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The Malacological Society of Japan 

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1. Brief Schedule of the Symposium

Friday, September 14, 2007 Registration and oral presentation. Evening welcome party.

9:00am-	Start of registration
10:00am-10:10am	Opening address
10:10am-11:25am	Oral session - Paleobiological Aspects of Fossil Cephalopods 1
11:25am-11:45am	Taking a Souvenir Photo in front of the Conference Hall
11:45am-1:30pm	Lunch Break
1:30pm-3:00pm	Oral session - Paleobiological Aspects of Fossil Cephalopods 2
3:00pm-3:30pm	Afternoon Break
3:30pm-4:30pm	Biological Aspects of Modern Coleoida
18:00pm-20:00pm	Welcome Party

Saturday, September 15, 2007 Oral and poster presentations.

9:00am-10:15am	Oral session - Cephalopod Taphonomy and New Techniques
10:15am-10:45am	Morning Break
10:45am-12:00pm	Oral session - Paleobiology and Systematics of Mesozoic Ammonoidea
	and Coleoidea
12:00pm-1:30pm	Lunch Break
1:30pm-3:00pm	Poster session - Core time for ODD-NUMBERED POSTERS
3:00pm-4:45pm	Oral session - Biostratigraphic and Paleobiogeographic Aspects of Ammonoidea

Sunday, September 16, 2007

Oral and poster presentations and farewell party.				
9:00am-10:15am	Oral session - New Approaches to Cephalopod Biology and Paleobiology			
10:15am-10:45am	Morning Break			
10:45am-12:00pm	Oral session - New Approaches to Cephalopod Paleobiology and			
	Biogeography			
12:00pm-1:30pm	Lunch Break			
1:30pm-3:00pm	Poster session - Core time for EVEN-NUMBERED POSTERS			
3:00pm-4:45pm	Oral session - Paleoecology, Biostratigraphy and Extinction of			
	Ammonoidea			
17:15pm	Assemble in front of the Conference Hall. Going to Sapporo Beer			
	Garden			
18:00pm-20:00pm	Farewell Party at Sapporo Beer Garden			

2. Detailed Schedule of the Symposium

Friday, September 14, 2007

9:00am. Starting of Registration at entrance hall

10:00am-10:10am Opening address and general information *Kazushige Tanabe*

PALEOBIOLOGICAL ASPECTS OF FOSSIL CEPHALOPODS 1 - 10:10am-11:25am

Chairs- Kazushige Tanabe and Cyprian Kulicki

10:10am-10:25am O1 ON THE ORIGIN OF BACTRITOIDS (CEPHALOPODA) Björn Kröger and Royal H. Mapes

10:25am-10:40am O2 ORIGIN OF INTRASPECIFIC VARIABILITY IN THE EARLIEST AMMONOIDEA Kenneth De Baets and Christian Klug

10:40am-10:55am O3 SOME EXCEPTIONALLY WELL PRESERVED SPECIMENS OF *AGONIATITES VANUXEMI* FROM THE MIDDLE DEVONIAN CHERRY VALLEY LIMESTONE OF NEW YORK STATE, U.S.A. *Susan M. Klofak and Neil H Landman*

10:55am-11:10am O4 SOFT-TISSUE IMPRINTS IN FOSSIL AND RECENT CEPHALOPOD SEPTA AND PHRAGMOCONE EFFICIENCY Christian Klug and Dieter Korn

11:10am-11:25am O5 PSEUDOSUTURES AND SIPHUNCULAR MEMBRANES IN LATE CRETACEOUS *RHAEBOCERAS* FROM MONTANA *Kristin Polizzotto, Neil H. Landman and Elvis Le Benz*

Taking a Souvenir Photo 11:25am-11:45am (in front of the Conference Hall)

LUNCH BREAK 12:00pm-1:30pm

PALEOBIOLOGICAL ASPECTS OF FOSSIL CEPHALOPODS 2 - 1:30pm-3:00pm

Chairs- Federico Olóriz and Pascal Neige

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1:45pm-2:00pm O7 UNIQUE SIPHONAL STRUCTURE IN AN ORTHOCONIC NAUTILOID FROM THE BOGGY FORMATION, PENNSYLVANIAN, USA Harry Mutvei and Elena Dunca

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AN OVERVIEW OF THE CEPHALOPOD FAUNA OF THE UPPER MISSISSIPPIAN (NAMURIAN) BEAR GULCH LIMESTONE, MONTANA, U.S.A. *Melissa A. Lindholm, W. Bruce Saunders and Emily G.*

Allen

2:15pm-2:30pm O9

A CARBONIFEROUS RADIATION IN THE EVOLUTION OF COLEOID CEPHALOPODS AS INDICATED BY THEIR MORPHOLOGICAL PLASTICITY

Larisa A. Doguzhaeva, Royal H. Mapes and Harry Mutvei

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2:45pm-3:00pm O11 EOCENE CEPHALOPODS FROM DUDAR, TRANSDANUBIAN HUNGARY András Galácz

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BIOLOGICAL ASPECTS OF MODERN COLEOIDEA - 3:30pm-4:30pm

Chairs- Tsunemi Kubodera and Takenori Sasaki

3:30pm-3:45pm O12 MOLECULAR PHYLOGENY AMONG EAST-ASIAN CUTTLEFISHES USING THREE MITOCHONDRIAL GENES Masa-aki Yoshida, Kazuhiko Tsuneki and Hidetaka Furuya

3:45pm-4:00pm O13 HOW MANY SPECIES WITHIN *SPIRULA* EXIST? A MORPHOMETRIC APPROACH Pascal Neige and Kerstin Warnke

4:00pm-4:15pm O14 NEUROPEPTIDES AND PEPTIDE HORMONES IN THE OCTOPUS BRAIN *Hiroyuki Minakata*

4:15pm-4:30pm O15 CLOSE BUT DISTANT? —GEOGRAPHICAL DISTRIBUTION OF SHALLOW WATER BENTHIC OCTOPUS OF THE RYUKYU ARCHIPELAGO AND ADJACENT AREAS Natsumi Kaneko and Tsunemi Kubodera

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Saturday, September 15, 2007

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Dan Stephen, Kevin Bylund, Paul Bybee and Wes Ream

9:15am-9:30am O17 MASS MORTALITIES OF COLEOID CEPHALOPODS IN THE JURASSIC OXFORD CLAY OF ENGLAND: ORIGIN AND TAPHONOMY

<u>Philip R. Wilby</u>, Keith L. Duff, Kevin N. Page, Mike J. Norry and Christopher H. Vane

9:30am-9:45am 018

HOW TO RECOGNIZE IN SITU FOSSIL CEPHALOPODS: EVIDENCE FROM EXPERIMENTS WITH MODERN NAUTILUS Ryoji Wani

9:45am-10:00am 019

LOOKING AT FOSSIL CEPHALOPODS IN A NEW LIGHT Neal L. Larson, Neal A. Larson, Peter L. Larson, Robert W. Morton, Ken G. Huntly, Jon F. Geibel, Nick A. Morton and Uwe Bergmann

10:00am-10:15am O20 AMMONITE IMAGING USING DIGITAL PHOTOGRAPHY Jason D. Biederman

MORNING BREAK 10:15am-10:45am

PALEOBIOLOGY AND SYSTEMATICS OF MESOZOIC AMMONOIDEA AND COLEOIDEA 10:45am-12:00pm

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11:00am-11:15am O22 STRUCTURE AND FUNCTION OF *BACULITES*, *POLYPTYCHOCERAS* AND *JELETZKYTES* APTYCHI *Isabelle Kruta*, *Neil H. Landman*, *Isabelle Rouget*, *Kazushige Tanabe and Fabrizio Cecca*

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11:30am-11:45am O24 PALAEOCTOPUS N. SP. (CEPHALOPODA: COLEOIDEA), A PELAGIC OCTOPOD FROM THE LATE CRETACEOUS OF VALLECILLO, NE MEXICO Christina Ifrim and Dirk Fuchs

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LUNCH BREAK 12:00pm-1:30pm

POSTER PRESENTATIONS

CORE TIME FOR ODD-NUMBERED POSTERS 1:30pm-3:00pm

at meeting rooms #3 and #4

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3:15pm-3:30pm O27 NEW DATA ON GUADALUPIAN AND EARLIEST LOPINGIAN *TIMORITES* OF FAR EAST (JAPAN AND RUSSIA) AND BIOSTRATIGRAPHICAL AND PALEOGEOGRAPHICAL SIGNIFICANCE OF CYCLOLOBID AMMONOIDS

Yuri D. Zakharov and Masayuki Ehiro

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4:30pm-4:45pm O32 MODE AND TEMPO OF EVOLUTION IN PHYLOGENY OF THE LATE JURASSIC FAMILY ATAXIOCERATIDAE (AMMONOIDEA) S. Bardhan and S. Shome

Sunday, September 16, 2007

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Chairs- Margaret M. Yacobucci and Takao Ubukata

9:00am-9:15am O33 CRYSTALLOGRAPHIC TEXTURES OF CEPHALOPOD NACRE: ITS EVOLUTION, TIME STABILITY, AND PHYLOGENETIC SIGNIFICANCE Jiri Frýda, Wolfgang Weitschat, Patricie Týcová, Jakub Haloda and Royal H. Mapes

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NAUTILUS AS A CONCHIFERAN MOLLUSC: COMPARATIVE ANATOMY AND PHYLOGENY Takenori Sasaki, Shuichi Shigeno and Kazushige Tanabe

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Shuichi Shigeno, Takenori Sasaki and Takeya Moritaki

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RECONSTRUCTING THE LIFE HISTORY OF MODERN AND FOSSIL NAUTILOIDS BASED ON NITROGEN ISOTOPIC COMPOSITION OF THE SHELL ORGANIC MATTERS AND AMINO ACIDS

<u>Yuichiro Kashiyama</u>, Nanako O. Ogawa, Yoshito Chikaraishi, Napussakorn Kashiyama, Saburo Sakai, Kazushige Tanabe, Hiroshi Kitazato and Naohiko Ohkouchi

10:00am-10:15am O37 THE EVOLUTIONARY RADIATION OF MODERN NAUTILUS

James Bonacum, Neil H. Landman, Royal H. Mapes, Matthew M. White, Alicia Jeannette White and Justin Irlam

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NEW APPROACHES TO CEPHALOPOD PALEOBIOLOGY AND BIOGEOGRAPHY 10:45am-12:00pm

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LUNCH BREAK 12:00pm-1:30pm

POSTER PRESENTATIONS

CORE TIME FOR EVEN-NUMBERED POSTERS 1:30pm-3:00pm

at meeting rooms #3 and #4

PALEOECOLOGY, BIOSTRATIGRAPHY AND EXTINCTION OF AMMONOIDEA

3:00pm-4:30pm

Chairs- Hiromichi Hirano and Ryoji Wani

3:00pm-3:15pm O43 NEW APPROACH ON THE LATE VALANGINIAN AMMONITE HABITAT IN THE POLISH BASIN *Izabela Ploch*

3:15pm-3:30pm O44 EARLY APTIAN HETEROMORPH AMMONITES FROM ULYANOVSK AREA (VOLGA RIVER, RUSSIAN PLATFORM) *Irina Mikhailova and Evgenij Baraboshkin*

3:30pm-3:45pm O45 APTIAN – CAMPANIAN AMMONITES OF HUNGARY: AN OVERVIEW *Ottilia Szives*

3:45pm-4:00 O46 CEPHALOPOD BIOSTRATIGRAPHY OF THE CRETACEOUS OF SOUTH INDIA *Krishnan Ayyasami*

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4:15pm-4:30pm O48 CEPHALOPODS AT THE CRETACEOUS/TERTIARY BOUNDARY IN NEW JERSEY *Neil H. Landman, Ralph O. Johnson, Matthew P. Garb, Lucy E. Edwards and Frank T. Kyte*

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Farewell Party 18:00-20:00 at Sapporo Beer Garden Assemble at entrance of the Conference Hall, Hokkaido University at 17:15pm.

Poster presentations

P1 PERMIAN AMMONOIDS OF JAPAN: THEIR STRATIGRAPHIC AND PALEOBIOGEOGRAPHIC SIGNIFICANCE Masayuki Ehiro

P2 NEW SPECIES OF *PSEUDAGATHICERAS* (MIDDLE PERMIAN AMMONOIDEA) OF PAKLAY DISTRICT, WESTERN LAOS

<u>Masayuki Fujikawa</u>, Bounthung Xayaseng, San Assavapatchara, Denchok Monjai, Udom Jamratwai and Apsorn Sardsud

P3 MORPHOLOGICAL STUDY OF GENUS PROTOGRAMMOCERAS (EARLY JURASSIC AMMONOID) FROM THE TOYORA GROUP IN SOUTHWEST JAPAN Kentaro Nakada and Atsushi Matsuoka

P4 BIOMETRICAL ANALYSIS ON MIDDLE JURASSIC AMMONOID *PSEUDONEUQUENICERAS YOKOYAMAI* (KOBAYASHI & FUKADA) AND ITS RELATED FORMS *Atsushi Matsuoka, Junko Anso, Kentaro Nakada, Kazunobu Terabe and Tadashi Sato*

P5 A TRANS-PACIFIC DISPERSAL OF NEUQUENICERATIDS, EVIDENCE FROM TIBET Jiarun Yin and Xiaoqiao Wan

P6 THE ORIGIN OF *PROHECTICOCERAS* SPATH 1928 AND ITS EVOLUTIONARY SIGNIFICANCE IN THE SUBFAMILY HECTICOCERATINAE (AMMONOIDEA): A HISTORICAL AND CLADISTIC APPROACH *Pinaki Roy and <u>Subhendu Bardhan</u>*

P7 AMMONITE FAUNA OF THE MIDDLE-JURASSIC (UPPER AALENIAN-UPPER BAJOCIAN) OF LA BAUME (CASTELLANE, ALPES DES HAUTES PROVENCE) AND SYSTEMATICS OF THE SONNINIIDAE Kenneth De Baets and Fabrizio Cecca

P8 UPPER BAJOCIAN TO BATHONIAN AMMONITES

OF NORTH IRAN Mahmoud Reza Majidifard

P9 BELEMNITES OF THE JURASSIC/CRETACEOUS BOUNDARY INTERVAL FROM NORDVIK PENINSULA (NORTHERN SIBERIA) Oksana S. Dzyuba, Viktor A. Zakharov and Martin

Košt'ák

P10 GENUS *DELPHINITES* (AMMONOIDEA) IN THE VALANGINIAN OF RUSSIA

Yury Bogomolov and Vasily Mitta

P11 ALBIAN AMMONITE PALEOBIOGEOGRAPHY IN THE NORTH PACIFIC

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P12 CENOMANIAN/TURONIAN BOUNDARY EVENT IN THE NORTHWESREN PACIFIC: MARINE BIODIVERSITY AND PALEOCEANOGRAPHIC BACKGROUND *Ken'ichi Kurihara*

P13 TAXONOMIC REVISION OF TRAGODESNOCEROIDES AND DAMESITES SPECIES (UPPER CRETACEOUS DESMOCERATINE AMMONOIDS) FROM THE CRETACEOUS YEZO GROUP Tomohiro Nishimura, Haruyoshi Maeda and Yasunari Shigeta

P14 *PSEUDASPIDOCERAS FLEXUOSUM*: AN AMMONITE WITH FLEXIBLE SPINES FROM THE EARLY TURONIAN (LATE CRETACEOUS) OF NE MEXICO <u>Christina Ifrim</u>, Eberhard Frey and Wolfgang Stinnesbeck

P15 METHANE INDUCED FOSSILIZATION PROCESS OF AMMONOIDS: A CASE FROM A LATE CRETACEOUS METHANE-SEEP IN NAKAGAWA AREA, NORTHERN HOKKAIDO, JAPAN

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P16 TWO CAMPANIAN (LATE CRETACEOUS) NOSTOCERATID AMMONOIDS FROM THE TOYAJO FORMATION IN WAKAYAMA, SOUTHWEST JAPAN Akihiro Misaki and Haruyoshi Maeda

P17 TOWARDS A DATABASE OF THE CRETACEOUS AMMONOIDS IN JAPAN

Seiichi Toshimitsu and Hiromichi Hirano

P18 SUPPOSED DEEP-WATER TEMPERATURE FLUCTUATIONS IN THE CENTRAL PACIFIC DURING LATEST CRETACEOUS TIME: FIRST EVIDENCE FROM ISOTOPIC COMPOSITION OF BELEMNITE ROSTRA Yuri D. Zakharov, Mikhael E. Melnikov, Olga P. Smysh-Iyaeva, Peter P. Safronov, Alexander Popov, Tatiana Velivetskaya and Tamara B. Afanasyeva

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P20 UPPER CRETACEUS NAUTILOIDS OF EPICONTINENTAL SEAS IN CETRAL EUROPE - BOHEMIAN CRETACEOUS BASIN Jiří Frank

P21 *ATUROIDEA* (NAUTILIDA) FROM UPPER CRETACEOUS SADA LIMESTONE IN SHIMANTO CITY, KOCHI PREFECTURE, JAPAN <u>Yasuyuki Tsujino</u> and Hirohide Iwata

P22 DISCOVERY OF A NAUTILOID UPPER JAW FROM THE MAASTRICHTIAN OF HOKKAIDO, JAPAN Toshifumi Neomoto and Kazushige Tanabe

P23 THE NEOGENE CEPHALOPOD FOSSILS OF JAPAN Susumu Tomida

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P26 SOFT TISSUES IN AMMONOID CEPHALOPODS FROM THE BEAR GULCH *LAGERSTÄTTE* (LOWER CARBONIFEROUS), MONTANA, USA *Neil H. Landman, Royal H. Mapes and Chris Cruz*

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P29 DEVELOPMENT OF THE EMBRYONIC SHELL STRUCTURE IN MESOZOIC AMMONOIDEA Kazushige Tanabe, Cyprian Kulicki and Neil H. Landman

P30 COLEOID CEPHALOPODS FROM THE LATE CRETACEOUS NORTH EASTERN PACIFIC Dirk Fuchs, Graham Beard, Kazushige Tanabe and Rick Ross

P31 LATE SILURIAN EVENTS AND THE CEPHALOPOD EXTINCTIONS IN THE PRAGUE BASIN Štěpán Manda

P32 EMBRYONIC SHELLS IN SOME LECHRITROCHOCERATIDS (NAUTILOIDEA, BARRANDEOCERINA) *Vojtěch Turek*

P33 LATERALITY OF BEHAVIORAL AND MORPHOLOGICAL FEATURES IN SEPIA LYCIDAS Ryo Ihara, Takashi Hirao, Yasuhisa Matsuda, Michio Hori and Kosaku Yamaoka

P34 GENETIC SEPARATION OF THREE SPECIES AMONG THE STHENOTEUTHIS OUALANIENSIS- COMPLEX <u>Toshie Wakabayashi</u>, Mitsuo Sakai, Taro Ichii, Yasuo Odani, Kotaro Yokawa and Akihiko Yatsu **3. Abstracts of Oral Presentations**

ON THE ORIGIN OF BACTRITOIDS (CEPHALOPODA)

Björn Kröger¹ and Royal H. Mapes²

¹Museum für Naturkunde and the Humboldt University, Invalidenstrassen 43, D-10115, Berlin, Germany; <e-mail: bjoekroe@gmx.de> ²Department of Geological Sciences, Ohio University, Athens, Ohio 45701, U.S.A.; <e-mail: mapes@ohio.edu>

The Bactritoidea are an important cephalopod order in the Phanerozoic because this group is considered to be the ancestral lineage for all the Ammonoidea and the Coleoidea. Both of these cephalopod orders are very important in modern and fossil studies. Despite the fact that the bactritoid lineage is very important, the precise connection of how the coleoids arose within the bactritoid lineage is completely unknown. Fortunately, the origin of the Ammonoidea is better understood with an origin in the Early Emsian (Early Devonian) when the ancestral bactritoid *Lobobactrites* Schindewolf developed a cyrtoconic shell. This relationship was well documented by Erben (1964). An additional problem with the evolution of the bactritoid lineage is when did the lineage evolve. That the bactritoid lineage evolved from an orthoceratid nautiloid ancestor is not a contested conclusion; however, when this event occurred has not yet been resolved with an Ordovician candidate (*Bactroceras* Holm 1899), an upper Silurian candidate (*Bactrites* Sandberger, proposed by Erben 1964). We have focused on this last situation to resolve the probable origin of the Bactritoidea.

Bactritoids and their related ancestral and descendant forms are lacking in many critical diagnostic features that are useful in determining phylogenetic relationships within the Cephalopoda. Some of these features are internal deposits, significant variations in suture patterns, and septal neck variations. The critical morphological features that are available in the Bactritoidea include overall shape and size of the protoconch or apices, shafts that are straight, variations in growth stage morphology, and to a lesser extent the siphuncle position.

The initial chamber of the Emsian Bactrites, Devonobactrites Shimansky, and Lobobactrites is an elongated spherical structure that is larger in diameter than the slender, smooth shaft located adoral of the initial chamber. All are accepted as being important genera within the Bactritoidea. All have ventral marginal siphuncles, simple orthochoanitic septal necks, a relatively low apical angle, and relatively closely spaced septa. Similar apices that are larger than the shaft adoral of the initial chamber occur in a number of Late Silurian sphaerorthoceridans with central siphuncles. Sphaerorthoceridans with a Bactrites-like apex and an eccentric siphuncle position, known from the Early Devonian, are indeterminate between Bactrites and orthocerids.

By contrast, the Late Silurian "*Bactrites*" bohemicus displays an initial chamber that is smaller in diameter than the shaft located adorally of the initial chamber (see Fig. 1). Moreover, the apex of Middle Ordovician *Bactroceras* is similar in apex shape with orthocerids of similar age but differs strongly in shape and dimension from the Devonian *Bactrites*. Therefore, displacement of the siphuncle from subcentral or eccentric positions toward the conch margin occurred at least three times during the

Ordovician–Early Devonian evolution of the Orthocerida, and bactritoid-like orthocones of the Middle Ordovician and Late Silurian are homeomorphs of Bactritoidea with different early growth stage morphologies. Thus, it is highly probable that a marginal shift of the orthocerid siphuncle occurred in post-Early Emsian time, too. Based on the features that are available, the earliest questionable *Bactrites* occurs in the Pragian. By the Early Emsian time, the bactritoids are a common element of the cephalopod faunas. Thus, the Ordovician and Silurian taxa should be removed from the bactritoid (s.s.) lineage, and the time interval between the first appearance of *Bactrites* and the origin of ammonoids can now be pinpointed to the Pragian–earliest Early Emsian, which is a five million year interval in the Early Devonian.



Figure 1. Phylogram of selected Siluro–Devonian sphaerorthocerids and bactritoids. Illustrations are from Erben (1960: fig 2.3), Ristedt (1968: figs. 3.1b, 4.1a; 1981: fig. 1), Serpagli and Gnoli (1977: text-figs. 5, 7), and Schindewolf (1933: pl. 3.2).

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ORIGIN OF INTRASPECIFIC VARIABILITY IN THE EARLIEST AMMONOIDEA

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It is largely accepted by palaeontologists that ammonoids originated from bactritids (Klug and Korn 2004). The early ammonoids themselves are loosely coiled and members of the subfamily Anetoceratinae with their loose, gyroconic coiling are considered the closest to their bactritoid ancestors. A fairly high number of taxa have been introduced worldwide for the loosely coiled forms among the early ammonoids. For example, at least eight genera (*Anetoceras*; *Erbenoceras*, *Metabactrites*, *Teneroceras*, *Borivites*, *Haletoceras*, *Ruanites*, *Luofoceras*) and 24 species are in use for Emsian Anetoceratinae (see Klug 2001 and Korn and Klug 2002 for reviews). This seeming diversity might have its origin in a significant intraspecific variability which may tentatively be interpreted as a result from the morphogenetic constraints of loose coiling. Largely because of the intraspecific variability of the earliest ammonoids has never been examined. Another interesting aspect of ammonoid conch morphology and geometry is the pronounced covariance of some characters. It is interesting to study this covariation (e.g. rib strength and number is more or less strongly correlated to coiling) at the dawn of ammonoids.

A statistically relevant number of specimens were collected from a limited stratigraphical interval (*Erbenoceras* beds) in the Anti-Atlas (Morocco). In order to quantify the intraspecific variation, several conch parameters (diameter, whorl height, whorl width, whorl interspace), their ratios (umbilical width index, whorl width index, whorl width/ whorl height ratio, whorl expansion rate, whorl interspace rate) and rib spacing were plotted throughout ontogeny in bivariate diagrams. In these plots the whorl height was used as a proxy for the ontogeny. Analysis of such bivariate plots could help us identify those growth stages with higher variability and the parameters most suitable to investigate intraspecific variability among these ammonoids.

Preliminary results seem to suggest, that the pre-adult whorls are indeed the most variable. Apparently, the ultimate whorl actually is morphologically much more similar to other specimens, even if these have rather different earlier whorls, otherwise.



Ruanites, Erbenoceras, early Emsian, Early Devonian, Morocco

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SOME EXCEPTIONALLY WELL PRESERVED SPECIMENS OF AGONIATITES VANUXEMI FROM THE MIDDLE DEVONIAN CHERRY VALLEY LIMESTONE OF NEW YORK STATE, U.S.A.

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Representatives of *Agoniatites vanuxemi* (Hall, 1879) occur in discrete beds in the Cherry Valley Limestone (Middle Devonian) of New York State, U. S. A. These beds are thought to represent mass mortality events of immigrant populations during times of transgression. The Seneca Stone Quarry preserves such a bed on the top surface of the quarry. After death, the agoniatites fell to the sea floor and were buried rapidly, but incompletely, leaving their topside exposed and subject to dissolution. The shells rested on their sides, which may have favored the preservation of the innermost whorls. By removing these inner whorls from the quarry floor it was possible to examine the internal structures of the juvenile whorls, including the ammonitella. The specimens were embedded in epoxy, ground and polished in median section and etched with 5 % HCL. The calcite in the specimens dissolved leaving the organic membranes and structures, which are preserved as pyrite. The specimens were then examined with a scanning electron microscope. Two of the specimens exhibit remarkable preservation and are presented here.

The internal structure of the ammonitellas of the Agoniatitida is less well known than the external morphology. A few examples of median sections do exist in the literature (Schindewolf, 1934; Chlupáč and Turek, 1983). The internal morphology has also been studied on the ventral surface of weathered ammonitellas, where the caecum and prosiphon have been exposed in the initial chamber (Clarke, 1899; Petter, 1959; Klofak et al., 1999). Clarke's example is particularly important, because it is the same species and from the same formation studied here.

The caecum is visible, and as in the externally weathered specimen, it originates deep into the initial chamber. It is rounded and is attached to the wall of the initial chamber by a short prosiphon. The diameter of the caecum and siphuncle in the initial chamber is $\sim 200 \mu m$, but by the second chamber the diameter of the siphuncle is reduced by half. In the initial chamber on the dorsal side of the siphuncle are membranes that look like elongate blisters or bubbles.

The opening of the initial chamber was very large as indicated by the height of the dorsal portion of the first septum. The first three septa join the dorsal wall of the initial chamber at the junction where the initial chamber is folded into the ammonitella coil. The first septum is strongly adapically concave and is continuous with the wall of the initial chamber. The first two septa of one of the specimens shows septal-siphuncular membranes (Landman *et al.*, 2006).

The thickness of the wall of the initial chamber can also be estimated from these specimens. The thickness at the dorsalmost part is much thinner, about two-thirds that of the rest of the initial chamber. This thickness difference can be correlated to changes in the ornament observed in the Agoniatitida. The thinner part of the shell corresponds to the apical part of the initial chamber, which is smooth and devoid of ornament (the "bald spot"). The thicker parts of the initial chamber correspond to the areas covered by lirae, which surround the apical area. The location of the thin apical area indicates that the closing of the umbilical perforation and tighter coiling in *A. vanuxemi* were accomplished by reducing the dorsal side of the initial chamber. In members of the Anarcestina it has already been demonstrated that the dorsal side of the initial chamber is shorter than the ventral side (Klofak *et al.*, 2007).

The end of the ammonitella is also visible. It is marked as an area where the shell thins, and many organic layers are present. It lays approximately 360° from the first septum. A small approximation occurs between septa 5 and 6. If this is taken to represent the point of hatching, then the ammonite hatched with a body chamber of approximately 270° . Immediately after hatching, the shell layers become thicker by a factor of two.

The differences in size, shape and ornament have always made it difficult for workers to relate the embryonic shells of Devonian ammonoids to their post Devonian relatives. The data on the internal structures of the ammonitellas of *Agoniatites vanuxemi*, reveal many similarities in structure and offer an opportunity to better define the evolutionary changes which transformed the ammonitella.

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SOFT-TISSUE IMPRINTS IN FOSSIL AND RECENT CEPHALOPOD SEPTA AND PHRAGMOCONE EFFICIENCY

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Several, previously undescribed structures, here interpreted as soft-tissue imprints and attachment sites, have been discovered on the inside of the shell wall and on the septum of various fossil and Recent ectocochleate cephalopods. Internal moulds of the body chambers of the bactritoid Devonobactrites and the Emsian ammonoids Anarcestes, Chebbites, Erbenoceras, Gyroceratites, and Metabactrites from the Moroccan (Klug 2001) as well as from the German Emsian (Early Devonian) sedimentary rocks display various kinds of striations (Kröger et al. 2005); some of these striations are restricted to the mural band, some start at the suture and terminate at various parts of the annular elevation (especially the mantle myoadhesive band). Some of these features were also discovered in various specimens of Mesozoic and Recent nautilids (compare Willey 1902; Deecke 1913; Blind 1976; Mutvei et al. 1993). These structures are here interpreted as the septal furrow as well as imprints of blood vessels and contractile fibres of the septal mantle (subepithelial musculature of Blind 1976). Most of these structures were not found in ammonoids younger than Middle Devonian yet. The nature of these imprints was examined by sectioning the marginal septal mantle of Recent Nautilus specimens; longitudinal and transverse sections of contractile fibre bundles (or muscles) and of blood vessels were found therein, arranged exactly like the imprints on nautilid septa.

What is the reason for the differing shapes in early and derived ammonoid septa?

We suggest that the tension produced by the contractile fibres of the septal mantle was higher in derived ammonoids than in all other ectocochleate cephalopods (compare Henderson 1984 and Hewitt et al. 1991). Presuming this hypothesis is correct, the contractile fibres cover a larger portion of the septum surface than in early ammonoids and other cephalopods because of the folded margin of the septal mantle which was attached at the mural band (Blind 1975, 1976; Mutvei et al. 1993). Additionally, these fibres pulled the not yet mineralised septum in opposing directions and offered a significantly larger attachment surface than in early ammonoids. Consequently, the organic septum was possibly much more tightly stayed with the outer shell wall.

Organs which are directly in contact with the septal mantle or which are part of it leave imprints only in septa of those cephalopods which have simple dome-shape septa with a low number of sutural elements, depending largely on specimen preservation (even in Recent nautilid shells). This includes certain malformations of these organs which rarely left traces on the septa. The septum surface is completely smooth only in derived ammonoids (except for lobes and saddles).

Removal of cameral liquid from new chambers where septum mineralisation was not yet terminated as well as replacement by gas probably started earlier than in cephalopods with simple dome-shaped septa. A similar conclusion was drawn previously by Daniel et al. (1997) based on a mathematical model for septal strength. The higher growth rates of ammonoids compared to nautiloids (compare Lécuyer & Bucher 2006) agree also with this hypothesis.

Therefore, the new formed chambers of derived ammonoids were functional earlier and thus, the buoyancy apparatus was perhaps more efficient than in nautiloids, bactritoids or early ammonoids. Consequently, the function of ammonoid septa was probably not predominantly to enhance resistance of the shell towards hydrostatic pressure but rather to create an efficient buoyancy apparatus.

In combination with their generally improved manoeuvrability compared to orthocones (Klug & Korn 2004), this partially explains the evolutionary success of early ammonoids: Ammonoids potentially were able to deal with adverse conditions like anoxic bottom waters by more quickly migrating to shallower water depths. Additionally, early gnathostome fish were probably not able to follow the more highly mobile ammonoids (in horizontal and vertical directions) because of the constructional morphology of these fish which was adapted to a demersal mode of life.

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PSEUDOSUTURES AND SIPHUNCULAR MEMBRANES IN LATE CRETACEOUS RHAEBOCERAS FROM MONTANA

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We examined Late Campanian *Rhaeboceras* from the Pierre Shale of north-central Montana. The original aragonitic mineralogy of the shells is preserved and many of the phragmocones are hollow, indicating that the specimens did not sit on the sea floor for very long, but were instead rapidly buried in sediment. The body chambers are commonly broken, although most of the fragments are still present. The presence of jaws in a high proportion of the body chambers suggests that the ammonites died as a result of predation and fell to the sea floor almost immediately with no post-mortem transport. The presence of original shell material and hollow phragmocones make these specimens ideal for studies of cameral membranes and pseudosutures.

In one exceptional specimen, we observed both siphuncular membranes and pseudosutures preserved on the interior surface of the chambers. The siphuncular membranes were probably originally organic. They are spaced evenly along the ventral part of the (missing) siphuncle, approximately 200 μ m apart. There may have been up to 18 membranes in each chamber, although in this specimen only those near the adoral end of the chamber have been preserved. The pseudosutures, which mimic the shape of the lobules in the external lobe, are evenly spaced as well, but at intervals of only 100 μ m. There may have been up to 35 ridge-like pseudosutures in each chamber. They have a distinctive cross-section, which is gradual adapically and steep adorally. Drag lines are also visible, forming continuous, tube-like ridges extending from the apical ends of the lobules across the entire chamber. The pseudosutures are generally continuous with the drag lines. We anticipate that further examination of these specimens will shed light on the process of chamber formation and soft body translocation in these ammonites.

ENDOCOCHLEATE MODEL OF THE SHELL IN THE SILURIAN ORTOCERATOID SPHOOCERAS

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The orthocone cephalopod Sphooceras Flower, 1962, characterised by its short, finger-like shape and blunt asymmetric and markedly thickened posterior portion of the shell, was widespread in the Silurian subtropical and tropical seas of Europe and Asia. It displays a striking affinity with coleoids and demonstrates that the boundary between fossil ectocochleate and endocochleate cephalopods is problematic. Reported natural truncation of the apical part of phragmocone from the rest of the shell (Barrande 1860), sometimes later challenged (Dzik 1984), is reaffirmed unequivocally. This process is substantiated especially by: a) The shell has very short phragmocone with a limited number of gas chambers - three to eight (documented in specimens with dorsoventral diameter ranging from 3 to 78 mm), b) A characteristic structure of the apical portion of the shell with strongly narrowed and then plugged siphonal perforation and thickened apical end of the shell in different ontogenetic stages, c) Secretion of two shell layers on the convex apical surface formed by naked cameral deposits - the inner one with characteristic finger print pattern and outer layer which is smooth, d) Discontinuity of growth traced in the boundary between truncated part and the rest of the shell annular groove development and sometimes thickening of the shell along this boundary, disrupted course of growth lines and sudden disappearance of colour pattern e) Presence of cameral deposits at the centre of gravity of the shell discovered in one specimen – supposed symptom preceding later truncation, f) Co-occurrence of complete shells of Sphooceras with isolated apical parts, which may represent truncated portions of the shells.

Periodical natural removal of the apical part of the shell (4 to 5 gas chambers) preceded formation of episeptal deposits and a calcareous plug closing the septal foramen. The truncated portion of the shell must not have been covered by soft tissue before this process. After truncation the mantle completely surrounded the apical region and two calcareous layers mentioned above had also been secreted. The repeated ability of the animal to cover entirely the shell by the mantle in these growth stages was facilitated by a very short phragmocone and a long body chamber. This process is substantiated by the discovery of colour pattern in the apical region of the shell, which could not be secreted by cameral mantle (comp. Gnoli and Kiselev 1994). Dark brownish longitudinal strips are present on the dorsal half of the shell only. This pattern, together with general morphology of the shell, supports the idea of a horizontal living position in this orthocone cephalopod for which a nectobenthic mode of life is presumed. Functionality of the colour pattern depends on its display; it is supposed that after secretion of outer prismatic layer containing colour pigments the mantle was retracted from the new apex. A camouflage effect could be improved by pigmentation of the soft tissue. Discontinuities of growth expressed in the shell morphology (comp. point ,,d"), as well as entirely smooth shell surface or indistinct growth lines support the idea already expressed by Blake (1882) that the shell of Sphooceras was "more nearly internal than in Nautilus". The co-occurrence of different growth stages of S. truncatum within one type of embryonic shell is remarkable and indicates the possibility that all these shells could belong to an identical species. The early juveniles, probably representing individuals shortly after hatching, are 4 to 5 mm long. The spherical initial chamber is very small and it is separated from adjacent chamber by a conspicuous constriction. These embryonic shells resemble embryonic shells of *Parasphaerorthoceras* Ridsted, 1968.

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Unique siphonal structure in an orthoconic nautiloid from the Boggy Formation, Pennsylvanian, USA

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Numerous orthoconic nautiloids occur in the asphalt-rich bed of the Boggy Formation (Pennsylvanian, Desmoinesian) of south of Sulphur, Oklahoma (Buckhorn Asphalt). The shells of these nautiloids are fractured into small fragments, usually consisting of a few chambers. To judge from the descriptions and illustrations by Gordon (1964), one of the dominant nautiloid in this formation belongs to the genus *Mitorthoceras*. The shell structure in this nautiloid has been previously described by Ristedt (1971), Mutvei (1972) and Hewitt (1982). We have restudied its siphonal structure and compared it with that in other nautiloids.

The septal neck is orthochoanitic. The nacreous layer of the septal neck gradually decreases in thickness in distal direction. The septal neck therefore is characteristically pointed in longitudinal sections. A calcareous layer, here termed the transitional siphonal layer (tsl, Fig. 1A; Siphowulst by Ristedt, 1971, modified nacreous layer by Mutvei, 1972), emerges from the outer surface of the distal half of the septal neck (sn, tsl, Fig. 1C). This layer increases in thickness and terminates a short distance adapical to the septal neck where it passes into the connecting ring proper (tsl, cr, Fig. 1B). As indicated by growth lines, the transitional layer is a direct continuation of the nacreous layer of the septal neck but has a porous, irregularly spherulitic-prismatic structure (sn, tsl, Fig. 1C). The connecting ring proper is composed of an exceptionally thick, single organic (glycoprotein) layer (cr, Fig. 1A, B). It is a direct continuation of the transitional layer but has a distinct boundary towards that layer (tsl, cr, Fig. 1A, B). It consists of thin lamellae of organic substance that show an indistinctly fibrous, fine-globular structure. It seems to be perforated by numerous pores of 0.1-0.2 µm in diameter (cr, Fig. 1B). Owing to the high porosity, the majority of the studied connecting rings have been postmortally penetrated by prismatic layers from the adjacent cameral deposits. The connecting ring extends adapically to the preceding septal neck and is attached on its inner surface.

The structure of the connecting ring in *Mitorthoceras* differs from that in hitherto described nautiloids. In the living *Nautilus*, the connecting ring is composed of an outer, calcified, spherulitic-prismatic layer and an inner, organic, glycoprotein layer. In fossil ellesmerocerids, tarphycerids and nautilids, the connecting ring consisted of similar two layers as that in *Nautilus* but the inner organic layer has been always destroyed by diagenesis (Mutvei, 2002). In plectrocerids, orthocerids and actinocerids, the inner layer of the connecting ring is not organic but calcified and perforated by numerous pore canals (Mutvei, 2002; Mutvei et al., 2007). Only in prosiphonate ammonoids the connecting ring is composed of a thick, single, organic layer, similar to that in *Mitorthoceras*. This layer in ammonoids, as well as in *Mitorthoceras*, was probably tanned and therefore often well preserved. In order to make the connecting ring permeable for cameral liquid it is perforated by numerous pores (Mutvei and Dunca, 2007). Further studies will clarify the taxonomical position of this nautiloid.

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Figure 1. A- Longitudinal section of *Mitorthoceras*, (LM); B, C- Detailed view (SEM)

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AN OVERVIEW OF THE CEPHALOPOD FAUNA OF THE UPPER MISSISSIPPIAN (NAMURIAN) BEAR GULCH LIMESTONE, MONTANA, U.S.A.

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The Bear Gulch Limestone is a Konservat-Lagerstätte that is best known for its unique preservation of fishes, particularly sharks. Cephalopods are the most common invertebrates in the Bear Gulch. A combined sample of 560 cephalopod specimens from localities throughout the basin are available from museum collections (Carnegie Institution, University of Montana) and include a comprehensive collection (n=327) made at a single locality during 2006. The combined collections include orthoconic (n=189; 33.8%), cyrtoconic (n=2; 0.36%), and coiled nautiloids (n=131; 23.4%), ammonoids (n=151; 27.0%), possible bactritoids (n=11; 2.0%), and two different groups of coleoids (n=63; 11.3%). There is a relatively high incidence of soft part preservation among the cephalopods, including *in situ* mandibles (n=36), gut contents (n=4), possible ink sacs (n=7), and arm hooks (n=6). The presence of coleoid arm hooks and ink sacs in the Bear Gulch cephalopods extends the fossil record of these structures back ~20 Ma. Analysis of the taxonomic composition of the cephalopod fauna from three different parts of the Bear Gulch basin permits evaluation of whether the distribution of taxa Rarefaction indicates that differences in taxonomic within the basin is random. richness between sites are likely due to differences in sample size. A Monte Carlo simulation measuring the Shannon and Simpson diversity indices of random subsamples from each site indicates only subtle spatial variation in the cephalopod community Analysis of lithological associations reveals no obvious correlation composition. between rock type and cephalopod diversity.

A CARBONIFEROUS RADIATION IN THE EVOLUTION OF COLEOID CEPHALOPODS AS INDICATED BY THEIR MORPHOLOGICAL PLASTICITY

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Discoveries in the 1950's and 1960's revealed the existence of definitive coleoid features such as the rostrum (*Hematites*) and arm hooks (*Jeletzkya*) on carboniferous cephalopods. During the last 10 years new discoveries in the Carboniferous have added unexpected innovative morphologic features that are unique to coleoids. Moreover, the Carboniferous coleoids are shown to possess a remarkable morphological plasticity because of their ability to innovate new features and to recombine in different ways the new and old features. This plasticity even concerns relatively stable structures, such as the radula. In the Carboniferous a coleoid with a unique radula having two marginal plates adjacent to each other has been illustrated (*Saundersites*). This is an example of the ability to innovate new features and to recombine these new features with the older features. This ability seems to be absent in the evolution of Mesozoic coleoids.

Knowledge of Carboniferous coleoids is relatively limited; however, to begin to understand Late Paleozoic evolution in the Coleoidea, significant morphological features that are preserved in Late Paleozoic and Mesozoic coleoids must be considered. These include the following morphological elements: a short final chamber that only contained a small part of the body mass, a long body chamber that contained the majority of the body mass, a lamello-fibrillar nacre in the septa, rostrum morphology and ultrastructure, pro-ostracum morphology and ultrastructure, radula structure, arm-hook morphology, shell/septum attachment arrangement, shell wall and septum ultrastructure, the presence or absence of mineralized shell, and presence or absence of the ink sac. The analysis of these features led to the reevaluation of the widely accepted hypothesis on the evolutionary morphology of coleoids by Naef (1922) and later Jeletzky (1966) that suggested there was a gradual elimination of the ventral and lateral sides of the body chamber shell wall that led to the formation of the pro-ostracum and later to the formation of the chitinous gladius. This evolutionary concept can now be rejected because of new data from several Mesozoic belemnoids on the essential differences between the pro-ostracum and body chamber shell wall ultrastructure. It is now apparent that the pro-ostracum must have appeared as innovative feature rather than as a remnant of the dorso-lateral portion of the body chamber shell wall. Therefore, the mantle secreting epithelium had to be modified, and a new secretional zone must have been added to the secretional zones responsible for the body chamber wall formation.

Five orders are now necessary to accommodate the known Carboniferous coleoid genera. The following is a listing of these orders and their main characteristics:

<u>Order Hematitida</u>: (example: *Hematites*) Phragmocone breviconic with closely spaced septa, not completely covered by the mantle during early ontogeny, but became covered in the last growth; body chamber very diminished (slightly longer than last chamber), no pro-ostracum like structure; rostrum prominent with longitudinal ridges and grooves, complex ultrastructure; conotheca multi-layered and lacks nacreous layer.

<u>Order Aulacocerida</u>: (example: *Mutveiconites*) Rostrum small, cone-like structure surrounding the protoconch and early phragmocone; phragmocone longiconic; body chamber long and tubular, at least in early ontogenetic stages; conotheca with nacreous layer.

<u>Order Donovaniconida</u>: (examples: *Rhiphaeoteuthis, Donovaniconus, Saundersites*) Longiconic body chamber present either through the entire ontogeny (*Donovaniconus, Saundersites*), or only at the early ontogeny (*Rhiphaeoteuthis*); pro-ostracum like structure comparatively short (*Donovaniconus*) to moderate in length (*Saundersites*); breviconic phragmocone length much shorter than the body chamber (*Donovaniconus, Saundersites*); rostrum weakly calcified (*Saundersites*), sheet-like or absent (*Donovaniconus*); conotheca with nacreous layer; mural parts of septa long (up to 2/5 camera length) and embedded into shell wall; septa consist of lamello-fibrillar nacre (*Donovaniconus*); ink sac present (*Donovaniconus, Saundersites*), arm hooks in double rows (*Saundersites*) and rosettes (undescribed new genus).

<u>Order Spirulida</u>: (example: *Shimanskya*) Body chamber and phragmocone longiconic; shell wall lacks nacreous layer and consists of an inner and outer plate; septa with thick and extensive organic membranes suggesting lamello-fibrillar nacre.

<u>Order Octopoda</u>: (example: *Pohlsepia*) Lacking any trace of a mineralized shell, probable ink sac present, arms without arm hooks.

To summarize: Based on the new features described above, the Carboniferous was a time of extensive coleoid experimentation in search of a new and more competitive architecture. Recognition of these new features allows the testing of the empirical rule in evolutionary theory that the morphological plasticity should be higher in the earliest stages of the evolution of a lineage, and that the plasticity tends to become less variable in the later stages of evolutionary development of that lineage. The relatively high plasticity in the Carboniferous coleoids signals the presence of an evolutionary radiation. During such a radiation, it can be expected that numerous innovations can develop, and that most of these evolutionary experiments will tend to be short lived and become extinct. For this reason we anticipate that additional new coleoid taxa with new combinations of features will be discovered from the Upper Paleozoic in the future and these discoveries will profoundly impact our ideas of early coleoid evolution.

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RECOVERY OF NAUTILOIDS IN THE EARLY TRIASSIC

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As with most other organisms, the nautiloids underwent a major biotic crisis during the Permian-Triassic (P/Tr) transition. Unfortunately, the fossil record for this particular cephalopod group is poorly understood during this interval. However, recent discoveries from Lower Triassic deposits in southern Primorye, Far Eastern Russia, provide an important key to understanding nautiloid recovery during the Early Triassic.

The following four genera of grypoceratid nautiloids have been found in Lowest Triassic Induan deposits in southern Primorye: 1) *Grypoceras*, with an moderately involute conch and a central siphuncle, 2) *Gyronautilus*, characterized by a gyroconic conch with a sub-central siphuncle, 3) *Xiaohenautilus*, with an evolute conch and a sub-central siphuncle, and 4) *Menuthionautilus*, distinguished by an involute, rapidly expanded conch and siphuncle in an extreme ventral position.

The Grypoceratidae, one of the more successful nautiloid families, flourished during the Permian and developed diverse shell forms and siphuncle positions. During the P/Tr transition, most genera of the family became extinct, and only one genus, an ancestor of *Grypoceras*, survived. Nautiloids from the Induan of southern Primorye suggest that this survivor rapidly diversified after the P/Tr mass extinction and by the end of the Induan, morphological diversity had recovered to pre-extinction levels.

After the Induan, the Grypoceratidae and two other survivors, the Tainoceratidae and Liroceratidae, diversified and gave rise to several new families. The total number of genera increased and taxonomic diversity recovered to pre-extinction levels during the Upper Triassic. Thus, the taxonomical recovery of nautiloids was much slower than their morphological recovery.

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EOCENE CEPHALOPODS FROM DUDAR, TRANSDANUBIAN HUNGARY

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The Middle Eocene mollusc fauna of Dudar in the Transdanubian Central Range, Hungary has been yielded by the subsurface brown-coal mining activity, when the nummulitic-mollusc limestone, the overhanging rock of the coal was dumped as waste around the shafts. The greyish-brownish limestone gave fossils in great profusion and exceptional preseration. Some early works in the 1950's and 60's resulted in extended faunal lists which mentioned Nautiloids and Coleoids.

The nautiloids are represented by several examples of *Cimomia crassiconcha* (Vogl), the only Cephalopod species which was recorded and described formerly from here. New specimens are from the nummulitic-mollusc limestone from the waste dump and additionally from collecting in a nearby open pit coal-mine worked in the 1980's. Previous collecting at the locality and inspection of museum materials yielded some

Previous collecting at the locality and inspection of museum materials yielded some Bayanoteuthis rugifer (Schloenbach) rostra and Belosepia blainvillei Deshayes rostra-periostraca. The latter species is firstly reported now from Hungary.

Eocene coleoids are rare fossils even in rich mollusc materials because preservation needs circumstances favourable for very fragile skeletal elements. Thus all records could substatially extend our knowledge on cephalopod faunas of the European Tertiary. The here introduced records support other data suggesting a uniform nekton fauna of the Eocene Mediterranean Sea.

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MOLECULAR PHYLOGENY AMONG EAST-ASIAN CUTTLEFISHES USING THREE MITOCHONDRIAL GENES

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Phylogenetic relationships among sixteen species of sepiids were studied using three mitochondrial genes, cytochrome *c* oxidase subunit I (COI), Cytochrome *b* (Cytb), and NADH dehydrogenase subunit 5 (ND5). We analyzed nucleotide sequences of these genes (totally 2,200 bp) and translated amino acid sequences (732 aa) with the outgroups, teuthoids and octopods, using the maximum likelihood method. Our molecular phylogenetic analyses revealed that these sepiids comprise four clades, *Acanthosepion* clade, *Metasepia+Sepia latimanus* clade, *Sepiella+Sepia* clade, and *Doratosepion* clade (Fig. 1). Khromov *et al.* (1998) classified cuttlefishes into six species complexes. *Acanthosepion* and *Doratosepion* were consistent with our molecular clades. However, the species complex *Sepia* didn't form a single clade as by our previous analysis suggested using COI, 12S and 16S rRNA genes (Yoshida *et al.*, 2006). The present analyses also suggested Asian *Acanthosepion* species are ancestral to the sepiids.



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HOW MANY SPECIES WITHIN SPIRULA EXIST? A MORPHOMETRIC APPROACH

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One of the most unusual recent cephalopods is *Spirula* with a well-developed internal chambered shell (Figure 1). These shells can be found in great numbers on oceanic beaches. *Spirula* is widely distributed in the Atlantic and Indo- or Indo-West Pacific (Bruun 1943, Clarke 1966). But its distribution range is disjunct like that of many other epi- and mesopelagic circumtropical species and apparently there is no gene flow between the Atlantic and Indo-Pacific parts of their ranges around South Africa (Nesis 1998).



Figure 1. Spirula shell (Canary Islands)

However, well-preserved material of whole *Spirula* is scarce, therefore a molecular study to examine the diversity of geographically fragmented populations has been carried out. Additionally, most collections of *Spirula* were preserved in formol therefore it is a big problem to get ethanol fixated tissue which is useful for DNA molecular analyses. However, a first study of four *Spirula* animals catched near Fuerteventura (Canary Islands, Spain) and sequences (from the gene bank) of one *Spirula* from New Caledonia were examined to get hints about the diversity of geographically fragmented populations (Warnke, in press). Because there were just sequences from one *Spirula* of New Caledonia in the gene bank available, this analysis did not come to a clear answer to the question if there is more than one *Spirula* species or not. Therefore in this study we used the morphometry of the shells to get additional hints to investigate the question.

We explore morphology of the shell from 4 main geographical areas: West Atlantic (Brazil), East Atlantic (Canary Islands, Morocco), West Indian Ocean (Madagascar, Mocambique) and West Pacific (New Zealand, Australia). Growth patterns of the shell are quantified and compared between these populations. First results seem to indicate no differences, and thus give no advice to separate the species. Further explorations are needed on other anatomical aspects including both shell and soft parts and on molecular analysis before, to accept or reject the occurrence of more than one species.

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NEUROPEPTIDES AND PEPTIDE HORMONES IN THE OCTOPUS BRAIN

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Cephalopods have highly developed sensory and motor systems, and large multi-lobed brains that are capable of complex analysis, learning, and social behavior. Despite decades of studies on neuroanatomy, physiology, endocrinology, and behavior, very little has been known about the molecular mechanisms mediating their advanced skills. Immunohistochemical studies have been carried out on the central and peripheral nervous systems using heterologous antibodies against vertebrate peptides and hormones, suggesting occurrences of vertebrate peptide-like substances. However, reports about isolation and characterization of endogenous peptides have been limited. Neuropeptides and peptide hormones involved in control of cardiovascular system and gonadal maturation will be presented.

1. Cardioactive peptides isolated from the brain and the vena cava neurosecretory system of the octopus

Cephalopods are the only animals other than vertebrates to form a high-pressure closed vessel system. Similar to the vertebrate system, cardiac and vascular regulation is controlled by an antagonistic innervation of excitatory and inhibitory fibers involving peptidergic mechanisms. Cardioexcitatory peptides (Ocp-1: Gly-D-Phe-Gly-Asp, Ocp-3: Gly-Ser-Trp-Asp) were isolated from the brain of *Octopus minor*. The D-/L-stereoisomers at position 2 were also isolated (Ocp-2: Gly-Phe-Gly-Asp, Ocp-4: Gly-D-Ser-Trp-Asp), but their activities are only 1/10³-1/10⁴ those of the corresponding stereoisomers. The presence of the peptides in the systemic heart was confirmed by mass spectrometry analysis. The results suggest that Ocp-1 and Ocp-3 are involved in excitatory control of the octopus cardiovascular system.

A number of neurosecretory cells in the visceral lobe send a voluminous neuropil inside the vena cava forming the vena cava neurosecretory system, which secretes cardioactive substances. A novel member of the oxytocin/vasopressin superfamily, octopressin, was isolated from *Octopus vulgaris*. Octopressin causes contractions of smooth muscles of the oviduct, aorta, and rectum, and has cardiac-stimulating activity.

2. Regulatory peptide hormone in the gonadal maturation

The optic glands are small rounded bodies found on the upper posterior edges of the optic tracts of octopus. In matured octopuses, the optic glands enlarge and secrete a gonadotropic hormone. Gonadotropin-releasing hormone (GnRH) plays a pivotal role in the regulation of reproduction in vertebrates. A dodecapeptide, named oct-GnRH, with structural features similar to GnRH was isolated from the brain of *Octopus vulgaris*. GnRHs from chordate species are decapeptides, so that the $-Asn^2$ -Tyr³- residues of oct-GnRH are inserted. However, oct-GnRH appears to satisfy the structural requirements for gonadotropin-releasing activity such as the <Glu¹- residue at the N-terminus, -His⁴- and $-Ser^6$ - residues, and $-Pro^{11}$ -Gly¹²-NH₂ at the C-terminal region (Table 1).

origin	structure
O. vulgalis	<glu-asn-tyr-his-phe-ser-asn-gly-trp-his-pro-gly-< td=""></glu-asn-tyr-his-phe-ser-asn-gly-trp-his-pro-gly-<>
	$ m NH_2$
mammal	<glu-his-trp-ser-tyr-gly-leu-arg-pro-gly-nh<sub>2</glu-his-trp-ser-tyr-gly-leu-arg-pro-gly-nh<sub>
guinea pig	<glu-tyr-trp-ser-tyr-gly-val-arg-pro-gly-nh<sub>2</glu-tyr-trp-ser-tyr-gly-val-arg-pro-gly-nh<sub>
chicken-I	<glu-his-trp-ser-tyr-gly-leu-gln-pro-gly-nh<sub>2</glu-his-trp-ser-tyr-gly-leu-gln-pro-gly-nh<sub>
chicken-II	<glu-his-trp-ser-his-gly-trp-tyr-pro-gly-nh<sub>2</glu-his-trp-ser-his-gly-trp-tyr-pro-gly-nh<sub>
frog	<glu-his-trp-ser-tyr-gly-leu-trp-pro-gly-nh<sub>2</glu-his-trp-ser-tyr-gly-leu-trp-pro-gly-nh<sub>
salmon	<glu-his-trp-ser-tyr-gly-trp-leu-pro-gly-nh<sub>2</glu-his-trp-ser-tyr-gly-trp-leu-pro-gly-nh<sub>
whitefish	<glu-his-trp-ser-tyr-gly-met-asn-pro-gly-nh<sub>2</glu-his-trp-ser-tyr-gly-met-asn-pro-gly-nh<sub>
seabream	<glu-his-trp-ser-tyr-gly-leu-ser-pro-gly-nh<sub>2</glu-his-trp-ser-tyr-gly-leu-ser-pro-gly-nh<sub>
medaka	<glu-his-trp-ser-phe-gly-leu-ser-pro-gly-nh<sub>2</glu-his-trp-ser-phe-gly-leu-ser-pro-gly-nh<sub>
catfish	<glu-his-trp-ser-his-gly-leu-asn-pro-gly-nh<sub>2</glu-his-trp-ser-his-gly-leu-asn-pro-gly-nh<sub>
herring	<glu-his-trp-ser-his-gly-leu-ser-pro-gly-nh<sub>2</glu-his-trp-ser-his-gly-leu-ser-pro-gly-nh<sub>
dogfish	<glu-his-trp-ser-his-gly-trp-leu-pro-gly-nh<sub>2</glu-his-trp-ser-his-gly-trp-leu-pro-gly-nh<sub>
lamprey-I	<glu-his-tyr-ser-leu-glu-trp-lys-pro-gly-nh<sub>2</glu-his-tyr-ser-leu-glu-trp-lys-pro-gly-nh<sub>
lamprey-II	<glu-his-trp-ser-his-asp-trp-lys-pro-gly-nh<sub>2</glu-his-trp-ser-his-asp-trp-lys-pro-gly-nh<sub>
Ι	
tunicate-I	<glu-his-trp-ser-asp-tyr-phe-lys-pro-gly-nh<sub>2</glu-his-trp-ser-asp-tyr-phe-lys-pro-gly-nh<sub>
tunicate-II	<glu-his-trp-ser-leu-cys-his-ala-pro-gly-nh<sub>2</glu-his-trp-ser-leu-cys-his-ala-pro-gly-nh<sub>

Table 1. Primary structures of GnRH family peptides

Actually, oct-GnRH shows luteinizing hormone-releasing activity in the anterior pituitary cells of the Japanese quail *Coturnix coturnix*. Oct-GnRH-like immunoreactive signals were observed in the glandular cells of the optic gland, which is analogous to the anterior pituitary in the context of gonadal maturation. Oct-GnRH stimulates synthesis and release of sex steroids from the ovary and testis, and exhibits contractions of the oviduct. Oct-GnRH receptor, which was cloned from the brain, was expressed in the gonads and accessory organs such as oviduct, oviducal gland, and vas deferens. These results suggest that oct-GnRH induces the gonadal maturation and oviposition by regulating sex steroids via oct-GnRH receptor as an optic gland hormone.

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CLOSE BUT DISTANT? —GEOGRAPHICAL DISTRIBUTION OF SHALLOW WATER BENTHIC OCTOPUS OF THE RYUKYU ARCHIPELAGO AND ADJACENT AREAS

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Shallow-water (<50 m) benthic octopus fauna in the Ryukyu archipelago was investigated and compared with those of other four localities of East Asia (southern Japan, Taiwan, Philippines and Hong Kong), for which relatively comprehensive and reliable information is available from literature and stored specimens. Although Ryukyu archipelago is close to Taiwan and southern Japan, cluster analysis of similarity indices indicated that species composition of octopuses in the Ryukyus was much similar to that of the Philippines, while its similarities to those of southern Japan, Taiwan, and Hong Kong were distinctly lower. Most species found in the Ryukyus and the Philippines are also share with other, more southern, such as Sunda archipelago or Great Barrier Reef (north Australia), whereas southern Japan, Taiwan and Hong Kong were also associated with each other faunistically. Such geographic patterns of similarity in the species composition of shallow water octopuses may reflect that in available habitat types. We also discuss the influence of the Kuroshio Current to distribution of octopus fauna in East Asia.

AMMONOID MASS MORTALITY BEDS IN THE LOWER TRIASSIC THAYNES FORMATION OF WESTERN UTAH, USA

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The Thaynes Formation was deposited in the Sonoma Foreland Basin during the Early Triassic (Olenekian). Outcrops of these epicontinental marine rocks can be seen now in the Confusion Range of Utah. Most of the Thaynes Formation in western Utah consists of yellow-gray fissile shale and gray-brown limestone that reflect deposition in relatively calm conditions equivalent to basin to outer shelf facies. Occasional, short-term regressions produced a few thin layers of inner shelf siltstone, sandstone, and/or limestone.

The Thaynes Formation is well known by professionals and amateurs alike for its densely concentrated ammonoid beds. Indeed, the best locality in the Confusion Range seems to be inexhaustible, despite the sporadic but dedicated efforts of collectors over at least the past several decades. We recognize three distinct Smithian ammonoid assemblages in the Thaynes Formation of western Utah. Each assemblage occurs within thin, isolated beds of about 20-30 cm thickness. We refer to the lowest of these as the Meekoceras Bed, which is dominated by *Meekoceras*, *Arctoceras*, and *Aspenites*. The middle occurrence is the Inyoites Bed, dominated by *Inyoites*, *Lanceolites*, and *Pseudosageceras*. The uppermost of the occurrences is referred to as the Anasibirites Bed, and is dominated by *Anasibirites* and *Wasatchites*. The lower and middle occurrence appear to fall within the Romunderi Zone, whereas the upper occurrence appears to fall within the Tardus Zone. These beds can be confidently identified in outcrops within the study area (~100 km²) and even beyond (*e.g.*, in southeastern Utah).

There are numerous possible explanations for dense concentrations of ammonoids, including reproductive mass mortality (semelparity), taphonomic biases (*e.g.*, condensed intervals and post-mortem hydrodynamic transportation), and mass mortality generated by environmental catastrophe. There is some evidence that the Lower Triassic ammonoid beds of the Thaynes Formation in western Utah may have resulted from several different causes. However, we believe the primary cause of these ammonoid beds is related to the unusual ocean conditions documented for the Early Triassic by many other workers. Multiple lines of evidence (*e.g.*, sedimentology, paleontology, geochemistry) indicate that anoxia and hypercapnia are likely culprits for large-scale death horizons during the Early Triassic in general. The fact that these ammonoid beds can probably be traced across hundreds of kilometers strongly suggests that they were produced by basin-wide (and possibly global) catastrophic environmental events.
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MASS MORTALITIES OF COLEOID CEPHALOPODS IN THE JURASSIC OXFORD CLAY OF ENGLAND: ORIGIN AND TAPHONOMY

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Exceptionally well-preserved coleoid cephalopods retaining details of their soft-part anatomy, including the ink sac, gonads, brain cartilage, mantle and arms with suckers, are well known from the Middle Jurassic Peterborough Member of the Oxford Clay Formation of England. They comprise three species: the belemnoid *Belemnotheutis antiquus* (see Donovan and Crane, 1992), the probable decapod *Mastigophora brevipinnis* (Vecchione et al., 1999) and a rare form provisionally identified as *Romaniteuthis* (Page and Doyle, 1991). Their soft tissues are replaced by apatite (calcium phosphate) and preserve cellular histological details; the ink retains molecular derivatives of the original melanin.

Most of the specimens, amounting to over 100 individuals, were collected from a small (now inaccessible) excavation near Christian Malford in the mid nineteenth century. Their distribution at outcrop was not recorded, but their remarkable abundance implies that they probably originated from one or more high density mass accumulates. This is consistent with numerous specimens recently collected from the same level nearby which consist of "pairs" of *en echelon* coleoids. Individuals within each "pair" may be conspecific and of similar size, or of two different species, but in every case one individual is preserved clasping the other. Palaeoecological analysis of the Peterborough Member indicates that the sea floor at this time repeatedly experienced periods of anoxia and was overlain by a water column that was at least intermittently stratified. It is proposed that the coleoids formed large schools that were killed *en masse*, together with other elements of the associated fauna (e.g. fish), in one or more catastrophic anoxic events. During the event(s), the coleoids preyed upon moribund fish and other coleoids before being overcome themselves (Wilby et al., 2004).

Detailed vertical geochemical sampling of the sequence is helping to elucidate the frequency of anoxic events in this part of the Peterborough Member sea, their effect on the cephalopod faunas, and the sedimentary conditions required for soft tissue preservation. Pronounced TOC (total organic carbon) excursions correlate well with isolated occurrences of exceptionally well-preserved coleoids at other levels in the sequence and may, for the first time, assist with prospecting for new taxonomically significant specimens.

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018

HOW TO RECOGNIZE IN SITU FOSSIL CEPHALOPODS: EVIDENCE FROM EXPERIMENTS WITH MODERN NAUTILUS

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Field and flume experiments with modern Nautilus pompilius establish two prerequisites to recognize in situ preservation of fossil cephalopod shells (soft parts were within body chamber in situ at the time of fossilization): occurrence of the upper jaw within the body chamber and the position of jaws within the body chamber. Morphology of shells and jaws in modern and fossil nautiloids are so similar that these prerequisites can be applied for fossil nautiloids and provide implications for ammonoids. The upper jaws of *Nautilus* start to move at a water velocity of >0.2 m/s, when the shells are reoriented with the aperture downstream; jaws are therefore unlikely to be secondarily deposited near the shell aperture by bottom currents. The lower jaws, moved at the velocity of >0.1 m/s, can be deposited around the shell aperture by weak current (0.1-0.2 m/s in velocity), but never enter the inside of body chamber. Neither jaw is likely to be separately and selectively displaced from the inside of the body chamber through scavenging of the soft parts by burrowing infaunal animals. An upper jaw preserved inside the body chamber, together with a lower jaw, is thus a reliable indicator of in situ preservation; a sole lower jaw preserved around the shell aperture is likely to be secondarily deposited. Sedimentary structures inferring rapid burial events and jaw size are useful as additional evidence. Smaller jaws were more likely to be displaced from the body chamber by scavenging by infaunal animals after in situ burial, so that smaller jaws preserved within the body chamber suggest less scavenging. These findings are crucial to interpreting the taphonomic history and paleoecology of fossil cephalopods.

019

LOOKING AT FOSSIL CEPHALOPODS IN A NEW LIGHT

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We normally view fossils using visible wave-lengths of light. Other techniques such as CAT scans, SEM images, x-rays and immersion are used to see things that are otherwise invisible to the naked eye. Very rarely, are new procedures discovered that enable us to see fossils in different ways, but we keep looking. Although Ultra Violet (UV) imaging is not new, the use of UV imaging in conjunction with macro, UV photography has shed a new light on the fossil cephalopods from Hakel, Lebanon (lower, upper Cenomanian). This imaging has helped to show the remarkable similarities between fossil squids and their extant relatives. Looking at fossil cephalopods in UV fluorescent, UV LCD, UV mercury, and UV sunlight has enabled us to examine their gladii, pens, arms, eyes, ink sacs and other organs in a manner not normally seen. As a result, UV imaging will aid in the descriptions and classifications of these and other fossil In addition to UV imaging and macro-photography, some of the cephalopods. specimens from Lebanon were taken to Stanford University, CA where they were scanned with a monochromatic beam of electrons in a linear accelerator. The information gleaned from these scanned fossils has also resulted in important discoveries regarding the soft parts of cephalopods through single and composite element images not able to be seen with any other method. These new techniques of imaging may one day enable us to see the soft parts of ammonites and fossil nautilids as well.

AMMONITE IMAGING USING DIGITAL PHOTOGRAPHY

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High quality photographs are critical to the study of ammonites. Digital photography increases the control in producing an image and thereby increases the quality of the photograph. This topic can be divided into three areas: equipment, photographic technique, and digital editing of the image.

A 35 mm DSLR (digital single lens reflex) camera having a full frame sensor (CMOS or CCD) with at least a 12-megapixel resolution is the optimum choice for the camera body. The lenses required are a macro lens (1:1), normal lens, and a special close up lens or bellows for magnifications that are greater than 1:1. A stable copy stand and focusing rack are also necessary. A cable release and mirror lock-up are needed for non-flash photographs to prevent blurring of the image. Lighting can be accomplished using flash, fiber optics or diffuse lighting. Color temperature of the light source is not important because it can be corrected using the camera's software. A circular polarizing filter is needed with reflective surfaces.

Lighting techniques allow for greater or lesser mottling (shadows). The more diffuse the light, the more subtle the shadowing. Conversely, the more concentrated the light source, the greater definition of the shadows. Low angle lighting is extremely useful for showing texture, while lighting that is perpendicular to the specimen all but eliminates shadows. Reflectors and diffusers further modify mottling.

Digital editing of the image is the final step in producing a high quality image. The use of RAW format is recommended because it allows you more control of white balance and exposure than TIFF. Never use JPEG, as the image degrades each time it is manipulated and saved. The sequence of editing is Level adjustment, Shadow / Highlight adjustment, and Unsharp Mask adjustment. Further manipulation of the image can be done after the initial editing sequence is completed. Use CombineZM to increase depth of field when necessary. **O21**

CEPHALOPOD JAWS FROM THE LOWER CALLOVIAN OF KOSTROMA REGION, RUSSIA

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Numerous mostly isolated remains of ammonoid jaws have been found in different stratigraphical horizons of the Lower Callovian of the River Unzha Basin/Russia. Only one specimen of a Praestriaptychus (lower beak) have been found within the body chamber of a perisphinctid (fig. 1). Complete jaw apparatuses of cardioceratid microconchs and rare findings of the Early Callovian kosmoceratid aptychi from Russian platform have been described recently (Mitta & Keupp, 2004). However the new material is unique because of its undamaged preservation, quantity of findings and diversity of material. They are preserved in phosphoritic concretions and phosphated sandstones of a sandy-argillaceous facies deposited under conditions of a sublithoral environment and are associated with representatives of Cardioceratidae, Kosmoceratidae and Perisphinctidae (micro- and macroconchs). The aptychophor ammonites changed their lower jaw functionally from a biting instrument into an operculum, while the upper jaws remain more or less rudimentary as an abutment for the mandibular muscle system and reduced often their outer lamellae.

The different types of ammonitic jaw apparatuses, both aptychi and anaptychi, can be used for reconstructions of phylogenetic relationships (Engeser & Keupp 2002), showing besides of other that the kosmoceratid granulaptychi link to the derived group of perisphinctids rather than to the basic perisphinctid group or to the stephanoceratids characterized by smooth praestriaptychi.

The new remains of upper beaks exhibit their inner and outer lamellae quite clearely (figs. 2-4). By the first impression, these rests belong to miscellaneous taxa, probably to Cardioceratidae. But the strong outer lamella which creates a sharp biting tip do not fit with the former described beaks of *Costacadoceras* (Mitta & Keupp, 2004).

We hope to enrich our material so that its study will allow to obtain more differentiated data on distinctions in structure of the jaw apparatuses of Middle Jurassic Ammonitina and the way they fed.

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Explanations of figures:

1. Lower Jaw (= *Praestriaptychus*) in body chamber of the perisphinctid ammonite *Elatmites* sp. [m]. 2. Upper beak in dorsal view. 3. Upper beak in dorsal (a) and lateral view (b) exhibiting the outer lamella very clearly. 4. Outer lamella of an (?) upper beak. 5. The cardioceratid ammonite *Cadoceras* sp. [M] with prominent inner lamella of upper jaw. The outer lamella seems to be reduced or lost by taphonomic processes. Figs 1-3 – Calloviense Zone; 4,5 – Elatmae Zone. Scale bar 5 mm.

O22

STRUCTURE AND FUNCTION OF BACULITES, POLYPTYCHOCERAS AND JELETZKYTES APTYCHI

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The microstructure of the lower jaws of the Late Cretaceous ammonites *Baculites*, *Polyptychoceras* and *Jeletzkytes* is here described for the first time on the basis of well-preserved and in situ materials from the U.S. Western Interior and Hokkaido (Japan). Most of the lower jaw specimens occur inside the living chamber of their ammonites retaining original aragonitic shell mineralogy. The *Polyptychoceras pseudogaltinum* specimen was recovered from the Lower Campanian in the Wakkawenbetsu Creek, Nakagawa, N. Hokkaido. The *Jeletzkytes nebrascensis* (Scaphitidae) and *Baculites* sp. (smooth) specimens came from the U.S Western Interior (South Dakota, Lower Maastrichtian Fox Hills Formation, Timber Lake Member)and from Alabama (U.S.A. – Lower Campanian, Moorville Chalk, Greene County, Alabama)respectively.

The lower jaws of these ammonites consist of an inner chitinous layer with a ridge along the midline. The outer layer consists, in the aptychus-type jaw, of a pair of calcareous valves.

The aptychus of the *Polyptychoceras* is very thin, approximately 30 μ m thick, and is smooth on the outside. The aptychus in the *Jeletzkytes* is thicker (500 μ m thick) with thin round ridges on the outside. The aptychus in *Baculites* is slightly thicker (700 μ m thick) and is covered with prominent ridges.

All of these aptychi are thinner than those in Jurassic ammonites, such as *Laevaptychus* or *Punctaptychus*. The microstructure is also different and may be interpreted as an evolutionary trend. In the Cretaceous forms calcite occurs in regular layers whereas in the Jurassic forms most of the calcite occurs in a sponge like structure. An electron probe analysis has also been done with the specimens.

Observations on the size and structure of the jaws in relation to the size and shape of the whorl section prove that aptychi are lower jaws.

These elements and the understanding of the growth pattern may provide additional characters that can be used in reconstructing phylogeny in the Ancyloceratina.

O23

LATE CRETACEOUS LARGE OCTOBRACHIATE COLEOID JAWS FROM THE CIRCUM-NORTH PACIFIC REGIONS

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Several well-preserved cephalopod jaw fossils were recovered from the Late Cretaceous (Santonian and Campanian) deposits of Vancouver Island, Canada and Hokkaido, Japan. They occur individually in calcareous concretions and favorably retain their three-dimensional architecture. Seven of them consist of widely open outer, and posteriorly projected inner lamellae, with a pointed rostrum. Both Lamellae are made of fluorapatite $[Ca_5(PO_4)_3F]$ which may represent diagenetically altered chitin, and lack a calcareous element. Based on these diagnostic features, the five jaw fossils are identified as the lower jaws of the Coleoidea.

Comparison with the lower jaws of modern coleoids (e.g., Clarke, 1986; Kubodera, 2000) indicates that one jaw specimen with a sharply pointed rostral tip and a weakly opened outer lamella is attributed to the new genus and species of the Order Vampyromorphida, and that the rest four jaw specimens with a obtusely pointed rostral tip and a widely opened outer lamella are assigned to two new species of a new genus of the Order Cirroctopodida. The lower jaws of these new taxa are clearly distinguished by having a much less projected inner lamella from those of the species of the Superorder Decabrachia and the Order Octopodida. The maximum lengths of the outer lamella of the jaws of these new taxa (37.5 - 67.0 mm) are much larger than those of modern vampyromorph and cirroctopodid species (< 25 mm), suggesting large body size and weight of living animals.

Extant Coleoidea is currently divided into two superorders: Decabrachia and Octobrachia. The Decabrachia contains the Orders Teuthida (open- and closed-eyed squids), Sepiida (cuttlefishes), Sepiolida (bobtail and bottletail squids), Idiosepiida (pigmy squids), and Spirulida (ram's horn squid). They are characterized by a modification of the fourth pair of arms into tentacles. The Octobrachia comprises the Orders Octopodida (benthic and pelagic octopuses without fins and cirri), Cirroctopodida (deep-sea finned octopuses with cirri), and Vampryomorphida (vampire squid), all of which share the outer capsule of the statocyst, the modified second pair of arms, and the position of superior buccal lobe of the brain as synapomorphies (Young and Vecchione, 1996). Divergence time analysis using multiple genes suggests that the Decabrachia and Octobrachia were branched in the Devonian and the Vampryomorphida and the clade comprising the Cirroctopodida and Octopodida in the Permian (Strugnell et al., 2006). However, this hypothesis has not yet been verified by sufficient fossil evidence. Our knowledge on the extinct coeloids other than the Aulacocerida and the Belemnitida has been virtually restricted to the exceptionally well-preserved fossils with compressed soft tissue remains ("fossil teuthids") from the "Konservat-Lagerstätten" of Late Paleozoic to Cretaceous ages.

Our discovery of well-preserved coleoid jaws fills the gap of the poor fossil record of the "nonshelled" coleoids and clearly demonstrates that large Octobrachia existed in the Late Cretaceous Pacific, together with teuthids (*Yezoteuthis*; Tanabe et al., 2006), sepioids (*Naefia* and *Groenlandibelus*), ammonoids, and nautilids.

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PALAEOCTOPUS N. SP. (CEPHALOPODA: COLEOIDEA), A PELAGIC OCTOPOD FROM THE LATE CRETACEOUS OF VALLECILLO, NE MEXICO

024

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The fossil Lagerstätte Vallecillo has become famous for its well-preserved fishes. Near this village in NE Mexico, platy limestone quarried for commercial purposes yields marine fossils with exceptional preservation. Both ammonites and inoceramids provide an early Turonian age for the assemblage. Planktic foraminifers, calcispheres and recrystallized radiolarians indicate a pelagic environment, consistent with the palaeogeographic position of Vallecillo; the nearest palaeocoasts were >500 km to the NE or W, and islands or submarine topographic heights did not exist due to the high global sea-level of the early Turonian.

The only benthic organisms known from both the micro- and the macrofossil assemblage are inoceramids. Apparently, the conditions at the sea-floor were very hostile, and only these bivalves could bear this environment. It seems that the late Cenomanian Oceanic Anoxic Event 2 persisted on the Mexican shelf.

During a scientific excavation in 2003, the gladius vestige of a fossil octopod was excavated. *Palaeoctopus n. sp.* represents the first record of a fossil octopod from America and the second species of its genus. The other species, *P. newboldi* from the Santonian of Lebanon, is characterised by a bipartite shell vestige in the posterior part of a sack-like body, a pair of sub-terminal fins, eight equal arms and circular suckers. It possibly inhabited to benthic or benthopelagic environments on the Lebanese Carbonate Platform. The carcasses probably drifted into the small basin of Sahel Aalma.

The Mexican specimen preserves one half of an originally bipartite gladius vestige which is different from *P. newboldi*; soft parts are unknown. The palaeoenvironment of Vallecillo clearly suggests that *Palaeoctopus n. sp.* inhabited a pelagic environment. Desertic hostile low oxygen conditions on the sea floor preclude a benthic mode of life for *Palaeoctopus n. sp*, whereas it could live under normal marine conditions near the surface and feed on floating carcasses of fishes and ammonites or hunt small prey. This new Mexican specimen is the oldest fossil octopod known and casts new light on the mode of life of early Octopods. **O25**

THE "PROOSTRACUM" IN SPIRULID COLEOIDS AND ITS PHYLOGENETIC IMPLICATIONS

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The proostracum, a dorsal protrusion of a coleoid phragmocone, apparently plays a key role in the phylogeny of the Coleoidea. It is commonly considered as the result of a ventral reduction of the body chamber and well-known from belemnoids (phragmoteuthids, belemnitids, diplobelids). Although the general morphology of so-called proostraca found in Late Cretaceous spirulids, *Naefia* and *Groenlandibelus*, clearly differ from belemnoid proostraca, both structures are widely regarded to be homologues. However, Fuchs (2006, in press) recently expressed his doubts about the homology of the two types of proostraca and suggested that the spirulid type is the result of allometric dorsal growth of a tubular (ventrally closed) body chamber, rather than the relict of a ventrally opened body chamber.

Since shell preservation is very common in the Santonian – Campanian Haborogawa Formation of Hokkaido (north Japan), *Naefia matsumotoi* is ideal for ultrastructural analyses. Hence, to obtain more details on the enigmatic shell morphology a large set of specimens available from various collections in Japan (Waseda University, University of Tokyo, National Science Museum of Tokyo, Ehime University) was investigated. For comparisons, the investigation included furthermore specimens of *Groenlandibelus rosenkranzi* from the Late Cretaceous of Greenland and *Groenlandibelus* spec. from the Late Cretaceous of Vancouver Island (British Columbia, Canada).

It turned out that in both, *Naefia* and *Groenlandibelus*, only the very thin sheath enveloping the shell exhibits forward projecting growth increments. The shell wall (conotheca), in contrast, shows no evidence of proostracal growth lines. These observations clearly indicate that the body chamber is most likely tubular and not involved into the formation of the "proostracum". Instead, the "proostracum" is formed by the sheath; similar to Cenozoic spirulirostrids (*Beloptera, Spirulirostra*) and different to belemnoids, where the rostrum thins out towards the anterior parts of the phragmocone. This evidently supports the idea about a convergent development of belemnoid and spirulid proostraca.

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CEPHALOPOD ASSEMBLAGES IN THE UPPER CARBONIFEROUS PART OF THE AKIYOSHI LIMESTONE GROUP, SOUTHWEST JAPAN

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The Akiyoshi Limestone Group, Southwest Japan comprises an organic reef complex that was deposited on a seamount during Early Carboniferous to Middle Permian time. It is distributed as a large $(8 \times 16$ km across) allochtonous body in the accretionary Akiyoshi Terrane with synchronous siliceous and Permian terrigenous clastic sediments in Southwest Japan. Eleven cephalopod assemblages which are represented by abbreviated CA1 to CA11 in ascending order, have been discriminated in the Upper Carboniferous part of the group. The limestone sequences that yield the CA1 to CA10 are successively distributed in groove-like narrow belts (less than 50 meters in width). The belts obliquely intersect with general attitude of limestone. The sequence which yields the CA11 is discontinuously distributed above that of the CA10. Each assemblage consists of large quantity of ammonoids in which bactritoids are included and small quantity of nautiloids. The lists of cephalopods of each assemblage are given with individual numbers. In addition to the list of ammonoids of the CA6, list of ammonoids from the one meter cube of limestone of extraordinary rich in cephalopods is given. The species of Pseudoparalegoceras and Syngastrioceras of goniatite are predominant and Pseudopronorites arkansiensis of prolecanite is fairly abundant in all assemblages. As the rare elements the combinations of species of shistoceratid and welleritid goniatite are recognized in almost assemblages and very useful for regional correlation. The sequences of the eleven cephalopod assemblages are distributed in the five successive fusulinacean zones in ascending order as follows; upper part of Pseudostaffella antiqua Zone (CA1), Profusulinella beppensis Z. (CA2~CA4), Fusulinella biconica Z. (CA5~CA9), Beedeina akiyoshiensis Z. (CA10) and Pseudofusulinella hidensis Z. (CA11) respectively. In all cephalopod assemblages, two or more (maximum six) endemic species are present. It is interested that *Pseudopronorites arkansiensis* known widely from North America to China and Minepronorites takahashii known only in the group co-exist in all assemblages.

NEW DATA ON GUADALUPIAN AND EARLIEST LOPINGIAN *TIMORITES* OF FAR EAST (JAPAN AND RUSSIA) AND BIOSTRATIGRAPHICAL AND PALEOGEOGRAPHICAL SIGNIFICANCE OF CYCLOLOBID AMMONOIDS

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The evolution of the Cyclolobinae followed several divergent tendency. In its phylogeny one conservative lineage (*Demarezites – Changhsingoceras*) and three progressive ones (*Demarezites – Waagenoceras – Timorites*, Waagenoceras – *Cyclolobus* (with primitive *Persulcatum* and advanced *Walkeri* groups, which seem to be its subgenera) and *Demaresites – Mexicoceras - ?Paramexicoceras*) can be recognized. Since almost all known cyclolobid ammonoid genera and their immediate ancestors were formed originally in low latitudes, just near the paleoequator, areals of all cyclolobid ammonoid genera reflect apparently the location of the both paleoequatorial realms (Tethyan Paleoequatorial and American Paleoequatorial), as well as transition zones. Our assumption seems to be in accordance with some results on isotopic paleotemperature calculation and data on paleogeography of ceratitid ammonoids and some other fossil invertebrates. New *Timorites* species from the Lower Wuchiapingian of the Kitakami Massif is described (Figure).



Figure. External and internal suture lines of *Timorites* **sp. nov. and** *Timorites takaizumi* **Ehiro & Araki**. A-H – *Timorites* **sp.** nov., based on holotype (IGPS 86886; eastern coast of Ishihama, Utatsu-cho, Motoyoshi-gun, Miyagi Prefecture; Wuchiapingian, Suenosaki Formation, *Araxoceras* Zone.): A-C - ventral lobe and two first lateral saddles at H = 57 mm (A), H = 48 mm (B) and H = 49 mm (C); D-E – external suture, saddles 1-12 at H = 62 mm (D) and H = 49 mm (E, mirror image); F – external suture (near umbilical area, saddles 10-13) at H = 128? mm); G – internal suture, saddles 4-13, at H = 130 mm; H – dorsal lobe of *Timorites takaizumi* Ehiro & Araki, at H > 55 mm, based on holotype IGPS 103125; Kurosawa River basin, northern Kesennuma; upper Capitanian, Ochiai Formation.



LATE SCYTHIAN TO MIDDLE ANISIAN AMMONOIDS FROM THE ALAM FORMATION IN NAKHLAK AREA, CENTRAL IRAN

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A distinctive succession of Triassic sedimentary strata with a thickness of 2724 m is well exposed in the Nakhlak area of central Iran (Fig. 1). These rocks are subdivided into three formations: the Alam, Baqoroq and Ashin formations (Fig. 2) with Late Scythian to Early Carnian? age that have been named as the Nakhlak Group (Davoudzadeh and Seyed-Emami, 1972; Tozer, 1972; Vaziri, 1996). Lithologically, paleontologically and depositional environments of the Triassic strata of Nakhlak differ completely from the shallow carbonatic and platform successions of lower and middle Triassic of Iran. The only correlative Triassic succession to the Nakhlak Group is Triassic succession of Aghdarband area (Ruttner, 1991) in northeastern Iran.

The up to 1298 m thick, mainly turbiditic, siliciclastic Alam Formation consists-besides some conspicuous carbonatic intercalations at the lower and middle part-predominantly of a sequence of shallowing and coarsening-upward marine turbidities with frequent volcanic components, deposited on a forearc side of an active margin in a continental shelf to slope setting (Fig. 2). Ammonoids collected from different levels of the Alam Formation indicate a Late Scythian to Middle Anisian age for the formation (Tozer, 1972; Vaziri, 1996). The recognized ammonoids belong to 35 genera and 31 species, and including Epacrochordiceras sp., Pseudosageceras sp., Procladiscites sp., Sturia sp., Acrochordiceras aff. hyatti, Propthyhitoides decipiens, Paragoceras mediterraneum, Kazahstanites dolnapensis, Isculitoides seyedemamii, Dagnoceras nopscanum, Columbits ventroangusts, Subcolumbites perrinismithi, Prenkites cf. malsorensis, Stacheites undatus, Alanites triadicus, Tirolites cassianus, Metadognoceras amiidi, Eophylites davoudzadehi, Leiophyllites stoecklini, Leiophyllites aff. pitamaha, Hollandites tozeri, Norites gondola, Nicomedites cf. toulai, Hungarites cf. Proponticus, Stenopapnoceras transiens, Ussurites arthaberi, Semibeyrichites ruttneri, Aghdarbandites ismidicus, Paraceratites aff. binodosus, Parapinacoceras cf. damesi, Ptychites aff. pauli, Gymnites religiouscus, Gymnites palmai, Gymnites asseretoi and Monophyllites kieperti.

The mentioned ammonoids belong to a single bio-province at southern margin of Turan continent and have commonality faunas (*Leiophyllites* sp., *Procladiscites* sp., *Gymnites* sp., *Semibeyrichites ruttneri*, *Aghdarbandites ismidiscus* and *Gymnites asseretoi*) with the Nazarkardeh Formation (Ruttner, 1991) in Aghdarband area of northeastern Iran (Fig. 1). The position of *ismidicus* ammonoida zone with Middle Anisian (Bithynian) age introduced by Krystyn and Tatzeriter (1991) in the Nazarkardeh Formation (fossil horizon number 1) is in the upper part of the Alam Formation.

The paleobiogeographical relationships of Triassic ammonoids in Nakhlak area with other areas show the existence of a certain province in the southern margin from the eastern most to western most portion of Paleothetys Ocean. This distribution shows the bio-district distinction of Lurasia continent (to the north) from Gondwana (to the south) and also boundary between Lurasia continent (at north) and Gondwana continent (at south) in northern Iran.

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Fig. 1: Location of Nakhlak and Aghdarband areas in central and northeastern Iran. Fig. 2: Stratigraphic units and recognized ammonoids of the Nakhlak Triassic succession.

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AMMONITE BIOGEOGRAPHY: FROM DESCRIPTIVE TO DYNAMIC, ECOLOGICAL INTERPRETATIONS

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Concerning to pelagic organisms, biogreography usually focuses on large scale patterns of distribution, which result from evolutionary adaptation to dynamic teleconnections in the ocean-atmosphere-geosphere system.

Recent improving of biogeographical interpretation of extant cephalopods resulted from ongoing research on biochemical and molecular genetics (and barcoding in the near future), remote monitoring, chemical tags and isotope geochemistry of water masses (e.g. Jackson et al., 2007; Semmens et al., 2007; Sinclair et al., 2007). Mainly focused on commercial species, the ecological dynamics underlying area distribution is being elucidated through stable isotope, fatty acid and heavy metal signatures, as well as precise identification of cephalopod beaks. On this basis, potential metapopulation structure has been assumed to be approached (e.g. Semmens et al., 2007). However, in such a stimulating context, the informal use of terms such as dispersal, dispersion and migration introduces noise when interpreting dynamic biogeography (e.g. Dingle, 1999).

In contrast to increasing interpretation of extant cephalopods in terms of dynamic biogeography, the interpretation of biogeographical patterns in ammonoids has been logically limited and basically descriptive (but see Cecca, 2002), and submitted to a rather vague use of terms when referring to the underlying palaeobiological, ecological dynamics. The abiotic, palaeoenvironmental context of reference has been approached through uneven allusions to so-called major environmental parameters, depth included, and/or more recently to relative sea-level fluctuations at different scales. Less common were references to the crucial, eco-evolutionary relevance of water masses forcing both "capture-effect" and eco-evolutionary traits in ammonoids (e.g. Olóriz, 2000 and references therein).

A revision of selected biogeographical concepts and terms applied to interpretations of ammonoid biogeography is made, and metacommunity and metapopulation dynamics (e.g. Gilpin & Hanski, 1991; Sterelny, 1999) are envisaged as a useful template for interpreting ammonite biogeography under acceptance of some assumptions: (i) Ecospace for pelagic to demersal ammonoids operated at mainly upper waters, even in oceanic-epioceanic environments; (ii) modern nautilids are closer analogues to standard-ammonoid behaviour, especially in that concerning basic ecological targets and costs related to animal's movements (e.g. swimming, foraging, feeding, metabolism); and (iv) variable within-biogeographic range post-mortem transport overwhelmingly prevailed. To exemplify, some ammonite records from the upper Jurassic are discussed.

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AMMONITE BIOSTRATIGRAPHY OF THE DALICHAI FORMATION (MIDDLE JURASSIC) SOUTHEAST OF LAKE URMIA, SOUTHWEST ALBORZ, NORTH IRAN

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Middle Jurassic strata (Dalichai Formation) are widely distributed along the Alborz Range, consisting of an alternation of bluish-grey lime stones and marls and containing a fairly rich ammonite fauna.

The studied ammonites come from southeast of Maragheh (southeast of Lake Urumia), where the Dalichai Formation with a thickness of about 203m is well exposed. It consists of an alternation of grayish marls and lime stones and contains a fairly rich and well-preserved ammonite fauna, mainly in the lower part. These comprise the following families: Oppelidae, Stephanoceratidae, Parkinsoniidae, Morphoceratidae, Reineckeidae and Perisphinctidae. Contrary to the other occurrences of the formation, the scarcity of Phylloceratidae (2%) is remarkable. Paleobiogeographically the fauna is closely related to the taxa from northwestestern Europe and Submediterranian areas, allowing a similar biozonation.

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UPPER BAJOCIAN TO TITHONIAN AMMONITES OF THE NORTHEASTERN IRAN

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The Middle and Upper Jurassic sedimentary successions of Alborz in northern Iran and Koppeh Dagh in northeastern Iran comprise six formations; Shal, Dalichai, Lar (Alborz) and Kashafrud, Chaman Bid and Mozduran (Koppeh Dagh).

The Middle and Upper Jurassic sediments in North Iran constitute a more or less continuous sequence, being confined by two tectonic events, at the base, in the uppermost part of the Shemshak Formation the so-called Mid-Cimmerian Event (Bajocian), and the so-called Late-Cimmerian Event (early Cretaceous) at the top. The upper part of the underlying siliciclastic Shemshak Formation contains a fairly abundant ammonite fauna ranging in age from Aalenian to early Bajocian. The Dalichai, Shal and Kashafrud formations begins everywhere with a significant marine transgression of late Bajocian age.

Based on ammonites, the formations strongly diachronous: The Dalichai Formation ranges from the Upper Bajocian to the Lower Tithonian, Lar Formation from the Upper Callovian to the ?Neocomian, Shal Formation from the Upper Bajocian to the ?Neocomian. In the Koppeh Dagh the Kashafrud Formation ranges from the Upper Bajocian to the Upper Bathonian, Chaman Bid Formation from the Upper Bathonian to ?Neocomian and Mozduran Formation from the Upper Bathonian to the ?Neocomian.

Among the taxa Phylloceratidae are most abundant, followed by Ataxioceratidae, Perisphinctidae, and Cardioceratidae. Pachyceratidae are the least common family. The ammonite fauna is of low diversity and is concentrated in several levels. Some of the ammonite genera and species are recorded from Iran for the first time. These include Pachyceras lalandei, Cardioceras praecordatum, Microbajocisphinctes sp., Geyssantia geyssanti, Larcheria schilli, Passendorferia sp., Sequeirosia sp., Phanerostephanus subsenex, Nothostephanus sp., Nannostephanus cf. subcomutus, Parawedekindia callomoni, Physodoceras sp., Extrenodites sp.. Biostratigraphically, thirty ammonite zones have been recognized for the Middle and Upper Jurassic successions at the North Iran.

MODE AND TEMPO OF EVOLUTION IN PHYLOGENY OF THE LATE JURASSIC FAMILY ATAXIOCERATIDAE (AMMONOIDEA)

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Ataxioceratidae is an important Late Jurassic ammonite family and all subfamilies viz Ataxioceratinae, Lithacoceratinae and Virgatosphinctinae share the virgatatome style of ribbing. The origin of the family remains one of the most difficult to understand in terms of mode and tempo of evolution (Callomon, 1981).

Kutch, in western India, is famous for Late Jurassic ammonites which are found in near-continuous Oxfordian to Tithonian sections. 11 genera and 74 species within Ataxioceratidae have been reported from Kutch (Spath, 1927-33). Although the family is excessively split, all the subfamilies appeared very rapidly within a span of about two million years, straddling the Oxfordian – Kimmeridgian boundary. Refinement of stratigraphic data suggests overlapping of all the subfamilies at the base of Kimmeridgian. From the Late Oxfordian to Middle Kimmeridgian five genera already appeared and they include 52 species. This indicates that evolution of Ataxioceratidae is marked by burst of radiation with frequent overlapping of species.

Spaciotemporal distribution of Ataxioceratidae indicates that oldest species of all subfamilies originated in Kutch which seems to be the site of early evolution of the clade. Detailed regional distribution of genera suggests that each subfamily originated first in the eastern Kutch and then soon spread to the entire region.

Closer examination on one of the diverse genera, *Katroliceras* of Virgatosphinctinae reveals similar mode and tempo of evolution which also took place at the higher taxonomic category. The possible progenitor *Torquatisohinctes* originated in the eastern Kutch, it soon spread to mainland where it gave rise to *Katroliceras*. Both genera include equal number of species (12) and many species are contemporary and are found in the same beds. The origin of descendant *Katroliceras* is believed to have resulted from rapid speciation. *Torquatisphinctes* in Kutch is strongly dimorphic, the microconchs are lappeted with biplicate ribbing but macroconchs have body chamber ornamented by trifid virgatatome ribs. In *Katroliceras*, microconchs (previously known as *Pachysphinctes*) attain trifid stage and larger macroconchs bear triplicate ribs in early stage and multifurcate virgatatome ribbing in late phargmocone – early body chamber stage. The evolution has been driven by allometry induced by peramorphosis.

Thus it appears evolution of Ataxioceratidae and the subfamily Virgatosphinctinae was caused by cladogenetic macroevolution where species selection (cf. Stanley, 1979; Gould, 2002) was the driving mechanism. They originated "out of India" and subsequently migrated to different provinces/climatic belts where they gave rise to several endemic groups.

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CRYSTALLOGRAPHIC TEXTURES OF CEPHALOPOD NACRE: ITS EVOLUTION, TIME STABILITY, AND PHYLOGENETIC SIGNIFICANCE

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Analyses of crystallographic texture and microstructure of molluscan shells provide non-redundant characters of pivotal value for molluscan phylogeny. Molluscan shells having the same microstructure (a shape of biocrystals) can have a different crystallographic texture (arrangement of crystal axes of biocrystals) and *vice versa*. We analyzed the crystallographic textures of nacre (mother of pearl) of living and fossil cephalopods to understand its evolution, time stability, and phylogenetic significance. Nacre is considered to be the simplest of molluscan shell structures, and it has been recorded in some members of the classes Gastropoda, Cephalopoda, Bivalvia, and Monoplacophora. Its sharing by different molluscan classes has been used for its interpretation as a plesiomorphic shell structure in some evolutionary models. To fill a gap in our knowledge on the crystallographic textures of nacre in living and fossil members of the class Cephalopoda, we have applied several diffraction techniques providing complementary information about the crystallographic texture of the nacreous layer.

In contrast to previous studies (Chateigner et al. 2000), our study has revealed that the cephalopod nacreous layer described as columnar nacre is not uniform in terms of its crystallographic texture. The nacre in living cephalopods (species of *Nautilus*) has perfect preferred orientation of all axes providing a single crystal-like X-ray pattern. The same crystallographic texture was documented in Tertiary and Mesozoic nautiloids and was also found to be present in Carboniferous cephalopods. By comparison, a quite different crystallographic texture, and perpendicular directions [100]* and [010]* random) was documented in Mesozoic ammonoids belonging to the suborders Ceratitina, Ammonitina, Lytoceratina and Phylloceratina (Frýda et al. 2004, and in prep.). The same nacre type was also documented in some Carboniferous cephalopods. The latter type of cephalopod nacre is identical (in term of its crystallographic texture and microstructure) with gastropod nacre, but it has not yet been discovered the other molluscan groups.

Sharing of the same type of nacre in members of the Cephalopoda and Gastropoda has been interpreted as a new line of evidence for a close evolutionary relationship of these classes (Frýda et al. 2006, and in prep.). Our analyses also demonstrated for the first time that both texture patterns of cephalopod nacre (the *Nautilus* pattern as well as the ammonoid pattern) were unchanged for a relatively long time (more than 300 Ma.). It should be noted that in the Mesozoic nautiloid genera *Cymatoceras* and *Paracenoceras*, a transitional nacreous crystallographic texture (from the ammonoid type to *Nautilus* type) is present.

All of the above-mentioned facts support the conclusion that cephalopod nacre evolution was rather complex. The presence of different nacre textural patterns in nautiloid and ammonoid lineages as well as the extreme time stability of those patterns supports the conclusion that these patterns can be used as tools to resolve cephalopod phylogenetic relationships.

Thus, it presently appears that nacre textural analysis can help resolve problems of the degree of relatedness of different orders within the Class Cephalopoda at the higher levels of the existing classification (i.e. Subclass and ordinal levels). Future phylogenetic reconstructions of the higher levels of the classification of the cephalopod (and molluscan) phylogeny should consider integrating these nacre crystallographic relationship patterns into future classification schemes to clarify higher level ancestor and descendent relationships within the Class Cephalopoda and ultimately the classes of the Phylum Mollusca.

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NAUTILUS AS A CONCHIFERAN MOLLUSC: COMPARATIVE ANATOMY AND PHYLOGENY

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The living *Nautilus* is a key taxon in understanding the phylogenetic relationships between cephalopods and other molluscan classes. In the systematics of molluscs, cephalopods have been allocated to the subphylum Conchifera together with Gastropoda, Scaphopoda, Monoplacophora, Bivalvia and Rostroconchia against basal groups (Solenogastres, Caudofoveata and Polyplacophora). The monophyly of Conchifera is supported by several synapomorphic characters such as the shell entirely covering the visceral mass, the protoconch, the absence of spicules in the mantle, the jaw, the statocysts and the subrectal commissure in contrast to the suprarectal commissure of primitive groups.

Within Conchifera, some phylogenetic hypotheses have been proposed. From paleontological view point, Conchifera has been classified into two large groups, Diasoma and Cyrtosoma. Until the late 1990s this view had mostly been consistent with analyses using anatomical characters of Recent groups, except that Gastropoda and Cephalopoda were more closely related (as Visceroconcha). Recent phylogenetic analyses after the 1990s have revealed another possibility that Scaphopoda + Cephalopoda + Gastropoda form a clade (e.g. Haszprunar, 2000). Thus, possible close relationships exist among Monoplacophora (Tryblidiida), Scaphopoda, Gastropoda and Cephalopoda. In contrast, Bivalvia does not have any feature uniquely shared with Cephalopoda. Extinct class Rostroconchia is probably distantly related to Cephalopoda.

The connection of Monoplacophora and Cephalopoda has been suggested by fossil records (*Knightconus - Plectronoceras*). The embryonic shell of *Nautilus* is cup-shaped and similar to the shells of monoplacophorans. However, the closeness of two classes is not obviously detected by comparative anatomy of extant Monoplacophora (e.g. *Neopilina*) and *Nautilus*.

The phylogenetic relationship of Scaphopoda and Cephalopoda is justified by a limited number of characters. One possible character is the presence of cerebrally innervated tentacular structures (captacula and arms/tentacles) around the mouth, but their homology is not always acceptable in terms of structure, position and ontogeny. The shell ontogeny and shell microstructure of *Nautilus* and scaphopods do not support their monophyly.

The sister relationship of Gastropoda and Cephalopoda, especially basal gastropods and *Nautilus*, has been most robustly supported by phylogenetic analyses using anatomical characters (e.g. Sasaki, 1998; Haszprunar, 2000). The shared characters are: obvious distinction of the head-foot and visceral mass; cerebrally innervated eyes (in contrast to

pallially innervated photoreceptors of other groups), the head retractor muscles, the visceral nerve loop inside of dorsoventral musculature, and the mantle innervated only from the cerebropleural ganglia. Cup-shaped open eyes lacking lens are shared between *Nautilus* and Patellogastropoda. The double-layered jaw of patellogastropods may correspond to the upper beak of cephalopods. Common type of nacreous structure of basal cephalopods and gastropods (Frýda et al., 2006) also supports their sister relationship.

Through comparison among *Nautilus*, coleoid cephalopods and other molluscs, the cephalopod common ancestor is inferred to have acquired the following characters: the loss of pedal sole, five pairs of arms, the funnel, the siphuncle, dorsoventrally paired beaks, simplification of esophageal inner structures, loss of connection between the kidney and gonoduct, reduction of the visceral nerve loop and pedal cords and direct development.

Extant cephalopods are further characterized by numerous characters such as the arm suckers, the chromatophores, the ink sac, simplification of stomach inner structures, enlargement of the stomach caecum, the branchial hearts, a well-developed closed circulatory system, concentration of the central nervous system, and the brain and statocysts encased in a cartilaginous cranium. However, these are not general characters of cephalopods but actually apomorphies diagnosing Coleoidea.

The developmental studies of *Nautilus* provide important clues to the origin of cephalopod body plan (Shigeno et al. submitted). For example, the tentacles originate ontogenetically from pedally innervated region, and this fact suggests that cephalopod arms are the foot, not the head, in origin. The tentacle anlagen are five pairs, which means that a large number of tentacles in adult *Nautilus* is a result of secondary multiplication. The origin of two pairs of ctenidia in *Nautilus* (in contrast to a single pair in other cephalopods and part of other Conchifera) is also an interesting topic, but their ontogeny is unfortunately unknown. The comparison of organogenesis across conchiferan molluscs is a crucial future subject in understanding the diversification of molluscan body plan.

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EVOLUTIONARY ORIGINS OF CEPHALOPOD BRAINS AND HEAD COMPLEX: EVIDENCE FROM *NAUTILUS* AND COLEOID EMBRYOGENESIS

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Cephalopod brains and head parts are among the most complex occurring in all invertebrates. Hypotheses for the evolutionary process require a drastic structural transition in relation to the life-style changes from benthos to active nekton. Determining these transitions, however, has been elusive due to scarcity of fossil records of soft tissues and lack of some of the early developmental stages of nautiloids. Here we show the first embryological evidence in the nautiloid cephalopod Nautilus pompilius for the morphological development of the brain and associated head complex by a unique assembly of multiple archetypical molluscan body parts. Using an aquarium system, we successfully obtained a series of developmental stages that enabled us to test previous controversial scenarios. Our results demonstrate that the embryonic brain cords and organs exhibit simple plans that are primarily bilateral and antero-posteriorly elongated at stereotyped positions (Figure). The distinct cephalic compartment, the brain cords, foot, mantle, and shell resemble the body plans of monoplacophorans and basal gastropods. The numerous digital tentacles of Nautilus develop from simple serial and spatially-patterned bud-like anlagen along the anterior-posterior axis, indicating that origins of digital tentacles or arms of all other cephalopods develop not from the head but from the foot. In middle and late embryos, the primary body plans largely change to those of juveniles or adults, and finally form a massive brain and 'head' complex assembled by anlagen of the foot, cephalic hood, collar, hyponome (funnel), and the foot-derived epidermal covers. We suggest a new scheme to explain the evolutionary origins for the brain and head complex in cephalopods.



Figure. Early embryonic body plan of Nautilus

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RECONSTRUCTING THE LIFE HISTORY OF MODERN AND FOSSIL NAUTILOIDS BASED ON NITROGEN ISOTOPIC COMPOSITION OF THE SHELL ORGANIC MATTERS AND AMINO ACIDS

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Molluscan shells preserve biogeochemical signatures of their life time. For example, quantitative or semi-quantitative information on their ecology can be extracted from isotopic composition of oxygen in their carbonate minerals of not only modern but also extinct species (e.g., Oba et al., 1992; Moriya et al., 2003). In the present work, we studied isotopic composition of nitrogen ($\delta^{15}N$) in the bulk organic matter as well as that of compound-specific amino acids in nautiloid shells as proxies of its trophic life history. Isotopic composition of nitrogen of animal tissues has been widely used in various ecological studies; it is known to reflect that of nutrient sources (e.g., diets, nutrients from symbionts) and systematically increases relative to the source by approximately 3.3‰ (e.g., DeNoro and Epstein, 1981; Minagawa and Wada, 1984), being quantitative tool for elucidating trophic position of organisms and the food web structure (Fry, 2006). On the other hand, isotopic composition of nitrogen in amino acids is a recently developed proxy for the trophic analysis with better sensitivity (Chikaraishi et al., in press), where $\delta^{15}N$ value of glutamate increase approximately 7.6% relative to that of diets. Because of additive formation of the molluscan shell, continuous records of the isotopic signature on the nutrient source are expected to be preserved. Thus. we examined modern nautilus shells to test if the changes in nitrogen isotopic composition of shell organic matter reasonably reflect the expected changes in the nutrient source during its life time. We used the specimens of juvenile Nautilus pompilius captured in Balayan Bay, Philippines, and cultured for a substantial period. Pulverized shell material was obtained by micro-milling from each septa and various part of the phragmocone along its growth and analyzed for isotopic composition of nitrogen by an elemental analyzer/continuous flow/isotopic ratio mass spectrometry with improved sensitivity. The results demonstrated that the nitrogen isotopic composition of the bulk shell organic matter fairly recorded the change in the nutrient sources along the life Namely, $\delta^{15}N$ values of both embryonic septa and history of the specimens. phragmocone have constant and rather high (12.0-14.2%; varying among specimens), but they sharply drops about 3-4‰ in the shells formed during the earliest stage of post-embryonic growth. This change is likely to reflect the change in the nutrient source from yoke (having the $\delta^{15}N$ value of adult nautilus) to the diets (presumably having relatively low δ^{15} N value of one-trophic level lower animals). The δ^{15} N values in the shells formed afterward were relatively stable, which indicates the specimens had fed on similar diets during their growth in nature. The δ^{15} N value shapely drops again in the phragmocone formed during culturing, which is interpreted to reflect the change in the diet from natural food sources to cultivated shrimps that had exceptionally low δ^{15} N value. Similar results were obtained from analyses of nitrogen isotopic

composition of amino acids extracted from selected samples that used for the bulk analyses. Thus, we concluded that the shell organic matter of nautilus indeed records their nutritional life history. This technique is potentially applicable for reconstruction of life history of the extinct cephalopods such as ammonoids. We will also reports preliminary data on fossil nautiloids.

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THE EVOLUTIONARY RADIATION OF MODERN NAUTILUS

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The extensive fossil record of coiled nautiloids from the mid-Paleozoic through the Early Oligocene indicates that they comprised a diverse assemblage of species in the ancient oceans. Today they are represented by a single genus, *Nautilus* (including *Allonautilus* of Ward and Saunders 1997) that can be found inhabiting reef systems throughout the Indo Pacific region.

Some individual populations of *Nautilus* show subtle differences in shell morphologies. It has been suggested that these subtle morphological differences represent distinct species (e.g., N. macromphalus, N. belauensis, and N. stenomphalus and others); however, an alternative view is that these morphological variations are subspecies level differences that are localized variants of the broadly distributed taxon generally referred to as N. pompilius. Although as many as twelve species of Nautilus have been proposed (see the discussion and references by Saunders 1987), only two, N. pompilius, and N. scrobiculatus, have been previously diagnosed in a phylogenetic context (Wray et al. 1995.) Here we present a phylogenetic hypothesis for modern Nautilus using molecular characters for two mitochondrial gene regions, 16s rDNA and Cytochrome Oxidase subunit I. Included are broader sampling for three populations of N. pompilus in Vanuatu (New Hebrides Islands), Ndrova [Admiralty Islands, Papua New Guinea (PNG)], and Lizard Island (Great Barrier Reef, Queensland, Australia), and two populations of N. macromphalus (southern tip of New Caledonia). The gastropod Crepidula striolata, is included as an outgroup to develop a biogeographic hypothesis for the radiation of modern Nautilus populations.

Based upon the strict consensus of 24 most parsimonius trees (Length 552 steps, CI 0.832, RI 0.828) our results indicate significant differentiation and that modern *Nautilus* may be undergoing a period of evolutionary radiation throughout the Indo-Pacific region. The basal divergence in *Nautilus* is represented by *N. scrobiculatus*. The topology of the strict consensus tree suggests that this occurred in the waters surrounding present day PNG and the northern part of the Great Barrier Reef in northeast Australia. This was followed by a migration to New Caledonia by the common ancestor of *N. macromphalus*, and the *N. pompilius* populations in Vanuatu, Fiji, and American Samoa. The samples representing *N. macromphalus* form a monophyletic assemblage, although neither of the individual populations are themselves monophyletic. Similarly, the population of *N. pompilius* in Vanuatu also forms a monophyletic assemblage in the consensus tree. These results are consistent with a pattern of migration to the northeast from New Caledonia. Our results also suggest that the present day populations of *Nautilus* in

Palau, Indonesia, Western Australia and the Philippines derive from a migration from PNG and northeastern Australia (The Great Barrier Reef). Neither the PNG nor Great Barrier Reef (Manus Island, Ndrova Island, and Lizard Island, respectively) populations that are represented by multiple samples is monophyletic. This suggests that gene flow has occurred among these populations. Our results indicate that *N. macromphalus* and *N. scrobiculatus* are true phylogenetic species. However, *N. pompilius* is interpreted as a paraphyletic assemblage of populations. In cases where geographic isolation occurs, as is the situation in Vanuatu, these populations have become highly differentiated. Less isolated populations such as those found on the reefs surrounding PNG may experience gene flow and the entire central clade including *N. stenomphalus* likely represents a single broadly distributed species. Further sampling is required to assess populations in the western Pacific. Our results suggest that many geographically isolated populations of *Nautilus* may represent distinct phylogenetic species.

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A DISCRETE WAVELET ANALYSIS OF AMMONOID SUTURES

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Ammonoid septum is a partition which subdivides the shell interior into chambers. The periphery of the septum is folded and frilled to form a complicated suture line where the septum intersects the external shell wall. The complex septa had been conventionally thought to have helped reinforce the shell wall with its fluted structure against hydrostatic pressure. The 'strength paradigm' is in part based on a correlation between suture morphology and external shell curvature (Jacobs, 1990). However, previous analyses often failed to demonstrate a clear relationship between a suture complexity index and external shell geometry (Saunders and Work, 1996). Nevertheless, the failure of finding the relationship may be attributed to ambiguity of complexity measures of suture line hitherto been available. For example, disparate suture forms are often represented by near-identical values of such measures as fractal Comparison of suture morphology with gross shell geometry requires a dimension. rigorous description of suture form itself rather than proxies of complexity. One of promising attempts is a Fourier-based method in which a series of morphometric data transformed into a periodic function is decomposed into sine and cosine functions with various frequencies. However, predominant frequency often changes with position along the suture line, and Fourier-based analyses tend to fail to catch signals with non-stationary frequency, without few exceptions (Allen, 2006). Here I introduce an alternative method based on a discrete wavelet transform for comparison of suture forms with external shell morphology of ammonoids. Prior to measurements, a figure of an external suture line was installed in an x-y coordinate system by putting the point of ventral extreme onto the origin of the coordinate and placing the straight line traced from venter to umbilical seam along the x-axis. A series of v coordinate data along the suture line was measured, and was used as periodic function of the cumulative chordal length of the suture line. Wavelet transform is defined as a kind of correlation of the periodic function with a short and localized function called mother wavelet. Wavelet transforms were calculated for individual mother wavelets with various wavelengths and positions. A power spectrum was obtained for each mother wavelet as an absolute value of the wavelet transform. An average power spectrum was calculated for each portion of the shell which is represented by x-coordinate value. Series of average spectra with position were compared with breadth/height ratio of the whorl cross section by use of multiple regression analyses. The analyses on 60 Paleozoic and Mesozoic species demonstrated significant relationships between suture form and cross-sectional shape of whorl.

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FUNCTIONAL AND PHYLOGENETIC SIGNIFICANCE OF THE SEPTAL LOBE IN THE LYTOCERATACEAE

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The septal lobe (Is) is generated by median dorsal septal recesses of the internal lobe (I) which are curved backwards to a short tube and attached on the septal surface of the preceeding septa. Thus a funnel shaped septate tunnel lying within the phragmocone on the dorsal part of the chamber is formed. The attached part of the septal lobe is fluted in a complex manner like that of the septal periphery in contact with the outer shell wall (fig. 1a-e). This feature of the internal shell only occurs in the Lytocerataceae Neumayr 1875 (which represent a monophyletic taxon of the Ammonitida sensu Guex 1995 & 2004 and Shigeta 2006). The character described above emerge within the Lytocerataceae Neumayr 1875 during the early Liassic through the continuously backwards drifting of the internal lobe.

D' Orbigny (1845) first represented a septal lobe of the Jurassic (late Bajocian) ammonite *Lytoceras eudesianum* and Yabe (1903) called this structure a "septal lobe" for the first time. Within the last two years, more than 150 septal lobes from a great variety of lytoceratid taxa have been found in the literature and more than 200 specimens with septal lobes have been discovered in various museum collections.

In contrast to the recognised significance of the development of the septal apparate for the ammonoid systematic, it is still remarkable that the phenomenon septal lobe was just little noted and not seriously investigated in a systematical and functional morphological way (see Schindewolf 1961-1968).

The complex structure of the septal lobe and the fact that it only occurs in the Lytocerataceae Neumayr 1875 leads, unlike Arkell et al. 1957, to the assumption that all lytoceratid taxa with such a septal lobe can be combined into a monophyletic group.

Functional interpretations are given by Westermann (1971) and Henderson (1984). Westerman (1971) states that the last septum is reinforced against hydrostatic pressure transmitted through the soft body and perhaps also to the strength of the entire loosely coiled phragmocone and Henderson (1984) favours the muscle attachment proposal. However, both theories are rejected by Keupp (2000) and Hoffmann & Keupp (2006).

As the septal lobe is built simultaneously with the whole septum, the septal tunnel must be completely filled with liquid. Therefore we propose a hydrostatic function for this complex structure. The complex fluted margin of the attached part of the septal lobe provides a large surface. In this way, the loss of space can be compensated and the hydrostatic apparatus is not influenced in its function. Furthermore, the septal lobe provides a mechanism for stabilisation of the swimming position because of the stored liquid depots lying at the dorsal part of each whorl, next to the center of buoyancy.



Fig. 1; a) septal lobe attached on the preceeding septum, b) view into the septal tunnel, c-d) median section with septal tunnel, e) ct-scan of the septal lobe structure

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CLADISTIC ANALYSIS OF THE GENUS *DAYICERAS* (SPATH 1920) AND THE QUALITY OF THE FOSSIL RECORD

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Attempts to construct ammonoid phylogenetic trees are known since the last part of the XIX century. From this time to the present, two types of data are used to resolve ammonite phylogenies: (1) stratigraphic ordering of taxa, and (2) morphological shell features. In most available phylogenetic studies, authors gave priority to stratigraphic data in the sense that they constrained morphological data with regard to the stratigraphic distribution of taxa (Donovan *et al.* 1981). The level of integration of the stratigraphic and morphologic data in analyses depend on the authors conceptions (*e. g.* choice of model of speciation) and on paleontological practices (*e.g.*, the improvement of biostratigraphy has favoured the importance given to stratigraphic data in phylogenetic reconstructions).

The recent use of a cladistic approach to infer phylogeny has demonstrated that this method is not unsuitable for ammonite phylogenetic reconstructions, as it was expected among the ammonitological community (Landman *et al.* 1991; Neige & Dommergues 1995; Korn 1997; Yacobucci 1999; Monks 1999, Rouget *et al.* 2004). Nonetheless, cladograms obtained could be in conflict with stratigraphic occurrences of taxa involving the presence of "ghost lineages," which are more or less important in duration (Monks1999; Cecca & Rouget 2006). These kinds of results could be interpreted as evidence of the incompleteness of the fossil record, or as an inappropriate choice of characters or coding technique. Going back to characters and field data could then provide arguments to decide between the two solutions.

A cladistic analysis performed on the ammonite genus *Dayiceras* from the Lower Jurassic (Pliensbachien) is presented as an example to illustrate the problem of disagreement between cladograms and the fossil record. Results show that the confrontation of stratigraphic data and character analysis could provide some relevant information to improve our hypotheses on evolutionary trends of ammonites.

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USING GIS, TOPOGRAPHIC SOFTWARE, AND SIMPLE EXCEL SPREADSHEETS TO EXPLORE GEOGRAPHIC RANGE OF WESTERN INTERIOR UPPER CRETACEOUS AMMONOIDS

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It may be possible to answer many questions related to cephalopod diversity, ecology, evolution, extinction, and morphology using quantifiable biogeographic information provided by GIS. Only recently have GIS and PaleoGIS been applied to address these important paleobiogeographic questions (Rode and Lieberman, 2004; Stigall and Lieberman, 2006). A new database of ammonoid localities was constructed to produce quantifiable biogeographic information using simple techniques and EXCEL and GIS software (MacKenzie, 2007, and this volume).

Maps displaying the minimum geographic ranges for all Cretaceous Western Interior ammonoids have been constructed from a digital inventory using GIS techniques. The inventory was compiled from over 200 sources, including several museum collections, published databases, and relevant publications, to provide information on over 20,000 individual ammonoid occurrences in over 2,000 different localities. The inventory is divided into three sections, each providing a required type of information needed to construct an ammonoid's minimum geographic range. Fossil nomenclature contains all available information on an ammonoid specimen's identity, including intraspecies variations. Other data contained within this section are information on the publication or museum collection from which the information was collected, and the identifier and collector of the fossil. Geospatial information is completed down to the highest level available, including Global Positioning System (GPS) data with less than 1.5 meter resolution. This section also contains coordinates indicating the current geospace where the fossil was discovered, and the paleogeospace, that is, the fossil's spatial location during the Cretaceous at the highest resolution obtained by the collector. All localities were mapped in current geospace using ArcMap GIS 9.1 software (ESRI, 2004), and were rotated to their paleocontinental position using Scotese's PaleoGIS software (Scotese, 2003). Temporal data are recorded to the highest level provided, including current standard biozones and sub-zones. Also provided in this section are lithologic data if included in the source. The inventory was constructed using a simple spreadsheet format with EXCEL 2003 providing easy sorting and modification using standard EXCEL queries. The EXCEL spreadsheet is easily imported into GIS software for geospatial analysis. It is hoped that this inventory and subsequent biogeographic range maps will provide information on morphologic variation in geospace, geographic range variation comparison with an ammonoid taxon's origination and extinction rates, and the geography of mass extinction and recovery.

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APPLICATIONS OF A NEW GIS DATABASE OF CEPHALOPOD OCCURRENCES IN THE CRETACEOUS WESTERN INTERIOR SEAWAY OF NORTH AMERICA: THE CENOMANIAN-TURONIAN OCEAN ANOXIC EVENT (OAE2), SEA LEVEL RISE, AND AMMONOID TURNOVER

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Many questions related to the ecology, evolution, and extinction of fossil cephalopods require paleobiogeographic data to be answered. Paleobiogeographic patterns can also assist in developing a better understanding of paleoenvironmental parameters (such as temperature, salinity, nutrients, and oxygen), paleoceanographic features, sea level fluctuations, and the structure and tectonic history of basins (Lieberman, 2000, 2003).

Paleobiogeographic data has in the past been difficult to compile, visualize, and interpret. Fossil locality information has often been of a limited nature, and has not been recorded in a quantitative form. Manipulating and comparing geographic distributions has been time-consuming and labor-intensive. In recent years, the use of Geographic Information Systems (GIS) has expanded in many areas of the geosciences. GIS offers easy management and analysis of spatial data, but GIS techniques have rarely been used to address paleobiogeographic problems (Rode and Lieberman, 2004; Stigall and Lieberman, 2006).

A new GIS database of fossil cephalopod occurrences within the Cretaceous Western Interior Seaway (WIS) of North America has been compiled (MacKenzie, 2007, and this volume). This database offers numerous opportunities to explore the paleobiogeographic dynamics of ammonoids within the WIS. In this study, we focus on the Cenomanian-Turonian boundary interval, a time of second-order global sea level rise, the expansion of the oxygen minimum zone in many parts of the world ocean (OAE2), and extensive turnover of both macroinvertebrates and microfossil groups.

Cenomanian-Turonian ammonoid genera present in the GIS database were placed into one of three groups: (1) became extinct in the Late Cenomanian, (2) crossed the C/T boundary, (3) originated in the Early Turonian. Digital maps showing the distribution of occurrences within North America were created for each genus separately for the Late Cenomanian, Early Turonian, Middle Turonian, and Late Turonian substages, as appropriate. The geographic areas spanned by these occurrences were calculated using minimum spanning polygons, and the maximum northern, southern, and eastern extent of each genus at each time interval was recorded.

While as a general rule animals tend to show a relationship between geographic area and extinction probability (with more narrowly distributed taxa having increased vulnerability to extinction), survivors of the C/T event do not have significantly larger geographic ranges within the WIS during the Late Cenomanian than victims. Notably, surviving genera that are widespread in the WIS in the Late Cenomanian become restricted to the southwestern portion of the seaway in the Early Turonian. This restricted pattern is not an artifact of sampling – numerous ammonoid genera are known from Early Turonian localities in other portions of the WIS, but these localities do not contain C/T boundary crossers. C/T survivors and Early Turonian originators both expand their geographic ranges northward and along the relatively shallow eastern margin of the WIS throughout the Turonian.

The restriction of C/T survivors within the southwestern portions of the WIS during the Early Turonian suggests that these genera may have persisted in existing, stable, relatively deep water niches, while new immigrants and taxa originating locally refilled vacated niches in the rest of the WIS ecosystem. The pattern of survivorship and recovery may also reflect the collapse of the shelf-break front and incursion of deeper, stratified, oligotrophic waters into shelf settings as sea level peaked in the Early Turonian (Hay, 1995; Gale et al., 2000).

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043

NEW APPROACH ON THE LATE VALANGINIAN AMMONITE HABITAT IN THE POLISH BASIN

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Various fossil groups from the same horizon served to improve the habitat reconstruction of the late Valanginian ammonites. Previous detailed studies of numerous fossil groups in the Polish Lowlands, correlated with analyzes of depositional sequences and cyclicity of the basin fill caused by relative and eustatic sea-level changes (Dziadzio et al., 2004) allowed to interpret the late Valanginian paleoenvironment. Relationship between cephalopods, foraminifers, ostracods, and calcareous nannoplankton reflected influences of between the Tethys and the Boreal basins. The studied area - Polish basin, because of Tethyan-Boreal mixed influences is crucial for correlation both palaeogeographic realms and character of migrations between them. Ammonite assemblages associated microfauna, and calcareous nannoplankton were studied in the sections of wells in Poland Lowland (Dziadzio et al., 2004). Nevertheless, only the exposure in the Wawał clay-pit near Tomaszów Mazowiecki (central Poland) provided material suitable for a detailed study of the ammonite assemblages and their succession. Stable isotope analyzes of shells provided additional information about ammonites habit and paleoenvironment.

The most interesting are two time intervals – upper part of *verrucosum* and *triptychoides* Zones. During relatively transgressive and highstand system track, ammonite assemblages changed from the Mediterranean species (the upper part of *verrucosum* Zone) to the Boreal assemblages (the *triptychoides* Zone), while nanno- and microfossil assemblages still yield Tethyan taxa. Ammonite species at the upper part of *verrucosum* Zone represent forms, which could migrated seasonally and at the end of their life. Boreal forms from the *triptychoides* Zone possibly migrated to warmer Polish basin and dislodged forms from the Tethys. Boreal ammonites are mainly of the same species like in the German basin – *Dichotomites*, but they have specific features typical for Polish basin, suggested local adaptation. This adaptation and their abundance could suggest favorable environment for them in the Polish basin. Thus fossil assemblage changes reflect paleoenvironment perturbations in post-*triptychoides* period of time.

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EARLY APTIAN HETEROMORPH AMMONITES FROM ULYANOVSK AREA (VOLGA RIVER, RUSSIAN PLATFORM)

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Heteromorph ammonites from Ulyanovsk region (middle stream of Volga River) are well-known due to their excellent preservation. We have already published the new data on the heteremorph ammonite assemblages, their stratigraphic and geographic distribution and environmental control (Baraboshkin, Mikhailova, 2002). Some unique finds like jaw apparatus inside the *Australiceras* body chamber were published (Doguzhaeva, Mikhailova, 2002). Recently the new data on the muscle impressions and ontogenetic development of *Audouliceras* were received (see the plate).

Protoconch is elliptical with high ventral and low dorsal saddles. The embryonic shell is transformed into the short shaft and then into the non-touched plain spiral, which finally is evolved into the normal plane spiral second whorl. In the end of the third whorl the spiral starts unroll again getting ancyloconic in shape. Primasuture is five-branched: VUU¹ID. First umbilical lobe is divided by the seam in the middle and reducing soon. The following transformations lead to the complexity of the suture-line, but the new saddles and lobes do not appear.

This style of ontogenesis is inherited by monomorph descendants of heteromorphs and it is necessary to mind it dealing with taxonomy.

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Figs. 1, 2. Muscle impressions of *Audouliceras* sp. Samples: 1 – 4426/44; 2 – 4426/651. Scale bar is 0,5 cm. Collection of M. Agafonov. Arrows indicate ventral (1) and dorsal (2) muscles.

Fig. 3. Ontogenesis of *Audouliceras* ex gr. *renauxianum* (d'Orbigny). Sample SH-493. Scale bar is: a-e, h-k = 5 mm; f, g, i, l, p = 10 mm; m-o = 3 mm; q = 30 mm. Collection of I.Shumilkin.

All samples are from the Lower Aptian of Ulyanovsk, Audouliceras renauxianum zone.

Seventh International Symposium Cephalopods – Present and Past, 2007, Sapporo, Japan. Abstracts of Oral Presentations



045

APTIAN – CAMPANIAN AMMONITES OF HUNGARY: AN OVERVIEW

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The Cretaceous ammonite record of present Hungary is very hectic considering both the numbers of collected specimens and the documentation as well. Researches on Cretaceous ammonites started in the mid XIXth century with the scientific discovery of the marvellous Late Albian fauna of "Schichten von Nána" (Hauer, 1862). The Early Cretaceous assemblages are accurately collected, show high taxonomic diversity and great numbers considering the more than 13.000 specimens but they are out of focus this time. In the frame of a monographic study, the author collected and studied the most important surface and borehole Aptian-Campanian ammonite assemblages that contain approximately 7,000 specimens. In the present lecture this monographic work is outlined.

Hungary is located in Europe, in between the chain of the Carpathians. Ammonite bearing surface outcrops and borehole materials are restricted to two certain areas: the Transdanubian Range and the southern Villány Mountains (Fig. 1.).



Fig. 1. Map of Western Hungary. Mesozoic outcrops shown lilac. Fig. 2. Sedimentary megacycles of the Hungarian Cretaceous. After Pocsai & Csontos (2006).

Cretaceous sedimentation of the Carpathian Basin was determined by the Alpine orogeny and three sedimentary megacycles can be recognized in the present sediment record (Fig. 2.). Ammonite-bearing strata are abundant in Lower Cretaceous and getting more rare after the Albian due to the more intensive orogenic movements that caused environmental changes. Reef complexes, brackish-coal and subaerial environments dominated the sedimentation from the Cenomanian and this caused almost the complete lack of the ammonites in the area of present Hungary.

Fülöp (1975) have made collected fossils from tata, from condensed basal "pockets" that lie between a Tithonian hardground and a massive Late Aptian - Early Albian crinoidal limestone. Fossils preserved as glauconitized and phosphatized internal moulds and show sorting by size – this also suggest the reworking and transportation of the assemblage. The great number of *Tetragonites*, *Silesitoides*, *Diadochoceras*, *Acanthohoplites* and *Hypacanthoplites* is remarkable. The ammonite assemblage contain Middle Aptian to Late Aptian species besides echinoids, gastropods and belemnites. Early Albian ammonites only known from boreholes and contain *Douvilleiceras*, *Brancoceras* and *Beudanticeras* species. There is no ammonite data from the Middle Albian due to the lack of the ammonite-bearing facies.

Late Albian ammonite assemblages are represented in great specimen number and high taxonomic diversity. Thanked to the impressive macrofauna, the fossils of the "Turrilitenmergel" (Böckh, 1909) are in the mainstream of the Hungarian paleontology, even H. Douvillé (1933) also published data about the Late Albian ammonites of Tiloserdő. The most accurate and well-known work about "Vracon" ammonites of the Bakony Mountains is of Scholz (1979). Fossils also collected from a condensed basal layer and recently from the above 2 meters as well. The assemblage is useless for biostratigraphic purposes but the presence of *Zuluscaphites*, *Engonoceras*, *Ficheuria* and the extreme diversity of *Salaziceras* makes the assemblage unique. From borehole materials the most important is Jásd-42 section. This section was nominated as an Albian/Cenomanian Boundary Candidate but not have much support (Birkelund et al., 1984) because of the "boreal" affinity of the ammonite fauna. The decision is more understandable if we consider the lack of surely Cenomanian taxa. Other remarkable borehole section is Bóly-1 which is known from description of *Worthoceras pygmaeum* Bujtor, 1991.

In contrast to previous researches, there is no ammonite evidence from the Cenomanian.

Late Cretaceous, consecutively Santonian-Campanian ammonites are unique, due to the brackish water and reef environments that dominated the region by then. There is only a single Santonian ammonite is discovered by Partényi (1986) from a borehole.

Campanian ammonite record contain two dozen specimens, mainly *Texanites* and Pachydiscus species, but *Glyptoxoceras*, *Scaphites hippocrepis* II (De Kay), *Brahmaites* and *Menabites* are also present.

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CEPHALOPOD BIOSTRATIGRAPHY OF THE CRETACEOUS OF SOUTH INDIA

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Excellent preservation of ammonites and other cephalopod fossils in the Cretaceous rocks of southern India facilitate their use in precise geological dating. Ammonites are common in the Albian to Maastrichtian succession and these show considerable variations in ornamentation and diversity. The changes in the morphological characters in various ammonite lineages help in developing the stratigraphy of the Cretaceous succession and in turn, the geological dating. The positions of many important genera in the geological sections offer scope for the identification of stratigraphic gaps in the succession that may or may not be accompanied by unconformity. Their occurrence along with other cephalopod assemblages, especially nautiloids and belemnites, in the Cretaceous sediments of southern India is marked for recognition of zonal indices and for correlation.

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LATE CAMPANIAN CEPHALOPOD FAUNA FROM NORTHERN JORDAN

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The Campanian-Maastrichtian Al Hisa Phosphorite Formation cropping out on western and central Jordan is rich in cephalopods. It consists of alternating thin- bedded limestone, more-or-less silicified or calcified phosphorite layers, thick-bedded and cross-bedded oyster lumachells, and lenses and layers of minable phosphate. The sphenodiscid ammonite Libycoceras ismaeli (Zittel) predominantly occurs in the middle part of this formation. Libycoceras ismaeli is associated with different nautiloid and baculitid species. The paleontological description led to recognition of six cephalopod species belong to 6 genera (Libycoceras ismaeli (Zittel), Cymatoceras honmai Matsumoto & Miyauchi, Cymatoceras pseudoatlas (Yape & Shimizu), Angulites sp., Baculites vertebralis Lamarck and Baculites obtusus Landes), that described systematically in detail for the first time from Jordan. The presence of Libycoceras ismaeli (Zittel), previously known from North Africa, Middle East, Mali, Niger and Peru dated the assemblage as early but not earliest Late Campanian age. The range of all taxa are fully documented and provide the basis for two-fold division of the Late Campanian of Jordan, with the zones of Libycoceras ismaeli Zone (oldest) and Baculites vertebralis Zone (youngest). These are the first biostratigraphically well dated Late Campanian cephalopod fauna from Jordan, which show close affinities to the Campanian cephalopod faunas from the Tethyan Realm and having formed part of a southerly paleobiogeographical subprovince of the Mediterranean Province.

Keywords: Cephalopods, ammonites, nautiloids, Campanian, Jordan.

CEPHALOPODS AT THE CRETACEOUS/TERTIARY BOUNDARY IN NEW JERSEY

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investigations in County, Jersey, Geological Monmouth New reveal a Cretaceous/Tertiary succession consisting of approximately 2 m of the Tinton Formation overlain by 2 m of the Hornerstown Formation. The top of the Tinton Formation consists of a very fossiliferous unit (the Pinna Layer), which is truncated at the top by an unconformity and overlain by the Hornerstown Formation. The Pinna Layer is abundantly fossiliferous and represents a diverse, near shore marine community. It contains approximately 110 species of bivalves, gastropods, cephalopods, echinoids, sponges, annelids, bryozoans, crustaceans, and dinoflagellates. The cephalopods include Eutrephoceras dekayi (Morton), Pachydiscus (Neodesmoceras) mokotibensis Collignon, Sphenodiscus lobatus (Tuomey), Eubaculites carinatus (Morton), E. latecarinatus (Brunnschweiler), Discoscaphites gulosus (Morton), D. iris (Conrad), D. jerseyensis Landman et al., D. minardi Landman et al., and D. sphaeroidalis Kennedy and Cobban. The ammonites and dinoflagellates are indicative of the uppermost Maastrichtian, corresponding to the upper part of calcareous nannofossil Subzone CC26b. The mode of occurrence of the fossils in the Pinna Layer suggests an autochthonous accumulation with little or no post-mortem transport. Specimens of Pinna laqueata Conrad are in life position and monospecific clusters of echinoids, oysters, baculites, and scaphites are common. Scaphite jaws are also present, which represent the first reports of these structures in the Upper Cretaceous of the Atlantic Coastal Plain. Iridium analyses reveal an elevated concentration of iridium of 520 pg/g, on average, at the base of the Pinna Layer. If this enriched concentration of iridium marks the bolide impact, it implies that the animals in the *Pinna* community, including the ammonites, were living at the moment of impact and may even have persisted for some time afterward. The community was subsequently buried by a rapid pulse of sedimentation, possibly related to enhanced riverine discharge following the impact. The early Danian marine community was greatly reduced in diversity, with only a few Cretaceous species of bivalves, gastropods, and echinoids surviving.

4. Abstracts of Poster Presentations

PERMIAN AMMONOIDS OF JAPAN: THEIR STRATIGRAPHIC AND PALEOBIOGEOGRAPHIC SIGNIFICANCE

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Since Mabuti (1935) described an ammonoid *Stacheoceras* from the Middle Permian Iwaizaki Limestone in the South Kitakami Belt, Northeast Japan, only few ammonoids had been known from the Japanese Permian until the mid-1980s. When Koizumi (1975) published his monograph titled "Paleozoic Cephalopods of Japan", only 14 genera of Permian ammonoids were listed, including ones without description and photos. Recent progress in ammonoid study during the past quarter century gave rise it up to 37 genera. Of which Middle Permian ammonoids are abundant and 25 genera (including 2 genera ranging from the Early Permian) have been known. Late Permian genera are 12 (including 4 ranging from the Middle Permian) and Early Permian ones are rather few and only 6.

Permian ammonoids of Japan have been mostly known from the South Kitakami Belt (Lower to Upper Permian in the Southern Kitakami Massif and Middle Permian in the eastern marginal part of the Abukuma Massif). Lower Permian of the South Kitakami Belt yields 2 genera: Agathiceras and Artinskia. Twenty-three genera are from the Middle Permian: Agathiceras, Altudoceras?, Roadoceras, Cardiella, Adrianites, Popanoceras, Tauroceras, Jilingites, Pseudagathiceras, Prostacheoceras, Stacheoceras, Parastacheoceras, Perrinites, Demarezites, Mexicoceras?, Waagenoceras, Newellites, Timorites, Propinacoceras, Medlicottia, Eumedlicottia, Paraceltites and Cibolites, and twelve from the Upper Permian: Pseudogastrioceras, Stacheoceras, Timorites, Cyclolobus, Eumedlicottia, Neogeoceras, Araxoceras, Vescotoceras, Eusanyangites, Dzhulfoceras, Xenodiscus, and Paratirolites. Permian strata in the South Kitakami Belt deposited in a shallow marine on the continental shelf of the South Kitakami Paleoland (Ehiro, 1997).

Other Permian ammonoid localities are in the Southwest Japan. Two Early Permian ammonoids, *Aktastioceras* and *Propopanoceras* and a Middle Permian *Paraceltites* have been known from the Hida-Gaien Belt. Middle Permian in the Kurosegawa Belt yields *Cibolites*. These are from the shallow marine terrigenous deposits. The rest have been recovered from the exotic blocks in the latest Permian (Chugoku Belt) or Jurassic (Mino Belt) accretionary complexes. The Akiyoshi Limestone of the Chugoku Belt contains two Early Permian ammonoids, *Paraperrinites* and *Stacheoceras*, and unnamed strata at Miharanoro in the Chugoku Belt yielded Middle Permian *Agathiceras*, *Popanoceras*, *Peritrochia*?, *Waagenoceras*?, *Pseudogastrioceras* (probably not *Pseudogastrioceras*) and *Adrianites*?. From the Middle Permian Akasaka Limestone in the Mino Belt, *Agathiceras*, *Adrianites*?, *Perrinites*?, *Stacheoceras*? and *Propinacoceras*? have been reported.

As shown above Permian ammonoid occurrences in Japan are rare and sporadic except for the South Kitakami Belt. Middle Permian Roadian ammonoids from Kitakami are characterized by *Adrianites*, *Perrinites* and *Demarezites*. Wordian ones are *Tauroceras*, *Mexicoceras*?, *Waagenoceras* and *Paraceltites*, and Capitanian ones *Timorites* and *Cibolites*. Among the Upper Permian ammonoids, araxoceratid such as *Araxoceras*, *Vescotoceras, Eusanyangites* and *Dzhulfoceras* are Wuchiapingian indexes and *Paratirolites* is Dorashamian one.

The Middle to Late Permian ammonoids from South Kitakami consist of the Tethys type (equatorial type) and cosmopolitan genera, without Boreal type ones (Ehiro, 1997, 2001; Ehiro and Misaki, 2005; Ehiro et al., 2006). Therefore it is considered that the South Kitakami Paleoland had located near equator during the Middle to Late Permian. The Equatorial Tethys type ammonoid genera from the Middle Permian are Cardiella, Adrianites, Tauroceras, Pseudagathiceras, Perrinites, Demarezites, Mexicoceras?, Newellites, Timorites, Paraceltites and Cibolites. Ones from the Late Permian are Pseudogastrioceras, Timorites, Araxoceras, Vescotoceras, Eusanyangites and Dzhulfoceras.

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NEW SPECIES OF *PSEUDAGATHICERAS* (MIDDLE PERMIAN AMMONOIDEA) OF PAKLAY DISTRICT, WESTERN LAOS

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In Laos (=Lao People's Democratic Republic; Lao PDR), Permian ammonoid has been reported only *Xenodiscus*? sp. by Mansuy in 1912, from the beds of Luang Prabang. On the other hand, Permian ammonoid has been reported from various areas of Southeast Asia, especially from Thailand, Malaysia and Timor. In order to compare and discuss the affinity of their fauna, we need more basic paleontological data on Late Paleozoic ammonoids. In recent years the joint project of geological survey by Department of Geology and Mine, Laos and Department of Mineral Resources, Thailand, has been done at the western Laos. We could collect some fossil samples in some locations, and in this time new species of Permian ammonoid *Pseudagathiceras* is identified and presented from the bed of Pak Lay Formation distributed in the Paklay district, western Laos. *Pseudagathiceras* has been reported from Middle Permian (from Wordian (Murgabian) to Capitanian (Midian)) age, but for the insufficiently paleontological data, it is difficult to determine the age of this bed strictly in this study. This is the second report of the Permian ammonoid from Laos.

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MORPHOLOGICAL STUDY OF GENUS *PROTOGRAMMOCERAS* (EARLY JURASSIC AMMONOID) FROM THE TOYORA GROUP IN SOUTHWEST JAPAN

P3

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The Toyora Group, Lower to Middle Jurassic continental shelf sediments, is known as the major source of Early Jurassic ammonoid fossils. Among the ammonoid assemblages, the genus *Protogrammoceras* is one of the most common taxa in this area. The genus is characterized by evolute whorls, by fine and numerous ribs, and by a prominent keel. Three species described by Matsumoto & Ono (1947) and Hirano (1971) are as follows; *Protogrammoceras nipponicum* (MATSUMOTO), *Protogrammoceras yabei* HIRANO, *Protogrammoceras onoi* HIRANO. Hirano (1971) pointed out the following differences among these species: *P. nipponicum* is distinguished from *P. yabei* by its more involute whorls and narrower/weaker ribs, and is distinguished from *P. onoi* by its weakly falciform ribs and the vague keel. In this study, we have reexamined the morphological classification for the three *Protogrammoceras* species from the Toyora Group on the basis of scatter diagrams concerning the umbilical diameter (U)/diameter (D), whorl height (Wh)/diameter (D) and the number of ribs in half a whorl (Rnh)/diameter (D), and ontogenetic trajectories of rib density (Fig. 1). As a result, the scatter diagram of U/D and Wh/D shows that it is difficult to separate into different groups among the



Fig. 1. Number of primary ribs per half a whorl (Rnh) for 30 specimens belonging to the genus *Protogrammoceras* from the Toyora Group, southwest Japan. Primary ribs are counted per half a whorl at every 90°. Broken line and dash-dotted line show the grouping of the three species.

three species. By contrast, the ontogenetic trajectories of Rnh/D (Fig. 1) show that it is possible to recognize 2 groups from them: one increases the rib density with growth, while the second, Rnh is nearly constant with growth. The former includes *P. nipponicum*, and the latter includes *P. yabei* and *P. onoi*. This result suggests the necessities of analysis on stratigraphic division and sexual dimorphism of these species.

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BIOMETRICAL ANALYSIS ON MIDDLE JURASSIC AMMONOID PSEUDONEUQUENICERAS YOKOYAMAI (KOBAYASHI & FUKADA) AND ITS RELATED FORMS

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Pseudoneuqueniceras yokoyamai (Kobayashi & Fukada) is one of the most abundantly occurring ammonoid species from the Middle Jurassic in Japan. This species and its related forms, *P. yokoyamai alticostatum* (Sato) and *P. maedai* (Sato), are found from the same localities in the Kuzuryu Subgroup of the Tetori Group in the Kuzuryu area, Fukui Prefecture, central Japan. To clarify the relationship among these three forms, hereafter called as the *Pseudoneuqueniceras yokoyamai* group, biometrical analysis is performed.

Materials come from the University Museum of the University of Tokyo, the Fukui City Museum of Natural History (mainly Mr. Shimonoya's collection), and Mr. Miyakita's personal collection (Niigata City). All of the holotypes are registered and deposited in the University of Tokyo. More than 50 individuals from the above three collections are biometrically analyzed. The relationship between diameter and the number of primary ribs of 45 specimens including the holotype specimens is depicted in Fig. 1. The holotype of *P. yokoyamai yokoyamai* cannot be presented in Fig. 1 due to its poor preservation.

The *P. yokoyamai* group shows a wide variation in the number of primary ribs. Twice number of primary ribs is recorded at most ontogenic stages. The primary ribs degrease in number through ontogenic development. At a mature stage, the number of primary ribs is somewhat constant. This diagram clearly shows that the holotype of *P. maedai* is an individual with extremely small-numbered primary ribs and is located at an end member in the distribution chart. On the other hand, the holotype of *P. yokoyamai alticostatum* is situated at the center in the diagram.

Individuals with a lappet range from 45 mm to 75 mm in diameter as presented in Fig. 1. The maximum diameter of specimen with a lappet is 95 mm in our materials (not shown in Fig. 1). Because lappet is indicative of mature stage of microconch (male), the adult size of male is equal to or less than half of the largest specimen in the *P. yokoyamai* group. Larger specimens without a lappet are probably macroconch (female). The wide variation in the number of primary ribs in the *P. yokoyamai* group can be resulted from a mixture of male and female individuals which express a different spacing pattern of primary ribs and their own variation.



Fig. 1. The relationship between diameter and the number of primary ribs of 45 specimens including the holotype specimens of *Pseudoneuqueniceras yokoyamai* alticostatum (Sato) and *Pseudoneuqueniceras maedai* (Sato). Primary ribs are counted per a single whorl at every 90° . When the number of primary ribs is obtained successively, data points are connected with a line. Thick lines are for holotypes while thin lines are for others.

A TRANS-PACIFIC DISPERSAL OF NEUQUENICERATIDS, EVIDENCE FROM TIBET

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Two species of *Neuqueniceras* have recently been recognized in northern and southern Tibet. The first, *N. tibeticum* Yin, is from the Himalayas. This species is close to the Andean species *N. bodenbenderi* (Tornquist)which is of earliest Callovian age. The bed bearing *N. tibeticum* overlies the *Oxycerites orbis* Assemblage which corresponds to the European Retrocostatum (or Orbis) Zone. The second species, *N. cf. yokoyamai*, is found in the Upper Bathonian of northern Tibet. This species exhibits a close faunal relationship with *N. yokoyamai* (Kobayashi et Fukada) of Japan, suggesting an alliance between northern Tibet and Japan during Middle Jurassic times.

The appearance of neuqueniceratids in Tibet is also significant for trans-Pacific paleobiogeography. The Family Reineckeidae consists of two subfamilies, Reineckiinae and Neuqueninae. These two groups show clear provincialism. Until now, the Reineckiinae were believed to include the Callovian forms of Europe and western India while the Neuqueninae were thought to be endemic to the eastern Pacific (Argentina, Mexico and Chile). The Tibet occurrences of *Neuqueniceras* indicate the first trans-Pacific dispersal within the Neuqueninae.

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THE ORIGIN OF *PROHECTICOCERAS* SPATH 1928 AND ITS EVOLUTIONARY SIGNIFICANCE IN THE SUBFAMILY HECTICOCERATINAE (AMMONOIDEA): A HISTORICAL AND CLADISTIC APPROACH

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Prohecticoceras belongs to the subfamily Hecticoceratinae which is believed to have evolved from Oppelinae (Arkell et al. 1957). But, workers differ whether the propensity lies in *Oxycerites* Rollier 1909 (Spath 1928), *Oecotraustes* Waagen 1869 (Bonarelli 1893 in Arkell 1951-58), *Paroecotraustes* Spath 1928 (Arkell et al. 1957) or in *Eohecticoceras* Zeiss (Elmi 1967). *Oecotraustes* and younger *Paroecotraustes* are now considered to be the microconchs of the Lower Bathonian *Oppelia* Waagen 1869 and the Upper Bathonian *Oxycerites* (*Alcidellus*) respectively (see Westermann & Callomon 1988). The confusion regarding the true ancestor of *Prohecticoceras* has a taxonomic reality. Many early species of *Prohecticoceras* retain primitive oppelin characters. These have been adequately discussed in historical perspective.

A new species of *Prohecticoceras* Spath 1928, *P. manjalense* sp. nov. is described by us from the Middle Bathonian of Kutch, western India (Roy et al., in press). This is also the first record of *Prohecticoceras* from the Indo-Madagascan Faunal Province. Sexual dimorphism has been established within the present species, which was unknown until recently in *Prohecticoceras*. The nature of dimorphism discriminates *Prohecticoceras* from the contemporary oppelin taxa. Cladistic analysis reveals that *Prohecticoceras* evolved from *Eohecticoceras* Zeiss. The evolution appears to have involved paedomorphosis in which microconchiate characters of the ancestral taxa contributed greatly. Ecologically, the evolution reflects the change from deeper water ancestral habitat to nectobenthic, shallow water living.

Key words: Hecticoceratinae, Middle Jurassic, Cladistic analysis, Paedomorphosis.

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AMMONITE FAUNA OF THE MIDDLE-JURASSIC (UPPER AALENIAN-UPPER BAJOCIAN) OF LA BAUME (CASTELLANE, ALPES DES HAUTES PROVENCE) AND SYSTEMATICS OF THE SONNINIDAE

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Upper Aalenian to Upper Bajocian ammonites were sampled bed-by-bed from the 68mthick pelagic marls and limestones of the Calcaires à *Zoophycos* formation in the outcrop of La Baume for stratigraphic and taphonomic purposes. This succession paraconformably overlies Lower Jurassic shallow-water limestones and is overlain by basinal marls ("Terres noires"). The pelagic succession studied can be roughly subdivided in a marl-dominated member 1 (from bed 1 up to bed 23), followed by a limestone-dominated member 2 (from bed 24 up to bed 109) with Zoophycos traces, that is overlain by a new marl-dominated member 3.

In the section we have distinguished 122 beds. Almost 400 ammonites belonging to 6 superfamilies and 13 families have been collected together with other fossils (belemnites, bivalves, brachiopods, gastropods, nautiloids). The aragonitic shells of ammonites, nautiloids, gastropods and bivalves have been dissolved and only internal molds remain, sometimes with replacement shell. The subvertical to oblique position of smaller ammonites with a narrow venter and belemnites seems to indicate a marked bioturbation before lithification.

At the base of the pelagic succession, *Haplopleuroceras* gr. *mundum*, *Graphoceras limitatum* and *G*. cf. *decorum* indicate the Late Aalenian Concavum Zone. At meter 10 (bed 14) we have found *Hyperlioceras* cf. *mundum*, which allows us to identify the position of the base of the Bajocian. All the Zones of the Lower Bajocian seem to be represented and the main paleontological interest therein is the richness and the diversity of the family Sonniniidae, which is known to show great "intraspecific" variability. All the main macroconch genera (*Witchellia, Dorsetensia, Sonninia*) are present, often associated with their microconchs. They can be found associated with members of biostratigraphic significant superfamilies like the Stephanoceratoidea, which is not always the case in some historical sonniniid study areas (e.g. Germany). The hammatoceratid genus *Fissilobiceras*, which is homeomorphic to some large sonniniids, was also found.

A major gap of both Niortense and Garantiana Zones was detected at the boundary between members 2 and 3. In fact, member 3, which contains ammonites of the Parkinsoni Zone (*Parkinsonia* cf. *rarecostata* in bed 114 and *Parkinsonia* cf. *parkinsoni* in bed 118a), directly overlies the top of member 2, ascribed to the top of the Humphriesianum Zone on the basis of the occurrence of *Teloceras blagdeni* (bed 107) and *Normannites* (bed 108b). The occurrence of *Lobosphinctes* cf. *tmetolobus* and

Planisphinctes tenuissimus in bed 121d might indicate that these beds still belong to the Parkinsoni Zone at the top of the "Calcaires à *Zoophycos*". The limit between the Calcaires à *Zoophycos* formation and the "Terres Noires" formation (Lower Callovian – Oxfordian age) coincides with another gap.

One Upper Aalenian Zone (Concavum Zone) is represented, all Lower Bajocian Zones (Discites Zone, Laeviuscula Zone (including Ovale Subzone), Humpriesianum Zone) are represented and one Upper Bajocian Zone (Parkinsoni Zone). Further research could investigate the nature of this gap, which was not described before in the literature. Twenty-two percent of the Lower Bajocian ammonites belong to Phylloceratidae and Lytoceratidae documenting communication with oceanic waters. The Upper Bajocian ammonites are dominated by nannolytoceratids (forty-two percent vs twenty-five percent of Phylloceratidae and thirty-three percent of Ammonitina).

UPPER BAJOCIAN TO BATHONIAN AMMONITES OF NORTH IRAN

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The Dalichai Formation ranges from 97 to 567m of light-grey to bluish-grey limestone with thin intercalations of marl. The lower boundary of the Dalichai Formation is an unconformity due to the Mid-Cimmerian tectonic event (the marine transgression of the Dalichai Formation over the Shemshak Formation is diachronous). In many areas the upper boundary of the Dalichai Formation is, however, gradational. In a few areas it is continuous but sharp and followed by the Lar Formation. The sedimentary environments, in which this formation was deposited, are the lower shelf to continental slope. The Dalichai Formation is rich in ammonites.

Ammonites are described from the Dalichai Formation of the Alborz (northern Iran). The material comes from four localities of Alborz. The ammonites belong to the following genera and subgenera respectively:

Phylloceras sp., Holcophylloceras sp., Spiroceras orbignyi (Garantiana Zone), Spiroceras annulatum (Niortense and Garantiana zones), Oxycerites sp., Oxycerites yeovilensis, Oxycerites cf. oxus, Cadomites (Polyplectites) sp., Cadomites (Polyplectites) dorni (Lower Bathonian), Sphaeroceras tuttum (Garantiana and Parkinsoni zones), Bullatimorphites sp., Bullatimorphites (Kheraiceras) bullatus (Lower to ?Middle Bathonian), Strenoceras sp., Garantiana (Orthogarantiana) cf. densicostata, Garantiana (Pseudogarantiana) dichotoma (Garantiana Zone), Parkinsonia radiata, Parkinsonia parkinsoni (Parkinsoni Zone), P. depressa, Morphoceras multiforme, M. macrescens, M. egrediens, Ebrayiceras cf. sulcatum, Microbajocisphinctes sp., Microbajocisphinctes cf. pseudointerruptus.

Homoeoplanulites (Homoeoplanulites) cf. bugesiacus (Discus Zone), Homoeoplanulites (Parachoffatia) arkelli (Discus Zone), and Homoeoplanulites sp..

BELEMNITES OF THE JURASSIC/CRETACEOUS BOUNDARY INTERVAL FROM NORDVIK PENINSULA (NORTHERN SIBERIA)

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Stratigraphically, the most complete Boreal section of the J/K boundary interval is located on the Nordvik Peninsula (NP). The successions of ammonite and buchiid zones are recognized in great details. The belemnite zonal scheme for the Boreal J/K boundary interval is based on the North Siberian belemnite successions. NP belemnites were studied in the past by Saks, Nalnyaeva, Shenfil and Dzyuba. In 2003, a new stratigraphically significant fauna has been collected on Urdyuk-Khaya Cape (NP) during the common field work of Geological Institute (Moscow) and Charles University Prague. According to a new finds of ammonites, the base of the section is assigned to be Middle Oxfordian in age (Rogov, Wierzbowski, in press). Thus, the Middle Oxfordian belemnite assemblage on the whole is established herein for the first time (Fig. 1) for the NP and North Siberia. The Middle Oxfordian Siberian belemnite fauna is taxonomically almost identical to those belemnites in the Russian Platform. Stratigraphic ranges of the species: Cylindroteuthis (Cylindroteuthis) cuspidata Sachs et Naln., following C. (Arctoteuthis) septentrionalis Bodyl. and Simobelus (Simobelus) mamillaris (Eichw.) were specified. Simobelus (Liobelus) prolateralis (Gust.) was recorded at the same stratigraphic level as in the European sections. Lagonibelus (Lagonibelus) parvulus (Gust.), known only from Lower-Middle Volgian transitional beds of the Russian Platform, was recently recorded from the NP section. According to the belemnite distribution, the Kimmeridgian/Volgian boundary is located within 4,0-4,5 m interval below the level 2D (Fig. 1) - probably at the horizon with rare phosphatic and calcareous nodules with fossilized wood. Index Volgian belemnites appear just above this interval. The significant faunal (ammonite, belemnite) change shows a gap in sedimentation of a significant part of the Lower-Middle Volgian, albeit sedimentologic evidences are still missing. The Middle Volgian Variabilis Zone show both high diversity and abundance of belemnites, which could be considered to be a belemnite events (Fig. 1). The increase in faunal diversity in this stratigraphic interval is a typical feature in northern Siberian seas. It is accompanied by transgressive events and climate warming. The lowest belemnite diversity is recorded in the Volgian/Boreal Berriasian boundary beds. Only rare representatives of genera Cylindroteuthis and Lagonibelus with elongate rostra are distributed here, higher abundance was recorded only just above the iridium anomaly bed. Taxa with shorter robust rostra from genera Pachyteuthis and Simobelus are absent, that indicates a deepening and size-increase of the basin. There are no changes in belemnite assemblages at the J/K boundary (inside the Taimyrensis Zone), newly recognized by magnetostratigraphy. The study was supported by RFBR grants 06-05-64284, 06-05-64439 and Earth Sciences Department RAS Program 14; GAČR: 205/06/0842, 205/07/1365 and MSM 0021620855.

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GENUS DELPHINITES (AMMONOIDEA) IN THE VALANGINIAN OF RUSSIA

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On Russian platform ammonites of the genus *Delphinites* Sayn, 1901 (subfam. Platylenticeratinae, incertae familiae) are characteristic of Undulatoplicatilis Zone of the Lower Valanginian. Formerly these ammonites were assigned to the genera *Pseudogarnieria* and *Proleopoldia*, the type species of which are described from the Volga River Basin. The authors have studied a new material from the type locality (River Menya, Chuvashia, the middle reaches of the Volga River) and also the collections of W. Stchirowsky, A. Pavlow, I. Sasonova. Up to now all doubtless Central Russian *Delphinites* originate from this locality and were described as 7 species: *Oxynoticeras tuberculiferum* Stchirowsky, 1893; *O. undulatoplicatile* Stchirowsky, 1893; *Hoplites menensis* Stchirowsky, 1893; *H. kurmyschensis* Stchirowsky, 1893; *Platylenticeras* (*Pseudogarnieria*) alatyrense Kemper, 1961; *Pseudogarnieria securis* Sasonova, 1971, *Proleopoldia stchirowskyi* Sasonova, 1971. The ammonites occur in a thin (up to 0.8 m) sandstone bed overflown by bivalves and ammonites (*Buchia, Surites, Menjaites*, etc.) and having obvious signs of condensation.

Representatives of *Delphinites* from this section may be arranged in a single morphoseries. This series begins from oxycone shells with the ventral side very narrow and only weak rugae and striate ornamentation on lateral sides (*D. undulatoplicatilis*). Several following morphs developed the primary ribs raised in umbilical part (*D. tuberculiferus*, *D. securis*, *D. alatyrense*). In the next morph curved primary ribs well developed on the juvenile whorls are modified with the shell growth into umbilical tubercles, short ribs ("denticles") near ventrolateral shoulder are observed, and the venter remains very narrow (Fig. 1). This still undescribed morph represents a transition from "*Pseudogarnieria*" to "*Proleopoldia*". These latter have trapezoid section of whorls with flattened venter; the primary ribs raised in umbilical part, and more or less expressed tubercles on ventrolateral shoulder (*D. kurmyschensis*, *D. menensis*, *D. stchirowskyi*). This series is culminated with one more still undescribed form showing sharp tubercles on the midflanks, disappearing as the shell grows (Fig. 2). This form closely resembles *Delphinites (Pseudogarnieria) donovani* described from Greenland (Alsen & Rawson, 2005).

In our opinion, in the Undulatoplicatilis Zone in the type locality the ammonites from 3–4 faunal horizons are condensed, each of them being characterized by only one species of *Delphinites*. The species of Kemper (1961) and Sasonova (1971) are subjective synonyms of species described by Stchirowsky (1893).

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Explanations of figures:

1. *Delphinites* sp., transition from "*Pseudogarnieria*" to "*Proleopoldia*", Vernadsky State Geol. Museum N II-108/402, Moscow, lateral view.

2. *Delphinites* sp. (sp. nov.?), Vernadsky State Geol. Museum N II-117/788, Moscow, a – lateral view, b – apertural view. Scale bar 15 mm.

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ALBIAN AMMONITE PALEOBIOGEOGRAPHY IN THE NORTH PACIFIC

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Cretaceous marine faunas in the North Pacific Province markedly differ both taxonomically and ecologically, from those in the Tethys regions. Recently, it was demonstrated that the Albian time was the most important for considering the establishment of the North Pacific biotic province (Iba and Sano, 2007). Abundant ammonite shells preserved in the Cretaceous marine deposits are particularly useful in reconstructing paleobiogeography and marine paleoenvironment of this period. In this study, mid-Cretaceous (especially, Albian) ammonite faunas from the Budden Canyon Formation in northern California and from the Yezo Group in northern Japan were analyzed from the paleobiogeographic and palaeoclimatologic viewpoints, in order to elucidate a major ammonite faunal change in the North Pacific.

The Budden Canyon Formation exposed along the North Fork Cottonwood and Huling creeks can be classified into nine sedimentary facies which represent depositional settings from the outer shelf to the distal basin plain via proximal basin plain. Based on the yielded ammonites, six ammonite zones were recognized in the Aptian to Albian strata. However, the *Leymeriella taldefrucata* zone, which characterizes the lower Lower Albian in the Tethys and western European regions, is missing in the northern California section. Aptian–Albian ammonites from northern California can be classified into five biogeographic types on the basis of their distribution patterns; 1) Tethys-type (distributed only in the subtropical–tropical realm), 2) Cosmopolitan type 1 (distributed both in Tethys and western European realms), 3) Cosmopolitan type 2 (worldwide distribution), 4) North Pacific type (distributed only in N. Pacific), 5) endemic type (distributed only in northern California).

Paleobiogeographic analyses of the ammonite faunas have been done on the basis of generic composition and their individual composition for each of the bio-zones. The results reveal the dominance of the Tethys-type genera (e.g., *Lytoceras*, *Holcophilloceras*, *Valdedorsella*, *Acanthoplites*) in the Late to latest Aptian, indicating a strong faunal affinity between northern California and Tethys regions. In particular, the latest Aptian ammonite assemblage from northern California is represented by Tethys-type genera only. The same trend is widely recognized in other North Pacific regions. Tethys-type genera such as *Acanthoplites* became extinct in northern California at Aptian/Albian boundary interval, and thereafter, no Tethys-types exist in earliest Albian assemblages. The ammonite faunas in this region consisted mostly of North Pacific and endemic types (e.g., *Leconteites* and *Brewericeras*) during Early Albian to Middle Albian, especially in earliest Albian (North Pacific and endemic type occupied 60% in generic composition, 86% in individual composition). These lines of evidence strongly suggest that an ammonite fauna "vicariance event" occurred during the latest Aptian–Early Albian interval.

An Early Albian Arctic-type ammonite *Arcthoplites* was discovered from the Kj5 Member of the Kamiji Formation (Yezo Group) in the Nakagawa area of northern

Hokkaido, Japan, together with other ammonites (i.e., *Brewericeras?*, *Tetragonites*, *Cleoniceras?*) and a belemnitid *Neohibolites*. This is the first reliable record of a hoplitid ammonite from Japan that indicates the immigration of an Arctic fauna into the middle latitudes of the North Pacific at that time. Synchronously with the appearance of this Arctic-type ammonite, the tropical Tethyan biota (Mesogean taxa) disappeared from Hokkaido and elsewhere in the Northwest Pacific (Iba and Sano, 2007). These biogeographic changes seem to suggest a presence of the Early Albian "cooling" condition in the North Pacific during the Greenhouse Cretaceous period.

Thus, it is strongly suggested that major paleobiogeographic changes occurred extensively in the Early Albian in the North Pacific.

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Iba, Y., Sano, S., 2007, Mid-Cretaceous step-wise demise of the carbonate platform biota in the Northwest Pacific and establishment of the North Pacific biotic province.

Palaeogeography, Palaeoclimatology, Palaeoecology 245, 462–482.

CENOMANIAN/TURONIAN BOUNDARY EVENT IN THE NORTHWESREN PACIFIC: MARINE BIODIVERSITY AND PALEOCEANOGRAPHIC BACKGROUND

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The faunal changes of ammonoids, inoceramids and foraminifers across the Cenomanian/Turonian boundary (CTB; 93.5 Ma) in the Yezo forearc basin, Hokkaido, Japan revealed the expansion process of the oxygen-minimum zone (OMZ) in an open ocean setting. The faunal changes from shallow to deep environments (inner shelf, outer shelf and slope sections) across the CTB were examined in Hokkaido. They indicate that (1) the high extinction rates (extinction rate > 50%) were concentrated during 0.6-0.7m.y. before the CTB; (2) the timing of the high extinction rates was slightly different in each section ("stepwise extinction"), which was the earliest in the outer shelf section; and (3) the species diversity increased drastically in the 93.4 to 93.3 Ma in all sections (origination rate = 70 %). Moreover, *Rotalipora*, a planktonic foraminifer living in mid water, became extinct earlier than most benthic foraminifers and planktonic foraminifers living in surface water such as Praeglobotruncana in the continental slope section. Weakly laminated mudstones, suggesting dysoxic conditions, were dominant in the extinction interval. These facts suggest that the mid-water OMZ were expanded upward and downward in water column near the CTB in Hokkaido. This expansion process is different from that in enclosed basin settings (e.g., Western Interior Seaway, USA), where the OMZ was expanded upward from the sea floor.

Furthermore, the thickness ratio of ammonoid shells (breadth/diameter of shell) decreased across the CTB in Hokkaido, and the ammonoids with slender shells tend to survive despite the several oceanic anoxic events (OAEs) during the Cretaceous period. These tendencies presumably suggest that the slender ammonoids could avoid the OAEs.

The expansion and intensification of the OMZ has been suggested as a major cause of the OAEs during the mid-Cretaceous period, known as one of the green house ages. The OAEs triggered off large turnovers in marine biota, so that this finding is important to recognize an impact of the OAEs on marine organisms and to prospect the future of the modern Earth, which is currently undergoing global warming.

TAXONOMIC REVISION OF *TRAGODESNOCEROIDES* AND *DAMESITES* SPECIES (UPPER CRETACEOUS DESMOCERATINE AMMONOIDS) FROM THE CRETACEOUS YEZO GROUP

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Taxonomic revision of the six morph(sub)species of *Tragodesmoceroides* and *Damesites* in the subfamily Desmoceratinae from the Cretaceous Yezo Group were addressed based on detailed observation on the ontogenetic shell-development. Adequacy of several characters, such as the shape of growth lines, whorl expansion ratio, shell surface ornament, whorl breadth and umbilical width were tested from the ontogenetic point of view (e. g., Nishimura et al., 2006). Results of reevaluation of diagnostic characters revealed that five evolutionary bio(sub)species, including one new species, are discriminated. They were morphologically classified into the C- and S groups as follows.

C group: Growth lines form single concave (C) pattern throughout the growth. The shell surface is almost smooth with periodical constrictions throughout the growth. Whorl expansion ratio is small. Two *Damesites* species, *Damesites* sugata and *Damesites* n. sp. are included in this group.

S group: Growth lines changes from single concave (C) pattern to sigmoid (S) pattern in the latter growth stage (larger than 50 mm in diameter). The shell surface ornament is similar to the C type up to 30 mm in diameter. Then, sigmoidal ribs are often developed after the middle stage. Whorl expansion ratio is large. Three (sub)species, *Tragodesmoceroides subcostatus*, *Damesites damesi* and *D. damesi intermedius* are included in this group.

Difference of the ontogenetic shell-development suggests that the two groups were phylogenetically isolated. This view is also supported by the paleobiogeographic distribution. In the Turonian, S group was locally distributed in the western Pacific realm, but this group temporally decreased during the latest Turonian to Coniacian. During this interval, the cosmopolitan C-group species, *Damesites sugata*, migrated from Gondowana area, and succeeded to stay in the western Pacific realm. In the Santonian and the early Campanian, C group (*Damesites* n. sp.) and S group (*D. damesi* and *D. damesi intermeidus*) coexisted in the western Pacific realm. Similar changing pattern of ammonoid fauna is observable among several groups, e.g., *Yokoyamaoceras* of Kossmaticeratidae (Maeda, 1993).

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PSEUDASPIDOCERAS FLEXUOSUM: AN AMMONITE WITH FLEXIBLE SPINES FROM THE EARLY TURONIAN (LATE CRETACEOUS) OF NE MEXICO

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The platy limestone quarries near Vallecillo in NE Mexico have become famous for excellently preserved fossils during the last years. Commercial quarrying, but also a series of scientific excavations, provided fossils with exceptional preservation. Many ammonites preserve their aptychi *in situ* and, in cases, stomach contents.

The long-lasting survey by quarrymen and scientists provided a detailed overview of the fossil assemblage, including quantitative data. *Pseudaspidoceras flexuosum* turned out to be the most abundant ammonite species at Vallecillo, with a long stratigraphic range throughout most of the early Turonian.

About one third of the >100 specimens collected of this species yields long ventrolateral, hollow spines. They are present on smoothly ornamented shells, whereas shells with a more stout ornamentation always lack spines. This suggests the presence of a sexual dimorphism, hitherto unknown for *P. flexuosum*. The long spines are exclusively preserved on the living chamber. They are not rigid extensions of the shell, but were articulated with the shell at the base. The spines were possibly mobile. Similar appendices have never been reported for ammonites before. The function of the spines is not known at present. Current research focuses on detailed study of the construction of these spines.

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METHANE INDUCED FOSSILIZATION PROCESS OF AMMONOIDS: A CASE FROM A LATE CRETACEOUS METHANE-SEEP IN NAKAGAWA AREA, NORTHERN HOKKAIDO, JAPAN

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In the Cretaceous Yezo Group in Hokkaido and Sakhalin, ammonoid fossils preserved in calcareous concretions are mostly well preserved, with retaining their original threedimensional shape. In contrast, those from clastic rocks have been more or less flattened by sediment compaction. However, we found a rare example of three-dimensionally well-preserved ammonoid fossils without external calcareous cementations, but with internal calcareous cementations. They occur in a Late Cretaceous methane-seep deposit at the Yasukawa site (Jenkins et al., 2007) in the Nakagawa area, Hokkaido, Japan. To reveal fossilization process of these peculiar ammonoid fossils, we observed their mode of occurrence and slab- and thin-sections, and analyzed carbon and oxygen isotopic compositions of the calcareous cementations.

Four carbonate bodies, larger than 50 cm in diameter, are exposed at the Yasukawa site. Jenkins et al. (2007) interpreted that these carbonate bodies were formed under influence of Late Cretaceous methane-seep activities based on paleontological, lithological, and geochemical properties. We examined a sandstone layer (ca. 40 cm in thickness) 5 m laterally away from the largest carbonate body at the site. The sandstone contains a large number of small concretions (smaller than 10 cm in diameter) and ammonoid fossils.

Slab- and thin-section observations show that the cavity of the phragmocone of each specimen is almost occupied by calcareous cements. Carbon isotopic compositions of early-precipitated cements show as low as -42 ‰ (vs. PDB). The last-precipitated cements have a higher value than -15 ‰ (vs. PDB) for carbon isotopic compositions.

The negative carbon isotopic compositions of early cement phase indicate that the cement was formed under the influence of methane activity, because biogenic methane usually has strong depletion of ¹³C. Thus, the cementation in the cavity of ammonoid shells induced by methane-seep activity had reinforced and had prevented the ammonoid shells from the compaction during burial.

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TWO CAMPANIAN (LATE CRETACEOUS) NOSTOCERATID AMMONOIDS FROM THE TOYAJO FORMATION IN WAKAYAMA, SOUTHWEST JAPAN

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Many specimens of the nostoceratid heteromorph ammonoids, Eubostrychoceras elongatum and Didymoceras awajiense, were obtained from the Campanian to Maastrichtian Toyajo Formation in the Aridagawa area, Wakayama, southwest Japan. The Toyajo Formation is divided into three members, Nakaibara Siltstone Member, Hasegawa Muddy Sandstone Member, and Buyo Sandstone Member in ascending order. E. elongatum occurs in the Middle Campanian Nakaibara Siltstone Member, and D. awajiense is contained in the Upper Campanian Hasegawa Muddy Sandstone Member. Although E. elongatum has been known in the northeast Pacific region, the occurrence of this species has been uncertain in the northwest Pacific region before. The occurrence of E. elongatum in the northwest Pacific region indicates the strong similarity of the faunas between the northwest Pacific region and the northeast Pacific region. The present species has been remarked to have helical whorls touching each other and distinct retroversal hook. On the other hand, the specimens from the Toyajo Formation show a wide range of variation. The coiling pattern varies from whorls in contact to not in contact. Additionary, some specimens have last part slightly facing obliquely upward, and others have distinct retroversal hooks. Both dextral and sinistral forms were collected within the species. In the lower horizon, sinistral forms outnumber the dextral ones, then the dextral forms increase upward. Finally, dextral shells become dominant in the upper horizon (see Figure). Ward (1976) remarked that the ratio of sinistral individuals to dextral ones of E. elongatum on the Vancouver Island and Orcas Island approximated one to one, and that the possibility of sexual dimorphism can not be disregarded. However, different coiling forms in Eubostrychoceras are difficult to be regarded as a sexual pair because of presense of closely related Nipponites whose shell consists of a combination of dextral-, sinistral-, and planispiral coiling within an individual. So far, no evidences suggesting that the opposite coiling directions are ecophenotype have ever been obtained. Different coiling patterns may rather be controlled genetically in these populations, and stratigraphic change of their ratios may be attributable to the genetic floatation. Another species, D. awajiense also has helically coiled phragmocone followed by a body chamber forming a vertical retroversal hook. Two rows of ventral tubercles are present through the early to late growth stages. Almost same number of the dextral and sinistral forms were obtained in each horizon. On the other hand, some specimens of *D. awajiense* collected in the upper horizon have more planar whorls. Pravitoceras sigmoidale, flat coiling nostoceratid ammonoids, is well known in the Izumi Group on Awaji Island, southwest Japan. Matsumoto et al. (1981) and Morozumi (1985) suggested that P. sigmoidale had been evolved from D. awajiense because of their successive occurrence and similarity on their ornamentation and juvenile shell forms. The planar shaped D. awajiense of the Toyajo Formation confirms their suggestion.



Figure: Change in proportion of dextral and sinistral specimens of Eubostrychoceras elongatum.

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TOWARDS A DATABASE OF THE CRETACEOUS AMMONOIDS IN JAPAN

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Ammonoids are one of the most common fossil animals in the Late Paleozoic and Mesozoic Eras, and a great many species of ammonoids have been reported until now. The Japanese Cretaceous System yielded many ammonoid species so far, too. Some lists, catalogues and/or databases on the Japanese Cretaceous ammonoid species have been published, to date, e.g., Matsumoto (1942, 1943), Tanabe et al. (2000), Toshimitsu and Hirano (2000), and Tanabe and Shigeta (2002). Among them, Tanabe et al. (2000) and Tanabe and Shigeta (2002) mainly dealt with illustrated and/or type specimens described in Japan. On the other hand, Toshimitsu and Hirano (2000) collected all records of ammonoid species reported from the Japanese Cretaceous deposits, from literature in geology, stratigraphy, and paleontology, and 790 "species" (bearing subspecies, varieties and other undescribed ones) are regarded in the list, with their stratigraphic distributions. Now, we try to renew and modify the data of Toshimitsu and Hirano (2000) and make database of the Japanese Cretaceous ammonoids for Web, adding information of synonym, strata bearing fossils, and literature. We will introduce to a part of the preparing work, in this symposium.

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SUPPOSED DEEP-WATER TEMPERATURE FLUCTUATIONS IN THE CENTRAL PACIFIC DURING LATEST CRETACEOUS TIME: FIRST EVIDENCE FROM ISOTOPIC COMPOSITION OF BELEMNITE ROSTRA

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An oxygen isotope paleotemperature study of belemnites from open ocean paleoenvironments was done for the first time, having the 55 well-preserved rostra recently collected from Late Campanian-Maastrichtian limestones of the DVGI, Gelendzhik and Butakov guyots, Magellan Rise (Zakharov et al., 2007). According to plate-tectonic reconstructions, the Magellan Rise at late Campanian time could have been at the paleolatitude of 18-19°S in the Central Pacific. For the preliminary isotopic investigation, only two belemnite rostra were selected: no. 8D8-G(MR12) from the DVGI Guyot and no. 37D110-A(IR1) from the Gelendzhik Guyot. The values of δ^{18} O and δ^{13} C in the calcite material obtained from the rostrum 8D8-G(MR12) are -1.3% (the corresponding paleotemperature is 17.1°C) and +0.2‰, respectively. 83 samples for our detailed isotopic analyses were taken from successive growth portions in the belemnite rostrum 37D110-A(IR1). The values of δ^{18} O and δ^{13} C in the analyzed material fluctuate from -0.4 to +0.8‰ and from +0.1 to +3.1‰, respectively. Judging from the data obtained, the lowest paleotemperature calculated from the rostrum 37D110-A(IR1) is 9.0°C, the highest is 13.6°C. New data on the isotopic composition of the Late Cretaceous belemnite rostra from the tropical Pacific are consistent with the hypothesis suggesting a considerable vertical range of the migration of belemnites in the seawater column. It is possible that, in Magellan Rise region, they submerged down to depths of 1000-1500 m, where the water temperature near the guyots could have approached, to some extent, the temperature of the abyssal waters, taking into consideration a possible effect the Taylor-Hogg topography vortices (Mikhalik et al., 2003), which originate around guyots because of the Earth's rotation and stimulate the influence of cold abyssal waters on the thermal regime near the guyot slopes.

Near-bottom paleotemperatures close to 9°C and 9.3-11.5 °C have been estimated for the subequatorial zone of the Pacific from early Early Maastrichtian benthic foraminifera shells by Boersma & Shackelton (1981) and Douglas & Savin (1973), respectively. Surface paleotemperatures of 10-17.8 °C have been estimated for the South Atlantic from early Early Maastrichtian planktic foraminifera by Barrera et al. (1987) and Huber et al. (1995). Saltzman & Barron (1982) suggest that deep water was formed both by cooling at high latitudes and by evaporation in the subtropics. In view of new facts it seems likely that at least in the tropical Pacific (Southern hemisphere), bottom waters were produced mainly by sinking of surface waters in polar regions. Judging from signs of possible seasonal temperature fluctuation, fixed for the rostrum 37D110-A(IR1), very likely reflecting some surface seasonal conditions in polar regions in general, we assume that near bottom temperatures in the Magellan Rise area were a few degrees higher in

the Campanian-Maastrichtian southern summer (paleotemperatures were not lower than $11.3-11.7^{\circ}$ C) than in the Campanian-Maastrichtian southern winter (not lower than 9.0-10.2 °C) (Figure). This research was made under the financial support of DVO RAN grant (07-III-B-08-080).



Oxygen and carbon isotopic composition of the belemnite rostrum. 37D110-A(JR1) in its different ontogenetic stages (interpretation from 83 samples).

PRELIMINARY REPORT ON THE REVISION OF THE CRETACEOUS AMMONITES OF THE COQUAND COLLECTION

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Henri Coquand (1813, Aix en Provence – 1881, Marseille) was a well-known geologist of his age. During decades he was collected a marvellous fossil material containing ammonites, ostreas, brachiopods besides other types of fossils mainly from North-Africa, Southern-France and Spain. After his death the collection was sold out by the family and bought by a great patron of the Hungarian geology, a nobleman, Andor Semsey in 1892. Semsey donated the whole collction to the Museum of the Hungarian Royal Geological Institute. The last wish of H. Coquand was that his collection have to be intact and deposited and exhibited in one place.

The so-called "Coquand Collection" was a great attraction of the Hungarian Geological Institute as it "[...includes more than 10.000 species with a great number of 30.000 specimens.]" (Guide to the collections of the Museum of the Hungarian Royal Geological Institute, 1909). In 1909 the Geological Institute was moved to a new building and the former president, J. Böckh exhibited the whole fossil collection as it was desired by the collector.

According to Coquand's instruction, the collection was exhibited and aggregated into groups (parts containing Cretaceous cephalopods are shown in **bold**).

- 1. General stratigraphic fossil collection
- 2. Collection of Cretaceous oysters
- 3. Brachiopod Collection
- 4. Echinoid Collection
- 5. Africa Collection (Coquand, 1881)
- 6. Aptian Fossils from Spain (Coquand, 1865)

Decades of wars, the decay of the Austro-Hungarian Monarchy and the socialism resulted the Coquand Collection was splitted into groups and unfortunately many specimens are lost. In the revolution in 1956 the Hungarian Natural History Museum had a tank-attack and most of the collections are burned and destroyed. The Geological Institute offered the Jurassic part of the Coquand Collection - and absolutely negligated the last wish of Coquand – to the Natural History Museum, so since then the Jurassic part is still housed there.

The Cretaceous fossils were remained at the Hungarian Geological Museum at Stefánia street. On the basis of an ongoing project, the revision of the type specimens of the Cretaceous ammonites of the Coquand Collection have been started in 2006 with the contribution of W. J. Kennedy (Oxford) and M. Company (Granada). Coquand described at least 25 ammonite species in his works (Coquand 1852, 1854, 1858-1860, 1862, 1865, 1881) but some holotypes were separated from the Hungarian Coquand Collection and housed in various other museums.

In the Hungarian Geological Museum 12 Cretaceous ammonite holotypes were found:

- 1. Ammonites cicer
- 2. Ammonites baborense
- 3. Ammonites rebouli
- 4. Ammonites nicaisei
- 5. Ammonites favrei
- 6. Ammonites solarium
- 7. Ammonites pauli
- 8. Ammonites jubae
- 9. Ammonites villei
- 10. Ammonites martimpreyi
- 11. Ammonites lhotellerieri
- 12. Ammonites brossardi

The holotype of Ammonites stanleyi is lost, only the original designation remained in the box.

In total 189 ammonite specimens were found as a repository numbered item in the Cretaceous Ammonite Collection part apart from the holotypes. It is also likely that some specimens are in the Jurassic part because of Early Cretaceous forms could be determined as Tithonian. Finding of uninventored specimens is still on the way. Unfortunately it seems that half of the Cretaceous ammonite collection is disappeared according to the list from 1984 which contain 450 items. We try our best to find the missing specimens. After collecting all the available material and literature the revision of type specimens can start.

The author is grateful to Prof. W. J. Kennedy (Oxford University Museum) to his enthusiastic help and consultation. Prof. Kennedy also kindly sent his notes and manuscripts of his former investigations on the Coquand Collection which gesture is also fully appreciated.

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UPPER CRETACEUS NAUTILOIDS OF EPICONTINENTAL SEAS IN CETRAL EUROPE - BOHEMIAN CRETACEOUS BASIN

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Nautiloidea of the Bohemian Cretaceous Basin (BCB) represent a group with rather rich taxonomic diversity. Currently, six species belonging to three genera are known from BCB. Genus *Eutrephoceras* constitutes three species: *Eutrephoceras columbinum* (FRIČ & SCHLÖNBACH), *Eutrephoceras sublaevigatum* (D`ORBIGNY) and *Eutrephoceras* sp. (Frank and Košták 2004). The last mentioned species is provisionally kept in open nomenclature. Genus *Deltocymatoceras* includes two species: *Deltocymatoceras rugatus* (FRIČ & SCHLÖNBACH) and *Deltocymatoceras galea* (FRIČ & SCHLÖNBACH). The last genus *Cymatoceras* is represented by only one species *Cymatoceras* aff. *elegans*. Generally, representatives of nautiloidea range from the Upper Cenomanian (Korycany member of Peruc-Korycany Formation; zone *Inoceramus pictus*), to the middle-upper Coniacian (Chlomek member of the Merboltice Formation; zone *Volviceramus koeneni*) and they are known from all sedimentary formations of the BCB. All specimens studied show no dependence on sediment character and they occurred both in sediments of shallow and deeper water environments (post mortal transport of nautiloid shells).

Some interesting interspecies differences and even intraspecies dimorphisms have been discovered during the study of fossil material. For example, in some species of genus *Deltocymatoceras* a possible dimorphism between juveniles and adults has been observed. This dimorphism is characterized by well developed ventral keel in adult specimens. Almost all specimens of species *Deltocymatoceras galea* from BCB have mistakenly been classified as *Deltocymatoceras rugatus* or *Eutrephoceras sublaevigatum* in the past, as it has been recognized during the taxonomic revision.

Interesting ascertainment is the presence of genus *Cymatoceras*, which is represented by one species, still left in an open nomenclature - *Cymatoceras* aff. *elegans*. This species is very close to species *Cymatoceras elegans* (SOWERBY). However, *C. elegans* is known from the Cenomanian, while the *Cymatoceras* aff. *elegans* from the BCB ranges from the Upper Turonian to the Middle Coniacian.

Specimens of *Eutrephoceras* sp. are probably juveniles of species *Eutrephoceras sublaevigatum*, although this is difficult to prove due to their mediocre preservation. Another opinion is that some of these specimens can possibly represent initial whorls of adults.

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Obr.1: Nautiloids of the BCB: *Eutrephoceras, Deltocymatoceras* a *Cymatoceras*: **1.** *Eutrephoceras columbinum* (1/2 of original size); **2.** *Deltocymatoceras galea* (1/4 of o. s.); **3.** *Deltocymatoceras rugatus* (1/2 of o. s.); **4.** *Cymatoceras* aff. *elegans* (1/3 of o. s.).

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ATUROIDEA (NAUTILIDA) FROM UPPER CRETACEOUS SADA LIMESTONE IN SHIMANTO CITY, KOCHI PREFECTURE, JAPAN

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The first specimen of *Aturoidea* (Cephalopoda: Nautilida) to be recorded in East Asia was discovered in Upper Cretaceous Sada limestone in Shimanto City, Kochi Prefecture, Japan. *Aturoidea* is of the nautiloid genus, known to exist in the Upper Cretaceous to Eocene strata with a nearly worldwide distribution. While at least 13 species of *Aturoidea* have been reported, their occurrence is so rare that each species is represented by one or only a very few specimens (Kummel, 1956). Particularly, only 3 species of *Aturoidea* from the Upper Cretaceous are known. Specimens of these species have been discovered in Libya, Angola and India. No species have previously been reported from the East Asia area.

The specimen is of moderate size, measuring 82 mm in diameter, and is characterized by thick sublenticular whorls with a roundish trapezoidal cross section, involute, very narrow umbilicus, and adorally convex fine and dense ribs. A rounded infundibuliform suture can be observed on the surface of the internal mold.

Aturoidea are very closely related to *Hercoglossa*, which has a sinuous suture, and *Aturia*, with an infundibuliform suture, and is approximately intermediate between them. Miller (1951) suggested an evolutionary lineage of *Hercoglossa* to *Aturia*, through *Aturoidea*. Among species of *Aturoidea*, the characteristics of their sutures differ slightly according to their age. In primitive *Aturoidea* from the Upper Cretaceous, the suture is rounded and is similar to that of *Hercoglossa*. However, *Aturoidea* from the Eocene resembles *Aturia* in its typical infundibuliform suture. Our specimen has an intermediate suture between the Upper Cretaceous and Eocene types.

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DISCOVERY OF A NAUTILOID UPPER JAW FROM THE MAASTRICHTIAN OF HOKKAIDO, JAPAN

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A partial cephalopod jaw was discovered solitarily from the shallow-water fine-grained sandstone unit (Heitaro-zawa Member), the lower part of the Hakobuchi Formation, Yezo Group in the Nakatonbetsu area, northern Hokkaido. The horizon yielded the jaw fossil belongs to the Sphenoceramus hetonaianus Zone of early Maastrichtian age (Ando and Tomosugi, 2005). The jaw remain consists mainly of a calcified portion, about 15 mm in axial length and 12 mm in maximum width, whose basal margin is connected with a black chitinous lamellar fragment (Fig. 1A-C). The calcified portion is characterized by having an arrowhead-shaped head that is strongly notched and set off from the shaft by a deep and narrow indentation. Although an anterior calcified jaw element has been known in modern and fossil Nautiloidea (e.g., Saunders et al., 1978; Klug, 2001) and some Mesozoic lytoceratid ammonoids (Tanabe et al., 1980), the overall morphological features of the jaw remain examined fit well with those of the anterior calcified tip (rhyncholite) of the upper jaws of extant Nautilus (Saunders et al., 1978; Fig. 1G-I) and fossil nautiloids (Klug, 2001). Hence, it is identified as a partial remain of the upper jaw of Nautiloidea. The upper (dorsal) side of the calcified portion has a median rounded elevation, and the lower (ventral) side has a prominent median ridge with a sharp top that extends onto the relatively short shaft. Based on these characteristics, our rhyncholite corresponds to the form genus Rhynchoteuthis d'Orbigny, 1847 (Fig. 1D-F) that is known to occur from the Lower Permain to the Upper Cretaceous.

The range data of the previously known nautiloids suggest that the following genera can be considered as the source of the jaw examined; *Carinonautilus* and *Eutrephoceras* of the Nautilidae, *Cymatoceras*, *Deltocymatoceras*, *Epicymatoceras*, *Syrionautilus*, and *Anglonautilus* of the Cymatoceratidae, and *Hercoglossa*, *Aturoidea*, *Cimomia*, and *Deltoidonautilus* of the Helcoglossidae. Of these genera, shell remains of *Eutrephoceras*, *Cymatoceras*, and *Anglonautilus* have been described from the Campanian of Hokkaido (Matsumoto and Miyauchi, 1983), but no nautiloid shells have been known from the Maastrichtian of the region. The perfect preservation of a calcified portion without suffering abrasion as well as the partial association of a chitinous lamella suggests that the jaw examined was not transported a long distance after the death of the animal.

The present report is the first reliable record of a nautiloid jaw from the Upper Cretaceous of Hokkaido, and provides an important information about the paleoecology and taphonomy of the nautiloid animals in the Yezo forearc basin.

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Fig. 1. Comparison of the Nakatonbetsu rhyncholite specimen (A-C) with *Rhynchoteuthis astieriana* (D-E; from the Aptian of France; Teichert et al., 1964) and the rhyncholite of *Nautilus pompilius* (G-I; Recent , from the Philippines; Saunders et al., 1978). Outer (A, D, G), lateral (B, E, H) and inner (C, F, I) views.

THE NEOGENE CEPHALOPOD FOSSILS OF JAPAN

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The Neogene cephalopod fossils are described from the Miocene and Pliocene deposits in Japan, and these are shown in the following lines.

<Nautiloid>

Aturia aturi (Basterot, 1825): ?Miocene; *Aturia cubaensis* (Lea, 1841): Early-Middle Miocene; *Aturia formae* Parona, 1898: late Early Miocene; *Aturia coxi* Miller, 1947: Late Miocene; *Aturia complanata* Sturani, 1958; late Early Miocene.

<Argonautid>

Argonauta hians Lightfoot, 1786: Late Pliocene (to Recent); Argonauta tokunagai Yokoyama, 1913: Middle Miocene; Argonauta itoigawai Tomida, 1983: Late Miocene; Izumonauta lata Kobayashi, 1954: Middle Miocene; Izumonauta kagana (Kaseno, 1955): Middle Miocene; Izumonauta kasataniensis (Kaseno, 1955): Middle Miocene; Mizuhobaris izumoensis (Yokoyama, 1913): Middle Miocene; Obinautilus awaensis (Tomida, 1983): Late Miocene.

<Spirulirostrid>

Spirulirostra mizunamiensis (Tomida and Itoigawa, 1981): late Early to early Middle Miocene.

My field studies of Neogene cephalopod fossils in Japan have shown the clear correspondence between stratigraphic levels with warm-water faunas and the times of major eustatic sea level rises deliminated by Haq *et al.* (1987) and Malmgren and Berggren (1987). Additional study has shown that cephalopod fossils occur in all major transgressions. These were belong to a group of pelagic mollusks that floated at the surface of tropical seas and drifted on warm ocean currents, or after death, so that these are accompanied by warm-water mollusks and a clear indicator of strong, warm ocean currents. These occurrences show that the vigorous, warm Kuroshio current flowed along the Pacific coast of Japan in the late Early Miocene (N.7), early Middle Miocene (N.8), middle Miocene (N.9), Late Miocene (N.17), and Late Pliocene (N.21).

A considerable number of argonautid fossil specimens were reported from the Middle Miocene (e. g., Hilber, 1915; Martin, 1929; Kobayashi, 1954b; Kaseno, 1955; Noda *et al.*, 1986). The diversity of argonautid genera also peaked during the Middle Miocene and seven species of four genera flourished: above mentioned five species and *Argonauta joanneus* Hilber, 1915, and *Kapal batavus* Martin, 1929. All the species disappeared prior to the Late Miocene, and only three species of three genera, above mentioned two species and *Mizuhobaris lepta* Saul and Stadum, 2005, were reported from the upper Miocene (Tomida, 1989, 1996; Yanagisawa, 1990; Saul and Stadum, 2005; Tomida *et al.*, 2007). Finally, the genus *Argonauta* is the only survivor through the Pliocene to the present. This declining trend of argonautid abundance and diversity is similar to that of the nautiloid *Aturia*. Most of the Neogene *Aturia* species became extinct at the mid-upper Miocene boundary, and only two species *A. coxi* Miller, 1947 and *A. cubaensis*

(Lea, 1841), survive to the end of the Miocene (Beu, 1973; Ozawa and Tomida, 1996), and since then *Aturia* was extinct. This decline of the Neogene cephalopods was probably caused by the remarkable regressions and climatic cooling in relation to the intensified Antarctic glaciation at 10 Ma (Robin, 1988) and terminal Miocene event of cooling (e. g., Beu, 1990).

ECOLOGICAL CHANGE DURING THE EARLY EMSIAN (DEVONIAN) IN THE ANTI-ATLAS (MOROCCO) AND THE ORIGIN OF THE AMMONOIDEA

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Early Emsian claystones and marls of the Tafilalt yielded two diverse and prolific faunas with nearly 5000 specimens belonging to at least 100 species having been recovered. The older of the two faunas contains what may be the oldest bactritoids, a number of rare fossil groups and a diverse and largely infaunal bivalve assemblage. The younger fauna is marked by the appearance of the first ammonoids, which are represented by the genera *Chebbites*, *Erbenoceras*, *Gracilites*, *Gyroceratites*, *Irdanites*, *Lenzites*, and *Metabactrites* (see Klug 2001b). These are accompanied by other cephalopods such as the bactritoids *Devonobactrites* and *Cyrtobactrites*, predominantly epibyssate bivalves, and gastropods; infaunal organisms are rare in this fauna.

Based on the differences in the identified faunal elements of the two assemblages, the preservation of the fossils and the lithology from which the fossils were recovered, it can be concluded that the paleoenvironment had more or less normal oxic conditions with intermittent dysoxic and anoxic phases. Both phases produced reducing conditions that allowed some of the organisms to be preserved as pyrite (later transformed into limonite), and the latter phase resulted in local accumulations of minute bivalves that died shortly after hatching. Based on the sedimentology, the water depth was moderate with the deeper part of the photic zone being below storm wave base. The high diversity of the infaunal benthonic community of the older fauna and the sediment itself indicate a soft bottom paleoenvironment.

The older fauna is represented by machaerids, infaunal bivalves, hyolithids, brachiopods, trilobites (low diversity), phyllocarids and stalked edrioasteroids. The younger fauna, in addition to the bactritoids and ammonoids previously mentioned, contains numerous invertebrate taxa including gastropods, epibyssate bivalves, brachiopods, and much more abundant orthocones (Klug et al. in press). By comparison, the younger fauna has fewer infaunal representatives compared to the older fauna. In addition to the arthropods and echinoderms, vertebrates are less abundant in the younger fauna; this is not surprising given that these animals were part of the nektobenthonic community (as can be demonstrated by the worn tips of their fin spines).

The change in faunal composition between the two faunas strongly suggests that the paleoenvironment of the younger fauna had a decreased oxygen content in the sediment and possibly also in the deepest part of the water column. It is possible that the environmental stresses created regionally by the periodic oxygen reduction in the deeper part of the water column facilitated and stimulated the early radiation of bactritoids and ammonoids during the Emsian. When looking at bactritoid abundance (42% in the older fauna) compared to ammonoid and nautiloid abundance (16% in the older fauna), it appears the bactritoids (3% in the younger fauna) were largely displaced by the other two cephalopod groups (64%) in the younger fauna. This dramatic faunal shift in bactritoid abundance and the extraordinary rapid radiation of the Ammonoidea seen in the vounger fauna may be partly explained by the presumed life mode differences of the two cephalopod groups (see also Klug 2001a and Klug and Korn 2004) and the fluctuating oxygen levels. Bactritoids probably had a demersal life style and they probably suffered near extinction when anoxic phases developed. The ammonoids and nautiloids probably had a more flexible life style and could live higher in the water column (nektoplanktonic). This allowed the ammonoids and nautiloids to escape most of the lethal effects of the anoxic bottom waters. When bottom waters became more oxygenated, the ammonoids and nautiloids were able to exploit the nearly empty paleoenvironmental niche previously occupied and dominated by the bactritoids. Globally, the rising sea level and the radiation of the Gnathostomata also played additional important roles (Kröger 2005) in early bactritoid and ammonoid evolution in early Devonian time.

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AN EARLY CARBONIFEROUS COLEOID CEPHALOPOD SHOWING A TENTACLE WITH ARM HOOKS, AND AN INK SAC (MONTANA, USA)

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Only two locations in North America (Arkansas and Utah) have previously yielded Lower Carboniferous coleoid cephalopods. Recently, a new coleoid assignable to a new genus was discovered by reinterpretation of a previously described "orthoconic nautiloid" specimen and other undescribed specimens from the Lower Carboniferous Bear Gulch Limestone *Lagerstätte* in Montana, U.S.A. These specimens exhibit a combination of morphological features that are typically seen in ectocochleates (i.e. a long body chamber) and endocochleates (i.e. ink, arm hooks, and a tentacle).

In specimen UM 5743 the crushed rostrum, phragmocone and body chamber is 90 mm long and is 25 mm broad at the aperture. The body chamber is long, is about a half of the total length of the shell and is 55 mm long. In the body chamber approximately 20 mm apicad from the aperture there is the remains of the ink sac. The oval shaped ink sac is partly crushed. The surface of the structure is covered with polygonal structures filled with black, shiny, coaly material. Additionally, black material, which is interpreted to be ink, is dispersed around the ink sac making the area darker than the surrounding limestone. There is the possibility that there are traces of soft tissues preserved in three places around the conch based on the texture of the fracture surface that exposed the fossil. From one of these presumed tissue patches there is a long (85+ mm) carbon impression that is 2 to 4 mm wide that stretches to the side of the body chamber. In the carbon impression there are numerous carbonized paired arm hooks; some of the hooks appear to be arranged in rosettes. Each hook is about 1.0 mm long and 0.2 mm wide. Based on the preservation as a carbon impression and the presence of arm hooks, this narrow structure is interpreted to be a tentacle. No other signs of arm hooks, arms, or tentacles are preserved on the specimen; although, there is a large amount of organic debris in the sediment. This is the oldest know occurrence of ink, arm hooks, and a tentacle. The presence of a tentacle suggests that arm differentiation and specialization occurred by the late part of the Early Carboniferous time in the Coleoidea. *

One of the specimens with a short rostrum, longiconic phragmocone, and long body chamber contains mandibles at the orad end of the body chamber and the imprint of the cephalic region (without arm crown) in front of the aperture. There are also food balls of macerated fish scales (intact and fragmentary fossil fish are moderately common in the Bear Gulch limestone beds) in the presumed intestinal tract in the body chamber.

Based on their rostrum shape, phragmocone shape, septal spacing, and body chamber length, this new genus is assignable to the Order Donovaniconida. There are three slightly older Lower Carboniferous coleoid genera from Arkansas and Utah that are currently accepted as coleoids. These genera are *Hematites*, *Paleoconus*, and *Bactritimimus*. Only *Hematites* is well known, and it has a rapidly expanding breviconic phragmocone with closely spaced septa, a very short body chamber, and a massive, bluntly pointed rostrum. These taxa are very different than the new genus. The new genus has a long body chamber, a longiconic phragmocone with closely spaced septa, and a short rather modest rostrum on the apical end of the phragmocone. Additionally, these slightly older coleoids from Arkansas and Utah are not known to have arm hooks or ink.

The Carboniferous is now known to contain a number of new genera belonging to at least five different orders. Until now, there was only one coleoid order known in the Lower Carboniferous. With the discovery of the new genus from the Bear Gulch Limestone in Montana, there are now two coleoid orders (Hematitida and Donovaniconida) that can be placed at this time. The diversity of coleoids, most of which have become known in the past decade, suggests that early Coleoidea evolution has been much more rapid than previously expected.

*We wish to acknowledge that W. Bruce Saunders and Melissa Lindholm were the first to discover the presence of arm hooks and ink associated with coleoids in the Bear Gulch fossil collections and they made that information known to us. We subsequently discovered these features on one of the specimens in our collection.

SOFT TISSUES IN AMMONOID CEPHALOPODS FROM THE BEAR GULCH *LAGERSTÄTTE* (LOWER CARBONIFEROUS), MONTANA, USA

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The Lower Carboniferous (Upper Mississippian) Bear Gulch *Lagerstätte* in Montana is famous for its extraordinary preservation of vertebrate and invertebrate fossils (see Hagadorn, 2002 for details). Among the invertebrates that are preserved are the impressions of ammonoid cephalopods. These fossils are apparently moderately common, and their impressions are preserved in very fine-grained limestone. Diagenetic processes have destroyed the aragonitic shell material of the body chambers and phragmocones after burial. Because the shell material has been removed and the impressions tend to split into parts and counterparts, the internal contents, including traces of internal organs in the body chambers, are sometimes exposed for examination.

A total of 95 specimens were available for study. Most of these specimens were donated and precise collecting localities are unknown. These specimens cannot be precisely identified because all ornament and suture patterns were destroyed by dissolution. However, based on age-equivalent ammonoids described by Saunders (1973) from the Imo Formation in Arkansas, only *Rhadinites* and *Anthracoceras* have conchs of comparable diameters with umbilical openings of the same shape as the ammonoids from the Bear Gulch Limestone. In examining the material for soft tissues and other structures, it was discovered that these features were more easily detected when the specimens were immersed in ethyl alcohol.

The most common organs preserved are the jaws. These semi-soft tissues composed of chitinous material are present in 80% of the specimens studied. In some instances, the beaklike shape of the jaws is visible, but, more commonly, the jaws simply appear as patches of black material. Usually, the jaws are found 20-40 degrees adapical of the aperture. The presence of these jaws supports the conclusion that the remainder of the soft body must have been present in the body chamber and that there must have been little or no scavenging of these specimens before or during burial.

Other internal features include 1) a thin, short tentacle/arm-like structure in one specimen, which is tantalizing close to, but not in touch with, the ammonoid shell impression; 2) black masses of material at the adapical ends of the body chamber, which presumably represent stomach and/or intestinal tract contents; and 3) a dark brown, spiral band on the dorsum of the body chamber, which we interpret as the dorsal muscle. This muscle was presumably responsible for the retraction and extension of the head and arm crown while the animal was alive. Significantly, as the animal died, this muscle must have contracted, pulling the soft body, including the head and arm crown along with the jaws, back into the body chamber.

While it is well understood that modern *Nautilus* is not a perfect model for ammonoid reconstruction, it is informative that when *Nautilus* dies, it withdraws into the shell, and the hood tightly seals the aperture. Such a withdrawal pulls the jaws and the arm crown back into the body chamber. This apertural seal by the hood can be sufficiently tight that a living animal can eventually suffocate. That this same withdrawal reaction may be applied to the Bear Gulch ammonoids is supported by the position of most of the jaws 20-40 degrees adapical of the aperture.

Thus, by combining the observations of modern *Nautilus* and the position of the dorsal muscle and jaws in the Bear Gulch ammonoids, we suggest that at the time of death, the Bear Gulch ammonoids withdrew into the body chamber. Additionally, if a soft tissue hood was present and the arms were short and thin, the arms would have been trapped inside the body chamber. This conclusion is consistent with other reports of the positions of *in situ* jaws in the body chambers of Late Paleozoic and Mesozoic ammonoids. It may explain why, despite almost two centuries of collecting and study, unequivocal ammonoid arms have not yet been discovered despite the fact that ammonoids have been recovered at the same localities as arm-bearing coleoids (i.e., Mazon Creek, Bear Gulch Limestone, etc.).

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STRUCTURE AND PRESERVATION OF THE AMMONITE CONNECTING RING

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The most distinctive and important element of the hydrostatic organ of ammonites and nautiloids is the siphuncular tube. It consists of mineral and organic segments (the socalled connecting ring.) The connecting ring of ammonites never preserves its original organic matter in its mineralized state, usually having undergone diagenetic phosphatization, more rarely, calcification, or even complete loss. Our knowledge about its original ultrastructure is based upon comparisons with Recent Nautilus and phosphatized or calcified ammonite fossils. We show that, depending on taphonomic history, both calcium phosphate and calcite can participate in the diagenesis of the Under standard light microscopy, the phosphatized elements are connecting ring. indistinguishable from the calcified ones. Both are dark brown in color, due to an excess of carbon. The structure of the phosphatized siphuncle does not closely replicate the structure of its original organic components. This casts doubts on the conclusions of Mutvei et al. (2004) who described a complex, porous structure in ammonite siphuncles, which is completely different from that of Recent Nautilus, suggesting to these authors that this organ functioned differently in ammonites. SEM observations using a BSE detector on the calcified parts of the walls of ammonite connecting rings revealed a multilayered structure, with perpendicular elements connecting particular layers, resembling the structure of stacked nacre.

In ammonites with prochoanitic septal necks, the mineralized segments are connected to the nacreous septal necks and consist of spherulitic-prismatic or prismatic elements called auxiliary deposits and cuffs. In *Nautilus*, the connecting ring is a simple, nonmineralized extension of the retrochoanitic septal neck. Differences between retrochoanitic and prochoanitic conditions were described by Kulicki (1979, 1996). According to generally accepted interpretations, the mineralized segments are impermeable to cameral liquid, while the organic segments are conductive to fluid. Such a siphuncular cord allows osmoregulation of the liquid content of the phragmocone chambers, thus controlling the buoyancy of the living animal. This process occurs at a molecular level.

The mineral segments fossilize comparatively well, preserving the shape and ultrastructural details during diagenesis and only the original metastable mineral aragonite changes into stable calcite in some cases. The connecting ring of ammonites is usually phosphatized with francolite (Andalib, 1972; Hewitt and Westermann, 1982; and the authors' own observations). The ontogenetically newest sections of the connecting rings are usually not preserved. Only in exceptionally well preserved phylloceratids with the "siphuncular tube" protruding into the body chamber is a fully preserved siphuncular tube observed in the last phragmocone chamber and in the living chamber. In the case of a representative of the Ammonoitida, *Damesites*, the part protruding into the body chamber is a very elongated prochoanitic septal neck (Tanabe et al., 2005). In the case of other Phylloceratida described by Tanabe et al. (2005), the elements protruding into the body chamber are precursory siphuncular membranes, equivalent to the outer component of the siphuncular tube of prochoanitic ammonites (Kulicki, 1979, 1994). Tanabe et al. (2000) described a similarity in the anatomical features between exceptionally well-preserved soft tissue remains in the Permian ammonite *Akmilleria* and the siphuncular cord of Recent *Nautilus*. The anatomical similarity of their siphuncular epithelia also suggests a functional similarity, as well as a similarity in the structure of the secretory products, i.e., the siphuncular tube. In 2004, Mutvei et al. described phosphatized connecting rings with perpendicular pores in fractured specimens of *Aconeceras* and *Grammoceras*. They interpreted the pores as canals housing cytoplasmic extensions of the siphuncular cord. Such an interpretation is completely at odds with Recent *Nautilus* and our own observations of ammonite connecting rings.

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PRESERVATION OF CONNECTING RINGS OF THE APTIAN AMMONITE EOGAUDRYCERAS, THE NORTH-WESTERN CAUCASUS (RUSSIA), AND THEIR SUGGESTED MICROPOROSITY

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The permeability of the connecting ring in siphuncle of phragmocone-bearing cephalopods is inadequately known, although it must have played an important role in their buoyancy control. In ammonoid evolution the siphuncular structure went through essential transformation, but there is little information on the connecting rings in this respect. One can assume that the appearance of prochoanitic septal necks - first in the late ontogenetic stages of Carboniferous members of Goniatitina (see Druschits et al., 1976; Doguzhaeva and Mutvei, 1986) - was possibly accompanied by changes in connecting ring ultrastructure. The presence of the connecting ring in the posterior portion of the body chamber in *Phyllopachyceras* (Druschits and Doguzhaeva, 1974; Tanabe et al., 2005) and *Melchiorites* (Doguzhaeva, 1988) exhibited additional difference in siphuncle between "prochoanitic" ammonoids and Recent Nautilus. Connecting rings are more often preserved in Mesozoic ammonoids than in Palaeozoic, but in all ammonoids they were apparently organic, possibly chitinous, and post mortally pseudomorphed by phosphorus-containing minerals. Contrary to the living *Nautilus* and Spirula, in each chamber of most ammonoids the siphuncular surface lacked calcareous covering but was originally organic. Based on the ultrastructural examination of two ammonite genera (Aconeceras and Grammoceras) Mutvei with co-authors (Mutvei et al., 2004) suggested, for the first time, that tiny pore canals penetrated the connecting ring and provided for a permeability of siphuncle in ammonites.

The recent study was aimed to examine the preservation of connecting rings and to reveal ultrastructural features that could help to understand the permeability of siphuncle in ammonoids. For these purposes five shells of the Aptian lytoceratid *Eodaudryceras* Spath, 1927 from the north-western Caucasus were studied with the scanning electron microscope (SEM) and energy dispersive spectrometer (EDS) at the Swedish Museum of Natural History. The Aptian ammonoids from the north-western Caucasus are known to have exceptional preservation of the siphuncular structures (Druschits, Doguzhaeva, 1974, 1981). The material studied was collected in the R. Belaja Basin, Adygeya Republic, Russia, by Doguzhaeva.

The connecting rings were examined on their exposed surfaces after the shells had been crushed in a way to remove the calcite filling the chambers of the shell. High quality of the nacre preservation in the shell wall and septa indicates an exclusive preservation of studied ammonites.

EDS examination of *Eogaudryceras* demonstrated that the shell wall, septa and filling of siphuncle and chambers in this ammonoid contain Ca, C, O but lack P. The connecting rings additionally contain P, in places together with Fe, Mg or F. Inside the connecting

rings, close to its inner surface, there are globular clusters of crystals that show Fe and S. Thus, the post-mortem phosphatization selectively occurred in connecting rings but did not involve the shell wall, septa and filling of the chambers and siphuncle.

SEM examination revealed that the connecting ring consists of the inner and outer layers, each of which show indistinct lamination. Both are made either of globular aggregates (ca. 1 µm) of smaller globular particles, or of crystal-shaped units of calcium phosphate. In fractured planes the connecting rings show a "step-shaped" pattern that is similar to that of broken chitinous mandibles in dried condition in Recent squids. This might be an indirect indication of chitinous composition of the connecting rings. On the inner and outer surfaces the connecting rings exhibit numerous micro-pores, which create their microporosity in the studied genus. The diameter of each micro-pore is approximately 0.2 µm. The arrangement of phosphate particles around the micro-pores demonstrate that they apparently existed during pseudomorphing and therefore it is excluded that they represent traces of boring of micro-organisms. Besides, the micropores were not observed to penetrate the crystals or grains of phosphate as it happens in a case of boring. The boring traces are present in the nacreous layer in the shell wall. They are of about the same size as the structures that are supposed to be micro-pores but differ from the latter in being continued in distinct canals, mainly perpendicular to the crystal surface. Such canals are missing in the connecting rings. The innermost, thin layer of the connecting ring has a fibrous structure. The fibres are about 1.0 µm in diameter and have a parallel orientation transverse to the length axis of the siphuncle. The fibres are in some places closely spaced, in other places separated by narrow interspaces. The fibres running around the pores were observed.

To summarize: EDS and SEM analyses of the shell in the Aptian lytoceratid *Eogaudryceras* suggested, with high probably, that (1) the selective phosphatization of the connecting rings occurred due to their primary organic composition and significant role of phosphorus-accumulating bacteria in their fossilization, (2) the siphuncle possessed permeability evidently provided by microporosity of connecting rings with the micro-pores being about 0. 2 μ m in diameter.

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DEVELOPMENT OF THE EMBRYONIC SHELL STRUCTURE IN MESOZOIC AMMONOIDEA

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Micro- and ultrastructural features of the shell wall and tuberculate ornamentation at the embryonic stage of Mesozoic ammonoids were investigated on the basis of 14 Jurassic and Cretaceous species from Russia, Poland, Japan, and the United States. SEM observations of exceptionally well-preserved early Aptian Aconeceras embryonic shells (ammonitellae) from Simbirsk, Russia, confirm the previous observations of these shells from the same locality by Kulicki and Doguzhaeva (1994), and reveal that they can be classified into the following three groups with different wall microstructures: Group 1, with a thin (ca. 5 µm thick) double-layered shell wall, consisting of inner prismatic and outer homogeneous layers, the former of which is absent in the adapical portion and becomes thicker adorally, Group 2, with a three-layered shell wall terminating at the primary constriction, and consisting of inner prismatic, middle homogeneous, and outer prismatic layers, with minute tubercles on the outer layer, and Group 3, with a thick nacreous swelling (primary varix) on the anteroventral side near the constricted aperture. The middle homogeneous layer of the embryonic shells of Groups 2 and 3 is comparable to the outer homogeneous layer of embryonic shells of Group 1. It is made up of calcium carbonate (possibly calcite), and is comparable in its microstructure to amorphous calcium carbonate (ACC) that appears in the early larval shell of extant gastropods and bivalves (Weiss et al., 2002; Marxen et al., 2003).

In modern Nautilus and gastropods, embryonic or larval shell development is initiated by the secretion of a cup-shaped fully organic shell prior to the deposition of calcium carbonate (Arnold et al., 1987; Tanabe et al., 1997; Weiss et al., 2002; Marxen et al., 2003). This stage was not recognized in the material examined, but might exist in the Ammonoidea. Based on our observations and data from extant Nautilus and gastropods, we propose a model for the development of the embryonic shell structure of Mesozoic ammonoids, starting from secretion of an organic primary shell, followed by secretion of ACC and subsequent transformation of ACC into inner and outer prismatic layers, and ending in the deposition of a primary varix on the inner ventrolateral side just before the aperture. Minute tubercles begin to appear on the exposed surface of the embryonic shell after the formation of ACC. They show remarkable variation in their ultrastructure, size, shape, and distribution patterns on the embryonic shells of the Mesozoic ammonoids examined. In some cases, two contiguous tubercles cover a single prismatic tablet, and in other cases, a single large tubercle spreads over several contiguous prisms. These observations strongly suggest that the tubercles were formed by remote mineralization of calcium carbonate bearing ambient egg fluid, without the direct influence of an undifferentiated mantle (shell gland).

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COLEOID CEPHALOPODS FROM THE LATE CRETACEOUS NORTH EASTERN PACIFIC

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Coleoid cephalopods from the Late Cretaceous of North America were previously reported only from the Western Interior Seaway. However, for some time the existence of various coleoids from the Pacific coast is well-known to amateur collectors from Vancouver Island, Canada (Ludwigsen & Graham, 1997). More recently, Tanabe et al. (see the abstract in this volume) discovered well-preserved large jaws that can be assigned to new taxa of octobrachiate coleoids from the Santonian-Campanian strata of Vancouver Island. The material described herein came from the Upper Campanian Northumberland Formation (Nanaimo Group) exposed on the northern coast of Vancouver Island. The occurrence of phylogenetically distant taxa is striking.

Actinosepia canadensis Whiteaves 1897, a trachyteuthid vampyropod with a wide distribution in the Western Interior, exhibits numerous well-preserved and comparatively large gladii. A single poorly preserved specimen shows a kelaenid gladius, similar to those of *Tusoteuthis longa* Logan 1898 that is also widely distributed in the Western Interior. Another three-dimensionally preserved gladius shows remarkable similarities to *Boreopeltis soniae* Wade 1993 from the Upper Albian of Queensland (Australia). A concretion contains a comparatively large plesioteuthid gladius. Many orthoconic phragmocones preserved as coprolite remains are very similar to those of *Groenlandibelus rosenkranzi* (Birkelund 1956), a spirulid from the Campanian of Greenland. An outstanding record represents a three-dimensionally preserved butterfly-like gladius vestige. It is the first discovery of a cirroctopod in the fossil record at all.

The aim of the poster is to present preliminary conclusions about this peculiar coleoid fauna.

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LATE SILURIAN EVENTS AND THE CEPHALOPOD EXTINCTIONS IN THE PRAGUE BASIN

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The cephalopod fauna of the Prague Basin is well known since famous work of Joachim Barrande, who described and figured more than 600 species. It represents the most diversified Silurian cephalopod fauna over the world even when the Perunica was located at the northern margin of peri-Gondwana in temperate waters of the Rheic Ocean. In the Prague Basin, few cephalopods appear as calcareous shale replaced anoxic graptolite shale in early Wenlock. Rapid onset of diversified cephalopod fauna in the late Wenlock coincided with appearance of shallow water areas with carbonate sedimentation and suggests large-scale immigration followed by radiations in place. The cephalopods have became generally common since the late Wenlock in the Prague Basin, but the diversity of cephalopod faunas fluctuated markedly trough the time.

The main turnovers in cephalopod fauna correlate with extinction events previously recognized at graptolites and conodonts. The most prominent Silurian changes in sedimentary successions, faunas, and isotopic composition of seawater took place at Lundgreni (i.e. Mulde) Event (LE), Kozlovskii (i.e. Lau) Event (KE), and Silurian-Devonian boundary Event (SDE). These events have been explained by change in global ocean regime including eustatic oscillations, stratification and changes in productivity.

The latter events are accompanied by almost total local extinction of cephalopod fauna except few pelagic and long-ranging taxa. At the late Wenlock LE, the majority of disappearing taxa and evolutionary lines reappeared together with additional immigrants at the base of the Ludlow. No genera extinct, true extinction affected only few rare species. KE had similar effect; the extinction was followed by interval containing few survivals and subsequent rapid radiation and immigration. 23 species, 5 genera and one family became extinct. SDE was the most sever and comparable with prominent Phanerozoic cephalopod extinctions, many evolutionary lines disappeared fully from fossil record during the latest Přídolí; namely 2 orders, 9 families, more than 10 genera and over 32 species. The recovery after SDE is connected with appearance of low diversified fauna consisting mostly of few in place survival clades.

The cephalopod extinctions coincided with events previously recognised at graptolites and conodonts. Nevertheless, the severity of extinctions at graptolites, conodonts and cephalopods do not correlate; similarly there is no clear correlation with benthos. The cephalopod extinction in all cases coincided with beginning positive carbon isotope excursion. There is no correlation between severity of extinction and carbon isotope values reflecting change in primary production, although the KE posses the strongest carbon isotope Phanerozoic excursion, the number of extinct taxa is much lower than at SD Event. In addition, rapid eustatic oscillation coincided with extinctions; the extinction interval occurs during high stand and/or early regressive tract while full recovery falls into low stand. All three extinctions are followed by interval with few survivals and later by rapid onset of re-established cephalopod fauna. The cephalopod fauna recovery drops behind graptolites or benthos and does not took place at certain position to the carbon isotope curve (as extinction). The recovery depends at cephalopod immigrations from tropical platforms to the temperate peri-Gondwanan area. The LE and KE are followed by radiation of few survivals taxa, Lazarus taxa and exotic immigrants; the total diversity become rapidly higher than before the extinction.

The recovery after the SDE is represented by low diversity cephalopod fauna consisting of lines survival extinction; only one genus could be regarded as immigrant. The SDE Event was severest not due to strongest change in ocean chemistry or more rapid eustatic oscillation, but probably due to large-scale palaeogeographic change. The Baltica, Laurentia and Avalonia formed Old Red continent during latest Silurian and consequently shallow tropical sea areas rapidly decrease, what caused local extinction of several taxa, which occurs during Přídolí only in the Prague Basin. The SDE strongly affected that fauna of the Prague Basin, but in the contrary to the previous events there was not a source area of immigrants. Thus, few cephalopod lines surviving the SDE in the peri-Gondwana gave rise to certain Early Devonian cephalopod clades appearing since latest Lochkovian (egg. Nephriticeratidae, Rutoceratidae). North belt of peri-Gondwana become evolutionary centre of cephalopods during Přídolí instead of former continents grouping now Old Red continent. Thus except eustatic oscillations and changes in primary production, the global palaeogeography should be considered as a prominent factor of long-term evolution of cephalopods.

EMBRYONIC SHELLS IN SOME LECHRITROCHOCERATIDS (NAUTILOIDEA, BARRANDEOCERINA)

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Nautiloids of the family Lechritrochoceratidae Flower *in* Flower et Kummel, 1950 form an important Silurian group of the suborder Barrandeocerina. They are considered by some palaeontologists (Dzik and Korn 1992) as possible ancestors of Nautilida and are characterised by a cyrtocone to low-spired dextrally torticone ribbed shell. The cylindrical narrow siphuncle is located ventrally from the centre, and retractor muscle scars are situated laterally. Lechritrochoceratids were widely distributed in the tropical and subtropical shallow seas of Laurentia, Baltica and Perunica; representatives of some species are locally abundant. However, published information concerning their embryonic shell is sporadic due to their very rare preservation. More or less complete embryonic shells have been discovered for four species of this family. Regrettably, only its outer morphology is known.

Barrande (1866, pl. 199. fig. 44, 45) illustrated embryonic shell in *Cyrtoceras cognatum*, later selected as the type species of the genus *Callocyrtoceras* Foerste, 1936. The genus, commonly attributed to Orthocerida, very probably belongs to Lechritrochoceratidae. Slightly curved embryonic shell is about 5 mm long, and almost circular in cross section. The diameter of the protoconch is about 1.5 mm. Sculpture is characterised by densely spaced longitudinal lirae, but transverse sculpture is hardly discernible. The start of annulation is interpreted as the beginning of the post-hatching phase. The shell shape and sculpture is almost identical to the morphology of newly discovered an early juvenile stage of *Peismoceras pulchrum* (Barrande, 1865) (Shary collection, Museum of Comparative Zoology, Harvard) and it confirms the position of *Callocyrtoceras* within the same family. Well-preserved sculpture in *P. pulchrum*, documented by use of SEM, is characterised by dominating longitudinal lirae. The embryonic shell surface closely resembles the surface illustrated in the Lower Carboniferous pseudorthoceratids *Reticycloceras* Gordon, 1960 and *Euloxoceras* Milller, Dunbar and Condra, 1933 (Kröger and Mapes 2004).

A complete juvenile shell of a cyrtocone assigned to *Callocyrtoceras*(?) cf. *simulans* (Barrande, 1865) comes from Gotland (deposited in the Museum of Natural History, Stockholm). Although the embryonic shell is damaged by dislocation, it shows characteristic features observed in above-mentioned lechritrochoceratids. In comparison with the type species of *Callocyrtoceras* longitudinal lirae are not so densely spaced.

Schematic drawing published by the author (Turek 1975) shows early juvenile growth stage in the type species of *Kosovoceras* Turek, 1875 - K. *sandbergeri* (Barrande, 1865). The embryonic shell is very slightly curved bearing fine reticulate sculpture. Although the author has at his disposal several hundred specimens from different localities, some of them in very good state of preservation, unfortunately the protoconch has not been

observed. The termination of the first growth stage is characterised by the sudden occurrence of annulations.

Small slightly cyrtocone embryonic shells of the representatives Lechritrochoceratidae are very similar in size (maximum diameter about 3 mm, the lengh 4.5–10 mm). Its only slightly curved shape is in contrast with the perfect coiling of the other part of the shell in torticone forms. The apex is bluntly rounded, cicatrix due preservation has not been observed. Nepionic constriction has not been ascertained. Appearance of annuli on the shell is interpreted as the beginning of posthatching phase. Longitudinal lirae are invariably the dominating feature of the embryonic surface sculpture. Limited data concerning embryonic shells, fundamental for tracing phylogenetic and systematic relationship of lechritrochoceratids, are in this way extended. Their evaluation depends on additional comparative study of this feature in the related nautiloids. The shape of embryonic shell leads to search ancestors of lechritrochoceroids among Upper Ordovician nautiloids possessing curved shells.

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LATERALITY OF BEHAVIORAL AND MORPHOLOGICAL FEATURES IN SEPIA LYCIDAS

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We examined experimentally whether handedness in prey capture of the marine invertebrate, Sepia lycidas, whose body shape appears superficially symmetrical was detectable or not, using 19 cuttlefish juveniles twice from both behavioral and morphological points of view. In the first experiment in which 7 individuals were used from May to Octorber 2002, two kinds of prey (shrimp and mysis) were shown to them and the same trends of capture behaviors toward the different kind of preys were given. Significant difference was present between the frequency of right and left attacks in every individual, suggesting that there exists the handedness of each individual in the prey capture behavior. Each cuttlebone showed warp toward right or left and its warp direction was in accord with its behavioral handedness. In the second experiment in which 12 individuals were used from may to Octorber 2006 and only one kind of pray was given, same result about the handedness as in the first one was gained. By the examination of cuttlebone warp, it seems possible to determine the handedness of each individual. Byrne et al. (2004) found the lateralized eye use and populational lateralization in Octopus vulgaris. The present study clearly showed the laterality for behavioral and morphological features in the cephalopods which have been considered to have superficially symmetrical body shape.

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GENETIC SEPARATION OF THREE SPECIES AMONG THE STHENOTEUTHIS OUALANIENSIS- COMPLEX

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Sthenoteuthis oualaniensis is an oceanic squid distributed in tropical and sub-tropical Indo-Pacific. S. oualaniensis is generally recognized by a large dorsal mantle photophore and fusion of the funnel-mantle locking cartilages. However, considerable morphological variation occurs within S. *oualaniensis*; at present, the following three main forms of S. oualaniensis are recognized in the Indo-Pacific: the dwarf photophoreless form, the middle-sized form, and the giant late-maturing form. In this study, allozym differentiation and mitochondrial cytochrome oxidase I (COI) gene sequence data of 3 forms of S. oualaniensis were analyzed to resolve the controversy regarding their taxonomic classification. Thirty-seven putative enzyme-coding loci were examined in 6 ommastrephid squids (included the 3 forms). The electophoretic patterns of OPDH and 6PGD revealed that the three forms are clearly separated on the locus encoding to these enzymes, and indicated that the three forms of S. oualaniensis exist without reproductive mixing. The COI sequence data (603 bp) were analyzed in 16 ommastrephid squids (included the 3 forms). The percentage of nucleotide substitution between the dwarf and giant forms, the dwarf and middle forms, and the middle and giant forms were 6.3%, 8.4%, and 8.8%, respectively. Since the percentage of nucleotide substitution of COI sequence within the species was low (<1.3%: Wakabayashi unpublished data), it suggests that the three forms are clearly distinct. A dendrogram based on Nei's genetic distance from the allozyme differentiation data and a neighbor-joining (NJ) phylogenetic tree based on Kimura's two-parameter distance from the COI sequence data showed that the dwarf and giant forms were more closely related than to the middle form.