



# **Charles University of Prague**

## **Faculty of Science**

**2nd International Symposium "Coleoid Cephalopods Through Time"**  
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**Short papers / Abstracts Volume**

**Martin Košťák & Jaroslav Marek (eds.)**  
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# **Charles University of Prague - Faculty of Science**

## **2nd International Symposium "Coleoid Cephalopods Through Time"**

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## Editorial

**Charles University** was founded on the 7<sup>th</sup> of April 1348 by a charter of Charles IV, King of Bohemia and Emperor of the Holy Roman Empire. In this way one of the three great ideas of Christian medieval times – *universitas* – was fulfilled. Thanks to Charles' foresight and his good relations with Pope Clement VI, the newly founded university had four faculties – theological, law, medical and arts – a pattern which corresponded to medieval concepts of a complete university. The university was based on the Sorbonne model and it is the oldest university in Central Europe.

However, the **Faculty of Science** is not as old; it was established in 1920, when it became quite obvious that it was no longer possible to teach sciences in the Faculties of Philosophy and Medicine. The enormous development and differentiation of the natural sciences since the nineteenth century and their rapidly growing importance in the life of mankind necessitated the formation of independent institutions providing for education and research in this field; the Faculty is one of them. There have been many changes in the life of Charles University during the turbulent twentieth century, accompanied by various organizational adjustments. At present, the entire field of science is shared by two faculties - the Faculty of Mathematics and Physics and the Faculty of Science which deals with Biology, Chemistry, Geology and Geography and contains a special Institute for environmental studies.

It is a compliment for us, that the 2<sup>nd</sup> *International Symposium – „Coleoid Cephalopods Through Time, Prague 2005“* is hosted by Charles University which combines tradition with the modern life and living in Prague, one of the most beautiful cities in the world which has inspired scores of scientists, artists and sensitive people throughout history.

Let's have a nice time in Prague

Martin Košťák & Jaroslav Marek

*University of Charles in Prague  
Košťák & Marek*

## Coleoid research in Bohemia – a brief historical view

Marek Jaroslav and Košťák Martin

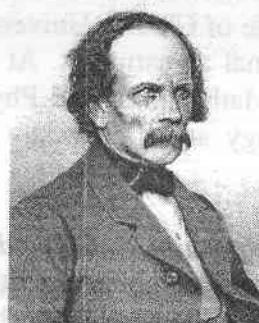
Institute of Geology and Palaeontology, Charles University Prague, Albertov 6, 128 43, Czech Republic; [marekj@natur.cuni.cz](mailto:marekj@natur.cuni.cz); [kostak@natur.cuni.cz](mailto:kostak@natur.cuni.cz)

However, the coleoid fossils are not so common in Bohemian sedimentary formations and units, they represent a small but important stone in mosaic which completes the data of their evolution. They were studied in detail by very few authors in the past. The following part is dedicated to them.

Between 1527 - 1533, a famous **Georg Bauer**, known as **Georgius Agricola** (\*24.3.1490 in Glaucau - †21.11.1555 in Chemnitz) worked as a medicine doctor in Jáchymov (Joachimsthal).



*Georgius Agricola*



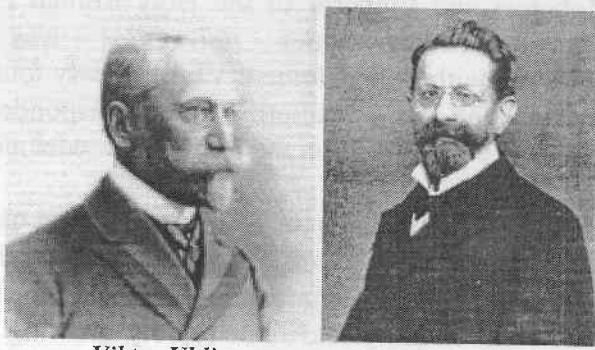
*A. E. Reuss*

He is considered to be a father of mineralogy, however, for palaeontologists and biologists is especially known as an author of many names of fossils. Inside of them, especially a term „belemnite“ (*De natura fossilium libri 1546, IV, cap. VIII; "Belemnites - a javelin shape"*) is topical for coleoid workers.

**August Emanuel Reuss** (\*8.7.1811 in Bílina - †26.11.1873 in Vienna) - professor of the Mineralogy in Prague University (since 1849) and University of Vienna (since 1863) described (1854) an unique discovery of strongly mineralized gladius of „*Glyptiteuthis ornata*“ from Turonian deposits (Upper Cretaceous) of Bílá Hora in Prague. (Plate 2)

**Karl Alfred Zittel** (\*25.9.1839 in Bahlingen - †5.1.1904 in Munich) - professor in Vienna and Karlsruhe Universities (since 1863) and Munich University (since 1866). Since 1899 director of the Bavarian Academy of Science. He described a Late Jurassic and Early Cretaceous belemnite fauna from Štramberk, Northern Moravia (1868, 1870). (Fig.1).

**Viktor Uhlig** (\*2.1.1857 in Lískovec - †4.6.1911 in Karlovy Vary (Karlsbad)) - professor of the Prague Polytechnic University (since 1891) and the Vienna University (since 1900), and also the first President of the „*Geologischen Gesellschaft*“ in Vienna.

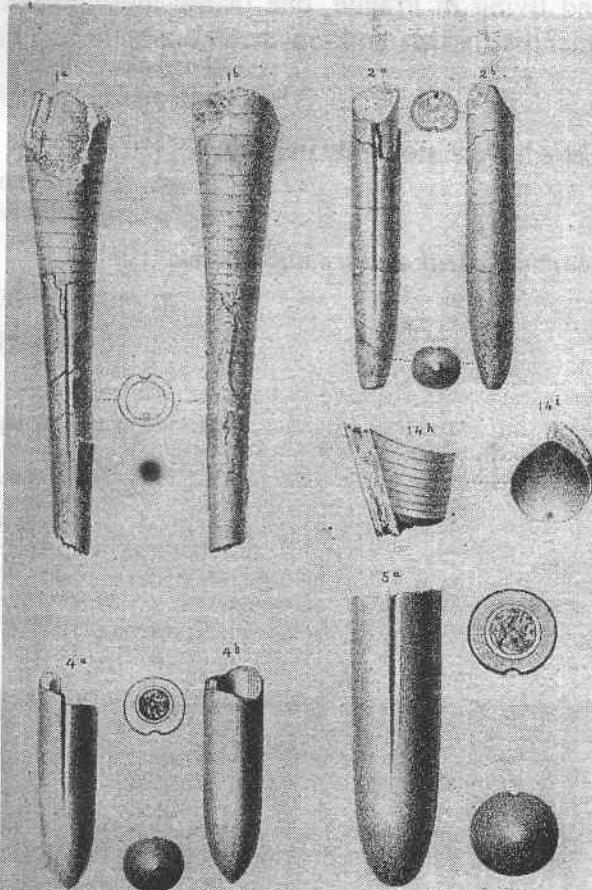


*Viktor Uhlig*

*K. A. Zittel*

His research was concentrated into Geology and Tectonics of Alps and Carpathians and also to Palaeontology (ammonites and also belemnites). He described a quite rich Lower Cretaceous belemnite fauna from Štramberk – Northern Moravia (1883, 1902, 1902 - with A. Liebus; - Veřovice, Těšín and Hradiště Formations, Early Cretaceous).

*Zittel. Cephalopoden der Štramberger Schichten*



*Fig.1. A part of K. A. Zittel's Plate 1, 1868.*

**Antonín Frič** (\*30.7.1832 in Prague - †15.11.1913 in Prague), professor of Zoology and Comparative Anatomy at Prague University (since 1862) and director of the Geological-Palaeontological Collections of the National Museum Prague. He is an author of many monographies and also a prize winner of the Cuvier na Lyell prizes. His very important studies were concentrated into Carboniferous – Permian coal deposits (Vertebrates and Insects) in Central Bohemia and also to the Bohemian Cretaceous sedimentary formations and palaeontology, especially to Crustaceans, Vertebrates and Cephalopods. Coleoid cephalopods were studied in details in his basic works:

Fritsch, A. - Schlönbach, U. (1872): *Cephalopoden der böhmischen Kreideformation*.

Fritsch, A. (1910): *Miscellanea Palaeontologicca. II. Mesozoica. Pt. 2. Neue Cephalopoden aus der Kreideformation Böhmens.*

(Plates 1, 2).

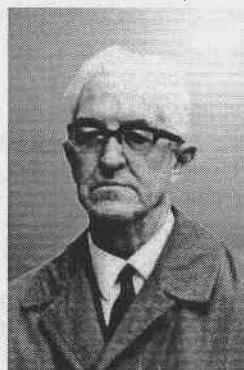


Antonín Frič

**Georg Bruder** (\*1856 in Innsbruck - †10.12.1916 in Ústí nad Labem) - assistant of Geological Institute of German University in Prague (1882-1890), later he worked as a professor at Gymnasium in Žatec and Ústí nad Labem. He described a very rare Jurassic fauna from northern Bohemia (1888) including also a poorly preserved belemnites.

**Vlastislav Zázvorka** (\*3.10.1903 in Simferopol - †4.12.1986 in Prague) – director of the Geological-Palaeontological Collections of the National Museum Prague. He studied especially a „problematic“ Upper Cretaceous belemnite species of „*Actinocamax plenus*“

– its systematics, taxonomy and stratigraphy (1929, 1930, 1965, 1968).



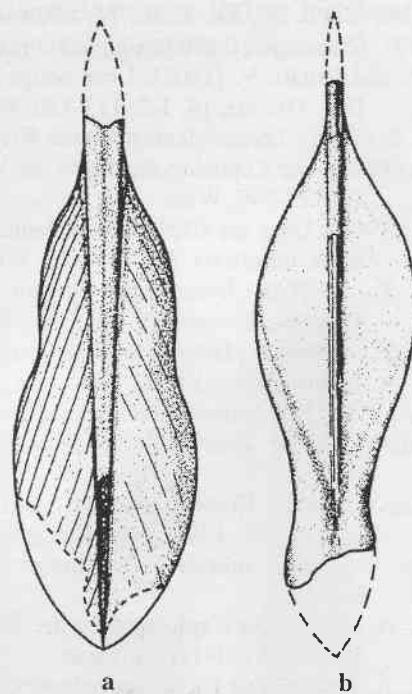
Vl. Zázvorka



Zdeněk Vašíček

**Zdeněk Vašíček** (\*11.7.1937 in Frýdek-Místek) – professor of the VŠB Technical University Ostrava. He is an outstanding specialist on the Lower Cretaceous ammonites, however, some his important works are concerning also the Lower Cretaceous belemnites from Northern Moravia and the Carpathians (1978 a,b; 1996 – with P. Pemza and A. Grmela).

The Lower Cretaceous belemnites from Northern Moravia and the Carpathians were also partly studied by another authors - i.e. **H. Frajová** (1960) and **J. Horák** (1988).



**Fig.2.** Gladii of the Bohemian Cretaceous „teuthoids“ - a) *Marekites* and b) *Eoteuthoides* (After Kostak, 2002; cf. Plate 2).

The Upper Cretaceous coleoid cephalopods from the Bohemian Cretaceous Basin (i. e. belemnites and „teuthids“) were recently revised and studied in details by **M. Košták** (1996, 1997, 2002, 2003, 2004) (Fig. 2).

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## PLATE EXPLANATIONS

### PLATE 1 (p. 5)

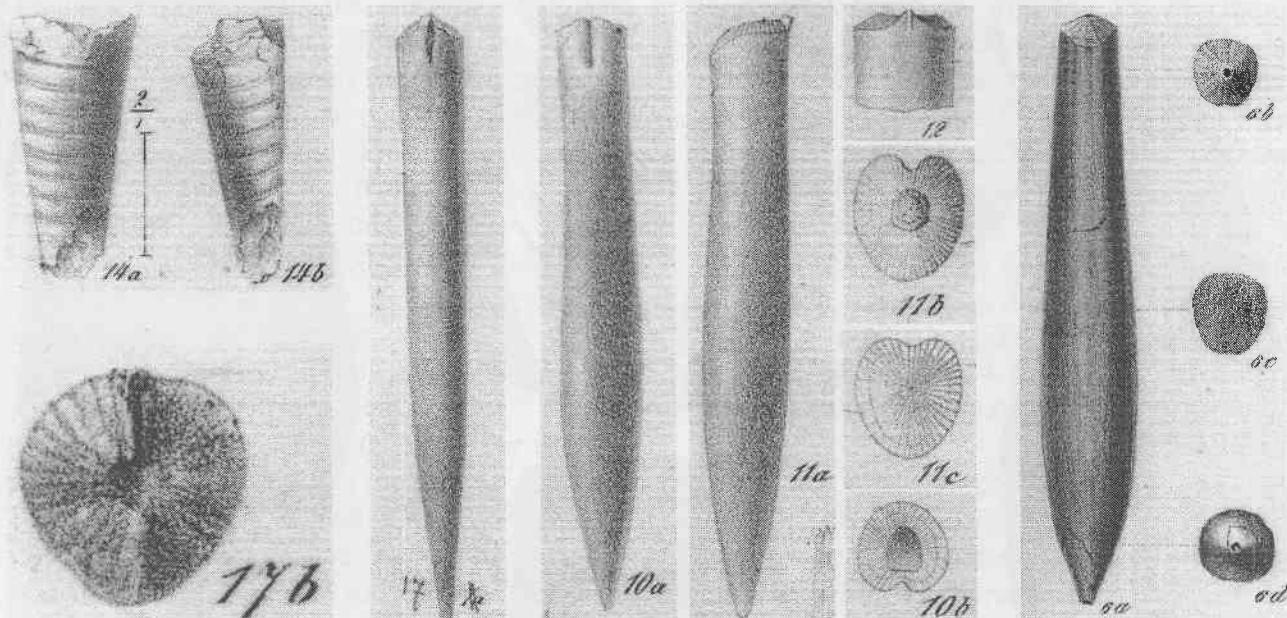
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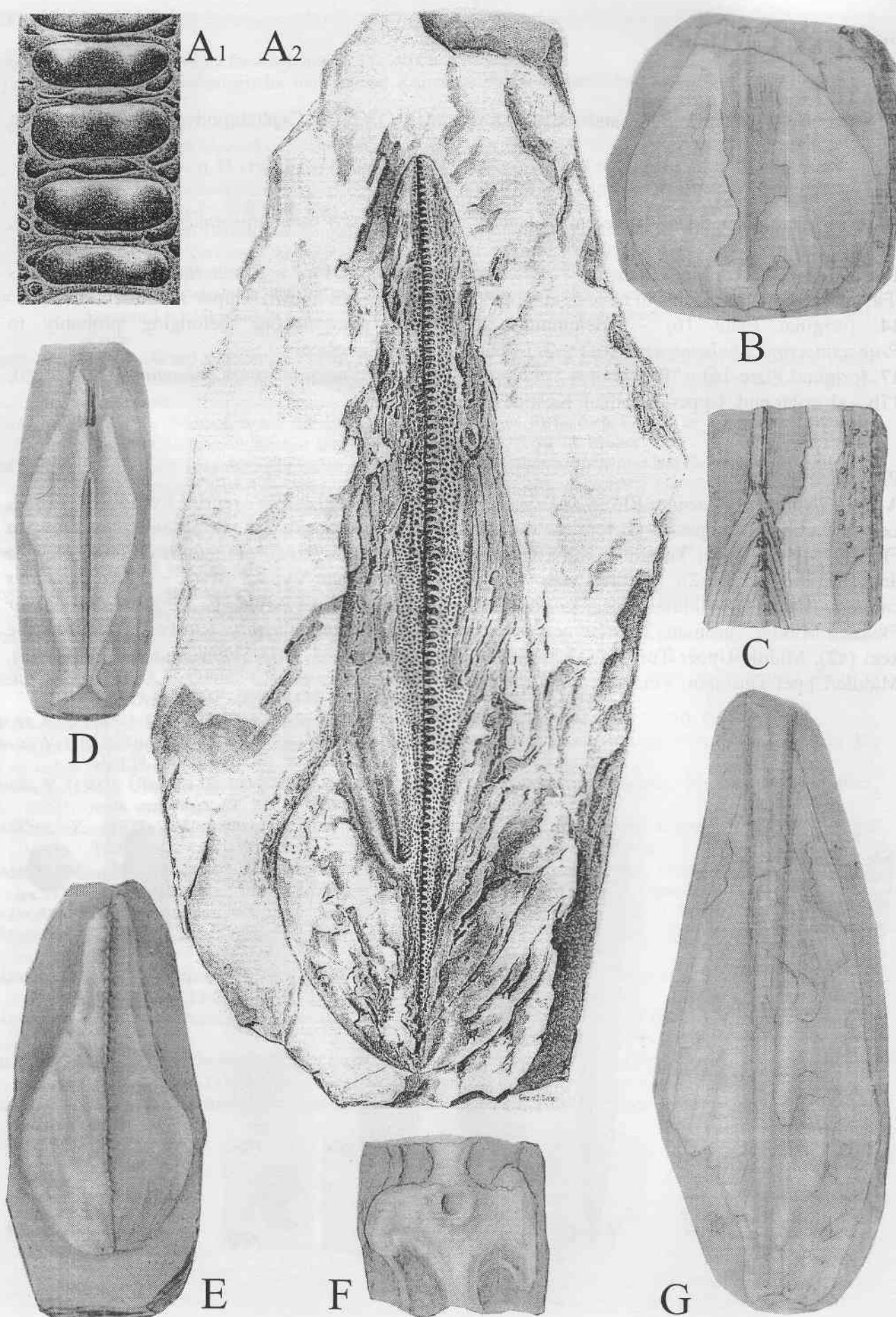
Fritsch's indexes:

- 6a-d.** (original Plate 11) - “Belemnites lanceolatus, SOW.” = *Praeactinocamax plenus* (BLAINV.). Upper Cenomanian.  
**10a-b, 11a-c, 12.** (original Plate 16) - “Belemnites Strehlensis, FR.” = *Praeactinocamax strehlensis* (FR.). \*The holotype seems to be lost, another specimens are not known. Upper Turonian. Strehlen.  
**14.** (original Plate 16) - “Belemnites sp.?” - a phragmocone belonging probably to *Praeactinocamax bohemicus* (STOLLEY). Upper Turonian. Lenešice.  
**17.** (original Plate 16) - “Belemnites Strehlensis, FR.” = (*Praeactinocamax boemicus* (STOLLEY)), 17b – alveolar end. Upper Turonian. Koštice u Loun.

### PLATE 2 (p. 6)

**A<sub>1</sub>-A<sub>2</sub>.** *Glyphiteuthis ornata* REUSS (x 0.5), **A<sub>1</sub>** - detail of the keel, x2,5) - reprint from REUSS, 1854, Lower Turonian, Prague. **B-G:** reprints from Fritsch 1910, Orig. Plate 5. **B.** *Styloleuthis convexa* FR.(x2), Middle/Upper Turonian, Vinary near Vysoké Mýto. **C.** *Paraglyphiteuthis crenata* (FR.) - a detail of the keel, (x2), Middle/Upper Turonian, Vinary near Vysoké Mýto. **D.** *Eoteuthoides caudata* (FR.)(x2), Middle/Upper Turonian, Vinary near Vysoké Mýto. **E.** *Glyphiteuthis minor* FR.(x2), Middle Turonian, Ždánice near Kouřim. **F.** *Glyphiteuthis ornata* REUSS - a detail of the keel (x2), Middle/Upper Turonian, Vinary near Vysoké Mýto. **G.** *Marekites vinarensis* (FR.)(x3), Middle/Upper Turonian, Vinary near Vysoké Mýto.





# Allopatric speciation of the teuthid fauna on the shelf and slope of Northwest Africa

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**ABSTRACT:** Habitats and life cycle strategies of nektonic squid occurring off the Northwest African coast are described. Evolutionary pathways of their allopatric speciation on the shelf and continental slope are discussed.

**Key words:** Coleoid cephalopods, nektonic teuthids, depth distribution, speciation, NW Africa

The shelf and slope of the Northwest African coasts between 19° and 26°30 N is one of the most productive regions in the Atlantic because of a strong upwelling occurring here throughout the year. Unlike rather uniform landscape of the Sahara desert, the adjacent oceanic habitats are diverse including a complex of the different streams, meanders and gyres. The major regional current, the Canary Current, moves southward along the entire shelf and continental slope. At about 22-24°S it splits into two branches - the Saharan Current (inshore branch), which runs also southwards on the shelf between 50 and 200-m depth contours, and the mainstream that follows the deeper part of continental slope. The convergence between the cold upwelling and warm waters of the Canary Current is known as the Oceanic Front. Northbound extension of the North Equatorial Countercurrent (NECC) runs over the depths ranging from 200 m to 900 m, with the main stream locating at ~ 50 m deep from the surface to ~ 300-m depth, wedges between Saharan Current and the mainstream, and achieves 22-24°S (Mittelstaedt, 1991).

The nektonic squid fauna in the region consists of eight species belonging to two families, Loliginidae and Ommastrephidae. Interestingly, squid species seem to be segregated by depth, with only one-two species dominating near the bottom and in the water column between the certain depth ranges.

Two sympatric species of the loliginid genus *Alloteuthis*, *A. subulata* and *A. africana* are the shallowest squid of the local teuthofauna. They are encountered in the coastal waters of Saharan Current, mostly at depths of about 15-100 m. These relatively small squid have a half-year life cycle and the lowest potential fecundity of hundreds or several thousand eggs of 1.5-2.3 mm (Arkhipkin and Nekludova, 1993; Laptikhovsky et al., 2002).

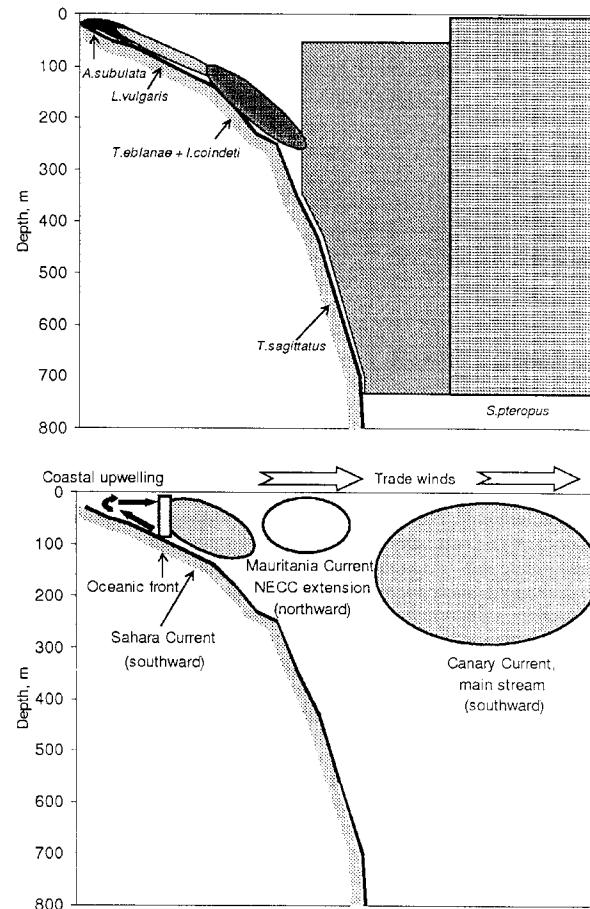
Another loliginid squid, *Loligo v. vulgaris*, occupies deeper waters of the same origin, mainly between 30 m and 130 m, penetrating down to 400 m. Its maximum abundance was observed in the Saharan Current inflows on the shelf. Immature squid move offshore down the shelf, and upon their maturation return to shallow waters to spawn. Two main spawning peaks (autumn and spring) were observed. Squid belonging to both spawning cohorts have annual life cycle (Arkhipkin, 1995). Egg dimensions are 2.0-2.2 x 1.5-1.6 mm, the potential fecundity was estimated as 28,500-74,200 oocytes including 3,500-30,500 yolk oocytes (Laptikhovsky, 2000).

Two ommastrephid squid, *Todaropsis eblanae* and *Illex coindetii*, occupy the next depth range. Both species may be encountered over the wide depth range (between 38 and 719 m), but *T.eblanae* is more deep-water (mostly 150-300 m vs 100-250, Hernández-García, Castro, 1995). Their main habitat is the

waters occupied by the Oceanic Front and Saharan Current. *T. eblanae* is a demersal squid, spending its entire life cycle near the bottom. *I. coindetii* is more pelagic (=benthopelagic), making diel vertical migrations into the water column, but not raising to the surface. Life cycle of *T. eblanae* is one year (Arkhipkin, Laptikhovsky, 2000). Spawning of *T. eblanae* is all year round, with peaks in spring and autumn. Eggs are about 1.2 mm in diameter, potential fecundity ranges between 103,000 – 236,000 eggs. *I. coindetii* also spawns throughout the year, with much less pronounced spring spawning peak (Hernández-García, Castro, 1995). Two cohorts are present off the NW African coast, large squid with annual life cycle, and small squid having 0.5-year life cycle (Arkhipkin, 1996). Ripe egg size is 0.7-1 mm, potential fecundity is 80,000-800,000 (Laptikhovsky, Nigmatullin, 1993).

Another ommastrephid squid, *Todarodes sagittatus* occurs mostly between 250 and 800 m. Juveniles inhabit pelagic waters of the NECC (mostly above 300-800 m depths) undertaking diel vertical migrations to deepwater layers. Upon maturation, squid move to near-bottom layers of the continental slope. Spawning is throughout the year, with the prominent winter peak. Lifespan duration is 1 year (Arkhipkin et al., 1999). Ripe eggs are of 0.9-1.0 mm in diameter, the potential fecundity is 215,000-950,000 (Nigmatullin et al., 2002).

*Sthenoteuthis pteropus* is an abundant oceanic ommasterphid squid, widely distributed in the tropical and subtropical Atlantic. Off the NW Africa, *S. pteropus* inhabits the waters of the Canary Current (above 1000 m depths). Paralarvae occur in the superficial water layers, whereas juveniles migrate to thermocline. Adults undertake extensive diel vertical migrations from mesopelagic waters during the day to the surface at night. Lifespan is 1 year (Arkhipkin, Mikheev, 1992). Spawning takes place throughout the year, but mostly in summer-autumn. Ripe egg size is 0.73-0.87 mm, the potential fecundity increases with body size from 560,000 to 17,900,000 (Laptikhovsky, Nigmatullin, in press).



#### Figure caption

Scheme of spatial and vertical distribution of nektonic squid (up) and main oceanographic features (down) off the Northwest African coast at 21°N latitude.

Generally, the teuthofauna off the NW African coast consists of benthopelagic species belonging to the Lousitaine -Mediterranean faunistic province (Nesis, 1985), that appeared here with the Canary Current, and epimesopelagic tropical *S. pteropus*. For shelf and slope squid this region is the southern periphery of their ranges in the Atlantic. It seems that speciation of squid fauna in the region happened ‘horizontally’, with one-two dominant species occupying each depth habitat. Similar “stratification” could be observed between the local horse mackerel genera *Decapterus* and *Trachurus*. Similar to other areas of the world ocean (Nesis, 1985), loliginids dominated on the inner shelf, whereas the waters of the outer shelf and slope were occupied by ommastrephids. From

inshore to offshore direction, squid species have smaller eggs and larger fecundity, possibly due to higher non-selective mortality

at early stages in oceanic habitats related to increasing egg dispersal.

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## ***Naefia* WETZEL, 1930 from Quiriquina Formation (Maastrichtian), a relative of the Spirulida (Coleoidea, Cephalopoda)?**

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**ABSTRACT:** The genus *Naefia* WETZEL, 1930 is based on *Naefia neogaeia* WETZEL, 1930 from Quiriquina Formation, Maastrichtian of Quiriquina Island, Concepción, southern Central Chile. *Naefia* has been described quite some time ago (Wetzel, 1930), before *Groenlandibelus* BIRKELUND, 1956 became known, but both fossil cephalopods have been interpreted to represent shells of *Spirula*- like composition but straight orientation (Haas, 1997, 2003). The two genera were interpreted to compose the Groenlandibelidae JELETZKY, 1966.

**Key words:** Coleoid cephalopods, *Naefia*, Upper Cretaceous, Chile, shell morphology.

### **1. Redescription of *Naefia***

The shell of *Naefia* based on its type *Naefia neogaeia* from Quiriquina Formation in Chile consists of a straight phragmocone with simple watch glass like septa, a width of more than 12 mm and an apical angle of about 14°. The apertural margin on the ventral side is straight and on the dorsal side it extends into a narrow projection, the proostracum. The intermediate zone of sharply forwards curving growth increments on both sides of the proostracum is narrow. This dorsal proostracum is part of the outer phragmocone layer forms that has fine elongate striation and represents the periostracal layer of the shell. It is bordered by a marginal keel on each side and a double keel in its middle. Growth lines from the narrow dorsal projection of the proostracum are partly disconnected from the margin.

Attachment scars of tissue to the shell interior are well expressed on chamber fills (steinkern) in part of the phragmocone (Pl. 1, Figs B,C,E). The rectangular scars lie at the very end of the dorsal side of each chamber. The scar in the anterior part of each chamber

is surrounded by a groove, which the ridge that surrounded the tissue attachment to the shell interior.

The initial chamber is globular in shape and attached to the tube of the shell a little inclined to the ventral side. In thin section it documented no siphon indicating that the siphon as well as first chamber closure were organic in original composition. Later chambers are about three times wider than high. The siphonal tube lies marginal and consists of a tube with mineralized septal necks extending for about one third of chamber height and remaining tube portions organic in composition. The largest shell is about 20 mm long and 5 mm wide and has about 9 chambers preserved.

The median dorsal ribbon found in *Naefia neogaeia* represents a projection of the aperture of unrecognized length and very narrow marginal zone, since growth lines of the phragmocone otherwise are simple and straight (Pl. 1, Figs B,D,F). The aperture of the phragmocone was, therefore connected to a narrow spine-like projection already found on the shell of young individuals as well.

*Naefia neogaeia* from Quiriquina Formation documents that the exterior of the phragmocone is covered by a thin external layer differing from the underlying wall of the shell. This underlying wall shows simple growth lines, and the thin outer layer has growth lines as well as fine longitudinal stripes, which are connected to a proostracum. Wetzel (1930) extracted two small phragmocones from concretions containing many *Baculites* individuals which occur rather commonly in the upper portion of Quiriquina Formation. There is no trace of a rostrum. Wetzel's (1930, Pl.14, Fig.3) illustration shows two fragments of chambered cones. Therefore, his description is not very detailed. Biro- Bagoczky (1982) added new specimen and new information on *Naefia* from Quiriquina and the mainland near Lirquén and Cocholgue (both at the shore north of Concepción). He found specimen of up to 14 mm in length, which usually had an apical angle of 15°. Biro- Bogoczky (1982) noted some deposits on the outside of the phragmocone, which he considered transitional to *Belemnoteuthis*. Such layer could not be confirmed. He also noted that *Naefia* should probably be placed with the same genus as *Groenlandibelus rosenkrantzi* BIRKELUND, 1956. Stinnesbeck (1986) noted dorsal lines on the phragmocone.

## 2. About other species described to belong to *Naefia*

A *Naefia* was described from the Ariyaloor Group of Pondicherry, southern India, by Doyle (1986). It belonged to the fossils collected in the Tiruchirappalli area with obviously unknown exact locality. Here fossil bearing strata from Aptian to Maastrichtian may be encountered (for references see Bandel, 2000) so that the age of this fossil is in question. The three fragments of phragmocones called *Naefia* aff. *neogaeia* have an apical angle of only up to 8,5° and the largest specimen 24,5 mm long and has 7 chambers preserved. Their dorsal wall bears a median field with a median keel. This proostracum resembles that found in *Naefia neogaeia* but differs in details. The later consists of two marginal longitudinal

ribs and a double rib with a groove between in the middle, while *Naefia* aff. *neogaeia* from India has no double keels. *Naefia neogaeia* has next to the dorsal ribbon growth lines that strongly curve forwards and connect to the ribbon margin without continuing in the ribbon. This zone appears to be narrower than that described from *Naefia* aff. *neogaeia* from India.

The siphonal tube lies on the ventral side. As internal character a median dorsal line was noted on the steinkern that reflects the presence of a furrow on the dorsal side of the phragmocone wall (Normallinie) (Doyle 1986, fig.2b). This differs from the situation in *Nafia neogaeia* and resembles features as were noted in *Naefia kabanovi*. No further details were presented from these fossils which may be of Aptian to Maastrichtian in age. Doyle (1986) noted as difference to *Groenlandibelus* the shape of the "proostracum" and suggested that one (*Naefia*) lived in the cold sea of the Southern Hemisphere during the Late Cretaceous, while *Groenlandibelus* preferred the Northern Hemisphere at about the same time.

*Naefia kabanovi* as described by Doguzhaeva (1996, Textfig.4, Pl.6, Figs.1-5, Pl.7, Figs1,2, Pl.8, Figs.1-4, Pl.9, Figs.1-3) consists of a phragmocone that is wider at first (up to 14°) and later may have an apical angle as narrow as 7°. The chambers are about on third of their width in height. Septa are simple and interpreted to be constructed of *Spirula-nacre* (lamello-fibrillar-nacre). The siphonal tube is a little expanded in the chamber and lies ventral. The septum curves into the siphonal tube but the mineralized portion of shell apparently is not continuous for long distance into the chamber space. The construction of the siphonal tube is described as consisting of two spherulitic-prismatic layers. The final chamber is short. The shell wall supposedly consists of a prismatic compositionl with a thin outer coating layer which is thicker ventrally than dorsally. No nacre was found in the outer walls of the phragmocone. Elongate shell body attachment scars are found dorsally preserved on the inner mould of the phragmocone. These are longitudinal, slender, spindle-shaped,

corresponding to the “Normallinie” as may be noted in the phragmocones of rather unrelated cephalopods, especially such with a conical shell. These attachment scars differs strongly from the rectangular ones of *Naefia neogaeia*. Doguzhaeva (1996) found in *Naefia kabanovi* that the sutures are normal to the shell axis whereas she supposed that in *Naefia neogaeia* they are oblique, which can not be confirmed. The proostracum in *Naefia kabanovi* is not known.

Doguzhaeva (1996) suggested that the structure of the siphon of *Naefia kabanovi* is like that described in *Groenlandibelus*, and interpreted the outer layer of the siphon to represent a structurally modified continuation of the septal neck, and the inner layer to represent the remains of a slightly calcified or organic composition.

Hewitt & Jagt (1999, Fig.3D) illustrated a fragment of a Campanian *Naefia* derived from the Royal Ontario Museum and found in it sheets of nacreous microstructure. They suggested, therefore, that the Aptian *Naefia kabanovi* DOGUZHAEVA, 1996 from Russia had *Spirula*-nacre as defined by Mutvei (1964, 1970) composing its septa. The outer layer of the same shell is described as having been of prismatic structure, the inner layer also.

A prominent difference between *Naefia neogaeia* from Chile and the other two species placed in the same genus from Russia and India lies in the shape of the attachment scar of tissue to the interior of the shell wall. These attachment scars in case of *Naefia* sensu strictu are as wide as the dorsal outer ribbon and as high as one third of a chamber positioned in the anterior part in each chamber. The shape is rectangular and the scar is surrounded by a furrow. It is found on several of the individual fossils preserved in several consecutive fine grained fillings of the chambers. The well developed attachment scars of *Naefia kabanovi* DOGUZHAEVA, 1996 are quite different and consist of elongate scars that cross the whole chamber height.

Hewitt et al. (1991) suggested that in *Naefia* the shell wall could be nacreous on the outside and prismatic on the inner side and that the septa are of *Spirula*- nacre

construction. This would than be as in case of belemnites where such structure has been preserved and documented (Bandel & Kulicki 1988). But neither *Naefia* nor *Groenlandibelus* are preserved well enough to document their original shell structure. With the shell features of *Naefia neogaeia* taken as characteristic to the genus, the other two species described as *Naefia* aff. *neogaeia* from the Cretaceous of India and *Naefia kabanovi* from Russia do not fit these characters sufficiently to include them in the same genus. Especially the rectangular attachment scar of *Naefia neogaeia* is a character not found in *Naefia kabanovi*, that has an elongate scar resembling that of modern *Spirula*. The “Normallinie” seen in *Naefia* aff. *neogaeia* from India indicates its resemblance to the Russian fossil. While the Indian fossil had a proostracum, the Russian fossil did apparently not preserve one or had none. But the proostracum of the Indian coleoid is wider and of different ornament to that of *Naefia* sensu strictu.

### **3. Comparison of *Naefia* with *Groenlandibelus* BIRKELUND 1956, and evaluation of the family Groenlandibelidae**

The family Groenlandibelidae was erected by Jeletzky (1966) around *Belemnoteuthis rosenkrantzi* BIRKELUND, 1956 and was placed within the order Sepiida. The shell of *Groenlandibelus* is essentially straight, and narrow with apical angle amounting to 12°-15°. The phragmocone has watch-glass-like septa and simple suture. According to Birkelund & Hansen (1974) the septa are like those of belemnites. Chambers are about one third as high as wide and walls of the phragmocone may show corrugations. The apical shell is covered by a short, wrinkled cone representing deposits onto the outside of the phragmocone reconstructed as short rostrum. The dorsal side carries a ridged elongate structure that is reconstructed as proostracum (see also Doyle, 1986 for schematic drawing, Haas - 1997, 2003 for reconstruction). The proostracum is narrow and has sharp margins, and was not noted to connect to growth lines (Birkelund, 1956). There may also be a dorsal keel on it.

According to Jeletzky (1966) it resembles the Diplobelina among the belemnites.

The ventral siphonal tube is relatively wide, not mineralized, but may have been double walled according to the interpretation of Jeletzky (1966, Pl.20-22). But if double walled, both walls were organic. The septal necks change during ontogenesis from relatively long to short and end on the margin of the siphonal tube. The begin of the siphonal tube is of blind sausage-like shape extending into the bulbous first chamber. This earliest part of the siphonal tube measures three-quarters of the height of the chamber in length. It consists totally of organic material and is attached to the inside of the chamber by a sheet (prosiphon) (Jeletzky, 1966, Pl.20, figs.1A,B). The siphonal tube of *Groenlandibelus* has a different structure than that of *Spirula*, judging from the description provided by Jeletzky (1966) and Birkelund & Hansen (1974, Pls.13-15). The septum apparently did not continue into an outer mineral tube, but mineralized layers ended right in the margin to the hole through which the siphonal tube passed.

Jeletzky (1966) suggested that *Groenlandibelus* as well as *Naefia* represent members of the Groenlandibelidae. But *Groenlandibelus rosenkrantzi* differs from *Naefia neogaeia* in the composition of the siphon, in the presence of a rostrum in the first (Jeletzky, 1966), and no rostrum in the later, in the shape of the dorsal shell projection (Doyle, 1986) and, especially, the attachment scar of the visceral mass to the shell. Haas (1997, Fig.2) provided a model reconstruction of *Groenlandibelus* and *Naefia* united into one. According to this the proostracum is reconstructed as short and the rostrum also as short but present. Both these features cannot be confirmed from the restudy of *Naefia neogaeia* as we know it now, which appears to have had a slender narrow elongate proostracum and no rostrum. But the reconstruction could serve for *Groenlandibelus* as described by Birkelund (1956), Birkelund & Hansen (1974) and Jeletzky (1966).

#### 4. Comparison of *Naefia* with *Spirula*

Naef (1922) noted that the siphonal tube of *Spirula* consists of an external tube that is the continuation of the septum. This mineralized tube is coated on the inside by an organic tube. Gregoire (1961) was the first to note that the nacre of the septa of *Spirula* differs from the nacre seen in other mollusks, and also that of *Nautilus*. Dauphin (1976, Fig.23) noted that the siphon begins with a calcareous tube that continues in a organic attachment sheet (prosiphon). Mutvei (1970) had identified the septum and the outer siphonal tube to consists of nacre of a type that may not be found in *Nautilus*, but is characteristic of *Spirula*. It consists of needles of about 0,2 micron in diameter arranged in layers oriented along the growth surface instead of platelets (Bandel 1990). This layer was called to consists of lamello-fibrillar structure. The layer on the interior of the outer mineral tube of the siphon is porous and has prismatic needles (Dauphin 1976, Figs. 18-21). The construction of the siphonal tube of *Spirula* as double tube with a calcareous outer wall, a porous intermediate layer and an organic inner wall was worked out in detail by Bandel & Boletzky (1979). A similar tube but with shorter fully calcified outer wall has been noted to have been constructed by in the late Triassic aulacocerid *Dictyoconites* by Bandel (1985), and a double tube with similar construction but *Nautilus*-type nacre has also been proven in case of *Aturia* (Nielsen et al. 2005).

The siphonal system is responsible for buoyancy regulation and thus is very important in shell construction. The tube of *Naefia* differs from that of *Spirula* considerably. The septal neck of *Spirula* is continuous for the width of a whole chamber, so that the siphonal tube has a solid outer wall, while its outer wall is only solid for a part of the chamber width in *Naefia*. There is no dorsal projection on the apertural margin in case of *Spirula*, the shell is spirally arranged in *Spirula* and straight in *Naefia*. The initial chamber of *Naefia* is larger than that of *Spirula*, and the shell layer added from the outside to the phragmocone is thicker in *Spirula* than that noted on *Naefia*. Attachment

to the inner side of the shell results in a ribbon in case of *Spirula* and is quite different to the rectangular scar found in *Naefia*. Visceral mass connects to the shell of *Spirula* along a

dorsal ribbon and retractor muscles end in the tissue of the mantle lateral to it (Bandel, 1982).

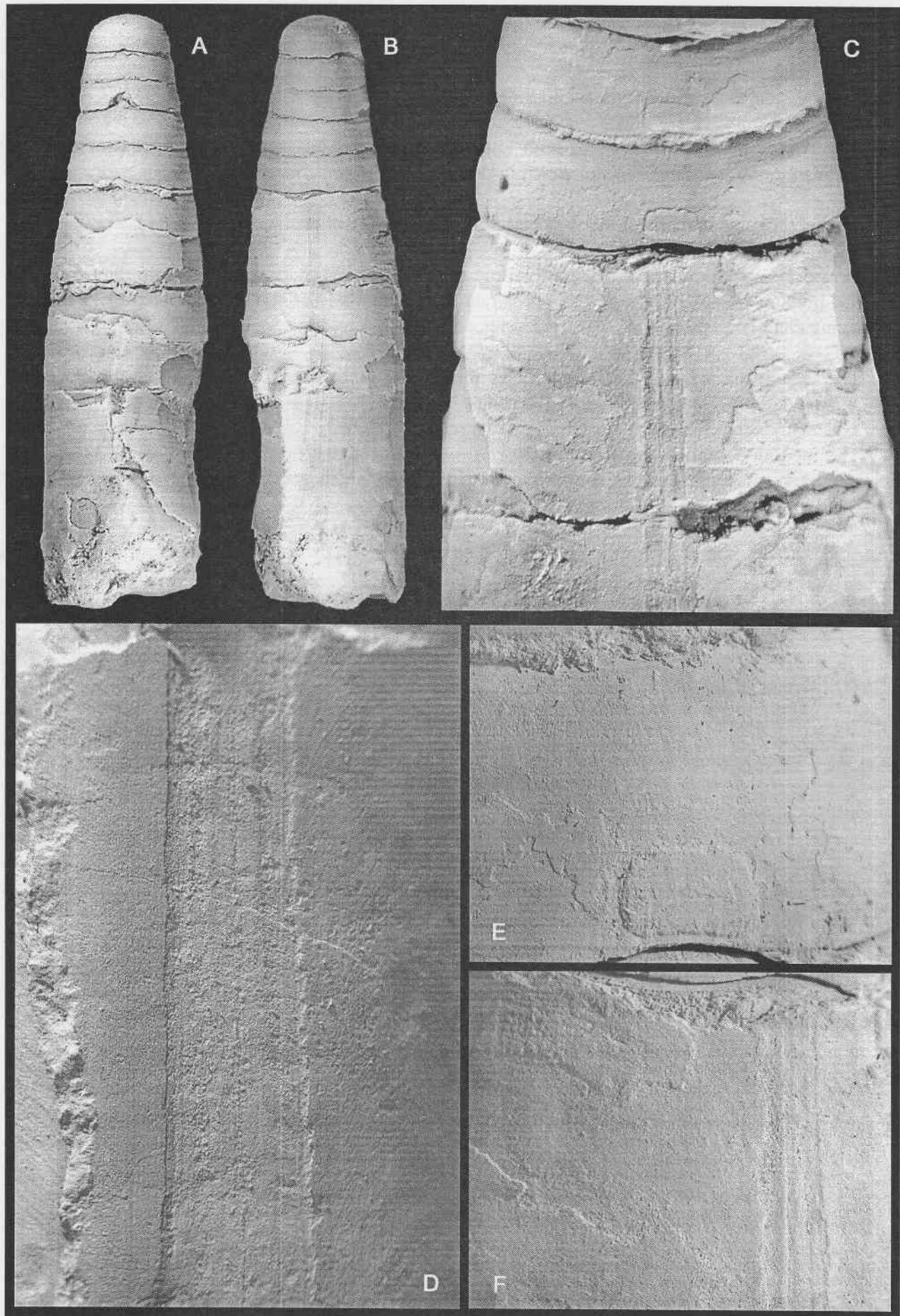
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## PLATE 1 - EXPLANATION

- A. Ventral side of *Naefia neogaeia* (20 mm long).
- B. Dorsal side of *Naefia neogaeia* with attachment scars of tissue to the shell interior are well expressed on chamber fills (steinkern) in part of the phragmocone.
- C. The rectangular scars lie at the very end of the dorsal side of each chamber.
- D. Dorsal side with attachment scars in some of the posterior chambers of the phragmocone and the median dorsal ribbon of the proostracum on the shell of the anterior chambers and the living chamber.
- E. The scar in the anterior part of each chamber is surrounded by a groove, which the ridge that surrounded the tissue attachment to the shell interior.
- F. The median dorsal ribbon found in *Naefia neogaeia* represents a projection of the aperture of unrecognized length and very narrow marginal zone, since growth lines of the phragmocone otherwise are simple and straight.



## The Late Hauterivian - Barremian belemnite succession of the Russian Platform

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**ABSTRACT:** Recent studies of Late Hauterivian – Barremian belemnite successions from the Volga River Basin (Russian Platform, RP) allowed for the first time to compare the belemnite successions of NW Europe (N Germany, NE England) and NE Europe. The new belemnite succession of the RP differs from the late Hauterivian belemnite zonation of NW Europe. Close similarities between NW Europe and NE Europe, however, are indicated for the Barremian.

**Key words:** Coleoid cephalopods, belemnites, Lower Cretaceous, Russia, stratigraphy.

### 1. Localities and material

The Lower Cretaceous succession of the Ulyanovsk – Saratov area is represented by an alternation of claystones and sandstones, which crop out over a distance of 400 km from Ulyanovsk in the north to Saratov in the south along the Volga River. Thirteen sections, which expose late Hauterivian – Barremian beds have been logged and sampled for belemnites in three areas: Ulyanovsk, Syzran and Saratov City regions (Fig.1). The composite lithological succession includes XII Units and was described before (Guzhikov et al., 2003; Baraboshkin & Mutterlose 2004).

Belemnites are overall quite rare in the studied sections. Usually rostra found *in situ* are replaced by gypsum. Nevertheless their preservation is sufficient for determination. Rostra, which were washed out from outcrops and found on the beach, are much better preserved. Both types of rostra were collected and the original position (possible zonal intervals) of the removed belemnites was defined in accordance with the distribution of belemnites *in situ*. Poorly

preserved rostra were not deposited in the collection and the numbers of belemnites in the description of the composite section reflect only a part of the material available.

About 200 guards were collected in total. The figured material is deposited in the Museum of the Earth (Moscow State University, Russia; = MSU, collections No.97, 99, 104).

### 2. Belemnite assemblages and zonation scheme

The Upper Hauterivian-Barremian stratigraphy of the RP (Ulyanovsk – Saratov area) has been studied for more than 150 years. The Upper Hauterivian deposits contain lots of ammonites and their biostratigraphy was outlined in detail, while the Barremian stratigraphy has been the subject of controversial discussions for three reasons. Ammonites are essentially absent, *in situ* findings of belemnites have been extremely rare and extended landslides along the Volga River make it difficult to study the

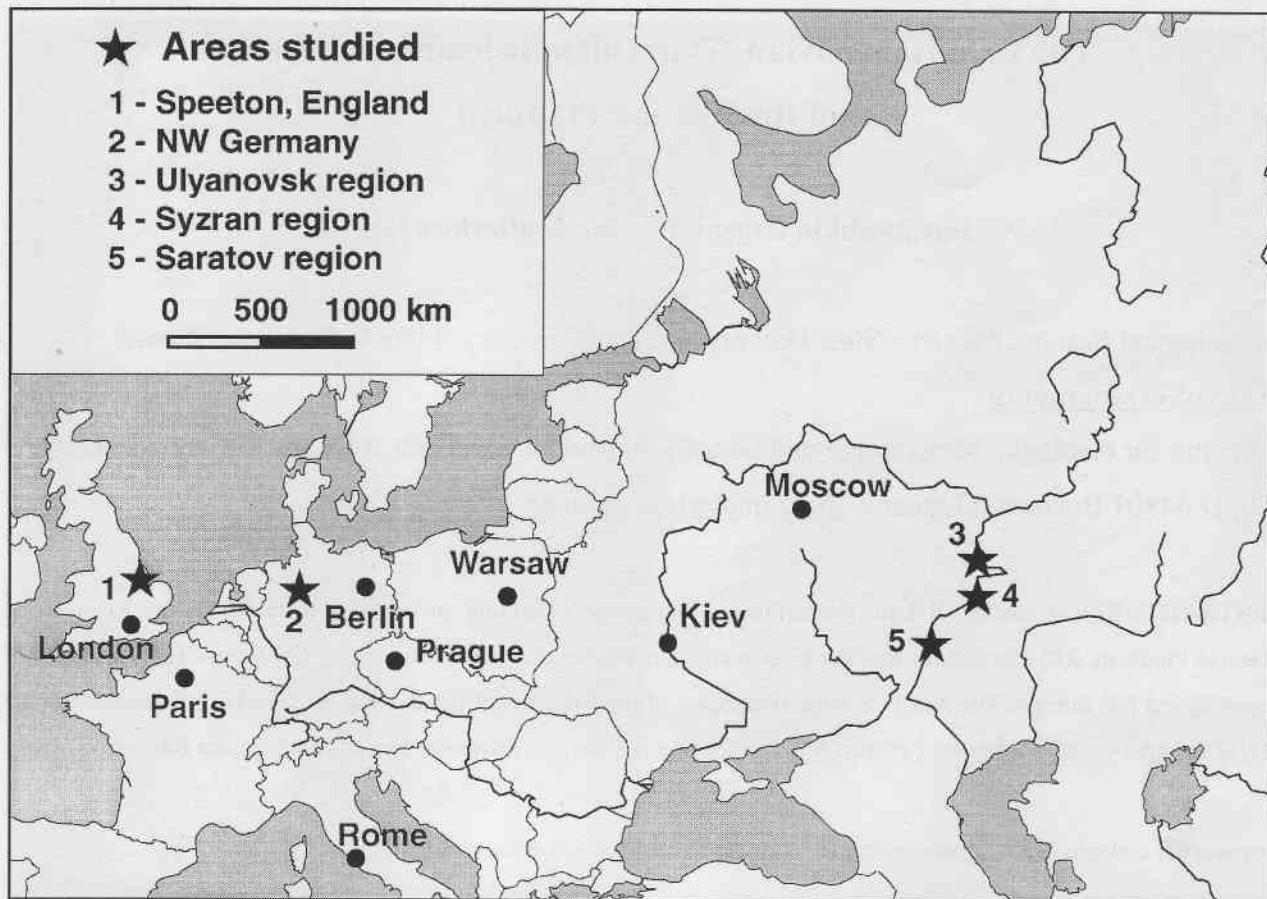


Fig. 1. Locality map of the studied areas.

Barremian succession bed-by-bed. Recent works of the authors fills this gap (Baraboshkin, 2001; Mutterlose & Baraboshkin, 2003; Baraboshkin & Mutterlose, 2004).

The Hauterivian belemnite succession needs, however, further study. At the present state, the belemnites were recognised in the following succession:

#### UPPER HAUTERIVIAN.

**"Pseudoaulacoteuthis absolutiformis" (sensu I.Sinzow) Zone:** The belemnite assemblage consists of "*Pseudoaulacoteuthis absolutiformis* (SINZOW)", "*P.* "tenebrosus" GLASUNOVA, *Acroteuthis* (A.) sp. indet. and *Acroteuthis* (*Boreioteuthis*) aff. *rawsoni* (Plate 1). The distribution of the assemblage corresponds to the ammonite *Speetoniceras versicolor* Zone. The ventrally extremely displaced apical line of "*Pseudoaulacoteuthis absolutiformis*" suggests that this species should be included in the Cylindroteuthidae and re-named (for discussion see Mutterlose & Baraboshkin, 2003).

#### Acroteuthis (A.) pseudopanderi Zone:

*A. (A.) pseudopanderi* (SINZOW) (Plate 1). The Zone coincides with ammonite *Milanowskia speetonensis* - *Craspedodiscus discofalcatus* Zones.

#### LOWER BARREMIAN.

##### Praeoxyteuthis hibolitiformis Zone:

The belemnite assemblage consists of *P. hibolitiformis*, *P. ex gr. jasikofiana*, *P. sp.* (Plate 1).

**Praeoxyteuthis jasikofiana Zone:** The belemnite assemblage is made up by *P. jasikofiana*, *P. cf. & aff. jasikofiana*, *P. sp.* (Plate 1).

**Praeoxyteuthis pugio Zone:** Typical belemnites of this zone are *P. pugio*, *P. cf. & aff. pugio*, *P. jasikofiana* (at the base only), *P. sp.* (Plate 1).

##### Aulacoteuthis descendens Zone:

Belemnites of this assemblage are *A. cf. descendens*, *A. speetonensis* and *A. sp.* (Plate 1).

**UPPER BARREMIAN.**

**Oxyteuthis brunsvicensis Zone:** The belemnite fauna includes *O. brunsvicensis* and *O. sp.* (Plate1).

**Oxyteuthis germanica Zone:** *O. cf. germanica* and *O. sp.* are typical belemnites of this zone.

**Oxyteuthis lahuseni Zone:** The assemblage of this zone contains *O. lahuseni*, *O. barremicus* and *O. sp.* (Plate1). The zone is of latest Barremian age and extends into lower part of the Aptian succession.

**3. Correlation**

The Upper Hauterivian belemnite assemblage of the RP is of low diversity and differs from NW European significantly. Only two belemnite Zones were recognized, both of them are based on the endemic species. Some resemblance with European belemnites has *Acroteuthis* (*Boreiteuthis*) aff. *rawsoni*

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(Plate1), but it is more depressed and characterises the basal part of the Upper Hauterivian, which strongly differs from Europeans sections.

For the Barremian both the RP and NW Europe are characterised by an evolutionary lineage leading from ungrooved *Praoxyteuthis* over grooved *Aulacoteuthis* to ungrooved *Oxyteuthis*. Apart from early Barremian *P. hibolitiformis* and the latest Barremian/early Aptian *O. lahuseni* belemnite Zone, all zones observed on the RP corresponds to belemnite zones in NW Europe.

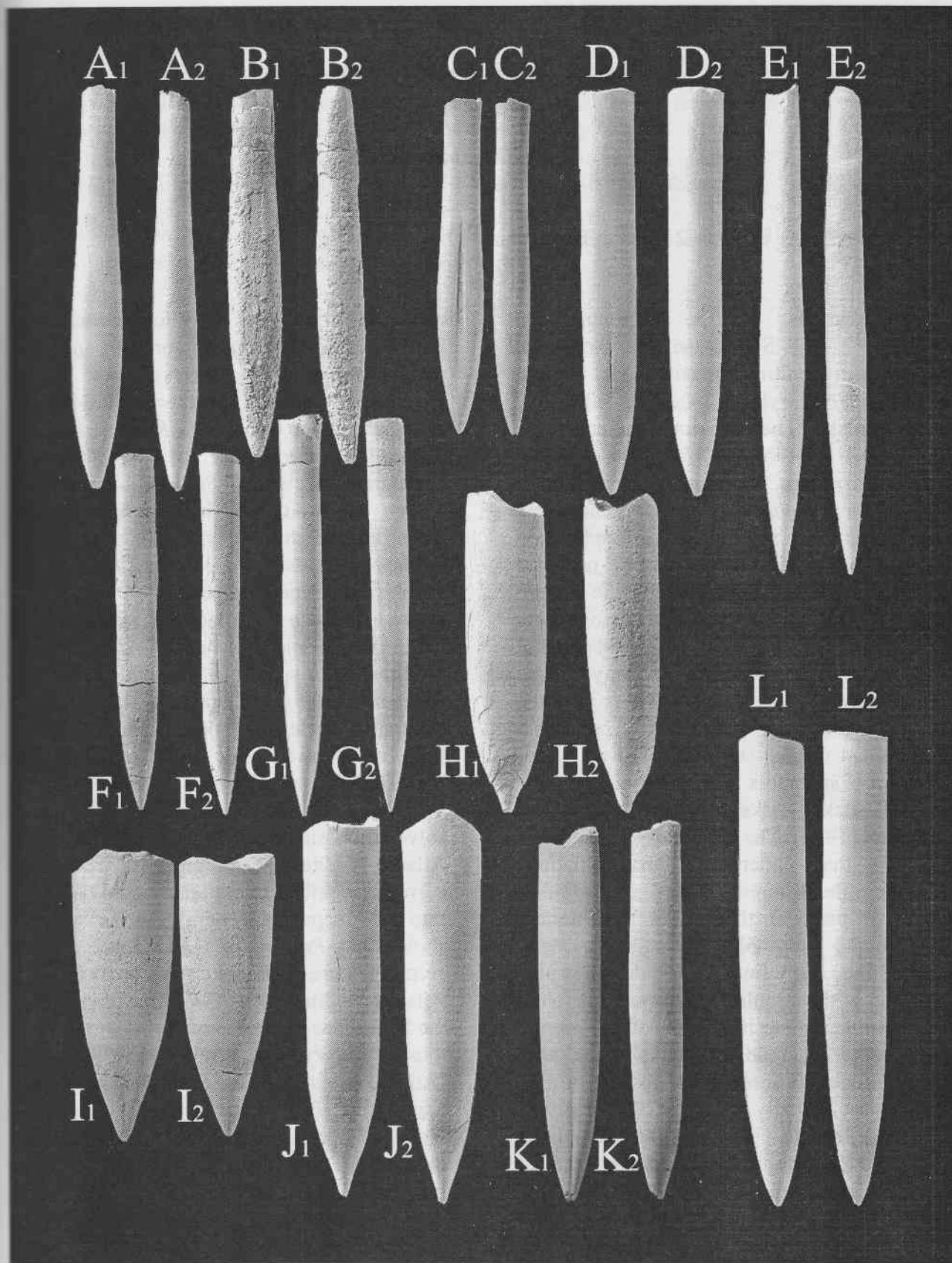
**Acknowledgements:** We are grateful to Russian Foundation for Basic Research (grants 04-05-64503, 04-05-64420, 04-05-64424) and "Scientific schools" (grant 326.2003.5) for financial support of the investigation.

## PLATE 1. - EXPLANATION

### Belemnites from the Ulyanovsk–Saratov area (Russian Platform).

Specimens are from the right bank of Volga River, **Syzran region**: Fig. 1, 2, 5, 7 - Forfos Mt.; **Ulyanovsk region**: Fig. 3 - Zakharievsky Rudnik; Fig. 4, 10, 12 - Bueraki Village; Fig. 8 - Kremenki Village; Fig. 9 - Novaya Bedenga Village; Fig. 11 – Polivna Village; **Saratov region**: Fig. 6 - Tcherny Zaton Village. Samples 1-8, 10-12 collected by E.J.Baraboshkin, sample 9 – by I.A.Shumilkin (Ulyanovsk).

- A. *Praeoxyteuthis hibolitiformis* (STOLLEY, 1811). No. MSU 104/1. A1 – ventral view, A2 – lateral view, venter to the left. L. Barremian, Praeoxyteuthis hibolitiformis Zone, on a beach.
- B. *Praeoxyteuthis jasicofiana* (LAHUSEN, 1874). No. MSU 97/2. B1 – ventral view, B2 – lateral view, venter to the left. L. Barremian, Praeoxyteuthis jasicofiana Zone, bed No.5.
- C. "*Pseudoaulacoteuthis absolutiformis* (SINZOW, 1877)". No. MSU 99/1. C1 – ventral view, C2 – lateral view, venter to the left. U. Hauterivian, Speetoniceras versicolor Zone.
- D. *Aulacoteuthis speetonensis* (PAVLOW, 1892). No. MSU 104/2. D1 – ventral view, D2 – lateral view, venter to the left. L. Barremian, Aulacoteuthis descendens Zone, on a beach.
- E. *Praeoxyteuthis pugio* (STOLLEY, 1925). No. MSU 97/10. E1 – ventral view, E2 – lateral view, venter to the left. L. Barremian, Praeoxyteuthis pugio Zone, on a beach.
- F. *Praeoxyteuthis pugio* (STOLLEY, 1925). No. MSU 104/4. F1 – ventral view, F2 – lateral view, venter to the left. L. Barremian, Praeoxyteuthis pugio Zone, bed No.4.
- G. *Praeoxyteuthis pugio* (STOLLEY, 1925). No. MSU 97/3. G1 – ventral view, G2 – lateral view, venter to the right. L. Barremian, Praeoxyteuthis pugio Zone, bed 19.
- H. *Oxyteuthis barremicus* GLASUNOVA, 1969. No. MSU 104/5. H1 – ventral view, H2 – lateral view, venter to the left. U. Barremian, Oxyteuthis lahuseni Zone, on a beach.
- I. *Acroteuthis (A.) pseudopanderi* (SINZOW, 1877). No. 641. I1 – ventral view, I2 – lateral view, venter to the right. U. Hauterivian, Craspedodiscus discofalcatus Zone, Unit IV.
- J. *Oxyteuthis lahuseni* (PAVLOW, 1901). No. MSU 104/7 [Y97-27/4]. J1 – ventral view, J2 – lateral view, venter to the left. U. Barremian, Oxyteuthis lahuseni Zone, on a beach.
- K. *Acroteuthis (Boreioteuthis) aff. rawsoni* PINCKNEY, 1987. No. Y2003/5-6. K1 – ventral view, K2 – lateral view, venter to the left. U. Hauterivian, Speetoniceras versicolor Zone, Unit II.
- L. *Oxyteuthis brunsvicensis* (STROMBECK, 1861). No. MSU 104/9 [Y97-27/6]. L1 – ventral view, L2 – lateral view, venter to the right. U. Barremian, Oxyteuthis lahuseni Zone, on a beach.



\* All specimens have been coated with NH<sub>4</sub>Cl and are figured 1 : 1.

# Cladistic analysis of the Sepiolinae (Cephalopoda: Sepiolidae)

## based on the hectocotylus

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Peculiarities of the Sepiolinae, a subfamily of the Sepiolidae, are the *bursa copulatrix* in the female mantle cavity and the matching *hectocotylus* – modified left dorsal arm – in males. The Sepiolinae include some 30 species distributed into five genera, namely *Euprymna*, *Inioteuthis*, *Rondeletiola*, *Sepietta*, and *Sepiola*. The main characters which the generic subdivision is based on are the hectocotylus morphology and the presence and shape of light organs inside the mantle cavity. Purpose of this paper is to contribute to the systematic revision of the Sepiolinae based on the hectocotylus diversity. Three parts may be distinguished in the hectocotylized arm: the basal part that includes 1-4 normal suckers, followed by the copulatory apparatus consisting of a few modified sucker stalks, followed by the distal part (Naef, 1923). The copulatory apparatus is the part that undergoes most variations throughout the different species groups (either genera or parts of them). An evolutionary trend in its morphology is quite evident. Within the Sepiolinae the plesiomorphic condition of the copulatory apparatus is found in *Euprymna*, where it consists of 1-3 nipple-like papillae, i.e. modified stalks of the outer row of suckers, sometimes bearing a tiny sucker. Incidentally Naef (1923) placed *Euprymna* at the base of the Sepiolinae phylogenetic tree; this opinion is corroborated by the cladograms in Bello (1998) and Vecchione & Young (2004). The closest apomorphic condition is represented by the rostrum-like modified stalks of the 3<sup>rd</sup> and 4<sup>th</sup> suckers of the outer row in the three *Sepiola* species from the Indo-Pacific Ocean, viz. *S. parva*, *S. birostrata*, and *S. trirostrata*. A further evolutionary step is the rostrum-like

modification of stalks involving suckers from both the outer (3<sup>rd</sup> and 4<sup>th</sup> suckers) and inner (two corresponding suckers) rows. All of these stalks are fused together with each other at their base in the genera *Rondeletiola* and *Sepietta*, or throughout their length in the remaining species of *Sepiola* (all of them from the Atlanto-Mediterranean area). According to this analysis, the Indo-Pacific species of *Sepiola* share with *Euprymna* the synplesiomorphic character “copulatory apparatus made of modified suckers from outer row only”, whereas the Atlanto-Mediterranean species of *Sepiola* display the synapomorphic character “copulatory apparatus made of modified suckers from both outer and inner rows” shared with *Rondeletiola* and *Sepietta*. Hence the genus *Sepiola* is indeed paraphyletic. In order to solve this situation, the Indo-Pacific and Atlanto-Mediterranean groups of species currently ascribed to *Sepiola* should be placed into two separate genera. Further analysis shows that *Rondeletiola* and *Sepietta* share certain features that make them apart from the Atlanto-Mediterranean *Sepiola*. To sum up, the Sepiolinae cladogram may be summarized thus: (*Euprymna* (Indo-Pacific *Sepiola* (Atlanto-Mediterranean *Sepiola*(*Rondeletiola*, *Sepietta*))). The genus *Inioteuthis* was not included in this analysis because of its quite different copulatory apparatus which seemingly does not pertain to the above reported evolutionary cline; other characters, in addition to the hectocotylus, must be taken into account to complete the cladistic analysis of the Sepoliniae.

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# No hands – but arms: The morphological and functional diversification of brachial appendages in the evolution of coleoid cephalopods

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The arm crown is the most conspicuous part of the pedal complex («molluscan foot») of cephalopods. Whereas *Nautilus* has two concentric series of uniform, radially arranged brachial appendages (Naef, 1922, Fig. 3), coleoid cephalopods have only one fully developed brachial series; it is a supposed homologue of the outer series of *Nautilus*, the inner one (the so-called buccal arm crown, or buccal funnel) being vestigial (in Decabrachia) or lacking (in Vampyropoda; Boletzky, 1992). Compared to a *Nautilus* tentacle, which comprises a proximal sheath and a distal cirrus with adhesive ridges (Kier, 1987), a coleoid arm (or a specialized decabrachian tentacle; see below) exhibits a greater number of variable structures that occupy well defined areas of the brachial surface (cf. Kier and Thompson, 2003).

Individual arms, and pairs or groups of arms perform complex motor actions that are – to a certain degree – comparable to the performance of the hand of primates (cf. Sumbre et al., 2005). In addition to the basic functions of grasping and manipulating food, fending off would-be predators, or attaching themselves to a hard substrate, the arms can produce visually effective signals, sometimes in combination with light emission by brachial photophores (Hanlon and Messenger, 1996) or luminescent suckers (Johnsen et al., 1999a, b).

The adhesive function (which is achieved by the ridges of a brachial cirrus in *Nautilus*) is optimized in the brachial suckers of coleoid arms and tentacles. In some decabrachian squids of the taxon Oegopsida, certain suckers are transformed into hook-shaped claws during juvenile development. Naef (1922, Fig. 68) compared oegopsid hooks with the fossil hooks of belemnoids.

The question whether they are really homologous structures, i. e. horny structures derived from the “chitinous ring” of a normal sucker, was discussed by Engeser and Clarke (1988). The observations of Donovan and Crane (1992) speak in favor of this homology. They also draw attention to the possibility that simple muscular suckers do not necessarily exhibit a distinct, permanent central depression (as in extant octopus suckers; cf. Schmidtberg, 1999).

When alluding to coleoid arms and tentacles, the term tentacle should only be used to designate the members of one particular pair of arms within the decabrachian arm crown (which is composed of a series of five pairs of brachial appendages). Traditionally, the arm pairs of a ten-armed coleoid cephalopod are numbered from the “upper” or “anterior” arms (I) to the “lower” or “posterior” arms (V), and the tentacles then are number IV. They are characterized by the differentiation of a special “fast” musculature in the stalk (Kier and Curtin, 2002). “Upper” here alludes to the (horizontal) swimming position of e. g. *Sepia*, and the upper part of the animal is then called “dorsal” (in the so-called physiological orientation). “Anterior” alludes to the normal head-down drifting position of e. g. *Spirula*, which also corresponds to the position of the embryo cap (the epibolic gastrula) lying on top of the yolk mass, *when viewed from above* (Boletzky, 2003, Fig. 2). This is the so-called morphological or embryological orientation (Fioroni, 1978, Fig. 12) that permits a morphological comparison with other molluscs.

The above-mentioned *physiological orientation* of living cephalopods, and the (*pseudo*) *radial arrangement of the arms*

surrounding the mouth in cephalopods, are two singularities that tend to obscure the *basic antero-posterior polarity* of the embryonic arm crown.

The problem of the pseudo radial arrangement becomes particularly acute when defining the orientation of the arm surfaces that bear suckers; one normally refers to the mouth in talking about the *adoral* surface of the arm that bears suckers or hooks. Likewise, the buccal arms (or buccal lappets) of decabrachian coleoids appear to be adoral derivatives of the (sessile) arms. Although the (final) central position of the mouth is undeniable, it is a secondary position which is attained rather late in the course of embryogenesis. The question thus is how to reconcile a final “adoral” position with the previous, ostensibly “admedian” position of the “inner surfaces” of the arms. At first sight this question may appear futile; it becomes more pressing once the contrast between the

brachial appendages proper and the *dorsal extensions* (in the morphological orientation) of the arm rudiments are recognized (Boletzky, 2003, Fig. 2). These dorsal extensions provide a series of paired pedal derivatives, starting with the rudiments of the funnel tube, continuing with the primary lid rudiments and ending with the anterior folds covering the buccal complex. Although these structures ontogenetically become increasingly distinct from the arm crown proper (at least in the coleoids), their respective positions may nevertheless be indicative of some particular functional relationships, e. g. with the hectocotylisation of certain arms in males.

A thorough morphological and developmental analysis of the arm crown is necessary for a better understanding of the functional specializations of arms and associated brachial structures that must have occurred in the course of coleoid evolution.

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## Comparison of adhesive organ between *Idiosepius* sp. and *Euprymna scolopes*

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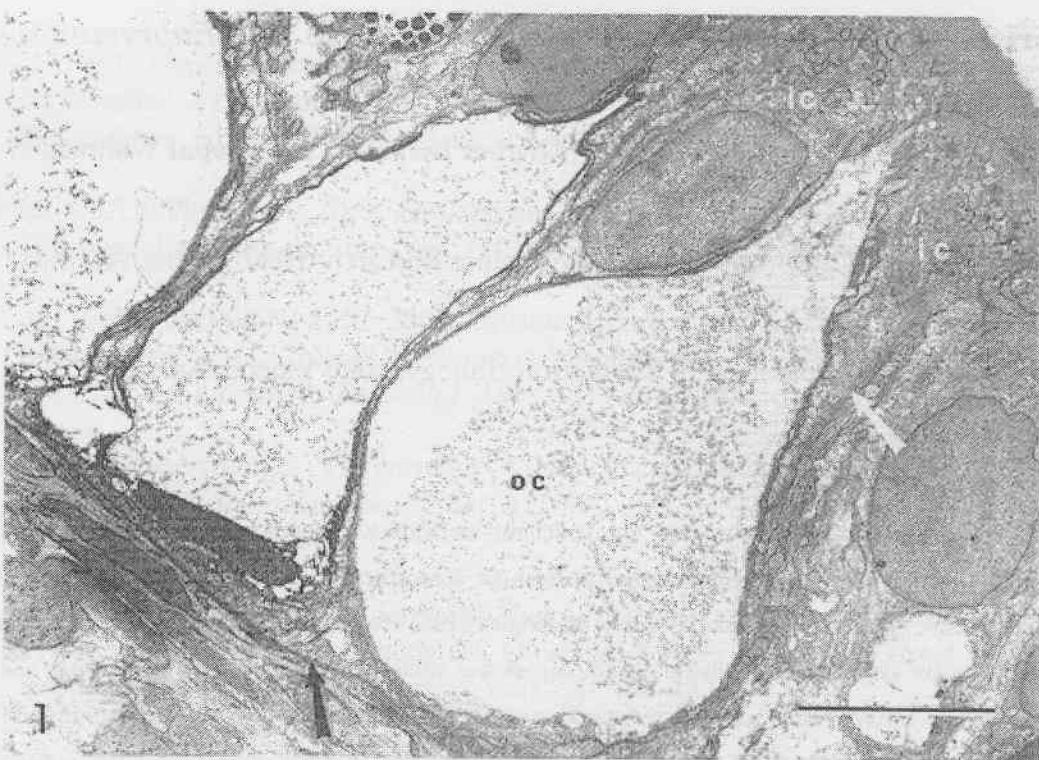
**ABSTRACT:** Histological, histochemical and ultrastructural methods were applied to elucidate the nature of the secretion in the epithelial cells of three *Idiosepius* species (*I. biserialis*, *I. paradoxus* and *I. pygmaeus*). Previous analysis of the adhesive organ of *Euprymna scolopes* by Singley (1981) reveals that adhesion and deadhesion is caused by a duo-gland adhesive system. The epithelium of *Idiosepius* was studies to elucidate their morphology and the nature of their secretion. The current results show that the adhesive organ of *Idiosepius* consists of three different glandular cells. Histochemical results indicate that each cell type contains its specific sugar units, associated with proteins. The nature of the secretory products suggests that all cell types are responsible for adhesion. Acid proteins were not found in the adhesive organ of *Idiosepius*. A duo-gland adhesive system as in *Euprymna scolopes* can therefore be excluded for *Idiosepius*. The results indicate that *Idiosepius pygmaeus* holds on to the substrate by Stefan-type adhesion. This form of adhesion maybe the result of adaption to habitat and behavior of *Idiosepius*.

**Keywords:** Coleoid cephalopods, adhesion, adhesive gland, glue compounds, *Idiosepius*, *Euprymna scolopes*, duo-gland-system, Stefan-type-adhesion

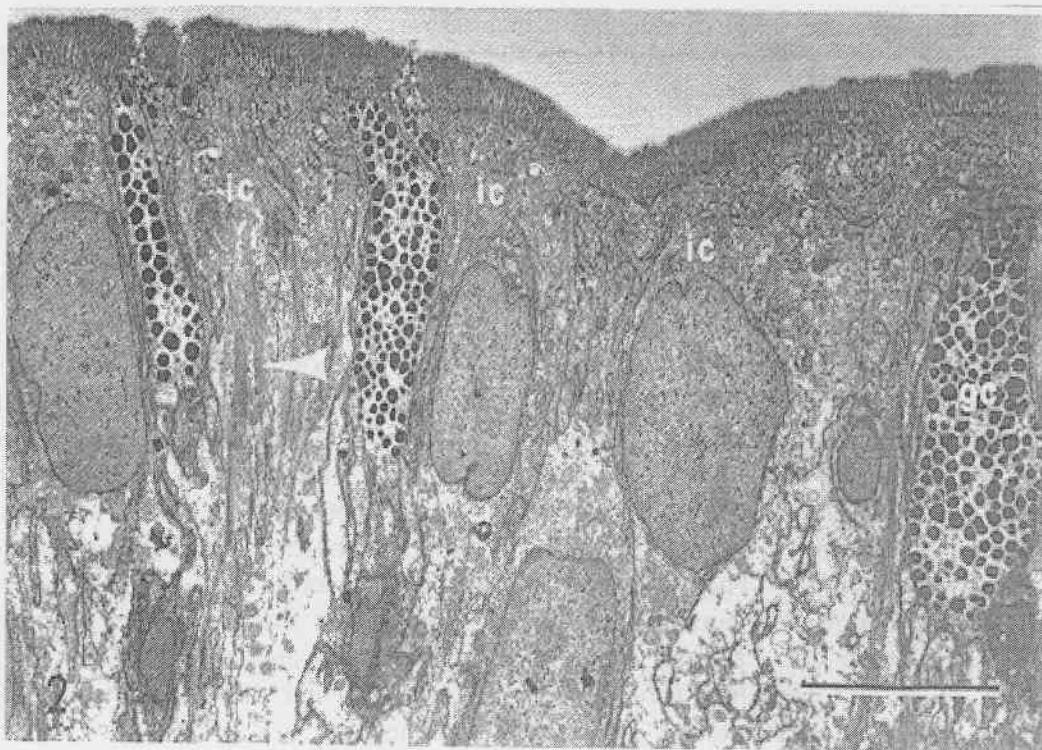
Attachment in cephalopods is primarily achieved by reduced pressure systems as in suckers on the arms, tentacles or defined dermal structures on the mantle (von Boletzky and Roeleveld, 2000). Two sepiolid genera of cephalopods (*Euprymna*, Sepiolidae; *Idiosepius*, Idiosepiidae) produce glue in adhesive glands, also termed adhesive organ (Nesis, 1982; Norman, 2000).

*Euprymna scolopes* live in near-shore benthal habitats and hide during the day in the sediment (Moynihan, 2002). The animals secrete glue to coat themselves totally with sand. In case of danger they release sand instantaneously to deflect predators (Shears, 1988; Norman, 2000). Ultrastructural and

histochemical examinations show that *Euprymna scolopes* has goblet and ovate cells in a duo-gland adhesive system all over the body. Between these cells are non-secretory interstitial cells (Figures 1 and 2, Singley, 1982). The goblet cells contain large, electron dense granules (glucose units), responsible for adhesion. The finely granular secretory material of the ovate cells, located in a large vesicle appears to be basic proteins. During secretion these proteins transform to highly sulphated acidic proteins. Singley (1982) assumes that the rate of secretion of acidic mucoproteins are secreted relatively from the ovate cells and that they are responsible for de-adhesion.



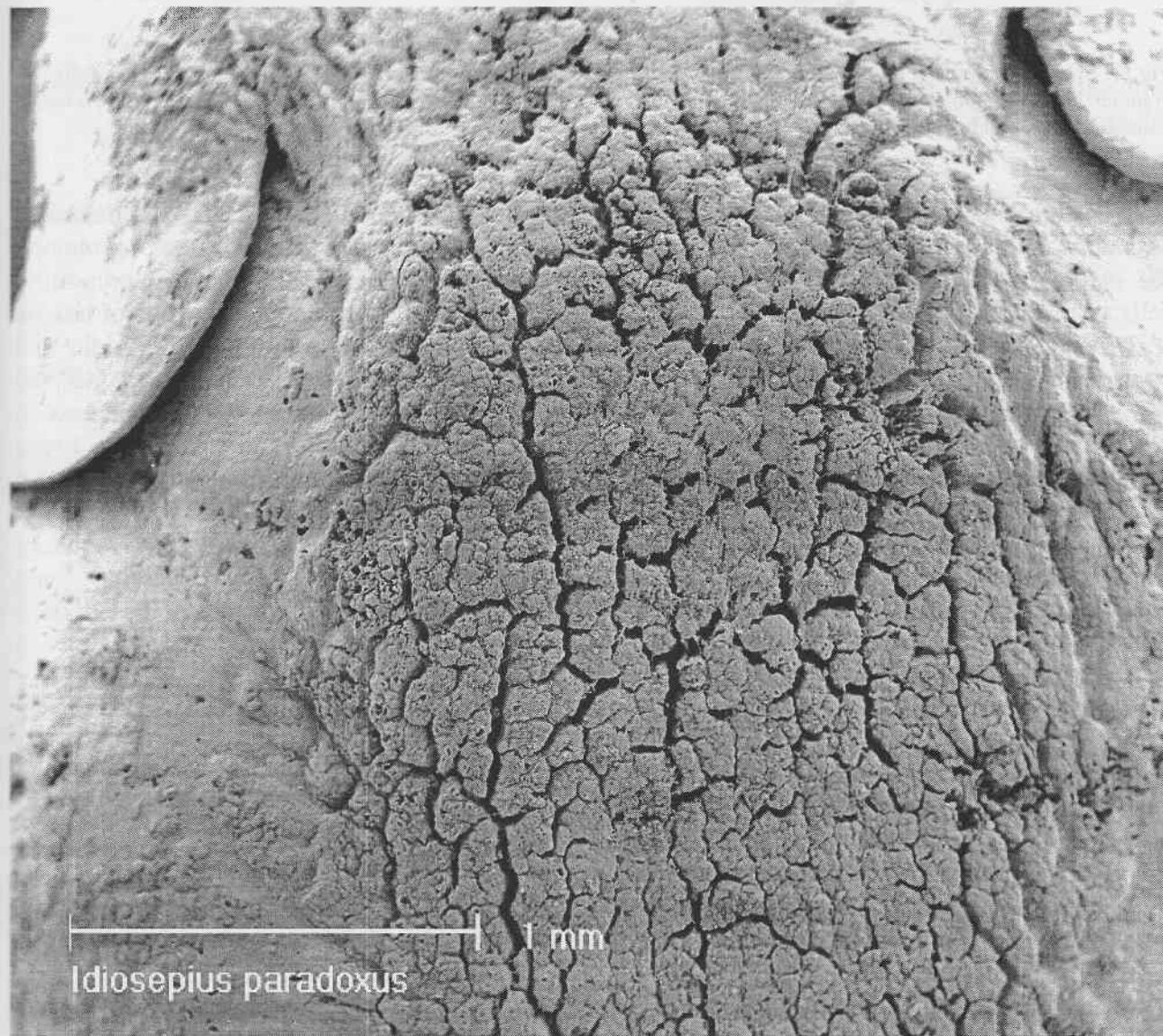
**Fig.1.** Cross section of dorsal epithelium at *Euprymna scolopes*. Sac-like ovate cells (oc) with fine granular material occur in the adhesive organ, presumably responsible for deadhesion. Interstitial cells (ic) possess intracellular filaments (arrow). Figure from Singley (1982).



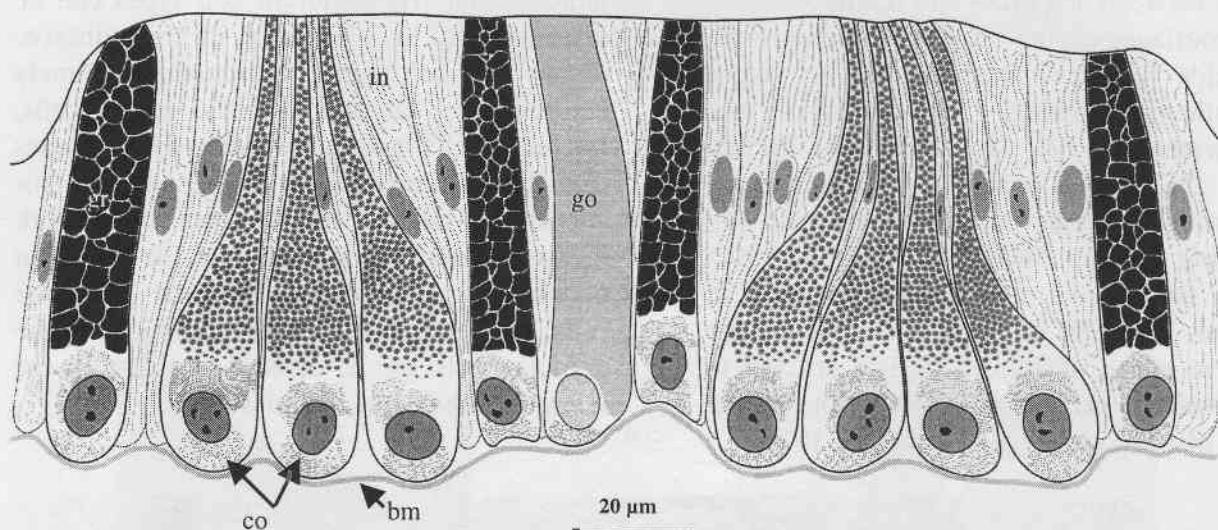
**Fig.2.** Goblet cells (gc) have a long, tube-shaped form and are filled with large granules. Its secretion product is responsible for adhesion at *Euprymna scolopes*. Figure from Singley (1982).

*Idiosepius* lives in near-shore shallow waters between sea grass and mangrove area. It camouflages during the day, sticking to the underside of sea grass leaves or algae (Moynihan, 1983; Hylleberg and Nateewathana, 1991; Jackson, 1992). Hiding there, the animals wait to capture prey swimming by, and females adhere also for spawning (Natsukari, 1970; Jackson, 1992; Lewis and Choat, 1993; Kasugai, 2000; Kasugai, 2001). In contrast to *Euprymna*, the adhesive organ of *Idiosepius* is restricted to the posterior part of the fin region of the dorsal mantle side (Figure 3, Sasaki, 1921).

Previous results of Sasaki (1921) indicate that five different cell types can be distinguished histologically in the adhesive organ of *Idiosepius paradoxus*, namely columnar cells, granular cells, goblet cells, fusiform cells and basal cells. He assumes that the columnar cells are responsible for adhesion whereas the fusiform cells work pressure-induced and stimulate the secretion of adhesive substances from the columnar cells. Information about the function of the granular cells, goblet cells and basal cells the release mechanisms are missing.



**Fig.3.** SEM picture of the adhesive organ of *Idiosepius paradoxus*. Sasaki (1921, p. 210) describes the adhesive organ as follows: "It is represented by a longitudinal corrugated area extending along the posterior three-fourths of the back. The folds run quite irregularly without any definite mode of arrangement, and show also fine furrows and pits".



**Fig. 4.** Schematic drawing of the adhesive organ of *Idiosepius* sp. with its characteristic cells: co-columnar cells, granular cells, go-goblet cells and in-interstitial cells. The dermal layers below the basal membrane (bm) contain collagen, muscle and nerve fibres and chromatic elements. Image published with permission of Norbert Cyran.

Histological, histochemical and ultrastructural methods were applied to elucidate the nature of the secretion in the epithelial cells of three *Idiosepius* species (*I. biserialis*, *I. paradoxus* and *I. pygmaeus*). The adhesive organ of all species consists of four different cell types (columnar cells, granular cells, goblet cells and interstitial cells), which can be distinguished morphologically and on account of their chemistry of their secretion (Figure 4). A further fifth cell type (basal cells), postulated by Sasaki (1921), seems doubtful. The vacuoles of the columnar cells are filled with fine granules while the granular cells contain large spherical to polygonal granules. The secretory material of the goblet cells is finely granular whereas the interstitial cells are free of secretory components.

Histochemical tests show that the three glandular cell types (columnar, granular and goblet cells) contain periodate-reactive substances (neutral hexose sugars) and basic proteins. There is no difference in the composition of the secretory products between the species of *Idiosepius*. The different staining reactions indicate that the ratio of proteins and polysaccharides varies strongly between the glandular cells, forming different protein-polysaccharide complexes. Columnar cells have a high proportion of glucose sugar units and less fractions of

protein(s). Granular cells have a balanced ratio of different sugar units and protein(s) while the goblet cells have higher proportion of protein fractions and a lower one of hexose sugar units other than glucose. Acidic and sulphated substances are absent in all *Idiosepius* species. The surface layer next to the glandular cells of the adhesive organ consists of sugar units too, presumably also secretion product of these cells.

The histochemistry of the secretory products suggests that adhesion and deadhesion of *Idiosepius* is not based on a duo-gland adhesive system as found in *Euprymna scolopes* (Singley, 1982) and other molluscs (Grenon and Walker, 1978; Shirbhate and Cook, 1987) but follows rather a Stefan-type adhesion.

The different adhesive substances and mechanisms of these two squid taxa serve different purposes and can be explained as ecological and behavioral adaptations. *Euprymna scolopes* uses the glue to cover itself with a coat of soft sediment parts (sand, mud) and release the glue fast and over the whole-body.

*Idiosepius* attaches with a small adhesive area to hard surfaces (seaweeds, seagrass leaves, roots). The three glandular cells with different composition of secretory material give the strength necessary for the

attachment. It also enables an easy disconnection without special deadhesive substances. The break of connection might be effected by contraction or other mechanical release. So far observations do not allow any conclusions.

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## Pharmacological and histochemical examination of the *Vena cephalica* of *Sepia officinalis* L. (Cephalopoda)

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**ABSTRACT:** This study reveals results on the mechanisms modulating peristalsis of the Vena cephalica in *Sepia officinalis* (L.) (Cephalopoda). The pharmacological data provide evidence for two antagonistic receptor systems in the Vena cephalica. Cholinergic transmitters, like acetylcholine and nicotine, have a positive effect on peristalsis of the Vena cephalica whereas aminergic transmitters cause a standstill of peristalsis in the Vena cephalica. Histochemical and immunohistochemical tests confirm the presence of a cholinergic transmitter system. The regulation of peristalsis in the Vena cephalica resembles closely the neuroregulation of the gastrointestinal tract of other invertebrates and vertebrates than to other circulatory organs of *Sepia officinalis*.

**Key words:** Coleoid cephalopods, cholinergic transmitter system, Circulatory system, nicotinergic acetylcholine receptor, peristalsis, *Sepia officinalis*, Vena cephalica.

Functionally, the circulation system of the dibranchiate cephalopods is subdivided into a systemic and respiratory part (Tompsett, 1939; Schipp, 1987a). Like in vertebrates all cephalopods the thick-walled arteries enable a high-pressure circulation by an air vessel function, (Shadwick and Nilsson, 1990). In cephalopods, however, the reflux of deoxygenated blood towards the respiratory system is effected by large propulsive veins (de Wilde, 1956; Schipp, 1987a). Especially the Vena cephalica of *Sepia officinalis* produces powerful peristaltic waves posteriorly along this vein, driving the blood from the head region towards the Venae cavae (Tompsett, 1939). The peristalsis of the Vena cephalica in *Sepia officinalis* is based on two muscle systems of different function (Alexandrowicz, 1965). The periadventitial, longitudinal muscle layer (PLM) effects cranial to caudal contraction waves, while the circular muscle fibre layer of the Tunica media (cMF) is responsible for peristaltic contractions of the vessel (Schipp, 1987b).

In addition, the Vena cephalica takes part in regulating the hemodynamics of the

systemic and branchial hearts, the Bulbus cordis branchialis, the arterial system and the contractile branchial gill artery. Initial evidence for this is provided by studies demonstrating that this organ together with nerve fibers form a neuronal plexus (NSV-system) which tends to produce transmitters such as hormones, FMRFamide and other cardioexcitatory peptides into the circulatory system (Alexandrowicz, 1964; Alexandrowicz, 1965; Martin, 1968; Young, 1969; Young, 1971; Martin and Voigt, 1987). This neurosecretory system of the Vena cephalica is comparable with the adrenaline system in vertebrates (Wells, 1983).

The physiological results of denervated vein preparations show that a myogenic automatism is responsible for the peristalsis of the Vena cephalica of *Sepia officinalis*.

The pharmacological data presented here provide evidence for two antagonistic receptor systems in the Vena cephalica. Cholinergic transmitter, like Acetylcholine (ACh) and nicotine, the nicotinic acetylcholine receptor agonist dimethylphenylpiperazinium iodide (DMPP) and FMRFamide induce a positive

inotropic and chronotropic effect on Vena cephalica peristalsis. The neuromuscular blocking agent decamethonium has no effect on peristalsis, amplitude and frequency remains constant. Muscarine and cholinergic antagonists like Tetraethylammonium (TEA), d-Tubocurarin and  $\alpha$ -Bungarotoxin ( $\alpha$ -BTX) reversibly block the peristalsis in the Vena cephalica. Also aminergic transmitter (adrenaline, isoprenaline, noradrenaline) and serotonin (5-hydroxytryptamine) cause a reversible peristalsis standstill.

The histological results provide evidence that nerve fibres in the longitudinal and circular muscles of the Tunica media and Tunica periadventitia form dense nerve plexi. The function of these structures remains unknown, but the nerve plexi may be responsible for muscle contraction and involved in the neuroregulation of peristalsis by modulation the tonus of the circulatory system. The present histochemical data provide evidence for Acetylcholinesterase (AChE) in fibrous structures of the longitudinal muscle of the Tunica periadventitia and Nervus visceralis, indicating a cholinergic transmitter system. The  $\alpha 7$ -subunit of a nicotinergic ACh receptor subunit (sc-5544) of vertebrates (Santa Cruz Biotechnology Inc., 2001) show

clear brown precipitations in the longitudinal muscles of the Tunica periadventitia and Nervus visceralis in the Vena cephalica of *Sepia officinalis*. The used toxin FITC  $\alpha$ -Bungarotoxin allows no clear conclusions about the presence of muscular nicotinic receptors in the Vena cephalica of *Sepia officinalis*.

This study successfully demonstrates that a cholinergic transmitter system or acetylcholine-catabolic system takes part in peristalsis of the Vena cephalica in *Sepia officinalis*. The regulation mechanisms of Vena cephalica peristalsis apparently have great similarity with the peristaltic waves of the gastrointestinal tract of other invertebrates and vertebrates, which are regulated by similar excitatory cholinergic and inhibitory aminergic mechanisms (Jensen and Holmgren, 1985; Johnson et al., 1987; Furness and Costa, 1987; Schmidt and Thews, 1997).

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## Distribution pattern of a minimalist – new records for *Idiosepius biserialis* (Idiosepiidae, Cephalopoda)

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**ABSTRACT:** New records of *Idiosepius biserialis* in Indonesia and Japan indicate that this species has a wider distribution than assumed before. Its occurrence in “cooler” Japanese waters next to the related species *Idiosepius paradoxus* indicates that the distribution of *Idiosepius biserialis* is not limited to tropical waters.

**Key words:** Coeloid cephalopods, behaviour, habitat, Idiosepiidae, *Idiosepius pygmaeus*, Thailand, Phuket Island.

Idiosepiidae are represented by a single genus with seven species: *Idiosepius biserialis* (Voss, 1962), *I. macrocheir* (Voss, 1962), *I. notoides* (Berry, 1921), *I. paradoxus* (Ortmann, 1888), *I. picteti* (Joubin, 1894), *I. pygmaeus* (Steenstrup, 1881) and *I. thailandicus* (Chotiyaputta, Okutani, and Chaitiamvong, 1991). Their distribution stretches from Japan, Thailand to South Australia and Moçambique. Morphologically the species can be identified by the arrangement of suckers on the club (two or four rows) and the number of suckers on the ventral arms (Hectocotylus) (Nesis, 1982). One conspicuous morphological character of this family is the adhesive organ (also known as adhesive gland) located on the posterior part of the dorsal mantle side.

*Idiosepius biserialis* differs from the other species of this genus by occurrence at two distant geographical locations. Voss recorded it 1962 in Moçambique but not in South Africa and 1991 it was found in Thailand by Hylleberg and Nateewathana.

Apart from *Idiosepius biserialis* a second species, *Idiosepius thailandicus*, also has a biserial arrangement of suckers on the tentacles (Chotiyaputta, Okutani, and

Chaitiamvong, 1991). Both species resemble each other. They differ only marginally in size (*Idiosepius thailandicus* 5.03 mm males and 9.85 mm females - *Idiosepius biserialis* 6.5 mm males and 9.05 mm females). Only scanning-electron-microscope (SEM) images of the tentacle suckers point to a morphological difference between both species (Chotiyaputta, Okutani, and Chaitiamvong, 1991).

The new record of *Idiosepius biserialis* in Indonesia confirms that this species has a widespread distribution in the Indo-Pacific region. The finding in Japanese waters may raise questions not only about the geographical distribution but also about the habitat conditions of this minimalist. This new record shows that the occurrence of *Idiosepius biserialis* is not limited to sea grass and algae of “warm” tropical water (25-30°C). Like other *Idiosepius* species (Kasugai, 2000; Nesis, Katugin, and Ratnikov, 2002; Kasugai and Ikeda, 2003) this pygmy squid can also be found in “cooler” (15-20° C) climatic zones. This species possesses the largest geographical distribution within the family Idiosepiidae

and, because of its size, presumably within the cephalopods.

The recently collected specimen of *Idiosepius biserialis* from Indonesia and Japan were identified following Voss (1962) and compared with *Idiosepius biserialis* and *Idiosepius thailandicus* from Thailand by SEM-analysis.

## 1. Localities

### *Idiosepius biserialis*

- Thailand: Bang Rong, Phuket Island ( $8^{\circ} 02.156^{\prime}\text{N}$ ;  $98^{\circ} 25.487^{\prime}\text{E}$ ) (J. von Byern unpubl. data); Ko Pratong, Ranong (Hylleberg and Nateewathana, 1991)
- Moçambique: Inhaca Island ( $26^{\circ} 00.215^{\prime}\text{S}$ ,  $32^{\circ} 54.721^{\prime}\text{E}$  and  $26^{\circ} 02.300^{\prime}\text{S}$ ,  $32^{\circ} 54.166^{\prime}\text{E}$ ); Inhambane Bay ( $23^{\circ} 51.184^{\prime}\text{S}$ ,  $35^{\circ} 22.553^{\prime}\text{E}$ ); Linga Linga ( $23^{\circ} 42.911^{\prime}\text{S}$ ,  $35^{\circ} 23.684^{\prime}\text{E}$ ); Monque ( $23^{\circ} 41.331^{\prime}\text{S}$ ,  $35^{\circ} 22.281^{\prime}\text{E}$ ) (J. von Byern unpubl. data); San Jose Mission Station, Morrumbene (Voss, 1962); Vilanculos (M. Roeleveld unpubl. data)

### *Idiosepius thailandicus*

- Thailand: Marine Station Ban Phe, Rayong; Chantaburi River ( $12^{\circ} 32.424^{\prime}\text{N}$ ;  $102^{\circ} 02.842^{\prime}\text{E}$ ) (J. von Byern unpubl. data) and (Nabhitabhata, 1998); Donsak Surat-tani, Ban Phe Rayong

## New records of *Idiosepius biserialis*

- Indonesia: 1 male and 2 females taken from the surface by dip net on 2 May 2004; eastern part of Ekas-Bay, Lombok Island, Indonesia ( $08^{\circ} 52.020^{\prime}\text{S}$ ;  $116^{\circ} 27.541^{\prime}\text{E}$ ). Collector: J. von Byern
- Japan: 7 males and 4 females taken from the surface by dip-net on 3 August 2000; Takasu, Japan. Collector: S. Shigeno

## 2. Description

The morphology of the body and the presence of an adhesive organ clearly place specimens into the genus *Idiosepius*. The body size of all collected specimens agrees well with the descriptions of *Idiosepius biserialis* Voss, 1962; Hylleberg and Nateewathana, 1991a. The animals are small (Table 1), dorso-ventrally compressed and cigar-shaped; the mantle ends in a blunt point.

The body is spotted with reddish brown chromatophores. The fins are small and kidney-shaped. Both arms IV in the males are hectocotylized, bearing 3-4 suckers on the left respectively 4-6 suckers on the right basal area of ventral arm. In the male, the hectocotyl arms are unequal in length contrary to the holotype specimen of Voss (1962). The suckers on the tentacles of all caught specimens have about the same size (100 µm) in the basal area, decreasing towards the tip of arms.

**Table1:** Morphometric data of the collected specimens.

	Indonesia			Japan			
	Female 1	Female 2	Male	Males (n=7)		Females (n=4)	
				Mean	Range	Mean	Range
Total length [mm]	10	7	5	11.8	9.2-13.4	16,70	14.2-18
Mantle length [mm]	5.5	5	3	6.3	4.7-7.6	9,39	8.1-10
Weight [g.]	0.04	0.02	0.01	0.141	0.14-0.15	0,157	0.15-0.16
Mantle width [mm]	5	3	2.5	3.1	2.4-4.0	4,24	3.7-4.4
Head width [mm]	2.5	2	2	2,81	2.7-2.9	3,19	2.9-3.5
Fin length [mm]	2	1.8	1.2	2,86	2.7-2.9	3,01	2.9-3.2
Fin width [mm]	1.25	0.6	0.6	1,73	1.6-1.8	1,76	1.7-1.8
Arms I [mm]	2	1.6	1.0	contracted	-	contracted	-
II	3	1.85	1.3	contracted	-	contracted	-
III	1.5	1.6	1	contracted	-	contracted	-
IV	2.5	2	1.1	contracted	-	contracted	-
Tentacles [mm]	4	contracted	1.65	contracted	-	contracted	-

Based on the biserial arrangement of suckers on the tentacles the specimens from the new locations belong either to the species *Idiosepius biserialis* and/or to *Idiosepius thailandicus*. The differences between the two species are marginal and reduced to the arrangement of peg rows in the distal portion of tentacle suckers (Chotiyaputta, Okutani, and Chaitiamvong, 1991). Comparison of SEM photographs of arm and tentacle suckers (Fig. 1) with data of *Idiosepius biserialis* from Thailand and Moçambique respectively *Idiosepius thailandicus* reveals that the recently collected specimen from Indonesia and Japan are morphological closely related to *Idiosepius biserialis*.

### 3. Distribution and habitat

*Idiosepius biserialis* and the specimens from Japan can be caught easily by handnets in shallow seagrass and algal beds of Moçambique and Thailand (Voss, 1962; Hylleberg and Nateewathana, 1991). The

specimens from Indonesia were caught at the water surface in a sandy area next to a small mangrove sapling. No seagrass beds have been reported in the Ekas-bay, so it remains unclear where the animals stay at low tide.

Currently no information about the origin of settlement (Moçambique or Thailand), the period and route of migration (e.g. along the coast, directly through the Indian Ocean or abduction) are available. Molecularbiological investigations are planned to provide new insights in the degree of relationship of *Idiosepius biserialis* and *Idiosepius thailandicus*.

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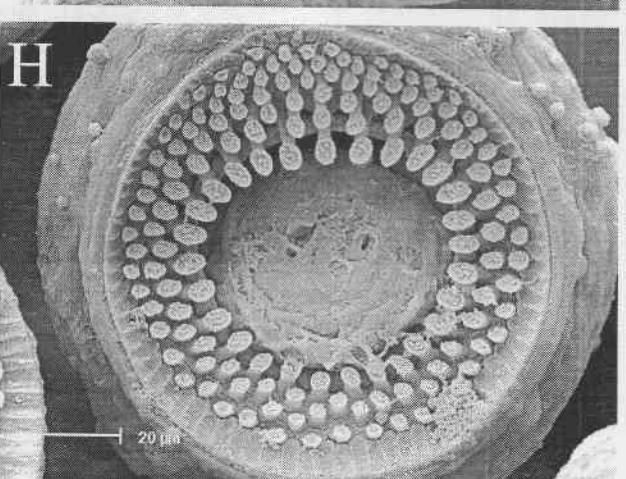
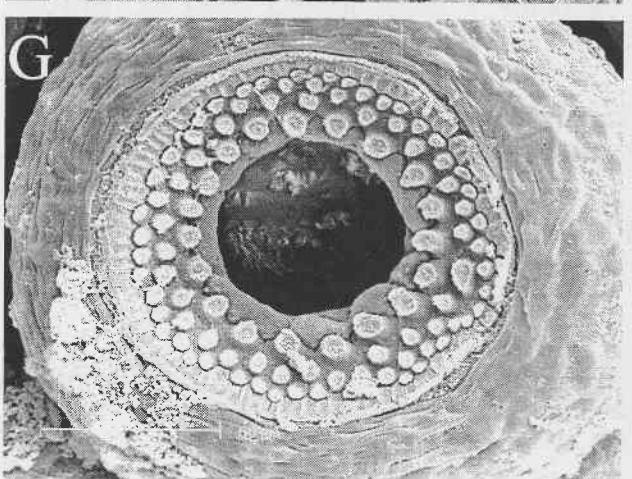
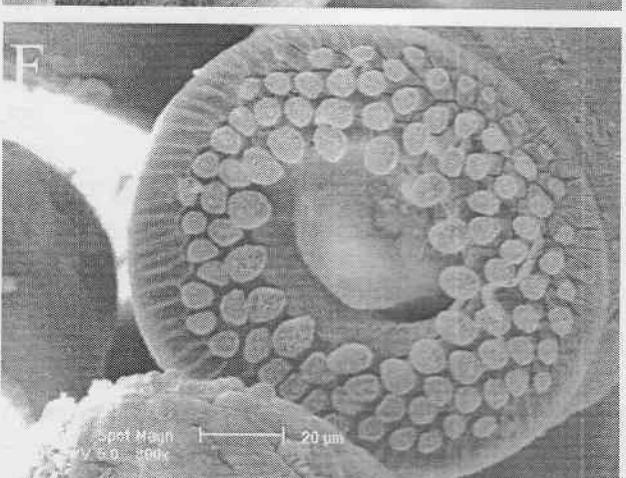
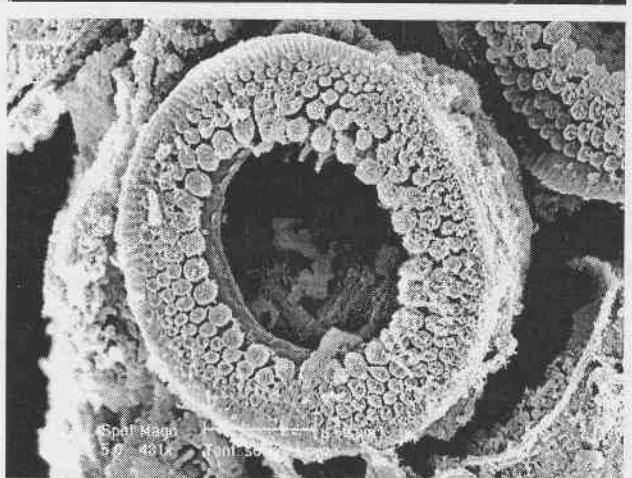
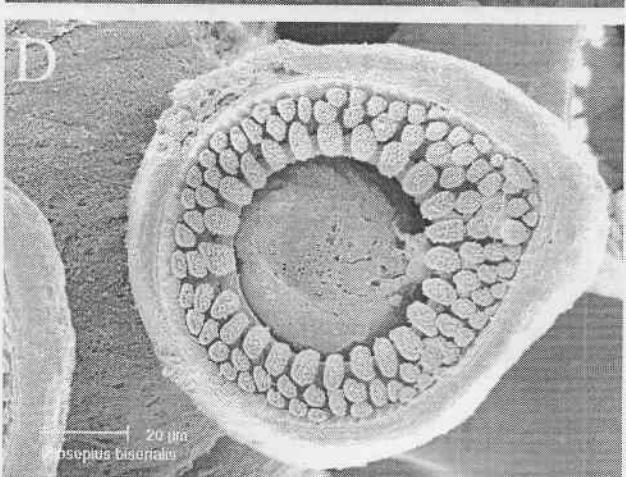
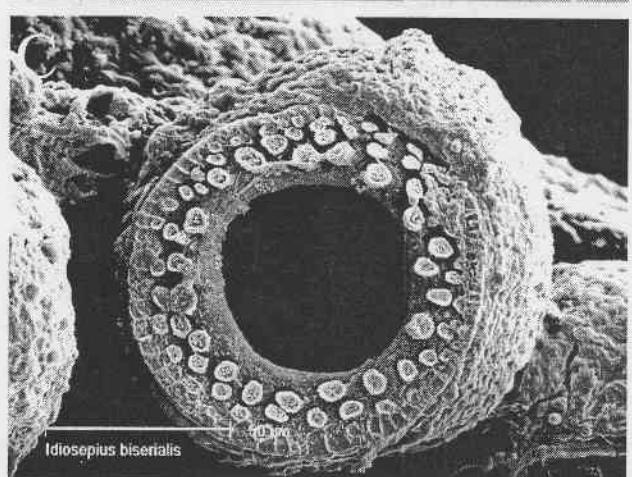
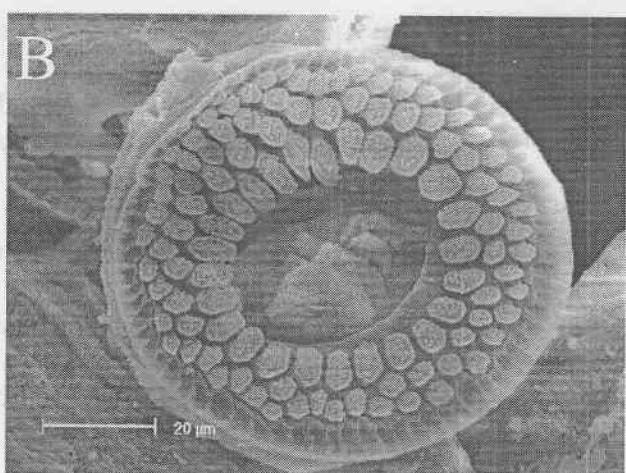
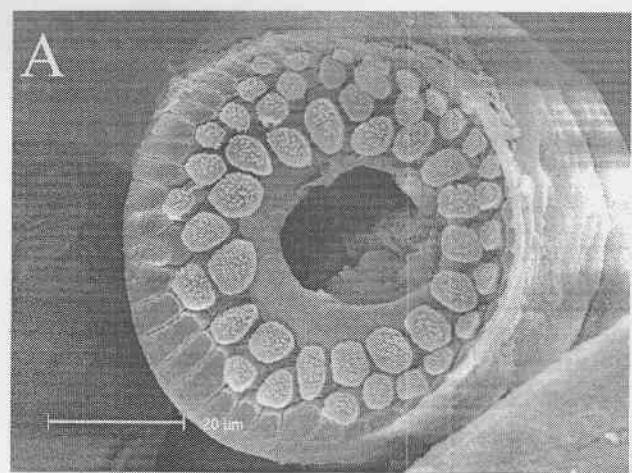
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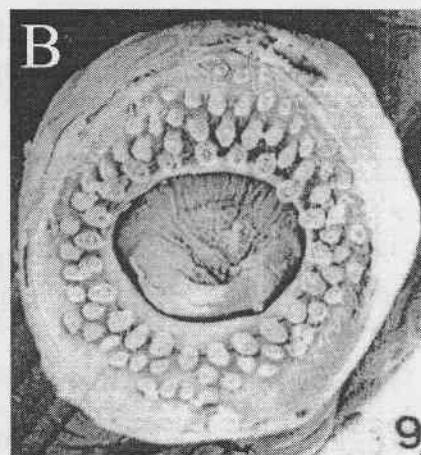
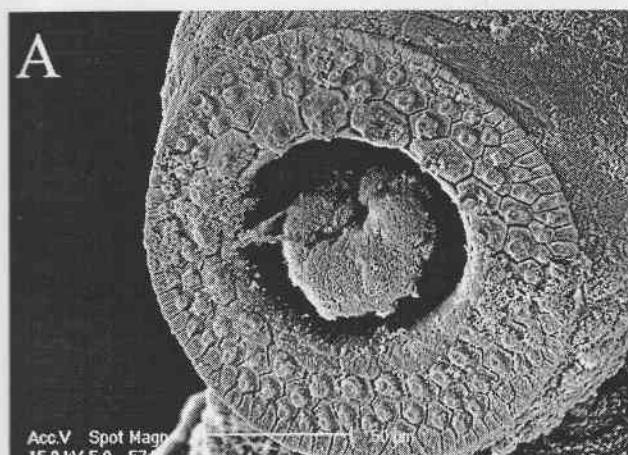
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## PLATE EXPLANATIONS

### PLATE 1 (p. 42)

A-B. Arm and tentacle sucker of *Idiosepius biserialis* from Thailand.

C-D. Arm and tentacle sucker of *Idiosepius biserialis* from Moçambique.

E-F. Arm and tentacle sucker of *Idiosepius biserialis* from Indonesia.

G-H. Arm and tentacle sucker of *Idiosepius biserialis* from Japan.

### PLATE 2 (p. 43)

A-B. Arm and tentacle sucker of *Idiosepius thailandicus* from Thailand. Image of the tentacle sucker (x750) from Chotiyaputta, Okutani and Chaitiamvong, 1991.

## Multiple spawning in *Sepiola affinis* (Cephalopoda: Sepiolidae)

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In order to gather information on the reproductive strategy of the sepiolid squid *Sepiola affinis*, direct observation of egg-laying in the aquarium by 14 wild collected females were combined with the examination of their ovaries and the ovaries of 21 females,

which did not spawn in the laboratory. The record of multiple spawning events in five aquarium-kept females (two to 14 events) and the co-existence in the ovaries of oocytes at various stages of maturation, showed that *Sepiola affinis* is a multiple spawner.

# The rostrum, conotheca and pro-ostracum in the Jurassic coleoid

## *Belemnoteuthis* PEARCE from Wiltshire, England

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**ABSTRACT:** Three specimens of *Belemnotheutis* PEARCE, 1842 from the Oxford Clay (Jurassic; Callovian) of Christian Malford, Wiltshire, England, are studied with the goal of elucidating the structural relationship of rostrum, conotheca and pro-ostracum in this genus. SEM examination has revealed the following ultrastructural data: (1) the apical part of the rostrum is composed of a dense, outer prismatic portion and a porous, inner prismatic portion; towards the aperture the rostrum decreases in thickness, losing first the porous inner portion and finally the outer dense portion; (2) in the middle part of the shell the conotheca consists of outer prismatic, nacreous and inner prismatic layers; towards the aperture it gradually decreases in thickness: first, the outer prismatic layer disappears and then the nacreous layer; the most anterior portion of the conotheca is solely formed by the thin, inner prismatic layer; (3) the pro-ostracum differs distinctly from the conotheca and rostrum in the following features: (a) it is mainly an organic formation, consisting of horizontally laminated vertical columns; (b) the distal end of each column represents a polygonal field that in its periphery is composed of numerous, irregularly shaped, radially arranged plates, and in its central portion of several angular, smaller elements separated by interspaces of various widths. Delicate lamination of the pro-ostracum in *Belemnotheutis* is similar to the lamination of the chitinous material in the gladius of modern squids (see Doguzhaeva & Mutvei, 2003: Fig. 4a, b). Our SEM observations demonstrate that the pro-ostracum in *Belemnotheutis* is a shell element with unique structure without any similarity to that of the conotheca or rostrum.

**Key words:** Coleoid cephalopods, *Belemnoteuthis*, Jurassic, England, shell morphology, microstructures.

### Introduction

Since the erection of the genus *Belemnotheutis* PEARCE, 1842 it has been known that this coleoid has a pro-ostracum, in addition to a short rostrum and a phragmocone (Huxley, 1864; Naef, 1922; Makowski, 1952; Jeletzky, 1966; Bandel & Kulicky, 1988; Donovan & Crane, 1992). The present paper contains results of the SEM examination of the shell structure in *B. antiquus* PEARCE.

### 1. Material and preservation

Three specimens of *B. antiquus* from the Oxford Clay (Jurassic; Callovian) of Christian Malford, Wiltshire, England were studied with

the SEM. They are about 80 mm, 60 mm and 50 mm in length. All specimens have been flattened and the shell material is fractured into a mosaic of pieces that retain their original positions. A rostrum and a conotheca were originally aragonitic but have been diagenetically replaced by calcium phosphate. Two shells are deposited in the British Museum (Natural History), and the third shell in the Swedish Museums of Natural History. The shells were examined without etching. The shell ultrastructure was studied in broken pieces of the shell taken from different distances from the apex. In two specimens the hyperbolar zone of the pro-ostracum was exposed by removing

the shellac that covers the shells in front of the wedged-out rostrum..

## 2. Observations

**Rostrum.** In the apical part of the shell the rostrum is solid and therefore less compressed than the rest of the shell. The rostrum consists here of an outer and an inner layer. The outer layer has a solid, simple prismatic structure with needle-shaped crystallites. The inner layer is composed of similar prismatic units but they are loosely packed. Towards the aperture the rostrum loses its inner layer and the outer layer becomes spherulitic-prismatic in that the crystalline units form sectors in which they radiate towards the shell surface and become loosely packed. Small interspaces are left between some of the crystalline units that indicate higher organic content. The outer surface of the rostrum is covered by a thin, possibly originally organic layer.

**Conotheca.** In an apical part (up to approximately 50 mm from the shell apex), it consists of a thin outer prismatic, a thick nacreous and a thin inner prismatic layer. Samples taken a somewhat greater distance from the apex show that the conotheca is composed only of the nacreous and the inner prismatic layers, both having the same thickness of ca 0.6 mm. In our largest specimen the samples taken at a distance of 65 mm from the shell apex show that the conotheca is here composed only of the inner prismatic layer that is about 0.1 mm thick. Thus, at earlier growth stages the conotheca has three layers but at older stages first the outer prismatic layer and finally the nacreous layer wedge out.

**Pro-ostracum** (Pl. 1; Figs. A-F). The surface of the pro-ostracum is exposed laterally in the anterior parts of two specimens where the rostrum has wedged out or been removed. The hyperbolar zone is clearly visible due to longitudinal striation on its surface. In higher magnification the striae have a somewhat compact, plate like structure, and the interspaces between them a porous net- or lace-like structure (Pl. 1; Fig. F). The surface of the pro-ostracum is penetrated, both vertically and horizontally, by a great number of canals of boring organisms, with a diameter somewhat less than 1 µm. The presence of these

organisms indicates that the pro-ostracum mainly consisted of organic substance that is only partially calcified. Immediately beneath the pro-ostracal surface there follows a thin layer, ca 15 µm thick, that is clearly visible on vertical fracture surfaces of all three shells. Because it is rich in organic substance this layer shows a great difference in mode of preservation, in contrast to the calcified, uniformly well preserved prismatic and nacreous layers in the same shell. This layer of the pro-ostracum is in places composed of columnar units about 5 µm in diameter (Pl. 1, Fig. B). These columns seem to be composed of predominantly organic, very thin laminae (Pl. 1, Figs. C, D), ca 0.05 µm thick. In surface view (Pl. 1, Fig. E) the distal end of each column forms a polygonal field; its periphery is composed of numerous, irregularly shaped, radially arranged plates in contact with each other; in its central portion it consists of several angular, smaller elements separated by interspaces of various widths. In other places the pro-ostracum consists of vertical elements of highly variable diameter separated by interspaces of irregular shapes and sizes. Some of these elements seem to be plate-like and show series of deep, horizontal, narrow incisions (Pl. 1, Fig. A). Thus, the pro-ostracum has an unique structure that has no resemblance either to the adjacent, outer prismatic layer of the conotheca, or to the prismatic layers of the rostrum.

## 3. Discussion

As described above, the pro-ostracum in *Belemnotheutis* consists of vertical columns of predominantly organic lamellae, ca 0.05 µm thick. Their thickness corresponds to that of the lamellae forming the chitinous gladii in living squids (Pl. 1, Fig. G). On the basis of our SEM observations on the pro-ostracum in *Belemnotheutis* we propose the name “organic lamello-columnar ultrastructure” as a new type of shell ultrastructure in cephalopods.

Huxley (1864, p. 18) observed a specimen of *Belemnotheuthis* in which “from one lip of the phragmocone there obviously proceeds the horny-looking plate (*a*, *a*), the two lateral contours of which, obscurely defined from the matrix, pass into one another at an acute angle

at *b*. A narrow band of horny-looking matter, marked by oblique striae, is discernible at *c*, and is quite distinct from the remains of the mantle (*f*), under which it seems to pass.” The ultrastructural features of the pro-ostracum, presented herein, agree with Huxley’s interpretation of the pro-ostracum as a “horny” structure. The concept of the pro-ostracum as

an innovation in coleoid cephalopods was based on SEM studies of “ordinary” belemnites (Doguzhaeva et al. 2002, 2003).

Our present results support this idea, but they do not support the earlier view according to which the pro-ostracum is a dorsal remnant of the body chamber of coleoid precursors.

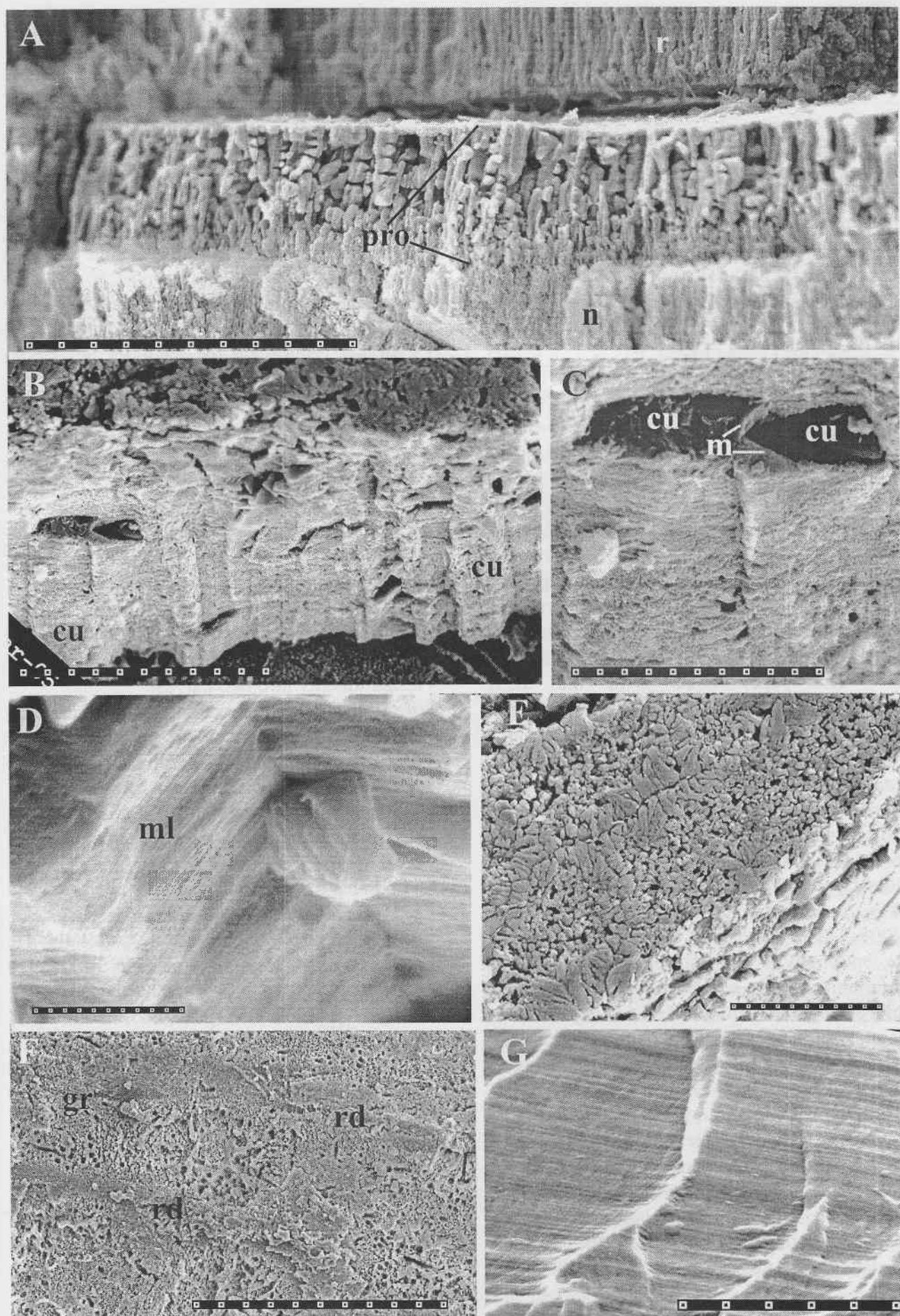
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## PLATE 1. - EXPLANATION

**Pro-ostracum ultrastructure in *Belemnotheutis antiquus*; Oxford Clay, Jurassic; Callovian, Christian Malford, Wiltshire, England:**

- A. Specimen No. SMNH 90284; B – F. Specimen. No. BMNH 37412. G. Lamination in chitinous gladius (cross section) in living squid *Berryteuthis magister* BERRY; scale bar – 30 µm.
- A. Middle part of the shell; the pro-ostracum (pro) is situated between the rostrum (r) and the nacreous layer (n) of the conotheca; scale bar - 30 µm.
- B. Columnar units (cu) of the pro-ostracum separated by an organic membrane (m); anterior part of the shell; scale bar - 15 µm.
- C. Close-up of B to show thin lamination of the columnar units; scale bar - 6 µm.
- D. Micro-laminae (ml) of the columnar units; scale bar 1.2 µm.
- E. Surface view of the pro-ostracum; scale bar – 6 µm.
- F. Close-up of striae (rd) and grooves (gr) of the hyperbolar zone ; scale bar – 60 µm.



# The original composition of the gladius in the Aptian plesioteuthid *Nesisoteuthis*, Central Russia, based on its ultrastructure

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**ABSTRACT:** A thin, delicate, small-sized (less than 30 mm in length) gladius with an ink sac in *Nesisoteuthis simbirskensis* DOGUZHAEVA from the Lower Aptian of the Shilovka Lagerstätte, Middle Volga, Central Russia, is examined with the SEM with the aim of clarifying the original composition of the gladius – whether it was organic or formed of calcium phosphate. Its ultrastructure is compared with the originally organic but secondarily phosphatized scales of pelagic fish and aptychi from the same beds. In addition, a gladius of modern squid *Loligo* is also examined for comparison. It is shown that the gladius and ink in *N. simbirskensis*, as well as fish scales and aptichii, have a globular ultrastructure. The gladius in *N. simbirskensis* was originally a laminated, organic structure like that in living squids but became secondarily phosphatized during fossilization.

**Key words:** Coleoid cephalopods, plesioteuthid, *Nesisoteuthis*, Early Cretaceous, Central Russia, shell morphology.

## Introduction

The paper deals with the SEM examination of shell and ink substance in a small-sized, less than 30 mm in length, thin-walled, slender gladius, covering an underlying ink sac. The specimen comes from the Lower Aptian *Lagerstätte* Shilovka, Ulyanovsk region, near the village of Shilovka, Middle Volga region, Central Russia. It is described as a plesioteuthid: *Nesisoteuthis simbirskensis* DOGUZHAEVA, 2005. The locality has also yielded exceptionally well-preserved aragonitic ammonite shells exhibiting rarely observed morphological features such as large ventro-lateral muscle scars and buccal apparatus preserved in situ (Doguzhaeva & Mutvei, 1991, 1992). The ammonite shells from Shilovka contain about 90 % of aragonite (x-ray data); however, the aptychi and coleoid ink that were analysed with EDAX are phosphatized (Doguzhaeva & al., 2004). The gladius lies in a dense, dark-grey siderite concretion that has preserved the detailed structure of this fragile fossil. When the

concretion was broken the gladius was split longitudinally into two halves

Aptian gladius-bearing coleoids are rare the world over, including Central Russia. Since the first find of a gladius in late 1940<sup>s</sup> (Hecker & Hecker, 1955) our specimen is the fifth recorded (Doguzhaeva, 2005). The five specimens are the only known Aptian gladius-bearing coleoids from Russia so far.

## 1. Material studied and method

The gladius under examination is the holotype of *N. simbirskensis* (PIN 3871/391) consisting of two halves split longitudinally (Doguzhaeva, 2005, Figs. 1A-D). The larger, thicker half is 26 mm long and 6 mm broad. The thinner counterpart is 23 mm long and 4 mm in maximum width. Both halves show split surfaces. The ink sac is exposed in cracks of the gladius. For comparison, aptychi and scales of pelagic fish from the same beds, and a gladius of a living squid *Loligo*, were studied with the SEM without etching. The fish scales are examples of fossils that are known to have been originally of organic

composition but were phosphatized post-mortem.

## 2. Observations

Gladius in *N. simbirskensis*. The gladius consists of thin laminae, ca 1-2 µm in thickness, each of which is composed of a set of thinner lamellae (Pl. 1 A,B). The lamellae consist of globules that are more or less regularly shaped (Pl. 1B,C). The globules are ca 0.05 – 0.2 µm in diameter and each one is an aggregate of still smaller particles. In some laminae the globules are loosely packed, in others the globules are distributed within a material that looks structureless, similar to pure organic substance. This probably depends on the degree of coagulation of the particles into globules. Where the particles were not coagulated into globules they look like structureless matter. The laminae have micro-pores with diameters of ca 0.05 - 0.2 µm, being close to the size of the globules. About 100 pores were counted on a square of 5 µm side in the central keel region. In the same region the globules form aggregates that are larger and more compactly packed than those outside the keel. However, in some other places the pores are less numerous or not visible. Numerous cracks in the gladius, caused by compaction, are filled by heterogeneous debris including angular and globular particles, the latter having diameters of ca 0.3 µm.

Ink sac content. The ink sac, exposed in cracks of the gladius, contains two dominant substances: globules of ca 0.3 µm diameter (Pl. 1 D), and a structureless mass consisting of small particles, not coagulated into globules. Besides, the ink sac contains undetermined debris, and probably pieces of gladius and remnants of soft tissues. They might have penetrated into the ink sac in early postmortem time.

Fish scales and aptychi. Both are laminated with a globular ultrastructure in each lamina. The globules are ca 0.03 µm in diameter (Pl. 1 E), and consequently about ten times smaller than the globules in the gladius and ink sac. In the aptychi the globules are arranged in fibres.

Modern gladius. It is laminated and each lamina has a fibrous ultrastructure (Pl. 1 F). Each fibre is ca 0.06 µm in diameter. The gladius is perforated by micropores with a diameter of ca 0.3 – 0.6 µm. Thus, their diameter corresponds to that of the micropores in the gladius of the extinct *N. simbirskensis*.

## 3. Ultrastructural comparison with other fossil gladii previously studied

The ultrastructure of the gladius has been described in the Jurassic *Loligosepia*, *Trachyteuthis* and *Teudopsis* (Doguzhaeva & Mutvei, 2003). All these gladii are multi-laminated, each lamina being composed of globular, tablet-like or chain-like aggregates of tiny granules with a diameter of ca 0.3 - 0.4 µm. The globular chains in the laminae represent fossilized fibres, which reveals the organic composition of the Jurassic gladii. The Aptian gladius of *N. simbirskensis* examined herein shows a similar ultrastructure: it is laminated and each lamina is composed of granules that are arranged in indistinct fibres (Pl. 1; Fig. B).

## 4. Palaeoenvironmental conclusions

*N. simbirskensis* lived in the epicontinental Early Aptian Sea on the East-European Platform characterized by dysoxic or anoxic environments (see Doguzhaeva, 2002). Existence of the latter conditions can be proved by analysis of the ink sac preservation. The deformation of the gladius gives the impression that the ink sac was solid and became hardened prior to the compaction of the sediment and fracture of the gladius. The rapid solidification of ink needed slightly acid or neutral conditions that existed in the dysoxic or anoxic marine environments (see Doguzhaeva & al., 2004). In an alkaline environment the ink is dispersed colloidally (FOX, 1966).

## 5. Phylogenetic conclusions

The ultrastructural investigation of the gladius material in the Early Aptian plesiotethid *Nesisoteuthis* reveals that it can be interpreted as an initially organic substance that became secondarily replaced by calcium

phosphate. Thus, this is the fourth squid-like fossil, in addition to the three Jurassic taxa previously studied (Doguzhaeva & Mutvei, 2003), in which the gladius has been shown to be of originally organic composition. This data leads to the conclusion that either loss of mineralization of the gladius in extinct squid-like coleoids occurred in pre-Jurassic time, or

that the gladius in pre-Jurassic time was originally mainly organic in composition.

**Acknowledgements:**

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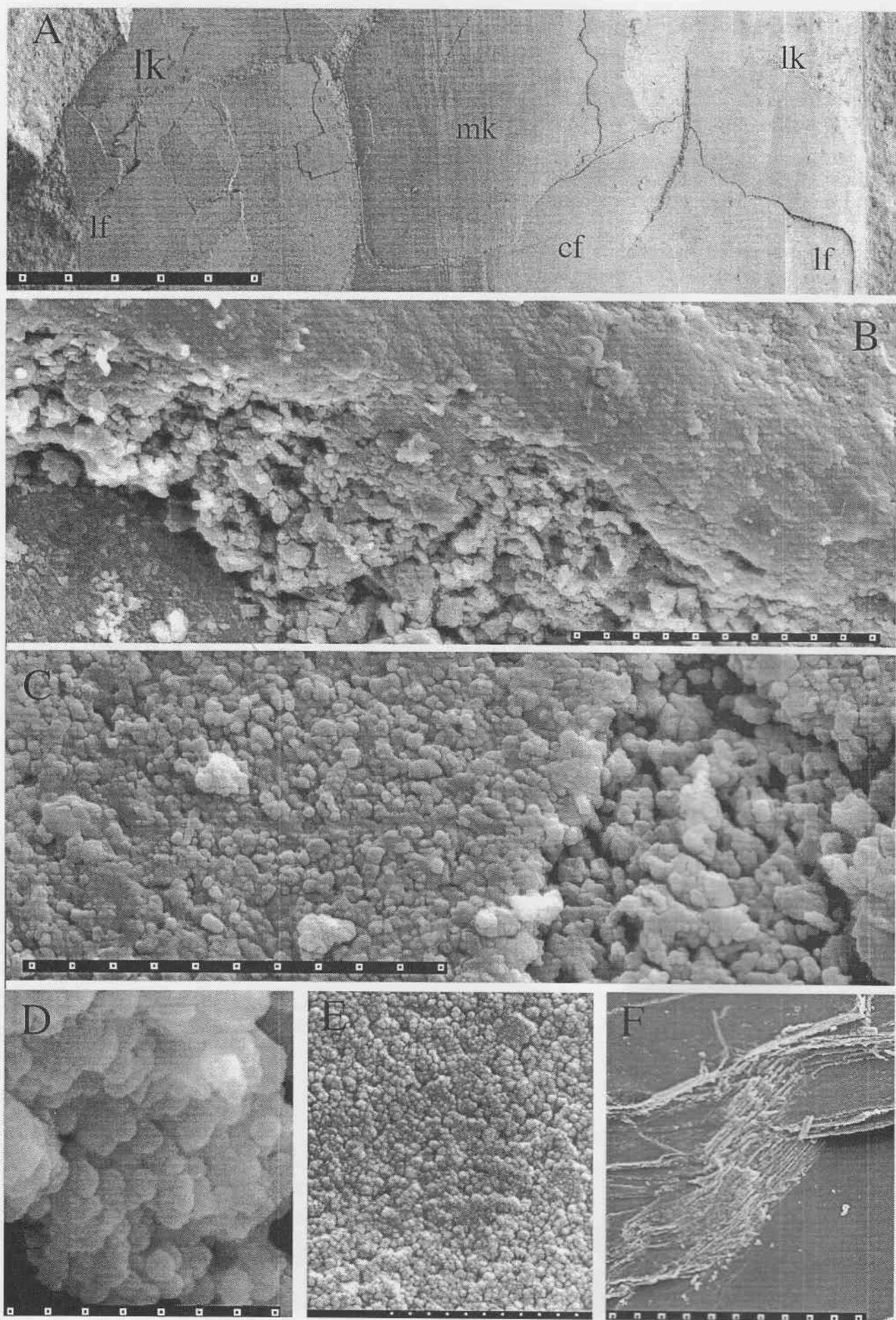
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## PLATE 1. – EXPLANATION

**A-D. *Nesisoteuthis simbirskensis*, sp. nov. PIN 3871/391; Lower Aptian; village of Shilovka, Uljanovsk region, Middle Volga area, Central Russia.**

- A. Anterior part of the gladius showing central (cf) and lateral (lf) fields, median (mk) and lateral (lk) keels, and lamination of gladius material; scale bar - 1. 5 mm.
- B. Enlarged view on the gladius to show two laminae (right top and left bottom corners) and infilling of a crack between them, scale bar – 12 µm.
- C. Two laminae of the gladius exposing globular ultrastructure, the upper has compactly packed globules and the lower has loosely packed globules; scale bar – 12 µm.
- D. Globular ultrastructure of the ink; scale bar – 0. 6 µm.
- E. Globular ultrastructure of the fish scale, scale bar – 0. 6 µm.
- F. Lamination of the gladius in living squid *Loligo*, scale bar – 120 µm.



# A late Triassic coleoid from the Austrian Alps: The pro-ostracum viewpoint

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**ABSTRACT:** The discovery of a new and as yet unnamed Late Triassic coleoid with a pro-ostracum from the Carnian beds of Lower Austria is reported. The new taxon is represented by a tiny (about 10 mm broad and 5 mm long) fragment of a small-sized shell together with black organic jaws (about 4 mm long) lying immediately in front of the anterior edge of the shell and slightly contacting it. The shell is dorso-ventrally compressed and exposes the dorsal and lateral sides. It comprises the phragmocone and the pro-ostracum. Mural parts of the septa are distinguishable but indistinct. The pro-ostracum is narrow, about 1/7-1/8 of the shell circumference. It has a narrow median field with convex growth lines, and hyperbolar zones with ribs converging anteriorly. The shape is remarkably different from the broad (about three-quarters of shell circumference) fanlike tripartite pro-ostracum in the contemporaneous *Phragmoteuthis* MOJSISOVICS, 1882, and can be defined as of the "belemnoid type" (Huxley, 1864). SEM examination revealed that the pro-ostracum is formed by two layers: (1) the inner layer of vertical columnar units formed by micro-lamellae, and (2) the outer layer of micro-plates arranged parallel to the surface. Neither prismatic nor nacreous layer is present in the pro-ostracum. This ultrastructure is essentially similar to that of the pro-ostracum in the Jurassic *Belemnotheutis* (Doguzhaeva et al., 2005). In both cases the fine lamination of the pro-ostracum material shows a close similarity to the lamination of the chitinous material in the gladius of living squids. Therefore, the pro-ostracum in the extinct coleoids is considered to have been composed of partially calcified, mostly organic material. SEM examination revealed also that the jaws of the specimen studied have a laminated ultrastructure similar to that of chitinous jaws of living squids. Our study shows that coleoids with a narrow "belemnite"-like type of pro-ostracum and those with a broad pro-ostracum of the *Phragmoteuthis*-type (Jeletzky, 1966) are now known to occur in Late Triassic. The micro-laminated ultrastructure of the pro-ostracum in the Carnian coleoid described herein supports the concept that the pro-ostracum was originally a predominately organic and innovative morphological structure in coleoid evolution (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, 2003b, 2005).

**Key words:** Coleoid cephalopods, Triassic, Austrian Alps, shell morphology, pro-ostracum.

## Introduction.

This is the first report of a new narrow, "belemnite"-like pro-ostracum. The as yet unnamed coleoid specimen is from the Late Triassic Austrian Alps. It contains a crushed orthoconic phragmocone and jaws that apparently belonged to the same individual. The shell shows a narrow pro-ostracum with well preserved shell material. The shell and the jaws were examined with SEM. The specimen

was discovered by splitting the shale around the shells of the ceratid ammonoid *Austrotrachyceras*. The *Austrotrachyceras* shells in the shale were collected more than hundred years ago for the Austrian Geological Survey and for the Museum of Natural History in Vienna. The exceptional preservation of the shell material in these ammonoids from this locality has been elucidated earlier (Doguzhaeva et al., 2004).

## 1. Material studied and method.

The studied specimen represents a tiny (about 10 mm broad and 5 mm long) fragment of a small-sized shell together with black organic jaws (about 4 mm long) lying immediately in front of the anterior edge of the shell. The specimen comes from the Lower Carnian - Austriacum Zone, Upper Triassic; locality Schindelberg, Lunz, Lower Austria. The specimen is compressed, flattened and split longitudinally into a main part and a counter-part. The external surface of the dorsal and lateral sides of the phragmocone are exposed, and the inner surface of the ventral side of the phragmocone is also partly exposed (Pl. 1, Fig. A). The deformation of the shell is similar to that of the recently studied Jurassic specimens of *Belemnotheutis* (Doguzhaeva et al., 2005); both have longitudinal fractures and fractures along the mural rings that produce rectangular fragments in a mozaic pattern. The estimated diameter of the phragmocone is about 5 mm. The preserved pro-ostracum is discernible by its typical growth lines on the central zone and by the longitudinal ribs on its hyperbolar zone. The specimen was examined without etching with SEM at the Swedish 3. Museum of Natural History, Stockholm, Sweden and is reposed in the Museum of Natural History, Vienna, Austria.

## 2. Morphology and ultrastructure of the pro-ostracum (Pl. 1, figs. A-E).

The width of the pro-ostracum is about 3 mm, which is approximately 1/6 - 1/7 of the estimated shell circumference (Pl. 1, Fig. A). It has a narrow median field with narrowly rounded growth lines, and hyperbolar zones with longitudinally converging ribs. In the adoral part of the median field the growth lines form an acute angle of ca 60° - 80°. The growth lines are of two orders. The preserved fragment has about 5 broad and 30 narrow growth lines. The pro-ostracum covers 5 or 6 camerae of the phragmocone; the camerae are about 0.8 mm in length. The thickness of the pro-ostracum is ca 50 µm. It consists of two layers of about the same thickness. The inner layer is composed of vertical columnar units about 4-5 µm in diameter (Pl. 1, Fig. B). The columns are separated by interspaces and

composed of micro-laminae of ca 0.05 µm in thickness (Pl. 1, Fig. C). In a surface view the distal end of each column has an irregular polygonal shape. The outer layer consists of horizontally arranged micro-plates that are ca 0.2 – 0.3 µm in thickness (Pl. 1, Figs. B, D). They seem to have been originally organic as are the lamellae in the chitinous jaws (compare Pl. 1, Fig. D and Fig. E). Thus, the ultrastructure of the pro-ostracum is unique and lacks any ultrastructural resemblance to either the prismatic or nacreous layers of the phragmocone.

**The Jaws.** The jaws of the specimen show thin laminations that are fractured in a “step-like” pattern (Pl. 1, Fig. E). This fracture pattern is similar to that seen in the broken jaws and gladii of living squids consisting of organic material. Similar fracture patterns have also been observed in broken gladii of fossil squid-like coleoids (Doguzhaeva & Mutvei, 2003). The resemblance between the ultrastructure of the outer layer of the pro-ostracum and the jaws indicates that both are composed of organic material.

## 3. Discussion:

Up-to-now *Phragmoteuthis* has been the only known Triassic coleoid preserved with a pro-ostracum. In this genus the pro-ostracum is broad and different from the pro-ostraca in Early Jurassic phragmocone-bearing coleoids. Therefore, *Phragmoteuthis* has been interpreted as an intermediate stage between the bactritoids with a long body chamber and belemnoids with a narrow pro-ostracum (Jeletzky, 1966). This view is based on the assumption that there was a gradual reduction of the ventral side of the body chamber in the ancestral bactritoids that resulted in the formation of the initially broad pro-ostracum in early coleoids. Our study demonstrates that the morphological variability of pro-ostraca in Triassic coleoids was not restricted to a single *Phragmoteuthis*-like type. Moreover, the newly discovered specimen gives a new information for discussion of the possible origin and transformation of the shell in coleoid cephalopods. As described above, neither the prismatic nor nacreous layer is present in the pro-ostracum. The characteristic

ultrastructure of the pro-ostracum in the new coleoid is the micro-lamination. The micro-lamellae are arranged in vertical columns in the inner layer and in micro-plates in the outer layer. The thickness of the micro-lamellae corresponds to that of the micro-lamellae forming the chitinous gladii in living squids and in the pro-ostracum of *Belemnotheutis* (Doguzhaeva et al., 2005, herein). This

observation leads to the conclusion that the pro-ostracum in the specimen studied was originally mainly organic material. This conclusion provides additional proof for the concept that the pro-ostracum originated as an innovative morphological structure in coleoid evolution and not as a shell reduction feature from the ancestral bactritoids (Doguzhaeva, 2002; Doguzhaeva et al, 2002, 2003, 2005).

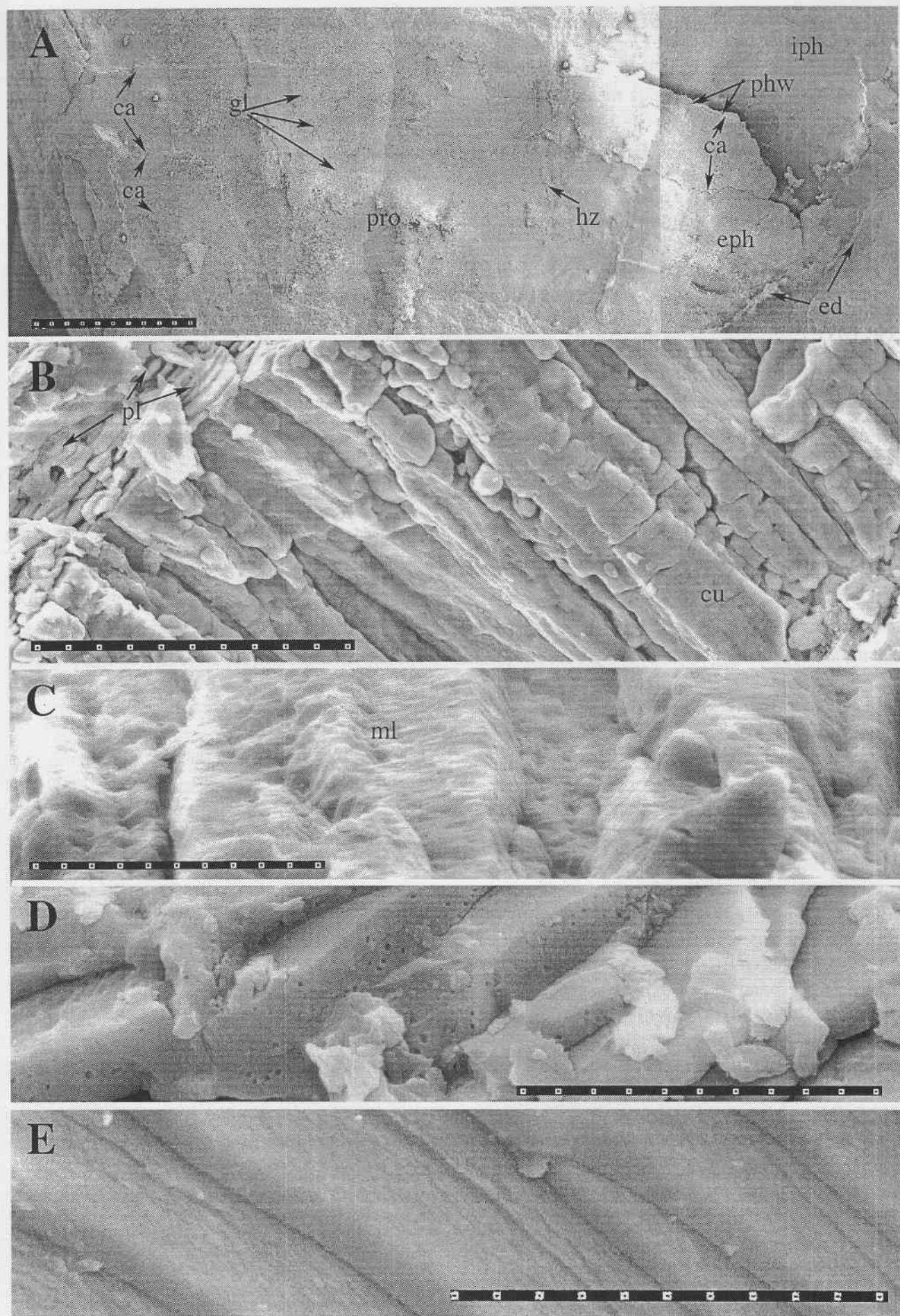
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**PLATE 1. – EXPLANATION,**

**Unnamed coleoid; sp. no. NHMW 2005z0005/0001; Lower Carnian, Upper Triassic; Lower Austria.**

- A. General view on a dorso-ventrally compressed shell (ed – lateral edge of the shell) showing the dorsal side of the phragmocone with the exposed external (eph) and internal (iph) surfaces, camera (ca), growth lines (gl) of the central and ribs of the hyperbolar (hz) zones of the pro-ostracum (pro), and thickness of the phragmocone wall (phw); scale bar – 1.2 mm.
- B. Pro-ostracum composed of the two organic layers: the inner one is of columnar units (cu) and the outer one is of micro-plates (pl) arranged parallel to the surface; scale bar – 15 µm.
- C. Close-up of B to show micro-lamination of the columnar units (ml); scale bar - 6 µm.
- D. The ultrastructure of the micro-plates of the outer layer; scale bar - 3 µm.
- E. Thin lamination and step-like fracture pattern in a jaw; scale bar – 6 µm.



# Analysis of growth increments in rostra of Middle Jurassic belemnite *Megateuthis* from Germany

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**ABSTRACT:** Seven rostra of *Megateuthis giganteus* from the Middle Jurassic of Hannover area, Germany, were studied with the scanning electron microscope (SEM) and energy dispersive spectrometry (EDS) in order to elucidate the potentialities of using belemnite rostrum as a data archive of growth periodicity. It is revealed that (1) alternation of the dark and light lamellae is caused by regular changes in density of a rostrum material rather than alternations in organic content; (2) in dark regions the number of increments is less (ca 30) while in light regions it is higher (ca 110); (3) the rostra contain (in per cent to atomic weight): calcium (ca 35%), carbon (ca 15%) and oxygen (ca 50%) that indicate calcium carbonate, apparently in a calcite form; (4) the higher content of carbon (ca 30%) is restricted to the spaces between the calcium carbonate prisms dominantly near the outer surface of the rostra while the dark and light regions show no differences in carbon content; (5) up to 700 increments were counted in the rostra with 40 mm in diameter; (6) in large-sized rostra there are up to six regions with higher growth rate (evidenced by broader increments) and the same number of periods of low growth rate (evidenced by narrow increments); (7) the relatively highest growth rate period corresponds to the middle part of the rostrum (the third region).

**Key words:** Coleoid cephalopods, belemnites, Middle Jurassic, Germany, shell composition and growth.

## Introduction

Rostra of *Megateuthis giganteus* from Middle Jurassic of Hannover area, Germany (collections of Swedish Museum of Natural History) were examined using scanning electron microscopy (SEM) and energy dispersive spectrometry (EDS) in order to elucidate the potential of using the rostrum of belemnites as data archive of growth periodicity and life-span estimation of the genus.

To begin with, we concentrated on finding out whether the rostra in *M. giganteus* have any periodicity in the width, density and elemental composition of the growth increments. Next, in order to check the feasibility of the idea of regular secretion of organic matter as the primary cause of the alternation of light and dark lamellae we paid special attention to content in organic

matter in the rostra. For this purpose we selected very well preserved belemnite rostra in which earlier studies by Doguzhaeva et al., 2002, demonstrated that there are traces of an organic content.

## 1. Material and method of study.

Growth increments of seven large-sized rostra with the maximum diameter of 30 - 40 mm were investigated in cross and longitudinal sections. All the rostra were cut through the protoconch in cross and median sections. In order to enhance the visibility of the growth rings the cross sections were made parallel to the c-axes of the calcite prisms (that are not precisely perpendicular to the axis of the rostrum) and then the sections were treated with Mutvei's solution, (a 1:1 mixture of glutaraldehyde 25% and acetic

acid 1% to which alcian blue was added) for ca 2 hours. This is an etching technique used in structural studies of recent bivalve shells (Mutvei, 1979; Dunca & Mutvei 2001; Schöne et al., 2003, 2004, 2005; Dunca et al., 2005).

The etched sections of the seven rostra were then examined using the light microscope AxioCam HRc Zeiss and the scanning electron microscope Hitachi S 4300. The elemental distribution within the rostra was analysed using the Energy Dispersive X-Ray Microanalysis (EDS).

Furthermore, the width of growth increments was measured in the ventral part of the rostra using Image J 1.33u, Wayne Rasband, National Institutes of Health, USA (<http://rbs.info.nih.gov/ij/>) and a growth curve was established for every specimen.

## 2. Results

- (1) The ultrastructure of rostra in *M. giganteus* shows that alternation of the dark and light lamellae seen in light microscope corresponds with ridges and depressions in SEM. The dark lamellae or the ridges are more etch resistant due to more dense structure comprised of smaller prisms in comparison to the light lamellae or the depressions;
- (2) The number of growth increments (the distance between two dark lamellae) is less in the dark regions of the rostra (ca 30) while in light regions is much higher (ca 110);
- (3) All seven rostra of *M. giganteus* in this study show the following content (in per cent to atomic weight): calcium (ca 35%), carbon (ca 15%) and oxygen (ca 50%) indicating a calcium carbonate composition (apparently in a calcite form);
- (4) The higher content of carbon (up-to ca 30%) is restricted to the interspaces between the calcium carbonate prisms dominantly near the outer surface of the

rostra. The dark and light lamellae show no differences in carbon content;

- (5) Between 500 and 700 lamellae were counted in specimens of 30 to 40 mm in diameter.
- (6) The growth measurements revealed up to six regions with higher growth rate that are delimited by regions with lower growth rate and more dense lamellae;
- (7) The growth increments are the largest in middle part (the third region) in all the rostra;
- (8) No correlation was found between the growth measurements of the seven rostra.

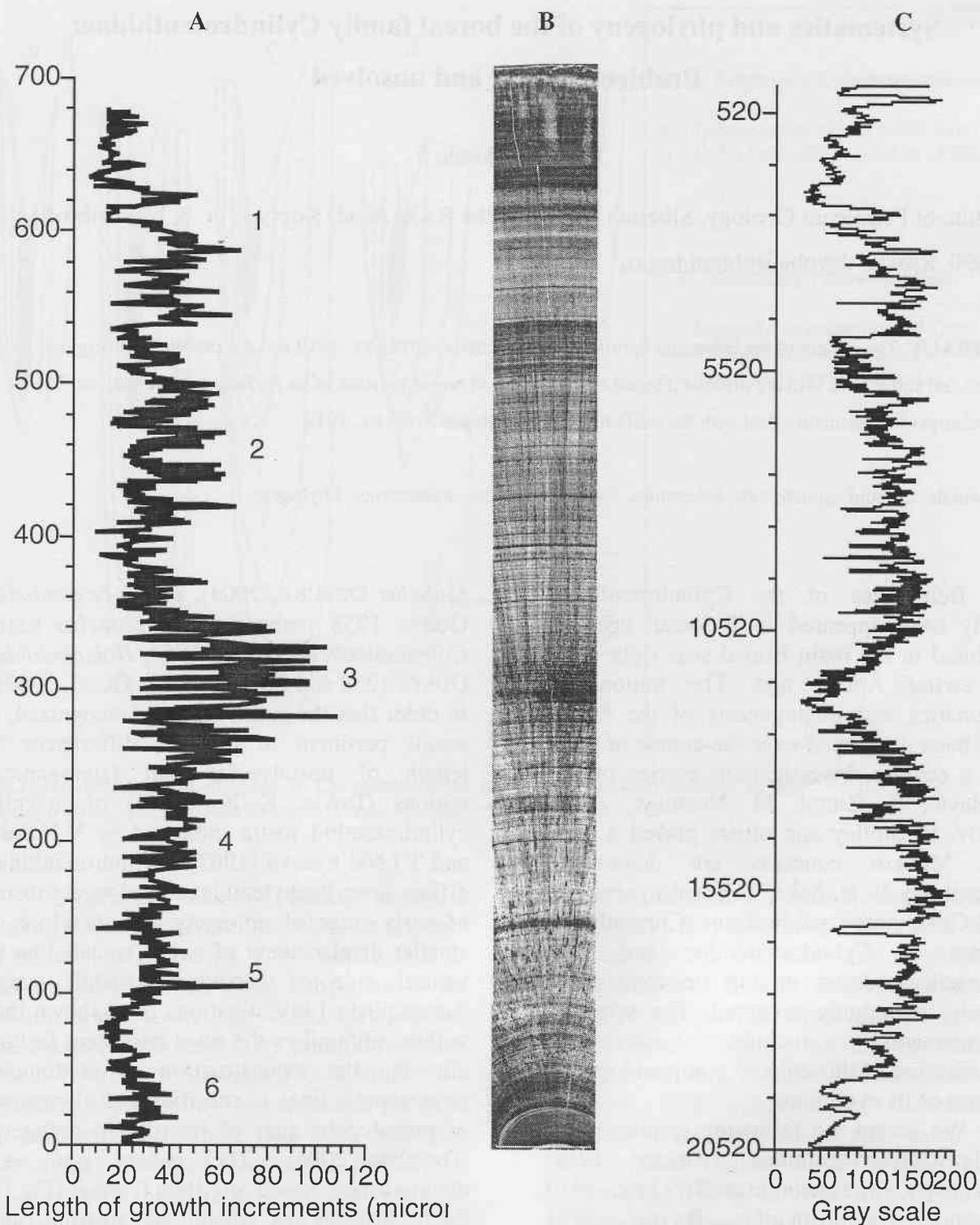
## 3. Interpretations

- (1) Rostra in *M. giganteus* were originally calcite rather than aragonite;
- (2) Higher content of carbon in the interspaces between the prisms of calcite, especially near the periphery of rostra seem to be traces of organic material originally contained in rostra;
- (3) The light regions of the rostra characterized by a larger number of lamellae and larger growth increments corresponds to periods of intensive shell growth while the dark regions with fewer lamellae and smaller growth increments corresponds to periods of slow growth of the shell;
- (4) During the time of rostrum secretion five to six periods of intensive growth alternated with the same number of slow growth periods;
- (5) In each intensive growth period ca 110 increments were added;
- (6) In periods of slow growth ca 30 increments were added.

Further analyses of these well-preserved *Megateuthis* shells (as Sr levels and O<sup>18</sup>/O<sup>16</sup> ratios) are planned to be carried out this year in order to bring more detail to their growth scheme.

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#### PLATE 1 - EXPLANATION:

- A. Diagram showing measurements of the length of each increment (the distance between two dark lamellae) in micromes. Numbers 1-6 are the regions with higher growth rate.
- B. Profile of a cross-section (the ventral part of the rostrum and through the protoconch) of a belemnite rostrum showing the growth lamellae and the increment measurements.
- C. Diagram representing the grey scale profile obtained with ImageJ program (0 is for black and 250 is for white).

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

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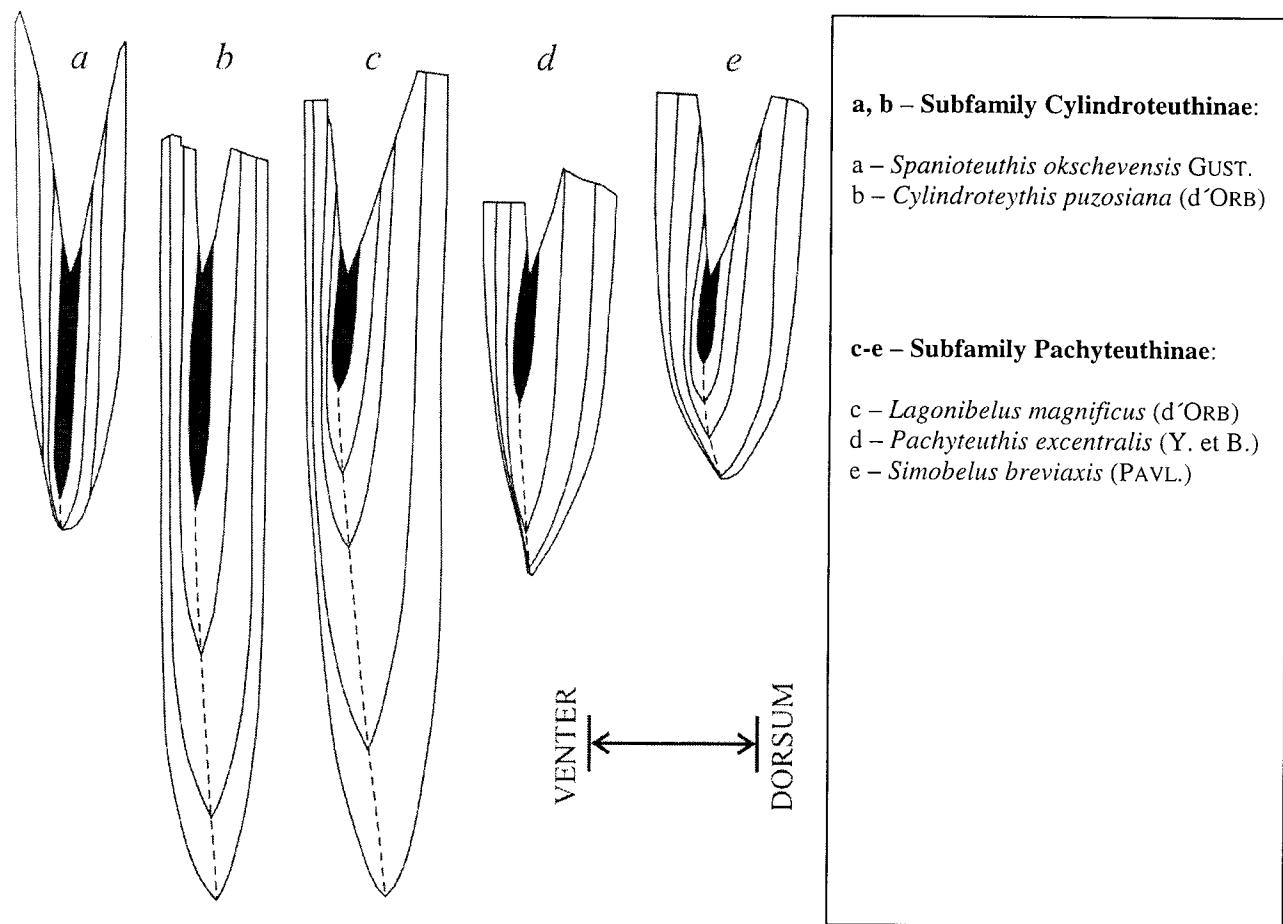
**ABSTRACT:** The system of the belemnite family Cylindroteuthidae STOLLEY, 1919 and the problems of origin of its generic and subgeneric taxa are discussed based on the results of recent revision of its Jurassic representatives. The main changes in systematics deal with the subfamily Pachyteuthinae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

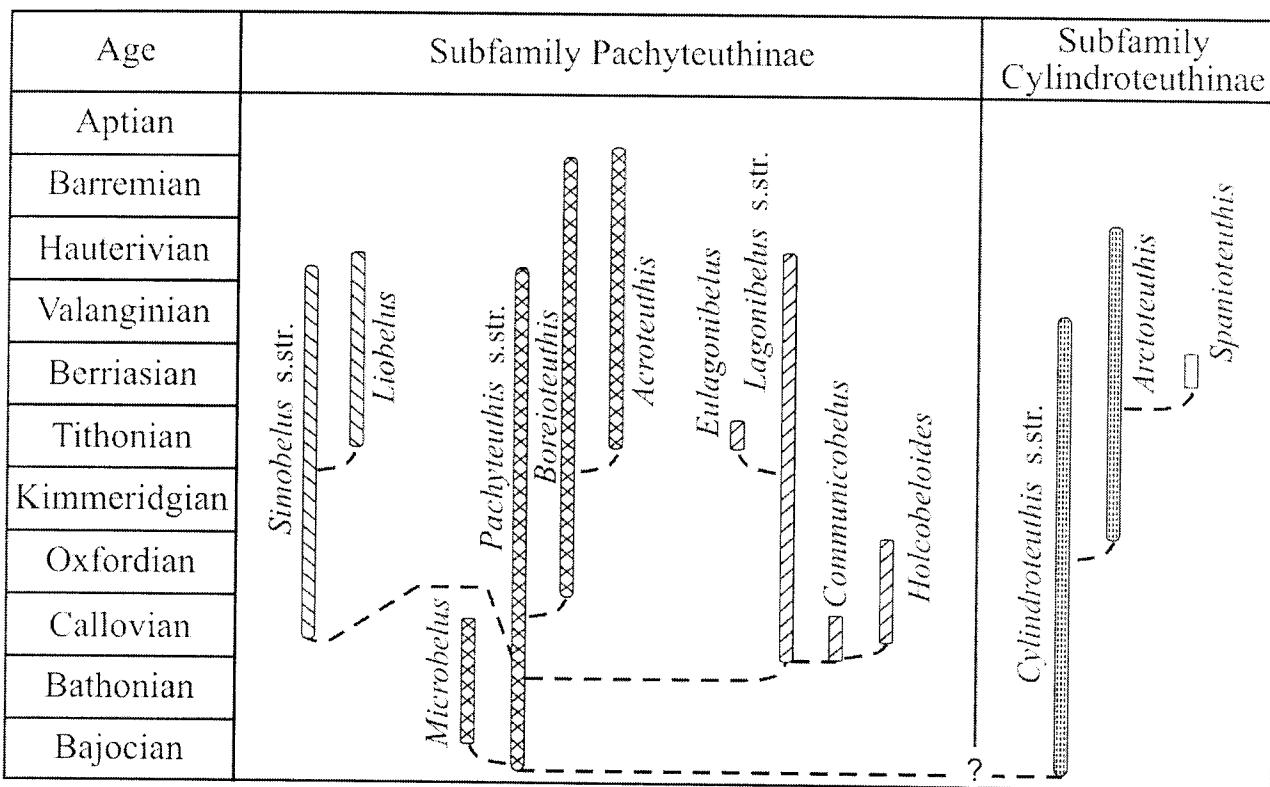
*Liobelus* DZYUBA, 2004), genus *Lagonibelus* GUST., 1958 (subgenera *Lagonibelus* s.str., *Communicobelus* GUST., 1964, *Holcobeloides* GUST., 1958 and *Eulagonibelus* GUST., 1989). In order that the subfamilies be recognized, it seems pertinent to use the differences in length of postalveolar part (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 Naln. 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*, *Boreoteuthis* 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 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.) prolateralis* (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* NAL.N.) 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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## About the phylogeny on the Coleoidea

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Reconstruction of the phylogeny of the Coleoidea based solely on recent forms is still difficult. To some extent, this is due to problematic out-group comparisons with *Nautilus* (Young & Vecchione 1996, Vecchione, Young *et al.* 2000). Thus, some significant character states within the Decabrachia as well as the Vampyropoda are ambiguous.

Because ancestral character states can be easily inferred from the fossil record neontologists should resort to fossil data. The aim of the present work was therefore to investigate the phylogenetical potential of preservable characters in order to polarise ancestral character states.

Within this context, a large number of fossil coleoids (more than 1000 specimens) from 25 collections were investigated in order to find phylogenetically significant characters. Comprehensive morphological analyses suggest that complexes of characters such as the embryonic shell, conotheca, rostrum, proostracum, gladius or arm crown are of notable phylogenetic significance. Combined, these fossil characters reveal a surprising coleoid phylogeny.

The presence of suckers is widely considered to be an autapomorphy of the Neocoelioidea (Doyle, Donovan *et al.* 1994; Young, Vecchione *et al.* 1998; Haas 2002, Haas 2003). However, Boletzky (2003) doubts a sister-group relationship between the Decabrachia and Vampyropoda. As shown by Donovan & Crane (1992), the supposed presence of muscular structures on the inner surface of arms within extinct belemnoids may perhaps indicate that possession of suckers is actually not an autapomorphy of neocoelioids. In addition, neontologists consider the loss of tabular nacre (*Nautilus*-

nacre, Type 1) within the Vampyropoda and Decabrachia as synapomorphic, but from the paleontological point of view, reduction of nacre must have occurred independently in these taxa. Hence, there is no reasonable apomorphic character that justifies the taxon Neocoelioidea.

Apart from this, it is widely accepted that the vampyropod gladius originated from a proostracum-bearing phragmocone of a belemnoid through demineralisation (Haas 2002, Bizikov 2004). The assumption that all Mesozoic gladii without any exceptions belong to vampyropod coleoids suggests a sister-group relationship between the Belemnoidea and the Vampyropoda. On the other hand we have no evidence for the existence of a proostracum in fossil Decabrachia (*Shimanskyia*, *Adygeya*). So-called proostraca in *Naefia* and *Groenlandibelus* can hardly be homologous with a belemnoid proostracum and are rather the result of allometric dorsal shell growth instead of a ventral opening of the living chamber. None of the Cenozoic spirulids and sepiids (*Spirulirostra*, *Beloptera*, *Ceratisepia*, *Belosepia*) possesses a proostracum. Recent *Spirula* definitely does not bear a proostracum. The chambered cuttlebone of *Sepia* is often called proostracum but this is a terminological mistake. Hence, both paleontological and neontological data suggest that the decabrachian body plan (*bauplan*) does not include a proostracum and there is no reason to regard the teuthid and sepiolid gladii as a derivation of a proostracum-bearing phragmocone.

For these reasons Vampyropoda and Belemnoidea seem to be sister taxa. Vampyropoda and Decabrachia represent a monophylum only if fossil taxa were

excluded. Therefore, the taxon "Neocoledoidea" is paraphyletic. Additionally, within the Belemnoidea the Aulacocerida were commonly considered to be the sister taxon of the Uncinifera. Because the hook-bearing Uncinifera is treated as the sister taxon of the Vampyropoda, the taxon "Belemnoidea" becomes also a paraphylum. The synapomorphies of the Vampyropoda and Uncinifera mainly include mineralised phragmocone characters, which become secondarily lost in the course of demineralisation within the Vampyropoda. But the opening of the living chamber and the development of a proostracum are sufficient to constitute a sister-group relationship between the Vampyropoda and Uncinifera.

Until now, unambiguous fossil representatives of recent Sepiolida or Teuthida are unknown in the fossil record. Therefore, information about ancestral character states within the Decabrachia cannot be obtained from the fossil record so far. Aside from phylogenetic aspects, the fossil record strongly implies that Decabrachia existed already in Carboniferous times (*Shimanskyia*) but played a minor role during Palaeozoic and Mesozoic times in comparison with the "Belemnoidea" and Vampyropoda. Only the mass extinctions in the context of the K/T-boundary enabled them to radiate remarkably and to develop their present diversity.

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# Fossil record and DNA-Sequences: a working hypothesis about the time of origin of Decabrachia and Vampyropoda

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The molecular clock hypothesis (Zuckerlandl and Pauling, 1965) is based on the neutrality theory of molecular evolution (Kimura 1968). This theory predicts that the rate of molecular evolution is approximately constant over time. Thus the molecular clock can be used for approximately timing past evolutionary events. Although justifications for the hypothesis of a molecular clock are not beyond any doubt, the use is widely applied. Because the published opinions about the age of Decabrachia and Vampyropoda are rather different from one another, we should like to combine both molecular and fossil data.

In the present work DNA-sequences coding for the nuclear 18S rRNA gene were used. The sequences are from the following Decabrachia: *Spirula spirula*, *Histioteuthis* sp., *Heteroteuthis* sp., *Loligo vulgaris*, *Illex coindetii*, *Sepia officinalis*, *Sepiella* sp., and from the octopod *Eledone cirrhosa* as a member of the Vampyropoda (Warnke et al. 2003). Additionally, *Nautilus scrobiculatus* (AF120504) sequences from the EMBL data bank were used as an outgroup representative. Sequences were aligned with Clustal W using MegAlign (DNASTar Lasergene; GATC, Konstanz) and checked by eye. Analysis was limited to reliably aligned regions, which included 1694 nucleotide positions. Using the computer program PAUP (Version 4.0b10 by D. L. Swofford 2002) uncorrected ("p") and corrected ("Tajma-Nei") distances were studied. A relative rate test was enforced to assess the relative rate of nucleotide substitution between two sequences, to determine whether one sequence is accumulating more substitutions than another. To calibrate the molecular clock for

estimating the divergence time between Decabrachia and Vampyropoda we used the splitting away of the Spirulida lineage from the Sepiida lineage.

The fossil indications for the sepiid – spirulid separation are the following: Doguzhaeva (1996, 1999) showed that the absence of tabular nacre (type I-nacre, *Nautilus*-nacre) in the conotheca of *Shimanskyia* (Late Carboniferous, Upper Pennsylvanian, USA), *Adygeya* (Early Cretaceous, Aptian, Russia), *Groenlandibelus* (Late Cretaceous, Maastrichtian, Greenland) as well as recent *Spirula* is a typical feature of the Spirulida. However, neither fossil sepiids such as *Ceratisepia* (Danian), *Belocephelia* (Eocene) nor recent *Sepia* possesses tabular nacre within their conotheca (Meyer 1993, Fuchs, this volume). Unambiguous information concerning teuthids, sepiolids or idiosepiids is missing for the Mesozoic fossil record (so-called "fossil teuthids" are considered to be vampyropods) and most probably this is not a preservational artefact. According to Haas (2003) teuthids, sepiolids or idiosepiids are Cenozoic offshoots of sepiids. It is therefore likely that *Shimanskyia* as well as *Adygeya* represent stem-lineage-representatives of the Decabrachia.

*Ceratisepia* without any doubt already is a sepiid (inclined septa, opening of the siphonal canal). If *Groenlandibelus* is really a spirulid, branching apart of the sepiid-spirulid-clade must have happened between the Albian (~100 mya) and the Campanian (~70 mya). Thus we are able to calibrate the molecular clock with a value between 70 and 100 mya. The results of the molecular clock calculations reveal an average time span of 364 mya to 520 mya for an origin of

## Decabrachia and Vampyropoda.

Earlier discussions on the origin of Decabrachia and Vampyropoda concentrated on the Triassic (~220 – 250 mya). However, recent findings on Palaeozoic coleoids (e.g. *Shimanskyia*, *Jeletzkyia*) indicate that these forms have occurred in the Late

Carboniferous (~300 mya) and therefore branching apart of the Decabrachia and the Vampyropoda should have been already completed at that time.

Our present calculations suggest even a much earlier origin. The plausibility of these results will be discussed on the poster.

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# Can the bathymetric distribution of cephalopods be studied with commercial fishing gears?

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**ABSTRACT:** The species composition and bathymetric distribution of cephalopods close to the island of Fuerteventura (Canary Islands, Central-eastern Atlantic) were investigated. For this purpose, a total of 27 trawls were carried out in March 2002, including two series of 4 tows in four discrete depth levels during day and night times, using a commercial fishing gear. Fishing depths ranged between 0-1000 m. A total of 27 cephalopods species were identified; the sample was dominated by Oegopsida, being Sepiida and Octopoda less numerous (2 and 3 species respectively). Cephalopods were mainly represented by their early life stages, post-larvae and juveniles; captured adults were of species reaching short maximal sizes (i. e. the genus *Spirula*, *Abraliopsis*, *Abrolia*, *Pterygioteuthis* and *Pyroteuthis*). The most important families, in number and frequency of occurrence, were Pyroteuthidae and Enoplateuthidae with relatively low diversity (3 and 2 species respectively). The two fishing series let us verify the vertical migration of several cephalopod species. Both, the number of species (13 and 20 respectively) and total number of specimens was larger for the night hauls. The last shows the considerable possibilities of the technique used.

**Key words:** Coleoid cephalopods, Canary Islands, depth distribution, diversity and methods.

## Introduction

Research on pelagic cephalopods off Canary Islands is scarce. Previous studies were carried out during the 60's and 70's on board the *Sond Cruise* and *R.R.S. Discovery* (Clarke, 1969; Clarke and Lu, 1974); and, short notes have been published on stranded or accidental catches of one specimen (Lozano, 1991).

This study was planned as a complement of the research program focused on the analysis and evaluation of the pelagic resources around the Canary Islands, a research financed by the Fisheries Department of the Canary Islands Government (Viceconsejería de Pesca del Gobierno de Canarias). Thus, the aim of this work was to determine and study the pelagic cephalopod species inhabiting around Canary Islands, with emphasis on those species found in the epipelagic, mesopelagic and the upper batipelagic layers.

## 1. Material and methods

Between 4 and 18 March 2002, in South-eastern waters off Fuerteventura (Central-eastern Atlantic), a fishing survey was carried out on-board the S/V "La BOCAINA". The objectives were both the acoustical evaluation of the epipelagic fishery resources (i. e. *Scomber japonicus*, *Trachurus picturatus*, *Sardinella aurita*) and the study of the species composition from the deep sea scattering layer (DSL). A total of 27 trawls were carried out between 0-1000 m, including two series of 4 tows in different discrete depth levels. Out of the 27 tows, 19 were epipelagic. A commercial gear with an internal net in the cod-end with mesh-size 10.4 mm was used. The status of the gear and its performance were continuously monitored by means of a Scanmar Net Sounder and physical parameters were measured with a CTD. In order to analyze the possibilities to

study the cephalopod vertical migration as function of changes in light conditions with the available infrastructure, the following sampling was designed: two series of 4 consecutive tows within the same geographical zone (from 28° 00' to 28° 05' N and from 14° 08' to 14° 12' W) in the depth levels 50, 200-225, 325-350 and 675-700 m during daylight and darkness (Table 1).

For interpretation purpose, the catch data were combined with the oceanographic, acoustic and meteorological data registered. All cephalopods, including free fragments, were considered. Dorsal mantle length (DML) was measured (in mm). The percentage in number and the frequency of occurrence were calculated for each species.

## 2. Results

### General results

The initial number of specimens estimated was 425. A total of 27 species were identified, belonging to 15 families and 3 orders. In general, all cephalopods were of small size, they were mainly represented by their early life stages, post-larvae and juveniles; also, adults of species reaching short maximal sizes (ca. 2-7 cm) were caught (i. e. of the genus *Spirula*, *Abraaliopsis*, *Abralia*, *Pterygioteuthis* and *Pyroteuthis*).

**Table 1.** Data of the two sequence trawls: FT= fishing time; sFT=fishing time of the stable period; FD=fishing depth; sFD=fishing depth of the stable period; T= temperature; sT= temperature of the stable period; S= speed.

Trawl	Date	Tour	FT/ sFT (min.)	FD / sFD (m)	T / sT (°C)	S (knots)
<i>Daylight sequence</i>						
15	15/03/02	10:55	35 / 30	30-98 / 30-58	-	4.05
16	15/03/02	12:52	38 / 30	185-211 / 200-211	15.4 (15.4-15.6)	3.75
17	15/03/02	15:06	39 / 30	311-378 / 311-338	13.2 (12.9-13.6)	3.73
18	15/03/02	16:50	55 / 40	470-695 / 677-695	9.07 (8.9-9.2)	2.74
<i>Darkness sequence</i>						
19	15/03/02	21:09	36 / 30	34-139 / 34-62	18.4 (18.3-18.6)	4.46
22	16/03/02	22:14	36 / 30	215-261 / 215-230	15.0 (14.9-15.3)	3.61
23	17/03/02	00:24	41 / 30	310-427 / 310-363	13.3 (12.8-13.6)	3.78
24	17/03/02	02:47	53 / 40	565-980 / 671-691	9.3 (9.2-9.4)	2.73

The most important families, in number and frequency of occurrence, were Pyroteuthidae and Enoploteuthidae (N = 36.24%, F = 77.77% and N = 27.29%, F = 85.19% respectively); although with a low species diversity (3 and 2 species respectively).

### 3. Depth distribution and migration

Due to the local weather conditions, the last 3 tows of the second sequence were carried out the next night. On the basis of the results obtained, the behaviour displayed by the cephalopods was diverse: there were species keeping the distribution pattern along the day cycle (e. g. *Belonella belone*) while others changed from a defined layer to be disperse in the water column (e. g. *Heteroteuthis dispar*).

However, in general, the consecutive fishing series showed the following:

- a) the concentration of the cephalopod species in deep waters during day-light. The number of specimens increased with depth, *from 3 in upper tow to 16 in the deeper tow* (Table 2).
- b) the migration of several species toward the upper layers, which inhabited deeper waters during the daylight; and the presence of other species at night in deeper waters.
- c) an increase of the number of specimens and species at night: during day-time, a total of 44 cephalopods were caught, while at night they were as many as 91 and the species number passed from 13 to 20, respectively.

The values showed keep the proportions between both sequences even when taking out the first tow (i. e. comparing only the second, third and fourth tows). Thus, the number of specimens passed from 41 to 78. These results show that the technique and methods used are useful for the study of the distribution and migration of these species.

The physical parameters did not show relevant structures with depth. The water column down to a depth of 900 m appeared to be as a homogeneous structure of layers within the studied zone. The largest differences were observed in the surface layers. The temperature and salinity decreased significantly between 60 - 200 (to 3.4° C and 0.7 ‰ respectively) after which further decreases were slight. We consider that such changes do not impose any significant barriers to the vertical migration, mainly for the muscular species.

#### 4. Discussion

The sample may not be a complete representation of the cephalopod fauna inhabiting the area, as an important bias is due to the catch method: large muscular cephalopods are able to avoid the net. The samples studied herein may be an intermediate representation between those obtained with RMT, IKMT or Bongo nets (Clarke and Lu, 1974, 1975), catches obtained with very large commercial nets (Rebik and Kukharev, 1998) and other gears, and samples from the stomach contents of large predators, as well (Hernández-García, 1995).

The species diversity ( $N= 27$ ) was close to that obtained at 30° N - 23° W ( $N= 29$ , Clarke and Lu, 1974) and smaller than the 40 species found in the geographical range at 18° N - 25° W (Clarke and Lu, 1975). However, should be stressed that species diversity gradually increases as latitude decreases and the sampling depth range from the referred studies was from surface to 2000 m, i. e. it

doubled the depth range in our study. The effort was considerably higher, 76 tows and a total of 160 hours. For a very close area, the southern end of Fuerteventura, was identified a total of 18 species (Clarke, 1969); the difference could be in part due to the mass effect of the island (see Sangrá, 1995).

In relation to the diel migration, the results cannot be compared in detail as different techniques and a shorter depth range was considered. However, some of the results obtained for some of the species are coincident with the ones observed by those authors. Moreover, a sampling bias may have occurred (particularly in the fourth tow) as some individuals may be caught during the time previous to the stabilization of the gear. However, it is necessary to keep in mind that there were no superposition of the fishing ranges in any of the series. In the same way, the depth error till the stabilization of the gear for the first three tows in each of the series was small (15-35 m) as well as the stabilization time (3-5 minutes). Therefore, we considered the catches mainly from the planned strata or depth layers. This shows the considerable potential of the technique used. Also, the observed diversity (ca. 4% of the species of the Class) showed the importance of this research as their ecological implications and its socioeconomic values, as a potential resource, are considered.

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#### \* DEDICATION

This work is dedicated to Enrique Hernández-García

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Table 2.

Table 2. Percentage in number of the cephalopods caught during the daylight and darkness sequences. N is the number of specimens caught in each depth level. Under "other species" are included the family Mastigoteuthidae, *Octopoteuthis sicula* and the specimens (pieces) no identified. (*P. gemmata* = *Pterygioteuthis gemmata*; *P. g. giardi* = *Pterygioteuthis g. giardi*; *H. dispar* = *Heteroteuthis dispar*; *V. infernalis* = *Vampyroteuthis infernalis*; *A. lichenstini* = *Ancistroteuthis lichensteinii*)

## Abundance trend of *Octopus vulgaris* CUVIER, 1797 and *Eledone cirrhosa* (LAMARCK, 1798) in the southern Tyrrhenian Sea (Central Mediterranean)

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**ABSTRACT:** In this paper, the temporal abundance trends of two cephalopod species, *Octopus vulgaris* CUVIER, 1797 and *Eledone cirrhosa* (LAMARCK, 1798) related to ten years of trawl survey are shown. The data were recorded during the GRUND (Evaluation of demersal resources in the Italian Sea) national project from 1994-2004 (Greco *et al.*, 1998, 2003).

**Key words:** Coleoid cephalopods, Octopoda, Mediterranean Sea, abundance trend and biomass index.

The common octopus *Octopus vulgaris* and the horned octopus *Eledone cirrhosa* are two of the most important commercial species in the Mediterranean Sea.

*O. vulgaris* is a typical inhabitant of littoral waters, existing up to the limit of the continental shelf (Mangold-Wirz, 1963), while *E. cirrhosa* displays a wide bathymetrical distribution, generally down the 700m bathymetric line (Belcari *et al.*, 2002). In the Mediterranean Sea, octopods catches from trawlers that operate on the continental shelf constitute an important fraction of the total landings of these ship (Relini and Orsi Relini, 1984; Tursi and D'Onghia, 1992; Belcari and Sartor, 1993; Giordano *et al.*, 1998). The study area was comprised between Suvero Cape (Calabria) and San Vito Cape (Sicily).

Ten annual bottom trawl surveys that were mainly aimed to obtaining estimates of abundance indices for ten target species were carried out in autumn from 1994 to 1998 and from 2000 to 2004. Selection of sampling stations was based on a depth-stratified sampling scheme, taking into account the

surface area of each stratum; five depth zone were considered: 10-50, 50-100, 100-200, 200-500 and 500-800m. Specimens were counted, weighed, measured (dorsal mantle length, DML) sexed and assigned to a maturity stage by macroscopic analysis of the gonads.

Catch data (number and weight of *O. vulgaris* and *E. cirrhosa* collected) were analysed by means of specifically developed software (Souplet, 1996), taking into account the surface of each haul and depth stratum, in order to obtain estimates of abundance indices expressed in terms of both number of specimens and kg per km<sup>2</sup>. The abundance estimations of the two species were calculated as a mean value per year of samplings, bathymetric stratum, shelf (10-200m) and slope (200-800m). The above estimates indicated that the abundance of *O. vulgaris* was negligible in waters deeper than 200m. For this reason further analysis for this species was confined to depth strata down to 200m. The results shown a decreasing trend of the overall annual abundance ( $r^2=0.506$ ;  $p<0.05$ ) of *O. vulgaris* (fig.1), while *E. cirrhosa* abundance presents more fluctuations.

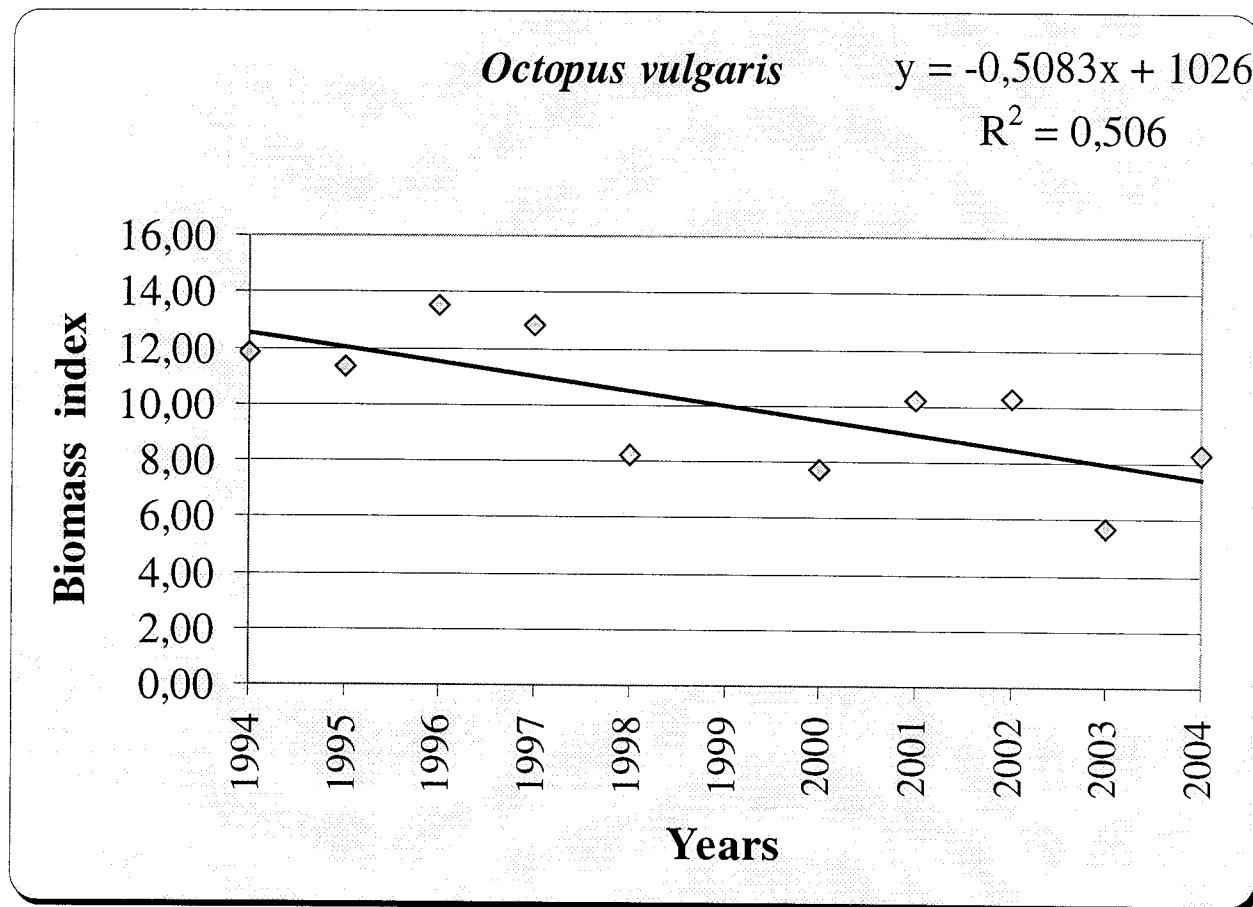


Fig. 1 - Temporal trend of the biomass index ( $\text{kg}/\text{km}^2$ ) in the overall strata (10-800 m) for *O. vulgaris*.

The biomass indices values of the overall annual abundance for *O. vulgaris* decreasing from  $13.55 \text{ kg}/\text{km}^2$  (Dev. St.= 1.13, CV=21.81%) in 1996 to  $5.63 \text{ kg}/\text{km}^2$  (Dev. St.= 0.80, CV=39.50%) in 2003. On a total of 682 samples, the length-frequency distribution of *O. vulgaris* during the ten years shown that the species present a range of dorsal mantle length that ranged from 25 to 200 mm with a peak of percentage (13.49%) at 80mm DML.

The density indices values of the stratum A for *Octopus vulgaris* shown an increment from 1994 ( $56 \text{ N}/\text{km}^2$ ; Dev. St. = 4; CV=36%) to 2004 ( $127 \text{ N}/\text{km}^2$ ; Dev. St. = 5; CV=35%).

The biomass indices values of the overall annual abundance for *E. cirrhosa* decreasing from  $6.35 \text{ kg}/\text{km}^2$  (Dev. St.= 0.88, CV=35.75%) during the 1995 to  $0.35 \text{ kg}/\text{km}^2$  (Dev. St.= 0.06, CV=43.86%) in the 1998 and from  $4.39 \text{ kg}/\text{km}^2$  (Dev. St.= 0.50,

CV=30.67%) in 2003 to  $0.87 \text{ kg}/\text{km}^2$  (Dev. St.= 0.09, CV=30.75%) in the 2004.

The density indices values of the shelf for *Eledone cirrhosa* shown an increment from 1994 ( $61 \text{ N}/\text{km}^2$ ; Dev. St. = 4; CV=22%) to 2003 ( $111 \text{ N}/\text{km}^2$ ; Dev. St. = 6; CV=21%). While in the 2004 year this index decreasing to a value of  $22 \text{ N}/\text{km}^2$  (Dev. St.= 2; CV=32%).

A total of 717 samples of *E. cirrhosa* were analysed. The size-distribution shown a range of dorsal mantle length that ranged from 20 to 130 mm of DML, with a peak of percentage (14.09 %) at 50 mm DML.

The present results confirm the discontinuous pattern in the catches presented by both octopods. Apart from environmental conditions that may markedly affect the stocks, annual fluctuations in abundance should be related to the peculiarities of species dynamics and to fishing strategies.

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## Phylogeny of *Praeactinocamax* NAIDIN (Belemnitellidae, Upper Cretaceous)

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**ABSTRACT:** The origin of *Praeactinocamax* NAIDIN, 1964 (i. e. Belemnitellidae PAVLOW, 1914) has not been exactly explained to date. Jeletzky (1946) derived their origin from the Aptian Belemnopseidae – probably from *Neohibolites ewaldi* (STROMBECK) or *N. clava* STOLLEY on the basis of a similar alveolar part structure. Doyle (1987, 1992) supposed that belemnitellids are derived from some northern (boreal) endemics. Naidin and Alekseev (1975) supposed the origin of the first belemnitellid species – *Praeactinocamax primus* (ARKHANGELSKY) – from *Neohibolites repentinus* NAIDIN et ALEKSEEV (early middle Cenomanian) with respect to the similar shape of the guard and the structure of the alveolar part. This opinion is incorrect – *P. primus* occurs in the same time interval and/or sooner than *N. repentinus*. Christensen (1997) admitted a **polyphyletic origin** of the family Belemnitellidae. *P. primus* and *N. repentinus* have probably a common ancestor in the *Neohibolites* group.

**Key words:** Coleoid cephalopods, belemnites, Belemnitellidae, *Praeactinocamax*, Upper Cretaceous, Phylogeny.

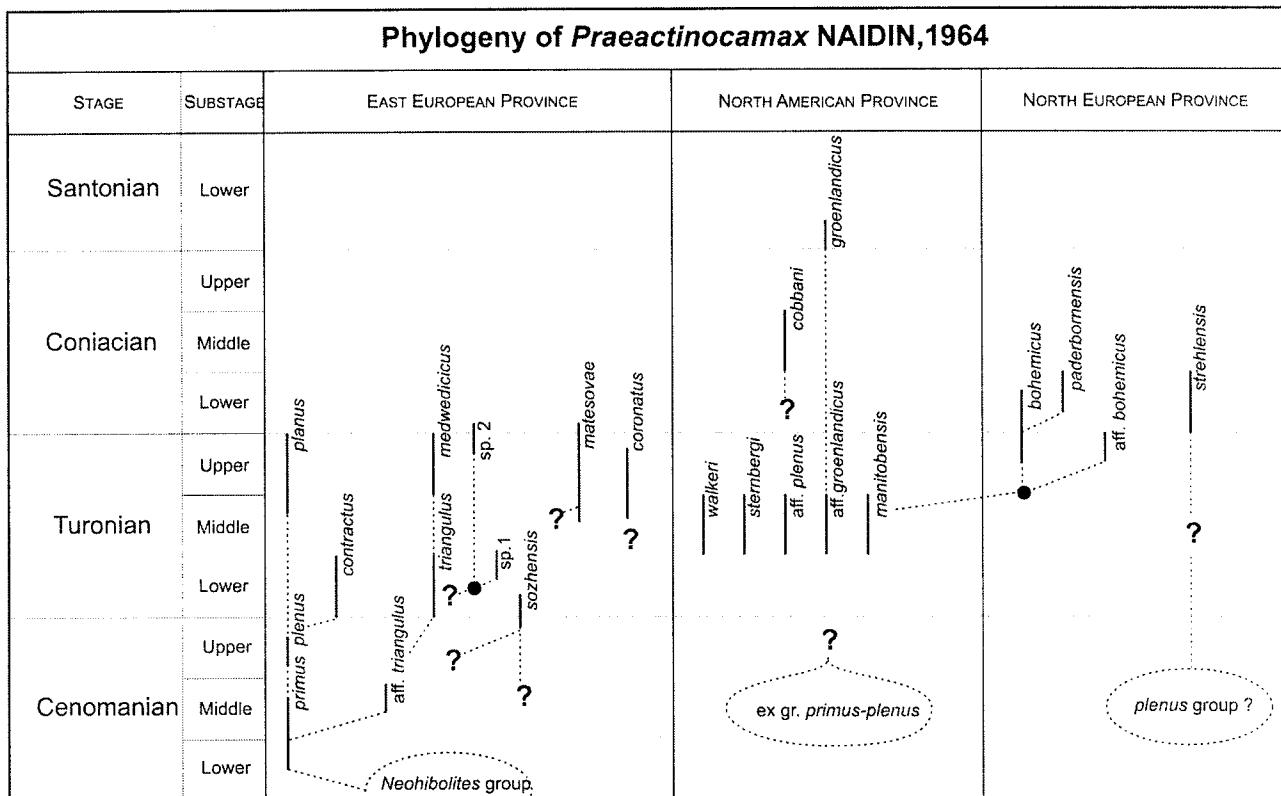
*Praeactinocamax primus* (ARKH.) is the earliest representative of Belemnitellidae PAVLOW, 1914. It occurs in the lower Cenomanian – at upper levels of the *Mantelliceras mantelli* Zone – and continues to lower parts of the *Mantelliceras dixoni* Zone in NW Europe.

*Praeactinocamax plenus* (BLAINVILLE) is considered to be a direct phylogenetic descendant of *P. primus*. Christensen (1974, 1990) perfectly analysed the differences between these two species and confirmed a direct evolutionary lineage.

The rare and endemic lower Turonian species of *Praeactinocamax contractus* NAIDIN is widespread in the Central Russian Subprovince (CRS). In spite of the opinion of Christensen (1974), I consider *Praeactinocamax contractus* an independent species especially with respect to its specific morphology: shorter and stout massive guards and poorly calcified alveolar fracture. *P. contractus* is considered to be a descendant of

the *primus/plenus* evolutionary lineage – derived and specialized species, respectively. This species is known from the Volga River region and eastern Belarussia (Košťák, 2004).

*Praeactinocamax triangulus* NAIDIN has recently been raised to rank of independent species (Košťák, 2004). This species is derived from *P. primus* and/or especially from *P. aff. triangulus* rather than from *P. plenus*, as suggested by the guard shape and partly by ontogeny (not so marked allometric growth as in *P. plenus*). The single complete specimen of *P. aff. triangulus* known has a similar triangular shallower pseudoalveolus. Hypothetical evolutionary lineage is going to *P. triangulus* and can be possibly defined as follows: A common ancestor of *P. primus* (middle Cenomanian) and *P. aff. triangulus* (middle Cenomanian) – ? – *P. triangulus* (lower Turonian). During this evolution, a gradual calcification of alveolar part continued, a deeper pseudoalveolus formed, and the guard size increased.



**Fig.1.** *Praeactinocamax* NAIDIN, 1964 species. Phylogenetic evolutionary lineages in the East- European, North- American and North- European Provinces (Modified after Košťák, 2004).

A similar calcification trend was described by Ernst (1964), and Christensen (1997) in *Gonioteuthis* BAYLE, 1879.

The origin of *Praeactinocamax sozhensis* (MAKHLIN, 1973) with poorly calcified alveolar fracture is not clear. This species probably represents a lineage parallel to *P. plenus* or convergence. Some morphological similarities like the shape and size of the guard could prove this opinion.

The late Turonian *Praeactinocamax planus* (MAKHLIN) has probably its origin also in the *primus/plenus* evolutionary lineage. The morphology of *P. plenus* and *P. planus* is conservative and did not change during the Turonian.

Middle Turonian species of North American Province (NAP) – *P. manitobensis* (WHITEAVES), *P. sternbergi* (JELETZKY), *P. walkeri* (JELETZKY), *P. aff. groenlandicus* and *P. aff. plenus* – are close to one another by having a similar alveolar fracture and partly also the shape of the guard. They are typical inhabitants of the NAP (including North America and Greenland). *Praeactinocamax* phylogeny is poorly recorded here. *Praeactinocamax cobbani* (CHRISTENSEN) is

known from the middle Coniacian and *P. groenlandicus* (BIRKELUND) from the lower Santonian. *P. groenlandicus* is the last representative of *Praeactinocamax*. Middle Turonian *Praeactinocamax* group in the NAP may be derived from *primus/plenus* ancestors, too. Their evolution passed independently in the North European Province (NEP) and in the East European Province (EEP). This group represents a typical parallel model of belemnitellid evolution (Plate 1).

Species of the NEP – *P. bohemicus* (STOLLEY), *P. aff. bohemicus* and *P. paderbornensis* (SCHLÜTER) – probably have their evolutionary roots in this group. *P. bohemicus*, *P. aff. bohemicus* (Košťák, 1996) and *P. paderbornensis* are extremely rare in Europe: they were described from the Upper Turonian through the lower Coniacian deposits of the Central European Subprovince (CES) and Baltoscandia. They may prove a connection between the NAP and NEP in the Turonian (Košťák et Wiese, 2002). On the other hand, the EEP was completely isolated from the NEP during the whole Turonian stage. Several “transitive forms” existed between *Praeactinocamax* and *Goniocamax*

NAIDIN, 1964 during the early through late Turonian: *P. matesovae* (NAIDIN), *P. coronatus* (MAKHLIN), and *P. sp. 1* (KOŠTÁK, 2004). I suppose their morphology to be the result of convergence with *Goniocamax*. Some representatives of *Praeactinocamax* resemble the first species of *Goniocamax*, especially by having a similar shape of the guard and by the depth of the pseudoalveolus. The origin of *P. matesovae*, *P. coronatus*, and *P. sp. 1* is not clear. *P. matesovae* shows marked similarities to *Goniocamax* but its very shallow and well calcified pseudoalveolus is typical for genus

*Praeactinocamax*. *P. coronatus* has a relatively deep (about 6 mm) pseudoalveolus (typical for *Goniocamax*), but its slender and subcylindrical to high conical guards somewhat resemble the middle Turonian species of *Praeactinocamax* from the North American Province (*P. manitobensis*) and the rare upper Turonian belemnites from the Central European Subprovince and Baltoscandia (*P. bohemicus*, *P. aff. bohemicus*). *P. matesovae*, *P. coronatus*, and *P. sp. 1* are very rare species of the Central Russian Subprovince. They show a high endemicity and diversity in this region.

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## PLATE 1 – EXPLANATION

A-J, M: *Praeactinamax* NAIDIN from the East European Province; K-L: *Praeactinamax* from the North European Province, N-P: *Praeactinamax* from the North American Province. Index 1 – alveolar ends (x1,5), I (x2,5). Index 2 – dorsal views: (A-D, F-G, J, M-O), ventral views (E, H, K-L, P) (x1,2).

A-J, M. - A. *Praeactinamax primus* (ARKHANGELSKY), Middle Cenomanian, Ukraine; B. *Praeactinamax plenus* (BLAINVILLE), Upper Cenomanian, Kazakhstan; C. *Praeactinamax sozhensis* (MAKHLIN), Uppermost Cenomanian, Russia; D. *Praeactinamax contractus* NAIDIN, Lower Turonian, Russia; E. *Praeactinamax* aff. *triangulus*, Middle Cenomanian, Russia; F. *Praeactinamax triangulus* NAIDIN, Lower Turonian, Russia; G. *Praeactinamax* sp. 1, Lower Turonian, Russia; H. *Praeactinamax* sp. 2, Turonian/Coniacian boundary, Turkmenistan; I. *Praeactinamax coronatus* (MAKHLIN), Upper Turonian, Russia; J. *Praeactinamax planus* (MAKHLIN), Upper Turonian, Russia; M. *Praeactinamax matesovae* (NAIDIN), Upper Turonian, Russia. (after Košťák, 2004).

K-L. K. *Praeactinamax bohemicus* (STOLLEY), Upper Turonian, Czech Republic; *Praeactinamax* aff. *bohemicus*, Upper Turonian, Czech Republic. (after Košťák, 1996).

N-P. N. *Praeactinamax cobbani* (CHRISTENSEN), Middle Coniacian, USA (reprint from Christensen, 1997); O. *Praeactinamax walkeri* (JELETZKY), Middle Turonian, USA (reprint from Jeletzky, 1961); P<sub>2</sub>. *Praeactinamax manitobensis* (WHITEAVES), Middle Turonian, USA (reprint from Jeletzky, 1961).



# Cenomanian – Coniacian (Upper Cretaceous) belemnitellid distribution and belemnite events in the East European Province

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**ABSTRACT:** Belemnite (belemnitellid) geographic distributions are established for the East European Province, a biogeographic unit established and characterized by endemic representatives of *Praeactinocamax*, subspecies of *Actinocamax* and by the first representatives of *Goniocamax*. Marked abundance of index belemnitellid species guards inside their range zones combined with their wide geographic distribution can be understood as belemnite events.

**Key word:** Coleoid cephalopods, belemnites, Upper Cretaceous, palaeobiogeography.

Belemnitellids show a cosmopolitan distribution in middle to late Cenomanian in the whole European Paleobiogeographic Region (= NEP *sensu* Christensen, 1976).

*Praeactinocamax primus* (ARKHANGELSKY, 1912) is the earliest representative of Belemnitellidae PAVLOW, 1914. *P. primus* is widespread from the northern Caspian Sea area in the east to Northern Ireland in the west. Geographic distribution of this species represents a belt 4000 km long and about 1000 km wide (Fig.1).

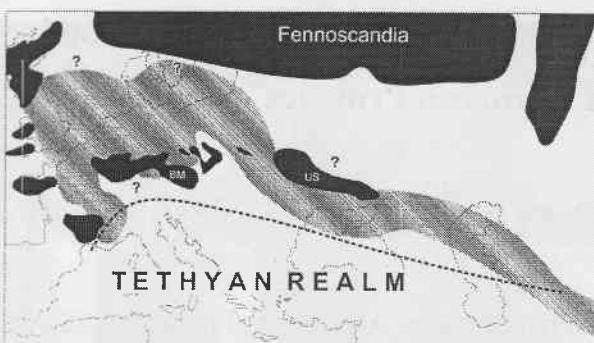
Geographic distribution of *P. plenus* (BLAINVILLE, 1825), which is considered to be a phylogenetic descendant of *P. primus*, extends more than 1000 km to the east (to the Afghanistan/Tadzhikistan border) and also to the south (Tethyan Realm), central European basins, Crimea and southern Turkestan (Fig.2).

The low belemnitellid diversity in the Cenomanian/Turonian boundary interval is presumably connected with a major eustatic Cenomanian/Turonian event. Only the highly endemic species *P. sozhensis* (MAKHLIN, 1973) survived this time interval in the area

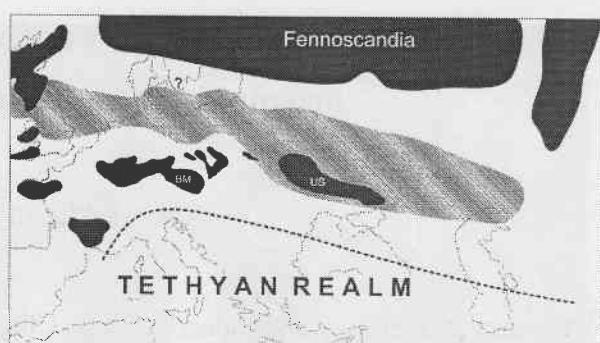
between the present Russia/Belorussia and the Russia/Kazakhstan borders (Fig.3).

The eastern part of the European Paleobiogeographic Region (East European Province, EEP) is considered an **independent province** (Košťák et Wiese 2002; Košťák et al. 2004; Košťák 2004) with respect to the occurrence of 100% endemic taxa in the latest Cenomanian through the earliest Coniacian. This province existed for about 5 million years. The Russian Central Subprovince is well distinguishable from the early Turonian to the earliest Coniacian. Communication with other areas is limited to the southeast (Transcaspian area), east (western Siberia, Yenisei River), and north (Russian Arctica – Taimyr Region, Norilsk District).

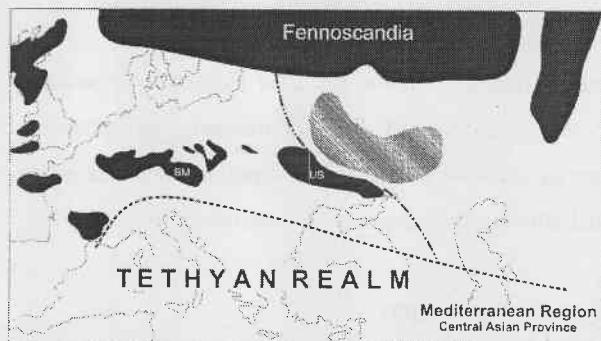
*Praeactinocamax triangulus* NAIDIN, 1964 and *P. contractus* NAIDIN, 1964 belong to taxa typical for the EEP in the early Turonian. Geographic distribution of *P. triangulus* extends from Belarussia in the west as far as to Uzbekistan and western Turkmenistan in the southeast (Figs 4-5).



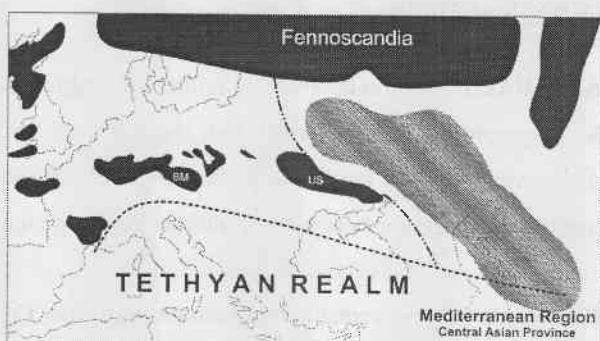
**Fig.1.** Palaeobiogeographic distribution of *P. primus*. Middle Cenomanian. BM – Bohemian Massif, US – Ukrainian Shield.



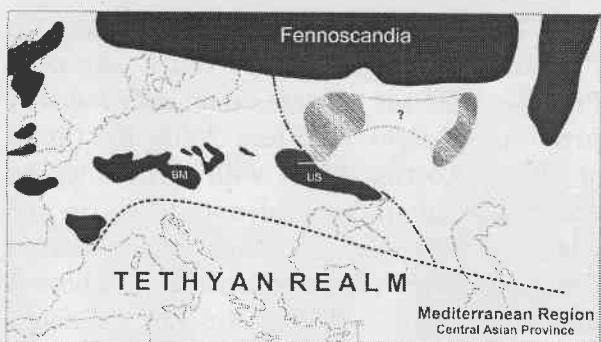
**Fig.2.** Palaeobiogeographic distribution of *P. plenus*. Late Cenomanian. BM – Bohemian Massif, US – Ukrainian Shield.



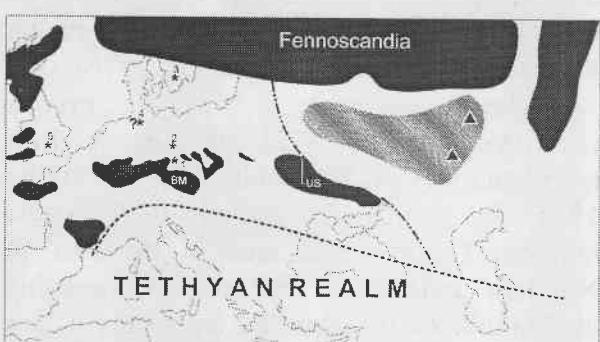
**Fig.3.** Palaeobiogeographic distribution of *P. sozhenensis*. Cenomanian/Turonian boundary interval. BM – Bohemian Massif, US – Ukrainian Shield.



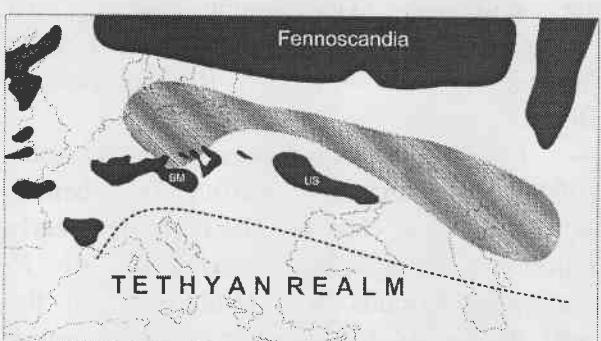
**Fig.4.** Palaeobiogeographic distribution of *P. triangulus*. Early Turonian. BM – Bohemian Massif, US – Ukrainian Shield.



**Fig.5.** Palaeobiogeographic distribution of *P. contractus*. Early Turonian. BM – Bohemian Massif, US – Ukrainian Shield.



**Fig.6.** Palaeobiogeographic distribution of *G. intermedius* (late middle to upper Turonian) and *G. christensenii* ( $\Delta$ ; upper Turonian – the base of the Coniacian). The upper Turonian distribution of *Praeactinocamax bohemicus* (\*) in Central and Northern Europe. BM – Bohemian Massif, US – Ukrainian Shield.



**Fig.7.** Palaeobiogeographic distribution of *G. lundgreni*. Early Coniacian. BM – Bohemian Massif, US – Ukrainian Shield. (Figs 1-7 after Košťák, 2004).

*Goniocamax intermedius* (ARKH., 1912) and *G. christensenii* (Košťák, in prep.) are the middle Turonian through the lowermost Coniacian EEP endemics of the CRS (Fig.6).

*Goniocamax lundgreni* (STOLLEY, 1916) is the typical Coniacian species. The easternmost occurrence of *G. lundgreni* was recorded from the Azovsk Sea area and probably from Mangyshlak Peninsula (Fig.7).

Free belemnite migration continued during the Santonian, Campanian and Maastrichtian – genera *Gonioteuthis*, *Belemnitella* and *Belemnella* are almost cosmopolitan in the whole North European Region.

### Belemnite events

Marked abundance and frequency of index belemnitellid species guards inside their range zones combined with their wide geographic distribution can be understood as belemnite events (Fig.8). High abundance of *P. primus* – the **primus event** was recorded north of the Caspian Sea (NW Kazakhstan) (lower part of the *Acanthoceras rhotomagense* Zone). This event approximately corresponds to those in NW Europe.

Stratigraphic range of *P. plenus* is very short and corresponds to the *Metoicoceras geslinianum* Zone in central and NW Europe and the *Inoceramus pictus boemicus* Zone on the Mangyshlak Peninsula (between the *Acanthoceras jukesbrownei* Zone and *Neocardioceras juddii* Zone) – see Marcinowski et al. (1996). This range and the wide geographic distribution have the character of a separate event – the **plenus event**.

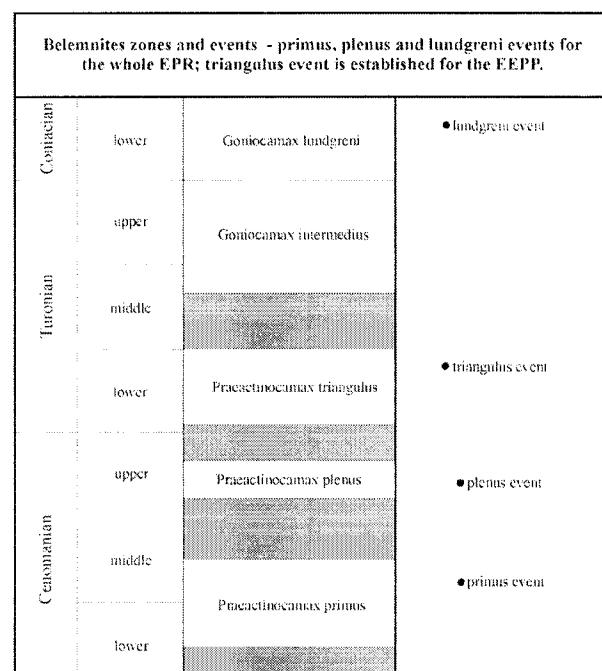


Fig.8. Belemnitellid biozones and events in the Eaest European Province. Cenomanian through the lower Coniacian interval. (modified after Košťák, 2004).

Maximum geographic distribution of *P. triangulus* (from Belarusia in the west to Uzbekistan and Turkmenistan in the southeast) and high abundance of guards were recorded in the late lower Turonian (*Mytiloides labiatus* Zone and *Mammites nodosoides* Zone) – the **triangulus event**.

Coniacian species of *G. lundgreni* rarely penetrated also to the central European basins (*Cremnoceramus crassus* Zone; Košťák, 1996; Košťák et al., 2004). The appearance of this species finished the existence of the independent EEP. The belemnite fauna became cosmopolitan again. The easternmost occurrence of *G. lundgreni* was recorded from the Azovsk Sea area (Naidin, 1964), and probably from the lower Coniacian of the Mangyshlak Peninsula (i. e. *Actinocamax cf. lundgreni*; Marcinowski and al., 1996). The **lundgreni event** could be established for the late lower Coniacian.

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## Non associative learning in the common octopus (*Octopus vulgaris*)

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**ABSTRACT:** Non associative learning is one of the basic manifestations of behavioral flexibility. In order to document this behavioral trait in *Octopus vulgaris* we test the animal's habituation to a repeatedly presented prey-like stimulus. During the 15 min experiment a plastic model of a lobster is presented every minute for 15s. Experiments are repeated 6h and 24h after the first presentation. The animals habituated to the stimulus during all experimental sessions. Habituation is faster in the experimental sessions repeated 6h and 24h after the initial trial. In order to understand the neural mechanism underlying this habituation, single cells activity is recorded at the level of the median superior frontal lobe (MSF) and the vertical lobe (VL). This electrophysiological approach enables discerning whether and which of the synaptic connections are involved in mediation of behavioral habituation.

**Key words:** Coleoid cephalopods, *Octopus vulgaris*, behaviour.

The acquisition of knowledge about the environment and its changes is probably one of the principal tasks each organism has to face. There have been numerous studies on learning and other cognitive abilities, in the genus *Octopus* (Boal 1996, Fiorito 1992, for reviews see: Hanlon & Messenger 1996, Nixon & Young 2003, Wells 1978). Nevertheless, studies on non-associative learning are scarce, including Wells & Wells (1957), Angermeier & Dassler (1992), and Mather & Anderson (1999). Wells & Wells (1956) concentrated on the tactile habituation of blinded *Octopus vulgaris* to repeatedly presented objects. Angermeier & Dassler (1992) demonstrated inhibitory learning in *Eleodone cirrhosa* and the transfer of a learned inhibition to a natural feeding situation. Mather & Anderson (1999) documented habituation in *Octopus dofleinii* and also investigated the relation to the influence of habituation on exploratory behavior and object play. In addition to those studies Byrne et al. (2004) gave a first description of habituation to a prey-like stimulus presented outside the tank. Given the importance of the vertical lobe (VL) and

median superior frontal lobe (MSF) for learning and memory in *Octopus vulgaris* (Nixon & Young 2003, Wells 1978) we investigate these areas brain activity during a non associative learning test. This is done using the method for *in vivo* extra cellular recording developed by Zullo (2004) and Zullo & Hochner (in prep).

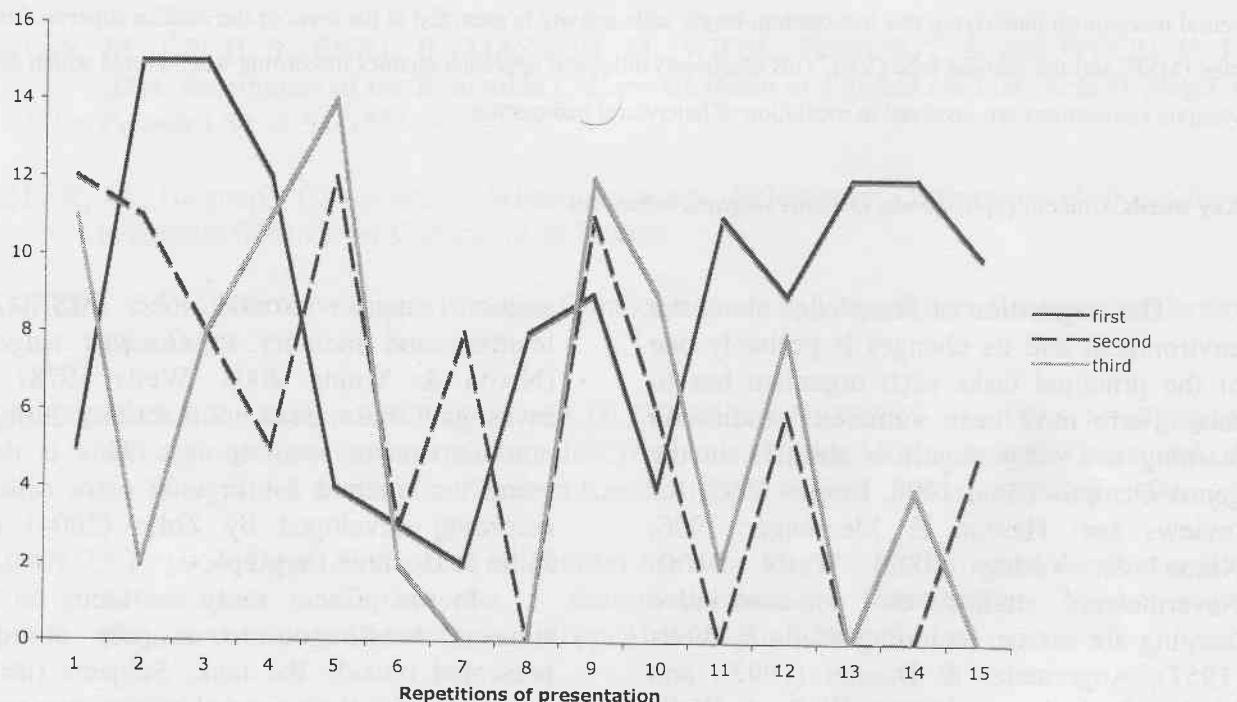
In the present study we focus on the subjects habituation to a prey stimulus presented outside the tank. Subjects (n=10) are chosen for their general responsiveness to stimuli outside their home tanks (see Boycott 1954 for a description of this behavior of *O. vulgaris* in captivity). Once the animal reacts to human presence in the room by approaching the front glass of its home tank it is transferred to a different room where the experimental tank is situated. The animals are given a 24h period to adjust to the new environment and are then tested. Each animal is tested three times for 15min. During this 15min period a plastic lobster is presented outside the tank for 15s at the beginning of every minute. These 15min testing-periods are repeated twice, 6h and 24h after the initial presentation.

In Figure 1, the performance of animal 2 is shown. The three experimental sessions are different in terms of qualitative changes as the number of visual attacks on the target decreases significantly (Kendall's W,  $p=0.004$ ,  $N=15$ ,  $\chi^2 = 10.889$ ). The total time spent at the front glass trying to get hold of the prey item also significantly decreases from the first to the second and third experimental session (Chi-square,  $p=0.001$ ,  $\chi^2 = 14.144$ ,  $df=2$ ).

The results of these experiments show that *O. vulgaris* does habituate to a visual stimulus. The single unites recording during habituation will test whether the habituation process involves depression of the response to

the prey stimulus at either the MSF, the VL or both levels. Further experiments are conducted in order to pin point the sites involved in this behavioral habituation. The possibility of combining a simple learning paradigm with *in vivo* recording will enable us to get a better insight into the neuronal bases of behavioral processes.

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**Fig.1.** Exemplary graphs of animal number 2 during the three experimental sessions. The x axis shows the number of repeated presentation per session, while the y axis shows the total amount of time the animal spent on the front glass trying to catch the prey item.

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## Rare evidences of shark predation in Upper Cretaceous belemnites

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### Introduction:

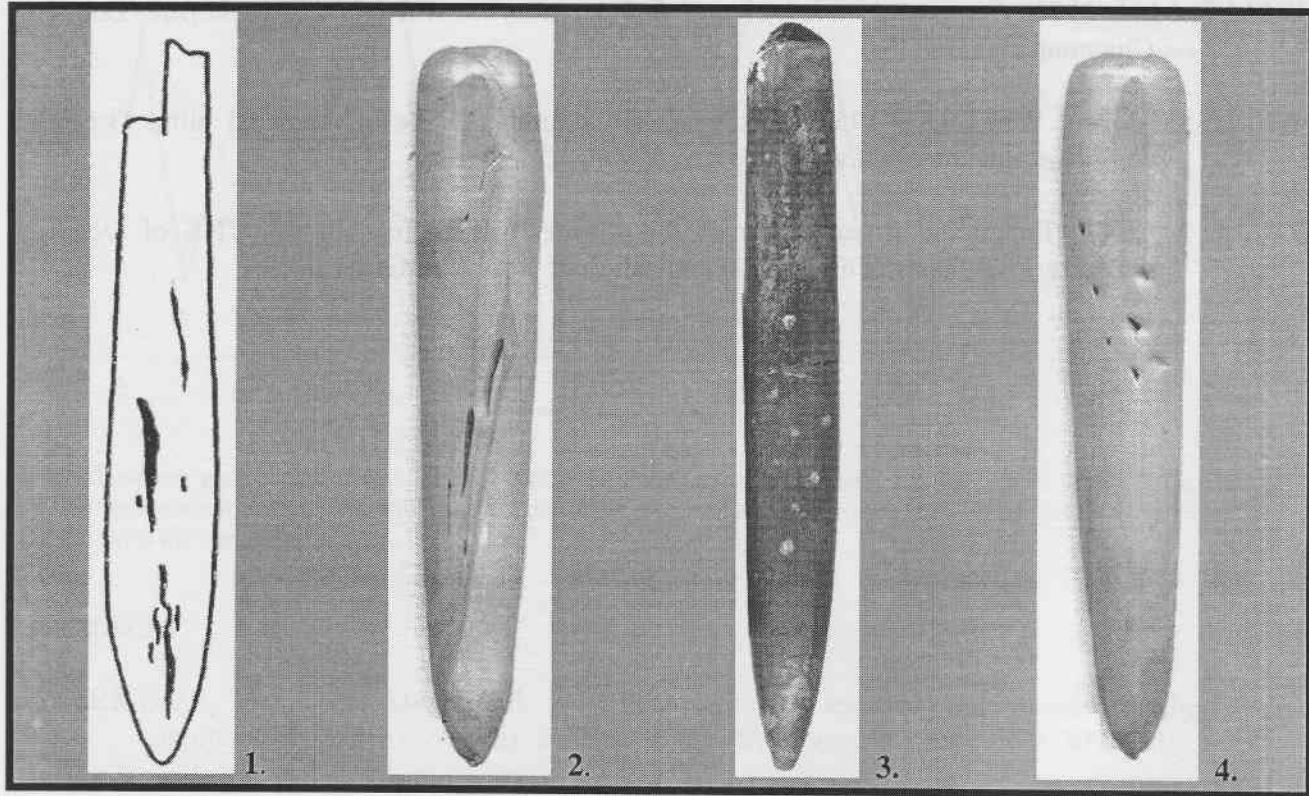
The Upper Cretaceous belemnite family Belemnitellidae Pavlow, 1914 is exclusively distributed in the Northern Hemisphere. Calcitic belemnite rostra are known from various near shore facies. Belemnites were also a prey of several predators – i. e. larger fishes, sharks and marine reptiles. Some imprints (grazes and furrows) on the rostra surface could have been caused by a predator attack.

Naidin (1969) showed also grazes and furrows on the rostra surface. Although their

origin seems to be unknown, some of them could prove the predator attacks (fishes, sharks, marine reptiles). These imprints were classified by Naidin (1969) into four groups:

1. smaller circular to oval imprints.
2. large irregular imprints.
3. longitudinal furrows (Figs - 1, 2)
4. double-faced grazes (Figs - 3, 4)

The last two mentioned groups may have originated during a shark attack.



Figs 1-4. 1,2. longitudinal furrows (from Naidin, 1969), 3,4. double-faced grazes. Figs. 2,4. Experimental bites on plasticine guards.

The belemnite rostrum model has been moulded from plasticine and an experimental bite was re-enacted by a complete shark jaw. The imprints on the surface are shown in Figs 3-4.

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## Stable isotope signatures of Cretaceous belemnites: The approach of a palaeobiologist

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### Introduction:

Belemnite guards are currently being used in two fields of geosciences:

- a) taxonomy, evolution and biostratigraphy are aspects considered by palaeontologists.
- b) stable isotope studies are performed by geochemists. Only few studies cover aspects of both fields.

For more than 50 years the calcareous guards of belemnites have been used to gain  $\delta^{18}\text{O}$ - and  $\delta^{13}\text{C}$  data of the Cretaceous. Fluctuations of the  $\delta^{18}\text{O}$  data indicate variations of the ice volume and palaeotemperature, those of the  $\delta^{13}\text{C}$  value are explained by changes in the bioproduction of the oceans. The observed data have been used to postulate seasonal or secular temperature or productivity variations of the sea water. All of these studies have serious setbacks, in so far as they neglect biological aspects. One of the problems is that taxonomically heterogeneous groups have been used. Data derived from different species or even genera have been lumped together, ignoring possible species dependant fractionation of the stable isotope signature. A second drawback is the neglection of ontogenetic and ecological aspects of belemnites.

We have analysed trace elements and stable isotopes of belemnites from the mid Jurassic of Germany and the early Cretaceous

of Germany and NE England in order to check ontogenetic and taxonomic variations of both parameters. The investigations of mid Jurassic megateuthids indicate no significant variation of the  $\delta^{18}\text{O}$ -values during ontogeny, indicating no changes in the habitat throughout life.

Observations on Cretaceous belemnites show, that a biofractionation of the stable isotopes and trace elements occurs on a generic level. Various belemnite genera from the Valanginian – Barremian show different  $\delta^{18}\text{O}$ - and  $\delta^{13}\text{C}$ -signatures. The  $\delta^{18}\text{O}$ -values of the endemic *Hibolites*, are higher („cooler“) than those of the genus *Acroteuthis*. These differences may indicate either secular changes of the isotope signature or different modes of life for both genera. The latter implies a rather shallow water habitat for the relatively thick *Acroteuthis* and a deeper habitat for the slender *Hibolites*.

Consequently stable isotope curves should be solely based on one taxon only, if possible. Long ranging taxa should be preferred over short living species, several species from one genus over several species of several genera. Ecological factors (way of life, habitat, migration) have to be considered.

## The cephalopod embryo: Testing 3D visualization methods

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Even in the era of modern genetics it is necessary to observe the anatomy and development of an organism for a better understanding of its function in the ecological context. Since cephalopods represent important nutritional resources and research objects in applied sciences, such as fisheries and aquaculture, it is necessary to provide exact data of their development. It is important that such data can be quantified for statistical analyses of growth and other developmental parameters. This presentation aims to test the use of 3D reconstruction methods in the developmental analysis of *Octopus vulgaris* and *Loligo vulgaris* embryos. Thirteen days old *Octopus vulgaris* embryos (approximately stage XIII of Naef) and eighteen days old *Loligo vulgaris* embryos (approximately stage XIX of Naef) were harvested, sectioned, and digitized according to the EFIC protocol (Weninger

and Mohun 2002), using a Voxelsize of 1,09 x 1,09 x 2. JVision and EMVIS were used for 3D visualizations of several stages of these cephalopod embryos.

The histological preparation of the early embryonic stages was more complicated than the preparation of later stages, due to the large external yolk sac and the inpenetrable chorion. Various treatments were applied to avoid poor fixation and embedding artifacts.

The resulting images were of high quality and sufficiently complete for 3D reconstruction of external and internal embryonic structures. It was shown that modern imaging procedures, such as the EFIC protocol, can be used for the analysis and quantification of embryonic shape and internal organ primordia such as the nervous system and the circulatory system of cephalopodembryos.

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WENINGER, W. J., MOHUN, T. 2002. "Phenotyping transgenic embryos: a rapid 3-D screening method based on episcopic fluorescence image capturing." *Nature genetics*, 30: 59-65.

## Oxygen isotopes of *Sepia officinalis* – implications for fossil cephalopod studies

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Studies of stable isotope ratios ( $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$ ) on belemnites have been widely used in palaeoenvironmental reconstructions.  $\delta^{18}\text{O}$  is used as a proxy for paleotemperatures and changes in polar ice volumes,  $\delta^{13}\text{C}$  as an indicator for the overall marine bioproductivity and metabolic activity of the studied specimens. But these studies encounter some problems. First of all, diagenetic influence has a strong impact on isotope ratios and is able to cause a serious shift in the results of paleoclimatological reconstructions. Secondly, these studies neglect possible biofractionation and ecological and ontogenetic factors. On one hand metabolic functions might favor one isotope over another during intra-cell precipitation of  $\text{CaCO}_3$  on the other hand changes in the mode of living and associated changes of the environment might influence the results.

Specimens of wild and aquarium-reared *Sepia officinalis* have been used for studies concerning these factors. Interpretation of the data is easy, because diagenetic effects can be neglected and the ecology of these organisms is very well known.

Results show no discernible biofractionation or ontogenetic influence on the oxygen isotope ratios, the isotopic composition is in equilibrium with the seawater and reflects the actual temperature conditions. On the other hand, migrational patterns and seasonal changes are clearly visible and affect the results strongly.

The carbon isotope signature shows no direct correlation to the oxygen signature and proofs difficult to be explained.

# New data on Middle Jurassic - Lower Cretaceous Belemnotheutidae of Russia. Their habit and possible mode of life

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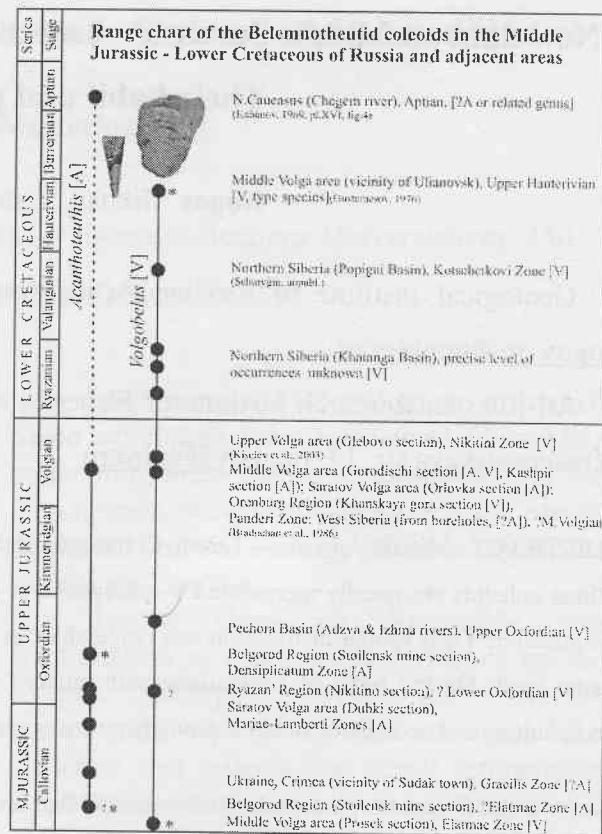
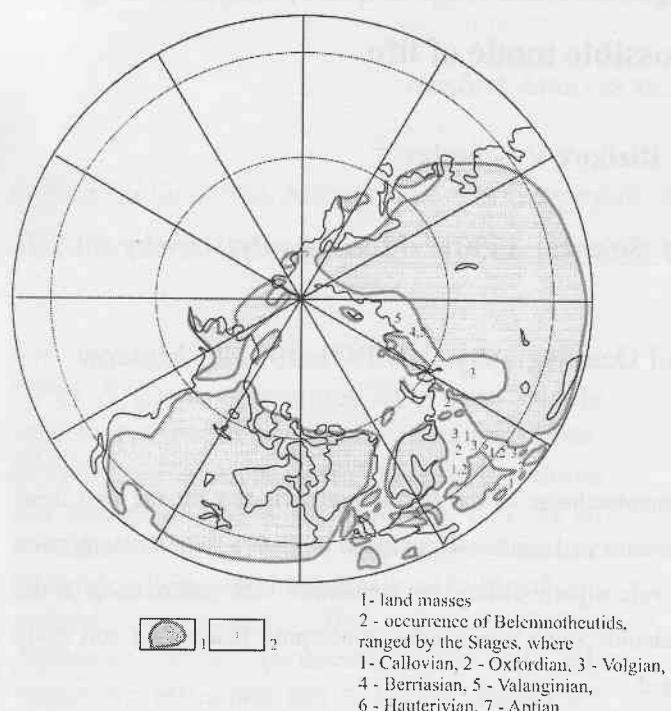
**ABSTRACT:** Middle Jurassic – Lower Cretaceous Belemnoteuthidae of the Russia are reviewed for the first time. These coleoids are usually represented by phragmocone remains and cautiously assigned to genera *Acanthoteuthis* and *Volgobelus*. Their spatial distribution and range chart as a rule slightly differs, but sometimes both genera occur at the same level. On the basis of comparison with modern coleoids some conclusions concerning features of soft body morphology and ecology of Belemnoteuthidae were suggested.

**Key words:** Coleoid cephalopods, Belemnoteuthidae, Jurassic – Cretaceous, Russia, Palaeoecology.

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 and usually lost 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 latter were generally ignored during field works by collectors who often misinterpreted them as isolated belemnoid phragmocones. 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 (Donovan & Crane, 1992; Doyle & Shakides, 2004). However, the

information on distribution and fauna of Belemnotheutidae in Russia is still fragmentary and is actually restricted by several brief mentions (Gustomesov, 1976; Kiselev et al., 2003, among others). 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.

As the conotheca is often lost in belemnotheutid phragmocones the main problem in their study is to distinguish them from isolated belemnitid phragmocones. Recently, Doyle and Shakides (2004) showed that the apical angle in belemnotheutids is somewhat less 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 recorded from the same level.



\*Localities where belemnite guards are entirely absent marked by asterisks.

**Fig.1.** Distribution of the Middle Jurassic – Lower Cretaceous Belemnoteuthidae of Russia and adjacent areas in space and time.

The material collected by the authors as well as obtained from publications show that Belemnotheutidae are widely spread in the Callovian – Lower Cretaceous sediments of Russia and former USSR (Fig.). The fossils in authors' collection can be distinctly classified into three groups. The first group consisted of small (1-5 cm length; 2-3 cm width) crushed isolated phragmocones with characteristic low v-shaped ridges in the apical part on the dorsal side. These fossils were tentatively identified as *Acanthoteuthis* sp. The second group consisted of 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*. One specimen represented almost entire shell (only apical part was missing). It was 34 cm length; 10 cm width, and consisted of crushed phragmocone (18 cm length), tongue-shaped proostracum (16 cm length) and remains of the ink sac. This fossil combine some features of the 1<sup>st</sup> and 2<sup>nd</sup> groups and was tentatively

identified as ? *Acanthoteuthis* sp. Geographic and stratigraphic distribution of *Acanthoteuthis* and *Volgobelus* in Russia is different. Within the studied area only in the Middle Vologian they occur together.

Comparison with living coleoids provides opportunity to reconstruct some features of soft body morphology and ecology of Belemnotheutidae. Dorsal v-shaped ridges in the apical part of conotheca – one of the most distinctive features of *Acanthoteuthis* – 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 the shell of *Acanthoteuthis* indicates that in this form the fins apparently attached to dorso-lateral surface in apical part of conotheca. The bases of fins were separated, possibly merging apically. The fins were terminal, probably broad-oval or rhomboidal. Their length could slightly exceed the length of the ridges: 3/5ths of the length of the

phragmocone (Donovan & Crane, 1992). Considerable width and flat profile of proostracum in *Acanthoteuthis* indicates that it was not covered by the mantle muscles from the dorsal side. Most probably, the mantle attached to lateral edges (hyperbolar zones) of proostracum, as in recent *Vampyroteuthis*. Thickening of hyperbolar zones found in *Acanthoteuthis* as well as in other belemnite proostraca provide another prove for this hypothesis. Tongue-like proostracum of belemnoids, including *Acanthoteuthis*, lacks broadened vanes (lateral plates) that usually present in the gladii of recent squids providing place for the funnel retractors attachment (Bizikov, 1996; Bizikov & Arkhipkin, 1997). Absence of similar structures in belemnoid proostraca indicates that funnel retractors in Belemnitida attached either to the inner surface of thickened hyperbolar zones (like in recent Sepiidae) or to the inner side of the mantle wall, like in recent squids (Ommastrephidae and Chiroteuthidae). In the latter case there must be some strong funnel locking-apparatus of complex structure, or fusion of the funnel corners with the mantle. The presence of the

ink sac in *Acanthoteuthis* indicates that this species inhabited upper layers of Mesozoic seas, apparently above 200 m. The arm length in *Acanthoteuthis* comprises about 40% of the total length (Donovan & Crane, 1992). 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 *Acanthoteuthis* signifies that living position of this animal was vertical head-down, like in recent *Spirula* and some planktonic squids, for example, *Mastigoteuthis*.

Taking into account all above-mentioned considerations it is possible to draw some conclusions on possible way of life of Belemnoteutidae. Apparently, these were middle- to large-sized planktonic forms inhabiting epipelagic (possibly upper mesopelagic) horizons over shelf and slope of continental seas in Mesozoic era.

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# Meso- and neohibolitid belemnites from the Albian (lower Cretaceous) of NE Mexico

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The belemnite bearing locality Sierra de La Silla is situated in northeastern Mexico in the northern part of Nuevo León between Monterrey in the north and Montemorelos in the south. The Sierra is a narrow anticline separated from the eastern frontrange of the Sierra Madre Oriental in the west by a wide valley of some ten km. The steeply inclined flanks of the range generally consist of Lower Cretaceous carbonates with a narrow stripe of Jurassic clastics in the center of the Sierra and Upper Cretaceous carbonates in its outer slopes. Some twenty km south of Monterrey the village of El Alamo is situated with an abandoned quarry nearby. In this section on the western flank of the Sierra, the following regional lithostratigraphic units are exposed: the upper part of the Tamaulipas Superior Formation (KiTS, Aptian to Middle Albian), the Cuesta del Cura Fm. (KiCC, Middle Albian to Cenomanian), the Agua Nueva Fm. (KiAN, Cenomanian/Turonian), and a greater part of the San Felipe Fm. (KiSF, Turonian to lowermost Coniacian).

The top of the KiTS is characterized by thick-bedded dolomitic limestones, the beds being separated from each other by stylolithic joints. The base of the overlying KiCC consists of a bundle of several erosion surfaces followed by flaser-bedded and undulated light and dark grey limestone. It is sparitic in the lower part of the formation where erosion and omission surfaces / hardgrounds dominate, and micritic and darker in the upper part where flaser-bedding and undulation are less developed. Light grey

chert occurs in nodules or stratiform bands of *Thalassinoides* shape.

The KiTS is assumed to be deposited in an open and deeper sea, whereas the KiCC was accumulated in a shallow water environment at this location. In contradiction to the opinion of some authors to represent entirely deep-water conditions, the KiCC shows here special depositional environments in accordance with its paleogeographic position. Thus, a coincidence with inundated Jurassic land masses is obvious, the structures of which are strongly basement controlled. Biostratigraphic assignment of the upper KiTS is made by the occurrence of *Neohibolites* ex gr. *minimus* and undeterminable mesohibolitids giving a basal Mid-Albian age. The lower part of the KiCC is biostratigraphically fixed by belemnites, too, among which several species and subspecies of the genus *Neohibolites* are diagnostic for Middle and Upper Albian, and which are often accumulated in condensation, and arranged by currents. The same age is given by ammonites of the genera *Mortoniceras*, *Worthoceras*, *Anisoceras*, and *Mariella*. Other faunal content comprises brachiopods (*Sellithyris*, *Rectithyris*, and *Terebratulina* s.l.), echinoids (*Holaster*, and *Hemiaester*), inoceramids, and microocrinoids of *Roveacrinus* affinity.

The Mid-Albian part of the KiCC is characterized by *Neohibolites* ex gr. *minimus* (MILLER), occurring in different formtypes, together with *N. minimus clavaformis* SEIBERTZ et BUITRON, here represented by larger and thicker rostra than at its type

locality Tepexi de Rodríguez in the State of Puebla (Seibertz and Buitron, 1987). In the basal beds of the KiCC two forms are cooccurring with several specimens strongly resembling the Upper Albian *N. praeultimus* SPAETH, and the Lower Cenomanian *N. ultimus* (D'ORBIGNY) respectively, both being looked upon as new subspecies of *N. minimus* showing an iterative radiation. Besides these neohibolitids two species of *Mesohibolites* are cooccurring, *M. semicanaliculatus* (BLAINV.) (Seibertz and Spaeth, 2002, 2005), and *M.*

*spicatus* (SWINNERTON). Originally described by Swinnerton (1936-55) under reservation as *Neohibolites*, the Mexican specimens confirm the doubts and lead to a generic change (Seibertz and Spaeth, in prep.).

The lower Upper Albian part of the KiCC is characterized by *Neohibolites oxycaudatus* SPAETH together with the last occurrences of the *N. minimus* group. The higher Upper Albian part of the KiCC can be determined by the real *N. praeultimus* SPAETH.

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## New morphological and functional data on the fork in the cuttlebone of *Sepia officinalis*

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The fork (fig.1) of the sepiid cuttlebone has been investigated several times during the last century by many authors (Appellöf 1983, Naef 1922, Spiess 1972, Bandel & Boletzky 1979, Dauphin 1981, Haas 2003) and it seemed that the main issues seem to be well established. However, ultrastructural details remain unclear such as:

1. How does the fork expand within the cuttlebone and how does its structure change?

2. Which connections exist between the fork and the chamberwalls and is there a border layer between the two structures ?
3. How does the fork develop from the embryonic stage up to the adult animal?
4. What is the fork's possible function in the organism?



**Fig.1.** Scheme of the fork in the cuttlebone of *Sepia officinalis*.

The investigated embryonic, postembryonic, juvenil and adult cuttlebones of *Sepia officinalis* were collected in the Mediterranean Sea and were kindly provided by Sigurd v. Boletzky, Banyuls-sur-mer (France). Some cuttlebones were crossfractured near the fork and analysed with SEM. Serial cross- and longitudinal sections through a freeze-dried and in resin embedded animal were used to detect the relationship of muscle and mantle tissue on the fork. Serial sections through a resin-embedded cuttlebone were used for observation with a light microscope.

REM analyses clearly demonstrate that both chamber septa and fork septa are composed of lamello-fibrillar nacre (type II nacre, *Spirula* nacre). Phylogenetic considerations suggest the homology of the fork with the ventral part of the phracmocone, this appears in the structural comparison with the forklayers and the chamberseptum.

Especially the anterior part of each fork septum appears to continue into the chamber septa. Serial cross sections support this assumption. Additionally, a distinct semi-prismatic layer and a thin organic layer covering the ventral side of the fork were not mentioned in previous investigations.

Although a one-chamber stage was not available, observations on a five to six chamber stage show, that the fork is already present during embryogenesis. The fork septa can clearly be recognized at this stage. In the longitudinal view, it looks as if the forksepta were moving on the wall of the first chamber during embryogenesis.

Viewing a dissected adult animal, the fork does not appear as an attachment site for the mantle musculature. Some of the observations made were previously unknown, others contradict previous investigations. Detailed illustrations as well as interpretations of these findings will be given in a poster.

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## Divergence time estimates for major cephalopod groups: Evidence from multiple genes

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This is the first study to use both molecular and fossil data to date the divergence of taxa within the coleoid cephalopods (octopus, squid, cuttlefish). A dataset including sequences from three nuclear and three mitochondrial genes (3415 bp in total) was used to investigate the evolutionary divergences within the group. Divergence time analyses were performed using the Thorne/Kishino method of analysis which allows multiple constraints from the fossil record and permits rates of molecular evolution to vary on different branches of a

phylogenetic tree. The data support a Paleozoic origin of the Orders Octopoda and Vampyromorpha, the majority of the extant higher level decapodiform taxa. These estimated divergence times are considerably older than paleontological estimates.

The major lineages within the Order Octopoda were estimated to have diverged in the Mesozoic, with a radiation of many taxa around the Cretaceous/Cenozoic boundary. Higher level decapodiform phylogenetic relationships appear to have been obscured due to an ancient diversification of this group.

## Observation of *Idiosepius pygmaeus* (Cephalopoda, Idiosepiidae) at Klong Bangrong, Phuket Island, Thailand

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**ABSTRACT:** This report reveals impressions and observations about sampling *Idiosepius pygmaeus* in a selected mangrove area. *Idiosepius pygmaeus* is shown to inhabit the whole tidal range of a small tributary of the Bangrong River Phuket Island, Thailand. Males are predominantly located in the upper and lower reaches of the tributary. Females are observed in the lower part and at the mouth of the tributary, sometimes together with males. Bank vegetation has a greater influence on the presence of specimens, than current speed or sudden weather changes.

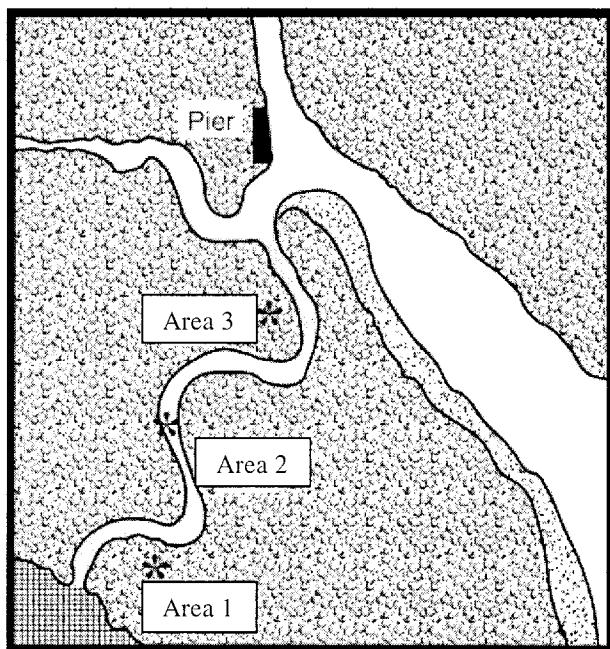
**Keywords:** Behaviour; Cephalopoda; habitat; Idiosepiidae; *Idiosepius pygmaeus*; Phuket Island; Thailand.

Several studies have been published on the geographical distribution (Hylleberg and Nateewathana, 1991), seasonal abundance (Jackson, 1992; Jackson, 1993), behaviour and postures in captivity (Moynihan, 1983) of *Idiosepius pygmaeus*. Less is known about the behaviour of Idiosepiidae in its natural habitat. The following report will describe under which conditions *Idiosepius pygmaeus* may be found and to describe our impressions and observations during sampling of *Idiosepius pygmaeus* in a selected habitat (Bangrong River, Phuket Island, Thailand). The collection site was restricted to a smaller tributary of Bangrong River (Fig. 1) because of the depth and current speed in the main stream (Kristensen et al., 2000; Holmer et al., 2001).

The tributary is about 0.8 km long, has a mean width of 15 m and a depth of about 3 m. The tributary is lined on both sides by mangroves, mainly *Rhizophora* and *Avicennia*.

From April to May 2004, 9 females (mean mantle length 12.5 mm) and 46 males (mean mantle length 11.28 mm) of *Idiosepius pygmaeus* were caught in the small tributary of the Bangrong River (8° 02.945'N; 98° 25.030'E). The animals were trapped with dipnets downstream during falling tide and flood tide. Work on foot during high tide was impossible because of the water depth. At high tide animals were also caught occasional by boat, but the dense mangrove made his strategy difficult and ineffective.

A recognizing of these pygmy squids in its natural habitat is difficult, although their unchangeable eye colour (blue-green with a white ring) simplify their localization. Moreover, during swimming *Idiosepius pygmaeus* produced a clear big bow wave on the surface which provided possibility for interception.



**Fig.1.** Klong Bangrong with study areas. Scale bar: 500 m.



Males were differently distributed in the tributary (Fig. 1). In the upper part (Area 1), 19 males of *Idiosepius pygmaeus* were caught. Fewer males (totally 6) were captured in the middle part (Area 2), while in the lower part (Area 3) and at the mouth of the tributary many specimens (totally 21) were found. Females were only observed in the lower part (totally 4) and at the mouth of the tributary (totally 5), sometimes mating with males. It is clear why males were only present in low numbers in the middle part of the tributary. Unsuitable food (shrimps and mysids) or different bank vegetation can be excluded as cause because all three sections of the tributary had obviously the same ecological conditions. Males and females retain the same pattern of distribution throughout the complete tidal cycle.

The animals were mainly caught near the mangrove belt (distance 10 cm to 1m) in zones, characterised by bank vegetation. No specimens were collected at riverbanks with *Avicennia* sp. roots and sand banks. This type of habitat provides poor hiding-places. Most specimens were caught between looping aerial roots of *Rhizophora* sp. and under overhangs (distance to water surface 10-20cm).

The current speed had no influence on the distribution of *Idiosepius pygmaeus*.

Animals were caught both in strong currents (up to 10 km/h) and in almost stagnant areas. During cloudy or rainy periods and/or “cooler” outdoor temperatures (28-30° C) the animals presumably retreated to deeper water and were no longer visible in the muddy brown water (visibility: 10-20 cm). Short cloudy or rainy periods (up to 30 minutes) and sudden changes in weather had less influence on the catch. At higher temperatures (30-35°C), specimens were located near the surface and could easily be netted.

*Idiosepius pygmaeus* adapted their camouflage to prevailing light conditions. In bright sunlight they took on a light brown to ochre colour. In dark areas their colour changed to black. Only their eye colour did not change (see above). During changes from clear to shady areas and back, the animals adapted to prevailing light conditions within seconds.

Our study showed that the distribution of *Idiosepius pygmaeus* is restricted to a small tributary of Bangrong River. Further investigations are planned to find out whether females spawn in mangroves and whether this habitat serves as a nursery area for juvenile stages or hatchlings.

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## The « Fossil Dibranchiate Cephalopods » by Adolf Naef – a commentary

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*The recent publication of an English Edition\* of Naef's (1922) „Die fossilen Tintenfische“ offers an opportunity to recall the general background of this work.*

Adolf Naef (1883-1949) was a zoologist who specialized in comparative anatomy and embryology of molluscs, in particular cephalopods (before he moved on to vertebrate zoology; see Boletzky, 1999). He became most widely known as the author of a very large monograph of cephalopods (Naef, 1921-1928) published in the series "Fauna and Flora of the Bay of Naples". His book on fossil coleoids appeared as a companion volume to this monograph, as emphasized by the many quotations and reproduction of illustrations. While the Naples monograph has become a bible to cephalopod taxonomists and developmental morphologists (who rarely cite the book on fossil coleoids), "Fossil Dibranchiate Cephalopods" is a true classic for cephalopod paleontologists. However, as much as in cephalopod neontology a reading problem existed with the Naples monograph before it was translated into English, Naef's paleozoological prose was also difficult to understand for paleontologists not familiar with the German language. This difficulty no longer exists, and given the larger format of the English Edition, Naef's original figures are now more easily decipherable than in the original book. Additionally, a list of synonyms was supplemented by Theo Engeser.

We could conclude by simply emphasizing that Naef's texts and figures can now be understood by any (English speaking)

neontologist or paleontologist interested in cephalopods – in other words, no longer is there any excuse for ignoring Naef's work as "unintelligible".

A better conclusion may be recalling Naef's morphological approach, highlighted as "systematic morphology": «Systematic morphology is the rational synthesis of comparative anatomy, paleomorphology, embryology and natural systematics» (Naef, 1917). In particular, let us consider the following reminder: «In the history of Biology (Zoology) we find two forms of systematic morphology, namely an idealistic one, and a historical one (phylogenetics)» (Naef, 1919), and let us keep in mind what Naef said on the precedence of the former: «Idealistic morphology (by creating the "natural system" of organisms) not only was prerequisite – in the history of science – to the introduction of phylogenetics, but for logical reasons it has – even today – precedence over phylogenetics (because we cannot investigate directly, without such prerequisites, into things that are no longer in existence)» (Naef, 1919).

That Naef definitely aimed at robust hypotheses on phylogenetics is sometimes obscured by statements such as: «...authors like Naef... virtually returned to the principles of idealistic morphology» (Mayr, 1982). Fortunately recent literature offers more instructive ways of viewing Naef's

approach: «Naef represents a systematic morphology of the structuralist sort; he therefore proposes a structuralistic definition of homology, as do the transformed cladists. With the transformed cladists he also shares the view that the theory of derivation has to

be deduced from morphology rather than the other way round» (Reif, 1998). Certainly we are not wasting our time when considering Naef's work in earnest.

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# The mysterious origin of the belemnites: New records from the Hettangian of Belgium and Luxembourg

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**ABSTRACT:** The order Belemnitida, suborder Belemnitina appeared in Europe not earlier than the basal Lower Hettangian. These ancestral forms, present in the Hettangian of Southern Germany, Northern Ireland and Belgium are so rare that every single specimen may bring new light on the dawn of the first true belemnites. New field research by the authors in the Lower and Middle Hettangian of Belgium and Luxembourg yielded some isolated rostra assignable to *Schwegleria* RIEGRAF and aff. *Subhastites* GUSTOMESOV. This new material shows an extraordinary elevated heterogeneity of morphological features.

**Key words:** Coleoid cephalopods, belemnites. Lower Jurassic, Belgium and Luxembourg, Phylogeny.

## The origin of belemnites: some clues, little evidence

The origin of belemnites remains still uncertain. Following Riegraf (1996), belemnites s.str. appeared in the Lower Jurassic. According to this author, they may descend from Triassic Aulacoceratida STOLLEY or Phragmoteuthidida JELETZKY, or a yet unknown ancestor. These Hettangian belemnites have been figured by Tate (1869), Schwegler (1939), Delsate and al. (2002) and Weis & Delsate (2005). Stratigraphically anterior findings have been reported amongst others by Flower (1945), Flower & Mackenzie (1959), Johnson and Richardson (1968). In a short review, Doyle and al. (1984) however support the opinion that these specimens represent either other coleoid groups or are of doubtful provenience, with exception of the Sinobelemnitiidae described by Zhu & Bian (1984) from the Triassic of Sichuan, China: "Certainly, these are the only serious contenders in the search for pre-Jurassic belemnites" (p.8). These Chinese records however need further research in order to confirm their phylogenetic position.

Another coleoid cephalopod from the Permian of Greenland, *Permitethis groenlandica* ROSENKRANTZ has been classified by Riegraf (1995) amongst the Belemnoteuthidida ZITTEL and consequently excluded from the Belemnitida sensu Riegraf. There is still some discussion on the position of the family Belemnotheutididae ZITTEL: Doyle and al. (1984) suggest a suborder Belemnotheutidina STOLLEY inside the order Belemnitida. In contrast to this opinion, Riegraf (1995) proposes to maintain the Belemnoteuthidida as an outstanding order distinct from the Belemnitida s.str.

Currently, the only evidence about the first occurrence of belemnites appears to be the presence of the suborder Belemnitina STOLLEY, with the genus *Schwegleria* RIEGRAF in the Hettangian *Liasicus*-zone of Southern Germany and Belgium (Weis & Delsate, 2005).

## The first true belemnites in the European Lower Jurassic - a short synopsis

In Europe, the order Belemnitida, represented by the suborder Belemnitina is first known in the Hettangian with the genus

*Schwegleria*. Aside from some doubtful mentions in literature, the first to figure a true belemnite from the Hettangian of Ireland was Tate (1869): “*Belemnites praematurus*” from the Hettangian *Angulata*-Zone of Northern Ireland. There was, however, little attention drawn to this isolated record and for many years, the unofficial title of “the oldest belemnite” was generally attributed to *Nannobelus acutus* (MILLER) from the Lower Sinemurian. This picture changed with the work of Schwegler (1939) who described three new species from the Hettangian *Liasicus*-Zone of Steinenberg bei Nürtingen (SW-Germany). Riegraf (1980) created the genus *Schwegleria* for these dwarf ancestral forms. Later on, Riegraf (1996) described cephalopod arm hooks, *Paraglycerites* EISENACK, from the *Planorbis*-Zone of Tübingen-Bebenhausen (SW-Germany) which he linked with the *Schwegleria* rostra.



Fig.1. “*Belemnites praematurus*” TATE, 1869 (original figure). Scale 1cm.

#### New records of belemnites in the Hettangian of Belgium and Luxembourg

During the last 10 years, the micropalaeontological research in marly Hettangian sediments of SE-Belgium resulted in the discovery of some isolated belemnite rostra and fragments. The site of Fontenoille, *Liasicus*-Zone, yielded 3 determinable rostra of *Schwegleria* belonging to *S. feifeli* (SCHWEGLER, 1939) and *S. psilonoti* (SCHWEGLER, 1939), 1 fragment of ?*Schwegleria* sp. and a belemnite phragmocone (Delsate et al., 2002). Further research in the *Planorbis*-Zone of Vance yielded a stem-fragment which diverges considerably from the conical *Schwegleria* shape and approaches the hastate genus *Subhastites* GUSTOMESOV from the Pliensbachian (Weis & Delsate, 2005). Additionally to these findings demonstrating

the presence of early belemnites in the Belgian Hettangian, Delsate & Thuy (2005) mention fragmentary coleoid arm hooks from the *Planorbis*-Zone of Bourglinster, Luxembourg. All specimens are stored at the palaeontological department of the Natural History Museum Luxembourg.

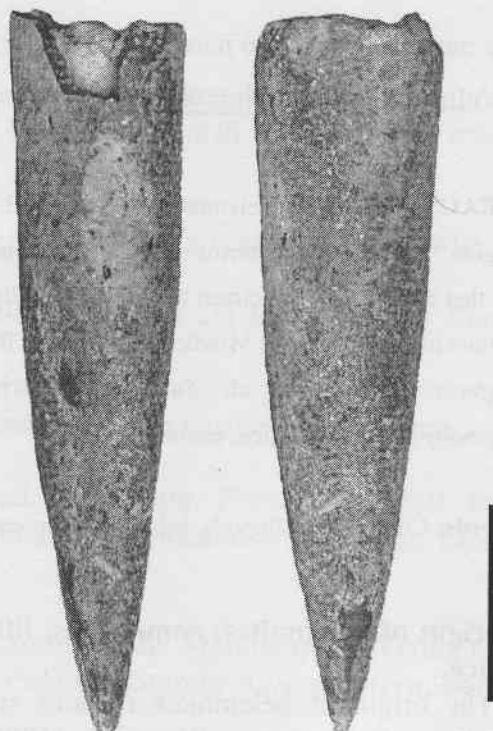


Fig.2 *Nannobelus acutus* (MILLER, 1826), from the Lower Sinemurian of Aspert, Luxembourg. Scale 1cm.

These new fossil records from Belgium and Luxembourg confirm:

- the presence of true belemnites in marly sediments of middle Hettangian age (*Liasicus*-Zone): 2 of the 3 species present in SW-Germany have until now been identified in Belgium
- the presence of coleoid arm hooks as soon as the *Planorbis*-Zone, probably assignable to belemnites
- the rarity of these early belemnitids (5 rostra and 1 phragmocone found in 10 years)

Further, they brought in some new elements:

- The heterogeneity of these ancestral forms is remarkably elevated: beside forms with a ventral groove (*Schwegleria feifeli*), dorsolaterals (*S. psilonoti*) and both ventral and

dorsolateral (*S. praecox*) there already existed forms with a subhastate shape (?*S. praematura*, ?*Schwegleria* sp., aff. *Subhastites* sp.)

## Discussion

The records of *Schwegleria* in the last 10 years in Belgium have been isolated and mostly fragmentary. The 5 located rostra belong to 4 different species. Thus each single new specimen may bring new evidence. To continue the research on these early belemnites, more field research is needed. The disappearance of the classical German site Nürtingen under the effects of urban

development adds a supplementary scientific value to the Belgian sites. Unfortunately, one of them is currently inaccessible (Fontenoille). Field research is periodically set on by scientific collaborators of the Natural History Museum Luxembourg in order to gather new material as well as new sites in the NE of the Paris Basin (Lorraine, Luxembourg and Belgium).

Concerning taxonomy, future findings should allow splitting the heterogeneous *Schwegleria*-group into some new genera. The genus *Schwegleria* with the type species *Schwegleria feifeli* would consequently be restricted to forms with a ventral groove.

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#### PLATE 1 - EXPLANATION

- A. *Schwegleria feifeli* (SCHWEGLER, 1939), complet rostrum, lateral view. Specimen QB268a. Hettangian, *Liasicus*-Zone of Fontenoille, Belgium.
- B. Idem, ventral view.
- C. *Schwegleria feifeli* (SCHWEGLER, 1939), fragment, ventral view. Specimen QB268b. Hettangian, *Liasicus*-Zone of Fontenoille, Belgium.
- D. Idem, transverse section.
- E. *Schwegleria psilonoti* (SCHWEGLER, 1939), fragment, lateral view. Specimen QB269. Hettangian, *Liasicus*-Zone of Fontenoille, Belgium.
- F. Idem, transverse section.
- G. Belemnitid phragmocone. Specimen QB271. Hettangian, *Liasicus*-Zone of Fontenoille, Belgium.
- H. ?*Schwegleria* sp., fragment, lateral view. Specimen QB270. Hettangian, *Liasicus*-Zone of Fontenoille, Belgium.
- I. Idem, transverse section.
- J. Idem, ventral view.
- K. aff. *Subhastites* sp., fragment, lateral view showing the lateral line. Specimen HE366. Hettangian, probably *Planorbis*-Zone of Vance, Belgium.
- L. Idem, transverse section.
- M. Idem, ventral or dorsal view.

