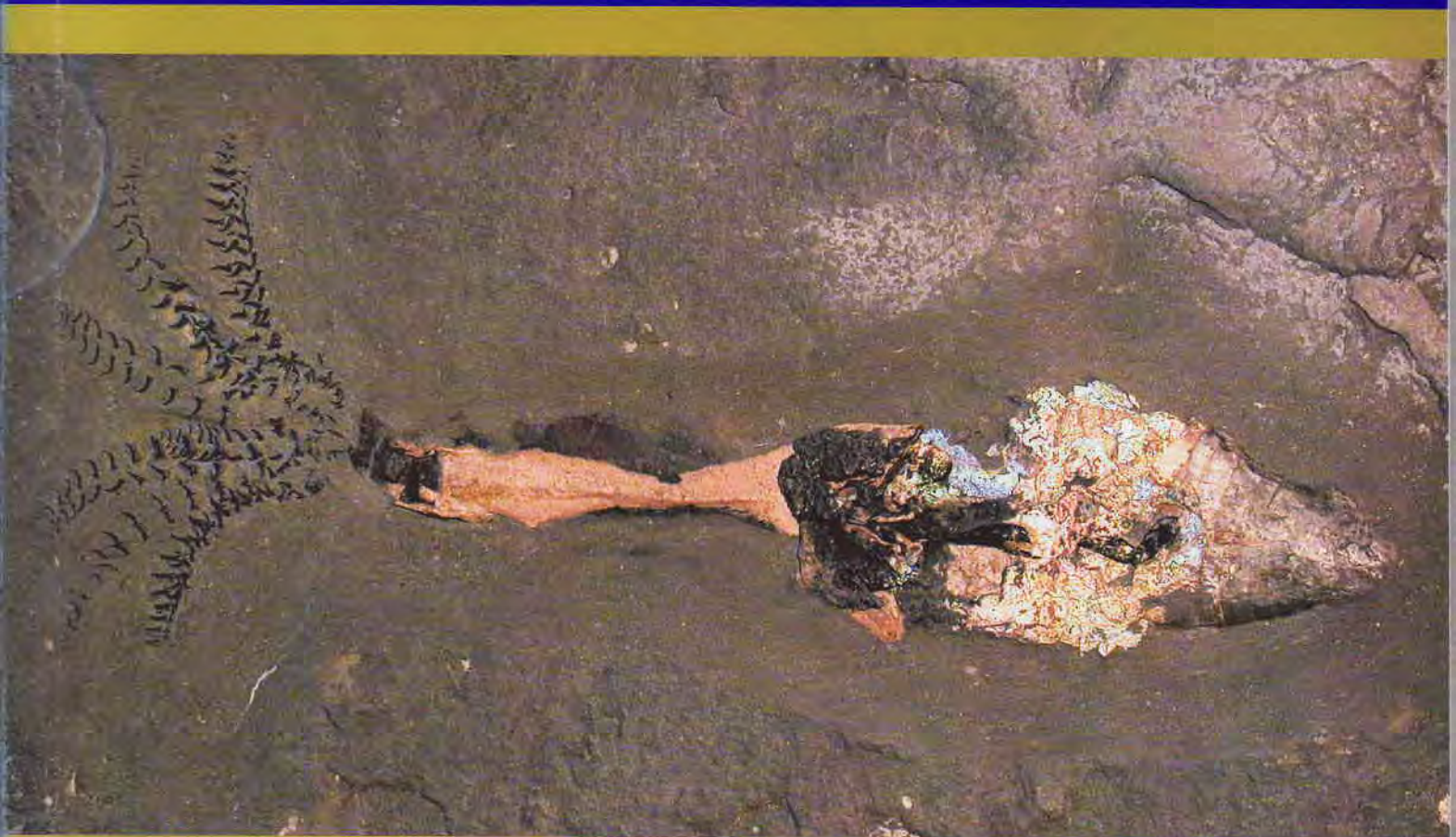




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Systematics and phylogeny of the boreal family *Cylindroteuthidae*: Problems solved and unsolved

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ABSTRACT: The system of the belemnite family *Cylindroteuthidae* STOLLEY, 1919 and the problems of origin of its generic and subgeneric taxa are discussed based on the results of recent revision of its Jurassic representatives. The main changes in systematics deal with the subfamily *Pachyteuthinae* STOLLEY, 1919.

Key words: Coleoid cephalopods, belemnites, *Cylindroteuthidae*, Systematics, Phylogeny.

Belemnites of the *Cylindroteuthidae* family have appeared in Bajocian age and inhabited in the main Boreal seas right up to the earlier Aptian age. The notions of systematics and phylogenesis of the family have been developed over the course of more than a century. Investigations carried out by E. Bayle, K. Zittel, M. Neumayr, A. P. Pavlov, E. Stolley and others played a great role. Modern concepts are determined primarily by V. N. Saks, T. I. Nal'nyaeva and V. A. Gustomesov publications. Currently the volume of *Cylindroteuthidae* and their systematic position among belemnites are virtually commonly accepted. The principal disagreements include intrafamily classification of this coleoid group and special features of its evolution.

We accept the following system of the family *Cylindroteuthidae* STOLLEY, 1919: subfamily *Cylindroteuthinae* STOLLEY, 1919 – genus *Cylindroteuthis* BAYLE, 1878 (subgenera *Cylindroteuthis* s.str. and *Arctoteuthis* SACHS et NALNAEVA, 1964), genus *Spanioteuthis* GUSTOMESOV, 1958; subfamily *Pachyteuthinae* STOLLEY, 1919 – genus *Pachyteuthis* BAYLE, 1878 (subgenera *Pachyteuthis* s.str., *Microbelus* GUST., 1958, *Boreioteuthis* SACHS et NALN., 1966 and *Acroteuthis* STOLLEY, 1911), genus *Simobelus* GUST., 1958 (subgenera *Simobelus* s.str. and

Liobelus DZYUBA, 2004), genus *Lagonibelus* GUST., 1958 (subgenera *Lagonibelus* s.str., *Communicobelus* GUST., 1964, *Holcobeloides* GUST., 1958 and *Eulagonibelus* GUST., 1989). In order that the subfamilies be recognized, it seems pertinent to use the differences in length of postalveolar part (stem+apical regions (Doyle, Kelly, 1988)) of juvenile *Cylindroteuthid* rostra indicated by V.N.Saks and T.I.Nal'nyaeva (1967): *Cylindroteuthinae* differs from *Pachyteuthinae* in elongate rostra of early stage of ontogeny and therefore in smaller displacement of axial (apical) line to ventral side of rostrum of adult stage. Accomplished investigations have shown that within subfamilies the most persistent feature allowing the reconstruction of continuous phylogenetic lines is specificity of elongation of postalveolar part of rostrum in ontogeny (Dzyuba, 2004). The genera are well distinguished based on this feature (Fig.1). Such features as shape of rostrum and transverse section, specificity of ventral apical groove hold more low systematic rank in features hierarchy of *Cylindroteuthidae*. They manifest themselves in a similar way and independently in different phylolines of *Cylindroteuthids*, however they are comparatively persistent within small groups of closely allied species. These features may serve good criteria of subgeneric rank.

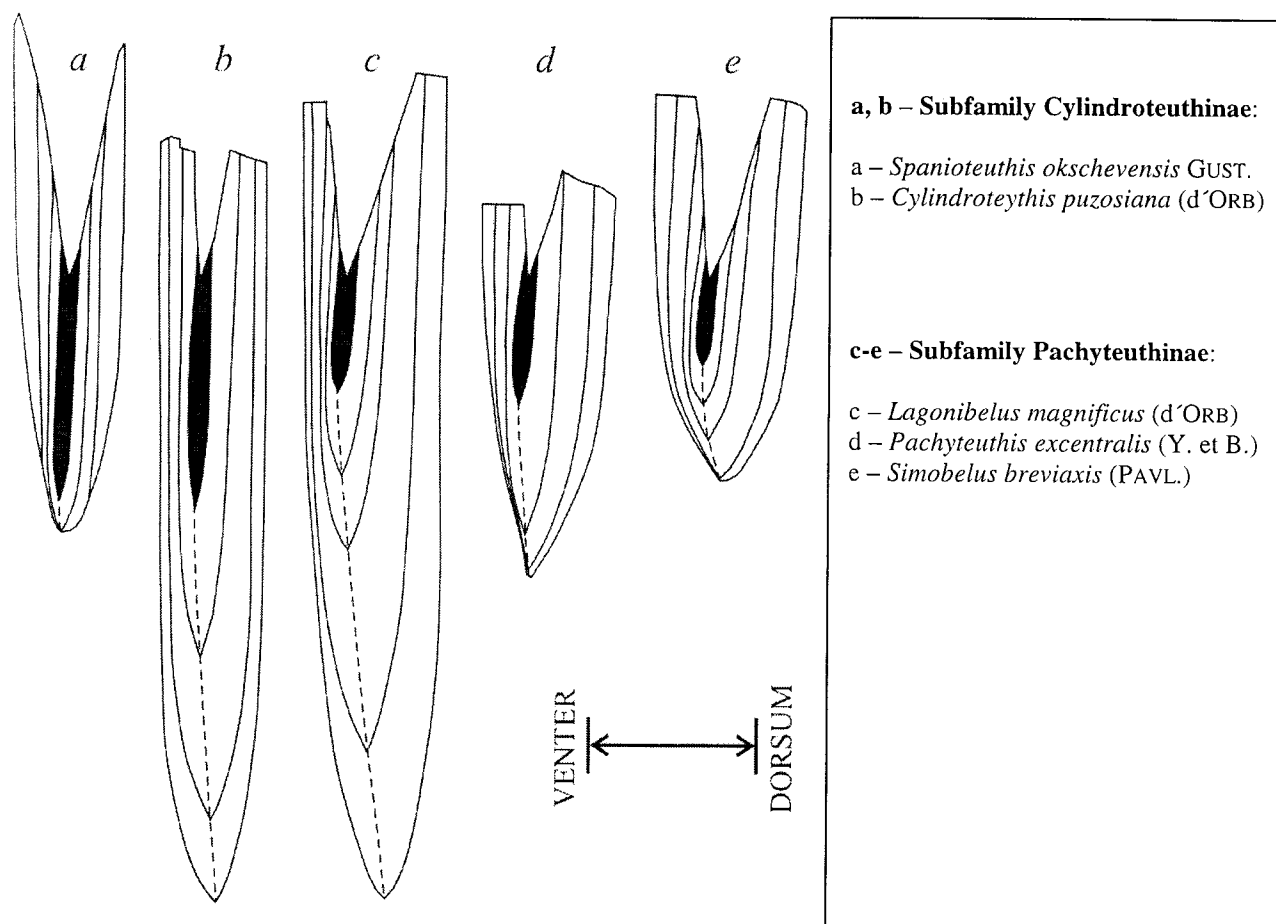
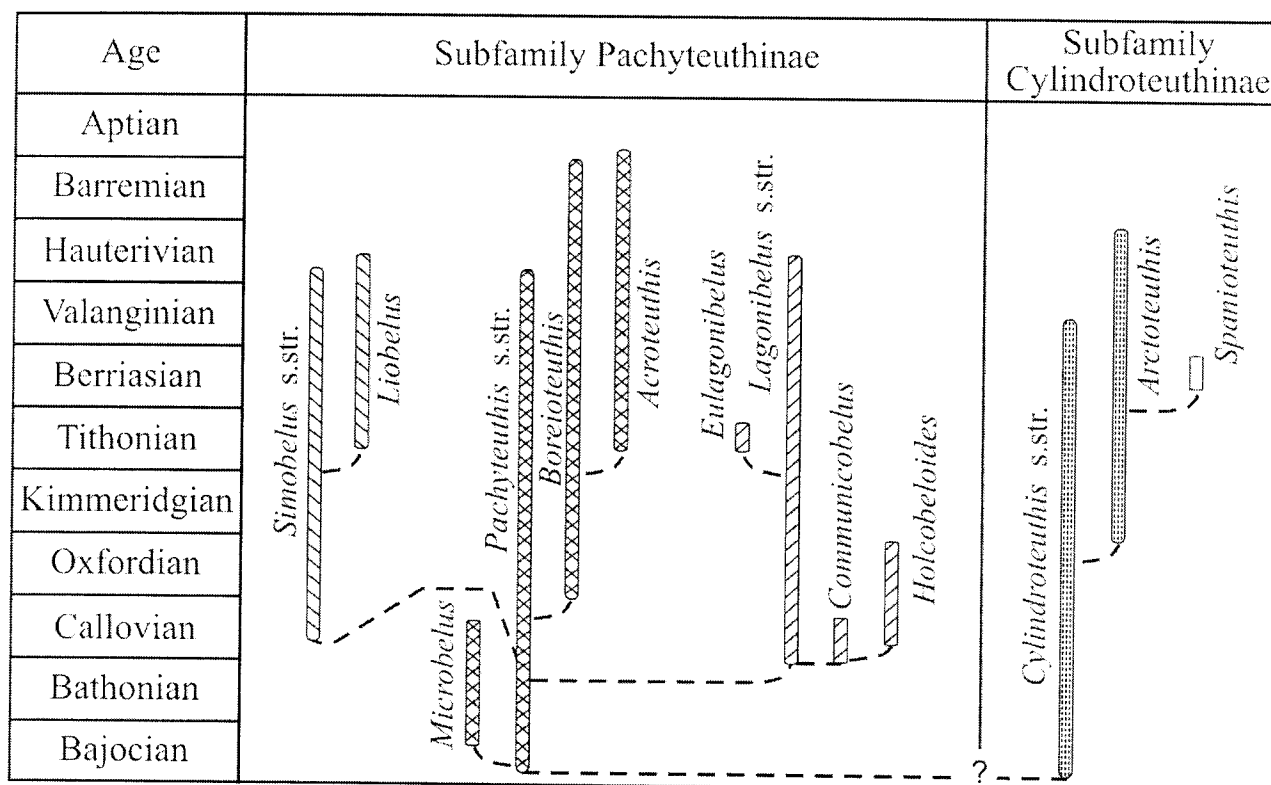


Fig.1. Internal structure of rostra in Cylindroteuthidae genera (longitudinal sections in dorso-ventral plane for type species). *Black colour points to rostra at early ontogeny stages.

At present there is widely accepted generic status for *Acroteuthis*. A great number of researchers following V. N. Saks and T. I. Nal'nyaeva identified three subgenera in its composition: *Acroteuthis* s.str., *Microbelus* and *Boreioteuthis* united by common feature (dorso-ventrally depressed section of relatively short rostra). Nevertheless, the idea on development of these taxa from one stem was already subjected to question (Mutterlose et al., 1987). Based on revision of type species of *Boreioteuthis* (we consider the *Acroteuthis* (*Boreioteuthis*) *niiga* Sachs et Nal'n. as a synonym of the *Pachyteuthis* (*P.*) *subregularis* SACHS et NALNAEVA) and reconsideration of genetic relations between some species of Pachyteuthinae we have changed species composition in Jurassic *Boreioteuthis* (Dzyuba, 2004). For example, such species as *Pachyteuthis* (*P.*) *subregularis*

SACHS et NALNAEVA., *Belemnites troslayanus* D'ORBIGNY, *B. explanatus* PHILL. and others were included in this subgenus. In diagnosis of the subgenus *Boreioteuthis* such character as transverse section were refined: sections are depressed to slightly laterally compressed, subquadrate to rounded subquadrate or pyriform. The subgenus is assumed to originate from *Pachyteuthis* s.str. rather than *Microbelus* as it was believed before (Saks & Nal'nyaeva, 1966). It was established that *Microbelus* (Bajocian–Callovian age range) and *Boreioteuthis* (Oxfordian–Barremian) have originated (independently of one another) from the representatives of *Pachyteuthis* s.str. Only the subgenus *Acroteuthis* s.str. (Tithonian–Aptian) in its origin is probably related to *Boreioteuthis* (Fig.2).



Genera: ▨ *Simobelus* ▩ *Pachyteuthis* ▧ *Lagonibelus* ▦ *Cylindroteuthis* □ *Spanioteuthis*

Fig. 2. Phylogenetic chart for Cylindroteuthidae genera and subgenera.

Consequently, depressed transverse section, i.e. the basic feature for genus recognition, arose independently in the species of abovementioned taxa. The assignment of *Acroteuthis*, *Boreioteuthis* and *Microbelus* to the genus *Acroteuthis* is correspondingly man-made. We treat these taxa as subgenera of the genus *Pachyteuthis*. The subgenus *Acroteuthis* as we see it stands more close by its species composition to *Acroteuthis* s.str. in the V. N. Saks and T. I. Nal'nyaeva sense. It also includes *Belemnites mosquensis* PAVL. and *B. souichei* d'Orb., which were assigned by V. N. Saks and T. I. Nal'nyaeva to *Acroteuthis* (*Microbelus*). Some species with very robust rostrum on the contrary were excluded from subgenus *Acroteuthis* and were assigned to *Simobelus* (*Liobelus*). The subgenus *Acroteuthis* thus unites the species with robust (not very robust) or moderately elongate rostrum, flattened on ventral side, with a short, indistinct ventral apical groove. Transverse sections are depressed and subquadrate to rounded subquadrate. The volume of

subgenus *Microbelus* is enlarged a little in comparison with those of proposed by V. A. Gustomesov (1964) at the sacrifice of Bajocian - Bathonian *Pachyteuthis* (*Pachyteuthis*) *parens* SACHS et NALN. and *Cylindroteuthis themis* Crick, assigned to it.

There was distinguished the genus *Simobelus* GUST. which apart from *Simobelus* s.str. includes also the species characterized by robust or very robust rostra showing the same type of growing in ontogenesis however being strongly depressed dorso-ventrally. This group of species is recognized as a new subgenus *Liobelus* DZYUBA (Tithonian-Hauterivian age range), which is direct descendant of *Simobelus* s.str.: *S. (L.) praecorpulentus* (GERAS.), *S. (L.) russiensis* (D'ORB.), *S. (L.) uralensis* (SACHS et NALN.), *S. (L.) prolatensis* (GUST.), *S. (L.) partneyi* (SWINN.), *S. (L.) lindseyensis* (SWINN.), *S. (L.) lateralis* (PHILL.), *S. (L.) acrei* (SWINN.), *S. (L.) posterior* (SACHS) and others.

The volume of subgenera and phylogenetic chart within the genus *Lagonibelus* are adopted according to those

established for genera with the same names identified by V. A. Gustomesov (1977, 1989) in subfamily Lagonibelinae. Subgenus *Lagonibelus* is an exception. It includes a number of species singled out by V. A. Gustomesov as isolated genus *Boreiolagonibelus*. These species differ from other *Lagonibelus* s.str. in more long ventral groove developed at late stages of ontogeny. We arrived at the conclusion that they were not independent genetically allied group of species but rather have originated at different time from different representatives of *Lagonibelus* s.str.

The question of descendant forms of the family is still an open one. The first

representatives of the genera *Cylindroteuthis* (*C. (C.) confessa* NALN.) and *Pachyteuthis* (*P. (P.)* sp. indet. SACHS et NALNAEVA) making their appearance in Early Bajocian time in North Pacific show significant morphologic differences and essential divergence in ontogeny. Conceivably the idea of the origin of subfamilies Cylindroteuthinae and Pachyteuthinae from the same descendant might be corrected.

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