

# *8<sup>th</sup> International Symposium Cephalopods – Present and Past*

August 30 – September 3, 2010

## Abstracts Volume

University of Burgundy & CNRS  
Dijon - France

<http://www.u-bourgogne.fr/cephalopods/>



**BIOGÉOSCIENCES**



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# *8<sup>th</sup> International Symposium Cephalopods – Present and Past*

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# *8<sup>th</sup> International Symposium Cephalopods – Present and Past*

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**August 31 - September 3, 2010**  
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## **Program**

.....  
**University of Burgundy \_ CNRS**

**Dijon (France)**  
.....





# Brief schedule of the 8<sup>th</sup> International Symposium, Cephalopods – Present and Past

## Tuesday, August 31, 2010

### Registration

### Opening address

### Social events –

- Photo
- Icebreaker

### Scientific events -

- Oral Sessions:           Ontogeny  
                                  Anatomy & Morphology
- Poster Session

## Wednesday, September 1, 2010

### Social events –

- Wine Testing Party

### Scientific events -

- Oral Sessions:           Behavior, Ecology & Paleoecology
- Poster Session

## Thursday, September 2, 2010

### Presentation of the candidates for the organization of the next International Symposium, Cephalopods – Present and Past (9ISCPP)

### Social events –

- Farewell Dinner

### Scientific events –

- Oral Sessions:           Phylogeny & Systematic  
                                  Evolutionary Patterns and Processes: from Micro- to Macroevolution  
                                  *Nautilus* as an endangered species
- Poster Session

## Friday, September 3, 2010

### Closing Address

### Vote for the organizer of the 9ISCPP

### Scientific events –

- Oral Sessions:           Paleobiogeography & Biostratigraphy  
                                  Mass Extinctions and their Aftermaths
- Poster Session

## Saturday, September 4, 2010

**Fieldtrip #1** (optional): from 8:00am to 7:00pm

## Sunday, September 5, 2010 to Wednesday, September 8, 2010

**Fieldtrip #2** (optional): departure September 5, 8:00am, return September 8, 7:00pm





# Detailed schedule of the symposium

**Tuesday, August 31, 2010**

9:00am. Starting of Registration at Symposium venue (University of Burgundy, Main Campus, Building Gabriel)

**10:00am-10:30am • Opening address and general information**

P. NEIGE & I. ROUGET

**10:30am-11:15am • Keynote lecture**

**The molluscan shell: formation, origin, evolution**

**F. MARIN (CNRS, Dijon – France)**

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## ONTOGENY

*Chairs: N.H. LANDMAN & K. TANABE*

11:15am-11:30am

Morphogenesis in cephalopod embryos: description of slow changes using motion pictures

S. VON BOLETZKY

11:30am-11:45am

Internal Features of the Ammonitellas of some Tornoceratids from the Cherry Valley Limestone, New York State, U. S. A.

S.M. KLOFAK, N.H. LANDMAN

11:45am-12:00pm

Quantitative aspect of oocyte follicular epithelium development in two ecological groups of octopod

C.M. NIGMATULLIN

**12:00pm-2:00pm • Lunch**

2:00pm-2:15pm

Evo-Devo in early Ammonoidea: links between embryonic and post-embryonic ontogeny?

K. DE BAETS, C. KLUG, D. KORN

2:15pm-2:30pm

Ontogeny of *Didymoceras* Hyatt, 1894, in the Late Cretaceous (Middle and Upper Campanian) U. S. Western Interior

S.D. JORGENSEN, N.L. LARSON, N.H. LANDMAN, W.A. COBBAN

2:30pm-2:45pm

The evidence of the maturity of genus *Angulithes* Montfort, 1812 (Cretaceous–Oligocene, Nautiloidea)

J. FRANK

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## ANATOMY & MORPHOLOGY

*Chairs: V. BIZIKOV & C. KLUG*

2:45pm-3:00pm

Did belemnoid coleoids have suckers?

D. FUCHS, S. VON BOLETZKY, H. TISCHLINGER

3:00pm-3:15pm

*Sepia* type of connecting rings

L.A. DOGUZHAEVA, H. MUTVEI

3:15pm-3:30pm

Pseudosutures in *Baculites mariasensis*

K. POLIZZOTTO

### 3:30pm-4:00pm • Afternoon Break

4:00pm-4:15pm

The microstructure and mineralogy of anaptychus-, aptychus-, and rhynchaptychus-type lower jaws in the Cretaceous Ammonoidea

K. TANABE, N.H. LANDMAN, I. KRUTA

4:15pm-4:30pm

Portable XRF instruments in the elemental analysis of ammonite shell and matrix

N.L. LARSON, L.A. LARSON, J. SHERMAN

4:30pm-4:45pm

Raup's shell coiling ammonoid morphospace, geometric alternatives and impact on disparity estimates

S. GERBER

4:45pm-5:00pm

A morphometric method for simultaneously describing whorl shape and its ontogenetic change in ammonoids

T. UBUKATA

5:00pm-5:15pm

On the deepwater origin of teuthoid coleoids

A.I. ARKHIPKIN, V.A. BIZIKOV

5:15pm-5:30pm

Empirical relationships between shell expansion and septal spacing in Devonian ammonoids

M. HUBERS, R.T. BECKER

5:30pm-5:45pm

Well preserved buccal mass in two Late Cretaceous ammonites

I. KRUTA, I. ROUGET, N.H. LANDMAN, P. TAFFOREAU, F. CECCA

### 5:45pm-6:00pm • Outdoor photo of the participants

### 6:00pm-7:00pm • Icebreaker and Poster Session

**Wednesday, September 1, 2010**

## **BEHAVIOR, ECOLOGY & PALEOECOLOGY**

*Chairs: N.H. LANDMAN & G. BELLO*

9:00am-9:15am

Modifications and adaptations of arm use in *Octopus vulgaris*

M.J. KUBA, R.A. BYRNE, J. RICHTER, L. ZULLO, B. HOCHNER

9:15am-9:30am

Visual control of precision single arm use by *Octopus vulgaris*

T. GUTNICK, R.A. BYRNE, B. HOCHNER, M.J. KUBA

9:30am-9:45am

Constructing a language from skin displays of squid

J.A. MATHER

9:45am-10:00am

Evolutionary trends in sperm transfer and storage in cephalopods

A. ARKHIPKIN, V. LAPTIKHOVSKY, C. NIGMATULLIN

10:00am-10:15am

Seasonal trends of reproductive cycle of *Octopus vulgaris* in two environmental distinct coastal areas

S. LOURENÇO, A. MORENO, J. PEREIRA

10:15am-10:30am

New insights into the ecology and evolution of the *Ceratites* fauna of the Muschelkalk Basin from phylogenetic analysis

A.J. McGOWAN

**10:30am-11:00am • Morning Break & Poster Session**

11:00am-11:15am

Population structure of Hawaiian Octopuses : *Octopus cyanea* (Gray, 1849) and *O. oliveri* (Berry, 1914)

P.J. SIMION, C.E. BIRD, N. VELASCO, R.J. TOONEN

11:15am-11:30am

Abundance of pelagic cephalopods in the central Mediterranean Sea (Strait of Messina and southern Tyrrhenian Sea): information obtained from swordfish diet

T. ROMEO, C. PEDÀ, P. BATTAGLIA, P. CONSOLI, A. POTOSCHI, F. ANDALORO

11:30am-11:45am

A synthesis on Hg bioaccumulation in cephalopods

P. BUSTAMANTE, T. CHOUVELON, T. LACOUÉ-LABARTHE, J. SPITZ, F. CAURANT

11:45am-12:00pm

Isotopic signature for depth habitat of the late Cretaceous Nautiloid, *Eutrephoceras*

K. MORIYA, K. TANABE, H. NISHI, H. KAWAHATA

12:00pm-12:15pm

Paleobiological interpretation of the early Turonian (Late Cretaceous) *Pseudaspidoceras flexuosum* (Cephalopoda: Ammonitina)

C. IFRIM

12:15pm-12:30pm

Preferential peeling: ammonoid versus nautiloid shells from the Upper Carboniferous of Texas, USA

R. WANI, R.H. MAPES

**12:30pm-2:00pm • Lunch**

**2:00pm-2:45pm • Keynote lecture**

**Mode of Life and Habitat of *Scaphites***

**N.H. LANDMAN (AMNH, New York – USA)**

2:45pm-3:00pm

Observations of *Baculites* from the lower Campanian, Western Interior

N.L. LARSON, S.D. JORGENSEN, J. SIME, M.A. WILSON, L.A. LARSON, P.D. TAYLOR

3:00pm-3:15pm

New ammonite data from the Lower Cretaceous Puez key-section in the Dolomites (Southern Alps; N-Italy; FWF project P20018-N10)

A. LUKENEDER

3:15pm-3:30pm

Taphonomy of dense concentrations of juvenile ammonoids in the Mancos Shale, east-central Utah, USA

D.A. STEPHEN, K.G. BYLUND, H.J. CARTER, P. GARCIA

3:30pm-3:45pm

Devonian and Carboniferous Ammonoid faunas in the Uralian Ocean: paleoenvironments and migration pathways

S. NIKOLAEVA, V. KONOVALOVA, M. BOIKO

**4:00pm • Departure to Beaune for the Wine Testing Party**

**Departure from the entrance of the Conference Hall, University of Burgundy**

**Return Dijon circa 7:30pm**

9:00am-9:45am • Keynote lecture

Evolution of the shell in Coleoidea

V.A. BIZIKOV (Russian Federal Research Institute of Marine Fisheries and Oceanography, Moscow – Russia)

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## PHYLOGENY & SYSTEMATIC

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*Chairs: M. YACOBUCCI & I. ROUGET*

9:45am-10:00am

*Rhabdobelus* biodiversity from the Toarcian of Crimea and the problem of *Rhabdobelus-Pseudobelus* relationship

A.P. IPPOLITOV

10:00am-10:15am

*Chalalabelus* finds from the Middle Volgian of Moscow city and the nature of enigmatic Diplobelida

A.P. IPPOLITOV, V.A. BIZIKOV, M.A. ROGOV

10:15am-10:30am

A groenlandibelid spirulid from the Campanian/Maastrichtian of Vancouver Island (Canada)

D. FUCHS, H. KEUPP

### 10:30am-11:00am • Morning Break & Poster Session

11:00am-11:15am

Is the Endocerida polyphyletic? – A possible new order of lower Palaeozoic nautiloids

D.H. EVANS, A.H. KING

11:15am-11:30am

Reconstruction of the body plan and possible way of life of ancient nautiloid cephalopods

V.A. BIZIKOV, B. KRÖGER

11:30am-11:45am

Meta-analysis of character utility and phylogenetic information content in cladistic studies of ammonoids

M.M. YACOBUCCI

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## EVOLUTIONARY PATTERNS AND PROCESSES: FROM MICRO- TO MACROEVOLUTION

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*Chairs: E. FARA & D. KORN*

11:45am-12:00pm

Devonian pearls and ammonoid-endoparasite coevolution

C. KLUG, K. DE BAETS, D. KORN

12:00pm-12:15pm

The chance of evolutionary success - the case of the oldest (Tournaisian) ceratitoid ammonoids (Prodromitidae, Tornoceratina)

R.T. BECKER

12:15pm-12:30pm

Recurrent patterns of covariation in ammonoid shell characters: how do they relate to growth dynamics?

S. URDY, N. GOUDEMANT, H. BUCHER, C. MONNET

### 12:30pm-2:00pm • Lunch

2:15pm-2:30pm

Evolution and morphologic trends in the Upper Cretaceous belemnite family Belemnitellidae Pavlow, 1914.

M. KOSTAK

2:30pm-2:45pm

Evolutionary pattern in the Upper Campanian (Upper Cretaceous) belemnites – an example of parallel evolution

Z. REMIN

2:45pm-3:00pm

Systematics, phylogeny and adaptive radiation in the squid of family Ommastrephidae

C.M. NIGMATULLIN

3:00pm-3:15pm

The phylogenetic distribution of extinctions in Early Jurassic ammonite communities

C. HARDY, E. FARA, P. NEIGE, C. MEISTER, J.L. DOMMARGUES

3:15pm-3:30pm

Temporal patterns in disparity and diversity of the Jurassic ammonoids of southern Germany

M. SIMON, D. KORN, S. KOENEMANN

3:30pm-3:45pm

Large-scale morphological evolutionary trends of Acrochordiceratidae (Ammonoidea, Middle Triassic) and Cope's rule

C. MONNET, H. BUCHER, J. GUÉX, M. WASMER

**3:45pm-4:15pm • Afternoon Break**

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## **NAUTILUS AS AN ENDANGERED SPECIES**

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*Chairs: N.H. LANDMAN*

4:15pm-4:30pm

Is *Nautilus* an endangered taxon?

N.H. LANDMAN, R.H. MAPES

4:30pm-4:45pm

*Nautilus pompilius* fishing and population decline in the Philippines; a comparison with an unexploited Australian *Nautilus* population

A.J. DUNSTAN, O. SALIH, J. MARSHALL

4:45pm-5:00pm

Record of live specimens of Emperor Nautilus, *Nautilus pompilius* (Linnaeus 1758) from the east Andaman Sea, Thai waters

J. NABHITABHATA, K. WONGKAMHAENG

5:00pm-5:15pm

Nautilid conservation and international trade

P.S. De ANGELIS

5:15pm-5:30pm

Evolution and formation of *Nautilus macromphalus* nacre: biochemistry and proteomic of the shell organic matrix

B. MARIE, F. MARIN

**5:30pm-6:00pm • Presentation of candidates for the organization of the next International Symposium, Cephalopods – Present and Past (9ISCPP)**

**7:00pm • Farewell Dinner at the 'Cellier de Clairvaux', Dijon**

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## PALEOBIOGEOGRAPHY & BIOSTRATIGRAPHY

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*Chairs: M. KOSTAK & P. NEIGE*

9:00am-9:15am

Early Carboniferous palaeogeography based on ammonoids

D. KORN

9:15am-9:30am

Controlling factors of the paleogeographic distribution of nautiloid cephalopods along the Northern Gondwana margin during the Silurian: a case study from the Carnic Alps (Austria)

K. HISTON

9:30am-9:45am

A macroecological study of early Pliensbachian ammonites from western Tethys and adjacent areas

E. FARA, J-L. DOMMERGUES, C. MEISTER, B. VRIELYNCK

9:45am-10:00am

Paleobiogeographical changes in ammonite faunas during the Pliensbachian-Toarcian interval (Early Jurassic)

G. DERA, P. NEIGE, J-L. DOMMERGUES, A. BRAYARD

10:00am-10:15am

Migration pathways of the late Campanian and Maastrichtian shallow facies ammonite *Sphenodiscus* in North America

C. IFRIM, W. STINNESBECK

10:15am-10:30am

Ammonite, inoceramid and nannofossil biostratigraphy across the Turonian–Coniacian boundary in the Aquitaine and Vocontian basins (France) and Diego Basin (Madagascar)

F. DIEBOLD, P. BENGTON, J.A. LEES, I. WALASZCZYK

### 10:30am-11:30am • Morning Break & Poster Session

11:30am-11:45am

Dienerian (Early Triassic) ammonoid successions of the Tethys: preliminary results from Pakistan and India

D. WARE, H. BUCHER, T. BRÜHWILER, N. GOUEMAND

11:45am-12:00pm

Co-occurrence of ammonite and radiolarians from the Upper Cretaceous Izumi Group in southwestern part of Awaji Island, Hyogo Prefecture, southwest Japan

K. YOSHINO, A. MATSUOKA

12:00pm-12:15pm

Taxonomic and biostratigraphic analyses of the genus *Amaltheus*, Late Pliensbachian (Early Jurassic) ammonite, from East Asia

K. NAKADA, C. MEISTER, A. MATSUOKA

12:15pm-12:30pm

Cephalopods from the Jurassic 'Minette' Ironstone Formation of Luxembourg and Lorraine (NE Paris Basin): an update

R. WEIS, N. MARIOTTI, A. DI CENCIO, A. FABER, D. FUCHS, S. GUÉRIN-FRANIATTE

### 12:30pm-2:00pm • Lunch

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## MASS EXTINCTIONS AND THEIR AFTERMATHS

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*Chairs: A. BRAYARD & D. KORN*

2:00pm-2:15pm

Ammonite mass mortality (200 000 000 !!! specimens) as proxy for the Carnian Crisis (Taurus, Turkey) – 3D modelling of the Carnian Crisis (FWF Project P22109-B17)  
S. MAYRHOFER, A. LUKENEDER

2:15pm-2:30pm

The ammonoid recovery after the end-Permian mass extinction: evidence from the Iran-Transcaucasia area, Siberia, Primorye, and Kazakhstan  
Y.D. ZAKHAROV, N. MOUSAVI ABNAVI

2:30pm-2:45pm

Evolutionary significance of cephalopod egg size during mass extinctions  
V. LAPTIKHOVSKY, M. ROGOV, S. NIKOLAEVA, A. ARKHIPKIN

2:45pm-3:00pm

The Devonian Nekton Revolution  
C. KLUG, B. KRÖGER, W. KIESSLING, G.L. MULLINS, T. SERVAIS, J. FRYDA, D. KORN, S. TURNER

3:00pm-3:15pm

Extinction of the ammonoids: Chixculub impact or Deccan flood basalt volcanism?  
S. GOOLAERTS

**3:30pm-4:00pm • Closing Session, Vote for the organizer the 91SCPP**

## Poster Session

Updated biostratigraphy of the Agrio Formation, Early Cretaceous of the Neuquen Basin, Argentina  
B. AGUIRRE-URRETA & P.F. RAWSON

The role of cephalopods as a vector for the transfer of cadmium to swordfish in the Mediterranean Sea  
S. ANCORA, N. BIANCHI, S. FORTINO, M.C. FOSSI, F. ANDALORO, T. ROMEO

Spectral analysis of Late Anisian (Middle Triassic) ammonoid faunas from Prezzo Limestone (Southern Alps)  
M. BALINI

Cladistic treatment of continuous characters: Example from representatives of Hildoceratoidea, Hyatt 1967  
J. BARDIN, I. ROUGET, F. CECCA

Late Albian (Early Cretaceous) ammonites (Cephalopoda, Ammonoidea) from the Provincial Formation of Cuba  
R. BARRAGÁN-MANZO & O. SZIVES

A biogeographical quantitative analysis of early triassic ammonoid faunas using bootstrapped spanning



networks

A. BRAYARD, G. ESCARGUEL, H. BUCHER

Good genes and good luck: ammonoid diversity and the end-Permian mass extinction

A. BRAYARD, G. ESCARGUEL, H. BUCHER, C. MONNET, T. BRUHWILER, N. GOUDEMANT, T. GALFETTI, J. GUÉX

Coniacian (Late Cretaceous) ammonoid fauna of eastern Utah, USA

K.G. BYLUND & D.A. STEPHEN

Early Triassic ammonoids from the Pahvant Range, Utah, USA

K.G. BYLUND, D.A. STEPHEN, A. BRAYARD, H. BUCHER, J. JENKS, R.D. McSHINSKY

Testing indirect effects of fishing on the European squid *Loligo vulgaris* (Lamarck 1798)

M. CABANELLAS-REBOREDO, J. ALÓS, M. PALMER, B. MORALES-NIN, R. GRÄEL

The Floian eothinoceratid radiation in northwestern Argentina (southern Central Andean Basin)

M. CICHOWOLSKI & L.F. MARENGO

Stable isotopes in well-preserved shells of a methane seep fauna from the Upper Cretaceous (Campanian) Pierre Shale, U.S. Western Interior

J.K. COCHRAN, N.H. LANDMAN, P.J. HARRIES, N.L. LARSON, M.P. GARB, S.M. KLOFAK, C. MYERS, J. BREZINA

*Crioceratites* and *Pseudothurmannia* (Ammonoidea) from the uppermost Hauterivian (Lower Cretaceous) of the Mediterranean region. Taxonomic and stratigraphic considerations

M. COMPANY, J. SANDOVAL, J.M. TAVERA

Global changes recorded in the Oxfordian Ammonite associations (Paris Basin, France)

P. COURVILLE & D. MARCHAND

Palaeobiology, stratigraphy and systematics of Early Emsian Ammonoidea from the Hunsrück Slate (Rhenish Massif, Germany)

K. DE BAETS, C. KLUG, D. KORN, C. BARTELS, M. POSCHMANN

Olcostephanidae (Cephalopoda, Ammonoidea) from the Taraises Formation (upper Valanginian, Peregrinus Zone) from Durango State, Mexico

C. GONZÁLES-ARREOLA & R. BARRAGÁN-MANZO

Alive and fossil Cephalopods in the National Nature Reserve of Haute-Provence: how to protect and make discover this exceptional heritage

M. GUIOMAR

An Alpine immigrant: *Phragmoceras* Broderip, 1839 from the Silurian of the Carnic Alps (Austria)

K. HISTON

On the systematics of Lytoceratoidea (Jurassic-Cretaceous)

R. HOFFMANN

Morphometry and palaeopathology of Orthoceratida from the Middle and Upper Devonian of the Dra Valley (SW Morocco)

B. HUMBERG & R.T. BECKER

Anatomy and function of spines in post-Triassic ammonites

C. IFRIM, W. STINNESBECK, P. BENGTSON, G. SCHWEIGERT

*Stramentum* on ammonites from Mexican Late Cretaceous Platy Limestones

C. IFRIM, F.J. VEGA, W. STINNESBECK

Age determination using stylets in genus *Eledone*

Z. IKICA, S. KRSTULOVIC SIFNER, A. JOKSIMOVIC, M. PETRIC

Tethyan affinity of new Smithian (Early Triassic) ammonoids from Crittenden Springs, Elko County, Nevada (USA)

J.F. JENKS, A. BRAYARD, T. BRÜHWILER, H. BUCHER

Dienerian (Early Triassic) ammonoids from the Candelaria Formation, Mineral County, Nevada (USA)  
J. JENKS, D. WARE & H. BUCHER

First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany)  
C. KLUG, G. SCHWEIGERT, D. FUCHS, G. DIETL

Parallel evolution controlled by adaptation and covariation in ammonoids (Cephalopoda)  
C. KLUG, K. DE BAETS, C. MONNET

Middle Permian (Roadian) Cephalopods of the Volga-Urals Region  
T.B. LEONOVA, I.S. BARSKOV, V.A. KONOVALOVA

Early ontogeny of a Late Carboniferous Bactritoid (Cephalopoda) from Kansas, USA  
R.H. MAPES, S. von BOLETZKY, L. DOGUZHAEVA

New records of Early Middle Jurassic belemnites in the French Subalpine Basin and their paleobiogeographic relevance  
N. MARIOTTI, R. WEIS, A. CLEMENT, A. DI CENCIO

Central Russian ammonites at the Jurassic / Cretaceous boundary  
V. MITTA & Y. BOGOMOLOV

Taxonomic revision of *Puzosia*, ammonite of the Lower Cenomanian: *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841), a species not announced in the Onilahy sector of the Morondava Basin (Madagascar)  
H. RANDRIANALY & A.H. RASOAMIARAMANANA

Changes in some Cretaceous ammonoid assemblages (planispirals versus heteromorphs) and their link to palaeoceanography and climate  
S. REBOULET, F. GIRAUD, E. MATTIOLI, B. PITTET, B. GRESELLE, A. CARPENTIER

*Fusiteuthis polonica* – an intergeneric belemnite hybrid; proofs and discussion  
Z. REMIN

Ammonite jaws at the base of the Danian (?) Hornerstown Formation, Monmouth County, New Jersey  
R. ROVELLI, M.P. GARB, N.H. LANDMAN

Latest Toarcian-Earliest Bajocian (Jurassic) Grammocerotinae (Hildoceratidae, Ammonitina) of the western Tethys: palaeobiogeographic significance  
J. SANDOVAL, M.H. HENRIQUES, M. URETA, R. CHANDLER

*Aturia* from the Miocene Paratethys: an exceptional window to nautilid habitat and lifestyle  
J. SCHLÖGL, R. CHIRAT, V. BALTER, M.M. JOACHIMSKI, N. HUDÁKOVÁ, F. QUILLÉVÉRE

Quantification of ontogenetic change in Triassic ammonoids  
M. SIMON & D. KORN

Late Cretaceous nautiloids from eastern Utah, USA  
D.A. STEPHEN & K.G. BYLUND

New and additional records of Late Cretaceous octobrachiata coleoid jaws from the Western Interior Seaway and the Northwestern Pacific  
K. TANABE, N.L. LARSON, Y. HIKIDA

Stable nitrogen isotope analysis of soft and hard tissues of three modern coleoid species *Sepia officinalis*, *Sepia latimanus*, and *Spirula spirula*  
R. TSUDA, Y. CHIKARAISHI, N. OGAWA, Y. KASHIYAMA, N. OHKOUCI, K. TANABE

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# *8<sup>th</sup> International Symposium Cephalopods – Present and Past*

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**August 31 - September 3, 2010**  
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## **Abstracts**

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**University of Burgundy \_ CNRS**

**Dijon (France)**  
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**Abstracts of oral sessions**  
**(authors in alphabetical order)**

## On the deepwater origin of teuthoid coleoids

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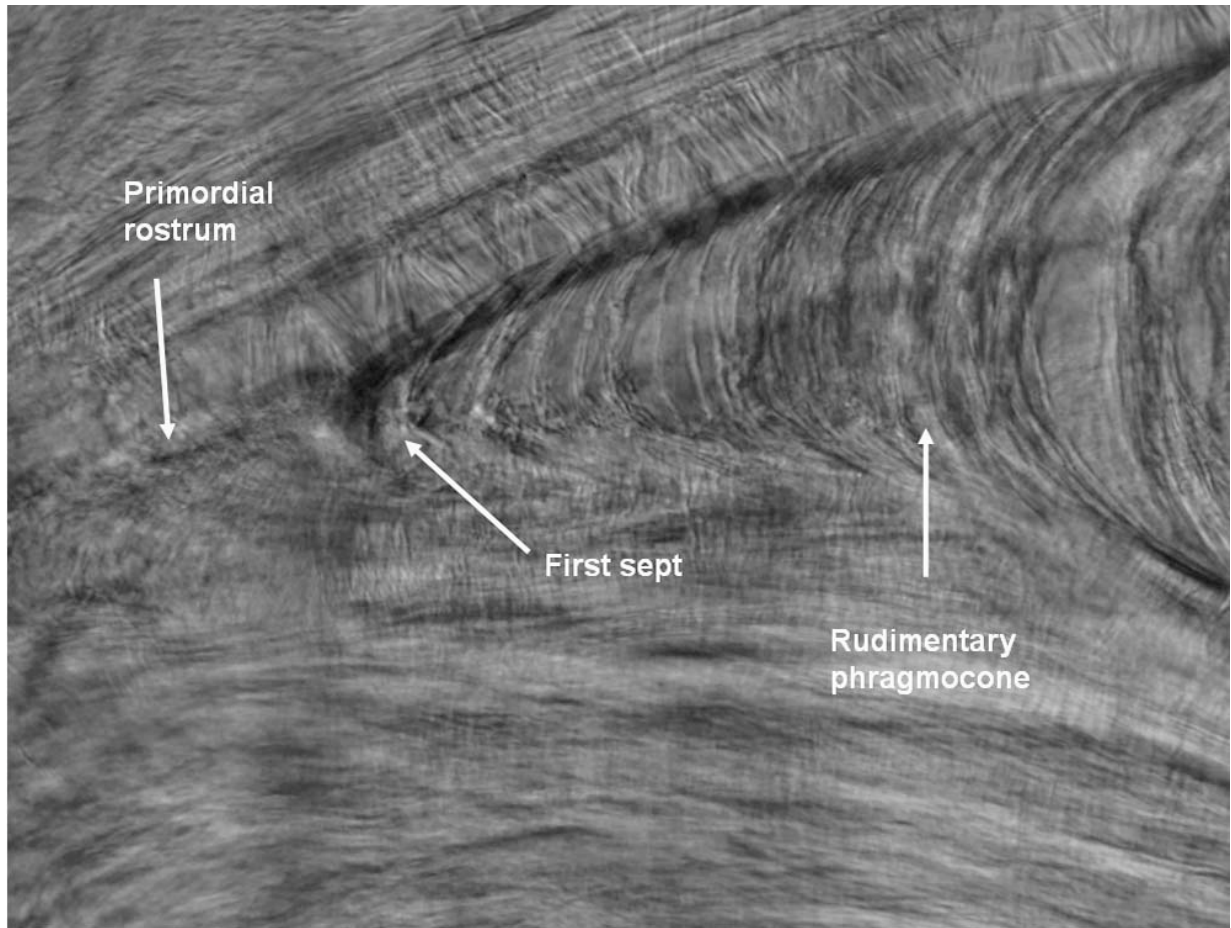
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It is generally accepted that evolution of the shell in teuthoid coleoids followed the reduction of the gas-filled phragmocone, decalcification of the shell, and development of the rod-like proostracum (Naef, 1921/23). The outcome of this process, the chitinous gladius, represents one of the most characteristic features of squids. Acquisition of the gladius enabled coleoids to develop several life forms based mainly on the 'rocket propulsive movement', from fast nektonic predators (Ommastrephidae, Onychoteuthidae) to slow planktonic forms (Cranchiidae, Histioteuthidae), that are competitive with pelagic fishes.

Squids lack the phragmocone as such. However, Steenstrup (1881) and Pfeffer (1912) described septa-like layers in the gladius cone of recent Gonatidae. Chun (1910) assumed that similar septa in Chiroteuthidae were homologous to the transverse septa in the phragmocone of other cephalopods. Naef cautiously suggested that 'the homology between these structures and the phragmocone can only be general'. However, Bizikov (2008) concluded that these structures could not be a rudiment of phragmocone but developed later, as they lack the siphon and mural attachment of septa.

We re-examined the gladius of *Illex argentinus* (Ommastrephidae) and found septa-like layers in the apical part of its cone that have strong resemblance to the phragmocone of extinct belemnoids (Fig. 1). The first septum is situated close to the cone apex, with the primordial rostrum forming at its other end. These septa-like layers were separated from the cone walls by a distinct layer. Based on these features, these septa may represent a decalcified rudiment of the phragmocone that lost the siphon and gas-filled chambers.

The hydrostatic function of the gas-filled phragmocone has been important to control movements with depth both in extinct nektonic belemnoids and recent sepiids. However, its relative fragility confines animals' distribution to the shelf and upper slope. The decalcification of the phragmocone with interstitial filling of spaces between septa by chitinous substance (originating from the hypostracum) resulted in complete loss of its hydrostatic function. This could be an evolutionary leap that happened in squid ancestors during their movement to deepwater habitats away from competition pressure on the shelf. It could also have allowed the squid to perform deep diel vertical migrations in the open ocean that boosted their growth by active feeding in warm epipelagic waters at night, and slow metabolic demand in cold bathypelagic waters during daytime. The great variety in proostracum structure in recent squid families may be explained by their polyphyletic origin from different groups of the phragmocone-bearing coleoids that had moved to the deep ocean. A deep oceanic origin may further explain why geological records of early teuthids are extremely sparse in otherwise deposit-rich shelf environments.



*Figure: Illex argentinus. Sagittal section of the apical part of the conus*

*(Abstract: Arkhipkin & Bizikov)*



## Evolutionary trends in sperm transfer and storage in cephalopods

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Primitive molluscs (Monoplacophora, Polyplacophora) possess a pallial groove in which gills, nephridiopores and gonopores are located. In modern molluscs the pallial groove has evolved to a closed form as the mantle (pallial) cavity. This evolved mollusc body plan may be advantageous to protect gills, especially with the development of long or convoluted shells. However, excretory and gonadal openings are also enclosed in the mantle cavity. The need to ventilate the mantle cavity for respiration makes it more difficult to retain the sperm and direct it to the female genital openings. Subsequent evolution appears to have 'tried' to overcome this disadvantage by a variety of ways in different Molluscan groups.

Cephalopods acquired another function of the mantle: using it for jet propulsion. This function facilitates water ventilation through the gills, but aggravates sperm (or spermatophore) retention in the mantle cavity because of faster water exchange. As a result, their spermatophores are the most complicated in the animal kingdom, with special devices (ejaculatory tube and cement body) to anchor them to a female body.

Two main pathways in the co-evolution of male sperm transfer and female sperm storage can be distinguished in coleoid cephalopods. One pathway has been evolved mainly by deepwater squid that developed subcutaneous injection of spermatophores. Females of this group do not have specialized seminal receptacles. Males have a long and muscled extension of the distal part of their spermatophoric sac (penis). During copulation, spermatophores are placed by a long penis virtually everywhere outside the body and inside the mantle (places of attachment vary by species). After attachment, spermatophores dissolve the outer tissues and penetrate through the muscles to remain there until egg fertilisation. A second pathway has been evolved by sepiids, sepiolids, incirrate octopods and mainly shelf and epipelagic squid families. Their females have either special seminal receptacles or sites located either externally (skin ring around the mouth, and back of the head) or internally (oviductal glands). Males have a short penis that does not extend beyond the mantle margin. One or (rarely) several male arms are modified (hectocotylized) to be able to pick up spermatophores ejaculated from the penis, and hold and transfer them to a female during copulation. As females lack a vagina, it is likely that a highly articulated arm (hectocotylus) is more precise for targeted placement of spermatophores on special attachment sites of the female body than the comparatively poorly articulated penis. Aside from these two mainstream pathways, Vampyroteuthis, cirrate octopods and argonautids have evolved their specific ways of sperm transfer and storage. Thus the development of specific organs and mechanisms for the transfer and storage of sperm has enabled cephalopods to adapt their reproductive needs to a body plan designed for jet propulsive locomotion.

## The chance of evolutionary success - the case of the oldest (Tournaisian) ceratitoid ammonoids (Prodromitidae, Tornoceratina)

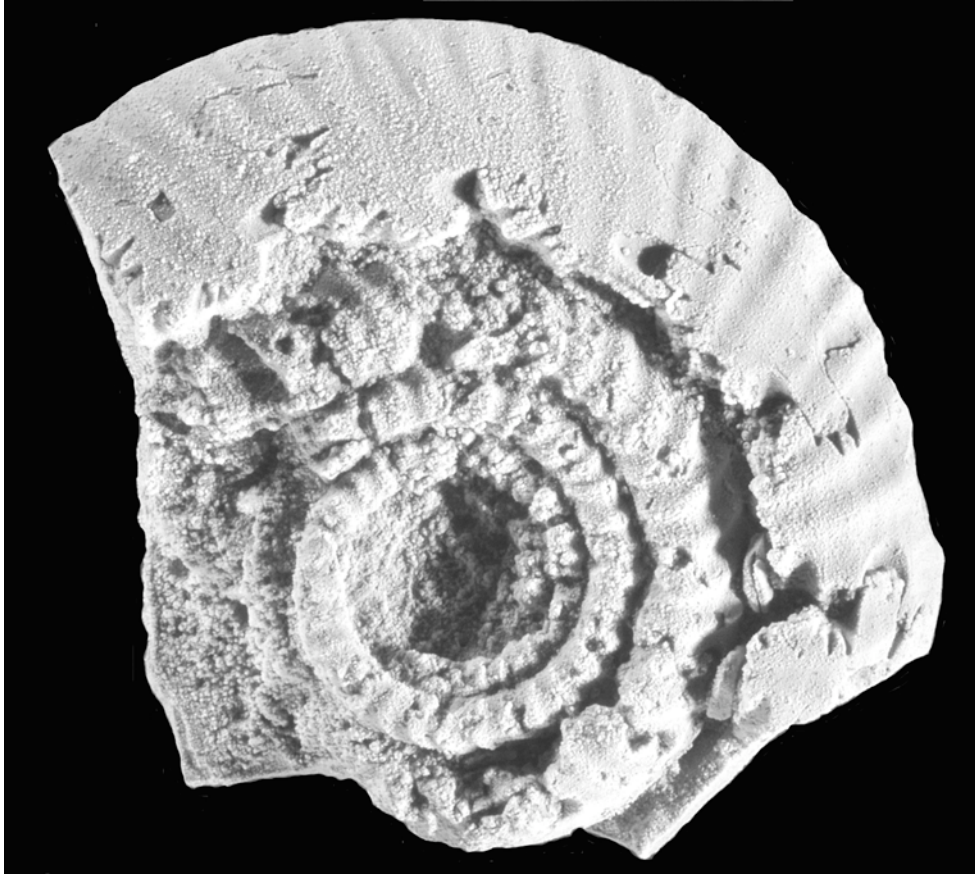
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It is textbook knowledge that most Palaeozoic ammonoids had simple to moderately complex sutures with rounded (agoniatitic) or pointed (goniatitic) lobes, whilst Upper Permian/Triassic ceratites had ceratitic and most Jurassic/Cretaceous groups ammonitic sutures. The rapid complication of septa appears to be one significant reason for the 340 Ma evolutionary success of ammonoids.

The basal Middle Tournaisian Oued Znaigui Formation of El Atrous (S-Tafilalt, Anti-Atlas, Morocco) yielded a new and the oldest ammonoid genus with fully ceratitic A- and L-lobes, predating the times of true ceratites by at least 100 Ma. Apart from a very different, serpenticonic shell form, its sutures show clear affinities with the endemic *Prodromites* lineage from the Tournaisian of eastern North America. Very similar shell form and ornament of the new genus clarify the systematic position of the enigmatic *Goniatites ammonitiformis* from the Tournaisian of Queensland, which sutures were unknown. A related third taxon may occur in the Tournaisian of northern Spain.

The evaluation of the evolutionary success of any group has to consider several aspects. Short-term success can be expressed by abundance, by wide geographic distribution, occupation of different habitats, and by high intra-clade diversity and disparity. Long-term evolutionary success can be measured by the total longevity and diversity of a clade, including their descendents. In comparison with associated other goniatite families, and despite their distinctive morphological innovation, the Prodromitidae were rather unsuccessful. They were mostly rare (only 2.5 % of the El Atrous fauna), geographically restricted in hemipelagic facies, species-poor (three genera with six species), and are currently known from less than ten regions (but of four continents). The contemporaneous Prionoceratidae comprise globally at least 13 genera (known from 34 regions), early Pericyclidae at least 5 genera (from 22 regions), and the early prolecanitids also only 3 genera, but from 34 regions. The longevity of the Prodromitidae is 4-5 Ma compared to > 40 Ma in the Prionoceratidae and ca. 35 Ma in the Prolecanitidae. The Pericyclidae, which enter at the same time, last three times as long, until the middle Viséan. Much longer longevities characterize other Palaeozoic ammonoid groups that developed iteratively ceratitic or even ammonitic septa, such as the Draelitidae (ca. 65 Ma, 3 genera), the Thalassoceratidae (ca. 35 Ma, 8-9 genera), Neopronorites (25-30 Ma), and the Lower/Middle Permian Pseudohaloritidae (ca. 15 Ma, 4 genera). The very different evolutionary success of groups that iteratively expressed a similar morphological innovation implies that it is chance, the coincidence of environmental changes, that shaped the main course of cephalopod evolution. It is more the capability of iterative evolution in clades, by variable gene expression in time and space, that appears to be a key for long-term evolutionary success.



*Figure: Prodomitidae n. gen. n. sp. from the Middle Tournaisian of El Atrous, SE Morocco*  
*(Abstract: Becker)*

## Evolution of the shell in Coleoidea

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Spreading of mantle over the shell in ancestors of coleoid cephalopods initially could serve for two purposes: camouflage and locomotion. The latter could be accomplished by longitudinal mantle folds – evolving fins. Formation of the shell sac tightly fitting to the shell created the necessary prerequisites for the attachment of muscles to the external surface of the shell that, in turn, initiated the development of muscular mantle and its supportive element – proostracum.

Submersion of the shell inside the body in ancestors of Coleoidea was accompanied by the changes of its functions. In Coleoidea the shell transformed into inner skeleton providing support to the muscles of new locomotory apparatus: fins, mantle and funnel.

Proostracum represents the major evolutionary acquisition of coleoid cephalopods. In phyletic lineages that lost phragmocone proostracum became the main structural part of the shell. Evolution of the shell in coleoids occurred principally as evolution of proostracum.

To enhance the strength of the muscles attachment to the shell sac, its walls were reinforced with the connective tissue that in the course of evolution transformed into cartilage. Morphological and histological similarity of cartilaginous tissue between Coleoidea and Chordata represents a striking example of parallel evolution.

The shell in Coleoidea remained calcified as long as it retained the phragmocone. On the contrary, loss of phragmocone inevitably and apparently rather quickly lead to complete decalcification of the shell.

Coleoid cephalopods have two types of contacts between muscles and the shell: primary, inherited from ectocochleate ancestors, and advanced contacts that appeared after enclosing of the shell by mantle. Primary contacts (direct adhering of the muscles to the shell) are highly conservative. On the contrary, the advanced contacts – indirect attachment of muscles to the shell through the shell sac – are highly variable but usually are realized with participation of the cartilage. Distinction between primary and advanced contacts provides necessary clue for homological comparison of the shells in different groups of Coleoidea.

Recent fauna of Coleoidea consists of descendants of four evolutionary clades: spiruloid, sepioid, teuthoid and vampyropodian. Members of the clades differ in the structure of proostracum and phragmocone (in the case of phragmocone loss – by the structure of the cone).

Evolutionary trend of gradual reduction of the shell can be traced in all four evolutionary branches of Coleoidea. Final loss of the shell was related with the development of benthic life form (Incirrata, Sepiida) or planktonic form (some Incirrata, Sepiolida, Cranchiidae). Usually, the loss of the shell was accompanied by major decrease in the ability to jetting swimming but did not induced the changes in bauplan; the latter remained the same in closely related forms with and without shell.

The squids – coleoids with decalcified shell (gladius) – do not represent a monophyletic taxon but a certain stage of convergent evolution in different clades of Coleoidea, that comes after reduction of the gas-filled phragmocone.

## Reconstruction of the body plan and possible way of life of ancient nautiloid cephalopods

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Basing on the data from paleontology, embryology and comparative morphology we attempted to reconstruct possible body plan and the way of life of ancient nautiloids from the first evolutionary wave of cephalopods: *Plectronoceras*, the oldest cephalopod, *Levisoceras*, *Ectenolites* (Ellesmeroceratida), *Phragmoceras* (Discosorida) and *Richardsonoceras* (Oncocerida). Body plan of *Plectronoceras* could be derived from primitive monoplacophorans (Tryblidiida). The foot apparently was differentiated into five pairs of bipartite tentacles (arms) arranged into one circular row postero-laterally from the head – the same way they originate in embryogenesis of recent *Nautilus*. Such arms could serve for grasping, keeping the prey and for crawling. The head was small, with a pair of lateral stalked eyes. The mouth may be equipped with a chitinous beak and surrounded by the buccal lip. Paired dorso-ventral muscles attaching to the shell close to the last septum powered the head and the arms. Most probably, there were six pairs of such muscles, and they were in functional correlation with the head/pedal parts: anterior pair of muscles operated the head while posterior muscles operated five pairs of bipartite arms. Four epipodial muscular folds were situated on the foot above the arms and head: anterior fold (the hood), paired lateral folds (collar folds) and posterior fold (the funnel). The collar folds fused posteriorly with the funnel. The funnel was directed ventro-posteriorly. Respiratory ventilation of the mantle cavity was generated by undulation of the collar and funnel folds. Slow jetting swimming generated by respiratory ventilation, together with crawling were possibly the principal modes of locomotion in *Plectronoceras*. Thus, the body plan of *Plectronoceras* combined ancestral molluscan characters with evolving cephalopodan design. Most probably, *Plectronoceras* was a shallow-water benthic mollusk that could either crawl over substratum or swim sluggishly near the bottom using its slow-jetting mode. Three modifications of the body plan could be traced among ancient nautiloids, all being related with the shell shape: endogastric, straight and exogastric. The forms with endogastric shell (some Ellesmeroceratida, Discosorida) had the body tilted head-downward and were bottom-oriented benthic-pelagic animals. Having posteriorly directed funnel, these forms evolved unique mode of forward jetting-swimming combined with respiration. Contracted shell aperture of some discosorids may enhance jetting capacity and support the funnel. The straight forms (*Ectenolites*) were head-down oriented planctonic animals with the funnel co-axial with the head. Exogastric coiled forms developed from the straight forms in the course of evolution toward more active necto-pelagic swimmers. They could have the body plan similar with recent *Nautilus*.



*Figure: Plectronoceras : plasticine reconstruction of the soft body; lateral view*

*(Abstract: Bizikov & Kröger)*

## **Morphogenesis in cephalopod embryos: description of slow changes using motion pictures**

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Cephalopod embryogenesis strongly differs in early developmental patterns compared to other molluscs. It is characterized by partial cleavage without relics of the ancestral spiralian mode, and epibolic gastrulation without flexion of the egg axis (cf. embolic gastrulation). The slow progression of the blastopore lip along the surface of the uncleaved yolk mass is easily grasped by an observer looking at the same embryo day after day until the blastopore is closed. In contrast, the subtle changes occurring subsequently both at the surface and inside the embryo are much more difficult to view (or visualize) in their respective developmental contexts. Due to the strict bilateral symmetry of the embryo, anterior and posterior (dorsal and ventral in the prospective "physiological" orientation) aspects are virtually identical as long as the embryo is semi-transparent, but "linking" the changes thus observed to those seen in lateral aspect is rather difficult. Such a lateral aspect may show the increasingly distinct differences of the anterior and posterior sides, in particular the slow invagination of the stomodaeum on the anterior side and the slow elevation of the intestinal complex below the posterior surface, which again can be followed directly, by observing the same embryo day after day. However, the actual fusion of the foregut and midgut rudiments, for example, is not observable in the living embryo; it has to be "reconstructed" from histological sections made from embryos preserved at successive developmental stages. From such an ontogenetic time series, one can build a motion picture that overcomes the difficulties of viewing morphogenetic changes by looking at different aspects of the embryo at successive developmental stages. Moreover, time-lapse photography obtained from living embryos over days (possibly weeks) provides an essential tool for showing the true dimensions of organs, unaltered by the form changes related to fixation procedures used in histological work. Ultimately a combination of (a) time-lapse photography of living embryos and (b) sequences of reconstructions based on serial sections of preserved embryos provides the four-dimensional motion picture necessary for a thorough understanding of morphogenesis. This reflection offers an opportunity to remember that more than 50 years ago Jean Painlevé (Paris, 1902-1989), an internationally renowned pioneer of scientific cinematography, produced an excellent time-lapse film of octopus morphogenesis, a unique document that will soon become available as DVD.

## **A synthesis on Hg bioaccumulation in cephalopods**

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Cephalopods are characterised by their particular capacity to accumulate very high concentrations of various essential and non essential metals. Because most of cephalopod species are short lived, metal concentrations in their tissues reflect the environmental variations of metal concentrations. Nonetheless, metal levels are governed by the physiological processes that determine metal bioaccumulation according to the rates of the uptake, assimilation and elimination, the role of the organs in the detoxification and storage, and the molecules involved in the processes of transfer within the organisms. These levels also depend on biological (sex, size/age, diet, trophic level) and environmental (habitat, latitude) factors. In this context, the objective of the present work is to provide an overview of the processes that governs the bioaccumulation of mercury (Hg) which is one of the more toxic heavy metals, bioaccumulates in marine organisms and biomagnifies along food webs. Results concerning field investigations showed that 1) the digestive gland generally had the highest metal concentrations suggesting this organ is involved in Hg detoxification; 2) the muscles contained most of Hg contained in animals where it was mainly under organic form in the muscle tissues suggesting it binds to the sulphhydryl groups of proteins; 3) there was a correlation between size/age and Hg concentrations however not always related to a change in the diet/trophic level. Results concerning experimental investigations with <sup>203</sup>Hg showed that 1) Hg was transferred from peripheral tissues to the digestive gland when cephalopods were exposed to waterborne metal; 2) Hg was highly assimilated following ingestion of radiolabelled food but subsequently rapidly eliminated through the digestive gland, strongly supporting the major detoxification role of this organ; 3) between dissolved and dietary pathways, food mainly contributed to Hg bioaccumulation in cephalopods. These results imply that cephalopods can be used to biomonitor Hg variations in marine systems taking into account the relative importance of the factors cited above.



## Nautilid Conservation and International Trade

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Nautilids (including *Allonautilus* and *Nautilus spp.*) are internationally traded as shell products, unworked shell, trim, and jewelry; as dead specimens for curio and tourist markets; and as live specimens for public and private aquariums. Global trade data are not available. However, U.S. import data indicate that more than 579,000 specimens were imported between 2005 and 2008, mainly from China, Indonesia, and the Philippines. Nearly all of these specimens were wild-harvested. Israel, the European Union, and Thailand are among the other known non-range countries involved in international nautilid trade. Certain intrinsic life history traits (such as longevity, delayed maturation, lengthy gestation, and small number of eggs produced per breeding season), in combination with extrinsic factors (such as selective harvest, predation, habitat fragmentation, and climate change), render nautilids more susceptible to unregulated harvest and increase their risk of extinction. The Convention on International Trade in Endangered Species (CITES) is a multinational agreement that entered into force in 1975 to ensure that international trade in certain animal and plant species does not threaten their survival by regulating their import, export, and re-export. Under CITES, species may be listed in one of three Appendices, each conferring a different level of regulation through CITES documentation and permits. Commercial trade is not allowed for Appendix-I species. Commercial trade is permissible for Appendix-II species, but must be biologically sustainable and legal. Countries may also include native species in Appendix III to enlist assistance of international trading partners to better control trade. More than 34,000 species are listed in the CITES Appendices, a little over 5,000 animals and nearly 29,000 plants. The majority of species are listed in Appendix II, which allows biologically sustainable and legal commercial trade. A CITES Appendix-II listing could provide regulation of international nautilid trade, complementing national and local management. Some of the marine species listed in Appendix II include queen conch, black corals, some dolphins, all giant clams, all stony corals, basking sharks, Great White sharks, whale sharks, and seahorses. CITES Parties have established biological and trade criteria to assess whether a species should be included in Appendices I or II (i.e., listing criteria). Of particular importance to nautilids in trade is the decline and vulnerability of this taxon, as these terms are defined by the CITES listing criteria. However, there is currently insufficient biological information to assess the status of wild populations and the impact of trade. Biological information, including range-wide population size estimates, and additional data, including trade and industry information, would assist in determining whether to submit a listing proposal at the next meeting of the Conference of the Parties.

## Evo-Devo in early Ammonoidea: links between embryonic and post-embryonic ontogeny?

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Several groups (bactritoids, ammonoids, dacroconarids, gastropods, nautiloids) show an increase in shell coiling during the Devonian, which might be related to the “Devonian nekton revolution”. These changes are usually interpreted to reflect increased predatory, selective pressures. These changes are particularly interesting in early ammonoids as they show a progressive coiling of both the ammonitella (embryonal conch) and the post-embryonal conch. This evolution must have happened very fast as more derived forms with a tightly coiled, oxyconic conch are associated with their loosely coiled relatives in Morocco, the Urals and Uzbekistan. Forms with loosely coiled post-embryonal whorls disappear at the end of the early Emsian (Lower Devonian) before the Daleje event, while the last forms with a perforated ammonitella (umbilical window) disappear shortly after the Chotec event in the early Eifelian (Middle Devonian). Parameters of the embryonal conch and first whorl are compared in a morphospace through time. There is trends toward a more coiled, smaller ammonitellae and smaller protoconch, although some lineages show an enlargement of the protoconch. The variability and changes in early ontogeny are also investigated over time in some well-dated lineages (*Gyroceratites* and *Erbenoceras-Mimosphinctes* lineage).

The ontogenetic change of the shape of the aperture is investigated through time and in relation to the amount of whorl overlap and coiling. Major evolutionary trends are an increasingly allometric growth, more thinly discoidal or more globular whorls and narrower umbilici from the earliest ammonoids towards more derived Devonian ammonoids. The coiling trends in early ontogeny and post-embryonal ontogeny are compared.

## Paleobiogeographical changes in ammonite faunas during the Pliensbachian-Toarcian interval (Early Jurassic)

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The Pliensbachian-Toarcian crisis (183 Ma; Early Jurassic) is generally regarded as one of the most important extinction events of the Mesozoic. It affected both marine and continental faunas (Caswell *et al.* 2009), and was temporized by successive extinction pulses with different selective dynamics (Dera *et al.* 2010). The origin of these disturbances is still debated and includes different processes such as the Karoo-Ferrar volcanism, strong climate and sea-level changes, an oceanic anoxic event (T-OAE), and a carbonate production crisis. Contemporaneous with these paleoenvironmental events, important paleobiogeographical changes have been reported, in relation with latitudinal expansions or retractions of marine species (Zakharov *et al.* 2006; Arias & Whatley 2009). For instance, several authors have qualitatively suggested a total disruption of the provincialism of Tethyan ammonites (Euro-boreal vs. Mediterranean) during the Early Toarcian (Enay & Mangold 1982; Cecca & Macchioni 2004).

Here, we attempt to test in a quantitative way the temporal changes in the biogeographical structure of ammonite faunas during this major biotic crisis. Our work lies on the analysis of an extensive and revised database of 772 ammonite species, including information on the stratigraphical range and the spatial distribution of each taxa according to 17 Arctic and NW Tethyan areas. Different analyses (HCA, NMDS, BSM) were conjointly used in order to characterize the provincialism and the faunal exchanges during the 13 biochronozones of the Pliensbachian-Toarcian interval.

Our principal results show: 1) a strong faunal dichotomy between Euro-boreal and Mediterranean areas during the Early Pliensbachian; 2) the first appearance of the Arctic biome during the Late Pliensbachian; 3) an increase in faunal exchanges and a progressive disruption of provincialism during the Early Toarcian; 4) its reappearance during the Middle and Late Toarcian. In parallel, we discuss the possible influence of climatic and eustatic factors on these paleobiogeographical events.

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# Ammonite, inoceramid and nannofossil biostratigraphy across the Turonian–Coniacian boundary in the Aquitaine and Vocontian basins (France) and Diego Basin (Madagascar)

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Detailed study of Turonian–Coniacian boundary sections in the Aquitaine Basin in southwestern France has yielded ammonites and inoceramids previously not reported from this basin. The ammonite *Forresteria petrocoriensis* (Coquand, 1859) occurs with inoceramids of the group of *Mytiloides incertus* (Jimbo, 1894), which confirms that this classical zonal index ammonite actually has its first occurrence in the upper Turonian as currently conceived. Calcareous nannofossils indicate Burnett et al.'s (1998) "standard" biozones UC9a to UC9c. In the Vocontian Basin, in southeastern France, *Prionocyclus germari* (Reuss, 1845) occurs with *Didymotis costatus* (Fri\_, 1893).

Collignon (1954) introduced an ammonite zonation for the Cretaceous of Madagascar, based on outcrops in the Menabe region (central western Madagascar), the Onilahy valley (southwestern Madagascar) and the Montagne des Français near Antsiranana (Diego Basin, northern Madagascar). However, this zonation, particularly that for the upper Turonian to Coniacian, suffers from many discrepancies and cannot be directly correlated with the "standard zonation".

The rock succession exposed in the Diego Basin was studied in detail and ammonites and inoceramids collected bed-by-bed. A rich ammonite fauna with *Prionocyclus germari* (Reuss, 1845), *Barroisiceras onilahyense* Basse, 1948, *Nostoceras* (*Eubostrychoceras*) *indopacificum* Matsumoto, 1967 and *Baculites yokoyamai* Tokunaga & Shimizu, 1926 was collected, together with inoceramids indicating the *Mytiloides incertus* Zone or the lower part of the *M. scupini* Zone. The ammonite fauna indicates the *Prionocyclus germari* Zone (introduced by Kaplan & Kennedy 1996 for northern Germany) and the presence also in northern Madagascar of Collignon's (1960) *Kossmaticeras theobaldi*–*Barroisiceras onilahyense* Zone. Calcareous nannofossils indicate Burnett et al.'s (1998) "standard" biozones UC9b to UC11b. The zonal scheme of Collignon is clearly in need of revision.

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## ***Sepia* type of connecting rings**

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Cuttlebone of recent *Sepia* (*Acanthosepion*) *cf. savignyi* Blanville was examined with a goal to clarify whether *Sepia* retains homologous structure of connecting ring developed in Spirula and extinct spirulids, Nautilus and fossil nautiloids as well as in belemnoids, ammonoids, bactritoids and orthoceroids.

The studied material comprises five cuttlebones of *S. (A.) cf. savignyi* from the Bay of Aqaba, Red Sea (Israel, Eilat) collected by Mutvei in 1980s. Untreated and treated with glutaraldehyde - acetic acid - alcianblue solution cuttlebones were examined with scanning electron microscope and energy dispersive spectrometer.

The surface of the cuttlebone reveals sheets which have the shape of a strip and cover narrow slit-like openings of chambers between septa. The sheets are attached to two neighbouring septa along their edges that show narrow sheet/septum attachment scars. It was demonstrated that the sheets represent multi-laminated formations, where each lamina consists of fibres. The sheets exhibit pores of two size categories: comparatively large pores with diameter equal to 0.4-0.6  $\mu\text{m}$  and micro-pores that are ca. 0.1  $\mu\text{m}$  in diameter, or less. The sheets contain C, O, Na, K and lack Ca.

It is concluded that:

- (1) *Sepia* possesses segmented non-mineralized, apparently chitinous, multi-laminated micro-porous strip-like sheets that cover the outer side of chambers of the phragmocone but lack a ring-like shape of "connecting ring". Therefore the sheets are named "connecting strips";
- (2) Connecting strips of *Sepia* represent a homologous structure of connecting ring of phragmocone-bearing cephalopods;
- (3) Connecting strips of *Sepia* reveal a micro-porosity that is typical for connecting rings in orthoceroid/bactritoid/ammonoid evolutionary branch and distinct from the Nautilus branch that has no pores in the connecting rings;
- (4) *Sepia* uses porosity of connecting strips to change the buoyancy and regulate cameral liquid volumes in chambers during diurnal vertical migrations;
- (5) *Sepia* apparently inherited the mechanism for buoyancy regulation from orthoceroid / bactritoid / ammonoid evolutionary branch.

# *Nautilus pompilius* fishing and population decline in the Philippines; a comparison with an unexploited Australian *Nautilus* population

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The low fecundity, late maturity and long life span of *Nautilus* ensure their vulnerability to overfishing. Demand from the ornamental shell trade and restricted habitat preferences contribute to their rapid decline. This study reports fishing effort and related changes to *Nautilus* populations in the Philippines as compared to an unexploited population in Australian waters. Baseline capture, mark and release studies of *Nautilus pompilius* conducted at Osprey Reef, Coral Sea, Australia show this unexploited population to demonstrate a stable CPU over 12 years, a marked difference to the exploited *Nautilus* populations of the Philippines. Data from a detailed interview questionnaire of *Nautilus pompilius* fishers and traders in Palawan, Philippines highlight a fishery which is both unsustainable and culturally unimportant. The results show up to 80% declines in catch rates during periods ranging from 1980 to the present. Protection of *Nautilus* from fishing would provide minimal long term impact on the local culture or economy as there is no cultural relevance to local communities and the fishery only provides approximately 10 - 20 years of economic return before becoming non-viable. Identification of new *Nautilus* fishing sites and training of locals by buyers from distant depleted fishing areas shows the value and demand *Nautilus* shells have to generate fishing effort. Similar international demand has driven the introduction and subsequent decline of shark and beche de mer fisheries to the same developing Indo-Pacific nations of known *Nautilus* populations. *Nautilus* populations have been shown to be genetically different where divided by deep (>800m) ocean barriers to connectivity. This precludes recolonisation of depleted sub-populations and supports a strong argument for protection of all *Nautilus* stocks to maintain genetic diversity. Strong evidence exists for *Nautilus pompilius* (and by ecological association, other *Nautilus* species) to be assessed as 'ENDANGERED' in the IUCN Red List and provides impetus for CITES listing.



## Is the Endocerida polyphyletic ? – A possible new order of lower Palaeozoic nautiloids

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The pilocerids are a group of mainly Early Ordovician cephalopods, and form a characteristic component of many low latitude assemblages, especially in North America and China. With some notable exceptions, the remains of these organisms are restricted to siphuncles containing massive endosiphuncular deposits, the presence of which has conventionally been taken as evidence of their taxonomic position within the Order Endocerida. The ancestry and early phylogeny of the Endocerida has been discussed for over 75 years, and several workers have made important contributions to the debate, including Kobayashi, Flower, Dzik and Kröger & Landing. Crucially, analysis has focused on the detailed morphology and stratigraphical occurrence of the two earliest known 'endocerid' families, the Piloceratidae and Proterocameroceratidae, and their relationship with the ancestral Ellesmerocerida.

Endocones or endocone-like structures are known from a number of distantly related groups of 'nautiloid' cephalopods apart from the Endocerida, such as the Discosorida and the Dissidocerida. Furthermore, siphonal structures that represent either conical endosiphuncular diaphragms (or possibly even endocones) are present in a number of ellesmerocerids assigned to at least three different families. Consequently, cephalopods possessing endocones may have originated from more than one lineage within the Ellesmerocerida.

Although the stratigraphic relationships between the earliest known pilocerids and proterocameroceratids is equivocal, study of the endosiphuncular deposits suggests that those of the Piloceratidae, Manchuroceratidae and the younger Allotrioceratidae and Najaceratidae, are distinctly different to those of the Proterocameroceratidae and Endoceratidae. Other differences include overall shell shape (cyrtobreviconic in the Piloceratidae and Manchuroceratidae, longiconic in the Proterocameroceratidae) and septal neck morphology (holochoanitic to macrochoanitic throughout the Piloceratidae, Manchuroceratidae, Allotrioceratidae and Najaceratidae). There may also be differences in the form of muscle attachment scars, but the evidence for these is debatable.

Considering all available evidence together, we suggest that the Endocerida as currently defined is a polyphyletic taxon, from which we propose the Piloceratidae and related families should be separated and regarded as a new Order of lower Palaeozoic nautiloids.

## A macroecological study of early Pliensbachian ammonites from western Tethys and adjacent areas

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The early Pliensbachian (Early Jurassic) is known as a time of marked provincialism in the marine realm, notably between the Mediterranean Tethys and North–West Europe. We compiled 104 locality-level species lists from those areas based on a comprehensive revision of early Pliensbachian ammonites. With this dataset, we explore various macroecological and biogeographical patterns at the scale of the chronozone and sub-chronozone. Although there is a sharp contrast between the NW European (NWE) and the Mediterranean (MED) ammonite provinces in terms of taxonomic composition and richness, they both record similar trends in richness and endemism.

First, ammonite richness is low in the Davoei chronozone. That observation may be related to a coeval warming of seawaters, but the latter was insufficient to affect biotic interchanges between the domains as is usually observed elsewhere. This persistent compartmentalisation probably reflects a major palaeogeographical structure, such as an emerged or near-emerged barrier running from the Betic range to the Briançonnais ridge.

Second, biogeographic patterns are characterized by significantly high proportions of endemic and cosmopolitan species (occurring respectively in less than 10 % or in more than 90% of localities), suggesting a strong control of ammonite distribution during early Pliensbachian times.

Further spatial analyses for this dataset will be possible in a near future thank to the current computation of locality paleo-coordinates. In addition, we are currently exploring the relation between alpha and beta diversities within and across the two domains, as well as the correlation between diversity, morphology, and phylogeny.

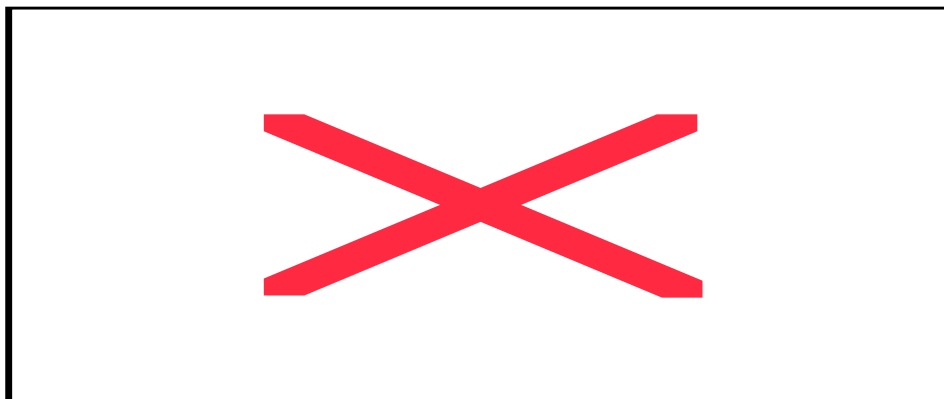


Figure: Sample-based rarefaction curves and their 95% confidence intervals for ammonites in the Mediterranean (MED) and NW European (NWE) provinces. Each curve corresponds to an early Pliensbachian chronozone (Jam. = Jamesoni chronozone; Ibex = Ibex chronozone; Dav. = Davoei chronozone). Note the significant decrease in species richness between the Ibex and Davoei chronozones in both provinces. (after Dommergues, Fara & Meister 2009)



## The evidence of the maturity of genus *Angulithes* Montfort, 1812 (Cretaceous–Oligocene, Nautiloidea)

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During the revision of genus *Angulithes* Montfort, 1812, significant morphological changes corresponding to maturity achievement of living *Nautilus* (e.g. Stenzel, 1964; Collins & Ward, 1987) and also new features specific only for the fossil representatives were recognized. The features which correspond with the maturity of recent *Nautilus* are follows: apertural contraction; rounded broadening of the fully mature body chamber; thickened apertural edge; change in shell coiling and increase in the length of the mature body chamber. The approximation of the last phragmocone chambers is a reliable indicator of approaching maturity rather than of full maturity (Collins and Ward 1987).

Characteristic for *Angulithes* is narrower ventral side with obtusely sagittate to triangular whorl cross section with significant ventral keel in several cases. The keel is gradually decreasing on the last whorl of the fully grown shell close to the apertural area. The whorl cross section is changes its shape to the broadly rounded, because of increasing space inside of the living chamber probably to accommodate enlarging reproductive organs. Ventral keel played most probably hydro dynamically important function (e.g. Chamberlain & Westerman, 1976) and still fulfils its function even after its decrease during adult stage, because his large part still persists on the last whorl. The thickening of apertural edge is in several cases accompanied by significant changing of shell ornamentation with strong radial "ribbing". The functional morphology of the strong apertural ribbing and ribbing its self is a topic opens to debate (e.g. Chirat, 2001); however, several hypotheses have been suggested: e.g. significantly strengthening of the aperture as a defence against damage or increasing stability of the mature shell. Such hypotheses are probably in some ways complementary.

The interpretation of these morphological changes of *Angulithes* as evidence of maturity achievement brings new knowledge about paleoecology of this group and help with the interpretation of similar features of other fossil nautilids. The research is supported by GAUK 22207.

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## A groenlandibelid spirulid from the Campanian/Maastrichtian of Vancouver Island (Canada)

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So far, *Groenlandibelus rosenkrantzi* (Birkelund, 1956) from the Maastrichtian of Greenland represents the only fossil coleoid that is known to have a protoconch with a caecum and a prosiphon (Jeletzky 1966). Although the holotype appears in some other features as a belemnoid, Jeletzky (1966) recognized more similarities with spirulids and sepiids than with belemnoids. Most coleoid workers subsequently followed this assumption. The character complex of *Groenlandibelus* is today crucial for comparative analyses that shall decide whether a phragmocone belongs to the Decabrachia or the Belemnoidea. However, the small number of phragmocones from Greenland studied by Jeletzky (1966) and later again by Birkelund & Hansen (1974) could not resolve all morphological and phylogenetical problems. Numerous phragmocones from the Campanian/Maastrichtian Northumberland Formation of Vancouver Island (British Columbia, Canada) and previously illustrated in Ludwigsen & Beard (1997) show remarkable similarities with *Groenlandibelus*, more than with the closely related genus *Naefia*, which were recently thought to be transitional between belemnoids and spirulids by Fuchs & Tanabe (2010). The groenlandibelid-like phragmocones are preserved in concretions and are therefore in an extraordinarily good condition, i.e. they exhibit significant characters such as protoconcha, proostraca and unaltered shell material. Preliminary results based on macroscopic observations indicate that the conotheca shows no evidence of forward curved growth increments and that the proostracum is instead distinctly formed by the outer sheath and an underlying most probably organic layer. This condition is also typical for co-existing *Naefia* as well as for Cenozoic spirulids and unknown in belemnoids (Fuchs & Tanabe 2010).

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## Did belemnoid coleoids have suckers?

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The 10 arms of belemnoid coleoids are well known to be equipped with hooks. Since Mantell (1852: p. 19, Fig. 4) and Donovan & Crane (1992: p. 286) it is clear that in addition to hooks there must have been muscular structures in close association with the hooks. However, it is still uncertain whether these presumed “suckers” have been functional or not. Engeser & Clarke (1988: p. 139), Young et al. (1998: p. 395) and Fuchs (2006a: p. 71, 77, Fig. 3.7-3) believed that these structures rather represent muscular bases that moved the hooks and that they were hardly functional suckers. Nevertheless, a new record of a belemnoid arm crown from the Late Jurassic Solnhofen Limestones yielded indeed strong evidence of functional suckers. The specimen unambiguously shows that the hooks are definitely not rooted in the suckers. As the “presence of suckers” is widely regarded to be the single autapomorphy of the “Neocoleoidea”, the discovery of suckers in the “Belemnoidea” has a striking impact on the higher-level phylogeny of the Coleoidea. Moreover, it opens the discussion whether the Ammonoidea, the presumed sister-group of the Coleoidea, had also suckers.

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# **Raup's shell coiling ammonoid morphospace, geometric alternatives and impact on disparity estimates**

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About forty years ago, David Raup in a series of influential papers devised and implemented an elegantly simple model for describing shell coiling in various taxa, and set the bases of Theoretical Morphology. In this fixed-frame geometric model, most shells exhibiting spiral growth can be efficiently described with only four parameters defining translation along and revolution around the coiling axis of an expanding generating curve (i.e., shell aperture).

Here we focus only on the 'D-W plane' (D and W standing for distance of the generating curve from axis and expansion rate, respectively), which can be viewed as a 'subspace' of the general three-dimensional block, and within which most ammonoids can be depicted.

Using the morphometric traits needed for computing Raup's parameters, we develop two alternative morphospaces, also based on a geometric concept of shape: the first one corresponds to geometric morphometrics of sets of collinear landmarks, and is similar to common 2D and 3D approaches. The shape space of forms described by  $p$  collinear landmarks is the  $p-2$  surface of a unit radius hypersphere and is identical to the preshape space, since the rotational fit of Procrustes analysis is not required. In contrast, the second morphospace considers interlandmark distances instead of the landmarks themselves and, based on their relative proportions, does allowing ammonoids to be pictured in a third way by means of ternary diagram, a classical tool for visualizing compositional data in geology.

Within the context of morphospace and disparity analyses, we heuristically explore the properties of these three spaces built from similar morphometric inputs, so as to find possible connections among them, and discuss the various notions of intershape distances that can be drawn from different morphospaces and their effects on disparity estimates in empirical studies.

## **Extinction of the ammonoids: Chixculub impact or Deccan flood basalt volcanism?**

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Since Alvarez et al. (1980) and Smit & Hertogen (1980), hypothesis and theories including catastrophic events explaining the fossil record (re)gained a lot of attention. The extraterrestrial origin of the anomalous iridium concentrations seemed highly controversial at first, but since years passed, nowadays scientists generally agree upon the 'accident' Chixculub caused. The impact level even became the marker horizon for the GSSP of the Paleogene. However, alternative theories explaining the huge diversity loss of the last of the 'big five' mass extinctions life on planet Earth yet experienced remain being published. Of them, the Deccan flood basalt stepped prominently forward as one of the main causes, especially when trying to explain the gradual diversity decline the fossil record preserves.

The inconsistencies between the proposed theories root in too narrowly geographically and geologically spread datasets. This is for most fossil groups, and especially for the ammonoids. A recent compilation of worldwide ammonoid occurrences of Late Maastrichtian age by Kiessling & Claeys (2002) evidences the lack of a globally well distributed set of data. In this compilation, North Africa was left as a blind spot, while Tunisia has been the centre of the K/Pg mass extinction debate for more almost three decades already, with the GSSP (El Kef) and many other well suited sections in its basin. Also, the Tunisian Upper Cretaceous sediments are thick, well exposed and continuous, and, more importantly, ammonoid bearing till high up in the Maastrichtian, the last Stage of the Cretaceous. Therefore, Tunisia was chosen as our primary research area.

In several sections, spread across several areas in the Tunisian Trough Basin, ammonoids were found within the topmost 20 m of the Maastrichtian, until very near the K/Pg boundary level. A collection of 896 uppermost Maastrichtian ammonoids was obtained, all from within the last 420.000 years of the Cretaceous, with the highest find about 50.000 years before the boundary. The Tunisian fauna is the most diverse uppermost Maastrichtian fauna yet recorded, with 22 species, belonging to 10 families, with representatives of each the four large suborders; the Phylloceratina, Lytoceratina, Ammonitina and Ancyloceratina.

When the observed ammonoid species richness is plotted next to all time constraints of the possible causes, the possibility of Deccan flood basalt volcanism negatively influencing ammonoid diversity is refuted. A major extinction caused by the Chixculub impact seems the single plausible theory at present. The short survival of ammonoids into the earliest Danian as proposed for The Netherlands (Jagt, 2002), Denmark (Machalski & Heinberg, 200) and New Jersey (Landman et al., 2007) in recent literature may also fit here (<20kyr).

## Visual control of precision single arm use by *Octopus vulgaris*

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Controlling eight flexible arms the octopus carries out many complex tasks, such as crawling, exploring, mating and swimming. With all their infinite options of movement researchers have found them disappointing, as they consistently failed in operant tasks requiring them to combine central nervous system reward information with visual and peripheral knowledge of the location of their arms in precision control movement. Wells (1978) postulated that the octopuses did not possess the feedback mechanisms required for mastering such tasks. Using an operant behavioral task we now show that *Octopus vulgaris* is capable of visually guiding a complex arm movement to a specific location. We developed a transparent Plexiglas 3 choice maze, building on the natural exploration movements of the octopus arm, to investigate the relationship between vision and the control of complex arm movement. Following a random sequence, in each trial only 1 of the 3 compartments contained a visual stimulus and a reward. Octopuses were trained to guide a single arm through a central tube, out of the water and into the visually marked goal compartment. 6 of 7 octopuses reached criterion for learning, 5 correct trials in a row, within 61-211 trials. We found a strong negative correlation between not seeing the target and success ( $R^2=0.136$ ,  $n=5$ ,  $\text{corr.coef}=-0.923$   $p<0.001$ ). In a control experiment, using an identical opaque maze, octopus performance returned to chance levels. This is the first study that clearly shows the ability of *Octopus vulgaris* to learn an operant task that requires visual guidance of complex arm movement. Complex goal oriented arm movements require constant online control and feedback, and perhaps cross-referencing between different sensory inputs. Recent results showing no somatotopic organization in the higher motor centers of the octopus brain raise interesting questions about the mechanisms behind such single arm complex movement control.

## The phylogenetic distribution of extinctions in Early Jurassic ammonite communities

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Exploring the phylogenetic structure of communities has become a major challenge for ecologists in the last decade. Indeed, the co-occurrence of species into biological communities is not only the result of present processes but also the result of the evolutionary history of those species. Here we investigate in a phylogenetic perspective the mechanisms that have structured extinction patterns among ammonite species. Our study focuses on assemblages from the Early Pliensbachian (Early Jurassic) in western Tethys and adjacent areas. That part of the ammonite fossil record is particularly well-suited because it has been recently revised at the species level and it is now associated to a robust phylogenetic hypothesis that includes 214 species.

In order to explore the phylogenetic distribution of extinctions, we use a spatial autocorrelation index called the Moran's I. Its values and associated confidence intervals indicate whether extinctions are phylogenetically clustered, overdispersed, or random in successive biozones. This index is considered in two ways. First, we computed separately the Moran's I for various levels of the phylogenetic hierarchy. Second, we computed the Moran's I with overall phylogenetic distances among species, thus yielding a single value for the entire phylogenetic tree.

Our first results show that most extinctions were significantly clustered, suggesting a strong signal from extinction-prone clades. We are also currently quantifying the phylogenetic structures of ammonite assemblages in order to test their response to paleoenvironmental and paleogeographic changes. This work shall provide an interesting insight into the evolution and structure of ancient marine biodiversity from a phylogenetic perspective.

# **Controlling factors of the paleogeographic distribution of nautiloid cephalopods along the Northern Gondwana margin during the Silurian: a case study from the Carnic Alps (Austria)**

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Faunal gradients from Baltica and Avalonia, across peri-Gondwanan Europe, to the North African shelf basins may have been chiefly controlled by marine water temperature gradient and, consequently, the surface current system. During the Silurian there are rapid facies shifts, which reflect very differing environments but seem to have a recurrent global pattern. Carbonates from the North Gondwana area include cephalopod limestones characterized by mass occurrences of orthoconic nautiloids and bivalves (the famous "Orthoceras Limestones"). Studies of the development of the Silurian Cephalopod Limestone Biofacies have shown that it may be traced from Siberia, Bohemia, the Carnic Alps, Sardinia, Montagne Noire and the Ossa Morena in Spain (Kriz, 1998; Gnoli, 2003).

The Carnic Alps is a key locality along the Northern Gondwana margin regarding Silurian biostratigraphical correlation. Recognition of environmental and water depth changes based on the fossil assemblages (mostly trilobites, brachiopods and bivalves) from the Silurian depositional sequences developed there (Brett et al, 2009) places a tight control on small scale bioevents within well-defined conodont, graptolite and chitinozoan biozones. Particular emphasis is placed on establishing the response of marine faunas to oscillations in sea-level and to the oceanic variations (chemistry, temperature, currents) recorded during this time interval on a local scale for comparison with data from other North Gondwana terranes such as Sardinia and Bohemia and on a global scale with some sectors of Avalonia (the British Isles) and Laurentia (North America).

Correlation of the nautiloid faunal assemblages and their taphonomic signatures from the Carnic Alps successions with evidence for global eustatic/climatic events, pronounced redox changes, surface currents, regression/transgression sequences within precise intervals may identify common controlling factors in the palaeogeographic distribution and migrational routes of these faunas. This approach may provide further evidence for the reconstruction of reliable palaeobiogeographic models of the northern Gondwana margin and its derived "terranes" based on pelagic as well as benthonic faunas (Cocks & Torsvik, 2002).

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## Empirical relationships between shell expansion and septal spacing in Devonian ammonoids

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Since the pioneer work of Trueman (1941) and Saunders & Shapiro (1986) it is known that the body chamber length controlled the orientation and mode of life of ammonoids. Neutral shell buoyancy was only possible with a balance between total animal weight and the buoyancy of the gas-filled phragmocone parts. A large part of the weight was formed by the growing body chamber shell. Consequently there is a strong correlation between body chamber length and whorl expansion rate (Okamoto 1996, Klug (2001). Shells with high whorl expansion rates, as in the extant *Nautilus*, are brevidomic, those with slowly expanding shells are longidomic. Chamber formation cycles are also correlated with whorl expansion since, in order to maintain neutral buoyancy, the increase of shell weight at the apertural margin had to be balanced at an upper limit by the secretion of a new gas-filled chamber. The large size and shell weight increase in fast expanding shells resulted in a generally closer septal spacing (smaller cameral angle) than in slowly expanding forms. Slowed apertural growth, for example towards maturity, is long known to result in even closer septal spacing since the genetically fixed septal formation could be delayed but not completely stopped.

The relationships between whorl expansion rate (WER) and septal spacing were empirically ascertained in more than 900 Middle/Upper Devonian ammonoids that represent more than 130 species and 76 genera. In general, specimens with a high WER show low maximum cameral angles and vice versa. Plotting both parameters, the upper limit of measured values is represented by a distinctive curve with a steep slope between 25° at ca. WER 3.0 and 80° at WER 1.5. Most specimens plot below this limit, either because of slowed growth, high shell weight (e.g., thick shell walls), or reduced buoyancy (partial water filling of the phragmocone). Sudden ontogenetic changes in WER rates may cause some errors in plots but are reflected in changing cameral angle values. The large variability of maximum septal spacing within species shows that it can be used as an important proxy for variable living conditions of individuals and populations. Strong differences between specimens from single units probably reflect time-averaging during sedimentation and/or sampling. The previously recognized rhythmic changes of cameral length may have been caused by seasonal variations. Two pathological specimens were episodically incapable of septal secretion and must have survived a phase of negative buoyancy by active swimming. A single non-pathological clymeniid (*Rectoclymeniidae* n. gen. n. sp.) with extremely long chambers defies all other specimens but its stream-lined shell form speaks against a benthic, non-buoyant life-style. Systematically lower maximum cameral angles in all Givetian than in Upper Devonian taxa suggests that chamber emptying was less efficient at that time and first advanced in the Frasnian Gephurocerataceae.

## **Paleobiological interpretation of the early Turonian (Late Cretaceous) *Pseudaspidoceras flexuosum* (Cephalopoda: Ammonitina)**

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*Pseudaspidoceras flexuosum* was a common species in lower and middle latitudes of the early Turonian and is thus widely used as index fossil. It was thus a surprise to find specimens of this species wearing long spines, hitherto unknown for that species, in the early Turonian Vallecillo Platy Limestone (see Figure 1, specimen VCII/95B, scale in cm). *P. flexuosum* is the most abundant ammonite in this locality. The large amount of information about the palaeoenvironment of the Vallecillo fossil Lagerstätte includes sedimentological, geochemical, statistical, and biostratigraphical data. In addition, there are quantitative data on *P. flexuosum* from a series of scientific excavations. Further material was loosely collected by the author and by the quarrymen, in part with stratigraphic data. Altogether, 150 specimens of *P. flexuosum* are available for statistical tests. Their interpretations allows for conclusions on taphonomy, dimorphism, shell secretion, functions of the spines and dwelling depth.

*P. flexuosum* was part of a pelagic ecosystem on the outer shelf. The well-known early Turonian fauna preserved at Vallecillo allows for the discussion of possible food sources for this ammonite. In addition, there is evidence that *P. flexuosum* was preyed upon.

Three shells were colonized by Stramentum, which provides further information about the mode of life of *P. flexuosum*, as well as its comparison to other spined species from different localities and ages. The spines of *P. flexuosum* were mostly restricted to its body chamber. Apparently, they were removed subsequently during growth, although the mechanism of removal is unclear.

The abundant data on *P. flexuosum* at Vallecillo, on the paleoenvironment and on the early Turonian ecosystem are combined here to a palaeobiological model for the mode of life of this ammonite.



*Figure: Obliquely embedded specimen of Pseudaspidoceras flexuosum from the Platy Limestone at Vallecillo, Mexico. This specimen shows long, fragile spines preserved on the ventrolateral tubercles of the body chamber. Early Turonian, UANL-FCT-VC1195B, Scale in cm.*

*(Abstract: Ifrim)*

## Migration pathways of the late Campanian and Maastrichtian shallow facies ammonite *Sphenodiscus* in North America

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Records of the ammonites *Sphenodiscus lobatus* and *Sphenodiscus pleurisepta* from the latest Cretaceous Gulf of Mexico region, the Western Interior Seaway and the Atlantic coast have repeatedly been used as a stratigraphic index for a Maastrichtian age. In recent years, however, high-resolution biostratigraphy on north-eastern Mexican occurrences and its combination with other correlation tools, such as sequence stratigraphy, as well as a refined definition of the Campanian–Maastrichtian boundary, led to a different interpretation regarding the age of the earliest *Sphenodiscus*. The FA of *Sphenodiscus* in north-eastern Mexico is thus latest Campanian in age. However, before this formal definition of the boundary, the level of its FA in Mexico was in the Maastrichtian. *Sphenodiscids* dispersed and radiated during the latest Campanian and Maastrichtian, until they went extinct at or near the Cretaceous–Palaeogene boundary.

There is evidence for migration pathways of *S. lobatus* and *S. pleurisepta* in North America which results from precise dating of many occurrences throughout this continent. During the latest Campanian and early Maastrichtian, the two species immigrated to North America from the South; they did not evolve on this continent. Both species used changes of the sea level to migrate or disperse over the continent. The dispersal route of *Sphenodiscus* during the Maastrichtian does not reflect a general dispersal pattern for ammonoids in North America, as is indicated by an opposing north to south-directed migration trend of *B. ovatus*.

Both *S. lobatus* and *S. pleurisepta* are long-ranging species, not suited as high-resolution biostratigraphic markers for correlation over large distances. Instead, they are excellently suitable as facies indicators for proximal near-shore environments. Their short local ranges in different regions of the North American continent results from this characteristic and the fact that *Sphenodiscus* followed shallow water areas and shorelines during times of changing sea levels.

## ***Rhabdobelus* biodiversity from the Toarcian of Crimea and the problem of *Rhabdobelus*-*Pseudobelus* relationship**

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*Rhabdobelus* Naef, 1922 is a belemnite genus common for Upper Toarcian. Despite it is very common for this interval, their sudden appearance and dramatic disappearance do not allow to trace relationship with possible ancestors and descendants. There are no common opinion among researchers about the composition of the genus, but two species are obviously form the «nucleus» of the genus – *R. exilis* and *R. serpulatus*. They obtain peculiar rostrum cross-section, similar to «8» numeral created by deep lateral furrows, unusual among belemnites. These rostra were erected to a family Rhabdobelidae by Nalnjaeva in 1967.

In Upper Jurassic - Lower Cretaceous (Tithonian - Hauterivian), similar belemnite rostra can be found, attributed to genus *Pseudobelus* and family Duvaliidae. There is no certain opinion about *Rhabdobelus*-*Pseudobelus* relation: early authors united both in *Pseudobelus*, A.Naef considered possible relationship between *Rhabdobelus* and Duvaliidae via *Pseudobelus*; Jeletzky shared this opinion, and these genera became a link between suborders Belemnopseina and Belemnitina of his classification. Modern authors usually separate them in different families, thus considering convergent, or consider *Rhabdobelus* to be a synonym of *Pseudobelus* (R. Combemorel). The reasons for separating *Rhabdobelus* and *Pseudobelus* in separate families are: 1) large stratigraphic gap between *Rhabdobelus* and *Pseudobelus* and 2) the presence of the dorsal furrow underlying with a split in *Pseudobelus*.

First reason is not sufficient because of its "geological" nature, plus, there are some finds of *Pseudobelus*-like rostra in the gap: «*B. coquandus*» (Callovian-Oxfordian) and some Bathonian finds mentioned by H. Pugaczewska (1961).

The second reason was the subject of our investigation. Material from a unique locality Lozovoe of Upper Toarcian in Crimea (Ukraine) showed, that morphological variety of the genus is higher than it was considered. Among numerous *R. exilis* and *R. serpulatus* rostra, there were two unusual rostrum fragments found. One of them shows a median dorsal furrow, but split presence remains uncertain. In another one, there are three parallel shallow U-shaped furrows. Each fragment represents an undescribed species. Comparative morphological study of *Rhabdobelus* and *Pseudobelus* rostra has shown that:

1. Furrows on unusual *Rhabdobelus* fragments are dorsal, like in *Pseudobelus*.
2. Lateral furrows in both genera have similar origin – from «Doppellinen».
3. *Rhabdobelus* rostra has principal arrangement of furrows approaching to *Acrocoelites* and *Pseudohastites*, and this marks its origin.

So, there are strong morphological data showing that *Rhabdobelus* and *Pseudobelus* are part of a one phyletic line. The generic separation is still possible based on angular subquadrate cross-section in *Rhabdobelus*. So, *Pseudobelus* is better to remove from Duvaliidae to Rhabdobelidae. Anyway, hypothesis of convergence based on similar ecological habitat, now cannot be completely rejected.

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## ***Chalalabelus* finds from the Middle Volgian of Moscow city and the nature of enigmatic Diplobelida**

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Diplobelida is a coleoid order, combining rare isolated finds of peculiar Mesozoic coleoids, representing such genera as *Diplobelus*, *Vectibelus*, *Chalalabelus* and others. This group was erected by Naef (1922) as a family, and modern considerations on this taxon are based mostly on a detailed review made by Jeletzky (1981). The definitive characteristics are narrow proostracum and dorsal saddle at the suture line.

Our investigation is based on numerous finds of well-preserved *Chalalabelus* rostra (>40 specimens attributing to 2 species to be described), coming from Middle Volgian (virgatus-nikitini boundary interval) of Kuntsevo locality in Moscow, and numerous (>50 specimens) *Pavloviteuthis*-like (undescribed genus and species) rostra from the same locality. Phragmocone walls have not preserved in any specimen. We've also reviewed materials held in funds and described by previous Russian researchers (V.N.Shimansky, G.K.Kabanov, L.A.Doguzhaeva). Careful morphological study and systematic measurements of «diplobelid» phragmocones, both from collections and publications, has shown the distinct heterogeneity of the order. Despite for many Diplobelida finds described in literature some important features remain uncertain, even now all Diplobelida can be divided in two major groups:

1. Ventrally incurved phragmocones with wide angle (30-56°), narrow proostracum – 12-21% of camera width, suture line usually bearing chevron-like saddle, rostrum reduced or with rounded apex (genera *Chalalabelus*, *Vectibelus*, *Conoteuthis*). Stratigraphically these genera are like to form a phyletic line with a trend to gradual rostrum reduction and development of a chevron-like saddle.

2. Straight phragmocones with moderate apical angle (18-32°) and proostracum width about 28-33% of camera width, suture usually with rounded dorsal saddle; rostrum short, belemnite-like (genera *Diplobelus*, *Quiricobelus*, *Pavloviteuthis*, *Tauriconites* and possibly some more). There are no clear apomorphies and no obvious stratigraphic trends for this group, so this group needs to be restudied.

Next step of investigation was comparative microstructural study of rostra for both groups. *Chalalabelus* has shown that its rostra consist of pure aragonite and have specific microstructure, closely resembling such of *Kostromateuthis* and spirulids – from one side, and of Triassic *Belemnococeras* – from the second side. Surface texture of *Chalalabelus* rostra are identical to Tertiary spirulid rostra. All these genera are interpreted by us as a Mesozoic spirulid branch.

*Pavloviteuthis* rostra, both from our collections (Lower Jurassic) and Shimanky ones (Lower Cretaceous) consist of aragonite, and have typical «belemnite» microstructure. Their rostrum surfaces are smooth or slightly wrinkled, and there are some details approaching these rostra to Belemniteuthidae.

Thus, Diplobelida as it was recognized by Jeletzky, is an artificial group, fancifully combining Mesozoic Spirulidae and belemnite-like coleoids.

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## Ontogeny of *Didymoceras* Hyatt, 1894, in the Late Cretaceous (Middle and Upper Campanian) U. S. Western Interior

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Because of their striking and distinctive appearance, and wide spread occurrences, Scott and Cobban (1965) designated *D. nebrascense* (Meek and Hayden, 1856), *D. stevensoni* (Whitfield, 1877), and *D. cheyennense* (Meek and Hayden, 1856) as biostratigraphic zone-index species. Kennedy, Cobban and Scott (2000) designated *D. binodosum* (Kennedy and Cobban, 1993) and *D. jorgenseni* (Kennedy, Cobban and Scott, 2000), as sub-zone index species. Close examination of each of these species indicates that there are at least four distinct ontogenetic stages beginning immediately after the ammonitella. These include juvenile, adolescent, sub-adult, and adult stages.

The juvenile stages of *Didymoceras binodosum*, *D. jorgenseni* and *D. cheyennense* consist of an open planispiral coil of approximately two whorls while early whorls of *D. stevensoni* show an open planispiral coil of maybe one whorl. Unlike the other species, *D. nebrascense* appears to begin with the ammonitella followed by a straight limb before bending back. The adolescent stage varies greatly in the genus from one or two straight limbs to gently descending, non-contacting coils. The sub-adult stage varies from three to six helical coils that may or may not be in contact with adjacent coils, and may be either loosely or tightly coiled. The adult body chamber of all of the species is a retroversal hook that bends back so the animal, in most cases, would have been almost facing the earlier helix.

Extreme intraspecific variation within each species is the norm. Dimorphism is apparent and is based on the wide variation in absolute dimensions of the adults. Additionally, sinistral and dextral coiling of individuals is remarkably consistent, with about half of the specimens being one or the other. However, one extraordinary specimen of *Didymoceras nebrascense* indicates that the direction of coiling can change. The juvenile stage of this specimen grew in a sinistral coiling pattern, the animal then appears to have inverted its orientation, and the animal then grew with a dextral coiling pattern as an adolescent.

The apparent differences between the juvenile growth stage of *Didymoceras nebrascense* and the other *Didymoceras* species may have interesting taxonomic implications. Additionally, the similar appearance of the juvenile growth stages of co-occurring genera, especially *Spiroxybeloceras* and *Solenoceras*, may require further taxonomic revision.

# Internal Features of the Ammonitellas of some Tornoceratids from the Cherry Valley Limestone, New York State, U. S. A.

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The documentation of a similar septal structure in the ammonitellas of *Agoniatites vanuxemi* to that already described for tornoceratids has led to a reexamination of ammonitellas of tornoceratids. The specimens of *A. vanuxemi* and tornoceratids used in these studies are from the Middle Devonian Cherry Valley Limestone of New York State, U. S. A., but they come from very different units within it. The *Agoniatites* come from a black limestone rich in pyrite and phosphate, which promoted the preservation of organic structures within the blocky calcitic matrix. The ammonitellas studied were extracted from adult specimens. The tornoceratids come from a weathered friable shale layer. The ammonitellas examined are from juvenile specimens, many of which appear to be loose ammonitellas. The ammonitellas are preserved as blocky calcite and lack the pyrite and phosphate, making analysis more difficult. Specimens were embedded in an epoxy resin, ground down to a median plane, polished and etched with 5% HCL for ~ 10 seconds. Shell walls and septa appear as more heavily etched grooves surrounded by the large blocks of calcite. Septal membranes were associated with several postembryonic septa in one specimen. A primary varix was also documented. The septal junction at the dorsalmost point of the initial chamber was examined. The first two septa join together with the shell wall at this point. The first septum (= proseptum) is asymmetrically concave adapically and attaches to the dorsal wall of the initial chamber which extends into the first chamber. The second septum attaches at the end of this extension. The third septum attaches to the dorsal wall of the ammonitella coil. This arrangement differs from *Agoniatites*, where all three septa join the dorsal wall of the ammonitella at a single point. This difference is likely the result of a more tightly coiled ammonitella and a further shortening of the dorsal wall of the initial chamber. As the dorsal wall of the initial chamber of tornoceratids is forced inward, it bends and drags the attachment point of the first septum inside of the initial chamber. An examination of this junction in different taxa offers a promising approach to understanding the evolution of the ammonitellas of ammonoids.



## The Devonian Nekton Revolution

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Impressive discoveries of Neoproterozoic and Early Palaeozoic Fossilagerstaetten drew the attention on evolutionary and ecological processes of these timespans. It almost seemed that, except for some of the "Big Five", nothing essential happened after the Ordovician. Such a scenario is certainly not true.

Contrariwise, some major ecological fluctuations have been recorded from the Devonian, several of which have less prominent Silurian precursors. Famous examples are the radiation of land plants and jawed fish (both known already from the pre-Devonian). During the Devonian, several animal groups conquered the land (various arthropods and possibly tetrapods). Marine invertebrates show significant ecological and morphological changes: Important cephalopod groups such as bactritoids as well as ammonoids evolved and reef growth increased until the Late Devonian crises. Both the global rise and fall of dacroconarids occurred, graptolites became extinct, and various mollusc clades modified early ontogenetic strategies during the Devonian, documenting a planktonic turnover. In addition, there is a macroecological change in marine faunas from a demersal (swimming close to the sea-floor) and planktonic habit towards a more active nektonic habit.

Various interpretations are at hand to explain this Devonian Nekton Revolution: (1) Demersal and nektonic modes of life were probably initially driven by competition in the diversity-saturated benthic habitats as well as (2) the availability of rich planktonic food resources (as reflected in evolutionary alterations in early ontogenetic stages of many mollusks). Escalatory feedbacks probably promoted the rapid evolution of nekton (jawed fish and some derived cephalopod groups in particular) in the Devonian, as suggested by the sequence and tempo of water-column occupation. Potentially, both these radiations and the Givetian to Famennian mass-extinctions were linked to a pronounced increase in nutrient input to sea surface waters during eutrophication episodes.

## Devonian pearls and ammonoid-endoparasite coevolution

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Pits in internal moulds of Devonian ammonoids are already known since several decades. These pits are the moulds of pearl-like structures on the inner shell wall. New specimens from Morocco revealed novel details of these structures: Most, if not all, of these pits are lined by ammonoid shell covering tiny tubes which are attached to the outer shell wall. In this article we discuss the nature of these encapsulated tubes. Based on differences in pit morphology, size, and arrangement, we group the pits in five types. We used these traits for a simple cladistic analysis and compared the resulting consensus tree to the phylogeny of ammonoids. It appears likely that the parasites underwent a coevolution with the ammonoids over 10 to 15 Ma including evolutionary events like cospeciation, “drowning on arrival” (end of parasite lineage near base of a new host clade) and “missing the boat” (parasite lineage misses a new host clade), while “swapping the boat” (changing from one to another host clade) did probably not occur. Because of the lack of fossilised soft-tissues only speculations can be made on the parasite’s systematic affiliation, its life-cycle, its strategy and the ecological framework, but we interpret them as documents from trematode infestations. This extends the fossil record of parasitic trematodes to the Early Devonian.

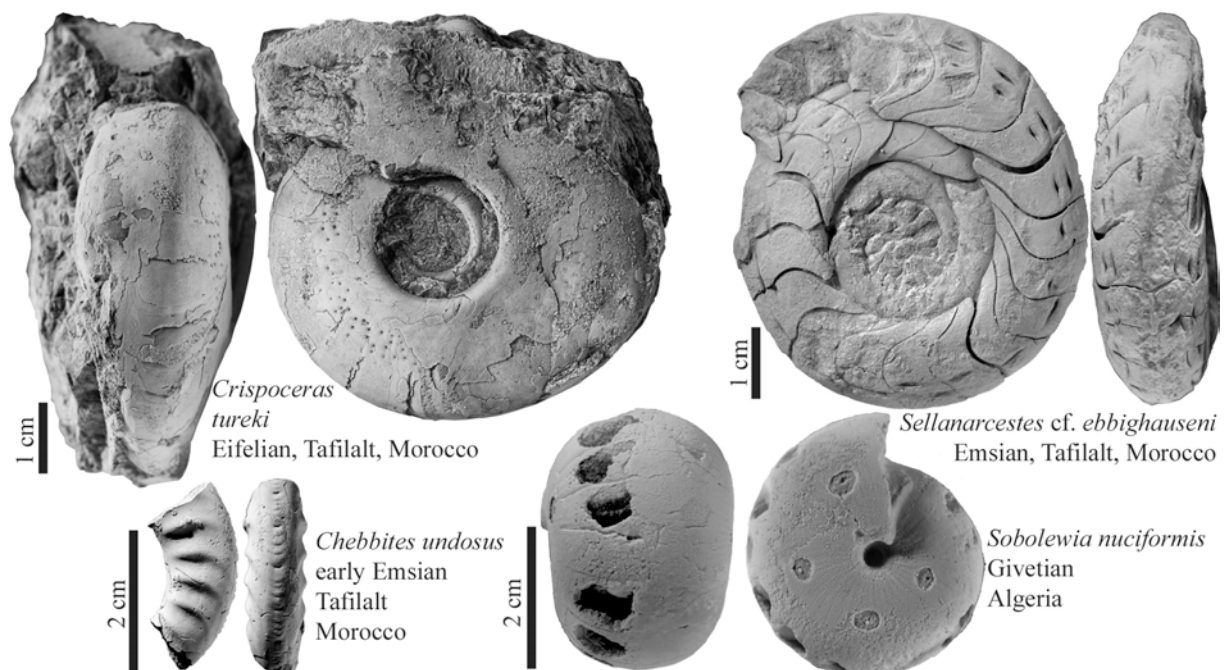


Figure: Examples of ammonoids with Housean pits, showing four of the five different types of pits which we documented from the Emsian to Givetian (Devonian). Note the differences in pit size, number per whorl, localisation, and arrangement.

## Early Carboniferous palaeogeography based on ammonoids

*Dieter Korn*

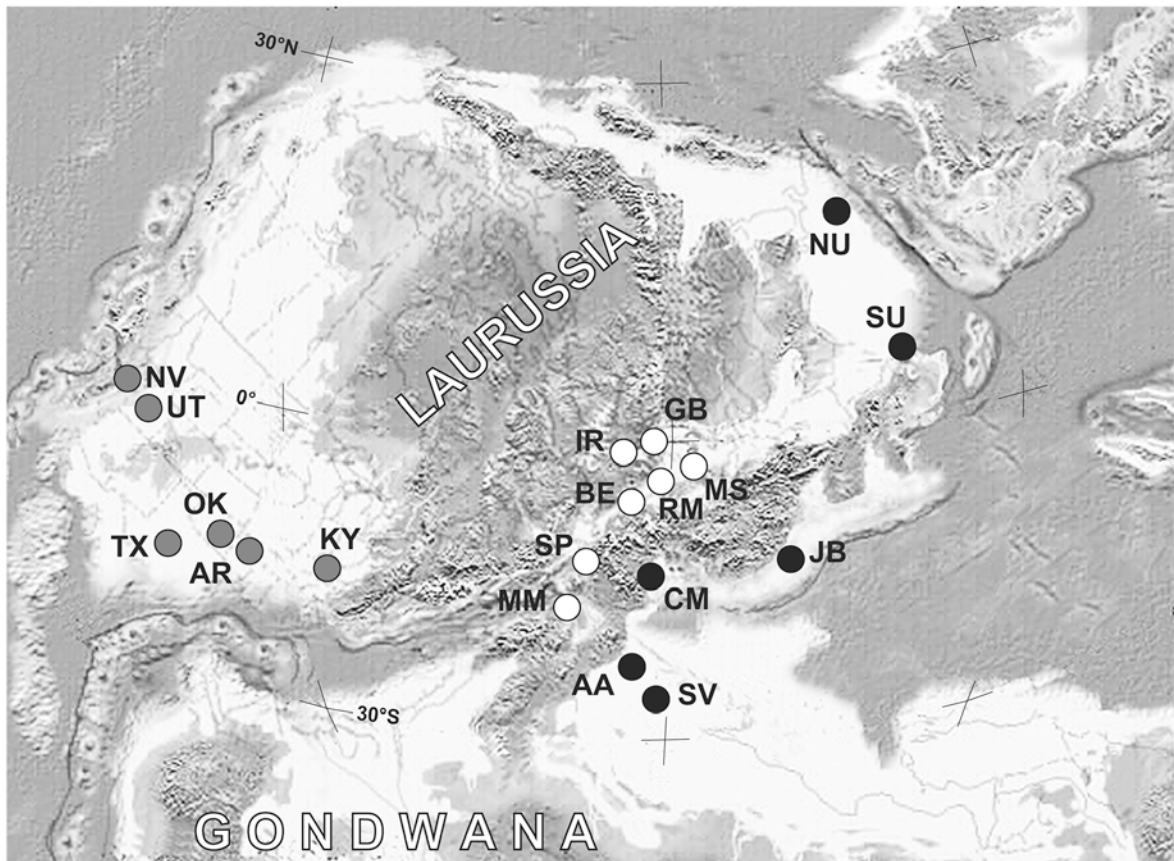
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The abundance of ammonoids and their rapid evolution make them valuable tools for palaeogeographic investigations. The Early Carboniferous (Mississippian) was a time in which a rather cosmopolitan world of pelagic organisms has changed into provincialism. Major plate movements, causing e.g. the Variscan Orogeny, may have played a crucial role for this development. They dismembered the large shelf of the Rheic Ocean between Laurussia and Pangaea, resulting in smaller basins, which were characterised by distinct oceanographic properties. In the process towards the formation of a Pangaea, the convergence of Laurussia and Gondwana produced a land barrier between the European, North American, and Mediterranean ammonoid occurrences.

Iberian and north-western African occurrences of Early Carboniferous (Mississippian) ammonoids show a distinct pattern of increasing provincialism during the Late Viséan. Clear separation of northern Variscan and southern Variscan/north Gondwanan ammonoid provinces took place during the Brigantian regression by decreasing numbers of common genera and higher taxa in both realms. The north-westernmost African occurrences, i.e. the Moroccan Meseta and the Jerada Basin north of the South Atlas Fault show very close biogeographic relationships to the North Variscan occurrences (South Portuguese Zone as well as the British Isles and Central Europe). Latest Viséan occurrences south of the High Atlas Fault, such as the Anti-Atlas of Morocco and the Saoura Valley of Algeria differ strikingly in their composition of genera and are much closer related to the Palaeotethyan occurrences in the Cantabrian Mountains, the Montagne Noire, and the South Urals. The ammonoids provide firm evidence for the continuation of the Subvariscan/Rhenohercynian sea into the north-westernmost part of Africa. Close similarity of ammonoid communities suggest the existence of a connection of the South Variscan and north Gondwanan shelves in Viséan times and a narrow Palaeotethyan Ocean.

The quantitative analysis of the regions with sufficiently rich ammonoid occurrences (Antler Foreland Basin of Nevada and Utah, American Midcontinent, North England, Rhenish Mountains, Cantabrian Mountains, Jadar Block of Serbia, South Portuguese Zone, Jerada Basin, Anti-Atlas, South Urals) shows the following biogeographic patterns:

Two major realms can be separated for the Viséan-Serpukhovian boundary, both composed of two provinces. (1) A south-eastern realm includes (1a) a Uralian-North Gondwanan province (including the South Urals and the Saoura Valley of Algeria) and (1b) a South Variscan province (Cantabrian Mountains and Balkan terranes). (2) A north-western realm is composed (2a) of a North Variscan province (Central and North-western Europe) and (2b) a North American province (American Midcontinent and Antler Foreland Basin).



(image after Ron Blakey)

- Occurrences of the *Dombarites-Platygoniatites-Hypergoniatites* assemblage
- Occurrences of a *Dombarites* assemblage without *Platygoniatites* and *Hypergoniatites*
- Occurrences without *Dombarites*

*Figure: Latest Viséan/earliest Serpukhovian palaeogeography*

(Abstract: Korn)

## Evolution and morphologic trends in the Upper Cretaceous belemnite family Belemnitellidae Pavlow, 1914.

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Morphology of the alveolar part of rostrum belongs to a very important taxonomic features in belemnitellids. In genera *Actinocamax* Miller and *Praeactinocamax* Naidin it is formed by conical (highly conical in *Actinocamax*) alveolar fracture or less and more deep pseudoalveolus (in *Praeactinocamax*), and by a short part of the ventral notch preserved (in *Praeactinocamax* and partly in *Goniocamax* Naidin ancestors). In phylogenetically advanced belemnitellids (i. e. genera *Goniocamax*, *Goniot euthis* Bayle, *Belemnelloamax* Naidin, *Belemnitella* d'Orbigny, *Belemnella* Nowak and *Fusiteuthis* Kongiel), the ventral notch is well developed and it is connected with important morphological structures.

The origin of the Upper Cretaceous belemnite genus *Goniocamax* and consequently *Belemnitella* stock, is explained by the gradual calcification of the anterior part of the rostrum and by the pseudoalveolus deepening. The ancestors of both genera are derived from genus *Praeactinocamax*. The pseudoalveolus deepening and, equally, its walls calcification happened selectively in different evolutionary lineages. The Upper Cretaceous genus *Goniocamax* played an important role in *Goniot euthis* and *Belemnitella* evolution. Whereas, the evolution of *Goniot euthis* and *Belemnitella* has been described in great details (Ernst, 1964; Naidin, 1964; Christensen et Schulz, 1997), the origin of *Goniocamax* was considered to be unclear, however, it was partly suggested to lie in some species of *Praeactinocamax* in the Central Russian Subprovince (CRS), especially in some rare endemics (Christensen 1997; Košťák, 2004). The earliest species of *Belemnitella* (*B. schmidí*) is considered as the transitional taxon possessing characters in common with the genera *Goniocamax* and *Belemnitella* (Christensen et Schulz, 1997). It has probably been evolved from *G. lundgreni* by allopatric speciation (Christensen, 1997). During belemnitellid evolution, the pseudoalveolus deepening, the true alveolus forming and changes in the rostrum sizes are well recognized in major evolutionary lineages.

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## Well preserved buccal mass in two Late Cretaceous ammonites

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We report the first detailed evidence of a radula in two Late Cretaceous (70-80 Myr-old) ammonites from the U.S Western Interior, *Baculites* sp. (smooth) and *Rhaeboceras halli* (Meek and Hayden 1856) revealed by propagation phase contrast Synchrotron X-ray microtomography (PPC-SR- $\mu$ CT) (Tafforeau et al 2006). Both of these ammonites are members of a monophyletic group of Jurassic and Cretaceous ammonites, the Aptychophora (Engeser & Keupp 2002), that possess a unique type of lower jaw. These jaws are covered with two calcareous plates (an aptychus). The buccal mass elements were found *in situ* between the valves of the aptychi. Three specimens of *Baculites* sp. from the Pierre Shale had the radula preserved between the valves of the aptychus. (AMNH 66253, AMNH 55901, AMNH 66267).

In *Baculites* sp. the upper jaw and food remnants were found as well (AMNH 66253). The upper jaw has a blunt anterior margin and is extremely thin (140 $\mu$ m thick at the anterior margin). Each radular row consisted of nine elements, including seven teeth and two marginal plates. The teeth are delicate, multicuspidate, "comb-like", and the marginal teeth are extremely prominent and sabre-shaped. One radula was found in *Rhaeboceras halli* (AMNH 55901) in a specimen presenting the upper and lower jaw and the hook like structure described by Kennedy *et al.* as a radula (2002). Fewer teeth were preserved in *Rhaeboceras*, the teeth are multicuspidate and more robust than in *Baculites* sp, the sabre-shaped marginal tooth is also present. The radulae were compared to the radular morphology of recent mollusks; similar structures are found in pelagic mollusks, with plankton feeding habits. Moreover, crustaceans remnants as well as a shell of a pelagic gastropod were found between the jaws of *Baculites* sp.. All the elements belong to zooplankton. Therefore, *Baculites* sp., and probably other aptychiphorans, such as *Rhaeboceras halli* fed on zooplankton. Authors (Kennedy et al 2002, Lehmann 1981, Morton & Nixon 1897, Seilacher 1993) have already suggested that the aptychophoran buccal mass was an adaptation for feeding on small prey. The discovery of the buccal mass elements in *Baculites* sp. supports this hypothesis and gives new insights on ammonoid paleobiology.

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## Modifications and adaptations of arm use in *Octopus vulgaris*

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The motor control of the eight highly flexible arms of the common octopus (*Octopus vulgaris*) has been the focus of several recent studies. In our present studies we investigate modifying feed forward systems through learning and the impact on the online motor control output by sensory feedback. The aim of these studies is to elucidate, on which system the motor control programs are depending to perform tasks like reaching, fetching, grasping or movement correction.

Therefore we forced our animals to perform tasks challenging their standard repertoire of arm movements: In our first experiment we introduced a physical constrain to the base of the octopus arm to investigate its influence on motor primitives like reaching, fetching and the bend propagation (a feed forward program). Animals were placed inside a transparent Perspex box (40x40x40cm) with a hole at the center of every surface that allowed the insertion of a single arm only (1.5cm Ø). During the experiment the subjects had to reach out through a hole towards a target, to retrieve a food reward. While the accuracy of the reaching movement towards a target did not improve in consecutive experimental sessions, the accuracy and speed of fetching movements improved both within and across sessions.

A second set of experiments was conducted to investigate the ability of octopuses to use proprioceptive information on the position of the arm (i.e. sensory feedback) during a learning task.

Here the octopuses had to learn to turn a single arm left or right in an opaque Y shaped maze to get rewarded. They received no visual, chemical or tactile cues that would help them to complete this task. Five out of six subjects were able to successfully complete the task in less than 90 trials. These experiments show that octopuses are able to modify the execution of motor output and use sensory feedback for on-line motor control, even in movements that more resemble searching and probing. This suggests that octopuses have a more elaborate control over their arm movements than previously thought.



## Is *Nautilus* an endangered taxon?

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*Nautilus* and *Allonautilus* are the last surviving externally shelled cephalopods. Consequently, researchers on extinct cephalopods are extremely interested in all aspects of these living fossils. In fact, in the past 100+ years, fossil cephalopod researchers have lead the way in discovering much of what we know about these animals. Present-day nautilids occur in the Indo-Pacific, but their distribution is spotty, probably because of poor sampling of the deep habitats in which they live. Recent phylogenetic work using molecular characters suggests that these animals are undergoing a period of evolutionary radiation. The basal divergence between *Nautilus* and *Allonautilus* probably occurred in the waters surrounding the present-day island of New Guinea and the northern part of the Great Barrier Reef in northeast Australia. This was followed by a migration to the east by the common ancestor of *N. macromphalus* and the *N. pompilius* populations in Vanuatu, Fiji, and American Samoa. A subsequent migration to the west led to the founding of populations off the west coast of Australia, the Philippines, as well as Palau and Indonesia. The life history of these animals makes them susceptible to over-exploitation. They are slow growing and reach sexual maturity in 10-15 years. Females produce few large, yolk-rich eggs, which require almost one year to hatch. Over fishing of nautilus has been reported in some areas in the Indo-Pacific, for example, the Philippines. As a result, it has been proposed that both genera be placed on the CITES list of endangered species. However, additional work is necessary to develop a better understanding of the population dynamics of nautilus at different sites before such a decision is made.

## Mode of life and habitat of *Scaphites*

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Scaphitid ammonites (scaphites) are among the most common ammonites in the Upper Cretaceous of the U.S. Western Interior. We have examined species of Hoploscaphites from the Campanian and Maastrichtian Pierre Shale and Bearpaw Shale for clues about their mode of life and habitat. Like many other ammonites, scaphites exhibit determinate growth. The “morphogenetic” countdown begins at the point at which the shell departs from the spiral coil and develops into a shaft and recurved hook. This is accompanied by a reduction in the spacing of ribs and tubercles on the hook and the formation of a constriction and varix at the aperture. Internally, this coincides with a decrease in septal spacing. The common association of scaphites and benthic fossils (e.g., *Inoceramus*) is interpreted as reflecting oxygen-rich episodes in the history of the Western Interior Seaway. Habitat depths are estimated at less than 100 m, based on faunal associations and studies of the mechanical strength of the septa and siphuncle. Analyses of the isotopic composition of the shells suggest that the animals lived near the sea floor. The high angle of orientation of the aperture at maturity (approximately 90°) seems incompatible with a nektobenthic mode of life. The constricted aperture ending in a thin lip would also have restricted unimpeded movement of the soft body outside of the aperture. Adults were probably poor swimmers, based on a comparison of their musculature (as inferred from their muscle scars) with that of nautilus (assuming that such a comparison is valid). The lack of a hyponomic sinus on the midventer would have prevented the animal from extending its hyponome below the shell in order to swim forward. As a consequence, scaphites may have been limited in their movement to swimming backward or downward, and may have exploited a low-energy lifestyle, remaining at a single site for an extended period of time. They may have behaved as floating filter feeders consuming small prey in the water column, which is consistent with the presence of an aptychus-type lower jaw. The large ventrolateral tubercles on the body chamber served as an anti-predatory device against attacks from behind. Indeed, healed injuries, as well as lethal injuries, are common on the adapical end of the body chamber. It is possible that the calcified aptychi of the lower jaws may have provided additional protection against predators in the apertural region. The male may have been equipped with a specially modified arm covered with hook like structures (the hectocotylus) that would have allowed the transfer of spermatophores from the male to the female during copulation.

## Evolutionary significance of cephalopod egg size during mass extinctions

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The Ammonoidea and Nautiloidea were the most abundant and diverse cephalopods inhabiting the Middle - Late Palaeozoic and Mesozoic seas. The Nautiloidea survived both the P/T and K/T-extinctions. The Ammonoidea narrowly passed through the P/T boundary and became extinct at the end of the Cretaceous, even though they were the more diverse group, both morphologically and ecologically than Nautiloidea.

The small egg size of ammonoids evolved to reproduce in pelagic layers with high unpredictable mortality because of unstable environment. They evolved high diversity and had relatively short stratigraphic ranges (Stephen, Stanton, 2002). The colonisation of the oceanic epipelagial was accompanied by a further decrease in egg size in Ancyloceratina, as happened in extant cephalopods. The move of Lytoceratina to colder mesopelagic waters provoked a progressive increase in egg size, which also is the case of modern coleoids. The egg size varied with environmental temperatures: Mesozoic boreal ammonoids produced larger eggs than tropical species (Drushchits, Doguzhaeva, 1981). During the Turonian global warming it decreased both in shelf-dwelling Ammonitina and mesopelagic Lytoceratina, with a gradual increase during the subsequent cooling. Ammonoidea became extinct simultaneously with another dominant small-egged cephalopod group – the Coleoid Belemnitida. The most prominent teleost fish that became extinct at the same time were five families of ecological siblings of modern large-bodied predators like tunas and billfishes (Friedman, 2009), which also are small-egged broadcast spawners.

Nautiloids laid large eggs on the sea floor in a relatively predictable and stable environment. Such an attachment to near-bottom habitats prevented an expansion into open oceanic waters. They were low diverse in respect to ammonoids and had longer stratigraphic ranges. Possibly, the absence of a vulnerable paralarval stage saved them from extinction at the K/T boundary. This boundary was also crossed by Sepiida - another large – egged cephalopod group as well as by squids and octopods. Among fish, the extremely large-egged Elasmobranchii and Coelacanthiformes persisted through K/T boundary as well as through many other extinction events.

The appearance of these two types of cephalopod reproductive strategies is in agreement with Vance's (1973) hypothesis that only the extremes of egg size are evolutionary stable strategies. Small – egged, high fecund species are more vulnerable to disasters of a climatic / abiotic character through sudden impact on vulnerable early stages. Low fecund, large-egged species with larger and more resilient offsprings are more vulnerable to disasters of ecological / biotic character influencing later stages of ontogenesis, such as the appearance of new competitors, new predators and fishery.

## **Portable XRF instruments in the elemental analysis of ammonite shell and matrix**

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Portable X-Ray Fluorescent (XRF) instruments (“material analyzers”) were developed in the 1970’s to detect lead in paint. Since that time they have been greatly improved and are now commonly used to search for hazardous substances in toys, food and other products that come in close contact with humans and are consumed or absorbed. Currently, XRF spectroscopy is widely used in the elemental analysis of environmental, industrial and biological waste; testing of geological and mining samples; and confirmation of exotic metals for medical device manufacturing. Compared to other XRF techniques such as synchrotron radiation (see Larson et al., 2010), the handheld XRF has the advantage of being non-destructive, fast and cost-effective. Furthermore, it allows for remarkably accurate detection in either percentages or parts per million (ppm) across much of the Periodic Table for elements heavier than fluorine.

We are using a handheld, portable XRF material analyzer from Oxford Instruments, the XMET 5000, for the study of ammonite shell and rocks containing ammonites. The goal is to determine whether or not shell color is determined by elemental differences in aragonite. At the same time, samples are also taken of their host rock in the attempt to learn if ammonite-bearing rocks from one location had similar percentages of the same elements; and if they differ significantly enough to distinguish them from ammonite-bearing rocks from other locations. Portable XRF may be a method to determine if a “signature” exists for confirmation of different localities; thus allowing us to determine where fossils without field notes were originally collected. We are also considering the use of portable XRF in other novel and, as of yet, untested ways that could benefit paleontology and further the study of fossil cephalopods.

Larson, N.L., R.W. Morton, P.L. Larson and U. Bergmann, 2010. A new look at fossil cephalopods. In Tanabe, K., Shigeta, Y., Sasaki, T. & Hirano, H. (eds.), *Cephalopods - Present and Past*, Tokai University Press, Tokyo, p. 303-314.

## Observations of *Baculites* from the lower Campanian, Western Interior

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A large concentration of baculite steinkerns and phragmocones occurs near Belle Fourche, South Dakota, in the *Baculites* sp. smooth Range Zone of the Western Interior. The abundance and preservation of these ammonites holds the keys to much of the biological secrets of the genus while representing the ontogeny and taphonomy of a single species of ammonite. The preservation of these ammonites is exquisite and a high percentage exhibit beautiful, iridescent muscle scars as well as other intricate markings under their shells. Jaws and radula have been discovered within the body chambers of some specimens (Landman, Larson and Cobban, 2007). These fossils may also provide insights into the breeding habits of baculites. The sheer numbers of mature ammonite shells suggest that, like many modern cephalopods, generations of baculites probably returned to the same areas year after year to spawn and die.

Occasionally, multitudes of pits are visible on the body chamber steinkerns, giving the specimens a spotted appearance. The pits are shallow, circular to elliptical, flat-bottomed and typically <1 mm in diameter. They are impressed into the sediment that fills the body chamber and appear in positive relief as pedestals on the inner surfaces of shell fragments exfoliated from the body chambers. They were interpreted to be the result of an infestation by an unknown parasitic organism by Kennedy and Klinger (2001). Gill & Cobban (1966) interpreted identical spots in baculites from the Red Bird section of Wyoming as sites where epibionts (sclerobionts) were attached to the inside of the shell, locally protecting the aragonite from post-mortem dissolution. This phenomenon has since been termed 'epibiont shadowing' by Palmer et al. (1993). The epibiont that created the spots remains enigmatic. Although it may have been a small species of cryptic sclerobiont, the spots could alternatively mark sites where individual eggs from egg masses were attached in a protected habitat afforded by the body chamber of the dead baculite. However, the lack of morphological detail offered by the spots makes these hypotheses very difficult to test. A speculative scenario is that the egg-laying animal was also a baculite that took advantage of the presence of shells from earlier generations of conspecific baculites at spawning grounds where adult mortality rates were high.

## Seasonal trends of reproductive cycle of *Octopus vulgaris* in two environmental distinct coastal areas

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*Octopus vulgaris* is a bottom-dwelling species with pelagic paralarvae. The species is widely distributed over mainland shelf waters, as well as in distant oceanic islands and seamounts of the eastern Atlantic, with mature individuals found all year around, although with specific intensive breeding seasons. The paralarval phase can represent up to 25% of the longevity of the species and is highly sensitive to environmental conditions, including water mass characteristics and food availability. Data on maturation and other biological parameters collected between January 2007 and December 2009 are used to define breeding seasons for octopus landed by artisanal fisheries in two oceanographically distinct Portuguese coastal areas: the northwest (western Iberia upwelling ecosystem) and the south (Gulf of Cadiz ecosystem). In order to identify the specific breeding seasons we follow monthly the proportion of mature specimens and the maturity ogive characteristics as population parameters, as well as the Gonad-Somatic Index and the Hayashi Index as biological parameters. Mature males and females are found all year around. The proportion of mature females presents important breeding indications in both coastal areas but at different timings. The indication of different breeding seasons between geographical areas is confirmed by the monthly evolution of female gonad-somatic indices. Size at maturity of both females and males is also studied in order to evaluate reproductive differences between both areas. The spawning strategies of octopus on the Portuguese coast and other upwelling systems show that the species is capable of adjusting its population dynamics in terms of spatial and temporal optimisation of the survival of the planktonic paralarvae.

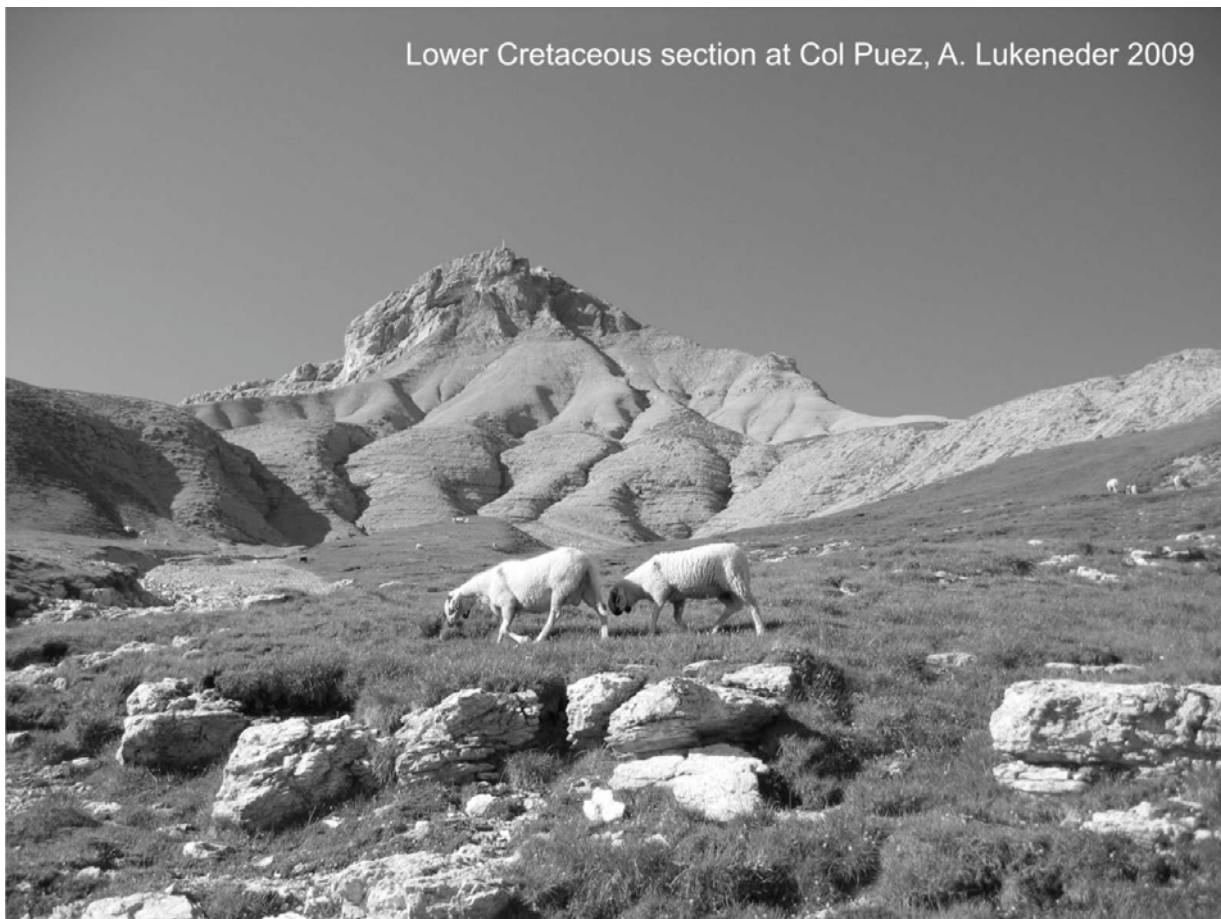
## New ammonite data from the Lower Cretaceous Puez key-section in the Dolomites (Southern Alps; N-Italy; FWF project P20018-N10)

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Investigations on different fossil groups within fields of isotopic, magneto- and cyclostratigraphic and geochemical analysis are combined to extract the Early Cretaceous history of environmental changes as displayed by the sea level and climate. This results in calibrating ammonite biostratigraphy and magnetostratigraphy through isotope data. The main investigation topics of the submitted project within the above-described framework are the biostratigraphic, palaeoecological, palaeobiogeographic, lithostratigraphic, cyclostratigraphic and magnetostratigraphic development of the Early Cretaceous of the Puez area. The main locality within the project is located in huge outcrops located at the southern margin of the Puez Plateau. It is located within the area of the Puez-Geisler Nature park in the northern part of the Dolomites (Trentino-Alto Adige; South Tyrol). Lower Cretaceous ammonoids ( $n = 640$ ) were collected at the Puez locality in the Dolomites of Southern Tyrol. The cephalopod fauna from the limestones to marls indicates Late Valanginian to Late Albian age. The underlying Biancone Formation is of Early to Late Valanginian. The ammonoid fauna comprises 48 different genera, each apparently represented by one to three species. The complete occurrence at the Puez section is dominated by the Phylloceratina (30%) and the Ammonitina (34%). *Phyllopachyceras* (17%) and *Phylloceras* (13%) from the Phylloceratina are the most frequent components, followed by *Lytoceras* (12%) from the Lytoceratina, and *Barremites* (10%) and *Melchiorites* (8%) from the Ammonitina. The following index ammonites could be detected so far: the latest Valanginian *Criosarasinella furcillata* (C. furcillata Zone and Subzone), for the middle Early Hauterivian *Olcostephanus (Jeannoticeras) jeannoti* (O. (J.) jeannoti Subzone), and *Toxancyloceras vandenheckii* for the early Late Barremian (T. vandenheckii Zone). The ammonoid fauna contains only descendants of the Mediterranean Province (Tethyan Realm). Most affinities of the cephalopod fauna are observed with faunas from the adjacent areas of Italy (Lessini Mountains, Belluno, Trento Plateau), the Northern Calcareous Alps and the Bakony, Geresce and Mecsek Mountains of Hungary. This is explained by the neighbouring position of the latter areas during the Early Cretaceous on the Apulian/Adria block and the Alpine-Carpathian microplate. Lower Cretaceous (Valanginian-Albian) deposits of the Puez locality yield remarkable amounts of specimens of different ammonoid taxa showing unique epifaunal encrustations by the scleractinian, ahermatypic solitary coral ?*Cycloseris* Lamarck, 1801. The pattern of infestation clearly documents a preference of the adherent taxa for the outer shell surface of the ammonoids, whereas the inner surface remains barren. The exact stratigraphically dating of the ammonoid fauna allows synchronously to clear the age of the infested corals and the autecological history of this new ammonoid/coral palaeocommunity.

Lower Cretaceous section at Col Puez, A. Lukeneder 2009



*Figure: Lower Cretaceous section at Col Puez, A. Lukeneder 2009*

*(Abstract: Lukeneder)*



## Evolution and formation of *Nautilus macromphalus* nacre: biochemistry and proteomic of the shell organic matrix

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In mollusks, the shell formation is a genetically controlled process handled by the calcifying mantle cells. One of the most studied shell texture is the nacre, also called mother-of-pearl, the lustrous aragonitic layer that constitutes the internal part of the shell of several bivalves, a few gastropods and one cephalopod, the nautilus. Like other shell texture, nacre contains a minor organic fraction, which displays a wide range of functions in relation with the biomineralization process. Here, we have characterized biochemically the nacre matrix of the cephalopod *Nautilus macromphalus*.

The acido-soluble matrix contains a mixture of polydisperse and discrete proteins, glycoproteins and proteoglycans, which inhibits the *in vitro* precipitation of  $\text{CaCO}_3$ , interacts with the formation of calcite crystals, and binds  $\text{Ca}^{2+}$  ions in solution. Although the saccharidic moieties are not involved in binding calcium, they participate to the modulation of the shape of calcite crystals grown *in vitro*. On 2-DE, the different components of the nacre matrix migrate either at very acidic or at very basic pI. In addition, we have used a 'shellomic' approach (proteomics applied to the shell matrix) on the acetic soluble and acetic insoluble matrices, as well as on spots obtained after 2-D electrophoresis. Our data demonstrate that the so-called insoluble and soluble matrices contain numerous shared peptides. Furthermore, while most of the obtained partial sequences do not fit with known molluscan shell proteins, few of them partly match with shell proteins of bivalvian origin. Nautilin-63, a 63 kDa glycoprotein was purified, partially sequenced and biochemically analyzed. These findings have implications in the knowledge of the macro-evolution of molluscan shell matrices.

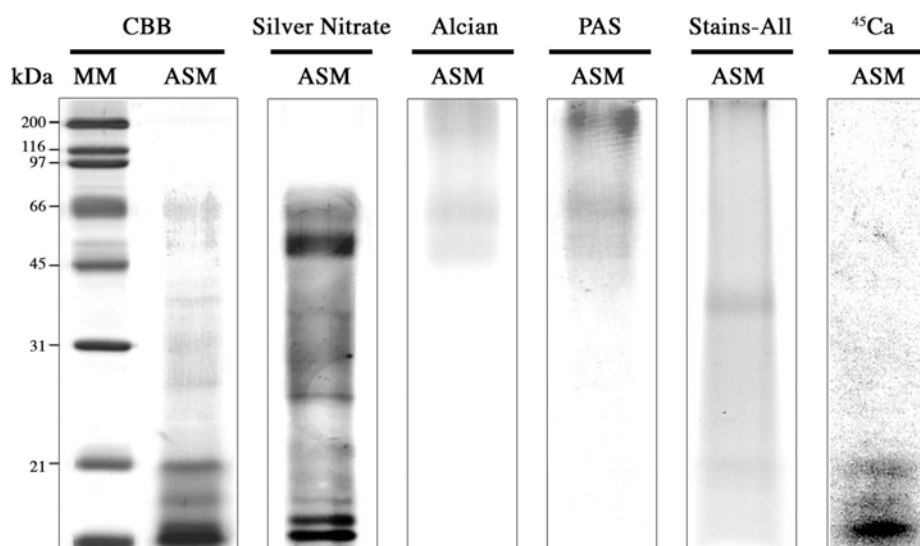


Figure: SDS-PAGE analysis of the ASM of *Nautilus macromphalus* nacre. 12% acrylamide gels were stained with CBB, silver nitrate, Alcian blue, PAS, Stains-All, from left to right. The last right lane corresponds to the result of the calcium overlay test ( $^{45}\text{Ca}$ ). MM, molecular mass markers.

## The molluscan shell: formation, origin, evolution

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For a decade, the field of mollusc shell biomineralization has accomplished remarkable progresses. The most recent advances deal more particularly with the structure of shell biominerals at the nanoscale, and with the identification of an increasing number of shell matrix protein components. Although the organic matrix represents usually less than 5% of the shell weight, it is however the major component that controls different aspects of the shell formation process. Until recently, the classical paradigm was to consider that the control of shell synthesis at the biocrystal scale was performed primarily by two mechanisms: crystal nucleation and growth inhibition. New concepts and emerging models try now to translate a more complex and dynamic reality, which is remarkably illustrated by the wide variety of shell proteins, characterized in the last few years (Marin *et al.*, 2008). These proteins cover a broad spectrum of *pI*, from very acidic to very basic. The primary structure of a number of them is composed of different domains, suggesting that these proteins are multifunctional. Some of them exhibit enzymatic activities. Others may be involved in cell signalling. Some others have remarkable crystal-binding properties, and may even have an effect at the level of crystal lattice. Today, the extra-cellular calcifying shell matrix appears as a whole integrated system, which regulates protein-mineral and protein-protein interactions as well as feedback interactions between the biominerals and the calcifying epithelium that synthesized them.

From an evolutionary viewpoint, the analysis of shell proteins offers fascinating perspectives for understanding how calcification was implemented in molluscs at the dawn of the Cambrian times, and for following the long-term evolution of calcifying systems. The example of nacre is particularly striking: nacre is one of the microstructures, known since the Cambro-Ordovician, and which is present in four molluscan classes, the monoplacophorans, the bivalves, the gastropods and the cephalopods. Because of its temporal stability, nacre is supposed to be evolutionary constrained. The question whether all nacres are truly homologous from class to class, *i.e.*, whether they share similar/homologous matrix protein assemblages can be tackled by using proteomics alone or proteomics supported by existing transcriptomic data. Our approach, applied on selected nacro-prismatic mollusc genera (*Unio*, *Pinctada*, *Mytilus*, for bivalves; *Nautilus* for cephalopods; *Haliotis* for gastropods) shows that the proteins constitutive of the nacre matrix are much more diverse than expected, and that many of them present in one class do not have homologous representatives in the other classes. Only a limited number of key molecular functions, such as carbonic anhydrase, or protease inhibitor, would be shared by all tested genera. This example gives a glimpse on the unexpected "evolutionary plasticity" of shell matrix assemblages.

Marin, F., Luquet, G., Marie, B., and Medakovic, D., 2008. *Curr. Topics Dev. Biol.*, 80, 209-276.

## Constructing a language from skin displays of squid

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The variety of pigmented and reflective elements on the skin of cephalopods allows for a diversity in display components. Moynihan (1985) has suggested that the resulting spatial array of main and secondary components of displays may be analogous to human word categories. He proposed that peripheral displays may modify central ones, like adjectives and adverbs, to change the 'meaning' of central ones. Alternately, peripheral components may simply enhance the emphasis of the central one, making the display more intense. Observational data from the study of *Sepioteuthis sepioidea* Caribbean reef squid allows for testing of these two alternates. Different peripherals, such as the fin base stripe and brown fins, may combine with central ones such as the zebra pattern. The results suggest that the presence of peripheral components does not change the meaning of central ones, but may correlate with higher intensity of central ones. Thus the combinations do not represent a parallel to language formed on the cephalopod skin.

## **Ammonite mass mortality (200 000 000 !!! specimens) as proxy for the Carnian Crisis (Taurus, Turkey) – 3D modelling of the Carnian Crisis (FWF Project P22109-B17)**

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The Upper Triassic in general, and the Carnian stage in detail was devastated by one of the most severe ecological crisis of the Mesozoic Era, the Carnian Crisis (= Carnian Pluvial Event), when the carbonate platforms demised and with them most of the reef-builders disappeared. The *Orthocelites* assemblage (ammonoids, cephalopods) was formed in the Carnian Crisis, now located at the boundary from Kartoz and Kasimlar Formation (Anatolia, Turkey), can act as proxy for the environmental activities and biotic crisis in the Carnian time. It has to be noted that the ultimate cause of this drastic Mesozoic crisis is still under comprehensive discussion. The main investigation topics of the project are the palaeoecologic, palaeobiogeographic, litho-, cyclo- and magnetostratigraphic development of the Upper Triassic (Carnian) ammonoid mass-occurrence at the Asagiyaylabel section in Anatolia (Turkey), formed during the Carnian Crisis. This area is a key section within the Taurids and has a connecting and intermediate position. Situated on the western end of the Cimmerian System at that time it shows connection to both, the Neo-Tethys and the Palaeo-Tethys Oceans. New insights into the taxonomy and the palaeoecology of the investigated ammonoids and associated macro- and microfossils are expected. The abundant ammonoid *Orthocelites*, at least 200 000 000 !!! specimens, is assumed to be a new species. Further topics of investigation are the original position and environmental conditions of the sedimentation area at the Asagiyaylabel section, located in the Taurids. 3D modelling results will be essential to reach geodynamic, palaeoceanographic and palaeobiological conclusions. As a multitasking project, one aim is to underline a crucial fact in working within different sciences as the Structural Processes Group at the Departments of Geodynamic and Sedimentology (University of Vienna) and the Geometric Modelling and Industrial Geometry group (3D technology at the Vienna University of Technology). Interdisciplinary collaboration with other scientists is essential in modern times. Statistical analysis of the orientation and relative position (e.g. imbrication) of the ammonoid shells can hint to current or transport directions. 3D modelling of calcite-cement distribution (representing geopodal structures) and post-diagenetic calcite-veins displacing several ammonoids will complete the geometrical reconstruction and shed light on the biostratigraphic and additional diagenetic processes. The combination in analysing different fossil groups with additional analysis of isotopic, magnetostratigraphic, cyclostratigraphic and geochemical features will help to extract details of the Upper Triassic history around one of the most severe crisis in the Mesozoic time, the Carnian Crisis. Investigations, undertaken at sections (e.g. Asagiyaylabel) possessing this time interval, can work as proxy for the major Upper Triassic Tethyan crisis.

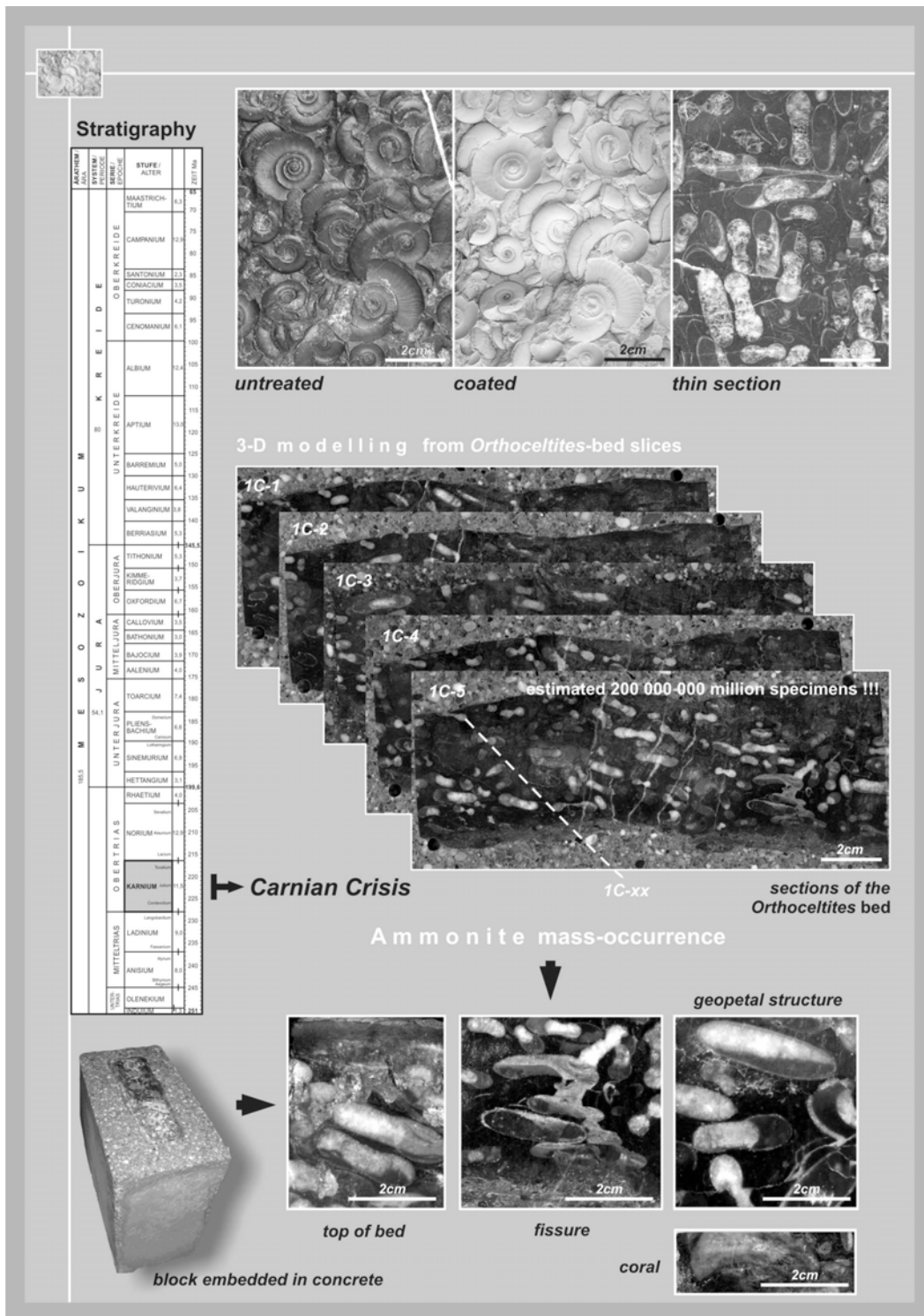


Figure: The remarkable Upper Triassic monotonous ammonoid assemblage of a single bed at Asagiyaylabel. At the top rock samples and right a polished section through the Orthoceltites beds. In the middle several polished slices for 3D calculation of the fossiliferous bed. At the bottom details of the concrete block (left) with from left ammonoid-bivalve association (white material is calcite), fissures, geopetal structures and shallow water components (corals).

(Abstract: Mayrhofer & Lukeneder)

# New insights into the ecology and evolution of the *Ceratites* fauna of the Muschelkalk Basin from phylogenetic analysis

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The evolutionary radiation of the genus *Ceratites* in the Germanic Basin (Anisian/Ladinian) of Central Europe is a putative case of a rapid radiation within an epicontinental sea. Studies of such evolutionary processes require robust phylogenetic hypotheses to perform rigorous testing with modern quantitative methods. Previously published phylogenies of Muschelkalk ammonoids have been based on phenetics and have relied to a great extent upon the stratigraphic occurrence order of taxa. I re-examined the phylogenetic relationships among *Ceratites* and other ammonoid taxa known from the Muschelkalk Basin by cladistic analysis using parsimony criteria. A growing body of recent work has confirmed the applicability of cladistic methods to ammonoids. Cladistics represents the application of the most up-to-date methods for inferring phylogeny, but it is not an infallible guide. What is more important for ammonoid palaeobiology is the access to other techniques and that cladograms allow (e.g. cladistic biogeography; phylogenetically independent contrasts) and the explicit thinking and publication of characters can help to focus the debate on certain characters and taxa that are the source of either strong signal or are particularly problematic.

A suite of 46 taxa characters and 69 characters covering both external and internal character comprised the total data set. A series of analyses was conducted. One analysis included all 46 taxa regardless of stratigraphic occurrence and a series of analyses that subdivided the taxa into stratigraphic intervals. The cladograms also allowed me to test Ulrichs (2006) claims for sexual dimorphism in *Ceratites*. If sexual dimorphs were present, then each pair of dimorphs should be sister taxa.

After a single round of reweighting based on the rescaled consistency index, PAUP found 11 most parsimonious trees with a consistency index (CI) of 0.55 for the matrix based on all taxa and characters. The analyses that time-sliced the taxa into five subgroups based on their stratigraphic occurrences showed a gradual increase in CI before reaching a plateau at a level similar to the overall CI (0.39, 0.48, 0.57, 0.55) while the retention index (RI) rises and falls through the four intervals.

These new analyses challenge previous stratophenetic interpretations of the evolutionary relationships. Subgenera such as *Paraceratites*, *Acanthoceratites* and *Discoceratites* did not form monophyletic groups, although this was partly attributable to missing data. Increasing CI through time indicates the emergence of more stable morphological difference among the genera comprising the *Ceratites* fauna that could reflect ecological specialization within an endemic habitat. The cyclical change in RI is explained by changes in characters that define individual species. Ulrichs claims for sexual dimorphism were not supported by the phylogenies. The new phylogenies support an endemic radiation driven by ecological specialization.

## Large-scale morphological evolutionary trends of Acrochordiceratidae (Ammonoidea, Middle Triassic) and Cope's rule

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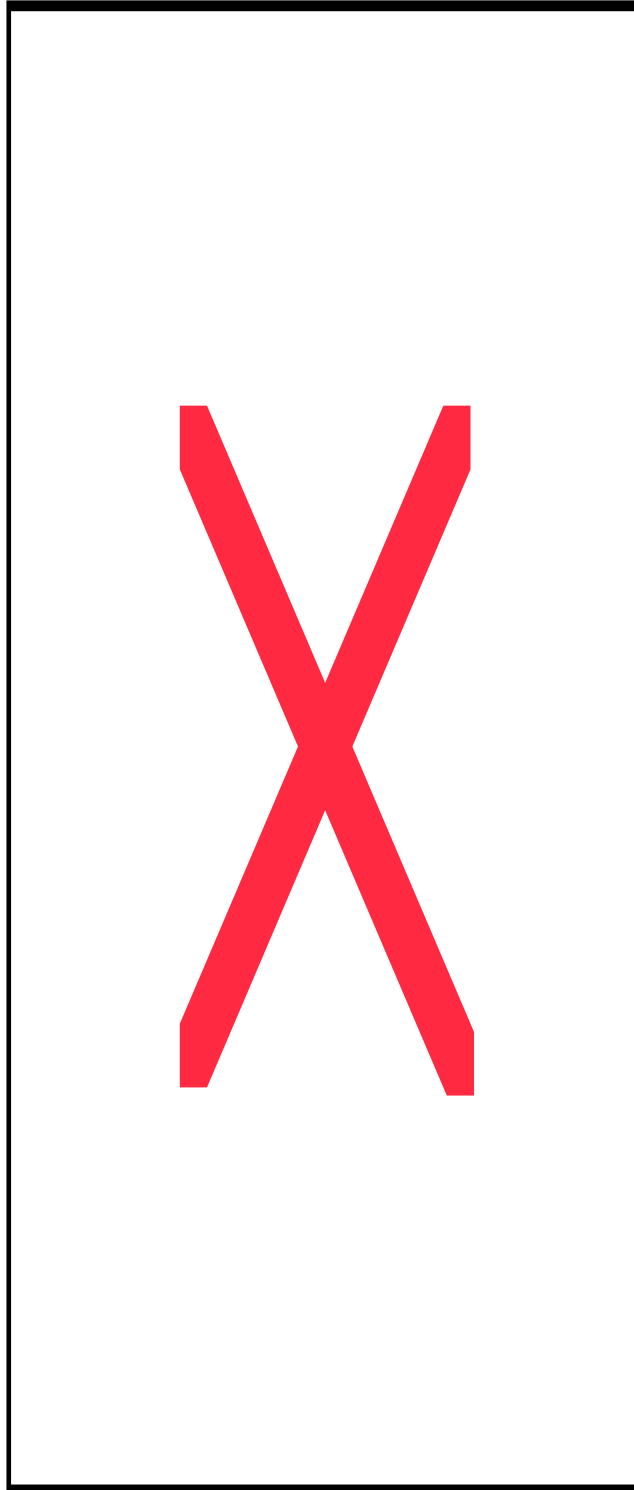
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Directed evolution of life through millions of years, such as increasing complexity and increasing adult body size, is one of the most intriguing patterns displayed by fossil lineages. The general tendency for body size to increase during the evolution of a group of animals is known as Cope's rule. However, processes and causes of such evolutionary trends remain controversial. Among fossils, ammonoid shells (marine cephalopods) are well known to experience repetitive morphological evolutionary trends of their adult size, shell geometry and ornamentation.

This study analyses the evolutionary trends of the family Acrochordiceratidae Arthaber, 1911 from the Early–Middle Triassic (251–228 Ma). Exceptionally large collections of this ammonoid family were obtained from North America. They enable quantitative and statistical analyses of its morphological evolutionary trends. This study highlights that (1) the monophyletic clade of Acrochordiceratidae follows the classical evolute to involute evolutionary trend (i.e. increasing coiling of the shell); (2) the lineage shows a stepwise increase of its shell adult size (shell diameter); (3) the clade records increasing complexity of its suture line; and (4) the lineage is characterized by an increase of the intraspecific variation of its shell morphology. These morphological trends persisted during about 3 myr (fig.).

These large-scale morphological evolutionary trends are statistically robust and seem more or less gradual. Furthermore, they can be considered as non-random with the sustained shift of the mean, the minimum and the maximum of studied shell characters. These results can be classically interpreted as being constrained by the persistence and common selection pressure on this mostly anagenetic lineage characterized by relatively moderate evolutionary rates. Increasing involution of ammonites is traditionally interpreted by increasing adaptation mostly in terms of improving hydrodynamics. However, this trend in ammonoid geometry can also be explained as a case of Cope's rule (increasing adult body size) instead of functional explanation of coiling, because both shell diameter and shell involution are two possible paths for ammonoids to accommodate size increase.



*Figure: Large-scale morphological evolutionary trends for Acrochordiceratidae during the Anisian (Middle Triassic). Global trends affecting successive spectra of variants for Acrochordiceratidae are increasing adult shell size, increasing involution, decreasing ribbing density, increasing suture complexity, and increasing intraspecific variability*

*(Abstract: Monnet, Bucher, Guex & Wasmer)*



## Isotopic signature for depth habitat of the late Cretaceous Nautiloid, *Eutrephoceras*

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Chambered nautilus (species of *Nautilus* and *Allonautilus*) which belong to the Order Nautilida of the Subclass Nautiloidea are one of the well-known living fossils, because of their order-level long evolutionary history since the early Devonian. The Nautilida had been flourished in the world's oceans during the Devonian to the Cretaceous, together with other ectocochliate cephalopod subclass, the Ammonoidea, but their diversity has become decreased in the Cenozoic, and only several species of *Nautilus* and *Allonautilus* are distributed in the relatively deep waters of the modern tropical to subtropical Southwest Pacific. Considering the fact that these two groups coexisted in the Mesozoic ocean, and only ammonoids completely disappeared at the end Cretaceous, it is hypothesized that ecological niches, such as depth habitat, food habit, and/or reproductive strategy, of these two groups were segregated within an ancient water column.

Here, we present oxygen isotopic records of the Cretaceous nautiloid *Eutrephoceras dekayi*. Because the genus *Eutrephoceras* could survive after the end Cretaceous extinction event and belongs to the Nautilidae which include modern chambered nautilus, it is the best representative for understanding the niche segregation between the Cretaceous ammonoids and nautiloids. We calculated shell secreting temperature from isotopic records of *E. dekayi*. Then we discussed depth habitat of the Cretaceous nautiloid by superimposing those isotopic temperature on thermal structure of the Cretaceous water column in which the analyzed nautiloid occurred.

We utilized a well-preserved juvenile specimen of *E. dekayi* (42.4 mm shell diameter), recovered from the late Campanian Coon Creek Formation in McNairy County, Tennessee, USA. For isotopic analyses, the aragonitic nacreous outer shell layer was milled with micro-drill of 300 micrometer diameter at almost every 1 mm interval. Subsamples were milled in the later ontogenetic stage of this individual (larger than 30.0 mm shell diameter). In addition with this *E. dekayi* specimen, we also analyzed oxygen isotopic compositions of the co-occurring planktic foraminiferal tests of *Rugoglobigerina rugosa* and *R. hexacamerata*. Sea surface water temperature calculated from these foraminiferal oxygen isotopes is 30°C. Isotopic temperatures of *E. dekayi* show almost constant through the interval analyzed at around 16°C. While oxygen isotopic composition stays almost constant, carbon isotopic composition indicates sigmoidal fluctuation in the interval analyzed. Significant isotopic temperature offset of 14°C between *E. dekayi* and planktic foraminifers obviously indicates that *E. dekayi* inhabited much cooler water mass than planktic foraminifers. This significant temperature offset and constant isotopic temperature of *E. dekayi* imply that this nautilid species dwelled near the seafloor in the interval analyzed.

## **Record of live specimens of Emperor Nautilus, *Nautilus pompilus* (Linnaeus 1758) from the east Andaman Sea, Thai waters**

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Four live specimens of *Nautilus pompilius* Linnaeus, 1758 were collected from the East Andaman Sea, eastern Indian Ocean. Their occurrence is the evidence of the distribution of this species in the region. The specimens are larger and the depth they are caught is shallower compared to those reported in the literature. The morphological variations and the geographic distance in this study might reveal the existence of another distinct clade.

## Taxonomic and biostratigraphic analyses of the genus *Amaltheus*, Late Pliensbachian (Early Jurassic) ammonite, from East Asia

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The late Early Jurassic (Late Pliensbachian-Early Toarcian) ammonite assemblages have been recognized in the Lower Jurassic epicontinental deposits exposed in Southwest Japan. They provide important biostratigraphical and paleobiogeographical data. Especially, the genus *Amaltheus*, characterized by having involute whorl and a crenulated keel, is one of the most important taxa in Late Pliensbachian because of their paleontological usefulness. During the Late Pliensbachian, Boreal Realm faunas are dominated by the Amaltheidae. In addition, the genus *Amaltheus* has a high biostratigraphical resolution because the standard ammonite zonation of this substage established in NW European province was discussed in detail by the phylogeny of this genus (Dean et al., 1961).

In Japan, the genus *Amaltheus* has been obtained from two areas, *Amaltheus* sp. (Sato, 1955) from the Kuruma Group and "*A. cf. stokesi* (SOWERBY)" (Hirano, 1971) from the Toyora Group. However the taxonomical discussions of this genus have been disturbed by a small number of specimens, some well preserved specimens were recently collected from the both areas. The purposes of this study are to identify the genus *Amaltheus* from Japan at specific level and to discuss their biostratigraphical and paleobiogeographical significances.

A total of 12 specimens, nine specimens from the Teradani Formation (middle part of the Kuruma Group) and three specimens from the Nishinakayama Formation (middle part of the Toyora Group), are utilized for this analyses. Three species identified in the Teradani Formation are *A. stokesi*, *A. margaritatus* MONTFORT, and *A. repressus* DAGIS. *Amaltheus stokesi* is characterized that each ribs pass onto the keel as crenulation. *Amaltheus margaritatus* have various surface ornaments, and the ribs are not connected with chevron. *Amaltheus repressus* is similar to *A. margaritatus* in surface ornaments but is distinguished by the constrictions on the whorl flank. On the materials from the Nishinakayama Formation, only one species, *A. margaritatus*, is recognized.

The biostratigraphical analysis is carried out on the basis of these identifications. *Amaltheus stokesi* is the index species of the Stokesi Subzone (Margaritatus Zone) in NW European province, and *A. repressus* co-occur with *A. stokesi* in Russian province. *Amaltheus margaritatus* is characterized by the restricted range from the Subnodosus Subzone (Margaritatus Zone) to the Apyrenum Subzone (Spinatum Zone). As a result, two assemblage zones based on this genus are established in the Teradani Formation, and these zones enable to correlate this formation with the Toyora Group. In addition, the faunal specific composition from the Teradani Formation is characteristic in the mixing of NW European species (*A. stokesi*) and Russian endemic species (*A. repressus*). This suggests high paleobiogeographical similarity between the East Asian and the Northeast Russian fauna in this period.

## Systematics, phylogeny and adaptative radiation in the squid of family Ommastrephidae

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Ommastrephid squid are one of the most abundant (biomass ~55 million t and annual production ~400 million t), widely distributed and ecologically active nektonic cephalopods. They occur throughout the World Ocean from sub-Arctic to sub-Antarctic; including waters of the shelf, slope and open ocean from the surface to 2000 m depths. Traditionally, the family has been subdivided into three subfamilies, Illicinae, Todarodinae and Ommastrephinae. Critical analysis of 19 morphological features enabled to distinguish two new subfamilies and develop the phylogenetic tree to the species level. The new family macrotaxonomy comprises: 1. Subfamily Illicinae Posselt, 1891. Genus *Illex* Steenstrup, 1880: 3 species. 2. Subfamily Todaropsinae Nigmatullin, 2000. Genus *Todaropsis* Girard, 1890: 1 sp. 3. Subfamily Todarodinae Adam, 1960. Genus *Martialia* Rochebrune & Mabile, 1889: 1 sp., *Todarodes* Steenstrup, 1880: 4 sp., *Nototodarus* Pfeffer, 1912: 3 sp. 4. Subfamily Ornithoteuthinae Nigmatullin, 1979. Genus *Ornithoteuthis* Okada, 1927: 2 sp. 5. Subfamily Ommastrephinae Posselt, 1891. Genus *Dosidicus* Steenstrup, 1857: 1 sp., *Ommastrephes* Orbigny, 1834: 1 sp., *Sthenoteuthis* Verrill, 1880: 2 sp., *Eucleoteuthis* Berry, 1916: 1 sp., *Hyaloteuthis* Gray, 1849: 1 sp. Taxonomically, the most complicated situation is in *Todarodes* (probably there are 3-4 new species), *Todaropsis* and *Sthenoteuthis oualaniensis*. Most of primitive features are concentrated in Illicinae and Todaropsinae, the intermediate features in Todarodinae and Ornithoteuthinae, and the most advanced ones in Ommastrephinae.

Three main ecological groups are distinguished by their habitats: 1. Slope-shelf group. Main habitats include waters of continental slope and shelf: *Illex*, *Todaropsis*, *Todarodes pacificus*, *T. angolensis*, *T. sagittatus* of the North African coast, *Nototodarus sloani*, *N. gouldi*. 2. Nerito-oceanic group. Main habitats include waters of continental slope, oceanic seamounts and islands, and adjacent oceanic waters: *Todarodes sagittatus* of the North Atlantic, *T. filippovae*, *Nototodarus hawaiiensis*, *Martialia*, *Ornithoteuthis*, *Dosidicus*. 3. Oceanic group. The whole life cycles takes place in oceanic waters and there are not connections with the bottom: *Ommastrephes*, *Sthenoteuthis*, *Eucleoteuthis*, *Hyaloteuthis*. From both morpho-functional (development of organization of active nektonic swimmer) and ecological (shift from shelf-slope to oceanic realm) points of view of the family evolution, there are three main (slope-shelf Illicinae ; nerito-oceanic Todarodinae ; true oceanic Ommastrephinae) and two intermediate (slope-shelf Todaropsinae and nerito-oceanic Ornithoteuthinae) groups. Large species of ommastrephins are at the "top" of squid progressive evolution towards nektonization.

## Quantitative aspect of oocyte follicular epithelium development in two ecological groups of octopod

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One of the important traits in cephalopod evolution is the embryonization of early development on basis of follicular type of oogenesis with the formation of large yolky eggs. The follicular epithelium (FE) is the only source of yolk in vitellogenesis. Additionally, FE function is further intensified by formation of deep FE intra-oocyte folds that increased the contact of FE surface with ooplasm. This is a unique feature of cephalopods that however has not been studied quantitatively. The simplest type of FE invaginations into oocyte in form of longitudinal folds occurs in octopods. Six octopod species were investigated to examine degree of FE folding on cross-sections across the middle part of pre-vitelline (phase of FE folds formation) and vitelline (midway of vitellogenesis) oocytes. This study included description of oocyte and ripe egg shape, measurement oocyte length and diameter, estimation of the number of FE folds and as well as the depth of their invaginations. A special index of FE surface (IFS) calculated as the ratio of total FE perimeter on the oocyte section to the oocyte perimeter has been used to compare different octopod species. Maximal filling of oocyte by FE folds were observed in the end of pre-vitelligenous phase. In small-sized egg (< 6 mm) octopods formed minimal numbers of FE folds: 4-5 in *Octopus vulgaris* and 6-8 in *Enterocopus dofleini*. In these species degree of oocyte fillings by FE folds is not more than 30% oocyte volume. In large-sized egg (15-29 mm) octopods (*Adelieledone polymorpha*, *Paroctopus conispadiceus*, *Bathypolypus salebrosus*, *Benthooctopus sp. cf. abruptus*) number of FE folds varied from 10 to 27, and folds occupied up to 80-95% oocyte volume. During pre-vitelligenous phase the oocyte size increased due to FE folds from 2 (*O. vulgaris*) to 13 (*Benthooctopus*) times. In vitelline oocytes IFS value as well as number of FE folds depend on ripe egg size and varied from 1.4-1.5 in small-sized egg octopods to 1.7-4.3 (mainly 3-4) in large-sized egg ones. These two octopod groups – r-strategists (*Octopus*, *Enterocopus*) and K-strategists (rest species) differ by oocyte shape, number of FE folds, IFS value, egg size and post-hatching mode of life. The most developed vitelline oocyte of the first group differs in length (2-3 times larger) and shape from the ripe egg. The oocyte shape in the second group is similar up to the ripe egg and egg size is not significantly smaller (by 5-10% only) than most developed vitelline oocyte. Thus these alternative reproductive strategies based on clear differences in quantitative development of FE during oogenesis, and its patterns depend on species ecological strategy but not from species taxonomic position.

## **Devonian and Carboniferous Ammonoid faunas in the Uralian Ocean: paleoenvironments and migration pathways**

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Paleozoic ammonoids are iconic fossils of the Urals and have been explored for over 100 years. However, the current state of knowledge of their regional and facial preferences is insufficient, not matching the high level of resolution of the paleogeographical history of the Urals achieved in the past two decades. We plotted successive distributions on paleotectonic maps and profiles of the Uralian Ocean in the Devonian and Carboniferous to record changes in regional and local diversities in an attempt to estimate to what extent changes in diversity were facially and ecologically biased. Changes in taxonomic diversity were then compared with the global evolutionary history of this group, focusing on important geochronological levels. Two major realms of the Uralian Ocean corresponding to the western slope (marginal sea of Baltica continent) and eastern slope (open seas facing Kazakhstania) maintained different ammonoid assemblages throughout the Devonian and Carboniferous, and their role as sources of regional diversity changed as Kazakhstania collided with Baltica. Ammonoids first appeared in the Urals with the onset of a large transgression in the Emsian across the eastern open seas, which brought in common Emsian mimosphinctids, possibly from the Turkestan Ocean. The first big increase in ammonoid diversity was in the Frasnian and was associated with anoxic and hypoxic basins developed in troughs supporting manticoceratid-tornoceratid associations. The Frasnian-Famennian extinction is clearly pronounced in the Urals being followed by a regional diversification in the southern carbonate-shale basin, a source for several waves of immigrants to the northeast. The earliest Mississippian pericyclid-muensteroceratid faunas are also recorded in the southwest and spread northward, a direction maintained throughout the Carboniferous. Tournaisian and Viséan faunas reached the basins of the Subpolar Urals, Pai-Khoy and Novaya Zemlya, but the mid-Viséan regression resulted in their almost complete elimination. The Late Viséan diversification began in the south, but this time in the carbonate Dombur basin. However, most of this fauna's descendants in the Bashkirian time switched to predominantly terrigenous-carbonate basins of the nearby Zilair Depression on the western slope. In the basins of the eastern slope, isolated small faunas persisted in shoals and around carbonate buildups, but perished in the mid-Bashkirian. Moscovian ammonoids are uncommon and are confined to the western slope. Kasimovian faunas were more diverse, and seven out of nine families were new for this region. The community was re-established in the Gzhelian. Diverse ammonoid faunas of this age are also found on the western slope which was by the end of the Carboniferous involved in the Pre-Uralian Foredeep. These ammonoids preferred regions with flyschoid sedimentation in the south (eastern slope of the Foredeep) and avoided shallow carbonate basins in the north.

## Pseudosutures in *Baculites mariasensis*

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Pseudosutures have been reported in numerous ammonoid species, particularly within the Ammonitina. Previous work has interpreted these structures as traces of partially formed septa. Presumably, the animal would have had to pause during forward movement in order to secrete these structures. Therefore, pseudosutures provide important evidence about the pace and timing of chamber growth. Pseudosutures have been studied in some detail in several coiled ammonites; in baculites, however, while their presence has been noted, pseudosuture structure and patterns of occurrence have never been analyzed. In this presentation, I share my initial observations of pseudosutures in *Baculites mariasensis* Cobban 1951, from the Upper Cretaceous Marias River Shale in north central Montana, USA. Numerous individuals can be found in concretions that appear to have formed rapidly, and so the specimens, though usually missing the embryonic shell and apex, are otherwise exceptionally well preserved. Aragonitic shell is often present, and where it has exfoliated the sutures are clearly visible on the surface of the brown calcite inner mold. At least 2% of the specimens examined have pseudosutures visible to the naked eye, and more may be found with the aid of lenses. The pseudosutures occur mainly on the lateral aspect of the molds, in contrast to some other late Cretaceous ammonites where sutures seem to be most common on the venter. As in other ammonites, the pseudosutures are partial rather than complete replicas of the suture, and most commonly mimic the shape of the lobules. These observations support the idea that pseudosutures served as temporary points of mantle attachment during chamber growth, and that the animal paused repeatedly during forward motion within the newly forming chamber. Additional details about pseudosutures in baculites are essential in comparing growth strategies among various ammonite taxa, which in turn aids in the reconstruction of evolutionary patterns in the group.

## Evolutionary pattern in the Upper Campanian (Upper Cretaceous) belemnites – an example of parallel evolution

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Within the Upper Campanian belemnites of the genus *Belemnitella* two phylogenetic lineages are commonly recognizable (i.e. Christensen, 1997): *Belemnitella mucronata* group and *Belemnitella langei* group. In my last studies concerning the Upper Campanian belemnites from the Vistula section (central Poland), based on new taxonomical and methodological approach with use of artificial neural networks (i.e. Remin, 2008), similar phylogenetic lineages have been recognized. However, these new studies reveal some evolutionary trends, not recognized previously.

In the Vistula section the *Belemnitella mucronata* group contains *B. mucronata* (oldest) *B. minor* and *B. posterior* (youngest); the *Belemnitella langei* group contains *B. langei* (oldest), *B. sp. a* and *B. najdini* (youngest).

*B. mucronata* and *B. langei* are the ancestor form for the other studied Upper Campanian *Belemnitella* species. Both possess relatively wide stratigraphic range and occur throughout the Upper Campanian as well as in the Lower Maastrichtian.

The species of the *B. mucronata* group are characterized by markedly larger guards than the representatives of the *B. langei* group. In these two groups similar evolutionary trends have been recognized. The succeeding species: *B. minor* and *B. sp. a*, a representatives of two compared groups, enter almost simultaneously in the section studied and are characterized by markedly larger guards, as in case of length and diameters and similar fissure angle to ancestor forms (*B. mucronata* and *B. langei* respectively).

Higher up in the section, there appear the youngest of studied species – *B. posterior* and *B. najdini*. These forms, again appear almost simultaneously, within narrow stratigraphic interval, and again reveal very similar evolutionary trends in both phylogenetic lineages. The youngest species, *B. posterior* and *B. najdini* are characterized by smaller guards, smaller diameters and all the internal characters in comparison to the ancestor form (*B. mucronata* and *B. langei* respectively), however possess markedly larger fissure angles than in the initial species. Concluding, in the successively appearing species in both lineages, the trends of changes of selected biometric features are the same. It suggest, that in the same time, environmental condition force similar evolutionary changes of belemnite guards in these two parallel phylogenetic lineages. However, the factor of environmental stress that force these changes remain unsolved so far.

Christensen, W.K. 1997. Bulletin of the Geological Society of Denmark, 44, 59-88.

Remin Z. 2008. Przegląd Geologiczny, 56, 58-66.



## Abundance of pelagic cephalopods in the central Mediterranean Sea (Strait of Messina and southern Tyrrhenian Sea): information obtained from swordfish diet

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Available information on pelagic cephalopod communities are still very poor because of the difficulty in sampling and the lack of commercial interest in most species. Accordingly, the best way to fill in this gap is to collect precious information from studies carried out on top predator diet. The pelagic cephalopod fauna of the central Mediterranean Sea (Strait of Messina and southern Tyrrhenian Sea) was thus investigated by carrying out an analysis of swordfish stomach content. It is well known that swordfish, *Xiphias gladius* L. 1758, largely preys on cephalopods, feeding mainly on this food item. One hundred and twenty-four swordfish individuals were collected by harpoon fishery during 2002-2008 and their stomachs analyzed. Whenever digestion was at too advanced a stage, mandibular beaks were taken as the best taxonomic feature to the purpose of classification. Overall, 1,032 cephalopod preys were identified, belonging to 20 different species. *Todarodes sagittatus* (n = 315) and *Ancistroteuthis lichtensteini* (n = 202) resulted to be the most common food items. Ommastrephidae represented the most important family in number (%N = 43.90) and weight (%W = 49.74). The high number of items preyed in terms of species (i.e. 20 species), as recorded in swordfish stomachs, is related to swordfish hunting behaviour of performing large vertical movements across a broad portion of the water column. This can explain the presence of both epipelagic (*Tremoctopus violaceus*, *Argonauta argo*, etc.) and deep-water cephalopod preys (*Chiroteuthis veranyi*, *Histioteuthis bonnellii*, *Histioteuthis reversa*, *Octopoteuthis* see *sicula*, *Abralia veranyi*) in swordfish diet. The study of top marine predator diet, such as *X. gladius*, also gives the opportunity to improve knowledge on distribution, biology and ecology of poorly known cephalopod species.

## **Population structure of Hawaiian Octopuses : *Octopus cyanea* (Gray, 1849) and *O. oliveri* (Berry, 1914)**

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Shallow-water octopuses are very common in Hawai'i where they inhabit the endangered coral reefs and are important for local commercial, recreational and subsistence fisheries. With the current popularity of using Marine Protected Areas to manage critical natural resources, it is important to understand the population boundaries and dispersal patterns of the targeted organisms. Here we report the first insight into the population structures of two common Hawaiian octopuses : *Octopus cyanea* and *O. oliveri*. It is notoriously difficult to find DNA markers that are informative for population genetic studies of octopuses.

To assess the phylogeographic distribution pattern and the associated gene flow within the Hawaiian archipelago, we tested 24 different molecular markers to determine their success and usefulness. Of those markers which were successfully amplified and relevant, population partitioning was analyzed using analysis of molecular variance in Arlequin 3.5. Different levels of structural resolution were found, demonstrating individual marker potential to assess population genetic structure. In addition, population structures between the two species were found to be distinct. On the basis of these results, we will discuss the recent genetic history of octopuses in the Hawaiian archipelago and the Pacific Ocean. This comparison of various molecular markers also has implications for future studies of octopuses and for the determination of fisheries management policies in Hawai'i.

# Temporal patterns in disparity and diversity of the Jurassic ammonoids of southern Germany

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We investigated the Jurassic ammonoids of southern Germany with respect to their temporal morphospace occupation adapted from their whorl cross-sections. A Fourier analysis of whorl outline shapes was performed based on 1,200 species within 72 discriminated biostratigraphic zones. Successive Jurassic ammonoid faunas of southern Germany show characteristic patterns. While Early and Middle Jurassic ammonoids occupy limited areas of the morphospace range, the Late Jurassic ammonoids cover the entire spectrum. The ammonoids are characterised by an overall increase of both taxonomic diversity and morphological disparity in the course of the Jurassic.

Three general modes of temporal patterns in morphospace occupation can be distinguished by combining the sum of range, the sum of variance, and the position of the centroid of the morphological spectrum: (1) morphospace stasis, (2) morphospace enlargement, and (3) morphospace reduction. We applied this classification scheme in the study of the Jurassic ammonoids, demonstrating that the evolutionary history of Jurassic ammonoids in southern Germany can be subdivided into three phases with increased morphological range. These phases end with incisions in the early Aalenian, late Bathonian, and Tithonian.

Patterns of morphological variance differ partly from the morphological range, showing a general increase during the Jurassic with incisions at the Toarcian-Aalenian boundary, within the Callovian, and in the Tithonian. Neither temporal patterns in diversity nor disparity support the hypothesis of a mass extinction event that is settled in the Early Toarcian.

Significant changes in diversity and disparity in the early Callovian support the hypothesis of a migration event of Boreal ammonoids into the Tethyan realm. This is particularly evident because of the sudden occupation of new areas within the morphospace, for which an explanation by gradual evolution is not likely.

The comparison of disparity analyses of different temporal resolutions shows strikingly varying effects in morphospace patterns. Longer time intervals provide a somewhat blurred picture, in which short-term events such as immigrations are not detectable.

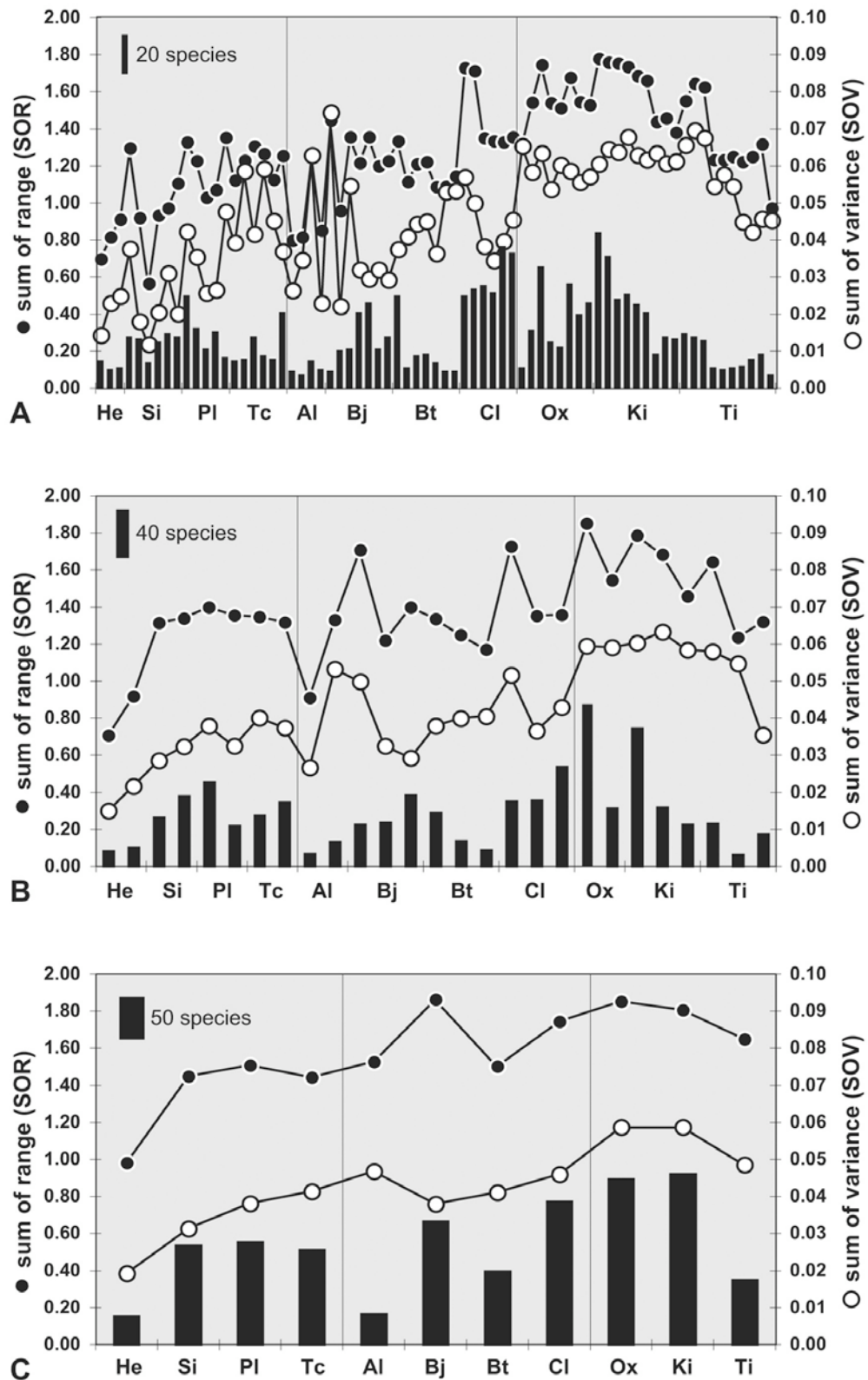


Figure: Temporal patterns in disparity and diversity of the Jurassic ammonoids of southern Germany

(Abstract: Simon, Korn & Koenemann)

# **Taphonomy of dense concentrations of juvenile ammonoids in the Mancos Shale, east-central Utah, USA**

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The Upper Cretaceous Mancos Shale reflects the approximate peak of deposition for the Zuni cratonic sequence, near the highest eustatic sealevel stand of the Mesozoic Era. At that time, an enormous epeiric sea covered much of North America, stretching from the Gulf of Mexico to the Arctic Ocean. The eastern side of this Western Interior Seaway was dominated by limestone facies, whereas a heavy influx of siliciclastic sediment on the western side of the basin was provided by the Sevier Orogeny. Such was the context for the Mancos Shale, which occurs across a vast area of several western states including Utah, in some places exceeding 1500 m in thickness. Outcrops of the mostly siliciclastic mudrocks of this unit can be observed now throughout a large part of the desert of east-central Utah.

We document here the recent discovery of dense concentrations of post-embryonic juvenile ammonoids in the main body of the Mancos Shale southeast of the town of Green River, Utah. This unusual ammonoid occurrence lies about 5 m above the Juana Lopez Member, in thin limestone lenses essentially devoid of siliciclastic sediment and composed almost entirely of tightly packed, small mollusks (ammonoids, gastropods, and bivalves), which even fill the inside of many of the larger ammonoid shells. The fossils are internal molds, some retaining recrystallized shell material, but otherwise the preservation is quite good. The Upper Turonian ammonoid assemblage includes adult representatives of *Scaphites whitfieldi*, *Prionocyclus novamexicanus*, and *Baculites yokoyamai*. Fossil-bearing lenses are biosparite/skeletal grainstone (~calcarenite), and ammonoids occur in the same lithology in the underlying *Prionocyclus wyomingensis* Zone. Another fossil bed a few meters higher in the section is interpreted as a shell lag, chiefly comprised of broken bivalves in a siltstone matrix, but containing the same ammonoids, though not as abundant and notably lacking the tiny constituents. The lenses with the mass accumulations of juvenile ammonoids occur sporadically over a large area (a few hundred square kilometers), thus there must have been a gargantuan number of embryonic and hatchling ammonoids in the region at times. All of these fossil beds lie within the soft, fissile, gray shale typical of the Mancos, previously interpreted as a low-energy, low-oxygen depositional environment.

Although the mechanism responsible for the fossil concentrations is not clear, the production of so many juvenile ammonoids was likely associated with spawning activity. There is no sign of hydrodynamic transport. Instead, lithologic and geochemical evidence suggests that these fossil beds may have been generated as a consequence of the adverse oceanographic conditions common during the extreme greenhouse climate regime of the Cretaceous, manifested by the well-known Ocean Anoxic Events around the time when these deposits were formed.

# The microstructure and mineralogy of anaptychus-, aptychus-, and rhynchaptychus-type lower jaws in the Cretaceous Ammonoidea

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Fossilized remains of jaws are occasionally preserved within the body chambers of ammonoids whose taxonomic relationships are known. Previous work using in situ material has shown that the lower jaws of ammonoids exhibit remarkable taxonomic variability in their relative size, overall shape, and the degree of development of an outer calcified element, in contrast to the morphological conservatism of the upper jaws (e.g., Lehmann 1976, 1990; Tanabe et al. 2002). Based on these lines of evidence, the lower jaws of Ammonoidea have been classified into four morphotypes, namely, normal, anaptychus, aptychus, and rhynchaptychus types (Lehmann et al. 1980; Tanabe and Landman 2002). One of the serious problems in reconstructing the morphology of ammonoid jaws is ignorance about the taphonomic modification or loss of the calcified and chitinous jaw elements, which is a common phenomenon in the fossil record of ammonoid jaws.

In this study, we examined the microstructure and mineralogical composition of well-preserved lower jaws of the following Late Cretaceous ammonoids from Hokkaido (Japan), U.S. Western Interior, and southern Alaska; *Pachydiscus kamishakensis*, *Damesites sugata*, *Anagaudryceras limatum*, and *Baculites sp.* (smooth or weak flank ribs). Each of these lower jaws was preserved in situ within the body chamber which retains an aragonitic shell wall. The lower jaws can be assigned to the anaptychus-type for the first two species, the rhynchaptychus-type for the third species, and the aptychus-type for the fourth species. Micro XRD and SEM analysis indicates that the lower jaws of all four species possess a calcareous layer on the outer phosphatized chitinous lamella. The calcareous layer is composed of aragonite in *D. sugata* and *A. limatum*, and calcite in *P. kamishakensis* and *B. sp.* The microstructure of the outer calcareous layer differs among the four species, i.e., granular in *A. limatum*, spherulitic prismatic in *D. sugata*, prismatic in *P. kamishakensis*, and lamellar in *B. sp.* Our study demonstrates that the aptychus-, anaptychus- and rhynchaptychus- type lower jaws all possess an outer calcareous layer on the outer lamella, although its mineralogy, microstructure, and relative thickness differ among taxa.

# **A morphometric method for simultaneously describing whorl shape and its ontogenetic change in ammonoids**

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The cross-sectional shape of outer whorls is one of the principal features that characterize ammonoid shell form. It has been traditionally represented by its breadth/height ratio, and recently a variety of Fourier-based methods are utilized for analyses of the whorl outlines. A conventional Fourier method in morphometrics decomposes each contour into a set of harmonics. However, the cross-sectional shape of the ammonoid whorl commonly changes through growth and the manner of the ontogenetic change in its shape provides useful intelligence to ammonoid paleobiology. In this talk, I propose a morphometric method designed for describing cross-sectional shapes of a series of ammonoid whorls; the present method allows us to perform analyses of each outline and its ontogenetic change simultaneously. In the conventional elliptic Fourier analysis, the coordinate data collected along the outline curve are expressed as the functions of the length traversed along the curve from the starting point, or the relative position on the curve ( $l$ ). The present method based on a set of series of the coordinate data obtained from a series of outline curves in various growth stages. A set of data is decomposed into position and size domains; the size of each outline is represented by its total perimeter ( $s$ ).

In the present study, the outline of the whorl cross-section was first digitized by locating series of  $x$  and  $y$  coordinates halfway along the periphery of the outer whorl. The digitized curve was connected with its laterally reflected one, and the midpoint between the right and left umbilical margins of the outer whorl was redefined as the starting point of the trace. A series of coordinate points was interpolated such that the outline was represented by 50 equally spaced points. The  $x$  and  $y$  coordinates that were normalized for size, location and orientation depends on  $s$  and  $l$ . Each of  $x(s, l)$  and  $y(s, l)$  was then described in terms of a distinct set of harmonics.

Series of  $x$ - and  $y$ -functions can be decomposed into  $s$ - and  $l$ -domains by use of a three-dimensional morphometric technique because the present method deals with "three dimensions"; growth (time) dimension in addition to the two-dimensional outline. A way to perform such analysis is a two-dimensional Fourier transform which is a generalized Fourier method to higher dimensions and is commonly used for image processing. An alternative is a method using spherical harmonics which is an extension of Fourier methods to three dimensions and are recently used for 3D morphometrics of closed surfaces. Application of 3D morphometrics to the analyses of ontogenetic change in shape may be promising not only for the whorl shape in ammonoids but also for various contours of many marginally growing animals.

## Recurrent patterns of covariation in ammonoid shell characters: how do they relate to growth dynamics?

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The comparison of shell shape among and within different clades of molluscs can be informative with regards to the basic rules of accretionary growth. Indeed, patterns of variation of shell shape and its associated growth features (like growth halts) in ammonoids and gastropods suggest that common rules of accretionary growth underlie the morphogenesis of the shell and its evolution in both clades.

Moreover, in some phylogenetically distant ammonoids species, covariations among the intensity of ornamentation, the lateral compression of the aperture and the degree of whorl overlap have been described (Buckman's laws). Similarly, these shell characters covary with the spacing between growth halts during ontogeny and among specimens in some of these highly variable ammonoids species.

Does a comparable pattern of covariation exist in gastropods as well? Could the documentation of modes of growth in gastropods support the view according to which some recurrent patterns of covariation could reflect basic constraints tied to accretionary growth?

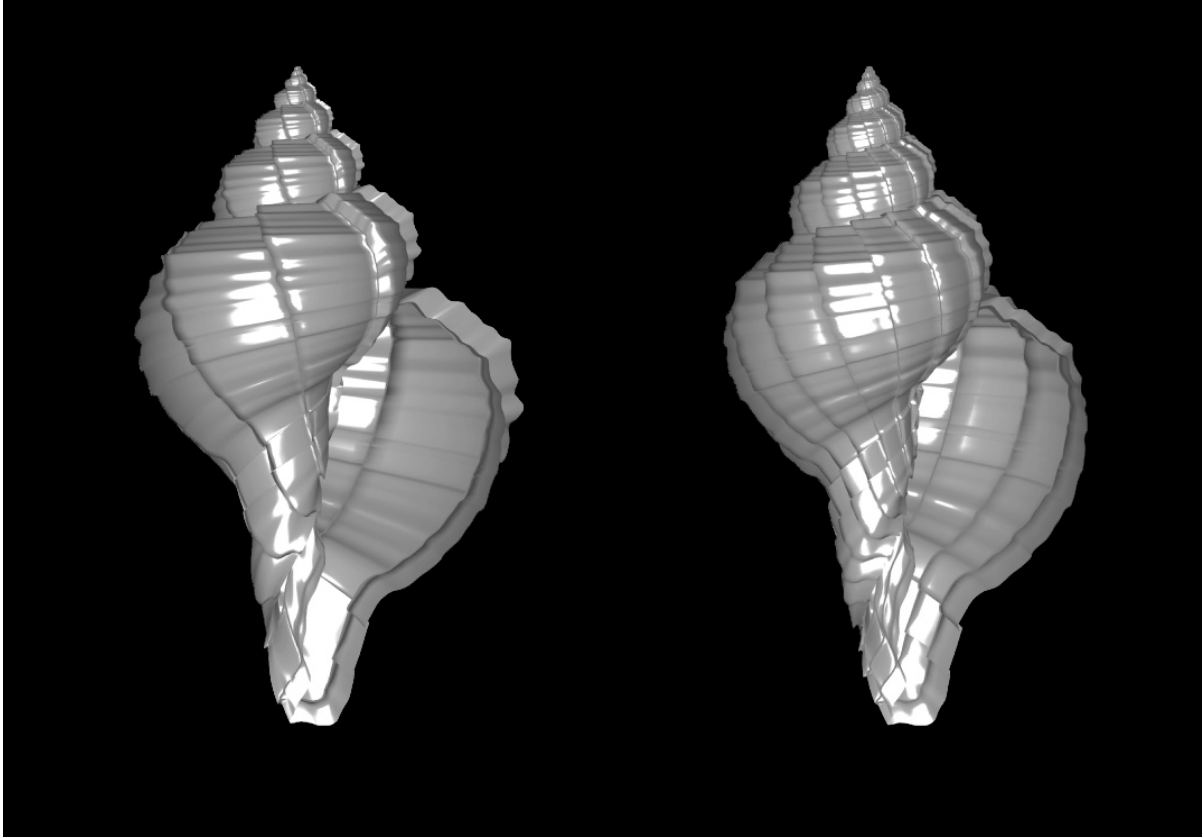
In this study, we investigate the ontogenetic patterns of variation in aperture shape, intensity of ornamentation and spacing between growth halts in a population of gastropods (*Hexaplex trunculus*, Muricidae) reared under controlled laboratory conditions from the age of approximately 100 days to 550 days after hatching.

This study highlights a covariation among growth halts spacing, aperture allometry and intensity of ornamentation:

- Variation in shell shape is analysed by geometric morphometrics of landmarks located on the aperture. We document an ontogenetic allometry of aperture, which becomes relatively wider with size.
- Variation in the 'strength of ornamentation' and intensity of allometry is related to the mean spacing between growth halts: smoother, narrower snails tend to exhibit more closely spaced growth halts.
- The mean number of growth halts per month ('growth rhythm') is related to the global shape of the growth curve and to the mean spacing between growth halts: the more frequent the growth 'pulses', the shorter the time spent on a growth halt (down to nearly continuous growth), the more linear the growth curve and the smaller the growth segments between successive growth halts.

Additionally, we develop a growth vector model in order to simulate the formation of growth halts phenomenologically. This model is able to account for some patterns of covariation among specimens. In particular, variation in growth rhythm is regarded as critical in generating the observed covariation between growth halts spacing and ornamentation (Fig.1). Based on these simulations, we suggest that this covariation mainly results from simple scaling among the aperture dimensions and the lengths of shell segments between successive growth halts. Then, the important structuration of phenotypic variation in some ammonoids species could be a generic outcome of underlying variation in growth rhythm.





*Figure: Variation in growth rhythm seems sufficient to generate a covariation between growth halts spacing and intensity of ornamentation (the number of growth halts per time unit increases from left to right)*

*(Abstract: Urdy, Goudemand, Bucher & Monnet)*

## Preferential peeling: ammonoid versus nautiloid shells from the Upper Carboniferous of Texas, USA

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Unusual, nearly parallel, relatively narrow excavations on or near the venter in some cephalopod shells from the Upper Carboniferous in Oklahoma and Texas were reported by Mapes and Chaffin (2003). However, beyond some speculation about possible perpetrators, no detailed examination of this type of feature was given. These groove-like excavations are formed by the removal of many small chips of shell on the venter and ventrolateral part of the conch. An analysis of Upper Carboniferous cephalopod collections from Texas of more than 9,000 specimens of ammonoids, coiled and orthoconic nautiloids, bactritoids, and coleoids was undertaken to determine more information about this unusual shell damage.

The presence of these chipped excavations is relatively rare in the available collections. Excavations were not seen in the bactritoids, orthoconic nautiloids or coleoids; this may be due to the relative scarcity and fragmentary nature of these cephalopod groups in this collection. Ammonoids have the larger incidence of this excavation condition (1.2% of ca. 3,500 specimens), while coiled nautiloids are less frequently damaged (0.5% of ca. 2,960 specimens); these differences are statistically significant ( $p < 0.01$ ). Thus, there is a selective preference for ammonoids over coiled nautiloids.

The amount of shell breakage is also different between ammonoids and nautiloids: in ammonoids the narrow chipped grooves that extend along the body chamber are relatively longer and penetrate the phragmocones in a higher percentage of specimens than those in coiled nautiloids. The penetration of the grooves into phragmocones suggests that some of the chipping happened after death. But, this does not rule out the possibility that the chipping perpetrator did not kill the cephalopod or that the chipping was caused by a scavenger excavating to reach the soft parts of dead animals. Annelids are sometimes attached to exposed septal surfaces inside the phragmocone, indicating that the grooves are not due to dissolution during diagenesis and the chipping had been done before the burial. The differences between the ammonoids and coiled nautiloids (percentages of chipped specimens, length of the chipped grooves, and tendency of penetration into phragmocones) suggest that the unknown predators/scavengers did not create a "home place" to avoid predation, but instead selectively utilized the inside of only ammonoid phragmocones (for ingestion of much organic matter?).

## Dienerian (Early Triassic) ammonoid successions of the Tethys: preliminary results from Pakistan and India

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In the aftermath of the Permian/Triassic mass extinction, ammonoids are one of the two fastest animal marine clades to recover (Brayard et al. 2009). It is generally assumed that diversity remained low during the Griesbachian, increased slowly during the Dienerian, and then reached a first peak in middle Smithian times. However, Dienerian faunas are only poorly known, and most recent works deal with boreal faunas whose record is strongly affected by the paucity of carbonate rocks. Recent fieldwork conducted in the Lower Triassic of the Northern Indian Margin (Salt Range, Pakistan and Spiti Valley, NW Himalaya) allow us to reassess the hypothesis of a slowly increasing diversity during the Dienerian: late Griesbachian and Dienerian ammonoid taxonomy is being completely revised and a preliminary, high resolution biochronological scheme has been constructed.

This paper focuses on the Nammal section (Salt Range), which possesses the best stratigraphic record so far (17 ammonoid-bearing beds within this 12 m interval of the section; the duration of the Griesbachian, Dienerian and lowermost Smithian together being of ca. 1.4 My, Galfetti et al. 2007). This time interval can be divided here into 6 major ammonoid zones: the first one is late Griesbachian, characterised by ophiceratids, and the other five zones are Dienerian, characterised by a succession of five phylogenetically related gyronitid genera: *Gyronites*, *Ambites*, gen. nov. A, gen. nov. B, and *Prionolobus* (in stratigraphical order). Preliminary results from other sections in the Salt Range and Spiti show that these five Dienerian zones can be recognised easily in every of these.

Diversity in the latest Griesbachian and Dienerian stays rather low and constant, with 5 to 7 species per zone, but this time interval is characterised by very high turnover rates. The supposed low increase of diversity during the Dienerian is therefore not obvious, and may just be a consequence of the previous lower time resolution combined with high turnover rates. In the earliest Smithian zones, diversity remains low (6 to 8 species), and starts increasing only at the end of the lower Smithian (Brühwiler et al., submitted).

We also note a drop of the morphological disparity among Dienerian ammonoids. The most striking fact is the loss of ornamentation: ribbed forms are still known in the *Gyronites* zone, but they completely disappear in the *Ambites* zone, and reappear only in the earliest Smithian faunas. Cadiconic forms are also absent during this time interval.

Brayard et al., 2009. *Science* 325, pp. 1118-1121

Brühwiler et al., submitted. *Palaeogeography, Palaeoclimatology, Palaeoecology*

Galfetti et al., 2007. *Earth and Planetary Science Letters* 258, pp. 593–604

# Cephalopods from the Jurassic 'Minette' Ironstone Formation of Luxembourg and Lorraine (NE Paris Basin): an update

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The Minette Ironstone Formation (Late Toarcian – Late Aalenian) is exposed in southern Luxembourg, northern Lorraine and south-eastern Belgium ; it played a key role in the economical development of these areas. The oolitic iron ore was extensively extracted between 1860 and 1980, partially in enormous open air pits that are still accessible. Over the last 150 years, numerous paleontologists have described fossils coming from the Ironstone Formation, e.g. Benecke (1905) and Maubeuge (1950). The cephalopod fauna includes several ammonite and belemnite species, a few nautilids and a single, fragmentary record of a vampyropod coleoid (Teudopsis). However, this fauna has not been revised for several decades, except some limited contributions (Weis, 1999; Fuchs & Weis, 2010; Guérin-Franiatte & Weis, 2010). It is therefore the aim of the present study to revise the type material (Lower Jurassic cephalopods) of the historical collections, stored at the Natural History National Museum of Luxembourg. In a second step, a new biostratigraphic scheme for the NE Paris Basin will be established. This scheme is based on ammonites and belemnites coming from historical as well as new collections. The type material is constituted by *Pleydellia buckmani* Maubeuge, *P. spathi* Maubeuge, *P. falcifer* Maubeuge, *P. arkelli* Maubeuge, *P. pseudoarctuata* Maubeuge, *P. hinsbergi* Benecke, *P. grandjeani* Benecke, *Dumortieria leesbergi* Branco, *D. kochi* Benecke, *D. nicklesi* Benecke, *D. bleicheri* Benecke, *P. lotharingica* Branco, for ammonites, and '*Belemnites subgigantea*' Branco, *Brevibelus breviformis* Voltz, *Acrocoelites meta* Blainville, for belemnites.

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## **Meta-analysis of character utility and phylogenetic information content in cladistic studies of ammonoids**

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Rouget et al. (2004) and Neige et al. (2007) argued persuasively that ammonoid workers should use cladistic approaches to reconstruct phylogeny. An essential yet challenging part of cladistic analysis is the selection of characters. Are certain types of characters more likely to show homoplasy? Are certain aspects of shell anatomy more likely to contain phylogenetically informative characters? Are datasets with more characters inherently better? To answer these questions, I performed a meta-analysis of character data from published ammonoid phylogenies.

I compiled 14 datasets, published between 1989 and 2007, representing parsimony-based phylogenetic analyses of ammonoids. The majority of studies focused on single families or smaller clades of Jurassic-Cretaceous ammonoids. These studies defined a combined total of 323 characters, which I grouped into categories reflecting different aspects of anatomy: shell shape and size, ornament, suture, early ontogeny, body chamber and apertural modifications. Tree searches were re-run using PAUP to determine overall tree statistics, and retention and consistency indices for each character were calculated using the program Mesquite.

Several aspects of the datasets raised concerns. Most studies had a low character/taxon ratio, typically less than two. Five studies ordered at least one character a priori (i.e., forced a particular sequence of character state changes). A surprisingly large number of studies included phylogenetically uninformative characters (e.g., autapomorphies, constant characters) in their datasets, representing up to 90% of the characters included. My analyses revealed that studies with higher character/taxon ratios did not necessarily produce trees with more information content and less homoplasy, as measured by retention or rescaled consistency indices, because additional characters were often parsimony-uninformative. Rather, studies with relatively few characters could produce high-quality trees if the characters were well-chosen and character states carefully defined. Characters related to the body chamber and adult aperture typically had retention indices of either 0 or 1, rarely in between, indicating that they either worked perfectly or not at all. Suture characters tended to have higher indices than shell shape or ornament characters, suggesting more phylogenetic information / less homoplasy in the suture line than shell traits. These results should aid in the selection of characters for future cladistic studies of ammonoids.

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# Co-occurrence of ammonite and radiolarians from the Upper Cretaceous Izumi Group in southwestern part of Awaji Island, Hyogo Prefecture, southwest Japan

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The Upper Cretaceous Izumi Group is distributed along the Median Tectonic Line from western Shikoku to the Izumi Mountains on the Kii peninsula. This group is considered to be deposits from Campanian to early Maastrichtian mainly by molluscan fossils. Many researchers believe that the Campanian/Maastrichtian boundary must be located within the Izumi Group in southwestern Awaji Island. Therefore, this area is important for chronostratigraphy. A considerable number of ammonites including heteromorphs were found from this area (Yabe 1901, 1902, 1915; Matsumoto and Maeda, 1951; Matsumoto et al., 1981; Morozumi, 1985; Iwaki and Maeda, 1989 etc).

Morozumi (1985) reported 20 species yielded and defined five ammonite zones within this group; the *Didymoceras awajiense* Zone, the *Pravitoceras sigmoidale* Zone, the *Pachydiscus awajiensis* Zone, the *Nostoceras hetonaiense* Zone, and the *Pachydiscus aff. subcompressus* Zone in ascending order. It is difficult to compare these zones with other ammonite zones because they were defined by endemic species. However, magnetostratigraphic study clarified that normal polarity horizons and reversed polarity horizons in this area were compared polarity chrons from Chron 33 to Chron 32 (Kodama, 1990). Therefore, these fossil zones could be corresponded with zones of A Geologic Time Scale (Ogg et al., 2004). Ammonite zones of Awaji Island are compared with two intervals from the upper *Didymoceras cheyennensis* Zone to the lower *Pachydiscus neubergius* Zone in the Tethyan and from the *Baculites reesidei* Zone to the lower *Baculites baculus* Zone in North America.

Bivalves, foraminifers, and radiolarians were also found from Awaji Island. Many studies on late Cretaceous radiolarian fossils have been done, but their stratigraphic ranges remain unclear. We tried to find radiolarian and clarify stratigraphic ranges by giving ammonite zone of radiolarian-bearing horizons. As a result, foraminifers and radiolarians were obtained from horizons 7.5m above and 26m below of *Pravitoceras sigmoidale* Yabe bearing beds in the Anaga, Minamiawaji City.

*Pravitoceras sigmoidale* Yabe, one of heteromorphs yielded from the Izumi Group, belongs to the family Nostoceratidae. Moreover, stratigraphic range of this ammonite was short (Matsumoto et al., 1981). The *Pravitoceras sigmoidale* Zone matches the middle of lower normal polarity chron of the Chron 32. This part of standard paleomagnetic stratigraphy corresponds to the upper *Didymoceras cheyennensis* Zone of the Tethyan and the upper *Baculites reesidei* Zone of the North America, which show a late Campanian age (Ogg et al., 2004). Therefore, the stratigraphic ranges of radiolarian must include late Campanian.

# The ammonoid recovery after the end-Permian mass extinction: evidence from the Iran-Transcaucasia area, Siberia, Primorye, and Kazakhstan

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The Upper Permian of Transcaucasia and Iran is characterised by 28 and 19 ammonoid genera, respectively. Most of them (about 82%) are representatives of the order Ceratitida. Among early Wuchiapingian and late Changhsingian ammonoids the families Araxoceratidae (Otoceratoidea) and Dzhulfitidae are dominated, respectively. In the lower Induan of the Transcaucasia-Iran area only ceratitid ammonoids *Lytosphiceras*, *Ophiceras*, *Kymatites*, *Gyronites*, and *Koninckites* (representatives of Mesozoic type families Ophiceratidae and Meekoceratidae) were documented. In the Verkhoyansk area, as well as other regions of the Boreal realm, no Late Permian (Wuchiapingian and Changhsingian) ammonoids were discovered. However, some Palaeozoic type ammonoid groups are known in the Induan of the Verkhoyansk area: the families Episageceratidae (*Episageceras*) and Dzhulfitidae (*Tompophiceras*) and the superfamily Otoceratoidea (*Otoceras* and *Vavilovites*), which demonstrates the survival of the three mentioned ammonoid groups during the Permian-Triassic boundary extinction and their prompt diversification into higher latitude ecological niches, together with representatives of the Mesozoic type families. Induan-Olenekian ammonoid successions in South Primorye, Mangyshlak and Arctic Siberia illustrate the high rate of Early Triassic ammonoid recovery in both the Tethys and the Boreal realm, having restored and exceeded their former Tethyan taxonomic diversity and abundance towards the beginning of the Olenekian (Figure). The absent of both Wuchiapingian and Changhsingian ammonoids in the Boreal realm may be caused by several reasons, without excepting of abnormal salinity of Boreal basin waters during Late Permian time.

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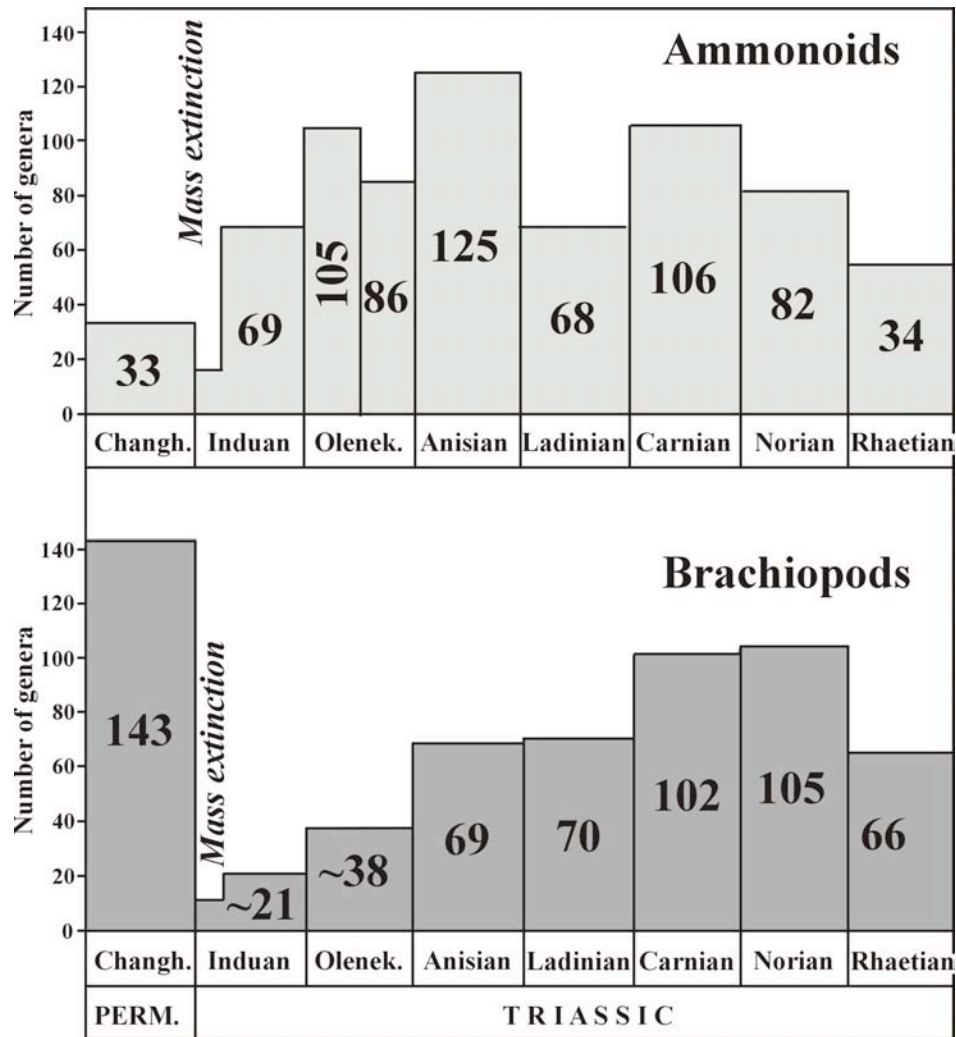


Figure: Early to Late Triassic recovery of the brachiopod and ammonoid faunas from the end-Permian mass extinction

(Abstract : Zakharov & Mousavi Abnavi)





**Abstracts of poster session**  
**(authors in alphabetical order)**



## Updated biostratigraphy of the Agrio Formation, Early Cretaceous of the Neuquen Basin, Argentina

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Our continuous studies in the marine sedimentary succession of the Agrio Formation in the Neuquén Basin of west-central Argentina have permitted the improvement of the ammonoid biostratigraphy of the Valanginian-?Early Barremian. The *Olcostephanus* (*Olcostephanus*) *atherstoni* biozone represents the time interval of the basal beds on the Agrio Formation in the center of the basin (late Early Valanginian-early Late Valanginian). It has been subdivided in three subzones, from bottom to top: *O. (O.) atherstoni*, *Karakaschiceras attenuatum* and *O. (Viluceras) permolestum*. Following the proposal of Klein (2005) we agree to consider *Viluceras* a valid genus, thus changing the name of the subzone to *Viluceras permolestum*. The following zone of *Pseudofavrella angulatiformis* of the Late Valanginian was also subdivided into three subzones: *P. angulatiformis*, *Chacantuceras ornatum* and '*Neocomites*'sp. Our recent taxonomic revision of the Late Valanginian neocomitids (Aguirre-Urreta & Rawson, 2010) allowed us to rename the upper subzone as the *Decliveites crassicostatum* subzone. The Valanginian-Hauterivian boundary is marked by the replacement of neocomitids by the first holcodiscid genus to invade the basin, *Holcoptychites*. The zone of *Holcoptychites neuquensis* is also divided in three subzones: *H. neuquensis*, *H. agrioensis* and *Olcostephanus (O.) laticosta*. The *Hoplitocrioceras gentilii* and *Weavericeras vacaensis* zones represents the Early Hauterivian in the basin. The revision of new material of *Spitidiscus* may lead to the subdivision of the *Spitidiscus riccardii* in two subzones of the early Late Hauterivian. The crioceratitids are represented at the moment in the *C. schalagintweiti* and the *C. diamantensis* zones of the Late Hauterivian. However, the study of a very coarsely ribbed, open coiled crioceratitid fauna on the top part of the diamantensis zone will allow us to propose an additional zone below the *Paraspitoceras groeberi* zone. The topmost Agrio Formation bears still undescribed coiled and uncoiled ancyloceratids. These appear close to *Sabaudiella simplex*, a species characteristic of the Late Hauterivian of the Mediterranean region (Busnardo et al., 2003). This assemblage would represent the topmost ammonoid zone of the Early Cretaceous Neuquén Basin.

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## The role of cephalopods as a vector for the transfer of cadmium to swordfish in the Mediterranean Sea

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Cephalopods are regarded as key species in many marine ecosystems and represent an essential link in marine trophic chains. Cephalopod species, however, are well known as Cd accumulators. In fact, several studies have highlighted the capacity of cephalopods' digestive gland of concentrating Cd. In particular, cephalopods have been indicated as a vector for the transfer of Cd to top marine predators.

Despite the recognized high contribution of cephalopods to swordfish total Cd intake, no studies have been carried out aimed at investigating a direct relationship between Cd levels in swordfish tissue.

Compared to other top marine predators, available data on Cd levels in swordfish are quite limited and not well structured. Starting from the assumption that food is the main route for Cd intake, after passing through the digestive tract, metals reach the different tissues in the body via the bloodway.

Accordingly, in this study we have relied on stomach content analysis for its cadmium content, which was then compared to Cd concentrations determined at blood and liver level for the ecophysiological studies in swordfish specimens from the Mediterranean Sea. The investigation was carried out on 60 swordfish individuals collected in the Central Mediterranean Sea from 2002 to 2008.

Results on the stomach content analysis confirmed that the most preyed upon taxon is cephalopods with the following results: (Frequency of occurrence %F = 80.6; Numerical abundance %N = 75.2). *T. sagittatus* is the dominant food item in swordfish diet, as reported also from other Mediterranean areas.

Regarding Cd concentrations, swordfish analysed in the present work showed mean Cd levels totalling to 0.042 mg/kg d.w for blood and 22.97 mg/kg d.w. for liver.

Overall results allow us: (1) to assess the importance of cephalopods' contribution as a source of Cd for the diet of Mediterranean swordfish; (2) to underline the use of blood to estimate recently assimilated metals (mainly Cd)

## **Spectral analysis of Late Anisian (Middle Triassic) ammonoid faunas from Prezzo Limestone (Southern Alps)**

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Prezzo Limestone is an Anisian formation of the Southern Alps known since the XIX century for the rich ammonoid faunas recovered from several tens of fossil-bearing localities. The formation is 60-80m thick and consists of a rather monotonous alternation of marly limestone beds with marl/shale interbeds, with almost 1:1 ratio. The megafossil record consists of cephalopods, bivalves, brachiopods with more rare gastropods and is mostly recorded in the marly limestone beds. The unit has been studied following a strict bed-by-bed sampling approach in seven sections, with a total number of collected specimens of about 6,000 specimens. The number of fossil bearing levels recognized in the same section of the unit is up to 40.

The very rich fossil record of the Prezzo Limestone is surely unusual, especially for a Triassic formation, but it is not easy to be interpreted. Ammonoids do not show any indication of post-mortem drifting, pre- or post burial dissolution or reworking. Sedimentology of the marly limestone beds is very poor and rather constant in the studied sections, but this notwithstanding faunal content of the beds sometimes shows surprising changes. Ammonoid faunas are mostly composed of Ceratitidae and Pinacocerataceae, with more rare Noritaceae and Danubitidae. Composition of the assemblages changes not only from the base to the top of the unit, but sometimes from bed to bed, with sudden changes from faunas dominated by Pinacocerataceae to faunas dominated by Ceratitaceae.

The complex faunal changes were probably controlled by a combination of factors interplaying at different scale. The productivity of the Prezzo basin was surely controlled by the interplay of subsidence, sea-level rise, very fine grained siliciclastic supply, development of both carbonate platform and "pelagic" communities, but it is here suggested that the main factors directly controlling the ammonoid assemblages were the variation of O<sub>2</sub> and of the organic productivity in the deepest part of the water column and sea bottom.

## **Cladistic treatment of continuous characters: Example from representatives of Hildoceratoidea, Hyatt 1967.**

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Recent advances in ammonite phylogenetic reconstructions have demonstrated that coding discrete characters of ammonoid shells (e.g. ornamentation, coiling, suture line) offers a reliable data set to propose testable phylogenetic hypotheses. This presents a new challenge for the cladistic development of ammonoid systematics by increasing the number of taxa under study to investigate phylogeny at larger taxonomic scales. By including quantitative morphologic characters in the analysis is particularly important as it takes into account shell morphology and, can be used to compare taxa that are not closely related. However, this approach is problematic because quantitative characters do show degrees of overlap. These types of continuous characters have been considered problematic in phylogenetic reconstructions because there is no solid ground to recognize discrete states among them (Pimentel & Riggins 1987).

Several methods of coding continuous data in cladistic analyses have been proposed over the last 30 years. For instance the simple gap coding (Mickevitch & Johnson 1990), the segment gap coding (Chappill 1989) or the "Thiele's method" (Thiele 1993). These methods have been rarely compared and discussed. In this study we propose a cladistic analysis of 27 taxa included in the Hildoceratoidea. Among the 49 characters defined, 11 are continuous and coded using segment gap coding method and Thiele's method. In our analysis, continuous characters have been withdrawn in order to assess the effect of adding continuous characters in parsimony optimisation. The analysis produced three cladograms on the basis of the three distinct methods. Two of which are consensus trees whilst the third obtained using Thiele's method, is the sole parsimony-based tree. All trees were compared in order to evaluate the effect of discretisation. The main results show (1) that traditional gap-coding methods are strongly biased to be used routinely in cladistic analysis; (2) for any given character, Thiele's method is appropriately sensitive to the magnitude of mean values amongst taxa and; (3) the latter method is biased by the number of character states: when these increase the number of most parsimonious trees decrease. Our work shows the phylogenetic relevance of continuous characters in ammonoid phylogeny and suggests the improvement of discretisation methods.

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## Late Albian (Early Cretaceous) ammonites (Cephalopoda, Ammonoidea) from the Provincial Formation of Cuba

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The Provincial Formation is a unit that crops out in broad areas of central Cuba. It is composed of calcareous and terrigenous marine and volcano-sedimentary deposits characterized by a series of micritic limestones, with an intercalation of marls, sandstones, calcareous conglomerates, and ash and tuffaceous material. These facies represent sediments of Albian-Cenomanian age typical of a volcanic arc that developed during the Cretaceous in the Caribbean Tethys. A late Albian ammonite assemblage was sampled from calcareous biomicrites and marls of an exposed portion of this formation within the Villa Clara Province, in central Cuba. Despite the lack of precise local Albian ammonite biostratigraphy, the ammonite-bearing strata of this work have been studied intensively for their stratigraphical characterizations. This research employs the comprehensive Tethyan and European standard ammonite zonal schemes by Reboulet et al. (2009) and Owen (1999) respectively. A rich assemblage of taxa typical of the rostratum subzone (sensu Owen, 1999) of the upper Albian *Stoliczkaia* (*Stoliczkaia*) *dispar* Zone conforms to the studied material. The record of *Protetragonites* cf. *aeolus* (d'Orbigny), *Desmoceras* (*Desmoceras*) cf. *latidorsatum* (Michelin), cf. *Discohoplites* sp., *Mortoniceras* sp., *Cantabrigites spinosum* (Pervinquiére), *Cantabrigites wenoensis* (Adkins), *Stoliczkaia* (*Stoliczkaia*) *clavigera* (Neumayr), and *Algerites* sp., confirms the idea that the age of the studied stratigraphic section is late Albian. The ammonites show a strong tethyan affinity, as the typical boreal forms of coeval ages, such as the members of the Hoplitidae Family, are underrepresented. Until this point, these upper Albian ammonite species were not recorded for Cuba or for any Caribbean locality. Thus, their records broaden their paleobiogeographic significance and allow for precise long distance correlations of standard Albian ammonite zonations between Cuba and other areas of the world.

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# A biogeographical quantitative analysis of Early Triassic ammonoid faunas using bootstrapped spanning networks

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A systematic data set of twenty Early Triassic basins allows the investigation of diversity and biogeographic patterns of ammonoids. The study of latitudinal diversity gradients indicates that the maximum differentiation of ammonoids faunas was reached during the Spathian (Brayard et al. 2006, 2009a). In order to investigate more precisely the corresponding biogeographical relationships between the studied localities and their evolution through Early Triassic times, we develop a new clustering method allowing the construction of a "Bootstrapped Spanning Network" (BSN, Brayard et al. 2007). This approach basically relies on a Bootstrapped Similarity Analysis (in this work, we use the Bray-Curtis distance for binary data) of the Presence/Absence  $M$  taxa  $\times$   $N$  localities matrix using undirected Minimum Spanning Networks (MSN). The BSN is then deduced from the set of bootstrapped MSN as the best compromise between the number of edges linking vertices ( $\geq N-1$ ), which is minimized, and its (maximized) overall bootstrapped probability. The latter can be approximated from the bootstrapped Confidence Intervals estimated for each individual edge in the complete Network (considering such C.I. as 1st order estimates of the probability that a given edge is "real", *i.e.*, non-random). On the one hand, by connecting vertices without inferring additional ("ancestral") nodes, this clustering technique is particularly well suited to biogeographic analysis, as it does not require any post hoc hypothesis about the existence of potentially meaningless (as historically non-functional) biogeographic units (the internal nodes of classical, metric or ultrametric clustering techniques). On the other hand, the statistical backgrounds of this technique make it immune to well-know flaws of the Minimum Spanning clustering techniques, particularly when the computed pairwise biogeographical distances are small.

The biogeographical relationships identified using the BSN method indicate that during the Dienerian, strong latitudinal affinities already exist between basins. Dienerian high-latitudes localities appear separated from lower latitudes localities, but an antitropical relationship links these two provinces. The same tendencies are accentuated during the Smithian with almost no antitropical relationship. All basins surrounding the Tethys were linked to its geographic center (Afghanistan), suggesting a certain degree of endemism. This paleoceanographic pattern was markedly altered during the Spathian, possibly indicating significant modifications of oceanic circulation at that time, as illustrated by the development of a marked intertropical faunal belt across Tethys and Panthalassa. The BSN method also allows to suggest paleopositions for Panthalassic terranes (Brayard et al. 2009b).

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## Good genes and good luck: Ammonoid diversity and the end-Permian mass extinction

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Two hundred fifty-two million years ago, the Permian/Triassic boundary (PTB) marked the largest documented mass extinction in the history of life by removing more than 80% of marine genera. In the World Ocean, ammonoid cephalopods were among the leading organisms deeply affected by this crisis. A time-calibrated analysis of a diversity dataset of ammonoid genera covering a ~106 m.y. timespan centered on the PTB shows that Triassic ammonoid actually reached levels of diversity higher than in the Permian only 1 m.y. after the PTB. The available data clearly favors a Hierarchical rather than Logistic model of diversification coupled with a Niche Incumbency hypothesis. This diversification stands in striking contradiction with the widely-accepted slow and delayed character of the Triassic biotic recovery.

Early Triassic ammonoid diversity first peaks during the Smithian, when numerous Lazarus taxa among mollusks also reappear. Then, a new diversity crisis, well comparing with the end-Permian for ammonoids, ends the Smithian times. This global event corresponds to major global changes in the Carbon cycle and climate. Nevertheless, it did not markedly delay the "fireworks" dynamics of Ceratitid ammonoids. Combined with the lack of previous time-calibrated studies, this poly-phased scenario accounts well for the generally accepted delayed character of this recovery, which appears now to be the spurious consequence of still inadequate sampling and/or time resolution in the very first million years after the PTB.

## Coniacian (Late Cretaceous) ammonoid fauna of eastern Utah, USA

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The Mancos Shale is an extensive marine unit, present at the surface and in the subsurface through a vast area of several western states including Utah, where in some places its thickness is in excess of 1500 m. The mostly siliciclastic mudrocks of this unit reflect deposition within the Western Interior Seaway of North America, and outcrops of these Upper Cretaceous rocks can be seen now across a large part of the desert of east-central Utah. Several recent discoveries in the Blue Gate Member of the Mancos Shale in Emery County, Utah, have significantly expanded our understanding of the Coniacian cephalopod fauna in this part of the basin. All fossils were collected from concretionary masses in rocks belonging to the *Scaphites preventricosus* Zone, indicative of the Lower Coniacian Substage. The high diversity ammonoid assemblage includes the zonal name-bearer, as well as *Scaphites impendicostatus*, *Forresteria alluaudi*, *Placenticeras kaffrarium*, *Baculites mariasensis*, and *Allocrioceras hazzardi*. In addition, we document the first *Scaphites frontierensis* and the first Coniacian *Yezoites* sp. in Utah. Also, we report the first *Peroniceras* found in Utah, *P. tridorsatum*; other species of this genus have previously been reported from as far north as Montana, but from the overlying *Scaphites ventricosus* Zone (Middle Coniacian Substage). Finally, the cephalopod fauna also includes nautiloids, provisionally identified as *Anglonutilus* sp., and described in another contribution to this symposium. Along with the cephalopods, abundant inoceramids occur here and may enable us to further refine our zonal identifications in the future.

## Early Triassic ammonoids from the Pahvant Range, Utah, USA

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In this contribution, we describe the Smithian ammonoid assemblages from the Pahvant Range of central Utah. The Thaynes Group is a marine unit that thins from northwest to southeast across Utah, where it interfingers with the terrestrial Moenkopi Group. The intertonguing relationship of these two famous units is conspicuous in the Dog Valley area of the Pahvant Range. The limestones and shales of the Thaynes Group were deposited within the Sonoma Foreland Basin, while the Moenkopi Group reflects deposition in the adjacent coastal plain.

We measured two sections at separate localities in the Dog Valley area of the Pahvant Range. Both of these sections encompassed a large portion of the Thaynes Group. We systematically collected fossils from the limestone beds; fossils are extremely rare in the intercalated shales. Ammonoids are abundant, though generally poorly preserved, in the upper beds of both measured sections. We recognize these upper layers as the *Anasibirites* Beds, which are dominated by the eponymous taxon. In the underlying beds, which we refer to as the *Meekoceras* Beds, the ammonoid fauna is much more diverse and includes: *Inyoites*, *Wyomingites*, *Churkites*, *Guodunites*, *Owenites*, a ussuriid (?*Lanceolites*), and an unidentified proptychitid. The upper beds are assignable to the informal *Anasibirites kingianus* Zone, while the underlying beds belong to the upper part of the *Meekoceras gracilitatis* Zone. Furthermore, the *A. kingianus* Zone correlates with the *A. multiformis* Zone (Upper Smithian), while the upper part of the *M. gracilitatis* Zone correlates with the *Owenites* Beds (Middle Smithian) of the Tethyan Paleoequatorial Zonation.

Our results complement recent reports of the occurrence of the Upper Smithian *Anasibirites* fauna in the Sinbad Formation (Thaynes Group) at several sites in southern and southeastern Utah. The Pahvant Range assemblages described herein provide an important geographic link between localities to the east and south and those to the west and north. Interestingly, ammonoids of the Middle Smithian *Meekoceras* fauna appear to be absent in the correlative Sinbad Formation localities to the south and east. Therefore, the occurrence of the *Meekoceras* fauna in the Pahvant Range represents the farthest southeast this fauna has been reported in Utah. The lower beds of the Thaynes Group in the Pahvant Range also contain ammonoids, which continue to be investigated and may soon yield more significant discoveries.

## Testing indirect effects of fishing on the European squid *Loligo vulgaris* (Lamarck 1798)

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A detailed description of the fishing effects are recommended to assess with the sustainable yield to maintain the exploited population stable and prevent over fishing. Direct fishing effect, such as changes in abundance or age/size structures are widely studied in exploited stocks. However, indirect effects received less attention. It seems the case of the European squid, one of the most important species targeted by commercial and recreational fisheries in the NW Mediterranean. In this study, we copy with the consequences of drop-off of the tentacles caused by fishing with jigs (i.e. the most common gear). In order to disentangle the ecological effects of the loss of the tentacles and the possible adaptation to this disability, a series of depredation and competence experiments with squids in captivity were tested.

The Sea Bass *Dicentrarchus labrax* and the Common Prawn *Palaemon serratus* were chosen to represent the two main types of potential preys which differ in mobility and imply different tactics and possibilities of the squid's predation. The individual experiments consisted in counting the number of attacks and depredation time of the squids over these two different preys, independently. These squids were subjected to the following BACI (Before-After-Control-Impact) experiment: In a first step (before), all squids hunted with both tentacles. In a second step (after), three treatments were applied: a) control squids (2 tentacles), b) one-tentacle squids and c) without-tentacle squids. Moreover, the two types of preys (fish and shrimp) were offered separately to two classes of competence experiments (control vs. one-tentacle and control vs. no-tentacles). Additionally, the prey-selectivity was tested: squids were given an equal choice of two preys, fish and shrimp simultaneously.

The results demonstrated that, for preys with high swim response, such as fishes, the one-tentacle and without-tentacles squids showed a decreased predation effectiveness, executing a greater number of attacks in more time than the control squids. Nevertheless, for preys with reduced mobility, such as shrimps, the lost of one or both tentacles had not consequences since the control and disabled squids captures the preys at similar time and they perform similar number of attacks. In the competence experiments, the shrimps catch from different squids (2, 1 and without tentacles) was indistinct while the control squids (2 tentacles) were clear winners in fish predation. Moreover, the results of prey-selectivity trials showed that squids preferred fish instead shrimp. We conclude that the survival of the disabled squids depends of the adaptation to feed preys with reduced mobility (crabs and shrimps). Furthermore, these novel and first study to copy with the drop-off of the tentacles in the squid showed how these phenomena can play a key role in the life-history of squid.



*Figure: Detail of a broken tentacle caused by fishing with jigs*  
(Abstract : Cabanellas-Reboredo, Alós, Palmer, Morales-Nin & Gräel)

## The Floian eothinoceratid radiation in northwestern Argentina (southern Central Andean Basin)

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The Central Andean Basin is the southern continuation of the extended Andean belt that also comprises the Cordillera Oriental of Peru, as well as the Cordillera Oriental and Central of Bolivia. The southern part of this basin is exceptionally exposed in the Cordillera Oriental in northwestern Argentina. Siliciclastic successions of the Cordillera Oriental of Argentina and Bolivia were deposited along the western Gondwanan margin of South America.

The oldest known cephalopods in the Central Andean Basin, and particularly in NW Argentina, belong to the family Eothinoceratidae. Their remains come from the Middle Tremadocian of the Sierra de Mojotoro (Cordillera Oriental), and were identified as *Saloceras* cf. *sericeum* Evans, due to similarities with the Avalonian species.

The diversity and abundance of the Tremadocian record of cephalopods from the NW Argentina are very low, although during the Floian an important radiation existed, corresponding to the great diversification occurring globally for this group of mollusks. The family Eothinoceratidae would have been importantly represented in this radiation at the western margin of Gondwana. Even though until recently its presence in this region passed almost occult, now it is noticed that they are not only the oldest record of nautiloids in the basin, but also various taxa exist in Floian strata. New records from NW Argentina are added to the already described species from Bolivia (corresponding to the genera *Eothinoceras* and *Margaritoceras*). Several specimens were collected from different localities in the Cordillera Oriental. *Margaritoceras* is also present in Argentina, and new taxa have to be described. The concentrations of eothinoceratids are very common in the Acoite Formation, along with specimens of the family Protocycloceratidae.

Other Ordovician cephalopods of Argentina come from the Precordillera Basin, where the family Eothinoceratidae seems to be absent. This is important from a paleogeographic point of view, since the Precordillera is considered to have been part of Laurentia up to Cambrian times, when it detached during the Ordovician crossing the Iapetus Ocean until its collision against the South American margin of Gondwana. During the Floian this microcontinent has probably been located at low paleolatitudes, at the time when the San Juan Limestone (main unit with cephalopods) was deposited.

## Stable isotopes in well-preserved shells of a methane seep fauna from the Upper Cretaceous (Campanian) Pierre Shale, U.S. Western Interior

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Methane seep deposits are common in the Upper Cretaceous Pierre Shale of the U.S. Western Interior. They contain a rich fauna including *Baculites*, *Hoploscaphites*, *Didymoceras*, *Placentoceras*, *Solenoceras*, *Lucina*, gastropods, sponges, and crinoids. In an effort to understand the ecology and environment of these systems, we have examined a vent from the upper Campanian *Didymoceras cheyennense* Zone in Custer County, South Dakota, in which the molluscs retain their original microstructure. Measurements of the oxygen and carbon isotopic composition of *Inoceramus*, *Lucina*, *Hoploscaphites*, and *Baculites* from the central part of the vent as well as from the surrounding sea floor are surprisingly consistent for each kind of organism, and the  $\delta^{13}\text{C}$  values suggest differences in their habitats relative to the source of methane. The oxygen isotopic values for specimens of *Lucina*, *Hoploscaphites* and *Baculites* average  $-1.8 \pm 0.9\text{‰}$ , corresponding to water temperatures of  $\sim 23 \pm 4^\circ\text{C}$  (assuming  $\delta^{18}\text{O}$  of the water =  $-1\text{‰}$ ). Values of  $\delta^{13}\text{C}$  for these specimens range from  $\sim -6\text{‰}$  in *Hoploscaphites* to  $\sim -3\text{‰}$  in *Baculites* to  $\sim -1\text{‰}$  in *Lucina*. The unusually light  $\delta^{13}\text{C}$  values in the scaphite and baculite specimens suggest that their shells incorporated dissolved inorganic carbon derived from seep methane and that these mobile animals were living in close proximity to the vent fluids. In contrast, *Inoceramus* shells from both the central part of the vent as well as from the surrounding sea floor display  $\delta^{18}\text{O}$  ranging from  $-5.7$  to  $-3.4\text{‰}$  and  $\delta^{13}\text{C}$  ranging from  $3.6$  to  $5.2\text{‰}$ . These results suggest non-equilibrium precipitation of carbonate in the shells of *Inoceramus*, consistent with results from prior studies.



## *Crioceratites* and *Pseudothurmannia* (Ammonoidea) from the uppermost Hauterivian (Lower Cretaceous) of the Mediterranean region. Taxonomic and stratigraphic considerations

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The ammonite stratigraphy of the uppermost Hauterivian (Lower Cretaceous) in the Mediterranean region has traditionally been based on the distribution of species belonging to the genera *Crioceratites* L veill  and *Pseudothurmannia* Spath. Most of these species, however, were defined in classic papers with poor illustrations and little indication about their stratigraphic position. Subsequent reviews, during the second half of the past century, complicated even more the systematics of the group by erecting many new taxa founded on minor morphologic differences. The confusion about the interpretation and the exact stratigraphic position of this group of species still persists today and hinders the correlation of the results obtained in more recent works.

In order to solve some of these problems, we have undertaken a systematic revision of these species, based on the analysis of more than 3000 specimens systematically collected from 15 sections located in different paleogeographic domains of the Betic Cordillera (SE Spain). The amount of material studied has allowed us to assess the morphologic variability of the different species recognized (including a conspicuous sexual size dimorphism) and, in consequence, to put in synonymy with them many other nominal taxa.

In the current standard zonation for the Mediterranean region, the uppermost Hauterivian interval is represented by the *Crioceratites balearis* and *Pseudothurmannia ohmi* Zones (see figure). The *Crioceratites balearis* Zone can be subdivided into four subzones defined by the consecutive appearance of four species belonging to the same *Crioceratites* lineage. These species are *Cr. balearis* (Nolan), *Cr. binelli* (Astier), *Cr. krenkeli* (Sarkar), and *Cr. angulicostatus* (d'Orbigny), which seem to correspond to four successive steps in an evolutionary trend towards a stronger ornamentation in the middle ontogenetic stages. In addition to these species, we have also identified *Cr. majoricensis* (Nolan), which probably represents a member of the same lineage showing a more prolonged trituberculate stage (trituberculate ribs are present in the innermost whorls of the other members of the group).

The genus *Crioceratites* is succeeded by *Pseudothurmannia* at the base of the *Ps. ohmi* Zone. This zone can also be subdivided into three subzones, which are characterized by different species of *Pseudothurmannia*. The oldest representative of this genus is *Ps. ohmi* (Winkler), which gives place to *Ps. mortilleti* (Pictet & de Loriol) and *Ps. pseudomalbosi* (Sarasin & Sch ndelmayer) in the intermediate subzone. *Ps. picteti* Sarkar would be the last member of this lineage characterized by a trend towards a more involute coiling and a longer persistence of ventrolateral tubercles along the ontogeny.

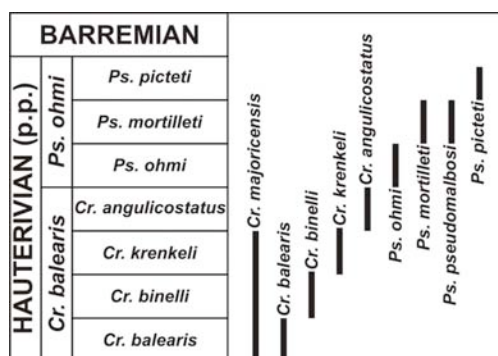


Figure: Stratigraphic distribution of the identified species

## Global changes recorded in the Oxfordian Ammonite associations (Paris Basin, France)

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In the Paris basin, the Oxfordian ammonite faunas are mainly consisting of two palaeobiological unities : an older (Lower Oxfordian) one, dominated by successive species of the genus *Cardioceras sensu lato*, heir to the Upper Callovian *Quenstedtoceras*. In the Middle to Upper Oxfordian the associations are suddenly, and definitely, dominated by various representative of the family Perisphinctidae, even if Cardioceratids are still easy to collect in the older Vertebrale subzone. The Cardioceratids are sure of boreal origin, as the Perisphinctids may be tethysian groups. But we can notice that the Perisphinctid ammonites collected in the Paris basin, from the Middle Oxfordian (Vertebrale subzone and Transversarium zone), really match with the 'british species', rather than with the subtethysian ones (southern Poland, Italy, Spain).

If we compare the northern and southern margins of the Paris Basin, some obvious differences can be observed. For example, the Cardioceratids remain quite abundant in the oldest Middle Oxfordian horizons, around its northern part (North of Lorraine, Ardennes, etc.), than in the southern (Burgundy, North Poitou, Berry, etc.). These differences may be related to large-scale ecological factors (palaeobiogeographical origin).

The homogeneousness of both associations do not prevent brutal and short variations ('bio-events'), that can be observed all over the studied area. These 'events' introduce boreal associations within tethysian ones, as well as tethysian associations amongst boreal ones :

1. In the Lower Oxfordian three 'tethysian bio-events' are located in the Middle Scarburgense subzone (*Taramelliceras*) and 2. Middle Praecordatum subzone (*Peltoceratoides* 1), and Bukowskii subzone-Costicardia subzone boundary (*Peltoceratoides* 2), respectively.

2. In the Middle and Upper Oxfordian, five 'boreal bio-events', traduced by small cardioceratids associations, occur (1) in the oldest Vertebrale subzone (*C. tenuistriatum*) ; (2), in the Middle Luciaeformis subzone (*Amoeboceras* of the *glosense* group) ; (3), in the Upper Bifurcatus zone (*A. serratum*) ; (4), in the Upper Semimammatum subzone (*A. ovale* + *Ringsteadial*) ; (5), in the oldest Hauffianum subzone (*A. gr. bauhini*).

Such variations are of great interest, in both bio-stratigraphical and palaeo-ecological fields. Some comparable, if not identical faunic events have been pointed out in many european areas : if the synchronism can be proved, they provide the best tool for precise long-distance correlations, all over Europe. Concerning their ecological interpretation, such biological horizons induce questions and problems, instead of solving them. In fact, it is attractive to relate these variations to cyclic, eustatic factors, necessarily control by general (climatic) fluctuations; but how to imagine such short environmental changes, if compared to the absence of changes recorded in the sedimentary series yielding the faunas themselves?

# Palaeobiology, stratigraphy and systematics of Early Emsian Ammonoidea from the Hunsrück Slate (Rhenish Massif, Germany)

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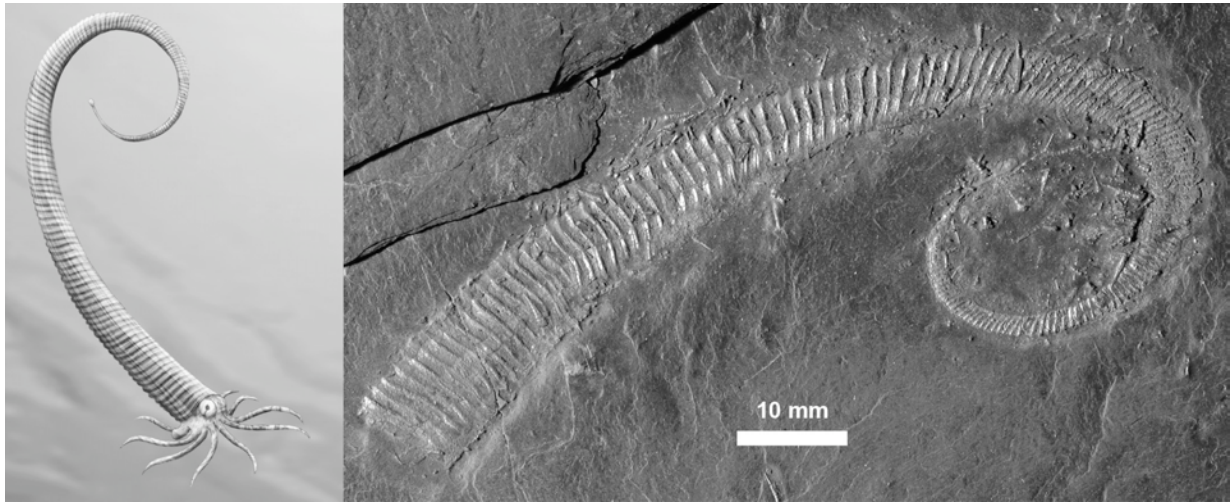
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The Hunsrück ammonoids have not been intensively studied since the publications of Erben and Chlupáček in the sixties and seventies. Meanwhile, additional early Emsian (Devonian) ammonoid finds were described from Algeria, Canada, Czech Republic, France, Germany, Kazakhstan, Morocco, the northern Caucasus, Novaya Zemlya, Russia, South China, Tibet, Turkey and Uzbekistan. Hunsrück Slate ammonoids have often been overlooked by roof slate splitters, but they are one of the most important groups (together with dactyloconarids) to help correlate and date the Hunsrück Slate. Due to the fact that most collections were made in the phase of roof slate splitting, the exact stratigraphical position of ammonoids (and of most of the other groups) was unknown and in some old collections, their origin was only listed as Hunsrück or Taunus.

The Hunsrück ammonoids were long thought to be the oldest in the world. This is confirmed as at least some come from the *Nowakia praecursor* Zone, while others are younger (probably *Barrandei* Zone). The transitional evolutionary series of the Hunsrück ammonoids from bacitritoid to coiled ammonoids has been repeatedly figured, but never been stratigraphically tested. For the first time, we assigned the ammonoid discoveries to members of a new stratigraphical scheme proposed for the Bundenbach region by Schindler et al., some of which contain the exceptionally preserved, pyritised faunas, and correlated these occurrences with those of other regions.

Several new taxa are described, including a new species of *Gyroceratites* with a very large umbilical window and loosely coiled inner whorls, and the first complete *Borivites* with protoconch (see figure below). The Hunsrück Slate offers a preservational window on the early ontogeny of early ammonoids, which is corroborated by the discovery of the protoconchs from four additional Hunsrück taxa (*Borivites*, *Ivoites*, *Mimagoniaticites* and *Gyroceratites*) in addition to the ones described by Erben. Other taxa could be synonymized (for example the endemic *Mimagoniaticites "falcistriae"* with the geographically more widely distributed *M. fecundus*). Ammonoids were previously only reported from the Central Hunsrück region and the Taunus. We also discovered ammonoids (albeit poorly preserved) in the Hunsrück Slate of Altlay in the northern Hunsrück/Mosel region. We also studied the taphonomy of the Hunsrück ammonoids, which lead to some additional insights on the depositional and diagenetic history of the Hunsrück Slate.

Some specimens of *Ivoites* show peculiar spirally arranged, paired pits on the internal mould, which affect rib spacing and sometimes also rib angularity and septal spacing. They formed during the lifetime and affected growth at the aperture. They are reminiscent of "Housean pits" and megastriae. At least one specimen shows a spiral trace of these pits indicating possible irritation of the mantle tissue. They might have been caused by parasitic infestation as not all specimens show them.



*Figure: Reconstruction (left) and pyritic, internal mould (right) of Borivites n. sp. from the middle Kaub Formation (Hunsrück Slate) of Bundenbach. The specimen is completely preserved from the protoconch until the adult body chamber.*

*(Abstract: De Baets, Klug, Korn, Bartels & Poschmann)*

## **Olcostephanidae (Cephalopoda, Ammonoidea) from the Taraises Formation (upper Valanginian, Peregrinus Zone) from Durango State, Mexico**

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Previous studies regarding ammonites of the Taraises Formation from the upper Valanginian have provided valuable data to the understanding of the systematics, evolution, and paleobiogeography of this fossil group in northeast Mexico.

Current research discusses about the origin, depositional environment, and paleobiogeographic significance of an assemblage of Valanginian ammonites recovered from a stratigraphic section of the area of Cuencamé, in the State of Durango.

The stratigraphic section of this study is located within the "Palotes" Anticlinorium at 103° 30' west and 24° 42' north. It is made up of 628 cm consisting of an alternation of facies made of limestones, marly limestones, marls, and shales typical of an outer neritic environment. In the stratigraphic section, stands out a fossiliferous horizon that records a rich assemblage of representatives of the Family Olcostephanidae, such as *Olcostephanus (Olcostephanus) atherstoni*, *Olcostephanus (O.) balestrai*, *Olcostephanus (O.) nicklesi*, and *Olcostephanus (O.) nov. sp.*

It is worth to mention that this family of ammonites appeared in the East Tethys at the time interval elapsed by the Verrucosum Zone at the beginning of the late Valanginian. Its subsequent migration towards the West Tethys was facilitated by a global sea level rise.

Associated to the first records of the olcostephanids in this work, stand out other ammonites with biostratigraphic value, such as *Karakaschiceras sp.*, *Ceratotuberculus linguituberculatus*, *Rodighieroides belimelensis*, *Oosterella begastrensis*, *O. gaudryi*, *O. cultrata* and *O. cultrataeformis*. This assemblage can be regarded as belonging to the Peregrinus Zone from the upper Valanginian, which according to the standard scheme for the Tethyan domain represents a younger age than that of the Verrucosum Zone. Thus, this work confirms the preconceived idea that the entrance of elements of the Family Olcostephanidae along with other associated ammonoids into the Mexican basins, occurred during the late Valanginian, a time after that family was originated within European basins.

## **Alive and fossil Cephalopods in the National Nature Reserve of Haute-Provence: how to protect and make discover this exceptional heritage?**

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The "Réserve Naturelle Géologique de Haute Provence" is a National Nature Reserve the mission of which is the protection of the geological heritage. Created in 1984 it is one of the former French Geologic Reserves. Today its territory extends on 2300km<sup>2</sup>. The Region covered by the reserve offers a geological heritage of exception: 300 million years of history are recorded in sedimentary series, which can reach 4500 meters in thickness. The Mesozoic series is almost complete, and sediments left by the sea, which occupied the region from the Hettangian to the Campanian, contain abundant faunas of cephalopods (ammonites, nautilus, belemnites). The region of Digne and Barrême is known for its faunas and its geological sections since the works of Alcide d'Orbigny. Its wealth of ammonites in addition involved many plunderings for the trade of the fossils. Today the geological Reserve leads at the same time, actions of protection, educational, scientific research, and tourist development. The territory of the Reserve is conceived as an open-air museum; ammonites are in the free air (Digne) or covered (Fontbelle). The ammonites are also presented in the museum of the Reserve in Digne or in the museums of Sisteron, Castellane, Barrême. Sites as that ammonite slab of Digne (320m<sup>2</sup>), with its 1500 *Coroniceras multicoatum* (Sinemurian), allow to make sensitive and to educate several thousand persons every year, in private individuals of the school, in the brittleness of the natural heritage. Marine aquariums make the link between the past and the present. *Nautilus* alive, ammonites fossils, ask at the same time a follow-up and studies to improve the knowledge and improve the management of aquariums and sites; for it scientific teams are associated with the works of the Reserve. A partnership is required for the follow-up of *Nautilus*.

## **An Alpine immigrant: *Phragmoceras* Broderip, 1839 from the Silurian of the Carnic Alps (Austria)**

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Numerous species of the distinctive Silurian genus *Phragmoceras* Broderip, 1839 (Discosorida, Phragmoceratidae) have been documented from Laurentia, Baltica and Perunica (Prague Basin) whereas occurrences recorded from Avalonia are often represented by numerous although poorly preserved individuals of these endogastric breviconic nautiloid cephalopods. They form characteristic elements of the tropical faunas of Laurentia and Baltica and seem to be indicative of a change to warmer environmental conditions at other palaeolatitudes at precise intervals as, for instance, during the Homerian (Wenlock) and early Ludlow in the Prague Basin (Holland & Stridsberg, 2004; Manda 2008). To date findings of "stray" poorly preserved specimens of *Phragmoceras* from the upper Silurian of SW Sardinia (Gnoli, 1996) document the presence in the Mediterranean area of species occurring in Bohemia and Baltica. Their distribution may be related to the deposition of the cephalopod limestone biofacies at certain intervals and transport by surface currents active along the North Gondwana margin. Differing opinions prevail with regard to prolonged post-mortem drift of such specimens and as to whether they represent thanatocoenoses or biocoenoses. Collecting bias may also be a factor as even in areas such as the Prague Basin representatives of the numerous species continue to be found. Specimens have also been documented from Estonia, Podolia, Siberia, the North Urals and elsewhere. Manda (2008) suggests that immigration events of this genus took place which seem to coincide with global eustatic lowstands thus facilitating faunal exchange along shallow carbonate shelves. He has documented several such events into the Prague Basin ranging from late Llandovery to Ludlow in age.

A finding of a phragmocerid specimen in the Wenlock strata (Homerian: Ozarkodina sagitta sagitta conodont biozone) of the Rachkofel Boden section, Carnic Alps (Austria) together with data from studies on sequence stratigraphy, correlation of nautiloid assemblages and study of their taphonomic signatures in relation to Silurian global biotic events would seem to support this hypothesis. The presence of this genus in the Alpine area adds further evidence with regard to faunal exchange for documenting the relative positions of various Peri-Gondwana Terranes during the Silurian.

Gnoli, M. (1996) Occurrence of a Bohemian type phragmoceratid (Nautiloidea) from the Silurian of South-Western Sardinia. *Accad. Naz. Sci. Lett. Arti. di Modena Collana di Studi* 15, 355-360.

Holland, C.H. & Stridsberg, S. (2004). Specific representation of the Silurian cephalopod genus *Phragmoceras* in Gotland and Britain. *GFF*, vol. 126, 301-310.

Manda, \_\_. (2008). Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia). *Bulletin of Geosciences* 83(1), 39–62.

## On the systematics of Lytoceratoidea (Jurassic-Cretaceous)

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After major taxonomic revision of all genera (65) ascribed to traditional Lytoceratoidea it turned out that only 30 genera are presently valid (Hoffmann in press). These findings are based on careful morphological investigations on the septal lobe (Is) and additional characters (e.g. general shell morphology, ornamentation and suture line). The septal lobe is the apomorphic character for all valid Lytoceratoidea, thus substantiating a monophylum. It appears in the lowermost Jurassic and is generated by median dorsal septal recesses of the internal lobe. Accordingly, the following 15 genera are excluded from the Lytoceratoidea, because of the lack of typical lytoceratoid characters (septal lobe, suture line, ornamentation) and dominance of non-lytoceratid characters, or scarce material with insufficient preservation. Although, 17 genera were regarded as junior subjective synonyms due to the lack of apomorphic characters, most of them were established without diagnosis. Three taxa were identified as sexual dimorphic relatives of other lytoceratid taxa: *Derolytocras* being the microconch of *Lytocras* (Meister, 1986), *Trachyltocras* being the microconch of *Lytocras* (Rulleau, 1998), and *Zelandites* proved to be the microconch of *Anagaudryceras*, which is recorded here for the first time. Finally, the cladistic approach was applied to elucidate the phylogenetic relationship of the remaining 30 valid lytoceratid genera using StrataPhy (Marcot & Fox, 2008).

Following Guex (1995) the Lytoceratoidea are derived from the Ammonitina being the sister taxon of Psiloceratoidea and treated here as superfamily. The Lytoceratoidea consist of the sister groups Lytoceratidae and Tetragonitidae. For the Lytoceratidae five subfamilies (Ectocentritinae, Pleuroacanthitinae, Lytoceratinae, Alcolytoceratinae and Megalytoceratinae) and for the Tetragonitidae three subfamilies (Gabbioceratinae, Gaudryceratinae and Tetragonitinae) were recognised.

This revision caused the reduction of valid taxa by more than 50%. The use of the cladistic approach allows us to represent a complete phylogenetic tree for all remaining Jurassic and Cretaceous lytoceratid ammonites on the generic level.

Guex, J. 1995. Ammonites hettangiennes de la Gabbs Valley Range (Nevada). Mémoires de Géologie (Lausanne), 27: 1-130.

Hoffmann, R. (in press). New insights on the phylogeny of the Lytoceratoidea (Ammonitina) from the septal lobe and its functional interpretation. Revue de Paléobiologie, Genève.

Marcot, J. D. & Fox, D. L. 2008. StrataPhy: A new Computer Program for Stratocladistic analysis. Palaeontologia Electronica, 11 (1): 1-16.

Meister, C. 1986. Les ammonites du Carixien des Causses (France). Schweizerische Paläontologische Abhandlungen, 109: 1-159.

Rulleau, L. 1998. Evolution and systematics of the phylloceratids and lytoceratids of the Toarcian and early Dogger of the Lyon area. Documents des Laboratoires de Géologie Lyon, 149: 1-167.



# Morphometry and palaeopathology of Orthoceratida from the Middle and Upper Devonian of the Dra Valley (SW Morocco)

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Orthoconic cephalopods from the Devonian of South Morocco, especially from the Dra Valley (Anti Atlas), have hardly been investigated. 117 specimens from the middle Givetian and upper Frasnian of the Tata region have been assigned to three genera of the Orthoceratidae: *Hastula* Zhuravleva 1978, *Plagiostomoceras* Teichert & Glenister 1952, and *Bogoslovskya* Zhuravleva 1978. They occur as limonitic/haematitic moulds in hypoxic, goniaticite-rich shales of the Ahrerouch and Anoû Smaira Formations. The environment was dysphotic and dysoxic but subordinate neritic fauna indicates a shallow hemipelagic setting. The orthoceratids have been investigated in order to use morphometry and palaeopathology for taxonomic and palaeoecological interpretations.

The material shows a large variability of chamber height at comparable diameter or of chamber height/diameter ratios, especially in *Plagiostomoceras*, less in *Bogoslovskiya*. There are no data for *Hastula*, which is mostly preserved as body chamber fragments. Septal spacing is apparently not a species character within *Plagiostomoceras* and *Bogoslovskiya* but indicates a rather high variability of individual growth rates, despite the relative stability of litho- and biofacies. Immature specimens with close septal spacing lived beyond their palaeoecological optimum. The fluctuating oxygen availability may have slowed metabolism rates and apertural growth, which was probably partially coupled with chamber formation.

All three genera were investigated for types and rates of sublethal, healed shell injuries. This is a proxy for contacts with shell-breaking or punctuating predators, such as epibenthonic arthropods, which have a poor Palaeozoic fossil record. Shell anomalies are placed in categories according to their course and strength. The total number of anomalies was normalized against the preserved length of specimens and the percentage of sufficiently preserved surface. *Hastula* has a fourfold higher sublethal injury rate than *Plagiostomoceras* from the same sections; the shell damage is on average also much stronger. None of the 11 *Bogoslovskya* specimens show shell anomalies, despite good preservation. *Bogoslovskya* seems to have lived in the free water column, without regular contact with the sea-floor or with shell-breaking or punctuating predators. *Plagiostomoceras* did interact moderately with predators, whilst *Hastula* visited regularly or diurnally the sea-floor. Its high failed predation rate correlates with its distinctive feature, the regular, concavo-convex internal shell thickenings. The course of these varices is not parallel to the rursiradiate, convex ornament. As in contemporary demersal goniaticites, the shell thickenings developed as a protection against shell breaking predators. When attacked, the animal retracted behind the last varix, which must have been secreted well behind the aperture. This is supported by their variable profile and course. Their spacing varies, too, but increases slightly with growth.

## **Anatomy and function of spines in post-Triassic ammonites**

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Spined ammonites evolved twice in post-Triassic times. In both cases, entire groups were concerned, namely the subfamily Euomphaloceratinae in the Late Cretaceous and the family Aspidoceratidae in the Late Jurassic. Spined ammonites from Mexico studied here derive from the lower Turonian Vallecillo Platy Limestone, which has become famous during the last two decades for its well-preserved macrofossils, particularly fishes, ammonites and marine reptiles. Lower Turonian spined ammonites from Venezuela are uncompressed and partly preserved with shell, including fine details of the ornamentation such as striae and growth lines. Ammonites from the lower Turonian of Brazil are preserved as three-dimensional internal moulds with striation, and in places with epizoic bivalves and bryozoans attached to the body chambers. The conchs are slightly compressed and, comparable to the ammonites from Vallecillo, the body chambers are better preserved than the inner whorls. The spined Jurassic ammonites studied here are aspidoceratids which are preserved three-dimensionally, or flattened in Lithographic Limestone from Nusplingen, with spines also present on the inner whorls.

The basic construction of spines is similar in all taxa, irrespective of their position on the shell, length and geological ages of the taxa. A conspicuously shaped gap is developed at the adoral base of the spine. It is also recognized in growth lines on internal moulds and thus an indicator for the formation of spines where these are not preserved. Ammonites of Jurassic and Cenomanian age retain their spines throughout ontogeny and include them into succeeding whorls, but in post-Cenomanian ammonites spines are restricted to the last whorl, possibly even to the body chamber. The mechanism of their removal from the phragmocone remains unclear.

Many functions have been suggested for the spines. The most widely accepted explanation for their formation is that they served as a balancing aid for resting on the sea-floor in a demersal mode of life. However, this cannot be applied to Jurassic and Cretaceous taxa preserved in platy limestones, because a demersal mode of life is excluded there by hostile palaeoenvironments. Among further possible functions of the spines, several can be excluded, and some others are plausible.

## ***Stramentum* on ammonites from Mexican Late Cretaceous Platy Limestones**

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The thoracic crustacean *Stramentum* spp. is widespread in sediments of Cenomanian-Coniacian age. During recent years, the discovery of platy limestone deposits in north-eastern Mexico led to the collection of well-preserved Stramentids of early Turonian age at Vallecillo, state of Nuevo León, and of early Coniacian age at El Carranza, state of Coahuila. The Vallecillo Platy Limestone has been noted for well-preserved fossils, particularly fishes, ammonites and marine reptiles during the last decades, and the palaeoenvironment is well known from previous studies. El Carranza is less understood, but precise biostratigraphic data exist.

While the nacreous shells of the ammonites were dissolved during early diagenesis, the calcite of their epizoans is preserved, but recrystallized in some specimens from Vallecillo. The detailed taphonomic analysis of both hosts and epibionts showed that the ammonite shells were colonized during their lifetime in all cases. The Stramentids may have survived the death of the ammonite, but the shell did not float for a long time. The well-preserved Stramentids seem to have been embedded alive.

*Stramentum* colonized the shells of various ammonite species, but their target shells were restricted to few morphotypes. In addition, the cirripedians were mapped on the ammonite shells. The interpretation of these quantitative data allows for new insights into the palaeobiology of the epibionts and the host ammonites.

## Age determination using stylets in genus *Eledone*

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An attempt was made at age determination of two eledonid species abundant in the Adriatic Sea, *Eledone cirrhosa* and *E. moschata*, by means of growth increments within the stylet structure (a remnant of internal shell reduced to a pair of fine, long structures embedded in mantle, near the base of each of the gills). Until now, age determination for these octopod species was primarily based on the length frequency distribution data, a method proved to be highly unreliable for these short-lived species. So far, several studies at age determination by stylet growth increment analysis have been undertaken in several octopod species, but none have included species from the genus *Eledone*. The experiment was performed on wild specimens obtained through commercial trawling fisheries in the Central Adriatic Sea. Several methods were used for the preparation of stylets for reading of growth increments. The best results were obtained when after dissection stylets were preserved in 4% formalin using tap water. All prepared transverse stylet sections were vertically mounted in thermo-plastic cement and then ground and polished using lapping sheets. The final thin sections were analysed under a microscope. In both species sections included several areas differing in coloration and visibility of growth increments. A comparison of results obtained for the two species and comparison with results of similar studies on the same structure in other octopod species was discussed. Promising results were obtained for both eledonid species, but further, more detailed studies are needed to improve the preparation techniques and reading processes of stylets and to validate the periodicity of the increments for both species.

## **Tethyan affinity of new Smithian (Early Triassic) ammonoids from Crittenden Springs, Elko County, Nevada (USA)**

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Ten new records of Smithian (Early Triassic) ammonoid taxa recently reported from Crittenden Springs, northeastern Nevada by Jenks (2007) and Jenks et al., (2010) include six newly described taxa, but of even more importance is the fact that six of the taxa (an arctoceratid, two proptychitids, a flemingitid, a hedenstroemid and an aspenitid) are very similar or identical to forms from such Tethyan localities as Guangxi (South China), Oman and South Primorye. These occurrences not only add to the growing list of ammonoids common to the Tethys and the Eastern Panthalassic basins, but they also further demonstrate the paleotropical nature of these basins. They also further corroborate the very significant low paleolatitude faunal exchange that existed between opposite sides of the Panthalassic Ocean during Smithian time. These common taxa include: *Churkites noblei*, *Pseudaspidites silberlingi*, *Galfettites lucasi*, *Pseudosageceras augustum*, *Pseudaspenites balinii* and *Guodunites cf. G. monneti*.

## Dienerian (Early Triassic) ammonoids from the Candelaria Formation, Mineral County, Nevada (USA)

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A well-preserved ammonoid fauna of Early Dienerian age has long been known from the lower portion of the Candelaria Formation in the old Candelaria silver mining district in Mineral County, Nevada, but for a variety of reasons, this fauna has never been studied in detail nor illustrated. In 1936, Muller and Ferguson named and described the Candelaria Formation and recognized that its fossils represented two of the earliest Triassic marine faunas then known from North America, namely an older bivalve fauna consisting largely of *Claraia stachei* and a slightly younger *Proptychites* ammonoid fauna. Then, Muller and Ferguson (1939) documented the close affinity of their Candelaria ammonoids with those described by Waagen (1895) from the Salt Range of Pakistan and by Krafft and Diener (1909) from the NW Himalaya. Subsequently, they tentatively identified these ammonoids as: "*Meekoceras*" cf. *lilangense*, "*M.*" cf. *tenuistriatum*, *Proptychites* cf. *ammonoides* Waagen, *P.* cf. *trilobatus* Waagen and *Hedenstroemia* (*Clypites*) cf. *evolvens*. Later, Silberling and Tozer (1968) assigned a late Griesbachian age to the *Claraia* bivalve assemblage and correlated the ammonoid fauna with the early Dienerian *Proptychites candidus* Zone of Canada.

Currently, the Candelaria ammonoid assemblage is undergoing rigorous taxonomic analysis at the University of Zurich. This work includes detailed comparisons with early Dienerian ammonoids from various Tethyan localities such as the Salt Range, Spiti, and South China. Not surprisingly, the low-paleolatitude Candelaria ammonoid fauna tends to more closely resemble the Tethyan faunas than the higher paleolatitude Canadian faunas. This observation is supported by the presence of *Proptychites haydeni* and *Ambites lilangensis*, which are present in the Southern Tethys, but not in the boreal realm. Further corroboration is provided by the presence of early Hedenstroemiids, which appear only at the end of the *Vavilovites sverdrupi* Zone in the boreal realm. These similarities at least demonstrate that some degree of equatorial faunal exchange occurred between opposite sides of the Panthalassic Ocean during early Dienerian time, and the slight dissimilarity in North American faunas also suggests the possible existence of a weak latitudinal diversity gradient during this time as well (Brayard et al., 2006).

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Waagen, W.H., 1895, *Palaeontologia Indica (Salt Range Fossils)*, ser. 13, v. 2.

# First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany)

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A recent discovery of an unusually preserved belemnite from Nusplingen comprises the extraordinarily rare remains of beaks and nearly in situ arm-hooks as well as the ink sac and the incomplete phragmocone. So far, *Hibolithes semisulcatus* (Münster, 1830) is the only larger belemnite known from the Nusplingen Lithographic Limestone (Upper Jurassic, Late Kimmeridgian, Beckeri Zone, Ulmense Subzone; SW Germany) which has the same phragmocone shape and size, thus we assign the new specimen to this taxon. The rostrum was probably lost due to a lethal predation attempt in which the prey was killed but not entirely eaten. For the first time, a specimen reveals details of the belemnite beak morphology, which we compare to the beaks of other Jurassic cephalopods. This specimen presently represents the only known rostrum-bearing belemnite of post-Toarcian age which has been preserved with non-mineralised body parts. As *Hibolithes semisulcatus* is known to possess one pair of mega-onychites, the absence of those in the present specimen provides evidence of sexual dimorphism in *Hibolithes semisulcatus*. This phenomenon was previously presumed for all belemnites, but it is known only from *Passaloteuthis* with certainty since the rostrum of the latter is unambiguously associated with an arm crown that occasionally includes one pair of mega-onychites. The imperfect preservation of the belemnite beaks hampers a detailed comparison with other Recent and fossil coleoid beaks. Some morphological characters (low width of the outer lamella, double lateral lobes of the dark parts of rostrum and hood, possibly short internal lamella) of the lower beak of *Hibolithes* more closely resemble Recent decapods than Recent octopods. The upper beak of *Hibolithes* differs in the long, narrow and curved rostrum from those coleoid beaks previously known from Nusplingen. The dark part of the lower beak also shows a unique outline with a short and pointed rostrum, an elongate posteroventral extension and two small rounded sinuses which pointed towards the wings (sometimes similarly developed in Recent *Sepioteuthis*). It appears likely that this beak form is quite characteristic and it might reflect a special diet of the belemnites. Taking their probably high swimming velocity (fins, stream-lined body, and horizontal orientation of the longest body axis) with the arm hooks and the sharp beaks into account, it appears quite likely that belemnites were fast-swimming, effective, medium-sized predators. With the new discovery, Nusplingen now represents the only locality which has yielded complete beak apparatuses from all major Jurassic cephalopod groups.

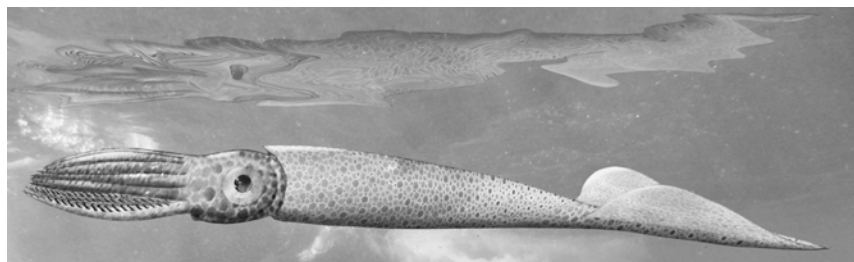


Figure: Life reconstruction of *Hibolithes semisulcatus* (Münster, 1830) from the Kimmeridgian. The entire adult animal attained a length of approximately 500 mm.

## **Parallel evolution controlled by adaptation and covariation in ammonoids (Cephalopoda)**

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Parallel evolution among extinct lineages is a poorly studied phenomenon. Usually, it is difficult to differentiate between functional or adaptive aspects of morphological evolution and aspects which are controlled by covariation and morphogenetic constraints. Herein, we present a case study of two lineages of early ammonoids (extinct cephalopods with chambered shells) where the most derived species of both display a strikingly high quantity and quality of homoplasies. Among ammonoids, parallel evolution is often linked to covariation of shell parameters which plays a central role in the morphogenesis of mollusc shells. Nevertheless, selective pressure on some shell parameters did most likely direct evolution while other parameters simply followed because of covariation. We document their parallel evolution and discuss in detail, how some of their derived character states can be explained by covariation whereas others represent probably adaptations to improve the hydrodynamic properties of the shell. We thereby show that parallel evolution can be driven simultaneously by different factors such as covariation (fabricational constraints) and adaptation (natural selection).



## Middle Permian (Roadian) Cephalopods of the Volga-Urals Region

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New cephalopod records from the Kazanian of the Volga-Urals Region (over 1000 specimens of nautiloids and 150 of ammonoids from 15 localities) provide for the first time the age and correlation of the Kazanian Regional Stage of the Permian System, and an insight into biogeography and ecology of this fauna.

*Ammonoids.* About 80% of the collection are species of *Sverdrupites* (*S. harkeri*, *S. amundseni* and *Sverdrupites* sp.), 15% are species of *Biarmiceras* (*B. esaulovae*, *B. kremeshkense* and *B. barskovi*), medicottiids are ca. 5% (*Medlicottia postorbignyana*), while a few more were identified as *Neouddenites* and *Anuites*, which indicates Roadian age. Interestingly, no pseudogastrioceratids have been found, while in synchronous faunas from Novaya Zemlya, this family is present, with no *Biarmiceras* or medicottiids, while the assemblage from Arctic Canada includes all the above genera. No medicottiids are known from the Verkhoyansk Region. These differences may partly result from sampling, but also suggest different ecological situations. Species of *Sverdrupites* are known from all northern regions where Roadian ammonoids have been found and are reliable indicators for the beginning of the Middle Permian in the Biarmian Region. Almost all genera of this assemblage (excluding *Medlicottia*) are typical of and restricted to the temperate Biarmian Province. There was a considerable faunal exchange between different regions within the province. *Sverdrupites* and *Biarmiceras* originated in the east (Verkhoyansk Region), and later migrated westward, reaching the basins of the Volga-Urals Region and of Arctic Canada.

*Non-ammonoid cephalopods.* About 95% of these are Nautilida (at least 10 genera and 200 species), and a few bactritoids. The genera *Domatoceras*, *Liroceras*, *Peripetoceras*, *Millkoninckioceras* existed from the Early-Middle Carboniferous to the end of the Permian, allowing a study of migration pathways. *Liroceras* appeared in the Early Carboniferous and became widespread in the basins of the Russian Platform, UK and North America. From the end of the Carboniferous and Early Permian it is recorded from the UK and North America, but is absent in the Russian Platform and the Urals. In the mid-Permian it was present in the Urals, while in the Late Permian it occurred in the Paleotethys (Madagascar, Japan), which indicates its northward migration. The same applies to other nautilids in the assemblage. Nautilids include only involute and semi-involute shells similar to modern *Nautilus* and are also connected with reefs suggesting a benthopelagic living form. Differences in the whorl cross-section, whorl overlap degree and differences in the suture and hyponomic sinus may indicate depth preferences and ability for active swimming. Presence of shells with characteristic aperture modifications in adults (*Permonautilus*) suggests a high-energy environment requiring adaptations for shell orientation.

## Early ontogeny of a Late Carboniferous Bactritoid (Cephalopoda) from Kansas, USA

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More than a thousand pyritized internal molds of bactritoids from a dysoxic black shale (Eudora Member - Stanton Formation: U. Carboniferous) provide a morphological series of embryonic and early post-embryonic shells: (1) apical half of incomplete protoconch, (2) sub-spherical protoconch (0.6 mm wide and 0.5 mm long) with a formed aperture; a few are attached to each other forming possible "twins", (3) a sub-spherical protoconch and a short orthoconic shaft with no septum between them; sometimes these are "twins", (4) a protoconch and a short orthoconic body chamber separated by a septum; (5) a protoconch, two septa (one chamber) and a body chamber; (6) a protoconch, three septa (two chambers) and a body chamber with a primary constriction forming at a distance about three times longer than the protoconch length from the first septum; (7) Time of hatching - protoconch and four septa (three chambers) with a formed primary constriction, and (8) post-hatched specimens with more than four septa.

The reason for possible "twinning" is uncertain, but they may represent twinned embryos within the same egg capsule. Based on modern coleoid embryology, such pairing could have resulted from "repeating" the first cleavage step so that each of the second cleavage furrows lying on either side of the first furrow became the respective first cleavage furrow of a prospective twin. Apparently, the pairs do not survive into later embryo growth, possibly because of insufficient egg yolk volume or because the organism could not survive beyond a certain growth development stage due to organ dysfunctions (including the shared yolk sac envelope) of co-joined individuals.

The Eudora bactritoids occur in a dysoxic bottom environment (based on mineralization and lack of benthic fauna). This indicates that bactritoids laid their eggs in the upper water column. The studied embryonic shells at different developmental stages within different egg masses (see stages 1- 7 above) apparently sank to the bottom where the oxygen deficiency killed the embryos. Post-hatchlings (beyond stage 7) were deposited on the dysoxic bottom for unknown reasons, perhaps because of physiological and/or predation problems and/or the inability to avoid the deadly bottom environment.

The embryonic development of ammonoids and *Nautilus* follow different developmental paths than bactritellas. Because higher levels of classification consider early development differences to be important, the bactritoids should be maintained as a separate subclass – the Bactritoidea.

## New records of Early Middle Jurassic belemnites in the French Subalpine Basin and their paleobiogeographic relevance

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Recently, Weis & Mariotti (2007) and Mariotti et al. (2007; 2010), described early Middle Jurassic belemnite faunas from Luxembourg, SW Germany, NW France and Italy, supposing that a belemnite provincialism developed at the Aalenian-Bajocian boundary inside the European archipelago. Particularly, a subboreal Belemnitina-dominated fauna has been recognized in Luxembourg, Germany, NE France and NW Switzerland while a submediterranean *Pachybelemnopseina*-dominated fauna is described for Italy and southern France. The western Anglo-Paris Basin (Normandy, Dorset) represented a transitional area.

Recent fieldwork in the French Subalpine Basin area has yielded a previously unknown fauna characterized by Late Aalenian to Early Bajocian belemnites. The new records from Gap, Castellane and Digne (Subalpine Basin, SE France) seem to confirm this scenario and greatly contribute to a more detailed distribution pattern. The specimens were found in hemi-pelagic marl-limestone alternations in the lower part of the 'Calcaire à Zoophycos' Formation together with early Middle Jurassic ammonites. In the northern areas of the Subalpine Basin (Gap), *Megateuthis elliptica* is abundant, meanwhile it is unknown in the southern area (Castellane); "*Belemnitida incertae sedis*" (sensu Mariotti et al., 2007) and *Holcobelus munieri* are well represented in all the outcrops, while *H. tetramerus* and *H. tchegemensis* have been found in Castellane. The belemnites coming from the Castellane area (Lac du Castillon and La Baume sections) show great similarities with the fauna of the Calabro Peloritani Arc (southern Italy, Mariotti et al., 2007); this can be explained by the peculiar paleogeographic position of the later during the Middle Jurassic, when the Calabro Peloritani Arc was the continuation of the Sardinia-Corsica European margin.

Mariotti N., Santantonio M. & Weis R. 2007. Aalenian-Early Bajocian belemnite assemblage from peri-mediterranean Tethyan sediments (Calabria, southern Italy). *Geologica Romana*, 40: 1-19.

Mariotti N., Santantonio M. & Weis R. 2010. New data on the paleobiogeographic and biostratigraphic distribution of *Holcobelus* Stolley, 1927 and its allies (Belemnitida) in the Middle Jurassic. In Fuchs D. (ed.), Proceedings of the 3rd international symposium Coleoid Cephalopods Through Time. Luxembourg 8th-11th October 2008. *Ferrantia*, 59: 137-147. Musée national d'histoire naturelle, Luxembourg.

Weis R. & Mariotti N. 2007. A belemnite fauna from the Aalenian-Bajocian boundary beds of the Grand Duchy of Luxembourg (NE Paris Basin). *Bollettino della Società Paleontologica Italiana*, 46 (2-3): 149-174. Modena

## Central Russian ammonites at the Jurassic / Cretaceous boundary

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The Jurassic/Cretaceous boundary beds in the central part of Russian platform are presented by *Craspedites nodiger* Zone of the Volgian Stage and *Riasanites rjasanensis* Zone of the Ryazanian Stage. The beds with *Hectoroceras*, still insufficiently studied, are established between these zones in recent years.

*Craspedites* and *Garniericeras* typify the Volgian terminal zone. Apparently, in each faunal horizon of this zone there is one species of *Craspedites*, in association with *Garniericeras subclypeiforme* (Milashevitsch). In layers lying above only *Hectoroceras tolijense* (Nikitin) are found. Still above follow the beds with typical *Hectoroceras kochi* (Spath) (fig. 1), with which solitary *Craspedites?* sp. juv., are found.

The basal zone of the Ryazanian is subdivided into two subzones, lower Rjasanensis and upper Spasskensis (Mitta & Bogomolov, 2008). This zone contains various assemblages of ammonites: except *Craspeditidae*, ammonites of the Tethyan origin (*Neocomitidae* and *Himalayitidae*) are found here.

The lowest faunal horizon of the Rjasanensis Subzone contains numerous *Riasanites swistowianus* (Nikitin), and rare *R. rjasanensis* (Nikitin). Also here are established ammonites of the new genus, related to *Riasanites*, with four new species. *Neocomitids* are presented by *Subalpinites* (4), *Mazenoticerias* (3), *Malbosiceras* (1), *Pomeliceras* (1). *Craspeditids* are presented by *Craspedites*, *Pseudocraspedites*, *Hectoroceras* – each genus by one species. For panboreal correlations it is important, that is not *Hectoroceras kochi* that occurs in Rjasanensis Zone, but another species, which have thicker whorls and wider umbilicus (fig. 2).

The *Riasanites rjasanensis* faunal horizon except a numerous specimens of index-species contains rare *R. swistowianus* and *Subalpinites* (1), *Mazenoticerias* (1); and also *Pseudocraspedites* (1), *Praesurites* (1).

In the Spasskensis Subzone, the *Riasanites* (3), *Transcaspiites* (3), *Subalpinites* (1), *Malbosiceras* (1), *Pomeliceras* (1), and also *Surites* (2), *Pronjaites* (1), *Gerassimovia* (1), *Externiceras* (1), are found.

Apparently, Rjasanensis Zone is an equivalent of the Occitanica zone of the standard Berriasian. The beds Tolijense/Kochi may correspond to the Jacobi/Grandis Zone.

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Mitta V.V., Bogomolov Yu.I., 2008. Subdivision of the Ryazanian Stage of Russian Platform. In: The Cretaceous System of Russia and adjacent countries: problems of stratigraphy and paleogeography. Publ. House SB RAS, Novosibirsk. P. 126-129.

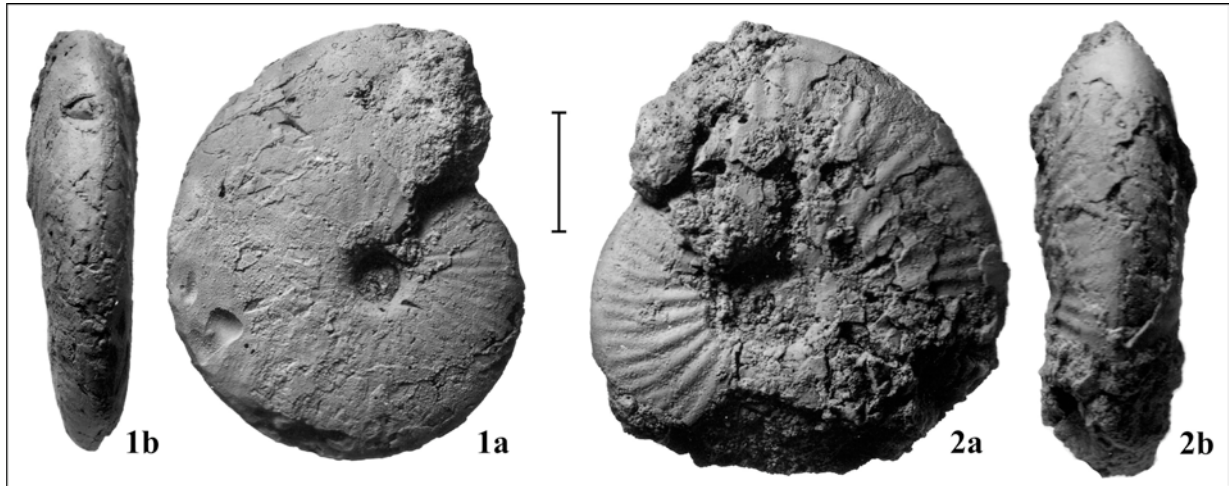


Figure: (1): *Hektoroceras kochi* (Spath), (2) *Hektoroceras* sp. nov. Moscow region near Voskresensk. Scale bar 15 mm

(Abstract: Mitta & Bogomolov)

**Taxonomic revision of *Puzosia*, ammonite of the Lower Cenomanian:  
*Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841), a species not  
announced in the Onilahy sector of the Morondava Basin (Madagascar)**

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Several ammonites recovered from the Onilahy area (South of the Morondava Basin, Madagascar) have been studied to reappraise the systematic of the genus *Puzosia*. This work is based on the analysis of morphological variations and shell growth of several specimens in order to identify possible dimorphism. Based on biometric considerations, six species of *Puzosia* previously described by Collignon (1928, 1961, 1964) are attributed to dimorphs of the same species: *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1981). This species, never announced in Madagascar, is a very important taxon to characterise the lower Cenomanian. Consequently, these systematic results allow the simplification of the current nomenclature of the genus *Puzosia* and make easier the regional and intercontinental stratigraphical correlations.

## Changes in some Cretaceous ammonoid assemblages (planispirals versus heteromorphs) and their link to palaeoceanography and climate

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The aim of this work is to investigate the possible connections between ammonoid evolution and palaeoenvironmental changes. The results and their interpretations are based on the studies of Valanginian and Cenomanian faunas, mainly from the Vocontian basin successions (France). Some comparisons will be made with the Upper Albian fauna.

The major extinction event in the Valanginian ammonoid faunas occurs across the Lower-Upper Valanginian boundary (Biassalense/Verrucosum subzones), simultaneously with the first positive  $\delta^{13}\text{C}$  excursion (Valanginian Weissert OAE). This faunal caesura is followed by the evolution of some planispirals (from involute *Neocomites* to evolute *Rodighieroites*; *Pronocostatum*-*Peregrinus* subzones) that will be at the origination of *Himantoceras* (criocones; appearance at the base of Nicklesi subzone); it coincides with the decrease of carbon isotope values. Perturbations in the global carbon cycle are the final expression of large-scale and rapid environmental changes which could have affected the biota. The first positive  $\delta^{13}\text{C}$  excursion is probably linked to a higher basin primary productivity stimulated by high trophic levels; a synchronous increase of calcareous nannofossils and clay fluxes is observed. This interval is characterized by important palaeoenvironmental changes as a decrease in sea-water temperature, sea-level fluctuations (sharp transgression followed by a regression resulting to the exposure of platforms in the Upper Valanginian), and an intensification of continental weathering and run-off related to cold and humid climates (fresh-water input, increasing turbidity due to clay accumulation and introduction of associated nutrients into marine realm). These unstable conditions could partly explain the extinction of numerous Lower Valanginian ammonoid (and belemnites) taxa and their abundance variations, for instance due to modifications in their habitat space in proximal palaeoenvironments and/or due to variations in trophic resources. The change in geometry shell (from coiled to uncoiled) seems to take place during high environmental stress generated by a major sea-level lowstand and the maximum sea-water cooling which takes place during the *Peregrinus* subzone.

The Lower-Middle Cenomanian boundary is characterized by a change in the ammonoid assemblages: decrease in abundance of *Schloenbachia*, disappearance of *Mantelliceras*, appearance of *Acanthoceras* and *Cunningtoniceras* and abundance of *Sciponoceras baculoides* (orthocones). This faunal event occurs simultaneously with the Mid-Cenomanian Event 1 (positive  $\delta^{13}\text{C}$  excursion) and an important sea-level variation. The dominance of *S. baculoides* coincides with the sea level rise, as observed for 3 other *Sciponoceras* species that generally occur in mass in the lower part of transgressive system tracts and, in some cases, after the occurrence of Belemnites.

## *Fusiteuthis polonica* – an intergeneric belemnite hybrid; proofs and discussion

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*Fusiteuthis polonica* Kongiel, 1962 represent one of the most bizzare belemnite form amongst all the Upper Cretaceous belemnite. Here it is interpreted not as separate species but as an example of intergeneric hybrid. Until now, only couple of specimens of this form have been found, make it the rarest representatives of the Upper Cretaceous belemnite (i.e. Christensen 2002). However, paleogeographically, it is very widespread, being known from Germany, Poland and as far east as the Crimea, in the eastern Ukraine. *F. polonica* is simultaneously one of the longest ranging Upper Cretaceous belemnite form and what is surprising, the most stable morphologically.

Its external morphology, especially very delicate alveolar part, markedly hinders its comparison with co-occurring representatives of the genera *Belemnitella* d'Orbigny, 1840 and *Belemnella* Nowak, 1913, which are characterized by well developed and powerful alveolar part of the guard.

The so far records of this species are restricted to the traditionally understood Maastrichtian stage based on the first occurrence of the representatives of the genus *Belemnella*. It is the time, when the genus *Belemnella* appears suddenly across the Europe and co-occur with the genus *Belemnitella*. These two genera differ significantly in the microstructural development of the guard (Remin in prep) and in the internal characters.

The working hypothesis that *F. polonica* represent an intergeneric hybrid could be confirmed by following observations:

1. The guards of *F. polonica* shows development patterns observed both for *Belemnitella* and *Belemnella*. The microstructural development of the guard duplicated that of *Belemnitella*, whereas the internal characters distinctly duplicate that of *Belemnella*.
2. The external morphology of *F. polonica* is significantly distinct from all other Upper Campanian and Maastrichtian belemnite species and this form can not be placed neither in *Belemnitella* nor in *Belemnella* lineages.
3. *F. polonica* appears almost immediately after the entrance of the genus *Belemnella*, therefore it occurs only in the time when genera *Belemnitella* and *Belemnella* co-occur. No records are known from the traditionally understood Upper Campanian.
4. Morphologically, it is a very stable form. Starting from the lowermost Maastrichtian up to the uppermost Maastrichtian, about 6 millions of years, is invariable. It is strange, since all the other Upper Campanian and Maastrichtian belemnites are very fast evolving animals.
5. And finally there are no reasonable ancestor neither in the Upper Campanian nor in the Maastrichtian belemnites.

All these data led to a conclusion that *F. polonica* is not a separate species, but may represent an intergeneric hybrid, not able to sex, however strong enough to live and left its fossils.

Christensen, W.K. 2002. *Acta Palaeontologica Polonica* 47: 679–683.

Kongiel, R. 1962. *Prace Muzeum Ziemi*, 5, 1–148.



## **Ammonite jaws at the base of the Danian (?) Hornerstown Formation, Monmouth County, New Jersey**

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Our investigations have revealed the presence of the K/P boundary in the Manasquan River Basin in Monmouth County, New Jersey. The section includes the topmost Tinton Formation represented by a richly fossiliferous unit that Landman et. al (2007) referred to as the Pinna Layer. The Pinna Layer is overlain by the Hornerstown Formation. In down dip sites, an additional unit occurs between the Pinna Layer and the rest of the Hornerstown Formation referred to as the Burrowed Unit. The Pinna Layer and Burrowed Unit are Maastrichtian in age based on the fossil content, but an Ir anomaly (~700ppt) occurs at the base of the Pinna Layer suggesting a lowermost Danian age. The current investigation focuses on the fossil content of the Burrowed Unit. The Burrowed Unit consists of a light green, muddy, glauconitic sand with sparse large quartz grains. It is heavily burrowed by dark green, glauconitic sand piped down from the overlying Hornerstown Formation. The matrix is relatively unfossiliferous both in macro and micro fossils compared to the Pinna Layer below. The fauna includes 4 species of bivalves, 4 gastropods, 3 ammonites, 1 arthropod, and several shark teeth. Of particular interest are 4 specimens of ammonite aptychi which include the first recorded baculite jaws on the Atlantic Coastal Plain. Within the burrows, the oyster *Ostrea pulaskensis* (Harris 1894) dominates comprising close to 90% of the fauna. Also common in the burrows are reworked Cretaceous forms preserved as siderite nodules most likely representing a hiatus within the base of the Hornerstown Formation. The preservation of aptychi suggests that the ammonites lived, died and were buried during the deposition of the Burrowed Unit. If the Ir anomaly is in place, the depauperate fauna of the Burrowed Unit could represent a unique window recording the last gasp of the Cretaceous ecosystem, including ammonites.

# **Latest Toarcian-Earliest Bajocian (Jurassic) Grammoceratinae (Hildoceratidae, Ammonitina) of the western Tethys: palaeobiogeographic significance**

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Grammoceratinae (Hildoceratidae, Ammonitina) are abundant in the Toarcian of many west Tethyan localities, where they are useful tools for biostratigraphy. They become progressively scarcer in the Aalenian and disappear in the lowermost Bajocian. The genera *Asthenoceras* Buckman 1889, *Vacekia* Buckman 1899, *Fontannesia* Buckman 1992 and *Nadorites* Elmi & Caloo-Fortier 1985 are traditionally cited among the latest Toarcian-earliest Bajocian Grammoceratinae. Likewise some species of *Osperlioceras* Krimholz, also occur in latest Toarcian rocks. Some of these taxa have been studied in detail. So, Linares and Sandoval (1988, 1992) carried out monographic studies, where they described and figured the Subbetic ammonites included in the genera *Vacekia*, *Asthenoceras* and *Fontannesia*. The Grammoceratinae are especially abundant in the Lusitanian Basin, from where Henriques (1992) described and figured four new "species": *Vacekia striata*, *V. robusta*, *Asthenoceras* sp and *A. vacekiformis*. Apart from western Tethys, the Grammoceratinae are also common in east Pacific, especially in Oregon and Alaska, and they are also probably present in east Tethys (Thailand). The Subbetic and Lusitanian material is reviewed in this work which includes data from other palaeogeographic areas.

The revision of original collection of Linares & Sandoval shows that most of the Subbetic material represents Grammoceratinae (genera *Vacekia* and *Asthenoceras*) and that only some specimens are representatives of *Fontannesia* (eg. *F. tortiva* Buckman). The specimens there described as *F. montillanensis* Linares & Sandoval, subsequently also cited in the High Atlas, do not correspond to the morphological characters of the genus *Fontannesia* (genus that must be included in the family Sonniniidae rather than in Grammoceratinae), but they clearly belong to the subfamily Grammoceratinae and they represent, probably, the last western Tethys Grammoceratinae. Most Aalenian specimens from the Lusitanian Basin described by Henriques as *Vacekia* clearly correspond to forms of this genus, while their Upper Toarcian specimens could correspond to the subgenus *Nadorites*. The "type" of "*Asthenoceras vacekiformis*" from the Opalinum Subzone, can likewise represent a primitive *Vacekia*.

The analysis of the temporal succession of genera and species of Grammoceratinae shows a progressive uncoiling (more evolute) throughout the time, which is sometimes coupled with a decrease in size. Palaeogeographic analyses support the hypothesis that during the Early-Middle Jurassic transition the west Tethys and east Pacific were, at least temporally, well connected, perhaps through the Hispanic Corridor, as shows the similarity between Tethyan (especially Subbetic and Lusitanian) and East Pacific (Oregon and Alaska) Grammoceratinae.

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Linares, A. & Sandoval, J. 1988. Rev. esp. Paleont. 3, 3-12.

Linares, A. & Sandoval, J. 1992. Rev. esp. Paleont. Ext., 91-100.

## ***Aturia* from the Miocene Paratethys: an exceptional window to nautilid habitat and lifestyle**

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Drifted *Nautilus* shells are found on beaches sometimes thousands of kilometers outside distribution areas of living animals. This post-mortem drift constitutes a potential caveat for the interpretation of the paleobiology and paleoecology of chambered cephalopods and the extent to which this process biases their paleobiogeographic distribution remains difficult to evaluate. An exceptional Lower Miocene deposit from the Vienna Basin of Central Paratethys yielded an abundant and very well-preserved upper bathyal (240 – 330 m paleodepth) fossil assemblage. *Aturias* are distributed within a 7.5 m thick section in which about 500 specimens have been collected. *Aturia* assemblages comprise adult (as indicated by approximation of last septa, black band along the shell edge, thickened peristome and crowded growth lines on the body chamber) as well as juvenile and newly hatched specimens, associated in the sediments with their jaws, representing the first unequivocal case of autochthonous *Aturia* and one of the most exceptional nautilid deposits reported so far. We performed stable oxygen isotope analyses on embryonic and post-embryonic shells of *Aturia* as well as on associated calcareous shells of organisms including planktonic foraminifera, bivalves, gastropods and scaphopods. Comparisons of multi-organismic stable isotope ratios show that *Aturia* was like *Nautilus*, nekto-benthic at all stages of its development. The presence of well preserved newly hatched individuals (in the range of 7-15 mm) suggests close proximity of spawning grounds. Contrary to *Nautilus*, no major shift in  $\delta^{18}\text{O}$  occurs between embryonic and post-embryonic shells, suggesting that newly hatched individuals and adults lived at a similar depth where the eggs were laid.

Based on calculations of the benthic foraminiferal oxygen index (BFOI), we show in addition that the section deposited under dysoxic conditions. Such dysoxic paleoenvironmental setting in which *Aturia* occurs in abundance may be interpreted in light of the capacity of *Nautilus* to exploit oxygen-depleted waters, and molecular phylogenetic tree of cephalopods, altogether suggesting plesiomorphic physiological traits associated with hypoxia tolerance.

## Quantification of ontogenetic change in Triassic ammonoids

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The integration of developmental processes in evolutionary studies is one of the main topics of Evolutionary Biology. However, palaeontologists can contribute much less to developmental studies, simply because palaeontological objects and assemblages are often too incomplete for such studies or the organisms under study do not allow the postulation of ontogenetic series. Ammonoids can serve as valuable objects for studying ontogeny and may thus play an important role in Evo Devo research of extinct organisms. The distinct growth modus of their conchs offers some advantages that are rare in other fossil organisms. The conch grows accretionally, i.e. early ontogenetic stages are preserved within adult specimens. Using grinding or scanning techniques, the entire ontogeny can be studied.

Ontogenetic trajectories are a very characteristic feature of taxa of various hierarchical order; they are important to study evolutionary change and are key characters for the classification of the Ammonoidea. The study of Palaeozoic ammonoids demonstrates that most species show a complex ontogeny with regard to their conch geometry. Isometrically growing conchs are extremely rare, and ontogenies with constant allometry index also play a subordinate role. The vast majority of the Palaeozoic ammonoids undergo several successive ontogenetic stages with an instable but strictly determined temporal pattern of the allometry index.

The ontogenetic change of Triassic ammonoid conchs will be quantified with the aim to correlate ontogenetic processes with phylogenetic hypotheses. The morphological disparity of selected Tethyan and eastern Pacific assemblages of Triassic ammonoids are analysed and compared with Palaeozoic faunas. It is tested if the ammonoids, after their dramatic decline near the Permian-Triassic Boundary, reached similar grades of morphological variation in ontogeny like their Palaeozoic predecessors.

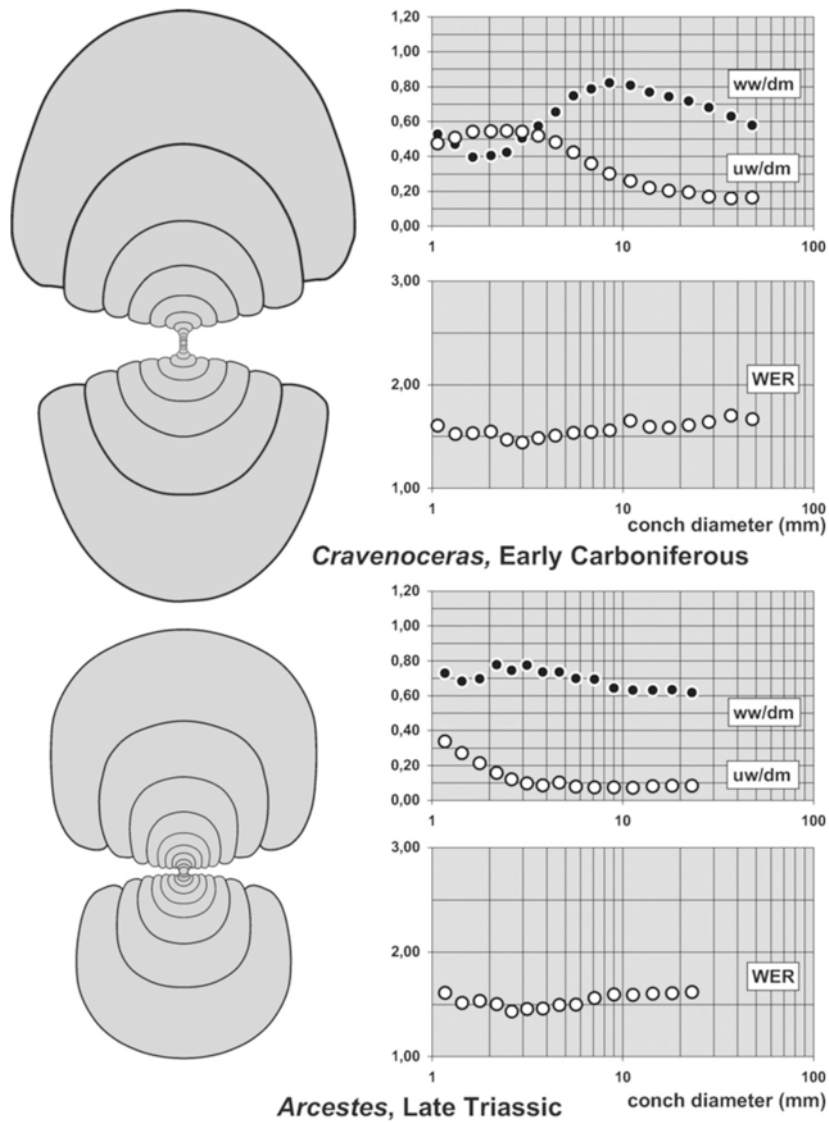


Figure: Two examples of ontogenetic change. *Cravenoceras* (Early Carboniferous) shows conspicuous allometric growth in the whorl width and umbilical width ratios, whereas *Arcestes* (Late Triassic) shows an almost isometrically increasing whorl width.

(Abstract: Simon & Korn)

## Late Cretaceous nautiloids from eastern Utah, USA

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The Mancos Shale is an extensive marine unit, present at the surface and in the subsurface through a vast area of several western states including Utah, where in some places it is over 1500 m thick. The mostly siliciclastic mudrocks of this unit reflect deposition within the Western Interior Seaway of North America, and outcrops of these Upper Cretaceous rocks can be seen now across a large part of the desert of east-central Utah. Recent discoveries in the Blue Gate Member of the Mancos Shale in Emery County, Utah, have significantly expanded our understanding of the Coniacian cephalopod fauna in this part of the basin. All fossils were collected from concretionary masses in rocks belonging to the *Scaphites preventricosus* Zone, indicative of the Lower Coniacian Substage. The high diversity ammonoid assemblage is described in a separate contribution to this symposium.

As is typical, nautiloids are a much less common component of the cephalopod fauna. Elsewhere in eastern Utah, we find *Eutrephoceras* sp. higher in the Upper Cretaceous strata. However, here we document specimens that we have referred to *Anglonautilus* sp., which may represent a new, undescribed species. The fossils are internal molds; very little shell material is preserved. The conch is involute, and the whorl section is broad and rounded. Siphuncle position is approximately central. The suture is only gently sinuous, being rather straight across the venter though with a very shallow but distinct ventral adapical deflection, which could be interpreted as a lobe, and modest lateral and umbilical lobes and saddles. One specimen, apparently representing an adult, shows the coarse, "fold-like" ribs on the internal mold of the living chamber, a key diagnostic feature of the genus. The ribs are strongly but smoothly curved, and are more pronounced on the venter, somewhat fading in strength on the flanks towards the umbilicus. Fine lirae or growth lines can also be seen between the ribs. If we are correct in our identification of these specimens, then it is the first report of *Anglonautilus* in Utah, and to the best of our knowledge the first report of the genus in North America.

## New and additional records of Late Cretaceous octobrachiata coleoid jaws from the Western Interior Seaway and the Northwestern Pacific

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Well-preserved isolated coleoid jaw fossils referable to the Teuthida, Vampyromorphida, Cirroctopodida and Octopodida were recently described from the Upper Cretaceous of Hokkaido (Japan) and Vancouver Island (Canada) (Tanabe et al., 2006, 2008). In the course of searching for additional fossil material, we have discovered six well-preserved Cretaceous coleoid jaws; two from the Turonian of Hokkaido and four from the Campanian and Maastrichtian of South Dakota, USA. All are preserved in calcareous nodules and retain their three-dimensional morphology. They are identified as lower jaws in having a more widely open outer lamella than an inner lamella, as observed in the lower jaws of modern coleoids.

As a result of direct comparison with the lower jaws of known modern and fossil coleoids, we distinguished the following three taxa from the Superorder Octobrachia: 1) *Nanaimoteuthis* sp. nov., Order Vampyroteuthida, is represented by two lower jaws from the Turonian of Hokkaido that consist of equally sized outer and inner lamellae with the crest portion of the latter wholly covered by the former. The maximum length of the holotype (UMUT MM 30337) attains 63.7 mm, suggesting a remarkably large body size of the living animal. 2) *Nanaimoteuthis* ? sp., represented by a single jaw specimen (BHI-5492), 34.4 mm in maximum length of the outer lamella, from the *Baculites compressus* zone (late Campanian) of the Pierre Shale, Meade County, South Dakota, and 3) Cirroctopodida, genus and species indeterminate (possibly *Actinosepia landmani* Larson, 2010), represented by a single lower jaw (BHI-5973) from the *Hoploscaphites nicolletii* Zone (upper Maastrichtian) of the Fox Hills Formation, Corson County, South Dakota. As seen in the lower jaws of modern cirroctopodids, the lower jaw is characterized by a posteriorly elongated wing and a relatively short hood, The inner lamella is not exposed so presently its state of development is unknown.

Shell and soft tissue remains of vampyropods and octopods have been reported from the Upper Cretaceous strata deposited in two other bioprovinces: one from the upper Cenomanian and upper Santonian Konservat-Lagerstätten of Lebanon in the Tethys realm (e.g., Fuchs, 2006; Fuchs et al., 2009) and the other from the Campanian and Maastrichtian in the Late Cretaceous Western Interior Seaway of North America (Whiteaves 1898; Waage, 1965; Miller & Walker, 1968; Nicholls and Isaak, 1987; Larson et al., 1997; Larson, 2010). The latter fauna includes *Actinosepia canadensis* Whiteaves 1898, *A. landmani* and *A. mapesi* Larson, 2010; *Enchoteuthis melanae* Miller & Walker, 1968; *Tusoteuthis longa* Logan, 1898; and *T. cobhani* (Larson, 2010) and shows taxonomic affinity with the Late Cretaceous coleoid fauna from the North Pacific region. These lines of evidence strongly support the hypothesis that highly diversified octobrachiata coleoids flourished in the world's oceans during the Late Cretaceous.

## **Stable nitrogen isotope analysis of soft and hard tissues of three modern coleoid species *Sepia officinalis*, *Sepia latimanus*, and *Spirula spirula***

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Reconstruction of trophic levels is one of the important subjects in cephalopod biology and paleobiology. Although most modern cephalopods have predatory-scavenging modes of feeding, a variety of dietary habits has been postulated for the Ammonoidea on the basis of comparative anatomical observations of jaw apparatuses and analysis of stomach-oesophagus contents preserved in the body chambers of ammonoids (e.g., Lehmann 1988, 1990; Westermann, 1996; Tanabe and Fukuda 1999). For example, Lehmann (1988) speculated that some Jurassic ammonoids fed on small benthic organisms (ostracods, crinoids, crustaceans, and foraminifers) found as their stomach-oesophagus remains by using their highly specialized aptychus-type lower jaw like a shovel. However, a question about post-mortem mixing still remains for these “preys” found in the body chambers, and another new and reliable approach is required for reconstructing feeding habits of fossil cephalopods.

Compound-specific nitrogen isotope analysis of amino acids by gas chromatography / combustion / isotope ratio mass spectrometry (GC/C/IRMS) is one of the most useful methods to estimate the food sources of organisms in a given food web (Chikaraishi et al. 2009; Kashiyama et al. 2010). We applied this method to the hard tissues (internal shells, jaws and a radula) of three modern coleoid species *Sepia officinalis*, *Sepia latimanus*, and *Spirula spirula*, as a basis for reconstruction of trophic levels in fossil cephalopods, especially ammonoids, because these hard tissues have preservation potential as fossils. Our study demonstrates that in each species, the amino acid compositions of the shell, jaws and a radula are similar, suggesting that the nitrogen isotopic composition in amino acids preserved in the intra-crystalline organic fractions can be used as a proxy of the trophic level of these species in the food web. We will present nitrogen isotopic compositions of amino acids in the soft and hard tissues of these species and discuss their ecological implications.



# Biological response to damage of the phragmocone and siphuncle in recent nautiloid: *Nautilus pompilius* Linnaeus

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Recent *Nautilus* has phragmocone and siphuncle which pass through the septa serving to separate individual chambers as a buoyancy device. Such *Nautilus* maintains neutral buoyancy by removing the cameral liquid from the phragmocone via the siphuncle. Extinct chambered cephalopods also had the phragmocone and siphuncle similar to *Nautilus*. In both *Nautilus* and extinct chambered cephalopods, the physiologic function of the phragmocone and siphuncle serve an important role in the buoyancy control. If any predators attack chambered cephalopods or some other kind of accident occurs, it is highly probable that the phragmocone and siphuncle may be injured. Particularly, the phragmocone and siphuncle of early growth portion are prone to damage. In normally coiled ammonoids and nautiloids, the young shells are rarely damaged, because the successive whorls overlap and the shells are protected. On the other hand, heteromorph ammonoids and loosely coiled, orthocone nautiloids have a high risk that the young shells suffer serious damage. Because they are open-coiled cephalopods. Based on our field observations, many heteromorph ammonoids often suffer from breakages of the phragmocone and siphuncle in young shells. Although there may be many examples that shells of heteromorph ammonoids show damage after death, it is also possible that individuals survive after damage to the phragmocone and siphuncle. Previously, many studies on the buoyancy mechanisms of chambered cephalopods have been carried out. However, there has little related to the influence on the living body of the chambered cephalopods when the phragmocone and siphuncle have been damaged. In order to estimate the biological response to damage of the phragmocone and siphuncle in chambered cephalopods, we had performed laboratory experiments with *Nautilus* whose phragmocone and siphuncle were partially severed artificially. Next we observed the progress following severance of the siphuncle over a period of four months. As a result, we confirmed the following:

- (1) *Nautilus* survived after damage to the phragmocone and siphuncle, although they lost neutral buoyancy.
- (2) After completion of the experiment, the severed part of remain of siphuncle healed by the siphuncular epithelium.
- (3) The injured area of the phragmocone was covered by the hood and the dorsally extending mantle of the soft parts, then the thin shell layer developed to recover on the injured area. We revealed that damage of the phragmocone and siphuncle in *Nautilus* is not a lethal injury, although the neutral buoyancy is significantly affected. If the phragmocone and siphuncle of heteromorph ammonoids also suffer such damage during their lifetime, it is possible that such damage is not a lethal injury and they survive.

## Early ontogeny of some Silurian tarphycerids (Nautiloidea)

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Early ontogeny of coiled nautiloids of the suborders Tarphycerina and Barrandeocerina is still poorly understood. More complex data concerning early ontogeny of the Silurian tarphycerid *Boionutilus* have been assembled and compared with early ontogeny of the Recent *Nautilus*. As the nepionic constriction of shell characterising the end of embryonic stage of post-Triassic nautilids is missing in Early Palaeozoic nautiloids, the other features characterising the embryonic shell of Recent *Nautilus* had to be applied. The change in shell coiling, character of growth structures, increasing roughness of sculpture, irregularities in spacing of growth lines, reticulate sculpture, striking deepening of the hyponomic sinus, eventual appearance of annulation and first injuries are the main features useful in determination of a probable border between embryonic and postembryonic growth stages (i.e. hatching time). Most reliable changes coincide with an abrupt change in shell coiling, which occurs in shell length 11–13 mm, i.e. approximately in 1/6 of the whorl. The first marked repair of an injured shell was observed at the midpoint of the first whorl.

Embryonic shells are known in three species of the genus *Boionutilus* forming an evolutionary lineage (*B. sacheri*-*B. tyrannus*-*B. bohemicus*) ranging from late Ludlow to latest Prídolí. Morphological changes observed in early juvenile shells are expressed in tighter coiling of the first whorl and appearance of annulation in the postembryonic phase in *B. sacheri*. *B. bohemicus* frequently differs from *B. tyrannus* by a more rapidly increasing dorsoventral length in early growth stages. Widely cup-shaped protoconch is low, its height is, however, highly variable, which is expressed in length of the caecum. The second chamber is usually higher than the third one. The height of the phragmocone chambers then generally increases. Early hatched shell in *Boionutilus* had, besides the protoconch, only one or two phragmocone chambers. This is inferred from the relative length of the juveniles and distance between the first three septa.

Hatched *Boionutilus* resembles immature embryo of Recent *Nautilus*. The short phragmocone apparently was not sufficient to buoy the relatively thick-walled shell. Consequently, freshly hatched juveniles very probably dwelt near the bottom. Owing to increasing volume of phragmocone accompanied by a quick development of the hyponome, the animal soon acquired an active swimming ability. The high regeneration ability of juveniles is proved by healing of serious shell damages appearing as early as in 3/4 of the first whorl. Very good preservation of embryonic shell of *Ophioceras* and *Graftonoceras* (from Gotland, Sweden) enables comparative study of early ontogeny in Early Palaeozoic nautiloids.

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## A new Berriasian species of *Andiceras* Krantz from the Neuquén Basin, Mendoza, Argentina

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Since Krantz (1926) raised the genus *Andiceras* from Late Tithonian-Early Berriasian sediments from two localities of the Neuquén Basin, west-central Argentina, new records of this genus outside this country are dubious and scarce. From a thin interval of the last portion of Vaca Muerta Formation (Lower Tithonian-Lower Valanginian), in the Real de las Coloradas section, Mendoza, 27 well preserved specimens of a new species assignable to *Andiceras* had been recovered. *Andiceras sp. nov.* has a medium sized, strongly evolute, discoidal shell, with almost parallel flat flanks, venter gently convex and whorl section remarkably compressed, higher than wide, with its maximum whorl breadth around the umbilical border. The very shallow rounded umbilical wall tends to be slightly more pronounced on outer whorls. The ornamentation is characterized by low relief, gently rursiradiate fine ribs on umbilical wall, bended forward at the umbilical angle and rectiradiated over the flanks. Most of the primary ribs bifurcate near the middle of the flanks, while some remain simple and in a few cases some virgatotome branching does occur. Ribs may be interrupted on inner whorls of internal moulds but are only depressed where shell is preserved. On outer whorls ribbing is continuous and straight in the venter. Portions of body chamber preserved do not denote any change in ornamentation. Suture line appears to be well indented and characterized by narrow saddles and a deep trifid lateral lobe. All the specimens appear between levels yielding *Parodontoceras callistoides* and *Groebericeras bifrons*, of the *Substeueroceras koeneni* and *Argentinceras noduliferum* assemblage biozones respectively. The former one has traditionally been considered of Late Tithonian age (Leanza 1981, Riccardi 1988), but based on new findings and correlations with the Tethys now it is proposed to embrace the Tithonian-Berriasian boundary (Leanza 1996, Riccardi 2008). Therefore *Andiceras sp. nov.* would be of early Berriasian age in the classic scheme, but middle Berriasian in the new one. A systematic review of the perisphinctids of Vaca Muerta Formation is being currently carried out, thus we expect to refine the Andean Biozonation scheme in the nearby future.

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## How useful are AFLPs to analyse population genetics of Cephalopoda?

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Amplified fragment length polymorphism (AFLP) is a technique based on the selective PCR amplification of restriction fragments from a total digest of genomic DNA. This random DNA fingerprinting technique is commonly used in botany for population genetics. Microsatellites are the favourite markers for investigations of genetic diversity and population genetic structure in cephalopod population samples, but their development and application are expensive and time-consuming. AFLP markers are specific to restriction sites and thus are reliable, indeed large numbers of polymorphisms can be developed quickly without prior knowledge of DNA sequence. As we obtained only 13 specimens of *Spirula spirula* and *Pyroteuthis magaritifera*, respectively, we analysed the genetic variability within the populations using AFLP. As no AFLP data of cephalopods existed in the literature, we decided to test this technique as a potential tool to measure genetic variability in cephalopod species.

The midwater cephalopods *Spirula* and *Pyroteuthis* were caught in the waters between Morocco and the Canary Islands. We also analysed shallow water cephalopods from the Mediterranean. *Sepia officinalis* and *Loligo vulgaris* were caught in the waters around Mola di Bari (Italy, donation from Gianni Bello). *Octopus vulgaris* tissue samples from various locations in the Mediterranean were collected in France (Sigurd von Boletzky), Italy and Israel (Michael Kuba), Croatia, Greece and Turkey.

After DNA extraction of tissue samples from the arm tips AFLP was performed following the method described by Vos et al. (1995). 60 primer combinations were screened to choose 5-6 primer combinations for the selective PCR of every taxon. AFLP products were analysed in denaturing polyacrylamide gel using an automated DNA sequencer (CEQ 8000 Genetic Analysis System). The AFLP bands obtained were converted, and scored as present or absent using the program Genographer. Only distinct bands were selected, resulting in a dataset containing between 135 and 165 loci for each taxon (except *Pyroteuthis* which contained less loci). Analyses were performed using the programs PAUP, ARLEQUIN and AFLPsurv. First results show that the octopus samples from remote locations are more heterogeneous than *Spirula*, *Sepia* and *Loligo*. *Sepia* shows homogeneity to a certain degree. More detailed results will be presented on the poster.

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## Ammonoid and brachiopod fossils from the Pacific floor: evidence from the Upper Cretaceous of the Magellan Seamounts

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Findings of ammonoid remains in Mesozoic sediment sequences of the Recent oceanic floor are very restricted, and apparently no Mesozoic brachiopods have been discovered there. However, both Late Cretaceous ammonoid (*Hypophylloceras*, *Phyllopachiceras*, *Zelandites*, *Gaudryceras*, *Saghalinites*, and *Tetragonitidae* gen. and sp. indet.) shells and a single valve of the Late Cretaceous rhynchonellid brachiopod (*Basiliolidae*) shell were recently (since the 2004) discovered by us in the Magellan Seamounts, Pacific (Figure). According to palaeontological data, the ammonoid assemblages of the Butakov, Fedorov, Kotsebu, Il'ichev, Govorov, and Pallada guyots, as well as the belemnite assemblages of the Butakov, Gelendzhik, and Govorov guyots (Zakharov et al., 2007, 2009), are Late Campanian-Maastrichtian in age. Judging from data on carbon isotopic correlation, we assume that the age of cephalopod-bearing limestone of the Fedorov, Govorov and possibly Gelendzhik guyots seems to be the middle Maastrichtian; however, the age of cephalopods from the Butakov Guyot is more likely early Maastrichtian. According to plate-tectonic reconstructions, the Magellan Rise at late Campanian time could have been at the palaeolatitude of 18-19 degrees S in the Central Pacific (Douglas and Savin, 1973), which allows us to suggest that during late Cretaceous, as well as in Recent time, it was located at the tropical area. Late Cretaceous cephalopods, found in the Magellan Seamounts, migrated apparently from both the southern higher latitudes of the Australia area (*dimitobelid* belemnite fauna) and the northern higher latitudes of the Hokkaido-Sakhalin and/or Kamchatka areas (ammonoid fauna), possibly following directions of major surface palaeocurrents of the early-middle Maastrichtian Pacific Ocean.

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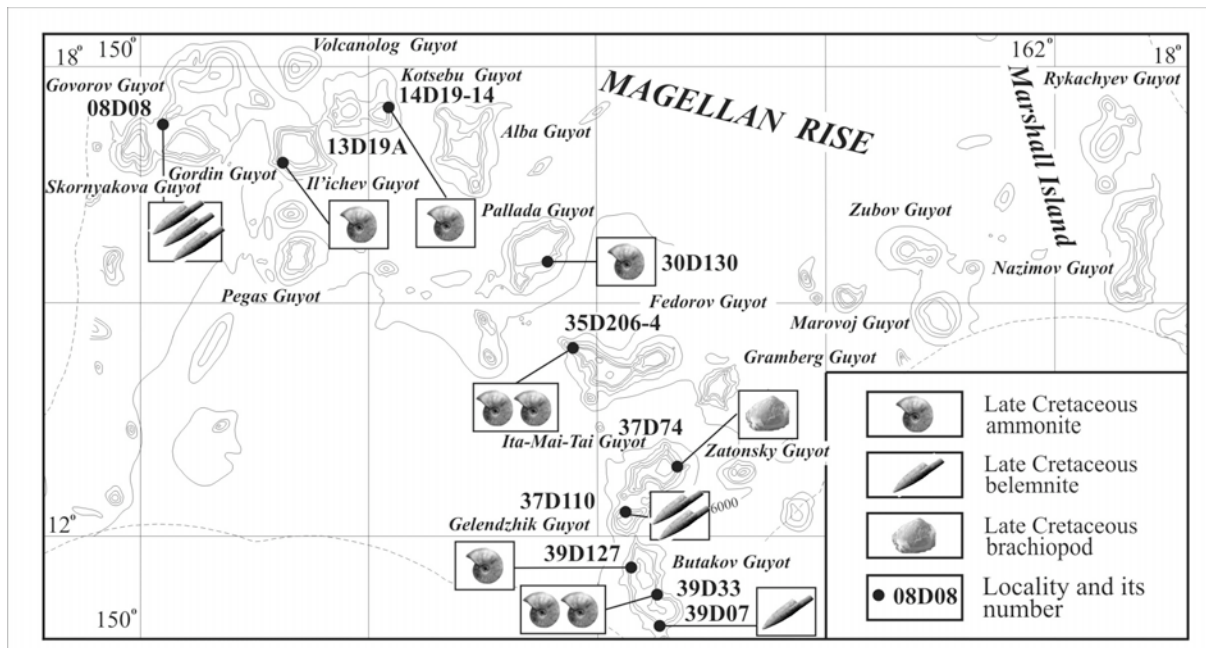


Figure: Distribution of Late Cretaceous cephalopod and brachiopod fossils in the Magellan Rise area, Pacific

(Abstract: Zakharov, Melnikov, Popov, Khudik, Punina & Pletnev)

