

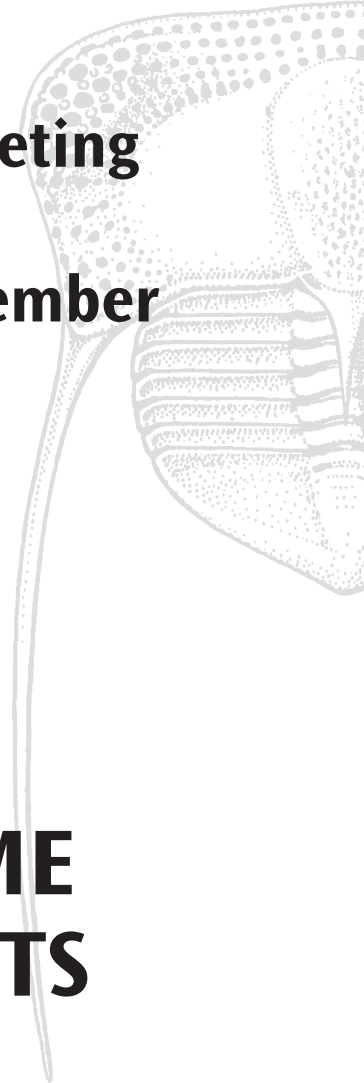
**The
Palaeontological
Association**

67th Annual Meeting

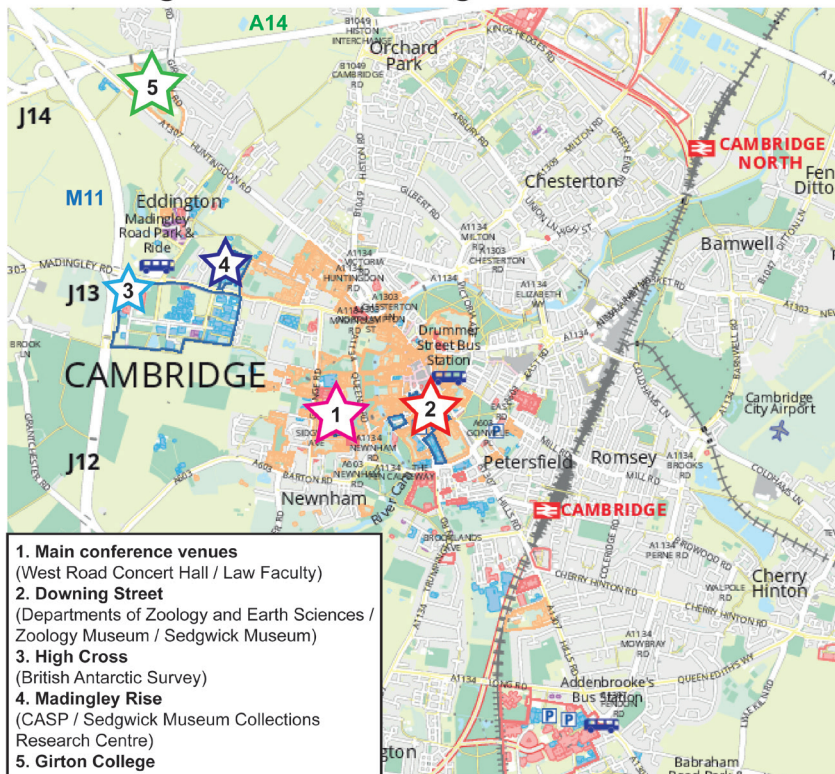
**11th–15th September
2023**

*University of
Cambridge, UK*

**PROGRAMME
& ABSTRACTS**

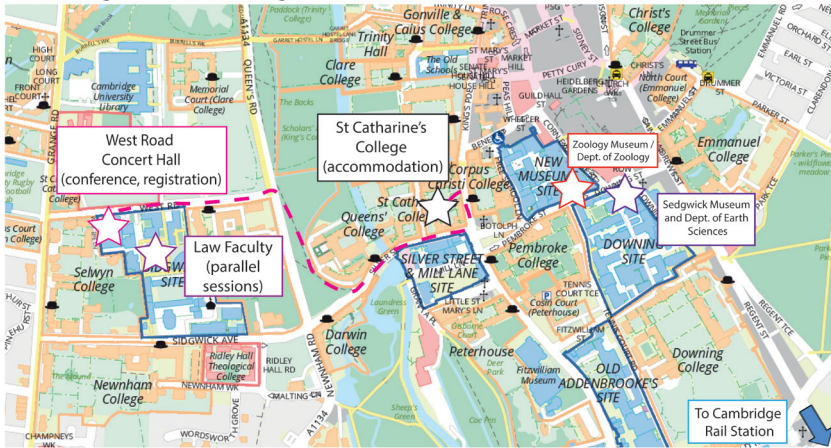


Cambridge Annual Meeting event venues

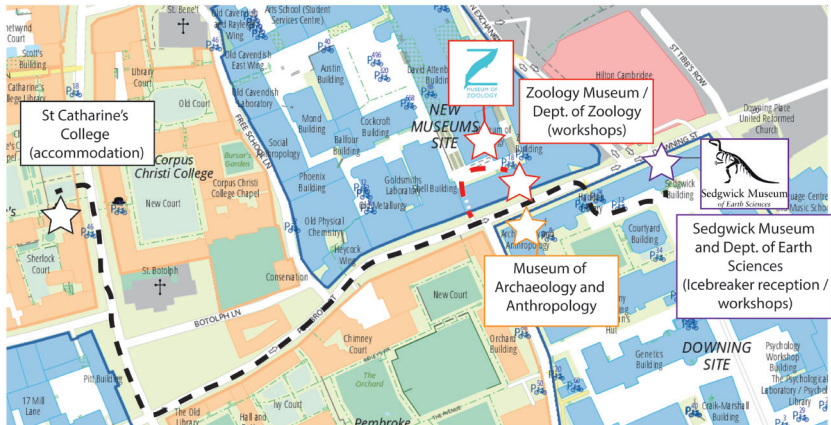


An interactive digital map showing all meeting venues, local transport hubs, local attractions and recommended food and drink venues is available for delegates to explore on the Annual Meeting website, at <<https://www.palass.org/meetings-events/annual-meeting/2023/annual-meeting-2023-cambridge-uk-maps>>.

Cambridge Annual Meeting scientific session venues

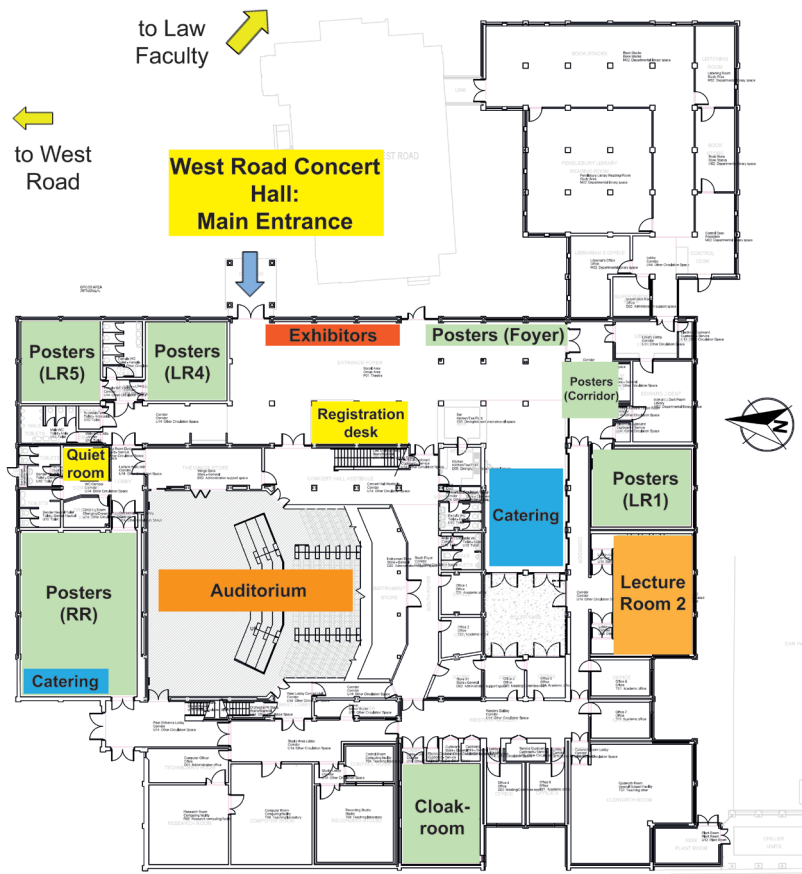


Cambridge City Centre workshop and accommodation locations

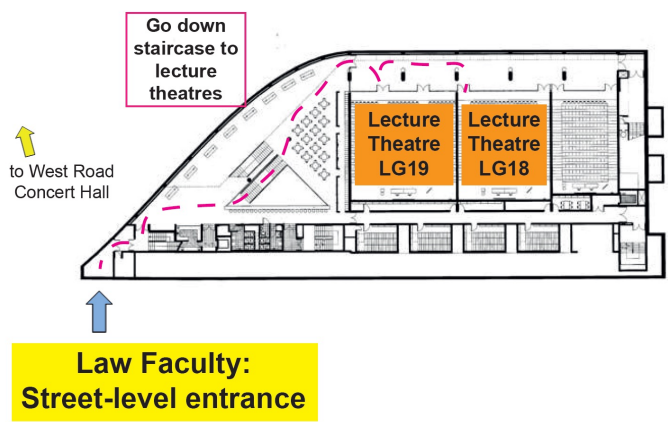


N.B. Enter the Department of Earth Sciences and Sedgwick Museum via an archway off Downing Street, proceeding into a central courtyard. The Sedgwick Museum entrance is up a staircase flanked by bears, to your left as you enter the courtyard. The Department entrance is the wooden door beneath that staircase.

West Road Concert Hall floor plan, ground floor



Law Faculty floor plan, lower ground floor





The Palaeontological Association

67th Annual Meeting

11th–15th September 2023

University of Cambridge

The programme and abstracts for the 67th Annual Meeting of the Palaeontological Association are provided after the following information and summary of the Meeting.

Venue

The Annual Meeting will take place at various University of Cambridge locations. All scientific sessions, the Symposium and the Annual Address will take place on the University's Sidgwick Site campus, at West Road Concert Hall or the Faculty of Law (parallel session lecture theatres). Workshops, the icebreaker reception and the early-career researcher event will take place in the Department of Earth Sciences (which contains the Sedgwick Museum) on Downing Street, central Cambridge. Collections tours will take place in their respective locations either in the city centre, or on the High Cross (British Antarctic Survey) or Madingley Rise (CASP, Sedgwick Museum Collections Research Centre) sites. There are bus stops on Trumpington Road and Silver Street, close to the Downing Street meeting venues, for the U-bus, which departs roughly every 15 minutes or less for the High Cross and Madingley Rise sites (journey time 10 minutes), or in the opposite direction to Cambridge Rail Station (journey time 10-15 minutes depending on traffic). Staff or students in education are eligible for a 'purple ticket' (£1.50 per ride, or £2 for the day) if you show the driver your university ID (for journeys on the U-bus only). You can download the most up-to-date timetable here from <<https://www.go-whippet.co.uk/routes-timetables/busway-routes/>>. The scientific session venues on West Road are a 10-15 minute walk from the city centre.

Registration

On-site registration will be possible on Monday 11th September (13:00 – 18:00) and Tuesday 12th September (08:30 – 12:00) in the Watson Gallery of the Sedgwick Museum, Department of Earth Sciences, Downing Street. From 12:30 to 17:30 on Tuesday 12th September, registration will be available in the foyer of West Road Concert Hall, on West Road. The registration desk there will be open from 08:00 – 17:30 on Wednesday 13th and Thursday 14th September.

Oral presentations

Apart from the four invited Symposium speakers, all speakers have been allocated 15 minutes. It is therefore expected that you prepare to speak for no more than 12 minutes to allow time for questions and switching between presenters. We have a number of parallel sessions in adjacent lecture theatres (those in the Faculty of Law are ~2 minutes' walk from the West Road Concert Hall), so timing will be especially important. All lecture theatres have an AV projector linked to a large screen. All presentations should be in PowerPoint or PDF format. If you do not wish for content from your poster or talk (or specific slides therein) to be shared electronically or on social media, please use the PalAss social media symbols in your presentation. Those presentations not submitted



to the local organizers prior to the meeting must now be uploaded to the local system and checked. This should be done as soon as possible, and at least an hour before the allotted time for the presentation.

Poster presentations

Poster boards will accommodate an A0-sized poster presented in portrait format only. Velcro dots to affix your poster to the boards are available. Posters will be displayed in several adjacent rooms in West Road Concert Hall. Please put up your posters either on Tuesday afternoon, or first thing on Wednesday morning (between 08:00 and 09:00). A designated poster session will take place on the afternoon of Wednesday 13th September from 15:00 to 16:30.

Travel grants to student members

Students who have been awarded a PalAss travel grant should see the Executive Officer, Dr Jo Hellawell, at the Association's stand to receive their reimbursement. Those who have received an IAS travel grant must see Dr Alex Liu to sign a form confirming meeting attendance prior to departure from Cambridge.

Childcare

Baby changing facilities are available at the Sedgwick Museum and the Department of Earth Sciences, as well as a nursing room in West Road Concert Hall.

Accessibility

All meeting venues are accessible via ramps and/or lifts. A quiet room will be available for individual use if required. The meeting venues have taken steps to mitigate against the transmission of communicable respiratory diseases, to ensure the safety of all attendees. These steps include mechanical ventilation systems in our lecture venues that provide predominantly fresh air, sanitizer stations, CO₂ monitors to indicate air quality, and natural ventilation that users can adjust in the foyer areas.

Cambridge

The historic city of Cambridge has been inhabited since Bronze Age times, and bears evidence of Iron Age, Roman, Viking and Saxon settlement. The University of Cambridge, founded in 1209, currently hosts over 24,000 students, and comprises 31 colleges alongside over 150 faculties, departments and associated institutions. World-class museums include the striking Fitzwilliam Museum (housing art and antiquities from across the globe), Kettle's Yard (twentieth century and contemporary art), the Polar Museum (history of Antarctica and the Arctic) and the Whipple Museum of the History of Science. Walking or punting along the picturesque River Cam offers an excellent way to see the University and College buildings, including the iconic King's College Chapel. For recommendations of things to do, places to see, and food and drink options, please see our online interactive map at <https://www.palass.org/meetings-events/annual-meeting/2023/annual-meeting-2023-cambridge-uk-maps>. We hope you enjoy your stay.



The Palaeontological Association thanks the Organizing Committee:

Chair:

Dr Alex G. Liu

Core Organizing Committee:

Prof. Nicholas J. Butterfield

Prof. Neil S. Davies

Prof. Daniel J. Field

Dr Liz Hide

Dr Aaron W. Hunter

Tasnuva Ming Khan

Dr Emily G. Mitchell

Dr Stephen Pates

Dr Simon Schneider

Dr Rowan J. Whittle

Klara E. Widrig

Broader Organization:

Dr Robert J. Asher

Catherine E. Boddy

Katie M. Delahooke

Oliver E. Demuth

Dr Mark Evans

Katrina van Grouw

Prof. Elizabeth M. Harper

Zoë Hughes

Mathew Lowe

Dr Javier Luque

Dr Luke Parry

Dan Pemberton

Matthew Riley

Nile P. Stephenson

Robert J. Theodore

Grace Varnham

Philip B. Vixseboxe

Dr Junya Watanabe



**The Palaeontological Association
Annual Meeting**

Meeting volunteers:

Bassel Arnaout

Christine Bordean

Princess Buma-At

Carmen Barroso Carmona

Madeline Carruthers

Dr Albert Chen

Alex Colesmith

Sean Herron

Grace Kinney-Broderick

Dr William J. McMahon

Giovanni Mussini

Jessica White

Rocky Yu



Sponsors

The organizers of the Annual Meeting gratefully acknowledge the support of:

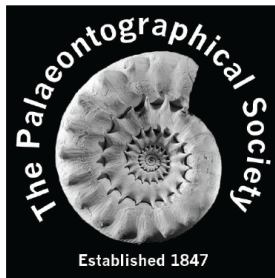
- Agisoft Metashape (Sponsor of the Photogrammetry workshop)
- Cambridge Philosophical Society
- Elsevier
- Prof. D. J. Field
- *Fossils*
- The Geological Society
- The International Association of Sedimentologists (IAS)
- Indiana University Press
- Palaeocast
- Palaeontographical Society (Sponsor of the Annual Meeting field-trip)
- *PeerJ*
- Scudamore's
- Sedgwick Museum of Earth Sciences
- *Treatise on Invertebrate Paleontology* (Sponsor of the Annual Address)
- Trinity College, Cambridge



Cambridge
Philosophical
Society



Sedgwick Museum
of Earth Sciences



Field Palaeobiology
Research Group



TREATISE
on Invertebrate Paleontology



fossils
an Open Access Journal by MDPI



INDIANA UNIVERSITY PRESS



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CAMBRIDGE



ELSEVIER



The
Geological
Society



Summary of Schedule

Monday 11th September: Early-career researcher event

Registration for the conference will be available in the Watson Gallery, on the ground floor of the Department of Earth Sciences, Downing Street, from 13:00 to 18:00.

A half-day early-career researcher (ECR) event, 'Palaeontologists for the Future', will take place in the Department of Earth Sciences, University of Cambridge. The event will include workshops on inclusivity, publishing and elevator pitches, and is aimed at students and those at key early-career transition points. It will run from 14:00 to 17:30, and will be followed by an informal buffet networking event. Delegates must be pre-registered for this event.

Tuesday 12th September: Workshops, museum tours, Symposium and icebreaker reception

Registration will be available in the Department of Earth Sciences (Downing Street) from 08:30 to 12:00 on Tuesday 12th September, and will move to the foyer of West Road Concert Hall (WRCH) from 12:30 to 17:30.

Poster setup will be available from 12:30 to 17:30 on Tuesday 12th September, or from 08:00 on Wednesday 13th September.

Our four workshops will take place at locations in the city centre, in the departments of Earth Sciences and Zoology, and the Sedgwick Museum, all starting at 09:00. Concurrent with these workshops, there will be tours of the palaeontology collections of the Zoology Museum, Sedgwick Museum, British Antarctic Survey, and CASP and the Sedgwick Museum Collections Research Centre. All tour and workshop places are now taken. Those delegates registered should have received information on tour start times and meeting points by e-mail. Volunteers will be on hand at each venue to help direct delegates to the correct locations.

The Annual Symposium, running from 13.30 to 17.30, has the theme 'Ecosystem engineering through deep time'. The Symposium will be held in the main auditorium at West Road Concert Hall.

Following the Symposium there will be an icebreaker drinks reception in the Sedgwick Museum of Earth Sciences, Downing Street (central Cambridge) from 18:00 to 20:00. You will need to show your reception ticket upon entry.

Wednesday 13th September: Scientific sessions, LGBTQ+ event, Annual Address and Annual Dinner

Registration will be open in the foyer of WRCH from 08:00 to 17:30 on both Wednesday 13th and Thursday 14th September.

Scientific sessions will start at 09:00 in the auditorium of West Road Concert Hall. Following a coffee break, we will divide into three parallel scientific sessions running concurrently in the WRCH



auditorium and two lecture theatres in the neighbouring Faculty of Law building. Please follow the signage to move between these venues.

Delegates who have pre-ordered lunch will be able to collect it from the foyer at WRCH.

At 12:30 there will be a friendly and informal LGBTQ+ gathering of community and allies for cordial conversation and a talk by Cambridge PhD student and Sedgwick Museum *Bridging Binaries* tour volunteer Klara Widrig, in Lecture Theatre 2 of WRCH. Klara will present a portion of their *Bridging Binaries* museum tour on the fabulous adventures of nineteenth century Hungarian palaeobiologist Franz Nopcsa. All are welcome.

From 15:00 to 16:30 there will be a dedicated poster session. Poster presenters are requested to stand next to their posters during this time. Refreshments will be available.

The Annual Address will take place at 16:30 in West Road Concert Hall (delivered by Dr **Greg Edgecombe** FRS), and is entitled 'Fossils, molecules and arthropods'. We are grateful to the *Treatise on Invertebrate Paleontology* for sponsoring this year's Annual Address.

The Annual Dinner will be held in the beautiful and historic surroundings of Girton College, the UK's oldest residential institution to offer higher education to women. Buses to the venue will leave Queen's Road (at the Silver Street junction) at 18:30. Please do not be late! You will need to show your dinner ticket for entry. Dinner in the Great Hall (starting at 19:45) will be preceded by a drinks reception (from ~19:00) in the College gardens. After dinner, delegates are welcome to continue discussions in the College Bar (NB: only card payments accepted). Buses will bring delegates back to the city centre and Queen's Road, leaving Girton College at c. 22:30, 23:15 and 00:00.

Thursday 14th September: Scientific sessions

Thursday 14th September will feature a full day of talks (09:00 – 17:15) in the West Road Concert Hall and Law Faculty lecture theatres. Lunch and coffee breaks will take place in the WRCH foyer.

Talks will end at 16:45, after which time the conference will close with presentations by the organizing committees of upcoming Palaeontological Association meetings, the award of the President's Prize and the Council Poster Prize, and concluding remarks.

Friday 15th September: Field-trip to Bawdsey, Suffolk

Delegates will visit Eocene and Pliocene sites in the London Clay and Red Crag along the coast of south Suffolk, reflecting deposition and fauna in the proto-North Sea. The field-trip will begin with a visit to the Red Crag in Rendlesham Forest. Subsequently, while waiting for the tide to fall, delegates will benefit from the region's archaeological heritage, visiting the Sutton Hoo burial site that sits within the field area on top of Pleistocene marine and river deposits. In the afternoon, delegates will visit the extensive coastal sections of the London Clay and Red Crag around Bawdsey.

The trip will depart from Downing Street, Cambridge at 08:00, returning to the same location at approximately 18:30. We are grateful to the Palaeontographical Society for sponsoring the field-trip. Participants must be pre-registered as spaces are limited.

Trip leaders: Prof. Neil S. Davies and Dr Simon Schneider.



Schedule of events and timetable of presentations

Monday 11th September

Registration for the conference will be available in the Watson Gallery, on the ground floor of the Department of Earth Sciences, Downing Street, from 13:00 to 18:00.

Early-career researcher (ECR) event: Palaeontologists for the future

Rooms: 1A Laboratory and Harker Lecture Theatres, Department of Earth Sciences, Downing Street, from 14:00 to 17:30. Please meet in the Watson Gallery, Department of Earth Sciences (just inside the main entrance).

Delegates must be pre-registered for the ECR event as spaces are limited.

14:00 – 14:15 Welcome, introductions

14:15 – 14:45 Developing and sharing elevator pitches

14:45 – 15:30 Inclusive palaeontology: workshop on addressing inequality and bias

15:30 – 16:00 Refreshments break
Watson Gallery, Department of Earth Sciences

16:00 – 16:45 Palaeontological research in the context of global climate change

16:45 – 17:15 Publishing for ECRs
Peter Llewellyn, Elsevier

17:15 – 17:30 Reflections and feedback / developing action points
Liz Hide, Stephen Pates

ECR Reception

18:00 – 20:00 Informal buffet and networking
Watson Gallery, Sedgwick Museum of Earth Sciences, Downing Street

Tuesday 12th September

Workshops, collections tours, Symposium and Icebreaker reception

Registration for the conference will be available in the Watson Gallery, on the ground floor of the Department of Earth Sciences, Downing Street, from 08:30 to 12:00. In the afternoon, registration will be available in the Entrance Foyer of West Road Concert Hall, West Road, from 12:30 to 17:30.



Workshops

The workshops will take place in either the Department of Earth Sciences or the Department of Zoology, both on Downing Street. Participants must be pre-registered as spaces are limited.

09:00 – 12:30 **Photogrammetry**

Instructor: Stephen Pates

Room: Demonstration Room, Zoology Museum (meet at the Zoology Museum entrance, outside the Whale Hall)

09:00 – 12:30 **Palaeoart: observational drawing and digital 3D modelling**

Instructors: Katrina van Grouw and Oliver Demuth

Room Harker 2, Department of Earth Sciences

09:00 – 12:00 **Best practice for specimen-based and taxonomic research in palaeontology**

Instructors: Luke Parry and Zöe Hughes

Room Harker 1, Department of Earth Sciences

09:00 – 12:30 **Pop-up Palaeo Museum**

Instructors: Liz Hide and Rob Theodore

Sedgwick Museum

Collections tours of Cambridge palaeontological collections

Collection tours have different start times at each location. Participants must be pre-registered as spaces are limited; participants have been pre-assigned to a specific tour, and will have received an e-mail prior to the conference stating their tour start time. The meeting point for each tour is stated below.

British Antarctic Survey collections tour

Leaders: Rowan Whittle and Mark Evans

Start times: 09:30, 11:00 (1 hour duration)

Meeting point: British Antarctic Survey main entrance, High Cross, West Cambridge Site

CASP and Sedgwick Museum Collections Research Centre tour

Leaders: Simon Schneider and Dan Pemberton

Start times: 09:00, 10:45 (1.5 hour duration)

Meeting point: A.G. Brighton Building, Madingley Rise Site

Sedgwick Museum gallery tours

Leader: Klara Widrig and Matt Riley

Start times: 09:00, 10:00, 11:00 (50 minutes duration)

Meeting point: Sedgwick Museum main entrance, Downing Street (enter via the staircase in the Downing Site courtyard, meet opposite the gift shop)

Zoology Museum collections tour

Leader: Mathew Lowe

Start times: 09:00, 10:00, 11:00 (1 hour duration)

Meeting point: Zoology Museum main entrance, Downing Street (either outside the entrance (09:00), or in the whale hall (10:00, 11:00)).



Symposium: “Ecosystem engineering through deep time”

Auditorium, West Road Concert Hall, West Road. Chair: Nicholas Butterfield.

13:15 – 13:30 Welcome address

13:30 – 14:00 **Understanding niche construction as a cause of natural selection**

[Kevin N. Lala](#)

14:00 – 14:15 **Exploring the macroevolutionary impact of ecosystem engineers using an individual-based eco-evolutionary simulation**

[Luke A. Parry](#), Thomas J. Smith, Frances S. Dunn and Russell J. Garwood

14:15 – 14:30 **Modern and ancient root-related calcretes: calcium carbonate biomineralization in the rhizosphere as a soil ecosystem engineering mechanism**

[Adrijan Kosir](#)

14:30 – 15:00 **The deep-time record of bioturbators as ecosystem engineers**

[M. Gabriela Mángano](#)

15:00 – 15:15 **Did the onset of terrestrial carnivory SPICE up marine animal biodiversity?**

[Jakob Vinther](#) and Benjamin J.W. Mills

15:15 – 15:45 Tea/coffee break (Foyer, West Road Concert Hall)

15:45 – 16:15 **Body size evolution as a driver of Phanerozoic nutrient availability**

[Christopher E. Doughty](#), Yadvinder Malhi and Adam Wolf

16:15 – 16:30 **Neoichnology as a lens for studying ecosystem engineering across the Ediacaran–Cambrian transition**

[Katherine A. Turk](#), Achim Wehrmann, Simon A.F. Darroch and Marc Laflamme

16:30 – 16:45 **The first plants changed the planet and they used mud to do it**

[William J. McMahon](#), Neil S. Davies, Stefan C. Loehr and Cassandra A. Wheeler

16:45 – 17:15 **Biogeochemical interactions between life and the environment during the Ediacaran Period**

[Graham A. Shields](#)

17:15 – 17:30 **How to engineer a habitable planet: new frameworks for understanding the rise and fall of marine ecosystem engineers through Earth history**

[Alison Cribb](#), Simon A.F. Darroch and Thomas Ezard

Icebreaker Reception

Sedgwick Museum, Department of Earth Sciences, Downing Street. Note that refreshments will be served both in the main gallery and in the Watson Gallery (ground floor level).

18:00 – 20:00 Sedgwick Museum of Earth Sciences, Downing Street



Wednesday 13th September

Scientific sessions, Annual Address and Annual Dinner

Registration for the conference will be available in the Entrance Foyer of West Road Concert Hall, West Road, from 08:00 to 17:30.

Underlined author denotes designated speaker.

* Candidates for the President's Prize are marked with an asterisk.

08:00 – 09:00 Poster set-up in West Road Concert Hall (multiple adjacent rooms)

Session 1

Auditorium, West Road Concert Hall. Chair: Orla Bath-Enright.

09:00 – 09:15 **The nature of the last universal common ancestor and its impact on the early Earth system**

Edmund R. R. Moody, Holly Betts, James Clark, Nina Dombrowski, Stuart Daines, Richard Boyle *et al.*

09:15 – 09:30 **Ediacaran marine animal forests and the ventilation of the oceans**

Susana Gutarra, Emily G. Mitchell, Frances S. Dunn, Brandt M. Gibson, Rachel A. Racicot, Simon A. F. Darroch and Imran A. Rahman

09:30 – 09:45 **Juvenile arthropleuroids from the Montceau-les-Mines Lagerstätte (305 Ma) help explain the phylogenetic affinities of these giants myriapods**

*Mickaël Lheritier, Adrien Buisson, Alexis Gerbe, Jean Vannier, Gilles Escarguel, Gregory D. Edgecombe *et al.*

09:45 – 10:00 **Estimating the origin of angiosperms based on quantitative analysis of the fossil records and the molecular clock**

*Ruolin Wu, Daniele Silvestro, Harald Schneider, Yue Tong, Shan Wan, Davide Pisani and Philip C. J. Donoghue

10:00 – 10:15 **Repeated evolution of extreme sabre-tooth morphology explained by optimality**

Tahlia Pollock, William J. Deakin, Narimane Chatar, Pablo S. Milla Carmona, Olga Panagiotopoulou, William M. G. Parker *et al.*

10:15 – 10:30 **Predicting extinction risk by range loss: evidence from the fossil record**

Eileen Straube, Gregor Mathes and Manuel Steinbauer

10:30 – 11:00 Tea/coffee break and posters

Foyer, West Road Concert Hall

**Session 2A**

Auditorium, West Road Concert Hall. Chair: Phil Mannion.

- 11:00 – 11:15 **Neoselachian diversification dynamics and age dependent extinction**
*[Kristína Kocáková](#), Daniele Silvestro, Amanda M. Gardiner, Jaime A. Villafaña and Catalina Pimiento
- 11:15 – 11:30 **Iron-coated varanid teeth and the dental specializations of ziphodont reptiles**
[Aaron LeBlanc](#), Alexander P. Morrell, Slobodan Sirovica, David Labonte, Domenic D'Amore and Owen Addison
- 11:30 – 11:45 **Ontogeny and tooth replacement in the Brazilian cynodont**
Brasilodon quadrangularis
[Nuria Melisa Morales Garcia](#), Agustin G. Martinelli, Pamela G. Gill, Heitor Francischini, Pedro H. Fonseca, Ian J. Corfe and Emily J. Rayfield
- 11:45 – 12:00 **Tempo and mode in the evolution of dinosaurian (Archosauria: Dinosauria) climatic niche landscape**
[Alfio Alessandro Chiarenza](#), Alexander J. Farnsworth, Lewis A. Jones, Juan L. Cantalapiedra, Sara Gamboa, Sofia Galvan *et al.*
- 12:00 – 12:15 **Evaluating homoplasy and evolutionary constraint in the passerine bird appendicular skeleton**
*[Elizabeth M. Steell](#), Neil Brocklehurst, Roger B. J. Benson, Matthieu Chotard, Jacqueline Nguyen and Daniel J. Field

Session 2B

Lecture theatre LG18, Law Faculty. Chair: Ricardo Pérez-de la Fuente.

- 11:00 – 11:15 **Reconstructing the phylogeny of longest existing gastropod group Pleuromariida (Ordovician–Recent) with Parsimony and Bayesian methods**
*[Baran Karapınar](#), Sebastian Höhna and Alexander Nützel
- 11:15 – 11:30 **The secret history of sea spiders (Arthropoda: Pycnogonida)**
[Romain Sabroux](#), Morena Nava, Gregory D. Edgecombe, Russell J. Garwood, Philip C. J. Donoghue, Derek J. Siveter *et al.*
- 11:30 – 11:45 **Euarthropod horseshoe carapace convergence shaped by hydrodynamics?**
[Stephen Pates](#) and Harriet B. Drage
- 11:45 – 12:00 **Developmental and functional constraints drove ontogenetic change in protective enrolment in an ancient arthropod**
[Jorge Esteve](#) and Nigel C. Hughes
- 12:00 – 12:15 **Convergent ventral adaptations for enrolment in trilobites, crustaceans and millipedes – insights from the Middle Ordovician Walcott-Rust Lagerstätte**
*[Sarah Losso](#), Pauline Affatato, Karma Nanglu and Javier Ortega-Hernández

**Session 2C**

Lecture theatre LG19, Law Faculty. Chair Fred Bowyer.

- 11:00 – 11:15 **A new rangeomorph from Newfoundland illuminates the origin of a lost body-plan**
Frances S. Dunn, Luke A. Parry and Alexander G. Liu
- 11:15 – 11:30 **Community development in the Avalonian Ediacaran**
*Nile P. Stephenson, Katie M. Delahooke, Charlotte G. Kenchington, Andrea Manica and Emily G. Mitchell
- 11:30 – 11:45 **Macroalgae, cyanobacteria and a late Ediacaran ‘diversity crisis’ in the Mackenzie Mountains, NW Canada**
Heda Agic, Martin R. Smith and Alex Kovalick
- 11:45 – 12:00 **Reconstructing the skeletal and soft tissue of the Ediacaran metazoan *Namacalathus***
*Ruaridh Alexander and Rachel A. Wood
- 12:00 – 12:15 **No mass extinction at the Ediacaran–Cambrian boundary**
*Mariana Yilales, Fred T. Bowyer and Rachel A. Wood
- 12:15 – 13:30 Lunch, West Road Concert Hall foyer
- 12:30 – 13:30 LGBTQ+ meet up, Lecture Room 2, West Road Concert Hall

Session 3A

Auditorium, West Road Concert Hall. Chair: Sam Giles.

- 13:30 – 13:45 **A new species of actinopterygian from the Upper Carboniferous (Bashkirian) of northern England, and the problem of phylogenetically forgotten fishes**
*Struan Henderson and Sam Giles
- 13:45 – 14:00 **Extreme lower jaw elongation in a ‘placoderm’ reflects high disparity in early vertebrate evolution**
*Melina E.M. Jobbins, Martin Rücklin, Hervé Lelièvre, Eileen Grogan, Piotr Szrek and Christian Klug
- 14:00 – 14:15 **Resorption and remodelling in the dermal skeleton of an early chondrichthyan**
Plamen Andreev, Qiang Li, Wenjin Zhao, Lijian Peng, Lars Brakenhoff, Martin Rücklin *et al.*
- 14:15 – 14:30 **Reconstructing feeding behaviour and diet in Devonian ctenacanth chondrichthyans using tooth wear analysis and finite element analysis**
*Merle Greif, Ivan Calandra, Stephan Lautenschlager, Thomas Kaiser and Christian Klug
- 14:30 – 14:45 **Testing hypotheses on heterostracan feeding**
*Madleen Grohgan, Antonio Ballell Mayoral, Humberto G. Ferron, Zerina Johanson, Emily J. Rayfield and Philip C.J. Donoghue
- 14:45 – 15:00 **How has shark functional diversity changed through geological time?**
Jack Cooper and Catalina Pimiento

**Session 3B**

Lecture theatre LG18, Law Faculty. Chair: Alex Dunhill.

- 13:30 – 13:45 **'morphospace': an R package for building and depicting multivariate ordinations of shape data**
Pablo S. Milla Carmona, Oscar E. R. Lehmann, William J. Deakin, Eduardo M. Soto, Ignacio M. Soto, Philip C. J. Donoghue and Emily J. Rayfield
- 13:45 – 14:00 **Fossilization can mislead analyses of phenotypic disparity**
*Thomas J. Smith, Robert S. Sansom, Davide Pisani and Philip C. J. Donoghue
- 14:00 – 14:15 **Temporal trajectory of geographic occupancy is an informative predictor of extinction risk across fossil microplankton taxa**
Isaiah Smith, Ádám T. Kocsis and Wolfgang Kiessling
- 14:15 – 14:30 **Carboniferous wildfire revisited: wildfire, post-fire erosion and deposition in a Mississippian crater lake**
Andrew C. Scott
- 14:30 – 14:45 **Climate-mediated vegetation changes during the Smithian–Spathian cooling event (c. 249.2 Ma) at southern subpolar latitudes (Sydney Basin, Australia)**
*Marcos Amores, Tracy D. Frank, Christopher R. Fielding and Chris Mays
- 14:45 – 15:00 **A century of imaging the Rhynie chert: using confocal microscopy to model the first land animals, plants and fungi in 3D**
*Emma J. Long, Gregory D. Edgecombe, Paul Kenrick, Alexander D. Ball and Xiaoya Ma

Session 3C

Lecture theatre LG19, Law Faculty. Chair: Karma Nanglu.

- 13:30 – 13:45 **Tooth origins and the convergent evolution of sensory structures**
*Yara Haridy, Karma Nanglu, Mark Rivers, Javier Ortega-Hernández and Neil Shubin
- 13:45 – 14:00 **Preservation of the organic carbon remains in the Chengjiang biota – an integrated story**
*Xiangtong Lei, Peiyun Cong, Wenwen Wen and Fan Wei
- 14:00 – 14:15 **Integration and modularity in the Cambrian diversification of arthropods**
*Joseph Moysiuk and Jean-Bernard Caron
- 14:15 – 14:30 **A look inside the ancestral arthropod**
Martin R. Smith, Emma J. Long, Alavya Dhungana and Katherine J. Dobson
- 14:30 – 14:45 **A fresh North American view into the Cambrian Explosion – new insights from the Drumian Marjum Konservat-Lagerstätte of western Utah, USA**
Rudy Lerosey Aubril, Robert Coleman, Lucas del Mouro, Robert Gaines, Luke A. Parry, Jacob Skabelund and Javier Ortega-Hernández
- 14:45 – 15:00 **The non-cryptic, diachronous origins of animal phyla**
*Alavya Dhungana and Martin R. Smith



15:00 – 16:30 Tea/coffee break and **dedicated poster session**
Foyer and adjacent rooms, West Road Concert Hall

Annual Address

Auditorium, West Road Concert Hall

16:30 – 17:30 **Fossils, molecules and arthropods**
Gregory D. Edgecombe

Annual Dinner

Girton College, Huntingdon Road

18:30 Coach transport from Queen's Road, next to the Silver Street junction

18.50 – 19:30 Reception in the Fellows' Gardens, Girton College

19:45 – 22:30 Dinner and President's speech

22:30 Return transport to Cambridge city centre (Queen's Road, next to the Silver Street junction), close to local bars. A shuttle service will operate from Girton College bringing delegates back, also at c. 23:15 and 00:00.

Thursday 14th September

Scientific sessions

Registration for the conference will be available in the Entrance Foyer of West Road Concert Hall, West Road, from 08:00 – 17:30

Session 4A

Auditorium, West Road Concert Hall Chair: David Bond

09:00 – 09:15 **Landmark-free morphometrics suggests different paths of mammalian evolution through the Cenozoic**
*James M. Mulqueeney, Thomas H. G. Ezard and Anjali Goswami

09:15 – 09:30 **Dietary niche shifts are coincident with mammalian body size reduction during a Paleocene hyperthermal**
*Neil F. Adams, Stephen L. Brusatte, Thomas E. Williamson, Ross Secord and Mark A. Purnell

09:30 – 09:45 **Regional aridification drove changes in Asian mammal faunas by the middle Eocene: implications for the timing and magnitude of the Mongolian Remodelling**
Gemma L. Benevento, Niels Meijer, Julia Brugger, Andreas Mulch, Thomas Hickler and Susanne Fritz



- 09:45 – 10:00 **Indications for major ‘out of Asia’ proboscidean migrations during the Middle Miocene**
*[Nora Carolin](#) and Sunil Bajpai
- 10:00 – 10:15 **The virtual endocast of the Late Miocene hedgehog *Postpalerinaceus vireti* (Eulipotyphla, Mammalia)**
[Raquel Moya Costa](#), Ornella C. Bertrand, Àngel H. Luján, Isaac Casanovas-Vilar and Marc Furió
- 10:15 – 10:30 **Cementochronology reveals the evolution of life history amongst the earliest mammals**
[Pamela G. Gill](#), Elis Newham, Philippa Brewer, Julia Schultz, Kai Jaeger, Ian J. Corfe and Thomas Martin

Session 4B

Lecture theatre LG18, Law Faculty. Chair: Valentina Rossi.

- 09:00 – 09:15 **Understanding fossil preservation patterns and processes using decay experimentation**
[Allison C. Daley](#), Orla G. Bath Enright, Harriet B. Drage, Farid Saleh and Jonathan B. Antcliffe
- 09:15 – 09:30 **Life after death: characterizing the microbial communities responsible for decomposition and fossilization**
[Robert S. Sansom](#), Christopher Boothman and Sophie L. Nixon
- 09:30 – 09:45 **Proliferation of microbial collagenase as a constraint on soft tissue preservation**
*[Philip B. Vixseboxse](#), Edmund R. R. Moody, Philip C. J. Donoghue, Sean McMahon and Alexander G. Liu
- 09:45 – 10:00 **Kaolinite causes mineralization and stabilization of soft tissues within days during marine shrimp decay experiments**
*[Nora Corthésy](#), Farid Saleh, Allison C. Daley and Jonathan B. Antcliffe
- 10:00 – 10:15 **A new taphonomic model for the Eocene Geiseltal Konservat-Lagerstätte, Germany**
*[Daniel Falk](#), Oliver Wings and Maria E. McNamara
- 10:15 – 10:30 **The experimental effects of wave processes on arthropod taphonomy: implications for Lagerstätten and small carbonaceous fossils**
*[Laura Devine](#) and Nicholas J. Minter

Session 4C

Lecture theatre LG19, Law Faculty. Chair: Imran Rahman.

- 09:00 – 09:15 **An Ordovician vertebrate neurocranium**
[Richard P. Dearden](#), Agnese Lanzetti, Sam Giles, Zerina Johanson, Andy Jones, Stephan Lautenschlager *et al.*



- 09:15 – 09:30 **A new luolishaniid from the early Ordovician and the autecology of suspension feeding lobopodians**
*[Jared Richards](#) and Javier Ortega-Hernández
- 09:30 – 09:45 **Epibionts and trace fossils on stem- and crown-group euarthropod carapaces from the Early Ordovician Fezouata Shale**
*[Jonathan Pople](#), Gaëtan J.-M. Potin and Allison C. Daley
- 09:45 – 10:00 **Trilobite mass extinction events in the Early Ordovician (Tremadocian) of North America**
Jonathan M. Adrain and *[Francesc Pérez-Peris](#)
- 10:00 – 10:15 **Two new Lagerstätten shed light on Ordovician animal ecosystems**
[Farid Saleh](#)
- 10:15 – 10:30 **An early Palaeozoic ostracod psychrosphere?**
*[Anna McGairy](#), Christopher P. Stocker, Mark Williams, Phong Duc Nguyen, Thomas H. P. Harvey, Toshifumi Komatsu and C. Giles Miller
- 10:30 – 11:00 Tea/coffee break and posters
Foyer, West Road Concert Hall

Session 5A

Auditorium, West Road Concert Hall. Chair: Juan Benito Moreno.

- 11:00 – 11:15 **Anatomy of the skeleton and soft tissues of a 290-million-year-old amphibian revealed using elemental and multispectral imaging**
[Antoine Logghe](#), Pierre Gueriau, Phillip L. Manning, Roy A. Wogelius, Victoria M. Egerton, Uwe Bergmann *et al.*
- 11:15 – 11:30 **Melanosome geometry informs on the functional evolution of melanin in Reptilia and Amphibia**
*[Aaron Quigley](#), Beatriz Carazo del Hoyo, Daniel Cirtina, Catherine McCarney, Jane Brennan, Soudeh Ziapour and Maria E. McNamara
- 11:30 – 11:45 **Characterization of melanin-based colour expression and melanosome attributes across the avian phylogeny**
*[Hollie Bean](#), Daniel J. Field and Maria E. McNamara
- 11:45 – 12:00 **Trait-mediated speciation and human-driven extinctions in proboscideans revealed by unsupervised Bayesian neural networks**
[Torsten Hauffe](#), Juan L. Cantalapiedra, Fernando Blanco and Daniele Silvestro
- 12:00 – 12:15 **A new approach to the reconstruction of fragmentary fossil long bones; the case study of *Homo naledi***
[Julia Aramendi](#) and Lloyd A. Courtenay

**Session 5B**

Lecture theatre LG18, Law Faculty Chair: Heda Agic

- 11:00 – 11:15 **Organic-walled microfossils of the late Palaeoproterozoic Limbunya Group and implications for early eukaryotic evolution**
Leigh Anne Riedman, Susannah M. Porter, Angelo Dos Santos, Maxwell A. Lechte and Galen P. Halverson
- 11:15 – 11:30 **Multicellular microfossils from the c. 930–820-million-year-old Veteranen Group of Svalbard**
Ross P. Anderson, George O. Wedlake, Luke A. Parry, Timothy M. Gibson, Alexie E. G. Millikin, Karsten Piepjohn *et al.*
- 11:30 – 11:45 **Heterochronic processes in the evolution of planktonic foraminifera**
Bridget S. Wade, Christopher Poole, Thomas Ezard and Anieke Brombacher
- 11:45 – 12:00 **Enigmatic Silurian jawless vertebrate *Lasanius* evaluated with new synchrotron data**
*Jane Reeves, Roy A. Wogelius, Joseph N. Keating, Phillip L. Manning and Robert S. Sansom
- 12:00 – 12:15 **Current issues with conodont tissues**
*Bryan Shirley and Emilia Jarochowska

Session 5C

Lecture theatre LG19, Law Faculty. Chair: William McMahon.

- 11:00 – 11:15 ***Osedax* bioerosion in marine reptiles: the evolution of an ecosystem engineer**
*Sarah Jamison-Todd, Adrian Glover, Philip D. Mannion and Paul Upchurch
- 11:15 – 11:30 **From the tiny ant to the elephant: engineering impacts of the vertebrate and invertebrate denizens of Mesozoic terrestrial ecosystems**
Anthony Shillito and Maximiliano Paz
- 11:30 – 11:45 **Insect diversity from the late Eocene Xiede locality (central Tibetan Plateau) and a preliminary review of Hymenoptera**
*Xiaoting Xu, Isabelle Deregnacourt, Jérémie Bardin, Cecilia Waichert, Alexandre Somavilla, James M. Carpenter *et al.*
- 11:45 – 12:00 **Palaeoecologic turnovers in the Ediacaran-Cambrian Chapel Island Formation, Newfoundland, Canada and the early steps of the Cambrian Explosion**
*Romain Gougeon, M. Gabriela Mángano, Luis A. Buatois, Guy M. Narbonne, Brittany A. Laing and Maximiliano Paz
- 12:00 – 12:15 **Early Cambrian trace fossils in shallow-marine quartzites from Baltica and their implications for sedimentary stasis and anactualistic sedimentation**
*Yorick Veenma, Neil S. Davies, Ben J. Slater and Graham E. Budd
- 12:15 – 13:30 Lunch, West Road Concert Hall foyer

**Session 6**

Auditorium, West Road Concert Hall. Chair: Erin Saupe.

- 13:30 – 13:45 **Bretskyan hierarchy—the structure and evolution of biota in time and space**
Andrej Spiridonov and Niles Eldredge
- 13:45 – 14:00 **Unveiling the third eye of the earliest vertebrates**
*Sihang Zhang, Xiangtong Lei, Peiyun Cong, Jakob Vinther and Sarah E. Gabbott
- 14:00 – 14:15 **Challenges of ancestral state estimation: the practical case of feather evolution**
Pierre Cockx, Joseph N. Keating and Michael J. Benton
- 14:15 – 14:30 **The impact of fossil tips on reconstructing trait evolution using phylogenetic comparative methods**
Bethany J. Allen, William Gearty, Pedro Godoy and Alfio Alessandro Chiarenza
- 14:30 – 14:45 **Ecosystem structural changes following a marine megafaunal extinction**
*Amy E. Shipley, Tracy Aze, Catalina Pimiento, Andrew P. Beckerman, Jennifer A. Dunne, Jack O. Shaw and Alexander M. Dunhill
- 14:45 – 15:00 **Echoes from the past: unveiling deep-time functional dynamics through network analysis**
*Fernando Blanco, Johannes Müller, Daniele Silvestro and Juan L. Cantalapiedra
- 15:00 – 15:30 Tea/coffee break and taking down of posters
Foyer, West Road Concert Hall

Session 7

Auditorium, West Road Concert Hall. Chair: Javier Ortega-Hernández.

- 15:30 – 15:45 **Evolution in the mesopelagic twilight zone is regulated by a temperature-dependent biological pump**
Paul N. Pearson, Bridget S. Wade, Flavia Boscolo-Galazzo, Katherine Crichton, Tom Dunkley Jones, Eleanor John *et al.*
- 15:45 – 16:00 **A new quantitative framework to determine the producers of marine locomotory trace fossils**
Zekun Wang and Imran A. Rahman
- 16:00 – 16:15 **Exceptional preservation in the Rhynie chert: molecular fingerprints resolved *in situ* down to sub-micron scales**
Corentin Loron, Ferenc Borondics, Edwin Rodriguez Dzul, Patrick J. Orr, Andrei V. Gromov, Nick C. Fraser and Sean McMahon
- 16:15 – 16:30 **Palynofloral change through the Palaeocene–Eocene Thermal Maximum in the Bighorn Basin, Wyoming**
Vera Korasidis and Scott L. Wing
- 16:30 – 16:45 **Early tetrapod jaw shape and mechanical performance during the water-land transition**
Laura B. Porro and Emily J. Rayfield



Closing business

Auditorium, West Road Concert Hall

16:45 – 16:50 Presentation from the PalAss Council Diversity Officer

16:50 – 17:05 Presentation from the organizing committee of PalAss 2024

17:05 – 17:15 Presentation of the President's Prize and the Council Poster Prize followed by closing remarks

Friday 15th September

Post-conference field-trip

Departure time is 08:00 from Downing Street, boarding the coach by the Department of Zoology entrance archway. We expect to arrive back in Cambridge by c. 18:30 on Friday 15th September.

Field-trip leaders: Neil S. Davies and Simon Schneider.



The Palaeontological Association

Registered Charity Number: 1168330

Code of Conduct for Palaeontological Association meetings

The Palaeontological Association was founded in 1957 and has become one of the world's leading learned societies in this field. The Association is a registered charity that promotes the study of palaeontology and its allied sciences through publication of original research and field guides, sponsorship of meetings and field excursions, provision of web resources and information, and a programme of annual awards.

The Palaeontological Association holds regular meetings and events throughout the year. The two flagship meetings are the Annual Meeting, held at a different location each year, and the annual Progressive Palaeontology (ProgPal) meeting, run by students for students with the support of the Palaeontological Association. The Association Code of Conduct relates to the behaviour of all participants and attendees at annual events.

Behavioural expectations: It is the expectation of the Palaeontological Association that meeting attendees behave in a courteous, collegial and respectful fashion to each other, volunteers, exhibitors and meeting facility staff. Attendees should respect common-sense rules for professional and personal interactions, public behaviour (including behaviour in public electronic communications), common courtesy, respect for private property, and respect for intellectual property of presenters. Demeaning, abusive, discriminatory, harassing or threatening behaviour towards other attendees or towards meeting volunteers, exhibitors or facilities staff and security will not be tolerated, in either personal or electronic interactions.

Digital images and social media: Do not photograph a poster or record a talk without the author's express permission. While the default assumption is to allow open discussion of presentations on social media, attendees are expected to respect any request by an author to not disseminate the contents of their talk or poster.

Reporting unacceptable behaviour: If you are the subject of unacceptable behaviour or have witnessed any such behaviour, you can report it to us (anonymously if you choose to) via our online reporting form at <https://www.palass.org/meetings-events/report-meeting-code-conduct-violation>.

Anyone experiencing or witnessing behaviour that constitutes an immediate or serious threat to public safety, or a criminal act, is expected to contact the appropriate law enforcement agency. Those witnessing a potential criminal act should also take actions necessary to maintain their own personal safety.



Annual Address

The Annual Address will be given on Wednesday 13th September at 16:30.

Fossils, molecules and arthropods

Gregory D. Edgecombe

Natural History Museum, London, UK

Palaeontologists have persuasively made the case that fossils improve morphological phylogenetic analyses. The fossil record provides otherwise unknowable insights into the sequence of character acquisition in ancient stem lineages, as exemplified by the lobopodian roots of the panarthropod phyla. As is the case across the tree of life, many questions in arthropod phylogeny were effectively answered as molecular phylogenetics transitioned from analyses of a few loci to the genomic scale; some clades that were not widely anticipated by morphologists (*e.g.* several major groups within Pancrustacea) are now part of an extant-taxon scaffold into which fossil taxa are integrated. The necessity of fossils for total-evidence / tip dating has revitalized the nexus through which fossils and molecular sequences speak a common language – coding phenotypic characters for extant organisms. The evolution of arthropod appendages illustrates a methodology for reconstructing the origin of complex phenotypic novelties that draws on similarities in morphology and gene expression, phylogenomic evidence for a single origin, the sequence of character transformations in exceptionally preserved fossils, and gene knockdown. Advances in knowledge of early arthropods will continue to be triggered by discoveries from new Konservat-Lagerstätten, improvements in morphological imaging, and refinements in how we build and date trees.



Abstracts of symposium presentations

Ecosystem engineering through deep time

How to engineer a habitable planet: new frameworks for understanding the rise and fall of marine ecosystem engineers through Earth history

Alison Cribb¹, Simon A. F. Darroch^{2,3} and Thomas Ezard¹

¹*University of Southampton, UK*

²*Vanderbilt University, USA*

³*Senckenberg Museum of Natural History, Germany*

The structure and function of Earth systems today are a result of nearly 4 billion years of the co-evolution of life and the environment. Ecosystem engineers – taxa that influence the habitability of their environment by changing its physical characteristics and resource flows – are particularly important for understanding these co-evolutionary processes throughout Earth history. As ecosystem engineers have evolved and dispersed, modifying and creating new habitats, they have had wide-ranging impacts on the spatio-temporal patterns of biodiversity. In particular, it has been hypothesized that the evolution of new ecosystem engineer groups drove increased biodiversity, and those groups' demise during mass extinctions exacerbated extinction severity and delayed ecosystem recovery. Here, we present new methodological and conceptual frameworks that quantitatively link the fossil record of ecosystem engineers and their behaviours to ecological outcomes. These new approaches allow us to address longstanding questions regarding the impact of marine ecosystem engineers on biodiversity in the early Palaeozoic, the lag times between the appearance of ecosystem engineers and their ecological outcomes, and the importance of ecosystem engineers for understanding past, present, and future ecological collapse.

Body size evolution as a driver of Phanerozoic nutrient availability

Christopher E. Doughty¹, Yadvinder Malhi² and Adam Wolf³

¹*Northern Arizona University, USA*

²*University of Oxford, UK*

³*Eion Corp, USA*

Cope's rule postulates that population lineages increase in body size over evolutionary time. Here we explore the impacts of Cope's rule on global nutrient dynamics over the Phanerozoic. We start by examining the impact of the Pleistocene Megafauna extinctions, when 97 genera of large animals went extinct. We find nutrient diffusion potential is size dependent, with large animals disproportionately important for the spread of nutrients, and following extinctions animal nutrient movement decreased by almost two orders of magnitude. This resulted in strong decreases in phosphorus availability in, for example, eastern Amazonia away from fertile floodplains, a decline that may still be ongoing. We then scale globally and find in the past marine mammals, seabirds, anadromous fish and terrestrial animals likely formed an interlinked system recycling nutrients from the ocean depths to the continental interiors, with marine mammals moving nutrients from



the deep sea to surface waters, seabirds and anadromous fish moving nutrients from the ocean to land, and large animals moving nutrients away from hotspots into the continental interior. We then test these ideas further back in time by comparing a time period with the biggest herbivores, the Cretaceous, to a period of Earth's history prior to the evolution of tetrapod herbivores, the Carboniferous. We use a coal dataset to suggest that large herbivore–plant interactions are important in reducing spatial heterogeneity of nutrient supply and, possibly, increasing the supply of important nutrients. Combining Cope's rule with large animals' inherent role in nutrient distribution means that the planet may have an intrinsic mechanism for improving nutrient dispersal over time.

Modern and ancient root-related calcretes: calcium carbonate biomineralization in the rhizosphere as a soil ecosystem engineering mechanism

Adrijan Kosir

Research Centre of the Slovenian Academy of Sciences and Arts, Slovenia

Calcium carbonate precipitation around roots of vascular plants has been considered as one of the fundamental mechanisms of biogenic calcrete formation. However, cementation of the active rhizosphere with CaCO_3 appears to be at least undesirable for the efficient nutrient and water uptake by absorptive fine roots, if not largely detrimental for the functioning of roots involved in resource acquisition. Although accumulations of secondary soil carbonate appear to be highly restricting for both root growth and water percolation, it has also been shown that even highly cemented calcrete horizons can exhibit high water-holding capacity. Furthermore, precipitation of specific forms of microcrystalline calcite, characteristically associated with root systems in modern highly permeable calcareous soils and forming a typical microporous fabric in palaeocalcretes, appears to be essentially induced by biogeochemical processes in the rhizosphere. Particularly in semi-arid climates with pronounced seasonal moisture deficit, physical modification of the soil environment through massive accumulation of biologically induced, porous CaCO_3 deposits within laterally extensive horizontal root systems may represent a mechanism for enhanced short-term water retention capacity and longer-term maintenance of a complex underground ecosystem. Presented examples include modern Mediterranean calcretes, associated with pine and eucalyptus root systems, and potential analogues in the geological record.

Understanding niche construction as a cause of natural selection

Kevin N. Lala

University of St Andrews, UK

For most evolutionary biologists, fitness differences cause trait frequency changes in populations, and natural selection explains the evolution of adaptations. However, treating fitness differences as a cause is a convention. Philosopher Elliott Sober (1984) distinguished between 'source laws' and 'consequence laws': "the former describe the circumstances that produce forces; the latter describe how forces, once they exist, produce changes in the systems they impinge upon". Sober argued that evolutionary theory is rich in consequence laws, which are "the province of population genetics", but "impoverished" with respect to source laws. Unfortunately, the historical assumptions



that the complexities of development leave the origins of phenotypic variation unpredictable, and that ecological processes are idiosyncratic, has hindered the development of source laws for selection. A rarely appreciated consequence is that explanations reliant on selection potentially mask particular causal patterns important in evolution. Using examples of niche construction, I will highlight how the activities of organisms co-determine the nature of the response to selection in an often surprisingly well-regulated manner. Niche construction biases the phenotypic variation exposed to selection, often generating axes of covariation with plastically expressed morphological traits. Taxonomically shared developmental mechanisms aggregate across populations to generate statistical regularities that are easy to miss because the developmental causes of fitness differences are not currently central to the study of evolution. Theory and experiments suggest that how organisms develop and what organisms do cause and strengthen the relationship between key traits and fitness, thereby part-determining the characteristics of natural selection. In this manner, organismal niche construction can modify the adaptive landscape, create pathways through morphospace and exert a long-term influence on evolutionary dynamics and equilibria. The findings have implications for understanding parallel evolution, macroevolutionary trends and variation in evolvability.

The deep-time record of bioturbators as ecosystem engineers

M. Gabriela Mángano

University of Saskatchewan, Canada

The trace-fossil record provides a wealth of information to reconstruct the role of bioturbators as ecosystem engineers in space and time. The Multidimensional Ecospace and Ecosystem Engineering Analysis provides valuable insights to unravel modes of sediment reworking and ecospace utilization during evolutionary breakthroughs and mass extinctions. This approach results from the articulation through the lens of ichnology of two different research traditions: functional groups from marine benthic ecology and ecospace utilization from palaeobiology. The trace fossil record provides hard data to evaluate bioturbation as a driving force in ecosystem restructuring and as a key factor in geobiological cycles. Models assessing these fundamental issues should be rooted in empirical trace fossil data at both autoecologic and synecologic scales using the rich ichnologic toolbox. Systematic analysis of the Ediacaran–Ordovician trace fossil record along the marine depositional profile underscores the significance of the Cambrian Explosion in the establishment of modern-style shallow-marine ecosystems and of the Ordovician Radiation for their deep-marine counterparts. Comprehensive datasets for the rest of the Phanerozoic are not available yet. However, preliminary information suggests that colonization of ultra-deep tiers, increased compartmentalization of the endobenthic ecospace, and the rise to prominence of regenerators were a product of the Mesozoic Marine Revolution.



The first plants changed the planet and they used mud to do it

William J. McMahon¹, Neil S. Davies¹, Stefan C. Loehr² and Cassandra A. Wheeler³

¹*University of Cambridge, UK*

²*University of Adelaide, Australia*

³*Macquarie University, Australia*

Hypotheses about the deep history of vegetation as an eco-engineering force are contested. Questions have been raised about whether diminutive Palaeozoic plants had the capacity to stabilize landscapes, or whether they could have enhanced silicate weathering. If evidence were found for either, there would be profound implications for a shift in the abundance and location of muddy sediment on Earth, with ramifications for global biogeochemical cycles. Here we show how the clay mineral component of terrestrial mudstones can act as an archive of plant-induced planetary change. Deciphering this record requires a robust understanding of clay origin, information unattainable via conventional petrography. Recent technological developments in scanning electron microscope-energy dispersive spectroscopy (SEM-EDS) have made it possible to assess individual clay mineral morphology, petrological context and likely origins. We have employed this tool to assess clay mineral character before and during the evolution of land plants, revealing a striking concomitant change that can be attributed to the power of plants as weathering agents. These new data provide empirical evidence for a stratigraphic shift in clay mineral motifs that mirrors the timing of other fundamental changes in processes and environments triggered by the greening of the continents.

Exploring the macroevolutionary impact of ecosystem engineers using an individual-based eco-evolutionary simulation

Luke A. Parry¹, Thomas J. Smith¹, Frances S. Dunn¹ and Russell J. Garwood^{2,3}

¹*University of Oxford, UK*

²*The University of Manchester, UK*

³*Natural History Museum, London, UK*

Feedbacks between organisms and their environment can drastically alter ecosystems over a range of spatial and temporal scales. The introduction or removal of ecosystem engineers, organisms capable of inducing extraordinary ecological change, from otherwise stable ecosystems can impact the diversity of co-occurring species. This process is thought to have played a significant role in several major transitions in Earth history (*e.g.* the appearance of extensive bioturbation during the Cambrian substrate revolution, and associated Ediacaran–Cambrian turnover). Here we use an emerging eco-evolutionary simulation framework and assign lineages the ability to impact the fitness of co-occurring taxa through phenotype–environment feedback. We explore numerous conditions, including varying the niche space into which ecosystem engineers are introduced, and isolated versus persistent impact of ecosystem engineers over long timescales. We show that there is no general expected outcome from the introduction of an ecosystem engineering species. In a minority of runs, ecosystem engineering lineages completely dominate, rendering all others extinct, but in others they persist (but do not dominate) or die out. We suggest that ecosystem engineers have complex impacts but possess the capacity to profoundly shape diversity, and it is appropriate to consider them alongside other exogenous extinction drivers in deep time.



Biogeochemical interactions between life and the environment during the Ediacaran Period

Graham A. Shields

University College London, UK

The Ediacaran Period encompasses the transition to modern marine ecosystems, exemplified by the invention of bioturbation, biomineralization and muscular carnivory. The Ediacaran Period also marks a fundamental transition in carbon cycling, with episodic transfers of oxidizing power between sedimentary sulphur and carbon reservoirs, accompanied by opportunistic habitation of oxidized seafloor. Throughout the Ediacaran Period, newly emergent metazoans needed to navigate wild swings in climate, nutrient and redox regimes, likely adding to the pace of innovation. Sulphur-utilizing microbes, acting in concert with metazoans, catalysed changes but the broader Earth system, including tectonic movements, drove the runaway positive feedbacks that characterize this time. Towards the end of the period, bioturbation and metazoan respiration enhanced oxidative back reactions by greatly increasing the area over which oxidation could take place, helping to buffer against perturbations. Biomineralization, which arose around the same time, was triggered perhaps by rising carbonate saturation and calcium toxicity due to a combination of weathering and seafloor oxidation. Here I outline how positive feedbacks likely contributed to environmental instability and evolutionary bottlenecks during the Ediacaran Period, and how negative feedbacks resulting from biological innovations emerged during the Ediacaran–Cambrian transition.

Neoichnology as a lens for studying ecosystem engineering across the Ediacaran–Cambrian transition

Katherine A. Turk^{1,2}, Achim Wehrmann², Simon A. F. Darroch^{1,3} and Marc Laffamme⁴

¹*Vanderbilt University, USA*

²*Senckenberg am Meer, Germany*

³*Senckenberg Museum of Natural History, Germany*

⁴*University of Toronto Mississauga, Canada*

The Ediacaran–Cambrian transition (ECT; *c.* 550–539 Ma) records a widespread increase in the diversity and intensity of metazoan ecosystem engineering behaviours coincident with one or more pulses of apparent biotic turnover and the establishment of more modern-looking, animal-dominated ecosystems. Understanding the deep-time evolution of ecosystem engineering is thus key to understanding potential drivers of this unique interval in Earth history. One group hypothesized to have had a variety of ecosystem engineering impacts is marine bioturbators; modern representatives exert significant control over environments, influencing seafloor sediment characteristics and habitable ecospace distribution. The ECT emergence and spread of these behaviours is thought to have resulted in several critical downstream effects, including downwards transport of surficial materials, porewater chemistry changes, and increased subsurface oxygenation. However, there remains a dearth of empirical data as to exactly how and at what magnitude these behaviours alter environments. Here we provide an overview of neoichnological experimentation aimed at addressing these knowledge gaps and present an evolving framework for quantifying the bioturbative impacts of taxa thought to have evolved during or before the ECT. Lastly, we present a case study where neoichnology can be used to reinterpret ECT trace-maker behaviours with important implications for understanding their ecosystem engineering impacts.



Did the onset of terrestrial carnivory SPICE up marine animal biodiversity?

Jakob Vinther¹ and Benjamin J. W. Mills²

¹*University of Bristol, UK*

²*University of Leeds, UK*

The onset of life on land opened up a whole new ecosystem. It also had an impact on biogeochemical cycles as increased terrestrial weathering by plants and fungi stimulated primary productivity in marine ecosystems. Molecular clock evidence consistently demonstrates an older origin of both land plants and several arthropod groups than hitherto thought, which can be explained by a practically non-existent pre-Silurian terrestrial rock record. Here we argue that the late Cambrian Steptoean positive inorganic carbon excursion (SPICE) resembles Late Devonian events interpreted as effects of increased terrestrial weathering by plants. The coincidence with terrestrial carnivores (arachnids) rather than the earlier inception of land plants and soil invertebrates already in the mid Cambrian suggests a top-down control. Similar to the early Cambrian perturbations to the carbon cycle by marine bioturbation, one could surmise that carnivory would prompt soil detritivores to have become burrowers hence creating deeper soil profiles. If the SPICE event was initiated by stepwise shifts in terrestrial ecosystems in this way, it can potentially be linked to the subsequent expansion of marine phytoplankton and, more generally, the Great Ordovician Biodiversification Event (GOBE). Using biogeochemical modelling, we will explore the likelihood of top-down terrestrial-to-marine drivers for the SPICE and GOBE.



Abstracts of oral presentations

* Candidates for the President's Prize are marked with an asterisk.

Underlined author denotes designated speaker.

Dietary niche shifts are coincident with mammalian body size reduction during a Paleocene hyperthermal

***Neil F. Adams**^{1,2}, **Stephen L. Brusatte**³, **Thomas E. Williamson**⁴, **Ross Secord**⁵ and **Mark A. Purnell**²

¹Natural History Museum, London, UK

²University of Leicester, UK

³University of Edinburgh, UK

⁴New Mexico Museum of Natural History and Science, USA

⁵University of Nebraska–Lincoln, USA

The idea that ecological niches remain stable during periods of rapid climate change has long been central to methods used to assess extinction risk. However, evidence to test this assumption, particularly beyond recent timescales, remains scarce. Here we examine how a terrestrial mammal responded to rapid climate warming during the Latest Danian Event (LDE; ~62.3 Ma) in the early Paleocene. *Tetraclaenodon puercensis* is an archaic ungulate that exhibits a size reduction during the LDE in the San Juan Basin of New Mexico, USA. The drivers of this phenomenon – hyperthermal dwarfism – remain poorly resolved and are often linked to biogeographic range shifts rather than *in situ* ecological responses. Using a novel multi-comparator approach to dental microwear texture analysis, we show that *T. puercensis* shifted from frugivorous to folivorous diets during the LDE. Such a shift is often observed among extant forest mammals during times of food scarcity and moisture stress, which are likely during Palaeogene hyperthermals. Our results provide the first robust evidence for mammalian ecological responses and adaptation to lower quality resources during a Palaeogene hyperthermal. Dietary niche shifts therefore provide a means of dealing with rapid warming without requiring broad changes in biogeographic ranges.

Trilobite mass extinction events in the Early Ordovician (Tremadocian) of North America

Jonathan M. Adrain and ***Francesc Pérez-Peris**

University of Iowa, USA

The Great Basin contains one of the most complete and well exposed Lower Ordovician sequences in the world. Intensive fieldwork carried out over a more than a 20-year period has revealed much greater trilobite diversity than previously known. Subsequent taxonomic and biostratigraphic works have suggested the existence of two major trilobite mass extinction events in the Tremadocian of the northern margin of Laurentia. However, these extinction events have yet to be studied in detail. For the first time, a comprehensive study of the Tremadocian trilobite extinction events is performed. In order to identify the critical intervals, proportional genus extinction and boundary



crosser diversity for all the biozones has been calculated. As a result, two major trilobite mass extinctions have been exposed. The oldest extinction interval lies between the Skullrockian and Stairsian regional stages, featuring 84 % trilobite genus extinction. The younger extinction occurs between the Stairsian and the Tulean regional stages, with 100 % genus extinction. The trilobite extinctions are abrupt and characterized by a complete generic turnover and noticeable changes at higher taxonomical levels within the trilobite assemblage.

Macroalgae, cyanobacteria and a late Ediacaran ‘diversity crisis’ in the Mackenzie Mountains, NW Canada

Heda Agic¹, Martin R. Smith¹ and Alex Kovalick²

¹Durham University, UK

²University of California, Riverside, USA

The terminal Ediacaran to early Cambrian transition records a seeming decline in diversity, in contrast to older units which preserve rich communities of macroscopic Ediacara-type biota worldwide. Our understanding of this biotic change and its environmental drivers suffers from stratigraphic incompleteness, as mid-upper Ediacaran and Cambrian strata are rarely exposed in a continuous sequence in the same area, and often represent different depositional settings. An almost continuous succession of Ediacaran to mid-Cambrian siliciclastics and carbonates in the Mackenzie Mountains, Northwest Territories, Canada records a broadly uniform depositional setting and allows us to assess biotic and environmental changes through this interval. Ediacara-type biota, including newly-reported occurrences, appear in the siliciclastic, mid-shallow shelf Blueflower Formation. The overlying Ingta Formation represents a similar environment, but lacks macrofossils except scarce traces (*Planolites*, *Treptichnus*) and a lamellar uniserial macroalga similar to kelp. The organic microfossil record consists of bacterial filaments (*Oscillatorioopsis*, *Siphonophycus*) and minor prasinophyte-like *Tasmanites*, but lacks complex forms or metazoans. The overlying (pre-trilobitic) Vampire Formation records increased complexity of traces, but no body fossils. The primary producer-dominated environment and the absence of organically-preserved metazoan remains in a setting conducive to organic preservation implies a true diversity crisis of complex life through the Ediacaran–Cambrian transition.

Reconstructing the skeletal and soft tissue of the Ediacaran metazoan *Namacalathus*

***Ruaridh Alexander and Rachel A. Wood**

University of Edinburgh, UK

The Ediacaran–Cambrian transition (c. 574–521 Ma) is host to the emergence of metazoans and crown groups of modern phyla. The phylogenetic affinities and lifestyles of many Ediacaran taxa remain uncertain, however, making it difficult to link Cambrian fauna to those in the Ediacaran. One such fossil is *Namacalathus hermanastes*, a sessile, benthic, goblet-shaped biomineralizer, which possessed a skeleton that was variably populated with spines. Initially interpreted as a cnidarian, recent interpretations have placed it as a total group lophotrochozoan, partly due to soft tissue preservation in specimens from the Nama Group, Namibia (c. 551–539 Ma), some internal features



which have been interpreted as partial gut structures. *Namacalathus*' mode of reproduction is also uncertain as it has been suggested that it may have reproduced via asexual external bilateral budding, although definitive evidence is yet to be presented. Here we present analyses of specimens which display soft tissue preservation, showing novel external spine morphologies and further evidence for possible internal soft tissue structures. Furthermore, specimens which display apparent attachment (possible budding sites) appear to be common, suggesting budding may have been a major mechanism for dispersal along the sea floor.

The impact of fossil tips on reconstructing trait evolution using phylogenetic comparative methods

Bethany J. Allen¹, William Gearty², Pedro Godoy³ and Alfio Alessandro Chiarenza⁴

¹ETH Zürich, Switzerland

²American Museum of Natural History, USA

³University of São Paulo, Brazil

⁴Universidad de Vigo, Spain

Collecting data for use in constructing phylogenies is a valuable but time- and resource-consuming pursuit. Indicators of the potential value of including certain species in a phylogeny *a priori* could therefore prove useful when planning this stage of research. We used a simulation approach to investigate whether there are trends in the ability for phylogenetic comparative methods to recover the correct model of trait evolution based on certain characteristics of the phylogeny. First, we used an array of different diversification rates to simulate phylogenies containing a varying number of fossil and extant tips. We then simulated the evolution of a single trait across each phylogeny using multiple continuous trait evolution models. We then calculated the fit of the correct and incorrect models to the simulated traits. Finally, we assessed the importance of the phylogenetic and functional uniqueness of the individual fossil tips to recovering the correct model of evolution. This quantitative evaluation allows us to discern whether there are certain tip characteristics or phylogeny shapes associated with identifying the correct trait evolution models. Our results provide valuable insights into the conditions under which continuous trait evolution can be successfully characterized using phylogenetic comparative methods, especially when fossil taxa are included.

Climate-mediated vegetation changes during the Smithian–Spathian cooling event (c. 249.2 Ma) at southern subpolar latitudes (Sydney Basin, Australia)

***Marcos Amores¹, Tracy D. Frank², Christopher R. Fielding² and Chris Mays¹**

¹University College Cork, Ireland

²University of Connecticut, USA

The Sydney Basin in southeastern Australia provides a valuable record of the recovery of subpolar (c. 60–65°S) continental ecosystems after the end-Permian extinction event (c. 252 Ma). Stable carbon isotopes ($\delta^{13}\text{C}$) facilitated correlation to global carbon cycle changes across a cooling event known as the Smithian–Spathian Event (SSE; c. 249.2 Ma). High-resolution spore-pollen analyses during the SSE revealed that isoëtalean lycophyte plants initially dominated the basin's alluvial environments, represented by the spore genera *Densoisporites* and, subsequently, *Aratrisporites*. Later, as the world cooled, seed plants such as the Umkomasiales, Peltaspermales and stem group



conifers resurged at southern high latitudes. The SSE coincided with the deposition of thick, oxidized Fe-rich mudrock facies ('red beds'); despite intense post-depositional oxidation, these beds yielded well-preserved palynological assemblages. *Aratrisporites* remained abundant throughout the red bed facies, suggesting a relationship between this lycophyte group and the cooling conditions during the SSE. Quantitative palynology combined with geochemical weathering proxies will further elucidate the influence of oxidation on microfossil preservation. Since red bed facies are common to several mass extinction events, characterizing their preservation potential has broad implications for resolving the continental records of other deep-time biotic crises.

Multicellular microfossils from the c. 930–820-million-year-old Veteranen Group of Svalbard

**Ross P. Anderson¹, George O. Wedlake¹, Luke A. Parry², Timothy M. Gibson³,
Alexie E. G. Millikin³, Karsten Piepjohn⁴, Nicholas J. Tosca⁵, Alan D. Rooney³ and
Justin V. Strauss⁶**

¹University of Oxford, UK

²University College London, UK

³Yale University, USA

⁴Bundesanstalt für Geowissenschaften und Rohstoffe, Germany

⁵University of Cambridge, UK

⁶Dartmouth College, USA

The Neoproterozoic diversification of complex multicellular life marks a pivotal turning point for life on Earth. Molecular clocks predict that major groups of eukaryotes emerged by ~1,000 million years ago (Ma) but few early fossils are known. Here we report new microfossils from mud- and siltstone facies of the c. 930–820 Ma Veteranen Group of Svalbard. This sedimentary succession is c. 4.5 km thick and records deposition largely in marginal marine environments. Microfossil data from clay-rich samples collected at Faksevågen, Spitsbergen and across multiple sites on Nordaustlandet and Lågøya indicate a community with a modest diversity of eukaryotes. This contrasts with younger deposits from Svalbard, such as the c. 790 Ma Svanbergjellet Formation, which are among the most diverse Neoproterozoic assemblages worldwide. However, new exceptionally preserved multicellular taxa are recorded in the Tonian Veteranen samples, in addition to the known green alga *Proterocladus*. The new taxa may have affinities with red or green algae. One of the new taxa evidences a regular and symmetrical pattern of branching, indicating algae already had access to developmental pathways that gave significant control over their morphology by the middle of the Tonian period.



Resorption and remodelling in the dermal skeleton of an early chondrichthyan

Plamen Andreev^{1,2}, Qiang Li^{1,2}, Wenjin Zhao^{2,3,4}, Lijian Peng¹, Lars Brakenhoff⁵, Martin Rücklin⁶, Federica Marone⁷ and Min Zhu^{2,3,4}

¹*Qijing Normal University, China*

²*Institute of Vertebrate Paleontology and Paleoanthropology, China*

³*CAS Center for Excellence in Life and Palaeoenvironment, China*

⁴*University of Chinese Academy of Sciences, China*

⁵*Leiden University, Netherlands*

⁶*Naturalis Biodiversity Center, Netherlands*

⁷*Swiss Light Source, Paul Scherrer Institut, Switzerland*

The external skeleton of living chondrichthyans consists largely of dermal scales, each representing a distinct tooth-like element. Stem chondrichthyan lineages, however, demonstrate shoulder girdle armour of fin spines and ventral dermal plates that are regarded as homologues of median and paired plates of other jawed vertebrates ('placoderms' and osteichthyans). Here we challenge this view by supplying new data on the growth of the dermal skeleton of the stem chondrichthyan *Fanjingshania renovata* from the lower Silurian of China. Examined fragments of fused pectoral fin spines and paired (pinnal) plates reveal that the latter constitute extensions of the lamellar bone of the spine wall that bind together modified body scales. The fin spines' ornamenting ridges become discontinuous near the spine base and change their tissue composition from bone to atubular dentine, indicating that they are the remnants of resorbed scales. These results show that the pinnal plates of *Fanjingshania* represent the modified, growing ends of pectoral spines, unlike the concentric deposition of independent dermal plates in stem jawed vertebrates. This condition could have wider distribution in the chondrichthyan stem (*e.g.* in climatiids and diplacanthids) and raises the possibility for the independent origin of large dermal ossifications in the chondrichthyan total group.

A new approach to the reconstruction of fragmentary fossil long bones; the case study of *Homo naledi*

Julia Aramendi¹ and Lloyd A. Courtenay²

¹*University of Cambridge, UK*

²*Université de Bordeaux, France*

Our understanding of primate evolution is limited by an incomplete fossil record, which often consists of fragmentary remains. One of the possible means of overcoming these limitations relies on the use of different reconstruction techniques. Unfortunately, some of these approaches have raised several methodological questions. To address this issue, we have developed a novel approach to reconstruct hominoid long bones, utilizing morphological variables extracted from modern anatomical data. Our approach implements a new technique called the 'Reverse Engineering' method, which leverages landmark-based information to predict the morphology of entire bones, based on morphological variables extracted from the portions of preserved bone represented by highly fragmented fossil specimens. With the aid of both landmarks and semi-landmarks, we tested this approach on modern great apes, including anatomically modern humans, chimpanzees, gorillas and orangutans, and found that it significantly reduces the reconstruction error of estimated missing landmarks compared to other methods. We then successfully applied this methodology to



reconstruct some of the long bones of the South African human fossil taxon *Homo naledi*. These promising results have important implications for the study of human and primate evolution, particularly for the analysis of fragmentary fossils, thus contributing to ongoing efforts in reconstructing the human evolutionary tree.

Characterization of melanin-based colour expression and melanosome attributes across the avian phylogeny

***Hollie Bean¹, Daniel J. Field² and Maria E. McNamara¹**

¹*University College Cork, Ireland*

²*University of Cambridge, UK*

Melanin pigments contribute to the expression of black, brown, grey and rufous colours in feathers and play an important role in visual communication. Fossil feathers that preserve evidence of melanin, such as organelles termed melanosomes, can potentially inform us on fossil behaviour. However, current models for predicting fossil feather colouration yield low accuracies of less than 60 %, and visually assigned categories for melanin-based colours lack statistical support. In this study we aim to improve these models with an approach that includes data from melanosome geometry and chemistry, plus quantitative data on feather colour. We sampled feathers that express melanin-based colouration from 112 birds that represent all 44 extant avian orders. We characterized feather colour using reflectance spectrophotometry and compared spectral data for feathers with different colours using multivariate statistics. Our data show that spectrally derived colour parameters such as brightness, saturation and RGB values can successfully differentiate visual reflectance spectra of feathers with different melanin-based colours. Future analyses will use scanning electron microscopy to characterize the geometry of feather melanosomes. Integration of these data with chemical data, plus a fuller understanding of feather taphonomy, will provide a new opportunity to improve existing predictive models of fossil feather colour.

Regional aridification drove changes in Asian mammal faunas by the middle Eocene: implications for the timing and magnitude of the Mongolian Remodelling

Gemma L. Benevento¹, Niels Meijer¹, Julia Brugger¹, Andreas Mulch^{1,2}, Thomas Hickler^{1,2} and Susanne Fritz^{1,2}

¹*Senckenberg Biodiversity and Climate Research Centre (BiK-F), Germany*

²*Goethe University Frankfurt, Germany*

In Asia, previous studies have shown changes across the Eocene–Oligocene transition (EOT, a global cooling event; 34 Ma) from perissodactyl-dominated faunas to those dominated by smaller-bodied Glires, better adapted to dry environments with limited resources (the Mongolian Remodelling). However, recent palaeoenvironmental records and novel climate models show drying already occurring in Central Asia during the mid-Eocene due to global cooling, the growing Tibetan Plateau, and the retreating Paratethys Sea. We calculated sampling-corrected fossil mammal taxonomic richness across the Palaeogene of Central Asia. We recover substantially lower diversity in the mid-Eocene, concurrent with the onset of regional aridification. Mammal richness increased throughout



the remainder of the Eocene but declined again across the EOT and throughout the Oligocene. In addition, we recover increased mammal turnover and decreases in mean and maximum body size in the mid-Eocene and across the EOT, concurrent with shifting environmental conditions. This suggests that regional mid-Eocene aridification in Central Asia may have driven faunal shifts similar in magnitude to those linked to the EOT global cooling event. Furthermore, our analyses indicate declines in both perissodactyl and rodent diversity across the EOT, suggesting that the Mongolian Remodelling may be partially influenced by sampling biases in the fossil record.

Echoes from the past: unveiling deep-time functional dynamics through network analysis

***Fernando Blanco**^{1,2}, **Johannes Müller**³, **Daniele Silvestro**⁴ and **Juan L. Cantalapiedra**⁵

¹University of Gothenburg, Sweden

²Gothenburg Global Biodiversity Centre, Sweden

³Museum für Naturkunde Berlin, Germany

⁴University of Fribourg, Switzerland

⁵Universidad de Alcalá, Spain

Ecosystem functional structures are complex systems shaped by the interplay between living organisms and their environment. One way to characterize these systems is to decompose them into their individual elements and the connection between them. Network analysis emerges as a powerful tool that enables us to characterize these systems and study their behaviour. By incorporating geohistorical records, we add a layer of information to this framework, providing valuable insights into functional dynamics over evolutionary time. Here we develop a novel analytical framework based on network analysis to characterize and examine deep-time functional dynamics. First, we test this new framework in a regional setting, the Iberian Peninsula mammalian record over the past 21 Ma. We find that functional aggregates of mammalian communities (functional faunas) experienced long periods of stability punctuated by rapid changes associated with major abiotic events. Second, we apply our validated framework over a global dataset of large herbivores spanning the past 60 Ma. Our results reveal that even at global scale there are long periods with stable functional assemblages interrupted by rapid reorganizations likely driven by abiotic factors. Network analyses provide a powerful approach to understand the evolution of functional systems and their response to changing environments.

Indications for major ‘out of Asia’ proboscidean migrations during the Middle Miocene

***Nora Carolin** and **Sunil Bajpai**

Indian Institute of Technology Roorkee, India

The proboscideans recently identified from the Middle Miocene of Kutch, India include *Prodeinotherium pentapotamiae*, *Miomastodon metachinjensis*, *Choerolophodon corrugatus* and a gomphotheroid. The M3 and d3 of *P. pentapotamiae* show close affinity to *D. levius*, the earliest *Deinotherium* species in Europe. A P4 of *C. corrugatus* corroborates the presence of premolars reported previously for *Afrochoerodon palaeindicus*. Upper premolars are also known for



“*C.* *guangheensis* from the Linxia basin (China), suggesting all the known Asian choerolophodontids retained premolars, and are hence ancestral. Molars assigned to *Zygodolophodon turicensis* from the MN6 of Turkey are referable to *M. metachinjiensis*, suggesting its northward dispersal. Moreover, *M. metachinjiensis* d4 and “*Mammut*” *obliquelophus* molars are comparable in the degree of gracility, implying their close relationship. The major proboscidean immigration suggested for Europe’s Vallesian/Turolian boundary involved primarily immigrants from the Indian subcontinent. *Afrochoerodon palaindicus*, *Prodeinotherium pentapotamiae* and *Miomastodon metachinjiensis* dispersed northward during the Middle Miocene and were ancestral to the European species of *Afrochoerodon choticus*, *Deinotherium levius* and “*Mammut*” *obliquelophus*, respectively. Choerolophontidae, however, dispersed northward earlier than the other two clades. These migrations were possibly Middle Miocene Climatic Optimum (MMCO)-driven, and record the earliest major northward dispersal of proboscideans out of Asia.

Tempo and mode in the evolution of dinosaurian (Archosauria: Dinosauria) climatic niche landscape

Alfio Alessandro Chiarenza¹, Alexander J. Farnsworth², Lewis A. Jones¹,

Juan L. Cantalapiedra³, Sara Gamboa^{1,4}, Sofía Galvan¹, Graciela Sotelo¹ and Sara Varela¹

¹Universidad de Vigo, Spain

²University of Bristol, UK

³Universidad de Alcalá, Spain

⁴Universidad Complutense de Madrid, Spain

Earth system changes had a long-term influence on dinosaurian biology during their Mesozoic legacy, making them ideal candidates for investigating the interplay between climate and macroevolution. We built a comprehensive dataset of specimen-based dinosaur occurrences recording their geographic location. Palaeorotations based on tectonic models were computed for the Carnian–Maastrichtian interval (237–66 Ma), and calibrated with HadCM3L palaeoclimatic models, reproducing physical conditions for variables like temperature and precipitation. Phylogenetic matrices were assembled with >300 operational taxonomic units for each subclade (Ornithischia, Sauropodomorpha and Theropoda) and analysed within a Bayesian framework. We finally investigated the occupation of dinosaurian climatic niche space using phylogenetic comparative methods, which combine ancestral state reconstruction and multi-regime Ornstein–Uhlenbeck models. We evaluated whether the evolution of their climatic niches followed directional trends, and whether niche shifts were coincident with global climatic changes (e.g. Mesozoic hyperthermals like the Early Jurassic oceanic anoxic events or the Cenomanian–Turonian boundary). Multiple evolutionary regimes were exhibited by theropods, with a burst towards a cooler niche in the Middle Jurassic (170 Ma). Ornithischian climatic landscape appears unconstrained from the earliest Jurassic, while sauropodomorphs shifted to a warmer niche in the Triassic/Jurassic, maintaining a temperature-constrained niche throughout the Mesozoic.



Challenges of ancestral state estimation: the practical case of feather evolution

Pierre Cockx, Joseph N. Keating and Michael J. Benton

University of Bristol, UK

Ancestral state estimation is among the most fundamental tools for exploring evolution. These methods combine information from a phylogenetic tree with observations in modern species or fossil specimens. By estimating character states in ancestors, it offers a unique insight into the evolutionary histories of the groups studied for the characters of interest. Although the challenges of these methods have already received some attention, a full assessment of the parameters influencing the results is yet to be done. The evolution of feather function represents an ideal practical case. It is subjected to very strong research and public interest, and ancestral state estimation has been used recently to formulate hypotheses surrounding the deep time origin and subsequent diversification of feathers. We ran a series of analyses to assess maximum likelihood reconstruction sensitivity to the following parameters: outgroup selection, branch lengths, model, and coding strategy. Our initial findings suggest that the outgroup selection does not affect our results. On the other hand, the time scaling method employed, evolutionary model and coding strategy significantly influence ancestral estimates. These results greatly inform our understanding of the origin and early evolution of feathers, together with the limitations and reliability of ancestral state estimation more generally.

How has shark functional diversity changed through geological time?

Jack Cooper¹ and Catalina Pimiento^{1,2,3}

¹*Swansea University, UK*

²*University of Zurich, Switzerland*

³*Smithsonian Tropical Research Institute, Panama*

Modern sharks have a long evolutionary history, during which they have persisted through numerous environmental changes and played key ecological roles such as predation-induced top-down control of prey populations. Here we assess how shark ecological functions have changed over time by quantifying their functional diversity throughout the Cenozoic (66–0.01 Ma) using their well-preserved and abundant fossil teeth. To do so, we compiled a dataset of over 8,500 shark teeth from museum collections and scientific literature and took different dental measurements previously demonstrated to be proxies of ecological traits such as body size and diet. We found functional richness (FRic, volume of trait-space occupied, representing range of functions) to be generally high, with >60 % of trait-space being consistently occupied over time. While maximum FRic was reached in the Eocene, the minimum took place in the Pleistocene. Interestingly, we found the FRic of the last ~10 Ma to be generally lower than expected based on species-richness. Despite these changes in FRic, functional redundancy (number of taxa sharing trait-values and hence functions) remained generally stable, with 3-4 species/function over time. Overall, our results indicate that shark functional diversity experienced important changes over the Cenozoic, most notably a reduction in trait-space from the Miocene onwards.



Kaolinite causes mineralization and stabilization of soft tissues within days during marine shrimp decay experiments

***Nora Corthésy, Farid Saleh, Allison C. Daley and Jonathan B. Antcliffe**

University of Lausanne, Switzerland

Decay experiments constrain the factors involved in the early stages of fossilization, when labile anatomical information is lost or preserved. One of the most important of these experiments is the sediment associated with the carcass, with burial in various clay minerals showing differing preservation profiles. However, the effect of clays on decaying animals on top of sediments without burial is still unknown. The decay of the marine shrimp *Palaemon varians* deposited on three clay types was assessed. Results show kaolinite minerals slow decay rates. Further, by 120 hours on kaolinite substrate, a fine black film forms around the carcass replicating the cuticle in microscopic detail and stabilizing the morphology. Cryo-SEM analysis shows the film consists of newly formed aluminosilicate minerals, confirming silicification can occur rapidly after death on the seafloor. The other clays do not show these effects, and with kaolinite they only took place at marine salinities and never in freshwater. Thus, kaolinite not only slows down decay, but it also facilitates the mineralization of soft parts even in the absence of complete burial. This questions whether rapid burial is necessary for soft tissue preservation and demonstrates experimentally a crucial missing step of silicification in the early fossilization process.

Understanding fossil preservation patterns and processes using decay experimentation

Allison C. Daley¹, Orla G. Bath Enright^{1,2}, Harriet B. Drage¹, Farid Saleh¹ and Jonathan B. Antcliffe¹

¹*University of Lausanne, Switzerland*

²*State Museum of Natural History Stuttgart, Germany*

Decay experiments are an experimental taphonomy approach that investigates the interactions between the biosphere, lithosphere and hydrosphere during the decomposition of a carcass. A series of decay experiments on arthropods, molluscs and cnidarians at the University of Lausanne has been conducted to help understand patterns in the fossil record, and to gain insight into preservation processes. Body size influences the rate and type of decay, with smaller carcasses generally showing less disarticulation and significantly differential rates of decay compared to larger carcasses. Moulded arthropod exoskeletons tend to degrade much less quickly than carcasses, despite being marked by initial disarticulation. Certain anatomical features, notably appendages, are resistant to morphological change during decay. These results can guide our interpretation of arthropod fossils. Oxygen levels were recorded during decay experiments of arthropods, corals and gastropods, and revealed that oxygen declined more quickly than previously known, with open vial systems showing drastically reduced oxygen levels within 36 hours. Early decomposition creates local anoxia extremely rapidly, in many cases before any major visible loss of anatomical features through decay. The mineralogy of the substrate can also slow decay rates and help to stabilize anatomy. These data, taken together, allow for a better understanding of fossil preservation pathways.



An Ordovician vertebrate neurocranium

Richard P. Dearden^{1,2}, **Agnese Lanzetti**^{1,3}, **Sam Giles**^{1,3}, **Zerina Johanson**³, **Andy Jones**¹, **Stephan Lautenschlager**¹, **Emma Randle**¹ and **Ivan J. Sansom**¹

¹University of Birmingham, UK

²Naturalis Biodiversity Center, Netherlands

³Natural History Museum, London, UK

The evolutionary origins of the vertebrate head are obscured by the large temporal and phylogenetic gap that separates the oldest Cambrian vertebrate fossils from the earliest three-dimensionally preserved vertebrate skulls from the Silurian. We know that armoured vertebrates existed in the Ordovician, which spans this gap, but nothing is known of the anatomy of these animals beyond their outer skeleton of dermal scales and plates. We used computed tomography to image an articulated specimen of *Eriptychius americanus*, an Ordovician armoured vertebrate from the Sandbian (458.4–453.0 Ma) Harding Sandstone of Colorado, USA. Scanning reveals that this specimen harbours a set of symmetrical paired and midline cartilages, which we interpret as the front of the cranial endoskeleton surrounding the mouth, olfactory bulbs, pineal organ and orbits. These cartilages are separate from but closely wrapped by the dermal skeleton, suggesting that they filled and framed the head as in osteostracans and galeaspid, but unlike those taxa are not united into a single unit with each other and the splanchnocranium. *Eriptychius* represents the oldest three-dimensionally preserved endocranial skeleton of a vertebrate known in the fossil record, revealing a hitherto unknown way of constructing the neurocranium in the earliest armoured fishes.

The experimental effects of wave processes on arthropod taphonomy: implications for Lagerstätten and small carbonaceous fossils

***Laura Devine and Nicholas J. Minter**

University of Portsmouth, UK

Arthropods are one of the most significant groups of animals through Earth history, so it is important to determine if there are any taphonomic processes affecting the preservation quality of certain taxa and the fidelity of their fossil assemblages. Actualistic experiments, using analogue organisms, provide some of the best ways to test hypotheses about any such taphonomically induced biases. Using the marine arthropod *Ligia oceanica* as a modern analogue to segmented, multipodus arthropods, we conducted repeated measures taphonomic experiments using a wave-generating flume tank to investigate the effects of both the exposure to waves (wave exposure versus static decay) and time (0 to 96 hours) on decay and disarticulation. From our results, we identified the stages of decay and disarticulation for *L. oceanica*. A non-parametric longitudinal analysis (nparLD) demonstrated overall statistically significant effects of both wave exposure and time, and *post hoc* tests identified specific pairwise differences. Our results will be compared with certain fossil assemblages to identify the processes involved in how a deceased arthropod can become exceptionally preserved as a complete fossil in a Konservat-Lagerstätten or whether its ultimate fate is to become the disarticulated and fragmented remains found in small carbonaceous fossil (SCF) deposits.



The non-cryptic, diachronous origins of animal phyla

***Alavya Dhungana and Martin R. Smith**

Durham University, UK

The apparently 'sudden' appearance of most animal phyla in the early Cambrian is interpreted as reflecting the onset of favourable taphonomic conditions, capturing the aftermath of a cryptic Precambrian radiation. This 'cryptic origin' hypothesis explains the disconnect between the deep molecular clock divergence dates and the later, almost simultaneous appearance of animal phyla in the Cambrian. We test this hypothesis against the fossil record by compiling a dataset of the first occurrences of metazoan micro-, trace- and body-fossils. If taphonomy is the major control on first occurrences, this would lead to a phylogenetically random appearance of different metazoan clades. We instead find early-diverging clades appear in older strata, and late-diverging clades appear in younger strata, suggesting that the true origin of these clades corresponds closely in time to their appearance, without a need to invoke an ad-hoc cryptic radiation. Our results suggest there is sufficient time in the early stages of the Cambrian (prior to Burgess-Shale type preservation) for different animal clades to have evolved. The asynchronicity of evolution between different animal lineages indicates that the Cambrian 'explosion' did not have a single environmental trigger, but rather comprised multiple distinct radiations with different interplays of evolutionary and environmental factors.

A new rangeomorph from Newfoundland illuminates the origin of a lost body-plan

Frankie S. Dunn¹, Luke A. Parry¹ and Alexander G. Liu²

¹*University of Oxford, UK*

²*University of Cambridge, UK*

Late Ediacaran macrofossils record assemblages of early animals with distinctive forms that have no counterparts among living phyla. Detailed study of the development and anatomy of the enigmatic rangeomorphs has identified them as stem-group eumetazoans, possessing true tissues and body axes but likely phylogenetically pre-dating the origins of a gut and other eumetazoan synapomorphies. However, the origin of the rangeomorphs is poorly constrained, and it is unclear which of their morphological features are plesiomorphic, obscuring their relevance to broader questions in animal evolution. Here we describe a new rangeomorph taxon that possesses different branching architectures on either side of the midline of a unifoliate frond, and a stolon emerging directly from the frond base. The consistent structural asymmetry we demonstrate is unique to living eumetazoans. Furthermore, these characters are chimeric, uniting disparate rangeomorph groups and allowing us to polarize character transformations in rangeomorph evolutionary history and reconstruct the rangeomorph ancestor. Our new phylogenetic analysis of rangeomorphs and living animals recovers *Fractofusus* and other traditionally reclining forms as the earliest diverging rangeomorph taxa, suggesting rangeomorphs evolved from a reclining, colony-like, stoloniferous ancestor and 'organs' (e.g. the stalk) observed in some taxa were likely acquired independently of organs in living eumetazoans.



Developmental and functional constraints drove ontogenetic change in protective enrolment in an ancient arthropod

Jorge Esteve¹ and Nigel C. Hughes²

¹*Universidad Complutense de Madrid, Spain*

²*University of California, Riverside, USA*

New insights via 3D kinematic models into enrolment mechanics of the 429-million-year old trilobite *Aulacopleura koninckii* demonstrate marked change in enrolment style during development. In earlier growth phases, enrolment was spheroidal but later growth segmental growth dynamics required an alternative, non-spheroidal enrolment style. Results suggest adoption of a posture in later growth in which the posterior trunk extended beyond the front of the head. This change in enrolment accommodated a pattern of notable variation in the number of mature trunk segments, well known to characterize the development of this species. It suggests how an animal whose early segmental development was remarkably precisely controlled was able to realize marked variation in final mature segment number. The pattern was related, apparently, to life in a physically challenging, reduced oxygen setting. Understanding of functional morphology thus reconciles two paradoxical aspects of *A. koninckii*: strict ontogenetic regulation of individual segment size and shape accompanied by remarkable plasticity mature segment number.

A new taphonomic model for the Eocene Geiseltal Konservat-Lagerstätte, Germany

***Daniel Falk¹, Oliver Wings², Maria E. McNamara¹**

¹*University College Cork, Ireland*

²*Natural History Museum Bamberg, Germany*

The Geiseltal Konservat-Lagerstätte (Eocene, Germany) is represented by c. 25,000 fossil vertebrate specimens that were recovered from open lignite mines in central Germany in the early twentieth century. The taphonomy of the biota, including the preservation of soft tissues, is poorly understood. Early studies of the vertebrates reported remarkable (sub)cellular details of muscle, cartilage, blood vessels, feathers, hair, reptile scales and bacteria, all replaced in three dimensions in silica. This mode of preservation is unknown from other vertebrate Konservat-Lagerstätten and the claims of cellular fidelity lack verification by modern techniques. We examined soft tissues of the anurans using electron microscopy, electron probe microanalysis, Fourier-transform infrared spectroscopy, Raman spectroscopy and synchrotron rapid scanning-X-ray fluorescence analysis. Our data reveal that the soft tissues are not preserved as silica replacements. The Eberth-Katschenko layer of the mid-dermis, unique to anurans, is preserved in calcium phosphate. Preserved melanosomes have a sulphur-rich carbonaceous composition, probably due to sulphurization. Phosphatized skin and sulphurized melanosome films recur in vertebrates from other Konservat-Lagerstätten, albeit with variation in the fidelity of preservation among biotas. Recognition of this recurring dual mode of preservation informs on the taphonomic pathways available for preservation of vertebrate soft tissues in the fossil record.



Cementochronology reveals the evolution of life history amongst the earliest mammals

Pamela G. Gill^{1,3}, Elis Newham^{2,4}, Philippa Brewer³, Julia Schultz⁴, Kai Jaeger⁴, Ian J. Corfe^{5,6} and Thomas Martin⁴

¹*University of Bristol, UK*

²*Queen Mary University of London, UK*

³*Natural History Museum, London, UK*

⁴*Rheinische Friedrich-Wilhelms-Universität, Germany*

⁵*University of Helsinki, Finland*

⁶*Geological Survey of Finland, Finland*

The Jurassic radiation of crown mammals has been linked to the acquisition of key physiological innovations, including the evolution of determinate patterns of rapid juvenile growth truncated at sexual maturity. These patterns are intrinsically related to the evolution of mammals' endothermic physiology, the timing and mechanisms of which remain under considerable debate. We use synchrotron X-ray tomographic imaging of annual growth increments in the dental cementum of Early-to-Late Jurassic mammaliaforms (mammals and their closest ancestors) to map the origin and evolution of mammalian determinate growth. Non-mammalian mammaliaforms exhibited slow growth-rates with relatively little change through life. Early crown mammals developed significantly faster juvenile growth-rates that reduced at the attainment of sexual maturity, showing distinct contrasts in structure between juvenile and adult cementum. All fossils studied retained lower growth-rates, longer estimated maximum lifespans and delayed sexual maturity relative to comparably sized extant mammals. Estimation of basal-metabolic-rates (BMRs) using lifespan also suggests that non-mammalian mammaliaforms retained low BMRs, while some fossil crown mammals had BMRs approaching the lowest values of extant mammals. These patterns suggest that the mammalian determinate growth strategy first evolved amongst early crown mammals during the mid-Jurassic mammalian adaptive radiation, although growth remained slower than in extant mammals.

Palaeoecologic turnovers in the Ediacaran–Cambrian Chapel Island Formation, Newfoundland, Canada and the early steps of the Cambrian Explosion

***Romain Gougeon¹, M. Gabriela Mángano¹, Luis A. Buatois¹, Guy M. Narbonne^{1,2}, Brittany A. Laing¹ and Maximiliano Paz¹**

¹*University of Saskatchewan, Canada*

²*Queen's University, Canada*

The Chapel Island Formation in southeastern Newfoundland, Canada contains a continuous late Ediacaran to Cambrian Age 2 trace fossil record starting hundreds of metres below the oldest trilobites in the area. Since 1992, the >1,000-metre-thick, mostly siliciclastic succession has been renowned for hosting the Cambrian GSSP at Fortune Head. Recent restudy of six localities focused on gathering new ichnologic and sedimentologic datasets comprising bioturbation intensities, burrow width and depth, trace-fossil identification, and stratal packages and their sedimentary structures. Three palaeoecologic stages are identified for shallow-marine seafloors: an Ediacaran matground ecology, dominated by simple horizontal trails associated with microbially-stabilized



surfaces and limited vertical bioturbation; a Fortunian matground/firmground ecology, with evidence of penetrative shallow-tier bioturbation and a burst in trace-fossil diversity; and a late Fortunian/Cambrian Age 2 mixground ecology, with high bioturbation intensities and the formation of modern-style seafloors. In addition, an ecosystem engineering cube analysis demonstrates that a significant increase in the modes of engineering took place in early to middle Fortunian offshore and shelf environments. This study underscores the relevance of the Cambrian Explosion as a breakthrough in benthic ecosystems.

Reconstructing feeding behaviour and diet in Devonian ctenacanth chondrichthyans using tooth wear analysis and finite element analysis

***Merle Greif¹, Ivan Calandra², Stephan Lautenschlager³, Thomas Kaiser⁴ and Christian Klug¹**

¹University of Zurich, Switzerland

²Leibniz-Zentrum für Archäologie, Germany

³University of Birmingham, UK

⁴Leibniz Institute for the Analysis of Biodiversity Change (LIB), Germany

In fossil chondrichthyans, there is little evidence for their diet. Direct evidence can be digestive tract contents while indirect evidence stems from coprolites, tooth marks or stable isotopes. Dental microwear texture analysis (DMTA) can provide further information regarding diet and is used frequently to reconstruct diet in terrestrial and marine vertebrates. In chondrichthyans, DMTA has only been applied to modern species and Cenozoic fossil taxa, which share a high tooth replacement rate. In some Devonian chondrichthyans, the tooth replacement rate was much lower and significantly more food-tooth contact occurred. This research focuses on *Ctenacanthus*, the largest chondrichthyan genus of the Devonian. Heavily worn teeth from the Moroccan Tafilalt were analysed by combining DMTA with finite element analysis. Here we reconstruct feeding behaviour and diet of this hypothetical apex predator. Initial examinations of the tooth wear indicate two main scratch directions. In the apical part of the wear facet, scratches are mainly oriented vertically, while horizontal scratches dominate in the basal areas. This pattern indicates a feeding behaviour combining biting involving hard object contacts and head shaking movements to reduce prey size, which is a derived behaviour. The high abundance of co-occurring large clymeniids suggests that they might have been important prey.

Testing hypotheses on heterostracan feeding

***Madleen Grohganz¹, Antonio Ballell Mayoral¹, Humberto G. Ferron^{1,3}, Zerina Johanson², Emily J. Rayfield¹ and Philip C. J. Donoghue¹**

¹University of Bristol, UK

²Natural History Museum, London, UK

³University of Valencia, Spain

Teeth constitute a key innovation underpinning the evolutionary and ecological development of jawed vertebrates. To learn more about the evolutionary origin of teeth we study the tooth-like structures of heterostracans, a group of extinct, jawless vertebrates. We integrate evidence from different computational biomechanics methods and morphology to test feeding hypotheses. To test if the anteriorly-facing denticles on the oral plates are an adaption to suspension feeding, we



performed computational fluid dynamics (CFD) analyses. Independent of denticle orientation, similar velocity and turbulence patterns develop in the spaces between the denticles and on their upper surface, which allows us to reject this hypothesis. Internal growth dynamics analysis indicates a similar histology to the dermal skeleton and does not show patterns of replacement in the denticles, which we would expect if they were homologous to teeth. We performed finite element analysis (FEA) and bone density calculations to further test the mechanical function hypothesis. FEA stresses in the shaft of the oral plate are negatively correlated with bone density. The anterior part of the oral plate shows the highest bone density indicating a specific adaptation of the microstructure to a mechanical function. The heterostracan oral plates most likely performed a mechanical function, possibly deposit feeding.

Ediacaran marine animal forests and the ventilation of the oceans

Susana Gutarra¹, Emily G. Mitchell², Frances S. Dunn³, Brandt M. Gibson⁴, Rachel A. Racicot^{4,5}, Simon A. F. Darroch^{4,5} and Imran A. Rahman¹

¹*Natural History Museum, London, UK*

²*University of Cambridge, UK*

³*University of Oxford, UK*

⁴*Vanderbilt University, USA*

⁵*Senckenberg Museum of Natural History, Germany*

Marine forests play a vital ecological role in modern environments, but their importance during the rise of animal-dominated ecosystems over half a billion years ago is unknown. Here we use ecological modelling and computer simulations of flow to explore how Earth's oldest marine animal forests from the Ediacaran of Mistaken Point, Newfoundland, Canada influenced their fluid environment. Our results reveal how organism morphology, community structure and composition combined to impact vertical mixing of the surrounding water. We find that Mistaken Point communities were capable of generating high-mixing conditions, likely enhancing oxygenation of the water column. Our work suggests that Ediacaran marine animal forests may have been major contributors to the ventilation of the oceans, potentially catalysing the emergence of motile eumetazoans in marine ecosystems.

Tooth origins and the convergent evolution of sensory structures

***Yara Haridy¹, Karma Nanglu², Mark Rivers¹, Javier Ortega-Hernández² and Neil Shubin¹**

¹*University of Chicago, USA*

²*Harvard University, USA*

There is limited information about the origin of the fundamental tissues of the vertebrate skeleton. Dentine, enameloid and bone appear simultaneously in the odontodes of jawless vertebrates in the middle Ordovician. Yet, little is known about the impetus for the initial evolution of odontodes; historical hypotheses propose scenarios ranging from defence, to hydrodynamics, to sensation, but consensus has yet to emerge. Early vertebrate fossils are scarce and understudied, with fragmentary plates of the putative earliest vertebrates with odontodes such as the controversial Cambrian *Anatolepis* being key. *Anatolepis* reportedly has vertebrate tissues akin to those of heterostracans, and a pore-system like in ostracoderms. Despite these observations, *Anatolepis* has also been



argued to be an arthropod, rendering its significance for early vertebrate evolution controversial. We examined *Anatolepis* and related material: high contrast and high-resolution scan data aligned with descriptions of *Anatolepis* but also allowed visualization of novel complex structures which were revealed to be a complex pore system of Cambrian Aglaspid arthropod sensillae. The similarities between odontodes and arthropod cuticle sensillae are remarkable and reveal that odontodes are convergently akin to mechanoreceptors. Additionally dental studies support a parallel mechanosensory function of dentine, thereby lending credence to the sensory origins of odontodes.

Trait-mediated speciation and human-driven extinctions in proboscideans revealed by unsupervised Bayesian neural networks

Torsten Hauffe^{1,2}, Juan L. Cantalapedra³, Fernando Blanco⁴ and Daniele Silvestro^{1,2,4}

¹University of Fribourg Switzerland

²Swiss Institute of Bioinformatics, Switzerland

³Universidad de Alcalá, Spain

⁴Gothenburg Global Biodiversity Centre, Sweden

Species traits, palaeoenvironment and interactions among taxa are thought to control speciation and extinction rates that ultimately shape species richness through time. Recently, birth-death models have been developed to infer the impact of these factors on speciation and extinction rates from fossil occurrences. However, these models typically assume monotonic relationships between single predictors and rates, limiting our ability to assess their relative importance and interaction. Here we present a Bayesian birth-death model that uses a neural network to infer the multifactorial and nonlinear influence of continuous and categorical traits, time-dependent variables, and their interactions on speciation and extinction rates. Our model allows for the estimation of lineage- and time-specific rates from fossil occurrence data, and we use methods from explainable artificial intelligence to disentangle the effects of different predictors. After benchmarking the model with simulations, we apply it to a fossil dataset of proboscideans including ecomorphological traits, regional palaeoclimate and spatiotemporal overlap with hominins and modern humans. We found an increase in proboscidean speciation rate associated with traits that enhanced their dietary flexibility and that the emergence of modern humans is linked with a 12-fold increase in extinction rate, with a lower predicted impact of regional climate change.

A new species of actinopterygian from the Upper Carboniferous (Bashkirian) of northern England, and the problem of phylogenetically forgotten fishes

***Struan Henderson¹ and Sam Giles^{1,2}**

¹University of Birmingham, UK

²Natural History Museum, London, UK

The British Isles are among the most heavily sampled Carboniferous deposits globally, yet specimens in regional museums are often overlooked in favour of larger national museum collections. Here we describe a specimen from the Manchester Museum that has been known since the late nineteenth century but never described, recognizing it as a new genus and species of actinopterygian from



the Bashkirian of England. It exhibits distinctive features such as a posterior process of the operculum and an opercular process of the hyomandibular. We also conduct a phylogenetic analysis, significantly expanding character and taxon sampling to encompass historically excluded groups of Palaeozoic actinopterygians. Additionally, we visualize treespace explored by different methods of phylogenetic inference as a means of comparing parsimony (equal and implied weights) and likelihood-based methods. This study highlights that taxonomic reassessment of Carboniferous material, particularly material in smaller regional museum collections, is critical, and can reveal hidden diversity. It also shows that the failure to capture the totality of the Palaeozoic actinopterygian radiation in phylogenetic analyses has impacted our understanding of the sequence of character evolution along the stem-lineage and among early crown members.

***Osedax* bioerosion in marine reptiles: the evolution of an ecosystem engineer**

***Sarah Jamison-Todd^{1,2}, Adrian Glover², Philip D. Mannion¹ and Paul Upchurch¹**

¹University College London, UK

²Natural History Museum, London, UK

The bone-eating worm *Osedax* is found today on whale carcasses on the ocean floor, and in the fossil record of whales and marine reptiles. It is known only from vertebrate remains in marine environments and inhabits a unique and novel ecological role in the taxonomic assemblages associated with large marine vertebrate falls. By degrading bone, *Osedax* increases nutrient availability to the benthos and contributes to the diversity and prevalence of other specialist taxa associated with marine tetrapod falls. The origins of this taxon are hazy, and it is not clear when it became an important component of these niche ecosystems. The only previously described occurrence of *Osedax* borings in the fossil record of marine reptiles is from the Late Cretaceous of England. Here we examine additional Mesozoic marine reptile material for these traces. Bones containing putative borings were CT-scanned and compared to modern-day examples in whalebone. Definitive examples of *Osedax* were found in the Late Cretaceous of both the United Kingdom and North America, expanding the geographic range of Mesozoic *Osedax*. Tentative examples of borings were found in a Late Jurassic pliosaur, indicating that additional examples should be sought to define the temporal range of this taxon.

Extreme lower jaw elongation in a ‘placoderm’ reflects high disparity in early vertebrate evolution

***Melina E. M. Jobbins¹, Martin Rücklin^{2,3}, Hervé Lelièvre⁴, Eileen Grogan⁵, Piotr Szrek⁶ and Christian Klug¹**

¹University of Zurich, Switzerland

²Naturalis Biodiversity Center, Netherlands

³University of Leiden, Netherlands

⁴Independent

⁵Saint Joseph's University, USA

⁶Polish Geological Institute–National Research Institute, Poland

Morphological diversity of arthrodires is believed to reach a peak in the Middle to early Late Devonian, to then collapse before their extinction. Here we describe a unique ‘placoderm’ from the



Famennian of Morocco and Poland with a strong lower jaw elongation, reminiscent in proportions to extant halfbeaks. Currently, it is the oldest known vertebrate species with such extreme lower jaw protrusion. Initially described as a “fin spine”, the original material was later recognized as part of an arthrodire jaw. Key characters of this taxon include slender elongated inferognathals, gnathal elements with posteriorly recurved teeth, a pronounced rostrum, large eyes, a large nuchal gap and a single point of contact between the paired central plates. Phylogenetic analyses place *Alienacanthus malkowskii* within the derived Selenosteidae. Teeth anterior to the occlusal surface were probably functional during earlier ontogenetic stages, occluding with their upper jaw counterpart, and later grew past the occlusion. The recurved teeth were suitable for grasping and holding prey. The large size of the hyoid coincides with the need for strong mechanical support for the long inferognathals. The jaw proportions suggest a specialized feeding strategy and emphasize even higher ‘placoderm’ diversity and disparity, particularly in the Late Devonian.

Reconstructing the phylogeny of longest existing gastropod group Pleurotomariida (Ordovician–Recent) with Parsimony and Bayesian methods

***Baran Karapınar**^{1,2,3}, **Sebastian Höhna**² and **Alexander Nützel**^{1,2}

¹SNSB– Bayerische Staatssammlung für Paläontologie und Geologie, Germany

²Ludwig-Maximilians-Universität München, Germany

³Universität Hamburg, Germany

Pleurotomariida has the longest fossil record among extant gastropod groups, which extends back to the Cambrian–Ordovician. Pleurotomariida is a major clade in gastropod evolutionary history, comprising around 25–30 % of late Palaeozoic global gastropod generic diversity. Diversity of Pleurotomariida dropped significantly at the end-Permian mass extinction and remained low throughout the Triassic due to low origination rates and selective extinction in the Carnian. Here we present results of the first comprehensive phylogenetic analyses of Pleurotomariida using Parsimony and Bayesian inference (fossilized birth-death [FBD] model) with 93 shell characters and 109 taxa (Ordovician–Recent). In the most parsimonious tree, members of the same genus were recovered in distant clades and the topology was incongruent with stratigraphic data. The FBD tree is stratigraphically more congruent because the FBD model incorporates age information of the fossil tips. According to the FBD topology, two major clades survived into the Triassic, and only the least diversified clade survived until today. In contrast to previous assumptions, axial shell characters are not more homoplastic than the spiral shell characters. The early ontogenetic shell characters are more stable compared to late ontogenetic characters, indicating that early shell ontogeny is phylogenetically more informative.



Neoselachian diversification dynamics and age dependent extinction

***Kristína Kocáková¹**, **Daniele Silvestro^{2,3,4}**, **Amanda M. Gardiner¹**, **Jaime A. Villafaña^{5,6}** and **Catalina Pimiento^{1,7,8}**

¹*University of Zurich, Switzerland*

²*University of Fribourg, Switzerland*

³*Swiss Institute of Bioinformatics, Switzerland*

⁴*Gothenburg Global Biodiversity Centre, Sweden*

⁵*Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Chile*

⁶*Universidad Bernardo O'Higgins, Chile*

⁷*Swansea University, UK*

⁸*Smithsonian Tropical Research Institute, Panama*

Neoselachians – modern sharks, rays and skates and their extinct relatives – have an abundant fossil record and long evolutionary history. Previous studies suggest that after the K–Pg extinction event (~66 Ma), they did not suffer any other major global extinctions, except for the current human-driven decline. We compiled a comprehensive global dataset of neoselachian occurrences spanning the last 145 million years, and used a Bayesian framework accounting for sampling and preservation biases to assess their diversification dynamics and test for age-dependent extinction. We identified three hitherto unknown global extinctions in the upper Cretaceous (73.2 – 71.8 Ma), the Eocene–Oligocene (37.8 – 32.9 Ma) and from Pliocene onwards (5.3 Ma – Recent). Speciation rates were found to increase around times of elevated extinction suggesting high turnover, except during the last 13 million years, when there is prolonged negative diversification. We further found age-dependent extinction, with young species persistently displaying higher extinction rates than old species. Taken together, our results uncovered new patterns in the evolutionary history of neoselachians, suggesting that this group is more vulnerable to extinction than previously thought, especially as they approach the Recent. Importantly, species' age seems to be a key predictor of extinction, with short-lived species being particularly vulnerable.

Palynofloral change through the Palaeocene–Eocene Thermal Maximum in the Bighorn Basin, Wyoming

Vera Korasidis^{1,2} and **Scott L. Wing²**

¹*University of Melbourne, Australia*

²*Smithsonian Institution, USA*

To better understand the effect of the Palaeocene–Eocene Thermal Maximum (PETM) on continental ecosystems, we studied 40 new palynological samples from the Bighorn Basin (BHB) in Wyoming, USA. Abundances of palms and ferns increased slightly in the last 20–30 kyr of the Palaeocene, then dramatically with the onset of the carbon isotope excursion (CIE) defining the base of the PETM. Most tropical palynomorphs are restricted to the CIE body, whereas many temperate palynomorphs have gaps in their temporal ranges during the CIE. During the CIE, recovery pollen of mesophytic or wetland plants became more common while tropical taxa persisted. Palynofloral changes are consistent with warming in the latest Palaeocene, rapid warming and drying at the onset of the CIE followed by tropical temperatures throughout the CIE body, a return to wetter floodplains in a very warm climate during the CIE recovery, and cooler wet conditions in the post-PETM early Eocene.



The observation that pollen and leaves of temperate taxa have range gaps corresponding to the body of the CIE suggests that extirpation of these lineages was a basin-wide phenomenon rather than being restricted to streamside vegetation. The same is true for the invasion of tropical taxa during the body of the CIE.

Iron-coated varanid teeth and the dental specializations of ziphodont reptiles

**Aaron LeBlanc¹, Alexander P. Morrell¹, Slobodan Sirovica², David Labonte³,
Domenic C. D'Amore⁴ and Owen Addison¹**

¹King's College London, UK

²Queen Mary University of London, UK

³Imperial College London, UK

⁴Daemen University, USA

Reptiles have evolved serrated, blade-shaped (ziphodont) teeth several times, most notably within the theropod dinosaurs. However, ziphodonty is rare among extant reptiles. Among these, the Komodo dragon (*Varanus komodoensis*) is the most popular analogue for understanding ziphodont tooth form and function. Our understanding of the similarities in material properties of the teeth of *V. komodoensis* and extinct ziphodonts are, however, poorly understood. Here we provide the first elemental and structural characterization of the enamel and dentine in *V. komodoensis* teeth and describe specialized coatings on the enamel of their serrations and tooth tips. Electron microscopy and elemental imaging techniques revealed a thin, iron- and zinc-rich layer covering these regions of each tooth, creating orange-coloured serrations in erupted and developing teeth. Extrapolating this feature to the ziphodont teeth of theropod dinosaurs is difficult due to diagenetic alterations to the enamel and dentine in fossil teeth. Despite this, structural imaging revealed that the serrations of tyrannosaurid dinosaurs exhibit an unusual 'wavy' form of enamel elsewhere seen in the grinding dentitions of hadrosaurid dinosaurs. These comparisons highlight the hidden diversity within the thin veneer of enamel in ziphodont reptiles, emphasizing the need to explore dental adaptations in other reptilian groups and tooth morphotypes.

Preservation of the organic carbon remains in the Chengjiang biota – an integrated story

***Xiangtong Lei, Peiyun Cong, Wenwen Wen and Fan Wei**

Yunnan University, China

The exceptional preservation of various nervous and digestive tissues as carbonaceous residues in Cambrian fossil Lagerstätten (e.g. the Chengjiang biota in South China) has provided important new anatomical details to elucidate the evolution of early Cambrian animals. However, the preservation mechanism of these graphitized soft tissues remains controversial. Here we report on new data, from Raman spectroscopy and SEM-EDX analyses, in a range of fossil taxa from the event beds (EB) and the background beds (BGB) of the Chengjiang biota. In the EB pyritization is the main taphonomic pathway that occurred during early decay, a process that functioned as a 'taphonomic filter' that exhausted metabolizable carbon but left the early graphitized (relatively inactive) carbon in the soft tissues. This is corroborated by the presence of more disordered



carbon in the recalcitrant tissues that might escape from pyritization. In contrast, the BGB fossils are characterized by heavy graphitization, exhibiting a lower occurrence of common diagenetic mineralization such as pyritization and phosphatization. Our results provide a new view of the preservation of organic carbon in Burgess Shale-type (BST) fossil Lagerstätten and reveal that the Chengjiang BGB fossils represent a typical example of BST preservation without significant alteration by diagenetic mineralization.

A fresh North American view into the Cambrian Explosion – new insights from the Drumian Marjum Konservat-Lagerstätte of western Utah, USA

Rudy Lerosey Aubril¹, Robert Coleman², Lucas del Mouro^{1,5}, Robert Gaines³, Luke A. Parry⁴, Jacob Skabelund² and Javier Ortega-Hernández¹

¹Harvard University, USA

²Independent

³Pomona College, USA

⁴University College London, UK

⁵University of São Paulo, Brazil

Burgess Shale-type (BST) biotas preserve soft-bodied fossils that critically inform the biodiversity and ecological complexity of the Cambrian Explosion. In North America, the Wuliuan Burgess Shale has fundamentally shaped our understanding of this major evolutionary event, and although the USA also contains several BST biotas, they typically feature much lower preservation quality and species richness. New investigations on the Drumian Marjum biota from Utah reveal that it fundamentally complements our perspective on the early evolution of animal-dominated communities in Laurentia. With 149 species, *c.* 57% of which are soft-bodied, this remarkable fossil assemblage is the most diverse Cambrian BST biota in North America after the Burgess Shale. The Marjum biota is dominated by panarthropods and sponges in both species richness and abundance. The high preservation quality is evidenced by the common observation of internal organs and the presence of animal clades with extremely scarce Cambrian fossil records (*e.g.* comb jellies, tunicates, vertebrates). The Marjum Formation shares broadly comparable depositional and palaeogeographic contexts to the Burgess Shale, including quiet, deep-water, recurrently oxygen-depleted environments at the offshore margin of a carbonate platform, which were located several thousands of kilometres apart, but along the same subequatorial northern margin of Laurentia.

Juvenile arthropleurids from the Montceau-les-Mines Lagerstätte (305 Ma) help explain the phylogenetic affinities of these giant myriapods

***Mickaël Lheritier¹, Adrien Buisson¹, Alexis Gerbe¹, Jean Vannier¹, Gilles Escarguel¹, Gregory D. Edgecombe², Russell J. Garwood^{2,3} and Vincent Perrier¹**

¹Université Claude Bernard Lyon 1, France

²Natural History Museum, London, UK

³The University of Manchester, UK

The Montceau-les-Mines Lagerstätte is located in the northeast of the Massif Central in France and is Late Carboniferous in age (Kasimovian, around 305 Ma). The associated wet and swampy



palaeoenvironments are characterized by a diversified flora and fauna preserved in three dimensions inside sideritic nodules. The fauna is dominated by arthropods (*e.g.* crustaceans, arachnids) and also has some molluscs, annelids and some vertebrates (*e.g.* fishes, tetrapods). Among the arthropods a notable group is the myriapods, with diplopods and arthropleurids. Arthropleurids are an extinct group of myriapods which lived during the Carboniferous and early Permian. They distinguished themselves from other myriapods by their gigantic size, reaching 3 m in length and 50 cm in width for the biggest specimens. Our study focuses on the juvenile arthropleurids from this site. We restudied these specimens with X-ray micro-tomography (μ CT). We reconstituted for the first time their body and appendices anatomy in three dimensions. The presence of antennae, mandibles and stalked eyes is observed on several specimens. These new data helped us to reassign the arthropleurids in the myriapod phylogeny, specifying their phylogenetic relationships with the diplopods (millipedes) and the chilopods (centipedes).

Anatomy of the skeleton and soft tissues of a 290-million-year-old amphibian revealed using elemental and multispectral imaging

Antoine Logghe¹, Pierre Gueriau², Phillip L. Manning³, Roy A. Wogelius³, Victoria M. Egerton³, Uwe Bergmann⁴, Sophie Sanchez^{5,6} and Jean-Sébastien Steyer¹

¹*Sorbonne Université, France*

²*Université Paris-Saclay, France*

³*The University of Manchester, UK*

⁴*University of Wisconsin-Madison, USA*

⁵*Uppsala University, Sweden*

⁶*European Synchrotron Radiation Facility, Grenoble, France*

Fossil amphibians from the Carboniferous–Permian period are diverse and well-studied: within the temnospondyls, the dissorophoids and eryopoids have been studied in depth in terms of anatomy and skeletal ontogeny. However, soft tissue analyses are rare. Here we describe in detail the skeletal and soft tissue anatomy of an exceptionally preserved early Permian eryopoid from Franchesse (Massif Central, France) using advanced imaging techniques, namely synchrotron X-ray fluorescence mapping of major to trace elements and multispectral UV-visible-near-infrared laboratory imaging. The newly revealed details of the skull and postcranial bones allow the systematic attribution of this specimen to the genus *Onchiodon* and its identification as a juvenile individual. In addition, the phosphorus and sulphur distributions reveal a possible dermal pattern in the lateral scales, with the presence of linearly organized holes in the skin. These holes most likely reflect the earlier presence of more labile soft tissues, such as glands (*e.g.* mucus glands). Chemical characterization of these dermal remains using X-ray absorption spectroscopy indicates that they preserve endogenous organic compounds, including degradation products of protein remains probably derived from keratin. These results open up new perspectives on the analysis of soft tissues (morphology, chemistry and preservation), which have often been neglected until now.



A century of imaging the Rhynie chert: using confocal microscopy to model the first land animals, plants and fungi in 3D

***Emma J. Long¹, Gregory D. Edgecombe¹, Paul Kenrick¹, Alexander D. Ball¹ and Xiaoya Ma²**

¹Natural History Museum, London, UK

²University of Exeter, UK

Colonization of the land has profoundly influenced life on Earth. Scotland's Lower Devonian Rhynie chert (~408 Ma) houses the earliest diverse terrestrial ecosystem ever discovered. Preserved within a translucent matrix, plant cells, arthropod cuticle and fungi reveal vascular tissues, spores, hyphal networks, muscle tendons, articulated setae, chemosensory sensilla and the earliest instances of lungs in the fossil record. For over a century, Rhynie has been studied using traditional light microscopy, with more recent advances including stereo-pair imaging and 3D reconstructions of serial sections. Confocal laser scanning microscopy (CLSM) has revolutionized the field by rendering fossils with clarity in 3D, from fungi, amoebae, cyanobacteria and crustacean eggs to a eurythecarid arthropod. While previous CLSM-led research has focused on generating intensity projections, this study takes a more three-dimensional approach by segmenting and modelling high-resolution Z-stack tiles. From the tangled loops of fungal hyphae in an arachnid carcass to the springing apparatus of the first collembolans, our methods shed light on the intricate anatomical adaptations of some of the earliest terrestrial organisms. The Rhynie chert's evolutionary significance, combined with the autofluorescent properties of the fossils within it, makes it an ideal case study for demonstrating the power of confocal imaging in specimen-based palaeontology.

Exceptional preservation in the Rhynie chert: molecular fingerprints resolved *in situ* down to sub-micron scales

Corentin Loron¹, Ferenc Borondics², Edwin Rodriguez Dzul¹, Patrick J. Orr³,

Andrei V. Gromov¹, Nick C. Fraser⁴ and Sean McMahon¹

¹University of Edinburgh, UK

²Synchrotron SOLEIL, France

³University College Dublin, Ireland

⁴National Museums Scotland, UK

The c. 407 Ma-old Rhynie chert of Aberdeenshire hosts one of the world's most iconic and complete fossil ecosystems: plants, algae, fungi, bacteria, animals and protists all preserved organically in 3D with intact cellular and subcellular details. We have recently used *in situ* Fourier transform infrared spectroscopy (FTIR) to show that these fossils also retain palaeobiologically informative chemical signatures. For example, multivariate statistics and machine-learning approaches applied to FTIR spectra correctly classify Rhynie organisms of known affinity while helping to resolve more ambiguous taxa (*e.g.* nematophytes). Here we present the first application to fossil material of a new spectroscopic technique: optical photothermal infrared spectroscopy (O-PTIR). O-PTIR achieves molecular characterization at an extremely fine spatial resolution (~100 nanometres) and overcomes many of the challenges previously associated with bench-top FTIR spectroscopy. We show that O-PTIR can be used to map the molecular composition and spatial heterogeneities of small organic fossils in the Rhynie chert. For example, such heterogeneities in the cuticle on an Aglaophyton plant suggest a compositional organization comparable to modern



plants. These results validate these approaches as powerful tools for analytical palaeontology of chert-hosted biota and provide a strong positive control for the interpretation of older, more ambiguous, assemblages.

Convergent ventral adaptations for enrolment in trilobites, crustaceans and millipedes – insights from the Middle Ordovician Walcott-Rust Lagerstätte

***Sarah Losso, Pauline Affatato, Karma Nanglu and Javier Ortega-Hernández**

Harvard University, USA

Trilobites with preserved appendages were originally discovered from the Walcott-Rust Quarry (New York, USA) by Charles D. Walcott in the 1870s, but the calcite cast preservation proved difficult to interpret due to the three-dimensional structures being prepared as two-dimensional thin sections. Appendicular morphology of the trilobites *Ceraurus pleurexanthemus* and *Flexicalymene senaria* was controversial with various authors proposing spiral branchiae, presence or absence of endites, exopodites with up to seven segments. Comprehensive study of thin sections from the Walcott-Rust Quarry allows for more accurate understanding of the three-dimensional morphology, functional morphology and comparisons with extant euarthropods. Here we present updates to the appendages of *C. pleurexanthemus* and *F. senaria* including subtriangular protopodites with gnathobasal spines and long endites along the ventral edge. The exopodite of *C. pleurexanthemus* is composed of a proximal and distal lobes with dumbbell-shaped lamellae extending from the posterior edge of the former. The updated exopodite morphology of *C. pleurexanthemus* closely resembles that of the early Ordovician *Anacheirus adserai* from Morocco, showing conservation within the clade. Both *C. pleurexanthemus* and *F. senaria* exhibit wedge-shaped protopodites in cross section, allowing for complete enrolment of the body. One specimen preserved sternites in an enrolled position, demonstrating convergent evolution between trilobites, isopods and millipedes.

An early Palaeozoic ostracod psychrosphere?

***Anna McGairy^{1,4}, Christopher P. Stocker¹, Mark Williams¹, Phong Duc Nguyen², Thomas H. P. Harvey¹, Toshifumi Komatsu³ and C. Giles Miller⁴**

¹University of Leicester, UK

²Vietnam Institute of Geosciences and Mineral Resources, Vietnam

³Kumamoto University, Japan

⁴Natural History Museum, London, UK

Ostracods have been used as key biogeographical index species for the early Palaeozoic due to their assumed benthic ecology and lack of pelagic larval stage. However, some ostracod taxa do not appear to conform to this pattern, and are palaeogeographically widespread. Here we analyse a new ostracod assemblage from the Upper Ordovician (Katian, c. 453 Ma) of northern Vietnam, preserved *in situ* in sedimentary deposits from a deeper marine arc setting, below storm wave base, but with oxygenated bottom-water conditions. Whilst all the ostracod species appear to be endemic to the South China palaeo-plate, at least four of the genera are very widespread, being known from distant palaeocontinents including Baltica and Laurentia. The deep-marine shelf setting, together with the occurrence of Baltic and Laurentian-affinity taxa, suggests that a component of this fauna is



representative of an early ostracod radiation into psychrospheric (cold, deeper-water) environments. Therefore, future studies may need to distinguish palaeobiogeographically-informative, shallow-shelf taxa from more cosmopolitan, deep-water forms.

‘morphospace’: an R package for building and depicting multivariate ordinations of shape data

Pablo S. Milla Carmona^{1,2}, Oscar E. R. Lehmann³, William J. Deakin¹, Eduardo M. Soto², Ignacio M. Soto², Philip C. J. Donoghue¹ and Emily J. Rayfield¹

¹*University of Bristol, UK*

²*Universidad de Buenos Aires, Argentina*

³*Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Argentina*

Methods for the rigorous assessment of morphology are essential for palaeontologists. In particular, geometric morphometrics (GM) emerges as a powerful framework for the statistical analysis and visualization of morphological variation that allows devising and testing a range of taxonomic, ecological and evolutionary hypotheses. The implementation of landmark- and outline-based approaches within programming environments such as R has enabled incorporation of GM with other statistical and graphical methods into fully integrated workflows with improved reproducibility. Here we present ‘morphospace’, an R package specifically devoted to building and depicting multivariate ordinations of shape data. This package integrates a series of tools aiming to generate insightful visualizations that facilitate heuristic exploration of morphological patterns. Three main aspects of the ‘morphospace’ workflow are outlined: data refinement, or the analytical removal of variational ‘noise’ introduced by unwanted sources; multivariate ordination, which summarizes high-dimensional shape spaces by reorganizing variation – a process that can be ‘supervised’ by non-shape information to improve interpretation; and projection of different elements into the resulting axes, including theoretical shapes, convex hulls, confidence ellipses, phylogenetic relationships, shape vectors and landscapes. This workflow is illustrated using two examples of fossil bivalves from Argentina, quantified as elliptic Fourier and 3D landmark data, respectively.

The nature of the last universal common ancestor and its impact on the early Earth system

Edmund R. R. Moody¹, Holly Betts¹, James Clark¹, Nina Dombrowski⁴, Stuart Daines², Richard Boyle², Xi Chen³, Graham A. Shields³, Gergely Szöllösi⁵, Anja Spang⁴, Davide Pisani¹, Tom A. Williams¹, Timothy M. Lenton² and Philip C. J. Donoghue¹

¹*University of Bristol, UK*

²*University of Exeter, UK*

³*University College London, UK*

⁴*Royal Netherlands Institute for Sea Research (NIOZ), Netherlands*

⁵*Eötvös Loránd University, Hungary*

The nature of the last universal common ancestor (LUCA), its age and impact on the Earth system have been the subject of vigorous debate among diverse disciplines based on disparate data. Age estimates for LUCA are usually based on the fossil record, varying with every reinterpretation.



The nature of LUCA's metabolism has proven equally contentious, with some attributing all core metabolisms to LUCA, while others infer it to have been half alive, subsisting only with the aid of geochemistry. Here we show, using a set of pre-LUCA gene duplications, calibrated with eukaryote fossils to infer that LUCA was older than 3.9 Ga, thus predating the end of the Late Heavy Bombardment. We estimated a 1.24 Mb genome for LUCA encoding 1,297 proteins including metabolic genes similar to that of modern prokaryotes. Specifically, LUCA was inferred to be a thermophilic, anaerobic organism encoding the Wood-Ljungdahl pathway (WLP) supporting growth as an acetogen. Furthermore, we infer the presence of an early CRISPR-cas anti-viral defence system. Thus, our results support the hypothesis of the importance of hydrogen-fuelled metabolisms in this early ecosystem in which LUCA thrived, and the likely metabolic functional types with which LUCA coexisted.

Ontogeny and tooth replacement in the Brazilian cynodont *Brasilodon quadrangularis*

Nuria Melisa Morales Garcia¹, Agustin G. Martinelli², Pamela G. Gill^{1,3}, Heitor Francischini⁴, Pedro H. Fonseca⁴, Ian J. Corfe^{5,6} and Emily J. Rayfield¹

¹University of Bristol, UK

²Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina

³Natural History Museum, London, UK

⁴Universidade Federal do Rio Grande do Sul, Brazil

⁵University of Helsinki, Finland

⁶Geological Survey of Finland, Finland

Brasilodon quadrangularis is a probainognathian cynodont from the Late Triassic (Norian) of southern Brazil that is phylogenetically positioned close to Mammaliaformes. This taxon is based upon several skulls and isolated jaws, including the junior synonyms *Brasilitherium riograndensis* and *Minicynodon maieri*, from a range of ontogenetic stages. To investigate the tooth replacement pattern in *Brasilodon*, several specimens were micro-CT scanned. We observed that: postcanines vary from five to seven functional tooth positions, with the loss of at least four anterior postcanines during ontogeny (indicating at least 11 positions during life); there is more than one tooth replacement at anterior loci in juvenile forms, and the diastema enlargement is a result of the loss of incisor-like canines of juveniles and the anteriormost postcanine teeth; as the middle postcanines are replaced alternately, new posterior postcanines are added; and larger individuals have a more disparate postcanine morphology than smaller individuals, indicating that replaced teeth are simpler than new ones. These data demonstrate that *Brasilodon* has not acquired a diphyodont tooth replacement, which is a major apomorphy for mammaliaforms. Tooth replacement mechanisms amongst non-mammaliaform cynodonts are highly diverse, and *Brasilodon* indicates a unique replacement pattern among probainognathians, sharing resemblances with *Sinoconodon*.



The virtual endocast of the Late Miocene hedgehog *Postpalerinaceus vireti* (Eulipotyphla, Mammalia)

Raquel Moya Costa^{1,2}, Ornella C. Bertrand², Àngel H. Luján^{2,3}, Isaac Casanovas-Vilar² and Marc Furió^{2,4}

¹Universidad de Zaragoza, Spain

²Institut Català de Paleontologia Miquel Crusafont, Spain

³Masaryk University, Czechia

⁴Universitat Autònoma de Barcelona, Spain

The holotype of the erinaceid *Postpalerinaceus vireti* is an almost complete cranium from the site of Can Trullars 1 (Late Miocene; Viladecavalls, Spain). We reconstructed the virtual brain endocast of *P. vireti* to study it from a palaeoneurological perspective. The cranium was scanned using microcomputed tomography and segmented to generate the brain endocast. Then, we measured the volumes of different brain regions and estimated the body mass and the encephalization quotient for this specimen. We applied the same methodology to a representative sample of extant erinaceids and other eulipotyphlans. Our results show that the total volume of the brain endocast of *P. vireti* is approximately 3.4 cm³, the olfactory bulb volume ratio is 10 % and the petrosal lobe volume ratio 0.7 %. These values are similar to extant erinaceids. The estimated body mass is close to 1 kg, which is relatively heavy for an erinaceid. This results in an encephalization quotient of 0.36, which is lower than values observed in extant erinaceids (0.48–0.72), and closer to the basal eulipotyphlan *Solenodon* (0.40). The brain endocast of *P. vireti* is morphologically similar to extant erinaceids, suggesting that vision and olfaction may have been relatively static in Erinaceinae since the Late Miocene.

Integration and modularity in the Cambrian diversification of arthropods

***Joseph Moysiuk^{1,2} and Jean-Bernard Caron^{1,2}**

¹University of Toronto, Canada

²Royal Ontario Museum, Toronto, Canada

Varied explanations for the Cambrian Explosion, such as changing ecological opportunity or developmental constraints, have been proposed. The latter is particularly challenging to test since we lack direct access to developmental systems of extinct species. However, integration or modularity of morphological traits – describing their relative covariation or independence – can provide a proxy for underlying developmental interactions. Trait integration is expected to constrain accessible morphospace relative to the case in which the same traits are modular. We developed a novel approach to quantify the evolution of both integration/modularity and disparity in arthropod appendages since the Cambrian. We generated superimposed phylomorphospaces for the first five appendage pairs of fossil and extant arthropods (124 taxa and 57 discrete characters). We measured integration as the correlation of phylogenetic trajectories between adjacent appendages in morphospace. Integration is higher on average in the Cambrian than in the post-Cambrian. Between ancestral and descendent nodes, integration is associated with marginally reduced range expansion in morphospace, but also surprisingly with higher centroid displacements. This suggests that while integration may restrict the directions of morphological change, it can also increase directional divergence between lineages, indicating that it could have contributed to the rapid divergence of major arthropod clades.



Landmark-free morphometrics suggests different paths of mammalian evolution through the Cenozoic

***James M. Mulqueeney**^{1,2}, **Thomas H. G. Ezard**¹ and **Anjali Goswami**²

¹*University of Southampton, UK*

²*Natural History Museum, London, UK*

Quantifying anatomical shape is crucial for understanding phenotypic evolution. Traditionally, this has been achieved through 3D geometric morphometrics using manual landmark placement. However, these methods are time-consuming, prone to observer bias, and lack repeatability. New automated approaches have emerged to address these limitations, including automated landmarking and landmark-free techniques. Nevertheless, the effectiveness of rapid automated approaches at higher taxonomic levels remains largely untested. In this study, we compared manual and automated approaches applied to 322 craniums of crown and stem placental mammals to evaluate the trade-offs in speed, repeatability and accuracy. The results demonstrate significant similarities in shape variation patterns, but the landmark-free methods show less constrained variation than their landmark-based counterparts, indicating differences between the two approaches. These differences may be attributed to the landmark-free methods' ability to analyse continuous structures rather than discrete points. The findings highlight the robustness of automated methods for large-scale data analysis, providing repeatable results in a shorter time-frame, enabling the analysis of larger datasets across a wider range of taxonomic groups and research areas.

Euarthropod horseshoe carapace convergence shaped by hydrodynamics?

Stephen Pates¹ and **Harriet B. Drage**²

¹*University of Cambridge, UK*

²*University of Lausanne, Switzerland*

Euarthropods with horseshoe-shaped carapaces have lived in the oceans near continuously for over 500 million years, with this carapace shape having evolved multiple times within the group; for example in trilobites, radiodonts and horseshoe crabs. The vaulted semi-circular carapace is considered an adaptation to a benthic marine lifestyle, which in horseshoe crabs facilitates positive lift avoidance, increases stability and prevents overturning. However, the extent to which the horseshoe-shaped carapaces of trilobites, radiodonts and horseshoe crabs are morphologically and/or hydrodynamically similar has not yet been quantified. Thus, the extent to which this similarity represents convergent evolution resulting from hydrodynamic pressures of a benthic mode of life remains unresolved. We modelled the carapace morphology of these three groups in 2D and 3D using outline analysis and surface semi-landmark analysis, respectively. The hydrodynamic importance of certain features, such as carapace brim width and angle, length of posterior projections and convexity of the carapace were then tested using computational fluid dynamics simulations. We thereby quantified the extent of convergence between these groups, and determined the role of a horseshoe-shaped carapace morphology in facilitating a benthic life mode for euarthropods from the Cambrian to the present day.



Evolution in the mesopelagic twilight zone is regulated by a temperature-dependent biological pump

Paul N. Pearson¹, Bridget S. Wade¹, Flavia Boscolo-Galazzo², Katherine Crichton³, Tom Dunkley Jones⁴, Eleanor John⁵, Amy Jones⁴, Andy Ridgwell⁶ and Jamie Wilson⁷

¹University College London, UK

²MARUM, University of Bremen, Germany

³University of Exeter, UK

⁴University of Birmingham, UK

⁵Cardiff University, UK

⁶University of California, Riverside, USA

⁷University of Liverpool, UK

Environmental temperature is a master variable in ecology because metabolic rates approximately double with every 10°C while respiration is significantly more temperature-dependent than photosynthesis. This has far-reaching consequences when Earth's climate shifts between warm and cold modes. One instance is the ocean's 'biological pump', wherein organic matter is fixed in the photic zone and sinks to deliver food to mesopelagic habitats and the sea floor. We developed a new temperature-dependent configuration of the Earth system model cGenie to show how refrigeration of the ocean interior during global cooling since the Eocene slowed decomposition, improved subsurface food supply and reduced extreme oxygen depletion. Site-by-site, we linked this to the globally distributed fossil record of depth-stratified calcareous microplankton (foraminifera and algae) to explain large and hitherto unexplained changes in depth distribution and carbon geochemistry. Cenozoic cooling steps increased deep ocean biomass, produced new habitats and promoted speciation. Unusual phylogenetic patterns of groups from ctenophores to pelagic fish may also be explained by relatively recent bursts of evolution in deep-dwelling habitats. Our work reveals how anthropogenic ocean warming currently threatens the twilight zone and has implications for the deep sea fossil record across other climate transitions in Earth history.

Repeated evolution of extreme sabre-tooth morphology explained by optimality

Tahlia Pollock^{1,2}, William J. Deakin¹, Narimane Chatar³, Pablo S. Milla Carmona¹, Olga Panagiotopoulou², William M. G. Parker², Douglass S. Rovinsky⁴, Justin W. Adams^{2,5}, David P. Hocking⁶, Philip C. J. Donoghue¹, Emily J. Rayfield¹ and Alistair R. Evans^{2,5}

¹University of Bristol, UK

²Monash University, Australia

³Université de Liège, Belgium

⁴Australian Museum, Australia

⁵Museums Victoria, Australia

⁶Tasmanian Museum and Art Gallery, Australia

'Sabre teeth' – elongate blade-like canines – have evolved repeatedly throughout mammalian history. However, the functional drivers of this reoccurring morphology remain unclear. To effectively bite into prey, all canine teeth must strike a balance between being slender enough to reduce puncture force, while being sufficiently robust to resist breakage. We explored this trade-off in sabre-tooth canines by comparing these against teeth from living carnivores, integrating



three-dimensional shape data with mechanical performance metrics within a functional optimality framework. Shape was captured via 3D geometric morphometrics in a sample representing 67 non-sabre and 21 sabre-tooth species. We then quantified two mechanical performance metrics in a subset of teeth, applying finite element analysis to model tooth stress and undertaking physical puncture tests to quantify puncture force. These data were combined using a Pareto rank approach, constructing an adaptive landscape to assess optimality. Extreme sabre-tooth forms, like *Smilodon*, *Barbourofelis* and *Thylacosmilus*, exhibit a combination of slenderness, lateral compression and curvature not found in living carnivores, resulting in high stress values and low puncture forces. Interestingly, this form sits on a peak of optimality in our adaptive landscape suggesting high adaptive value, which may help to explain the repeated evolution of this iconic morphology.

Epibionts and trace fossils on stem- and crown-group euarthropod carapaces from the Early Ordovician Fezouata Shale

***Jonathan Pople, Gaëtan J.-M. Potin and Allison C. Daley**

University of Lausanne, Switzerland

The Early Ordovician Fezouata Shale of Morocco is a Burgess Shale-type Lagerstätte providing a unique record of soft-bodied organisms during the transition from the Cambrian Explosion to the Ordovician Radiation. Stem- and crown-group euarthropods are highly diverse in the Fezouata Shale and include giant suspension-feeding radiodonts. A survey of hundreds of specimens has revealed that arthropod carapaces, especially those of radiodonts, attracted sessile epifauna, the most abundant of which is an indeterminate brachiopod species interpreted as an ectosymbiont of living giant nektonic radiodonts based on its exclusive association and implied long development. Less common epibiotic taxa include the conulariid *Eoconularia*, the brachiopod *Nanorthis* and the tubular fossil *Sphenothallus*. Non-mineralized arthropod carapaces from Fezouata are also associated with abundant burrows preserved as positive and negative imprints. These are simple, shallow-tier structures that sometimes form dense assemblages, and are interpreted to represent the activity of small endofauna grazing on microbial mats growing on decaying carapaces. A preservational model for these traces is proposed, whereby bioturbation-driven deformation of microbial mats associated with carapaces is preserved by cementation and differential compaction. Traces from the Fezouata Shale are comparable to those in Cambrian assemblages, but reach much larger sizes, reflecting the increased size of substrate carapaces.

Early tetrapod jaw shape and mechanical performance during the water-land transition

Laura B. Porro¹ and Emily J. Rayfield²

¹*University College London, UK*

²*University of Bristol, UK*

The colonization of the land by vertebrates was a key moment in the history of life, marked by dramatic changes in skull shape, sutures, the size and distribution of teeth, and jaw muscle arrangement. These changes are assumed to be associated with new feeding mechanisms and diets, and/or differing environmental constraints. We explore the anatomy and mechanics of



fossil tetrapod lower jaws spanning the water-land transition – from the Late Devonian to Early Triassic – as well as those of extant relatives and analogues. High-resolution CT scanning was used to capture lower jaw shape – including sutures – and damage and deformation removed to produce three-dimensional models of the lower jaws of such iconic taxa as *Eusthenopteron*, *Acanthostega*, *Crassigyrinus* and others. Finite element analysis was applied to these models to test the mechanical response of the lower jaws to feeding loads. Results suggest complex shifts in the relative strength of the lower jaw through the lineage. Basal taxa exhibited high stress on the biting side, whereas the highest stresses occurred on the balancing side of more derived taxa, potentially linked to changes in symphyseal morphology, which permitted greater force transfer from balancing side jaw muscles to the bite point.

Melanosome geometry informs on the functional evolution of melanin in Reptilia and Amphibia

***Aaron Quigley¹, Beatriz Carazo del Hoyo¹, Daniel Cirtina¹, Catherine McCarney², Jane Brennan², Soudeh Ziapour² and Maria E. McNamara¹**

¹University College Cork, Ireland

²University College Dublin, Ireland

Melanosomes are melanin-rich organelles that, in extant vertebrates, occur in the integument, eyes and internal tissues. Although melanin underpins critical physiological functions, certain fundamental aspects of melanin biology remain poorly understood. Previous studies reported tissue-specific melanosome geometries in a limited number of extant vertebrates. Whether that dataset is representative of vertebrates more broadly is unclear. To test this, our new expanded dataset incorporates 18 taxa and 11 tissue types, including three tissue types not studied previously. We used an enzymatic digestion process to extract melanosomes from 143 tissues from four reptile and two amphibian taxa, yielding 86 melanin extracts. Scanning electron microscopy and image analysis in *ImageJ* confirms tissue-specific melanosome geometry in Reptilia and Amphibia, thus validating existing models. The range of melanosome geometries observed is consistent with that previously reported in amphibian and reptilian tissues but is distinct from melanosome geometries in mammals and birds. This suggests high-level taxonomic controls on the biology of non-integumentary melanosomes. Future work combining data on melanosome chemistry and geometry may shed light on the biological controls underlying these trends and on the functional evolution of melanin through deep time.

Enigmatic Silurian jawless vertebrate *Lasanius* evaluated with new synchrotron data

***Jane Reeves¹, Roy A. Wogelius¹, Joseph N. Keating², Phillip L. Manning¹ and Robert S. Sansom¹**

¹University of Manchester, UK

²University of Bristol, UK

The fossil record of non-biom mineralizing taxa is our only direct evidence of early vertebrate history. Robust reconstruction of their affinities is critical to unlocking vertebrate origins and the



evolution of skeletal tissues, but these taxa invariably have unstable, poorly supported phylogenetic positions. At the cusp between mineralized bony vertebrates and entirely soft-bodied vertebrates is the enigmatic *Lasanius*, a purported anaspid from the Silurian of Scotland. Our analysis using traditional methods has been powerful in reconstructing aspects of its morphology and putatively identifies *Lasanius* as a biomineralizing cyclostome, raising important questions about the nature of *Lasanius* tissues and the timeline of vertebrate biomineralization. Here we present new data from synchrotron-XRF analysis and CT-scanning. We identify distinct regional differences in the unusual 'cage-like' torso biomineralized area: evidence for potential functional differentiation. This supports previous interpretations of this structure as two anatomical features, a branchial region and an ambiguous feature. The findings have implications for the evolution of respiratory structures in cyclostomes and vertebrates and may support modularity in the origin of fins. The work demonstrates a link between early gnathostome and cyclostome anatomy, reducing the morphological gap, and highlights how focusing on key taxa can dramatically improve our knowledge of evolutionary events.

A new luolishaniid from the early Ordovician and the autecology of suspension feeding lobopodians

***Jared Richards and Javier Ortega-Hernández**

Harvard University, USA

Lobopodians are a diverse clade of soft-bodied, vermiform marine invertebrates crucial to understanding panarthropod evolution in deep time. We describe a new luolishaniid lobopodian from the early Ordovician Fezouata Shale biota of Morocco with adaptations for suspension feeding. The Fezouata Shale luolishaniid features at least nine relatively robust and annulated limb pairs. The five anterior-most limb pairs are elongated with setiform structures emerging from either side of the limb in a chevron pattern. The remaining posterior limb pairs are shorter and likely end in a terminal claw. The Fezouata Shale lobopodian extends the evolutionary history of luolishaniids, previously only known from early and mid-Cambrian deposits in North America, South China and South Australia. We also explore the autecological implications of the suspension feeding morphology of all described luolishaniid taxa. Luolishaniids sifted particles and organisms out of the water column that are on the larger end of the micro-planktonic spectrum (20 μm – 200 μm) and on the smaller end of the meso-plankton spectrum (200 μm – 20 mm). We find a statistically significant, positive relationship between luolishaniid maximum body size and setae mesh size, suggesting that larger luolishaniids specialized on meso-plankton while smaller taxa specialized on micro-plankton.

Organic-walled microfossils of the late Palaeoproterozoic Limbunya Group and implications for early eukaryotic evolution

Leigh Anne Riedman¹, Susannah M. Porter¹, Angelo Dos Santos², Maxwell A. Lechte² and Galen P. Halverson²

¹*University of California, Santa Barbara, USA*

²*McGill University, Canada*

Fine-grained siliciclastic units of the $>1642\pm 3.9$ Ma Limbunya Group, northern Australia host a rich and well-preserved organic-walled microfossil assemblage that includes several known



and several new, likely eukaryotic, taxa. These include process-bearing taxa such as *Tappania plana*, *Gigantosphaeridium fibratum* and *G. floccosum*; platy taxa such as *Satka favosa* and a newly described tubular, platy form; lined taxa such as *Valeria lophostriata*, *V. elongata* and *Spiromorpha segmentata*; a new operculate taxon and a large septate filamentous form. Considering the morphological characters of these fossil taxa in context of modern protists with similar features, we suggest a late Palaeoproterozoic minimum age for eukaryotic cytoskeletons, endomembrane systems and Golgi bodies. We also present a new within-assemblage richness estimate for Palaeoproterozoic through to Tonian units, focusing on organic-walled microfossils likely to have been eukaryotic. This estimate indicates that the oldest eukaryote-bearing units already show species richness levels similar to those of the much younger and more heavily sampled Tonian period. Further, even the oldest eukaryotic assemblages display significant morphological disparity, particularly in vesicle construction. These high levels of eukaryotic species richness and morphological disparity suggest that although late Palaeoproterozoic units are our oldest record of eukaryotes, the total-group eukaryotic clade has a much deeper history.

The secret history of sea spiders (Arthropoda: Pycnogonida)

Romain Sabroux¹, Morena Nava^{1,2}, Gregory D. Edgecombe³, Russell J. Garwood^{3,4}, Philip C. J. Donoghue¹, Derek J. Siveter⁵, Denis Audo⁶, Derek E. G. Briggs⁷, David J. Siveter⁸, Mark D. Sutton⁹, Sylvain Charbonnier⁶, Laure Corbari⁶, Alexandre Hassanin⁶ and Davide Pisani¹

¹University of Bristol, UK

²University of Milano-Bicocca, Italy

³Natural History Museum, London, UK

⁴The University of Manchester, UK

⁵University of Oxford, UK

⁶Muséum national d'Histoire naturelle, Paris, France

⁷Yale University, USA

⁸University of Leicester, UK

⁹Imperial College London, UK

Sea spider fossils (Chelicerata: Pycnogonida) are restricted to eleven species sparsely distributed from the Silurian to the Jurassic. Their morphology and relationships to extant pycnogonids are poorly understood. To improve their description, nest them in the chelicerate phylogeny and decipher the timing of Pycnogonida's evolution, we conducted a comprehensive reinvestigation of the sea spider fossil record. We studied approximately 60 fossils, published or new, from the Konservat-Lagerstätten of Herefordshire, UK (Silurian), the Hunsrück Slate, Germany (Devonian), La Voulte-sur-Rhône, France and Solnhofen, Germany (Jurassic). Using X-ray microtomography, Reflectance Transformation Imaging, serial grinding and microtopography, we illustrate the past diversities of Pycnogonida. We show that while Palaeozoic fossils exhibit a stunning diversity of forms and adaptations unmatched in extant species, Mesozoic fossils share the same body plan as extant sea spiders, suggesting they belong to the crown-group Pycnogonida, *i.e.* Pantopoda. By performing the first total-evidence phylogeny of Chelicerata including the eleven sea spider fossil species, we further support our taxonomic interpretations. We demonstrate that Mesozoic fossils are nested within extant families or superfamilies, while Palaeozoic species belong to the stem-group Pycnogonida. Finally, we date the phylogeny of Pycnogonida using both node-dating and tip-dating strategies and estimate the divergence time of major Pycnogonida lineages.



Two new Lagerstätten shed light on Ordovician animal ecosystems

Farid Saleh

University of Lausanne, Switzerland

Lagerstätten, with their exceptional fossil preservation, provide more comprehensive insights into past ecosystems compared to those that preserve shells and bones. While Lagerstätten are highly abundant from the Cambrian period, their numbers decrease thereafter. In this study, we present two recently discovered Lagerstätten. One site originates from Early Ordovician strata of France, while the other is located in the Middle Ordovician of Morocco. The French site exhibits a dominant presence of algae, sponges, trilobites, bivalved arthropods, and contains some chelicerates. It also preserves armoured lobopodians, indicating their survival beyond the Cambrian–Ordovician boundary. Echinoderms are absent from this Lagerstätten but are very abundant and diverse in the Middle Ordovician Moroccan site, which represents a slightly older lateral extension of the Tafilalt Biota previously known from Upper Ordovician strata. Within the Moroccan site, a clear differentiation in body size is observed across different environments, and mineralized taxa such as trilobites, hyolithids and cnidarians are preserved in high detail within certain facies. This site has yielded non-biomineralized arthropods. Numerous fragments of an enigmatic organism are also abundantly preserved, and they may potentially represent fragments of the earliest placoderm fish.

Life after death: characterizing the microbial communities responsible for decomposition and fossilization

Robert S. Sansom, Christopher Boothman and Sophie L. Nixon

The University of Manchester, UK

Microbes play a fundamental role in the degradation of organic matter, but their role is poorly characterized in the context of fossil formation. The action, and inaction, of bacteria has been central to a wide range of hypotheses relating to preservation of soft-tissue fossils. However, very little is known about the marine ‘necrobiome’, *i.e.* the community of organisms associated with decay. We undertook experiments to directly characterize the microbes responsible for the post-mortem decay of plant and animal tissues in marine sediments, both fresh and sterile. We extracted DNA from decaying tissues and used 16S rRNA gene sequencing to identify the bacterial communities. Results enabled us to survey the succession of bacterial taxa as decay progressed over 56 days in a laboratory environment, and to contrast the decay of plants and animals in terms of endogenous and environmental microbial sources. Characterizing these necrobiome communities is an important first step towards constraining and testing hypotheses of exceptional soft-tissue preservation and fossilization processes.



Carboniferous wildfire revisited: wildfire, post-fire erosion and deposition in a Mississippian crater lake

Andrew C. Scott

Royal Holloway University of London, UK

Fires have been shown to have been common in many Carboniferous ecosystems worldwide, yet we still have little understanding of the detail of what, where and how such fires occur or indeed their effects both on the local ecosystem as well as on the Earth system as a whole. The Kingswood Limestone, of late Viséan (Mississippian) age, found near Pettycur in Fife, Scotland, is interpreted as being deposited within a crater lake. The limestone contains a range of volcanic clasts together with charcoaled and uncharred plants. Two distinctive communities existed. One dominated by the herbaceous lycopsid *Oxroadia* that is permineralized, and one dominated by a range of pteridosperms and other gymnosperms preserved as charcoal. Fires surrounding a crater lake charred the plants that were then washed into the lake by post-fire erosion. All plant organs are found as charcoal including woody axes, leaves, pollen organs and ovules. *Oxroadia* that was living close to the lake was not affected by fire. Rising lake and sea levels allowed saline water to be introduced to the lake and connection to the sea was established. Many new charcoaled plants have still to be formally described.

From the tiny ant to the elephant: engineering impacts of the vertebrate and invertebrate denizens of Mesozoic terrestrial ecosystems

Anthony Shillito and Maximiliano Paz

University of Saskatchewan, Canada

Invertebrates and vertebrates both affect the world around them in significant, but often different, ways. Invertebrates make up the vast majority of bioturbating organisms, recycling nutrients and increasing connectivity between the atmosphere and geosphere. With their greater size and mass, vertebrates frequently act as geomorphic agents, altering landscapes through the direct and indirect consequences of their behaviours. The Mesozoic is considered as the age of dinosaurs, when terrestrial vertebrates were at their largest. However, during this interval, terrestrial invertebrate diversity dramatically increased, and their engineering impacts were magnified as they occupied new niches. We will discuss the ways in which animals sculpted their surroundings using two case studies: the Jurassic Lastres Formation, Spain, and the Cretaceous Ashdown Formation, UK. Studies on the Lastres Formation have largely focused on its exceptional record of dinosaur footprints, with evidence for extensive dinoturbation. However, the formation also bears a high diversity of invertebrate ichnofauna, recording the significant ecological impacts of bioturbating arthropods and molluscs. The Ashdown Formation has also been recognized for its diverse dinosaur ichnofauna, with less attention paid to the corresponding invertebrate traces. Here we will consider how the engineering impacts of the dinosaurs and invertebrates combine to form the complete picture.



Ecosystem structural changes following a marine megafaunal extinction

***Amy E. Shipley¹, Tracy Aze¹, Catalina Pimiento^{2,3}, Andrew P. Beckerman⁴, Jennifer A. Dunne⁵, Jack O. Shaw⁵ and Alexander M. Dunhill¹**

¹University of Leeds, UK

²University of Zurich, Switzerland

³Swansea University, UK

⁴University of Sheffield, UK

⁵Santa Fe Institute, USA

Despite increasing threats of extinction, it is not well understood how marine ecosystems may be impacted following losses of taxa in different trophic levels. Reconstructing extinct ecosystems can inform on how community dynamics shift following extinction events. An end-Pliocene marine extinction resulted in global losses of megafauna, including the giant apex predator *Otodus megalodon*. Using a trait-based model, we constructed metacommunity webs for pre- and post-extinction North Atlantic communities. Using this method, we found similar distributions of taxa to those found in modern marine ecosystems, with *O. megalodon* at the top of the web in trophic level 6. This trophic role appears not to be replaced in the Pleistocene. As modern food webs exhibit a standard link distribution across trophic levels, we enforced this distribution on the constructed metacommunity webs by randomly removing links, producing 50 iterations of these 'realized' webs for both time bins. Our analyses indicate consistency in structure across the extinction in the metacommunity and realized webs, suggesting this ecosystem was robust to losses in higher trophic levels. However, a slight decrease in vertical complexity and increase in generalism in the Pleistocene could indicate a drop in primary productivity, a potential driver for this extinction event.

Current issues with conodont tissues

***Bryan Shirley^{1,2} and Emilia Jarochovska¹**

¹Utrecht University, Netherlands

²Friedrich-Alexander-Universität Erlangen-Nürnberg, Germany

Understanding the histology, chemistry and crystallography of biominerals unlocks valuable information on the growth, ecology and function of the organisms that created them. Conodonts are a highly diverse group of vertebrates that thrived in prehistoric oceans and are widely known from their teeth. The structure and chemical composition of these teeth are universally used to reconstruct palaeoenvironments and the animal's ecology. The teeth grew by lateral accretion of enamel-like hydroxyapatite throughout the animal's life which provides a somewhat continuous record of growth. A key innovation in conodont evolution was the appearance of hypermineralized enamel analogue, the hyaline crown tissue. Many taxa also bear a type of tissue unique to this group, the white matter, which often appears as single porous crystals filling entire tooth denticles. Although conodonts offer an astonishing sclerochronological record, the identification of their crown tissues has been based on, in the majority of cases, optical microscopy. We undertook a systematic analysis of conodont crown tissues in terms of *in situ* crystallography, Raman spectroscopy and backscatter electron microscopy. Here we re-evaluate previous descriptions of these tissues while highlighting the conodonts' unrivalled ability to regenerate their teeth and restore their function.



Temporal trajectory of geographic occupancy is an informative predictor of extinction risk across fossil microplankton taxa

Isaiah Smith, Ādám T. Kocsis and Wolfgang Kiessling

Friedrich-Alexander-Universität Erlangen-Nürnberg, Germany

Although standing geographic occupancy (range) is frequently acknowledged as an important extinction risk factor, the trajectory of geographic occupancy through time is not always considered. The extinction risk of four microplankton groups – foraminifera, calcareous nannofossils, radiolarians and diatoms – was examined with respect to their occupancy and the temporal trajectory of their occupancy, based on their record in the Neptune Sandbox Berlin database. Using logistic modelling, the relationship between occupancy, occupancy change and extinction was explored for each group. Relative importance and the proportion of total deviance reduction attributable to each model term were calculated for each dataset. Our findings confirm that the temporal trajectory of geographic occupancy is an important predictor of extinction risk. Additionally, the relative importance of occupancy trajectory in predicting extinction is approximately four times higher in siliceous microplankton than in calcareous microplankton. We suggest that the more opportunistic life mode of siliceous microplankton might contribute to this difference. The fact that temporal trajectory of occupancy can be used as an informative predictor of extinction risk demonstrates the utility of incorporating palaeontological data into modern conservation efforts.

A look inside the ancestral arthropod

Martin R. Smith¹, Emma J. Long^{1,2,3}, Alavya Dhungana¹ and Katherine J. Dobson^{1,4}

¹*Durham University, UK*

²*Natural History Museum, London, UK*

³*University of Exeter, UK*

⁴*University of Strathclyde, UK*

Arthropods are one of the most enduringly successful animal phyla, and their rapid diversification epitomizes the Cambrian Explosion. Their colonization of diverse lifestyles and ecologies is made possible by the adaptable feeding appendages of the differentiated head. To understand arthropod head evolution, it is necessary to resolve the ambiguous segmental affinity of the head, and to correctly interpret the contested brains and nervous tissue in Burgess Shale-type compression fossils. Developmental data can resolve such issues in extant arthropods, but are unavailable for fossil taxa. X-ray tomography of a three-dimensionally preserved larva from Chengjiang-age phosphorites provides the first snapshot into the early development of stem-group euarthropods. Its lobopod appendages, midgut glands and a ventral mouth demonstrate a close relationship with gilled lobopodians. The anatomy of its sophisticated circulatory system suggests that putative nervous tissue in certain Cambrian macrofossils in fact represents impressions of a lacunar haemolymph system. Internal voids replicate the structure of the single body segment that houses the brain. These data underpin a new model for the origin of brains in panarthropods through the dorsal elaboration of an ancestrally 'cycloneuralian-like' circumoral nerve ring.



Fossilization can mislead analyses of phenotypic disparity

***Thomas J. Smith^{1,2}, Robert S. Sansom³, Davide Pisani¹ and Philip C. J. Donoghue¹**

¹*University of Bristol, UK*

²*University of Oxford, UK*

³*The University of Manchester, UK*

Palaeontological datasets are routinely employed in analyses of morphological disparity that seek to understand how phenotypic variation changes through time. However, taphonomic processes introduce non-random patterns of data loss in fossil data and their impact on perceptions of disparity is unclear. To address this, we characterize how measures of disparity change when simulated and empirical data are degraded through both random and non-random data loss. We demonstrate that fossilization can misrepresent the disparity of clades, even when fossil taxa are unrealistically complete. These distortions vary depending on the combination of distance metric and disparity index used. Inclusion of extant and exceptionally preserved fossil taxa mitigates the effects of non-random patterns of data loss resulting from taphonomic processes on estimations of disparity. These reference taxa are essential for understanding the full extent of the data loss, most of which would otherwise go uncharacterized, as they facilitate the use of ancestral state estimation to control for these losses. Where this is not possible, we urge caution in the extrapolation of general patterns in disparity from palaeontological datasets that characterize subsets of phenotype, which may represent no more than the traits that they sample.

Bretskyan hierarchy – the structure and evolution of biota in time and space

Andrej Spiridonov¹ and Niles Eldredge²

¹*Vilnius University, Lithuania*

²*American Museum of Natural History, USA*

The dual hierarchy approach states that the biological world can be understood from two perspectives: i) hierarchy of economic entities, which are internally and externally interacting and clearly defined in space; and ii) the Linnaean or genealogical hierarchy which is a hierarchy of genetic information book-keeping and transfer without explicit functional significance or spatial and temporal structure. Here we present a complementary and hybrid in nature concept of the Bretskyan hierarchy of holobionts and geobiomes. All ecological interactions, as well as all genetic information transfer, is localized in space and time. The communities at many scales have both ecological and genealogical significance. At smaller scales such communities can merge into holobionts (strongly integrated polyphyletic individuals). At large scales this integration assumes a different nature: it is determined by geological spatio-temporal structures. Large scale polyphyletic biotic individuals exhibiting ecological and genealogical properties here are called geobiomes. This contribution explains how this hybrid hierarchy, which combines features of both eco- and genealogical hierarchies, and the hierarchy of abiotic structures can merge themes of the major transitions in evolution, megatrajectories in the history of life, and the whole range of other evolutionary patterns in a single multi-scale theoretical framework.



Evaluating homoplasy and evolutionary constraint in the passerine bird appendicular skeleton

***Elizabeth M. Steell¹, Neil Brocklehurst¹, Roger B. J. Benson², Matthieu Chotard³, Jacqueline Nguyen^{4,5} and Daniel J. Field¹**

¹*Department of Earth Sciences, University of Cambridge, UK*

²*American Museum of Natural History, USA*

³*The Chinese University of Hong Kong, Hong Kong*

⁴*Flinders University, Australia*

⁵*Australian Museum Research Institute, Australia*

Passeriformes (passerines) exhibit unparalleled diversity among crown birds, accounting for over 60 % of extant bird species. Passerines radiated rapidly into one of the most species-rich and widespread vertebrate groups in Earth history, yet disproportionately few studies have attempted to understand their skeletal evolution. Within the wing and hindlimb, the carpometacarpus and tarsometatarsus are proving to be particularly variable skeletal elements. However, passerine morphology exhibits considerable homoplasy, suggesting constraints to their evolution. Here we explore patterns of homoplasy in the passerine appendicular skeleton by analysing discrete character matrices of the carpometacarpus and tarsometatarsus with a novel metric, the Relative Homoplasy Index, as well as character state exhaustion analyses. We show that passerines generally endure significantly relaxed constraints to morphological evolution when the deepest divergences occur, suggesting rapid exploration of new morphologies early in their evolutionary history. However, oscines – the most diverse major subclade – show significant evolutionary constraint in the latter stages of lineage diversification, in contrast to their sister clade, the suboscines. This aligns with the patterns of homoplasy we observe in extant oscines and suboscines, and hints at contrasting evolutionary modes between subclades of the largest avian radiation.

Community development in the Avalonian Ediacaran

***Nile Stephenson, Katie M. Delahooke, Charlotte G. Kenchington, Andrea Manica and Emily G. Mitchell**

University of Cambridge, UK

Bedding planes from the Avalonian Ediacaran (~580–560 Ma) record some of the first animals as near-census deep-sea, benthic communities. Community composition is highly variable, yet the drivers behind this variability are not well understood. Prior models of Avalonian succession have suggested that community composition changes systematically driven by competitive tiering, similar to modern systems. We calculate the degree of community succession by comparing the relative abundance and areal coverage (a proxy for biomass) using the W-statistic, where early-stage communities have relatively high abundance, whereas late stages have relatively high areal coverage. We mapped out 20 Avalonian communities from Newfoundland, Canada and Charnwood Forest, UK, using a combination of laser-line probe, LiDAR, and photogrammetry, covering a total 795 m², with 18,060 specimens and 42 taxa. We quantified community composition using NMDS and LDA to determine how community composition and tiering metrics were correlated to degree of succession. We found four early, 11 middle, and five late-stage communities with a variety of community compositions at each successional stage. Our results suggest multiple different



successional pathways in the Avalon driven by metacommunity dynamics and reproductive processes over and above the impacts of competitive tiering.

Predicting extinction risk by range loss: evidence from the fossil record

Eileen Straube¹, Gregor Mathes^{1,2} and Manuel Steinbauer¹

¹University of Bayreuth, Germany

²University of Zurich, Switzerland

Species extinction and biodiversity loss as reported by the IPCC are predicted from climate change related reduction in the geographic range (range loss). This builds on the well-established IUCN Red List criterion, in which a species is considered critically endangered (>50 % extinction risk) if it loses 80 % of its geographic range. However, while there is clear evidence that extinction risk is related to the absolute geographic range of a species, its relationship to range loss has not been investigated. Building on fossil evidence of true extinctions (Neogene – Holocene), this study implements a Bayesian hierarchical weighted generalized additive model to investigate how extinction risk changes with the percentage decrease or increase in geographic range of a genus. Results clearly indicate how extinction risk increases with range loss. Taxon-dependent differences in the relationship between extinction risk and range loss indicate a potential need for adapting its application in extinction risk predictions as well as the IUCN criteria.

Early Cambrian trace fossils in shallow-marine quartzites from Baltica and their implications for sedimentary stasis and anactuality sedimentation

***Yorick Veenma¹, Neil S. Davies¹, Ben J. Slater² and Graham E. Budd²**

¹University of Cambridge, UK

²Uppsala University, Sweden

The interplay between erosion, deposition and stasis controlled how time was archived within the strata and bedding planes that make up the Cambrian rock record. To explore whether this interplay may have variably diluted or condensed palaeoenvironmental data (e.g. trace fossils), here we present new data from the Lower Cambrian of southern Scandinavia. We describe a new trace fossil assemblage from the Redalen Member (Lower Cambrian; Series 2) of the Mjøsa area, southern Norway. This new assemblage reflects a range of architectural styles, which are discussed in the context of the depositional environment and the Cambrian diversification of early animals. We then compare the Redalen Member to other units of the Lower Cambrian of Baltica and use trace fossils, along with specific sedimentary structures, as a proxy for stasis in the depositional environment. We show how local sedimentary conditions control the abundance of bedding planes that reflect stasis at the sediment-water interface (*i.e.* 'true substrates') and suggest that ichnological motifs may be influenced by the anactuality sediment supply to the shallow-marine realm. The further application of such an integrated sedimentological–ichnological approach is expected to improve our understanding of the distribution of stratigraphic time in the rock record of non-uniformitarian sedimentary systems.



Proliferation of microbial collagenase as a constraint on soft tissue preservation

***Philip B. Vixseboxse¹, Edmund R. R. Moody², Philip C. J. Donoghue², Sean McMahon³ and Alexander G. Liu¹**

¹University of Cambridge, UK

²University of Bristol, UK

³University of Edinburgh, UK

Collagen synthesis – a trait acquired within stem Metazoa – was a key innovation in the development of the metazoan bauplan, affording a flexible extracellular matrix with the structural integrity necessary for complex multicellularity in animals. Prior to metazoan scavenging and predation, collagen degradation was primarily catalysed by two processes: endogenous enzymes for collagen remodelling *in vivo*, and exogenous microbial collagenases. Prokaryotes cannot synthesize collagen, therefore instances of prokaryotic collagenase biosynthesis must reflect adaptation to metabolize collagen within the environment. Leveraging 700 archaeal and bacterial proteomes, we classified protein function and identified the highly substrate-specific microbial collagenase U32 for further investigation. We inferred a maximum likelihood phylogeny and identified deviations from known relationships between taxa – likely lateral gene transfer events – which were temporally constrained by molecular clock estimates. We show microbial collagenase U32 exhibits numerous instances of lateral gene transfer between 580 and 250 Ma. These results indicate a lag-time between the origination of metazoan collagen synthesis and the proliferation of microbial collagenases, and predict a fundamental shift in collagen degradation rate during the Proterozoic–Phanerozoic transition – perhaps explaining the profusion of exceptionally-preserved soft-bodied animals in the late Ediacaran, and hinting at the closure of an important taphonomic window during the Cambrian Explosion.

Heterochronic processes in the evolution of planktonic foraminifera

Bridget S. Wade¹, Christopher Poole¹, Thomas Ezard² and Anieke Brombacher^{2,3}

¹University College London, UK

²University of Southampton, UK

³Yale University, USA

Planktonic foraminifera are extremely well-suited to study evolutionary processes in the fossil record due to their high-resolution deposits and global distribution. Species are typically conservative in their shell morphology with the same geometric shapes appearing repeatedly through iterative evolution, but the mechanisms behind the architectural limits on foraminiferal shell shape are still not well understood. To understand when and how these developmental constraints can be overcome, we studied morphological change leading up to the origination of the unusually ornate species *Globigerinoidesella fistulosa*. Our results show that the origination of *G. fistulosa* from the *Trilobatus sacculifer* plexus involved an amalgamation of three different heterochronic expressions: addition of chambers (hypermorphosis), earlier onset of protuberances (pre-displacement), and steeper allometric slope (acceleration) as compared to its ancestor. We argue that the protuberances unique to *G. fistulosa* were necessary to sustain a surface-area:volume ratio that could host sufficient numbers of photosymbionts. Our work provides a case study of the complex combination of processes required to produce unusual shell shapes and highlights the importance of developmental processes in evolutionary origination.



A new quantitative framework to determine the producers of marine locomotory trace fossils

Zekun Wang and Imran A. Rahman

Natural History Museum, London, UK

Trace fossils record the interactions between organisms and their surroundings, and can therefore provide unique insights into the coevolution of trace-makers and the environment. However, identifying the producers of trace fossils is often challenging because different animals can produce similar traces. Hence, many traces can only be attributed to broad morphological grades, such as vermiform worms, and this uncertainty makes it difficult to decipher their palaeobiological significance through major evolutionary events and episodes of environmental change. To quantify this, we have developed a new mathematical approach for identifying previously unrecognized signatures left by the trace-makers of simple marine locomotory traces. We mapped the variation of turning angles of self-crossing traces made by extant molluscs, isopods, gastropods and nematodes, and calibrated their repeating patterns using two mathematical metrics (frequency spectrum and autocorrelation function). Evident differences in these indices can be recognized between the traces left by animals from different phyla. Using these results, we are able to identify the trace makers of several archetypical *Gordia* ichnospecies, allowing us to correlate the first appearances of certain traces with specific trace-makers. This new mathematical framework has great potential for identifying trace-makers through deep time, consolidating the link between ichnology and palaeobiology.

Estimating the origin of angiosperms based on quantitative analysis of the fossil records and the molecular clock

***Ruolin Wu¹, Daniele Silvestro^{2,3,4}, Harald Schneider⁵, Yue Tong⁶, Shan Wan⁶, Davide Pisani¹ and Philip C. J. Donoghue¹**

¹*University of Bristol, UK*

²*University of Fribourg, Switzerland*

³*University of Gothenburg, Sweden*

⁴*Swiss Institute of Bioinformatics, Switzerland*

⁵*Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China*

⁶*Independent*

Angiosperms dominate modern plant diversity but the timing of their diversification remains the subject of dispute. Molecular clock analyses invariably estimate crown angiosperms to have diverged in the Triassic or earlier whereas there are no unequivocal fossil representatives of the clade prior to Cretaceous. In large part, this discrepancy must arise because of the often simplistic interpretations of the fossil record that both underpin molecular clock calibration and many palaeobotanical perspectives. Here we use a revision of the Bayesian Brownian Bridge (BBB) model which estimates the ages of clade origin and extinction based on extant and historical diversity to analyse a revised database of approximately 15,000 records of fossil angiosperms. The BBB model yields probabilistic estimates of clade age at the family level that we employ as calibrations within a molecular clock analysis based on a dataset of 83 genes from 644 taxa; amounting to an unparalleled 175 calibrations. The results of our analysis allow us to reject a post-Jurassic



origin of angiosperms. However, our analysis estimates that the bulk of angiosperm diversity did not appear until later, in the Cretaceous, suggesting increasing concordance between the molecular timescale and raw palaeontological records when angiosperms become ecologically and geographically widespread.

Insect diversity from the late Eocene Xiede locality (central Tibetan Plateau) and a preliminary review of Hymenoptera

***Xiaoting Xu^{1,2,3}, Isabelle Deregnacourt³, Jérémie Bardin³, Cecilia Waichert⁴, Alexandre Somavilla⁵, James M. Carpenter⁶, Weiyudong Deng⁷, Tao Su^{1,2} and Olivier Béthoux³**

¹Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China

²University of Chinese Academy of Sciences, China

³Sorbonne Université, France

⁴University of Brasília, Brazil

⁵Instituto Nacional de Pesquisas da Amazônia, Brazil

⁶American Museum of Natural History, USA

⁷University of Bonn, Germany

Considering its geographic range, the insect fossil record of the Tibetan Plateau (TP) is scarce. It is not until recent years that more than 4,000 insect fossil specimens have been excavated from the Upper Eocene (~39 Ma) Niubao Formation, at the Xiede section, central TP. These specimens provide a unique opportunity for understanding the diversity, systematics and biogeographic relevance of the fauna. A preliminary taxonomic overview shows that the site contains six orders (Hymenoptera, Coleoptera, Hemiptera, Diptera, Orthoptera and Odonata), including at least 47 morphotypes, making it the most diverse insect fauna on the TP. Among them, Hemiptera and Orthoptera are the most abundant for specimen numbers, while Hymenoptera are one of the most diverse, with about 15 morphotypes. Vespidae and Ichneumonidae are the most common families in Hymenoptera. Representatives of this order were investigated using various photographic processing, including sides-merging and UV light. New records include a paper wasp (Vespidae, *Polistes*); a blue-black spider wasp (Pompilidae, *Anoplius*); and five Darwin wasps (Ichneumonidae), including a morphotype which geometric morphometrics revealed as closely related to the extant genus *Theronia* (parasitoid wasp of Lepidoptera). Further investigation of the Xiede biota will provide critical insights on the evolution of the TP insect fauna.

No mass extinction at the Ediacaran–Cambrian boundary

***Mariana Yilales, Fred T. Bowyer and Rachel A. Wood**

University of Edinburgh, UK

Whether a mass extinction separates the Ediacaran biota from the Cambrian biota at the base of the Cambrian (c. 538.8 Ma) is unresolved, even though this is of fundamental importance to understanding the rise of animals. Mass extinction has been suggested due to the disappearance of the Ediacaran biota coincident with a marked negative $\delta^{13}\text{C}$ excursion (the BAsal Cambrian carbon isotope Excursion, BACE), inferred to be a global perturbation of the marine carbon cycle. Using two global end-range age models for the 543–533 Ma interval we integrate known metazoan fossil distribution with global (U isotopes) and local (Fe speciation) marine redox data. Fossil



biostratigraphic ranges show substantial overlap between Late Ediacaran biota, and Cambrian small skeletal fossil fauna throughout the boundary interval and across all plausible age models, revealing only a modest biotic turnover, where the most moderate overlapping scenarios show at least the co-occurrence of erniettomorphs, cloudinomorphic and protoconodonts. Available geochemical data remain insufficient to support any kill mechanism associated with an expansion of anoxic waters, while statistical analyses show only a limited rise of oxygenated sea floor across the BACE. We conclude that no mass extinction marks the Ediacaran–Cambrian boundary.

Unveiling the third eye of the earliest vertebrates

***Sihang Zhang¹, Xiangtong Lei¹, Peiyun Cong¹, Jakob Vinther² and Sarah E. Gabbott³**

¹*Yunnan University, China*

²*University of Bristol, UK*

³*University of Leicester, UK*

The pineal complex is a key evolutionary innovation that contributes to the visual and neuroendocrine systems of vertebrates. It has long been hypothesized that this structure evolved through the degeneration of an ancestral eye, known as the third eye theory. However, whether such a third eye existed in early vertebrates remains unknown. The Cambrian myllokunmingids from the Chengjiang biota, China are the oldest vertebrates known. These fossils bear paired lateral dark spots, interpreted as eyes, and a single median (unidentified) dark spot in their head. Examination of specimens with a range of techniques (SEM, ToF-SIMS, FIB, and TEM) reveals that all of these structures comprise melanosomes, a feature considered specific to screening pigments. In each species of myllokunmingids, the melanosomes of the paired lateral dark spots and the median dark spot show a similar and consistent morphology. This corroborates an eye interpretation for the lateral dark spots and indicates that the median dark spot was also photoreceptive, an interpretation suggesting that it may represent the precursor of the pineal complex. These findings support the third eye theory and demonstrate that the pineal eye probably had the same function, perhaps being photoreceptive or image forming, as the paired lateral eyes in earliest vertebrates.



Abstracts of poster presentations

* indicates a poster eligible for the Council Poster Prize.

Underlined author denotes designated presenter.

Dietary diversity among early Paleocene periptychid ‘condylarths’ revealed by multi-proxy analysis

***Neil F. Adams**^{1,2}, **Stephen L. Brusatte**³, **Thomas E. Williamson**⁴, **Sarah L. Shelley**³ and **Mark A. Purnell**²

¹*Natural History Museum, London, UK*

²*University of Leicester, UK*

³*University of Edinburgh, UK*

⁴*New Mexico Museum of Natural History and Science, USA*

The Periptychidae were one of the most prolific families of archaic ungulates (‘condylarths’) in the earliest Paleocene. From among their ranks emerged some of the first mammals to attain larger body sizes after the Cretaceous–Palaeogene (K–Pg) mass extinction. Despite their high diversity and body size disparity, studies of periptychid palaeobiology have remained few. Previous hypotheses suggest periptychids were omnivorous, herbivorous, or frugivorous. Some have even proposed co-evolutionary links between the appearance of large-bodied periptychids (purported hard-object feeders) and the diversification of plants with large fruits/seeds, just ~300 kyr after the K–Pg boundary. Here, we provide tests of these hypotheses by applying dental microwear texture analysis and multi-proxy dental morphology analysis to periptychids for the first time. Our sample consists of nine genera from the early Paleocene Nacimiento Formation in the San Juan Basin, New Mexico, USA. Through comparisons with extant frugivores we find no support for hypotheses of hard-object feeding in larger-bodied early periptychines. Phylogenetic mapping of palaeodietary data indicates that high dental complexity evolved in periptychids first as an adaptation to process tough foliage but was later co-opted to diets of increasing hardness. Our results reinforce the rapid ecological recovery and radiation of placentals after the K–Pg mass extinction.

Unravelling diversification patterns in Anseriformes.

***Darcy Adhami**^{1,2}, **Eloise Hunt**^{1,2}, **Christopher D. Dean**³, **Daniel J. Field**⁴, **Philip D. Mannion**³ and **Anjali Goswami**¹

¹*Natural History Museum, London, UK*

²*Imperial College London, UK*

³*University College London, UK*

⁴*University of Cambridge, UK*

The Anseriformes, comprising a diverse array of waterfowl including ducks, geese and screamers, encompasses more than 160 extant species along with numerous globally distributed fossil lineages. Previous investigations employing phylogenomic analyses have proposed a Plio–Pleistocene origin for the diversification of Anseriformes. However, scrutiny of raw fossil data seemingly challenges this hypothesis, potentially stemming from inherent biases in the fossil record’s sampling. This



study aims to elucidate the apparent discrepancy by exploring the influence of sampling biases on the inferred evolutionary timeline of Anseriformes. Here we use shareholder quorum subsampling to show that major diversification occurred some 15 million years earlier than genomic estimates: during the Oligocene, with connections to eustatic sea level. Our analyses reveal major reductions in relative diversity of Anseriformes at the Oligocene–Miocene transition and Plio–Pleistocene boundary with peaks around the Mid-Miocene Climactic Optimum and Miocene–Pliocene boundary. Global diversity patterns generally match continental patterns, with the exception of greater relative diversity in Asia in the mid-Miocene and in North America across the Miocene–Pliocene boundary. Our results suggest the possible influence of environmental factors such as eustatic sea level on anseriform diversity, highlighting the need to include both fossil and extant taxa in estimates of diversity.

New morphological features and terminology for the trilobite order Olenida

Jonathan M. Adrain

University of Iowa, USA

The Order Olenida is a major clade of Cambrian–Ordovician trilobites characterized by a complex synapomorphy featuring new morphological features involved in a complex articulation between the librigenal anterior projections and the cranidium. This articulation has not previously been discovered and new terms are required to describe it. The overall feature is termed the stylidium. It consists of a series of stylidial pillars produced dorsally from the inner edge of the doublure of the anterior projection. These are matched ventrally by librigenal pits. The pillars dock with the underside of the anterior cranidium via a matching series of ventral pits, each of which receives a process-like pillar. On the dorsal surface of the cranidium, the position of the ventral stylidial pits can be marked by dorsal tubercles, but these are effaced in many taxa. The stylidium is present in all checked species of olenids, aphelaspidiids, asaphiscids, cedariids, dokimocephalids, idahoiiids, loganellids, parabolinoiids, pteroccephaliids and remopleuridiids. It has never been observed in any other group and is demonstrably absent from most. It appears to represent a rare, complex, fully conserved high-level synapomorphy indicating a major evolutionary group.

Doushantuo–Pertatataka acritarchs from the lower Ediacaran of Ghana

Heda Agic¹, Andrey Bekker² and Muhamuda Abu³

¹*Durham University, UK*

²*University of California, Riverside, USA*

³*University for Development Studies, Ghana*

Ornamented organic-walled microfossils are important for understanding eukaryotic evolution in the aftermath of the Snowball Earth and prior to the rise of macroscopic life. They are also useful to biostratigraphically date and correlate Ediacaran successions. Here we report an assemblage of Doushantuo–Pertatataka acritarchs (DPA) from the Voltaian basin of the West African craton, Ghana. The Neoproterozoic Ota–Pendjari Group contains tillite and cap carbonates at the base, overlain by 1 km of green-grey mudstones. The fossiliferous samples are from the middle megasequence, the Pendjari Formation. Palynological acid-maceration yielded DPA microfossils characteristic of lower Ediacaran strata and compositionally most similar to assemblages of South-Central Australia. The assemblage contains 26 taxa, dominated by acanthomorphs *Tanarium conoideum* and



Variomargosphaeridium litoschum. Species richness declines up-section. The assemblage broadly corresponds to the *Tanarium-Schizofusa-Variomargosphaeridium* zone established in Australia. However, in Ghana, some taxa diagnostic of other zones (*Ceratosphaeridium*, *Appendisphaera*) appear throughout the sequence. These data establish the Ediacaran age for the Pendjari Formation and confirm the global stratigraphic significance of DPA. However, this also shows that biozonation established in Australia and South China might not be entirely applicable to other Ediacaran sedimentary basins. The Pendjari microfossils further demonstrate a rapid diversification of eukaryotic microbiota following the Marinoan glaciation.

Measuring ornithischian tooth complexity using patch count rotated analysis (OPCR)

Isaura Aguilar Pedrayes, David J. Button, Emily J. Rayfield and Michael J. Benton

University of Bristol, UK

Ornithischians were a diverse clade of Mesozoic dinosaurs that independently evolved multiple different craniodental character combinations to increase relative bite force and jaw mechanical processing ability as adaptations towards high-fibre herbivory. Previous studies suggest that an increase in tooth occlusal surface complexity was linked to increased bite efficiency in ornithischians, but this idea has yet to be tested. The orientation patch count (OPC) and orientation patch count rotated (OPCR) methods measure tooth surface complexity and appear to be reliable ways to identify non-homologous dental features corresponding with diet. Herbivores have significantly higher OPC and OPCR values than carnivores among both living and extinct mammals and, to some extent, reptiles, but these metrics have yet to be systematically compared across Ornithischia. Here we perform a sensitivity analysis of tooth crown 3D models with different numbers of mesh faces, from micro-CT data, of the upper and lower jaws of one specimen of *Hypsilophodon foxii*, to measure the impact of mesh resolution on OPCR analyses. With this preliminary work we will quantify tooth surface complexity of other ornithischian species to trace evolutionary shifts in ornithischian tooth complexity, quantify its relationship with bite performance, and explore patterns of dietary adaptation across the clade.

Comparative embryonic development of the galloanseran skull

***Bassel Arnaout, Benjamin Steventon and Daniel J. Field**

University of Cambridge, UK

The Galloanserae is composed of Galliformes (chickens and their relatives) and Anseriformes (ducks and their relatives), subclades exhibiting divergent cranial morphologies. Anseriformes generally exhibit flattened, elongated bills with comparatively dorsoventrally deep and rostrocaudally short braincases, while Galliformes generally exhibit shorter, pointed beaks with wide, globe-like braincases. The stem lineage of Galloanserae is hypothesized to have exhibited a mosaic combination of these morphologies, as seen in the stem galloanseran *Asteriornis maastrichtensis*. In order to understand the evolution of cranial form among total-group galloanserans, the developmental underpinnings of their cranial disparity need to be examined. We compared the skull development of mallard ducks and chickens to determine the differences in cranial developmental trajectories and ossification patterns that ultimately give rise to morphologically



divergent hatchlings. Our comparisons reveal an earlier onset and accelerated process of skull ossification in chickens compared to ducks. Moreover, we document identifiable clade-specific differences first arising during the second stage of skull ossification. Our results indicate that the disparity in cranial form between these clades evolved in part by shifts in the onset and rate of ossification of key cranial components, on top of sometimes subtle differences in the geometry of the initial ossifications of the skull.

Divergent strategies in cranial biomechanics and feeding ecology of the ankylosaurian dinosaurs

***Antonio Ballell Mayoral, Bohao Mai and Michael J. Benton**

University of Bristol, UK

Ankylosaurs were key megaherbivorous dinosaurs of Jurassic and Cretaceous ecosystems. Their distinctive craniodental anatomy and mechanics differentiated them from coexisting hadrosaurs and ceratopsians, and morphological evidence suggests dietary niche partitioning between sympatric ankylosaurids and nodosaurids. Here we investigate the cranial biomechanics of *Panoplosaurus mirus* and *Euoplocephalus tutus* using finite element analysis and lever mechanics, aiming to compare feeding functional performance between nodosaurids and ankylosaurids. We also compare jaw performance across a wider sample of ankylosaurs through lever mechanics and phylogenetic comparative methods. Mandibular stress levels are higher in *Euoplocephalus*, supporting the view that *Panoplosaurus* consumed tougher foodstuffs. Bite force and mechanical advantage (MA) estimates indicate that *Panoplosaurus* had a relatively more forceful and efficient bite than *Euoplocephalus*. There is little support for a role of the secondary palate in resisting feeding loads in the two ankylosaur clades. Several ankylosaurs converged on similar jaw mechanics, while some nodosaurids specialized towards high MA and some ankylosaurids evolved low MA jaws. Our study confirms divergent evolutionary pathways in skull biomechanics and feeding habits by the two main clades of ankylosaurs.

The eyes and vision of ichthyosaurs

***Matteo Battini¹, Benjamin C. Moon², Matt Williams³ and Michael J. Benton⁴**

¹*University of Leicester, UK*

²*Office for Standards in Education, UK*

³*Bath Royal Literary and Scientific Institution, UK*

⁴*University of Bristol, UK*

Ichthyosaurs – dolphin-like marine reptiles that thrived throughout most of the Mesozoic – are famous for having incredibly large eyes. However, the function of such large eyes in ichthyosaurs is still debated; whether for increased sensitivity in low-light conditions (either at night, depth or in turbid waters), or improved prey, conspecific and/or predator detection at a distance. Fortunately, it is possible to infer aspects of the visual capabilities of extinct animals from *f*-numbers – a measure of the light-gathering capabilities of an optical system – calculated using fossil material. Here we re-describe two three-dimensionally preserved sclerotic rings attributed to the ichthyosaur *Hauffiopteryx typicus* from the early Toarcian (Lower Jurassic) Strawberry Bank Lagerstätte, Somerset, UK. Using CT scan data, we provide the first detailed representation of the sclerotic ring, and



hence eyeball shape, in three dimensions. We find that *H. typicus* had asymmetrical eyeballs, with flattened outer corneal portions. Analysis of *f*-numbers of ichthyosaurs with well-preserved skulls shows that these were more variable during the Triassic, compared to generally lower values in the Jurassic and Cretaceous. This corresponds with a decrease in morphological disparity among ichthyosaurs across the Triassic–Jurassic boundary, which resulted in survivors specializing as open water pursuit predators.

New data on Late Cretaceous stem birds clarifies the plesiomorphic condition of the neornithine postcranial skeleton

***Juan Benito Moreno, Elisabeth M. Steell, Klara E. Widrig and Daniel J. Field**

University of Cambridge, UK

Neornithes (the bird crown group) originated during the Late Cretaceous, yet their pre-Cenozoic fossil record is extremely scarce. Many fragmentary Late Cretaceous avian remains exhibit affinities to Galloanserae (waterfowl and landfowl), and the only two well-supported Cretaceous neornithines are thought to belong to this clade. Similarly, total-group Anseriformes (waterfowl) are amongst the most common early Cenozoic neornithines. Recent insights on the ancestral crown bird palate suggest that a galloanseran-like palate may be ancestral for Neornithes, yet the plesiomorphic condition of numerous additional aspects of the neornithine postcranial skeleton remain uncertain. Here we re-evaluate a crownward stem bird specimen from North America, and reveal that several aspects of its pectoral and forelimb anatomy are remarkably similar to those of early Cenozoic Anseriformes. However, these ‘galloanseran’ features are combined with hindlimb morphologies shared with stem palaeognaths, raising the intriguing possibility that numerous aspects of the postcranial anatomy of early total-group Anseriformes could be plesiomorphic for Neornithes. These results may force reconsideration of the purported galloanseran and neornithine affinities of several Cretaceous and early Cenozoic fossil birds, with potential implications for assessing the age of the deepest divergences among Neornithes in the Cretaceous and the ecology of the earliest crown birds.

A new artiopodan from the lower Cambrian Sirius Passet Lagerstätte (North Greenland) and its phylogenetic implications

Harry Berks¹, Morten L. Nielsen^{1,2,3}, Joseph Flannery-Sutherland¹, Arne T. Nielsen⁴, Tae-Yoon Park³ and Jakob Vinther¹

¹*University of Bristol, UK*

²*British Geological Survey, UK*

³*Korea Polar Research Institute, Republic of Korea*

⁴*University of Copenhagen, Denmark*

Artiopoda is a diverse and important group of Palaeozoic euarthropods yet to be fully understood. Here we describe a new non-trilobite artiopodan from the Lower Cambrian Sirius Passet Lagerstätte, North Greenland. The new taxon is a large species with an ovoid outline, a broad, domed cephalon, followed by fifteen trunk tergites and a small pygidium. Preliminary cladistic analyses recover it as the sister-taxon to *Squamacula*, a genus found in the Chengjiang and Emu Bay Shale biotas which



has previously been recovered as the sister to all other artiopodans. The new taxon is shown to be distinct from *Squamacula* because the anterior trunk tergites bear articulating half-ring-like structures and the pleural tips and genae are rounded. Posteriorly, the half-ring structures are absent, and the pleura form short spines. Its phylogenetic position means it is potentially important for understanding the ancestral states of Artiopoda and the group's origin.

***Carcharopsis* sp. from the Spanish Mississippian, a Carboniferous marine giant shark**

Silvia Blanco-Ferrera¹, Héctor Botella², María Ciudad Real³ and Javier Sanz-López¹

¹University of Oviedo, Spain

²University of Valencia, Spain

³Universidad Nacional de Educación a Distancia, Spain

Carcharopsis is a Carboniferous chondrichthyan genus originally described on the basis of its distinctive teeth which have a central, broad, triangular crown and serrated margin. It is an extremely rare morphology in Palaeozoic fishes. Here two fragments of one tooth of *Carcharopsis* sp. are studied from the Cantabrian Mountains of Spain. This is the first report of the genus in the margins of Gondwanaland. The conodonts studied from the limestone correlate with the *Lochriea zieglerei* Zone in the upper Viséan (Middle Mississippian). The size of this probably mesial tooth is among the largest described, and suggests a fish body length of at least 4-5 m. A review of the known occurrences of *Carcharopsis* shows a distribution from the upper Viséan (*Gnathodus bilineatus* Conodont Zone) to the end of the Serpukhovian (*Nuculoceras nuculum* Ammonoid Zone), except for two doubtful Pennsylvanian finds. Size, morphology and histology of *Carcharopsis* teeth, together with a wide ecological distribution from coastal to pelagic marine areas and from temperate to warm waters, suggests an active pelagic swimming hyper-carnivore. The occurrence in the Middle-Late Mississippian indicates and coincides in time with the recovery of marine diversity after the end of Devonian Hangenberg biotic crisis.

Determining environmental controls on Ediacaran microfossil and matground distributions

***Catherine E. Boddy, Brennan O'Connell, William J. McMahon and Alexander G. Liu**

University of Cambridge, UK

The Ediacaran macrobiota include some of the earliest known large, complex multicellular eukaryotes, and provide insights into the early evolutionary history of animal life. However, environmental controls on microfossil distribution remain poorly resolved. In the relatively deep-marine deposits of Newfoundland, Canada and Charnwood Forest, UK, distal turbiditic rapid burial events were likely separated by long intervals of sedimentary stasis, facilitating preservation of diverse assemblages of Ediacaran microfossils. In the same basins, shallower marine environments contain no microfossils, despite evidence of intervening stasis and known Ediacaran organisms at comparable bathymetries in contemporaneous global localities. Here we test hypotheses regarding global fossil-facies relationships via detailed sedimentological and palaeontological comparison of late Ediacaran shallow marine and deltaic successions from Newfoundland and Shropshire, UK with well-characterized shallow marine settings in Namibia and Australia. We describe a range of surface



textures, and consider the influence of sediment deposition, tectonic framework and matground maturity on fossil preservation. Our findings suggest that the observed distribution of Ediacaran fossils, and any subsequently drawn inferences on community ecology, may be highly dependent on both the rate and style of accompanying sedimentation.

Patterns of predation on pea urchins: past and present

Christine Bordean and Elizabeth M. Harper

University of Cambridge, UK

The potential of the minute clypeasteroid *Echinocyamus pusillus* (OF.Müller 1776) to preserve evidence of drilling predation throughout the Cenozoic has not been fully appreciated until recently. A total of 1,216 individuals were analysed for signs of drilling, making this the largest study of its kind. Both fossil and modern specimens were measured from 12 locations across Europe. Overall predation rate was 19 %, higher than previous studies. This can be explained by multiple behaviours acting simultaneously, including size and non-size selective predation and parasitism. Predation frequency could have changed with time across the whole study area but is far more likely to be affected by local conditions. What has remained consistent over time and space is the tactic used by predators. Piercing the test is achieved by secretion of acid and muscular rasping with the radula. ‘Pore theory’ encapsulates how a predator detects advantageous sites and why they are attracted to them. The tactics used for urchin predation differ from those used to hunt bivalves due to the heterogeneous nature of the urchin test. The site chosen by predators is such that the acid volume secreted, and drilling time, are minimized, so net energy gain is maximized.

When and where did the first skeletal metazoans appear?

Fred T. Bowyer¹, Collen-Issia Uahengo², Kavevaza Kaputuaza², Junias Ndeunyema^{1,2}, Mariana Yilales¹, Ruaridh Alexander¹, Andrew Curtis¹ and Rachel A. Wood¹

¹*University of Edinburgh, UK*

²*University of Namibia, Namibia*

The advent of metazoan skeletonization (biomineralization) marks a fundamental transition in Earth’s history, facilitating the diversification of novel body plans and biological control of carbonate sediment production, and permanently restructuring the global carbon cycle. The terminal Ediacaran fossil record hosts a number of tubular organisms, some of which such as *Cloudina* probably represent the earliest biomineralizing metazoans. Precisely when, where and why metazoans first acquired the ability to biomineralize is poorly understood. Assessing possible environmental triggers for this key event requires accurate constraint of the age, palaeoenvironmental setting and geochemical context of the earliest *Cloudina*. Here we present new stratigraphic, sedimentological and geochemical ($\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$) data from the oldest strata of the Ediacaran Nama Group, exposed in the Tsau Mountains of southwest Namibia. These new insights constrain the first appearance of *Cloudina* to limestones that record dominantly negative $\delta^{13}\text{C}_{\text{carb}}$ values, and were deposited in shallow waters after a transition from semi-restricted, evaporitive–dolomitic to open marine carbonate settings, laterally-equivalent to more proximal siliciclastic settings that host well-known Nama assemblage soft-bodied fossils. *Cloudina* first appeared during an interval of dominantly low oxygen and unstable, regional marine redox conditions, and colonized the sea floor during short-lived oxic intervals.



Anthropic palaeodiversity

John Brenner

Independent

Anthropic palaeodiversity is a hypothesis that explains the trajectory of palaeodiversity as a multi-billion year within-world sequence of sub-anthropogenic outcomes that eventually lead to an anthropogenic mass extinction. In which case, the maximum range and scope of the biodiversity is finite (and so are all subsets of it). Earth is the accessible type specimen; the trajectory can be translated into an understandable multi-billion-year palaeontological narrative that motivates social, industrial, geopolitical and cultural change to mitigate the impending anthropogenic mass extinction on Earth. A tentative corollary is that this is the only feasible kind of palaeodiversity trajectory in the universe.

Putative algal microfossils from the Ediacaran Doushantuo Formation

***Princess Buma-at¹, Dominic Papineau^{1,2,3} and Zhenbing She³**

¹University College London, UK

²Birkbeck College London, UK

³China University of Geosciences, Wuhan, China

A rapid diversification of complex multicellular life occurred during the Ediacaran, coinciding with a significant rise in atmospheric oxygen. This study presents new undescribed spheroidal microfossils recovered from granular phosphorites of the Ediacaran Doushantuo Formation. A size range of 200–700 μm , a $\sim 2 \mu\text{m}$ outer boundary, and abundant dark-coloured cell units characterize these spheroidal specimens. Micro-Raman analyses revealed internal cells dominated by organic matter, and alongside an observed Gaussian distribution for their diameters, is indicative of a biological origin. Most circular cell units were therefore deemed to represent somatic cells while larger cells ($>20 \mu\text{m}$) were interpreted as gonads. From this, a potential asexual life cycle history was constructed, and additional evidence for the presence of possible cytoplasmic bridges has enabled green algal affinities to be elucidated. However, these putative algal microfossils are 20% larger than the largest modern *Volvox*, so this size disparity is attributed to the sudden influx of nutrients following Neoproterozoic glaciation events. If further analyses reinforce the tentative phylogenetic placement of these new specimens within an extinct stem-crown group of Volvocaceae (Chlorophyta), it could drastically alter the current consensus that Volvocaceae diverged from its green algal ancestors during the Triassic, predating molecular clock estimates by ~ 400 million years.

Impact of MISS on the ecological community dynamics of an Avalonian Ediacaran community

***Princess Buma-at¹, Nile P. Stephenson², Charlotte G. Kenchington² and Emily G. Mitchell²**

¹University College London, UK

²University of Cambridge, UK

The Ediacaran (635–539 Ma) is one of the most critical intervals in Earth's geological time because it encompasses the transition from microbially-dominated Proterozoic ecosystems to ones hosting the first complex macrofossils. In Newfoundland, Canada, fossil communities of enigmatic, sessile



organisms are exceptionally well preserved under volcanic ash layers, recording a snapshot of their life-histories. As such, quantitative ecological statistics provide a novel approach for investigating fossil community dynamics. In the Discovery Geopark, Newfoundland, the LC13 surface is unusually highly textured compared to other Avalonian bedding planes, including with microbially-induced sedimentary structures (MISS). Therefore, it provides a novel insight into the potential influence of MISS on community dynamics. To investigate this influence, we applied spatial point process analyses to the LC13 surface to reconstruct Ediacaran marine benthos interactions. LC13 was mapped out using a laser-line probe, LiDAR and photogrammetry to a 40-micron resolution, covering 26.9 m² with eight abundant taxa across 327 specimens. We found the community dynamics of LC13 to be remarkably different to that of other analysed Avalonian communities, with high instances of intra- and inter-specific competition and interactions with the local habitat. This suggests that microbial environments had the potential to strongly influence Ediacaran species dynamics.

Direct quantification of skeletal pneumaticity in birds sheds light on the evolution and function of this key trait

***Maria Grace Burton**¹, **Roger B. J. Benson**² and **Daniel J. Field**¹

¹*University of Cambridge, UK*

²*American Museum of Natural History, USA*

Skeletal pneumaticity (*i.e.* epithelial-lined, air-filled cavities within bones) is a defining trait of avian structure and biology. While birds are the only living vertebrates with postcranial skeletal pneumaticity, evidence of this trait has been found in various extinct ornithodiran archosaurs, implying its deep evolutionary history in this lineage. The presence or absence of pneumatic bones across the avian skeleton has been categorically assessed in specific clades and shown to vary across taxa, related primarily to ecology and body size; however, until now, a comprehensive quantitative investigation into the true extent of skeletal pneumaticity has been lacking, hindering fundamental insights into the evolution of this key avian feature. We used microCT scans of fresh, frozen birds to directly quantify the fraction of humerus volume occupied by bone, marrow and air across a phylogenetically diverse taxon sample. Among other insights, we provide clarity on the drivers of cortical bone thickness and its long-hypothesized association with pneumaticity, with our results providing strong support that humeral size, body mass, aquatic diving and the presence or absence of pneumaticity all have independent effects on cortical bone thickness. Furthermore, our results suggest that the last common ancestor of crown birds possessed a highly pneumatized humerus.

The Fezouata brachiopod fauna: an Early Ordovician diversification at high latitudes

Yves Candela¹, **David A. T. Harper**² and **Michal Mergl**³

¹*National Museums Scotland, UK*

²*Durham University, UK*

³*West Bohemia University, Czechia*

The Fezouata Biota has been a focus of much attention, exposing an incredibly diverse and exceptionally-preserved fauna of soft-bodied taxa, some displaying Cambrian-like features.



Brachiopods remain a neglected part of the fauna. Brachiopods occur at distinct horizons: in the lower part of the Fezouata Shale (upper Tremadocian) and in the upper part of the Fezouata Shale (lower Floian). The fauna is dominated by a mixture of lingulides, siphonotretides and orthides. The Tremadocian assemblage is more diverse (over 20 species) than the Floian assemblage (some ten species). So far, six new species and three new genera have been identified. The total brachiopod fauna shows high γ -diversity, whereas at a local scale, α -diversity is low. This is interpreted as a rapid turn-over of short-lived populations of opportunistic taxa, living in shallow-water environments above storm-wave base. Multivariate analysis confirms that the Tremadocian fauna has a close affinity with faunas from Peri-Gondwanan terranes and from Eastern Avalonia, then marginal to Gondwana. Numerically dominant elements of the Moroccan fauna share a common identity with those from Bohemia, especially the non-articulates *Celdobolus* and *Orbithele*. The younger Floian fauna shows an increased affiliation with faunas from Baltica, as Avalonia rifted and moved northward closer to Baltica, acting as a stepping stone for faunas migrating southward.

Phylogenetic variation in tissue-specific melanosome geometry in mammals and birds

***Beatriz Carazo del Hoyo**¹, **Aaron Quigley**¹, **Daniel Cirtina**¹, **Catherine McCarney**², **Jane Brennan**², **Soudeh Ziapour**² and **Maria E. McNamara**¹

¹*University College Cork, Ireland*

²*University College Dublin, Ireland*

Melanins are pigments that in extant and extinct vertebrates are stored in melanosomes in integumentary and non-integumentary tissues. Characterizing phylogenetic variation in key melanosome characters could improve our understanding of the evolution of melanins and their functions through deep time. Previous studies reported tissue-specific chemistry and geometry in a limited dataset of modern and fossil melanosomes. Here we test whether the reported data trends apply to vertebrates more broadly. We used an enzymatic digestion procedure to isolate melanosomes from the internal and external organs of three replicate specimens of each of twelve mammal and bird species. These two groups were chosen because they present more variable melanosome geometries in non-integumentary tissues than reptiles or amphibians. The geometry of extracted melanosomes was analysed using scanning electron microscopy. Preliminary results reveal tissue-specific geometries consistent with previous studies. Future analysis of the organic chemistry and metallome of our samples will inform on any trends in melanosome chemistry. Understanding the tissue-specific chemistry and geometry of melanosomes across a broad phylogeny of vertebrates will facilitate reconstruction of the internal anatomy of fossils and will shed light on the links between melanins and metal homeostasis.



Redescription of *Pteronisculus gunnari* (Nielsen, 1942), from a juvenile specimen from East Greenland

***Iacopo Cavicchini**¹, **Thodoris Argyriou**² and **Sam Giles**^{1,3}

¹University of Birmingham, UK

²Ludwig-Maximilians-Universität München, Germany

³Natural History Museum, London, UK

The Early–Middle Triassic actinopterygian *Pteronisculus* (White, 1933) is part of the Triassic early fish fauna (TEFF), a group of cosmopolitan genera that thrived in the aftermath of the end-Permian mass extinction. Phylogenetic relationships are debated for many of these genera, including *Pteronisculus*, and the topology of the evolution of crown actinopterygian lineages during the Early Triassic remains unclear. *Pteronisculus* is an essential outgroup for works dealing with the interrelationships of early crown actinopterygians. The species *P. gunnari* (Nielsen, 1942), from eastern Greenland, was described in less detail than other species of the genus. Here, CT is employed for the first time on a three-dimensionally preserved specimen of *P. gunnari* to thoroughly redescribe the species, thanks to the preservation of very fine morphological details (e.g. braincase, sensory canals, gill skeleton). The specimen reveals juvenile features (e.g. long bone extremities not fully ossified), details of the ossification pattern of the unfused braincase and palatoquadrate, as well as morphological features previously undescribed for the genus (e.g. interclavicle, pharyngeal parotic toothplates). New information from the endoskeleton of *P. gunnari* enriches our understanding of both the morphological complexity as well as the inter-relationships of morphologically generalized actinopterygians from the TEFF.

New exceptionally preserved spheroidal microfossils from the late Ediacaran Gaojiashan biota, South China

Shu Chai^{1,2}, **Alexander G. Liu**², **Cédric Aria**³, **Yu Wu**^{1,2} and **Hong Hua**¹

¹Northwest University, China

²University of Cambridge, UK

³University of Toronto, Canada

The late Ediacaran Gaojiashan biota (c. 551 Ma) of the Dengying Formation, Shaanxi Province, China encompasses abundant and diverse exquisitely preserved phosphatic microfossils that have great potential to cast light on the origin and early evolution of multicellular organisms. However, our knowledge of the anatomy and affinities of these fossils remains limited. Here we describe new material of spheroidal microfossils from the Lijiagou section of the Gaojiashan biota. New morphological information revealed by high-resolution scanning electron microscopy and X-ray tomographic microscopy allows us to interpret these fossils as a diverse assemblage with affinities to possible unicellular protists, multicellular protists, metazoan embryos and unicellular algae. This study not only provides further evidence for the presence of diverse embryos in the Gaojiashan biota, but also contributes to our understanding of the biological attributes, affiliation and evolution of late Neoproterozoic spheroidal microfossils.



The early evolution of crown birds: phylogenetic and morphological case studies

***Albert Chen and Daniel J. Field**

University of Cambridge, UK

Despite substantial recent advances in understanding crown bird evolution, their timing of origin and phylogenetic inter-relationships remain difficult to resolve. In this work, we performed several case studies integrating morphological data with findings from molecular phylogenetics to investigate specific problems in crown bird origins. For one of these studies, we used combined molecular–morphological analyses to resolve the controversial phylogenetic inter-relationships within the avian clade Strisores, the results of which suggest a novel scenario for their evolutionary history. A second case study used a similar approach to investigate the affinities of the Late Cretaceous *Asteriornis maastrichtensis*, one of the oldest known fossil crown birds, placing it close to the phylogenetic root of the clade Galloanserae. A final case study focused on assembling a morphological dataset that comprehensively samples osteological traits from the pectoral girdle and forelimb across crown bird diversity. Using this dataset, we identify sources of conflict among previous analyses as well as highlight potential morphological synapomorphies of major avian clades that had previously been recognized only using molecular data. Our results indicate that the integration of information from avian morphology and fossils with insights from genetic studies is both feasible and illuminating regarding the subject of avian evolution.

A deep dive into the anatomical distribution and geometry of melanosomes in fish

***Dan Cirtina and Maria E. McNamara**

University College Cork, Ireland

Melanins are ubiquitous pigments in extant eumetazoans and, in vertebrates, are synthesized in specialized organelles termed melanosomes. The potential for melanosomes to survive decay and diagenesis provides a pathway for organic preservation of soft tissues, with most research to date focused on melanin in fossil feathers. Consequently, our understanding of the origin(s) and functional evolution of melanin within the vertebrate clade remains poorly understood. Fish melanosomes are of particular interest as they have putative functions in immunity and, unlike other vertebrates, may be synthesized in internal tissues. The biology of fish melanosomes, however, is largely unknown. Here we resolve these issues by sampling ten tissues in twelve species of extant fish, representing a wide phylogenetic spread of early-diverging vertebrates. Scanning electron microscopy reveals tissue-specific trends in the anatomical distribution and geometry of melanosomes. Actinopterygii contains abundant melanosomes in the spleen and kidney, while Chondrichthyes lack melanosomes in both organs. Further, eye melanosomes differ significantly in geometry between the two groups, with large, spheroidal melanosomes present in Chondrichthyes and long, rod-shaped melanosomes in Actinopterygii. Comparative analysis of melanosome characters in extant amphibians and reptiles will further inform on broader trends in the biology and evolution of melanin during the Phanerozoic.



Rates of phenotypic evolution between salinity habitats in fishes globally

John T. Clarke

Ludwig-Maximilians-Universität München, Germany

Classic and contemporary theories expect differences in phenotypic rates between marine, freshwater and other salinity lifestyles/habitats. Actinopterygian fishes, which possess ~32,000 species that have repeatedly explored many salinity habitats at multiple scales, represent a model system to test for the influence of these factors on evolutionary rate. By quantifying evolutionary rates in body size using datasets of up to 27,000 species with two rate methods, I reveal that rates do not differ in a consistent manner between salinity habitats in the sense that patterns are not repeated at multiple phylogenetic scales. Instead, patterns vary widely by scale with one exception: freshwater-brackish taxa possess higher rates than euryhaline taxa in most comparisons across most phylogenetic scales. The search for additional factors that explain differences in rate revealed notable roles for species richness, branch duration, size variance, size itself and living exclusively in lakes.

Reconsidering the phylogeny of Radiodonta: a sister group or an evolutionary grade of euarthropods?

Peiyun Cong^{1,2} and Jin Guo²

¹*Yunnan University, China*

²*Chengjiang Science Museum, China*

Radiodonts (*Anomalocaris* and its relatives) are pervasively regarded as a monophyletic group and are widely recovered as the sister group to a clade including all the upper-stem and crown groups of euarthropods. It is upon this phylogenetic framework that the acquisition sequence of euarthropod diagnostic characters has been evaluated, such as compound eyes and segmented appendages. Growing evidence indicates that several other key characters of euarthropods also evolved within radiodonts (e.g. *Amplectobelua*), such as potential biramous limbs (complex of gnathobase-like structure and reduced flap), and sternites. However, the status of a sister group between radiodonts and euarthropods (including the upper-stem groups) forces all these shared characters to be plesiomorphic or due to convergent evolution. Re-examination of the enigmatic fossils *Parapeytoia* and *Cucumericrus* reveals more character-sharing between radiodonts and euarthropods. For example, radiodont flaps are homologous with the exopods of euarthropods and a homologous structure of euarthropod protopodite is probably present in all radiodonts. This increasing body of evidence suggests that radiodonts more likely represent an evolutionary grade from which euarthropods originated, rather than sharing a very complex ancestor with euarthropods or evolving these diagnostic characters of euarthropods independently.

High-resolution confocal laser scanning microscopy (CLSM) imaging of 'phloem-like' tissue from the Rhynie chert

***Laura Cooper and Alexander J. Hetherington**

University of Edinburgh, UK

The Rhynie chert is an Early Devonian Lagerstätte renowned for exceptional cellular, three-dimensional preservation of an early terrestrial ecosystem. *Asteroxylon mackiei* is the most complex plant found in the Rhynie chert, possessing complex traits such as rooting axes and



leaves. By exhibiting exceptional preservation at a crucial point in plant evolution, *A. mackiei* can provide insight into the origin and evolution of key plant tissues. Phloem is the specialized sugar-conducting tissue of vascular plants. As the origin of phloem is associated with increased size and complexity, phloem can be considered a key innovation in plant evolution. Phloem is defined by the presence of sieve pores, which enable movement of sugar between cells. Though *A. mackiei* possesses so-called 'phloem-like' tissue, the presence of sieve pores in this tissue has not been confirmed – in part due to the resolution limit of light microscopy. Airyscan confocal laser scanning microscopy (CLSM) is a high-resolution form of microscopy that can overcome the limits of light microscopy in resolving small subcellular structures. Here we demonstrate how Airyscan CLSM can be used to image the walls of the 'phloem-like' tissue of *A. mackiei*, enabling a greater understanding of the origin of a major plant tissue.

Estimating biodiversity through time using deep learning

***Rebecca Cooper**^{1,2}, **Daniele Silvestro**^{1,2,3} and **Joseph T. Flannery-Sutherland**⁴

¹University of Fribourg, Switzerland

²Swiss Institute of Bioinformatics, Switzerland

³University of Gothenburg, Sweden

⁴University of Bristol, UK

Palaeodiversity estimates are challenged by the incompleteness of the fossil record and recent studies have demonstrated that spatial and temporal variation in preservation and sampling invariably hamper global estimates, even when state-of-the-art methods are applied to correct these biases. Here we develop a new software package, DeepDive (Deep learning estimation of Diversity), that combines biodiversity simulations and a deep learning model to estimate richness through time while accounting for spatial, temporal and taxonomic heterogeneities. We assess model performance under simulated conditions of strong temporal, taxonomic and spatial biases and compare accuracy with that of a widely-used alternative method, SQS. DeepDive consistently outperforms alternative methods and demonstrates particular improvement under conditions of strong spatial bias. We apply our model to estimate the diversity dynamics of two empirical datasets of different taxonomic and temporal scope: the Permian–Triassic record of marine animals and the Cenozoic evolution of proboscideans. DeepDive estimates reveal hidden diversity from both datasets and recover evidence for a smaller effect of the Permian–Triassic mass extinction in marine groups than previously estimated. The inferred diversity curve for proboscideans shows rapid diversification of the clade following its expansion out of Africa, and a recent 12- to 20-fold drop in elephant diversity.

Characterizing the microbial communities during marine shrimp decay using 16S ribosomal RNA sequencing

***Nora Corthésy**, **Farid Saleh**, **Allison C. Daley** and **Jonathan B. Antcliffe**

University of Lausanne, Switzerland

Fossilization favours the preservation of mineralized structures over soft tissues, which are rarely retained in deep time. To understand exceptional fossil preservation, experimental taphonomy is essential to identify factors influencing fossilization potential. Of the biotic factors involved in



preservation, bacteria are known to play a major role in carcass recycling and degradation. Bacterial growth can be limited in the presence of certain clays. However, the impact of clays on bacterial community composition during animal decay is unknown. The microbial communities of marine shrimps decaying on three different clays were identified using 16S ribosomal RNA sequencing for the first time. Marine shrimps decaying on kaolinite minerals were the least degraded as kaolinite not only limits bacterial growth but also favours the growth of Proteobacteria over that of the Firmicutes, with the latter being more efficient in recycling the polysaccharides that are the principal component in shrimp cuticle. This highlights that the primary observation of kaolinite limiting bacterial growth may not be as important as which specific bacteria it inhibits. Thus, kaolinite promotes the growth of bacteria that are less efficient in recycling complex organic compounds present in exoskeletal elements of many animal groups, which increases soft tissue preservation potential.

Quantifying and visualizing biomineral preservation

Matthew Cowen¹, Loic Segalen², Marc de Rafelis³, Benjamin Kear⁴, Maitena Dumont⁵ and Živilė Žigaitė¹

¹*Uppsala University, Sweden*

²*Sorbonne Université, France*

³*Géosciences Environnement Toulouse, France*

⁴*Evolutionsmuseet Uppsala, Sweden*

⁵*Hebrew University of Jerusalem, Israel*

Geochemical signatures from fossil bioapatite contribute greatly to palaeoenvironmental and palaeoecological reconstruction. The reliability of these signals depends upon the preservation of primary elementary composition, which is often lost due to diagenetic alteration. In this study we attempt to visualize and quantify fossil vertebrate dental tissue geochemistry and infer the state of bioapatite preservation by combining analysis of *in situ* major, trace and rare earth element (REE) compositions in plesiosaur and lungfish dental remains from the Lower Cretaceous Wonthaggi and Eumeralla formations of southeastern Australia. Tissue-selective REE values were obtained using laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS), indicating areas of REE enrichment. Optical cathodoluminescence (CL) imaging was also performed to visualize potential compositional changes. Energy dispersive X-ray spectroscopy (EDS) mapping was used to identify major elemental components and identify areas of secondary replacement. The REE profiles we present are indicative of limited diagenetic alteration, overlapping with the secondary element distributions seen in the CL imaging and EDS maps. The degree of preservation in some analysed tissues is such that the geochemical signature of the samples can be interpreted as primary. REE and trace element distribution between tissue types highlights the influence of histology on the likelihood of primary preservation.



Quantifying tiering of crinoid communities using a new echinoderm Lagerstätte from the Jurassic of Wiltshire, UK

Ebony Cutcliffe¹, Emily G. Mitchell², Jeffrey Thompson³, Timothy Ewin¹ and Imran A. Rahman¹

¹Natural History Museum, London, UK

²University of Cambridge, UK

³University of Southampton, UK

Tiering, the vertical subdivision of space by organisms within a community, has been proposed as a key driver of diversification in benthic marine ecosystems. Owing to their extensive fossil record, crinoids are potentially an ideal group with which to study this process in deep time. However, crinoid fossils are often found partly disarticulated and/or incomplete, hindering our ability to reconstruct their heights. A new Middle Jurassic echinoderm Lagerstätte from Wiltshire, UK provides an ideal opportunity to test for possible correlations between crinoid height and other aspects of their morphology because it contains abundant, near-complete crinoid specimens that have undergone minimal transportation. For this study, we measured key morphological features of complete and incomplete fossils from the Wiltshire site. Data were analysed with general linear regressions to determine if there are any relationships between stalk length and dimensions of the crown, which would allow us to reconstruct heights for partial fossil specimens. Preliminary results suggest a correlation between stem length and cup height, primibrachial length and number of plates in the secundibrachials. This work will help deliver a powerful new method for quantifying tiering and its effects on evolutionary dynamics.

An overview of biogeographical and evolutionary trends in non-avian theropods (Dinosauria; Saurischia) of the Indian subcontinent

Arunaditya Das¹ and James L. King^{2,3}

¹Birbal Sahani Institute of Palaeosciences, India

²Institute of Vertebrate Paleontology and Paleoanthropology, China

³University of Bristol, UK

Theropod fossils from the Indian subcontinent are typified as being rare since their first descriptions in 1933. Due to this, theropod taxa have always been enigmatic, thanks in part to their morphology, taxonomic affinity and geographical isolation during the Late Cretaceous. Fossiliferous formations from across the Mesozoic preserve theropod fossils from a broad temporal range. Triassic formations preserve neotheropods and the basal saurischian *Alwalkeria*. Jurassic specimens are rare with only *Grallator* and *Eubrontes* ichnotaxa and an isolated indeterminate tooth described to date. Cretaceous theropod descriptions are dominated by abelisauroids and potentially noasaurids with up to eight species known for both groups. Both groups suffer from many dubious taxa and the inter-relationships of abelisauroids and noasaurids from the Indian subcontinent still remain contentious. One other notable fossil, a troodontid tooth, has been recovered from Cretaceous deposits. Coalescing taxonomic and temporal specimen data indicate that theropods – and their progenitors – were present in the Indian subcontinent early on in dinosaur evolutionary history. Identifiable Indian and Pakistani taxa imply that the subcontinent reflected Gondwanan taxa that were typical of Africa until rifting events began moving India and Pakistan northward. Post-rifting isolation gave rise to theropod endemism that favoured abelisauroids during the Late Cretaceous.



The interplay of animal life, plant life and landscape in a Middle Devonian distributive fluvial system: the Hangman Sandstone Formation, SW England

Neil S. Davies and William J. McMahon

University of Cambridge, UK

The Eifelian-aged Hangman Sandstone Formation, UK has previously been interpreted as alluvial sheetflood deposits, relatively barren of trace or body fossil evidence for ancient life. The unit has significance in the context of the 'Old Red Sandstone' (ORS), recording deposition on the Cornubian terrane and thus being different in its climatic context to other British ORS settings. Recent work has revealed a number of sedimentological and ichnological characteristics that challenge previous environmental interpretations, and new fossil and trace fossil discoveries reveal it to be a previously under-appreciated window onto the diversification of life–sedimentary interactions in Devonian non-marine environments. We reveal that the unit contains a notably diverse arthropod ichnofauna, comprising >20 different ichnotaxa, shedding light on arthropod–sediment interactions in the Devonian. In addition, an abundance of 'true substrates' in the unit provide evidence for varied arthropod walking and furrowing behaviour, in addition to several striking microbially-induced sedimentary structures, including mat roll-ups, desiccation and rip-up features. The unit is also shown to yield an exceptional array of previously unreported vegetation-induced sedimentary structures and *in situ* plant fossils, which, combined with new sedimentary facies information, provide a high-resolution window onto plant-related biogeomorphic sedimentary processes in some of Earth's earliest forests.

Evolutionary allometry of the eusuchian palate (Crocodyliformes, Eusuchia)

***Ane de Celis, Iván Narváez and Francisco Ortega**

Universidad Nacional de Educación a Distancia, Spain

Eusuchia is the only living lineage of crocodylomorphs and has a reduced number of extant species, but its rich fossil record and morphological variability provide an important source of information for interpreting its evolutionary history and involved drivers. One of the most important structures for interpreting the evolution of the crocodylomorph lineage is the morphological evolution of the palate, a structure that is indeed key to the establishment of Eusuchia. However, most previous studies that have quantitatively analysed cranial evolution in Eusuchia have focused on its dorsal aspect and have not analysed the evolution of the palate. Herein a study of the eusuchian palate was conducted to characterize its morphological evolution and size–shape relationship using 2D geometric morphometrics and phylogenetic comparative methods. The dataset comprises 251 craniums of adult individuals from all extant species and several fossils, providing considerable phylogenetic coverage and morphological variation. Most of the shape variation is related to the length of the snout, but variability in the shape of the suborbital fenestrae is also relevant, among other traits. Analyses show that there is a shape–size relationship in eusuchians, but that alligatoroids do not exhibit evolutionary allometry, presenting similar palatal shapes with strikingly different sizes.



Reconstructing Pleistocene filoviruses from endogenous viral elements

***Alice de Sampaio Kalkuhl¹** and **Robert J. Gifford²**

¹*Trinity College Dublin, Ireland*

²*University of Glasgow, UK*

The genomes of eukaryotic species frequently contain vertically inherited, virus-derived sequences called endogenous viral elements (EVEs). These EVEs likely arose in ancestral host species when virus-derived DNA was integrated into the nuclear genome of infected germline cells. Some EVEs have become fixed and can provide insight into the ancient genomic diversity and evolutionary timeline of contemporary viruses. Where multiple orthologous copies are identified, ancestral sequences can be reconstructed that better represent the ancient ‘palaeoviruses’ from which EVEs are derived. Filoviruses (family Filoviridae) are RNA viruses that occasionally cause outbreaks of haemorrhagic fevers in humans and other mammals. Here we used DIGS (database-integrated genome screening) to identify filovirus-derived EVEs in published genome sequences, and to identify orthologous EVE copies. We used these data to estimate the minimum ages of distinct filovirus lineages, and to derive ancestral sequence estimates for ancient filovirus genes. We show that while estimates based on contemporary sequences place the origin of extant filoviruses in the mid to late Holocene, EVEs demonstrate that they originated millions of years earlier, allowing calibration of the filovirus evolutionary timeline. In addition, we obtain an overview of ancient filovirus genome diversity, revealing that conserved motifs in filovirus genomes were present in ancient ancestors.

Quantification of MISS textures to untangle the relationships between Ediacaran matgrounds and macrofossils

***Katie M. Delahooke, Alexander G. Liu, Nile P. Stephenson, Charlotte G. Kenchington and Emily G. Mitchell**

University of Cambridge, UK

The late Ediacaran Period (580–539 Ma) records the earliest evidence for diverse and complex macro-organisms. The Ediacaran seafloor was often bound by microbial mats, which are preserved as a disparate range of microbially-induced sedimentary structures (MISS) alongside the macrofossil communities. Here we quantify MISS textures in a novel way, using surface metrology and persistent homology, to objectively classify different texture types and determine the impact of matground heterogeneity on Ediacaran ecological dynamics. Analyses were applied to high-resolution (15 micron) 3D scans of 5.97 m² of the Pigeon Cove surface (~ 574 Ma) in Mistaken Point Ecological Reserve, Newfoundland, Canada. Surface metrology and persistent homology were used to characterize different morphotypes of ivesheadiomorphs (‘pizza-disc’ like structures), recovering three distinct clusters likely relating to different formative processes. Surface metrics were then calculated via a moving window to map textural changes across the entire surface, allowing application of inhomogeneous Poisson, random forest and maximum entropy models to ascertain whether the spatial position, and thus life-histories, of small rangeomorph fossils (n = 68) were correlated to the textural heterogeneity, and by extension mat characteristics. We thus provide a direct test of the existence of fine-scale habitat associations between matgrounds and Ediacaran macrofossils.



New sponge from the Marjum Formation of Utah supports a Cambrian origin of the hexactinellid body plan

Lucas Del Mouro^{1,5}, Rudy Lerosey-Aubril¹, Joseph Botting², Robert Coleman³, Robert Gaines⁴, Jacob Skabelund⁴ and Javier Ortega-Hernández¹

¹*Harvard University, USA*

²*Amgueddfa Cymru – National Museum Wales, UK*

³*Pomona College, USA*

⁴*Independent*

⁵*University of Sao Paulo, Brazil*

Poriferans play important ecological roles in marine ecosystems and are predicted to become more significant with climate change. Despite a simple anatomy, these filter-feeding organisms are formidable ecological engineers, influencing bioerosion, geochemical cycles and nutrient transfers. They have also critically impacted the history of the biosphere, aiding in the recovery of marine life after extinctions and contributing to the emergence of animals in the Cambrian. Modern poriferans are classified into four main classes: Calcarea, Demospongiae, Hexactinellida and Homoscleromorpha. However, the classification of fossil forms most exclusively relies on spicule morphology. Cambrian poriferans are highly diverse in morphology and many display anatomical characteristics that challenge the classification of modern taxa. For instance, hexactin spicules – a synapomorphy of modern hexactinellids – are found in many Cambrian taxa that do not fit within the hexactinellid body plan. Here we report a new poriferan from the Marjum Formation in Utah, which exhibits a uniquely complex anatomy for a Cambrian form: a syconoid-like organization, a thick body wall, and a hexactin-based skeleton. The discovery of this species and its hexactinellid-like body wall architecture supports a Cambrian origin of the hexactinellid body plan and provides valuable insights into character evolution in early glass sponges.

Disparification and extinction trade-offs shaped the evolution of Permian to Jurassic Odonata

Isabelle Deregnaucourt, Jérémie Bardin, Loïc Villier, Romain Julliard and Olivier Béthoux
Sorbonne Université, France

Owing to their prevalence and unparalleled diversity in modern terrestrial ecosystems, insects are a target group to assess the impact of mass extinctions on emerged land. Their evolutionary history is currently depicted as a major Late Palaeozoic diversification burst followed by a more progressive increase at low taxonomic levels. However, temporal and geographic limitations of the fossil record and a taxonomic impediment make it difficult to address the effect of mass extinctions on insects based on taxonomic diversity metrics alone. To bypass these issues and complement current data, we documented trends in disparity. Wings, the most frequent insect fossil remain, and that of Odonata in particular, offer a suitable model, as they offer a wide range of wing venations conforming to a single, generalized pattern. Our results show that Odonata experienced a decrease in disparity while species richness increased. Both the Permian–Triassic and Triassic–Jurassic transitions are revealed as episodes of strong morphospace restructuring due to selective extinction. In each case, a recovery was assured by the diversification of new forms. Early representatives of Odonata continuously evolved new shapes, a pattern contrasting with the classical assertion of a morphospace fulfilled early and followed by selective extinctions and specialization within it.



Phylogenetics across the Ediacaran–Cambrian boundary

Rory Devlin and Rachel A. Wood

University of Edinburgh, UK

The Ediacaran–Cambrian radiation of animals represents the first major radiation of animal life. Many previously enigmatic taxa from the Ediacaran have been allied to Metazoa. However, their position wherein remains unclear, as does their relation to the more recognizable fauna of the Cambrian. This thesis aims to place several Ediacaran taxa on the animal tree of life by compiling a morphological character dataset using novel characters and those taken from previous literature. The resulting trees show that many Ediacaran taxa occupy the eumetazoan stem-lineage, and that some nest within the Bilateria, thus drawing the origin of these groups, and by extension the Cambrian Explosion, back into the Ediacaran.

Novel form of moulting in cirolanid isopods?

Harriet B. Drage¹ and Matúš Hyžný²

¹*University of Lausanne, Switzerland*

²*Comenius University Bratislava, Slovakia*

Isopods are a diverse group of extant crustaceans, occupying a range of ecological niches from the Carboniferous. Isopods are characterized by a unique biphasic moult cycle in which they first shed the posterior section and, following a variable delay, the anterior section. The two sections are often found separately in modern environments and the fossil record because it is usually hours to days before the anterior section is moulted. Biphasic moulting may be an adaptation to various ecological modes such as parasitism, but its origin and evolutionary selection are unknown. New specimens of the extinct cirolanid isopods *Cirolana feldmanni* (Miocene; Slovakia) and '*Palaeoga' collinsi* (Eocene; UK) may show deviant moulting. The exoskeleton disarticulates into posterior and anterior sections, as in other isopods, but the anterior section is consistently found overturned, with both sections anteriorly orientated. Further, both sections are preserved in close association, with little/no sediment between them, suggesting moulting of both sections either close to simultaneously or within burrows. The overturned anterior section is alike the overturned cephalon in Salter's configuration for trilobites, though is otherwise dissimilar. Isopod moulting and its biochemical control are poorly understood, and it is possible this moulting style could be found in other isopods.

Trilobite cephalon morphology varies with taxonomic assignment and geological age, but cannot inform on moulting behaviour

Harriet B. Drage¹ and Stephen Pates²

¹*University of Lausanne, Switzerland*

²*University of Cambridge, UK*

Trilobites had strongly biomineralized exoskeletons with a diversity of morphological adaptations to different niches across the Palaeozoic. Like all euarthropods, trilobites moulted their exoskeletons repeatedly throughout their lives to grow and develop. Exoskeleton moulting behaviour in trilobites



appears to have been uniquely variable, both intra- and interspecifically, compared to modern arthropod groups, partly because of their cephalon morphological diversity. We used a dataset of *c.* 1,000 trilobite cephalon outline curves to create an expansive morphospace exploring the full extent of trilobite cephalon morphometric diversity. We then used these data to analyse the differences in morphospace occupation across the Palaeozoic and between taxonomic families, and to test for an association between cephalon morphometry, facial suture morphology and moulting behaviour. Elliptical Fourier analysis and clustering analyses suggest cephalic shape has little overall impact on moulting behaviour, with the behavioural groups almost entirely nested in morphospace. However, cephalon outline morphometry is informative on family-level grouping, and the dataset shows broad changes in cephalon morphometry through geological time; demonstrating that this data source is broadly useful. Perhaps trilobites demonstrated high phenotypic plasticity in moulting that cannot be explained by individual variables or evolutionary drivers such as morphometry.

Building a new publication model for palaeontology: a community-driven open access journal with preregistration

Harriet B. Drage¹ and Thomas Wong Hearing²

¹*University of Lausanne, Switzerland*

²*Ghent University, Belgium*

The academic publishing landscape is systemically unfit for purpose, dominated by a few large publishing houses that extract substantial profit from public resources whilst adding little value to published work and removing copyright from authors. Traditional publishing models bake-in gatekeeping practices that control who and what is published; single-blind peer review has long been suggested to suppress original thought, be biased against marginalized groups and be ineffective at improving the quality of flawed work. There is also increasing recognition of a reproducibility crisis in science, partly driven by pressure to publish novel work in high-impact journals. The result is systemic inaccessibility, opacity and lack of accountability. We present a publishing model rooted in financial accessibility, transparency and accountability to directly address these issues. The new model draws on best practice from across the academic publishing landscape, including diamond open access to mitigate financial inaccessibility, innovative broad-access and transparent peer review procedures, and preregistration integrated with article publication. We also propose a flexible approach to publishing ongoing research at various stages of intellectual development. We intend to establish a new palaeontology journal founded on these principles, and put out an open call for collaboration to do so.



Entitlement: the naming and claiming of dinosaur species

Emma M. Dunne¹, Nussaibah B. Raja¹, Sarah E. Greene², Sibusiso Biyela³, Riley Black⁴, Lawrence Bradley⁵, Daniel Cashmore^{1,2}, Katie Collins⁶, William J. Foster⁷, Bryan Gee⁸, Aline Ghilardi⁹, Agness Gidna¹⁰, Ana Rosa Gomez Canor¹¹, Thomas Halliday², Thomas Wong Hearing¹², Paula Medina-García¹³, Bolortsetseg Minjin¹⁴, Emanuel Tschopp⁷ and Evangelos Vlachos¹⁵

¹*Friedrich-Alexander-Universität Erlangen-Nürnberg, Germany*

²*University of Birmingham, UK*

³*ScienceLink, South Africa*

⁴*Independent*

⁵*University of Nebraska Omaha, USA*

⁶*Natural History Museum, London, UK*

⁷*Universität Hamburg, Germany*

⁸*University of Washington, USA*

⁹*Federal University of Rio Grande do Norte, Brazil*

¹⁰*Ngorongoro Conservation Area Authority, Arusha, Tanzania*

¹¹*Transmitting Science, Spain*

¹²*Ghent University, Belgium*

¹³*Technische Universität Berlin, Germany*

¹⁴*Institute for the Study of Mongolian Dinosaurs, Mongolia*

¹⁵*Museo Paleontológico Egidio Feruglio, Argentina*

Linnaean taxonomy is fundamental to organizing and managing our knowledge of the history of life on Earth. In this system, species are assigned a binomial (two-part) name and designated a holotype (name-bearing) specimen. The choice of whom or what to honour in a species' name is a power held by those describing the holotype within the constraints of the Codes of Nomenclature. Holotype specimens are typically housed in national repositories but practices, such as scientific colonialism, have led to some specimens residing far from their country of origin. In our study focusing on Mesozoic dinosaurs, we examined how historical patterns in the naming of species and the repositing of holotype specimens reflect and reinforce global inequalities in palaeontological research. Among our findings, we demonstrate that dinosaur species naming is dominated by countries from the Global North, particularly the USA and UK, and frequently reflects perceptions and prejudices of society (e.g. with respect to geography or gender). Furthermore, of the holotypes not repositing in their country of origin (15% of total), all were transported to countries in the Global North (87% originating in the Global South). Together, these patterns reinforce inequity and colonial structures that persist in our discipline today.

Taxonomy and phylogeny of Scottish 'cephalaspids' and the origin of paired fins

***Amin El Fassi El Fehri, Joseph N. Keating, Madleen Grohganz and Michael J. Benton**

University of Bristol, UK

Osteostracans are a group of jawless fishes from the Silurian and Devonian periods and are the first vertebrates to show true paired fins. Many specimens from the Old Red Sandstone of Scotland were assigned to the genus *Cephalaspis* when described. Recent re-analyses have revealed



significant morphological disparity, which is not reflected in their taxonomy. Many specimens have subsequently been re-assigned to existing or novel genera. We aim to explore the variation in Scottish 'cephalaspids' to inform osteostracan phylogeny. We will collect morphological data using photography and microscopy, which will be analysed using principal component analysis. Preliminary results show multiple clusters, suggesting morphologically disparate taxa. Where appropriate, these will be re-assigned to potentially new species or genera. We will then add these taxa to an updated phylogenetic dataset of Osteostraci, and perform parsimony and Bayesian analyses. The latter has never been attempted on this group. Using our new trees, we will then conduct ancestral state reconstruction of paired-fin characters. Our goal is to explore the evolution of paired fins by testing a modern hypothesis based on the classical 'lateral fin fold theory'. It proposes paired lateral fins evolved from a single ventrolateral fold, which is genetically homologous to median fins.

Gait modelling sheds light on trilobite evolutionary and ecological history

Jorge Esteve¹ and Pedro Rubio²

¹*Universidad Complutense de Madrid, Spain*

²*Burashi S.L., Spain*

An understanding of how animals move is essential to proper contextualization of their evolutionary history and ecological impact. Trilobites were one of the first animals on Earth to produce traces on the seafloor. Such traces are behavioural traces related to feeding or protection, in both cases implying different types of locomotion. In order to understand their evolutionary history and ecological impact on marine substrates, modelling of how trilobites moved is essential. Locomotion in trilobites is approached through three-dimensional models, which yielded two main gaits that reflect basic behaviours: burrowing and walking. Our model shows that trilobites could change their gait and consequently increase their speed rapidly, varying the amplitude of the metachronal wave, a change independent of their biological structure. Fast increases in speed enhanced the protection of trilobites against predators and sudden environmental crises. Finally, our models point out how the trilobite body pattern constrained their gaits, controlled by the distance between the pair of legs and between legs in a same segment.

Tracing archosauromorph origins through space, time and climate in the TARDIS

Joseph Flannery Sutherland

University of Bristol, UK

The diversification of archosauromorph reptiles from the Late Permian to Late Triassic is a classic example of an adaptive radiation. It has received significant attention from phylogenetic, morphological and ecological perspectives, but its spatial signature is understudied. Here I reconstruct the geographic origins of early archosauromorphs using a taxonomically updated, time-calibrated super tree. I then couple landscape connectivity analysis and high-resolution reconstructions of deep time climate and topography in a novel workflow (TARDIS – Traversal And Routes of Dispersal In Spacetime) to infer the phylogeographic structure of their radiation across the ecologically anachronous stage presented by Pangaea. Finally, I quantify their rates and



routes of dispersal and rates of climate adaptation to examine the biogeographic constraints on their early evolutionary success. Preliminary results highlight that the deepest archosauromorph divergences took place in European Pangaea but later cladogenetic events were geographically disparate and frequently involved trans-equatorial dispersals. This indicates that extreme climates across the supercontinent were not as robust biogeographic barriers as previously suspected, and demonstrates the role that landscape connectivity analysis can play in reconstructing the spatial dynamics of evolutionary radiations.

Determining developmental sequences in *Megaclonophycus* from the early Ediacaran using approximation methods

***Kirsten Flett, Kelsie Cracknell, Philip C. J. Donoghue, Davide Pisani and John A. Cunningham**
University of Bristol, UK

This study investigates the use of approximation methods to determine consistency in the volume of embryos with increasing cell counts in *Megaclonophycus*-stage development. The Weng'an Biota, found in the Doushantuo Formation in Southern China, is host to calcium phosphate preserved globular microfossils which have been interpreted by some to be of metazoan affinity. The purpose of this study is to assess whether the embryos follow reductive cleavage divisions which are characteristic of metazoan embryos. *Megaclonophycus*-stage embryos were scanned using the TomCat beamline for tomographic microscopy. Fifteen of these embryos were then counted accurately using Avizo software by counting each cell to calculate volume before using an approximation method to increase the dataset. The approximation method uses a 3D sample area consisting of a disc measuring three cells in width with differing volumes which is then multiplied by the fraction of the total specimen volume to give an accurate count for the total cell number in the embryo. Early results show that cell division in *Megaclonophycus*-stage embryos is not palintomic as would be expected for metazoan embryos. These *Megaclonophycus*-stage embryos also lack evidence of gastrulation or blastocoel formation, features consistent with early metazoan embryos.

Unearthing the diversity and evolution of phloem in ferns

***Zishan Fu and Alexander J. Hetherington**
University of Edinburgh, UK

Phloem is vital for vascular plants because of its fundamental role in transporting photosynthate and comprehensive roles in signalling. Despite its importance, the evolution of phloem is not well understood. Phloem structure is poorly preserved in the fossil record. Little attention has been paid to early-derived lineages such as ferns, the sister group of all euphyllophytes. This limits our ability to characterize phloem evolution over long periods of geological time. Therefore, our research focuses on exploring the phloem traits in ferns. We are using histology and microscopy techniques to study phloem structure in a range of extant fern species, which enable us to quantify key phloem traits such as the size of phloem conducting cells. Current results suggest that the size of conducting cells is significantly correlated with the body size of extant ferns. Ancestral state reconstruction is applied to predict phloem structure in the past. To test the prediction, we are investigating some historic thin sections made of Carboniferous coal balls from the Lancashire and Yorkshire coal



fields, UK. Phloem was well preserved in these fossils. Combining data from extant and extinct ferns, the anticipated outcomes are to quantify what phloem traits changed and how they evolved through geological time.

Life and death in the deep: modelling benthic ecosystem engineering over evolutionary time

***Euan Furness**^{1,2} and **Mark D. Sutton**¹

¹*Imperial College London, UK*

²*Grantham Institute, UK*

Marine diversity is the dominant contributor to the fossil record throughout geological time. However, the eco-evolutionary processes driving diversity in the marine realm, particularly the deep marine realm, are not well understood. One suggested mechanism is the ‘biological cropping hypothesis’, which proposes that widespread, non-selective predation (termed “cropping”) in benthic ecosystems reduces competition among prey within those ecosystems and, in so doing, prevents competitive exclusion. This hypothesis is 50 years old but, owing to difficulties with working on the deep marine benthos and over evolutionary timescales, has never been conclusively evaluated. Here we test the predictions of the biological cropping hypothesis using the REvoSim eco-evolutionary simulator, which performs individual-level simulations of ecosystems over geological timescales. We find that biological cropping pressure alone is insufficient to generate new species, but that it does have the capacity to increase and preserve genetic variation. However, this increase in genetic variation may be offset by an increase in homogenizing sexual selection, given the pressure to breed rapidly in the presence of intense predation. Depending on the balance between these two mechanisms over the Phanerozoic, this hypothesis suggests that ecological differences may have often been unimportant in maintaining species diversity in the deep marine realm.

Can the size, shape and form of the tribosphenic molars tell cryptic bat species apart within the Pleistocene fossil record?

Julia Galán¹ and **Julia Aramendi**²

¹*University of the Basque Country, Spain*

²*University of Cambridge, UK*

This work focuses on the cryptic complex of large-sized mouse-eared bats, *Myotis myotis*, *Myotis blythii* and *Myotis punicus*, currently sympatric in some Mediterranean areas. According to molecular data, the first two species differentiated in the Middle Pleistocene, while the latter one is an earlier branch, separated at c. 6 Ma. Here we studied the upper and lower molars of this complex using biometric analyses (BA) and geometric morphometrics (GMM). Two fossil samples from the Gran Dolina site, Spain were added to the study (Early and Middle Pleistocene). The PCAs considering only size (BA) show two main clusters, with the fossil samples grouped with *M. myotis*. The overlapping degree between clusters is greater for third molars, with fossil samples somehow occupying intermediate positions. The PCAs considering only shape show a very high degree of overlapping among groups and different patterns for each molar. If anything, Early Pleistocene specimens fall close to *M. blythii* for the third molars. In the PCA plots in form space the fossil



samples are separated from the extant species, more evidently in the case of the first and second molars. Results suggest that further work on the allocation of the fossil specimens is necessary.

Silurian brachiopods from the Pentland Hills: the status of the Pentlandian

Emma Gallagher¹ and David A. T. Harper²

¹National Museums Northern Ireland, UK

²Durham University, UK

The brachiopod fauna from the Silurian (upper Llandovery–lower Wenlock) rocks of the Pentland Hills, Scotland is abundant, diverse and historically important. Its distinctive associations in generally deep-water siliciclastic facies on soft substrates encouraged Archie Lamont in the early 1950s to erect a new chronostratigraphic unit for upper Llandovery strata, the Pentlandian, now correlated with the upper Llandovery and lowest Wenlock global stages. The majority of some 55 species are distributed across the following superfamilies (numbers of species, including those in open nomenclature, in parentheses): Linguloidea (7), Craniopsoidea (1), Discinoidea (4), Strophomenoidea (9), Plectambonitoidea (2), Chonetoida (1), Childiopoidea (2), Skenidioidea (1), Dalmanelloidea (3), Pentamerioidea (2), Rhynchonelloidea (4), Atrypoida (4), Athyridoidea (5), Cyrtioidea (5) and Delthyridoidea (3). New species of the following genera are present: *Leptaena*, *Isorthis* (*Ovalella*), *Dicoelosia*, *Oglupes* and *Lissatrypa*. Nevertheless in terms of abundance the fauna is dominated by individuals belonging to the Strophomenoidea, Plectambonitoidea and Dalmanelloidea, having a distinctly Ordovician essence. The species have also been organized into four palaeoecological associations evolving against a background of regression through the upper part of the Telychian and lowest Sheinwoodian (*crenulata* to *centrifugus* zones). The composition of the fauna, its deeper-water setting associated with finer-grained siliciclastic substrates, characterize the Pentlandian.

Neoselachian diversity through deep time

Amanda Gardiner¹, Rebecca Cooper³, Kristína Kocáková¹, Jaime Villafaña⁴, Daniele Silvestro³ and Catalina Pimiento^{1,2}

¹University of Zurich, Switzerland

²Swansea University, UK

³University of Fribourg, Switzerland

⁴Universität Wien, Austria

Modern sharks, rays and skates (Neoselachii) have a long evolutionary history that started in the Early Triassic (~250 Ma). Different studies have shown that neoselachians reached their maximum diversity in the Late Cretaceous (~72 Ma), declined during the K–Pg (66 Ma), and maintained relatively stable diversity throughout the Neogene. However, our current knowledge of neoselachian diversity is likely biased by their inherently incomplete and patchy fossil record. Here, based on a novel deep-learning approach of artificial intelligence and an unprecedented dataset of over 30,000 occurrences spanning the last 145 million years, we re-assess neoselachian diversity through time while accounting for numerous biases. We found an increase in neoselachian diversity throughout the Cretaceous, followed by the loss of 42% of species richness around the K–Pg. However, unlike previous



assessments, we found a second peak in diversity from the Paleocene to the early Eocene (62–48 Ma), with a 63 % increase in species richness. This was followed by a near-continuous decline from then onwards, only temporarily interrupted in the Middle Miocene (16–12 Ma), which resulted in the loss of 48 % of species in the last ~12 million years. Our approach revealed hitherto unrecognized patterns in the neoselachian past, suggesting we inherited an already depleted diversity.

Back to the ocean II: evolution of ecospace occupancy in Cenozoic marine tetrapods

***Piero Giuffra¹, Michael J. Benton¹ and Thomas L. Stubbs²**

¹*University of Bristol, UK*

²*The Open University, UK*

After the K–Pg event, a variety of ancestrally terrestrial tetrapods transitioned into the marine realm. By overcoming the difficulties that come with shifting towards a subaqueous medium, they radiated into a disparate spectrum of morphological ecospace associated with distinct feeding strategies, innovative swimming modes and unique physiological adaptations. In this work we mapped and quantified the evolution of the functional morphospace distribution of secondarily aquatic tetrapods (SATs) during the Cenozoic using principal coordinate analyses (PCoA). Based on a discrete character matrix, we studied the evolution of ecological diversity in tetrapod-dominated oceanic ecosystems, measured how ecological diversity changed over time and evaluated ecospace changes in the light of both intrinsic and extrinsic factors. We found that despite the occurrences of incomplete evolutionary convergence, generally widespread carnivory and similar modes of evolution, there are major divergences in the trophic spectrum, morphological constraints and rates of evolution in Cenozoic taxa with respect to Mesozoic SATs analysed in previous work. Our results also allow us to compare past diversity to modern ocean ecosystems and help us to better understand the structuring of modern marine trophic webs.

Theoretical morphology and functional optimality in chondrichthyan mandible evolution

***Benjamin Griffin, William J. Deakin, Philip C. J. Donoghue and Emily J. Rayfield**

University of Bristol, UK

Chondrichthyans are a successful clade of widely distributed aquatic vertebrates that have occupied a variety of trophic levels from the Devonian to the present, as reflected in their disparate jaw morphologies. To determine the factors that have impacted chondrichthyan jaw morphology we undertook a theoretical morphospace analysis of mandibular morphology for 194 species, representing 29 orders of both extant and extinct chondrichthyans. Mandibular morphological variation was captured using elliptical Fourier shape analysis and these data were used to derive and project a theoretical morphospace that was subjected to functional analysis. Theoretical shapes were analysed for proxies of speed and strength, allowing us to project functional surfaces into theoretical morphospace, as well as the Pareto optimal trade-off between these functional parameters. The disparate empirical morphologies present in chondrichthyans do not occupy the functionally optimal regions of the theoretical morphospace. Despite this there is a consistent trend towards more optimal and robust mandible forms within the morphospace through evolutionary



time. The shift towards more optimal shapes means that, while extant low trophic level chondrichthyans encompass a greater range of morphospace than do the top predators at higher trophic levels, this is only a portion of the morphospace chondrichthyans have previously occupied.

Potential and perils in using morphological characters for phylogenetic inference

Nicola Heckeberg¹, Alessio Capobianco¹, Gustavo Darlim², Basanta Khakurel³ and Sebastian Höhna¹

¹Ludwig-Maximilians-Universität München, Germany

²Eberhard Karls Universität Tübingen, Germany

³Southeastern Louisiana University, USA

Morphological characters play a crucial role in reconstructing systematic relationships, especially of extinct organisms. However, incorporating morphological data into analyses of evolutionary taxonomic history has received increasing interest in the past decade. While molecular data are available in large quantities for many organisms and their variability, evolutionary rates and parameter settings can be easily assessed, morphological data are not available in comparable dimensions and the models describing their parameters and evolutionary rates are under-developed. Morphological characters are more complex regarding the scoring, variability and estimation of parameters. For example, a 'T' always has the same meaning in molecular data, whilst a '1' in morphological data has a different meaning in each character. Different characters have different evolutionary rates, which should be accounted for when modelling characters across a phylogeny. Traditional partitioning into anatomical subregions might not always be the best approach. Here we provide a state-of-the-art overview of current modes of modelling morphological character evolution in phylogenetic inference. We show selected examples of scoring in vertebrates where defining, describing and/or delimiting character states is challenging. We present approaches to improve setting up morphological models and how to incorporate these into phylogenetic inferences of large-scale macro-evolutionary studies.

Developmental models shed light on the earliest dental tissues: an example based on *Astraspis*

Guillaume Houee¹, Jérémie Bardin¹, Damien Germain¹, Philippe Janvier¹ and Nicolas Goudemand²

¹Sorbonne Université, France

²Université Claude Bernard Lyon 1, France

Skeletal remains of extinct jawless vertebrates are pivotal to deciphering the evolutionary paths that led to the various forms of the vertebrate skeleton. For example, Pteraspidomorphs (stem-gnathostomes), such as the Ordovician *Astraspis*, display some of the oldest remains of bony and 'dental' tissues. However, the identification of the very nature of these early mineralized tissues has been hitherto hampered by a lack of unambiguous markers. As development is key to identifying the derivation of these tissues, we developed an integrative and generic histogenetic model, testing several ontogenetic scenarios. We illustrate our approach on the basis of the well-preserved *Astraspis* samples and show how this can be used to infer key developmental features from extinct species. This study suggests that in the odontodes of *Astraspis*: the initial curvature



of the epithelium was close to the shape of the final external surface; the mesenchymal cells differentiate synchronously in the whole inner periphery; and the capping tissue was produced by both mesenchymal–epithelial cells (enameloid rather than enamel). Incidentally, *Astraspis* specimens also evidence a dual growth periodicity that could be homologous to Andresen and von Ebner growth lines observed in amniotes, suggesting this type of dual periodicity may be shared by most vertebrates.

Micro-computed tomography reveals new information on the process of pterygoid segmentation in neognathous birds

***Annabel K. Hunt¹, Olivia Plateau¹, Juan Benito Moreno¹, Louis Fisher¹, Adam Urantówka² and Daniel J. Field¹**

¹University of Cambridge, UK

²Uniwersytet Przyrodniczy we Wrocławiu, Poland

Pterygoid segmentation is the process whereby the rostral portion of the pterygoid separates into a so-called ‘hemipterygoid’ and subsequently fuses with the palatine during neognath ontogeny. An unfused hemipterygoid has been identified in several stem-group birds, and a neognath-like pterygoid has recently been documented in the stem-bird *Janavis*, challenging long-held views regarding the ancestral neornithine palate. Despite frequent references in the literature, pterygoid segmentation remains poorly understood due to inconsistent anatomical terminology and difficulties interpreting the three-dimensional inter-relationships of palate bones from line drawings/photographs. A thorough re-assessment of the developmental underpinnings of avian palate morphology is therefore warranted. Here we applied micro-computed tomography to examine the skulls of late embryonic and early post-hatchling neognaths to elucidate the inter-relationships and three-dimensional morphologies of bones involved in the pterygoid segmentation process: the palatine, pterygoid and hemipterygoid. Based on our observations, we propose that the rostrally projecting process of the pterygoid found in some juvenile neoavians and juvenile and adult anseriforms represents the unsegmented ‘hemipterygoid’. Overall, our study helps clarify the process of pterygoid segmentation across Neognathae – a key component for reconstructing early neornithine palate evolution.

Odaraia is a Cambrian suspension-feeding arthropod with notostracan-like mandibles

***Alejandro Izquierdo Lopez^{1,2} and Jean-Bernard Caron^{1,2}**

¹University of Toronto, Canada

²Royal Ontario Museum, Toronto, Canada

Mandibulate arthropods, which include myriapods and pancrustaceans, are a highly disparate group with few synapomorphies. One of these is the mandibles, a pair of stout, dentate appendages. Mandibles are increasingly being uncovered across ‘bivalved arthropods’ from Cambrian Konservat-Lagerstätten, a group which was previously regarded as basal euarthropods. Unfortunately, cephalic features in this group remain unknown in many taxa, especially small ones where such features are too small to be observed or prepared mechanically. We revisit the large problematic ‘bivalved arthropod’ *Odaraia* from the Cambrian (Wuliuan) Burgess Shale, Canada, based on over



100 specimens housed in the Royal Ontario Museum. More than a dozen specimens of *Odaraia* preserved ventrally, or disarticulated, show mandibles: these are ellipsoidal and have an inner edge of large teeth, reminiscent of extant notostracans. *Odaraia* also shows a hypostome-labrum complex, a pair of post-mandibular appendages and a trident-shaped foregut ossicle, showcasing an unexpected complexity in the mandibular apparatus. Strong similarities to the cephalic limbs of *Waptia* reinforce the position of 'bivalved arthropods' (except isoxyids) in the mandibulate stem. Newly revealed arrays of short and long endopod spines represent one of the clearest lines of evidence for a suspension-feeding mode of life amongst all Cambrian euarthropods.

Patterns of marine benthic macrofaunal diversity across the late Pliensbachian, and early Toarcian (Lower Jurassic; ~183 million years ago) Oceanic Anoxic Event (TOAE, or Jenkyns Event) in the Llanbedr (Mochras Farm) borehole

***Meghan Jenkinson and Crispin T. S. Little**

University of Leeds, UK

Hyperthermal conditions and accompanying environmental perturbations linked to Karoo–Ferrar large igneous province volcanism caused widespread marine anoxia and benthic macrofaunal extinctions across much of Europe during the early Toarcian. Extinction and recovery patterns are well constrained in the Cleveland Basin of Yorkshire, but little equivalent is known elsewhere in the UK. Benthic assemblages in the Mochras borehole (Cardigan Bay Basin, North Wales) differ significantly compared to coeval strata in Yorkshire. Diversity remained relatively high in the early Toarcian and is accompanied by pyritized *Chondrites* burrows, suggesting marine redox conditions differed between the two sites. At Mochras, bivalves are the most abundant benthic representatives, followed by brachiopods and gastropods. These groups comprise many taxa which are rare or absent in Yorkshire. Infaunal bivalves are surprisingly uncommon in the late Pliensbachian and become scarce in the early Toarcian. Epifaunal disaster taxa *Bositra* and *Meleagrinnella* are extremely rare, and *Pseudomytiloides* are restricted entirely to the *falciferum* Zone. Infaunal *Dacromya*, diagnostic of improving environmental conditions in Yorkshire, are missing at Mochras, their niche instead occupied by astartids and lucinids. Aphorhaid gastropods and rhynchonellid brachiopods are common throughout the early Toarcian, but disappear briefly during the upper *falciferum* Zone, where *Lingula* and *Discinisa* prevail.

Tooth replacement pattern of *Incisivosaurus gauthieri* and its implications on the dental evolution of theropod dinosaurs

***Yihui Ke, Rui Pei and Xing Xu**

Institute of Vertebrate Paleontology and Paleoanthropology, China

The loss of teeth is a key evolutionary event in the early evolution of birds, but little is known about the tooth replacement pattern in early birds or their closest theropod relatives. Here we present 3D reconstructions of tooth rows based on high-resolution CT data of *Incisivosaurus gauthieri*, a putative herbivorous oviraptorosaurian with enlarged incisciform first premaxillary teeth on both sides. The reconstructions show two generations of replacement teeth on the lingual side of the right incisciform tooth, which is unprecedentedly reported in maniraptorans. However, there is only one replacement tooth present for the left incisciform tooth, displaying an asymmetrical pattern



possibly to prevent the simultaneous shedding of the paired incisiform teeth. This asymmetrical pattern is present in the whole premaxillary dentition in terms of the tooth replacement phase, probably related to the dental function. Meanwhile, replacement teeth are developed in alternating alveoli in the maxilla and dentary, which is similar to the condition of *Archaeopteryx*, possibly an ancestral state of avialans, with a more sporadic distribution of replacement teeth than that in the early-diverging coelurosaurians. We hypothesize that the slowdown of tooth replacement happened prior to avian origin.

Using ancestral state reconstruction to understand the simplification of the tetrapod skull

***Kim Julia Kean, Celeste Perez Ben, Marylène Danto and Nadia Fröbisch**

Museum für Naturkunde Berlin, Germany

One of the best documented phenomena in tetrapod evolution is the repeated loss of bones in the skull. This trend is first seen in the tetrapodomorphs as the number of elements of the skull roof reduces from ~75 in the bony fish *Eusthenherpeton*, to ~30 in *Acanthostega* and *Ichthyostega*. The loss in complexity is even more extreme in lissamphibians which have ~20 components to their skull roof. However, little research has been done to understand the patterns and evolutionary and developmental drivers behind this reduction. Here we investigate the simplification of the temporal series across the early tetrapod phylogeny. The temporal series shows the greatest variation in the skull roof and contains the intertemporal, supratemporal and tabular. By tracing the ancestral state of the presence/absence of each temporal series component, we see different patterns emerge. In the anamniote lineage the intertemporal disappears first, followed by the supratemporal and tabular. A similar pattern is seen in lepospondyls. In the amniote lineage, however, the supratemporal is maintained and the tabular lost in many neodiapsids. These different patterns raise questions regarding the modularity and homology of the tetrapod skull roof, and highlight the need to further study the evolution of skull simplification.

A new model of morphological evolution

Joseph N. Keating

University of Bristol, UK

Morphology is essential for estimating evolutionary relationships in deep time. Unfortunately, its utility is hindered by a lack of realistic models necessary for accurate evolutionary inferences. The standard Mk model assumes that changes between character states are instantaneous. In reality, morphological change occurs iteratively via cumulative modifications to underlying gene regulatory networks. Alternatively, the Threshold model approximates underlying gene regulatory evolution as a continuous process, termed liability. However, the Threshold model is inherently ordered, meaning that only transitions between adjacent states are possible. Here I present a novel 'Spherical' model, which better approximates current understanding of morphological evolution. The 'Spherical' model addresses the limitations of both the Mk and Threshold models: it incorporates underlying evolutionary 'liability' whilst permitting any conceivable state ordering (including unordered states) for any number of states. It can be implemented in two ways: liability can be modelled as a continuous process, akin to the Threshold model, or as a discrete hidden



process, drawing inspiration from hierarchical models of character evolution. I demonstrate that the Spherical model has desirable behaviour: It appropriately models both among-lineage rate heterogeneity and hierarchical dependencies between states. The Spherical model thus offers a promising avenue towards more accurate evolutionary inferences from morphology.

From malformations to mass extinctions: what spore and pollen exines can tell us about Earth's past

Matthew Kent¹, Feng Liu², Huiping Peng², Wenzhe Yin¹, Shuya Shi¹, Benjamin Bomfleur³, John E. A. Marshall⁴, Wesley T. Fraser⁵, Zoe A. Wilson¹, Philip E. Jardine³ and Barry H. Lomax¹

¹University of Nottingham, UK

²Nanjing Institute of Geology and Palaeontology, China

³University of Münster, Germany

⁴University of Southampton, UK

⁵Oxford Brookes University, UK

The chemical composition of fossilized spore and pollen exines holds clues as to the environmental conditions in which the parent plants grew. Exines contain plant-like 'sunscreen' chemicals, ultraviolet-absorbing compounds (UACs), which can be used as a proxy for a plant's level of exposure to ultraviolet-B radiation (UV-B). In cases of extreme UV-B exposure, the UAC content of exines may be very high and can indicate a damaged ozone layer. We found elevated amounts of UACs in fossilized conifer pollen from across the Permian–Triassic Boundary coinciding with a carbon-isotope excursion and elevated terrestrial organic matter to mercury concentration. The latter phenomena were caused by massive volcanism at the Siberian Traps, releasing sufficient organohalogens to significantly damage the ozone layer. This finding provides the first direct evidence to support a long-held hypothesis that ozone layer destruction may have been a primary kill mechanism which led to the End-Permian (terrestrial) mass extinction. We present this with related work from our group and colleagues that highlights the deleterious effects that elevated UV-B can have on plants, via disruption of their potential to reproduce. Being primary producers, we explain how UV-B-caused sterility could cause a collapse of the terrestrial biosphere.

Fossil insects from Aix-en-Provence at Oxford University Museum of Natural History

Beatrice Kerry¹, Leonidas-Romanos Davranoglou² and Ricardo Pérez-de la Fuente²

¹Harper Adams University, UK

²Oxford University Museum of Natural History, UK

Fossiliferous localities from the Aix-en-Provence Formation, in southeastern France, have been studied since the early-mid nineteenth century. Fish, plant remains and insects were deposited in a lagoonal or lacustrine setting under a subtropical climate during the late Oligocene (Chattian, ~25–23Ma). We have digitized and preliminarily assessed an almost completely unidentified, largely neglected fossil insect collection comprised of about 250 specimens from Aix-en-Provence at Oxford University Museum of Natural History (OUMNH), UK. Samples were collected by Rev. F. W. Hope during the 1840s and incorporated into his collection. About 80 % of the samples have been determined to, at least, order level, and more than half to family level. Dipterans are



the most abundant insects, clearly dominated by March flies (Bibionidae), followed by beetles, particularly weevils (Curculionidae), hemipterans, namely seed bugs (Lygaeidae), and diverse hymenopterans. Tentative, single occurrences of insect orders include a partial dragonfly nymph, a thrips and a moth. These data are in overall agreement with those from much larger Aix-en-Provence collections, suggesting that the OUMNH collection is unsorted. Aside from its historical significance and despite its small size, this 'rediscovered' collection has the potential to provide unusual taxa and contribute to the palaeoecological knowledge of this classic fossil site.

Controls on monticule height and spacing in Permian stenolaemate bryozoans with colony-wide feeding currents

Marcus Key¹, Eckart Hakansson² and Benjamin Edwards¹

¹Dickinson College, USA

²University of Western Australia, Australia

One of the challenges for bryozoans is avoiding refiltering of water which has already had its plankton removed. Larger colonies develop colony-wide maculae-centred feeding currents to avoid refiltering water. Elevated maculae (monticules) are ubiquitous on larger colonies. We hypothesize that height and spacing of monticules is inversely proportional to curvature of the colony surface. Larger flatter colonies should have higher and more closely spaced monticules. We compare two Permian palaeostomate bryozoans whose colonies form branches with elliptical cross-sections: the smaller and more elliptical cystoporate *Evactinostella crucialis* from Western Australia ($n = 17$) and the larger and flatter trepostome *Amphiporella* sp. from eastern North Greenland ($n = 15$). Using calipers and digital elevation models we measured curvature, monticule height and number of monticules per area. Results indicate that *Evactinostella* branches are twice as curved as those of *Amphiporella*, their monticules are half the height of *Amphiporella* and their monticules 22 % less densely spaced than those of *Amphiporella*. In *Evactinostella* colonies, surface curvature is inversely proportional to monticule height and spacing, which is not true for *Amphiporella*. Therefore, we conclude that the smaller and more curved the colony surface, the less need there is for robust colony-wide feeding currents created by tall closely spaced monticules.

Dynamics of community structure of Antarctic invertebrates over the end-Cretaceous extinction event

***Tasnuva Ming Khan^{1,2}, Rowan J. Whittle², Huw J. Griffiths², Katie M. Delahooke¹, Nile P. Stephenson¹, Andrea Manica¹ and Emily G. Mitchell¹**

¹University of Cambridge, UK

²British Antarctic Survey, Cambridge, UK

Seymour Island, Antarctic Peninsula, has one of the most highly expanded onshore Maastrichtian–Danian sedimentary successions in the world. The López de Bertodano Formation (~70–65.6 Ma) covers fluctuating sea surface temperatures, including several cold snaps, as well as warming due to Deccan Trap volcanism. Here we determine a novel network structure of the community using Bayesian network inference (BNI), using fossils from the Zinsmeister Collection of Paleontological Research Institution, USA. BNI statistically infers causal relationships or dependencies between



variables, *e.g.* taxonomic abundance, palaeoenvironment or geography, creating a network representation of the ecosystem. Data consisted of 7,400 fossils from 85 genera across bivalves, gastropods, cephalopods, echinoderms, brachiopods, scaphopods, polychaetes and octocorals, from 324 localities spanning six sub-units, KLBs 4–9. Results show the number of significantly non-random taxonomic co-occurrences increases towards the end of the Cretaceous, indicating increasing ecosystem complexity through time. However, variation in sampling effort, temporal uncertainty and taxonomic updates could potentially affect our results, so we applied different subsampling regimes to investigate their effects on network structure. Sample corrected results show a pattern of increasing ecological complexity throughout the Cretaceous, providing further insight into the ecological impact of catastrophic mass extinctions.

Evolution of coleoid neuroanatomy

Christian Klug¹, René Hoffmann², Helmut Tischlinger³, Dirk Fuchs⁴, Alexander Pohle^{1,2}, Alison Rowe⁵, Isabelle Rouget⁵ and Isabelle Kruta⁵

¹*University of Zurich, Switzerland*

²*Ruhr-Universität Bochum, Germany*

³*Jura-Museum, Eichstätt, Germany*

⁴*SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Germany*

⁵*Sorbonne Université, France*

Although molluscs lack mineralized structures protecting the main parts of their nervous system, coleoid fossils from Palaeozoic and Mesozoic conservation deposits worldwide occasionally preserve visible parts thereof. We have collected neuroanatomical information of several main clades of mainly Mesozoic coleoids. For the first time, we documented and compared the axial nerves of several groups, mostly of Jurassic forms. Similarly, we examined the cephalic cartilage of the same taxa, including the statocysts where preserved. For some of the groups, we documented these fossilized neuroanatomical details for the first time. We have put this information into phylogenetic context and compared their nervous systems to their modern relatives. Using these actualistic comparisons, we discuss potential links with morphology and proportions of parts of the nervous system with habitat depth and other aspects of their mode of life through coleoid evolution.

Shift to animal pollination during the Paleocene–Eocene Thermal Maximum

Vera Korasidis^{1,2}, Scott L. Wing², Paul Morse³, Natasha Vitek^{3,4} and Jon Bloch^{3,5}

¹*University of Melbourne, Australia*

²*Smithsonian Institution, USA*

³*Florida Museum of Natural History, USA*

⁴*University of Colorado, USA*

⁵*Stony Brook University, USA*

Major changes to terrestrial plant communities and biotas occurred globally ~56 Ma in response to the rapid warming during the Paleocene–Eocene Thermal Maximum (PETM). To better understand the effect of the PETM on pollination, we studied 38 palynological samples from the Bighorn Basin, Wyoming, USA. Pollen size, pollination mode of nearest living relatives (NLR), and pollen clump



prevalence all changed during the PETM. The proportion of taxa in the wind-pollinated size range (20–40 μm) decreased. The proportion of taxa with animal-pollinated NLR increased, as did the proportion of taxa preserved as pollen clumps. These three lines of evidence are consistent with a shift in pollination mode from wind to animal dispersal during the PETM. The shift to animal pollination is associated with a major change in floral composition and may reflect the arrival in the mid-latitude study area of biotically pollinated tropical species that maintained their pollination mode even as their ranges shifted north. Previous studies have presented evidence for higher abundance and diversity of insect feeding traces on plants during the PETM, and for higher diversity of small mammals that are potential pollinators. Warming climate and biome shifts during the PETM may have strengthened plant–animal interactions at middle latitudes.

Ecomorphology and macroevolution of the avian quadrate

***Pei-Chen Kuo**¹, **Guillermo Navalón**¹, **Roger B. J. Benson**^{2,4} and **Daniel J. Field**^{1,3}

¹*University of Cambridge, UK*

²*American Museum of Natural History, USA*

³*Natural History Museum, London, UK*

⁴*University of Oxford, UK*

In birds, the quadrate bone acts as a hinge between the lower jaw and the skull, playing an important role in cranial kinesis. As a result, it is expected that the evolution of avian quadrate morphology may have been influenced by selective pressures related to feeding ecology. However, the variation of quadrate morphology in living birds and its potential relationship with ecology have never been quantitatively characterized. Here we used three-dimensional geometric morphometrics and phylogenetic comparative methods to quantify morphological variation of the quadrate and its relationship with an array of key ecological features across 200 bird species covering all major lineages of extant birds. We found non-significant association between quadrate shape and ecology across different phylogenetic scales. Instead, other factors such as allometry and phylogeny exhibit stronger relationships with quadrate shape. Furthermore, our results suggest that the avian quadrate evolved as an integrated unit, yet it exhibits strong associations with the morphologies of neighbouring bones with which it articulates. Our results collectively suggest a more complex macroevolutionary scenario than originally envisioned in which quadrate morphology evolved jointly with other elements of the avian kinetic system, with the major lineages of birds exploring alternative quadrate morphologies.

The evolution of beaks in the Permian and Triassic

***Damiano Landi**¹, **Suresh Singh**¹, **Logan King**^{1,2}, **Emily J. Rayfield**¹ and **Michael J. Benton**¹

¹*University of Bristol, Bristol, UK*

²*Institute of Vertebrate Paleontology and Paleoanthropology, China*

Beaks are compound feeding structures, present today only in birds and turtles. However, they were much more widespread in the past, emerging initially in Middle Permian synapsids and then appearing in multiple sauropsid clades after the end-Permian extinction. Our goal is to explore the biomechanical characteristics of these early beaked amniotes and identify potential cases



of morphological or functional convergence. Here we examine the evolution of beaks across dicynodonts, rhynchosaurs, allokotosaurs, aetosaurs, poposauroids and basal dinosauriforms using a combination of elliptical Fourier analysis and two-dimensional semi-landmark analysis to assess mandibular shape variation and beaked portions of the upper and lower jaws. We also use multivariate approaches to quantify variation in key functional traits of the mandibles. We find a contrasting pattern of synapsid and diapsid beak morphospace occupation across the upper and lower jaws; there is a strong separation between synapsid and archosauromorph beaks, except in the beaked portion of the mandibles, which exhibit some overlap between dicynodonts and rhynchosaurs. Functional analysis confirms a broad distinction between synapsids and diapsids, while also highlighting how rhynchosaurs shared some beak functionality with dicynodonts. This suggests similar functions in food acquisition for the beaked lower jaws of these two otherwise very distinct clades.

No jaws? No problem. Morphological diversity in the feeding apparatus of heterostracan jawless “fishes” (Agnatha: Heterostraci)

Agnese Lanzetti^{1,2}, Richard P. Dearden^{1,3}, Andrew S. Jones¹, Sam Giles¹, Zerina Johanson², Stephan Lautenschlager¹, Emma Randle¹ and Ivan J. Sansom¹

¹University of Birmingham, UK

²Natural History Museum, London, UK

³Naturalis Biodiversity Center, Netherlands

The evolution of the jaw marks a dramatic shift in vertebrate evolution, but, before that, jawless forms diversified and dominated Palaeozoic environments. Heterostracans are a morphologically diverse group of armoured, jawless stem-gnathostomes that were a major component of marine ecosystems in the Silurian and Devonian. In this project, we aim to characterize the anatomical and functional diversity of heterostracans by analysing 3D preserved complete fossils with high-resolution CT scanning, and we were able to identify evolutionary patterns and polarize the character evolution. We delimit three main functional groups based on the number and morphology of the oral and post-oral plates. The multi-plated forms have more than ten oral plates articulated with a post-oral plate on the ventral surface. They likely represent the ancestral state of the group and are found across the evolutionary tree. We also found two additional forms, showing a progressive reduction in plate number and complexity: *Anglaspis*-like forms, with a reduced post-oral plate in the centre and 2–3 elongated oral plates on each side, and *Poraspis*-like forms, with only an enlarged post-oral plate and small accessory plates on the side. This variety of morphologies points to these animals occupying a variety of feeding niches and environments.



A new bubble-headed trilobite species from the Upper Ordovician of southwest Wales

***Manus Leidi**¹, **Lucy M. E. McCobb**², **Patrick D. McDermott**³ and **Alan W. Owen**⁴

¹*Cardiff University, UK*

²*Amgueddfa Cymru – National Museum Wales, UK*

³*Independent*

⁴*University of Glasgow, UK*

The Sholeshook Limestone Formation of southwest Wales, UK preserves a diverse trilobite fauna of upper Katian age (Ashgill, Cautleyan-Rawtheyan), comprising over fifty species which were documented in detail by Price over 40 years ago. He concluded that the formation probably represents deposition on the upper part of the slope between the platform edge and basin. An important new locality near Llanddowror in Carmarthenshire has yielded the richest fauna collected from any single locality in the Sholeshook Limestone, and includes abundant echinoderms (crinoids and cystoids) and brachiopods, along with rarer bryozoans, gastropods, cephalopods, ostracods and corals. The abundant trilobites include over 200 specimens of a new species of the bubble-headed trilobite *Staurocephalus*, previously considered uncommon in the formation. Although no fully articulated specimens were found, the material is the most abundant and well-preserved of any Ordovician *Staurocephalus* species known from Britain and Ireland, and enables the complicated 3D structure of its cephalon to be reconstructed. *Staurocephalus* sp. nov. is the earliest representative of the genus recorded in Avalonia, following its presumed migration into the area from Laurentia or Baltica, and its occurrence has significant palaeoecological and stratigraphical implications.

How predation could explain the unique morphology of ammonites

Robert Lemanis and **Igor Zlotnikov**

B CUBE-Center for Molecular Bioengineering, Germany

Predation is a powerful driver for evolutionary change, and molluscs have long been a common group to study the role of predation and escalation in shaping morphological change through time. It is interesting then to note the lack of investigation into the potential connections between predation and one of the more mysterious evolutionary trends in the clade, the ammonitic septum. The persistent increase in complexity from the Palaeozoic through the Mesozoic has traditionally been explained as an adaptation to increasing habitat depth. As this hypothesis falls out of favour, we propose predation as a potential driver behind this increasing complexity. We produced tomographic models of two end-member septal morphologies and several theoretical septal morphologies based on a minimum surface algorithm. Finite element based buckling simulations were used to study the robustness of these structures. We show how more complex septa are better able to resist unrecoverable, and potentially fatal, deformation by increasing the force needed to buckle the structure. Septal morphology has been shown to respond to ecological changes, such as transgression–regression cycles. Understanding why these changes might have occurred will deepen our understanding of the biological aspect of such shifts.



Macroalgae from the early Cambrian Chengjiang biota

***Gaorong Li¹, Fan Wei^{1,2}, Jin Guo^{1,3} and Peiyun Cong^{1,2}**

¹*Yunnan University, China*

²*Nanjing Institute of Geology and Palaeontology, China*

³*Chengjiang Science Museum, China*

The Chengjiang biota of South China documents crucial information about the early Cambrian marine ecosystem. However, the macroalgae therein as primary producers have not been comprehensively investigated until now. Here we systematically (re-)describe and revise the Chengjiang macroalgae based on the collection over the last four decades. A total of 13 macroalgal genera with 17 species are now validated, including one new genus (*Yunnanospirellus* gen. nov.) with two new species (*Y. typica* sp. nov. and *Y. elegans* sp. nov.) and six species of five genera (*Tawuia* sp., *Morania fragmenta*, *Liulingjitaenia alloplecta*, *Longfengshania stipitate*, *Lo. spheria* and *Paralongfengshania sicyoides*) that have not been previously reported in the Chengjiang biota. The Chengjiang macroalgae can be briefly grouped into two ecological categories, the attached and the unattached, based on the presence/absence of holdfasts. The presence of diverse attached algae (nine species of six genera) adapted to Proterozoic firm substrate (PFS) from the Chengjiang biota reinforces the claim that the PFS extended at least into the early Cambrian. Nevertheless, it is the diverse and abundant unattached macroalgae that function as an important driver in the diversification and ecological expansion (into the water column) of metazoans during the Cambrian Explosion.

Bivalve-barnacle pseudoplanktonic colonization of wood from the Toarcian (Lower Jurassic) Strawberry Bank Lagerstätte, Somerset, UK

Crispin T. S. Little¹, Andy S. Gale², Matt Williams³, Øyvind Hammer⁴ and Vincent Fernandez⁵

¹*University of Leeds, UK*

²*University of Portsmouth, UK*

³*Bath Royal Literary and Scientific Institution, UK*

⁴*Natural History Museum, University of Oslo, Norway*

⁵*European Synchrotron Radiation Facility, Grenoble, France*

Pseudoplankton are organisms that are adapted for a mode of life attached to floating objects. In modern oceans common examples are lepadid barnacles, which attach themselves to man-made and natural objects, especially wood logs. In the fossil record, pseudoplankton examples are commonly found in black shales, such as the lower Toarcian Posidonia Shale Formation of Germany. One example from this unit is the occurrence of the numerous disarticulated specimens of the phosphatic-shelled eolepadid barnacle *Toarcolepas mutans* associated with a piece of fossil wood, which constitutes the oldest example of pseudoplanktonic barnacles in the fossil record. Here we record a limestone concretion from the lower Toarcian Strawberry Bank Lagerstätte (Ilminster, Somerset, UK) that preserves a piece of fossil wood with a pseudoplanktonic colony comprising at least a hundred specimens of *Toarcolepas mutans* that attached onto a layer of *Pseudomytiloides dubius* bivalves, that had already attached onto the wood. This is one of very few examples of temporal succession for pseudoplankton in the Toarcian and is also unusual in being preserved in a mixed carbonate-siliciclastic facies rather than a black shale. The occurrence of *T. mutans* in the



Strawberry Bank Lagerstätte concretion represents the second record of the species and also the equal oldest example of pseudoplanktonic barnacles in the fossil record.

Morphological evolution of marine animals during the Permian–Triassic mass extinction

Xiaokang Liu^{1,2}, Haijun Song² and Daniele Silvestro¹

¹*University of Fribourg, Switzerland*

²*China University of Geosciences, China*

The Permian–Triassic mass extinction (PTME), is the most severe biotic crisis in Earth's evolutionary history, with over 80 % of marine species estimated to have gone extinct. The magnitude and duration of the biodiversity crisis during the PTME have been thoroughly studied. Yet, the consequences of this mass extinction on morphological disparity of marine animals and their evolution during this critical interval remains largely debated. Here we develop a new approach based on deep learning to extract morphological matrices from images of fossil specimens and use it to explore the evolution of disparity across the PTME. We apply our pipeline to a newly compiled high-resolution dataset of 730 species of six marine clades. We found that the mass extinction led to different disparity patterns across clades, with ammonoids and brachiopods showing a morphological reduction and selectivity, while extinctions in bivalves did not significantly alter their morphospace. We found that species with complex ornamentations and specialized shells were more vulnerable to extinction, while morphological generalist species were more resilient. Our approach offers new opportunities to study morphospace dynamics in deep time across large datasets. Our preliminary findings show that the magnitude and selectivity of mass extinctions had nuanced impacts on morphological disparity among clades.

Liquid feeding in the palaeocharinid trigonotarbid of the Lower Devonian Rhynie chert

***Emma J. Long¹, Gregory D. Edgecombe¹ and Xiaoya Ma²**

¹*Natural History Museum, London, UK*

²*University of Exeter, UK*

Trigonotarbids, an extinct order of armoured, spider-like arachnids, were key terrestrial predators in the Devonian. Body fossils detailing their exoskeletal architecture span ~125 million years between the late Silurian and early Permian. Characteristic morphologies include a trilobate opisthosoma, clasp-knife chelicerae, paired book lungs and an intricate preoral filtration apparatus that facilitated liquid feeding on land. However, the compression-fossil preservation of many Devonian trigonotarbids has limited our understanding of their detailed morphology. Scotland's Rhynie chert, an exceptional Lower Devonian (~408 Ma) deposit containing the earliest recorded complex terrestrial ecosystem, provides a remarkable opportunity to study trigonotarbid anatomy. Within this deposit, cuticle of the genus *Palaeocharinus* is preserved in three dimensions with extraordinary fidelity. Here we present the first confocal laser scanning microscopy (CLSM) data for *Palaeocharinus*. These data illustrate the three-dimensional morphology of the tiered filtration apparatus, shown to comprise a coarse outer mesh of interlacing plumose setae and a fine inner filter, its comb-like setae



bearing delicate ventral spines. The combined actions of the cheliceral teeth and fangs, the palpal denticles and the tiered filtration system paint a vivid picture of a sophisticated terrestrial predator with an architecturally modern feeding mechanism.

A beginner's guide to 3D modelling: a 'fantastic voyage' through Cambrian organ systems

***Emma J. Long**^{1,2,3}, **Martin R. Smith**³, **Katherine Dobson**⁴ and **Alavya Dhungana**³

¹Natural History Museum, London, UK

²University of Exeter, UK

³Durham University, UK

⁴University of Strathclyde, UK

Three-dimensional Cambrian body fossils are exceptionally rare, with notable examples from the Orsten of Sweden and Kuanchanpu of China. Recent studies have even demonstrated the recovery of volume data from compression fossils, like China's Chengjiang fauna. Unlike the compression fossils of the Burgess Shale and Chengjiang, relatively undistorted 3D specimens offer clear, unobstructed insights into the anatomy of early arthropods. In the last two decades, micro-computed tomography (CT) techniques, such as synchrotron X-ray radiation tomography (SXRT), have revealed the internal and external features of Cambrian arthropods. Various post-acquisitional methodologies have emerged, involving imaging software like Drishti, Blender, Dragonfly and Avizo. However, the complexity of software and the high turnover of trained researchers, particularly students who may not continue in academia, contribute to knowledge gaps within institutions. Here we present a post-acquisitional workflow for modelling volume data in Avizo using a SRXT dataset of a Cambrian larva from the Yu'anshan Formation of China. This fossil exhibits exceptional preservation, with voids replicating the internal anatomy of the nervous, digestive, and circulatory systems in 3D. The presented workflow aims to highlight the challenges of modelling in palaeontology, while providing systematic and replicable techniques for researchers entering the field of 3D modelling.

Moulting and development in a freshwater prawn from the Late Cretaceous of Morocco

***Sinéad Lynch**¹, **Pierre Gueriau**¹, **Harriet B. Drage**¹, **Didier B. Dutheil**², **Sylvain Charbonnier**² and **Allison C. Daley**¹

¹University of Lausanne, Switzerland

²Sorbonne Université, France

Cretapenaeus berberus Garassino, Pasini & Dutheil, 2006 is a freshwater prawn (Dendrobranchiata, Penaeidae) from the Upper Cretaceous (Cenomanian) Kem Kem Group of Morocco. *C. berberus* is the only known freshwater penaeid, among the uncommon freshwater-dwelling species in Dendrobranchiata. New *C. berberus* specimens enable us to refine its morphological description and analyse growth. Of the ~100 specimens of *C. berberus* examined, most are carcasses and a few are moults. Moults can be recognized by their displaced cephalothorax, resulting from opening of an exuvial gape at the cephalothorax posterior to enable shedding of the old exoskeleton.



Exceptionally preserved muscles, found only in carcasses, provide additional evidence to distinguish moults from carcasses. Multispectral imaging and geochemical characterization will be used to investigate further differences in carcass and moult composition. Preliminary analysis shows a wide size range in the sample, with cephalothorax lengths measuring from ~2 to 23 mm. All moults are from fairly large specimens. Early larval stages appear to be absent, and the smallest specimens are either late larval or early juvenile stages. As in all decapods, no segments are added during post-larval growth. *C. berberus* provides Late Cretaceous evidence of the moulting mechanism commonly observed in modern decapods and possibly indeterminate growth.

Environmental controls on animal distribution and soft-bodied fossil preservation of early Cambrian eastern Yunnan

Xiaoya Ma^{1,2}

¹*Yunnan University, China*

²*University of Exeter, UK*

The Cambrian Explosion is now universally accepted as a genuine rapid evolutionary event, but the co-evolution of life and environment during the Ediacaran–Cambrian transition remains largely unanswered or highly controversial. One of the key difficulties is that palaeoenvironmental data are often not well correlated with fossil data in a temporal and spatial framework, and the local and global signals are not well constrained. Therefore, to address these challenges and to constrain the timing of bio- and geo-events, it is essential to conduct a case study on a regional scale among Ediacaran–Cambrian successions that allows integrating multiple high-resolution datasets within a chronostratigraphic framework. Eastern Yunnan in Southwest China, with its unique combination of complete and richly fossiliferous Ediacaran–Cambrian strata, is one of the best candidates for such a study. Therefore, I will review our latest understanding on the palaeontological, geochemical, sedimentological and taphonomic datasets of early Cambrian eastern Yunnan, to establish the causal relationship between palaeoenvironmental changes and animal distribution or exceptional soft-bodied fossil preservation, which will contribute to identify triggering factors for the origin and early evolution of bilaterian animals.

The origin of loopy leaf venation networks: a consequence of herbivory?

Luke Mander¹, **Andres Baresch**² and **Hywel Williams**³

¹*The Open University, UK*

²*Stanford University, USA*

³*University of Exeter, UK*

Networks vary widely in their architecture and functional properties. Modelling work has shown that networks optimized for transportation efficiency are branching trees, while networks optimized for resistance to damage are characterized by loops. Illustrations of these two architectures are found in leaf venation networks, and branching networks are found in ferns as well as the seed plant *Ginkgo*, while networks with loops are typical of flowering plants and some ferns. The first evolutionary transition from branched to loopy venation is recorded by leaf fossils in the Westphalian of the Carboniferous, but there is currently a lack of data on the effects of damage in



extinct leaf venation networks. Consequently, it is unclear whether loopy leaf venation networks could be a possible outcome of selection for resistance to damage. We address this issue here with a computational analysis of venation network robustness that is focused on fossil leaves from the Westphalian. We compare the responses of real-world fossil leaf venation networks to simulated damage and interpret the results in the context of the Carboniferous record of herbivory. We suggest that herbivory may have played a role in driving the evolution of loopy architectures in Carboniferous leaf venation networks.

Upper Paleocene–Lower Eocene tropical rainforests in West Africa: descriptive systematics of pollen and spores from southeastern Nigeria

Luke Mander¹, Carlos Jaramillo² and Francisca Oboh-Ikuenobe³

¹*The Open University, UK*

²*Smithsonian Tropical Research Institute, Panama*

³*Missouri University of Science and Technology, USA*

Tropical rainforests are the most structurally complex and diverse land ecosystems on Earth, and fossil pollen and spores are a vital source of information on the geological history of these unique ecosystems. However, such information relies on a sound underpinning taxonomic framework, which is challenging to achieve in the tropics because of the large number of pollen and spore morphotypes that are encountered in low latitude sediment samples. Fossil pollen and spores from tropical West Africa are in particular need of taxonomic work as there are numerous species that have not been described and because of the widespread use of illegitimate names in this region. In order to begin this work we have undertaken a descriptive systematic study of pollen and spores from 15 sediment samples spanning the Upper Paleocene–Lower Eocene of southeastern Nigeria. A palynoflora consisting of 29 spores, two gymnosperm pollen grains and 138 angiosperm pollen grains is described. Two new spore species are proposed, and one new genus and 18 new species of angiosperm pollen are proposed. The richness of each sample ranges from 29 to 76 taxa, and rarefaction analysis indicates diversification of rainforests from the Paleocene to the Eocene in tropical West Africa.

Conodonts occupied high trophic levels in the Middle Triassic

Carlos Martinez Perez^{1,2}, Victor Gines Vidal¹ and Emilia Jarochowska³

¹*University of Valencia, Spain*

²*University of Bristol, UK*

³*Utrecht University, Netherlands*

Conodonts, extinct marine vertebrates possessing mineralized tooth-like structures, exhibit a vast array of tooth morphologies. This disparity suggests specific adaptations to a wide range of trophic niches. However, the diet of conodonts and their role in ecosystems remain a controversy. We used a novel proxy for the relative position in the trophic network, Sr/Ca and Ba/Ca ratios, to estimate the position of conodonts with respect to other vertebrates. We focus on the Middle Triassic ecosystem preserved at Henarejos, Spain, which developed in a restricted Tethyan basin. Reconstructions based on chondrichthyans, osteichthyans, placodonts and conodonts show that each taxon occupied



a distinct trophic niche with limited overlap. The relative positions of fish are consistent with reconstructions based on functional morphology and other proxies. By the Middle Triassic, marine ecosystems were occupied by a wide range of fish and reptile predators reaching large body sizes. It has been hypothesized that this led to the demise of conodonts, who would not be able to compete for food with larger and more efficient feeders. However, our findings indicate that conodonts, similar to other vertebrates, occupied a trophic niche that, given the small size of the animals, might be consistent with parasitic or scavenger feeding.

Protecting Newfoundland's palaeontological heritage: mitigating anthropogenic and environmental damage to the Ediacaran fossils of Upper Island Cove

***Christopher McKean¹, Jack J. Matthews^{1,2} and Duncan McIlroy¹**

¹*Memorial University of Newfoundland, Canada*

²*Oxford University Museum of Natural History, UK*

Over 200 fossils belonging to the Ediacaran biota have been recognized from a single site in the town of Upper Island Cove, Newfoundland, Canada. These fossils preserve high-relief, sub-mm morphological detail providing an opportunity to further our understanding on some of the earliest Ediacaran organisms. Unlike many other Ediacaran localities the site is at risk to both high impact anthropogenic and environmental events, due to its location in the town and close proximity to the ocean. As part of a year-long study cameras were set up to record the erosional events impacting the fossiliferous surface. Rare high impact anthropogenic events such as vandalism have been noted at the site, alongside the potential for inadvertent damage caused by misuse through poor footwear and inappropriate activities. Environmental events are more common and present the highest risk of damage to the fossils through high energy waves covering the surface and the formation of large ice sheets during the winter which engulfed the fossils on numerous occasions. Work is now under way to implement methods that will mitigate the challenges that the site faces and minimize any future damage. Some of these methods may be pertinent to other at-risk fossil localities found across the world.

The snapshot effect: could faster decay sometimes translate into better fossil preservation?

Sean McMahon¹ and Russell J. Garwood^{2,3}

¹*University of Edinburgh, UK*

²*The University of Manchester, UK*

³*Natural History Museum, London, UK*

Fossilization is often characterized as a race between decay and preservation. Intuitively, a lower decay rate favours the formation of higher-fidelity fossils by allowing more time for preservation to act. This is true when processes of preservation act slowly. However, many important fossil assemblages were preserved by abrupt events that captured still-living organisms, as well as already-deceased and decaying ones. Using a novel birth–death model incorporating decay, we suggest that this creates a ‘snapshot’ effect that inverts the normal relationship between decay rate and preservation potential: organisms that tend to decay slowly are more likely to be captured in a state of advanced decay (since they exist in this state for a long time), while organisms that tend



to decay quickly are more likely to be very well preserved (since they only exist briefly in a state of decay). This effect may be seen in certain Konservat-Lagerstätten (e.g. the Rhynie chert). However, lifespan is also a contributing factor: the longer the lifespan, the fewer dead/decaying individuals are captured in any random snapshot. Overall, the relationship between average decay rate and average state of preservation is not as straightforward as it may appear.

Associated material of small-bodied pterosaurs from the Middle Jurassic of Skye, Scotland

***Luke E. Meade¹**, **Roger B. J. Benson²** and **Richard J. Butler¹**

¹*University of Birmingham, UK*

²*American Museum of Natural History, USA*

The Middle Jurassic was a crucial time of pterosaur diversification including the transition between non-pterodactyloid and pterodactyloid body plans, but the pterosaur fossil record during this interval is sparse, mostly comprising isolated elements. Recently, a couple of well-preserved Middle Jurassic pterosaurs have been described from Scotland. The Kilmaluag Formation (Bathonian) of Skye preserves one of the most diverse Middle Jurassic tetrapod fossil assemblages globally, including associated pterosaur remains, and has potential as a vital site for examining pterosaur evolution during this interval. We present two new small pterosaur specimens (estimated wingspan <50 cm) from fieldwork in the Kilmaluag Formation. One comprises shoulder girdle (coracoid) and forelimb material, including well-preserved and associated wrist material. A second specimen includes much of the post-cranial axial skeleton, pelvis and hindlimb. Both are preserved in three-dimensions and CT-scanning reveals detailed anatomy. These specimens show similarities to a new Kilmaluag pterosaur taxon, currently under description, but also differences that may be taxonomically informative. Examination of this new material provides important insights into pterosaur evolution during an interval of morphological innovation and diversification. In particular, we are able to provide new information on the evolution and functional morphology of the pterosaur wrist, with implications for locomotion.

High-density 3D geometric morphometrics of otolith shape in Sciaenidae (Osteichthyes: Actinopterygii) reveals phylogenetic signal

Dominique Mediodia^{1,2,3}, **Siao-Man Wu¹**, **Hao-Chun Hsu¹**, **Roland B. Sookias⁴**, **Valentin Fischer⁴** and **Chien-Hsiang Lin¹**

¹*Academia Sinica, Taiwan*

²*National Taiwan Normal University, Taiwan*

³*University of the Philippines Visayas, Philippines*

⁴*Université de Liège, Belgium*

The fish otolith is vital in sensing vibrations and balance, and its shape is strongly affected by both ecology and phylogeny. Otoliths fossilize well, and are thus of utility in assessing diversity change through time. Sciaenidae – croakers – are a widespread, ecomorphologically diverse and speciose clade, with major importance in assessing past environment; quantifying their otolith shape has the potential to greatly assist in our understanding of marine climatic/biodiversity change. We employ a new protocol for high-density geometric morphometrics (HDGMM) to a large 3D scan (light, CT)



dataset of sciaenid extant and fossil otolith 3D scans to investigate the degree of phylogenetic and ecological signal. We focus on the extant genera *Panna*, *Nibea*, *Pennahia*, *Cynoscion* and *Larimichthys* due to data availability and species richness. We find significant phylogenetic signal in extant otolith shape and good generic and species assignment accuracy. We find no significant association with ecology once phylogeny is removed. Phylogenetic inference from otolith shape accurately assigns species and genera, but interspecific/intergeneric relationships are less accurate. HDGMM provides a useful new toolset, allowing more objective, accurate taxonomic assignment and thus biodiversity assessment, and facilitates placement of fossils. This in turn will shed light on ecosystem and climatic change in Cenozoic marine systems.

Molecular characterization of acritarchs: applying infrared spectroscopy to better infer biological affinities with other organic-walled microfossils

***Pjotr Meyvich**¹, **Hanne François**¹, **Philippe Steemans**², **Victoria García Muro**³, **Kenneth N. Mertens**⁴, **Pieter R. Gurdebeke**¹, **Thomas Servais**⁵, **Vânia Correia**⁶, **Francesca Sangiorgi**⁷, **Kasia K. Śliwińska**⁸, **Henk Vrielinck**⁹, **Stephen Louwye**¹

¹Department of Geology, Ghent University, Belgium

²Département de Géologie, Evolution and diversity dynamics lab, Université de Liège, Belgium

³Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET, Universidad Nacional de Cuyo (UNCuyo), Mendoza, Argentina.

⁴Ifremer, LITTORAL, Station Concarneau, France

⁵Unité Evo-Eco-Paléo (EEP), CNRS / Université de Lille, Sciences et Technologies, France

⁶Natural Resources Canada, Geological Survey of Canada, Atlantic, Canada

⁷Earth Sciences, Laboratory of Palaeobotany and Palynology, Utrecht University, Netherlands

⁸Geological Survey of Denmark and Greenland, Denmark

⁹Department of Solid-State Sciences, Ghent University, Belgium

Acritarchs are an informal, polyphyletic, and morphologically heterogeneous group of organic-walled microfossils of unknown biological affinity. Some acritarchs share morphological similarities with certain microplankton resting stages (from *e.g.* dinoflagellates, prasinophycean-, chlorophycean- and zygnematophycean green algae), others with miospores, egg cases of zooplankton, or even skeletal fragments of higher organisms. For most extant organism groups able to produce organic-walled micro-remains, the structural, fossilizable molecular compounds are relatively well known. These are dinosporin in dinoflagellate cysts, algaenan and cellulose in green algae, sporopollenin in spores and pollen, proteinaceous polysaccharides in zooplankton eggs, chitin in higher animals and cellulose/lignin/cutin in higher plants. While considering the taphonomy of such compounds, molecular parallels can be drawn between acritarchs and microfossils with known biological affinities which, together with possible morphological parallels, provide a stronger argument for inferring biological assignments. Here we used attenuated total reflection micro-Fourier transform infrared spectroscopy to collect a large dataset from a wide range of Quaternary to Palaeozoic micro-remains, including many acritarch species. These data reveal a – sometimes large – molecular variability in samples with taxonomically and morphologically heterogeneous assemblages. This shows that chemo-specific signatures can survive diagenesis and can sometimes be used to better infer the biological affinity of acritarchs.



Unravelling the molecular taphonomy of organic-walled dinoflagellate cysts via infrared spectroscopy

***Pjotr Meyvisch¹**, **Hanne François¹**, **Kenneth N. Mertens²**, **Pieter R. Gurdebeke¹**, **Vera Pospelova³**, **Gerard J. M. Versteegh^{4,5}**, **Kasia K. Śliwińska⁶**, **Vânia Correia⁷**, **Mariusz Niechwedowicz⁸**, **Francesca Sangiorgi⁹**, **Viktória Baranyi¹⁰**, **Manuel Bringué⁷**, **Henk Vrielinck¹** and **Stephen Louwye¹**

¹*Ghent University, Belgium*

²*Ifremer, Concarneau, France*

³*University of Minnesota, USA*

⁴*MARUM, University of Bremen, Germany*

⁵*Jacobs University Bremen, Germany*

⁶*Geological Survey of Denmark and Greenland, Denmark*

⁷*Geological Survey of Canada, Canada*

⁸*Stanisław Józef Thugutt Geological Museum, University of Warsaw, Poland*

⁹*Utrecht University, Netherlands*

¹⁰*Croatian Geological Survey (HGI-CGS), Croatia*

Dinoflagellates are an extant group of unicellular, eukaryotic microalgae occurring in a wide range of aquatic environments. They can form resistant, organic-walled resting stages (dinocysts); the earliest body fossils appear in the Middle Triassic. Dinocyst walls are composed of a heavily cross-linked, nitrogenous, cellulose-like carbohydrate, 'dinosporin', which is compositionally distinct from other resistant biomacromolecules such as sporopollenin (pollen and spores) and algaenan (green algae). Macromolecular analyses of modern dinosporin via attenuated total reflection micro-Fourier transform infrared (ATR micro-FTIR) spectroscopy revealed a variable compound: sometimes strongly influenced by the presence of brown colour-inducing (possibly eumelanin) pigments, or with additional aromatic ('sporopollenin-like') or aliphatic ('algaenan-like') moieties. Here we used ATR micro-FTIR spectroscopy to collect a large dataset from a wide range of Meso- and Cenozoic dinocysts to investigate their molecular taphonomy. These data reveal an expected increase in the aliphaticity of dinosporin over time, likely related to early-diagenetic *in situ* polymerization of lipids. Furthermore, modern dinosporin variability was detected in fossil dinocysts up to the late Paleocene, highlighting the palaeoecological and taxonomical value of these chemospecific signatures. Finally, it is hypothesized that some dinosporin types might be better suited for low-salinity (aliphatic type) or high-UV (pigmented and aromatic types) aquatic environments.

Ediacaran ecological dynamics across large spatial scales

Emily G. Mitchell, ***Nile P. Stephenson**, **Katie M. Delahooke** and **Charlotte G. Kenchington**
University of Cambridge, UK

The Ediacaran strata of Newfoundland, Canada (580–560Ma) record some of the first animal communities. The *in situ* preservation of these sessile organisms means that the positions and sizes of specimens on the bedding planes encapsulate their life-histories, enabling spatial analyses to reconstruct their ecological dynamics. However, it is not known how representative the ecological dynamics of individual outcrops are across large spatial scales. Fortunately, the E and G surfaces at Mistaken Point outcrop at multiple locations, providing the opportunity to compare ecological



dynamics between communities separated by large spatial scales (800 m between outcrops). In this study we collected data from two outcrops each of E and G surfaces using a combination of laser-line probe, LiDAR and photogrammetry. To account for preservational and area-mapped differences, we subsampled the larger (E surface Yale and G surface Watern Cove) to the size of smaller surfaces (main G surface, E surface West). Accounting for these sampling differences, we found that the G and E surfaces exhibited remarkably similar ecological dynamics. Our results demonstrate the consistency of Mistaken Point dynamics over large spatial scales, which suggests that analyses of even small outcrops could be good representations of eco-evolutionary dynamics during the Ediacaran.

First record of a possible synziphosurine from the Middle Ordovician of Baltoscandia

Dmitry Molodtsov¹, Maria E. McNamara² and Yakov Tarasov¹

¹*Independent*

²*University College Cork, Ireland*

The Ordovician carbonate succession of the eastern Baltic is renowned for rich and well-preserved trilobite fauna. However, there were no records of non-trilobite arthropods, except ostracods. Here we report articulated, non-biomineralized arthropod remains from the limestones of the Aseri Regional Stage (Darriwilian), *Asaphus kowalewskii* zone. The specimen is preserved as a powdery carbonaceous film retaining the overall three-dimensional shape of the exoskeleton, with deformations suggesting the lack of biomineralization at the time of burial. Cephalic shield without visible eyes on the dorsal side, followed by at least nine articulated somites; tergites 2-7 are transversally trilobed, 7-9 mm long (sag., including the articulating half-ring), with a single node/cusp on each flank of the axis; wide doublure is present in the pleural regions; tergites 8-9 lack pleurae, sternite of the segment 9 is exposed in cross-section; no appendages visible. These characters suggest a synziphosurine affinity, although other possibilities (e.g. Tremaglaspididae) cannot be ruled out without studying the ventral morphology. Synziphosurines are unknown between the Tremadocian and the Silurian, so the present find significantly adds to the group's evolutionary history. It also suggests a revision of the potential for 'soft-body' preservation in the Ordovician storm-generated carbonate sequences of eastern Baltoscandia.

Clams over time: imprint of global climate changes on the Phanerozoic palaeobiodiversity of bivalves

***Coraline Montariol, Claude Monnet and Sébastien Clausen**

Université de Lille, France

Although bivalves constitute a major and key component of modern and past ecosystems, their global diversification throughout the Phanerozoic and its major environmental drivers remains poorly known. Therefore, to investigate palaeobiodiversity patterns of clams in deep time, we analysed the occurrences of marine bivalves from the Paleobiology Database through the Ordovician–Neogene interval and by applying modern measures of taxonomic richness. Our results show that the evolutionary history of these organisms is characterized by increasing



palaeobiodiversity across the Phanerozoic. Nevertheless, this pervasive trend is also punctuated by four major extinction events (during the Hirnantian and at the Permian/Triassic, Jurassic/Cretaceous and Cretaceous/Tertiary boundaries) from which bivalves recovered quickly. To gain further insights, we conducted a factor analysis of within-families genus richness to establish the evolutionary faunas of bivalves. Interestingly, our study shows four successive faunas in time, only partly related to the events previously mentioned. Finally, several factors are involved in bivalve palaeobiodiversity history. Both results can be correlated to the abundance of plankton, the marine level and the sea-water chemistry, but more broadly to global climate changes. Furthermore, the major changes in the biodiversity dynamics and the evolutionary faunas of bivalves are concomitant with shifts in their ecological habits.

Evaluation of cophylogenetic methods and extinction risk among parasites

***Laura Mulvey¹, Tim Brandler¹, Wade Dismukes² and Jordan Satler³**

¹*Friedrich-Alexander-Universität Erlangen-Nürnberg, Germany*

²*Iowa State University, USA*

³*The Ohio State University, USA*

As the effects of climate change become more extreme, parasites are anticipated to undergo changes that will influence relationships with their hosts, and their potential transmission to new hosts. Understanding and predicting the response of parasites to climate change is therefore an important goal for conservation biology. Cophylogenetic methods estimate the evolutionary history between parasites and their hosts, allowing us to understand how they have co-evolved together through time and to make predictions about co-extinction risk. Recent studies have suggested that the use of model-based cophylogenetic methods may out-perform parsimony-based approaches. Yet, up to now, no available approaches have been thoroughly validated. Novel cophylogenetic simulation tools create the opportunity to test such methods. Here we test and compare the performance of competing cophylogenetic methods using simulated datasets. We demonstrate scenarios in which output from cophylogenetic methods can reliably provide insight into how different parasite groups may respond to the extinction of their host, whether by coextinction or host switching. We also highlight scenarios in which further model development will be crucial to better understand the impact of stress on host parasite interactions.

Life under a Cambrian Sun: reviving an early Phanerozoic mudflat biota

***Giovanni Mussini and Nicholas J. Butterfield**

University of Cambridge, UK

The aftermath of the Cambrian Explosion in intertidal environments remains poorly understood, largely due to a sparse body fossil record hampering attribution of local ichnofossils to their animal tracemakers. We tackle the gaps in our picture of these critical ecological settings by combining evidence from trace fossils and small carbonaceous fossils (SCFs) from the mid-Cambrian (late Guzhangian, Series 3) Pika Formation of Jasper National Park, Alberta, Canada. Fine-grained, finely laminated mudstones with abundant mudcracks and U-shaped *Diplocraterion* burrows record a periodically subaerial mudflat that likely witnessed strong variations in temperature, salinity and



oxygenation. The same facies yield abundant priapulid, annelid and wiwaxiid SCFs together with sparse brachiopod macrofossils, reflecting a diverse metazoan biota. Animal body fossils co-occur with dense *in situ* aggregates of compact, pill-shaped faecal pellets, which accumulated both on bedding plane surfaces and inside *Diplocraterion* burrows. The recurrent co-occurrence and physical association between the pellets and *Diplocraterion* suggest a shared tracemaker, identifiable as a deposit- or nonselective suspension-feeding polychaete based on the local SCF record and actualistic comparisons. Our findings map novel Cambrian feeding strategies and sediment engineering far beyond deepwater Burgess Shale-type settings, suggesting that lophotrochozoans and scalidophorans outclassed arthropods as key architects of early animal-dominated intertidal ecologies.

Diet of the endemic pygmy hippo *Phanourios minor* from Aghia Napa (Cyprus) based on carbon isotope analysis ($\delta^{13}\text{C}$) and Hypsodonty Index calculation (HI)

***Maria Anna Nakasi¹, Elizabeth Stathopoulou¹, Maria Tassi², Petros Karalis²,
Elissavet Dotsika², Georgios Theodorou¹ and Efthymios Tsiolakis³**

¹National and Kapodistrian University of Athens, Greece

²National Center of Scientific Research "Demokritos", Greece

³Geological Survey Department, Cyprus

The pygmy hippopotamus *Phanourios minor* lived in Cyprus during the late Pleistocene, 11–13.5 ka BP. This species became extinct during the Younger Dryas cold event that started at 12.85 ka BP. Our objective was to reconstruct the palaeodiet of the pygmy hippo, based on carbon isotope analyses ($\delta^{13}\text{C}$) of fossil skeletal material (bone bioapatite and tooth enamel) excavated from a fossiliferous site in Aghia Napa. $\delta^{13}\text{C}$ values were combined with hypsodonty index (HI) measurements. The HI is a measure of the molar crown height relative to the occlusal width. Calculated values of the HI from 20 upper M3 molars indicate a browser with anatomical features that testify to a terrestrial lifestyle. The range of carbon values for C3 plants is -19.2‰ to -28.7‰. Following the appropriate corrections, our carbon isotope results showed that *P. minor* preferred C3 plants (the average value was 21.03‰) that thrive in cold and wet environments. The study of material of *Phanourios minor*, from Aetokremnos, Cyprus, indicates a diet that includes, in addition to C3 plants, several C4 plants but more C3 plants than the modern hippopotamus. The endemic hippopotamus of Cyprus seems to have preferred more closed environments characterized by tree coverage rather than grass.

Investigating why collagen wasn't preserved in skeletal material from the site of Aghia Napa (Cyprus) through soil analyses

**Maria Anna Nakasi¹, Christos Vorriss², Stilianos Dallas², Elizabeth Stathopoulou¹,
Ioannis Massas², Georgios Theodorou¹ and Efthymios Tsiolakis³**

¹National and Kapodistrian University of Athens, Greece

²Agricultural University of Athens, Greece

³Geological Survey Department, Cyprus

In previous work, fossil skeletal material of the endemic pygmy hippopotamus *Phanourios minor* (11–13.5 ka BP) from the fossiliferous site in Aghia Napa, Cyprus was used to reconstruct the



palaeoenvironmental conditions. Such isotopic studies are based either on the extracted collagen or the skeletal material's bioapatite. In our case, all attempts to extract collagen failed so the isotopic analyses were realized on the bioapatite of bone and tooth samples. The preservation of collagen in bone and soil depends on factors such as pH, salinity, carbonates and microbial activity. Therefore, analyses were realized on soil samples from the fossil site to investigate why collagen is not preserved. Measurements of soil pH were made by an electronic pH meter, while the determination of the calcium carbonate percentage was done using the Bernard method, by measuring the released CO₂. The measurement of the soil organic matter was made using the Walkley-Black method. The presence of calcium carbonate and the microbial activity shown to be present are unfavourable conditions for collagen preservation. Mineral staining of the skeletal material, also present at the site, may also have played a role.

Patterns of tube-building behaviour across early animal communities: insights from the Ordovician Fezouata Shale biota

Karma Nanglu and Javier Ortega-Hernández

Harvard University, USA

The construction of tubular dwellings is a complex trait that can be achieved through a wide variety of behaviours and physiological mechanisms. Notably, this character is found in disparate metazoan taxa and in high abundance in several early Palaeozoic Lagerstätten. This suggests that the strategy was highly advantageous early in the history of complex animals, and may provide ecological links between temporally disparate faunas. Here we present three new examples of tubiculous taxa from the Ordovician Fezouata Shale biota of Morocco. First, we report a striking case of tube-building hemichordates that have colonized a cephalopod phragmocone, which draws parallels with hemichordate symbioses from the Cambrian. Second, the discovery of the typically Cambrian scalidophoran *Selkirkia* expands the temporal range of this genus by roughly 30 million years. Finally, we present new, enigmatic tube clusters that are unlike anything else reported from the Fezouata Shale to date. Comparisons of Fezouata Shale tubiculous taxa to Cambrian and Ediacaran organisms has several implications. Tube-building was ecologically important in several early animal lineages, but many of these organisms secondarily lost this trait. Finally, fossils may be misidentified as empty burrows or algae but are in fact the constructed dwellings of non-preserved soft-bodied taxa.

Ontogeny-dependent palatal characters in Eusuchia and implications for character-scoring

Iván Narváez, Ane de Celis and Francisco Ortega

Universidad Nacional de Educación a Distancia, Spain

Although assessing the approximate ontogenetic stage of fossil crocodyliforms is sometimes straightforward when dealing with complete skulls, this can become challenging when dealing with highly fragmentary specimens. In such cases, the specimen may be a juvenile or subadult individual rather than an adult and, if unrecognized, immature individuals could be included in phylogenetic analyses. Since scoring immature specimens in character matrices is discouraged,



it is therefore relevant to identify the ontogenetic stage of the specimens. Previous studies of the ontogeny of extant eusuchians have focused primarily on the dorsal view of the skull, and current knowledge of the ontogenetic morphological transformations in the palatal region is limited. Therefore, the present study analyses the ontogenetic variability of the palate using two-dimensional geometric morphometrics on a large sample of extant crocodylians, including 334 craniums from hatchling to adult individuals of 23 species. The analysis allowed the identification of certain palatal structures whose shape and relative position vary considerably throughout ontogeny, and whose variability could affect the scoring of specimens depending on their ontogenetic stage. Furthermore, several recently published character matrices for the Eusuchia clade have been evaluated in order to detect these character states, which may vary depending on the ontogenetic stage.

Ediacaran insights into the origins of the eumetazoan body plan

***Arsham Nejad Kourki**

University of Cambridge, UK

Our understanding of early animal body plan evolution has been revolutionized in the past few decades via incorporating the role of the expression patterns of transcription factors and morphogen gradients in underpinning body plans. Conflicting developmental genetic evidence, however, has left key puzzles unresolved: what are the homology relations between the bilaterian anterior–posterior (AP) and dorso–ventral (DV) body axes and the cnidarian oral–aboral (OA) and directive axes; and how, and in what order, did these body axes and the gastric cavity/tract first evolve? Here I argue that a successful integration of palaeontological evidence from the Ediacaran promises the resolution of these puzzles. I will first highlight two prominent hypotheses of eumetazoan body plan evolution (OA=AP; OA=DV) and recent support for each from developmental genetics, followed by showing that present palaeontological evidence, though currently patchy, only supports one of the hypotheses (OA=DV). The putative evolutionary scenario resulting from this integration elucidates both neontological and palaeontological evidential gaps, and generates a range of testable hypotheses and gives direction to existing ones; in other words, it serves as a framework offering a roadmap for future research and as a bridge between distinct fields that combines their explanatory power and scope.

Testing for a signal of solar irradiance in fern spores from the K–Pg boundary

Hendrik Nowak¹, Barry H. Lomax¹, Wesley T. Fraser², Phillip E. Jardine³ and Luke Mander⁴

¹*University of Nottingham, UK*

²*Oxford Brookes University, UK*

³*University of Münster, Germany*

⁴*The Open University, UK*

The K–Pg boundary is famously marked by one of the most prominent mass extinction events. It is generally accepted nowadays that the main cause was an extraterrestrial impact and its subsequent effects on the global climate. The model proposed by Alvarez *et al.* (1980) involves an “impact winter” caused by a dust cloud formed by ejecta in the stratosphere. This is thought to have hindered photosynthesis in plants. Our study aims to test this theory. In many sections preserving



the boundary, palynofloras right above it are dominated by fern spores. The sporopollenin making up the spore walls is chemically complex and variable, including UV-B absorbing compounds. The concentration of these compounds can be measured using Fourier-transform infrared (FTIR) spectroscopy. It has previously been shown with this method that the relative abundance of UV-B absorbing compounds correlates with the UV irradiance during plant growth. We are now analysing fern spores obtained from dense sampling around the K–Pg boundary in North America to show whether they document a drastically reduced irradiance immediately above the boundary consistent with the influence of a dust cloud.

Shifting sands: are late Ediacaran fossil assemblages reliable records of original ecosystems?

***Brennan O'Connell, William J. McMahon and Alexander G. Liu**

University of Cambridge, UK

The Ediacaran Nama Group of Namibia (~549–539 Ma) preserves soft-bodied and biomineralized macrofossils of early metazoans. Using sedimentological evidence from over 40 fossil-bearing beds in the Witputz sub-basin, we demonstrate ubiquitous transport of macro-organisms within sediment gravity flows in shoreface and deep-marine palaeoenvironments. Transported *Cloudina* and *Namacalathus* are preserved in debris flow, linked 'hybrid' flow and turbidite beds; transported *Pteridinium* are preserved in shoreface event beds; transported *Rangea* and *Ernieetta* are preserved in ungraded-unsorted mud-sand debris flow beds. Individual fossil specimens act as clasts within beds, with orientations (horizontal, mixed or chaotic) reflecting sediment transport mode (laminar, transitional or turbulent flow, respectively) rather than life position or feeding behaviours. Some transported *Ernieetta* specimens may have been able to re-orient during or post transport, potentially bioturbating the substrate. Recognition of sediment gravity flows, sourced from up-slope environments, implies that Namibian macrofossils are preserved in settings that potentially do not reflect their original geochemical and life habitat. Conversely, storm event beds preserve taxonomically distinct deep-marine *in situ* matground assemblages with novel taxa and species-substrate interactions. Distinct *in situ* and transported fossil assemblages are preserved in close stratigraphic proximity but may not have been in close environmental proximity or interacted in terminal Precambrian ecosystems.

Early evolutionary trends of the Hymenoptera (xyelid sawflies) in relation to ovipositor preserved fossils

Nozomu Oyama^{1,2}, Haruyoshi Maeda², Alexandr P. Rasnitsyn^{3,4}, Kenji Shinoda⁵ and Humio Takahashi⁵

¹*Sorbonne Université, France*

²*The Kyusyu University Museum, Japan*

³*Russian Academy of Sciences, Russia*

⁴*Natural History Museum, UK*

⁵*Mine City Museum of History and Folklore, Japan*

A well-preserved fossil assemblage of family Xyelidae (Hymenoptera) is described from the Upper Triassic of Japan. It is the first discovery of intact body fossils of subfamily Madygellinae, which represents the important basal representatives of xyelid sawflies. Information from the intact fossils



is expected to be useful for updating the classification of Madygellinae, especially those possessing ovipositors. Despite their ecological importance, fossil ovipositors remain largely under-studied. Consideration of several ovipositors from preserved Xyelidae fossils in addition to those from extant species reveals that while needle-like ovipositors appeared in the Triassic, the diversification of ovipositor morphologies occurred later in the Jurassic, with the appearance of flat-type ovipositors. This shift can be interpreted as increasing the variation of egg-laying strategies in the mid-Mesozoic. The Middle Jurassic was also the time when other wasps evolved hyper-needle-like ovipositors. This was associated with functional change, relating to a rise in parasitic wasps laying eggs in larvae in the Jurassic, and further, to venomous stingers of wasps. The morphology of ovipositors is an important key to understand the early evolution of basal Hymenoptera, and the needle-like type of ovipositor suggests that the Triassic Madygellinae host the origin of various forms and functions of ovipositors of Symphyta that diversified after the Middle Jurassic.

Orsten-type Lagerstätten yield three-dimensionally preserved phosphatized microfossils of microscopic organisms.

Jonathan Pople, Pierre Gueriau and Allison C. Daley

University of Lausanne, Switzerland

The Upper Cambrian Orsten locality in Sweden has yielded abundant three-dimensionally preserved phosphatized arthropods, revealing much about their anatomy, systematics and ontogeny. However, the processes that led to their exceptional preservation have yet to be described. Combining synchrotron radiation X-ray microtomography (SR- μ CT) with scanning electron microscopy (SEM) and energy dispersive X-ray spectroscopy (EDX), we undertook a taphonomic examination of over 60 bivalved phosphatocopine arthropods that we collected from an Upper Cambrian alum shale outcrop in the Kinnekulle region of Västergötland, Sweden. Intact shield valves contain soft tissues representing a grade of taphonomic states, ranging from highly detailed and complete external cuticle, through various stages of incompleteness and lack of detail, to specimens consisting only of an indistinct mass of globules bearing a vague resemblance to the anatomy. No internal anatomical structures can be distinguished, and instead spherical phosphatic globules fill the internal space, which we propose represent autolithified bacteria preserved inside the cuticle. We also observed highly localized filamentous structures, interpreted as bacterial biofilms, and pyrite framboids with sizes correlating to preservation quality. These observations provide direct evidence for the involvement of internal and external microbial activity in Orsten-type preservation and allow for a step-by-step reconstruction of phosphatization processes.

A new Tonian Konservat-Lagerstätte? Diverse, organically preserved vase-shaped microfossils from the <770–730 Ma Chuar Group, Grand Canyon, USA

Susannah M. Porter¹, Aidan Tydings¹, Dean Mantelzak¹ and Kelly E. Tingle²

¹*University of California, Santa Barbara, USA*

²*Vanderbilt University, USA*

Vase-shaped microfossils (VSMs), thought to be the remains of testate amoebae, are widespread in late Tonian strata, typically preserved as mineralized casts and moulds. Here we report a diverse assemblage of organically preserved VSMs from shales in the Awatubi and Walcott members,



Chuar Group, USA. Eighteen species have been provisionally identified, ten of them new. Test wall ultrastructure is preserved in many specimens: in some the wall appears to be fibrous; in others it is multi-layered with an inner layer covered in hollow $<1 \mu\text{m}$ bumps. Some tests also show scratches or dents similar to those sometimes found in modern testate amoebae. One species preserves a pliable collar-like structure extending from the test aperture with a fringe of 'tentacles' around it; to our knowledge similar structures are not known from modern testate amoebae. One specimen shows a semi-circular hole in the side of the test, perhaps from predation. We suggest these fossils represent a new Precambrian Konservat-Lagerstätte, one that could easily be overlooked under traditional acid maceration and light microscopy.

Radiodont diversity from the Fezouata Shale Formation (Early Ordovician, Morocco): palaeoecology and taphonomic implications

***Gaëtan J.-M. Potin**¹, **Pénélope Claisse**^{1,2}, **Jonathan Pople**¹, **Pierre Gueriau**^{1,3} and **Allison C. Daley**¹

¹*University of Lausanne, Switzerland*

²*Université de Lille, France*

³*Université Paris-Saclay, France*

Early Ordovician Lagerstätten are rare; however, they are crucial in understanding the transition between the Cambrian Explosion and the Great Ordovician Biodiversification Event (GOBE). The Fezouata Shale of Morocco is the most complete of them owing to the richness of fossils of marine organisms, including radiodonts (Arthropoda). These nektonic predators, emblematic from the Cambrian Explosion, are dominated by suspension-feeders in the Fezouata Shale, with sediment sifters being rare and active predators absent. Their frontal appendages and carapaces indicate a huge size range of radiodonts representing at least six different species. Their abundance and diversity reveal the important ecological roles they had, both pre- and postmortem, in the community. Frontal appendages inform about the feeding strategy, and their carapaces are colonized with epibionts and traces testifying to interactions with other species and a potential role in providing a stable living substrate for other taxa both pre- and postmortem. A complete vision of the preservation can be inferred from their degree of disarticulation in different environments. Radiodonts can be preserved either in concretions or as compressed fossils, depending on the anatomical part, size and preservation conditions, as inferred from synchrotron luminescence, Raman spectroscopy and computed tomography (CT scanning) of the specimens.

New snakeflies from the Cretaceous amber of Spain

William Potter Herrera¹ and **Ricardo Pérez-de la Fuente**²

¹*University of Portsmouth, UK*

²*Oxford University Museum of Natural History, UK*

Snakeflies (Neuropterida: Raphidioptera) are predatory insects characterized by long 'necks' (pronota) and an ovipositor in females. Although the group is known from about 250 extant species living in cold temperate regions of the Northern Hemisphere, snakeflies were globally distributed and more disparate during the Mesozoic. We have studied five new specimens, ranging from largely



complete to fragmentary, preserved in Early Cretaceous amber from El Soplao in northern Spain. All the specimens belong to the family †Mesoraphidiidae. One represents a new species within the genus *Necroraphidia*, with its type and only current species also described from El Soplao. The new material also provides a second specimen of *Amarantoraphidia ventolina*, also described from El Soplao based on a single specimen, as well as a specimen that could be classified within the genus *Proraphidia*. One of these amber pieces also contains several charcoaliified plant fibres, including a gymnospermous wood fragment preserving some elements of the tracheid ultrastructure. This finding reinforces the hypothesis that the palaeobiology of these insects was linked with recurrent palaeofires, as the dead wood resulting from these would have increased the available substrate for the snakeflies' xylophagous and/or xylophilous prey to develop.

Modelling the evolution of the mammalian jaw joint and middle ear in 3D

***James Rawson**¹, **Pamela G. Gill**^{1,2}, **Agustín Martinelli**³, **Marina Soares**⁴, **Cesar Schultz**⁵ and **Emily J. Rayfield**¹

¹University of Bristol, UK

²Natural History Museum, London, UK

³Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina

⁴Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil

⁵Universidade Federal do Rio Grande do Sul, Brazil

Previous research has described morphological changes to the jaw and postdentary bones across the cynodont/mammaliaform transition. However, more recently discovered non-mammaliaform probainognathian cynodonts from South America have thus far not been wholly integrated into comparative anatomical studies, despite being represented by numerous specimens. In this study, micro-CT data from twelve cynodont species, including nine specimens of *Brasilodon quadrangularis*, the sister taxon to mammaliaforms, and ten specimens of the tritheledontid *Riograndia guaibensis*, were segmented to produce 3D descriptions of jaw articulations, many for the first time. Hitherto unknown morphology visible in our scans overturns previous descriptions and demonstrates homoplasy in the approach to mammaliaforms, similar to that seen in the independent acquisition of the definitive mammalian jaw joint and middle ear in Mesozoic mammals. *Brasilodon*, contrary to previous interpretations, lacks a clear squamosal-dentary articulation and instead relies solely on a quadrate-articular joint, while *Riograndia* possesses a developed squamosal-dentary contact to reinforce the already robust primary jaw joint. We find that jaw joint evolution accelerates crownwards in cynodonts, beginning with the acquisition of a secondary jaw joint in eucynodonts and followed by a notable increase in morphological experimentation in derived probainognathians, that occurred alongside the evolution of other key mammalian features.



An examination of gomphodont material from the *Cynognathus* assemblage zone of the Burgersdorp Formation of South Africa and the identification of three new species

***Romy Rayner¹, Richard J. Butler^{1,3}, Christian F. Kammerer² and Jonah N. Choiniere³**

¹University of Birmingham, UK

²North Carolina Museum of Natural Sciences, USA

³University of the Witwatersrand, South Africa

The Burgersdorp Formation of South Africa is a richly fossiliferous rock sequence at the top of the Permian–Triassic Beaufort Group, known for its abundance of Early–Middle Triassic vertebrates, particularly cynodonts. Fossils from the Burgersdorp Formation are referred biostratigraphically to the *Cynognathus* Assemblage Zone (CAZ), which is further divided into three subzones. Each subzone is characterized by a distinct species of trirachodontid, a group of gomphodont cynodonts found abundantly throughout the CAZ. The uppermost subzone yields trirachodontids of the largest size, these specimens have previously been referred to *Cricodon metabolus*, a taxon known from Tanzania and Zambia. Conclusions have been drawn about stratigraphical correlations between these formations, partially based on this taxonomic referral. Identification of these specimens as three new taxa will be presented; the already formally described and named *Guttigomphus avilionis*, a novel genus; a new species of the traversodontid *Impidens*; and a new species of *Cricodon*. No occurrence of *C. metabolus* is currently documented from the Burgersdorp Formation. This project will present the distinguishing features of postcanine morphology that are the primary basis for differentiation of the new taxa and other closely related gomphodonts, along with a discussion of phylogenetic uncertainty among these taxa.

Infrared spectroscopy reveals chemical signatures of micro-eukaryotic diversity in the ~1 Ga Torridon Group, Scotland

***Edwin Rodriguez Dzul¹, Corentin C. Loron¹, Heda Agic², Sherri Donaldson¹,**

Andrei V. Gromov¹ and Sean McMahon¹

¹University of Edinburgh, UK

²Durham University, UK

Precambrian organic-walled microfossils (OWM) preserved in fine-grained sedimentary rocks constitute the earliest fossil record of eukaryotes. In some assemblages such fossils are preserved three-dimensionally within a phosphate matrix, retaining fine and delicate structural features. Despite this exceptional preservation, the biological affinity (prokaryote/eukaryote) of many OWM remains elusive because they have few morphological characters and lack obvious synapomorphies. Spectroscopic techniques such as Fourier-transform infrared spectroscopy (FTIR) can complement traditional morphological analysis by providing molecular fingerprints with the potential to discriminate between morphologically similar taxa. Here we studied OWM from the ~1 Ga Torridon Group of northwest Scotland, an important fossil assemblage formed during a critical interval for the evolution of eukaryotic cells, the Meso–Neoproterozoic transition. We applied FTIR to multiple microfossils including representative specimens of the Torridon biota *Eohalothecce lacustrina* and *Bicellum brasieri* (the latter previously interpreted as a possible holozoan), the ubiquitous Precambrian morphotaxa *Siphonophycus* sp., and *Leiosphaeridia* sp., plus two new taxa presented



here for the first time, including a probable eukaryotic alga. Our results reveal the fossilization products (CH, COO-, C=C, C=O, N-moieties) of organic precursors modified by diagenesis. These molecular fingerprints differ consistently between taxa, providing new insights into their original affinities.

A novel method for discriminating ancient melanins using Raman spectroscopy

Valentina Rossi, Richard Unitt and Maria E. McNamara

University College Cork, Ireland

Raman spectroscopy (RS) is an emerging tool in palaeontology to investigate the preservation of biomolecules in fossils. Recent studies have applied RS to identify fossil melanin in vertebrate soft tissues. These claims have been challenged because Raman spectra for melanin cannot readily be discriminated from those for kerogen – both spectra are dominated by broad bands for disordered (D) and graphitized (G) carbon. We used a comprehensive programme of maturation experiments (250 °C for 24 h) on melanin- and non-melanin-rich soft tissues from diverse modern organisms, including vertebrates, invertebrates, plants, fungi, bacteria and algae, to systematically test whether thermally matured melanin can be discriminated from other thermally matured biological materials using Raman signatures. After maturation, the chemistry of all samples converges toward that of kerogen, yielding similar spectra dominated by D- and G-bands. Our new approach to analysing Raman spectra, using peak deconvolution and rigorous multivariate statistics, however, reveals strong tissue-specific signals. Application of these results to diverse fossils from the Eocene Bolca Lagerstätte (Italy) confirms that kerogen-like Raman signatures from plant and vertebrate soft tissues can be readily discriminated. Our approach indicates that RS coupled with deconvolution and statistical analyses is a powerful tool to identify melanin signatures in fossils.

The fusioolithid dinosaur eggshells from Poyos (Campanian–Maastrichtian, Guadalajara, Spain) and its implications for the interpretation of the variability of *Fusioolithus baghensis*

***Fernando Sanguino, Ane de Celis, Adán Pérez-García and Francisco Ortega**

Universidad Nacional de Educación a Distancia, Spain

A considerable portion of the fusioolithid oological remains from the Poyos site (Villalba de la Sierra Fm., central Spain) show the diagnostic features of *Fusioolithus baghensis*. However, the thickness of most Poyos eggshells is at the lower end or even below the diagnosed thickness range of *F. baghensis*, with a portion of them showing an increased presence of anastomosed structures and larger internodal spaces than most specimens from other sites. Though eggshell thickness is a highly variable feature and many known eggshells of the Villalba de la Sierra Fm. (both Megaloolithidae and Fusioolithidae) share this low thickness (compared to specimens from coeval formations), comparing its spherolith dimensions with published *F. baghensis* thin sections reveals significant statistical differences between the latter and both subsets from Poyos. Therefore, if all these Poyos eggshells belong to *F. baghensis*, this ootaxon exhibits higher variability than previously recognized. The significance of these differences in a widespread genus such as *F. baghensis* (including the specimens from Poyos) could possibly be related to biotic conditions (*i.e.* having



different productors), abiotic conditions, (*i.e.* denoting different environmental conditions) and/or methodological biases (*i.e.* ambiguous diagnosis producing a wastebasket ootaxon effect); and should therefore be carefully assessed in the future.

Multi light imaging of small compression fossils – proper tools and a neat shortcut

Mario Schädel

Eberhard Karls Universität Tübingen, Germany

The interpretation of compression fossils can be very challenging due to multiple structures overlying each other. Therefore, it is often not sufficient to use only one image modality. Photographs taken with grazing light from multiple directions can be used in order to highlight small-scale surface details that are not apparent from the colour of the fossilized material. Yet, when presenting the findings this can come at the cost of needing many images to illustrate various parts of a fossil. However, there are several techniques that can harvest the information from a set of images taken with different illumination settings (Multi Light Image Collections) by creating digital models of the fossils. One such set of techniques is centred around the reflectance properties (Reflectance Transformation Imaging), while other techniques aim to recover the surface shapes (Photometric Stereo). Both sets of techniques have been successfully used to study fossils; however, they have not become widespread in palaeontology. Here I aim to explain methods of adapting the techniques to the study of compression fossils by means of overcoming photographic limitations, custom hardware and automation, as well as to present a way to capture similar datasets using a flatbed scanner.

A world of tyrants: the biogeography of Tyrannosauroida

***Charlie R. Scherer**

University College London, UK

Tyrannosauroida are an extremely successful superfamily of theropods with an undisputed Laurasian distribution. However, a complete biogeographical hypothesis for the dispersal of these dinosaurs is yet to be formulated. Here, I collate numerous works into the occurrence of tyrannosauroids across the Northern Hemisphere and combine them with palaeogeographical reconstructions of the latter half of the Mesozoic in an attempt to formulate such a hypothesis for tyrannosauroid biogeographical history. Tyrannosauroids originated in Asian biotas ~170 Ma and were widespread in Eurasia by ~145 Ma. Tyrannosauroids first appear in Laramidia in the middle Jurassic, and disappear until the Albian–Cenomanian (99–97 Ma). In Appalachia, the tyrannosauroid fossil record is limited to non-tyrannosaurid eutyranosaurians, likely due to isolation from Laramidia as a result of the Western Interior Seaway throughout the Late Cretaceous. Tyrannosauridae emerged in Laramidia ~90 Ma, with numerous distinct contemporary clades occurring at separate latitudes, with little spatial overlap. Approaching the K–Pg boundary (68–66 Ma), tyrannosauroid diversity was reduced with only one form present in Laramidia and occurring at all latitudes – *Tyrannosaurus rex*. The dispersal of tyrannosauroids between Asia and North America was facilitated by the Bering land bridge, which episodically linked the two landmasses throughout the Cretaceous.



Re-analysis of a dataset refutes claims of anagenesis in ‘Tyrannosaurus-line’ tyrannosaurines (Theropoda, Tyrannosauridae)

***Charlie R. Scherer**¹ and **Christian Voiculescu-Holvad**^{1,2}

¹University College London, UK

²GeoCenter Møns Klint, Denmark

The recently described tyrannosaurine species *Daspletosaurus wilsoni* was suggested to show evidence for anagenesis with the genus and wider Tyrannosaurinae. Here we evaluate the methodology and conclusions of the authors. Re-analysis of their dataset with the addition of a potentially novel species of *Daspletosaurus* and consistently applied methodologies shows no strong evidence for a single anagenetic lineage within ‘Tyrannosaurus-line’ tyrannosaurines throughout the uppermost Cretaceous, although anagenesis within *Daspletosaurus* remains possible. Instead, our study shows that Tyrannosaurinae is composed of four morphologically and geographically distinct clades, two of which we formally define and diagnose: Tyrannosaurini and Teratophoneini clade nov. Teratophoneini is currently restricted to the southern latitudes of Campanian Laramidia while Tyrannosaurini is present in both Campanian and Maastrichtian strata in Asia and Laramidia. We also demonstrate that *Daspletosaurus wilsoni* does not currently fulfil previously established prerequisites for anagenesis and advise against prematurity when making conclusions concerning significant processes surrounding the mode of evolution of extinct taxa with sparse and often incomplete fossil records. Future detailed anatomical descriptions of more complete specimens representing the possible fourth species of *Daspletosaurus* will further aid in elucidating the evolution of this genus and tyrannosaurines more generally.

The stratigraphical Anthropocene in the birth area of the Industrial Revolution

***Hannah Sellers, Amy Wrisdale, Juan Carlos Berrio, Stefano De Sabbata and Mark Williams**

University of Leicester, UK

The Anthropocene is a proposed new epoch of geological time with its beginning in the mid-twentieth century. Its definition requires the precision of a GSSP, but it is part of an episode of human-induced changes to the Earth system that have unfolded over millennia. Here we attempt to identify the Anthropocene in a sedimentary archive from the English Midlands, in one of the most heavily human-modified landscapes in the UK, and the birth area of the Industrial Revolution. We have found that whilst palaeontological signals indicate significant landscape changes prior to the twentieth century, the stratigraphical signal from radiogenic fallout events and from fossil-fuel combustion yield a clear mid-twentieth century Anthropocene signature, one that dovetails with the Great Acceleration of the post-WW II era, being the phase of accelerated human impacts on the planet. We contend that the stratigraphical Anthropocene will be recognizable even in some of the most long-lived, heavily human-impacted settings on planet Earth.



Carnivory in the forerunners of mammals: using tooth morphology to reconstruct therapsid feeding behaviour and trophic evolution through the Permian

Suresh Singh¹, Tahlia Pollock¹, Adam Huttenlocker² and Michael J. Benton¹

¹University of Bristol, UK

²University of Southern California, USA

Non-mammalian synspsids emerged as some of the first fully terrestrial, macrocarnivorous tetrapods in the late Palaeozoic, establishing themselves as the dominant large predators on land until the end of the Permian. During this time, synspsids evolved superior feeding, locomotory and respiratory efficiency as they became less 'reptilian' and more 'mammalian' in nature. One such advance was the evolution of regionalized dentitions in therapsid synspsids, marking the earliest origins of mammalian heterodonty. Such innovation is undoubtedly linked to changes in feeding behaviour. Here we investigate how growing dental disparity and regionalization in carnivorous therapsids supported their ecological and taxonomic diversification through the Middle and Late Permian. Applying morphometric methods, we compare the tooth morphologies of carnivorous therapsids and extant mammals to reconstruct potential therapsid feeding behaviours through the Permian and Triassic. Our results show marked shifts towards greater niche specialization and ecological diversity in theriodont therapsids, generating likely feeding behaviours reminiscent of later mammalian predators. Additionally, we demonstrate how broader functional improvements across therapsid anatomy supported this evolution and the ecological diversification that created the complex and rich carnivore communities of the Late Permian.

Two birds with one stone: the taphonomy of feather proteins and the biochemical evolution of feathers

***Tiffany Slater¹, Nicholas P. Edwards², Samuel M. Webb², Fucheng Zhang³ and Maria E. McNamara¹**

¹University College Cork, Ireland

²Stanford Synchrotron Radiation Lightsource, USA

³Linyi University, China

Fossil feathers offer the intriguing potential to elucidate the biochemical processes underpinning the macroevolutionary transition from dinosaurs to birds. Recent evidence that *Eoconfuciusornis* feathers comprise primarily (α -)keratins paints a revised picture of feather evolution, as feathers in extant birds comprise primarily corneous beta proteins (CBPs; with β -sheet conformation) plus minor keratins (with α -helix structure). This interpretation, however, does not consider feather taphonomy. Here we use taphonomic experiments, coupled with Fourier transform infrared (FTIR) and sulphur-X-ray absorption near-edge structure (XANES) spectroscopy, to probe changes in the molecular structure of feather proteins during thermal maturation. We matured feathers from the domestic chicken (*Gallus gallus*) and little egret (*Egretta garzetta*) for one hour at temperatures up to 250 °C. Our results show that feather CBPs can survive moderate maturation. This supports our new evidence that CBPs are preserved in *Confuciusornis* and *Sinornithosaurus*, confirming the potential for protein remnants to persist in Mesozoic fossils. Critically, our experiments show that the predominantly β -sheet structure of CBPs is progressively altered to α -helices with increasing temperature, revealing the keratin-rich composition of some fossil feathers to be a taphonomic artefact. Collectively, these data indicate that modern feather biochemistry predates Aves.



Site-accessibility is a significant predictor of palaeontological research output in fossil-bearing regions

Isaiah Smith

Friedrich-Alexander-Universität Erlangen-Nürnberg, Germany

The USA is characterized by relatively strict private property laws, which greatly reduce public access to privately held plots of land. Publicly administered land in this country, however, is often relatively accessible for research purposes. This ownership-based discrepancy in site-accessibility, along with the existence of detailed land administration records and palaeontological collections data, make for an interesting case study in the relationship between site-accessibility and palaeontological research output. Exhaustive data sets were downloaded from the Paleobiology Database for each of the 3,143 counties in the USA. For each county, the raw number of reported palaeontological collections, as well as the number of reported collections per reported formation, were modelled in relation to population density and the proportion of publicly accessible land in each county. Model results suggest that the proportion of publicly accessible land is a significant predictor of palaeontological research output, with reduced site-accessibility inhibiting palaeontological research. While these results are based strictly on US data, the relationship between site-accessibility and ease-of-research can be applied to other parts of the world. Three case studies dealing with site-accessibility and palaeontological research output, including localities in the USA, UK and Germany, are discussed in the context of these results.

Vetulicolians are early-diverging echinoderms

Martin R. Smith

Durham University, UK

The origins of the deuterostome phyla – chordates, hemichordates and echinoderms – are difficult to disentangle, largely because the extant representatives are so morphologically distinct. The Cambrian fossil record contains the intermediate morphologies necessary to piece together early deuterostome evolution, but these are often difficult to recognize. Here I revisit one of the most controversial Cambrian groups, the vetulicolians. Although these are recognized as deuterostomes based on their gill slits, other aspects of their anatomy – a segmented ‘tail’ and ‘tooth-ringed mouth’ – are impossible to reconcile with this affinity. Based on a re-examination of exceptional Burgess Shale fossils, I propose and substantiate a solution to this paradox: vetulicolians have been interpreted back-to-front. The ‘tail’ is in fact an anterior feeding appendage homologous to the arms of starfish; the ‘mouth’ is in fact a plate-rimmed anus. This interpretation can be reconciled with the earliest-diverging echinoderm groups, and reveals the pre-mineralization format of this phylum. By illuminating these deep reaches of deuterostome phylogeny, it is possible to identify deep anatomical homologies within this superphylum, and to infer the timing of deuterostome origins directly from the fossil record.



New lungfish from the Lower Coal Measures of Scotland

Timothy R. Smithson¹, Francis M. Elliott² and Thomas J. Challands³

¹*University of Cambridge, UK*

²*University of Glasgow, UK*

³*University of Edinburgh, UK*

Until now, only two lungfish taxa have been recorded in the Scottish Coal Measures: *Ctenodus* and *Sagenodus*. Here we describe a suite of new lungfish specimens, including tooth plates and a parasphenoid, from sites in the Central Coalfield that represent at least four taxa: *Sagenodus*; *Conchopoma*; and two new forms. They are rare members of an extensive vertebrate fauna recently discovered in the colliery waste from mining the Upper and Lower Drumgray Coal. These coals lie within the *communis* Zone and are of Langsetian age. The basihyal tooth plates of *Conchopoma* are the first record of this genus in the Pennsylvanian of Europe and one of the new taxa has a heterodont dentition not previously described from the Pennsylvanian. The specimens are much smaller than those found previously in the Scottish Coal Measures and are preserved in thin, laminated shales, containing a diverse shelly fauna, suggesting a small lake environment rather than the typical coal swamp. These new discoveries demonstrate that Pennsylvanian lungfish were more diverse than previously realized and add to the growing evidence that the rate of lungfish evolution did not decline significantly after the Devonian but remained high throughout the Carboniferous.

Integration of track and skeletal data yields novel insights into pterosaur ecology

***Robert S. H. Smyth**

University of Leicester, UK

Tracks have contributed greatly to our understanding of pterosaur terrestrial locomotion, but the ecological and evolutionary implications of tracks (pteraichnites) remain largely unexplored. Photogrammetric approaches reveal a strong correlation between pteraichnites and skeletal anatomy. Multivariate analyses incorporating skeletal and track records allow referral, for the first time, of particular track morphologies to specific clades. Application of this approach to multiple pterosaur tracksites from the Upper Jurassic (Oxfordian–Kimmeridgian) of the western USA indicates that, in all cases, the tracks were generated by ctenochasmatooid pterosaurs, ground-based feeders that visited intertidal flats on the margins of the Sundance Sea. Behaviours revealed by these trackways include persistent walking parallel to the palaeoshoreline and foot-propelled swimming, an unusual locomotory mode in pterosaurs that cannot be confidently inferred from skeletal morphology. The broad geographic and temporal distribution of the ctenochasmatooid tracks reveals that these pterosaurs were already common and widespread in marginal marine environments in the early Late Jurassic, considerably earlier than indicated by the body fossil record. Further integration of pteraichnites into our conception of the pterosaur fossil record could greatly improve our understanding of pterosaur palaeobiogeography, evolution and behaviour, far beyond that which can be derived from the body fossil record alone.



Coordination of acritarch and graptolite turnovers before and during the onset of Lau Event (Ludlow, Silurian)

Robertas Stankevič¹, Agnė Venckutė-Aleksienė², Sigitas Radzevičius¹ and Andrej Spiridonov¹

¹*Vilnius University, Lithuania*

²*Nature Research Centre, Vilnius, Lithuania*

The Silurian Period was a time of some of the most profound climatic perturbations and macroevolutionary turnovers in the pelagic realm during the Phanerozoic. Some of these extinction and turnover episodes have their own names: Ireviken, Mulde, Lau, Šilalė and Klonk Events. The effects of these oceanic perturbations on the trophic pyramids of the oceanic plankton are essentially unknown. Here we present the distributional and abundance data of acritarchs (the dominant phytoplankton) and compare the taxonomic and compositional changes with changes in graptolite (dominant zooplankton) assemblages before and during the onset of the mid-Ludfordian (Wenlock, upper Silurian) Lau Event. The application of recurrence plot technique and the recurrence quantification analysis revealed that there is a distinct periodic structure in biotic compositional changes and also in variability of stable oxygen and carbon isotopic ratios of carbonates. The duration of compositionally recurring episodes and recurring climatic states suggests that long eccentricity cycles (400 ka period length) along with long-term climatic trends played a major role in the onset and timing of Lau event.

Mass extinctions and close calls: using experimental Earth system and ecophysiological modelling to investigate what makes a catastrophic extinction

Richard G. Stockey¹, Erin E. Saupe², Benjamin Mills³ and Alexandre Pohl⁴

¹*University of Southampton, UK*

²*University of Oxford, UK*

³*University of Leeds, UK*

⁴*University of Burgundy, France*

Ancient warming events are commonly proposed as deep-time analogues for modern climate change. However, comparisons are complicated by differences in the rate and magnitude of warming, and changes in key Earth system boundary conditions such as continental configuration. These differences make it difficult to compare ancient extinctions to the modern biodiversity crisis, and to mechanistically understand why some ancient warming events resulted in more severe marine extinctions than others. The synergistic effects of ocean warming and deoxygenation are proposed as key mechanisms in driving marine animal extinction through Earth history, emphasizing the importance of spatially explicit palaeoceanography for providing direct links between climate and animal physiology. We first address how oxygen minimum zones respond to different rates and magnitudes of global warming under different Mesozoic–Cenozoic continental configurations using the *cGENIE* Earth system model. Then, we use ecophysiological and macroecological modelling approaches to simulate how the combined physiological impacts of marine oxygen, temperature and productivity dynamics control the ability of marine organisms to track their physiological niches in response to warming. Using this integrated modelling framework, we investigate why well-characterized Mesozoic–Cenozoic hyperthermal events resulted in markedly different marine biodiversity responses and their potential relevance to modern climate change.



Testing the resilience of the penguin (Spheniscidae) phylogeny to fossil sampling using the stratigraphic ranges model

Ugnė Stolz¹, Bethany J. Allen¹, Alexandra Gavryushkina², Tanja Stadler¹ and Timothy Vaughan¹

¹*ETH Zürich, Switzerland*

²*University of Canterbury, New Zealand*

Selecting the best method for inferring a phylogeny remains a contentious issue. However, Bayesian methods are growing in popularity, particularly due to the increasing choice of constituent models available for various evolutionary and sampling processes. One such model is the recently developed stratigraphic ranges model. Unlike previous models that inform the placement of fossil branches based on independent single fossil occurrences, this new approach summarizes multiple occurrences of each species into a range, explicitly representing information on the existence of a species through time. Uncertainty on the beginning and end of this range is also taken into account. Here we use this model, newly implemented in the phylogenetics software BEAST2, to infer the phylogeny of penguins. Both molecular sequences for living penguins and morphological characters for living and extinct penguins are used. While the topology of the inferred phylogeny is largely consistent with previous analyses, changes in the posterior probabilities placed on clades, and in tip and node ages throughout the phylogeny, are evident. These results demonstrate the usage of the stratigraphic ranges model, which has potential to greatly improve the compatibility of inferred phylogenies with the fossil record.

Two new species of insect from the Mesozoic of the UK

***Emily Swaby¹, Angela L. Coe¹, Deborah Hutchinson², Luke Mander¹, André Nel³, Lee Riva⁴, Bryony A. Caswell⁵ and Scott A. L. Hayward^{6,7}**

¹*The Open University, UK*

²*Bristol Museum and Art Gallery, UK*

³*Muséum national d'Histoire naturelle, Paris, France*

⁴*Lovell Stone Group, UK*

⁵*University of Hull, UK*

⁶*University of Birmingham, UK*

⁷*Birmingham Institute of Forest Research, UK*

Insects form a critical part of ecosystems, yet their response to past periods of environmental change is understudied. There are numerous good collections of fossil insects in UK museums; however, many specimens still require taxonomic revision before they can be used to reconstruct palaeontofaunas and draw conclusions about insect diversity and evolution. Here we describe two new insect species housed at Bristol Museum and Art Gallery. Whilst the damselfly dragonfly family Liassophlebiidae (Odonata: Heterophlebioidea) is well-established during the Early Jurassic, the occurrence of Liassophlebiidae is only recorded from three very fragmentary specimens from the Rhaetian (Upper Triassic). Here we report from the uppermost Rhaetian of Somerset, UK, a fourth, better-preserved specimen representing a new species. This discovery provides confirmation of Liassophlebiidae during the latest Rhaetian. The Blattodea (cockroach) diversity of Early Toarcian sites is considered low; therefore any new specimens are important for better understanding their diversification during this time. Here we report a new species of cockroach from the Toarcian



(Lower Jurassic) of Gloucestershire, UK. Initial analysis of the specimen suggests it likely represents a new species due to its unique wing venation. The specimen also possesses distinct wing spots, a feature previously unreported in Toarcian cockroaches.

Taphonomic variation in vase-shaped microfossils from carbonate nodules of the late Tonian Chuar Group, Grand Canyon, Arizona, USA

***Kelly E. Tingle¹, Susannah M. Porter², Elizabeth C. Teeter¹ and Simon A. F. Darroch¹**

¹*Vanderbilt University, USA*

²*University of California, Santa Barbara, USA*

Vase-shaped microfossils (VSMS) are found in late Tonian rocks worldwide and are interpreted as the earliest evidence for testate amoebozoans. In the Walcott Member of the upper Chuar Group, VSMS are reported in a variety of preservation modes and lithologies, including (sometimes pyrite, iron oxide or organic coated) siliceous and calcareous casts and moulds in chert and carbonate nodules, and as pyritic casts and organic tests in shales. Here we focused on the taphonomy of VSMS in shale-hosted carbonate nodules of the upper Walcott Member, collecting samples at ~5 m intervals spanning ~50 m of stratigraphy. Most VSMS are preserved either as siliceous casts (39 %) or as casts that are partially siliceous, partially composed of pyrite or iron oxide (35 %). The remaining specimens are preserved as calcareous internal moulds (23 %) and rarely, as internal moulds of framboidal pyrite (3 %). Elemental mapping reveals that one third of VSMS, independent of preservation, show aluminium and/or potassium enrichment around tests; in some specimens, SEM imaging reveals that clay minerals are coating microfossils. These results demonstrate that VSM preservation is highly variable at the mm-scale or smaller within carbonate nodules but is fairly consistent among individual carbonate nodules collected at different stratigraphic levels.

Biogeomorphology in Ireland's oldest fossil forest: plant-sediment and plant-animal interactions recorded in the Late Devonian Harrylock Formation, Co. Wexford

***Yorick Veenma¹, Neil S. Davies¹, Ken T. Higgs² and William J. McMahon¹**

¹*University of Cambridge, UK*

²*University College Cork, Ireland*

The mid-Palaeozoic was a significant interval in the evolution of plants, during which their biogeomorphological influence on terrestrial landscapes increased substantially. Yet, while such interactions are well known from Carboniferous strata, evidence in the Devonian record is less common. We present new evidence for plant-sediment interactions from the Late Devonian (Famennian) Harrylock Formation of County Wexford, Ireland, that hosts standing trees that represent Ireland's oldest reported fossil forest. The formation records deposition in fluvial and lacustrine environments, the former of which is here shown to host Earth's earliest known logjam and early examples of vegetation-induced sedimentary structures (VISS) and a vegetation-sustained chute channel. Fossil driftwood debris preserved in lacustrine facies within the unit also contains the earliest evidence for arthropod(?) borings, which serve to narrow the prolonged gap between the first occurrence of fossil wood and the earliest borings in vascular plant material. Together these early examples show that plant-related phenomena, frequently associated with Carboniferous strata,



were already in existence by the Devonian and may have been previously overlooked. Considering evolutionary changes in flora across the Devonian–Carboniferous boundary, the sparse early record of plant-related sedimentary phenomena can be explained by a lesser abundance and/or longevity of such features in Devonian landscapes.

Settlers in the Netherlands, passers-by in Denmark? A critical assessment of the causes of mosasaur occurrence disparities in the latest Cretaceous chalk of Europe

***Christian Voiculescu-Holvad^{1,2}**

¹*University College London, UK*

²*GeoCenter Møns Klint, Denmark*

Mososauridae are a family of predatory marine squamates which, in Europe, have a particularly widespread distribution during the Campanian and Maastrichtian. Chalk deposits in the Netherlands, Belgium, Denmark, Germany, Sweden and Poland have yielded diverse records of the European mosasaur fauna. Within these deposits, there are notable geography-linked disparities in the occurrence of mosasaur remains. For instance, while being relatively common in the Maastrichtian-type area (Netherlands; Belgium), mosasaur material is exceedingly rare in the Danish Chalk. It was largely considered that the relative abundance of mosasaur remains at particular localities is indicative of preferential habitat selection, and that mosasaur fossil rarity reflects their actual rarity in certain areas of the European Chalk Sea. Potential explanations for such occurrence disparities are reviewed here. Factors including prey availability, water palaeodepth and palaeotemperature are shown to be somewhat unlikely to cause near absence of mosasaurs in particular regions. Instead, there is tentative support for the assessment that mosasaur fossil scarcity is an artefact of taphonomic and palaeoceanographic processes, and is not necessarily an indication of actual mosasaur absence in particular regions of the Chalk Sea.

A giant, late-surviving member of Belemnotheutidae (Coleoidea, Belemnitida) from the Maastrichtian (Late Cretaceous) of Denmark: preliminary findings

***Christian Voiculescu-Holvad^{1,2}**

¹*University College London, UK*

²*GeoCenter Møns Klint, Denmark*

Belemnotheutidae is a family of small-bodied coleoids (Order Belemnitida) characterized by thin rostra and hook-bearing arms. Belemnotheutids existed mostly during the Late Jurassic, and are considered to have disappeared during the Early Cretaceous. Based on a single arm hook from the Maastrichtian deposits of Møns Klint (Late Cretaceous, Denmark), a novel belemnotheutid taxon is described. Belemnotheutid affinities of the material were determined based on morphological characters including profuse striations, spur absence, and gentle curvature with a shallow shaft-uncinus angle. Features including an uncinal notch allow this taxon to be distinguished from other belemnotheutids. This Maastrichtian specimen significantly extends the stratigraphic range of Belemnotheutidae, revealing that this family persisted until the terminal Cretaceous. Additionally, the hitherto undescribed arm hook is around ten times larger than hooks from other belemnotheutid taxa, and a ~4 m body length is estimated. Preliminary findings on this new taxon



are here reported, emphasising palaeoecological implications. A predatory mode of life is inferred, with the notched arm hooks suggesting increased grasping ability. Additionally, gigantism would have allowed it to occupy a high trophic level in European Chalk Sea food-webs. The large size of this belemnite provides further support for gigantism trends observed across Coleoidea during the Late Cretaceous.

Do optimal bird wings exist: using theoretical morphospace to examine optimality and trade-offs in bird wing evolution

***Benton Walters, Philip C. J. Donoghue and Emily J. Rayfield**

University of Bristol, UK

Historically, study of wing morphology has focused on variation in observed taxa to draw conclusions about characteristics such as flight style and niche partitioning. Theoretical morphospace analysis provides a useful companion to these traditional analyses, producing a space populated with all possible wing shapes, whether realized by evolution or not. By mapping aerodynamic traits onto theoretical space rather than observed taxa, we take advantage of this quality to examine the optimality of bird wings. The visibility of un-accessed and even impossible areas of morphospace is key as optimal wing forms may not be realized and positioning of observed taxa relative to optimal peaks can inform about trade-offs in evolutionary development. Using a classic dataset of extant birds we demonstrate that optimal wing shapes for flight performance exist within un-accessed theoretical space. This further reinforces that aerodynamic properties are not the primary drivers of variation in bird wing shape but rather represent a minimum threshold which must be overcome to achieve flight. This analysis forms the basis for a larger comparative study of wing shape across all volant vertebrate groups to examine convergence in evolutionary path and whether trade-offs in the mechanics of flight affect vertebrate lineages similarly.

Calibrating the diversification of early animals during the Ediacaran–Cambrian using a newly proposed beta ichnodiversity index

Zekun Wang and Imran A. Rahman

Natural History Museum, London, UK

Trace fossils are the product of complex interactions between organism, substrate and fluid flow, and can thus provide important insights into the body plan, motility and behaviour of the trace maker. One interval when the trace fossil record is especially important is the Ediacaran–Cambrian transition, which records the diversification and evolution of Earth's earliest animals. To quantify variation in the diversity of trace fossils across this critical interval, a new measure of beta ichnodiversity based on vector calculation is proposed. The obtained results enable us to quantify the diversification rate of traces over this transition, and allow us to infer when different behaviours (*e.g.* grazing, foraging, resting, parenting) first appeared. By interpreting these results in the context of evolutionary and environmental change, we can pinpoint the timing and pattern of the Fortunian Diversification Event, Cambrian Information Revolution and Agronomic Revolution, shedding light on the diversification of animal body plans, behaviours and locomotory capabilities during the Ediacaran to Cambrian transition. Furthermore, applying this newly proposed metric to the ichnological records from shallow and deep marine settings reveals a more rapid diversification



rate in shallow marine settings at this time, with a progressive niche partitioning process during the Ediacaran to Cambrian identified.

The evolution of Southern Ocean seafloor ecology

Rowan J. Whittle¹, Emily G. Mitchell², Tasnuva Ming Khan^{1,2}, James D. Witts³, Aaron W. Hunter² and Huw J. Griffiths¹

¹*British Antarctic Survey, Cambridge, UK*

²*University of Cambridge, UK*

³*University of Bristol, UK*

Assessing ecological change in fossil communities provides crucial insights into how modern communities will react to environmental change. Modern Southern Ocean sea-floor invertebrate communities are described as having an archaic retrograde ecology, as they are dominated by epifaunal suspension feeding organisms. The current understanding is that these patterns started to develop in the Eocene, with cooling decreasing durophagous predation. However, our data show that not all Antarctic fossil occurrences follow this pattern. The Southern Hemisphere fossil record (and particularly Antarctica) is not studied in as much detail as the rest of the world, but it represents a huge area of the globe. We show that Southern Hemisphere evolutionary ecological patterns can differ to the Northern Hemisphere. Additionally, more factors may have affected ecological evolution, including water depth and environmental setting of fossil sites, and a greater degree of cooling potentially into the Pliocene. There is a long way to go to understand Southern Ocean ecology. The timing of community structure origin, and even the distribution of modern predator and prey organisms, and their relative proportions underpinning community structure, are still in need of study. This hinders our understanding of how polar ocean communities will adapt to anthropogenic environmental change.

Birds of Stone: two lithornithid specimens provide insights into early palaeognath evolution

***Klara E. Widrig and Daniel J. Field**

University of Cambridge, UK

While only representing a tiny fraction of extant bird species diversity, the clade Palaeognathae encompasses a great variety of body sizes and ecologies, from giant flightless forms such as the ostrich to the volant, partridge-like tinamous of the Neotropics. Lithornithids, a group of presumably volant stem palaeognaths from the Palaeogene of Europe and North America, represent the earliest known occurrence of this clade in the fossil record. Here we use high-resolution micro-CT scanning to characterize the morphology of two lithornithid specimens from the early Eocene London Clay Formation, UK: the neotype of *Lithornis vulturinus* (NHMUK A5204) from the Isle of Sheppey, and a newly discovered clay nodule from the nearby locality of Seasalter. The neotype contains an endocast and semicircular canals that were hitherto uninvestigated. We refer the Seasalter specimen to *L. vulturinus* on the basis of numerous apomorphies and its provenance from a nearby penecontemporaneous locality. The Seasalter specimen contains postcranial material that provides new insight into bones damaged or missing in the neotype, including a three-dimensionally preserved sternum. We hope that this investigation will assist in the identification



of other early total-clade palaeognath fossils, and shed light on the skeletal morphology and neuroanatomy of early crown group birds.

Organic-walled microfossils from the c. 766–730 Ma Moosehorn Lake formation, Uinta Mountain Group, Utah

***Christina R. Woltz¹, Susannah M. Porter², Carol M. Dehler³ and Leigh Anne Riedman²**

¹Stanford University, USA

²University of California, Santa Barbara, USA

³Utah State University, USA

The Tonian Period is characterized by a rise in eukaryotic diversity and ecological complexity. Organic-lean shales of the late Tonian Moosehorn Lake formation, an informal unit in the Uinta Mountain Group, Utah, USA, preserve a diverse assemblage of organic-walled microfossils that includes many eukaryotic species. In total, we describe 22 species and four unnamed forms using transmitted light and scanning electron microscopy. Fourteen of these species also appear in the coeval Chuar Group of Arizona, including *Kaibabia gemmulella*, *Microlepidopalla mira* and *Volleyballia dehlerae*. Similarities in microfossil assemblages support the idea that the Uinta and Chuar basins, together with the Pahrump basin of Nevada, formed an epeiric sea. Also preserved is *Bicellum brasieri*, a possible holozoan (a group containing animals and their protistan relatives), described previously from the c. 1,000 Ma Torridon Group, Scotland. Originally interpreted as a fluvio-lacustrine deposit, the presence of *B. brasieri* in the Torridon Group supports the hypothesis that terrestrial environments were important to early eukaryote diversification. Given the larger stratigraphic context of the Moosehorn Lake formation and the co-occurrence of globally widespread marine species, *B. brasieri* either inhabited marginal marine environments, migrated to marine settings during the Tonian or had a broad salinity tolerance.

What controlled the distribution of early Cambrian metazoan-supported reefs?

Thomas Wong Hearing

Ghent University, Belgium

The Archaeocyatha are an extinct class of calcifying sponges and were the first animals to be globally important producers of calcified reef structures. Calcimicrobe–archaeocyath associations were the dominant type of reef for approximately 15 million years, from mid-Cambrian Age 2 (Terreneuvian Epoch) when archaeocyaths first appeared until their sharp and near-total demise in late Cambrian Age 4 (Epoch 2) in what is often considered the first major Phanerozoic extinction. Archaeocyaths are interpreted as having a limited ecological tolerance, being stenobathyal, stenothermal, stenohaline filter feeders that lived in tropical shallow (photic zone) marine environments with normal salinity and low turbidity. Indeed, their assumed tropical distribution has historically been used to evaluate the validity of palaeomagnetism-derived palaeocontinental reconstructions. However, the hypothesized relationships between calcimicrobe–archaeocyath reefs and environmental parameters like temperature, salinity, nutrient availability and light intensity have not been properly tested with palaeoclimate model data or using recent palaeocontinental reconstructions. Advances in plate reconstructions over the last decade now permit detailed analyses of Cambrian biogeography, and advances in palaeoclimate modelling make it possible



to integrate climatic data with these analyses. Here I examine the 15-million-year evolution of calcimicrobe–archaeocyath reef biogeography and evaluate potential environmental factors controlling their distribution.

Exceptionally preserved radiodont arthropods from the Lower Cambrian (Stage 3) Qingjiang Lagerstätte of Hubei, South China

Yu Wu^{1,2} and Dongjing Fu¹

¹Northwest University, China

²University of Cambridge, UK

The early Cambrian (Series 2, Stage 3) Qingjiang Lagerstätte of South China is one of the world's top-tier exceptionally-preserved deposits besides the Chengjiang biota and Burgess Shale. It yields diverse and abundant soft-bodied taxa with high fidelity including radiodonts, a taxonomically and ecologically diverse stem-euarthropod group, which have been generally thought to be apex predators during the early Palaeozoic Era. Here we present several new radiodont taxa from Qingjiang, including *Stanleycaris* sp. nov. A, which represents the earliest occurrence of *Stanleycaris* as well as the first record of this genus outside Laurentia. This articulated specimen preserved a pair of frontal appendages and a lateral element of cephalic carapace. Additional specimens include cephalic carapaces attributed to a new hurdiid taxon and possible *Hurdia*, a new type of triradial oral cone with possible anomalocaridid or tamisiocaridid affinities, as well as partial frontal appendages belonging to ampletobeluids and hurdiids. Compared to other radiodont families, Hurdiidae appears to have an advantage in being both diverse and abundant. It thus supports the view that hurdiids may have a preference for deeper water environments. The new material also substantially increases our understanding of the early diversification of radiodonts.

A new anomalocaridid radiodont from the lower Cambrian Chengjiang Lagerstätte, South China with implications for internal relationship and disparity of radiodonts

Yu Wu^{1,2}, Stephen Pates² and Dongjing Fu¹

¹Northwest University, China

²University of Cambridge, UK

As a diverse clade of early Palaeozoic stem-euarthropods, radiodonts occupied a pivotal position in early animal ecosystems and early evolution of arthropods. The well-known Chengjiang Lagerstätte (Cambrian Stage 3, c. 518 Ma) has yielded the highest known diversity of radiodonts of any Cambrian Konservat-Lagerstätten, and therefore become a crucial site for radiodont research. One important but under-appreciated Chengjiang radiodont taxon, previously identified as *Anomalocaris* sp. or Radiodont C, is herein designated as the type species of a new monotypic genus of Anomalocarididae, *Shucaris ankylosskelos* gen. et sp. nov. Here we describe dozens of new Chengjiang specimens of *S. ankylosskelos* showcasing exceptionally preserved soft tissues, allowing for the first comprehensive reconstruction of its anatomy, palaeoecology and evolutionary significance. Reinvestigation of the morphology of radiodont frontal appendages prompts us to recognize two appendage types, namely 'A-appendage' and 'H-appendage', leading the erection of Anomalocarida subord. nov., which groups together Tamisiocarididae, Anomalocarididae and



Amplectobeluidae. The divergence between Anomalocarida and Hurdiidae has been supported by our phylogenetic and morphospace analyses, challenging traditional views concerning the internal relationships within Radiodonta. This study not only illuminates the early diversification of Radiodonta, but also provides fresh insights into radiodont systematics and phylogeny.

Absolute growth and mortality estimates for the Cambrian apex predator

Amplectobelua symbrachiata

Yu Wu^{1,2}, Daniel Pauly³ and Dongjing Fu¹

¹Northwest University, China

²Department of Zoology, University of Cambridge, UK

³University of British Columbia, Canada

Radiodonta, an extinct stem-euarthropod group, has been considered to include the largest predators of Cambrian marine ecosystems. Despite its importance for our understanding of the evolution and ecology of the group, the post-embryonic development of radiodonts has remained scarce. Here we describe the post-embryonic development of the frontal appendage in *Amplectobelua symbrachiata*, the most common radiodont from the Cambrian (Series 2, Stage 3, ~518 Ma) Chengjiang biota in South China using ELEFAN (Electronic Length-Frequency Analysis). The analysis of 224 measurements yielded for an estimated asymptotic length $L_{\infty} = 14.1$ mm, and suggests that this radiodont probably lived up to nine years. A length-converted catch curve provided an estimate of mortality rates of $M = 0.92$ year⁻¹, with a 95 % confidence interval of 0.75-1.08 yr⁻¹. This corresponds to 60 % of a population dying every year, which is rather high, whereas the ELEFAN estimate $K = 0.33$ year⁻¹ appears low. In comparison with recent crustaceans, *A. symbrachiata* had an exceptionally rapid growth. Therefore, this study provides quantitative information on the absolute growth characteristics of a radiodont for the first time. The ELEFAN approach used here may also be applied to other radiodonts for which suitable length–frequency data exist.

Experimental phosphatization of shrimps in a freshwater setting

Zixiao Yang and Maria E. McNamara

University College Cork, Ireland

Preservation of fossil soft tissues with (sub-)cellular fidelity is often associated with replication in calcium phosphate and can provide important insights into the evolution of anatomy, providing any biases in preservation are known. Taphonomic experiments are critical to understanding the fossilization process, but experimental phosphatization of soft tissues has been investigated only in simulated marine settings. Here we test whether the factors known to promote phosphatization in marine settings apply to freshwater settings. We degraded the shrimp *Neocaridina davidi* at 20 °C for 21 days in freshwater from a natural lake. Experimental conditions promoted phosphatization by limiting diffusion, promoting anaerobic microbial activity and adding a source of phosphate ions. We observed a significant drop in pH, reaching the pH window for calcium phosphate precipitation (below 6.38) within the first two days. After 21 days, most of the soft tissues had degraded completely. Small pieces of connective tissues were replicated in calcium phosphate and the gills in calcium carbonate. This tissue-specific mineralization may reflect different tissue chemistry *in vivo*.



This study represents the first attempt to understand phosphatization in freshwater systems using laboratory experiments. Fossils with extensive soft tissue phosphatization may have entered the phosphatization window early and/or experienced slow decay.

Three-dimensional preservation of skin ultrastructure in a feathered dinosaur

Zixiao Yang¹, Baoyu Jiang² and Maria E. McNamara¹

¹University College Cork, Ireland

²Nanjing University, China

Despite recent advances in understanding feather evolution, the critical transition from scaled to feathered skin remains poorly understood. Here we investigate a new specimen of *Psittacosaurus*, a non-avian dinosaur known to preserve feathers on the tail and scales in other body regions. We identified patches of mineralized skin in the (non-feathered) torso. Scanning electron microscopy revealed that the fossil skin is replicated in silica in three dimensions and shows two distinct layers. The upper layer comprises c. 10-20 sublayers that represent preserved corneocytes of the stratum corneum. The thinner lower layer lacks internal structure and represents the remains of the uncornified inner epidermis. Compared with extant analogues, the thickness of the *Psittacosaurus* stratum corneum is consistent with a primary composition of corneous beta protein rather than keratin. Our study also reveals moulds of microbodies, interpreted as melanosomes, that can occur in the uncornified inner epidermis or in both the cornified and uncornified layers. This anatomical distribution of melanosomes is consistent with that in crocodylian scales. Our findings confirm that the *Psittacosaurus* skin retained the plesiomorphic condition of its scaled ancestors in non-feathered body regions. Deviation from this ancestral condition may have only occurred locally, in the feather tracts.

Shrews bite: anatomy and evolution of soricids (Lipotyphla, Mammalia)

***Haobo Yuan and Robert J. Asher**

University of Cambridge, UK

Among the most remarkable anatomical features of extant soricids is their double jaw joint, positioned anteriorly to overlap with the posterior ethmoidal region. Even within the crown group, there exist several anatomically distinctive, supra-generic clades, and the fossil record further documents the evolution of soricids. Here we discuss a well-preserved, early Oligocene specimen from Wyoming, USA and present results from a new matrix of hard tissue characters in light of recent hypotheses on soricid phylogenetics. We show that some heterosoricines, which lack the pocketed coronoid and dual mandibular condyle, have a surprisingly modern squamosal side of the jaw articulation. Furthermore, we describe a set of new characters concerning the hard palate. *Sorex* generally exhibits a single pair of incisive foramina with the oral opening of vomeronasal canals located posteriorly. In many non-*Sorex* soricines and crocidurines, an additional foramen is present posteromedial to the incisive foramina with which the vomeronasal canals are often confluent. Our Oligocene fossil shows only a pair of incisive foramina without vomeronasal canals. Living and fossil shrews possess many hard tissue features in common, but are still a diverse clade with several morphologically cohesive units. Their fossil record exhibits mosaic evolution relative to their non-soricid, lipotyphlan common ancestor.



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