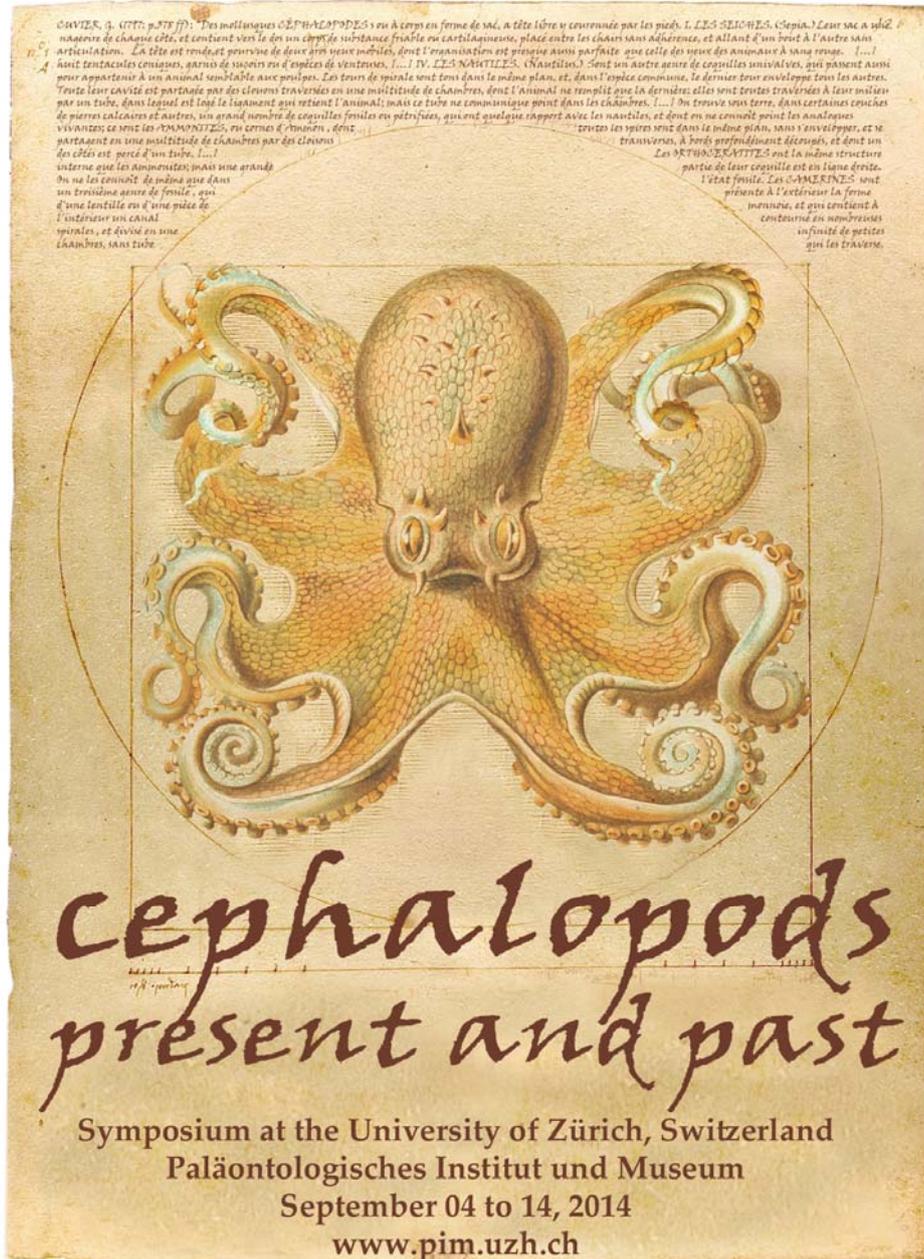




University of  
Zurich <sup>UZH</sup>

Paläontologisches Institut und Museum



in combination with the

## 5<sup>th</sup> International Symposium Coleoid Cephalopods through Time

Abstracts and program

Edited by Christian Klug (Zürich) & Dirk Fuchs (Sapporo)

Paläontologisches Institut und Museum, Universität Zürich



**University of  
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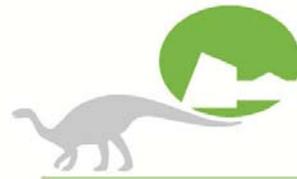
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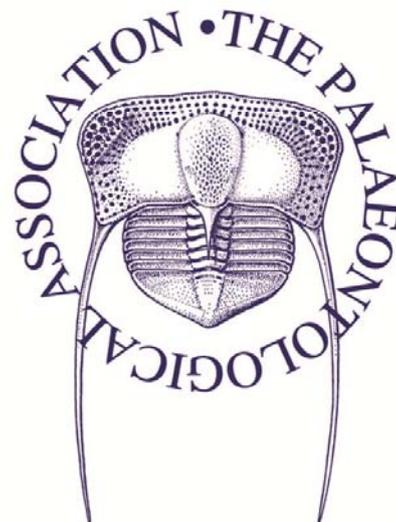
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# 9<sup>th</sup> International Symposium Cephalopods – Present and Past

in combination with the

# 5<sup>th</sup> International Symposium Coleoid Cephalopods through Time



Edited by

Christian Klug (Zürich) & Dirk Fuchs (Sapporo)

Paläontologisches Institut und Museum  
Universität Zürich, September 2014

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## 9th International Symposium Cephalopods – Present and Past

in combination with the

### 5<sup>th</sup> International Symposium Coleoid Cephalopods through Time

#### Schedule of events and timetable of presentations

**Thursday, September 4<sup>th</sup> to Saturday, September 6<sup>th</sup> 2014**

**Pre-conference field-trip**

Mesozoic Fossilagerstätten of the Jurassic of southern Germany

Guides: Günter Schweigert, Annette Schmid-Röhl, Christian Klug

Thursday, 04.09.2014, 9.00 am - departure from Zürich, meeting point: entry Zoological Museum

Saturday, 06.09.2014, 7.00 pm - arrival at Zürich, entry Zoological Museum

**Saturday, September 6<sup>th</sup> 2014**

**Evening and night: Lange Nacht der Museen**

This evening, most museums in Zurich are open to the public. You can get one ticket, which is valid for all museums + public transport from 6 pm to 2 am (Sunday). **Tickets are not included in the conference fee and have to be purchased at the museum entrance.**

### Lectures

**Sunday, September 7<sup>th</sup> 2014**

09.00-10.00      **Registration** (at the entrance of the Palaeontological Institute:  
[http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png))  
**Coffee** (Lichthof: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png))

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10.00-10.15      **Welcome and introductory remarks**

**Session 1: Evolution**

**Chair: Christian Klug, Björn Kröger**

10.15-10.30      **Key note: The palaeogeography of the initial cephalopod diversification during the Cambro-Ordovician**  
Björn Kröger (Finnish Museum of Natural History, Helsinki)

10.30-10.45      **Tracing key innovations and the tempo of cephalopod evolution using molecular paleobiology**  
Jakob Vinther (Schools of Biological and Earth Sciences, Bristol), Dirk Fuchs (Earth and Planetary System Science, Sapporo) & Björn Kröger (Finnish Museum of Natural History, Helsinki)

10.45-11.00      **Origin and evolution of the Gephuroceratina (Ammonoidea, Agoniatitida)**  
R. Thomas Becker (Westfälische Wilhelms-Universität Münster)

11.00-11.15      **A model for speciation in ammonoid cephalopods**  
Margaret M. Yacobucci (Bowling Green State University, Ohio)

11.15-11.30      **Morphological changes of the genus *Baculites* from the Coniacian to lower Campanian in Japan**  
Yasuyuki Tsujino (Tokushima Prefectural Museum, Tokushima) & Haruyoshi Maeda (The Kyushu University Museum, Fukuoka)

11.30-11.45      **Complete dorsal ammonoid shell - A facultative character of phylogenetic importance?**  
Gregor Radtke (Free University Berlin)

11.45-12.00      **The evolution of ammonites versus eustatic variations: case study from the Aptian from the NW Tethyan margin**  
Antoine Pictet (University of Lausanne)

12.00-13.30      **Lunch**

**Session 2: Ontogeny****Chair: Neil H. Landman, Ryoji Wani**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 13.30-13.45      **Key note: Iterative ontogenetic development of ammonoid conch shapes from the Devonian through to the Jurassic**  
Sonny A. Walton & Dieter Korn (both Museum für Naturkunde Berlin)
- 13.45-14.00      **Early ontogeny of Silurian tarphycerid Ophioceras; a comparison with some other tarphycerids and earliest nautilids**  
Vojtěch Turek (National Museum, Praha) & Štěpán Manda (Czech Geological Survey, Praha)
- 14.00-14.15      **Early ontogeny of well preserved ammonoids from the Middle Devonian Cherry Valley Limestone (NY, USA)**  
Susan M. Klofak (American Museum of Natural History & City College of the City of New York, New York) & Neil H. Landman (American Museum of Natural History, New York)
- 14.15-14.30      **Ontogenetic morphometry, taxonomy and biogeographic aspects of Famennian (Upper Devonian) Prionoceratidae**  
Tobias Fischer & R. Thomas Becker (both Westfälische Wilhelms-Universität Münster)
- 14.30-14.45      **Cladistic coding of ontogeny: application with the Amaltheidae (Lower Jurassic)**  
Jérémie Bardin, Isabelle Rouge, Fabrizio Cecca (all Sorbonne Universités, UPMC Univ Paris 06, Paris)
- 14.45-15.00      **Sutural complexity covaries with whorl shape: evidence from the intraspecific analyses of Cretaceous desmoceratid ammonoid from Madagascar**  
Daisuke Aiba & Ryoji Wani (both Yokohama National University)
- 14.45-15.00      **Relationship between ontogenetic change in shell shape and aperture map in ammonoids**  
Takao Ubukata (Kyoto University)
- 15.00-16.00      **Coffee and poster session**

**Session 3: Methods, tomography, 3D, History****Chair: Rene Hoffmann, Isabelle Kruta**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 16.00-16.15      **Key note: Advances in paleobiological reconstructions in cephalopods**  
Isabelle Kruta (American Museum of Natural History, New York)
- 16.15-16.30      **New Insights into Ammonite Palaeobiology from Tomographic Data**  
Robert Lemanis (Ruhr-Universität Bochum), Rene Hoffmann (Ruhr-Universität Bochum) & Stefan Zachow (Zuse Institute, Berlin)
- 16.30-16.45      **Virtually reconstructed growth trajectories and buoyancy of some major Palaeozoic ammonoid clades**  
Carole Naglik, Amane Tajika & Christian Klug (all University of Zürich)
- 16.45-17.00      **CONCH - new software for quantitative morphological analyses of ammonite shells**  
René Hoffmann (Ruhr-Universität Bochum) & Peter Göddertz (Steinmann-Institut für Geologie, Mineralogie und Paläontologie Bonn)
- 17.00-17.15      **3-dimensional analysis of the middle jurassic ammonite normannites and its functional morphology**  
Amane Tajika, Carole Naglik & Christian Klug (all University of Zürich)
- 17.15-17.30      **Early ideas about fossil cephalopods**  
Walter Etter (Naturhistorisches Museum Basel)
- 18.00-22.00      **Icebreaker party with Apéro riche**  
Zoological Museum

**Monday, September 8<sup>th</sup> 2014****Session 4: Palaeozoic****Chair: Kenneth De Baets & Dieter Korn**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 09.00-09.15      **Key note: The taxonomic geometry of the Palaeozoic ammonoids**  
Dieter Korn (Humboldt-Universität zu Berlin), Björn Kröger (Finnish Museum of Natural History), August Ilg (affiliation)
- 09.15-09.30      **The Endocerida – are the Lower Palaeozoic ‘gas pipes’ viable or not?**  
Andy King (Geckoella environmental consultants, , Taunton, Somerset)
- 09.30-09.45      **Latitudinal shifts of Palaeozoic marine invertebrate gigantism and global change**  
Christian Klug (University of Zürich), Kenneth De Baets (Universität Erlangen), Björn Kröger (Finnish Museum of Natural History), Mark A. Bell (University College London), Dieter Korn (Humboldt-Universität zu Berlin) & Jonathan L. Payne (Stanford University)
- 09.45-10.00      **New records of silurian ascocerids from the Prague Basin (Bohemia) and their significance**  
Martina Aubrechtová & Ladislav Zedník (both Charles University in Prague)
- 10.00-10.15      **Untangling the Striae: Ammonoid Biostratigraphy of the Carboniferous Shannon Basin, Western Ireland**  
Anthea Lacchia (Trinity College Dublin)
- 10.15-10.45      **Coffee and poster session**

**Session 5: Triassic (organized and supported by the Subcommittee on Triassic Stratigraphy)****Chair: Hugo Bucher & Marco Balini**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 10.45-11.00      **Key note: The timing of cephalopods survival after the Permian-Triassic mass extinction**  
Hugo Bucher, Max Meier & David Ware (all University of Zürich)
- 11.00-11.15      **Intraspecific variability among Ophiceratidae Arthaber, 1911 (Ammonoidea, Early Triassic) from NE Greenland: implications for taxonomy and diversity in the immediate aftermath of the Permian-Triassic boundary mass extinction**  
Max Meier & Hugo Bucher (both University of Zürich)
- 11.15-11.30      **High resolution biostratigraphy and biodiversity dynamics of Dienerian (Early Triassic) ammonoids from the Northern Indian Margin**  
David Ware & Hugo Bucher (both University of Zürich)
- 11.30-11.45      **Additional information on Spathian (late Olenekian) ammonoids from South Primorye and their palaeobiogeographic significance**  
Yuri Zakharov, Olga P. Smyshlyaeva & Alexander M. Popov (all Far Eastern Geological Institute of Russian Academy of Sciences, Vladivostok)
- 11.45-12.00      **Evolutionary trends of ammonoids during the Triassic in a Boreal basin (Canada)**  
Claude Monnet (University of Lille)
- 12.00-12.15      **New Trachyceratidae from the Upper Ladinian (Middle Triassic) of Guizhou, China, and their paleobiogeographic relationships**  
Marco Balini (Università degli Studi di Milano), Xiaodong Zou (Peking University), Da-yong Jiang (Peking University), Zuo-yu Sun (Peking University) & Yuan-lin Sun (Peking University)
- 12.15-12.30      **Key note: Geographic differentiation of the Late Triassic nautilids and biogeographic zoning of Late Triassic marine basins**  
Evgeny S. Sobolev (Trofimuk Institute of Petroleum Geology and Geophysics SB RAS, Novosibirsk)
- 12.30-14.00      **Lunch**

**Session 6: Jurassic****Chair: Günter Schweigert & Horacio Parent**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 14.00-14.15      **Key note: Ammonite aptychi: functions and sexual dimorphism**  
Horacio Parent (Universidad Nacional de Rosario) & Gerd E.G. Westermann (Burlington, Canada)
- 14.15-14.30      **Biogeography of early Pliensbachian ammonites: integrating distribution, phylogeny and morphology**  
Axelle Zacaï (Université de Bourgogne), Emmanuel Fara (Université de Bourgogne), Arnaud Brayard (Université de Bourgogne), Jean-Louis Dommergues (Université de Bourgogne), Christian Meister (Muséum d'Histoire Naturelle de Genève) & Bruno Vrielynck (Université Pierre et Marie Curie - Paris 6)
- 14.30-14.45      **The Callovian and Upper Jurassic of Western Siberia and West European classic stage standards: ammonite zonation and correspondence in lithostratigraphy and sequences**  
Alexander Alifirov, Svetlana Meledina & Alexander Beisel (all Trofimuk Institute of Petroleum Geology and Geophysics SB RAS, Novosibirsk)
- 14.45-15.00      **Systematics, endemism and phylogeny of Indian proplanulids (Ammonoidea) from the Bathonian-Callovian of Kutch**  
Rakhi Dutta & Subhendu Bardhan (both Jadavpur University, Kolkata)
- 15.00-15.15      **Age, Systematics and Palaeobiogeography of the Late Jurassic Ataxioceratid Ammonoids from Kutch, India: A New Light on Origin and Migration**  
Arindam Roy (Geological Survey of India, Lucknow) & Subhendu Bardhan (Jadavpur University, Kolkata)
- 15.15-15.30      **Soft-tissue preservation in Jurassic ammonites from Central Russia**  
Aleksandr Mironenko (Moscow)
- 15.30-15.45      **The systematic and taxonomic revision of the 'Pleydellia-group' ammonites from the Minette ironstones (Late Toarcian), southern Luxembourg**  
Andrea Di Cencio (National Museum of Natural History, Luxembourg)
- 16.00-16.15      **Exceptional preservation of ammonites from the Late Jurassic Nusplingen Plattenkalk**  
Günter Schweigert (Stuttgart)
- 16.15-17.00      **Coffee and poster session**

**Session 7: Cretaceous I****Chair: Christina Ifrim & Margret Yacobucci**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 17.00-17.15      **Key note: Muscle and mantle attachment marks and body chamber lengths indicative of diverse life styles of coexisted Aptian ammonites of the Russian Platform**  
Larisa A. Doguzhaeva (Swedish Museum of Natural History, Stockholm)
- 17.15-17.30      **Speculations on ethology of some (turricone, colchicone) heteromorph ammonites**  
Mikheil V. Kakabadze (Ivane Javakishvili Tbilisi State University)
- 17.30-17.45      **Ammonoid buccal mass and jaw apparatus: comparative morphology, functional morphology and taxonomic variation**  
Kazushige Tanabe (University of Tokyo), Isabelle Kruta (American Museum of Natural History, New York) & Neil H. Landman (American Museum of Natural History, New York)
- 17.45-18.00      **Aptychi of the Boreal and Subboreal Middle Jurassic - Early Cretaceous ammonites: new records and review of published data**  
Mikhail Rogov (Geological Institute of Russian Academy of Sciences, Moscow) & Aleksandr Mironenko (Moscow)

**Tuesday, September 9<sup>th</sup> 2014****Session 8: Cretaceous II****Chair: Otilia Szives & Stijn Goolaerts**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 09.00-09.15      **Report on the revision of the Cretaceous ammonites of the Coquand Collection**  
Otilia Szives (Hungarian Natural History Museum, Budapest)
- 09.15-09.30      **Reevaluation of the upper Maastrichtian ammonite biostratigraphy based on Discoscaphites occurrences along the Gulf Coastal Plain**  
Ekaterina Larina (Brooklyn College, New York), Matthew Garb (Brooklyn College, New York), Neil Landman (American Museum of Natural History, New York), Remy Rovelli (Brooklyn College, New York), Corinne Myers (Harvard University, Cambridge, MA)
- 09.30-09.45      **Fluctuations of the oxygen minimum zone at the end of Oceanic Anoxic Event 2 and the response of ammonites: A case study from Mexico**  
Christina Ifrim (Ruprecht-Karls-Universität, Heidelberg)
- 09.45-10.00      **Ammonites from the uppermost Campanian (Late Cretaceous) in Central Montana**  
Jamie A. Brezina (South Dakota School of Mines & Technology, Rapid City) & Neal L. Larson (Larson Paleontology Unlimited, Hill City)
- 10.00-10.15      **Key note: Ammonites on the brink of extinction**  
Neil H. Landman (American Museum of Natural History, New York), Stijn Goolaerts (Royal Belgian Institute of Natural Sciences, Brussels), John W.M. Jagt (Natuurhistorisch Museum Maastricht), Elena A. Jagt-Yazykova (Uniwersytet Opolski, Opole), Marcin Machalski (Instytut Paleobiologii, Warsaw) & Margaret Yacobucci (Bowling Green State University)
- 10.15-11.00      **Coffee and poster session**

**Session 9: Ammonoid ecology****Chair: Benjamin J. Linzmeier & Alexander Lukeneder**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 11.00-11.15      **Stable isotope evidence of habitat change during early ontogeny in Cretaceous *Hoploscaphites***  
Benjamin J. Linzmeier (University of Wisconsin-Madison), Neil H. Landman (American Museum of Natural History, New York), Reinhard Kozdon (University of Wisconsin-Madison), Shanan E. Peters (University of Wisconsin-Madison) & John W. Valley (University of Wisconsin-Madison)
- 11.15-11.30      **Ammonoid Habitats and Life History**  
Alexander Lukeneder (Natural History Museum, Vienna)
- 11.30-11.45      **Knowledge of parasitism in ammonoids: importance for paleoecology**  
Kenneth De Baets (University Erlangen-Nuremberg), Helmut Keupp (Freie Universität Berlin) & Christian Klug (University of Zürich)
- 11.45-12.00      **Studies compared in Westermann Morphospace with the goal of understanding ammonoid life mode**  
Kathleen Ritterbush (University of Southern California, Los Angeles)
- 12.00-12.15      **Breaking the waves: suture line complexity indicates types of life style in nautiloids and ammonites**  
Alexander Arkhipkin (Falkland Islands Fisheries Department)
- 12.15-12.30      **Getting hooked: the role of a U-shaped body chamber in the shell of adult heteromorph ammonites**  
Alexander Arkhipkin (Falkland Islands Fisheries Department)
- 12.30-14.00      **Lunch**

**Session 10: Nautilida****Chair: Peter. D. Ward & Jiří Frank**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 14.00-14.15      **An advanced workflow for taxonomic research: case study on Cretaceous Nautilids**  
Jiří Frank (National Museum & Charles University, Prague)
- 14.15-14.30      ***Epicymatoceras*: an exotic evolute nautilid from the European latest Cretaceous that does it all different**  
Stijn Goolaerts (Royal Belgian Institute of Natural Sciences, Brussels) & Jiří Frank (National Museum & Charles University, Prague)
- 14.30-14.45      **What about nautilids at the Cretaceous/Paleogene boundary?**  
Stijn Goolaerts (Royal Belgian Institute of Natural Sciences, Brussels), John W.M. Jagt (Natuurhistorisch Museum Maastricht), Elena A. Jagt-Yazykova (Uniwersytet Opolski, Opole), Neil H. Landman (American Museum of Natural History, New York), Marcin Machalski (Instytut Paleobiologii, Warsaw) & Margaret Yacobucci (Bowling Green State University)
- 14.45-15.00      **Key note: *Allonautilus* and *Nautilus*: Post-Jurassic phylogeny, shift from shallow to deep water habitats based on isotopic evidence, new evidence concerning mode of life, and conservation issues**  
Peter. D. Ward (University of Adelaide)
- 15.00-15.15      **A historical and modern approach to assess the current state of *Nautilus* populations in the Indo-Pacific**  
Greg J. Barord (City University of New York), Andrew J. Dunstan (Queensland University), Anthony Ilano (San Carlos University), & Peter. D. Ward (University of Adelaide)
- 15.15-15.30      **Bioerosion in shells of the modern *Nautilus***  
Barbara Seuss (Universität Erlangen-Nürnberg), Max Wisshak (Senckenberg am Meer, Wilhelmshaven), Royal H. Mapes (North Carolina Museum of Natural Sciences, Raleigh) & Neil H. Landman (American Museum of Natural History, New York)
- 15.15-15.30      **The study of the type series of *Nautilus pompilius* Linnaeus, 1758**  
Svetlana V. Nikolaeva (Natural History Museum, London & Borissiak Paleontological Institute, Moscow)
- 15.30-16.15      **Coffee and poster session**

## 5<sup>th</sup> International Symposium Coleoid Cephalopods through Time

### Session 11: Fossil Coleoidea

Chair: Dirk Fuchs & Royal H. Mapes

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- 16.15-16.30      **Key note: On the locomotion system of fossil Coleoidea (Cephalopoda) and its systematic and phylogenetic significance**  
Dirk Fuchs (Hokkaido University, Sapporo), Christian Klug (University of Zürich), Helmut Tischlinger (Stammham, Germany) & Helmut Keupp (Freie Universität Berlin)
- 16.30-16.45      **Arm hooks of Early Carboniferous-Late Permian coleoids, and their phylogenetic implication**  
Larisa A. Doguzhaeva (Swedish Museum of Natural History, Stockholm) & Royal H. Mapes (North Carolina Museum of Natural Sciences, Raleigh)
- 17.45-18.00      **Upper Paleozoic coleoids (Cephalopoda) from North America: Observations on their paleoecology, taphonomy and phylogeny**  
Royal H. Mapes (North Carolina Museum of Natural Sciences, Raleigh) & Larisa A. Doguzhaeva (Swedish Museum of Natural History, Stockholm)
- 17.00-17.15      **Is *Proteroctopus ribeti* an Octopoda? Reappraisal of *Proteroctopus ribeti* characters in the light of X-ray microtomography**  
Isabelle Rouget (Sorbonne Universités, UPMC Univ Paris 06), Isabelle Kruta (American Museum of Natural History, New York), Damien Germain (Sorbonne Universités, UPMC Univ Paris 06), Arnaud Brayard (Université de Bourgogne, Dijon), Sylvain Charbonnier (Sorbonne Universités, UPMC Univ Paris 06), Vincent Fernandez (European Synchrotron Radiation Facility, Grenoble), Neil H. Landman (American Museum of Natural History, New York) & Fabrizio Cecca (Sorbonne Universités, UPMC Univ Paris 06)
- 17.15-17.30      **Staloliths and other microfossils associated with the Christian Malford Lagerstätte**  
Malcolm B. Hart (Plymouth University), Alex De Jonghe (Plymouth University, Robertson: a CGG Company, Llandudno), Kevin N. Page (Plymouth University), Gregory D. Price (Plymouth University), Christopher W Smart (Plymouth University) & Philip R. Wilby (British Geological Survey, Nottingham)
- 17.30-17.45      **A review of biostratigraphy and palaeobiogeography of Boreal latest Jurassic–earliest Cretaceous belemnites**  
Oksana S. Dzyuba (Trofimuk Institute of Petroleum Geology and Geophysics, Novosibirsk)
- 17.45-18.00      **The Cenozoic fossil record of the Coleoidea: an overview**  
Dirk Fuchs (Hokkaido University, Sapporo), Yasuhiro Iba (Hokkaido University, Sapporo), Martin Kosták (Charles University in Prague), Alexander Lukeneder (Naturhistorisches Museum Wien), Alexander Nützel (Bayerische Staatssammlung München) & Patricia Weaver (North Carolina Museum of Natural Sciences, Raleigh)
- 18.00-19.30      Walk to the venue of the conference dinner, Aperitif
- 19.30-23.00      **Conference dinner**  
  
**Restaurant Weisser Wind**  
Altstadt, Oberdorf, Oberdorfstr. 20"

### Wednesday, September 10<sup>th</sup> 2014

#### Session 12: Fossil coleoids: Belemnoids

Chair: Isabelle Rouget & Alexei Ippolitov

KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 09.00-09.15      **Key note: Early evolutionary history of belemnites, revisited: New perspectives from East Asia**  
Yasuhiro Iba (Hokkaido University, Sapporo), Shin-ichi Sano (Fukui Prefectural Dinosaur Museum), Dirk Fuchs (Hokkaido University, Sapporo), Jingeng Sha (Nanjing Institute of Geology and Palaeontology), Jian Liu (Chengdu University of Technology) & Jörg Mutterlose (Ruhr-University Bochum)
- 09.15-09.30      **Belemnite “Doppellinien”: myths and realities**  
Alexei Ippolitov (Geological Institute of Russian Academy of Sciences, Moscow)

- 09.30-09.45 **Belemnitids as pelagic meso-predators evidenced by radula and fin preservation**  
Christian Klug (University of Zurich), Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart), Dirk Fuchs (Hokkaido University, Sapporo), Helmut Tischlinger (Stammham, Germany) & Isabelle Kruta (American Museum of Natural History, New York)
- 09.45-10.00 **Diversity and palaeobiogeography of belemnites during the Early Jurassic**  
Jean-Daniel Pinard (National Museum of Natural History, Luxembourg & University of Burgundy, Dijon), Pascal Neige (University of Burgundy, Dijon), Robert Weis (National Museum of Natural History, Luxembourg) & Emmanuel Fara (University of Burgundy, Dijon)
- 10.00-10.15 **Infrazonal belemnite stratigraphy of the Lower Callovian of East European Platform**  
Alexei Ippolitov (Geological Institute of Russian Academy of Sciences, Moscow) & Denis Gulyaev (Interdepartmental Stratigraphical Committee (ISC) of Russia, Yaroslavl)
- 10.15-11.00 **Coffee and poster session**

**Session 13: Recent coleoids I****Chair: Henk-Jan Hoving & Yasuhiro Iba**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 11.30-11.45 **Key note: A Molecular Search for the Giant Squid**  
Inger Winkelmann (University of Copenhagen), M. Jan Strugnell (La Trobe University, Bundoora) & MTP Gilbert (University of Copenhagen)
- 11.45-12.00 **Morphometry of the shell of *Spirula spirula* based on nano-CT data**  
René Hoffmann (Ruhr-Universität Bochum)
- 12.00-12.15 ***Sepia*-type connecting rings and septa**  
Larisa A. Doguzhaeva & Elena Dunca (both Swedish Museum of Natural History, Stockholm)
- 12.15-12.30 **Abrupt changes of distance between succeeding septa at the hatching event in modern *Sepia* and *Spirula***  
Ayaka Yamaguchi, Yuichiro Kumada & Ryoji Wani (all Yokohama National University)
- 12.30-14.00 **Lunch**

**Session 14: Recent coleoids II****Chair: Inger Winkelmann & Alexander Arkhipkin**KO2-F-180: [http://www.plaene.uzh.ch/floormaps/KOL\\_D.png](http://www.plaene.uzh.ch/floormaps/KOL_D.png)

- 14.00-14.15 **Key note: Life Cycles of Deep-Sea Cephalopods: Past, Present and Future**  
Henk-Jan Hoving (GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel)
- 14.15-14.30 **Shell construction during embryonic life of *Sepia officinalis*: what does it tell for evolution?**  
Laure Bonnaud-Ponticelli (Museum National d'Histoire Naturelle, Paris) & Dirk Fuchs (Hokkaido University, Sapporo)
- 14.30-14.45 **Analysis of genetic variability and phylogeny of the oval squid *Sepioteuthis lessoniana* around Japan**  
Satoshi Tomano (Hiroshima University), Yukio Ueta (Tokushima Agriculture, Forestry and Fisheries Technology Support Center, Naruto, Tokushima), Noriyasu Kasaoka (Nakayama Steel Works Ltd, Fukuoka) & Tetsuya Umino (Hiroshima University)
- 14.45-15.00 **'Tailed' coleoid cephalopods through time**  
Alexander Arkhipkin (Falkland Islands Fisheries Department), Jean-Daniel Pinard (National Museum of Natural History, Luxembourg), Robert Weis (National Museum of Natural History, Luxembourg), Nino Mariotti (Sapienza University, Rome) & Zhanna Shcherbich (Falkland Islands Fisheries Department)
- 15.00-15.15 **All life-stages of the tropical arrow squid around the Sao Sebastiao Island, SE Brazil**  
Maria A. Gasalla (University of São Paulo)

**Post-conference field trip 1: Jurassic ammonoid localities of Switzerland**

Bathonian and Oxfordian of Holderbank, Early Jurassic of Frick

Guide: Heinz Furrer

Thursday, 11.09.2014, 09.00

departure from Zürich, meeting point: entry Zoological Museum

Thursday, 11.09.2014, ca. 19.00

arrival at Zürich, entry Zoological Museum

**Post-conference fieldtrip 2: Mesozoic ammonoid localities of Switzerland and eastern France**

Guides: Walter Etter, Peter Kürsteiner, Karl Tschanz, Antoine Pictet, Peter Bitterli, Bernhard Hostettler, Christian Klug

Wednesday, 10.09.2014, 16.00

departure from Zürich, meeting point: entry Zoological Museum

Sunday, 14.09.2014, ca. 19.00

arrival at Zürich, entry Zoological Museum

# Talks

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## **Sutural complexity covaries with whorl shape: evidence from the intraspecific analyses of Cretaceous desmoceratid ammonoid from Madagascar**

Daisuke Aiba\* & Ryoji Wani\*\*

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Intraspecific variations of complexity of suture lines and shell morphology (whorl shape, external shell thickness, and septal thickness) of the Cretaceous ammonoid *Desmoceras latidorsatum* from Madagascar were analyzed. These analyses are carried out at the diameter of 15, 20, 25, and 30 mm in each specimen. The results are: 1) More compressed or depressed shells have more complex suture lines. More depressed or compressed shells are generally expected to be weaker in shell strength than intermediate ones. 2) The consistent correlation between the sutural complexity and thickness of both external shells and septa was not observed during ontogeny. 3) The correlations between the complexity balance of suture line (the lateral vs. the ventral sections) and the whorl shape demonstrated that more compressed shells have a high complexity rate at the lateral section. Although more compressed shells generally have a relatively shorter distance of whorl width, the more significant attributes on the sutural complexity are developed by this lateral section. These results suggest that the complex suture line of *Desmoceras latidorsatum* supported the weak phragmocone that would derive from the more depressed or compressed whorl shape.

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## The Callovian and Upper Jurassic of Western Siberia and West European classic stage standards: ammonite zonation and correspondence in lithostratigraphy and sequences

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\*\*Novosibirsk State University, Pirogova St., 2, 630090, Novosibirsk, Russia

The Callovian and Late Jurassic represent a time of widespread marine boreal transgression beginning at the end of the Bathonian. Its maximum was reached during the Callovian, further demonstrating several waves. They left traces in sedimentary sequences and had impacts on ammonite populations. West Siberian Callovian-Upper Jurassic marine sequences are combined into greater lithostratigraphic units referred to as Vasyugan, Georgiev and Bazhenov regional horizons consisting of formations and other subdivisions.

The Callovian, Oxfordian, Kimmeridgian, and Volgian refined and detailed zonal chart is proposed after revision of more than thousand ammonites belonging to these sequences from core samples of West Siberian boreholes. The Callovian, Oxfordian and Kimmeridgian stages (Vasyugan and Georgiev Formations) of Western Siberia are characterized by boreal ammonites of the Cardioceratidae and the rarer Kosmoceratidae and Aulacostephanidae. The Volgian (Bazhenov Fm.) is subdivided into zones by ammonites of the families Dorsoplanitidae and Craspeditidae. The Oxfordian zonal chart is practically equivalent to Northwest European one. The Callovian and Volgian Stages consist of a boreal zonal succession, whereas the Kimmeridgian is divided by the boreal *Amoeboceras* and subboreal Aulacostephanidae (*Pictonia*, *Rasenia*, *Aulacostephanus*). Studying sections of numerous boreholes drilled in Western Siberia has led to a clear idea of cyclic construction of the West Siberian Callovian to Upper Jurassic and has allowed to associate West Siberian formations with the ones of the English Callovian, Oxfordian, and Kimmeridgian.

The most impressive example of the correlation between West Siberian and Northwest European sections is a comparison of the Vasyugan Formation with the Cornbrash, Kellaways, Oxford Clay, and Corallian Formations. Particular phases of sedimentation dated by the bases of the ammonites zones Jason, Densiplicatum, and Glosense are reliably identified in the Vasyugan Fm. The base of the Kimmeridge Clay Fm. tentatively matches the Georgiev Fm. The base of the oil-producing Bazhenov Formation presumably corresponds to oil shales in the upper part of the Kimmeridge Clay Fm. near the Wheatleyensis/Hudlestoni boundary. Coincidences are observed when local lithostratigraphic units of both regions correspond to the sequences or system tracts. In that case, maximum flooding surfaces and bases of transgressive system tracts are especially important boundaries.

This is a contribution to the RFBR projects *14-05-31026 and 12-05-00453 and RAS Programs 23 and 28.*

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## **Breaking the waves: suture line complexity indicates types of life style in nautiloids and ammonites**

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One of the most intriguing problems in nautiloid and ammonoid shell structure is the great variety in the shape of the suture lines, from very simple in most nautiloids and early Palaeozoic ammonoids to complexly fluted in Mesozoic Ammonitida. There is a plethora of hypotheses about the reasons that led to the complexity of the ammonoid suture structure. Buckland (1836) put forward a hypothesis on strengthening the shell walls against implosion, which is the most popular point of view until now. Von Buch (XIX century) and Seilacher (1975) hypothesized that the fluted suture line strengthened the muscle attachment to the septal wall. Kulicki (1979) suggested that folding of septal margins should result in the retention of the cameral liquid, kept in place by the action of surface tension forces, and therefore preventing the overflow of liquid in the chambers. Hewitt and Westermann (2003) further noted that the fluted suture line, secondary to providing shell strength, also served as water storage preventing the water present in the largest chambers from sloshing around. Barskov (1999) assumed that an increase of the inner surface of chambers laid with organic membrane should lead to extensive water exchange in ammonites with the fluted suture.

In the present study, the movement of cephalopods with an external shell was analysed based on the modern nautilids. Two main features were taken into account; the type of movement and the simultaneous presence of water and air in the last chambers of the phragmocone. Shelled cephalopods, similar to coleoids, had a jet propulsive mode of locomotion, either to migrate spatially, attack prey or escape from predators. The main characteristic of jet propulsion is a change in acceleration; from positive acceleration during the start of a ‘thrust’ to deceleration before the next ‘thrust’. There is a trade-off between continuous growth of the mollusc body and periodic formation of new chambers in the phragmocone in keeping neutral buoyancy of the whole animal. Hence, the presence of water in the phragmocone is needed to compensate for continuous growth of the body.

During locomotion by jet propulsion, inertia forces periodic water displacement to the anterior wall of the chamber during positive acceleration and to the posterior wall during deceleration. This periodic water movement (‘sloshing’) would constantly displace the centre of gravity of the shell and make the movement less stable and less energy efficient. It is notable that this effect only happens when both water and air are present in one phragmocone chamber. There are many ways to decrease the water movement in a chamber such as to increase the water’s viscosity, make the chamber narrower in the moving direction or to make partitions within the chamber. The ammonites evolved yet another way. Both the shape of the suture lines and their more complex structure in the wider part of the chamber suggest that they worked effectively as ‘wave breakers’ dissipating the ‘wave’ on the boundary between water and air and therefore decreasing the energy of displaced water. Slow movers (like nautiloids and primitive ammonites) had a simple suture line and were mainly planktonic, whereas the complex suture line in advanced ammonites indicates a nektonic life style. Similar assumptions could apply to ontogenetic stages of ammonites, as their juveniles with simpler suture lines were planktonic, whereas adults with more complicated suture lines were nektonic. Once evolved, the complex suture line persisted in a line even if some representatives became secondarily planktonic or did not use their jet propulsion much, as in adult heteromorph ammonites for example.

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## Getting hooked: the role of a U-shaped body chamber in the shell of adult heteromorph ammonites

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Cretaceous heteromorph ammonites of the suborder Ancyloceratina underwent a striking ontogenetic change in their shell shape. Juveniles had virtually all possible types of coiling of their shells, ranging from regular planispiral and orthoconic to torticonic, hamitoconic, and gyroconic. The adults uncoiled the last whorl of their shell forming a U-shaped recurved body chamber with the aperture facing upward. Examination of ribbing pattern and its resolution in various parts of the living chamber in eleven species revealed that the ribs were less developed and had some traces of wear on the inner surface of the hooked chamber, being well developed both on the lateral and outer lower parts. This could indicate that the adult animals were semi-loosely hooked (*Ancyloceras*, *Macroscaphites*) or permanently clipped (*Scaphites*, *Hoploscaphites*) onto either horizontal or upwardly angled stipes of non-calcified algal macrophytes or branched animals. Comparison of the adult mode of life with those of modern cephalopods suggested that ammonites of the suborder Ancyloceratina had developed a stationary brooding phase that could have several ecological advantages over free-swimming monomorph ammonites.

Location of the adult brooding ammonite among kelp fronds could have given several ecological advantages to heteromorphs in comparison with planispiral ammonites. First, hiding the shells of adult ammonites among the macroalgal stipes would have concealed them from pelagic predators and also made them less accessible to benthic predators such as crabs. A similar reproductive strategy is utilized by spawning females in some loliginid squid (e.g. *Doryteuthis gahi*) that attach their egg masses to kelp fronds well above the bottom. Second, stationary brooding females would have expended less energy for active metabolism than free-floating ones and therefore channelled more resources into reproduction. This is especially important in cases of ovoviviparity when animals spend their internal resources on larval development. Third, as macroalgae are located in warmer and more productive shallow waters nearshore (down to 25-30 m), the temperature-dependent egg development would have been faster and food resources more abundant for hatchlings and juveniles than in offshore habitats. As they grew, juveniles could have been dispersed further offshore by tidal currents to exploit the resources of the shelf. A similar scheme of inshore-offshore ontogenetic migration is observed in the majority of Recent loliginids. And, fourth, inshore stationary brooding would have kept the adults away from offshore anoxic zones. This also might explain the fact that adult heteromorphs were found away from these anoxic zones. Owing to the complete extinction of all ammonites at the end of Cretaceous, they did not encounter the later radiation of brown algal kelps that occurred during climate cooling in the Miocene.

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## ‘Tailed’ coleoid cephalopods through time

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Adults of some extinct and recent coleoid cephalopods develop a special morphological feature at the posterior end of their body. The apical tip of their mantle elongates (sometimes with the posterior part of the fin) forming an attenuated ‘tail’. The tails may form just in one sex, commonly in males like in modern squid *Alloteuthis* spp. (Loliginidae) and in cuttlefish *Sepia confusa*, or in both sexes like in squid *Uroteuthis bartschi* (Loliginidae) and *Onykia robsoni* (Onychoteuthidae). The ethological and ecological roles of the tail formation in those recent adult cephalopods remain unknown. On the other hand, the extinct belemnites (order Belemnitida) developed in some cases an additional epirostrum on the posterior part of their orthorostrum, the functional role of which is yet unknown.

We have studied the anatomy and development of the tails both in extinct and recent coleoid cephalopods and revealed substantial differences in their formation in different groups of animals. Males of the recent subtropical squid *Alloteuthis africana* form their tail (sometimes as long as the rest of the mantle) by increased growth of the anterior part of the gladius with simultaneous growth of the posterior part of the mantle. As a result, the gladius rolls longitudinally in the tail forming a pseudoconus. Similar process takes place in the tail formation in *Alloteuthis subulata*. The attenuated tail in males of the squid *Lycoteuthis springeri* (Lycoteuthidae) is formed by growing the special rod-like fin with vacuolated cartilage covered by a thin layer of muscle and skin. The posterior tip of the gladius (with small rostrum) does not enter into the tail being located at the level of the fins. Adults of both sexes of recent *Onykia robsoni* and *O. robusta* form a carrot-like flexible chitinous rostrum that supports the attenuated tail and anteriorly elongated parts of the fin. Adults of the extinct belemnites *Dactyloteuthis semistriata* and *Acrocoelites riegrafi* formed an elongated epirostrum posteriorly to their orthorostrum with both structures differing in their growth mode. Adult belemnites of *Megateuthis* spp. also increased their rostral growth by forming non-dense aragonite layers in the inner part of their otherwise calcitic epirostrum. By counting growth micro-increments within the orthorostrum and epirostrum it was possible to date the formation of these parts of belemnite body and estimate their growth rates assuming daily periodicity of increment formation as suggested by Dunca et al. (2006). Taking into account ontogenetic changes in the body shape, a new hypothesis on possible ecological role of tail formation in adult coleoid cephalopods has been suggested.

## Stratigraphy of ascocerids from the Silurian of the Prague Basin (Bohemia)

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Ascocerids are morphologically unique cephalopods that have been rather rarely found within the Ordovician and Silurian strata of N. America and Europe. The largest collections of Silurian ascocerids counting up to tens of specimens were collected and described from Gotland and Bohemia during the 19<sup>th</sup> century by G. Lindström and J. Barrande, respectively. Since then, no relevant material has been collected, which would help to resolve the largely unexplored issues related to ascocerid morphology, phylogeny, ontogeny and ecology. However, about seventy stratigraphically well-calibrated specimens of ascocerid cephalopods were collected in the last two decades as part of an extensive study of Silurian assemblages of the Prague Basin. In the Prague Basin, the first ascocerid was illustrated by Barrande (1877) and assigned by him to the species „*Glossoceras gracile*“. The age of the illustrated specimen corresponds to the early Gorstian *N. nilssoni* Biozone. In the late Gorstian and most of the Ludfordian, the ascocerids occur with only two species. The species is *Ascoceras verneuilli* of the *L. scanicus*-*S. chimaera* and *S. leintwardinensis* (*S. linearis*) Biozones. The second species is *Glossoceras gracile* of the *N. kozlowskii* Biozone. In the following *P. dubius postfrequens* Biozone, no ascocerids were recorded possibly due to the *Kozlowskii* Event. The ascocerids re-appeared in the *P. latilobus*-*S. balticus* Biozone with the species *Parascoceras decipiens*. In the Prague Basin, ascocerids reached their highest diversity in the latest Ludfordian and early Přídolí (*P. fragmentalis*, *M. parultimus* and *M. ultimus* Biozones) where up to five ascocerid species have been recorded. Presumably, migration from Baltica and Avalonia occurred at that time as species from both regions are present in the Prague Basin. Further evolution of immigrants and the subsequent origination of endemic forms (Manda 2008) might have taken place in the early Přídolí. During the late Přídolí, ascocerids are represented by *Parascoceras* sp. in the *M. bouceki* and *M. transgrediens* Biozones and *Ascoceras purchisoni* in the *M. transgrediens* Biozone. The latter species marks the stratigraphically youngest occurrence of ascocerids in the Prague Basin.

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## **New Trachyceratidae from the Upper Ladinian (Middle Triassic) of Guizhou, China, and their paleobiogeographic relationships**

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The Falang Formation (Ladinian to Lower Carnian) is widely exposed in South China and is known since the mid of the 20<sup>th</sup> century for its ammonoid record. Ammonoid faunas collected and reviewed by Wang (1983) provided support to the definition of three ammonoid zones of the South China regional scale, the *Xenoprotrachyceras primum*, *Protrachyceras deprati* and *Trachyceras multituberculatum* zones, attributed respectively to the Lower and Upper Ladinian as well as the Lower Carnian.

Recent excavations carried out at Nimaigu (near Xingyi, Guizhou) allowed the bed-by-bed sampling of the Zhuganpo and Wayao members for the first time. The taxonomic analysis of the ammonoid collection leads to the introduction of three new genera of the Trachyceratidae comprising four species. Additionally, *Xenoprotrachyceras*, *Detoniceras*, *Trachyceras*, *Clionitites*, *Parasturia*, and *Ptychites* occur there.

Three biostratigraphic units have been recognized. The lower one is dominated by the new genera of the Trachyceratidae, which show various combinations of rows of nodes with deeply indented ceratitic to subammonitic suture lines. Correlation of this biostratigraphic unit is quite complex due to the abundance of new taxa. Its position is comprised between the upper Meginae to the lower Sutherlandi zones (Upper Ladinian) of the North American scale. The second and third biostratigraphic units are assigned to the Carnian, because of the occurrence of *Trachyceras*.

The new results improve the knowledge of Ladinian ammonoid paleobiogeography. The Late Ladinian has never been considered a time of significant ammonoid differentiation. Moreover, ammonoid faunas from the western and southern Tethyan realm to North America are characterized by a high similarity at least at the genus level, but often also at the species level. Instead, the studied ammonoid succession of Guizhou is characterized not only by endemic taxa but also by the lack of several Trachyceratidae such as *Meginoceras*, *Maclarnoceras* and *Frankites* that are usually widespread at low and mid paleolatitudes.

### Reference

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## Cladistic coding of ontogeny: application with the Amaltheidae (Lower Jurassic).

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Ontogeny is rarely included in ammonoid cladistic analyses. When used, the developmental information is reduced to one character for two or three different ontogenetic stages despite an important literature describing ontogenetic variations of morphological characters (e.g., Alberch et al. 1979). Works on ammonites have highlighted the importance of ontogeny to reconstruct the evolutionary history (e.g., Dommergues et al. 1986). The objective of this work is to explore how to include the ontogenetic information more accurately in a cladistic coding scheme despite the intractable problem of age standard. The approach is based on classic ontogenetic trajectories proposed by Alberch et al. (1979). Their framework has the benefits to take both discrete and continuous characters as well as their rate of development into account. Our method consists in the recognition of homologous stages in each ontogenetic trajectory and to code them. A main difference between our approach and other attempts to code ontogeny is that stages are not *a priori* defined (e.g., inner whorls, outer whorls). We use the family Amaltheidae (Early Jurassic) as a model. Development and phylogeny of this taxon has been well-documented and discussed in the literature (Howarth 1958; Meister 1988) allowing to critically analyse the results. We show that transformations of different characters through development may not be correlated and thus, some characters have to be treated independently with regard to their ontogeny. Heterochronies in the evolution of the Amaltheidae is reviewed and newly interpreted thanks to this geometric approach showing some important differences to the traditional view.

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## **A historical and modern approach to assess the current state of *Nautilus* populations in the Indo-Pacific**

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Nautilus are disappearing, presumably as a result of unregulated fisheries throughout the Indo-Pacific created to support a world-wide demand for nautilid shells. Possessing a reproductive strategy similar to sea turtles and large sharks, nautilus are therefore unable to repopulate these depleted populations quickly. To support needed conservation initiatives, a comprehensive assessment of nautilid populations was conducted. The study was performed in four locations to compare a fished population (Philippines) to non-fished populations (Australia, Fiji, and American Samoa). The process relied upon historically accepted methods, such as baited traps, to calculate catch per unit effort (CPUE), and modern techniques utilizing baited remote underwater video systems (BRUVS) to calculate population densities. Additionally, genetic samples were collected from each specimen and ultrasonic tracking studies were conducted. The CPUE in the Philippines was significantly lower than the CPUE in non-fished populations. Likewise, the population density in the Philippines was significantly lower than the three non-fished areas. The genetic analysis is to be completed but initial results suggest that isolated populations are genetically distinct. Our migration results point to nautilus with short migrations, living in their local habitat primarily. The results suggest that fisheries not only have a negative impact on nautilid populations, but non-fished populations are small and vulnerable to exploitation. These data provide the first comprehensive analysis of the destructive impact of nautilid fisheries, while also providing baseline data for future climate change studies. Nautilus are sensitive to temperature change and may be an important indicator species of climate change. Protective measures not only benefit nautilus and its ecosystem, but may also assist humans in developing effective climate change models.

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## Origin and evolution of the Gephuroceratina (Ammonoidea, Agoniatitida)

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The higher systematics of the Ammonoidea has traditionally been based on their sutures but more recently, aspects of early ontogeny and general shell form (e.g., whorl expansion and body chamber length) have been re-considered. This ongoing revision will lead to a new, non-cladistic systematic scheme. The suborder Gephuroceratina was established by Ruzhencev (1957) for all imperforate Agoniatitida with subdivided ventral lobe. Korn (1998) suggested that the superfamilies Pharcicerataceae and Triainocerataceae arose independently and created a new suborder Pharciceratina. This is rejected based on stratigraphic and morphologic data. Rich middle Givetian faunas from southern Morocco suggest an important additional apomorphy for monophyletic Gephuroceratina, the lack of embryonic growth ornament. It is well-preserved on the very large protoconchs of agoniatitids (including “*Meragoniatites*”) but not visible on the smaller protoconchs of maenioceratids and pharciceratids from the same locality and beds and has never been seen in any Frasnian gephuoceratid. In *Manticoceras*, Ritzstreifung, the mould imprint of peculiar ornament of the inner shell layer, clearly begins only after hatching. This gives further evidence for a complex early ontogeny in the Gephuroceratina.

The Maenioceratidae are the oldest family of the Pharcicerataceae although typical genera show a divided ventral saddle (with an A-lobe) and not a divided ventral lobe. They originated in the last Eifelian beds, probably from *Holzapfeloceras* (Anarcestaceae). Advanced new *Maenioceras* species are homoemorphic to some Famennian goniatites and include an alleged *Sporadoceras* from Bolivia. The early whorls of the oldest Pharciceratidae closely resemble associated *Afromaenioceras*, which underlines the placing of both in the same superfamily. A new intermediate genus from Morocco proves that the upper Givetian Taouzitidae, with a trend towards rapidly expanding whorls, also evolved from *Afromaenioceras*. They are no Gephurocerataceae, as suggested by Korn (2001). Within the Triainocerataceae, new genera from southern Siberia provide a complete evolutionary series from upper Givetian Tamaritidae to the Frasnian Triainoceratidae. Sutures and ammonitellae of the top middle Givetian *Atlantoceras* are closer to associated *Afromaenioceras* than to the slightly older, youngest agoniatitids. New rare lower Frasnian forms link the genus with the upper Frasnian/lower Famennian *Archoceras*. *Pseudoproboloceras*, the undoubted oldest member of the Gephurocerataceae, shares more similarities with *Atlantoceras* than with other known upper Givetian ammonoids. The type of *Ponticeras* is a maternoceratid; therefore, a new name is needed for the oldest Gephurocerataceae subfamily, which gave rise in the basal Frasnian both to the oldest *Manticoceras* and the Koenenitidae. As shown by Bockwinkel et al. (2013), the Belocerataceae derived via *Scaturites* (Acanthoclymeniinae) slightly earlier, still in the upper Givetian.

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## **Ammonites from the uppermost Campanian (Late Cretaceous) in Central Montana**

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Ammonites from the uppermost Campanian (Late Cretaceous) within the Bearpaw Shale of Montana have a diverse fauna that includes *Baculites*, *Pseudobaculites*, *Hoploscaphites*, *Rhaeboceras*, *Didymoceras*, *Pachydiscus*, *Placentoceras*, and *Sphenodiscus*. The Bearpaw Shale was deposited as a transgressive event in the U.S. Western Interior Seaway over terrestrial sediments in Montana, Wyoming, and Canada from *Didymoceras nebrascense* through *Baculites clinolobatus* Range Zones (75.19-69.59 MYA). Herein, we examine some recently collected fauna from the *Baculites reesidei* through the *Baculites jenseni* zones. Post depositional structural events including faulting, anticlines & synclines occurred providing obstacles following stratigraphic zones and measuring individual beds from one outcrop to the next.

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## **Shell construction during embryonic life of *Sepia officinalis*: what does it tell for evolution?**

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Among extant cephalopod molluscs, cuttlefish and spirulids are the only groups that retained an internal calcified shell. The morphogenetic origin of their shells and thus the homologies of their substructures are still poorly understood and remain to be specified. The aragonitic cuttlebone is composed of a superimposition of flat chambers delimited by septa and supported by pillars linked together in a continuous wall. The origin and the formation processes of both the pillars and the different layers of the septa are not yet fully understood. Despite its fundamental importance for understanding the evolution of the coleoid shell, no spatio-temporal analysis of the construction of the shell has been performed in the first stage of the development. To approach this question, we have studied the development of the shell during the embryonic life of the European cuttlefish, *Sepia officinalis* in four steps:

- 1) Analysis of the 3D structure in the first five chambers built before hatching
- 2) Study of the dynamics of mineralisation both in the pillars and in the septa
- 3) Identification of the mineral and organic components in the different parts of the shell
- 4) Characterization of the molecular processes (expression of target genes involved in mineralisation)

The chitinous matrix is formed at stage 24 (stage 14 of Naef) and the mineralization begins at stage 25. Preliminary results show that the building of the pillars is not complete before the formation of the next septum suggesting that mineralization process occurs in several steps, the last one leading to complete walls by accretion rather than by cellular mechanisms.

Our aim is to compare embryonic, juvenile, and adult *Sepia* shells. Because of the different environmental pressure, inside the egg and after hatching, we cannot exclude differential regulation processes. The observation of fossil shells in the light of these results should allow to infer evolutionary hypotheses on the formation mechanisms in coleoid shells.

## The timing of cephalopod survival after the Permian-Triassic mass extinction

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Ammonoid were one of the marine invertebrates clades most strongly affected by the Permian-Triassic mass extinction (Brayard et al. 2009). Prolecanitida and Ceratitida are the only orders that crossed the boundary (Tozer 1981). Triassic Prolecanitida includes only the Episageceratidae, whose discontinuous stratigraphic occurrence is restricted to the Griesbachian and the early and middle Smithian. No episageceratid has been recorded from the Dienerian yet. Episageceratidae left no post middle Smithian descendants as the Triassic near-homeomorphic Sagecerataceae are phylogenetically linked to Ceratitida and not to Prolecanitida. Among the Ceratitida, Otocerataceae occur in the the Griesbachian (Otoceratidae) and in the middle Smithian (*Proharpoceras*; see Brayard et al. 2007), but otocerataceans are presently unknown from Dienerian strata. Among Ceratitida, the morphologically simple Xenodiscaceae cross the boundary and form the rootstock of all other Ceratitida. *Xenodiscus* ranges from the Permian into the Griesbachian, where it is accompanied by several close derivatives or synonyms (e.g., *Tompohiceras*, *Hypohyceras*, *Metophiceras*). To date, no Xenodiscaceae is documented from the Dienerian. They diversified during the Smithian with a new family (Xenoceltitidae) in which much of the Spathian diversification roots. A typical Permian nautiloid (*Tainionautilus*) also re-occurs briefly in the early-middle Smithian (Brühwiler et al. 2012). The main timing pattern that emerges is that the Dienerian was the harshest interval for all clades that survived the Permian-Triassic mass extinction. Their abundances were so low that they temporarily disappeared from the Dienerian record. Their final and sporadic reappearance during the Smithian coincides with the first Early Triassic massive diversification of newly evolved Triassic ammonoid clades. The second major diversification took place in the Spathian, immediately following the most severe Triassic ammonoid extinction at the end of the Smithian. Correlations with sea-level changes, sea-surface temperature, and oxygenation of the sea-water (Romano et al. 2013) are discussed and the preponderant role of abiotic parameters in the shaping of these survivor clades is underlined.

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## Knowledge of parasitism in ammonoids: importance for paleoecology

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Extant cephalopods are commonly infested by parasites making it plausible that also ammonoids had parasites. We reviewed the fossil evidence of parasitic infestations in ammonoids. Due to low preservation potential of soft-tissues in ammonoids and parasites, traces of parasitoses are largely restricted to pathologies interpreted to be caused by parasites. *Nautilus* is of little help to interpret these structures as it is only known to harbour parasitic copepods on the gills. Analogues to ammonoid pathologies are caused by parasites in extant bivalves and gastropods. Characteristics of these structures such as their position deep within the soft-tissues, low prevalence within a species, high host specificity or their gradual and/or temporary development later in ontogeny can also corroborate their parasitic nature.

The most-convincing traces of parasitoses in ammonoids are blister pearls, which encase remains of parasitic organisms, which speak for a long-term coevolution between ammonoids and their parasites. The restriction of these structures to particular specimens or populations of certain taxa suggest not only the influence of phylogeny, but also ecology (habitat, predator-prey interactions) on infection risks – a phenomenon, which is well-known from extant coleoids. The study of ammonoid paleobiology would therefore benefit from more studies and reports of such structures, which have often been overlooked.

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## The systematic and taxonomic revision of the ‘*Pleydellia*-group’ ammonites from the Minette ironstones (Late Toarcian), southern Luxembourg

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Here, I propose the systematic and taxonomic revision of the group of *Pleydellia sensu lato* (Dumortierinae, Graphoceratidae, Hildoceratoidea), by the means of the ammonites stored at the National Museum for Natural History in Luxembourg (MNHN-L). Most of the ammonites originate from the historical collections (studied by W. Branco, E.W. Benecke, and P.L. Maubeuge) with several holotypes and particularly well preserved material. The specimens originate from several outcrops of the Minette Ironstone Formation situated in southern Luxembourg (Differdange, Esch-sur-Alzette subbasins) and the adjoining French Lorraine region. Other material sampled recently (by R. Weis, D. Delsate, R. Haas, and V. Rebizant) completes the study and gives new information about the biostratigraphy of the uppermost Toarcian of this area, which corresponds to the NE margins of the Paris Basin.

Since the first description of *Pleydellia*, this group of ammonites underwent several systematic revisions at generic level. The four genera which belong to the group (*Pleydellia sensu stricto*, *Cotteswoldia*, *Walkericeras*, and *Canavarina*) were considered as sub-genera or synonyms. Furthermore, the French and German palaeontological schools historically developed their own independent classification systems.

In the context of taxonomic revision of the ammonites from the National Museum of Natural History in Luxembourg, an alternative third way of classification of the *Pleydellia s.l.* group without ambiguities is proposed here, combining the best of the work of these two schools.

The analysis of the morphological characters of all taxa historically included into *Pleydellia s.l.* has made it possible to individuate the elevation at generic taxonomic hierarchy for the following taxa: *Cotteswoldia*, *Pleydellia s.s.*, *Walkericeras*, *Canavarina*. All of these genera have an own set of distinctive morphological features. By studying features such as ribs, external area, periumbilical walls and sutural lines it is possible to distinguish between each genus and to reconstruct a probable phylogenetic lineage.

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## ***Sepia*-type connecting rings and septa**

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The evolutionary shell transformation that resulted in elimination of tubular siphuncle in *Sepia* is poorly understood. Micro-laminated micro-porous band-like sheets (connecting stripes) sealing the slit-like ventral and ventrolateral “openings” of chambers of the phragmocones of *S. (Acanthosepion) cf. savignyi* are presumable homologous structures of the connecting rings of tubular siphuncle (Doguzhaeva and Mutvei 2010). The presence of connecting stripes in the cuttlebones is herein confirmed by a SEM testing of 16 shells of *S. officinalis* from a shore in Vale do Lobo, southern Portugal. It is shown for the first time that the connecting stripes are inorganic-organic structures firmly fused with septa by prominent contacting ridges on the adoral septal surfaces along the septal edges where they regularly leave - when partially broken - band-like attachment scars. The contacting ridges have an inorganic-organic composition and a complex ultrastructure not found so far in any other cephalopods. These ridges consist of fused globular crystalline structures within an organic matrix. Each globular crystalline structure is formed by a stack of rounded micro-laminas parallel to the septal surface. Small isolated carbonate globules are observed on the adoral septal surfaces within the chambers near the connecting stripes. Each micro-lamina consists of carbonate micro-granules imbedded in organic substance. The posterior and anterior slopes of the contacting ridge show different mineralization; the former has plate-like elements while the latter lacks them. The contacting ridge contains numerous interspaces between spheres filled with organic material and has also numerous micro- and nano-pores of about 0.1-0.01  $\mu\text{m}$  in diameter. Therefore, the contacting ridge is considered to be a homologous structure of a pillar zone of the tubular siphuncle of *Spirula* shell. Both structures are permeable and apparently serve for shell buoyancy regulation. In *Spirula*, the permeable pillar zone is situated within the long septal necks that are strongly attached to the shell wall. The inner surface of the pillar zone is uneven and shows non-mineralized interspaces between the pillars. In *Sepia*, the contacting ridges are situated along the edges of the achoanitic septa; their inner surfaces also show numerous non-mineralized interspaces. In *Spirula*, septa consist of lamella-fibrillar nacre. In *Sepia*, septa have granular ultrastructure but their surfaces are lined with thin sub-layers distantly resembling lamella-fibrillar nacre.

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## Muscle and mantle attachment marks as well as body chamber lengths indicative of diverse life styles of coexisting Aptian ammonites of the Russian Platform

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The diverse muscle and mantle attachment marks observed in the body chambers of coexisting ammonites from the Aptian epicontinental Sea in the Russian Platform are thought to indicate different ammonoid life styles. Generally, the range of the body chamber lengths in adult ammonoid shells is about 180°-900°. Body chambers shorter than one whorl are associated with the large ventrolateral attachment marks extending to the midpoint of the body chamber. This fits with the precondition of the jet-powered swimming, namely the appropriate location of the attachment marks in the body chamber from where the cephalic and funnel retractor muscles would be able to extend straight across to the head and funnel area of the body. This is the case in *Aconeceras*. In the heteromorphs *Audouliceras* and *Ancyloceras*, the largest attachment marks are located in the umbilical corners of the hook-like terminal body chamber and show that the umbilical retractor muscles were the most powerful. The tongue-like umbilical marks extended over about one third to one fifth of the body chamber length so that they do not reach the place where the shell turns into the terminal straight shaft. Therefore, from these attachment marks, the retractor muscles would not be able to extend straight across to the cephalic area. However, the powerful umbilical muscles might have been useful for changing the mantle cavity volume for filter feeding. This suggests that the heteromorphs *Audouliceras* and *Ancyloceras* fed on small plankton or suspended organic particles. The morphology of the jaw apparatus of the co-occurring heteromorph *Australiceras* led to this idea; in this genus, the deep and wide lower jaw has a solid flat ventral side and the long wings of the upper jaw form a large cavity that could be used for sucking and filtering seawater (Doguzhaeva and Mikhailova 2002). Besides, the irregularly coiled spiral shell in these three heteromorph genera is perfectly suited for floating and perhaps vertical (diurnal) migrations. The *Audouliceras* and *Deshayesites* also show lateral V- and U- shaped mantle attachment marks continuing from the aperture to the back of the body chamber. These marks are indicative of pockets of the mantle cavity. In the heavily ribbed shell of *Deshayesites*, these marks (and thus pockets) are broader and deeper and associated with large lateral muscle attachment marks. This would also be essential for changing the mantle cavity volume and improvement of filter feeding. The presumed muscular mantle and well-developed funnel in the discussed ammonoids are supported by observation on the muscular mantle of the ceratitid *Austrotrachyceras*. Thus, the muscle and mantle attachment marks in association with the body chamber lengths distinguish the nektonic jet-powered swimming and the floating filter feeding life styles of the ammonites under consideration.

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## Arm hooks of Early Carboniferous-Late Permian coleoids, and their phylogenetic implication

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Ink sacs, arm hooks and lamella-fibrillar nacre are developed in extant coleoids but not in extant *Nautilus*. Thus, they are particularly important for the recognition of Paleozoic orthoconic coleoid cephalopods that lack a rostrum or have a reduced rostrum at the apex of the shell. Paleozoic coleoid recognition is also complicated by the mosaic combination of the ancestral (ectocochleate) and innovative (endocochleate) traits. In the record of Paleozoic arm hooks in association with other established coleoid features, the oldest occurrence is the ink-bearing *Gordoniconus* (late Early Carboniferous) with hooks that are unusually slender (1.0 mm long and 0.2 mm wide), relatively straight with a slight hook at the apical end of the shaft, and are arranged in rosettes. *Donovaniconus* (middle of the Late Carboniferous) was established as a coleoid on the basis of having an ink sac in the long body chamber. In the current examination of new specimens provisionally referred to *Donovaniconus*, arm hooks were found associated with the long body chamber and ink sac. These arm hooks are somewhat similar to those seen in *Gordoniconus* in that they are long and slender with only some curvature and differ in having a broad concave base. In *Saundersites* (time equivalent to *Donovaniconus*), the arm hooks are paired and relatively small (about 0.2-0.3 mm in length), and are associated with a coleoid radula. The hooks are short with a thick shaft and long distal part that is moderately hook-shaped. In *Jeletzkyia* (time equivalent to *Donovaniconus* and *Saundersites*), the 10 arms have small (length less than .4 mm), paired hooks that are swollen on their internal side, and their distal part is relatively thin. In an unnamed Late Carboniferous coleoid from Oklahoma (upper part of the Upper Carboniferous), the arm hooks are associated with the cartilaginous cephalic capsule and a radula; the hooks are of two sizes: about 0.6 mm and 1.8 mm in height; both are similar in shape and have comparatively long, thick shafts with a moderate hook shape. In the Late Permian *Glochinimorpha*, recently discovered arm hooks are associated with a gladius; there are three hook sizes - small (1 mm or less), medium (2 mm) and large (4 mm). All are robust and have a strongly curved internal edge with a semi-circular outline and have a shallow cup-shaped base. Based on these occurrences, arm hooks are a unique morphological and evolutionary innovation limited to coleoids, so they also serve as a reliable coleoid identification feature.

## Systematics, endemism and phylogeny of Indian proplanulids (Ammonoidea) from the Bathonian-Callovian of Kutch

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The Middle Bathonian of Kutch, western India, witnessed sudden migrations of many ammonite genera from different provinces (Roy et al. 2007) as soon as the Kutch basin opened up. Macrocephalitins, for example, invaded from the West Pacific Province (Indonesia) and displayed a spectacular radiation of many endemic taxa during the Late Bathonian-Early Callovian times (Spath 1931). Spath (1931) described many species within the genera *Sivajiceras*, *Obtusicoelites*, and *Kinkeliniceras* from the Upper Bathonian and entire Callovian successions of Kutch. All these genera were new and grouped within the subfamily Proplanulitinae of the Boreal Province. Since then, these new genera were continuously referred to as proplanulitids although their paleobiogeography was restricted to the Indo-Madagascan Province and not a single species of the Boreal *Proplanulites* has been recorded from Kutch or neighbouring regions. It was Callomon (1993) who expressed doubts about the phylogenetic affinity of the Kutch genera and predicted that a detailed study would reveal that these proplanulitids were unrelated and constitute an endemic lineage.

In the present study, we revisited Kutch's so-called proplanulitids. Our study included the type material archived in the Geological Survey of India, Kolkata, and numerous additional specimens collected by us from various sections with precise stratigraphic information. We revised the taxa in the light of new information about intraspecific variability and sexual diamorphism in these species. The concept of sexual dimorphism was not applied during the time of Spath (1931). The detailed systematic revision revealed that Spath's (1931) work suffered from excessive subjective splitting and many of the species were variants of a single, variable species. The genus *Hubertoceras* was considered as the microconch of *Obtusicoelites*. We finally described two species within each of the three genera. Dimorphism has been established in most of the species.

It is interesting to note that these three genera are overlapping both morphologically and stratigraphically. Callomon (1993) found strong similarities between *Sivajiceras congener* and the older *Procerites hians* from Kutch. He even insisted synonymising the two species. Roy et al. (2007) established *Procerites* and *Sivajiceras* as a group of genera that had an evolutionary plexus. *Procerites* was older in Europe (middle Upper Bathonian). We here envisaged that *Procerites* participated in a grand migrational event like many other ammonite genera and invaded the newly formed Kutch basin during the late Bathonian. It quickly speciated and gave rise to an endemic subfamily (nov. subfam.), which will soon be newly described. This is an example of allopatric speciation; the main European population of *Procerites* perhaps evolved into *Proplanulites*, which was essentially a Boreal genus. Because of the development of some converging characters (e.g., bullae-like primary ribs of the phragmocone), *Proplanulites* superficially resembled members of the *Sivajiceras-Obtusicoelites* lineage, but they differ at the subfamily level. For example, strong, dense primary ribs on the inner whorls and complex sutures of the Kutch genera are absent in proplanulitids (Callomon 1993).

## A review of biostratigraphy and palaeobiogeography of Boreal latest Jurassic–earliest Cretaceous belemnites

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In Boreal regions, the most detailed belemnite zonation of the Jurassic-Cretaceous (J-K) boundary sediments has been suggested for East Siberian sections. Two independent successions of biostratigraphic units based on belemnites of the family Cylindroteuthididae are defined there in the stratigraphic interval spanning the Volgian and Ryazanian stages: (1) *explanata* Beds, *russiensis* Zone, *gustomesovi* & *porrectiformis* Beds, and *curvulus* Zone; (2) *mamillaris* Zone, *napaensis* Zone, *tehamaensis* Zone, *knoxvillensis* Zone, and *curvulus* Zone. The East Siberian high-resolution succession of belemnite zones and beds is recorded in the West Siberian sections almost completely, excluding the *tehamaensis* Zone. In addition, the local *explorata* Beds and *compactus* Beds have been established there. Some Siberian zones (in the beds' rank) and beds are traceable to Pechora Basin (*mamillaris* Beds, *explorata* Beds, and *curvulus* Beds), NW Europe (*explanata* Beds) and northern California (*tehamaensis* Beds, and *knoxvillensis* Beds).

Cylindroteuthid belemnite zonations of the J-K boundary strata were also suggested for the NW Europe and East European (Russian) Platform. Almost all biostratons determined in the European Russia can be traced also in NW Europe, namely *magnificus* Beds, *volgensis* Beds, *russiensis* & *mosquensis* Beds, and *lateralis* Beds.

European belemnite scales most considerably differ from Siberian ones in the interval from the upper half of Volgian to the Ryazanian that is directly connected with peculiarities of development of Boreal-Atlantic and Arctic biogeographic realms. In the terminal Volgian the seas of Central Russia and NW Europe, belonging to the Boreal-Atlantic realm, became shallow basins with high-abundance but very low-diversity belemnite faunas. By the terminal Middle Volgian in the Boreal-Atlantic realm many genera and even subfamilies (Cylindroteuthidinae, Lagonibelinae, and the genus *Pachyteuthis*) disappeared sequentially, and temporarily the genera *Boreioteuthis* and *Simobelus* (re-occurred in the Early Cretaceous). In the Central Russian Sea, as well as in seas of NW Europe, at the Volgian–Ryazanian boundary only *Acroteuthis* and *Liobelus* with robust dorsoventrally depressed rostrum occurred as the most adapted to shallow environment. In the Arctic seas, various taxa of cylindroteuthids continued to exist and generated a number of new species. Some Arctic taxa from *Arctoteuthis*, *Cylindroteuthis* and *Lagonibelus* possessing slender elongate laterally compressed rostrum could have migrated over long distances through the epicontinental seaways between Siberia and Japan, between Siberia and California (or even Mexico). Thus, correlation of west and east European belemnite successions presents no problems. However, their correlation with Siberian belemnite successions is less precise. Three belemnite beds have been established for the J–K boundary interval in northern California; two from them are traced from Siberia. The distances over which precise correlations can be made are limited by the belemnite biogeography.

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## Early ideas about fossil cephalopods

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Ammonites and belemnites are among the most celebrated invertebrate fossils, and both groups played a crucial role in the early history of palaeontology. In the present talk, I want to give an overview of the sometimes twisted roads that led from the first descriptions and illustrations of ammonites and belemnites in the 16<sup>th</sup> century to the picture that emerged in the early 19<sup>th</sup> century.

Today, we have a pretty clear conception what a belemnite animal looked like and how it lived. They were pelagic predators, quite comparable to modern squid. We are much more insecure about ammonites. Our knowledge of their soft-part anatomy is rudimentary at most, and with respect to the number and form of the arms as well as the anatomy of the eyes, we are left with little more than educated guesses. Furthermore, many have strange jaws and in part a very peculiar sexual dimorphism. Therefore, there is much more argument about their ecological role. It may appear as surprising that for much of the last 500 years the situation was reversed.

**Establishing an organismic origin.** In the 16<sup>th</sup> and 17<sup>th</sup> century, when they appeared prominently in the first printed books on fossils, both ammonites and belemnites were seen as "sports of nature", as inorganic products that originated within the rocks by the action of a formative force ("vis plastica"). Yet, already in the works of Gessner, Aldrovandi, Worm, and others, a connection was seen between ammonites and marine snails, or snakes, although this similarity was not seen as a causal relationship. Belemnites, on the other hand, seemed to have their closest analogue firmly within the mineralogical/inorganic world, e.g., among the stalactites.

**The availability of a modern analogue.** The first definitive statement that ammonites are fossil cephalopods, "some kind of nautili", seems to be by Hooke in 1665, with a detailed comparison appearing posthumously in 1704. Although initially not widely accepted, this became the predominant notion with the establishment of the diluvian view of earth history. Belemnites on the other hand remained much longer in the realm of the inorganic. Although a relation with cephalopods (*Nautilus* and *Spirula*) was already suggested by Erhart in 1724/27, this was largely neglected and in 1750, it was still broadly contested that they were true fossils. The lack of a suitable modern analogue delayed any progress to the end of the 18<sup>th</sup> century, and during that time, the belemnites were assigned to almost every animal phylum.

**The question of extinction.** Once the biological origin was established, the obvious question remained: Where are they now? Belemnites could perhaps still dwell in the deeper parts of the ocean, and there were indeed some spectacular finds of "living fossils" in the second half of the 18<sup>th</sup> century. The same could be true for the ammonites, but things took an interesting twist during that time. The first foraminifer shells were described from beach sands, and for almost 50 years, they were described as modern shelled cephalopods and hence surviving ammonites.

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## Ontogenetic morphometry, taxonomy and biogeographic aspects of Famennian (Upper Devonian) Prionoceratidae

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The Prionoceratidae (Goniatitida, Tornoceratina) originated at the base of the upper Famennian and were the only ammonoid family that survived the global Hangenberg Crises at the end of the Devonian. They gave rise to all post-Devonian ammonoids. The understanding of ammonoid phylogeny and systematics in general, therefore, requires a careful revision of this group in the light of modern ontogenetic morphometry. Our work concentrated on Famennian Prionoceratinae from Germany and Morocco, from the northern and southern margin of the western Prototethys. In contrast to previous assumptions of a homogeneous distribution of species in that realm, we found significant differences between German and Moroccan faunas, especially with respect to early ontogeny.

All early forms from the Famennian IV were previously placed in the genus *Prionoceras*, which is characterized by involute early whorls and regularly-spaced, lateral shell constrictions until median stages. Beside the type-species, *Pr. divisum* (including its synonym *Postprolobites yakowlewi*), and the compressed *Pr. frechi*, there is a third Rhenish species with distinctive ontogenetic trait, for which the name *Pr. medius* is kept. Two new relatives of *Pr. frechi* range in the Tafelberg into the Dasberg Event Interval (basal UD V). A closely related new genus, which includes *Goniatites sulcatus* and several new species, shows evolute early whorls (uw/dm up to 0.4). It is transitional to the ancestral Prolobitidae, and gave rise to many subsequent taxa, especially in Morocco.

This second radiation occurred early in UD V. *Rectimitoceras* descended from *Prionoceras* by the loss of regular shell constrictions and varices and may be better recognized at subgeneric level. Involute species with complete shell constrictions bordered by lateral shell lips comprise the *liratum* Group, a new subgenus that includes several other species (*geminum*, *lentum*, *fuerstenbergi*). There are three groups in UD V/VI with slightly or marked evolute early whorls. Typical *Mimimitoceras* show subtriangular early whorls and regularly spaced constrictions with shell lips, the *pompeckji* Group has higher whorl expansion rates (> 1.8) than other Famennian Prionoceratidae and only internal varices, and most specimens from Morocco previously identified as *R. lineare* as well as *R. quadripartitum* proved to differ markedly from true *R. lineare*. The *pompeckji* Group was either homoemorphic or ancestral to *Acutimitoceras* (*Stockumites*) that entered in the topmost Famennian (UD VI-F) just after the global Hangenberg Blackshale. During the basal Carboniferous post-Event re-radiation, the involute, distinctive *simile* Group with weak shell constrictions, but without lips, comprise the last Prionoceratinae.

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## **An advanced workflow for taxonomic research: case study on Cretaceous Nautilids**

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The large amount of data gathered in a thorough taxonomic revision quickly becomes difficult to handle. The here proposed workflow allows an easy visualization of all acquired data/metadata and all types of descriptions, photo-documentations, illustrations and literature, and this with a minimal amount of invested time, money (app. 50 euros) and computer skills. The proposed workflow can be applied to any type of fossil group. It was elaborated during my PhD on the Upper Cretaceous Nautilids from the European epicontinental seas. Largely, it corresponds to the creation of a MS Access database specifically constructed for taxonomic purposes combined with the creation of a website using the Scratchpad platform for the overall taxonomic structure of the revised group and literature.

From the start of my PhD onwards, during numerous collection visits, I gathered huge amounts of information that were both on paper and distributed in various excel sheets, plus >10,000 photographs spread across many folders, datafiles, and drawings. In the end, I lost the overview. A solution that worked for me was the construction of a MS Access database, in which all the data can be displayed and also each specimen can be visualized and compared via the specimen form/card with defined fields. A script was created to connect the specimen cards with the corresponding photographs. By using the advanced filters and search options, the data become much more accessible and also can be visualized in various relations, making the sorting of data very effective. Because all data can be stored on an external hard drive, and MS software is readily available almost everywhere, even when your personal computer is not around, you are able to work with the data.

The second related solution, from which I benefited greatly, was the construction of a website using the Scratchpads platform, which is hosted and developed by the Natural History Museum London (<http://scratchpads.eu/>), and offered freely to scientists that want to sort and display their data and create their own research networks. I created my own website for the discussion of taxonomy within the Cretaceous Nautiloidea and sharing and effectively sorting the related literature. It allows to cross-reference the original description of the species, genera, families, and to add revised opinions and additional data, linked with publications, which can be effectively filtered by several advanced options. The Scratchpad interface is easy to use and it is possible to define several levels of editing for different users.

The proposed workflow is not revolutionarily new, and several variants are certainly possible, but because I benefited so greatly from it, I wanted to share my experience with the paleontological community, in particular with junior PhD students.

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## The Cenozoic fossil record of the Coleoidea: an overview

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Compared to Palaeozoic and Mesozoic coleoid cephalopods, where our morphological, systematical, and phylogenetical understanding has been considerably improved in the past 40 years, little has been changed since the last overview compiled by Naef (1922). It became now necessary - in the face of the upcoming *Treatise of Invertebrate Paleontology, Part M, Coleoidea* - to gather all available information on worldwide Cenozoic coleoids. It is hence the aim to provide an overview of the general morphology, systematics and phylogenetic relationships of Cenozoic coleoids.

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## On the locomotion system of fossil Coleoidea (Cephalopoda) and its systematic and phylogenetic significance

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One of the key innovations in the evolution of coleoid cephalopods was the development of a highly effective jet-propulsion. Apart from significant shell transformations, the re-organisation of the locomotion system involved also character complexes such as the muscular mantle, the fins and diverse retractor muscles. Naef (1921) proposed a convincing model that led to the main traits of modern subgroups but without providing fossil evidence for his ancestral character state reconstructions. Recently, Bizikov (2004, 2008) presented an impressive compendium in which he documented the different types of shell-muscular interactions in extant coleoids. Since a similar study on fossil forms is still missing, it was the objective of the present work to detect fossilized muscular attachment sites and to compare them with the observations made by Bizikov (2004, 2008).

The study included phragmocone-bearing as well as gladius-bearing coleoids from popular Konservat-Lagerstätten such as the Plattenkalks of Solnhofen (Late Jurassic: Tithonian) and Lebanon (Late Cretaceous: Cenomanian), where muscular tissues are extra-ordinarily well-preserved. Although muscle-shell interactions observed in Mesozoic gladius-bearing coleoids suggest - in contrast to Naef's view - vampyropod affiliations, our new approach largely support his ancestral character states. Detailed conclusions and how they impact existing systematics will be discussed in a phylogenetic context.

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## All life-stages of the tropical arrow squid around the Sao Sebastiao Island, SE Brazil

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A multidisciplinary research aiming to approach population structure, early life-stages, larval dispersal, growth, spawning, behavioral patterns, and the fishery of the squid *Doryteuthis plei* in SE Brazil allowed the integration of different surveys, observations, and models in order to understand the processes behind the population dynamics. The aim of this paper is to present the synthesis of the findings revealed by oceanographic surveys, biological samplings, filming, diving, the maintenance of living specimens, statoliths reading, interviews with fishers, and dynamic quantitative models of coupled ocean-particle tracking, all conducted by a large research group. Mature squid concentrate and spawn in soft bottoms in shallow waters during the summer where they became available to small-scale fisheries. The presence of *D. plei* egg mops were found on the seabed during some of the surveys allowing the description of embryonic stages. Behavioral body patterns were detected showing multiple chromatic and postural displays, including a “nuptial dance”. The somatic growth better fitted to the logistic model while juveniles grow in a Gompertz way. Longevity was estimated at 8 months. The population structure and the human dimension of the fisheries characterization also contributed to the knowledge of the species off this peculiar retentive area of SW Atlantic. Evidences indicated that some disaggregation of different life stages seems not to occur in waters around the island where all life stages of the tropical arrow squid were found.

## What about nautilids at the Cretaceous/Paleogene boundary?

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The differential extinction and survival of ammonites and nautilids at the Cretaceous/Paleogene (K/Pg) boundary has puzzled scientists for decades. These have been attributed to differences in reproductive strategies, early life, diet, preferred habitat, or a combination of one or more of these, and probably triggered by a transient period of ocean acidification in the immediate aftermath of the Chicxulub impact. During the past decades, K/Pg boundary ammonites have received a lot of attention. From having almost no records of ammonites just below the K/Pg boundary, today, we know of at least 29 sites with ammonites recorded from within the uppermost 0.5 myr of the Maastrichtian (Landman et al. 2014). Nautilids, in contrast, have received almost no attention. This seeming lack of interest may relate to the depleted number of shell characters that can be used in evolutionary and taxonomic studies, to their overall slow evolution, which makes them less useful for stratigraphic purposes, and more importantly, to their usual rarity in ammonite-bearing K/Pg boundary sections. For example, at Kalaat Senan, only a single nautilid was found associated with 800 ammonites within the interval corresponding to the last 0.5 myr of the Cretaceous.

Very little is actually known about their response to environmental stresses prior to, at, and shortly after the Chicxulub impact, other than that, at generic level, they seemingly did not suffer significant extinction, and that they underwent a period of intensive radiation in the early Paleogene, which may create the illusion of an undisturbed extension into the Cenozoic. However, when we zoom into the record of European shallow-water sections (e.g. the Mons Basin, Belgium; Maastrichtian type area, The Netherlands; Middle Vistula Valley, Poland) Maastrichtian and Paleocene nautilid faunas are quite different. These are evidence of significant responses to the changing conditions, including (local) extinctions of some species, in addition to migration and/or immigration of others. In other regions, slightly different scenarios seem to have been deployed. Achieving a better understanding of these evolutionary histories might allow an improved picture of the differential extinction and survival of nautilids vs ammonites.

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## ***Epicymatoceras*: an exotic evolute nautilid from the European latest Cretaceous that does it all different**

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It is a very well-kept secret that the Royal Belgian Institute of Natural Sciences (RBINS) hosts one of world's largest collections of uppermost Cretaceous nautilids. Apart from being included in some 19<sup>th</sup> century species lists describing the general geology of the area, hundreds of specimens from Campanian and Maastrichtian strata from the Mons, Campine, and Maastricht-Liège basins have never been thoroughly studied.

The major work on Maastrichtian nautilids from The Netherlands and Belgium is by Binkhorst van den Binkhorst (1861), who introduced four new taxa: *Nautilus depressus*, *N. heberti*, *N. vaelsensis*, and *N. lehardyi*. The first two are referred to *Eutrephoceras* and *Cimomia*, respectively, but the latter two are of specific interest and form the basis of a current revision of *Epicymatoceras*, a genus created by Kummel (1956) for *N. vaelsensis*. Like Kummel (1956) already partly mentioned, *Epicymatoceras* has several features that no other post-Triassic nautilid displays, in particular its evolute coiling throughout the entire ontogeny. Until recently, only a limited number of specimens were known, but in the collections of the RBINS, >80 specimens were recently discovered displaying several different taphonomies allowing a thorough revision, redescription of the species and genus, and (re)discussion of its origin, systematic position, and stratigraphic distribution. But more importantly, some of the newly discovered specimens are that well-preserved that they allow to study the change in morphological features from the pre- to post-hatching ontogenetic stages, including the changing surface morphology, chamber size, position of the siphuncle and the presence of the nepionic constriction.

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## Statoliths and other microfossils associated with the Christian Malford Lagerstätte

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In the 1840s, during construction of the railway line west of Swindon (Wiltshire, UK), a number of beautifully preserved coleoids (belemnites and squid-like cephalopods) were found. These famous specimens of *Belemniteuthis* and *Mastigophora*, as well as a number of fish, are described as a *Fossilagerstätte* under the name of the ‘Christian Malford Squid Bed’. Many of these specimens, which come from the Phaeinum Subzone (Athleta Zone, Callovian) of the Oxford Clay Formation, contain soft tissue, muscle fibres, and the content of their ink sacs.

In 2007, the British Geological Survey excavated a site, some ~100 m from the original borrow pits alongside the railway, as well as drilling a number of borehole cores. Our work (on BGS core No. 10) has recovered exceptionally large numbers of statoliths, otoliths (fish ‘ear’ bones), squid hooks, and foraminifera. Statoliths are the small, paired, aragonitic stones found in the fluid-filled cavities (or statocysts) within the cartilaginous heads of all modern and probably all fossil coleoids. Jurassic statoliths have yet to be described in any detail as there are only a few references to them in the literature. The exceptional abundance of statoliths and squid hooks recorded in the samples from the core may represent a Jurassic squid-breeding ground, which existed for an extended interval of late Callovian time. The annual spawning of female squid massively enlarges their ovaries and this breaks down the body wall leaving spent individuals to die. The highest numbers of statoliths occur over a 3 m thickness of strata associated with Christian Malford Squid Bed. The numbers recorded in this part of the Phaeinum Subzone are well above background levels in the rest of the Jurassic in the UK (Malcolm Clarke, *pers.com.*) where one has to wash several kg of sediment to recover <200 statoliths. In our samples 1kg of clay has yielded >400 statoliths.

The occurrence of abundant, though low diversity, assemblages of Foraminifera (especially *Epistomina* spp.) in the same samples point to an oxygenated, though possibly stressed, environment. The significant proportion of deformed Foraminifera in the assemblages appears to confirm that the environment was less than optimal but still able to support a relatively diverse and abundant population.

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## Morphometry of the shell of *Spirula spirula* based on nano-CT data

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*Spirula*, a deep-sea squid, possesses a well-developed internal chambered shell that can be found in great numbers washed ashore on marine beaches. Geographical distribution of *Spirula* is circumtropical but patchy and call the monospecific composition of that genus into question. Due to the lack of enough material suitable for DNA molecular analyses, morphometry of the shell seems promising to contribute to this question. However, recent attempts of morphometric analyses (inter-, intrapopulational, and ontogenetic) of empty *Spirula* shells from different geographical areas do not demonstrate the existence of two or more species. The development of new software (CONCH) for quantitative morphological analysis allows for the description of shell morphology down to 10° steps. CONCH is designed to minimize the time necessary to acquire these morphological data. High-resolution non-invasive imaging techniques (e.g., micro-computed tomography or nano-computed tomography) allow for the visualization and measurement of internal shell features (e.g., septal thickness, septal curvature or spacing, diameter of the siphuncle), but also 3D-data like chamber volumes. The combined use of CONCH and CT-derived images is demonstrated for a single shell of *Spirula spirula* from Fuerteventura. A shell feature that was not taken into account for *Spirula* so far is the whorl interspace, which appears to be highly variable. Another feature often observed but not yet quantified is the deviation of the whorl from the median plane. With our approach, we hope to support future morphometric analysis of *Spirula* shells from different geographical areas.

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## **CONCH - new software for quantitative morphological analyses of ammonite shells**

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Species description in palaeontology is based on the morphology of preserved hard parts (morphospecies concept). Traditionally, species were differentiated from each other utilizing a static (“Linnean”) rather than a dynamic (“Darwinian”) approach. This static method does not account for intraspecific variation, co-variation, and ontogenetic changes. Descriptions of species was usually rather narrative and included often only a single set of measurements, normally presented for the place of insertion of the last septum or the largest preserved diameter. Many species were thus validated on the grounds of subtle morphological differences of the adult or subadult stage. During the last decades, the way of species description has changed significantly, regarding ontogeny as well as the use of variability analyses. Hence, recent studies of Mesozoic ammonoids document a wide variability in conch parameters and ornamentation, though only when a sufficient amount of specimens was available. Quantitative morphological studies can improve our understanding of the species content of a genus and represent the state of the art of species description.

However, quantitative studies are often hampered by three problems: (i) limited number of fossils from bed-by-bed collections; (ii) well preserved, non-deformed material and (iii) it is a time-consuming process. We present new software called CONCH, which significantly reduces the amount of time needed to measure standard distances in spirally coiled shells such as diameter, whorl height, whorl interspace, umbilical width, and ornamentation. In addition, an angle measurement tool is available to measure orientation (inclination) or spacing of ribs or constrictions at the shell surface or septal spacing and septal curvature of sectioned specimens or in images derived from computed tomography. CONCH software allows obtaining more information in less time to describe the morphology of ammonite shells and supports quantitative morphological analyses of ammonite populations.

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## Life Cycles of Deep-Sea Cephalopods: Past, Present and Future

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Deep-sea cephalopods depend for a significant portion of their life cycle on the ocean below the euphotic zone. This group probably includes most cephalopods in terms of biomass. They play a crucial role in oceanic foodwebs, being preyed upon by a wide variety of oceanic predators. Many species migrate during the night to shallower waters to feed, and move to deeper waters during the day, and thereby contribute to the transport of carbon to deeper ocean layers. Despite the importance of this group of cephalopods, we know relatively little about their life cycles, with the exception of commercially important species. This paucity in information is in part the result of the difficulty in obtaining specimens, e.g. specialized deep-sea gear is required to sample the habitat of deep-sea cephalopods. Although our knowledge is still limited, evidence is accumulating that the life cycles of deep-sea cephalopods differ from those of their shallow water relatives.

In this talk, I will present an overview of our current state of knowledge of aspects of deep-sea cephalopod life cycles including feeding ecology and behavior and reproduction. Although many deep-sea cephalopods, are ‘ferocious carnivorous predators’, recent insights show a range of feeding strategies including opportunistic detritivory. Reproductive strategies show a variety of spawning and mating tactics, but for many species, sexually mature individuals have never been collected. The application of *in situ* observational methods has allowed the observation of deep-sea cephalopods in their natural habitat revealing unique feeding and reproductive behaviours. The further exploration of the oceans will likely result in answers to some of the many questions that remain about life cycles of deep-sea cephalopods. In the view of a changing climate, it is important to establish baseline information on abundance, diversity and distribution, in order to monitor and predict the impact of multiple stressors (inter)acting on deep-sea cephalopod populations.

## Early evolutionary history of belemnites, revisited: New perspectives from East Asia

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Belemnites (order Belemnitida), a very successful group of Mesozoic cephalopods, provide an important clue for understanding Mesozoic marine ecosystems and the origin of modern coleoid cephalopods. Following current hypotheses, belemnites originated in the earliest Jurassic (Hettangian, 201.6–197 Ma) with very small forms (e.g., *Schwegleria*: ~4 mm in rostrum diameter), whose rostrum is lacking a clear groove. According to this view, their paleobiogeographic distribution was restricted to northern Europe until the Toarcian (183–176 Ma). The fossil record is, however, biased by the fact that all the previous studies on belemnites so far focused on Europe.

Here, we report on true belemnite taxa from the Upper Triassic-lower Jurassic of East Asia. *Sichuanobelus* and *Sinobelemites* (Sinobelemitidae) occur in the Carnian of Southwest China, and the Hettangian-Sinemurian of Japan. The Sinobelemitidae, which has enigmatic morphological features (e.g., dorsal groove), may be included in the future in a new suborder. A large-sized taxon of the suborder Belemnitina (33 mm in diameter) also occurs in the Hettangian of Northwest Japan. This large diameter can be compared with that of *Megateuthis* (Middle Jurassic), the largest belemnite ever observed. In the Sinemurian, there are two belemnites from Northwest Japan; *Nipponoteuthis katana* and *Eocylindroteuthis yokoyamai* (Iba et al., 2014). These two belemnites have small to large rostra with one deep and long apical groove, a diagnostic character of the Belemnitina. Morphologically, these forms are completely different from coeval European genera of Hettangian-Sinemurian age. A Sinemurian belemnite also was discovered in South Tibet, which was located at the Gondwana margin at that time. The Tibetan belemnite resembles Sinobelemitidae or *Pachybelemnopsis* (Suborder Pachybelemnopseina). The Sinemurian belemnite from Tibet represents the earliest firm record of the Belemnitida from the Southern Hemisphere.

It is concluded that the earliest Jurassic (Hettangian-Sinemurian) Belemnitida had a much higher diversity, including extremely large taxa, and a wider distribution than previously thought. The Belemnitida did not originate in northern Europe, contrary to previous hypotheses. The Sinobelemitidae can be considered as a possible rootstock of all belemnites; the small European belemnites of the earliest Jurassic are here seen as an endemic offshoot. It is postulated here that the belemnites did not originate in the earliest Jurassic, but in the Late Triassic (Carnian). The fossil record of the Order Belemnitida is therefore extended by ~33 m.y. before the Triassic-Jurassic boundary, where one of the five largest mass extinctions in the Phanerozoic occurred.

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## Fluctuations of the oxygen minimum zone at the end of Oceanic Anoxic Event 2 and the response of ammonites: A case study from Mexico

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The latest Cenomanian to early Turonian (Late Cretaceous) section at Vallecillo, Mexico, contains a continuous and highly fossiliferous sedimentary record across the late Oceanic Anoxic Event (OAE) 2. The Vallecillo Platy Limestone provides insight into an early Turonian pelagic ecosystem with unique details. Similar distributions of benthic inoceramids and ornamented planktic foraminifers during this period of an expanded, but fluctuating oxygen minimum zone, are documented. Four phases of expansion and contraction of the oxygen minimum zone were reconstructed over the Vallecillo section (Ifrim et al. 2011a). Although the distributional mode of ammonites is similar to that of inoceramids (dispersal by hatchlings or larvae), strong differences in the extinction and recovery patterns were documented between the two groups. At Vallecillo, the abundances of ammonites do not correlate with those of inoceramids; they rule out a preservational bias but also indicate that ammonites and their hatchlings populated different water depths than inoceramid gametes and planktic foraminifers.

The size and abundance of ammonites appears to be related to changes of oxygen content of the water. Conclusions on ammonite paleobiology can be drawn for *Pseudaspidoceras flexuosum*, the most abundant species at Vallecillo. *P. flexuosum* clearly inhabited the open water column, supporting some and contrasting other interpretations on the mode of life of spinose ammonite morphotypes. A demersal mode of life can be excluded for this species based on the scarcity of oxygen and prey at the seafloor (Ifrim 2013). Instead, this species is interpreted to have dwelled in the well-oxygenated upper surface waters in a pelagic ecosystem with an active carbonate factory where it could have been colonized by epizoans (Ifrim et al. 2011b). It is among the first species to reappear at the end of OAE 2 (Ifrim & Stinnesbeck 2007) and may have been adapted to the layered water body. The improving conditions during the early Turonian led to a migration of *P. flexuosum* into other seas and oceans. In part, the interpretations on its paleobiology can be extended to the other ammonite present species. This study is an example for the complexity of species-based analyses, which is usually shadowed in the analysis of large databases.

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## **Infrazonal belemnite stratigraphy of the Lower Callovian of the East European Platform**

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The main result of the Jurassic biostratigraphy of European Russia achieved during the last two decades is the development of high-resolution infrazonal ammonite scales. Another cephalopod group, however, the belemnites, despite widely spread in the same deposits, do not allow detailed subdivision and consequently cannot provide precise age determinations. According to most actual schemes (Mitta et al. 2012) the whole Lower Callovian comprises a single belemnite zone, but the same interval contains 4 ammonite zones, the upper two of which are subdivided into 5 subzones, and more than 22 successive biohorizons (Gulyaev et al. 2002; Gulyaev & Ippolitov 2013; etc.). Unfortunately, published data on belemnites does not allow to review the stratigraphy, as most figured and determined specimens have indistinct positions in the sections, being tied in the best cases to ammonite zones.

During the 2011-2013 field seasons, the authors collected a huge number of belemnite rostra from many continuous sections in European Russia and Ukraine, together forming a full sequence of the Lower Callovian, well-characterized by ammonites. This material was studied biostratigraphically applying the concept of biohorizons (see Callomon 1985; Page 1995; Gulyaev 2002; Rogov et al. 2012; etc.). The remarkable point of this concept is that «ideally», phyletic biohorizons should represent successive elements of a single lineage.

The revision of the belemnite material has shown that the concept of phyletic biohorizons is fully applicable to the group. The Lower Callovian can be subdivided by belemnites into three parallel series of successive biohorizons, based on three different phyletic lines inside the boreal family *Cylindroteuthidae*, each covering a certain interval within the Lower Callovian and partly overlapping, so that in certain intervals, only one line can be used, while in other intervals two or even three. The number of successive units for the whole Lower Callovian is up to 14 biohorizons, which, in turn, can be grouped into 4 larger units (=zones), characterized by the well-recognizable appearance of the whole complex. Moreover, it is possible to select biohorizons based on immigration events, which are usually well-correlated with similar events in ammonites.

Thus, the concept of biohorizons looks to be fully applicable to belemnites, allowing to elaborate biostratigraphic scales, comparable in resolution with ammonite infrazonal scales.

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## Belemnite “Doppellinien”: myths and realities

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The term “Doppellinien” was first introduced by Stolley in 1911 for the designation of small lateral grooves on belemnite rostra, having the appearance of fine and straight double grooves. He paid special attention to peculiar appearance of lateral lines in *Oxyteuthis*, and this was the justification for the consequent elevation of the separate family Oxyteuthidae.

Now, more than a century later, Doppellinien remain poorly studied, and their biological nature is uncertain. Small lateral grooves, both double (=“Doppellinien”) and single, can be observed relatively rare, only in case of good preservation, and tracing them often requires a large set of specimens. As a result, almost no attention is paid to them in the classification of belemnites, unlike “normal” well-developed apical and alveolar grooves. The only attempts to summarize data about lateral lines in belemnites were made by V.A. Gustomesov (1962, 1973, 1978). He concluded that the appearance of lateral lines is characteristic for suborders, allowing to recognize the attribution in some problematic cases. Particularly, Doppellinien were considered to be characteristic of the suborder Belemnopseina only. However, lateral grooves did not strike roots in the common practice of taxonomic work, neither on species-level nor on genus-level. But in the case of the family Oxyteuthidae, the appearance of lateral lines (doppellinien in the posterior part, branching into two single grooves in the anterior part) still remains the main character defining the family. Moreover, this character makes a point for debates about phylogenetic affinities, as the morphology of lateral lines and the general morphology indicate mutually exclusive affinities.

New data were obtained from rostra of several families (Rhabdobelidae, Acrocoelitidae, Cylandroteuthidae, Mesohibolitidae, Oxyteuthidae); in all of them, typical Doppellinien were found. Thus, we can state a wide distribution of Doppellinien in belemnites even outside the suborder Belemnopseina. In all these cases within the suborder Belemnitina, the position of the Doppellinien is different from that known from Belemnopseina: they occupy the lower half of the lateral side of the rostrum, while the upper half is occupied by a single groove.

A key to the understanding of interrelations of different positions of the Doppellinien in both suborders is provided by the poorly known species “*Cylindroteuthis*” *kowalevi*, unusual among related Cylandroteuthidae in its hastate form. This species shows a combination of belemnitin- and belemnopsein-type Doppellinien, providing the idea that the formation of belemnopsein-type Doppellinien is mainly connected with the hastate rostrum form. This is well-supported by the configuration of lateral lines in non-hastate forms of Belemnopseina, which, vice versa, demonstrate lateral lines typical for Belemnitina. Thus, lateral lines in both suborders are derivatives of the same prototype, and their common modifications seem to be correlated with certain rostrum shapes.

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## Speculations on the ethology of some (turricone, colchicone) heteromorph ammonites

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The difficulties in assessing the swimming abilities of ammonites, their shell orientation, stability, and buoyancy attract the attention of many specialists. Many articles address these topics, and the respective authors have employed morphological analyses, included data from mock-ups, carried out computer calculations, etc. Nevertheless, there are still many unsolved questions concerning the reconstruction of lifestyle of heteromorph ammonites. We know only little about the animal's soft body shape, size, its possible maneuvering abilities within and outside of the body chamber, as well as about the animal's ability to change shell orientation, swimming direction and velocity by the regulation of phragmocone chambers liquid, the hyponome jet, and the tentacles (still very poor data about their size, number, etc.).

Some structural features in a few heteromorph ammonites may indicate the existence of semi-internal or internal shells (Doguzhaeva & Mutvei 1989, 1993). Also, movements of the animal's soft body within the body chamber might have significantly altered the distribution of mass and hence shell orientation (Monks & Young 1998). Additionally, representatives of *Ancyloceras* were presumably able to push a considerable part of the soft body out of the living chamber (Doguzhaeva & Mikhailova 1991). Such considerations should be taken into account.

The range of variability of parameters affecting the animal's buoyancy (even within the group of heteromorphs) is in many cases high. Hence, there is no doubt that data from functional morphology (ontogenetic alternation in coiling, cross section, sculpture, muscular scars, orientation of the aperture and siphuncle, etc.) combined with facies and taphonomical analyses can yield new insights into poorly understood aspects of the mode of life of various heteromorphs.

Ecological differentiation of ammonites took place directly after the planktonic ammonitella stage. Some have adapted to benthic via nektobenthic to nektonic or nektoplanktonic modes of life. The representatives of most groups of heteromorphs are characterized by rapid, repeated ontogenetic changes of shell morphology and accordingly, such hereditary changes had to be related to the changes in mode of life of the animal during ontogeny (Kakabadze 1981, 1988).

Heteromorph groups (turricone, colchicone) are characterized by helicoidal uncoiling directly after the ammonitella stage. The turricones have helically-coiled contiguous whorls up to the end of the gerontic stage. I believe that most representatives of turricones (as well as colchicones in the helicoidal ontogenetic stage) inhabited the sea with apex-upward shell orientation. Because of their ability of buoyancy regulation and actively functioning hyponome and arms, many of them were able to float more or less actively from one place to another one. Based on the variability in ornamentation (smooth, fine or coarse ribbing, spines, etc.) and differences in coiling, I suppose that turricones were adapted to differently habitats (mobile benthos, nektobenthos, etc.).

After the helicoidal stage, the colchicones and imericones are characterized by a planispiral stage with loosely coiled or contiguous whorls (e.g. *Colchidites*, *Kutatissites*, *Imerites*, etc.). The transition from helical to planispiral coiling is rather rapid and it is remarkable that together with coiling, the sculpture, the suture line, and the whorl cross section also became bilaterally-symmetric from the starting portion of the first planispiral whorl. Thus, the shell became similar to that of some monomorphic ammonites. Taking all these data into account, I am convinced that the transformations from helicoidal to planispiral indicate a transition to a more active, free

swimming lifestyle. Among the representatives of colchicones and imericones, there is a great variability in whorl cross section, sculpture, as well as in whorls number and coiling peculiarities, indicating on their varying maneuverability, swimming velocity, etc.

At the mature uncoiled stage, the representatives of colchicones have a shell similar to ancylocones with shaft and hook, where the living chamber occupies the whole hook and a considerable part of the shaft (on the whole, the living chamber length is variable in heteromorphs). Based on functional morphology and facies distribution, it can be assumed that they could migrate up and down, presumably not far from the sea-bottom in a near-vertical position of the shaft (with the aperture facing upward). Such shell orientation seems to be suitable for the animal's need for passively floating periods to gain neutral buoyancy. The same orientation allowed the animal to rest with the bottom of the shell's hook on the substrate, or to float passively close to it (Klinger 1981). Presumably, colchicones and ancylocones were able to "sit" on the substrate or to "hover" close to it with such a shell orientation. By contrast, such a position seems to hamper direct contact with the substrate and thus feeding from the substrate. I think that many adult colchicones and ancylocones were able to adjust their buoyancy and shell orientation to better reach the substrate (Kakabadze 1981; Kakabadze & Sharikadze 1993; Monks & Young 1998). The animal was not able to readjust buoyancy and thus shell orientation only by means of shifting of the soft body within the living chamber, by leaning out of the aperture, by cameral fluid mechanisms, or hyponome and tentacle action. On the contrary, I think that the animals altered their orientation by the simultaneous combination of all these mechanisms.

It is not the goal of the present paper to reconstruct the lifestyle of each turricone or colchicone species. Among, e.g., colchicones, there are species with shells with a fine (smooth whorls, fine ribs) and with a strong (coarse ribs with spines, etc.) ornamentation. Moreover, there can be differences also in whorl cross section, whorl coiling, peculiarities of muscular scars, etc. Probably, these animals had more or less different modes of life. Such studies require a combined analytical approach (changes in functional morphology during ontogeny, litho- and biofacial dependence, etc.) for each taxon.

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## **The Endocerida – are the Lower Palaeozoic ‘gas pipes’ viable or not?**

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Recognition that the former Order Endocerida was polyphyletic and required division – into the Order Bisonocerida (Evans & King, 2012) and remnant Endocerida – invariably leads to some important questions: what remains of the historic Order Endocerida and ‘allied families’, do the known genera exhibit a morphological distinctiveness, do they demonstrate a discernable phylogeny, do they still constitute a sensible and viable ‘group’ of Lower Palaeozoic cephalopods?

This presentation reviews current thinking and ongoing research on the Endocerida. Taxonomic problems undoubtedly persist - many genera are poorly defined and are only known from incomplete conchs or isolated endosiphuncles – and preservation often leaves much to be desired. However, a balanced approach that blends what is known with (reasonable) certainty about the endocerids with revision of key long-established taxonomic names and study of new Baltoscandian taxa, provides a ‘light at the end of the trench for the gas pipes’ (!). The classification scheme proposed here recognises a significantly revised Order Endocerida as a distinct, diverse and viable group of Ordovician and early Silurian cephalopods, which still includes some of the largest Palaeozoic invertebrates known.

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Evans, D. & King, A. 2012: Resolving polyphyly within the Endocerida: The Bisonocerida nov., a new order of early Palaeozoic nautiloids. *Geobios* 45: 19-28. (Supplementary data in the online version at doi: 10.1016/j.geobios.2011.11.015. Appendix A. Systematics of the Order Bisonocerida nov., and summary of the revised Order Endocerida Teichert, 1933 (emended herein). 9pp + Table S1).

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## Early ontogeny of well preserved ammonoids from the Middle Devonian Cherry Valley Limestone (NY, USA)

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The Middle Devonian Cherry Valley Limestone of New York State, U. S. A. contains a concentration of fossil cephalopods, believed to be a mass mortality event. Rapid influxes of sediment led to rapid burial. One of the most abundant fossils is *Agoniatites vanuxemi* (Hall, 1879). Specimens are preserved in beds as half shells, with the top portions eroded away, but the inner whorls preserved. In a previous study, the inner whorls of several specimens were removed and the internal morphology of the ammonitella was studied.

In this study, additional specimens are analyzed to both confirm the data from the previous study and to better understand the conditions required for such preservation. The specimens used in this study were removed from the bedrock itself.

The outermost whorls are mud filled. The inner whorls are filled with calcite. In some cases, the calcite does not fill the chambers and 0.5 - 1 whorls remain hollow and crystal lined. One specimen is completely mud filled. Pyrite is present in the mud as small bits and replacement of small faunal debris. It is also present in the calcite. Dolomite and quartz are present. The calcite in both the chambers and shell replacement forms large crystals. In spite of this, the surface details of the shell are remarkably well preserved. On a segment of one specimen, approximately 0.75 whorls long, the lirae go through numerous changes in size and spacing, suggesting growth spurts and life habit changes in the juvenile.

In median cross section, when etched with 5% HCl, the calcium phosphate-preserved structures are easily observed. These include chamber and septal linings. These linings are thin and seem to disappear by the second post embryonic whorl, making septa and shell walls nearly impossible to see. Some chambers are filled with calcium phosphate. Some septal siphuncular membranes are present. The dorsal and ventral shell walls of the specimen cannot be distinguished, suggesting that the outer surface of the shell had no periostracal linings.

The embryonic shells are not well preserved in most specimens. Where the initial chamber is filled with pyrite or mud, the internal structures are obliterated. The septa are preserved and shell thicknesses can be estimated. The best preservation is in those specimens where the embryonic shell is calcite-filled. In one specimen, the ammonitella is split in two by a calcite vein, but both halves of the ammonitella are preserved. Continued study of these specimens gives us insight into the embryonic development, early growth and life habits of these ammonoids.

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## Latitudinal shifts of Palaeozoic marine invertebrate gigantism and global change

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Since the Cambrian Explosion, giant marine invertebrate species have evolved iteratively in several groups. In the Palaeozoic, marine invertebrate gigantism was heterogeneously distributed through time and space; changes in maximum sizes show no clear relationship with atmospheric or oceanic oxygen and other environmental factors. Although gigantism has found an explanation for Carboniferous land invertebrates in the atmospheric oxygen peak, marine gigantism has not been studied empirically and explained comprehensively. By quantifying the spatiotemporal distribution of the largest representatives of some major marine invertebrate clades, we assessed links between ecological parameters and giant growth. These occurrence data suggest that temperature and latitude in combination with oxygen played important roles. Marine invertebrate gigantism developed in certain phases and regions with a greater number of extremely large species and their occurrences shifted independently from middle towards low latitudes during the Palaeozoic in all examined groups. This trend roughly coincides with the Late Devonian to Carboniferous cooling and regression as well as with a rise in atmospheric oxygen. This shows how global environmental changes can control the geographical distribution of organisms and that the optimal ecological requirements might differ depending on body size: extremely large organisms might react less flexibly to ecological changes.

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## Belemnitids as pelagic meso-predators evidenced by radula and fin preservation

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*Acanthoteuthis* is one of the more abundant coleoid genera from the Late Jurassic Fossilagerstätten of southern Germany. It is classically assigned to the Belemnitida and is often preserved with the shell, commonly showing both phragmocone and the proostracum. As far as other body parts are concerned, the arm crown with the strong hooks has been discovered repeatedly.

Because of similarities in the morphology of phragmocone, proostracum, and the hooks, the affinity to belemnites has been suggested. Some authors are convinced that the fossils of *Acanthoteuthis* represent members of the genus *Hibolithes*, which has somehow lost its rostrum. In the new specimen, this appears rather unlikely, because at the apical end, semicircular imprints are visible. These imprints are here interpreted as remains of the fins, which is corroborated by fin-preservation in an additional unpublished specimen. A taphonomic loss of an extensive rostrum when the fins are preserved appears unlikely.

In addition to the fins, the buccal mass with the radula is preserved. As seen under the light microscope, the radula resembles those of Recent coleoids, except for an accessory row of small multicuspitate teeth.

The fins, which indicate a nektonic habit, and the squid-like buccal mass suggest a carnivorous diet and a predatory habit. Therefore, *Acanthoteuthis*, and probably also the closely related belemnites with thick calcitic rostra, have to be considered as efficient nektonic predators, which might have preyed upon small fish and other moderately large nekton, nektoplankton, and plankton.

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## The taxonomic geometry of the Palaeozoic ammonoids

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Palaeozoic ammonoids have been classified in the Linnaean system for two centuries. In 1812, it was James Sowerby, who described '*Ammonites Listeri*' as the first ammonoid according to the binominal principles of classification. Today, more than 4,500 species, 860 genera, and 150 families of Palaeozoic ammonoids are catalogued in the AMMON database.

Until 1990, a nearly continuous number of newly described species can be seen; between 1850 and 1990, the number of Palaeozoic ammonoid species doubled every 35 years (1850: 200 species, 1885: 500, 1920: 1,000, 1955: 2,000, 1990: 4,000). The climax was reached in the 1970s and 1980s with about 700 new species per decade; thereafter, a decline to 320 species can be observed in the 1990s. The comparison of the four major 'scientific cultures' in Palaeozoic ammonoid research allows for a more detailed picture: In North America, the climax was passed already in 1940, in the Russian culture around 1980 and in the Chinese 1990. Only the European culture (which includes the research of the North African occurrences) does not show a significant decline.

The history of the description of genera is less continuous. James Parkinson described, in 1822, the first ammonoid genus *Ammonellipsites*, and thereafter, only four additional genera were added until 1875. The ratio of species per genus was then raised up to 45 in the 1880s. With the studies by Mojsisovics, Hyatt, and Gemmellaro in the 1880s, who between them introduced 45 new genera, the ratio dropped down to eight. Since then, the ratio has reduced to a very stable value of about five to six. Today, an average family of Palaeozoic ammonoids contains five genera and 27 species, an average genus represents five to six species, meaning that the *Hyatt Effect* is still working.

The ratio of species and genera is about five in all Palaeozoic ammonoid families and ranges between 3.92 (*Agoniatitida*) and 6.00 (*Prolecanitida*), the data sets of Devonian, Carboniferous and Permian ammonoids display similar values. If the 'scientific cultures' are treated separately, it can be seen that the ratio between species and genera is between 4.74 and 5.22 in the European, American, and Russian cultures but 8.97 in the Chinese culture. This difference cannot be explained by different methods; most probably, it has its reason in the later beginning of Palaeozoic ammonoid research in China at a time, when most genera have already been described from other regions.

The taxa with the smallest number of subtaxa are the most frequent in the system and that taxon–frequency distributions are nearly hypergeometric. The highest number of species in a genus is known from the long-ranging genus *Glaphyrites* with more than 70 species. On the other hand, more than 250 genera are monospecific.

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## **The palaeogeography of the initial cephalopod diversification during the Cambro-Ordovician**

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Cephalopods have their earliest occurrence in Late Cambrian shallow-water carbonates on the North China Platform and rapidly dispersed across the globe within the latest Cambrian. Latest Cambrian and initial Ordovician cephalopod occurrences are restricted to the palaeotropical realm. During the early Ordovician, cephalopods entered the open seas and also appeared for the first time in high palaeolatitudes.

The Ordovician records a mosaic-like pattern of appearance and disappearance of various higher groups, each with a specific palaeogeographical signature. Beyond this complex patterns of faunal change, one universal theme for the Ordovician is very apparent: the uninterrupted expansion of cephalopod diversity, disparity, abundance, and body size. Hence, every faunal change, and thus origination, disappearance or immigration of one group led to even higher total diversities, disparities and abundances.

The respective faunal changes often indicate a clear selectivity towards groups with more dynamic and more energy-efficient buoyancy regulations. A potential side effect of this evolutionary trend was an increased rate of geographical dispersal, because cephalopods were increasingly able to inhabit and migrate within the entire water column. This effect could contribute to the overall Ordovician trend of an increasing number of widespread taxa and the trend towards a decrease in beta-diversity amongst cephalopods. The potential mechanisms, which led to this unique diversification are still unknown. An increased ecosystem stability and food availability during the Ordovician certainly were major factors.

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## **Advances in paleobiological reconstructions in cephalopods**

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Soft tissue preservation is considered rare in fossil cephalopods. The increasing use of tomographic techniques (CT scan or synchrotron propagation phase contrast microtomography) has allowed for three-dimensional reconstructions and high-resolution data on remains still preserved in the matrix, unravelling the morphology of these delicate structures. Good examples are the buccal mass elements in ammonoids, previously difficult to study, such as the radula or the inner lamellae present on the inner part of the jaws that are important for muscle insertion. The high resolution of these data is essential for investigating new questions on the radular structures such as the morphological variability within closely related taxa or wearing patterns due to feeding habits. Other types of structures, such as hooks in Scaphitidae, are also discovered and studied in order to understand their morphology, distribution and function.

Data obtained with synchrotron propagation phase contrast tomography (ESRF, proposal ES 36) were also carried on the coleoid cephalopods from La-Voulte-sur-Rhône. The exceptional preservation of soft tissues within the matrix is revealed and allows one to obtain details on delicate structures such as cirri, suckers, digestive organs and gills.

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## Untangling the Striae: Ammonoid Biostratigraphy of the Carboniferous Shannon Basin, Western Ireland

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The basin fill of the Carboniferous Shannon Basin, Western Ireland, during the late Mississippian and Pennsylvanian consisted of deep-water shales succeeded by basin floor turbidite sandstones (Ross Sandstone Formation), and slope and delta deposits.

Ammonoids are present throughout the succession, but are concentrated in thin dark shales, which are thought to represent intervals of sediment starvation and are referred to as condensed sections. Ammonoid distribution is controlled by sedimentation rate, with greater numbers per unit volume of rock at times of lower sedimentation rates and fewer at times of higher sediment input.

Ongoing biostratigraphic work in the Shannon Basin suggests that ammonoid assemblages in the condensed sections are more diverse than previously thought and that it is not possible to pin point discrete, widespread ammonoid bands, each with a diagnostic species. Rather, the number of ammonoid bands, their fossil assemblages and their sedimentology are far more complex and variable than previously thought.

Ornament is the main tool in specific identification of Carboniferous ammonoids. However, since the ornament varies with ontogenetic growth of the organism, any robust taxonomic identification must rely on detailed knowledge of these changes. The systematic study of ontogeny can only be achieved by describing 3D ammonoid shells. This presents a significant challenge given that most ammonoids in the Ross Sandstone Formation are preserved as flattened, partial 2D moulds.

Ammonoids in the Ross Sandstone Formation span part of the Alportian and Kinder-scoutian Stages ( $H_{2a}$  to  $R_{1a}$  biozones) and in order to unravel the biostratigraphy within the  $R_1$  zone it is necessary to have a good understanding of the taxonomy of the *Reticuloceras/Phillipsoceras* group, which has not yet been fully resolved. An approach involving the ontogenetic study of all available 3D material has been employed to tackle this problem.

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## Ammonites on the brink of extinction

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We examine the “state” of ammonites on the brink of extinction at the end of the Cretaceous by compiling data on the stratigraphic and geographic distribution of ammonites just prior to, at, and just above the K/Pg boundary. According to our compilation, ammonites are abundant and diverse in the last 0.5 million years of the Maastrichtian. They are distributed across all four Cretaceous suborders (Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina) comprising six superfamilies (Phylloceratoidea, Tetragonitoidea, Desmoceratoidea, Acanthoceratoidea, Turrilitoidea, and Scaphitoidea) and 31 (sub)genera. The distribution of ammonites varies according to the environmental setting. Shallow-water environments (<100 m deep), represented by deposits in northern and central Europe and North America, favor sphenodiscids, diplomoceratids, and fast-evolving scaphitids and baculitids. Deeper-water settings (>100 m deep), represented by deposits in the Bay of Biscay, the Tunisian Trough, Antarctica, and Sakhalin, favor desmoceratoids and slow-evolving phylloceratids and lytoceratids, with occasional diplomoceratids and baculitids. Baculitids are probably the most abundant ammonites at the end of the Cretaceous in terms of number of individuals. Their wide distribution with respect to environmental settings suggests that they were facies independent. It is likely that the disappearance of ammonites at the end of the Maastrichtian was due to the asteroid impact. Because ammonites probably followed a planktic mode of life immediately after hatching, their extinction has been linked to a transient episode of surface water acidification. However, recent data from the Atlantic Coastal Plain, the Netherlands, and Denmark indicate that some ammonites (e.g., scaphitids and baculitids) may have survived for as much as several hundred thousand years after the impact. This pattern of extinction and short-term survival may be related to the geographic distribution of ammonite genera.

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## Reevaluation of the upper Maastrichtian ammonite biostratigraphy based on *Discoscaphites* occurrences along the Gulf Coastal Plain.

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An accurate stratigraphic reconstruction of upper Maastrichtian strata across the Gulf Coastal Plain (GCP) is essential for understanding the nature of events and biotic changes preceding the K/Pg mass extinction event. In contrast to well-resolved upper Maastrichtian microfossil biostratigraphy in the GCP, biostratigraphy of macrofossils has received little attention. The established macrofossil biostratigraphic indicators utilized within the *Haustator bilira* Assemblage Zone and the *Exogyra costata* Zone (Sohl and Koch 1986) are long ranging. This factor limits their utility for correlation of upper Maastrichtian strata. Cobban and Kennedy (1995) attempted a more refined ammonite biozonation, proposing the following biozones for the late Maastrichtian: the *Discoscaphites iris* Zone overlain by the *D. conradi* Zone. However, this succession contradicts the zonation established in the Atlantic Coastal Plain (ACP) by Landman et al. (2004). The current study evaluates the proposed GCP ammonite biozones using high-resolution biostratigraphic sampling of *D. minardi* (Landman et al., 2004), *D. iris* (Conrad, 1858), *D. conradi* (Morton, 1834), *Eubaculites carinatus* (Morton, 1834), *E. latecarinatus* (Brunnschweiler, 1966), *E. labyrinthicus* (Morton, 1834), *Baculites lomaensis* (Anderson, 1958) and *Baculites sp. C* (Cobban and Kennedy, 1995) from several sites in Mississippi, Alabama, and Missouri. Initial results based on stratigraphic superposition, abundance and associated ammonite faunal assemblages suggest that the ACP zonation is also present in the GCP and consists of three zones, from bottom to top: *D. conradi* Zone, *D. minardi* Zone and *D. iris* Zone. Further, results suggest that the *D. iris* Zone may be subdivided based on the relative abundance of *Eubaculites* compared to *Baculites sp. C*. This data plays an essential role in updating the correlation of the uppermost Maastrichtian strata across the GCP and linking it to the ACP region, which will in turn facilitate the reconstruction of depositional, lithological and paleoenvironmental changes over this broad area through time.

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## New insights into ammonite palaeobiology from tomographic data

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Computed tomography (CT) is a powerful and nigh universal tool in modern palaeontology, applied to such diverse fields as phylogenetics and biomechanics. Despite this, CT has had a limited application to ammonoids and other fossil cephalopods. Here, we present a new method that utilizes modern advances in high resolution CT technology such as Micro-CT, Nano-CT, and synchrotron microtomography (SR $\mu$ CT) to address standing questions in ammonoid palaeobiology. One such fundamental question concerning ammonoids is whether they possessed the capacity to inhabit the water column or were relegated to a benthic life-style. The answer to this question lies in the function of the chambered ammonoid shell and its efficiency as a buoyancy apparatus. Using exceptionally preserved hollow ammonite fossils and the shells of modern cephalopods, we demonstrate the high precision of CT based techniques to quantify the buoyant properties of the shell. Analysis of the shell of *Nautilus pompilius* demonstrates the importance of resolution and the sensitivity of CT volumetrics. SR $\mu$ CT analysis of the ammonitella of the Jurassic ammonite *Cadoceras* sp. demonstrates the high precision of this CT method. These tomographic techniques can quantify ammonite buoyancy and hydrostatics without oversimplifying the ammonite shell architecture as has been done in prior studies through the application of mathematical models. The potential biases in the calculations of stability and centres of mass and gravity are demonstrated for *Cadoceras* with a variable body length. The swimming mechanics of *Cadoceras* and similarities to the smallest of modern cephalopods, squid paralarvae, are explored. Computed tomography provides an unparalleled, high precision, non-destructive technique to explore internal and external shell morphology. The palaeobiological implications are clear; however, the understanding of ammonoid life-habits is also important for their utilization as archives for palaeoenvironmental data.

## Stable isotope evidence of habitat change during early ontogeny in Cretaceous *Hoploscaphites*

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Ammonite eggs and hatchlings are thought to have been planktonic. Juveniles are small (~600  $\mu\text{m}$ ), spherical and modern coleoids with eggs under 1000  $\mu\text{m}$  diameter have planktonic hatchlings. Ammonite shell aragonite is precipitated in oxygen isotope equilibrium with seawater. Therefore, change in habitat is reflected in the oxygen isotope ratio ( $\delta^{18}\text{O}$ ) of their shells. Variation in the carbon isotope ratio ( $\delta^{13}\text{C}$ ) can indicate a change in diet and/or the  $\delta^{13}\text{C}$  of dissolved inorganic carbon.

Sample sizes necessary for bulk isotope analyses of the ammonitella and neanoconch are impossible to extract using mechanical techniques because the shell wall is exceptionally thin (~10  $\mu\text{m}$ ). Secondary ion mass spectrometry (SIMS) allows for *in situ* measurement of isotope ratios in small domains (~10  $\mu\text{m}$ ,  $\pm 0.3\%$  2SD  $\delta^{18}\text{O}$ ,  $\pm 0.7\%$  2SD  $\delta^{13}\text{C}$ ) and thus provides a method for investigating ammonite habitat change during early ontogeny.

Analysis of five *Hoploscaphites* sp. (largest diameter ~2400  $\mu\text{m}$ ) was conducted to test for variation in isotope ratios indicating habitat change during early ontogeny. Samples are from one concretion that was collected at the contact between the Trail City and Timber Lake members of the Fox Hills Formation (Maastrichtian, South Dakota). This unit was deposited during regression of the Western Interior Seaway. All individuals preserve nacreous aragonite microstructure, suggesting that  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  are primary. To provide environmental context, diagenetic calcite and three coeval calcite bivalve fragments from within the same concretion were also analyzed by SIMS.

All five ammonites show  $\delta^{18}\text{O}$  changes with ontogeny (~3‰ range). The three ammonites analyzed for  $\delta^{13}\text{C}$  exhibit changes with ontogeny (~5‰ range). There is a difference between ammonitella and neanoconch  $\delta^{18}\text{O}$  (~1-2‰) and  $\delta^{13}\text{C}$  (~5‰). All five individuals have an additional  $\delta^{18}\text{O}$  transition at ~400° post-hatching rotational growth (~1200  $\mu\text{m}$  diameter) indicating that ammonites also changed habitat after hatching. The range of  $\delta^{18}\text{O}$  within the ammonites suggests either the seaway was stratified, possibly seasonally or the ammonites used habitats with different  $\delta^{18}\text{O}$  during early ontogeny. Change in  $\delta^{13}\text{C}$  suggests a yolk influence before hatching, similar to that observed in modern *Nautilus*. Thermohaline stratification is suggested by comparing ammonoids to bivalve shells (average difference  $\delta^{18}\text{O}$  ~2‰) and diagenetic calcite (average difference  $\delta^{18}\text{O}$  ~3.5‰). These differences demonstrate that the ammonite shells retain their original isotopic composition.

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## Ammonoid habitats and life history

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Our knowledge about the ammonoid/ habitat relation is reviewed and in part newly interpreted. The autecology of ammonoids, such as ontogeny and habitat, based on morphological and geochemical analyses in association with results from modern relatives, forms the foundation for subsequent interpretations. Synecological interactions (predator prey, infestation) are discussed with reference to sedimentary facies and the corresponding biofacies. Arguments for a possible mode of life and habitat are given based on the modern data on the food/ prey habits and predation habitats of ammonoids.

The state of the art in scientific investigations on ammonoid life and habitat is summarized, reviewed and in part reinterpreted. Traditional assumptions based on facies analyses are strengthened or contradicted by more recent methods such as morphospace and stable isotope analyses. Hypothetical assumptions, speculative methods and calculations are tested by correlating them with new geophysical data. Hard facts and evidence are predominantly missing in earlier data sets on ammonoid life and habitat: hypotheses and assumptions dominate over well-supported results.

The fairly new approach of ontogenetic studies using stable isotopes is introduced in detail. The importance of accurate measurements is predicted. New methods and the potential of stable isotope analyses along with the implications for ammonoid ontogeny and habitat are presented. Recent analyses on stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ) revealed ontogenetic stages that allow us to test older models. Distinct migration groups with different ontogenetic strategies were detected. The *wcw*-type (*warm-cool-warm* type) of *Cadoceras* resembles strategies in *Nautilus* and *Sepia*, which migrate from shallow into deeper environments and back in ontogeny; the *cw*-type (*cool-warm* type) of *Hypacanthoplites* resembles the first two migration phases of *Spirula* (*cwc*-type), which migrates from deeper into shallower and back into deeper habitats.

Highly variable migration histories in ontogeny are assumed for the huge group of morphologically diverse ammonoids. Most forms probably lived in shallow water in epipelagic seas. Ammonoids inhabited almost every ecological niche in the world oceans, preferring the neritic zones and preying mostly on plankton. Fossil evidence supports a life in the water column (pelagic mode of life), spending their life close to the seabottom (demersal), drifting as plankton or actively swimming as nekton. The distinct life strategy is linked to the ontogenetic stage, as a planktonic mode of life is suggested for ammonoid hatchlings. An active, swimming life strategy or at least considerable transport by oceanic currents is indicated by biogeographic data and isotope studies. At least a nektobenthic interaction is suggested by the data.

Evidence from morphological shell parameters alone can only give ideas on the ecological capabilities and the interpretation of highly diverse morphologies in ammonoids is insufficient, resulting in hypothetical diagrams. Future work on stable oxygen and carbon isotopes will promote our understanding and interpretation of ammonoid habitats, in combination with additional investigations on shell parameters, facies and biogeography.

## Upper Paleozoic coleoids (Cephalopoda) from North America: Observations on their paleoecology, taphonomy and phylogeny

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Sedimentary units that have produced Upper Paleozoic coleoids in North America provide insight into their preferred living conditions. Eighteen Upper Paleozoic coleoid genera are known from North America; 14 have been studied as to their paleoenvironmental occurrence.

Lower Carboniferous: Four rostrum-bearing coleoid genera (*Paleoconus*, *Hematites*, *Bactritimimus*, *Gordoniconus*) and two non-rostrum bearing bactritoid-like coleoids (“*Bactrites*” *quadrilineatus* and “*Ctenobactrites*” *lesliensis*) are known. All are from strongly dysaerobic to anoxic sedimentary environments in relatively deep water.

Upper Carboniferous: Sedimentary successions that formed during cyclic transgression-regression sequences (cyclothems) have yielded coleoids. In the Desmoinesian Stage, three genera (*Jeletzkyites*, *Saundersites*, *Pohlsepia*) are known from transgressive near-shore, shallow water prodeltaic shales. *Donovaniconus* occurs in relatively deep water sediments deposited during the early part of a cyclothem regression. In the Missourian Stage, “*Flowerites*” and three undescribed taxa are preserved in phosphatic black shales near the maximum deep water extent of the cyclothem. From the Virgilian Stage, two genera are known (*Shimanskya*, *Mutveiconites*); both come from oxygenated gray shales that were sedimented in the middle of a regression.

Middle Permian: Two genera are known; one (*Stenoconites*) is an Aulacocerida and the other (*Glochynomorpha*) has the earliest documented gladius. Both were deposited in deep-water sediments at an oceanic shelf edge or slope.

The Early Carboniferous coleoid occurrences have two basic morphologies (those with and those without a rostrum). All are from black, poorly oxygenated, black shales deposited in relatively deep water. We suggest that the earliest coleoid ancestors will be recovered from similar but older (Late Devonian/ earliest Carboniferous?) sedimentary paleoenvironments. By the Late Carboniferous time, a radiation of different coleoids had evolved to fill different niches including shallow water near shore delta environments to middle shelf in moderate water depths to offshore relatively deep-water environments.

Based on these occurrences, we suspect that many of the bactritoids recovered in the Late Paleozoic and perhaps some in the Middle Paleozoic are in fact coleoids similar to those bactritoid-like coleoids from the Early Carboniferous. Discovering new features that can separate the coleoids from the bactritoids needs to be accomplished to separate these two cephalopod groups.

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## **Intraspecific variability among *Ophiceratidae* Arthaber, 1911 (Ammonoidea, Early Triassic) from NE Greenland: implications for taxonomy and diversity in the immediate aftermath of the Permian-Triassic boundary mass extinction**

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A well preserved ammonoid fauna of Griesbachian age has long been known from the Wordie Creek Formation in the Kap Stosch area, NE Greenland. Although it was first reported in the beginning of the 20th century, ammonoid taxonomy and resulting biozonation can be significantly improved by collecting large samples *in situ*. Taxonomic over-splitting resulting from the traditional typological approach imposed by specimen-poor samples led to an overabundance of species and genera among which synonyms are frequent. The same typological approach and associated biozonation was still in use recently (e.g. Bjerager et al., 2006). A direct consequence of this over-splitting taxonomy is that the number of biostratigraphic subdivisions in the classic NE Greenland record can be legitimately questioned. The taxonomy of the Griesbachian ammonoid faunas from NE Greenland is thus in need of a revision that takes intraspecific and ontogenetic variations into account.

*Ophiceratidae* Arthaber, 1911 is the most common and most diversified family during Griesbachian times. *Ophiceras* Griesbach, 1880 is a key component of the NE Greenland biostratigraphic zonation. Being a cosmopolitan genus during the Griesbachian, there is also an additional and traditional bias towards erecting different species for each region.

The study of large samples, amounting to more than five hundred specimens, collected bed-by-bed in Kap Stosch area, coupled with precise biometry of ontogenetic trajectories, brings new insights into the intra-specific variability of *Ophiceras commune*, an iconic species of the Griesbachian. This leads to a clearer definition of the relevant parameters for distinguishing different species within this genus and leads to a decreasing number of *Ophiceras* species from 16 to 11 in NE Greenland. Such a reduction of species has major implications for both biochronology and diversity counts. On the one hand, it may significantly impact the classic ammonoid zonation from NE Greenland established by Trümpy (1969). Indeed, in the typological use of *Ophiceras commune* this species is restricted to the *O. commune* Zone, but the revised definition of the species implies a longer range for the species, encompassing the *O. commune* and *W. decipiens* zones. On the other hand, as over-splitting also likely applies to other Griesbachian genera, a less abrupt initiation of the explosive Early Triassic diversification of ammonoids will probably emerge.

## Soft-tissue preservation in Jurassic ammonites from Central Russia

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Several unique findings of Jurassic ammonites from Central Russia contain fossilized soft tissue remnants. There are well-preserved fragments of the posterior part of the mantle, presumably gill fragments and siphuncle blood vessels in Callovian and Volgian ammonites. A fragment of the posterior part of the mantle, imprints of the tissues of the annular elevation and presumably gill fragments were found on the ventral surface of the internal mould of the Lower Callovian ammonite *Cadoceras stupachenkoi* from Unzha river. The mantle fragment is a relatively small (6 x 2 mm) dark film (probably phosphatized) with clearly visible muscle fibers. Probably, it is the first finding of an ammonite mantle which is visible to the naked eye. Muscle fibers extend from the front edge of the annular elevation (mantle myoadhesive band) and point towards the midline of the body chamber. This fragment is probably a part of the longitudinal mantle musculature. Similar well visible longitudinal mantle muscles, seen as fine striations, were observed in the *Nautilus* soft body (Mutvei et al. 1993). As in adult *Nautilus*, longitudinal mantle musculature of the adult ammonite macroconch is sufficiently thin, but a difference can be seen: in *Nautilus* mantle, the muscle fibers are directed towards the aperture while in the ammonite, they are directed to the midline of the body chamber (however, it also can be explained by postmortem shifting of the soft tissues). Behind this mantle fragment, transverse soft-tissue folds (palliovisceral ligament attachment areas) are visible. Slightly ahead of the mantle myoadhesive band, small soft-tissue fragments are found, perhaps remnants of the gills. In several shells of Upper Volgian ammonites *Kachpurites fulgens* the fossilized blood vessels of the siphuncle tube were found. Until now, ammonoid siphuncle blood vessels have been described only twice: in the Upper Jurassic ammonite *Virgatites virgatus* (Drushchits & Doguzhaeva 1981; Barskov 1996) and in the Lower Permian prolecanitid *Akmilleria electraensis* (Tanabe et al. 2000). However, the structure and even the number of vessels described in each of these cases are very different. The *Kachpurites* blood vessels, although inferior in degree of preservation to *Akmilleria* siphuncle, seem to be similar in structure. The longitudinal ridges, similar to those observed in *Akmilleria*, are visible on the surface of the siphuncle soft-tissues. The internal structure is poorly preserved, but still, the presence of five blood vessels can be assumed: one large central and four small marginal, exactly as described in *Akmilleria* and Recent *Nautilus*.

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## **Evolutionary trends of ammonoids during the Triassic in a Boreal basin (Canada)**

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Evolutionary trends are a long standing and central theme in evolutionary biology and especially in paleontology thanks to the fossil record, which acts as a witness. Ammonoids have already been used successfully to provide insights into the understanding of evolutionary trends (e.g., suture complexity) of which patterns and processes remain debated. This topic is here investigated using the Triassic ammonoid record. Due to their near extinction at the Permian/ Triassic boundary, Triassic ammonoids constitute a quasi-monophyletic clade adequate to study evolutionary trends during a recovery and then in a more stable period.

Evolutionary trends of Triassic ammonoid are investigated by focusing on various traits such as adult shell size, taxonomic diversity and morphological disparity. This study also focuses on the Canadian record, which is a Boreal region characterized by a rich and regular record of ammonoids throughout the entire Triassic, for which an exhaustive morphological database with a revised taxonomic and stratigraphic framework is available. Triassic ammonoids cover a vast range of morphologies with regard to size, geometry (whorl shape and involution), ornamentation, and suture patterns. Their evolutionary trends are statistically evaluated and compared to known environmental changes in order to, e.g., decipher, which processes hold for generating evolutionary trends in ammonoids and in which conditions.

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## Virtually reconstructed growth trajectories and buoyancy of some major Palaeozoic ammonoid clades

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Ammonoids are ideal to study evolutionary changes in ontogeny through time due to their shell growth by accretion. But although they are studied for centuries now, some aspects of their palaeobiology remain poorly understood, especially for Palaeozoic ammonoids. So far, volumetric changes through ontogeny have not been quantified empirically although they bring additional information on growth, but most importantly, they contribute to the understanding of their buoyancy regulation by their phragmocones. For the first time, we documented (1) volumetric growth of septa and phragmocone chambers in detail and (2) ontogenetic changes between major ammonoid clades. Additionally, our data allowed the reconstruction of (3) their hydrostatic properties, their (4) *syn-vivo* shell orientation and their (5) buoyancy.

Standard methods were previously limited to two-dimensional data and volumes have been only estimated. In our materials, CT-scans could not be used due to the low contrast of absorption properties between the recrystallized shells and the carbonatic sediment matrix. Nevertheless, coupling grinding tomography and virtual three-dimensional reconstructions, we are now able to document volumetric changes in detail and ontogenetic changes between major clades throughout their early phylogeny. Although this method is destructive and requires working on abundant material, it provided very satisfying results and yielded data sets of various volumes.

Three representatives of these ammonoid clades have been investigated with this method: the Middle Devonian agoniaticid *Fidelites clariondi*, the Middle Devonian *Diallagites lenticulifer* and the Early Carboniferous goniaticid *Goniatites multiliratus*. Our volumetric data show that growth trajectories are more similar among the most derived *Diallagites* and *Goniatites* compared with the more widely umbilicate *Fidelites*. We also noticed a good correlation between certain 2-D and 3-D parameters. In all three species, both volumes follow exponential trends with deviations in very early ontogeny and near maturity (mature modification in shell growth). According to our models, measurements and calculations, these specimens had aperture orientations of 19°, 64° and 125° during their lives, which roughly corresponds to the values obtained for such shell forms by means of theoretical shell models. Additionally, our calculations also confirmed that the shorter the body chamber, the poorer was the hydrodynamic stability of the animal.

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## The study of the type series of *Nautilus pompilius* Linnaeus, 1758

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Few animals are treasured by zoologists more than *Nautilus*, and *Nautilus pompilius* Linnaeus, 1758, the type species of the genus, in particular. However, the type series of this species has not been studied in great detail. According to the rules of zoological nomenclature, the type series consists of all the specimens included by the author in the new nominal taxon (whether directly or by bibliographic reference), and any evidence, published or unpublished, may be taken into account to determine what specimens are included. The type series of *Nautilus pompilius* includes specimens in the Linnean society in London, the University Museum in Uppsala, and specimens figured by pre-Linnean authors indicated by reference by Linnaeus (1758). One specimen in London and four specimens in Uppsala, which are still extant, are likely to have been known to Linnaeus at the time when he prepared the 10<sup>th</sup> Edition of *Systema Naturae* (1758). However, it is widely believed that Linnaeus designated as lectotype a specimen figured by Rumphius (1705) in his *D'Amboinsche Rariteitkamer*, referred to in the 10<sup>th</sup> Edition. However, this presumed lectotypification is not valid because Linnaeus did not explicitly indicate that any particular specimen was considered to be the type of the species. His subsequent reference to “Fig. D” or “Fig. B” of Rumphius does not constitute a valid lectotype designation for the same reason. Most subsequent type designations of Rumphius’ illustration are not valid because the illustration includes drawings by Maria Sybilla Merian based on several specimens, while the lectotype designation should be based on a single specimen. It is likely that no valid type designation exists for *Nautilus pompilius*, although this is impossible to check because of the vast number of papers on *Nautilus pompilius* randomly using the word “type”. The extant physical specimens are better candidates for lectotypification, although the London specimen and two Uppsala specimens are subadult shells, whereas one Uppsala shell is decorated by etching and broken. One remaining Uppsala specimen is an adult *Nautilus*, but it is not certain whether Linnaeus saw it prior to 1764. It seems that the best approach, given the quality of the material and the lack of clarity as to its type status, is to apply to the ICZN asking to set aside all previous type fixations and designate a neotype, preferably a DNA sequenced specimen with known provenance.

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## Ammonite aptychi: functions and sexual dimorphism

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Nine proposals of aptychus (*sensu stricto*) function have hitherto been described. In historical order: micromorphic males; lower mandible; protection of gonades; protective operculum; ballast for lowering of aperture; flushing of benthic prey; filtering microfauna; pump for jet propulsion; and most recently, active stabilizer against rocking produced by the pulsating jet during forward foraging and backward swimming. Some ammonites bear exceptionally thick, laevaptychus- and lamellaptychus-type aptychi (e.g. aspidoceratids and haploceratoids) that may have improved lowering of the aperture by as part of a mobile cephalic complex, enabling most of these functions.

Aptychi were probably typically multifunctional, most commonly combining feeding (jaw, flushing, filtering) with protection (operculum). Others might have (also) used it for locomotion (ballast, pump, diving and stabilizing plane).

Some ammonites were sexually dimorphic, apparently also in their aptychi. *Lithacoceras* macroconchs (females) have praestriaptychus-type lower mandibles and at least the microconchiate '*Silicisphinctes*' (males) have more slender aptychi that are strongly curved along the growth axis. Some microconchiate haploceratoids show a similar curvature in their lamellaptychus-type lower mandibles, suggesting similar aptychus-type dimorphism also in haploceratoids.

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## The evolution of ammonites versus eustatic variations: case study from the Aptian from the NW Tethyan margin

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The Aptian witnessed an important episode of paleoenvironmental change, which has been linked to a major marine volcanic activity related to the formation of the Ontong-Java large igneous province. This phase culminated in the formation of hemipelagic and pelagic organic-rich sediments, whereas profound changes are also observed in shallow-water settings, with the disappearance of the northern Tethyan platform and its replacement by clastic and condensed sediments. Inside these heterozoan sediments, important sea level fluctuations are registered on the hemipelagic setting by the main sedimentological discontinuities and by ammonite turnover and speciations.

The compilation of the sections from the northern Tethyan platform (SE France, Swiss, Austrian and German Alps) and of the ammonite occurrences allows to recognise at least nine major crises in their evolution (turnovers, radiations, extinctions) during the Aptian. Each of these ammonite crises is closely preceded by a sea-level drop, with or without emersion phase, and closely followed by an anoxic event. The most important crises are briefly described in the following. The first one, reported from the middle early Aptian (*Deshayesites forbesi* zone), is important because it directly follows the replacement of the huge oligotrophic platforms (Urgonian limestones) by heterozoan ones, and because of the establishment of the first Early Cretaceous oceanic anoxic event, the Selli Episode (OAE1a). The neritic platform is replaced by a heterozoan carbonate production. The ammonite fauna witnessed an important diversification of hemipelagic forms, especially inside the heteromorph Ancyloceratacea. The third drowning phase that occurred in the late *D. furcata* zone, is marked by the complete disappearance of platforms in favour of marl deposits, having a significant impact on ammonites fauna. The seventh is characterised by a return of platform carbonates before a return to marl deposits with the eighth faunal crisis.

It is remarkable that the major ammonite crises often correspond to the ammonite biozone boundaries, which are linked to the main sea-level fluctuations and subsequently to the main platform emersion phases. Another notable point is the problem of definition of the biozones. Aptian biozones are not well defined and appear to start with the acme of the zonal index rather than with their first appearance; therefore, zonal indexes overlap during a short time interval at the base of the majority of the biozones.

In conclusion, the combined effect of the sea-level change and the subsequent oceanic anoxia as the consequence of climatic change is a key element in the platform crises and associated important faunal turnovers, which delimits the biozones.

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## Diversity and palaeobiogeography of belemnites during the Early Jurassic

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Belemnites (Belemnitida) were a major component of marine ecosystems during Jurassic and Cretaceous times. Their fossil record suggests a successful diversification already during the Early Jurassic, with a peak of diversity during the Toarcian. However, there is a current lack of synthetic studies about this diversification. The aim of the present study is to explore the radiation of belemnites at the scale of the western Tethys, from the Hettangian to the Aalenian.

A comprehensive bibliographic search and an original material-based study allowed us to obtain an up to date database of belemnite species. Using multivariate statistics and rarefaction techniques, we analyse the pattern in belemnites diversity and biogeography for the studied time interval.

Our study reveals that data on Early Jurassic belemnites predominantly concern the Toarcian stage and north-western Europe (Germany, Great Britain, Luxembourg, etc.), whereas little is known for the rest of Europe (Causses and Quercy Basins, Provence Platform, northern Spain, etc.) and from the Mediterranean areas (Italy, Austria, Southern Spain, North Africa, etc.). In these latter, data are still dramatically rare, outdated and/or they are not figured, especially for the earliest Jurassic. Therefore, it is currently difficult to establish a comprehensive exploration of the Early Jurassic belemnite radiation in the western Tethys. However, data from the northern part of the European province provide a first glimpse of the patterns of diversification.

In order to increase the knowledge in the understudied areas and periods, we recommend acquiring new field data, especially in the southern part of the north-west European province and in the Mediterranean province.

## Complete dorsal ammonoid shell - A facultative character of phylogenetic importance?

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In the last decades, multiple studies focused on the structure of the ammonoid shell and established the image of a reduced dorsal shell within planispirally coiled ammonoids. Whereas ventral and lateral shell portions are generally constructed of three distinct shell layers (outer prismatic layer, median nacre layer, inner prismatic layer), the dorsal shell portions are constructed only by the inner prismatic layer, sometimes accompanied by a previously secreted organic wrinkle layer, which forms an outer component (see Birkelund 1980; Kulicki 1996; Kulicki et al. 2001).

This common conception must be aligned. It is already known that several heteromorphic taxa form a complete dorsal shell within their loosely coiled portions (e.g., *Luppovia*, *Ptychoceras*, *Scaphites*; Doguzhaeva & Mikhailova 1982; Landman 1987; Doguzhaeva & Mutvei 1989). But studies on several planspiral lycoceratids (*Lobolytoceras*) and ammonites (*Amaltheus*, *Kosmoceras*, *Kranaosphinctes*, *Simbirskites*, *Euaspidoceras*, *Mirosphinctes*, *Aspidoceras*, *Pseudowaagenia*, *Puzosia*, *Douvilleiceras*) revealed nacreous structures of the dorsal shell, too. Within some taxa, dorsal nacreous shell material is restricted to local compensating structures like the relief of spines, which supports a secondary, optional formation of these structures. By contrast, a complete dorsal shell appears to be an aspect of (ongoing) ontogeny within several taxa: So *Lobolytoceras* and *Kranaosphinctes* developed a distinct nacreous layer only during late ontogeny ( $\emptyset > 20$  cm). A complete dorsal shell seems to be a general feature in the family Aspidoceratinae. Its development begins early in ontogeny ( $\emptyset < 3$  cm), where it is characteristically three-layered. Taxa of the sister taxon Peltoceratinae (*Peltoceratoides*) miss this feature. Therefore, the complete dorsal shell may have the potential for phylogenetic interpretations.

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## Studies compared in Westermann Morphospace with the goal of understanding ammonoid life mode

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Analyses of ammonoid shell shapes explore evolution and ecology in deep time in one of history's best temporally constrained and most dynamic fossil groups. Simplification of multidimensional shape data onto "agnostic axes" without prior expectations is well suited for open-ended explorations of shell shape evolution within specific ammonoid groups or samples. Plotting shell data along "generation axes" is helpful for understanding ontogenetic processes and shell constructional constraints. For ecological interpretations, new tools attempt to discover "functional axes" of shell shape variation. Presentation in multiple morphospaces can best stimulate collaboration in hypothesis generation and testing between research groups.

Westermann Morphospace compares ammonoid shell shape data to average shape distributions, and to previous research on hydrodynamic costs posed by the basic outer shape of the conch. It projects data into a single plane of variation between three end-member shapes (serpenticone, oxycone, spherocone) interpreted to impart distinct hydrodynamic challenges. It can test for expected shape variation in ammonoids in space, time, phylogeny, facies, isotopic signature, and predation scars.

Ammonoid shell shapes from different published studies are shown in Westermann Morphospace to compare the shape distributions consequent from important ecological scenarios in Earth history. Gradual change in shell shapes expressed by individuals within broadly-designated species are examined on sub-million year timescales. Examples from the Middle Triassic Germanic basin and from the Cretaceous Mowry Sea each show ammonoid populations collectively expressing trends in shell shape, with very different results. Shell shape data from ammonoid mass extinctions and subsequent diversifications allow examination of larger spatio-temporal scales. Data from different studies are compared to juxtapose ammonoid shell shape trends during the Devonian, Permian/Triassic, and Triassic/Jurassic events.

Discussion of possible interpretation schemes for life modes in the above comparisons yields two useful models and three possibilities for future work. Model 1: Hydrodynamic challenges posed by the outer shell shape as a hindrance to locomotion *must* have been met by the animal within, through either a minimally-active life mode, or through amelioration via shell ornamentation or soft-tissue behavior. Model 2: In contrast, hydrodynamic advantages of specific shell shapes may *not* have been utilized by animals lacking appropriate physiology. Clades with tight or broad shape variation may have had different capacities to utilize advantageous hydrodynamics.

Three possibilities are likely for future work. New hydrodynamic data may reveal gradients or thresholds between established life modes, which can be compared in Westermann Morphospace. If new hydrodynamic data suggest wholly different life modes, less dramatically-varied life modes, or life challenges that are more linked to size or another variable more influential than outer shell shape, wholly new axes may need to be used. If and when ecological data refute life modes inferred by hydrodynamics, physics and biomechanics must determine how the animal overcame those hydrodynamic challenges.

## Aptychi of the Boreal and Subboreal Middle Jurassic - Early Cretaceous ammonites: new records and review of published data

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Aptychi of Jurassic and Cretaceous ammonites are well-known from Mediterranean and Submediterranean areas. They were characterized by relatively thick calcite valves, while aptychi from Boreal and Subboreal sites remain relatively scarce. Siliciclastics typical for high-latitudes more likely preserve the thin organic layer of calcitic aptychi and of aptychi lacking a calcite layer. In the last decades, aptychi were discovered in some Boreal and Subboreal ammonite groups such as Bathonian-Callovian cardioceratids (Mitta 2006; Keupp & Mitta 2013), kosmoceratids (Schweigert 2000; Rogov 2004; Keupp & Mitta 2013), and Callovian proplanulitins (Rogov & Gulyaev 2001). Rare records of dorsoplanitid (Oates 1974) and simbirskitid (Engeser & Keupp 2002) aptychi are also known. In spite of the different evolutionary history of the high-latitude ammonite groups, they all have aptychi of a very similar type (praestriptychi), which are characterized by a thin smooth calcite layer, which differ mainly in outline and relative width of the valves. Only the latest kosmoceratids show small tubercles in the outer surface of their *Kosmogranulaptychus*. New aptychi records support a similarity of nearly all high-latitude aptychi. Praestriptychi were discovered in the early virgatitids (*Sarmatisphinctes*) and some dorsoplanitids (*Dorsoplanites*, *Laugeites*). Remarkably, the first record of an aulacostephanid aptychus should also be considered as *Praestriptychus*. Numerous aptychi of Late Volgian craspeditids were found since 2011 (Mironenko, in press). Some *Praestriptychus* were discovered inside the body chambers of *Kachpurites* and aptychi possibly associated with *Craspedites* are also known now. Ryazanian and Valanginian co-occurrences of aptychi with Boreal ammonites still remain unknown. In addition to *Simbirskites* (Engeser & Keupp 2002), a well-preserved *Praestriptychus* has been found in the body chamber of a *Speetonicer* megaconch. Aptychi of Aptian ammonites are common in the Lower Aptian shales of the Volga river, but they were not studied yet; information on their structure is based mainly on the investigation of thin sections (Doguzhaeva & Mutvei 1990, 1991). Recently collected material of *Sinzovia* aptychi may be assigned to *Lamellaptychus* (see also Thomson 1972). Surprisingly, aptychi of *Deshayesites* (Mikhailova & Bogdanova 1999) can also be considered as *Praestriptychus*. We found that aptychi of Middle Jurassic to Lower Cretaceous Boreal and Subboreal ammonoids are characterized by a set of common features and could be considered mainly within the *Praestriptychus* irrespective to the evolutionary history of ammonoid taxa. In addition to the aptychi occurrences mentioned above an interesting example of differences in aptychus type between macro- and microconch lineages has been recognized. As suggested by Trauth (1934), *Laevilamellaptychus* associated with *Sutneria* [m] differ from the *Laevaptychus* of their macroconchiate counterpart *Aspidoceras* s.l. *Laevaptychus* records are well-known from pre-Kimmeridgian macroconchs *Euaspidoceras*, while aptychi of the corresponding microconch *Mirosphinctes* remains unknown. Our discovery of *in situ* aptychi within the body chambers of Late Oxfordian *Mirosphinctes* indicates that they should be included in the same paragenus as the aptychi of *Sutneria*.

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## ***Is Proteroctopus ribeti* an Octopoda? Reappraisal of *Proteroctopus ribeti* characters in the light of X-ray microtomography**

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The systematic position of the Jurassic *Proteroctopus ribeti* among the Octopoda is still debated since its original description by Fischer and Riou (1982). The holotype, and only known specimen, from the La Voulte-sur-Rhône Lagerstätte has eight arms, a relatively short mantle, and an elongated funnel, which clearly suggests that *Proteroctopus* belongs to the Vampyropoda. The absence of cirri, the lack of a well-developed velum, and the presence of two fins and uniserial suckers are mixed characters of Recent Cirrata and Incirrata. On the basis of these observations and compared to the Cretaceous Palaeoctopodidae, *Palaeoctopus*, Fischer and Riou (1982) suggested that *Proteroctopus* is a stem Octopoda, exhibiting less derived characters than *Palaeoctopus*. Subsequently, the absence of a gladius and cirri has been questioned and attributed to fossilization artefact (Engeser 1988; Haas 2002; Fuchs et al. 2008). These authors regarded *Proteroctopus* as a member of a stem lineage of either Vampyromorpha or Octobranchia. In the La Voulte locality, pyritization processes have resulted in the preservation of the mantle of coleoids, preventing any direct observation of internal structures. Moreover, pyritization of soft tissues in framboidal pyrite crystals tend to form aggregates that could conceal slender features such as cirri. We used propagation phase contrast X-ray synchrotron microtomography (ESRF, proposal ES-36) to investigate the internal and external anatomy of *Proteroctopus*. In this work, we present new data obtained on the anatomy of this important taxon and discuss the place of *Proteroctopus* within the Vampyropoda.

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## Age, Systematics and Palaeobiogeography of the Late Jurassic Ataxioceratid Ammonoids from Kutch, India: A New Light on Origin and Migration

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Ataxioceratidae was an important Late Jurassic ammonite family and had wide spread biogeographic distribution, mostly in Europe. All the genera within this family were characterized by the development of virgatotome ribbing, which Callomon (1981) described as evolution “par excellence”. However, the origin of the family remained difficult to understand in terms of mode and tempo of evolution (Callomon 1981).

We revised the diversity of ataxioceratids previously reported from Kutch. Spath (1931) described 11 genera and 74 species within the Ataxioceratidae from the Late Jurassic of Kutch. The detailed systematic revision revealed that the family was excessively and subjectively split. We recognized three distinct genera within the subfamily Ataxioceratinae in Kutch, namely *Ataxioceras*, *Torquatisphinctes* and *Patchyplanulites*. *Patchyplanulites* was initially grouped within the Perisphinctinae by Spath, but we placed it in the Ataxioceratinae because of its virgatotome ribbing. Refinement of stratigraphic data suggested that all oldest members of the genera of Ataxioceratinae co-occurred with *Perisphinctes indogermanus* in the eastern part of the Kutch basin.

*Perisphinctes indogermanus* strongly resembles ataxioceratid genera of Kutch and it had virgatotome ribbing in its early development. We recently (Roy et al. 2012) envisaged that *P. indogermanus* gave rise to ataxioceratin genera in Kutch through allopatric speciation. *P. indogermanus* first appeared in the Lower Oxfordian in Kutch and was restricted mainly in the western part of the basin. During the middle Oxfordian transgression, it migrated to the shallow eastern part of the basin. The Kutch basin experienced a restricted interoceanic circulation during the Oxfordian. The semi-isolated population of *P. indogermanus* allopatrically evolved into many distinct genera which were all characterized by virgatotome ribbing. 52 species of 5 genera of Ataxioceratidae appeared between the Middle Oxfordian and Middle Kimmeridgian (Spath 1931; Roy et al. 2012). This indicates that the evolution was marked by a burst of radiation with a frequent overlapping of species. The younger subfamily Virgatosphinctinae also appeared during this time and was limited mainly to Kutch and neighboring areas.

Callomon (1981) correctly traced the ancestry of the Ataxioceratidae in the Perisphinctinae but could not indicate a specific ancestor. Atrops and Melendez (1981) suggested that *Ataxioceras* evolved from *Orthosphinctes* during the Late Oxfordian-Early Kimmeridgian transition, but *Orthosphinctes* lacked the virgatotome ribbing. We show that *Ataxioceras* and other early members were found from the Middle Oxfordian in Kutch. Kimmeridgian appearance of *Ataxioceras* in Europe and other areas rather indicated a grand migrational event which was triggered by the global marine transgression during the Oxfordian-Kimmeridgian transition. Thus, Kutch appeared to be the place of origin of a new family, the Ataxioceratidae and its rapid evolution from *P. indogermanus* suggested an allopatric speciation compatible with the punctuated equilibrium model of evolution.

## Exceptional preservation of ammonites from the Late Jurassic Nusplingen Plattenkalk

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The Nusplingen Plattenkalk is a Fossilagerstätte of Late Jurassic age located in the south-western part of the Swabian Alb (SW Germany). Already known since the middle of the 19<sup>th</sup> century, this locality has been exploited by scientific excavations of the Stuttgart natural History Museum since more than 20 years. More than 400 taxa of vertebrates, invertebrates, microfossils, and ichnofossils have been recorded (see Dietl & Schweigert 2004, 2011 for more details). Ammonites and their aptychi belong to the most common invertebrate fossils of the Nusplingen Plattenkalk. The moderately diverse ammonite fauna is of typical Submediterranean character and indicates a Late Kimmeridgian age for this Plattenkalk site (Schweigert 1998, 2007). Although most of the ammonites are strongly crushed and poorly preserved due to the dissolution of the aragonitic shell and the contemporaneous compaction of the sediment very early in diagenesis, numerous finds offer interesting information about ammonite autecology and anatomy. There are several hints that at least some of the ammonites lived permanently in the Nusplingen lagoon despite the presence of anoxic conditions at the seafloor. Stomach contents in various ammonite genera provide some ideas about the different preys and lifestyles. On the other hand ammonites had played an important role in the food web as it is demonstrated by isolated bitten shells and aptychi as well as aptychi remains within the stomach contents of predators (e.g., other ammonites, cuttlefish). Not only aptychi but also the corresponding upper jaws are recorded both isolated and sometimes still within or close to their body chamber. Especially aspidoceratids are rather common and show exceptionally preserved examples of their beak apparatuses, crop contents, and even carbonaceous remains of soft parts. Some specimens were overgrown with small oysters during lifetime, thus indicating that these ammonites had been able to compensate this additional load.

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## Bioerosion in shells of the modern *Nautilus*

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Over the past 20 years, Royal H. Mapes and colleagues caught specimens of the living *Nautilus* in various regions of the Southern Pacific Ocean. Many of these shells were encrusted by epiliths (foraminiferans, ostracods, goose barnacles). Additionally, the shells showed strong signs of bioerosion, i.e. numerous small irregular holes penetrating deep into the shell. Because bioerosion is a major factor in the degradation of carbonate skeletal material a study was carried out on four shells (one specimen of *N. pompilius* from Vanuatu, three specimens of *N. macromphalus* from New Caledonia) to investigate these holes in detail. The shells were broken into pieces and a set of epoxy resin casts was prepared for analyses with the scanning electron microscope.

The analyses revealed that the small holes are the openings of two, so far undescribed, microbioerosion traces which are most likely produced by naked foraminiferans. Traces of these foraminiferans commonly occur in dense clusters in the shell of up to many dozen individuals. Because these traces were not reported from other substrates before, we conclude, that these boring naked foraminiferans are host specific. In addition to the two boring foraminiferans we found two further traces on the shells outside of *Nautilus*. These etchings derive from test-bearing foraminiferans, likely from some genera of the Rosalinidae. As of now, there is no indication that any of the foraminiferans, naked or with a test, were parasitic but instead they used the *Nautilus* shells as substrate to settle respectively to live in. Our study presents the first report on syn-vivo bioerosion in *Nautilus* shells and demonstrates that shell degradation in *Nautilus* already starts during lifetime of the cephalopod.

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## **Geographic differentiation of the Late Triassic nautilids and biogeographic zoning of Late Triassic marine basins**

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The major patterns of paleobiogeographical distribution of the Late Triassic nautilids are discussed and a paleobiogeographic scheme for the Late Triassic seas is proposed. The zoning is based on a faunistic principle, which takes the spatial distribution of different taxa and the history of their formation into account. A systematic rank of specific (endemic) groups is adopted as the main criterion for the certain paleobiogeographic units (or biochores). Herewith, the rank of biochores relates not necessarily directly to the rank of taxa. The criteria used to distinguish the particular biochores are learned empirically as a result of successive comparisons of the taxonomic composition of fauna from different basins and specificity of the investigated groups and dynamics of their evolution. Negative features such as the absence of taxa, usually of generic and family ranks, are also significant for establishing of biochores.

For Triassic nautilids, the biochores of the first rank could be confidently distinguished. They are accepted as the realms, i.e. territorially limited water areas, which possess the unity of systematic composition of fauna and affinity of origin. The origin of realms is caused mainly by climatic factors (mainly the sea water temperature) and by the duration of isolation.

The study of Triassic nautilids revealed that biochores of the first rank are characterized by an almost complete endemism of species and appearance of peculiar taxa of generic and family ranks. Within the realms several allopatric communities were established. They are conditionally named as provinces and subprovinces. They have particular differences in the systematic composition of fauna and lower rank of endemism compared with realms. Based on nautilids, three biochores of the highest rank are recognized: Tethyan, Boreal, and Notal realms.

The low latitude Late Triassic nautilids from the Tethyan realm are characterized by a broad taxonomic diversity and a high degree of endemism. The high latitude fauna (Boreal and Notal realms) have been drastically reduced and during the Late Triassic, an endemism manifested mainly on the species level, rarely on the generic level. The degree of geographic differentiation of nautilids in the Late Triassic was not constant. It became maximal at Norian age, when the specific higher rank taxa appeared in Boreal regions.

In the Late Triassic, based on nautilid distribution (mainly endemic genera, rarely species) within realms, it is possible to allocate provinces (the Alpine-Carpathian and Himalayan-Indonesian – for the Tethyan realm; Canadian and Siberian – for the Boreal realm) and subprovinces (Novosiberian – for the Siberian province), those are clearly evident throughout the Carnian and Norian ages.

## Report on the revision of the Cretaceous ammonites of the Coquand Collection

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Henri Coquand (1813–1881) was a well-known geologist of his age. During decades, he collected a marvellous fossil material whose main part is called "Coquand Collection", which is housed in Budapest, Hungary, since more than a century. Ammonite-related scientific work of Henri Coquand had been done mostly on materials from France (1860), Spain (1865) and Algeria (1852, 1854, 1862, 1880), in some cases with co-authors (Coquand in Matheron 1878-1880; Bayle and Coquand 1851).

He described approximately 120 ammonite species in his works. Besides the published taxa, several ammonite forms had never been published but remained in manuscripts as the original handwritten labels of the Collection tell us. Coquand did the field-work and collecting with other geologists and friends, so some of the collected material remained in their collection: the Papier, Heinz, Hénon, the Rochebrune, and Lhotellerie Collections. Therefore, some of the published types of Coquand are housed in various other institutions. In the necrolog of Heinz written by Alexander Papier (1896), the detailed story of the whole Coquand Collection and the Algerian paleontologic works of Charles Heinz with Coquand and Gustave Sayn are described in detail among others.

The „Coquand Collection” was Henri Coquand’s private collection. When he died, the family sold his collection to a Hungarian nobleman, the greatest patron of the Hungarian science, count Andor Semsey, who bought the collection for the Hungarian Geological Institute in 1882. This collection was one of the greatest attractions of the Hungarian Geological Institute („...includes more than 10.000 species with a great number of 30.000 specimens”). According to Coquand’s instruction and last wish, the collection was kept in one intact body but exhibited and aggregated into groups (parts containing Cretaceous cephalopods are shown in **bold**).

1. **General stratigraphic fossil collection**
2. Collection of Cretaceous oysters
3. Brachiopod Collection
4. Echinoid Collection
5. **Africa Collection**
6. **Aptian Fossils from Spain**

The revision of type materials and additional specimens is very complicated due to their tiny pyritized state of preservation and lack of their proper description and illustrations. Most important species from Early Cretaceous were published by Szives & Company (2011). The original type material of *Holcodiscus diversecostatus*, *H. metamorphicus* and *Heinzia heinzi* shows that these species have been usually misidentified in the literature. We designate lectotypes for these species. In addition, the use of the nominal species “*Ammonites mazuca*” should be fully avoided, it is considered as a nomen dubium because its type material is apparently lost so its application is very doubtful. Other species are under current revision as well.

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### **3-dimensional analysis of the Middle Jurassic ammonite *Normannites* and its functional morphology**

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Some ammonoids have external shells with peculiar features in their terminal apertures such as an apertural shell thickening, an apertural constriction, changes in ornamentation and apertural appendages. These prominent features are referred to as mature modifications. In ammonoids, shell allometry including mature apertural modifications is of great importance because ammonoids used their shells as buoyancy devices and such modifications might have changed the orientation of the shell.

Two-dimensional approaches have been taken as the standard method to study ammonoids. However, the shell volume, which yields important clues to unravel the mystery of ammonoid palaeobiology, cannot be quantified by this approach. In our study, an ammonite is virtually reconstructed in three dimensions in order to calculate shell and chamber volumes. Two ammonite specimens were reconstructed, which belong to *Normannites*. It is commonly regarded as a microconch genus of the Stephanocerataceae (Ammonitina), partially because of its large lappets. The specimens are from the Middle Bajocian (Middle Jurassic) of northern Switzerland. In order to obtain empirical data, serial sections of the specimen were produced. Each section was automatically scanned. An obtained set of 114 scans was used to produce a virtual 3D-model of the ammonite. The resulting 2D-scans were imported into AdobeIllustrator® and manually traced. Each segment (shell, siphuncle and septa) was marked by different colors so that the volumes could be calculated separately. We use the software VGstudiomax®2.1, which constructs 3D-models out of 2D-stacks. These models were then used to measure shell volumes and to evaluate the spatial distribution of mass, which was then used to reconstruct the syn vivo shell orientation.

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## **Ammonoid buccal mass and jaw apparatus: comparative morphology, functional morphology and taxonomic variation**

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Current knowledge on the ammonoid buccal mass and jaw apparatus is synthesized on the basis of available *in situ* fossil records from 109 genera that are distributed in 30 superfamilies of 8 suborders of Devonian to Cretaceous age. As in those of modern cephalopods, the jaw apparatus of ammonoids consists of upper and lower elements. Comparative anatomical examination of the attachment scars of chitin-secreting cells (beccublasts) on the jaw lamellae allow us to reconstruct the buccal mass structure of ammonoids.

The jaw apparatuses of ammonoids can be classified into the normal, anaptychus, aptychus, intermediate, and rhychaptychus types based mainly on the differences in overall morphology and lamellar composition in the lower jaws. Both upper and lower jaws of the former two morphotypes are made mainly of a chitinous material, whereas the lower jaw of the aptychus-type has a bivalved calcitic plate (aptychus *sensu stricto*) on the outer chitinous lamella. The upper and lower jaws of the rhychaptychus-type are characterized by the development of a thick calcified rostral tip. The lower jaws of the intermediate-type exhibit intermediate features between the anaptychus- and aptychus-type ones.

The jaw apparatuses of the normal and rhychaptychus types are respectively known from the four pre-Jurassic ammonoid suborders (Goniitina, Gephuroceratina, Prolecanitina and Ceratitina) and the Cretaceous Phylloceratina and Lytoceratina. The anaptychus-type jaws are distributed in the Psiloceratoidea and Eoderoceratoidea of the Jurassic Ammonitina, whereas the aptychus-type jaws are widespread in the other superfamilies of the Jurassic and Cretaceous Ammonitina and in the Cretaceous Ancyloceratina. The lower jaws of the Desmoceratoidea (Cretaceous Ammonitina) exhibit intermediate features between anaptychus- and aptychus-type lower jaws; accordingly they are newly defined herein as the intermediate type.

Thick calcitic aptychi are developed in the lower jaws of some Jurassic and Cretaceous ammonoids; these would be effective during a predator's attack from the apertural side, if they were able to seal the shell aperture. The fairly large variation of the jaw morphology and the variety of food remains preserved in the crop/ stomach portion and buccal cavities in Mesozoic ammonoids may reflect diversity of feeding and dietary habits ranging from predatory-scavenging habits to microphagous (zooplankton-feeding) ones among them.

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## **Analysis of genetic variability and phylogeny of the oval squid *Sepioteuthis lessoniana* around Japan**

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### **Background**

The oval squid *Sepioteuthis lessoniana*, a member of the Loliginidae family, is one of the most economically important species of neritic fisheries, distributed over a broad geographical range throughout the Indo-Pacific region. Some genetic studies have shown that *S. lessoniana* in Japan is a complex species which includes the “Akaika type”, “Kwaika type” and “Shiroika type.” The last one has the largest fishery within this group, hence, is referred to as *S. lessoniana sensu stricto*.

However, the genetic diversity of the Shiroika type and the phylogenetic relationship among the three types are still poorly understood. An accurate evaluation of their genetic variability and phylogenetic relationship is a critical step for the conservation of this species.

### **Material & Methods**

First, microsatellite loci isolated from 740 individuals of the Shiroika type collected around Japan were used to evaluate genetic variation. Next, the mitochondrial DNA cytochrome oxidase I gene from the Shiroika type was sequenced to clarify the phylogenetic relationship between Shiroika type and others using neighbor-joining method. Additionally, nearly 170 sequences of this species from the Indo-Pacific area were obtained from GenBank and included in the phylogenetic analysis.

### **Results**

Microsatellites indicated high genetic variation but no significant genetic differentiation among 12 populations, which suggested the presence of a single population. The phylogenetic tree showed three distinct clades (clades A, B and C). Additionally, clade C was separated into two clades (clades C1 and C2) with high bootstrap support. The Shiroika type was only grouped in clade C1. Clade C1 also included samples from China, Vietnam and Indonesia while clade C2 was sampled from India, the Philippines, Vietnam and throughout Indonesia.

### **Conclusion**

DNA markers were useful in examining the population structure and phylogenetic relationship of the Shiroika type, which showed high genetic variability and a single genetic population around Japan. The phylogenetic tree clarified distinct groups in the Indo-Pacific region, which suggests the presence of three types there. Further genetic analysis of the Kwaika and Akaika types could help better understand genetic variability and phylogeny of the oval squid.

## Morphological changes of the genus *Baculites* from the Coniacian to lower Campanian in Japan

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The shell of *Baculites*, a Late Cretaceous heteromorph ammonoid, consists morphologically of a long straight shaft. Many *Baculites* species occur abundantly in the Upper Cretaceous deposits in Hokkaido, north Japan. Eleven species were reported from the Coniacian to lower Campanian sequence in Hokkaido (Matsumoto and Obata 1963). In our investigations, at least eight species of *Baculites* (Coniacian: *B. yokoyamai* and *B. cf. schenki*; Santonian: *B. bailyi*, *B. uedae*, *B. princeps*, *B. boulei* and *B. cf. capensis*; lower Campanian: *B. tanakae*) were found from the Tomamae section in north-west Hokkaido.

From the peramorphic tendency in development of shell ornaments, Tsujino et al. (2003) presumed a single evolutionary lineage from the Coniacian *B. yokoyamai* with a smooth surface throughout ontogeny to the lower Campanian *B. tanakae* with tubercles via *B. uedae* with faint ribbing. However, the evolutionary change of *Baculites* species during the Coniacian to early Campanian time remain to be examined in detail. Our recent investigations revealed the following:

- (1) *B. yokoyamai* with a smooth surface and *B. cf. schenki* with nodose ornaments co-occur in the same calcareous nodule. *B. cf. schenki* is intermediate type between *B. yokoyamai* and *B. schenki*.
- (2) Morphological continuity among *B. bailyi*, *B. uedae*, *B. princeps*, *B. boulei* and *B. cf. capensis* was recognized. There are intermediate forms between each species. A pair of species was obtained from a calcareous nodule.
- (3) *Baculites tanakae* shows a remarkable intraspecific variation in shell ornaments.

Taking the wide range of the intraspecific variation into consideration, the two Coniacian species *B. yokoyamai* and *B. cf. schenki* should be grouped into a single biospecies. Likewise, the five Santonian species *B. bailyi*, *B. uedae*, *B. princeps*, *B. boulei* and *B. cf. capensis* are also considered to be grouped together.

We infer the following: In the Coniacian, tuberculate groups such as *B. cf. schenki* appeared from a part of non-tuberculate *B. yokoyamai*. Then, in the Santonian, tuberculate groups such as *B. uedae*, *B. princeps*, *B. boulei* and *B. cf. capensis* showed an increase in population. In the lower Campanian, most of *Baculites* finally had remarkable shell ornaments. Such morphological changes of *Baculites* show a gradual tendency.

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## Early ontogeny of Silurian tarphycerid *Ophioceras*; a comparison with some other tarphycerids and earliest nautilids

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Early ontogeny of the Silurian nautiloid *Ophioceras* has been studied in detail and compared with ontogeny of some other tarphycerids. Remarkable variability of early juvenile growth stage has been documented in *O. simplex*. Changes in morphology and especially appearance of the first conspicuous growth anomalies on the shell surface clearly indicate that the embryonic shell of *Ophioceras* possessed only one high air chamber and a very low body chamber. Low cap-shaped cyrtconic shell thus attained less than one quarter of the whorl and freshly hatched specimens differed substantially from adults. A large air chamber probably resulting in positive buoyancy enabled the hatchling to live a planktonic mode of life. The whole embryonic shell was ornamented with fine densely spaced growth lines or the most apical part of the shell seems to be quite smooth. Before or soon after hatching, a reticulate sculpture appeared. Weak ribs appeared not immediately after hatching but usually at about the first half of the first whorl. Marked increasing density in septal spacing at the end of the first whorl (7<sup>th</sup> or 8<sup>th</sup> air chamber) is not connected with leaving the egg capsule by the animal. Shortening of these chambers at the beginning of the second whorl was related either to the change of shell shape in this stage or to ecological factors. Contrary to former opinions of some cephalopod workers a similar situation is expected in *Discoceras*. Earliest nautilids classified in the family Lechritrochoceratidae possessed embryonic shell with five to seven air chambers and a relatively long body chamber. Their first body chamber was very small. By contrast, the embryonic shell of *Boionutilus* (Uranoceratidae, Nautilida) was large, but the first chamber was low. None of the Early Palaeozoic nautiloids had an embryonic shell attaining more than half a whorl.

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## Relationship between ontogenetic change in shell shape and aperture map in ammonoids

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The shape of the ammonoid shell commonly changes through growth. Change in shell shape may require change in the pattern of relative rate of shell accretion for each point around the aperture, or aperture map. In a shell with a low expansion rate of the aperture such as ammonoids, the relationship between the aperture map and shell shape is also related to the manner of shell coiling as well as to the aperture shape. Substantial modification of the basic pattern of the aperture map requires a considerable change of behavior of cells around the mantle edge. The present study focused on the relationships between the aperture map and shell shape in ammonoids using theoretical morphologic models and morphometric analysis. The effects of ontogenetic change in the shape and the properties of shell coiling on the aperture map were taken into special consideration.

The shell shape of an ammonoid was represented by the Raupian parameters, i.e., whorl expansion rate ( $W$ ), umbilical width ( $D$ ) and whorl shape ( $S$ ). The aperture map was obtained from computer-produced shell forms with various values of the parameters. Since the aperture map of an ammonoid is symmetric in shape, it can be decomposed into a series of cosine functions with various frequencies. Synthetic aperture maps were reconstructed using inverse transforms to visualize the synthetic models represented by a given number of harmonics. The basic geometry of the aperture map was generated in the synthetic models based on the fifth and lower harmonics. Three dimensional contour maps of the Fourier coefficients depicted onto the theoretical morphospace indicated that the contours tend to run along diagonal from the low- $W$  and high- $D$  corner to the high- $W$  and low- $D$  corner in the morphospace. The ontogenetic changes in  $W$ ,  $D$  and  $S$  were estimated in a total of 114 ammonoid species through morphometric analyses. As a result, ontogenetic trajectories in the morphospace tend to be distributed along the contour of the Fourier coefficients. This result shows that the basic pattern of the aperture map is not as variable as the aperture shape and the manner of shell coiling throughout ontogeny in many ammonoids. In other words, ammonoids change their shell geometry with growth without major modification of the aperture map.

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## Tracing key innovations and the tempo of cephalopod evolution using molecular paleobiology

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The evolution of cephalopods is broadly speaking well understood from the rich fossil record. However, questions have been arising as to when crown cephalopods, coleoids, decabrachiates and vampyropods radiate. Using relaxed molecular clock analyses on a conserved set of 7 nuclear housekeeping genes, we have been able to trace the origin of the major lineages of cephalopods and compared it to the fossil record. The results are surprisingly congruent with earlier studies using the hemocyanin gene and different models, which speaks to a genuine consistent signal from the molecules, which are also fairly congruent with the fossil record.

We observe that the crown group of cephalopods (nautilids + coleoids) radiate around the Silurian-Devonian boundary. This is congruent with the fossil record of both bona fide stem coleoids, such as the ammonoids and bactritids appearing at this time. Convincing nautilids also traced back to the Devonian. A long standing scenario held that these two lineages saw their origin in the Early Ordovician descending from distinct early Palaeozoic lineages, such as oncocerids and orthocerids. With this new evidence we can pose that orthocerids alone gave rise to the crown group of cephalopods. A key innovation in this clade is the jaws, which saw their appearance in the fossil record also in the Devonian, which speaks to an origin in the latest common ancestor of crown cephalopods in the latest Silurian. Jawed vertebrates also radiated during this period in the so called Devonian Nekton revolution and we think that the crown group of cephalopods radiated as part of an evolutionary arms race with fishes.

Coleoids are radiate at the Permian-Triassic boundary. This speaks against the records of some fossils from the Carboniferous, which have been placed in the coleoid crown group. Instead, this evidence is congruent with stem vampire squids and other vampyropods from the Triassic and some belemnoids that might subtend the decabrachiate stem.

The vast diversity of modern cephalopods is in the octobrachiates and the decabrachiates. These seem to have radiated in parallel at the Jurassic Cretaceous boundary during the Mesozoic Marine revolution. Interestingly, this is also the time that teleost fishes radiate, and yet again we observe a turnover in cephalopod disparity in which skeletons are reduced almost completely to maximize efficient mantle pumping for jet propulsion.

The scenario emerging from this synoptic perspective is demonstrating that the cephalopod fossil record is remarkably faithful in its documentation of cephalopod evolution and that dubious fossils such as *Nectocaris* from the Cambrian can not be accommodated as part of the cephalopod or molluscan total group irrespective of its interpretation. The arms races between nektonic predators is an overarching theme for cephalopod evolution.

## Iterative ontogenetic development of ammonoid conch shapes from the Devonian through to the Jurassic

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The globular ammonoid conch is a recurring form found repeatedly in clades throughout the history of the group. The iteration of the same conch shape is a classic example of convergent evolution. We were interested whether the conch growth and the ontogenetic trajectories of the cardinal conch parameters, conch width index (CWI) and umbilical width index (UWI), were different between families and between different time bins.

Ammonoid ontogenetic trajectories can be divided into phases represented by changes in the direction of the trajectory or in periods of extreme deceleration or a levelling off. Conch cross sections of 184 globular specimens, ranging from the Devonian through to the Jurassic were analysed. The number of phases and their direction of change present in the CWI and UWI trajectories were recorded for each specimen, the length of the phases in terms of change in the overall maximum conch diameter were also taken. The percentage contribution of the CWI, UWI and whorl expansion rate (WER) to the growth of the conch was calculated and compared between the specimens.

The analysis revealed that there is a strong tendency for globular shaped ammonoid CWI ontogenetic trajectories to consist of three distinct phases (triphasic). In the majority of cases, the first phase is characterised by a relative reduction of the width of the conch in comparison with the conch diameter (CWI decrease), the second phase is represented by a reversal of this trend (CWI increase) and the third phase by another reduction in the conch width. There is also a strong tendency towards biphasic and triphasic trajectories for the UWI. However, the first phase is characterised by an increase in the relative size of the umbilicus in comparison with the diameter (the juvenile becomes more widely umbilicate) and the second phase a reversal. If a third phase is present then it consists of either a period of relative stability (little or no change in the UWI) or an increase in the relative size of the umbilicus. This pattern is repeated in unrelated families and in different geological periods. Almost all of the studied Palaeozoic and most of the Triassic species (particularly arcestid ammonoids) share some principal patterns in conch ontogeny: (1) the juvenile stage is often widely umbilicate (“serpenticonic”), (2) the intermediate stage is characterised by narrowing of the umbilicus and transformation towards a stouter, globular conch, (3) the adult conch shows a tendency to become more slender with the umbilical width index being stable or slightly increasing.

The general patterns show that not only adult conch shapes but also ontogenetic trajectories leading to these occur repeatedly within distant ammonoid clades. For instance, the Triassic genus *Arcestes* shows in its conch ontogeny, despite a strikingly advanced suture line, very close similarities to the early Carboniferous *Goniatites* and related forms. The reappearance of globular conch forms and similar conch ontogenies over a large time scale is indicative of not only the adult ammonoids creating similar niches but also the juveniles as well, in other words, life histories are repeated over time.

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***Allonautilus* and *Nautilus*: Post-Jurassic phylogeny, shift from shallow to deep water habitats based on isotopic evidence, new evidence concerning mode of life, and conservation issues.**

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In this talk, I will present new phylogenetic evidence demonstrating a Middle and perhaps Late Jurassic origin of the genus *Nautilus*, and show that it was both older and perhaps ancestral to the lineage producing species of *Hercoglossa*, and ultimately *Aturoidea* and *Aturia*. Additionally, I will use both sedimentological as well as new oxygen isotope data from species of Cretaceous *Nautilus*, *Eutrephoceras*, *Anglonautilus*, *Cymatoceras*, and *Cimomia*, as well as Paleogene *Nautilus*, *Cymatoceras*, *Eutrephoceras*, *Cimomia*, and *Aturia* to show that all specimens analyzed to date lived in water temperatures throughout life far exceeding mean habitation temperatures (and thus depths) of extant *Nautilus* and *Allonautilus* ( that latter here analyzed with oxygen isotopes for the first time). I will also present new tracking and depth and temperature records for *Nautilus* from New Caledonia, New Guinea, and the Philippine Islands (Bohol Island region) yielding new depth and movement information and also demonstrating what appears to be highly territorial behavior in specimens of *N. pompilius* from the Philippine Islands in which little lateral movement takes place over many month intervals. The re-catch of two healthy nautiluses from Panglao, Philippine Islands, taken, respectively four, and five months following attachment of Vemco acoustic transmitters validates the non-lethal use of such transmitters, while at the same time demonstrating the high fishing pressure being exerted on nautiluses in the Philippines, and perhaps elsewhere. I will also present data indicating that a perhaps genetically distinct population of dwarf nautiluses from Siquijor Island, Central Philippines, has apparently been fished to extinction, with living animals last caught nearly 20 years ago during intense fishing pressure on an island area surrounded by very deep water on all sides, and lethally hot surface water temperatures. This conclusion concerning the effects of fishing on nautiluses will be further documented using new data first presented here on a comparison of both predation pressure based on shell breaks as well as life history demographics (percentage of mature to immature specimens, the study conducted with Dr. Bruce Saunders) from both fished and unfished sites. The Philippine Islands nautiluses show the highest rate of shell break data of any known population, with with break frequency increasing in areas with highest human predation. All quantitative information from the Philippines suggests that a major extinction among stocks has or soon will have taken place, and it is argued strongly that international sanctions against the trade of shells or living nautiluses MUST be enforced if further disappearances are not to occur. The trade of living nautiluses from the Philippines should be banned, and the aquarium animals now found globally repatriated to the habitats from whence they came.

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## **High resolution biostratigraphy and biodiversity dynamics of Dienerian (Early Triassic) ammonoids from the Northern Indian Margin**

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Extensive new collections of ammonoids from the Dienerian of the Salt Range (Pakistan) and Spiti Valley (Himashal Pradesh, India) allowed us to thoroughly revise their taxonomy and propose a new, high resolution biostratigraphical scheme. A total of 47 species were collected, allowing the differentiation of 12 ammonoid zones, grouped into 3 intervals (early, middle and late Dienerian). This contrasts strongly with the previously established two-zone biostratigraphical scheme. This very high resolution permits a detailed study of biodiversity changes throughout this interval, which is crucial for a better understanding of the recovery following the end-Permian mass extinction. Ammonoid biodiversity first peaks in the early Dienerian. An extinction occurs at the early/middle Dienerian boundary, and the diversity remains low during the rest of the Dienerian. A slow increase in biodiversity occurs in the earliest Smithian, and a pronounced radiation occurs at the end of the early Smithian. Species turnover rates are high over the whole period, with generally more than 50% turnover, sometimes reaching 100%. The low diversity in the middle and late Dienerian can be correlated with an anoxic event associated with high temperatures. These results contradict the widely held hypothesis of a slow progressive recovery of ammonoids during the Dienerian.

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## A Molecular Search for the Giant Squid

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Despite its charismatic appeal to both scientists and the general public, remarkably little is known about the giant squid *Architeuthis*, one of the largest of the invertebrates. Although specimens are becoming more readily available, owing in part to the advancement of deep-sea fishing techniques, considerable controversy exists with regards to topics as varied as their taxonomy, biology, and even behaviour. In this study, we have used second-generation sequencing techniques to characterise the mitochondrial genome (mitogenome) diversity of 43 *Architeuthis* samples collected from across their known range, in order to use genetic information to shed new and otherwise difficult to obtain insights into the life of this animal. The results show no detectable phylogenetic structure on the mitochondrial level, and furthermore, that the level of nucleotide diversity is exceptionally low. This observation is consistent with the hypothesis that globally there is only one species of giant squid, *Architeuthis dux* Steenstrup, 1857, and furthermore, that it is highly mobile, possibly dispersing through a drifting paralarval stage. Demographic history analyses of the data indicate that there has been a recent population expansion, or possibly a selective sweep, which may explain the low level of genetic diversity. These findings provide a base upon which future nuclear genome studies can develop, in order to both refine these findings, and provide yet further insights.

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## **A model for speciation in ammonoid cephalopods**

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Ammonoid cephalopods experienced remarkably rapid rates of evolution and extinction. The processes that fueled this evolutionary volatility are not well understood. Ammonoid evolution is characterized by high degrees of homeomorphy, heterochrony, and other patterns that reveal a flexible developmental growth program. Ammonoid biodiversity through time appears to have been linked to changes in environmental variables, particularly sea level, water temperature, and oxygen content. Synthesizing these observations of ammonoid paleobiology with contemporary views on ecological speciation permits the creation of a new model for ammonoid speciation that may help explain the evolutionary volatility of the group.

In the model, a newly formed habitat space (e.g., a new seaway formed by sea level rise) plays host to the rapid endemic radiation of ammonoids from one or a few ancestral species. Within the seaway, anatomical variants are produced via changes in developmental timing and then sort into different niches based on microhabitats within the environment. Assortative mating and disruptive selection lead to reproductive isolation and speciation among these morphs. The same processes will occur each time sea level rises; given developmental constraints on shell form, homeomorphic species will result.

This model of speciation emphasizes the importance of both biological processes (developmental flexibility) and environmental factors (sea level change and a mosaic of microhabitats) in explaining high diversification rates among ammonoids. Neither by itself is sufficient to explain the rapid rate of ammonoid evolution. The inherent developmental flexibility of ammonoids can produce a great diversity of forms, but these will persist and diverge only when environmental conditions allow it.

Testing this model for ammonoid speciation will require detailed phylogenetic, morphometric, stratigraphic, paleogeographic, and environmental data for ammonoid clades. These data can be integrated using new quantitative and geospatial approaches in order to create a synthetic view of ammonoid evolution.

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## **Abrupt changes of distance between succeeding septa at the hatching event in modern *Sepia* and *Spirula***

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The analyses of distance between succeeding septa throughout the ontogeny reveal that the septal distances abruptly decrease at the hatching event, both in modern *Sepia* and *Spirula*. The examined species are *Sepia esculenta*, captured from the Seto Inland Sea, Japan, and *Spirula spirula*, stranded on the Taemaro Bay, New Zealand and the Canary Islands, northwest of Africa. The distances of succeeding septa were directly measured at the center of the septum in *Sepia*, and were measured as the central rotational angles in *Spirula*, because their shells are logarithmic spiral. The hatching timings are recognized by the literatures that modern observations of hatchlings (Oshima and Choe 1961; Choe 1962) and stable isotopic analyses (Lukeneder et al. 2008).

Similar abrupt decreases of distance between succeeding septa across the hatching events are well known in modern and fossil nautiloids (e.g., Davis and Mohorter 1973; Landman et al. 1983; Landman 1988; Chirat and Rioult 1998; Chirat 2001; Chirat et al. 2008; Wani and Mapes 2010). These facts suggest that the abrupt decrease of distance between succeeding septa across the hatching event is a common feature of cephalopods, although ammonoids are exception (e.g., Smith 1901; Drushchits and Khiami 1970; Landman 1982, 1985, 1988; Tanabe et al. 1993), in which the septa had not formed until hatching. This might be related to the different post-hatching modes of life among cephalopods.

## **Biogeography of early Pliensbachian ammonites: integrating distribution, phylogeny and morphology**

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One of the major issues of macroecology and macroevolution concerns the spatio-temporal fluctuations of biodiversity. Although distinct, those research fields treat two dimensions of biological evolution that are functionally related. The fossil record permits their unification by analyzing simultaneously the spatial organization of biodiversity and its temporal evolution.

Here, we address the following question: How - and to what extent - does phylogeny and morphology influence the macroecological properties of taxa?

Our study consists of an integrated approach that quantifies the relationships among the spatial distribution, phylogeny and morphological disparity of early Pliensbachian ammonites. We analyzed a comprehensive dataset that consists of 104 localities with known palaeocoordinates from the western Tethys and adjacent areas, 214 fully revised ammonite species, their morphology and phylogenetical relationships. This database covers the early Pliensbachian (Early Jurassic), a period of particular interest because of the marked faunal provincialism of some major marine groups and an increase in sea-surface temperature at the end of the interval.

We integrated our data into a GIS, allowing the spatial exploration of different variables. We evaluate patterns of similarity-distance decay and we highlight their sensitivity to the taxonomic and spatial scales. We perform SIMPER analyses between the NW European and Mediterranean domains to determine the main clades responsible for this biogeographical contrast over the three chronozones of the early Pliensbachian. We further characterize these clades in terms of shell size, morphological variations, phylogeny and geographical range.

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## **Additional information on Spathian (late Olenekian) ammonoids from South Primorye and their palaeobiogeographic significance**

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Ammonoids from the lower Spathian (Lower Triassic) are widely distributed, but still poorly studied. We focus in this paper on taxonomic diversity mainly of early and middle Spathian ammonoids from South Primorye to show their palaeobiogeographic significance. Till recently, early Spathian ammonoids in this region were known mainly from the shallow-water Schmidt Formation, characterised by *Bajarunia*, *Tirolites*, *Tchernyshevites*, *Bandoites*, and *Amphistephanites*.

The Kamenushka section in South Primorye, which has been studied recently in detail, contains an excellent record of the Smithian–Spathian boundary within deeper facies, where no indications of major sedimentary breaks have been found and the three ammonoid assemblages have been distinguished. The lower Kamenushka Formation (about 42 m thick) is characterised by the presence of the ammonoid *Arctoceras subhydaspis*, the conodont *Scythogondolella milleri* and some other fossils, common for the upper Smithian. The middle Kamenushka Formation (about 44 m thick) yields early Spathian *Bajarunia*, *Albanites*, *Tirolites*, and *Koninckitoides*, and is additionally characterised by the appearance of the ammonoid genera *Nordophiceratoides*, *Arctomeekoceras*, *Jeanbesseiceras*, and *Inyoceras*. The upper Kamenushka Formation (85–100 m thick) contains typical middle Spathian ammonoids (e.g., *Yvesgalleticeras*, *Kazakhstanites*, *Goricanites*, *Khvalynites*, *Eodanubites?*, *Palaeophyllites*, *Keyserlingitidae?*), as well as longer-lived ammonoids (*Tirolites*, *Nordophiceratoides*, *Arctomeekoceras*, and *Inyoceras*). Till recently, *Deweveeria*, *Yvesgalleticeras*, *Jeanbesseiceras*, and *Inyoceras* have been reported only from the middle Spathian of North America, and *Arctomeekoceras* only from the middle Spathian of North America and upper Spathian of Arctic Siberia. Spathian ammonoids in South Primorye are characteristically accompanied by articulated brachiopods, abundant in both the shallow-water facies of early Spathian age (Schmidt Formation) and the deeper facies of middle Spathian age (middle Kamenushka Formation).

Characteristics of early to middle Spathian ammonoids from Kamenushka and other regions of South Primorye appear to suppose, firstly, that some of those appear to be directly ancestral to the corresponding middle Spathian species from the western USA and, secondly, that the Spathian ammonoid migration across the Pacific have been especially marked during the middle Spathian. The new middle Spathian genus of the family Palaeophyllitidae and the new Spathian species of some genera (*Bajarunia*, *Albanites*, *Yvesgalleticeras*, *Tirolites*, *Arctomeekoceras*, *Koninckitoides*, *Palaeophyllites*, *Nordophiceratoides*, *Jeanbesseiceras*, *Inyoceras*, *Prenekites*) are described.

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# Posters

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## The role of environmental cues, their effect on navigational tactics, and its application to the natural ecology of *Nautilus*

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The genera *Nautilus* and *Allonautilus* are remnants of a lineage of cephalopods that appeared in the Cambrian Period (~500 million years ago). Nautiluses retain ancestral features of the cephalopod line, including neural development, allowing us to examine evolutionary and ecological pressures contributing to behavioral and neural complexity in modern cephalopods. *Nautilus* inhabit complex, coral-reef slopes in the Indo-Pacific and make daily migrations from cold, deep waters (500m) to warmer, shallow waters (75m) at night. Using spatial cues during these migrations may be adaptive for hunting and predator-avoidance behaviors. Here we focus on how environmental cues inform *Nautilus* orientation and navigation, the content and mechanisms of their spatial learning and memory, and how pressures in their natural habitat may relate. We tested the ability of nautiluses to locate an exit hole/deep water in a circular shallow-water maze. The exit was cued during training by a visual beacon: a white striped circle surrounding the hole. Nautiluses could learn the visual cue and/or their route to the goal during training. During memory testing, the beacon a) was rotated 45° from the exit or b) was rotated 90° from the exit. In addition, to determine whether beacon learning was overshadowing route learning we compared two more groups of nautiluses in a second experiment. One group was trained with a beacon and tested by removing the beacon while the second group was trained and tested without a beacon. Our results demonstrate that the navigational tactics of *Nautilus* shift depending on the reliability and location of a beacon. As the beacon was rotated further during testing trials, it appeared the nautiluses relied less on the beacon and more on route navigation. In the second experiment, nautiluses showed different success rates between the two conditions, supporting the notion of a shared memory space. Determining the mechanisms of behavioral complexity in nautiluses is crucial to understanding evolutionary pressures shaping neural and behavioral complexity in the cephalopod lineage as a whole.

## ***Placenticerias kaffrarium* Etheridge, 1904, in the Upper Cretaceous of the Mariquita Valley (Namibe Basin, Angola): Taxonomy and biostratigraphic implications**

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The Namibe Basin is the southernmost and least studied of the Meso-Cenozoic coastal Atlantic basins of Angola. Due to the desert environment, many exceptional exposures are available for palaeontologic studies. Most of the onshore series are transversally cut by valleys with vertical slopes ("dambas") tens of meters high and several km long. The stratigraphic succession is comprised of: (1) Aptian-Albian alluvial fan conglomerates and evaporites; (2) Albian inner shelf carbonates; (3) middle Turonian to lower Coniacian inner shelf carbonates and sandstones; (4) a Santonian to lower Campanian volcanic complex with basaltic flows; (5) Campanian shelf limestones interbedded with Gilbert delta conglomerates; and (6) a diverse Palaeogene and Miocene cover. The studied area of Mariquita Valley is located 50 km north of the Namibe Bay, near the modern seashore. Ammonites were sampled from the middle and upper parts of interval 3, which is a 43 m thick section of shallow marine, laminated, grayish marls interbedded with yellow marly sandstones and fine sandstones with abundant molluscs. Among them, the ammonite *Placenticerias kaffrarium* Etheridge, 1904, has been identified. It is represented by several highly compressed and involute discoidal specimens with narrow tabulate venter, broad convergent flanks and funnel-like small umbilici, absent ornamentation or limited to low bulges and tenuous falcate ribs, and complicated subphylloid sutures with numerous frilled elements. These very ammonites with fine falcoid or sickle-shaped striae and sharp ventrolateral shoulders correspond to the *umkwelanense* morphotype (Klinger & Kennedy, 1989). As a whole, *P. kaffrarium* exhibits extraordinary intraspecific morphological diversity. It has been reported from a wide range of Turonian-Coniacian sections in South Africa, Madagascar, India, Angola and the US. In southwest Angola, this taxon was identified previously in the middle Turonian-lower Coniacian beds of the middle and upper part of the São Nicolau Section (Salinas Fm, which is immediately overlain by the Ombe Volcanic Fm: Cooper 1998). The Mariquita record suggests the same biostratigraphic succession, and matches with data inferred from the benthic associations. Correlations between Mariquita and other areas of the Namibe Basin also indicate that the studied interval records the last transgressive episode that preceded the ~85-80 Ma South Atlantic peak of alkaline magmatism, which is expressed by interval 4.

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## The Coniacian ammonoid genus *Hemitissotia* Peron, 1897, in the Iberian Peninsula (Spain and Portugal): Sequential context and morphology

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After a revision of the types of the species of the Coniacian ammonite genus *Hemitissotia* Peron, 1897, from the Iberian Peninsula (Iberian Basin, Spain; W Portuguese Basin, Portugal), today kept in the Wiedmann (Universität Tübingen, Germany) and Choffat (Museu Geológico de Lisboa, Portugal) collections, and the study of new specimens of the taxa *H. ceadouroensis* Choffat, 1898, *H. celtiberica* Wiedmann, 1975 (= *H. ceadouroensis*), *H. turzoi* Karrenberg, 1935, *H. dullai* (Karrenberg, 1935) and *H. lenticeratiformis* Wiedmann in Wiedmann and Kauffman, 1978, their geographical and stratigraphical ranges have been determined and related to the Maximum Flooding Surface (mfs) and the Highstand System Tract (HST) of the UZA-3.2 (*sensu* Haq et al. 1988) 3rd-order depositional sequence. The UZA-3.2 mfs (middle upper Coniacian) is laterally continuous along the main part of both basins and contains numerous specimens of *H. ceadouroensis* and *H. turzoi*, corresponding to an acme-type interval. *H. turzoi* is so common in this interval that it is used as biostratigraphic marker along the W Tethys (Barroso-Barcenilla et al. 2013). The UZA-3.2 early HST (uppermost Coniacian) is well-developed in the Iberian Basin and contains many specimens of *H. dullai* and *H. lenticeratiformis*. All these ammonoids are oxycones (morphogroup 11 *sensu* Westermann 1996) and, thus, nektonic forms, well adapted to active swimming. Such forms had low drag coefficients and high max. swimming velocities. *H. ceadouroensis* and *H. turzoi* had nearly smooth, larger, more compressed and involute shells than *H. dullai* and *H. lenticeratiformis*. The differentiation of mfs and early HST is difficult based on cephalopod morphologies only. These oxycones show a tendency to become progressively smaller, more depressed and ornamented (hydrodynamically less efficient). Therefore, their relationship with mfs and early HST seems to be an adaptive response to sea-level changes, as a link between eustatic variations and ammonoid morphologies.

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## Comparisons between Belemnitida and Sepiida: Is the cuttlebone prong an analogue of the belemnite rostrum?

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Belemnite rostra are commonly used for performing palaeoenvironmental studies based on geochemical data. However, few detailed analyses of the belemnite microstructure and growth are available. The fossil order Belemnitida is included in the subclass Coleoidea, but most coleoids have completely reduced their calcareous shell. Only Sepiida has retained a calcareous internal shell still used as buoyancy device. Thus, studying Sepiida cuttlebone may be useful for understanding belemnite growth. In this study we compare the microstructure of the rostrum of Jurassic belemnites (*Belemnopsis* and *Hibolithes*) with that of cuttlefishes (*Sepia officinalis* and *S. dorbignyana*) in order to examine if their style of growth were similar.

In belemnites, calcite crystals of the rostrum solidum start growing along the apical line from successive centers of crystal growth that emerge radially towards the apex and the external wall of the rostrum as a spherulitic prismatic layer. If observed under SEM, calcite crystals are prismatic and thicken and become parallel as they grow outwards from the apical line and get closer to the outer part of the rostrum. When the rostrum is etched with glutardialdehyde, prismatic texture of crystals is not longer preserved and, in turn, several fans of smaller and radially distributed crystals are observed. These fans of crystals are very similar to those observed in the dorsal shield of cuttlebones of *Sepia*. Moreover, in longitudinal sections of the apical spine or prong of the cuttlebone, radially arranged, spherulitic-like crystals of aragonite are observed, which in turn display similar growth pattern than those observed in the apical line of the belemnite rostrum.

When the belemnite rostrum solidum is observed under the petrographic microscope, it is seem to be formed by concentric layers displaying radial structure which are separated by very thin layers without radial structure. This texture resembles that observed in the prong of *Sepia* where consecutive and concentric layers of prismatic and radial aragonite crystal are interbedded with organic-rich and not radially distributed layers.

Although it is not possible to observe the organic matter in fossil belemnite rostra, a growth pattern is observed in belemnites when studied with fluorescence microscopy suggesting that some growth layers or rings were organic-rich compared with others. Additionally, the fact that the apical line and some growth rings of belemnite rostra are diagenetically altered suggest that these areas could be in origin organic-rich like in the *Sepia* prong, and more suitable for being altered during the early diagenesis. In this sense, the *Sepia* prong is a good analog for belemnite rostrum and growth convergences suggest that growing of belemnites occurred similarly that the prong of sepiids does.

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## An example of taxonomic revision of an oversplitted cephalopod family: the Deshayesitidae

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The Deshayesitidae is one of the most significant Lower Aptian (Lower Cretaceous) ammonite families (fossil cephalopods) due to its wide paleogeographical extension, large morphological disparity and abundance. Moreover, this family provides almost all the species used for relative datation of the biostratigraphical units (zones and subzones) of the Lower Aptian. Unfortunately, this family has been taxonomically oversplitted in more than one hundred « species » and six genera. The diagnosis characters of these typological taxa are generally the rib density and the shell shape (characters known nowadays to be of potentially poor taxonomic significance due to high intraspecific variation) and the evolutionary characters were neglected in most of the cases. Due to its wide paleogeographical extension and its high typological diversity, a revision of this family using a “paleobiological” concept of species would be a considerable work. We performed a “first step” revision of this family based on literature data. In our opinion, the most complete literature data about this subject are the works of Casey (1961, 1963) and Casey et al. (1998) about the Deshayesitidae of Southern England. These authors recognized initially no less than 66 typological species and varieties and 3 genera. The results of this “first step” revision are as follows: (1) the general ontogenic sequence of the Southern England Deshayesitidae consist of five stages: post embryonic stages A and B, stage C with high growth in whorl height, narrow whorl section and slender ribbing, stage D with low growth in whorl height, broad whorl section and robust ribbing, and adult stage E with robust and smooth simple ribs. (2) Intraspecific variability of ornamentation and shell shape is similar throughout the Deshayesitidae evolutionary history and it is determined by three “rules”: the *variability of type 1* according to the Buckmann’s law of covariation and depending on the duration of the ontogenic stage C, and the *variability of type 2* which concerns the intensity of expression of the ornamental relief and a probable sexual dimorphism with macroconchs and microconchs. (3) The evolution of the Deshayesitidae is interpreted as being anagenetic. The evolutionary patterns are increasing complexity of suture lines, the emergence of a new ontogenic stage, and the emergence of three successive novelties on the inner whorls ventral area (smooth siphonal band, to subtabulate ventral area, then lateroventral tubercles) that evolve centrifugally through time (neotenic process). The group is reinterpreted as being composed by only one chronospecies divided into 2 genera, 8 successive paleospecies and 2 subspecies. Discordance in the “degree of evolution” of the English specimens attributed to one of the recognized species, *Deshayesites deshayesi*, and the type specimen of this species from the Paris Basin (France) is attributed to a diachronism between the English and French *D. deshayesi*.

## Factors of intraspecific variability in the ammonites

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Taxonomy is an important step that has a major influence over all other downstream fields of paleontological research. But when the aspect of variability is not (or too little) taken into account, the number of divisions in a given taxonomic group can artificially increase and no longer reflect the biodiversity they are supposed to materialize.

Oversplitting produced by the typologist approach tends to override the evolutionary signal and makes it undetectable or uninterpretable, and thus makes any attempt tedious to use a group in biostratigraphy. It also contributes to artificially overestimate biodiversity, to produce phylogenetically fictitious parallel lineages uninterpretable evolutionarily, etc. The study of intraspecific morphological variability associated with an evolutionary view is of primary interest to fight against this bias in ammonites.

There are several generic factors potentially at the origin of the patterns of intraspecific variability in the ammonites: (1) dimorphism, (2) changes in the ontogenic sequence, (3) changes in the rate of growth, which can affect the duration of ontogenic stages and adult size (heterochronies of development), (4) variation in shell proportions and ornamentation within one ontogenic stage (covariation), (5) phylogenetic changes (microevolution), and (6) geographic and environmental variations. These factors are materialized by

- (1) The dipolar covariation (i.e. 1st Buckman's Law of covariation).
- (2) The tripolar covariation. The existence of variability around three morphological poles in groups distant phyletically and stratigraphically, demonstrates that this variability is not a marginal case.
- (3) The heterochronies of the development, which can be morphological dependant or independant.
- (4) The secondary attenuation of ornamentation, which can occur regardless of the type of morphology, from the gracil forms with weak ornamentation to the hyper-ornated robust forms.
- (5) The dimorphism of sexual origin. The antidimorphes can be distinguished (macroconchs and microconchs) by differences in size, coiling (opening of the umbilicus or uncoiling of the shell), changes in the peristome, changes in ornamentation, or all four combined.
- (6) The coiling variation in heteromorphic ammonites, ornamental dependant or not.

The importance of the dipolar covariation is confirmed to explain intraspecific variability in ammonites. It seems to be the norm for a large number of cases, or at least to be dominant despite some of possible variants. However, it is not the only source of covariation and its influence must be relativized against the other factors cited. This list is not exhaustive, and it appears that the covariation is subject to several agents that reflect the expression of different mechanisms and causes, and whose action is nested but not necessarily interdependent. New research taking into account the maximum possible groups are needed to highlight their mechanisms, their constraints, their relationship to the environment, and their interactions (work in progress).

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## Evolutionary patterns and process of the Gassendiceratinae (Ammonoidea, Hemihoplitidae, Upper Barremian)

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The family Hemihoplitidae (Ancyloceratoidea, Ammonitina) is a key group for the North Tethyan Margin in the Upper Barremian due to its rapid diversification. The Gassendiceratinae contains three genera, *Gassendiceras*, *Pseudoshasticrioceras* and *Imerites*, which have close phyletic links; they range from the Vandenheckei Zone to the Giraudi Subzone. These genera are crioconic to ancyloceratic ammonites; their size varies from large (*Gassendiceras*) to small (*Imerites*, which bears an early turricon), and the ornamentation is characterized by the succession of several specific ontogenic stages.

The palaeontological approach leads to preferentially retain the characters that have proven to be an important source of phylogenetic informations. The anagenetic evolution of *Gassendiceras* is modulated by the interaction of heterochronies of the development (acceleration of ontogenetic development) associated with late novelties that fit the expression of a peramorphic process of palingenesis type. This evolutionary channelling leads to the expression of more and more innovative and original morphologies of the derived forms with respect to ancestral forms, but which are also more gracile. This evolution could be interpreted as the result of a constant selection of the most peramorphic individuals (and therefore the more gracile), which were favored at the expense of the most robust. It seems reasonable that this selection was to adapt to the environmental changes due to the transgressive sequence (increased water depth disadvantaging the most robust morphologies) that occurs during the Vandenheckei Zone and part of the Sartousiana Zone on the North Tethyan Margin.

*Pseudoshasticrioceras* evolved from *Gassendiceras*. But conversely to the latter, the *Pseudoshasticrioceras* lineage is characterised by a neotenic process up to *P. bersaci*. The later species *P. autrani* is characterised by a strong size decrease and a progenesis.

The presence of a helical early stage in *Imerites* is not a sufficient argument to classify it into the Heteroceratidae. Its ornamental features and most of all the succession of its ontogenetic stages attest an origin within the Gassendiceratinae. The turricon is an early novelty in the *Pseudoshasticrioceras-Imerites* lineage. The successive species are: (1) *P. autrani*, (2) *I. dichotomus* and (3) *I. giraudi*. This evolution is characterised by an acceleration of the ontogenetic stages and by the expression of an inflexion point from which the adult ornamentation is delayed.

All these transformations/ novelties at the origin of the genus *Imerites* from *Pseudoshasticrioceras* are perhaps linked with the eustatic variations and changes in the marine environment, considering the fact that the Dichotomus Horizon corresponds to the start of an important phase of marine transgression in the S-E of France. These changes are associated with a faunal turnover with the dominance of the Heteroceratidae, which probably led *Imerites* to an increase of the ecological competition with the neighboring morphological species (i.e. small sized with an early turricon, too), ultimately leading to their rapid extinction.

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## A New Smithian (Lower Triassic) Ammonoid Biostratigraphy from Utah (USA)

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As interest in the end Permian mass extinction event and the Triassic recovery has grown in recent decades, greater attention has necessarily been focussed on the time framework for this important interval. Intensive sampling of the lower portion of the Thaynes and Moenkopi Groups (Lower Triassic) in central and southern Utah (USA) has led to the recognition of a new key regional Smithian ammonoid succession. The new biostratigraphic zonation is comprised of twelve subdivisions, resulting in a sequence with much higher resolution than the long-recognized *Meekoceras gracilitatis* and *Anasibirites kingianus* Zone, that can be correlated not only with other western USA sites, but also with major localities worldwide. Middle and late Smithian faunas contain many taxa with wide geographic distributions allowing long-distance correlation with faunal successions from other regions such as British Columbia, the Canadian Arctic, South China, Spiti and Oman. Combined with Dienerian data from Nevada, and Spathian data from Nevada, Idaho, California, and Utah, a refined biostratigraphic scheme for the Lower Triassic of the Western USA can be achieved.

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## **Assembling the ammonite fauna of the Western Interior Seaway using a biogeographical framework**

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The repeated formation of extensive shallow seas throughout Earth history provides large-scale natural experiments that can be used to observe biotic response to novel environmental conditions and the concomitant ecological opportunities. Compared to open marine habitats, these epeiric seas are characterized by shallower depths and altered salinity, temperature, and circulation patterns. The fauna that become established within these environments must therefore be the evolutionary product of one or more of the following processes: uninhibited dispersal from open marine habitats; limited dispersal of open marine fauna, suggesting ecological filtering; and possible rounds of in situ speciation within the epeiric sea. The ecological tolerances and evolvability of the open marine source fauna therefore play crucial roles in determining how the epeiric sea is colonized and to what extent they are able to speciate within the new environment. Few studies, however, have used direct comparisons of epeiric fauna to their source fauna(s) in the broader biogeographic context to characterize the ecological attributes associated with occupying epeiric seas.

In this context, the ammonite fauna of the North American Western Interior Seaway is an ideal study system. It was host to a rich and diverse ammonite fauna from the Early through the Late Cretaceous, a time when high sea levels and inland flooding resulted in globally distributed shallow seas. Here I present a continental-scale study using a dataset containing over 1,500 ammonite species occurrences compiled from published literature and visits to key collections. The data span North America between the present-day Arctic Ocean and Gulf of Mexico and are focused on the Aptian and Albian, capturing the time of onset of the Western Interior Seaway. The occurrence dataset will be analyzed in conjunction with associated lithological data as well as body size data collected from the literature. By comparing these attributes and the evolutionary history of the early fauna in the Western Interior Seaway with that of fauna(s) in the immediately adjacent open marine environments, I explore environmental and ecological variables that influence the potential of lineages to invade and diversify in environmental conditions they had not previously experienced.

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## Methane seeps as ammonite habitats: evidence from O, C and Sr isotopes in well-preserved shells from methane seeps in the Upper Cretaceous (Campanian) Pierre Shale

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Methane seeps in the Upper Cretaceous Pierre Shale of the U.S. Western Interior contain a rich fauna including ammonites (*Baculites*, *Hoploscaphites*, *Didymoceras*, *Placentoceras*, *Solenoceras*), bivalves (*Lucina*), gastropods, sponges, and crinoids. Occasionally, the shell material in the seeps is very well preserved, retaining the original mineralogy and microstructure. We explored two such seeps from the upper Campanian *Didymoceras cheyennense* and overlying *Baculites compressus* Zones (74.7-73.5 Ma) in southwestern South Dakota. The values of  $\delta^{13}\text{C}$  in the micritic limestone of the seep are extremely light, ranging to as low as -47‰. These light values confirm the impact of anaerobic oxidation of methane on the isotopic composition of the dissolved inorganic carbon reservoir. We also observed light values of  $\delta^{13}\text{C}$  in well-preserved specimens of the ammonites *Hoploscaphites* and *Baculites*. These values are significantly lighter than those measured in specimens from age-equivalent non-seep deposits. We conclude that the ammonite shells incorporated isotopically light dissolved inorganic carbon derived from seep methane and that these mobile animals were living in close proximity to the vent fluids. Values of  $\delta^{18}\text{O}$  are comparable in both the micritic limestone and ammonite shells, and suggest precipitation temperatures of  $\sim 25^\circ\text{C}$ . Methane hydrates are thus unlikely to be involved in these seeps. The  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio is also elevated in the limestone core and well-preserved shells of ammonites compared with the coeval marine value, suggesting that the seep fluids are imprinted with a radiogenic Sr signature, perhaps derived from isotopic exchange with granitic deposits at depth associated with the Black Hills uplift.

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## Species Schedules: a new idea for Fossils' Data Sheets

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A paleontological museum, to be considered as such, must have an own collection representing its scientific richness and starting point for paleontological studies. In this regard, it is necessary to propose a new way to create a database of fossils belonging to such collections in order to obtain a global system of systematic and taxonomic information by using new technologies and communicative strategies. The database has to be constituted by data-sheets, which completely describe the species collections and show all their features.

Every data-sheet ought to have a certain number of pages, organized as suggested in the following:

- the logo of the structure, in which the species described is stored is present in each page, together with its scientific name, its storing code, the name of the fossils' classifiers and of who has compiled the data-sheet and the number of pages;
- on the first page: the image of the holotype of the species or the best preserved specimen, its systematic and taxonomic classification, its diagnosis, its biostratigraphic position;
- on middle pages: the list of synonymy; the complete description of species; remarks, geographic and stratigraphic distributions, information about the institution of holotype and references;
- on the last pages: images of all other specimens belonging to the same species of the collection in order to show intraspecific diversities.

The above described organization is realized starting from the available paleontological papers in order to create an applicative tool for museum activities. This instrument permits to keep all information at hand about a species. Such a scheme may be realized in every kind of computer format, particularly with HTML format that permits an increasing usability through their publication online.

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## Cephalopod accumulations in the Late Ordovician of northern England

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Concentrations or accumulations of cephalopods are relatively rare in the Ordovician successions of Britain. Most occurrences can only be recognised by an increase in abundance at a particular horizon. The state of exposure does not usually facilitate detailed observation of their mode of occurrence. The occurrence of two Late Ordovician cephalopod concentrations in northern England, in the late Katian, Troutbeck Siltstone Member of the Ash Gill Mudstone Formation and the Keisley Limestone Formation allow some investigation of their respective modes of occurrence. The concentration occurring in the Troutbeck Siltstone Member is associated with stromatolites, whilst the pattern of distribution of the cephalopods indicates that they are either influenced by, or influence the distribution of the stromatolites. The lack of other macrofossils may indicate that the conchs were stranded in shallow water, although the appearance of a *Hirnantia* fauna in the mudstones immediately above the cephalopod concentration may suggest rapid subsidence or sea-level rise. By contrast, dense accumulations of a monospecific association in the Keisley Limestone Formation exhibit telescoping as well features that provide additional evidence that this unit represents the remains of a carbonate mud-mound.

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## **Diversity and palaeoecology of early Devonian invertebrate associations in the Tafilalt (Anti-Atlas, Morocco)**

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The Anti-Atlas of Morocco is famous for its highly fossiliferous and well-exposed Palaeozoic rocks. Superb exposures of Early Devonian outcrops and their high abundance of mostly well-preserved fossils yield the possibility of studying faunal associations in their stratigraphical context. We collected five invertebrate associations of Early Devonian age (early Lochkovian to early Emsian) including a very rich Pragian fauna with well-preserved macrofossils from the south-west of Jebel Ouaoufilal (Filon 12) in the Tafilalt. All faunas were examined for alpha diversity and ecospace utilization by identifying the macrofossils, counting their frequencies and grouping them to ecological categories of tiering, motility and feeding behaviour. Quantitative analyses of the data showed a strong increase in diversity from the early Lochkovian to the late Pragian followed by a slightly reduced diversity in the early Emsian in the Taouz area of the Tafilalt. The ecospace use considerably extended during the Early Devonian and reached its maximum in the early Emsian. Especially, the abundance of benthic organisms was conspicuously high in the Pragian fauna and was significantly decreased in the early Emsian fauna. The increase followed by a decrease in species richness and the expansion of ecospace use may reflect regional environmental changes in the Early Devonian of the Tafilalt. In particular, the fluctuating benthic diversity led to the supposition that changes in oxygen content near the seafloor in combination with sea-level fluctuations occurred. These assumptions are supported by visible changes in the colour of sediments during the Early Devonian of the Tafilalt.

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***Amphispirula* nov. gen. from the Eocene of Southern Moravia (Czech Republic): a new ancestor of the Recent deep-sea squid *Spirula*?**

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A single specimen of an enigmatic coleoid cephalopod from the Eocene of southern Moravia (Czech Republic) represents the oldest record of a spirulid with a markedly, endogastrically coiled phragmocone. Distinctly oblique septa in *Amphispirula* show similarities to sepiid coleoids, but a ventrally closed siphuncle refers this taxon to the order Spirulida. The existence of a coiled-phragmocone-bearing coleoid in the Eocene significantly precedes Miocene records of *Spirulirostra* – a guard-bearing coleoid, which is suggested to be ancestral to Recent *Spirula*. A mosaic of morphological features in *Amphispirula* might point to an older and unknown ancestor of modern *Spirula*, but more likely represents a new evolutionary lineage within spirulid cephalopods.

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## First report on upper Frasnian cephalopods of the Lahonry quarry, Lompret, Belgium

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About three years ago, the Lahonry quarry at Lompret, 10 km west of Frasnes, Belgium, was quarried northwards, towards the old railroad, exposing upper Frasnian reefal limestones of the Petit-Mont Member. Since the summer of 2013, the surrounding and partially overlying peri-reefal Neuville Formation and younger Matagne Formation became progressively more exposed. Regular visits to the quarry allowed the assemblage of a large cephalopods collection from various levels within the upper Frasnian (Early and Late *rhenana* conodont zones).

The Neuville Formation consists of nodular limestones and shales, time-equivalent to the Petit-Mont reefal buildups. At Lompret, the Neuville succession varies from predominantly barren shales with bentonites to highly fossiliferous nodular limestones with abundant crinoids and corals. Cephalopods were found only in one of the studied outcrops, related to a fault zone in the northeastern corner of the quarry. Up to 30 large gephuroceratoids (*Manticoceras*) and three fragments of large nautiloids were found during the second half of 2013. The absence of small specimens and tornoceratoids, plus the nearly complete absence of *in-situ* benthic fauna may suggest these are drifted shells.

Fossiliferous shales of the Matagne Formation were exposed in two corners of the quarry. In the northeastern corner, a few meters above the sharp transition from the Neuville to the Matagne Formation, several limestone beds are rich in cephalopod remains. The lower one contains a concentration of small goniatites (mostly < 20 mm) and orthocones in the middle and upper part of the bed, plus an enrichment of medium sized (70-150mm) gephuroceratoids on top of the bed, about one every 2 m<sup>2</sup>. The highest concentration of cephalopods, however, is situated in a limestone nodule level. Tornoceratoids are fairly common within the entire interval. A fairly similar set of beds is exposed along the southeastern limit of the quarry. Several meters up-section, cephalopods are primarily preserved as small (<20 mm) pyritic internal moulds. Gephuroceratoids are again fairly common in this interval.

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## New finds of goniatite anaptychi from the Frasnian (Upper Devonian) of Belgium

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Detailed fauna sampling of the upper part (*jamieae* – Lower *rhenana* conodont zones) of the Boussu-en-Fagne Member (Grands Breux Formation, Frasnian) in the access road to the disused Lion quarry near Frasnes, Belgium (southern margin of the Dinant Synclinorium [DS]), by one of us (TH), gave four carbonaceous structures that can be identified as goniatite anaptychi. They are small, have a maximal length between 6 and 11 mm, and are well-preserved, allowing to reconstruct the change in their outer shape during growth.

Only a fairly limited number of goniatite anaptychi have been reported from Belgium by Maillieux (1935, 1936, 1940) from the Upper Frasnian ‘Schistes de Matagne’, which partly corresponds now to the Matagne Formation. To these records, we can add two specimens curated at the University of Liège that were previously assigned to phyllopod crustacean shields, namely *Ellipsocaris dewalquei* from the Upper Frasnian Aisemont Formation of Comblain-la-Tour (eastern part of the DS) and a specimen assigned by Van Straelen (1933) to *Spathiocaris chagrinsensis* from the Middle Frasnian Ermitage Member (Moulin Liénaux Formation) of Hotton (southeastern flank of the DS). All specimens are (re)figured and compared.

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## Unravelling Silurian nautiloid cephalopod distribution

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Study of the distribution of nautiloid cephalopods as tools for paleogeographical reconstruction is based on the premise that they are particularly sensitive to distance or water depth separating landmasses and to fluctuations in sea level and temperature. Distribution of Silurian nautiloids has to date been undervalued as a method for unravelling the record of oceanic/climatic global change. Most occurrences represent deposition within shallow water facies with the orthoconic shells in particular often being oriented either by current or wave action on the bedding plane. Various studies have been done with regard to their depositional environments and many theories and models have been proposed for the formation of concentrated accumulations of nautiloids (Histon 2012a). A study of these pelagic faunas in the Silurian sequences of the Carnic Alps (Histon 2012b) and the Graz Palaeozoic (Histon et al. 2010) in Austria complemented by data from detailed sequence stratigraphy and time specific facies analyses (Brett et al. 2012) has highlighted significant data regarding eustatic and climatic changes at precise intervals along the North Gondwana Margin during Silurian time. Clarification of ambiguities related to the taxonomy of Silurian nautiloids is a fundamental part of this study as the tracing of the migrational routes of these faunas also lies in the exact identification and comparison of taxa at least at generic level, if not even to species level. In this respect a comparative study has been done of collections of the British Silurian nautiloids and their stratigraphic distribution (Holland 2014) with potential biozone taxa from the North Gondwana Margin areas. The findings may have critical relevance within the context of identification of bioevents and their relation to oceanic/climatic cycles.

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## First results of the Jurassic ammonite distribution in North Bohemian and Moravian area (Czech Republic)

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Some localities in the North Bohemian (located near Krásná Lípa town) and Moravian area (Brno town and vicinity) have provided a great number of fossils, predominantly of ammonite faunas. In Moravia, abundant *Cardioceratidae* occur together with members of the *Aspidoceratidae* family and rarely with representatives of the *Oppeliidae* and *Perisphinctidae*. These occurrences suggest a stratigraphic near the Middle/Late Jurassic boundary.

The ammonite specimens, predominantly belonging to the family *Perisphinctidae*, *Ataxioceratidae*, and some of the *Aulacostephanidae* and *Cardioceratidae* from the Late Jurassic of the North Bohemian part, are currently revised based on the material rediscovered in the museum collections. The stratigraphic range was determined as the interval of the Upper Oxfordian to Kimmeridgian.

The systematic revision is in accordance with the first research executed in the 19<sup>th</sup> century and improved our view of the stratigraphy and paleogeography of the Czech Republic during the Middle and Late Jurassic. Ammonite composition and distribution shows the possibility that probably a wide marine strait crossed the Czech Republic with significant faunal migratory activity.

The occurrence of the Boreal families *Aulacostephanidae* and *Cardioceratidae* appears to be a key point of research, the presence of Upper Callovian *Hecticoceras* together with *Cardioceras* and *Peltoceras* shows the conclusive Callovian transgressive pulse demonstrable in Moravia.

## Belemnites from the Triassic of China extend their origin back by ~33 million years

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This study sheds new light on the debated existence of Triassic belemnites. Distribution and diversity patterns of belemnites in Middle Jurassic to Cretaceous times have been well recognized. Their evolutionary history in the Early Jurassic is, however, not fully understood. Current hypotheses of the early evolution of belemnites are summarized as follows. *Schwegleria* (Belemnitina), which is characterized by a small and short rostrum, occurs in the Hettangian of northern Europe. It is the oldest belemnite so far known, and was considered as a possible stock-group of all belemnites. It has been concluded that belemnites evolved in Europe in the Hettangian; their distribution was restricted to the European shelf seas until the Pliensbachian. (e.g., Doyle 1994).

Findings of pre-Jurassic “belemnites” (e.g., *Jeletzkyia* from the Carboniferous of North America, Palaeobelemnopsidae from the Permian of China, Sinobelemnitidae from the Triassic of China) challenged this view, but were reclassified later mostly as aulacocerid or phragmoteuthid coleoids (e.g., Doyle et al. 1994). The only exceptions are the Sinobelemnitidae, described by Zhu and Bian (1984) from the lower part of Ma’atang Formation in the Longmen Mountains region, China. We have re-studied the type specimens of these sinobelemnitids, which are stored at the Chengdu University of Technology, Chengdu, China. The Chinese sinobelemnitids have well preserved internal structures such as protoconch and siphuncle. They co-occur with ammonites indicating a Carnian age such as *Protrachyceras*, *Discotropites*, *Tropites*, and *Paratropites* (Gou 1993). The Sinobelemnitidae can be clearly distinguished from the Aulacocerida by the following diagnostic features of the Belemnitida: (1) a high apical angle of phragmocone (>12°), (2) short distance of each septa, and (3) ventrally inclined protoconch. Previous studies (e.g., Doyle 1993, 1994; Doyle et al. 1994) also considered the Chinese Sinobelemnitidae as belemnites s.s. (order Belemnitida). At the same time, the Triassic age assignment of these forms has been questioned (Doyle 1993, 1994; Weis and Delsate 2006) because the typical belemnite morphology (long rostra with a well-developed alveolar groove), superficially exposed by the Sinobelemnitidae, had not been recorded from pre-Middle Jurassic strata in Europe (Doyle 1993, 1994; Doyle et al. 1994). The Sinobelemnitidae have a long belemnite rostrum with, however, one well-developed deep groove on the dorsal side. This dorsal groove, which is only present in the Japanese Hettangian and Sinemurian belemnites (Iba et al. 2012), is a morphological feature that has been overlooked in previous European studies. The presence of Sinobelemnitids from the Triassic of China and earliest Jurassic of Japan therefore (1) extend the origin of the belemnites back by ~33 m.y. into the Triassic, (2) suggest that this group did not necessarily originate in northern Europe, and (3) imply that belemnites survived the Triassic–Jurassic extinction, one of the five big mass extinctions in the Phanerozoic.

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## Late Cretaceous fish cans: Fish preserved in ammonite body chambers from platy limestones in northeastern Mexico

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The study of fossils is mostly based on fossilized individuals, each group studied separately by experts. In addition, interactions between organisms are hard to reconstruct from the fossil record. The Upper Cretaceous platy limestones of northeastern Mexico preserve fossils in an exceptional way. Some findings include articulated fish preserved in ammonite body chambers (Nyborg et al. in press). Fish within ammonite shells are rarely observed in the fossil record and comprise mostly isolated individuals. We describe several fish occurrences in twodimensionally preserved ammonite shells, including the first report of multiple fish. We discuss several scenarios for such a preservation. Many of these scenarios can be excluded with arguments based on recent fish behavior, ammonite and fish taphonomy and paleoenvironment. The ammonites represent different morphotypes, and each shell preserves a different fish morphotype. The scenarios developed describe thus more general patterns in Cretaceous seas.

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## Nomenclatural review of *Polyptychoceras* spp. (Upper Cretaceous heteromorph ammonites) from Japan

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*Polyptychoceras* Yabe, 1927 from the Upper Cretaceous is a genus of heteromorph ammonites, which is characterized by a paper clip-like shell morphology. Until today, occurrences of 12 species have been reported from Japan, while there are still many unclear points in the species names of this genus. For example, *P. yubarensis* has been attributed by Yabe (1927) in many articles probably because he first proposed this name. In fact, Yabe (1927) provided not the original description of the species because this article only listed the name of this species and gave no biological description (the Code's Article 12.1).

In the present study, we examined the nomenclature of these 12 species on the basis of the *International Code of Zoological Nomenclature Fourth Edition* (International Commission on Zoological Nomenclature 1999, 2003, 2012), which is currently in effect. As a result, 10 species-names are available, while two species names are unavailable. The following is the reason why two species names are unavailable: One of them is an “unjustified emendation” (Art. 33.2.3) of an available name. The generic combination of this name is ambiguous, and the name is unavailable (Art. 11.9.3.4), although such an emended name is usually available. The other unavailable name is a *nomen nudum* (name without description or definition). These results will ensure the objectivity and reproducibility of relevant studies and will contribute to future taxonomic works.

For your information, this abstract is not issued for the purposes of zoological nomenclature (Disclaimer based on Art. 8.2).

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## **An asymmetric ammonite from the Toarcian of Cénaret (Lozère, France)**

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Ammonite pathologies are well-documented in the fossil record and they are helpful for understanding ammonite biology. This study focuses on a Toarcian ammonite specimen from Cénaret (Lozère, France) that shows a poorly-known pathology characterized by a strong, if not full, asymmetry in ornamentation. The specimen was found in marls that most probably belong to the Bifrons Zone. We identified this peculiar specimen taxonomically ourselves and also asked several ammonite workers to independently identify separately the two sides of the ammonite.

The left side of the specimen shows an ornamentation typical of *Hildoceras semipolitum*, whereas the right side indicates *Brodieia primaria*. Furthermore, the observation of the suture lines leads to the same identifications. Importantly, no evidence of injuries can be found on the shell after a careful observation of the entire ammonite coiling with a scanning electron microscope. Although the actual process responsible for the observed asymmetry remains elusive, most hypotheses challenge the phylogenetic relationship usually inferred for the genera *Hildoceras* and *Brodieia*.

Overall, this specimen from Cénaret shows that ammonite ornamentation, and to a lesser extent suture lines, can be subject to an intra-individual-level variability. Although similar pathological specimens seem to be rare, they are crucial for deciphering morphogenetic processes and for refining phylogenetic relationships.

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## Unusual umbilical modification in a Middle Smithian (Early Triassic) ammonoid from Crittenden Springs, Elko County, Nevada

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Early Triassic (Middle Smithian) ammonoids from Crittenden Springs are widely known for their superb preservation, especially the shell or test, which sometimes preserves unique features including relict color patterns, false color patterns, healed injuries, the black layer and associated wrinkle layer as well as the black apertural band (Klug et al. 2007). An additional feature, an umbilical plug together with its distinctive cover is newly reported for the very involute, oxyconic ussurid taxon *Parussuria compressa* Hyatt and Smith. Superficially, the cover imparts an occluded appearance to the umbilicus, and on a few very well-preserved specimens, it renders the open but involute nature of the umbilicus virtually undetectable with the naked eye. Adding to this deception is the presence of low-intensity bundled growth lines on the cover, making it indistinguishable from the adjoining lateral shell.

Cross-sectioned specimens reveal that the base of the slightly off-center plug, which consists of secondary shell deposits, begins on the umbilical shoulder of the second whorl and extends a short distance across the flank to the umbilical wall of the succeeding whorl, thus occupying about 2/3 of the umbilical width. The cover, formed by a deposit of outer or primary shell, wedges out against the lateral shell at the umbilical shoulder, making a smooth transition from the periphery of the cover to the lateral shell, while the inner margin of the cover folds tightly back on itself to form the occluded umbilicus. As the conch grows, primary shell is deposited on the old cover, eventually forming a new cover.

Also briefly discussed are possible evolutionary functions of this modification, including among others the streamlining of the shell or the prevention of encrustation by epizoic organisms in the umbilical region.

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## Quantitative stratigraphy of Late Devonian and Early Carboniferous ammonoid successions in the Rhenish Mountains (Germany)

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The application of modern biostratigraphical methods, especially concerning ammonoid stratigraphy, is a new and promising approach. These methods provide a finer stratigraphical resolution and a minimization of contradictions without new extensive sampling efforts being required.

We investigated the occurrences of 64 late Famennian (Late Devonian) ammonoid species from 13 sections and 52 early Tournaisian (Early Carboniferous) ammonoid species from 7 sections using three modern biostratigraphical correlation methods, (1) Unitary Associations (UA), (2) Constrained Optimization (CONOP) and (3) Ranking and Scaling (RASC). A test of the existing modern ammonoid zonation was carried out to see which of the three methods is the most suitable for refining it. The results obtained from these methods were compared with each other with respect to ammonoid succession and resolution; they were tested with the empirical data from selected reference sections.

Principally, the UA, CONOP and RASC methods lead to similar outcomes with respect to the succession of occurrence events of the analysed ammonoid species in the various sections and the fit with the reference sections is generally good. Of the three approaches, the UA method results in the lowest resolution, but it is the most robust. Application of the CONOP method results in a higher resolution than that obtained by the UA method but it is less robust and the highest resolution is provided by RASC. For the Devonian, only the results of the RASC method coincides with the existing modern ammonoid zonation, the *Effenbergia lens* Zone, the *Muesseniaergia parundulata* Zone and the *Muesseniaergia sublaevis* Zone cannot be resolved by the UA and CONOP methods. For the Carboniferous the results of all methods coincide with the existing modern ammonoid zonation.

On the basis of the results of the three analyses, the existing modern ammonoid zonation is confirmed for the Devonian dataset and partly refined for the Carboniferous dataset; the new *Weyerella molaris* Zone is separated.

Which method is the most suitable depends on the nature of the available data and the purpose of the investigation. For the biostratigraphical analysis, the RASC method is considered to be the most suitable but the more conservative UA method facilitates the separation of zones. The UA and RASC methods are fast and they can be used to complement one another, this gives them both an advantage over the CONOP approach, which is the least suitable as it is slow and produces contradictory stratigraphical occurrences of species.

## Ammonoids from the Tournaisian-Viséan beds of the Chatkal River Basin (Middle Tien Shan, Uzbekistan)

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Ammonoid occurrences in the Upper Tournaisian and Lower Viséan of the Middle Tien Shan have been known for over three decades, but until now they have not been systematically studied. This work is based on the material collected in 1980-1990 by Iskander Nigmatzhanov (Tashkent) from localities in the lower reaches of the Chatkal River (Uzbekistan). The ammonoids come from the Kuilyk Formation composed of deep water argillaceous, siliceous, laminated limestone with beds of cherts and calcareous-argillaceous mudstones and from synchronous limestone forming carbonate buildups of the Chatkal Group. Four ammonoid assemblages have been discovered of Late Tournaisian and Early Viséan age.

- (1) Assemblage 1 is from the base of the Kuilyuk Formation and includes *Muensteroceras* sp. nov. 1, *Muensteroceratoides aksuense*, *Imitoceras* sp., *Becanites* sp., *Pericyclus* sp. indicating the Late Tournaisian *Pericyclus* - *Progoniatites* Zone. The position of this zone coincides with the base of the conodont *D. bouckaerti* Subzone of the *G. semiglaber* Zone in the regional conodont scale of Central Asia.
- (2) Assemblage 2 comes from the carbonate buildups of the Chatkal Group («Aurakhmat» and «Kulosya») and includes: *Habadraitites* sp. nov. 1, *Nodopericyclus* sp. nov. 1, Gen. et sp. nov. 1, similar to *Asiacyclus* from the Terekty Beds of Eastern Kazakhstan and *Helicocyclus* sp. Conodonts from this level indicate the *D. bouckaerti* Subzone of the *G. semiglaber* Zone of the regional scale. *Habadraitites* and *Nodopericyclus* have previously been recorded only from North Africa (Argiles de Teguentour Group, Algeria), where they are found at different levels. *Habadraitites* comes from the *Pericyclus* – *Progoniatites* Zone, whereas *Nodopericyclus* was found in the younger Upper Tournaisian beds and indicates the regional *Helicocyclus* – *Ouaoufilalites* Zone (Korn et al., 2010). The Chatkal assemblage is probably synchronous with that of the *Helicocyclus* – *Ouaoufilalites* Zone.
- (3) Assemblage 3 is of a younger Tournaisian age and includes *Merocanites djaprakensis*, *Muensteroceratoides aksuense*, *Helicocyclus tianshanicus*, *Dzhaprakoceras sonkulica*, *Neopericyclus kokdzharensis*, *Ammonellipsites* sp., *Hammatocyclus* sp., suggesting the *Fascipericyclus* – *Ammonellipsites* Genozone. The taxonomic composition of the assemblage is similar to that of Zone F described by Popov (1968) from the lower horizons of the Dzhapryk Formation in the Son Kul Lake area (Kyrgyzstan). These beds also contain conodonts of the *G. semiglaber* (*D. bouckaerti* Subzone) and *S. anchoralis* – *G. pseudosemiglaber* Zones of the regional scale allowing a more precise placement of the F Zone of the Dzhapryk Formation.
- (4) Assemblage 4 from the upper part of the Kuilyuk Formation and the synchronous limestones of the Kulosya buildup contains *Helicocyclus* sp., *Dzhaprakoceras* sp., and *Bollandoceras* sp., of which *Bollandoceras* suggests the Early Viséan age.

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## **Cephalopod reproductive strategies through time and space: Database on cephalopod egg (Coleoidea) and embryonic shell (Ammonoidea and Nautiloidea) dimensions**

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Egg size is the most important feature of reproductive strategies in cephalopod molluscs. Species with smaller eggs tend to have a higher fecundity (so higher natural mortality), smaller hatchlings with longer duration of planktonic stage (if exists), and higher potential for dispersal. To promote evolutionary researches of cephalopod reproductive strategies through time and in different habitats, the authors created a database containing data on embryonic shell size in 531 species of Ammonoidea, 134 species of Nautiloidea, and on egg size of 330 species of extant Coleoidea. The database is available upon request and the authors expect to put it online soon.

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## **Mesozoic ammonoid cephalopods with iridescent colour patterns**

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Colour patterns in molluscs are sometimes exhibited on the exterior shell surface as shades of black, gray, brown, and red. A wide variety of shapes and designs are known including zigzag, chevron and wavy patterns, longitudinal and transverse bands, and spots. In the Ammonoidea (Early Devonian to Late Cretaceous), the oldest known colour patterns are transverse stripes and longitudinal bands from the early Triassic in Nevada, USA. It is unknown why ammonoids from rock units older than the Triassic have not yielded specimens with colour patterns, especially in places where Paleozoic orthoconic nautiloids with colour patterns co-occur with ammonoids.

In the last decade, hundreds of ammonite specimens with undescribed colour patterns have been discovered. These new patterns are iridescent longitudinal bands on the external surface (the outer prismatic layer) of the shell. These bands are probably the result of the prismatic shell ultrastructure selectively breaking down light into different wavelengths (i.e., different colours). Ammonoid sites that preserve an iridescent colour pattern have been collected from around the world including: the Upper Jurassic Callovian Stage of Saratov, Russia and Łuków, Poland; the Early Cretaceous Albian Stage of Mahajanga Province, Madagascar and Normandy, France; and the Late Cretaceous Campanian Stage from Coon Creek, Tennessee, USA and the Maastrichtian Stage of north-central South Dakota, USA.

These sites have incredibly good preservation with seemingly unaltered aragonite shell. The functions of these iridescent markings are probably similar to those of opaque colour patterns produced by modern Mollusca shells including camouflage, sexual attraction and light screening. In order to utilize these patterns these animals lived in the photic zone (shallow water) as part of the nektonic food web. Because we are not aware of any modern cephalopod (or Mollusca) that has this type of colour pattern, it appears that this pattern became extinct with the demise of the Ammonoidea at the K/T extinction event.

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## ***Nautilus* shells in a cenote: Lifou, Loyalty Islands, South Pacific**

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Exploration of a cenote on Lifou (Loyalty Islands, South Pacific) revealed more than 35 empty *Nautilus macromphalus* shells in saltwater on the cenote floor between 35-40 meters below the piezometric surface. This is the first known occurrence of modern *Nautilus* shells in a karstic system. The shells are scattered and oriented randomly on the rocky cenote floor. Most are unbroken mature individuals with faded brown stripes. Some are cemented by carbonate mud to the cenote floor and others have cemented carbonate mud partly filling the umbilical opening and body chambers. Seven shells were collected for analysis. These shells have a chalky outer surface. SEM analysis confirms there is no recrystallization of the aragonite shell material. No other organisms, living or dead, were observed on the *Nautilus* shell surfaces, attached to the limestone rubble, or in the cenote water column. Radiocarbon dating of the shells indicated ages of  $6380 \pm 30$  to  $7095 \pm 30$  y BP, making these the oldest *Nautilus* shells known since the Pleistocene. The  $^{238}\text{U}$  series radionuclides  $^{210}\text{Pb}$  (half-life = 22.3 y) and  $^{226}\text{Ra}$  (half-life = 1600 y) were also measured and generally showed radioactive equilibrium between these nuclides, consistent with their old radiocarbon ages. The taphonomic pathway of this *Nautilus* death assemblage is only partly understood. Human placement of the shells in the cave is rejected based on the radiocarbon age and cenote geometry. The restricted radiocarbon ages of the shells suggest that a connection to the adjacent marine waters existed for ~700 years and *Nautilus* occasionally entered from the seaward site through a flooded karstic system. Unable to find the exit, they were trapped and died - probably from starvation. After ~6400 y BP, the connection with the adjacent ocean was lost. This unique occurrence provides a minimum age for the appearance of *Nautilus* in the Loyalty Islands and provides insight into fossil cephalopod occurrences in karstic environments.

## A discovery of coleoid jaws in the Valanginian of the Russian Platform

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Cephalopod jaws were discovered in the bullions of gray calcareous micaceous sandstone in a gully on the right bank of the Unzha River (village of Unzha, Kostroma region, Central Russia). The sandstone contained abundant shells of the ammonites *Euryptychites* ex gr. *astierptychus* (Voronetz), *Siberites* cf. *ramulicosta* (Pavlov), and mainly distorted, and infrequent *Delphinites* sp. The same beds contain abundant bivalves *Buchia keyserlingi* (Trautschold) var. *siberica* (Sokolov), less commonly *Inoceramus taimyrensis* Zakharov, and infrequent belemnite rostra of the genus *Pachyteuthis* and onychites (Fig. 1). These fossils suggest that the sandstone belongs to the Lower Valanginian *Polyptychites michalskii* Zone. The collection contains elements of upper and lower jaws of coleoids (Figs. 2, 3). Apparently they belong to the same taxon, *Pachyteuthis*.



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## Biostratigraphy of the Bathonian Stage of the Russian platform based on ammonites and foraminifera

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The Bathonian Stage of the Russian Platform contains varying amounts of fossil remains. The middle part of the Bathonian contains only foraminiferal assemblages, whereas ammonites are found in the lower and upper parts (table).

Age	Volga River basin		Pechora River basin		
	Ammonite zonation	Foraminifera zonation	Ammonite zonation	Foraminifera zonation	
Lower Callovian	Cadoceras elatmae	Haplophragmoides infracallovienensis - Guttulina tatarensis	Cadoceras elatmae	Kutsevella instabile - Astacolus batrakiensis	
Bathonian	Upper Paracadoceras keuppi		Paracadoceras keuppi		H. infracallovienensis - G. tatarensis
	Mid- dle ammonites not found	Ammidiscus baticus	ammonites not found	Ammidiscus arangastachiensis - Recurvovoides anabarensis	
	Lower Arcticoceras ishmae	Lenticulina volganica - Vaginulina dainae	Arcticoceras ishmae		
	Oraniceras besnosovi		ammonites not found	Trochammina aff. praesquamata	Riyadhella sibirica
Upper Bajocian	Pseudocosmoceras michalskii	Ammidiscus subjurassicus - Lenticulina saratovensis	Arctocephalites arcticus		

**Ammonites.** Two zones are recognized in the Lower Bathonian in the middle reaches of the Volga River. The Besnosovi Zone based on the range of *Oraniceras* is equivalent to the Convergens and Macrescens Subzones of the standard Zigzag zone. The Ishmae Zone corresponding in its position in the section to the upper part of the Lower Bathonian is recognized both in the middle reaches of the Volga River and on the Pechora River (Izhma River and Dreshchanka River). No ammonites have been found in the middle part of the Bathonian of European Russia (including the Northern Caucasus). The Keuppi Zone was recognized in the Upper Bathonian, both in the basin of the Pechora River (Pizhma River), and in the basin of the Volga River.

**Foraminifers.** The Lower Bathonian in the basin of the Volga River contains beds with *L. volganica* – *V. dainae*. The foraminiferal assemblage of the upper part of these beds corresponds to those of the T. aff. praesquamata Zone of the basin of the Pechora River. The overlying beds are recognized as beds with *A. baticus*. The H. infracallovienensis – G. tatarensis Zone is established in the Upper Bathonian – Lower Callovian. The T. aff. praesquamata Zone has been recognized in the basin of the Pechora River in the Upper Bajocian and Bathonian. The A. arangastachiensis – R. anabarensis Zone is a stratigraphical equivalent of the above described zone. This region shows a wide distribution of the R. sibirica Zone. The Upper Bathonian of the Pechora River contains the foraminiferal assemblage of the K. memorabilis – G. tatarensis Zone.

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## **Of ammonite biostratigraphy, lithostratigraphic formations and geological maps in Switzerland.**

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Historically, the legend of Swiss geological maps was often based on terms referring to (pseudo-) chronostratigraphic subdivisions (e.g. “Séquanien”) or index fossils (e.g. “Blagdeni-Schichten”). Although they are now obsolete, some of these terms still remain in use as handy informal expressions, mainly due to the lack of a correctly defined alternative. In the meantime it also became obvious that many classical mapped units are definitely diachronous (e.g. Opalinus-Ton) or have a stratigraphic range that do not fully coincide with their age-based name (e.g. “Oxfordien”). Therefore, a clear separation between the descriptive definition and naming of mapped rock units (lithostratigraphy) and their interpretative attribution to time units (bio- and chronostratigraphy) was needed.

Nowadays, the mapping concept for the Geological Atlas of Switzerland 1:25'000 (AG25) is based on lithostratigraphy, i.e. descriptive, material-based units observable in the field, without direct age or genetic consideration. In order to clear up and update the legend of the AG25, a lithostratigraphic harmonization has been launched in 2011 by the Swiss Geological Survey in close collaboration with the Swiss Committee for Stratigraphy. A revised cartographic scheme is now available at national scale. The documentation of valid units, together with the current equivalence of superseded terminology, will progressively be integrated in the Lithostratigraphic Lexicon of Switzerland ([www.stratigraphie.ch](http://www.stratigraphie.ch)).

Although a relative succession of events leading to the present-day geometrical relationships can be reconstituted at a local to regional scale based on lithostratigraphy, further calibration methods are needed for larger scale correlations. Therefore, age assignment of the successive units remains crucial and much effort is still needed for documenting, updating and refining the bio- and chronostratigraphic framework in many regions. In this perspective, detailed ammonite biostratigraphy provides very precise and valuable information, also for the evaluation of the duration of stratigraphic gaps.

Biostratigraphic data – when available – will be incorporated in the description of the mapped lithostratigraphic units. This will ultimately permit to draw revised time-based correlation tables, as illustrated by a first provisional compilation of data for the Early Jurassic in Switzerland.

## Siphuncular structure in Jurassic belemnite *Megateuthis* and extant *Spirula*

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### Jurassic belemnite *Megateuthis*

The siphuncular structure in *Megateuthis* differs from that in all hitherto known shelled cephalopods (Mutvei 2014, in press). The cyrtconic septal neck is composed of two layers: a thick nacreous layer of the lamello-fibrillar type (type 2), and a thin, chitinous layer that covers its inner surface. Both layers are continuous from the same layers in the septum. The inner surface of the septal neck is covered by a thick, chitinous, tubular layer that appears on the adoral septal surface close to the septal neck. It consists of closely packed tubes that have about 2.0µm thick chitinous walls. The tubes are oriented at right angles to the siphuncular length axis. Each tube is distally divided into three branches that open into the siphuncular cavity. The connecting ring is composed of three layers. The nacreous layer of the septal neck continues into the connecting ring as an outer, non-calcified, chitinous layer that often is destroyed by diagenesis. The thin chitinous layer of the septal neck fuses with the tubular layer and forms the inner layer of the connecting ring. Thus, all three layers of the connecting ring are chitinous and highly elastic. The siphuncular cavity is traversed by diaphragms that consist of flat, thin, calcareous sheets.

**Aulacocerid belemnites** have similar siphuncular structure as the belemnite *Megateuthis*.

### Extant *Spirula*

As in *Megateuthis* (Mutvei 2014a, in press), the septa and septal necks in *Spirula* are composed of the nacreous layer of the lamello-fibrillar type. The septal necks are holochanitic. Instead of the chitinous tubular layer in *Megateuthis*, the inner surface of each neck in *Spirula* is covered by a calcareous pillar layer that thins out towards the distal end of the neck (Mutvei 2014b, in press). The pillars are oriented at right angles to the siphuncular long axis. The proximal portion of each pillar is composed of several columns of calcareous crystals. The crystals are arranged in numerous growth lamellae. In the distal portion of each pillar the crystalline columns are transformed into prisms that are oriented more or less obliquely towards the siphuncular cavity. The calcareous elements in the pillar are embedded into large amount of chitinous substance. The connecting ring has two layers: an outer, thin, spherulitic-prismatic layer that originates on the outer surface of the septal neck and covers the inner surface of the pillar layer of the preceding septal neck, and an inner chitinous layer that is non-mineralized continuation of the septal neck.

### Siphuncular structure in other coleoids

In remaining coleoids three additional types of the connecting rings are known: phragmoteuthid type (Mutvei & Donovan 2006), bactritid-like coleoid type (Mutvei et al. 2012) and *Sepia* type (Doguzhaeva & Mutvei 2012).

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## **Carboniferous ammonoids in the Natural History Museum, London: historical collections and their stratigraphic significance**

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Over the last 200 years the British Museum (subsequently NHM) has acquired a significant proportion of the Palaeozoic cephalopod material collected in the UK, including important historical collections described by James Sowerby, John Phillips and others, largely contributed by amateur geologists. Significant contributions have been made by William Gilbertson, William Bisat, Samuel Gibson, and Wheelton Hind, all non-professional palaeontologists or geologists. The re-examination of these parts of the NHM holdings has revealed not only interesting historical details of the procedures surrounding collection acquisition and curation in the 19th and early 20th centuries, but also allowed the recognition of the original type series of high-profile stratigraphic markers such as *Neoglyphioceras spirale* Phillips, 1841), *Nuculoceras nuculum* Bisat, 1924; *Bilinguites superbilinguis* (Bisat, 1924), *Cancelloceras cancellatum* (Bisat, 1923) and many others. Many specimens have never been photographed, or at least not since the 1920s. All 530 known historical specimens have been catalogued and photographed together with their labels, and type specimens have been photographed in detail to show their identification characters. Locality details have been verified where possible. The study is supported by a NHM Special Funds grant, by the Russian Foundation of Basic Research, project no. 14-05-00774, and the Program of Presidium of the Russian Academy of Sciences no. 28.

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## Carboniferous ammonoids in the Zilair Megasyclinorium

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At the end of the Mississippian, ammonoids widely populated the western subregion of the South Urals, which was a shelf of the continental margin of the Baltica continent. They particularly favoured the marginal trough of the Zilair Megasyclinorium (ZM), which was formed near the carbonate platforms of the continental shelf of Baltica during the beginning of its collision with the Kazakhstan continent. Ammonoids from this region are found in multiple occurrences and are well-known, but their habitats and ecological affinities need further study. We re-examined Serpukhovian and Bashkirian ammonoid localities in several ZM sections of the Bukharcha Formation (including the localities in Muradymovo, Kugarchi, Bogdanovka and Bolshoi Uskalyk) and analyzed ammonoid communities against the sedimentary settings. The ZM ammonoid fauna is very distinct from most contemporary assemblages in its diversity and endemism, showing similarities with the Western Kazakhstani and some Central Asian faunas. The Bukharcha Formation consists of rhythmic intercalation of bioclastic grainstone and packstone, thin-bedded wackestone and siliceous mudstones with interbeds of calcareous polymictic sandstone and sandy packstone with graded bedding showing the deposition of distal turbidites intercalating with contourites. In the southern ZM, the lower part of the Bukharcha formation is composed of argillaceous carbonates, with beds of deep water shale and siltstone, sometimes clastic limestones and limestone breccia, while the upper part is mostly limestone with cherty interbeds. The Lower Bashkirian has many beds of spongolites. In the north of the ZM, the formation contains considerably more carbonates. Other fossils include foraminifers, sponge spicules, gastropod protoconchs, ostracods, crinoids, occasionally bryozoans, brachiopods, and algae. Ammonoids from the Muradymovo Section (north) and Kugarchi section (south) are scarce in the late Serpukhovian and the basal Bashkirian but their diversity and endemism increased by the end the *Homoceras* phase. Beds with ammonoids represent bioclastic grainstone lenses interbedded with packstones. This lithology suggests impulsive deposition of bioclastic debris by storms or gravity flows. The change in the succession of cycles in the Lower Bashkirian shows the transition from the marginal deep outer shelf facies to slope and depression deposits, which contributed to the considerable increase in abundance and diversification of the ammonoid biota. The study is supported by the Russian Foundation of Basic Research, project no. 14-05-00774 and the Program of Presidium of the Russian Academy of Sciences no. 28

## Nautiloids from the Muschelkalk facies of the South-Iberian Triassic (Betic Ranges, Southern Spain)

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In the External Zones of the Betic Ranges (S Spain), epicontinental carbonates of Muschelkalk facies crop out extensively. These carbonates are constituted by 2 coeval units, the Siles Fm. and the Cehegín Fm. (Pérez-Valera & Pérez-López 2008), representing the lithostratigraphic variability from proximal to distal areas of the S-Iberian Palaeomargin in the Middle Triassic. Recently, the discovery of a great number of cephalopods in these units yielded a biostratigraphic framework in which 3 Ladinian ammonite biozones have been distinguished (Pérez-Valera et al. 2011). Numerous nautiloid specimens of five genera have been collected together with ammonoids in this Muschelkalk facies. In detail, moderately involute and subquadrate specimens have been attributed to *Germanonautilus* Mojsisovics, 1902; moderately evolute and ornamented to *Mojsvaroceras* Hyatt, 1883; subdiscoidal with broad ventral and lateral lobes to *Grypoceras* Hyatt, 1883; compressed and involute to *Indonautilus* Mojsisovics, 1902; and subquadrate with narrow funnel-like umbilicus to *Picardiceras* Parnes, 1986. Most of these nautiloid genera were historically described and they are known in the Germanic and Tethyan provinces. The presence in the Betic Ranges of the genus *Picardiceras*, typical of the Sephardic Province, also suggests that some of the species of the other genera could be endemic of this region and coinciding to those identified in Sinai (Egypt) and Negev (Israel). These nautiloids are currently being studied in order to improve the systematic, biostratigraphic and palaeobiogeographic ranges of these poorly known Triassic cephalopods in SW Europe.

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## Continuous or discontinuous? - The ultrastructure of flares, parabolae, constrictions and varices within ammonoid shell

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The sculpture of ammonoid shells encloses a high variety of structures like ribs, nodes, keels, etc., which were formed during a more or less constant growth of the shell tube. But it also includes several shell morphologies, which are thought to represent certain growth halts, e.g. flares, parabolae, constrictions or varices (see Arkell et al. 1957; Bucher et al. 1996). The question is whether the internal structure actually reflects this assumption: Does a general functional morphologic construction exist or do different constructional concepts evolve, which need an individual interpretation? Ultrastructural observations show differences between these structures. A better understanding could be the key for palaeobiological or phylogenetic considerations. Indeed, flares of *Argonauticeras* (Lytoceratoidea) and parabolae of *Binatisphinctes* (Persphinctoidea) represent temporary growth halts. The outer shell portions (outer prismatic layer, nacreous layer) form a distinct interruption, which forms a distinct "breaking edge". At flares, it is bent outward. The edge of the primary shell generation is underlain by a new shell package, which proceeded to grow. The inner prismatic layer is unaffected, which denotes its subsequent formation. The overall appearance resembles a healed injury. During the formation of the new shell generation, a certain withdrawal of the mantle edge can be assumed. Sectioned shell material of the edge may show a certain shell resorption (Kohn et al. 1979) or controlled breakage. The general construction of constrictions misses a distinct interruption of shell layers within phylloceratids, perisphinctids and desmoceratids. The typical furrow of the shell surface is formed by an undulation of the outer prismatic layer. The often accompanied inner thickening is formed by the nacre layer, which forms the internal ridges of varices, too. Within these thickening, some outer nacreous lamellae may wedge out. The inner prismatic layer thins to compensate the inner relief. The absence of a distinct interruption of the shell argues against a long lasting growth halt but the formation of the nacre thickening probably denotes a slowing of shell formation with probable pauses in the deposition of nacre as indicated by its "internal interruption". *Eotetragonites*, a member of the Lytoceratoidea, forms a weak discontinuity in the outer prismatic layer at its constrictions. At the adoral edge of constrictions, a new generation of the outer prismatic layer is added from within. The remaining features, nacre thickening, thinning of inner prismatic layer, are similarly developed as in other constrictions (and varices) and seem to be formed subsequently. This interruption is probably related to the construction of the lytoceratid flares, which raises the question of a general "episodic" growth pattern accompanied in flared and constricted Lytoceratids.

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## Bioerosion in shells of the modern *Nautilus*

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Bioerosion in shallow water deposited shells of *Nautilus macromphalus* - During two field trips to New Caledonia numerous shells of *Nautilus macromphalus* were collected by Royal H. Mapes and colleagues in two carbonate-sediment dominated bays near Mu, Lifou Island, in water depths of 1-3 m. Many shells were extensively encrusted and overgrown, especially by red algae but also by green algae, bryozoans and serpulids, and intensively bioeroded. Because bioerosion is one of the major factors responsible for the degradation of limestone and carbonate skeletal material, a detailed study on four shells of *N. macromphalus* was carried out to investigate the ichnocoenosis, i.e. the assemblage of ichnotaxa. Therefore, synthetic resin casts were prepared and studied with the scanning electron microscope.

The ichnocoenosis in the four shells contains a rich amount of bioerosion traces. Imprints of settling and encrusting organisms are present as well. Among the imprints, the thalli of coralline algae are especially abundant, while diatom imprints are less abundant. The ichnocoenosis comprises at least 22 ichnotaxa and is dominated (in abundance) by traces produced by autotroph organisms (seven ichnospecies are produced by cyanobacteria and four by chlorophytes). Our currently ongoing study may reveal even more ichnospecies as approximately 15 so far unidentified traces need to be investigated more closely. The ichnocoenosis, at the present state of the study, reflects a typical assemblage of ichnotaxa as is expected for shallow, tropical marine settings. The high abundance and density of traces in the shells demonstrates how bioerosion diminishes the chance of preservation of carbonatic shells by facilitating breakup and dissolution.

## Early Triassic flemingitid ammonoids of South Primorye and their palaeobiogeographic and phylogenetic significance

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The suborder Ussuritina Zakharov et Moussavi Abnavi appears to be directly ancestral to the suborder Phylloceratina Arkell, representatives of which are widely distributed in the Jurassic and Cretaceous. Flemingitid and palaeophyllitid ammonoids appeared in early Smithian and late Smithian times, respectively. They are the earliest groups of the Ussuritina. We focus in this presentation on the taxonomic diversity of the Flemingitidae in South Primorye, firstly investigated by Kiparisova (1961), and the geographic differentiation of Early Triassic representatives of the Ussuritina. The family Flemingitidae currently includes, in our opinion, the following 12 genera: *Flemingites*, *Pseudoflemingites*, *Subflemingites*, *Euflemingites*, *Anaxenaspis*, *Anaflemingites*, *Rohillites*, *Guangxiceras*, *Galfetites*, *Ussuriflemingites*, *Balhaeceras*, and *Subbalhaeceras*. Nine of them are known from South Primorye. The highest diversity of flemingitid ammonoids of South Primorye was found in the lower Smithian (*Mesohedenstroemia bosphorensis* Zone, *Euflemingites prinadai* beds). These include *Flemingites radiatus*, *F. trikamnaensis*, *F. alexanderi*, *Flemingites* sp., *Euflemingites prynadai*, *E. artyomensis*, *Euflemingites* sp. indet., *Ussuriflemingites abrekensis*, *U. primoriensis*, *Balhaeceras balhaense*, *Rohillites laevi*, and *R.?* *ambiguous*. Recently, some flemingitid ammonoids (*Pseudoflemingites* sp. nov. and *Rohillites* sp. nov.) were additionally discovered in the *Churkites* cf. *syaskoi* beds of the Tri Kamnya Cape area, which seems to be late Smithian in age (Smyshlyaeva and Zakharov, in press). *Guangxiceras tobisinense* was found earlier in a block of calcareous sandstone-coquina of the Tobizin Cape, originated from the uppermost Smithian (*Anasibirites nevolini* Zone) or lowermost Spathian (*Tirolites-Amphistephanites* Zone). In early Smithian time, most known genera of the family Flemingitidae occurred at low and middle palaeolatitudes, except the cosmopolitan genera *Euflemingites* and *Anaxenaspis*, which were widespread in both the Tethyan and Boreal realms. Tozer (1994) described “*Flemingites*” *reticulatus* from British Columbia in the Boreal Realm, but the assignment of this species to Flemingitidae is questionable because of insufficient data on its sutural morphology. During late Smithian time flemingitid ammonoids became rare at the low-middle (*Pseudoflemingites*, *Rohillites*, and ?*Guangxiceras*) and high (*Anaxenaspis*) palaeolatitudes. Late Smithian and early-middle Spathian palaeophyllitid ammonoids (e.g., *Burijites* and *Palaeophyllites*), another lineage of the suborder Ussuritina, are known only at the low and middle palaeolatitudes, including South Primorye. This work is partly financially supported by the grant RFBR (14-05-00011).

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## **Ammonoid fauna in the Teshionakagawa area, northern Hokkaido, Japan**

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The Cretaceous to Paleocene Yezo Group is extensively distributed in a north-to-south belt in central Hokkaido, the northernmost Japanese island. We have clarified the Upper Cretaceous ammonoid biostratigraphy and the features of ammonoid fauna of the Yezo Group in the Teshionakagawa area, northern Hokkaido. Abundant ammonoid species including heteromorphs occur in the six formations of the Teshionakagawa area, namely the Sakugawa, Saku, Nishichirashinai, Omagari, Osoushinai, and Hakobuchi Formations among the group, toward the top of the sequence. These formations of the group in the area yield well-preserved ammonoids and other molluscan organisms, which sometimes display aragonitic preservation. Based on the age-diagnostic species of the ammonoids and inoceramid bivalves, the Cenomanian/ Turonian boundary is located at the Sakugawa Formation, the Turonian/ Coniacian boundary is the adjacent to the boundary of the Saku/ Nishichirashinai Formations, the Coniacian/Santonian boundary at the Nishichirashinai Formation, and the Santonian/Campanian boundary at the upper part of the Omagari Formation.

The Obira, Kotanbetsu and Haboro areas are located northward in the northwestern Hokkaido. The ammonoid and inoceramid assemblages in the Teshionakawa area are exactly similar to those in the Haboro area, and generally similar to those in the Kotanbetsu area, whereas dissimilar to those in the Obira area. These natures are probably caused by similarity of the sedimentary environments or the difference of distances from the Teshionakagawa area.

Ammonoid species from the Teshionakagawa area are scarce from the Coniacian and Santonian Stages compared with the other Stages. It would be related with a local massive influx of coarse-grained sediments (Omagari Formation) into the low-oxygenated mud bottom associated with OAE3 at that time.

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## Durophagous predation and its effect on the body size of scaphitid ammonoids in the Late Cretaceous Western Interior Seaway

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Predator-prey interactions through geologic time played an important role for the evolution of the morphology of oragnims and their body size. Here, we report the predatory shell breakage on scaphitid ammonoids (*Scaphites*, *Hoploscaphites*, and *Discoscaphites*) in the Late Cretaceous Western Interior Seaway, focusing on whether the predation pressure facilitated an increase in body size of the scaphitid ammonoids or not.

A total of 1,009 specimens of scaphitid ammonoids recovered from the Upper Cretaceous (Turonian – Maastrichtian) of the South Dakota, USA, and repositied in the American Museum of Natural History and the University Museum, the University of Tokyo, were utilized in this study. A quantitative analysis were made for the ventral shell breakage in these specimens. A similar ventral shell breakage has already been reported in Jurassic and Cretaceous ammonoid collections from other regions.

As a result of our analysis, apparent ventral shell breakage was recognized in 69 scaphitid specimens. In most damaged specimens, the breakage occurs between 0° – 180° in the angular position towards the aperture, which is located in the back of the shell considering the angle of orientation of living scaphitids. The occurrence of the ventral breakage is extremely rare in the Turonian and Coniacian specimens, whereas it is fairly common in the Campanian (7%) and the Maastrichtian (10%) ones. The shell diameter of the adult scaphitid ammonoids tends to increase with time, though the ventral shell breakage appears to occur independently of shell diameter.

The high incidence of breakage and the absence of the repaired shell portion indicate that ventral breakage resulted from lethal predation. Based on the abundance and the breakage size, possible predators include other cephalopods such as *Placentiaceras* or the coiled nautiloid *Eutrephoceras*, coleoids, fish and mosasaurs. The increase in shell diameter of scaphitid ammonoids throughout the Turonian-Maastrichtian sequence in the study area indicates a possible anti-predatory function toward increasing predation pressure. However, statistical analysis did not detect any predatory characteristics such as size-selective predation and increase in the estimated body size of the predator, which would facilitate the increase in body size of scaphitid ammonoids. As the adult shell size of the macroconchs increased significantly with time, reproductive strategy might have been an important factor for the evolution of the larger body size of the scaphitid clade in the Late Cretaceous Western Interior Seaway.

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## New Records of cephalopod fossils (Cephalopoda) in Peninsular Thailand

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Sixteen species of nautiloid and ammonoid cephalopods were identified based on fossils collected from Peninsular Thailand. Fossils from Ordovician Strata are one ruedemannoceratid nautiloid –*Mediganella magna* Teichert & Glenister at Amphoe Ron Phibun, Changwat Nakhon Si Thammarat, one sactorthoceratid nautiloid –*Sactorthoceras banestanensis* Evan at Amphoe La-ngu, Changwat Satun. One goniatid ammonoid –*Neoglyphioceras subcirculare* (Miller) is from Devonian-Carboniferous Strata at Amphoe La-ngu, Changwat Satun.

Fossils from Triassic Strata are one orthoceratid nautiloid –*Michelinoceras* sp., one syringonautilid nautiloid –*Javavionautilus heterophyllus* (Hauer) at Amphoe Muang Phatthalung, Changwat Phatthalung. Eleven species of ammonoids were collected from the same locality and comprised one paranannitid –*Arianites musacchi* Arthaber, one ussurid –*Ussuria waageni* Hyatt & Smith, one noritid –*Bosnites clathratus* Hyatt & Smith, one acrochordiceratid –*Paracrochordiceras* sp., one beyrichitid –*Eutomoceras* sp., one ceratitid –*Halilucites plicatus* Hau., three hungarites –*Hungarites* sp., *Hungarites* sp. A and *Hungarites* sp. B, two aplococeratids –*Aplococeras* sp. and *Aplococeras parrus* (Smith) and one celtitid –*Indoceltites trigonalis* (Diener).

All taxa are new records in Thailand.

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## **An attempt to create a 3D digital model database for the type specimens of Cretaceous ammonoid in Japan**

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When finding a fossil, researchers need to decide whether the fossil is new or a known species by way of consulting systematic descriptions, photographs and illustrations from a huge number of past papers. Recently, development of electronic journals is removing the burden to gather numerous papers. However, the best way is to directly observe the type specimens, thus making it possible to check its characteristic features in detail. There is no easy way for researchers to gather numerous papers and to make a search of specimens housed in research institutes such as universities and museums.

Recently, many research institutes publicize databases of digital images of paleontological specimens on the Internet. Occasionally, digital images of type specimen are also made available online. The 3D digital models are useful, because they give us sterical recognition of a specimen. As a pioneering work, the GB3D type Fossils Online (<http://www.3d-fossils.ac.uk/home.html>) share 3D digital models of type specimens, held in British collections, via the Internet.

Cretaceous marine strata which yielded abundant ammonoids are widely distributed throughout Japan. Over 300 new species of Cretaceous ammonoids have been reported by researchers, and over 600 type specimens are held in Japan.

It is our aim to share on the Internet 3D digital models of the type specimens of Cretaceous ammonoids, which are housed in various research institutes of Japan. Using our 3D-scanner, I plan to put 3D-digitalised images of the type specimens on the Internet as an ongoing project. If this project spreads across catalogues and countries, it will become a significant contribution to research fields such as taxonomy and biostratigraphy.

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## **Allopatric variation of Pharaoh Cuttlefish *Sepia pharaonis* Ehrenberg, 1831, Species Complex in two oceans around Thai Peninsular based on mitochondrial DNA sequences**

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Allopatric variation of the pharaoh cuttlefish, *Sepia pharaonis* Ehrenberg, 1832, in Thai Waters is hypothesized to be partly initiated by a geographic barrier, the Peninsular Thailand. The Peninsular Thailand is the northern part of the Thai-Malay Peninsular, which separates the Pacific Ocean (the Gulf of Thailand) and the Indian Ocean (the Andaman Sea). The variations of the cuttlefish are recognized as different colour patterns on the dorsum. Specimens of pharaoh cuttlefish were collected from 9 coastal localities for partial sequencing of 16S and COI mitochondrial DNA. The phylogenetic trees revealed three likely clades, one in the Andaman Sea and two in the Gulf of Thailand. The cuttlefish in the Andaman clade are with mixed colour patterns but what in the Gulf of Thailand clades are with one colour pattern which mostly recorded in the Gulf of Thailand. Mixing of colour patterns in all clades indicate the current occurrence of gene-flow. The result suggested the origin of *Sepia pharaonis* in the Pacific and subsequent dispersion during the Cenozoic into the Indian Ocean.

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## Surprising diversity: Early Jurassic belemnites from Italy (Mediterranean Tethys)

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The Late Triassic and Early Jurassic were times of major changes in the evolution of coleoids. In particular, the belemnites s.s. (Belemnitida) appeared in the Late Triassic and achieved an almost worldwide distribution in the Early Jurassic. The phylogenetic relationships and the palaeobiogeography of the Early Jurassic belemnites are yet largely unknown. As a contribution to this debate, we report here new belemnites from the Peri-Mediterranean Tethys (Italy), an area which has been poorly investigated for belemnites.

The belemnite localities are situated in the Central Apennines and in western Sicily, two areas that have been intensively studied both from a stratigraphic and structural point of view. All specimens come from Lower Jurassic sediments (upper Sinemurian-upper Toarcian) and their exact stratigraphic occurrence could be established by accompanying ammonite faunas. The systematic and taxonomic analysis of the belemnites reveals a previously unknown diversity for Mediterranean Tethys, testified by several taxa belonging to the suborder Belemnitina (genera *Hastites*, *Passaloteuthis*, *Pseudohastites*, *Bairstowius*, *Cuspoteuthis* and *Megateuthis*). The coeval occurrence of rare “canaliculate” belemnites (suborder Pachybelemnopseina) was really unexpected. These are treated in open nomenclature and cannot be safely assigned to any known genus with the exception of a well preserved specimen of *Pachybelemnopsis* sp. (phragmocone, protoconch and siphuncle are preserved). The herein reported specimens represent thus the earliest records of pachybelemnopseins in Europe and adjoining Mediterranean domain.

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