# NEW DATA ON MIDDLE JURASSIC – LOWER CRETACEOUS BELEMNOTHEUTIDAE FROM RUSSIA. WHAT CAN SHELL TELL ABOUT THE ANIMAL AND ITS MODE OF LIFE

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**Abstract:** We present a new data on middle Jurassic – early Cretaceous coleoids family Belemnotheutidae form Russia. The palaeobiogeographic distribution of the family is summarized herein and new palaeobiogeographic data are connected within stratigraphic distribution. Based on well-preserved shells and soft bodies, the reconstruction of soft body structure of Belemnotheutidae has been completed in relation to recent coleoid families. The Belemnotheutidae mode of life and other ecological aspects are discussed in relation to recent coleoid ecology and taphonomy.

**Key words:** Coleoidea, Belemnoteuthidae, middle Jurassic – early Cretaceous, Russia, palaeobiogeography, stratigraphy, ecology

*"It is only the tradition to classify belemnites by their rostra that could possibly explain the fact that giant phragmocones (up to 15 cm in diameter) without rostra that occur in the Upper Jurassic sediments of the Russian platform have not been described yet" (Ivanov, 1979, p. 130)*

## INTRODUCTION

Fossil coleoids of the family Belemnotheutidae represent one of the most mysterious groups of Mesozoic Cephalopoda. From one hand, they are similar with other representatives of the order Belemnitida in having well-developed phragmocone with ventral siphuncle, tongue-shaped tri-partied proostracum and peculiar hooks on the arms (Naef, 1922; Jeletzky, 1966, etc.). From the other hand, they lack the main distinctive feature of belemnoid shell, the rostrum. Conotheca of Belemnotheutidae is very thin, shell-like. Usually it vanished in the course of fossilization, as well as fragile proostracum. Occurring much more rarely than belemnitids, Belemnotheutidae are usually represented by damaged phragmocones only. The later were generally ignored during field works by collectors. Apparently it was the main reason why Belemnotheutidae remained a scarcely studied group until the latest time. Investigations of the recent years marked substantial progress in our knowledge on Belemnotheutidae (Engeser & Reitner, 1981; Donovan & Crane, 1992; Hollingworth et al., 2001; Doyle & Shakides, 2004; Wilby et al., 2004). However, information on distribution and fauna of Belemnotheutidae in Russia is still fragmentary and is actually restricted by several brief mentions of 'giant phragmocones' that were usually misinterpreted as 'isolated phragmocones of belemnites' (Lahusen 1874; Pavlow, 1901; Gustomesov, 1976; Ivanov, 1979; Baranov, 1979; Ivanov et al., 1987; Bogomolov, Shenfille, 1991; Kiselev et al., 2003; Mitta, 2003; Keupp, Mitta, 2004). The material collected by the authors provided some new data on distribution of belemnotheutids on the Russian platform.

The aim of the present study is to describe fauna and distribution of Belemnotheutidae in Russia and to attempt to reconstruct some features of their soft body morphology and ecology basing on comparison with recent coleoids.

## MATERIAL STUDIED

As the conotheca is often absent in belemnotheutid phragmocones it is sometimes difficult to distinguish them from isolated belemnitid phragmocones. Recently Doyle and Shakides (2004) showed that the apical angle in belemnotheutids is somewhat smaller than in belemnitids, though their ranges overlap partly. Our data proved that this criterion is quite unambiguous while comparing belemnotheutid and belemnitid phragmocones of similar size/age group (Fig. 1). The problem of identification is greatly facilitated by different spacio-temporal distribution of these two groups: phragmocones of Belemnotheutidae are often found in localities and levels where belemnite rostra either rare or absent altogether.

The material collected by the authors as well as literature data show that Belemnotheutidae are widely spread in the Callovian – Lower Cretaceous sediments of Russia and former USSR (Fig. 2). The fossils in authors' collection can

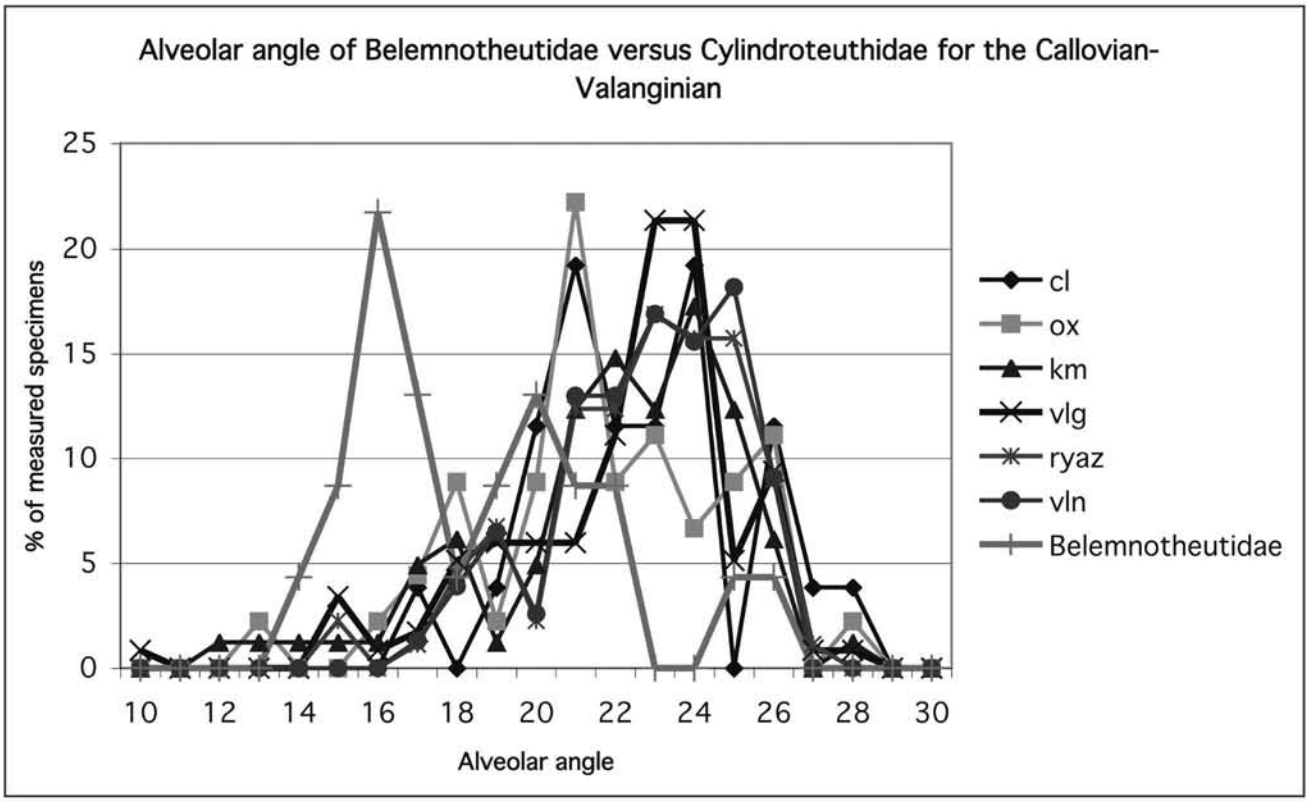


**Fig. 1 Comparison of the alveolar angle in Belemnotheutina and true belemnitids from the Callovian-Ryazanian of Panboreal Realm (Cylindroteuthidae). Data on alveolar angles in Cylindroteuthidae were obtained from papers of Mikhailov, 1964; Sachs & Nalnyaeva, 1964, 1966; Dzyuba, 2004. Total of measured specimens: Cylindroteuthidae – 435 (including Callovian – 26; Oxfordian – 45; Kimmeridgian – 81; Volgian – 117; Ryazanian – 89; Valanginian – 77); Belemnotheutidae were measured by the authors, total of 23 specimens from all studied levels (Lower Callovian to Aptian).**

be classified into two groups. The first group included small (1–5 cm length; 2–3 cm width) crushed isolated phragmocones with characteristic low V-shaped ridges on the dorsal side in apical part. These fossils were tentatively identified as *Acanthoteuthis* sp. The second group included large (9–17 cm length; 7–10 cm width) uncrushed isolated phragmocones filled with sediments and lacking the dorsal ridges. These fossils were assigned to the genus *Volgobelus* Gustomesov, 1976. One specimen represented almost entire shell (only apical part was missing). It was 34 cm in length; 10 cm in width, and consisted of crushed phragmocone (18 cm long), tongue-shaped proostracum (16 cm long), remains of ink sac and muscular mantle. This fossil was tentatively identified as? *Volgobelus* basing on its large size and phragmocone structure.

Despite apparent differences in size and mode of preservation *Belemnotheutis* (= *Acanthoteuthis*) and *Volgobelus* are not easily separated from one another. Large specimens of *Belemnotheutis* (= *Acanthoteuthis*) sometimes are loosing characteristic V-shaped dorsal ridges and becoming similar with *Volgobelus* as it was described by Gustomesov (1976). Unfortunately, the characters listed by Gustomesov as diagnostic for *Volgobelus* – peculiar external sculpture of conotheca – can only be observed in a few specimens with exceptionally good preservation. From the other hand, reexamination of the type material of *Belemnotheutis* (Pearce, 1842) showed that it also included both small and large specimens (Donovan & Crane, 1992). Later large specimens were excluded from *B. antiqua* but the taxon that should encompass these forms as well as its systematic level was never


**Fig. 2 Map of the outcrops locations, 1. Stoilensk Mine (51.15° N; 37.43° E); 2. Glebovo (58° N; 38.4° E); 3. Adzva river basin, near Adzvavom village (66.6° N; 59.3° E); 4. Prosek-Isady (56.05° N; 45.07° E); 5. Gorodischi – Polivna (54.34° N; 48.24° E), Kashpir (53.04° N; 48.25° E); 6. Dubki Quarry (51.40° N; 46.01° E), Orlovka (52.33° N; 48.65° E); 7. Khanskaya gora (51.25° N; 55.25° E); 8. Perchem Mt. near Sudak (44.51° N; 34.55° E); 9. Bojarka river basin (70.4° N; 96.3° E); 10. Putyatin Island (42.85° N; 132.4° E).**

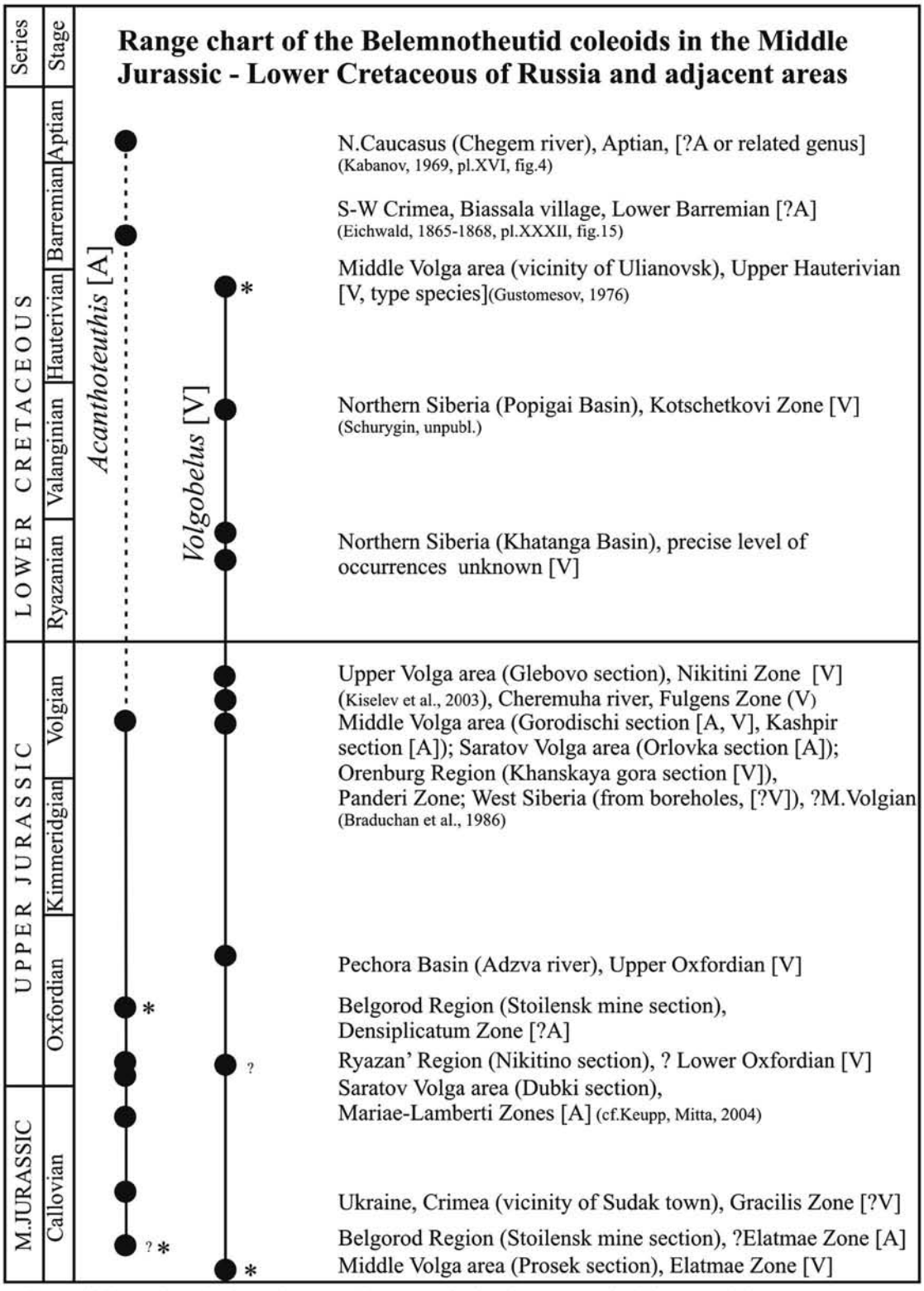


**Fig. 3 Ranges of Belemnotheutina in the studied region and their distribution through localities. V. – Volgobelus, A – Acanthoteuthis.**

specified (Donovan & Crane, 1992). It could not be ruled out that the sculpture of conotheca changed in ontogeny and the differences between large and small belemnotheutoid shells in our collection correspond to systematic differences of subgeneric or species level. Geographic and stratigraphic distribution of *Acanthoteuthis* and *Volgobelus* in Russia is different. Within the studied area they occur together only in the Middle Volgian sediments.

Most specimens described in this paper were collected by the authors from different localities of Russian platform (Fig. 2). Several specimens of exceptionally good quality were kindly provided for study by Dr. V. M. Efimov (Paleontological Museum of Undory; Ulianovsk region). Two well-preserved phragmocones were kindly grunted by Dr. D. N. Kiselev (Yaroslavl Pedagogic University). Three specimens from Ryazanian Stage (Boreal Berriasian) of Bojarka river (Eastern

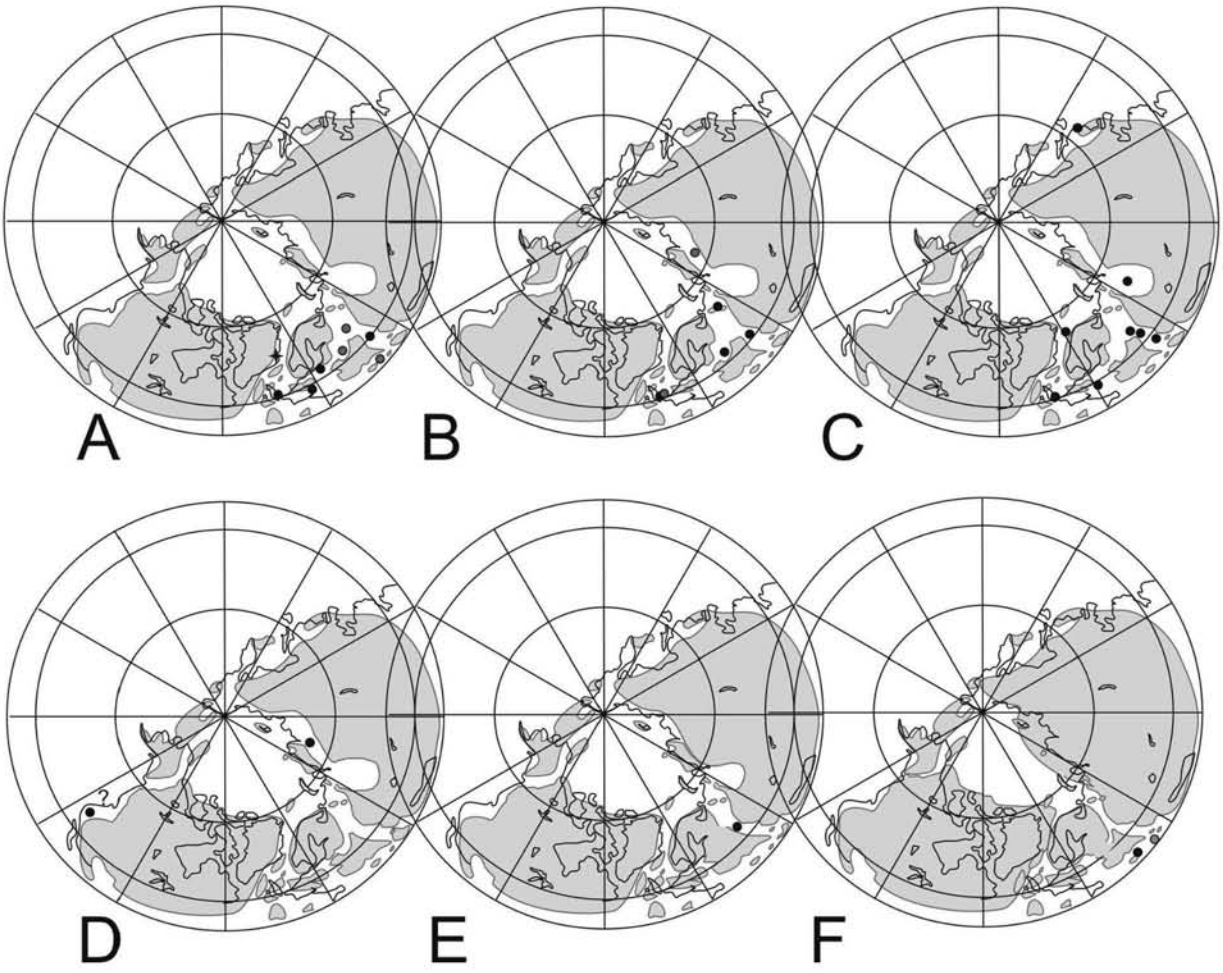


**Fig. 4 Belemnotheutids of the Bathonian – Aptian age in space and time (paleogeography is simplified). A Bathonian (asterisk), Lower (gray circles) and Upper (dark circles) Callovian. B. Oxfordian (dark circles) to Kimmeridgian (gray circles). C. Volgian. D. Ryazanian and Valanginian (but note: belemnotheutids records from California are doubtful and recently has been reinterpreted as phragmocone of the belemnite by Th. Engeser). E. Hauterivian; F. Barremian (dark circles) to Aptian (gray circles).**

part of Taimyr Peninsula) were kindly provided by A. Savitski (All-Russian Research Geological Institute (VSEGEI); Saint-Petersburg). Single small specimen from Russian Far East (Primorie region) was kindly presented by Dr. I. I. Sei and Dr. E. D. Kalacheva (All-Russian Research Geological Institute (VSEGEI); Saint-Petersburg).

**Abbreviations for the museums and institutes that housed the specimens examined here are:** CNIGR – F. N. Chernyshev Central Research Geological Museum, Saint-Petersburg; GIN – Geological Institute of Russian Academy of Science, Moscow; GM – Museum of the Saint-Petersburg State Mining Institute; IGPUW Institute of Geology, University of Warsaw; NMS – National Museum of Scotland (Edinburgh; UK); SPbSU – Saint-Petersburg State University, Museum of the Historical Geology Department; UPM – Paleontological Museum of Undory (Ulianovsk region; collection of Dr. V. M. Efimov).

## GEOLOGICAL SETTINGS OF BELEMNOTHEUTIDAE IN RUSSIA

In this section we briefly describe the most important locations of Belemnotheutidae in Russia in stratigraphic sequence, starting from the oldest ones.

**1. Lower Callovian.** Belemnotheutidae from Lower Callovian were found at three sites: Belgorod region (Stary Oskol), Nizhni Novgorod region (Prosek-Isady) and Southern Crimea (Perchem, Sudak region). At the first two locations belemnitid rostra in Lower Callovian deposits are absent, while in the Southern Crimea belemnitid rostra from Lower Callovian are rare and represented by small forms only. In Nizhni Novgorod region two large specimens of *Volgobelus* in excellent condition were found by V. M. Efimov in a single marl concretion from Eltamae Zone, *elatmae* faunal horizon in Prosek-Isady section; bed 2 (after Gulyaev, 2001). The specimens represent two straight uncrushed phragmocones with remains of conotheca and camera filled with sediments (Plate 1; Fig. 1). The length of phragmocones is 145 mm and 155 mm; apical angle is about 21°. The rostrum has an appearance of thin egg-like layer preserved in some places on the outer surface of conotheca. Septa are simple watch glass like, circular in transversal plane. The distance between septa comprises 0.08–0.10 of their diameter. No traces of proostracum can be found in either of specimens.

In Southern Crimea a single middle-size phragmocone of *Volgobelus* sp. was found near Sudak (Perchem Mt.) in Gracilis Zone, bed 13 (after Rogov et al., 2002). The speci-

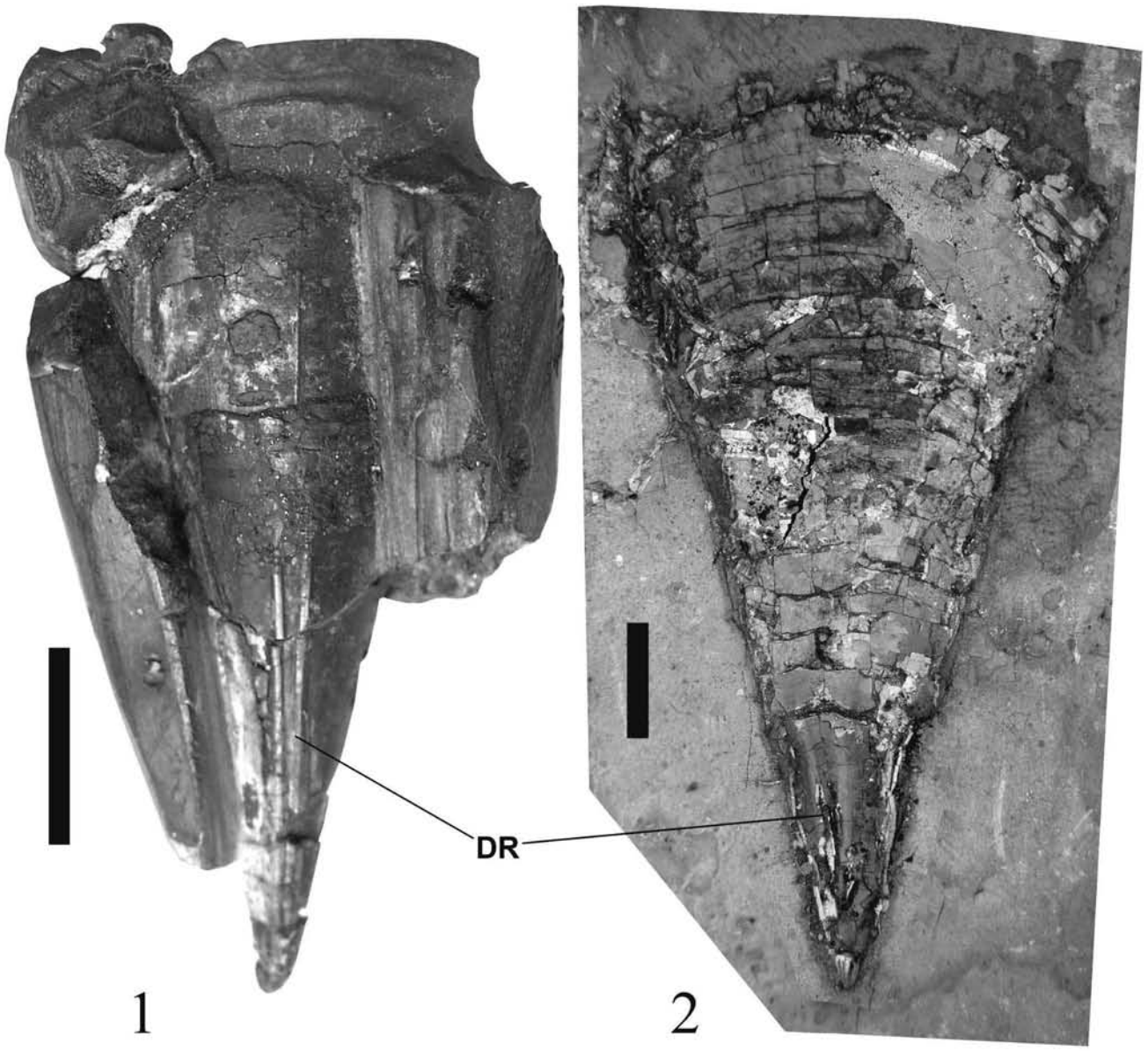


**Fig. 5 Upper Callovian Belemnotheutids from Europe. 1. *Acanthoteuthis polonicum* (Makowski), holotype IGPUW ZI/02/174, Łuków, Poland; 2. A. antiqua (Pearce), NMS G 1972.1.115, Christian Malford, UK. Abbreviations: DR – dorsal ridges of the rostrum. Scale bars = 1 cm.**

men represented a fragment of stright circular phragmocone with camera filled with sediments (Table 1; Fig. 2). In Belgorod region one small pyritized specimen of *Acanthoteuthis* sp. was found in Stoilensk mine not *in situ* from beds 1–2 (after Rogov, 2003). The specimen represented a pyrite mould of partly crushed phragmocone 42 mm in length (Plate 1; Fig. 3). Apical angle comprised about 27°.

**2. Upper Callovian – Lower Oxfordian.** Several specimens of *Acanthoteuthis* were found in Dubki section (near Saratov) in stratigraphic range between Upper Callovian, Lamberti Zone, *henrici* faunal horizon and Lower Oxfordian, Mariae Zone, *scarburgense* faunal horizon. Phragmocones *Acanthoteuthis* were reported earlier from Lamberti Zone of Dubki section by Mitta (2003), who identified them as *A. polonicum*, but they have never been neither figured, nor described. It should be noted, however, that systematics of *Acanthoteuthis* is somewhat confusing. Two species of this genus were described from Upper Callovian from the Europe: *A. antiqua* (Pearce, 1842) and *A. polonicum* (Makowski, 1952). Later Bandel and Kulicki (1988) noted that these two species are difficult to distinguish as their diagnoses uses the same characters (thin rostrum covering with paired dorsal longitudinal ridges). We had a chance to compare holotype of *A. polonicum* with exceptionally well-preserved specimen of *A. antiqua* from the type locality, Christian Malford; England (Fig. 5a). To our opinion, these two species differ mostly by their preservation condition rather than by their morphology: *A. antiqua* was described basing on crushed specimens while *A. polonicum* was described on uncrushed ones. Rare examples of uncrushed *A. antiqua* are virtually indistinguishable from *A. polonicum* (Doyle, Shakides, 2004; text-fig. 2). In our collection most specimens of *Acanthoteuthis* from Dubki section represented uncrushed phragmocones filled with sediments (Plat 1; Fig. 4). Some specimens retained characteristic dorsal ridges in apical part of the phragmocone.

**3. Middle Oxfordian.** Isolated middle-size phragmocones apparently belonging to *Acanthoteuthis* sp. are often found in Stoilensk mine (Belgorod region; Stary Oskol) in Densiplicatum Zone, bed 5 (after Rogov, 2003). Usually these specimens represent fragments of straight circular phragmocones with widely spaced watch glass like septa (Plate 2; Fig. 1). Distance between septa comprises about 0.13 of their diameter. Preservation conditions in bed 5 is not favorable for fossilization of belemnite rostra as all calcite structures (in bed 5b also aragonite structures) have been dissolved. However, it is important to note, that in bed 5b even imprints of rostra are absent, and in the rest of bed 5 a few small rostra of *Hibolithes* were found only in Lamberti Zone (Upper Callovian).

**4. Upper Oxfordian.** Large phragmocone tentatively identified as *Volgobelus* sp. was found in the Komi region, in Adzva river basin, near Adzvavom settlement (Plate 2; Fig. 2). The specimen is currently deposited in the collection of Dr. A. V. Medvedev (CNIGR; Saint-Petersburg). It could be aged by the imprint of *Amoeboceras* sp. visible in the anterior part of the sample. The specimen represents large (176 mm in length) fragment of straight circular phragmocone filled with sediments. It has relatively small apical angle (14°) and widely spaced septa: distance between septa comprises about 0.15 of septa diameter. On the ventral side suture lines of the septa make characteristic shallow incision, apparently corresponding to the position of siphuncle. Presence of ventral incision on septa and unusually low apical angle indicate that *Volgobelus* from Adzva river apparently represent a different species than Lower Callovian *Volgobelus* from Prosek-Isady; Nizhni Novgorod region (Plate 1; Fig. 1).

**5. Middle Volgian.** Belemnotheutidae are quite abundant stratotype of the Volgian stage near Gorodischi village (Ulyanovsk region). Numerous specimens were found not *in situ* in lower part of *regularis* horizon; bed 2/12 (after Rogov, 2005). One small specimen of *Acanthoteuthis* sp. was found in upper part of *scythicus* horizon. All these specimens represented small crushed phragmocones with partly preserved rostrum forming characteristic V-shaped ridges on the dorsal side (Plate 2; Fig. 6).

One exceptionally well-preserved specimen with almost complete shell, remains of the ink sac and the mantle was found in large block of oil shale fallen out from the bed 2/12. The specimen is exposed by its ventral side up (Plate 3). It is 34 cm long and about 10 cm wide. The phragmocone is crushed but its original aragonite composition is preserved. The septa are visible in anterior part of the phragmocone as widely spaced thin lines. Proostracum is thin brown tongue-shaped non-calcified structure protruding from the anterior part of the phragmocone. Its lateral zones in some places reveal fine oblique striation apparently corresponding to hyperbolar zones of belemnitid proostracum (Naef, 1922). Median zone of proostracum is comprehensively fractured into polygonal fragments (2–5 mm) that partly displaced beyond the shell contour. The ink sac is preserved as a black granular substance of irregular shape situated near anterior margin of the phragmocone. Analysis of the ink sac content under SEM showed that it consisted of clusters of uniform ink globules ranging from 0.2 μm to 0.4 μm in diameter (Plate 3; Fig. 3). Quite similar globular ultrastructure of the ink sac content was reported earlier in recent, Jurassic and Carboniferous Coleoids (Doguzhaeva et al., 2003). In anterior right part of the proostracum imprints of mantle muscles preserved as fine transversal striation overlaying the shell margin from dorsal side. In posterior part of the fossil faint wing-like contour is visible that possibly may represent imprint of the fins. This specimen was tentatively identified as *Volgobelus* sp. on the basis of large size of its phragmocone.

Phragmocones of *Acanthoteuthis* sp. and *Volgobelus* sp. from the same stratigraphic level (lower part of *regularis* horizon) were found also in Saratov, Samara and Orenburg regions. In Saratov region small specimen of *Acanthoteuthis* sp. was discovered in a steep side of Solionyi Dol ravine near Orlovka village (Plate 2; Fig. 6). It represents posterior part of crushed phragmocone embedded with its dorsal side up. The conotheca is whitish, calcareous, with traces of widely spaced septa. The rostrum layer is thin, egg-like, brownish. It forms the outer cover of conotheca with characteristic V-shaped dorsal ridges in apical part. In Samara region several specimens of *Acanthoteuthis* sp. were found by Dr. V. M. Efimov near Kashpir (Plate 2; Fig. 4). All of them consisted of fragments of crushed phragmocones, some of them with the traces of septa and dorsal ridges. In Orenburg region single large phragmocone of *Volgobelus* sp. was found in Panderi Zone, from Khanskaya Mountain section (Plate 2; Fig. 3).

Thus, all findings of Belemnotheutidae from Panderi Zone originate from relatively narrow stratigraphic interval, which in the Middle Volga region is represented by thick layer of oil shales. It is interesting to note that upper stratigraphic limit of occurrence of Belemnotheutidae in Volga region matches to Pallasioides Zone of Kimmeridge Clay Formation, which is the upper limit of occurrence of *Acanthoteuthis* in England (Donovan & Crane, 1992), and also to Bazhenov Formation in the Western Siberia where Belemnotheutidae phragmocones were found as well (Braduchan et al., 1986). Phragmocones be replaced by *Acanthoteuthis* sp. reported by Sokolov (1912; Pl. 1, Fig. 5) from Andøya Island (Norway) basing on a large hook, apparently originated from similar stratigraphic level, but may belong to some other coleoid.

Belemnotheutidae have never been reported from Virgatus Zone of Russia. However, they appear again in Nikitini Zone. Incomplete phragmocones sometimes with partly preserved conotheca were repeatedly described from Nikitini Zone of Glebovo section; Yaroslavl region (Baranov, 1979, Fig. 4–6; Ivanov et al., 1987, Plate 12; Fig. 6; Kiselev et al., 2003, Plate 39; Fig. 13). One of these specimens was kindly granted for our investigation by Dr. D. N. Kiselev (Plate 4; Fig. 1). The specimen represented a part of straight circular uncrushed phragmocone with remains of conotheca on its dorsal side. The surface of conotheca bore fine longitudinal striation (Plate 4; Fig. 1b). Distance between septa comprised about 0.13 of their diameter. The size of phragmocone is intermediate between 'typical' size of *Acanthoteuthis* and *Volgobelus*. Apparently, it should be tentatively identified as *Acanthoteuthis*, as small phragmocones with dorsal sculpture were also common in this Glebovo section (Baranov, 1979).

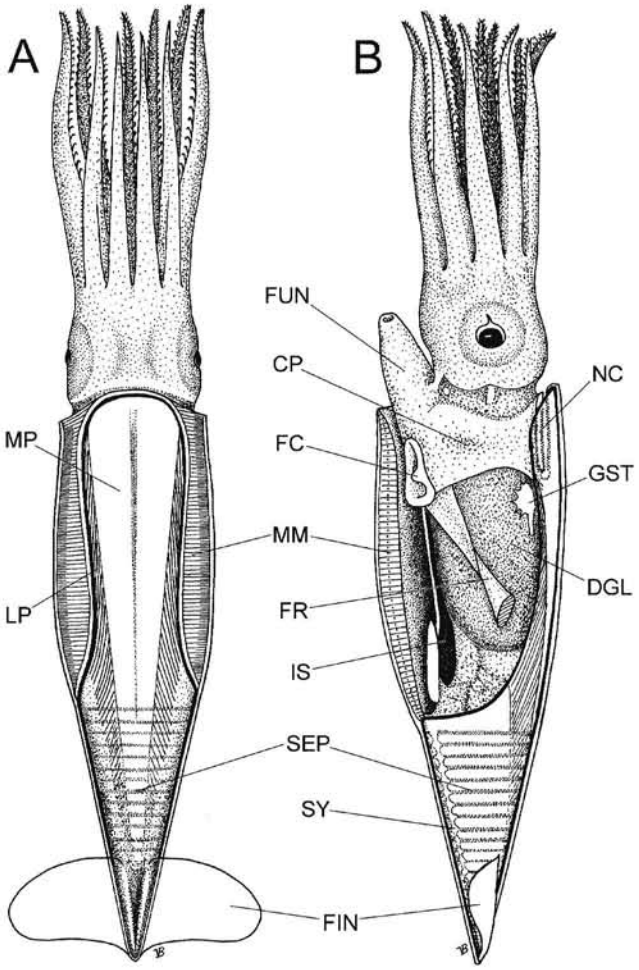


**Fig. 6 Reconstruction of the soft body in *Acanthoteuthis*. A. Dorsal view. B. Sagittal section. Abbreviations: MP – median plate of proostracum; LP – lateral plates of proostracum; SY – siphuncle; SEP – septa; MM – mantle muscles; IS – inc sac; DGL – digestive gland; GST – stellar ganglia; NC – nuchal cartilage; FC – funnel cartilage; FR – funnel retractor; CP – colar pockets; FIN – fins.**

**6. Upper Volgian.** Belemnoteuthidae from Upper Volgian up till now were found in Yaroslavl region only. One middle-size phragmocone apparently belonging to *Acanthoteuthis* sp. was grunted to authors by Dr. D. N. Kiselev (Yaroslavl Pedagogic University). It was found in Fulgens Zone in the basin of Cheriomukha river. Its size and mode of preservation is very similar with phragmocones found in Nikitini Zone of Glebovo.

**7. Ryazanian Stage = Boreal Berriasian.** Belemnotheutidae of this age were never reported from Russian Platform. However, they are known from the basin of Levaja Bojarka river in Hatanga depression; Eastern Taimyr. Several large phragmocones of *Volgobelus* were found in this location by A. S. Savitski (VSEGEI). Precise stratigraphic position of these specimens is unknown but they undoubtedly belong to Ryazanian Stage. *Volgobelus* from Bojarka represented fragments of straight uncrushed circular phragmocones filled with sediments (Plate 4; Figs 2, 3). Characteristic feature of these specimens is unusually wide distance between septa; it comprises about 0.2 of the septa diameter.

**8. Valanginian.** Authors do not have any Belemnotheutidae from Valangian. However, Bogomolov & Shenfille (1991) described small-size phragmocone with low apical angle from Lower Valangian of Sabyda river basin in Hatanga depression (Bogomolov et Shenfille, 1991, Table 27, Fig. 3). Conotheca is absent in this specimen preventing its identification at generic level, but small apical angle and widely spaced septa of this phragmocone indicates to its affinity with Belemnotheutidae. According to Dr. B. N. Shurygin (personal communication), extremely large phragmocones up to 40 cm in length occur in Upper Valanginian (Kotschetkov Zone) in the basin of Popigai river. Apparently, these phragmocones belong to *Volgobelus*.

**9. Haterivian.** Type material of *Volgobelus* Gustomesov, 1976 originated from Upper Haterivian of Ulyanovsk area of Volga region. This material included two specimens collected and named by N. M. Jasikov in 1830-es and later described by Lahusen (1874) as *Belemnites colossicus* (Plate 5; Fig. 1–2). Another exceptionally preserved specimen of *V. colossicus* was kindly grunted to authors by Dr. V. M. Efimov (Plate 5; Fig. 3). Huge phragmocones of *V. colossicus* from Upper Haterivian distinctly differ from and could not be assigned to rare small rostra of *Aulacoteuthis* sp. and *Acroteuthis* sp. found at the same horizon (Mutterlose & Baraboshkin, 2003; Baraboshkin & Mutterlose, 2004)

**10. Aptian.** Single phragmocone with small apical angle and remains of conotheca without rostra reported by Kabanov (1967, Table XVI; Fig. 4) from Aptian of the Northern Caucasus apparently belonged to Belemnoteuthidae (*Acanthoteuthis*?). The specimen represents small (approximately 5 cm long) fragment of straight circular uncrushed phragmocone filled with sediments. Its conotheca is thin, with fine parabolic growth lines and longitudinal ridge on the dorsal side.

## PALAEOBIOGEOGRAPHY OF BELEMNOTHEUTIDAE

The fragmentary knowledge of Belemnotheutidae makes it difficult to asses their distribution in the Middle Jurassic – Lower Cretaceous seas. Apparently, real distribution of this group was much wider than is currently known. Our data make possible at least to define the area and stratigraphic time where and when Belemnotheutidae were most abundant and played significant role in marine paleoecosystems.

The data available up to now indicate that in the Middle Jurassic – Lower Cretaceous Belemnotheutidae were distributed mainly in the Panboreal Superrealm. So far they have never been found in Aalenian – Bajocian sediments. Apparently the most ancient Belemnotheutidae are the forms mentioned from Cranocephaloide Zone (Boreal Bathonian) of the Eastern Greenland (Callomon, 2004). Relations of these forms with Lower Jurassic (Toarcian) Belemnotheutidae are not clear. It is possible that reduction of rostrum could happen independently in different phylogenetic lineages (Gustomesov, 1976). In Callovian Belemnotheutidae became distributed much wider. In Early Callovian the Middle-Rus-

sian sea was populated by both large *Volgobelus* with smooth conotheca and small *Acanthoteuthis* with characteristic dorsal ridges in apical part of conotheca. By the end of Early Callovian small- and middle-size *Acanthoteuthis*-like forms spread to the northern part of Tethys (Crimea) and to England (Doyle & Shakides, 2004). Similar distribution Belemnotheutidae had in Late Callovian. Apart from Russian Platform and England, *Acanthoteuthis* is known from France (Raspail, 1901; Couffon, 1919), Southern Germany (Naef, 1922) and glacial drift of Łuków in Poland (Makowski, 1952). In Oxfordian distribution of Belemnotheutidae was restricted to Russian Platform where they were represented by small forms tentatively identified as *Acanthoteuthis* sp. The northernmost findings of *Acanthoteuthis* at this time in the basin of Pechora river were larger than those from the Central Russia.

Kimmeridgian Belemnotheutidae have not been found in Russian Platform yet. However in the Western Europe small belemnotheutids (*Acanthoteuthis* sp.) were found in Upper Kimmeridgian in the Southern Germany (Naef, 1922) and England (Donovan, Crane, 1992). Single large phragmocone apparently belonging to *Volgobelus* sp. is deposited in collection of Dr. M. S. Mesezchnikov (All-Russian Oil & Geological Survey Research Institute (VNIGRI), Saint-Petersburg). It was found in Lower Kimmeridgian in the basin of Kheta river (Hatanga depression) by Dr. M. M. Romm.

In Lower Tithonian small phragmocones of *Acanthoteuthis* sp. are well known from lithographic shales of Hybonotum Zone of Germany. In Volgian sediments and their analogs Belemnotheutidae are the most abundant and widely spread. They were found from England (Donovan & Crane, 1992) and Norway (Sokolov, 1912) to the Western Siberia (Braduchan et al., 1986). At this time Belemnotheutidae (*Antarctiteuthis*) first appear in the South Hemisphere (Doyle, Shakides, 2004). In Berriasian Belemnotheutidae became less abundant and their distribution became bipolar. *Antarctiteuthis* apparently still inhabited in Antarctic, large *Volgobelus* occurred in the Northern Siberia (Eastern Taimyr) but in Europe Belemnotheutidae disappeared. In Valanginian Belemnotheutidae (*Volgobelus*) occurred only in the Northern Siberia. Supposed finding of Belemnotheutidae in the North America (*Belemnotheutis pacificus* Anderson, 1938) were later shown to be parts of belemnitids (Engeser, 1993).

Late Hauterivian was marked by substantial Boreal transgression (Baraboshkin et al., 2003). Apparently during this time *Volgobelus* together with boreal Ammonoids invaded from the north into the Middle-Russian sea. Isolation of Middle-Russian Basin from the Tethys in Barremian resulted in significant change of Belemnotheutidae distribution pattern. All post-Hauterivian Belemnotheutidae were quite rare and distributed in Tethys-Pantalassa Superrealm.

Single phragmocone that may belong to Belemnoteuthidae was described from Barremian of Crimea by Eichwald (1865, p. 1012). This specimen differed from other Belemnotheutids in having unusually long camera: the distance between septa comprised about 1/3 of their diameter (Plate 4; Fig. 4). Aptian Belemnoteuthidae in Russia are represented by a single phragmocone described by Kabanov (1967, Plate XVI; Fig. 4).

## RECONSTRUCTION OF THE SOFT BODY STRUCTURE

Morpho-functional correlations between the shell and soft body that were revealed in different group of recent Coleoidea (Bizikov, 1996; 2004) provide essential basis for reconstruction of general bauplan of the fossil coleoids by their shell and making some conclusions on their possible way of life. In case with Belemnotheutidae, such a reconstruction is greatly facilitated by numerous findings of exceptionally well-preserved complete shells and soft body parts (Engeser & Reitner, 1981; Donovan & Crane, 1992; Wilbi et al., 2004).

All characteristic features of the shell in Belemnotheutidae have important implications for soft body reconstruction which is shown on Fig. 5b. Considerable width of tongue-like proostracum in Belemnotheutidae as well as in other belemnoids indicates that it was not covered by the mantle muscles from the dorsal side. Most probably, the mantle attached to dorsal surface of the margins of thickened lateral plates (hyperbolar zones) of proostracum. Wilby et al. (2004, p. 1169) described narrow stripe of soft tissue running dorsally along the edges of lateral plates of proostracum of *Belemnotheutis*. This stripe apparently represents cartilaginous reinforcement of the shell sac at the site of mantle attachment. Similar cartilaginous rim encircles the gladius of recent *Vampyroteuthis* and serves for attachment of mantle muscles (Pickford, 1949; Bizikov, 2004). Posterior attachment of the mantle can also be defined for certain. Absence of the attachment sites on the outer surface of phragmocone, like the outer cone in recent Sepiidae or lateral wings and ventral process in fossil Spirulirostridae, testifies that the mantle wall in Belemnotheutidae apparently attached posteriorly to the aperture of phragmocone, namely to anterior margin of the living chamber. Circular profile of phragmocone (when it is not crushed) indicates that the mantle was cylindrical and its diameter was comparable with that of the living chamber. The phragmocone in Belemnotheutidae was covered by the skin integument only.

In recent coleoids each element of proostracum performs its specific function. Anterior part of the median plate provides support for the head through special nuchal cartilage. Broad shape and blunt anterior margin of the median plate indicates that nuchal cartilage in Belemnotheutidae was wide and flat like in recent Sepiidae. The width of nuchal cartilage apparently corresponded to the width of median plate; its length could not be less than its width. The funnel also received support from the shell: postero-lateral walls of the funnel in all coleoids form muscular folds (collar folds) that run alongside the visceral sac and attach anteriorly to the head, dorsally to the head component of nuchal cartilage and dorso-posteriorly to lateral margins of the proostracum. The stellar ganglia most probably were situated at the level of attachement of the collar folds to the shell, as they do in most recent coleoids. The function of lateral plates (paired elements adjacent to the median plate) is providing support for the head retractors (Bizikov & Arkhipkin, 1997). In Belemnotheutidae the head retractors could attach ventrally to the margins of lateral plates. Absence of the second paired elements in proostracum of Belemnotheutidae indicates that

the funnel retractors in these forms attached either to the inner surface of thickened lateral plates (like they do in recent Sepiidae) or to the inner mantle wall like in recent squids (Ommastrephidae, Mastigoteuthidae, Chiroteuthidae) and bob-tail squids (Sepiolidae). Attachment of the funnel retractors to the mantle is not as efficient as attachment to the shell. In recent forms it leads to development of strong funnel locking-apparatus with complex structure or to fusion of the mantle with the funnel. Similar complex structure of the funnel locking cartilages we may assume in Belemnotheutidae as well.

The presence of the ink sac in Belemnotheutidae indicates that these forms inhabited upper layers of Mesozoic seas, apparently above 200 m. Position of the ink sac is also important. In Belemnotheutidae it was situated next to anterior margin of the phragmocone. Taking into account that in all recent coleoids the ink sac, if present, is situated on the ventral side in posterior part of digestive gland one may come to conclusion that the digestive gland in Belemnotheutidae was very large and apparently occupied most part of the visceral sac. Similarly large digestive gland occurs in some recent squids families: Gonatidae, Octopoteuthidae, Ommastrephidae etc. Large digestive gland should create positive buoyancy that must be taken into account together with buoyancy generated by the phragmocone.

Dorsal v-shaped ridges in the apical part of conotheca – one of the most distinctive features of Belemnotheutidae – apparently represent a functional analogue to medial keel formed by the rachis in posterior part of the gladius in most recent squids. In squids this part of the gladius ensures articulation with the fins. Presence of similar keels in Belemnotheutidae indicates that the fins in these forms probably were small, terminal, broad-oval or oar-shaped and attached to dorso-lateral surface in apical part of conotheca. The bases of fins were separated anteriorly, possibly merging apically. The length of fins could slightly exceed the length of the ridges: 3/5$^{ths}$ of the length of the phragmocone (Donovan & Crane, 1992).

The arm length in Belemnotheutidae comprises about 40% of the total length (Donovan & Crane, 1992; Wilby et al., 2004). It is considerably longer than in recent nektonic squids (Ommastrephidae, Loliginidae, Thysanoteuthidae) but very close to planktonic species (some Gonatidae, Mastigoteuthidae, Octopoteuthidae).

The absence of rostrum in the shell of Belemnotheutidae signifies that living position of this animal was vertical head-down, like in recent *Spirula* and some planktonic squids (Mastigoteuthidae, Histioteuthidae, Bathyteuthidae etc). In deed, phragmocone of Belemnoteuthidae comprised about 50 % of the total shell length. Taking into account the head with the arms, the share of phragmocone would decrease to less than 30% of the total body length. Without a counter-weight (rostrum) such terminal position of phragmocone would turn the animal head-down. However, during jet swimming Belemnotheutidae could acquire horizontal orientation for a short period of time using fins (and possibly arms) as vertical rudders. Apparently phragmocone in Belemnotheutidae was not entirely filled with gas. Otherwise these animals would be floating on the sea surface. Frequent occurrence of belemnotheutid shell fossilized together with the soft parts indicates that phragmocone in these forms took the water and lost buoyancy quickly after animal death.

Taking into account all above-mentioned considerations it is possible to draw some general conclusions on possible way of life of Belemnotheutidae. Apparently, these were middle- to large-sized near-bottom slow-swimming or drifting forms inhabiting shallow depths (less than 150–200 m) in coastal and shelf areas of continental seas in Mesozoic era.

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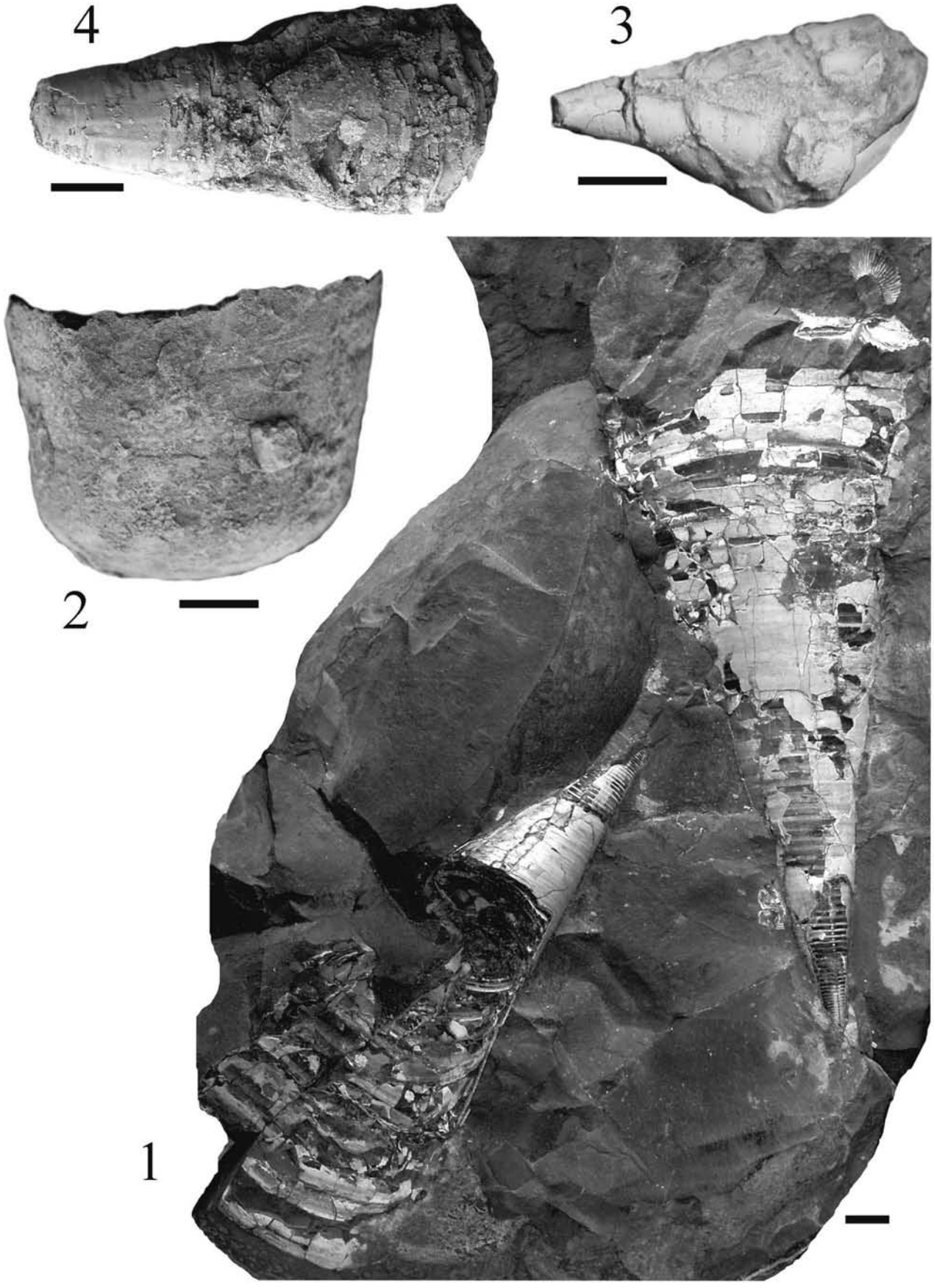


**Plate 1. Callovian Belemnotheutids. 1.** *Volgobelus* **sp., UPM, specimen without number, Prosek-Isady; Lower Callovian, Elatmae Zone,** *elatmae* **horizon (collected by V. M. Efimov). Orientation of the left shell is not clear; right shell is facing ventral side up. 2.** *Volgobelus* **(?) sp. Phragmocone; dorsal view. GIN MK1758, Perchem, Lower Callovian, Gracilis Zone, Michalskii Subzone, bed 13 after Rogov et al., 2002. 3.** *Acanthoteuthis* **sp. GIN MK1416, Stoilensk mine, Lower Callovian, ?Elatmae Zone (not in situ), pyrite mould. 4.** *Acanthoteuthis antiqua* **(Pearce). Dorsal view of the phragmocone; anterior end on the right. GIN MK1763, Dubki, Upper Callovian, Lamberti Zone,** *praelamberti* **horizon. Scale bars = 1 cm.**

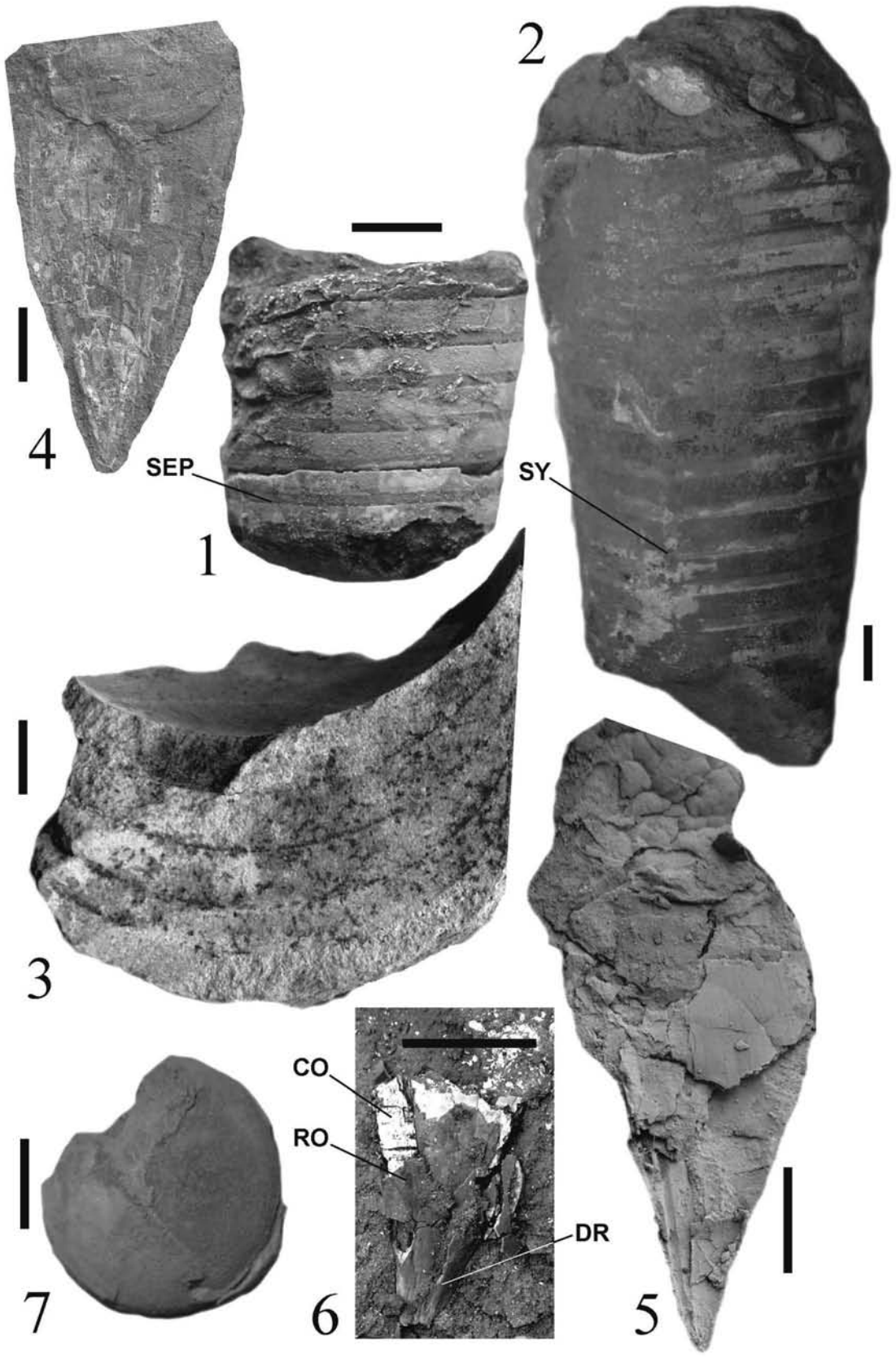


**Plate 2. Oxfordian – Volgian Belemnotheutids. 1.** *Acanthoteuthis* **(?) sp., dorsal view of phragmacone, GIN MK1417, Stoilensk mine, Middle Oxfordian, Densiplicatum Zone, near to base of bed 6 (after Rogov, 2003). 2.** *Volgobelus* **sp., ventral view of phragmocone, CNIGR 33/4390, Adzva river (?near Adzvavom), Upper Oxfordian (collected by A. V. Medvedev). 3.** *Volgobelus* **sp., sagittal fracture of phragmocone, GIN MK1758, Khanskaya gora, Middle Volgian, Panderi Zone. 4–6.** *Acanthoteuthis* **sp., dorsal views of posterior parts of phragmocones (crushed), Middle Volgian, Panderi Zone: 4. UPM, specimen without number; Kashpir, Samara region (collected by V. M. Efimov). 5. GIN MK1564, Gorodischi,** *regularis* **horizon (not** *in situ*). **6. GIN, specimen without number, Orlovka,** *regularis* **horizon. 7.** *Acanthoteuthis* **(?) sp., Putyatin Island, Middle Tithonian, Zitteli Zone (collected by I. I. Sey, E. D. Kalacheva). Scale bars = 1 cm. Abbreviations: CO – conotheca; SEP – septa; SY – siphuncle; RO – rostrum; DR – dorsal ridges of the rostrum.**

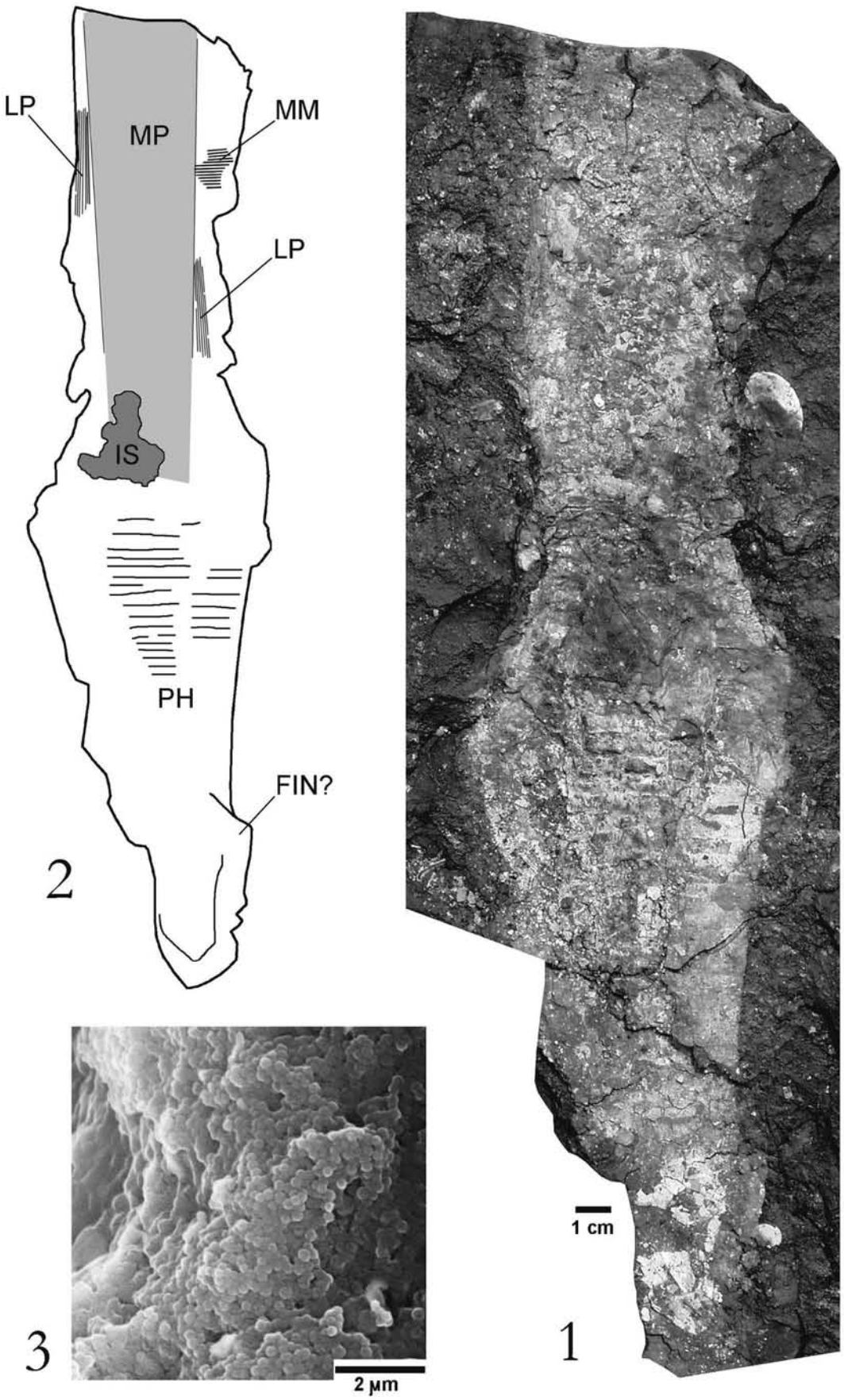


**Plate 3. Middle Volgian *Volgobelus* sp. of the exceptional preservation from the Gorodischi section, Panderi Zone, regularis horizon. 1. Specimen with preserved crushed phragmocone, proostracum and soft tissue remains. 2. Scheme of the specimen. 3. SEM micrographs of the ink sac content (characteristic ink globules). Abbreviations: MP – median plate of proostracum (parabola zone); LP – lateral plates of proostracum (hyperbole zones); MM – muscular mantle; PH – phragmocone; IS – ink sac; FIN? – contour of fins?**

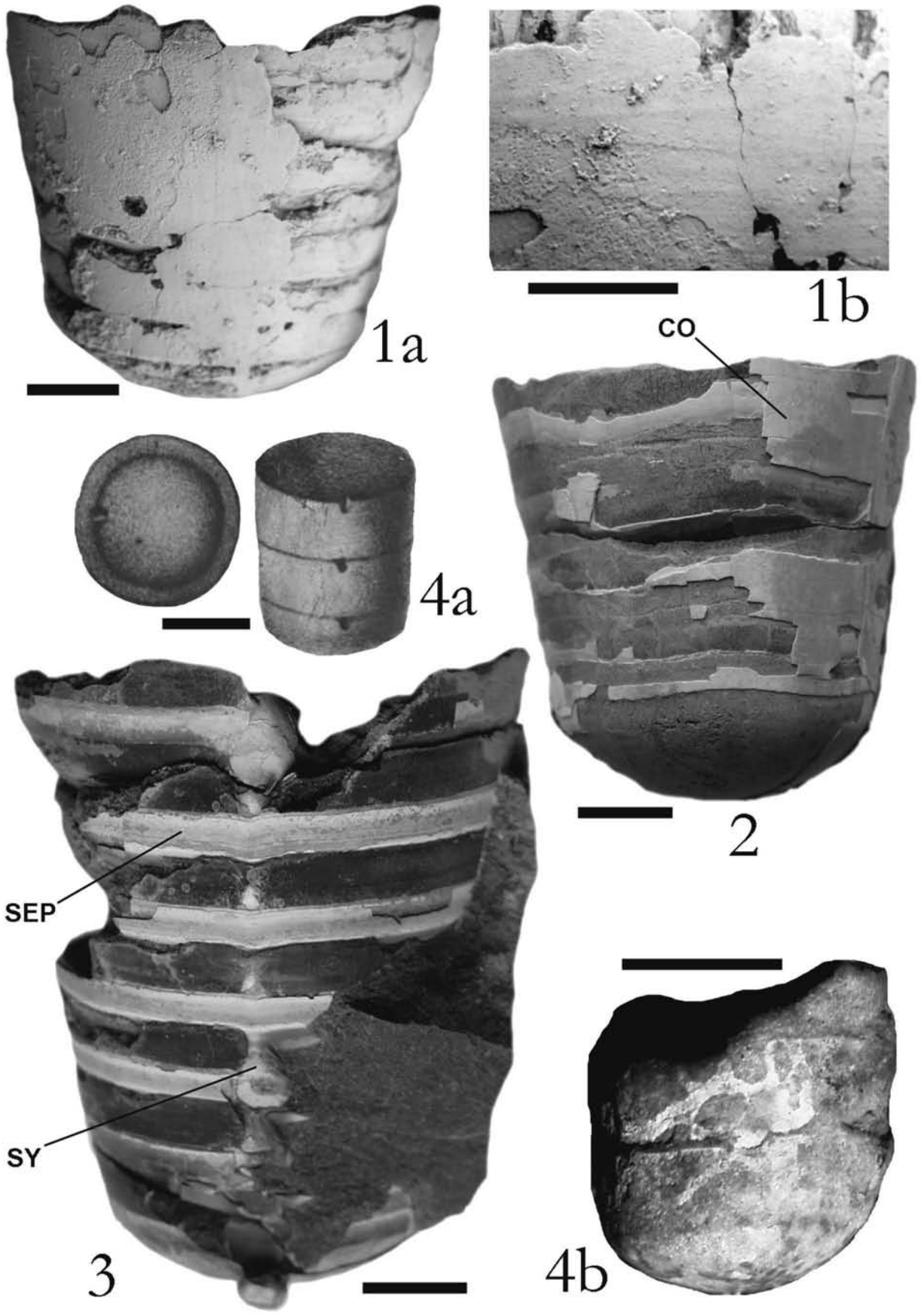


**Plate 4. Middle Volgian to Barremian Belemnotheutids. 1. ?*Acanthoteuthis* sp., GIN MK1759, Glebovo, Middle Volgian Nikitini Zone (collected by D. N. Kiselev), a – general view; b – details of the conotheca sculpture showing longitudinal ornament; 2, 3. *Volgobelus* sp., Ryazanian-Valanginian of Bojarka river basin, not in situ (collected by A. S. Savitsky), 2 – GIN MK 1754, dorsal view; 3 – GIN MK1755-1, ventral view; 4. *Acanthoteuthis* (?) sp., Biassala, Crimea, Lower Barremian (collected by E. Eichwald), a – refigured sketch from Eiuchwald, 1865–1868, pl. XXXII, fig. 15; b – original specimen of Eichwald, SPbSU 2/2039. Abbreviations: CO – conotheca; SEP – septa; SY – siphuncle. Scale bars = 1 cm.**

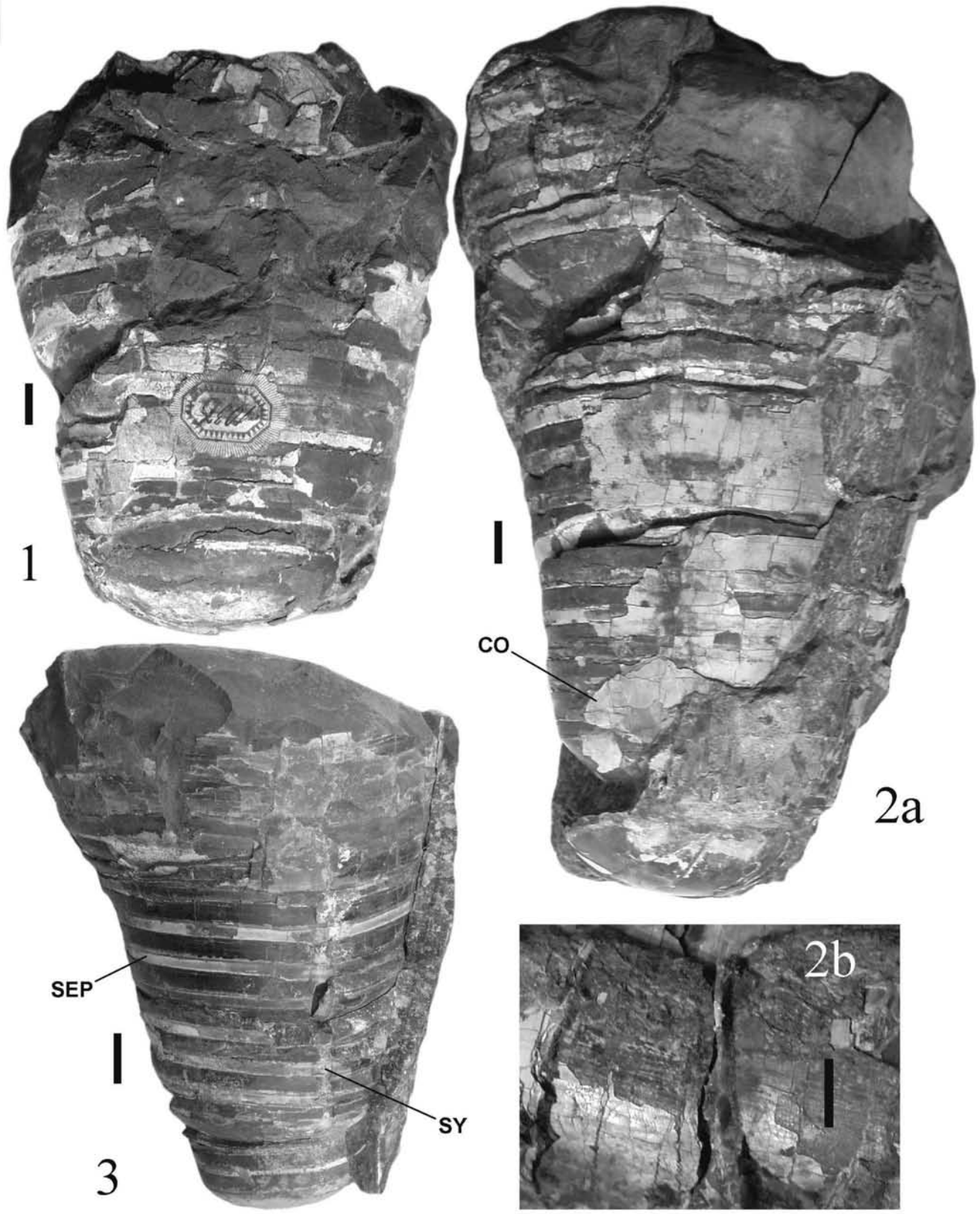


**Plate 5. Hauterivian *Volgobelus colossucus* (Jasikov) from the Ulyanovsk Volga area. 1. GM 495/464, Polivna (collected by P. M. Jasikov). 2. GM 25a/48, the specimen was collected by P. M. Jazykov and later described by Lahusen (1874). 2a – general view; 2b – detail of the longitudinal sculpture of conotheca. 3. UPM, specimen without number (collected by V. M. Efimov). Abbreviations as on Fig. 4. Scale bars = 1 cm.**