

A rare coleoid mollusc from the Upper Jurassic of Central Russia

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The shell of the coleoid cephalopod mollusc *Kostromateuthis roemeri* gen. et sp. n. from the lower Kimmeridgian of Central Russia consists of the slowly expanding orthoconic phragmocone and aragonitic sheath with a rugged surface, a weakly developed post-alveolar part and a long, strong, probably dorsal groove. The sheath lacks concentric structure common for belemnoid rostra. It is formed by spherulites consisting of the needle-like crystallites, and is characterized by strong porosity and high content of originally organic matter. Each spherulite has a porous central part, a solid periphery and an organic cover. Tubular structures with a wall formed by the needle-like crystallites are present in the sheath. For comparison the shell ultrastructure in Recent *Spirula* and *Sepia*, as well as in the Eocene *Belemmosis* were studied with SEM. Based on gross morphology and sheath ultrastructure *K. roemeri* is tentatively assigned to Spirulida and a monotypic family *Kostromateuthidae* nov. is erected for it. The Mesozoic evolution of spirulids is discussed.

Key words: Cephalopoda, Coleoidea, Spirulida, shell ultrastructure, Upper Jurassic, Central Russia.

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Introduction

The mainly soft-bodied coleoids (with the exception of the rostrum-bearing belemnoids) are not well-represented in the fossil record of extinct cephalopods that results in scanty knowledge of the evolutionary history of Recent coleoids and the rudimentary understanding of higher-level phylogenetic relationships of them (Bonnaud *et al.* 1997; Carlini & Graves 1999). Modern commonly accepted classification (Sweeney & Roper 1998) splits the coleoids into two superorders, the Decabranchia including the orders Spirulida, Sepiida, Sepiolida and Teuthida, and the Octobranchia including the orders Octopodida and Vampyromorphida.

Because of its shell a single extant spirulid *Spirula spirula* has great potentialities for the evolutionary morphology of cephalopods. Voss (1977) considered this form as a member of the order Sepioidea, but later it was demonstrated with the aid of the mo-

lecular phylogenetic analysis that *Sp. spirula* is linked neither to sepioids nor to teuthoids (Bonnaud *et al.* 1997; Carlini & Graves 1999). The evolution of spirulids is obscure, thus any shell found which might have belonged to this branch of coleoid cephalopods is of exceptional interest.

The Jurassic record of spirulids included a single Oxfordian form *Plagiot euthis moscoviensis* Roemer, 1890 (see Bülow-Trummer 1920). It is known by a sole rostrum-like structure with a deep alveolus and had no indications of conotheca, septa or siphuncle. Because of this the taxonomic assignment of the genus remains doubtful (Doyle *et al.* 1994). The present paper deals with a better preserved shell belonging to a previously unknown Early Kimmeridgian phragmocone-bearing orthoconic coleoid with a sheath-like structure instead of a real rostrum. It is described herein as *Kostromateuthis roemeri* gen. et sp. n. The sheath ultrastructure of *K. roemeri* studied with SEM yielded much new information concerning the ultrastructure of the coleoid shell that is useful for the comparison of *K. roemeri*, spirulids, sepiids, and belemnoids.

Materials and methods

The description of *Kostromateuthis roemeri* is based on a shell from the lower Kimmeridgian clay beds in the basin of the River Unzha, on its right bank near village Popovo, Kostroma Region, Central Russia. It was found together with several ammonites by a private collector, Mr. A.V. Stupachenko in 1998. V.V. Mitta (personal communication) assigned the ammonites to the following species: *Amoeboceras* (*Amoebobites*) ex. gr. *kitchini*, *A. (A.) pulchrum*, *Prorasenia* aff. *stephanoides*, and *Rasenoides?* sp. juv. The ammonoid assemblage indicates the standard *Cymodoce* Zone of the lower Kimmeridgian (Hantzpergue *et al.* 1998).

The specimen was studied with the scanning electron microscope (SEM) in the Paleontological Institute, Moscow. The micrographs were taken from the side showing the longitudinal groove and of the conical apical portion of the sheath; the latter being studied in fractured cross surface and from its outer surface. For comparison, the ultrastructure of the sheath of Recent *Spirula* from Cuba, *Sepia* from Australia, and *Belemnosis* from the Eocene of Turkey was studied with the SEM. The shells were etched with 5 per cent hydrochloric acid for 3–5 seconds.

The studied material is deposited in the Paleontological Institute of the Russian Academy of Sciences, Moscow, abbreviated as PIN.

Description

Class Cephalopoda Cuvier, 1794

Subclass Coleoidea Bather, 1888

Superorder Decabranchia Boettger, 1952

?Order Spirulida Pompeckj, 1912

Family Kostromateuthidae nov.

Type genus by monotypy: *Kostromateuthis* nov.

Diagnosis. — Small (approximately 2–4 cm in length) aragonitic orthocones, slowly expanding with bilaterally symmetrical sheath instead of rostrum. Sheath posteriorly conical; postalveolar portion absent or short; surface uneven; consisting of spherulites with much organic matter; thin (presumably) ventrally, thickened dorsally with the longitudinal central narrow part, which is thicker than elsewhere, bearing a groove, dorsally. The groove long, deep, bordered by two reinforced ridges with rows of tubercles along their crests and few smaller ridges on its floor. Phragmocone with simple camerae and straight septa; mural parts of septa long (about 1/3–2/5 of camera length); sutures non-sinuous.

Occurrence. — Upper Jurassic, lower Kimmeridgian; Unzha River, Kostroma Region, Central Russia.

Remarks. — The groove on the sheath is an apomorphy of the new family and distinguishes it from the older (Stephanian) family Shimanskyidae Doguzhaeva, Mapes, & Mutvei, 1998 and younger (Cretaceous) families Adygeyidae Doguzhaeva, 1996 and Groenlandibelidae Jeletzky, 1966, which have smooth shells, lacking grooves.

The family is tentatively referred to the Order Spirulida on the basis of the following common features: well developed slowly expanding phragmocone with comparatively short camerae, simple sutures, and septa with long mural parts; presence of a sheath with uneven surface and spherulitic ultrastructure instead of a real rostrum. The protoconch structure, namely: whether it had a closing membrane as in belemnoids, or a calcified first septum with a septal foramen, a caecum and a prosiphon as in spirulids, is so far unknown. But the family can hardly be referred to belemnoids because of the dimpled surface of the sheath which is a result of its spherulitic structure. Among belemnoids, the new family resembles diplobelids in having no postalveolar portion of the rostrum. However, diplobelids have breviconic phragmocones, sinuous sutures and crowded septae (Jeletzky 1981: p. 115), unlike the new family.

The reconstruction of the shell orientation is based on the fact that in coleoids the ventral side of the shell gradually lost its protective function and was replaced by a muscular mantle wall. For this reason the thickened side that bears the groove is considered as dorsal.

Genus *Kostromateuthis* nov.

Type species by monotypy: *Kostromateuthis roemeri* gen. et sp. n.

Derivation of name: From Kostroma, the capital of the region where the specimen was found.

Diagnosis. — Miniature orthocones with angle of expansion 18–20 degrees. Sheath conical with rounded apex and irregular rows of bean-shaped depressions apically, and smoother, 'pock-marked' adorally. Groove bordered by two ridges with rows of more than 10 tubercles along their crests; two or three smaller ridges on its floor.

Remarks. — In the uneven outer surface the sheath of *Kostromateuthis* is similar to partitions of the sheath of the Tertiary spirulid *Beloptera* (Dauphin 1985: fig. 3f) and the outer surface of the sheath of *Belemnosis*. Also the tubercles along the crests flanking the groove show similarity to the humps on the outer surface of a longitudinal partition of the *Beloptera* sheath (Dauphin 1985: fig. 4a). These were interpreted as unbroken spherulites (Dauphin 1985: p. 330). Spherulites with central depressions are known in the sheath of the Paleocene *Belopterina* (Dauphin 1986: pl. 2a–c).

***Kostromateuthis roemeri* gen. et sp. n.**

Fig. 1A–D.

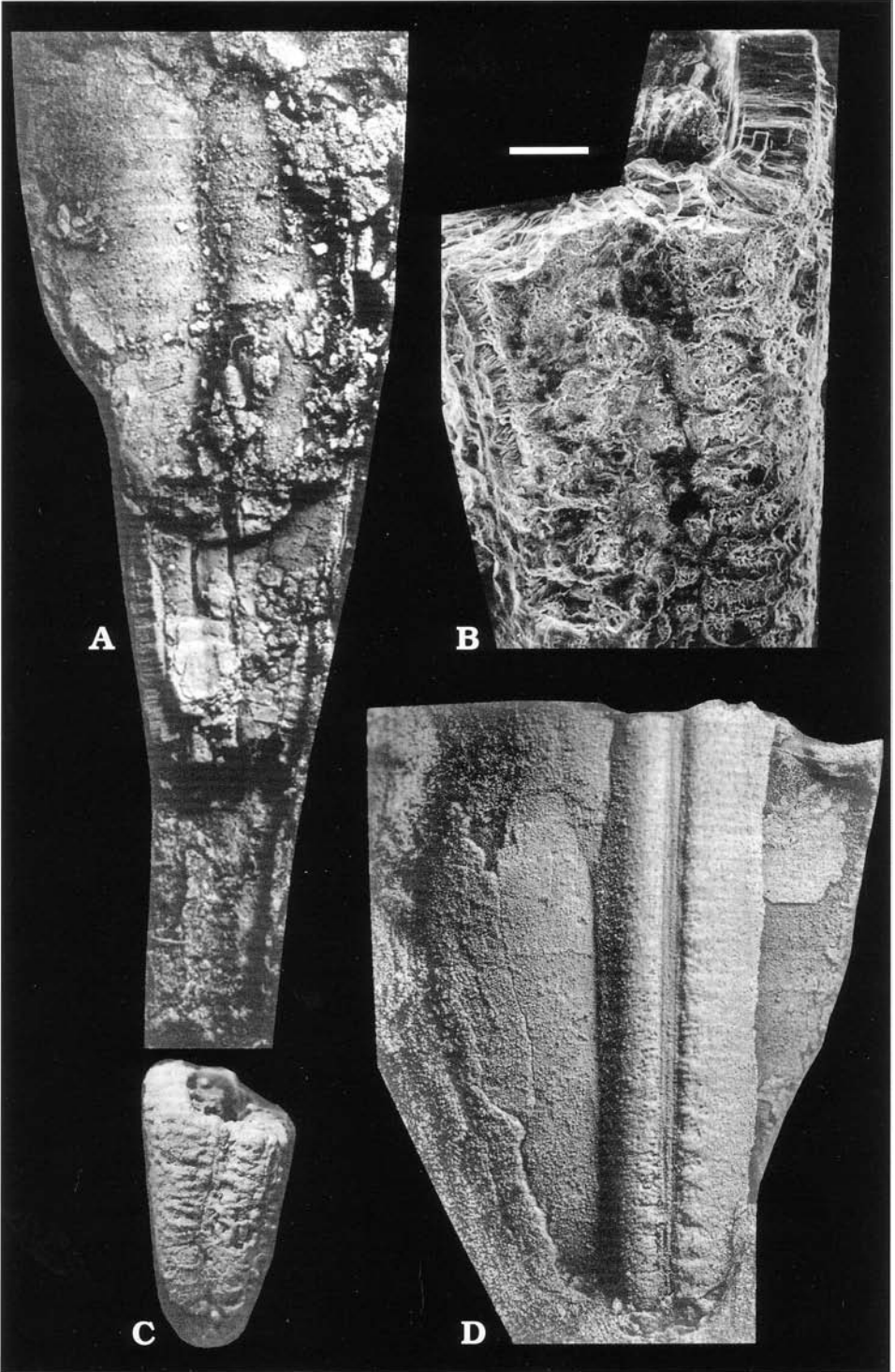
Holotype: PIN 3871/221 – the only specimen known.

Type horizon: Upper Jurassic, lower Kimmeridgian.

Type locality: Unzha River, right bank near village Popovo, Kostroma Region, Central Russia.

Derivation of name: in honour of Ferdinand Roemer, who described the first Jurassic coleoid shell which might have belonged to the Spirulida.

Diagnosis. — Same as for genus.



Description. — The shell is small (24 mm long, with maximum diameter about 8 mm), orthoconic, slowly expanding (angle of expansion 18–20 degrees), surface uneven, especially in its apical part where it is reticulated. Phragmocone and sheath seem to be of equal length; sheath probably ends near the apertural margin of the phragmocone and does not extend beyond the phragmocone. The sheath bears a strong medial, presumably dorsal, groove bordered by two ridges with rows of tubercles along their crests and has two or three smaller ridges on its floor. The length of the groove is approximately 3/4 of the shell length, or maybe longer. Adorally the sheath is thin but near the groove it is thicker. Apically the sheath is conical with a rounded apex; here the outer surface exhibits irregular rows of bean-shaped depressions oriented perpendicular to the longitudinal axis of the shell. In the adoral direction the bean-shaped depressions give way to a ‘pock-marked’ pattern and the surface becomes smoother. The phragmocone consists of approximately 25–30 camerae; sutures straight; mural parts of septa are long; their length is about 1/3–2/5 of the camera length. The conotheca (Fig. 1D) is as thin as a septum. Siphuncle and protoconch are unknown.

Shell wall ultrastructure of *Kostromateuthis*, *Belemnosis*, *Spirula*, and *Sepia*

***Kostromateuthis*.** — The sheath is the only part of the shell studied with SEM, as the conotheca that was observed with the light microscope on the surface of the phragmocone, illustrated on Fig. 1A, was accidentally destroyed during the preparation of the specimen. The conotheca (Fig. 1D) looks like a thin white layer. The septa were not studied with SEM because they were badly crushed. Under the light microscope they show nacreous lustre.

The sheath consists of spherulites formed of long thin crystallites of aragonite (Figs. 2A–D, 3A, B, 4A, B). The structure of the sheath changes remarkably from the apex towards the aperture, the apical portion of the sheath being more uneven than the adoral one (compare Fig. 1B and D). Close to its apical end the sheath contains many loosely packed spherical spherulites, each encased in an organic cover (Fig. 2A, B). Spaces between them probably were originally filled with organic matter. The spherulites exposed on the outer surface of the sheath exhibit a complex structure. Their central part is a porous crater-like depression while the periphery is a crest-like solid barrier separating adjacent spherulites (Figs. 2C, D, 3A, B). As a result the sheath has a rough, uneven surface with a ‘pock-marked’ pattern (Fig. 1B, C). The centres of the spherulites are less calcified than their periphery (Fig. 2A, B) and probably originally contained organic matter as well. The spherulites exhibit growth lines (Fig. 2D) indicating periodic accretionary growth. The outer surface of the conical portion of the sheath, and probably the entire surface of the sheath, has a covering that seems to represent an originally organic covering (Fig. 4A). Towards the aperture, the spherulites become more compactly arranged. In places where the originally organic covering is destroyed, numerous tiny tubular structures, terminated by pore openings, are exposed

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Fig. 1. *Kostromateuthis roemeri*, PIN 3871/221; lower Kimmeridgian; Unzha River, Kostroma Region, Central Russia. **A.** Presumably ventral view of the adoral portion of the preserved phragmocone, partly coated by a thin sheath, $\times 7$. **B.** The opposite side of the sheath than in C, to show reniform pattern on its surface; SEM micrograph; scale bar 0.3 mm. **C.** Conical apical portion of the sheath with uneven surface, rounded apex, and clearly visible alveola, $\times 10$. **D.** Presumably dorsal view of the shell showing strong medial groove of the sheath, its undeformed thick dorsal and thin dorso-lateral portions, and the fragment of a thin conotheca (to the right), $\times 10$.

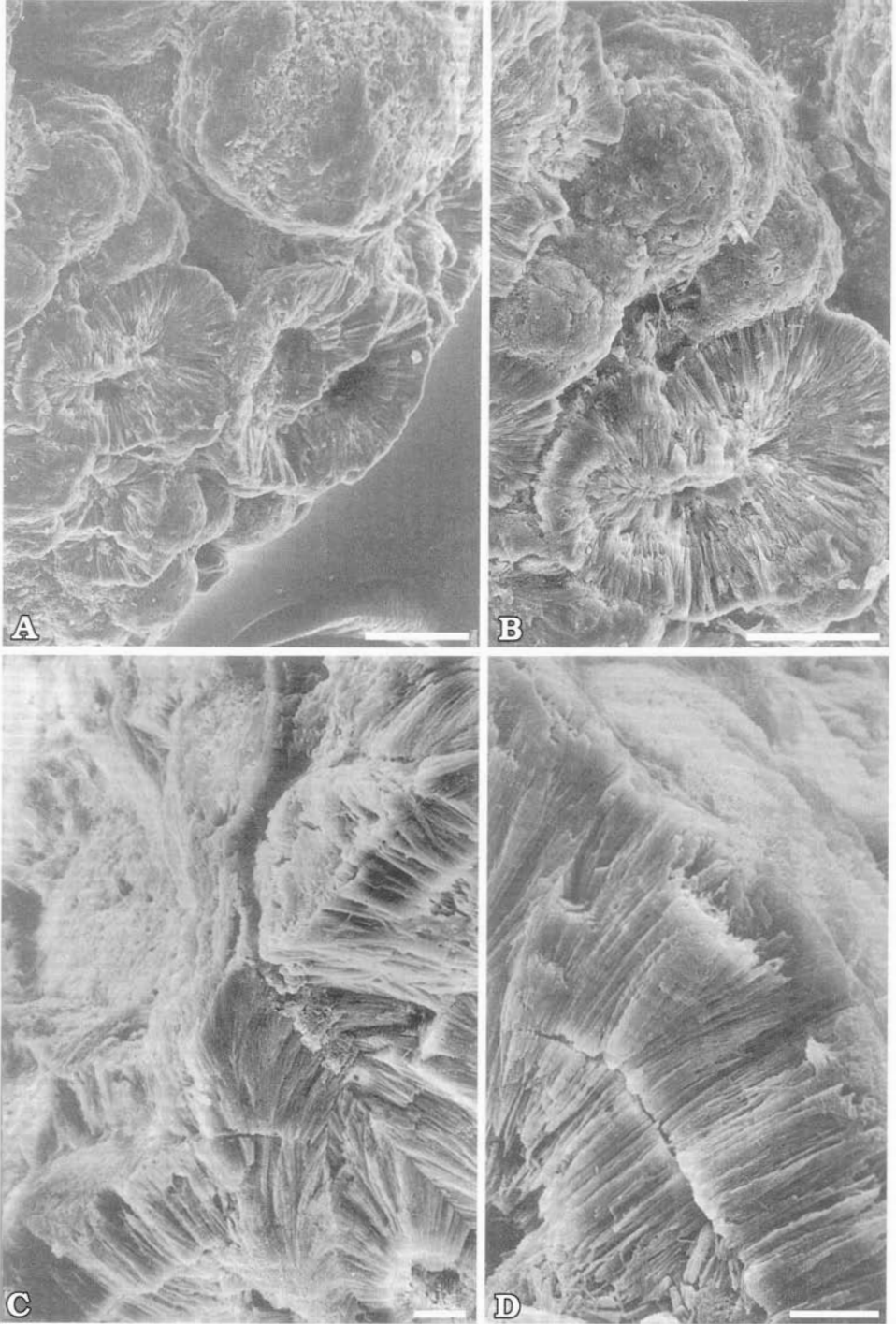


Fig. 2. *Kostromateuthis roemeri*, PIN 3871/221. A. The spherulites at the sheath apex; some spherulites are spherical (note their size differences) and coated by the originally organic capsule; others are hemispherical →

on the outer surface of the sheath (Fig. 4B). The walls of the tubes are formed by long thin crystals of aragonite parallel to the axis of the tube (Fig. 4C). Thus, strong porosity and high content of original organic matter seem to be characteristic features of the sheath of *Kostromateuthis*.

Belemnosis. — This Eocene genus is referred either to spirulids (Bülow-Trummer 1920; Doyle *et al.* 1994; Haas 1997; Doguzhaeva 2000) or to sepiids (Naef 1922; Krimgolts 1958; Jeletzky 1966). The protoconch is ovoid with a slightly curved axis and the phragmocone is gently curved as well so that the axis of the latter is a continuation of the former. The convex side is presumably dorsal and the concave side is presumably ventral (Fig. 6C). The sheath is bilaterally symmetrical with widely conical apical portion; it is swollen and short on the (presumably) ventral side, while thin and long on the opposite one (Fig. 6C). The axis of the sheath does not concur with those of the protoconch and phragmocone. The side of the sheath which is almost perpendicular to the axis of the protoconch is straight (in medial section); here the thickness of the sheath is less than in front of the lateral side of the protoconch. The swollen part of the sheath shows large, loosely packed spherulites with central hollow spaces. Here the spherulites are formed by long thin crystallites. The apical part shows radial sectors (Fig. 6C) which have also been reported in the sheath of the Eocene *Belopterinina* (Dauphin 1986: fig. 4). Adorally, on the convex side of the phragmocone there are two distinctly separated spherulitic-prismatic plates (Fig. 6C). The outermost plate is formed by the spherulites consisting of needle-like prisms and separated by the organic membranes. The tubular structures with the openings visible as numerous black spots are present here (Fig. 6D). The conotheca is a thin prismatic layer.

Spirula. — The shell wall of Recent *Spirula* (Fig. 5A, B) consists of two distinctly separated acicular-prismatic layers, termed the outer and inner plates (Appellöf 1893). The clear separation of the two plates is due to the thick layer of connecting tissue which is attached to the outer surface of the inner plate near the aperture, where the outer plate is absent as it is secreted just after the attachment place of connecting tissue (Chun 1898–1899: p. 335). The inner plate is an acicular-prismatic layer showing strongly oblique growth lines which make an angle of about 25 degrees with the inner surface (Doguzhaeva 1996: text-fig. 3a–c; figs. 2, 3). This indicates that the inner plate was secreted by the epithelium of the shell sac lining the inner surface of the last chamber. This acicular-prismatic layer shows alternations of black and white bands perpendicular to the growth lines and oblique to the shell surfaces (Doguzhaeva 1996: fig. 2). It is composed of prisms with a dendritic structure, a feather-like arrangement of acicular crystallites forming each prism (Doguzhaeva 1996: fig. 3). This layer seems to be rich in organic matrix that fills numerous narrow spaces between the crystallites and bundles of crystallites.

with hollow centres; the spherulites are formed by the needle-like crystallites; scale bar 0.3 mm. **B.** Close-up of A to show the organic cover and needle-like crystallites of the spherulites; scale bar 0.1 mm. **C.** The complex structure of the spherulites of the conical portion of the sheath, closer to the adoral portion of the shell where the spherulites are compactly arranged; their periphery is a solid crest-like barrier and the central part is porous depression; scale bar 0.3 mm. **D.** Fracture of the solid crest-like periphery of the spherulites showing needle-like prisms and their growth lines exhibiting their periodical secretion; scale bar 0.3 mm. SEM micrographs.

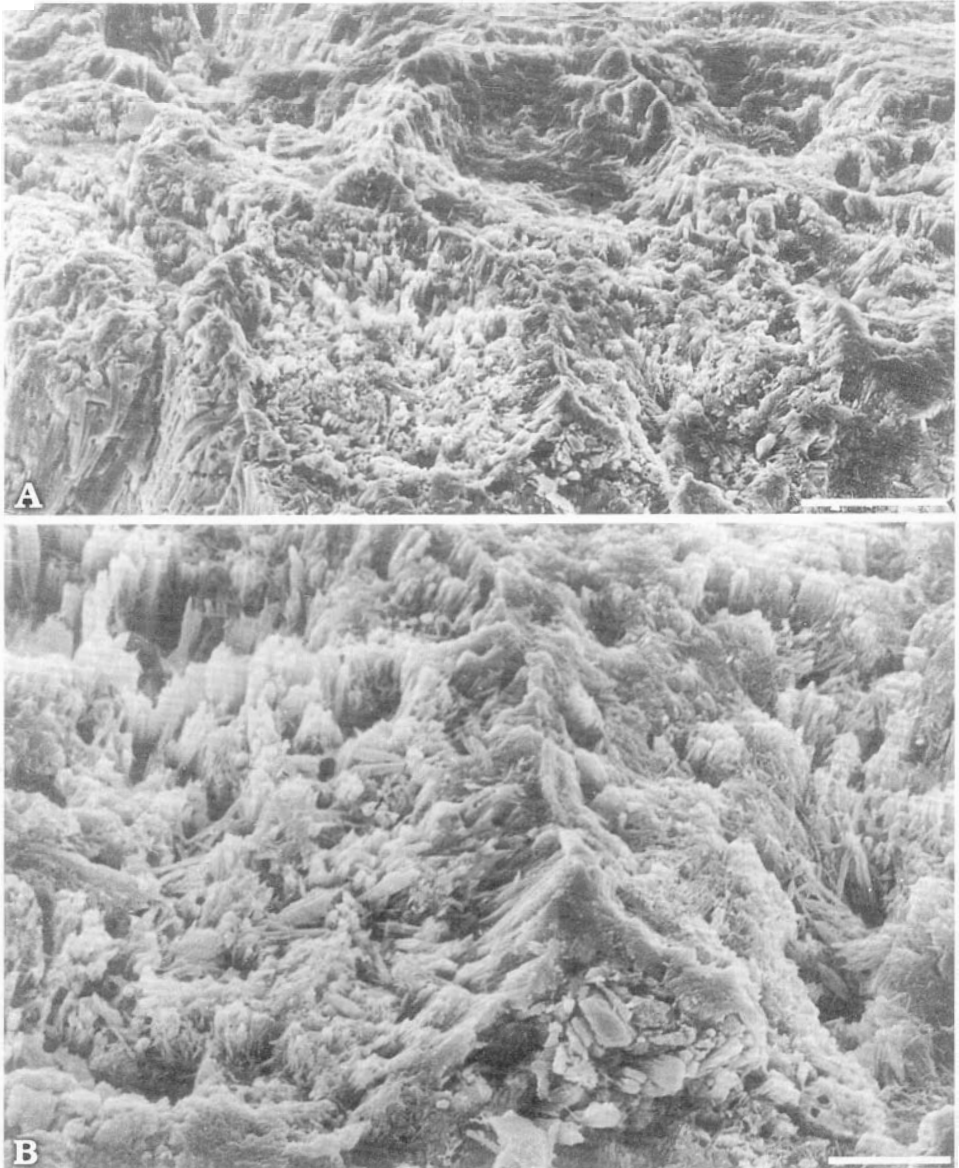


Fig. 3. *Kostromateuthis roemeri*, PIN 3871/221. **A.** The uneven surface of the sheath with 'pock-holes' which are central depressions of the spherulites surrounded by solid ridges; scale bar 0.1 mm. **B.** The crest-like solid barrier separating two adjacent spherulites; the central depressions are less calcified than their periphery and show numerous tubes; scale bar 0.03 mm. SEM micrographs.

The intermediate layer between the two plates is thin, lamellar and is only weakly calcified, consisting predominantly of organic matrix (Fig. 5B). The outer plate is represented by two layers: a thin acicular-prismatic layer and an outer coating layer (Fig. 5B). The acicular-prismatic layer has a simple prismatic structure consisting of acicular crystallites which are oriented more or less perpendicular to the layer bound-

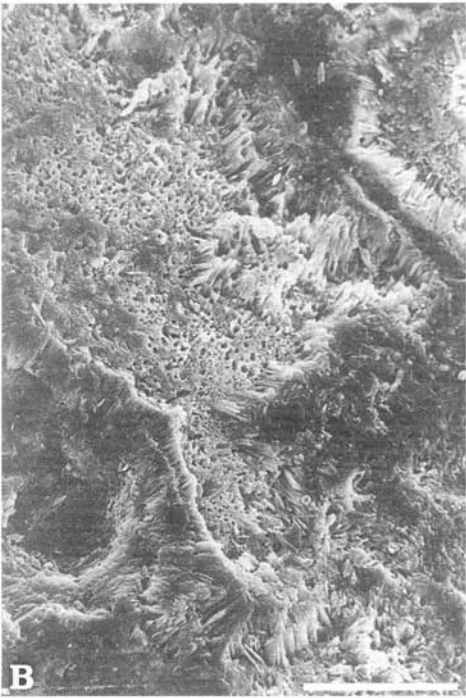
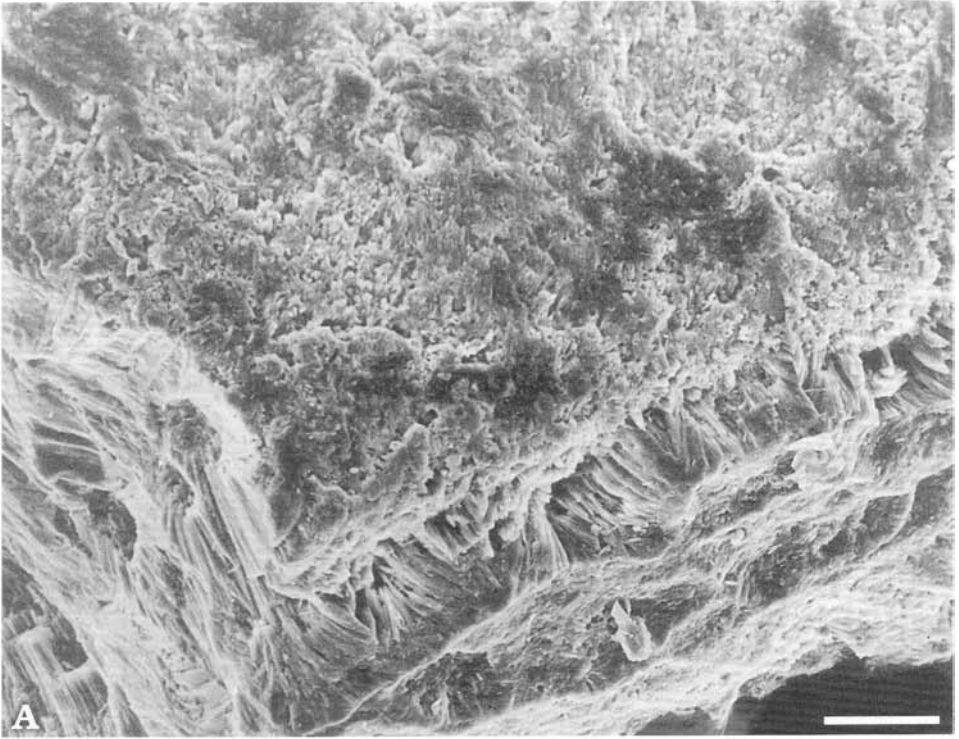
aries (Doguzhaeva 1996: fig. 3). The growth lines are uneven, more or less parallel to the shell surface. The coating layer covers the protoconch and forms the ventral ridge that is distinctly developed in the first whorl. The structure of the ventral ridge is strongly irregular, showing numerous interruptions of the oblique growth lines, resulting in a lenticular pattern. At the end of the first whorl it loses its ridge-like shape. The coating layer represents a lateral and dorsal continuation of this ventral ridge. It is absent in the apertural region and last appears at the penultimate camera. During ontogeny the coating layer grows proportionally thinner. It has a simple prismatic structure similar to that of the underlying layer; the growth lines are uneven, more or less parallel to the shell surface. The layer has a reticulate ridged outer surface.

Sepia. — The dorsal shield of the cuttle-bone shows an uneven outer surface and is formed by a thin laminated layer (the inner portion of the sheath) and a thick spherulitic-prismatic layer (the outer portion of the sheath). The former consists of several laminae more or less parallel to the inner surface of the sheath; the latter is formed by lens-like spherulites, which are composed of short acicular-prismatic crystallites. The spherulites are coated by thin organic films which separate them. The spine proper differs strongly from the rest of the sheath and does not seem to be a continuation of any of the layers of the sheath. It shows thin longitudinal laminations, granular structure between probably organic laminae, and numerous pores (Fig. 6A, B). Along the periphery there is a porous zone lacking growth lines. It is formed by the needle-like prisms and tubular structures of similar thickness, and with openings visible as numerous black spots like those in the sheath of *K. roemeri* (compare Fig. 6B and Fig. 4B).

Comparisons. — The sheath of *Kostromateuthis* is similar to that of spirulids and sepiids in being formed of spherulites consisting of thin long needle-like crystallites. As in *Kostromateuthis*, in *Belemnosis* and *Sepia* the sheath possesses tubular structures, the walls of which are formed by the needle-like crystallites as well. Among Tertiary sepiids the spherulitic-prismatic structure of the sheath has been observed in *Belosepia*, *Beloptera*, and *Belopterina* (Dauphin 1984, 1985, 1986). In contrast to these, the belemnites exhibit concentric structure of the rostrum, with radial prisms in each concentric growth ring. The diplobelids differ from all the other belemnoids and show a modified structure of the rostrum (Zittel 1868; Jeletzky 1966, 1981; Drushchits *et al.* 1984).

The dimpled surface of the sheath of the *K. roemeri* gen. et sp. n. also contrasts with the mainly smooth, or in rare cases weakly ornamented, rostrum of belemnoids. These differences are a result of the complex spherulitic structure of the sheath in *Kostromateuthis* and the radial-prismatic structure of the rostrum in belemnites. It should be noted that some fully-grown belemnoid rostra are coated by a layer of coarse prismatic structure (the epirostrum) slightly similar to the outer plate of the sheath of sepiids, or spirulids. In these forms the outer surface is not smooth but rather pitted; however, this feature seems not to be a general character of belemnoids.

Thus, the spherulitic-prismatic ultrastructure of the sheath of *Kostromateuthis*, taken separately, does not indicate affinity with any taxon of coleoids. Nevertheless, combination of features such as a fully developed phragmocone, comparatively short camerae, long mural parts of septa and simple sutures, strong fusion of septa and shell



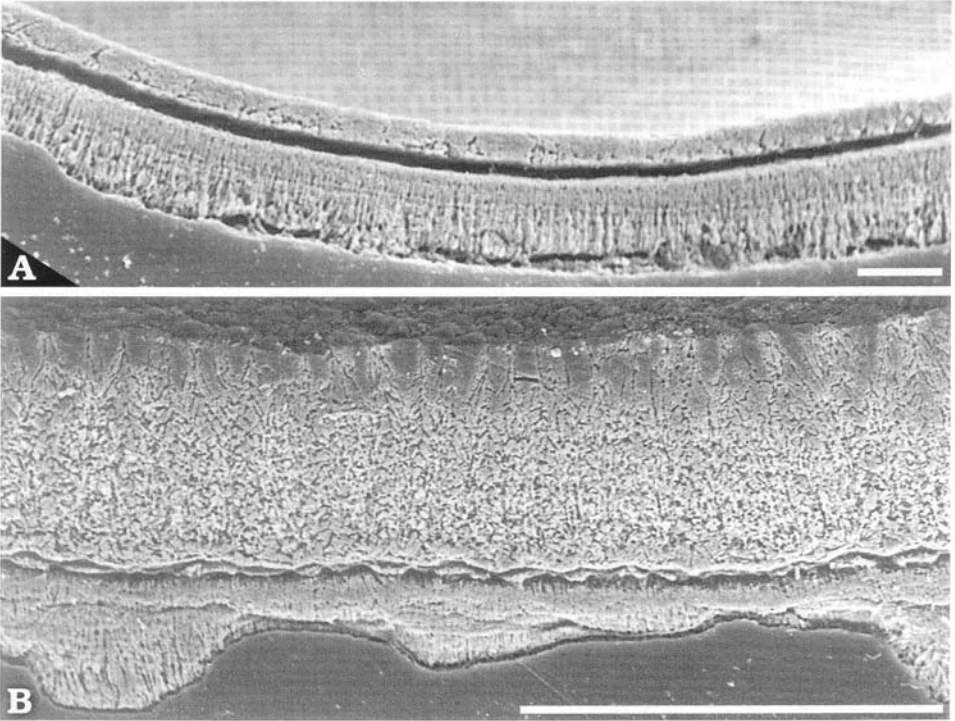


Fig. 5. Recent *Spirula*, PIN 3871/134; Cuba. Medial section of the shell wall consisting of outer and inner plates with the intermediate layer between them at a young (A) and late (B) ontogenetic stages. The plates show acicular-prismatic ultrastructure, the intermediate layer is irregularly calcified organic; the inner plate is thin and the outer plate is thick at the beginning (A) and vice versa later (B); scale bars 0.1 mm. SEM micrographs.

wall, uneven surface of the sheath which is often bilaterally symmetrical, and the absence of a nacreous layer in the shell wall (Doguzhaeva 1996, 2000; Doguzhaeva *et al.* 1998), suggests spirulid affinity of *Kostromateuthis*.

The Mesozoic evolution of spirulids and sepiids

Judging by the external appearance of the shell, *K. roemeri* could be assigned to belemnotheutids which are “a ‘catchall’ for most, or all, late Paleozoic and Mesozoic

Fig. 4. *Kostromateuthis roemeri*, PIN 3871/221. A. The surface, longitudinal and transverse fractures of the conical portion of the sheath to show the dark spots which are covered by presumably organic matter and the light ones which are porous and lack the organic covering; the transverse fracture (left side) shows the central cavities of the two spherulites and the radial needle-like prisms; the longitudinal fracture shows inclined prisms of the spherulites; scale bar 0.1 mm. B. The exposed porous area of the sheath surface showing numerous pores and tubular structures; the places where the pores are not visible are coated by presumably originally organic matter; scale bar 0.1 mm. C. Close-up of B showing three distinct tubular structures; their wall is formed by long, thin needle-like prisms; scale bar 0.01 mm. SEM micrographs.

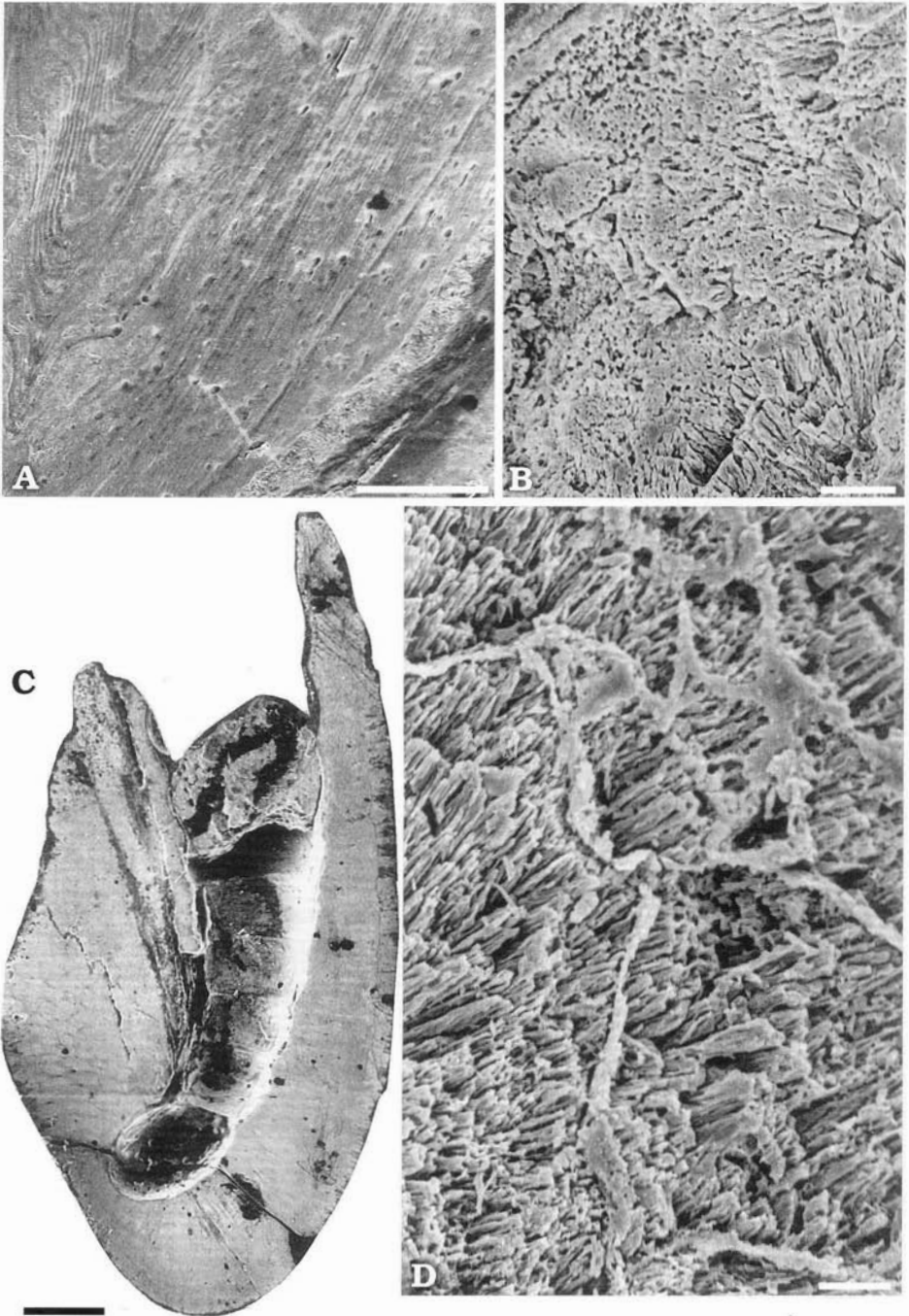


Fig. 6. **A, B.** Longitudinal section of cuttle-bone of Recent *Sepia*; PIN 3871/216; Australia. **A.** The spine showing the growth lines recording the ontogenetic changes of its shape and its high porosity; scale bar 0.1 mm. **B.** Close-up of **A**; the longitudinal peripheral porous zone of the spine showing numerous black spots which seem to be the openings of the tube-like structures like those in the sheath of *K. roemeri* (compare with

belemnite-like coleoids characterized by relatively weakly developed guards" (Jeletzky 1966: p. 144), or to the diplobelids. However, the belemnite-like coleoids have the typical belemnoid concentric structure of the rostrum (Makowski 1952; Bandel & Kulicki 1988); in diplobelids the sutures are more sinuous than in any other belemnoids, with a pronounced dorsal saddle and a weak ventral saddle, and the septa are usually considerably crowded (Jeletzky 1966, 1981), which is not the case in *K. roemeri*.

The idea of the possible existence of Jurassic sepiids was introduced by Roemer (1890) who described *Plagioteuthis moscoviensis* from the Oxfordian of Central Russia. The sole available specimen of this form is represented by a small (4 cm in length) slightly curved asymmetrical sculptured rostrum with deep slowly expanding alveola; one side of the rostrum is thicker than the other. Roemer compared *Plagioteuthis* with *Belosepia*, *Spirulirostra*, and *Diploconus* and believed that it belonged either to Belosepiidae, Belopteridae, or Belemnitidae (Roemer 1890: p. 362).

Kostromateuthis confirms Bülow-Trummer's idea (1920) of combining the Late Jurassic *Plagioteuthis* with Tertiary genera such as *Belemnosis*, *Beloptera*, *Belopterinina*, *Spirulirostra*, *Spirulirostrina*, and *Vasseurina* in the family Spirulidae, thus extending the lineage of the spirulids back to the Late Jurassic. However, Krimgolts (1958) considered *Plagioteuthis* as a conventional member of Belemnosidae. Naef (1922) and Jeletzky (1966) did not index *Plagioteuthis*. Doyle *et al.* (1994) listed it as *incertae sedis*. Nevertheless, several decades later the discovery of a caecum and a prosiphon within the protoconch of the Maastrichtian *Groenlandibelus rosenkrantzi*, which has a superficially belemnite-like appearance, provided strong evidence that the spirulid lineage existed in the Late Cretaceous (Jeletzky 1966). The finding of the Aptian *Naefia kabanovi* extended it to the Early Cretaceous (Doguzhaeva 1996).

Bülow-Trummer (1920) grouped the forms with normal phragmocones in the Suborder Phragmophori (Belemnoida, Belemniteuthidae, and Spirulidae) and separated them from the Suborder Sepioidei which included sepiids as well as teuthids. The idea of keeping the forms with fully developed phragmocones separate still seems to be acceptable. In light of this view the record of fossil spirulids probably includes, in addition to the six Tertiary genera mentioned above, the following: the Stephanian *Shimanskya* of the USA Mid-Continent (Doguzhaeva *et al.* 1998), the Aptian-Maastrichtian *Naefia* of Chile, India, Antarctica, Japan and the Caucasus (Wetzel 1930; Biro-Bagoczky 1982; Stinnesbeck 1986; Doyle 1986; Stilwell & Zinsmeister 1987; Hewitt *et al.* 1991; Doguzhaeva 1996), the Aptian *Adygeya* of the North-Western Caucasus (Doguzhaeva 1996), the Maastrichtian *Groenlandibelus* of West Greenland (Jeletzky, 1966) and the Miocene *Spirula*

Fig. 4B); scale bar 0.01 mm. C, D. *Belemnosis* sp.; PIN 3871/140; Eocene, Turkey; medial shell section. C. The ovoid protoconch and approximately 10 first camerae of the phragmocone; the curved axis of the phragmocone is a continuation of the curved axis of the protoconch; the sheath is bilaterally symmetrical: on the concave (presumably ventral) side of the phragmocone it is short and swollen, and on the convex (presumably dorsal) side it is thinner and longer than on the opposite one; the post-alveola portion is short; the reticulate pattern of the sheath is well visible in the swollen part; scale bar 0.1 mm. D. Close-up of C to show the differently oriented needle-like prisms and similarly thin tubular structures of the outermost portion of the sheath on the convex side of the phragmocone; the organic membranes separating adjoining spherulites are partly preserved; scale bar 0.01 mm.

mizunamiensis of Japan (Tomida & Itoigawa 1981). In the genera from this list, a spherical protoconch has so far been observed in *Groenlandibelus* (Jeletzky 1966), *Belemnosis* (Doguzhaeva 2000; herein) and *Spirula mizunamiensis* (Tomida & Itoigawa 1981). The caecum and prosiphon have been documented only in *Groenlandibelus* shell but they are still believed to be the characters of spirulids distinguishing their shells from those of diplobelids and other belemnoids.

The view that the spirulids (and sepiids) evolved from the belemnoid stock is still widespread (Dauphin 1985; Teichert 1988; Meyer 1993; Hewitt & Jagt 1999), but it is also widely questioned (Jeletzky 1966; Engeser & Bandel 1988; Doyle *et al.* 1994; Doguzhaeva 1996; Doguzhaeva *et al.* 1998). The origin of spirulids via reduction and loss of a rostrum in belemnoid-like ancestors was introduced by Volz (1830), supported by Schwarz (1895) and significantly elaborated by Naef (1922). Hewitt & Jagt (1999: p. 323) still believe that the spherulitic ultrastructure of the sheath in *Belosaepia* and *Sepia* was inherited from that of diplobelids. It has been known since Zittel (1868) that diplobelids apparently lacked the radially prismatic structure of the rostrum. According to Hewitt & Jagt (1999: p. 324), 'separate origins of the Sepiida and Spirulida within the Cretaceous diplobelid belemnites is still the most attractive hypothesis, until the case for pre-Aptian fossil record of spirulids becomes overwhelming.'

The available data on ultrastructure of the rostrum in diplobelids is so far scarce. Jeletzky (1981: p. 115) characterized the diplobelid belemnites as having a tapering pro-ostracum with an acute or very narrowly rounded tip and hyperbolic zones of belemnoid type; suture lines more sinuous than in any other belemnites, with a pronounced dorsal saddle and a small ventral lobe; crowded septa (the height of camera up to one-twentieth of their length); a usually breviconic phragmocone with the apical half curved endogastrically; and a rudimentary or short, stout, and apically bluntly rounded rostrum. Jeletzky (1966: p. 149) had noticed that, unlike in the other suborders of Belemnitida, the rostrum of diplobelids generally lacks radial-prismatic structure. However, after restudy and revision of a large collection of diplobelids, Jeletzky (1981: p. 116) concluded that 'apparent lack of the radially prismatic structure of the guard appears to be a result of post-mortem weathering in those forms where it is reduced to a very thin ... envelope.' In *Conoteuthis dupiniana* the rostrum has a smooth surface and shows radial striation suggestive of its primary radial-prismatic structure (Jeletzky 1981: p. 126). In the Early Cretaceous *Pavloviteuthis* the rostrum exhibits belemnoid-like radial-prismatic structure (Jeletzky 1981: p. 127). Nevertheless, in the Aptian *Chalalabelus* he showed the rostrum with lamellar structure (Jeletzky 1981: text-fig. 12a). Drushchits *et al.* (1984) studied the rostrum ultrastructure of the Valanginian diplobelid *Tauriconites nikolai* Kabanov, 1980. In this form the surface of the rostrum reflects the undulations of the phragmocone surface (Drushchits *et al.* 1984: fig. 2a) and shows transverse ridges and grooves on the ventral side. Similar undulations of the phragmocone surface are also known in Recent *Spirula* and in *Naefia*. These authors raised the diplobelids to the rank of Order Diplobelida Jeletzky, 1965 on the basis of differences in the structure of the rostrum between belemnoids and diplobelids. The apical portion of the rostrum in *Tauriconites* consists of spherulites resulting in a pattern of sectors in median section (Doguzhaeva, unpublished data) similar to that of several Tertiary sepiids (Dauphin 1984: fig. 6f, 1986: pl. 2d). However,

the anterior part of the rostrum exhibits concentric growth lines and a radial arrangement of short prismatic crystals more like the radial-prismatic structure of ordinary belemnite rostra. Thus, there are essential differences between the structure of the sheath of *K. roemeri* and the rostrum of diplobelids that exclude the new form from Diplobelidae.

Finally, following the idea of the inheritance of the spherulitic structure of the shell by the Tertiary sepiids and spirulids from their ancestors, one might expect that they evolved from the early Kimmeridgian *Kostromateuthis*-like forms rather than from the diplobelids which appeared in the Tithonian, later than *Kostromateuthis*. More probably, however, they inherited their ultrastructural characters from more remote still unknown precursors. The Stephanian *Shimanskya postremus* Doguzhaeva, Mapes & Mutvei, 1998 is the only older spirulid known so far. Being longiconic and having no grooves, the shell of this form has an external appearance that is essentially bacrtrid-like. However, contrary to bacrtritoids but similar to spirulids *Sh. postremus* lacks a nacreous layer in the shell wall (Doguzhaeva 1996; Doguzhaeva *et al.* 1998) which is porous, formed by the inner and outer prismatic plates. Thus, the Lower Carboniferous decapods probably were represented at least by the three orders: Aulacocerida (Shimansky 1960), Spirulida (Doguzhaeva *et al.* 1998), and Hematitida (Doguzhaeva *et al.* in press), that confirms the idea on a rapid radiation in evolution of decapods (Bonnaud *et al.* 1997).

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Редкий головоногий моллюск (Cephalopoda: Coleoidea) из верхней юры Центральной России

ЛАРИСА АСЛАМБЕКОВНА ДОГУЖАЕВА

Содержание

Раковина внутрэннераковинного головоногого *Kostromateuthis roemeri* gen. et sp. n., из киммериджских отложений Костромской области характеризуется небольшими размерами (около 30 мм в длину), медленно расширяющимся фрагмоконом с углом расширения примерно равным 18–20°, и арагонитовым чехлом с шероховатой поверхностью, короткой постальвеолярной частью и длинной и глубокой продольной, предположительно, дорсальной бороздой.

Чехол *K. roemeri* пористый, с высоким содержанием органического материала, сложенный сферулитами; не имеет радиально-концентрического строения, свойственного рострам белемнитов. Сферулиты образованы

тонкими игольчатыми кристаллитами; их центральные части менее обызвествлены, чем периферические; многочисленные промежутки между ними заполнены органическим материалом. В чехле присутствуют ранее неизвестные капиллярные трубочки, стенки которых сложены игольчатыми кристаллитами, идентичными тем, из которых состоят сферулиты.

Выявлено морфологическое и микроструктурное сходство раковины *K. roemeri*, эоценового *Belemnosis*, палеоценовой *Belopterina* и современной *Spirula*. Сходство заключается в наличии хорошо развитого фрагмокона с (1) небольшим углом расширения, (2) сравнительно короткими камерами, (3) простой лопастной линией, (4) длинными муральными частями септ, а также в наличии чехла с характерной неровной шероховатой поверхностью и сферурито-призматической микроструктурой. Установленное сходство рассматривается в качестве доказательства принадлежности *K. roemeri*, в составе монотипического семейства, к отряду Spirulida.

Отнесение киммериджского *K. roemeri* к спинулидам ставит под сомнение предположение о происхождении спинулид от белемноидного ствола, а именно, от меловых диплобелид.