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Zoë Hughes

Chair of the Organising Committee

*Candidates for a prize are noted with an asterisk

Underlined author denotes designated speaker

Exceptional preservation of organic periostracum in a Valanginian ammonoid from the Neuquén Basin, central Andes of Argentina

Beatriz Aguirre-Urreta[1], Luciana Marín[1], Darío G. Lazo[1], Maisa Tunik[2], Martin Parada[2] and Verónica V. Vennari[3]

1 Instituto de Estudios Andinos, CONICET and Universidad de Buenos Aires, Argentina
2 Instituto de Investigación en Paleobiología y Geología, CONICET and Universidad Nacional de Río Negro, Argentina
3 Instituto de Evolución, Ecología Histórica y Ambiente, CONICET and Universidad Tecnológica Nacional, Argentina

We report the exceptional preservation of organic periostracum in multiple specimens of *Bochianites neocomiensis* (d'Orbigny), a heteromorph ammonoid from the Valanginian of the Neuquén Basin, in the central Andes of Argentina. The fossils were recovered from the Vaca Muerta Formation, a monotonous succession of interbedded mudstones and wackestones. The level with the fossils is a micritic mudstone with abundant nannofossils, calcispheres, scarce foraminifera and undifferentiated fragmented bioclasts. There are only impressions of these ammonoids, and macroscopically it seems that the calcareous layers of the shell are not preserved. The periostracum is preserved as an organic film. Normally coiled ammonoids recovered from the same level are always impressions. The periostracum of *Bochianites neocomiensis* is dark to amber in color and generally peels off as soon as the surface of the slab with the fossil is exposed. Under the Scanning Electron Microscopy (SEM) the external surface looks smooth, and the thickness is around 2 µm. Preliminary energy dispersive X-ray analysis (EDAX) shows a high percentage of C (65.8%) with lesser amount of O (21.5%), Si (5.6), Al (2.9%) and Fe (2.9%). A combination of bottom entombment in fine grained carbonate sediment, early cementation, anoxia, and

sulfate reduction may seem to have played a role in the exceptional preservation of the still soft outer layer of the periostracum.

Iterative evolution (homoplasy) as the rule in cephalopod evolution – implications for phylogenetic reconstructions

Ralph Thomas Becker

Institute for Geology and Palaeontology, Westfalian Wilhelms University Münster, Germany

Based on their rich fossil record, phylogenetic reconstructions of ectocochleate cephalopods have classically been based on stratophenetic (chronophyletic) approaches, the observed changes of faunas in time. In recent years, cladistic methods were increasingly applied although character coding is a major challenge, because many species differ in ontogenetic conch parameter trajectories and quantitative character differences, often with high and fluctuating intraspecific variability. Furthermore, the fossil record provides no evidence that macroevolution operates by the division into descendent sister taxa; the splitting off from persisting stem taxa seems more common. A key problem is the identification of the most likely phylogenetic tree generated statistically by cladistic programs. Parsimony is widely used but this implies that trees with minimum iterative evolution (homoplasy) should be preferred.

A review of cephalopod shell evolution suggests that there are hardly any or even no morphological features that evolved only once. Iterative evolution was the rule, not an exception. Intriguing examples are presented for Bactritida, Palaeozoic Ammonoidea, and a Cretaceous homeomorph of the Devonian Kiaclymenia. Even the transformation towards non-accretionary embryonic shell growth happened at least twice, in Gephuroceratoidea and within the Goniatitida.

Cephalopod evolution suggests that the parsimony principle is not suitable to identify the correct phylogenetic tree. Cladistics is useful to formulate phylogenetic hypotheses but, as in all clades with a rich fossil record, must be accompanied by chronophyletic considerations. There should be emphasis on trees with high homoplasy that are congruent with the fossil record and the shortest ghost ranges, and paraphyla should be accepted.

Is *Pohlsepia mazonensis* a cirrate octopus? A reassessment of a controversial Carboniferous fossil.

Thomas Clements[1], Christian Klug[2], Dirk Fuchs[3], Imran Rahman[4] and Pierre Gueriau[5]

1 University of Birmingham, Birmingham, UK
2 Universität Zürich, Switzerland
3 Bayerische Staatssammlung für Paläontologie und Geologie, Germany
4 The Natural History Museum, U.K.
5 Muséum national d'Histoire naturelle, France

Pohlsepia mazonensis (Kluessendorf & Doyle, 2000) is a controversial coleoid cephalopod from the Late Carboniferous (Pennsylvanian) Mazon Creek Lagerstätte, Illinois, USA. Known from a single specimen found within an iron carbonate (siderite) concretion, it was first described as a member of the Cirrata, a suborder within the Octopoda, but has not been reinvestigated since its original description – and many studies question whether *P. mazonensis* is even a mollusc, let alone a cephalopod. Reassessment of *P. mazonensis* is vital — well supported fossil and molecular clock evidence suggest that octopods originate during the Triassic/Jurassic, however, if *P. mazonensis* is indeed an octopod, then this would indicate that this group originated during the Early Carboniferous – over 150 million years earlier than our current estimates. Here we re-examine this enigmatic fossil and present new anatomy of *P. mazonensis* based on data acquired from scanning electron microscopy, X-ray microtomography, and synchrotron X-ray fluorescence.

Into the digital cephalopod world: tales from digitizing the Cephalopoda from the RBINS type-and-figured collections

Stijn Goolaerts, Cédric D'Udekem D'Acoz, Annelise Folie, Camille Locatelli, Aurore Mathys, Bernard Mottequin, Yves Samyn, Patrick Semal

Royal Belgian Institute of Natural Sciences, Belgium

With about 200.000 types and 38.000.000 general specimens, the results of nearly two centuries of intensive collecting and research, the Royal Belgian

The Unitary Associations method in ammonoid biostratigraphy

Romain Jattiot, Centre de Recherche en Paléontologie – Paris, Sorbonne Université, France.

Claude Monnet, Unité Evo-Eco-Paléo, Université de Lille, France.

Owing to their abundance, high evolutionary rates and widespread geographical distribution, ammonoids represent major biostratigraphical fossils. In biostratigraphical works, ammonoid zones are usually defined as interval zones, which correspond to continuous zones generally bounded by the first occurrence (FO) and/or last occurrence (LO) of an index species. However, the local range of any particular ammonoid by itself is not necessarily informative and accurate in time, since the fossil record is incomplete, discontinuous and reflects ecological partitioning. Thus, the use of interval zones often leads to diachronous correlations and biostratigraphical contradictions.

Differing from interval zones, the Unitary Associations method is based on discrete, discontinuous zones defined by the occurrence of characteristic species or of characteristic pairs of species. Thus, this method is much more robust for detecting and solving biostratigraphical contradictions in a given dataset, and it also provides a laterally constant sequence of zones without any crossings, whatever their resolution.

We will show some examples where this method has already been proved to be very efficient in providing robust quantitative ammonoid biostratigraphical schemes in the Triassic and in the Cretaceous. Additionally, we will present a project whose prime objective is to reassess uppermost Albian biostratigraphy by means of the Unitary Associations method. Utilizing for the first time this method in the debate over the highly controversial Vraconnian stage, this project is expected to yield unprecedented results towards disentangling this biostratigraphical conundrum. We also aim to subsequently decipher couplings between major palaeoecological and environmental changes observed during this time interval.

Exceptionally preserved cephalopod fossils from conservation deposits

Christian Klug[1], Alexander Pohle[1], Dirk Fuchs[2], René Hoffmann[3]

1 Paläontologisches Institut und Museum, Universität Zürich, Switzerland
2 Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
3 Institute of Geology, Mineralogy & Geophysics, Ruhr-Universität Bochum, Germany

Ectocochleate cephalopods (with an external mineralized aragonitic shell) yield a much greater number of fossils than endocochleates (with internal shell, which is in some cases partial or non-mineralized). In most cases, ectocochleate cephalopod soft tissues are not preserved. Nevertheless, conservation deposits bear the potential of such a unique preservation. Additionally, even if ectocochleate shells or remains thereof are preserved, their soft tissues tend to be concealed and hence, they are poorly known. Among endocochleates and ectocochleates, soft tissue-preservation occurs only under exceptional conditions. In the past years, we reported soft tissue-remains from some of the main clades of cephalopods, which we will portray here. We could demonstrate the potential of pabulites (prey remains lost by the predator) of ectocochleates such as ammonoids and nautilids. This taphonomic window occurs rarely but has a great potential for future discoveries. With such fossils, we visualized remains of all main organs of various cephalopod clades. As demonstrated for other fossil groups, we suspect that coprolites and cololites of cephalopod predators bear a comparable potential and are regarded as an underexplored type of conservation deposit.

Uniquely preserved Turonian belemnites shed light to cryptic mineralogy of Late Cretaceous belemnitellids: implications for evolution and original shell composition

Martin Košťák[1], Lucie Vaňková[1], Alexei P. Ippolitov[2], Mikhail A. Rogov[2], Dirk Fuchs[3], Martin Mazuch[1], Rastislav Milovský[4], Adam Culka[5], Juraj Šurka[4], Viktor A. Zakharov[2]

1 Institute of Geology and Palaeontology, Faculty of Science, Charles University,

Czech Republic
2 Geological Institute of Russian Academy of Sciences, Russia
3 SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Germany
4 Earth Science Institute, Slovak Academy of Sciences, Slovakia
5 Institute of Geochemistry, Mineralogy and Mineral resources, Faculty of Science, Charles University, Czech Republic

The original biomineralization of belemnite rostra is subject to a long lasting and highly complex discussion. The unusual rostrum architecture of Upper Cretaceous belemnites particularly complicates this enigma. We therefore scutinized exceptionally well preserved rostra of the Belemnitellidae by using modern geochemical and visualization methods (Raman spectroscopy, XRF, ICP-MS + LA, ICP-OES, WDS, TIMS, SEM, MicroCT). The studied specimens obtained from concretions exposed at river Nizhnaya Agapa, Siberia (Lower Turonian strata) consist of calcitic/aragonitic rostra and phragmocones possessing remains of the conotheca and the pro-ostracum. The original aragonite composition (basal prismatic, thin lamello-fibrillar and thick multiply prismatic layers) of the rostrum has been recorded in the anterior part – beginning at the protoconch area. The stable isotope record clearly documents markedly different δ13C and δ18O values in both - calcitic and aragonitic parts of the rostrum (significantly lower in the aragonite part). We assume a secondary, probably partly postmortem calcification of the protoconch area. This idea is supported by evidence of the penetration of opaque calcite into aragonitic prismatic layers. The calcitic/aragonitic boundary forms an "alveolar fracture", typical for early belemnitellids (*Praeactinocamax*, *Actinocamax*). A newly observed layer resembling a "membrane", enriched by organic matter, forms an additional barrier in the calcite spreading into aragonite part. Its role and origin, however, remains unclear. The long ventral fissure, known in the younger members of Belemnitellidae, has also been observed in our material, showing its presence in the early representatives of the family. It is directly linked to the aragonite part of the rostrum.

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Getting hooked by a scaphite

Isabelle Kruta[1], Jérémie Bardin[1], Neil Landman[2]

1 Sorbonne Université-MNHN-CNRS-CR2P, Paris, France.
2 American Museum of Natural History, USA.

In the last few years our knowledge on the anatomy of ammonite soft tissues has improved thanks to the discovery of well-preserved specimens and the use of powerful imaging techniques. Nonetheless, the morphology of the brachial crown remains enigmatic. One family, the Scaphitidae, seem to have preserved some hooklike structures that belong to the ammonite brachial crown. A detailed study of the disparity and position in space of these structures was recently made on *Rhaeboceras halli*. The present work broadens the study and investigates all the known occurrences of these hooklike structures in the family. The study includes six species of Scaphitidae: *Hoploscaphites gilberti*, *Hoploscaphites nicolletii*, *Hoploscaphites nebrascensis*, *Hoploscaphites comprimus*, and *Rhaeboceras halli*. The specimens were all investigated using X-ray based imaging techniques (CT scan, PPC SRμCT-ESRF) and the hooks were virtually reconstructed in order to compare their morphology. All the hooks are bicuspidate and have a similar overall morphology, but variations occur such as in the shape of the aperture, erection of the hook, and length and curvature of the cusps. The number of elements also varies, with the highest number still found in *Rhaeboceras halli* (up to a 168 hooks in AMNH 66350). So far, these hooklike structures were only found in *Hoploscaphites* and *Rhaeboceras* from the U.S. Western Interior. This raises many questions: did these hooks only appear in this clade of Scaphitidae? Is this a fossil artifact due to the specific taphonomic conditions needed to preserve these hooks? What was the advantage of such structures for this group of ammonites?

Evolution of the Scaphitidae (Ammonoidea, Ancyloceratina) (Albian to Danian)

Neil Landman[1], Selina Cole[2,3], David Wright[2,3], Melanie Hopkins[1]

1 American Museum of Natural History, New York, USA
2 Sam Noble Museum, Norman, Oklahoma, USA
3 University of Oklahoma, Norman, Oklahoma USA

Scaphitid ammonites represent a long lived family extending from the late Albian to the late Maastrichtian (and possibly into the early Paleocene). We performed a phylogenetic analysis of the group using approximately 500 morphological characters and including representative species from all genera within the family. The analysis was conducted using both maximum parsimony and Bayesian tip-dating (BTD) methods. Where applicable, we incorporated temporal data by placing uniform distributions on species occurrences corresponding to their earliest known appearance (biozone). Informative characters include shape of the internal lobe, presence/absence, distribution, and shape of the umbilicolateral, lateral, ventrolateral, and ventral tubercles; presence/absence of apertural lappets in microconchs (males); presence/absence of a bulge on the umbilical shoulder of the shaft of macroconchs (females); degree of branching and intercalation of ribs; bifid or trifid first lateral lobes; relative size of the spire, shaft, and hook; degree of recurvature of the hook; and projection of the ribs on the venter of the spire, shaft, and hook (backward, straight across, or forward). Although results are still preliminary and require the incorporation of more taxa and characters, we document the iterative appearance of new lineages with uncoiled body chambers, followed by a gradual trend toward recoiling. The next order of business is mapping character transformations (involving ribbing, tubercles, whorl shape, etc.) against environmental changes (sea level, temperature, distance from shore, etc.). This is particularly revealing for the *Hoploscaphites* (reasonably well adapted for swimming) versus the hook shaped Scaphites, although even in this clade, subtle patterns are apparent.

From Palaeozoic to bathyal: temporal and spatial aspects of the evolution of cephalopod reproductive strategies.

Vladimir Laptikhovsky[1], Svetlana Nikolaeva[2] and Dirk Fuchs[3].

1 Centre for Environment, Fisheries and Aquaculture, Lowestoft, U.K.

2 Natural History Museum, London, UK

3 Bayerische Staatssammlung für Geologie und Paläontologie

Since the Ordovician, the ectocochleate cephalopods have exhibited two alternative reproductive strategies based on the trade-off between egg size and offspring number with lower fitness of intermediate egg and offspring size (Vance model). This phenomenon is exemplified by the morphologically similar but reproductively different ammonoids and nautiloids. Coleoids appeared in the late

Paleozoic and there is no evidence that they ever produced large eggs before the end of the Cretaceous. Modern cephalopods still exhibit the same two major strategies, with large-egged reproduction occurring throughout the taxon range, whereas reproduction with small eggs is restricted to shelves and upper pelagic waters.

Is there a relationship between septal morphology and predation?

Robert Lemanis

Technische Universität Dresden; Germany

The highly folded septa of ammonites represent a perennial paleontological problem. A conflux of factors, such as: a lack of modern analogue structures to study in living organisms, an unknown mode of formation, and difficulty in habitat depth reconstructions, all conspire together to create a problem that has driven over 100 years of research. In that time there have been many functional hypotheses but no reliable, widely agreed upon conclusions. The application of sophisticated computer methods and techniques such as 3D printing have recently begun more rigorously quantifying some of these hypotheses and pruning away others. Here we examine the solid mechanics of the septum and focus on the hypothesis of septal complexity being driven by predation. Using finite element analysis to study static loading, and linear perturbation simulations to analyze buckling behavior, I show that an increase in some types of complexity mitigate unwanted displacement of the structure under discrete loads and increases the critical load necessary to destabilize the shell structure. This data builds upon older, somewhat neglected ideas of septal functions, and presents a working hypothesis that can be further addressed with future ecological studies.

3D-reconstruction of mineralised belemnoid cephalic cartilage from the Late Triassic Polzberg Konservat-Lagerstätte (Austria)*

Petra Lukeneder[1], Alexander Lukeneder[2], Christina Kaurin[1], Valentin Blüml[1]

1 University of Vienna, Vienna, Austria

2 Museum of Natural History Vienna, Vienna, Austria

1 Paläontologisches Institut und Museum, Universität Zürich, Switzerland
2 Finnish Museum of Natural History, University of Helsinki, Finland
3 GeoZentrum Nordbayern, Friedrich-Alexander Universität Erlangen-Nürnberg, Erlangen, Germany
4 Geckoella Ltd, Watchet, United Kingdom
5 Natural England, Bridgwater, United Kingdom
6 Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague, Czech Republic
7 Institute of Geology, Czech Academy of Sciences, Prague, Czech Republic
8 Instituto de Estudios Andinos "Don Pablo Groeber", CONICET and Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina
9 State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing, China
10 School of Earth Sciences, The University of Queensland, St. Lucia QLD, Australia

Classical taxonomy divides cephalopods into three major subclasses: Coleoidea, Nautiloidea and Ammonoidea. However, it has long been known that this system does not accurately reflect the evolution of the group, because the Nautiloidea is paraphyletic. Numerous attempts to divide nautiloids into further subgroups have been complicated by difficulties in deciphering the evolution of the earliest forms in the Cambrian and Ordovician, the time of the first major radiation of cephalopods. We show here how new methods, such as Bayesian phylogenetic inference applying the fossilized birth-death model can help to resolve longstanding questions of phylogenetic relationships within "nautiloid" cephalopods. Our results reveal a paraphyletic group at the base of the cephalopod tree and a rapid diversification into three major clades near the Cambrian-Ordovician boundary: Endoceratoidea, Multiceratoidea and Orthoceratoidea. While the Orthoceratoidea contains the probable ancestors of the Ammonoidea and Coleoidea, the ancestral group of the Nautilida is to be found within either Orthoceratoidea or Multiceratoidea, with profound consequences for the extent of the cephalopod crown and stem group. Despite the potential of these methods, further taxonomic work remains fundamental. We demonstrate this with the example of a rich fossil collection from the

Cambrian-Ordovician boundary of Queensland, Australia that has been known at least since the 1970's but remained undescribed to this day. Specimens from this collection provide valuable insights into early cephalopod evolution, as it contains the first three-dimensionally presented "protactinocerids", confirming their re-interpretation as plectronocerids. In addition, we report the oldest member of the Endoceratoidea from the earliest Ordovician.

Dynamic frontiers in ammonoid locomotion

Kathleen Ritterbush[1], Nicholas Hebdon[2], David Peterman[1], YunJi Choi[1], Mikelia Heberer[1]

1 University of Utah, USA
2 Chapman University, USA

Ammonoids produced an unparalleled record of change in life through time. Human understanding of that record shifts alongside our perceptions of ammonoids' potential locomotion strategies. We highlight approaches to interpret ammonoid motility from conch fossil architecture.

Conch size, velocity, and gross coiling geometry exert primary control over resistance to forward motion. Cephalopod locomotion is awfully complex, so classic palaeoecological approaches address first-order biomechanics of the conch as a rigid structure that must be propelled through the water. Emerging technologies allow greater precision in experimental, and computer simulated measurements of water flow around the conch. Flow patterns impart varied intensities of drag and lift, which can exhibit constructive feedback with acceleration. Adding variance in ammonoid conch ornamentation, posture (including soft body), or propulsive jet rhythm allows us to create more realistic reconstructions of ammonoid locomotion. At present, we isolate variables to observe their individual impacts on dynamic water flow, and to predict how combined nuances will alter motility.

Maturing methods to incorporate results across this dynamic adaptive landscape allow sophisticated ways to conceive of ecological complexity among ammonoids through deep time. First, we must incorporate hydrodynamic consequences of flow around the conch alongside hydrostatic consequences of conch architecture (including internal structures). Different conch configurations would allow different combinations of acceleration and manoeuvrability. We explore Bayesian

methods to merge these 'apples-to-oranges' observations into coherent and predictive ecospace. Ultimately, advances in this field will require an upcoming generation to employ equal application of imagination and rigor.

Contribution of 2D and 3D geometric morphometrics to the study of cephalopod fossil beaks.

Isabelle Rouget[1], Marjorie Roscian[1], Anthony Herrel[2], Royal Mapes[3] and Isabelle Kruta[1].

1 UMR 7207 Centre de Recherche en Paléontologie – Paris, CNRS-MNHN-Sorbonne Université, Muséum national d'Histoire naturelle, - France
2 Mécanismes Adaptatifs et Evolution (Mecadev), Muséum National d'Histoire Naturelle, CNRS, France
3 Division of Paleontology (Invertebrate), American Museum of Natural History, USA.

Though quite rare, fossil coleoid beaks have been documented in the fossil record dating back to the Carboniferous, a few million years after the estimated divergence between coleoids and nautiloids. Most are fragmentary and preserved as two-dimensional carbon imprints, but there are a small number of remarkably well-preserved 3D fossils whose morphology is comparable to that of recent coleoids. Tanabe et al. (2015) have successfully used a geometric morphometrics approach to investigate the morphological similarity of Cretaceous fossil beaks to recent cephalopod groups and, more recently, Roscian et al. (2022) used 3D geometric morphometrics to show that the beak shape of modern coleoids is not only driven by phylogeny but is also correlated with the habitat and trophic level of the species. All of these results open up new perspectives for the study of fossil beaks. However, just how effective these methods are on fragmentary remains, which comprise the majority of the fossil sample, still needs to be explored. Here we propose to test this by comparing two fragments of Carboniferous jaws, one preserved in 2D (AMNH 82601, Late Visean from Arkansas), and the other in 3D (AMNH 66475, Late Mississippian, Chesterian from Oklahoma) with recent cephalopod beaks using 2D and 3D geometric morphometrics. The results show that both fragments are morphologically closer to living Octopods than Decapods, and that these approaches should, in the future, be particularly relevant to the

study fossil beaks including those partially preserved and not found in association with the rest of the body.

New Jurassic Vampyromorph from La Voulte sur Rhône Lagerstätte, France*

Alison Rowe, Isabelle Kruta, Loïc Villier, Isabelle Rouget

Sorbonne Université-Muséum national d'Histoire naturelle-CNRS-Centre de Recherche en Paléontologie, Paris, France.

The increased utilization of powerful imaging techniques over the last decade has enabled the reappraisal of many fossil Lagerstätte specimens, as well as the discovery of previously unknown anatomical and palaeoecological information. The unique 3D preservation of coleoid specimens from the Jurassic La Voulte-sur-Rhône Lagerstätte (Callovian, Ardèche, France) is ideal for these X-ray-based approaches and provides unparalleled opportunities for the observation of internal and external morphology. Multiple Vampyromorph specimens have been recovered from this site, roughly 20 of which have been assigned to the species *Vampyronassa rhodanica*. Recent re-analysis of three of these *V. rhodanica* specimens (including the holotype) using Propagation Phase Contrast Synchrotron Microtomography (PPC-SR-μCT), recorded new observational data on the internal organs, confirming the characteristic absence of an ink sac. New work on an undescribed coleoid from this locality was conducted using the same PPC-SR-μCT methodology. The data obtained revealed the presence of an ink sac, and two possible internal light organs. These characters preclude this specimen as belonging to *V. rhodanica*. Instead, the combination of characters observed suggest this specimen represents a new Vampyromorph species with a combination of defence mechanisms not yet known from the fossil record. The increasing amount of data on La Voulte-sur-Rhône is beginning to provide the outline of a complex ecosystem, where the ecological diversification of cephalopods is consistent with the prey-predator escalation of the Marine Mesozoic Revolution.

The impact of the Lower Kellwasser Event (Devonian, upper Frasnian) on ammonoids (Tornoceratidae) at Büdesheim (Rhenish Massif, Germany)

Till Söte, Ralph Thomas Becker

Institute for Geology and Palaeontology, Westfalian Wilhelms-University of Münster, Germany

The pyritic Frasnian ammonoid fauna from Büdesheim (Eifel Mountains, Rhenish Massif) has been collected and studied for nearly 200 years and became world-famous. We investigated the regional impact of the Lower Kellwasser Event on the long-neglected tornoceratids based on taxonomic revisions of old, extensive collections from the pre-Kellwasser interval (Upper Devonian I-J, *Neomanticoceras* Genozone) and the investigation of a new, stratigraphically younger fauna from the intra-Kellwasser level (UD I-K, "*Archoceras*" Genozone). By comparisons of species richness and relative abundance, the regional impact of the Lower Kellwasser Event on the Tornoceratidae can be characterized.

The Büdesheim faunas comprise 25 tornoceratid taxa from seven genera, including one new genus, seven new species, and new local records. Our analyses confirm an exceptionally high alpha diversity of tornoceratids, at the level of the locally diverse gephuroceratoids. It is the highest on a global scale but this has to consider the bias of rich collections. There is no significant difference between the pre- and intra-Kellwasser intervals in terms of alpha diversity, but the faunal composition differs strongly. Buckman's Rules of Covariation apply to the stratigraphically younger fauna, where there is a tendency towards more evolute, depressed, and more coarsely ornamented forms with more simplified sutures. The results underline that tornoceratids living in a permanent low-oxygen shelf basin environment were only slightly harmed by the Lower Kellwasser Event. The complete absence of UD I-L faunas may reflect a deadly extension of anoxia in the water column, as indicated by biomarkers of phototrophic green sulphur bacteria.

Exploring the metabolic rate of different ectocochleate cephalopods using stable carbon isotopes of shell material

Amane Tajika[1,2], Neil H. Landman[1], J. Kirk Cochran[1,3]

1 American Museum of Natural History, USA

2 University of Tokyo, Japan

3 Stony Brook University, USA

Reconstructing the metabolic rate of fossil organisms is key to understanding their evolution. The metabolic rate of extant organisms is commonly determined by measuring the oxygen consumption in laboratory experiments. However, direct observations are difficult in extinct organisms. Therefore, palaeontologists attempt to reconstruct the metabolic rate of extinct organisms using different approaches. For example, in cephalopods, a recent study suggested that ammonoids possessed a higher metabolic rate than nautiloids based on the pattern of chamber volume development. To test this hypothesis, another approach is needed to determine the metabolic rate of extinct organisms. The carbon isotopic value (δ 13C) of the shell is a function of both metabolic carbon in modern cephalopods and the dissolved inorganic carbon (DIC) in the water. Furthermore, another recent study reports that the metabolically derived carbon in modern cephalopods is correlated with metabolism-related factors. In this study, we use the fraction of metabolic carbon (Cmeta) as a proxy for the metabolic rate of cephalopods. We analyzed the δ 13C of the shell in the modern nautilid *Nautilus macromphalus* to estimate the fraction of metabolic carbon (Cmeta). Additionally, we explore the metabolic rate of extinct ectocochleate cephalopods (ammonoids and nautilids) using published values of δ 13Cshell and δ 13Cmeta to determine which group possessed a higher metabolic rate.

The planktic post-embryonic stage of Cretaceous ammonoids: estimation from the ontogenetic trajectory of septal spacing

Ryoji Wani

Yokohama National University, Japan

In marine organisms, the planktic ontogenetic stage (e.g., larval stage in gastropods and bivalves) plays an important role in the expansion and

diversification of geographic distribution. Understanding the planktic embryonic and/or post-embryonic stages is also important to studying the diversification and speciation in ammonoids. Most ammonoid hatchlings are thought to have a planktic mode of life. However, several Jurassic–Cretaceous ammonoids of the post-embryonic ontogenetic stage had a demersal mode of life, based on oxygen isotopic data. When did the planktic mode of life during the post-embryonic stage end and how large was the shell diameter at this ontogenetic stage?

Based on the ontogenetic trajectory of septal spacing of several lineages of Cretaceous ammonoids (Ammonitina, Lytoceratina, and Phylloceratina), their planktic post-embryonic stages were estimated. In some groups, the planktic post-embryonic stages could be supposed, considering the theoretical calculation of density within seawater in the previous studies and the overlaps with the transitions in the ontogenetic trajectories of outer shell shape (e.g., whorl expansion rate, WER). On the other hand, the ontogenetic trajectories of septal spacing in some species or groups show unique tendencies, from which their planktic post-embryonic stages could not be estimated.

Comparative trophic levels of Jurassic-Cretaceous ammonites and Jurassic-Recent nautiloids, based on carbon and nitrogen isotopes of extinct and extant species: the present as key to the past

Peter Ward[1], Greg Barod[2], Christian Klug[3], Job Veloso[1]

1 University of Washington,USA
2 Department of Marine Science, Central Campus, Iowa, USA
3 Universität Zürich, Switzerland

We sampled tissue and pristine shell material from extant *Nautilus* and *Allonautilus* species and ten species of extant sepiids as well as from shells of Mesozoic planispiral and heteromorphic ammonites and Jurassic through Miocene nautiloids, Our results demonstrate that 1) in extant *Nautilus, Allonautilus* and *Sepia,* and $\delta^{13}C_{org}$ and $\delta^{15}N$ from shell samples, average 95% of tissue values, and thus show the utility of obtaining these values from extant and fossil shells only, and thus providing a means of comparing trophic levels of extant nautilids and sepiids from centuries-old shells when available; 2) *Allonautilus scrobiculatus* demonstrated Isotopic Niche levels significantly different from all

Nautilus species, and much higher values than any sepiids, with $\delta^{15}N$ averaging between 15-17 ‰, which exceeds that of *Architeuthis;* all sampled *Nautilus* species average ~ $\delta^{15}N$ of 10‰. In extant sepiids, the deepest living species yielded the highest nitrogen levels, equivalent to those of *Nautilus* but shallow-water species were always lower, while sepiid values were approximately the same as sampled ammonites. Extant nautiluses and allonautiluses also were atypical of all other cephalopods in their functional allometry in that they showed decreasing nitrogen isotopes through growth, which is also seen in similarly long-lived vampire squids; sepiids showed increasing nitrogen isotopic levels through ontogeny. The functional allometry of extant nautiloids compared to that for mid-water cephalopods plots in a distinctly different field compared to results of Murphy et al, 2021.

A new phylogeny of Post-Jurassic nautiloid cephalopods, including a summary of the extinct and extant species of Cretaceous to Recent Nautilus and Allonautilus

Peter Ward[1], Greg Barord[2], David J. Combosch[3]

1 University of Washington, USA
2 Department of Marine Science, Iowa, USA
3 University of Guam, Guam, USA

The systematics of post-Triassic nautiloids has little changed since 20th century work of Spath (1927), Kummel (1956), and the Genus-level definitions proposed in those works were mainly followed in the nautiloid volume of the Treatise on Invertebrate Paleontology. Since that time, the most notable, recent addition to higher level nautiloid taxonomy has been through the novel use of muscle scars. However, one of the major, continuing problems in arriving at a modern systematic treatment of the post-Triassic nautiloids has been the continued use of one single character, the presence (and specific morphology) of shell ribbing, to define post Triassic, and especially Cretaceous nautiloid genera. The most diverse of the Cretaceous nautiloid species, assigned mainly to *Cymatocer*as, (but also in *Anglonautilus),* should be placed in other genera (mainly *Nautilus, Eutrephoceras, and Pseudocenoceras*) based on the presence of ribbed and non-ribbed species in multiple post-Triassic genera, including *Cenoceras* in the Jurassic and *Allonautilus*

in the both the Cretaceous and Recent. If ribbing becomes a species-, rather than Genus-level character, it requires a fundamental new systematics. Here we present information about multiple new species of extant *Nautilus* and extinct *Nautilus* and *Allonautilus.* We reject the validity of the genus *Euciphoceras* (Schultz 1977), and consider it a junior synonym of *Nautilus.* The oldest species that can be assigned to *Nautilus* are ribbed, and include *Nautilus elegans, and Nautilus radiatus*, while in the Late Cretaceous we accept multiple ribbed species in both *Nautilus* and *Allonautilus.* We also present new genetic analyses of all known extant species of the genus *Nautilus.*

Fossil coleoid phylogeny sheds light on belemnoid and decabrachian interrelationships

Christopher D. Whalen[1,2], Mark Sutton[3], Neil H. Landman[1]

1 American Museum of Natural History, New York, NY 10024, USA
2 Yale University, New Haven, CT 06511, USA
3 Imperial College, London, UK.

Formal phylogenetic analyses of fossil cephalopods have primarily focused on gladius-bearing forms. Partially as a result of these efforts, most fossil "squids" have now been reclassified as octobrachians, exposing a problematic dearth of fossil decabrachians. Furthermore, molecular evidence has struggled to provide consistent picture of phylogenetic interrelationships among the higher decabrachian taxa. This increases the importance of fossil data in a group that appears to lack such evidence. Belemnoids present a possible solution to this problem, and all analyses conducted thus far seem to agree that belemnoids ar related to decabrachians. However, the small number of sampled belemnoids have only been compared to vampyropods (= total-group octobrachians) and Recent decabrachians. This is not a consequence of limited evidence – sepiids spirulids possess a rich fossil record. Here we present a comprehensive phylog of evolutionary interrelationships among coleoid cephalopods, which is the fir analysis to explicitly test the affinity and monophyly of all coleoid higher-taxa.

New data on the Bear Gulch (Carboniferous, Serpukhovian) coleoid *Syllipsimopodi*

Christopher D. Whalen[1,2], Isabelle Kruta[3], Pierre Gueriau[4], Derek E. G. Briggs[2], Neil Landman[1]
1 American Museum of Natural History, New York, USA.
2 Yale University, New Haven, USA.
3 Sorbonne Université-MNHN-CNRS-CR2P, Paris, France.
4 University of Lausanne, Switzerland

Syllipsimopodi is a fossil coleoid from the Carboniferous (Mississippian, Serpukhovian) Bear Gulch Limestone of Montana, USA. The genus is known from a single exceptionally well-preserved specimen, which possesses ten sucker-bearing arms and a large proostracum (interpreted as a gladius) with a prominent median rib. Bayesian tip-dated phylogenetic analysis recovered *Syllipsimopodi* as the earliest-diverging vampyropod (= total-group octobrachian). This significantly extends the known stratigraphic range of Vampyropoda and by extension Neocoleoidea. Here we present new results from XRF spectroscopy of the *Syllipsimopodi* holotype. These new data help clarify the taxon's apical anatomy and phylogenetic affinity.

Stasis over evolutionary timescales in Late Cretaceous ammonoids from North America

James Witts[1], Corinne Myers[2], Neil H. Landman[3], Melanie Hopkins[3], Matthew Garb[4], Kayla Irizarry[5], Ekaterina Larina[6], Anastasia Rashkova[3].

1 University of Bristol, UK
2 University of New Mexico, USA
3 American Museum of Natural History, USA
4 Brooklyn College, USA
5 The Pennsylvania State University, USA
6 University of Texas at Austin, USA

Ammonoid cephalopod molluscs (ammonites) are well known to have experienced significant diversification and increased disparity during the Late

Cretaceous; it has even been hypothesized that morphological "plasticity" contributed to their demise at the end-Cretaceous (K-Pg) mass extinction event (i.e., if disparity was related to specialization and/or geographic isolation). This potential "adaptability," and their abundant fossil record, make ammonites an excellent group with which to test the hypothesis of punctuated equilibrium. The family Scaphitidae is one of the most common and diverse Late Cretaceous ammonite clades, persisting to the K-Pg. We focused on two species: *Hoploscaphites nicolletii* (endemic to the North American Western Interior) and *Discoscaphites iris* (endemic to North America and abundant in the U.S. Atlantic and Gulf Coastal Plains). Variables capturing variation in whorl width, height, length, and shell compression were measured in over 1500 individual specimens to test for directional change vs. stasis of morphological characters across the entire spatial and temporal range of each species. These data were then compared to broad environmental proxies such as stable isotope reconstructed temperature estimates, dominant substrate type, and paleo- latitude and longitude to investigate potential ecophenotypic drivers of morphological variation. Results from both species demonstrate morphological change over space and time; however, this was reversible and showed no net directional change, supporting the dynamic stasis model observed in the fossil record of many other groups. Potential ecophenotypic changes observed within each species are further consistent with stasis driven by differential selection across paleoenvironments and/or stabilizing selection with a fluctuating optimum.

Species distribution modelling and ecomorphology of ammonoids during Oceanic Anoxic Event 2 (Late Cretaceous)

Margaret Yacobucci

Bowling Green State University, USA

During the Cenomanian-Turonian (C-T) interval of the early Late Cretaceous, warming and sea level rise helped to trigger Oceanic Anoxic Event 2 (OAE2), leading to the extinction of marine life, including ammonoid cephalopods. The Western Interior Seaway (WIS) of North America recorded OAE2 and its impacts in exceptional detail. Previous work has shown that, while globally, ammonoid species with larger geographic ranges were more likely to survive the C/T crisis,

this relationship breaks down when considering WIS ammonoids. Seeking an explanation for this difference, I compared ammonoid occurrences to a paleoceanographic model for the WIS during OAE2. I used species distribution modelling (SDM) to quantitatively relate the geographic distributions of 13 WIS ammonoid species to a suite of WIS environmental parameters for three ammonoid biozones spanning OAE2. Finally, I evaluated correlations between preferred habitat conditions and ecomorphology for nine ammonoid species using Westermann morphospace. While ammonoid species are widespread in the WIS prior to OAE2, during the peak of the event ammonoids became restricted to the southwestern margin of the WIS. SDM revealed that habitat suitability remained high in this location for most species, supporting the interpretation that this region within the WIS was a refugium during the C/T crisis. Oxygen level was the most important environmental parameter for species likely to be vertical migrants, while the three species sampled from the refugium at peak OAE2 were demersal or nektonic, suggesting that OAE2 preferentially eliminated ammonoids with a more passive mode of life.

*Candidates for a prize are noted with an asterisk

An 85-million-year-old diet: buccal mass and digestive system in fossil and extant Nautilida

Stijn Goolaerts[1], Isabelle Kruta[2], Amane Tajika[3], Zoë Hughes[4], Neil Landman[3]

1 Royal Belgian Institute of Natural Sciences, Belgium
2 Sorbonne Université, France
3 American Museum of Natural History, USA
4 Natural History Museum, UK

Ten specimens (five from the Natural History Museum, London, UK, and five from the Museum für Naturkunde, Berlin, Germany) of *Syrionautilus libanoticus* (Foord and Crick, 1890), from the famous Upper Cretaceous Konservat-Lagerstätte of Sahel Alma, Lebanon, with in-situ preserved remains of the buccal mass are reinvestigated with micro-focus computed tomography. Specimens from this Lagerstätte preserve some three-dimensionality allowing for this type of investigation, in contrast to the more recently discovered and published material from the Lebanese Lagerstätte Hadjoula, which is somewhat older (Cenomanian versus upper Santonian).

The µCT imaging allowed us to identify calcified and non-calcified remains of the upper and lower jaws, next to remnants of the digestive system (crop, stomach) as well as some enigmatic structures (possibly uroliths or renal concrements). This makes these specimens some of the very few nautilid fossils known to date that allow us to connect rhyncholite and conchorynch types with diet and feeding strategies, and to come up with palaeobiological considerations from a lineage which, according to current phylogenetic insights, is not directly connected to the two extant nautilid genera *Allonautilus* and *Nautilus*.

The findings on the fossil specimens are compared with the buccal mass and crop content of several extant specimens of *Nautilus pompilius* from Vanuatu (in the

collections of the American Museum of Natural History, New York, USA). Here, the identifiable parts of the crop content represent skeletal fragments of teleost fish, in surprisingly large pieces.

From minions to giants: exceptional upper Devonian cephalopods from the Lompret quarry, Belgium

Stijn Goolaerts[1], Kevin Houben[2], Natalie Tolisz[2], Joris Coron[3], Xavier Devleeschouwer[1], Sofie Gouwy[4]

1 Royal Belgian Institute of Natural Sciences, Belgium
2 Independent researcher, Belgium
3 Université de Mons, Belgium
4 Geological Survey of Canada, Canada

In the last few years, the 'Carrière de Lompret' quarry (Chimay municipality, Belgium) has become one of the most frequently visited mineral and fossil collecting spots in Belgium. The amazing richness and diversity in geology, mineralogy, and palaeontology of the middle and upper Frasnian limestones and shales sparks the interest of both collectors and researchers. A growing number of them is joining forces to preserve as many as possible of the scientifically important specimens, and to fully document the quarry's geodiversity.

Cephalopods are amongst the most searched-for fossils in the quarry. In certain beds, they are even the most common type of (macro)fossils. Over the past decade, many hundreds of specimens were carefully collected, facilitating detailed taxonomic studies. The entire sequence documents several successive faunas, wherein ammonoids are rare in the middle Frasnian part of the succession. In the upper Frasnian, Gephyroceratid ammonoids dominate most of the faunas, except for levels where Tornoceratid ammonoids are very abundant. To better comprehend the driving forces of these observed changes, studies on various other fossil groups (like crinoids, brachiopods, corals, graptolites, trilobites, ostracods, conodonts, chondrichthyans, placoderms) and detailed stratigraphical, sedimentological, and geochemical studies are ongoing

Some of the exceptional cephalopod finds from the Lompret quarry are presented here, spanning an array of taxonomic groups and displaying a remarkable variation in size, from minute Tornoceratids and Bactritids to middle-sized Manticoceras to large Carinoceras and Beloceras up to giant Crickites well over 30 cm in diameter.

Simulations of ammonoid conch hydrodynamics through ontogeny*

Mikelia Heberer[1], David Peterman[1], Casey Crawford[2], Nick Hebdon[3], Kathleen Ritterbush[1]

1 University of Utah, USA
2 University of Indianapolis, USA
3 Chapman University, USA

Ammonoids' extensive fossil record and variety of conch size and shape provide unique insight into ancient ecosystems. These extinct animals' fossils can retain the entire ontogenetic growth sequence of their external conch, which served as both a buoyancy device and their interface with water flow. Ongoing research emphasizes the importance of conch shape and size to interpretations of ammonoid livelihoods and habitat: hydrodynamic features of conch shape (streamlining, drag, etc.) depend on size as the first arbiter of flow regime (turbulence, Reynolds number, etc.)

To investigate ontogenetic influences on hydrodynamic function, we simulated water flow around conchs that change shape as they grow (allometry). We perform Computational Fluid Dynamics (CFD) simulations on four contrasting morphotypes: oxycone, serpenticone, sphaerocone, and an "averaged" morphospace center. Three morphotypes are represented by the species *Achguigites tafilaltensis*, *Dactylioceras commune*, and *Goniatites crenistria*, respectively, while the center is a theoretical, isometric average. Each of these 3D models are built with the true animal in mind, mimicking the correct ontogenetic projections that each species would have experienced. We divided each morphotype into 4 stages with set diameters of 10, 7, 3, 1cm. We simulate flow velocities as a function of shell diameter that show us the general hydrodynamic consequences across a wide spectrum of shape-size combinations. This approach

allows us to speculate cases in which certain ammonoids may have lost, maintained, or gained hydrodynamic advantages as an individual grew into adulthood.

Ammonoid Morphospace Occupation Through Time*

Lindsey Howard

University of Nebraska-Lincoln

Westermann Morphospace is a system by which planispirally coiled ammonoid cephalopod morphotypes and their expected swimming styles are depicted on a ternary graph. Key shell coiling parameters of an ammonoid are measured and then used to compute its position on a ternary graph showing the three end-member ammonoid shell forms: serpenticone, spherocone, and oxycone. These shell forms are associated with different life modes. Serpenticones and spherocones were poor swimmers, relying mainly on passive floating or vertical migration, respectively. Oxycones, on the other hand, had a compressed shell that allowed them to swim efficiently without relying on ocean currents. Most ammonoid species lie on a spectrum between these three end-member forms in Westermann Morphospace.

Climate change and changes in marine food webs over the long period that ammonoids were extant are expected to impact the overall distribution of shell types through time. Tracking shifts in occupation patterns within Westermann Morphospace through time may therefore reveal information on the changes in evolutionary impacts that the ammonoids faced over the 341 million years they survived in the oceans. In this study, I tested for changes in Morphospace occupation for ammonoids from the Carboniferous to the Cretaceous, a time of significant biotic change. Introduction of large predators to marine ecosystems such as plesiosaurs and mosasaurs in the Triassic and Late Cretaceous, respectively, may have impacted the ammonoid morphotypes, resulting in an increase in oxycones at this time. This impact could be tracked using Westermann Morphospace over the five periods sampled.

The ammonoid fossils used in this study came from the University of Nebraska-Lincoln's Invertebrate Paleontology collections. A total of 163 specimens were measured, ranging in age from the Carboniferous to the Cretaceous. Thirteen specimens were collected from areas in Europe, particularly France and Germany, 132 specimens had been collected from central and western areas in North America. A final 18 specimens were not labeled with a collection site. Seven parameters were measured on each specimen, including diameter, whorl width and heights of final whorl and earlier whorls, and larger and smaller radii of the shell. These measurement data were then used to compute the positions of the 163 specimens in Westermann Morphospace. Morphospace occupation was tracked through time, and graphs were produced of each period sampled along with a final overall graph that included all the sampled specimens.

In the Carboniferous samples, most specimens fell in the oxycone region of the Morphospace. This pattern continued through the four following periods, with very little variation in the placement on the Morphospace. Results show that the overall distribution of shell shapes did not change over the studied interval, even as the physical and biotic world, including predators and prey, did. The specimens, both European and American, were collected from areas that had relatively shallow waters, which may have selected for efficient swimming oxycones. The impact of the physical environment may therefore have had a greater effect on ammonoid morphology than the biotic environment. Further analysis of specimens from other areas of the world and different depths would help test this hypothesis that ammonoid shell shape is more strongly influenced by local environmental parameters like water depth than by food web changes.

Strength, toughness, and the "Just so" stories behind the evolution of biominerals.

Robert Lemanis[1], Kian Tadayon[1], Elke Reich[1], Gargi Joshi[1], Richard Johannes Best[1], Kevin Stevens[2], Igor Zlotnikov[1]

1Technische Universität Dresden; Germany
2Ruhr-Universität Bochum; Germany

The ability of evolution to shape organic form involves the interactions of multiple systems of constraints, including fabrication, phylogeny, and function. Historically, there was a tendency among biologists to emphasize natural selection as fully sufficient to explain the origins of form. Though not common in the modern day, a similar tendency sometimes occurs in biomineralization research, where features for which a mechanical function can be postulated, are treated as adaptations. Moreover, this postulated adaptation can be presented without any explicit consideration of the organism's ecology. We explore the consequences of this using two different systems: *Nautilus pompilius* and *Argonauta argo*, at different length scales and various relative humidities. Comparative dynamic mechanical analysis, nanoindentation, and EBSD analyses demonstrate the importance of multi-scale environmentally controlled characterization of biogenic materials. These results are then used to critique interpretations of adaptation sometimes presented in the literature. By integrating the hierarchical nature of biological structures and the environment in which they exist, biominerals testing can be a powerful tool for generating functional hypotheses that should be informed by how these structures are fabricated and their evolutionary history.

Jurassic coleoid statoliths from Central Russia

Aleksandr Mironenko

Geological Institute of Russian Academy of Sciences, Moscow, Russia

Statoliths are small aragonite structures located in the equilibrium organs of coleoid cephalopods. Their shape is related to the activity and habitat of their hosts, therefore the study of fossil statoliths can help to better understand the mode of life of extinct coleoids. Until now, Jurassic statoliths had been only known from several localities in Great Britain and Germany. Here we describe the first findings of Jurassic statoliths from Central Russia. Statoliths have been found in black clays (formed under dysoxic conditions) in 14 localities, in the Middle Jurassic (Callovian) and Upper
Jurassic (Oxfordian, Kimmeridgian, and Volgian) deposits. Statoliths belong to at least 5 morphotypes, some of them have not been previously described. The number of statoliths varies greatly in different sections. They are most numerous in the Middle Callovian localities, but there they almost all belong to Jurassic type

A, and in the Upper Oxfordian, where 4 morphotypes are found together. In the Callovian and Oxfordian sections, the statoliths markedly outnumber the fish otoliths. A large number of findings of different sizes makes it possible to trace changes in the statolith shape during ontogeny of their hosts. The taxonomic affinity of the statolith hosts is still an open question. However, it is extremely unlikely that they belonged to rostrum-bearing belemnites, since the abundance and diversity of statoliths does not correlate with the abundance and diversity of belemnite rostra. It is more likely that the statoliths belonged to belemnoids with a reduced rostrum, vampiromorphs, or squid ancestors.

Statoliths of Jurassic type A from the Upper Callovian, Mikhailov locality, Ryazan region, Russia.

Multi-approach imaging techniques shed new light on Lebanese gladius-bearing coleoids*

Alison Rowe[1], Isabelle Kruta[1], Pierre Gueriau[2], Aimie Doriath-Döhler[3], Robin Piguet-Ruinet[3], Isabelle Rouget[1]

1Sorbonne Université-Muséum national d'Histoire naturelle-CNRS-Centre de Recherche en Paléontologie, Paris, France.
2 Muséum national d'Histoire naturelle, UAR3461 IPANEMA, Gif-sur-Yvette, France. 3Sorbonne Université, Paris, France.

UV imaging is a standard form of analysis for the 2D fossils preserved in the Cenomanian Lebanese Lagerstätte sites of Hakel, Hadjoula, and Sahel Alma. This method produces excellent results when identifying certain characteristics, such as the remains of phosphatised soft tissues. Descriptions of prototeuthid coleoids from these localities, including the genus *Dorateuthis* Woodward, 1883, have utilized this imaging method to identify elements not visible with the naked eye. While the genus has defined parameters for body size, fin shape, as well as the proportions of the arm crown, and morphological detail of the gladius, there remains variation expressed in Dorateuthis fossil samples. Here, we analyse two undescribed specimens from the Hadjoula Lagerstätte. We used both classical observations along with a suite of non-destructive imaging methods including UV and RTI photography, and X-ray fluorescence elemental mapping. The results obtained allowed us to identify not just the well-preserved details, but also to visualize remains of tissues that are no longer visible. One of the specimens seems clearly to fit within the diagnosis of *Dorateuthis syriaca* Woodward, 1883. However, the other is more ambiguous and raises questions regarding the current systematic diagnosis of the genus. The additional data generated in the multi-approach imaging techniques provides a higher resolution for morphological studies of gladius-bearing coleoids from these Lebanese deposits. Additionally, it has shown to be a useful tool that can provide further information for the existing systematic descriptions of prototeuthids.

Review of the Lower Lias Nautiloids from the Dorset Coast

Heather Salmon, Paul Davis

A self-funded study supported by The Charmouth Heritage Coast Centre

The Nautiloids from this coast and of this age have been absent from recent literature and missing entirely from the Palaeontological Association Guide to the Fossils from the Lower Lias of the Dorset Coast of 2010. The Nautiloids found on these beaches can be exceptionally well preserved in some layers and identifiable in many. Recent improvements in preparation techniques, notably the use of iron powder abrasive, has allowed shell-on preparation. This has provided benefits in confirming published conjecture in French studies about the surface ornamentation and provided a possible new approach to identification and refined criteria for assignment to species. Different techniques and measurements for determining and defining conch shape have been investigated but the flaring of the mouth of mature specimens has defied a simple analysis in terms of a planar logarithmic spiral. Relatively obvious features of shape allow assignment to one of eight species. Useful comparisons have also been made to specimens prepared with shell-on and shell-off.

Rare Middle Triassic coleoids from Western Carpathians

Ján Schlögl[1], Martin Košťák[2], Dirk Fuchs[3], Milan Havrila[4], Tea Kolar-Jurkovšek[5], Attila Vörös[6], Juraj Šurka[7]

1 Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava, Slovakia
2 Institute of Geology and Palaeontology, Faculty of Science, Charles University, Czech Republic
3 SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Germany
4 Geological Institute of Dionýz Štúr, Slovakia
5Geological Survey of Slovenia, Slovenia
6Hungarian Natural History Museum, Hungary
7Earth Science Institute, Slovak Academy of Sciences, Slovakia

The two stratigraphically well labeled (by ammonites and conodonts) coleoid remains have been recorded in the Triassic dark-grey organodetritic limestones (Ráztoky Limestone) of Western Carpathians (Hronic Nappe). The facies originated between carbonate ramp and basinal development. It yields a diverse cephalopod fauna including nautiloids (2 taxa), ammonoids (7 taxa) and indetermined aulacoceratids. Two unusual coleoid specimens are putatively referred to genus *Mojsisovicsteuthis* (incomplete, 40 mm long, laterally compressed phragmocone with typical oval cross-section and slightly undulate suture lines) and possibly, a new taxon slightly resembling *Breviconoteuthis* (Phragmoteuthida; almost complete - 64mm long, cyrtoconic, dorso-ventrally compressed phragmoconus). Based on index ammonites and conodonts, both records are of the uppermost Trinodosus through the lowermost Reitzi zones (Anisian – Lower Illyrian).

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Peculiar microstructure of the outer shell wall in the Lower Miocene *Aturia* from the Central Paratethys.

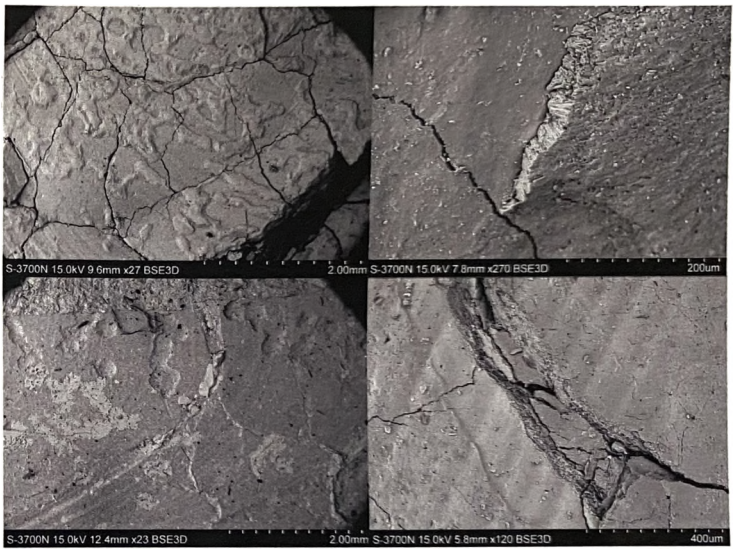
Ján Schlögl[1], Natália Hudáčková[1] , Adam Tomašových[2] ()

1 Comenius University, Slovakia
2 Slovak Academy of Sciences, Slovakia

The outer shell wall of Nautilus and ammonoids consists of four layers: (1) outermost organic periostracum, (2) outer prismatic-sphaerulitic or prismatic layer (OPL), (3) nacreous layer (NL), and (4) inner prismatic layer (IPL). Shells of *Aturia* preserved in the bathyal Miocene diatom-rich clays of the Vienna Basin show a unique outer shell structure: the OPL is either missing or represented by unique, irregular patchy coatings formed by prismatic crystals.

A thick NL is underlain by a distinct, thinner IPL (175-220 µm versus 40-110 µm for 18-25 mm D). Juvenile and subadult whorls possess very thin (3-8 µm), irregular, discontinuous, patchily-distributed prismatic aragonitic OPL-like coatings, overlying the NL. In plane views, they have conspicuous meandriform or labyrinthine contours. The prismatic crystals are variously oriented depending on

their position within the coatings. These coatings are fully missing on adult whorls. We suggest that this outer prismatic coating represents a conspicuous type of poorly-developed OPL. The crystal orientation, preservation of the nacreous layer, and epibionts directly attached to the NL indicate that these coatings are not altered by postdepositional dissolution, and the patchiness is the primary feature of the biomineralization process.



Aturia, Burdigalian, Cerová. A. Discontinuous OPL on the flank of *Aturia* at ~18 mm in D. B. Microstructure of the wedging out OPL coating. C. *Aturia* imprint with OPL coatings partly detached (white) or still attached on the counterpart (pits and furrows). D. Attachment scar of a polychaete tube on the NL with growth lines (*Aturia* D ~22 mm).

Rhyncholites and Rhynchoteuthis through time: unsuspected disparity and palaeoecological interpretations

Louise Souquet[1,2,4], Jérémy Andreoletti [1,2], Isabelle Kruta[1], Neil Landman[3], Anthony Herrel[2], Isabelle Rouget[1]

1 Centre de Recherche en Paléontologie-Paris, Muséum National d'Histoire Naturelle, Paris, France
2 Mécanismes Adaptatifs et Évolution, Muséum National d'Histoire Naturelle, Paris, France.
3 Department of Invertebrate Palaeontology, American Museum of Natural History, USA
4 Current affiliation: Department of mechanical engineering, University College London, UK

Rhyncholites, the arrow shaped calcite tips of the upper jaw of nautilus, are found abundantly in the fossil record from middle Triassic to nowadays, and are described as morphologically stable trough time. Another group of mineralized arrowed shaped fossils is found from Jurassic to Cretaceous: the *rhynchoteuthis*. Because they have never been found in situ, their affinity to nautiloids or ammonoids is still debated. With an overall morphology very similar to rhyncholites, they exhibit a greater shape diversity. Because of their feeding function, they should carry critical information related to their diet and environment. Yet, the morphological variability of these fossils has never been quantitatively investigated before. In this study, we thoroughly and quantitatively characterized the morphology of rhyncholites and rhynchoteuthis from Triassic to present-day. We digitized 262 specimens using an X-ray microtomograph (µCT) and performed a shape analysis using 3D geometrics morphometrics. The morphological continuum observed between rhyncholites and *rhynchoteuthis* along with the unfitting morphology of *rhynchoteuthis* with other contemporary cephalopods upper jaws, lead us to consider them as nautilids. Surprisingly, we observe broad variation in rhyncholites shape, ever since their apparition in Triassic. Specimens from that age are morphologically closer to modern ones,

probably sharing their opportunistic carnivorous diet and able to feed on hard items. This ability might have given them the upper hand during the Marine Mesozoic Revolution. Through this period of intense arms race, the increasing competition might have favoured the emergence of new forms such as *rhynchoteuthis*, as well as exploration of new niches.

Intraspecific variability of hatching size in nautilids

Amane Tajika[1,2], Neil H. Landman[1]

1American Museum of Natural History
2University of Tokyo

The size of eggs, embryonic shells, and hatchings has been considered of great importance in cephalopod evolution. However, our knowledge of size with regard to its variability in response to different factors in shelled cephalopods is largely lacking. We present a comprehensive overview of hatching size in all known species of modern nautilids to explore the relationship between size and abiotic and biotic factors. We find high intraspecific variation in hatching size in modern nautilids. When comparing the hatching size and temperature at which embryonic development takes place, there does not seem to be a clear correlation between the two parameters. Regarding embryonic duration, species with a longer embryonic development may exhibit a larger hatching size. In the fossil record, species in cold climates may produce a larger hatchling than those in temperate climates. However, these conclusions need to be further studied because the data pertaining to temperature and embryonic duration are not sufficient. We also find that the morphology of the embryonic shell is likely not constrained by hatching size. The three allopatric nautilid clades distinguished by molecular data do not show a clear pattern with respect to hatching size. Adult size and hatching size are positively correlated although this pattern is not apparent in all species. The positive correlation may be rooted in parental care strategy and/or predatory pressure. This proportional relationship between hatching size and adult size likely occurred at least in some Mesozoic nautilids.

Description of soft tissue preservation in the Cretaceous hoplitid ammonoid Neogastroplites from the Mowry Shale*

Kaylee Ann Walty

Bowling Green State University

The mid-Cretaceous Mowry Shale of North America is known for its unusual lithology, comprised of siliceous mudstones and bentonite beds. The Mowry is characterized by a low-diversity cold-water fauna, including the hoplitid ammonoid *Neogastroplites* as well as crustaceans, and a complex preservation environment for fossils. Typically, the ammonoid shells in the Mowry are found either compressed in mudstones or preserved in three dimensions in concretions. Here, I report on compressed specimens of *Neogastroplites* with preserved soft tissue, which does not normally fossilize, hinting at a more complex geochemical environment. These specimens are part of the collections at the Wyoming Dinosaur Center (WDC-Ms-101 and WDC-Ms-102) and were previously described by W. Wahl, who assigned them to *Neogastroplites americanus*; however, it is now believed that they are more likely the slightly younger *Neogastroplites maclearni*. The siphuncle is preserved, as well as the lower jaws and a possible crop. One specimen includes a faint preserved "shadow" where one might expect the soft body of the living organism to be. This discoloration requires geochemical analysis to determine if the living organism decayed in that spot. The unusual depositional environment of the Mowry Shale may have helped preserve these soft tissues, and investigation of other cold-water siliceous mudstone units may reveal other examples of soft tissue preservation.

Clumped isotope constraints on ammonoid palaeoecology and latest Cretaceous climate variability in the United States Gulf Coastal Plain

James Witts[1], Corinne Myers[2], Sierra Petersen[3], Jonathan Hoffman[3], Jone Naujokaityte[2], Remy Rovelli[2], Matthew Garb[4], George Phillips[5], Neil Landman[6]

1 University of Bristol, UK
2 University of New Mexico, USA
3 University of Michigan, USA
4 Brooklyn College, USA
5 Mississippi Museum of Natural Sciences, USA
6 American Museum of Natural History, USA

Geochemical records from well-preserved shell carbonate are used to reconstruct the paleoecology and habitat of ammonoid cephalopods (ammonites) and the evolution of ancient marine ecosystems and climate. Carbonate clumped isotope (Δ47) analysis is a promising tool which does not rely on assumptions of ancient seawater composition that hamper 'traditional' stable isotope studies. We present a multi-taxon dataset from the Maastrichtian Owl Creek Formation, Tippah County, Mississippi. This site contains an exceptionally preserved molluscan fauna constrained by macro- and microfossil biostratigraphy to the final ~300 kyr of the Cretaceous. Fossils of three ammonite genera, infaunal bivalves, and rare nautilids were systematically collected and sampled throughout a 9 m-thick section. Preservation was assessed using the SEM Preservation Index (PI). Clumped isotope palaeotemperatures and δ18OSeawater values reveal overlap in values and close agreement between all taxa. Ammonites and benthic bivalves thus secreted their shells in isotopic equilibrium with seawater of the same composition and probably lived in similar environments. We see no evidence that ammonites exhibit "vital effects" with respect to their clumped isotope composition. These data provide new constraints on the palaeoecology of extinct cephalopod taxa and marine climate evolution in the Gulf Coastal Plain immediately prior to the end-Cretaceous mass extinction.

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