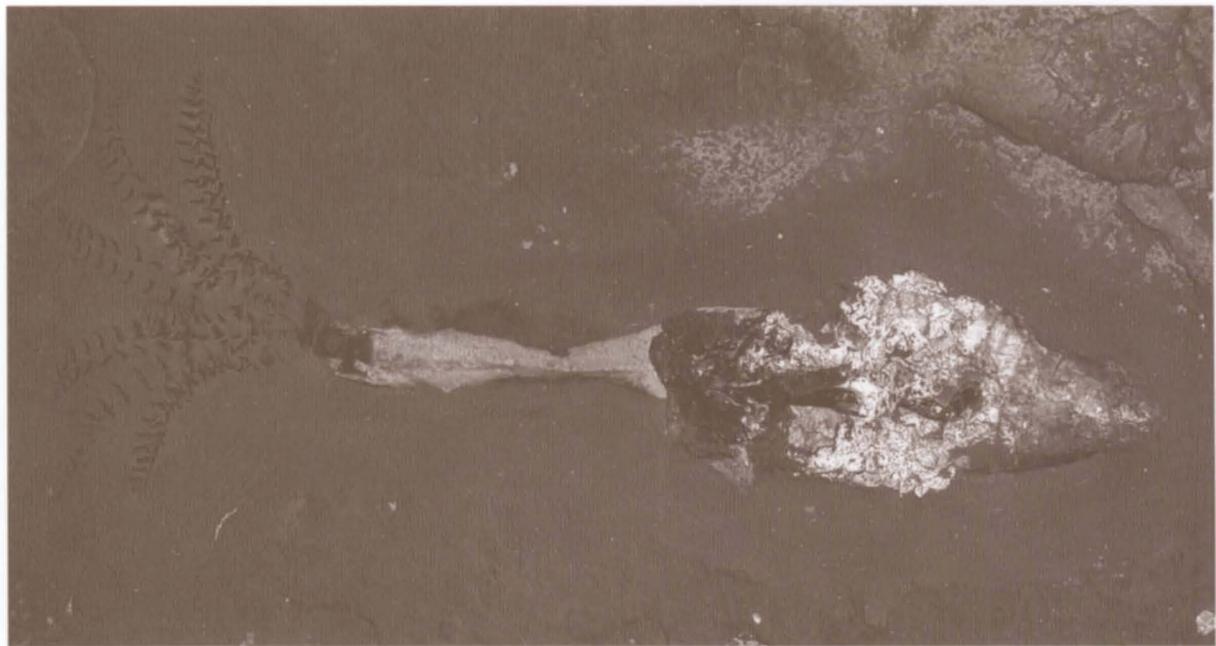


# ACTA UNIVERSITATIS CAROLINAE



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**PROCEEDINGS OF THE  
2<sup>nd</sup> INTERNATIONAL SYMPOSIUM  
*COLEOID CEPHALOPODS THROUGH TIME***

**Prague, 26–29 September, 2005**

**Edited by Martin Košťák and Jaroslav Marek**

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# FOREWORD

Having been a part of marine biota, the coleoid cephalopods played and recently still play an important role in nekton assemblages. As it has several times been mentioned, coleoid cephalopods belong to rarer fossils (except belemnites), thus the reconstruction of their evolution, palaeobiology and ecology suggests the combined actualistic – neontologic and palaeontologic approach. This completely opens a new view into a fascinating and amazing world of extinct and present coleoids, their habitat, relationships and evolution.

Historically, the first coleoid researchers meeting happened in September 17–19, 2002 at the Free University in Berlin. We hope, this was a basement for a long-termed tradition, which continued in 2<sup>nd</sup> International Symposium “Coleoid cephalopods Through Time” September 26–28, 2005 in Prague. The Symposium proceeding volume of the *Acta Universitatis Carolinae – Geologica* presents 20 papers concerning fossil and recent coleoids.

The first coleoid Symposium proceeding volume – *Berliner paläobiologische abhandlungen, Vol. 3* has been dedicated to Kir Nazimovich Nesis and Walter Kegel Christensen, both important figures of coleoid research, who passed away soon after the Berlin symposium. This was a large misfortune for coleoid research and both great men are always in our memories.

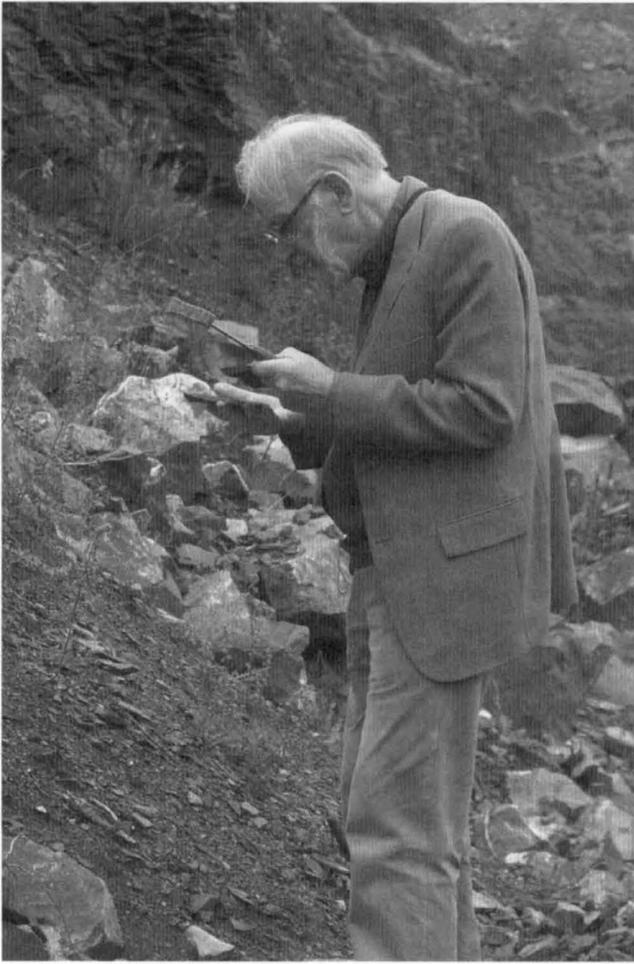
We would like to dedicate this Symposium proceeding volume of the *Acta Universitatis Carolinae* to doyen of coleoid research – prof. Desmond T. Donovan (\* 1921). We are indebted to his wife, Shirley Louise Donovan, who kindly provided us Desmond's *curriculum vitae* and many additional informations about prolific life of this great man.

Finally, we are indebted to all reviewers for their constructive tutorial and remarks. The editors thank to MSM 0021620855, GACR 205/06/0842 and 205/07/1365 for the support.

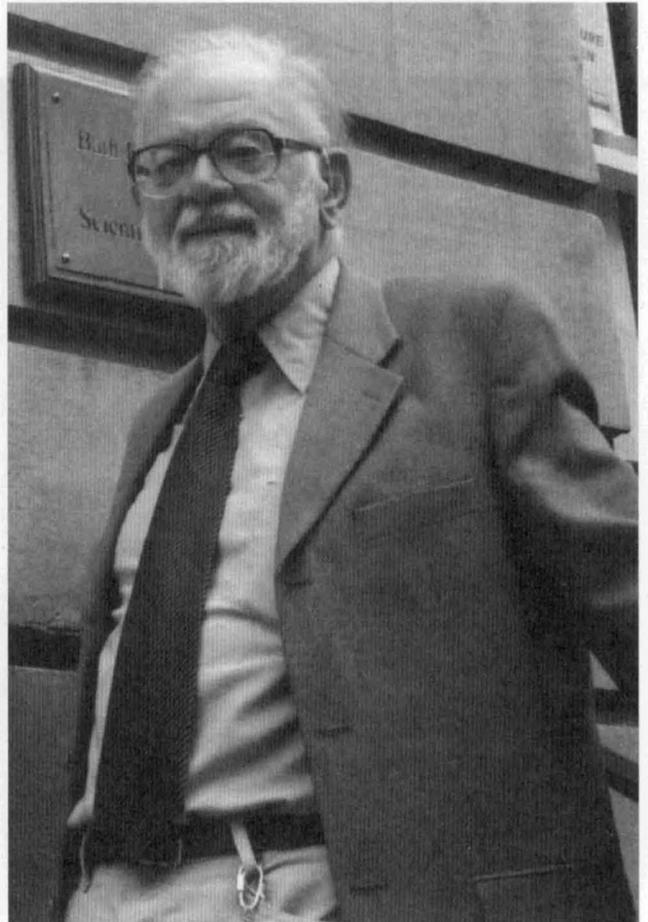
*Martin Košťák and Jaroslav Marek*



Participants of the Symposium, in front of the Faculty of Science, Charles University, 27<sup>th</sup> September 2005



**Prof. Desmond T. Donovan during the field trip at the Upper Silurian cephalopod locality of Lochkov close to Prague**



**Professor of the University College London, Department of Earth Sciences**

# PROFESSOR DESMOND THOMAS DONOVAN

SHIRLEY LOUISE DONOVAN

*University College London*

Born in Cheam, Surrey, England 1921 [16. 06. 21]

Son of Marie Augusta Benker, of Nurnberg, Germany, and Thomas Bartholomew Donovan, whose Irish greatgrandparents had moved to London from Skibereen, Co. Cork, Eire, in 1846 at the time of the great potato famine. Married 1959, a Bristol geology graduate [Shirley Louise Saward; paternal grandfather also from Ireland]; they have 3 children.

## Education

*Secondary school:* Epsom College, Surrey.

*University:* Royal College of Science, London 1938–39. He would have continued to the Royal School of Mines, of Imperial College London, but in 1939 at outset of war his parents moved to Bath, and he was enrolled at the University of Bristol, where he remained for much of his career.

*Bristol University:* 1939–42, BSc 1942; army 1942–46 (in UK & in 1945, Palestine). Bristol University 1946–62, Ph.D. 1951: Ph.D. Thesis (supervised by W. F. Whittard), “The Ammonites of the Blue Lias of the Bristol District”, printed 1952; D.Sc. 1960.

## Career

*Bristol University:* appointed Assistant Lecturer in 1947, Lecturer in 1950, in the Department of Geology. [on Senate – the academic part of the governing body – for much of this time]. Visiting Fellow [an honorary, ie unpaid, position] at University of Bristol 1982–2002.

*University of Hull,* 1962–1966: Chair, Department of Geology.

*University College London* 1966–1982, Yates-Goldsmid Professor and Head, Department of Geology. On retirement: Emeritus Professor UCL, where he still works.

Fellow, Geological Society of London 1942; member, Palaeontographical Society ca. 1950–, President 1979–84; member, Palaeontological Association 1960–, Fellow, Linnean Society of London 1960–; Yorkshire Geological Society 1962–, member 1938–1980s Geologists’ Association, London, for whom he led a field trip (1957, with T R Fry). International Subcommission on Jurassic Stratigraphy (various dates).

## Field mapping 1940s–50s

In the early 1950s, mapped Bathonian Fuller’s Earth of Cotswold Hills with W. J. Arkell, (publ. 1950, 1952); In the 1950s did water supply consulting for West Gloucestershire Water Co. in the Cotswolds; and for water from river gravels to Fry’s Chocolate factory at Keynsham. c. 1957. Wrote parts of chapter (pp. 23–28) in *Geology of the Bristol District* (in *Bristol and its adjoining area*, published for the Bristol meeting of the British Association for the Advancement of Science, 1955. 1958: contributed section on the geology to Nikolaus Pevsner’s *Buildings of England*, volumes on *North Somerset & Bristol* and *South & West Somerset*, Penguin Books.

## Greenland

In 1947–57 along with other young research geologists from Bristol spent 6 summers on field work in East Greenland, part of Danish expeditions run from Copenhagen by Dr. Lauge Koch. Mapped, logged sections and collected ammonite faunas in the mesozoic of Geographical Society Island, Traill Island and Wollaston Foreland. Reviewed the then known Jurassic and Cretaceous of East Greenland: published in *Meddelelser om Groenland* in 1957.

## Travel, systematics and cephalopod phylogeny

In the 1950s a large collection of unlocalised 1930s Greenland material at the British Museum (Natural History) needed sorting and weeding; Buckman’s systematics of Lower Jurassic ammonite genera was simplified and published in papers and memoirs in the 1950s, and in the Jurassic part (compiled by W. J. Arkell) of the first edition of the *Kansas Treatise on Invertebrate Paleontology, Part L: Ammonoidea* (1957).

Visited Stockholm (per British Council) in 1950s to help Dick Reyment with his study of the Lower Jurassic ammonites faunas of Skåne, southern Sweden. In 1953, field work (Royal Society grant) on Lower Jurassic Ammonitico Rosso of the

southern Alps (Switzerland & Italy), (paper on Toarcian zones 1958). In 1955 with Rudolf Trümpy of Zürich examined sections and fauna of various Lower Jurassic localities in the Swiss and Austrian Alps.

Compiled and edited *Lexique Stratigraphique International* Vol. 1, fasc. 3 a X, *Jurassique [of Great Britain]*, 1963, with J. E. Hemingway This had been initiated in 1960, (General Eds. Professors W. F. Whittard & Scott Simpson) at the Copenhagen International Geological Congress; Gave a paper on palaeobiogeography of L Jurassic ammonites at Cambridge Systematics Association meeting, 1966, published 1967 in Systematics Association Publ. No. 7, *Aspects of Tethyan biogeography*, (eds. C. G. Adams & D. V. Ager), London.

Several submissions to the International Commission on Zoological Nomenclature.

Book reviews (1960s): on stratigraphy, geological techniques etc. 1960s–70s: co-author of papers on systematics, on stratigraphic nomenclature codes, on standard Jurassic Stages 1961, 1966, 1974 (e. g. for GSL Jurassic working group of Mesozoic Era subcommittee), field guides, on scientific objectives for UKCS (Continental Shelf) drilling, etc. 1966: *Stratigraphy: an Introduction to Principles*, London: Thomas Murby (an imprint of George Allen & Unwin) was published. In 1967 contributed on cephalopods to GSL publication, *The Fossil Record*.

At the *International Field Symposium on the British Jurassic*, London, in 1969 (Convenors: DVAger, HSTorrens, N. Morton, DTD) joint leader (and contributor to field guide) of the North Somerset and Gloucestershire Excursion with DVAger, HSTorrens and others. Bulgaria 1969: British Council grant to meet geologists in Bulgaria and Romania, and visit site of an anomalous ammonite record in E. Bulgaria (the specimen was from an olistostrome). Traversed N. Turkey (1976): long field trip supervising UCL postgrad. student Füsün Alkaya, Ph.D. 1979, on Lower Jurassic ammonites of outcrops along the N. Anatolian Fault zone. In 1975, read a paper on coleoid mollusc evolution at the meeting *Biology of Cephalopods* convened by Dr. Marion Nixon and Professor John Messenger for the Zoological Society of London to mark the retirement of Professor J. Z. Young (of UCL), publ. 1977.

### **Archaeological interests**

1950s with archaeologist friends, investigation & measurement of the Roman remains in the spring chamber under the King's Bath, at the hot springs, Bath, Somerset; in 1950s–60s, many short contributions on Pleistocene records in caves in Somerset.

### **Offshore geology**

By the 1950s there were competing schemes for an English Channel Tunnel. In the late 1950s DTD was consultant to a company regarding a 'buried tube' solution to the proposed French-English Channel Tunnel. Became interested in early subsea investigation methods, and history of tunnelling beneath the Thames.

Early offshore surveys had made use of only topography and sea floor sampling. Surveys from Bristol in the late 50s early 60s used vessels of the Naval Hydrographic Office, the Plymouth Marine Biological Station (*Sarsia*), and the NIO (National Institute of Oceanography) oceanographic research ship *Discovery II*. Staff collaboration enabled this. In 1960–63 research surveys were undertaken in the Bristol Channel [Severn Estuary]. [A new *Discovery* came into Bristol's port at Avonmouth for the Colston Symposium marine geology meeting of 1965 (see publication), and was the first British ship purpose-built to enable geological survey].

Dr. Arthur Stride, of NIO (now absorbed into Southampton Oceanography Centre), a Bristol geology graduate, had in the 50s noticed geological features on sea floor records of vessels which were using wartime submarine detection sonar to find fish. Sidescan sonar revolutionised survey methods. In 1957 Desmond with Arthur Stride ran a pioneer sidescan sonar survey in the English Channel over the Weymouth Anticline (an Alpine fold long recognised onshore) (published by the Royal Society 1961). This led to publication of the first IGS (Institute of Geological Sciences) offshore geological map of British waters, and Britain's first offshore oil well, unfortunately dry, was soon drilled on the structure by BP. Cooperation between the two national geological surveys, the British IGS (under Sir Kingsley Dunham) and French BRGM, led to a joint publication programme for further Channel maps.

In Hull in 1963 geological survey offshore in the North Sea was begun, using an NIO-type gravity corer, and a sparker, designed and built locally in the Physics Department. This gave a sea floor profile and vertical sediment penetration of 20–30 m. Working from small trawlers they could only get 'ship's time' during the equinoxes, when it was too rough for fishing! Nonetheless, work was published, including the first North Sea papers, by Desmond with Hull postgraduate students (e. g. Dr. R. V. Dingle, Ph.D. thesis & publication).

Later work used an improved towed side-scan sonar tool loaned by BP, built to designs modified from those developed at the NIO (an example of co-operation between business and university research workers, enabled in this case by Norman Falcon, BP Chief Geologist and his successor Sir Peter Kent, later Head of NERC (National Environment Research Council). 1965 DTD, SLD visited Sweden to help operate BP's towed sidescan sonar in the Baltic for Prof I Hessland of Stockholm and his team. Papers at a 1967 conference on offshore geology held in Hull were published in 1968 as a book edited by DTD. Gave talks to the PESGB (Petroleum Exploration Society of Great Britain) in 1971 and 1973.

### **Further field mapping, stratigraphy & palaeontology**

In 1982 at age 61, without department responsibilities, research began anew, in stratigraphy and palaeontology. The IGS Bristol District Special Sheet 1:63 360 map had been published in 1962. Stratigraphy and palaeontology were revised for the accompanying L. Jurassic memoir (1984) co-authored by G. A. Kellaway and written by DTD. In the 1980s–90s he

collaborated with BGS geologists on revision mapping of two 1:50K Sheets of parts of Wiltshire and Somerset in SW England. The two new maps were published in 1996 & 2000, a memoir in 1999, [and a short report].

Lecturing and examining, student field teaching and mapping, in England regarded as of prime importance, continued. Occasional crates of mesozoic ammonites had formerly arrived for identification from oil company geologists; from 1956 he had acted as a consultant for IGS/BGS on L. Jurassic samples and borehole faunas. 1979: collaboration with BGS geologists, working from borehole records [cores & electric logs], led to a joint paper on rates of L. Lias transgression over the Paleozoic London Platform; also in 1979 co-author with Dr. E. J. W. Jones of paper on world-wide sea level change. Symposium on Ammonoidea, convened by Professor Michael House, held at UCL, London in 1991; (paper, and participant in field excursion to the Dorset Coast, based on Weymouth, led by Mike House).

The GSL in 1992 published an Atlas of Palaeogeography and Lithofacies, covering Great Britain and much of the UK Continental Shelf, eds. J. C. W. Cope et al.; DTD contributed to Lower Jurassic maps and text. In 1998–99: collaboration in work on Yorkshire Coast sections, for Dr. John MacArthur's belemnite 87/86 Sr analyses across the Toarcian anoxic event. Published 2000.

### Other interests

From student days Desmond had been interested in caves (see above), had published with others occasional work on palaeolithic sites and flint tools. Some of his latest papers are once again in this field, on stratified sediments and problematic old records of finds in caves in the Carboniferous Limestone of the Mendip Hills south of Bristol. He has long been involved with editing the University of Bristol Spelaeological Society Proceedings. Always having had an interest in the wellbeing of museums and old collections, he took an honorary post at Wells Museum, Somerset, for 3 years (1982–1985) curating, in particular, certain palaeolithic collections. Like many colleagues, contributed to the valuable work of local natural history societies [in Bristol and Bath] in recording and publishing sections and sensitive site conservation.

Desmond twice joined campaigns concerning historic buildings and sites [stimulated by SLD who worked & has contacts in this field]. In 1971 he contributed (a joint stability study) and gave evidence, along with architects and architectural historians of note, to a public local inquiry in Bristol into plans for commercial building at an environmentally sensitive site on the edge of the Avon Gorge, Bristol. Planning Permission was overturned by the Secretary of State. In 1981 he took part in a campaign against proposed demolition of NE galleries at the BM(NH), a Grade 1 'Listed' Building. Proposals abandoned. In the 1990s he took part (with sld) in the sustained campaign by the UK research community to protect the BGS from government privatisation plans.

A long-term interest in dimension stone used in historic buildings, its ancient sources and weathering characteristics resulted in study and joint reports on stone at Wells Cathedral, Salisbury Cathedral, Westminster Abbey and the Tower of London, among others, and participation in a seminar in Venice in 1987.

### Paleontology, continued

Part M of the Kansas Treatise was long overdue. Thus Desmond in the 1990s resumed work on coleoids, (see 1977 paper on evolution of dibranchiates, above) and took over the role of co-ordinating author in 1991 succeeding Jurij A. Jeletzky. Discussion with workers on modern cephalopods at Plymouth, Naples, Cambridge and UCL was of importance in this work. Through the generosity of Professor Harry Mutvei at Stockholm he has been able to work closely with Dr. Larisa Doguzhaeva of Moscow in her work on ultrastructure in cephalopods, particularly coleoids, and with Harry has led to their recent joint papers. New examples of otherwise poorly known or poorly preserved specimens continue to turn up [as recently in collections from the Dorset Kimmeridge Clay]. He has participated in many of the International Cephalopod Symposia and the more recent Coleoid Symposia.

In recent years discussion with younger workers has included: with a postdoc. student of Professor Derek Briggs: taphonomic studies (Amanda Kear, Bristol, in ca. 1991–3); with workers in molecular phylogeny of recent cephalopods (Jan Strugnell, Ph.D. Oxford, 2004); and Laure Bonnaud, Paris, for whom he was in 1995 a doctoral thesis adjudicator.

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\* indicates papers in which D. T. D. regards his contribution as significant



# 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 of genera *Alloteuthis*, *Loligo*, *Illex*, *Todarodes*, *Todaropsis*, and *Sthenoteuthis*, occurring off the Northwest African coast are described. The teuthofauna of the region consists of a mixture of boreal and tropical species, each associated with its specific water mass. Both boreal and tropical squid inhabit the ecotone zone, the main features of their life styles are common to that of the central part of their species ranges. Boreal species inhabit cold waters of either Sahara or Canary Currents, or inshore upwelling waters. They have the winter peak of the spawning. Species, which ranges extend into tropics, inhabit waters of tropical origin and tends to stay off the upwelling activities. As their southern counterparts, these species have a spring-summer peak in their spawning. In squid assemblage, fecundity increased about ten-folds at each step from the inner shelf to the shelf break and slope, and then to the open ocean. Egg size decreased in the same direction. The possible reason is an increase in mortality at early stages that forces species to produce more eggs at cost of egg size and offspring quality.

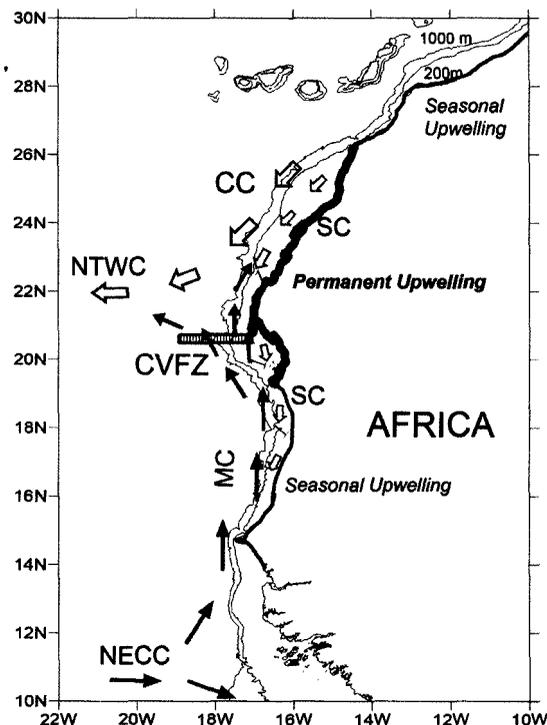
**Key words:** Nekton, squid, water masses, shelf, slope, Northeast Atlantic

## INTRODUCTION

Species ranges of marine plankton are closely associated with large-scale hydrographic features of the world ocean such as macro and meso-scale oceanic gyres, and their corresponding water masses (Beklemishev, 1969). Distribution of nektonic animals, such as squid, have similar but usually a weaker association. They may migrate from one water mass to another either at different phases of their ontogenesis or even during their diel vertical migrations (Nesis, 1985). Boundary layers between macro-scale hydrographic gyres, known as ecotones, are especially interesting as they may show to what extent nektonic squid associated with one major water mass can intermix with the squid belonging to a different water mass. Further, studies of the distribution of nektonic squid in different ecotones may reveal the evolutionary pathways of their adaptive speciation.

To fulfil this task we have chosen one of the most productive regions in the Atlantic, the shelf and slope waters off the Northwest African coasts between 19° and 26°30' N. This region (Mauritanian zoogeographic province) belongs to the subtropical Lusitano-Mediterranean Superprovince, which includes also the Mediterranean Sea and adjacent Atlantic up to the Ireland and to the English Channel (Nesis, 2003), and is populated by a mixture of boreal and tropical squid with some endemic species (Nesis, 1985). One of the main oceanographic features of the region is a strong near shore coldwater upwelling that occurs throughout the year (Fig. 1, 2). Unlike the rather uniform landscape of the Sahara desert, the adjacent oceanic habitats are diverse including a complex of different oceanic streams, meanders and gyres. The major regional

current, the Canary Current, moves southward along the entire shelf and continental slope (Fig. 1). At about 24–26° N it splits into two branches – the Sahara Current



**Fig. 1** Main oceanographic features in the subtropical and tropical Northeast Atlantic off the African coast: Canary Current (CC), Saharan Current (SC), Mauritanian Current (MC), North Equatorial Counter Current (NECC), North Trade Wind Current (NTWC) and Cabo Verde Frontal Zone (CVFZ).

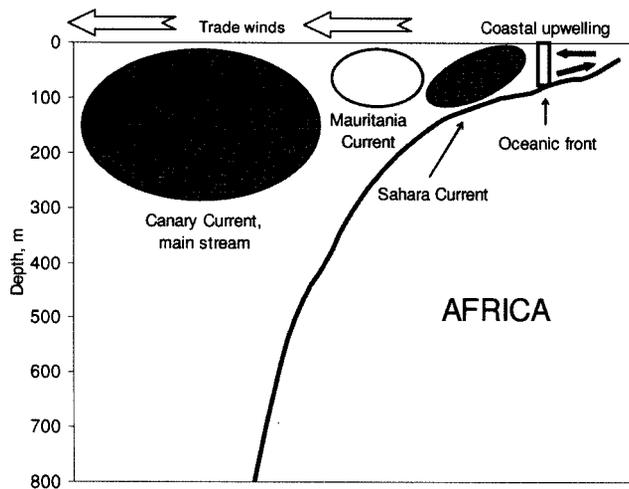


Fig. 2 Latitudinal transect over the shelf and slope at 24° N showing vertical and horizontal distributions of main currents off the African coast.

(inshore branch), which runs also southwards on the shelf between 50 and 200 m depth contours (Fig. 2), and the mainstream that flows over the deeper part of the continental slope. The convergence between the cold upwelling waters and the Canary Current is known as the Oceanic Front. The northbound extension of the tropical North Equatorial Counter Current (NECC) flows over the depths ranging from 200 m to 900 m, with the main stream located at depths between 50 and 300 m. The NECC wedges between the Saharan Current and mainstream, and reaches 22–24° S (Mittelstaedt, 1991; Peregrini et al., 2005).

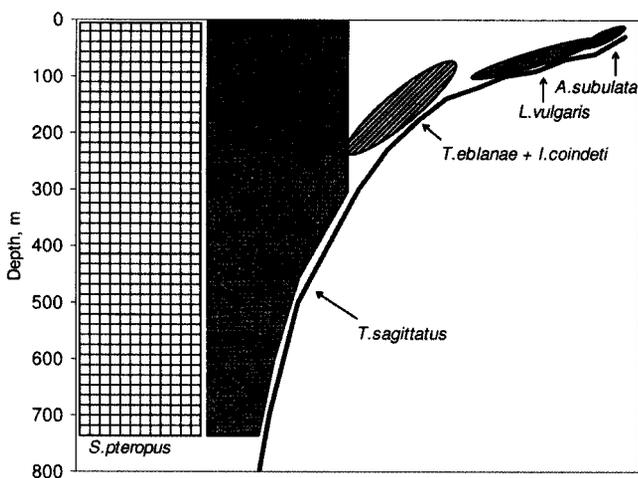


Fig. 3 Latitudinal transect over the shelf and slope at 24° N showing vertical and horizontal distributions of nektonic squid off the African coast.

The pelagic fish fauna of the region is diverse, consisting of at least 73 species (Froese and Pauly, 2003). On the contrary, the large nektonic squid fauna is rather poor, with only 6–7 species belonging to two families, Loliginidae and Ommastrephidae. Interestingly, the squid species seem to be segregated by depth, with only one or two species dominating near the bottom and the water column between certain depth ranges (Fig. 3). The main aim of the present study was to reveal the possible association of the distribution of squid species with the complicated water mass structure of the region.

## MATERIALS AND METHODS

Biological data were collected during many expeditions of the Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO, Kaliningrad, Russian Federation) on the shelf and continental slope off Morocco and Mauritania between 1969 and 1998. Squids were collected from the catches of bottom and pelagic trawls of different constructions. Targeted trawl hauls were carried out at depths range between 10 and 1500 m during day and night in all months of the year. To describe the geographic and bathymetric distribution, a total of 34,218 squid from the catches of 6,898 trawls hauls were analysed. Dorsal mantle length (ML) and total body weight (BW) were measured, and sex and maturity stage were assigned according to a scale for ommastrephid squids (Nigmatullin, 1989). Statoliths were taken from subsamples of squid (1,804 animals) and stored in 70% ethyl alcohol. A total of 183 reproductive systems were stored in 6–8% formaldehyde and investigated onshore. Details of methods used and numbers of animals sampled of each species are given in the papers cited below as are the papers from which data was used to describe the species biology and distribution.

## RESULTS

### Nektonic squid species

Several abundant squid species inhabit waters of the Saharan Bank. Two loliginid squids, the large European common squid, *Loligo v. vulgaris* and the small (Table 1) *Alloteuthis subulata* are distributed over the shelf of the East Atlantic from the southern Norway to Mauritanian-Senegalese waters (Nesis, 1987). The latter species is substituted in the tropical African waters by *A. africana*, whereas another

Table 1. Squid maximum and minimum sizes off NW Africa and a relation between the maximum male and maximum female sizes (M/F).

Species	Maximum size mm			Source
	Male	Female	M/F	
<i>Loligo v. vulgaris</i>	640	362	1.8	Moreno et al., 2001
<i>Alloteuthis subulata</i>	200	120	1.7	Roper et al., 1984
<i>Illex coindetii</i>	263	300	0.9	Sanchez et al., 1998
<i>Todaropsis eblanae</i>	160	270	0.6	Roper et al., 1984
<i>Todarodes sagittatus</i>	280	350	0.8	Nigmatullin et al., 2002
<i>Sthenoteuthis pteropus</i>	280	630	0.4	Zuev et al., 2002

subspecies of *Loligo vulgaris*, *L. v. reynaudi*, occurs only in cold waters of the Benguela upwelling system of South Africa. Both ommastrephid species of the outer shelf and slope, *Todaropsis eblanae* and *Illex coindetii*, have uninterrupted distributions in the East Atlantic from temperate European waters to South Africa. The latitudinal distribu-

tion of arrow-squid, *Todarodes sagittatus*, is similar to those of *L. vulgaris* and *A. subulata*, though the waters of NW Africa are inhabited by a population with a distinctive biology (Nigmatullin et al., 2002). The orange-back squid, *Sthenoteuthis pteropus*, is a "pure" oceanic species and occurs in the East Atlantic from Canary Islands to Namibia, mostly between 20° N and 20° S (Zuev et al., 1985).

### Bathymetric distribution

An analysis of bathymetric distribution of nektonic squids highlighted an important segregation by depth between them (Table 2). Both loliginid species tended to live on the inner shelf (depths < 100 m) although some squids were found far beyond the shelf edge. *I. coindetii* and *T. eblanae* inhabited the outer shelf (depths >100 m) and shelf break (200–250 m). *T. sagittatus* occurred in both pelagic (juvenile) and near-bottom (adults) waters above the continental slope sometimes entering the outer shelf. *S. pteropus* inhabits the waters of the open ocean.

**Table 2. Depth ranges of nektonic squids off West Africa.**

Species	Depth range	Max. abundance	Source
<i>Alloteuthis</i> spp.	20–300	20–50	Demersal...1992; Arkhipkin, Nekludova, 1993; Laptikhovskiy et al., 2005
<i>Loligo vulgaris</i>	< 25–400	< 100	Distribution...1982; Hernandez, Bas, 1993, Raya et al., 1999; our data
<i>Illex coindetii</i>	35–1000	90–250 100–400 100–250	Fisher et al., 1981 Sanchez et al., 1998 Hernández-García, 1991
<i>Todaropsis eblanae</i>	20–719	100–400 150–300	Fisher et al., 1981 Hernández-García, 1991
<i>Todarodes sagittatus</i>	65–2000	250–800 (100–)300–900*	Hernández-García, 1991 Nigmatullin et al., 2002
<i>Sthenoteuthis pteropus</i>	> 250–300	> 1000	Zuev et al., 1986.

\* generally occurs deeper than 300 m, but in some years invades outer shelf (depths 100–200 m).

### Age, growth and maturation

Among the squid studied, *A. subulata* had the lowest growth rates, averaging 0.1 g/day. This species is also characterized by a half-year life span and early maturation (Arkhipkin and Nekludova, 1993). Two species of ommastrephids occurring in the region (*I. coindetii* and *T. eblanae*) have higher growth rates than *A. subulata* (maximum 1.5–4 g/day in adults), but a similar longevity and early maturation (Arkhipkin, 1996; Arkhipkin and Laptikhovskiy, 2000). This is contrary to their boreal counterparts, inhabiting waters of the Southern Europe and having a 1-yr life span and late maturation (Gonzalez et al., 1994). It should be mentioned that the large-sized form of *I. coindetii* is also present near Morocco, but it is not abundant and occurs deeper than the bulk of the population (Arkhipkin, 1996).

Three other species, e. g. *L. vulgaris*, *T. sagittatus* and *S. pteropus*, have high growth rates (especially at the adult phase), attaining large sizes at the end of their 1-yr lifespan

(Table 3, Arkhipkin, 1995; Arkhipkin et al., 1999). The highest growth rates (up to 70 g/day) were observed in adult females of *S. pteropus* (Arkhipkin and Mikheev, 1992). All three squid mature quite late in their ontogenesis, at ages of more than 200 days.

A relation between the largest male size and the largest female size decreases in offshore direction (Table 1).

**Table 3. Lifespan, growth rates and maturity of nektonic squids off West Africa.**

Species	Lifespan	Growth rates	Maturity
<i>A. subulata</i>	0.5	low	early
<i>L. vulgaris</i>	1	high	late
<i>I. coindetii</i>	0.5	low	early
<i>T. eblanae</i>	0.5	low	early
<i>T. sagittatus</i>	1	high	late
<i>S. pteropus</i>	1	high	late

### Spawning seasonality

There is not much data on *Alloteuthis* spp. spawning off Northwest Africa. Most of the *A. subulata* and *A. africana* collected in August–September on the Saharan shelf hatched in March–May (Arkhipkin, Nekludova, 1993). The half-year life cycle revealed in this squid suggested that there should be another spawning peak in autumn. Another shelf inhabitant, *L. vulgaris*, spawns between 21–26° N all year round with a major peak in winter (November–February) and minor peak in spring (May) (Raya et al., 1999; Moreno et al., 2002). Correspondingly, hatching peaks were observed in December–March and June–July (Arkhipkin, 1995; Raya et al., 1999).

On the Northwest African shelf edge *Illex coindetii* reproduces throughout the year with a single weak spring – summer peak (Hernández-García, Castro, 1995; Sanchez et al., 1998). In the same habitat *T. eblanae* has two spawning peaks: April–June and October–January, the first being most important (Hernandez-García, Castro, 1995; Arkhipkin, Laptikhovskiy, 2000). Spawning in *T. sagittatus* clearly has an expressed peak in November–February, mostly off Cape Blanc (Nigmatullin et al., 2002). The peak in hatching occurs in February–March (Arkhipkin et al., 1999). Spawning in *S. pteropus* occurs throughout the year, but in the so-called Northeast Tropical Population, which inhabits the Northwest African waters, reproduction occurs mostly in summer–autumn (August–November; Zuev et al., 1985).

### Fecundity

The reproductive strategies are quite different between habitats (Table 4). On the inner shelf, where pelagic egg masses could be easily washed ashore, all squids and cuttlefish attach their eggs to the bottom. Squid fecundity is in the dozens of thousand of eggs and egg size is 1.4–2.7 mm. On the outer shelf and slope ommastrephid squid are still related to the bottom exhibiting a demersal life style when adult, but produce pelagic egg masses and use a system of border currents for their transport and incubation. Egg size decreases to 0.9–1.2 mm, fecundity increases to hundreds of thousands of eggs. In the pelagic waters of the open ocean where the species habitat is not related to the bottom any-

more, and where the system of trade wind currents and counter – currents is quite erratic and unpredictable, squid egg size decreases to 0.7–0.9 mm and fecundity increases to some millions of eggs.

**Table 4. Egg size and fecundity (F) of Northwest African squids.**

Species	Habitat	Egg size	F (10 <sup>3</sup> )	Source
<i>L. vulgaris</i>	Inner shelf	2.0–2.7	28–74	Laptikhovsky, 2000
<i>Alloteuthis</i> sp		1.4–2.3	1–4.5	Laptikhovsky et al., 2002
<i>I. coindetii</i>	Outer shelf and upper slope	0.9–1.0	80–780	Laptikhovsky, Nigmatullin, 2003
<i>T. eblanae</i>		1.2	40–240	Nigmatullin, Laptikhovsky, 1999
<i>T. sagittatus</i>		0.9–1.0	215–950	Nigmatullin, Laptikhovsky, 1999
<i>S. pteropus</i>	Open ocean	0.73–0.87	560–17.900	Laptikhovsky, Nigmatullin, 2005

## DISCUSSION

The results of the present study revealed a close association of nektonic squid species with different water masses of the shelf and slope off the Northwest Atlantic. Because of oceanographic variability, nektonic fish and squid could intrude following a “native” water mass into an adjacent habitat. It is characteristic not only for early stages (Rodríguez et al., 1999), but also for adults (Bukatin et al., 1982).

The teuthofauna of the region consists of a mixture of boreal and tropical species, each associated with its specific water mass. Interestingly, in both boreal and tropical squid inhabiting this ecotone, the main features of their life styles are common to that of the central part of their species ranges. Boreal species inhabit cold waters of either Sahara (*L. vulgaris* – Vovk, 1971) or Canary (*T. sagittatus*) Currents, or inshore upwelling waters (*A. subulata*). First two species have 1-yr life cycle, late maturation and high growth rates in adults (Table 5). As their northern counterparts, these species have a winter peak in their spawning. A dwarf *A. subulata* has 0.5-yr life style and the all year round spawning.

**Table 5. Life style features of nektonic squids.**

	Depth m	Life-span	Water mass	Water temp.	Peak of spawning
<i>A. subulata</i>	15–100	0.5	nearshore	high	End of spring
<i>L. vulgaris</i>	50–150	1.0	Saharan C.	low	Winter
<i>I. coindetii</i>	100–250	0.5	Mauritania C.	high	End of spring
<i>T. eblanae</i>	150–300	0.5	Mauritania C.	high	End of spring
<i>T. sagittatus</i>	300–800	1.0	Canary C.	low	Winter
<i>S. pteropus</i>	> 1000	1.0	Canary C.	low	Autumn

Species, which ranges extends into tropics, such as *I. coindetii* and *T. eblanae*, inhabit waters of tropical origin (NECC) and tend to stay off the upwelling activities. It prevents also their pelagic egg masses to be brought ashore by upwelling. Both of them have slow growth rates in adults and 0.5-yr life spans. As their southern counterparts, these species have a spring-summer peak in their spawning.

For the purely pelagic tropical species, *S. pteropus*, this region is the northernmost periphery of its species range. As with its large form in the tropics, this species has a 1-yr lifespan, but a summer-autumn peak in spawning, different to that of the boreal squid.

In squid assemblage, fecundity increased about ten-folds at each step from the inner shelf to the shelf break and slope, and then to the open ocean. Egg size decreased in the same direction. The possible reason is an increase in mortality at early stages that forces species to produce more eggs at cost of egg size and offspring quality (Nigmatullin, Laptikhovsky, 1994).

It seems that the speciation of squid fauna in the region occurred ‘horizontally’, with one-two dominant species occupying each depth habitat. Such “stratification” could be observed also 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.

By comparison with the mouth of a fish, the squid arm crown is large and much more versatile for capturing and handling prey. Cephalopods are opportunistic predators and they appear to be unselective in their choice of prey type (Boyle, Rodhouse, 2004). Squid also are able to consume prey of almost any “reasonable” size because they do not swallow it whole but use beaks to tear it apart into smaller pieces. This does not favour species radiation within a given eco-niche, resulting in a very poor diversity squid fauna, in contrast to fish, most of which swallow whole food items and therefore requires some kind of specialisation (mouth size, teeth morphology etc). Similar phenomenon is observed for sharks, which are also feeding generalists consuming food torn into pieces, and demonstrate low species diversity despite long evolutionary history – much longer than in predatory teleost fishes. For example, there are about 350 shark species in all habitats vs. 449 in groupers family Serranidae only (Froese, Pauly, 2006).

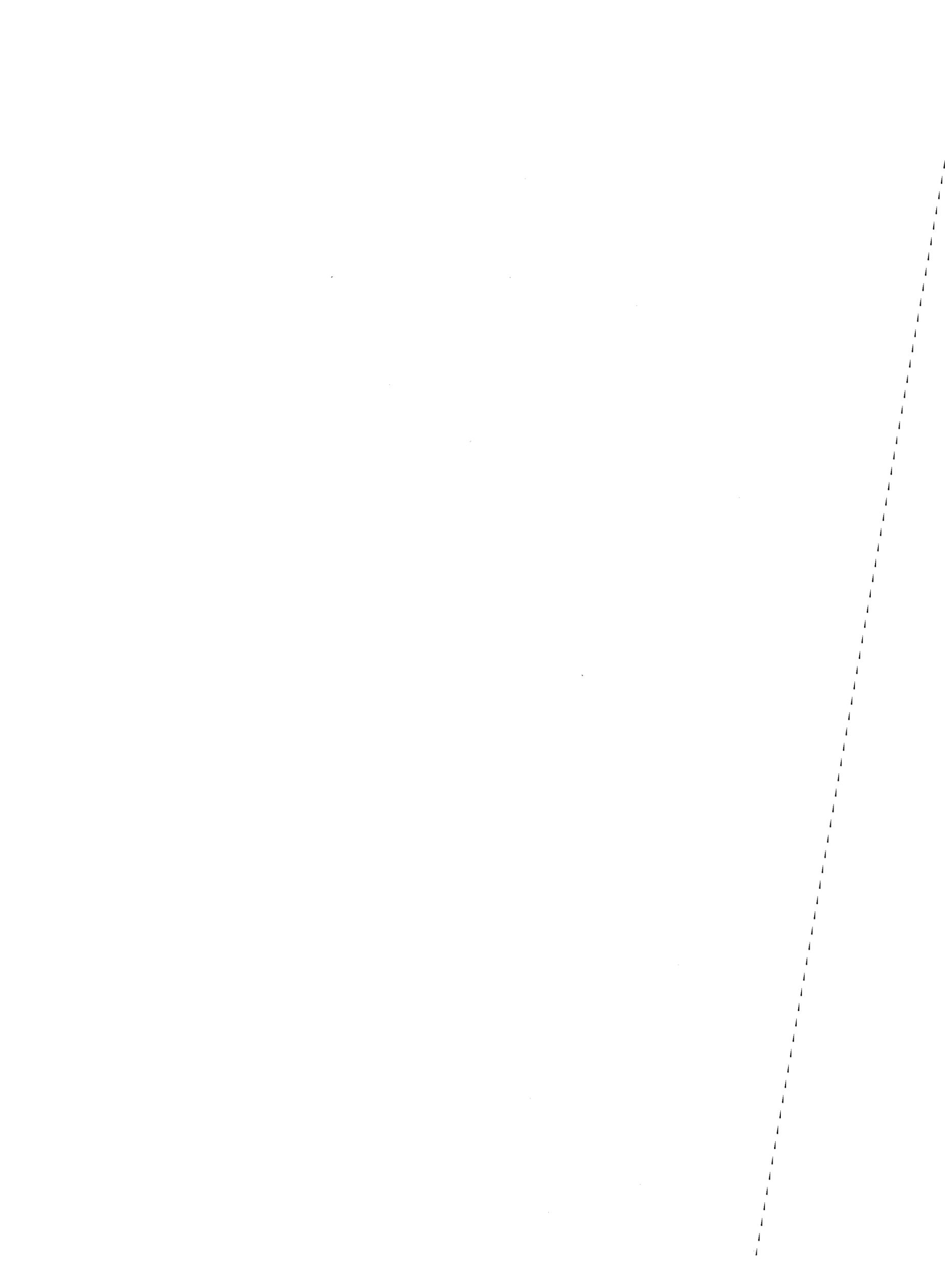
From inshore to offshore direction, squid species have smaller eggs and larger fecundity, possibly due to higher non-selective mortality at their early stages in oceanic habitats which is related to increasing egg dispersal. Also, species invest more in female growth enabling females to become the larger sex in oceanic species and the smaller one in inshore squids.

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# NAEFIA WETZEL 1930 FROM THE QUIRIQUINA FORMATION (LATE MAASTRICHTIAN, CHILE): RELATIONSHIP TO MODERN *SPIRULA* AND ANCIENT COLEOIDEA (CEPHALOPODA)

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**Abstract:** The shell of *Naefia neogaeia* Wetzel, 1930 from the Maastrichtian of Chile is revised and compared with other Cretaceous taxa placed in the Groenlandibelidae. *Naefia* differs from these species by the absence of a rostrum and other external layers of the shell, and a rectangular tissue attachment scar. The thorn-like dorsal proostracum is another distinctive feature of *Naefia*. Shell characters found in *Spirula* and *Sepia* do not favor a relation with *Naefia*, which would then not fit any group proposed in literature. *Naefia*, as well as *Groenlandibelus*, remain isolated regarding their taxonomic position among fossil coleoids.

**Key words:** Mollusca, Coleoidea, evolution, shell construction, cretaceous

## INTRODUCTION

The cephalopod genus *Naefia* Wetzel, 1930 is based on *Naefia neogaeia* Wetzel, 1930 from Quiriquina Formation, Maastrichtian of Quiriquina Island, southern Central Chile. The genus *Naefia* has been established by Wetzel, in 1930, and thus prior to *Groenlandibelus* Birkelund, 1956. Both *Naefia* and *Groenlandibelus* are Late Cretaceous in age and have been interpreted to represent relatives of *Spirula*, but with a straight orientation of their shell (Haas 1997, 2003). They were assigned to the Groenlandibelidae by Jeletzky, 1966. Their relationship to modern *Spirula* is primarily based on the presence of a siphuncular tube in the first chamber (Jeletzky 1966). In Aulacocerida and Belemnitida, the first chamber of the phragmocone is closed by an organic septum and no siphuncular tube crosses through it (Grandjean 1910, Jeletzky 1966). In *Spirula* and *Groenlandibelus*, in contrast, the siphuncular tube initiates within the first chamber and is here attached to its inner wall by a prosiphon (Appellöf 1893), similar to embryonic shells (ammonitellas) of the ammonites.

All recent cephalopods with the exception of *Nautilus* have an internal shell covered by muscular mantle. Only *Nautilus* is able to withdraw into its shell and close the aperture with a hood. This basic construction of the cephalopod shell is long known. Ehrhardt (1727) considered the chambered portion of *Nautilus* homologous to the phragmocones of belemnites, ammonites, and *Spirula*. Erhardt knew *Spirula* from the study of Rumpf (1704) (the genus was described as “Posthoorentje”) and considered it closely related to the ammonites.

The shell of coleoid cephalopods is entirely enclosed by soft tissue (Endocochleata). According to authors such as

Schindewolf (1933), Erben (1964) or Jeletzky (1966), endocochleat conditions established progressively when skin folds of the mantle edge gradually covered more and more of the shell of adult individuals. In contrast to the above hypothesis, Naef (1922), argued that this process initiated within the egg capsule and that the early ontogenetic shell was progressively covered by the embryo.

This latter view has since become more plausible. Muscular mantle covers the shell of embryos of many different mollusks that have a sheltered yolk-rich development (Bandel 1982). It connects to the shell from the outside and enables the embryo to concentrate on the manipulation of yolk and to retard the formation and attachment of retractor muscles. This is also the case in *Nautilus* (Tanabe 1989, Arnold 1987, Arnold & Carlson 1986). Recent squids have a hatching gland where the margins of the muscle meet in a position at the base of the fins. When the young is ready to hatch it lies attached to a special spot of the egg capsule and enzymes released by the hatching gland locally dissolve egg-envelopes. The embryo creeps through the hole with the aid of cilia that cover the body (Boletzky 1979, 1989, 1999).

This mode of hatching could well have developed during Late Silurian times, among the small and slender embryos of a group of michelinoceratid ectocochleates (Bandel et al., 1983, Bandel & Boletzky 1988). With embryonic endocochleat conditions carried into adult life, only muscular folds of the mantle had to evolve into fins and these cephalopods would have functioned as squid-like aulacoceratids.

Abel (1916), Naef (1922) and Jeletzky (1966) interpreted the belemnite rostrum to cover most or all of the phragmocone which was considered similar to the shell of

*Orthoceras*. They interpreted the rostrum to represent part of the periostracum. However, in all conchiferan mollusks the periostracum is produced by special cells on the edge of the mantle. In belemnites, the periostracum consequently lies below the rostrum and covers both the phragmocone and proostracum (Bandel et al., 1984). It is segregated by the cells of a gland at the margin of the mantle. The periostracum thus forms a basal layer onto which the mantle that lies behind that zone segregates additional layers of calcareous biominerals, such as nacre in the case of the class Cephalopoda.

Construction of the siphuncular tube is variable in belemnite-like cephalopods and may help to distinguish different groups (Naef 1922). For instance, belemnites from the Jurassic and Cretaceous have a simple organic tube (Jeletzky 1966), while Triassic Aulacoceratidae are characterized by a double-walled tube that resembles that of modern *Spirula* (Bandel 1985). Abel (1916) was the first to assume a buoyancy control in chambered cephalopods, long before the fundamental discussions on this function by Denton & Gilpin Brown (1961, 1971). He stated (translated): It appears to be likely that belemnites were deliberately able to fill the chambers of the phragmocone with gas or liquid to dive up or down. Abel's correct assumption was rejected by Naef (1922) who saw "no reason" for such a process. Finally, Denton & Gilpin Brown (1961, 1971), Denton et al. (1967) and Denton (1974) explained the function of the chambered shell and buoyancy control of the cephalopods became apparent.

The basic design of Coleoidea has been presented by Naef (1922). Their origin lies in the Ectocochleata of Late Silurian to Early Devonian age as documented by Bandel et al. (1983) and further discussed by Bandel & Boletzky (1988). Coleoidea are characterized by a functional siphuncular tube with a construction as found in Orthoceratida. They may well have had ten arms and a buccal apparatus resembling that of modern squids. Their hallmark is the internal shell whereas shell additions to the outside of the phragmocone such as a rostrum are possible but not necessarily present. The distinction from Ectocochleata is, therefore, difficult (Bandel 1982, Bandel & Stanley, 1988) because it is not always evident in fossil material whether a phragmocone was covered by mantle or not. In case no additional shell material is added to the outside of a phragmocone, the presence of muscle mantle can not be reconstructed with certainty.

## REDESCRIPTION OF *NAEFIA*

The genus *Naefia* has been described by Wetzel (1930), 36 years before *Groenlandibelus* became known (Birkelund 1956, Jeletzky 1966). Both genera have a shell that has been interpreted to resemble that of modern *Spirula* but with a straight orientation of the phragmocone. *Naefia* is based on its type *Naefia neogaia* Wetzel, 1930 from the Quiriquina Formation, Maastrichtian of Quiriquina Island, in the bay of Talcahuano near Concepción, southern Central Chile.

For the present research we have revised the five specimens housed in the collections of the Geological Department of the University of Concepción, Chile, in addition to new material collected by one of us (Wolfgang Stinnesbeck) in

the type localities of the Quiriquina Formation. These specimens will also be housed in the University of Concepción.

The best preserved specimen consists of a straight phragmocone with an apical angle of about 14°. It is about 20 mm long and 4.5 mm wide and consists of 13 chambers, with the earliest chambers broken off. Septa are simple watch glass-like and round to oval. The teleoconch in other specimens studied has a width of more than 12 mm. Other shell fragments indicate that the shell may have grown to at least 100 mm in length and 15 mm in width.

Growth lines demonstrate the presence of a straight apertural margin on the ventral side of the shell, as is also indicated by the position of the siphuncular tube within the shell. A narrow projection is present on the dorsal side of the apertural margin. It consists of two narrow zones with sharply forward curving growth increments on both sides. This proostracum forms a double keeled dorsal ribbon seen on the outer layer of the phragmocone. It thus represents a narrow dorsal projection of the shell margin, with dense lateral growth lines which are steeply inclined and disconnected from the margin. The proostracum was narrow, elongate and relatively long, although its actual length can not be determined.

On the dorsal inner shell wall, a rectangular scar of tissue attachment is present on the anterior dorsal part of each chamber (Plate 1). It was imprinted by tissue to that posterior position of the shell tube next to last formed septum of the chambered shell (phragmocone). The rectangular scar is surrounded by a groove, which therefore corresponds to a thickening of the shell. The scar is about one third of chamber in height.

The initial chamber is globular in shape, about 4 mm wide, and attached to the shell tube with an inclination towards the ventral side (Plate 2). No remains of the siphuncular tube are preserved in the initial chamber. In polished section, an elongate sausage-like structure is present. It contains sediment of different composition than the remainder of the chamber. This suggests that a siphuncular tube of originally organic composition may have existed which disappeared due to the activity of microbial organisms.

Later chambers are about three times wider than high. The siphuncular tube is in a marginal position and consists of a single organic layer with very short mineralized septal necks (Plate 2). Each mineral neck ends at a short distance posterior to the septum to which it belongs. These mineralized portions of the siphuncular tube continue only for about one fourth of the height of a chamber. The tube extends for one chamber height and individual segments are attached to the interior of the septal neck of the chamber formed before. The septal necks are also mineralized and the siphuncular tube ends within the septal neck of the previous chamber. The tube diameter is about 3 mm in a chamber that measures 10 mm in diameter.

### Remarks

Wetzel (1930) extracted his type material of *Naefia neogaia*, two small phragmocones, from concretions containing abundant *Eubaculites carinatus* which occur commonly in the upper portion of Quiriquina Formation. The age of this formation was determined by ammonites (Stinnesbeck 1986, 1996) to represent the Late Maastrichtian. According

to Wetzel (1930) the chambered conical fossils have an apical angle of about 13°. The diameter is round and the siphuncular tube lies marginal. The septa are simple, with an even convex-concave curving and a distance between each other of about 0.6 mm from each other in the juvenile shell, and up to 4 mm in later shell portions. Wetzel's (1930, Pl. 14, Fig. 3) illustration shows two fragments of chambered cones, one of which is reproduced by Haas (1997). There is no trace of a rostrum, as has been suggested by Haas (2003).

Biro-Boguskoy (1982) added new specimens and new information on *Naefia* from Quiriquina Island and the mainland villages of Lirquén and Cocholgue, both at the sea shore to the north of Concepción. His specimens are up to 14 mm in length, with an apical angle of 15°. Biro noted some deposits on the outside of the phragmocone, which he considered transitional to *Belemnoteuthis*. He also suggested that *Naefia* should best be placed in the proximity of *Groenlandibelus rosenkrantzi* (Birkelund 1956). Stinnesbeck (1986) added several new specimens from Lirquén and Tomé and identified dorsal lines on the phragmocone which represent the projecting narrow proostracum.

Filled chambers resembling *Naefia neogaea* were described from the Maastrichtian of northeastern Mexico (Ifrim et al., 2004, Text-fig. 2A–B). These steinkerns of single chambers of a phragmocone with a marginal siphuncular tube neither show remnants of a dorsal proostracum, nor imprints of a tissue attachment scar. Only a longitudinal striation on the dorsal side may indicate the former presence of a proostracum. In consequence, this fossil could just as well represent the phragmocone of a belemnite. They remain enigmatic. If they were to belong to belemnites these would be the only ones known from the Late Cretaceous of that region.

Haas (1997, Fig. 1, 4) illustrated a dorsal view of the phragmocone of *Naefia neogaea* from the Quiriquina Formation, demonstrating the presence of slender narrow proostracum. Haas (1997, Fig. 2) considered an evolutionary reduction of the proostracum to represent one of the important characters of *Groenlandibelus* and *Naefia*. In his idealized reconstruction of a groenlandibelid cephalopod, he united characters of both genera and the resulting animal has a relatively short proostracum, a ventrally open body chamber and a short rostrum. The whole shell is reconstructed as resting in the dorsal portion of a *Sepia*-like animal.

### Special characters of *Naefia*

1. The protoconch is spherical, quite large in comparison to that of *Spirula* (more than four times); it contains the beginning of the organic siphuncular tube.

2. The phragmocone is slender, with a narrow apical angle of about 14°, and without a cover of external shell material added from the outside.

3. The septa are simple and evenly rounded. The siphuncular tube resembles that of belemnites. It corresponds to an organic continuation of the short calcareous septal neck.

4. The living chamber (camera terminalis) has a narrow proostracum on its dorsal side and was open in unknown length at its ventral side. The median dorsal ribbon represents a projection of the aperture and very narrow marginal zone. The aperture of the phragmocone was therefore con-

nected to a narrow spine-like projection with unknown dimension and an otherwise simple margin. This projection was already present in young individuals.

5. A rectangular attachment scar of the body is identified internally, in a posterior position on the dorsal side.

## DISCUSSION OF OTHER SPECIES THAT HAVE BEEN PROPOSED TO BELONG TO *NAEFIA*

A single phragmocone considered to represent a *Naefia* was described by Doyle (1986) from the Campanian-Maastrichtian Ariyaloor Group of Pondicherry, southern India. It belongs to the fossils collected in the Tiruchirappalli area by Forbes (1846), obviously with unknown exact locality and stratigraphic position. This area of Tamil Nadu exposes fossil bearing strata that range from Aptian to Maastrichtian (Bandel 2000).

The apical angle of the phragmocone is about 8.5°. The largest fragment is 24.5 mm long and has 7 chambers preserved. The dorsal wall of the phragmocone bears a median keel. This structure is interpreted to represent the proostracum and resembles the one found in *Naefia neogaea* but differs in details. According to Doyle (1986, Fig. 1d, Fig. 4) the Indian material differs from *Naefia neogaea* from Chile by having a double keel. *Naefia neogaea* is characterized by dorsal ribbon growth lines that strongly curve forwards. This zone appears to be narrower than that described from *Naefia* aff. *neogaea* from India.

A siphuncular tube is present at the ventral side and a median dorsal line was noted on mould that reflects the presence of an internal furrow on the phragmocone (Doyle 1986, Fig. 2b). Such a dorsal line is not present in *Naefia neogaea* from Chile but resembles features noted in *Naefia kabanovi* from Russia (see below). Doyle (1986) noted that the Indian fossil differs from *Groenlandibelus* by the shape of the "proostracum". The south Indian phragmocone could possibly be derived from a belemnite.

*Naefia kabanovi* from the Aptian of Russia was described by Doguzhaeva (1996, Text-fig. 4, Pl. 6, Figs. 1–5, Pl. 7, Figs. 1, 2, Pl. 8, Figs. 1–4, Pl. 9, Figs. 1–3). It consists of a phragmocone that reaches an apical angle of 14° when younger and later may be as narrow as 7°. The chambers are about three times wider than high. Septa are simple and reported to be constructed of lamello-fibrillar nacre, as is found in the septa of *Spirula*. The siphuncular tube lies ventral and continues into the septa with short septal necks. It is described as consisting of two spherulitic-prismatic layers. The final chamber (body chamber) is reported to be short. The shell wall shows a prismatic structure, coated by an outer layer which is thicker ventrally than dorsally. No nacre is reported from the walls of the conotheca. On the inner mould of the phragmocone, body attachment scars are found. They are longitudinal, slender, spindle-like and thus differ strongly from the rectangular attachment scar of *Naefia neogaea*. Instead, they may correspond to the "Normallinie" which is noted in many cephalopods and is not specific to Coleoidea (in case of the orthoceratids see discussion by Bandel & Stanley 1988).

According to Doguzhaeva (1996) the suture line is normal to the shell axis in *Naefia kabanovi* and oblique in *Naefia neogaeia*. However, this difference does not exist and septa in *Naefia neogaeia* are also oriented normal to the shell axis as well. Doguzhaeva (1996) further suggested that the outline of the proostracum of the two species is identical. However, this character is not preserved in *Naefia kabanovi*, and its first chamber is also unknown.

Hewitt & Jagt (1999, Fig. 3D) illustrated a fragment of a Campanian *Naefia* derived from the collection of the Royal Ontario Museum. The specimen preserves sheets of a nacreous microstructure. They consequently suggested that the Aptian *Naefia kabanovi* Doguzhaeva 1996 should also have presented nacre, composing its septa, similar to the modern *Spirula*. This nacre should have been of lamellar-fibrillar type as defined by Mutvei (1964, 1970). Both, the outer and the inner shell layer of *Naefia kabanovi* are described as prismatic in structure. 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 nacreous construction of septa are of *Spirula*-type.

The attachment scar distinguishes the Chilean *Naefia neogaeia* from the Russian *Naefia kabanovi* and *Naefia* aff. *neogaeia* from India. The Chilean *Naefia* is characterized by rectangular attachment scars surrounded by a furrow. The scar is positioned in the anterior part of each chamber. It is as wide as the dorsal outer ribbon and as high as one third of each chamber. In contrast, attachment scars of *Naefia kabanovi* Doguzhaeva, 1996 are elongate and cross the entire chamber in height, as is noted in the phragmocone of belemnites.

The two species described as *Naefia* aff. *neogaeia*, from the Cretaceous of India, and *Naefia kabanovi*, from Russia do not fit the characters of *Naefia* sufficiently to include them in the same genus as *Naefia neogaeia* from Chile. 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. The proostracum of the Indian coleoid is a little wider and of different ornament to that of *Naefia neogaeia*. Both these fossils should not be included in the genus *Naefia*, but rather be placed with belemnite-like endocochleates.

A *Naefia* described from Mexico by Ifrim et al. (2004) may belong here or not. The fossil consists only of internal chamber-fills which present no features that would allow a decision that this was a phragmocone of a belemnite or of *Naefia*.

### **Comparison of *Naefia* with *Groenlandibelus*, evaluation of the family Groenlandibelidae**

The family Groenlandibelidae has been erected by Jeletzky (1966) around *Belemnoteuthis rosenkrantzi* Birkelund 1956. Jeletzky (1966) later excluded the genus *Belemnoteuthis* from the group based on differences in the first chamber. Even though the phragmocone of *Naefia* and *Groenlandibelus* may be similar to belemnites in shape, Jeletzky (1966) noted that differences exist with regard to the beginning of the siphuncular tube. While belemnites are characterized by an organic first septum, the siphuncular tube of *Groenlandibelus* begins with a blind sack extending into the first

chamber of the phragmocone, as is the case in modern *Spirula*.

The shell is essentially straight in both *Naefia* and *Groenlandibelus*, and apical angles are narrow, between 12°–15°. Watch-glass-like septa and simple sutures characterize the phragmocone in the two genera and chambers are about three times wider than high. Birkelund & Hansen (1974) found these septa to resemble those of belemnites. In *Groenlandibelus*, however, the apical part of the phragmocone walls is covered by a short, wrinkled cone forming a short rostrum. *Naefia*, on the other hand, does not present a rostrum, even though the phragmocone grew longer and wider.

The dorsal side of *Groenlandibelus* carries a ridged elongate structure that is reconstructed as proostracum (see also Doyle 1986 for schematic drawing). This ribbon is narrow and presents sharp margins. It was apparently unconnected to growth lines (Birkelund 1956). A dorsal keel may also be present, which according to Jeletzky (1966) resembles the one found in the belemnite *Diplobelina*, and is similar to the proostracum of *Naefia*.

The ventral siphuncular tube is relatively wide, not mineralized, but may have been double-walled (Jeletzky 1966, Pl. 20–22). Even then, both walls were of organic composition. The septal necks are relatively long in early chambers and gradually shorten. Their mineral composition ends on the margin of the siphuncular tube. It initiates in the first globular chamber. It is of sausage-like shape and continues for three-quarters of the height of the first chamber. It consists of organic material and is attached to the inside of the chamber by a sheet (prosiphon) (Jeletzky 1966, Pl. 20, Figs. 1A, B). The siphuncular tube could have been similar in *Naefia*, but the first chamber of *Groenlandibelus* as documented by Jeletzky (1966, Pl. 20, Fig. 1A) is much smaller, with only about 0.5 mm, contrasting to 4 mm in *Naefia*.

According to Jeletzky (1966) the Groenlandibelidae represent members of the order Sepiida. In *Groenlandibelus*, Jeletzky (1966) noted a "prismatic structure" of the phragmocone wall and a double walled siphonal tube. In a thin section, Jeletzky (1966, Pl. 23, Fig. 1A) documented vertical structures in both the phragmocone wall and the septum. They could represent remnants of columnar nacre. His interpretation of the original structure of the outer shell wall as prismatic is thus doubtful.

Doguzhaeva (1996) suggested that the structure of the siphon of *Naefia* resembles *Groenlandibelus*, based on information gathered from *Naefia kabanovi*. Since this species is not a member of the genus *Naefia*, the Russian phragmocone can not be assigned properly. Doguzhaeva (1996) interpreted the outer layer of the siphon to represent a structurally modified continuation of the septal neck, whereas the inner layer would represent the remains of a slightly calcified wall, or a wall of organic composition.

According to Jeletzky (1966, Pl. 23, Figs. 1D, 1E) and Birkelund & Hansen (1974, Pls. 13–15), the siphuncular tubes of *Groenlandibelus* and *Spirula* differ. In both genera, the septum apparently did not continue into an outer calcareous tube, but mineralized layers ended right next to the hole through which the siphuncular tube passed. This tube is predominantly of organic composition. *Naefia*, in contrast, has mineralized septal necks, similar to those found in belemnites.

Jeletzky (1966) suggested that both *Groenlandibelus* and *Naefia* represent members of the Groenlandibelidae. However important differences exist between *Groenlandibelus rosenkrantzi* and *Naefia neogaeia* regarding the presence of a rostrum (Jeletzky 1966, Pl. 20, Fig. 1A), the shape of the transition of the septum into the siphuncular tube, and the size of the first chamber. Haas (1997, Fig. 2, 2003) provided a model in which *Groenlandibelus* and *Naefia* both present a short proostracum and a rostrum. Both features could serve for a reconstruction of *Groenlandibelus* as described by Birkelund (1956), Birkelund & Hansen (1974) and Jeletzky (1966). For *Naefia*, however, they can not be confirmed. According to our restudy, *Naefia neogaeia* may have had a slender narrow elongate proostracum and no rostrum.

### Comparison of *Naefia* with *Spirula*

*Spirula* is characterized by an internal open coiled shell with smooth apertural margin. The shell is calcareous, located in the posterior end of the animal and contains over 30 chambers in adults, connected by a siphuncular tube. *Spirula spirula* (Linné 1758), a member of the Spirulidae Orbigny, 1826, corresponds to an animal without a radula (Kerr 1931). It lives at about 600–700 m depth during the day and rises to about 300 m during night. The initial chamber of its shell is globular and the siphuncular tube has a double wall (Bandel & Boletzky, 1979). Naef (1922) noted that the external layer of the siphuncular tube 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 observed in septa of *Spirula* differs from the nacre seen in other mollusks, including that of *Nautilus*. The ultra-structure of the shell of *Spirula* was described by Mutvei (1970), and by Dauphin (1976). The latter author noted that the calcareous siphuncular tube begins with an organic tube that initiates in an organic attachment sheet (prosiphon) (Dauphin 1976, Fig. 23). In *Spirula*, the nacre of the septum and the outer siphuncular tube consists of needles of about 0.2 micron in diameter arranged in layers oriented along the growth surface and not in platelets. This structure was called lamello-fibrillar by Erben (1972). Between the outer calcareous and the inner organic layer of the siphuncular tube, a porous intermediary layer exists of prismatic needles (Dauphin 1976, Figs. 18–21). The detailed three-layered construction of the siphuncular tube of *Spirula* was first described by Bandel & Boletzky (1979). A similar tube but with shorter fully calcified outer wall has been present in the late Triassic aulacoceratidid *Dictyoconites*, analyzed by Bandel (1985).

The permeable zone within the siphuncular tube of *Spirula* is as long as one chamber is high. In consequence, much of the chamber liquid is in contact with the living siphuncle. Liquid is actively moved in and out of the buoyancy system by a salt pump of the siphuncular mantle. While much of the vertical movements of *Spirula* may simply relate to its weight, – the animal is heavier when well fed and lighter when digestion is completed –, the buoyancy of the shell may also change fairly rapidly (Bandel & Boletzky, 1979).

The siphonal system is responsible for buoyancy regulation and thus represents an important feature in shell

construction. It is therefore important to note that the siphuncular tube of *Naefia* differs considerably from that of *Spirula*. In *Spirula*, the septal neck is continuous through the entire chamber, forming a solid outer wall, whereas in *Naefia* only a part of the siphuncular tube forms a solid outer wall. The initial chamber of *Naefia* is about five times larger than that of *Spirula*, and there is a shell layer in *Spirula* added from the outside to the phragmocone that is not found on the *Naefia* shell. Visceral mass is connected to the shell of *Spirula* along a dorsal ribbon. On both sides of this ribbon retractor muscles end in the tissue of the mantle (Bandel 1982).

### Hypothesis of a transition from a *Spirula*-like shell to the cuttlebone of *Sepia*

Modern *Sepia* has a characteristic internal shell, the cuttlebone. It varies quite a lot in shape and size among the living species, but is always of similar construction. *Sepia* is not found in the Americas and most of the Central and Eastern Pacific. About 120 species exist of the genus and the similar *Sepiella* (Adam & Rees, 1966, Voss & Williamson, 1971, Roeleveld 1972). The cuttlebone of *Sepia* has been described by Appellöf (1823) and his terminology has largely been utilized and adopted by Bandel & Boletzky (1979). Accordingly, the cuttlebone consists of a dorsal shield and the ventral chamber zone. The mid-dorsal line close to the posterior end of the dorsal shield bears a more or less well developed spine or rostrum. The ventral surface the chamber zone has the siphuncular zone anterior and the last formed chamber posterior. This chamber zone is embraced by the fork. The cuttlebone serves as backbone with solid lateral attachment to the large marginal fins and as buoyancy regulator due to ventral chambers.

The construction of the *Spirula* shell was compared to that of *Sepia* by Bandel & Boletzky (1979). The authors found that the phragmocone wall and the septa are built of a specific nacre, but that the prismatic shell walls are otherwise similar to the ones found in *Sepia*. While the shell structure is similar, the embryonic shell of *Spirula* and *Sepia* differs very strongly. While *Spirula* has a rounded initial chamber that of *Sepia* is an open cup-like structure. The first chamber of *Spirula* is closed by the first septum, while the initial shell of *Sepia* grows on its anterior edge and chambers are added to it in consecutive layers on top of each other. It was suggested by Appellöf (1893), Bandel & Boletzky (1979), Haas (1997), Hewitt & Jagt (1999) that the septa as in *Spirula* developed into the inner plate of the cuttlebone of *Sepia*, and that the siphuncular tube as in *Spirula* was opened to form the *Sepia* septa and supporting walls. The siphuncular tube is, therefore, interpreted to be homologous to the flat chambers of the cuttlebone of *Sepia*.

Squires (1983) described a cuttlebone of a sepiid from the Eocene of California. Transitional species should therefore be older. They should present chambers not connected to a flat ventral chamber zone on one side and a globular initial chamber on the other, thus resembling neither *Sepia* nor *Spirula*. *Groenlandibelus* or *Naefia* do not provide any similarity regarding their siphuncular tube, which rather resembles that of belemnites instead.

Bonnard et al. (1997) and Carlini & Graves (1999) carried out a molecular phylogenetic analysis comparing *Spirula*

with other coleoids and noted neither a link to *Sepia* nor to teuthoids. The results of Warnke et al. (2003) also support this analysis. Woodward (1856) placed the Sepiidae on equal level to the Belemnitidae and the Spirulidae. This interpretation has in principle been confirmed by the molecular data, as the distance stated by Young et al. (1998) between Sepiidae and Spirulidae.

Coleoids with ten arms (Decabrachia Boettger, 1952 (= Decapoda)) according to Haas (1997, 2003) are considered to form the two sister groups Uniductia Berthold & Engeser, 1987 and Oegopsida. The first have lost their calcified shell and are considered to have had ancestors similar to the Groenlandibelidae which are interpreted to be representatives of the stem group of the Uniductia by Berthold & Engeser (1987, Fig. 8). *Groenlandibelus*, on the other hand, is considered close to the stem group to the Spirulida by Haas (2003). According to that interpretation it was a member of the Uniductia which have the ventral living chamber open, as in the belemnites but convergent to them. The Uniductia, thus, remain to be a rather artificial construct, and the resemblance of a stem group represented by *Groenlandibelus* is only assumed. This construct has not been improved by creating a reconstruction of an animal that unites the features of *Groenlandibelus* and *Naefia* (Haas 1997, Fig. 2).

#### SHELL CHARACTERS THAT CAN BE UTILIZED IN THE ANALYSIS OF CEPHALOPOD EVOLUTION AND IN DISCRIMINATION OF NAEFIA FROM OTHER COLEOIDS

The shell is interpreted in terms used with Ectocochleata and Mollusca in general.

**a.** The organic shell is formed by the mantle edge and its special glandular cells (periostracum gland). It is usually organic in construction and is also present in cases where the shell is formed covered by mantle, as is the case among coleoids. Periostracum is present in all conchiferan mollusks including the cephalopods, at least at some stage of their ontogeny. In case of the Endocochleata the periostracum is secreted below the cover of the muscular mantle. In this group the shell secreting epithelium is progressively covered by muscular mantle during embryonic development. The shell is formed below this muscular mantle, that in ectocochleate cephalopods is found in front of the periostracal gland zone. In *Naefia* the periostracum is not covered by additional shell (Pl. 1 and 2), in contrast to *Spirula*, *Groenlandibelus* and *Sepia*.

**b.** The mineralized shell is produced by the mantle behind the periostracal gland zone and is formed within and by the extrapallial liquid secreted by the mantle. The characteristic biomineral of the shell is nacre which is found in all phragmocone-bearing cephalopods. Nacre can be organized as platelets forming pillars (*Nautilus*-nacre), or as lamellar structures composed of needles (*Spirula* – nacre). *Spirula*-nacre is also called lamellar prismatic nacre and is only found in the phragmocone of Endocochleata. Among these it helps to distinguish such groups that also have *Nautilus*-nacre as

dominant biomineral of the inner layer in the phragmocone wall, and *Spirula*-nacre in the septa and other taxa, where only *Spirula*-nacre is present. This latter case is present in *Spirula* and *Sepia*, and the former in belemnites and aulacoceratids. Nacre is aragonitic and, thus, commonly replaced diagenetically by calcite or other substances. During this process crystal morphology changes, as in case of all individuals of *Naefia* and *Groenlandibelus* that have been studied.

**c.** A more simple construction is present in the mineral shell that is produced outside the shell mantle behind the periostracal gland by the cells of the muscular mantle. It does not consist of nacre or other characteristic molluskan biominerals. An outer shell layer secreted by the muscle mantle can be organic, calcitic, or aragonitic or all three, but it may also be totally absent, as is the case in *Naefia*. Deposits formed in the shell sac by the cells of the muscular mantle may be calcitic or aragonitic with organic material added to it. In either case, characteristic textures are developed. Aragonitic morphologies are commonly spherulitic or consist of spherulite sectors, as on the cuttlebone of *Sepia* and the rostrum of many aulacoceratids. Calcitic structure is regularly prismatic on a base of spherulites as is the case in the rostrum of belemnites. The composition of the rostrum may change from calcitic to aragonitic or vice versa during shell growth. In *Spirula*, the aragonitic outer layers are spherulitic and prismatic (Pl. 3). The latter structure was likely developed in the rostrum of *Groenlandibelus* before its transformation into calcite.

**d.** The siphuncular tube may resemble that of *Nautilus* with a calcareous and porous outer layer and an organic inner layer, but it may also be a single organic tube as in belemnites where it grades into the mineralized septa at the septum – tube contact. In advanced ammonites the siphuncular tube may be distinct from the septa, and it may be double walled as in *Spirula* and *Aturia*. In case of some of the Paleozoic Ectocochleata even more complex structures are known to exist. In case of *Spirula* the tube may occasionally have been sealed and filled with organic shell. The siphuncular tube of *Naefia* is like that of belemnites (Pl. 2), while that of *Groenlandibelus* appears to differ in regard to its attachment to the septum.

**e.** The first shell developed, or embryonic shell may reflect eggs rich in yolk, such as in *Sepia* or *Nautilus*. In these organisms, it is larger than 0.5 mm in diameter. Eggs that are relatively poor in yolk exist in the Recent *Spirula*, in ammonites, belemnites and aulacoceratids, among fossil forms. The shape of this first shell is quite stable within the groups. Ammonites always develop an “Ammonitella” that remains similar in shape and size from the Devonian to the end of the Cretaceous. Similar conditions can be expected in other groups with external or internal shell. Apparently, Belemnitida and Aulacoceratida form another large unit. They are closely connected to their common stem group, the Bactritida. The first shell of *Naefia* and *Groenlandibelus*, in contrast, resembles that of those bactritids that developed into the ammonites and present a siphuncular tube entering the first chamber (Pl. 3).

f. Anterior of the last septum, the shell is more or less tubular in *Spirula*, and short. It is elongate in Aulacocerida, closely resembling that of the Bactritida. In Belemnitida, it is short on the ventral side and extended into a more or less elongated dorsal lobe or spine, the proostracum. In this respect, *Naefia* and *Groenlandibelus* resemble the belemnites.

g. The visceral mass of that part of the body that enters the "living chamber" leaves a scar on the dorsal side. This scar reflects the shape of attachment of the soft tissue to the shell. It is elongate in the Belemnitida and Aulacocerida and also in *Spirula* (Pl. 3), and short and rectangular in *Naefia* (Pl. 1).

In conclusion *Naefia* differs from *Groenlandibelus* in regard to its tissue attachment scar, the connection of the septum to the organic siphuncular tube, the size of the first globular chamber of the phragmocone and the absence of a rostrum. It is distinguished from belemnites by the shape of the attachment scar, the composition of the siphuncular tube in the initial chamber of the phragmocone and the absence of a rostrum. *Naefia* differs from *Spirula* by the shape of the tissue attachment scar, the composition of the siphuncular tube, and the presence of a proostracum, besides not having a coiled shell. *Naefia* differs from the aulacoceratid *Dictyoconites* in regard to the tissue attachment scar, the composition of the siphuncular tube in the initial chamber of the phragmocone, the presence of a proostracum and the absence of a rostrum. If *Naefia* would have been found in strata of the Late Paleozoic it could be connected to Bactritidae and would then differ from this group by the attachment scar to the interior of the protoconch, as well as by the presence of a proostracum. In conclusion, *Naefia* represents a Late Cretaceous coleoid that does not fit into the Groenlandibelidae, the Spirulidae, the Belemnitidae, the Aulacoceratidae, and the Bactritidae.

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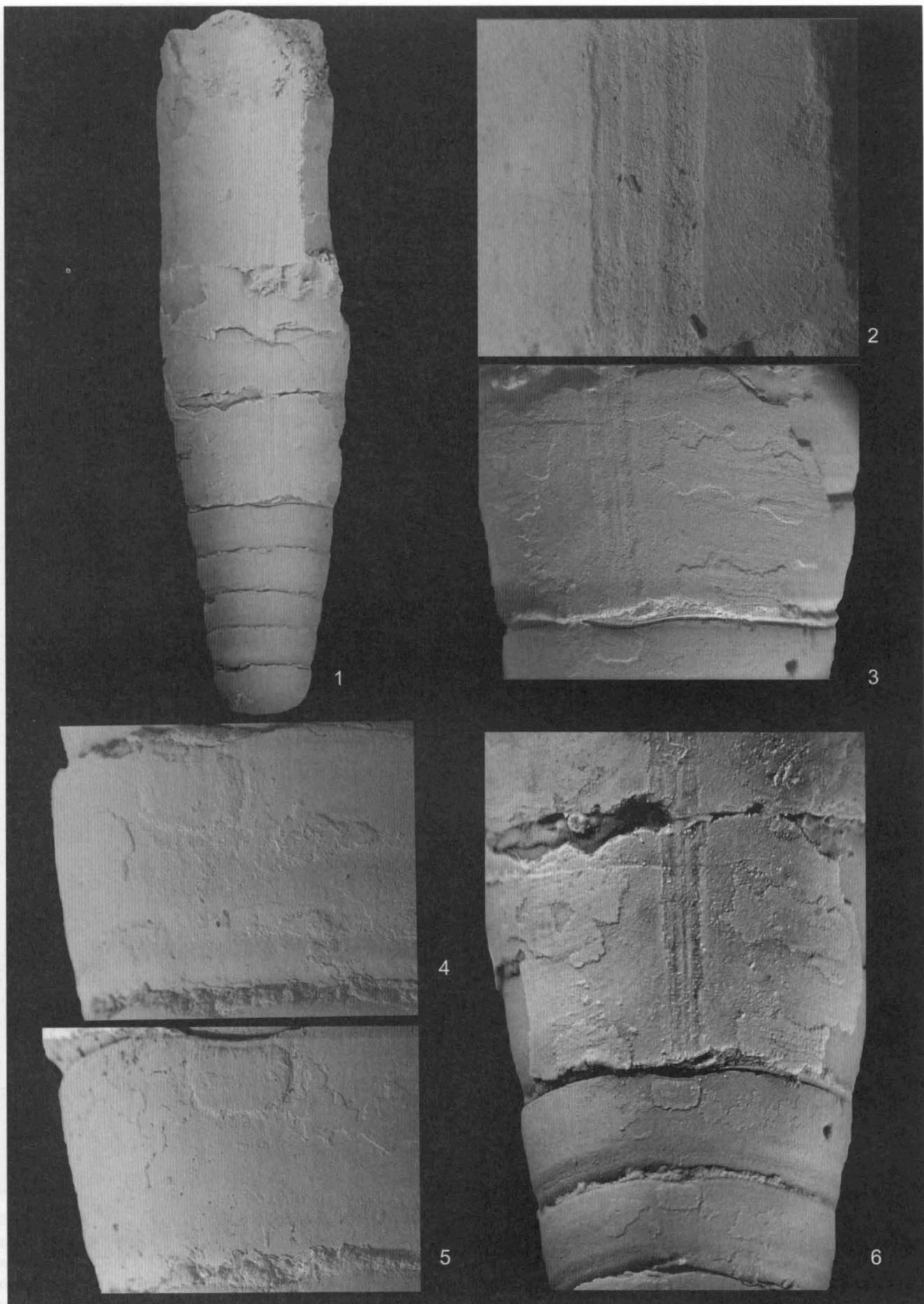


Plate 1. Fig. 1 Dorsal view of 20 mm long phragmocone of *Naefia neogaeia*. Details are present in figures 2–6. Fig. 2 Proostracum with two keels and growth lines at its margin. Fig. 3 Part of the shell with proostracum and with internal chamber filling. Fig. 4 and 5 Attachment scars of the body to the shell in consecutive chambers with rectangular shape preserved on sediment of the filled chamber.

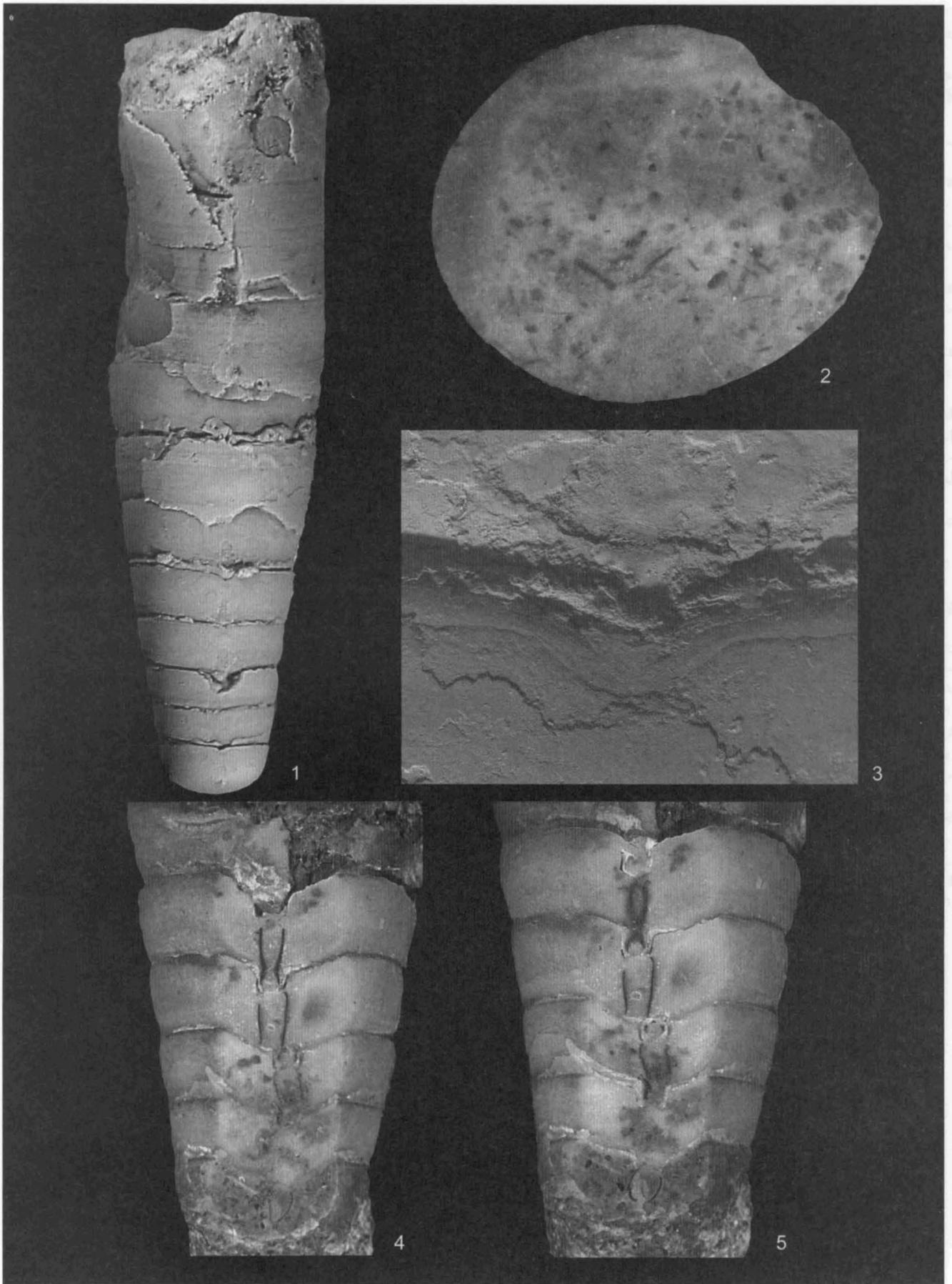


Plate 2. Fig. 1 Ventral side of the shell of *Naefia neogaeia*. The 20 mm long shell is seen in dorsal view on Plate 1. Fig. 2 Polished section of the globular first chamber of 4 mm in width and 4.5 mm in greatest diameter with traces of the rounded blind end of the siphuncular tube in the sediment filling the chamber. Fig. 3 Suture line of the fifth septum in detail with traces of the attachment lamellae of the siphuncular canal to the inner side of the shell wall. Fig. 4 and 5 Sections of the siphuncular tube on the 8 mm long cambered part representing the mineralized septal necks and the succeeding organic tube. The whole specimen is 20 mm long and composed of 11 chambers.

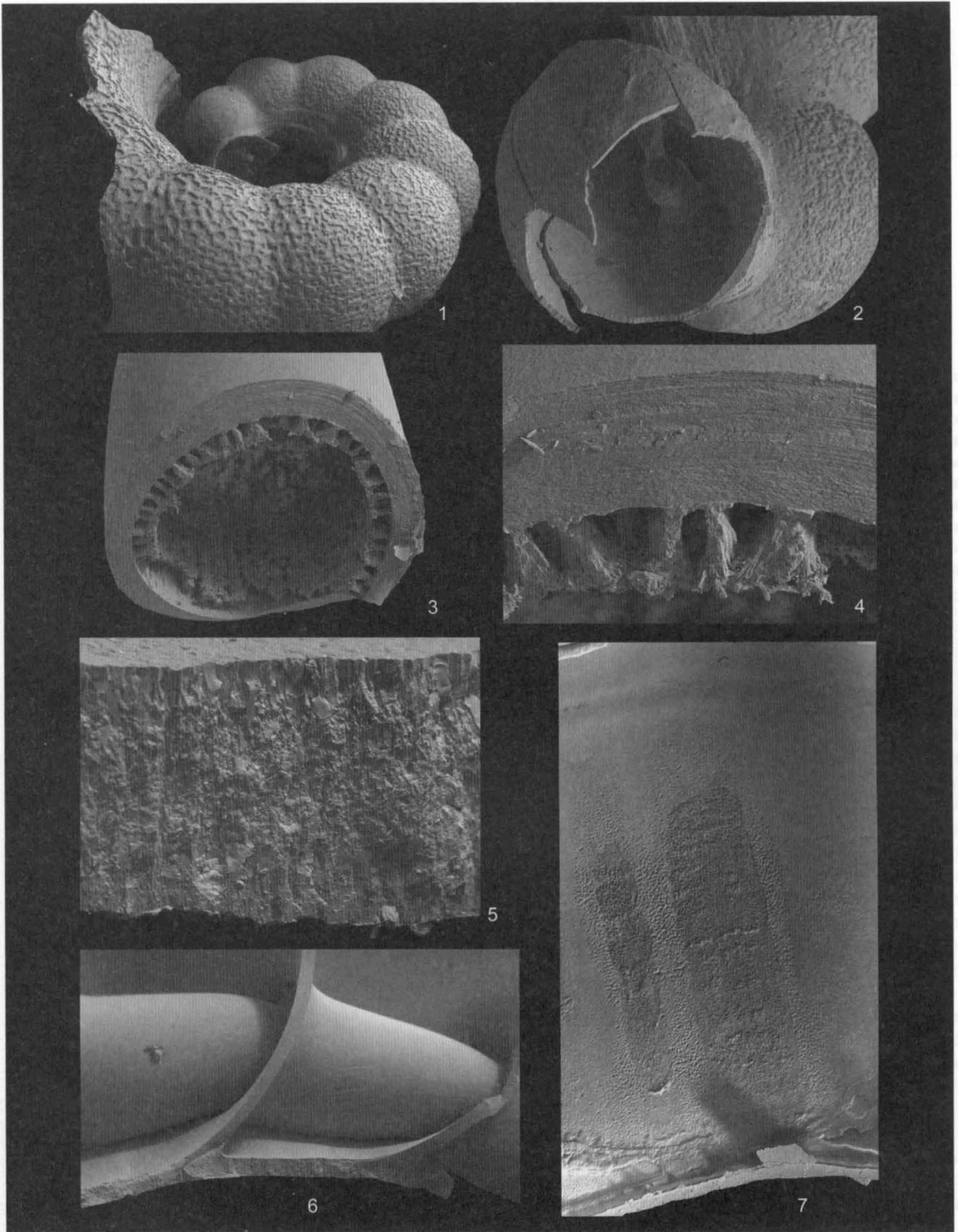


Plate 3. All figures are from *Spirula* from the Indo Pacific of Western Australia. Fig. 1 Shell with about 3 mm in diameter with opened first chamber and outer side of phragmocone covered by external calcareous deposits. Fig. 2 Opened first chamber of about 0.5 mm width with the beginning of the siphuncular tube. An organic sheet (prosiphon) connects the initial organic layer of the tube to the shell. This organic cap continues in a mineralized elongate septal neck. Fig. 3 Siphuncular tube with nacreous outer wall, porous pillar zone and thin organic inner tube here dissolved. Fig. 4 Detail to Fig. 3 with laminated nacre of outer tube and prismatic structure of pillar zone. Fig. 5 Section of outer wall (detail to Fig. 6) with fine grained central shell layer and inner and outer prismatic structure. Fig. 6 Shell opened to expose siphuncular tube and two fractured septa. Fig. 7 Elongate attachment scar of the body to the interior of the shell opposite to the siphuncular tube. The septa cover it, so it forms a continuous dorsal scar on the shell interior.

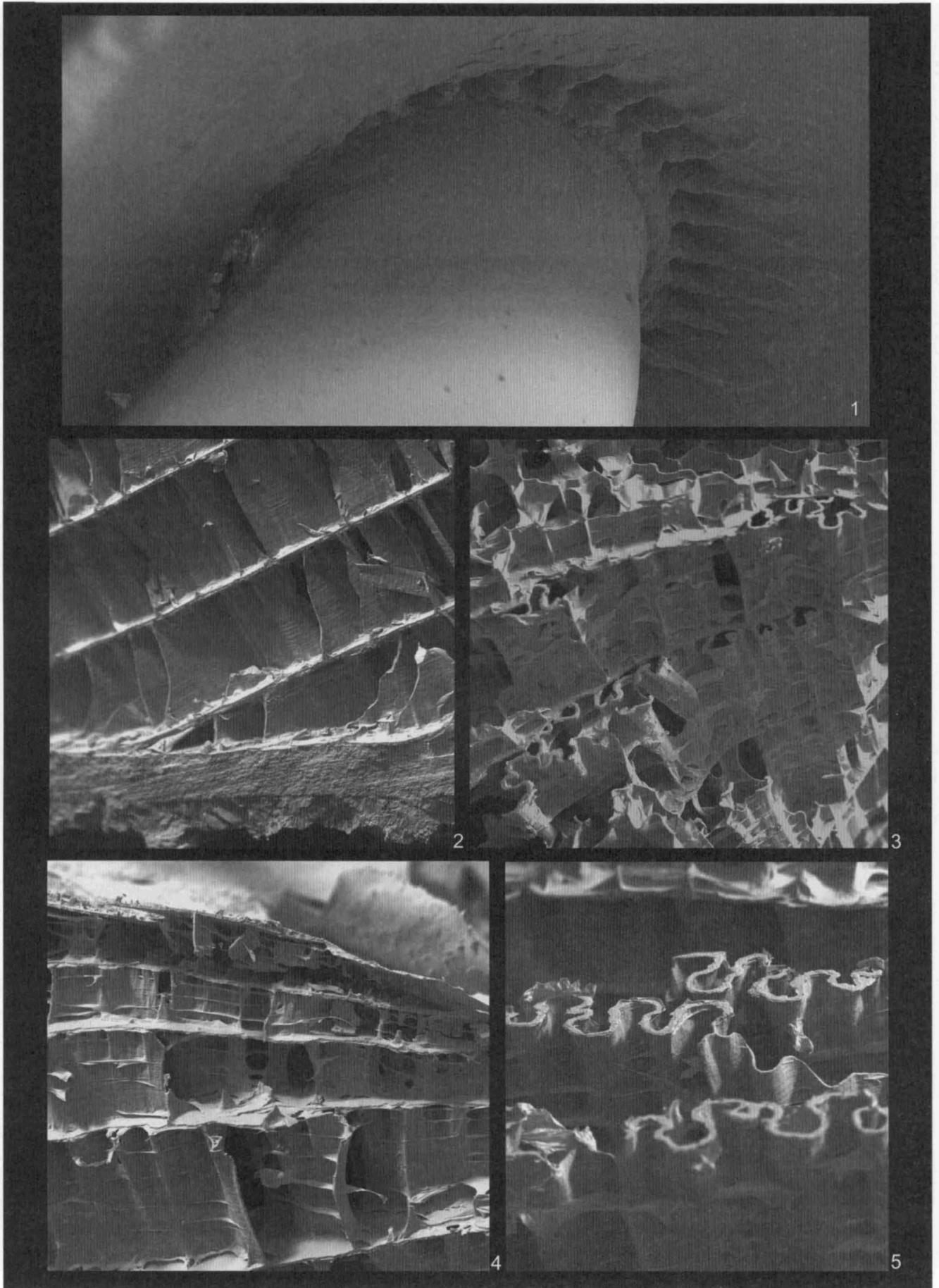


Plate 4. Fig. 1 Siphuncular tube of *Spirula*. Entrance from the chamber to the space between nacreous and organic layer. Note that pillars are not unlike those found in the cuttlebone of *Sepia*. Figures 2–4: *Sepia pharaonis* from the Red Sea. Fig. 2. Fractured cuttlebone with attachment of the septa to the outer wall. Fig. 3. Central fracture of consecutive chambers. Fig. 4. Outermost chambers and zone of chambers next to the pumping epithelium. Fig. 5. Attachment suture of chamber pillar walls to the septum. About three chambers above each other amount to 1 mm in height.

# FROM HEAD TO FOOT – AND BACK AGAIN: BRACHIAL CROWN DEVELOPMENT IN THE COLEOIDEA (MOLLUSCA, CEPHALOPODA)

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**Abstract:** The so-called arm crown (brachial crown) of the Cephalopoda is the most conspicuous part of the pedal complex in this class of molluscs (earlier reports claiming a cephalic nature of arms notwithstanding). In contrast to what is expected of an archetypal “molluscan foot”, the brachial appendages of coleoid cephalopods are able to perform very complex motor actions, individually, in pairs (e. g. ejectible tentacles) or in concert (whole arm crown, with or without web). The brachial armament (suckers, sucker-derived structures) adds another level of functional integration to those of the brachial crown and of the individual arms. Proximally the arm crown of cephalopods is very closely associated with the cephalic complex, as reflected by the technical term cephalopodium (designating the “head-foot”). In the ontogeny of cephalopods, this close morphological association and functional integration of the foot and the head is achieved during advanced stages of embryogenesis. The ventral parts are finally marked by a *pseudo-radial* arrangement, in that the brachial appendages encircle the mouth (“circum-oral” appendages), whereas the dorsal parts (funnel tube, secondary head cover with extraocular eye muscles) continue to reveal the original bilateral symmetry.

**Key words:** cephalopoda, coleoidea, arm-crown, brachial appendages, foot-derivatives

## INTRODUCTION

The evolution of coleoid cephalopods is normally envisaged in relation to their respective predators and prey, taking account of an apparent functional “convergence” between coleoids and fish (Packard, 1972). In discussions about the actual causes of this convergence, the supposed role of competition between coleoids and bony fish during their evolutionary history is controversial, however (O’Dor & Webber, 1986). Whatever the emphasis chosen, it is undeniable that collectively the coleoids have been successful as active predators feeding on living crustaceans, teleost fish and other cephalopods, with only a few exceptions related to microphageous or scavenging modes. Most coleoids catch fast-moving prey and get out of the way of other predators by using very efficient sense-organs such as lens eyes and statocysts (Budelmann & Tu, 1997) and equally efficient neural control circuits for the main effector systems (Nixon & Young, 2003), namely a strong muscular propulsive system which is formed by the mantle-funnel complex (O’Dor et al., 1990), and a strong muscular brachial crown (Kier & Thompson, 2003).

The series of brachial appendages (arms and tentacles) forms the actual armament of the animal. Generally speaking, armaments are likely to change in form and function if they have to be adapted to changing tactical objectives or a need for overall functional perfection. In a biological context, prey predator relations in particular may entail something reminiscent of an arms race, as exemplified by the similarity of the coleoid eyes and statocysts with teleost eyes and otocysts. Other suggestive examples of “fish-like” structures are the lateral line-analogue of decabrachian cephalopods (Budelmann &

Bleckmann, 1988), or the horny beaks of cephalopods (Clarke & Maddock, 1988). In contrast, the brachial crown of cephalopods bears no analogy to any teleost organ complex. To allude here to an arms race-like process may seem far-fetched. However, the development of increasingly sophisticated tools (especially ejectible tentacles) having allowed coleoids to catch increasingly fast swimming prey (especially fish and shrimp) seems a likely scenario at least for squids and cuttlefish. However, the “multi purpose” character of the brachial appendages was a likely impediment to thorough change. The diverse morphologies observed in living and fossil coleoids indeed suggest a cumulation of relatively small adjustments rather than radical changes in existing equipment.

This article surveys extant coleoid arm crown arrangements, viewing the observed structural and functional diversity against the background of a morphogenetic ground pattern that is remarkably conservative throughout embryonic and juvenile development. Brief discussions are included in successive paragraphs rather than assembled at the end of the article. The resulting overall picture of developmental morphology finally helps to address the question of arm crown homology in a context of molluscan systematic morphology (Naef, 1922, 1928).

## THE BRACHIAL CROWN OF COLEOIDS: ARMS AND TENTACLES, BUCCAL LAPPETS AND WEBS

In contrast to *Nautilus*, in which the arm crown consists of two concentric “rings” of brachial appendages (Naef, 1922:

Fig. 3), the coleoid cephalopods have only one fully developed brachial series. It is supposed to be homologous to the outer brachial series of *Nautilus*. An inner series does exist in the Decabrachia (except in the pygmy squid *Idiosepius*), but it is vestigial, forming the so-called buccal arm crown, or buccal funnel (comprising the “buccal lappets”); it is lacking in the Vampyropoda (Vampyromorpha + Cirroctopoda + Octopoda; see Boletzky, 1992, 2003). Compared to an individual nautiloid arm (also called “tentacle”), which comprises a proximal sheath and a distal cirrus with relatively simple, transverse, adhesive ridges (Kier, 1987), a coleoid arm – or a specialized decabrachian tentacle (Fig. 1A) – bears some more variable adhesive structures that occupy well defined areas of the brachial surface (Kier and Thompson, 2003). This observation raises the question whether coleoid suckers and sucker-derived structures are homologous to single adhesive ridges of *Nautilus* (Boletzky, 1978–79).

In coleoid cephalopods, individual arms and pairs or groups of arms (or the decabrachian pair of specialized tentacles; Fig. 1A, D) may perform very complex motor actions involving their adhesive devices, i. e. suckers and/or hooks (Hanlon & Messenger, 1996; Sumbre et al., 2005). There are essentially ‘mechanical’ functions related to: grasping and manipulating food (Nixon, 1985); seizing a sexual partner during copulation (Hanlon & Messenger, 1996); transferring spermatophores from male to female, or – in females – attaching eggs to a support structure (Boletzky, 1986); gathering substrate particles for concealment (Boletzky & Boletzky, 1970); attaching the animal to a hard substrate (Fig. 1F); fending off would-be predators (cf. Fig. 1D); or stabilising swimming movements (Fig. 1B, C). But arms may also function as signal effectors, by taking on visually effective postures (Fig. 1E), sometimes in combination with light emission by brachial photophores (Hanlon and Messenger, 1996; Robison et al., 2003) or luminescent suckers (Johnsen et al., 1999a, b).

Figure 1 illustrates very common acts and attitudes involving the arms (or the ejectible tentacles). There are much more spectacular patterns, some of which were observed only recently. For example, *in situ* observations of deep-sea cephalopods indicate that cirroctopods may use their interbrachial membranes (or “web”; see further below) for likely tactile camouflage (Boletzky et al., 1992); that mastigoteuthid squids trail their extended tentacles as sticky plankton catchers (Roper & Vecchione, 1997); and that magnapinnid squids (Vecchione & Young, 1998) trail the extremely long, terminal filaments of their arms and tentacles, possibly for similar purposes (Vecchione et al., 2001).

As far as is known, most arm postures and actions show a bilateral symmetry, one side representing a mirror image of the opposite side (Fig. 1E). Exceptions are the “split V” display of the loliginid squid *Sepioteuthis sepioidea* (Moynihan & Rodaniche, 1982), in which the arms and the tentacle of one side point upwards while those of the other side point downwards, and a similar display observed in an undescribed Caribbean octopus (Rodaniche, pers. comm. 1990).

**An aside on terminology.** When describing coleoid arms and tentacles, terms used should be unambiguous. The term *tentacle(s)* designates the two 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 arm pairs are numbered, from the “upper” or “anterior” arms (I) to the “lower” or “posterior” arms (V), and the decabrachian tentacles then form the pair number IV (Fig. 4B). When fully formed the tentacles are characterized by the differentiation of a tentacular shaft (Fig. 1D), also called stalk, with a special ‘fast’ musculature allowing them to be ejected (Fig. 1A) at very high speed for the capture of live prey (Kier & Curtin, 2002).

The designation “upper” here refers to the horizontal swimming position of e. g. an octopus (Fig. 1B), squid (Fig. 1C), or cuttlefish (Fig. 1E). This is the so-called *physiological orientation* which is adopted in most textbooks; by extension the upper part of the animal is generally called “dorsal”. In contrast, the designation “anterior” used above alludes to a head-down position as in a hovering *Mastigoteuthis* (Roper & Vecchione, 1997) or cirroctopod (Boletzky, 2001). This position happens to correspond to that of an embryo in relation to the “underlying” yolk mass (Fig. 2A–D). It is called the *morphological* or *embryological orientation* (Fioroni, 1978: Fig. 12); it allows one to compare the body plan of cephalopods with that of other molluscs. In this orientation the apex of the mantle represents the dorsal side, while the arms extend from the ventral side. This is the orientation used here.

## BRACHIAL ARMAMENTS AND THE ORIENTATION OF BRACHIAL APPENDAGES

If the whole arm crown can be said to provide an armament for the animal, each arm or tentacle has its own armament in the form of numerous suckers or sucker-derived structures. In other words, below the integration levels of the arm crown and of individual arms, we see another level of functional integration concerned with special muscular modules that are able to make contact with other animals or with a substratum (accompanying “cirri” present in certain groups are discussed in the next paragraph). In the course of embryonic development, sucker rudiments first appear on the lower surface of arm rudiments (Fig. 2D). In the morphological orientation the sucker rudiments thus appear as differentiations of the *ventral* arm surfaces. In consequence, the interbrachial web (which appears much later during embryonic or post-embryonic development and connects the arm surfaces) can be considered a *dorsal* differentiation of the arms (Fig. 1F).

Although suckers may take on rather different forms during post-embryonic development, sucker rudiments always start out as low crests or buds aligned in a single file on each brachial rudiment (Fig. 3A). Each sucker bud soon forms a central depression. Towards the base of the arm or tentacle rudiment, the sucker buds take up alternating positions, thus forming a zigzag pattern, from which biserial, quadriserial and multiserial arrangements can subsequently arise due to a “crowding” process (Boletzky & Boletzky, 1973). Exceptions to this rule are forms in which suckers always remain in a single file, namely many octopods (Boletzky, 1978–79) and all the cirroctopods and vampyromorphs (Boletzky, 1982; Budelmann et al., 1997).

The arm surfaces bearing suckers are normally referred to with reference to the mouth; when describing juvenile

and adult cephalopods one usually mentions the *adoral* arm surface which bears suckers (or hooks). Likewise, the buccal arms (or buccal lappets) of the Decabrachia appear to be *adoral* derivatives of the (sessile) arms (Naef, 1928: Plates 21, 22). Although here “adoral” is an appropriate designation for late embryonic and post-embryonic stages, it is rather inappropriate when referring to the early embryonic stages during which the first sucker rudiments are formed; at these stages, the rudiment of the buccal mass (formed from the stomodaeum) is still excentric in relation to the arm crown (Fig. 2A–D).

Figure 3C shows the onset of a change leading from the early arrangement (which emphasized the bilateral symmetry of the arm crown) to the final pseudo-radial arrangement of the arms. Progressively the arms are growing in length and become more and more closely aligned with the dorso-ventral axis (i. e. the prospective longitudinal axis of the body); thus the suckers are increasingly directed to this axis (transiently represented by the “yolk neck”; see Boletzky, 2002a), long before the buccal mass occupies its final (central) position (Fig. 3E).

#### DIFFERENTIATION OF SUCKERS AND SUCKER-DERIVED STRUCTURES

Final differentiation of the originally uniform sucker rudiments may lead to ostensibly simple, soft suckers, as in octopus (Fig. 3D). An interesting possibility offered by these suckers is that later, when they have grown larger, they can fold around a thin object (e. g. a crab leg) and thus can grasp an item to which otherwise only extremely small suckers could become attached by suction. Alternatively, differentiation may lead to rigid suckers with horny rings as in cuttlefish and squids (Fig. 1D; for details see Schmidtberg, 1997), or to more complex suckers in which the horny rings become transformed into claw-like hooks (Naef, 1922: Fig. 68). This last transformation (see further below) takes place only during post-embryonic development; indeed no cephalopod hatchling is known to have already transformed suckers.

An intriguing condition exists in the vampyromorph hatchling, in that the arms have no suckers yet; biserial palp-like cirri are the only “armament” of the early juvenile arms (Pickford, 1949, Young & Vecchione, 1999). The vampyromorph suckers appear much later during post-hatching development, along with additional cirri. The hatchling armament thus is vaguely reminiscent of the armament of belemnoids, if one views the biserial cirri of vampyromorph arms as analogues of the biserial hooks of belemnoid arms. But this vague similarity involves clearly different morphological elements. Indeed the vampyromorph (and cirroctopod) cirri are very unlikely homologues of belemnoid hooks.

An equally intriguing adult feature is the virtual return to apparently primitive, crest-like structures replacing the suckers, especially in the copulatory arms (hectocotyli), in many coleoid males (Boletzky, 1978–79).

The adhesive function is obvious in the normal brachial suckers of coleoid arms and tentacles, especially in decabrachian suckers where adhesion is further enhanced by traction (Smith, 1996). However, one should also remember

that each sucker is under combined peripheral and central nervous controls enabling the animal to cancel adhesion (Budelmann et al., 1997).

As mentioned above, in some teuthid squids (among the Oegopsida) certain suckers are transformed definitively during juvenile development to become hook-shaped claws that lose their adhesive function. Naef (1922, Fig. 68) compared oegopsid hooks with the fossil hooks of belemnoids. The question whether they are homologous structures, i. e. horny structures derived from the so-called 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, which has interesting consequences for hypotheses on the phylogenetic position of belemnites (Boletzky, 2002b). These observations also draw attention to the possibility that simple muscular suckers do not necessarily exhibit a distinct, permanent (i. e. likely conserved in a fossil) central depression as in extant octopus suckers (Fig 3D; cf. Schmidtberg, 1999).

If the belemnoids had suckers on their arms, and if their hooks were formed as parts of these suckers (in a way similar, but certainly not identical, to the transformation of sucker rings in modern teuthid squids), then the following question will have to be considered: did the belemnoid hatchlings have suckers without hooks? Unless a fossil record provides evidence for belemnoid hatchlings equipped with hooks, it seems likely that they had relatively simple suckers (with or without horny rings).

#### THE ANCHORING STRUCTURES OF THE ARM CROWN

The head-foot – or cephalopodium – is an organ complex representing an integration level above that of the arm crown. Final integration here results from thorough rearrangements of components that started out as separate rudiments in the early course of embryonic development (Fig. 4A, B).

As to the dorsal side of the arm crown, the ultimate formation of a web (Fig. 1F) has already been mentioned in relation to the orientation of the brachial appendages. We now focus attention on Figure 3C and view it in relation to B and E. In C the bases of the arms are extending dorsally (downwards in the figure), thus encroaching upon the anterior head surface (a similar process occurs on the posterior surface of the head), while the buccal mass and the eyes remain free. Figure 3B shows a more advanced stage where the eye becomes encircled by a fold (called the primary lid) which is formed from the edges of corresponding extensions of the arm bases. Figure 3E shows the final stage where the buccal mass has disappeared and the eye is entirely covered by the membrane formed as an extension of the primary lid folds. Only in the oegopsid squids (plus a few other coleoids), a large primary lid pore remains open in front of the eye lens, as can be seen in Figure 1C, D. The secondary head cover produced by these arm base extensions not only fixates the arm crown to the head, it also provides several eye muscles, which are not visible in a surface view. What does show up in Figure 1C and D is another part derived from two arm bases, namely the funnel tube.

At a very early stage, a pair of inconspicuous streaks of embryonic tissue splits off dorsally from the posterior arm rudiments ('fu' in Fig. 4A). These streaks will later form the ridges from which the funnel tube is made, in close connection with similar ridges derived from the palleo-visceral complex that will form the funnel pouch (collar). By the time the first sucker rudiments appear (Figs. 2D, 3A), the other arm rudiments produce similar ridges extending dorsally to embrace the eye complex on either side, and the buccal mass at the anterior end (Fig. 3C, E). During the same embryonic period, vesicular organs are formed by invagination between arms I and II (probably III in Octobranchia; cf. Note at the end of explanation to Fig. 4) and between arms IV and V. These are the so-called metabranchial vesicles (Boletzky et al., 1970; Lee et al., 2003).

Since the ridges extending from arms III and IV form the so-called primary lid, they allow one to distinguish pre-ocular and post-ocular regions in the brachial crown (Fig. 4B). In Octobranchia the pre-ocular group contains I and (probably) III, the post-ocular group IV and V (Bandel & Boletzky, 1988). The term primary lid was coined by Naef (1928) who already described in great detail how the integumental folds extending from the middle arm rudiments grow around the eye on each side and finally cover it partly (e. g. in oegopsid squids) or completely; he used these folds as landmarks to demonstrate the likely homology of two octopodan arms (3) with the specialized tentacles (IV) of Decabranchia (see Fig. 2C).

Figure 4A illustrates the onset of the funnel tube derivation, which occurs much earlier than the primary lid formation. What is most important here is the fact that the funnel tube rudiments are derived from the posterior arm rudiments in exactly the same way as the primary lid and epibuccal folds are derived (subsequently) from the middle and anterior arm rudiments. The basic similarity of these morphogenetic processes is emphasised in the cartoon of Fig. 4B, which gives a condensed representation of stages IX to XII of Naef (1928). Furthermore, Figure 4B indicates "pedal segments forming arm rudiments", in other words the arms are defined as parts of the foot, and the foot is considered to be segmented. These two assumptions are briefly discussed below.

### FOOT OR NOT FOOT?

When the embryological orientation is adopted describing the embryonic pattern of brachial development in cephalopods, there can be little doubt that the arm crown represents a major part of the "molluscan foot" (Brooks, 1880, Naef, 1928, Seidel, 1960). Indeed, all the embryological arguments (Boletzky, 1988, 1993, Marquis, 1989, Shigeno et al., 2001a-c) plead in favour of the hypothesis that the brachial crown of cephalopods is pedal in origin – in other words, is likely homologous to the greater part of the foot of e. g. gastropods. A recent study of cephalopod *Hox* genes (Lee et al., 2003) strongly supports the view adopted by the afore-mentioned authors. The opposing representation given by Salvini-Plawen (1980) and maintained by Salvini-Plawen & Steiner (1996) takes no account of the significance of early ontogenetic processes. Based on some indications

from earlier literature, these authors place emphasis on the (clearly secondary) connection of the brachial complex with the supra-oesophageal part of the central nervous system; they ignore the studies pleading against the old "siphonopod" hypothesis, which they wish to re-activate. There is no evidence that would justify a specification like the one added in parentheses in the following description: "Tentacles (cephalic in origin) surround the mouth..." (Lindberg et al., 2004: 271).

As Budelmann (1995) noted earlier: "...the extreme complexity of the cephalopod brain and the differentiation of most of its ganglia into several subunits (lobes) makes it often very difficult to identify, or just to discuss, homologues of individual parts of the cephalopod and the mollusc brains..."; as an example he mentioned the "difficulty aris[ing] when one tries to explain why the extraocular eye muscles are innervated by sub-oesophageal motoneurons that are located in the anterior lateral pedal lobe...". This difficulty is overcome when the eye muscles are recognized as belonging to the dorsal extensions of arm rudiments (Fig. 4B; Budelmann et al., 1997).

### FOOT SEGMENTATION

How are the five pairs of arms formed in the embryo? Early gastrular stages show a roughly U-shaped foot anlage, each side of which soon becomes subdivided into five arm rudiments (four in Octobranchia, likely corresponding to the rudiments I, III, IV and V of Decabranchia and Vampyromorpha) (Fig. 4A). Pairs of arm rudiments thus form a metameric pattern reminiscent of a polarized series of segments. One may therefore use the term pedal segment for each one of the cephalopod arm pairs (Fig. 4B), with individual numbers emphasizing the antero-posterior polarity. This polarity is clearly recognizable in the "dynamic temporal and spatial pattern of *Hox* expression in the brachial crown and funnel tube during development" (Lee et al., 2003).

That the paired elements of each of the segments are separated from one another is related to the presence of an outer yolk sac (Seidel, 1960). Schwartz (1973: 266–267) has drawn attention to the fact that the positional relationship of the yolk sac to the pedal complex in cephalopod embryos is reminiscent of the accumulation of yolk in the foot anlage in the embryos of certain pulmonate gastropods: "In cephalopods the yolk sac at late stages indeed appears as a protuberance of a part of the foot". So, the subdivision of the foot into a right and a left half, which is related to the partial "extrusion" of the large yolk mass, appears to be closely related to the particular mode of yolk storage in cephalopods (Boletzky, 2002a).

As indicated above, the (medially split) segments can be grouped in a "pre-ocular" (I–III) and a "post-ocular" (IV, V) group (Fig. 4B) according to the respective final positions of the arm rudiments providing the components of the so-called primary lid (Fig. 3C). But in the gastrula, the middle arm rudiments are still situated far behind the eye rudiments. It is only during the organogenetic phase following stage X of Naef that a general contraction of the embryo cap (or bell) will bring them into their definitive position relative to the eye complex on either side (Fig. 3C).

## CONCLUSION

The embryos of coleoid cephalopods (Naef, 1928) and those of *Nautilus* (Arnold & Carlson, 1986, Boletzky, 1989) demonstrate the existence of a uniform pattern of early organogenesis in all living cephalopods. It is reasonable to assume that this pattern is representative for fossil cephalopods, so that the (incompletely known) morphological and (supposed) functional diversification of brachial appendages in fossil cephalopods can be viewed as resulting from basically the same processes of differentiation.

Considering the functional diversity of the brachial appendages in coleoids, it is significant that the related morphological diversification always starts out from a strikingly uniform (topologically constant) ground pattern in early development (Fig. 4A). Diversification of structures occurs relatively late in embryonic development, drastic modifications of modules (e.g. suckers transforming into hooks) being strictly terminal (although this remains to be confirmed for the belemnoid hooks). Nothing is known of the evolutionary rates at which the underlying developmental programs were modified, but the progressive transformation of arm and sucker rudiments in early ontogeny suggests additive innovations in the course of coleoid phylogeny. A particularly interesting example is offered by the muscle development in decabrachian tentacles (Kier & Curtin, 2002); indeed the novel fast muscle fibres (allowing the specialized tentacles to be ejected at very high speed) develop only after the formation of the normal slow muscle system. At least in some teuthid squids (not in cuttlefish or sepiolid squids) the slow muscle system remains functional in the tentacles so they can still be used like other arms (Fig. 1D; Flores, 1983).

If embryonic development of cephalopods demonstrates that the arms, the metabrachial vesicles, the funnel tube, and the extraocular eye muscles are derived from a single foot anlage, this common origin also draws attention to the high degree of co-ordination between the ultimately achieved arm actions, eye movements, and (funnel)jet-propelled locomotion or manoeuvring.

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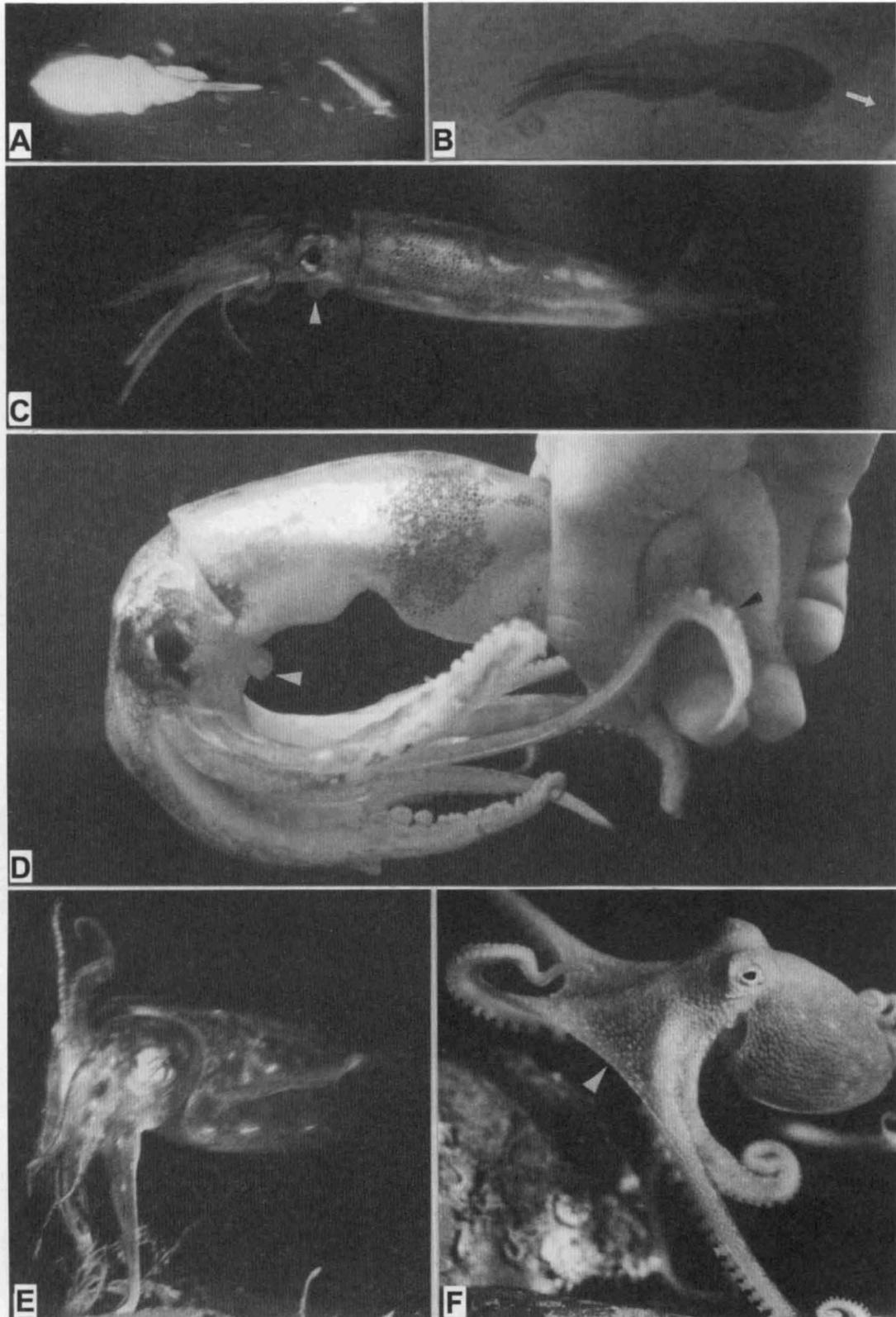


Plate. 1. A–F. Arm actions and postures of cuttlefish (A, E), squid (C, D) and octopus (B, F) observed under aquarium conditions. A. Top view of a young *Sepia officinalis*, 3 days after hatching, approaching a mysid shrimp, the tentacles being extended before final ejection (3× nat. size). B. Top view of a swimming *Eledone cirrhosa* (arrow indicating swimming direction), trailing the arms, with lateral arms slightly bent outwards to form a “stabilizer” (0.2× nat. size). C. Lateral view of a subadult *Illex coindetii* hovering, arms partly spread, fins at the beginning of a down beat, the funnel tube (arrow head) directed downwards (0.6× nat. size). D. Lateral view of an adult *Illex coindetii* being grasped by an experimenter; the animal begins to fold down and reaches backwards trying to free itself (the black arrow head points at the left tentacular club, white arrow head at funnel tube) (0.7× nat. size). E. Frontolateral view of an adult *Sepia orbignyana*, immediately after capture; the neutrally buoyant animal is virtually hovering, but rests on the tips of two arms (arm V) while the first arm pair (arm I) is stretched upwards in a “flambuoyant” posture (0.5× nat. size). F. Lateral view of an adult *Scaevurgus unicirrhus* “exploring” the aquarium setting; one arm reaching the substrate at the lower end (arrow head pointing at the interbrachial membrane) (0.5× nat. size).

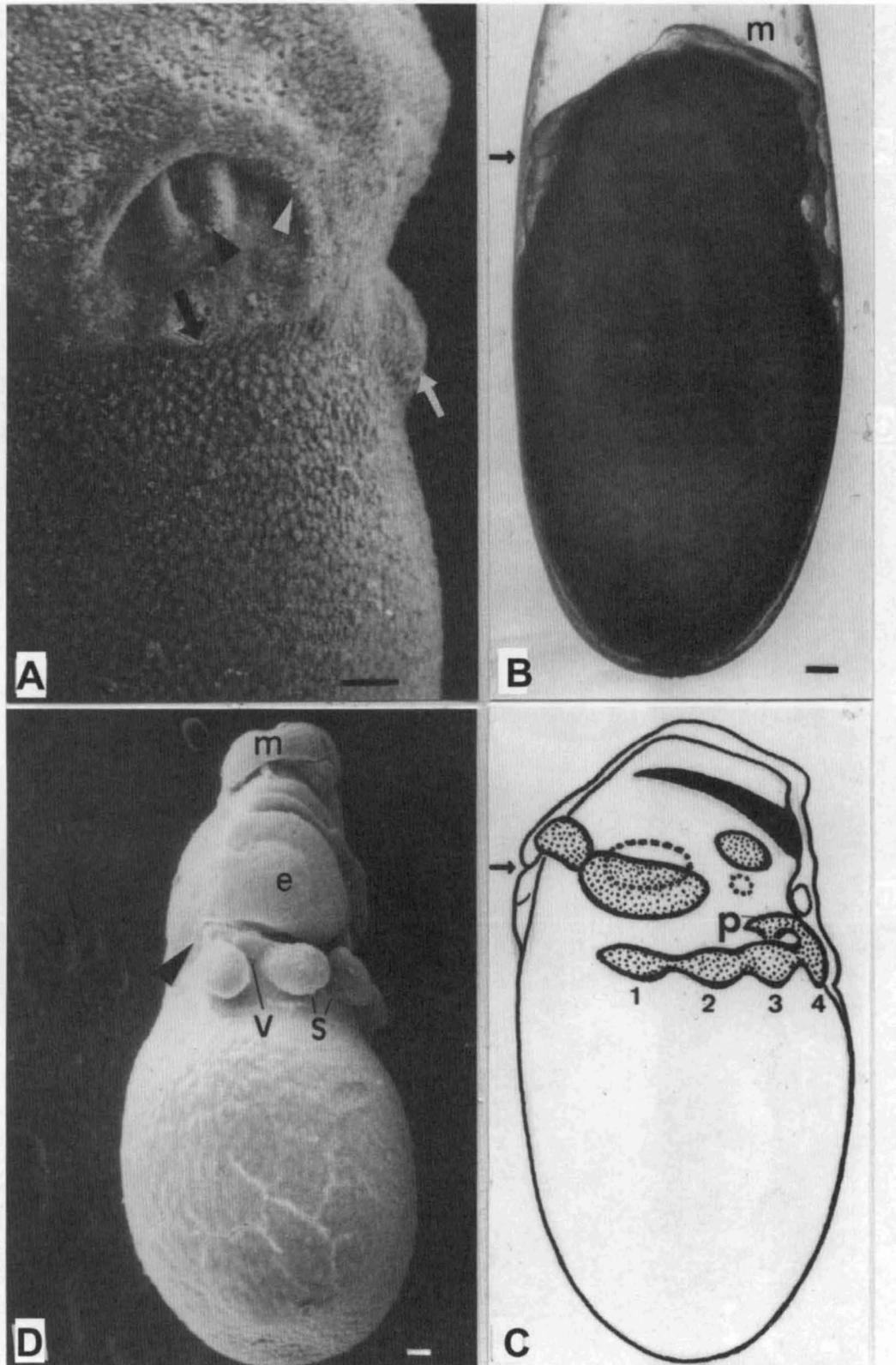


Plate 2. A-D. Early organogenetic stages of *Octopus vulgaris*. A. A low power SEM front view of an embryo at stage IX of Naef (1928), showing the stomodaeal invagination (white arrow head pointing at one side of the invagination lip) and the secondary invagination (black arrow head) of the posterior salivary gland, which is at the point of disappearing below the stomodaeal lip; the black arrow points at the limit of the densely ciliated surface of the outer yolk sac envelope (below), the white arrow points at the first arm bud of the left side (arm I). B. Lateral view of living embryo at stage IX of Naef (slightly earlier than A!). The arrow points at the stomodaeal lip; the secondary invagination (immediately below) giving rise to the posterior salivary gland is not yet drawn into the stomodaeum. m = mantle rudiment. C. A sketch representing B, inner organ rudiments being added (dark band: midgut rudiment; stippled parts: rudiments of central nervous system (after Marquis, 1989); dotted ovals: eye (large) and statocyst (small); p = pedal ganglion, 1-4 = brachial ganglia corresponding to arm I (1), arm III? (2), arm IV (3), and arm V (4). Note the continuity of 'p' and '4'. D. Lateral view of stage XI. The arrow head points at the anterior edge of the left arm series. v = metabrachial vesicle invaginated between first and second arm; s = sucker buds, e = eye, m = mantle. (Scale bars = 0.1 mm).

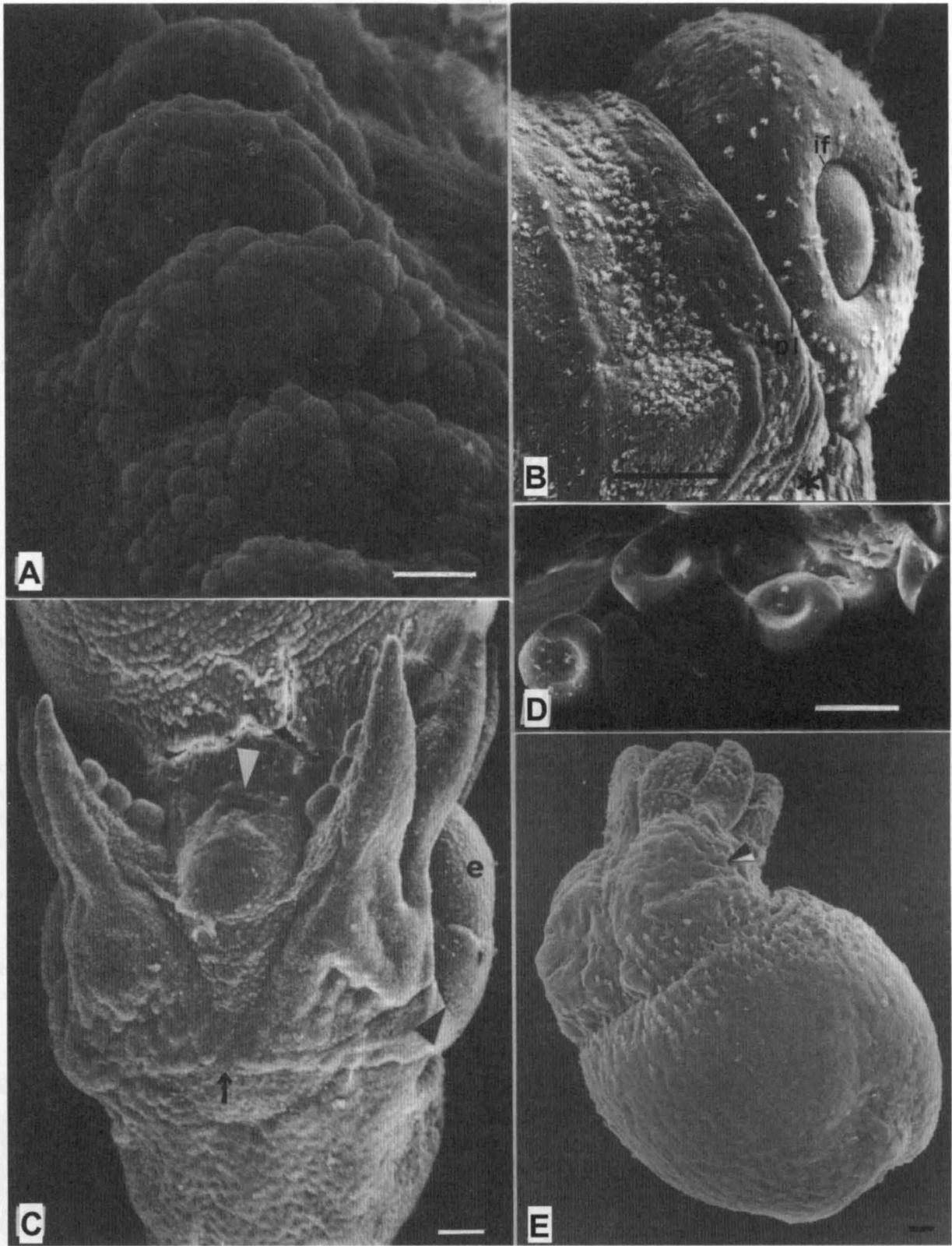


Plate 3. A–E. Low power SEM views of embryos of *Loligo vulgaris* (A), *Sepia officinalis* (B) and *Octopus vulgaris* (C–E). A. Sucker rudiments in single file on the tentacular anlage at stage XI of Naef (scale bar: 0.01 mm). B. Antero-lateral view of right eye at stage XVI of Naef, showing the eye ball with its iris fold (if) tightly surrounded by the primary lid (pl) which is now continuous with a wrinkled connecting part (\*) uniting the anterior (visible here) and posterior elements (scale bar: 0.2 mm). C. Anterior view of stage XV–XVI of Naef showing the eye (e) more widely exposed than in B, the anterior element of the primary lid still ends (black arrow head) without forming a connection to the posterior element. The small arrow points at the narrow gap between the two ends of the secondary head cover. The white arrow head points at the mouth and buccal mass. Note the 3 large sucker rudiments on each arm. D. Oblique view of suckers in a hatchling (cf. E). E. Antero-lateral view of hatchling with contracted arm crown; the eye is completely covered by the cornea made from primary lid folds (arrow head). The light ‘grains’ sticking out from the integument of the nuchal area are the Kölliker tufts (this is a fixation artifact; see Boletzky, 1978–79). (Scale bars in D–E: 0.1 mm).

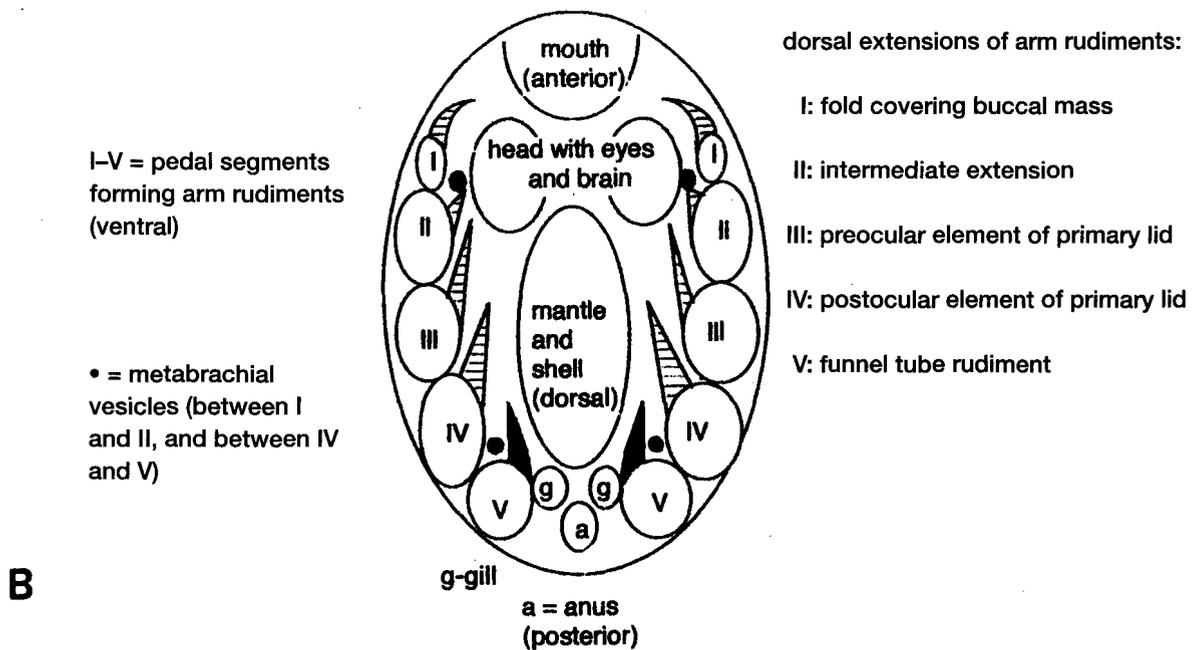
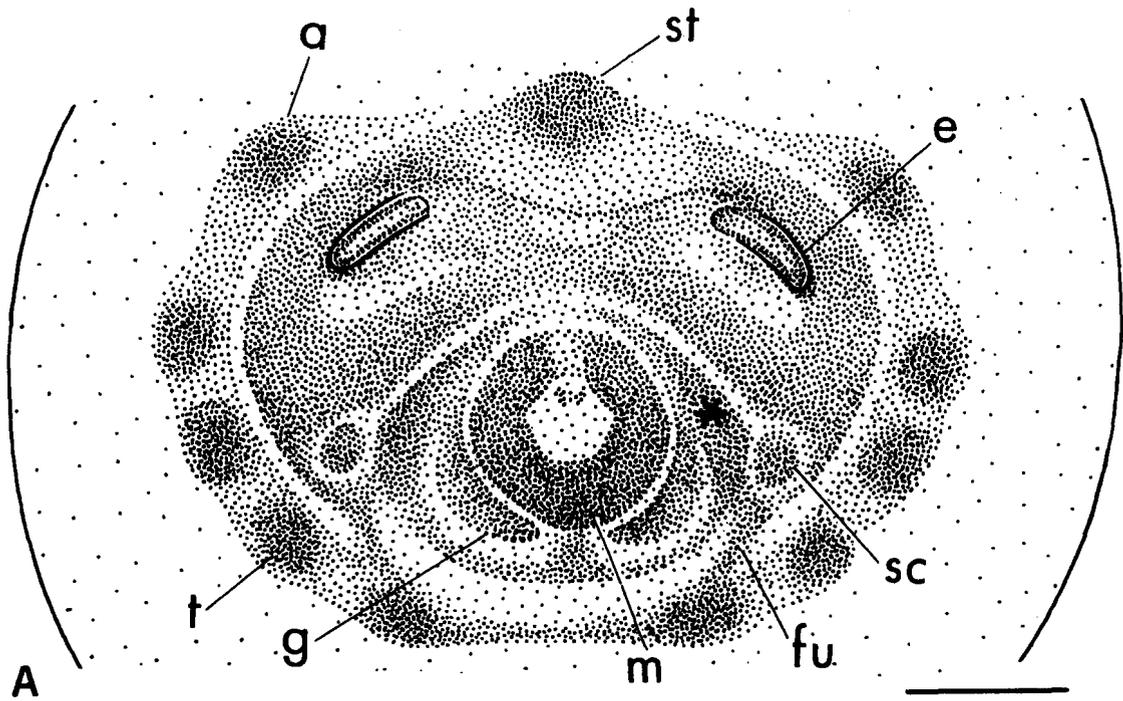


Plate 4. A-B. Dorsal view of a *Rossia macrosoma* embryo at stage VII of Naef (drawn after preserved material). The arm crown anlage shows 5 pairs of individual arm buds (a, t: prospective tentacles); the anterior end of the embryo is marked by a placode (st) from which the stomodaeum will be formed by invagination (cf. Fig. 2A). Invagination has already started for the formation of the eye chambers (e). On either side of the mantle (m) and gill (g) rudiments lies the paired anlage of the collar (\*) which is joined, close to the statocyst placodes (sc), by the funnel tube rudiments (fu) which are still connected to the posterior arm buds (after Boletzky & Boletzky, 1973). Scale bar: 1 mm. B. A schematic representation of the "phylotypic phase" of cephalopods (cf. Boletzky, 2003), combining stages IX to XII of Naef, i. e. from early funnel tube formation (by dorsal extension V) to covering of the buccal mass (by dorsal extension I). Note: the position of the anterior metabranchial vesicles between arms I and II (between 1 and 2 in Octobranchia) indicates that arm I is likely homologous to the octobranchian arm 1; it does not, however, *prove* that II is missing in Octobranchia (theoretically III could be missing, but the modification and miniaturization of II in Vampyromorpha strongly suggests that II was further reduced and finally disappeared in the octobranchian ancestor).

# COMPARISON OF ADHESIVE ORGAN OF *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 (1982) reveals that adhesion and de-adhesion is caused by a duo-gland adhesive system. The epithelium of *Idiosepius* was studied to elucidate its morphology and the nature of its secretion. The current results show that the adhesive organ of *Idiosepius* consists of three different glandular cells and two non-secretory cell types. Histochemical results indicate that each glandular cell type contains sugar, 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*. *Idiosepius* presumably uses the “Stefan-type” of adhesion. This form of adhesion involves the presence of two flat surfaces with a thin film of liquid in between. The different adhesive substances and mechanisms are discussed in relation to habitat choice and behaviour.

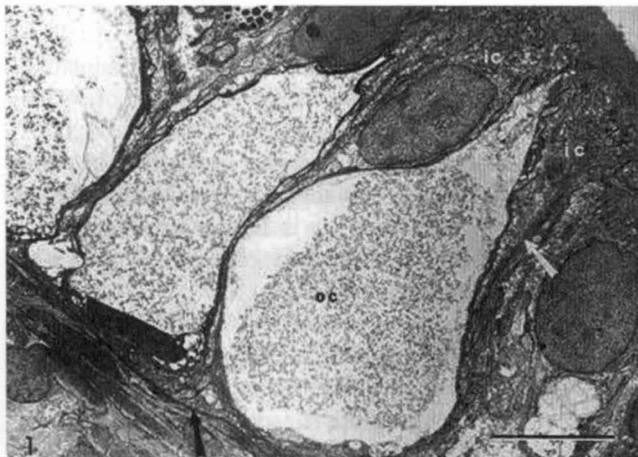
**Key words:** Adhesion, adhesive gland system, glue compounds, histochemistry, *Euprymna*, *Idiosepius*, protein-polysaccharide complex

## INTRODUCTION

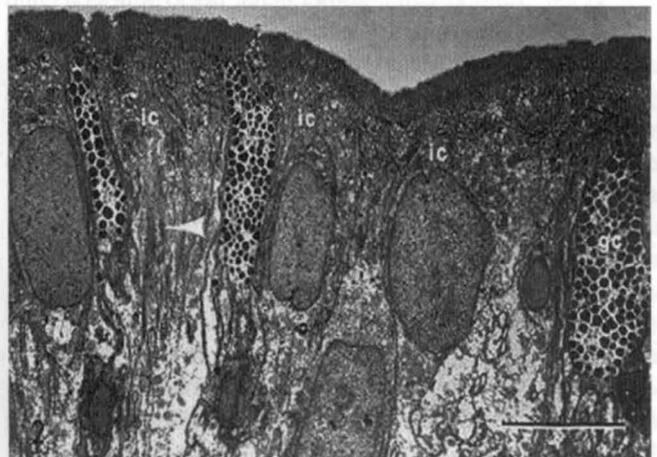
Attachment in cephalopods is primarily achieved by reduced pressure systems as in suckers on the arms, tentacles or defined dermal structures on the mantle and tentacles (Muntz and Wentworth, 1995; von Boletzky and Roeleveld, 2000). Two genera of cephalopods (*Euprymna*, Sepiolidae; *Idiosepius*, Idiosepiidae) produce glue in adhesive glands, also termed adhesive organ (Nesis, 1982; Norman, 2003).

*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.

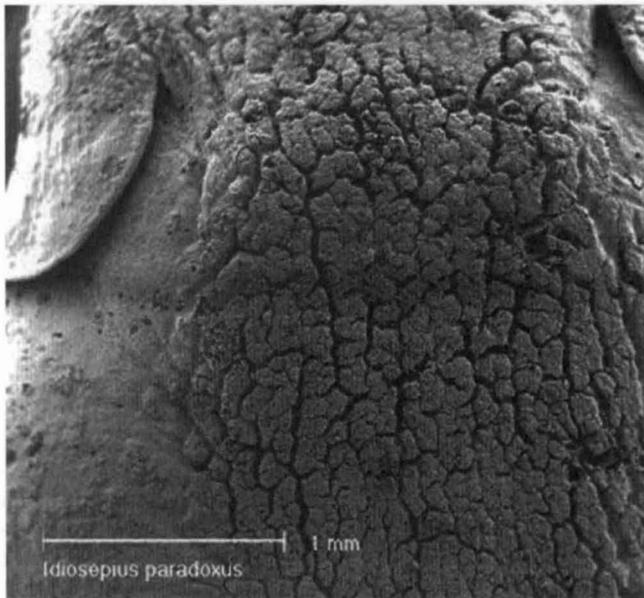
In case of danger they release sand instantaneously to deflect predators (Singley, 1983; Shears, 1988). Ultrastructural and histochemical examinations show that *Euprymna scolopes* has goblet and ovate cells in a duo-gland adhesive system all over the body (Singley, 1982). Between these cells are non-secretory interstitial cells (Fig. 1 and 2). The goblet cells contain large, electron dense granules (neutral mucopolysaccharides), 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 acidic mucoproteins cause 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 de-adhesion. Interstitial cells (ic) possess intracellular filaments (white arrow). Scale bar = 10 m 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*. The white pointer marks the intracellular filament of the interstitial cells (ic). Scale bar = 10 µm Figure from Singley (1982).



**Fig. 3** SEM image 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”.

*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 (Fig. 3).

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, interstitial cells and basal cells. He assumes that the columnar cells are responsible for adhesion whereas the interstitial cells work pressure-induced and stimulate the secretion of adhesive substances from the columnar cells. No information is available on the function of the granular cells, goblet cells and basal cells or on the de-adhesion mechanisms (Sasaki, 1921).

## MATERIAL AND METHODS

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*). For light microscope examinations, mantle tissue samples were fixed in two different acetic-alcohol-formalin mixtures (AAF I Lillie, 1949 and AAF II Böck, 1989) or for 1 h at room temperature in Carnoy solution (Kiernan, 1999); embedded in

paraffin (melting point 51–53 °C), cut in 7 µm sections, mounted on glass slides and dried at room temperature before use.

For ultrastructural investigations, specimen of *Idiosepius paradoxus* were fixed in 70% EtOH, dehydrated in a graded series of ethanol, washed several times in acetone, dried with HMDS (Hexamethyldisilazane) mounted on stubs, coated with gold in a Polaron 5800 sputter coater and examined using a Philips XL 20 scanning electron microscope.

Following Singley's (1982) methods on *Euprymna scolopes* several histological and histochemical tests were employed to elucidate the nature of the epithelial secretions of *Idiosepius*.

The trichrome method AZAN (Heidenhain, 1905) was used to provide an overview of the glandular system and structural details. The periodic acid-Schiff (PAS) method (McManus and Mowry, 1960) was used to detect neutral hexose sugars units in the adhesive organ.

To differentiate between neutral and acidic mucosubstances in the adhesive organ, the following staining methods were used: the periodic acid-diamine method (PAD) according to Spicer and Jarrels, 1961 and Spicer, 1965 for 7, 24 and 48 h at pH 4.0; alcian blue 8GX (AB) (McManus and Mowry, 1960) at pH 1.0 and 2.5 (for 2 h at 20 °C) combination with PAS; azure A (AA) (Spicer, 1960) in different buffers (HCl-phosphate or phosphate-citrate) at graded pH levels (30 min in pH 0.5; 1.0 and 3.2); toluidine blue (TB), 0.1% in 30% ethanol for 20 min (Kramer and Windrum, 1954).

Proteins were detected with Biebrich Scarlet (BS) for 1 h at 20 °C (0.04% BS in phosphate buffer) at pH 6.0 (Spicer and Lillie, 1961) and at pH 8.0, 9.5 and 10.5 in Laskey's glycine buffer (McManus and Mowry, 1960) and Fast Green FCF (FG) (0.1% FG for 30 min at pH 8.1) (Böck, 1989).

### Key to Abbreviations

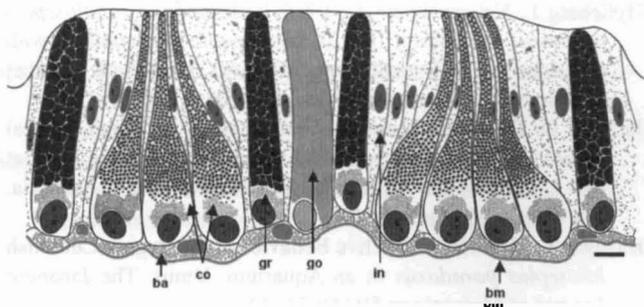
AA	Azure A	HMDS	Hexamethyldisilazane
AAF	Acetic-Alcohol- -Formalin fixative	ML	Mantle length
AB	Alcian Blue 8GX	PAD	Periodic acid- -p-Diamine
BS	Biebrich Scarlet	PAS	Periodic acid-Schiff
FG	Fast Green	TB	Toluidine Blue O

## RESULTS

The adhesive organ in all *Idiosepius* species can be distinguished easily from the remaining body epithelium (30 µm in *Idiosepius biserialis*, 40 µm in *Idiosepius pygmaeus*) by its greater thickness (60–80 µm in *Idiosepius biserialis* and 80–100 µm in *Idiosepius pygmaeus*).

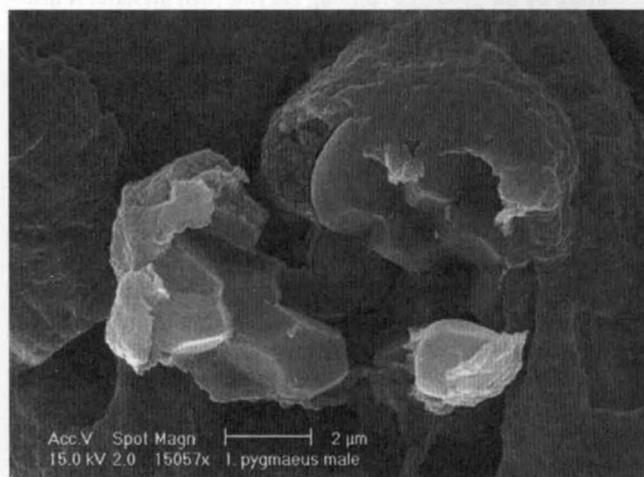
The adhesive organ consists of five different cell types (Fig. 4) (columnar, granular, goblet, interstitial and basal cells), which can be distinguished morphologically and on account of their chemistry of their secretion (von Byern et al., 2005; Cyran, von Byern, and Klepal, 2005):

Columnar cells are pear-shaped and tapering towards the surface; the cells are densely filled with fine granules (1 µm in diameter). Granular cells are oblong and tube-shaped and contain large spherical to polygonal granules (Fig. 5) (3–5 µm in diameter) of uniform density. Gob-



**Fig. 4** Schematic drawing of the adhesive organ of *Idiosepius* with its characteristic cell types: bm-basal membrane, co-columnar cells, gr-granular cells, go-goblet cells, in-interstitial and ba-basal cells. Scale bar = 2µm Drawing by N. Cyran, et al., 2005.

let cells are round to sac-shaped, tapering towards their apical ends; its secretory material is finely granular. Interstitial cells between the secretory cells are long and slender; the cells are free of secretory material. Basal cells line the basal membrane and contain vacuoles of uniform density.

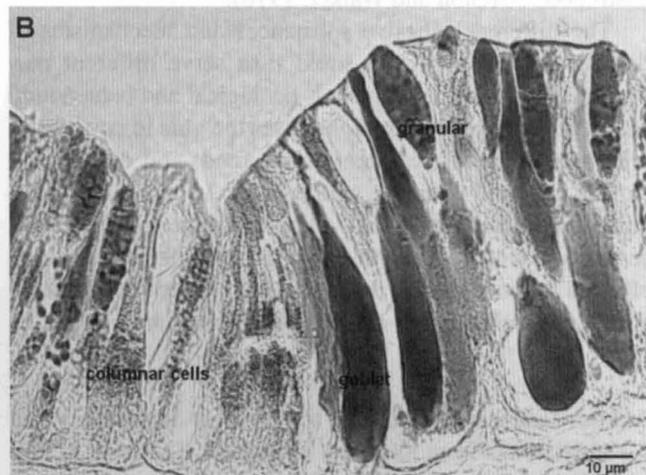
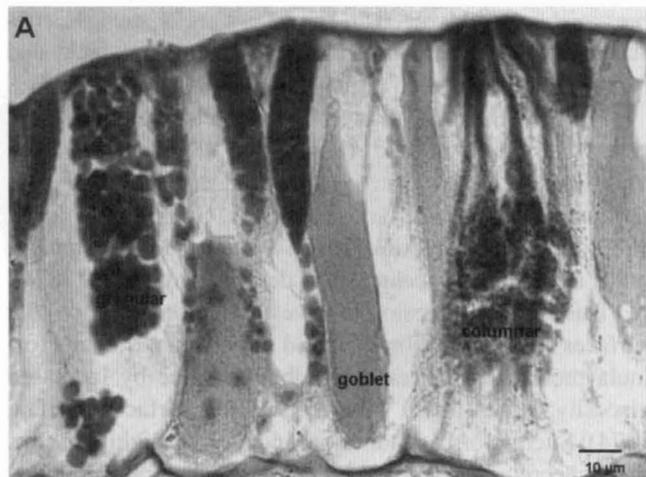


**Fig. 5** The granular cell type with larger polygonal granules, packed tightly together.

Histochemical tests (Fig. 6a and b) show that the three glandular cell types (columnar, granular and goblet cells) are periodate-reactive (PAS) and moderately reactive with PAD. No  $\gamma$ -metachromasia is effected with Toluidine Blue and Alcian Blue, demonstrating acid groups. Biebrich Scarlet at all pH levels and Fast Green show weak (columnar cells), positive (granular cells) to strong positive (goblet cells) reactions for basic proteins.

## DISCUSSION

The histochemical results of *Idiosepius* indicate that the secretory material consists of a protein-polysaccharide complex. Anyhow, the ratio of protein and polysaccharide varies strongly between the cells. Columnar cells contain a high proportion of



**Fig. 6** Histochemical reactions of the cell types in the adhesive organ of *Idiosepius*. A. PAS with glutaraldehyde fixation, B. Biebrich scarlet. Interstitial and basal cells don't react with any of the applied histochemical tests.

sugar and few fractions of proteins. Granular cells have a balanced ratio of sugar and proteins, while the goblet cells have a higher proportion of proteins and a lower fraction of sugar units. Acidic substances are absent in all *Idiosepius* species.

In comparison with *Euprymna scolopes* (Singley, 1982) the adhesive organ in *Idiosepius* shows similarities and differences in the morphology and secretory components of the glandular cell types<sup>1</sup> (Despite the morphological similarities of the cell types in the two genera we follow the terminology used by Sasaki (1921) (see also Packard, 1988; Budelmann, Schipp, and von Boletzky, 1997). The goblet cells of *Euprymna* resemble the granular cells of *Idiosepius* and contain both neutral hexose sugars. The ovate cells of *Euprymna* correspond morphologically to the goblet cells of *Idiosepius*. Anyhow the basic proteins in this cell type in *Euprymna* become highly acidic during secretion (Singley, 1982). On the contrary, a change of the associated protein-polysaccharide complex to an acidic complex in this cell type can be excluded for *Idiosepius*. The appropriate tests (AB, AA, TB) were negative, even on secreting cells. The interstitial cells of *Euprymna scolopes*, *Idiosepius biserialis* and *Idiosepius pygmaeus* do not show any histochemical reaction and are

<sup>1</sup> Despite the morphological similarities of the cell types in the two genera we follow the terminology used by Sasaki (1921) (see also Packard, 1988; Budelmann, Schipp and von Boletzky, 1997).

presumably not involved in the secretion of mucous substances for adhesion or de-adhesion. The columnar cells and basal cells are restricted to the adhesive organ of *Idiosepius*.

The histochemical nature of the secretory products suggests that adhesion and de-adhesion is not evoked by a duo-gland adhesive system such found as that in *Euprymna scolopes* (Singley, 1982) and gastropods (Grenon and Walker, 1980; Shirbhate and Cook, 1987). Adhesion in *Idiosepius* is rather effected by a mechanism as described by Stefan (1874).

This form of adhesion involves the presence of two flat surfaces with a thin film of liquid in between. Stefan's formula predicts an increase of adhesion force by increased viscosity of the liquid between two flat surfaces (Stefan, 1874). Such a form of adhesion, induced by highly viscous mucus secreted from the pedal glands, can be found in many gastropods (Grenon and Walker, 1978).

The different adhesive substances and mechanisms of de-adhesion in these two squid taxa serve different purposes. They can be explained as ecological and behavioural adaptations. *Euprymna scolopes* uses the glue to cover itself with a coat of soft sediment (sand, mud) and disconnects from it fast and over the whole body. *Idiosepius* attaches with a small adhesive area to different substrates (seaweeds, seagrass leaves, roots). An easy but slow disconnection is effected without special de-adhesive substance but presumably by a mechanical or dissolving mechanism.

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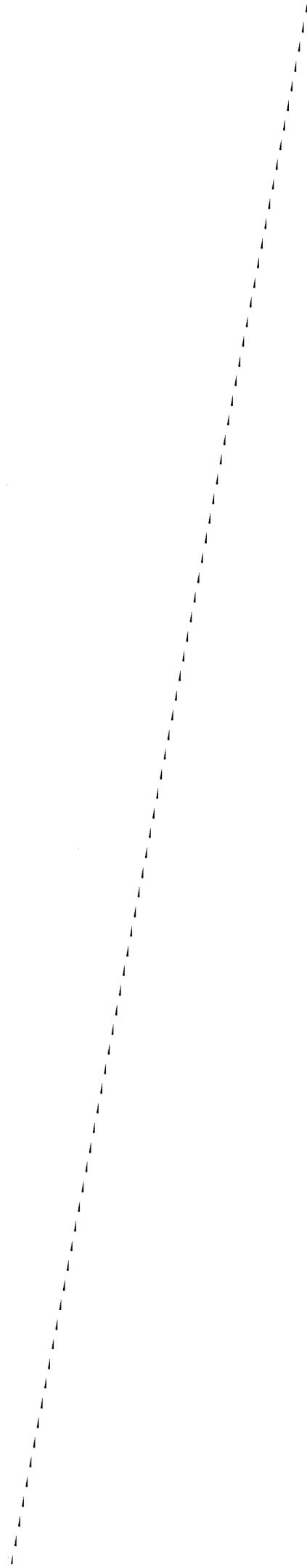
Thanks go to the Austrian Science Fund (FWF, Project No. P 17 193 – B 12), which allowed the collection of *Idiosepius pygmaeus* in Thailand and *Idiosepius biserialis* in Moçambique. The Japan Society for the Promotion of Science (JSPS, Grant No. 04567) made possible the collection of *Idiosepius paradoxus* in Japan.

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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*.

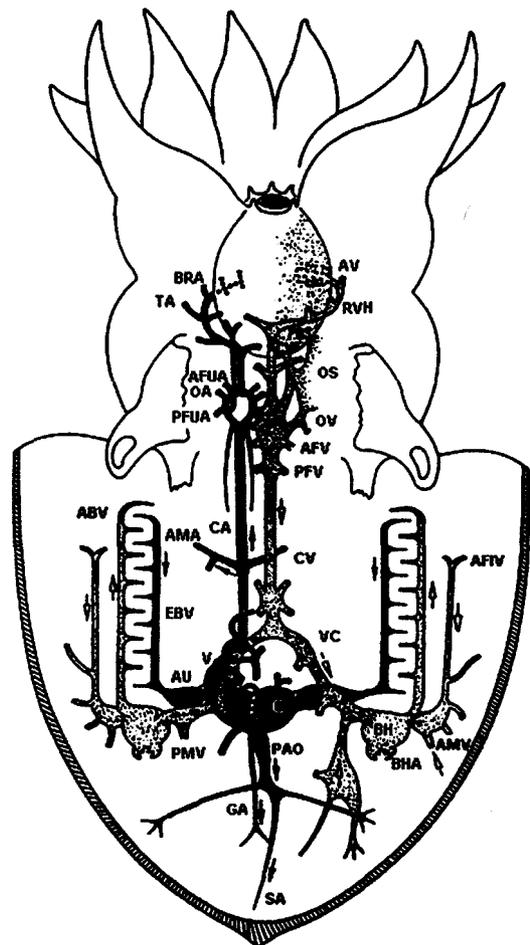
**Key words:** Acetylcholine, cephalopoda, cholinergic receptor system, circulation system, nicotine, peristalsis, *Sepia officinalis*, Vena cephalica

## INTRODUCTION

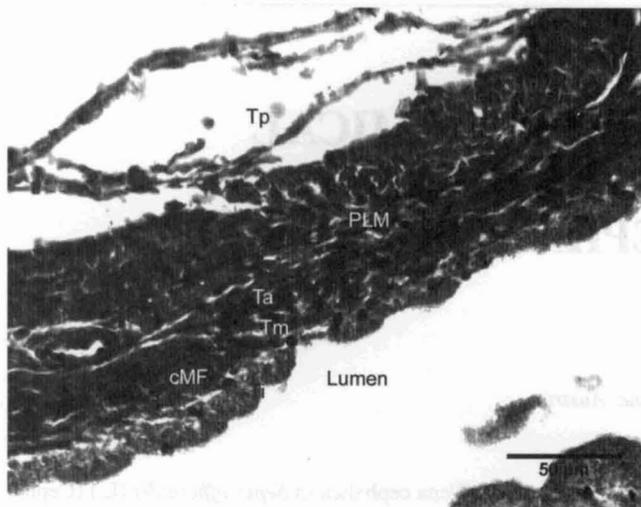
Functionally the circulation system of the dibranchiate cephalopods is subdivided into a systemic and respiratory part (Fig. 1) (Tompsett, 1939; Schipp, 1987a). Like in vertebrates at cephalopods the thick-walled arteries enable a high-pressurise circulation by an air vessel-function, (Shadwick and Nilsson, 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 (CV) 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 wall of this vein is composed of four-layers (Fig. 2) (Smith, 1962; Barber, 1966; Schipp and Schäfer, 1969; Schipp, 1987b). 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) of the Tunica periadventitia effects cranial to caudal contraction waves, while the circular muscle fibres of the Tunica media (cMF) are 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 fibres form a neuronal plexus (NSV-system = Neurosecretory system of the Vena cephalica) 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).



**Fig. 1** Ventral view of the circulatory system of *Sepia officinalis*. The arterial circulation system is shown black and the venous system grey. Explanations to anatomy and function of the blood circulation system and abbreviations can be found in Schipp (1987a).



**Fig. 2** Cross section through the wall of the ventral vessel. The vein is composed by four layers (Tunica intima (Ti), Tunica media (Tm), Tunica adventitia (Ta) and Tunica periadventitia (Tp). Two muscle systems, the periadventitial longitudinal muscle layer (PLM) and the circular muscle fibres (cMF), are responsible for peristaltic contractions of the vessel. AZAN

This neurosecretory system of the Vena cephalica is comparable with the adrenaline system in vertebrates (Wells, 1983).

The present study focuses on the nature of the cholinergic and aminergic mechanisms modulating the peristalsis of the Vena cephalica in *Sepia officinalis*. Histochemical and immunohistochemical tests will provide information on the nature of the cholinergic mechanisms.

## MATERIAL AND METHODS

Animals were anaesthetised, opened from the ventral side and the Vena cephalica, including the cephalic bulb and attached visceral nerves, were dissected out. Tissue and nerves were removed from the vein while myogenic components like the periadventitial muscle layer were not removed from preparations. In the isolated vein an afferent and an efferent cannula were inserted, closed by a ligature and all existent flows towards the vein were tied up. The preparations were removed freshly without any time interval and fixed horizontally in an organ bath (Fig. 3).

The two-walled water-jacketed organ bath was filled with physiological solution (filtered seawater with 0.16% glucose, maintained at 18–19 °C, pH 8.5). The pharmacological solutions were perfused over a four-tap-system into the vein or through the bypass. These solutions, by peristalsis, evoked pressure-signals that were registered by a pressure transducer, amplified and recorded by a pen recorder. This experimental set-up has already been successfully employed in other experiments (Schuck, 1988; Agnisola and Houlihan, 1994). All veins were perfused orthograde under constant conditions (preload pressure 10 cm water pillar; afterload pressure 1 cm water pillar) initially with physiological solution in order to obtain a solid starting condition and to wash out the remaining hemolymph.

## DRUG APPLICATION

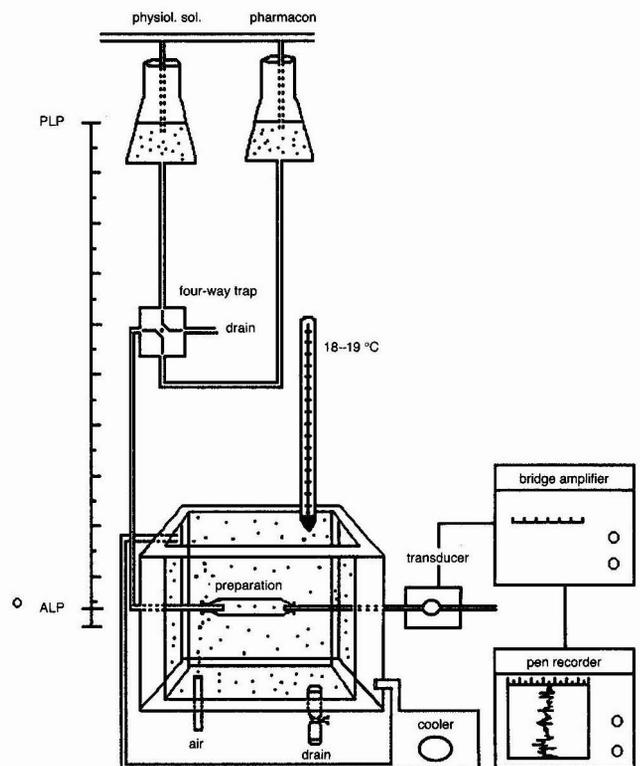
The drugs (acetylcholine (ACh), adrenaline, dimethylphenylpiperazinium iodide (DMPP), d-Tubocurarin isoprenaline, nicotine, noradrenaline, muscarine, tetraethylammonium and  $\alpha$ -BTX) were freshly dissolved in physiological solution and perfused cumulatively through the vein at increasing concentrations ( $10^{-9}$  mol/l to  $5 \times 10^{-5}$  mol/l in tenth power steps). For every series of concentrations in the perfusions, an actogram with physiological solution only was first recorded; this was related to a specific transmitter effect. From this recorded curve the amplitude and frequency were determined and computed in the calculation as the "0"-value in the dose-response curves.

## IMMUNHISTOCHEMISTRY

Isolated vein preparations from adult specimen were freshly removed, fixed in Bouin solution and 4% saline formalin for 24 h. at RT, washed in 70% Ethanol or running water, embedded in paraffin, cut in 7  $\mu$ m sections and mounted on slides. For fluorescence histochemical examinations, preparations were embedded in Tissue Tec<sup>®</sup> (Sakura Inc.) and frozen in liquid nitrogen.

The investigations provided proof of Acetylcholinesterase (E. C. Nr. 3.1.1.7) at the Vena cephalica (Karnovsky and Roots, 1964).

For immunohistochemical marking, a polyclonal antibody (Santa Cruz Biotechnology SC-5544) was used, binding specifically on a protein of the  $\alpha 7$  subunit at nicotinic acetylcholine receptors (Santa Cruz Biotechnology Inc., 2001).



**Fig. 3** This scheme represents the set-up for the pharmacological experiments. The preload Pressure (PLP) was adjust to 10 cm and the afterload Pressure (ALP) to 1 cm opposite preparation level. Scheme from Schuck (1988) modified by von Byern.

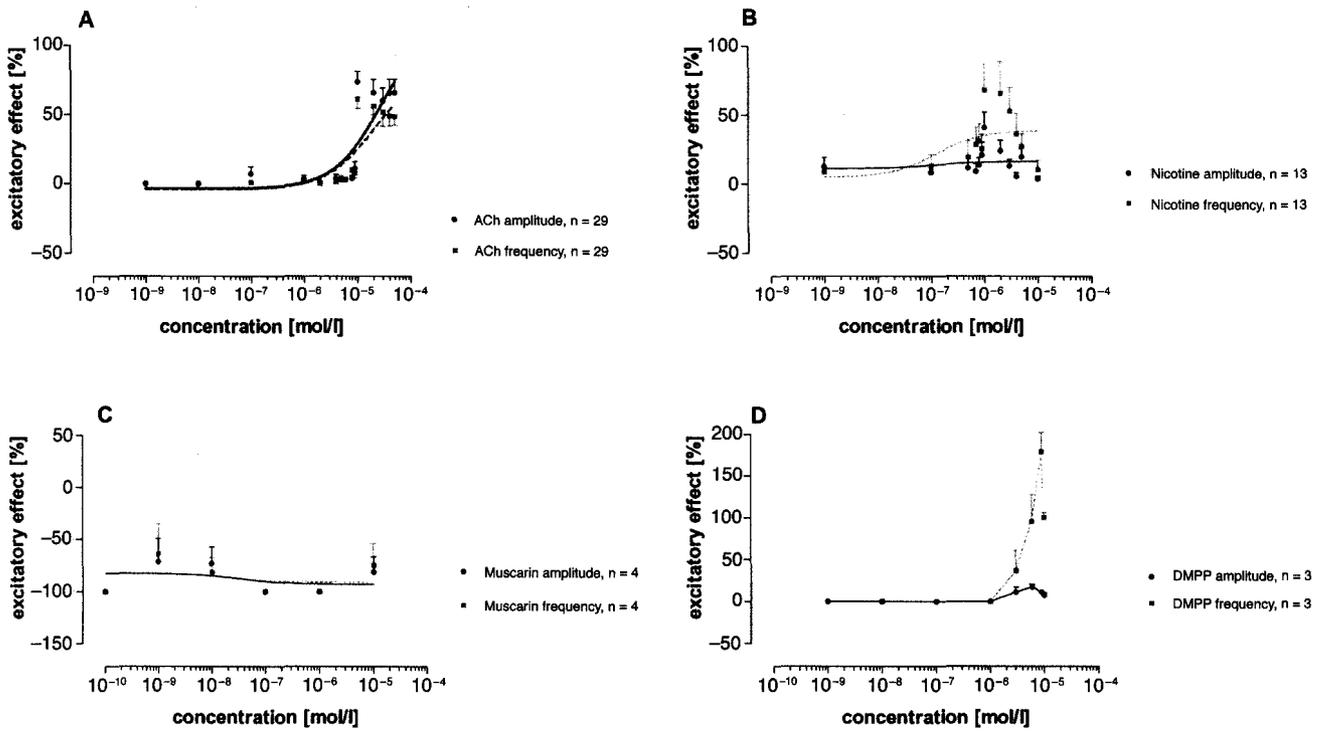


Fig. 4. Binomial concentration-response curve of a) acetylcholine (ACh), b) nicotine, c) muscarine and d). DMPP on the amplitude and frequency of the perfused Vena cephalica. Values are expressed as mean  $\pm$  SD.

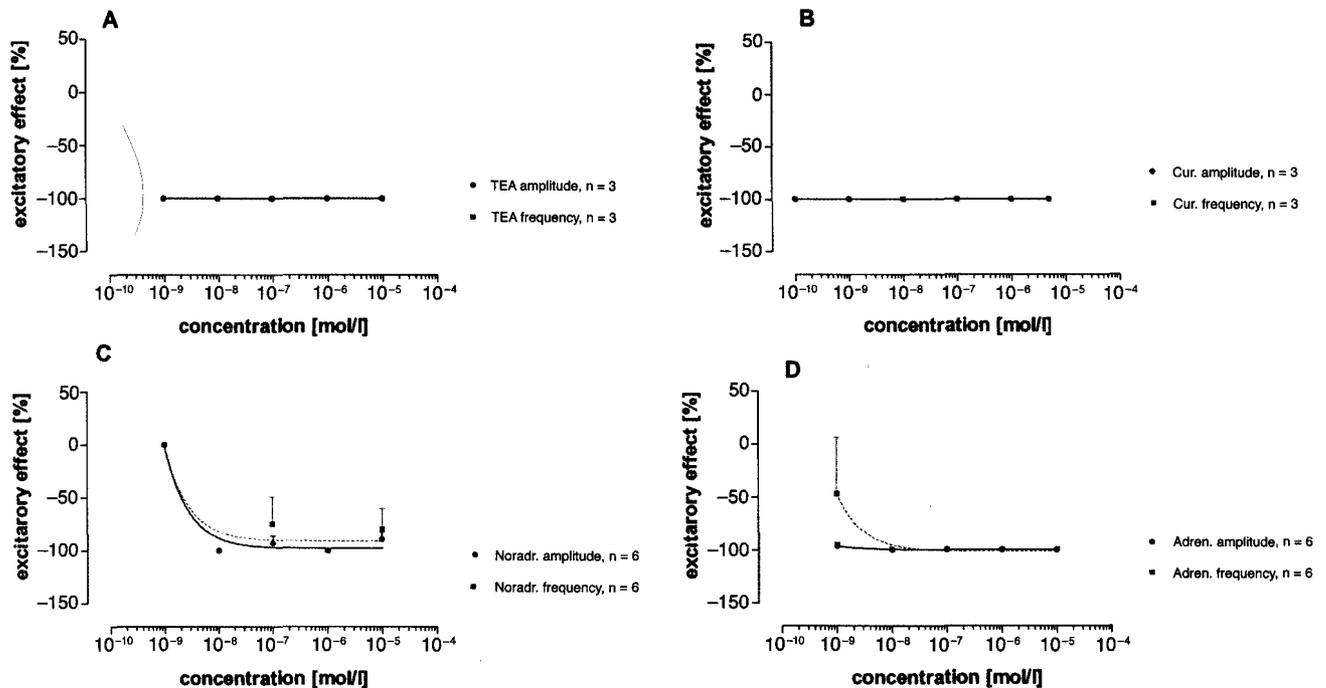


Fig. 5 Binomial concentration-response curve of a) TEA, b) d-Tubocurarin (Cur.), c) noradrenaline (Noradr.), d) adrenaline (Adren.) on the amplitude and frequency of the perfused Vena cephalica. Values are expressed as mean  $\pm$  SD.

For fluorescence marking of FITC with  $\alpha$ -Bungarotoxin (Sigma-Aldrich T-9641), preparations were first perfused in the organ-bath with acetylcholine (concentration  $5 \times 10^{-5}$  M) for 20 min. The isolated vessels were then fixed for 1 hour in the dark in  $10^{-7}$  Mol FITC- $\alpha$ -Bungarotoxin. Cryostat sections of the samples were photographed (wave length 355–425 nm, barrier filter 460 nm) with a fluorescence microscope. For controls, only FITC was used.

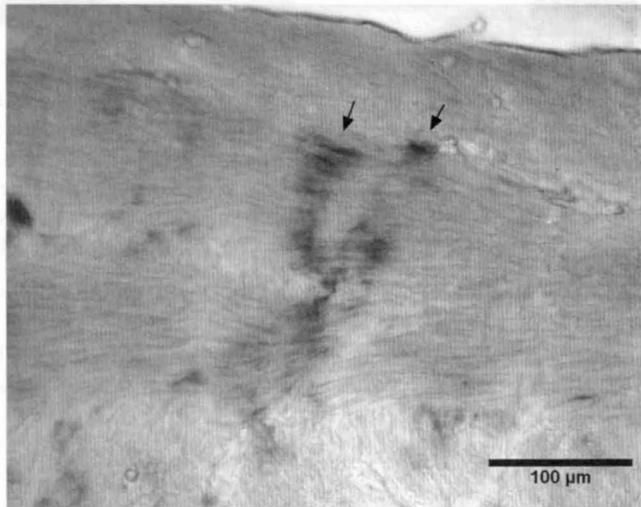
## RESULTS

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 and

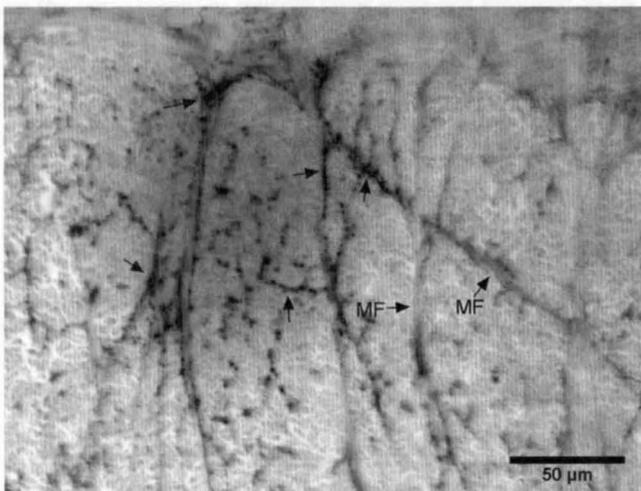
nicotine, the nicotinic acetylcholine receptor agonist dimethylphenylpiperazinium iodide (DMPP) induces a positive inotropic and chronotropic effect on Vena cephalica peristalsis (Fig. 4). Muscarine and cholinergic antagonists like Tetraethylammonium (TEA), d-Tubocurarin and  $\alpha$ -Bungarotoxin ( $\alpha$ -BTX) reversibly block the peristalsis in the Vena cephalica. Also aminergic transmitter (adrenaline, isoprenaline, noradrenaline) causes a reversible peristalsis standstill (Fig. 5).

The present immunohistochemical 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 (Fig. 6).

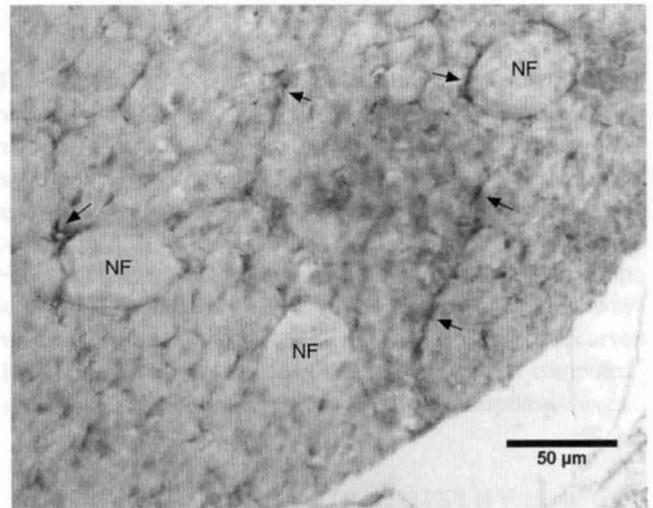


**Fig 6** Hatchett-Brown enzyme reactions of AChE (arrows) can be found at muscle fibres of longitudinal muscle layer of the Tunica periadventitia.

The  $\alpha 7$ -subunit of a nicotinic 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* (Fig. 7 and 8).



**Fig. 7** Immunohistochemical precipitations (arrows) of the antibody against the  $\alpha 7$  subunit of nicotinic acetylcholine receptor yield positive results at muscle fibres (MF) of the Tunica periadventitia.



**Fig. 8** Immunohistochemical precipitations of the antibody (arrows) around nerve fibres (NF) of the visceral nerve.

The used toxin FITC  $\alpha$ -Bungarotoxin allows no clear conclusions about the presence of muscular nicotinic receptors in the Vena cephalica of *Sepia officinalis*.

## DISCUSSION

Pharmacological studies on the physiology of the systemic heart, the arterial system and the branchial hearts point at an antagonistic transmitter system with cholinergic (inhibitory) and monoaminergic (excitatory) neuronal mechanisms (Schipf, Schmidt, and Fiedler, 1986; Kling, 1987; Kling and Schipp, 1987; Schipp, Jakobs, and Fiedler, 1991; Fiedler, 1992; Schipp and Fiedler, 1994; Gebauer and Versen, 1998; Versen et al., 1999; Lehr and Schipp, 2004a; Lehr and Schipp, 2004b).

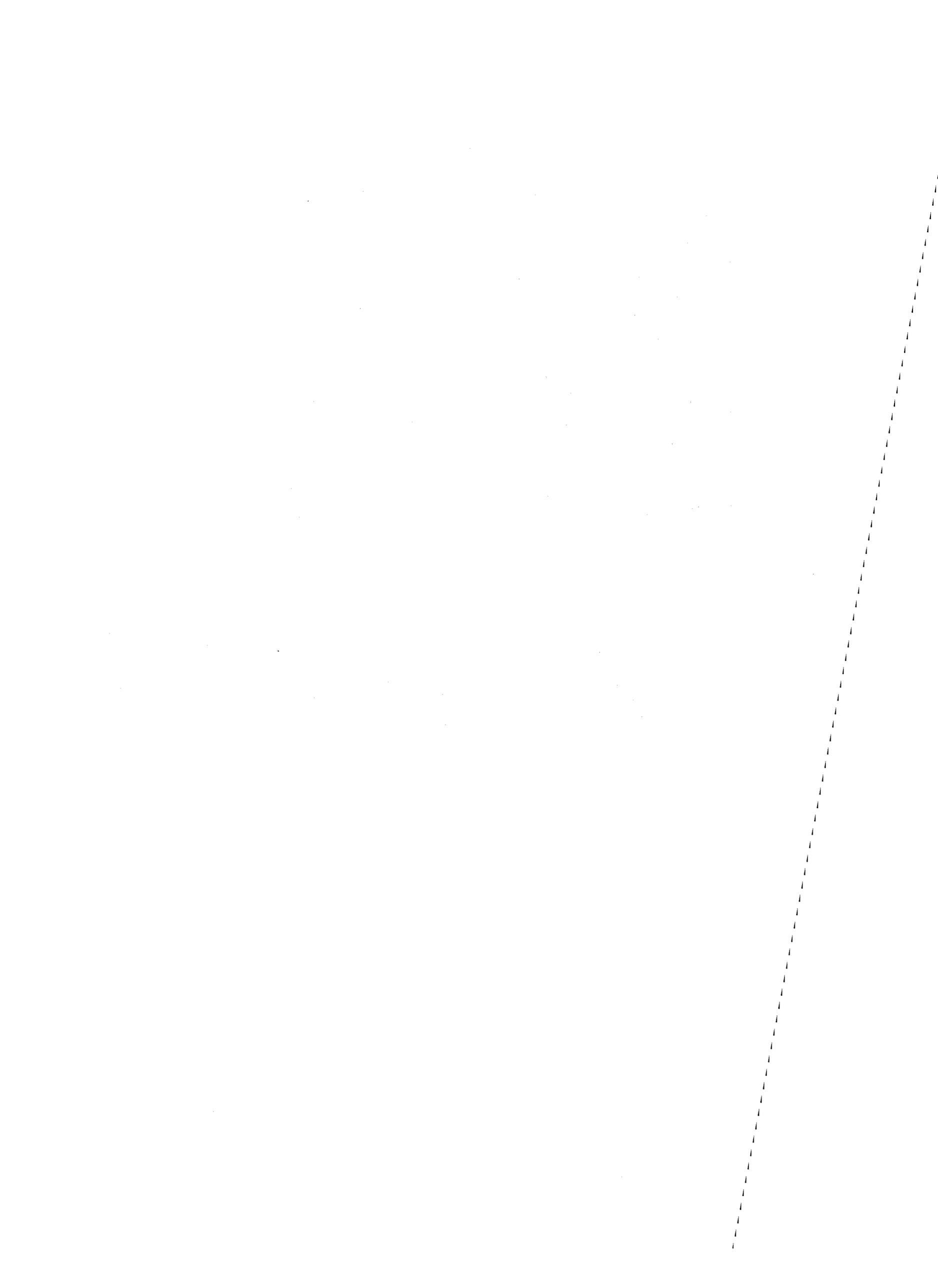
The present pharmacological data provide evidence for a functionally different regulation of the Vena cephalica different from the remaining circulatory system of *Sepia officinalis*. Cholinergic transmitters, like acetylcholine, nicotine and the nAChR agonist DMPP, excite the peristalsis while aminergic transmitter (adrenaline, isoprenaline, noradrenaline) and muscarine cause a reversible standstill of peristalsis.

The regulation mechanisms of Vena cephalica peristalsis are apparently similar to the peristaltic waves of the gastrointestinal tract, which is regulated by similar excitatory cholinergic and inhibitory aminergic mechanisms (Johnson et al., 1987; Furness and Costa, 1987). The immunohistochemical results successfully demonstrate that a cholinergic transmitter system or acetylcholine-catabolic system takes part in peristalsis of the Vena cephalica in *Sepia officinalis*.

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# A LATE CARBONIFEROUS ADOLESCENT CEPHALOPOD FROM TEXAS (USA), WITH A SHORT ROSTRUM AND A LONG BODY CHAMBER

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**Abstract:** Three longicones (Virgilian, Upper Pennsylvanian, Texas, USA) with a ventral marginal siphuncle, a shell wall with a nacreous layer, and a long body chamber were examined. The smallest is a 25 mm long adolescent, protoconch-bearing shell with a short rostrum. The rostrum has a small post-protoconch part that is about as long as the protoconch (ca 0.25 mm), and extends along about first ten camerae. The rostrum is loosely calcified and strongly pyritized, and this suggests that it originally had a combined organic and carbonate primary composition. The first septum is mineralized, with long prismatic mural parts that extend along about ten camerae and form the shell wall. At latter growth stages a nacreous layer and then an inner prismatic layer appear. The septal necks are retrochoanitic, short dorsally and long (about 1/3 camera length) ventrally. The connecting rings are thin and were probably originally organic in composition. Thin cameral deposits are distinct in the protoconch and the first two camerae. In the latter camerae the deposits are less distinct but show pyritized membranes on their surfaces.

The adolescent longicone falls within the concept of *Mutveiconites* Doguzhaeva, 2002, known from the Upper Carboniferous (Orenburgian) of south Urals, and is described as *Mutveiconites milleri* sp. n. The other two larger longicones possibly represent older growth stages of *Mutveiconites*, which is considered to be the earliest aulacocerid coleoid so far known. Also this occurrence represents the first report of this genus in North America.

**Keywords:** Late Carboniferous coleoid, shell morphology and ultrastructure, rostrum, evolutionary morphology, Texas

## INTRODUCTION

The present study concerns the early evolution of aulacocerid coleoid cephalopods. It deals mainly with a fully preserved adolescent Late Carboniferous (Virgilian = Stephanian) longicone specimen with a short rostrum from Texas, USA. This is the second confirmed find of such a shell. The first recovery of an adolescent longicone with a short rostrum was from the Late Carboniferous (Orenburgian) in the southern Urals. These two shells belonged to two individuals that are nearly synchronous (in scale of geological time), but remarkably remote from each other in geographic space.

The adolescent longicone from Texas was recognized during examination of new material of the oldest known spirulid coleoid *Shimanskya postremus* Doguzhaeva, Mapes, Mutvei, 1999. This genus was initially referred to *Bactrites postremus* Miller, 1930 but it was separated from the bactritoids because of ultrastructural details of the shell by scanning electron microscopy study (see Doguzhaeva et al., 1999). Specimens of *Shimanskya* are known from the Virgilian deposits of Texas and Oklahoma (USA) and occur with several species of *Bactrites* (see Mapes, 1979: p. 35).

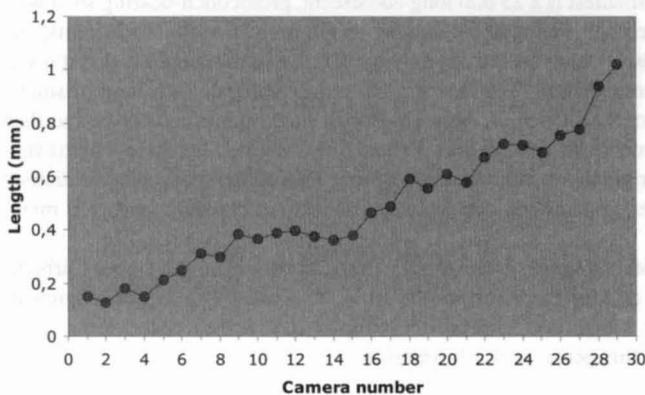
The two adolescent longicones, one from Urals and the other from Texas, with preserved initial parts of the

shell, are important because they show details of the early evolutionary stages of aulacoceratids. These details include a rarely observed combination of morphological features including: a short rostrum, a small (ca 0.3 mm) protoconch, a longiconic phragmocone with a marginal siphuncle, a shell wall with a nacreous layer and a long body chamber. The order Aulacoceratida was established by Jeletzky (1966, p. 20) who accepted Abel's (1916) and latter Schwegler's (1949) and Erben's (1964) conclusions on independent origin of aulacocerids and belemnites. A long tubular body chamber and pro-ostracum were considered to occur in aulacocerids by many authors (Mojsisovics, 1871, 1882, 1902; Gemmellaro, 1904; Wanner, 1911; Bülow, 1916; Abel, 1916; Dunbar, 1924). Naef (1922) assumed that for keeping a horizontal position, the aulacoceratids with their long slender rostrum, needed a long pro-ostracum. However, as was noticed by Bandel (1985, p. 232), there was no direct evidence for these two assumptions. No adult shell showing a morphological combination of long slender rostrum, tubular body chamber and pro-ostracum have been reported to our knowledge. Also, to our knowledge, the two Late Carboniferous adolescent shells mentioned above are the only documented coleoid longicones that have a short rostrum and a long body chamber.

## MATERIAL AND STATE OF PRESERVATION

The studied material comprises three longicones from Virgilian, Upper Pennsylvanian (= Stephanian, Upper Carboniferous) beds of Texas, USA.

**Specimen 1** (OUZC 5205): (Pl. 1, Figs. A, B, D, E; Pl. 3, Figs. A–F; Pl. 4, Figs. A–F; Text-fig. 1). A unique 25 mm long adolescent shell preserved inside the long body chamber of the medium-sized longiconic specimen OUZC 5206. It has a small protoconch, a short rostrum, 29 chambers in the phragmocone and a long body chamber. The body chamber is 11 mm long, which is 2/5 of shell length, and with two exceptions is filled with uniformly tan matrix identical to that seen in the body chamber of specimen 2. The conch diameter near the aperture of the body chamber is 3 mm. The phragmocone is characterized by an irregular increase in camera length (Text-fig. 1). The camerae of the phragmocone are filled with light peach-colored calcite.



Text-fig. 1 *Mutveiconites milleri* sp. n., Graphic representation of the 29 camera length measurements showing a periodicity of the shell growth.

**Specimen 2** (no. OUZC 5206): (Pl. 1, Fig. A). An incomplete shell segment 70 mm long with a 64 mm long portion of tubular body chamber and two camerae of the phragmocone. The shell diameter at the anterior broken edge is 17 mm while near the last septum the diameter is 9 mm. The body chamber, which is filled with a uniform textured matrix, also contains the adolescent longicone of specimen 1 with its initial parts preserved together with numerous undetermined pieces of organic debris and material reworked by bacteria (Pl. 4, Figs. D, E).

**Specimen 3** (no. OUZC 5207): (Pl. 2, Figs. A–C). The specimen consists of a 50 mm long fragment of a longicone buried in a dense dark grey medium-sized carbonate concretion. The shell comprises eight camerae of the phragmocone and an incomplete body chamber. All but one of the camerae of the phragmocone is filled with white calcite. The camera that is the exception and the preserved apical portion of the body chamber are filled with numerous coprolites, and the interspaces between the coprolites is extensively pyritized. The maximum diameter of the shell is 9 mm, and its minimum diameter is 7 mm. This specimen is cut longitudinally through the ventral marginal siphuncle. The siphuncle is strongly pyritized inside and outside the siphuncular tube. It also has strongly pyritized layers on

the adapical septal surfaces and near the septal necks on adoral surfaces. Additionally the specimen has pyritized cameral membranes on the surface of cameral deposits. The adapical surfaces of the septa are strongly pyritized while the adoral ones are weakly and irregular pyritized mainly near the septal necks. An exception is the septum near the damaged edge of the shell, which is pyritized on both surfaces. Serious damage that was partly repaired, followed by a shell breakage, occurs at the adapical margin of the shell.

The three specimens available have a similar phragmocone structure. In all specimens the shell exhibits a slowly expanding phragmocone with moderately curved septa and a long body chamber. A narrow ventral marginal siphuncle is observed in the two larger specimens (specimens 2, 3), while in the adolescent shell (specimen 1) the siphuncle is not exposed because the section of the shell is not median. However, the siphuncle of the adolescent specimen is also considered to be marginal, because if the siphuncle had been central, it would have been visible in the longitudinal section running through the central part of the septa.

The body chamber of specimen 2, where the adolescent longicone (specimen 1) was preserved, contains a substantial amount of undetermined organic debris. EDS analyses of the sediment inside the body chamber show a content of O (24–48%), Ca (21–40%), Si (0–45%), P (0–12%), Na (0–1.6%), Al (0–1.9%), Mg (0–0.82%), Fe (0–3%), S (0–2.8%), K (0–0.8%) (C was not registered). This means that the body chamber was filled by heterogeneous material. The first two elements (O, Ca) have a more homogenous distribution in comparison with the other eight elements. In some places of the body chamber the sediment was phosphatized, in others either silicified or pyritized. This pattern of elemental distribution is possible evidence of high content in organic material during fossilization. Decay of soft body possibly occurred inside the body chamber, which influenced formation of the microenvironment that favored good preservation of the fine delicate adolescent shell within the body chamber.

The material is deposited at the Ohio University, Zoological Collections (OUZC), Athens, Ohio, USA.

## GEOLOGICAL SETTING AND OCCURRENCE

The outcrop that yielded the specimens described herein is an excavated exposure in the Finis Shale Member of the Graham Formation (Lower Virgilian = Stephanian B/C). The excavation serves as the emergency spillway for Lost Creek Lake, which serves as a water supply for the community of Jacksboro, Jack County, Texas. The lake is located 3.2 km northeast of Jacksboro where Texas highway 59 crosses the northern tip of the lake. The fossiliferous outcrop is located near the dam on the southern end of the lake.

The exposure contains parts of both a transgressive and the regressive marine cycle. During the Upper Carboniferous more than 75 marine transgressive–regressive (T-R) units have been documented on the North American Mid-continent region (see Heckel 1986, 1994 for summaries). Boardman et al. (1984) analyzed the invertebrate megafauna of many of these T-R units in this region and identified and named a series of invertebrate communities that occur repeatedly in the T-R sequences.

Several marine megafaunal communities including a transgressive dysaerobic or juvenile molluscan dominated community that is separated by an unconformity from the overlying regressive mature molluscan dominated community; both communities make up the Finis Shale. This shale is capped by the Jacksboro Limestone, which has a distinct community containing phylloid algae in its upper portion (see figure 2 of Rothwell et al., 1996 for a measured section and a more complete discussion of the exposure).

The bactritoid and coleoid-bearing interval is in the regressive phase of Mature Molluscan Community. At the exposure in the spillway excavation, this community consists of approximately four meters of dark grey, when fresh and weathering, to a tan color shale, immediately above the storm deposit where shell debris and reworked phosphate concretions are concentrated (see figure 2 in Rothwell et al., 1996). The mega fauna of the bactritoid/coleoid bearing unit is dominated by cephalopods and other molluscs.

### DEPOSITIONAL ENVIRONMENT

The paleoecology of the interval bearing the bactritoid/coleoid cephalopods is interpreted as being moderately deep water (more than 25 meters but probably less than 100 meters) and having a moderately well oxygenated water column with a lesser, but still oxygenated, bottom sediment. This conclusion is based in part on the overall lack of phosphate and pyrite deposition in the shale interval, which indicates that the bottom water conditions were not strongly reducing. Other supporting evidence includes the presence of an extensive benthic fauna including corals, brachiopods, and numerous different molluscs as well as complete mixing of the sediment bedding by bioturbation. However, below the water/sediment interface probably no deeper than a few centimeters, reducing conditions must have been more intense around local places where there was more organic material.

Preservation of the shelled invertebrate organisms within this community is primarily by calcium carbonate with many specimens being discrete concretions. Some original aragonite shells are preserved, especially where weathering has not appreciably altered the sediment. Some pyrite is present in freshly excavated shale micro samples, but this kind of mineralization is minor in the fossilization of the larger invertebrates. The original aragonite of the molluscan shells appears to be only partly altered to calcite.

Virtually all of the cephalopods preserved in this interval are the partial remains of shells that were partly destroyed by predators. Indeed, all the shells of some species of coiled nautiloids and ammonoids from this interval are interpreted as having been broken during the act of predation (Mapes and Chaffin, 2003). None of the bactritoids and coleoids from this interval in the Finis Shale are complete specimens, and, while they have not been studied in detail, these shells also bear the similar marks of predation that were documented on some of the cephalopods from the Finis Shale by Mapes and Chaffin (2003) including circular and oval holes produced by tooth punctures and missing shell segments produced by crushing teeth. Some specimens exhibit crushing by lithostatic pressures that occurred after burial; however, specimens excavated *in situ* are always incomplete, and because of this, the preda-

tion breakage that caused the demise of the animal can usually be separated from diagenetic crushing.

### METHODS OF STUDY

**Scanning electron microscopy.** The initial portion of the adolescent shell as well as the shell ultrastructure was studied with scanning electron microscope (SEM) Hitachi S-4300 at the Swedish Museum of Natural History, Stockholm. The specimens were cut longitudinally, polished and etched with a water solution of 25% glutardialdehyde for 30 min. The specimens were repolished and re-etched with 5% acetic acid for 2–5 min. The etched specimens were glued to holders and coated with gold.

**Energy dispersive spectrometry.** EDS was used for analysis of the (a) sediment inside the body chamber of the largest shell (specimen 2) where the adolescent shell (specimen 1) was preserved, (b) the juvenile rostrum of specimen 1, (c) the shell wall, cameral deposits, septa and sediment inside the camerae and body chamber in the same specimen, and (d) the shell wall and septa in specimens 2 and 3.

**Measurements of cameral length.** The length of the camerae was measured on SEM images of the phragmocone, with a magnification of 40x, along the longitudinal central axis.

### OBSERVATIONS ON SHELL MORPHOLOGY, ULTRASTRUCTURE AND ELEMENTAL ANALYSIS

**Specimen 1 (no. OUZC 5205):** (Pl. 1, Figs. A, B, D, E; Pl. 3, Figs. A–F; Pl. 4, Figs. A–F; Text-fig. 1).

The specimen is the holotype of a new species *Mutveiconites milleri* sp. n. Shell morphology and ultrastructures are described in the systematic paleontology section herein.

**EDS data.** EDS analyses of the rostrum show S (ca 45%) and Fe (ca 38%) in places with numerous crystals of pyrite. Beyond them, the following elements are detected: O (19–44%), Ca (0–55%), Fe (0–6.8%), Mg (0–2.3%), S (0–0.7%), Si (0–1%), Al (0–0.7%), Mn (0–0.5%), P (0–0.4%). Analyses of the chambers show peaks of Ca (33–62%), O (33–55%), Fe (0–13%), Mg (0–6%), Al (0–0.5%), P (0–0.4%), K (0–0.4%), Mn (0–0.3%), Si (0–0.2%). Spectra of the shell wall show peaks of O (29–36%), Ca (34–47%), S (0–1%), Mg (0–0.7%), K (0–0.2%). EDS analyses of the cameral deposits show O (19–50%), Ca (44–50%), Fe (0–1.7%), Mg (0–1%), S (0–0.6%), Al (0–0.4%), K (0–0.4%), P (0–0.3%). Thus, the shell wall lacks P, Fe, and Si, and in this respect, it differs from the rostrum, chambers and cameral deposits. The latter three parts of the shell seemed to contain significant amount of organic material, which is not the case with the shell wall.

**Camera length periodicity.** (Text-fig. 1). The septa are irregularly spaced. The first camera of the phragmocone is short; its length is equal to 3/4 protoconch length; the second camera is shorter than the first one; the third camera is longer than the preceding ones but it is still shorter than the protoconch length; the fourth camera is as long as the first one; the fifth camera is slightly longer than the third one; next

camerae show a gradual but slightly irregular increase in length. This early initial shorting between septa 2 and 3 is probably due to development of the bactritella in the egg. With the gradual septal distance lengthening beginning at the 3<sup>rd</sup> and 4<sup>th</sup> septa and the gradual lengthening of the septal spacing from that point on, the 3<sup>rd</sup> and 4<sup>th</sup> septa probably correspond to the apertural position which is also the position of the primary constriction between the 8<sup>th</sup> and 9<sup>th</sup> septum that marks the time of hatching of the animal. The measurements of the 29 camerae indicate fluctuation of shell growth with increasing and decreasing length in 6 cycles.

**Specimen 2 (no. OUZC 5206):** (Pl. 1, Fig. A).

**Phragmocone.** The preserved portion includes the last two camerae before the body chamber. The last camera is shorter than the one before the last (3 mm and 5 mm respectively); this septal approximation may indicate the terminal mature growth stage. Siphuncle is narrow, ventral, and marginal. Because of the adolescent shell (specimen 1) lies in the paramedian plane about 2 mm from the median plane of specimen 2 the siphuncle was not cut. However, it is visible on the ventral side and the oval septal foramen indicates the ventral position of the narrow siphuncle, which is exposed on the next to last septum.

**Body chamber.** It is long slowly expanding; the length of the preserved portion is 65 mm, the diameter near the last septum is 9 mm and "aperture" diameter is 17 mm. The body chamber is 20 times as long as the last camera of the phragmocone.

**Shell ultrastructure.** The shell wall consists of thick nacreous and thin inner and outer prismatic layers. Septa, which are as thick as the shell wall, are nacreous. A wrinkle layer that has delicate wrinkles oriented perpendicular to the shell axis lines the body chamber. The wrinkle layer is located between the nacreous inner layer and the prismatic outer layer. In co-occurring coleoid *Shimanskya* the wrinkle layer is between the inner and outer acicular prismatic layers of the outer shell. Interestingly, the wrinkle layer in the co-occurring bactritoids occurs on the innermost surface of the nacreous layer of the shell wall, and this characteristic difference, together with ultrastructural studies and other subtle morphological features can help identify and separate the coleoids from the bactritoids as described by Miller (1930) and Mapes (1979) that occur in the Finis Shale in Texas.

**Specimen 3 (no. OUZC 5207):** (Pl. 2, Figs. A-C).

**Phragmocone.** The slowly expanded phragmocone is a 50 mm long fragment including nine camerae. The width of the camerae is slightly larger than their length (ca 7 : 5 respectively).

**Siphuncle.** It is marginal and narrow. Septal necks are retrochoanitic. Their dorsal portions are about twice as long as ventral. Connecting rings are thin, non-calcified, and were probably organic. In each camera their posterior ends are attached to the inner surface of the septal necks with the aid of the annular deposits. Their anterior ends are attached to the posterior edge of each septal neck.

**Septa.** The septa are thin, moderately curved, and nacreous. On dorsal side, the mural parts of the septa are short, but on ventral (siphuncular) side, they are long, about 1/3 camera length.

**Body chamber.** Only a partly complete body chamber (maximum diameter 9 mm) is preserved. Where the shell layers are separated on the body chamber the outer surface of the nacreous layer is lined with a delicate wrinkle layer. The wrinkles are aligned perpendicular to the shell axis like the wrinkle layer of the specimen 2.

**Cameral deposits.** At the growth stage of the specimen, the cameral deposits are indistinct.

**Cameral membranes and deposits.** The membranes can be distinguished under a standard dissecting microscope because of differences in color between the white calcite filling the camerae and black or dark brown material of membranes. The membranes line the shell wall, septal surfaces and the thin, indistinct cameral deposits on the shell wall. On the adapical septal surfaces, the deposits are essentially thicker than the septa. On the adoral surfaces, they occur irregularly and do not coat the entire septal surface but are restricted to the area near septal neck.

**EDS data.** The analyses of the cameral membranes taken from the surfaces facing the camerae show Fe (43–67%), S (15–34%) and O (8–23%). Analyses of the cameral membranes taken from the surfaces matching the shell wall show O (22–38%), Fe (55–62%), S (6–15%), Si (1.3–3.3%). Therefore, the cameral membranes were presumably originally organic material, but diagenetically they were replaced by black pyrite and reddish marcasite.

## SYSTEMATIC PALEONTOLOGY

Subclass Coleoidea Bather, 1888

Order Aulacocerida Stolley, 1919

Family Mutveiconidae Doguzhaeva, 2002

**Differences.** The family Mutveiconidae is erected by monotypy. A short rostrum is a characteristic feature of the family that distinguishes it from bactritoids because they lack a rostrum. Comparison with younger aulacocerids is difficult since the young growth stages are known for none of them in detail.

Genus *Mutveiconites* Doguzhaeva, 2002

**Type species.** *Mutveiconites mirandus* Doguzhaeva, 2002

**Diagnosis:** Slender longiconic orthocones with oval (in median section) protoconch; short rostrum coating protoconch and about first ten camerae, its conical post-protoconch part shorter than protoconch length, small ventral marginal siphuncle, septal necks short; camerae comparatively long; long body chamber present at least in young growth stages, shell wall of thin inner prismatic and thick nacreous layers; a gradual primary constriction is present between the eighth and ninth septum 8; there is no primary varix.

**Remarks:** The diagnosis was originally based on the adolescent shell described by Doguzhaeva, (2002a, Pl. 17, Figs. 1–4); adults were unknown. The family is established on the basis of the following features: longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle; short rostrum coating protoconch and adult first ten camerae, its conical post-protoconch part shorter than protoconch length; long body chamber present at least in early stages of growth. In *Mutveiconites* the conotheca includes a nacreous layer that makes up the bulk of its thickness as in Bactritoidea (Doguzhaeva et al., 1996). If it was

a spirulid genus it would lack a nacreous layer like Recent *Spirula*, the Cretaceous *Adygeya* Doguzhaeva, 1996a and *Naefia* Wetzel, 1930 and the Late Carboniferous *Shimanskyia* (Doguzhaeva & al., 1999a), in all of which the shell wall consists of inner and outer acicular-prismatic plates.

The adolescent specimen from the Finis Shale under consideration fits within the diagnosis of this family. The diagnosis of the genus is the same as for the family. Therefore, there are no morphological features that would contradict with the diagnosis of the genus as well.

The two other medium-sized longicones (specimens 2 and 3) from the same locality that yielded the adolescent shell (specimen 1) described below are referred to the family and genus, with reservation. However, they are not used for the systematic description because they do not preserve the diagnostic young shell growth stages, and without these early shell growth stages, a comparison with the type genus cannot be made.

*Mutveiconites milleri* sp. n.

Pl. 1, Figs. A, B, D, E

**Derivation of name:** In honour of A. K. Miller, a famous researcher of fossil cephalopods.

**Holotype.** Holotype, specimen no. OUZC 5205, Ohio University Zoological Collections, Ohio University, Department of Geological Sciences, Athens, OH 45701, USA.

**Type locality.** The specimen was collected from the emergency spillway at Lost Creek Lake approximately 3.2 km northeast of the community of Jacksboro, Jack County, Texas. The locality is designated as TXV-200 in the Ohio University fossil collections.

**Type Horizon.** Upper Carboniferous, Virgilian Stage, Finis Shale Member of the Graham Formation, Texas.

**Description.** The holotype is a 25 mm long adolescent longiconic shell. It consists of a small hemispherical, or cup-shaped protoconch, a rostrum, in which a post-protoconch part is about as long as the protoconch, 29 camerae are present in the phragmocone and a long body chamber. The protoconch is two times broader than long; the maximum diameter is near the aperture; it is 0.50 mm and its length is 0.25 mm. There is no constriction between the protoconch and first camera of the phragmocone, which may be due to the plane of the section, or this may be a diagnostic feature that separates the coleoids from the Bactritoidea. The protoconch wall has a thin unilayered shell, possibly prismatic, that wedges out near the first septum. There is no observable closing membrane. First septum is prismatic with thick organic membranes on the surfaces; it has long mural parts and in these two respects differs from the second and all other succeeding septa. The long mural parts of the first septum form the shell wall in several (5–10) of the initial camerae before the nacreous layer appears on its inner surface. The rostrum has a 0.25 mm long post-protoconch part, which surrounds the protoconch and extends as a sheath along the first ten or so camerae. The rostrum is loosely calcified and in places strongly pyritized, presumably because of its original essentially organic composition.

The diameter of the phragmocone increases in the first two camerae, then it gradually decreases during the next 6 camerae. Between the 8<sup>th</sup> and the 9<sup>th</sup> camera the shell is at its most constricted diameter, and from this gentle constriction, the shell gradually increases towards the aperture where it achieves a maximum diameter of about 1.8 mm. The gra-

dually expanding body chamber is 11 mm long, and that is about 2/5 of the shell length. Near the last septum, the diameter is 1.7 mm, and near the aperture it is 3 mm. Its shell wall thins towards the aperture. In ontogeny the shell wall shows the following ultrastructural modifications (Pl. 4, Figs. A–D). It is prismatic until approximately 7–10<sup>th</sup> camerae then a nacreous layer appears. There is no observable primary varix; however, this may be due to the plane of the section. The nacreous layer gradually becomes thicker and starting approximately from the 20<sup>th</sup> camera, it forms the main bulk of the shell wall thickness. The inner prismatic layer appears approximately at the position of the 20<sup>th</sup> camera. The outer and inner prismatic layers are comparatively thin. The septa are thin, moderately curved, and nacreous, with the exception of the first one that is prismatic. It appears that the adapical septal surfaces were originally coated by thick organic membranes. The adoral septal surfaces lack such membranes, or they are thin. Since the section of the shell is not median a siphuncle is not exposed, however, due to indirect evidence the siphuncle must have been ventral and marginal. Thin layering of cameral deposits is present in the protoconch and in the first camera. In the protoconch they are thin near the apex (or even absent there) and become thicker toward the aperture: At a distance of half the protoconch length, they are two times and near the aperture three times thicker than the protoconch wall. The adapical surface of the first septum lacks cameral deposits. In the first camera, they also have a maximum thickness in the adoral part of the camera, where they coat the shell wall and adoral septal surface. On the shell wall, they are as thick as the shell wall but become thinner and almost wedge out on the septum towards its central part. The cameral deposits have cameral membranes lining their surfaces. The membranes occur on thin loosely calcified portion of cameral deposits along the shell wall, on septal surfaces and in the corners between the shell wall and adapical septal surfaces. These membranes may be responsible for secretion of cameral deposits.

**Differences.** *M. milleri* sp. n. differs from *M. mirandus* in the shape of the protoconch, which is cup-like in the former and oval in the latter (compare Pl. 1, Fig. 2; Pl. 3, Fig. 1 and Pl. 5, Figs. A, B) and by presence of cameral deposits in the protoconch and also in camerae. This can be explained by the fact that the shell of the former is at an older growth stage since it has 29 camerae, against ten camerae in the latter. Besides, in *M. milleri* sp. n. the phragmocone is less curved than in *M. mirandus* but this can be explained by the different section plane of the two shells as follows: in *M. milleri* specimen the section is not median and in *M. mirandus* specimen the section is median. Therefore, the shell in *M. milleri* sp. n. could be slightly curved.

## CARBONIFEROUS PHRAGMOCONE-BEARING COLEOIDS – COMPARISON WITH HEREIN STUDIED LONGICONES

The limited data available on the initial part of the shell, phragmocone structure, and shell ultrastructure in Carboniferous phragmocone-bearing coleoids allows a systematic

comparison of the studied specimens from Texas with some of these taxa. Additionally the longicones examined are compared with Early Permian bactritoids and Mesozoic belemnoids.

### List of Carboniferous phragmocone-bearing coleoids

Order Hematitida Doguzhaeva, Mapes and Mutvei, 2002 – Early Carboniferous

Family Hematitidae Gustomesov, 1976

*Hematites* Flower and Gordon, 1959 – Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovian), Utah, Arkansas, USA

*Bactritimimus* Flower and Gordon, 1959 – Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovian), Arkansas, USA

*Paleoconus* Flower and Gordon, 1959 – Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovian), Arkansas, USA

Order Donovaniconida Doguzhaeva, Mapes and Mutvei (in press) – Late Carboniferous

Family Donovaniconusidae Doguzhaeva, Mapes and Mutvei, 2002

*Donovaniconus* Doguzhaeva, Mapes and Mutvei, 2002 – Upper Pennsylvanian, Desmoinesian, Oklahoma, USA.

Order Aulacoceratida Stolley, 1919–? Devonian; Carboniferous–Jurassic

Family Mutveiconitidae Doguzhaeva, 2002

*Mutveiconites* Doguzhaeva, 2002 – Upper Carboniferous, Orenburgian, southern Urals, Kazakhstan; Pennsylvanian (Virgilian), Texas, USA

Order Phragmoteuthida Jeletzky in Sweet, 1964

Family Rhiphaeoteuthidae Doguzhaeva, 2002

*Rhiphaeoteuthis* Doguzhaeva, 2002 – Upper Carboniferous, Orenburgian, Southern Urals, Kazakhstan

Order Spirulida Pompeckj, 1912

Family Shimanskyidae Doguzhaeva, Mapes and Mutvei, 1999

*Shimanskyia* Doguzhaeva, Mapes and Mutvei, 1999 – Upper Pennsylvanian, Virgilian (= Stephanian); Texas, USA

Order uncertain

? *Eobelemnites* Flower, 1945 – Upper Mississippian, Chesterian, Alabama, USA

? Unnamed coleoid from Czech Republic (Košťák et al., 2002) – Early Carboniferous, Moravice Formation, Northern Moravia, Czech Republic

“*Bactrites*” *woodi* Mapes, 1979–Eudora Shale Member, Stanton Formation, Pennsylvanian, Kansas, USA. (MAPES, 1979)

Undescribed Stark coleoids (Doguzhaeva, Mapes, Mutvei and Pabian, 2002) – Upper Pennsylvanian, Missourian (= Kasimovian), Nebraska, USA

### Comparison

***Hematites*.** The similarity of this genus and the Texas longicones under examination concerns: (a) presence of a rostrum, (b) irregular mineralization of the rostrum that seemed to be of essentially organic material in both, and (c) longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle with what appear to be organic connecting rings. Unlike the longicones under consideration, in *Hematites*: (a) the shell wall consists of five layers and lacks a nacreous layer; (b) the rostrum is a com-

plicated folded structure that coats the total length of the phragmocone; its post-phragmocone part is rather long as compared to the length of the body chamber, (c) the final chamber (= body chamber) is short, equal to 1.5 camera length, and (d) the protoconch and the initial part of the phragmocone are commonly truncated.

***Shimanskyia*.** The similarity of this genus and the Texas longicones under examination concerns: (a) longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle with thin and presumably organic connecting rings and septal necks that are longer on ventral side and shorter on dorsal side and (b) a long “tubular” body chamber. Unlike the longicones under examination, in *Shimanskyia* the shell wall consists of inner and outer acicular prismatic plates and lacks a nacreous layer, which is present in the Texas specimens.

***Donovaniconus*.** The similarity of this genus and the Texas longicones under examination concerns: (a) a sheath-like rostrum (its early stage form, near the protoconch, is unknown), (b) a long body chamber, (c) a phragmocone with narrow marginal siphuncle, septal necks that are short dorsally but long ventrally and septa with comparatively long mural parts, and (d) a shell wall with a dominant nacreous layer. This genus has a moderately breviconic shell, and in this respect differs significantly from the longicones under examination.

***Mutveiconites* (Pl. 5, Figs. A, B).** The similarity of this genus and the Texas longicones under examination concerns: (a) a longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle, (b) a long slowly expanded “tubular” body chamber, (c) protoconch with its maximum diameter near the aperture, (d) the lack of a constriction between the protoconch and first camera, (e) a short rostrum coating the protoconch and about first ten camerae, its post-protoconch part is about the length of the protoconch, and in front of the protoconch it is sheath-like, (f) irregular mineralization of rostrum that is supposed to be rich in organic material, (g) no distinct primary constriction, (h) no primary varix, and (k) shell wall ultrastructure with a dominant nacreous layer.

***Rhiphaeoteuthis*.** The similarity of this genus and the Texas longicones under examination concerns: (a) a phragmocone with narrow marginal siphuncle, septal necks that are short dorsally but long ventrally. This genus has a moderately breviconic shell, and in this respect differs significantly from the longicones under examination. Although the protoconch and early stages are unknown, a long slowly expanded body chamber at early ontogeny is possible as it was observed in undetermined juvenile shells from the same beds (see Doguzhaeva, 2002a: Pl. 15, Fig. 1; Pl. 16, Figs. 1, 6).

***Hemibactrites* (Bactritida):** The protoconch has a primordial dome (Doguzhaeva, 1996b, c) that can be erroneously interpreted as a short rostrum because of their similar positions in the shell. However, in *Hemibactrites* the protoconch wall consists of three prismatic layers, and near the apex there is a space between the outermost layer and two other layers. This space was named a “primordial dome”. The base of the primordial dome is marked by a ring of modified micro-ornamentation on the outer surface of the protoconch. The primordial dome lacks any traces of mine-

ralization or organic filling. It looks like an originally empty space on the apex of the protoconch. Contrary to that, in the studied adolescent Texas longicone, the rostrum is loosely mineralized and has no separate layer around it. The phragmocone structure is similar in the two genera, and in both (a) the longiconic phragmocone has comparatively long camerae and a narrow marginal siphuncle, and (2) a nacreous layer is the dominant element in the ultrastructure of the shell wall. Additionally, both genera have a long "tubular" body chamber.

*Conobelus*, *Passaloteuthis* (Pl. 1, Fig. C) (Belemnitida). The similarities in these genera and the Texas adolescent longicones under examination concerns: (a) the long mural parts of first septum that form a shell wall in first more than 20 camerae, where conotheca proper is missing, and (b) the irregular mineralization and high content of organic material of the primordial rostrum in belemnites (Pl. 1, Fig. C) and in the juvenile rostrum of *M. milleri* sp. n. (Pl. 1, Fig. B; Pl. 3, Fig. A).

## EVOLUTIONARY IMPLICATION

Nowadays, early evolution of aulacocerid coleoid cephalopods is poorly documented and, therefore, their origin is obscure. The coleoids, including the aulacocerids, evidently arose from bactritoids. Therefore, it is reasonable to assume that the "pioneers" of the aulacocerids were similar in gross morphology to bactritoids. However, for a long time, *Hematites* has been considered as an Early Carboniferous aulacocerid (Shimansky, 1960; Gordon, 1966; Gustomesov, 1976; Reitner and Engeser, 1982; Doyle, 1990; Doyle et al., 1994; Mariotti and Pignatti, 1999). The reasons for that were that this genus represented the earliest recorded cephalopod possessing a rostrum, and in chronological order, the next group having a rostrum is the aulacocerids. Besides, in both, the rostrum is a folded complex structure. Jeletzky (1966) erected the order Aulacocerida because of the pronounced morphological differences between the aulacocerids and belemnitids, such as a long body chamber, an aperture with short dorsal and ventral crests, a conotheca with growth lines, a rostrum built mainly of organic material, and prochoanitic adult septal necks. He considered the aulacocerid rostrum as analogous but not homologous to that in belemnitids. Jeletzky (1966) formally assigned *Hematites* to the order Aulacocerida, but for unknown reasons, omitted this genus in his classification. Doguzhaeva et al., (2002) restudied with the scanning electron microscope newly recovered material of *Hematites*. Their study revealed a set of features that did not fit within the diagnosis of the Aulacocerida. These features are: a short posterior "free" (post-phragmocone) part of a rostrum, short terminal (= "body") chamber, a peristome with a broad U-shaped ventral or ventro-lateral sinus, multi-layered conotheca without a nacreous layer, absence of ventral and dorsal apertural projections and growth lines, and absence of a pro-ostracum. On the basis of the differences listed above the order Hematitida Doguzhaeva, Mapes and Mutvei, 2002 was erected. Simultaneously with this, a juvenile orthoconic shell was found that shows a long body chamber, a narrow marginal siphuncle, a small protoconch, a short irregular mineralized rostrum. The post-

protoconch part of that is approximately as long as a protoconch and a shell wall has a nacreous layer. The specimen comes from the Upper Carboniferous of southern Urals, north-western Kazakhstan. This form was described as *Mutveiconites* (Doguzhaeva, 2002a). It has been considered as the earliest recorded member of the Aulacocerida. With the exception of the rostrum, it is remarkably like a bactritid shell (compare: Doguzhaeva, 2002: Pl. 1, Fig. 1 and Pl. 17, Fig. 1). The discovery of the Late Carboniferous adolescent longicone with a short rostrum from Texas, that is under examination herein, confirms the concept that the evolution of the aulacocerids started with bactritid-like forms that had a short irregularly mineralized, partly organic rostrum, which was, in its post-protoconch part, as small as a protoconch itself. From this viewpoint, the lineage of the aulacocerids is documented from the Late Carboniferous.

The striking feature of early shell ontogeny observed in the Late Carboniferous adolescent longicone from Texas, referred to the genus *Mutveiconites*, is the absence of the conotheca proper at the early growth stages. This feature has been known in some Jurassic and Cretaceous belemnites, for instance in Lower Cretaceous *Conobelus* (Doguzhaeva & al., 1999) and Lower Jurassic *Passaloteuthis* (Doguzhaeva & al., 2003), in which the long mural parts of the first septum continue along the initial portion of the phragmocone and form its shell wall. Another striking feature common for *Mutveiconites* and some belemnites is the irregular mineralization of the rostrum, in the former, and the primordial rostrum, in the latter (compare Pl. 1, Fig. B and Fig. C), indicating that both structures probably had an essentially organic composition. Further investigations are needed for discussion of these similarities.

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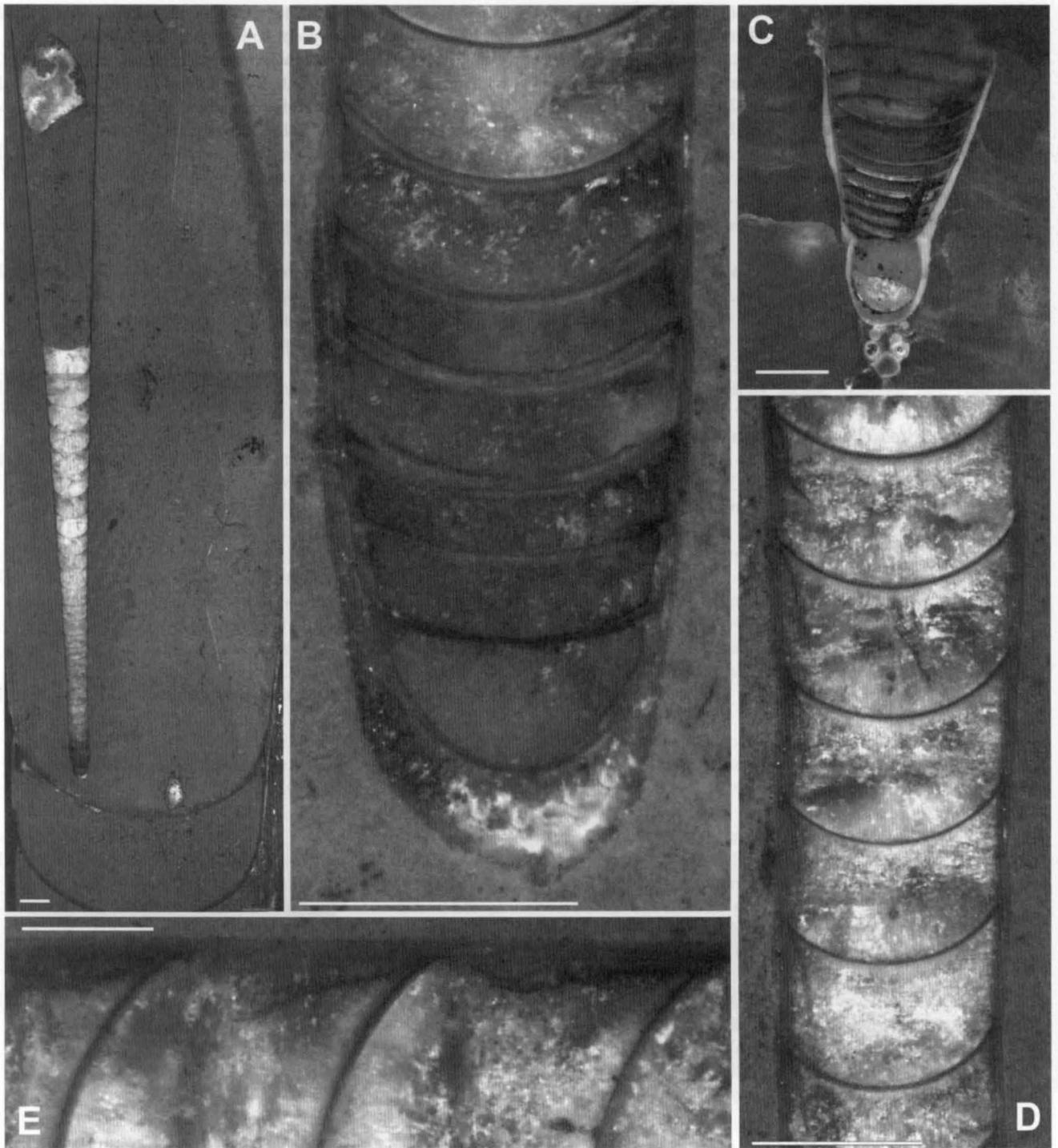


Plate 1. A–E. *Mutveiconites milleri* sp. n., Upper Carboniferous (Virgilian, = Stephanian), Texas, USA, holotype (OUZC 5205), longitudinal section. A. The adolescent longicone preserved inside the body chamber of the larger shell (OUZC 5206), showing a long body chamber and a phragmocone, scale bar is 1 mm. B. Enlarged view on the initial portion of the shell on Fig. A to show a short rostrum surrounding the protoconch and extending along the camerae, hemispherical protoconch, short irregularly spaced septa and cameral membranes on the inner surfaces of the shell; note that in the first septum the membranes are thicker than in the next septa; scale bar is 0.5 mm; D. Seven camerae of the phragmocone showing cameral membranes (left side) with their adoral ends attached to the corners between the shell wall and septa, scale bar is 0.5 mm; E. Enlarged view of the cameral membranes to show that they lie on the surface of the cameral deposits occurring along the shell wall; within the right camera the cameral membrane are coating the cameral deposits and from both ends they are attached to the septal membranes, in the next camera (to the left) the membrane is attached to the adoral septal surface but broken near its adapical end and shifted to the centre of the camera, the color photo emphasizes the presence of the cameral deposits along the shell wall, scale bar is 0.2 mm. C. *Passaloteuthis* sp. Lower Jurassic, north-western Germany. The median shell section showing a primordial rostrum exhibiting similarity with the rostrum in adolescent *M. milleri* sp. n. (compare with Fig. B). In both the apical part is loosely mineralized and evidently originally contained much organic material (for details see Doguzhaeva et al., 2002, 2003), scale bar is 0.5 mm.

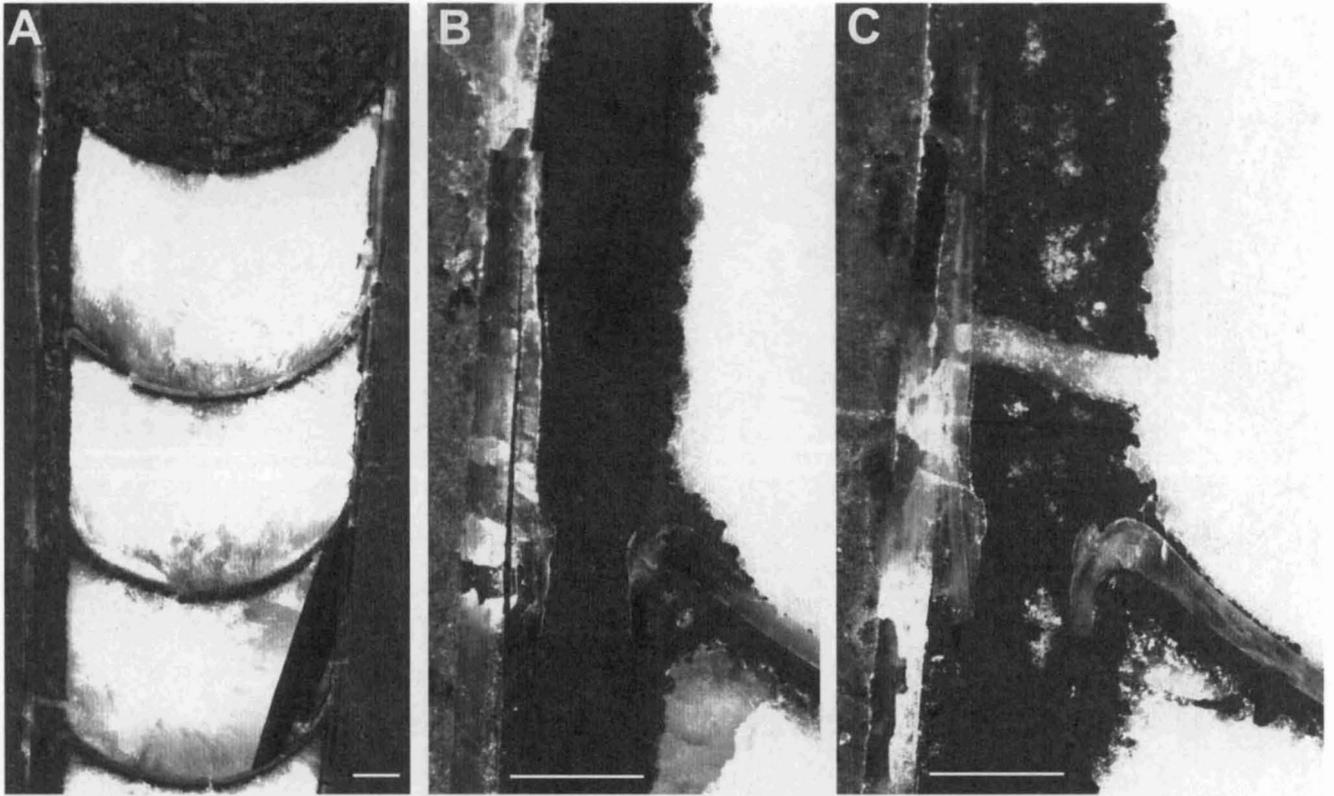


Plate 2. A–C. ? *Mutveiconites* sp., OUZC 5206, Upper Carboniferous (Virgilian = Stephanian), Texas, USA. Median shell section of medium-sized longicone showing the back part of a body chamber and last three camerae. A body chamber, a narrow marginal siphuncle and membranes on the adapical septal surfaces are strongly pyritized; camerae have no cameral deposits, scale bar is 1 mm. B, C. Enlarged view on two septal necks and connecting rings on Fig. A to show that septal necks have short dorsal portion and long ventral portion; connecting rings are thin, possibly nonmineralized, originally organic, their adapical ends are attached to the septal necks with the aid of the annular deposits inside the necks and their adoral ends are attached to the adapical tips of necks, scale bar is 0.5 mm.

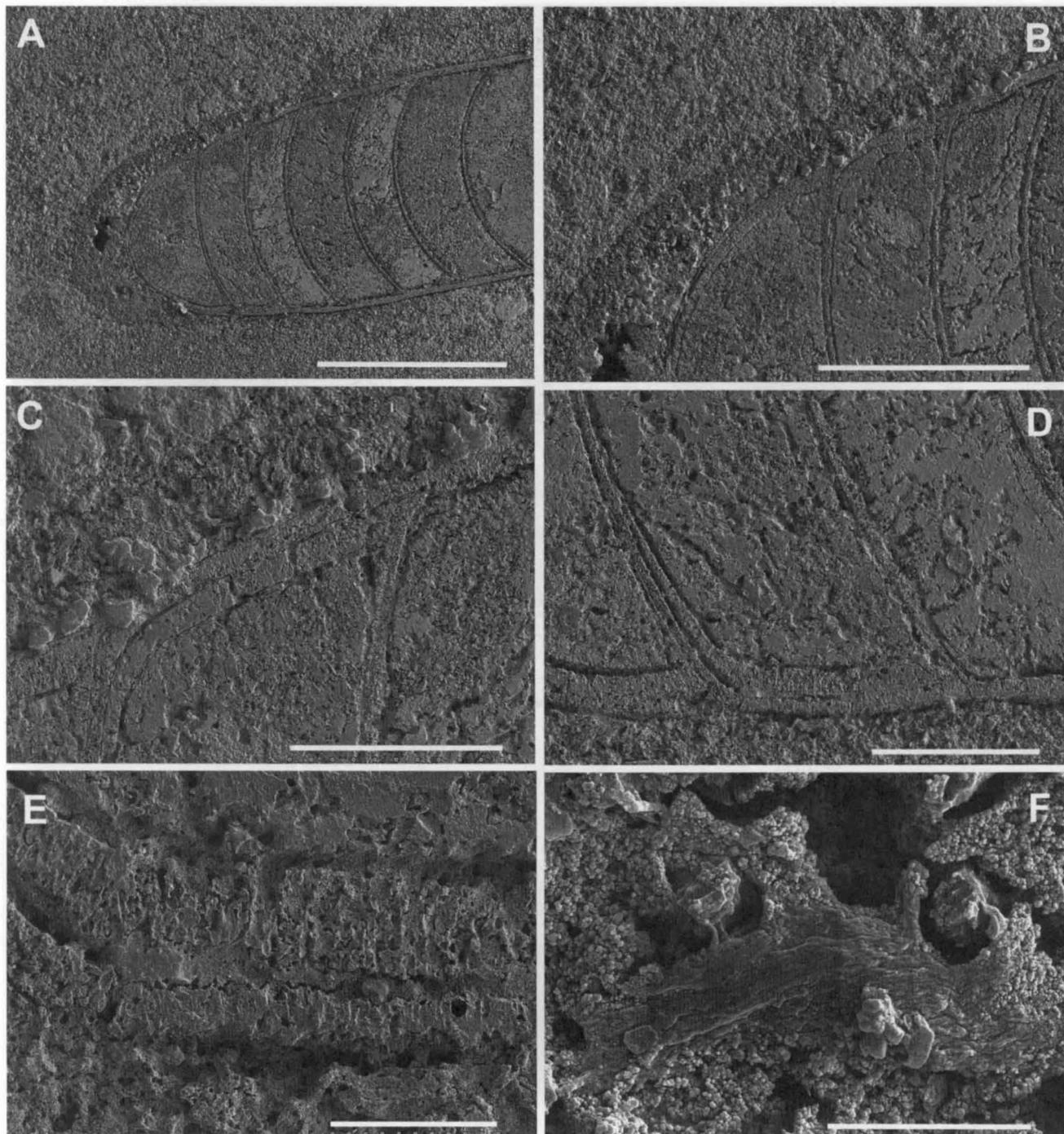


Plate 3. A–F. *Mutveiconites milleri* sp. n., Upper Carboniferous (Virgilian = Stephanian), Texas, USA, holotype (OUZC 5207), longitudinal section, SEM images. A. The initial portion of the shell to show a presence of a rostrum around the protoconch and first camerae and its length in ratio to the length of the protoconch, and camerae, scale bar is 600  $\mu\text{m}$ . B. Close up of Fig. A to show irregular mineralization and strong pyritization of the rostrum, scale bar is 300  $\mu\text{m}$ . C. Close up of Fig. A to show a long mural part of first septum constructing the shell wall and cameral deposits, scale bar is 120  $\mu\text{m}$ . D. Close up of Fig. A to show that the cameral deposits in the protoconch and first camerae, scale bar is 120  $\mu\text{m}$ . E. Enlarged view on Fig. D to show that the mural part of the first septum forms the shell wall in first camera and an interspace between them, scale bar is 30  $\mu\text{m}$ . F. Enlarged view of the coprolites showing they are oval clusters composed of digested material from an unknown organism, scale bar is 3  $\mu\text{m}$ .

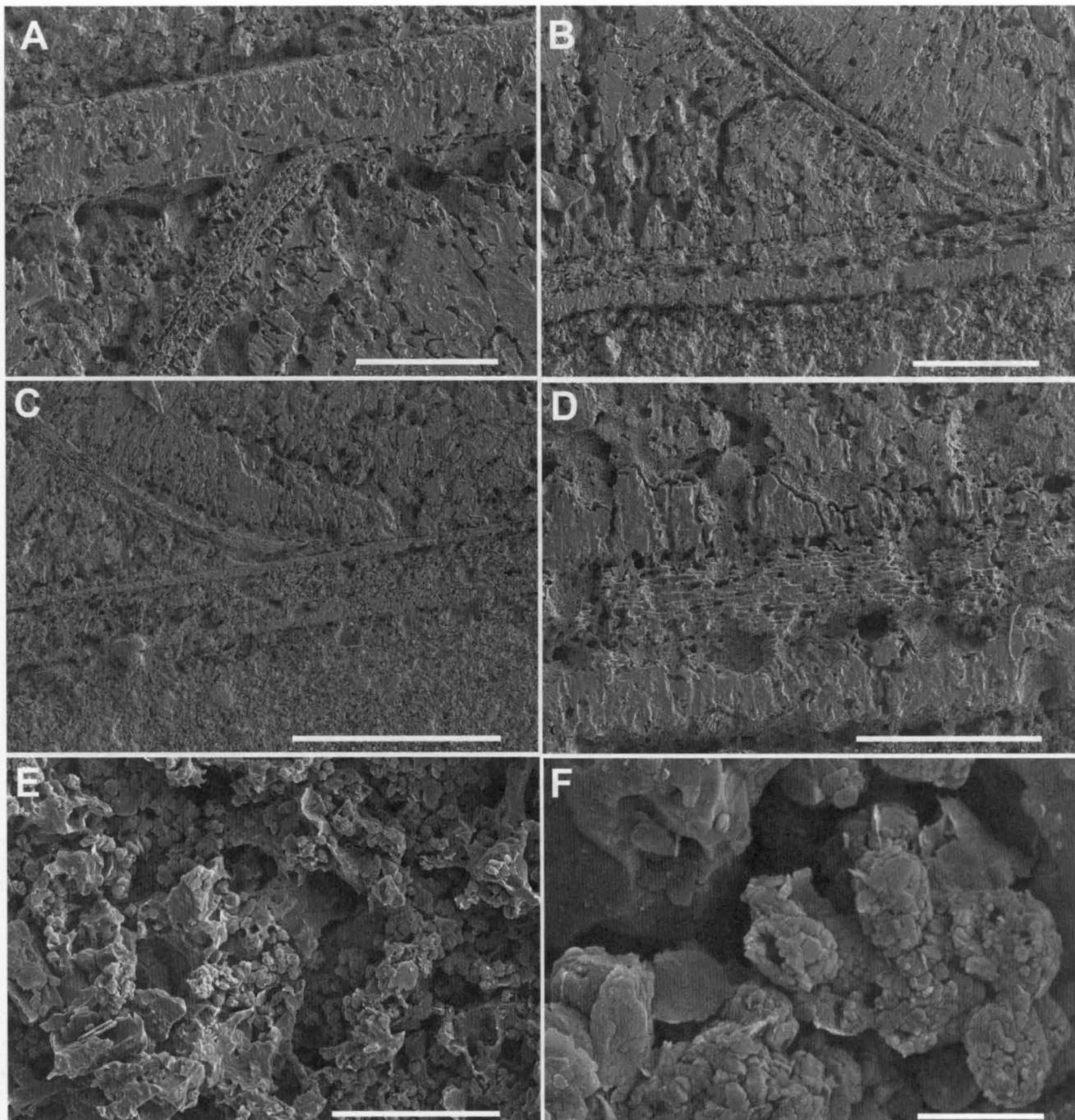


Plate 4. A–D. Shell wall ontogeny in *Mutveiconites milleri* sp. n., Upper Carboniferous (Virgilian = Stephanian), Texas, USA, holotype (OUZC 5205), longitudinal section, SEM images. A. Unilayered prismatic shell wall in first camera, scale bar is 30  $\mu$ m. B. Next growth stage, a nacreous layer is added to the outer prismatic layer, scale bar is 60  $\mu$ m. C. Next growth stage, an inner prismatic layer is added, scale bar is 120  $\mu$ m. D. Close up of Fig. C to show horizontal lamination of nacreous layer, scale bar is 30  $\mu$ m. Figs. E, F. ?*Mutveiconites* sp., OUZC 5206, Upper Carboniferous (Virgilian = Stephanian), Texas, USA. View on heterogeneous sediment in the body chamber, scale bar is 12  $\mu$ m. F. Close up of Fig. D to show microstructures evidently evidencing possible role of microorganisms (?bacteria) in reworking of the material inside the body chamber. The latter made possible fine preservation of a delicate adolescent longicone inside, scale bar is 1.2  $\mu$ m.

DISCUSSION

The shell wall ontogeny in *Mutveiconites milleri* sp. n. shows a clear progression from a unilayered prismatic structure to a more complex, multi-layered structure with an inner prismatic layer and an outer nacreous layer. This suggests a process of incremental growth and modification of the shell wall over time. The presence of horizontal laminations in the nacreous layer (Fig. D) is characteristic of nacreous growth. The heterogeneous sediment in the body chamber (Figs. E, F) and the microstructures within it (Fig. F) provide evidence for the possible role of microorganisms in reworking the material, which allowed for the fine preservation of a delicate adolescent longicone inside.

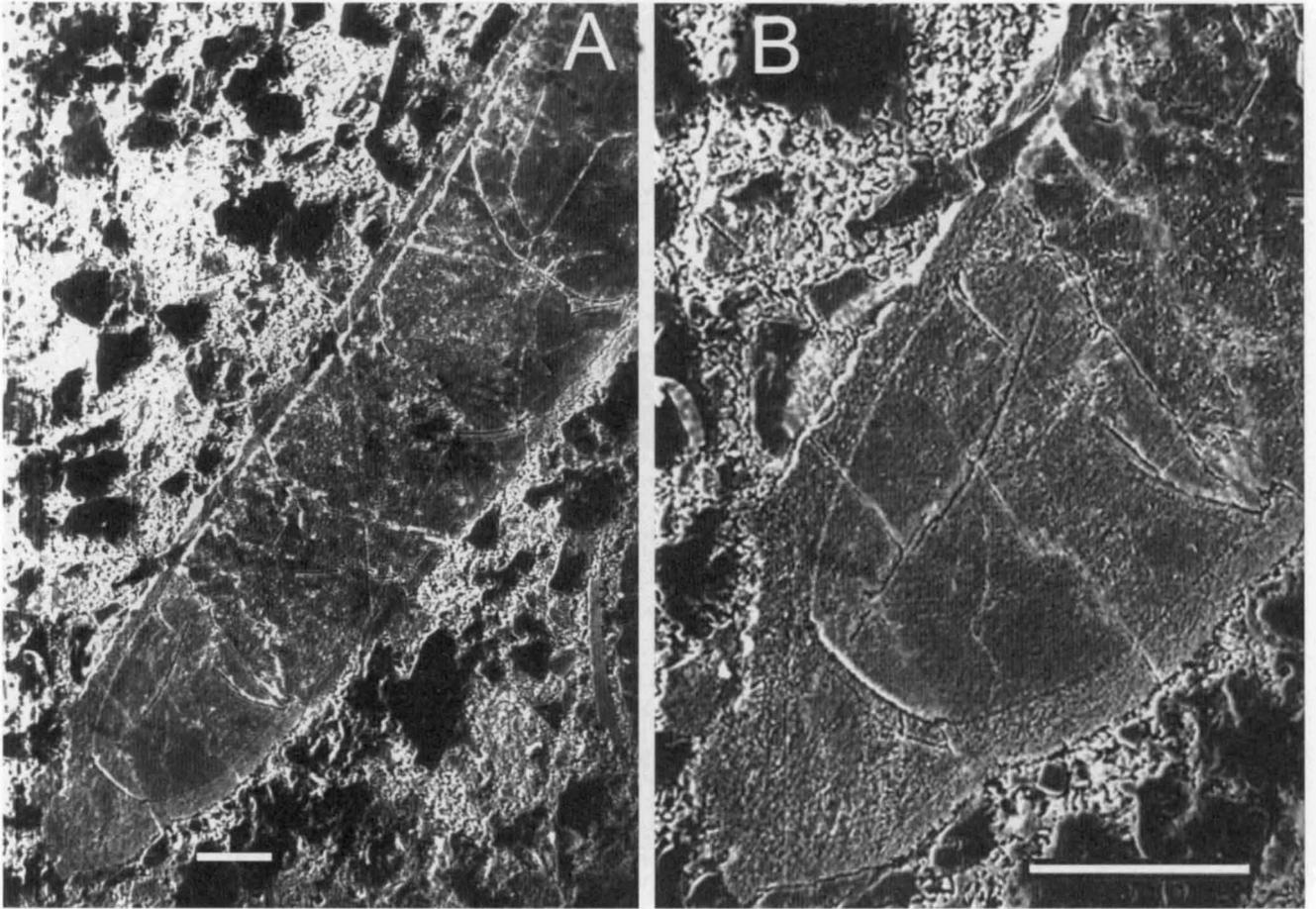


Plate 5. A–B. *Mutveiconites mirandus*, sp. PIN 3871/370, Coll. of Paleontological Inst., Russian Academy of Sci., Moscow, Upper Carboniferous, Orenburgian, south Urals, Kazakhstan (former USSR) (modified from Doguzhaeva, 2002, Pl. 17, Figs. 1–4). A. The median section of the initial portion of the shell showing a cone-like rostrum, an oval protoconch and first camerae, scale bar is 0.1 mm. B. Enlarged detail of A to show a rostrum with a short post-protoconch part and sheath-like part Vextending along the phragmocone, scale bar is 0.1 mm.

# AN UNIQUE UPPER TRIASSIC COLEOID FROM THE AUSTRIAN ALPS REVEALS PRO-OSTRACUM AND MANDIBULE ULTRASTRUCTURE

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**Abstract:** A recently discovered Late Triassic (Lower Carnian) coleoid (Doguzhaeva & al., 2005a) from the Austrian Alps (locality Schindelberg, Lunz, Niederösterreich) is described as *Lunzoteuthis schindelbergensis* n. gen. et sp. The remnants of the small-sized coleoid comprise (1) a fragmentarily preserved, breviconic phragmocone compressed by compaction (about 10 mm broad and 5 mm long; estimated apical angle ca. 15–20°), (2) a proostracum that is discernible by the growth lines on the dorsal side of the phragmocone, and (3) a lower mandible that is relatively large, broad (about 4 mm long), black and glassy. The rostrum is absent.

The proostracum in *L. schindelbergensis* is similar to that in Early Jurassic *Belemnotheutis* but differs by its narrow central field, bordered by hyperbolic zones, from the tripartite proostracum of the contemporaneous *Phragmoteuthis*, Middle Triassic *Breviconoteuthis* and Upper Permian *Permoteuthis*. Contrary to *Belemnotheutis*, it has no rostrum. The lower mandible in *L. schindelbergensis* is similar to that in recent squids and bears no resemblance to the structure described as mandibles in *Phragmoteuthis* (Mojsisovics, 1882).

SEM examination shows that the proostracum material in *L. schindelbergensis* is finely laminated, making it similar to (1) the chitinous gladii in modern squids *Loligo* and *Berryteuthis* here studied, (2) the fossil gladii of several squid-like coleoids (Doguzhaeva & Mutvei, 2003; 2005, 2006 herein) and (3) the proostracum of *Belemnotheutis* (Doguzhaeva et al., 2005b; 2006b herein). The proostracum in *L. schindelbergensis* has neither prismatic nor nacreous layers and therefore is not considered to be a projection of the phragmocone wall (conotheca). It is built up of two layers: (1) the inner layer of vertical columnar units formed by micro-lamellae (“organic lamello-columnar” ultrastructure), (2) the outer layer of micro-plates that have a wedge-like shape and are arranged more or less parallel to the surface. The new data supports the concept that the proostracum is an innovative morphological element in coleoid evolution (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, b, 2003a, b, 2005a, b; 2006b herein).

The presumable lower mandible of *L. schindelbergensis* is characterized by broad wings and a distinct beak (= rostrum) that has a thickened anterior edge. The wings are formed by inner and outer laminae fused near the rostrum. The length ratio of the two laminae is unclear because the posterior portion of the mandible was destroyed during preparation. The mandible has a micro-laminated ultrastructure similar to that of chitinous mandibles in *Loligo* and in the contemporaneous ceratitid *Austrotrochyceras* from the same locality (Doguzhaeva et al., 2007a in press). In: *L. schindelbergensis* the mandible must therefore have been originally chitinous.

The initial shell ontogeny in *Lunzoteuthis* n. gen. remains unknown, and the systematic position of the new genus is uncertain. In the gross morphology of the phragmocone and proostracum it is comparable with *Belemnotheutis* but is distinguished by having no rostrum. It is temporarily referred to the Suborder Belemnoteuthidina Stolley.

**Key words:** Late Triassic coleoid, shell morphology and ultrastructure, pro-ostracum, mandibles evolutionary morphology, Austria

## INTRODUCTION

Starting from the Early Jurassic, ca. 135 MY ago, belemnites were widespread all over the world. All were characterized by a proostracum, an important component of the soft body/skeleton architecture. However, the record of the pre-Jurassic proostracum-bearing coleoids is restricted to a few taxa; since most of these were represented by only one or two available specimens, the pre-Jurassic “history” of the proostracum remains obscure. Among Triassic coleoid cephalopods, the

proostracum has been observed in *Phragmoteuthis* (Bronn, 1859; Suess, 1865; Mojsisovics, 1882) and *Breviconoteuthis* (Rieber, 1974). The Upper Triassic *Phragmoteuthis bisinuata* BRONN from the black fish shales of Raibl in Carinthia (formerly in the Austro-Hungarian Empire, now: Cave del Predil in Italy) is well illustrated and represented by about 100 specimens stored at the Museum of Natural History and Austrian Geological Survey in Vienna. The broad (ca. 3/4 of the circumference of the phragmocone) tripartite proostracum of the above two genera differs essentially from that of Jurassic-

Cretaceous Belemnoida, which is tongue-like and flanked by hyperbolic zones. The proostracum of the "*Phragmotheuthis*" type has been considered as a "morphological bridge" between the bacritoids, which have a long body chamber with a deep ventral sinus in some taxa (*Pseudobacrites bicarinatus* Ferronnière), and the belemnoids, which lack a body chamber but have a proostracum. The proostracum is generally interpreted as a dorsal remnant of the body chamber wall in the precursors (see Naef, 1922; Jeletzky, 1966; Donovan, 1977). This interpretation remains convincing and valid, although it has not been reevaluated taking into account new data obtained since its introduction. Recently, the conotheca and proostracum were found to differ essentially at the ultrastructural level (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, b; 2003a, b; 2005a, b; 2006b herein). If, however, the proostracum is a remnant of the body chamber wall, then the proostracum and conotheca should be similar ultrastructurally. This inconsistency calls for additional data to help elucidate the evolutionary transformation of an external skeleton into an internal one in cephalopod evolution.

The present paper deals with a recently reported, unique Upper Triassic coleoid from the Austrian Alps (Doguzhaeva et al., 2005a). It shows a rarely observed combination of a shell and a mandible preserved in one and the same fossil (Pl. 1 A–C; Pl. 2). Moreover, the shell surface is well preserved and bears growth lines indicating the presence of a proostracum. This study provides new morphological data that helps to elucidate the evolutionary morphology of the coleoid skeleton. Apart from the shell, the mandible in extinct coleoids is itself a rare and important fossil. In the present case, the mandible material, which was originally organic, is of special interest for ultrastructural comparison with the material of the proostracum in the same specimen.

The paper contains (1) a systematic description of the Upper Triassic coleoid, and (2) comparisons between the ultrastructure of the proostracum and mandible in this coleoid and the gladii and mandibles of the living squids *Berryteuthis* Berry and *Loligo* Lamarck, and (3) a discussion on the evolutionary morphology of the proostracum.

## MATERIAL, LOCALITY, STATUS OF PRESERVATION AND METHOD

The studied material comprises: (1) a single shell and a mandible of the Late Triassic coleoid from the Lower Carnian – *Austriacum* Zone at Lunz (locality Schindelberg), Lower Austria and (2) five gladii and mandibles of the Recent squids *Berryteuthis* and *Loligo*.

The fossil specimen (Pl. 1–7) was found in the old collections of the ceratitid *Austrotrachyceras*. More than 100 years ago, the material was excavated with the permission of Mr. Haberfelner, the director of the coal mine at Lunz, in 1885 for the Geological Survey of Austria and in 1902 for the Museum of Natural History in Vienna. The sites are now inaccessible for collecting. The remains of this coleoid, comprising a tiny shell and a mandible, were buried near a comparatively large (ca. 50 mm diameter) shell of *Austrotrachyceras*. The larger ammonoid shell possibly hindered the post-mortem disintegration of the shell and mandible of this small-sized coleoid. The exceptional preservation of

the shell material in *Austrotrachyceras* from this locality has already been elucidated (Doguzhaeva et al., 2004). All the ammonoid shells here are crushed by compaction, with the left and right body chamber walls more or less in contact with each other. Nevertheless, the pieces of the shells remain together in a fractured mosaic pattern. At the Schindelberg locality the mandibles are known to be associated with the ammonoid specimens and located in front of or partly within the body chamber (Trauth, 1935; Krystyn, 1991; Doguzhaeva et al., 2004, 2007a in press). Shiny, black, asphalt-like material is located between the body chamber shell walls in places. The ultrastructural and energy dispersive analyses of this black material revealed that it represented bituminous soft body tissues (Doguzhaeva et al., 2004). The low-oxygen, near-bottom depositional environment of the shales helped preserve the originally non-mineralised organic material (Griffin, 1977).

The studied Carnian coleoid is crushed by dorso-ventral compaction. The shell deformation is similar to that of the recently studied Jurassic specimens of *Belemnotheuthis* (Doguzhaeva et al., 2005b). In both, the longitudinal and transverse (along the mural rings) fractures exhibit a mosaic pattern formed by rectangular fragments. The proostracum is discernible by the typical growth lines of its central field and by the longitudinal ribs on its hyperbolic zones. The mode of preservation and dislocation of the shell and mandible (dorso-ventral compression of the shell, mandible positioned immediately in front of the anterior edge of the phragmocone) indicates that the mandible must have been buried and protected by the proostracum before it was partially destroyed, and that these two structures apparently belonged to the same individual. The shell/mandible size ratio points to a relatively large jaw apparatus. In modern squids the ratio between the length of the body and buccal apparatus is approximately 1/10 (Morton & Nixon, 1987; Tanabe et al., 2006).

The ultrastructure of gladii and mandibles of the modern squids *Berryteuthis* and *Loligo* was studied after one-year drying.

The specimens were examined without etching with a scanning electron microscope Hitachi 4300 at the Swedish Museum of Natural History, Stockholm, Sweden.

The fossil specimen is deposited in the Museum of Natural History, Vienna, Austria, under the inventory number NHMW 2005z0005/1.

## PRO-OSTRACUM MORPHOLOGY AND ULTRASTRUCTURE (FIGS. 1; 3–7)

The proostracum is about 3 mm wide, which is approximately 1/6–1/7 of the estimated shell circumference (Pl. 1, A). It has a narrow central field with narrowly rounded growth lines, and hyperbolic zones with longitudinally converging ribs but no asymptotes (Pl. 1, A–C). In the adoral part of the central field, the growth lines form an acute angle of ca. 60–80°. The narrow growth lines are of two orders: about 5 broad and 30 narrow lines. The proostracum covers five or six camerae of the phragmocone; the camerae are about 0.8 mm long.

The proostracum is ca. 50 µm thick. It consists of the two layers of about the same thickness (Pl. 3, A, B). The inner

layer is composed of vertical columnar units about 4–5 µm in diameter (Pl. 4, A–B; Pl. 5, A–B). The columns are separated by interspaces and composed of ca. 0.05µm-thick micro-laminae (Pl. 5, A–B). In 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 thick (Pl. 4, A; Pl. 5, A). They were probably originally organic, as were the lamellae in the chitinous mandible of living coleoids (Pl. 8, A–B). Thus, the proostracum ultrastructure is unique and bears no resemblance to either the prismatic or nacreous layers of the phragmocone wall.

## MORPHOLOGY AND ULTRASTRUCTURE OF THE LOWER MANDIBLE (FIGS. 2, 7)

Judging from its broad, spoon-like shape, the preserved mandible is the lower mandible (Pl. 2; Pl. 7, A). In modern coleoids the lower mandible is usually broader than the upper one (Clarke, 1962; Hernández-García, 2003). The mandible consists of broad wings, a flattened crest (the bottom of the mandible) and a beak (= rostrum), the latter having a thickened anterior edge (Pl. 7, A–B). The wings are formed by inner and outer laminae fused near the beak. The length ratio of the two laminae is unclear because the posterior portion of the mandible was destroyed during preparation. The mandible has a micro-laminated ultrastructure (Pl. 7, C), being in this respect similar to the chitinous mandibles in *Loligo* (Pl. 8, A–B) and in the contemporaneous ceratitid *Austrotrachyceras* from the same locality (Doguzhaeva et al., 2007a in press).

The beak (= rostrum) is fractured in a “step-like” pattern (Fig. 7, C), similar to the fractioned chitinous mandibles and gladii in the living squids *Berryteuthis* and *Loligo* (Pl. 8, A–B). Similar fracture patterns have also been observed in broken gladii of fossil squid-like coleoids (Doguzhaeva & Mutvei, 2003; Pl. II, Fig. 1a; Pl. III, Fig. 1a). In modern squids this pattern is determined by a “glassy” ultrastructure of the chitin material both in the mandibles and gladii (Pl. 8, A–B). Based on this ultrastructural similarity, the fossil mandibles are considered to have been originally composed of chitin.

## SYSTEMATIC PALAEOONTOLOGY

Class Cephalopoda CUVIER, 1794  
Subclass Coleoidea BATHER, 1888  
Ordinal status uncertain  
? Suborder Belemnoteuthididina STOLLEY, 1919  
? Family

Genus *Lunzoteuthis* n. gen.

Type-species: *Lunzoteuthis schindelberensis* n. sp.

Derivation of name: From the town of Lunz (Lower Austria), close to where the specimen was found.

Diagnosis: Small-sized breviconic phragmocone with apical angle ca. 15°–20°, short camerae with broad (ca. 1/3 of camera length) mural parts of septa. Proostracum shorter than phragmocone; with narrow central field (ca. 1/6 of phragmocone circumference) and hyperbolar zones; no asymptotes;

curvature of growth lines in central field ca. 70–80°; hyperbolar zones with thin longitudinal converging ribs; angle between them and median line of proostracum about 40°. No rostrum. Lower mandible with broad wings and a distinct beak (= rostrum).

Notes: The genus is erected based on a tiny fragment of a single, small-sized shell and mandibles positioned in front of the anterior edge of the shell (Pl. 1, A–B; Pl. 2; Pl. 7, A). The apical portion of the shell is unknown. Based upon the solid mandible the specimen might have belonged to a small-sized mature individual. In living squids the juveniles have a solid beak (= rostrum) but the hood is softer (Hernández-García, 2003).

Discussion. The systematic position of the new genus is unclear. The gross morphology of the phragmocone and proostracum may allow a placement of the genus within the Suborder Belemnoteuthididina. However, the apical portion of the shell is unknown and whether it had a rostrum, like in *Belemnoteuthis*, is uncertain. Should this coleoid have no rostrum at early ontogenetic stages, it should be placed in a new suborder.

Geographical range: locality Schindelberg, Lunz, Lower Austria.

Stratigraphical range: Lower Carnian, *Austriacum* Zone, Upper Triassic.

*Lunzoteuthis schindelbergensis* n. sp.

(Figs. 1A–C; 2)

Holotype: NHMW 2005z0005/1 is an incompletely preserved, small-sized (about 10 mm broad and 5 mm long), breviconic phragmocone, compressed by compaction, with exposed dorso-lateral surface and a black, organic, lower mandible located near an anterior edge of the shell.

Derivation of name: From the name of the locality Schindelberg.

Type locality: Schindelberg, Lunz, Lower Austria, Northern Calcareous Alps.

Stratum typicum: Lower Carnian, *Austriacum* Zone, Upper Triassic

Diagnosis: As for the genus.

Description: The remnants of the small-sized coleoid comprise (1) a fragmentarily preserved, breviconic phragmocone (about 10 mm wide and 5 mm long; estimated apical angle ca. 15–20°), compressed by compaction, (2) a proostracum that is discernible by the growth lines on the dorsal side of the phragmocone, and (3) a lower mandible that is relatively large, broad (about 4 mm long), black and glossy.

The shell wall is thin and, by compression, crushed into small rectangular pieces forming a mosaic pattern. The camerae are short and the mural parts of septa are broad; camerae with a length ratio ca. 3:1. The dorsal and lateral shell surfaces and a small piece of the inner surface on the ventral side are exposed (Pl. 1, A). The estimated shell diameter near the aperture is 5 mm. The total length of the phragmocone is estimated to be ca. 20 mm. The proostracum has a central field, typically ornamented by curved growth lines, and hyperbolar zones, ornamented by longitudinal, converging ribs. The asymptotes are not developed. The proostracum length is estimated approximately to be one half of the phragmocone length. The lower mandible is partly exposed and has a broad, flattened crest (bottom),

broad wings and a non-calcified beak (= rostrum). It consists of a black, anthracite-like, glossy material. The wings are formed by the inner and outer laminae. Because of imperfect preservation, the size and three-dimensional shape of the mandible are unknown. The maximum size of the preserved mandible fragment is equal to the maximum diameter of the phragmocone.

Geographical and stratigraphical range: as for the genus.

## DISCUSSION

In Paleozoic coleoids the proostracum is known in the Late Permian *Permoteuthis groenlandica* Rosenkrantz and in the Late Carboniferous *Donovaniconus oklahomensis* Doguzhaeva, Mapes & Mutvei. In *P. groenlandica* the proostracum has only been observed in a single shell fragment (Rosenkrantz, 1946: p. 161, Fig. 6); according to Jeletzky (1966: p. 38), all other phragmocones referred to this taxon show no traces of proostraca and belong to the parabactritid genus *Tabantaloceras* Shimansky. The proostracum in *P. groenlandica* represents the long and broad, tripartite “*Phragmoteuthis*” type (see Jeletzky, 1966: p. 38). In *D. oklahomensis* the proostracum covers the entire shell but has a short, dorsal, lobe-like, broadly rounded anterior projection beyond the aperture with a length of approximately 1.5–2 camerae length. Its thickness is approximately 1/2–2/5 of the conotheca thickness. The proostracum is composed of a thin outer prismatic sublayer and a thick inner sublayer with an irregularly granular ultrastructure containing numerous empty spaces, probably originally filled by organic material. Transverse and longitudinal smooth ridges ornament the external and internal surfaces of the proostracum. On the dorsal external surface the transverse ridges are strongly curved adorally. They show no indications of the tripartite pattern (Doguzhaeva et al., 2002b: Fig. 2; 2003a: Fig. 2) and therefore the proostracum in *D. oklahomensis* cannot be referred to the “*Phragmoteuthis*” type.

In the Middle Triassic *Breviconoteuthis* (Rieber, 1974) and Late Triassic *Phragmoteuthis* (Bronn, 1858; Suess, 1865; Mojsisovics, 1882) the proostracum is long (exceeding the phragmocone length) and broad (3/4 of the phragmocone circumference), tripartite, without hyperbolar zones, and differs from the proostraca in all other coleoids with the exception of *Permoteuthis*.

Huxley (1864) and subsequent authors (Suess, 1865; Mojsisovics, 1882; Naef, 1922; Jeletzky, 1966; Donovan, 1977) emphasized the phylogenetic significance of the peculiar proostracum in *Phragmoteuthis*. Based on this characteristic, Mojsisovics 1882 erected the family Phragmoteuthidae that Jeletzky later ranked as an order Phragmoteuthida Jeletzky (in SWEET, 1964). The “*Phragmoteuthis*” type of a proostracum has been considered as a feature indicating the bactritoid/coleoid affinity (Jeletzky, 1966). This concept assumes that a gradual reduction of the ventral side of the body chamber in ancestral bactritoids resulted in the formation of the initially broad proostracum in early coleoids. The broad proostracum was believed to gradually narrow and create a “*Belemnite*” type of the proostracum. Naef (1922), however, believed that the earli-

est coleoids had a narrow proostracum, although at that time the earliest known proostracum-bearing coleoid was *Phragmoteuthis* with broad proostracum.

In the Late Triassic *L. schindelbergensis* n. gen. et sp. the external dorsal surface of the phragmocone bears two kinds of ornament. The median part exhibits anteriorly curved growth lines and is therefore probably the central field of the proostracum. On each side of the central field there is a longitudinal zone with straight, longitudinal, anteriorly converged lines. The latter zones are considered to be the hyperbolar zones of the proostracum. The genus lacks asymptotes that, in the “*Belemnite*” proostracum type, lie between the central field and the hyperbolar zones. Judging of the Early Jurassic juvenile belemnites in which the proostracum was observed in the first camera of the phragmocone (Doguzhaeva et al., 2002c: p. 42, Figs. 1, 4; 2003b: p. 81, Figs. 1–3), the asymptotes are present throughout the ontogeny in the “*Belemnite*” type. This leads to a conclusion that the proostracum of *L. schindelbergensis* cannot be referred to the “*Belemnite*” type. Nevertheless, it shows certain elements of differentiation (central field and hyperbolar zones) of the “*Belemnite*” type. The proostracum morphology clearly demonstrates that *L. schindelbergensis* is not a juvenile or adolescent individual of the contemporaneous *Phragmoteuthis*.

The proostracum of *L. schindelbergensis* yields new ultrastructural data for the discussion on the origin and transformation of the shell in coleoid cephalopods. The proostracum lacks the nacreous and prismatic layers that are typical for the aragonitic conotheca but possesses a fine lamination that characterizes organic substances such as chitin. 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. Similar micro-lamellae are observed in the proostracum of the Early Jurassic *Belemnite* (Doguzhaeva et al., 2005b, 200Xb, herein). Thus, the proostracum in the specimen studied was originally mainly composed of an organic material. This provides additional proof for the concept (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, 2003a, b; 2005a, b, 2006b herein) that the proostracum originated as an innovative morphological structure in coleoid evolution rather than as a derivate of the conotheca in the precursors.

Mandibles of extinct coleoids are rare, especially in association with a shell or gladius. Mojsisovics (1882) described the mandibles in the contemporaneous *Phragmoteuthis bisinuata*. Accordingly, the mandibles commonly lie in front of the proostracum at a distance of about 1/2 – 3/4 the proostracum length (Mojsisovics, 1882: Taf. XCIV, Figs. 1, 4a, 5, 6). They are glossy, black and small, and consist of two symmetrical branches with two upwards pointed, tubercular processes. The tentacles with double rows of hooks are linked up to the mandibles. According to the illustrations the mandibles are partly exposed from the shale and their real shape can hardly be reconstructed based on the illustrations. They appear to differ essentially from the mandibles in living coleoids.

In Late Jurassic *Trachyteuthis hastiformis* Rüppell the lower and upper mandibles were found in association with a gladius, being still articulated in one of the two specimens

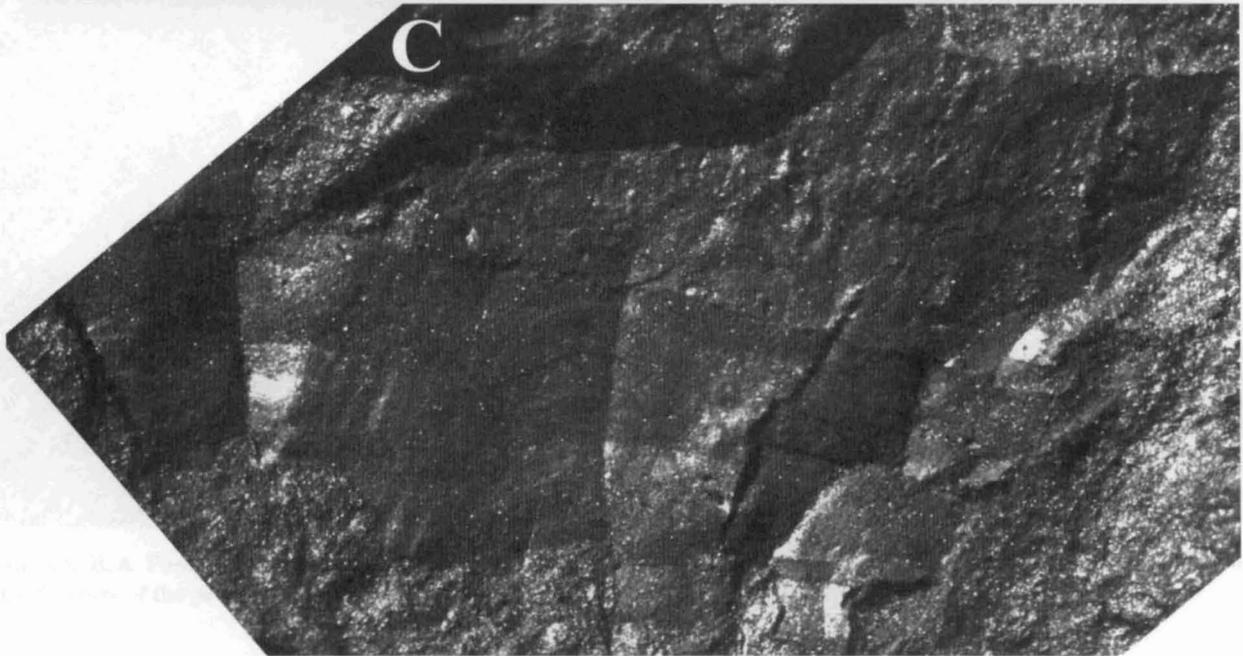
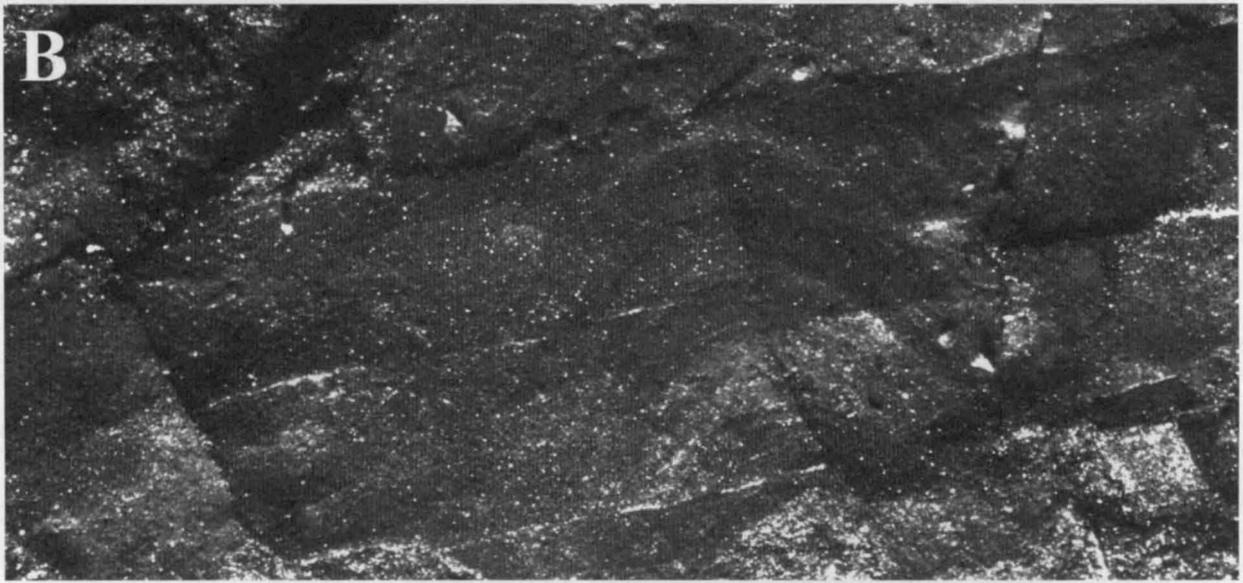
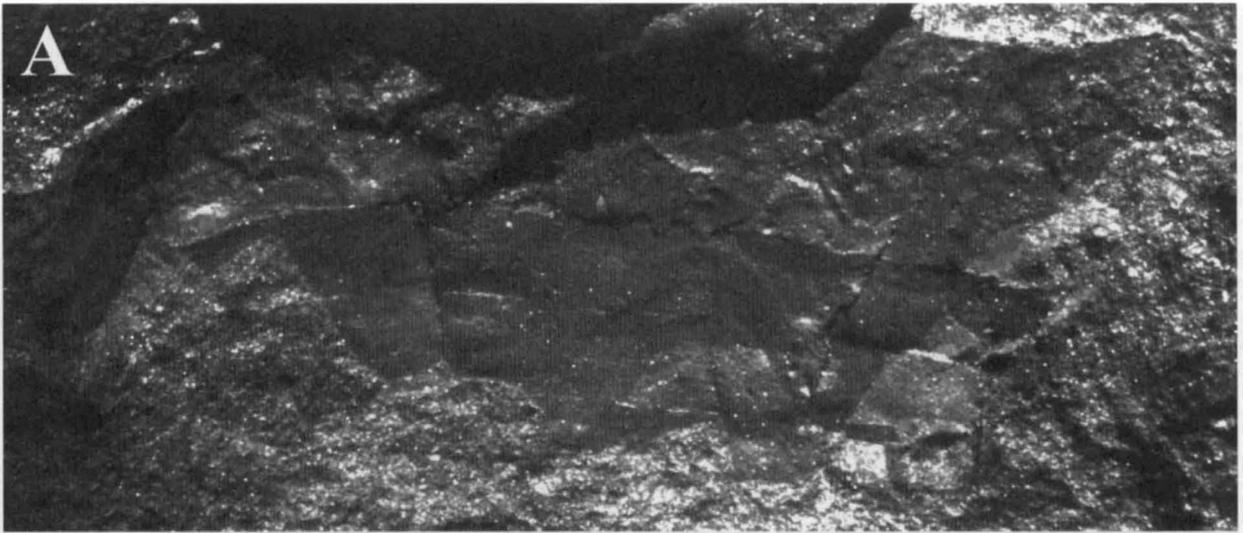
(Klug et al., 2004). The mandibles lie a short distance in front of the anterior edge of the gladius. In having a short hood (the outer lamina) and a long crest (the inner lamina), the reconstructed lower mandible of *T. hastiformis* is similar to that of modern *Octopus* but different from that in *Vampyrotheuthis infernalis* Chun (Klug et al., 2004: Fig. 1A, B, C, E).

The lower mandible of *L. schindelbergensis* n. gen. et sp. consists of black shiny “glassy” material. The mandible is characterized by the broad wings and distinct beak (= rostrum). The wings are formed by the inner and outer lamellae fused near the rostrum. The length ratio of the two laminae is unknown because the posterior portion of the mandible is damaged. The mandible has a micro-laminated ultrastructure similar to that of the chitinous mandibles of *Loligo* (Pl. 8, A–B) and of the contemporaneous ceratitid *Austrotrachyceras* from the same locality (Doguzhaeva et al., 2007a in press). In *L. schindelbergensis* the mandible must have been originally chitinous.

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Plates 1–7 – *Lunzoteuthis schindelbergensis* n. gen. et sp.; NHMW 2005z0005/0001; Lower Carnian, U. Triassic; Lower Austria

Plate 1. A–C. A. General view of the breviconic shell, strongly fractured by compression;  $\times 15$ . B. Closeup of A to show forwardly curved growth lines of the central field of the proostracum and three fracture lines along the septum/shell wall attachment; distances between the lines correspond to the camera length,  $\times 40$ . C. Closeup of A to show longitudinal ridges of the hyperbolar zone of the proostracum on the left side of the central field; two camerae of the phragmocone are visible,  $\times 20$ .

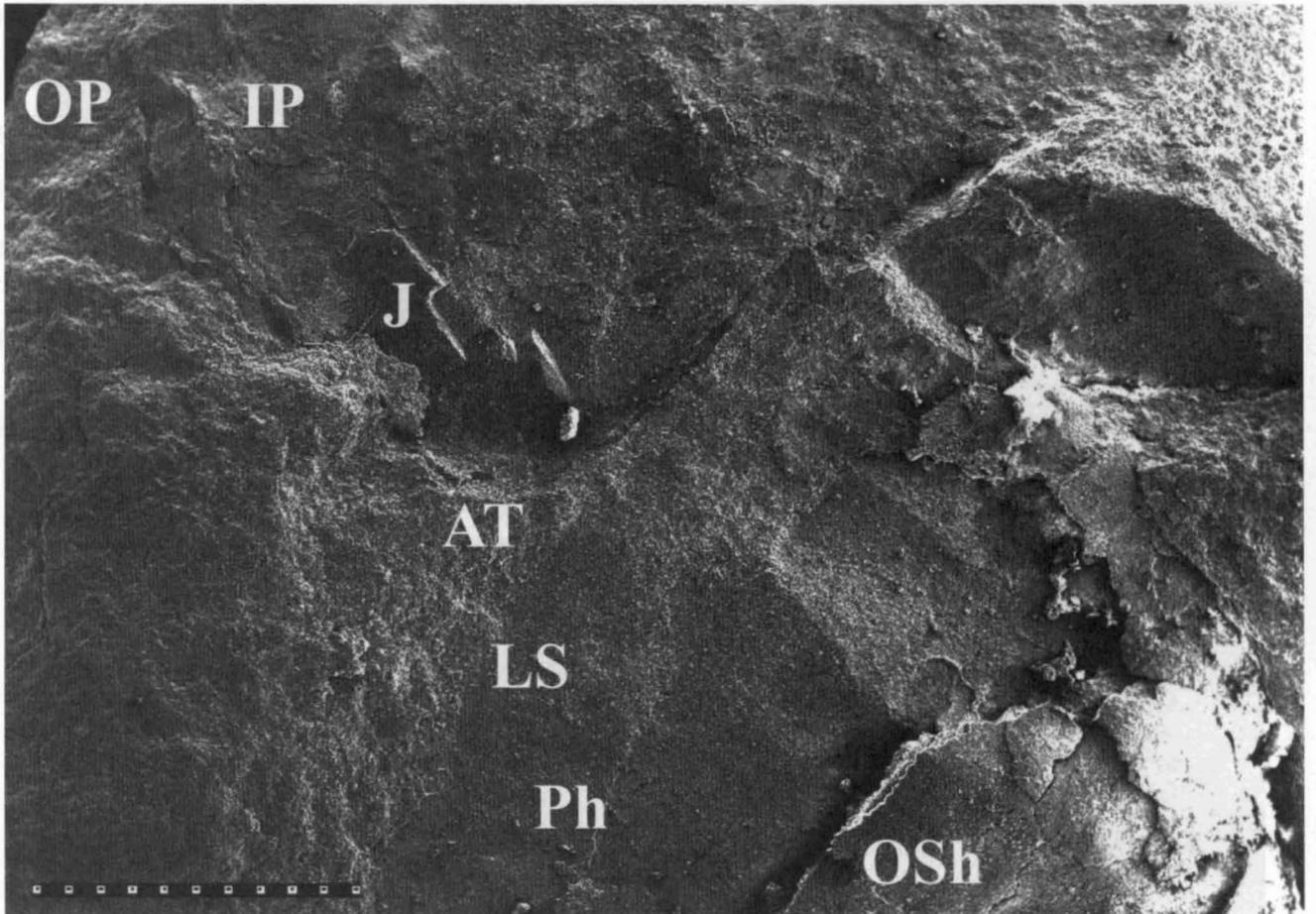


Plate 2. Lower mandible (anterior part) positioned in front of the anterior edge of the phragmocone: M – mandible; IP – inner plate; LS – last septum, OP – outer plate, OSh – outer shell surface, Ph – phragmocone; scale bar is 12 mm.

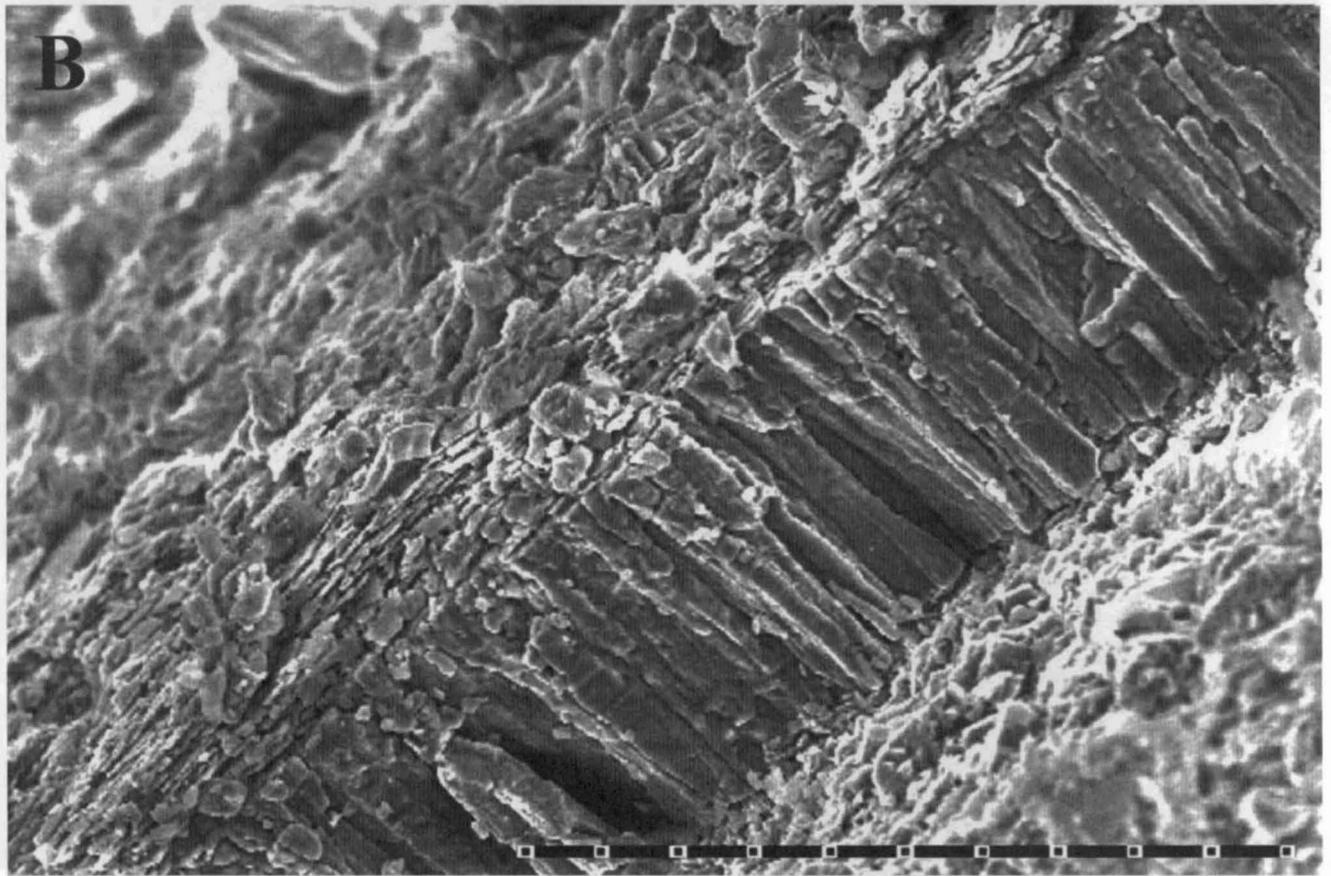
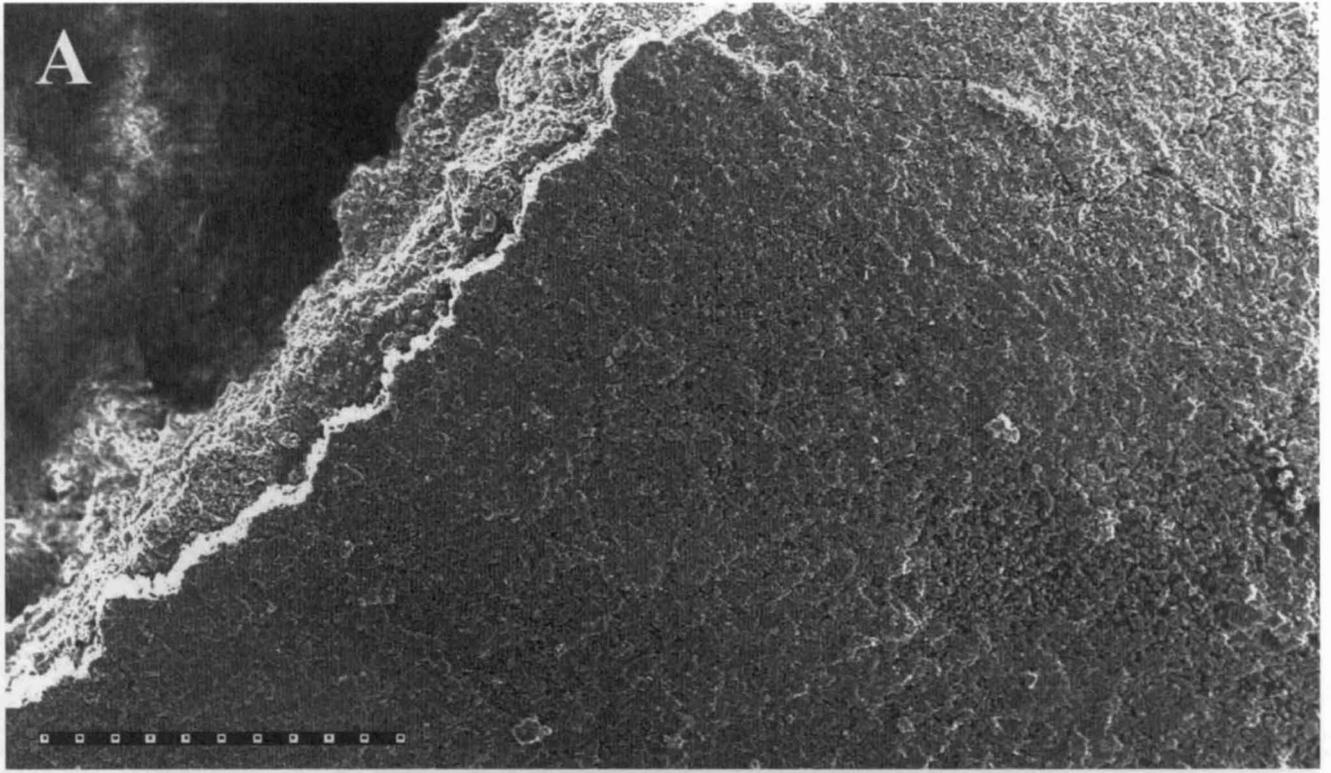


Plate 3. A–B. A. Porous outer surface of the proostracum (external surface, dorso-lateral side), scale bar is 150  $\mu\text{m}$ ; B. Longitudinal fracture of the proostracum showing the two layers, scale bar is 6  $\mu\text{m}$ .

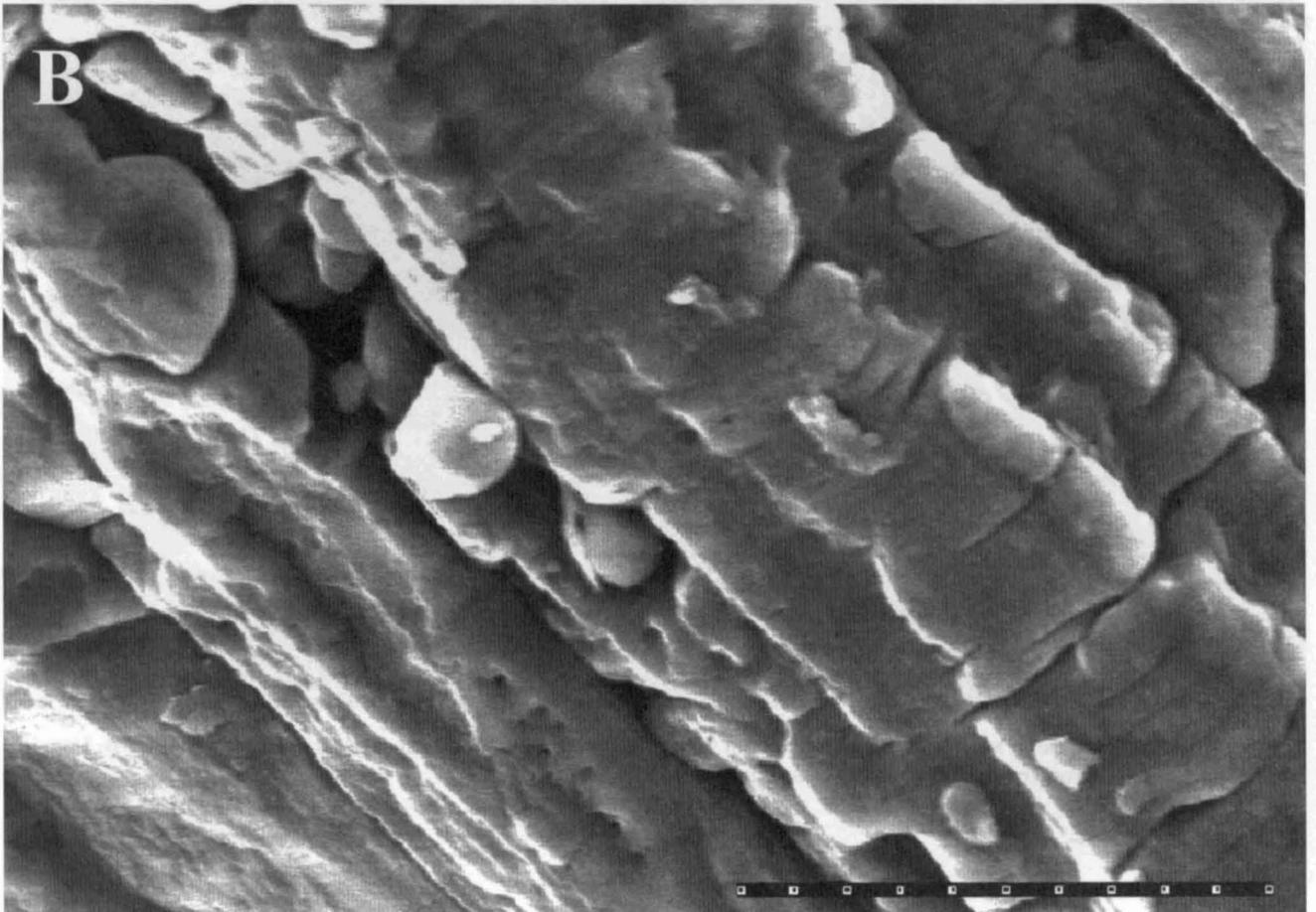
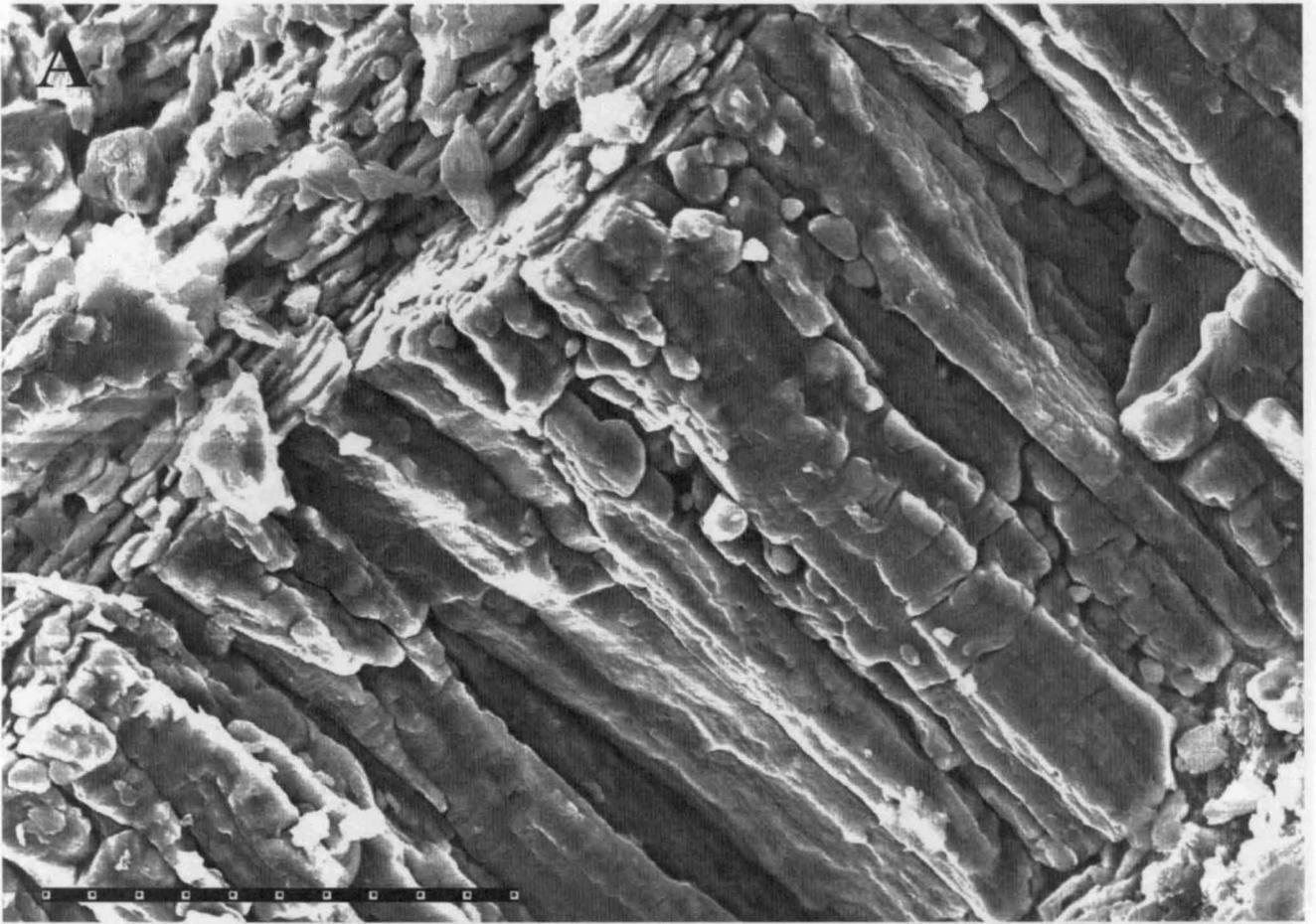


Plate 4. A–B. Closeup of 3B to show the micro-plate structure of the outer layer and the lamello-columnar structure of the inner layer of the proostracum, scale bar is 15  $\mu\text{m}$ . B. Closeup of the columnar units of the inner layer showing horizontal micro-lamellation, scale bar is 6  $\mu\text{m}$ .

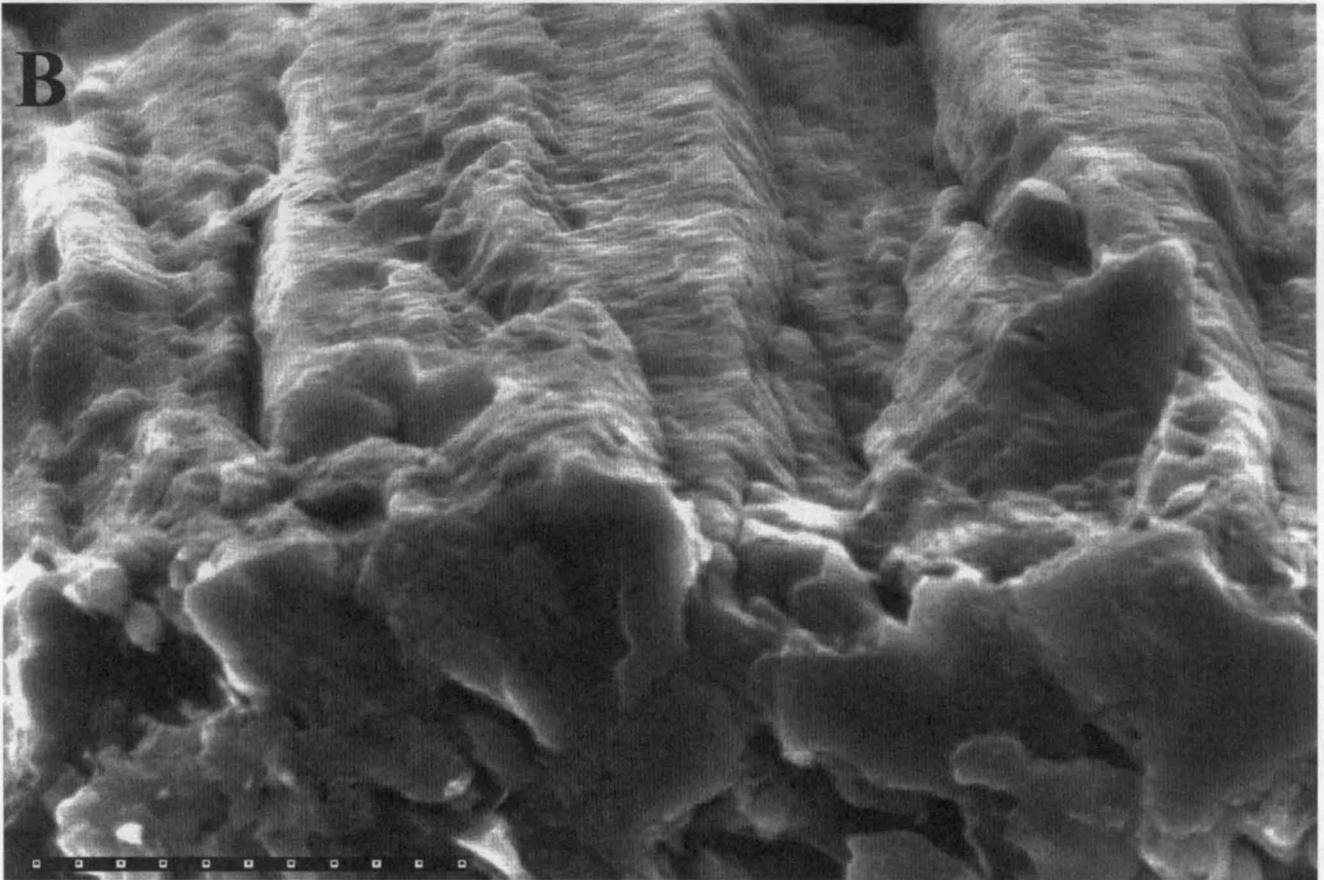
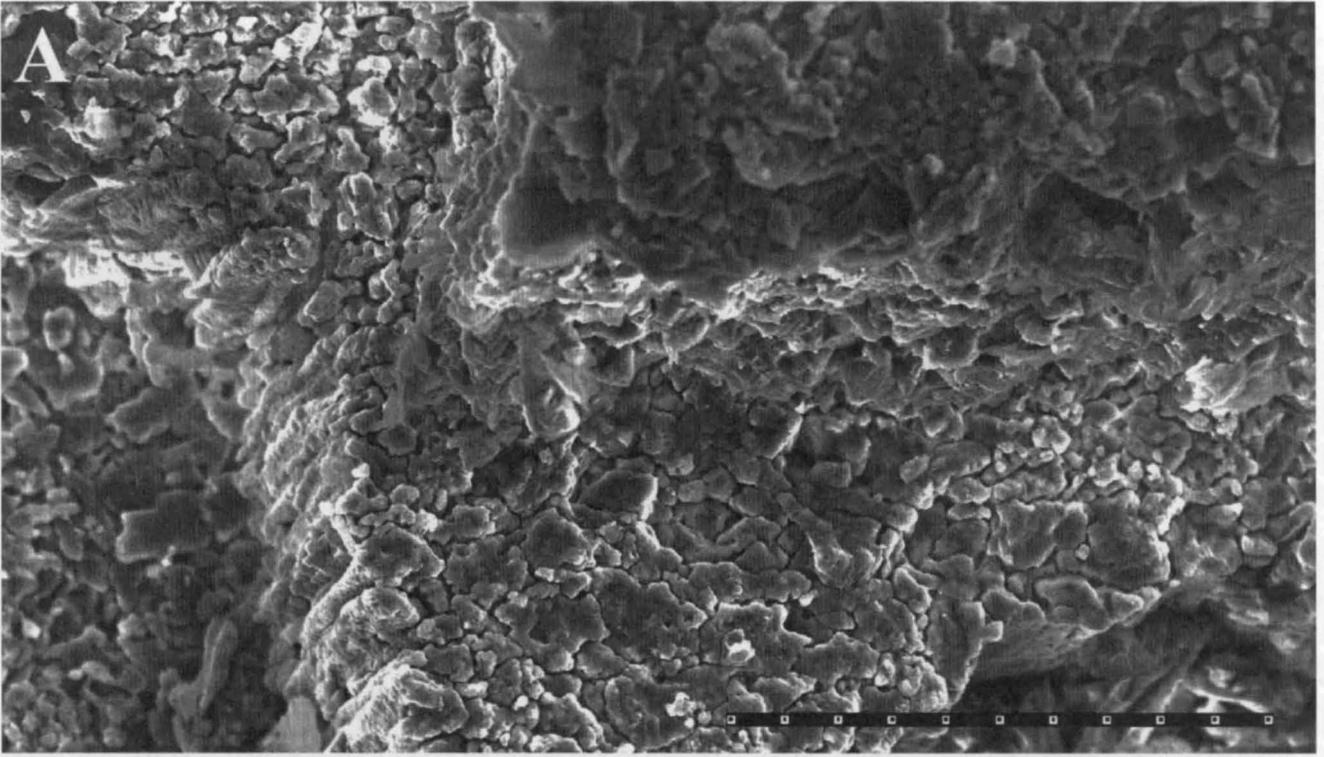


Plate 5. A–B. Surface view on the proostracum to show irregularly shaped end surfaces of the columnar units of the inner layer, scale bar is 30  $\mu\text{m}$ ; B. Micro-lamination of the columnar units of the inner layer of the proostracum, scale bar is 6  $\mu\text{m}$ .

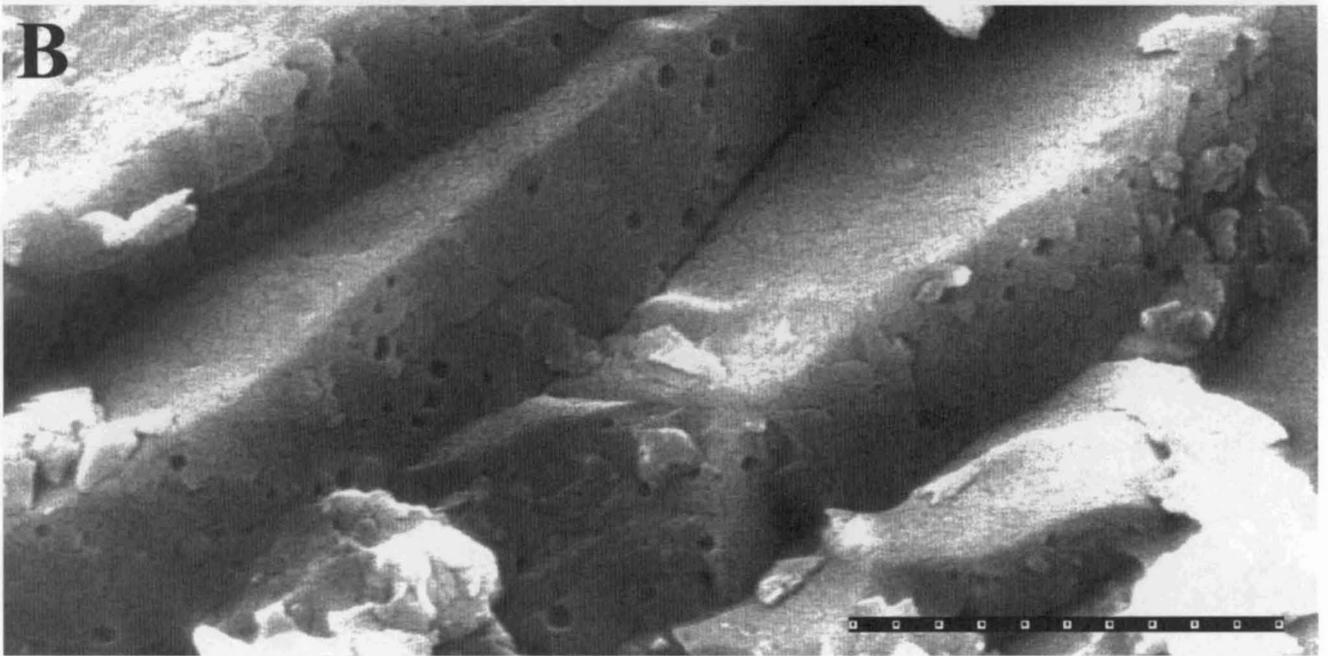
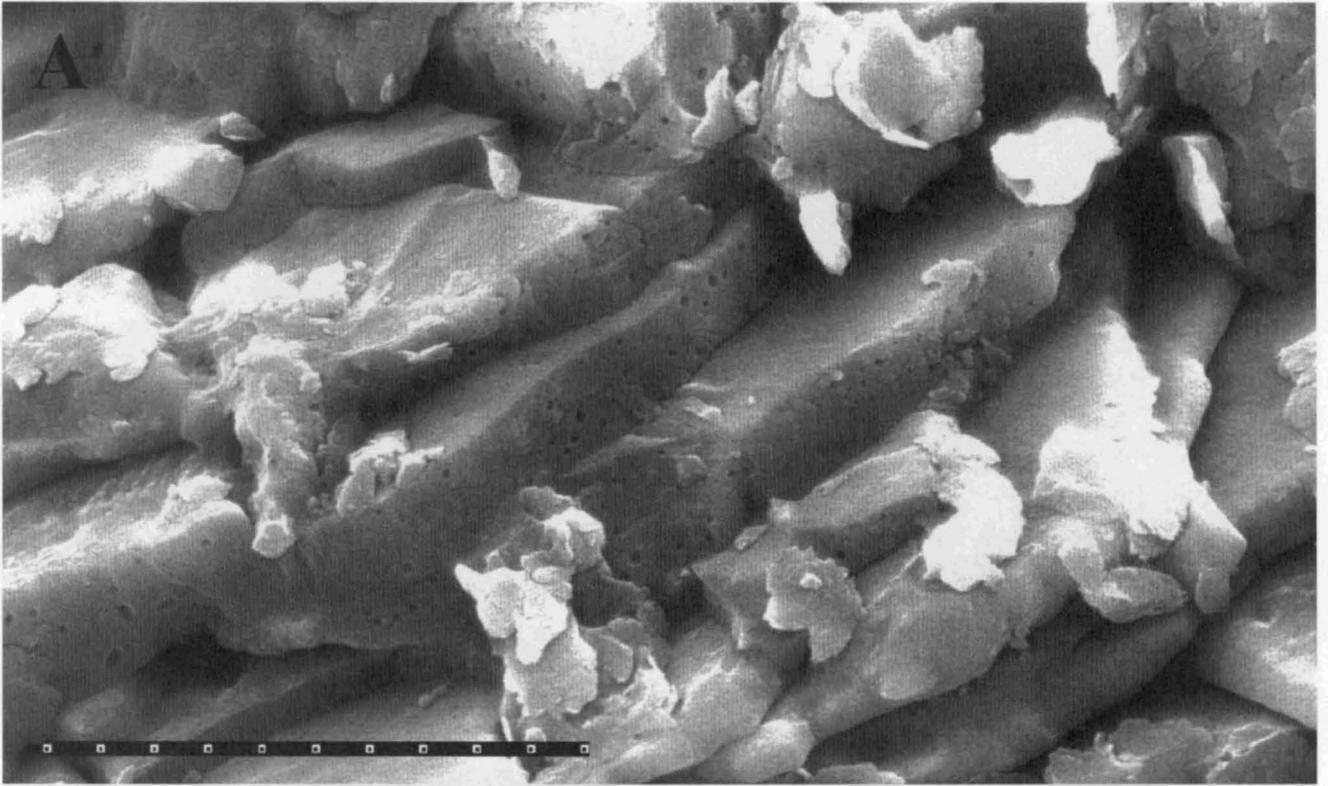


Plate 6. A-B. Vertical oblique fracture plane of the outer layer of the proostracum to show the micro-plates, scale bar is 3  $\mu\text{m}$ ; B. Closeup of A to show the wedge-like shape of the plates, scale bar is 1.2  $\mu\text{m}$ .

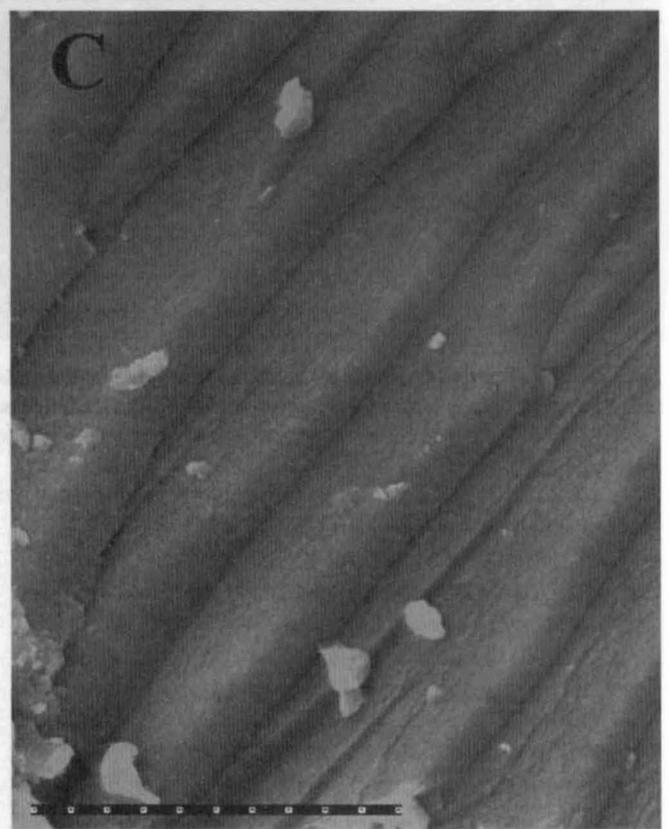
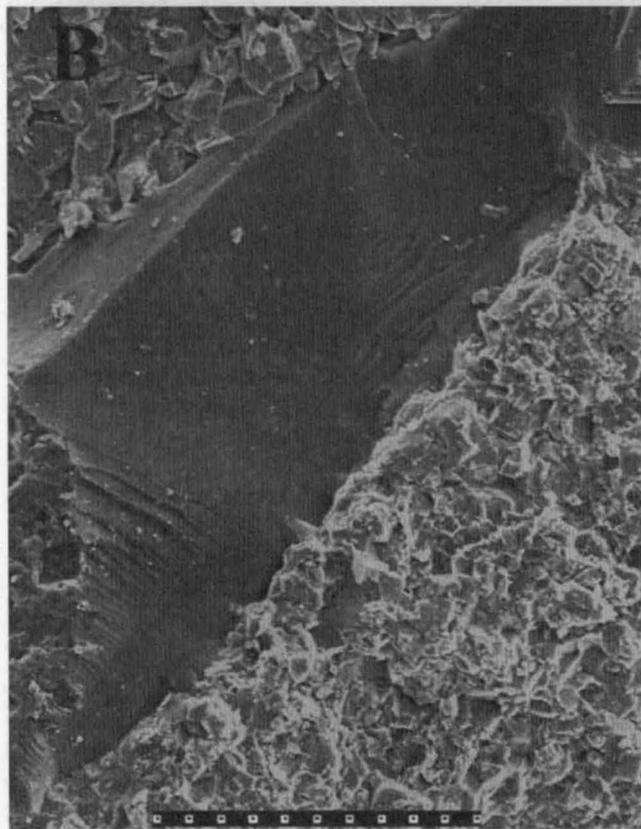
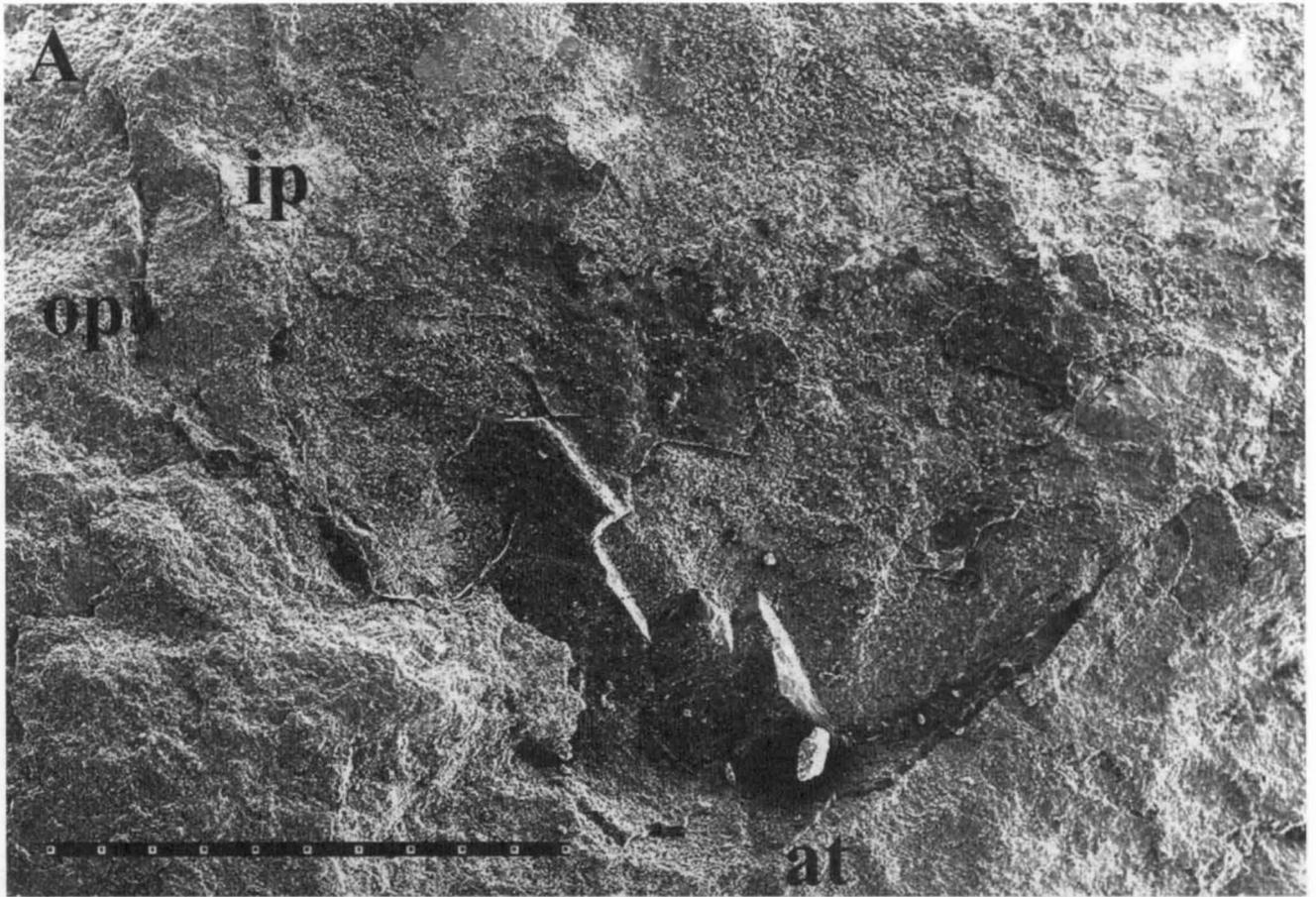


Plate 7. A–C. General view of the mandible located in front of the anterior edge of the shell, scale bar is 1.2 mm. B. Fracture of the beak (= rostrum) showing “glassy” material of the mandible, scale bar is 60 $\mu$ m. C. Step-like pattern of the fracture plane in the mandible, indicating a laminar structure, scale bar is 6  $\mu$ m.

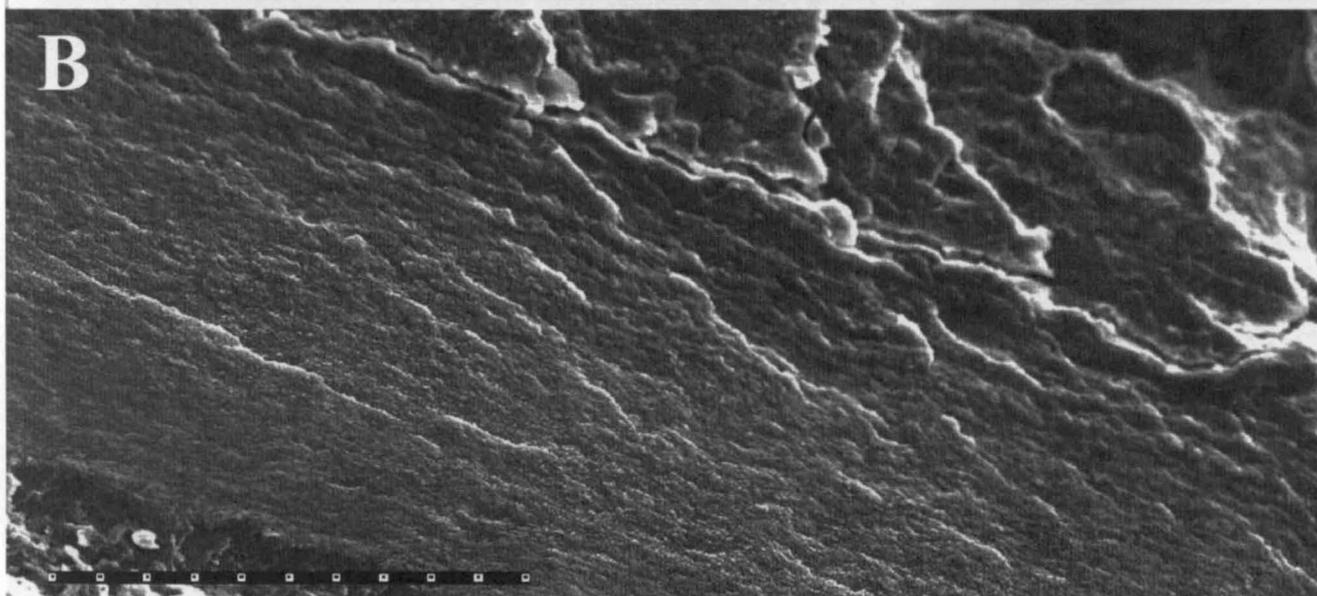
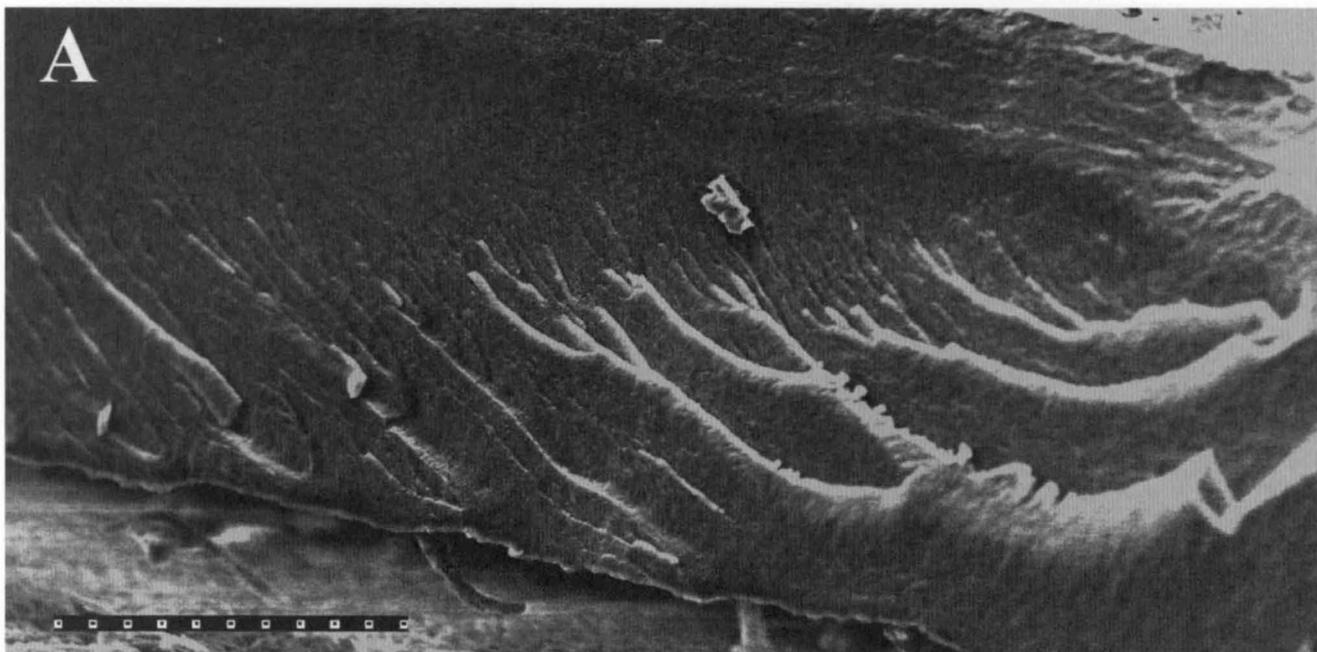


Plate 8. A-B. Vertical fracture plane of the mandible in living *Loligo* to show a step-like pattern formed by fractured chitinous material, scale bar is 60  $\mu\text{m}$ ; B - Micro-lamination of two layers forming the mandible in *Loligo*, scale bar is 60  $\mu\text{m}$ .

# ULTRASTRUCTURAL AND CHEMICAL COMPARISON BETWEEN GLADII IN LIVING COLEOIDS AND APTIAN COLEOIDS FROM CENTRAL RUSSIA

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**Abstract:** The paper reports ultrastructural and chemical studies on gladii of living and fossil coleoids in order to elucidate the original composition of the fossil gladii. Gladii of the Aptian *Nesisoteuthis simbirskensis* Doguzhaeva and of the living coleoids *Berryteuthis magister* Berry and *Loligo* sp. were studied with scanning electron microscopy (SEM) and energy dispersive spectrometry (Link). In all three taxa the gladius is laminated, being composed of alternating solid and less solid laminae. In living coleoids each lamina consists of fibrous sheaths. In the fossil *N. simbirskensis* the laminae are composed of globular aggregates of tiny granules. The globules are ca. 0.1–0.4 µm in diameter and arranged in chains.

Link analyses on the gladii of living coleoids show the elements: S, P, Si, Fe, Cl, Al, K and Ca. The first two elements, S and P, are dominant, whereas Ca has the lowest concentration. The fossil gladius and ink were analysed with the same instrument in the holotype of *N. simbirskensis* and in an imperfectly preserved, unnamed Aptian coleoid (Hecker & Hecker, 1955, p. 37, note 2). In the two specimens the gladius and ink both show Ca as the dominant element followed by P and S. This indicates that they are composed of calcium phosphate. In *N. simbirskensis* the split surfaces between the part and counterpart of the gladius are covered by a thin layer of barite.

The fossil ink in the two Aptian specimens, like the dried ink in the living *B. magister* and *Loligo* sp, has a globular ultrastructure. Originally organic, but post-mortally phosphatized, fish scales, which co-occur with *N. simbirskensis*, also have a globular ultrastructure but the globules are smaller than those in the gladius. Also the “horny” siphonal tube in ammonites found in the same beds has a globular ultrastructure, whereas the ammonite shell wall and septa show a well-preserved nacreous structure.

The role of bacteria in the post-mortem phosphatization which gives rise to the globular ultrastructure of the fossil gladius, ink and organic debris in *N. simbirskensis* is discussed. The presence of morphologically similar globules is shown in the soft tissues of Recent *Loligo* after a year of drying, and in the muscle tissue of Recent *Nautilus* after 20 years in alcohol. In *Loligo* the globular aggregates represent colonies of bacteria; in *Nautilus* they seem to be formed by coagulation of proteins in the muscle fibres.

The laminated gladius in *N. simbirskensis* is here interpreted as originally composed of an organic, probably chitinous, material that became phosphatized during fossilization. This agrees with the results previously obtained in Jurassic “fossil squids” (Doguzhaeva & Mutvei, 2003). It is still unclear whether the gladius in extinct squid-like coleoids lost its mineral composition in pre-Jurassic times or whether it was composed of organic material from the beginning. In belemnoids the mainly organic pro-ostacum seems to have developed as an innovative structure (Doguzhaeva & al., 2002, 2005a, b).

**Key words:** Early Cretaceous coleoid, shell morphology and ultrastructure, gladius, ink sac, evolutionary morphology, Russia

## INTRODUCTION

The available interpretations of the original composition of the gladii in “fossil squids” are contradictory. All gladii of “fossil squids” which have been analysed, found either in the Solnhofen Formation in Bavaria, in the Kimmeridge Clay in southern England, and in Upper Jurassic and Aptian beds in Central Russia, consist of calcium phosphate. Gladii were therefore considered to have been originally mineralized (Naef, 1922; Jeletzky, 1966; Hewitt, Lazer, Moorhouse, 1983; Donovan & Toll, 1988; Hewitt & Whyte, 1990; Engesser & Keupp, 2002). Hecker & Hecker (1955) assumed that the Upper Jurassic and Aptian gladii from Central Russia were mainly organic in life, as in the case of modern squids. Bandel & Leich (1986) were of the opinion that the origi-

nal mineral of the gladius in *Trachyteuthis* was aragonite. Hewitt and Jagt (1999) shared this interpretation of the primary aragonitic mineralization of the gladii in *Trachyteuthis* and *Loligosepia*, and accepted the idea of their post-mortem replacement by francolite. However, Hewitt & Wignall (1988, p. 153) thought that “the shell of *Trachyteuthis* was largely composed of a laminar fabric of chitin material, with a crystalline material concentrated in folded layers over the median dorsal surface”. They assumed that the chitin in this fossil might have been secondarily replaced by brushite. According to Doguzhaeva & Mutvei (2003), the gladii of the Jurassic squids *Loligosepia*, *Trachyteuthis* and *Teudopsis* were originally of organic, apparently chitinous composition.

The present paper describes scanning electron microscopic (SEM) and energy dispersive spectroscopic (Link)

studies on the gladii of the Aptian *Nesisoteuthis simbirskensis* Doguzhaeva from Central Russia and the living squids *Berryteuthis magister* Berry and *Loligo* sp. The object of the study is to elucidate the original composition of the gladius of *N. simbirskensis*.

## MATERIAL STUDIED AND METHODS

The material studied includes: (1) gladius of the holotype of *N. simbirskensis* Doguzhaeva (no. PIN 3871/391) from the Lower Aptian, vicinity of the village Shilovka, Uljanovsk region, Middle Volga, Central Russia (Doguzhaeva, 2005; Doguzhaeva & Mutvei, 2005); (2) gladius and ink from an unnamed "fossil squid" (Hecker & Hecker, 1955, p. 37, footnote 2), together with scales of pelagic fish and aptychi from the same beds, and (5) five gladii each of the living squids *Berryteuthis magister* Berry and *Loligo* sp.

The well preserved gladius of *N. simbirskensis* was extracted from a small, ca 50 mm long, dense, dark-grey, sideritic concretion that was split into two halves. The fractured surfaces of the concretion expose a longitudinally split gladius. The larger, thicker portion is 26 mm long and 6 mm wide and the thinner counterpart is 23 mm long and 4 mm in maximum width. The specimen has an ink sac distinguished by its flask-like shape and its content of black ink. The ink sac could be observed through the thin gladius that became transparent in alcohol. At the location of the ink sac the gladius is deformed and broken. The black ink fills the cracks.

Both split surfaces of the gladius, and a cross section through its anterior edge, were studied with the SEM without etching. The structure of pelagic fish scales, which consisted originally of organic substance, and which occur abundantly in the same sideritic concretion, was compared with that of the gladius. The fossil gladius, ink and fish scales were also analysed for their elemental composition with Link. The samples were coated with gold for ultrastructural examination, and either with carbon or nickel for Link analysis.

The study was carried out at the Palaeontological Institute of the Russian Academy of Sciences, Moscow, and at the Department of Palaeozoology at Swedish Museum of Natural History, Stockholm.

The specimens are stored at the Palaeontological Institute of the Russian Academy of Sciences, Moscow.

## OBSERVATIONS

### 1. The ultrastructure of the gladius, ink and organic debris in *N. simbirskensis*

#### 1. 1. Gladius (Pl. 1, A–B; 2, A–F)

The gladius consists of ca 1–2  $\mu\text{m}$  thick laminae, each composed of a set of thinner lamellae (Pl. 2, A–C). The lamellae consist of globules that are more or less regularly shaped and 0.05–0.2  $\mu\text{m}$  in diameter (Pl. 2, C–E). In some laminae a fibrous arrangement of granules is present (Pl. 2, F). Each globule is formed of an aggregate of still smaller particles (Pl. 2, E). In some laminae the globules are loosely packed (right side of Pl. 2, D), whereas in others they are compactly

packed (left side of Pl. 2, D). In the central keel region of the gladius the globules form aggregates that are larger and more compactly packed than those outside the keel. The laminae are traversed by vertical micro-pores with diameters of ca 0.05–0.2  $\mu\text{m}$ , being close to the size of the globules (Pl. 2, E). About 100 pores were counted on a square with 5  $\mu\text{m}$  sides in the central keel region. 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.

A longitudinal scar occurs on the right side of the median keel on the dorsal surface of the gladius (sc, Pl. 1, B). Along the scar the growth lines are irregular and form a V-shaped lobe indicating the the gladius was damaged during life and that the injury was repaired by the animal. Similar scars have been described in gladii of living sepiida (Bello & Paparella, 2003).

#### 1. 2. Fossil ink (Pl. 3, A–D)

Because of compaction of the gladius the ink sac is partly destroyed and the ink is exposed in cracks in the gladius (Pl. 3, A). In addition to the ink, the ink sac probably contains pieces of gladius and remnants of soft tissues (Pl. 3, B) that penetrated into the ink sac during the early post-mortem period. Under low magnification the ink looks like a glassy, structureless substance (Pl. 3, C). Under higher magnification aggregates of globules, ca 0.3  $\mu\text{m}$  in diameter, can be distinguished. They are embedded in a mass of small particles that do not form globules (Pl. 3, D). Each globule consists of smaller particles (Pl. 3, D). The globular ultrastructure is similar to that seen in the ink of living and extinct coleoids of different geological ages (see Doguzhaeva & al., 2004).

#### 1. 3. Soft tissue debris (Pl. 3, B, E–F)

Debris of soft tissues is observed within the ink sac (Pl. 3, B), in cracks of the fractured laminae of the gladius, and also around the gladius. In all these places the debris has an angular or globular shape and seems to be mixed with sediment from the concretion. Besides, the ink sac contains indeterminate micro-fragments of unknown origin in the shape of distinct bands of criss cross fibres (Pl. 3, F). The organic debris also contains numerous micro-organisms that are often organized in colonies (Pl. 3, E).

### 2. Aptian fish scales (Pl. 5, A) and aptychi

The Aptian fish scales are laminated, consisting of several (five or six) laminae of globular ultrastructure (Pl. 5, A). The globules are ca 0.03  $\mu\text{m}$  in diameter and, thus, about ten times smaller than the globules in the gladius and ink substance. Each globule is composed of smaller particles.

The Aptian aptychi studied also have a globular ultrastructure. The globules are ca. 0.2  $\mu\text{m}$ . in diameter and arranged in fibre-like chains.

### 3. Gladius and ink in the living squids *Berryteuthis magister* (Pl. 4, A–G) and *Loligo* sp. (Pl. 5, B, F)

The gladius is laminated (Pl. 4, G; 5, B) and flexible when wet, but fragile, longitudinally folded (Pl. 4, A), deformed (Pl. 4, B) or crushed into elongated fragments, when dried.

It seems to absorb and retain water between the laminae. This possibly explains why the gladius is flexible in wet condition and fragile in dried condition.

The dorsal surface of the gladius bears a mid-dorsal rib, known as the rib of rigidity (e.g. by Bizikov, 1996), that encloses a hollow, ventrally open, tunnel (Pl. 4, A, C). The dorsal surface of the rib bears growth lines whereas the rest of the dorsal surface is smooth (Pl. 4, A). The gladius is thickened along the crest of the rib and along a narrow, longitudinal thickened zone on each side of the rib (Pl. 4, A–C). The laminae are separated by empty interspaces in the central part of the thickened zones but they become tightly packed close to the dorsal and ventral surfaces of the gladius (Pl. 4, E). Under high magnification the lamination is not homogenous but consists of alternating compact and porous laminae (Pl. 5, F). The latter are perforated by numerous micropores, 0.3–0.6 µm in diameter. Each lamina has a fibrous ultrastructure, the diameter of the fibres ca 0.06 µm.

The dried ink has a globular ultrastructure. Each globule has a diameter of 0.2–0.5 µm and consists of tiny particles. As experimentally demonstrated, regular or less regular shape of globules depends on the mode of drying. If the ink is dried slowly within the opened ink sac the globules are regularly shaped. If the ink is placed between cover glasses and heated the globules do not form but the ink consists of flattened, irregularly shaped, structural units.

#### 4. Results of chemical analysis

##### 4.1. The gladius of the Aptian *Nesisoteuthis* and an unnamed coleoid (Pl. 6, A–B), fossil ink (Pl. B–D), aptychi and fish scales (Pl. 5A)

The dominant elements in the gladius of *Nesisoteuthis simbirskensis* and an Aptian unnamed coleoid (Hecker & Hecker, 1955) are Ca, P, S, Fe, followed by the minor elements, Si, Ti, Al, Zn, Md, K. In strongly pyritized spots the peak of S is almost as high as for Ca and the peak of Fe higher than that of P (Pl. 6, A). In other places the peaks of Ca and P are the highest (Pl. 6, B). In *N. simbirskensis* the split surfaces between the part and counterpart of the gladius are covered by a thin layers of barite.

The dominant elements in the fossil ink of *Nesisoteuthis simbirskensis* and the Aptian unnamed coleoid are Ca, P, S and Fe, and the minor elements Al, Mg, U.

Also in the Aptian aptychi and fish scales the dominant elements are Ca, P and S, and the minor elements Fe, Si, Mg.

The results clearly demonstrate that the fossil gladius, ink, aptychi and fish scales, co-occurring in Aptian beds, consist of calcium phosphate.

##### 4.2. The gladii in the living squid *Berryteuthis magister* (Pl. 6, C–D)

The dominant elements are S, P, Si, and the minor elements Cl, K, Ca, Fe. The elements show quantitative variations, although S always has the highest peak. In some places the peak of Si is higher than that of P (Pl. 6, C) but lower in others (Pl. 6, D).

#### 5. Discussion

##### 5.1. Ultrastructural and chemical comparisons with gladii previously studied

The ultrastructure of the gladius has previously been described in the Jurassic *Loligosepia*, *Trachyteuthis* and *Teudopsis* (Doguzhaeva & Mutvei, 2003). All these gladii are multi-laminated, each lamina being composed of tablet-like or chain-like aggregates of tiny globules with a diameter of 0.3–0.4 µm. The globular chains in the laminae represent fossilized fibres, which reveal the organic composition of the Jurassic gladii. The gladius of the Aptian *N. simbirskensis*, examined herein, shows a similar ultrastructure: it is laminated and each lamina is composed of globules that are arranged in indistinct fibres (Pl. 2, F).

In the living coleoids *Berryteuthis* and *Loligo* the gladii are laminated and consist of fibrous sheaths. It seems reasonable to assume that also the laminae in the fossil gladii originally consisted of organic fibres that have been transformed diagenetically into chains of globules.

According to previous elemental analysis (Doguzhaeva & Mikhailova, 2002) the mandibles in the Aptian heteromorph ammonite *Australiceras* are also composed of calcium phosphate like the Lower Aptian fossils studied herein, whereas the ammonite shells are unaltered aragonitic.

##### 5.2. Potential role of microorganisms in preservation of the Aptian gladii from Volga

The spectra of the gladius in *Nesisoteuthis* exhibit the barite on the split surfaces of the main part and counter-part. The marine microorganisms can precipitate this mineral. The recently obtained data on the chemistry of the marine water column demonstrate the presence of suspended marine barite. The particles of barite are a universal component of water in the Atlantic and Pacific oceans. Barite has been previously reported in benthic protozoans (see Church, 1986). It has been found in the siphuncle of the Carboniferous orthoconic cephalopods from the Buckhorn asphalts (unpublished data by Doguzhaeva & Mapes). These data indicate the potential role of the microorganisms participating in barite precipitation and in the exceptional preservation of the gladii examined.

##### 5.3. The role of Recent marine bacteria in decomposing chitin, and its bearing on the interpretation of mineral replacement of chitin in ancient environments

Million of tons of chitin are deposited in the exoskeletons of marine crustaceans every year. Although chitin is a water-insoluble and chemically resistant substance there are no large accumulations of chitin on the sea bottom. Marine bacteria play a dominant role in the decomposition of chitin. These bacteria were studied in the Black Sea where accumulations of chitin are produced by gammarids and other amphipods (Crustacea) by shedding their exoskeletons 40–50 times per year (Imsheneckiy, 1933; Kopp & Markianovich, 1950; Markianovich, 1959). The chitin-decomposing bacteria are widespread all over the Black Sea where they live in various environments at the depths from 100 m to 2000 m. They occur most abundantly in zones with a high content of hydrogen sulphide (Kopp & Markianovich, 1950). This led first to

the conclusion that the decomposition of chitin by bacteria mainly occurred in anaerobic conditions. Later it was shown that bacteria also decompose chitin in oxygen-rich zones (Markianovich, 1959). Long-term experiments with the chitin-decomposing bacteria from the Black Sea show that the chitin became soft in three months and total decomposition was usually achieved after 3–7 months. The experiments carried out in aerobic conditions showed that the appearance of ammonium hydrate marks the end of the total decomposition, resulting in the formation of mineral components. The rate of destruction of the chitin by different chitin-decomposing bacteria depends on environmental conditions, being higher in water that is rich in sulphuric acid. The chitin-decomposing bacteria in the Black Sea include several species, most having a stick-like shape of length ca. 0.2–1  $\mu\text{m}$ .

The recent findings suggest that in the Mesozoic also marine bacteria played a significant role in decomposition of chitin in skeletons. As shown above, the globular ultrastructure of the fossil gladius is hitherto known in three Jurassic and one Lower Cretaceous genera of coleoid cephalopods. Besides, the Aptian fish scales and aptychi have a globular ultrastructure. All the globules consist of tiny particles. In the gladius the globules are 0.3–0.5  $\mu\text{m}$  in diameter but in fish scales about ten times smaller. This shows that the size of the globules does not exceed the size of the modern chitin-decomposing bacteria that have a diameter of about 1  $\mu\text{m}$  or less. The bacteria seem to rework the chitinous material of the gladius and accumulate P. The possible step-by-step scenario of the replacement of chitin by calcium phosphate cannot so far be reconstructed. The size of the granules suggests that they are at least partly a product of bacterial metabolism. The chitin-decomposing bacteria could create a microenvironment favouring the precipitation of phosphates. The latter occurred in low oxygen condition, such as in the Lower Aptian of the Uljanovsk region. Here the Lower Aptian black claystones and shales contain abundant bituminous organic material, numerous druses of gypsum crystals, dispersed pyrite, marcasite, siderite and ankerite-siderite concretions. The lamination in the calcareous concretions and claystones, interlayered with beds of fine-grained glauconitic sandstones, laminated aleurolite limestones and marls, indicate a generally shallow water environment with variable depth regime. Such a lithology indicates an unstable, deoxygenated milieu favouring the precipitation of phosphorus (Doguzhaeva, 2002).

After drying for one year the gladius of living *Loligo* shows laminae that are disintegrated into small, plate-like elements (Pl. 5, C–D). Colonies of globular bacteria were found in the soft tissue surrounding the gladius (Pl. 5, E). The ink in living *Loligo* sp., *Berryteuthis magister* and other coleoids studied has also a globular ultrastructure even after being dried and heated for ca. 30 min. Fossil coleoid ink has a similar globular ultrastructure. In the latter case the aggregates of globules were apparently formed as a result of coagulation of melanin into small particles (the pigment melanin is the main component of ink in living coleoids) and thereafter transformed into bigger globules. In the compressed ink sac of the Aptian *N. simbirskensis* the fossil ink has in places a globular ultrastructure, in other places it is structureless, apparently because the particles were not

coagulated into globules. In Recent *Nautilus* after 20 years in alcohol the muscular mantle shows a globular ultrastructure. This is probably caused by a coagulation of proteins in the muscle fibres into globules.

Recent studies show that the exposed surfaces of the bacteria include reactive chemical compounds, e.g. phosphates and carboxylates, which are responsible for ionic interaction with solutes. Once an ion is added to such a chemical group, it becomes a nucleation site for further precipitation. The bacteria have the highest surface area-to-volume ratio that makes them highly interactive with the surrounding elements. This explains their great productivity in the precipitation of ions from the environment and development of fine-grained minerals (Fortin et al., 1997).

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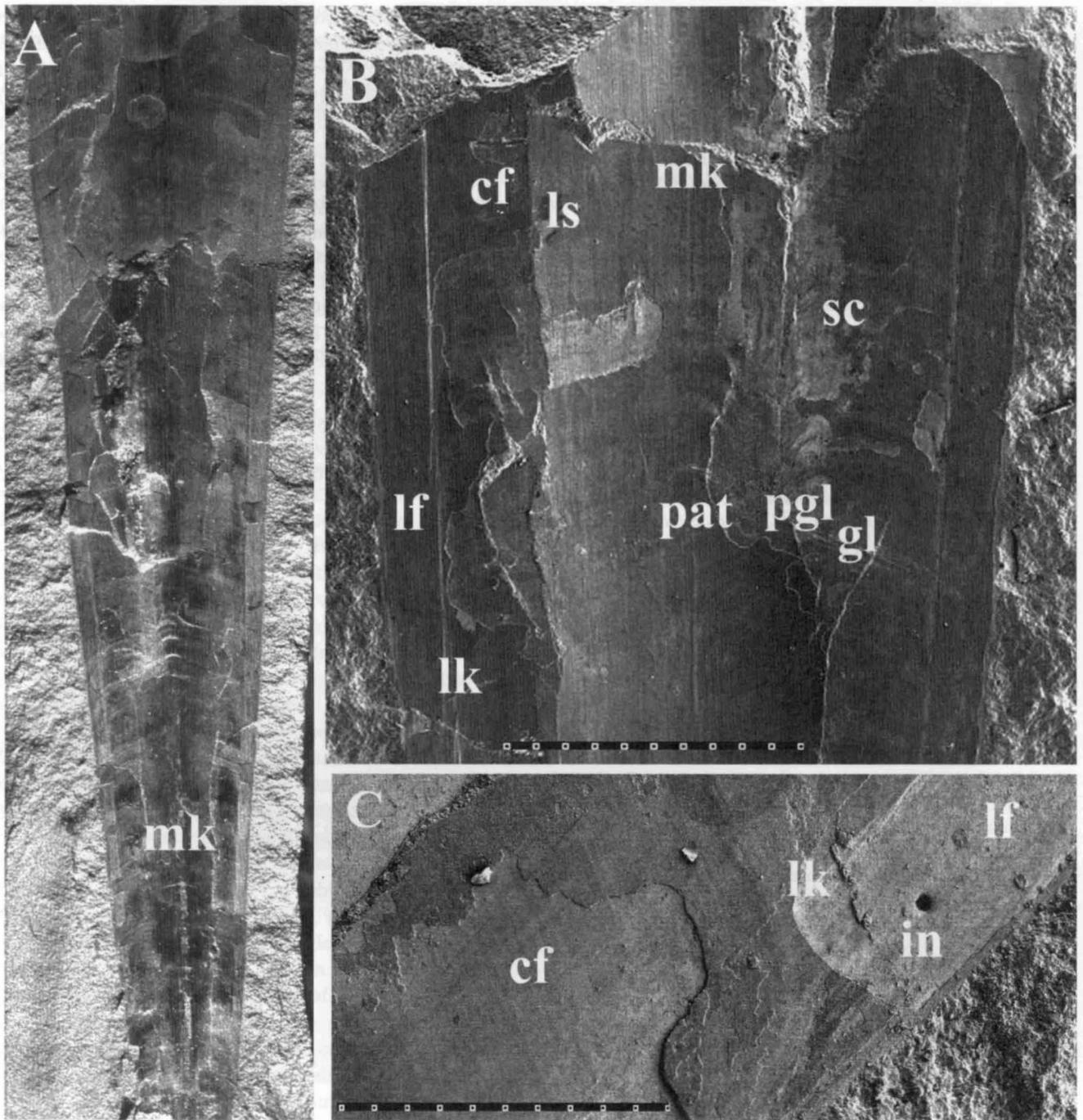


Plate 1. A–C. *Nesisoteuthis simbirskensis* ( no. PIN 3871/391). A. General view of the gladius exposed along the split surface;  $\times 2$ . B. Anterior portion of the counterpart of the gladius in Fig. 1A to show the central (cf) and lateral (lf) fields, the median (mk) and lateral (lk) keels, growth lines (gl), longitudinal striation (ls), crest of the median keel (pat), healed longitudinal scar (sc); scale bar is 1.5 mm.

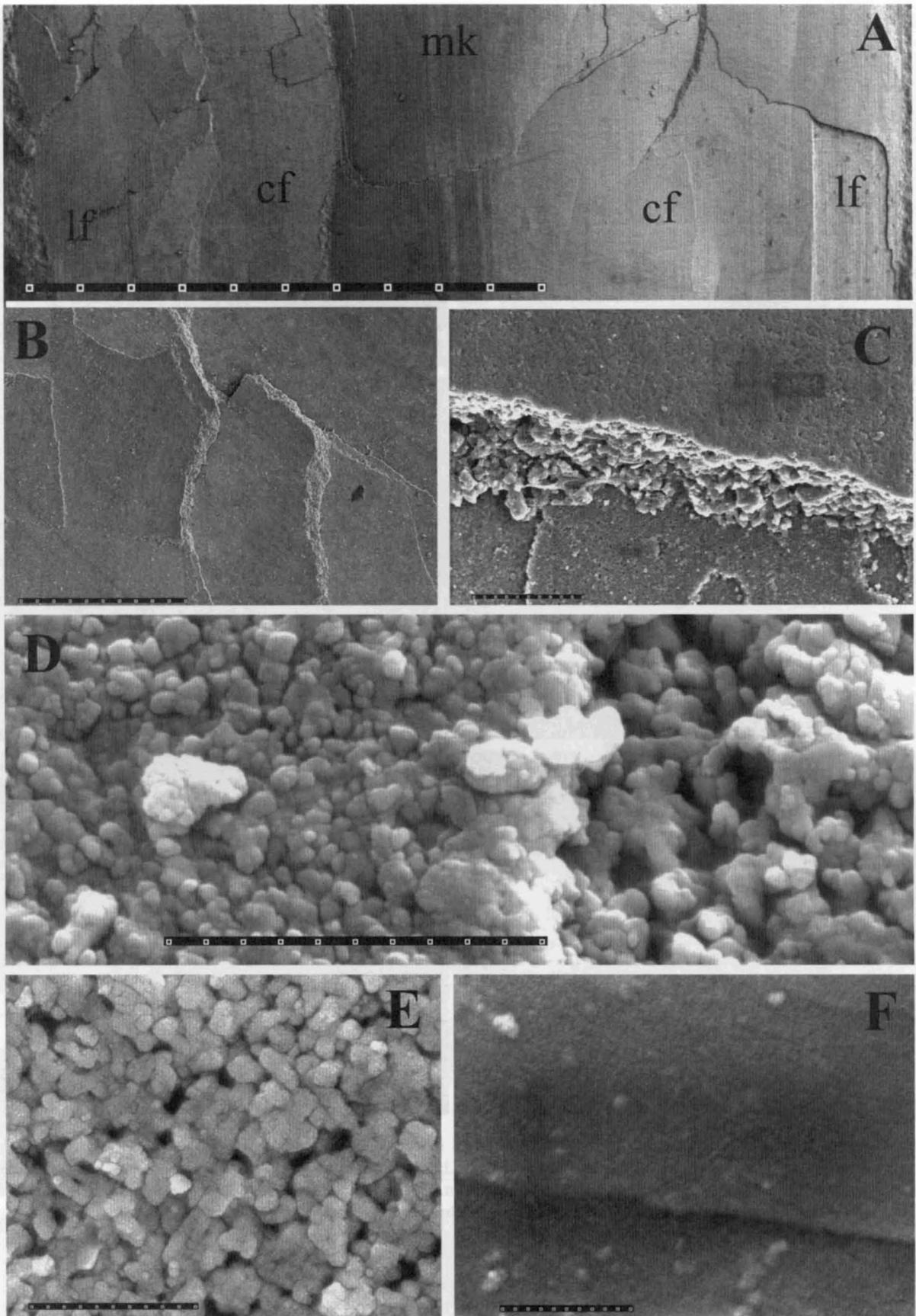


Plate 2. A–F. *Nesisoteuthis simbirskensis* (no. PIN 3871/391). A. Portion of the dorsal surface of the gladius in higher magnification; scale bar is 1 mm. B. Detail of Fig. 1 to show sublayers in the fractured gladius; scale bar is 3 mm. C. Close-up of 2B to show the globular structure in the fractured gladius; scale bar is 300  $\mu\text{m}$ . D. Close-up of 2C to show the globular ultrastructure of the laminae; the globules are compactly packed on the left hand side but loosely packed on the right hand side; scale bar is 3  $\mu\text{m}$ . E. Globular ultrastructure of the gladius; each globule consists of numerous tiny particles; note the micro-pores between the globules; scale bar is 1.2  $\mu\text{m}$ . F. Surfaces of two laminae of the gladius to show fibrous ultrastructure; each fibre consists of chains of small globules; scale bar is 0.6  $\mu\text{m}$ .

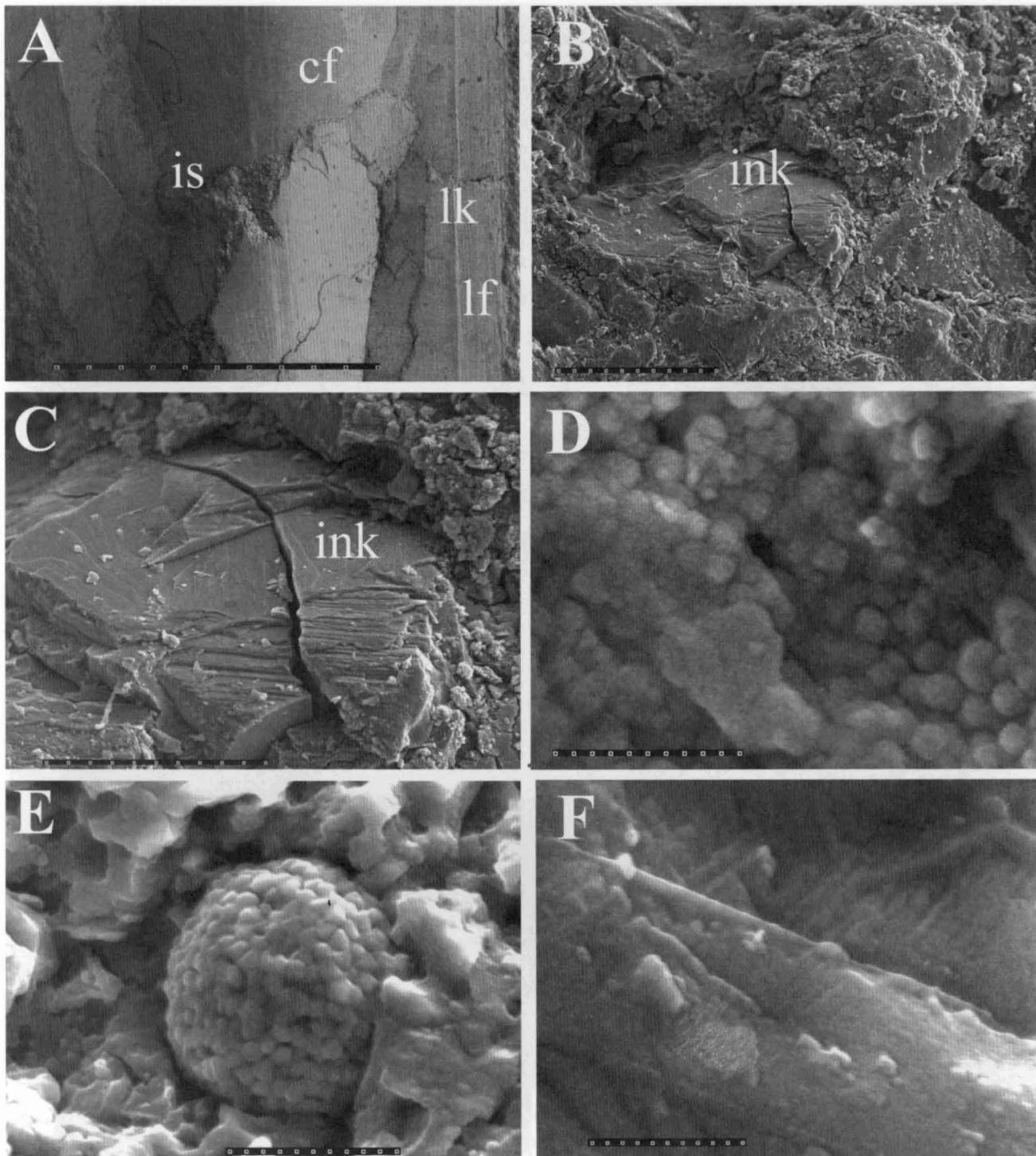


Plate 3. A–F. *Nesisoteuthis simbirskensis* (no. PIN 3871/391). A. Fractured gladius above the ink sac (is); scale bar is 3 mm. B. Organic debris within the ink sac; scale bar is 60  $\mu\text{m}$ . C. Fossil ink in low magnification; scale bar is 30  $\mu\text{m}$ . D. Globular structure of the fossil ink in higher magnification; scale bar is 0.6  $\mu\text{m}$ . E. Colony of micro-organisms in ink sac; scale bar is 3  $\mu\text{m}$ . F. Undetermined fragments of distinct bands with fibrous structure in ink sac; scale bar is 1.2  $\mu\text{m}$ .

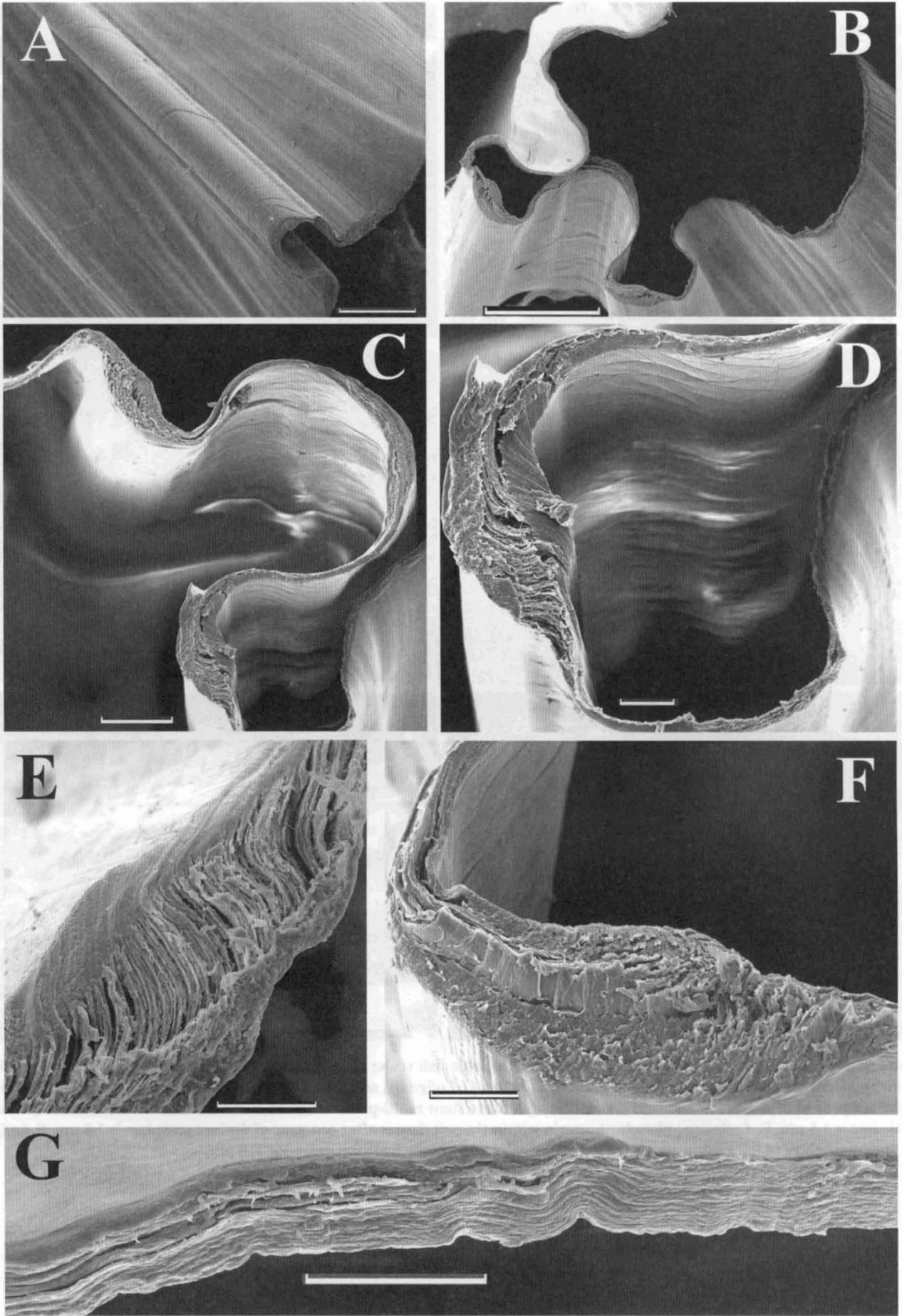
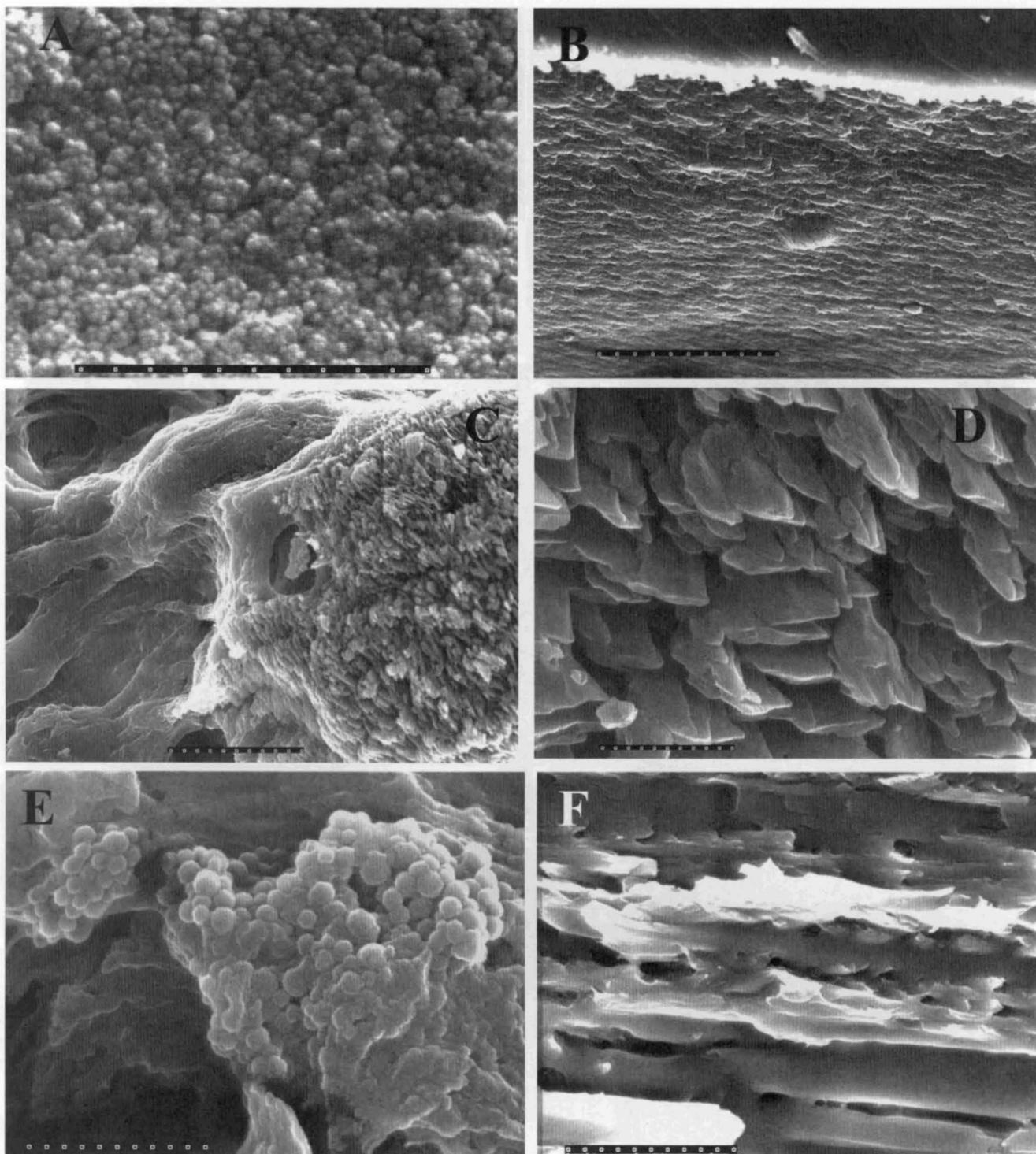


Plate 4. A–G. Gladius ultrastructure in the modern squid *Berryteuthis magister*. A. Surface view of the gladius; scale bar is 1 mm. B. Cross section of the gladius; scale bar is 1 mm. C. Thickened portions of the gladius along the crest of the mid dorsal rib and lateral ribs; scale bar is 300  $\mu\text{m}$ . D. Thickening of the gladius in higher magnification; scale bar is 100  $\mu\text{m}$ . E, F. Close ups of lateral thickenings in Fig. C; scale bar is 100  $\mu\text{m}$ . G. Cross section of the gladius; scale bar is 100  $\mu\text{m}$ .



Palte 5. A–F. Globular ultrastructure of Lower Aptian pelagic fish scale; scale bar is 0.6  $\mu\text{m}$ . B. *Loligo sp.*, fractured gladius showing micro-laminated ultrastructure; scale bar is 30  $\mu\text{m}$ . C. *Loligo sp.*, soft tissues on the left side and gladius on the right side after one year of drying; scale bar is 15  $\mu\text{m}$ . D. detail of 5C to show multi-plate structure of the chitinous laminae of the gladius; scale bar is 1.5  $\mu\text{m}$ . E. *Loligo sp.*, globular bacteria within the soft tissues after one year of drying; scale bar is 1.5  $\mu\text{m}$ . F. *Loligo sp.*, ultrastructure of the gladius showing alternating solid and porous laminae; scale bar is 6  $\mu\text{m}$ .

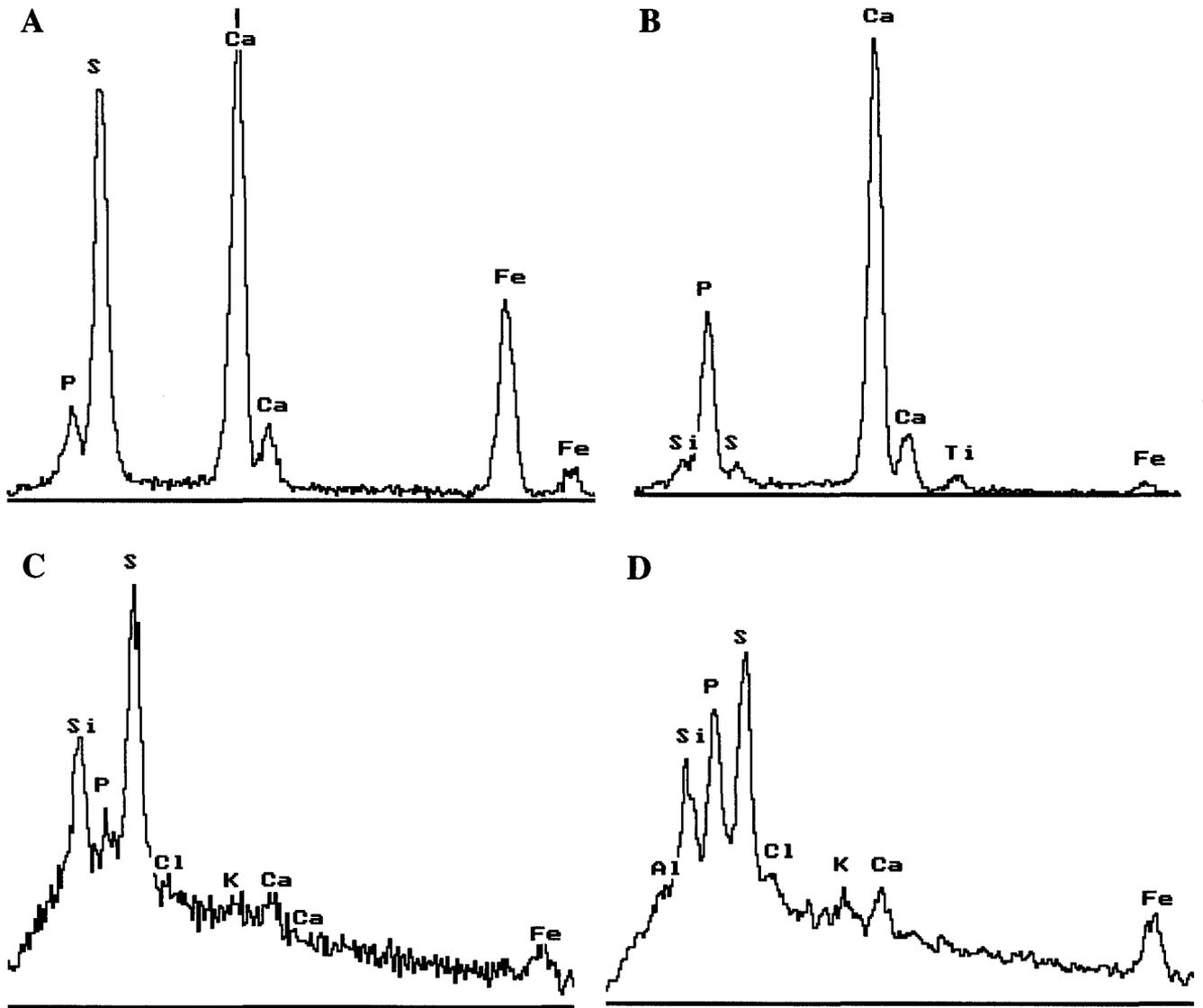
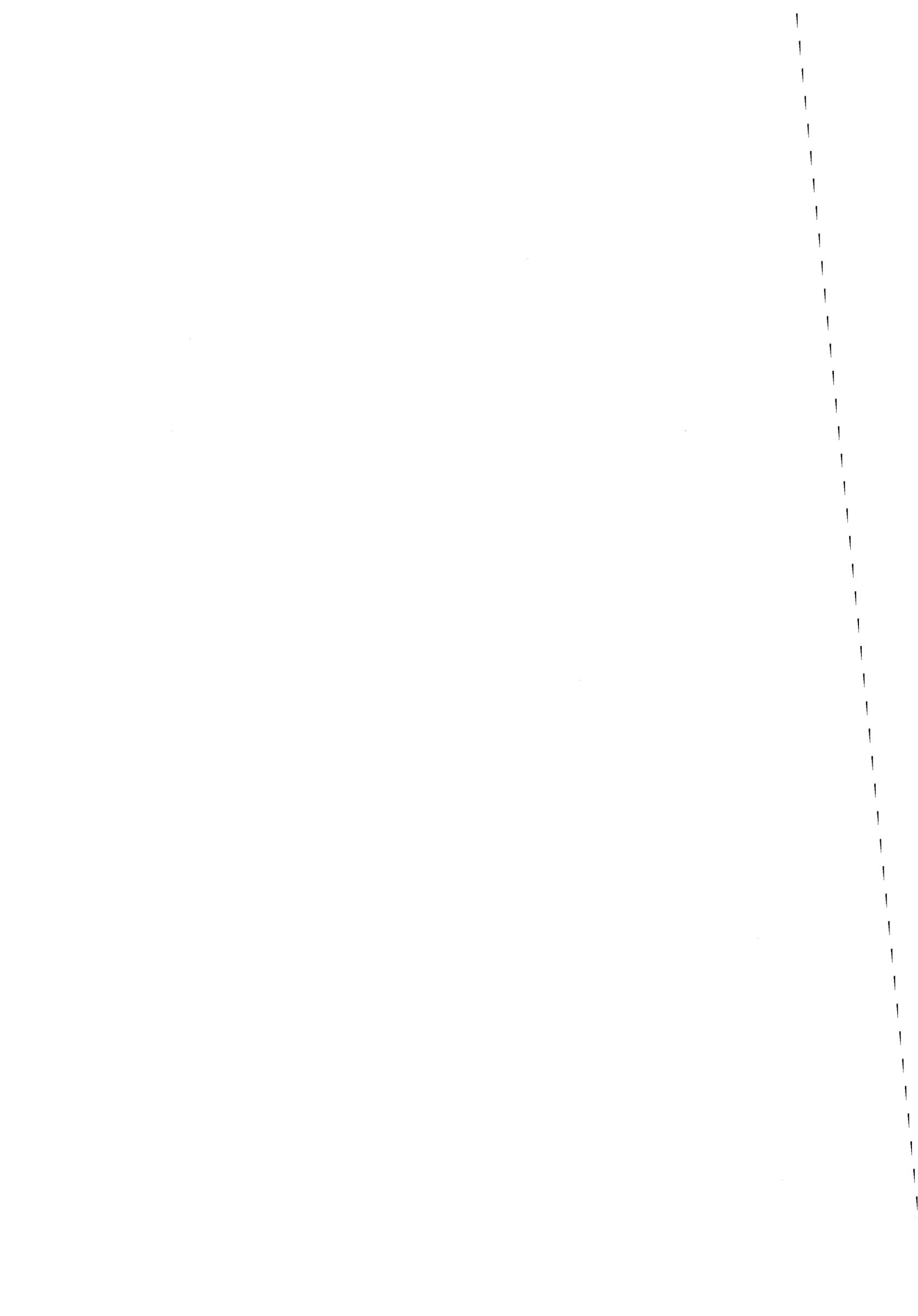


Plate 6. A-D. Elemental composition of an unnamed Lower Aptian gladius (Hecker & Hecker, 1955), Shilovka village, Middle Volga, Central Russia. C-D. Elemental composition of gladius in living squid *Berryteuthis magister*.



# ULTRASTRUCTURE OF *BELEMNOTHEUTIS* FROM THE OXFORD CLAY (CALLOVIAN), ENGLAND, AS A KEY FOR ELUCIDATING THE ORIGIN OF THE PRO-OSTRACUM

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**Abstract:** The postulate that the pro-ostracum of extinct coleoids is a dorsal extension of the phragmocone wall (conotheca), and is therefore a homologue of the shell wall of ectocochleate precursors (Naef, 1922; Jeletzky, 1966) is analysed in the light of the shell ultrastructure in *Belemnotheutis antiquus* Pearce.

Three shells of *B. antiquus* from the Oxford Clay (Middle Jurassic, Callovian) of Christian Malford, Wiltshire, England, were examined with the SEM. For comparison, additionally five gladii of the living squids *Loligo* and *Berryteuthis* were studied with the SEM. It is shown that in *B. antiquus* (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) the conotheca from the apical to the middle part consists on the dorso-lateral sides of the outer prismatic, nacreous and inner prismatic layers; towards the aperture it loses, first, the outer prismatic layer and then the nacreous layer; (3) the pro-ostracum differs remarkably from the conotheca – it exhibits irregular mineralization while the nacreous and prismatic layers of the conotheca and the prismatic rostrum are standard in their ultrastructure; the pro-ostracum is a micro-laminated, possibly mainly organic, structure, made up of vertical, horizontally micro-laminated, columns; (4) fine micro-lamination of the pro-ostracum is similar to the micro-lamination of the chitinous gladius in modern squids.

The ultrastructural data on *Belemnotheutis* favours the concept of the pro-ostracum as a separate, innovative part of the skeleton in coleoids (Doguzhaeva, 2002; Doguzhaeva et al., 2002a, 2003, 2005a, b; 2006 in press) rather than a dorsal projection of the conotheca.

**Key words:** Middle Jurassic coleoid, shell morphology and ultrastructure, pro-ostracum, evolutionary morphology, England

## INTRODUCTION

The pro-ostracum is a key skeletal element from which it was inferred that in belemnite-like cephalopods the body was not wholly surrounded by the body chamber of the shell but had “open” ventral and ventro-lateral sides covered by an elastic muscular wall, or mantle (Voltz, 1830; Mantell, 1848). The fossilized muscular mantle from the outside of the pro-ostracum was reported in the Middle Jurassic *Belemnotheutis* Pearce (Owen, 1844; Pearce, 1847) and more recently was studied in detail with the scanning electron microscope (Kear et al., 1995). Imprints of the mantle tunic on the side of the shell, marking the attachment of the mantle to the lateral margins (hyperbolar zones) of the pro-ostracum were described in the Middle Jurassic *Megateuthis* (Doguzhaeva et al., 2002a).

The pro-ostracum is a fragile structure, seldom preserved, that has been observed in the Late Triassic *Phragmoteuthis* (Bronn, 1859; Suess, 1865; Mojsisovics, 1882) and Jurassic *Cylindroteuthis* (Mantell, 1848), *Chondroteuthis* (Crick, 1896) and *Acanthoteuthis* (Crick, 1897;

Rogov & Bizikov, 2005). More often the pro-ostracum is preserved as imprints on the dorsal side of the phragmocone and/or on the internal surface of the rostrum (see Phillips, 1865–70; Naef, 1922). This was possible because of the relief on its external and internal surfaces. On the external (dorsal) surface the crescent-shaped growth increments along a median line form a central field bordered laterally in phragmoteuthids by the lateral lobes and in belemniteuthids, belemnitids and diploconitids by the hyperbolar zones, marked by thin, longitudinal, forwardly converging ribs and grooves. The internal (ventral) side of the pro-ostracum is even more rarely exposed. It is known in belemnitids in which it has a fine feather-like pattern formed by slightly curved or straight discrete lines diverging from both sides of the median line (Crick, 1896; Doguzhaeva et al., 2002a). In Early Jurassic belemnitids and probably in younger taxa as well, the pro-ostracum was present from early growth stages. This is shown by the impression of the pro-ostracum on the surface of the first camerae of the phragmocone (immediately after the protoconch) in the Early Jurassic *Passaloteuthis* (Doguzhaeva et al., 2003a). This indicates

that the pro-ostracum was already present in belemnite hatchlings.

Morphological investigations are here combined with analysis of shell ultrastructure to provide new data to help elucidate the evolutionary morphology of the pro-ostracum. This double method was applied for the first time to the Middle Jurassic belemnite *Megateuthis* (Doguzhaeva et al., 2002a) and then to the Early Jurassic *Passaloteuthis* (Doguzhaeva et al., 2003a). The ultrastructural observations revealed the significant difference between the pro-ostracum and the conotheca in these two genera (Belemnitida Zittel, 1895) and thereby threw doubt on the concept of the pro-ostracum as a dorsal continuation of the phragmocone wall. If that concept was correct one would expect the conotheca and pro-ostracum to be ultrastructurally similar.

In the present paper the double method, combining morphological and ultrastructural investigations, is applied to the study of the pro-ostracum in *Belemnotheutis* (Belemnitheutida Stolley). In this genus the presence of the pro-ostracum has been known since the genus was erected (Pearce, 1842). This "atypical belemnite" with a short rostrum forming a thin sheath-like covering of a breviconic phragmocone has been a focus of many investigations (Huxley, 1864; Naef, 1922; Makowski, 1952; Jeletzky, 1966; Bandel & Kulicky, 1988; Donovan & Crane, 1992; Funchs et al., 2004; Doguzhaeva et al., 2005a). Makowski (1952: Fig. 8) illustrated the pro-ostracum in *B. polonica* Makowski as a comparatively narrow, long tongue-like structure covering about one half of the circumference of the phragmocone.

#### MATERIAL STUDIED, STATE OF PRESERVATION AND METHODS

Three specimens of *B. antiquus* from the Oxford Clay (Jurassic; Callovian) of Christian Malford, Wiltshire, England were studied. They were collected in the nineteenth century and purchased by the British Museum (Natural History) (two specimens) and the Swedish Museums of Natural History (one specimen). The specimens are slabs of dark grey clay each with a flattened shell, coated with shellac in an attempt to preserve the shell.

All three shells have been strongly compressed approximately in a dorso-ventral direction so that their dorsal and ventral sides are almost in contact (Pl. 1). The shells are ca. 80 mm, 60 mm and 50 mm in length. They expose dorso-lateral and lateral sides. In the apical part of the shell the rostrum is comparatively thicker than at later ontogenetic stages and solid, and therefore the shell is less deformed there than anteriorly where the shell wall is fractured into a mosaic. The fragments retain their original positions. Horizontal fractures run along the mural parts of the septa.

In two specimens the shellac was removed, firstly by solution in acetone and then by cautious scraping. In places the sheath was removed together with the shellac because they were strongly bound together. Due to this removal, mainly near the aperture where the sheath is thin, the pro-ostracum became partly exposed. The lateral surface of the pro-ostracum is exposed in the anterior parts of two specimens. It is characterised by fine longitudinal striation at some distance from the median line. In places these hyperbolar zones have

a thin coating of black material. In *B. antiquus* the position of the hyperbolar zones corresponds to that in *B. polonica* (Makowski, 1952: Fig. 8) so that the proportion of the central field to the hyperbolar zones in these two species is similar. The curved growth lines of the central field between two hyperbolar zones were not observed in the material examined. During the "cleaning" of the shell the pro-ostracum must have been partly removed together with the shellac and the rostrum.

The samples of the shell wall selected for scanning electron microscope (SEM) examination were taken from the dorsal and dorso-lateral sides including places where the hyperbolar zones were exposed. To observe the ontogeny of the shell ultrastructure small pieces of the shell were taken at different distances from the apex. The samples were not etched. Fractured surfaces of the fragments of shell wall were examined with the SEM.

The gladii of the modern squids *Loligo* and *Beryteuthis* were dried before they lost water and became brittle and then studied with the SEM. Fractured surfaces of the gladii were investigated.

The samples were studied with a scanning electron microscope Hitachi 4300 at the Swedish Museum of Natural History, Stockholm, Sweden.

#### OBSERVATIONS: SHELL ULTRASTRUCTURE IN *BELEMNOTHEUTIS*

##### Rostrum (Pl. 1; 2, A; 3, A; 4, C)

The apical portion of the rostrum consists 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. The two portions of the rostrum differ in colour – the external one is shiny yellowish and the internal is chalky white. Towards the aperture the rostrum loses its inner layer and the outer layer becomes spherulitic-prismatic in structure. The crystalline units form sectors in which they radiate towards the shell surface and become loosely packed. Small interspaces between some of the crystalline units indicate higher organic content. The outer surface of the rostrum is covered by a thin, possibly originally organic, layer.

##### Conotheca (Pl. 2, E; 3, C; 4, A, C)

The apical part of the conotheca (up to approximately 50 mm from the apex) 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 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; 2, A–F; 3, A–E; 4, A–F)

In higher magnification a criss-cross pattern of the pro-ostracum is observed below the rostrum (Pl. 2A). 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  $\mu\text{m}$ . The presence of these canals indicates that the pro-ostracum consisted mainly of organic matter that was only partially calcified. The striae of the hyperbolar zones of the pro-ostracum have a somewhat compact, plate like structure, and the interspaces between them have a porous net- or lace-like structure (Pl. 2, C–D). Immediately beneath the pro-ostracal surface there follows a thin layer, ca 15  $\mu\text{m}$  thick, that is clearly visible on vertical fracture surfaces of all three shells. Because it is rich in organic matter this layer shows a great difference in mode of preservation from the calcified, uniformly well preserved prismatic and nacreous layers of the same shell. This layer of the pro-ostracum is in places composed of columnar units about 5  $\mu\text{m}$  in diameter (Pl. 4, D). These columns seem to be composed of predominantly organic, very thin laminae (Pl. 4, E–F), ca 0.5  $\mu\text{m}$  thick. In surface view (Pl. 2, F) the distal end of each column forms a polygonal field; its periphery composed of numerous, irregularly shaped, radially arranged plates in contact with each other; its central portion consists of several smaller, angular, 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 (Pl. 4, D–E). Some of these elements seem to be plate-like and show series of deep, horizontal, narrow incisions (Pl. 3, C–E; 4, A–B). Thus, the pro-ostracum has a unique structure that has no resemblance either to the adjacent, outer prismatic layer of the conotheca, or to the prismatic layers of the rostrum.

#### DISCUSSION: THE EVOLUTIONARY MORPHOLOGY OF THE PRO-OSTRACUM

The evolutionary morphology of the skeleton in coleoid cephalopods, including the pro-ostracum, is at present inadequately known. For a long time the evolutionary morphology of the skeleton in coleoids was based mainly on the shell morphology in Jurassic-Cretaceous, and a smaller number of Triassic representatives. However, a coleoid archetype was evidently developing in the Carboniferous when the coleoids (although relatively few of this age are known) displayed the high morphological diversity and plasticity (Doguzhaeva, 2002a) that is a typical feature of the early evolutionary stages of any group of animals or plants (Mamkaev, 1968). Therefore elucidating the evolutionary transformation of the skeleton on the basis of Mesozoic members only can hardly be effective any longer.

The Early Carboniferous coleoid *Hematites* Flower & Gordon yielded important information for the question under consideration. This form has a short body chamber (less than two camerae in length) in combination with the absence of a pro-ostracum (Doguzhaeva et al., 2002b: Pl. 1, Figs. 1–3). According to the classic concept (Naef, 1922; Jeletzky, 1966) a gradual elimination of the ventral and ventro-lateral sides of the body chamber resulted in the formation of a pro-ostracum on the dorsal side. In other words, the pro-ostracum is the dorsal part of the body chamber remaining after the reduction of the long body chamber

in the supposed bactritoid ancestors. Hence a morphological combination such as a short body chamber and absence of the pro-ostracum, according to this concept, would be impossible. On the other hand, a long body chamber is combined with an ink sac and a short pro-ostracum in the Late Carboniferous coleoid *Donovaniconus oklahomensis* Doguzhaeva, Mapes & Mutvei (2002d, 2003b: Figs. 1, 2, 4). This observation also conflicts with the classic concept, because coleoids were believed to have no body chamber. Moreover, the Late Carboniferous coleoids preserved with a phragmocone and an ink sac seemed to be diverse in a respect of the pro-ostracum/terminal chamber development (Doguzhaeva et al., 2002c; 2004: Figs. 1A, B; Mapes et al., in prep.). These data on Palaeozoic phragmocone-bearing coleoids require, for their explanation, re-evaluation of the classic concept of the formation of the main characters of the skeleton in coleoids (Doguzhaeva, 2002a).

The ultrastructural approach has also revealed new data that conflict with the classic concept. For the classic concept to be true, (1) the pro-ostracum should have the same or comparable ultrastructure to that of the conotheca, and (2) in the section of the shell there should be no layers between the rostrum and the conotheca. To be a homologue of the shell wall in coleoid ancestors (bactritoids), the pro-ostracum in belemnite-like coleoids and the shell wall in bactritoids should have a similar or a comparable ultrastructure. In bactritoids the shell wall consists of a thin outer prismatic and a thick nacreous layer. The inner prismatic layer was absent or secreted only at late ontogenetic stages (Doguzhaeva, 2002b: Pl. 3, Fig. 5). It is now clear that the structure of the conotheca in belemnite-like coleoids is remarkably variable. It is practically impossible to identify the shell layers without tracing them forwards from the protoconch stage. This opinion is close to the views of Grandjean (1910), Christensen (1925) and Müller-Stoll (1936) who thought that the conotheca differs essentially from the shell wall of ectocochlians. However, the contrary idea on the conotheca or phragmocone wall retaining the structure of the ectocochleate shell wall has been dominant (Voltz, 1830; d'Orbigny, 1842; Flower, 1945; Flower & Gordon, 1959; Mutvei, 1964; Barskov, 1973; Dauphin, 1985; Bandel, 1989; Bandel et al., 1984; Bandel & Kulicky, 1988). Nevertheless, SEM study of well preserved shells of the Valanginian *Conobelus* (Duvallidae) revealed that in the first 20 or so camerae the conotheca proper is missing, and the wall of the phragmocone consists of the long mural parts of the septa and/or a thin prismatic sheath-like continuation of the primordial rostrum (Doguzhaeva et al., 1996). This continuation of the primordial rostrum in *Conobelus* seems to correspond to the outer prismatic layer of the conotheca of Christensen (1925) and Müller-Stoll (1936). Christensen (1925) observed that in belemnites the outer layer of the two calcified layers forming the conotheca is a continuation of the prismatic wall of the protoconch. Müller-Stoll (1936) described presumably aragonitic outer and inner layers in the conotheca, with a thin, apparently mainly conchiolin layer between the first two. Mutvei (1964) emphasized that the outer calcified layer in the conotheca is formed by alternation of thin aragonitic lamellae and conchiolin membranes. He assumed that this layer was correlated with the nacreous layer of the shell wall in Recent *Nautilus*. Barskov (1973) observed that in the Late

Jurassic *Pachyteuthis* and the Lower Cretaceous *Conobelus* and *Neohibolites* the inner prismatic layer of the conotheca corresponds to the long part of the first septum that runs along the whole phragmocone. Similarly in juvenile *Hibolites* the inner layer of the conotheca is formed by a continuation of the mural part of the first septum (Bandel et al., 1984). Druschits et al. (1984) found that in the Lower Cretaceous *Tauriconites* (Diplobelida) the conotheca is formed by a prismatic layer that was a continuation of the prismatic wall of the protoconch. In the conotheca of *Belemnotheutis* and *Megateuthis*, Bandel & Kulicky (1988) described the periostracum, outer prismatic, nacreous and inner prismatic layers. According to Doguzhaeva et al. (2002a) in *Megateuthis* the conotheca consists of two layers: inner prismatic and nacreous. In juvenile Lower Jurassic *Passaloteuthis* the conotheca proper is missing and the phragmocone wall is formed by a continuation of the mural part of the first septum (Doguzhaeva et al., 2003a).

To be certain of observing the true ultrastructure of the pro-ostracum one must restrict observations to the thickness of the shell between the outer and inner surfaces of the pro-ostracum, recognisable by their characteristic patterns. In *Megateuthis* this revealed that the pro-ostracum was formed of organic fibres with different orientations, alternating with irregularly calcified sublayers which are built of loosely packed, criss-crossed crystallites lying parallel to the surface; the outer and inner surfaces are covered by thin, compact pellicles (Doguzhaeva et al., 2002a). A similar case was found in *Passaloteuthis* in which the description of the ultrastructure of the pro-ostracum was based on the SEM examination of the wall thickness between the outer and inner surfaces exposing the relief of both sides of the pro-ostracum (Doguzhaeva et al., 2003a). In this belemnite the pro-ostracum is described as consisting of two compact prismatic layers with a fine lamellar, loosely calcified, originally organic-rich layer between them. The original high content of organic material was indirectly confirmed by the presence of numerous borings on exposed broken surfaces of the pro-ostracum (Doguzhaeva et al., 2003a: Pl. 4).

As described above, the pro-ostracum in *Belemnotheutis* consists of vertical columns made up of predominantly organic lamellae, ca 0.05 µm thick. Their thickness is similar to that of the lamellae forming the gladius, formed of chitin-protein complexes (Hunt & Nixon, 1981), in living squids (Pl. 5). On the basis of our SEM observations on the pro-ostracum in *Belemnotheutis* we propose the name “organic lamello-columnar ultrastructure” (Pl. 4, D–F) as a new type of shell ultrastructure in cephalopods.

The pro-ostracum would have had an ultrastructure close to that of the conotheca if it arose from the latter. The concept of the pro-ostracum as an innovation in coleoid cephalopods was originally based on SEM studies of “ordinary” belemnites (Doguzhaeva et al., 2002a, 2003). Our present results on the “abnormal” belemnite *Belemnotheutis* support this idea.

Huxley (1864, p. 18) observed a specimen of *Belemnotheutis* 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 dis-

cernible 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.

To summarize, the SEM study shows that in *Belemnotheutis*: (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 consists of horizontally laminated vertical columns; the distal end of each column represents a polygonal field that at 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 chitin-protein material in the gladius of the living squids *Loligo* and *Berryteuthis* as examined with the SEM. The pro-ostracum in *Belemnotheutis*, is thus a shell element with unique structure without any similarity to that of the conotheca or rostrum.

The ultrastructural data on *Belemnotheutis* favour the concept of the pro-ostracum as a separate, innovative part of the shell rather than a dorsal projection of the conotheca.

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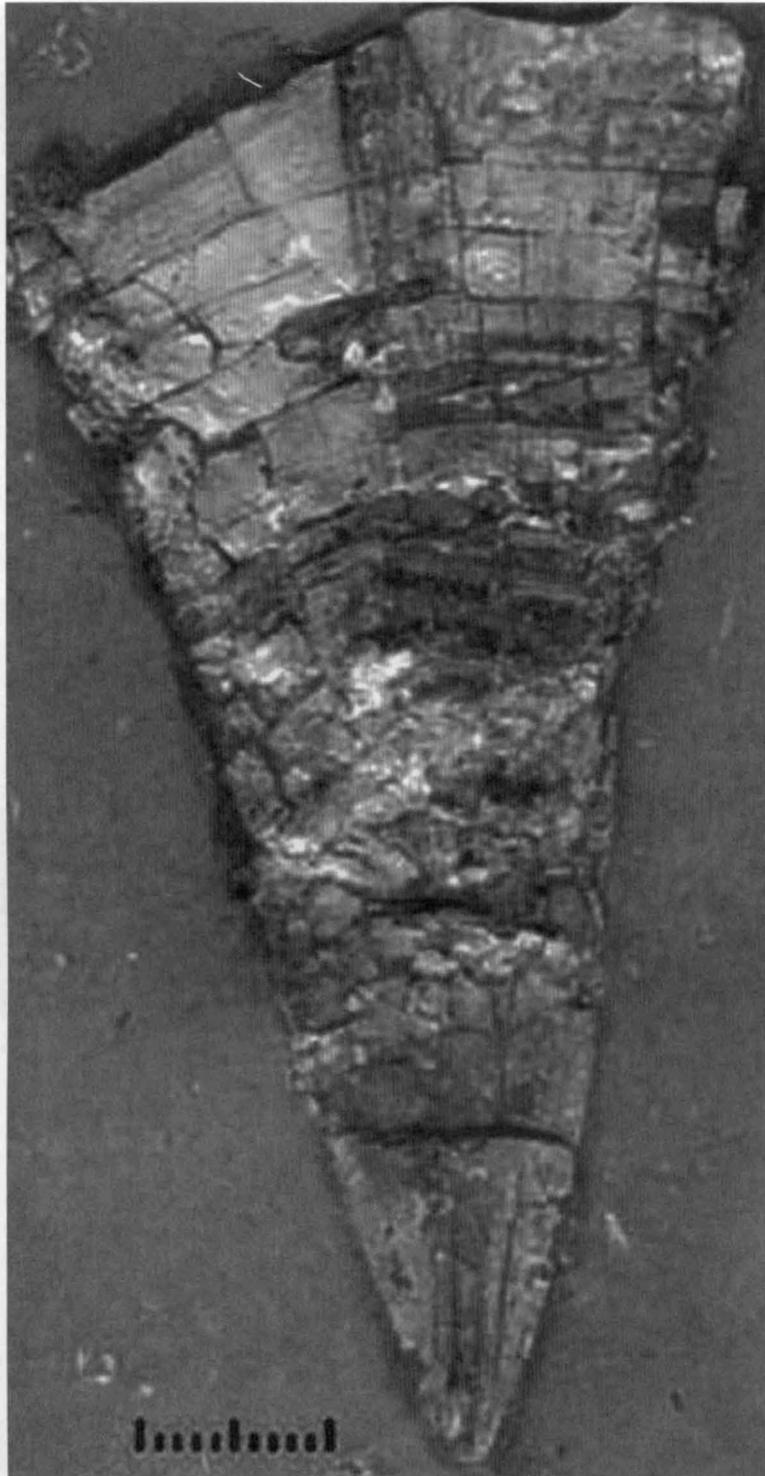


Plate 1. *Belemnite antiquus*, specimen no. BMNH 37412; Oxford Clay, Jurassic; Callovian, Christian Malford, Wiltshire, England: 1 – General view of the shell deformed by compaction. The smooth apical portion, about 1/3 of the total length shows a rostrum; two short ridges separated by a short groove mark the dorsal side; anteriorly the rostrum becomes thinner and the phragmocone is less protected against compaction, being more strongly crushed and slightly shifted to the right; the shifting results in an artifact that gives an erroneous view as if the hyperbolic zone is situated along the median line that in the apical part is between the two ridges. The transverse lines of the phragmocone are fractures along the mural parts of septa; scale bar is 10 mm.

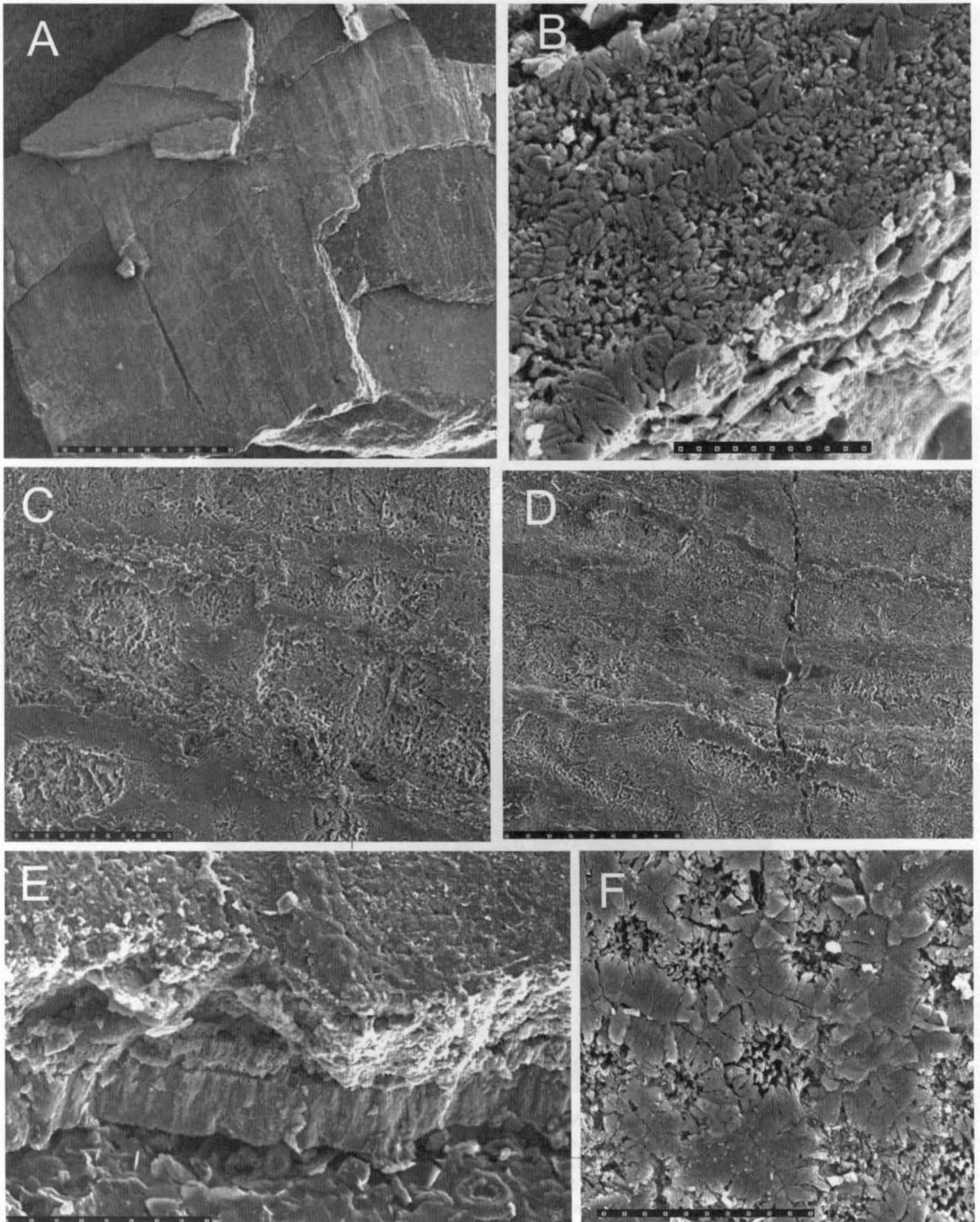


Plate 2. A–F. Surface view of a fragment of the anterior portion of the shell: a criss-cross pattern of the surface of the pro-ostracum, above is a fragment of the rostrum; scale bar is 0.6 mm. B. Close up of A: two views of the pro-ostracum: from the surface and from the longitudinal fracture plane to show its high porosity in combination with a lamination; scale bar is 6  $\mu\text{m}$ . C, D. Surface view of the hyperbolar zone to show the porosity of the material within the grooves and more compact material of the ridges; scale bar: C is 60  $\mu\text{m}$ ; D is 150  $\mu\text{m}$ ; E. Close up of A (centre) to show the laminated pro-ostracum (upper part) and inner prismatic layer of the conotheca; the outer prismatic and nacreous layers are missing at the apertural part of the shell but present at early and middle ontogenetic stages; scale bar is 30  $\mu\text{m}$ ; F. The porous outer surface of the pro-ostracum shows a “rosette”-like pattern formed by a combination of porous centres and elongated plates around them; scale bar is 12  $\mu\text{m}$ .

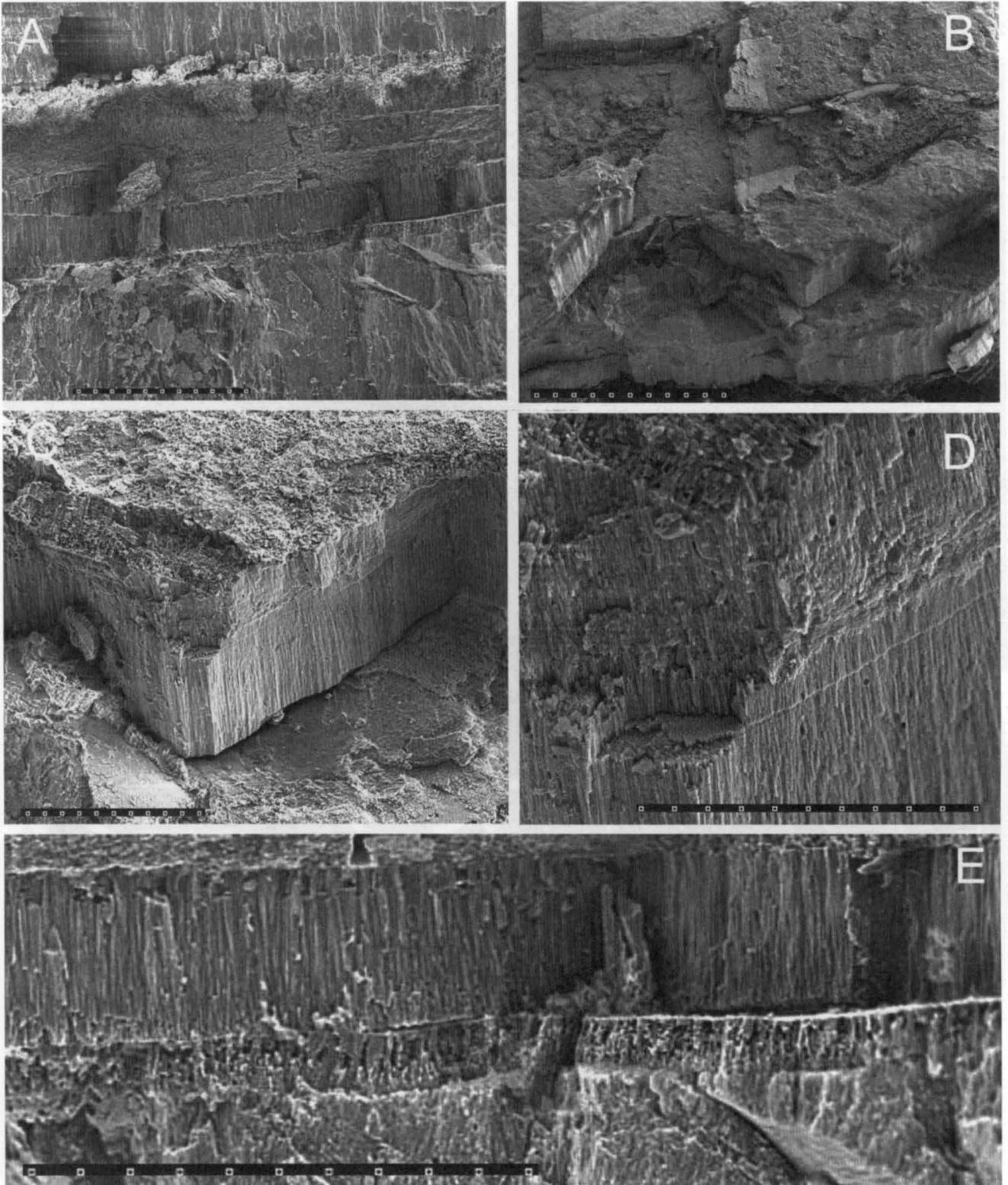


Plate 3. A–E. Fracture of a compressed shell with a rostrum running through the middle part of the photo, below a thin pro-ostracum and a thick nacreous layer of the conotheca; scale bar is 150  $\mu\text{m}$ . B. General view of the compressed and fractured shell exposing different structural elements; the hyperbolar zone of the pro-ostracum is at the top; scale bar is 0.6 mm. C. Detail of B (central part) to show a fragment of the shell with a thin pro-ostracum that is distinguished by its porous ultrastructure; scale bar is 120  $\mu\text{m}$ . D. Closeup of C with a fragment of the pro-ostracum exposed at top left corner; scale bar is 60  $\mu\text{m}$ . E. Middle part of the shell with a thin porous pro-ostracum situated between a rostrum (top) and a nacreous layer of the conotheca (bottom); scale bar is 120  $\mu\text{m}$ .

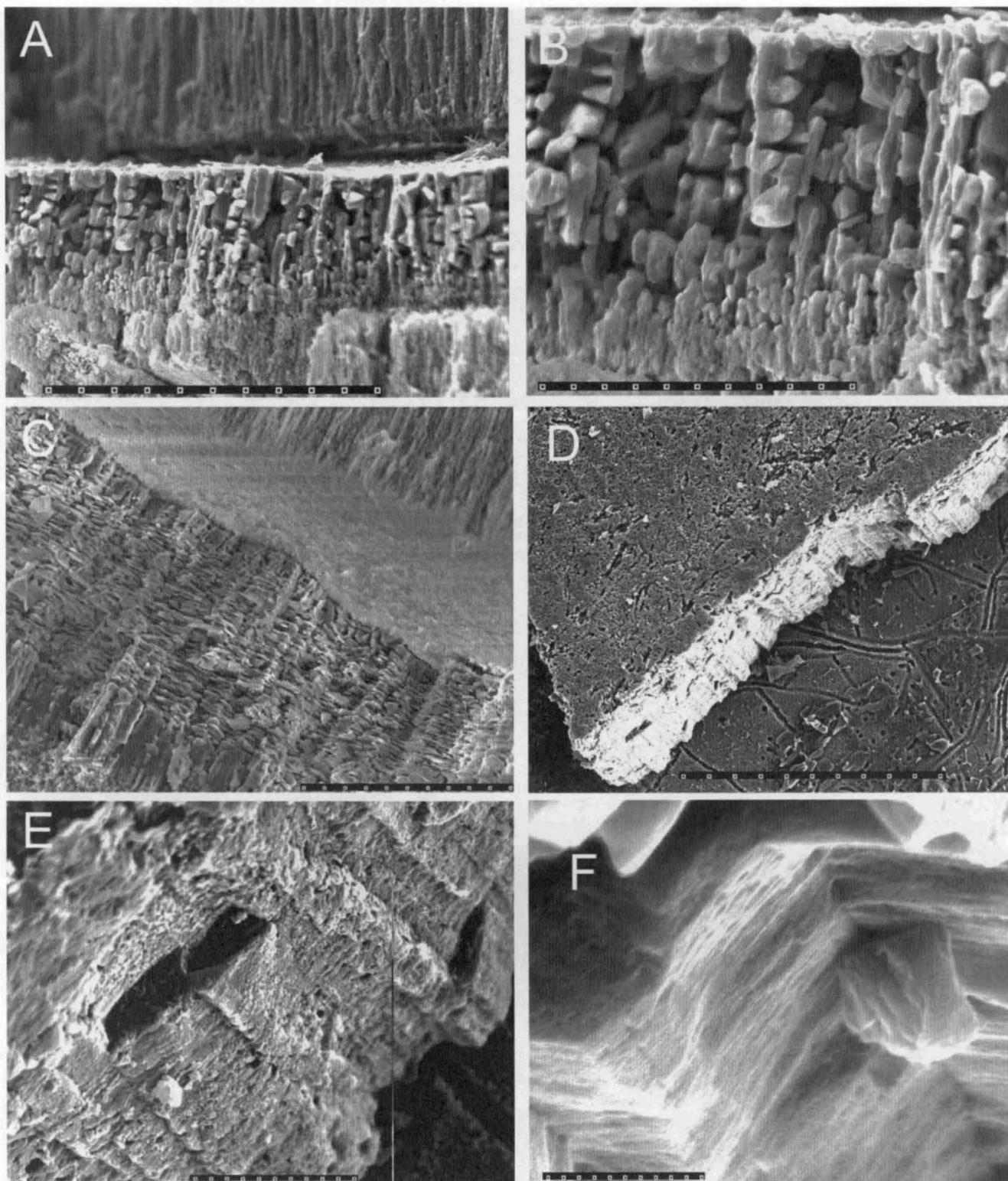


Plate 4. A–F. Close up of 3E to show a distinct contact between the pro-ostracum and the rostrum (top); scale bar is 30  $\mu\text{m}$ . B. Enlarged detail of A: the pro-ostracum is formed by vertical elements of varying shape with regular horizontal incisions, the inner portion of the pro-ostracum is comparatively more compact; scale bar is 12  $\mu\text{m}$ . C. Middle part of the shell showing (from the top right corner to the bottom left corner): a prismatic rostrum with an exposed whitish plane of the basal part, a pro-ostracum (a thin layer below the whitish layer) and two layers of the conotheca: a nacreous and an inner prismatic one; the outer prismatic layer is missing; the inner prismatic layer is about twice as thick as the pro-ostracum; scale bar is 30  $\mu\text{m}$ . D. A fragment of the pro-ostracum at a late ontogenetic stage; scale bar is 60  $\mu\text{m}$ . E. Enlarged detail of D to show columnar units of the pro-ostracum; scale bar is 6  $\mu\text{m}$ . F. Enlarged detail of E to show the micro-laminae of the columnar units probably indicating its initially organic composition; scale bar is 1.2  $\mu\text{m}$ .

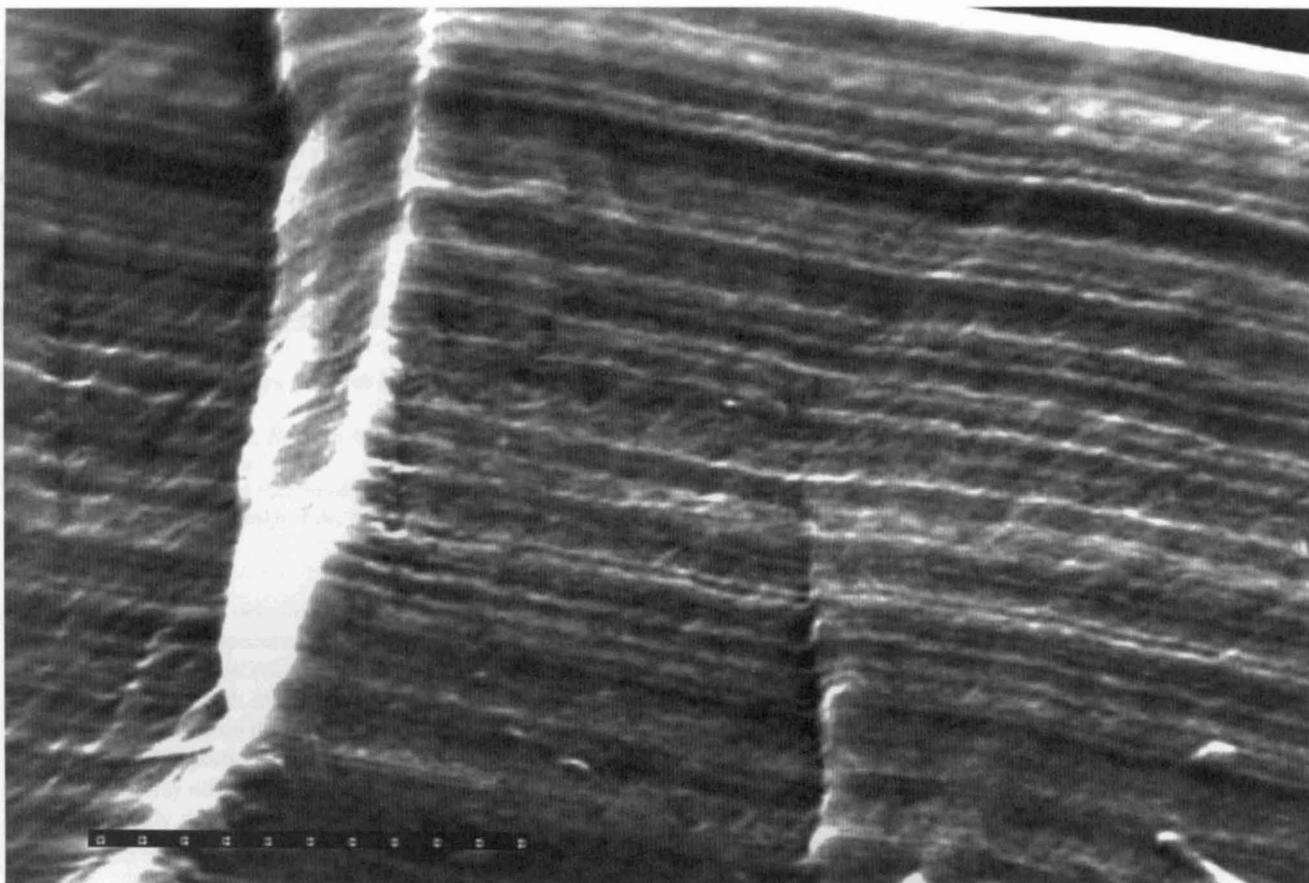
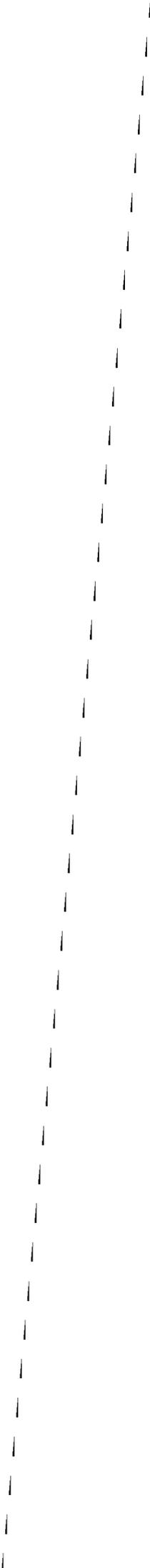


Plate 5. Micro-lamination of a chitinous gladius in a living squid *Berryteuthis magister*; scale bar is 12  $\mu\text{m}$ .



# GROWTH PATTERNS IN ROSTRA OF THE MIDDLE JURASSIC BELEMNITE *MEGATEUTHIS GIGANTEUS*: CONTROLLED BY THE MOON?

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**Abstract:** In order to determine the timing of growth of belemnite rostra, we analyzed microgrowth patterns of seven, excellently preserved specimens of *Megateuthis giganteus* (v. Schloth.) from the Middle Jurassic of the Hannover area, Germany. Spectral analysis (single spectrum analysis, continuous wavelet transformation) of microgrowth curves suggests that the microgrowth increments and lines formed on a lunar daily basis. Microincrements are arranged in fortnight bundles of 15. Based on this interpretation, we estimated that the ontogenetic age of the studied specimens (at least the well-preserved visible portions) ranged between one and two years. Furthermore, chemical (energy dispersive spectrometry) and structural (X-ray diffractometry, scanning electron microscopy) analyses and monochromatic cathodoluminescence were employed to study the degree of diagenetic alteration, interpret the original mineralogical composition of the guards and explain the reason for the distinct alternation of dark and light laminae (microgrowth lines or rings). We found that the alternation of dark and light laminae in the rostrum is caused by regular changes in density of calcium carbonate rather variable organic content. Orthorostra were originally composed of low-Mg calcite rather than aragonite. The overall high carbon content (35 to 65% higher amounts than expected for pure calcite) indicates the presence of pristine intra-crystalline (and perhaps inter-crystalline) organic matrix. Despite the overall mint preservation, some portions of the rostra (stained blue by Mutvei's solution) have undergone diagenetic alterations such as cementation and/or recrystallization.

**Key words:** Belemnites, microstructures, growth patterns, lunar periodicity, Jurassic

## INTRODUCTION

Belemnite rostra have been used in numerous studies for the reconstruction of paleoenvironmental conditions (e.g., Urey et al., 1951; Podlaha et al., 1998; Price et al., 2000; Longinelli et al., 2002, 2003; McArthur et al., 2000, 2004; Niebuhr & Joachimski, 2002; Voigt et al., 2003; Florek et al., 2004; Rosales et al., 2004; Wierzbowski 2004; van de Schootbrugge et al., 2005). These studies focused on stable isotopes and trace and minor elements to infer ancient water temperatures, interpret seawater isotopic composition and paleoceanography. Yet, little is known about the structure and the growth periodicity of belemnite rostra. Urey et al. (1951) interpreted the oscillations of oxygen isotopes of the belemnite low-Mg calcite as annual temperature variations and used these cycles to estimate the ontogenetic age of these belemnites (four years of age). However, age determinations based on sclerochronological (growth pattern) studies of belemnite rostra have not been employed.

The rostra of most Jurassic and Cretaceous belemnites have three parts with different structures: (1) the primordial and early juvenile rostrum is considered to be organic-rich and often aragonitic in composition, (2) the orthorostrum is a solid calcitic structure that covers the primordial rostrum and (3) the epirostrum is covering the orthorostrum. Bandel and Spaeth (1988) stated that the epirostrum was originally

composed of the aragonite polymorph. The ortho- and epirostrum show concentric laminae interpreted as alternating organic (*laminae obscurae*) and inorganic laminae (*laminae pellucidae*) (Müller-Stoll, 1936; Jeletsky, 1966; Barskov, 1970; Spaeth, 1971; Sælen, 1989). These laminae, also called microgrowth lines or microgrowth rings form a specific microgrowth pattern for each rostrum and are considered to have been formed periodically throughout the entire life-span. Similar microgrowth patterns are found in skeletons of many organisms including bivalve shells (e.g., Berry and Barker, 1968; Clark, 1975, 2005a; Evans, 1972; Richardson et al., 1979; Schöne et al., 2002), corals (e.g., Wells, 1963; Cohen and McConnaughey, 2004), fish otoliths (e.g., Pannella, 1971; Gutiérrez and Morales-Nin, 1986), squid statoliths (e.g., Archipkin and Murzov, 1986; Bettencourt and Guerra, 2001), beak and gladius of octopus (Hernández-Lopez et al., 2001; Perez et al., 1996) and have been interpreted as daily growth periodicities. In these organisms, precipitation of skeletal hard parts is regularly retarded resulting in the formation of distinct growth lines. Such structures might thus be useful in estimating precise ontogenetic ages and adding a time axis to geochemical analyses.

Two major reasons may explain the lack of sclerochronological studies of belemnite guards. Firstly, the poor preservation of most specimens prevents the recognition of

pristine microgrowth structures. Secondly, the lack of appropriate techniques required to visualize internal microgrowth patterns in belemnite rostra over larger portions of the belemnite. Mietchen et al. (2005) used magnetic resonance imaging (MRI) to study pathological deformations of belemnites and to reveal internal growth patterns. However, the resolution of present MRI techniques is insufficient to resolve  $\mu\text{m}$ -scale structures. Microgrowth patterns are much better visible in standard petrographic thin-sections viewed under polarized light or gently etched polished thick-sections viewed under reflected light (Mutvei, 1964; Sælen, 1989; O'Neill et al., 2003).

In the present study, we use a new approach to the analysis of microgrowth patterns of belemnite rostra using sclerochronological techniques similar to those applied to bivalve shells (Dunca and Mutvei, 2001; Schöne et al., 2004; Dunca et al., 2005): immersion in Mutvei's solution (Schöne et al., 2005), digital image processing and time-series analyses (Mallat, 1989; Keppenne and Ghil, 1992; Torrence and Compo, 1998). Our aim was to determine whether the microgrowth increments in the rostra of *Megateuthis giganteus* (v. Schloth.) reflect periodicities in the width and density. In order to elucidate the primary cause of the alternation of light and dark laminae we paid special attention to the content of organic matter in the orthorostra. For this purpose, we selected exceptionally well-preserved belemnite rostra with traces of organic matter (Doguzhaeva et al., 2002). Results of the present study will help to better understand life history traits of belemnites and to estimate the timing contained in certain shell portions.

## MATERIAL AND METHODS

Seven specimens of *Megateuthis giganteus* (v. Schloth.) from the Middle Jurassic of the Pfullingen, Würtenberg, southern Germany (belonging to the collections of Swedish Museum of Natural History, Stockholm) were chosen for our study. The same specimens were previously used by Doguzhaeva et al. (2002) to describe the general morphology of the pro-ostracum as well as the ultrastructure of the shell wall and the mantle tunic. The maximum diameter of the specimens ranged between 30 and 40 mm.

We prepared median- and cross-sections of the protoconch of all specimens. In order to enhance the visibility of the microgrowth rings, the cross-sections were also made parallel to the c-axes of the calcite prisms and not perpendicularly to the growth axis of the rostrum. The sections were immersed in Mutvei's solution (SCHÖNE et al., 2005) for ca. two hours. This agent is a 1:1 mixture of glutardialdehyde (25%) and acetic acid (1%) to which Alcian blue powder (ca. 5 to 10 g per liter solution) was added. Mutvei's solution is ideal to make fine structural details of biogenic carbonates and phosphates visible in three dimensions (Mutvei, 1979; Dunca and Mutvei, 2001; Schöne et al., 2004; Dunca et al., 2005) and is superior to simple acid treatment (e.g., Sælen, 1989; O'Neill et al., 2003).

Etched sections of the seven rostra were examined using reflected light microscopy (Nikon SMZ 1500; oblique and axial light) as well as scanning electron microscopy (SEM; Hitachi S 4300) at magnifications ranging from ca 20 to 2000

X. The elemental distribution within the rostra was analyzed with energy dispersive spectrometry (EDS) with a spatial resolution of ca 30  $\mu\text{m}$  and detection limit down to ca 1% atomic weight. X-ray diffractometry (XRD) was employed to determine which calcium carbonate polymorph (aragonite, calcite) prevails of the rostra. Possible diagenetic effects were studied with monochromatic cathodoluminescence (CL).

The smallest growth increment (microgrowth increment) in the rostra was defined as the distance between two dark laminae. The width of the microgrowth increments was measured in digital images of the ventral part of the rostra using the Panopea® image processing software (developed by Peinl and Schöne, University of Frankfurt). Then, the microincrement widths were plotted against microincrement number, linear trends removed and the data were standardized. Spectral analyses of the standardized microincrement time-series included single spectrum analysis (SSA; Keppenne and Ghil, 1992), and continuous wavelet transformation (CWT; Mallat, 1989; Torrence and Compo, 1998). SSA enables decomposition of the chronology into discrete sinusoidal waves and analyses of signal strength (amplitude) through time. Eigenvalues determine the relative proportion of each wavelength in the entire time-series. The focus was on the eight strongest eigenvalues. CWT (here: Morlet function, wavenumber six), however, enables recognition of non-stationary signals, i.e. changes in the amplitude of the dominant (amplitude) wavelengths and frequency evolution of signals through time.

## RESULTS

**Ultrastructure.** Mutvei's solution revealed crisp ultrastructural details in the seven *M. giganteus* rostra. The alternation of the light *laminae pellucidae* and dark *laminae obscurae* seen in the light microscope corresponded to etch-resistant ridges and less etch-resistant depressions seen in SEM (Pl. 1). However, not all the transversal sections were etched homogeneously. Portions of the rostrum were more etch-resistant and more deeply blue stained by the Mutvei's solution (Pl. 2). Neither the *laminae pellucidae* or *laminae obscurae* were interrupted when crossing from blue stained to unstained portions, but they had a different microstructure (smaller crystals with less organized orientation; Pl. 2). Also, the cement that was precipitated in the microcracks of the rostra and the spherulitic structure near the protoconch were strongly bluish stained by the Mutvei's solution (Pl. 2). The blue stained, spherulitic structure within the central part of the juvenile rostrum changed into a colorless prismatic structure after approximately 30 microgrowth increments from the center of the rostrum.

In the colorless portions of the rostra the calcitic prisms were radially arranged and showed a continuous growth toward the outer surface. The prisms were thinner, but not interrupted at the *laminae obscura* (Pl. 3).

All studied rostra exhibited darker regions that had less numerous and narrower laminae. These regions were often stained blue and contained intrusions of spherulitic carbonate.

**Microgrowth patterns.** We counted up to 567 microincrements in the rostra. The average microincrement width

**Table 1. Measurement results.**

Specimen no	Museum collection no	Microincrement number	Microincrement width ( $\mu\text{m}$ )			Maximal diameter of the rostrum (mm)
			min	max	average	
1	Mo160885	384	4	29	10	30
2	Mo160886	465	4	23	11	42
3	Mo160887	500	6	51	19	34
4	Mo160888	418	3	18	07	37
6	Mo160890	567	2	10	11	44
7	Mo160891	494	4	25	12	43
8	Mo160892	370	4	24	12	31

ranged from 2  $\mu\text{m}$  in specimen no. 6 and 51  $\mu\text{m}$  in specimen no. 3 (Tab. 1). Microgrowth increment measurements revealed up to eight regions with broader microincrements which in turn were separated by regions with narrower microincrements (Pl. 4). Within each specimen, broadest microgrowth increments were found midway between the center and the rim of the cross-section. Growth curves of all studied specimens exhibited distinct periods (eigenvalue pair 7 and 8 in specimens 1–7, eigenvalue pair 3 and 4 in specimen 8) of around  $15 \pm 2$  microincrements (Pl. 5; 6: eigenvalue decomposition and CWTs of decomposed signals). Specimens 1, 3, 4 (eigenvalue pair 3 and 4), 2 (eigenvalue 5) and 7 and 8 (eigenvalue 6) also showed spectral power at frequencies corresponding to approx.  $30 \pm 2$  microincrements. Other spectral power occurred at periods of about 100, 20 and 8 microincrements. In all series, eigenvalues 1 and 2 plotted far away from each other and characterized lower-frequency oscillations. CWTs showed that the  $15 \pm 2$  and the  $30 \pm 2$  microincrement oscillations were nearly stationary in all growth curves. Lower frequency cycles, however, were strongly transient (examples: Pl. 5, A, specimen no. 1 and Pl. 6, C, specimen no. 7).

**Chemical analyses.** EDS analyses of the seven rostra of *M. giganteus* revealed the following content (in atomic weight %): Ca (ca. 35%), C (ca. 15%) and O (ca. 50%). Trace and minor elements (particularly Mg, Mn, Fe) were lower than the detection limit of the machine. Close to the outer surface of the rostra, EDS showed a higher content of carbon (up to 30%) at the interspaces between the calcium carbonate prisms. The dark and light laminae, however, did not differ in carbon content. CL analyses demonstrated that the portions of the rostrum stained by the Alcian blue have higher luminescence than the unstained portions of the same rostrum.

XDS analysis of specimen no. 7 indicated that the rostra consist of 100% calcite and no aragonite.

## DISCUSSION

**Ultrastructure and mineralogy.** Low amounts of Mg, Mn and Fe within the rostra indicates that the orthorostra of *M. giganteus* were originally composed of (low-Mg) calcite rather than aragonite. This interpretation would be in concert with previous assumptions (Mutvei, 1964; Sælen, 1989; Veizer, 1974) and is supported by the excellent preservation of microgrowth patterns and by the higher carbon content. For pure  $\text{CaCO}_3$ , we would expect 37.7% Ca (atomic weight), 11.3% C and 50.9% O. Our analysis, however,

revealed 32.5% higher carbon values than expected in light portions of the rostra and even higher amounts (up to 65% higher than expected) near the outer surface. This observation suggests the presence of original organic matrix in the biominerals and is supported by some previous investigations (Müller-Stoll, 1936; Jeletzky, 1966; Barskov, 1970; Spaeth, 1971; Sælen, 1989).

Preservation of pristine organic matter is not unusual in well-preserved fossil material (Clark, 1999), especially within the crystallites (intra-crystalline organic matrix; Clark, 2005b). Apparently, the dense skeleton of the belemnite rostrum prevented extensive diagenetic alteration, except for portions near the periphery of rostra, within microcracks and in the youngest parts (center) of the rostra. We observed patchy recrystallization through the use of monochromatic CL and immersion in Mutvei's solution. Our findings confirm previous observations on low diagenetic alteration of belemnites (e.g. Podlaha et al., 1998; O'Neill et al., 2003; Rosales et al., 2004).

There is no evidence that organic laminae alternate with inorganic laminae as previously stated (Müller-Stoll, 1936; Jeletzky, 1966; Barskov, 1970; Spaeth, 1971; Sælen, 1989). We did not find a difference in carbon content of dark and light laminae. Rather, the organic material seems to be homogeneously distributed within the rostrum (except for C-enriched outer rim portions), while the alternating lightness of the laminae seems to be the result of different crystal size and density.

**Timing of growth of the belemnite guard; micro-growth patterns.** Spectral analyses of the microgrowth patterns suggest that the formation of the belemnite guards of *M. giganteus* was controlled by lunar cycles. In all micro-growth increment time-series of *M. giganteus*, sinusoidal components reflecting bundles of 15 and 30 microincrements were among the eight most prominent signals. We assume that these cycles are indicative of fortnight periods of shell formation. Today, however, one fortnight period is slightly shorter and comprises only 13.5 to 14.5 lunar days (perigee and apogee fortnight periods, respectively). Yet, according to astronomical calculations and sclerochronological analyses of other Jurassic biogenic skeletons, days in the Jurassic were shorter, because the rotation of the earth around its own axis was faster and the distance between earth and moon closer than today (e.g., Rosenberg, 1977). During the Jurassic, each fortnight period was about one day longer than today. This finding adds support to our hypothesis that the 15 and 30 microincrement bundles reflect fortnight periods and that each microincrement was formed during one lunar day. But can the microincrements

also represent semi-diurnal cycles? This seems unlikely because the 15 microincrement cycle would be much weaker or absent from the chronology. Components of the time-series with lower frequency can be attributed to harmonics of these fortnight periods or were strongly transient indicating growth trends rather than cycles. The hypothesis of a tide-controlled growth of the belemnite guard was also previously suggested by Anisimov et al. (1984), based on optical heterogeneity of orostrostra sections.

Circadian (ca. 24hr period) and circalunidian (two circadian clocks linked in antiphase, hence 12.4 hr intervals, intertidal organisms; term coined by Palmer et al., 1994) periods were observed in a variety of living organisms including humans (sleeping cycle), bivalves (Richardson et al., 1980; Kim et al., 1999), crabs (Palmer et al., 1994) and coleoid cephalopods (Kristensen, 1980; Radtke, 1985). Circadian or circalunidian periodicity of shell growth was also observed in several ammonoid genera (Doguzhaeva, 1982, 1984, 1986, 1990; Checa, 1987).

Laptikhovsky (2002) observed diurnal feeding rhythms in the short-finned squid *Illex argentinus* off the Falkland Islands. Perhaps, similar causes can be assumed for the rhythms retrieved from the belemnite rostra. Biological clocks help organisms to anticipate changes of the environment such as changes of the food supply, light availability etc. (Pittendrigh, 1979; Rensing et al., 2001). Circadian biological clocks are genetically determined and are entrained and constantly reset by environmental pacemakers (Young and Kay, 2001).

Gravitational forces of the moon and sun exert a major control on marine ecosystems (Palmer, 1996). For example, spawning of corals and many other organisms is induced by the tides (e.g., McGuire, 1998). Even deep sea environments are affected by the tidal bulges. Current velocity in deep sea environments varies diurnally and on a fortnightly basis. Near hydrothermal vents, these currents can significantly influence the temperature regime (Johnson et al., 1994) and hence the biological productivity of organisms that directly (chemosymbionts) or indirectly (organisms with chemosymbionts) depend on hydrothermal effluents (Schöne and Giere, 2005).

If our hypothesis on the timing of growth of the rostra is true, the belemnites of our study formed during a period of about one or two years. Such age estimates closely match those of modern cephalopods (e.g. Jackson, 1998).

## CONCLUSIONS

- (1) Guards of *M. giganteus* formed with lunar daily periodicity. Lunar daily microgrowth patterns were revealed by immersion in Mutvei's solution and can be used to estimate the ontogenetic age of the belemnite and add a precise time axis to geochemical data obtained from the rostra.
- (2) The ontogenetic ages of the studied specimens of *M. giganteus* ranged between one to two years.
- (3) Orthorostra of *M. giganteus* were originally composed of (low-Mg) calcite.
- (4) Carbon is enriched in the rostra by 35 to 65% possibly reflecting the preservation of pristine intra- and inter-crystalline organic matrix.

- (5) There is no evidence that organic-rich laminae (micro-growth lines) alternate with inorganic laminae (micro-growth increments). The difference between microincrements and –lines seems to be the result of differences in crystal size and orientation.
- (6) Despite the overall excellent preservation, EDS, CL and XDS analyses demonstrate that non-homogenous diagenetic alteration occurred (radial microcracks, center of the guards, outer rim).

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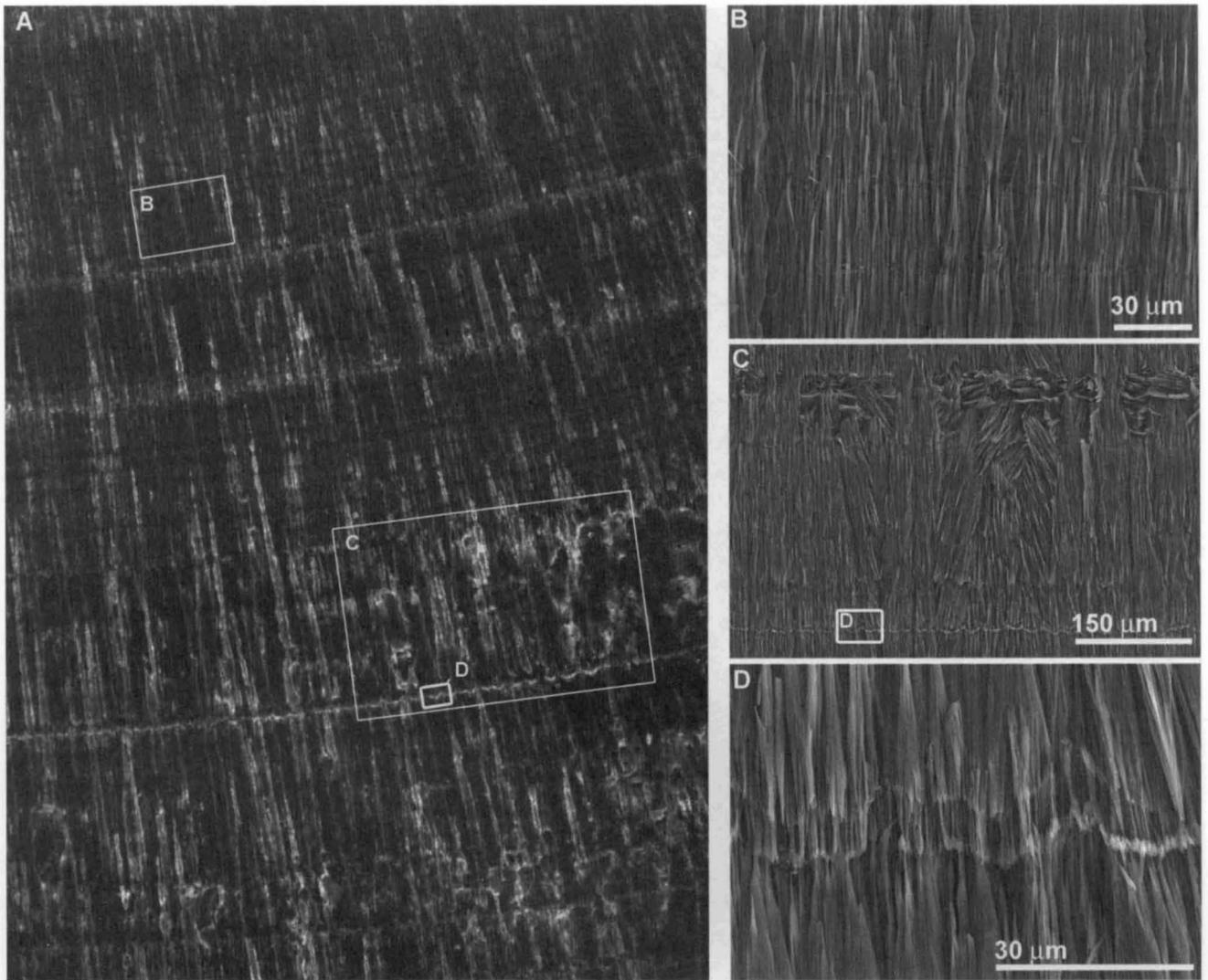


Plate 1. A–D. Thin section of the rostrum of *Megateuthis*, specimen 1, etched with Mutvei's solution. A. The section viewed under a reflective light stereomicroscope with axial light. B, C and D. Portions of the same rostrum viewed in a scanning electron microscope (SEM). The alternation of the light lamina and dark lamina (seen in light microscope) corresponds to ridges and depressions (seen in SEM). The light lamina (ridges) are more etch-resistant than the dark lamina (depressions).

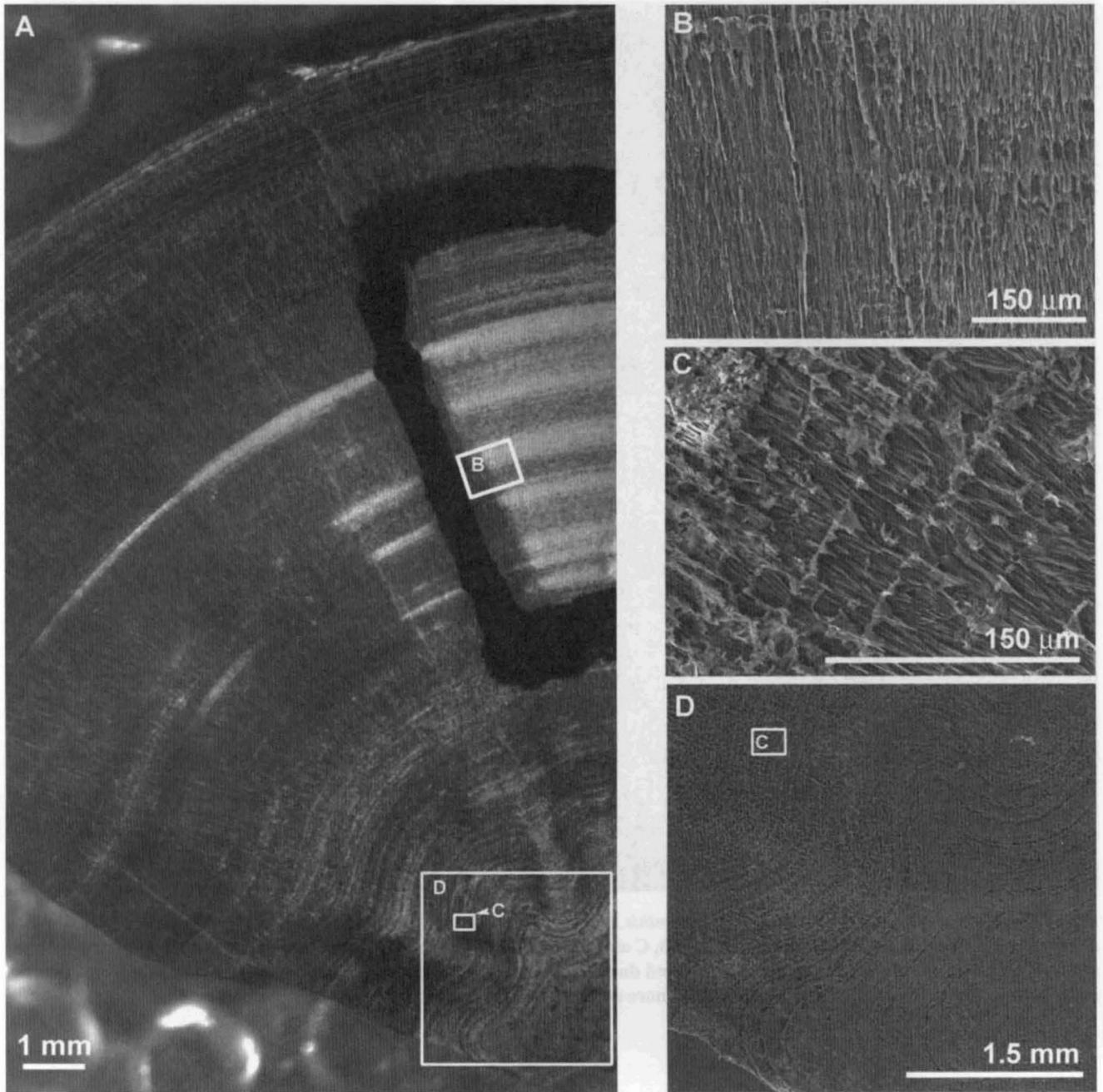


Plate 2. A–D. Portions of the rostrum (specimen 1) stained by Alcian blue are more etch-resistant (even the cement within the cracks) than the colourless portions. B. The growth rings are not interrupted when crossing from blue stained to colourless portions but they have different microstructure. C. The spherulitic microstructure of the juvenile rostrum is strongly stained by the Mutvei's solution and is more resistant to etching. D. Overview of the central part of the rostrum seen in SEM showing nonhomogenous etching.

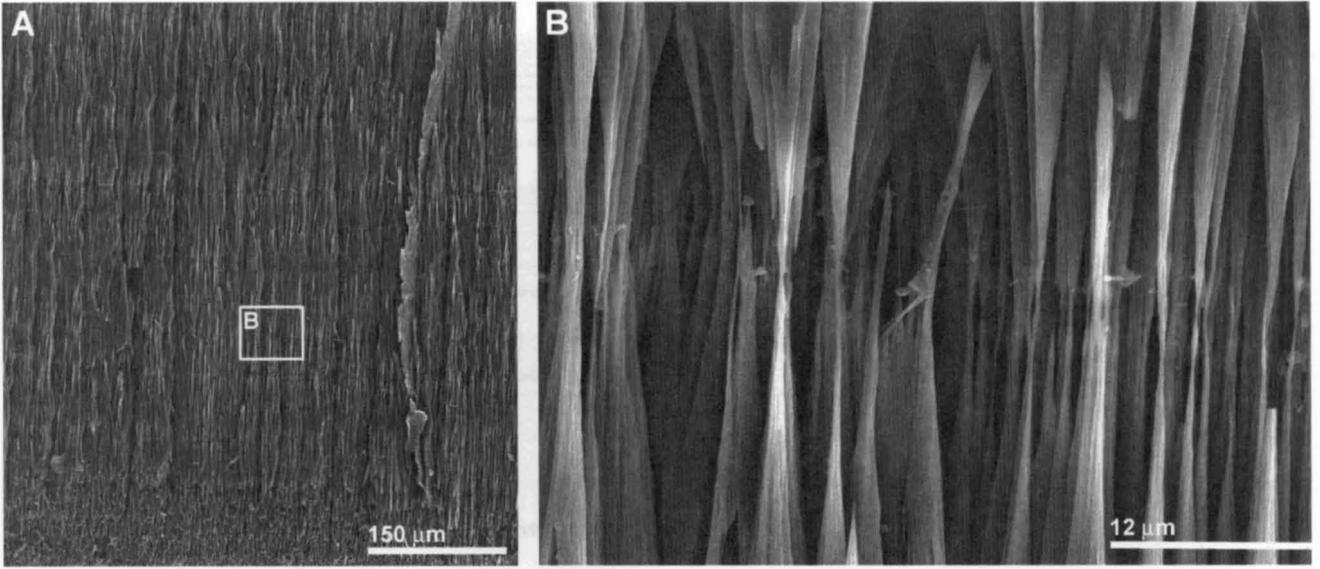


Plate 3. A–B. SEM picture of an unstained portion of the belemnite rostrum, specimen 3, showing that the calcite prisms grow radially and that their growth is not interrupted by dark lamina. B. Detail of a dark laminae that shows the continuous growth of the calcite prisms.

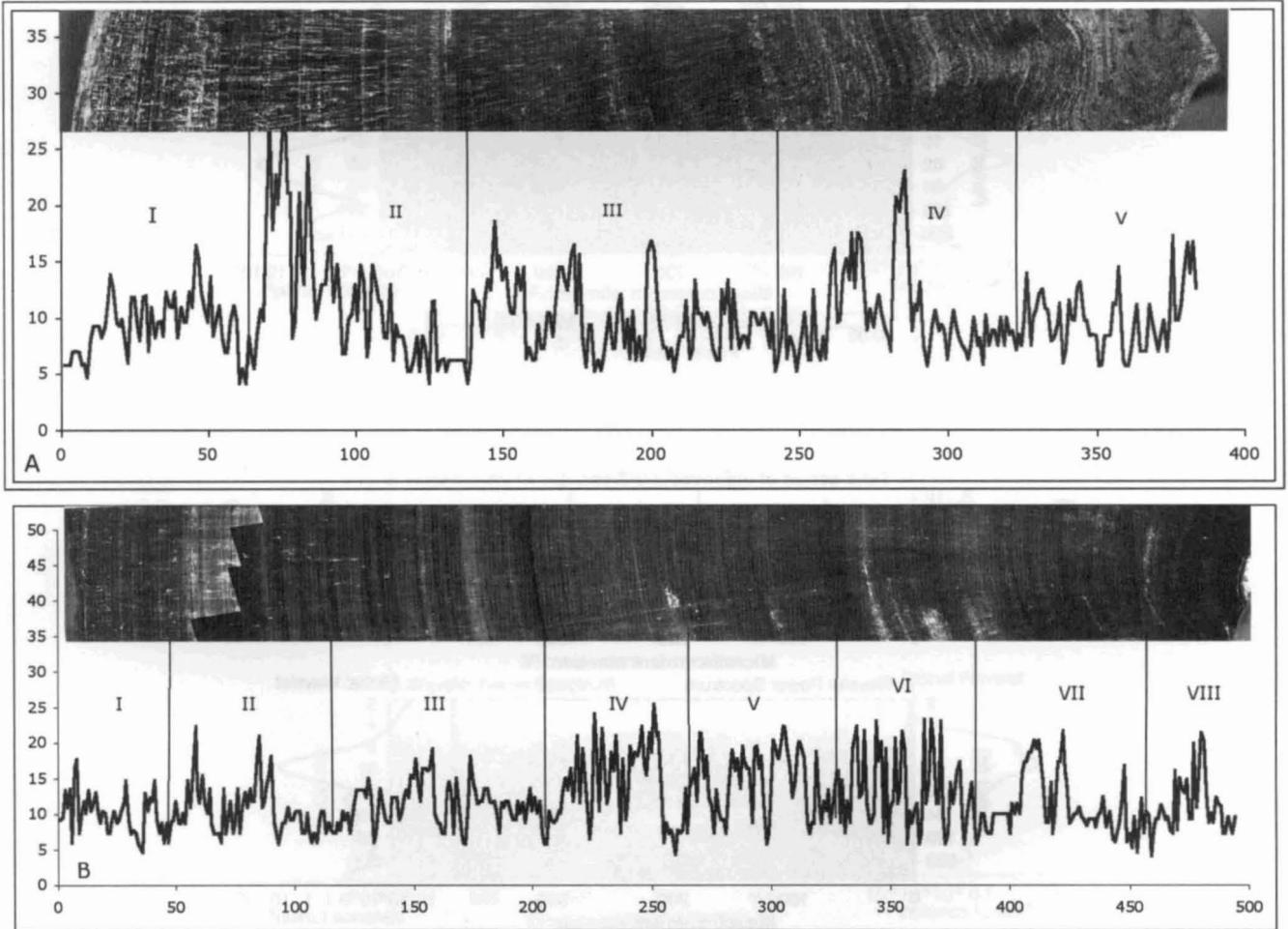


Plate 4. A–B. Growth measurements of two *Megateuthis* rostra: A. specimen no 1 and B. specimen no 7. I–VIII correspond to regions with higher growth rate separated by regions with lower growth rate (darker regions).

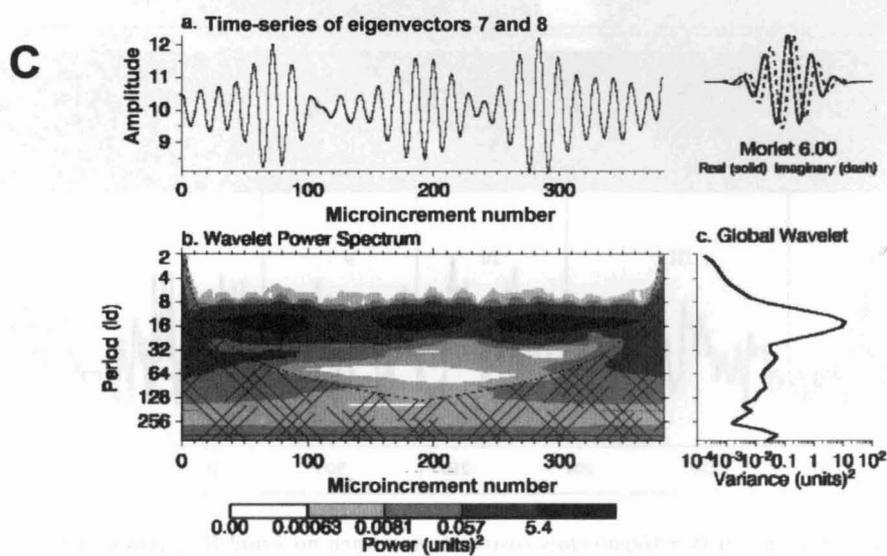
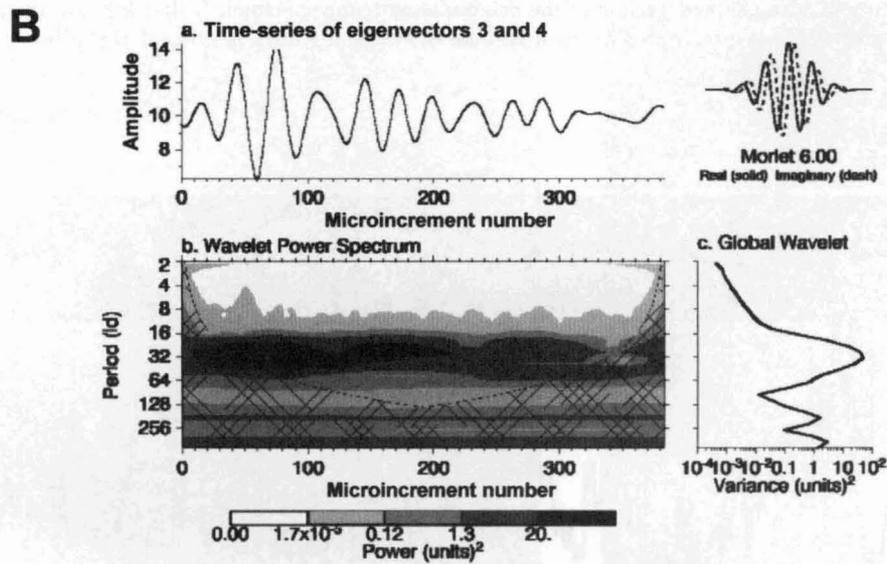
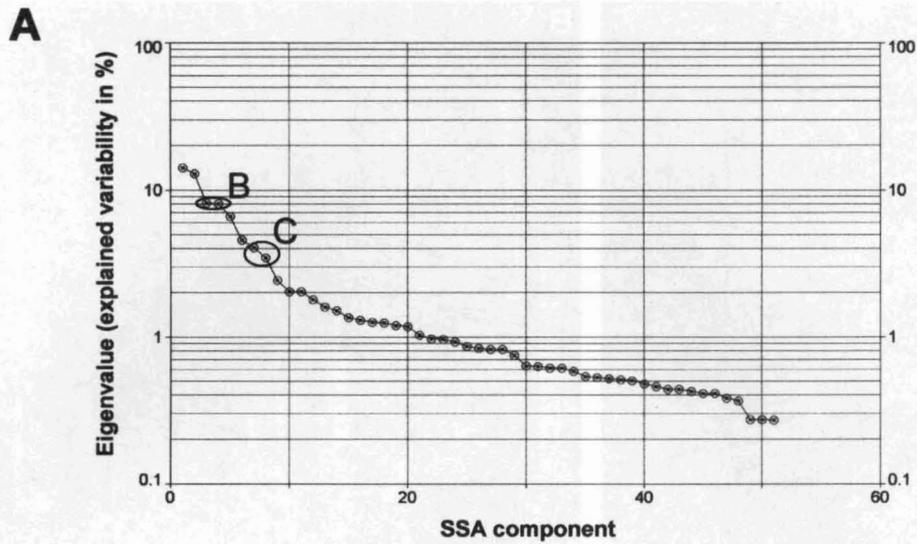


Plate 5. A–C. Single spectrum analysis (eigenvalue decomposition) of specimen 1 (A) and continuous wavelet transforms of selected eigenvalues (B, C). Eigenvalues 3 and 4 explain about 16% (A; 8% and 8%) of the chronology and resemble microincrement width periods of ca. 15 laminae (B), whereas eigenvalues 7 and 8 stand for periods of ca. 30 microincrements (C) and explain 4% and 3% of the time-series, respectively. These periods are interpreted as reflecting fortnightly periodicity of belemnite growth.

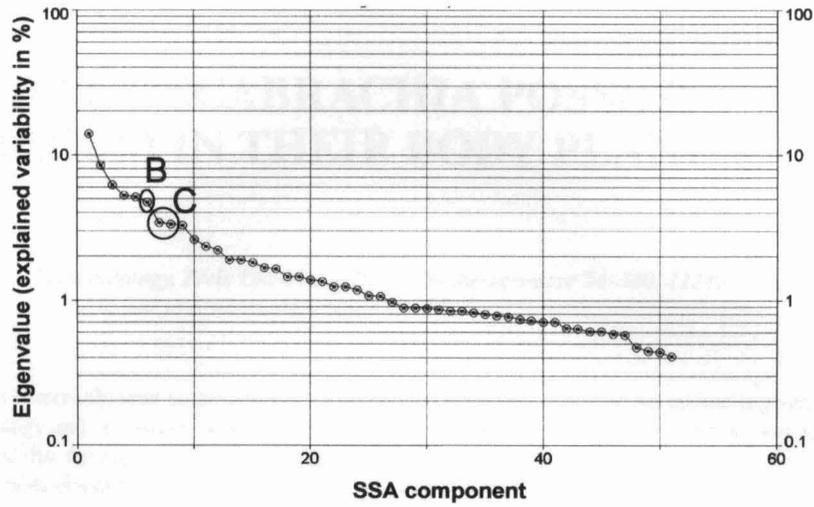
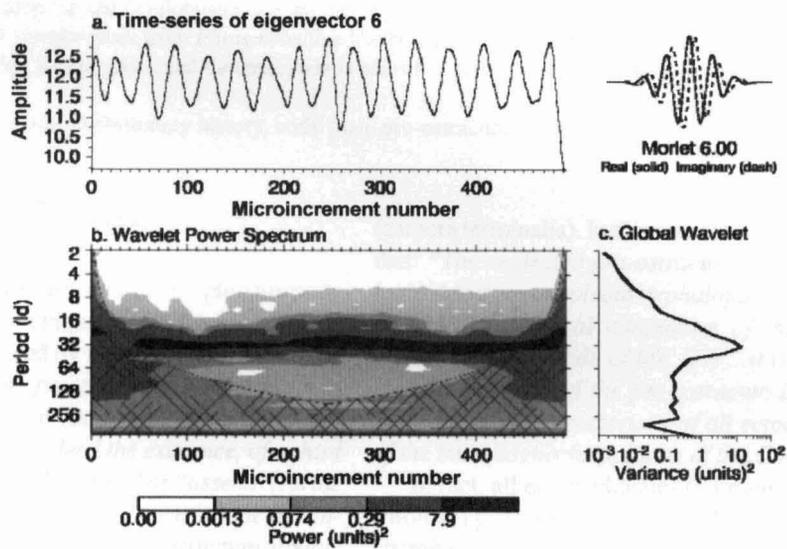
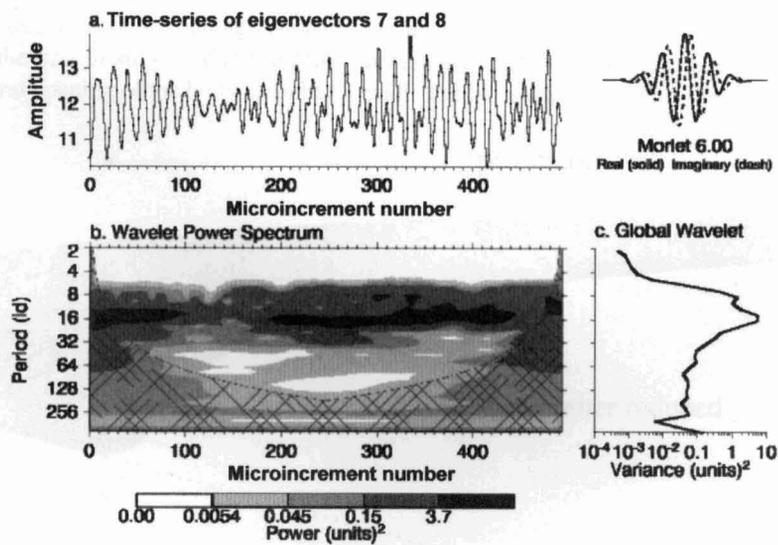
**A****B****C**

Plate 6. A–C. Single spectrum analysis (eigenvalue decomposition) of specimen 7 (A) and continuous wavelet transforms of selected eigenvalues (B, C). Eigenvalue 6 explains about 5% (A) of the chronology and resemble microincrement width periods of ca. 15 laminae (B), whereas eigenvalues 7 and 8 stand for periods of ca. 30 microincrements (C) and explain 7% (ca. 3.5% and 3.5%, respectively) of the time-series. These periods are interpreted as reflecting fortnightly periodicity of belemnite growth.



# DID ANCESTRAL DECABRACHIA POSSESS A PRO-OSTRACUM IN THEIR BODY PLAN?

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**Abstract:** A pro-ostracum is commonly seen as the result of a ventrally opened body chamber. An outline is given of present knowledge about the morphology and occurrence of pro-ostraca in different coleoid groups. It turns out that most fossil Decabrachia lack a pro-ostracum and that the presumed pro-ostracum of *Naefia* and *Groenlandibelus* is more likely a dorsal growth allometry of a long and tubular body chamber and merely the result of an opened body chamber. The existence of a “true” pro-ostracum is therefore most probably restricted to phragmoteuthids, belemnitids and diplobelids. The sepiid clade demonstrates that reduction of the ventral phragmocone side can be alternatively achieved by vaulting the phragmocone and tilted septa. This, in turn, suggests that the loss of calcification, i.e. the development of a gladius might have occurred independently in Decabrachia and Vampyropoda. Since derivation of vampyropods from *Phragmoteuthis*-like belemnoids is widely accepted, a sister-group relationship between pro-ostracum-bearing Belemnoidea and Vampyropoda is plausible. As a result the taxon Neocoleoidea describes a paraphylum.

**Key words:** Coleoidea, Decabrachia, evolutionary history, body plan, pro-ostracum

## INTRODUCTION

The pro-ostracum is a dorsal protrusion of the phragmocone and generally considered to be unique within fossil Coleoidea (Fig. 1). The term was introduced by Huxley (1864: p. 3): “All observers are agreed as to the presence of the parts hitherto mentioned in a Belemnite, but a great diversity of opinion prevails respecting the nature, and indeed the existence, of a third constituent of the fossil, the so-called “pen” or “osselet”. As the part which commonly goes by the name of “pen” in the Belemnite, however, corresponds to only a part of the structure already known as the “pen” in recent Cephalopoda, I shall endeavour to avoid ambiguity, by using it for the appellation of pro-ostracum”. Thus, Huxley believed that the gladius (“pen”) of modern squids is a relict of a pro-ostracum-bearing phragmocone.

Naef (1922: p. 31) was the first to suggest that the pro-ostracum is the result of ventral opening of the body chamber

(camera terminalis). In this context Jeletzky (1966: p. 8) stated that: “The neglected pro-ostracum is a fundamental morphological feature to coleoid cephalopods and represents a most important biological adaptation of their characteristically active, nektonic mode of life. (...) ...it is sufficient to mention that the presence of the pro-ostracum instead of the tubular body chamber characteristic of all ectocochlian forms is one of the best diagnostic features of the Coleoidea.”

In fact, all ectocochleates (ammonoids, nautiloids, “bactritoids”) possessed a long, tubular and entirely closed body chamber. In recent *Nautilus*, it still encloses and protects the visceral mass. By contrast, in belemnoid coleoids ventral (and in some taxa even lateral) parts of the body chamber wall have been lost. They were replaced by the muscular mantle, which became attached to the margins of the remaining spatulate-like dorsal part of the body chamber wall, the pro-ostracum. The development of a pro-ostra-

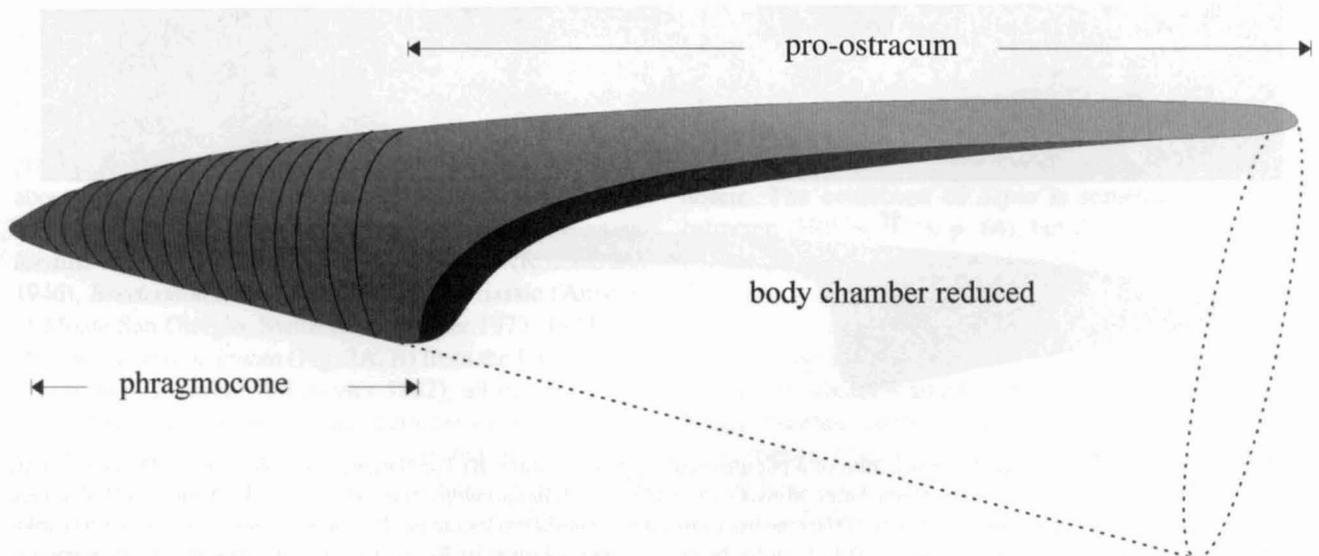
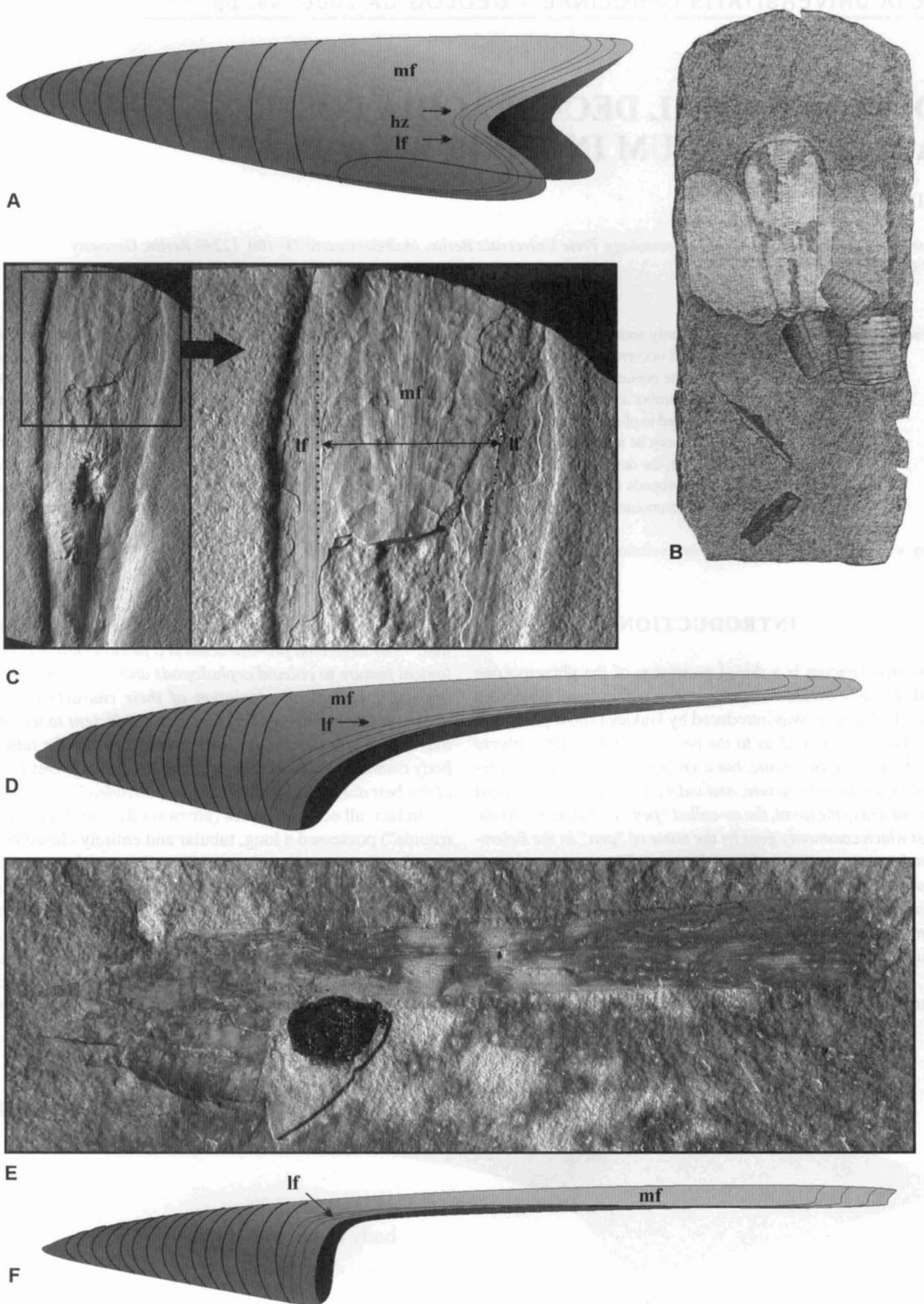


Fig. 1 The pro-ostracum as a relict of a reduced body chamber.



**Fig. 2** Belemnoid pro-ostraca. A) Reconstruction of a phragmoteuthid pro-ostracum. B) The flattened pro-ostracum of *Phragmoteuthis bisinuata* (Phragmoteuthida, Carnium, Raibl, after Mojsisovics 1882). C) *Acanthoteuthis spec.* (Belemnitida, Tithonian, Solnhofen, Staatliches Museum für Naturkunde Stuttgart). D) Reconstruction of a belemnitid pro-ostracum. E) *Chondroteuthis wunnenbergi* (Diplobelida, Toarcian, Luxembourg, Musée National D'Histoire Naturelle Luxembourg). F) Reconstruction of a diplobelid pro-ostracum. Note that rostra are not considered in the reconstructions. Abbreviations: hz = hyperbolar zone, lf = lateral field, mf = median field.

cum was therefore an important step towards perfecting jet propulsion.

Naef (1922) and Jeletzky (1966) believed that both modern vampyropod and decabrachian gladii derive from a proostracum. Especially Naef (1922) therefore assumed a proostracum in so-called "Tertiary Sepiids", such as *Belosepia*, *Beloptera* and *Spirulirostra*. To date, however, fossil evidence for these assumptions is weak.

The present contribution summarises and discusses the knowledge about the morphology and occurrence of so-called proostraca in fossil Coleoidea and demonstrates their phylogenetical significance.

## MODES OF PRESERVATION

In general, pro-ostraca have a comparatively poor preservational potential. In most cases, phragmocones are preserved without their pro-ostraca. Imprints of pro-ostraca are well preserved only in finely laminated deposits such as the Oxford Clay of Christian Malford (UK), the Posidonienschiefer of Holzmaden (Germany) and the Solnhofen Plattenkalks (Germany). In these cases, surface structures, outline and length-width indices are easily analysed.

Sometimes the existence of a pro-ostracum can be reconstructed from characteristically forward-curved growth lines, whether on the dorsal outer surface of the conotheca or on the dorsal inner surface of the rostrum (Flower 1945, Birkelund 1956, Doguzhaeva et al., 2002, 2003b, Donovan 2006). In that mode of preservation, pro-ostracum length is difficult to determine because growth lines cannot be tracked owing to dense striations. To date, no 3-dimensional pro-ostracum has been found *in situ*.

## PROOSTRACA IN BELEMNOIDS

Pro-ostraca occur in phragmoteuthids, belemnites and diplobelids (Fig. 2). Most authors agree that the body chamber of the Aulacocerida is still tubular and ventrally closed.

The oldest known pro-ostracum was presumed to occur in *Eobelemnites caneyensis* from the Late Carboniferous (Mississippian) of USA (Flower 1945), but Doyle et al., (1994: p. 7) emphasised that the stratigraphical age of this taxon is more than ambiguous. Doguzhaeva et al., (2003a: p. 65) reported on a Late Carboniferous (Pennsylvanian) coleoid (*Donovaniconus*) that yielded a structure which they interpreted as a pro-ostracum. Unfortunately, reliable information about the presumed pro-ostracum is still insufficient. The first well-preserved pro-ostraca are shown by *Permoteuthis groenlandica* from Late Permian of East Greenland (Rosenkrantz 1946), *Breviconoteuthis* from the Middle Triassic (Anisian) of Monte San Giorgio, Switzerland (Rieber 1973, 1974) and *Phragmoteuthis bisinuata* (Fig. 2A, B) from the Late Triassic (Carnian) of Austria (Mojsisovics 1882), all of which look very similar. On the basis of the characteristic pro-ostracum of *Phragmoteuthis*, Jeletzky (1965) erected the new taxon Phragmoteuthida. In his diagnosis Jeletzky (1966: p. 31) claimed a "...tripartite, fan-like pro-ostracum which is considerably longer than phragmocone and attached to about three quarters of its circumference...". Tripartite means that

three different fields can be distinguished on a phragmoteuthid pro-ostracum. A broad median field with parabolic growth lines is delimited from likewise parabolic lateral fields by narrow hyperbolic zones ("notches" or "re-entrants"). Donovan (2006) recently presented the first post-Triassic record of phragmoteuthid pro-ostraca. The three-lobed growth lines are easily visible on the surface of the conotheca of *Phragmoteuthis huxleyi* from the Middle Jurassic (Sinemurian) of Dorset (UK).

Close similarities between the phragmoteuthid pro-ostracum and the likewise three-lobed gladius of the vampyromorph *Loligosepia aalensis* from the Toarcian Posidonienschiefer of Holzmaden (Germany) have led many authorities to derive a gladius from a phragmoteuthid phragmocone (Naef 1922: p. 32; Jeletzky 1966: p. 8; Donovan 1977: p. 43; Doyle et al., 1994: p. 4; Toll 1998: p. 55).

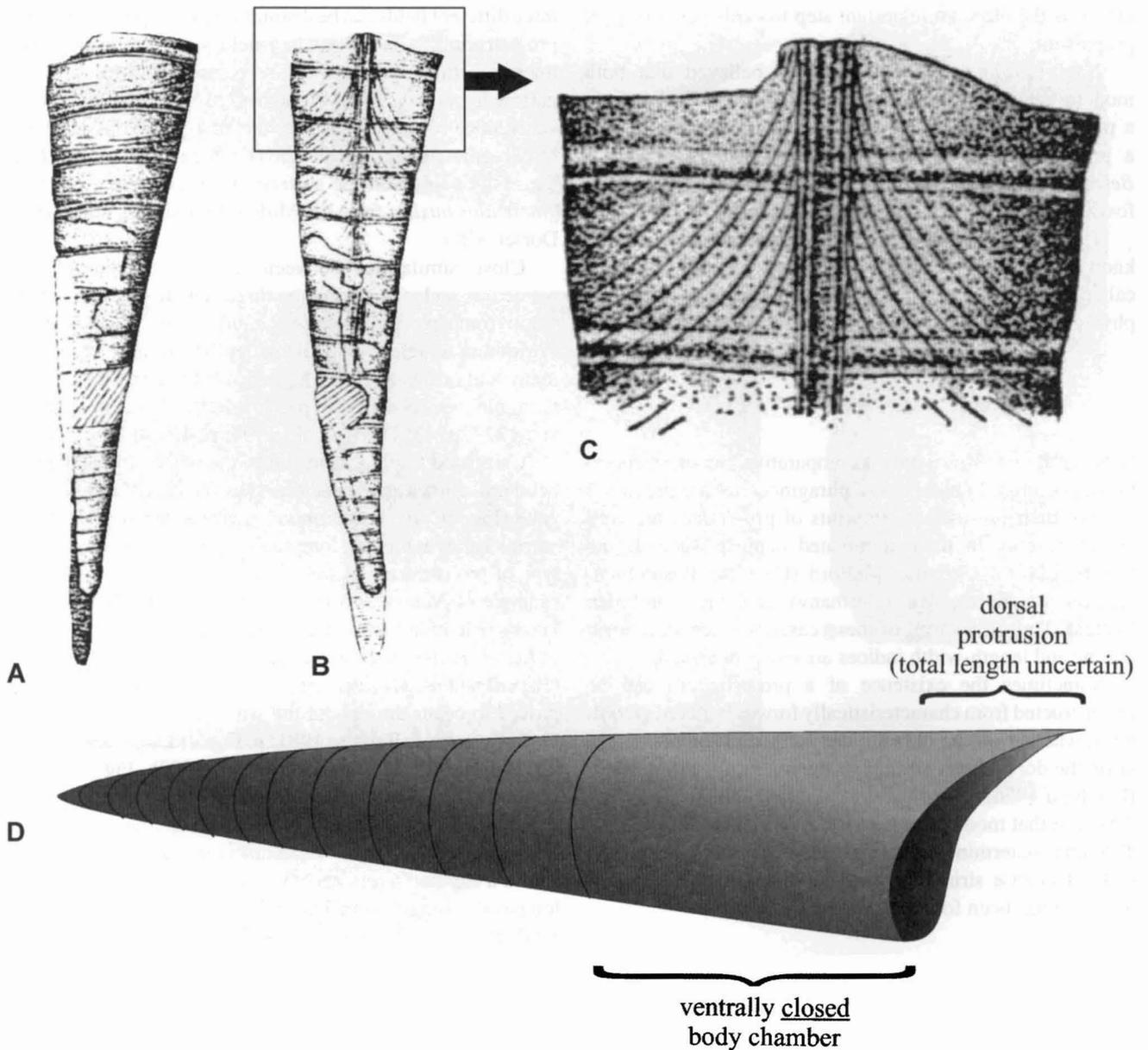
Compared to phragmoteuthids, the belemnite and diplobelid pro-ostraca are characterised by the lack of a hyperbolic zone (Fig. 2C–F). Furthermore, lateral fields are reduced to narrow bands exhibiting longitudinal growth increments. This type of pro-ostracum is well documented from a Hettangian example of *Nannobelus* (Hölder 1973), probably the oldest known belemnite pro-ostracum (this depends on the true age of *Eobelemnites caneyensis*). Quite similarly built pro-ostraca (*Passaloteuthis*, *Megateuthis*, *Hibolithes*, *Acanthoteuthis*) are proved to occur throughout the whole Jurassic (Crick 1896: Pl. 9; Engeser & Reitner, 1981: p. Fig. 1; Doguzhaeva et al., 2002: p. text-fig. 1; Doguzhaeva et al., 2003b: Fig. 7). Cretaceous records of belemnite pro-ostraca are scarce.

The Toarcian *Chondroteuthis wunnenbergi* provides a typical diplobelid pro-ostracum (Fig. 2E, F). This taxon shows a comparatively narrow pro-ostracum that is twice as long as its phragmocone length (Bode 1933: Pl. 11; Jeletzky 1966: Pl. 7, Fig 7; Doyle & Shakides 2004: text-fig. 3; Fuchs 2006: Pl. 10, Fig. C, D). Distinct median ribbons reinforce the pro-ostracum. Lateral ridges correspond to the lateral fields of belemnites. Similar rod-like pro-ostraca are also known from Early Cretaceous *Pavloviteuthis* and *Vectibelus* (Jeletzky 1981). As a result of narrowing, the belemnite pro-ostracum takes up only two-thirds, the diplobelid even only one-third of the total phragmocone circumference.

## PROOSTRACA IN SPIRULIDS AND SEPIIDS

*Spirula* and *Sepia* are the only living representatives of the Decabrachia that have kept a buoyant phragmocone. The body chamber of *Spirula* is closed, i.e. a pro-ostracum is definitely absent. The cuttlebone of *Sepia* is sometimes called pro-ostracum (Hölder 1973: p. 64), but this is a terminological mistake, because the morphological chain "*Ceratisepia* – *Belosepia* – *Sepia*" markedly demonstrates that shell reduction includes the entire ventral phragmocone (not only the ventral body chamber as in belemnites). The last formed (youngest) septum is attached to the anteriormost edge of the dorsal conotheca (dorsal shield).

Although Naef (1922: Fig. 12, 14, 21, 23, 30) reconstructed pro-ostraca in Cenozoic sepiids and spirulids such as *Belosepia*, *Beloptera*, *Belemnosella*, *Belemnosis* and *Spirulirostra*, not a single fragment of a pro-ostracum has ever been found (despite a great number of Cenozoic specimens).



**Fig. 3** *Groenlandibelus rosenkrantzi* (Spirulida, Maastrichtian, East Greenland). A) Lateral view (after Rosenkrantz 1946). B) Dorsal view. C) Close-up of B). Forward curved growth increments meet in the mid-dorsal line. D) Reconstruction of the phragmocone. Note that the body chamber is long and tubular by contrast to belemnoids.

Owing to anterior projections of the guard-like sheath, Naef (1922) concluded that a pro-ostracum must have existed. In this case pro-ostracal growth lines should be detectable either on the inner surface of the sheath or on the outer surface of phragmocones. But these are unknown, either on isolated sheaths or on isolated phragmocones (Jeletzky 1969, Janssen & Müller, 1984, Fornasiero & Vicariotto, 1997, Monks & Wells, 2000), Jeletzky (1969: Fig. 2, 3) considered belemnoids, spirulirostrids, beloapterids and belosepiids therefore as pro-ostracum-less and reconstructed their phragmocones with a closed body chamber.

Haas (1997: Fig. 3; 2003: Fig. 6) assumed a broad pro-ostracum in *Vasseuria* (Eocene). On the basis of an internal mould of an empty alveola, he recognized pro-ostracal growth lines on the inner chamber surface. However, present author's own observations on *Vasseuria* phragmocones cannot confirm this assumption. The inner chamber surface is smooth without growth lines. Pro-ostracal growth lines are

usually found on the inner surface of the guard-like sheath and/or on the outer surface of the conotheca.

Forward-curved growth increments on the dorsal conotheca of Late Cretaceous *Groenlandibelus rosenkrantzi* and *Naefia neogaeia* indeed show signs of a narrow dorsal projection (Fig. 3A–D). Birkelund (1956: p. 17), Jeletzky (1966: p. 94), Doyle (1986: p. 136), and Haas (1997: p. 64, Fig. 1) interpreted the projection as a pro-ostracum. However, compared to the belemnitid and diplobelid pro-ostracum neither lateral fields with longitudinal growth lines nor a parabolic median field are visible. Instead, hyperbolic growth increments on the dorsolateral and dorsal conotheca meet at the mid-dorsal line and appear to form a median keel. Owing to the striae density, the length of this protrusion cannot be determined.

According to the definition of Jeletzky (1966), the existence of a pro-ostracum presupposes a ventrally opened body chamber. Previously, body chambers had never been recorded in specimens of *Groenlandibelus* or *Naefia* (Fuchs

2005, 2006: p. 46). However, Bandel & Stinnesbeck (2005) recently presented the first specimen of *Naefia* from the type locality (Quriquina Formation, Chile, Maastrichtian) with a distinctly long and ventrally closed body chamber (see this volume). This observation excludes the presence of a “true” pro-ostracum. It is therefore also likely to assume a closed body chamber in *Groenlandibelus* (Fig. 3D).

Evidence of a pro-ostracum is also unknown in *Naefia kabanovi* and *Adygeya adyensis* (both Early Cretaceous), *Kostromateuthis* (Late Jurassic) and *Shimanskya* (Late Carboniferous), the oldest presumed representatives of the Decabrachia (Doguzhaeva 1996, 2000, Doguzhaeva et al., 1999).

## DISCUSSION

Many authorities favoured a Late Triassic origin of neocoleoids (Vampyropoda + Decabrachia) within a belemnoid rootstock that possessed a distinct pro-ostracum. Moreover, the gladius is believed to represent the organic components of a pro-ostracum-bearing phragmocone (Toll 1998: p. 56). This idea is partly based on *Plesioeteuthis*, a Late Jurassic (Tithonian) coleoid from the Solnhofen Plattenkalks. *Plesioeteuthis* is often considered to be a stem-oegopsid (Young et al., 1998, Vecchione et al., 1999), because its comparatively narrow gladius is very similar to ommastrephid gladii. The discovery of ten arms including a pair of tentacular arms (an unambiguous decabrachian character) would confirm this assumption. Naef (1922: Fig. 42) speculated about the existence of tentacular arms in a specimen from the Munich collection, but the present author’s own re-investigations of Naef’s specimen clearly support those made by Bandel & Leich (1986: p. 135), who rejected the presence of tentacular arms in this specimen (Fuchs 2006: Pl. 22, Fig. D). A comprehensive analysis based on 150 specimens of *Plesioeteuthis* yielded dozens of more or less well-preserved arm crowns, none of which displayed more than eight arms (Fuchs et al., in press). Despite the remarkable preservation in the Solnhofen Plattenkalks, a ninth or tenth arm has never been found. Coleoid researchers, who questioned vampyropod affiliations, argued that tentacular arms might have been lost during sinking down of the carcass or hidden within their pouches (Kear et al., 1995: p. 125). According to Kear et al., (1995) sinking of a dead squid usually causes the tentacles to slide from their pouch. Stellate imprints of arms in association with *Plesioeteuthis* clearly demonstrate that the carcasses met the sea-floor in an oral-end down position, and they never show more than eight arms. This fact, together with the combined presence of cirri and interbranchial web, makes vampyropod affiliations plausible.

Apart from *Plesioeteuthis*, the search for “fossil teuthids” has also focused on the Middle Jurassic (Callovian) *Mastigophora brevipinnis*. Vecchione et al., (1999) recognized filamentous appendages in this taxon and interpreted them as tentacular arms. Indeed, a specimen from La Voulte-sur-Rhone (Callovian), which is very similar to *Mastigophora*, shows an elongated arm pair, but this is without doubt a dorsal arm pair (Fuchs 2006: p. 74, Pl. 24, Fig. C). Haas (2002: p. 344) interpreted the filamentous structures as cirri. As postulated in Fuchs (2006: p. 74), elongation of dorsal arm pair is common in fossil (*Vampyronassa*, *Gramadella*, *Trachyteuthis*)

and recent vampyropods (Nesis 1987). Konservat-Lagerstätten such as Christian Malford, La Voulte, Solnhofen and especially the Late Cretaceous Plattenkalks (“fish beds”) of Lebanon certainly possess the potential to conserve complete arm crowns. As long as an elongated arm pair in an unambiguous ventrolateral position cannot be shown among dozens of preserved arm crowns, not a single decabrachian soft-part character is yet known in the fossil record.

Hence, “fossil teuthids” (whether loliginids or oegopsids) are still unknown, since they are apparently not preserved in Cenozoic deposits. Therefore, only a handful of pre-Cenozoic Decabrachia have been described without any information about their soft-part morphology: *Shimanskya* (Late Carboniferous), *Kostromateuthis* (Late Jurassic), *Adygeya* (Early Cretaceous), *Naefia* (Early – Late Cretaceous), *Groenlandibelus* (Late Cretaceous) and *Ceratisepia* (Late Cretaceous). Each of them is characterised by a more or less straight phragmocone and, as already suggested above, with no evidence of a pro-ostracum that can be derived from a belemnoid ancestor. The Carboniferous *Shimanskya* is variously treated as a stem-decabrachian (Fuchs 2006: p. 29) or a stem-spirulid (Doguzhaeva et al., 1999). In any case, derivation of the Decabrachia from phragmoteuthid-like ancestors seems also stratigraphically improbable, because *Shimanskya* is older than the Permian *Permoteuthis*, the earliest phragmoteuthid with a distinct pro-ostracum.

With regard to these considerations, evidence for the existence of a pro-ostracum in the Decabrachia rests on the ambiguous “pro-ostracum” of *Groenlandibelus* and *Naefia*. According to Fuchs (2006: p. 46), their so-called “pro-ostracum” more likely indicates positive allometric dorsal growth of a tubular (i.e. closed) body chamber. If early Decabrachia never exhibited a “true” pro-ostracum (in the sense of a ventrally opened body chamber) in their body plan, it appears unlikely that they derive from phragmoteuthid belemnoids. Consequently, the origin of “teuthid” gladii is still difficult to explain. Young et al., (1998: p. 409) stated: “...if myopsids belong on the sepioid line, then the gladii probably have evolved at least four times (*Vampyromorpha*, *Oegopsida*, *Myopsida*, *Sepiolidae*), and the problem becomes even more complex. As most calcareous coleoid shells probably have a gladius buried within the structure, evolution of a gladius is probably not a difficult step.” This is not surprising if one considers that the gladius is a product of the shell sac epithelium (Toll 1998: p. 56). Fuchs (2006: p. 18) suggested that the belemnoid pro-ostracum is dominated by the organic periostracum, the initial matrix of the mollusc shell for subsequently deposited calcareous layers. In this context, a gladius simply evolves through decalcification of a cephalopod phragmocone, whose ventral side is partly reduced. Ventral opening of a long body chamber leading to a vampyropod gladius is only one possibility to reduce parts of the ventral phragmocone.

The sepiid lineage developed differently. The morphological chain *Ceratisepia* – *Belosepia* – *Sepia* clearly demonstrates the evolutionary pathway that has modified the sepiid phragmocone (cuttlebone). A progressively vaulted phragmocone in combination with obliquely positioned septa reduced the ventral phragmocone length (Fig. 4A). In *Sepia* the visceral mass became situated below the flattened and ventrally opened phragmocone. Decalcification of a modern cuttlebone with acetic acid leaves behind a purely

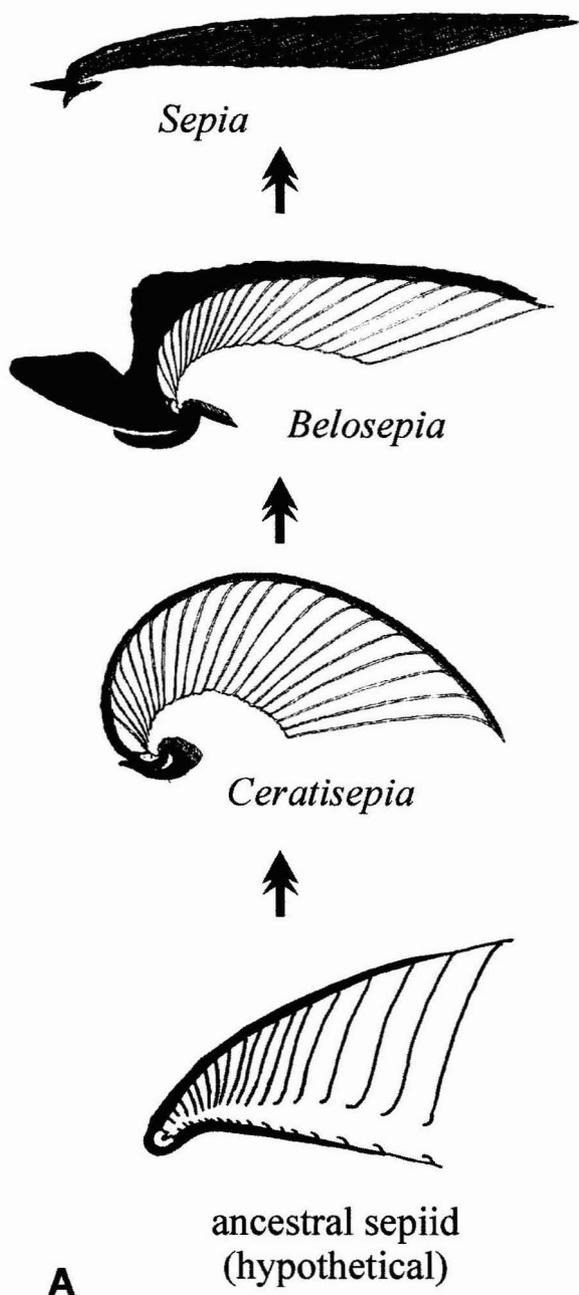


Fig. 4 A) Evolutionary development of the sepiid cuttlebone. B) The cuttlebone of recent *Sepia spec.* after decalcification with acetic acid.

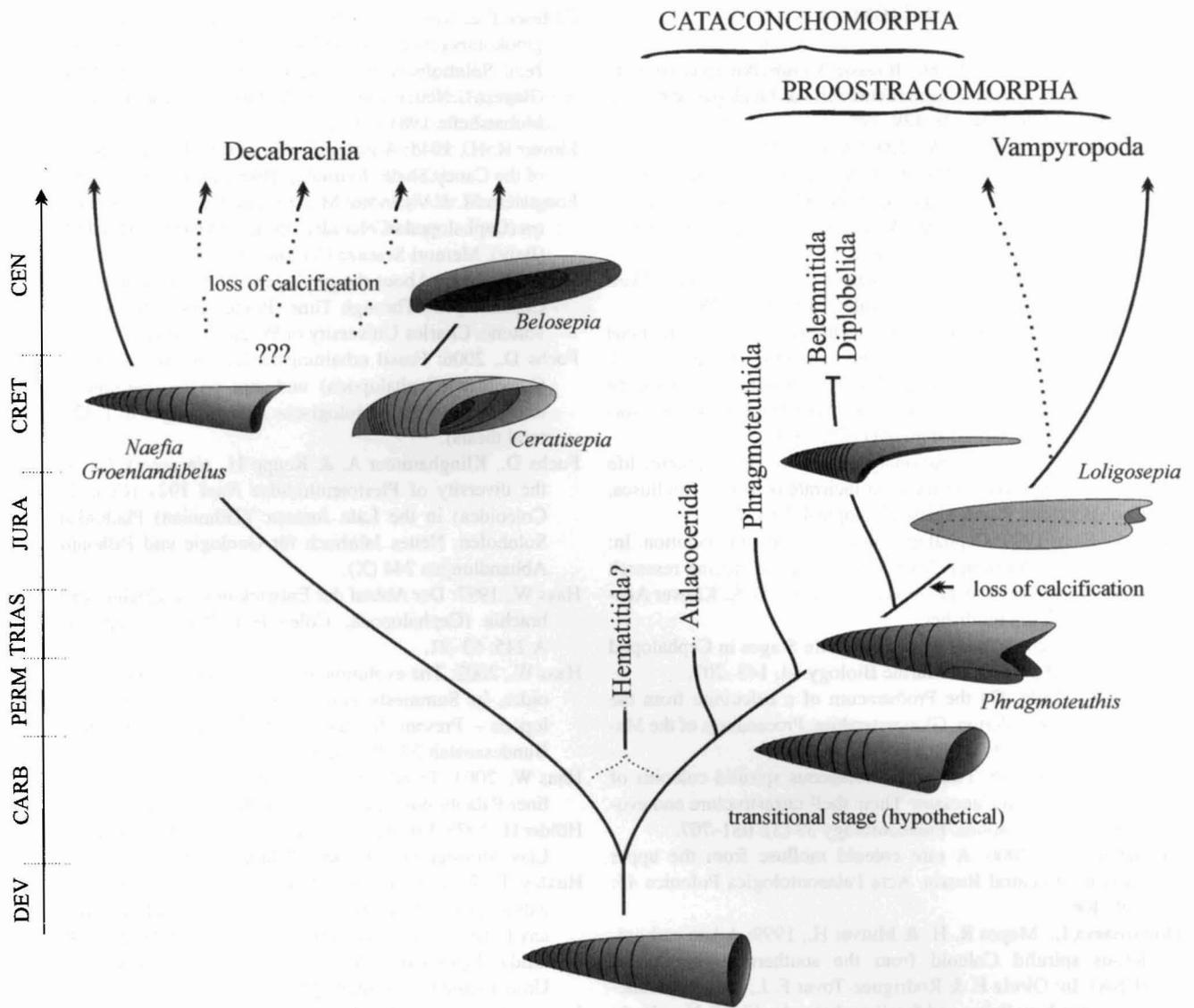
organic structure (the periostracum) that is very similar to a “teuthid” gladius (Fig. 4B). Such a scenario is also conceivable in early “teuthids”. In this case the gladius would be the result of a reduction of the entire ventral phragmocone wall rather than a ventral opening of the body chamber.

Haas (1997, 2003) also favoured a convergent development of a pro-ostracum. He regarded the Eocene *Vasseuria* as a primitive loliginid. *Vasseuria* possessed a straight phragmocone enveloped by a guard-like sheath. The presence of an oval primordial shell as well as oblique septa implicates sepiid affinities. Haas (1997, 2003) assumed a very long pro-ostracum, which is already present in embryonic stages. Although the evolutionary development of this presumed pro-ostracum is not clear (as already mentioned above, the observations by Haas need further confirmation), origin of

early “teuthids” during Cenozoic times is likely, because some recent oegopsid teuthids still have kept rudimental septa, while others show rudiments of a guard-like sheath (Toll 1998, Haas 2003). This is another striking argument against oegopsid relationships of the Late Jurassic *Plesio-teuthis*, because in the light of this fact, one should expect also a septated conus and/or at least remnants of a rostrum in this taxon. As these structures are obviously absent, *Plesio-teuthis* is hardly a precursor of living oegopsids.

## CONCLUSION

On the basis of the present fossil record, evidence about pro-ostraca (in the sense of a ventrally opened body chamber) is



**Fig. 5** Phylogeny of the Coleoidea inferred from the phragmocone development. Decabrachia and Vampyropoda reduced their phragmocones in two different ways. A “true” pro-ostracum (in the sense of an opened body chamber) is developed only in the vampyropod lineage, whereas in the decabrachian lineage ventral shell reduction is realised by a vaulted phragmocone and tilted septa. Based on this scenario, the loss of calcification (= development of a gladius) occurred independently. Nevertheless, the origin of the oegopsid, myopsid and sepiolid gladius remains eventually open (for a more detailed phylogenetic tree including apomorphies and plesiomorphies see Fuchs 2006).

scarce if not absent in decabrachian precursors. It has been shown that reduction of ventral parts of the phragmocone happened in at least two different ways (Fig. 5): 1) ventral opening of the body chamber (belemnoids) and 2) vaulting of the entire phragmocone in combination with tilted septa (sepiids). This observation suggests that the loss of secreting calcareous shell material (= development of a gladius) occurred independently in Vampyropoda and Decabrachia (and probably also independently in Oegopsida, Myopsida, Sepiolida). However, the origin of the decabrachiate types of gladii remains obscure, despite the very useful approaches of Haas (1997, 2003).

Nevertheless, assuming the lack of a “true” pro-ostracum in the decabrachian body plan greatly impacts the coleoid phylogeny. Because the derivation of a vampyropod gladius from *Phragmoteuthis*-like ancestors is morphologically and stratigraphically well established and widely accepted, a sister-group relationship between Vampyropoda (Ooctabrachia + Vampyromorpha) and Decabrachia is not beyond any doubt. Since belemnoids were proved to have possessed

sucker-homologous organs, the monophyly of neocoleoids was weakened anyway (Donovan & Crane, 1992). This is furthermore in accordance with Boletzky (1992, 1999, 2003), who repeatedly suggested a paraphyletic origin of the Neocoleoidea, for different arm modifications in Decabrachia and Vampyropoda must have been achieved in two transformational steps. On the other hand, a sister-group relationship between pro-ostracum-bearing belemnoids and Vampyropoda appears plausible (Fig. 5). Because aulacocerids and hematitids retained a closed body chamber in contrast to phragmoteuthids, belemnitids and diplobelids, the taxon “Belemnoidea” is a paraphylum, too. In Fuchs (2006: Fig. 4.1–1) Aulacocerida, Hematitida, Belemnitida, Diplobelida and Vampyropoda were combined as Cataconchomorpha. The presence of a closing membrane establishes this monophylum. Phragmoteuthida, Belemnitida, Diplobelida and Vampyropoda constitute the taxon Proostracomorpha, which is characterised by the development of a pro-ostracum.

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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. The cephalopods were caught in 27 trawls carried out in March 2002, including two trawl series of 4 tows at four discrete depth levels during day and night times, using a commercial fishing gear. Fishing depths ranged between 0–1000 m. A total of 28 cephalopods species belonging to 15 families were identified; the samples were 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*, *Abralia*, *Pterygioteuthis* and *Pyroteuthis*). The families in highest number and frequency of occurrence, were Pyroteuthidae and Enoploteuthidae with a relatively low diversity (3 and 2 species, respectively). Cephalopods concentrated in deeper waters during the day. The two fishing series let us verify the vertical migration of several cephalopod species. Both, the number of species (from 13 to 20) and total number of specimens (from 44 to 91) were larger for the night hauls. The later suggests a considerable potential of the technique used to study cephalopod populations.

**Key words:** Cephalopods, bathymetrics distribution, fishing gear, Central-eastern Atlantic

## INTRODUCTION

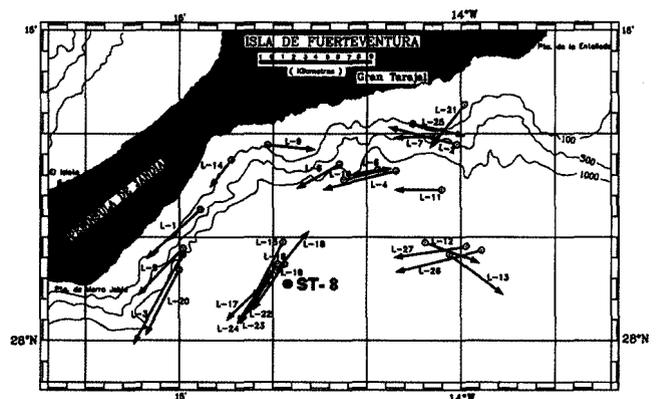
Research on pelagic cephalopods off Canary Islands is scarce. Previous studies were carried out during the 60's and 70's on board the *Sond Cruise* and *R.R.S. Discovery* (Clarke, 1969; Clarke and Lu, 1974); recent studies were carried out through the analysis of the stomach contents of large predators (e. g. Hernández-García, 1995; 2002) as they consume cephalopods; and, some short notes have been published on stranded or accidental catches of one specimen (e. g. Lozano, 1991).

In previous fishing surveys focused on the evaluation of fish pelagic resources around Canary Islands (Bordes et al., 1997), several cephalopod species were caught. The experiment presented in this paper was planned as a complement of the research program on the analysis and evaluation of the fish pelagic resources, a research financed by the Fisheries Department of the Canary Islands Government (Viceconsejería de Pesca del Gobierno de Canarias) which allowed us to work on cephalopods off Canary Islands.

The aim of this work was to determine and study the pelagic cephalopod species inhabiting around these islands, with emphasis on those species found in the epipelagic, mesopelagic and the upper batipelagic layers. The possibility to develop fishing trawls with commercial fishing gear at different depth levels was considered as an important opportunity to evaluate the viability to study the vertical migration of cephalopods.

## MATERIAL AND METHODS

Between the 4–18<sup>th</sup> March, 2002, in South-eastern waters off Fuerteventura (Central-eastern Atlantic; Fig. 1), 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



**Fig. 1** Map of the southeast of Fuerteventura (Canary Islands) showing the position of the trawls and the hydrographical station N° 8.

**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	Hour	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

**Table 2.** Cephalopods caught during March 2002 (*BOCAINA-0302*). N is the percentage in number and F the frequency of occurrence (h = head, m = mantle).

Species	N (%)	F (%)	Size range (mm)	Specimens identified from pieces
<i>Spirula spirula</i>	7.29	33.33	7–37	–
<i>Heteroteuthis dispar</i>	4.47	29.63	13–22	–
<i>Chiroteuthis v. veranyi</i>	0.94	14.82	40–44	–
<i>Chiroteuthis joubini</i> (?)	0.47	7.40	–	1 (h)
<i>Chiroteuthis mega</i>	1.65	11.11	92–184	–
<i>Chiroteuthis</i> sp.	0.24	3.70	–	1 (1/2 arm crown)
<i>Belonella belone</i>	1.88	11.11	140–235	3 (m)
<i>Leachia (P.) atlantica</i>	2.82	25.93	50–84	1 (m)
<i>Abraliopsis pfefferi</i>	11.76	48.15	11–37	2 (h)
<i>Abralia veranyi</i>	15.53	37.04	17–43	–
<i>Histioteuthis c. corona</i>	0.71	11.11	11–36	–
<i>Histioteuthis</i> sp. (A)	0.94	11.11	8–19	–
<i>Joubiniteuthis portieri</i>	0.24	3.70	–	–
<i>Mastigoteuthis grimaldii</i>	0.47	3.70	–	–
<i>Mastigoteuthis</i> sp. (A)	2.36	22.22	47–108	4 (h)
<i>Idioteuthis hjorti</i>	0.94	3.70	61–68	1 (h)
<i>Octopoteuthis sicula</i>	0.47	7.40	71–95	–
<i>Taningia danae</i>	0.47	3.70	22–27	–
<i>Illex coindetii</i>	6.12	40.74	23–58	3 (m)
<i>Onykia carriboea</i>	0.24	3.70	–	–
<i>Onychoteuthis banksii</i>	0.47	7.40	37–58	–
<i>Ancistroteuthis lichtensteini</i>	0.47	7.40	14–42	1 (?)
<i>Pyroteuthis margaritifera</i>	1.88	14.81	10–45	1 (?)
<i>Pterygoteuthis gemmata</i>	33.18	48.15	14–28	2 (h)
<i>Pterygoteuthis g. giardi</i>	1.18	14.81	–	–
<i>Octopus vulgaris</i> (?)	0.24	3.70	5	–
<i>Haliphron atlanticus</i> (?)	0.24	3.70	3	–
<i>Vampyroteuthis infernalis</i>	0.47	7.40	27–34	–
Oegopsid cephalopods no identified	1.41	11.11	–	1 (m); 1 (h); 1 arm crown; 1 gladius; fins

(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

on board the R/V “*TALIARTE*” to the S/V ‘*La Bocaina*’” navigating in parallel [NAVIGATING IN PARALLEL]. 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

**Table 3. 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.**

CEPHALOPOD SPECIES ↓	Daylight sequence				Darkness sequence			
	15	16	17	18	19	22	23	24
<i>Spirula spirula</i>			7.14	37.5		11.11	21.74	
<i>Heteroteuthis dispar</i>		72.7			15.38	2.78	8.69	15.79
<i>Chiroteuthis</i> spp.				6.25		11.11	4.35	5.26
<i>Belonella belone</i>				25				15.79
<i>Leachia</i> (P.) sp.		9.09	21.42	6.25				
<i>Abraliopsis pfefferi</i>		9.09		6.25	15.38	2.78		10.53
<i>Abralia veranyi</i>	100		7.14			13.88		
<i>Histioteuthis c. corona</i>					7.69	2.78		
<i>Taningia danae</i>				12.5				
<i>Illex coindetii</i>		9.09	7.14		7.69		4.35	5.26
<i>Onykia carriboea</i>						2.78		
<i>Onychoteuthis banksii</i>						2.78		
<i>Ancistroteuthis lichtensteini</i>						2.78		
<i>Pyroteuthis margaritifera</i>			28.57			5.56	4.35	
<i>Pterygioteuthis gemmata</i>			21.42		53.84	25	34.78	26.32
<i>Pterygioteuthis g. giardi</i>			7.14					
<i>Vampyroteuthis infernalis</i>							4.35	
Other species				6.25		16.67	17.39	21.05
<b>N</b>	<b>3</b>	<b>11</b>	<b>14</b>	<b>16</b>	<b>13</b>	<b>36</b>	<b>23</b>	<b>19</b>

the depth levels 50, 200–225, 325–350 and 675–700 m during both daylight and darkness (Table 1). Depth distributions during daylight and darkness trawls were compared using the Chi-Square test. Also, catch data was matched with oceanographic, acoustic and meteorological recordings. All cephalopods, including free fragments, were considered. Dorsal mantle length (DML) was measured (in mm). Percentages in number and the frequency of occurrence were calculated for each of the species.

## RESULTS

### General results

A total of 425 cephalopods were caught. Some specimens were counted only from a free body parts (e.g. a head or a mantle), which did not belong to other cephalopods or fragments. A total of 28 species were identified (Table 2), belonging to 15 families and 3 orders. In general, all cephalopods were of small size 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*, *Abraliopsis*, *Abralia*, *Pterygioteuthis* and *Pyroteuthis*). Juveniles (near 6 cm DML) of some species have been caught (e.g. *Illex coindetii* and *Onychoteuthis banksii*) (Table 2). The most important families, in number and frequency of occurrence, were Pyroteuthidae and Enopteuthidae (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).

### Depth distribution and migration

The results presented herein are referred to the 8 tows (the two series) developed under controlled conditions and in

four discrete depth levels. 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 become 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 3).

b) the migration of several species toward the upper layers at night, which inhabited deep waters during the day-light; and the presence of new species at night in deeper waters (Table 3).

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 (Table 3).

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 increased from 41 to 78. Results of the Chi-Square analysis of the depth distributions in both daylight and darkness trawls showed they were significantly different ( $p < 0.05$ ,  $df = 3$ ). These results show that the technique and methods considered could be useful to study the distribution and migration of these cephalopod species.

The physical parameters did not show relevant structures with depth. The water column from a depth of 900 m presented a thermal stratification extended almost to the surface, and the surface mixed layer was shallow. The larg-

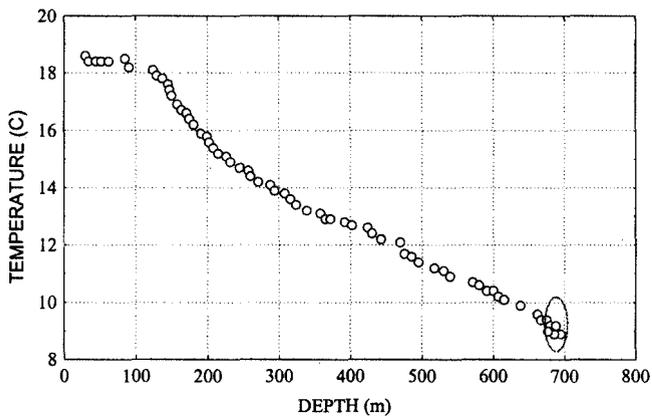


Fig. 2 Temperature curve obtained with data derived from the Scanmar Net Sounder during the daylight trawl N° 18 on 15 March 2002 southward Fuerteventura Island. The ellipse contains temperature data of the fishing stable period.

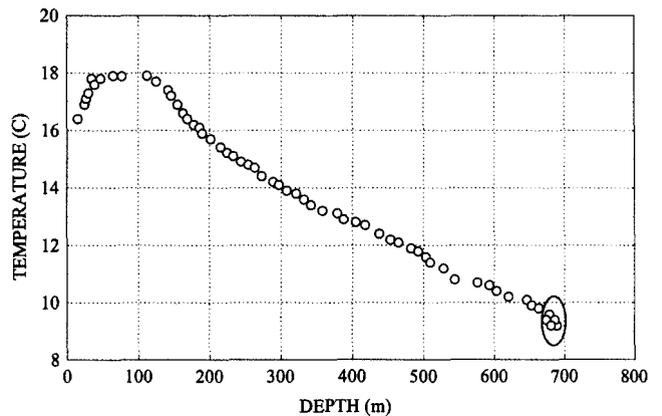


Fig 3 Temperature curve obtained with data derived from the Scanmar Net Sounder during the darkness trawl N° 24 on 17 March 2002 southward Fuerteventura Island. The ellipse contains temperature data of the fishing stable period.

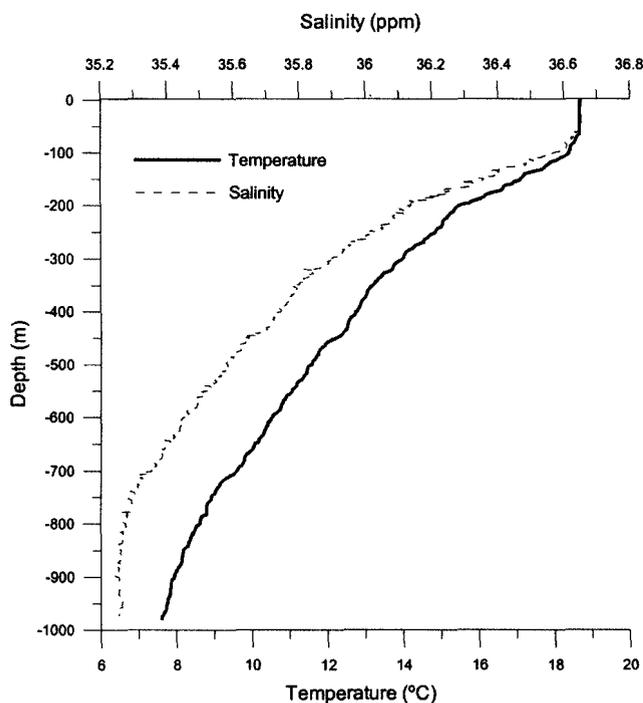


Fig 4 Temperature and salinity curves taken at 28°04' N and 14°08' W (Station 8, southward Fuerteventura) measured with a CTD.

est differences were observed in the surface layers (Figures 2, 3, 4 and 5). 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. However, important changes in vertical fauna distribution take place in the day cycle (Figures 6 and 7).

## 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 (e. g. large *Ommastrephes bartramii* or *Thysa-*

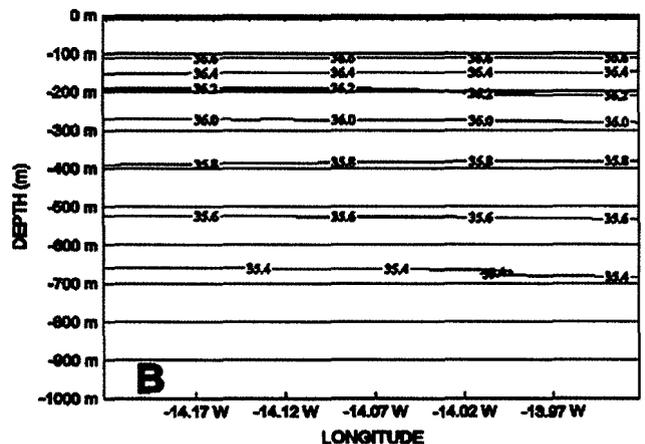
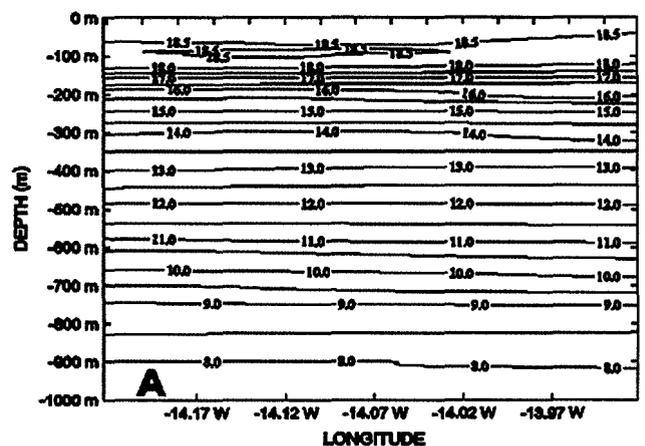


Fig 5 Vertical temperature and salinity profiles along a E-W transect in parallel 28°07' N derived from the CTD data.

*noteuthis rhombus*). The samples studied herein may be an intermediate representation between those obtained with RMT, IKMT, MOCNESS or Bongo nets (Clarke and Lu, 1974, 1975; Piatkowski, 1998), catches obtained with very large commercial nets (Rebik and Kukharev, 1998) and other gears (e. g. the common traps used in artisanal fisheries in Canary Islands) (Hernández-García et al., 1998), and samples from the stomach contents of large predators (Hernández-García, 1995) as well.

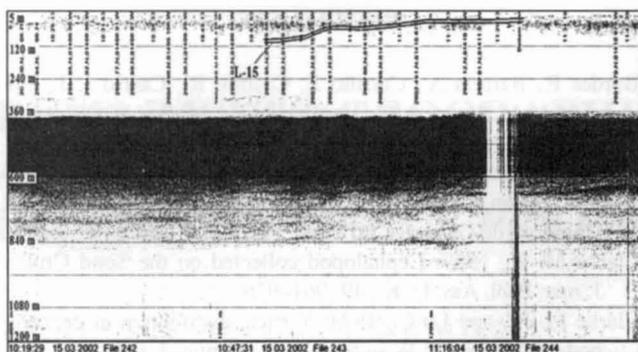


Fig 6 Echogram obtained during the daylight trawl N° 15 on 15 March 2002 southward Fuerteventura Island.

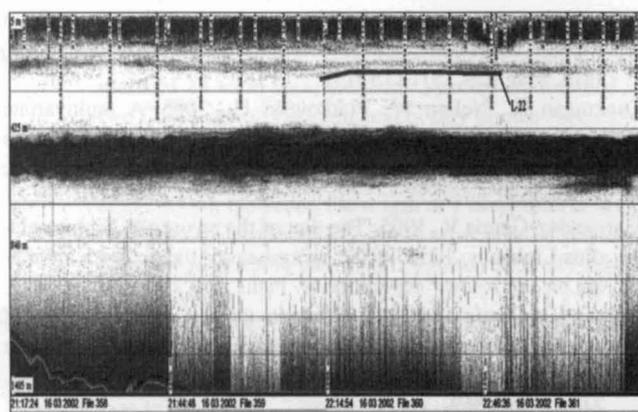


Fig. 7 Echogram corresponding to the darkness trawl N° 22 on 16 March 2002 southward Fuerteventura Island.

The species diversity ( $N=28$ ) was close to that obtained at  $30^{\circ}N-23^{\circ}W$  ( $N=29$ , Clarke and Lu, 1974) and smaller than the 40 species found at  $18^{\circ}N-25^{\circ}W$  (Clarke and Lu, 1975). However, it 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 of our study. The effort was considerably higher in that study, 76 tows and a total of 160 hours (we carried out 27 tows and no more than 30 hours). For a very close area at the southern end of Fuerteventura, a total of 18 species was identified (Clarke, 1969); the difference could be in part due to the mass effect of the island (see Sangrá, 1995). Diekmann and Piatkowski (2004) reported a close number of families and species (18 and 31 respectively) at approximately  $30^{\circ}N$  and  $28^{\circ}W$ , as well as the concentration of the species in deeper waters by day than at night.

In relation to the diel migration, the results may not be compared in detail with those reported by other authors as different techniques, a shorter depth range and lower fishing effort characterised our study. However, the results obtained for some of the species (e. g. *Belonella belone*) are coincident with observations done by those authors. Clarke and Lu's data (1974) are compared in Table 4 for those species which were captured in our samplings, as well; it can be appreciated that for most of the species the day and night vertical distribution is similar. Most of the differences are in the number of specimens, which could be as result of the different efforts in each work. If we take into account the fishing time, our catch rates are significantly larger than those reported by Clarke and Lu (1974). Also, it should be

Table 4. The Clarke and Lu's data (1974) are compared with data of the cephalopods caught in two fishing series (8 tows) during the BOCAINA-0302 (March, 2002) for those species present in both collections.

CEPHALOPOD SPECIES	Daylight sequence				Darkness sequence				
	This study DEPTH (m)	30-58	200-211	311-338	677-695	34-62	215-230	310-363	671-691
	Clarke & Lu, 1974	0-200	200-300	300-500	500-870	0-200	200-300	300-500	500-870
<i>Spirula spirula</i>				1	6 8	5	4	5	
<i>Belonella belone</i>				8* <sup>3</sup>	4 5			7* <sup>3</sup>	3 3
<i>Abrialopsis pfefferi</i>		3	1		1	2 70	1		2
<i>Histioteuthis c. corona</i>					3	1	1 1	3	
<i>Taningia danae</i>		3			2		1		
<i>Onychoteuthis banksii</i>		2		1	1	32* <sup>2</sup>	1		
<i>Pyroteuthis margaritifera</i>		16		4 5* <sup>1</sup>		12	2	1	
<i>Pterygioteuthis gemmata</i>				3		7 3	10	8	5
<i>Pterygioteuthis g. giardi</i>		9		1 22		18			
<i>Vampyroteuthis infernalis</i>					2* <sup>4</sup>			1	3* <sup>4</sup>

\*<sup>1</sup> = 4 squids caught by IKMT at depth ranges 410-(200) and 640-(400) m and 1 squid at 600-500 m by RMT.

\*<sup>2</sup> = 3 squids caught at 270-(100) m.

\*<sup>3</sup> = squids caught at depth range 400-500 m.

\*<sup>4</sup> = caught deeper than 900 m.

considered that tows were developed in a quite narrow layer (horizontal tows) as we were not searching for squids in the water column. The results for the families Onychoteuthidae, Enoploteuthidae and Pyroteuthidae are coincident with those reported by Diekmann and Piatkowski (2004) and Diekmann et al., (2006), as a diel vertical migration was registered for the last two families and the concentration of the representatives of the first in surface waters at night, and the last even these workers covered a shorter depth range (0–290 m).

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, we should keep in mind that there were no overlapping in 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). To the last could contribute the thermal stratification observed, which coincides with the data obtained by other workers (Rodríguez et al., 2006) in the Canaries-African coastal-transition zone. Therefore, we considered the catches mainly come from the planned strata or depth layers.

The aims of this research was to verify whether it is possible work on this topic using the technique employed rather than contribute to the knowledge on the vertical distribution and migration in cephalopods just at this moment. The potential of the technique used is high. On the other hand, 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 larger than expected.

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*Dedication. This work is dedicated to the memory of Enrique Hernández García (Rest In Peace).*

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# REMARKS TO GEOGRAPHIC DISTRIBUTION AND PHYLOGENY OF THE UPPER CRETACEOUS BELEMNITE GENUS *PRAEACTINOCAMAX* NAIDIN

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**Abstract:** According to present knowledges, the belemnite genus *Praeactinocamax* Naidin, 1964 (Belemnitellidae Pavlow, 1914) includes 14 valid taxa, another 7 species are retained in the open nomenclature due to a shortage of specimens known, and two Coniacian problematic and poorly known species – *P. aralensis* (Arkhangelsky) and *P. munjakensis* (Naidin) with strong affinities to genus *Goniocamax* Naidin need to be revised and reevaluated. After the revision of collected material from the East European Province, the palaeobiogeography and stratigraphic distribution were partly completed (Košťák 2004; Košťák et al., 2004). However, the origin of *Praeactinocamax* (and the Upper Cretaceous family Belemnitellidae in general) has not been exactly explained yet, some aspects of its phylogeny seem to be much more clear at present time, and the evolution in three biogeographic provinces (regions) is briefly summarized herein.

**Key words:** Upper Cretaceous, belemnites, *Praeactinocamax*, paleogeography phylogeny

## INTRODUCTION – THE GENUS ORIGIN

The origin of *Praeactinocamax* Naidin (i. e. Belemnitellidae Pavlow) 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, 1988, 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 and 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 (1997a) admitted a polyphyletic origin of the family Belemnitellidae. Some morphological differences between genera *Actinocamax* Miller and *Praeactinocamax* Naidin could prove this opinion. The first species of *Praeactinocamax* (*P. primus*) and *N. repentinus* have probably a common ancestor in the *Neohibolites* group.

## NOTES ON SYSTEMATICS, STRATIGRAPHY AND PALAEOBIOGEOGRAPHY

The guards of Upper Cretaceous (Cenomanian – Santonian) belemnite genus *Praeactinocamax* are of a medium size (65–115 mm), predominantly lanceolate in dorsoventral view. The maximum lateral diameter is situated mostly at one half of the guard. Ventral side is markedly flattened. Alveolar fracture has a low conical shape with a shallow pit in the centre.

The pseudoalveolus is oval to triangular in cross section. Ventral furrow is sometimes developed. Dorsolateral compressions and furrows are usually fully developed. Striation is usually present. Vascular imprints may be significant. Granulation is present rarely.

Christensen and Schulz (1997) raised the subgenus of *Praeactinocamax* Naidin, 1964 to generic rank and established its stratigraphic range at Cenomanian – Lower Santonian.

The geographic distribution of the genus is restricted to the Northern Hemisphere: North-, NW-, Central Europe, Baltoscandia, Russian Platform, Transcaspiian area, Northwestern Siberia; Tethyan Realm (SE France), Mediterranean Region (Turkmenistan, Tadjhikistan – Afghanistan border); North America, Greenland. (Fig. 1).

## NORTH EUROPEAN PROVINCE, EAST EUROPEAN PROVINCE, CENTRAL RUSSIAN SUBPROVINCE

The *North European Province* (NEP) was defined by Christensen (1976) on the base of belemnitellid distribution. Naidin (1978) recommended using a term *European Palaeobiogeographic Region* (EPR). Both terms actually mean a *biogeographic province*, including the *Central European Subprovince* (CES), *Baltoscandia*, and the *Central Russian Subprovince* (CRS). The CRS was also a part of the *East European Province* (EEP – persisting only during the latest Late Cenomanian to the beginning of the Coniacian – Naidin & Košťák, 2000; Košťák & Wiese, 2002; Košťák 2004, Košťák et al., 2004). The EEP was also a territory of *Praeactinocamax* speciation and radiation. Especially, the margins

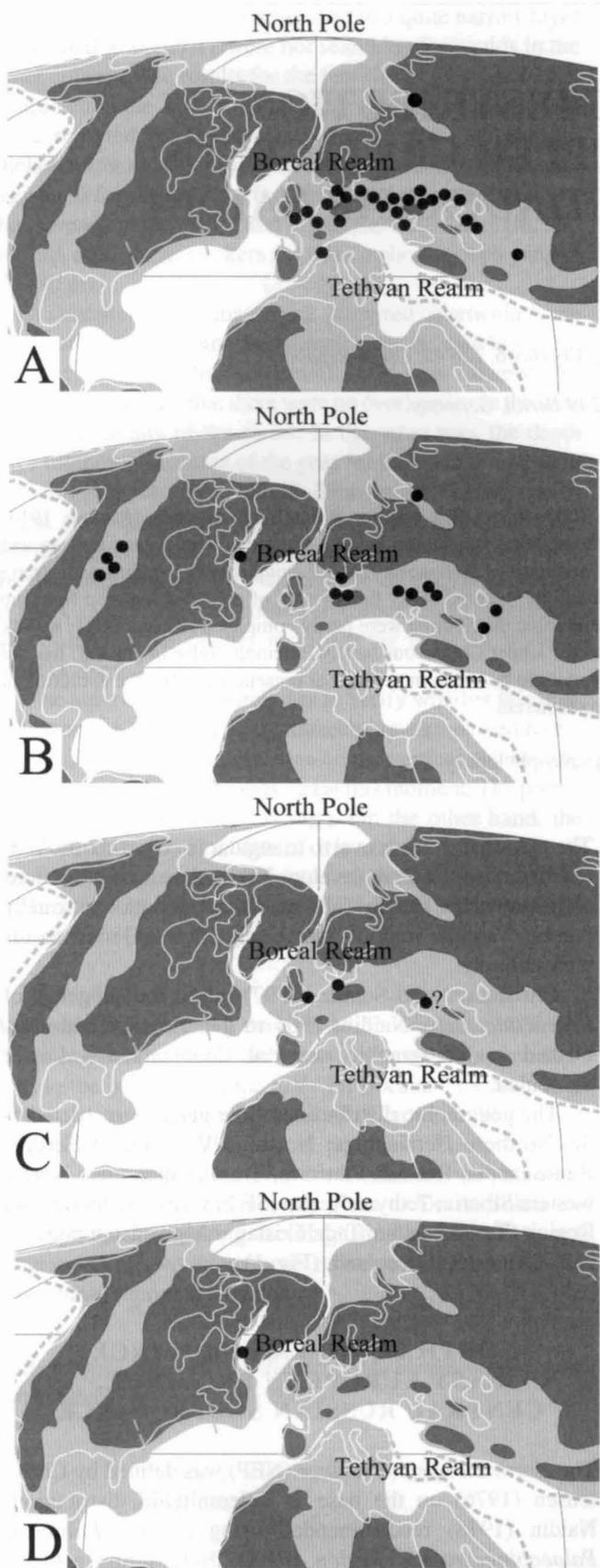


Fig. 1 Geographic distribution of *Praeactinocamax* A. Cenomanian, B. Turonian, C. Coniacian, D. Santonian, light grey – shallow seas, dark grey – lands.

of this province were probably also habitats of allopatric speciation, the CRS was an areal of the genus radiation.

*Praeactinocamax* showed a cosmopolitan distribution from the Mid- to the Late Cenomanian throughout the NEP

(EPR). The first belemnitellid, *Praeactinocamax primus* (Arkhangelsky) is widespread from the north Caspian Sea area in the east to Northern Ireland in the west. It occurs in the lower Cenomanian – at upper levels of the *Mantelliceras mantelli* Zone – and continues to lower parts of the *Mantelliceras dixonii* 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 occurrence of *P. plenus* is probably identical with the *Metoicoceras geslinianum* range zone in its the whole paleobiogeographic distribution area.

The rare and endemic lower Turonian species of *Praeactinocamax contractus* Naidin is widespread in the CRS. In spite of the opinion of Christensen (1974), *Praeactinocamax contractus* is considered to be an independent species especially with respect to its specific morphology – shorter and stout massive guards and poorly calcified alveolar fracture (Košťák 2004). *P. contractus* is probably a descendent of the *primus/plenus* evolutionary lineage – derived and specialized species, respectively. This species is known from the Volga River region and eastern Belarussia.

*Praeactinocamax triangulus* Naidin has recently been raised to the 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 margins of alveolar part (“fracture”) continued, a deeper pseudoalveolus formed, and the guard size increased (Košťák 2004).

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*. Some morphological similarities like the shape and size of the guard could prove this opinion. The main dissimilarities are observable in poorly calcified alveolar part.

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*, including also alveolar structure, is conservative and did not change during the Turonian.

Barskov & al. (1997) described microstructures of the “*Goniocamax*” rostrum from the Russian Arctic region (the Taymyr Region, Norilsk town vicinity). This Late Cenomanian-Early Turonian belemnitellid taxon definitely belong to *Praeactinocamax* (observation MK). However, this belemnite still lack systematic treatment and its position within the *Praeactinocamax* is still unclear.

Several “transitive forms” existed between *Praeactinocamax* and *Goniocamax* during the Turonian: *P. matesovae* (Naidin), *P. coronatus* (Makhlin), and *P. sp. 1* (Košťák 2004). Their morphology could be the result of convergence with *Goniocamax*. Some representatives of *Praeactinoca-*

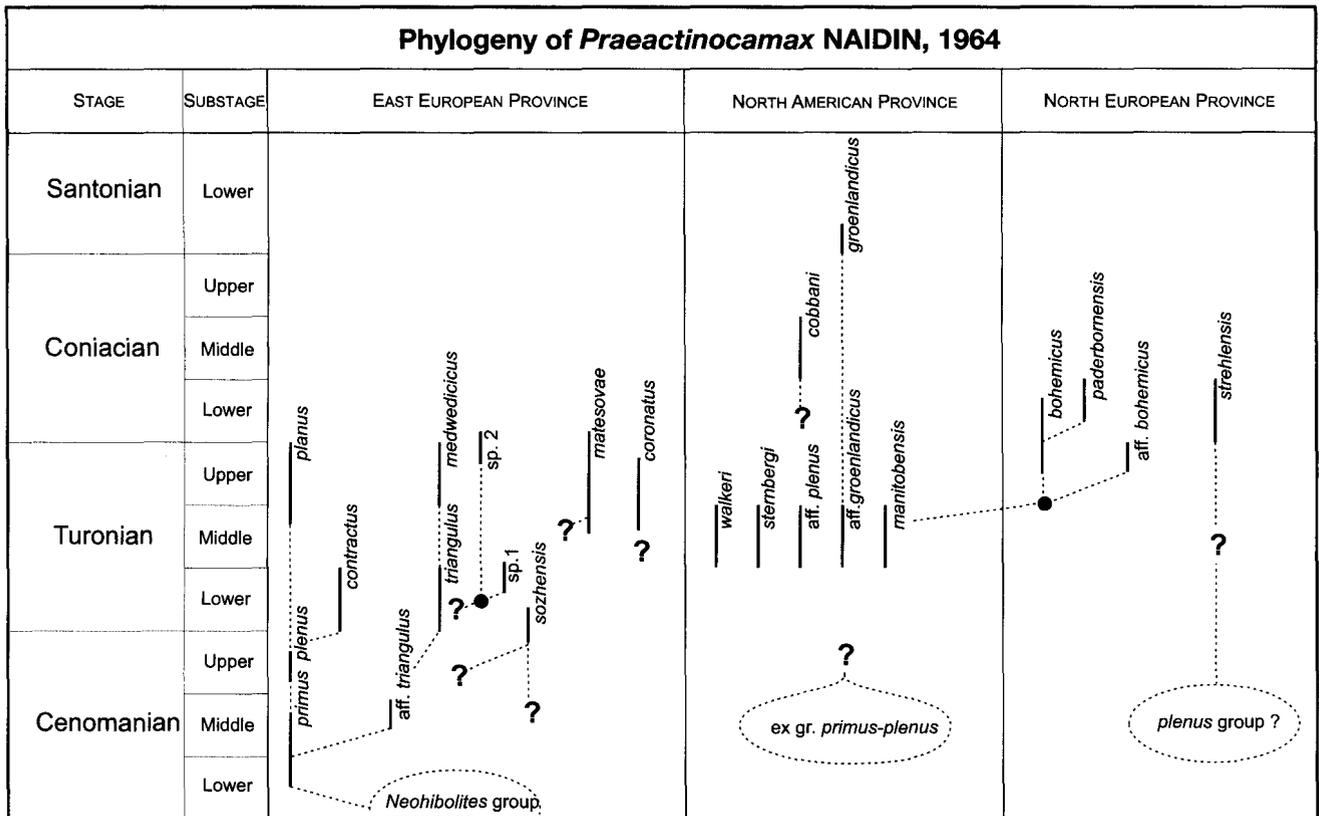


Fig. 2 *Praeactinocamax* species phylogenetic evolutionary lineages in the East European-, North American- and North European Provinces (Modified after Košťák 2004).

*max* resemble the first species of *Goniocamax*, especially by having a similar shape of the guard and by the depth of the pseudoalveolus. Some of them, respectively their ancestors were equally ancestors of *Goniocamax* (Košťák, in prep.). 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 NAP (*P. manitobensis* group – see below) and the rare upper Turonian belemnites from the CES and Baltoscandia. *P. matesovae*, *P. coronatus*, and *P. sp. 1* are very rare species of the CRS. They show a high endemism and diversity in this region. From Early Coniacian, the *Praeactinocamax* became extinct, and it was substituted by evolutionarily modern species of *Goniocamax*, and a bit younger *Goniot euthis* Bayle. However, this trend started in the latest middle Turonian and, especially, during the Late Turonian. In this time interval, we can observe the largest diversification, morphological modifications and convergence trends with earliest *Goniocamax* (*G. intermedius*, *G. surensis*). These trends probably were a response to rising of role of *Goniocamax* in the EEP ecosystems. Just after a “modern” *Goniocamax* origination (*G. christenseni*, *G. lundgreni*), the rapid fall of *Praeactinocamax* diversity is well documented (Figs. 1, 3; see also Košťák 2005).

Two problematic and poorly known Coniacian species – *P. aralensis* (Arkhangelsky) and *P. munjakensis* (Naidin)

show strong affinities to genus *Goniocamax* Naidin. They need to be revised and reevaluated, and included into *Goniocamax* on the base of morphological coincidence.

#### NORTH EUROPEAN PROVINCE, CENTRAL EUROPEAN SUBPROVINCE, BALTOSCANDIA

Turonian species of the NEP – *P. bohemicus* (Stolley), *P. aff. bohemicus* (Košťák 1996) and *P. paderbornensis* (Schlüter) – probably have their evolutionary roots in NAP (Košťák et al., 2004; Košťák 2004). Slightly different species of *P. strehlensis* (Fritsch) was figured by Fritsch et Schlönbach (1872) (for more details see Košťák 2004) and its origin is unknown. *P. bohemicus*, *P. aff. bohemicus* a *P. paderbornensis* are extremely rare in Europe, they were described from the Upper Turonian through the lower Coniacian deposits of the CES, ?England and Baltoscandia (*P. bohemicus*). They may prove a connection between the NAP and NEP in the Turonian (Košťák et Wiese, 2002; Košťák et al., 2004). Conversely, the NEP was completely isolated from the EEP during the whole Turonian stage.

#### NORTH AMERICAN PROVINCE

Christensen (1976) divided the North “Temperate” Realm (= Boreal) into the NEP (including CES) and NAP (including North America and Greenland) based on belemnite

(belemnitellid) distribution. Belemnitellids of the NAP are characterized especially by *Praeactinocamax* Naidin, ?*Actinocamax* Miller, and *Belemnitella* d'Orbigny.

Middle Turonian species of NAP – *P. manitobensis* (Whiteaves), *P. sternbergi* (Jeletzky), *P. walkeri* (Jeletzky), *P. aff. groenlandicus* a *P. aff. plenus* – are close to one another by having a similar alveolar fracture and partly also the shape of the guard (Jeletzky 1950, 1961). Cobban (1991) described also indetermined *Praeactinocamax* from Middle Turonian deposits of Central Western Montana. *Praeactinocamax* phylogeny is poorly recorded here. Middle Turonian *Praeactinocamax* group in the NAP may be derived from *primus/plenus* ancestors. Their evolution passed independently in the NEP and in the EEP. This group represents a typical parallel model of belemnitellid evolution.

*Praeactinocamax cobbani* (Christensen) is known from the middle Coniacian and *P. groenlandicus* (Birkelund) from the lower Santonian (Christensen 1993; Christensen & Hoch, 1983). *P. groenlandicus* is equally the last representative of *Praeactinocamax*, probably with a stock in North American Turonian species.

Seibertz and Spaeth (1995) described Upper Cretaceous belemnites from Mexico as *P. cf. primus* (Middle Cenomanian) and *P. manitobensis* (Early Turonian). Both taxa are, however, poorly preserved and especially the absence of alveolar part (significant for genus *Praeactinocamax*) does not enable exact determination. The single specimen of “*P. manitobensis*” known, represents another belemnite taxon (author's observation), surprisingly belonging probably to family Belemnopseidae, of which genera and taxa are virtually unknown from younger deposits than Cenomanian.

## CONCLUSIONS

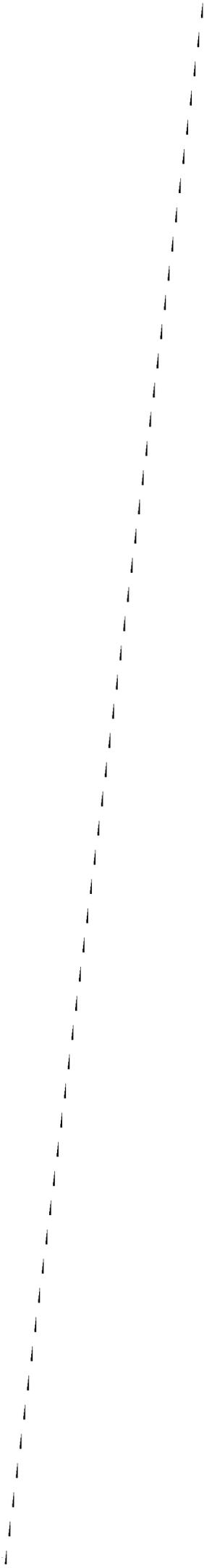
Species of genus *Praeactinocamax*, the first representatives of Upper Cretaceous family Belemnitellidae appeared for the first time in Early Cenomanian, probably such as descendents of some neohibolitid (family Belemnopseidae). They expanded from contemporeaneous area of Caspian Sea towards the West, and during two large Cenomanian belemnite events (i. e. *primus* and *plenus*) pervaded large epicontinental seas covering majority of European land from Russian Platform to Great Britain. Some of early praectinocamaxid reached also Northern Siberia and North American Western Interior Sea. The largest evolutionary events (i. e. speciation and radiation) happened in the Russian platform and adjacent areas. The *Praeactinocamax* evolution is well recorded here and some phylogenetic lineages are sufficiently documented from the Cenomanian through Coniacian time interval (see also Košťák 2004). The genus became extinct in Early Santonian by *Praeactinocamax groenlandicus*, the last species survived in the North American Province. This biogeographic unit was not influenced by commencement of *Goniocamax* (and *Goniot euthis*). From the earliest Coniacian, the *Praeactinocamax* was substituted in the NEP by *Goniocamax*, and a bit younger *Goniot euthis*, both direct ancestors of famous *Belemnitella* stock.

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# VISUAL HABITUATION 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 tested the animal's habituation towards a repeatedly presented prey-like visual stimulus. A plastic model of a lobster was presented outside the tank for 15 times for 15 seconds at the beginning of each minute of the experimental session. Sessions were repeated 6 h and 24 h after initial presentation. Eight out of ten animals habituated to the stimulus they could only visually inspect during all experimental sessions. The animals showed significant short-term effect in habituation between the first session (0 h) and the second session (6 h). However, no clear long-term differences between the first session (0 h) and the third session (24 h) were present. Our finding that octopuses do show strong short-term habituation but no long-term habituation is consistent with earlier findings, but in our study we used a purely visual stimulus. This set-up enables us to apply the already established technique of extra-cellular recording from the octopus' central nervous system to monitor the activity of the MSF (median superior frontal lobe) and VL (vertical lobe) during non-associative learning.

**Key words:** Invertebrates, cephalopods, octopus vulgaris non-associative learning, habituation

## INTRODUCTION

The acquisition of information about the environment and its changes is one of the principal tasks each organism has to face. Habituation, one of the most basic manifestations of behavioral plasticity, is defined as a decrease of response to a repeated stimulus (Thompson & Spencer, 1966). It has been extensively studied in whole animals, semi-intact animals and isolated cells of nervous tissue (Chase, 2002, Zaccardi et al., 2001, Mongeluzi & Frost 2000, Hawkins et al., 1998, Brown 1998, 1997). Studies on non-associative learning in cephalopod mollusks are scarce.

A study by Wells & Wells (1957) concentrated on the tactile habituation of blinded octopuses to repeatedly presented objects. They used metal cylinders and showed that the animals did have shorter and less intense contacts during repeated encounters with the objects. However, they also reported that non-blinded octopuses did not learn to habituate to objects by sight as they always approached an object that was dropped into their tank. These findings of the non-habituation of *O. vulgaris* towards visual stimuli need re-examining. Mather & Anderson (1999) not only investigated exploration and habituation, but also the interplay of exploratory behavior and object play. They showed that octopuses habituated to a stimulus they can explore using visual and tactile information. Habituation to a visual stimulus has been demonstrated in bay squids (Long et al., 1989), showing the decline of escape jets and ring patterns on the mantle with repeated presentation of a fish predator model. The squids showed dishabituation to the predator model after a threat stimulus. Angermeier & Dassler (1992) demonstrated visual habituation towards

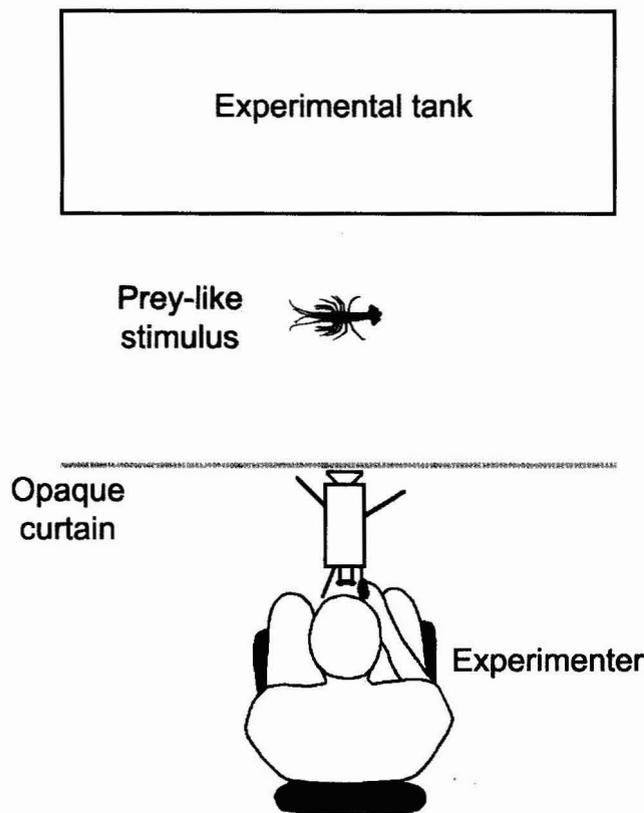
a crab-shaped model in *Eleodone cirrhosa*. They also showed the transfer of a learned inhibition to a later natural feeding situation. In addition to these studies, Byrne et al. (2004) gave a first description of habituation to a prey-like stimulus (crab) presented outside the tank. Byrne et al. (2004) tested for lateralization of eye use and reported visual habituation as a 'byproduct' in their study. Their experimental set-up was not rigorous enough to test a learning paradigm, as the human experimenters were visible for the octopus during the experiment. In addition the stimulus was moved directly by one of the two experimenters without a standardized pattern of movement. Given the small number of habituation studies, some of the critics of octopus work therefore drew the conclusion that octopus-learning research tried to run before it could walk (Boal 1993; Bittermann 1975).

In contrast to this, there have been numerous studies on learning and other cognitive abilities in the genus *Octopus* (for reviews see: Boal 1996, Hanlon & Messenger, 1996, Mather, 1995, Nixon & Young, 2003, Wells, 1978). However, learning studies in cephalopods were criticized (Bitterman, 1975, Boal 1996) for their lack of proper control and their techniques, which were often rough to the animals.

The aims of this study are threefold. The first aim is to show that octopuses can habituate to visual stimuli outside the aquarium. The second aim is to compare our findings to previous studies and to document the problems that arise using a less controlled protocol as criticized by Bitterman (1975) and Boal (1996). The third aim of this study is to develop a protocol for future electrophysiological investigation of learning and memory related processes in the octopus brain.

## MATERIAL AND METHODS

This study took place at the Department of Neurobiology at the Hebrew University in Jerusalem between March 2005 and September 2005. Subjects were 10 adult *Octopus vulgaris* obtained from local fishermen. Animals were 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 reacted to human presence in the room by approaching the front glass of its home tank it was transferred to the experimental tank situated in a different room. The animals were given a 24 h period to adjust to the new environment and were then tested. All sessions took place between 1100 and 2100 hours and were recorded with a digital video camera (Panasonic DVC30E). Thirty minutes before the start of each experiment the animals were visually isolated and the camera was positioned in front of the tank, but behind the curtain. While filming, an operator followed the movement of the octopus (Figure 1). The experimenter sat on a chair and used a monofilament line to pull up a small plastic lobster model (resembling *Homarus sp.*, 12.5 cm length) into the field of view of the subject.



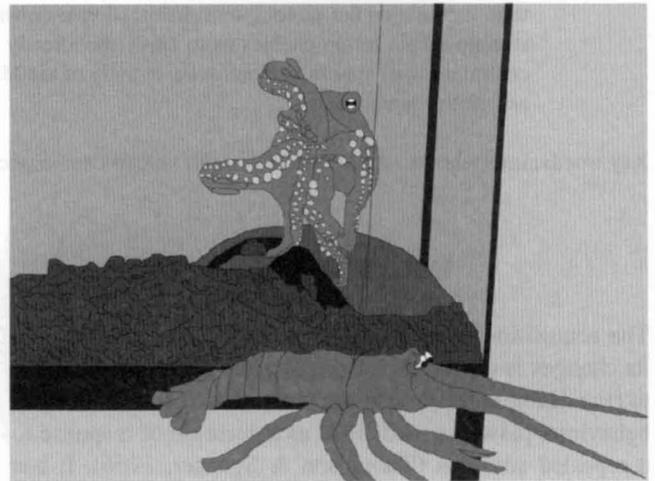
**Fig. 1** Experimental set-up, the stimulus was moved up and down using a clear monofilament line.

Each animal was tested three times for 15 min. During this 15-min period the plastic lobster was presented outside the tank for 15 s at the beginning of every minute. These 15-min testing periods were repeated twice, 6 h and 24 h after the initial presentation. For each presentation of the stimulus we recorded the time the octopus was out of his den and inspecting the stimulus. This classification of

inspective behavior is based on Byrne et al. (2004). Chi square tests were used to document differences within the experimental sessions (0 h, 6 h, 24 h). Data were then compared for differences in habituation across sessions using Wilcoxon tests. In order to show differences in habituation between the sessions, we divided each session (0 h, 6 h, 24 h) into three 5-min blocks. These blocks were then compared to one another using Friedman signed rank tests.

## RESULTS

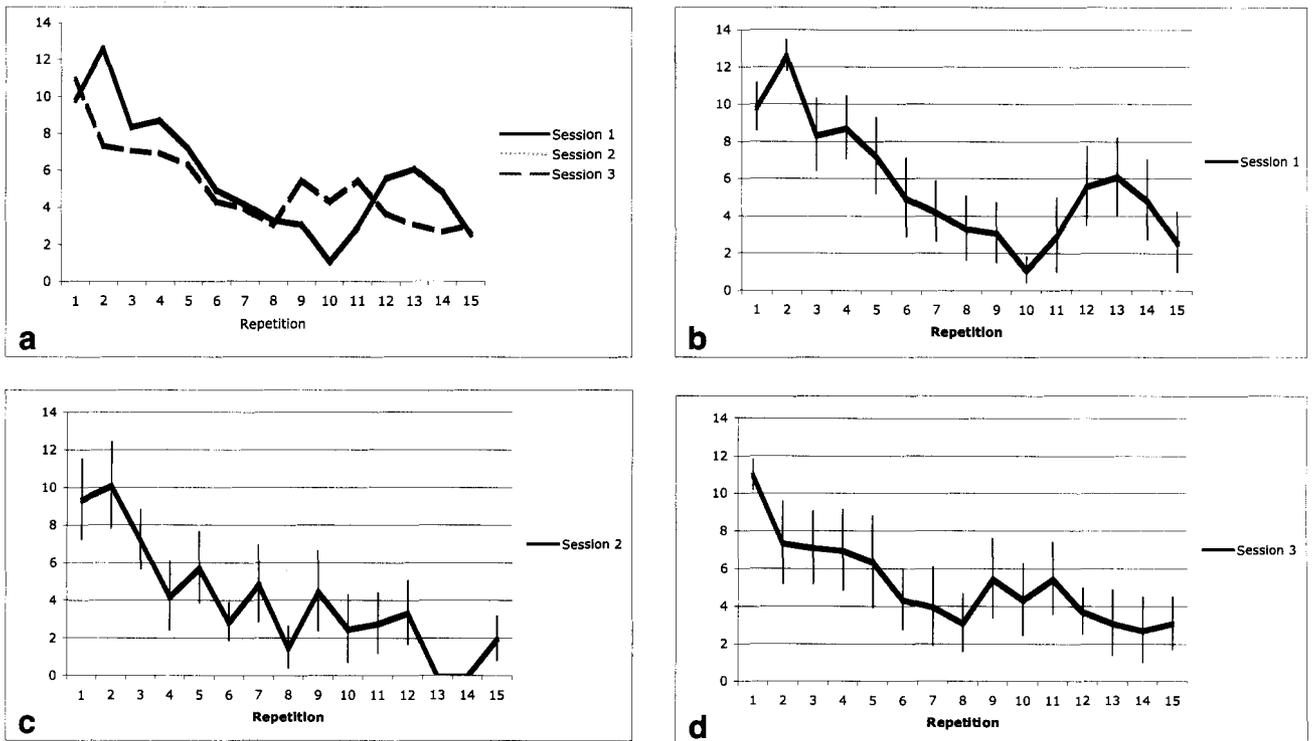
Eight out of the 10 experimental subjects showed behavioral response to the repeatedly presented stimulus. These 8 animals reacted to the initial presentations of the stimulus by leaving their house and approaching the front screen of the tank (Figure 2). In later presentations the animals either retreated to their den after initially approaching the stimulus or did not react to the stimulus at all. A Chi-square test showed



**Fig. 2** Screen shot of animal 2 trying to get hold of the prey-like stimulus.

significant habituation in each of the experimental sessions (0 h:  $N = 120$ ,  $\chi^2 = 221.86$ ,  $df = 14$ ,  $P = 0.0001$ ; 6 h:  $N = 120$ ,  $\chi^2 = 460.00$ ,  $df = 14$ ,  $P = 0.0001$ ; 24 h:  $N = 120$ ,  $\chi^2 = 218.25$ ,  $df = 14$ ,  $P = 0.0001$ ). The Figures 3 a-d show the performances of animals during the experimental sessions.

The amount of attentiveness decreased significantly in the second experiment (6 h) compared to the first (Wilcoxon,  $Z = -2.825$ ,  $P = 0.005$ ). However, there was no significant difference in attentiveness between the first and the third (24 h) presentation (Wilcoxon,  $Z = -0.675$ ,  $P = ns$ ). In the second session attentiveness was significantly lower than in the third experimental session (Wilcoxon,  $Z = -2.419$ ,  $P = 0.01$ ). Further statistical tests were carried out to document the differences in habituation within the experimental sessions (see Figure 3 a). Experiments were divided into three 5-min blocks, each of these blocks were then compared across the three experimental sessions. Notice that in the last 5 min (Figure 3 a) of the initial session (0 h) showed a significant increase in inspective behavior towards the stimulus compared to the later sessions (6 h, 24 h; see Figure 3 a;



**Fig. 3 a.** These graphs compares the decline in response during session 1 (0 h), session 2 (6 h) and session three (24 h). Individual sessions including error bars are shown in (b–d).

$N = 40$ ,  $\chi^2 = 10.344$ ,  $df = 2$ ,  $P = 0.006$ ). There were no significant differences in the process of habituation for the other two thirds of the experiment's duration (first 5 min:  $N = 40$ ,  $\chi^2 = 1.121$ ,  $df = 2$ ,  $P = ns$ ; second 5 min:  $N = 40$ ,  $\chi^2 = 1.213$ ,  $df = 2$ ,  $P = ns$ ).

## DISCUSSION

We were able to demonstrate that *Octopus vulgaris* does habituate to a stimulus that can only be visually explored. This finding contrasts earlier results by Wells & Wells (1957). Perhaps the findings of Wells & Wells (1957) were influenced by the barren tanks in which the octopuses were kept (Bitterman, 1975), because a stimulus poor environment can lead to an increase in exploration of novel stimuli (Toates, 1983).

In this study we showed that the only difference in the process of habituation was an increase of inspection behavior during the last five minutes of the first experimental session (0 h) compared to the same period of time in later sessions 6 h and 24 h. This and the fact that the overall decrease in inspective behavior was not significantly different between the first (0 h) and the last (24 h) session supports the findings by Byrne et al. (2004) that habituation was stronger within rather than across days of experiments. In the study by Mather & Anderson (1999), *Octopus dofleini* exhibited clear habituation towards the stimuli on the first day of the experiments. But on successive days the patterns of response were more complex and sometimes led to exploratory play. The similarities in habituation across days is interesting as the animals in Mather and Anderson's study (1999) had visual as well as tactile contact to the objects.

This raises the important question of how non-associative learning in the common octopus could be influenced by multi-modal sensory inputs. Further testing will be required to answer this question. The lack of clear long-term effects found in the present study might be a result of the life history of octopuses. In a study on habitat use, Mather (1991) reported that octopuses changed their small home ranges after periods of about 10 days. Although octopuses have the potential for long-term memory (Nixon and Young, 2003; Wells 1978) short intervals for habituation to stimuli can be more important for the animals than long-term ones in a quickly changing natural environment.

Although the general trend reported here and the one previously documented by Byrne et al. (2004) is the same, the habituation was considerably slower in the study by Byrne et al. This difference shows that increased activity outside of the animal's tank can alter the habituation process. Further studies will investigate different protocols in order to shed light on the differences in habituation between a permanently and a repeatedly presented stimulus. Therefore, the differences between this and earlier studies on non-associative learning in *Octopus vulgaris* show the importance of controlled conditions that were so often lacking in learning studies of *O. vulgaris*.

The possibility of combining a simple learning paradigm, like habituation, with a well established *in vivo* recording technique (Zullo, 2004) would enable us to get stronger insights on the neuronal bases of behavioral processes. One of the advantages showed in this study is the use of a stimulus located outside the experimental tank. This greatly simplifies methodological difficulties encountered when using a non-wireless recording technique. Monitoring brain activity during habituation will provide information

on whether the habituation process does involve a depression of the brain activity at the level of memory-associated areas in the central nervous system such as the MSF (median superior frontal lobe), the VL (vertical lobe), or both. This study represents a first step to close a gap in our knowledge of the learning processes in this advanced invertebrate.

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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 supposed before. Its occurrence in “cooler” Japanese waters (15–20 °C) waters next to the related species *Idiosepius paradoxus* indicates that the distribution of *Idiosepius biserialis* is not limited to tropical waters (25–30 °C).

**Key words:** coleoidea, idiosepius, geographic distribution

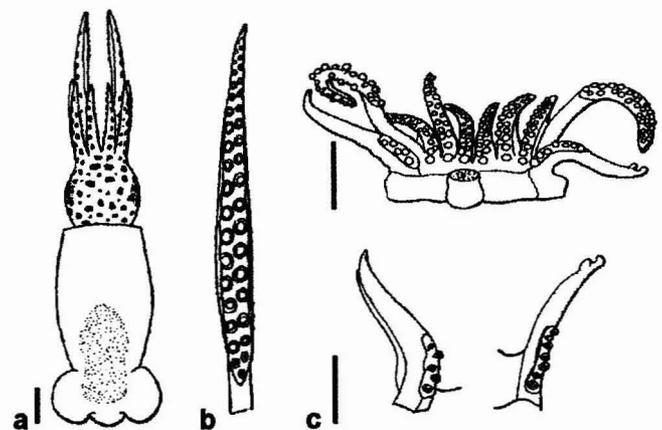
## INTRODUCTION

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 (Fig. 1). 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 an adhesive gland) located on the posterior part of the dorsal mantle side (Fig. 2). *Idiosepius biserialis* differs from the other species of this genus by occurrence at two distant geographical locations. Voss (1962) recorded this species in Moçambique but not in South Africa and it was found in Thailand by Hylleberg and Nateewathana (1991).



**Fig. 1** Geographical distribution of various *Idiosepius* species. In particular *I. biserialis* shows a widespread distribution within the genus.

Apart from *I. biserialis* a second species, *I. thailandicus*, also has a biserial arrangement of suckers on the tentacles (Chotiyaputta, Okutani, and Chaitiamvong, 1991). Both species strongly resemble each other. They differ only marginally in size (*I. thailandicus* 5.03 mm males and 9.85 mm females – *I. biserialis* 6.5 mm males and 9.05 mm females). Only scanning electron microscopic (SEM) images of the tentacle suckers point to a morphological difference between both species (Chotiyaputta, Okutani, and Chaitiamvong, 1991).



**Fig. 2** Images of *I. biserialis* (a) with its 2-rowed tentacle club (b), arms and hectocotylus. Images from Voss (1962). All scale bars 1 mm.

The new record of *I. 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 restricted habitat conditions of this cephalopod minimalist. The present results show that the occurrence of *I. biserialis* is not limited to sea grass and algae of “warm” tropical water (25–30 °C) and can also be found in “cooler” (15–20 °C) climatic zones. The species thus exhibits the largest geographical distribution in this family (Kasugai, 2000; Nesis, Katugin,

**Table 1. Morphometric data of the collected *I. biserialis* from Indonesia and Japan.**

	Indonesia		Japan				
	Female 1	Female 2	Males (n = 7)		Females (n = 4)		
			Male 1	Mean	Range	Mean	Range
Total length [mm]	10	7.0	5.0	11.8	9.2–13.4	16.7	14.2–18
Mantle length [mm]	5.5	5.0	3.0	6.30	4.7–7.6	9.39	8.1–10
Weight [g]	0.04	0.02	0.01	0.14	0.14–0.15	0.16	0.15–0.16
Mantle width [mm]	5.0	3.0	2.5	3.10	2.4–4.0	4.24	3.7–4.4
Head width [mm]	2.5	2.0	2.0	2.81	2.7–2.9	3.19	2.9–3.5
Fin length [mm]	2.0	1.8	1.2	2.86	2.7–2.9	3.01	2.9–3.2
Fin width [mm]	1.3	0.6	0.6	1.73	1.6–1.8	1.76	1.7–1.8
Arm I [mm]	2.0	1.6	1.0	contracted	–	contracted	–
II	3.0	1.9	1.3	contracted	–	contracted	–
III	1.5	1.6	1.1	contracted	–	contracted	–
IV	2.5	2.0	1.1	contracted	–	contracted	–
Tentacle	4.0	contracted	1.7	contracted	–	contracted	–

and Ratnikov, 2002; Kasugai and Ikeda, 2003), and very unique in all cephalopods due to its body size.

In this study, we report new characteristics of *I. biserialis* from Indonesia and Japan were evaluated based on the criteria of Voss (1962) and compared with other species by SEM-analysis.

## LOCALITIES

### *Idiosepius biserialis*

- Thailand: Bang Rong, Phuket Island (8°02.156' N; 98°25.487' E) (J. von Byern unpubl. data); Ko Pratong, Ranong (Hylleberg and Nateewathana, 1991)
- Moçambique: Inhaca Island (26°00.215' s, 32°54.721' E and 26°02.300' s, 32°54.166' E); Inhambane Bay (23°51.184' s, 35°22.553' E); Linga Linga (23°42.911' s, 35°23.684' E); Monque (23°41.331' s, 35°22.281' 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°32.424' N; 102°02.842' E) (J. von Byern unpubl. data and Nabhitabhata, 1998); Donsak Suratani, 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°52.020' s; 116°27.541' 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

## 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 *I. biserialis* (Voss, 1962; Hylleberg and Nateewathana, 1991a). The animals are small (Table 1),

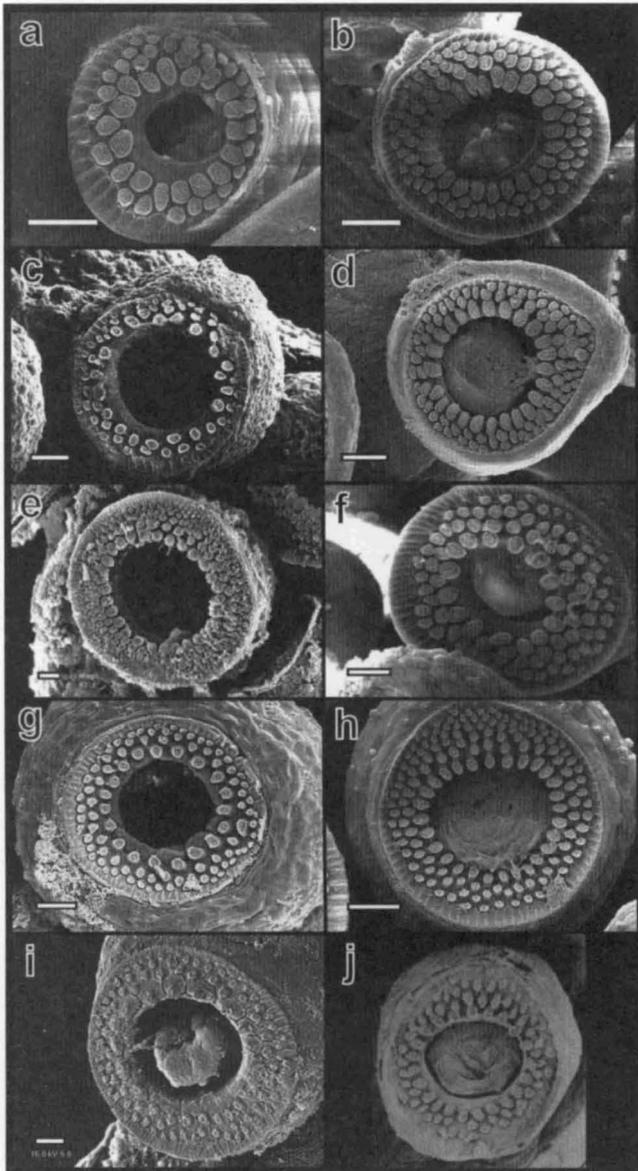
dorso-ventrally compressed and cigar-shaped; the mantle ends in a blunt point. The body is spotted with reddish brown chromatophores. The fins are small and kidney-shaped. Both arms IV in the males are hectocotylyzed, bearing 3–4 suckers on the left respectively 4–6 suckers on the right basal area of ventral arm. In the male, the hectocotyly arms are unequal in length contrary to the holotype specimen of Voss (1962). The suckers on the tentacles of all examined specimens have about the same size (100 µm) in the basal area, decreasing towards the tip of arms (10 µm).

Based on the biserial arrangement of suckers on the tentacles, the specimens from the new locations belong either to the species *I. biserialis* or to *I. 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 arm and tentacle suckers using SEM (Fig. 3) and *I. thailandicus* reveals that specimens of *I. biserialis* from Indonesia and Japan are morphological closely related to those of *I. biserialis*. The species *I. thailandicus* carries 2 rows of pegs, which becomes triple in the distal portion of tentacle suckers. In contrast the individuals from Japan and Indonesia possesses a distinct tripe circlets arrangement of pegs like *I. biserialis* from Moçambique and Thailand.

## Distribution and Habitat

*I. biserialis* can be caught easily by handnets in shallow seagrass and algal beds of Moçambique, Thailand, and Japan (Voss, 1962; Hylleberg and Nateewathana, 1991; Kasugai, 2000). The specimens from Indonesia were caught at the water surface in a sandy area next to a small mangrove sampling. No seagrass beds have been reported in the Ekas-Bay (Fig. 4), so it remains unclear where the animals stay at low tide. Currently no information about the geographic 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. Molecular biological studies are planned to provide new insights into the phylogenetic relationships and genetic flow of *I. biserialis* and *I. thailandicus*.

**Acknowledgments.** We are very grateful to Prof. Dr. W. Klepal, the head of the current research project, for kind support,



**Fig. 3** SEM images of arm (a, c, e, g) and tentacle (b, d, f, h) suckers of *I. biserialis* from Thailand (a, b), Moçambique (c, d), Indonesia (e, f) and Japan (g, h). For comparison, arm and tentacle suckers (i, j) of *I. thailandicus* from Thailand. An image of the tentacle sucker (x750) was retraced from Chotiyaputta, Okutani and Chaitiamvong, 1991.

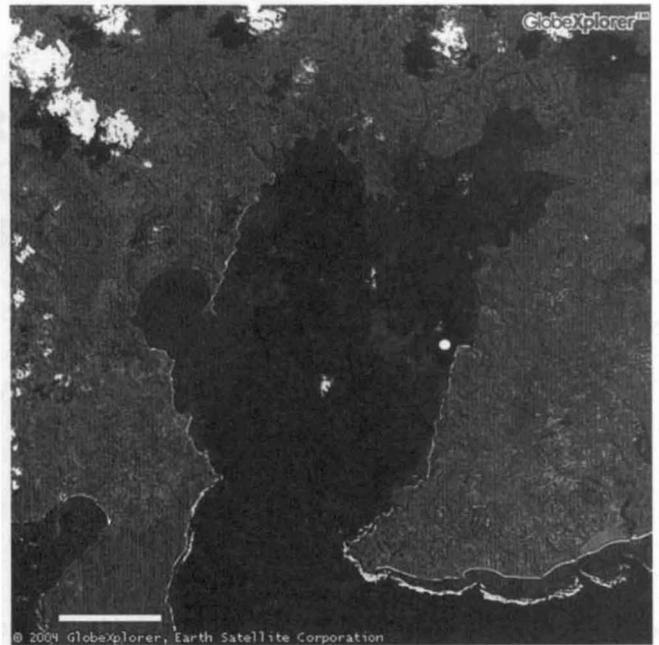
promotion of this study and critical reading. Our thanks go in particular to the Austrian Science Fund (FWF Project No. P 17193-B 12) and the Japan Society for the Promotion of Science (JSPS Grant No. 04567).

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**Fig. 4** Ekas-Bay, Lombok Island, Indonesia. The satellite image gives an overall view of Ekas-Bay. Only the passage in the southern part effects the water exchange. The white point on the right side (eastern part) mark the hunting area. In this area mangrove forests are mixed with sandy areas along the coast. Image published with permission of Terraserver.com. All copyrights preserved by Terraserver.com, GlobeExplorer, and Earth Sat. Scale Bar: 1.18 km.

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

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

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

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

## INTRODUCTION

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

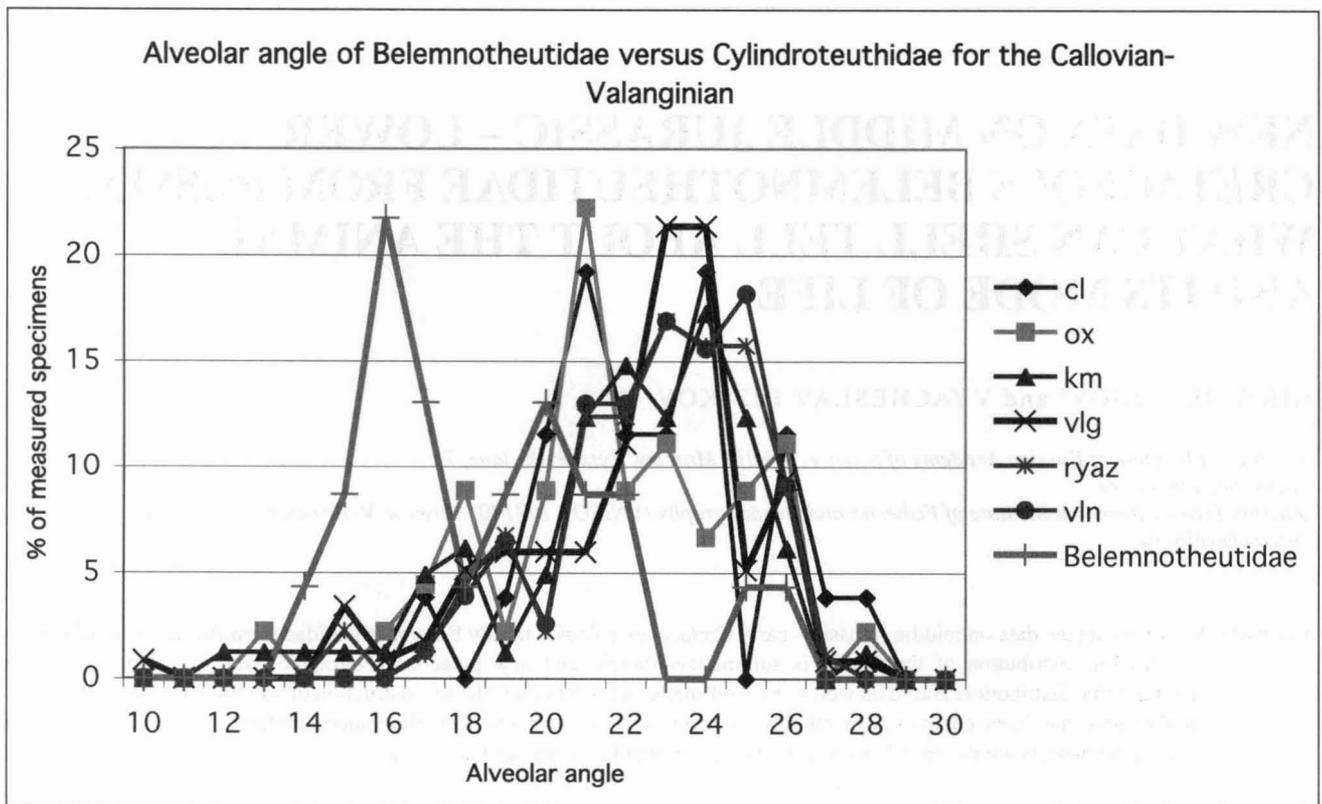
molov, Shenfille, 1991; Kiselev et al., 2003; Mitta, 2003; Keupp, Mitta, 2004). The material collected by the authors provided some new data on distribution of belemnotheutids on the Russian platform.

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

## MATERIAL STUDIED

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

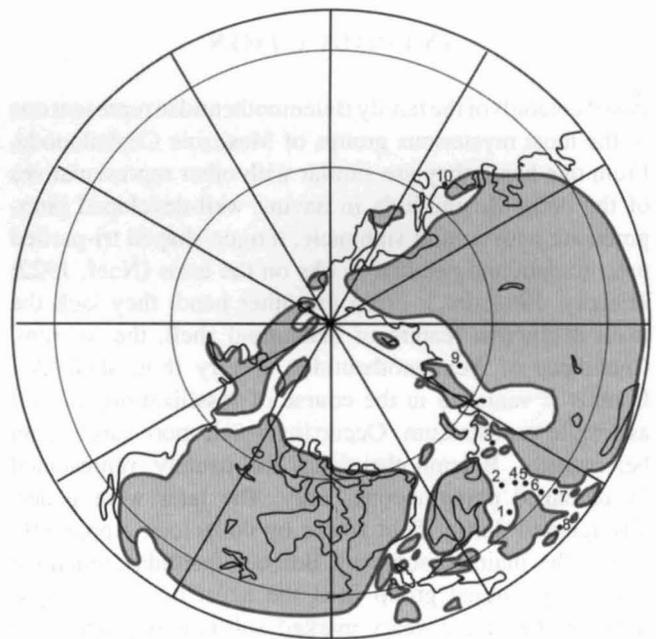
The material collected by the authors as well as literature data show that Belemnotheutidae are widely spread in the Callovian – Lower Cretaceous sediments of Russia and former USSR (Fig. 2). The fossils in authors’ collection can



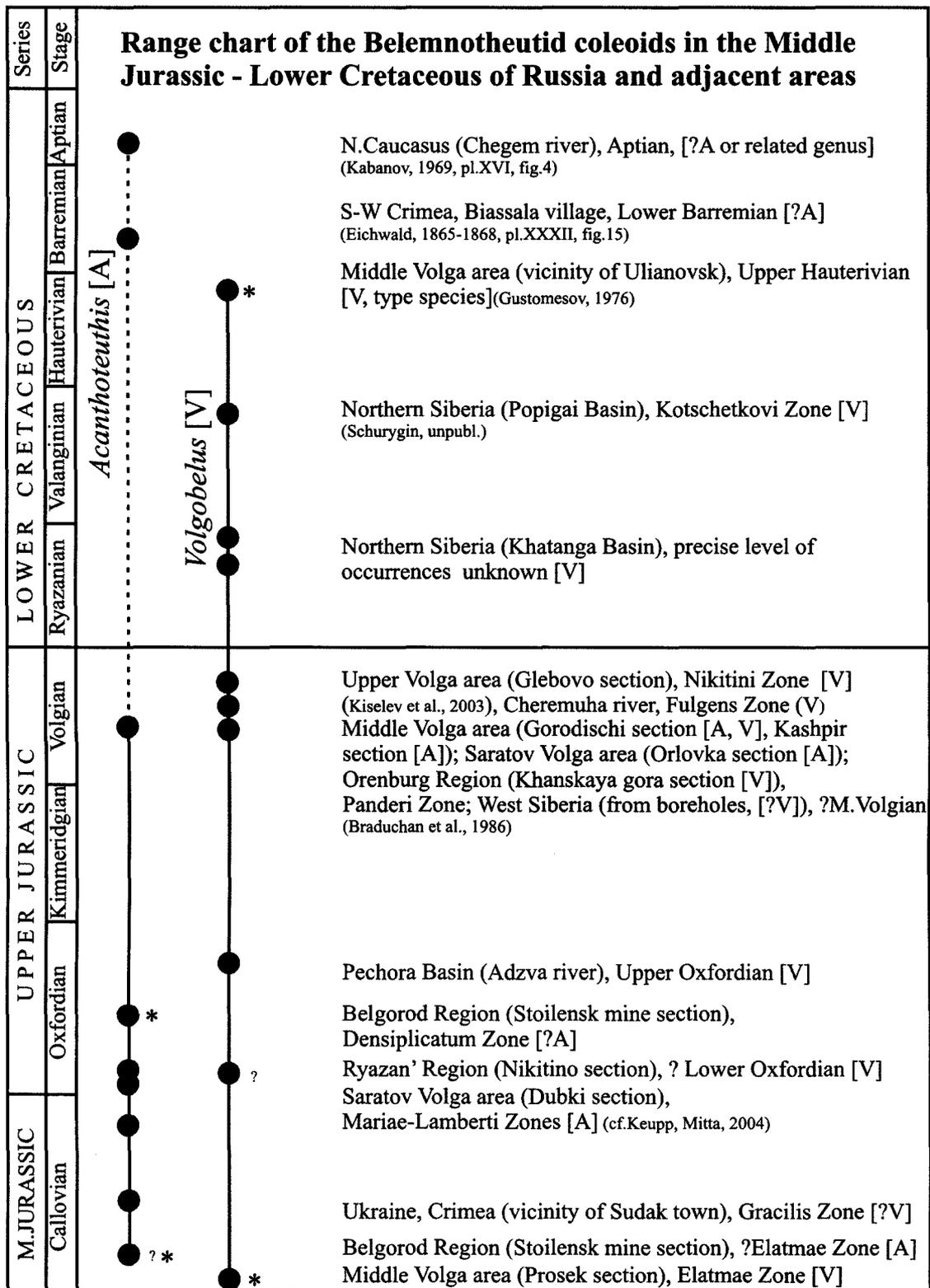
**Fig. 1** Comparison of the alveolar angle in Belemnotheutina and true belemnites from the Callovian-Ryazanian of Panboreal Realm (Cylindroteuthidae). Data on alveolar angles in Cylindroteuthidae were obtained from papers of Mikhailov, 1964; Sachs & Nalnyaeva, 1964, 1966; Dzyuba, 2004. Total of measured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

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

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



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

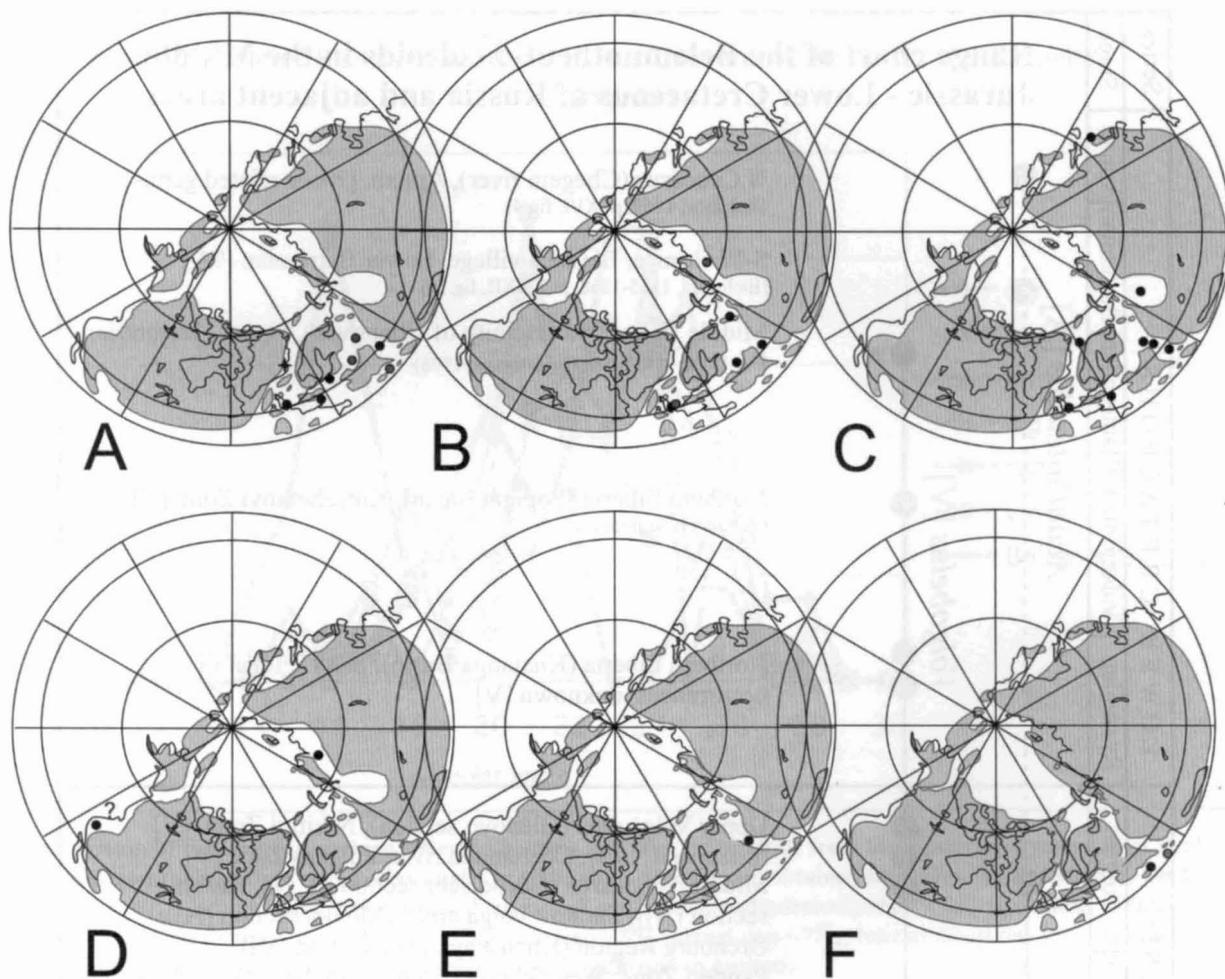


\*Localities where belemnite guards are entirely absent marked by asterisks.

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

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

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



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

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

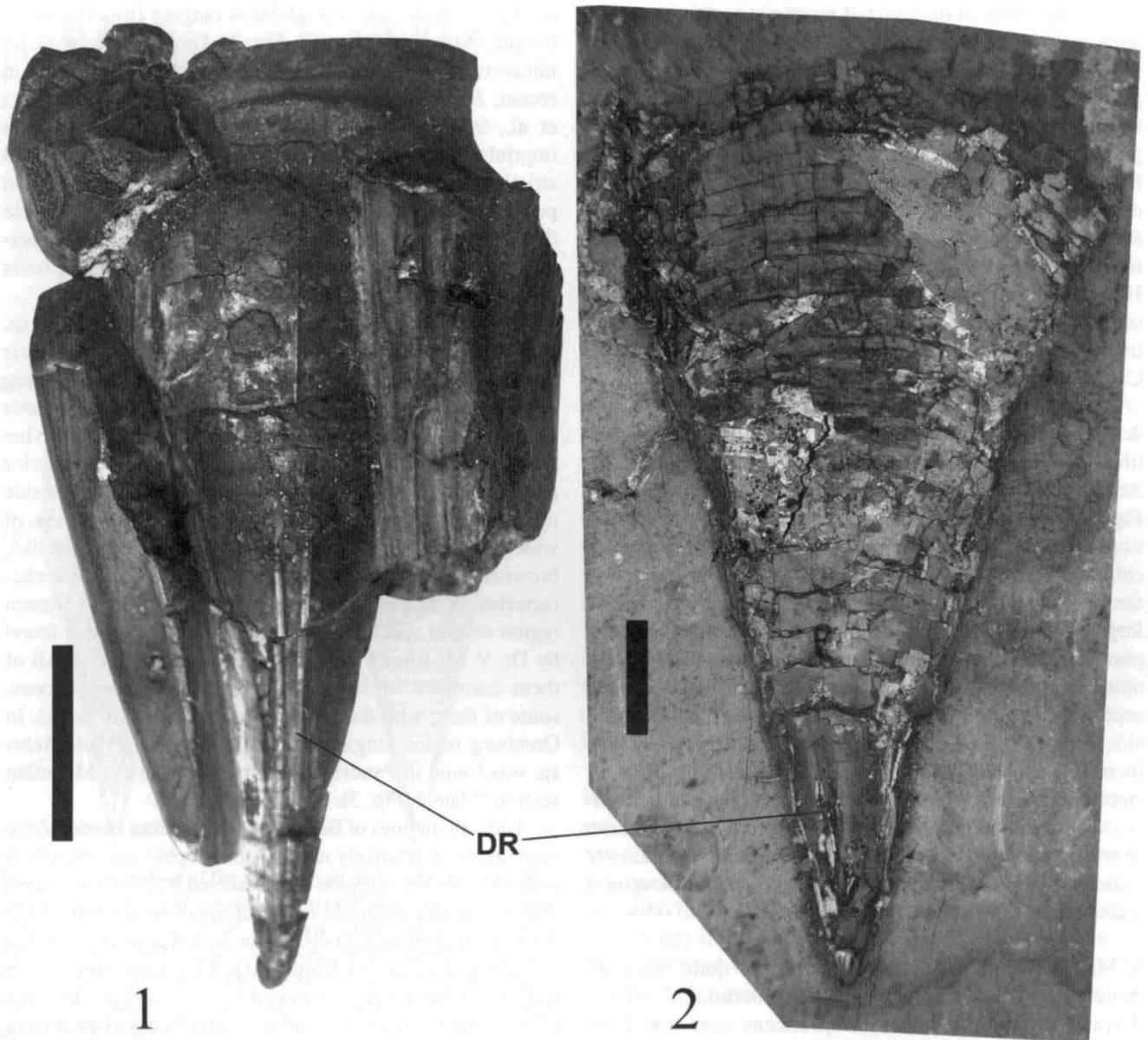
**Abbreviations for the museums and institutes that housed the specimens examined here:** CNIGR – F. N. Chernyshev Central Research Geological Museum, Saint-Petersburg; GIN – Geological Institute of Russian Academy of Science, Moscow; GM – Museum of the Saint-Petersburg State Mining Institute; IGPUW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

#### **GEOLOGICAL SETTINGS OF BELEMNOTHEUTIDAE IN RUSSIA**

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

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

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



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

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

**2. Upper Callovian – Lower Oxfordian.** Several specimens of *Acanthoteuthis* were found in Dubki section (near Saratov) in stratigraphic range between Upper Callovian, Lamberti Zone, *henrici* faunal horizon and Lower Oxfordian, Mariae Zone, *scarburgense* faunal horizon. Phragmocones *Acanthoteuthis* were reported earlier from Lamberti Zone of Dubki section by Mitta (2003), who identified them as *A. polonicum*, but they have never been neither figured, nor described. It should be noted, however, that systematics of *Acanthoteuthis* is somewhat confusing. Two species of this genus were described from Upper Call-

ovian from the Europe: *A. antiqua* (Pearce, 1842) and *A. polonicum* (Makowski, 1952). Later Bandel and Kulicki (1988) noted that these two species are difficult to distinguish as their diagnoses uses the same characters (thin rostrum covering with paired dorsal longitudinal ridges). We had a chance to compare holotype of *A. polonicum* with exceptionally well-preserved specimen of *A. antiqua* from the type locality, Christian Malford; England (Fig. 5a). To our opinion, these two species differ mostly by their preservation condition rather than by their morphology: *A. antiqua* was described basing on crushed specimens while *A. polonicum* was described on uncrushed ones. Rare examples of uncrushed *A. antiqua* are virtually indistinguishable from *A. polonicum* (Doyle, Shakides, 2004; text-fig. 2). In our collection most specimens of *Acanthoteuthis* from Dubki section represented uncrushed phragmocones filled with sediments (Plat 1; Fig. 4). Some specimens retained characteristic dorsal ridges in apical part of the phragmocone.

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

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

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

One exceptionally well-preserved specimen with almost complete shell, remains of the ink sac and the mantle was found in large block of oil shale fallen out from the bed 2/12. The specimen is exposed by its ventral side up (Plate 3). It is 34 cm long and about 10 cm wide. The phragmocone is crushed but its original aragonite composition is preserved. The septa are visible in anterior part of the phragmocone as widely spaced thin lines. Proostracum is thin brown tongue-shaped non-calcified structure protruding from the anterior part of the phragmocone. Its lateral zones in some places reveal fine oblique striation apparently corresponding to hyperbolic zones of belemnite proostracum (Naef, 1922). Median zone of proostracum is comprehensively fractured into polygonal fragments (2–5 mm) that partly displaced beyond the shell contour. The ink sac is preserved as a black granular substance of irregular shape situated near anterior margin of the phragmocone. Analysis of the ink sac content under SEM showed that it consisted

of clusters of uniform ink globules ranging from 0.2  $\mu\text{m}$  to 0.4  $\mu\text{m}$  in diameter (Plate 3; Fig. 3). Quite similar globular ultrastructure of the ink sac content was reported earlier in recent, Jurassic and Carboniferous Coleoids (Doguzhaeva et al., 2003). In anterior right part of the proostracum imprints of mantle muscles preserved as fine transversal striation overlaying the shell margin from dorsal side. In posterior part of the fossil faint wing-like contour is visible that possibly may represent imprint of the fins. This specimen was tentatively identified as *Volgobelus* sp. on the basis of large size of its phragmocone.

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

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

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

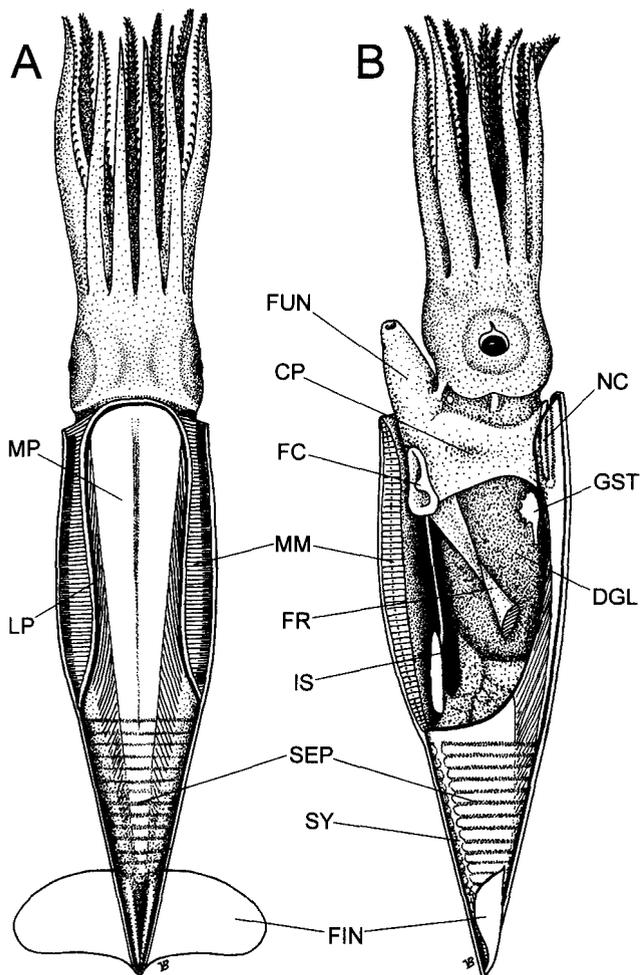


Fig. 6 Reconstruction of the soft body in *Acanthoteuthis*. A. Dorsal view. B. Sagittal section. Abbreviations: MP – median plate of proostracum; LP – lateral plates of proostracum; SY – siphuncle; SEP – septa; MM – mantle muscles; IS – inc sac; DGL – digestive gland; GST – stellar ganglia; NC – nuchal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

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

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

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

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

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

## PALAEOBIOGEOGRAPHY OF BELEMNOTHEUTIDAE

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

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

## RECONSTRUCTION OF THE SOFT BODY STRUCTURE

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

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

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

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

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

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

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

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

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

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

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

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

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

these forms took the water and lost buoyancy quickly after animal death.

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

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We wish to express our heartily thanks to Lyall Anderson for access to the collections of fossil coleoids in the National Museum of Scotland (Edinburgh; UK) and Marcin Barski (Warsaw, Poland) for access to holotype of *B. polonicum* from paleontological collection in Museum of the Faculty of Geology, University of Warsaw.

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

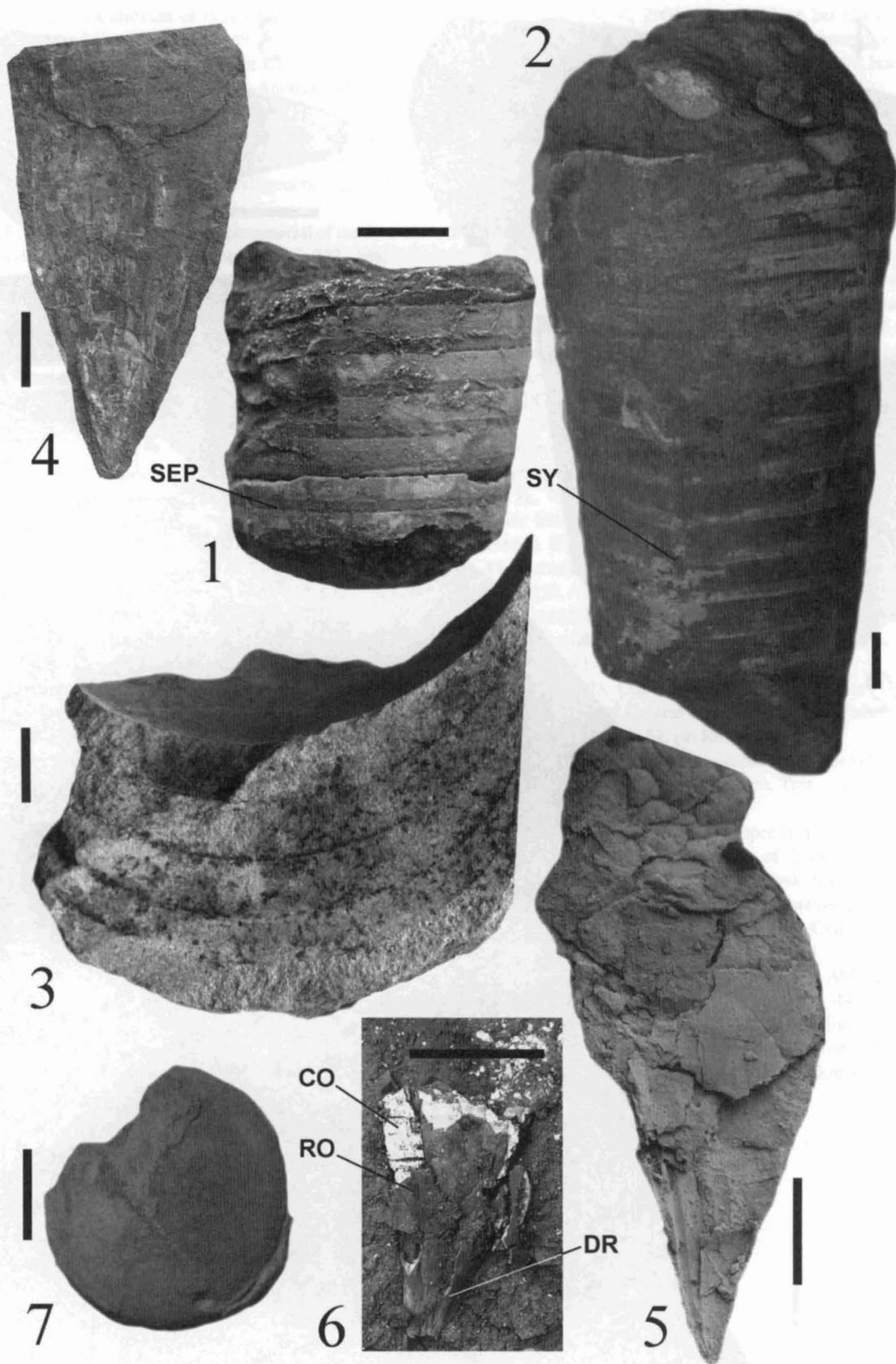


Plate 2. Oxfordian – Volgian Belemnotheutids. 1. *Acanthoteuthis* (?) sp., dorsal view of phragmocone, GIN MK1417, Stoilensk mine, Middle Oxfordian, Densiplicatum Zone, near to base of bed 6 (after Rogov, 2003). 2. *Volgobelus* sp., ventral view of phragmocone, CNIGR 33/4390, Adzva river (?near Adzvavom),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

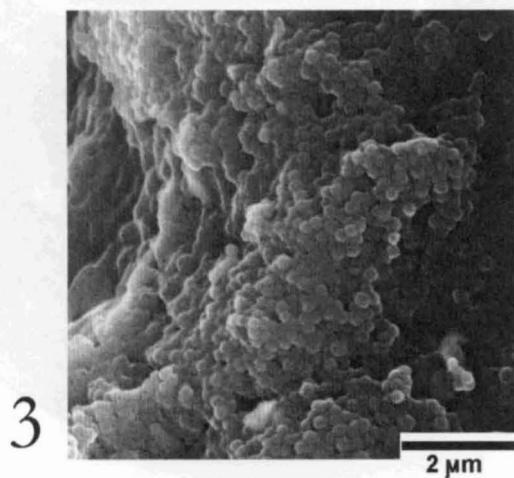
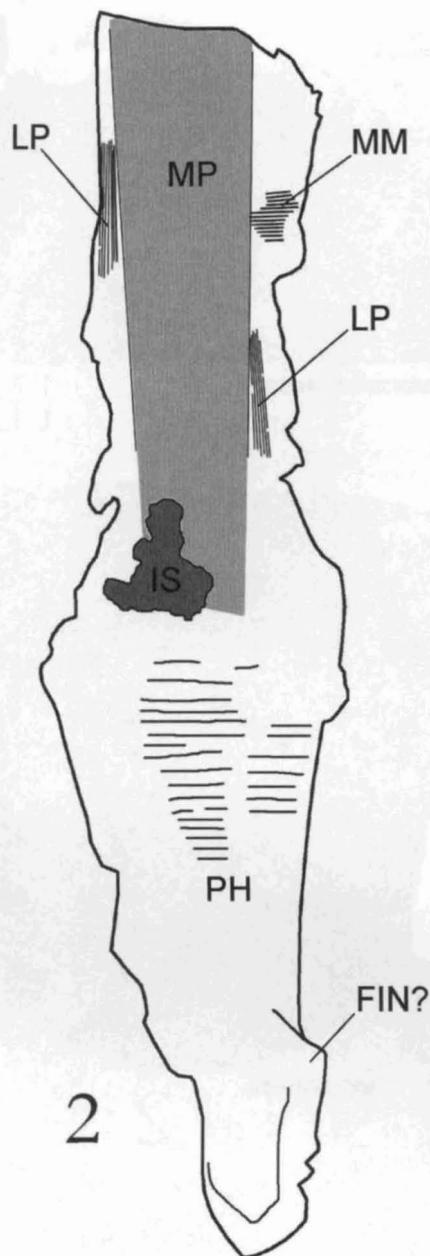


Plate 3. Middle Volgian *Volgobelus* sp. of the exceptional preservation from the Gorodischi section, Panderi Zone, regularis horizon. 1. Specimen with preserved crushed phragmocone, proostracum and soft tissue remains. 2. Scheme of the specimen. 3. SEM micrographs of the ink sac content (characteristic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

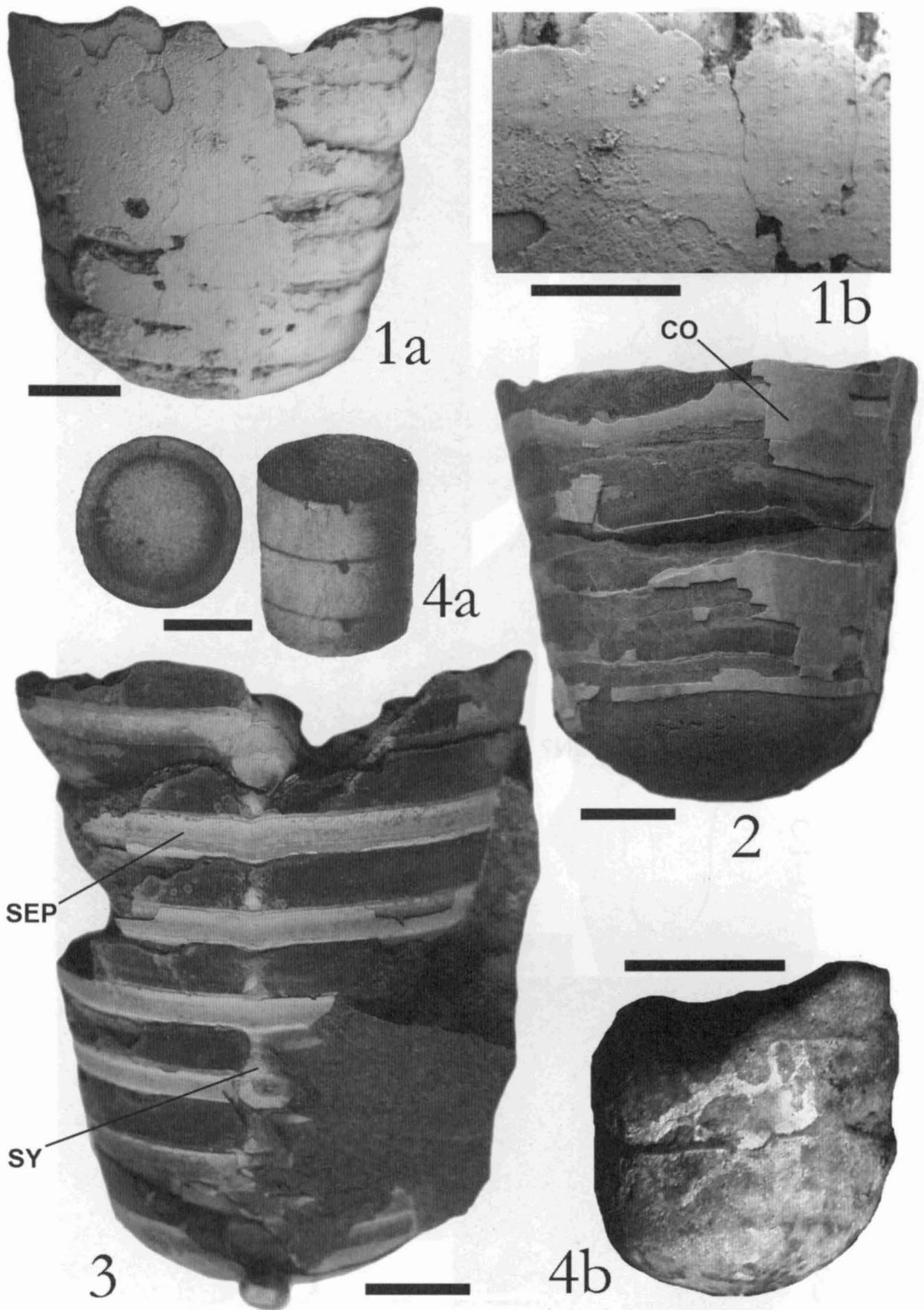


Plate 4. Middle Volgian to Barremian Belemnotheutids. 1. *?Acanthoteuthis* sp., GIN MK1759, Glebovo, Middle Volgian Nikitini Zone (collected by D. N. Kiselev), a – general view; b – details of the conotheca sculpture showing longitudinal ornament; 2, 3. *Volgobelus* sp., Ryazanian-Valanginian of Bojarka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

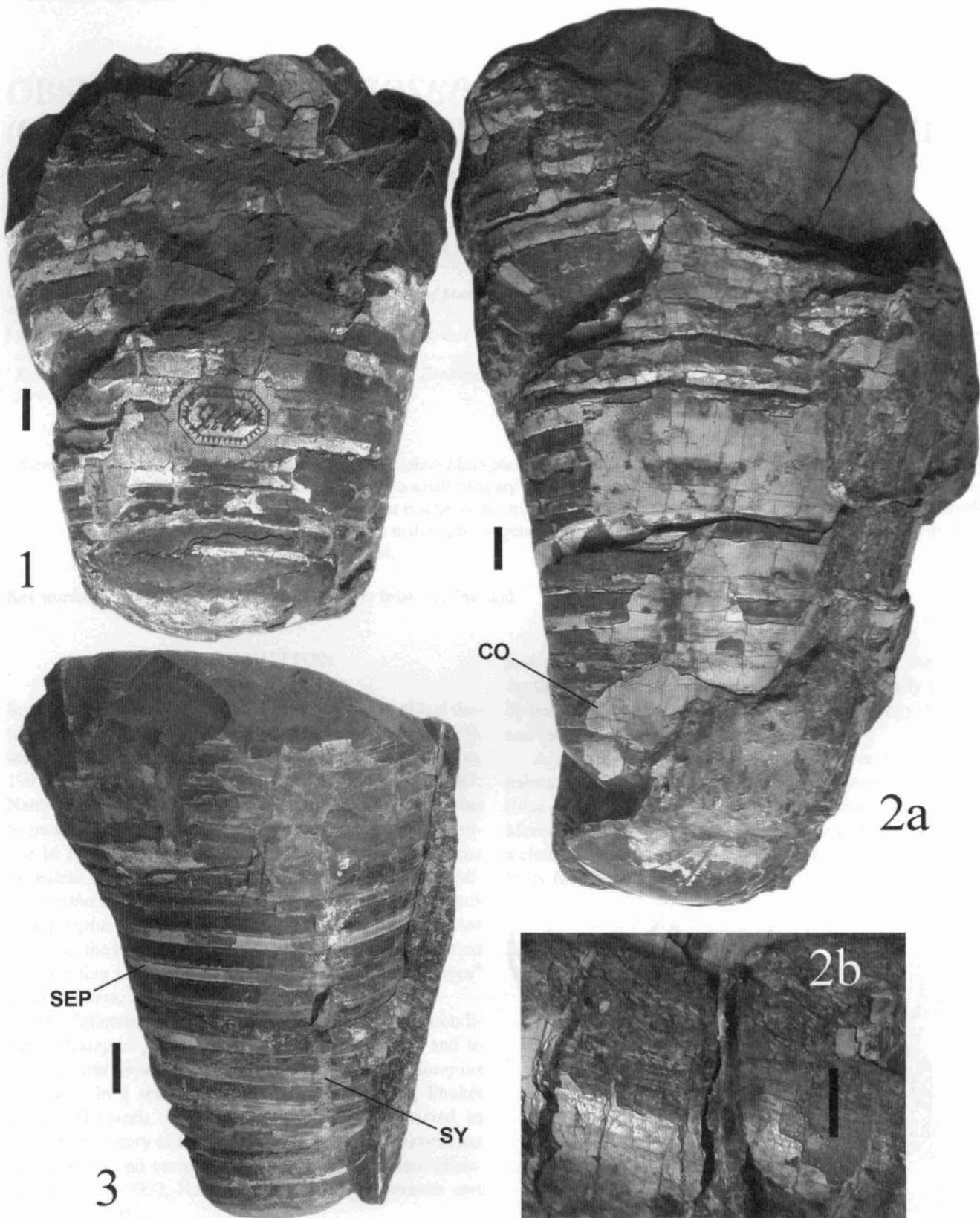


Plate 5. Hauterivian *Volgobelus colossucus* (Jasikov) from the Ulyanovsk Volga area. 1. GM 495/464, Polivna (collected by P. M. Jasikov). 2. GM 25a/48, the specimen was collected by P. M. Jazykov and later described by Lahusen (1874). 2a – general view; 2b – detail of the longitudinal sculpture of conotheca.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



# OBSERVATION OF *IDIOSEPIUS PYGMAEUS* (CEPHALOPODA, IDIOSEPIIDAE) AT BANGRONG RIVER, PHUKET ISLAND, THAILAND

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**Abstract:** This report reveals 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.

**Key words:** Coleoidea, *Idiosepius*, Bangrong River tributary, Thailand

## INTRODUCTION

Several studies have been published on the geographical distribution (Nesis, 1982; Hylleberg and Natewathana, 1991), seasonal abundance (Jackson and Choat, 1992; Jackson, 1993), behaviour and postures in captivity (Moynihan, 1983; Nabhitabhata, Nilaphat, and Promboon, 2004) of *Idiosepius pygmaeus*. Less is known about the behaviour of *Idiosepiidae* in its natural habitat. In Thailand next to *Idiosepius pygmaeus* two smaller species, *Idiosepius biserialis* and *Idiosepius thailandicus*, can be found. Preliminary observations of *Idiosepius thailandicus* have shown that these species “occur in the littoral zones, free swimming or in association with floating sea weeds, and in estuaries, and mangroves” (Nabhitabhata, 1998).

The following report will describe under which conditions *Idiosepius pygmaeus* (Fig. 1) may be found and to describe our 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. 2 and 3) because of the depth and current speed in the main stream (Kristensen et al., 2000; Holmer et al., 2001; Kristensen and Suraswadi, 2002).

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* (Fig. 4 a–d).

From April to May 2004, 9 females (mean mantle length  $12.5 \pm 2.18$  mm) and 46 males (mean mantle length  $11.28 \pm 2.10$  mm) of *Idiosepius pygmaeus* (Fig. 4) were caught in the small tributary of the Bangrong River (8°02.945' N; 98°25.030' E). The animals were trapped with dip-nets downstream during ebb tide and flood tide (Fig. 5). Work on

foot during high tide was impossible because of the water depth. At high tide animals were also occasionally caught by boat, but the dense mangrove made his strategy difficult and ineffective.

A recognizing of these pygmy squids in their 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.

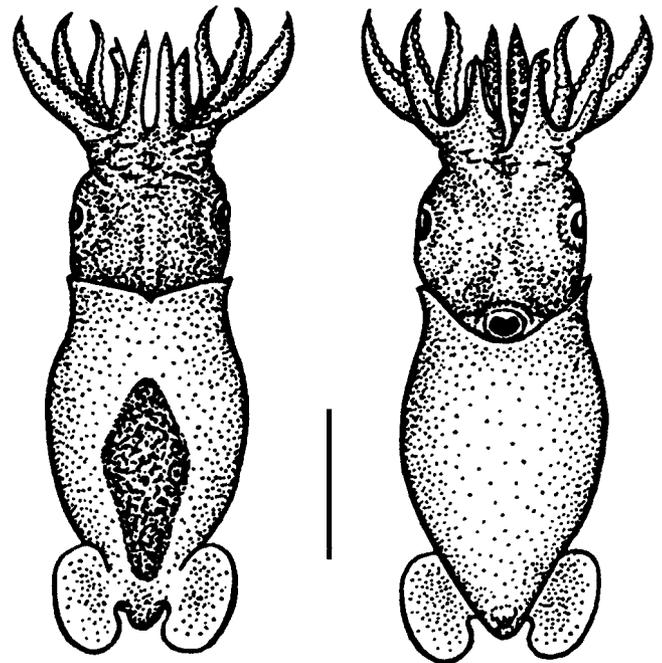


Fig. 1 Male specimen of *Idiosepius pygmaeus*. Figure from Nesis (1987). Scale bar: 0.54 cm.

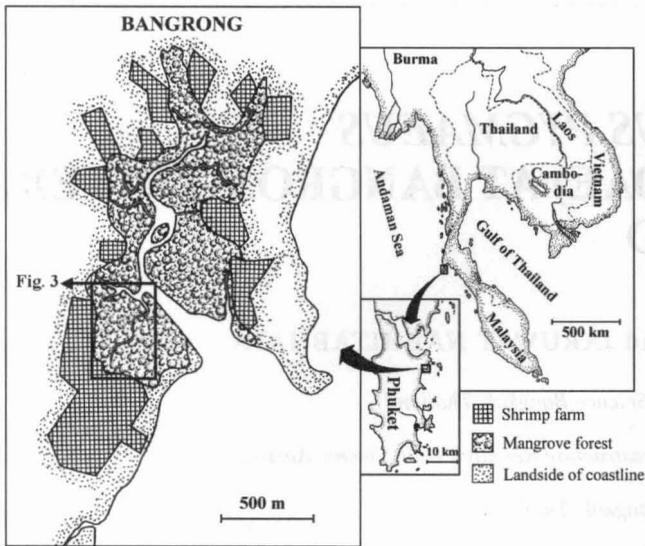
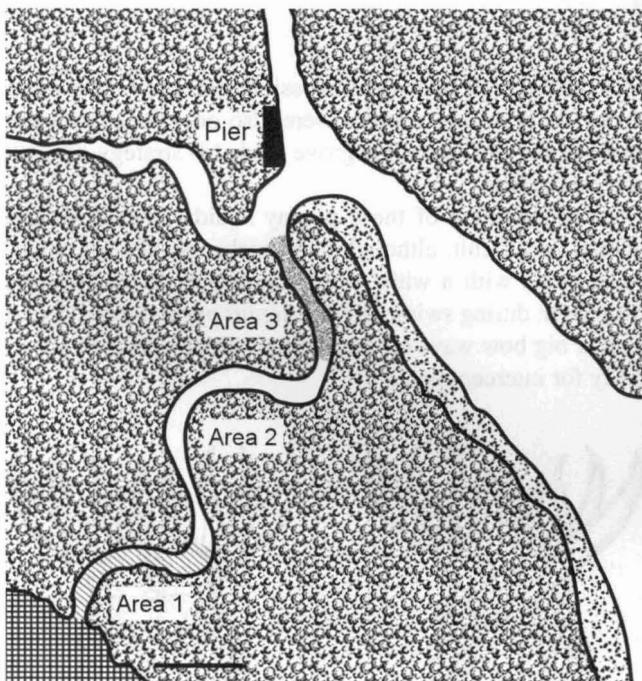


Fig. 2 Drawing from satellite photo of Bangrong River. The estuary is fed by one main and several smaller streams surrounded by an enormous mangrove swamp. The following observations and collections were made in the smaller marked tributary (Fig. 3). Image published with permission of Erik Kristensen. All copyrights preserved by Kristensen and Surawadi (2002).



- Mangrove Forest
- Sand bank
- Shrimp farm
- Area 1 Tributary
- Area 2 Tributary
- Area 3 Tributary

Fig. 3 Bangrong River with study areas. Scale bar: 50 m.

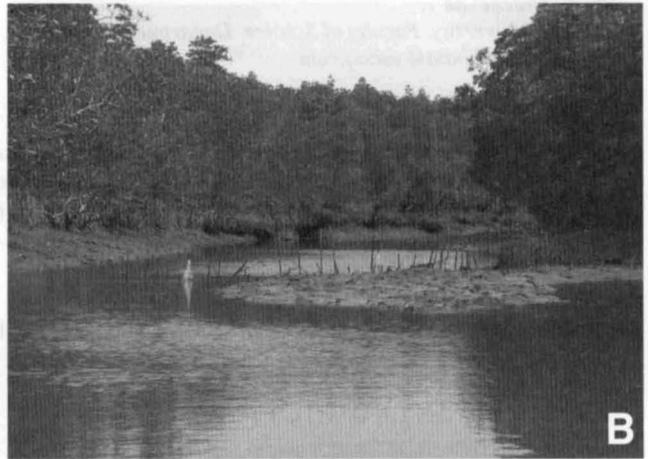


Fig. 4 Tributary of Bangrong River at flood tide (A) and ebb tide (B). The tributary is lined on both sides by mangroves, mainly *Avicennia* (C) and *Rhizophora* (D). Scale bar: 80 cm.



Fig. 5 Attempt to catch *Idiosepius pygmaeus*. Image by J. N.

Males were differently distributed in the tributary (Fig. 2). 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 (Fig. 6). It is not 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 to 100 cm) in zones, characterised by bank vegetation. No specimens were collected at riverbanks with *Avicennia* sp. roots and sand banks (Fig. 4C). 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 10–20 cm) (Fig. 4D).

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.

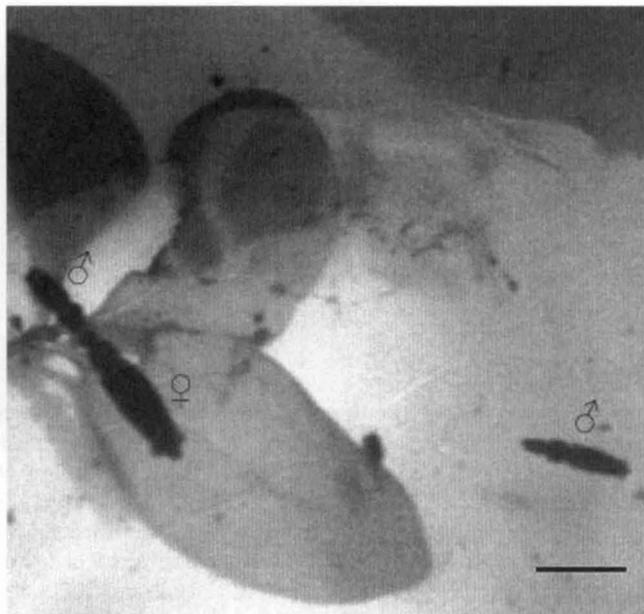


Fig. 6 Male (upper) and female (lower) mating in bucket. Scale bar: 2 cm.

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# HERCYNIAN CRETACEOUS AND “PLENUS EVENT”

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**Abstract:** The so called “Plenus event”, characterized by occurrence of belemnite *Praeactinocamax plenus*, is stratigraphically situated into the Late Cenomanian (geslinianum Zone, G. bentonensis Subzone, W. archaeocretacea Zone) extensive eustatic transgressive cycle (similar to those in Early Turonian M. nodosoides zone). The constant rise of sea level caused influx of cooler water masses from Arctica, and the new counter stream started circulate over Czech Massif. During the next eustasy, the surface of epicontinental sea increased, and the bottom counter stream disappeared. Inside of the geslinianum zone, large hiatus are reported from Anglo-Paris Basin in the West through to Kazakhstan in the East. The Czech Massif was continually uplifted, however the Labe lineament and probable Bohemia-Bavarian channel showed a continuous ebb. The similar event has been recorded in the M. nodosoides zone including also the bottom counter stream, however without any belemnite incursion.

**Key words:** Hercynian Cretaceous, Bohemia Cretaceous Basin, Late Cenomanian, sea level changes, praeactinocamax plenus, rudists

## INTRODUCTION

It is possible to find *Praeactinocamax plenus* (Blainv.) on a number of various localities in the Bohemian Cretaceous (BCB). It is the development from the Vltava-Beroun, Kolín and Szczeliniec regions and quite different development from boreholes in Labe and Jizera regions. There is an erosion boundary above sediments at all localities with *Praeactinocamax plenus* (Blainv.). Sediments of *Mammites nodosoides* zone are situated above this boundary. Hiatus includes the uppermost part of zone *Metoicoceras geslinianum*, probably the zone *Neocardioceras juddi* and at least *Watinoceras devonense*. Different development is documented from the Saxony in the north direction, also from German-Polish Basin and Anglo-Paris Basin. Recently published literature dealing with the uppermost Cenomanian enables new comparison of each site in Europe and the Tethyan Realm.

## THE DEVELOPMENT OF CENOMANIAN SEDIMENTS OF THE BCB

### The development before the plenus event

The last work on stratigraphy of Cenomanian from the Hercynian Cretaceous (Svoboda, 2004) was based on the development at Vltava-Beroun region. It was found that sandstones and siltstones from the base of *Praeactinocamax plenus* (Blainv.) in other regions are not of the age of E complex in Vltava-Beroun region. Due to this, there are longer hiatuses in the Bohemian Cretaceous Basin. Apart of this the basic scheme remains the unchanged. The Bohemian Massif was uplifting the world ocean level was rising even after the end of *guerangeri* zone. The occasional basins of SW-NE direction were arising. The oldest units are the lagoonal Peruc Member *s. s.* and their analogues from southeast part of Vltava-Beroun region. They are of zone

*jukesbrownei* age. The so-called “Hořice sandstone” from the central part of the basin probably belongs also to the zone *jukesbrownei*. Following complexes A and B from the Vltava-Beroun region are of zone *guerangeri* and it includes *Newboldiceras newboldi* (Kossmat). The so-called “Mochov sandstone” is with the highest probability equivalent of the so-called sea interbed from Vidoule (Svoboda, 2004). The complex C includes typical fauna from the end of zone *guerangeri*: *Calycoceras naviculare* (Mantell), *Newboldiceras newboldi* (Kossmat), *Thomelites cf. sornayi* (Thomel) and *Thomelites flandrini* (Thomel). The complex D includes: *Calycoceras naviculare* (Mantell), *Metoicoceras geslinianum* (d’Orb.), *Euomphaloceras* sp. and *Proplacentoceras memoriaschloenbachi* (Laube et Bruder). The complex E rarely contained: *Metoicoceras geslinianum* (d’Orb.), *Sciponoceras gracile* (Shumard) and *Allocrioceras annulatum* (Shumard). *Metoicoceras geslinianum* (d’Orb.) and *Praeactinocamax plenus* (Blainv.) were quite abundant within complex F at some sites. The lagoonal and marine sediments occur in Orlice-Žďár region on the southeast, which represent the local development.

### Plenus event in the BCB

Complex F is composed of seemingly monotonous beds of marlites, spiculites, siltstones and sandstones whose parts differ with content of fauna. Inside the complex F, there is a layer with *Praeactinocamax plenus* (Blainv.). The highest abundance of belemnite guards represents the plenus event. The layer of siltstone with *Calycoceras* sp., *Inoceramus pictus bohemicus* (Leonh.), *Lunatia* sp. and *Terebratula* sp. (Svoboda, 1999) was found on the base of complex F at sites Zlončice II. and Odolena Voda II. Only above follow the spiculitic siltstones, which include bed with *Praeactinocamax plenus* (Blainv.). Similar development in limestone facies was described by Frič (1869) at Holubice, by Svoboda (1989, 1999) at Dolany (direction to Debrno) and on site Zlončice III. Spiculitic siltstones are developed from Holubice up to

Odolena Voda and they include: *Metoicoceras geslinianum* (d'Orb.), *Inoceramus pictus bohemicus* (Leonh.) and *Hep-teris septemsulcata* (A. Roem.) (Košťák, 1996, Košťák et al., 2004). The thickness of these spiculites varies from 0.9 m to 2 m (Fig. 1, 2). From the Veliká Ves hills towards Neratovice the complex F developed as marl with maximal thickness of 1.5 m. *Praeactinocamax plenus* (Blainv.) is reported from 0.1 m above the base of complex F at sites Neratovice I. and Jiřice II. On sites Veliká Ves I. and Neratovice II. it is found in

*suborbiculatum* (Lam.) but even *Exogyra sigmoidea* Reuss and *Praeactinocamax plenus* (Blainv.) (Svoboda, 1987). The thickness of the complex F in vicinity of Kostelec nad Labem and Polerady is 1.4 m. In vicinity of Kolín, the complex F is developed as sandstones with *Rhynchostreon suborbiculatum* (Lam.) and layers of biodetrital limestones (Urbánek, 1924). Above the level with *Praeactinocamax plenus* (Blainv.) were reported big corals *Saxuligyra maior* Eliášová and *Ovalas-traea facilis* (Počta), rudists *Petalodontia* and gastropods *Actaeonella gigantea* Sow. and *Trochoacteon briarti* (Gein.). The limestones with big rudist *Radiolites sanctaebarae* Poč. appear already around Chocenice and Radovesnice. The thickness of complex F is here up to 15 m (Fig. 3, 4). The sandstones proceed horizontally into biodetrital limestones with *Radiolites sanctaebarae* Poč. in vicinity of Kutná Hora and it is up to 32 m thick (Klein, 1962). Two cases of finding of *Praeactinocamax plenus* (Blainv.) were reported from sandstones (Fejfar et al., 2005). The sandstones around

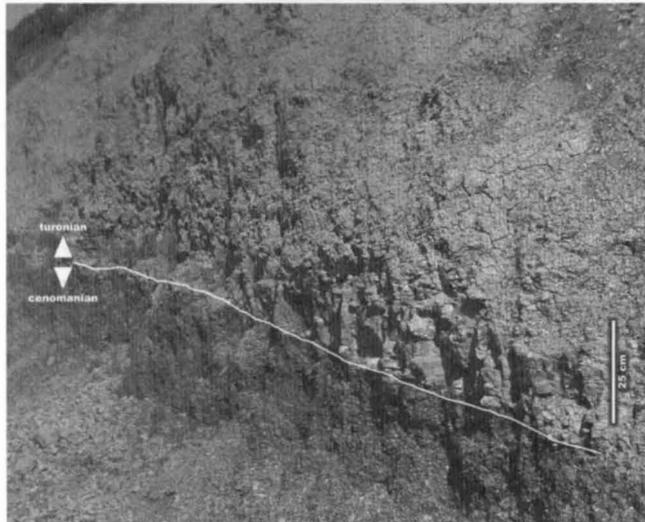


Fig. 1 Locality Kozomín – excavation from 1968; southeast from Kralupy nad Vltavou. Transgression of the glauconitic claystones (lower Turonian) on spongilites with *P. plenus* (upper Cenomanian).



Fig. 2 Lokality Holubice – limestone quarry, 1971; southwest from Kralupy nad Vltavou. Spongilites with plenus event in down part. Scale 1 m.

the upper part of profile. By Polerady on basement sandstones of complex C is found strongly glauconitized argillous sandstone with the lyditic gravel and abundant fauna: *Torquesia cenomanensis* (d'Orb.), *Lunatia* sp., rarely *Trigonia sulcata* Lam. and *Rhynchostreon suborbiculatum* (Lam.). A glauconitite follows to the top into glauconitic marlite. The upper level of this marlite includes *Praeactinocamax plenus* (Blainv.). To the northwest, the sandstones with *Rhynchostreon suborbiculatum* (Lam.) diminish and marlites are situated directly on basement. The glauconites and lydite in southeast direction at site Černá skála contain *Rhynchostreon*

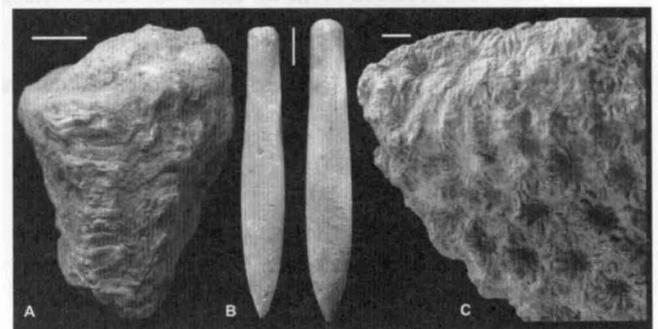


Fig. 3 Important fossils from complex F. A – *Radiolites sanctaebarae* Počta, B – *Praeactinocamax plenus* (Blainville), C – *Saxuligyra maior* Eliášová. Scale 1 cm.

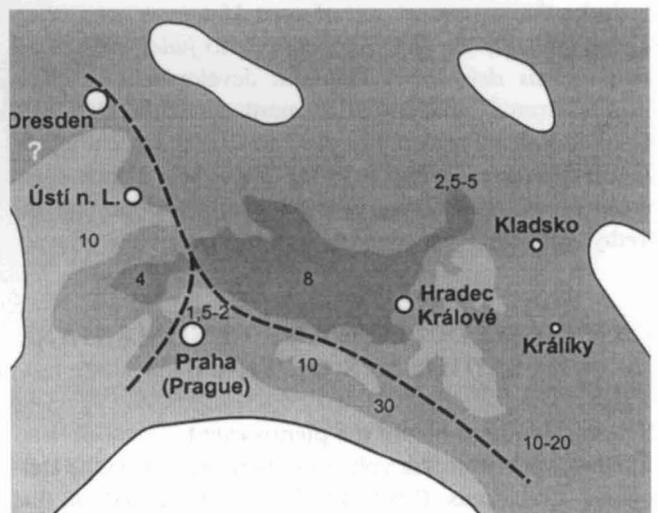


Fig. 4 Map of thickness of complex F in BCB (in m).

Čáslav are divided into the lower limonitic fine-grained sandstones, upper calcareous and upper glauconitic. The *Rhynchostreon suborbiculatum* (Lam.) and *Opis bicornis* (Gein.) can be found within. The limonitic sandstones include *Praeactinocamax plenus* (Blainv.). *Praeactinocamax plenus* (Blainv.) can also be found redeposited in basal lower Turonian beds in Orlice-Žďár region. Its basement consists of glauconitic coarse-grained sandstone with rare fauna. It was

reported directly in these sandstones alongside Nové Hradky by dr. Soukup and dr. Klein from Czech Geological Survey (S. Čech – oral communication 2005). Sandstones are thus the equivalent of the lower part of complex F. In Szczelinię region, the complex F is formed by spiculitic siltstones to sandstones with spiculitic chert. These contain *Praeactinocamax plenus* (Blainv.), *Inoceramus pictus bohemicus* (Leonh.) and *Hepteris septemsulcata* (A. Roem.). It reaches the thickness from 2.5 m to 5 m. The glauconitic beds are situated at its base and at the top. The so-called siltstone formation was reported from Jizera and Labe regions (Pražák, 1989, Uličný et al., 1993). Lower subcycles are the siltstones with abundant fauna reminiscent of the so-called Pennricher Fauna from Saxony: *Perna cretacea* Reuss, *Neithea aequicostata* (Lam.), *Neithea notabilis* (Muenst.), *Rhynchostreon suborbiculatum* (Lam.) and *Exogyra reticulata* Reuss. *Merklinia aspera* (Lam.) can be found rarely. Upper subcycles are spiculitic siltstones with rare fauna: *Torquesia cenomanensis* (d'Orb.), *Perna cretacea* Reuss, *Neithea aequicostata* (Lam.), *Neithea notabilis* (Muenst.), *Pseudoptera anomala* (Sow.), *Rastellum carinatum* (Lam.) and *Rhynchostreon suborbiculatum* (Lam.). *Entolium orbiculare* (Sow.), *Pycnodonte vesicularis* (Lam.) and *Trigonia sulcataria* Lam. occur commonly. The uppermost part 0.1 m below the base of Turonian rarely contains *Praeactinocamax plenus* (Blainv.) (S. Čech, oral communication 2004) and commonly *Pycnodonte vesicularis* (Lam.) or *Entolium orbiculare* (Sow.). The thickness of this siltstone formation varies from 4 m to 10 m. The 4 m thick, units P3 and P4 from the Pečínov Member (Uličný et al., 1997) at the west of Vltava-Beroun and Ohře region probably belong to complex F.

## COMPARISON WITH GERMAN-POLISH BASIN AND ITS SOUTH BOUNDARY

Upper Cenomanian is divided in two parts in the north Germany. The lower part is composed of the so-called Arme rhotomagensis Schichten, coccolith limestones of thickness around 10 m. The observations of fauna are rare. Beds with oyster occur at the base (Amphidonte Event) (Kaplan et al., 1998, Wilmsen, 2003). Upper part of the upper Cenomanian begins in north Germany by 1.8 m thick Bunter complex in which the beds of ochre, ferruginous, green-grayish and black-grayish marlites are interlaced with beds of yellowish marly limestones (Diedrich, 2001). Bunter complex ends up with dark marlites of Chondrites-Horizon. The I. Pictus Horizon III in the lower part of Bunter complex includes: *Inoceramus pictus pictus* (Sow.) and *Inoceramus pictus concentricundulatus* Troeger. The Chondrites-Horizon includes: *Calycoceras naviculare* (Mantell) and *Inoceramus pictus pictus* (Sow.). The Karbonat-Komplex is 2.4 m thick. The base consists of Puzosia-Event I with accumulation of ammonite shells and abundant bioturbations. It includes: *Metoicoceras geslinianum* (d'Orb.), very abundant *Puzosia dibleyi* (Spath), *Inoceramus pictus bohemicus* (Leonh.) and end of occurrence of *Rotalipora cushmani* (Morrow). The so-called Plenus Event with *Praeactinocamax plenus* (Blainv.) is located above. It is followed by Rotpläner Bank and bright marlite. Schwarzschiefer Komplex with thickness of 3.2 m is the rotation of black-gray marls with gray-green calcareous marls. It

includes: *Neocardioceras juddi* (Barrois et Guerne), *Sciponoceras* sp. and *Allocrioceras* sp. The 4 m thick, Grüngrauer Mergelkalk Komplex is rotation of olive dark calcareous marl – marly limestones with hard bright marly limestones. Probably it is of zone *devonense* age. The above sediments are already of lower Turonian age Unter Rotpläner. On the south of Westphalian, the sediments with *Praeactinocamax plenus* (Blainv.) are found in two facies. In the first as the glauconitic marls and in the second as the so-called Knollenkalk above the Essener Grünsand (Fiege, 1927, Kaplan et al., 1998). The whole development is the analogy of Beds A, B and C from the Anglo-Paris Basin. The marls with mytiloides event in the upper part are situated above this development. Eastwards at the Lower Lusatia, the described development passes into argillaceous marls to silty sandstones (Musstow, 1968).

The lower Cenomanian Meissen Schichten are on the base of north Dresden region. Silty marls Mobschatz Schichten with *Rotalipora cushmani* (Morrow) are situated above. The basal sediments with fauna at site Oberau (Dietze, 1961) have not been precisely classified yet.

Fauna includes majority of elements that are reminiscent of sites at elevations on the south. However, it can be older. Glaukonitreicher Pläner in lower beds of marls with *Praeactinocamax plenus* (Blainv.) is probably equivalent of the lower part of complex F. In addition, Häntzschel (1933) reports *Hepteris septemsulcata* (A. Roem.) and *Cidaris sorigneti* Desor from Pläner.

On the south of Dresden region in Saxony the base consists of Niederschöna Schichten. Above them are the upper Cenomanian Oberhäslich and Dölzschen Schichten. Oberhäslich Sch. are developed as sandstones with abundant *Neithea aequicostata* (Lam.) and rare *Calycoceras naviculare* (Mantell), *Calycoceras newboldi* (Kossmat), *Inoceramus pictus pictus* (Sow.), *Inoceramus pictus bannewitzensis* Troeger and *Merklinia aspera* (Lam.). On the base of Dölzschen Sch. are the clays and marls. On elevations, their equivalent is the conglomerate with corals, abundant bivalves including rudists, gastropods and starfish (Svoboda, 2004). Partial equivalent of the complex F and or just of plenus event is Pennricher Sandstein with the so-called Pennricher Fauna: *Praeactinocamax plenus* (Blainv.), *Neithea notabilis* (Muenst.), *Inoceramus pictus bohemicus* (Leonh.), *Pteria raricosta* (Reuss), *Hepteris septemsulcata* (A. Roem.) a very rarely *Aequipecten arlesiensis* (Woods) (Uhlig, 1941). On elevations is the equivalent of Pennricher Sandstein, the limestone with abundant gravel and abundant fauna: *Cyclothyris* aff. *difformis* (Val.), *Praeactinocamax plenus* (Blainv.), *Opis bicornis* (Gein.), *Chlamys elongata* (d'Orb.), *Chlamys acuminata* (Gein.), *Pycnodonte vesicularis* (Lam.), *Exogyra sigmoidea* Reuss, *Exogyra reticulata* Reuss, *Exogyra haliotoidea* (Sow.), *Lophia diluviana* (Linné), *Cidaris vesiculosa* (Goldf.) and *Cidaris sorigneti* Desor. The fauna is similar to fauna from Minice and Zlončice in Czech Republic (Svoboda, 1996a). On the base above Pläner is also found: *Metoicoceras geslinianum* (d'Orb.), *Euomphaloceras septemseriatum* (Cragin) and *Pseudocalyoceras angolaense* (Spath) (Tröger, 2003, 2004). The rest of plenus Pläner belongs probably to the *juddi* zone.

In the north Sudetic Cretaceous, the sandstones with *Merklinia aspera* (Lam.) are below the dark marls containing shark teeth and only upon them are the gray marls with

*Praeactinocamax plenus* (Blainv.) and *Hepteria septemsulcata* (A. Roem.) and even higher are the marls with *Inoceramus pictus bohemicus* (Leonh.) (Fig. 5). According to Scupin (1913) the lower marls contain *Ptychodus mammillaris* Ag. the species, which was not found with *P. plenus* (Svoboda, 1996a). This is the question of the older horizon whose precise age is not clear at the present. Fauna described by Williger (1881) is different of the plenus event. The findings of foraminifers prove that marls contain the even the

1996, Naidin, 1964, Košťák, 2004, Košťák et al., 2004). In Kazakhstan, *Praeactinocamax plenus* (Blainv.) is reported together with *Inoceramus pictus bohemicus* (Leonh.). In Mangyshlak peninsula and in Kopet Dag, the Late Cenomanian sediments are partly missing below the plenus beds.

## COMPARISON WITH THE DEVELOPMENT IN BAVARIA AND HELVETIC

On the base of Bavarian Cretaceous are developed non-marine lower Cretaceous sediments filling up the karst. The lower part is formed by Amberger Erzformation and the upper by Schuttfelsschichten. The marine sedimentation starts not until Cenomanian. According to the new literature, the part of Regensburger Grünsandstein is of middle Cenomanian age and in basal beds even of lower Cenomanian age (Kauffman et al., 2000). Findings of *Aequipecten arlesiensis* (Woods) and *Actinocamax* cf. *plenus* Blainv. from Regensburger Grünsandstein (Dacqué, 1939) may belong to the primus event. Upper part Regensburger Grünsandstein and Regensburger Kalksandstein are of upper Cenomanian age. It includes abundant: *Neithea aequicostata* (Lam.), *Merklinia aspera* (Lam.) and *Rhynchostreon suborbiculatum* (Lam.) (Dacqué, 1939). Above situated Eibrunner Mergel is of upper Cenomanian to lower Turonian age. Part of the formation may belong to the *Calycoceras guerangeri* zone. The level of the so-called chondrites event is found on site Benberg up to 1.7 m from the base and level of plenus event up to 2.1 m from the base (Förster et al., 1983, Hilbrecht, 1986). The chondrites event includes: *Calycoceras naviculare* (Mantell), *Metoicoceras geslinianum* (d'Orb.), *Euomphaloceras septemseriatum* (Cragin), *Worthoceras vermiculum* (Shumard), *Hemiptyloceras* cf. *reesidei* Cobban, *Pseudocalyoceras angolaense* (Spath), *Pseudocalyoceras* cf. *harpax* (Stoliczka) and *Vascoceras diartianum* (d'Orb.). Only *Metoicoceras geslinianum* (d'Orb.) of the ammonites is found in layer with *Praeactinocamax plenus* (Blainv.). With respect to character of the sedimentation, it was the question of deep basin dividing the Bohemian Massif from Helveticum. The depression of the bottom did not continue during the Turonian and the basin was filled with inverse cycles. The evidence is also the development during upper Turonian eustatic regression.

The Cenomanian is developed in strongly condensed and reduced thickness in Helvetic. It is the part of Aubrig-Schichten and only sediments from the boundary Cenomanian-Turonian can be on the base of Seewerkalk (Hilbrecht, 1991, Weidich et al., 1983). The lower part of zone *Whiteinella archaeocretacea* is missing here.

The site Les Lattes is located on the southeast from Anglo-Paris Basin in Alpes de Haute-Provence (Thomel, 1993, Gale et Christensen, 1996). Lower parts of the upper Cenomanian are the marls with *Calycoceras guerangeri* (Spath), *Eucalycoceras pentagonum* (Jukes-Browne), *Pseudocalyoceras lattense* (Thomel), *Calycoceras naviculare* (Mantell), *Thomelites sornayi* (Thomel) and *Inoceramus pictus* Sow. The silty marls with glauconitic-sandy base are located on the silty marls of the *guerangeri* zone. Glauconitic base is 1.07 m thick and the marls 4.6 m. In the upper levels occur: *Metoicoceras geslinianum* (d'Orb.), *Worthoceras* sp.

LANDMASS IN CENTRAL EUROPE ON BOUNDARY UPPERMOST CENOMANIAN / LOWER TURONIAN

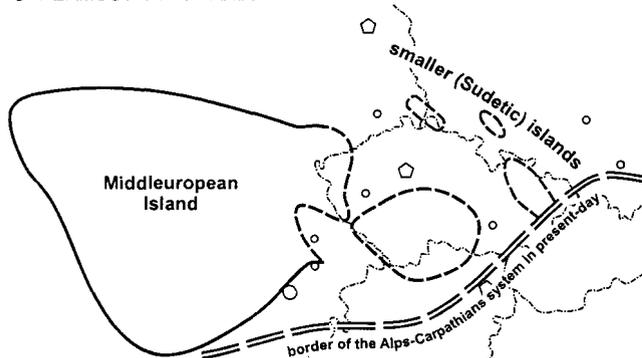


Fig. 5 Palaeogeographic map of Hercynian Cretaceous during uppermost Cenomanian and lower Turonian.

older Cenomanian (Gorczyca-Skala, 1977). In the Opole Cretaceous, the sandstones from site Groszowice (Leonhard, 1897) according to fauna *Acanthoceras rhotomagense* (Brong.), *Turrilites costatus* (Lam.) and finding of belemnite belong to primus event. Sites in vicinity of Osoblaha and Glubyczyz are equivalent to sandstones from surroundings of Hořice. Upon sandstones are found the dark marls with glauconitic base and findings of upper Cenomanian foraminifers (Alexandrowic et Radan, 1973, Klapciński et Teisseyre, 1981). Upper dark marls are of the lower Turonian age. Basement sandstones fill up the canyon like pre-Cenomanian surface and only dark lower Turonian marls level up the bottom (Kotański et Radwański, 1977). These sites are analogous to Eibrunner Mergel from the Bavarian Cretaceous. Opole Cretaceous was located on the area out of the main sea-currents during the plenus event.

On elevation of the Polish Jurassic is the upper Cenomanian developed as condensed horizon of calcareous conglomerates with *Schloenbachia* cf. *lymensis* Spath, *Praeactinocamax plenus* (Blainv.), *Inoceramus pictus bohemicus* (Leonh.), *Conulus subrotundus* (Mantell) and *Pyrina ovalis* d'Orb. (Marcinowski, 1972, 1976). Further to the east in surroundings of Annopol, it similarly develops into only 0.5 m thick horizon of sandy marls on the phosphatized hardground. It contains: *Schloenbachia lymensis* Spath and *Praeactinocamax plenus* (Blainv.) (Marcinowski, 1980).

## RUSSIAN PLATFORM AND ADJACENT AREAS, KAZAKHSTAN

The "Plenus event" is recorded also from Lithuniana, Belarussia, Ukraine, Kazakhstan, Turkmenistan to Tadjhikistan (Gale et al., 1999, Marcinowski, 1980, Marcinowski et al.,

and *Inoceramus pictus* (Sow.). These are sharply overlain by glauconitic sandy siltstones with abundant bivalves fauna, brachiopods and worms. Rarely it contains: *Metoicoceras geslinianum* (d'Orb.) and *Sciponoceras gracile* (Shumard). Often are found: *Praeactinocamax plenus* (Blainv.), *Hamulus* sp. and *Oxytoma seminudum* (Dames). Lower marls are equivalent of Jeffries Beds 1–3. Glauconitic siltstones are equivalent to Beds 4–5. The findings from the lower marls are reminiscent of site Benberg in Bavaria.

## THE DEVELOPMENT IN ANGLO-PARIS BASIN

The basic division of Plenus Marls was assigned already by Jeffries (1962, 1963a, 1963b). Further studies led to specification of the ammonites and foraminifers distribution (Robaszynski et al., 1987, Keller et al., 2001, Gale et al., 2005).

The uppermost levels of Grey Chalk of *Calycoceras guerangeri* age form the basement of Plenus Marls. It is the gray bioturbated chalk. Against the Plenus Marls, it is finished with erosion boundary with washouts and bioturbations into the basement. It includes: *Aequipecten beaveri* (Sow.), *Entolium orbiculare* (Sow.), *Neithea quinquecostata* (Lam.), *Plicatula inflata* Sow., *Inoceramus pictus* Sow., *Pycnodonte vesicularis* (Lam.) and *Holaster trecensis* (Leymerie).

Bed 1 is formed by marls passing upwards into the marly chalk. Fauna: *Aequipecten beaveri* (Sow.), *Inoceramus pictus* Sow., *Entolium orbiculare* (Sow.), *Neithea quinquecostata* (Lam.), *Pycnodonte vesicularis* (Lam.), *Holaster trecensis* (Leymerie), *Orbirhynchia multicostata* Pettitt, *Ctenothrissa* sp. Very rarely it includes: *Metoicoceras geslinianum* (d'Orb.) and *Calycoceras* sp. Bed is finished with erosion boundary.

Bed 2 is represented by the marls passing into the marly chalk. It includes: *Metoicoceras geslinianum* (d'Orb.), *Scaphites equalis* Sow., *Puzosia dibleyi* Spath, *Calycoceras naviculare* (Mantell), *Aporrhais* sp., *Solarium* sp., *Gramatodon* cf. *cenomanense* (d'Orb.), *Neithea quinquecostata* (Lam.), *Entolium membranaceum* (Nilss.), only at the base *Pycnodonte vesicularis* (Lam.), *Rhynchonella lineolata carteri* Davidson. and *Calliderma smithiae* (Forbes).

Beds 2–3 and 3 are marly chalks passing upwards into the gray chalks. Fauna is very rare. In Beds 2–3 it is similar to Bed 2. In Bed 3 *Metoicoceras geslinianum* (d'Orb.) is found and occurrence of *Rotalipora cushmani* (Morrow) ends up. The bed is finished with erosion boundary.

Beds 4–5 are marls passing upwards into the marly chalk. Fauna: *Praeactinocamax plenus* (Blainv.), *Metoicoceras geslinianum* (d'Orb.), *Sciponoceras gracile* (Shumard), *Oxytoma seminudum* (Dames), *Aequipecten arlesiensis* (Woods) and *Ditrupa difformis* (Lam.). Bed 5 is the last bed with *Globigerinelloides bentonensis* (Morrow) and it is finished with erosion boundary.

Bed 6 is composed of the marls containing the redeposited fauna from the basement and *Globigerinelloides bentonensis* (Morrow) is absent in this bed. Bed 7 is the chalk with *Metoicoceras geslinianum* (d'Orb.), *Pseudocalycoceras angolaense* (Spath), *Euomphaloceras septemseriatum* (Cragin), *Sciponoceras gracile* (Shumard), *Cidaris hirudo* Sorignet and *Orbirhynchia wiesti* (Quenstedt). Bed 8 is the gray chalk with *Euomphaloceras septemseriatum* (Cragin). The basal beds of the nodular chalk from Ballard Cliff Member belong also to the zone *Metoicoceras geslinianum*.

The lower Cenomanian beds in the southwest England are build into the condensed development similarly to bed C (Kennedy, 1970). The most typical example is the site White Hart Sandpit (Wilmington, Devon) (Wright et Kennedy, 1981, Hilbrecht, 1986). On the middle Cenomanian limestones of Bed B is deposited glauconitic sandy chalk with phosphate concretions and quartz pebbles. On the base are redeposited phosphatised cores of upper Cenomanian ammonites from the *guerangeri* zone: *Euomphaloceras euomphalum* (Sharpe), *Schloenbachia lymensis* Spath., *Calycoceras naviculare* (Mantell), *Newboldiceras* sp., *Protacanthoceras bunburianum* (Sharpe) and *Scaphites equalis* Sow. Above is found redeposited *Praeactinocamax plenus* (Blainv.) and above it in hardground are *Euomphaloceras septemseriatum* (Cragin) and *Allocrioceras annulatum* (Shumard). Together with both species occurs *Metoicoceras geslinianum* (d'Orb.). In the uppermost part of the hardground is found the *Sciponoceras* sp. together with *Cidaris hirudo* Sorignet. Upward is the chalk of *Watinoceras devonense* age with redeposited fauna of *Neocardioceras juddi* zone at the base. Due to that Bed C is of same age as Jeffries Beds 1–8.

Next condensed development is located in Normandy. Craie d'Antifer is developed as nodular chalk with hardgrounds and here and there. Because of the base development, it is located directly on the chalk of *jukesbrownei* zone. The redeposited fauna forms the analogy to Bed C (Juignet et Kennedy, 1976).

The upper Cenomanian is represented by two units on the southwest of Anglo-Paris Basin. The lower are Marnes à Ostracées, marls passing into limestones, which include lumachelles with *Pycnodonte biauriculata* (Lam.) and *Rhynchostreon suborbiculatum* (Lam.). On the base they include: *Puzosia austeni* (Sharpe), *Calycoceras bruni* (Fabre), *Pseudocalycoceras moustieriensis* Thomel, *Pseudocalycoceras cf. lattense* Thomel, *Thomelites sornayi* (Thomel) and *Thomelites prerusticum* (Thomel). The upper layers contain *Calycoceras naviculare* (Mantell) (Juignet et al., 1973, Amédro et al., 1981, Kennedy et al., 1981). Upwards are located Sables à *Catopygus obtusus*. These are sandy marls or chalky sandstones sharply deposited on the basement. It includes: *Calycoceras naviculare* (Mantell), *Metoicoceras geslinianum* (d'Orb.), *Euomphaloceras septemseriatum* (Cragin), *Sciponoceras gracile* (Shumard), *Metengonoceras dumbli* (Cragin), *Proplacenticeras cf. memoriaschloenbachi* (Laube et Bruder), *Forbesiceras* sp., *Vascoceras diartianum* (d'Orb.), *Rhynchostreon suborbiculatum* (Lam.), *Rastellum carinatum* (Lam.), *Gryphaeostrea canaliculata* (Sow.), *Terabratala phaseolina* Lam. and *Hamulus deformis* (Lam.). The fauna is similar to the lower part of the *geslinianum* zone from the Bohemia and chondrites event from Bavaria. Above is found the glauconitic chalk of *Neocardioceras juddi* zone. It is possible to find redeposited fragments of basement with fauna within this zone at some sites (Juignet et al., 1973, Kennedy et Juignet, 1977). The finding of redeposited *Praeactinocamax plenus* (Blainv.) on base of glauconitic chalk (Jefferies, 1963a) is very interesting.

The glauconitic clayey marls with quartz pebbles and dark silicites called Tourtia de Mons (Cornet, 1923) are located on the basement of various age in Belgium. Within these is found: *Praeactinocamax plenus* (Blainv.), *Merklinia aspera* (Lam.), *Entolium orbiculare* (Sow.), *Chlamys robinaldina* (d'Orb.), *Neithea quadricostata* (Sow.), *Rhynchostreon suborbiculatum* (Lam.), *Lopha diluviana* (Linné), *Pycnodonte vesicularis* (Lam.), *Exogyra haliotoidea* (Sow.) and *Ditrupa deformis* (Lam.). The sediments above the Tourtie are formed at some sites of Dièves inférieures by the marls with *Praeactinocamax plenus* (Blainv.) at the base. Tourtia de Mons is an equivalent of Jeffries Beds 4–5 and Dièves inférieures possibly of Beds 6–7.

## AQUITANIA AND PROVENCE

In Aquitania is on the base of upper Cenomanian found subunit Dm. These are marls with thickness of 1.5 m contain *Thomelites lattense* (Thomel) and *Pseudocalycoceras* sp. The subunit Es with thickness of 3.5 m is formed by sandstones with *Pycnodonte bauriculata* (Lam.). Subunit Fc are limestones with *Ichthyosarcolithes triangularis* Desm. Subunit G1s are sandstones with *Rhynchostreon suborbiculatum* (Lam.) and *Neolobites vibrayanus* (d'Orb.). Subunit G2c are limestones of 3 m thickness with *Calycoceras naviculare* (Mantell), *Euomphaloceras septemseriatum* (Cragin) and *Metoicoceras geslinianum* (d'Orb.) on the base. Subunit G2m are marls with *Rhynchostreon suborbiculatum* (Lam.). It contains *Metoicoceras geslinianum* (d'Orb.) on the base. Upper part of unit possibly belongs to the zone *juddi* (Francis, 1984, Moreau et al., 1983, Moreau, 1996).

The upper part of Marcouline formation belongs to the upper Cenomanian in Provence. These are the biodetritic limestones with *Calycoceras gentoni* (Brong.) and sandstones to sandy marls with *Pseudocalycoceras harpax* (Stoliczka). Above the sandstones is the Fontblanche formation with thickness of approximately 20 m. It includes zones *guerangeri*, *geslinianum* and *juddi*. The sequence passes into the micritic and biomicritic limestones to biodetritic ones. The environment developed from the deeper into the shallower. On the base is found *Eucalycoceras* cf. *pentagonum* (Jukes-Browne) and rudists *Caprinula* start to appear. Above is the erosion boundary. The limestones at the top gradually diminish in zone *geslinianum* the rudists of family Caprotinidae and the reduction of the family Caprinidae and genus *Eoradiolites*, *Neoradiolites* and *Praeradiolites* takes place. At the end of zone *juddi* Caprinidae and genus *Eoradiolites* disappear. In whole of the Cenomanian occur: *Durania arnaudi* (Choffat), *Radiolites lusitanicus* (Bayle) and *Radiolites peroni* (Choffat). In the *juddi* zone rudists of genus *Vaccinites* appear. On the rudist limestones is the erosion boundary and above it are already the lower Turonian marls with *Mammites nodosoides* (Schloth.) and *Fagesia superstes* (Kossmat) (Philip, 1974, 1978, 1998).

## THE MIDDLE EAST

Upper Cenomanian ammonite *Neolobites vibrayanus* (d'Orb.) is found in upper dolomites and limestones of the Hazera formation at south Negev in Israel. Green clays passing upwards into the silts and limestones with total thickness of 12 m form

the lowest part of the formation. In the clays is found: *Costagrya olisiponensis* (Sharpe), *Eucalycoceras rowei* (Spath) and *Calycoceras* sp. In the lower part of the limestones is found: *Vascoceras cauvini* Chudeau, *Metoicoceras geslinianum* (d'Orb.) and *Euomphaloceras* sp. In the upper part of limestones is found *Vascoceras cauvini* Chudeau only. The clays and marls with *Vascoceras pioti* (Peron et Fourtau) appear above. In the northeast Negev on dolomites of the Hazera formation is found white chalk of 7 m thickness with *Costagrya olisiponensis* (Sharpe) and with two layers with *Neolobites vibrayanus* (d'Orb.). After the chalk follows 0.5 m of yellow-pink limestone with *Metoicoceras geslinianum* (d'Orb.), *Vascoceras cauvini* Chudeau, *Calycoceras* sp. and *Euomphaloceras* sp. Above is situated 0.5 m of limestone with *Vascoceras cauvini* Chudeau and 4 m of pinkish chalk with *Vascoceras pioti* (Peron et Fourtau) (Lewy et al., 1984, Buchbinder et al., 2000).

## AFRICA

Brown siltstones are found on brown limestones finished with bottom transgressive cycle at site Salinas in Angola. Lower siltstones with thickness of 3 m rarely contain *Calycoceras naviculare* (Mantell). The brown siltstones at the top with thickness of 6 m include 8 rows of gray calcareous concretions with abundant *Rhynchostreon suborbiculatum* (Lam.). Only 2.5 m above the base are found abundant ammonites: *Calycoceras naviculare* (Mantell), *Puzosia dibleyi* (Spath), *Pseudocalycoceras angolaense* (Spath), *Euomphaloceras septemseriatum* (Cragin), *Metoicoceras geslinianum* (d'Orb.), *Sciponoceras gracile* (Shumard), *Vascoceras* cf. *cauvini* Chudeau and *Watinoceras coloradoense* (Henderson). The presence of the last two species here documents the occurrence of zones *juddi* and *devonense* (Cooper, 1978).

## NORTH AMERICA

Upper Cenomanian is developed as marly Hartland Shale Member and Bridge Creek Limestone with rhythmic rotation of limestone layers with dark marls and interbeds of bentonites. On basis of Bridge Creek Limestone is Bed 63 with *Calycoceras naviculare* (Mantell), *Pseudocalycoceras angolaense* (Spath) and *Metoicoceras geslinianum* (d'Orb.). *Rotalipora cushmani* (Morrow) disappears at Bed 66. The Bed 67 contains: *Pseudocalycoceras angolaense* (Spath), *Euomphaloceras septemseriatum* (Cragin), *Metoicoceras geslinianum* (d'Orb.), *Sciponoceras gracile* (Shumard) and *Allocrioceras annulatum* (Shumard). Bed 68 is the last with *Globigerinelloides bentonensis* (Morrow). Bed 69 is composed of bentonite. In Bed 77 is found *Sciponoceras gracile* (Shumard) and *Worthoceras vermiculum* (Shumard). In Bed 79 appears *Neocardioceras juddi* (Barrois et Guerne) (Keller et Pardo, 2004, Kennedy et al., 2000).

## COMPLETION OF PROFILES

The hiatuses are reported in Anglo-Paris Basin between Beds 3 and 4, again between Beds 5 and 6 and again between Bed 8

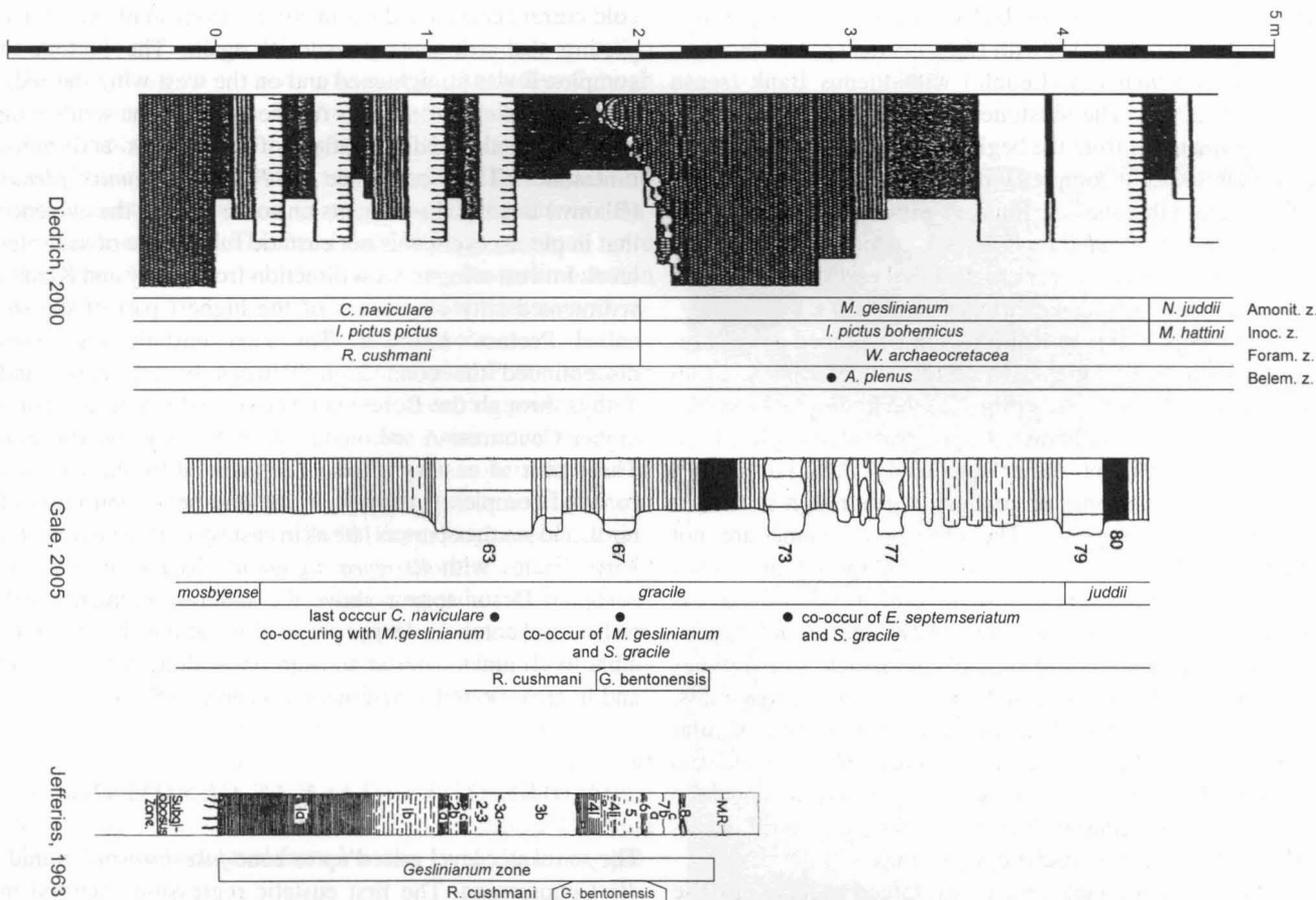


Fig. 6 Stratigraphic correlation of the *geslinianum* zone between northern Germany, North America and Anglo-Paris basin.

and Ballard Cliff Member. It is caused by the flow condition, basin depth and differing environment production in each layer. In Beds 4–5 the productivity was extraordinary high. The beds are thicker than elsewhere as it is documented by presence of *Praeactinocamax plenus* (Blainv.). But the equivalent of the Plenus Bank (sensu Diedrich, 2001) is completely missing there (Fig. 6). The Plenus Bank originated in deep basin and under increased environmental production during the hiatus between Beds 3–4, which corresponds to Bed 67 from Greenhorn Sea. The Bed C includes *Ditrupa difformis* (Lam.) and similarly to occurrence of redeposited *Praeactinocamax plenus* (Blainv.) in Bed 6, it is with the highest probability redeposited material. Another hiatuses are in the uppermost part of the zone *geslinianum*, *juddii* and *devonense* and in the marginal parts of the basin above the Bed C and Sables à *C. obtusus*. In the Bohemian and Saxonian Cretaceous sometimes wedge out the basal parts of complex F. The equivalent of upper part of complex F above plenus event is missing at the upper subcycle of the siltstone formation.

#### COMPARISON OF OCCURRENCE OF UPPER ZONE *GESLINIANUM* IN BOHEMIA AND GERMANY

With the deepening of Bavarian and North Sudetic Cretaceous Basins is coherent, even the genesis of intermittent basins of SW-NE orientation in central Bohemia on both

sides of Unhošť-Tursko elevation during complete upper Cenomanian. Only the complex F generated the first axis of the basin detectable from Bavaria through the north territory from Unhošť-Tursko elevation and from there through České středohoří mountains into Saxony down to Oberau.

Unlike the Bohemia, where on the complex F is developed the basal lower Turonian strata, in Saxony the spiculit the so-called Obere Plenus Zone developed on the Pennricher Sandstein. In its lower part are found ammonites, which correspond to findings from Jeffries Beds 6 to 8. The above-located spiculit is poor in fossils and is probably of the *juddii* zone age. Even the spreading of fauna with *Exogyra sigmoidea* and *Cidaris sorigneti* is fixed on equivalents of Pennricher Sandstein. The findings of big gastropods *Cerithium bircki* Gein. and *Pleurotomaria* sp. together with *Opis bicornis* (Gein.) at sites Kahlbusch (Dohna) and Gamühügel hopefully represent the shallowing. Again, the findings of *Synhelia gibbosa* (Muenst.) are documenting greater depth as it occurs in Bohemia as late as in Turonian.

The complex F begins in vicinity of Odolena Voda by wedging bed with *Calycoceras* sp. and *Inoceramus pictus bohemicus* (Leonh.) and after that follow marls and spiculites. In vicinity of Kostelec, there is sandy bed on the base with *Rhynchostreon suborbiculatum* (Lam.). At sites where this layer is missing the level with *Praeactinocamax plenus* (Blainv.) is directly at the base of complex F and marls above it are thicker. The equivalent of marls close to the level with *Praeactinocamax plenus* (Blainv.) is the lowest

level Pennricher Sandstein. Unfortunately, it is not possible to compare the basal bed with *Calycoceras* sp. and *Inoceramus pictus bohemicus* (Leonh.) with Plenus Bank (sensu Diedrich, 2001). The siltstone formation are rapidly sedimented siltstones from the beginning of plenus event. Fauna is similar to that of complex F base from vicinity of Kostelec nad Labem. Siltstones are finished with level containing the *Praeactinocamax plenus* (Blainv.), which is sometimes eroded and the guards occur in the basal early Turonian bed. Its partial equivalent is Pennricher Sandstein s. s.

The complex F is in Kolín region developed as calcareous sandstones or limestones divided in two parts. From the boundary of both parts originate the findings of *Praeactinocamax plenus* (Blainv.). Upper part of complex is in the same facies but either the sandy material amount decreases in limestones or contrary it gets rough in case of sandstone developments. The species of fauna are not changing. The findings of corals and rudists are rather exotic. Rudistic fauna at sites Radovesnice and Zibohlavý is prevailingly composed of genus *Petalodontia* and *Caprotina* at it is reminiscent of older Cenomanian. The findings of gastropods *Actaeonella* and *Trochoacteon* approach this. Rudist fauna on sites Miskovice and Mezholezy is similar to fauna from the uppermost Cenomanian in France and Portugal. But the species vary. It is possible to find here *Puzosia austeni* (Sharp). It concerns the most north occurrence of Cenomanian rudistic limestones.

The mentioned facts may be explained as large eustatic transgression, which occurred during subsidence of two narrow basins at the beginning of genesis of complex F. The extent of this transgression reached the extent of eustatic transgression from the beginning of zone *nodosoides*. The sea covered even the area outside of these basins. The first basin retained the direction SW-NE and the second was along the Elbe line direction. In the deepest parts of basin sedimented the calcareous sandstones and marls with spicules. Gray siltstones sedimented in the northeast wing of the lower part of upper subcycle of siltstone formation. On the south wing sedimented sandstones with *Rhynchostreon suborbiculatum* (Lam.) and limestones with rudists. During this time only warm currents from the Tethys occurred. Either the next eustatic transgression followed or the large ascent of cold water. In this time appeared the low cold counter current from the Arctic, which caused extension of fauna in facies with *Exogyra sigmoidea* Reuss and *Cidaris sorigneti* Desor. Boreal *Praeactinocamax plenus* (Blainv.) extended from eastwards. Wide areas were flooded, which formerly were the source of silt material for lower part of complex F. The extent of eustasy was so large that from plenus event we only know the redeposited coastal fauna from Pennricher Sandstein and from Tourtia de Mons in Belgium. Further, it is possible that coastal sediments from age of complex F are dark claystones and siltstones from around Teplice with brakish fauna described by Čech and Váně (1988). Cenomanian sediments are covered by middle Turonian sandstones, only. That would mean temporal change of climate from semi-arid to humid in age of complex F. This would also indicate the development from Anglo-Paris Basin where in Bed 4 and in Tourtia de Mons strongly increases the amount of clayey material. After plenus event sedimentation passed back into pre-plenus state. The low

cold current ceased and warm current from south was transporting the sedimentary material again. The bottom of complex F was straightened and on the west wing the sedimentation of claystones was regenerated. On the south wing regenerated the sedimentation of sandstones and rudist limestones. The occurrence of *Praeactinocamax plenus* (Blainv.) in coastal sediments on south wing is the evidence that in plenus event was not eustatic subsidence of seawater level. In west wing in west direction from Slaný and Kladno sedimented silty claystones of the highest part of the so-called Pecínov Member. The next eustatic regression discontinued the connection between boreal region and Tethys through the Bohemian Massif and stratigraphically higher Cenomanian sediments are in Saxony and Bavaria. The extent of eustasy is also documented by the fact that basin of complex F kept declining and next connection of north and south occurs as late as in eustasy during *nodosoides* zone. Facies with *Exogyra sigmoidea* Reuss and *Cidaris sorigneti* Desor appear above the shallow sediments with rudists and corals in deeper parts on elevations. It is not possible to eliminate shorter transgression along the Elbe line and in areas bound to sedimentation area in Silesia.

#### MODEL OF EUSTASY IN CENOMANIAN

The sea water level raised up to zone *jukesbrownei* in middle Cenomanian. The first eustatic regression occurred in the middle of zone *guerangeri*. It is recognized by genesis of sandstones in Aquitania (Bed E) and in Provence (sandstones in the highest part of Marcouline formation). After that, the water level started to increase again. At the end of zone *guerangeri* the water level decreased and again it started to increase. In Anglo-Paris Basin sedimented the Bed 1, in Aquitania sedimented Bed G1, in Saxony sedimented Oberhäslich Schisten, in German-Polish Basin the sedimentation was changed and Bed 63 appeared in Greenhorn Sea. During the next increase of water level in Anglo-Paris Basin Beds 2 and 3, in Aquitania lower part of unit G2, in Saxony base Dölzchen Schichten, in German-Polish Basin and in Bavarian Cretaceous appears the Chondrites Event. The following decline of the seawater level lasts through the extinction of foraminifers *Rotalipora cushmani* (Morrow) and after sedimentation of Puzosia Event I appears the so-called Plenus Bank and Bed 67 in Greenhorn Sea. This bed must not necessarily have equivalent outside of Vocontian trough with basin of Alpes de Haute-Provence. Gradual increase of seawater level, which is greater than the recent greatest eustasy. During the plenus event, the flow regime is changed what causes the extension of the so-called fauna with *Exogyra sigmoidea* and *Cidaris sorigneti* caused by genesis of low cold current from the Arctic. Sediments with *Praeactinocamax plenus* (Blainv.) originate in greater depths. From elevations rising above the seawater level is eroded before all the clayey material due to climate change during this eustasy. After plenus event pre-plenus sedimentation continues on the Bohemian Massif. In Anglo-Paris Basin sediments the upper part of Bed C, in Aquitania unit G2. Bed 68 in Greenhorn Sea probably corresponds with complex F and plenus event. After another short decline, the seawater level reaches back to its level before complex F.

On the margin of the Bohemian Massif and in the Saxony continues the sedimentation of spiculites the so-called Obere Plenus Zone without connection with Tethys through the Bohemian Massif. In Provence the sedimentation of rudist limestones and in Anglo-Paris Basin sediments Bed 7–8, Ballard Cliff Member and Craie du Cap Fagnet, the beds at the top of Sables à *C. obtusus* and in Aquitania subunits G2m and T1m. This level does not vary as much up to the zone *nodosoides*, which is proved by the sedimentation of rudist limestones in Provence or the siltstones with *Rhynchostreon suborbiculatum* (Lam.) in Angola.

During the sedimentation of complex F the seawater level probably continued ascending. In certain point (Fig. 7), the penetration of cold water from the Arctic occurred and it established low counter flow through the Bohemian Massif. During another seawater level rise the surface level of warm water extended and low counter flow disappeared. During eustasy during *nodosoides* zone seawater level rapidly reached the former level present during sedimentation of the upper part of complex F and the plenus event did not repeat. During another seawater level increase the low counter current through the Bohemian Massif regenerated.

Keller et al., (2001) assume that decrease of seawater to level Bed 1, gradual decrease of level in Bed 2 to 3, decrease of level between Bed 3 to 4 and in Bed 4 another gradual rise. Contrary to Keller et al., (2001) assumes Diedrich (2001) decrease of level from Puzosia Event including plenus event.

## CONCLUSIONS

The Bohemian Massif kept constantly ascending in Cenomanian. During single declines without faults were generated basins of each complex in direction SW-NE with depths of couple tenths of meters and width of tenths of kilometers. Sedimentation of complexes concluded with gradual uplift of massif and eustatic regressions. The complexes in direction SW-NE appeared during eustatic transgressions at marginal parts of ascending area and it belongs actually to south boundary of the recent North Sudetic Cretaceous. Unlike the previous basins of complex F basins from end of Cenomanian and beginning of Turonian kept ascending. One in direction SW-NE was connecting Saxony and Bavarian Cretaceous Basin and the second was in direction of Elbe line.

After genesis of the complex F basins eustatic transgression occurred, which flooded the area even outside this basin. The sediments of complex F were preserved on the Bohemian Massif only due to their constant decline in direction of basin axis. This decline was similar to above Lower and Middle Turonian shoreface sediments. The occurrence of *Praeactinocamax plenus* (Blainv.) in shoreface sediments is an evidence that plenus event was not the eustatic sea-level fall. Absence of equivalents in the uppermost part of *geslinianum*, *juddi* and *devonense* zones means that even during genesis of constantly declining basin the gradual uplift of the Bohemian Massif occurred! The complex F is a lithologic unit generated during eustasy comparable to beginning of eustasy in zone *nodosoides* and in its Middle part the plenus event occurred. Facies with

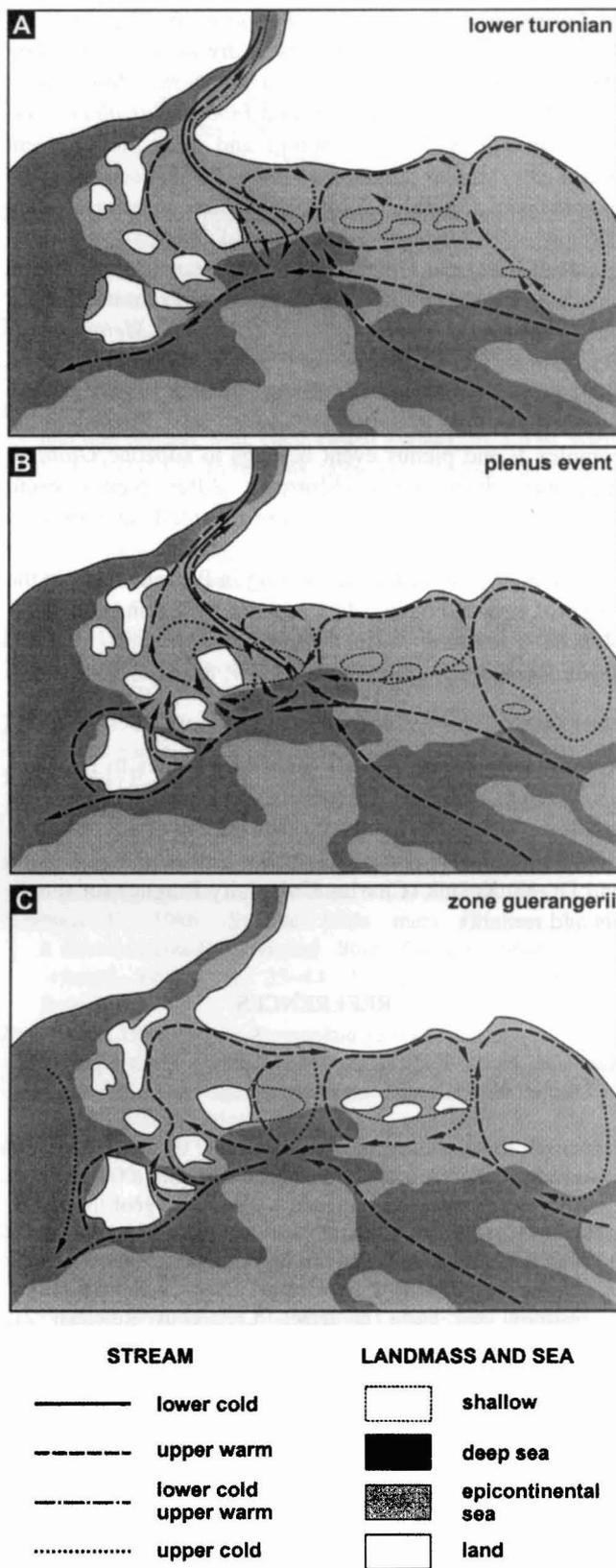


Fig. 7 Palaeogeographic maps of Europe with sea streams in upper Cenomanian and lower Turonian.

*Exogyra sigmoidea* Reuss and *Cidaris sorigneti* Desor is found together with *Praeactinocamax plenus* (Blainv.), which may not have been the direct part of the ecosystem on sea scarps. Its dispersion is determined by area with main currents.

On the base of zone *geslinianum* is found poor fauna with the most common species: *Calycoceras naviculare* (Mantell), *Inoceramus pictus pictus* Sow., *Inoceramus pictus bannewitzensis* Troeger and *Inoceramus pictus concentricoundulatus* Troeger. Before and after plenus event occurs the similar ammonites fauna: *Pseudocalycoceras angolaense* (Spath), *Euomphaloceras septemseriatum* (Cragin), *Metoicoceras geslinianum* (d'Orb.), *Sciponoceras gracile* (Shumard), *Allocrioceras annulatum* (Shumard) and *Vascoceras diartianum* (d'Orb.). In plenus event itself occur only: *Praeactinocamax plenus* (Blainv.), *Metoicoceras geslinianum* (d'Orb.), *Sciponoceras gracile* (Shumard) and *Hepteria septemsulcata* (A. Roem.), which is *Ditrupa difformis* (Lam.) and *Hamulus deformis* (Lam.). Eustasy of the complex F and plenus event belongs to subzone *Globigerinelloides bentonensis* (Morrow). After plenus event disappears *Calycoceras naviculare* (Mantell) and *Puzosia dibleyi* (Spath).

The zone *geslinianum* is missing in Provence within the range of Lower Plenus Marl and after breaking the Fontblanche formation base follows the highest part of *geslinianum* zone equivalent to Bed 7, 8 and of zone *juddi*.

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# THE EARLIEST BELEMNITES: NEW RECORDS FROM THE HETTANGIAN OF BELGIUM AND LUXEMBOURG

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**Abstract:** Belemnites s. str. (Belemnitida) appeared in Europe not earlier than the basal Lower Jurassic with the earliest representatives of the suborder Belemnitina. These ancestral forms, present in the Hettangian of Germany, Northern Ireland and Belgium are so rare that every single specimen may shed new light on the dawn of the first true belemnites. Recent field research by the authors in the Hettangian of Belgium and Luxembourg yielded some isolated rostra assignable to the Passaloteuthididae (*Schwegleria*) and the Hastitidae (aff. *Subhastites*) as well as coleoid armhooks. This new material shows a formerly unrecognized heterogeneity of morphological features in early belemnites. Though the records are isolated, two lineages can be hypothesized in the Hettangian and Sinemurian Belemnitina: the Passaloteuthididae and the Hastitidae, both present as soon as the *liasicus* Zone. However, more complete and stratigraphically well set material is needed in order to confirm this working hypothesis.

**Key words:** Belemnites, Hettungian, Luxembourg

## INTRODUCTION

The Belemnitida (belemnites s. str.) represent the most important order within the fossil Coleoidea by number of species and frequency of the fossil record. Nonetheless, little is known about their origin: reliable fossil data about early belemnites is scarce, so that every single specimen gains a certain importance. The opinions about the earliest belemnites have diverged notably in the past. Most authors agree that the first belemnites were simple, conical Passaloteuthididae from the Early Lower Jurassic (Doyle et al., 1994). These are at the same time the first representatives of the suborder Belemnitina whilst the Pachybelemnopseina (sensu Rieggraf et al., 1998) are not documented before the Middle Jurassic. The recent description of new material assignable to the early Hettangian genus *Schwegleria* (Weis & Delsate, 2005) represents an opportunity to address the problem and reconsider the facts under the light of these new records from the Belgian Lower Jurassic.

## THE EARLIEST BELEMNITES: HISTORICAL REMARKS

Pre-Jurassic belemnite records have been reported occasionally but were reclassified mostly as aulacocerid or phragmoteuthid coleoids. *Eobelemnites caneyensis* from the Mississippian of Oklahoma (Flower, 1945) represents a belemnite phragmocone but its stratigraphical position is considered as dubious. *Jeletzkyia douglassae* from the Upper Carboniferous of Illinois (Johnson & Richardson, 1968) displays ten hook-bearing arms, but no phragmocone or rostrum and is just likely to be a phragmoteuthid or aulacocerid arm-crown (Doyle et al., 1994). *Permoteuthis groenlandica*, from the Permian of East Greenland (Rosenkrantz, 1946) has been redefined a phragmoteuthid proostracum by Jeletzky (1966: 38). The Sinobelemnitidae,

described by Zhu & Bian (1984) from the Triassic of Sichuan, are considered by Doyle et al. (1994) to be “the only serious contenders in the search for pre-Jurassic belemnites” (p. 8). These Chinese records however need further investigations in order to specify their true nature. Judging by the figures, they could represent true belemnites, showing remarkable similarities with representatives of the Pachybelemnopseina, known from the Middle and Upper Jurassic.

According to most authors, belemnites s. str. appeared in the Early Lower Jurassic and may descend from Triassic Aulacocerida or Phragmoteuthida, or a yet unknown ancestor. Hettangian belemnites have been figured by Tate (1869), Schwegler (1939) and Weis & Delsate (2005). In Europe, the Belemnitida are first known in the Hettangian with the genus *Schwegleria*. Tate (1869) was the first to figure a Hettangian belemnite: “*Belemnites praematurus*” from the *angulata* Zone of Northern Ireland (Fig. 1). There was, however, little attention drawn to this single record and for many years, the unofficial title of “the oldest belemnite” was attributed to *Nannobelus acutus* from the Sinemurian (Quenstedt, 1845–1849; Naef, 1922). This picture changed with the work of Schwegler (1939) who described three new species, *Nannobelus feifeli*, *Nannobelus praecox* and *Holcoteuthis* (?) *pilonoti*, from the Hettangian *liasicus* Zone of Steinberg bei Nürtingen

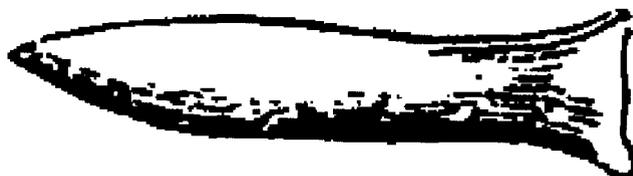


Fig. 1 “*Belemnites praematurus*” Tate, 1869 (original figure, scale 1 cm).

(Southwest Germany). Riegraf (1980) created the genus *Schwegleria* for these dwarf ancestral forms. The same author figured a belemnite phragmocone from the *angulata* Zone of Oldentrup bei Bielefeld, Northern Germany (Riegraf, 1982). Later on, Riegraf (1996) described cephalopod arm hooks, *Paraglycerites*, from the *planorbis* Zone of Tübingen-Bebenhausen (Southwest Germany) which he linked with the *Schwegleria* rostra. Some ambiguous records are specified in Riegraf (1996). Schlegelmilch (1996) redescribed the original material of Schwegler (1939), and compared it with *Nannobelus acutus* from the Sinemurian, considering this species to be a direct descendant of *Schwegleria feifeli*.

### NEW RECORDS OF BELEMNITES IN THE HETTANGIAN OF BELGIUM AND LUXEMBOURG

During the last 10 years, micropalaeontological research in marly Hettangian sediments of Southeast Belgium resulted in the discovery of some isolated belemnite rostra and fragments. The site of Fontenoille, *liasicus* Zone yielded 3 determinable rostra of *Schwegleria* (Belemnitina, Passaloteuthididae) belonging to *S. feifeli* and *S. psilonoti*, 1 fragment of *Schwegleria* sp. and a belemnite phragmocone, similar to the one figured by Riegraf (1982) from the *angulata* Zone of Oldentrup. Further research in the *planorbis/liasicus*-Zone of Vance yielded a stem-fragment which diverges considerably from the conical *Schwegleria* shape and is similar to the hastate genus *Subhastites* (Belemnitina, Hastitidae) from the Pliensbachian. These new records from the Belgian Hettangian are detailed in Weis & Delsate (2005). Furthermore, Delsate & Thuy (2005) mention fragmentary coleoid arm hooks from the Hettangian *planorbis* Zone of Bourglinster, Luxembourg.

### DISCUSSION

The fossil record reveals that the Belemnitida are represented since the Early Jurassic Hettangian by the suborder Belemnitina, with the Passaloteuthididae and the Hastitidae. The Pachybelemnopseina are documented since the Middle Jurassic (Bajocian/Aalenian) (Fig. 2). The position of the Sinobelemnitidae from the Upper Triassic is ambiguous, but currently we can not exclude with certainty that they are

early representatives of the Pachybelemnopseina. The Sinobelemnitidae certainly need further investigation in order to determine their true nature.

The isolated records of belemnites in the European basal Jurassic allow a hypothesis of two lineages in the Belemnitina during the Hettangian and Sinemurian (Fig. 3): the Passaloteuthididae (with *Schwegleria*, *Nannobelus* and *Coeloteuthis*) and the Hastitidae (with *Subhastites*). This idea

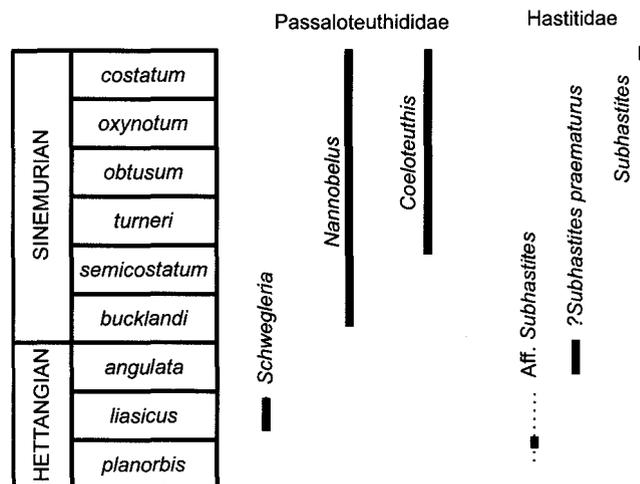


Fig. 3 Stratigraphic position of early Jurassic belemnite records in Southwest Germany, Belgium, Normandy and Northern Ireland (Riegraf, 1980; Weis & Delsate, 2005; Weis, pers. obs., 2005; Tate, 1869).

was already advanced by Naef (1922), who states about the Hastitidae: "It is noteworthy that from the beginning (Lias  $\beta$ - $\gamma$ ) the long- and thin-stemmed forms occur [...]. I do not consider their direct derivation from *Nannobelus* [...] as probable. Such extremely "clavate" rostra placed at the very posterior end of the phragmocone require a special structure and strengthening to be biologically functional, and such an adaptation would have to be recognizable in stepwise transitions in the zone of Lias  $\beta$  to  $\gamma$ . Such transitional stages are not known to date" (in Warnke et al., 2004: 134). The earliest "clavate" belemnites known to Naef come from the Sinemurian-Pliensbachian boundary (Naef, 1922: 227). The specimen described by Weis & Delsate (2005) as aff. *Subhastites* sp. demonstrates that these "clavate" forms already existed in the Hettangian. The specimen described by Tate (1869) as "*Belemnites praematurus*" from the Upper Hettangian has to be assigned to the Hastitidae as well, showing a subhastate profile, lateral lines and lacking the apical grooves (Fig. 1). The author (Tate, 1869: 167) regards it as "distinct from, though closely allied to *B. clavatus* [*Subhastites pseudoclavatus* = *Hastites clavatus* in lit.]". Dwarf Sinemurian hastate forms have also been recorded in the Upper Sinemurian of Subles, Normandy, France (Plate 1; Fig. E-F).

Jeletzky (1966: 143) considered the Hastitidae as an early off-shot of the Passaloteuthididae. If this was to be true, the off-shot would have to be located before the Hettangian *liasicus* Zone.

Furthermore, more complete future findings should allow us to split the heterogeneous *Schwegleria*-group into

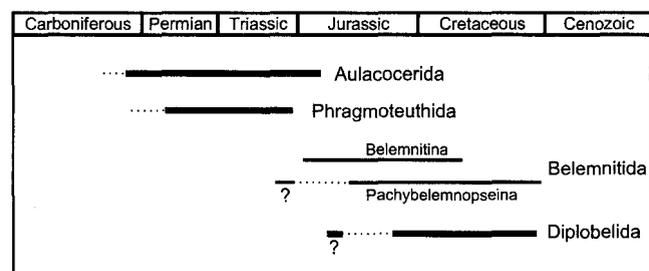


Fig. 2 Simplified stratigraphic range of the "Belemnoidea". If the Sinobelemnitidae from the Upper Triassic represent true Belemnitida has not been established yet.

some new genera. The genus *Schwegleria* with the type species *Schwegleria feifeli* would consequently be restricted to forms with a ventral groove. Whether the Hettangian hastate forms can be integrated in the genus *Subhastites* or need a new generic attribution can only be established by more complete material.

## CONCLUSIONS

Currently, the unambiguous evidence of the first occurrence of belemnites appears to be the presence of the suborder Belemnitina (sensu Riegraf et al., 1998), with *Schwegleria* and aff. *Subhastites* in the Hettangian *liasicus* Zone of Southwest Germany and Belgium. Coleoid armhooks, possibly attributable to belemnites, are already present in the *planorbis* Zone of Southwest Germany and Luxembourg. The new records from Belgium confirm the presence of true belemnites in the Hettangian. The Hettangian material is remarkable by the heterogeneity of its morphological features: among forms belonging to the Passaloteuthididae (*Schwegleria*) the Hastitidae are represented by two single records (aff. *Subhastites* and ?*Subhastites praematurus*). These two lineages would consequently have been separated as soon as the *liasicus* Zone and can be followed by isolated records through the upper Hettangian and Sinemurian. However, in order to confirm and precise this hypothesis, we need more complete and stratigraphically reliable material, considering that Hettangian belemnites have proved to be excessively rare. Attention should be paid also to Sinemurian belemnites, especially the hastate pre-Pliensbachian forms.

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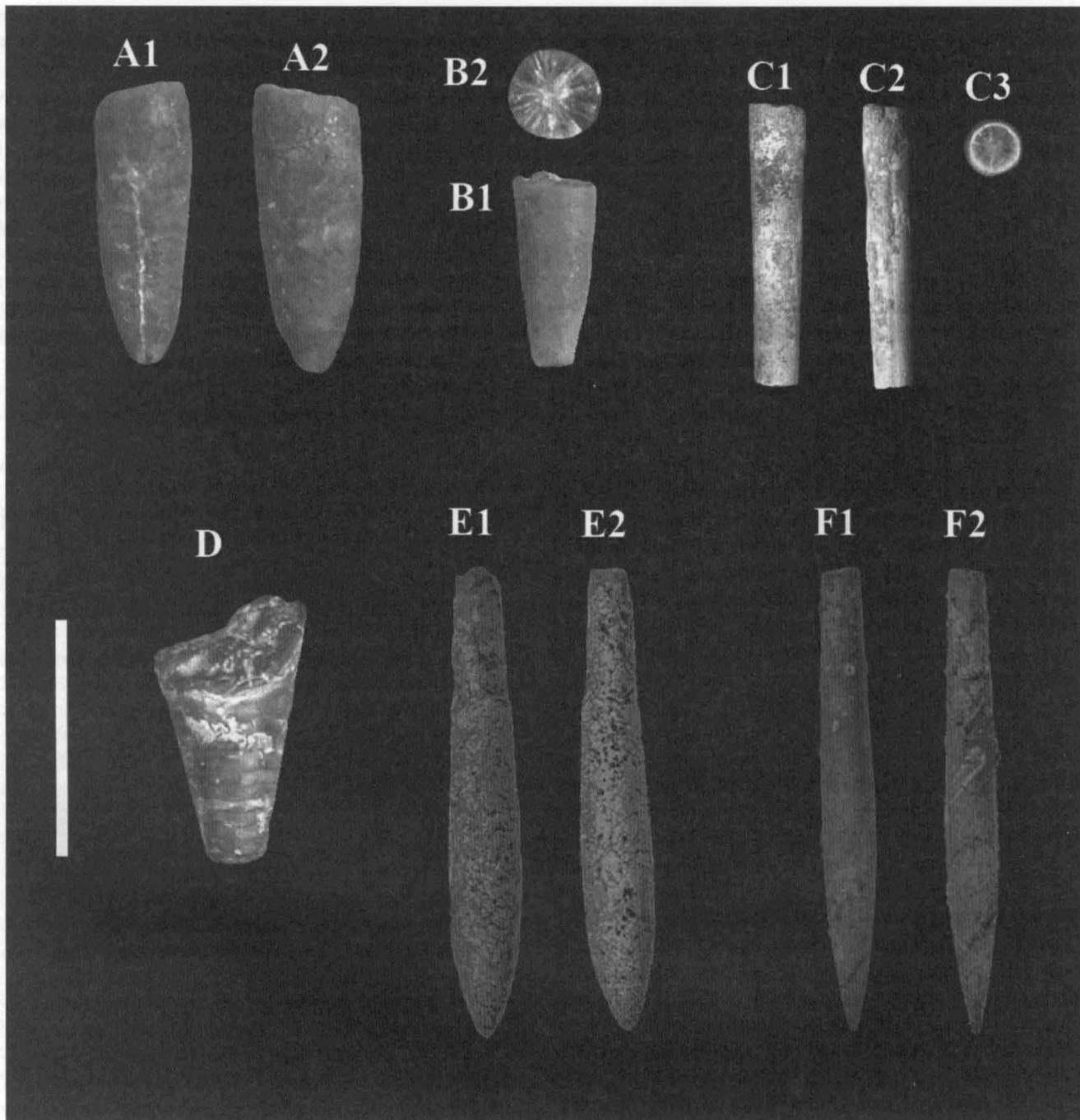


Plate 1. Early Jurassic belemnites from the Hettangian-Sinemurian of Belgium and Normandy (France). A. *Schwegleria feifeli* (SCHWEGLER, 1939), complet rostrum. Specimen QB268a. A1. Ventral view, A2. Lateral view. Hettangian, *liasicus* Zone of Fontenoille, Belgium. B. *Schwegleria psilonoti* (SCHWEGLER, 1939), fragment. Specimen QB269. B1. Lateral view, B2. Transverse section. Hettangian, *liasicus* Zone of Fontenoille, Belgium. C. aff. *Subhastites* sp., stem-fragment. Specimen HE366. C1. Ventral view, C2. Lateral view with lateral line in evidence, C3. Transverse section. Hettangian, *planorbis* or *liasicus* Zone of Vance, Belgium. D. Belemnite phragmocone. Specimen QB271. Hettangian, *liasicus* Zone of Fontenoille, Belgium. E. *Subhastites* sp. E1. Ventral view, E2. Lateral view. Upper Sinemurian of Subles, Normandy, France. F. *Subhastites* sp. F1. Ventral view, F2. Lateral view. Upper Sinemurian of Subles, Normandy, France. Scale 1cm. Specimens A–D stored at the National Museum of Natural History, Luxembourg. Specimens E–F exposed at the Maison du Fossile, Dubrulle Collection (Lion-sur-Mer, Normandy, France).

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