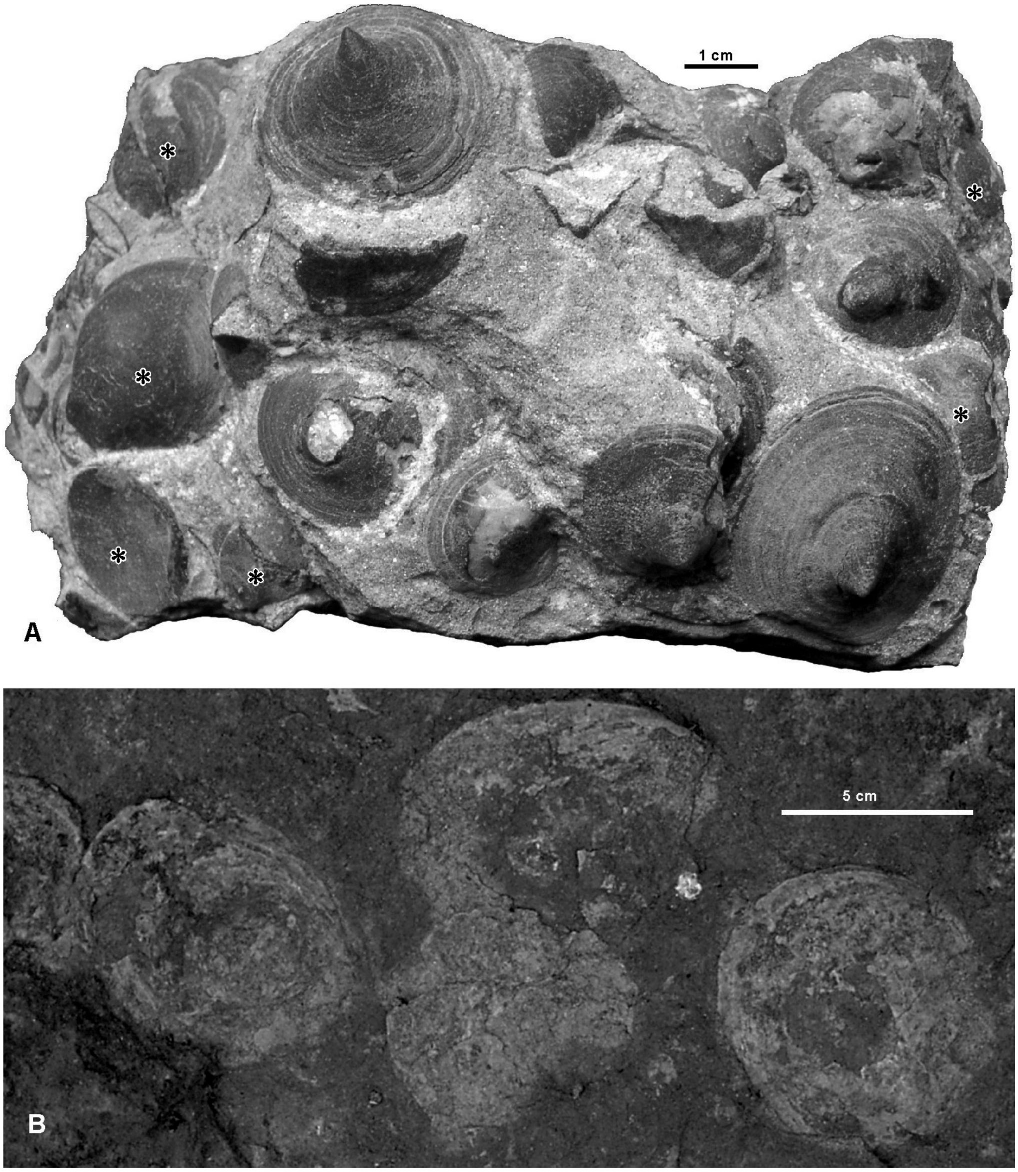

FIG. 1. Species of *Angarella* from the Ordovician of the Angara River region, Siberia. A: Mass occurrence of *Angarella jaworowskii* Asatkin, 1932, shells in light coarse-grained calcareous sandstone of the lower Badaranovo Formation; loose block ZPAL Bp 62/12 collected at Pashino near Kodinsk. Ventral valves are marked with asterisks; B: Large ventral valves of *Angarella* at the bedding surface of red muddy calcareous sandstone of the lower Mamyry Formation at the bank of Vikhoreva River near Bratsk (field photo).

Amphitheatre geological structure in southern Siberia (Divina et al., 1984). Frequently they are rock-forming skeletal elements. Their preservation is generally poor, and morphological details of the shell surface or interior are rarely discernible. The specimens used in this study come from a loose block of calcareous sandstone collected on the left bank of Angara near Ko-

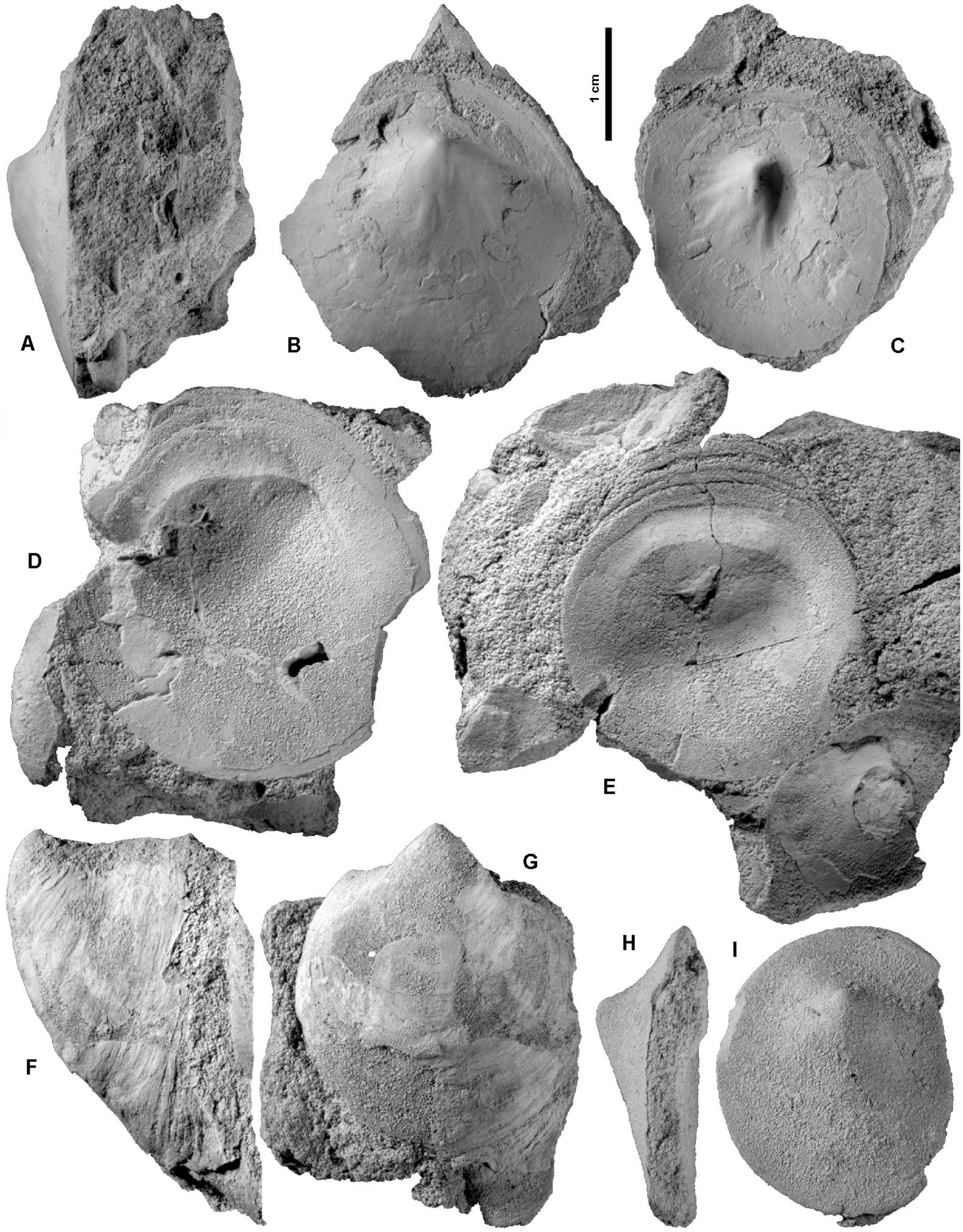

FIG. 2. Morphology of *Angarella jaworowskii* Asatkin, 1932. Shells from a loose block of sandstone of the lower Badaranovo Formation collected at the bank of Angara at Pashino near Kodinsk, Siberia. A–C: Dorsal valve ZPAL Bp 62/6 with muscle attachment scars, lateral and external views of part (A–B) and internal view of counterpart (C); D: Ventral valve ZPAL Bp 62/8 in internal view; E: Same for ventral valve ZPAL Bp 62/7; F–G: Lateral and external view of extremely high-conical dorsal valve ZPAL Bp 62/25 with thin wall; H–I: Same views of small-conical dorsal valve ZPAL Bp 62/27 with thick wall.

dinsk upstream of Verkhnaya Kezhma Creek, where formerly the village Pashino was located. The material is relatively informative owing to weathering of the rock, which then easily disintegrates along the shell surfaces. The block probably derived from the 1.5 m thick bed 43 of the Badaranovo Formation, where a mass occurrence of *Angarella* was reported by Kniazev (1978). There was little sorting, as ventral and dorsal valves seem to be equally frequent in the rock (Figs. 1A, 2). The fossil assemblage in the block is monospecific, but in other beds of the formation *Angarella* is sometimes associated with sinuitid bellerophonts.

This material of *Angarella* Asatkin, 1932, almost certainly represents the type species of the genus, *A. jaworowskii* Asatkin, 1932, and derives from its type stratum, the Badaranovo Formation. The type locality is within the same region on Angara at the mouth of the Koda River. Each sample of *Angarella* shells from the Badaranovo Formation shows so much variability in the shape of both ventral and dorsal valves that discrimination seems hardly possible. Originally four species of the genus were named, and Yadrenkina (1984) reduced their number to three, but all occur together in various horizons of the formation.

In relatively pure reddish sandstone of the lower Badaranovo Formation on Angara, specimens with marginal concentration of growth increments are mostly of 3 cm diameter and rarely approach 4 cm. Specimens possibly representing a more advanced segment of the *Angarella* lineage or a local population living in a different environment occur in olive-gray marly sandstone of the upper Badaranovo Formation exposed near Kodinsk a few kilometers upstream from the place where specimens with muscle scars were collected (near the former village Rozhkovka). The stratum probably represents the basal horizon in the upper Badaranovo Formation. Specimens of *Angarella* reach there oyster size, up to 12 cm long (Fig. 3B). At Rozhkovka the large *Angarella* is a member of a rather diverse fossil assemblage with conodonts, suggestive of an open-sea environment with normal salinity. Similar, but usually poorly preserved specimens of *Angarella* occur in the cliff of Vikhoreva River, a tributary of Angara near Bratsk (Fig. 1B). The stratigraphically highest occurrence of *Angarella* at Vikhoreva is in the marly oolithic limestone of the lower Mamyry Formation in an abandoned quarry on the other side of the road (exposure 755 in Divina et al., 1984). Large *Angarella* are associated with the raphistomatic gastropods and bellerophonts indicative of more open marine conditions than lower in the section.

Specimens are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warszawa, Poland (ZPAL).

GEOLOGICAL AGE OF THE FAUNA

In the Ordovician, the Siberian Platform was a separate continent with faunas biogeographically distinct from those of other regions of the world. Only some species of pelagic organisms had their distribution wide enough to enable age correlation. In the Angara section, the conodonts may serve this purpose, but our knowledge about them is at a rather preliminary stage, with the standard apparatus-based taxonomy applied to only a few species, none from the Badaranovo Formation. A brief overview of the evidence thus seems necessary.

Conodont samples rich enough to enable the apparatus study have been obtained from two glauconitic limestone beds near the base of the formation. They are underlain by mudstone beds, and overlain by reddish sandstone, with the *Angarella*-rich horizon a few meters higher. Glauconite is the main component of the rock in the basal bed of the Badaranovo Formation (Ang-3), whereas quartz sand dominates in the bed 40 cm higher in the section (Ang-2). Conodont faunas from these beds are closely similar to each other.

The most common conodont is a species of *Drepanoistodus* (141 specimens in Ang-3; 122 in Ang-2) with rather robust elements lacking any additional ribs (Moskalenko, 1984). Some elements resemble *Drepanodus* and were classified as such by Moskalenko (1984), but no symmetrical S_0 or geniculate M elements in the samples represent this genus. The second in number (19 specimens in Ang-3; 30 in Ang-2) is a similarly generalized species of *Acodus* with minute elements (possibly *A. deltatus*).

Conodonts with coniform elements in the apparatus are not common in the assemblages studied, the most important of them being *Glyptoconus*, probably *G. quadraplicatus* (there is a possibility that "*Oneotodus*" *rotundus* Moskalenko, 1967, is a P element of the same apparatus) (29 specimens in Ang-3; 24 in Ang-2). Hyaline *Drepanodus*-like specimens with the S_0 element distantly resembling *Ulrichodina* may be related to "*Drepanodus*" *concavus* as interpreted by Ji & Barnes (1990).

Of the greatest correlative value are two species of conodonts with incipient denticulation of some elements. The more elaborate of them is *Jumudontus sigmoidalis* (Moskalenko, 1984), different from its cosmopolitan relative *J. gananda* in having a narrow base and sinuous orientation of denticles in P_1 elements (22 specimens in Ang-3; 16 in Ang-2). The Siberian material does not support identification of M elements by Nicoll (1992), who attributed to *Jumudontus* probable specimens of *Protoprioniodus*. Instead, associated elements of the Siberian *Jumudontus* have a much less derived appearance (Moskalenko, 1984: pl. 16:18). *Jumudontus gananda* is widespread in the late *Oepikodus evae* Zone of the Arenig. The Siberian species, as suggested by its narrow base, may be transitional between *J. brevis* and *J. gananda* within the same lineage (see Nicoll, 1992), or represents a separate lineage that split out near this point. This interpretation is supported by the co-occurrence of an early member of the *Histiodella* lineage in Siberia (11 specimens in Ang-3; 9 in Ang-2). *Histiodella sibirica* (Moskalenko, 1967) (= *Histiodella angulata* Moskalenko, 1982) may be ancestral to *H. altifrons*, known to occur above the range of *J. gananda* (e.g., Pyle & Barnes, 2003).

Among the numerous relatively shallow-water conodonts reported from the lower Mamyry Formation by Moskalenko (1984), the most distinctive is the pterospathodontid "*Polyplacognathus*" *angarense* Moskalenko, 1984, of limited vertical distribution, but unknown outside Siberia. Higher up in the section it co-occurs with *Phragmodus flexuosus* Moskalenko, 1973, which indicates the *Pygodus serra* Zone of the Llanvirn.

Angarella is thus known to occur from the Mid Arenig to Late Llanvirn in terms of the British subdivision of the Ordovician.

Phosphatized ellesmeroceratid nautiloids were extracted from a detrital limestone intercalation in the stromatolithic Ust-Kut Formation at Pashino, stratigraphically much below the Badaranovo Formation. Associated specimens of *Cordylodus rotundatus* indicate its own Zone, that is early Tremadoc.

SHELL MORPHOLOGY AND STRUCTURE OF *ANGARELLA*

The shell of *Angarella* was bivalved, the upper (dorsal) one being of conical appearance and the lower (ventral) almost flat. Dorsal valves are very variable in outline and height of the cone (Figs. 2A, F, H, 3A). The sample taken to the laboratory is too small to offer a reasonable biometric evaluation of variability, but field observations suggest that there is a complete gradation in the shell geometry. The most common shell outline is oval, somewhat elongate, and with the greatest width at the level of the apex (Fig. 1A). Specimens circular in outline or slightly wider than long also occur. The apex is located in the posterior third of the dorsal valve in most specimens, but it may overhang the margin in the tallest ones (I apply here descriptives as for brachiopod shells, not molluscan conchs). Usually the length of the valve is about 3.5 times its height, but in the tallest specimens it is about 2.5, whereas in the flattest it may reach 4.0.

The apex of the dorsal valve, smooth and hemispherical in shape, is about 1 mm in diameter. Its surface is too crudely preserved, with imprints of sand grains, to allow discrimination of the larval stage.

The ventral valve was cemented to hard objects, as shown by attachment scars replicating the rough substratum surface of undetermined nature. Rarely it is cemented to other *Angarella* shells. Prominent irregular growth increments are discernible on an area of variable extent in the posterior region of the valve. This area is more or less concave, in connection with a slight dorsoventral curvature of the whole valve. Generally, the valve is almost flat and near its posterior margin it attains the greatest thickness. In specimens from marly facies (possibly separate species) this thickness exceeds 1 cm (Fig. 3B).

Shell Structure

The shell thickness is clearly correlated with its mode of growth. Tall-conical specimens are thin-walled (Figs. 2F, G, 3A), whereas low-conical dorsal valves and all ventral valves are thick-walled (Fig. 2H, I).

Internal structures of the *Angarella* shell are well preserved even in strata where aragonitic gastropod conchs are recrystallized into calcitic sparite or dissolved, which proves its originally calcitic composition. There is no evidence of secondary mineralisation or recrystallisation in specimens from Pashino but, as a result of mechanical weathering, the shell is cut by numerous cracks obliterating the original structure. The shell wall structure is laminar and imporous. Because of this structure, the shell matrix of weathered specimens easily splits into fine glossy blades. In the SEM, rhythmic banding is recognizable, with laminae thickness about 1.5 µm (Fig. 3E), with rhythmicity suggestive of daily increments (e.g., Goodwin et al., 2001).

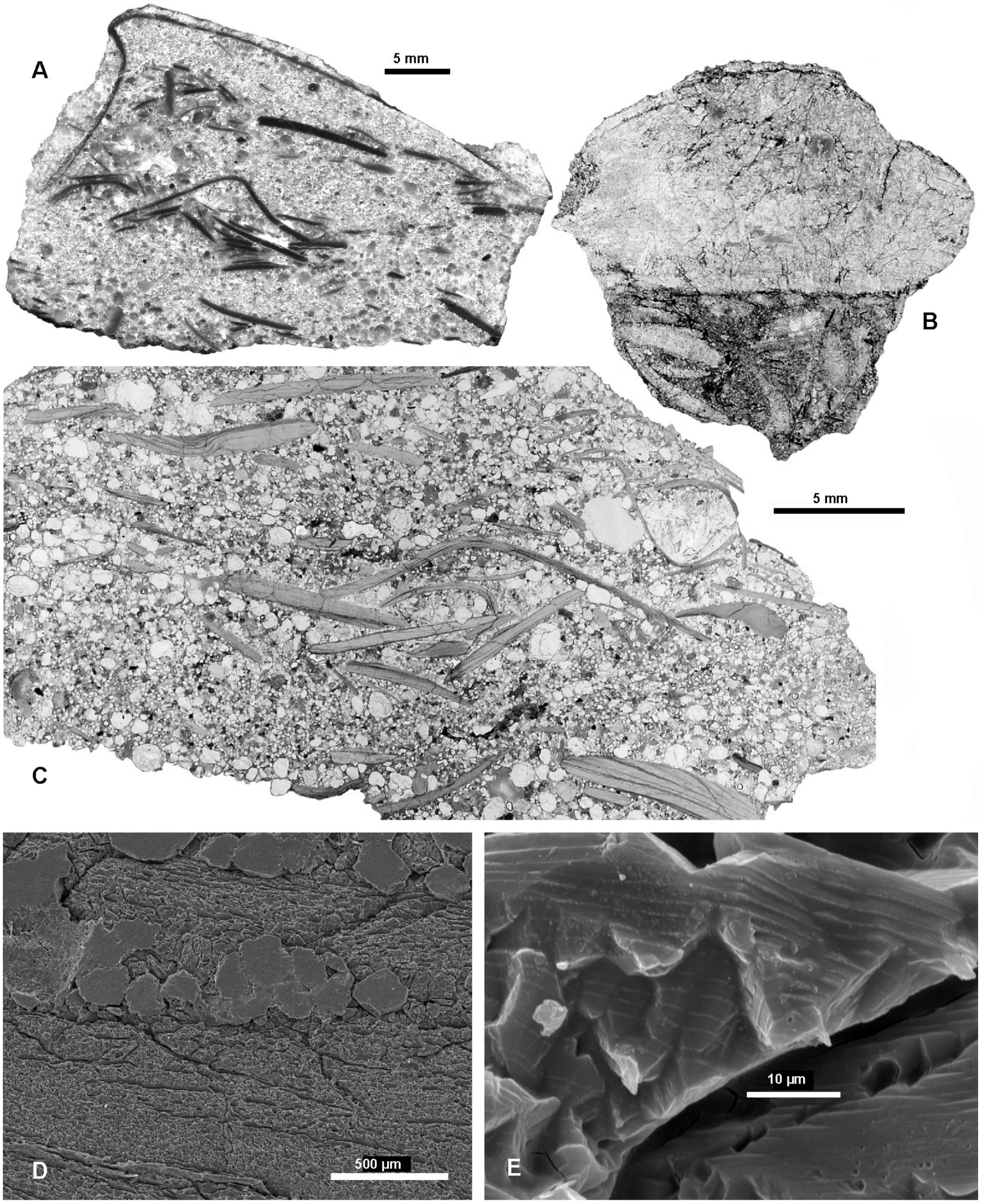

FIG. 3. Wall structure of *Angarella* from the bank of Angara. A, C–E: *Angarella jaworowskii* Asatkin, 1932, high-conical specimen ZPAL Bp 62/24 from the lower Badaranovo Formation at Pashino; polished section (A), thin section showing shell detritus in the sandstone (C), and SEM pictures of shells in transverse section etched with dilute acetic acid (D, E) note polished quartz sand grains in the upper part of the area shown (D) and fine lamination of the shell matrix, possibly daily increments (E); B: Very large and thick *Angarella* sp. ventral valve ZPAL Bp 62/13 from the upper Badaranovo Formation at Rozhkovka; thin section of the anterior margin of diageneticaly altered shell; note detritus of thinner parts of shells in the rock matrix below.

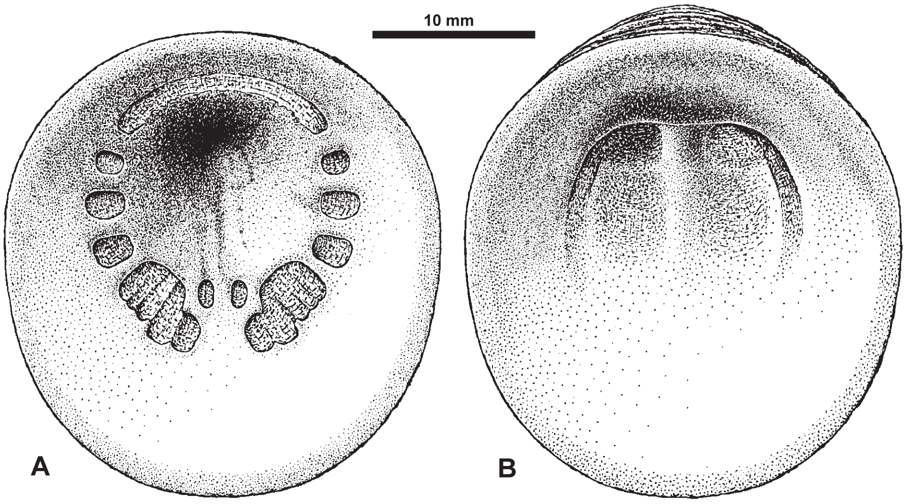

FIG. 4. Restoration of interiors of *Angarella jaworowskii* Asatkin, 1932, from the Badaranovo Formation of the Angara River region, Siberia. A: Interiors of dorsal valves based on ZPAL Bp 62/6; B: Interiors of ventral valves based on ZPAL Bp 62/8.

Muscle Attachments

Muscle attachment scars of *Angarella jaworowskii* were identified and illustrated by Yadrenkina (1984, pl. 8: 1a, b, pl. 9: 3). In her paper, they are shown as large dark-stained fields separated from each other by a narrow strip of lighter matrix. Their exact shape is hard to visualize based on published photographs.

More informative is the part of a mature dorsal valve from the Pashino block split along its internal surface (Fig. 2A–C). The valve represents the flat morphotype that has a relatively thick shell. Consequently, muscle attachment scars are relatively deep for the species. Moreover, roughness of the surface of the muscle attachment area, as compared with the rest of the shell interior, permitted the shell matrix to remain in places on the nucleus, demarcating the limits of muscle attachments. These are symmetrically distributed on both sides of the shell, excluding a possibility of being artifactual.

There are five paired scars and a probably continuous, narrow posterior band. The three lateral scars are of similar size (Fig. 4). A pair of large scars occupies the anteriormost position. These seem to be internally subdivided into smaller fields, perhaps five in each scar. Minute scars are near the midline of the valve at the level of posterior margin of the largest scars.

No ventral valve of comparable quality in representation of muscle attachments is available. The two best preserved specimens with the interior of the valve visible (Fig. 2D, E) show only indistinct areas of muscle attachments. They are clearly delimited by the thickened posterior region of the valve and the low medial ridge. An indistinct, very low transverse elevation may suggest that two pairs of large oval attachments are represented in the posterior part of the ventral valve floor, but their boundaries cannot be traced with confidence. There are two tear-like elongated belts of different coloration along the lateral margins of the valve floor that may also represent muscle attachments. This is definitely not enough to make restoration of ventral attachments reliable, and I hesitate to speculate about the relationship between dorsal and ventral muscle attachments in *Angarella*.

RELATIVES OF *ANGARELLA*

Siberian Species

Conical shells with muscle attachments virtually indistinguishable from those of *Angarella* are known from other rock units of the Early Ordovician and Late Cambrian of Siberia. The stratigraphically and geographically closest is probably *Nyuella bjalyi* Rosov, 1975, collected from sandy limestone near the base of the Ust-Kut Formation of the Kima stage, left bank of the Nyuia River, a tributary of the Lena River. The Ust-Kut Formation underlies the Badaranovo formation in the region, but it is not certain that everywhere they are of the same age. Muscle attachments are preserved as a dark carbonaceous(?) staining (Rosov, 1975) of the same kind as in the *Angarella* specimens of Yadrenkina (1984). There is a possibility that, like the Yadrenkina (1984) material, not all muscle scars are there reproduced with the stain and that these are actually specimens of *Angarella*.

Another form collected from the lower Ust-Kut Formation in the same area is *Lenaella octobinaria* Bjaly, 1973. The type locality is on the Kirenga River, 7 km upstream from Kluchi Village. *Lenaella octobinaria* differs from *Angarella jaworowskii* only in having a taller conical shell with the apex located in its center. It may well be ancestral to the lineage. In fact, Bjaly (1973) reported the species also from the Angara River at Rozhkovo, that is from the same locality from which the material of *Angarella* described here comes. He refers to concentric growth increments on the external surface of the shell, which means that it is preserved in at least some specimens.

The stratigraphically oldest Siberian member of the group and its name-giver is *Kirengella ayaktchica* Rosov, 1968. Its shell form is closely similar to that of *Lenaella*, and the muscle attachments pattern is virtually the same as in *Angarella*. *Kirengella ayaktchica* occurs in sandy limestone of the Khandin Formation on the Kirenga riverbank near the mouth of Ayaktcha stream in the same area of southern Siberia. Based on the co-occurrence of the trilobite *Delgeuloma*, characteristic for the Mansy regional stage, the age of the strata is believed to be Late Cambrian (Rosov, 1968). Specimens frequently preserve the shell, with concentric growth increments visible on the surface and, when the external shell layer is exfoliated, the surface is shiny and smooth (Rosov, 1968: 1429). This description suggests that the shell is of lamellar structure, presumably originally calcitic, as in *Angarella*.

Doguzhaeva (1972) named four species attributed to *Kirengella* and a new genus, *Romaniella*, from the Tremadoc (thus coeval to the southern Siberian Ust-Kut Formation) strata of the southern Urals, on the bank of the Ebit River near the mouth of Kultabasay Creek based on nuclei preserved in sandstone. Muscle scar attachments there are deep, which indicates reasonable thickness of the shell. Its original mineralogy remains undetermined. Specimens were separated to two genera because on specimens attributed by her to *Kirengella* two additional small anterior (posterior, if the molluscan interpretation is preferred) attachments are discernible. Otherwise the distribution of scars is virtually the same in all specimens. *Kirengella kultavasensis*, based on four specimens, *Romaniella aebitensis*, *R. getlingi* and *R. zverevi* of Doguzhaeva, 1972, are all from the same stratum. By analogy with *Angarella*, with which these Uralian form shares a similar shell appearance, one may suggest that they represent variability in shell form within a single population. Three separate small scars of *Romaniella* appear to correspond to each of the large scars of the anterior pair in *Angarella* and *Kirengella*. The admedial scars are between them, that is, somewhat anteriorward in respect to their position in *Angarella*.

Still within the Siberian Platform but near its northern margin is the type locality of *Moyerokania miagkovae* Rosov, 1970, found on the right bank of the Moyerokan River, a tributary of Moyero, near the mouth of the Superechi Stream. The species is known only from nuclei with muscle attachment scars (Rosov, 1970). They show a characteristic subquadrate outline, with the posterior margin almost straight. *Moyerokania miagkovae* is reported to co-occur with *Angarella*. The main difference between these genera is that in *Moyerokania* admedial scars are located anteriorward of the largest muscle scars.

European Species

Such disposition of muscle attachments characterizes also *Pygmaeoconus porrectus* (Barrande, in Perner, 1903) from the Llanvirn Šárka Formation of Bohemia (Horný, 2006). The shell of *P. porrectus* was thick, highly variable in its geometry and with irregular growth. Interestingly, the shell of this animal was precisely fit to the complex geometry of the substratum. This clearly resulted from its sessile growth mode. The ventral valve was apparently thin or even non-mineralized. A similar fossil, 11 mm long, still attached to the shell of a Mid Ordovician orthoconic nautiloid, was identified as *Archinacella* by Rudolph (1997: 33, fig. 11). The shell aperture in those specimens apparently replicate the substratum morphology, and this may explain unusual geometry of the shell

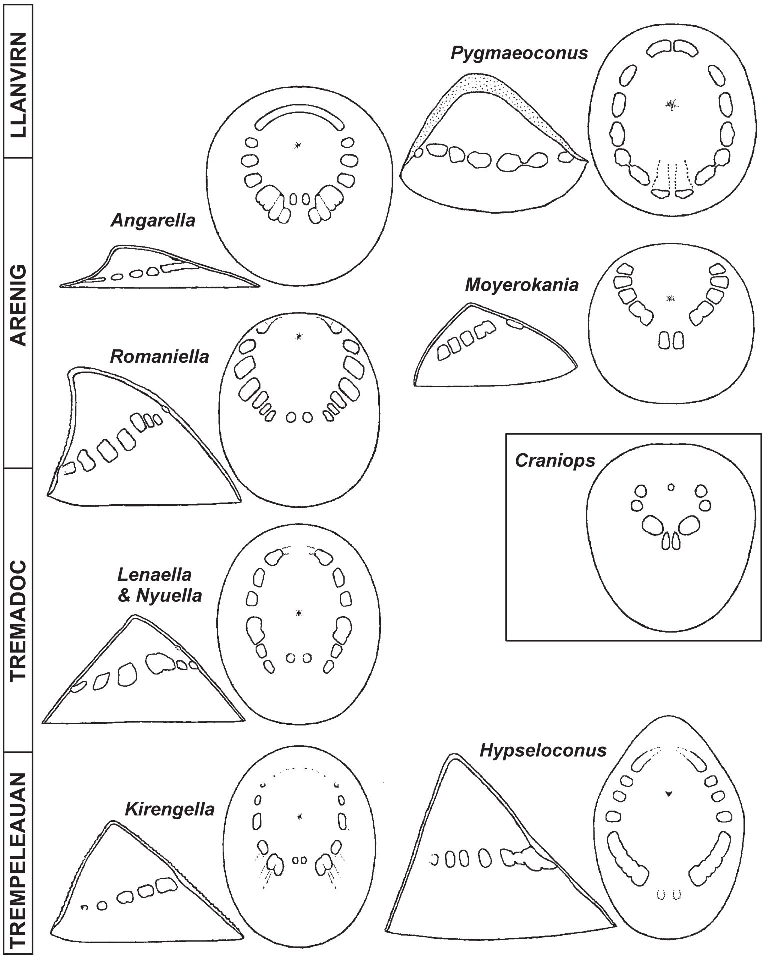

FIG. 5. Stratigraphic distribution of members of the Kirengellidae with known muscle attachments in the dorsal valve; diagrammatic representation of *Craniops* inserted. Restorations of muscle attachments distribution are based on literature sources reviewed in the text.

in the Uralian *Romaniella aebitensis*, to which aspect of morphology Doguzhaeva (1981) paid much attention. She interpreted the presence of a sinus at the adapical shell margin as evidence for a shell curvature opposite to that in *Kirengella*.

North American Midcontinent Species

Pygmaeoconus is geologically younger than *Romaniella* and *Moyerocania*, and the anterior disposition of its admedial attachment scars may be a derived character. If so, the alleged patellacean gastropod *Floripatella rousseaui* Yochelson, 1988, from the Whiterockian Kanosh Shale of Utah may be even more derived. Numerous muscle attachments form there an almost continuous horseshoe belt (Yochelson, 1988).

Serial muscle scars associated with conical shell shape have also been identified by Stinchcomb (1980) in another North American form, *Hypseloconus* cf. *H. stabilis* Berkey, 1898, from the Late Cambrian Davis Formation of Missouri. Although rather superficially described, the disposition of muscle attachments in this form seems similar to that in the type species of *Kirengella*, and because of this Webers et al. (1991) and Stinchcomb & Angeli (2002) placed *Hypseloconus stabilis* Berkey, 1898, and other American species earlier classified in this genus in *Kirengella*, namely *H. washingtonensis* Stinchcomb, 1975 (nom. corr. herein; *Hypseloconus* is of masculine gender, not neuter), and *H. simplex* Berkey, 1898. Stinchcomb & Angeli (2002) also added to *Kirengella Hypseloconus compressus* Ulrich & Bridge, 1931, *H. ozarkensis* Ulrich & Bridge, 1931, *Gasconadaeconus expansus* Stinchcomb, 1986, and *Kirengella oregonensis* Stinchcomb & Angeli, 2002. The family Kirengellidae was supplemented with his new genus and species *Irondalia irondalensis*. These all are forms of generalized morphology with unknown musculature, and their congenerity with *Kirengella* does not seem well substantiated.

If these nomenclatorial transfers were accepted, the muscle scars of true *Hypseloconus* (its type species is *H. recurvus* Berkey, 1898), as well as the original shell mineralogy, would remain unknown. However, shells of all the American species differ from the Siberian type species of *Kirengella* in being much taller, having an ovate cross-section and an anteriorly displaced apex. In stratigraphically higher Eminence and Gasconade Formations of Trempealeauan and earliest Ordovician age in Missouri more elongate and septate *Shelbyoceras* occurs. Muscle scars are unknown in it, but general shell form makes the ancestor-descendant relationship between *Hypseloconus* and *Shelbyoceras* likely. The North American lineage is likely to be separate of the Siberian one. A wide range of hypseloconid shell morphologies is known in the North American Midcontinent province (Greenland) as early as in the late Mid Cambrian (Peel, 1988).

The only other Cambrian fossil shell with preserved serial muscle attachments is that identified as *Scenella* sp. undet. by Rasetti (1954; Peel, 1991: 56). The almost centrally located shell apex and the arrangement of muscles make it more similar to the kirengellids than to the tergomyan monoplacophorans. In the latter, the “muscle scars form a ring located posterior to the shell apex, such that the apex lies outside of the muscle field” (Peel, 1991: 14).

The unavoidable consequence of the above review is that the family-rank taxa Hypseloconidae Knight, 1956, Kirengellidae Starobogatov, 1970, Romaniellidae Rosov, 1975, Hypseloconellacea (*recte* Hypseloconacea) Stinchcomb, 1986, and Pygmaeoconinae Horný, 2006, are subjective synonyms. The same refers to the orders Kirengellida Rosov, 1975, Romaniellida Doguzhaeva, 1981, and Hypseloconida Peel, 1991. Ironically, the arrangement of muscle attachments in the Kirengellida is rather different from that in unquestionable Monoplacophora, which appear to be unknown before the Late Ordovician. Instead, there are some Cambrian fossils exhibiting much similarity to the kirengellids in this respect.

CAMBRIAN PROBLEMATICA POSSIBLY RELATED TO A*NGARELLA*

In the Early Cambrian several species of phosphatic shells with muscle attachment scars of disposition similar to that in *Angarella* occur (Fig. 6). They are referred to as mobergellans (e.g., Conway Morris & Chapman, 1997; Skovsted, 2003) with the family name Mobergellidae Missarzhevsky, 1976, available. Although originally described as brachiopods, they are known exclusively from their “dorsal” valves that make such affinity difficult to support. Their brachiopod affinities are generally also considered unlikely because in some species shells are concave, which makes them similar rather to opercula of tubular skeletons (Bengtson, 1968). No such tubes fitting mobergellid and co-occurring with them have been identified yet.

However, some mobergellans have high vaulted shells (e.g., *Aktugaia* and *Thorslundella*) and with irregular outline and growth bands distribution making them similar to the kirengellids such as *Pygmaeoconus*. The lack of ventral valves in fossil assemblages could have resulted from their being unmineralized or cemented to hard bottom environments not represented in the fossil record. A taphonomic analogue may be offered by the Ordovician acrotretid *Eoconulus*, which cemented to the substratum by its ventral valve. Although its phosphatic dorsal valves are common fossils, known after incomparably more numerous specimens than mobergellas, it took some time until the rare ventral valve was identified (Holmer, 1989: 147). One may speculate that the ventral cementing valve of mobergellans was flat or reduced in a manner suggested here for the kirengellid *Pygmaeoconus*.

Despite the similarity in overall form, the phosphatic composition of the mobergellans makes them basically different from the kirengellids. The difference is original (Nyers, 1987; Skovsted, 2003), because at least in *Aktugaia triangula* Missarzhevsky, 1976, from

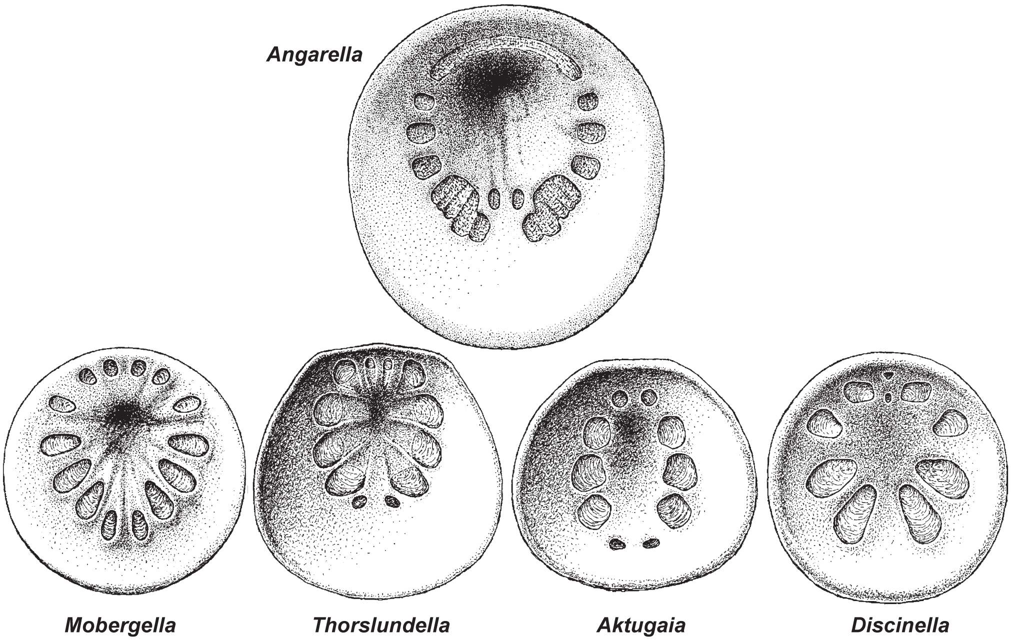

FIG. 6. Comparison of muscle attachments in the dorsal valve of *Angarella* with those of various members of the Mobergellidae. Restorations are based on literature sources reviewed in the text.

the Geres Member of the Shabakhty Formation in Malyi Karatau Range, Kazakstan, the shell differs from secondarily phosphatized co-occurring mollusk shells in its shiny appearance (Skovsted, 2003).

Genera of the mobergellans differ from each other in number of muscle attachments (Skovsted, 2003). The pattern of attachments, with a circle of oval attachments surrounding apex, makes them remotely similar to the "cyclomyan" bellerophontids, and such affinity has been proposed for them by Nyers (1987). However, in their roughly similar size decreasing posteriorly (brachiopod orientation applied), and the presence of a pair of distinctly smaller scars at the anterior end, they more closely resemble the pattern represented in the kirengellids. The small anterior attachments pair are in the ring, thus in position like *Hypseloconus* rather than *Kirengella*. There is a long time span separating the oldest kirengellids from the mobergellans, which makes a relationship between them only a highly hypothetical possibility. However, the mobergellans remain the only fossil organisms preceding the kirengellids with a similar body plan.

BRACHIOPOD AFFINITIES OF *ANGARELLA*

Originally *Angarella* was attributed to the Craniidae. This affinity was questioned by Yadrenkina (1984), because, unlike recent craniids, the four pairs of large muscle attachment scars she identified inside the dorsal valve of *Angarella* leave only one third of the internal shell volume for the mantle cavity. She noticed that there was virtually no space for the lophophore and that the virtually flat ventral valve did not protect the animal against ingestion of the mud from the sea bottom. Therefore, she proposed that *Angarella* represents a new unknown group of animals with bivalve shells of the brachiopod ground plan.

Lophophore of *Heliomedusa*

The problem of the space for the lophophore in the shell of *Angarella*, raised by Yadrenkina (1984), has been indirectly solved by *Heliomedusa*, an Early Cambrian mickwitziid (Holmer & Popov, 2007) with a thin organic or organophosphatic shell. This brachiopod had a surprisingly simple lophophore, with a row of radially oriented tentacles forming a relatively narrow belt along the anterior part of the shell. Its extent was virtually the same as, or at least closely similar to, the area outside the muscle scar belt in *Angarella* (Chen et al., 2007: fig. 3: 4). A large visceral mass may be plesiomorphic for brachiopods, as suggested by its entering the base of the pedicle in some Early Cambrian lingulids (Zhang et al., 2005, 2007; Holmer & Caron, 2006). *Heliomedusa*, as restored by Chen et al. (2007), had a simple organization of adductors, with a pair of large anterior and another pair of small posterior muscles surrounding the large visceral mass with pedicle in the center. Although *Heliomedusa* is not a craniopsid, its ancestral position with respect to craniopsids and perhaps also kirengellids seems likely (at least it is a more parsimonious solution than assuming completely independent origin of calcareous and organophosphatic skeletons). Transition from a shortened pedicle to shell cementation may have occurred in a way analogous to the shift from a massive shortened byssus to cementation in the anomiid bivalves (Fürsich & Palmer, 1982).

Kirengellid and Craniopsid Shells

Apart from the disposition of the dorsal valve muscle attachments, the *Angarella* shell is similar to that of the craniopsid inarticulate brachiopods. In particular, the general appearance of shells of the Devonian *Lingulapholis*, free lying on the sediment surface in its postlarval stage, is like that of *Angarella*. The Mid to Late Ordovician (Caradoc-Ashgill) *Pseudopholidops* differs from *Lingulapholis* only in the distribution of muscles, whereas *Craniops* (Caradoc-Tournaisian) was attached apically by cementation (Popov & Holmer, 2000).

The calcitic secondary shell of *Craniops* has a laminar structure (Williams, 1997: fig. 249.1), thus similar to that of *Angarella*. The *Angarella* shell matrix shows increments similar to those in the Ordovician *Petrocrania* (Cusack & Williams, 2007: fig. 1648a) or Recent *Novocrania* (Cusack & Williams, 2007: fig. 1644). It is possible that the shell of *Angarella* underwent some diagenetic changes of a similar kind as those in fossil craniids, but its originaly calcitic and laminar structure seems to be not in doubt, being visible in thin sections, on etched surfaces and in the pattern of exfoliation. Under SEM, the shell matrix of *Angarella* (Fig. 3E) shows growth banding resembling that in the primary calcitic shell layer of brachiopods, for instance in the advanced Recent *Notosaria* (Williams et al., 1997: fig. 11.1).

The main and possibly fundamental difference between the Craniopsida Gorjansky & Popov, 1985, and the Kirengellida is in the distribution of shell muscles. In *Angarella*, instead of three pairs of lateral muscle scars recognized in *Craniops* (Popov & Holmer, 2000), there are four. Instead of the single posterior attachment there is a posterior belt. Presence of paired posterior and anterior adductors is considered plesiomorphic to all brachiopods by Holmer et al. (1995) and rather conservative in their evolution. If the kirengellids are truly brachiopods, a secondary complication of their musculature took place in their early evolution, perhaps in connection with cementation to the substratum and under selection pressure, of a kind similar to that acting on limpet-like molluscs.

Ancestry of Kirengellids

To resolve the question of the origin of the discrepancy in musculature, the evolution of the kirengellids and craniopsids has to be traced backward up to the identification of their putative common ancestor. This does not seem possible at the moment.

Probably the geologically oldest craniopsid with well-known musculature is *Pseudopholidops stolleyana* (Huene, 1900) from the Caradoc (Baltic Nabala-Vormsi stages) of Belorussia (Popov & Pushkin, 1986). It is still much younger geologically than the last kirengellids. Juvenile shells with a shape similar to those of *Angarella* from the latest Early Ordovician (Kunda-Aseri boundary) were tentatively attributed to the craniids (Madison, 2007). The craniids, which are more derived than craniopsids, are known already from the Tremadoc (Mergl, 2002; Sdzuy et al., 2001), which implies a “ghost” lineage of the craniopsids exists before this date. Only putative craniopsid relatives, with strongly convex larval shell, are known from the Early Cambrian Upper Bastion Formation of Greenland (Skovsted & Holmer, 2005). Other Cambrian brachiopods with calcareous shells (Balthasar, 2008) are rather unlikely to be related to the craniopsids or kirengellids.

A possibility remains that the mobergellans are near the ancestry of both the craniopsids and kirengellids. The Mid Cambrian *Scenella* of Rasetti (1954) may represent the connecting link, although it is too incompletely known for this purpose. The mobergellan and kirengellid anterior admedial pair of small muscles would represents the brachial protractor (Popov & Holmer, 2000), homology of other muscles remaining obscure (Fig. 6).

The difference in shell composition may not be of great importance, as in the early brachiopods organic, phosphatic, aragonitic and calcitic shells are known, and the gap between lineages characterized by different skeletal mineralogy does not need to be wide (Balthasar, 2008). This is suggested also by the apparent craniopsid affinities of the trimerellid brachiopods with presumably originally aragonitic shell (Gorjansky & Popov, 1985, 1986). Probably also shells of some of the kirengellids were aragonitic. This could have been the case with unnamed forms I collected from the upper part of Ust-Kut Formation at Angara near Kudinsk and the Krivaya Luka Formation at the Lena River. In shell shape they are similar to *Kirengella* or even taller, resembling the North American *Hypseloconus*. They frequently show their shell matrix recrystallised into calcitic sparite, as if originally aragonitic. Obviously, a possibility remains that the aragonitic *Kirengella*-like Ordovician fossils are truly monoplacophorans. Nevertheless, additional evidence for this has to be provided, as the serial distribution of muscle attachment is misleading.

Whether the bivalved kirengellids are brachiopods or not, they have to be removed from considerations on the early evolution of mollusks, in which these fossils were assumed to play the main role. It appears that the pre-Late Ordovician history of the tergomyan Monoplacophora has to be rewritten. More specifically, the brachiopod affinity of the celebrated high-conical *Hypseloconus* calls for reconsideration of the theory about the ancestry of Cephalopoda.

ORIGINS OF THE CEPHALOPODS

It is generally accepted that the body plans of cephalopods, monoplacophorans, and basal gastropods are closely similar. There is a significant progress in understanding the origin and early evolution of the nominal cephalopod organs: head and arms. Embryological evidence is now available that the unique digital tentacles of *Nautilus* or arms of other cephalopods developed from the foot of an ancestral mollusk (Shigeno et al., 2008). Comparative anatomical data suggest that the adhesive function of carbohydrates and proteins secreted on tentacles of *Nautilus* was probably gradually taken over by muscular suckers in more advanced forms (von Byern & Klepal, 2006). Such interpretations of the evolution of soft parts are difficult to test with the paleontological evidence, but the modifications of shell in the evolution of cephalopods have a rather good fossil record. An exception is the origin of the phragmocone, which probably took place not later than in the early Late Cambrian. In this respect we have to rely only on speculations.

Peel (1991) reaffirmed Yochelson et al.'s (1973) hypothesis that cephalopods originated from a benthic monoplacophoran similar to *Hypseloconus*. Based on endogastric curvature, he proposed aenigmatic helcionellid molluscs as possible ancestors to the cephalopods, the idea supported by molecular phylogenetic proximity of scaphopods (probable distant successors of the helcionellids) to cephalopods (Steiner & Dreyer, 2003). The main argument used by Yochelson et al. (1973) and Webers & Yochelson (1989) was the presence of diaphragms (septa) in the apex. Dzik (1981), Chen & Teichert (1983), and Teichert (1988) pointed out that it is the siphuncle, not septa, that makes a cephalopod and that septa occur widely in high-conical shells of unrelated invertebrates. Cephalopods from the beginning of their palaeontologically documented history differ from the monoplacophorans in the shape of their larval shells. In their subspherical apex and cylindrical appearance, they resemble rather larval shells of gastropods. A flat discoidal larval shell is known to occur in the tryblidiid monoplacophorans at least since the Silurian (Dzik, 1994: 294, fig. 30A). Possibly they had such shells already in the Early Cambrian, although mollusks of that age with low cap-like larval shells have not been shown to have serial pedal musculature (Dzik, 1994: 265, fig. 12A). Such shell morphology of the Cambrian limpet-like mollusks means that the early development within the egg capsule without free-living larva characterized tryblidiid monoplacophorans for all their evolution. Thus, according to the Yochelson et al. (1973) theory, the pelagic mode of life was a complete novelty in the lineage of benthic monoplacophorans adapted to life among stromatolites. Such was the ecology of *Hypseloconus* and related forms (Stinchcomb, 1975) interpreted as molluscs.

On the contrary, I proposed (Dzik, 1981) that the origin of the phragmocone in the early evolution of cephalopods was a result of extension of the pelagic mode of larval life of their ancestors to mature stages, in a way similar to pteropods. I suggested that the

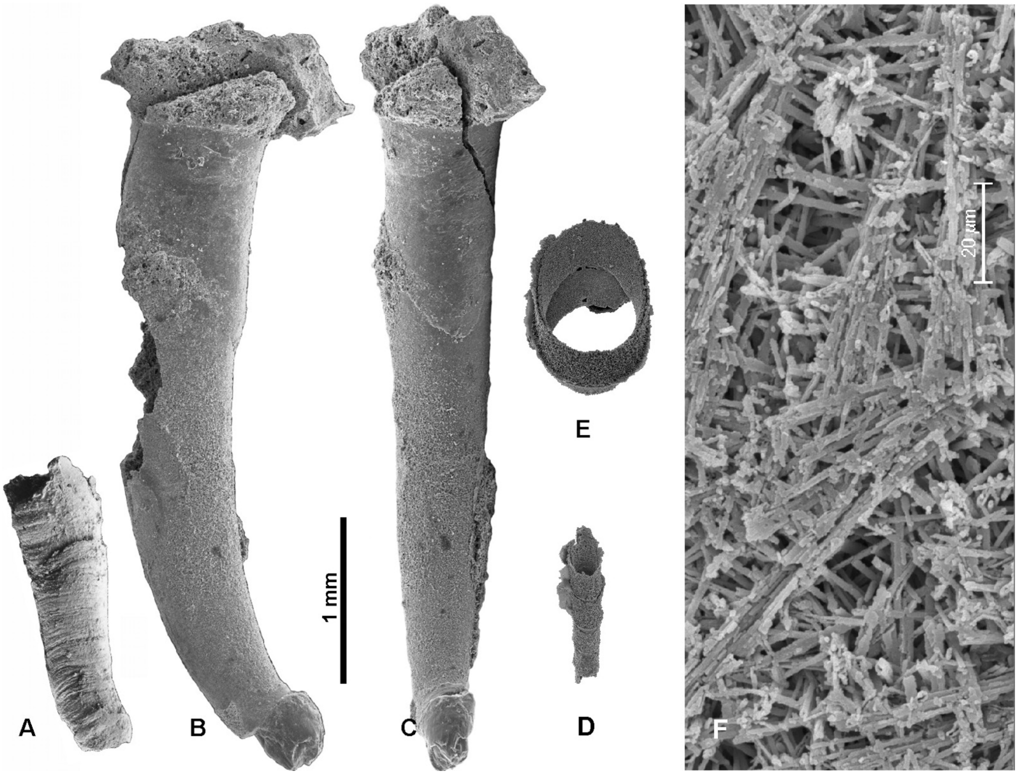

FIG. 7A–C. Possible relative of earliest cephalopods, *Turcutheca crassaecochlia* Syssoiev, 1962, from the Tommotian (*Dokidocyathus lenaicus* Zone) at Bydyangaia on the Lena River, central Yakutia; phosphatized specimens photographed under SEM. A: Specimen with well preserved surface of embryonic part (destroyed while removed from the stub); B, C: Probably mature specimen (largest known) with partially phosphatized shell wall and displaced embryonic part preserved as glauconitic internal mold, lateral and posterior ('ventral') views; D–F: Pieces of phosphatized siphuncles (mineralized fibres of the connecting ring enlarged in F) of ellesmeroceratid nautiloids from the earliest Ordovician (early Tremadoc) Ust-Kut Formation at Pashino, Angara River, southern Yakutia; note that inferred larval conch size was similar to that of *Turkutheca* but mature specimens were many times larger.

positive buoyancy by replacing liquid with gas in the phragmocone chambers (Greenwald et al., 1982, 1984; Greenwald & Ward, 1987) was preceded by a plain removal of sodium ions from the liquid inside the conch tip as a result of the siphonal epithelium sodium pump action, in a way analogous to that of the Recent cranchiid squids. This requires that the cephalopod ancestor already had a pelagic veliger-like larva with subspherical embryonic and cylindrical larval conchs. Such conchs characterized the orthoceratid and presumably also ellesmeroceratid cephalopods (Dzik, 1981); note that the smallest piece of the oldest known Late Cambrian cephalopod *Plectronoceras* was less than 1 mm in diameter (Webers & Yochelson, 1989: fig. 3), which suggests the presence of a minute pelagic larva. From the earliest Ordovician Ust-Kut Formation at Pashino fragmentary phosphatized conchs of ellesmeroceratid nautiloids were recovered with siphuncle diameter 160 µm; the conch apex diameter was thus less than 0.8 mm. The size of the embryonic conch was not much larger than in other early mollusks. Larvae with elongate cylindrical conches were also typical for the Cambrian bellerophontids, gastropods, and hyoliths (Dzik, 1994).

Possible ancestors of the lineage leading to the cephalopods are known from the Early Cambrian. *Turcutheca* is an Early Cambrian mollusk with the general conch form closely resembling that of the earliest ellesmeroceratid cephalopods: endogastrically curved and laterally compressed, with relatively large subspherical embryonic part (Fig. 7). As usual for any high-conical shells, diaphragms may occur in the apex of *Turcutheca* or related forms, but no sign of anything similar to a siphuncle is known. Despite its unusual conch form *Turcutheca* seems related to hyoliths (they have a depressed and straight or exogastric conch). Perhaps it had a morphologically simple calcified operculum, like its relative *Ladatheca* (Dzik, 1994: 268). If it is truly related to cephalopods, not only did the siphuncle have to develop in the course of evolution to the Late Cambrian cephalopods but also the size of the conch, both mature and embryonic, had to increase. Together with reduction of the foot, the operculum was probably transformed into the lower jaw (Dzik, 1981; the idea presented also without attribution to its source in Seilacher, 1993).

ACKNOWLEDGEMENTS

I am grateful to Aleksandr Kanygin (Institute of Petroleum Geology and Geophysics, Novosibirsk) and Andrey Dronov (St. Petersburg State University) for introducing me into the Irkutsk Amphitheatre geology. My participation in the expedition to the Cambrian exposures near Yakutsk in 2006 (led by V. M. Sundukov) and to the Angara and upper Lena Rivers in 2007 (led by Taras Gonta) was possible owing to the exchange program between the Polish Academy of Sciences and the Russian Academy of Sciences. My visit to The Natural History Museum, London, was supported by SYNTHESYS in 2008. Lars Holmer (Uppsala Universitetet) and Andrzej Baliński (Instytut Paleobiologii PAN, Warsaw) read the manuscript and provided very helpful comments on it.

LITERATURE CITED

BALTHASAR, U., 2008, *Mummpikia* gen. nov. and the origin of calcitic-shelled brachiopods. *Palaeontology*, 51: 263–279.

BENGTSON, S., 1968, The problematic genus *Mobergella* from the Lower Cambrian of the Baltic area. *Lethaia*, 1: 325–351.

BJALY, V. I., 1973, Novyie ranneordovikskiye monoplakofory Sibiri. *Paleontologicheskiy Zhurnal*, 1973 (3): 47–51.

CHEN, J.-Y. & C. TEICHERT, 1983, Cambrian cephalopods. *Geology*, 11: 647–650.

CHEN, J.-Y., D.-Y. HUANG & S.-H. CHUANG, 2007, Reinterpretation of the Lower Cambrian brachiopod *Heliomedusa orienta* Sun and Hou, 1987a as a discinid. *Journal of Paleontology*, 81: 38–47.

CONWAY MORRIS, S. & A. J. CHAPMAN, 1997, Lower Cambrian halkieriids and other coeloscleritomorphs from Aksu-Wushi, Xinjiang, China. *Journal of Paleontology*, 71: 6–22.

CUSACK, M. & A. WILLIAMS, 2007, Biochemistry & diversity of brachiopod shells. Pp. 2373–2395, in: P. A. Selden, ed., *Treatise on Invertebrate Paleontology*, *Part H, Brachiopoda*, Vol. 6. Geological Society of America, Boulder, Colorado.

DIVINA, T. A., A. V. KANYGIN, V. G. MATUKHINA, T. A. MOSKALENKO & A. G. YADRENKINA, 1984, Opisanie razrezov. *Trudy Instituta Geologii i Geofiziki SO AN SSSR*, 529: 5–46.

DOGUZHAEVA, L. A., 1972, Novyie tremadokskiye monoplakofory Yuzhnogo Urala. *Paleontologicheskiy Zhurnal*, 1972(1): 24–28.

DOGUZHAEVA, L. A., 1981, Sinus kolpachkovidnykh monoplakofor. *Doklady Akademii Nauk SSSR*, 258: 209–211.

DZIK, J., 1981, Origin of the Cephalopoda. *Acta Palaeontologica Polonica*, 26: 161–191.

DZIK, J., 1994, Evolution of ‘small shelly fossils’ assemblages of the early Paleozoic. *Acta Palaeontologica Polonica*, 39: 247–313.

FÜRSICH, F. T. & T. J. PALMER, 1982, The first true anomiid bivalve? *Palaeontology*, 25: 897–903.

GOODWIN, D. H., K. W. FLESSA, B. R. SCHÖNE & D. L. DETTMAN, 2001, Cross-calibration of daily growth increments, stable isotope variation, and temperature in the Gulf of California bivalve mollusk *Chione cortezi*: implications for paleoenvironmental analysis. *Palaios*, 16: 387–398.

GORJANSKY, W. J. & L. Y. POPOV, 1985, Morfologia, sistematicheskoye polozhenie i proiskhozhdenie bezzamkovykh brachiopod s karbonatnoy rakovinoy. *Paleontologicheskiy Zhurnal*, 1985 (3): 3–19.

GORJANSKY, W. J. & L. Y. POPOV, 1986, On the origin and systematic position of the calcareous-shelled inarticulate brachiopods. *Lethaia*, 19: 233–240.

GREENWALD, L., C. B. COOK & P. D. WARD, 1982, The structure of the chambered nautilus siphuncle: the siphuncular epithelium. *Journal of Morpholog*y, 172: 5–22.

GREENWALD, L., G. VERDERBER & C. SINGLEY, 1984, Localization of Na-K ATPase activity in the nautilus siphuncle. *Journal of Experimental Zoology*, 229: 481–484.

GREENWALD, L. & P. D. WARD, 1987, Buoyancy in *Nautilus*. Pp. 547–560, in: W. B. Saunders & N. H. Landmann, eds., *Nautilus*. Plenum Publishing Corp., New York.

HOLMER, L., 1989, Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna. *Fossils and Strata*, 26: 1–172.

HOLMER, L., L. E. POPOV, M. G. BASSETT & J. LAURIE, 1995, Phylogenetic analysis and ordinal classification of the Brachiopoda. *Palaeontology*, 38: 713–741.

HOLMER, L. E. & J.-B. CARON, 2006, A spinose stem-group brachiopod with pedicle from Middle Cambrian Burgess Shale. *Acta Zoologica*, 87: 273–290.

HOLMER, L. E. & L. E. POPOV, 2007, Incertae sedis: Organophosphatic bivalved stem-group brachiopods. Pp. 2580–2590, in: P. A. Selden, ed., *Treatise on Invertebrate Paleontology, Part H Brachiopoda, revised Volume 6: Supplement*, Geological Society of America, Boulder, Colorado.

HORNÝ, R. J., 2006, The Middle Ordovician tergomyan mollusc *Pygmaeoconus*: An obligatory epibiont of hyolithids. *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, 62: 81–95.

JI, Z. & C. R. BARNES, 1990, Apparatus reconstruction of Lower Ordovician conodonts from the Midcontinent province. *Courier Forschungsinstitut Senckenberg*, 118: 333–351.

KNIAZEV, S. A., 1978, Ordovikskiye otlozheniya shirotnogo techenia Angary. *Geologia i geofizika SO AN SSSR*, 10: 54–61.

KRÖGER, B., 2007, Some lesser known features of the ancient cephalopod order Ellesmerocerida (Nautiloidea, Cephalopoda). *Palaeontology*, 50: 565–572.

MADISON, A. A., 2007, Pervyie nakhodki lichinochnykh rakovin kraniid v ordovikie Pskovskoi oblasti. *Paleontologicheskiy Zhurnal*, 2007(3): 16–18.

MERGL, M., 2002, Linguliformean and craniiformean brachiopods of the Ordovician (Třenice and Dobrotivá Formations of the Barrandian, Bohemia. *Acta Musei Nationalis Pragae, Series B, Natural History*, 58: 1–82.

MOSKALENKO, T. A., 1984, Konodonty. *Trudy Instituta Geologii i Geofiziki SO AN SSSR*, 529: 65–105.

NICOLL, R. C., 1992, Analysis of conodont apparatus organization and the genus *Jumudontus* (Conodonta), a coniform—pectiniform apparatus structure from the Early Ordovician. *BMR Journal of Australian Geology & Geophysics*, 13: 213–228.

NYERS, A. J., 1987, *Thorslundella*: a proposed early Cambrian protogastropod that secreted a phosphatic shell due to environmental constraints. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 174: 171–192.

PEEL, J. S., 1988, Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland. *Meddelelser om Grønland, Geoscience*, 20: 145–168.

PEEL, J. S., 1991, The classes Tergomya and Helcionelloida, and early molluscan evolution. *Grønlands Geologiske Undersøgelse, Bulletin*, 161: 11–65.

POPOV, L. E. & L. E. HOLMER, 2000, Craniopsida. Pp. 164–168, in: R. L. Kaesler, ed., *Treatise on Invertebrate Paleontology, Part H Brachiopoda revised Volumes 2–3: Linguliformea, Craniiformea, and Rhynchonelliformea (part)*. Geological Society of America, Boulder, Colorado.

POPOV, L. E. & V. I. PUSHKIN, 1986, Ordovikskiye bezzamkovyie brachiopody yuzhnoi Pribaltiki. Pp. 11–22, in: R. G. Garecki, S. F. Zubowicz & V. I. Pushkin, eds., *Novyie i maloizvestnyie vidy iskopayemykh zhivotnykh i rastenii Belorussii*, Nauka i Technika, Minsk.

PYLE, L. J. & C. R. BARNES, 2003, Conodonts from a platform-to-basin transect, Lower Ordovician to Lower Silurian, northeastern British Columbia, Canada. *Journal of Paleontology*, 77: 146–171.

RASETTI, F., 1954, Internal shell structures in the Middle Cambrian gastropod *Scenella* and the problematic genus *Stenothecoides*. *Journal of Paleontology*, 28: 59–66.

ROSOV, S. N., 1968, Novyi rod pozdnekembriyskikh molluskov iż klassa monoplakofor (yuzhnaya chast Sibirskoi Platformy). *Doklady Akademii Nauk SSSR*, 183: 1427–1430.

ROSOV, S. N., 1970, Novyi predstavitel ranneordovikskikh monoplakofor Sibiri. *Paleontologicheskiy Zhurnal*, 1970(2): 109–112.

ROSOV, S. N., 1975, Novyi otriad monoplakofor. *Paleontologicheskiy zhurnal*, 1975(1): 41–45.

RUDOLPH, F., 1997, Geschiebefossilien. Teil 1: Paläozoikum. *Fossilien*, *Sonderheft*, 12: 1–64.

SDZUY, K., W. HAMMANN & E. VILLAS, 2001, The Upper Tremadoc fauna from Vogtendorf and the Bavarian Ordovician of the Frankenwald (Germany). *Senckenbergiana lethaea*, 81: 207–261.

SEILACHER, A., 1993, Ammonite aptychi; how to transform a jaw into an operculum? *American Journal of Science*, 293: 20–32.

SHIGENO, S., T. SASAKI, T. MORITAKI, T. KASUGAI, M. VECCHIONE & K. AGATA, 2008, Evolution of the cephalopod head complex by assembly of multiple molluscan body parts: Evidence from *Nautilus* embryonic development. *Journal of Morphology*, 269: 1–17.

SKOVSTED, C. B., 2003, Mobergellans (Problematica) from the Cambrian of Greenland, Siberia and Kazakhstan. *Paläontologische Zeitschrift*, 77: 429–443.

SKOVSTED, C. B. & L. E. HOLMER, 2005, Early Cambrian brachiopods from North-East Greenland. *Palaeontology*, 48: 325–345.

STEINER, G. & H. DREYER, 2003, Molecular phylogeny of Scaphopoda inferred from 18S rDNA sequences – support for a Scaphopoda-Cephalopoda clade. *Zoologica Scripta*, 32: 343–356.

STINCHCOMB, B. L., 1975, Paleoecology of two new species of Late Cambrian *Hypseloconus* (Monoplacophora) from Missouri. *Journal of Paleontology*, 49: 416–421.

STINCHCOMB, B. L., 1980, New information on Late Cambrian Monoplacophora *Hypseloconus* and *Shelbyoceras* (Mollusca). *Journal of Paleontology*, 54: 45–49.

STINCHCOMB, B. L., 1986, New Monoplacophora (Mollusca) from the Late Cambrian and Early Ordovician of Missouri. *Journal of Paleontology*, 60: 606–626.

STINCHCOMB, B. L. & N. A. ANGELI, 2002, New Cambrian and Lower Ordovician monoplacophorans from the Ozark Uplift, Missouri. *Journal of Paleontology*, 76: 965–974.

TEICHERT, C., 1988, Main features of cephalopod evolution. Pp. 11–75, in: M. R. Clarke & E. R. Trueman, eds., *The Mollusca 12, Paleontology and Neontology of Cephalopods*, Academic Press, Orlando, Florida.

VON BYERN, J. & W. KLEPAL, 2006, Adhesive mechanisms in cephalopods: a review. *Biofouling*, 22: 329–338.

WEBERS, G. F. & E. L. YOCHELSON, 1989, Late Cambrian molluscan faunas and the origin of the Cephalopoda. *Special Publications of the Geological Society of London*, 47: 29–42.

WEBERS, G. F., E. L. YOCHELSON & T. KASE, 1991, Observations on a Late Cambrian cephalopod. *Lethaia*, 24: 347–348.

WILLIAMS, A., 1997, Shell structure. Pp. 267–320, in: R. L. KAESLER, ed., *Treatise on Invertebrate Paleontology Part H Brachiopoda revised Volume 1: Introduction*, Geological Society of America, Boulder, Colorado.

WILLIAMS, A., M. A. JAMES, C. C. EMIG, S. MACKAY & M. C. RHODES, 1997, Anatomy. Pp. 7–188, in: R. L. KAESLER, ed., *Treatise on Invertebrate Paleontology Part H Brachiopoda revised Volume 1: Introduction*, Geological Society of America, Boulder.

YADRENKINA, A. G., 1984, Brachiopody. *Trudy Instituta Geologii i Geofiziki SO AN SSSR*, 529: 48–62.

YOCHELSON, E. L., 1988, A new genus of Patellacea (Gastropoda) from the Middle Ordovician of Utah: The oldest known example of the superfamily. *New Mexico Bureau of Mines and Mineral Resources Memoir*, 44: 195–200.

YOCHELSON, E. L., R. H. FLOWER & G. F. WEBERS, 1973, The bearing of the new Late Cambrian monoplacophoran genus *Knightoconus* upon the origin of the Cephalopoda. *Lethaia*, 6: 275–310.

ZHANG, Z., J. HAN, X. ZHANG, J. LIU, J. GUO & D. SHU, 2007, Note on the gut preservation in the Lower Cambrian *Lingulellotreta* (Lingulata, Brachiopoda) from southern China. *Acta Zoologica*, 88: 65–70.

ZHANG, Z., D. SHU, J. HAN & J. LIU, 2005, Morpho-anatomical differences of the Early Cambrian Chengjiang and Recent lingulids and their implications. *Acta Zoologica*, 86: 277–288.

Revised ms. accepted 9 October 2009