



School of
Biological, Earth and
Environmental Sciences

2017 International Workshop on Konservat- Lagerstätten

Cork, Ireland 15-16 July 2017



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Welcome

Dear delegates,

It is our pleasure to welcome you to the 2017 International Workshop on Konservat-Lagerstätten at University College Cork, Cork (Ireland), 15-16 July 2017.

Konservat-Lagerstätten are fossil deposits that include exceptionally preserved soft tissues of plants and animals and are widely recognised as essential archives of palaeobiological information. Research in the field is accelerating rapidly and is becoming increasingly multidisciplinary, with the integration of new methodological approaches, new fossil discoveries, and refinement of current methods.

This meeting will explore frontier research on Konservat-Lagerstätten and will bring together experts in imaging, chemical analysis, organismal palaeobiology, sedimentological analysis and experimental taphonomy. Our exciting program reflects the diversity of research in the field. Day 1 of the meeting focuses on current research, with five keynote presentations, regular presentations, lightning presentations and poster sessions. Day 2 is based on a series of workshop sessions on key techniques in the study of fossil soft tissues with a strong practical and logistical focus; poster sessions also feature in the day's programme.

Venue

Cork is Ireland's second city and is full of character and culture. University College Cork is situated within beautiful tree-lined grounds through which flows the River Lee. The university is a 15-minute walk from the city centre and is served by excellent public transport. The scientific programme will take place in UCC's historic Main Quadrangle, known as "The Main Quad", built between 1847 and 1849. All talks, posters and daytime refreshments will take place under the same roof. The evening reception and dinner on the 15th will take place in the atmospheric surrounds of UCC's Glucksman Gallery, and will be followed by an incredible evening of music at UCC's annual *A Summer Evening on the Quad* event. All key locations will be signposted. See map on p. 5 of this programme.

Registration

Registration will be open from 08:00 on Saturday 15th July in the Aula Maxima, which is on the ground floor of the northern wing of the Main Quadrangle. You will need to register in order to collect your abstract booklet and tickets for lunch and dinner. There will be signage at all entrances to the university campus directing you to the building.

Posters

At registration you may collect materials for affixing your posters to the posterboards and an A4 sleeve for disseminating scaled-down versions of your poster (if desired). Poster setup will be available from 8.00 am until 8.50 am; assistants will be on hand to help you set up. The poster sessions will be located in the Aula Maxima, which is the location for registration and all tea/coffee breaks and lunches. Posters will remain on display for the duration of the workshop; poster

presenters are asked to remain by their poster for as much of the duration of the breaks as possible. Posters should be taken down following the final session on the 16th.

Oral presentations

All oral presentations will take place in the Council room, which is on the first floor of the northern wing of the Main Quadrangle. The system in the Council room is PC-based. If you intend to prepare your presentation using a Mac, please ensure file compatibility in advance. Powerpoint files can be uploaded between 8:00 am and 8:50 am in the Council room on the morning of the 15th, or in the break immediately before your session. Speakers who upload their presentations in a timely manner will have the facility to check briefly their presentation following upload.

Lunches and refreshments

Lunch and tea/coffee breaks will take place in the Aula Maxima, which will also house the posters. The extended tea/coffee break on the morning of the 16th is a dedicated poster session.

Evening reception

The evening reception on the 15th will take place at 17.30 in the riverside garden outside Fresco's restaurant, which is a 2-minute walk away from the Main Quad.

Conference dinner

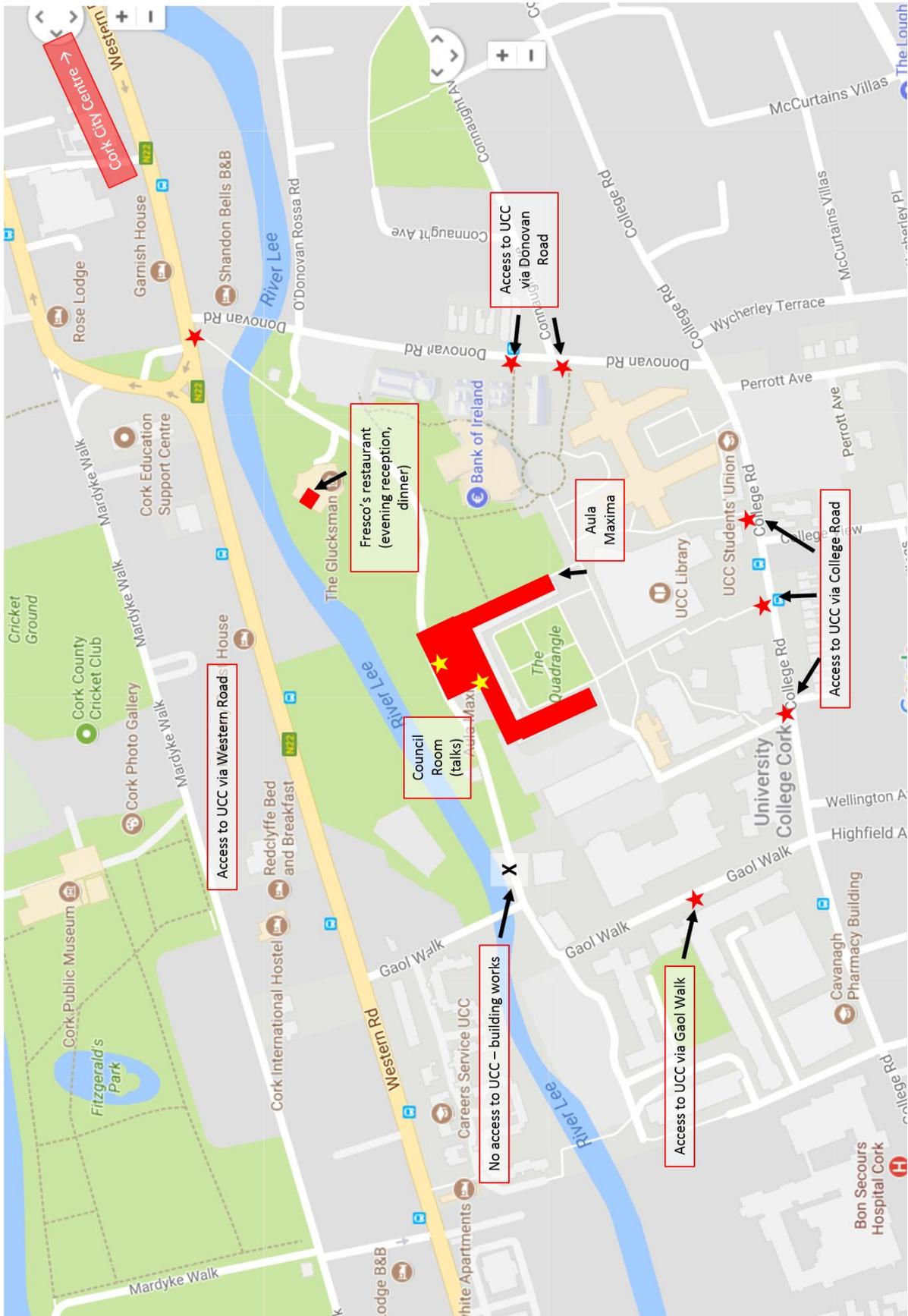
The conference dinner on the 15th will take place in Fresco's restaurant at 18.30. Delegates who have not elected to attend the conference dinner can find diverse dining options in the various bars and restaurants on Washington Street and the city centre (a 15-minute walk from main campus).

A Summer's Evening on the Quad

This open-air concert commences at 20:00 in the Main Quadrangle. At the date of circulation, a limited number of tickets are still available and can be purchased for €30. The event is likely to be sold out in advance of the concert.

Post-conference dinner

The post-conference dinner will take place in *Holy Smoke* restaurant on Washington Street (a 15-minute walk from main campus) at 18:30. Delegates who have not elected to attend the post-conference dinner can find diverse dining options in the various bars and restaurants on Washington Street and the city centre.



Schedule of events

Saturday 15th July 2017

Asterisk (*) denotes designated speaker

Council Room, North Wing, Main Quadrangle, UCC

09:00–09:10 **Welcome and introductory remarks**

09:10–10:45 **Session 1: Experimental taphonomy I**

09:10–09:30 **Keynote 1: Research on Konservat-Lagerstätten – a SWOT analysis**
Prof. Derek Briggs

09:30–09:45 **The value of experimental decay in analysis of exceptionally preserved fossils**
Mark A. Purnell*, Duncan J. E. Murdock, Robert S. Sansom, Sarah E. Gabbott

09:45–10:00 **Biases in the fossil record of patterned insects**
Nidia Álvarez Armada*, Maria E. McNamara, Stuart L. Kearns, Samuel M. Webb,
Fiona L. Gill, Kevin J. McGraw

10:00–10:15 **Microbial mats: the implications of microbial communities in the early stages of fossilization**
Miguel Iniesto*, Angela D. Buscalioni, M. Carmen Guerrero, Ana I López-Archilla

10:15–10:30 **Preservation of soft-bodied organisms in coarse-grained siliciclastic environments**
Sharon Newman*, Sirine C. Fakra, Tanja Bosak

10:30–10:45 **What is a pigment granule? - and why you should care**
Tim Astrop*, Christopher S. Rogers, Maria E. McNamara

10:45–11:10 *Tea / Coffee and posters (Aula Maxima)*

11:10–12:45 **Session 2: Experimental taphonomy II and synchrotron-aided analyses**

11:10–11:30 **Keynote 2: Decoding the fossil record of the earliest animals and their embryology**
Prof. Philip Donoghue

11:30–11:45 **Rotten livers, guts and gills: can carcasses generate organ specific microenvironments?**
Thomas Clements*, Mark Purnell and Sarah Gabbott

11:45–12:00 **Insights into exceptional preservation processes: the study of crustaceans from La Voulte-sur-Rhône, France**
Clément Jauvion*, Sylvain Bernard, Pierre Gueriau, Sylvain Charbonnier

12:00–12:15 **Trace element chemistry of melanosomes revealed by synchrotron-X-ray fluorescence: a tool for interpreting fossil vertebrate soft tissue**
Valentina Rossi*, Maria E. McNamara, Sam Webb

12:15–12:30 **Tissue-specific trace element chemistry of melanosomes in cyclostomes and gnathostomes revealed by synchrotron X-ray fluorescence**
Christopher S. Rogers*, Maria E. McNamara, Sam Webb

12:30–12:35 **Preliminary report of the mineralization potential of tissues**
Lindsay MacKenzie*, Cameron Cummings

- 12:35–12:40 **Experimental taphonomy of circularly polarizing nanostructures in scarab beetles (Coleoptera: Scarabaeidae)**
Giliane Odin*, Maria E. McNamara
- 12:40–12:45 **Probing the speciation of carbon in fossils at high energy using synchrotron-based X-ray Raman scattering**
Pierre Gueriau*, Jean-Pascal Rueff, Sylvain Bernard, Josiane A. Kaddissy, Sarah Goler, Christoph Sahle, Dimosthenis Sokaras, Roy A. Wogelius, Philip L. Manning, Uwe Bergmann, Loïc Bertrand
- 12:45–13:45 *Lunch (Aula Maxima)*
- 13:45–15:35 Session 3: Biomolecules and morphology
- 13:45–14:05 **Keynote: The Eocene Fur Formation of Denmark – exceptional preservation exemplified by sea turtle soft tissues**
Prof. Johan Lindgren
- 14:05–14:20 **Revelations by hard parts: ammonoid examples from the Hunsrück Slate Konservat-Lagerstätte**
Kenneth De Baets*, Christian Klug, Markus Poschmann, Trisha Smrecak, Julia Stilkerich
- 14:20–14:35 **Dinosaur eggshell calcite as a closed system: ‘molecular Konservat-Lagerstätten’**
Evan Saitta*, Kirsty Penkman, Jakob Vinther
- 14:35–14:50 **The Mazon Creek cnidarian *Essexella*: The world turned upside down**
Roy Plotnick*, James W. Hagadorn, Graham Young
- 14:50–15:05 **Integumentary structures and soft-tissues in the gobiconodontid *Spinolestes* from the upper Barremian of Las Hoyas (Huérquina Formation, southwestern Iberian Basin, Cuenca)**
Angela Buscalioni*, Thomas Martin, Jesús Marugán-Lobón, Romain Vullo, Hugo Martín-Abad, and Zhe-Xi Luo
- 15:05–15:20 **A variable geometry tail in early birds and feathered dinosaurs: evidence from Archaeopteryx and Microraptor**
Nick Longrich*, Christian Foth, Xu Xing
- 15:20–15:25 **An exceptionally preserved specimen of *Aurorazhdarcho* (Pterosauria, Aurorazhdarchidae) from the Jurassic Solnhofen of Germany**
Hebert Bruno N. Campos*, Michael Pittman, Thomas G. Kaye, Heinrich Mallison, Eberhard Frey
- 15:25–15:30 **3D preservation of gills in the first fossil crabs from the Kerguelen Islands**
Ninon Robin*¹, Barry W. Van Bakel², Marie-Madeleine Blanc-Valleron¹, Sylvain Charbonnier
- 15:30–15:35 **Fluoridation of a lizard forelimb in Miocene Dominican amber**
Jonas Barthel*, Jes Rust, Thorsten Geisler
- 15:35–16:00 *Tea / Coffee and posters (Aula Maxima)*
- 16:00–17:25 Session 4: Palaeoenvironment
- 16:00–16:20 **Keynote: Mechanisms for exceptional preservation of fossils in lakes associated with volcanism**
Prof. Baoyu Jiang
- 16:20–16:35 **Upper Cretaceous marine arthropods relied on terrestrial organic matter as a food source: geochemical evidence from the Coon Creek Lagerstätte in the Mississippian Embayment**

Matthew B. Vrazo*, Aaron F. Diefendorf, Brooke E. Crowley, and Andrew D. Czaja

- 16:35–16:50 **Selective taphonomic processes in the Fezouata Konservat-Lagerstätte (Lower Ordovician, Morocco): storm influence on the brachiopod record**
Farid Saleh*, Yves Candela, Bertrand Lefebvre, Bernard Pittet
- 16:50–17:05 **Sedimentology and paleoecology of two Miocene maar-Lagerstätten in New Zealand**
Uwe Kaulfuss*, Daphne E. Lee and Jon K. Lindqvist
- 17:05–17:25 **Keynote: The Early Phanerozoic “Taphonomic Window”**
Prof. Bob Gaines
- 17:25 Close
- 17:30–18:30 *Icebreaker reception (Glucksman Gallery)*
- 18:30–19:45 *Dinner (Fresco’s restaurant, Glucksman Gallery)*
- 20:00–23:00 *Summer on the Quad*

Sunday 16th July 2017

Council Room, North Wing, Main Quadrangle, UCC

- 09:00–09:50 **Electron microbeam analysis of exceptionally preserved fossils**
Stuart Kearns
- 09:50–10:40 **Transmission electron microscopy of fossil soft tissues**
Maria McNamara
- 10:40–11:25 *Tea / Coffee and posters (Aula Maxima)*
- 11:25–12:40 **Best practice in experimental decay: design, analysis and application**
Duncan Murdock & Rob Sansom
- 12:40–13:30 *Lunch (Aula Maxima)*
- 13:30–14:20 **The skeletal taphonomy of vertebrates in exceptional biotas**
Patrick Orr
- 14:20–15:10 **The light at the end of the tunnel: synchrotron methods and ancient life**
Roy Wogelius
- 15:10–15:30 *Tea / Coffee and posters (Aula Maxima)*
- 15:30–16:20 **Palaeoproteomics**
Michael Buckley
- 16:20–17:10 **Applying X-ray computed tomography to exceptionally preserved fossils**
Imran Rahman
- 17:10 Close
- 18:30–late *Dinner in Holy Smoke restaurant*

Abstracts of keynote presentations

Research on Konservat-Lagerstätten – a SWOT analysis

Derek E.G. Briggs

Department of Geology and Geophysics, and Yale Peabody Museum of Natural History, Yale University, New Haven, CT 06520, USA

Strengths: Konservat-Lagerstätten have long ceased to be regarded as on the fringe of palaeontology. Together with the analysis of large databases, and the development of novel imaging techniques, the discovery of Konservat-Lagerstätten catalyses much current palaeobiological research. This is particularly true of the Precambrian and early Palaeozoic because addressing many questions related to that time requires the evidence of exceptionally preserved fossils. **Weaknesses:** In spite of significant progress based on field observations, experiments, and data analysis our understanding of the controls on exceptional preservation remains incomplete. This hinders the search for new Konservat-Lagerstätten and can even compromise the interpretation of specimens – we run the risk of over- or underinterpreting soft-bodied fossils. **Opportunities:** Advances in sedimentary geochemistry and analytical methods offer the possibility of identifying patterns from the specimen to the global level that may help to target new discoveries, a particular concern in pre-Ediacaran sequences. Such research is also relevant to the identification of sampling sites for future Mars missions. **Threats:** Although our ultimate agenda, understanding the history of life, promises limitless research, the sensational nature of the fossils will not always justify funding. We must continue to use Konservat-Lagerstätten to address major evolutionary questions with an interdisciplinary approach.

Decoding the fossil record of the earliest animals and their embryology

Phil Donoghue

School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

The 609 Ma Doushantuo biota of South China has yielded important fossils that include the oldest widely accepted record for the establishment of the animal evolutionary lineage, as well as a suite of specimens with alleged bilaterian affinity. However, interpretations of these fossils have been criticized on the basis that inference of affinity is contingent on the presence of key biological structures that may alternatively represent artefacts of diagenetic mineralization. Furthermore, preserved fossils are limited to the earliest stages of embryonic development and the absence of equivalent adults has led to the suggestion that preserved clusters of cells may rather represent clusters of vegetatively dividing bacterial cells. We attempted to discriminate among these competing hypotheses by first characterizing the mineral phases that replicate original biological structure and later diagenetic void filling using BSE, EPMA, EBSD and SRXTM. The results demonstrate that structures interpreted hitherto as evidence for derived animals are characteristic of void-filling mineralization that occurred long after the original biological structures decayed. To discriminate between animal- versus bacterial interpretative models we undertook decay experiments on modern animal embryos and giant bacteria. The taphonomy of the Doushantuo fossils is compatible with animal embryos, but not bacteria. Furthermore, the fossilised remains of nuclei within the Doushantuo allows us to reject the bacterial model. It does not follow, however, that the animal model is correct and new developmental stages in the Doushantuo assemblage provide compelling evidence against their interpretation as animal embryos. Thus, while these fossils

may no longer be considered direct evidence of Ediacaran animals, they may represent a stage in the deep evolutionary origins of animal-grade multicellularity.

The Early Phanerozoic “Taphonomic Window”

Robert R. Gaines

Geology Department, Pomona College, Claremont, CA 91711 USA

Exceptional fossil assemblages provide a unique record of animal life in the immediate aftermath of the Cambrian “explosion”. While most soft-bodied biotas in the rock record were conserved by mineral replication of soft tissues, the Cambrian signal is dominated by Burgess Shale-type preservation, which involved the conservation of whole assemblages of soft-bodied animals as primary carbonaceous remains, often preserved in extraordinary anatomical detail. Burgess Shale-type preservation resulted from a combination of influences, operating at both local and global scales, which acted to drastically slow microbial degradation in the early burial environment, resulting in incomplete decomposition and in the conservation of soft-bodied remains. Here, I will review the circumstances that led to the preservation of Burgess Shale-type fossils in Cambrian strata worldwide and consider the hierarchy of controls that regulated the operation of Burgess Shale-type preservation in space and time, ultimately determining the taxonomic richness and the fidelity of preservation in each deposit. While Burgess Shale-type preservation is a unique taphonomic mode that ultimately was regulated by the influence of global seawater chemistry upon the early diagenetic environment, physical depositional (biostratinomic) controls were critical in regulating many of the important differences among Burgess Shale-type deposits.

Mechanisms for exceptional preservation of fossils in lakes associated with volcanism

Baoyu Jiang

Center for Research and Education on Biological Evolution and Environments, School of Earth Sciences and Engineering, Nanjing University, Nanjing 210023, China

The Mesozoic Yanliao and Jehol Biotas in northeast China have yielded numerous complete and articulated skeletons of fossils that include feathered non-avian dinosaurs, birds, pterosaurs, mammals, insects, and plants. Most specimens show various types of exceptional preservation, ranging from impressions of the body outlines to traces of soft tissues (e.g., teleost air sac, eye spots, muscles, skins) and external body coverings (e.g., scales, feathers, hairs). The fossils are preserved primarily in lakes that were closely associated spatially with frequent volcanic eruptions. The impact of volcanic eruptions on the preservation process in these lakes is poorly understood. Detailed analysis of the state of preservation of these fossils, including the degree of fragmentation, density and diversity, plan-view orientation, size frequency, type of biomineralization, and lithofacies of the fossil-bearing layers as well as the relationship between the host lithology and associated volcanic rocks, sheds light on the causes of mass mortality events and mode of transport and burial of the organism remains in these lakes are discussed. The dominant environmental factors that influenced exceptional preservation of fossils in these volcanism-associated lakes are frequent mass mortalities, transport and rapid burial of the remains by pyroclastic sediments, and maturation of soft tissues by charcoalification.

The Eocene Fur Formation of Denmark – exceptional preservation exemplified by sea turtle soft tissues

Johan Lindgren

Department of Geology, Lund University, Sölvegatan 12, 223 62 Lund, Sweden

The Fur Formation (or Mo-clay) of western Limfjord region, Denmark, is a tephra-bearing and clayey marine diatomite of earliest Eocene (Ypresian) age. The formation is sub-divided into the lower Kudeklint and upper Silstrup Member, and a large number of isochronous volcanic ash layers have facilitated precise local correlations of the sedimentary succession. A moist sub-tropical to tropical climate, local upwelling and volcanic eruptions in nearby areas during the Ypresian ensured a continuous flow of detrital minerals, dust and microorganisms (mostly diatom frustules) some distance out to sea. The fine-grained material accumulated in the neritic zone under poorly oxygenated bottom conditions, and the deposits have since experienced only a mild geothermal history. Strata of the Fur Formation are replete with exquisitely preserved fossils, including birds, reptiles, bony fishes, insects, and plants; these reflect the organismal diversity immediately after the most pronounced greenhouse event of the Cenozoic (that is, the Paleocene–Eocene Thermal Maximum). Here, I review current knowledge on soft tissue structures and primary biomolecules obtained from sea turtle fossils, and show how this novel information can be used to elucidate traits that contributed to the evolutionary success of chelonids during the Paleogene.

Abstracts of workshop sessions

Palaeoproteomics

Mike Buckley

Manchester Institute of Biotechnology, The University of Manchester, Manchester M1 7DN, UK

Proteomics is the study of sets of proteins within a particular tissue or extraction, and arose from the development of soft ionization mass spectrometry. This allowed for the mass spectrometric analysis of large biomolecules in such a manner as to retrieve amino acid sequence information, the constituents of proteins coded for by DNA. ‘Palaeoproteomics’ is the analysis of ancient proteomes where some proteins are known to have much greater longevity than ancient DNA. Although it is usually the mere preservation of ancient biomolecules that forms the focus of many palaeobiological studies, the extraction and analysis of protein from extinct species can offer insights into evolution beyond that observed by morphological interpretation alone. As a result, over the past decade the application of proteomics to ancient fossils has been a growing field of research. However, this has not been without controversy, particularly with respect to claims of ancient protein sequences from dinosaur fossils. In this workshop, I will introduce the fundamentals of proteomic techniques and, using case studies, will illustrate the wider benefits of using proteomics for species identification to characterise palaeobiodiversity of faunal assemblages as well as examples in molecular phylogeny. I will also discuss the limitations of such techniques in their application to ancient remains in terms of sensitivity, contamination and the utilization of complementary techniques in screening for palaeontological material most likely to yield endogenous protein information.

Electron microbeam analysis of exceptionally preserved fossils

Stuart Kearns

School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

Scanning electron microscopy (SEM) is a tool routinely used in palaeobiological studies. It offers the potential to investigate morphology, mineral chemistry and structure. Different modes of exceptional preservation yield a range of materials from organic carbon to crystalline solids. As with other branches of materials science, each requires a particular set of operating conditions and detector types to characterise those materials in the fullest detail. A prerequisite for electron beam analysis is that the fossil samples, almost always dielectric, are rendered conductive. This is accomplished by the addition of a conductive coating or by the presence of a charge neutralising gas inside the instrument chamber. This latter case, Variable Pressure SEM, offers the potential of observing pure secondary signals (i.e. not attenuated/enhanced by the coating) coming from the sample and may offer additional information e.g. Charge Contrast Imaging; conversely, however, other signals will be compromised. Where data on either chemistry (X-ray microanalysis) or mineralogical structure (electron backscatter diffraction - EBSD) are required then the sample must be polished to yield accurate results. Surface roughness will compromise both techniques. Traditionally mechanical or electro-polishing will provide a suitable surface but for ultra-fine detail sampling, focussed ion beam (FIB) offers the highest possible resolution.

Transmission electron microscopy of fossil soft tissues

Maria McNamara

School of Biological, Earth and Environmental Sciences, University College Cork, Cork T23 TK30, Ireland

Transmission electron microscopy (TEM) is routinely used in the biological and material sciences to image sample structure, particularly internal details, at a sub-micron scale. The technique is increasingly combined with scanning electron microscopy (SEM), i.e., scanning transmission electron microscopy (STEM), which allows users to probe sample chemistry using backscattered electron imaging, energy-dispersive X-ray mapping, and electron energy loss analysis. Despite this, TEM is a relatively underused technique in palaeontology. This may reflect, in part, a lack of awareness of potential applications and preconceptions regarding sample suitability and preparation. In reality, almost any carbonaceous fossil can be prepared for, and imaged using, TEM, but sample preparation is relatively labour-intensive (compared to SEM) and requires specialist skills. Ultrathin sections can be prepared using focussed ion beam analysis (FIB) or conventional ultramicrotome sectioning; each have advantages and disadvantages. For conventional sectioning, tissue samples must be trimmed to less than 1 mm wide, embedded in resin and stained prior to imaging. Mineralised fossil tissues can also be prepared and sectioned using an ultramicrotome, but at a cost, i.e. the risk of irreversible damage to the diamond knife that is used to prepare the sections. Ultrathin sections can also be prepared using a FIB-SEM but the quality of resulting TEM images is typically lower than for those obtained using conventional microtomy. TEM images and chemical data offer information that is complementary to SEM and can be critical to interpretations of the structure and nature of preserved soft tissues in fossils.

The skeletal taphonomy of vertebrates in exceptional biotas

Patrick J. Orr

UCD School of Earth Sciences, University College Dublin, Dublin 4, Ireland

The taphonomic histories of fossil vertebrate skeletons in Konservat-Lagerstätten can be difficult to resolve. The simplest methods for assessing skeletal fidelity use verbal descriptors, comparative visual indicators of different preservational states, and assess the skeleton as a whole. The most complex involve counting the presence/absence of individual bones and whether each joint is articulated or not. A compromise is the division of the skeleton into parts, the completeness and articulation of each of which is scored semi-quantitatively, and from which an overall value for each variable can be derived. The effect of biostratinomic processes on the loss of skeletal fidelity is controlled by variables related to the biology of the taxon, environmental conditions, and the physical environment; how these interact is notoriously difficult to predict *a priori*. Analysis of the presence/absence of Voorhies Groups assumes the skeleton is reduced first to isolated bones, the size, shape and density of which control their transport potential. This, and more complex scenarios, e.g. the transport potential of defleshed but articulated bones, are amenable to experimental testing. What elements are removed is also strongly impacted by whether carcasses become locally adhered to the substrate as they decay before being subjected to the winnowing effects of currents.

Applying X-ray computed tomography to exceptionally preserved fossils

Imran A. Rahman

Oxford University Museum of Natural History, Oxford OX1 3PW, UK

X-ray computed tomography (CT) is a powerful technique for non-destructive visualization of the interior of objects, such as fossils. It has been applied to a wide range of preservation types and specimen sizes, including exceptionally preserved material from Konservat-Lagerstätten. However, not all fossils are well suited to CT (e.g. flattened and chemically homogeneous specimens), and the exact system, settings and software used to analyse the sample can greatly influence the quality of the results. In this presentation, I will outline the main steps in applying CT to fossils and discuss how to optimize them. Assuming the sample is suitable, the first step is to determine which CT variant (e.g. medical-CT, micro-CT or synchrotron CT) to use, given their differing capabilities in terms of sample size, resolution and contrast. Establishing the optimal scan settings is also important and may require some trial and error. By far the most time-consuming part of any CT-based study is reconstructing the scan as a three-dimensional computer model, and a variety of free and commercial software packages are available for this purpose. Lastly, researchers should consider how to make their datasets available to other workers when the analytical results are published.

Best practice in experimental decay: design, analysis, and application

Robert S. Sansom¹, Duncan J. E. Murdock²

¹School of Earth & Environmental Sciences, University of Manchester, Manchester M13 9PL, UK

²Oxford University Museum of Natural History, Oxford OX1 3PW, UK

All exceptionally preserved soft tissue fossil data have been filtered and transformed during the complex processes of decay and preservation; as such, it is always necessary to frame interpretations in light of taphonomy, be it the nature of the Cambrian explosion or the colour of feathers. Rather than making intuitive assumptions about the likelihood of different kinds of characters being preserved, researchers are increasingly turning to experimental analyses to make

informed interpretations. Patterns and processes of soft tissue decay can be studied over laboratory time scales and hold much promise in providing new insights, but how should those experiments be conducted and applied? How should they not? Here we outline points of consideration for design, analysis and application of experiments. Aims and hypotheses need to be stated *a priori*. Consideration and constraint is needed for the relevant variables of decay (organismal and environmental) and the possible measures of decay (morphological and chemical). Furthermore, application to fossil data requires consideration of geological context; for example, decay can act as either agonist or antagonist to preservation, depending on local conditions. A rich array of possibilities for further decay experiments exists and it is hoped that the methodologies outlined herein will provide guidance and a conceptual framework for future studies.

The light at the end of the tunnel: synchrotron methods and ancient life

Roy A. Wogelius¹, Phillip L. Manning^{1,2}, Uwe Bergmann³, Nicholas P. Edwards⁴, Loic Bertrand^{5,6}, Pierre Gueriau^{5,6}

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Beyond the structural details that may be recovered from exceptionally preserved fossils, the chemical residue may contain important details of both the fossilization pathway and the original biochemistry of the organism. Ancient specimens, however, present a number of analytical challenges. Here we will discuss a recently developed methodology which exploits the advantages of synchrotron radiation. The high photon flux of the synchrotron makes it possible to resolve, map, and quantify elements present at trace levels within fossil specimens non-destructively. Synchrotron Rapid Scanning - X-Ray Fluorescence Imaging allows chemical maps of large specimens to be produced quickly. Quantification of the XRF signal can be used to determine exact concentrations of elements. Once the inventory of elements has been determined via imaging, X-ray Absorption Spectroscopy (XAS, which is not possible in conventional X-ray sources) provides unambiguous information about the coordination chemistry of specific elements within the fossil and thus may indicate whether detected trace elements are part of the organic inventory of the preserved material and if the preserved chemical structures can be derived from biomolecules present in the living organism. Techniques will be explained using examples of vertebrate, invertebrate, and plant specimens. Related spectroscopic methods will also be discussed.

Abstracts of regular presentations

Biases in the fossil record of patterned insects

Nidia Álvarez Armada*¹, Maria E. McNamara¹, Stuart L. Kearns², Samuel M. Webb³, Fiona L. Gill⁴, Kevin J. McGraw⁵

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Insects exhibit some of the most diverse and striking colouration in the animal kingdom. Evidence of pigmentation in fossil insects can inform on their original colours and thus on the evolutionary history of pigments and their functions. Previous studies on the coloration of fossil insects have focussed on structural colours; the fossil record of insect pigments has yet to be investigated. Many fossil insects preserve evidence of patterning, but the taphonomic factors that control such preservation, and the nature of the pigments responsible, are unknown. Here we use an experimental approach to understand the taphonomy of pigmentary colours in insects. Specimens of *Harmonia axyridis* (n = 150) were degraded in acidic and basic pH conditions at 25°C for 6 months; a subset of these specimens (n = 32) were then tumbled for 5.5 weeks to simulate transport. Our results show that the preservation potential of pigmented cuticles is controlled by the pH of the decay medium and by the original pigment content of the cuticle. Future studies will elucidate the impact of these profound biological and environmental biases on the fossil record of different insect groups.

What is a pigment granule? - and why you should care

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The discovery that melanosomes (sub-spherical to ellipsoidal micron-sized organelles that contain the pigment melanin) persist in the fossil record and can be linked to colour patterns in fossil feathers has instigated a plethora of studies on fossil melanin over the last nine years. Accurate interpretations of fossil melanosomes, particularly in enigmatic fossils, are contingent upon a comprehensive understanding of their biology in extant animals. It is generally accepted that melanosomes occur in various tissues of extant vertebrates. Recalcitrant black/dark pigment granules of similar sizes to melanosomes, however, have also been recorded in the eyes of gastropods, cuttlefish and cubozoan jellyfish and in the integument of echinoderms, pterobranchs and nematodes. Here we present a review of these 'pigment granules' in invertebrates and a discussion of their possible identities. We also present new evidence of 'melanosome-like' structures in the eyes of modern cephalopods and experimental data on the resistance of these melanosome-like structures to decay. The occurrence and recalcitrance of multiple 'types' of pigment granule, many of which manifest as near-identical to melanosomes in gross morphology and chemistry, has major implications for the interpretation of the phylogenetic affinities of fossils based on the presence of melanosomes. Further research into the identity, origin, function and recalcitrance of

'pigment granules' in extant taxa is of paramount importance in moving forward the burgeoning field of fossil colour.

Integumentary structures and soft-tissues in the gobiconodontid *Spinolestes* from the upper Barremian of Las Hoyas (Huérquina Formation, southwestern Iberian Basin, Cuenca)

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The sediments from Las Hoyas are finely laminated limestones with a small fraction of clay and organic matter. The deposits accumulated in a periphyton-dominated carbonatic subtropical wetland which was covered by thick microbial mats and was influenced by cyclical oscillations of the climatically driven water level. *Spinolestes* is a largely articulated skeleton associated with preserved integument. Our analyses indicate that the skin ruptured during the gas decomposition phase of decay, resulting in detachment and slight displacement of the skull. The exceptional preservation of *Spinolestes* soft-tissues includes integumentary structures of different types, lung ducts and sacs, and the visceral contour of the liver; all tissues are preserved via phosphatisation. Both light microscope and scanning electron microscope examination revealed the histology of the hairs at cellular scale, keratinized epidermal cells, hair roots, bulbs and hair follicles. The possible biostratinomic processes that were involved in *Spinolestes* preservation will be discussed.

Rotten livers, guts and gills: can carcasses generate organ specific microenvironments?

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Exceptionally preserved soft tissues are found in many Lagerstätten and are invaluable in reconstructing ancient life. The most important control on the replacement of organics by authigenic minerals is the generation of suitable geochemical conditions, notably pH, during decay. Various studies using fossil material have concluded that that localised and chemically distinct 'microenvironments' corresponding to specific organs occur within a carcass during decay and that this may affect mineralisation processes and composition. Experimental designs investigating this phenomenon have relied on external conditions around a carcass as a proxy for whether internal conditions are suitable for mineral precipitation. We have designed a novel experiment to investigate the formation of microenvironments inside a carcass by recording the varying chemical conditions within specific organs in real time. Our experiments demonstrate that (i) pH within and around the carcass drops rapidly post-mortem, (ii) internal chemical gradients are more pronounced than immediately around the carcass, and (iii) organs have variable decay resistance and trajectories. Our data also suggest that decaying organs, such as the stomach, have little influence on surrounding tissues and do not cause 'pH-cascades' during integrity failure.

Revelations by hard parts: ammonoid examples from the Hunsrück Slate Konservat-Lagerstätte

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Research on Lower Devonian Lagerstätten around Bundenbach (Germany) has focused on fossils with remarkable preservation, including fully articulated echinoderms and vertebrates as well as soft tissues of annelids, arthropods and other groups that are typically preserved without hard tissues. Although some fossils reveal remarkable preservation, all of them are typically flattened and deformed. Moreover, it is difficult if not impossible to prepare specimens from both sides and subsequently study them without micro (μ)CT-scanning. Ammonoids found within the Hunsrück Slate are not only used to constrain the age of the deposit but their preservation and associated encrusters also reveal important details about the paleoenvironment and taphonomic history of assemblages they are found in. We studied 341 ammonoid specimens representing seven taphonomic groups, based on preservation and EDS analysis, which corroborated the most recent interpretations of depositional environment and diagenesis for the host sediment. Ammonoid conchs are only rarely encrusted when compared with nautiloids, inferring habitats in deeper shelf environments. A μ CT investigation revealed an in situ encrustation by hederelloids in at least one specimen, which supports depositional conditions within the photic zone with maximal depths around 100 m.

Microbial mats: the implications of microbial communities in the early stages of fossilization

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Microbial mats have been frequently invoked as a potential factor to explain exceptional preservation in different Konservat-Lagerstätten. However, the influence of these mats in preservation needs to be reconsidered in the light of long-term experiments. We summarize the effects of microbial mat communities in early fossilization of flies, fish, anurans and plants during experiments that lasted up to 5.5 years. The body is isolated within a microbial sarcophagus that develops within a few days. This microbial mat controls microenvironmental conditions within the carcass and favours the preservation of inner organs by delaying decay, maintaining the hydration of the body, and favouring an alkaline environment inside the body. The detailed structure of muscles, tendons, and bone marrow are identified in a frog after 5 years using SEM. Tissues mineralize in the form of a talc-like Mg-rich silicate replacing bones in fish, or in the case of the mid-brain of frogs, calcium carbonate. Lastly, the inner face of the sarcophagus generates detailed impressions, in negative, of external structures. These impressions were enabled by the action of the exopolymeric substances (EPS) produced by the mat, and by the small size of cells inside the sarcophagus.

Insights into exceptional preservation processes: the study of crustaceans from La Voulte-sur-Rhône, France

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Konservat-Lagerstätten are considered the source of the most reliable palaeontological data given the quality of fossil preservation. However, a better understanding of the processes leading to the formation of exceptionally preserved fossils is necessary to uncover potential biases and assess the robustness of paleontological reconstructions (relating to anatomy, biology, and palaeoenvironment). Here, we report the mineralogical study of exceptionally preserved crustaceans fossilised within carbonate-rich concretions from the Jurassic Konservat-Lagerstätte of La Voulte-sur-Rhône (Ardèche, France). Semi-quantitative elemental mapping was performed using SEM-EDS and synchrotron-based XRF. Mineralogical phases were identified using XRD and Raman spectroscopy. Combining these techniques allowed identification of the mineralogical phases composing the fossils (Ca-phosphates, Fe-, Zn-, Pb-sulfides, Ca-sulfates, Fe-oxides and Ca-, Mg-, Fe-carbonates) and the surrounding matrix (Fe-carbonates, K-rich clays and detrital silicates), and documented their complex textural relationships. As a result, we propose a new taphonomic scenario for these exceptionally preserved fossils: phosphates and sulphides precipitated first, iron sulphides were later oxidised in sulphates and iron oxides. This change in the redox environment appears to have been related to inflows of detrital material. Different tissues may have promoted the precipitation of different mineralogical associations, reflecting the precise chemical conditions at different stages of the mineralisation process and/or the inherent geochemistry. This specificity allows potential taphonomic biases to be assessed.

Sedimentology and paleoecology of two Miocene maar-Lagerstätten in New Zealand

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Some of the most spectacular Konservat-Lagerstätten are associated with maars (small, deep volcanic craters) in which finely laminated biogenic sediments accumulated under anoxic conditions. These settings may allow preservation of soft-bodied organisms in exquisite detail and preserve entire terrestrial ecosystems. We present two examples of maar-type Lagerstätten of Miocene age from southern New Zealand. At the early Miocene Foulden Maar, the fossiliferous sediment comprises finely laminated diatomite. In contrast, at the mid-Miocene Hindon Maar, the sediments include carbonaceous gyttja, spiculite and thin intervals of diatomite. At both sites, plant remains from the surrounding palaeoforests include abundant, highly diverse leaves, flowers, fruits, seeds and wood. Of particular significance are flowers and conifer cones with in situ pollen and fertile fern fronds. The fauna includes numerous insects, some with structural colour and near 3-D preservation, entire fish with soft tissue preservation and bird feathers. Insects include mainly forest-taxa such as ants, termites and beetles; (semi)aquatic insects such as flies, dragonflies and caddisfly larvae are rare. Fish are of low diversity but include the oldest records of galaxiids and the only Southern

Hemisphere freshwater eel fossils. The sedimentary setting, taphonomy and biodiversity of these significant Southern Hemisphere Konservat-Lagerstätten will be highlighted.

A variable geometry tail in early birds and feathered dinosaurs: evidence from *Archaeopteryx* and *Microraptor*

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The tail of birds serves multiple roles in flight, generating lift, reducing drag, and providing control via passive stability or active steering. Control is a prerequisite for the evolution of gliding or powered flight, and the tail is therefore likely to have played a critical role in the origin of flight. However, the tail of basal birds is thought to be unable to alter span and area, limiting its effectiveness. New observations of the early bird *Archaeopteryx* and the feathered dromaeosaur *Microraptor*, show that despite a number of primitive features of the plumage, the feathers were not fixed to the tail skeleton and could fan to increase span and area. The tail of *Archaeopteryx* and *Microraptor* lack a one-to-one correspondence between rectrices and vertebrae, indicating that rectrices were supported by soft tissue, rather than attaching to the skeleton. Both *Archaeopteryx* and *Microraptor* exhibit variation in the extension of rectrices, ranging from approximately 20° to 30°, suggesting that rectrices could be fanned and furled. The combination of a sophisticated control structure with primitive wings and pectoral girdle in *Archaeopteryx* and *Microraptor* suggest that aerodynamic control was critical in early bird flight and preceded the evolution of sophisticated flapping flight in birds.

Preservation of soft-bodied organisms in coarse-grained siliciclastic environments

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During the Ediacaran Period, soft-bodied organisms were commonly preserved in coarse-grained siliciclastic sediments. The exceptional preservation of these organisms during the terminal Proterozoic/early Cambrian, and their relative absence from the fossil record later in the Phanerozoic, suggest that temporally unique environmental conditions may have facilitated preservation. In the absence of grazing and bioturbating metazoans, microbial mats were widespread in benthic Precambrian environments, and have a hypothesized role in the preservation of soft tissues. We investigated the preservation of soft-bodied organisms (scallops and jellyfish) incubated in siliciclastic sand. The experiments tested the ability of photosynthetic microbial mats and clay minerals (illite and kaolinite) to preserve soft tissues. Control experiments were performed in the absence of photosynthetic mats. Micro-focused Fe K-edge X-Ray Absorption Near Edge Structure (μ XANES) spectroscopy and X-ray diffraction (μ XRD) revealed that Fe (II), such as Fe (II) sulfates, and Fe (II, III) mixed oxides (clays) accumulated on soft tissues after 45 days of incubation. Although larger soft tissues were recovered in the presence of clay minerals and photosynthetic

mats, the results indicate that microbial processes within sediments were most important for the overall preservation of soft tissues.

The Mazon Creek cnidarian *Essexella*: The world turned upside down

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Essexella asherae is the most common animal in the Pennsylvanian Mazon Creek Biota of Illinois, USA. Foster (1979) assigned the taxon to Scyphozoa, based primarily on the occasional presence of small gastropods on the “skirt” region, analogous to a modern species that feeds on planktic cnidarians. The skirt was described as “a membranous curtain of rather resistant material that hangs below the bell”, although a similar feature is not found in modern scyphozoans. Various pustules and ridges occurring in that region were suggested to be “oral lobes, tentacles...or gas bubbles from decay of structures.” We propose an alternative interpretation: the animal represents an anemone, possibly a burrower. The great variation in preserved morphology is probably due a combination of original orientation in the sediment, degree of post-burial decay, and the superimposition of upper and lower features due to compaction. The specimens have substantial relief compared to other Mazon Creek animals, indicating a relatively tough and firm structure. “Tentacles” are re-interpreted as contracted mesenterial muscles. The “bell”, which is highly variable in shape and size, is instead suggested to be an inflated pedal disk. *Essexella* is a candidate for the tracemaker of *Conostichus*, a common Pennsylvanian ichnofossil attributed to burrowing anemones.

The value of experimental decay in analysis of exceptionally preserved fossils

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The use of experiments to understand post-mortem processes and their role in exceptional preservation goes back decades, but recent papers have strongly questioned their value. We argue that this reflects a misunderstanding regarding the objectives of taphonomic experiments, partly arising from a lack of clarity in terminology. Focussing on character-based experimental decay we have developed methods that allow clear analysis and quantitative testing of the repeatability and comparability of experiments, differentiating factors that retard onset of decay from those that reduce the rate of character loss. This approach demonstrates that sequences of character loss are generally unaffected by the environment in which carcasses decay. Empirically derived sequences can thus be applied to exceptionally preserved fossils to disentangle the relative importance of, and interactions between, decay, maturation and preservation, and to inform our interpretations of fossil morphologies. Far from being of limited value, data from well-designed taphonomic experiments provide fundamental new insights into the processes and biases that have produced exceptionally preserved fossils, and the degree to which they distort our view of the past.

Tissue-specific trace element chemistry of melanosomes in vertebrates revealed by synchrotron X-ray fluorescence

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Melanosomes are micron-sized spheroidal to oblate organelles that contain the pigment melanin and occur in various vertebrate soft tissues including the eyes and integument. Fossilized examples of melanosomes have been applied primarily to studies of melanin and melanin-based coloration in fossils. The broader significance of melanosomes in evolutionary studies is, as yet, poorly understood; only a single study has attempted to use melanosome geometry to infer the anatomy and phylogenetic position of fossils. This stems, in large part, from our limited understanding of which, if any, characteristics of melanosomes (e.g. geometry, chemistry) correlate with anatomy. Certain trace elements, such as copper, iron and magnesium, are known to chelate with melanin *in vivo*. Here, we use synchrotron-based X-ray fluorescence (XRF) to quantify the concentrations of various trace elements in melanosomes extracted from the eyes and other tissues in the cranial region of vertebrates. Our results reveal that specific suites of trace elements are associated with individual tissues; for certain tissues, the trace element chemistry of melanosomes in homologous tissues is consistent among taxa. These data help constrain the extent to which the chemistry of melanosomes from the cranial region of vertebrates can be used to infer anatomy.

Trace element chemistry of melanosomes revealed by synchrotron-X-ray fluorescence: a tool for interpreting fossil vertebrate soft tissue

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Melanosomes are important components of integumentary tissues in modern vertebrates and have been reported from various vertebrate and invertebrate fossils ranging in age from the upper Palaeozoic to the Cenozoic. Much previous work on fossil melanin has focused on reconstructions of integumentary colour in fossils. Modern vertebrates, however, also possess melanin pigmentation in internal tissues. The impact of these internal melanosomes on interpretations of fossil soft tissues has not been assessed and, critically, there is no known mechanism to discriminate between melanosomes from different tissue sources. Here we present the first systematic analysis of the anatomical distribution, morphology and chemistry of melanosomes in different vertebrate taxa. Melanin extracts from various tissues from extant amphibians, reptiles, birds and mammals were analysed using scanning electron microscopy (SEM) and synchrotron X-ray fluorescence (XRF). Our results reveal striking differences in trace element chemistry both within individual animals and among taxa. These findings can be applied to fossils to allow integumentary and non-integumentary melanosomes to be discriminated, offering a new tool for the investigation of the preservation potential of soft tissues in the fossil record and more accurate interpretation of the internal anatomy in extinct animals.

Dinosaur eggshell calcite as a closed system: 'molecular Konservat-Lagerstätten'

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Mesozoic protein survival is unlikely given known rates of hydrolysis and diagenetic reactions. As proteins hydrolyze in open systems (e.g., bone), released peptides/amino acids can leach from the specimen and be microbially metabolized or further degraded. Given the thermodynamic instability of peptide bonds, closed systems are the most likely repository for trapped breakdown products of what were once endogenous proteins. Recent amino acid racemization analysis suggests that avian eggshell calcite crystals can act as closed systems, trapping endogenous amino acids. Here, HPLC shows that Late Cretaceous (~80 Ma) sauropod eggshell contains only the three most stable amino acids (Glx, Gly, Ala) and all three are fully racemic, including Glx, the slowest racemizing amino acid. Such results match expected trends from modern, sub-fossil, and 3 Ma avian eggshell, and 30 Ma closed system mollusc shell. These results represent the first robustly supported dinosaur or Mesozoic protein-derived biomolecules, and the selective survival of only three amino acids strongly supports a loss of the majority of the peptide chain sequence. Crystal matrices can impart preservational potential to labile organic molecules, but the significant loss of most amino acids raises doubt about reports of proteins from dinosaur bone.

Selective taphonomic processes in the Fezouata Konservat-Lagerstätte (Lower Ordovician, Morocco): storm influence on the brachiopod record

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Taphonomic processes are responsible for the transition of an organism from the biosphere to the lithosphere. In marine settings, these processes involve both pre-mortem and post-mortem biological, chemical and physical parameters in the water column and in the sediments. Previous detailed studies focused on the influence of these parameters on the fossil record (Lilliput effect, fossil sorting, presence of mineralized organisms and organic matter). The pre-mortem physical conditions of the water column, however, have not been considered important. The brachiopod record in the Fezouata Shale suggests that these physical processes should be taken into consideration to explain the size composition of the brachiopod assemblages. In this Formation, epibenthic brachiopods show an abnormal distribution (small-sized individuals only) in proximal sites and a normal demography in distal localities, while the distribution of endobenthic brachiopods was standard in both proximal and distal sites. This discrepancy can be related to storm intensities influencing the Fezouata palaeoenvironments. In shallow settings, living epibenthic brachiopods were more influenced by weak storms than deeply-burrowing endobenthic taxa, which were only affected by stronger events. This indirect ecological defence strategy provided more time for endobenthic individuals to grow, therefore displaying a wider range of sizes in proximal settings than epibenthic communities.

Upper Cretaceous marine arthropods relied on terrestrial organic matter as a food source: geochemical evidence from the Coon Creek Lagerstätte in the Mississippian Embayment

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We tested the integrity of organic stable carbon isotope signatures ($\delta^{13}\text{C}$) in exceptionally preserved Mesozoic-age decapod arthropod cuticle and their utility in paleoenvironmental interpretations. Crab, mudshrimp, and samples of the associated matrix were obtained from the Upper Cretaceous Coon Creek Formation Lagerstätte of Tennessee. These samples were examined using elemental analysis, biomarker, bulk TOC and n-alkane $\delta^{13}\text{C}$ analyses, and Raman spectroscopy. Thermal maturity indices indicate that specimens underwent limited post-burial heating. Comparison of total organic carbon and nitrogen, and C:N ratios from fossil specimens to those from modern chitin indicate that the former are heavily depleted in nitrogen, but do preserve organic carbon, up to 13 wt %, as kerogen. Using published inorganic $\delta^{13}\text{C}$ values, we produced a model of the Coon Creek carbon isotope systematics that defines potential marine (phytoplankton) and terrestrial (plant) dietary sources. Mean fossil crab and shrimp organic $\delta^{13}\text{C}$ values (-25.1‰ and -26.0‰ , respectively) fall closer to those estimated for terrigenous plant matter than marine phytoplankton, indicating that decapods were feeding primarily on terrigenous organic matter. From this model, we infer that the Coon Creek Formation was deposited in a shallow back-bar-type setting where terrestrial organic matter was occasionally washed into otherwise normal marine conditions in the northern Mississippi Embayment.

Abstracts of lightning presentations

Fluoridation of a lizard forelimb in Miocene Dominican amber

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Amber deposits represent a remarkable subset of Konservat-Lagerstätten, characterized by three-dimensional preservation of the soft tissues of organisms as organic remains. Discoveries of vertebrate fossils in amber are extremely rare, and thus such specimens are highly valuable and are often not accessible to scientific study. Consequently, almost nothing is known about the quality of preservation of vertebrate fossil inclusions in amber. Here, we present the results of a study on the left forelimb of a fossil lizard, *Anolis sp.*, preserved in Miocene Dominican amber. The lizard appears to have been trapped in the resin while alive and exhibits evidence of predation, including an edema. Thin sections of the lizard and associated resin were analysed using confocal Raman spectroscopy. Analysis of the bones reveals the degradation of collagen to amorphous carbon and to more complex organic compounds, and fluoridation of the bone apatite. Whilst the latter process is common for fossils preserved in sediment, it is unexpected for material trapped in amber. Our study will stimulate new questions concerning the taphonomic pathway of amber in general.

An exceptionally preserved specimen of *Aurorazhdarcho* (Pterosauria, Aurorazhdarchidae) from the Jurassic Solnhofen of Germany

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A skeleton of a small pterodactyloid pterosaur assigned to *Aurorazhdarcho micronyx* (Aurorazhdarchidae) from the Early Jurassic Solnhofen limestone (early Tithonian of Southern Germany) was analysed under UV light and laser-stimulated fluorescence (LSF) imaging, revealing new information on the anatomical diversity of pterosaur wing shape and the functionality of pedal webbing. The specimen MB.R.3531 consists of a slab preserving most of the skeleton and some soft tissue as well as a counter slab. The counter slab preserves external moulds of some skeletal elements including portions of the wing skeleton. The preserved skeleton comprises both wings and hindlimbs as well as vertebrae from the neck and trunk and includes some ribs. Soft tissue preservation includes remains of the wing membrane (a complete right dactylopatagium and partial left dactylopatagium; partial right and left plagiopatagiums) and pedal webbing. The complete actinofibrils of the right dactylopatagium allow for a reconstruction of the distribution and position of these structures and their functional significance for the pterosaur wing membrane.

Probing the speciation of carbon in fossils at high energy using synchrotron-based X-ray Raman scattering

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Identifying carbon species in fossils using X-ray absorption spectroscopy allows the signature of relict organic molecules to be recognized (e.g. sporopollenin and chitin), and their biological origin and/or their alteration to be traced through time. Conventional X-ray absorption spectroscopy at the carbon K-edge (~290 eV) imposes stringent constraints on sample type, preparation (extremely thin micro-samples) and analytical environment (vacuum) due to the short penetration of soft X-rays. Here, we show that the use of X-ray Raman scattering at ~6 keV incident energy is a practical and powerful complementary technique that can discriminate carbon compounds in palaeontological macro-remains. The method also has potential applications in the analysis of additional light elements such as oxygen and nitrogen. Both the capacities and the limitations of this hard X-ray speciation probe are presented.

Preliminary report of the mineralization potential of tissues

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Exceptionally preserved fossils occur throughout the Phanerozoic and include diverse tissue types. The type of tissue fossilized and the quality of preservation varies greatly between localities, and the specific taphonomic factors controlling mineralization are still incompletely understood. Here, we present preliminary results from an experimental taphonomic study designed to simulate the pyritisation of soft tissues. Plant leaves and stems, chitons, and polychaetes were buried under similar conditions; the experiment was stopped after 6 weeks of decay and samples were analysed using light microscopy and SEM-EDS. The presence of pyrite was not identified conclusively in any of the samples. Nonetheless, the different tissues showed different taphonomic histories. The soft tissues of the chitons and polychaetes were completely replaced by mineral films, the plant stems retained their original composition but showed incipient mineral precipitation along the ends of the stems, and the leaves showed no substantial mineral film development. Although this study is ongoing, it is clear that the timing of mineralization is strongly impacted by tissue composition.

Experimental taphonomy of circularly polarizing nanostructures in scarab beetles (Coleoptera: Scarabaeidae)

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Insect cuticles comprise chitin-based composite structures that can be coloured using both pigments and photonic nanostructures, either in isolation or in combination. In certain scarabaeid sub-families, chitin nanofibrils assemble to form helicoidal photonic structures that reflect circularly polarized light. Intriguingly, the evolutionary history of these structures is unknown: they have not been reported from the fossil record. Whether this reflects a real biological signal, or a taphonomic artefact, has not previously been investigated. To address this, we decayed circularly polarizing cuticles from three scarab beetle genera for three months in controlled laboratory experiments. We assessed changes in cuticle colour, structure and polarization using polarizing filters, reflectance spectrophotometry, scanning- and transmission electron microscopies. Our results reveal taxonomic controls on the preservation potential of circular polarizing structures in insects. Optical and structural features survive decay in *Ischiopsopha* and *Gymnopleurus*, but not *Chrysina*, possibly due to the unusual cusp-like arrangement of the helicoidal ultrastructure in *Chrysina*. These results indicate that preservation of circularly polarizing structures is feasible in fossil insects. Future studies will identify diagenetic controls on the preservation of these structures to constrain potential target localities for the preservation of polarizing cuticle structures in the insect fossil record.

3D preservation of gills in the first fossil crabs from the Kerguelen Islands

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The Kerguelen Islands possess rare fossil localities. Those that do occur yield marine invertebrates of Miocene age, including decapod crustaceans. These crabs correspond to a new monospecific assemblage (Brachyura, Cancridae) preserved in approximately one hundred phosphate nodules.

Some specimens reveal exceptional preservation of fragile internal structures which rarely fossilize, such as the endoskeleton and, more remarkably, three-dimensionally preserved gills with branchial lamellae. The preserved tissues were imaged using scanning electron microscopy. Petrographic and geochemical analyses were performed using energy dispersive X-ray spectroscopy and X-ray diffractometry. The morphology and organization of the gills preserved in the fossil Cancridae is similar to that observed in modern representatives of the group. The three-dimensional preservation of soft tissues is attributed to phosphatization during the early stages of diagenesis and, most likely, the formation of a thin clayey layer adhering to the surface of the soft tissues. The extent to which internal sources of phosphorous have impacted on the quality of preservation of different tissues is difficult to determine.

Abstracts of posters

X-ray fluorescence as a tool for interpreting fossilized pigmentary colours

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Many insects exhibit striking colour patterns on their cuticle, which are produced primarily by pigments such as melanins, carotenoids and pterins. Fossil specimens can exhibit similar patterns, but the origins of their patterning and the nature of the pigments responsible are unknown. We resolve these issues using non-destructive synchrotron-based X-ray fluorescence (XRF) to characterize the spatial distributions of trace elements in the cuticles of both fossil and modern insects. We mapped the concentrations of eleven trace elements in cuticle regions that possess different pigments. Principal component analysis (PCA) of the concentrations of each element reveals a strong taxonomic signal whereby members of the same family show similar concentrations of trace elements. Within families, cuticle regions with different pigments have distinct trace element chemistries, suggesting that the broad taxonomic signal is overprinted by a strong pigment-specific signal. The trace element chemistry of fossil insect cuticle differs to that of the modern analogues, indicating diagenetic overprinting. These results will enhance our ability to interpret the original pigmentary colours of fossil insects, thus informing models of the evolution of colour and its ecological functions in insects through deep time.

Multiple paths that cross into the integration of the Las Hoyas Early Cretaceous ecosystem

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The Early Cretaceous Las Hoyas biota (Spain) includes approximately 200 known species that are highly representative of a subtropical wetland ecosystem. Research to date includes on the recovery of taxonomic, but also sedimentological and taphonomic, data from the excavated layers. Taphonomic research at the Las Hoyas deposit has focused on the characterization of biostratigraphic patterns and processes. The search for a coherent and comprehensive biostratigraphic scenario

requires the combination of sedimentological, biological and ecological information, including data on fossil production, fossil assemblages and fossil associations retrieved *in situ*. Taphonomic experimentation is essential to this goal and affords a deeper understanding of the biostratigraphic processes responsible for preservation. Resulting improvements to excavation design are coupled with a better understanding of (a) the link between seasonality and fossil abundance, (b) exceptional fossil preservation, and (c) the structure of the ecosystem. The reconstruction of the trophic network is a current focus of research.

Synchrotron micro X-ray fluorescence (μ XRF) and X-ray near-edge absorption spectroscopy (μ XANES) suggest the presence of eumelanin pigment in the protofeathers of *Kulindadromeus zabaikalicus* (Middle Jurassic of Siberia)

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Since the first discoveries of feathers closely associated with the skeletons of non-avian theropod dinosaurs, it is widely recognized that the ancestors of birds also possessed feathers. More recently, elongated integumentary structures interpreted as protofeathers have been reported in association with remains of ornithischian dinosaurs, the dinosaurian clade that is not related to birds. The study of such epidermal appendages in non-theropod dinosaurs reveals new data about the origin and evolution of feathers. Here, we investigate the chemical composition of the elongated filaments from the basal neornithischian dinosaur *Kulindadromeus zabaikalicus* (Middle Jurassic of Siberia) using synchrotron μ XRF elemental mapping and μ XANES spectroscopy. μ XRF mapping shows that the structures interpreted as protofeathers are enriched with Cu compared to the surrounding sedimentary matrix. μ XANES performed at the Cu K-edge reveals that the coordination chemistry of the Cu is similar to organic Cu in modern bird feathers and in natural eumelanin, as previously reported for Cretaceous and Eocene fossil bird feathers. This would indicate that the protofeathers of *Kulindadromeus* were pigmented by eumelanin, suggesting that diverse primitive feathers contained pigments.

The evolution of colour patterns in fossil insects

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Wing colour patterns are the basis of diverse communication strategies in insects, with major roles in camouflage, mate choice and as warning signals, in addition to physiological functions and in aiding species identification. In the fossil record many insect specimens exhibit colour patterns. These consist of monochrome stripes, blotches, and eyespots, and can resemble those observed in modern insects. The variable wing colour patterns of extant insects are critical to our understanding of evolutionary processes, especially the respective roles of innovation, homology, and convergence in driving trends in colour pattern evolution. However, there has been no systematic investigation of colour patterns in fossil insects; thus the potential of the latter to contribute to evolutionary hypotheses is untested. This project represents the first rigorous and phylogenetically broad study of colour patterns in fossil insects and uses geometric morphometric analysis of high-resolution photographs of specimens to classify and compare fossil insect colour patterns. Preliminary work is focussing on the order Neuroptera from the Jurassic Daohugou Lagerst tte, China; the morphospace

of the preserved patterns will be compared with those present in other insect groups (e.g. Orthoptera, Hemiptera) and other sites (e.g. Messel, Germany). Patterns will be mapped onto a phylogenetic framework to infer the evolution of colour patterns in fossil insects and the relative importance of different evolutionary drivers controlling patterning.

Relevance of Konservat-Lagerstätten to past ecosystems: the paradigmatic case of the Paris Biota (Early Triassic)

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After the end-Permian mass extinction, the Early Triassic (~251.9 to 247 Ma) is characterized by several biotic crises that particularly affected marine benthic fauna; accordingly, marine ecosystems from this unstable interval have been described as heavily depauperate in diversity and abundance. This assumption, however, may relate to bias in the fossil record. The discovery of taphonomic windows, like Konservat-Lagerstätten, in the Early Triassic would help to reveal the true composition of ecosystems at that time. The Paris Biota (Idaho, USA) is a highly diverse fossil assemblage from the earliest Spathian (Middle Olenekian, ~250.6 Ma) that includes at least seven phyla and twenty metazoan orders, representing a remarkably complex marine ecosystem. However, the taphonomy of these fossils has not been investigated. Here we report the mineral characterization of two of the most abundant groups in the biota: brachiopods and leptomitid sponges. For this purpose, we combine data from Raman spectroscopy, FTIR, and SEM-EDS. Despite preservation of tissues in both groups in calcium phosphate, the morphology and organization of the preserved tissues are very dissimilar at a micron scale. Better understanding of such preservation would help identify potential bias on observed diversity signals and their interpretation.

The influence of resin chemical compounds on common components of fruit fly gut microbiota: implications for a resin chemistry bias in the amber fossil record

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Fossils in amber are an important palaeobiological resource for understanding extinct organisms and ancient ecosystems. However, inclusions in amber exhibit preservational variation – they range from preserved labile tissues to empty moulds – indicating that the amber fossil record is influenced by preservational biases; in particular, variable resin chemistry is thought to influence preservation. We have shown experimentally that fruit flies decay far more quickly when embedded in *Pinus sylvestris* resin (specimens were empty cuticle after 6 months) than in *Wollemia nobilis* resin (specimens retained most of their labile soft tissue after 1.6 years). Resin influences preservation in the early stages of fossilization in 2 ways: (1) it creates a physical barrier against the activity of external bacteria; (2) the volatile resin compounds infiltrate the tissues, and influence the activity of gut biota, which, in fruit flies, is dominated by *Acetobacter pomorum* and *Lactobacillus plantarum*. There are 26 volatile compounds that differ in presence or quantity between the two resins, and we

have reviewed the literature to determine which are most effective at inhibiting the activity of *A. pomorum* and *L. plantarum* and, therefore, which are most likely to explain the differences in decay between the two experimental treatment groups.

Diverse 3D photonic nanostructures in fossil insect scales

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Beetles represent the most populous order amongst extant insects, with many species displaying vibrant, iridescent colours that result directly from interactions between incident light and the beetles' cuticle ultrastructure. The majority of animals, including beetles, typically use 1D multilayer reflectors to produce these 'structural colours'. However, some weevils and longhorn beetles have evolved complex 3D photonic crystal (3DPC) nanostructures, which form within scales adorning the beetles' exoskeleton. Although abundant in extant species, structural colours are comparatively rare in the insect fossil record, partly due to the paucity of preserved scales. Specifically, 3DPCs have thus far been reported in only a single fossil weevil and, thus, the evolutionary history of these tissue architectures, and the driving forces behind their evolution, are unknown. Here, we report the discovery of distinct 3DPC assemblies in diverse fossilised scale structures. We adopted a multi-faceted approach to identify and diagnose nanostructures in thirteen Pleistocene weevil specimens collected from Canadian localities. Scanning electron microscopy (SEM), transmission electron microscopy (TEM), Fourier analysis and small-angle X-ray scattering (SAXS) corroborate the presence of complex 3DPC nanostructures in fossil insect scales, which correspond to those reported for extant species. These data will serve as a platform to deliver novel insights into the evolution, development and functionality of scales in coleopteran species.

Preliminary report of the mineralization potential of tissues

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Exceptionally preserved fossils occur throughout the Phanerozoic and include diverse tissue types. The type of tissue fossilized and the quality of preservation varies greatly between localities, and the specific taphonomic factors controlling mineralization are still incompletely understood. Here, we present preliminary results from an experimental taphonomic study designed to simulate the pyritisation of soft tissues. Plant leaves and stems, chitons, and polychaetes were buried under similar conditions; the experiment was stopped after 6 weeks of decay and samples were analysed using light microscopy and SEM-EDS. The presence of pyrite was not identified conclusively in any of the samples. Nonetheless, the different tissues showed different taphonomic histories. The soft tissues of the chitons and polychaetes were completely replaced by mineral films, the plant stems retained their original composition, with incipient mineral precipitation along the ends of the stems, and the leaves showed no substantial mineral film development. Although this study is ongoing, it is nonetheless clear that the timing of mineralization is strongly impacted by tissue composition.

Skin shedding and the coevolution of skin and feathers in fossil birds and feathered dinosaurs

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Feathers are remarkable evolutionary innovations that in modern birds are associated with complex adaptations of the skin. Fossilized feathers in dinosaurs and early birds provide insights into feather evolution, but how associated integumentary adaptations evolved is unclear. Here we report the discovery of fossil skin in feathered dinosaurs and an early bird from the Cretaceous Jehol biota (NE China). The fossil skin comprises patches of epidermal corneocytes (dandruff) that preserve a cytoskeletal array of helically coiled α -keratin tonofibrils. This shows that reptilian-style partial- or whole-body molting had already been replaced by shedding of small epidermal flakes as in modern mammals and birds, albeit with lower body heat production. Feathered epidermis in dinosaurs and primitive birds had acquired many anatomically modern attributes by the Early Cretaceous.

Experimental taphonomy of circularly polarizing nanostructures in scarab beetles (Coleoptera: Scarabaeidae)

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Insect cuticles comprise chitin-based composite structures that can be coloured using both pigments and photonic nanostructures, either in isolation or in combination. In certain scarabaeid sub-families, chitin nanofibrils assemble to form helicoidal photonic structures that reflect circularly polarized light. Intriguingly, the evolutionary history of these structures is unknown: they have not been reported from the fossil record. Whether this reflects a real biological signal, or a taphonomic artefact, has not previously been investigated. To address this, we decayed circularly polarizing cuticles from three scarab beetle genera for three months in controlled laboratory experiments. We assessed changes in cuticle colour, structure and polarization using polarizing filters, reflectance spectrophotometry, scanning- and transmission electron microscopies. Our results reveal taxonomic controls on the preservation potential of circular polarizing structures in insects. Optical and structural features survive decay in *Ischiopsopha* and *Gymnopleurus*, but not *Chrysina*, possibly due to the unusual cusp-like arrangement of the helicoidal ultrastructure in *Chrysina*. These results indicate that preservation of circularly polarizing structures is feasible in fossil insects. Future studies will identify diagenetic controls on the preservation of these structures to constrain potential target localities for the preservation of polarizing cuticle structures in the insect fossil record.

Preservation of soft-bodied xylophagous mollusks (Bivalva, Teredinidae) and evolutionary implications

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Teredinidae, also known as shipworms, are obligate xylophagous bivalves that colonise driftwood. The valves of xylophagous bivalves are highly derived and reduced in size relative to other bivalves. Key mineralized features of xylophagous bivalve anatomy are terminal aragonitic structures (pallets) and calcitic linings. The vast majority of their anatomy, however, consists of soft tissues and thus most occurrences in the fossil record are attributed either to ichnofossils or to isolated valves and pallets. Here, we report on exceptionally preserved Teredinidae from the Early Cretaceous of the Envigne Valley (Vienne, France). We investigated the interior of two pieces of fossilized wood in which the silicified feet of Teredinidae were observed protruding from the surface. Three-dimensional images of these specimens were produced using computed tomography, allowing the distribution and anatomical preservation of the xylophagous bivalves to be reconstructed. Our data reveal that fragile soft tissues such as the mantle and respiratory siphons are preserved. Surprisingly, the pallets, which are mineralised *in vivo*, are absent. Analysis of the preserved morphological details of these early shipworms will provide insights as to the morphological evolution of pallet features among this taxon.

Polychromatic UV-induced photoluminescence provides new insights into the fossilization of hard and soft tissues in *Pesciara di Bolca* fossils

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Since the 17th century, the *Pesciara di Bolca* Konservat-Lagerstätte (Verona province, Italy) has yielded thousands of fossils of exceptionally preserved plants, crustaceans, fish and other vertebrates, preserved in lithographic limestones deposited in an undisturbed lagoon during the Ypresian (Lower Eocene, ca. 50 Ma). This unique snapshot of the Eocene is continuously disclosing even more new palaeontological, palaeobiological and paleoecological information. However, the processes leading to such exceptional preservation remain poorly understood. Recently, it has been noted that Bolca fossil vertebrates exhibit a peculiar tissue-specific fluorescence when exposed to UV light, allowing better visualization of the anatomy of preserved tissues and for better preparation and conservation. In particular, the preserved soft-tissues can be more easily discriminated from the surrounding sedimentary matrix and bone. This interesting phenomenon has been observed also in fossil fish from the Cenomanian (Lower Cretaceous, ~95 Myr) of Lebanon (Hjoula, Haqel, Nmoura and Sahel Alma localities). Here, we compare the polychromatic UV-induced fluorescence in fossil

chondrichthyans and actinopterygians from these Konservat-Lagerstätten. Similarities between the Bolca and Lebanese fossils suggest a new taphonomic scenario for exceptional fossilization in the Bolca Lagerstätte.

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