

64TH  
PALAEOLOGICAL ASSOCIATION  
ANNUAL MEETING

16–18 DECEMBER 2020

OXFORD UNIVERSITY MUSEUM  
OF NATURAL HISTORY

The Palaeontological Association



2020  
Virtual Annual Meeting



**The  
Palaeontological  
Association**

**64th Annual Meeting**

*Virtual meeting*

**16th–18th December  
2020**

*Oxford University  
Museum of  
Natural History*

**PROGRAMME  
ABSTRACTS  
AGM papers**







# The Palaeontological Association

## 64th Annual Meeting

16 –18 December 2020

Hosted online by

Oxford University Museum of Natural History

The programme and abstracts for the 64th Annual Meeting of the Palaeontological Association are provided after the following information and summary of the meeting.

### Platforms

The Annual Meeting will take place online, hosted by the Oxford University Museum of Natural History, UK. All talks will be broadcast via the WebinarJam platform. We recommend using Google Chrome when attending WebinarJam events. The poster sessions will take place on the Discord platform, which you will be able to access via your web browser, or by downloading the Discord application. Delegates will be e-mailed a set of personal links to access all content, as well as guidance on how to access the conference sessions. Fringe events should be registered for separately.

### Presentation formats

The Organizing Committee would like to emphasize that all presentation formats – standard talks, flash talks and posters – have equal importance. The three different presentation styles offer varied ways to present research and discuss it with colleagues. In all cases presenting authors will be able to deliver their research and debate the content with delegates at the Annual Meeting.

### Oral Presentations

Presenters giving standard talks have been allocated 15 minutes; these talks should last for no more than 12 minutes to allow time for questions and switching between presenters. Speakers giving flash talks have been allocated five minutes and may only present a maximum of three slides. Questions and a short panel discussion will take place at the end of each flash talk session, rather than after each talk. Unless there are extenuating circumstances, presentations will be given live over the WebinarJam system, with attendees able to ask questions via the chat function, which will then be put to the speakers by the Session Chair. All presentations should be in PowerPoint or PDF format and should not contain animations, although videos can be accommodated. All presentation files should be less than 80 MB and must be submitted in the week prior to the Annual Meeting, including any URLs for videos. Having presentations securely pre-loaded into the presentation system 'cloud' eliminates the need to use bandwidth-consuming screen-sharing, and in so doing makes the meeting more accessible to those with varying levels of Internet connection.

### Poster presentations

Posters may be portrait or landscape and presenters should consider designs that will work well when viewed on a typical screen. Posters will be submitted and be available to view through a password-protected portal on the PalAss website. Posters should be submitted in PDF format. Online, interactive poster sessions will take place on Discord to promote live debate and discussion between presenters and attendees.



### Illustrations

This year the Organizing Committee have arranged for a number of illustrators to attend the Annual Meeting. Inspired by the presentations being made, they will make their illustrations available online using the conference hashtag #PalAss20. Keep an eye on social media to catch your favourite talks in artistic form.

### Virtual field-trips

Throughout the Annual Meeting the Oxford University Museum of Natural History will be running a number of virtual field-trips, using material from the collections to guide delegates around a number of otherwise inaccessible localities from around the world. These events will be advertised to all delegates and will not require separate registration.

### Oxford University Museum of Natural History

Oxford University Museum of Natural History was established in 1860 to draw together scientific studies from across the University of Oxford. Today, the award-winning Museum continues to be a place of scientific research, collecting and fieldwork, and plays host to a programme of events, exhibitions and activities for the public and school students of all ages. The palaeontology collections include one of the world's most important collections of Middle Jurassic dinosaurs, exceptionally-preserved specimens with intact soft tissues and enigmatic fossils representing the earliest complex multicellular organisms. They feature around 400,000 fossils, ranging from the Archaean at around 2.7 billion years ago to the end of the Pleistocene 11,700 years ago. Highlights in the collections include the world's first scientifically described dinosaur – *Megalosaurus bucklandii* – and the world-famous Oxford Dodo, the only soft tissue remains of the extinct dodo.

### Logo

For the virtual Annual Meeting it seemed appropriate that the logo should feature a virtual fossil. This model of a trilobite, an enrolled *Bailliaspis ? glabrata*, is based on CT scans and 3D reconstructions by Imran Rahman, Deputy Head of Research at the Oxford University Museum of Natural History and member of the Organizing Committee. The model is part of 3D computer simulations associated with a paper in *Palaeontology* by Jorge Esteve and colleagues on modelling enrolment in Cambrian trilobites.





The Palaeontological Association wishes to thank the Organizing Committee:

**Chair:**

- Dr Jack J. Matthews

**Organizing committee:**

- Dr Frankie S. Dunn
- Dr Duncan J. E. Murdock
- Dr Elsa Panciroli
- Dr Ricardo Pérez-de la Fuente
- Dr Imran A. Rahman
- Prof. M. Paul Smith
- Dr Lauren H. Sumner-Rooney

**The Science Committee:**

- Dr Ross P. Anderson
- Dr Neil Brocklehurst
- Dr Richard P. Dearden
- Dr Frankie S. Dunn
- Dr Isabel S. Fenton
- Hiu Wai Lee
- Dr Jack J. Matthews
- Dr Duncan J. E. Murdock
- Dr Elsa Panciroli
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- Prof. M. Paul Smith
- Dr Lauren H. Sumner-Rooney
- Dr James D. Witts
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**Sponsors**

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

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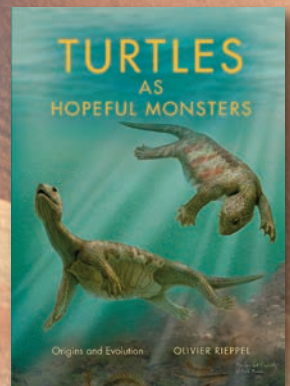
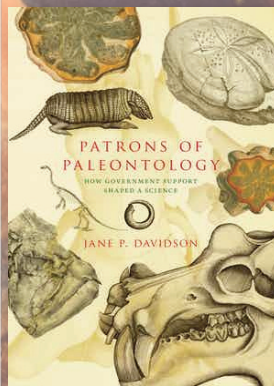
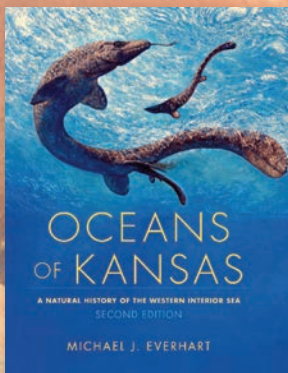
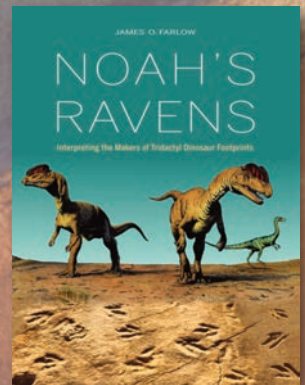
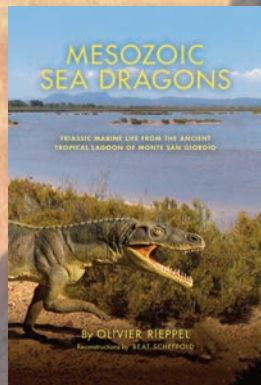
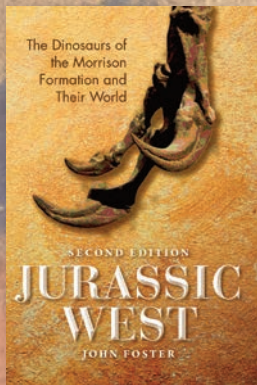
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## *Summary of Schedule*

Please note: all times given are in GMT.

### **Tuesday 15th December: Pre-conference fringe events**

A number of fringe events associated with the Annual Meeting are available to book separately online. These include a Palaeoethics Workshop to discuss ethical issues in palaeontology from fieldwork to collections and publication.

### **Wednesday 16th December: Conference and Symposium**

The conference will begin with opening remarks at 09.00 on the morning of 18th December. The morning features single sessions of standard and flash talks, with the first poster session from 11.20 to 12.20. The conference continues after lunch with two parallel sessions of standard talks.

The afternoon will conclude with the Symposium entitled “New Ideas on Old Fossils: A Symposium of Early Career Palaeontologists from Around the World”, featuring five speakers.

### **Thursday 17th December: Conference, AGM and Annual Address**

The conference will start at 09.00 with single and parallel sessions of standard and flash talks throughout the morning. The conference continues in the afternoon with talks followed by the second poster session from 15.15 to 16.15.

The Annual General Meeting will begin at 16.30. The results of the recent election of new Council members will be announced, as well as the outcome of grant applications and the Association’s annual medals and awards. All members are strongly encouraged to attend the AGM, and non-members are also free to view the event. We suggest non-members join from around 17.00 for the announcements of the 2020 medals and awards.

The Annual Address will be given at 19:00 by Prof. Rachel Wood of the University of Edinburgh and is entitled “Tales from the Cambrian Explosion”. This is a public event and all are welcome.

### **Friday 18th December: Conference, prizes and social events**

The conference will start at 09.00 with single and parallel sessions of standard and flash talks continuing throughout the day. Talks will end at 16.45, followed by an update from the Association’s Diversity Officer and presentations by the organizing committees of upcoming meetings. The main conference will then close with the award of the President’s Prize, the Council Flash Talk Prize and the Council Poster Prize, followed by concluding remarks.

This year’s Annual Meeting will end with ‘The Palaeovision Fossil Contest’, an online, interactive, international competition to decide the Annual Meeting’s favourite fossil for 2020, starting at 19:30.



## 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 December, 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 commonsense 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: <<https://www.palass.org/association/report-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.



# Schedule of events and timetable of presentations

## Wednesday 16th December

### *Conference and symposium*

Underlined author denotes designated speaker.

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

#### Session 1

09.00 – 09.15 **Opening remarks**

09.15 – 09.30 **Multiple branching and attachment structures in mat-dwelling cloudinomorphs, Nama Group, Namibia**

\*Amy Shore, Rachel Wood, Andrew Curtis and Fred Bowyer

09.30 – 09.45 **The origin of Ecdysozoa and an Early Cambrian stem group Ecdysozoan**

\*Richard J. Howard, Gregory D. Edgecombe, Xiaomei Shi, Xianguang Hou and Xiaoya Ma

09.45 – 10.00 **Appendage specialization in the Cambrian trilobite *Olenoides serratus* from the Burgess Shale**

\*Sarah Lusso and Javier Ortega-Hernández

10.00 – 10.15 **Small carbonaceous fossils (SCFs) from North Greenland: new light on metazoan diversity in early Cambrian shelf environments**

\*Elise Walleit, Ben J. Slater, Sebastian Willman and John S. Peel

10.15 – 10.30 **Synchrotron X-ray tomography of *Hyperblastus reimanni* provides the first comprehensive 3D reconstruction of various internal soft tissue structures in a fossil blastoid**

\*Nidia Alvarez Armada, Imran A. Rahman and Jennifer E. Bauer

10.30 – 10.45 **Break**

#### Session 2

10.45 – 10.50 **New, unique pterosaur remains from the Great Estuarine Group of Scotland**

\*Natalia Jagielska, Stephen L. Brusatte, Michael O'Sullivan, Ian Butler, Thomas J. Challands, Neil D. L. Clark, Nicholas C. Fraser, Amelia M. Penny, Dugald A. Ross and Mark Wilkinson

10.50 – 10.55 **Evolutionary and ontogenetic changes of the anatomical organization and modularity in the skull of archosaurs**

\*Hui Wai Lee, Borja Esteve-Altava and Arkhat Abzhanov

10.55 – 11.00 **Refinement of palaeocolour reconstruction using machine learning**

\*Arindam Roy, Satyaki Roy, and Michael Pittman



- 11.00 – 11.05 **The unique dentition of the rhynchocephalian *Clevosaurus brasiliensis*, and rhynchocephalian diversity in the Late Triassic of the southern hemisphere**  
\*[Sofia Chambi-Trowell](#), David I. Whiteside, Michael J. Benton, Agustin G. Martinelli and Emily J. Rayfield
- 11.05 – 11.10 **Ontogenetic patterns of the crocodylian palate (*Eusuchia*, *Crocodylia*)**  
\*[Ane de Celis](#), Iván Narváez, Alejandro Serrano-Martínez and Francisco Ortega
- 11.10 – 11.20 **Questions and panel discussion**
- 11.20 – 12.20 **Poster session 1**
- 12.20 – 13.15 **Break**

### Session 3A (in parallel with session 3B)

- 13.15 – 13.30 **Diversification dynamics of total-, stem- and crown-groups are compatible with molecular clock estimates of divergence times**  
\*[Alan J. S. Beavan](#), Davide Pisani and Philip C. J. Donoghue
- 13.30 – 13.45 **Tree shape warps perceptions of morphological disparity in analyses of cladistic discrete character datasets**  
\*[Thomas J. Smith](#), Mark N. Puttick, Joseph E. O'Reilly, Davide Pisani and Philip C. J. Donoghue
- 13.45 – 14.00 **The brain evolutionarily and developmentally shapes the skull**  
\*[Matteo Fabbri](#), Daniel Smith Paredes, Miccaella Vergara, Laurel Yohe and Bhart-Anjan S. Bhullar
- 14.00 – 14.15 **Phylogenetic utility of the avian pectoral girdle and forelimb skeleton**  
\*[Albert Chen](#), Roger B. J. Benson and Daniel J. Field
- 14.15 – 14.30 **Reassessment of the evolutionary history of Late Triassic and Early Jurassic sauropodomorph dinosaurs**  
\*[Omar Rafael Regalado Fernandez](#), Paul Upchurch, Philip D. Mannion, Paul M. Barrett and Susannah C. R. Maidment

### Session 3B (in parallel with session 3A)

- 13.15 – 13.30 ***In situ* spores of *Asterotheca merianii*: morphological variability and effects of preparation**  
[Hendrik Nowak](#) and Evelyn Kustatscher
- 13.30 – 13.45 **Zechstein forests thrived up to the Permian–Triassic mass extinction event**  
[Martha Gibson](#) and Charles H. Wellman
- 13.45 – 14.00 **Late Triassic terrestrial invertebrate and plant trace fossils from the Mid-Zambezi Basin, Zimbabwe**  
[Lara Sciscio](#), Timothy J. Broderick, Paul M. Barrett, Darlington Munyikwa, Michel Zondo and Jonah N. Choiniere



14.00 – 14.15 **Latitude induced climatic forcing as a driver for bioregionalization during the Devonian period: a case study from high latitudinal regions of West Gondwana**  
Cameron Penn-Clarke and David A.T. Harper

14.15 – 14.30 **Heat stress indications in the shells of benthic foraminifera: insights from a thermally polluted field laboratory**  
Danna Titelboim, Oliver Lord and Daniela N. Schmidt

\*

**Symposium:** *“New Ideas on Old Fossils: A Symposium of Early Career Palaeontologists from Around the World”*

14.45 – 15.15 ***Dickinsonia costata* from the Late Precambrian of the White Sea**  
Maria Zakrevskaya and Andrey Ivantsov

15.15 – 15.45 **The influence of extinction on the rise and fall of trilobite disparity**  
Diego Balseiro, Arnaud Bignon and Fernanda Serra

15.45 – 16.15 **Growing with dinosaurs: an interdisciplinary approach to getting to know South Africa’s iconic *Massospondylus carinatus***  
Kimberley E. J. Chapelle, Paul M. Barrett, Stephan Lautenschlager, Jennifer Botha, Vincent Fernandez and Jonah N. Choiniere

16.15 – 16.30 **Break**

16.30 – 17.00 **Breaking new ground in the study of Egypt’s ancient prehistory**  
Sanaa El-Sayed and Hesham Sallam

17.00 – 17.30 **Phytolith analyses from modern Herbivore molars: testing reliability of using phytoliths to reconstruct herbivore diets/habitats in the fossil record**  
Rahab N. Kinyanjui, Doris Barboni and Jean-Philip Brugal

## Thursday 17th December

### *Conference, Association AGM and Annual Address*

Underlined author denotes designated speaker.

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

#### Session 4

09.00 – 09.05 **Heterophyllous ferns from Las Hoyas (Cuenca, Spain) and El Montsec (Lleida, Spain): highlighting their importance in the evolution of vegetation during the Early Cretaceous**  
\*Candela Blanco Moreno and Ángela D. Buscalioni

09.05 – 09.10 **Microanalytical investigation of exceptionally preserved microbial fossils in the Rhynie chert**  
\*Edwin Rodriguez-Dzul, Sean McMahon and Bryne T. Ngwenya



- 09.10 – 09.15 **Scientometric trends in Burmese amber research**  
\*[Emma Dunne](#) and Nussaibah B. Raja
- 09.15 – 09.20 **Creating a link between schools and palaeontologists: how the use of valuable fossils can encourage scientific literacy**  
\*[Lara de la Cita García](#) and Angela Delgado Buscalioni
- 09.20 – 09.25 **In search of the Cheshire Cat: the appearance and disappearance of the planet's first eumetazoans**  
[Dmitriy V. Grazhdankin](#)
- 09.25 – 09.35 **Questions and panel discussion**
- 09.35 – 09.40 **Break**

#### Session 5

- 09.40 – 09.45 **Characterization of intraspecific variation of the European stem turtle *Pleurosternon bullockii* (Paracryptodira)**  
\*[Andrea Guerrero](#) and Adán Pérez-García
- 09.45 – 09.50 **Convex hull estimation of mammalian body segment parameters**  
\*[Sam Coatham](#), William Sellers and Thomas A. Püschel
- 09.50 – 09.55 **Morphological evolution in the tribe Cricetodontini (Cricetidae, Rodentia) during the Miocene**  
\*[Patricia Carro-Rodriguez](#), Paloma López-Guerrero, Pablo Peláez-Campomanes and M<sup>a</sup> Ángeles Álvarez-Sierra
- 09.55 – 10.00 **Modelling skeletal enrichment as a result of mixing, advection and disintegration of skeletal remains**  
\*[Niklas Hohmann](#) and Adam Tomašových
- 10.00 – 10.05 **Multi-proxy dental morphological analysis: a quantitative approach to inferring diet across distantly related taxa**  
\*[Christopher Stockey](#), Neil Adams, Philip C. J. Donoghue, Thomas H. P. Harvey and Mark A. Purnell
- 10.05 – 10.15 **Questions and panel discussion**
- 10.15 – 10.20 **Break**

#### Session 6A (in parallel with session 6B)

- 10.20 – 10.35 **The ever-browsing Deinotheriidae (Mammalia, Proboscidea): did climate change affect conservative herbivory during the Miocene?**  
\*[Alexandros Xafis](#), Erik Wolfgring, Nagel Doris and Friðgeir Grímsson
- 10.35 – 10.50 **Charting new waters: changes in skull ecomorphology during the initial aquatic radiations of mosasaurs and cetaceans**  
\*[Rebecca Bennion](#), Jamie MacLaren, Ellen Coombs, Felix Marx, Olivier Lambert and Valentin Fischer



- 10.50 – 11.05 **On the anatomy of *Conoryctes*: insights into the evolution of Paleocene mammals following the end-Cretaceous mass extinction**  
\*[Zoi Kynigopoulou](#), Sarah L. Shelley, Thomas E. Williamson and Stephen L. Brusatte
- 11.05 – 11.20 **Insular gigantism in giant dormice: divergence from the non-giant allometric trajectory**  
\*[Jesse J. Hennekam](#), Roger B. J. Benson, Victoria L. Herridge, Nathan Jeffery, Enric Torres-Roig, Josep A. Alcover and Philip G. Cox
- 11.20 – 11.35 **High resolution rapid thermal neutron tomographic imaging of fossiliferous cave breccias from Southeast Asia**  
\*[Holly Smith](#), Joseph Bevitt, Ulf Garbe, Jahdi Zaim, Yan Rizal, Mika Rizki Puspaningrum, Aswan, Agus Trihiscaryo, Gilbert Price, Gregg Webb and Julien Louys

#### Session 6B (in parallel with session 6A)

- 10.20 – 10.35 **Evolution of dental topographic disparity in African anthropoid and strepsirrhine primates from the Eocene into the Miocene**  
[Dorien de Vries](#) and Erik R. Seiffert
- 10.35 – 10.50 **Morphological variability of petrous bone in extant and extinct suids (Mammalia, Artiodactyla): taxonomic and phylogenetic implications of a new morphometric protocol**  
[Karl Baltazart](#), Antoine Souron, Bastien Mennecart and Jean-Luc Guadelli
- 10.50 – 11.05 **Incongruent species delimitation among extant and extinct lacertid lizards, and how to overcome the “species problem” using morphology**  
[Emanuel Tschopp](#), James G. Napoli, Lukardis C. M. Wencker, Massimo Delfino and Paul Upchurch
- 11.05 – 11.20 **Otolith taphonomy: can we estimate the age-since-death of an otolith based on its preservation state?**  
[Konstantina Agiadi](#), Michele Azzarone, Quan Hua, Darrell S. Kaufman, Danae Thivaïou and Paolo G. Albano
- 11.20 – 11.35 **Sea-level history and species ecology control the scale of time-averaging in molluscan fossil assemblages on the northern Adriatic shelf**  
[Rafal Nawrot](#), Daniele Scarponi, Adam Tomašových and Michał Kowalewski
- 11.35 – 11.50 **Break**

#### Session 7A (in parallel with session 7B)

- 11.50 – 12.05 **Using computer flow simulations to explore the hydrodynamics of extreme body morphology and size in derived Mesozoic marine reptiles**  
\*[Susana Gutarra Diaz](#), Thomas L. Stubbs, Benjamin C. Moon, Colin Palmer and Michael J. Benton
- 12.05 – 12.20 **Resolving the pterosaur bauplan using a quantitative taphonomic approach**  
\*[Rachel Belben](#)





- 12.20 – 12.35 **Skin patterning and internal anatomy of a 50 Ma moonfish from the Monte Bolca Lagerstätte**  
\*[Valentina Rossi](#), Roberto Zorzin, Richard Unitt, Maria E. McNamara and Giorgio Carnevale
- 12.35 – 12.50 **Skeletal and soft tissue completeness of the acanthodian fossil record through time**  
\*[Lisa Schnetz](#), Richard J. Butler, Michael I. Coates and Ivan J. Sansom
- 12.50 – 13.05 **Reinvestigating the ‘Maastricht ichthyornithine’ from the latest Cretaceous of Belgium**  
\*[Juan Benito](#), John W. M. Jagt and Daniel J. Field

#### Session 7B (in parallel with session 7A)

- 11.50 – 12.05 **Informing the 3D morphology of the Ediacaran rangeomorph *Fractofusus misrai* through detailed taphonomic analysis**  
[Rod S. Taylor](#), Robert Nicholls, Jenna Neville and Duncan Mclroy
- 12.05 – 12.20 **The palaeogeographic distribution of the Ediacaran macrobiota**  
[Catherine E. Boddy](#), Emily G. Mitchell, Andrew Merdith and Alexander G. Liu
- 12.20 – 12.35 **Crossing the boundary: small carbonaceous fossils (SCFs) as a means of tracking Ediacaran–Cambrian ‘survivors’**  
[Ben J. Slater](#), Thomas H. P. Harvey and Nicholas J. Butterfield
- 12.35 – 12.50 **A reduced labrum in a Cambrian great-appendage euarthropod**  
[Javier Ortega-Hernandez](#), Yu Liu, Dayou Zhai and Xianguang Hou
- 12.50 – 13.05 **Life in a Cambrian back-reef environment: insights from a new Dyeran Konservat-Lagerstätte from British Columbia, Canada**  
[Rudy Lerosey-Aubril](#), David Comfort, Robert R. Gaines, John R. Paterson, Jacob Skabelund and Javier Ortega-Hernández
- 13.05 – 14.00 **Break**

#### Session 8A (in parallel with session 8B)

- 14.00 – 14.05 **The making of a Lagerstätte: taphonomic artefacts associated with the Ediacaran biota of Spaniard’s Bay, Newfoundland**  
\*[Christopher McKean](#), Duncan Mclroy and Rod S. Taylor
- 14.05 – 14.10 **Preliminary observations of potential reproductive structures in the rangeomorph *Culmofrons plumosa* from the Ediacaran of Newfoundland, Canada**  
\*[Giovanni Pasinetti](#), Duncan Mclroy and Rod S. Taylor
- 14.10 – 14.15 **Fronnduplication in a new rangeomorph: insights into growth, adaptability and development**  
\*[Anna McGairy](#), Charlotte G. Kenchington, Frankie S. Dunn and Alexander G. Liu



14.15 – 14.20 **Spiralling out of control: morphology and ecology of *Eoandromeda octobrachiata* from Nilpena, South Australia**

\*[Tory Botha](#), Emma Sherratt, Mary L. Droser, James G. Gehling and Diego C. Garcia-Bellido

14.20 – 14.25 **Biostratinomy of carbonate-hosted Ediacaran macrofossils in the Khatyspyt Formation, northeastern Siberia**

\*[Olzhas Zharasbayev](#), Natalia Bykova and Dmitriy V. Grazhdankin

14.25 – 14.35 **Questions and panel discussion**

**Session 8B (in parallel with session 8A)**

14.00 – 14.05 **Humeral diaphysis structure across mammals**

[Eli Amson](#)

14.05 – 14.10 **New data on the *Nacholapithecus* elbow show close affinities with *Equatorius* and living papionins**

[Marta Pina](#) and Masato Nakatsukasa

14.10 – 14.15 **Could Lucy run? Reconstructing lower limb musculature in *Australopithecus afarensis***

[Sian McCormack](#), Evie Donald, Sam Coatham, Charlotte A. Brassey, Thomas O'Mahoney, William Sellers and Karl T. Bates

14.15 – 14.20 **Ginglymostomatid-like multicuspid teeth in an elusive rajid skate from the Tuscan Pliocene**

[Alberto Collareta](#), Frederik H. Mollen, Marco Merella, Simone Casati and Andrea Di Cencio

14.20 – 14.25 **New insights in morphology and histology of Triassic Hybodontiform shark fin spines**

[Matthew Cowen](#) and Živilė Žigaitė

14.25 – 14.35 **Questions and panel discussion**

14.35 – 14.40 **Break**

**Session 9A (in parallel with session 9B)**

14.40 – 14.45 **Finding the worm: first palaeoscolecid from the middle Cambrian Marjum Formation of Utah, USA**

\*[Wade Leibach](#), Rudy Lerosey-Aubril, James D. Schiffbauer, Anna F. Whitaker and Julien Kimmig

14.45 – 14.50 **Testing hypotheses of trilobite head modularity with emphasis on the eyes**

\*[Ernesto Vargas-Parra](#) and Melanie Hopkins

14.50 – 14.55 **What triggered coccolithophore calcification?**

\*[Mariana Yilales](#), Rachel Wood, Rosalind E. M. Rickaby, Fabio Nudelman, Tianchen He, Sylvain Richoz and Matthew O. Clarkson



14.55 – 15.00 **Two-dimensional dental microwear indicates different feeding behaviours amongst three mosasaur taxa of the Campanian Bearpaw Fm., Alberta, Canada**  
\*[Femke M. Holwerda](#)

15.00 – 15.05 **Defining the preservational variability of *Funisia dorothea* and related insights on morphology from the Ediacara Member of South Australia**  
\*[Rachel Surprenant](#) and Mary L. Droser

15.05 – 15.15 **Questions and panel discussion**

#### Session 9B (in parallel with session 9A)

14.40 – 14.45 **Early post-embryonic stages of marrellomorph euarthropod from Morocco**  
[Lukáš Laibl](#), Pierre Gueriau, Farid Saleh, Frances Pérez-Peris, Lorenzo Lustri, Orla G. Bath Enright, Jonathan B. Antcliffe and Allison C. Daley

14.45 – 14.50 **The freshwater Devonian arthropod *Oxyuropoda*: the oldest peracarid crustacea (Eumalacostraca)?**  
[Ninon Robin](#) and Maria E. McNamara

14.50 – 14.55 **Predation by Octopodoidea in the fossil record**  
[Adiel A. Klompmaker](#), B. Alex Kittle and Neil H. Landman

14.55 – 15.00 **Can we reconstruct limb motion from fossil footprints?**  
[Barbara Grant](#), James Charles, Peter L. Falkingham, Kristiaan D'Août and Karl T. Bates

15.00 – 15.05 **Unravelling the legacies of empire in palaeontology: examples from the Sedgwick Museum**  
[Liz Hide](#) and Robert Theodore

15.05 – 15.15 **Questions and panel discussion**

15.15 – 16.15 **Poster session 2**

16.15 – 16.30 **Break**

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### *Annual General Meeting*

16.30 – 18.00 **Annual General Meeting and presentation of Association medals and awards**

18.00 – 19.00 **Break**

### *Annual Address*

19.00 – 20.30 **Tales from the Cambrian Explosion**  
Rachel Wood



## Friday 18th December

### *Conference and social events*

Underlined author denotes designated speaker.

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

#### Session 10A (in parallel with session 10B)

- 09.00 – 09.15 **Evolution of feeding mechanics in the dietary diversification of theropod dinosaurs**  
\*Wai Sum Ma, Stephan Lautenschlager, Michael Pittman, and Richard J. Butler
- 09.15 – 09.30 **The first multi-individual assemblage of a Mesozoic dinosaur from Italy: systematic, osteohistological and morphological re-evaluations of *Tethyshadros insularis* (Dinosauria: Ornithopoda)**  
\*Alfio A. Chiarenza, Matteo Fabbri, Marco Muscioni, David C. Evans and Federico Fanti
- 09.30 – 09.45 **The cranial anatomy of *Qianzhousaurus sinensis***  
\*William Foster, Stephen L. Brusatte and Lü Junchang
- 09.45 – 10.00 **Micro-computed tomography of the aistopods from the Jarrow Assemblage, Ireland**  
\*Aodhán Ó Gogáin, Patrick N. Wyse Jackson and John Murray
- 10.00 – 10.15 **Constraining quadrupedal launch: range of motion in *Coloborhynchus***  
\*Benjamin Griffin, Elizabeth Martin-Silverstone, Oliver E. Demuth, Colin Palmer and Emily J. Rayfield

#### Session 10B (in parallel with session 10A)

- 09.00 – 09.15 **Evolutionary stasis in the ammonite *Discoscaphites iris* from the US Gulf and Atlantic Coastal Plains prior to the end-Cretaceous (K–Pg) mass extinction**  
James D. Witts, Neil H. Landman, Ekaterina Larina, Matthew Garb, Anastasia Rashkova, Kayla Irizarry, Jone Naujokaityte, Remy Rovelli and Corinne E. Myers
- 09.15 – 09.30 **Growing up big: the largest known cowrie and the evolution of giant cypraeid gastropods**  
Stefano Dominici, Mariagabriella Fornasiero and Luca Giusberti
- 09.30 – 09.45 **Going round the twist: an empirical analysis of shell coiling in helicospiral gastropods**  
Katie S. Collins, Roman Klapaukh, James S. Crampton, Michael F. Gazley, C. Ian Schipper, Anton Maksimenko and Benjamin R. Hines
- 09.45 – 10.00 **Offspring size evolution in a colonial marine invertebrate lineage**  
Emanuela Di Martino and Lee Hsiang Liow
- 10.00 – 10.15 **Niche partitioning and hydrodynamics of *Isoxys*: implications for the Cambrian biological pump**  
Stephen Pates, Allison C. Daley, David A. Legg and Imran A. Rahman
- 10.15 – 10.30 **Break**

**Session 11A (in parallel with session 11B)**

- 10.30 – 10.45 **Diverse communities of Bacteria and Archaea flourished in Earth's earliest ecosystems**  
\*[Keyron Hickman-Lewis](#), Frances Westall and Barbara Cavalazzi
- 10.45 – 11.00 **Growing pains of the Agronomic Revolution: Ediacaran–Cambrian bioturbators stimulated sulfide production in shallow sediment tiers**  
\*[Alison Cribb](#), Sebastiaan J. van de Velde, Simon A. F. Darroch, David J. Bottjer and Frank A. Corsetti
- 11.00 – 11.15 **The colonization of anoxic, matground-dominated sedimentary environments during the Early Phanerozoic**  
\*[Catherine Mascord](#), Liam G. Herringshaw, Krysia Mazik, Duncan McIlroy and Daniel Parsons
- 11.15 – 11.30 **The initial colonization of desert ecosystems – insights from the Mereenie Sandstone, Australia**  
\*[Anthony P. Shillito](#) and Neil S. Davies
- 11.30 – 11.45 **Fossilization potential of marine assemblages and environments**  
\*[Jack O. Shaw](#), Derek E. G. Briggs and Pincelli M. Hull

**Session 11B (in parallel with session 11A)**

- 10.30 – 10.45 **A Late Jurassic marine reptile fauna from Helmsdale, Scotland**  
[Kim Kean](#), Stephen L. Brusatte and Davide Foffa
- 10.45 – 11.00 **The evolution of body shape, locomotion and ecology in terrestrial vertebrates**  
[Alice Maher](#), Philip G. Cox, Thomas Maddox and Karl T. Bates
- 11.00 – 11.15 **Challenging hegemonic narratives: the rise of the naked pterosaur**  
[David M. Unwin](#)
- 11.15 – 11.30 **The first age of reptiles? Comparing reptile and synapsid diversity during the Carboniferous and early Permian**  
[Neil Brocklehurst](#)
- 11.30 – 11.45 **Early tetrapods: testing the boundaries**  
[Michael I. Coates](#), Benjamin Otoo, Vishruth Venkataramen, Kailin Wu, Peishu Li and Reese Fulgenzi
- 11.45 – 12.00 **Break**

**Session 12**

- 12.00 – 12.05 **Intrinsic or extrinsic? Untangling the impact of taphonomic, phylogenetic and ontogenetic factors on morphological variance in exceptionally preserved fossils**  
\*[Jane Reeves](#) and Robert S. Sansom
- 12.05 – 12.10 **Using evolutionary simulation to improve biodiversity-area models**  
\*[Euan Furness](#), Russell J. Garwood, Philip D. Mannion and Mark D. Sutton
- 12.10 – 12.15 **The changes of seawater chemistry during the Cambrian Explosion**  
\*[Yi Xiong](#) and Rachel Wood



12.15 – 12.20 **The invasion hierarchy: quantifying ecological and evolutionary consequences of invasions in the fossil record**  
[Alycia L. Stigall](#)

12.20 – 12.25 **Active trends and higher extinction of smaller lineages drove body mass increase in brontothers**  
[Juan L. Cantalapiedra](#), Oscar Sanisidro and Matthew C. Mhlbachler

12.25 – 12.35 **Questions and panel discussion**

12.35 – 13.30 **Break**

**Session 13A (in parallel with session 13B)**

13.30 – 13.45 **The impact of morphological clocks and fossil tips in inferring the tree of life**  
\*[Nicolas Mongiardino Koch](#), Russell J. Garwood and Luke A. Parry

13.45 – 14.00 **A new Euchelicerate from the early Ordovician Fezouata Biota, and its significance for “synziphosurine” phylogeny**  
\*[Lorenzo Lustrì](#), Pierre Gueriau, Peter Van Roy and Allison C. Daley

14.00 – 14.15 **Searching for macroevolutionary early bursts through 156 million years of ammonoid evolution**  
\*[Christopher D. Whalen](#), Pincelli M. Hull and Derek E. G. Briggs

14.15 – 14.30 **The palaeoenvironmental reconstruction of the Lower Toarcian (Lower Jurassic) Lower Sulphur Band, Cleveland Basin, UK**  
\*[Connor O’Keeffe](#), Crispin T. S. Little, Christian März, Fiona L. Gill, Christopher H. Vane and Simon W. Poulton

14.30 – 14.45 **Exceptionally preserved Cambrian paraconodonts hold key insights into the diversity of the earliest vertebrates**  
\*[Will Crabbe](#) and Thomas H. P. Harvey

**Session 13B (in parallel with session 13A)**

13.30 – 13.45 **Foot anatomy, walking energetics and the evolution of human bipedal locomotion**  
[James Charles](#), Barbara Grant, Kristiaan D’Août and Karl T. Bates

13.45 – 14.00 **Could the bat-winged dinosaurs fly? An assessment of powered flight ability in the Scansoriopterygidae**  
[Sophia Anderson](#), Stephen L. Brusatte and Graeme D. Ruxton

14.00 – 14.15 **How reliable are bite force estimates in extinct dinosaurs and mammals?**  
[Manabu Sakamoto](#)

14.15 – 14.30 **Investigating the evolution of forelimb anatomy and function in ornithischian dinosaurs**  
[Matthew Dempsey](#), Susannah C. R. Maidment and Karl T. Bates

14.30 – 14.45 **For your eyes only: evolution of orbit shape in archosaurs and its functional implications**  
[Stephan Lautenschlager](#)

14.45 – 15.00 **Break**

**Session 14**

- 15.00 – 15.15 **Organic matter preserves biosignatures in deepest time and drives soft tissue permineralization**  
*\*[Jasmina Wiemann](#)*
- 15.15 – 15.30 **Trouble in the ocean: a PETM record captured by planktic foraminifera species**  
*\*[Monsuru Adebawale](#), Ruby Barrett, Heather Birch, Jamie Wilson and Daniela N. Schmidt*
- 15.30 – 15.45 **The Metabolic Index: a flexible framework to predict biological responses to changing marine temperature and oxygen levels in deep time**  
*[Erik A. Sperling](#), Thomas H. Boag, Curtis Deutsch, Murray I. Duncan, Andy Marquez, Jonathan L. Payne, Justin L. Penn and Richard G. Stockey*
- 15.45 – 16.00 **Decreasing Phanerozoic extinction intensity as a consequence of Earth surface oxygenation and metazoan ecophysiology**  
*\*[Richard G. Stockey](#), Alexandre Pohl, Andy Ridgwell, Seth Finnegan and Erik A. Sperling*
- 16.00 – 16.15 **A case for arachnid monophyly and a single terrestrialization within chelicerates**  
*[Jesus Lozano-Fernandez](#), Richard J Howard, Mark N Puttick and Gregory D Edgecombe*
- 16.15 – 16.30 **Break**

**Session 15 and closing business**

- 16.30 – 16.45 **Carbon isotope measurements of single organic-walled microfossils from the Tonian Chuar Group, USA reveal taxon-specific water column habitats**  
*[Heda Agić](#), Phoebe Cohen, Susannah Porter and Christopher Junium*
- 16.45 – 16.55 **Presentation by the Association Diversity Officer**  
*[Rachel C. M. Warnock](#)*
- 16.55 – 17.15 **Presentations from the organizing committees of PalAss 2021 and Progressive Palaeontology 2021**
- 17.15 – 17.30 **Presentation of the President's Prize, Council Flash Talk Prize and the Council Poster Prize followed by closing remarks**
- 19.30 **The Palaeovision Fossil Contest**



## Abstracts of symposium presentations

### New Ideas on Old Fossils: A Symposium of Early-Career Palaeontologists from Around the World

The Symposium will take place on Wednesday 16th December

**Growing with dinosaurs: an interdisciplinary approach to getting to know South Africa's iconic *Massospondylus carinatus***

**Kimberley E. J. Chapelle<sup>1</sup>, Paul M. Barrett<sup>2</sup>, Stephan Lautenschlager<sup>3</sup>, Jennifer Botha<sup>4,5</sup>, Vincent Fernandez<sup>2</sup> and Jonah N. Choiniere<sup>1</sup>**

<sup>1</sup>University of the Witwatersrand, Johannesburg, South Africa

<sup>2</sup>Natural History Museum, London, UK

<sup>3</sup>University of Birmingham, UK

<sup>4</sup>National Museum Bloemfontein, South Africa

<sup>5</sup>University of the Free State, South Africa

In the last decade, digital methods for studying fossils have come into their own, allowing for the use of multiple methods to examine the same material in order to test hypotheses previously out of reach. Using an interdisciplinary approach including micro-computed-tomography, synchrotron radiation, digital retrodeformation, geometric morphometrics and osteohistology, we can reassess longstanding hypotheses regarding the identity and growth strategies of *Massospondylus carinatus* and their implications in the macroevolution of dinosaurs. *Massospondylus carinatus* was one of the first dinosaurs named from southern Africa in 1854 by Sir Richard Owen. Since then, hundreds of specimens have been discovered and referred to the taxon, meaning it is one of the most iconic dinosaurs from South Africa. These abundant fossils range in size from embryo to adult, making it an ideal study system for looking at dinosaur life histories. The phylogenetic position of this Early Jurassic plant-eating dinosaur also entails that understanding its development has inferences for the evolution of sauropodomorphs.

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### Phytolith analyses from modern Herbivore molars: testing reliability of using phytoliths to reconstruct herbivore diets/habitats in the fossil record

**Rahab N. Kinyanjui<sup>1</sup>, Doris Barboni<sup>2</sup> and Jean-Philip Brugal<sup>3</sup>**

<sup>1</sup>National Museums of Kenya, Kenya

<sup>2</sup>CEREGE, Aix-en-Provence, France

<sup>3</sup>CNRS, Aix-en-Provence, France

Phytolith are plant's silica cells formed when silica is deposited within and/or around plants' cells producing cell casts that are taxonomically related to source, hence, if extracted from secondary environments or source, they can be traced back to their primary source. Grass short cell phytoliths (GSCP) are particularly significant and more diagnostic than those associated with woody and herbaceous sources. East African herbivores are specialized grazers/browsers or mixed feeders depending on what is available in their habitats. Specialized grazers are ecologically associated with open grasslands while specialized browsers are ecologically associated with wooded vegetation cover (forests, shrublands, bushlands). In the palaeontological record, preservation of teeth is favoured





by all depositional environments, therefore in most cases, it is the only part of the animal that is used to accurately identify the animals' species in the fossil record. Over the years, isotopic analyses have been used to study the teeth to identify animals' diets and, by extension, the environments they interacted with. Here we explore how reliable phytolith analyses can be in reconstructing diets of herbivore species with known feeding behaviour and assess their application in reconstructing herbivore diet in the fossil record. We present the preliminary data analysed from six specialized grazers, six specialized browsers and six mixed feeders collected from different habitats.

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### The influence of extinction on the rise and fall of trilobite disparity

**Diego Balseiro, Arnaud Bignon and Fernanda Serra**  
*CONICET, Universidad Nacional de Córdoba, Argentina*

Of the many contributions of palaeontology to evolutionary biology, the analysis of the evolution of morphological diversity – *i.e.* disparity – is probably among the most relevant. In particular, the rise and fall of disparity throughout the evolutionary history of a clade has been a widely studied aspect of the fossil record. The temporal dynamics of morphological disparity are usually studied by comparing the trajectories of taxonomic and morphological diversity. However, comparing trajectories alone is not enough to understand true macroevolutionary dynamics of disparity, because it analyses net diversification but does not individualize extinction and origination rates. In this contribution we analyse trilobite disparity during the Cambrian–Devonian history of the clade, integrating the largest morphometric database to date with stratigraphic ranges obtained from the Paleobiology Database. We generate time series of taxonomic and morphological diversity, extinction and origination rates, and individualize the selectivity of extinction and origination with respect to morphology using logistic regression. Net diversification is unable to explain the trend in disparity because the largest increases in trilobite morphological diversity occur at intervals of relatively stable taxonomic diversity. However, studying the selectivity of extinction and origination sheds light on the dynamics underlying the trend in disparity. In particular, a modified measure of the macroevolutionary influence of extinction and origination shows how these processes complement each other to generate the observed patterns, underscoring that both extinction and origination can individually produce increases and decreases in disparity. For trilobites in particular, extinction is the main cause of morphospace expansion and contraction, highlighting that the classic idea of extinction as a constraining factor for morphological evolution is a limited view.

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### Breaking new ground in the study of Egypt's ancient prehistory

**Sanaa El-Sayed<sup>1</sup> and Hesham Sallam<sup>1,2</sup>**

<sup>1</sup>*Mansoura University, Egypt*

<sup>2</sup>*The American University in Cairo, Egypt*

Mansoura University Vertebrate Paleontology center (MUVP) is a research unit within the Department of Geology, created in 2010 to be a pioneer centre in Egyptian universities and institutions. It is the only high-level research unit in the field of vertebrate palaeontology in Egyptian universities, and indeed in the entire Middle East. Since its foundation, MUVP has become a centre for the study of fossil vertebrates where students and researchers can exchange ideas and collaborate on projects that build upon Egypt's fascinating geological past. MUVP is engaged in multiple projects in the Egyptian deserts that are diverse in scope, ranging from Late Cretaceous



dinosaurs to Oligocene mammals, with other groups (*e.g.* fishes) or questions (*e.g.* stratigraphy) sprinkled in between. Late Cretaceous projects aim to recover vertebrate fossils, in particular archosaurs and mammals, from the exposures in the Western Desert. Recovery of such fauna from this area will help us to understand the final phase of non-avian dinosaur evolution and the subsequent rise of mammals. In the Cenozoic, MUVP is interested in understanding the possible impacts of hyperthermal events like the Paleocene Eocene Thermal Maximum (PETM) and the Late Danian event (LDE), both of which are represented by fossil-bearing marine beds in the Eastern Desert. MUVP also has active palaeontological fieldwork in the Fayum Depression excavating the micromammal-bearing quarries north of Birket Qarun (late Eocene to early Oligocene in age). Expeditions there have led to the recovery of remarkable and unparalleled collections of fossil mammals, including primates and representatives of many other groups. Fossil whales represent an additional area of interest for MUVP, and are the focus of excavations in the middle to late Eocene deposits south of Birket Qarun. This work has led to a series of remarkable discoveries including the oldest record of Basilosauridae in Africa (early middle Eocene), which will help to fill in an important biogeographic and evolutionary gap in our understanding of the early evolution of whales. The results of these projects have made substantial contributions to scientific understanding of the vertebrate fossil record of Egypt through publications led by Egyptian students. Another critical aspect of the MUVP's work is its public outreach. MUVP has come to play an indispensable role in helping to communicate the new palaeontological discoveries to the general public via accessible social media, presented free of jargon, in Arabic. This endeavour has raised public engagement in science and provided a model that other Middle Eastern institutions seek to apply.

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### ***Dickinsonia costata* from the Late Precambrian of the White Sea**

**Maria Zakrevskaya and Andrey Ivantsov**

*Borissiak Paleontological Institute, RAS, Russia*

*Dickinsonia costata*, one of the most recognizable Ediacaran macrofossils, has been found in abundance in the siliciclastic deposits of the Flinders Ranges (South Australia) and the White Sea coast (northeastern Europe). However, the main information about it is based on the Australian material. In the White Sea Basin, *D. costata* lived in quieter environments. Its remains are found in more fine-grained, slightly altered rocks and, in addition to imprints and feeding traces, are also represented by organic 'compressions'. This allows us to expand the data on age-related changes in *D. costata*, going beyond the documented range of body length (4.1–140.5 mm). The smallest specimens that show the main features of *D. costata* (rounded outline, with length only slightly exceeding width, wide 'half-segments' or isomers) are 1.7 mm long, and the number of visible isomers does not exceed 3–4 pairs. However, in the White Sea localities, there are also similar rounded imprints of smaller size, highlighted by organic matter. Transverse dissection is less noticeable in them, and in the smallest ones (up to 1.2 mm) does not appear at all. This can be explained by the unfavourable ratio of the density of the thin body and the grain size of the surrounding rock. However, based on the trend of a decrease in the number of isomers with a decrease in body size, such *D. costata* specimens could lack transverse dissection, and the putative planktonic *Dickinsonia* larva could be nonmetameric. The largest *D. costata* specimen is 395 mm in length and has 225 pairs of visible isomers. The White Sea material shows that the appearance of *D. costata* in the benthic community occurred at a body diameter of slightly more than 1 mm, and the addition of isomers occurred during the entire observed interval of a lifetime.



## Abstract of Annual Address

The Annual Address will be given on Thursday 17th December at 19.00 GMT. All Annual Meeting delegates will automatically be registered for this event. The event is also open to the public, and we welcome the support of members and attendees in helping advertise this free annual palaeontological outreach event. Sign-up information for those who wish to attend but are not registered for the Annual Meeting will be circulated in due course.

### Tales from the Cambrian Explosion

**Prof. Rachel Wood**

*University of Edinburgh*

The Cambrian Explosion marks the rise of diverse animal groups *c.* 540 million years ago, but the triggers for this revolution remain poorly understood. I will explore the differing roles of changing climate, oceanic redox, nutrient availability and ecosystem feedbacks across the critical Ediacaran–Cambrian transitional period. The fossil record now reveals that the roots of the Cambrian Explosion are to be found in the Ediacaran. We can now document a series of pulses of enhanced seawater oxygen availability over the Ediacaran to Cambrian interval. These coincide with pulses of diversification and increased body size in animals, but the biological control of carbonate production was driven by ecosystem feedbacks including the rise of predation.



# Abstracts of oral presentations

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

Underlined author denotes designated speaker.

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## Trouble in the ocean: a PETM record captured by planktic foraminifera species

\***Monsuru Adebawale, Ruby Barrett, Heather Birch, Jamie Wilson and Daniela N. Schmidt**  
*University of Bristol, UK*

Climate change is causing warming, acidification, deoxygenation and increasing stratification of the ocean. These changes are projected to impact marine ecosystems causing migration of species, changes in biodiversity, and reducing productivity and carbonate production. Impacts are usually quantified in laboratory studies that are mostly too short to assess potentials for acclimation and adaptation. This study uses the Paleocene–Eocene Thermal Maximum (PETM, 56 Ma) as an analogue to modern climate disruptions to assess the impact on the planktic ecosystem. The PETM is associated with warming of up to 10°C in high latitudes, ocean acidification and lower open ocean productivity. Consequently, planktic foraminifers, major carbonate producers in the modern ocean, migrated to polar and subpolar regions and short-lived excursion taxa appeared. Here we generate a record of foraminiferal test sizes, fragmentation and calcification reconstructed via size normalized weights (SNW) in the tropics, mid and high latitudes. We combine the results with a numerical model of plankton ecosystems that resolves foraminifera embedded in a 3D Earth system model (EcoGENIE) to upscale our results to global assessments. We ascribe different climate forcing scenarios to assess the impact of anthropogenic climate change on plankton ecosystems.

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## Otolith taphonomy: can we estimate the age-since-death of an otolith based on its preservation state?

**Konstantina Agiadi<sup>1</sup>, Michele Azzarone<sup>1</sup>, Quan Hua<sup>2</sup>, Darrell S. Kaufman<sup>3</sup>, Danae Thivaoui<sup>4</sup> and Paolo G. Albano<sup>1</sup>**

<sup>1</sup>*University of Vienna, Austria*

<sup>2</sup>*Australian Nuclear Science and Technology Organization, Australia*

<sup>3</sup>*Northern Arizona University, USA*

<sup>4</sup>*National and Kapodistrian University of Athens, Greece*

The extent of time-averaging in death and fossil assemblages is crucial for quantifying the temporal resolution of the fossil record. One approach to quantify scales of time-averaging is the taphonomic clock: older skeletons show a higher degree of alteration because of the accrual of skeletal damage with increasing post-mortem age. Here we test the taphonomic clock hypothesis for marine fish otoliths for the first time. We radiocarbon dated and taphonomically scored 77 otoliths from three sites along a 10 to 40 m gradient on the shallow Mediterranean Israeli shelf. Otolith ages range between 4 and 7,961 years, with considerable variation along the transect. At 30 m depth and for the pelagic component of the otolith assemblage, taphonomic degradation correlates positively with post-mortem age. In contrast, no correlation occurs for the demersal fish assemblages at 10 and 30 m depth, mostly because of the paucity of very young (<150 yr) otoliths. Young otoliths



are little damaged, possibly because of fast burial protecting them from the damaging processes at the sediment–water interface. At 40 m depth, all dated otoliths are young but damaged because of chemically aggressive sediments, thus showing no correlation between taphonomic grade and post-mortem age.

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## Carbon isotope measurements of single organic-walled microfossils from the Tonian Chuar Group, USA reveal taxon-specific water column habitats

**Heda Agić<sup>1</sup>, Phoebe Cohen<sup>2</sup>, Susannah Porter<sup>1</sup> and Christopher Junium<sup>3</sup>**

<sup>1</sup>University of California, Santa Barbara, USA

<sup>2</sup>Williams College, USA

<sup>3</sup>Syracuse University, USA

Ancient eukaryotic cells are represented in the rock record as organic-walled microfossils (OWM). Although OWM constitute the bulk of the Precambrian record, little is known about their affinities, habitats or trophic preferences. Organic carbon isotope analyses of single microfossils grant information about short-term environmental variability and ecology. To gain insight into palaeoecology of Neoproterozoic eukaryotes, we analysed C-isotopic composition of individual OWM from shales of the Tonian Chuar Group, using a nano-EA-IRMS method for single microfossil analysis. OWM (>100) include smooth, ornamented and envelope-bearing acritarchs, plus cell-aggregates and filaments that were components of benthic microbial mats. Microfossils show a wide spread of  $\delta^{13}\text{C}$  values/sample (up to 22 ‰). Depleted values of mat-building prokaryotes *Rugosoopsis*, *Polytrichoides* and *Symplastosphaeridium* (-33 to -26 ‰), lighter from bulk rock  $\delta^{13}\text{C}_{\text{org}}$  within sample by 5–16 ‰, are consistent with utilization of  $^{13}\text{C}$ -depleted C-sources from diffusing underlying pore waters, or DIC derived from respired planktonically-produced organic carbon. Ornamented *Simia* and *Germinosphaera* have enriched  $\delta^{13}\text{C}$  values (c. -15 ‰). *Simia* is consistently heavier than mat-builders within sample by up to 15.8 ‰, which suggests it probably incorporated  $^{13}\text{C}$ -enriched in surface waters, or utilized an alternative C-metabolism (e.g. bicarbonate pumping). The highest range in  $\delta^{13}\text{C}_{\text{OWM}}$  occurs in anoxic samples (FeHR/FeT >0.38), supporting the presence of a biological pump.

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## Synchrotron X-ray tomography of *Hyperblastus reimanni* provides the first comprehensive 3D reconstruction of various internal soft tissue structures in a fossil blastoid

**\*Nidia Alvarez Armada<sup>1</sup>, Imran A. Rahman<sup>2</sup> and Jennifer E. Bauer<sup>3</sup>**

<sup>1</sup>Independent

<sup>2</sup>Oxford University Museum of Natural History, UK

<sup>3</sup>University of Michigan Museum of Paleontology, USA

Preservation of internal soft tissues in fossil echinoderms, although rare, has been reported for fossil representatives of most classes in the phylum. Blastoids, along with other extinct groups of echinoderms, illustrate the challenges of interpreting soft tissues in enigmatic organisms lacking an extant analogue. Here, synchrotron X-ray tomography is applied to a well-preserved fossil blastoid, *Hyperblastus reimanni*. The coelomic system appears entirely preserved as a coiled arrangement partially enclosing a U-shaped structure, which is interpreted as the gut. The coelom is divided into two posteriorly interconnected compartments by a vertical membrane, enclosing two symmetric structures interpreted to



be part of the reproductive system, possibly a brooding chamber and associated organs. Hydrospires constrain the coelomic system anteriorly in the thecal cavity, attaining pseudo-pentaradial symmetry. The coelom system is crowned by a partially preserved water vascular system on its anterior-most part. Modern representatives of the phylum, such as crinoids, possess comparable internal characteristics to those described in this specimen. This is the first attempt to non-destructively reconstruct the coelomic system and associated internal organs of any representative of the class Blastoidea. Resolving the internal anatomy of this extinct group will inform on the evolution of key organ systems in early pentaradial echinoderms.

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### Could the bat-winged dinosaurs fly? An assessment of powered flight ability in the Scansoriopterygidae

**Sophia Anderson<sup>1,2</sup>, Stephen L. Brusatte<sup>2</sup> and Graeme D. Ruxton<sup>3</sup>**

<sup>1</sup>Durham University, UK

<sup>2</sup>University of Edinburgh, UK

<sup>3</sup>University of St Andrews, UK

The Scansoriopterygidae are a family of theropod dinosaurs from the Yanliao Biota (Mid-Late Jurassic, approximately 163 Ma) in Hebei Province, China. From the first description of *Scansoriopteryx* (= *Epidendrosaurus*) in 2002 (Zhang *et al.* 2002; Czerkas and Yuan 2002) to the recent description of *Ambopteryx* (Wang *et al.* 2019), discussion has arisen surrounding their elongated forelimb, styliiform and forelimb membrane. It is clear that the scansoriopterygids were experimenting with unusual forelimb morphology, but were they wings? Could these animals achieve powered flight? Here we provide a qualitative analysis of mechanical flight capability in scansoriopterygids and, for the first time, compare their 'wings' to those of bats. We also use multivariate analyses to quantitatively compare the flight characteristics (wingspan, body mass, wing area, wing loading and aspect ratio) of scansoriopterygids to eight species of pterosaurs, 14 species of birds and 213 species of bats which are under 1 kg in body mass, all from data available in published literature. We find strong evidence that at least one of the currently known scansoriopterygids – *Yi* – was capable of powered flight, falling in the morphospace of pterodactylomorph pterosaurs and extant pteropodid bats, and with wings mechanically comparable to both.

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### Morphological variability of petrous bone in extant and extinct suids (Mammalia, Artiodactyla): taxonomic and phylogenetic implications of a new morphometric protocol

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Suids are a suitable taxonomic group for understanding evolutionary mechanisms owing to their rich fossil record and their high morphological and ecological variability. Establishing a correct taxonomy is a crucial prerequisite for any palaeontological study. The petrous bone displays a complex morphology and is an important source of taxonomic/phylogenetic characters, but their use is hindered by a poor understanding of intraspecific variability. We therefore developed an original protocol to quantify morphological variation of lateral and medial faces of the petrous bone by combining 3D traditional morphometrics (linear



distances and areas) on surface models from CT scans and 2D geometric morphometrics (landmarks, semilandmarks) on photographs, drawings and standardized views from 3D models. We applied this protocol to 74 petrous bones encompassing 12 taxa to disentangle intraspecific and interspecific components of variability of main morphological structures (bone outline, position and shape of main foramina). Using two reference groups of more than 20 specimens, the extant wild boar (*Sus scrofa*) and an extinct suid from Ahl al Oughlam, Morocco (previously attributed to *Kolpochoerus*), we identified characters varying intraspecifically (e.g. length of medial process of protympanum). Based on this enhanced understanding of petrous bone variability, we discuss implications for taxonomic delineation and phylogenetic reconstructions.

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### Diversification dynamics of total-, stem- and crown-groups are compatible with molecular clock estimates of divergence times

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Molecular evolutionary timescales are expected to predate the fossil evidence and can imply a long period of total-group evolution before the origin of the crown-group, particularly for the evolutionary radiations of major clades including animals, mammals, birds and flowering plants. Hence, it has long been debated whether molecular clocks actually overestimate real divergence times. We use macroevolutionary simulations to describe the range of total-group and crown-group ages expected under a model with constant rates of speciation and extinction. Further, we show that predictions can be made about the time of origin of crown- and total-groups, as well as the extinction of the stem-group, and that there is a high degree of variance in these predictions. We show that under constant rates of speciation and extinction, the distribution of expected arthropod total-group ages is consistent with molecular clock estimates.

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### Resolving the pterosaur bauplan using a quantitative taphonomic approach

\***Rachel Belben**

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Despite more than 200 years of research, the pterosaur bauplan remains unresolved. A key issue concerns the structural and functional linkage of the limbs as determined by their inclusion or exclusion in the flight apparatus, *i.e.* wing membranes. In exceptionally well preserved non-pterodactyloid specimens the hind limbs appear attached to each other via a uropatagium, while in pterodactyloids they are separated. However, the applicability of these models for the vast majority of species, which lack soft tissue evidence of the uropatagium, is unknown. This study tests these models using quantitative taphonomic data on limb bone geometries (posture), with coverage of almost the entire stratigraphic and taxonomic range of Pterosauria. Context is provided by bats and birds, where the construction is known, and fossils show significant differences in limb posture. Bat limbs exhibit conservative, symmetrical postures, while in birds a much wider range of postures reflect their limbs' functional and anatomical independence. Plots for limb posture consistently show symmetrical 'bat-like' posture in non-pterodactyloids, while pterodactyloid plots closely match those of birds. This supports the widespread or universal models of hind limbs being independent of each other in pterodactyloids, and hind limbs connected by the uropatagium in non-pterodactyloids.



## Reinvestigating the 'Maastricht ichthyornithine' from the latest Cretaceous of Belgium

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Ichthyornithes may be more representative of the ancestral condition of crown birds than any other Mesozoic avialans. However, diversity and morphological disparity within the group is severely under-studied, and only one well-known taxon is currently recognized, *Ichthyornis dispar*. An unnamed specimen from the Maastricht Formation of Belgium (~66.7 Ma) has been previously suggested to show affinities with the 20 Ma older *Ichthyornis* from North America. Previously identified material from the specimen includes several elements encased in matrix, including limb bones, jaws, some vertebrae and a tooth, although the material has not received further attention. Here we investigate the specimen using high-resolution  $\mu$ CT, revealing the preservation of a partial skeleton including several new elements, and casting doubt on several previously-identified skeletal elements, such as the lower jaws. Beyond its much larger size, the morphology of the Maastricht bird is remarkably similar to that of *Ichthyornis*, sharing several of its diagnostic features. Phylogenetic analyses including the Maastricht bird recover it in a well-supported clade with *Ichthyornis*, stemward of the clade uniting Hesperornithes and crown-group birds. Improving our knowledge of Ichthyornithes and other crownward Mesozoic ornithurines might have crucial implications for clarifying patterns of morphological evolution preceding the origin of crown birds.

## Charting new waters: changes in skull ecomorphology during the initial aquatic radiations of mosasaurs and cetaceans

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The repeated return of tetrapods to water provides many iconic examples of convergent evolution, with various groups of mammals and reptiles independently evolving streamlined body shapes and similar feeding strategies. One comparison which has received little attention is that of cetaceans (whales and dolphins) and mosasaurs (a group of Late Cretaceous marine squamates). The earliest fully aquatic members of both groups had serpentine bodies and swam by axial undulation, before evolving more efficient caudal oscillatory locomotion and colonizing open ocean niches. Here we investigate possible parallel evolutionary trajectories of skull morphology that occurred during these initial aquatic radiations. A series of functionally informative ratios were calculated from 32 species of mosasaur and early cetacean. These were subjected to ordination techniques to reconstruct patterns of functional morphospace occupation. Preliminary results show that the earliest mosasaurs had gracile skulls specialized for smaller prey, from which they radiated in several waves across the morphospace. By contrast, basilosaurid





cetaceans occupied a relatively constrained megapredatory niche, and only evolved new ecomorphologies after the Late Eocene split into odontocetes and mysticetes. The results also suggest cranial convergence between the toothed mysticete *Janjucetus* and the mosasaur *Prognathodon*. Future work will investigate these results further using 3D landmarks.

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## The palaeogeographic distribution of the Ediacaran macrobiota

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Late Ediacaran macrofossils (580–539 Ma) document a diverse array of large, complex multicellular eukaryotes, including early animals. Distinguishing between evolutionary and ecological controls on the observed global distribution of Ediacaran macrofossils is vital if we are to identify early metazoan evolutionary trajectories, or causal links between environmental perturbations and biotic responses. The roles of temporal, palaeoenvironmental and lithological factors in shaping the modern geographic distribution of Ediacaran taxa have been widely investigated, but the influence of palaeogeography has received relatively little attention. Using a new database that compiles data on the age, location, morphogroup and body composition of 163 Ediacaran macrofossil genera across 31 localities, we investigated the influence of palaeolatitude on the spatial distribution of Ediacaran macrobiota through the late Ediacaran. The presence of candidate bilateral taxa, and frondomorphs, is significantly different between sites from low and high palaeolatitudes, whereas relationships between palaeolatitude and overall taxonomic diversity were not determined to be statistically significant. Proposed biomineralizing, algal and tubular taxa show no statistically different presence between high and low palaeolatitudes. In summary, palaeolatitude does appear to have significantly influenced the spatial distribution of some Ediacaran morphogroups, in conjunction with previously recognized factors including water depth and age.

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## The first age of reptiles? Comparing reptile and synapsid diversity during the Carboniferous and early Permian

**Neil Brocklehurst**

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Terrestrial ecosystems during the late Carboniferous and early Permian are usually described in the literature as dominated by synapsids, the mammal-line amniotes. The pelycosaurs (a paraphyletic grade of synapsid families) are considered more speciose, abundant and ecologically diverse than contemporary reptile-line amniotes. However, in recent years the amniote phylogeny has undergone numerous revisions, with suggestions that varanopids and recumbirostran microsaurians fall within reptiles, and that diadectomorphs may be pelycosaurian-grade synapsids. An examination of species richness in synapsids and reptiles during the Carboniferous and early Permian shows that these taxonomic revisions have substantial impacts on relative diversity patterns of synapsids and reptiles. Synapsids are only found to be consistently more diverse through the early Permian when using the 'traditional' taxonomy. The recent taxonomic updates produce diversity estimates where reptile diversity is consistent with, or in some cases higher than that of synapsids. Moreover, biases in preservation may affect patterns. Where



preservation favours smaller vertebrates, *e.g.* Fort Sill, reptiles overwhelmingly dominate. If smaller vertebrates are expected to make up the bulk of amniote diversity, such localities may be more representative of true diversity patterns.

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## Foot anatomy, walking energetics and the evolution of human bipedal locomotion

**James Charles, Barbara Grant, Kristiaan D'Août and Karl T. Bates**

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The morphology of the human foot is unique among great apes and is hypothesized to have evolved several traits that enhance the mechanical efficiency of striding bipedalism. However, many of the form-function relationships in modern humans remain quantitatively untested, and it remains uncertain whether the evolution of the foot was driven by selective pressures for efficient walking or running. In this study, correlations between a range of functional musculoskeletal traits in the human lower limb and the metabolic cost of locomotion (CoL) during walking over compliant and non-compliant substrates were examined. It was found that CoL varied considerably between human individuals within and across substrate types, but this variation in CoL was not statistically correlated or explained by variation in musculoskeletal parameters considered to be adaptively important to efficient bipedal locomotion. This provides indirect evidence that the morphology of the human foot does not confer advantages to the efficiency of walking, and it is subsequently hypothesized that musculoskeletal parameters will show stronger correlations with CoL during running. These findings also cast doubt over the use of simple skeletal metrics in foot anatomy to infer walking behaviour in fossil species.

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## Phylogenetic utility of the avian pectoral girdle and forelimb skeleton

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Although recent phylogenomic analyses have clarified the inter-relationships among crown-group birds, the results of these studies nonetheless exhibit notable incongruities with each other and with morphology-based hypotheses. However, existing crown-avian morphological datasets are often limited by restricted sampling, inconsistent character construction and other factors, which in turn hampers our understanding of early crown-bird evolution and the affinities of enigmatic fossil avians. Here we focused on identifying phylogenetically informative characters of the avian pectoral girdle and forelimb skeleton, elements of which are commonly preserved as avian fossils. A dataset of 176 characters was assembled based on personal observations and previous literature. Characters were revised as necessary following established criteria for formulating morphological characters, then scored for a diverse range of 49 extant avian taxa and analysed in preliminary phylogenetic analyses. Although these analyses do not recover identical topologies to recent molecular analyses, implementation of molecular scaffolds allows identification of diagnostic character combinations for several clades previously only recognized through molecular data, and potentially provides an independent avenue with which to assess support for alternative molecular topologies. Future work will quantify the phylogenetic



utility of individual characters through homoplasy indices and evaluate the effects of different analytical parameters on morphological tree topology.

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### The first multi-individual assemblage of a Mesozoic dinosaur from Italy: systematic, osteohistological and morphological re-evaluations of *Tethyshadros insularis* (Dinosauria: Ornithopoda)

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*Tethyshadros insularis* Dalla Vecchia, 2009 was originally described as an insular, pygmy hadrosauroid closely related to hadrosaurids, based on a complete and articulated specimen from the Upper Campanian–Early Maastrichtian Liburnian Formation, northeastern Italy. Recent preparation of a second specimen (SC 57247) and additional information from a third skull (SC 57026) provide important new elements on the anatomy and systematics of this taxon. *T. insularis* was originally diagnosed on a mosaic of primitive and derived characters, the latter particularly present in the skull, such as a long anteorbital region due to elongated maxillae and nasal bones. SC 57247 represents a 20 % larger individual based on skull length, with more massive appendicular proportions. The skull is remarkably shorter and brachyrostrine, features also present in SC 57026, displaying proportions more reminiscent of iguanodontoid-grade ornithischians rather than hadrosauromorphs. Histological thin sections from the ribs of SC 57247 indicate this larger individual is approaching somatic maturity, with the development of an incipient external fundamental system. After the reinterpretation of the holotype as pertaining to an immature individual, the systematic position of the taxon shifts more basally towards affinities with smaller-bodied hadrosauroids, casting doubts on previous claims of insular dwarfism in this ornithopod dinosaur.

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### Early tetrapods: testing the boundaries

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Remarkably, species of late Devonian limbed tetrapods and their near-relatives now outnumber ray-finned fish contemporaries. Here we present the results of a maximally inclusive phylogenetic analysis of these tetrapodomorphs, undertaken with the aim of further investigating survivorship from the end Devonian into the Tournaisian. Notably, many of these taxa are known only from jaw or limb fragments and the resultant data matrix is a mere 36 % complete, despite buttressing from skeletally complete material such as *Tiktaalik*, *Acanthostega* and *Ichthyostega*, and Carboniferous tetrapods including new data from *Whatcheeria*. Weak results prompted a systematic investigation of signal strength and consistency. Although attenuation correlates with taxon incompleteness, signal erosion is stepped, allowing more informed than expected estimates of evolutionary pattern. These include maximum and minimum estimates of Devonian lineages persisting into, and thus populating, ‘Romer’s Gap’. Notably, under both scenarios, the whatcheeriids



emerge as Devonian hold-overs, with consequences for our understanding of Famennian tetrapod diversity. However, consensus trees also present a steady correlation between node-order and node-date (minimum estimate), and the likely extension of lineages and branching events into the Givetian, a result that is intriguingly exaggerated when analyses are subjected to character weighting regimes.

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### Going round the twist: an empirical analysis of shell coiling in helicospiral gastropods

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The logarithmic helicospiral has been the most widely accepted model of gastropod form since it was proposed. It is based on an explicit assumption that shells are isometric and grow exponentially, and an implicit assumption that the external form of the shell follows the internal shape, and thus, parameters of the spiral can be reconstructed from the external whorl profile. Using 176 fossil and modern specimens of 25 species, we show that both assumptions are false. Using synchrotron micro-CT and physical sectioning, we measure internal morphologies and fit models to the whorl expansion rate, translation rate, and rate of increasing distance from coiling axis, and demonstrate that the best model is not the same for each parameter. Using the three rate parameters plus aperture shape, we construct an empirical shell morphospace for a case study of change in shell form through geological time in the austral family Struthiolariidae, to demonstrate the utility of our approach for evolutionary palaeobiology. Shell form parameters in the Struthiolariidae highlight a hitherto-neglected hypothesis of relationship between Antarctic *Perissodonta* and the enigmatic Australian genus *Tylospira*, that fits the biogeographic and stratigraphic distribution of both genera.

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### Exceptionally preserved Cambrian paraconodonts hold key insights into the diversity of the earliest vertebrates

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Paraconodonts are among the earliest skeletonizing vertebrates in the fossil record and are known exclusively from their tooth-like phosphatic elements. However, unlike their more derived relatives the euconodonts, they are very poorly understood from a palaeobiological perspective. Particularly it is unknown how distinct element types are biologically related, meaning that diversity of this group is conspicuously understudied. A brand-new, diverse assemblage of paraconodont elements preserved as small carbonaceous fossils (SCFs) has been recovered from the upper Cambrian (Furongian) Deadwood Formation in Saskatchewan, Canada. These fossils preserve the internal growth structure of the elements with high fidelity and offer an unparalleled opportunity to identify early and late growth stages and illustrate divergent 'form-taxa' within single biological species. The ability to



reconstruct ontogeny is also afforded through the use of synchrotron-based tomographic microscopy. For the first time, ontogenetic sequences have been identified within elements of *Westergaardodina*. Elements develop from narrow, needle-shaped structures to broad elements with wing-like flanges, displaying distinct allometry with their morphogenesis. This raises issues with taxonomic over-splitting in paraconodonts which can have direct influence over biostratigraphic and palaeodiversity studies. An understanding of ontogenetic variation is therefore of critical importance for any disarticulated skeletal taxon.

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### Growing pains of the Agronomic Revolution: Ediacaran–Cambrian bioturbators stimulated sulfide production in shallow sediment tiers

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The evolution of complex bioturbation is suggested to have caused the shift from anoxic, microbial mat-dominated seafloors in the Ediacaran to more habitable, well-mixed, oxygenated seafloors in the Cambrian. However, not all bioturbation behaviours have equal impacts on seafloor geochemistry, so it is critical to understand when different modes of bioturbation evolved and precisely what role they played in early benthic ecosystem evolution. Here, we focus on the presence of biomixing (solids mixing) and bioirrigation (enhanced solute transport) in Ediacaran and Cambrian trace fossil assemblages from the Nama Group, Namibia and the White-Inyo Mountains, California, USA. We characterized biomixing and bioirrigation for these trace fossil assemblages and incorporated them into a reactive-transport model to predict changes in oxygen, organic matter and sulfur cycling. These trace fossil assemblages suggest an increase in biomixing intensity (more, larger *Planolites*, *Torrowangea* and *Psammichnites*) without a similar increase in bioirrigation. Our modelling results predict that this resulted in an increased bioavailability of organic matter to sulfate reducers, which in turn increased sulfide concentrations in the shallow sediment tier. We conclude that in these environments, intense biomixing may have actually led to less habitable conditions for many Ediacaran–Cambrian infaunal and semi-infaunal animals.

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### Evolution of dental topographic disparity in African anthropoid and strepsirrhine primates from the Eocene into the Miocene

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Even though strepsirrhine primates dispersed to Afro-Arabia before anthropoid primates did, anthropoids ultimately came to dominate Oligocene and Miocene primate faunas. This study quantifies dental disparity and lineage diversity through time and identifies key differences in the evolutionary histories of the two primate groups. We quantified dental disparity in African strepsirrhines and anthropoids using multiple variables (ariaDNE, RFI, OPCR and surface area) calculated on the lower m2 crowns of 66 fossil primate species



ranging in age from Eocene to early Miocene. Dental disparity and lineage diversity were analysed within a phylogenetic context provided by Bayesian tip-dating analyses of both clades. Ancestral trait values were calculated throughout the phylogenies at 0.5-million-year intervals. Our results reveal that after the arrival of anthropoid primates in Afro-Arabia, the clade underwent a period of high taxonomic diversification but showed relatively low dental disparity. In contrast, strepsirrhine taxonomic diversity decreased, but dental disparity increased. This may be due to anthropoids' competitive superiority over the endemic strepsirrhine clade, which allowed taxonomic diversification without the need to evolve novel tooth shapes. Strepsirrhines on the other hand may have been pushed into marginal ecological niches resulting in the evolution of more specialized dental adaptations.

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### Investigating the evolution of forelimb anatomy and function in ornithischian dinosaurs

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The evolution of quadrupedality from a bipedal ancestral state is unique to Dinosauria and its closest relatives. At least three independent reversions to quadrupedality occur in Ornithischia. Using 3D multi-body dynamic modelling, we are investigating biomechanical changes to the forelimbs of quadrupedal ornithischians. We focus on determining changes to muscle function that are mechanically linked to gait. Key fossil material was photogrammetrically digitized and reassembled with reference to articulated specimens. Muscle attachments and 3D paths were reconstructed using the extant phylogenetic bracket. Our analyses suggest that in ornithopods of a range of different body sizes, the deltoideus muscle groups were mainly humeral abductors, with the supracoracoideus groups acting as both abductors and extensors. However, modifications to the shape of the scapulae and coracoids shifted their origins in larger quadrupedal taxa such as hadrosaurs, altering their overall lines of action. Similar modifications to the shoulder may be a key factor in the evolution of quadrupedality across Ornithischia as a whole, but the changes vary across clades. Sensitivity analysis of subjectivities associated with less well-defined osteological correlates to specific muscles and variations in bone spacing resulting from differing epiphyseal cartilage reconstructions requires the generation of models representing ranges of plausible alternatives.

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### Offspring size evolution in a colonial marine invertebrate lineage

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Among life history traits, offspring size has one of the most direct impacts on the fitness of the individual, influencing its growth, recruitment and survival, therefore affecting population and, ultimately, macroevolutionary outcomes. Despite its ecological and evolutionary importance, little is known about how offspring size varies in lineages over macroevolutionary timescales, even less so when focusing on colonial organisms. Here we use the Miocene-to-Recent cheilostome bryozoan *Microporella* to investigate variation in offspring size over the history of the lineage. *Microporella* is the ideal model system because it is species-rich, cosmopolitan and the size of its reproductive structures, routinely



preserved in fossils, is a reliable proxy for offspring size. Based on a suite of biotic and abiotic factors, we ask: what best explains offspring/larval size variation in *Microporella*? Does this variation conform to Cope's Rule and/or the 'out of the tropics' hypothesis? Our results show that offspring size is best explained by a combination of module size and (palaeo)latitude. In addition, we found that the probability of a descendant species having larger offspring than its putative ancestor is higher than the null hypothesis, with the size difference between species-pairs little explained by a latitudinal shift happening over time.

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### Growing up big: the largest known cowrie and the evolution of giant cypraeid gastropods

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The cowries are the best-studied family of gastropods, with a global diversity distribution that parallels that of tropical corals, mangroves and seagrasses. The macroecological and macroevolutionary relationship between diversity and gigantism, two important ecological traits, has never been explored in this family (Cypraeidae). Here we introduce *Vicetia bizzottoi* sp. nov. based on a Priabonian fossil found in northeastern Italy, the largest documented cowrie found so far and the youngest of a lineage of Eocene Gisortinae species. Their stratigraphic distribution in western Europe indicates that species selection favoured large size and increased ornamentation. Palaeoecology and the stratigraphic distribution of species richness of the Cypraeidae suggest that gigantism occurs in peripheral habitats with respect to diversity hotspots, where smaller species are favoured. The Eocene–Oligocene boundary was marked by a turnover that favoured small-sized species of clades other than Gisortinae. Species selection leading to gigantism is again documented in Miocene lineages of Zoila and Umbilia, in the southern hemisphere, at the periphery of contemporaneous diversity hotspots. The decoupled relationship between size and diversity encountered in modern forms is thus a recurring pattern in the evolutionary history of cowries. Possible explanations include physiological and ecological phenomena, and life history constraints.

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### The brain evolutionarily and developmentally shapes the skull

**\*Matteo Fabbri, Daniel Smith Paredes, Miccaella Vergara, Laurel Yohe and Bhart-Anjan S. Bhullar**

*Yale University, USA*

The brain has a primacy in early cranial development. Extant birds show an enlarged brain in comparison to their dinosaur ancestors and other reptiles, causing anatomical changes to the braincase. Correlation between the boundary of brain regions and the suture of braincase elements suggests a deep evolutionary link. However, the pathways dictating such a link have never been properly addressed. CT scanning, confocal imaging and immunofluorescence were combined to track mesenchymal condensation forming the skull along the development of the brain in an embryological series of model and non-model organism reptiles, including birds. Mesenchymal cells condense early in organogenesis around the brain. We found that the physical pressure exercised by the brain ventricle is driving ossification of the skull elements of the braincase. Birds show a delayed patterning



of the skull in comparison to reptiles due to the positive allometry of the brain, contrary to the negative trajectory observed in reptiles. We regard the braincase as an example of a non-independent character, because it is strongly influenced by the evolution and development of the brain. This developmental pathway explains why bones composing the skull and not directly contacting the brain were lost along the evolution of the main branches of Amniota.

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### The cranial anatomy of *Qianzhousaurus sinensis*

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*Qianzhousaurus sinensis* represents the third entry to the alioramin sub-clade, a group of morphologically divergent tyrannosaurids from the Late Cretaceous of Asia. In this work we exhaustively describe the cranial anatomy of the holotype specimen, appending considerable depth to the original but cursory study of Lu *et al.* 2014. We recognize multiple discrete osteological characters that signify a more advanced degree of ontogeny than has been previously discussed, placing this individual as ‘intermediary’ in the tyrannosaurid growth sequence. We describe weak cranial sutures throughout the skull which would have decreased cranial integrity and, when coupled with reduced mandibular muscle attachment platforms, made it unlikely that *Q. sinensis* could have employed “puncture-pull” feeding behaviours. These observations have implications for the animal’s palaeoecology, suggestive that alioramins filled a divergent niche to the larger and more robust tyrannosaurids, thus allowing for sympatricity. Although tyrannosaurs are one of the best-represented of all dinosaur groups in regard to fossil content, there is certainly a high level of diversity still to be discovered and discussed.

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### Zechstein forests thrived up to the Permian–Triassic mass extinction event

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The Zechstein Sea was a large inland sea situated in northern Pangaea during the late Permian (~258–252 Ma) and is used in environmental reconstructions of central-western Europe. It was infilled by a remarkable carbonate-evaporite sequence consisting of up to seven evaporation-replenishment cycles. Previous palaeobotanical–palynological evidence shows that the hinterlands were vegetated with typical Euramerican gymnosperm forests during the earliest cycle. However, it is usually considered that these gradually declined and eventually disappeared as the environment became progressively hotter and drier approaching the Permian–Triassic mass extinction. High-resolution sampling of newly available cores from northeast England has enabled, for the first time, the recovery of pollen assemblages from the entire Zechstein sequence, facilitated by an improved technique for recovering pollen from evaporites. The dataset comprising >77,000 pollen grains indicates that the vegetation was little changed within cycles and between cycles, and persisted until the demise of the Zechstein Sea in the latest Permian–earliest Triassic. At this time desert sedimentation commenced, which yields no evidence for terrestrial vegetation until the early Triassic when evidence for a radically different flora appears. These observations suggest that vegetation loss at the Permian–Triassic boundary was rapid and catastrophic rather than representing the culmination of a slow decline.





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### Constraining quadrupedal launch: range of motion in *Coloborhynchus*

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Pterosaurs reached sizes significantly larger than modern flyers and as such there is uncertainty whether the largest pterosaurs were capable of flight. The quadrupedal launch hypothesis proposes that pterosaurs circumvented the size restriction seen in modern flyers by co-opting their forelimbs during take-off. We investigated the ability of the mid-sized ornithocheirid *Coloborhynchus* to assume the poses required to utilise quadrupedal launch. We applied range of motion (ROM) mapping methodology to the pelvic and pectoral girdles and identified unviable joint poses at varying levels of appendicular cartilage. Utilizing the novel Triangulated Minimum Stretch (TMS) methodology a connective tissue constrained ROM was determined. We found that the pelvic girdle could assume the required poses for quadrupedal launch with appendicular cartilage equivalent to an ostrich, while the pectoral girdle requires appendicular cartilage equivalent to alligators. The connective tissue ROM for the pelvic girdle found that the poses required for quadrupedal launch could be reached with low levels of ligamentous stretch. The poses required for quadrupedal launch could be reached by the pectoral girdle with muscular stretch values equivalent to modern birds. Our study indicates that *Coloborhynchus* would be capable of assuming the poses required to launch utilizing the quadrupedal launch hypothesis.

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### Using computer flow simulations to explore the hydrodynamics of extreme body morphology and size in derived Mesozoic marine reptiles

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Various groups of Mesozoic marine reptiles evolved streamlined body shapes and efficient lift-based swimming modes, as seen in modern aquatic mammals. Ichthyosaurs had low-drag bodies, akin to modern dolphins. Plesiosaurs on the other hand, had strikingly different morphologies with long hydrofoil-like limbs and greatly variable neck/trunk proportions, displaying some of the most extreme body shapes observed in aquatic tetrapods. Long necks evolved in this group are often assumed to add excess skin drag and raise the energy cost of swimming, constraining swimming speed. Despite recent attempts to evaluate the hydrodynamic impact of long necks, their effect on the energy expenses of swimming remain unexplored. Here we use computational fluid dynamics simulations on full-body reconstructions of derived plesiosaurs, ichthyosaurs and modern cetaceans at a range of speeds and sizes. Our results show that the limbless bodies of plesiosaurs generated low drag, similar to derived ichthyosaurs and modern cetaceans of the same mass, regardless of their fineness ratio, although drag is significantly higher if the flippers are accounted for. Additionally, necks that are about three times the trunk length substantially increase the cost of forward swimming for a constant trunk length. However, this effect was dampened by the enlargement of trunks during plesiosaur evolution.



## Insular gigantism in giant dormice: divergence from the non-giant allometric trajectory

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Mammals on islands often drastically adjust their body size and shape as a response to their isolated environment. A graded trend is proposed, with small animals getting larger and large animals becoming smaller, but some mammals appear more susceptible than others to this Island Rule, and insular dwarfism seems to occur more frequently than insular gigantism. Fossil dormice (Gliridae) appear to have increased their body size during isolation numerous times. Here we compared the cranial and mandibular morphology of fossil giant dormice from Mallorca (*Hypnomys* spp.) and Sicily (*Leithia melitensis*) with their nearest living relative, the garden dormouse (*Eliomys quercinus*). We developed a new method (Predicted Size vs Actual Size model), allowing us to predict morphologies at hypothetical sizes, based on the allometric trajectory within non-giant dormice. By comparing the actual shape of giants with the shapes proposed by our model, we concluded that only part of the morphology in giants can be explained by allometry. Other features appear to be idiosyncratic, presumably associated with adaptation to specific niches. Finite element analyses indicate the morphological variation to have a direct effect on the masticatory apparatus, predicting faunivory in some giants and herbivory in others.

## Diverse communities of Bacteria and Archaea flourished in Earth's earliest ecosystems

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Limited taxonomic classification is possible for Archaean microbial mats; this fundamentally limits the constraints placed on early ecosystems. Applying Fourier transform infrared spectroscopy (FTIR), we identified fossilized biopolymers in 3.5–3.3 Ga microbial mats from the Barberton greenstone belt, South Africa. Despite high aromaticity, the carbonaceous fraction of microbial mats exhibits significant variation in taxonomically informative aliphatic and carboxylic contents. Since all horizons underwent similar grades of metamorphism, this variation reflects precursor biological heterogeneity. High CH<sub>3</sub>/CH<sub>2</sub> absorbance ratios in mats from the 3.472 Ga Middle Marker horizon signify short, highly branched *n*-alkanes residues interpreted as isoprenoid chains forming archaean membranes. Mats from the 3.45 Ga Hooggenoeg Chert H5c, 3.334 Ga Footbridge Chert and 3.33 Ga Josefsdal Chert exhibit higher CH<sub>3</sub>/CH<sub>2</sub> ratios suggesting mixed bacterial



and archaeal precursors, dominated by longer, unbranched fatty acids from bacterial lipid residues. This exceptional preservation denotes early, rapid silicification preventing the alteration of primary biogeochemistry. Since silicification commenced during the lifetime of the microbial mat, FTIR signals estimate the affinities of the architect community and may be used, when coupled with detailed palaeoenvironmental geochemistry, to reconstruct Archaean ecosystems. In summary, diverse biomes flourished in Earth's earliest habitable environments.

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### The origin of Ecdysozoa and an Early Cambrian stem group Ecdysozoan

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Ecdysozoa are the moulting protostomes, including arthropods, tardigrades and nematodes. Both the molecular and fossil records indicate that Ecdysozoa is an ancient group originating in the terminal Proterozoic, and exceptional fossil biotas show their dominance and diversity at the beginning of the Phanerozoic. However, the nature of the ecdysozoan common ancestor has been difficult to ascertain due to the extreme morphological diversity of extant Ecdysozoa, and the lack of early diverging taxa in ancient fossil biotas. Here we redescribe *Acosmia maotiania*, a worm from the early Cambrian Chengjiang biota of Yunnan Province, China and assign it to stem group Ecdysozoa through morphological phylogenetic analysis. Subsequently, ancestral state probabilities were calculated for key ecdysozoan nodes, in order to test characters inferred from fossils to be ancestral for Ecdysozoa. Results support an ancestor of crown group ecdysozoans sharing an annulated vermiform body with a terminal mouth like *Acosmia*, but also possessing the pharyngeal armature and circumoral structures characteristic of Cambrian cycloneurians and lobopodians. Our study suggests acquisition of pharyngeal armature, and therefore a change in feeding strategy (*i.e.* predation), may have characterized the origin and radiation of crown group ecdysozoans from *Acosmia*-like ancestors in the late Ediacaran to early Cambrian.

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### A Late Jurassic marine reptile fauna from Helmsdale, Scotland

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Despite their abundance in continental Europe and England, there are only rare and isolated reports of marine reptiles from Scotland. The most famous discoveries are of plesiosaurian material from the nineteenth century by Patrick Duff (1842) and Hugh Miller (1858). More recently, the Inner Hebrides have proven to be a valuable source for Early and Middle Jurassic marine vertebrates, in particular the Isle of Skye, which was home to ichthyosaurs, plesiosaurs, turtles and crocodylomorphs. The mainland of Scotland has received less attention from researchers, despite bearing Jurassic-aged rocks. Here we report a marine reptile fauna from the Kimmeridgian-aged (Late Jurassic) Helmsdale Boulder Beds in Helmsdale, Sutherland. With an intermediate palaeolatitude



between the Boreal and sub-Boreal zones, the Helmsdale assemblage is important for understanding the biogeographical patterns of marine reptile distribution in the Late Jurassic. Consisting of 26 specimens of plesiosaur, pliosaur and ichthyosaur material held by museums across Scotland, the Helmsdale marine reptile fauna is similar to the southern and contemporaneous Kimmeridge Clay Formation. However, despite its diversity the Helmsdale fauna lacks thalattosuchian crocodylomorphs, raising important palaeobiogeographical questions regarding the distribution of metriorhynchids and which environments were habitable to them.

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### On the anatomy of *Conoryctes*: insights into the evolution of Paleocene mammals following the end-Cretaceous mass extinction

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Taeniodonta is a group of archaic mammals that potentially crossed the Cretaceous–Palaeogene mass extinction boundary and diversified in the early Palaeogene. They are known from North America and are characterized by their unique dentition adapted for an abrasive diet. There are nine genera of taeniodonts, traditionally arranged into two families. The smaller Conoryctidae, with a more generalized body plan, and the robust Stylinodontidae, adapted for digging. New fossils of *Conoryctes comma*, a conoryctid, were found in the Nacimiento Formation of the San Juan Basin, New Mexico, USA. We compared the new material to other taeniodonts and potential close relatives including *Procerberus* and *Escavadodon*. We find that they belong to *Conoryctes comma*, giving an almost complete picture of the skeleton. The postcranium of *Conoryctes* shares similarities with both basal taeniodonts like *Onychodectes* and with the derived *Stylinodon*. *Conoryctes* and *Escavadodon* have anatomical similarities, particularly in their distal limb bones with enlarged muscle attachments on the ulna olecranon, distal radius and distal tibia indicating powerful limb movements. Several tarsal features of *Conoryctes* are present in other taeniodonts and are very similar to *Procerberus*. The robust anatomical features point to digging behaviour for *Conoryctes*, indicating that digging was ancestral for all taeniodonts.

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### For your eyes only: evolution of orbit shape in archosaurs and its functional implications

**Stephan Lautenschlager**

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Vision is an important sense in vertebrates controlling a variety of behaviours, such as foraging, predator–prey interactions, navigation and species recognition. However, for fossil vertebrates, only the preserved hard tissues provide information on visual capabilities, for example in the form of orbit shape and size. Apart from housing the visual apparatus and other soft-tissues, the bony orbit plays an important role in the provision of muscle attachments, protection of the eye and the structural integrity of the whole skull. In fossil archosaurs, the orbit is generally circular but different species show a variety of orbit shapes. Using a geometric morphometrics approach, the orbit shape and morphological diversity were analysed and quantified for over 400 species of fossil archosaurs and their



kin (including Dinosauria, Pterosauria, Pseudosuchia and other Archosauromorpha). The results show that although a circular orbit shape is retained throughout archosaur evolution, several groups have convergently explored different orbit shapes, such as oblique or constricted orbits. Preliminary biomechanical analyses demonstrate that the deviation from the plesiomorphic circular orbit shape provided the functional means to counter feeding-related stresses, in particular in large carnivorous species.

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### Life in a Cambrian back-reef environment: insights from a new Dyeran Konservat-Lagerstätte from British Columbia, Canada

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Burgess Shale-type (BST) deposits are critical to our understanding of the taxonomic and ecological diversification of Cambrian animals. However, most BST Konservat-Lagerstätten were deposited in quiet, relatively deep-water settings near the shelf break, resulting in an impoverished picture of the diversity of faunal communities inhabiting the continental shelf at that time. We report the discovery of a new Cambrian Stage 4 Konservat-Lagerstätte within the Rosella Formation (Cassiar Mountains, western Canada), which preserves a biota that lived in a back-reef environment. The Dease River section exposes a *c.* 50 m-thick succession of skeletal limestone, interrupted by shaley intervals yielding non-biomineralized fossils. Sedimentological and biostratigraphic features suggest deposition in a rapidly changing environment landward of archaeocyathid-rich patch reefs. The biota comprises *c.* 20 predominantly soft-bodied species, including panarthropods, scalidophorans, vetulicolians, annelids, brachiopods, cnidarians, entoprocts, hyoliths and algae. The non-biomineralized fossils are preserved as carbonaceous compressions with subordinate apatite and pyrite. Panarthropods are rare and represented by pelagic forms, except for the trilobites that abounded on the seafloor along with various centimetric worms, but no sponges. These characteristics of the Rosella biota sharply contrast with most Cambrian BST assemblages, which suggests important variations in composition and structure of benthic assemblages along the shelf.

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### Appendage specialization in the Cambrian trilobite *Olenoides serratus* from the Burgess Shale

**\*Sarah Losso and Javier Ortega-Hernández**

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Trilobites are a dominant group of Palaeozoic euarthropods that despite boasting an impressive diversity of over 20,000 described species, details of their appendicular morphology are only known from 31 taxa. Trilobites with preserved appendages feature a pair of uniramous antenna followed by a homonomous series of biramous appendages. All the biramous trunk limbs have the same morphology, and the only evidence of differentiation consists of the presence of progressively smaller posterior appendage pairs. *Olenoides serratus* is a well-known corynexochid trilobite from the Burgess Shale (Wulian, Miaolingian; ~508 Ma, Canada) with preserved appendages known from over



70 specimens. However, *O. serratus* is unique among trilobites in having preserved cerci, thus showing a higher degree of limb tagmosis than other representatives. Here we demonstrate the first evidence of strong morphological differentiation of the biramous appendages in *O. serratus* based on undescribed material from the Burgess Shale. An exceptionally-preserved specimen shows differentiated appendages on the seventh thoracic and first pygidial segments consisting of greatly reduced endopods, each composed of seven podomeres, and a large sub-circular protopodite without endites. These specialized appendages demonstrate an unparalleled degree of limb tagmosis in trilobites, and carry broader implications for trilobite biology and reproduction.

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### A case for arachnid monophyly and a single terrestrialization within chelicerates

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The majority of extant arachnids are terrestrial, but other chelicerates are generally aquatic, including horseshoe crabs, sea spiders and the extinct eurypterids. It is necessary to determine whether arachnids are exclusively descended from a single common ancestor (monophyly), because only that relationship is compatible with one land colonization in chelicerate evolutionary history. Some studies have cast doubt on arachnid monophyly and recast the origins of their terrestrialization. These include some phylogenomic analyses placing horseshoe crabs within Arachnida, and from aquatic Palaeozoic stem-group scorpions. In this talk I will evaluate the possibility of arachnid monophyly by considering morphology, fossils and molecules holistically. I will argue that arachnid monophyly obviates the need to posit reacquisition/retention of aquatic characters such as gnathobasic feeding and book gills without trabeculae from terrestrial ancestors in horseshoe crabs, and that the scorpion total-group contains few aquatic taxa. Furthermore, I will present phylogenetic analyses from molecular matrices that retrieve arachnid monophyly, and time-trees that suggest a Cambrian–Ordovician colonization of land.

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### A new Euchelicerate from the early Ordovician Fezouata Biota, and its significance for “synziphosurine” phylogeny

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The Early Ordovician Fezouata Shale of Morocco preserves a wide variety of non-biomineralized taxa, including two undescribed but abundant euchelicerates: a modern-looking horseshoe crab, and a taxon ascribed to the “synziphosurines”. Specimens of the new synziphosurine taxon were examined, photographed and drawn, with some specimens being subjected to synchrotron radiation X-ray tomographic microscopy for a complete reconstruction of the anatomy. This taxon has a semi-circular prosoma bearing six pairs of appendages, five of which are biramous, followed by 11 post-cephalic tergites with a prominent central axis. The biramous prosomal appendages are characterized by the stenopodus exopods bearing brush-like setae, a structure that has only ever been identified



in two previously described synziphosurines from the Silurian Herefordshire Lagerstätte. To clarify the affinity of this group, we undertook a phylogenetic analysis using Bayesian methods. The new Fezouata Shale taxon resolves as a stem-euchelicerate, forming a monophyletic group together with the Herefordshire synziphosurines. Linking our new findings on euchelicerate diversity during the Great Ordovician Biodiversification Event to the earliest origin of the phylum, as recorded in the Cambrian Burgess Shale-type biotas, provides a more complete picture of euarthropod evolution during these major events and new insight for the resolution of the problematic phylogeny of “synziphosurines”.

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### Evolution of feeding mechanics in the dietary diversification of theropod dinosaurs

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Theropod dinosaurs underwent some of the most remarkable dietary shifts in vertebrate evolutionary history, shifting from carnivory to hypercarnivory and to herbivory. However, the mandibular adaptations accompanying the dietary shifts remain unclear. We conducted the first comprehensive study on the feeding mechanics of 46 non-avian theropods using 2D finite element analysis. We find that the mandibles of carnivorous theropods like dromaeosaurids and tyrannosauroids are less stress-resistant and less bite-efficient than those of herbivorous theropods like ornithomimosaurians, therizinosaurians and oviraptorosaurians. This suggests that the carnivores are less adapted to biting compared to the herbivores in general. An overall decrease in feeding-induced stress is identified in all studied lineages, suggesting a common tendency for structural strengthening of mandible regardless of diet, such as a post-dentary expansion of the mandible. However, different evolutionary pathways are identified in the dentary. Convergent evolution of a more down-turned dentary to enhance mandibular stability is observed in later-diverging herbivorous taxa whereas this is not observed in carnivores. Our study uncovers the pattern of mandibular adaptations accompanying dietary shifts in non-avian theropods, which represents a powerful case study for understanding dietary evolution in other vertebrates.

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### The evolution of body shape, locomotion and ecology in terrestrial vertebrates

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Body shape plays a fundamental role in organismal function and it is expected that animals evolve body proportions that best exploit their ecological niche. Terrestrial tetrapods have evolved a disparate array of body plans over the past 350 million years, but to date this diversity in body shape and its relationship to ecology and behaviour has not been systematically quantified. Here we analyse body proportions in 411 extinct and extant terrestrial tetrapods spanning most major taxonomic, locomotor and dietary groups. We show that most body segments scale with negative allometry across terrestrial tetrapods as a whole but find statistical support for quadratic relationships, which suggests differential scaling in small-medium versus large animals. Statistical analyses of shape differences and allometric trends in different locomotor and dietary groups highlight key adaptations



in body proportions that mechanistically underlie the exploitation of key ecological niches (such as flight and hyper-carnivory), as well as revealing patterns of changing body proportions during major macroevolutionary events (such as bipedal–quadrupedal transitions). Overall, our results emphasize that changing body proportions played an important role in the broad-scale ecological diversification of terrestrial tetrapods.

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### The colonization of anoxic, matground-dominated sedimentary environments during the Early Phanerozoic

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Burrowing organisms play a key role in controlling the physico-chemical conditions within marine sediments. Prior to their evolution, seafloor sediments were predominantly oxygen-deficient, hosting abundant microbial matgrounds. The physico-chemical conditions in these hypoxic Proterozoic environments were hostile to oxygen-dependent macro-organisms. Despite this, the Cambrian fossil record shows a rapid increase in the diversity of burrows, and thus the trace makers themselves, indicating that the earliest bioturbators were tolerant of or adapted to hypoxic/euxinic conditions. Our investigation of early Phanerozoic metazoan-microbial interactions preserved in the Cambro-Ordovician successions of Bell Island, Newfoundland documents settings in which the destruction of Ediacaran-like microbial matgrounds can be directly linked to the presence of dense assemblages of simple, near-surface, trace fossils. Matground break-up was followed by colonization by deeper-tier trace-makers that did not live concurrently with the matgrounds. Our field observations indicate that the colonization of microbially-dominated, early Phanerozoic marine sediments was initiated by small, probably opportunistic animals that were capable of creating oxygenated near-burrow sedimentary microenvironments. This would have engineered settings amenable to larger, more oxygen-dependent metazoans. Thus, the evolution of late Ediacaran and early Cambrian infaunal marine ecosystems may have been initiated by meiofaunal to small macrofaunal trace-makers.

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### The impact of morphological clocks and fossil tips in inferring the tree of life

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Incorporating fossils into phylogenetic hypotheses of extant taxa helps elucidate macroevolutionary patterns and processes. However, the effect fossils have on the inference of phylogenetic relationships from morphological data is controversial. Some studies have dismissed the impact of fossils due to their incompleteness, but others have championed their ability to uncover true relationships. More recent empirical analyses have highlighted the strong impact fossils can have on phylogenetic inference but have been unable to demonstrate that they improve tree topologies. The consequences of incorporating the stratigraphic ages of terminals in the process of inference also remains unclear. Here we simulate character data and associated phylogenies through an approach that does not rely on the stochastic models used for phylogenetic inference. We use these to explore how fossil sampling and missing data impact tree reconstruction across a range of inference





methods. Specifically, we focus on comparing inference of tip-dated trees under the fossilized birth–death process with traditional Bayesian and parsimony approaches that do not incorporate the temporal information of fossils. Our efforts elucidate the effect of fossils on phylogenetic reconstruction, and help establish the range of conditions under which we can expect their contribution to be significant.

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### Sea-level history and species ecology control the scale of time-averaging in molluscan fossil assemblages on the northern Adriatic shelf

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Time-averaging in fossil assemblages is controlled by net sedimentation rates, intrinsic skeletal durability and temporal changes in shell production, but the role of the latter factor remains poorly understood. We use carbonate-target radiocarbon ages of 191 shells to examine variation in time-averaging among four bivalve species collected from a 2.3 m-long core recording the post-glacial transgression on the northern Adriatic shelf. Within individual 5 cm-thick core samples, intraspecific time-averaging (interquartile age range) varied from 200 to 7,400 years, while interspecific differences in median age ranged from 2 to 6,400 years. Moreover, although the median ages of *Varicorbula*, *Timoclea* and *Parvicardium* increased with increasing burial depth, specimens of *Lentidium* appeared age-homogeneous throughout the core. The reconstructed timing of shell production pulses suggests that the four species replaced each other through time as the dominant component of the fauna in accordance with their bathymetric preferences and relative sea-level changes at the site. The diachronous shell production histories, combined with subsequent extensive bioturbational mixing under reduced terrigenous input, resulted in fossil assemblages characterized by multi-modal age distributions and millennial-scale age offsets between co-occurring species. These results underscore the importance of environmental history and species ecology in shaping the temporal resolution of fossil assemblages.

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### *In situ* spores of *Asterotheca merianii*: morphological variability and effects of preparation

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Spores or pollen from a single plant species or even an individual plant or sporangium may vary in shape to a point that equivalent dispersed forms have been described as different species or even genera. However, it is still not well understood to what degree this variability is affected by randomly differential development of characters in individual sporomorphs, different developmental stages within the fertile structures, environmental parameters or even maceration protocols. In order to determine possible adverse effects of acid treatment, we performed a series of variations of the standard technique (using the Schulze reagent) for the maceration of *in situ* sporomorphs on sporangia of *Asterotheca*



*merianii*, a marattiaceous fern that is common in Carnian floras in Europe. Our results show that variations in the treatment parameters had less impact on the observable characters than differences between individual plants and within sporangia. Depending on the individual, the spores may be weakly ornamented to smooth and smaller or larger on average, but sizes vary largely even within single sporangia. Notably, some spores are much smaller than normal, presumably representing malformations.

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### Micro-computed tomography of the aïstopods from the Jarrow Assemblage, Ireland

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The limbless stem-tetrapod clade Aïstopoda was first described from the Pennsylvanian coal-shales of the Jarrow Seam (Bashkirian stage, Langsettian regional substage) of southeastern Ireland. Recent revisions of aïstopod taxa have emphasized their importance in the evolution of early tetrapods; however, the Jarrow fauna remains largely overlooked. Here, micro-computed tomography is applied to two Jarrow aïstopod taxa: *Ophiderpeton brownriggii* and *Dolichosomatites emersoni*. Detailed analysis of *O. brownriggii* reveals previously unidentified characteristics in Ophiderpetontid aïstopods including lateral lines in the jugal. A new species of ophiderpetontid aïstopod is proposed from the syntypes of *O. brownriggii*, based on the presence of a relatively thinner skull table, slimmer jaws and the possession of a parietal foramen. The second Jarrow taxon, *D. emersoni*, is shown to have possessed skull characteristics more similar to primitive aïstopods, including paired postparietals, parietals and frontals, contradicting previous placement within the more derived phlegethontiid aïstopods. Temporal mapping of aïstopod occurrence suggests a conspicuous faunal change at the end of the Bashkirian, with ophiderpetontid-dominated faunas being replaced by faunas dominated by oestocephalids and phlegethontids. The Carboniferous was marked by profound palaeoclimatic fluctuations and the influence of these global perturbations on aïstopod fauna is apparent.

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### The palaeoenvironmental reconstruction of the Lower Toarcian (Lower Jurassic) Lower Sulphur Band, Cleveland Basin, UK

\***Connor O'Keeffe**<sup>1</sup>, **Crispin T. S. Little**<sup>1</sup>, **Christian März**<sup>1</sup>, **Fiona L. Gill**<sup>1</sup>, **Christopher H. Vane**<sup>2</sup> and **Simon W. Poulton**<sup>1</sup>

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In the Cleveland Basin, Yorkshire, the early Toarcian Grey Shales Member was deposited under oxic conditions, but it contains three decimetre-scale black shale units that may presage later reduced-oxygen events in overlying units. Here we present an ongoing study of the earliest of these units: the Lower Sulphur Band (LSB). The LSB is lithologically heterogeneous, containing bituminous, siliciclastic, cross-stratified and intensely bioturbated fabrics. Based on the iron speciation redox proxy, the whole of the LSB was deposited under anoxic conditions, despite the presence of *Chondrites* and *Rhizocorallium* traces at the base and top of the unit. Trace metal analysis shows that the LSB is also enriched



in Mn, implying a stratified water column, in a basin subject to a rapid transgression. Episodic enrichments in K/Rb and the presence of two sources of organic matter suggest that episodes of enhanced fluvial flux from surrounding hinterlands also took place. Our study highlights the importance of a multiproxy approach to palaeoenvironmental studies, and how a proper understanding of the biogeochemical dynamics in any studied basin is crucial for an accurate appraisal of Fe redox proxy data.

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### A reduced labrum in a Cambrian great-appendage euarthropod

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The euarthropod head is a versatile and functionally specialized body region whose complex evolution has been scrutinized through anatomical, developmental and palaeontological approaches. Cambrian fossils have allowed for the reconstruction of critical stages of the evolutionary history of the head, such as the origin of the labrum – an anteromedian flap-like structure that overlies the mouth opening in almost all extant representatives – from an ancestral pair of pre-ocular appendages. The position of the labrum makes it a valuable anatomical landmark for understanding the anterior segmental organization among extant and extinct euarthropods. However, the labrum appears absent in megacheirans, an extinct group characterized by enlarged raptorial ‘great appendages’ with a central role in hypotheses on the early evolution of the head. We used micro computed-tomography to demonstrate the presence of a three-dimensionally-preserved labrum in juvenile specimens of the megacheiran *Leancoilia illecebrosa* from the early Cambrian Chengjiang. The position of the labrum relative to the great appendages indicates that these limbs correspond to the deutocerebral segment, making them serially homologous with the first appendage pair of extant euarthropods. The reduced labrum and deutocerebral great appendages of *L. illecebrosa* strengthen the affinities of megacheirans as stem-group chelicerates, in line with recent palaeoneurological data.

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### Niche partitioning and hydrodynamics of *Isoxys*: implications for the Cambrian biological pump

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*Isoxys*, a nektonic arthropod with a distinctive bivalved carapace bearing anterior and posterior spines, is known from Cambrian deposits worldwide. Taxa are distinguished by the shape of the carapace, and the relative lengths of anterior and posterior spines. An elliptical Fourier analysis on valve outline shape split taxa into different morphotypes which were assessed for hydrodynamic performance using ANSYS Fluent. Morphotypes appear suited for reducing drag, increasing lift, or neither, implying that species of *Isoxys* occupied a number of distinct ecological niches. Importantly, some shapes were able to generate much more positive and negative lift than others, supporting the hypothesis that they were able to vertically migrate in the water column. Following the recent description



of numerous macroscopic primary consumers in Cambrian oceans, vertically migrating *Isoxys* species provide a second – and more efficient – avenue for the transportation of carbon from the shallow to deep oceans 500 million years ago.

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## Latitude induced climatic forcing as a driver for bioregionalization during the Devonian period: a case study from high latitudinal regions of West Gondwana

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The Early-Middle Devonian saw the development of biogeographic hotspots, especially in the marine realm. These hotspots were distributed as the tropic-subtropic latitude Old World, subtropic-temperate latitude Eastern Americas and subpolar-polar latitude Malvinokaffric realms. Only the Malvinokaffric Realm is a defined biogeographic area. Global eustasy or regional climatic differences may have acted as allopatric barriers for isolation and speciation. Towards the end of the Eifelian these hotspots collapsed, heralding cosmopolitanism. We compiled a large presence-absence brachiopod dataset from across West Gondwana and interrogated the data with multivariate statistics and network analysis. Regional climatic effects forced by latitudinal differences drove bioregionalization at high latitudes; these were coincident with a period of cooling during the Pragian-Eifelian. The Malvinokaffric Realm is reconfigured with a reduced area and as a second-order bioregion West Gondwana comprised two first-order, high-latitude (60°S – 90°S) and temperate-latitude (30°S – 60°S) bioregions. The temperate-latitude bioregion consists of only the Colombian–West African bioregion. Two second-order bioregions occur in the high-latitude bioregion, the Amazonian and Malvinokaffric. The Amazonian (~50°S – 70°S) was an intermediate region between the Colombian–West African (~30°S – 50°S) and Malvinokaffric (70°S – 90°S) end members.

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## Reassessment of the evolutionary history of Late Triassic and Early Jurassic sauropodomorph dinosaurs

**\*Omar Rafael Regalado Fernandez<sup>1</sup>, Paul Upchurch<sup>1</sup>, Philip D. Mannion<sup>1</sup>, Paul M. Barrett<sup>2</sup> and Susannah C. R. Maidment<sup>2</sup>**

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Early diverging sauropodomorphs have been thoroughly studied in recent years. Several hypotheses on the inter-relationships within this group have been proposed in the literature, and the grade-like hypothesis is the most accepted. Nevertheless, the relationships between the different taxa are not consistent through the literature. These inconsistencies have been attributed to missing data and unstable (*i.e.* poorly preserved) taxa; however, an extensive comparative cladistic analysis has shown that these inconsistencies arise instead from character coding and character selection, alongside combining dataset strategies. A detailed character analysis using information theory and mathematical topology as an approach for character delineation is discussed here to operationalize characters and reduce the



potential impact of missing data. This study also provided the largest and most detailed matrix after the reassessment and operationalization of each character. Partition analyses performed on this matrix have found consistencies in the inter-relationships within non-sauropod Sauropodomorpha and strong support for smaller clades. The results of these analyses also highlight a different scenario on how quadrupedality evolved, independently originating at least twice in the group, and provide a new framework to understand the palaeobiogeography and diversification rate of the first herbivore radiation of dinosaurs.

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### Skin patterning and internal anatomy of a 50 Ma moonfish from the Monte Bolca Lagerstätte

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The Monte Bolca Lagerstätte (50 Ma) of Veneto, Italy includes abundant teleost fish that preserve soft tissues and integumentary colour patterns in the form of stripes and spots. A recently excavated specimen of the moonfish *Mene rhombea* Volta, 1796 from the Pesciara site provides a timely opportunity to investigate the preservation of the soft tissues. The specimen preserves several features defined by dark carbonaceous films: striking longitudinal stripes in the epaxial region, an eyespot and discrete patches in the abdomen. Scanning electron microscopy reveals that all of these features comprise layers of melanosomes – melanin-bearing organelles – and thus the abdominal dark patches represent degraded internal organs. As with other vertebrate fossils, melanosomes from the skin and internal organs differ in geometry; melanosomes from two different regions in the abdomen exhibit different geometry, suggesting that the latter derive from two separate organs, likely to be the kidneys and liver based on the anatomical location. Raman spectra of all melanosome-rich soft tissues are consistent with eumelanin. The longitudinal striping suggests open water lifestyles and/or cooperative shoaling or other mutualistic interactions.

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### How reliable are bite force estimates in extinct dinosaurs and mammals?

**Manabu Sakamoto**

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Bite force is an important biomechanical performance measure associated with dietary ecology, and is often considered to be under natural selection. Bite force estimates thus offer a quantitative means to infer dietary ecologies in species for which such information is not available, most notably, extinct taxa. However, estimating bite force from fossils is associated with a degree of uncertainty owing to the reliance on reconstructed muscles in biomechanical models. Here I assess whether bite force estimates in extinct taxa (dinosaurs and mammals) are any more reliable than those of extant taxa, through phylogenetic predictions. I built a posterior predictive model using phylogenetic regression of bite force against phenotypic predictors (body size and skull size), and predicted bite force for extinct taxa, given their phylogenetic positions and Brownian motion evolution. I then compared biomechanical estimates of bite force to the posterior predictions. All biomechanical estimates of bite forces for extinct taxa fell within their posterior predictive distributions,



meaning that estimates based on muscle reconstructions are as reliable as statistical predictions given the variation in extant data. Biomechanical modelling remains a reliable and powerful tool to quantitatively infer the ecologies of extinct taxa.

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### Skeletal and soft tissue completeness of the acanthodian fossil record through time

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Acanthodians are a poorly understood grade of Palaeozoic fishes but play a pivotal role in our understanding of early vertebrate evolution as part of the chondrichthyan stem-group. However, much of their evolutionary history is poorly understood, largely due to the limited preservation of their mostly cartilaginous endoskeleton. Here we quantify the quality of the acanthodian fossil record by using a variation of the Skeletal Completeness Metric, an approach that calculates the completeness of skeletons, as well as introducing a novel Soft Tissue Completeness Metric. A database of >1,600 specimens comprising >300 taxa from museum collection visits and the literature reveals acanthodian completeness peaks in the Lochkovian, Givetian, Bashkirian–Moscovian and again in the Asselian, with lowest scores in the Llandovery. Acanthodians show a significantly lower completeness distribution than many tetrapods but a similar distribution to bats. Skeletons deposited in freshwater are significantly more complete than in marine environments where sea level significantly negatively correlates with observed completeness. Our assessment of completeness reveals only weak spatial biases influencing the acanthodian fossil record while environmental biases are much higher. Variation in completeness will have an impact on the utility of characters for assessing the phylogenetic positions and limits of the various acanthodian groups.

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### Late Triassic terrestrial invertebrate and plant trace fossils from the Mid-Zambezi Basin, Zimbabwe

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Rarely documented and described, invertebrate and plant trace fossils from the Triassic–Jurassic Upper Karoo Group (Mid-Zambezi Basin) of Zimbabwe are an overlooked source of biological information. These ichnofossils can be used to understand and expound local palaeoenvironmental and even palaeoecological settings. We present work conducted in the Late Triassic fluvial Pebbly Arkose Formation (Upper Karoo Group) as exposed on the southern shoreline of Lake Kariba, Zimbabwe. The Pebbly Arkose Formation preserves palaeo-pedogenically modified siltstones and mudstones that constitute floodplain deposits. These deposits are generally bioturbated with a low diversity but high density



of invertebrate ichnofossils and, often, carbonate-infilled plant-root traces and rhizohalos. Commonly occurring invertebrate ichnofossils are simple, horizontal, bedding plane-parallel burrows (*Planolites*) and adhesive meniscate burrows (*Taenidium* and *Taenidium*-like). Larval insects and vermiform animals are frequently credited as their trace makers. The morphologies of the rhizohalos and rhizoliths indicate smaller herbaceous plants, such as sphenophytes, not currently known from the Pebbly Arkose Formation. Altogether, ichnofossil and sedimentological evidence suggest that moist well-drained floodplains and fluvial channel areas, subjected to periodic and longer-term subaerial exposure, supported a diversity of invertebrates and plants.

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### Fossilization potential of marine assemblages and environments

\***Jack O. Shaw, Derek E. G. Briggs and Pincelli M. Hull**

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Only a small percentage of all life that ever existed is preserved in the rock record. Some animals and environments are particularly unlikely to fossilize – e.g. soft-bodied organisms and high-energy habitats – biasing fossil deposit faunal composition and resultant inferences about macroevolution and macroecology. To estimate the extent of information loss caused by non-preservation we compared diversity data in over 20,000 modern marine assemblages with fossil occurrence data to yield a global assessment of assemblage-level fossilization potential. We used two different metrics, taxon fossilization potential and within-environment fossilization potential, to assess the proportion of taxa in a modern community with Paleobiology Database occurrences or with Paleobiology Database occurrences in the same environment, respectively. We find that, on average, 38 % of taxa in modern assemblages are represented in the fossil record. However, an average of only 29 % of taxa in modern assemblages are recorded in the same environments in the fossil record as they are today, indicating the large control of environment on fossilization potential. Our results provide a means to include and compare palaeoecological dynamics across a broader range of settings in the fossil record, while accounting for differences in fossilization potential among environments.

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### The initial colonization of desert ecosystems – insights from the Mereenie Sandstone, Australia

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The Silurian was an interval of great change in terrestrial ecosystems, marking the onset of the first phase of colonization of land by animals. Whilst much is known about the transition from shallow marine to coastal habitats by pioneering animals, evidence for animal activity in contemporaneous aeolian strata is far rarer, so little is known about the establishment of desert ecosystems. The Mereenie Sandstone of Northern Territory, Australia can help to fill this knowledge gap, providing a unique insight into a fully aeolian succession from the Silurian, with trace fossil evidence indicating permanent habitation. This presentation describes the invertebrate trace fossil associations from the Mereenie Sandstone, and the implications that these have for our understanding of the colonization of aeolian environments. After introduction to the trace fossils of the Mereenie Sandstone, these signatures are compared to ichnofaunas from the underlying Stairway Sandstone,



to provide context for the transition from shallow marine to aeolian habitation. Finally, the Mereenie ichnofauna is compared and contrasted to other early aeolian ichnofaunas, such as the Lower Devonian Muth Formation and Middle Devonian Kilmurry Sandstone. This will explore how animals first dealt with the challenges of inhabiting an aeolian environment on local and global scales.

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### Multiple branching and attachment structures in mat-dwelling cloudinomorphs, Nama Group, Namibia

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The Ediacaran–Cambrian cloudinomorphs, including *Cloudina*, are the first putative skeletal metazoans. They have tubular, organic or biomineralized stacked funnel morphologies, and produced the first reef frameworks through mutual cementation, but have an unresolved phylogenetic affinity. First, we demonstrate the presence of multiple (polytomous) dichotomous branching in cloudinomorphs from the Nama Group, Namibia, as revealed by three-dimensional models. Branches share an open cavity and branching is achieved via external budding. Polytomous branching excludes a bilaterian affinity as proposed for other cloudinomorphs. Second, we show that areas between the cloudinomorph laminae consist of tangles of aragonitic needles nucleating from laminae, pre-dating the earliest marine cements. The composition of both the cements between *Cloudina* that form a framework, and the intra-*Cloudina* cements, share similarly low strontium concentrations (means = 1273.9 and 1358.3 ppm, respectively) compared to the first early marine cements (mean = 2514.7 ppm). These findings suggest that these structures are of biological origin, indicating biomineralization was under some degree of biological control. In sum, these observations raise the possibility that the Ediacaran tubular, funnel morphology is convergent, and that cloudinomorphs may represent taxa of diverse affinity, and that they were capable of producing biological-controlled benthic, reef frameworks.

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### Crossing the boundary: small carbonaceous fossils (SCFs) as a means of tracking Ediacaran–Cambrian ‘survivors’

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Only a handful of body-fossil taxa are known to span the Ediacaran–Cambrian boundary. This pattern has frequently been interpreted as signifying a terminal Proterozoic mass extinction; however, identification of such major evolutionary perturbations is heavily reliant on taphonomic continuity. Unfortunately, the traceability of taxa over this boundary is seriously compromised; the coincident opening and closure of several key taphonomic windows around the Ediacaran–Cambrian transition hampers any detailed tracking of taxonomic ranges from this interval, a problem that may amplify the apparent disconnect between Ediacaran and Cambrian biotas. Before a precise outline of the magnitude, timing and nature of this transition can reasonably be achieved, it is crucial to establish an improved record of non-biomineralizing taxa in order to distinguish genuine





macroevolutionary patterns from any obscuring taphonomic signals. The emerging record of small carbonaceous fossils (SCFs) exhibits a more-or-less continuous pattern of preservation spanning this critical interval. We focus on a number of distinctive SCF taxa (including possible metazoans) that range across the Ediacaran–Cambrian divide. These rare additions to the select club of ‘Ediacaran survivors’ highlight the wider significance of SCFs as a novel source of tracking evolutionary patterns over the Proterozoic–Phanerozoic transition.

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### High-resolution rapid thermal neutron tomographic imaging of fossiliferous cave breccias from Southeast Asia

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Southeast Asia has a rich and interesting palaeohistory; however, it can be incredibly difficult to discern the mechanisms of site formation, depositional history and vertebrate accumulation. This is in part due to dating complexities and poor preservation potential in tropical environments. Calcareous breccia deposits that accumulate in limestone caves may hold the key to resolving this issue. These deposits are often overlooked as they appear homogeneous and are often considered too difficult to work with. We demonstrate that these seemingly homogeneous breccia are an excellent source of data to aid in determining taphonomic and depositional histories of complex depositional sites such as tropical caves. We employ high-resolution rapid thermal neutron tomographic imaging (NT) to visualize internal diagnostic features of fossiliferous breccia from three Pleistocene cave localities in Sumatra, Indonesia. NT imaging reveals the internal composition and structure of buried fossils and consolidated sediment matrices in these deposits before any destructive mechanical or chemical preparation. The primary agents in the formation of the breccia and accumulation of incorporated vertebrate remains are several rapid depositional phases of water and sediment gravity flow. This study highlights the potential for analyses of breccia deposits in palaeontological studies in Southeast Asian caves in the future.

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### Tree shape warps perceptions of morphological disparity in analyses of cladistic discrete character datasets

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Cladistic datasets are routinely recycled in analyses of morphological disparity that are subsequently shaped by prior choices in taxon and character sampling, unconsciously biasing perceptions of evolutionary history. Here we explore the impact of sampling through tree shape variables including symmetry and branch length distribution, using analyses of simulated and empirical data. Our results demonstrate that both symmetry and stemminess (the apportioning of edge length between external and internal branches)



correlate with trait space occupation. Increases in tree symmetry and stemminess predict greater dispersal across trait space. Conversely, asymmetrical trees typically generate morphological datasets exhibiting more compact patterns of morphospace occupation. Trees with long external and short internal branches generate morphological datasets with greater divergence between morphological outliers. Of the two parameters, variations in stemminess introduce a much stronger bias on perceptions of disparity than symmetry. Our results caution against the uncritical recycling of cladistic datasets for analyses of morphological disparity. They also provide a null model for the interpretation of analyses of morphological disparity, helping to disambiguate patterns that are simply the product of tree shape from genuine macroevolutionary phenomena.

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### The Metabolic Index: a flexible framework to predict biological responses to changing marine temperature and oxygen levels in deep time

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Oxygen and temperature are the two most important environmental parameters in controlling habitable space for animals in the ocean, and changes in these parameters are often invoked as driving mechanisms for evolutionary radiations and mass extinctions. However, it is rare for only one parameter to change in isolation, and because oxygen and temperature interact synergistically in determining an animal's aerobic scope, it can be difficult to understand their relative importance or test the null hypothesis that environmental change is simply correlated with, rather than causally responsible for, major events in evolution. The recently developed Metabolic Index relates the oxygen supply to an organism to its oxygen demand, calibrated using experimental respirometry and biogeographic data. Here, using examples from the Permian–Triassic mass extinction, the Cambrian radiation and the modern ocean, we demonstrate how this framework can be used to understand the biological impact of oxygen and temperature change across a variety of timescales. Issues remain with: lack of physiological data from palaeontologically relevant marine invertebrates; determining the effect of cooling events; and timescales of migration and habitat occupancy requirements. Resolving these will lead to more nuanced understanding of the relationship between past environmental changes and biotic responses.

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### Decreasing Phanerozoic extinction intensity as a consequence of Earth surface oxygenation and metazoan ecophysiology

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The decline in background extinction rates of marine animals through geologic time is an established but unexplained feature of the Phanerozoic fossil record. There is also growing consensus that the ocean and atmosphere did not become oxygenated to near-modern levels until the mid-Palaeozoic, coinciding with the onset of generally lower extinction rates.



Physiological theory suggests that the synergistic impacts of oxygen and temperature on aerobic respiration would have made marine animals more vulnerable to ocean warming events during periods of limited surface oxygenation, linking these two observations. Here we present a combined Earth system and ecophysiological modelling approach to evaluate the feasibility of surface oxygenation as a first-order control on extinction rates through the Phanerozoic. Although continental configuration, the strength of the biological pump, habitat area thresholds and initial climate state all impact the magnitude of modelled biodiversity loss across simulated warming events, we find that atmospheric oxygen is the dominant predictor of extinction vulnerability in our analyses. We therefore propose that the relative frequency of high-magnitude extinction events (particularly those not included in the canonical Big Five mass extinctions) early in the Phanerozoic is a predictable consequence of limited Palaeozoic oxygenation and temperature-dependent hypoxia responses.

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### Informing the 3D morphology of the Ediacaran rangeomorph *Fractofusus misrai* through detailed taphonomic analysis

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The Ediacaran rangeomorph *Fractofusus misrai* is one of the best-preserved taxa at Mistaken Point, Newfoundland, with detailed impressions of its lower surface being cast due to its reclining epifaunal lifestyle. Many *F. misrai* have curves, kinks and ‘tousling’ that likely reflect directional growth or taphonomic factors. Consideration of such disrupted specimens has allowed us to revisit its 3D morphology and better explain its palaeobiology. Photographic and morphometric study of disturbed *F. misrai* demonstrates aspects of its three-dimensional morphology not present in idiomorphic specimens. *F. misrai* consists of two rows of primary order rangeomorph units emerging from a central axis. We consider that each primary order unit was a thin sheet of self-similar secondary order units that variably curled upwards from the seafloor, as evinced by the wide variety of distal edge morphologies. ‘Furled’ tertiary order branching can sometimes be determined on the lateral margins of secondary branches. It is inferred that the margins of most of these finest rangeomorph branches would have been curved upwards into the water column.

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### Heat stress indications in the shells of benthic foraminifera: insights from a thermally polluted field laboratory

**Danna Titelboim, Oliver Lord and Daniela N. Schmidt**

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Benthic foraminifera act as an archive of environmental conditions and biological responses through time via changes in morphology and the chemical and structural composition of their calcite. Their response to past intervals of climate change are often used as analogues to understand impacts of future climate change. However, direct interpretations are difficult as none of these geological examples are acting on the same species nor at the same rates. To overcome this shortcoming, we examine two benthic foraminifera species inhabiting a thermally-polluted area in the Mediterranean, mimicking future warming scenarios under field conditions. Mg/Ca analysis indicates continued calcification even under heat stress of ~40°C. However, X-ray tomography analysis suggests that under extreme warmth, *Pararotalia calcariformata* decreased calcification (less CaCO<sub>3</sub> with respect to test volume)



but did not change its surface area. In contrast, *Lachlanella* reduces surface area at warm temperatures, changing its surface-to-volume ratio. Raman spectroscopy indicates a response to hot conditions by alterations to their chemical composition and/or crystal structure that could allow better identification of thermal stress in the geological record. A change to the calcite crystal structure may impact the resilience of these important carbonate formers in shallow water environments to predation and breakage.

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## Incongruent species delimitation among extant and extinct lacertid lizards, and how to overcome the “species problem” using morphology

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The “species problem” has been debated since the 1940s. Species defined based on different species concepts cannot readily be compared, rendering the taxonomic unit “species” partially artificial. This issue is particularly marked when comparing extant with extinct species, where the only available data for species delimitation is derived from their preserved morphology. Here we quantify intraspecific osteological variability in extant lacertid lizards using pairwise disparity scores based on discrete morphological characters for 62 specimens referred to nine species. Ranges and mean values are consistent, with an average of 0.198 changes per character scored. Application of these methods to 26 fossil specimens of six extinct lacertid species revealed that intraspecific osteological variability is inconsistent, which can in part be attributed to different researchers having unequal expectations of skeletal disparity among species. This divergent interpretation of intraspecific variability among extant and extinct species reinforces the species problem. Lacertidae is an example where extant species defined and delimited based on different species concepts show comparable and consistent intraspecific osteological variability. Here, as well as in equivalent cases, application of those skeletal disparity values to palaeontological species delimitation potentially provides a way to ameliorate inconsistencies created by the use of morphology to define species.

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## Challenging hegemonic narratives: the rise of the naked pterosaur

**David M. Unwin**

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The image of fluffy, furry, perhaps even feathery, pterosaurs is beguiling – and is currently being woven into an emerging hegemonic narrative surrounding the origin of feathers, and birds. Non-mineralized, seemingly hair-like filaments have been reported in approximately 30 pterosaur specimens, though most of these have yet to be analysed in detail. We have reassessed all these records – in just over half of these cases by direct inspection using a range of imaging techniques (light microscopy, UV, laser UV, SEM). Filaments associated with wing-membranes appear to be aktinofibrils (wing fibres), composite dermal structures, ubiquitous in the flight patagia, that, when partially decayed and unravelled could adopt branching morphologies. Filaments fringing the dorsal margin of the skull were, most



likely, parts of soft cranial crests. Elsewhere (neck, body, tail) filaments are rare and seemingly dermal rather than epidermal in nature. Composite collagen macrofibres were a fundamental structural component of the pterosaur integument taking the form of fibres in the cranial crest, tail flap, foot webs and the skin enclosing the neck and body and aktinofibrils in the flight membranes. The external surface of the epidermis appeared smooth and glabrous but, viewed at fine scale, exhibited a slightly granular or irregular polygonal texture.

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### Small carbonaceous fossils (SCFs) from North Greenland: new light on metazoan diversity in early Cambrian shelf environments

**\*Elise Wallet, Ben J. Slater, Sebastian Willman and John S. Peel**

*Uppsala University, Sweden*

The Sirius Passet Lagerstätte of North Greenland provides one of the oldest Cambrian records of a metazoan-dominated ecosystem preserved in a Burgess Shale-type fashion. The Lagerstätte site itself is restricted to just a single ~1 km-long outcrop located offshore from the shelf margin, in an area that has been affected by metamorphic alteration. The recent recovery of small carbonaceous fossils (SCFs) further south has substantially expanded the known coverage of organic preservation into shallower-water depositional settings in this region. Here we describe additional SCF assemblages from the siliciclastic shelf succession of the Buen Formation (Cambrian Series 2, Stages 3–4). Newly recovered material reveals a rich diversity of non-mineralizing metazoans, including the filtering and grinding elements of a sophisticated crustacean feeding apparatus – the oldest crustacean remains reported to date – alongside an assortment of bradoriid sclerites encompassing almost complete, three-dimensional valves. Other metazoan remains include trilobite cuticles, diverse scaldiphoran sclerites and a range of fragments of uncertain affinities. These outer-shelf communities differ substantially from the deeper water Sirius Passet biota, providing some hints on the significance of lateral partitioning in early Cambrian ecosystems and its implications on the fossil record of soft-bodied metazoans.

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### Searching for macroevolutionary early bursts through 156 million years of ammonoid evolution

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The early burst model is among the most popular macroevolutionary explanations for increasing disparity through time. The fossil record is often perceived as rich with examples of macroevolutionary early bursts, but few studies explicitly address the impacts of diversity on observed disparity patterns. Ammonoids possess an exceptionally well-resolved stratigraphic record, have a proclivity for repeated instances of convergent evolution and possess a geometrically simple morphology that directly influences organismal ecology. These factors make ammonoids an exemplary clade to test the early burst model. We document the ecomorphometric evolution of Ammonoidea at origination and through six mass extinction recoveries. We interpret these data using a novel method to predict the expected disparity given standing diversity. Ultimately, we could not recover any evidence for an early burst through 156 million years of ammonoid evolution. Macroevolutionary early bursts are likely rare in fossil data.



## Organic matter preserves biosignatures in deepest time and drives soft tissue permineralization

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Structural biomolecules, such as proteins, lipids and sugars, are the fundamental building blocks of life. Proteins represent direct translation products of the genetic code, they facilitate metabolic function, and form, together with lipids and sugars, tissue structures. Resulting soft tissue morphologies preserve occasionally as permineralized remains in deep time, while case studies suggest that the original molecular building blocks and associated biological signatures are lost during fossilization. Here I analysed ~300 modern and Neoproterozoic–Recent animal tissues, as well as fossil sediments, using *in situ* Raman microspectroscopy. Subjecting the resulting data to statistical analyses revealed that biomolecules fossilize under oxidative conditions through transformation into N-, O-, S-heterocyclic polymers following Advanced Glycoxidation and Lipoxidation reactions. Comparisons between fossil and sediment composition demonstrated that fossil organic matter is endogenous, and preserves physiological and phylogenetic signatures. Analyses of differently permineralized fossils showed how tissue-specific molecular fossilization products engage in bioinorganic interactions with diagenetically precipitated minerals, explaining biases in the fossil record of soft tissues. Loss of certain functional groups in permineralized fossil organic matter indicates an intrinsic contribution to the formation of diagenetic minerals. Fossil organic matter is, regardless of age or permineralization, a powerful tool to reconstruct the history of life.

## Evolutionary stasis in the ammonite *Discoscaphites iris* from the US Gulf and Atlantic Coastal Plains prior to the end-Cretaceous (K-Pg) mass extinction

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The ammonite *Discoscaphites iris* occurs abundantly in upper Maastrichtian strata on the US Gulf and Atlantic Coastal Plains and is the zonal marker for the highest ammonite biozone in North America, representing the last 350 kyr of the Cretaceous prior to the K-Pg mass extinction. We performed a morphometric analysis of *Discoscaphites iris* to explore the relationship between shell evolution and environmental variation throughout the entire geographic and stratigraphic range of this species. Specimens were collected at sites from New Jersey, Missouri, Mississippi and Texas, representing a range of palaeoenvironments. Most sections are < 5 m thick except for the Owl Creek type locality in Mississippi, which is 10 m thick. We measured seven morphological parameters including maximum length, as well as width and height of the shell at different stages of ontogeny. Results indicate that despite intraspecific variation, the morphology of this species is invariant throughout its entire geographic range. In addition, no morphological changes were detected throughout the stratigraphic interval in which it occurs, suggesting evolutionary stasis. The record of *Discoscaphites iris* is not consistent with significant environmental changes prior to the K-Pg



mass extinction that might have affected the morphology of this species.

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### The ever-browsing Deinotheriidae (Mammalia, Proboscidea): did climate change affect conservative herbivory during the Miocene?

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The family Deinotheriidae includes middle- to large-sized proboscidean taxa, which were present in European palaeocommunities from the early to late Miocene. Deinotheriids have been considered exclusive browsers that did not shift their dietary behaviour over time. Nevertheless, dental wear data representing this group are limited, and the possible effects of major climatic events on their dietary ecology has never been investigated. For this study, a comprehensive dataset was established, utilizing dental microwear and mesowear analyses. The results demonstrate a typical leaf-browsing behaviour for the two deinotheriid genera: *Prodeinotherium* and *Deinotherium*. However, a time-based analysis indicates that the dietary habits of Deinotheriidae were unstable and fluctuated in response to climate. Specifically, during the middle Miocene Climatic Optimum deinotheres feasted on softer food resources such as soft foliage. Contrariwise, throughout cooler time intervals during the late Miocene, deinotheriids fed on harder food resources, possibly including drier vegetation and hard-shelled fruits. At the same time, a sudden decrease in abrasive food intake is observed, possibly corresponding to resource partitioning, due to newly radiated browsing megaherbivores. Conclusively, the results suggest that the ever-browsing dietary habits of Deinotheriidae were influenced by climatically controlled factors, such as temperature and vegetation changes, and possibly sympatry.



# Abstracts of flash talk presentations

\* Candidates for the Council Flash Talk Prize are marked with an asterisk.

Underlined author denotes designated speaker.

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## Humeral diaphysis structure across mammals

**Eli Amson**

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Long bones comprise articular ends (epiphyses) joined by transitional metaphyses and a diaphysis (shaft). The structure of the latter is often viewed as regularly tubular across tetrapods. However, assessments of the bone structure along the whole diaphysis are rare. Here I acquire whole-diaphysis profiles of global compactness (bone fraction) in over 160 species of extant and extinct therian mammals (marsupials and placentals). Generally terrestrial, mammals have acquired the highly specialized aerial, fully aquatic and subterranean lifestyles multiple times, allowing us to potentially associate specific traits with these lifestyles. I show that there is a consistent increase in global compactness along the diaphysis across mammals. This pattern is modified in a limited number of specialized species: aerial taxa (gliders and bats) have rather uniform and low values, while cetaceans' humeral diaphysis is marked with a slightly more compact central region. Among subterranean clades, structure alterations are most obvious in fossorial talpids (true moles) and their highly modified humerus. These results call for the investigation of bone structure in whole skeletal elements of key fossils in order to reconstruct the patterns of evolutionary modifications associated with lifestyle transitions.

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## Heterophyllous ferns from Las Hoyas (Cuenca, Spain) and El Montsec (Lleida, Spain): highlighting their importance in the evolution of vegetation during the Early Cretaceous

**\*Candela Blanco Moreno and Ángela D. Buscalioni**

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Two heterophyllous fern species, *Coniopteris laciniata* Diéguez and Meléndez, 2003 and *Sphenopteris wonmacottii* Dilcher and Hill, 2003, have been described from Las Hoyas (upper Barremian) and El Montsec (Barremian) respectively. The study of 45 hand specimens shows similarities in leaf size and shape, presenting both sphenopteroid and filiform pinnules in the same leaf. Identical rhizome branching and phyllotaxis is also observed. We therefore conclude that the two species are synonyms. The name *Coniopteris laciniata* is maintained following the rule of priority in botanical nomenclature, and due to doubts in the assignation to higher taxonomic rank. To explain the heterophylly of the plant, two interpretations for the reduction of the lamina in the filiform pinnules have been proposed: presence of fertile organs; or adaptation to submersion in water, similar to *Ranunculus aquatilis* L. The two hypotheses were tested using metric architecture analyses based on a new formulation of the Branching Algorithms method. Results show strong differences between the pinnule types, suggesting that the second hypothesis is more probable. Although further systematic analyses are necessary, this fern could be related to Polypodiales supporting the diversification of this group during the Early Cretaceous, associated to the origin of angiosperms, and linked to aquatic environments.





## Spiralling out of control: morphology and ecology of *Eoandromeda octobrachiata* from Nilpena, South Australia

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The Ediacara biota represents the oldest complex, multicellular life in Earth's history. South Australian fossil localities contain exceptionally-preserved fossils from the most morphologically and taxonomically diverse assemblage of this period. Nilpena Station National Heritage Site (South Australia), soon to be part of the state's National Park network, preserves more than 200 specimens of *Eoandromeda octobrachiata*, a poorly understood, 1–3 cm diameter, octoradial organism which has been interpreted as both benthic and pelagic. This study utilized the novel application of rotational geometric morphometrics on a fossil, in association with preliminary spatial tests and palaeoenvironmental conditions with the aim to better understand the morphology and ecology of *E. octobrachiata*. The expected shape during life and the shape changes associated with preservation/taphonomy were extracted using a generalized Procrustes analysis (GPA) and a principal components analysis (PCA), respectively. Preliminary nearest-neighbour cluster analyses and size measurements were conducted on the specimens from the three separate fossil beds where this fossil occurs to determine if there was a relationship between size and distribution. The size, spatial and shape results were checked against the interpreted palaeoenvironmental conditions and we infer that *E. octobrachiata* was most likely benthic and highly susceptible to deformation due to environmental and burial conditions.

## Active trends and higher extinction of smaller lineages drove body mass increase in brontotheres

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Brontotheres (a family within Perissodactyla) lived in North America and Eurasia in Eocene times. During the 20 million years of their evolutionary history, brontotheres underwent an average increase in mass of 20 % every million years, rapidly becoming the first Cenozoic dominant lineage within the megaherbivore guild and the largest terrestrial mammals of their time (many weighing between 4,000 and 7,000 kg). Brontotheres thus pose a key study group to understand the processes underpinning the rapid increase of mammalian body sizes during the Palaeogene. We combined mass estimates with phylogenetic modelling and a body mass-dependent diversification model that uses occurrence data for the 57 brontothere species. Our procedure reveals that phyletic increase (Cope's rule) was a common feature of brontothere evolution, although both the rate of size evolution and the strength of the active trend decayed over time likely due to structural limitations preventing sustained increases. However, active net increase across lineages alone cannot explain the rapid increase of body mass in this lineage. We found a strong correlation of extinction with size: smaller brontothere species had a higher extinction risk. Our results show that both microevolutionary (phyletic trends) and macroevolutionary processes (differential species survival) interweave to render macroevolutionary trends.



## Morphological evolution in the tribe Cricetodontini (Cricetidae, Rodentia) during the Miocene

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Tribe Cricetodontini is a group of large cricetids first recorded in the Early Miocene and becoming extinct during the Early Pliocene. This tribe was composed of four genera: *Cricetodon*, *Hispanomys*, *Ruscinomys* and *Byzantinia*. The morphological trends of these genera are increasing ectoloph complexity, increasing molar hypsodontology and simplification of molar morphology – although some species present a mosaic morphology that does not follow these trends. This makes their generic assignment difficult. Previous results indicated the presence of two outline morphologies, straight and trilobed for the upper first molar (M1). To assess the validity of this new criterion for the generic assignment of the species included in the tribe Cricetodontini, an outline morphology analysis of the M1 was performed. The study includes more than 350 M1 that belong to 49 species of *Cricetodon*, *Hispanomys* and *Byzantinia*. Our results show an increase in the trilobed morphology of the M1 throughout the stratigraphic record of the tribe. Further analyses are required to prove if this trend is the result of a phylogenetic signal and could be used as a new taxonomic criterion, or a morphological response to environmental changes that occurred during the Miocene with the expansion of the grasses.

## The unique dentition of the rhynchocephalian *Clevosaurus brasiliensis*, and rhynchocephalian diversity in the Late Triassic of the southern hemisphere

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Rhynchocephalia is an order of lizard-like reptiles that first appeared in the fossil record during the Triassic. Most of the oldest known taxa are the derived acrodont-toothed Sphenodontia. *Clevosaurus brasiliensis* is one of several sphenodontians known from the Late Triassic (Norian) of South America; these are some of the oldest sphenodontians known. Here we describe the CT scanning of three exceptionally-preserved skulls, revealing *Clevosaurus brasiliensis* to have a unique form of acrodonty with much of each individual tooth being encased within the jaw bones. In addition, we address the known rhynchocephalian diversity from the Late Triassic of South America and in particular we present new material for an as yet undescribed stem sphenodontian rhynchocephalian; this significantly enhances our understanding of the early evolution of rhynchocephalians.



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## Convex hull estimation of mammalian body segment parameters

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Obtaining accurate values for body segment inertial parameters (BSPs) is fundamental for gait analysis. BSPs comprise the specific mass and inertia properties of each body segment. Convex hulling, whereby the smallest-possible convex object that surrounds a set of points is calculated, has been suggested as an effective and time-efficient method to estimate these parameters in extinct animals, where soft tissues are rarely preserved. We investigated the effectiveness of convex hull BSP estimation in a range of extant mammals, to inform the potential future usage of this technique with extinct taxa. Using segmented CT scans, we compared the BSPs calculated from skin segments with parameters estimated from convex hull reconstructions based on the underlying bone morphology. Using both phylogenetic generalized least squares and ordinary least squares regressions, we found consistent predictive relationships between estimated and true BSPs for each body segment. The resultant regression equations can be used in future volumetric reconstruction and biomechanical analyses of mammals, both extinct and in extant species where such data may not be freely available.

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## Ginglymostomatid-like multicuspid teeth in an elusive rajid skate from the Tuscan Pliocene

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Among extant rays (Elasmobranchii: Batomorphii), those assigned to the order Rajiformes are known as ‘skates’ and number some 290 species. The fossil record of Rajiformes is scant, and the low number of diagnosable extinct rajiform species contrasts with the high alpha-diversity of the recent stock. Here we report on four unusual skate teeth from two Pliocene localities of Tuscany, central Italy. While being attributable to Rajiformes and somewhat reminiscent of *Dipturus* and *Rostroraja*, these specimens display an idiosyncratic multicuspid crown design that does not compare favourably with any skate species known to date; consequently, they are interpreted as representing a yet to be described taxon of Rajidae. In light of similarities between the rather large-sized teeth of the latter and those of extant ginglymostomatids (*i.e.* the nurse sharks), this extinct skate form might have been capable of actively foraging upon relatively large food items. This elusive rajid was likely an uncommon component of the Pliocene Tuscan elasmobranch fauna, and it inhabited littoral and shelf settings characterized by tropical climate conditions. The origin of this extinct skate form might be referred to an earliest Pliocene diversification phase that also saw the emergence of the Mediterranean endemic stock of extant rajid species.



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## New insights in morphology and histology of Triassic Hybodontiform shark fin spines

**Matthew Cowen and Živilė Žigaitė**

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Fin spines are skeletal elements found throughout the evolutionary history of chondrichthyans, now confined to two extant orders of elasmobranchs, Heterodontiformes (horned sharks) and Squaliformes (dogfishes), as well as one order of holocephalans, the Chimaeriformes (chimaeras). The extinct group of Hybodontiform (hybodont) sharks are well known for their fin spines, and were a major clade of elasmobranchs with high diversity in the Triassic and Jurassic. Here we present a histological and morphological assessment of three Triassic Hybodontiform shark fin spines from the Keuper Strata of southwest Poland. Hybodont fin spines are highly vascularized with an elaborate and varied dentine structure that develops continuously as the animal grows. The morphological characteristics of the spines differ between localities and suggest multiple taxa are represented, bearing Hybodontid and Lonchidiid affinities at Lisowice (Lipie Śląskie clay pit) and Poręba, respectively. In briefly discussing the challenges of accurately ageing fin spines we consider the role of histology in age determination and what can be learned from other fossil and extant sharks, identifying key features indicative of the growth and development of these specimens.

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## Ontogenetic patterns of the crocodylian palate (Eusuchia, Crocodylia)

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Changes in the ontogenetic trajectories are a potential evolutionary driving force. These changes have been recently characterized in the dorsum of the skull of crocodylians, but are still unknown in the palatal area, which is a key-structure for the interpretation of crocodylomorph evolutionary history. In order to understand the morphological diversity of the crocodylian palate and to characterize their growth patterns, we employed a geometric morphometric approach. The sample contains 333 crania of post-hatching to adult specimens from all extant crocodylian species. A 2D configuration of 20 landmarks was used to digitize the right half of the palate. Principal Component Analyses were performed to identify patterns of interspecific and intraspecific palate shape variation throughout their ontogeny. Regressions between shape and log-centroid size were performed to assess ontogenetic trajectories. The results indicate the existence of common patterns of ontogenetic shape change in their palate. However, the juvenile individuals of the main crocodylian lineages (Alligatoridae, Crocodylidae, Gavialidae) depart from different morphospace areas, and some species have distinct ontogenetic trajectories. This produces a wide variety of palate shapes clearly differentiated in each crocodylian lineage. As a next step, these results will allow us to interpret ontogenetic series in crocodylian fossils.



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## Creating a link between schools and palaeontologists: how the use of valuable fossils can encourage scientific literacy

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The project “A Participatory Science: Reconstruction of Life and Death of the First Fossil Mammal of Las Hoyas Deposit (Cuenca)” was born as a pilot programme to promote the collaboration between researchers, educators and heritage conservation agents. This project connects palaeontologists with compulsory schools using the fossil *Spinolestes xenarthrosus*, one of the most important fossils from the Las Hoyas deposit (upper Barremian, La Huérguina Formation, Cuenca, Spain), and the first Mammalia that preserved hair and other soft tissues, like the lungs and liver. Five primary and secondary schools, located in rural areas of Cuenca province, were selected to participate. With this experience, we aimed to facilitate the comprehension of evolutionary concepts through activities involving the study of variability using local micromammal species. Pupils studied the hair (pelage cleaning), trophic adaptations and skeletal preservation (dissection of 30 owl pellets) and compared them with the fossil mammal. We observed that enthusiasm and interest were enhanced by the development of a more direct scientific experience that includes the discovery of their own heritage. We will design an exhibition on this research programme at the Museum of Palaeontology of Castilla-La Mancha (MUPA), linking *Spinolestes xenarthrosus* with extant mammals in a phylogenetic context, bringing palaeontology and evolution closer to the public.

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## Scientometric trends in Burmese amber research

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Discoveries of fossil inclusions in Burmese (Myanmar) amber have attracted considerable attention due to their exquisite preservation, which offers an unparalleled window into Cretaceous forest ecosystems. However, research on Burmese amber has also attracted controversy due to its alleged role in funding internal conflict, resulting in a devastating humanitarian crisis. The palaeontological community is not yet unified on how to ethically adjust research practices in response to this situation. Using bibliometric methods and networks analyses, we investigated the scientometric trends in research publications on fossils in Burmese amber, and quantitatively examined the collaborative networks of their authors. We find that in the last 30 years, research activity on Burmese amber has generally increased, with a noticeable escalation within the last five years, coincident with the military takeover of the amber mines. The majority of publications are authored by researchers based in countries of the Global North and lack Burmese co-authors, indicating weak or absent collaborations with local researchers and communities. This practice of ‘parachute science’ is harmful generally, but in a conflict region it is acutely problematic because it erodes confidence about whether fossil specimens are – or even can be – ethically collected and traded.



## Using evolutionary simulation to improve biodiversity-area models

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The species-area relationship is a widely applicable ecological phenomenon often applied to palaeontological studies. It has been proposed to explain events as different as the Cambrian explosion and the Permo-Triassic mass extinction, but there is still a great deal of uncertainty over how it operates. Computational eco-evolutionary models provide an opportunity to determine the root causes of the species-area relationship, where empirical studies often fail. We employ the Rapid Evolutionary Simulator (REvoSim) to produce spatially explicit, individual-based simulations of evolving communities. Gradual extinction of species in these communities was used to fit curves of extinction rate against biodiversity, which were then used to calculate theoretical species-area relationships. Our results suggest that distinct habitat types are capable of acting as discrete units for the purposes of controlling biodiversity in the wider area, and that these units can interact to further increase or decrease biodiversity. A new mathematical model (equation) for predicting biodiversity, derived from our results, performed better than existing models when applied to datasets from both our synthetic experiments and from ecological literature. Advancement in our understanding of the controls on biodiversity in the present will better facilitate their application to the study of biodiversity over deep time.

## Can we reconstruct limb motion from fossil footprints?

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The transition to upright bipedalism is recognized as one of the primary adaptations that shaped human evolution. However, disparate interpretations of fossil footprints, stemming from a lack of understanding of the links between limb motion and footprint morphology, mean it remains uncertain exactly when our ancestors' transition from more flexed non-human ape-like postures to a more extended human-like gait took place. In this study we test two hypotheses that underpin interpretations of gait from fossil footprints: that limb flexion increases with footprint depth; and that these changes in motion result in differences in the relative topology of footprints. We quantified 3D kinematics, muscle activity and 3D footprint morphology in healthy human participants walking across a range of sandy sediments of variable moisture content. Three-dimensional footprint shapes were recorded using photogrammetry. Analysis suggests that in softer, more deformable substrates in which the foot sinks more deeply, participants adopt a more bent-hip, bent-knee gait, a slower walking speed and shorter stride length, thereby supporting the first hypothesis. However, preliminary analysis of footprint morphology suggests relative conservatism in shape as depth increases, suggesting (contrary to the second hypothesis) that changes in gait may not be detectable in footprint morphology.



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## In search of the Cheshire Cat: the appearance and disappearance of the planet's first eumetazoans

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The Ediacaran biota, representing the planet's first macroscopic organisms, formed global-scale recurrent ecological communities known as the Avalon-, White Sea- and Nama-type assemblages; however, the agents responsible for the pronounced ecological differentiation have remained elusive. Nor is there a satisfying explanation as to why it is the Avalon-type biota that first appears in relatively deep-water settings followed by shallow-water White Sea- and Nama-type biotas *c.* 20 million years later. The disappearance of the Ediacaran biota at the end of the Ediacaran Period is a mystery in itself. I argue that the 'Cheshire Cat' hypothesis (*i.e.* that the Ediacaran organisms were invisible to the known record although present in actuality) has not been falsified and therefore should not be dismissed. Several lines of evidence suggest that the Ediacaran biota was adapted to anoxic conditions and has been preserved due to early diagenetic authigenic cementation of the casting medium in response to sharp changes in marine redox conditions. The disappearance of the fossil soft-bodied biota in the geological record is a direct consequence of stabilization of marine redox conditions (the closure of the 'taphonomic window') coupled with a change in ecological niches resulting from gradual oxygenation of the ocean.

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## Characterization of intraspecific variation of the European stem turtle *Pleurosternon bullockii* (Paracryptodira)

**\*Andrea Guerrero and Adán Pérez-García**

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The European uppermost Jurassic to lowermost Cretaceous (Tithonian to Berriasian) turtle *Pleurosternon bullockii* corresponds to the best represented member of Pleurosternidae (Paracryptodira). Despite the high number of available individuals, and that most of them were found more than a century ago, the vast majority remain unpublished. In this context, a detailed study of the morphological variability of the mature stage of *P. bullockii* is carried out here. The great sample size (the largest documented for a Lower Cretaceous turtle in Europe), as well as its good preservation, allowed us to characterize the inter-individual variability (*i.e.* polymorphisms and sexual dimorphisms), integrating both qualitative and quantitative approaches. Specifically, a geometric morphometric approach has been applied to describe the shape changes, as well as to assess the role of different morphological factors which have an impact on adult disparity. The analyses revealed that most morphological variation can be explained by polymorphisms, which are recognized in several elements of the shell. In addition, two sexual dimorphs were recognized, the first such interpretation in Pleurosternidae. Additionally, due to the significant improvement in knowledge of this form, a new diagnosis is provided.



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## Unravelling the legacies of empire in palaeontology: examples from the Sedgwick Museum

**Liz Hide and Robert Theodore**

*Sedgwick Museum, University of Cambridge, UK*

Black Lives Matter activism has drawn new attention to the lack of racial diversity in palaeontology, and has reinvigorated calls to address embedded inequalities and racism. In order to meaningfully address these challenges, we need to recognize that the development of our discipline is intimately wrapped up in the history of European colonialism, and that this legacy continues to frame our scientific work. Using examples from the Sedgwick Museum's collections, we discuss ways in which we can acknowledge and address the legacies of empire, and contribute to building a more inclusive and global palaeontology.

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## Modelling skeletal enrichment as a result of mixing, advection and disintegration of skeletal remains

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The quality of the (sub)fossil record and of ecological inferences made from it is controlled by the interactions of physical, chemical and biological processes whose intensity and interactions determine the preservation of skeletal remains. Based on a reaction-diffusion-advection equation, we present a nonparametric model that determines the age-depth-distribution of skeletal remains in the sediment as a function of their mixing, advection and disintegration, and describes the taphonomic pathway from primary skeletal input via death assemblage and historical assemblage into the fossil record. We use this model to discuss how skeletal enrichment of fossil assemblages are affected by extrinsic (bioturbation, sedimentation) and intrinsic (skeletal robustness) taphonomic parameters, showing that mixing intensity is the dominant control on the preservation of less durable skeletal remains.

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## Two-dimensional dental microwear indicates different feeding behaviours amongst three mosasaur taxa of the Campanian Bearpaw Fm., Alberta, Canada

**\*Femke M. Holwerda**

*Royal Tyrrell Museum, Canada*

The Campanian Bearpaw Formation yields a rich marine fauna from the northern exposures of the Western Interior Seaway. Well-preserved mosasaur material is common. This allows complete tooththrows to be studied for dental microwear. Three common mosasaurs were sampled for two-dimensional microwear: *Mosasaurus missouriensis*, *Prognathodon* sp. and *Plioplatecarpus primaevus*. Microwear was categorized as small scratches, large scratches (gouges) and pits. *M. missouriensis* shows a high total and average of small scratches in the premaxillary and maxillary teeth, and a low amount in the dentary. This could indicate a difference in the use of the upper and lower jaws, and between the front and back of the mouth. *Prognathodon* sp. shows a high number of pits in both upper and lower tooththrows, and a large amount of gouges in the maxilla, suggesting feeding on harder food items. *Plioplatecarpus primaevus* teeth also show a





high quantity of gouges and pits, contrary to their tooth morphology. This phenomenon is seen in other plioplatecarpids and could indicate regular feeding on ammonites and belemnites by this taxon. This pilot study hints at different feeding strategies between the common mosasaurs, explaining their coexistence in the same ecosystem without too great a competition for resources.

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### New, unique pterosaur remains from the Great Estuarine Group of Scotland

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The European Middle Jurassic is one of the largest gaps in the pterosaurian fossil record. It is a period of apparent diversification, introducing the successful monofenestratan bauplan. Our discovery, a three-dimensionally preserved Bathonian non-pterodactyloid pterosaur, provides essential data for this time gap. The new pterosaur originates from the Middle Jurassic Lealt Shale Formation of Skye, Scotland. This formation is recognized for prolific dinosaurian ichnofossils and is a part of the fossiliferous Great Estuarine Group. The fossils originating from the Hebridean Jurassic are mostly partial, the good preservation of our pterosaur is therefore anomalous. It is one of the most complete vertebrate fossils from the Scottish Jurassic and is among the best-preserved pterosaurs from Britain, on par with *Dimorphodon* from 1828. The specimen represents a new genus and species of Rhamphorhynchinae, with autapomorphies including a slender humeral diaphysis and a large oval fossa on the lacrimal process of the jugal. The pterosaur fills the time gap between Toarcian Posidonia Shale and Tithonian Solnhofen Limestone. It helps to contextualize the largely disarticulated coeval Stonesfield material from Oxfordshire. Ongoing taxonomic research on the specimen will widen our understanding of major shifts in pterosaurian evolution.

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### Predation by Octopodoidea in the fossil record

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Octopodoid cephalopods are ferocious predators, with a diversity of ~250 extant species. Due to their low preservation potential, their body fossil record is restricted to a single species from the Late Cretaceous (Cenomanian). However, their presence can be tracked in a different way. Members of extant Octopodoidea prey upon molluscs and crustaceans and often leave behind a characteristic ~0.2–2 mm, oval to rounded drill hole (ichnospecies *Oichnus ovalis* and *O. simplex*). Some studies have reported on such holes from Plio–Pleistocene crustaceans and molluscs, and from Miocene and Eocene bivalves. As a result, the stratigraphic range of such holes, drilling intensity and octopodoid behaviour are poorly known. We present two case studies. First, a study on Plio–Pleistocene cypraeid



gastropods from Florida showing a relatively high drilling intensity (13 %) and strong site selectivity to where the columellar muscle anchoring the soft tissue to the shell interior is attached. Second, lucinid bivalve specimens from the Late Cretaceous (Campanian) of South Dakota exhibiting holes strongly resembling those produced by modern octopodoids. These studies demonstrate that the drilling traces produced by octopodoids are not necessarily rare and that their fossil record can be leveraged further to study the evolution of octopod occurrence and behaviour.

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### Early post-embryonic stages of marrellomorph euarthropod from Morocco

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Marrellomorphs are marine euarthropods known from Cambrian to Devonian strata worldwide. The post-embryonic development of Marrellomorpha is poorly known, as specimens of early stages are rare. Here we describe the early post-embryonic stages of the Fezouata Shale (Lower Ordovician) marrellomorph from Morocco. These early stages are small (ranging from 2 mm to 4 mm in sagittal length) and differ from the adults mostly with slender and straight spines on the cephalic shield and proportionally shorter secondary spines on the cephalic shield. Synchrotron X-ray tomography reveals a lower number of the trunk segments and proportionally shorter podomeres of the trunk endopods in early stages. The antenna, second appendage and trunk exopods are generally identical to those of adult specimens. The lower number of trunk segments in the early stages confirms anamorphic development in Marrellomorpha. The similarity between the early developmental stages and the adults implies that the development was without any significant metamorphosis, at least for the developmental sequence starting at about 2 mm in length onwards. This suggests that no niche differentiation took place during the development of this taxon, as is supported also by the co-occurrence of early stages and adults in the same facies.

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### Evolutionary and ontogenetic changes of the anatomical organization and modularity in the skull of archosaurs

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Comparative anatomy studies of the skull of archosaurs provide insights to the mechanisms of evolution for the morphologically and functionally diverse species of crocodiles and birds. One of the key attributes of skull evolution is the anatomical changes associated with the physical arrangement of cranial bones. Here we compare the changes in anatomical organization and modularity of the skull of extinct and extant archosaurs using an anatomical network analysis approach and node-based informed modularity strategy



(NIMS). We show that the number of bones, their topological arrangement and modular organization can discriminate birds from non-avian dinosaurs, and crurotarsans. We could also discriminate extant taxa from extinct species when adult birds were included. By comparing within the same framework, juveniles and adults for crown birds and alligators (*Alligator mississippiensis*), we find that adult and juvenile alligator skulls are topologically similar, whereas juvenile bird skulls have a morphological complexity and anisomerism more similar to those of non-avian dinosaurs and crurotarsans than of their own adult forms. Clade-specific ontogenetic differences in skull organization, such as extensive postnatal fusion of cranial bones in crown birds, can explain this pattern. The fact that juvenile and adult skulls in birds do share a similar anatomical integration suggests the presence of a specific constraint to their ontogenetic growth.

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### Finding the worm: first palaeoscolecid from the middle Cambrian Marjum Formation of Utah, USA

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The middle Marjum Formation is one of five Miaolingian Burgess Shale-type deposits in Utah, USA. It preserves a diverse non-biomineralized fossil assemblage, which is dominated by panarthropods and sponges. Infaunal components are particularly rare, which is best exemplified by the poorly diverse scalidophoran fauna, and the uncertain presence of palaeoscolecids amongst it. To date, only a single Marjum fossil has been tentatively assigned to a palaeoscolecid taxon (*Scathascolex minor*). This specimen and two recently collected worm fragments were analysed using scanning electron microscopy and energy dispersive X-ray spectrometry. The previous occurrence of a Marjum palaeoscolecid is refuted based on the absence of sclerites in the specimen. However, the two new fossils are identified as a new palaeoscolecid genus, which is characterized by the presence on each annulus of numerous, single-sized (20–30 µm), smooth rimmed plates. This is the first indisputable evidence for the presence of a palaeoscolecid in the Marjum Biota, and a rare occurrence of the group in the Cambrian of Laurentia. Palaeoscolecids are known from nine Cambrian Stage 3–Guzhangian localities in Laurentia, but they are typically rare and never represent dominant faunal components as they do in Gondwanan Konservat-Lagerstätten.



## Could Lucy run? Reconstructing lower limb musculature in

*Australopithecus afarensis*

**Sian McCormack<sup>1</sup>, Evie Donald<sup>1</sup>, Sam Coatham<sup>2</sup>, Charlotte A. Brassey<sup>3</sup>, Thomas O'Mahoney<sup>4</sup>, William Sellers<sup>2</sup> and Karl T. Bates<sup>1</sup>**

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Quantitative estimates of running ability in extinct animals rely on reconstructions of muscles, which generate the power underpinning locomotor movements. However, soft tissues are rarely preserved in the fossil record. Here we examine the relationship between lower limb muscle attachment areas and masses in extant Great Apes, using a combination of high-resolution MRI and published anatomical and 3D scan data sets. We find statistically significant relationships between attachment area and mass for almost all lower limb muscle groups, providing an objective basis to predict locomotor muscle mass in well-preserved hominid fossils. 3D scans of the famous Lucy fossil were used to estimate muscle attachment areas and subsequently generate quantitative estimates of lower limb muscle for *Australopithecus afarensis*. Overall our predicted muscle masses show greater similarity with human rather than non-human proportions. However, our results suggest that *A. afarensis* lacked the enlarged ankle extensor muscles seen in humans. Together with relatively shorter lower limbs, these results suggest that *A. afarensis* had lower maximal running performance than modern humans, supporting the idea that the evolution of enhanced running ability coincided with the appearance of the genus *Homo*.

## Fronnd duplication in a new rangeomorph: insights into growth, adaptability and development

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Late Ediacaran siliciclastic successions from Newfoundland, Canada record the oldest deep-marine palaeocommunities of complex macro-organisms. These palaeocommunities were dominated by rangeomorphs, a diverse group of frondose organisms characterized by a unique, self-similar branching architecture, which are considered to be amongst the oldest known macroscopic animals. We developed a robust, objective statistical approach to Ediacaran taxonomy, complemented by detailed analyses of growth. Using this approach, we identified two new species in the genus *Beothukis* from the Bonavista Peninsula, Newfoundland: one is always unifoliate, the other can be either unifoliate or bifoliate. This represents the first documented bifoliate rangeomorph, and the first example of multiple levels of foliate expression in a single rangeomorph taxon. We identify different developmental patterns in the two species, even when present in the same palaeocommunities; we interpret these as distinct, species-specific responses to some shared environmental stimulus. Together, our data imply a level and type of ecophenotypic variation that has not previously been documented in rangeomorphs, and allow us to constrain the point at which branching morphogenesis is fixed in their ontogeny.



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## The making of a Lagerstätte: taphonomic artefacts associated with the Ediacaran biota of Spaniard's Bay, Newfoundland

**\*Christopher McKean, Duncan McIlroy and Rod S. Taylor**

*Memorial University of Newfoundland, Canada*

Rangeomorph macrofossils preserved at Spaniard's Bay, Newfoundland exhibit a unique three-dimensional preservation not seen elsewhere in the Ediacaran of Avalonia. The study of specimens by casting and detailed photography has revealed previously undocumented taphonomic features which are inconsistent with previous taphonomic models. The currently accepted taphonomic model applied to the Spaniard's Bay biota considers that erect fronds were felled into erosive current scours generated in their lee. However, the observation of specimens that are orientated into the inferred palaeocurrent requires reconsideration of this accepted model. Many of the holdfasts at Spaniard's Bay are associated with obstacle scours that have been previously misinterpreted as stems. Additionally, in some cases there is a clear offset between the holdfasts and the adjacent fronds, suggesting that some apparently stemmed rangeomorphs may not have actually had stems. We note that many of the fronds are only partially exposed in the current scours with the remainder of the organism being buried beneath the overlying sediment, suggesting that the frondose organism was either endobenthic or previously entombed in the T<sub>d</sub> turbidite that underlies the Spaniard's Bay surface.

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## Preliminary observations of potential reproductive structures in the rangeomorph *Culmofrons plumosa* from the Ediacaran of Newfoundland, Canada

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The fossil record of the Ediacaran in Avalonia is dominated by the diverse but enigmatic Rangeomorpha that are characterized by up to five orders of fractal-like branching. Despite their abundance and morphological diversity, little is known about their biology and ecology, including their phylogenetic position. An exceptionally well-preserved specimen of *Culmofrons plumosa* reveals remarkable morphological details that provide insight into its palaeobiology. The possible reproductive structures are composed of three or more tertiary order branches, preserved as impressions below the apical portion of secondary order branches. The involved tertiary order branches are arranged in bundles, separated from the secondary branches at their point of attachment. We suggest that these might represent the first documented reproductive structures in the Rangeomorpha. It is proposed that the separation of bundled pre-existing tertiary order branches provides an asexual reproductive strategy that efficiently utilizes the modular anatomy of the rangeomorph epithelium. This mode of reproduction is consistent with it being an early stage in the growth models proposed for charniids such as *Charnia* and *Beothukis*, which are thought to have grown by insertion of new branches at their apical extremity.



## New data on the *Nacholapithecus* elbow show close affinities with *Equatorius* and living papionins

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The elbow is an important anatomical region in the evolution of hominoids, which share a set of plesiomorphic adaptations (e.g. short ulnar olecranon). *Nacholapithecus kerioi* is a kenyapithecine (Kenya; 16–15 Ma) whose elbow morphology has been described as derived compared to earlier proconsulids. Here we analyse a well-preserved ulnar proximal fragment (KNM–BG 38391B) and compare it with other extinct and living taxa to investigate its morphological and functional affinities. Seventeen linear measurements were taken on the proximal ulnae sample and were statistically analysed through PCA (size-related effects were removed by obtaining Mosimman variables). Additionally, AHC analysis (UPGMA algorithm) were performed to check for phenetic affinities. *Nacholapithecus* falls within cercopithecines (mainly papionins) and close to chimpanzees in the PC1–PC2 morphospace. The closest fossil taxon is *Equatorius* (KNM–TH 28860-K). Moreover, *Nacholapithecus* is grouped with papionins and *Equatorius* in the UPGMA cluster (CPC = 0.87). Our results reinforce the ulnar similarities between *Nacholapithecus* and *Equatorius* suggested by other authors and reveal closer resemblances with large papionins. The latter are dedicated terrestrial quadrupeds, a locomotor mode that has also been proposed for *Equatorius* based on some anatomical features. Similarities with these taxa might suggest previously unknown terrestrial affinities in *Nacholapithecus*.

## Intrinsic or extrinsic? Untangling the impact of taphonomic, phylogenetic and ontogenetic factors on morphological variance in exceptionally preserved fossils

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Exceptionally-preserved fossils provide invaluable information on the vibrant history of life on Earth, but they are also prone to conflicting morphological interpretations, leaving the fossil record littered with problematic taxa whose uncertain affinities prevent the accurate reconstruction of key evolutionary events. This occurs, in part, due to the complex influence of the multiple factors that create morphological variance, including phylogenetic constraints, ontogenetic and taphonomically-driven changes. Disentangling these factors to accurately distinguish between informative intrinsic variation and extrinsic biases during analysis can be difficult. Here we present a multivariate method which incorporates the combined influence of these factors during the comparison of fossil and modern taxa. Using soft-bodied early vertebrates as a case study, we are able to show its potential to infer the affinity of ambiguous problematic taxa as well as clearly visualize the impact of stemward slippage. This new approach enables the identification of the dominant causes of variance, and so can reduce ambiguity in the interpretation of fossil morphology and affinity.



## The freshwater Devonian arthropod *Oxyuropoda*: the oldest peracarid crustacea (Eumalacostraca)?

**Ninon Robin and Maria E. McNamara**

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*Oxyuropoda ligioides* from the Upper Devonian of Ireland (-370 Ma) was a freshwater to fully terrestrial arthropod. Since its discovery in 1908, it has been successively ascribed to arachnomorph chelicerates, euthycarcinoids and isopod peracarid relatives. Phylogenetic relationships among peracarid groups are not resolved, and their most widely accepted members (excluding pygocephalomorphs) are all known to be marine in the Devonian. However, when calibrated with the oldest fossils (-306 Ma), Isopoda phylogenies suggest a primary shallow-marine to freshwater ecological transition during diversification, which is assumed to have started in the Ordovician. This transition has never been studied, presumably due to lack of fossilized stem-isopods. Here we re-analyse *Oxyuropoda* anatomy using a set of recent imaging methods (particularly multispectral imaging) optimizing the recovery of anatomical details usually invisible on flat arthropods. These methods revealed the so far never observed legs, new details of buccal appendages, and an abdomen with six segments and a telson characteristic of Eumalacostraca. The interpretation of the presence of a carapace is complex, requiring the reassessment of features that could link *Oxyuropoda* to Peracarida, potentially pushing back the first appearance of the group by 40 Ma and shedding light on the timing of freshwater colonization within Peracarida.

## Microanalytical investigation of exceptionally preserved microbial fossils in the Rhynie chert

**\*Edwin Rodriguez-Dzul, Sean McMahon and Bryne T. Ngwenya**

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The ~407 Ma Rhynie chert Lagerstätte of Aberdeenshire, Scotland yields a unique, remarkably-preserved freshwater biota including early land plants, fungi, amoebae, algae and bacteria. These extraordinary fossils are preserved three-dimensionally as silica-permineralized organic matter. The microbial diversity of the Rhynie ecosystem is striking but remains under-explored. We are investigating new and previously described microorganisms in a variety of palaeo-microenvironments by using petrographic analysis of thin sections, Raman microscopy, and Fourier-transform infrared spectroscopy. Organisms of interest include streamer-mat-forming filamentous cyanobacteria, coccoids and sarcinoids interpreted as probable cyanobacteria (*e.g. Rhyniosarcina devonica*), fungi (*Glomites*-like) and amoebae (*Palaeoleptochlamys hassii*). A key challenge is to identify and reliably differentiate fossil bacteria from other microbes (*e.g. fungi and algae*). Preliminary spectral analysis suggests that important clues may be obtained from the aliphatic branching index (R3/2) and thermal maturity (I1350/I1600) intensity ratios in the carbonaceous matter. Using Principal Component Analysis (PCA), we may be able to extract further information both about the nature of these organisms (*e.g. prokaryotic or eukaryotic, where morphology is ambiguous*) and about the quality of carbonaceous preservation in different microenvironments or taphofacies. This should in turn inform future studies of the microbial diversity of this important ecosystem, and others.



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## Refinement of palaeocolour reconstruction using machine learning

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Melanin is a leading factor in palaeocolour reconstruction. Melanosomes have been detected in fossilized integuments and visceral organs. Palaeocolour prediction relies on statistical analyses to quantify and extrapolate the shape–colour relationships to fossil taxa. This has so far been achieved using quadratic discriminant analysis that leads to the basic tenets of ‘machine learning’. Machine learning is an emergent field in data science that works primarily on algorithms and models that take up a specific task and gradually improve their accuracy over time. We curated three comprehensive datasets on: feather melanosomes; vertebrate integument melanosomes; and vertebrate organ-specific melanosomes from prior publications on palaeocolour reconstruction. Unsupervised (data clustering) methods show that aspect ratio (long axis ÷ short axis) deemed highly significant by prior work, leads to information loss. Supervised learning techniques achieve an accuracy of ~73 % across all datasets. Finally, our use of deep neural network models show limited efficiency (~40–60 %) due to small sampling sizes, which was a limitation that prior studies had also suffered from. Therefore, we propose that a big data repository based on large-scale data collection may address the data scarcity and usher in drastic improvements in palaeocolour prediction accuracy.

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## The invasion hierarchy: quantifying ecological and evolutionary consequences of invasions in the fossil record

**Alycia L. Stigall**

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Species invasions are pervasive in Earth’s history, yet the ecological and evolutionary consequences vary greatly. Ancient invasion events can be organized in a hierarchy of increasing invasion intensity from ephemeral invasions to globally pervasive invasive regimes. Each level exhibits emergent properties exceeding the sum of interactions at lower levels. Hierarchy levels correspond to, but do not always exactly correlate with, geographic extent of invasion success. The ecological impacts of lower level impacts can be negligible or result in temporary community accommodation. Invasion events at moderate to high levels of the hierarchy permanently alter quantitative aspects of ecological communities, regional faunas and global ecosystems. The prevalence of invasive species results in quantifiable evolutionary changes by fostering niche evolution, differential survival of ecologically generalized taxa, faunal homogenization and suppressing speciation. These impacts can contribute to mass extinctions and biodiversity crises that alter the trajectory of ecological and evolutionary patterns of life. Examples are provided including ephemeral invasions in local strata, the regional Richmondian Invasion, the Great American Biotic Interchange and the Late Devonian Biodiversity Crisis. The fossil record provides a long-term record of how invasion impacts may scale up through time, which can augment ecological studies of modern species invasions.





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## Multi-proxy dental morphological analysis: a quantitative approach to inferring diet across distantly related taxa

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Diet is poorly constrained in many extinct taxa. Ecometrics quantifying 3D tooth morphology correlate with, and have been used to infer, diet. These ecometrics are hypothesized to be homology-free, allowing dietary inferences to be made from analysis regardless of phylogenetic affinity. However, this approach has been tested only on teeth and dentitions of gnathostome vertebrates, and its applicability to food processing structures in non-gnathostome vertebrates remains untried. Multi-proxy dental morphological analysis (MPDMA) combines several individual ecometrics, each capturing a single aspect of morphology, to provide a more accurate measure of 3D dental morphology. As a result, MPDMA is considered a more powerful tool for inferring diet than any single ecometric. Here we demonstrate that MPDMA produces metric values that are directly comparable between phylogenetically distant taxa with non-homologous dental tools. Specifically, we analysed the mandibles of 45 extant grasshoppers and crickets. We demonstrate that MPDMA of invertebrate mandibles can identify differences between dietary categories, correlates predictability with dietary intractability, and successfully predicts diet when trained by a vertebrate dataset. This suggests that MPDMA of 3D fossilized dental tools can produce accurate inferences about diet – providing a powerful new tool in identifying trophic interactions and ecosystem functioning throughout deep time.

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## Defining the preservational variability of *Funisia dorothea* and related insights on morphology from the Ediacara Member of South Australia

\***Rachel Surprenant** and **Mary L. Droser**

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The Nilpena Station Ediacara Fossil Site in South Australia houses 40 bedding planes, each of which represent the burial of *in situ* Ediacaran communities by discrete storm events, thus providing a unique opportunity to investigate the nature and drivers of taxon-specific biostratinomic variability in Ediacaran ecosystems. We utilize *Funisia dorothea*, the most abundant organism preserved at Nilpena, to illustrate the utility of such taxon-specific biostratinomic studies for constraining the morphology of Ediacaran taxa. *Funisia* is a hollow tubular organism composed of serially repeating modules and is most commonly preserved in large populations of densely packed individuals. The densely packed life habit of *Funisia* results in generally poor preservation which veils many aspects of *Funisia* morphology. To address this, biostratinomic data were collected on seven *Funisia*-dominated bedding planes, revealing four preservational modes and four biostratinomic grades of *Funisia*, reflecting distinct biostratinomic pathways and the extent of degradation, respectively. The nature and relative abundance of *Funisia*'s preservational modes and biostratinomic grades across the seven beds provide evidence for a recalcitrant body wall and a fluid-filled body cavity, and identifies population density, facies association and extent of pre-burial degradation as key controls on *Funisia* biostratinomy.



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## Testing hypotheses of trilobite head modularity with emphasis on the eyes

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The trilobite head served multiple functions and was composed of several fused segments. Yet, the underlying organization of the trilobite head, and whether patterns are conserved across trilobites, remains unclear. Modelling the head as being composed of modules, or subunits which evolve semi-independently, can reveal underlying patterns of organization. Hypotheses of modular organization based on functional and developmental assumptions were evaluated using an effect size measure derived from the covariance ratio (CR). Two-dimensional (semi)landmark datasets collected from the cranidia of two Ordovician trilobite species from different orders were analysed. When treating the eyes as a distinct module, the highest observed pairwise CR value in two species was that between the eyes and the anterior cranidia demonstrating high covariation between these modules, relative to covariation within modules, compared to other modules of the cranidia. Further, the best modular hypothesis identified for both species shows the eye and anterior cranidia integrated as a single module. These results can be interpreted as a developmental signal corresponding to the anterior-most ocular segment of early arthropods, especially considering modular hypotheses based on facial sutures were not well supported. Our findings further understanding of the underlying modular organization of the trilobite head.

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## The changes of seawater chemistry during the Cambrian Explosion

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The Cambrian explosion, witnessing the transition from soft-bodied eukaryotes in low diversity during the Ediacaran to burgeoning animal phyla with the development of ecological opportunities in the Cambrian, is a critical event for shaping the modern ecosystem. The diversification of animal species in the Cambrian happened with the appearance of diverse biomineralized skeletons, designating the onset of biomineralization. However, the causes of these evolutionary developments during the Cambrian Explosion remain complicated. We propose that the fluctuations of redox conditions might have facilitated the radiation of animal phyla, and variable seawater molar Mg/Ca influenced the precipitation of different carbonate mineralogy and the selection of carbonate skeletons. Here we collected carbonates in Mongolia, Siberia, Namibia and Labrador from Late Ediacaran to Lower Cambrian, and identified the oldest marine cements based on the optical and cathodoluminescence (CL) characteristics. We then rebuilt the changes of seawater molar Mg/Ca in the Cambrian combining the petrology and elemental compositions of the oldest marine cements, and used rare earth elements to reconstruct the variations of seawater redox conditions, explaining how oxygen concentrations shaped the ecosystem during the Cambrian Explosion.



## What triggered coccolithophore calcification?

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Coccolithophores are single-celled calcifying nannoplankton that were crucial in establishing modern ocean biochemical conditions and carbon cycling dynamics since the evolution of their calcification process in the Late Triassic, ~215 million years ago. The causes that triggered biomineralization in these organisms, however, remain unknown. Oxygen availability has been proposed as a driver for macroevolutionary novelty and innovation, but the relationship between coccolithophore evolution and ocean oxygenation has not been addressed. Here iodine-to-calcium ratios (I/Ca) and trace elemental analyses were used to build a high-resolution record of upper-ocean redox conditions during the Triassic in order to assess the relationship between oxygen concentration and the evolution of coccolithophore biomineralization. Initial measurements on carbonates from the Early Triassic of the Musandam Peninsula, UAE and the Late Triassic from the Austrian Alps yield evidence of local oxygenation increase prior to the onset of coccolithophore calcification, as shown by the appearance of the oldest fossil representatives of the group.

## Biostratinomy of carbonate-hosted Ediacaran macrofossils in the Khatyspyt Formation, northeastern Siberia

\***Olzhas Zharasbayev<sup>1,2</sup>, Natalia Bykova<sup>1</sup> and Dmitriy V. Grazhdankin<sup>1,2</sup>**

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Palaeobiology of Ediacaran soft-bodied organisms cannot be divorced from taphonomy, and both rely critically on the appreciation of the sedimentological processes; however, the common mouldic preservation of the fossils at the interface separating sediments of different texture has limited the biostratinomic detail that can be captured. The fossils are often studied in the context of the sediment that smothered the organisms, not of the sediment that the organisms lived in. Finely laminated (biolaminated) limestones of the Khatyspyt Formation, northeast Siberia host an assemblage of fossilized Ediacaran soft-bodied organisms and offer a unique opportunity to study both the overlying and the underlying sediment in thin sections. In the studied collection of 719 specimens of discoidal fossils we were able to differentiate between: fossils that only interfere with the biolamination in the underlying sediment; fossils that do not interfere with the biolamination; and fossils that only interfere with the biolamination in the overlying sediment. These three groups of fossils correspond respectively to: the areas of the localized concentrically degraded microbial substrate (Ediacaria-type fossils); the areas attributed to concentric growth of microbial substrate (*Cyclomedusa*-type fossils); and the holdfast structures (*Aspidella*-type fossils).



# Abstracts of poster presentations

\* indicates a poster eligible for the Council Poster Prize.

Underlined author denotes designated presenter.

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## Skull morphology of *Spheniscus urbinai* (Aves, Sphenisciformes) and the evolution of the cranial pneumatic system in penguins

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New data on the osteology, palaeoneurology and the pneumatic system of *Spheniscus urbinai* from the Miocene of southern South America are provided. Based on the examination of eight crania, and after extensive comparisons with living species of *Spheniscus*, we conclude that, even considering the intraspecific differences, the skull of *S. urbinai* is larger, the fossa temporalis is deeper, and the bill is characterized by the widening of the base and the rostrum, and the curvature of the apex. The marked reduction of the cranial pneumaticity of penguins in comparison, for example, with the albatross *Diomedea exulans* was present early in the Eocene, as observed in the Antarctic penguin MLP 12-I-20-1 (although not in the coeval *Anthropornis grandis*). *S. urbinai* exhibits slightly larger cranial pneumaticity than that observed in the living *Spheniscus* and *Pygoscelis*, and also that in the Miocene *P. calderensis*. Other differences include a reduction of absolute brain size, the wulst, the olfactory passages, and nasal cavities in living taxa. The skull cavities, restricted to the olfactory region, correspond to pneumatic trabecular cells in the Eocene specimens, whereas they merge forming passages and larger diverticula sinuses in the Miocene specimens. These structures also form a ring surrounding the cerebellar region dorsolaterally in living *Spheniscus* and *Pygoscelis*.

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## Organic-walled microfossils co-occurring with discoid problematica in the Neoproterozoic Xingmincun Formation, North China Craton

**Heda Agić<sup>1</sup> and Ying Zhou<sup>2</sup>**

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The Proterozoic fossil record is dominated by minute and soft-bodied fossils until the rise of macroscopic life in the Ediacaran. There are rare instances of macrofossils in older strata, among them enigmatic bedding plane discs from the Neoproterozoic (<924 Ma) Xingmincun Formation, upper Jinxian Group on the North China Craton. These macrofossils occur in shale representing a transgressive sequence. They are preserved as flattened discs with concentric annuli up to 3 mm in diameter. Two types of preservation are observed (following Luo *et al.* 2016): with a thin mineral cover and concentric relief; and lacking mineral covering. Well-preserved organic-walled microfossils (OWM) were recovered from the same shale horizons bearing the discs, via palynological maceration in hydrofluoric acid. OWM include early eukaryotes like envelope-bearing *Simia annulata*, and late Mesoproterozoic–Tonian taxa *Culcitolisphaera revelata*, *Microlepidopalla mira*, and *Squamosphaera colonialica*. Bacterial cellular aggregates are also present. No



differences in the OWM assemblage are observed between samples with different types of macrofossil preservation. *Culcitulispheera*, known mainly from units on Laurentia, is reported for the first time in China. The presence of characteristic Tonian OWM supports the older-than-Ediacaran age model for the Xingmincun Formation. The Xingmincun microfossil assemblage represents a rare instance of a co-occurrence of Precambrian micro- and macrofossils.

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## Recent advances in reconstructing Middle and Late Jurassic water temperatures of Gondwana based on stable oxygen isotopes of fossil shells

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Jurassic belemnites, brachiopods and bivalves were analysed for their stable oxygen isotope composition ( $\delta^{18}\text{O}$ ) to reconstruct temperature conditions for a series of Gondwanan localities including India, Madagascar, Jordan, Israel, Egypt, Tunisia, Morocco, Chile and Argentina. Results indicate comparatively stable temperatures for most of the represented time intervals and regions in western Gondwana, while eastern Gondwana experienced a nearly steady temperature decrease. This discrepancy is explained by the concomitant break-up of Gondwana during which the eastern part of the supercontinent drifted into higher (=colder) latitudes, while the western part did not change its position significantly. Data from fossils from low palaeolatitudes show the importance of considering a latitudinal gradient in seawater  $\delta^{18}\text{O}$  values for temperature reconstructions and point to a potential stress environment along the equator. Knowledge of seawater  $\delta^{18}\text{O}$  values is also fundamental for interpreting data from Argentina, where fossils indicate considerable freshwater influence in the central/northern parts of the Neuquén Basin during the Middle and Late Jurassic, which complicates temperature reconstructions. A combination of literature data with the present results allows the reconstruction of latitudinal temperature gradients, which seem to be as steep as today for most of the studied time intervals.

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## Evolution of bone cortical compactness in slow arboreal mammals

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Ecological and phenotypical convergences are pivotal in palaeobiological reconstruction. The convergent slow arboreality in the two genera of extant sloths probably explains their shared low bone cortical compactness (CC). Since evidence is limited to extant sloths and close relatives, the possibility of convergent evolution of low CC in other slow arboreal therian mammals was supposed. We explore this hypothesis, analysing humeral and femoral CC in several slow arboreal mammals and close ecologically-distinct



taxa. In this way, ecological effects are preponderantly taken into account. Our sample includes Patagonian Miocene medium-sized 'ground sloths' and the putatively slow arboreal subfossil lemurs Palaeopropithecidae and *Megaladapis*. Because of the high CC found in all the studied extinct sloths, the low CC retrieved in extant sloths (the lowest in the whole sample) is suggested to be a recent convergence. The relatively low CC in palaeopropithecids (mainly *Palaeopropithecus*) and *Megaladapis* might imply additional convergences of low CC and increases evidence of a tree sloth-like lifestyle for these enigmatic extinct lemurs. However, a straightforward relationship between low CC and slow arboreality cannot be drawn. Unexpected results for other slow arboreal groups suggest a multifactorial explanation of low CC in mammals.

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### Morphological disparity of the oldest ammonoids: a geometric morphometric approach

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The ammonoids appeared during the Lower Devonian (*c.* 405 Ma); they derived from the Bactritida which root in the Orthocerida in the latest Silurian or earliest Devonian. Earliest forms are found in Morocco (*e.g.* *Praechebbites debaetsi*) in early Emsian deposits. In the Anti-Atlas of Morocco, the Emsian ammonoids are abundant and well preserved. These faunas are well documented in the literature, and provide an interesting record of the morphological disparity changes that characterize the first step of the Ammonoidea evolution. The present study aims to investigate the morphological disparity of the early ammonoids during the Emsian (Lower Devonian), by analysing the shape of the whorl cross-section outline (aperture shape). Based on specimens from Morocco illustrated in the literature, we compile an exhaustive dataset (compilation of drawings representing the whorl cross-section outline for each Emsian species). We use a geometric morphometrics approach based on the acquisition of semi-landmark coordinates, to analyse the whorl cross-section outlines. Disparity indices are used to measure accurately the morphological disparity fluctuations through time. The analyses are performed considering the Moroccan ammonoid biozonation as temporal scale. Preliminary results suggest that the morphological disparity increased significantly during the late Emsian, with the appearance of numerous new shell morphologies.

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### The impact of the Permian and Triassic biotic crises on spatial patterns of origination and extinction in brachiopods and bivalves

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The Permian and Triassic (~300–200 Ma) represent an interesting time in Earth history, characterized by an icehouse–greenhouse transition followed by large-scale volcanic episodes and extreme greenhouse temperatures, resulting in biotic crises at the end of the Capitanian (Middle Permian) and the most severe known mass extinction event at the Permian–Triassic boundary. Two theories have been put forward to describe the spatial



distribution of extinctions during the end-Permian event: rising temperatures in the already-warm equatorial regions rendered them uninhabitably hot, driving poleward migration and/or high rates of extinction at low latitudes; and rising temperatures in the cooler polar regions meant the loss of niche-suitable habitat for cool-adapted organisms, driving high rates of extinction at high latitudes. Although these mechanisms have been invoked to explain patterns observed in the fossil record, neither has been explicitly, quantitatively tested. After building simulations to test the efficacy of our methods, we estimated rates of origination and extinction by latitude throughout the Permian and Triassic using a global database of fossil brachiopod and bivalve occurrences. We then used these results to examine whether one or both of the aforementioned mechanisms took place during the end-Capitanian and end-Permian extinctions and subsequent recoveries.

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## The response of conodont communities to the end-Ordovician mass extinction

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The Late Ordovician was the first of the five Phanerozoic mass extinctions. Each of these events had different long term impacts, and in some the drop in diversity was uncoupled from the ecological impact. Previous work on the Late Ordovician reports a greater effect on species diversity and not community structure, but these studies focus on benthic fauna. Notably, this event closely followed the Great Ordovician Biodiversification Event which notably increased diversity in planktonic and nektonic fauna. Conodonts flourished during this event and adopted an array of trophic niches. They survived the Late Ordovician mass extinction but never fully recovered. Despite this, conodonts have not been considered as to how the structures of communities changed. This project investigates whether conodont communities have been affected more severely in terms of community structure than other previously studied organisms. This study uses resources from the Paleobiology Database and contributed essential resources to the archive. It looks at studies across the Katian, Hirnantian and Rhuddanian to show the effect of the event and tests statistically how the diversity changed and if the community structure changed. Better understanding the effects of previous mass extinctions will help increase understanding of the long-term effects of the Holocene mass extinction.

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## A marine 'fish' assemblage from the Maastrichtian (Late Cretaceous) of Gavdos Island, Greece

**Thodoris Argyriou<sup>1</sup>, Lionel Cavin<sup>2</sup>, Jorge D. Carrillo-Briceño<sup>3</sup> and Apostolos Alexopoulos<sup>4</sup>**

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The global fossil record of marine vertebrates from the Maastrichtian stage, which immediately precedes the K–Pg mass extinction, is poor, hampering an accurate evaluation of the status of marine ecosystems before and after their sudden demise. Renewed collection and research efforts on K–Pg fossiliferous rocks of the Pindos Unit, Greece are opening windows into offshore pre-extinction vertebrate assemblages from the Tethys. In 2019, we conducted an exploration and salvage mission in the Maastrichtian of the Pindos



Unit on Gavdos Island. We salvaged many fossils from slabs already set in pavements, and collected additional material from the original fossil-yielding quarry. The new material expands the faunal list of Maastrichtian vertebrates from Gavdos, which now includes hexanchid sharks, †ichthyodectoids, †dercetids, a new species of †ichthyotringoid, †*Enchodus* cf. *dirus*, a new genus and species of †enchodontoid, and at least one unidentified teleost. The new †enchodontoid exhibits adaptations for the conceived shearing of soft-bodied prey. The recognition of new aulopiform taxa supports previous notions regarding the under-appreciated nature of aulopiform taxonomic diversity at the very end of the Cretaceous. Moreover, the overall character of the Gavdos assemblage is indicative of a healthy offshore ecosystem, in close temporal proximity to the K–Pg Extinction boundary.

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### Palaeoecology of the Hettangian–Sinemurian (Lower Jurassic) strata of Redcar, Cleveland Basin, northeast England

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Redcar (northeast England) presents the oldest Jurassic succession outcropping on the Yorkshire–Cleveland Coast. The section spans the Hettangian–Sinemurian (Lower Jurassic) boundary, providing insights into the timing of recovery following the end-Triassic mass extinction event. Despite the significance of the Redcar succession it has been largely neglected since the late nineteenth century due to beach sands frequently covering the outcrop. Temporary removal of these sands by winter storms early in 2018 allowed for a detailed study to be undertaken on a nearly 60 m thick foreshore section. The Redcar sequence comprises five cycles (parasequences) that grade upwards from mudstones into *Gryphaea*-dominated shell beds. The *Gryphaea* and the bivalve *Cardinia* commonly feature borings made by cirripedes and bryozoans. Although the abundant *Gryphaea* are the most notable component of the fauna, there is in fact a high invertebrate faunal diversity, including other bivalves, gastropods and solitary corals. These are not restricted to discrete shell beds but also occupy intervening mudstones and indicate advanced levels of marine recovery. Pyrite framboids are abundant in all lithologies in the cycles; however, their large size distribution suggests only weak dysoxia in the bottom waters. This is in contrast to repeated pulses of euxinia recorded in southern England.

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### A 2D geometric morphometric analysis of plesiosaur flippers

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Plesiosaurs existed from the Late Triassic to the end Cretaceous, during which time they diverged into two different morphotypes: large-headed, short-necked pliosauromorphs, and small-headed, long-necked plesiosauromorphs; additional differences include proportions of limb elements. These morphotypes are considered to have different predatory styles, from cruising ambush predators (plesiosauromorphs) to fast pursuit predators (pliosauromorphs). Plesiosaurs are limb-dominant locomotors, therefore differences in behavioural style that affect swimming biomechanics are expected to be reflected in morphology. This analysis compares flipper morphology of plesiosaurs using 2D geometric morphometrics, assessing





limb element proportions (fixed landmarks) and flipper shape (sliding landmarks) using a representative sample of Jurassic ( $n = 22$ ,  $n = 30$ ) and Cretaceous species ( $n = 16$ ,  $n = 24$ ). PCA indicates segregation of groups is more defined within the flipper proportion dataset than the flipper shape dataset. MANOVA confirms there are statistically significant differences for both datasets; however, these are more prevalent for the flipper proportions. These results indicate a convergent evolution of plesiosaur flippers across groups, in that while limb proportions vary, overall, they converge to form relatively similar flipper shapes. In order to further assess this, additional specimens for the flipper proportion dataset will have to be located.

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### Palaeoecology of vertebrates in the Cerro del Pueblo Formation (Campanian) at Porvenir de Jalpa, Coahuila, Mexico

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The municipality of General Cepeda has the largest number of palaeontological deposits in Coahuila, with an age between 73 and 72 Ma, from the Late Campanian within the Upper Cretaceous period. There are still unknown areas because the exposure of fossils around the Cerro del Pueblo Formation is discontinuous and it is hard to predict where other deposits may be. The study area discussed here was newly discovered by an amateur palaeontologist from the Museo del Desierto, Saltillo; he identified a complex diversity of fossils difficult to identify. When it was reported this project was assigned for a bachelor's degree thesis. Fieldwork consists of basic collecting of fossil material around where vertebrate faunas have been found. Hopefully, the material will be identifiable but much of it is eroded and some bone parts are impossible to identify to a specific taxonomic level. These are taken to the Museo del Desierto for cleaning and study (if required), so families can be identified from their biology along with recommended literature. Following this, a palaeoecology study of the site will be made. To date, we have been able to identify six families with teeth, vertebrae, fragmented shells, squamosal and parietal bones; phalanges and manual unguals belonging to Tyrannosauridae, Hadrosauridae, Parksosauridae, Trionychidae, Ceratopidae and Dromaeosauridae.

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### Biomechanical insights into the dentition of megatooth sharks (Lamniformes: Otodontidae)

\***Antonio Ballell Mayoral and Humberto G. Ferrón**

University of Bristol, UK

Evolution of gigantism in the extinct otodontid sharks was paralleled by a series of drastic modifications in their dentition, including the widening of the crown, the loss of lateral cusplets, and the acquisition of serrated edges. These traits have generally been interpreted as key functional features that enabled the transition from piscivorous to more energetic diets based on marine mammals, ultimately leading to the evolution of bizarre body sizes in the most recent forms (including the emblematic *Otodus megalodon*). To interrogate this hypothesis, we evaluate the biomechanical behaviour of anterior, lateral and posterior teeth of five otodontid species under different loading conditions using 2D finite element analysis. Stress distribution patterns vary among teeth with different degrees of crown curvature during puncture and draw (*i.e.* when subjected to vertical and lateral forces, respectively).



Contrary to the expected pattern, higher stress average values under both loading scenarios are detected in more recent species. Altogether, this supports little correlation between tooth morphology and stress in otodontids, making it difficult to frame the morphological trend of their detentions within an adaptive scenario. We propose that this pattern most likely emerged as a non-functional by-product of heterochronic processes driven by selection towards larger body sizes.

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### Virtual techniques help the study of two Early Pleistocene carnivorans

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Taphonomic deformation is one of the most common issues that affects fossil specimens, often obscuring the true development of the organism's structure, thus complicating, if not precluding, a correct interpretation of fossil anatomy. Here we present the virtual reconstruction of the type skulls of two of the most iconic Early Pleistocene carnivorans of southern Europe: *Canis arvensis* Del Campana, 1913 and *Homotherium crenatidens* Fabbrini, 1890. The specimens considered were collected from the Upper Valdarno Basin (Tuscany, central Italy) at the end of the nineteenth century and, although selected as types of the species, present a high degree of latero-lateral deformation. The 3D models of the holotypes were obtained with high-resolution laser scanners and the retrodeformation was developed using recently-published open-source protocols for 3D virtual reconstructions in R. This method, named Target Deformation, requires undeformed target specimens of the same species to be used as a guide for the fitting process, through a geometric morphometrics approach. The preliminary results of the retrodeformation provided new and valuable data for morphological and shape analyses for further investigation on evolution and adaptation of these emblematic fossil carnivorans. Furthermore, the results of virtual processing on these fossils may be used in a variety of educational initiatives.

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### Walking into the Oligocene: a revision of the early Oligocene Saignon tracksite (southeast France)

**Matteo Belvedere<sup>1</sup>, Emmanuel Fabre<sup>2</sup>, Stéphane Legal<sup>3</sup> and Pauline Coster<sup>3</sup>**

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Known since the 1980s, the Saignon tracksite bears a diverse early Oligocene ichnoassemblage. Geologically, the tracksite is located in the Apt syncline, within the Calcaires de La Fayette Formation dated to the earliest Rupelian (MP21). The tracksite is composed of two main track-bearing levels (labelled main and high). The main surface ichnoassemblage is dominated by perissodactyl tracks, co-occurring with artiodactyl ichnites, while the high surface yields bird footprints almost exclusively. The perissodactyl tracks belong to different ichnotaxa. The smallest ones, occurring only as few partial trackways and isolated prints, are assigned to *Plagiolophustipus* isp.; these tridactyl tracks are minute and show an overlapping of the fore and hindlimbs during walking. The most common perissodactyl tracks show clear manus and pes impressions, arranged in a variety



of relative positions dependant on gait and/or behaviour of the track-maker. Manus and pes impressions are similar in size, tridactyl, with subcircular digits and short, blunt hoof impressions. They have been identified as *Rhoncoceripeda voconcence* comb. nov. One trackway of a possible juvenile animal has been identified. The Saignon ichnoassemblage includes one of the earliest rhinocerotid records in Europe associated with endemic pre-Grande Coupure forms of ungulate.

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## Ostracods of the Ponto-Caspian region at the late Pleistocene–Holocene transition

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The Ponto-Caspian region is a system of inland basins and adjacent territories. The entire region's evolution reflects both global and regional climatic rhythms. The study area includes the North Caspian region, the Bulgarian part of the Black Sea (WBS), and the East Black Sea (EBS) near Anapa. Most of the studied ostracod species are Caspian. Thus, the ostracods of the Neuwexinian basin are common with the Khvalynian. This is probably a consequence of the unilateral water discharge from the Caspian. In the Caspian cores, Girkanian deposits abounded of *Paracyprideis* sp., *C. gracilis*, *C. cf. bogatschovi* and *B. dorsoarcuata*, while Khvalynian deposits contain 30 species of Caspian origin. In the EBS 57 species were identified, 52 of them having a Caspian origin, and five are Mediterranean. A smaller number – 25 species – were found in the sediments in the WBS, eight of the species are represented by Mediterranean migrants and 17 species have a Caspian origin. The most common are *Loxocochna lepida*, *Loxocaspiasublepida*, *Amnicythere martha*, *Euxinocythere relicta*, *Amnicythere stepanaitysae* and *Candona schweyerei*. Approaching the Late Pleistocene–Holocene border, the species diversity in both the Caspian and Black seas decreased.

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## Integrated multi-proxy approach reviews ecosystem dynamics during Holocene transgression in the northwest Adriatic Sea

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Holocene marine sediments preserve important information about environmental and ecological changes, often due to anthropogenic impact, which can be easily age-dated – a distinct advantage over deep time records. Our study approach combines sedimentology and palaeoecology to determine major environmental changes along a 3-m-long gravity core taken at 31 m water depth, off the Po River Delta in the late Holocene of the northern Adriatic Sea. Different age-dating techniques were used to define core chronology and to improve palaeoenvironmental reconstructions. Age-dating has been performed on shells of the bivalve *Corbula gibba* (by C14-calibrated amino acid racemization), bulk-sediment (210Pb isotope analysis) and plant remains (radiocarbon isotopes) to gain information about time-averaging, sedimentation rates and the complete core chronology. Different facies types have been identified, changing from laminated, lagoonal silts (transgressive system tract) to fully marine, bioclastic clayey silts (highstand system tract). A major environmental change has been identified in the highstand sediments. Geochemical and palaeoecological proxy



analyses indicate a drastic increase in eutrophication and heavy metal pollution coinciding with a major loss of molluscan abundance and diversity in the Northern Adriatic Sea during the twentieth century that can be related to anthropogenic impact.

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### Middle Miocene nautilids *Aturia* from the southwestern margin of the Central Paratethys, Croatia

**Marija Bošnjak<sup>1</sup>, Jasenka Sremac<sup>2</sup>, Tomislav Malvić<sup>2</sup> and Valentina Gašo<sup>2</sup>**

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Fossil nautilids of the genus *Aturia* have been recorded in the Middle Miocene (Langhian – Badenian) deposits in the Čučerje area near Zagreb, Croatia, at the palaeogeographical southwestern margin of the Central Paratethys sea. The specimens are housed today at the Croatian Natural History Museum in Zagreb, and determined at species level as *Aturia aturi* (De Basterot, 1825). Specimens are preserved as casts, with phragmocone and no last (living) chamber. In order to define complete size of the fossil shells, we chose 36 well-preserved samples for geomathematic modelling of the shell with the last chamber. Using the numerical analyses of the length, width and thickness of the cast we performed biometric analysis of the nautilid samples. Based on the biometrics and geomathematical modelling, results indicate possible sexual dimorphism present in the analysed samples. For further conclusions more specimens are necessary, as well as the comparison with neighbouring contemporaneous localities.

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### Arthropod head evolution in the Cambrian: a reappraisal

**Graham E. Budd**

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Cambrian arthropod phylogeny continues to be in a confused state, despite the (relatively) enormous amount of data now available – and nowhere is this more evident than in theories about head evolution. Although several such theories exist, they are underpinned by supporting hypotheses that have little empirical support. Here, then, I revisit (once more) the Cambrian fossil record of arthropods including some little-studied taxa, with the aim of understanding the key component of head evolution, the labrum – that which Rempel (1975) referred to as “the final, the central problem, the crucial point of the long-lasting controversy”. I shall argue that we should expect to see the transformation of a frontal appendage into the labrum reflected in the upper euarthropod stem group; we do in fact see this, and that with this insight comes resolution of a large portion of Cambrian euarthropod phylogeny. This framework, however, necessitates a (doubtlessly controversial) substantial reinterpretation of the preserved neuroanatomy of taxa such as the megacheirans and fuxianhuids, and indeed of the head structure of radiodontids and their relatives, with implications for the crown group too.



## The macroalgal assemblage from the late Ediacaran Khatyspyt Formation, Olenek Uplift, Siberia

**Natalia Bykova**

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Benthic marine macroalgae are key ecological players in oceans today and have been since the Proterozoic. In the Proterozoic, macroalgae reached the maximum morphospace occupation and diversity during the Ediacaran period, right before the animal ‘Cambrian Explosion’. The Khatyspyt Formation of northeastern Siberia hosts one of the richest assemblages of the Ediacaran macroalgae, preserved as carbonaceous compressions. The assemblage includes such taxa as *Beltanelloides*, *Chuaria*, *Globusphyton*, *Glomulus*, *Grypania*, *Juqunaoella*, *Liulingjitaenia*, *Longfengshania*, *Longifuniculum*, *Mezenia*, *Synocylindra*, as well as some yet undescribed, endemic forms: linguaforms, reniform bodies, lingulates with transverse banding, conical forms, diverse ribbons with longitudinal structures, blade-like bodies with holdfasts, tomaculate organisms with spaced annulation, bubble-like forms. In comparison with other macroalgal assemblages of the late Ediacaran, the Khatyspyt assemblage has a very low amount of branching forms (~3 % of the taxa; compare to ~30 % in the Miohe assemblage, South China). Furthermore, the Khatyspyt macroalgae are gigantic: the median is 84 mm, which is 2.5 times more than the size of macroalgae from Wenghui, South China. It is still unclear what provoked the peculiarities of the Khatyspyt macroalgae, but it is definite that it captures an essential interval of the macroalgal evolution during the Ediacaran.

## New insights into Middle Devonian chitinozoans from Bolivia

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The TCB X-1001 – Tacobo borehole, located in the foothills of Bolivia, eastern sub-Andean ranges, was palynologically analysed. It comprises the Middle Devonian shallow marine sedimentary succession of the Los Monos Formation. A late Eifelian? to middle Givetian age was already interpreted, based on organic-walled phytoplankton and miospores from the same samples. In total 669 chitinozoan specimens were examined under SEM. A moderately well preserved chitinozoan assemblage was recognized from the middle levels of the formation, allowing for the identification of five genera and 33 species. The lower and upper levels produced scarce and poorly preserved specimens. The formation yielded a typical late Eifelian to early Givetian chitinozoan fauna of western Gondwana. The assemblage is dominated by the genus *Ancyrochitina*, which constitutes 43 %, with representatives of *Ancyrochitina biconstricta* and *Ancyrochitina multibrachiata*, among others. It reveals strong similarities to assemblages previously recorded from the Middle Devonian of Bolivia. The presence of *Ramochitina stipbrospinata*, which is the index species of the eponymous early Givetian chitinozoan zone of western Gondwana, supports the age assignment based on other palynomorph groups. Other early Givetian characteristic species are *Ancyrochitina flexuosa*, *Ancyrochitina frankeli*, *Ancyrochitina morzadeci* and *Ramochitina boliviensis*, the latter being very abundant in the studied assemblage.



## Geometric morphometric analysis of the outline of *Megacricetodon* (Rodentia, Mammalia)

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*Megacricetodon* is an important rodent genus recorded during most of the Eurasian Miocene. Its distribution, diversity and short stratigraphic range make this genus a great stratigraphic marker of the continental Miocene of Europe. For this reason, morphological studies of its dentition are key in the Miocene European Chronology studies. In recent years, morphological studies of rodents have not been limited to the length and width of the cheek teeth but to multivariate analysis taking into account the complex morphology of molars, as occurs with the geometric morphometric analysis. In this work we present a geometric morphometric analysis based on the outline morphology of the molars of several species of *Megacricetodon* using elliptic Fourier analysis. We count with almost 2,000 dental pieces between upper and lower first molars of more than 20 species of *Megacricetodon*. In this analysis, we assess the morphological differences of the species among the upper and lower first molars, the relation between the outline morphology and the size of the species, and study the trend of different lineages described for this genus. Our results show differences among the species at the outline level but further analyses including other species are required.

## Target deformation of the *Equus stenonis* holotype skull: a new protocol for 3D virtual reconstructions

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We provide here the first application of a new digital reconstruction protocol, named Target Deformation (TD), which extends beyond traditional symmetrization and virtual aligning procedures by using target specimens as a guide for the reconstruction. We have tested this new method using the holotype of *Equus stenonis*, a nearly complete, yet medio-laterally crushed and badly compressed skull. As references to guide the virtual reconstruction, we have used two well-preserved yet fragmentary *E. stenonis* skulls from the Italian and Georgian localities of Olivola and Dmanisi (Early Pleistocene), respectively. The two specimens were retrodeformed and aligned on each other by using geometric morphometrics and eventually were used to restore the shape of *Equus stenonis* holotype via warping. The feasibility of TD was attested by showing how the TD 3D models



settle perfectly within the natural variability of European *E. stenonis* skulls. This case study shows the potential of using broken or otherwise fragmentary specimens to guide a virtual reconstruction for badly distorted and damaged specimens. The application of TD will increase the availability of comparative specimens for taphonomic, morphological, systematic and phylogenetic studies in palaeontology.

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### Sedimentology and palaeoecology of barnacle-dominated, *Amphistegina*-bearing facies from the lower Pliocene of Liguria (northwestern Italy)

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The lower Pliocene deposits of Pairola (Liguria, northwestern Italy) feature the otherwise uncommon occurrence of rock-forming amounts of barnacles (mostly belonging to the Neogene Euro-Mediterranean species *Concavus concavus*). Three main facies are recognized in the investigated succession: a barnacle-dominated facies, which formed along a shallow (<15 m deep) nearshore environment; a foraminifera-dominated facies from relatively deeper waters (40–100 m); and an intermediate transitional facies. These facies and their mutual relationships suggest deposition in a flooded valley, *i.e.* a ría (a kind of setting that was common along the Mediterranean coasts after the Messinian salinity crisis). Differing from other rías, the Pairola basin was exposed to strong waves, resulting in conditions favourable to barnacles. Although sedimentological and stratigraphic observations indicate that the Pairola succession formed within a timespan covering both cold and warm phases, the sub-tropical foraminifer *Amphistegina* is ubiquitous throughout the succession. *Amphistegina* occurs in the Pliocene and lower Pleistocene (Gelasian) of northern Italy, but not in the remainder of the Pleistocene. Crucially, this genus is currently recolonizing the Mediterranean and it is projected to reach the northern coasts of this basin soon, foretelling that Anthropocene Mediterranean temperatures might be approaching those typical of the Pliocene.

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### Early Miocene Erinaceids and herpetotherids from the Ribesalbes–Alcora Basin (Spain)

**Vicente Daniel Crespo Roures<sup>1,2,3</sup>, Francisco J. Goin<sup>1</sup>, Rafael Marquina Blasco<sup>3,4</sup>, Francisco Javier Ruiz-Sánchez<sup>3,4,5</sup> and Plini Montoya<sup>4</sup>**

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We present results obtained from a study of the mammalian assemblages from 45 sites included in the early Miocene deposits of the Campisano Ravine. These outcrops are located in the Araia/Mas d'Antolino area of the Ribesalbes–Alcora Basin, Spain. The faunal assemblages of these sites indicate an early Aragonian age (MN4, early Miocene), as inferred from the presence of rodent taxa such as *Megacricetodon*, *Democricetodon* and *Ligerimys*. The rodent assemblage allowed us to correlate levels bearing them with the



local Biozone C of the Calatayud–Montalbán Basin, Spain. These sites have yielded an assemblage of erinaceids and metatherians which is relatively rich for an Iberian site. The most common erinaceid is the gymnure *Galerix symeonidisi*, present in almost all of the studied sites. Other erinaceids in the faunal list are possibly indeterminate species of the genera *Lantanotherium* and *Atelerix*, in what constitutes one of their oldest occurrences in Europe. Metatherians are represented by the herpetotheriid *Amphiperatherium frequens erkertshofense*. We describe for the first time the lower dentition of this taxon in this basin, increasing our knowledge of the high variability of its decidual molars.

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### Revision of small mammal material (Rodentia, Lagomorpha, Eulipotyphla) from the early Pliocene sites of Berești and Mălușteni (eastern Romania): preliminary results

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The neighbouring sites of Berești and Mălușteni (eastern Romania) have yielded abundant remains which form the most diverse Pliocene vertebrate assemblage of this country. The most detailed descriptions of the small mammal material, made by Ion Simionescu in the early 1930s, included four species of insectivores, ten of rodents and two of lagomorphs, including four new species. Part of this material was revised by Costin Rădulescu and Petre Samson in the 1960s and the 1980s. They synonymized *Arvicola pliocenicus* with *Mimomys moldavicus*, described the new talpid *Talpa neagui*, and assigned all the leporid material to the new species *Trischizolagus dumitrescuae*. This contribution presents the first results obtained after revising what material still exists in the collections of the University of Bucharest (106 specimens). Most of the analysed specimens were confirmed as belonging to the lagomorphs *Trischizolagus dumitrescuae* and *Ochotona ursui*. The rodents still found in this collection were assigned to *Castor* sp., *Prospalax priscus*, cf. *Pseudocricetus* sp., *Spermophilus* cf. *praecox*, whereas one insectivore humerus was assigned to cf. *Archaeodesmana* sp. A more precise assessment is hindered by the fragmentary state of the material, but more data could be obtained by revising material housed in the Alexandru Ioan Cuza University in Iași.

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### A preliminary report on the Mid-Cambrian (Series 3, Guzhangian; Marjuman) trilobite *Arapahoia* from the Sullivan Formation, southern Canadian Rocky Mountains, Alberta and British Columbia

**Michael Cuggy**

University of Saskatchewan, Canada

The systematics of a few of the trilobites from the Sullivan Formation of the Southern Rockies of Canada have been briefly described by Walcott (1924;1925). The trilobites were then treated in more detail by Resser (1942) who was perhaps the most notorious





'splitter' in Cambrian palaeontology. Consequently, numerous species have been named but many are likely to be synonyms. Since this previous work was based on relatively few, small collections with little stratigraphic control, a great deal of systematic description and revision is still needed. One such taxon is *Arapahoia*, an abundant and species-rich genus that is poorly known from other locations across Laurentia. New collections of *Arapahoia* from the Sullivan Formation allow the species within this genus to be evaluated, new characteristics to be identified and hopefully for the first time allow the genus to be placed within a phylogenetic framework. Over seven species have been identified from the Sullivan Formation; as well, taxa from Montana and Wyoming have been re-evaluated. The diversity and high rate of turnover seen in *Arapahoia* in the Sullivan Formation makes it ideal for biostratigraphy.

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### Land–sea ecosystem connectivity during past global warming events

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Little is known about how climate change affects land–sea ecosystem connectivity in deep time. Here we reconstruct the timing of degradation and recovery of land-plants, marine primary producers and benthic macro-invertebrates over a period of four million years in response to the Early Toarcian warming event (Early Jurassic) and test for possible causal links between changes in land and sea ecosystems. Studied samples of pollen and spores, plankton and benthos derive from the coastal sections of Yorkshire, UK. Land-plants were more severely affected during the initial stages of warming, gradually changing from wet-temperate to hot and drought-adapted species at the peak of warming. Marine plankton and benthic animals experienced a muted response to initial warming, but as temperature peaked, suffered a rapid and extreme turnover. The loss of large trees, which contributed to increase weathering, runoff and seawater eutrophication, and the development of anoxia, explain changes in primary producers (from dinoflagellate- to prasinophyte-dominated), and is also linked to the local disappearance of all infaunal species. Although ocean systems have a stronger buffering system to climate perturbations, being initially more resilient than land-plants, they might be the last to recover, with a cascade effect from the planktonic to the seafloor environment.

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### The Devonian Landscape Factory: plant-sediment interactions in the Old Red Sandstone of Svalbard and the rise of vegetation as a biogeomorphic agent

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The Devonian period was a crucial interval in the evolution of land plants: it witnessed the successive evolution of roots, wood, trees and forests. An attendant effect of these



evolutionary innovations was that many of the biogeomorphic and ecosystem engineering phenomena that operate in modern terrestrial environments came online on Earth's surface for the first time. Such phenomena have left both direct and indirect signatures in the global sedimentary-stratigraphic record. The Old Red Sandstone of northwest Spitsbergen provides a near-continuous Silurian to Late Devonian record of land plant-colonized sedimentary environments so is a perfect natural laboratory to understand archetypal examples of early plant-related facies signatures. The purpose of this contribution is to describe a catalogue of features from the succession that provide tangible evidence for the stepwise appearance of novel plant–sediment interactions. We demonstrate how the unit hosts evidence for incremental changes in preserved plant material and rooting structures, early large woody debris accumulations, coal deposits, and the oldest known vegetation-induced sedimentary structures, in addition to typical vegetation-influenced facies motifs. These are used to reconstruct changes to non-marine sedimentary environments that were beginning to be influenced by novel land plant physiologies, materials and habitats in this Devonian ‘landscape factory’.

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### A snapshot of early Carboniferous floras: Tournaisian permineralized plants from Montagne Noire, France

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The early Carboniferous was an important time in plant evolution, with the diversification of several major groups of ferns s.l. and seed plants. The middle Tournaisian localities of the Montagne Noire in southern France include some of the oldest outcrops with anatomically preserved fossil plants from that time. Since the first discoveries in the late nineteenth century, over 400 permineralized specimens have been collected and more than 30 plant taxa have been identified, some of them unknown elsewhere. Thanks to their exceptional preservation, they provide information not only on the systematic diversity of Tournaisian plants but also on their biology. The assemblage is also important to understand floral changes between the Devonian and Carboniferous. It is largely dominated by seed plants (>60 %). Zygopteridalean ferns, cladoxyloids and lycopsids are also relatively abundant (+/- 10 %), while the progymnosperms and sphenopsids are rare (1–2 %). We will present a comprehensive review of this flora and highlight recent work on several emblematic taxa such as *Sphenophyllum* or *Cladoxylon*.

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### Addressing ambiguity in Acanthodes: the 3D pharynx of an iconic Permian stem-chondrichthyan revealed by computed tomography

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*Acanthodes confusus*, an anguilliform freshwater fish from the early Permian of Lebach, Germany is key to understanding the evolution of the jawed vertebrate pharynx. This significance is owed to *Acanthodes* being the only ‘acanthodian’ – the earliest-branching stem-chondrichthyan grade – known from numerous three-dimensional fossils preserving



articulated cranial skeletons. Unfortunately, the ironstone concretions containing these fossils require destructive preparation to create moulds, and ambiguities in these have led to diverse anatomical interpretations of the complicated series of bones forming *Acanthodes*' pharyngeal skeleton. We used computed tomography to image several unprepared specimens of *Acanthodes confusus* from Lebach, resulting in the first 3D models of its entire cranial anatomy. These confirm (and refute) aspects of previous accounts and show that *Acanthodes* had a mélange of osteichthyan-like and chondrichthyan-like morphologies in its pharyngeal skeleton. Consistent with other stem-chondrichthyans, *Acanthodes* has a basihyal with no hypohyals, and four pairs of posteriorly oriented pharyngobranchials. Like osteichthyans, *Acanthodes* possessed an interhyal between the ceratohyal and hyomandibular; however, it lacked the separate infra- and supra-pharyngobranchial elements seen in osteichthyans and the crown-chondrichthyan *Ozarcus*. We incorporate these data into a new phylogenetic dataset targeting the chondrichthyan stem-group, finding support for the hypothesis of an early branching 'Acanthodii' grade.

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### Soft tissue preservation in Solnhofen ichthyosaurs shows blubber and tail fin shape

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Ichthyosaur fossils with soft tissue preservation have been known for almost two centuries and have provided crucial knowledge on body shape. Still, soft tissue from the major middle Jurassic–middle Cretaceous family Ophthalmosauridae is known from fewer than five specimens. Two new specimens from the Solnhofen Lagerstätte are now described, and their soft tissue analysed for the first time for this family. One specimen, assigned to *Aegirosaurus* sp., is a rare case of a complete ophthalmosaurid, with large amounts of phosphatized soft tissue of several types. The majority of its body is preserved in its own decomposing blubber. Samples were analysed via X-ray diffraction (XRD) and scanning electron microscope (SEM), which confirms apatite, with phosphate most likely derived from the body itself, a finding which is interesting for understanding the taphonomical pathway for other Solnhofen vertebrates. Solnhofen is also the only locality with ophthalmosaurids preserved with a caudal fin outline. Two out of three such specimens are described here, and might have implications for swimming in derived ichthyosaurs.

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### Metacommunity analyses show increase in ecological specialization throughout the Ediacaran

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The first animals appear during the late Ediacaran (572–541 Ma); an initial diversity increase was followed by a drop, interpreted as catastrophic mass extinction. We investigate the processes underlying these changes using the 'Elements of Metacommunity Structure' framework. The oldest metacommunity was characterized by species with wide environmental tolerances, and limited specialization and inter-species interactions. Structuring increased in the middle metacommunity, with groups of taxa sharing



synchronous responses to environmental gradients, aggregating into distinct communities. This pattern strengthened in the youngest metacommunity, with communities showing strong environmental segregation and depth structure. Thus, increased specialization and resulting competitive exclusion, not external factors, led to diversity loss in the terminal Ediacaran, revealing that the complex eco-evolutionary dynamics associated with Cambrian diversification were established in the Ediacaran.

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## A developing picture of nervous system evolution and body regionalization in the oldest fossil animals

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Soft-bodied fossils of the Ediacara biota record the unfolding of animal life. The identification of developmentally relevant characters and the underlying genetic pathways responsible for their expression in several Ediacara biota taxa reveals conserved regulatory elements. In particular, we find that metazoan specific pathways responsible for axial differentiation, musculature and a nervous system were likely present in these ancient forms. We also recognize a distinct lack of evidence for a head with concentrated sensory machinery or regionalization of functional body units – characteristic of a variety of bilaterian clades – in taxa from this period. This supports previous interpretations suggesting the independent evolution of a centralized nervous system in different bilaterian groups. Thus, members of the Ediacara biota occupy a critical transition between the establishment of axial polarity and a rudimentary nervous system but before the evolution of more complex and familiar patterning.

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## Fieldwork in the lowermost Triassic Panchet Formation of India sheds light on the early archosauromorph radiation

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Proterosuchidae represents the oldest diversification of Archosauromorpha and the genus *Proterosuchus* is the first new taxon to appear in the Karoo beds of South Africa after the Permian–Triassic boundary. Thus, the diversity of Proterosuchidae plays a key role in understanding the biotic recovery after the mass extinction. The taxonomic content of this clade is currently limited to five species of the latest Permian of Russia and the Induan of South Africa and China. In addition, a few isolated proterosuchid bones have also been reported in the Induan Panchet Formation of India. Thus, we conducted fieldwork in this unit to expand our knowledge of the Panchet proterosuchid. We collected multiple vertebrate specimens, including several proterosuchid bones, mostly vertebrae. The Panchet proterosuchid possesses a unique combination of character states, indicating that it represents a new species. The new proterosuchid taxon shares apomorphies with the Early



Triassic Russian species *Chasmatosuchus rossicus* and *Chasmatosuchus magnus*, which are absent in other proterosuchids. A phylogenetic analysis recovered these three species within Proterosuchidae, closer to each other than to other proterosuchids. Thus, the taxonomic diversity of Proterosuchidae is substantially expanded here, indicating a broader diversification of the clade in the immediate aftermath of the mass extinction.

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## Controls on the skeletal taphonomy of anurans from the Eocene Geiseltal Konservat-Lagerstätte, Germany

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The taphonomy of anurans from the Eocene Geiseltal Konservat-Lagerstätte from central Germany is poorly understood. Most specimens are partial skeletons, many of which are near-complete and well-articulated. Disarticulated, scattered bones and isolated, articulated limbs are relatively rare. All specimens ( $n = 140$ ) are orientated with the sagittal axis of the body parallel to bedding. Specimens vary markedly in completeness and articulation; most include cranial elements, femura and the vertebral column. Bones of the lower torso (e.g. ischium, urostyle) and distal parts of the limbs are often absent. Completeness decreases systematically towards the distal parts of the forelimbs. Articulation is generally high: where bones are present, they are usually articulated. Joints in the distal fore- and hindlimbs are fully articulated in nearly all specimens, although their overall skeletal completeness is low. Articulation values are slightly lower for joints in the torso and lowest for the ischium-hip joint. Comparative analysis of patterns in completeness and articulation in these specimens and in fossil anurans from the well-known Lagerstätten of Enspel (Oligocene, Germany) and Libros (Miocene, Spain) reveal an interesting mosaic of shared features and some locality-specific differences, suggesting the presence of several taphonomic controls, especially transport, regimes for decay, environment of deposition and biology.

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## A functional assessment of morphological homoplasy in the stem-gnathostome headshields

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Osteostraci and Galeaspida are two Siluro–Devonian stem-gnathostome lineages occupying a key phylogenetic position for resolving the nature of the jawless ancestor from which jawed vertebrates evolved. Both groups are characterized by the presence of rigid headshields that present a number of common morphological traits, in some cases hindering the resolution of their inter-relationships and their affinities with jawed vertebrates. Here we explore the morphological and functional diversity of osteostracan and galeaspid headshields, by means of geometric morphometrics and computational fluid dynamics, to better constrain the underlying factors that promoted the evolution of similar morphologies. Phylomorphospace, Mantel analysis and Stayton metrics support the existence of a high degree of homoplasy. Convergent species show comparable hydrodynamic performances and flow patterns over the body, denoting the independent



acquisition of similar morphofunctional traits and, potentially, equivalent lifestyles. Therefore, many characters currently used in the phylogenetic analysis of early vertebrates, and in scenarios regarding the origin of jawed vertebrates, are environmentally-driven functional homoplasies which may obscure their true phylogenetic pattern. Our results further support that passive control of flow around the body, as a possible adaptation to enhance locomotion, was widespread among stem-gnathostomes and should be considered as an important factor underpinning their evolution.

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### La Invernada–Cerro Overo, Rincon de los Sauces, a hot spot in dinosaur palaeobiodiversity in the Upper Cretaceous (Bajo de la Carpa Formation, Santonian) of Patagonia, Argentina

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In the ‘La Invernada–Cerro Overo’ area (Rincón de los Sauces, Neuquén Province, Argentina), continental sediments of the Bajo de la Carpa Formation (Santonian, Upper Cretaceous) crop out. This area has shown a great diversity of vertebrates, including dinosaurs, such as the abelosaurid theropod *Viavenator exxoni*, the titanosaur sauropod *Overosaurus paradisorum*, the ornithopod *Mahuidacursor lipanglei*, and crocodyliforms, such as the peirosaurid *Kinesuchus overoi*, together with turtles, fresh water fishes, dinosaur eggs and fragments of petrified wood (the flora in general is unknown for this formation). As a result of the fieldwork carried out in 2019, a small titanosaur specimen (MAU-Pv-CO-660), partially articulated and integrated by axial and appendicular elements, two theropod specimens (Megaraptoridae indet., MAU-Pv-CO-659 and Abelisauridae indet., MAU-Pv-CO-661), preserving cranial, axial and appendicular bones, and isolated ornithopod bones were recovered. Other isolated remains correspond to turtle shells, fish teeth and osteoderms, and teeth and a mandible fragment of crocodyliforms. This great diversity of fossils allows us to carry out multidisciplinary studies, including palaeoecological, sedimentological, taphonomic and palaeobiogeographic aspects. The integral approach of this vertebrate and plant association will allow a palaeoenvironmental and palaeobiological reconstruction of the Cretaceous ecosystem in northern Patagonia, around 85 Ma.



## Rhaetian (Late Triassic) ostracods (Crustacea, Ostracoda) from the offshore prolongation of the North Dobrogean Orogen into the Romanian Black Sea shelf

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The Triassic was a turning point in the evolutionary history of marine organisms. This period remains challenging for ostracods (Crustacea) with the temporary dominance of Platycopida, the explosive radiation of ornate Bairdiidae, or the residual occurrence of Palaeozoic taxa in deep waters up to the Late Triassic. Only rare complete Rhaetian marine ostracod assemblages have been documented to date. Here we describe the first known Rhaetian assemblages from a drill core on the Romanian Black Sea shelf. They developed on an outer shelf with relatively normal marine oxygenation and demonstrate that *Pokornynopsis*, forerunner of modern troglobitic taxa, may not have been troglobitic in the Triassic. The internal structure of Bairdiidae carapaces has been observed by X-ray micro-computed tomography scanning (CT-scan) and previously inaccessible characters now allow for the clarification of the taxonomy of this family. Two traces of drill holes of predatory origin add to the oldest known of such records in the Carnian. These traces illustrate the improvement of the abilities of drilling predators on meiofauna from the Carnian to the Rhaetian and further demonstrate that the deep roots of the Mesozoic marine revolution are to be found in the Triassic.

## Spanish and Indian mammalian community structures during the Neogene in relation to the Middle Miocene climatic transition

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The effect(s) of climate change on past mammalian communities is a frequent topic in palaeoecological research. The climatic evolution of the Neogene, with long-term cooling disrupted by the Middle Miocene Climatic Transition (MMCT; 17–14.75 Ma), arises as a suitable baseline to analyse the effects of these transcendent climatic changes on the mammalian community structures. Thus, a comparison between extinct faunas from coeval intervals from different geographic locations provides a global perspective to the climatic evolution. In order to analyse the climatic evolution of the Miocene communities associated with the Global Cooling Event, a comparative study incorporating palaeo-synecological methodology (cenogram analysis) was applied to several Neogene fossil sites from the Madrid Basin (Spain), Kutch Basin (India) and the Himalayan Foreland Basin (India). The ecological faunal data from 100 modern localities uniformly distributed all around the world was established as a comparative framework for palaeoenvironmental inference based on multivariate discriminant analysis of the dataset containing both modern and fossil mammals. Overall, our analysis provided valuable insights into the varied habitats occupied by diverse mammalian communities across distant geographic areas that transited the MMCT interval.



## First study of the bat fossil record from Macaronesia

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The Macaronesian Region is made up of a group of five mid-Atlantic volcanic archipelagos (the Azores, Madeira, the Savage Islands, the Canary Islands and Cape Verde), with island ages ranging from 0.27 Ma (Pico, Azores) to 29.5 Ma (Savage Islands). They are assigned to a single biodiversity hotspot, the Mediterranean Basin. Although the extant bats in Macaronesia are well known, with 15 species including three endemic species and two endemic subspecies, the fossil record is poorly known. The Canary Islands are the only archipelago with fossil records formed by four unstudied sites: Cueva de la Enladrillada (800BP ± 50 years, Holocene) in Tenerife, Cueva Honda del Bejenado (700 ka–750 ka, Pleistocene) in La Palma, Cueva de los Verdes in Lanzarote and Cueva Roja in El Hierro. Cueva de los Verdes has been dated by <sup>40</sup>Ar/<sup>39</sup>Ar to 21,000 ± 6,500 years (Pleistocene), and its remains identified as *Pipistrellus kublii*, a species that does not currently inhabit the island. Cueva Roja is dated to between 4,000–2,000 years BP (Holocene). Two endemic species from the Macaronesian have been identified here, *Plecotus teneriffae* and *Pipistrellus maderensis*, both species currently inhabiting El Hierro. At the other three sites, the bat remains are undetermined.

## Evaluation of the validity of the British Upper Jurassic pleurosternid turtle ‘*Pleurosternon portlandicum*’

**\*Andrea Guerrero and Adán Pérez-García**

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Pleurosternidae (Paracryptodira) is a relatively diverse group of freshwater turtles recorded from the Kimmeridgian (Late Jurassic) to the Albian (Early Cretaceous) of North America and Europe. The known diversity of Pleurosternidae in the European record has been markedly increased over the last few years, providing a remarkable advance in the knowledge of this lineage of stem turtles. However, phylogenetic relationships within this clade still generate controversy due to the scarce information available from several representatives. In this context, a detailed analysis of the problematic ‘*Pleurosternon portlandicum*’ is performed, considering new information about the inter-individual variability of the type species of the genus *Pleurosternon*, as well as the current knowledge about other members of the clade Pleurosternidae. The putative anatomical differences recognized by some authors between the holotype and only known specimen of ‘*Pleurosternon portlandicum*’ and the species *Pleurosternon bullockii* are evaluated. All of them are compatible with the intraspecific variability recognized for this last form. Therefore, ‘*Pleurosternon portlandicum*’ is justified as a junior synonym of *Pleurosternon bullockii*. As a consequence, *Pleurosternon bullockii* represents the only species of a European turtle currently reported in both the Upper Jurassic (Tithonian) and the Lower Cretaceous (Berriasian) record.





## The locomotory eco-morphology and evolution of body plan in Mesozoic marine reptiles

\***Susana Gutarra Diaz, Thomas L. Stubbs, Benjamin C. Moon and Michael J. Benton**

*University of Bristol, UK*

The aftermath of the end-Permian mass extinction provided ecological opportunity for many groups of reptiles, setting the beginning of the reptile dominance of the Mesozoic oceans. Clades like ichthyosaurs, thalattosuchians, sauropterygians, mosasaurs and turtles explored a remarkable diversity of ecological niches, becoming important components of aquatic ecosystems. Locomotion is one key aspect of the ecology, crucial for many biological functions such as foraging or migration. However, the evolution of locomotory adaptations in the ensemble of Mesozoic marine reptiles remains unexplored at a large scale. Here we present multivariate and disparity analyses based upon body proportions, body size and post-cranial features with inferred functional value in 126 species of Mesozoic marine reptiles. This analysis captures the main anatomical transformations across time and within clades, highlighting key transitions between drag and lift-based swimming modes in both the axial and appendicular spectrum. Our results show that locomotory disparity increased gradually during the whole Mesozoic and was highest in the Cretaceous, providing important insight into the dynamics of the Mesozoic ocean ecosystems.

## Filling the palaeobiogeographic gap in mysticetes evolution: new records of baleen whales from the Neogene of the Atacama region, southeastern Pacific, Chile

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Mysticetes are an iconic group of marine mammals that include the most gigantic microphagous vertebrates that have ever lived on Earth. The fossil record of baleen whales dates back to the early Oligocene, reaching a diversification and widespread distribution during the Miocene, being present along most of the oceans (Atlantic, North and southwestern Pacific, and the Mediterranean). However, along the southeastern Pacific, especially at the Chilean coast, the fossil record of baleen whales remains a mystery. In recent years we increased fieldwork efforts in the Neogene Bahía Inglesa and Coquimbo formations, and performed a critical review of fossil specimens from national collections. At least three groups of mysticetes were recognized from diagnostic materials (skulls; tympano-periotic): Cethotheriidae (c.f. *Herpetocetus* sp.), Balaenidae (*Balaena* sp.) and Balaenopteroidea (*Balaenoptera* sp.). Both the cethotheriids and balaenids records are the first for the southeastern Pacific coast, greatly expanding their geographical distribution during the late Miocene. In the case of balaenids, presently unrepresented in the area, the new record implies a contraction of the distribution of right whales after the Neogene. Contrasting with their scarce representation in coeval formations along the southwestern Atlantic coast of Argentina, balaenopteroids are the most abundant mysticete remains in Chilean Miocene deposits.



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## The taxonomy of *Ortheastheria shupei* (Stephenson, in Stephenson & Stenzel, 1952) from the Cenomanian (Cretaceous) of Texas, USA

**Thomas A. Hegna**

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Originally described as belonging to the living genus *Cyzicus*, *Ortheastheria shupei* is a small clam shrimp from the Red Branch Member of the Woodbine Formation in Texas, USA. It has an ornamentation pattern consisting of slightly sinuous lirae formed perpendicular to the growth band. This is the only known record of clam shrimp from the Cretaceous of the USA. The genus, *Ortheastheria*, is also known from China and Argentina, and it is used in biostratigraphic schemes in China. *Ortheastheria* is very similar to another genus, *Nemestheria*, which is classified in a separate subfamily (Jilinestheriidae vs Fushunograptidae). The diagnoses for both are useless for telling the genera apart – both diagnoses exploit vague language that allow the admission of a broad array of taxa within a narrow stratigraphic range. Progress on deciphering clam shrimp phylogeny will only progress with meaningful diagnoses that circumscribe monophyletic groups.

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## Traces of Toarcian oxia

**Liam G. Herringshaw**

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The Toarcian stage (Early Jurassic) is well known as a period of environmental and biological upheaval, with multiple analyses leading to the identification of a Toarcian oceanic anoxic event. As *in situ*, non-transportable sedimentary structures, trace fossils of burrowing marine organisms have a key role to play in elucidating this story. Having searched for (and not found any) macroscopic trace fossils in the organic-rich shales of the Whitby Mudstone Formation (North Yorkshire, UK), I interpret the seafloor sediments as having been inimical to soft-bodied infauna for around a million years. This ties in with the Toarcian OAE hypothesis. However, when comparing the ichnology of the Whitby Mudstone Formation with other Toarcian successions from around the world, I found a very different and much more complicated story. Some successions show bioturbation throughout the Toarcian, others show frequent bioturbated intervals; very few show an ichnological pattern like that of the Whitby Mudstone Formation. I conclude therefore that Toarcian seafloor oxygenation was common in many basins; the duration of anoxia was anomalously severe in the Cleveland Basin; there was not a single, oceanic, Toarcian anoxic event; and that robust analyses of marine palaeoenvironments must incorporate ichnology.

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## In the wake of the pandemic, how might public engagement with palaeontology address the challenges faced by society?

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Engaging and inspiring the public with palaeontology through, for example, museum programmes, fossil festivals, schools outreach and digital initiatives is a hugely rewarding way to share our understanding and knowledge, and to inspire others to participate. It is a well-established means by which we can support young people's learning, encourage them into STEM careers and raise the profile of palaeontology amongst wide audiences. Less



common is the consideration of the role that public engagement with palaeontology might play in addressing the wider challenges faced by society. The pandemic has exacerbated already rising levels of social inequality across health and education, while recent events across the world have highlighted shocking examples of discrimination and social exclusion. Using examples, we demonstrate how the approach we take at the Sedgwick Museum involves considering how we respond to the broader needs of our audiences, and how our public engagement and work with schools can contribute to the challenges they are facing, be it discrimination, lack of opportunity, social isolation or poor health and wellbeing.

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## The evolutionary decay-clock: persistence versus decay of evolutionary biotas through the Phanerozoic

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We introduce a new measurement framework capturing the temporal persistence versus decay of sets of co-occurring species, called the evolutionary decay-clock. The process of evolutionary decay is the decrease in similarity between existing species sets as the time separating these sets increases. We present two specific measures: the probability of co-occurrence between species existing at two times, calculated using a machine learning embedding method, and the fraction of species shared between time windows, exhaustively calculated from fossil occurrence data. The process of evolutionary decay was tracked, looking back through time from a given base time, until the similarity of species sets falls below a given threshold, here  $\leq 10\%$  probability of co-occurrence or fraction of shared species. Measures of evolutionary decay calculated from global Paleobiology Database fossil occurrences for the Phanerozoic show the following results: the average time to over threshold decay in shared species fractions across the Phanerozoic was 19 Ma (co-occurrence probability 30 Ma); mass extinctions lead to rapid evolutionary decay, as they erode an original species set; what we call ‘mass radiations’ also cause rapid evolutionary decay as they dilute an original species set; and the Quaternary started with lower than average species persistence.

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## The flying ability of *Quetzalcoatlus northropi* in a reduced gravity

**Stephen W. Hurrell**

*Independent*

The envisaged flying ability of the gigantic *Quetzalcoatlus northropi* pterosaur has produced ongoing debate since its first discovery, mainly because aeronautical calculations show it is too large to produce continuous powered flight in our gravity. This problem has encouraged a number of authors to suggest that continuous powered flight might be possible in a reduced gravity. This study quantifies the flying ability of a *Quetzalcoatlus northropi* in a reduced gravity of 0.62 g (6.0822 m/s<sup>2</sup>). The results show that *Quetzalcoatlus northropi* was capable of producing continuous powered flight in this reduced gravity, allowing its flying ability to be comparable with the largest flying animals of today.



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## X-ray tomography and computer modelling of radiolarian skeletons: Bazhenov Fm., Late Jurassic–Early Cretaceous, Western Siberian Basin

**Alexandra Isaeva, Yu. A. Gatovsky and Georgy A. Kalmykov**

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Radiolarians are the matrix-forming silicious member of the petroleum-producing Bazhenov Formation in the Western Siberian Basin, and are a component of continuous potential reservoir. The thermal overprint of these rocks is from low to moderate, favouring good preservation of radiolarian fossils. A number of radiolarites samples were collected from deep cores of different localities in Western Siberia. X-ray tomography and computer modelling of washed radiolarian skeletons from the Bazhenov Formation (dated to the Late Jurassic–Early Cretaceous) were used to visualize the structure of individual species and digitally reconstruct skeletons. A set of images acquired by rotating an X-Ray source around the specimens was subsequently converted to a voxelated 3D file to reveal exterior and interior details and geometrical features of the specimens. Computer modelling was used for taxonomic study of radiolarian assemblages, for dating and reconstructing palaeogeography and palaeobathymetry of the area. The results were used to build a detailed stratigraphy of the Bazhenov Formation and to establish some regularities and the spatial concentration of radiolarian occurrence.

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## A giant multisegmented arthropod from the Burgess Shale highlights the complexity of Cambrian suspension feeding niches

**\*Alejandro Izquierdo-López<sup>1,2</sup> and Jean-Bernard Caron<sup>1,2</sup>**

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‘Odaraiids’, an informal group of hymenocarine Cambrian bivalved arthropods, including *Nereocaris*, *Odaraiia* and *Fibulacaris*, are characterized by reduced or absent antennae and a highly multisegmented body. Here we present a large new ‘odaraiid’ bivalved arthropod from the Burgess Shale Marble Canyon area in Kootenay National Park, British Columbia, Canada. With a body size of *c.* 20 cm, this new form represents the biggest Cambrian bivalved arthropod with soft tissues on record. This species has a short kidney-bean shaped carapace – greater in height than length – covering less than a quarter of the total body length. An elongate anterior sclerite covers the cephalic area, containing a pair of wide bilobate eyes and a pair of short but stout antennae. The thorax is elongated, with *c.* 20 homonomous segments bearing undifferentiated biramous limbs, with endopods subdivided into *c.* 20 podomeres and long elliptical exopods. The body terminates in a telson with two paddle-shaped caudal rami. We regard this species as a suspension feeder. Its distribution overlaps both geographically and stratigraphically with other suspension feeder ‘odaraiids’ (*e.g.* *Fibulacaris*), suggesting that size difference may have allowed ecologically similar species to coexist through niche partitioning.



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## An eye for a tooth: was *Thylacosmilus* really a “marsupial sabertooth” predator?

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*Thylacosmilus atrox* (Metatheria: Sparassodonta: Thylacosmilidae), from the Pliocene of Argentina, is popularly known as the “marsupial sabertooth,” and is well-known as a classic example of evolutionary convergence. However, its anatomy is anomalous for a sabertooth predator: it lacks incisors; the canines are triangular not blade-shaped; the jaw halves are unfused; there is little evidence for muscles exerting a powerful head strike; and it was non-cursorial, lacking retractile claws. Quantitative studies confirm distinct differences from placental sabertooths. Craniodental characters distinguish sabertooths from conical-toothed cats, but *Thylacosmilus* is distinctly different from all. Finite element analysis shows *Thylacosmilus*' skull is less stress-resistant to stabbing than the sabertooth *Smilodon*, but more resistant to a canine pulling-back motion. Dental microwear texture analysis shows *Thylacosmilus* ate soft food, either flesh or internal organs, but the postcanine teeth have blunt wear, not the shearing wear of meat-eaters. We conclude that *Thylacosmilus* was morphologically ill-equipped for proposed sabertooth predatory behaviour, although its actual mode of life is more difficult to determine. The lack of incisors, together with a domed palate, are suggestive of a large tongue; we propose that *Thylacosmilus* was a specialized scavenger, opening carcasses with its canines, and using its tongue to extract the internal organs.

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## Distal humeral anatomy indicates locomotory divergence between the extinct kangaroo *Protemnodon* and modern large kangaroos

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*Protemnodon* (Macropodoidea: Macropodidae) was a genus of giant Pleistocene kangaroo that achieved an estimated body mass up to 166 kg, almost double that of the largest extant kangaroos. Biomechanical constraints to hopping locomotion imposed by size pose questions about *Protemnodon*'s locomotory behaviour. *Protemnodon*'s postcranial anatomy, with long arms and short feet, is indeed unlike any large extant kangaroo. Nevertheless, the hopping ability of *Protemnodon* has rarely been addressed. Here we test the hypothesis that *Protemnodon* might have been primarily quadrupedal, supporting more weight on its forelimbs than extant large kangaroos. We use 2D geometric morphometrics to capture the shape of the distal humerus in extant marsupials of known locomotor mode, and show that distal humeral anatomy is distinct between terrestrial and arboreal forms. Including kangaroos in the analysis shows that unlike most other kangaroos, *Protemnodon* had limited forearm mobility with a distal humeral anatomy more similar to terrestrial taxa (specifically wombats), echoing previous studies on the proximal humerus. We infer from our results that *Protemnodon*'s forelimbs were more adapted to weight-bearing and hence stabilization for terrestrial locomotion than those of extant kangaroos, indicative of a greater degree of quadrupedal locomotion and less reliance on hopping.



## New azhdarchid pterosaur material from the Campanian Two Medicine Formation of northwestern Montana

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Azhdarchids are unique amongst pterosaurs not only for their enormous size, but also because of their frequent occurrence in terrestrial settings. Due to the relative rarity of azhdarchid material, understanding of the flight mechanics and palaeoecology of an animal of this scale remains controversial. The Campanian Two Medicine Formation of Montana, USA has produced some pterosaur material including the type specimen of the small-bodied *Montanazhdarcho*. In 1979, multiple large pterosaur elements, including a humerus, radius and carpals, were discovered at an associated site, Pterosaur Hill. These elements were identified as belonging to an indeterminate azhdarchid. Additional elements, including a large metacarpal IV, were surface collected in subsequent summers but never described. It was not until 2019 that quarrying at the site was undertaken, yielding nine new elements, including two identifiable wing-digit phalanges and a partial metacarpal, assessed here. Though they have undergone minor taphonomic crushing, many of the elements are three-dimensionally preserved. These new elements place this specimen among the largest and most complete of the North American azhdarchids, and include elements not previously described for this group. This specimen predates the Maastrichtian *Quetzalcoatlus* and may pertain to the large Campanian azhdarchid *Cryodrakon* or a new taxon.

## Modern clam shrimp ornamentation patterns as a key to the past

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Modern clam shrimp are classified based on their soft parts – their carapaces are ignored. Fossil clam shrimp are classified based on the morphology of their carapaces – in most instances, soft-parts aren't present. Thus, to unite the two systems of classification, we must thoroughly document the carapace ornamentation patterns of modern clam shrimp. Using the phylogenetic framework of Schwentner *et al.* (2020), we sampled modern clam shrimp from across the tree. Outside of Spinicaudata, Laevicaudatans have smooth, unornamented carapaces. Spinicaudatan carapaces vary. Most limnadiids have either smooth growth bands or weak, shallow-sided depressions. *Limnadopsis* has strong depressions. Leptestheriidae has a wrinkled texture. Cyzicids are variable with *Cyzicus* having a punctate pattern and *Ozestheria* having a ridge pattern. *Cyclestheria* has regular shallow depressions. These regular, shallow depressions may be a basal feature of Onychocaudata, and related to the underlying epidermal cells as in ostracods. There are many patterns present in fossil taxa that have no living representative.



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## Thylacocephalans from the La Voulte-sur-Rhône Lagerstätte (Ardèche, France): taxonomy, anatomy and palaeobiology

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Known from at least the Silurian to the Cretaceous, Thylacocephala is an enigmatic fossil euarthropod ingroup, often associated to Eucrustacea. Despite the remaining questions on their anatomy and tagmosis, thylacocephalans are characterized by key anatomical features: a folded shield enveloping the body, hypertrophied compound eyes, three pairs of raptorial appendages, a trunk made of eight up to 22 segments bearing appendages, and eight pairs of gills. Well-known for its diversity in euarthropods, the Jurassic La Voulte-sur-Rhône Lagerstätte (Callovian) has yielded remains of four species of Thylacocephala: *Dollocaris ingens*, *Kilianicaris lerichei*, *Paraostenia vouldensis* and *Clausocaris ribeti*. The revision of type and previously described specimens as well as the study of unpublished specimens allowed us to precisely determine the diversity of La Voulte thylacocephalans. Based on type specimens, we reassigned *Clausocaris ribeti* to *Ostenocaris ribeti* nov. comb. and we described a new species of *Clausocaris*. *Mayrocaris* is reported for the first time in the La Voulte Lagerstätte. Finally, a probable juvenile stage is described for *Paraostenia vouldensis*. This taxonomic work has led to the description of numerous anatomical details: cephalic, raptorial and trunk appendages, telson, shield ornamentation, eyes. Such information leads us to advance hypotheses on the palaeobiology and body organization of thylacocephalans.

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## Variation in frontal sinuses of selected Late Miocene bovids from Greece, via computed tomographic methods

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*National and Kapodistrian University of Athens, Greece*

The crania of Bovidae display a distinct and variable morphology as far as it concerns their frontal sinuses. Frontal sinuses, as part of the paranasal sinuses, are believed to form pneumatic spaces that develop opportunistically where bone is not mechanically necessary, leading to reduction of the skull mass, and so, improvement of its performance. However, these features have not been widely or virtually studied and their function has not yet been clarified. Herein we provide a description of their internal cranial structures based on three-dimensional reconstructions extracted by high resolution X-ray computed-tomography imagery. We demonstrate the variation in frontal sinus dimension and occupation of their volume in the skull, in order to determine the association between sinus dimension and frontal bone. Therefore, the crania of five fossil species from the Late Miocene (middle Turolian, MN12) locality of Pikermi, Greece – *Palaeoryx pallasii*, *Protoryx carolinae*, *Tragoportax amalthea*, *Protragelaphus skouzezi* and *Sporadotragus parvidens* – were examined using computed tomography to provide a volumetric assessment of the cranial sinuses.



## Southern Pachycormiforms: breaking the nordocentric mindset with southerly pachycormid exposures and origins

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Occupying a key-position within Actinopterygii as part of the Holostei–Teleostei transition, pachycormids are critical to understanding teleost origins. Arising in an explosive diversification in the Toarcian, pachycormids developed into two recognized tribes of ‘toothless’ (suspension-feeding) and ‘tusked’ (carnivorous) forms, persisting until the end of the Cretaceous. As a group they range greatly across three orders of magnitude, exhibiting a trend of reduced ossification for the skeleton with the increasing adult size of a given pachycormid taxon. Discoveries brought to light over the last decade have increased both the geographical and palaeogeographical extent of these animals in terms of their northern and southern limits, reflecting an ability to dwell in comparatively extreme environments. In the southern hemisphere, specimens from the Argentinian Tithonian have added *Notodectes* and *Leedsichthys* to South America’s record of Chile’s Oxfordian Antofagasta occurrence of the latter genus. Antarctica has yielded not only Tithonian cf. *Asthenocormus* material and a new suspension-feeding taxon, but also a Maastrichtian specimen. Finally, Australia has produced three Albian taxa (one a suspension-feeder), and a further Cenomanian–Coniacian specimen that may also prove new. These discoveries broaden our palaeogeographical understanding of the extent of this group, as well as providing clearer signals of their dispersal history.

## Hydrodynamic factors are a strong constraint on ichthyopterygian and sauropterygian jaw morphology

**\*Rob Loveday**, **William Deakin**, **Thomas Smith**, **Emily J. Rayfield** and **Philip C. J. Donoghue**  
*University of Bristol, UK*

Ichthyopterygians and sauropterygians were key members of Mesozoic oceans, but there has been little attempt to quantify the trade-offs they made between competing morphological constraints in becoming secondarily aquatic. Mandible shape should be highly determined by function and therefore enable such trade-offs to be isolated. Research was conducted to investigate whether hydrodynamic streamlining requirements constrain mandible morphology in Ichthyopterygia and Sauropterygia. Lateral mandible profiles were used to create an empirical morphospace, from which a theoretical morphospace was extrapolated. The hypothetical jaw shapes were subjected to 2D finite element analysis to assess strength via von Mises stress, speed of opening/closure via rotational inertia, and hydrodynamic performance via frontal area incurred drag. The resulting adaptive





landscapes show mandible morphologies of fast-swimming pelagic predatory taxa are poorly functionally optimized but strongly optimized for hydrodynamic performance. Conversely, shallow-water durophagous taxa were highly optimized for jaw strength, but poorly for hydrodynamics. A phylomorphospace was also constructed that showed a possible phylogenetic constraint, possibly reflecting niche partitioning or other factors. The results suggest hydrodynamics are a prime constraint on functional jaw morphology for fast-swimming taxa while the opposite is true for slow-swimming durophagous organisms, a trend that may apply to other secondarily aquatic tetrapod clades.

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## Evaluation of substrate affinities among phacopid trilobites in a phylogenetic framework

**\*Namiko Machida and James C. Lamsdell**

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Trilobites are an ecologically and morphologically diverse arthropod group occurring throughout the Palaeozoic with an excellent fossil record. This study focuses on a relationship between ecological affinity and species evolution among the trilobite family Phacopidae from the Ordovician–Devonian periods. Environmental factors are important as external regulations on morphological evolution; however, few studies have quantitatively tested their association within a phylogenetic framework. To see the distribution of substrate affinities (*i.e.* calcareous *vs* siliciclastic) along with phacopid evolutionary history, a phylogenetic analysis was conducted by compiling existing phacopid character matrices, which was followed by an overlaying of quantified affinity values at a species level. The data of substrate affinities are compiled from the primary literature and online databases such as the Paleobiology Database, Fossilworks and iDigBio, then a ratio of substrate types was taken for each species to calculate the affinity. The preliminary result suggests that the substrate affinities are dominated by carbonate settings, while a few species with strong siliciclastic affinities are seen in the Devonian period among phacopid trilobites. This study will be used to evaluate environmental constraints on the trend of morphological transitions such as heterochrony in future studies, which will contribute to our understanding of fundamental evolutionary processes.

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## Early Khvalynian ostracods in the northern Caspian region

**Radik Makshaev and Alina Berdnikova**

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The northern Caspian region (Middle and Lower Volga sections particularly) is unique for our understanding of Caspian history and correlation of palaeogeographic events with the glacial–interglacial rhythm and global/regional climate changes. We carried out microfaunal analyses on chocolate clay deposits and found representatives of several ostracod families – widely represented were Candonidae, Cyprididae, Leptocytheridae and Loxoconchidae. Sand sediments rarely contain a great variety of ostracods. Only *Leptocythere pirsagatica* (Liv.) is distinguished. According to Yakhimovich *et al.* (1986) and Sedaykin *et al.* (1987), more than 80 species of ostracods were described in the Lower Khvalynian deposits. The dominant ostracod species are *Caspiolla gracilis* (Liv.), *Cyprideis torosa* (Jones), *Leptocythere bacuana* (Liv.), *L. marta* (Liv.), *L. quinquetuberculata* (Schw.), *Loxoconcha umodensa* (Mand.), *L. lepida* (Step.), *L. gibboida* (Liv.) and *Paracyprideis enucleata* (Karm.). The ecological conditions of these species are diverse. In general,



the formation of the observed complex fauna took place under unstable hydrological conditions in a shallow basin. According to our data, Early Khvalynian basin salinity could have varied from brackish water (2–10 ‰) to slightly brackish water (0.5–3 ‰) conditions; typical marine species would be unable to live here because of insufficient salinity and freshwater ones.

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## A new approach to the step method for fractal ontogenies

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Fractal complexity is the number and configuration of self-similar subdivisions within a geometric entity. True fractals cannot exist in three dimensions; ammonite sutures sufficiently mimic fractals to be quantified geometrically via a method based on fractals. The step method, gleaned from the measurement of irregular coastlines, has historically been used to measure complexity of ammonite sutures. By generalizing the suture into its finite measurement intervals (steps), value is determined for the fractal dimension,  $D(f)$ , of that suture. However, a smaller interval, or step length, yields greater accuracy: over ontogeny, length, as well as further subdivision is added to the suture line of ammonites. Using the old step method, measuring ammonites (or coastline) over an ontogenetic sequence, plottable values that do not accurately depict the absolute rate of ontogenetic change in complexity. This is due to an inconstant step length that decreases proportionally to the subject it is measuring as size increases during ontogeny. I circumvent the dimensional aspect of step-method measurement instead by fractal complexity,  $C(f)$ , and demonstrate its greater accuracy in measuring ontogenetic change. The new method is proportional rather than dimensional, allowing it to remain constant relative to the stage of growth, and demonstrating the true rate of change.

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## UV-B radiation was the Devonian–Carboniferous boundary terrestrial extinction kill mechanism

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There is an unexplained terrestrial mass extinction at the Devonian–Carboniferous boundary (359 million years ago). The discovery in East Greenland of malformed land plant spores shows that the extinction was coincident with elevated UV-B radiation demonstrating ozone layer reduction. Mercury data through the extinction level proves that, unlike other mass extinctions, there were no planetary-scale volcanic eruptions. Significantly, the Devonian–Carboniferous boundary terrestrial mass extinction was coincident with a major climatic warming that ended the intense final glacial cycle of the latest Devonian ice age. A mechanism for ozone layer reduction during rapid warming is increased convective transport of naturally produced ozone destroying compounds. Hence, ozone loss during rapid warming is a possible process that is inherent to the Earth system. This leads us to the unavoidable conclusion that we should be alert for such an eventuality in the future warming world. Other suggested and now restated causes include a cosmic ray blast from an exploding star, *i.e.* a supernova.



## Neuroanatomical study and the sensory capabilities of the European Upper Cretaceous stem turtle *Kallokibotion bajazidi*

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*Kallokibotion bajazidi* is a putative terrestrial turtle from the Upper Cretaceous of the Haţeg Basin, Romania. It was described in the 1920s by the famous palaeontologist Franz Nopcsa through partial remains of several individuals. This poorly-known form was identified as an enigmatic taxon until the end of the twentieth century, but recent studies have provided new information significantly improving our knowledge of it. New and well-preserved remains of this turtle, including a relatively complete skeleton, allowed confirmation of its identification as a stem turtle, recognized as being closely related with the crown Testudines. The first three-dimensional osteological cranial model, and also the neuroanatomical reconstruction of this bizarre turtle, are presented here. These models have been generated from CT-scans of the best-preserved skull known so far for the species and the basicranium of another individual. This study allows us to improve our knowledge of the cranial osseous anatomy of the species, supporting its phylogenetic position as the sister taxon of the crown Testudines. A detailed comparison between the neuroanatomical structures related with the endocast, nasal cavities and labyrinthine system of *Kallokibotion bajazidi* and other stem turtles allows us to evaluate its interpretation as a terrestrial form.

## Identifying discrete fossiliferous levels using artificially intelligent systems

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Qualitative approaches have historically been used for the separation of discrete fossiliferous levels at archaeological or palaeontological sites with no clear stratigraphic horizons. These approaches generally rely on the interpretation of two-dimensional transversal and longitudinal projection planes. However, these interpretations can often be conditioned by the analyst's perspective. In order to create unbiased, discrete separations, Machine Learning algorithms have been used for pattern recognition tasks. The method can be divided into three main steps: unsupervised Machine Learning for density-based clustering; expert-in-the-loop Collaborative Intelligence Learning in order to integrate geological data; and supervised learning for the final fine-tuning of fossiliferous level models. These techniques have been tested at two sites of the Batallones Butte palaeontological complex (Late Miocene, Madrid, Spain): Batallones-3 and Batallones-10. Three discrete fossiliferous levels have been successfully identified in both Batallones-3 and Batallones-10.



## Marine origination rates linked to interactions of past temperature trends with short-term climate change

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Biodiversity dynamics are shaped by a complex interplay between current conditions and historic legacy. While a simple relationship is often used to link evolution with temperature, short-term climate change likely interacts with previous temperature trends when influencing the pace of origination. Such palaeoclimate interactions have been demonstrated for extinction risk, but the effect on evolutionary dynamics is untested. Here we show that origination probability in marine fossil groups is largely affected by palaeoclimate interactions. Short-term cooling adding to a long-term cooling trend increases the origination probability by 23.7 %. This large effect is consistent through time and all studied groups. Our results demonstrate that biodiversity is controlled by a complex array of ecological and evolutionary factors, with mutual interactions. The mechanisms of the detected effect might be manifold but are likely connected to eustatic sea-level drop caused by cumulative global cooling. Accounting for complex interactions using a dynamic modelling approach improves existing models and enables a better mechanistic discernment of processes that control biodiversity.

## The first digital cranial endocast of an ancestor of Steller's sea cow

*Dusisiren dewana*

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Sirenia is an order of mammals and includes two extant families, Dugonidae and Trichechidae. The “extant” Dugonidae includes two subfamilies, Dugoninae and Hydrodamalinae. Hydrodamalinae includes *Dusisiren* that appears to be used to feed on kelp at or near the surface, and *Hydrodamalis* is more derived than *Dusisiren*. *Dusisiren dewana* is known for the species that revealed intermediate teeth characteristics between *Dusisiren* and *Hydrodamalis*, but there is little information about their palaeoecology. Three-dimensional digital technology allows us to “see” brains or sensory organs of extinct animals. Notably, brain endocasts are correlated to palaeoecology and the evolution of extinct animals. Here we report on the digital endocast of *D. dewana* to understand the palaeoecology evolution of Hydrodamalinae. As a result of comparing *D. dewana* with other sirenians, *D. dewana* had character combinations with mosaic neuroanatomical features among Hydrodamalinae. *D. dewana* shared many characters with *Hydrodamalis*, but many characters with more basal dugonids too. This feature is consistent with their dental evolution. *D. dewana* had a tiny olfactory bulb, unlike other hydrodamalinae sea cows. These features indicate that olfactory retraction preceded the teeth loss.



## Reconstruction and functional morphology of the oviraptorosaurian theropod cranium

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Oviraptorosaurians were a theropod dinosaur group from the Cretaceous of North America and Asia that evolved robust toothless beaks and highly modified pneumatic skulls, leaving their cranial function, diet and ecosystem position uncertain. Three-dimensional models created from CT scanned oviraptorosaurian crania were retrodeformed to an in-life condition by removing the effects of taphonomic damage using the specialist software packages Avizo and Landmark. The oviraptorids *Citipati* and *Khaan*, and the earliest-diverging oviraptorosaurian *Incisivosaurus*, were subjected to finite element analysis (FEA) to assess how loading conditions resulted in patterns of stress and strain within their crania. The more derived *Citipati* and *Khaan* crania appear adapted for a strong symmetrical bite in multiple positions; greater stress is produced when force is applied asymmetrically. In contrast, the early diverging oviraptorosaurian *Incisivosaurus* exhibits higher and more generalized stress patterns, and its prominent incisor-like teeth appear adaptive for feeding. Initial results hint at a transition from a generalized feeding style in early oviraptorosaurians, towards a more specialized condition favouring stronger bite forces in later-diverging forms. Additional models informed by volumetric reconstructions of cranial musculature may reveal how complex functional patterns were throughout the Oviraptorosauria and more broadly elucidate the evolution of dietary diversity in theropod dinosaurs.

## A preserved disassociated rhamphotheca of the Cretaceous bird *Confuciusornis*

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*Confuciusornis* is the earliest known avialan to have a fully edentulous beak which evolved convergently to crown birds. We report a new specimen of *Confuciusornis sanctus* whose rhamphotheca (the horny covering of the beak) is visibly disassociated from the skull when imaged using laser-stimulated fluorescence (LSF). Three of the six known confuciusornithid rhamphothecae are disassociated from the skull while the skull remains attached to the body. This state is not reported in any decay studies of crown birds. This suggests that confuciusornithid rhamphothecae were anchored more loosely to the underlying bone than in crown birds. Reconstructing the rhamphotheca lets us confirm *in vivo* preservation of two other confuciusornithid rhamphothecae and comment on their extent and shape. Cranial extent of the rhamphotheca is consistent with crown birds, but the confuciusornithid rhamphotheca projects less post-rostrally than crown birds with the same rostral vascularity. Rhamphotheca curvature relative to the bone is like crown birds' in *C. sanctus* and *Eopengornis zhengi*, but like some turtles in *Confuciusornis dui*. Together, this evidence paints a picture of the confuciusornithid beak as a structure reminiscent of that in crown birds, but distinct in ways likely related to differing developmental pathways as relics of the groups' distinct evolutionary histories.



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## Early Palaeozoic Discinocarina and a new hypothesis of the appearance of cephalopod jaws

**Aleksandr A. Mironenko**

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The jaws of Cephalopoda are a unique structure among molluscs; however, their origin still remains a mystery. Whereas cephalopods appeared at the end of the Cambrian, their oldest jaws have been reported to date from the Upper Devonian, and belonged to ammonoids. However, in the Silurian and Devonian strata, initially organic structures related to cephalopods can be found. The most widely known among them is *Aptychopsis*, several specimens of which were found in the apertures of orthocerid shells. These structures had initially been interpreted as phyllopod crustaceans (suborder Discinocarina), but now their Devonian representatives are thought to be the lower jaws of ammonoids. Silurian discinocarins, including *Aptychopsis*, are considered as opercula of ammonoid ancestors – orthocerid nautiloids. However, it is unlikely that very similar structures appeared in the same evolutionary lineage twice, but in different body parts and for different purposes. It seems more possible that the Silurian discinocarins are basal proto-jaws. Here I propose a new hypothesis, according to which initially organic plates arose on the front of the nautiloid head around the radula to protect them not from predators, but from resisting prey. They had some mobility to release the radula and gradually evolved into a jaw apparatus.

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## Three-dimensional cameral membranes in the phragmocones of Jurassic ammonites

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Three-dimensional initially organic membranes can sometimes be found in well-preserved ammonoid phragmocones. Several types of membranes have been described to date. They are well studied in Permian and Triassic ammonoids but, until now, have been poorly known in Jurassic ammonites. I have studied membranes in Jurassic (Middle Callovian and Upper Volgian) ammonites from seven localities of Central Russia. In the shells of Jurassic ammonites, membranes have appeared starting from the first chamber of the phragmocone. In the earliest chambers they were located under the siphuncle tube, whereas in later whorls they were positioned by the sides of the siphuncle. The most common membranes in the studied ammonites belong to a previously unknown type and are herein called diagonal membranes. An unusual set of membranes was found in one shell of an Upper Jurassic ammonite of the genus *Kachpurites*. Most likely these membranes are phosphatized pseudosepta. The study of this finding and of other Jurassic membranes allows us to put forward a new hypothesis for the formation of cameral membranes, according to which all types of membranes were formed by adhesion of pseudosepta during pumping of water from the newly formed chamber.



## Quaternary megafauna from northwestern Iran

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The Moghan Basin (Dasht-e-Moghan) represents a small enclave of the Kura intermontane trough, which extends mainly in the northern and northeastern parts of the Moghan area in the Caucasus region. Although elephantids, equids and rhinocerotids are known by fragmentary material from the Quaternary of western, eastern and central Iran, recent discoveries in the Moghan area have brought new opportunities for better understanding of the Quaternary megafauna in Iran. Well-preserved cranial specimens of proboscideans and bovids have been discovered in four localities from the western, central and eastern parts of the Moghan area. The fossils are preserved in fluvial deposits and occur within fine grained sediments in the much coarser conglomerate settings. The molars of the proboscideans indicate the presence of two species, an anacid (*Anancus arvernensis*) and an elephantid (*Mammuthus meridionalis/trogotherii*). A large bovid skull with robust horns (*Leptobos*) with several postcranial elements is among the other fossils. The fossils are typical of the Eurasian Quaternary megafauna, indicating an early to late Pleistocene age for fossil localities. Similar occurrences can be traced in the Caucasus, Anatolia and eastern Mediterranean regions. The findings indicate the high potential of megafauna's preservation in this region of Iran and mark this area as the best place for further investigations.

## Palaeophytogeographical patterns across the Permian–Triassic boundary

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It has long been recognized that terrestrial floras underwent major and long-lasting changes during the Permian and Triassic, some of which have been attributed to the end-Permian mass extinction. However, these changes are still poorly understood with regard to the late Permian and Early Triassic. In particular, the impact that ecological disturbances around the Permian–Triassic boundary had on the composition and palaeogeographical distribution of land plant communities needs to be scrutinized. We analyse this impact based on fossil floras from across the world, covering the Wuchiapingian to Ladinian time interval. The plant assemblages are assigned to biomes representing particular environmentally-controlled community types. Variations in the distribution of biomes between stages indicate shifts in the environmental parameters affecting terrestrial floras, and provide insights into population turnover dynamics. A substantial shift towards increasing seasonality and a reduction of biome diversity occurs in the earliest Triassic and stabilized throughout the Middle Triassic. However, results also show that the stratigraphically and (palaeo-)geographically unequal distribution of sampled localities constitutes an important limitation for this kind of analysis.



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## New strides in macropodoid locomotion

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Studies of extinct kangaroos (Macropodoidea) have indicated a divergent locomotory mode for members of the subfamily Sthenurinae, proposing bipedal striding rather than hopping. Here we investigate the potential relationship between locomotory mode and the relative proportions of the macropodoid calcaneum. Ratios of the relative length of the calcaneal heel were measured for 88 extant and extinct macropodoid taxa (Pleistocene sthenurines and the basal Miocene sthenurines *Hadronomas* and *Rhizosthenurus*). Extant taxa were categorized by locomotor mode: hoppers, habitual quadrupeds (e.g. tree kangaroos) and obligate quadrupeds (the musky rat-kangaroo). Calcaneal ratios are associated with locomotory mode, with quadrupedal taxa having relatively shorter calcaneal heels. Calcaneal heel length scales with positive allometry in extant macropodoids, but isometric scaling or slight negative allometry in sthenurines. The long calcaneal heel of hoppers – a lever arm for the gastrocnemius (calf) muscle – likely counteracts torque experienced at the ankle while locomoting with an obligatorily crouched posture. Walking sthenurines would have had less need to counteract torque around the ankle joint, as reflected by their shorter calcaneal heel, resembling that of the quadrupedal kangaroos. Our results support the hypothesis of sthenurines as poorly-adapted for hopping locomotion. *Hadronomas* (but not *Rhizosthenurus*) shows calcaneal proportions like the Pleistocene sthenurines.

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## Middle Cambrian fossils of Nixon Gulch: taphonomy and taxonomic information

\***Hunter Olson**

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Relatively little is known about the organisms that lived in Montana during the Middle Cambrian (Miaolingian series, Wuliuan stage; ~509–504 Ma). Although rocks from this time are exposed throughout the state, outcrops from southwestern Montana remain largely unexplored. Here I describe a sample of fossils at the Museum of the Rockies (MOR) which were collected from the Wolsey Shale, near Manhattan, Montana. The Wolsey Shale is a lithostratigraphic unit that is a transitional unit between the Flathead Sandstone and the Meagher Limestone. The Wolsey Shale correlates in part with more notable Cambrian deposits such as the Spence Shale Member of the Langston Formation in Idaho and Utah and the Stephen Formation (Burgess Shale) in British Columbia. Members of four phyla – Arthropoda, Branchiopoda, Echinodermata and Porifera – are preserved in the MOR Horseshoe Hills sample, including taxa previously undescribed from Montana. Continued study of these fossils will increase understanding of how middle Cambrian taxa transitioned between the Burgess Shale (British Columbia) and the Spence Shale (Utah), an east–west palaeographic transect of the Cordilleran seaway.

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## Systematic revision of the Quaternary rhinoceroses of India

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A systematic revision of the rhinoceros material attributed to the genus *Rhinoceros* from different Quaternary localities of India, mainly the type specimens, is provided here, resulting in a new potential interpretation of the diversity and evolution of the fossil





rhinoceroses. Four species belonging to the genus *Rhinoceros* are considered here as valid taxa: *Rhinoceros platyrhinus*, *Rhinoceros sivalensis*, *Rhinoceros unicornis* and *Rhinoceros sondaicus*. A phylogenetic analysis based on 214 cranial and dental characters suggests that these four species are closely related and that “*Rhinoceros*” *deccanensis* is more closely related with northern Eurasian rhinoceroses than to the Indian or South East Asian species. The type material of *R. karnuliensis* closely resembles *R. sondaicus* and the Kurnool rhinoceros is here considered a younger synonym of the extant Javan species. *R. platyrhinus* displays grazer-like adaptative features of the teeth and it results as a sister taxon of the extant *R. unicornis*. The coexistence of two or more species in some areas, such as the Siwaliks, could be related with different specializations in diet.

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### A systematic revision of *Preaulophyseter gualichensis* (Cetacea, Odontoceti, Physeteroidea) from Argentinian Patagonia, and the phylogenetic signal of tympano-periotics in Physeteroidea

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Sperm whales (Physeteroidea) are known today from only two genera of disparate odontocetes: the largest toothed whale known (*Physeter macrocephalus*) and small-sized forms (*Kogia* spp.). In contrast, their fossil record indicates a high diversity during the Miocene, which is well documented in the marine sediments of Patagonia, Argentina. At least five species are identified, among which is *Preaulophyseter gualichensis*, from the Gran Bajo del Gualicho Formation (Miocene). This taxon was described from isolated teeth and periotics, which has contributed to the taxonomic uncertainty of this species. Here we re-describe the referred materials to *P. gualichensis*, revise its taxonomic status, and evaluate the phylogenetic signal of Physeteroidea ear bones. Our results show that in sperm whales the tympano-periotics morphology is poorly diagnostic at the species levels. Ontogenetic and intraspecific variation (including sexual dimorphism) and/or taphonomic processes could contribute to the minor differences observed. Based on the lack of diagnostic characters in both teeth and periotics, we consider *P. gualichensis* as nomen dubium and re-identify it as Physeteroidea indet. We suggest that tympano-periotics of sperm whales retain many plesiomorphies and a conservative morphology as a result of the morpho-functional constraints imposed by a highly specialized echolocation system.

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### Discovering ichthyosaurs in the border of glaciers in southern Chilean Patagonia by effects of actual climate change and ice melting

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In the year 2003 two almost complete ichthyosaurs were discovered in the rocks of the border of the Tyndall Glacier in southern Chilean Patagonia. Since then, several palaeontological expeditions have yielded the discovery of more than fifty almost-complete and exceptionally-preserved ichthyosaurs. Moreover, the ice melt from Grey Glacier in



Torres del Paine National Park has also led to exposed skeletons of ichthyosaurs. Both localities are Early Cretaceous in age (139–129 Ma). The skeletons are partially exposed from the hard rocks containing the fossils. The associated faunal assemblage is composed of ammonites, belemnites and bivalves, and different fishes are also present in both localities. So far, the most abundant species correspond to *Platypterygius hauthali*, from which it is possible to recognize adults, juveniles and even embryos contained in gravid females. However, most of the material is still *in situ* awaiting funding to continue the excavations, while glaciers continue retreating and new ichthyosaurs appear and are exposed.

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## Modelling marine ecosystem structure from palaeoecological trait data in the Middle Jurassic Peterborough Member, UK

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Reconstructing ancient community assemblages and the ecological relationships between extinct organisms is a major challenge due to the shortcomings of the fossil record. The uncertainty surrounding the life habits of extinct organisms has proven to be a major hurdle for our understanding of the evolution of ecosystem structure through time. One such period of interest is the Mesozoic marine revolution (MMR), where escalation is proposed to have driven major changes in marine food webs which led to the establishment of modern marine ecosystem structure. The timing of the MMR is heavily debated, with proposals ranging from an Early Triassic to a Cretaceous/Cenozoic origin. We present a meta-community analysis of the Peterborough Member (Callovian, UK) with the aim of constraining the timing of the MMR. We assigned traits (*i.e.* body size, feeding mode, motility, tiering) that define interactions in modern systems to all fossil organisms and used rules based on foraging behaviour to model meta-community food web structure. We then compare the modelled Peterborough Member food webs with those of well-constrained modern marine ecosystems to shed light on whether the modern marine ecosystem was established by the end of the Middle Jurassic.

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## On the phylogenetic relationships of Russian carditids *Aimicardita* and *Lunulicardita* (Bivalvia: Carditidae)

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Two genera of Carditidae were erected by Popov to group carditids from the east of Russia: *Aimicardita* and *Lunulicardita*. The former has an elongated elliptical outline with low umbones and strong cardinal teeth. In contrast, the latter has a high outline with strongly recurved umbones and enlarged cardinal teeth. Both taxa include large and massive shells. These genera were not considered in recently proposed systematics classifications of the family and herein are included for the first time. A cladistic phylogenetic analysis of the family is carried out with more than one species of each genus and the obtained placements are discussed. *Aimicardita* is a monophyletic taxon included within Venericorini as a sister clade of (*Megacardita*+*Bathycardita*). *Lunulicardita* is placed as sister taxon of the enigmatic living genus *Strophocardia*, and both are included within the clade Cyclocardida.



*Lunulicardita* and *Strophocardia* genera were synonymized in the past and could represent a unique lineage. Also, a relationship between the clades Venericorini and Cyclocardida are obtained.

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## On the validity and palaeobiogeographic distribution of the European Upper Cretaceous bothremydid turtle '*Polysternon*' *atlanticum*

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Bothremyidae represents the most abundant and diverse lineage of turtles for the end of the Cretaceous in southwestern Europe. Several members of Foxemydina are represented. The problematic '*Polysternon*' *atlanticum* is the most poorly characterized, lacking a diagnosis that allows confirmation of its specific validity. Its presence was exclusively proposed in its type locality, the upper Campanian quarry of Laño (Burgos Province, northern Spain). Despite the notable increase in knowledge of Bothremyidae, no study on '*Polysternon*' *atlanticum* has been conducted since its original description in the 1990s. The analysis of abundant unpublished material from its type locality, including all elements of the shell, allows us to confirm its specific validity. However, the generic attribution is refuted. It is recognized in several Spanish regions (being especially well represented in the fossil site of Lo Hueco, Cuenca Province, central Spain) but also in southern France, the new combination *Iberoccitanemys atlanticum* being proposed. Thus, the species '*Iberoccitanemys convenarum*', originally defined for the French record, and subsequently notified in Spain, is identified as a senior synonym of the species described in Laño. Consequently, only two members of Foxemydina are identified in the Iberian Peninsula, *Foxemys mechinorum* and *Iberoccitanemys atlanticum*, the latter species being the most abundant.

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## Anaga Palaeopark, a heritage proposal

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The PaleoParks conservation initiative proposed in 1996 by the International Palaeontological Association (IPA) has been successfully used in different parts of the world, including oceanic volcanic islands. The aim has been to conserve palaeontological sites *in situ* as tangible evidence of different palaeobiological and geological processes. We present the work accomplished in the Canary Islands for the application for PaleoPark status for the Anaga Massif Biosphere Reserve. This is located in the north of Tenerife in the mid-Atlantic Canary archipelago, which is of volcanic origin and dates to 11.9 Ma. Due to the geographic location of this archipelago, the islands have been sensitive to climate variations through the Quaternary, as recorded in marine and terrestrial sites with rich fossil records. Taking as references other international PaleoParks, we analyse the legislative framework for the current situation of the Anaga palaeontological sites, the evaluation criteria, and a methodological plan to establish the PaleoPark. The objective is palaeobiological conservation *in situ*, its application to the maintenance of ecosystems and biodiversity in a small area, and the promotion of educational interests and tourism. Anaga PaleoPark is a pioneering proposal for the maintenance of the palaeontology of the Canaries.



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## Comparative analyses of a new Miocene petrel (Aves: Procellariidae) from Patagonia, Argentina

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Procellariiformes are important components of South American modern assemblages but their Argentinian fossil record is scarce and poorly understood. A right carpometacarpus MLP 10-XII-11-1 from the early Miocene Gaiman Formation was examined and assigned, after extensive comparisons and morphogeometrical analyses, to Procellariidae. It shares with Procellariiformes a truncated os metacarpale alulare, a wide spatium intermetacarpale, a similar extension of metacarpalia, the absence of the processus intermetacarpalis, the ventral rim of the trochlea carpalis more caudally projected, a marked fossa infratrochlearis leaving cranially a crest bearing the processus pisiformis, and a sulcus extended proximally and along the synostosis metacarpalis distalis. The assignment to Procellariidae is supported by a sulcus tendineus restricted to the distal half, a small crest belonging to the m. ulnometacarpalis dorsalis scar, a notch and a tubercle on the ventral rim of the trochlea carpalis, a wide fovea carpalis caudalis not proximally delimited, a rounded, shallow, and proximo-cranial fossa supratrochlearis, and pneumatic foramina within the small fovea carpalis caudalis. Concordantly, the morphogeometric analyses show clear affinities with Procellariidae, and locate MLP-10-XII-11-1 close to *Daption capense*. To conclude, although the carpometacarpus is not a diagnostic element, MLP-10-XII-11-1 is definitively different from all Procellariidae and represents a new species.

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## Early origin of centre-out sequential flight-related moulting strategy revealed by *Archaeopteryx* feather sheaths

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Living flying birds moult to replace old and worn feathers that inhibit flight performance, but the origins of this are unclear. To address this, we present and evaluate a ~150 million-year-old record of moulting from the oldest known unequivocal bird *Archaeopteryx* from the Late Jurassic Solnhofen Limestone. Laser-stimulated fluorescence revealed feather sheaths that are otherwise invisible under white light. These are separated by one feather, are not in numerical sequential order and are mirrored in both wings. This indicates that a centre-out sequential moulting strategy was already present at the origins of flight, which is used in living falcons to preserve maximum flight performance. This strategy would have been a welcome benefit for early theropod flyers who had poorer flight capabilities. This discovery provides important insights into how birds refined their early flight capabilities before the appearance of key flight-related features such as the keeled sternum, pygostyle and triosseal canal.



## Suspension-feeding radiodont diversity in the Fezouata Shale

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The Ordovician Fezouata Shale Formation of Morocco yields exceptionally-preserved remains of marine organisms and is therefore a huge source of information about the GOBE (Great Ordovician Biodiversification Event). This Tremadocian Lagerstätte is rich in arthropod diversity, especially in remains of radiodonts (informally known as anomalocaridids). Frontal appendages are the most well-preserved part of this organism and such appendages are often found preserved in isolation, providing taxonomic information and informing on feeding behaviour. Two new radiodont species are described from appendages held in the collections of Fezouata Shale fossils at the University of Lausanne, Switzerland. The first belongs to the suspension-feeding *Aegirocassis*, and the other to the enigmatic genus *Pseudoangustidontus*. The discovery of more complete specimens allowed us to identify *Pseudoangustidontus* as a hurdiid radiodont that was also suspension-feeding. A study of the mesh size of these new appendages made it possible to estimate the size range of the plankton caught by each species. These appendages have revealed that the Fezouata Shale was characterized by the biggest suspension-feeder diversity within Radiodonta, which were more abundant and diverse than non-suspension feeding predatory radiodont taxa. This may be linked to the ‘Ordovician Plankton Revolution’, which saw a huge radiation in plankton diversity.

## Building a tetrapod: skull topology across the water-to-land transition

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The vertebrate skull has undergone periods of bone loss or fusion throughout its evolution. This trend, known as “Williston’s Law”, has been suggested to produce more mechanically efficient skulls. Major changes in cranial structure at the origin of tetrapods have been linked to consolidation of the skull as feeding mode changed across the water-to-land transition. It has therefore been inferred, but not tested, that Williston’s Law explains changes in skull anatomy across this event. We quantified skull architecture across the water-to-land transition, using a network-based approach to analyse topological features of 17 ‘fish’ and 93 tetrapod skulls. Moreover, we quantified the evolution of skull structural disparity from the Devonian to the present. We found that skull architecture changes significantly across the water-to-land transition, showing increased complexity and decreased modularity. This suggests that bone loss and fusion lead to greater connectivity among the remaining elements, disputing the assumption that Williston’s Law leads to anatomical simplification. Skull topological disparity decreases at the origin of Tetrapoda and again at the End-Devonian Hangenberg event, continuing into Romer’s Gap. We therefore conclude that tetrapod skull architecture has been shaped by mechanical constraints associated with bone loss as well as influence from external macroevolutionary events.



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## A new vertebrate locality at Presa San Antonio, Cerro del Pueblo Formation (Upper Cretaceous), Coahuila, Mexico

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The Cerro del Pueblo Formation is characterized by comprising many of the palaeontological studies of the Cretaceous in Mexico, resulting in a considerable number of fossiliferous localities in the state of Coahuila. Our work reports a new vertebrate locality near the communal land Presa San Antonio. The material found includes a partial skull of an indeterminate testudine and a possible mosasaur caudal vertebra. Also, different fragmentary specimens of hadrosaurid dinosaurs, including a left maxilla, a right dentary, two indeterminate fragments, possibly dentaries, embedded in a matrix with associated ichnofossils, and a cast of a long bone with skin impressions showing polygonal scales. The report of new fossiliferous localities complements the knowledge that we have of the Cerro del Pueblo Formation and the Campanian ecosystems in southern Laramidia.

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## Refined cladistics and phylogeny of the *Zaphrentis delanouei* species group

**William A. J. Rutter and Marios N. Miliorizos**

University of South Wales, UK

The generalized ontogeny of the Rugosa, outlined by Hill (1938), is not specific to the *Zaphrentis delanouei* species group. Some consensus exists on the phylogeny of the Rugosa, but without substantive evidence from diagnostic morphology. Here the morphology of the group was examined, and characteristics represented in a binary matrix. Statistically sound dendrograms relating the distance between morphometric features were constructed manually, with PAST (Hammer *et al.* 2001) and with Minitab™, using algorithms involving Euclidean distance, Ward's Method and complete linkage. Although the dendrograms are parsimonious, the last common ancestral trait varies between them, namely septal length, septal pattern and the position of the cardinal fossula. Each method listed considers the last common ancestor to have different characteristics. The manual tree considers the cardinal fossula to be analogous, PAST considers the presence and position of stereocolumns, and Minitab™ shows no analogy. The refined cladistics and phylogeny of the species group support analogous evolution of the cardinal fossula, as the morphology is controlled by the local environment of existence. However, further application of cladistics and phylogeny to the Rugosa as a whole is still uncertain due to their complexity, requiring consideration of additional characteristics to ensure parsimony.



## Insights into soft-part preservation from the Early Ordovician Fezouata Biota

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The Fezouata Biota in Morocco is the only Lower Ordovician Lagerstätte yielding a biologically diverse assemblage in a fully marine environment, whilst also containing organisms typical of Cambrian Burgess Shale-type (BST) ecosystems. Fossils from the Fezouata Shale share the same mode of preservation as Cambrian BST biotas defined by carbonaceous compressions and accessory authigenic mineralization. Most organisms of the Fezouata Biota were already dead and decaying on the seafloor when they were buried *in situ* by occasional storm deposits in a distal facies. Pre-burial decay in the Fezouata Shale was responsible for the non-preservation of completely cellular organisms such as jellyfish. These conditions contrast with the processes described for soft-tissue preservation in the Burgess Shale (Canada) and the Chengjiang biota (China). In these two Cambrian Lagerstätten, animals were transported alive or shortly after death by obrution events to a facies that was favourable for preservation. Despite preservational biases, the autochthonous assemblages of the Fezouata Shale offer a unique opportunity to decipher the structure of *in situ* communities and ecological dynamics in Early Palaeozoic seas, when compared to the allochthonous communities of most Cambrian BST biotas.

## First quantitative approach to the diversity of primitive teleosts from Las Hoyas Lower Cretaceous wetland using geometric morphometrics

**Carla San Román**, **Hugo Martín-Abad** and **Jesús Marugán Lobón**

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Most teleostean fishes from the Early Cretaceous are generally characterized by their small sizes, fusiform bodies and relatively short fins. The teleostean association from Las Hoyas fossil site is a great example of such a case. However, with a vast collection of thousands of individuals, the challenge of taxonomically defining details that allow classification of these forms remains unsolved. The aim of this project was to explore, for the first time, the geometric variation of teleostean fish shapes of this fossil association using geometric morphometrics. The results captured significant differences across the sample, including previously undetected variation related to cranial dimensions and to allometry. Unfortunately, the presence of different degrees of post-mortem body curvature in multiple individuals was an operative obstacle that made it difficult to factor out more subtle differences attributable to species identity and/or plasticity. The results thus far provide the first quantitative evidence for the presence of several taxa, opening an exciting prospect for future investigations to understand the diversity and ecological role of these fishes in the Las Hoyas wetland, as well as to provide new insight on the origin and early diversification of teleosts in the Cretaceous.



## Microanalytical study of organic integument composition in terminal Ediacaran animal *Sabellidites*

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The terminal Ediacaran (550–541 Ma) sediments on Baltica record the organically-preserved tubular metazoan *Sabellidites*, which is a morphologically simple soft-bodied fossil comprising resistant biopolymers with complex nanometre-scale microstructure of highly ordered fibres embedded in amorphous matrix. Previous studies are consistent with chitin. New exceptionally-preserved specimens from the transitional Ediacaran–Cambrian subsurface Rovno and coeval formations in western Russia are examined in order to further elucidate the original composition and biochemistry of fibres in the integument wall of the fossils. We applied several microanalytical techniques, including scanning electron microscopy (SEM), time-of-flight secondary ion mass spectrometry (ToF-SIMS), Fourier transform infrared (FTIR) spectroscopy and scanning transmission X-ray microscopy (STXM), to study the morphology and chemistry of the fibres of the fossils. Initial evaluation of the results is consistent with partial preservation of chitin within the fossils. The earliest known biosynthesis of chitin in early animals was an evolutionary innovation rendering the sturdy body construction and protection due to the recalcitrant properties of the chitin and its mechanical rigidity, and was successfully utilized in the Cambrian Explosion by various newly evolving clades of animals.

## Geometric expression of ichthyosaur paddle bone morphology using Archimedean and Catalan solids

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Ichthyosaur paddles are made of paddle bones which can be different shapes depending on species, their position within the paddle and limb positions. Specimens at the National Museum of Wales, UK were examined in detail. Archimedean and Catalan solids were used to express the paddles and therefore identify tangible geometric differences to provide species identification and paddle movement. The solid representation of the shapes of the phalanges may change from the centre of the paddle to other forms at the extremities, depending on preservation. This was observed in *Ichthyosaurus somersetensis* (M3550 and M3554) and *Leptonectes tenuirostris* (M3565). *Ichthyosaurus* sp. (M3551), however, consistently displays rhombicuboctohedronal distribution. The specimens range in quality of preservation, so the defining solids may not be immediately apparent. The taphonomic position of the paddle may also impact the assigned solid, due to the post-mortem distribution of bone within the substrate. Nevertheless, we can still determine the angularity and hydrodynamic efficiency of a given paddle using the solids. Furthermore, small-sided digits on the leading edge of the paddles could change the type of solid identified in the central mass. Splitting the paddle into ‘regions’ allows further developmental study as multiple solids may be observed in a single paddle.





## Lungfish from the early Pennsylvanian of Ireland and the phylogeny of Carboniferous Dipnoi

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Jarrow Colliery (Castlecomer, County Kilkenny, Ireland) is an important historic vertebrate site where fossil material was originally discovered in 1864 immediately above the Jarrow Coal (Coolburn Coal Formation, Langsettian = Westphalian A). Since then, the fauna has been largely neglected, partly because many of the specimens are preserved as bituminous residues with indistinct outlines which makes their preparation and study difficult. Here we describe all the available lungfish specimens for the first time. They represent a new species of *Sagenodus*, characterized by pterygoid tooth plates with up to six widely-spaced radiating ridges lacking teeth and a broad median furrow on the palatal surface of parasphenoid stem. *Sagenodus* is the longest lived and most widely distributed Palaeozoic lungfish genus. It first appears in the late Mississippian of Scotland and is last recorded in the late Lower Permian of Germany and the USA. Many species were named in the nineteenth century, but only six are here thought to be valid. Phylogenetic analysis of the Dipnoi, incorporating data from the present study and the recent redescription of *Sagenodus* from the British Carboniferous, found that the four key Carboniferous taxa were placed above all Devonian taxa in crown-ward order *Ctenodus*, *Uronemus*, *Sagenodus* and *Conchopoma*.

## Deep-fried calamari? The effect of Early Triassic global warming on cephalopod biogeography

**\*Polly Spruce, Bethany J. Allen, Paul B. Wignall and Alexander M. Dunhill**

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Ammonoids suffered substantial losses during the Permo–Triassic mass extinction (c. 252 Ma). Although the global environment remained hostile well into the Early Triassic, their recovery was apparently rapid. Sea surface temperatures reached 40°C during a thermal maximum in the Smithian (Early Triassic) and ammonoids are hypothesized to have moved poleward to escape extreme tropical heat. This suggests that sea surface temperatures played a significant role in the ammonoid latitudinal diversity gradient (LDG). Here we analyse the shape of the ammonoid LDG through the Middle Permian to Middle Triassic using a global dataset from the Paleobiology Database. Raw and subsampled LDGs were plotted at different temporal resolutions (Epochs, Stages and substages). The icehouse Permian plots generally show a unimodal distribution with diversity concentrated at low latitudes. A drastic change is seen across the Permo–Triassic boundary where there is a shift into an extreme greenhouse climate, with Triassic LDGs flatter across all latitudes, but the Middle Triassic shows hints of a recovery towards a unimodal LDG. The ammonoid LDG appears to strongly reflect sea surface temperatures throughout the Permo–Triassic and thus supports the hypothesis that broad climatic regimes (*i.e.* icehouse/greenhouse) are influential in controlling the LDG.



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## Morphological variation in the passerine carpometacarpus

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Passeriformes (passerines) is a hyperdiverse extant avian clade. Despite constituting over half of extant bird diversity, morphological variation across crown Passeriformes has not been adequately characterized to date. Relationships between passerine subclades, in addition to the phylogenetic position of extant outgroups to Passeriformes, have only recently become clear through well-supported molecular phylogenies. This longstanding lack of a comparative framework has hindered progress on understanding patterns of morphological variation across Passeriformes. As a result, the phylogenetic affinities of many crown and stem passerine fossils remain ambiguous, limiting our ability to interpret the passerine fossil record. The carpometacarpus (hand bone) is an important element in passerine comparative morphology, despite exhibiting several convergent characters within Passeriformes and with other avian clades. Carpometacarpi are among the most abundantly preserved passerine fossil elements. Here we investigate the passerine carpometacarpus as a case study to highlight previously uncharacterized morphological variation across Passeriformes. We present high-resolution 3D images of passerine carpometacarpi, sampling all major extant passerine subclades. We use the carpometacarpus to exemplify how character combinations are crucial for diagnosing isolated fossil elements, and expect that this work will facilitate the incorporation of additional fossils into a phylogenetic framework, thereby shedding new light on passerine evolutionary history.

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## Morphological and functional diversity of non-avian dinosaur manual unguals

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The distal-most phalanx of the tetrapod manus often undergoes selection to form a hoof or claw like structure called an ungual. This structure is present in non-avian dinosaurs where it has diversified into a broad range of morphologies, from highly curved claws to flattened hooves. These varied manual ungual morphologies evolved related to different functions, firstly associated with locomotion and then to more specific functions for bipedal taxa. However, there has been no investigation across the whole of Dinosauria into this relationship. We present the first quantitative study of manual ungual morphology across the whole of the non-avian dinosaurs. We used a two-dimensional geometric morphometric approach to investigate the shape variation on the unguals of digits I, II and III. Our dataset contained representatives of 113 genera from the Theropoda, Ornithischia and Sauropodomorpha. The data were Procrustes aligned and the variation was explored using phylogenetically-informed PCA. Diverse morphology was seen across the three digits with digit I showing lower variation than seen in digits II and III. The influence of allometry and phylogeny on ungual morphology was found to be minimal. Results from convergence testing show convergence in ungual morphology on the basis of locomotive stance across the quadrupedal Ornithischia.



## Mollusc and fish diversity in an early Miocene continental shelf of the proto-Mediterranean

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<sup>1</sup>National and Kapodistrian University of Athens

<sup>2</sup>University of Vienna, Austria

Reconstructing the Proto-Mediterranean biodiversity is challenging because aragonitic preservation is rare in this tectonically active domain during the Oligocene and the early–middle Miocene. Here we present a very rich and unique marine fish and mollusc fauna from the early Miocene deposits of northwestern Greece. Typical species of the molluscan assemblage are: *Bittium larrieyense*, *Turritella turris*, *Finella perpusilla*, *Smaragdia merignacensis*, *Ringicula minor*, *Alvania transiens* and *A. amphitrite*. More than 18 fish taxa are recognized based on their otoliths, including: *Ariosoma* aff. *moravica*, *Rhynchoconger pantanellii*, *Gnathophis* sp., *Conger* sp., *Apogon* sp., *Spicara* sp., *Trachurus* sp., *Lobianchia dofleini*, *Diaphus garmani*, *Diaphus dumerili*, *Vinciguerria* sp., *Sardinops* sp., *Solea senegalensis*, *Carapus nuntius*, *Cepola* sp., *Pomadasys incisus*, *Lesueurigobius suerii*, *Pomatoschistus quagga* and *Gobius* sp. The presence of several grazer species in the molluscan assemblage suggests a vegetated environment. Both the fish and mollusc assemblages indicate tropical conditions. The presence in the fish otolith assemblage of myctophids as well as gobies suggests that the water depth exceeded 50 m. Furthermore, we explore the palaeobiogeographic distributions of the studied assemblages.

## Analysis of skeletogenic gene evolution in echinoids and implications for body plan diversification

**Jeffrey Thompson**<sup>1</sup>, **Nicolás Mongiardino Koch**<sup>2</sup> and **Paola Oliveri**<sup>1</sup>

<sup>1</sup>University College London, UK

<sup>2</sup>Yale University, USA

Evolution of the skeleton across animal groups has resulted in the vast array of morphologies seen throughout the fossil record and on the planet today. The genomic underpinnings of why some animal groups evolve diverse body plans, while others stay remarkably similar over evolutionary timescales, are not well known. Amongst the sea urchins, regular echinoids have remained markedly constrained in their morphology throughout their ~270-million-year evolutionary history, while irregular sea urchins have diversified their body plans extensively. To understand differences in the biomineralization toolkit of these animal groups that may underlie their differing skeletal morphology, we surveyed the genomes and transcriptomes of numerous sea urchin and non-echinoid echinoderms. We focused on genes and gene families that may have undergone extensive duplication, and those that may have clade-specific heightened evolutionary rates. This work will lay the groundwork for understanding the molecular and genomic mechanisms which direct the disparate body plans of regular and irregular echinoids.



## Discovery of plywood structure in *Sphenothallus* from the Carboniferous of central Russia

**Olev Vinn<sup>1</sup> and Aleksandr A. Mironenko<sup>2</sup>**

<sup>1</sup>University of Tartu, Estonia

<sup>2</sup>Geological Institute, Russian Academy of Sciences, Russia

*Sphenothallus* cf. *S. angustifolius* specimens are reported for the first time from the Mississippian of central Russia. All *Sphenothallus* specimens have an apatitic composition and a characteristic laminar microstructure. Most of the lamellae in the tube wall are straight, but some have a wavy morphology and a few are so wrinkled that they form hollow 'ribs'. The lamellae forming hollow 'ribs' presumably had an originally higher organic content than straight lamellae. There are microborings on the surface of some lamellae that are morphologically similar to the bioerosional traces in various hard biomineral substrates. Lamellae in the inner parts of the tube wall are composed of fine fibres. The fibres are parallel to the surface of the tube wall and in successive laminae they differ in orientation by irregularly varying angles forming a plywood structure. It is possible that a plywood microstructure in *Sphenothallus* was originally organic and was later phosphatized during fossilization. Alternatively, but less likely, the plywood structure was originally mineralized and therefore is comparable to phosphatic lamello-fibrillar structures of vertebrates. Apatitic plywood structures have not been described previously in invertebrates.

## Bryozoan symbiosis in the Ordovician and Silurian

**Olev Vinn<sup>1</sup>, Mark A. Wilson<sup>2</sup>, Michał Zatoń<sup>3</sup> and Mikołaj K. Zapalski<sup>4</sup>**

<sup>1</sup>University of Tartu, Estonia

<sup>2</sup>The College of Wooster, USA

<sup>3</sup>University of Silesia in Katowice, Poland

<sup>4</sup>University of Warsaw, Poland

Ordovician bryozoan colonies were often inhabited by soft-bodied wormlike organisms, conulariids, rugose corals and cornulitids. It appears that the evolution of symbiotic relationships in bryozoans did not contribute much to their diversification during the Great Ordovician Biodiversity Event (GOBE). The GOBE may have been the catalyst that started the evolution of symbiotic relationships between bryozoans and other invertebrates. There was a progressive escalation in bryozoan symbiosis in the Ordovician, from the Darriwilian to Katian. There are several hypotheses to explain this escalation in bryozoan symbiosis in the Ordovician. Bryozoans with mutualistic relationships may have out-competed species without mutualistic relationships. Infestation strategies of bryozoan parasites likely improved with time, possibly at a faster pace than the anti-parasite strategies of their bryozoan hosts. Finally, those invertebrates that sought refuge from predators may have reacted to an increase in predation pressure with a more intense search for substrates suitable for an endobiotic life mode, such as large bryozoan colonies. There was a drop in bryozoan symbiosis in the Hirnantian possibly due to the end-Ordovician mass extinction. Silurian bryozoans were less symbiotic than those in the Ordovician, with the exception of Pridoli faunas, but this is most likely due to a study bias.



## Did earthworms cause the demise of the Carboniferous coal swamps?

**Jakob Vinther<sup>1</sup>, Luke A. Parry<sup>1,2</sup>, Jesus Lozano Fernandez<sup>1,3</sup>, Nicholas Mongiardino Koch<sup>4</sup>, Alistair R. Tanner<sup>1</sup>, Samuel James<sup>5</sup>, Elena K. Kupriyanova<sup>6</sup>, Stuart A. Robinson<sup>2</sup>, Benjamin Mills<sup>7</sup>, Alexander J. Hetherington<sup>8</sup> and Christoffer Bugge Harder<sup>9</sup>**

<sup>1</sup>University of Bristol, UK

<sup>2</sup>University of Oxford, UK

<sup>3</sup>Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain

<sup>4</sup>Yale University, USA

<sup>5</sup>University of Iowa, USA

<sup>6</sup>Australian Museum, Sydney, Australia

<sup>7</sup>University of Leeds, UK

<sup>8</sup>University of Edinburgh, UK

<sup>9</sup>Uppsala University, Sweden

One of the greatest terrestrial ecosystem engineers is the earthworm, key in recycling nutrients and remodelling soil profiles. Earthworms can also be a cause for destruction, as has been seen in North America where invasive earthworms are causing destruction of a unique earthworm-free forest ecosystem. Earthworms clearly must have changed land permanently when they first appeared. Here we show with molecular clock divergence estimates that earthworms colonized land at the end of the Carboniferous (320–295 Ma). Earthworms first radiated across the current Northern Hemisphere and then colonized Gondwana in the earliest Permian. This is consistent with patterns of floral and coal swamp transitions into a seed-plant-dominated realm from the previous more spore-plant-dominated world. Could earthworms have been integral in this event? Alternative mechanisms such as climate change may also have been important, but the change could also have been a consequence of earthworm activity. Introducing earthworm activity into the biogeochemical COPSE model suggests that earthworm activity could explain the large-scale patterns in O<sub>2</sub> and CO<sub>2</sub> fluctuations observed in this period. It suggests that we need to consider more seriously the role of animal ecosystem engineers in explaining many large-scale biosphere events.

## Taxon-specific bidirectional felling of Ediacaran fronds demonstrates constructional variability

**\*Philip B. Vixseboxse<sup>1</sup>, Frances S. Dunn<sup>2</sup> and Emily G. Mitchell<sup>3</sup>**

<sup>1</sup>University of Bristol, UK

<sup>2</sup>Oxford University Museum of Natural History, UK

<sup>3</sup>University of Cambridge, UK

The Ediacaran Period (635–539 Ma) records the first appearance of large, complex organisms in the fossil record around 570 Ma, at least some of which are likely to be animals. They record strange anatomies without obvious analogue, making it difficult to determine driving factors behind their morphological innovations. In this study we analysed the orientations of populations of five taxa from the Mistaken Point E surface, Newfoundland, Canada (565 Ma), which represent the disparity of body plans present. There was significant variation in the orientation distributions between the taxa, with the stemmed organisms *Primocandelabrum* sp., *Charniodiscus procerus* and *Charniodiscus* sp. showing significant unimodal orientations. In contrast, the stemless *Thectardis* showed



weak bimodal orientations, and the stemless *Bradgatia* was found to show significant bimodal directionality in felling. We suggest that stemless taxa were likely felled due to weak turbulent flow in the tip of the encroaching turbidite. However, stemmed taxa were rarely felled by this initial turbidity, instead remaining upright until stronger laminar flows felled the entire community in a unimodal distribution. This suggests the presence of a stem increased survivorship of taxa in lower energy turbidite flow events, protecting against the felling, and ultimately burial, of the organism.

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## Nomenclature has a new friend request: a network analysis of the PhyloCode

**Evangelos Vlachos<sup>1,2</sup>**

<sup>1</sup>*Museo Paleontológico Egidio Feruglio, Argentina*

<sup>2</sup>*Aristotle University of Thessaloniki, Greece*

Recently I have developed a new approach to use and understand codes of nomenclature by transforming them into networks. Conceptualizing a code as a network provides more efficient navigation and learning, and is a powerful tool for amendments and revisions. Also, this methodology allows the objective comparison between different codes in terms of their connectivity pattern and structure, both in a qualitative and quantitative way. From this starting point, I have constructed the network of the recently published PhyloCode and I compare it with the International Code of Zoological Nomenclature (ICZN). Although there are significant differences in the number and relative amount of articles and other text elements between the two codes, my experience is the same: in both codes, the user would have to consult three items on average and seven at most to reach a conclusion. However, and contrary to popular belief, I show that the PhyloCode is more complex than the ICZN. Placing both codes in the same network reveals that the PhyloCode is only loosely connected to the ICZN, focusing mainly on definitions and not names, and with a strong dependence on pre-existing/available names; PhyloCode is more focused on taxonomy than nomenclature.

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## The fossil record of turtles and tortoises (Reptilia: Testudines) in Greece

**Evangelos Vlachos<sup>1,2</sup>**

<sup>1</sup>*Museo Paleontológico Egidio Feruglio, Argentina*

<sup>2</sup>*Aristotle University of Thessaloniki, Greece*

Turtles are among the most common and easily identifiable elements of the vertebrate fossil record, especially in continental deposits. In Greece, turtle fossils have been identified in at least 68 continental and insular localities, ranging from the early Miocene to Holocene deposits. The review of the known turtle fossil record from Greece reveals the presence of at least 14 different species belonging to four cryptodiran clades (Trionychidae, Emydidae, Geoemydidae and Testudinidae) and a single pleurodiran clade. Seven of these species have been named based on type material from the country. The most diverse clade is Testudinidae, comprising more than half of the known diversity, with at least two giant and seven small-sized tortoise species. Although turtle fossils from Greece have been known since the first collections in the mid-nineteenth century, they have only recently received special attention and now contribute significantly to our understanding of the evolution of the palaeoherpetofaunas in the Eastern Mediterranean region during the last 25 million years.



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## A combined-evidence phylogeny of total group coleoid cephalopods

**\*Christopher Whalen**

*American Museum of Natural History, USA*

Coleoid cephalopods (octopuses, squids, cuttlefishes) are a keystone component of the modern and ancient marine biosphere; however, no matrix-based phylogeny of total group coleoids (octopuses, squids and cuttlefishes) has yet been proposed. Here I present results from the first combined-evidence total group coleoid phylogeny, incorporating morphological, stratigraphic and molecular data in a Bayesian framework.

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## Preservation and facies distribution of fossil cnidarian medusae (jellyfish) in Upper Carboniferous (Pennsylvanian) strata of the north-central United States

**Graham Young<sup>1</sup> and James W. Hagadorn<sup>2</sup>**

<sup>1</sup>*Manitoba Museum, Canada*

<sup>2</sup>*Denver Museum of Nature & Science, USA*

The palaeoenvironmental occurrence of fossil cnidarian medusae changed through the Phanerozoic. A broad Cambrian distribution in various marine palaeoenvironments was, by the Jurassic, replaced by occurrence only in muddy lagoons. Several occurrences during the Carboniferous Period, an approximate midpoint between these extremes, inform our understanding of factors affecting jellyfish preservation. In the North American midcontinent, medusae occur in shales, in two distinct types of setting. The first includes nodules of the Francis Creek Shale of Illinois (Middle Pennsylvanian, Moscovian), part of the Mazon Creek Lagerstätte. This unit was deposited in a tidally-influenced proximal marine to estuarine setting; associated fossils represent marine, brackish, freshwater and terrestrial environments. The pyrite- and siderite-mantled fossils were preserved by rapid burial and early mineralization. Medusae in the second palaeoenvironmental setting occur in black and grey shales. These include an Indiana exposure of the Mecca Quarry Shale (Middle Pennsylvanian, Moscovian), deposited in shallow nearshore conditions, and Iowa and Nebraska exposures of the Stark Shale (Upper Pennsylvanian, Kasimovian) that represent offshore locations and intermediate depths. Associated fossils include brachiopods, ammonoids, arthropods, fishes and plants. These black shales are unusually enriched in minerals incorporating heavy metals, which could have fostered early soft-tissue mineralization.

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## The organic-walled microfossil research from the Cambrian of China: implications for global phytoplankton diversity

**Shucan Zheng<sup>1,2</sup>, Xuesong Lu<sup>1</sup> and Qinglai Feng<sup>2</sup>**

<sup>1</sup>*Huanggang Normal University, China*

<sup>2</sup>*China University of Geosciences, Wuhan, China*

The present study constitutes a summary of a total of 30 investigations of Cambrian organic-walled microfossils from China. Most of these publications are written in Chinese and the available data are generally not included in previous compilations. In this study, the stratigraphic ranges of the organic-walled microfossils for each geographical region of China are listed in chronological order according to the most recent international stratigraphic chart, revealing 276 Cambrian fossil species belonging to 99 genera. The



localities of the investigated areas are mostly on the Cambrian Jiangnan slope and basin and the north continental shelf of the Yangtze plate, where the Ediacaran–Cambrian transition is continuous and the recorded facies are more favourable to acritarch preservation. The raw data from the reviewed literature are brought together to supplement the former published data of global acritarch diversity. The higher diversities in the early Cambrian Fortunian stage and Stage 2 in China point to a global diversity peak around the late early/early middle Cambrian reported in previous studies. The latest Cambrian diversification rise in China confirms the onset of the Ordovician plankton revolution. The Chinese Cambrian bears great potential for further research and additional studies are urgently needed.

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### Palaeoenvironmental context of early vertebrates from the Lower and Middle Devonian of Andrée Land, Spitsbergen

**Živilė Žigaitė<sup>1</sup>, Martin Whitehouse<sup>2</sup>, Gaël Clément<sup>3</sup>, Matthew Cowen<sup>1</sup> and Daniel Goujet<sup>3</sup>**

<sup>1</sup>*Uppsala University, Sweden*

<sup>2</sup>*Swedish Museum of Natural History, Stockholm, Sweden*

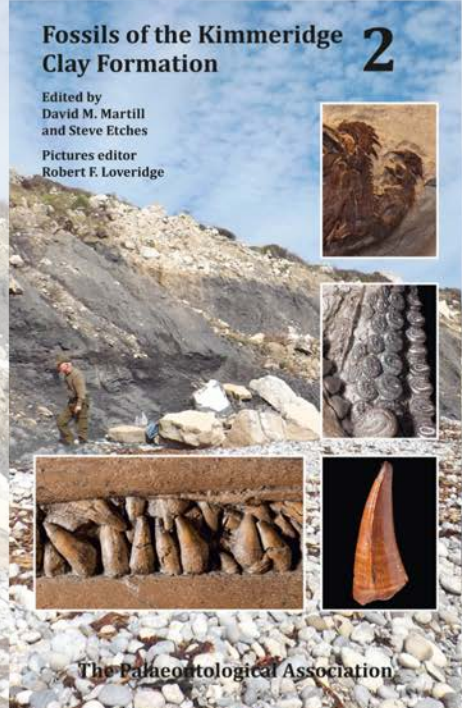
<sup>3</sup>*Muséum national d'Histoire naturelle, Paris, France*

Early vertebrates are known from a number of localities widely dispersed in the Lower and Middle Devonian of Andrée Land, northern Spitsbergen. These vertebrate fossils are mainly preserved as disarticulated exoskeleton remains, including microscopic scales of jawless fish and gnathostomes such as acanthodians, thelodonts and chondrichthyans. Their diversity reveals an endemic and complex biostratigraphic picture in the region, but palaeobiology and palaeoecology remain poorly understood. Here we present two new acanthodian species and one new chondrichthyan genus, and species based on morphology and histology of isolated scales from the Wood Bay and Grey Hoek formations of the Andrée Land Group. We also attempt to underline potential implications of these new taxa occurrences in terms of palaeobiogeography and palaeoenvironment, including new information from stable oxygen isotope ( $\delta^{18}\text{O}$ ) data.



# Field Guide to Fossils: Number 16

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**The  
Palaeontological  
Association**

**Annual  
General  
Meeting**

**14.30**

**Thursday**

**17th December**

**Papers**







# Annual General Meeting 2020

## AGENDA

1. Apologies for absence
2. Minutes of the 63rd AGM, University of Valencia
3. Trustees Annual Report for 2019
4. Accounts and Balance Sheet for 2019 and reappointment of financial examiner
5. Election of Council and vote of thanks to retiring members
6. Resolution to amend the Constitution
7. Report on Council Awards

## DRAFT AGM MINUTES 2019

Minutes of the Annual General Meeting held on Thursday 19th December 2019 at the University of Valencia, Spain.

- 1. Apologies for absence.** None.
- 2. Minutes.** The minutes of the 2018 AGM were agreed a true record by unanimous vote.
- 3. Trustees Annual Report for 2018.** The report was agreed by unanimous vote of the meeting.
- 4. Accounts and Balance Sheet for 2018.** The accounts were agreed by unanimous vote of the meeting.

### 5. Election of Council and vote of thanks to retiring members.

5.1 Prof. C.H. Wellman extended a vote of thanks to the following members of Council who were retiring from their positions this year: Dr C.J. Buttler, Dr B.H. Lomax, Dr L.M.E. McCobb, Dr A.R.T. Spencer, Dr D.P.G. Bond, Dr A.M. Dunhill, Prof. A.S. Gale and Ms Z.E. Hughes.

5.2 The following members were elected to serve on Council: President: Prof. C.H. Wellman, President-Elect: Dr P.J. Orr, Vice-Presidents: Dr F.L. Gill and Prof. T.R.A. Vandenbroucke, Treasurer: Dr P. Winrow, Secretary: Dr C.T.S. Little; Editor-in-Chief: Dr B.H. Lomax; Editor Trustees: Prof. N.J. Butterfield and Prof. M.A. Purnell, Newsletter Editor: Dr G.T. Lloyd, Book Review Editor: Dr T.J. Challands, Publicity Officer: Dr S.J. Lydon, Education Officer: Dr M.E. McNamara, Outreach Officer: Ms Z.E. Hughes, Internet Officer: Dr R.J. Garwood, Meetings Coordinator: Dr U. Balthasar, Diversity Officer: Dr R.C.M. Warnock, Ordinary Members: Dr T. Clements, Dr L. Hide, Dr S. Giles and Dr T.H.P. Harvey.

5.3 Dr R. Sansom and colleagues will organize the Annual Meeting in 2020 at the University of Manchester, UK. [See note above regarding the AGM and the coronavirus pandemic.]

### 6. Association Awards. The following awards were announced:

6.1 The Lapworth Medal was awarded to Prof. D.E.G. Briggs (Yale University).



- 6.2** The President's Medal was awarded to Dr M.D. Sutton (Imperial College London).
- 6.3** The Hodson Award was presented to Dr S. Danise (Università degli Studi di Firenze).
- 6.4** The Mary Anning Award was presented to Dr H. Hagdorn (Ingelfingen, Germany).
- 6.5** The Gertrude Elles Award for public engagement was presented to Ms E. Wallace (The University of Manchester/iCRAG).
- 6.6** Research Grants were awarded to: Dr N. Brocklehurst, University of Oxford, *Patterns of extinction and survival in early terrestrial herbivores*; Dr L.A. Riedman, University of California, Santa Barbara, *Eukaryotic evolution in heterogeneous Proterozoic seas*; and Dr E.A. Sperling, Stanford University, *Harnessing the power of the Metabolic Index for palaeontological studies*.
- 6.7** Under the Small Grants Scheme, the following awards were announced: the Whittington Award to Dr E.M. Dunne, University of Birmingham, *Harnessing the power of 'dark data' for enhancing estimates of tetrapod diversity*; the Callomon Award to Mr R. Smith, University of Portsmouth, *A new and unique Kem Kem beds (mid Cretaceous) locality near the oasis of Tarda, south eastern Morocco*; Stan Wood Awards to Ms R.F. Bennion, University of Liège, *Disparity and niche partitioning in toothed cetaceans from the early Miocene of Peru*, and Ms C. Shears-Ozeki, Kyoto University, *Bone modification of the Mesozoic marine vertebrates of south England*; and Sylvester-Bradley Awards to Ms N. Machida, West Virginia University, *The importance of environmental factors in driving paedomorphic evolution in the suborder Phacopina*, Dr N. Robin, University College Cork, *Investigating the enigmatic Devonian arthropod Oxyurotopoda*, and Mr J.O. Shaw, Yale University, *Elucidating connections between the Cambrian Explosion and Great Ordovician Biodiversification Event*.
- 6.8** Undergraduate Research Bursaries were awarded to: Mr T. Mackay-Champion, University of Oxford, supervised by Prof. R.B.J. Benson, *Anatomy of Hylonomus, the earliest amniote, based on high-resolution synchrotron tomography*; Mr J. Lovegrove, University of Bristol, supervised by Prof. M.J. Benton, *Investigating the Palaeotopography and Variations in Ecology of Rhaetian Bristol using the Westbury Formation bone bed*; Mr A.R.D. Payne, University of York, supervised by Dr K.E. Davis, *What happened to Pseudosuchia? Exploring the effects of past environmental change on a once diverse clade*; Ms L. Southan, University of Birmingham, supervised by Dr S.E. Greene, *Testing the biogenicity of ancient stromatolites using magnetic susceptibility*; Mr R. Carter, Imperial College London, supervised by Dr M.D. Sutton, *Analysing an exceptionally-preserved Silurian asterozoan*; and Mr H. Berks, University of Bristol, supervised by Dr J. Vinther, *A new Early Cambrian arthropod – a description and phylogenetic analysis*.
- 6.9** Engagement Grants were awarded to Dr C.D. Dean for *Fossil fact or fiction? Einstein's Garden palaeontology stall at Green Man Festival, 2019*; Ms Y. Haridy for *Velociraptor puppet workshops*; and Dr E.A. Hide for *Mary Anning's specimens and archives in the Sedgwick Museum*.
- 6.10** The 2019 Best Paper Awards were presented to Dr S.W. Evers and Prof. R.B.J. Benson, for their paper entitled 'A new phylogenetic hypothesis of turtles with implications for the timing and number of evolutionary transitions to marine lifestyles in the group' (*Palaeontology*), and to Dr W.J. Foster and colleagues for 'Early Triassic benthic invertebrates from the Great Bank of Guizhou, South China: systematic palaeontology and palaeobiology' (*Papers in Palaeontology*).
- 6.11** The President's Prize was presented to Dr J. Luque (Yale University).



6.12 The Council Poster Prize was presented to Dr E.M. Dunne (University of Birmingham).

7. **Annual Address.** A talk entitled 'Not just skin deep: probing the secrets of fossil melanin using taphonomic experiments and analytical chemistry' was given by Dr Maria E. McNamara (University College Cork).

## Trustees Annual Report 2019

The Trustees present their report with the financial statements of the charity for the year ended 31st December 2019. The Trustees have adopted the provisions of *Accounting and Reporting by Charities: Statement of Recommended Practice* applicable to charities preparing their accounts in accordance with the Financial Reporting Standard applicable in the UK and Republic of Ireland (FRS 102) (effective 1st January 2019).

### 1. OBJECTIVES AND ACTIVITIES

**1.1 Aims and objectives:** The aim of the Association is to promote research in Palaeontology and its allied sciences by (a) holding public meetings for the reading of original papers and the delivery of lectures, (b) demonstration and publication, and (c) by such other means as the Council may determine. In order to meet these objectives, the Association continues to increase its range and investment in public outreach and other charitable activities, whilst continuing to support research, publications, and student and speaker attendance at national and international meetings including our flagship Annual Meeting.

**1.2 Grants-in-aid for meetings and workshops:** The Association provided funds to support the following meetings and workshops: From molecules to macroevolution symposium, SVP 2019 (Prof. Derek E.G. Briggs, Yale University); 67th and 68th SVPCA (awards to Dr Martin Munt, Dinosaur Isle Museum and Dr Susannah C.R. Maidment, Natural History Museum, London).

**1.3 Public meetings:** Two public meetings were held in 2019, and the Association extends its thanks to the organizers and host institutions of these meetings.

*63rd Annual Meeting.* The Association's Annual Meeting is its flagship meeting and this year was held on 15–21 December at the University of Valencia. Dr C. Martínez-Pérez, together with local support from colleagues and PhD students, organized the meeting, which included a symposium on 'Virtual Palaeontology' and comprised a programme of internationally recognized speakers. There were 325 attendees. The Annual Address was entitled 'Not just skin deep: probing the secrets of fossil melanin using taphonomic experiments and analytical chemistry' and was given by Dr Maria E. McNamara (University College Cork). The President's Prize for best oral presentation by an early-career researcher was awarded to Dr J. Luque (Yale University). The Council Poster Prize for best poster presentation by an early-career researcher was presented to Dr E.M. Dunne (University of Birmingham).

*Progressive Palaeontology.* This is an annual, open meeting for research students in Palaeontology and allied sciences to present their work to an audience of their peers. The 2019 meeting was organized by Mr L.E. Meade and a team of other students, and held at the University of Birmingham on 6–8 June. There were 95 attendees.



**1.4 Publications:** The journals *Palaeontology* and *Papers in Palaeontology* are produced by Wiley. During 2019, the following volumes were published: *Palaeontology* volume 62, comprising six issues; and *Papers in Palaeontology* volume 5, comprising four issues. Council thanks Mr N. Stroud for assistance with the typesetting and production of the *Palaeontology Newsletter*.

**1.5 Research Grants:** A total of 13 applications for Palaeontological Association Research Grants were received. Three were recommended for funding in 2019, totalling £19,883, and were awarded to: Dr N. Brocklehurst (University of Oxford), 'Patterns of extinction and survival in early terrestrial herbivores'; Dr L.A. Riedman (University of California, Santa Barbara), 'Eukaryotic evolution in heterogeneous Proterozoic seas'; and Dr E.A. Sperling (Stanford University), 'Harnessing the power of the Metabolic Index for palaeontological studies'.

**1.6 Small Grants Scheme:** The scheme received 22 applications. Seven were recommended for funding in 2019, totalling £10,063.30. Small grants were awarded as follows: Dr E. M. Dunne (University of Birmingham) received the Whittington Award; Mr R. Smith (University of Portsmouth) received the Callomon Award; Ms R.F. Bennion (University of Liège) and Ms C. Shears-Ozeki (Kyoto University) received Stan Wood Awards; Ms N. Machida (West Virginia University), Dr N. Robin (University College Cork) and Mr J.O. Shaw (Yale University) received Sylvester-Bradley Awards.

**1.7 Undergraduate Research Bursary Scheme:** The scheme attracted 18 applications, of which six were recommended for funding in 2019, totalling £13,792.80. The awardees were as follows: Mr T. Mackay-Champion, University of Oxford, supervised by Prof. R.B.J. Benson; Mr J. Lovegrove, University of Bristol, supervised by Prof. M.J. Benton; Mr A.R.D. Payne, University of York, supervised by Dr K.E. Davis; Ms L. Southan, University of Birmingham, supervised by Dr S. E. Greene; Mr R. Carter, Imperial College, supervised by Dr M.D. Sutton; and Mr H. Berks, University of Bristol, supervised by Dr J. Vinther.

**1.8 Publicity, outreach and engagement:** The Association continues to promote Palaeontology and its allied sciences to print/online media, radio and television. The Association is a major financial supporter of the Lyme Regis Fossil Festival and the Yorkshire Fossil Festival. The Association developed new displays and activities for the public on the theme of fossilization, organized and staffed by members of Council and student members; Association members also delivered public lectures at the festivals. The Association launched a YouTube channel showcasing diverse aspects of palaeontology to the broader public. The Public Engagement Group (PEG), consisting of the Outreach Officer, Education Officer, Publicity Officer, Executive Officer, President and the Treasurer, decided on expenditure of the group budget (£30,000 for 2019), supporting recurring festival activities, Engagement Grants and commissioned projects.

**1.9 Engagement Grants:** The scheme received a total of six applications in 2019, of which three were recommended for funding, totalling £12,536. These were awarded to Dr C.D. Dean for 'Fossil fact or fiction? Einstein's Garden palaeontology stall at Green Man Festival, 2019'; Ms Y. Haridy for 'Velociraptor puppet workshops'; and Dr E.A. Hide for 'Mary Anning's specimens and archives in the Sedgwick Museum'.

**1.10 Diversity Group:** The Diversity Officer and Diversity Group (DG) are responsible for realizing the recommendations from the Diversity Study completed by Parigen Ltd in 2018. One of these was to revise the medals and awards nominations and selection procedures. To investigate alternative best





practices, the DG collected evidence and reached out to other scientific organizations. In response the DG updated the nominations and awards procedures, and is committed to re-evaluating these. In 2019 the Association launched the Carer's Bursary with a £250 maximum per individual to support those with caring responsibilities to attend Association meetings. The award recognizes the challenges faced by carers in obtaining equal access to the opportunities linked to scientific meetings. This year the Association supported two individuals with these bursaries. The organizers of the Annual Meeting and Progressive Palaeontology also made efforts to ensure these events were diverse and inclusive. A panel on diversity issues was hosted at the Annual Meeting and a guide to organizing inclusive meetings was published by the Progressive Palaeontology organizers. Throughout the year the DG commissioned articles promoting diversity and inclusion for the *Newsletter*, including a Special Report on gender bias in publishing in palaeontology.

**1.11 Palaeontological Association Exceptional Lecturer scheme:** The first Palaeontological Association Exceptional Lecturer, Dr S. Lautenschlager, gave six lectures in 2019/2020, at the Swedish Museum of Natural History, the Geological Society of London, University College Cork and the Universities of Plymouth, Cambridge and Oxford. Dr A.J. Hetherington was selected in a competitive process to be the Palaeontological Association Exceptional Lecturer for the academic year 2020/2021.

**1.12 Online activities:** The online activities of the Association continue to expand with greater emphasis on social media (Facebook, Twitter). The Association continues to be the sole host for the online-only journal *Palaeontologia Electronica*, as well as continuing to host websites for other societies (The Palaeontographical Society, International Organisation of Palaeobotany), palaeontological online resources (EDNA fossil insect database, the Kent Fossil Database, SPIERS Software), palaeontological networking sites (European Coalfield Conservation Opportunities) and online outreach projects (Palaeontology [Online]). The listserv PaleoNet also continues to be hosted. The Association continues to run its Internet activities on cloud-based services provided by AWS located on EU-based servers. At the end of 2019 members of the PalAss Facebook group numbered 1,697 and the @ThePalAss Twitter account had 6,025 followers. During 2019 a new Association Facebook page was implemented to allow for easier updates to members. The page is linked to the Facebook group and had 256 followers at the end of 2019.

**1.13 Awards:** The Lapworth Medal, awarded to people who have made a significant contribution to the science by means of a substantial body of research, was presented to Prof. Derek E.G. Briggs (Yale University). The President's Medal, awarded to a palaeontologist within 15 to 25 years of their PhD in recognition of outstanding contributions in their earlier career, coupled with an expectation that they will continue to contribute significantly to the subject in their further work, was presented to Dr Mark D. Sutton (Imperial College London). The Hodson Award, for a palaeontologist within ten years of award of their PhD who has made an outstanding contribution to the science through a portfolio of original published research, was awarded to Dr Silvia Danise (Università degli Studi di Firenze). The Mary Anning Award, for an outstanding contribution by an amateur palaeontologist, was made to Dr Hans Hagdorn (Muschelkalkmuseum Hagdorn, Ingelfingen). The Gertrude Elles Award for high-quality, amateur or institutional, public engagement projects that promote palaeontology was awarded to Ms Elspeth Wallace (The University of Manchester/iCRAG). The 2019 Best Paper Awards in *Palaeontology* and *Papers in Palaeontology* were given respectively to Dr S.W. Evers and Prof. R.B.J. Benson for their paper entitled 'A new phylogenetic hypothesis of turtles with implications for the



timing and number of evolutionary transitions to marine lifestyles in the group', **62(1)**, 93–134; and Dr W.J. Foster and colleagues for their paper 'Early Triassic benthic invertebrates from the Great Bank of Guizhou, South China: systematic palaeontology and palaeobiology', **5(4)**, 613–656. Council also awards undergraduate prizes to outstanding students in university departments worldwide where Palaeontology is taught beyond Level 1; a total of 19 were awarded throughout the year.

**1.14 Forthcoming plans:** The Association will continue to make substantial donations from General and Designated funds to promote the charitable aims of the Association. Resources will be made available to continue a similar programme of grants, meetings, outreach and public engagement activities. The 2020 Progressive Palaeontology conference will take place virtually due to the coronavirus pandemic. For the same reason the 64th Annual Meeting planned to be held in December 2020 at The University of Manchester will now also take place virtually. Volume 63 of *Palaeontology* and volume 6 of *Papers in Palaeontology* will be published; however, as announced at the AGM in 2019, paper copies will cease to be printed and publishing will move to online-only. The *Field Guide to Fossils of the Kimmeridge Clay Formation* is in production with publication expected in 2020. As of 2020, the Association will begin collecting diversity and equality data annually, supporting diversity and inclusion. Each year the membership will be asked to fill out an anonymous survey and given the opportunity to provide feedback. This provides a way to measure the impact of DG initiatives and to highlight critical areas for improvement. In addition, the DG has launched a survey to identify key areas for improvement at the Association's events.

**1.15 Public benefit:** The Trustees confirm that they have referred to the Charity Commission's guidance on public benefit when reviewing the charity's aims and objectives, in planning future activities and setting the grant-making policy for the year.

## 2. ACHIEVEMENTS AND PERFORMANCE

**2.1 Meetings support:** During 2019, the Association agreed to support a total of six palaeontological meetings, symposia or workshops worldwide (held in Australia, Spain and the UK). In addition, our Postgraduate Travel Grant scheme supported 12 postgraduate students to present their work at international conferences: Ms Valentina Brandolese (University of Ferrara), Ms Lucile Crete (Bournemouth University), Mr Panagiotis Kampouridis (Eberhard-Karls University Tübingen), Mr Romain Gougeon (University of Saskatchewan), Mr Calian Hazell (Northumbria University), Mr Pablo Sebastián Milla Carmona (University of Buenos Aires), Ms Maria Eugenia Pereyra (Facultad de Ciencias Naturales y Museo La Plata), Mr Hans Püschel (University of Edinburgh), Mr Miky Lova Tantely Raveloson (University of Antananarivo), Ms Lauren Sewell (Bournemouth University), Ms Amy Shore (University of Edinburgh) and Ms Danae Thivaïou (National and Kapodistrian University of Athens). The Association's support enabled the worldwide dissemination of research to the benefit of the global palaeontological community.

**2.2 Publications:** During 2019, 269 papers were submitted to either *Palaeontology* or *Papers in Palaeontology*. Of these, 127 (47 %) were considered to be within scope by the Editorial Board and 70 (26 %) were subsequently accepted following peer review; a further 29 papers are still awaiting submission of a revised manuscript before a final decision is made. A total of 97 papers were published online. The number of downloads of articles via Wiley Online Library was 14 % higher in 2019 relative to 2018 for *Palaeontology* and less than 1 % higher for *Papers in Palaeontology*. The Association continues to support data archiving by sponsoring Dryad data records; 75 papers



published online in 2019 had associated data files in Dryad, representing 77 % of all papers published (18 % more than 2018). Authors were also encouraged to use alternative data repositories if they wished, and some took this option instead. The Association published two books in 2019: *Fossils from the Lias of the Yorkshire Coast* edited by Prof. Alan R. Lord and *Trilobites, Dinosaurs and Mammoths* by palaeoartist Mr J. McKay.

**2.3 Support for research:** In 2019 the Association agreed to fund the research activities of 16 early-career researchers based in five countries (Belgium, Ireland, Japan, the UK and the USA). Apart from directly benefiting the career development of the individuals concerned, the Association's funds continue to enable more palaeontological research to be undertaken worldwide than would otherwise be the case. Overall, the number of grants funded in 2019 decreased from 2018 (from 22 to 16). Compared to 2018, applications for Research Grants decreased from 20 to 13, and thus the success rate increased from 15 % to 23 %. The applications to the Small Grants Scheme increased (from 14 to 22), and the success rate consequently decreased from 64 % to 32 %. Applications to the Undergraduate Research Bursary Scheme increased slightly in 2019 compared to 2018 (from 17 to 18) and the success rate decreased to 33 %.

**2.4 Mentoring scheme for early career palaeontologists:** In 2017 the Association established a mentoring scheme to assist palaeontologists at the start of their academic careers. Priority areas were identified and in the first instance the focus was on the transition from postdoctoral positions to permanent jobs. Other transition points such as late stage PhD to postdoctoral positions and mid-career to senior leadership roles will be considered later. Twenty-three palaeontologists in permanent positions offered to act as mentors and so far ten postdoctoral palaeontologists have taken part in the scheme. The Palaeontological Association mentoring scheme is via direct mentoring, via e-mail, video call or other forms of communication. In 2019 feedback was sought from all mentors and mentees about the scheme. Four responses were returned in total, two each from mentors and mentees. Three of the four responses were extremely positive and the fourth, from a mentor, was neutral.

**2.5 Outreach, education and public engagement:** During 2019, the Association supported two major fossil festivals in the UK, in Lyme Regis and Scarborough, which attracted an estimated 10,000 and 3,000 members of the public, respectively. The PEG developed a suite of novel activities based around the theme of adaptation for the Association stand at the festivals including: the 'Wheel of Misfortune'; exploring themes of organismal response to cataclysmic and gradual environmental and biotic change; 'How Fit are You', a card game based on Top Trumps; and 'Design-your-own-chimera', involving assembling and drawing novel arthropod 'species' from assorted heads, limbs, tails and body shapes. Palaeoartist Mr J. McKay provided watercolour interpretations of the children's drawings. In addition, workshops were delivered by Association volunteers to 133 children from five year classes of a primary school as part of the Lyme Regis Fossil Festival schools' day, and to 135 primary school children from five schools as part of the Yorkshire Fossil Festival schools' day. Association volunteers took part in a careers fair, 'Jobs that Rock', during the Yorkshire Fossil Festival, with a stand in the exhibition area and as part of a panel. The Association also took part in the Geological Society Careers and Industry Day at Imperial College London with a stand in the exhibition area. During 2019, PEG awarded three Engagement Grants (see 1.9). Continued use of social media, in particular the Association's Twitter and Facebook accounts, has enabled the rapid and regular dissemination of research news, including of new publications, meetings and other



information, to a growing audience (see section 1.12). The PEG launched a new YouTube channel (accessible at <<https://www.youtube.com/channel/UCVedLnMzG6RiZ8W6RY5QNFg>>) late in 2019. The channel currently hosts short videos featuring Council members speaking about exciting elements of their research, including trilobites, fossil colour, mass extinctions, fossil plants and fossil fish. It is hoped that members will contribute to the channel in 2020.

### 3. FINANCIAL REVIEW

**3.1 Reserves:** As of 31st December 2019, the Association holds reserves of £783,352 in General Funds, which enable the Association to generate additional revenue through investments, and thus to keep subscriptions to individuals at a low level, whilst still permitting a full programme of meetings to be held, publications to be produced, and the award of research grants and Grants-in-aid. They also act as a buffer to enable the normal programme to be followed in years in which expenditure exceeds income, and allow new initiatives to be pursued. The Association holds £130,612 in Designated Funds, which contribute interest towards the funding of the Sylvester-Bradley, Hodson, Callomon, Whittington and Stan Wood Awards and towards the Jones-Fenleigh Fund. Total funds carried forward to 2020 totalled £913,964.

**3.2 Reserves policy:** The Association maintains a minimum of General Fund reserves at a level sufficient to fund at least one year's expenditure, based on a three-year average of expenditure, in addition to Designated Fund reserves. This policy is reviewed and approved annually by the Trustees.

**3.3 Summary of expenditure:** Total charitable expenditure, through grants to support research, scientific meetings and workshops in 2019 was £432,957. Governance costs were £25,063. Total resources expended were £491,679. The Association continues its membership of the International Palaeontological Association and remains a Tier 1 sponsor of *Palaeontologia Electronica*, and the *Treatise on Invertebrate Paleontology*.

### 4. STRUCTURE, GOVERNANCE AND MANAGEMENT

**4.1 Nature of the governing document:** The Palaeontological Association was originally formed on 27th February 1957 as an unincorporated association, which was established as a registered charity (number 276369) on 21st August 1978. At an Extraordinary General Meeting on 16th March 2016, the membership voted in favour of the Association becoming a charitable incorporated organisation (CIO) under the Charities Act 2011. All contracts and assets were transferred to the new organization on 1st January 2017. As a CIO the charity is an independent legal entity and, in the unlikely event of its being wound up, the members (including the Trustees) will have no liability for any outstanding contractual debts that the CIO cannot meet. However, the Trustees will continue to have the normal trustee liability for negligence or fraudulence in managing the charity's affairs. The charitable objectives of the Association remain unchanged. The change in legal status means that there has been a different registration number (1168330) and constitution since 2017. The governing document of the Palaeontological Association is the Constitution adopted at the AGM on Thursday 15th December 2016.

**4.2 Management:** The Association is managed by a Council of up to 20 Trustees, which is led by the President. The Association employs an Executive Officer and a Publications Officer who serve on Council but are not Trustees. The Trustees are elected by vote of the Membership at the Annual General Meeting, following guidelines laid down in the Constitution.



**4.3 Membership:** Membership on 31st December 2019 totalled 1,177 (1,189 at end 2017). Of these, 581 were Ordinary Members, 192 Retired Members, 20 Honorary Members, 356 Student Members and 28 Institutional Members. There were 38 institutional subscribers to *Papers in Palaeontology*. Wiley also separately manage further institutional subscribers and arrange online access to publications for them on behalf of the Association.

**4.4 Risk:** The Trustees consider that the Association is in a sound financial position. Membership numbers and revenues from publications remain strong.

## 5. REFERENCE AND ADMINISTRATION

**5.1 Name and Charity Number:** The Palaeontological Association is a Charity registered in England and Wales, Charity Number 1168330.

**5.2 Address:** The registered office and contact address of the Association is The Palaeontological Association, Alport House, 35 Old Elvet, Durham DH1 3HN, UK.

**5.3 Trustees:** The following members were elected at the AGM on 15th December 2018 to serve as Trustees in 2019:

Prof. C. H. Wellman	President
Dr C. J Buttler	Vice President
Prof. T. R. A. Vandenbroucke	Vice President
Dr C. T. S. Little	Secretary
Dr P. Winrow	Treasurer
Dr B. H. Lomax	Editor Trustee
Prof. M. A. Purnell	Editor Trustee
Dr A. R. T. Spencer	Internet Officer
Dr G. T. Lloyd	Newsletter Editor
Dr T. J. Challands	Book Review Editor
Dr L. M. E. McCobb	Outreach Officer
Dr M. E. McNamara	Education Officer
Dr S. J. Lydon	Publicity Officer
Dr R. C. M. Warnock	Diversity Officer
Dr U. Balthasar	Meetings Coordinator
Dr D. P. G. Bond	Ordinary Member
Dr A. M. Dunhill	Ordinary Member
Prof. A. S. Gale	Ordinary Member
Ms. Z. E. Hughes	Ordinary Member

**5.4 Professional services:** The Association's Bankers are NatWest, Sheffield City Centre, 42 High Street, Sheffield S1 2GE. The Association's Independent Examiner is Ms M. R. Corfield ACA ACMA, Corfield Accountancy Ltd., Chartered Accountants, Myrick House, Hendomen, Montgomery, Powys, SY15 6EZ. The Association's investment portfolio is managed by Quilter Cheviot Investment Management, 1 Kingsway, London WC2B 6XD.



**EVENTS SINCE THE END OF THE YEAR**

Information relating to events since the end of the year is given in the notes to the financial statements.

Approved by order of the Board of Trustees on 19th June 2020.



## Independent Examiner's Report to the Trustees of The Palaeontological Association

I report to the trustees on my examination of the accounts of the above charity for the year ended 31st December 2019 set out on pages 14 to 22.

As the charity's trustees, you are responsible for the preparation of the accounts in accordance with the requirements of the Charities Act 2011 ("the Act").

I report in respect of my examination of the charity's accounts carried out under section 145 of the 2011 Act and in carrying out my examination, I have followed all the applicable Directions given by the Charity Commission under section 145(5)(b) of the Act.

The charity's gross income exceeded £250,000 and I am qualified to undertake the examination by being a qualified member of the Institute of Chartered Accountants in England and Wales (ICAEW) and the Chartered Institute of Management Accountants (CIMA), which are two of the listed bodies.

I have completed my examination. I confirm that no material matters have come to my attention in connection with the examination which give me cause to believe that in, any material respect:

- the accounting records were not kept in accordance with section 130 of the Charities Act; or
- the accounts did not accord with the accounting records; or
- the accounts did not comply with the applicable requirements concerning the form and content of accounts set out in the Charities (Accounts and Reports) Regulations 2008 other than any requirement that the accounts give a 'true and fair' view which is not a matter considered as part of an independent examination.

I have no concerns and have come across no other matters in connection with the examination to which attention should be drawn in this report in order to enable a proper understanding of the accounts to be reached.

Ms M. R. Corfield ACA ACMA  
Corfield Accountancy Limited  
Chartered Accountants  
Myrick House  
Hendomen  
Montgomery  
Powys SY15 6EZ  
Date: 19th June 2019



THE PALAEOLOGICAL ASSOCIATION

**Statement of Financial Activities  
for the Year Ended 31 December 2019**

	Notes	Unrestricted funds £	Designated funds £	31.12.19 Total funds £	31.12.18 Total funds £
<b>INCOME AND ENDOWMENTS FROM</b>					
Donations and legacies		55,148	6,423	61,571	62,552
<b>Charitable activities</b>					
Public Meetings		53,301	—	53,301	48,536
Publications		320,107	—	320,107	318,458
Investment income	2	<u>12,588</u>	<u>2,155</u>	<u>14,743</u>	<u>14,625</u>
<b>Total</b>		441,144	8,578	449,722	444,171
<b>EXPENDITURE ON</b>					
Raising funds	3	36,459	—	36,459	39,680
<b>Charitable activities</b>					
Public Meetings		73,364	—	73,364	72,542
Grants & Awards		55,356	10,138	65,494	65,866
Administration		51,479	—	51,479	55,756
Publications		239,820	—	239,820	195,332
Governance Costs		<u>25,063</u>	<u>—</u>	<u>25,063</u>	<u>44,557</u>
<b>Total</b>		481,541	10,138	491,679	473,733
Net gains/(losses) on investments		<u>94,878</u>	<u>—</u>	<u>94,878</u>	<u>(27,037)</u>
<b>NET INCOME/(EXPENDITURE)</b>		54,481	(1,560)	52,921	(56,599)
<b>RECONCILIATION OF FUNDS</b>					
<b>Total funds brought forward</b>		<u>728,871</u>	<u>132,172</u>	<u>861,043</u>	<u>917,642</u>
<b>TOTAL FUNDS CARRIED FORWARD</b>		<u>783,352</u>	<u>130,612</u>	<u>913,964</u>	<u>861,043</u>

**CONTINUING OPERATIONS**

All income and expenditure has arisen from continuing activities.

The notes form part of these financial statements.





## THE PALAEOLOGICAL ASSOCIATION

## Balance Sheet

### At 31 December 2019

	Notes	Unrestricted funds £	Designated funds £	31.12.19 Total funds £	31.12.18 Total funds £
<b>FIXED ASSETS</b>					
Investments	6	558,383	130,612	688,995	625,469
<b>CURRENT ASSETS</b>					
Debtors	7	175,564	—	175,564	189,454
Cash at bank		<u>90,743</u>	<u>—</u>	<u>90,743</u>	<u>91,305</u>
		266,307	—	266,307	280,759
<b>CREDITORS</b>					
Amounts falling due within one year	8	<u>(41,338)</u>	<u>—</u>	<u>(41,338)</u>	<u>(45,185)</u>
<b>NET CURRENT ASSETS</b>		<u>224,969</u>	<u>—</u>	<u>224,969</u>	<u>235,574</u>
<b>TOTAL ASSETS LESS CURRENT LIABILITIES</b>		<u>783,352</u>	<u>130,612</u>	<u>913,964</u>	<u>861,043</u>
<b>NET ASSETS</b>		<u>783,352</u>	<u>130,612</u>	<u>913,064</u>	<u>861,043</u>
<b>FUNDS</b>					
Unrestricted funds	9			<u>913,064</u>	<u>861,043</u>
<b>TOTAL FUNDS</b>				<u>913,064</u>	<u>861,043</u>

The notes form part of these financial statements.

The financial statements were approved by the Board of Trustees and authorized for issue on 19th June 2019.



## THE PALAEOLOGICAL ASSOCIATION

**Notes to the Financial Statements  
for the Year Ended 31 December 2019****1. ACCOUNTING POLICIES****Basis of preparing the financial statements**

The financial statements of the charity, which is a public benefit entity under FRS 102, have been prepared in accordance with the Charities SORP (FRS 102) 'Accounting and Reporting by Charities: Statement of Recommended Practice applicable to charities preparing their accounts in accordance with the Financial Reporting Standard applicable in the UK and Republic of Ireland (FRS 102) (effective 1 January 2019)', Financial Reporting Standard 102 'The Financial Reporting Standard applicable in the UK and Republic of Ireland' and the Companies Act 2006. The financial statements have been prepared under the historical cost convention with the exception of investments which are included at market value, as modified by the revaluation of certain assets.

**Income**

The charity's income principally comprises subscriptions from individuals and institutions which relate to the period under review, and sales of scientific publications.

All income is recognized in the Statement of Financial Activities once the charity has entitlement to the funds, it is probable that the income will be received and the amount can be measured reliably.

**Expenditure**

Liabilities are recognized as expenditure as soon as there is a legal or constructive obligation committing the charity to that expenditure, it is probable that a transfer of economic benefits will be required in settlement and the amount of the obligation can be measured reliably. Expenditure is accounted for on an accruals basis and has been classified under headings that aggregate all cost related to the category. Where costs cannot be directly attributed to particular headings they have been allocated to activities on a basis consistent with the use of resources.

**Allocation and apportionment of costs**

Administrative costs have been allocated to the various cost headings based on estimates of the time and costs spent thereon.

**Taxation**

The charity is exempt from corporation tax on its charitable activities.

**Fund accounting**

General Funds are unrestricted funds which are available for use at the discretion of the Council in furtherance of the general objectives of the charity and which have not been designated for other purposes.



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements – *continued* for the Year Ended 31 December 2019

**1. ACCOUNTING POLICIES – continued**

Designated funds comprise unrestricted funds that have been set aside by Council for particular purposes. The aim of each designated fund is as follows:

Sylvester-Bradley Fund: Grants made to permit palaeontological research.

Jones-Fenleigh Fund: Grants to permit one or more delegates annually to attend the Symposium of Vertebrate Palaeontology and Comparative Anatomy (SVPCA).

Hodson Fund: Awards made in recognition of the palaeontological achievements of a researcher within ten years of the award of their PhD.

Callomon Fund: Grants made to permit palaeontological research with a strong fieldwork element.

Whittington Fund: Grants made to permit palaeontological research with an element of study in museum collections.

Stan Wood Fund: Grants in the area of vertebrate palaeontology ideally involving fieldwork, due to generous donations in memory of the Scottish fossil collector Mr Stan Wood.

**2. INVESTMENT INCOME**

	31.12.19	31.12.18
	£	£
Deposit account interest	274	99
Investment Income	<u>14,469</u>	<u>14,526</u>
	<u>14,743</u>	<u>14,625</u>

**3. RAISING FUNDS**

	31.12.19	31.12.18
	£	£
<b>Voluntary Income Costs: Administration</b>	<b>32,759</b>	<b>35,481</b>
<b>Investment Management Costs: Stockbroker Fees</b>	<u>3,700</u>	<u>4,199</u>
	<u>36,459</u>	<u>39,680</u>

**4. TRUSTEES' REMUNERATION AND BENEFITS**

There were no Trustees' remuneration or other benefits for the year ended 31 December 2019 nor for the year ended 31 December 2018.

**Trustees' expenses**

The total travelling expenses reimbursed to 19 Members of Council (2018:19) was £12,308 (2018: £16,810).



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements – *continued* for the Year Ended 31 December 2019

**5. STAFF COSTS****Analysis of Staff Costs and Remuneration**

	£ 2019	£ 2018
Salaries	85,753	81,750
Social Security Costs	6,467	5,975
Pension Costs	<u>8,575</u>	<u>8,175</u>
Total	<u>100,795</u>	<u>95,900</u>

The average monthly number of employees during the year was as follows:

	2019	2018
Publications	1	1
Administration	<u>1</u>	<u>1</u>
	<u>2</u>	<u>2</u>

No employees received emoluments in excess of £60,000.

**6. FIXED ASSET INVESTMENTS**

Investments are initially recognized at their transaction value and subsequently measured at their fair value as at the balance sheet date. The statement of financial activities includes the net gains and losses arising on revaluation and disposals throughout the year.

**7. DEBTORS: AMOUNTS FALLING DUE WITHIN ONE YEAR**

	31.12.19	31.12.18
	£	£
Sundry Debtors	<u>175,564</u>	<u>189,454</u>

**8. CREDITORS: AMOUNTS FALLING DUE WITHIN ONE YEAR**

	31.12.19	31.12.18
	£	£
Trade creditors	19,734	27,945
Subscriptions in advance	<u>21,604</u>	<u>17,240</u>
	<u>41,338</u>	<u>45,185</u>



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements – *continued* for the Year Ended 31 December 2019

## 9. MOVEMENT IN FUNDS

	At 1.1.19 £	Net movement in funds £	At 31.12.19 £
<b>Unrestricted funds</b>			
General fund	728,871	54,481	783,352
Sylvester-Bradley	21,073	(3,465)	17,608
Jones-Fenleigh	27,503	873	28,376
Hodson	294	1	295
Callomon	3,368	(935)	2,433
Whittington	12,974	2,849	15,823
Stan Wood	<u>66,960</u>	<u>(883)</u>	<u>66,077</u>
<b>TOTAL FUNDS</b>	<u>861,043</u>	<u>52,921</u>	<u>913,964</u>

Net movement in funds included in the above are as follows:

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
<b>Unrestricted funds</b>				
General fund	441,144	(481,541)	94,878	54,481
Sylvester-Bradley	836	(4,301)	—	(3,465)
Jones-Fenleigh	873	—	—	873
Hodson	1	—	—	1
Callomon	365	(1,300)	—	(935)
Whittington	4,349	(1,500)	—	2,849
Stan Wood	<u>2,154</u>	<u>(3,037)</u>	<u>—</u>	<u>(883)</u>
<b>TOTAL FUNDS</b>	<u>449,722</u>	<u>(491,679)</u>	<u>94,878</u>	<u>52,921</u>



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements – *continued* for the Year Ended 31 December 2019

9. MOVEMENT IN FUNDS — *continued...*

## Comparatives for movement in funds:

	At 1.1.18 £	Net movement in funds £	At 31.12.18 £
<b>Unrestricted Funds</b>			
General fund	776,624	(47,753)	728,871
Sylvester-Bradley	26,394	(5,321)	21,073
Jones-Fenleigh	27,713	(210)	27,503
Hodson	1,719	(1,425)	294
Callomon	4,519	(1,151)	3,368
Whittington	13,974	(1,000)	12,974
Stan Wood	<u>66,699</u>	<u>261</u>	<u>66,960</u>
<b>TOTAL FUNDS</b>	<u>917,642</u>	<u>(56,599)</u>	<u>861,043</u>

Comparative net movement in funds included in the above are as follows:

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
<b>Unrestricted funds</b>				
General fund	439,541	(460,257)	(27,037)	(47,753)
Sylvester-Bradley	652	(5,973)	—	(5,321)
Jones-Fenleigh	1,370	(1,580)	—	(210)
Hodson	1	(1,426)	—	(1,425)
Callomon	349	(1,500)	—	(1,151)
Whittington	500	(1,500)	—	(1,000)
Stan Wood	<u>1,758</u>	<u>(1,497)</u>	<u>—</u>	<u>261</u>
<b>TOTAL FUNDS</b>	<u>444,171</u>	<u>(473,733)</u>	<u>(27,037)</u>	<u>(56,599)</u>



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements – *continued* for the Year Ended 31 December 2019

9. MOVEMENT IN FUNDS — *continued*...

A current year 12 months and prior year 12 months combined position is as follows:

	At 1.1.18 £	Net movement in funds £	At 31.12.19 £
<b>Unrestricted funds</b>			
General fund	776,624	6,728	783,352
Sylvester-Bradley	26,394	(8,786)	17,608
Jones-Fenleigh	27,713	663	28,376
Hodson	1,719	(1,424)	295
Callomon	4,519	(2,086)	2,433
Whittington	13,974	1,849	15,823
Stan Wood	<u>66,699</u>	<u>(622)</u>	<u>66,077</u>
TOTAL FUNDS	<u>917,642</u>	<u>(3,678)</u>	<u>913,964</u>

A current year 12 months and prior year 12 months combined net movement in funds included in the above are as follows:

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
<b>Unrestricted funds</b>				
General fund	880,685	(941,798)	67,841	6,728
Sylvester-Bradley	1,488	(10,274)	—	(8,786)
Jones-Fenleigh	2,243	(1,580)	—	663
Hodson	2	(1,426)	—	(1,424)
Callomon	714	(2,800)	—	(2,086)
Whittington	4,849	(3,000)	—	1,849
Stan Wood	<u>3,912</u>	<u>(4,534)</u>	<u>—</u>	<u>(622)</u>
TOTAL FUNDS	<u>893,893</u>	<u>(965,412)</u>	<u>67,841</u>	<u>(3,678)</u>



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements – *continued* for the Year Ended 31 December 2019

**10. RELATED PARTY DISCLOSURES**

There were no related party transactions for the year ended 31 December 2019.

**11. INVESTMENT GAINS AND LOSSES**

All gains and losses are taken to the Statement of Financial Activities as they arise. Realized gains and losses on investments are calculated as the difference between sales proceeds and their opening carrying value or their purchase value if acquired subsequent to the first day of the financial year.

Unrealized gains and losses are calculated as the difference between the fair value at the year end and their carrying value. Realized and unrealized investment gains and losses are combined in the Statement of Financial Activities.

Investment Gains/Losses	31st December 2019	31st December 2018
	£	£
Realized Gain/(Loss)	2,803	(518)
Unrealized Gain/(Loss)	<u>92,075</u>	<u>(26,519)</u>
Total per Statement of Financial Activities	<u>94,878</u>	<u>(27,037)</u>

**12. INVESTMENT PORTFOLIO 2019**

See pages 24–25.

**13. POST BALANCE SHEET EVENTS**

Since 31st December 2019, the pandemic related to COVID-19 has impacted the Association's investments and its activities during 2020. As at 31st March 2020, the fair value of the Association's fixed asset investments had reduced to £587,902 (a reduction of £101,095 (15%)) compared to the year ended 31st December 2019.

The ongoing extent of the COVID-19 outbreak and its impact on the Stock Market remains unclear at this time, although positive signs have been seen in two of the charity's investment funds (COIF) where a 9% loss in value for the first quarter of 2020 had regained its 31st December 2019 valuation level by early June 2020. Due to the continued uncertainty, these subsequent changes in the fair value of the Association's fixed asset investments and impact on the Association's activities are therefore not reflected in the financial statements as at 31st December 2019.

The Trustees are monitoring the situation and are taking account of the pandemic in making decisions that impact the Association's financial health including, but not limited to, expenditure on conferences which may be cancelled due to travel restrictions and replacement of the Association's flagship Annual Meeting with a virtual event.





## Detailed Statement of Financial Activities for the Year Ended 31 December 2019

	31.12.19 Unrestricted funds £	31.12.18 Total funds £
<b>INCOME AND ENDOWMENTS</b>		
<b>Donations and legacies</b>		
Donations	8,140	7,462
Subscriptions	53,431	55,090
	<u>61,571</u>	<u>62,552</u>
<b>Investment income</b>		
Deposit account interest	274	99
Investment Income	14,469	14,526
	<u>14,743</u>	<u>14,625</u>
<b>Charitable activities</b>		
Scientific Journals	309,605	314,201
Special Papers	573	828
Newsletter	80	243
Field Guides	9,129	2,944
Distribution	720	242
Scientific Meetings	53,301	48,536
	<u>373,408</u>	<u>366,994</u>
<b>Total incoming resources</b>	<b>449,722</b>	<b>444,171</b>
<b>EXPENDITURE</b>		
<b>Raising donations and legacies</b>		
Administration	32,759	35,481
<b>Investment management costs</b>		
Stockbroker Fees	3,700	4,199
<b>Charitable activities</b>		
Scientific Journals	67,050	56,630
Field Guides	25,622	—
Newsletters	18,990	18,265
Marketing	297	632
Publication Costs	82,544	81,825
Editorial Costs	45,317	37,980
Public Meetings & Costs	73,364	72,542
Grants & Awards	37,534	53,772
Research Grants	27,960	12,094
Administration	51,479	55,756
Consultancy	2,800	17,609
	<u>432,957</u>	<u>407,105</u>
<b>Support costs</b>		
<b>Governance costs</b>		
Trustees' expenses	12,308	16,810
Accountancy and legal fees	595	595
Administration	9,360	9,543
	<u>22,263</u>	<u>26,948</u>
<b>Total resources expended</b>	<b>491,679</b>	<b>473,733</b>
<b>Net income before gains and losses</b>	<b>(41,957)</b>	<b>(29,562)</b>
<b>Realized recognized gains and losses</b>		
Realized gains/(losses) on fixed asset investments	94,878	(27,037)
<b>Net income</b>	<b>52,921</b>	<b>(56,599)</b>

This page does not form part of the statutory financial statements.



## Palaeontological Association year ended 31st December 2019.

Nominal	Holding	Cost (bought pre 2019) £	Value end 2018 £
£10,000	UK 4.5% Gilt 07/03/19 GBP 0.01	10,046.50	10,210.00
£18,000	UK 4.75% Stock 07/03/20 GBP 100	18,145.87	19,112.00
49,685.81	COIF Charities Fixed Interest Fund	65,807.52	66,246.09
9,730.085	M&G Securities Limited Optimal Income J GBP Dis		
7,500	Royal London Unit Trust Mngrs Sterling Credit Z GBP NAV		
700	Pimco Global Advisors Irl Ltd Global Inv Grade Cred		
1,425	BP Ord 25c shares	5,047.35	7,067.00
600	Royal Dutch Shell B shares	4,422.42	14,040.00
600	BHP Billiton \$0.5 shares	4,341.48	9,910.00
180	CRH ord EUR 0.32	4,426.82	3,728.00
1,400	Smith(DS) ord GBP 0.10	4,569.69	4,190.00
370	Halma ord GBP 0.10	3,871.71	5,046.80
130	Halma ord GBP 0.10	1,360.33	1,773.20
437	IMI Ord 25p shares	4,267.00	4,125.00
350	Experian Ord 10C	2,870.79	6,667.50
70	Experian Ord 10C	574.16	1,333.50
200	Diageo Ord GBP 0.28	3,884.00	5,590.00
100	Diageo Ord GBP 0.28	1,942.00	2,795.00
200	Persimmon Ord 10p	2,258.00	3,860.00
70	Reckitt Benckiser Group ord GBP 0.10	5,325.75	4,209.00
150	Unilever PLC Ord GBP 0.031111	2,163.11	6,163.00
150	Unilever PLC Ord GBP 0.031111	2,163.11	6,163.00
120	Astrazeneca Ord 25c	5,749.41	7,047.53
50	Astrazeneca Ord 25c	2,395.59	2,936.47
450	Glaxo Smithkline Ordinary 25p shares	7,083.98	6,710.00
2,500	Tesco ord GBP0.05		
300	Relx Olc GBP 0.1444	4,438.20	4,850.00
300	Compass Group Plc ord GBP0.1105		
175	Carnival Plc Ord USD 1.66	3,996.49	6,585.00
1,000	BT Group Ordinary 5p shares	3,446.05	2,381.00
2,277	Vodafone Group Ord USD 0.11428571	3,434.00	3,482.00
641	National Grid Ord GBP 0.12431289	3,648.26	4,899.00
2,250	Barclays 25p Ord shares	4,867.00	3,387.00
1,465	HSBC Holdings Ordinary 0.5 US Dollar shares	4,534.00	9,477.00
982	Great Portland Estates Ord GBP0.15263157894	8,503.00	6,472.00
6,000	Mercantile Investment Tst Plc(The) ord GBP0.025	10,171.60	10,530.00
300	Findlay Park Partners US Smaller Companies	4,347.16	25,315.76
125	Findlay Park Partners US Smaller Companies	1,811.31	10,548.24
2,525	Ishares S&P 500 GBP	18,161.79	49,354.14
300	Ishares S&P 500 GBP	2,157.84	5,863.86
4250	Fidelity EUR Value Ordinary 25P shares	4,059.07	8,798.00
30	Roche Hldgs Ag Genusschein Nvp	3,335.33	5,829.00
6,600	Thesis Unit Trust Mngmt Ltd TM Crux European GBP Dis	7,140.00	12,699.00
9,000	Baillie Gifford & Co Japanese Income Growth W4 Dis	11,977.02	11,052.00
1,007	Eastspring Investments SICAV Japan Dynamic FGDY GBP	7,837.74	8,854.00
26	Veritas Funds Plc Veritas Asian D GBP Inc	8,182.27	14,924.00
900	JPMorgan Am UK Ltd Emerging Markets I Instl	5,043.10	7,313.00
650	RIT Capital Partners Ordinary £1 shares	4,903.90	12,415.00
800	BH Global Ltd ord GBP	10,226.25	11,860.00
4,400	Invesco Fund Managers Targeted Y Acc	9,770.33	9,538.00
37	Marshall Wace UCITS Funds Plc MW Tops UCITS G GBP	4,849.70	4,990.00
4,443	Aberdeen Investment Property Trust B	4,681.00	5,386.00
9,000	Charities Property Fund Income	11,043.28	11,711.00
1,021.54	COIF Charities Investment Fund Acc Units	59,678.69	158,032.03
	Total	388,960.96	625,469.12



## Schedule of Investments (Note 12 to the Accounts).

Proceeds (sold in 2019) £	Cost (bought in 2019) £	Gain realised during 2019 £	Value end 2019 £	Gain unrealised during 2019 £
10,000.00		-210.00		
			18,403.00	-709.00
			68,342.83	2,096.74
	10,060.08		10,130.00	69.92
	10,474.20		10,680.00	205.80
	9,620.07		9,828.00	207.93
			6,720.00	-347.00
			13,473.00	-567.00
			10,661.00	751.00
			5,476.00	1,748.00
			5,379.00	1,189.00
			7,829.00	2,782.20
2,145.25		372.05		
4,191.66		66.66		
			8,932.00	2,264.50
1,412.43		78.93		
			6,401.00	811.00
3,082.56		287.56		
			5,390.00	1,530.00
			4,290.00	81.00
			6,526.00	363.00
6,465.16		302.16		
			9,128.00	2,080.47
3,192.65		256.18		
			8,006.00	1,296.00
	5,953.09		6,380.00	426.91
			5,717.00	867.00
	5,399.53		5,670.00	270.47
6,332.31		-252.69		
2,034.57		-346.43		
2,846.11		-635.89		
			6,053.00	1,154.00
			4,042.00	655.00
			8,671.00	-806.00
7,250.71		778.71		
			15,720.00	5,190.00
			31,034.00	5,718.24
11,628.82		1,080.58		
			61,414.00	12,059.86
7,005.08		1,141.22		
			11,050.00	2,252.00
			7,345.00	1,516.00
			14,993.00	2,294.00
			12,519.00	1,467.00
			10,056.00	1,202.00
			18,585.00	3,661.00
			9,351.00	2,038.00
			13,748.00	1,333.00
			12,140.00	280.00
			9,860.00	322.00
			5,223.00	233.00
5,269.33		-116.67		
			11,592.00	-119.00
			192,239.12	34,207.09
72,856.64	41,506.97	2,802.38	688,996.95	92,075.12



## Nominations for Council

At the AGM in December 2020, the following vacancies will occur on Council:

- Vice President
- Treasurer
- Newsletter Editor
- Book Review Editor
- Education Officer
- Meetings Coordinator
- Diversity Officer
- Ordinary Member (up to one vacancy) \*

\* This positions is dependent on a Council member currently holding this post moving to another Council post.

Nominations received were as follows:

- Vice-President: Richard Butler
- Treasurer: Manabu Sakamoto, Paul Varotsis
- Newsletter Editor: Emilia Jarochovska
- Book Review Editor: Karen Bacon, Thomas Clements, Thomas Hegna
- Education Officer: Elspeth Wallace
- Meetings Coordinator: Konstantina Agiadi, Uwe Balthasar
- Diversity Officer: Farid Saleh
- Ordinary Member (0-1 position): Tracy Aze, Borja Cascales-Miñana, Sherri Donaldson, Christine Strullu-Derrien, Robert Theodore, Thomas Wong Hearing,

As there are multiple nominations for the Treasurer, Book Review Editor, Meetings Coordinator and Ordinary Member posts an election is being conducted prior to the Annual General Meeting. This is taking place electronically (or by post for those without electronic access) as per Schedule 14 clause 3(4) of the Corporate Insolvency and Governance Act 2020. Voting instructions were sent via e-mail (or post) to all voting members in late November, to allow for all votes to be cast and counted in time for election results to be announced at the AGM.





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